Modelling the Current and Potential Distribution of Woody Plants, with Special Emphasis on the Importance of Spatial Scale and Environmental Factors

Mathieu Rouget

THESIS PRESENTED FOR THE
DEGREE OF DOCTOR OF PHILOSOPHY
IN THE FACULTY OF SCIENCE
UNIVERSITY OF CAPE TOWN

DEPARTMENT OF BOTANY
FEBRUARY 2002

Table of Contents

Abstract

The relationship between species distribution and environment has always been a central issue in ecology. The primary aim of this thesis is to explore the role of abiotic and biotic factors in mediating the distribution of woody plants, particularly invasive alien species. Predictions of the future distribution of invasive species are required for management, conservation actions, and legislation. Using predictive geographical modelling, this thesis assesses the role of spatial scale in understanding the determinants of species distribution, modelling invasion spread, and taking conservation decisions.

The species distribution databases were collated in a Geographic Information System from various sources (from field mapping to remote-sensing data), and at various spatial scales (from local to sub-continental). Classification and regression trees, a flexible non-parametric statistical technique, were developed for each case study. I show that static modelling approaches, such as classification trees, are appropriate for modelling species distribution at regional to sub-continental scales. More mechanistic approaches, which include biological attributes, are required for accurate modelling of species abundance at local scale. A hierarchy of environmental factors was observed. Abiotic factors such as climate were more important for modelling species distribution at broad scales, whereas biotic factors were the fine-scale drivers of species distribution and abundance. This highlights the scale-dependence of prediction accuracy and of environmental drivers.

Predictive habitat modelling was also applied to modelling future land use changes (including invasive alien species) in the context of conservation planning for the Cape Floristic Region. Effective conservation planning requires a detailed assessment of current land use patterns and future land use scenarios. Conservation planning is generally derived at regional scale but implementation takes place at finer scales. I investigated the transition from broad-scale planning to fine-scale implementation. This work emphasises the importance of diverse and fragmented habitats in measuring conservation value.

This thesis concludes by linking predictive habitat modelling, species determinants, and application types to the spatial scale analysed.

Acknowledgements

I thank my supervisor Dave Richardson; his enthusiasm, his guidance and his constant support were much appreciated. I would also like to thank my other co-supervisors, Richard Cowling, Sandra Lavorel and Sue Milton, who encouraged me throughout the study. Special thanks to Fikile Hlatshwayo for her continued support during this work.

I am very grateful to the many other persons and institutions involved in the CAPE ("Cape Action Plan for the Environment") project for stimulating discussion and assistance in various ways during this work. Special thanks are due to Richard Cowling and Bob Pressey, co-ordinators of the terrestrial component of CAPE. Mandy Lombard, Charlotte Heijnis, Nicholas Cole assisted with providing GIS data. Nick Linderberg offered countless GIS advices during this study. The Centre for Ecological and Forestry Research (University Autonoma of Barcelona, Spain) kindly provided the species distribution database for Catalonia. I would like to thank F. Ninyerola for permission to use the climatic model for Catalonia. I am grateful to Doug Euston-Brown who undertook the marathon task of mapping the distribution of invasive trees and shrubs on the Agulhas Plain used in Chapter 3. Wendy Lloyd, Elna van der Berg, Leaza van Wyk, and Neil Fairall made significant contributions to the spatial mapping of habitat transformation in the Cape Floristic Region.

Many persons contributed by discussing ideas and reading manuscripts. They are acknowledged by chapter. I would like to thank F. Lloret, L. Mucina, R. Økland and M. Rejmánek for their very valuable comments on Chapter 2. I thank Dean Fairbanks and Wilfried Thuiller for their statistical advices on Chapter 3. I especially thank Bob Pressey, Steve Higgins, and Janet Franklin for their very useful comments and suggestions on Chapter 4. Adrian Armstrong, Curt Daehler, Karen Kirkman, Ingrid Parker and Peter Le Roux are thanked for their useful comments on Chapter 5. Bob Pressey is acknowledged for his very valuable advice on Chapter 6. Kimberly With suggested very useful comments on Chapter 7.

This work was carried out as part of the program Laboratoire Européen Associé "Dynamique des écosytèmes méditerranéens dans un monde changeant". Financial support was provided by a CNRS (France) - NRF (South Africa) joint project. Much of the data used in this study was collected as part of the Cape Action Plan for the Environment, with funding from the Global Environmental Facility through WWF-South Africa. Additional funding was provided by the National Research Foundation, the University of Cape Town's Research Committee, the Institute for Plant Conservation, the Terrestrial Ecology Research Unit, and the Agricultural Research Council – Institute for Soil, Climate and Water.

Introduction

This chapter provides the motivation for the work, discusses the main objectives, and gives an overview of the set of studies that make up the thesis.

Background and Objectives

This thesis aims, primarily, to develop a protocol for modelling the spatial patterns of plant species (particularly invasive species) at different spatial scales. Invasion by non-indigenous organisms has been recognised as the second major treat to biodiversity after direct habitat transformation worldwide (Wilcove et al., 1998). Over the last 50 years, and particularly in the last 20 years, invasion ecology has grown as a new discipline (Elton, 1958; Drake et al., 1989; Williamson, 1996; Groves et al., 2001) but its ability to predict which species will invade and in which habitats has been generally limited. The effect of environment, which is the most important factor for explaining patterns across a wide range of systems, has prevented the formulation of general answers, at least at scales that are helpful to managers (Rejmánek et al., in press). This thesis explores the role of environmental factors in mediating the distribution and the spread of invasive alien plant species in South Africa. Invasion by alien plants provides a superb natural experiment for exploring species-environment relationships and, thus, for inferring process from pattern. Natural experiments are also the only way to address large-scale ecological processes.

The issue of scale is a central problem in ecology (Levin, 1992). The scale of observations influences the description of ecological patterns and notably the understanding of plant distribution. Relatively few studies have analysed the same ecological phenomena at multiple spatial scales. Cross-scale studies are critical since ecological processes operating at many scales interact to affect community structure and composition. This motivated the need for assessing the effects of spatial scale in modelling species distribution. The thesis is therefore structured around several case studies that consider invasions of alien tree species at different spatial scales (from local to sub-continental, see Table 1). This thesis also addresses the issue of spatial scale in conservation planning, which requires detailed assessment of biodiversity features and land use pressures (including invasion by alien plant species). The scale at which these components are mapped greatly affects the outcomes of conservation planning, but this has been rarely addressed (Margules and Pressey, 2000).

Table 1: Spatial scales and main characteristics of case studies explored in this thesis.

Study area	Scale	Extent (km^2)	Resolution (m)	Characteristics
Agulhas Plain	Local	2200	250	Small region encompassing one to several plant communities
Catalonia	Regional	32000	180	Medium-size region encompassing a wide range of environmental conditions
Cape Floristic Region	Regional	88000	1700	Moderately large region encompassing a single biome
South Africa	Sub-continental	$1.2\ 10^6$	1700	Very large region encompassing several biomes

Models of invasive plant spread were recently developed for South Africa but they apply to fine-scale studies (< 500 km^2) and none address invasions at regional or sub-continental scales (Higgins et al., 1999, 2001). In order to understand the role of abiotic and biotic factors on species distribution patterns across various spatial scales, a statistical approach appeared more appropriate than a mechanistic one (Guisan and Zimmerman, 2000). Statistical habitat distribution models relate the geographical distribution of species to their present environment. Such models are static and probabilistic by nature. Static modelling approaches, focussing on identifying constraints, work best on large data sets, and are easy to implement in a Geographic Information System (GIS). The fitted model generated from the statistical analysis can be directly implemented into the GIS to derive maps of potential distribution. This approach also enabled me to identify the abiotic and biotic factors that limit or favour the spread of invasive organisms at various spatial scales. Information on the drivers of invasion operating at a local scale is needed by managers responsible for maintaining biodiversity in specific plant communities. On the other hand, information on the drivers operating at broader scales are needed for setting policies and legislation which are applicable over much larger areas (typically regions or countries).

Most of this work (except for Chapter 2) is based on case studies in South Africa, particularly in the Cape Floristic Region. Alien plant invasions (along with urbanisation and agriculture) are threatening biodiversity in the Cape Floristic Region, a global hotspot of biodiversity (Myers et al., 2000). Biological invasions have been relatively well studied in this area (see recent reviews by Richardson et al., 1997; Richardson and Higgins, 1998). The Cape Action Plan for the Environment (Cowling et al., 1999; Cowling and Pressey, in press), as well as the Forestry Inventory of Catalonia, generated vast amounts of data, which were used in this thesis. This provided excellent opportunities for exploring the determinants of species distribution, and the effect of spatial scale in modelling species distribution and in conservation planning.

Thesis structure

This thesis is organised as a series of scientific papers, each with its own aims, methods, and conclusions. The issues addressed in some parts of chapters 4 and 6 might deviate from the core subject of the thesis. All chapters, however, contribute to the overall aim of the thesis by focussing on modelling current and potential patterns of species distribution, or by addressing the issue of spatial scale.

Overview

Chapter 2 explores the determinants of distribution, abundance and regeneration for six *Pinus* species in part of their native range in northeastern Spain. This study quantifies plant-environment relationships at a regional scale (30 000 km^2) and introduces the statistical modelling approach used in the next chapters. Predictive geographical modelling recently gained importance following the development of new statistical techniques, improved computational capabilities, and geographic information systems (Guisan and Zimmerman, 2000). In this chapter, the role of abiotic and biotic factors is assessed for predicting spatial patterns of species distribution, abundance and regeneration.

Chapter 3 also explores the determinants of plant species distribution and abundance for the three most widespread invasive species in the Agulhas Plain (2 160 km^2): *Acacia cyclops, A. saligna*, and *Pinus pinaster*. The spatial scale (local vs. regional) and the type of species modelled (invasive vs. native species) are different to those examined in Chapter 2. This chapter tests the ability of static modelling (used in Chapter 2) to predict future patterns of invasive plant spread at a local scale. Propagule pressure (defined as the proximity from sites of initial introduction) is incorporated into the models to quantify the interactions between spread rate and environment. Such models are "quasi-mechanistic" because they integrate biological attributes (species dispersal modelled through propagule pressure). This chapter highlights the role of plant-environment interactions in determining the trajectory of invasions.

Chapter 4 brings the issue of invasive plant species into conservation planning. Effective conservation planning requires the spatially-explicit assessment of the current patterns of habitat transformation and a framework for predicting the likelihood of remaining habitat being transformed (Margules and Pressey, 2000). This chapter assesses the present and future extent of three important factors that threaten biodiversity in the Cape Floristic Region (80 000 km^2): agriculture, stands of invasive alien trees, and urbanisation. I identified the spatial determinants of each transformation factor and then compared two modelling approaches (rule-based and statistical modelling) for predicting future patterns.

Chapter 5 provides a spatially-explicit risk assessment of invasive woody plant species at a sub-continental scale. Objective methods for identifying areas where control measures should be focussed are required by managers, planners and policy-makers. Using regression tree-analysis and GIS, I developed maps of future invasion potential for South Africa and derived spatial guidelines for policy on alien plant management.

Chapter 6 focuses primarily on the effects of spatial scale in conservation planning for the Agulhas Plain (2 160 km^2). Regional conservation planning is based on broad-scale data but fine-scale assessments are generally required for implementation. This transition from broad-scale planning to fine-scale implementation has been rarely addressed. Two systems of notional reserves developed for this region using broad- and fine-scale data provided the unique opportunity to measure the implications of moving from broad- to fine-scale conservation planning. For each scale, I identified the factors affecting conservation value and reserve design efficiency. This chapter illustrates conditions where the adverse effects of broad-conservation planning are likely to be severe.

Chapter 7 collates the information from Chapter 3, 4 and 5, and quantifies the roles of environment and propagule pressure for understanding invasion patterns at different spatial scales. I identified determinants of distribution of invasive species using regression-tree analysis. This chapter concludes by highlighting the scale dependence of environmental determinants and of prediction accuracy.

References

Cowling, R.M., Pressey, R.L., in press. Context, characteristics and history of conservation planning. Biological Conservation.

Cowling, R.M., Pressey, R.L., Lombard, A.T., Heijnis, C.J., Richardson, D.M., Cole, N., 1999. Framework for a conservation plan for the Cape Floristic Region. Report 9902, Institute for Plant Conservation, Cape Town.

Drake, J.A., Mooney, H.A., di Castri, F., Groves, R.H., Kruger, F.J., Rejmánek, M., Williamson, M., 1989. Biological invasions. A global perspective. John Wiley & Sons, Chichester.

Elton, C.S., 1958. The ecology of invasions by animals and plants. Methuen, London.

Groves, R.H., Panetta, F.D., Virtue, J.G., 2001. Weed risk assessment. CSIRO Publisher, Collingwood.

Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135, 147-186.

Higgins, S.I., Richardson, D.M., Cowling, R.M., 2001. Validation of a spatial simulation model of a spreading alien plant population. Journal of Applied Ecology 38, 571-584.

Higgins, S.I., Richardson, D.M., Cowling, R.M., Trinder-Smith, T.H., 1999. Predicting the landscape scale distribution of alien plants and their threats to biodiversity. Conservation Biology 13, 303-313.

Levin, S.A., 1992. The problem of pattern and scale in ecology. Ecology 73, 1943-1967.

Margules, C.R., Pressey, R.L., 2000. Systematic conservation planning. Nature 405, 243-253.

Rejmánek, M., Richardson, D.M., Higgins, S.I., Pitcairn, M.J., Grotkopp, E., in press. Plant invasion ecology: State of the art. In: Mooney, H.A., Mc Neely, J.A., Neville, L., Schei, P.J., Waage, J. (Eds.), Invasive alien species: Searching for solutions, Island Press, Washington, D.C.

Richardson, D.M., Higgins, S.I., 1998. Pine as invaders in the southern hemisphere. In: Richardson, D.M. (Eds.), Ecology and biogeography of *Pinus*. Cambridge University Press, Cambridge, pp. 450-473.

Richardson, D.M., Macdonald, I.A.W., Hoffmann, J.H., Henderson, L., 1997. Alien plant invasions. In: Cowling, R.M., Richardson, D.M., Pierce, S.M. (Eds.), Vegetation of southern Africa, Cambridge University Press, Cambridge, pp. 535-570.

Wilcove, D.S., Rothstein, D., Dubow, D., Phillips, A., Losos, E., 1998. Quantifying threats to imperiled species in the United States. BioScience 48, 607-615.

Williamson, M.H., 1996. Biological Invasions. Chapman & Hall, London.

Determinants of distribution of six *Pinus* species in Catalonia, Spain

Abstract

This chapter explores the determinants of distribution, abundance and regeneration of six *Pinus* species (*P. halepensis*, *P. nigra*, *P. pinaster*, *P. pinea*, *P. sylvestris*, and *P. uncinata*) that occur naturally in Catalonia, northeastern Spain. The aim of this study was to generate accurate predictions of the distribution of each species using simple and readily available environmental variables. I used recursive partitioning and GIS analyses to relate the database of 10 600 field plots from the Forestry Inventory of Catalonia with abiotic and biotic characteristics of each plot. I present general patterns of distribution, dominance and regeneration for the six species and then focus on *P. halepensis*, the most abundant pine species in the western Mediterranean Basin. For all six species, the models correctly classified more than 80% of the distribution using abiotic factors, mainly altitude and rainfall variability. Biotic factors such as the basal area of other pine species were necessary to accurately predict patterns of pine species dominance. Biotic factors, especially the basal area of evergreen species (mainly *Quercus ilex*), were of overriding importance when predicting patterns of seedling occurrence. Potentially important factors such as land use and fire history were of little significance for predicting distribution at the scale of this study. The models failed to predict accurately which species (and in which number) co-occur with *P. halepensis*. Factors not included in this study, such as stand age, disturbance (cutting, clearing) and other human-induced factors, are probably the main determinants of co-existence patterns.

Introduction

In total, ten species of *Pinus* occur naturally in the Mediterranean Basin (including the Canary Islands), where they make up an important component of the vegetation over large areas. Pine-dominated ecosystems cover about 5% of the total area of this region and about 25% of the forested area in the region (Barbéro et al., 1998). Mediterranean pines occupy a wide range of substrata and grow mainly in humid and sub-humid climate types (annual rainfall > 600 mm (Quézel, 1985). They often occur in harsh environments (e.g. *Pinus halepensis* at the edge of the Sahara Desert; *P. uncinata* > 2300 m in the Pyrenées). The most abundant and widespread species in the region are the closely related and ecologically-similar *P. brutia* (in the east) and *P. halepensis* (in the west) which together cover 6.8 million ha. Other species that cover large areas are *P. nigra* (3.5 million ha), *P. pinaster* (1.3

million ha) and *P. pinea* (0.3 million ha). The remaining *Pinus* species together cover another 0.3 million ha (Barbéro et al., 1998).

In the Mediterranean Basin, the distribution of pines especially the most abundant and widespread ones, has been greatly affected by human activities over thousands of years. The role of humans in structuring pine forests is quite different in northern and southern parts of the region. For example, the area of pine forests (especially *P. halepensis*) has declined considerably in the Maghreb area as a result of clearing of forest for cultivation, cutting for various purposes (feeding of livestock, house building, charcoal), overgrazing and frequent fires (Quézel, 1980; Barbéro et al., 1990). In contrast, the area of pine forests is increasing rapidly in many parts of southwestern Europe where pines behave as invaders (early maturity, large seed crops, good germination success), occupying the abandoned fields resulting from the "set-aside" policy of the European Union (Acherar et al., 1984). Land use changes have also created many environmental and management issues with regard to pines. Outbreaks of insect pests have devastated planted, rather than natural, pine stands due to planting on inappropriate sites and inappropriate selection of provenances (Barbéro et al., 1998). Fires have caused major damages in pine-dominated ecosystems as a result of changes in fire regime (Agee 1998). In the 1980's, up to 550 000 ha yr^{-1} of Mediterranean forest and shrublands burned over. Only 2% of the affected area was ignited by lightning (Trabaud et al., 1993).

The broad-scale distribution of pine species across the Mediterranean Basin can, to a large extent, be accounted for by the division of the environment into *étages*; vegetation belts defined on the basis of topography, altitude and regional climate (see Quézel, 1974; Barbéro, 1998 for descriptions of the concept). Knowledge of the distribution of pines at different scales in their native habitat is important for many reasons, including: 1) changing conditions in the region as a result of changing land use and climate; 2) an increasing demand for the products and services supplied by Mediterranean pines both within the Mediterranean Basin and in other parts of the world; and 3) to shed light on invasions of Mediterranean pines in others regions (Richardson et al., 1994; Richardson and Higgins, 1998).

Catalonia in northeastern Spain has a rich native pine flora and comprises, within a relatively small area (31 930 km^2 or about 1.4% of the entire Mediterranean Basin as defined by Barbéro et al., 1998), a wide range of environmental conditions and land use classes. The six pine species that occur in Catalonia are, in order of decreasing area occupied: *Pinus sylvestris*, *P. halepensis*, *P. nigra*, *P. pinea*, *P. uncinata* and *P. pinaster*. The six species show very different distribution patterns due, among others, to the range of habitat conditions and the various and complex influences of humans over thousands of years. The existence of an extensive data base, incorporating results from 10 600 forestry plots throughout the region, for the distribution, abundance (basal area) and regeneration potential for all trees in Catalonia (see below) enabled me to explore the determinants of distribution of native pines in more detail than has been done in any other part of the Mediterranean Basin. The aim was to develop simple predictive models of the distribution, abundance and regeneration patterns of each *Pinus* species in Catalonia. For each *Pinus* species I used an hierarchical approach to relate environmental factors with: (1) the distribution of the species at the regional scale; (2) the basal area and relative abundance (dominance) of species within their respective environmental envelopes (i.e. where the species is predicted to occur based on environmental factors); and (3) the factors that distinguish sites where different *Pinus* taxa occur as adults from sites with prolific regeneration (large number of seedlings). I present the broad patterns for all *Pinus* species and then focus on *P. halepensis*, the most abundant pine species in the western part of the Mediterranean Basin. I also explore the distribution (presence and dominance) of *P. halepensis* in relation to the presence and relative abundance of other woody taxa (including other pine species).

Methods

Study site

Catalonia in northeastern Spain (31 930 km^2), comprising the provinces of Barcelona, Girona, Lleida, and Tarragona, is bounded on the north by the Pyrenees Mountains, on the west by the region of Aragón, and on the east by the Mediterranean Sea. The climate is mainly mediterranean with mild winters, and warm and dry summers. The Pyrenées mountains, reaching altitudes of over 3000 m create sharp topographical-climatic gradients where Mediterranean-type biomes gradually change to temperate, boreal-like (subalpine) and tundra-like (alpine) types, corresponding to the euro-siberian and boreoalpine phytogeographic regions. Furthermore, the increase in continentality and the decrease in rainfall from the coast to the central plains create another major gradient from a humid climate with warm winters (January minimum mean temperature of 1.5° C and mean annual precipitation of 750 mm) to a semi-arid Mediterranean climate with cold winters (January minimum mean temperature of –2° C), low annual rainfall (300-400 mm) and dominance of shrub subdesertic vegetation types.

Evergreen forests mainly dominated by *Quercus ilex* generally constitute end-points of many successional series (Barbéro et al., 1990; Polunin and Smythies, 1997). Most of *Q. ilex* forests have however been markedly degraded. A typical degradation stage is the maquis, brought by clearing, intensive cutting, grazing and frequent fire (Polunin and Smythies, 1997). Large parts of the forested area in Catalonia are dominated by *Quercus ilex* and *Pinus halepensis* in different mixtures. The structure and dynamics of these forests are determined mainly by water availability and time since disturbance (Espelta et al., 1992; Gracia and Retana, 1996).

Human activities became a pervasive factor in the vegetation dynamics in the region during the Roman Empire and have remained so ever since. Forests were exploited for wood (building houses and ships), wood charcoal, hunting and sheep, goat and cow grazing. The increasing human population in the region, especially in the 20th century, led to increased exploitation and associated impacts. Furthermore, forest dynamics has been influenced by the abandonment of large areas of cropland and grassland, followed by their colonisation by trees. The increase in industrial activities, recreational uses of forests, vehicle traffic, and the increasing incidence of ignition has changed the fire regime: the number of fires recorded per year has increased continuously from 1968 (Piñol et al., 1998). Fire-return times range from <25 years in some counties to >1000 years in others, depending on climate.

The data set

Forestry inventory

The forestry inventory of Catalonia (IFEC) is a database of 10 500 circular sampling plots (10 m radius) distributed throughout the region. Sampling was done between 1988 and 1994 at a density of one plot per km^2 of natural or managed forest. All trees with diameter at breast height above 5 cm were recorded. When more than five tree species occurred within the same sampling unit, only the five most abundant species were recorded (the case in less than 5% of the plots). The IFEC includes observations on 95 tree species (of which 33 are present in more than 10% of the plots) distributed into 43 genera (of which 17 are present in more than 10% of the plots). Genera with the greatest numbers of individual trees in the sampling plots were, in decreasing order of importance: *Pinus* (6 species), *Quercus* (13 spp.), *Acer* (6 spp.), *Fagus* (1 spp.), and *Arbutus* (1 spp.). The most abundant species were *Quercus ilex* (present in 18% of the sampling plots), *Pinus sylvestris* (13%), *P. halepensis* (11%), *P. nigra* (8%), and *Q. pubescens* (8%). For each representative tree of each diameter class, was recorded: species name, diameter, and basal area. For one fifth of the plots, the database also includes regeneration data (number of seedlings per m^2) (see Gracia et al., 1997 for a more detailed presentation of the IFEC). For each sampling plot, I computed the basal area of all evergreen species, the basal area of all deciduous species, the basal area of all *Quercus* species, and specifically that of *Q. ilex*, and the basal area of each *Pinus* species. For the regeneration data set, I recorded the following additional variables: total number of *Quercus* and *Pinus* seedlings per m^2 (see Table 1 for a list of factors used).

Table 1. List of potential predictors used to generate regression trees to explain the distribution of six *Pinus* species in Catalonia, Spain. Score value is a crude indicator of the relative importance of each variable summarised over all six species. Scoring was done as follows: when the variable was the first factor to explain the species distribution, a score of 4 was given; when it was the second factor, score of 2; the third factor, score of 1, the fourth factor, score of 0.5. The same factor can be used several times in the FIRM analysis. The most important factors are shown in bold.

Predictors	Abbreviation	Score		
		Distribution	*Dominance*	*Regeneration*
Topography				
Altitude	ALTI	**19**	4	0
Slope	SLOPE	0	0	0
Aspect	ASPECT	0	0	0
Solar radiation	SOLRAD	0	0	0
Climate				
Total rainfall	RN-AN	2	3	0
Winter rainfall	RN-WIN	**11**	5	4
Spring rainfall	RN-SPG	**11**	**6.5**	0
Summer rainfall	RN-SUM	3	0	0
Minimum annual temperature	TMP-AN	0	0	0
Minimum winter temperature	TMP-WIN	2	2.5	0
Minimum spring temperature	TMP-SPG	0	1	0
Maximum summer temperature	TMP-SUM	0	0	0
Land use	LDUSE	0	0	0
Geology	GEOL	5.5	1	0
Fire	FIRE	0	0	0
Species interaction				
Basal area of evergreen species	BA_E	2	2	**10**
Basal area of deciduous species	BA_D	4	**6**	0
Basal area of *Quercus* species	BA_Q	0	**10**	0
Basal area of *Q. ilex*	BA_ILEX	0	2	0
Basal area of *Pinus* species	BA_PINUS	2	**16**	0
Basal area of *P. halepensis*	BA_HAL	0	0	1
Basal area of *P. nigra*	BA_NIGRA	0	0	0
Basal area of *P. pinaster*	BA_PINAS	0	2.5	0
Basal area of *P. pinea*	BA_PINEA	0	0	0
Basal area of *P. sylvestris*	BA_SYLV	0	5	4
Basal area of *P. uncinata*	BA_UNCI	1	0	0
Number of *Quercus* seedlings	Q_SEED	-	-	**6.5**
Number of *Pinus* seedlings	P_SEED	-	-	2
Other seedlings	O_SEED	-	-	0

set, I recorded the following additional variables: total number of Quercus and Pinus seedlings per m^2 (see Table 1 for a list of factors used).

Environmental variables

A climate model (Ninyerola et al., 2000) was used to generate layers of monthly precipitation and monthly minimum and maximum temperatures for the entire study area. The climate model was created from a network of weather stations in Catalonia (160 stations for air temperature and 257 stations for precipitation), and was based on a multiple regression analysis between the meteorological variables and some geographic variables (altitude, latitude, continentality, solar radiation and a cloudiness factor). The independent variables were derived from a 180 m resolution digital elevation model. The accuracy of the climatic surfaces was then assessed and corrected with reference to an independent set of weather stations (40% of the initial weather stations). The correction factor improved the accuracy of the climate model, which ranges between 70 and 97% (model outputs were generally more accurate for temperature than for rainfall, and more accurate for lowlands than for mountains). Layers of mean annual rainfall, rainfall per season, minimum annual temperature, mean minimum winter and spring temperatures and mean maximum summer temperature were then derived from the original climate model. Topographic layers (altitude, slope, aspect, and solar radiation) were obtained from a Digital Terrain Model (180-m resolution). Coverages of fire history over the last 25 years (1975-1998) and current land use were obtained from CREAF (1:250 000 scale; Ibañez et al., 1997; Salvador et al., 1997). A geology layer was provided by the Institute of Cartography of Catalonia (1:250 000 scale). Biotic variables that could potentially influence the presence or abundance of pine species were derived from the IFEC database.

Statistical analysis

Determinants of species distribution

I used a recursive partitioning technique, Formal-based Inference Recursive Modelling (FIRM) (Hawkins, 1995), to describe the relationships between environmental variables and species distributions. Recursive modelling, also known as tree regression analysis, is a useful exploratory technique for uncovering structure in data with variables that may be hierarchical, nonlinear, or categorical (Breiman et al., 1984). Recursive modelling captures nonadditive behaviour, where the relationships between the response variable and predictor variables depend on the values of other predictors. These techniques do not rely on assumptions of linearity, and handle continuous and categorical data types. Recursive modelling is rapidly gaining popularity and has in several studies been shown to yield more accurate estimates than standard linear-models (Reichard and Hamilton, 1997; Iverson and Prasad, 1998; Vayssières et al., 2000; Rouget et al., 2001).

The data set is successively split by the FIRM analysis into smaller subsets, based on the values of the predictor variables. The grouping of classes is assessed by chi-squared tests between each pair, and the overall significance of the split is assessed by a Bonferroni procedure. Each split is designed to separate the cases in the node being split into a set of successor nodes that are maximally homogeneous. The output from FIRM is a dendrogram that provides an intuitive pictorial interface to understanding the structuring of the problem as well as an effective way of making further predictions.

stringent *p* values to avoid very large dendrograms with spurious splits. Since the addition of biotic factors did not significantly improve the model performance, only environmental factors were used in the final models. This allowed to define environmental envelopes for each *Pinus* species. In a second set of analyses, I examined the relative abundance (dominance) of each *Pinus* species within their environmental envelope. At this stage, both biotic and environmental factors were included (see Table 1). The dependent variable was grouped into three classes: species absent; species mixed with others; or species dominant (i.e. species with the highest basal area). Finally, regression trees were generated for each pine species, using presence/absence of seedlings as the dependent variable. This analysis was performed on the subset of plots with regeneration data.

Determinants of *Pinus halepensis* distribution and its interactions with other species were analysed by FIRM as follows: the distribution of the most abundant woody species co-occurring with *P. halepensis* were tested to find whether species co-occurrence was determined by environmental characteristics. Plots in which at least one of the following six species occurred were included in the analysis: *P. halepensis*, *P. nigra*, *P. pinea*, *Quercus ilex*, *Q. pubescens*, and *Q. cerrioides*. The five last-mentioned species occurred in more than 10 % of the sampling plots containing *P. halepensis*. The presence/absence of all the six species mentioned above was used as dependent variables in a single model. The aim of this general model was to isolate environmental conditions indicating where the six species occurred in pure or mixed stands. I then focused on the interaction between *P. halepensis* and *Q. ilex* in plots where either of the species occurred. The dependent variable, computed as the ratio [basal area of *P. halepensis*]/[sum of basal area for both species], was interpreted as a species dominance index.

To improve the understanding of species co-existence in pine ecosystems, I complemented the analysis with contingency tables of presence/absence data for adult and seedling individuals to highlight positive or negative associations between any pair of species among the 14 most common species in the plots. Different life stages were separated: I considered potential associations between adult trees, adult and seedling individuals, and seedlings only.

Table 2. Model accuracy for the distribution (presence/absence) of the six *Pinus* species occurring in Catalonia. Significant variables influencing the distribution are indicated (see Table 1 for explanation of abbreviations). Presence: number of plots where the species is present (% of correctly classified plots); Absence: number of plots where the species is absent (% of correctly classified plots); CA: classification accuracy ([total number of correctly classified plots]/[Absence + Presence] x 100).

Species	Presence	Absence	CA	Variables
P. halepensis	2675 (95.6)	7824 (92)	92.5	Rn-Spg, Rn-An, Tmp-Win
P. nigra	2061 (86.3)	8438 (78.3)	79.9	Rn-Win, Rn-Spg, Rn-Sum, Alti, Geol, Tmp-Win, Tmp-Spg
P. pinaster	302 (86.1)	10192 (82.6)	82.7	Alti, Rn-Win
P. pinea	971 (82.7)	9528 (77.8)	78.2	Alti, Rn-Win, Rn-Spg, Rn-Sum
P. sylvestris	3184 (82.3)	7315 (76.9)	78.5	Alti, Geol, Rn-Win, Rn-Spg, Rn-Sum
P. uncinata	774 (93.8)	9725 (91.8)	92.0	Alti, SolRad

Potential distribution maps

Dendrograms from the FIRM analysis and a GIS database for Catalonia of all recorded environmental variables were used to derive potential distribution maps for each of the six *Pinus* species. Environmental conditions useful for predicting the occurrence of each *Pinus* species were selected from the respective dendrogram. For each node of the dendrogram (i.e. for each combination of environmental factors), the species was considered likely to occur (probability of occurrence higher than 0.5) if the species was over-represented in the node (species with the highest frequency in this node). The accuracy of the model was estimated by the percentage of plots correctly classified by this method.

Results

General patterns for all pine species

Determinants of pine distribution

Regression trees were generated for each species. Among all potential predictors, only a few variables was found to significantly influence the distribution of the six pine species (Tables 1, 2). Physical and climatic factors were generally more important than biotic factors (Table 1). Moreover, the model performance was not significantly reduced when biotic factors were excluded. The distribution of the six *Pinus* species could then be accurately modelled using a few simple abiotic factors. For each species, between two and five environmental factors correctly classified more than 80 % of the species distribution (Table 2). Altitude was the most important factor for four *Pinus* species (*P. pinea*, *P. pinaster*, *P. sylvestris* and *P. uncinata*; Table 2). Winter and spring rainfall were the most important predictors of *P. nigra* and *P. halepensis* distribution respectively (Table 2). For all *Pinus* species,

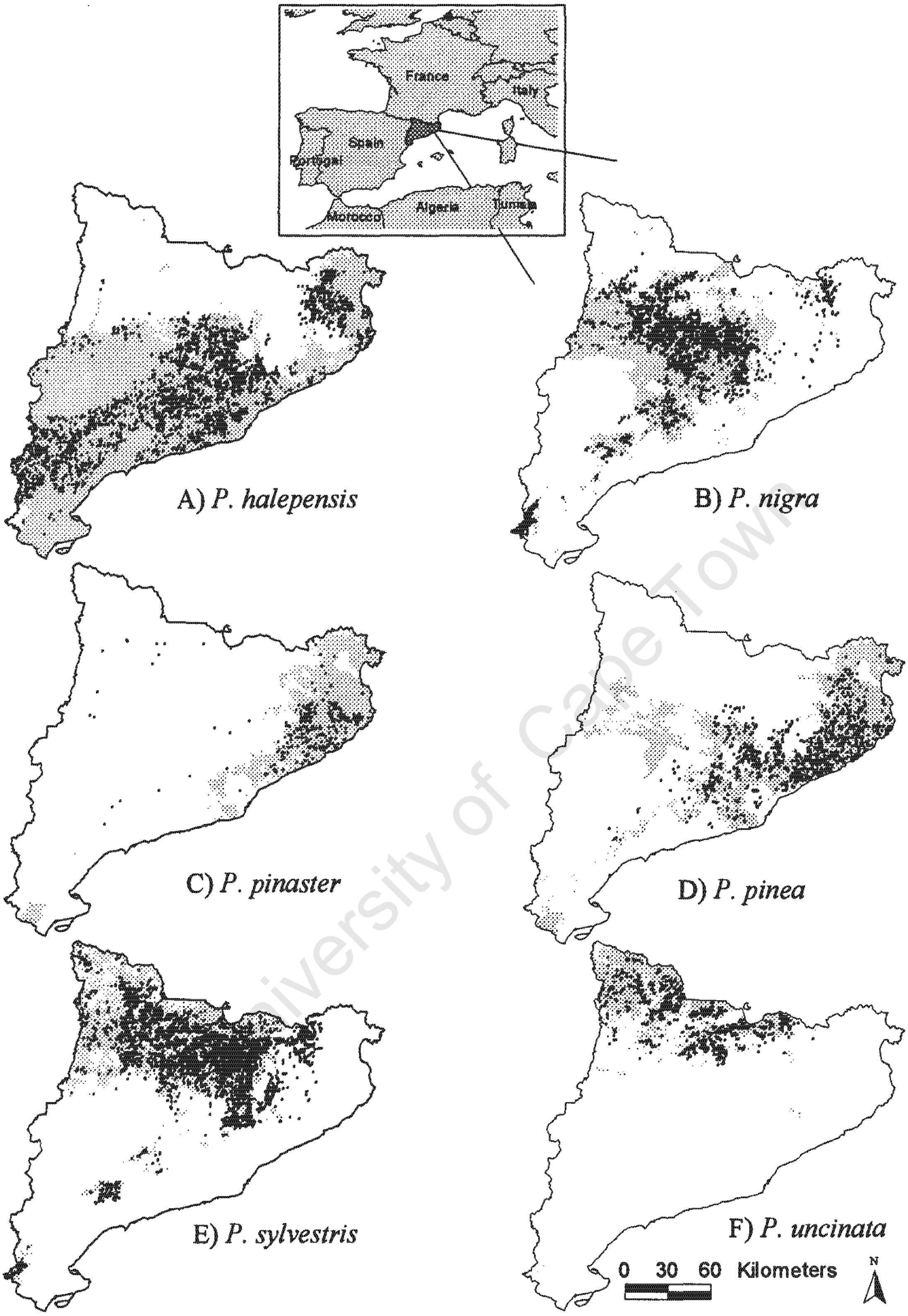


Figure 1. Potential distribution maps of six *Pinus* species in Catalonia: a) *P. halepensis,* b) *P. nigra,* c) *P. pinaster,* d) *P. pinea,* e) *P. sylvestris,* and f) *P. uncinata.* Shaded areas are suitable for pine occurrence (probability higher than 0.5). Plots where the species is present are represented by black dots. The geographic location of the study area within the Mediterranean Basin is shown.

rainfall variability was an important predictor of the species range whereas temperature was a secondary or tertiary factor (Table 1).

Fig. 1 shows the potential distribution maps for each *Pinus* species in relation to the environmental factors found to be important by FIRM analyses (Table 2). *Pinus sylvestris* and *P. uncinata* occurred only in the northern part of Catalonia at high altitudes. *Pinus nigra* occurred under intermediate conditions whereas *P. halepensis* was only found in dry areas (southern part). *Pinus pinaster* and *P. pinea* both occurred in more humid areas (>160 mm of winter rainfall per year) at low altitudes (<550 m, and <660 m, respectively) (Fig. 1).

Determinants of pine dominance

Biotic factors explained most of the variation in the pine dominance within their respective climatic envelopes (Tables 1, 3). The most important factors were the basal area of other *Pinus* species, the basal area of *Quercus* species, spring rainfall and the basal area of deciduous species (Table 1). The classification accuracy of the models ranged from 58 to 73% (Table 3). Prediction accuracy was higher for the most abundant pine species in Catalonia (*P. sylvestris* and *P. halepensis*). The model was generally very accurate in predicting the absence and the dominance of a given species within its environmental envelope (Table 3). However the model was weak in predicting species occurrence in mixed stands (i.e. species present but not dominant) (Table 3).

Determinants of pine seedling occurrence

Of thirty potential predictor variables, only six were found to influence the pattern of seedling occurrence of *Pinus* species significantly (see Table 1). Biotic factors were generally most important; notably the basal area of evergreen species and the number of *Quercus* seedlings, which both

Table 3. Model accuracy for the relative abundance of the six *Pinus* species within their climatic envelope. Significant variables influencing the distribution are indicated (see Table 1 for explanation of abbreviations). Dominance: number of plots where the species is dominant (% of correctly classified plots); Presence: number of plots where the species is present but not dominant (% of correctly classified plots); Absence: number of plots where the species is absent (% of correctly classified plots); CA: classification accuracy ([total number of correctly classified plots]/[Dominance + Presence + Absence] x 100).

Species	Dominance	Presence	Absence	CA	Variables
P. halepensis	1913 (91.2)	539 (50.8)	377 (36.1)	76.2	BA-Pinus, BA-Ilex, Alti
P. nigra	1135 (80.3)	640 (20.2)	1840 (65.9)	62.3	BA-Pinus, BA-Q, BA-Sylv, BA-D, BA-Ilex, Rn-Sum, Rn-Win, Tmp-Win
P. pinaster	99 (38.4)	161 (54.7)	1775 (68.4)	65.9	BA-Ilex, BA-Pinea, Rn-Win
P. pinea	271 (71.6)	530 (45.3)	2120 (60.1)	58.4	BA-Pinus, BA-Q, BA-D, Alti
P. sylvestris	1747 (80)	869 (35)	1756 (84.5)	72.9	BA-Pinus, BA-Q, Rn-Sum, Alti, BA-D
P. uncinata	473 (80.5)	253 (17.5)	795 (86.8)	73.3	Alti, BA-Pinus, BA-Sylv

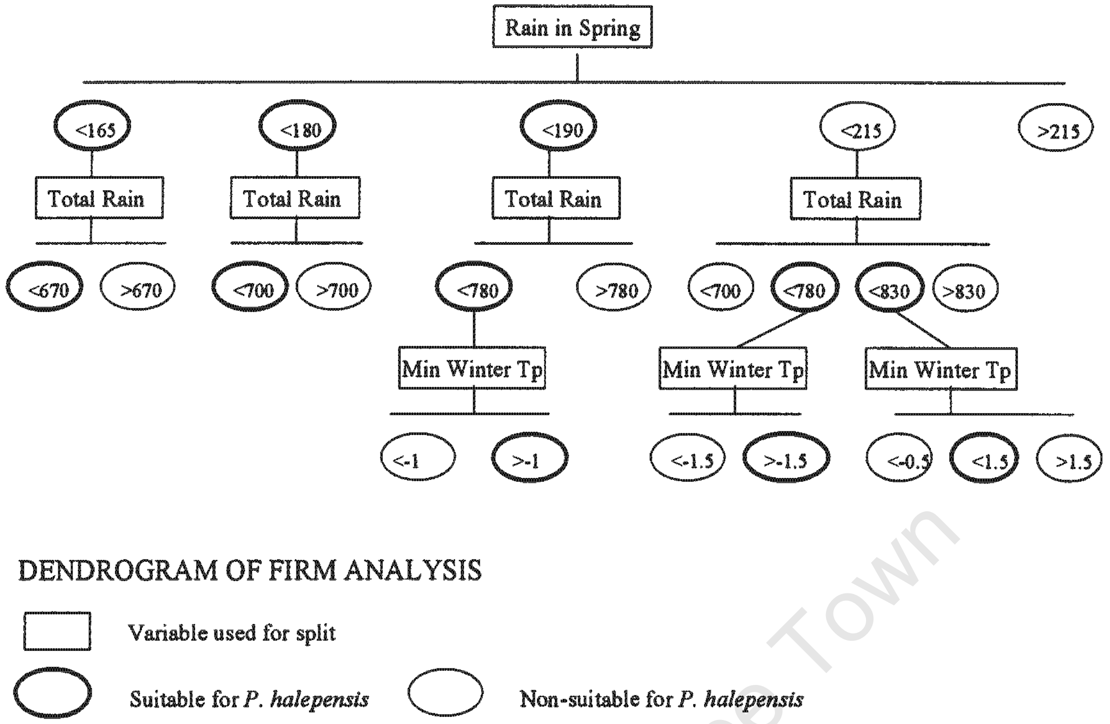


Figure 2. Determinants of *Pinus halepensis* distribution (presence/absence) in Catalonia as represented by a FIRM dendrogram. The boxes indicate variables that significantly influence the species distribution. The most important variable is shown on top. Combinations of variables that favour *P. halepensis* occurrence are shown in bold. Values are indicated in the ellipsoids (in mm for rainfall variables, in ° C for temperature). E.g., *P. halepensis* is predicted to occur with spring rainfall < 165 mm and total rainfall < 670 mm.

decreased the probability of occurrence of pine seedlings. The model was accurate for *P. halepensis* and *P. nigra*, the regeneration of which was influenced by several factors (Table 4). However, the model performance was weak for the other species where only one factor was found to be significant (Table 4).

Determinants of pine seedling occurrence

Of thirty potential predictor variables, only six were found to influence the pattern of seedling occurrence of *Pinus* species significantly (see Table 1). Biotic factors were generally most important; notably the basal area of evergreen species and the number of *Quercus* seedlings, which both decreased the probability of occurrence of pine seedlings. The model was accurate for *P. halepensis* and *P. nigra*, the regeneration of which was influenced by several factors (Table 4). However, the model performance was weak for the other species where only one factor was found to be significant (Table 4).

Table 4. Model accuracy for the occurrence of seedlings of five *Pinus* species in Catalonia (*P. pinaster* was excluded because the species was present in too few plots). Significant variables influencing the distribution are indicated (see Table 1 for abbreviations). Presence: number of plots where the species regenerate (% of correctly classified plots); Absence: number of plots where the species does not regenerate (% of correctly classified plots); CA: classification accuracy ([total number of correctly classified plots]/[Absence + Presence] x 100).

Species	Presence	Absence	CA	Variables
P. halepensis	363 (77.2)	212 (81.6)	78.6	BA-E, Q-Seed, P-seed
P. nigra	256 (80)	186 (61.9)	72.2	Rn-Win, BA-E, BA-Hal, Q-Seed
P. pinea	26 (57.6)	167 (85.6)	81.2	Q-Seed
P. sylvestris	389 (85.8)	275 (32)	63.6	BA-E
P. uncinata	107 (85)	53 (30.2)	66.9	BA-Sylv

Distribution, abundance and regeneration pattern of Pinus halepensis

Fig. 2 shows the determinants of the distribution of *Pinus halepensis*. Using spring rainfall only, the model correctly classified 83% of the current distribution, while the addition of total rainfall and minimum winter temperature improved the prediction accuracy to 92%. Areas with less than 190mm of precipitation in spring were most suitable for *P. halepensis*. Low annual precipitation (up to 830 mm, depending on spring rainfall value) and high minimum winter temperature (> -1° C) increased the probability of *P. halepensis* occurrence. Geology and altitude were less useful in explaining the distribution of this species. Almost 95% of the stations where *P. halepensis* was present were correctly classified by the model (Fig. 2).

Biotic factors were important in predicting dominance of *Pinus halepensis*. Using basal area of other *Pinus* species only, the model correctly classified 72% of the data set, while the addition of basal area of *Quercus* species and altitude improved the model accuracy to 75%. *Pinus halepensis* was predicted to be dominant when the basal area of other *Pinus* species was less than 1.25 m^2. *Pinus halepensis* was excluded from dense stands of other pine species, but could be present in dense stands of oaks. Within its environmental envelope, 92 % of the sites where *P. halepensis* is the dominant species were correctly classified, as were 51% of the sites where the species was present but not dominant (Table 3). The model failed to correctly predict sites where the species was absent in sites however climatically suitable (accuracy of 36%).

The occurrence of *P. halepensis* seedlings was influenced mainly by the basal area of evergreen species. Seedling occurrence was negatively affected by the basal area of evergreen species, the number of seedlings of other *Pinus* species and the number of *Quercus* seedlings (Fig. 3). The model accurately predicts more than 75% of seedling occurrence (Table 4).

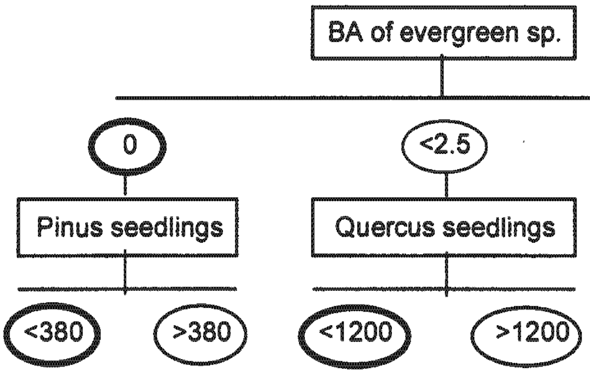


Figure 3. Determinants of *Pinus halepensis* seedling occurrence in Catalonia as represented by a FIRM dendrogram. Variables that significantly influence the seedling occurrence are indicated as well as values used for the split (in m^2 for basal area, in seedlings/m^2 for other variables). Combinations of variables that favour *P. halepensis* regeneration (i.e. where seedlings are predicted to occur) are shown in bold.

Determinants of the distribution of species co-occurring with *P. halepensis*

The most common species co-existing with *P. halepensis* were: *Quercus ilex* (43% of plots in which *P. halepensis* occurred), *Pinus nigra* (18%), *P. pinea* (15%), *Q. cerrioides* (11%) and *Q. pubescens* (10%). Their respective distribution was accurately predicted in one model with five environmental variables (Table 5), in which spring rainfall explained 63% of the variation. This global model generated a climatic envelope for each of these six species, with species occurrence accuracy ranging between 50.5% (*Quercus ilex*) and 85.5% (*Pinus nigra*). Model predictions were, however, not always accurate regarding species associations. Only the association of *P. halepensis* with *P. nigra* was correctly predicted, and the model was very poor at predicting where *P. halepensis* co-occurred with *Quercus ilex* or *Q. pubescens* (Table 5).

Table 5. Model accuracy for the distribution of species co-occurring with *Pinus halepensis.* All plots in which one of the mentioned species occurred were included in the model. Accuracy is given in percentages for occurrence data (a plot was correctly classified if the probability of a given species, present in the field plot, is higher than 0.5). The model included the following variables: spring rainfall, summer and winter rainfall, mean minimum temperature and altitude.

Species	Sample	Accuracy	Species	Sample	Accuracy
Pinus halepensis	2675	87	*P. halepensis / P. nigra*	472	73
P. nigra	2061	83	*P. halepensis / P. pinea*	392	68
P. pinea	976	78	*P. halepensis / Q. ilex*	1155	<1
Quercus ilex	4413	58	*P. halepensis / Q. pubescens*	250	<1
Q. pubescens	1995	68	*P. halepensis / Q cerrioides*	288	75
Q. cerrioides	890	73			

Regression trees generated to determine, from basal area of *P. halepensis* and *Q. ilex* respectively, where *P. halepensis* was dominant, where *Q. ilex* was dominant, and where the two species occurred in mixed stands, correctly classified 76% of the data set using only two factors, total rainfall and spring rainfall (see Fig. 4). When the total rainfall was lower than 668 mm, *P. halepensis* was predicted to be dominant; when the total rainfall was between 668 and 800 mm, the two species were predicted to co-occur; and, when the total rainfall was higher than 800mm, *Q. ilex* was predicted to be dominant. *Q. ilex* was also predicted to be the dominant species when spring rainfall was high (>180 mm) even when the total rainfall was low (Fig. 4). Seventy-five percent of the plots where *P. halepensis* was dominant and 78% of those where *Q. ilex* was dominant were correctly classified. Unlike the previous analysis based on occurrence alone, the model accurately predicted the distribution of mixed stands of *P. halepensis* and *Q. ilex* (accuracy of 54%).

Fig. 5 shows the associations between life-history stages of the most common species based on chi-squared tests from contingency tables. The occurrence of *Q. ilex* and *P. halepensis* appeared unrelated at the adult stage (Fig. 5, box A1 and A2). However, the occurrence of seedlings of *P. halepensis* was negatively associated ($p<10^{-5}$) with adult trees and seedlings of *Q. ilex* (Fig. 5, box B1 and C1). The occurrence of seedlings of *Q. ilex* was positively associated with adult trees of *P. halepensis* but not related with seedlings of *P. halepensis* (Fig. 5, boxes B2 and C2).

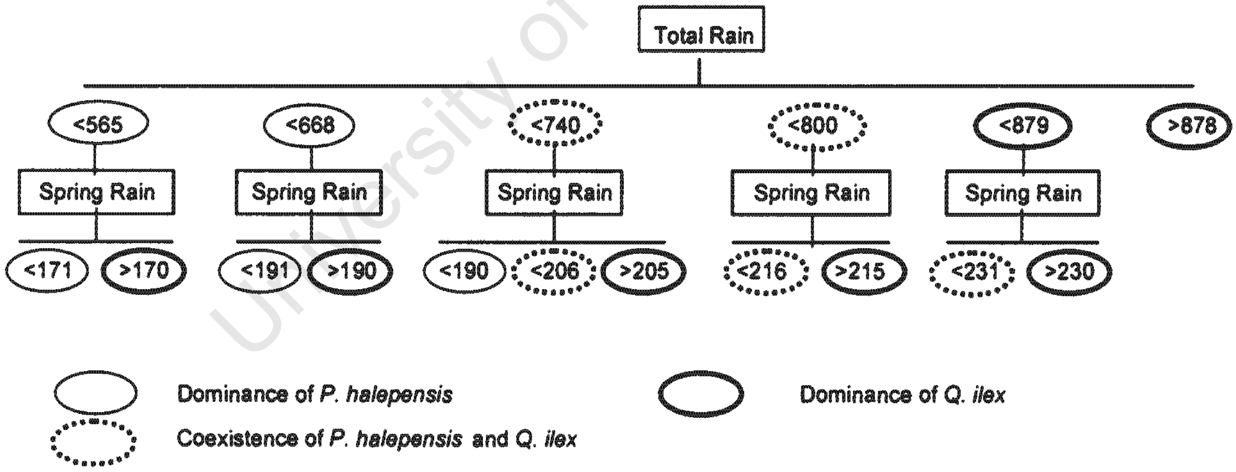
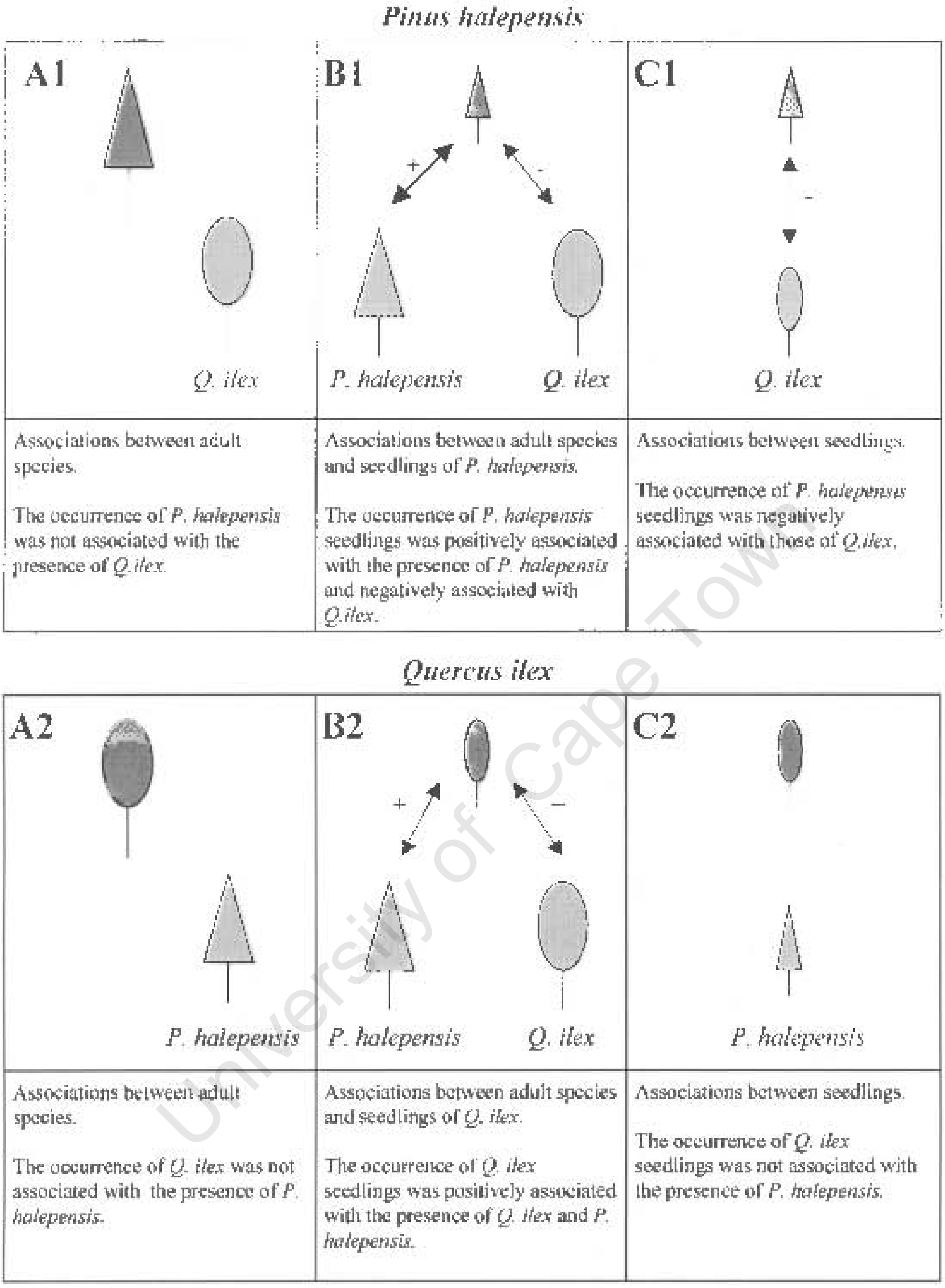


Figure 4. Determinants of *Pinus halepensis/Quercus ilex* distribution in Catalonia as represented by a FIRM dendrogram. The ratio [basal area of *P. halepensis*]/[sum of basal areas of both species] was used as the dependent variable. *Q. ilex* was interpreted to be the dominant species if the ratio (R) was less than 0.25, if R between 0.25 and 0.75 the species were considered to coexist, and if $R \geq 0.75$ then *P. halepensis* was interpreted as the dominant species. The boxes indicate the variables that significantly influence the distribution of both species. Values are indicated in the ellipsoids (in mm). The predicted species to occur is indicated.



Associations between adult species. The occurrence of *P. halepensis* was not associated with the presence of *Q. ilex*.	Associations between adult species and seedlings of *P. halepensis*. The occurrence of *P. halepensis* seedlings was positively associated with the presence of *P. halepensis* and negatively associated with *Q. ilex*.	Associations between seedlings. The occurrence of *P. halepensis* seedlings was negatively associated with those of *Q. ilex*.

Associations between adult species. The occurrence of *Q. ilex* was not associated with the presence of *P. halepensis*.	Associations between adult species and seedlings of *Q. ilex*. The occurrence of *Q. ilex* seedlings was positively associated with the presence of *Q. ilex* and *P. halepensis*.	Associations between seedlings. The occurrence of *Q. ilex* seedlings was not associated with the presence of *P. halepensis*.

Figure 5. Correlation between main species co-existing with *Pinus halepensis*, and with *Quercus ilex* of different life history stages in Catalonia. Contingency tables were generated for each species pair among adult trees of species co-occurring with adult trees of *P. halepensis* (box A1), and of *Q. ilex* (box A2). Then, contingency tables were generated for each species pair among adult tree of species co-occurring with seedlings of *P. halepensis* (box B1), and of *Q. ilex* (box B2). Finally, contingency tables were generated for each species pair among seedling of species co-occurring with seedlings of *P. halepensis* (box C1), and of *Q. ilex* (box C2).

Discussion

Predicting species distribution: the importance of climate

The models correctly classified more than 80 % of the species distribution using mainly climatic factors in a correlative approach (Table 2). Altitude is the variable most frequently included in the models, being the most important factor for two species *Pinus sylvestris* and *P. uncinata* of mountain habitats. The variable altitude in general refines the splits based on rainfall or temperature and I suggest that altitude might integrate the climatic variation in mountainous areas (in terms of temperature and rainfall gradients) better than the derived climatic variables themselves. Two of the best predictors describe aspects of rainfall variability (rain in winter and rain in spring). The inclusion in the models of measurements of energy (i.e. temperature parameters), water availability, as well as climate seasonality is likely to contribute strongly to their accuracy. Furthermore, the use of FIRM allows to detect automatically the effects of combined variables and interactions between factors.

Other potentially important predictors, such as geology, do not contribute significantly to model the distribution of *Pinus* species (Table 1). Furthermore a lack of correlation between the distribution of *Pinus* taxa and fire regime in Catalonia is unexpected as several authors have demonstrated that geology and fire are important in structuring *Pinus* communities (Lepart and Debussche, 1991; Agee, 1998; Barbéro et al., 1998; Pausas, 1999). The apparent lack of significance of fire in determining pine distribution in Catalonia may, however, be due to limitations of the fire data coverage (only the largest fires in the last 20 years are recorded).

The present study confirms the importance of climatic factors in explaining regional patterns of distribution in accordance with other studies at similar scales (Woodward, 1987; Prentice et al., 1992). Modelling of vegetation patterns at finer scales has generally focussed mainly on local variation of topography and geomorphology (Reed et al., 1993; Bridge and Johnson, 2000). However, this study reveals high importance of rainfall seasonality, a factor not considered in other studies of similar scope (Stephenson, 1998). This contrasts with other studies that have generally found temperature (minimum and maximum) to be the best predictor of species distribution (e.g. Woodward, 1987; Leathwick, 1995). The importance attributed to winter and spring rainfall for the distribution of *P. halepensis* confirms that *P. halepensis* is the most drought-tolerant *Pinus* species and therefore occurs only in harsh environments where its physiology enables it to survive. The importance of the annual distribution of rainfall will make it difficult to predict changes in distributions with climate change since these are aspects poorly predicted by climate models (Cubash et al., 1996).

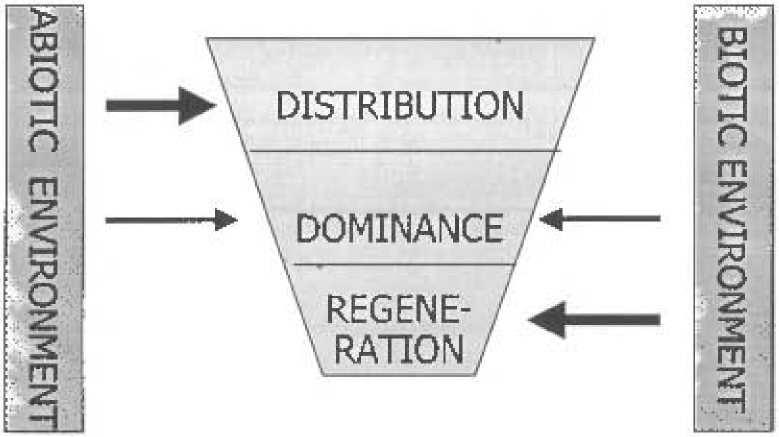


Figure 6. Conceptual model of abiotic and biotic variables that influence the distribution, dominance, and seedling occurrence patterns of *Pinus* species in Catalonia. The thickness of the arrows indicates the importance attributed to the factor.

The importance of species interaction

The results show that abiotic factors are of overriding importance in predicting the distribution (presence/absence) of the six native *Pinus* species in Catalonia (Fig. 6). However, biotic factors are as important as abiotic factors in predicting the dominance of pines, and were of overriding importance for predicting regeneration. The importance of biotic factors may have been underestimated in most related studies of vegetation distribution at a regional scale, which have mainly focused on the effects of environmental factors. Furthermore, stronger negative interaction *Pinus* - *Pinus* than *Pinus* – *Quercus* accords with *Pinus* dominance being more strongly determined by *Pinus* than *Quercus* basal area.

The models are not very accurate in predicting the distribution of species co-occurring with *P. halepensis* (Table 5), even though the distribution of the co-occurring species, modelled separately, can be accurately predicted. This indicated that species co-existence is regulated by factors other than those included in this analysis. Plant species composition in mediterranean-type ecosystems is related to water stress and nutrient availability (Cowling et al., 1996), and to the disturbance regime, especially fire (Pausas, 1999). However, Vilà and Sardans (1999) recently emphasise the importance of competition, a factor generally considered to be of secondary importance in shaping the composition of mediterranean-type communities. Many ecological questions remain unanswered, including the importance of competition compared to other biotic factors, and the response of a given species to competition at different life history stages. Whether or not competition affects co-existence can not be demonstrated directly in this study because of its broad scale. However, the increasing importance of biotic factors for predicting dominance and seedling occurrence patterns (Fig. 6) suggests that competition may play an important role in determining the distributions of woody plants in Catalonia.

Although statistical analyses of species associations have to be interpreted with great caution (Roxburgh and Chesson, 1998), the positive and negative associations found between *Pinus halepensis* and *Quercus ilex* at different life stages (Fig. 5) agree with general patterns of succession in mediterranean forests: according to Barbéro et al (1990), *Pinus* species (including *P. halepensis*) establish first after disturbance while *Q. ilex* seedlings later establish under the pine overstorey. Then, *Quercus* species progressively replace pioneer *Pinus* species in the absence of disturbance. This suggests that species co-existence may be a function of stand age (i.e. successional stage). The potential influence of stand age on species composition is masked in this study since stands of many ages and successional stages are analysed together. In future models of Mediterranean-type vegetation, stand age should be considered as a factor on its own to allow separation of effects of disturbance and temporal trends.

The role of human activities and land use

Centuries of human influence in the Mediterranean Basin makes it almost impossible to distinguish between human influences and the "natural" dynamics of these communities (Barbéro et al., 1990; Lepart and Debussche, 1992; Cowling et al., 1996). Therefore, because of ancient human management, including intensive tree planting, one would expect current species distributions to be poorly correlated with only environmental characteristics, and to depend much more on land use history and human disturbance. For example, several studies have documented the recent invasion of *P. halepensis* into abandoned fields associated with rural depopulation (Acherar et al., 1984; Lepart and Debussche, 1991). The expansion of *P. halepensis* has resulted from the abandonment of grazing in sclerophyllous shrublands, and the establishment of pines in secondary shrublands and grasslands follow abandonment of cultivated terraces (Barbéro et al., 1990).

With the above factors in mind, I was rather surprised at the high accuracy of these predictions based only on climatic and physical factors. Current land-use categories are not significant in explaining the distribution of any of the six *Pinus* species at the scale of this study (Table 1). However, one can not conclude that the broad patterns of pine species distribution in Catalonia are little affected by human activities. The net effects of human activities are probably already captured in the model. First, through human activity and planting, all the commercially valuable species have had the opportunity of sampling all available sites. Secondly, species were preferably planted in areas known to be most climatically suitable (e.g. *P. halepensis* in the driest areas). Consequently, the overriding factor determining management practices has been climate. Furthermore, current land use does not reflect historical changes that have favoured pine expansion especially over the last century.

To enhance timber production, the species composition and abundance of mediterranean-type ecosystems has been markedly altered by foresters (F. Lloret, pers. comm.). Clearance of understorey species and selective cutting have generally favoured *Pinus* species as they are more productive and economically important than *Quercus* species (Gracia et al., 2000). *Quercus* species were traditionally over-exploited to the point of being eliminated from woodlands in some areas. This probably explains the poor performance of the model in predicting the species co-occurring with *P. halepensis* (Table 5).

Modelling species distribution outside Catalonia and relevance to global change

Understanding and predicting plant species distribution has become more important recently in connection with global change modelling (e.g. Prentice et al., 1993; Sykes et al., 1996; Iverson and Prasad, 1998; Hughes, 2000). The high biodiversity, the transitional climate and the intense human activity in terrestrial ecosystems of the Mediterranean Basin create challenging opportunities for global change research (Lavorel et al., 1998). This requires a global understanding of the determinants of vegetation distribution in the Mediterranean Basin.

The six *Pinus* species present in Catalonia also occur naturally in other parts of the Mediterranean Basin (rest of Spain, southern France, Italy). Models similar to those derived in this study can be applied to, and compared with other parts of the Mediterranean Basin. As land use differs quite considerably within the Mediterranean Basin, such comparisons would be useful to examine the interactions between abiotic and anthropogenic factors. Lavorel et al. (1998) suggest a general framework for global change issues in the Mediterranean Basin. More valuable predictions of vegetation response to global change should include at least changes in fire regime, atmospheric change and land use. Results show that the amount and variability of rainfall are the main determinants of the distribution of pine species in Catalonia. While there is a general agreement on a 2-3° C increase of the average annual temperature, the direction and magnitude of precipitation change remain uncertain (Cubash et al., 1996). In order to predict effects of climate change, appropriate rainfall estimates are therefore required.

References

Acherar, M., Lepart, J., Debussche, M., 1984. La colonisation des friches par le pin d'Alep (*Pinus halepensis* Miller) en languedoc mediterraneen. Acta Oecologia 5, 179-189.

Agee, J. K., 1998. Fire and pine ecosystems. In: Richardson, D.M. (Ed.), Ecology and biogeography of *Pinus*. Cambridge Univ. Press, Cambridge, pp. 193-218.

Barbéro, M., Bonin, G., Loisel, R., Miglioretti, F., Quézel, *P.*, 1990. Changes and disturbances of forest ecosystems caused by human activities in the western part of the Mediterranean Basin. Vegetatio 87, 151-173.

Barbéro, M., Loisel, R., Quézel, *P.*, Richardson, D.M., Romane, F., 1998. Pines of the Mediterranean Basin. In: Richardson, D.M. (Ed.), Ecology and biogeography of *Pinus*. Cambridge University Press, Cambridge, pp. 450-473.

Breiman, L., Friedman, J.H., Olshen, R.A., Stone, C.J., 1984. Classification and regression trees. Wadsworth, Belmont.

Bridge, S.R.J., Johnson, E.A. 2000. Geomorphic principles of terrain organization and vegetation gradients. Journal of Vegetation Science 11, 57-70.

Cowling, R.M., Rundel, *P.*W., Lamont, B.B., Arroyo, M.K., Arianoutsou, M., 1996. Plant diversity in mediteranean climate regions. Trends in Ecology and Evolution 11, 362-366.

Cubash, U., von Storch, H., Waskewitz, J., Zorita, E., 1996. Estimates of climate change in Southern Europe derived from dynamical climate model output. Climate Research 7, 129-149.

Espelta, J. M., Gene, C., Retana, J., Terradas, J., 1992. Structure of mixed holm oak (*Quercus ilex*) Aleppo pine (*Pinus halepensis*) forests in Northeastern Spain. In: Teller, A., Mathy, *P.*, Jeffer, J.N.R. (Eds.), Response of forest ecosytems to environmental changes. Elsevier, London, pp. 892-894.

Gracia, M., Retana, J., 1996. Effects of site index and thinning management on the structure of the holm oak forests of the Montseny and Les Guilleries massifs (NE Spain). Annales des Sciences Forestières 53, 571-584.

Gracia, C.A., Burriel, J.A., Ibanez, J.J., Mata, T., Vayreda J. 2000. Forestry and Ecological Inventory of Catalonia. Forestry Region no 5. CREAF, Bellaterra. (In Catalan).

Gracia, C.A., Ibanez, J.J., Vayreda, J., Pons, X., Terradas, J., 1997. A nuevo concepto de inventario forestal. In Proceedings of the XI World Forestry Congress. Volume I. World Forestry Association, Antalya, TR.

Hawkins, D.M., 1995. Formal inference-based recursive modelling. Department of Applied Statistics. University of Minnesota, St Paul.

Hughes, L. 2000. Biological consequences of global warming: is the signal already apparent? Trends in Ecology and Evolution 15, 56-61.

Ibanez, J.J., Vayreda J., Pons, X., Burriel J.A., Tello, E., Calvet, S., Mata, T., Gracia, C.A., 1997. El sistema de información de los bosques de Cataluña: metodología, novedades y aplicaciones. In: Puertas, F., Rivas, M. (Eds.), Communicaciones del II Congreso Forestal Español / I Congreso Forestal Hispano Luso. Volume IV. Sociedad Española de Ciencas Forestales. Pamplona, pp. 351-356.

Iverson, L.R., Prasad, A.M., 1998. Predicting abundance of 80 tree species following climate change in the eastern United States. Ecological Monographs 68, 465-485.

Lavorel, S., Canadell, J., Rambal, S., Terradas, J., 1998. Mediterranean terrestrial ecosystems: research priorities on global change effects. Global Ecology and Biogeography Letters 7, 157-166.

Leathwick, J.R., 1995. Climatic relationships of some New Zealand forest tree species. Journal of Vegetation Science 6, 237-248.

Lepart, J., Debussche, M., 1991. Invasion processes as related to succession and disturbance. In: Groves, R.H., Di Castri, F. (Eds.), Biogeography of mediterranean invasions. Cambridge Univ. Press, Cambridge, pp. 159-177.

Lepart, J., Debussche, M., 1992. Human impact on landscape patterning: mediterranean examples. In: Hansen, A.J., Di Castri, F. (Eds.), Landscape boundaries: consequences for biotic diversity and ecological flows. Springer, New York, pp. 76-106.

Ninyerola, M., Pons, X., Roure, J.M., 2000. A methodological approach of climatological modelling of air temperature and precipitation through GIS techniques. International Journal of Climatology 20, 1823-1841.

Pausas, J.G., 1999. Mediterranean vegetation dynamics: modelling problems and functional types. Plant Ecology 140, 27-39.

Piñol, J., Terradas, J., Lloret, F., 1998. Climate warming, wildfire hazard, and wildfire occurrence in coastal eastern Spain. Climatic Change 38, 345-357.

Polunin, O., Smythies, B.E., 1997. Landform climate and vegetation. In: Polunin, O., Smythies, B.E. (Eds.), Flowers of South- West Europe, a field guide. Oxford Univ. Press, Oxford, pp. 1-39.

Prentice, I.C., Cramer, W., Harrison, S.*P.*, Leemans, R., Monseruds, R.A., Solomon, A.M., 1992. A global biome model based on plant physiology and dominance, soil properties and climate. Journal of Biogeography 19, 117-134.

Prentice, I.C., Sykes, M.T., Cramer, W., 1993. A simulation model for the transient effects of climate change on forest landscapes. Ecological Modelling 65, 51-70.

Price, R.A., Liston, A., Strauss, S.H., 1998. Phylogeny and systematics of *Pinus*. In: Richardson, D.M. (Ed.), Ecology and biogeography of *Pinus*. Cambridge Univ. Press, Cambridge, pp. 49-68.

Quézel, *P.*, 1974. Les forêts du pourtour méditerranéen. Notes techniques, pp. 9-34. UNESCO, Paris.

Quézel, *P.*, 1980. L'homme et la dégradation récente des forêts au Maghreb et au Proche-Orient. Naturalia Monspeliensia 147-152.

Quézel, *P.*, 1985. Definition of the Mediterranean region and the origin of its flora. In: Gómez-Campo, C. (Ed.) Plant conservation in the Mediterranean area. Junk, Dordrecht, pp. 9-24.

Reed, R.A., Peet, R.K., Palmer, L.W., White, *P.*S., 1993. Scale-dependence on vegetation environment correlation: a case study of a North Carolina piedmont woodland. Journal of Vegetation Science 4, 329-340.

Reichard, S.H., Hamilton, C.W., 1997. Predicting invasions of woody plants introduced to North America. Conservation Biology 11, 193-203.

Richardson, D.M., Higgins, S.I., 1998. Pine as invaders in the southern hemisphere. In: Richardson, D.M. (Ed.), Ecology and biogeography of *Pinus*. Cambridge Univ. Press, Cambridge, pp. 450-473.

Richardson, D.M., Williams, *P.*A., Hobbs, R.J., 1994. Pine invasions in the southern hemisphere: determinants of spread and invadability. Journal of Biogeography 21, 511-527.

Rouget, M., Richardson, D.M., Milton, S.J., Polakow, D. 2001. Predicting invasion dynamics of four alien *Pinus* species in a highly fragmented semi-arid shrubland in South Africa. Plant Ecology 152, 79-92.

Roxburg, S.H., Chesson, *P.*, 1998. A new method for detecting species associations with spatially autocorrelated data. Ecology 79, 2180-2192.

Salvador, R., Pons, X., Valeriano, J., Romeu, J., Pale, V., 1997. Un método de análysis de los incendios occuridos en Cataluña durante el periodo, 1975-1993 mediante imágenes de satélite. In:

Hernandez, C., Arias, J.E. (Eds.), Proceedings del Congreso de la Asociación Espanõla de Teledetección. Santiago de Compostela, Spain, pp. 212-214.

Stephenson, N.L., 1998. Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. Journal of Biogeography 25, 855-870.

Sykes, M.T., Prentice, I.C., Cramer, W., 1996. A bioclimatic model for the potential distribution of north European tree species under present and future climates. Journal of Biogeography 23, 203-233.

Trabaud, L., Christensen, N.L., Gill, A.M., 1993. Historical biogeography of fire in temperate and Mediterranean ecosystems. In: Crutzen, P., Goldammer, J.G. (Eds.), Fire in the environment: the ecological, atmospheric, and climatic importance of vegetation fires. Wiley, New York, pp. 277-295.

Tutin, T.G., Heywood, V.H., Burges, N.A., Valentine, D.H., Walters, S.M., Webb, D.A., 1964. Flora Europaea. Volume 1. Cambridge Univ. Press, Cambridge.

Vayssières, M.P., Plant, R.E., Allen-Diaz, B.H., 2000. Classification trees: an alternative non-parametric approach for predicting species distributions. Journal of Vegetation Science 11, 679-694.

Vilà, M., Sardans, J., 1999. Plant competition in mediterranean-type vegetation. Journal of Vegetation Science 10, 281-294.

Woodward, F.I., 1987. Climate and plant distribution. Cambridge Univ. Press, Cambridge.

Quasi-mechanistic models of invasive alien plant spread: Inferring process from pattern

Abstract

This chapter explores the relative importance of factors driving invasions using detailed data on the distribution and abundance of 39 alien tree and shrub species on the Agulhas Plain in South Africa. A correlative approach based on classification trees was first used to model species distribution. Spatially-explicit models invoking propagule pressure and environmental heterogeneity were then developed to explore the determinants of invasibility and spread for the three most widespread species (*Acacia cyclops*, *A. saligna* and *Pinus pinaster*) in more detail. Propagule pressure was modelled as a function of distance to probable source populations. Classification trees using geology, climate, land use and topography were appropriate for modelling species distribution with satisfactory accuracy, but failed to correctly simulate species abundance. I thus modelled species abundance using "quasi-mechanistic" models, which first predict species abundance on the basis of propagule pressure (assuming homogeneous spread rate), and then relate the residuals with environmental factors to improve model accuracy. This second type of model generated much better estimates of invasive plant distribution and abundance. A significant relationship was found between spread rate and environmental factors, but the interactions between spread rate and environmental factors were species specific. This chapter provides a method for quantifying the importance of different environmental factors, and the extent to which propagule pressure can negate the potential effects of various barriers in the invasion process. The importance of plant-environment interactions in determining the trajectory of invasions is highlighted.

Introduction

Many interacting factors determine the range and abundance of an organism at a given locality. Attempts at modelling the range/abundance of species make various assumptions, depending on the aims of the study and the nature of available data (e.g. spatial and temporal scale, precision and accuracy of data). The literature on spatial patterns and determinants of species distribution (mostly dealing with native species) is quite vast and the past decade has seen the resurgence of such studies (e.g. Huntley et al., 1995; Franklin, 1998; Guisan and Harrell, 2000). Due to the increasing availability of GIS data and the development of computational capability, many techniques can now be used to understand and model species distribution (Franklin, 1995; Guisan and Zimmerman, 2000). Over large spatial scales (from regions to continents), static approaches have been quite successful in modelling species distribution (Guisan and Zimmerman, 2000 and references therein). Such approaches rely on observed correlations between the environment and the species distribution and thus assume that the species is at pseudo equilibrium with its environment (Guisan and Zimmerman, 2000). Invasive alien species, especially when the invasion is still at an early stage, are generally not at equilibrium with the environment, and correlative approaches should be used with caution. Over small spatial scales (from stands to landscape), mechanistic models (also called process-based models) such as individual-based cellular automata models have been developed to model species distribution. Such models integrate biological attributes, space, and environmental stochasticity (Higgins and Richardson, 1996). Although they have clear theoretical advantages, they are quite complex to parameterise and can seldom be validated (Higgins et al., 2001). In a few cases, individual-based models have been developed with success for modelling spread of invasive alien species (Higgins et al., 2000).

Biological invasions provide ecologists with excellent opportunities for gaining improved insights on the determinants of distribution. Invasions provide useful natural experiments, which capture the combined effects of many interacting factors (Richardson et al., in press). Considerable understanding of the ecology of a given invasion episode can be gained by correlating observed spatial patterns (presence/absence; abundance; age distribution etc) with available environmental data (e.g. Higgins et al., 1999; Rouget et al., 2001). Information thus derived can be extremely useful for management. A fundamental understanding of the processes that drive invasions demands a more "mechanistic" approach, which explicitly includes these biological processes into the modelling procedure. Many recent studies have addressed key issues in invasion ecology using formal experiments, for example to determine the elements that influence invasibility. These studies may provide some robust, nontrivial generalisations in the future, but currently available evidence from such experiments offers little in the way of practical assistance to managers (see review in Rejmánek et al., in press). Also, such studies can only practically address the invasion ecology of short-lived species. For invasions of trees, shrubs, and other long-lived plants, distribution and population structure at any time reflects the cumulative effects of numerous factors, some of them rare events. Formal experiments offer little hope of improving the parameterisation of simulation models for long-lived species. I believe that much more attention needs to be given to finding ways of extracting as much information as possible from existing spatial patterns and whatever can be derived from available data on the processes that produced these patterns.

The invasion process can be conceptualised as a series of "barriers" that an invading organism must overcome to become fully integrated in an ecosystem (Richardson et al., 2000b). For many invasions, the trajectory of population development (population growth/decline; spatial spread/contraction) can be reconstructed to describe the eventual outcome of many interacting processes that mediate the fate of the immigrants. The strength of different barriers depends, at least to some extent, on the number of propagules - the greater the number of propagules, the greater the chance of a barrier being overcome and therefore invasion. The role of propagule pressure is clearly observable in many invasions, and has been assessed through the number of individuals introduced (Green, 1997), the number of times the species was introduced (Newsome and Noble, 1986), and the proximity from sites of initial introduction (Hutchinson and Vankat, 1997) (see also Williamson, 1996; Lonsdale, 1999). D'Antonio et al. (2001) provided a useful conceptualisation of the role of propagule pressure in mediating invasions. They suggest that high propagule pressure can overcome biotic resistance (to some extent), but that abiotic controls on invasibility are less open to amelioration by high numbers of propagules. Few studies have attempted to quantify the role of propagule pressure in plant invasion process (Williamson, 1996; but see Rejmánek et al., in press). Clearly, propagule pressure must be built into spatially-explicit invasions models. As Williamson (1996, p. 55) wrote: "Looking for real differences in invasibility requires looking at the residuals from the relationship between invasion success and propagule pressure". A major challenge is to parameterise models in this regard, particularly for long-lived species.

The main aim of this chapter is to explore the relative importance of factors driving plant invasions using extremely detailed data on the distribution and age structure of alien trees and shrubs on the Agulhas Plain in South Africa's Cape Floristic Region. I aimed to develop spatially-explicit models of the distribution and spread of invasive alien plants that are tractable, ecologically sound, and accurate over relatively large areas (> 1 000 km^2) and at a fine-scale resolution (≤ 250 m). In order to be useful for management, such models need to accurately estimate species abundance. For invasive alien plant species, abundance is largely influenced by propagule pressure and environmental suitability (Rejmánek et al., in press). I thus need a simple model that retains key biological attributes (notably dispersal ecology) and accounts for environmental heterogeneity. I also aimed to tease out the interactions between invasion spread and environment using the current pattern of invasion in the Agulhas Plain as a natural experiment. Natural experiments such as these offer great opportunities for inferring invasion process from landscape patterns (Richardson et al., in press). The Agulhas Plain is a superb locality to address these issues: many woody species have been introduced over the last century and widespread habitat fragmentation has increased the heterogeneity of the region.

The specific objectives of this chapter were: 1) to test the ability of correlative approaches to model species abundance at fine scale; 2) to develop a new approach for modelling abundance of invasive alien plant species in an heterogeneous environment; and 3) to explore the interactions between the spatial spread of invasion species and the environment for understanding how invading plants experience the environment.

Figure 1. Location of the Agulhas Plain within South Africa and the Cape Floristic Region (CFR). Areas transformed by agriculture and urbanisation are shown in grey and black respectively.

Methods

Study area

The Agulhas Plain lies in the southern part of the Cape Floristic Region (CFR, South Africa) and covers approximately 2160km^2 (Fig. 1). The area is a low-lying coastal plain (75% of the area below 150m elevation) broken by low (<800m) quartzitic hills. Largely because of the complex geology, the area has a rich mosaic of soil types, an important determinant of the high levels of beta diversity in the flora (Cowling, 1990). The area has a mediterranean-type climate, with a mean annual rainfall of between 450mm (in the east) and 650mm (in the north); 65-75% of rain falls in the winter (May-October. The Agulhas Plain is one of the centres of plant biodiversity within the Cape Floristic Province hotspot of plant diversity and endemism (Myers et al., 2000). It is host to 1751 plant species and most local endemic species are edaphic specialists, occurring in small and scattered populations (Cowling and Holmes, 1992). The predominant natural vegetation types on the Agulhas Plain are fynbos and renosterveld. Fynbos is an evergreen, fire-prone shrubland, occurring mostly on sandy, infertile soils; it always contains restioids (wiry, evergreen graminoids), and often ericoid shrubs (species of the Ericaceae and other structurally similar taxa), with proteoid shrubs forming an overstorey of highly variable cover and density. Renosterveld, also a fire-prone shrubland, grows on

Table 1: Description of environmental variables used for modelling species distribution and abundance. For each species, the numbers of time one factor was used for modelling species distribution using classification trees is indicated.

Factors	Mean (range)	*A. cyclops*	*A. saligna*	*P. pinaster*
Altitude	105m (0-780)	3	2	1
Slope	3° (0-35)			
Aspect	8 categories			
Wet index	35.5 (7-55)			
Proximity to river	2680m (0-11960)			
Land use	7 categories	1	1	
Proximity to fields	516m (0-5343)	1	2	2
Proximity to roads	1280m (0-6920)			
Mean annual precipitation	430 mm (310-647)		1	1
Annual minimum temperature	11.1° (10-12.2)		1	2
Growth days	135.5 (96-188)	1		1
Geology	13 categories	1		1
Vegetation groups	12 categories	2	2	2

more fertile, finer textured, clay-rich soils, and is usually dominated by the shrub *Elytropappus rhinocerotis* ("renosterbos"; Asteraceae). (Cowling et al., 1988). The area has been hugely affected and fragmented by agriculture, and 40% of the original natural vegetation has already been transformed (Lombard et al., 1997).

Data collection

Extensive field mapping was conducted to map as accurately as possible the distribution, density and height (age-class) structure of all invasive alien trees and shrubs for the entire Agulhas Plain. An extremely detailed survey was done over six months in 1998. Because of the structure of the native vegetation (low shrubland) and the flat topography of the area, alien woody species (mostly trees) were relatively easy to locate in the landscape and on aerial photographs. This ensured that the complete distribution of alien trees and shrubs was recorded for the study area. Over 100 recent orthophotos (scale: 1:10,000) were used for mapping the configuration of alien stands, and a Geographic Positioning System was used to verify localities. Mapping was done by driving on all roads and tracks in the area (2160 km^2). Areas that were inaccessible by road were traversed on foot. Within each stand of alien trees/shrubs (relatively uniform clumps larger than 0.5 ha), the percentage cover and average height (to the nearest meter) were recorded separately for each species. Cover estimates were made following the system devised by Le Maitre and Versfeld (1994). This consists of the following 8 density classes subdivided according to canopy cover: rare, occasional (< 1%), very scattered (1-5 %), scattered (5-25 %), medium (25-50%), dense (50-75 %), closed (> 75 %). Up to 13 alien species were recorded per stand (Euston-Brown, 1999). This survey produced the most detailed data set on the distribution of invasive plants, at the regional scale, for any part of South Africa.

The following environmental factors were available on a Geographic Information System (GIS): geology, vegetation types, land use, topography and a range of climate variables (see Table 1). The first three were developed for the "CAPE" project (see Cowling et al., 1999, Cole et al., 2000; Cowling and Pressey, in press). The Department of Geological Sciences, University of Cape Town, provided a coarse geology layer (scale 1:250 000). Vegetation types and land use (scale 1:10 000) were assessed and mapped during field surveys simultaneously with the alien vegetation (Euston-Brown, 1999). Thirty-six vegetation types, regrouped into 12 vegetation groups, were identified for the Agulhas Plain. These vegetation types were also reclassified in 13 geological types based on the predominant geology type known to be associated with each vegetation type (R.M. Cowling, unpublished data). The Chief Directorate: Surveys and Mapping provided digitised topographic information (resolution of 250 m) and the Computing Centre for Water Research (CCWR) supplied coarse climatic layers (scale 1: 250 000, resolution of 1 minute) (see Table 1 for the complete list of environmental factors used). The scale at which the environmental variables were available determined the modelling resolution and, to some extent, our ability to model species distribution. Climatic layers were only available at a coarse scale but due to the relatively low topographical heterogeneity, this was not considered a potential problem.

Building predictive models of the distribution and abundance of alien invasive species

The extent of invasion was summarised into density classes and percentage of total area invaded. I used five density classes relating to the total percentage cover of alien plants: <1% (considered as absent), 1 to 5%, 5 to 25%, 25 to 75%, and >75%.

Two approaches were used to model distribution and abundance for three of the most widespread invasive species (*Acacia saligna, A. cyclops,* and *Pinus pinaster*).

- A coarse approach using classification and regression trees for predicting presence/absence and abundance of invasive plant species.
  The ability of such model to predict invasive species distribution was demonstrated at larger spatial scale in South Africa (Chapter 4, 5). Here, this approach is applied at a much finer scale for modelling distribution and abundance.
- A refined approach using a "quasi-mechanistic" model for predicting species abundance.
  This new approach simulates very simplistically propagule pressure as a surrogate for species dispersal and integrates environment and spatial spread interactions. To our knowledge, such approach has not been used before. I explored the model ability to accurately predict species abundance. This also provided insights on how each invasive species perceived the natural environment.

Coarse approach

The study area was partitioned into cells of 250 m x 250 m (i.e. minimum mapping unit of 6.25 ha) under ArcInfo. For each alien species, a density grid of 25 m resolution was generated based on the original alien cover. The density grid was later re-sampled into a grid of 250 m resolution using an average function. For analysis of species distribution, a cell was considered "invaded" if the density was greater or equal to 5%. For each cell of the study area, a series of habitat predictor variables were defined: topography (altitude, aspect, slope), land use (7 categories), geology (13 categories), climate (mean annual precipitation, minimum temperature, growth days), and vegetation groups (12 categories). A training data set was created by randomly selecting 10 000 cells within the study area using standard GIS procedures. For each observation (i.e. cell), the values of the habitat variables were known, as were the response variables (distribution and abundance category of each invasive species). Later, all the observations of the training data set were entered into classification and regression tree analysis. Static models, such as classification and regression trees, assume equilibrium between the environment and species distribution patterns, in other words, they assume that species have had sufficient time to disperse in all suitable habitats and have reached pseudo-equilibrium. Thus, this approach, based on environmental correlates of species distribution, does not consider species dispersal as a limiting factor. In case of invasive species, such assumption is unlikely to be verified. This serious limitation motivated the development of the second approach in which dispersal is crudely modelled (see below).

Classification (for distribution data) and regression (for abundance data) trees were developed on S-Plus (Venables and Ripley, 1999). This technique has proved successful in similar studies that attempted to predict the distribution of plant species (see Iverson and Prasad, 1997; Rouget et al., 2001). Recursive partitioning is an attractive data-analytic tool for studying the relationship between a response variable and several predictor variables (De'ath and Fabricius, 2000). It makes no assumptions of linearity, and accommodates both categorical and continuous data. Recursive partitioning can also reveal complex interactions among variables. In the classification tree approach, the data set is successively split into smaller subsets, based on the values of the predictor variables. Each split is designed to separate the cases in the node being split into a set of successor nodes that are maximally homogeneous (Breinam et al., 1984). The output is a dendrogram or tree –diagram, which represents an intuitive pictorial interface to understanding the structuring of the problem as well as an effective way of making further predictions.

The factors identified in the regression tree analysis were used to derive potential distribution maps of alien species based on the dendrograms. Environmental conditions identified as suitable for the establishment of the target species were selected in ArcView to produce habitat suitability maps of species distribution.

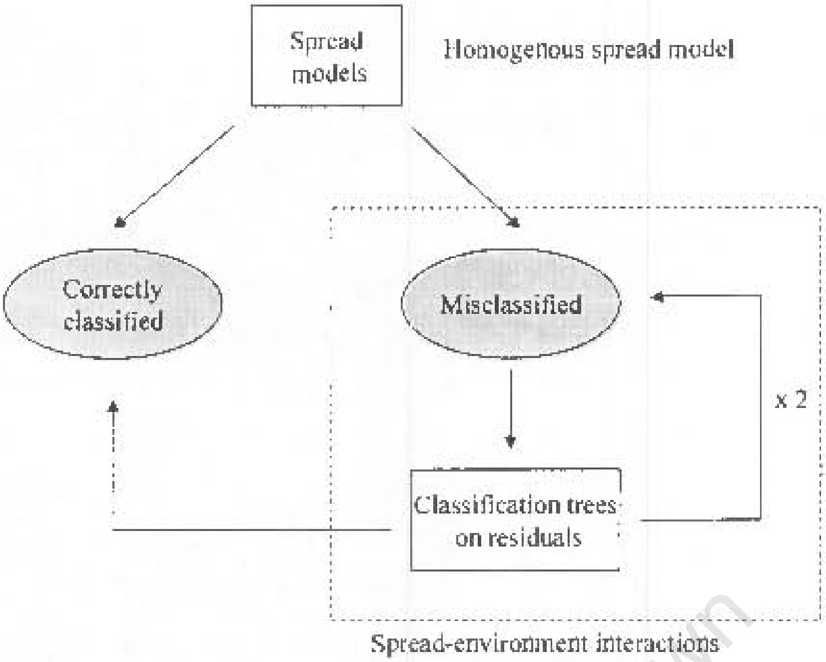


Figure 2. Conceptual diagram of quasi-mechanistic models. Spread rate is first modelled as a homogenous process based on distance to source population. Using this spread rate to predict species distribution and abundance, some observations are correctly classified, some are misclassified. Spread-environment interactions are then explored for misclassified observations using classification trees. Environmental conditions leading to higher or lower spread (i.e. abundance) than expected based on a homogenous spread rate are identified and used to refine the models. This generates new predictions of species abundance, some correctly classified, some not. Misclassified cases are re-analysed with classification trees as above.

Fine-scale approach

This is a new approach for modelling species abundance comprising two steps described in Fig. 2. Species abundance is first modelled as a homogenous spread from the source populations, using locally weighted regression smoothing. This first step considers propagule pressure (quantified as distance from source populations) as the only driver of invasion process. I refer to the first step-model as homogenous spread model (i.e. the interactions spread-environment are ignored at this stage). Then, the effects of environmental factors are assessed on residuals of the first model to determine how propagule pressure interacts with environmental factors. The first model (homogenous spread model) is thus refined by introducing the mediating effects (facilitating or limiting) of environmental factors (Fig. 2). I refer to the complete models as "quasi-mechanistic" models because they integrate biological processes (species dispersal through propagule pressure) but they capture plant-environment interactions in a static manner using classification trees.

For each species, probable source populations were identified on the basis of stand density and height (see Table 2). Centroids of tall and dense clumps were assumed to be the sources. This ignores past management practices, which have cleared some dense stands, and it is likely to introduce some unavoidable error to our models. A stratified random sample was generated for each invasive species consisting of 1000 points for each density category (1-5, 5-25, 25-50, 50-75, and >75 % cover) and

5000 points where the species does not occur. For each of these 10 000 points, the minimum distance to source population was derived based on a 25 m grid of Euclidean distance from probable sources. The percentage cover of each species was recorded for each of the 10 000 random points. For each point, a series of habitat predictor variables were defined (Table 1).

Locally weighted regression smoothing was applied to model the abundance of invasive species based on the distance to the nearest probable source using the data set of 10 000 random points described above. Local regression is a non-parametric regression technique, which relies on the data to specify the form of the model. A model is fitted to the data points locally, so that at any point the model depends only on the observations at that point and some specified neighbouring points (Chambers and Hastie, 1991). This approach was deemed appropriate for this study because of the nature (semi-quantitative abundance) and the non-linear relationship of the data. Local regression has the advantage of modelling interaction between variables, which generalised additive models (GAM) cannot do (Chambers and Hastie, 1991). This first model generated a homogeneous spread rate throughout the area, where the effect of environmental factors is assumed to be null [i.e. invasion is driven exclusively by propagule pressure].

To determine how environmental factors interacted with propagule pressure and to determine the abundance of invading plants, I analysed the relationship between residuals and environmental factors (Fig. 2). Regression and classification trees were used to identify the major environmental factors influencing residuals of the spread model for each invasive alien species. In this approach, I aim to explore how different invasive species perceive the environment. The focus of this model is more exploratory than predictive. I aimed to explore situations where a homogeneous spread model fails to accurately predict species abundance. The analysis of residuals therefore focussed on the misclassified cases (i.e. where the homogeneous spread model is inadequate) with the assumption that environmental heterogeneity would positively or negatively affect spread. Regression trees were used to identify environmental conditions where residuals are positive (species abundance is lower than expected by homogeneous spread model) or negative (species abundance is higher than expected by homogeneous spread model). The predicted residual values were used to correct the original spread model for the misclassified cases.

Table 2: Definition and characteristics of probable source populations (i.e. where the invasion presumably started) for the three most widespread invasive alien tree species modelled.

Species	Source type	Height	% cover	Number of sources	Area (% of total area invaded)
Acacia cyclops	1	≥8 m	>75	12	200 ha (0.17%)
	2	6-8 m	>75	54	2843 ha (2.5%)
Acacia saligna	1	≥8 m	>50	54	1227 ha (1.4%)
Pinus pinaster	1	>15 m		20	217 ha (0.28%)
		10-15 m	>75	56	256 ha (0.32%)
	2	≥10 m	50-75	46	923 ha (1.2%)

The analysis was performed in a stepwise manner to generate predicted distribution models for each species. The first correction on the original homogenous spread model generated new residuals, which were again analysed with regression trees in search of environmental correlation. A maximum of three corrections was performed for each species.

Model prediction ability

For distribution data, prediction ability was based on the percentage of correctly classified presence, the percentage of correctly classified absence, total accuracy (presence + absence), and Kappa value. For abundance data, prediction ability was based on the percentage of correctly classified cases in each density class category (<1, <5, <25, <50, <75, >75%) referred as total accuracy, Presence/Absence accuracy (% of correctly classified presence and absence), abundance accuracy (correct density class where the species occurs), and Kappa value. Accuracy was calculated based on the full data set (n = 34500).

Results

Patterns of invasion

The woody invasive alien flora of the Agulhas Plain comprises 39 species in 18 genera (Appendix 1). Almost the entire Agulhas Plain is invaded to a certain extent. Alien species occur in 72% of the total area and in 96% of the remaining vegetation (cultivated and urbanised areas excluded) (Fig. 3). Fig. 4 shows the frequency distribution of invaded areas grouped into percentage cover classes. For all

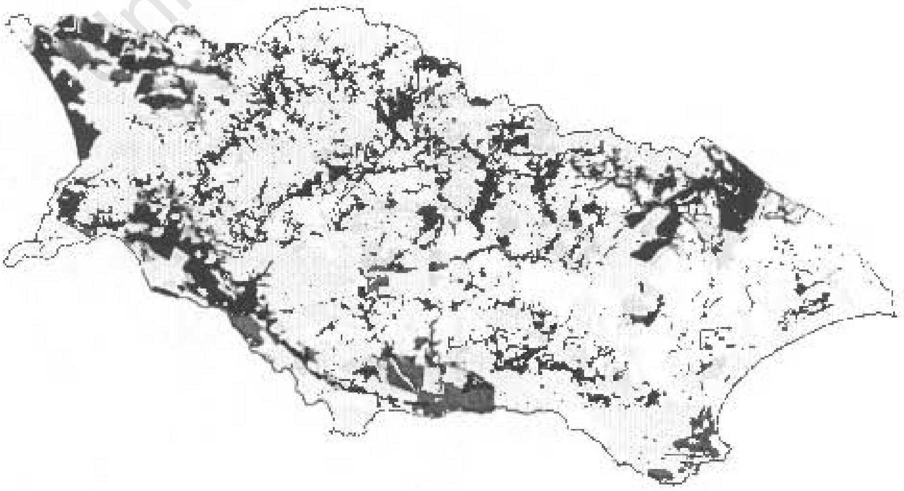


Figure 3. Distribution of alien plant species (all alien species combined) in the Agulhas Plain according to percentage cover.

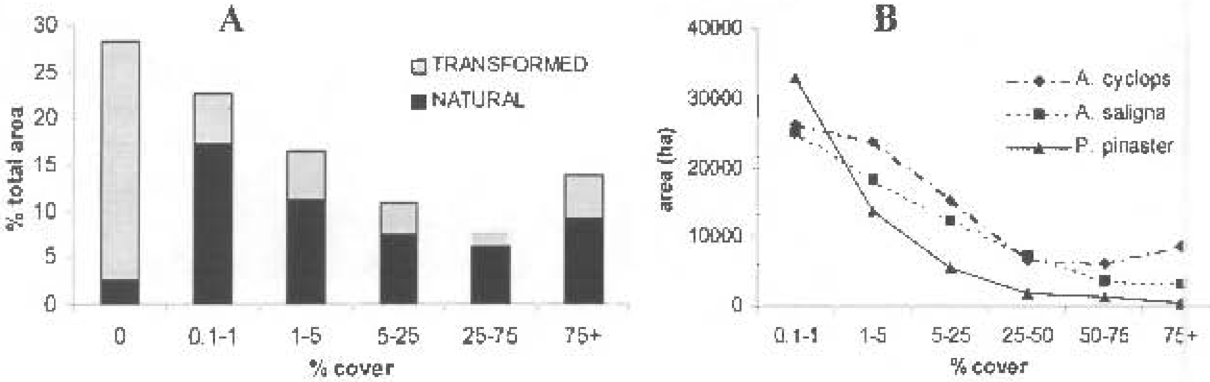


Figure 4. a). Percentage of Agulhas Plain invaded according to categories of invasion density; b) Extent of invasion for the three most widespread invasive species according to categories of invasion density.

species combined (see Fig. 4a), the distribution is bimodal, with most of the areas being little invaded (<1%) or highly invaded (>75%). A third of the remaining natural vegetation is invaded at low density (% cover <1), and 17% is densely invaded (% cover of all species combined >75) (Fig. 4a).

The top 10 species, in terms of area invaded, are (total invaded area is indicated in brackets): *Acacia cyclops* (113 817 ha), *A. saligna* (89 162 ha), *Pinus pinaster* (78 654 ha), *A. longifolia* (50 413 ha), *Leptospermum laevigatum* (38 535 ha), *Eucalyptus lehmanii* (32 957 ha), *Hakea gibbosa* (26 603 ha), *E. cladocalyx* (9 151 ha), *H. drupacea* (8 771 ha), *H. sericea* (5 532 ha), and *A. mearnsii* (4 716 ha). Fig. 4b indicates that the three most abundant species mostly occur at low density, but dense stands of *Acacia cyclops* occur over 8 700 ha. Eleven alien species still have a very limited distribution range (<50 ha invaded).

Correlative models to predict distribution and abundance of invasive alien species

Classification trees generated models of species distribution (presence/absence) with intermediate predictive power. Total accuracy was around 70% (Table 3). Model accuracy and species range appear to be positively correlated. The most widespread species (*Acacia cyclops*) was the best modelled species (Kappa value of 0.58).

Of all environmental factors considered, vegetation groups were the most important predictors of the distribution of invasive species for three species considered. As a second important factor for explaining species distribution, areas invaded by *P. pinaster* were characterised mostly by climate, areas invaded by *A. saligna* by land use, and areas invaded by *A. cyclops* by altitude (Table 1).

Acacia cyclops mostly occurs in dune asteraceous fynbos, forest and thicket, limestone proteoid fynbos, restioid fynbos, river and wetlands, and at low altitude (< 85m) in all other vegetation

Table 3: Predictive accuracy of modelling invasive species distribution using correlative approach. Percentage of correctly classified cases is indicated for each category. Classification trees were derived using the factors mentioned in Table 1.

Accuracy	All alien species	*Acacia cyclops*	*Acacia saligna*	*Pinus pinaster*
Presence	50.6	78.1	71.0	87.0
Absence	83.4	76.5	71.1	67.5
Total	68.3	77.1	71.1	70.0
Kappa	0.35	0.52	0.38	0.29

groups. *Acacia saligna* mostly occurs in untransformed areas of renosterveld, and in areas of high mean annual precipitation (>391mm), low altitude (<180m) in acid sand proteoid fynbos, Elim asteraceous fynbos, limestone proteoid fynbos, restioid fynbos, rivers and wetlands. *Pinus pinaster* mostly occurs in untransformed areas of Elim asteraceous fynbos and restioid fynbos, and in areas of low annual minimum temperature (<11.5 °C) in acid sand proteoid fynbos, ericaceous fynbos and wetlands.

Potential distribution maps (based on the environmental profile of each species as described above) were compared to their current distribution for the three species in Fig. 5. According to these environmental profiles, 29% of the Agulhas Plain could still be invaded by *P. pinaster* (i.e., the area is suitable), 20% by *A. saligna* and 14% by *A. cyclops*. Between 12 and 31% of the area currently invaded by each species did not match with the environmental profile identified.

The correlative approach described failed to adequately model species abundance (Table 4). Species abundance was very poorly related to environmental heterogeneity. Except for *P. pinaster*, model accuracy was in all cases lower than 20%. Regression trees could not identify specific environmental conditions for each density class. Each model failed to accurately predict the distribution of dense stands (>75 % cover). Regression trees were generally better to model low abundance values (% cover between 1 and 25). Sites where invasive species are absent could not be identified using regression trees for both *Acacia* species.

Table 4: Predictive accuracy of modelling species abundance using correlative approach. % of correctly classified cases for each category is indicated.

Accuracy	All alien species	*Acacia cyclops*	*Acacia saligna*	*Pinus pinaster*
Absence	0	0	0	79
1-5 % cover	-	55.4	77.7	36
5-25 % cover	69.2	35.3	28	22.3
25-50 % cover	33.4	40.9	6.1	6.1
50-75 % cover	12.3	4.7	0.7	7.5
> 75 % cover	1	0	0	0
Abundance	38.8	38.7	42.9	28.6
Total	17.8	13.6	12.9	72.5
Kappa	0	0	0	0.24

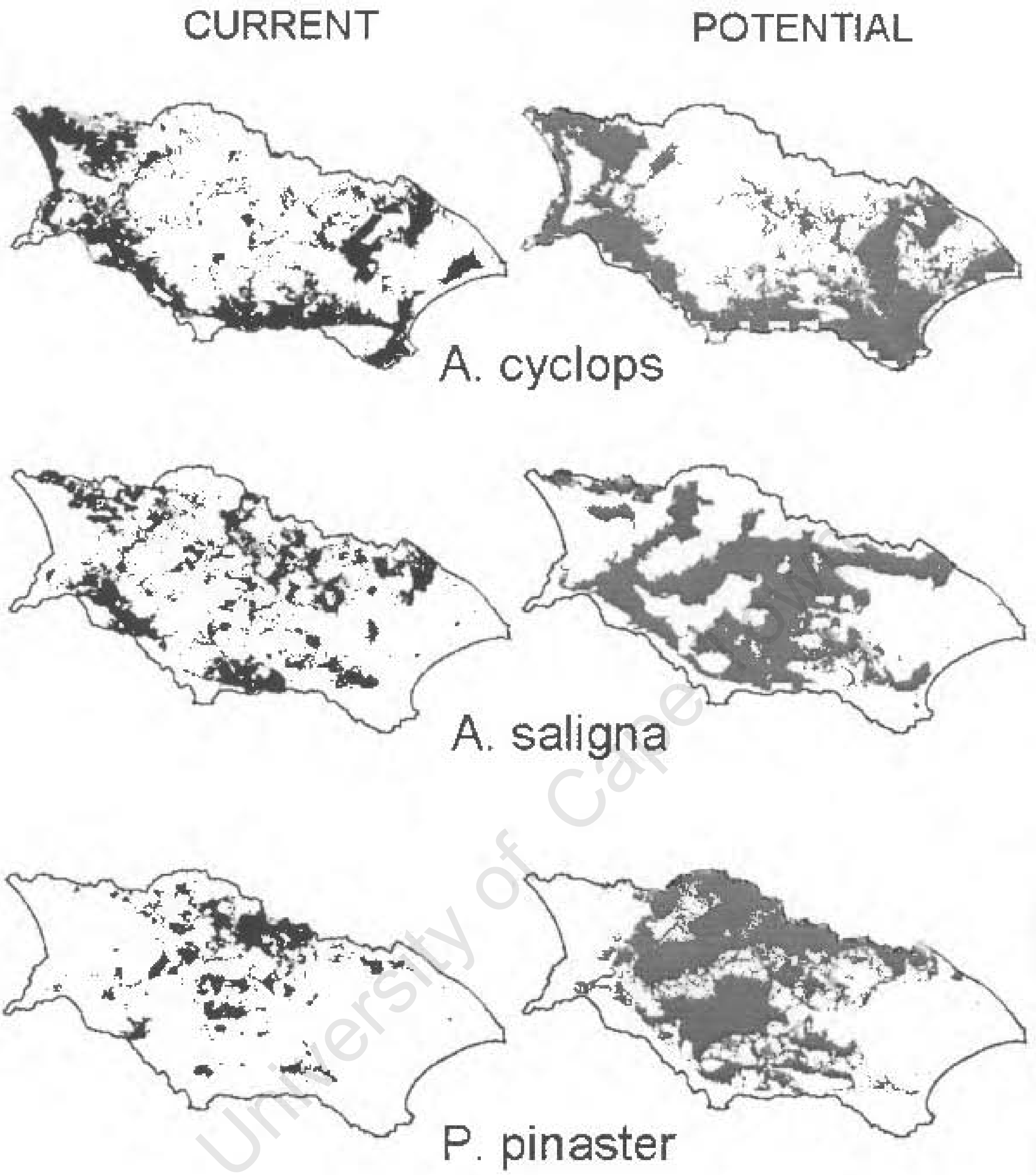


Figure 5. Actual and predicted distribution maps for the three most widespread invasive species on the Agulhas Plain. Predictions were based on classification trees, which identified an environmental profile for each species. Current distributions are shown in the left panel.

Quasi-mechanistic models of invasive alien plant spread

Modelling the spread of invasive species as a homogenous invasion spread

Local regression models were fitted on the density of *Acacia cyclops, A. saligna* and *Pinus pinaster* to simulate the process of invasion spread at a landscape scale. The predicted abundance (percentage

Table 5: Model parameters and model outputs for each species. A local regression model was used to predict the percentage cover of each species according to the minimum distance to probable source populations, which could be of two types. "DIST1" refers to source type 1, and "DIST2" refers to source type 2 (see Table 2).

	Acacia cyclops	*Acacia saligna*	*Pinus pinaster*
Model	Loess (DIST2*DIST1)	Loess (DIST)	Loess (DIST2*DIST1)
Span	0.5	0.4	0.35
Estimated number of parameters	10.2	7.5	14.3
Residual scale estimate	14.87	18.46	8.653
Residual median	-0.93	-1.19	-0.227

cover) for each species according to the minimum distance to probable source populations is shown in Fig. 6. *Acacia* species have the potential to spread much further than *P. pinaster*. A predicted cover of 50% was reached at 300m from the sources for *P. pinaster*, 450m for *A. saligna* and 600m for *A. cyclops*. This model predicted a cover of 5% for *A. cyclops* at 5000m from any source.

For *A. cyclops* and *P. pinaster*, the model could be improved (in terms of predictive accuracy of species distribution and abundance) by using a conditional function of distance to source 2 given distance to source 1 (see Table 2 for definition of sources). Parameters of the models for each species are shown in Table 5. The homogenous spread model, using minimum distance to probable source populations as unique predictor, produced a reasonable fit of the species distribution and some indications of the species abundance (Table 6). The best fit was obtained for *P. pinaster* for which the total accuracy of the spread model was 73% for predicting species distribution and 48% for species abundance (Table 6). The spread model alone provided similar classification accuracy for species

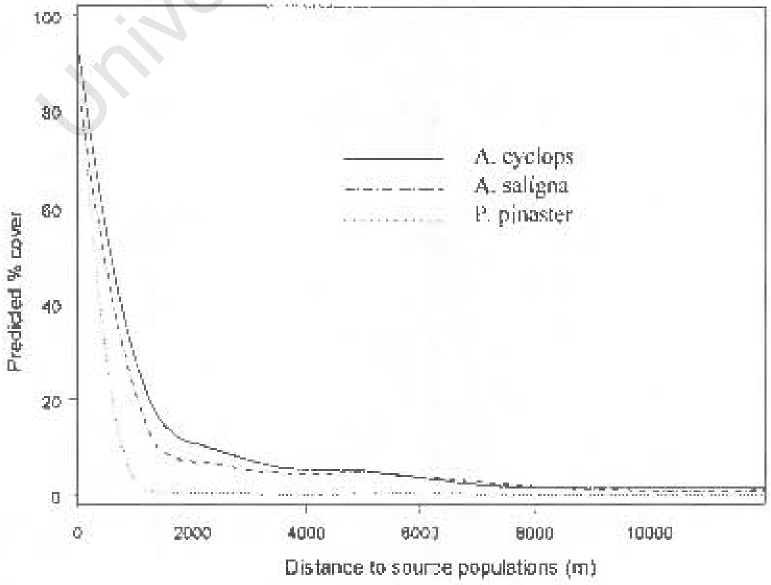


Figure 6. Local regression models for the spread of *Acacia cyclops*, *A. saligna* and *Pinus pinaster* spread on the Agulhas Plain. The abundance (percentage cover) of each species was modelled as a function of the minimum distance to probable source populations.

Table 6: Predictive accuracy of modelling species distribution and abundance using homogenous spread model (i.e. invasion is driven only by propagule pressure). The percentage of correctly classified cases is indicated for each category. Species abundance was classified into 5 categories of % cover (see methods). "Abundance only" refers to abundance accuracy for cases where the species is present. "Total" refers to all cases correctly classified (absence and 5 density categories).

Accuracy	*Acacia cyclops*	*Acacia saligna*	*Pinus pinaster*
Presence/Absence	57.7	58.4	72.8
Abundance only	23.8	23.1	29.5
Total	22.6	21.4	48.2
Kappa	0.16	0.15	0.46

distribution than the classification tree based on environmental factors (see Table 3). Spread models for *Acacia* species produced very low fit of species abundance (Table 6) and generally failed to accurately model species absence (both species are predicted to occur at low density (between 1 to 5 percent cover throughout most of the Agulhas Plain).

Modelling the spread of invasive species as an heterogeneous process (incorporating environmental factors)

I tested whether spread was regulated by environmental factors. The homogenous spread models partly explain the spatial patterns of species distribution and species abundance and a substantial amount of the residual variance remained unexplained. The analysis of the residual variance in relation to environmental variables revealed strong interactions between the environment and the spatial spread of the three invasive species. Each species reacted differently to changes in environment.

Table 7 shows the three most significant factors explaining variation in residuals of spread model. For the two *Acacia* species, variation in spread rate was correlated with altitude, geology and land use. The same factors were found to influence the residual variance of species abundance for both species. Spread rate was higher than predicted (from the homogenous spread model) at low altitudes (<75m for *A. cyclops*, and <68m for *A. saligna*), and in natural vegetation. Higher abundance (greater cover) than predicted by the homogenous spread model of *A. cyclops* was found on colluvium and wetlands. Greater cover than expected of *A. saligna* was found in alluvium, Bokkeveld shale, quaternary sand, and wetlands (Table 7). For *Pinus pinaster*, variation in rate of spread was correlated with number of growth days, distance to roads and mean annual precipitation (decreasing order of significance). Spread rate was higher than expected in areas where annual number of growth days was higher than 119, in areas less than 1250m from any road, and where mean annual precipitation was between 392 and 483mm (Table 7). These environmental conditions represent suitable conditions where the abundance of *P. pinaster* is higher than expected by the homogenous spread model.

Table 7: Variation in spread rate explained by environmental factors. For each species, residuals of spread model (based on propagule pressure) were regressed against environmental factors (one factor at a time) using regression trees in S-Plus. The three most significant factors are presented. "Positive effect" means that the spread rate was higher than expected based on the original spread model under these environmental conditions; "Negative effect" means that the spread rate was lower than expected.

Species	Factor	Positive effect	Negative effect
Acacia cyclops	Geology	Colluvium, wetlands	Bokkeveld shale, quaternary sand, Table Mountain granite sandstone
	Land use	Natural areas	Cultivated areas
	Altitude	< 72 m	> 72 m
Acacia saligna	Altitude	< 68 m	> 68 m
	Geology	Alluvium, Bokkeveld shale, Quaternary sand, wetland	Bokkeveld shale with ferricrete, Table Mountain granite sandstone
	Land use	Natural areas	Cultivated areas
Pinus pinaster	Growth days	> 119	< 119
	Distance to roads	< 1250 m	> 1250 m
	Mean Annual Precipitation	Between 392 and 483 mm	< 392 mm or > 483 mm

Stepwise analysis on the residuals of the homogenous spread model considerably improved the prediction of species abundance. Table 8 reflects the increase in predictive power for modelling abundance of *Acacia cyclops* using step-wise analysis. Each of these factors can be viewed as an environmental barrier. They are presented in Fig. 7 for the three species investigated. The barriers identified are species-specific and no hierarchy was found among environmental factors for the three species studied. Potential distribution maps of the three species are shown in Fig. 8. These are based on the homogenous spread models rectified by environmental factors identified on the basis of classification trees on the residual variance. As opposed to simple correlative models, the abundance pattern of each invasive species was predicted with greater accuracy (see Table 8 for *A. cyclops*).

Table 8: Classification accuracy of quasi-mechanistic model for *Acacia cyclops*. Species distribution and abundance is first modelled based on diffusion models and then rectified by interactions between spread rate and environment. This is the validation on the entire Agulhas Plain (n = 34500) of the spread model derived from the training data set (n = 10000).

Accuracy	loess	1st correction	2nd correction	3rd correction
Total	22.6	57.2	72.3	79.3
Presence/absence	57.7	78.0	82.9	91.5
Abundance	23.8	49.6	61.8	73.2
Kappa	0.09	0.44	0.54	0.73

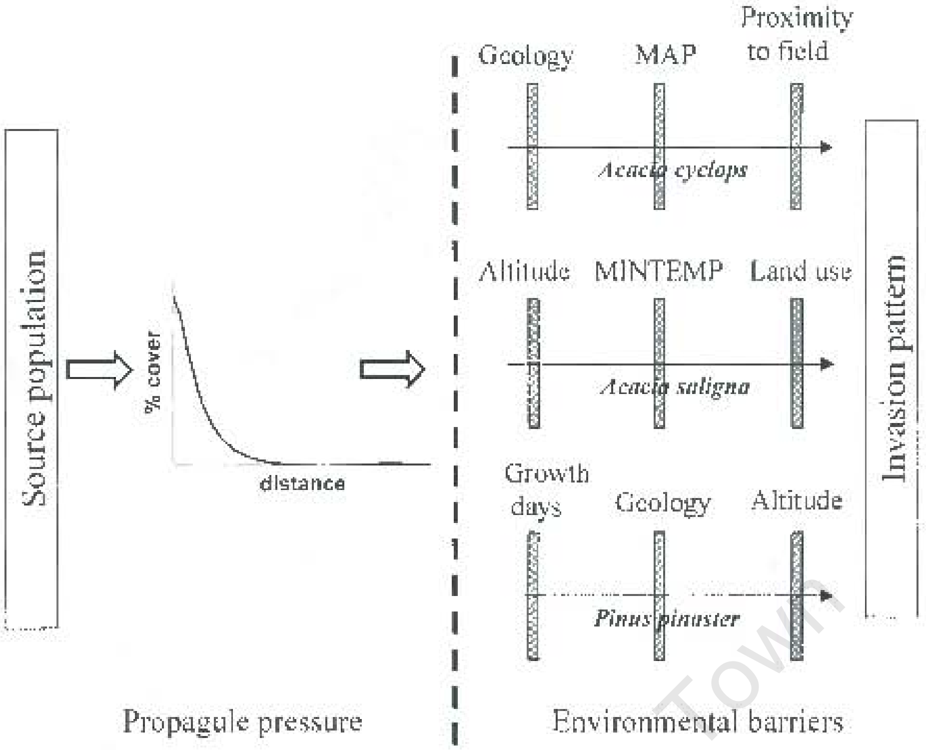


Figure 7. Quasi-mechanistic model for *Acacia cyclops, A. saligna* and *Pinus pinaster*. Homogenous spread models were first derived to predict species abundance as a function of propagulepressure only; environmental effects were then considered on the residual variance to model spread-environment interactions. Each environment factor acts as a successive barrier/vector to invasion spread. These are indicated for each species. MAP: Mean Annual Rainfall, MINTEMP: Annual Minimum Temperature.

Discussion

This study demonstrates the value of natural experiments in elucidating the mechanisms of tree invasions. Spatial patterns of invasion result from many different interacting factors, such as biological attributes of invader (e.g. seed dispersal), species response to abiotic environment, biotic interactions, and human activities (success of plant establishment) (Richardson et al., in press). In most cases, it is difficult to determine the relative roles of biological attributes and environmental factors. This study is an attempt to include species dispersal through propagule pressure and to account for plant-environment interactions. Previous studies that have focussed on local seed dispersal using spatial patterns of juveniles did not always consider the effects of environment (e.g., Schupp and Fuentes, 1995). On the other hand, statistical analyses of plant distribution in relation to environmental factors generally ignore ecological processes such as dispersal (Guisan and Zimmerman, 2000). By integrating propagule pressure and environmental determinants into the models, I was able to predict species abundance more accurately than by using environmental determinants alone. This study also enables to tease out the role of propagule pressure and environment, and to explore some of the interactions between spread rate and environment. The present study is however affected by several

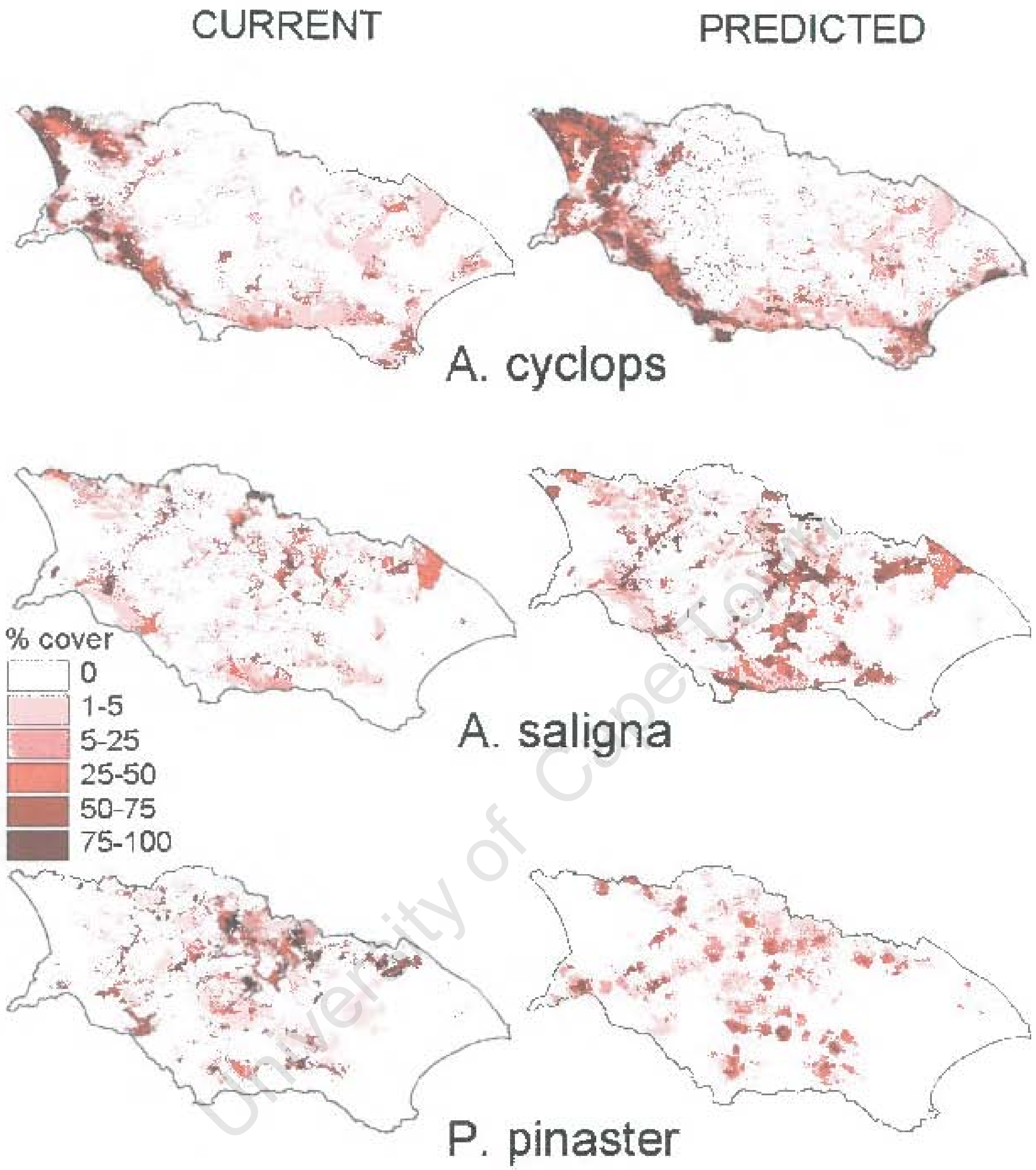


Figure 8. Current and predicted species distribution and abundance of *Acacia cyclops, A. saligna* and *Pinus pinaster*. Predictions are based on quasi-mechanistic models (see Fig. 7).

model limitations. Spread rate is modelled as a function of distance to probable source populations (i.e., the origin of invasions). The correct identification of source populations is a crucial aspect of the model. I assumed that the oldest (largest and densest) stands of trees to be the origin of self-sown populations. Individual trees can also act as foci of spread, but the contribution of such foci was not included in our simulations. Also, past management actions of alien plants and wood harvesting on the Agulhas Plain have probably eradicated some source populations. Finally, the availability of fine-scale environmental data limited the identification of plant-environment interactions. These factors contribute to the unexplained variance in the models. Despite these limitations, this study brings a deeper understanding of the main drivers of invasion process at a regional scale and provides a quantitative assessment of the role of propagule pressure in mediating environmental barriers.

Modelling species range/abundance

Species distribution could be modelled with satisfactory accuracy using classification trees (total accuracy of around 70%, Table 3). This confirms that correlative approach is appropriate for modelling species distribution. This view is supported by many other similar studies on plant distributions (Guisan and Zimmermann, 2000, and references therein). For invasive species, it was however shown that the predictive power of static modelling is limited (Higgins et al., 1999; Collingham et al., 2000). These techniques are appropriate for large-scale patterns but that they provide poor results at fine spatial scales. Natural vegetation categories seem to be the most general predictor of invasive species distribution (Table 1). More detailed environmental factors had value as determinants of invasibility, but different sets of variables were implicated for different species. Because no framework currently exists for modelling species distributions, the environmental determinants identified are likely to be specific to the species and the study area investigated. It is thus difficult to compare the factors identified as major determinants in this study with those identified in other studies. Pearce and Ferrier (2000) and Guisan and Harrell (2000) found that environmental factors could be used to model species abundance, but such factors were not good determinants of abundance for the three alien tree species studied on the Agulhas Plain.

Interestingly, propagule pressure (modelled as a function of distance to probable source populations) was a much better indicator of species distribution and abundance than any other environmental factor considered (see Table 3). In previous studies of invasive species distribution, species response to environment might have been confounded with simply propagule pressure. Few studies have assessed the relative importance of ecological interactions and propagule availability in producing observed patterns of species distribution at the local scale (Foster, 2001). Propagule pressure, although modelled rather simplistically, was crucial for simulating invasions of three alien tree species on the Agulhas Plain. I noted differences among species, and the effect of propagule pressure was more significant for *P. pinaster* than for the two *Acacia* species (Table 6). Rejmánek et al (in press) provided quantitative assessments that support the notion that high propagule pressure is positively associated with invasion success. Using data on extent of planting and naturalization/invasion of 57 *Eucalyptus* taxa, they found that propagule pressure (expressed as extent of planting) is much better correlated with invasive success than any set of traits that distinguish 'invasive' from 'non-invasive' taxa on the basis of life history, or any other features of biology.

Plant-environment interactions

Several studies have demonstrated the importance of plant-environment interactions in modelling species range/abundance (Higgins and Richardson, 1998 and references therein) but incorporating these interactions in modelling is challenging (Higgins and Richardson, 1996). This study reports on interactions between rate of spatial spread and environmental factors for three invasive species. The role of propagule pressure was isolated from the role of environment by looking at variation in residuals of spread rate in relation to environmental heterogeneity. For example, it was found that the spread rate of *Pinus pinaster* was regulated by climate (annual number of growth days and mean annual precipitation) and land use (distance to roads) (Table 7). This clearly highlights the importance of plant-environment interactions in modelling plant invasions, a view supported by several authors (Williamson, 1996; Higgins and Richardson, 1998). In future modelling studies of plant invasion, I suggest that spatial spread (or dispersal at a local scale) should be modelled in relation to environmental conditions. This implies that predictions about invasions must be context-specific.

In order to conceptualise and parameterise plant-interactions in the invasion process, several authors have suggested visualising invasion process of a series of barriers that an introduced species needs to overcome before becoming invasive (Richardson et al., 2000b). This study offers opportunities to identify some of these barriers and to quantify their effects on spread at a regional scale. For all three species, the amount/number of propagules available (propagule pressure) clearly affects the strength of various environmental barriers (Fig. 7). However, environmental barriers affecting rate of spread (i.e. once propagule pressure has been accounted for) are species-specific. Barriers could be geology, topography, climate, or land use without any consistent hierarchy among the three species (Fig. 7). Surprisingly, land use was not identified as the major barrier to invasion. There were some indications that spread was reduced in transformed habitats (cultivated fields mainly), but climatic or topographic factors were more significant (Table 7). The Agulhas Plain is however heavily fragmented, so one would expect invasive species to respond strongly to land use changes. Other studies, which focused on local dispersal, have shown that landscape structure can affect dispersal success. Dispersal success was considerably reduced in landscape with < 30-40% habitat, but the intensity of the effects was mitigated by habitat clumping (King and With, 2002). Modelling studies also suggest that invasive species might perform better than natives in fragmented ecosystems (Richardson et al., 2000a). Disturbance, natural or human-induced, is often mentioned as a factor-promoting invasion because it produces areas of bare ground permitting seedling establishment (Hobbs and Huenneke, 1992; Kolar and Lodge, 2001). At a local scale, the spatial configuration of bareground (e.g. large/small gaps, ramdomly/regularly-dispersed gaps) greatly affects the spread of invasive species (Bergelson et al., 1993). Predictions at landscape or regional scale, such as this study, could be improved by quantifying more rigorously aspects of disturbance regime and intensity, and the spatial structure of landscape, factors that are generally not accounted for in such studies (Chapter 7).

References

Bergelson, J., Newman, J.A., Floresroux, E. M., 1993. Rates of weed spread in spatially heterogeneous environments. Ecology 74, 999-1011.

Breinam, L., Friedman, J.H., Olshen, R.A., Stone, C.J., 1984. Classification and Regression Trees. Wadsworth, Belmont.

Chambers, J.M., Hastie.T.J., 1991. Statistical Models in S. Wadsworth & Brooks/Cole, Pacific Grove, California.

Cole, N.S., Lombard, A.T., Cowling, R.M., Euston-Brown, D., Richardson, D.M., Heijnis, C.E., 2000. Framework for a conservation plan for the Agulhas Plain, Cape Floristic Region, South Africa Institute for Plant Conservation, Cape Town.

Collingham, Y.C., Wadsworth, R.A., Huntley, B., Hulme, P. E., 2000. Predicting the spatial distribution of non-indigenous riparian weeds: issues of spatial scale and extent. Journal of Applied Ecology 37, 13-27.

Cowling, R. M., 1992. The ecology of Fynbos: nutrients, fire and diversity. Oxford University Press, Cape Town.

Cowling, R.M., 1990. Diversity components in a species-rich area of the Cape Floristic Region. Journal of Vegetation Science 1, 699-710.

Cowling, R.M., Campbell, B.M., Mustart, P., McDonald. D.J. Jarman, M.L., Moll, E.J. 1988. Vegetation classification in a floristically complex area: the Agulhas Plain. South African Journal of Botany, 54, 290-300.

Cowling, R.M., Holmes, P.M., 1992. Endemism and speciation in a lowland flora from the Cape Floristic Region. Biological Journal of the Linnean Society 47, 367-383.

Cowling, R.M., Pressey, R.L., in press. Context, characteristics and history of conservation planning. Biological Conservation.

Cowling, R.M., Pressey, R.L., Lombard, A.T., Heijnis, C.E., Richardson, D.M., Cole, N., 1999. Framework for a conservation plan for the Cape Floristic Region. Report 9902. Institute for Plant Conservation, Cape Town.

D'Antonio, C.M., Levine, J. and Thomsen, M., 2001. Ecosystem resistance to invasion and the role of propagule supply: A California perspective. Journal of Mediterranean Ecology 2, 233-245.

De'ath, G., Fabricius, K.E., 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. Ecology 81, 3178-3192.

Euston-Brown, D., 1999. Agulhas Plain field mapping final report. Institute for Plant Conservation, University of Cape Town, Cape Town.

Foster, B.L., 2001. Constraints on colonization and species richness along a grassland productivity gradient: the role of propagule availability. Ecology Letters 4, 530-535.

Franklin, J., 1995. Predictive vegetation mapping: geographic modelling of biospatial patterns in relation to environmental gradients. Progress in Physical Geography 19, 474-499.

Franklin, J., 1998. Predicting the distribution of shrub species in southern California from climate and terrain-derived variables. Journal of Vegetation Science 9, 733-748.

Green, R.E., 1997. The influence of numbers released on the outcome of attempts to introduce exotic bird species to New Zealand. Journal of Animal Ecology 66, 25-35.

Guisan, A., Harrell, F.E., 2000. Ordinal response regression models in ecology. Journal of Vegetation Science 11, 617-626.

Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135, 147-186.

Higgins, S.I., Richardson, D.M. 1996. A review of models of alien plant spread. Ecological Modelling 87, 249-265.

Higgins, S.I., Richardson, D.M., 1998. Pine invasions in the southern hemisphere, modelling interactions between organism, environment and disturbance. Plant Ecology 135, 79-93.

Higgins, S.I., Richardson, D.M., Cowling, R.M., 2000. A dynamic spatial model for managing alien plant invasions at the landscape extent. Ecological Applications 10, 1833-1848.

Higgins, S.I., Richardson, D.M., Cowling, R. M., 2001. Validation of a spatial simulation model of a spreading alien plant population. Journal of Applied Ecology 38, 571-584.

Higgins, S.I., Richardson, D.M., Cowling, R.M., Trinder-Smith, T.H., 1999. Predicting the landscape scale distribution of alien plants and their threats to biodiversity. Conservation Biology 13, 303-313.

Hobbs, R.J., Huenneke, L.F., 1992. Disturbance, diversity, and invasion: implications for conservation. Conservation Biology 6, 324-337.

Huntley, B., Berry, P.M., Cramer, W., McDonald, A.P., 1995. Modelling present and potential future ranges of some European higher plants using climate response surfaces. Journal of Biogeography 22, 967-1001.

Hutchinson, T.F., Vankat, J.L., 1997. Invasibility and Effects of Amur Honeysuckle in Southwestern Ohio Forests. Conservation Biology 11, 1117-1124.

Iverson, L.R., Prasad, A.M., 1998. Predicting abundance of 80 tree species following climate change in the eastern United States. Ecological Monographs 68, 465-485.

King, A.W., With, K.A., 2002. Dispersal success on spatially structured landscapes: when do spatial pattern and dispersal behavior really matter? Ecological Modelling 147, 23-39.

Kolar, C.S., Lodge, D.M., 2001. Progress in invasion biology: predicting invaders. Trends in Ecology and Evolution 16, 199-204.

Le Maitre, D.C., Versfeld, D.B., 1994. Field manual for mapping populations of invasive plants for use with the Catchment Management System. Unpublished CSIR report.

Levine, J.M., 2000. Species diversity and biological invasions: Relating local process to community pattern. Science 288, 852-854.

Lombard, A.T., Cowling, R.M., Pressey, R.L., Mustart, P.J., 1997. Reserve selection in a species-rich and fragmented landscape on the Agulhas Plain, South Africa. Conservation Biology 11, 1101-1116.

Lonsdale, W.M., 1999. Global patterns of plant invasions and the concept of invasibility. Ecology 80, 1522-1536.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853-858.

Newsome, A.E., Noble, I.R., 1986. Ecological and physiological characters of invading species. In: Groves, R.H., Burdon, J.J. (Eds.), Ecology of Biological Invasions: an Australian Perspective. Australian Academy of Science, Canberra, pp 1-20.

Pearce, J., Ferrier, S., 2001. The practical value of modelling relative abundance of species for regional conservation planning: a case study. Biological Conservation 98, 33-43.

Rejmánek, M., Richardson, D.M., Higgins, S.I. Pitcairn, M., Grotkopp, E., 2002. Plant invasion ecology: State of the art. In: Mooney, H.A., Mc Neely, J.A., Neville, L., Schei, P.J., Waage, J. (Eds.), Invasive alien species: Searching for solutions. Island Press, Washington, D.C. (in press).

Richardson, D.M., Bond, W.J., Dean, W.R.J., Higgins, S.I., Midgley, G.F., Milton, SJ., Powrie, L.W., Rutherford, M.C., Samways, M., Schulze, R.E., 2000a. Invasive aliens organisms and global change: A South African perspective. In: Mooney, L.H. A., Hobbs, R. J. (Eds.), The impact of global change on alien species. Island Press, Washington, pp 303-349.

Richardson, D.M., Pysek, P., Rejmánek, M., Barbour, M.G., Panetta, D.F., West, C.J. 2000b. Naturalization and invasion of alien plants - concepts and definitions. Diversity and Distributions 6: 93-107.

Richardson, D.M., Rouget, M. and Rejmánek, M., 2002. Using natural experiments in the study of plant invasions: Opportunities and limitations. In: Gordon. M., Bartol, S. (Eds.), Experimental approaches to conservation biology. University of California Press, Berkeley (in press).

Rouget, M., Richardson, D.M., Milton, S.J., Polakow, D., 2001. Predicting the dynamics of four invasive Pinus species in a fragmented semi-arid shrubland in South Africa. Plant Ecology 152:79-92.

Schupp, E.W., Fuentes, M., 1995. Spatial patterns of seed dispersal and the unification of plant population ecology. EcoScience 2. 267-275.

S-Plus 2000 Guide to Statistics, volume 1. Data Analysis Products Division, MathSoft, Seattle, WA.

Venables, W.M., Ripley, B.D., 1999. Modern applied statistics with S-plus. 3rd ed. Springer, New York.

Williamson, M., 1996. Biological Invasions. Chapman & Hall, London.

Current patterns of habitat transformation and future threats to biodiversity in terrestrial ecosystems of the Cape Floristic Region, South Africa

Abstract

The formulation of an effective strategic plan for biodiversity conservation in the Cape Floristic Region (CFR) requires an assessment of the current situation with regard to habitat transformation, and an explicit framework for predicting the likelihood of remaining habitat (i.e. that potentially available for conservation) being transformed. This chapter presents the results of a detailed assessment of the current and future extent of three important factors that threaten biodiversity in the CFR: cultivation for intensive agriculture (including commercial forestry plantations), urbanisation, and stands of invasive (self-sown) alien trees and shrubs. The extent of habitat transformation was mapped at the scale of 1:250,000, using primarily satellite imagery. I compared models derived from a rule-based approach relying on expert knowledge and a regression-tree technique to identify other areas likely to be affected by these factors in future.

Cultivation for agriculture has transformed 25.9% of the CFR and dense stands of woody alien plants and urban areas each cover 1.6%. Both models predict that at least 30% of the currently remaining natural vegetation could be transformed within 20 years. There was an overall accuracy of 73% between both models although significant differences were found for some habitat types. Spatial predictions of future agriculture threats derived from the rule-based approach were overestimated relative to the statistical approach, whereas future alien spread was underestimated. Threat assessment was used to derive conservation targets for subsequent stages of conservation planning for the CFR. The importance of integrating vulnerability knowledge into conservation planning is discussed. The choice of vulnerability analysis (future habitat degradation and/or impact on biological entities) and methods will depend on the complexity of the threatening processes and the availability of spatial data.

Introduction

The emphasis in conservation planning world-wide has been on identifying salient features of biodiversity (Franklin, 1993). Preserving biodiversity has for many years focused on the lower levels of biodiversity, namely species (ESA, 1973) or populations (Rojas, 1992). Because of the complexity of biodiversity, surrogates (e.g., habitat types, species assemblages) have also been used as indicators of biodiversity (Noss et al., 1997). This 'coarse-filter' approach assumes that by protecting a portion of every habitat type, all or most of the biodiversity in these habitats is preserved.

Less attention has been given to identifying, in spatially-explicit terms, the factors that threaten biodiversity now, and how these are likely to change in the future. Loss of habitat through land use practices has been recognised as the major threat to biodiversity (Wilcove et al., 1998). Detailed knowledge of threats to biodiversity should be an essential component of conservation planning for two main reasons. Firstly, conservation planning must operate within the constraints of current and likely future land use changes (transformed land usually has very low conservation value, and areas with high transformation potential are problematic for incorporating in reserve networks). Secondly, the spatial dimensions of land transformation (current and predicted) have implications for setting objective targets and for implementing conservation strategies (Margules and Pressey, 2000; Myers et al., 2000; Pressey and Cowling, 2001). Because conservation resources are scarce, there is an urgent need for identifying priorities for conservation actions. Habitats that are already modified should ideally receive more protection effort than those relatively free of human activities because the latter are in a way self-protected to a large extent by their harsh environmental characteristics (e.g. mountainous areas on unfertile soils – factors that have limited human development). Moreover, habitats susceptible to be transformed in future should receive priorities in conservation action. As implementation of conservation decisions is never immediate, the consideration of threats reduces the likelihood of losing important habitats following land use change before they can be protected. One strategy for implementing conservation decisions is to select areas on the basis of irreplaceability (contribution of the area in terms of conservation goal) and vulnerability (risk of the area being transformed) (Pressey et al., 1996; Pressey and Taffs, 2001). A conceptually similar approach has been suggested for identifying hotspots of biodiversity at a global scale whereby hotspots are defined as "areas featuring exceptional concentrations of endemic species and experiencing exceptional loss of habitat" (Myers et al., 2000).

Over the last decades, several models of land use change have been developed to project and quantify future land use and cover (see reviews in Riebsame et al., 1994; Veldkamp and Lambin, 2001). Most of the literature on threats to biodiversity in conservation planning has focused on identifying threats to biodiversity at the species level (Master, 1991; Rebelo, 1992; Sisk et al., 1994; Flather et al., 1998). Threats were categorised according to the Red Data Book species status or by estimating potential impacts following human development (Abbit et al., 2000). Fewer studies have assessed threat levels for plant communities or habitat types (however see Pressey et al., 1996; Margules and Pressey, 2000). Although the loss of habitat due to land use practices has been recognised as the main cause of decline in biodiversity (Soulé, 1991), conservation decisions seldom incorporate estimates of future changes in land use (Menon et al., 2001). White et al. (1997) estimated risks to biodiversity looking at the impact of future landscape alternatives on species distribution and abundance. Stoms (2000) investigated the potential impacts of land use conversions, human population growth and roads effect on ecological communities in relation to the Gap Analysis

Program. I present here an approach exploring future land use changes based on current land use pattern in the Cape Floristic Region.

The Cape Floristic Region covers 87 892 km^2 at the southern tip of Africa. It is home to over 9 000 plant species, of which 70% are endemic (Goldblatt and Manning, 2000), and 1 406 Red Data Book plant species, the highest known concentration of rare species in the world (Cowling and Hilton-Taylor, 1994). Previous assessments of conservation status in the CFR or part of it were based on species rarity or complementary indexes (Rebelo and Siegfried, 1992) or on threatened taxa (Rebelo, 1992; Richardson et al., 1996; Lombard et al., 1999). The CFR is extensively transformed by agriculture, alien plant invasions, and urban development (Rebelo 1992; Lombard et al., 1997). These are the major agents of habitat transformation that can be mapped and applied to spatially-explicit conservation plans. Other threats such as mining, unsustainable exploitation of natural products (e.g. harvesting of wild flowers) are certainly important in the CFR but their impacts cannot be accurately mapped for use in spatially-explicit models. Spatial pattern of current habitat transformation has been explored only for small parts of the CFR: the Agulhas Plain, which represents 2.5% of the CFR (Lombard et al., 1997), the Cape Peninsula, which represents less than 1% of the CFR (Richardson et al., 1996), and the coastal lowlands of the Western Cape (Heijnis et al., 1999).

This chapter aims to: 1) describe the extent of habitat transformation in relation to the main terrestrial habitat types and protected areas in the CFR; and 2) spatially identify and compare future areas likely to be transformed using two modelling approaches (rule-based and statistical models). Extent of current and future habitat transformation was included in the formulation of conservation targets for each habitat type (see Pressey et al., in press). Rouget et al. (in press) explored the extent of current and future habitat transformation in different categories of protected areas.

Methods

Mapping habitat transformation

LANDSAT Thematic Mapper imagery was identified as the most appropriate source of information for mapping the current spatial dimensions of habitat transformation posing the most immediate and widespread risk to terrestrial biodiversity at the scale required for this project. I mapped current land use (defined as urbanisation, forestry plantations, and cultivation) and alien plant cover (subdivided in three categories, see below). All these categories were spatially mutually-exclusive. In this chapter, current land use and alien plant cover are refered as habitat transformation factors whereas future changes in land use and alien plant cover are later refered as threats to biodiversity. A summary of the

LANDSAT mapping is provided below; further details on the mapping procedure are given in Lloyd et al. (1999).

The LANDSAT TM imagery was captured between December 1997 and February 1998 and was geometrically rectified at the scale of 1:50 000. The unsupervised (automatic) pattern-recognition algorithm in ERDAS Imagine (1997) was used to produce thematic layers containing discrete classes (i.e. clusters of pixels with similar spectral characteristics). The Iterative Self-Organising Data Analysis Technique (ISODATA) (Tou and Gonzales, 1974) was applied to all LANDSAT TM scenes covering the study area.

Each of the following classes was extracted by interpolation of these unsupervised classifications: urban areas; agriculture (cultivation, orchards, vineyards, bush cleared, heavily grazed); forestry plantations (mainly *Pinus* and *Eucalyptus* stands) and "natural vegetation" [later subdivided to reflect the cover of woody alien plants - none to low-density woody alien plant cover (<20% cover); medium-density woody alien plant cover (20-75% cover); high-density woody alien plant cover (>75% cover)]. "Water" and "sand" were also identified as classes.

The "natural vegetation" class was divided into the three alien plant density classes only after this broad category had been satisfactorily separated from other classes. The initial classifications resulted in a number of mixed classes in certain areas (e.g. natural vegetation and cultivation). Various techniques were applied to separate these mixed classes. There were fairly extensive misclassifications of alien plant density. Alien plants were defined as invasive species of *Acacia, Eucalyptus, Hakea, Eucalyptus, Leptospermum* and *Pinus* (see Richardson et al., 1992). Misclassifications were mostly the results of shadows caused by aspect and slope in the mountains, small areas of cloud cover, recently burnt areas, actively growing crops on centre pivots and cultivated lands, and clumps of certain indigenous trees and shrubs (notably *Sideroxylon inerme* and *Leucadendron* spp.) that have spectral signatures similar to those of the dominant alien trees and shrubs. In most cases, misclassifications were manually recoded to the relevant class based on knowledge of the project team and consultation with local authorities.

The relatively dense infestations of hakea in the mountains could not always be distinguished from native Proteaceae during the classification of the LANDSAT TM images. Existing *Hakea* data from the Protea Atlas Project (Rebelo, 1991) were coded and incorporated into the final layer. The boundaries of urban areas were delineated by visual interpretation of the LANDSAT image and screen digitising.

The thematic raster layers were then filtered (which outputs the class value representing the majority of the class values in a 7x7 window of pixels) to obtain a minimum mapping unit of 25 ha, appropriate for mapping at a scale of 1:250 000. Applying this filter to the relatively fragmented and patchy agriculture and natural vegetation classes (low-, medium- and high-density alien plants) caused the "loss" of smaller patches or linear strips of medium- and dense woody alien plant cover classes to the "none to low-density woody alien plant" class. The implications of losing small, clumped classes when filtering a thematic map has been discussed by Moody and Woodcook (1994).

Ancillary data sets and workshops: Workshops were held with officials from Western Cape Nature Conservation Board to capture local expertise to assist in the interpretation and classification of the LANDSAT TM imagery. Attention was focussed on delineating the "natural vegetation" class into the three classes of woody alien plant cover (high, medium and low). Existing ancillary data sets of alien plant distribution and density were also used to assist in assigning density classes to the classified images. Data for this purpose were supplied by the Working for Water Project (Department of Water Affairs and Forestry, Cape Town), CSIR (Stellenbosch), and South African National Parks.

Accuracy Assessment: In assessing the categorical accuracy of the final classification, a sample of 480 random points was taken across the CFR. The categorical accuracy of each point was assessed by an independent consultant who is well acquainted with the study area, and compared with the results obtained by the mapping team. The total accuracy of the overall classification was 93.9% ± 2.2 (at the 95% confidence level). The relative accuracy of the threats to biodiversity classes were 100% for urban (n=9); 86.9% for agriculture (n=61); 80.0% for plantations (n=10); 99.5% for none to low-density alien plant cover (n=382); 25.0% for medium-density alien plants (n=8) and 52.6% for high-density alien plants (n=19).

Standard GIS techniques in Arc View were used to compute the total area covered by each category of habitat transformation across the CFR, and the level of transformation by each factor in the 16 primary and 87 secondary Broad Habitat Units that comprise the CFR (Cowling and Heijnis, 2001).

Predicting future threats

Future changes in land use and alien plant cover are refered as threats to biodiversity. I spatially estimated threats associated with agriculture (including forestry), urbanisation and alien plants that are likely to materialise over the next two decades. I used and compared two different approaches -a rule-based approach relying on expert knowledge and a classification tree technique- for deriving spatial predictions of future habitat transformation. Threats were modelled in the first approach at a resolution of 1/16 degree cells. This was done to enable an analysis of priority for each planning unit when combined with irreplaceability values (see Cowling et al., in press). By using recursive partitioning (the second approach) I refined the resolution to 1 decimal minute (see below). Predictions of future land use / land cover changes are based on the current distribution of habitat transformation in both cases.

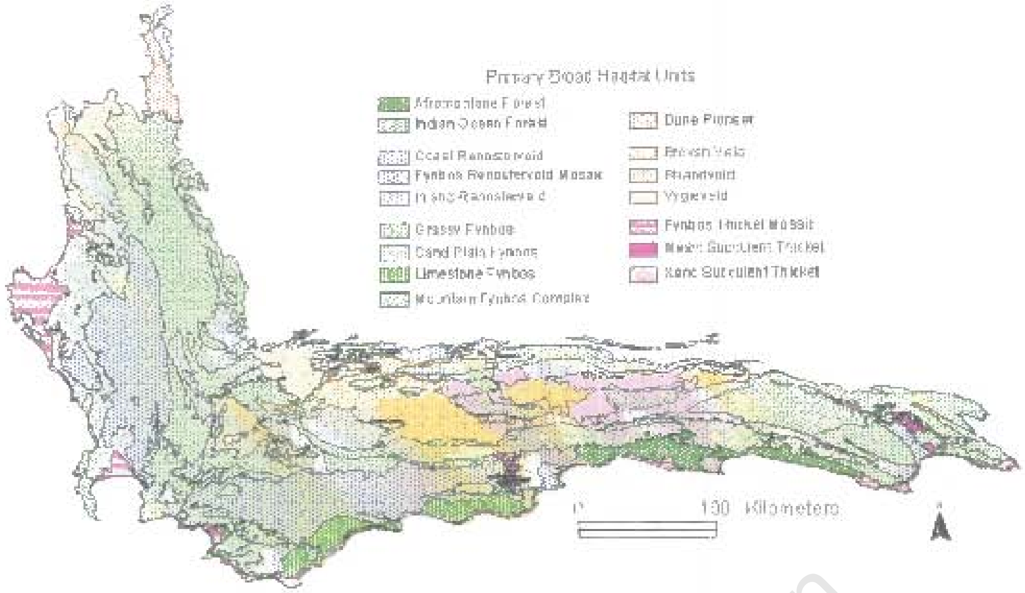


Figure 1. Map of primary BHUs (Broad Habitat Types) prior to human transformation within the Cape Floristic Region. These habitat types were derived on the basis of climate, geology and topography (see Cowling and Heijnis, 2001). They characterise major vegetation types which were later used to derive agriculture and urbanisation potential and alien plant spread (see Methods). Codes for primary BHUs are given in Table 2.

Method 1: Rule-based modelling based on expert knowledge

Agriculture: An agricultural threat was derived on the basis of Broad Habitat Units (BHUs). BHUs are a system of land classes that can be used as surrogates for biodiversity in the Cape Floristic Region (CFR) at a region-wide scale (Fig. 1; see for more details Cowling & Heijnis, 2001). The BHUs were derived by intersecting layers of homogenous climatic zones, geology and topography in a geographic information system. A total of 16 primary and 88 secondary BHUs were identified in the CFR (Fig. 1).

The agriculture threat index was developed by categorising the vulnerability of BHUs on the basis of soils (using soil parent material lithology as a surrogate), climate and topography. Thus, BHUs that were associated with fertile soils, sufficient rainfall for dryland agriculture, and level topography (e.g. Coast Renosterveld BHUs) were scored as High, whereas BHUs associated with poor soils, low rainfall and dissected topography (e.g. inland Mountain Complexes) were scored as Low. Further details regarding the allocation of threat classes is given in Cowling et al. (1999). Also, when allocating BHUs to classes, future threats were anticipated: for example, some coastal Mountain Complex BHUs (e.g. Bredasdorp, Klein River) were allocated High for agriculture on the basis of the expanding cut-flower industry.

In the final grid of agriculture threat, the extant habitat (currently untransformed by urbanisation or agriculture) within each planning unit was allocated to a category of agricultural threat based on the highest scoring BHU in the planning unit.

set of rules to cells of 1 700m (roughly one minute) instead of sixteen degree squares. Predictions for future alien plant spread were categorised as scattered (between 10 and 50% of the cell is likely to be invaded) and widespread (more than 50% of the cell is likely to be invaded). I used confusion matrix to calculate misclassification rate to compare the degree of similarities of both approaches. The comparison was also made at the level of primary BHUs (Table 2) to highlight major differences between habitat types.

Results

Spatial dimensions of current land transformation

Thirty per cent of the area of the CFR is currently transformed by urban areas, cultivated land (including forestry plantations), and medium- or high-density stands of invasive alien trees. There were considerable differences in the spatial extent of different land use categories across the CFR (Table 2; Appendix 1).

Urbanisation covers 1.6% of the CFR but it has severely impacted few habitat types due to its spatial concentration (Fig. 2). Two BHUs – Cape Flats Fynbos/Thicket Mosaic and Blackheath Sand Plain Fynbos- have lost more than 50% of their original area following urbanisation. Just five secondary BHUs contain 62.5% of the 1367 km^2 of urban areas.

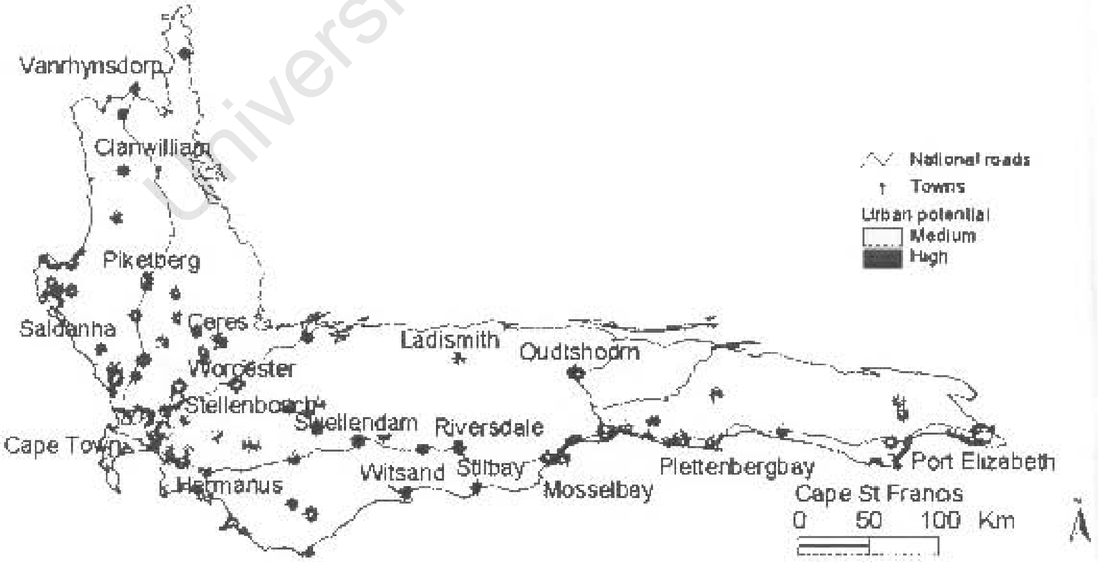


Figure 2. Current and predicted future patterns of urbanisation. Future urban development was derived from rule-based modelling. National roads and major towns within the CFR are shown.

Environmental correlates: The study relied on detailed data on biophysical and other features of the CFR at a scale of 1: 250 000. I used 12 environmental factors, among them those known to influence agriculture potential (such as roughness or growth days; Fairbanks and Scholes, 1999), plant distribution (e.g. minimum temperature; Woodward, 1987) (Table 1). Data were collected from many different sources to provide the necessary GIS layers (Table 1). The distance to the closest commercial forestry plantation was also derived.

Statistical analysis: I used Formal based Inference Recursive Modelling (FIRM) (Hawkins, 1995), a regression tree analysis technique, to relate the distribution of current habitat transformation (agriculture, forestry plantations, and invasion by alien plants) to environmental characteristics. For each land use factor (agriculture/forestry and invaded areas), I randomly selected 50% of the grid cells affected by this factor. Each cell contained information regarding the 12 environmental variables described above. This constituted the set of "presence" observations. A GIS layer of random points (then converted to a grid of 1 700 m by 1 700 m cells) was generated for areas not affected by agriculture or alien plants. This constituted the set of "absence" observations. Numbers of cells in both sets were similar. The same series of environmental variables was derived as for the "presence" cells. The distribution of "presence" cells versus "absence" cells was analysed in FIRM to identify environmental factors characterising areas affected by agriculture or alien plants. By including "presence" (area currently transformed) and "absence" (area currently untransformed) observations in the model, this approach identifies the spatial determinants of land use and land cover (i.e. the factors that distinguish transformed areas from untransformed).

I first analysed the top three independent factors that explain most of the variation for each habitat transformation factor. Then I applied the FIRM analysis to predict their spatial distributions (with likelihood of occurrence greater than 0.5). I excluded Broad Habitat Units (BHUs) from the analysis of prediction of threat occurrence because BHUs were derived on the basis of climate, soil and vegetation (Cowling and Heijnis, 2001), including many of the discrete environmental factors.

Potential maps of distribution for each threat factor were generated using the environmental factors identified as the major determinants of the distribution of each factor from the FIRM analysis. These maps were compared with the actual distribution of agriculture and alien plants. Prediction accuracy was calculated as the percentage of cells (both "absence" and "presence" data) correctly predicted by the model (Fielding and Bell, 1997). Areas currently untransformed but identified as suitable for agriculture or invasion by alien plants (i.e. they share the same environmental characteristics as areas currently cultivated or invaded) were considered under threat.

Model comparison

The outputs of both models were compared for spatial predictions of agriculture and alien plants future expansion. I adjusted the resolution of the rule-based approach to one-minute, by applying the same technique is described in more detail in Chapter 2). Recursive Modelling has also shown to yield more accurate predictions than standard linear models (Franklin, 1998; De'ath & Fabricius, 2000; Rouget et al., 2001). I modelled future land use change (expansion of agriculture and forestry) and land cover changes (spread of invasive alien plants). Future land use and land cover changes were derived for currently untransformed areas (i.e. under natural state); these changes are defined as threats to biodiversity. This approach enabled (1) to understand which factors influence agriculture expansion and alien spread, and (2) to derive spatially-explicit predictions of agriculture and alien spread that are likely to materialise in the near future (10 to 20 years). Understanding of spatial determinants of agriculture and alien plant cover were based on the current distribution of these factors. Once the spatial determinants of agriculture and alien plant cover were identified, I was able to predict based on these determinants where land use conversions are more likely to take place in the future. I did not attempt to model urbanisation, as the socio-economic factors most likely to influence future urban development (e.g. population growth, economic incentives) were not available in a spatially explicit manner for the entire region. I combined agriculture and forestry threats because no new afforestation is likely to occur in the CFR: indeed large areas under forestry will be transferred to other forms of land use in a 10 year planning horizon. Also most land that has high potential for forestry also has high potential for many types of agriculture (namely dairy, vineyards and deciduous fruit). I assumed that agriculture expansion would carry on over the next 10 years and would not decline. Thus, any area currently transformed by agriculture (as well as urbanisation, and alien plant invasion) would remain transformed in future.

Data conversion: The model resolution was determined by the scale of available climatic data (one-minute resolution). The original layer of current transformation was thus converted to a 1 700m grid (i.e. minimum mapping size of 289 ha, roughly 1 minute resolution). Slightly different approaches were required when assigning values to these cells for agriculture and alien plants. Cultivated areas (including forestry) cover a very large part (>25%) of the CFR and a very high proportion of the grid cells contained some cultivated land. I labelled only those cells where cultivation covers more than 50% of the cell area as "cultivated" (majority rule). As most of the areas occupied by alien plants occur in small patches, these areas would be lost in the grid conversion by using the majority rule. The percentage of the cell area occupied by alien plants was therefore considered as the cell value. I combined the medium- and high-density categories because there were too few cells of the latter for FIRM analysis and because preliminary analysis showed that there was no significant differences in the environmental correlates for the two classes. The percentage of alien plants in each cell was later grouped into three categories: "none", "patchy" (covering 10-50% of the cell area), and "widespread" (>50% of the cell covered). Cells where alien plants cover <10% of the cell (i.e. 29 ha) were ignored for the analysis.

Method 2: Statistical modelling based on classification tree

Unlike the method described above, this modelling technique required no understanding of processes, but was based exclusively on a statistical extrapolation of existing land use patterns. This approach assumed that the distribution of agriculture and invasive species is largely determined by environmental variables (such as climate, geology, or topography). An important assumption here was that current distribution of invasive species and agriculture approximate equilibrium distributions (i.e., that these factors have had sufficient time to sample all available environment in the CFR). Statistic models focus on identifying environmental constraints. They allow to better understand interactions between spatial determinants and the distribution of different land use/land cover changes. However, it is difficult to distinguish between causality and correlations. These models allow spatial predictions of land use changes but do not address the temporal component of these changes (Serneels and Lambin, 2001).

Numerous statistical methods are available to predict a response variable based on a series of environmental predictors (e.g. logistic regression, principal component analysis, and generalised additive models). I opted for recursive partitioning, a flexible non-parametric method, which has shown to accurately model landscape patterns (Reichard and Hamilton, 1997; Chapter 2). Recursive partitioning is an attractive statistical technique but requires large data sets (Vayssieres et al., 2000; the

Table 2: List of primary BHUs within the Cape Floristic Region. Major factors of current habitat transformation within the Cape Floristic Region are given in percentages of the area of each primary Broad Habitat Unit. Urban: proportion of BHU currently urbanised; Agric: proportion of BHU currently under cultivation (including agriculture); Alien-L: proportion of BHU currently invaded at low density (<20% cover and includes areas free of invasive alien plants); Alien-M: proportion of BHU invaded at medium density (20-75% cover); alien-H: proportion of BHU currently invaded at high density (>75% cover).

Primary BHUs	code	Area (km^2)	Urban	Agric	Alien-L	Alien-M	Alien-H
Dune Pioneer	DP	205.44	5.88	5.22	73.72	3.82	11.37
Fynbos / Thicket Mosaic	FT	2994.59	10.38	24.83	50.05	6.41	8.34
Sand Plain Fynbos	SPF	6771.11	6.91	40.07	50.40	1.46	1.16
Limestone Fynbos	LF	2068.24	0.12	14.73	75.62	5.45	4.08
Grassy Fynbos	GF	3655.67	3.04	25.98	65.05	1.50	4.43
Fynbos/Renosterveld Mosaic	FR	3531.76	1.04	40.36	54.55	0.79	3.27
Coast Renosterveld	CR	13989.82	1.23	80.58	17.07	0.37	0.75
Inland Renosterveld	IR	9184.72	0.35	16.63	82.28	0.21	0.53
Mountain Fynbos Complex	MFC	29475.33	0.32	7.50	89.91	1.02	1.24
Vygieveld	VY	2330.75	0.34	18.19	81.15	0.10	0.21
Strandveld	SV	962.76	0.46	22.03	77.40	0.09	0.02
Broken Veld	BV	7293.01	0.50	9.18	89.87	0.12	0.33
Mesic Succulent Thicket	MST	531.14	1.49	26.93	67.89	0.24	3.45
Xeric Succulent Thicket	XST	2443.05	0.18	3.25	96.22	0.05	0.29
Afromontane Forest	AF	2096.82	2.51	35.31	58.66	0.37	3.15
Indian Ocean Forest	IOF	357.38	3.92	11.44	71.74	1.56	11.35
Grand Total		87891.60	1.56	25.86	69.14	1.02	1.59

realistic value across the entire planning domain for these predictions (Le Maitre et al., 1996, Higgins et al., 2001).

4. I did not consider the spread of aliens between planning units.

Given a 7% average annual expansion rate, and taking into the account both the thickening-up of presently sparse and medium-density stands as well as spatial expansion of the invading population, planning units that currently have about 35% cover of dense aliens or 50% cover of dense and medium-density aliens combined, would have 80% coverage of dense stands within 20 years, assuming no intervention. Similarly, areas with currently low cover (> 5%) of moderate and dense stands of aliens would become 20 – 30% thus invaded after 20 years.

Therefore, alien threat was allocated for each planning unit using the following rules:

- if *N* > 80% of extant habitat, then alien threat = N (none);
- if *Dense* > 35% of extant habitat, then alien threat = High;
- if (*Dense* + *Moderate*) > 50% of extant habitat, then alien threat = High;
- if (*Dense* + *Moderate*) > 5% of extant habitat, then alien threat = Moderate;
- otherwise, alien threat = Low.

where *Dense* = area of dense aliens; *Moderate* = area of moderate-density aliens; *N* = area of extant habitat in non-susceptible BHUs.

Table 1: Environmental factors used for the statistical modelling of future agriculture expansion and alien plant spread in the Cape Floristic Region. CCWR = Computing Centre for Water Research, University of Natal, Pietermaritzburg; SG – Surveyor General; UCT – University of Cape Town; DEM = Digital Elevation Model. Data types: categorical (cat.; number of categories in brackets); continuous (cont.; units in brackets).

Environmental variables	Code	Source	Type
Geology	GEOLOGY	Dept. of Geological Sciences, UCT	Cat. (11)
Altitude	ALTITUDE	SG, derived from DEM	Cont. (m)
Slope	SLOPE	SG, derived from DEM	Cont. (°)
Roughness	ROUGHNESS	SG, derived from DEM	Cont.
C.V. of altitude	CVALTI	SG, derived from DEM	Cont. (%)
Growth temperature	GTEMP	CCWR	Cont. (oC)
Minimum temperature	MINTEMP	CCWR	Cont. (oC)
Mean annual precipitation	MAP	CCWR	Cont. (mm)
Number of growing days	GDAYS	CCWR	Cont.
Distance to the nearest main road	DISTROAD	SG	Cont. (km)
Distance to the coastline	DISTCOAST	SG	Cont. (km)

Urbanisation: Future urban development has been modeled using various approaches such as rule-based simulation (e.g. Swenson and Franklin, 2000) or complex socioeconomic and transportation simulations (e.g. Landis, 1994). To my knowledge, there is no conservation planning exercise that considered future urban development in a spatially-explicit manner at a regional scale. Modelling urban development requires detailed knowledge of social and economic interactions in the region (T. Leiman, personal communication). I modelled future urbanisation threat very simplistically and I acknowledge that a detailed study of the complex urbanisation processes within the CFR – including rapid growth in the luxury and informal sectors in some areas – may have produced (marginally) different results. Urbanisation threat was modelled at the same resolution as the planning units used in the conservation plan (i.e. 1/16th degree square). I modelled urban growth spreading from existing urban nodes into adjacent areas. I assumed that urban development could occur in areas currently cultivated. For each planning unit in the CFR, my approach was as follows:

- if ≥ 50% of the planning unit area is urbanised, then threat = High;
- if the area within 5 km radius from urban centre on level terrain (slope < 8°), including current urban areas, covers 35% of the planning unit then threat = High;
- if the area within 5 km radius from urban centre on level terrain (slope < 8°), including current urban areas, covers 10% of the planning unit then threat = Moderate;
- otherwise, threat = Low.

This simple model assumed equal likelihood of any urban centre spreading at the same rate. This could be improved in future modelling of urban development. I did not attempt to predict the growth of informal settlements.

Alien Plants: Extant habitat (i.e. natural vegetation not densely invaded) within each planning unit was classified as low, moderate, or high regarding future alien plant threat. Four assumptions were made for the categorisation of planning units:

1. Extant habitat in BHUs that were not susceptible to invasion by the alien species specified above, namely karroid (semi-arid) habitats, was regarded non-susceptible, even if alien plants had invaded azonal habitats such as drainage lines; those habitats mostly consist of inland Renosterveld, Vygielveld, Broken Veld, and Xeric Succulent Thicket.
2. Areas within susceptible BHUs that comprised dense stands of aliens were excluded from extant habitat, since these areas were, by definition, no longer susceptible to alien plant invasion.
3. When predicting likely increases in the extent of invaded areas in planning units over the next 20 years, I considered the role of thickening up of moderate-density stands as well as the spatial expansion of invading populations, the latter being mostly adjacent to currently dense stands. I based my predictions on recent studies (reconstruction of actual invasions using historical aerial photographs and modelling studies); an annual increase of 7% in spatial extent was taken as a

Agriculture, including commercial forestry plantations, covers 22 725 km^2 (25.9%) of the CFR; this form of land use is much more evenly distributed across the region than the other threat factors (Fig. 4). Xeric Succulent Thicket and Mountain Fynbos complex are the primary BHUs least affected by cultivation (Fig. 3a). Almost 80% of Coastal Renosterveld has been converted to agriculture. At the level of secondary BHUs, the top 10 BHUs (in terms of the area affected by agriculture) made up 68.7% of the total area of agriculture.

The area classified as "natural vegetation" in Figure 3 was subdivided according to the cover of woody alien plants. These results show that 1 394 km^2 of the CFR (1.6%) is covered by dense stands of alien trees and shrubs; 895 km^2 by medium-density stands (1.0%), and 60 067 km^2 by low-density stands (68.3%); the last category includes areas free of aliens (Fig. 5a). The primary BHUs with the greatest proportional cover of aliens were mainly those associated with mesic, lowland habitats, namely Dune Pioneer, Thicket and Forest and Fynbos/Thicket Mosaic (Fig. 6). In only three secondary BHUs was more than 25% of the area under "natural vegetation" (see above) covered with dense, or medium stands of woody aliens. These are: South East Dune Pioneer, Elgin Fynbos/Renosterveld Mosaic, and St Francis Fynbos/Thicket Mosaic. The primary BHUs Succulent Karoo and Inland Renosterveld, both associated with semi-arid to arid climates, had only tiny proportions of their remaining areas covered by woody aliens (Fig. 5a).

Spatial extent of future habitat transformation

Here, I present and compare the outcomes of rule-based and statistical modelling approaches for predicting the spatial extent of future land use changes. Patterns of future urbanisation are described first, as they were only modelled using the rule-based approach (see Methods).

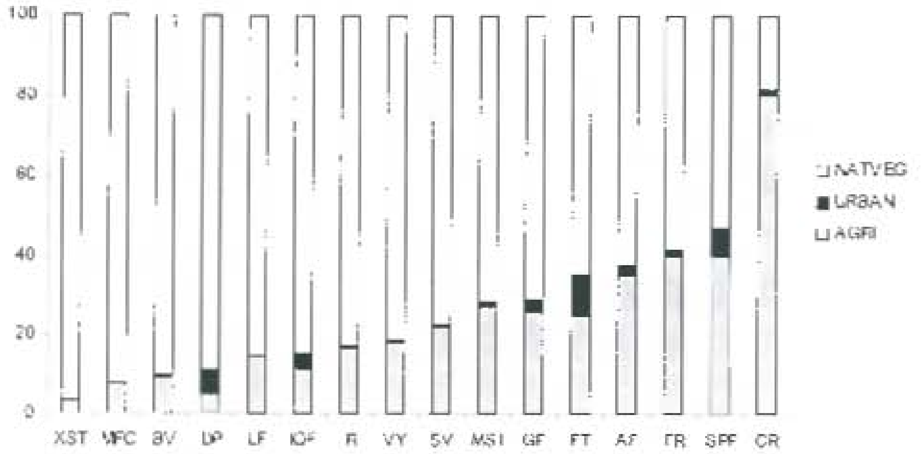
Future urban development

Figure 2 shows where urbanisation is most likely to occur in 20 years time within the CFR. According to this simple model, future urban development could affect 9% of the CFR. This spatially explicit model indicates that the coastal primary BHUs, Dune Pioneer, Indian Ocean Forest and Fynbos/Thicket Mosaic, will be most affected by future urban development (Fig. 3b).

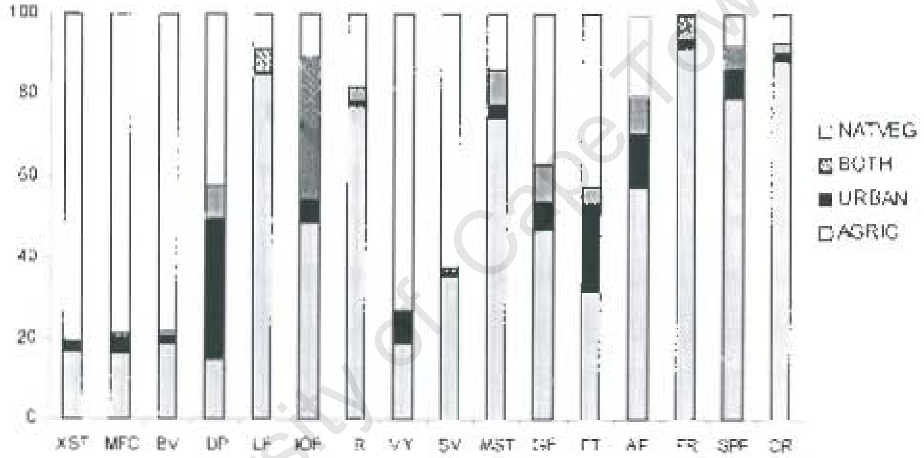
Future agriculture expansion

Figure 4 shows the predicted pattern of agriculture expansion for both approaches. This indicates that between 15.5% (statistical modelling) and 32.6% (rule-based modelling) of the currently untransformed land could be converted to agriculture. This is the most serious threat for the lowland primary BHUs, namely Coastal Renosterveld and Sand Plain Fynbos (Fig. 3b&c).

a) Current land use pattern



b) Future land use pattern: rule-based modeling



c) Future land use pattern: statistical modeling

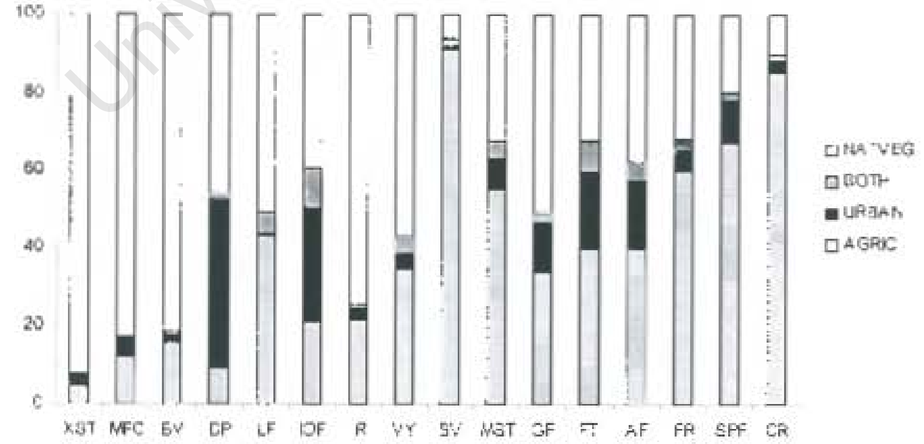


Figure 3. The current and predicted future extent of transformation by agriculture (including plantation forestry) and urbanisation in 16 primary Broad Habitat Units (BHUs) in the Cape Floristic Region. The area shown as "natural vegetation" indicates habitats not irreversibly transformed, and includes areas mapped as low, medium- and high-density stands of alien trees and shrubs. Predictions of future land use changes are derived from rule based and statistical modelling (see methods). Urbanisation was predicted using rule-based modelling only. Codes for primary BHUs are given in Table 2.

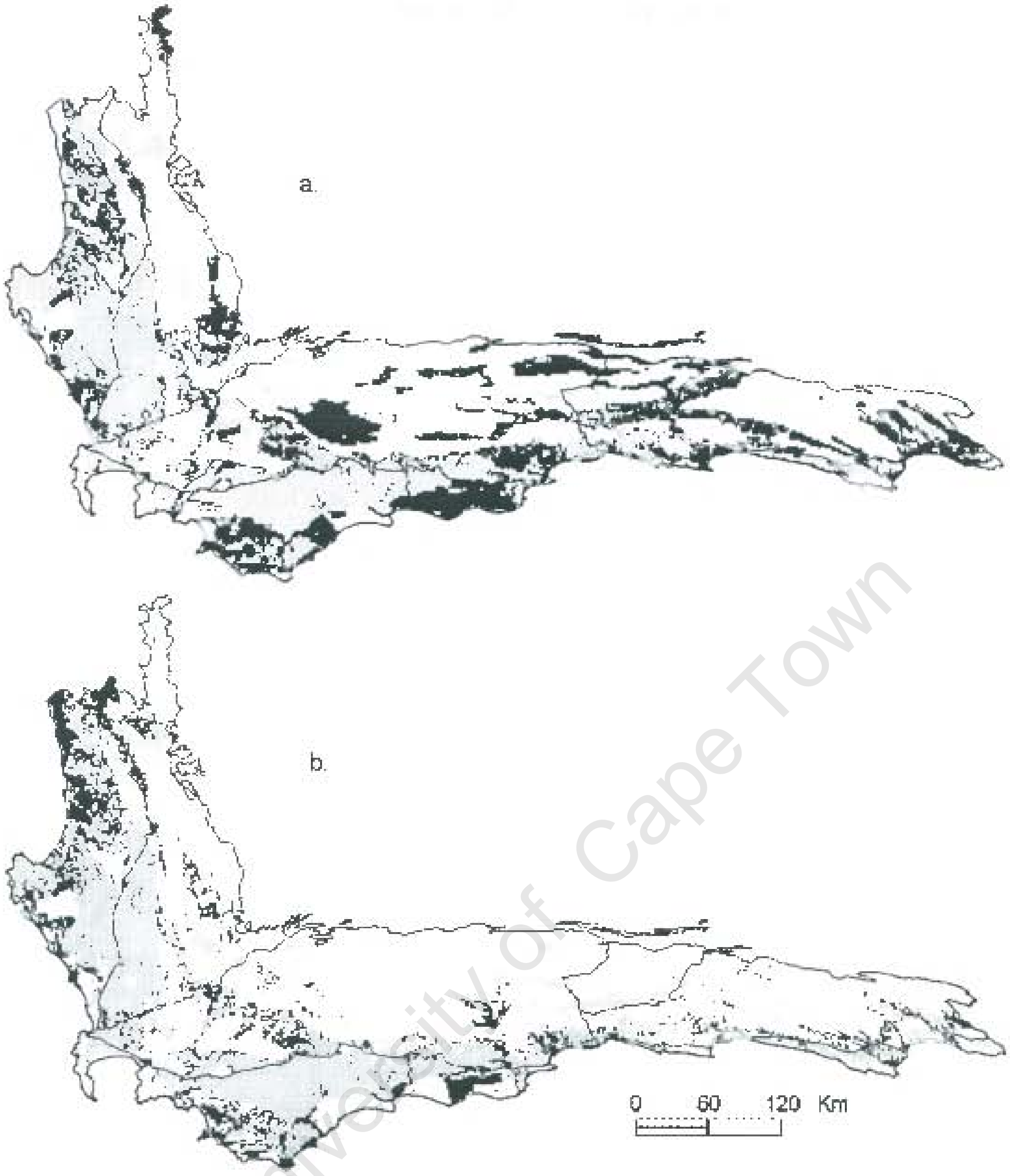


Figure 4. Current and predicted future distribution of agriculture (including forestry) in the Cape Floristic Region. The potential distribution was derived from rule-based modelling (a) and from FIRM modelling (b) using 8 biophysical factors as predictors of agricultural pattern (see dendrogram in Fig. 7). Shaded areas indicate the current extent of agriculture and urbanisation, red areas are suitable for future agriculture expansion

The use of FIRM (classification tree) allowed to identify the environmental determinants of cultivated areas within the CFR. Eight factors were required to model the current distribution of cultivated areas accurately (accuracy >85%) (Fig. 7). Suitable areas for agriculture were identified on the basis of topography (altitude, coefficient of variation of altitude, roughness, proximity to the coast), climate (growth days, growth temperature, mean annual precipitation), land use (distance to the roads) and geology. Altitude was the most significant factor, and very few areas above 300 m were predicted as being suitable for cultivation (Fig. 7). Spatial determinants of agriculture differed according to altitude: geology was the most significant factor in the lowlands (< 200m) whereas coefficient of variation in altitude was the most significant factor in the uplands (> 781 m). On the basis of primary BHUs only, a FIRM analysis predicted that Coastal Renosterveld, Fynbos Thicket Mosaic, Fynbos Renosterveld Mosaic, Sand Plain Fynbos, and Mesic Succulent Thicket were suitable for future agriculture development.

Invasions by alien plants

The future extent of alien plants in untransformed land (as defined by agriculture and urbanisation) is presented in Figure 5. Between 27.2% (rule-based modelling) and 32% (statistical modelling) of untransformed area are likely to be invaded by alien plants. The habitat types Limestone Fynbos, Grassy Fynbos, and Renosterveld Fynbos Mosaic are the most threatened by future alien plant spread (Fig. 6b & c).

Environmental determinants of alien plant invasions are shown in Figure 8. Using four factors (growth days, growth temperature, altitude and geology), I was able to accurately model 73% of the current distribution of alien stands in the CFR. Climatic factors appeared quite important in determining the distribution of alien stands. Annual number of growth days was the most significant factor and annual growth temperature the second most significant factor. Patchy invasion (i.e. occupying 10-50% of the cell area) could occur in areas with less than 107 growth days (high growth temperature or low altitude). Widespread invasion (> 50% of cell area invaded) was predicted on the basis of growth days and geology (Fig. 8). However, this model correctly classified only 45% of widespread invasions. The occurrence of widespread invasions was better predicted using primary BHUs only; they were predicted to occur in Dune Pioneer, Limestone Fynbos, Fynbos Thicket Mosaic, and Indian Ocean Forest (this is depicted in Fig 6c).

Comparison of modelling approaches

Although the two approaches differ considerably in their assumptions, they produced similar spatial patterns (Fig. 4 & 5). There was 73% agreement for agriculture and 74% agreement for alien plants (considering presence/absence of aliens only) between the two models. Spatial extent of future agriculture threats derived from the rule-based approach were higher than those derived from the statistical approach (Fig. 4). This created some important differences in levels of agriculture threat in the primary BHUs Limestone Fynbos or Inland Renosterveld (Fig 3b).

On the contrary, spatial extent of future alien threat derived from the rule-based approach were lower than those derived from the statistical approach (Fig. 5). There was a poor correspondence of alien plant density between the two approaches (Fig. 9). Fifty five percent of the areas categorised as widespread by the rule-based approach were classified as scattered by the statistical method (Fig. 9a); whereas 59% of the areas categorised as scattered by the statistical approach were classified as not invaded by the rule-based approach (Fig. 9b). Such differences are reflected in the predictions of alien

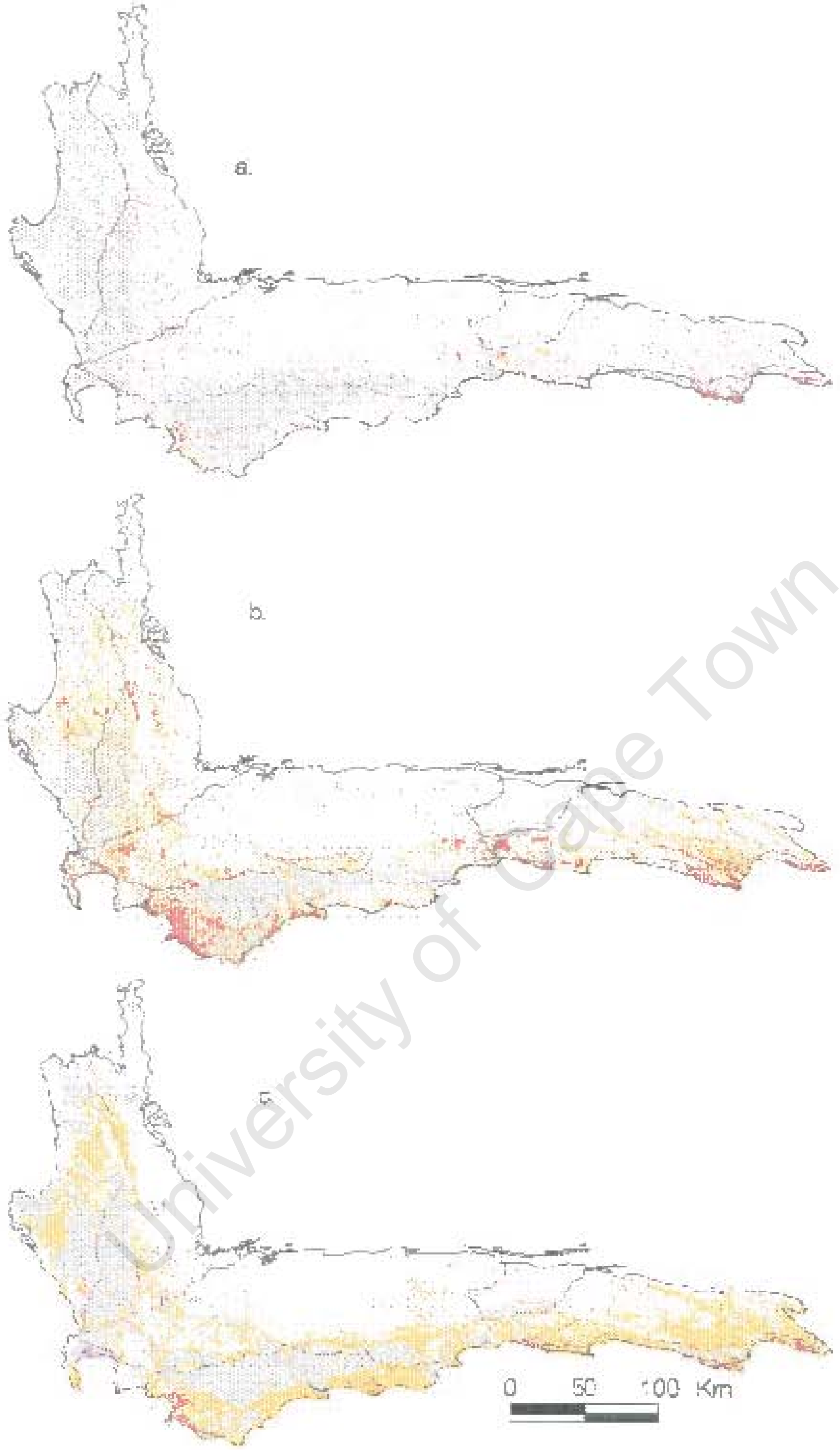
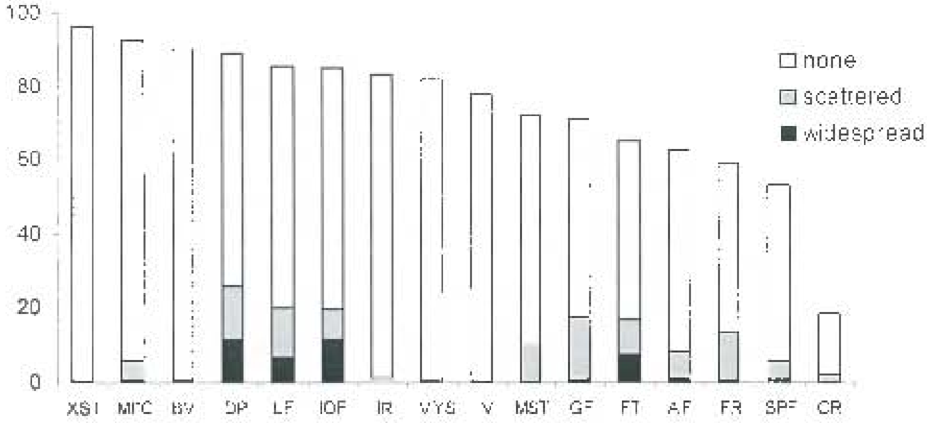
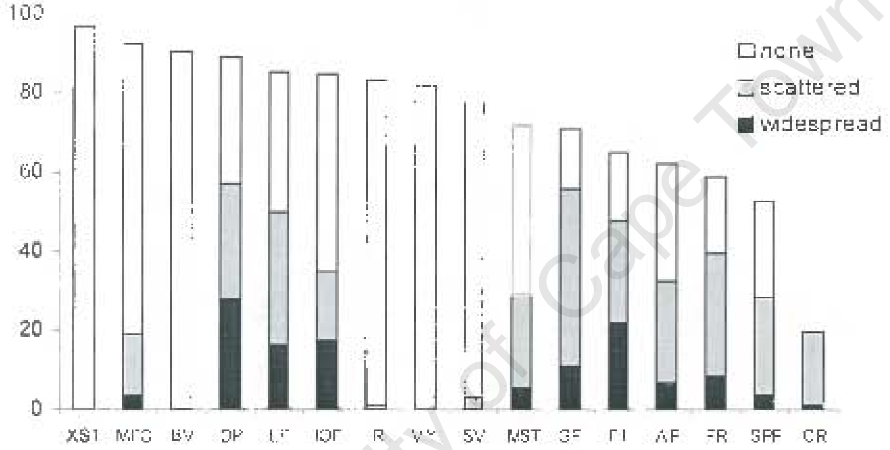


Figure 5. Current (a) and predicted future distribution of invasive alien plants in the Cape Floristic Region. The future extent of alien plants was derived from rule-based modelling (b) and FIRM modelling (c) using 4 biophysical factors as predictors of alien plant distribution (see dendrogram in Fig. 8). Shaded areas indicate the current extent of agriculture and urbanisation, areas of future scattered invasions are shown in orange, areas of future widespread invasions in red.

a) Current extent of alien plants



b) Future extent of alien plants: rule-based modeling



c) Future extent of alien plants: statistical modeling

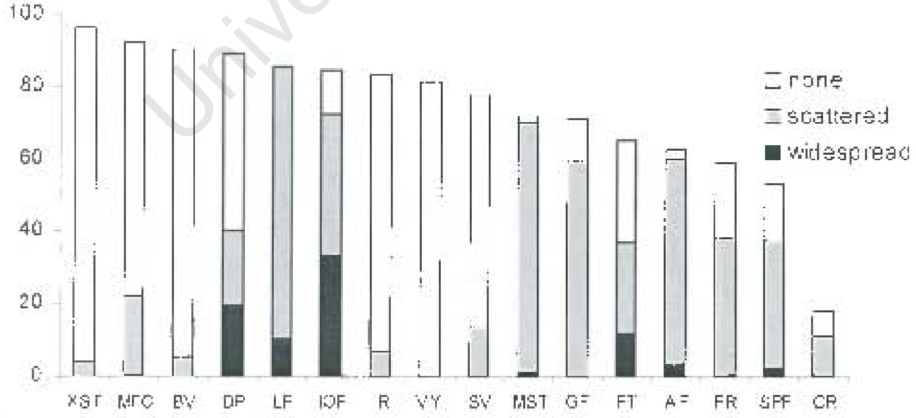


Figure 6. The current (a) and future extent of scattered and widespread stands of invasive (selfsown) alien trees and shrubs (see text for details on criteria for the classes) in 16 primary Broad Habitat Units (BHUs) in the Cape Floristic Region. The total area show here for the three classes is equivalent to the area shaded as "natural vegetation" in Fig. 2. Predictions of future alien plant spread are derived from rule-based and statistical modelling (b and c respectively). Codes for primary BHUs are given in Table 1.

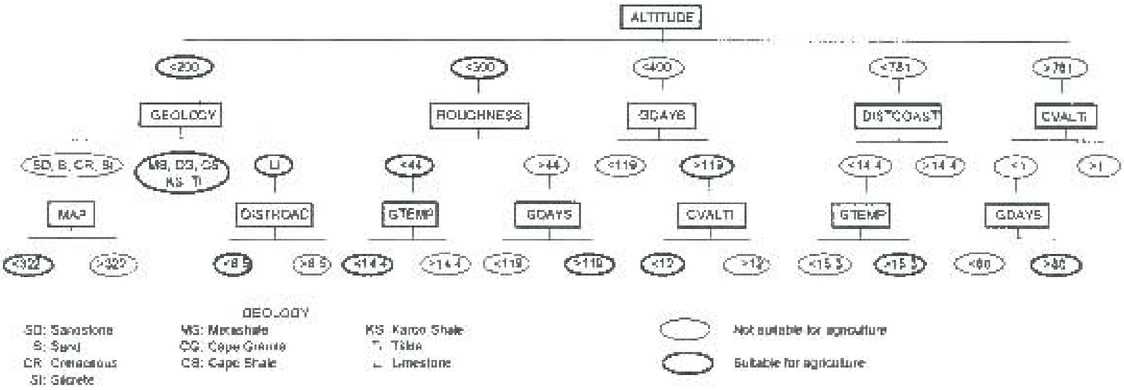


Figure 7. Determinants of the distribution of cultivated areas in the Cape Floristic Region. The dendrogram was generated by FIRM (see text). Significant factors are indicated in the boxes, significant values that distinguish suitable from non-suitable areas are indicated in the ellipsoids. The variables indicate: ALTITUDE (elevation above sea level in meters); GEOLOGY (11 geological categories of bedrock); ROUGHNESS (indicator of topographical heterogeneity); GDAYS (annual number of days suitable for plant growth); DISTCOAST (distance from the coast line, in km); CVALTI (coefficient of variation of altitude); MAP (mean annual precipitation in mm); DISTROAD (distance from major roads, in km); and GTEMP (growth temperature in°C); (for details of these and other variables used in modelling, see Table 1). The first factor is indicated on top the subsequent splits below. For example, areas at altitudes above 781 m, with a coefficient of variation of altitude < 1, and with > 80 growth days per year were classified as suitable for agriculture.

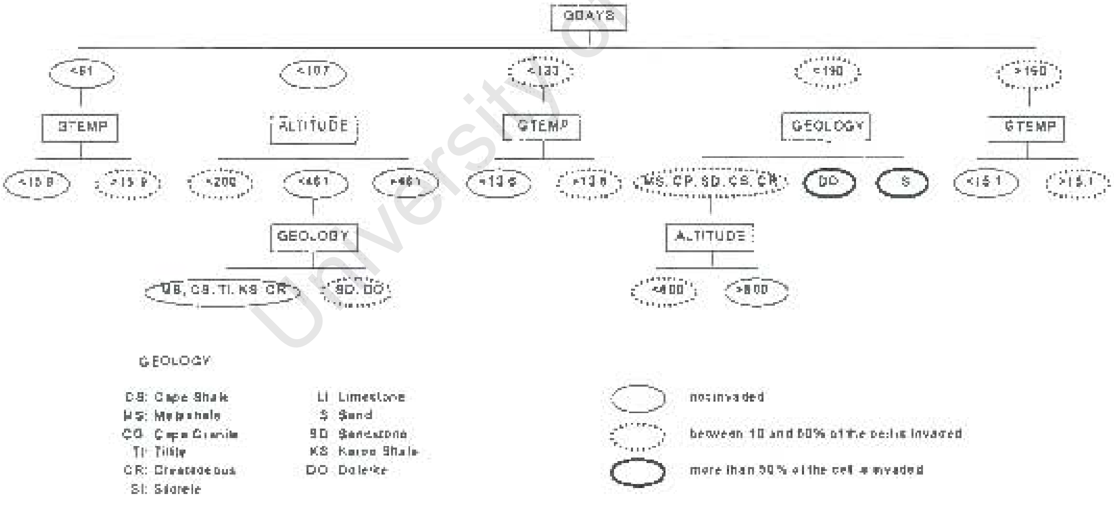


Figure 8. The determinants of invasion by alien trees and shrubs in the Cape Floristic Region (no distinction was made between species in the mapping, but the most widespread taxa are*Acacia cyclops*, *A. mearnsii*, *A. saligna*, *Hakea* spp., *Pinus radiata* and *P. pinaster*, with smaller areas of *Eucalyptus* spp.). The dendrogram was generated by FIRM analysis (see text). Significant factors are indicated in the boxes, significant values that differentiate between scattered invasions, widespread invasions, and non-invasible habitat are indicated in the ellipsoids. The variables indicate: GDAYS (annual number of days suitable for plant growth), GTEMP (growth temperature in °C); ALTITUDE (elevation above sea level in meters); GEOLOGY (11 geological categories of bedrock) (for details of these and other variables used in modelling, see Table 1). The first factor on the dendrogram is indicated on top, the subsequent splits below. For example, areas with > 190 growth days per year and with growth temperature values > 15.1°C were classified as suitable for scattered invasions (10 - 50% of cell affected).

plant invasions, for example, in the primary BHUs Afromontane Forest and Mountain Fynbos Complex (Fig. 6b & c).

Figure 10 shows the intensity of future habitat transformation according to both approaches. Predictions from rule-based modelling indicate that 31, 8.8, and 1.4% of currently untransformed land is likely to be affected by one, two or three threat categories, respectively. Similarly, predictions from statistical modelling indicate that 23.1, 8.5, and 1.3% of currently untransformed land is likely to be affected by one, two or three threat categories, respectively.

Discussion

Current pattern of habitat transformation

This study has shown that 30 % of the CFR is currently transformed by agriculture (including commercial forestry plantations), urbanisation and alien plants (Appendix 1). Estimates of agriculture and urbanisation extent for the CFR derived from the national land cover database were very similar (Fairbanks et al., 2000). Results of a recent country-wide survey of the distribution of alien and shrub species (Versfeld et al., 1998) gave similar estimates of the extent of dense stands of alien species int the CFR. This suggests that remote-sensing was an appropriate technique for quantifying the extent of alien plant invasions.

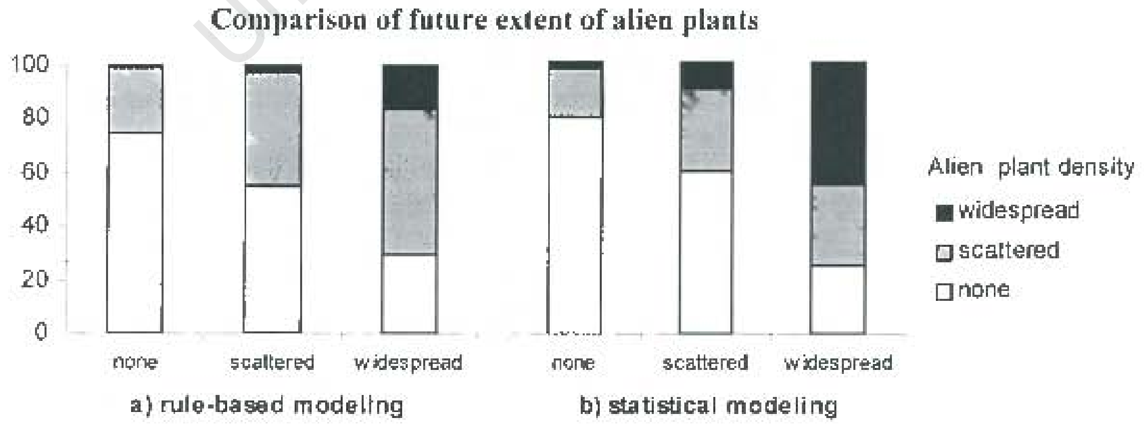


Figure 9. Comparison of modelling approaches for predicting future extent of alien plant invasion. Fig. 9a shows how categories derived from rule-based modelling were classified by FIRM modelling; Fig. 9b shows how categories derived from FIRM modelling were classified by the rule-based approach.

Urbanisation

Two types of urban development occur in South Africa. It must be borne in mind that these results reflect mainly formal development. The extent of informal settlements in the CFR has probably been underestimated, as they could not easily be identified on Landsat images. The development of informal settlements is highly dynamic and their impacts are likely to be high on the remaining lowland vegetation within the major metropolitan areas of the CFR, namely Cape Town and Port Elizabeth.

Urban development is currently limited to few areas in the CFR, especially the Cape Town and Port Elizabeth metropolitan areas, and the central south coast known as the Garden Route. This form of transformation affects 1 367 km^2 (1.6 % of the CFR). However its impacts can be severe in relation to the overall biodiversity pattern in the region. The Cape Town Metropole (the largest urban centre,

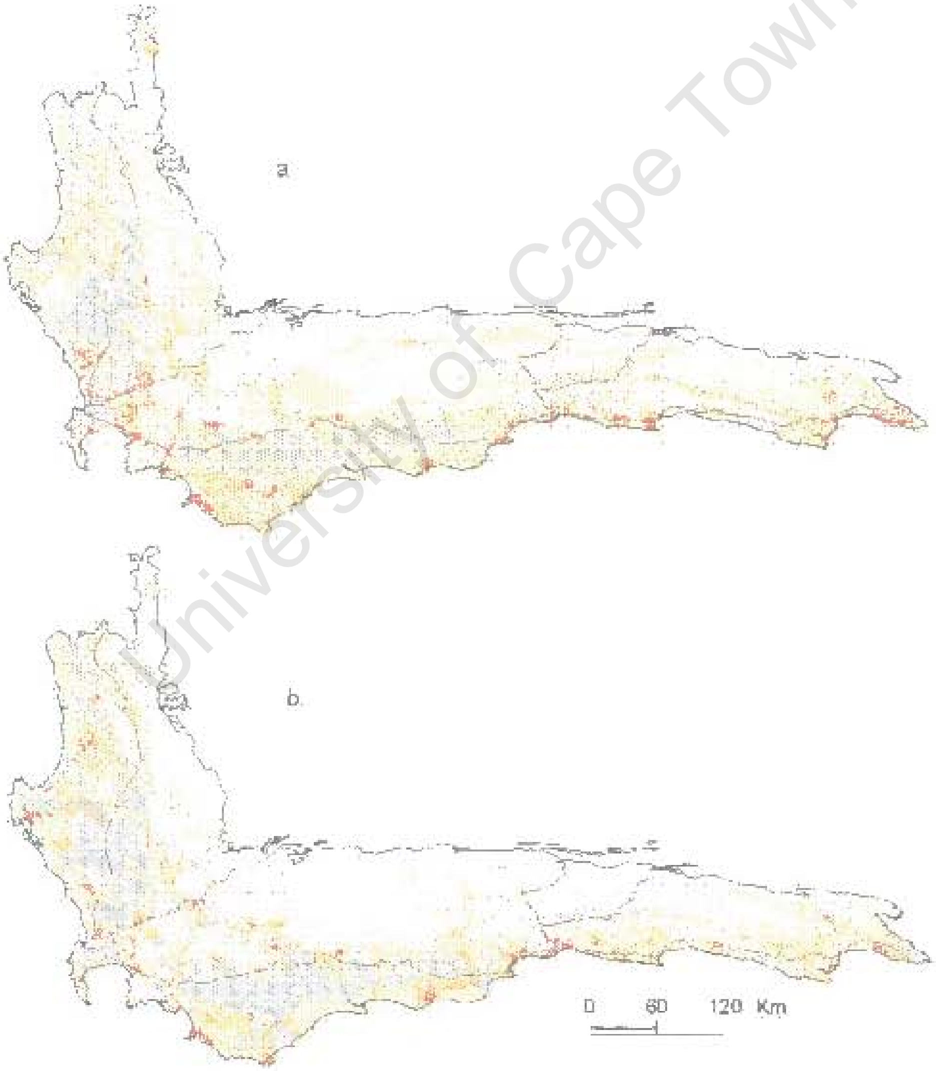


Figure 10. Intensity of future land use changes according to rule-based (a) and statistical (b) modelling approaches. The intensity was derived by superimposing each individual threat. Areas in yellow are predicted to experience one type of threat; areas in orange, two types of threat; and areas in red, three types of threat.

spreading over 50 km^2) is recognised as a centre of plant endemism, with 74 Red Data Book plant species occurring within the metropole, especially in small remnants of lowland habitats (Rebelo and Siegfried, 1990; Richardson et al., 1996). Some secondary BHU's, namely Cape Flats Fynbos/Thicket Mosaic and Blackheath Sand Plain Fynbos have been so heavily transformed (Wood et al., 1994) that more than all remaining habitats is required to achieve conservation targets (Pressey et al., in press). These remnants should receive immediate conservation effort for two reasons: 1) they score high on the basis of irreplaceability because of the high level of endemism (few options available in order to achieve conservation targets) (Maze and Rebelo, 1999), and 2) they are very vulnerable to habitat loss or degradation due to the threat intensity. Cowling and Bond (1991) found that small remnants (5-15 ha) of lowland Fynbos can sustain biodiversity provided they are subject to fires.

Agriculture

Agriculture (including plantation forestry) is the major agent of habitat transformation in the CFR, and covers 22 725 km^2 (25.9% of the CFR). The impacts are greatest on lowlands habitats (Fig. 4), especially those which have level topography, fertile soils and where rainfall is sufficient for agriculture. This has lead to a mosaic of remnants of natural vegetation (see Kemper et al., 1999 for a detailed study on renosterveld habitat fragmentation). As for urbanisation, some very diverse habitats have been massively transformed following agricultural expansion. This is the case in the Elgin Basin, the West Coast Renosterveld, and the Agulhas Plain -a highly fragmented and human-modified area of high species richness and endemism (Cowling, 1992; Lombard et al., 1997).

In some cases, transformation is so extensive that several habitats, occurring on fertile shale-derived soils of the coastal forelands, have lost more than 75% of their original extent (e.g. Overberg and Swartland Coast Renosterveld where 90% of their original extant have been converted to agriculture). Remarkably, plant species composition in small remnants of coastal renosterveld appears unaffected, relative to that on extensive tracts of habitat, suggesting that these remnants still have a role to play in species-level conservation (Kemper et al., 1999). Moreover, in the case of BHUs where the available habitat is less than the conservation target, these remnants represent the only option for achieving this target (see Cowling et al., in press; see also Margules and Pressey, 2000, Pressey and Taffs, 2001).

The degree of fragmentation was sometimes under-estimated due to the mapping resolution (25 ha) for the CAPE project (see Chapter 6). Another limitation of using land cover data derived from satellite images is that it fails to accurately estimate habitat degradation by overgrazing or chemical pollutants. While the latter is probably significant only around the two major metropolitan areas in the CFR (Cape Town and Port Elizabeth), overgrazing is a factor in many lowland and semi-arid (karroid) BHUs.

Alien plant invasions

The extent of stands of invasive alien trees and shrubs was estimated to cover 2.6 % of the CFR (2 290 km^2). Previous attempts of mapping invasion extent over the last few decades have reported higher estimates (see Macdonald and Richardson, 1986; Richardson et al., 1992, 1997 for recent reviews). For the fynbos biome only (which represents 87.9% of the CFR), Macdonald et al. (1985) estimated the combined extent of self-sown *Hakea* and *Pinus* species to be 6 641 km^2, and 8 092 km^2 for other thicket-forming alien tree/shrub invasions (mainly Australian species such as *Acacia cyclops*, *A. longifolia*, *A. saligna*, *Eucalyptus* spp., *Leptospermum laevigatum* and *Paraserianthes lophantha*). It is likely that these previous assessments have inflated estimates through inappropriate extrapolation from the small proportion of the CFR for which good data were available. In many previous assessments, areas mapped as "invaded" often contain large blocks of uninvaded land. Support for the estimates from this CFR-wide study come from the results of a recent countrywide survey of woody invasive plants (Versfeld et al., 1998). If I extract regional data from this survey to give as close an approximation as possible for the geographical extent of the CFR, I find that dense stands occupy 1.30% of the area. However, the rugged topography, cloud cover, and overlapping spectral signatures of alien and indigenous species were problems that undoubtedly influenced the accuracy of the mapping (Lloyd et al., 1999). Given the scale of this survey, many small stands of alien plant species were definitely missed. Nonetheless, the mapping methodology applied here enabled to obtain a CFR-wide map that is: 1) more consistent than any previous effort; and 2) very suitable for use in this modelling.

This assessment of the distribution of invasive alien plants dealt only with large trees and shrubs – these lifeforms are currently the greatest problem among all alien plants in the region. Herbaceous alien plants have notable impacts in some lowland ecosystems (Richardson et al., 2000). The extent and impacts of herbaceous invaders are likely to increase in the future as a results of the combined efffects of disturbance, agricultural activities, and changing fire and nutrient regimes (Richardson et al., 2000). Further work is needed before one could confidentially predict the spatial dimensions of likely future increases in extent and impact.

Assessing future threat to biodiversity

There has been a long debate on how to allocate priorities for conservation areas, and various approaches have been suggested based on threatened taxa (Master, 1991; Flather et al 1998); threatened ecosystems (Beissinger et al., 1996); per cent of remaining natural habitat and protection status (Dinerstein and Wikramanayake, 1993); endemism and vulnerability in "hotspots" (Myers, 1988; Mittermeier et al., 1998); and irreplaceability and vulnerability (Pressey, 1997). All these approaches include an analysis of threat level, in other words, the likelihood of losing a portion of extant biodiversity. However, only recently have studies attempted to identify threat patterns in a spatially explicit manner (Pressey et al., 1996; White et al., 1997; Higgins et al., 1999; Abbit et al., 2000; Stoms, 2000). Such approaches are essential for conservation planning for at least three reasons: 1) they enable explicit predictions of the magnitude and type of biodiversity loss (Abbit et al., 2000); 2) when combined with the conservation value of a parcel of land, an assessment of vulnerability to threatening processes enables the identification of priorities for conservation action (Pressey et al., 1996); and 3) they enable the identification of land parcels doomed by unavoidable threats and, hence, the early search for alternative options (Pressey, 1997) . What is clear is that rigorous studies of the spatial depiction and temporal manifestation of threats to biodiversity are essential for strategic conservation. No attention has been given to comparing different methods of threat analysis. The outcomes of the rule-based and statistical methods used to model the spatial distribution of future threats by urban development, agriculture expansion and alien plant spread are compared below.

Model limitations

Modelling future urban development requires detailed information on socio-economic factors, local and national policies, level of infrastructure, and terrain (Clarke et al., 1997). Compiling the necessary data for the Cape Floristic Region was beyond the scope of the project. Therefore the accuracy of this simplistic model of urbanisation threat is probably questionable, and the spatial outcomes should be considered as likelihood of urbanisation rather than true predictions. The factors used in this study (distance to urban centres and slope) have been used elsewhere to adequately model future urbanisation pattern (Wear et al., 1998; Gunter et al., 2000) although these studies were conducted at a finer scale. Based on these factors, the areas of future urban development identified by the model clearly have a higher probability for development than other areas.

I estimated the vulnerability of habitat types to agriculture based on expert knowledge and statistical modelling based on environmental factors. The first approach was done at a coarse scale since variations in the topography were not considered within each habitat type. Higher resolution in the threat estimation was provided by the classification tree method since it included the effects of terrain morphology, climate and geology on agriculture potential. This explains the higher proportion of the CFR predicted to be transformed by agriculture using the rule-based approach (Fig. 4). Both models consider agricultural expansion only and do not account for a reduction in agricultural practices. Crops currently in decline in the CFR include deciduous fruit and forestry. However, it is unlikely that the actual change in the extent of cultivated land will be substantial since these crops are likely to be replaced by alternatives that yield greater economic returns(e.g. grapes, cut flowers, and a new wave of indigenous crops, mainly teas and oil-yielding plants) (R.M. Cowling, personal observation). Moreover, land currently under plantations will also be reallocated to agriculture or other land uses.

Alien plant spread has been successfully modelled in some parts of the CFR using individual-based models (Higgins et al., 2001) and logistic regression (Higgins et al., 1999). Individual-based models require detailed knowledge of the species involved and their use has been limited to small geographical ranges (i.e. <50 km^2). This simple model of future spread of alien species, based on existing invasive stands, probably under-estimated the spread as it did not account for long-distance dispersal and species introduction into new areas. The importance of long distance dispersal was illustrated by Higgins et al. (2001). I also assumed a unique rate of alien spread regardless of the species involved or environmental conditions. The second model based on FIRM (classification tree method) estimated the potential distribution of alien plant species based on environmental factors. Although such models assume a quasi-equilibrium state of species distribution, they have been successful in predicting current and future species distribution in many systems (Chapter 2, Vayssieres et al., 2000; Rouget et al., 2001).

Rule-based versus statistical modelling

Although the overall threat pattern was similar using both approaches (Fig. 4 and 5), there were substantial differences in threat level predictions within habitat types (Fig. 3 and 6). Rule-based approaches, also called expert systems, have been used elsewhere to assess the extent of future threat (see Crist et al. 2000; Theobald et al., 2000). Statistical methods, such as logistic regression have also been applied to predict future threats (see Gunter et al., 2000 for predicting urbanisation). The classification tree used here can be considered as an extrapolation of the current patterns based on environmental correlates. The relatively good spatial agreement between both approaches (73%) suggests that future agriculture development and alien plant spread are likely to follow current distribution patterns. The rule-based approach was more appropriate to predict agriculture potential for crop types not yet developed wild-flowers and newly emerging indigenous crops that can be grown on soils unsuitable for conventional crops (Turpie and Heydenrych, in press). Such areas would have been missed by the statistical approach. Regarding future alien plant distribution, the rule-based approach probably better simulates the spread of existing stands, whereas the statistical method identifies sites where alien species are likely to spread if they were to be introduced. Thus, the latter approach gave higher estimates of future alien spread (Fig. 9). It should be however possible to combine rule-based and statistical models; while rule-based models can include processes such as rate of change, statistical models are appropriate for identifying constraints.

Choosing the most appropriate method will depend on the type of threat considered, the scale of the study, and data and knowledge availability. Static models based on environmental factors (such as the classification tree method used here) should perform better for modelling extensive habitat transformation. This is clearly the case for agriculture in this study. Agriculture development is also largely influenced by soil and climatic conditions. On the other hand, more dynamic threatening processes such as urbanisation can be accurately modelled by expert-systems (Crist et al., 2000) or mechanistic simulation models (Clarke et al., 1997). Since expert-systems or complex simulation models require detailed knowledge of the processes involved, which might not always be available for regional or broad-scale assessments, their use is mostly limited to well-investigated processes at a local scale. There is a growing literature on modelling species distribution using new computational methods (Guisan and Zimmermann, 2000; Peterson and Vieglais, in press). Many of these techniques are directly applicable to conservation planning, especially for predicting future threat distribution.

Type of threats and threatened taxa

Most of the studies which have explicitly integrated threats to biodiversity into conservation planning have focused on threatened taxa (Master, 1991; Rebelo, 1992, Beissinger et al., 1996; Dobson et al., 1997; Lombard et al. 1999). Surprisingly, relatively few studies have investigated quantitatively the factors directly responsible for species endangerment in relation to conservation (but see Flather et al., 1998; Wilcove et al. 1998). Both approaches described in this chapter enable the quantification of the extent of future threats for each biodiversity entity (BHU) considered. To be of real interest for conservation planning on the ground, threat assessment was developed here in a spatially-explicit manner, with knowledge of threat intensity for each planning unit (see Pressey et al., in press).

Although previous assessments in various parts of the world have focused on one type of threat (e.g. logging in New South Wales, Pressey et al., 1996; human population and development in the United States, Abbit et al., 2000), a multi-threat approach is recommended. Among the numerous factors leading to biodiversity reduction, habitat destruction and degradation is generally considered as the primary factor, followed by alien species (Wilson, 1992; Wilcove et al., 1998). I modelled separately future habitat transformation by urbanisation, agriculture and alien plant invasions. The relatively low level of overlap between these three threat categories (Fig. 10) suggests that future threat would have been under-estimated by considering one type of threat only. However, there is still no clear understanding on how to quantitatively combine threatening processes into a single value of threat intensity, as their impacts on biodiversity loss or habitat degradation vary (Flather et al.,1998; Pressey and Taffs, 2001).

Threats to biodiversity consist of two components: 1) the likelihood, and the extent, of habitat being degraded or lost, and 2) its impacts on species persistence or population viability (Pressey and Taffs, 2001). The relationships between those two aspects are quite complex and are likely to be species dependent. Except for global-scale assessments (see Beissinger et al., 1996), there have been almost no studies that use both components to define priority areas for conservation. Because information on species vulnerability to agriculture, urbanisation or alien plant invasion within the CFR is taxonomically biased and incomplete (Rebelo, 1992), this study explored the future extent of habitat degradation only. Analyses based on the geography of threatened species are likely to provide different spatial patterns of threat intensity due to the many different responses of species to environmental or anthropogenic stress (Sisk et al., 1994). Integrating vulnerability assessment into conservation planning based on future habitat degradation and impacts on biological entities is one promising way of ensuring the persistence of all levels of biodiversity.

References

Abbit, R.J.F., Scott, J.M., Wilcove, D.S., 2000. The geography of vulnerability: incorporating species geography and human development patterns into conservation planning. Biological Conservation 96, 169-175.

Beissinger, S.R., Steadman, S.C., Wohlgenant, T., Blate, G., Zack, S., 1996. Null models for assessing ecosystem conservation priorities: threatened birds as titers of threatened ecosystems in South America. Conservation Biology 10, 1343-1352.

Clarke, K.C., Hoppen, S., Gaydos, L., 1997. A self-modifying cellular automaton model of historical urbanization in the San Francisco Bay area. Environmental Planning B-Planning Design 24, 247-261.

Cowling, R.M., 1992. The ecology of Fynbos: nutrients, fire and diversity. Oxford University Press, Cape Town.

Cowling, R.M., Bond, W.J., 1991. How small reserves can be? An empirical approach in the Cape fynbos. Biological Conservation 58, 243-256.

Cowling, R.M., Heijnis, C.J., 2001. The identification of Broad Habitat Units as biodiversity entities for systematic conservation planning in the Cape Floristic Region. South African Journal of Botany 67, 15-38.

Cowling, R.M., Hilton-Taylor, C., 1994. Patterns of plant diversity and endemism in southern Africa: a overview. In: Huntley, B.J. (Ed.), Botanical diversity in southern Africa. National Botanical Institute, Pretoria, pp. 31-52.

Cowling, R.M., Pressey, R.L., Boshoff, A.F., Kerley, G.I.H., Lombard, A.T., Richardson, D.M., Rouget, M., in press. The identification of a system of conservation for terrestrial biodiversity. Biological Conservation.

Cowling, R.M., Pressey, R.L., Lombard, A.T., Heijnis, C.J., Richardson, D.M., Cole, N., 1999. Framework for a conservation plan for the Cape Floristic Region. Institute for Plant Conservation, Cape Town.

Crist, P.J., Kohley, T.W., Oakleaf, J., 2000. Assessing land-use impacts on biodiversity using an expert system tool. Landscape Ecology 15, 47-62.

De'ath, G., Fabricius, K.E., 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. Ecology 81, 3178-3192.

Dinerstein, E., Wikramanayake, E.D., 1993. Beyond "hotspots": how to prioritize investments to conserve biodiversity in the Indo-Pacific region. Conservation Biology 7, 53-65.

Dobson, A.P., Rodriguez, J.P., Roberts, W.M., Wilcove, D.S., 1997. Geographic distribution of endangered species in the United States. Science 275, 550-553.

Endangered Species Act, The (ESA), 1973. 16 U. S. C., Sections 1531-1543.

ERDAS Imagine, 1997. ERDAS Field Guide. Fourth Edition, Revised and Expanded. ERDAS, Inc. Atlanta, Georgia.

Fairbanks, D.H.K., Scholes, R.J., 1999. South African study on climate change: Vulnerability and adaptation assessment for plantation forestry. Report to National Research Facility (Sustainable Development Programme), Pretoria, South Africa.

Fairbanks, D.H.K., Thompson, M.W., Vink, D.E., Newby, T.S., van der Berg, H.M., Everard, D.A., 2000. The South African land-cover characteristics database: a synopsis of the landscape. South African Journal of Science 96, 69-85.

Fairbanks, D.H.K., Thompson, M.W., Vink, D.E., Newby, T.S., van der Berg, H.M., Everard, D.A., 2000. The South African land-cover characteristics database: a synopsis of the landscape. South African Journal of Science 96, 69-85.

Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessments of prediction errors in conservation presence/absence models. Environmental Conservation 24, 38-49.

Flather, C.H., Knowles, M.S., Kendall, I.A., 1998. Threatened and endangered species geography. BioScience 48, 365-376.

Franklin, J. F., 1993. Preserving Biodiversity - Species Ecosystems or Landscapes? Ecological Applications 3, 202-205.

Franklin, J., 1998. Predicting the distribution of shrub species in southern California from climate and terrain-derived variables. Journal of Vegetation Science 9, 733-748.

Goldblatt, P., Manning, J., 2000. Cape Plants: a conspectus of the Cape Flora of South Africa. Strelitzia 9. National Botanical Institute and Missouri Botanical Garden, Cape Town.

Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135, 147-186.

Gunter, J.T., Hodges, D.G., Swalm, C.M., Regens, J.L., 2000. Predicting the urbanisation of pine and mixed forest in Saint Tammany, Parish, Louisiana. Photogrammetric Engineering & Remote Sensing 66, 1469-1476.

Hawkins, D.M., 1995. Formal inference-based recursive modelling. Department of Applied Statistics, University of Minnesota, St Paul.

Heijnis, C., Lombard, A.T., Cowling, R.M, Desmet, P.G. 1999. Picking up pieces: a biosphere reserve for a fragmented landscape – The Coastal Lowlands of the Western Cape, South Africa. Biodiversity and Conservation 8: 471-496.

Higgins, S.I., Richardson, D.M., Cowling, R.M., 2001. Validation of a spatial simulation model of a spreading alien plant population. Journal of Applied Ecology, 38, 571-584.

Higgins, S.I., Richardson, D.M., Cowling, R.M., Trinder-Smith, T.H., 1999. Predicting the landscape scale distribution of alien plants and their threats to biodiversity. Conservation Biology 13, 303-313.

Kemper, J., Cowling, R.M., Richardson, D.M., 1999. Fragmentation of South African renosterveld shrublands: effects on plant community structure and conservation implications. Biological Conservation 90, 103-111.

Kemper, J., Cowling, R.M., Richardson, D.M., Forsyth, G.G., McKelly, D.H., 2000. Landscape fragmentation in south coast renosterveld, South Africa, in relation to rainfall and topography. Austral Ecology 25, 179-186.

Landis, J. D., 1994. The Californian urban future model: a new generation of metropolitan simulation models. Environmental Planning B: Planning Design 21, 399-420.

Le Maitre, D.C., van Wilgen, B.W., Chapman, R.A., McKelly, D.H., 1996. Invasive plants and water resources in the Western Cape Province, South Africa: modelling the consequences of a lack of management. Journal of Applied Ecology 33, 161-172.

Lloyd, J.W., van den Berg, E.C., van Wyk, E., 1999. CAPE Project The mapping of threats to biodiversity in the Cape Floristic Region with the aid of remote sensing and geographic information systems. Report GW/A1999/54. Agricultural Research Council, Institute for Soil, Climate and Water, Pretoria, South Africa.

Lombard, A.T., Cowling, R.M., Pressey, R.L., Mustart, P.J., 1997. Reserve selection in a species-rich and fragmented landscape on the Agulhas Plain, South Africa. Conservation Biology 11, 1101-1116.

Lombard, A.T., Hilton-Taylor, C., Rebelo, A.G., Pressey, R.L., Cowling, R.M., 1999. Reserve selection in the succulent Karoo, South Africa: coping with high compositional turnover. Plant Ecology 142, 35-55.

Macdonald, I.A.W., Jarman, M.L., Beeston, P., 1985. Management of invasive alien plants in the Fynbos biome. Report no. 111, South African National Scientific Programmes, Pretoria.

Macdonald, I.A.W., Richardson, D.M., 1986. Alien species in terrestrial ecosystems of the fynbos biome. In: Macdonald, I.A.W., Kruger, F.J., Ferrar, A.A. (Eds.), The ecology and management of biological invasions in southern Africa. Oxford University Press, Cape Town, pp. 77-91.

Margules, C.R., Pressey, R.L., 2000. Systematic conservation planning. Nature 405, 243-253.

Master, L.L., 1991. Assessing threats and setting priorities for conservation. Conservation Biology 5, 559-563.

Maze, K.E., Rebelo, A.G., 1999. Core flora conservation areas on the Cape Flats. Botanical Society of South Africa, Newlands.

Menon, S., Pontius, R.G., Rose, J., Khan, M.L., Bawa, K.S., 2001. Identifying conservation-priority areas in the tropics: a land-use change modeling approach. Conservation Biology 15, 501-512.

Mittermeir, R.A., Myers, N., Thomsen, J.B., 1998. Biodiversity hotspots and major tropical wilderness areas: approaches to setting conservation priorities. Conservation Biology 12, 516-520.

Moody, A., Woodcock, C.E., 1995. The influence of scale and the spatial characteristics of landscapes on land-cover mapping using remote sensing. Landscape Ecology 10, 363-379.

Myers, N., 1988. Threatened biotas: "Hotspots" in tropical forests. The Environmentalist 10, 243-255.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots conservation priorities. Nature 403, 853-858.

Noss, R.F., 1987. From plant communities to landscape in conservation inventories: A look at The Nature Conservancy (USA). Biological Conservation 41, 11-37.

Noss, R.F., O'Connell, M.A., Murphy, D.D., 1997. The science of conservation planning: habitat conservation under the Endangered Species Act. Word Wildlife Fund and Island Press, Washington, D C.

Peterson, A.T., Vieglais, D.A., in press. Predicting species invasions using ecological niche modelling. BioScience.

Pressey, R.L., 1997. Priority conservation areas: towards an operational definition for regional assessments. In: Pigram, J.J., Sundell, R.C. (Eds.), National parks and protected areas: Selection, delimitation and management. Centre for Water Research Policy, University of New England, Armidale, pp. 337-357.

Pressey, R.L., Cowling, R.M., 2001. Reserve selection algorithms and the real world. Conservation Biology 15, 275-277.

Pressey, R.L., Cowling, R.M., Rouget, M., in press. Formulation of conservation targets for biodiversity pattern and process in the Cape Floristic Region. Biological Conservation .

Pressey, R.L., Ferrier, S., Hager, T.C., Woods, C.A., Tully, S.L., Weiman, K.M., 1996. How well protected are the forests of north-eastern New South Wales? - Analyses of forest environments in relation to formal protection measures, land tenure, and vulnerability to clearing. Forest Ecology and Management 85, 311-333.

Pressey, R.L., Taffs, K.H., 2001. Scheduling conservation action in production landscapes: priority areas in western New South Wales defined by irreplaceability and vulnerability to vegetation loss. Biological Conservation 100, 355-376.

Rebelo, A.G., 1991. Protea Atlas Manual. Instruction booklet to the Protea Atlas Project. Endangered Plant Laboratory, National Botanical Institute, Kirstenbosch & Percy FitzPatrick Institute of African Ornithology, University of Cape Town.

Rebelo, A.G., 1992. Red data book species in the Cape Floristic Region: threats, priorities and target species. Transactions of the Royal Society of South Africa 48, 55-86.

Rebelo, A.G., Siegfried, W.R., 1990. Protection of fynbos vegetation: ideal and real-world options. Biological Conservation 54, 17-34.

Rebelo, A.G., Siegfried, W.R., 1992. Where should nature reserves be located in the Cape Floristic Region, South Africa? Models for the spatial configuration of a reserve network aimed at maximizing the protection of floral diversity. Conservation Biology 6, 243-252.

Reichard, S.H., Hamilton, C.W., 1997. Predicting invasions of woody plants introduced in North America. Conservation Biology 11, 193-203.

Richardson, D.M., Bond, W.J., Dean, W.R.J., Higgins, S.I., Midgley, G.F., Milton, S.J., Powrie, L.W., Rutherford, M.C., Samways, M., Schulze, R.E., 2000. Invasive aliens organisms and global change: A South African perspective. In: Mooney, H.A., Hobbs, R.J. (Eds.), The impact of global change on alien species. Island Press, Washington, pp. 303-349.

Richardson, D.M., Macdonald, I.A.W., Hoffmann, J.H., Henderson, L., 1997. Alien plant invasions. In: Cowling, R.M., Richardson, D.M., Pierce, S.M. (Eds.), Vegetation of southern Africa. Cambridge University Press, Cambridge, pp. 535-570.

Richardson, D.M., Macdonald, I.A.W., Holmes, P.M., Cowling, R.M., 1992. Plant and animal invasions. In: Cowling, R.M. (ed), The Ecology of Fynbos: Nutrients, Fire and Diversity, Oxford University Press, Cape Town, pp. 271-308.

Richardson, D.M., van Wilgen, B.W., Higgins, S.I., Trinder-Smith, T.H., Cowling, R.M., McKell, D.H., 1996. Current and future threats to plant biodiversity on the Cape Peninsula, South Africa. Biodiversity and Conservation 5, 607-647.

Riebsame, W.E., Meyer, W.B., Turner II, B.L., 1994. Modeling land use and cover as part of global environmental change. Climatic Change 28, 45-64.

Rojas, M. 1992. The species problem and conservation: what are we protecting? Conservation Biology 6, 170-178.

Rouget, M., in press. Measuring conservation value at fine and broad scale: the importance of diverse and fragmented habitats. Biological Conservation.

Rouget, M., Richardson, D.M., Cowling, R.M., in press. The current configuration of protected areas in the Cape Floristic Region, South Africa - Environmental determinants, representativeness, and opportunities. Biological Conservation.

Rouget, M., Richardson, D.M., Milton, S.J., Polakow, D., 2001. Predicting invasion dynamics of four alien *Pinus* species in a highly fragmented semi-arid shrubland in South Africa. Plant Ecology 152, 79-92.

Serneels, S., Lambin, E.F., 2001. Proximate causes of land-use change in Narok District, Kenya: a spatial statistical model. Agriculture, Ecosystems & Environment 85, 65-81.

Shoshany, M., 2000. Satellite remote sensing of natural Maditerranean vegetation: a review within an ecological context. Progress in Physical Geography 24, 153-178.

Sisk, T.D., Launer, A.E., Switky, K.R., Ehrlich, P.R., 1994. Identifying extinction threats: global analyses of the distribution of biodiversity and the expansion of the human entreprise. BioScience 44, 592-604.

Soule, M.E., 1991. Conservation: tactics for a constant crisis. Science 253, 744-750.

Stoms, D.M., 2000. GAP management status and regional indicators of threats to biodiversity. Landscape Ecology 15, 21-33.

Swenson, J.J., Franklin, J., 2000. The effects of future urban development on habitat fragmentation in the Santa Monica Mountains. Landscape Ecology 15, 713-730.

Theobald, D.M., Hobbs, N.T., Bearly, T., Zack, J.A., Shenk, T., Riebsame, W.E., 2000. Incorporating biological information in local land-use decision making for conservation planning. Landscape Ecology 15, 35-45.

Tou, J.T., Gonzales, R.C., 1974. Pattern Recognition Principles. Reading, Massachusetts: Addison-Wesley Publishing Company.

Turpie, J., Heydenrych, B.J., in press. The economic value of natural resources in the Cape Floristic Region: a preliminary analysis. Biological Conservation .

Vayssieres, M.P., Plant, R.E., Allen-Diaz, B.H., 2000. Classification trees: an alternative non-parametric approach for predicting species distributions. Journal of Vegetation Science 11, 679-694.

Veldkamp, A., Lambin, E.F., 2001. Predicting land-use change. Agriculture, Ecosystems & Environment 85, 1-6.

Versfeld, D.B., Le Maitre, D.C., Chapman, R.A., 1998. Alien invading plants and water resources in South Africa: A preliminary assessment. WRC, Pretoria.

Wear, D.N., Turner, M.G., Naiman, R.J., 1998. Land cover along an urban-rural gradient: implications for water quality. Ecological Applications 8, 619-630.

White, D., Minotti, P.G., Barczack, M.J., Sifneos, J.C., Freemark, K.E., Santelmann, M.V., Steinitz, C.F., Kiester, A.R., Preston, E.M., 1997. Assessing risks to biodiversity from future landscape change. Conservation Biology 11, 349-360.

Wilcove, D.S., Rothstein, D., Dubow, D., Phillips, A., Losos, E., 1998. Quantifying threats to imperiled species in the United States. BioScience 48, 607-615.

Wilson, E.O., 1992. The Diversity of Life. Belknap Press, Cambridge.

Wood, J., Low, A.B., Donaldson, J.S., Rebelo, A.G. 1994. Threats to plant species diversity through urbanization and habitat transformation in the Cape Metropolitan Area, South Africa. Strelitzia 1:259-274.

Woodward, F.I., 1987. Climate and plant distribution. Cambridge University Press, Cambridge.

Appendix 1. The area covered by urban areas (urban.), cultivated land including forestry (culti.) and different densities of invasive alien trees and shrubs in the Cape Floristic Region, South Africa, in 16 primary (in bold) and 87 secondary Broad Habitat Units (Cowling & Heijnis, 2001) (see text for details of criteria used in classifying threats). Total transformed area: (1) = summed % for urban areas and cultivated land; (2) = (1) plus the % affected by dense stands of invasive alien trees and shrubs.

BROAD HABITAT UNITS	**Total area km2**	**Urban** %	**Culti** %	**Alien trees and shrub** Low %	Medium %	Dense %	**Transformed** Total (1)	Total (2)
Dune Pioneer (DP)								
1. South West	119.65	7.36	8.90	72.85	4.55	6.33	16.26	22.59
2. South	57.98	0.00	0.09	82.54	3.71	13.66	0.09	13.75
3. South East	27.81	11.74	0.05	59.10	0.87	28.25	11.79	40.04
Total	**205.44**	5.88	5.22	73.72	3.82	11.35	11.09	22.46
Fynbos / Thicket Mosaic (FT)								
4. Langebaan	1603.40	4.70	41.66	52.89	0.57	0.19	46.35	46.54
5. Cape Flats	267.29	60.66	10.92	23.76	0.14	4.52	71.58	76.10
6. Agulhas	492.33	6.44	2.57	49.31	30.16	11.51	9.01	20.52
7. Stilbaai	230.09	6.23	6.43	76.33	5.09	5.91	12.66	18.58
8. Goukamma	142.24	5.22	8.93	61.64	6.61	17.61	14.14	31.75
9. St Francis	259.24	7.70	2.37	31.29	4.95	53.69	10.07	63.76
Total	**2994.59**	10.38	24.83	50.05	6.41	8.34	35.21	43.54
Sand Plain Fynbos (SPF)								
10. Leipoldtville	2110.85	0.10	43.48	55.77	0.23	0.42	43.58	44.00
11. Hopefield	2976.29	0.84	45.19	51.70	1.69	0.58	46.03	46.61
12. Blackheath	796.00	54.89	24.43	19.73	0.31	0.64	79.32	79.96
13. Springfield	440.41	0.05	10.69	69.81	9.30	10.14	10.74	20.88
14. Albertinia	447.54	0.83	46.64	51.86	0.11	0.56	47.47	48.03
Total	**6771.10**	6.91	40.07	50.40	1.46	1.16	46.98	48.14
Limestone Fynbos (LF)								
15. Hagelkraal	440.04	0.17	34.18	44.74	14.68	6.24	34.35	40.58
16. De Hoop	775.88	0.00	17.36	71.05	5.81	5.78	17.36	23.14
17. Canca	852.32	0.20	2.29	95.72	0.37	1.42	2.49	3.91
Total	**2068.24**	0.12	14.73	75.62	5.45	4.08	14.85	18.93
Grassy Fynbos (GF)								
18. Genadendal	488.98	1.30	37.57	55.91	1.82	3.41	38.87	42.28
19. Suurbraak	741.91	1.03	57.53	38.12	0.87	2.45	58.56	61.01
20. Keurbooms	140.79	6.59	9.09	66.68	16.26	1.38	15.68	17.06
21. Humansdorp	1987.25	0.50	14.32	78.38	0.77	6.02	14.82	20.85
22. Algoa	296.75	26.31	14.06	57.31	0.46	1.85	40.37	42.22
Total	**3655.68**	3.04	25.98	65.05	1.50	4.43	29.02	33.45
Fynbos/Renosterveld Mosaic (FR)								
24. Perdeberg	44.49	1.45	6.66	87.71	1.30	2.88	8.11	10.99
25. Elgin	136.10	2.10	85.85	11.76	0.23	0.05	87.95	88.01
26. Breede	378.18	1.81	56.58	35.26	1.87	4.49	58.38	62.87
27. Elim	594.07	0.08	55.05	37.56	2.28	5.03	55.13	60.16
28. Blanco	749.77	0.97	35.53	63.00	0.02	0.48	36.50	36.97
29. Langkloof	783.45	1.09	29.86	67.17	0.27	1.61	30.95	32.56
30. Kromme	845.71	1.20	31.24	61.05	0.48	6.04	32.43	38.48
Total	**3531.76**	1.04	40.36	54.55	0.79	3.27	41.40	44.67
Coast Renosterveld (CR)								
31. Swartland	4113.01	0.72	88.15	10.60	0.21	0.33	88.87	89.20
32. Boland	2416.92	4.20	70.90	22.54	0.65	1.71	75.10	76.81
33. Overberg	4296.89	0.34	87.86	10.32	0.53	0.95	88.20	89.15
34. Riversdale	3163.01	0.87	68.23	30.47	0.15	0.27	69.10	69.37
Total	**13989.8**	1.23	80.58	17.07	0.37	0.75	81.81	82.56

BROAD HABITAT UNITS	Total area km2	Urban %	Culti %	Alien trees and shrub Low %	Medium %	Dense %	Transformed Total (1)	Total (2)
Inland Renosterveld								
35. Nieuwoudtville	322.04	0.60	18.26	81.15	0.00	0.00	18.85	18.85
36. Kouebokkeveld	985.45	0.00	9.01	89.92	0.34	0.73	9.01	9.73
37. Waveren-Bokkeveld	802.72	1.67	48.49	45.92	1.07	2.86	50.15	53.01
38. Ashton	1267.40	0.93	35.01	62.72	0.42	0.92	35.94	36.85
39. Matjies	1141.35	0.00	0.54	99.37	0.07	0.02	0.54	0.56
41. Montagu	1280.45	0.36	4.62	94.74	0.06	0.22	4.97	5.20
42. Cannaland	494.70	0.00	16.18	83.69	0.10	0.03	16.18	16.21
43. Kango	1687.56	0.00	5.01	94.82	0.01	0.16	5.01	5.17
44. Uniondale	1203.06	0.03	26.34	73.55	0.00	0.08	26.38	26.45
Total	**9184.73**	0.35	16.63	82.28	0.21	0.53	**16.98**	**17.51**
Mountain Fynbos Complex (MC)								
45. Bokkeveld	983.56	0.00	5.99	93.95	0.02	0.04	5.99	6.03
46. Gifberg	2002.85	0.00	21.58	78.09	0.15	0.18	21.58	21.76
47. Cederberg	2278.20	0.00	6.22	91.46	0.78	1.54	6.22	7.76
48. Olifants River	1460.73	0.01	21.13	76.39	0.94	1.52	21.14	22.67
49. Swartruggens	1582.01	0.00	7.47	91.29	0.47	0.77	7.47	8.24
50. Piketberg	515.82	0.02	15.65	81.64	1.45	1.24	15.67	16.91
51. Groot Winterhoek	865.65	0.10	3.10	96.22	0.13	0.45	3.20	3.66
52. Matroosberg	714.19	0.04	0.51	99.16	0.15	0.14	0.55	0.69
53. Hawequas	1217.70	0.00	6.21	90.43	2.37	0.99	6.21	7.20
54. Franschhoek	551.02	0.45	14.22	80.61	1.53	3.19	14.66	17.86
55. Cape Peninsula	359.36	18.24	4.55	71.29	2.40	3.51	22.80	26.31
56. Kogelberg	728.52	3.03	15.11	79.38	1.16	1.32	18.14	19.46
57. Klein River	368.22	0.03	12.07	73.44	4.79	9.67	12.11	21.77
58. Caledon Swartberg	98.27	0.40	11.13	67.53	12.06	8.89	11.53	20.42
59. Riviersonderend	820.06	0.00	3.49	92.64	3.08	0.78	3.50	4.28
60. Koo Langeberg	736.67	0.00	1.56	98.25	0.07	0.11	1.56	1.68
61. Waboomsberg	279.97	0.00	20.85	79.09	0.07	0.00	20.85	20.85
62. Witteberg	450.22	0.00	0.27	99.50	0.22	0.01	0.27	0.28
63. Bredasdorp	333.71	0.00	10.35	75.14	3.44	11.06	10.36	21.42
64. Southern Langeberg	1505.97	0.00	6.97	91.52	0.35	1.16	6.97	8.12
65. Potberg	119.37	0.22	3.06	90.63	4.32	1.77	3.28	5.05
66. Klein Swartberg	813.94	0.00	0.12	99.74	0.00	0.14	0.12	0.26
67. Rooiberg	777.87	0.00	0.15	99.82	0.02	0.01	0.15	0.16
68. Groot Swartberg	1155.72	0.00	0.14	99.85	0.00	0.02	0.14	0.15
69. Outeniqua	1689.29	0.01	11.95	78.77	4.94	4.33	11.96	16.29
70. Kamanassie	549.75	0.00	2.05	97.94	0.00	0.01	2.05	2.06
71. Tsitsikamma	1619.41	0.04	3.44	93.61	1.84	1.07	3.48	4.56
72. Kouga	1749.12	0.00	2.39	97.07	0.06	0.48	2.39	2.87
73. Baviaanskloof	1683.40	0.00	0.58	98.91	0.07	0.44	0.58	1.02
74. Cockscomb	1464.76	0.00	9.37	89.54	0.13	0.97	9.37	10.33
Total	**29475.3**	0.32	7.50	89.91	1.02	1.24	**7.82**	**9.06**
Vygieveld (VY)								
76. Klawer	878.20	0.66	37.26	61.54	0.03	0.51	37.91	38.42
78. Tanqua	33.46	0.00	0.00	100.00	0.00	0.00	0.00	0.00
81. Touws	1419.08	0.15	6.83	92.84	0.15	0.04	6.97	7.01
Total	**2330.75**	0.34	18.19	81.15	0.10	0.21	**18.53**	**18.74**
Strandveld (SV)								
83. Lamberts	962.76	0.46	22.03	77.40	0.09	0.02	22.49	22.50
Total	**962.76**	0.46	22.03	77.40	0.09	0.02	**22.49**	**22.50**

BROAD HABITAT UNITS	Total area km2	Urban %	Culti %	Alien trees and shrub Low %	Medium %	Dense %	Transformed Total (1)	Total (2)
Broken Veld (BV)								
86. Witrantjies	207.90	0.00	9.76	90.02	0.08	0.15	9.76	9.90
87. Robertson	1276.59	1.52	33.83	63.03	0.53	1.09	35.35	36.44
88. Little Karoo	4456.55	0.01	1.21	98.63	0.03	0.12	1.22	1.34
89. Oudtshoorn	1351.98	1.24	12.10	86.30	0.00	0.36	13.34	13.70
Total	**7293.01**	0.50	9.18	89.87	0.12	0.33	9.69	10.02
Mesic Succulent Thicket (MST))								
93. Gouritz	182.80	0.00	28.98	70.68	0.04	0.30	28.98	29.28
94. Gamtoos	322.23	0.49	27.18	68.73	0.27	3.33	27.67	31.00
96. Aloes	26.11	24.11	9.61	38.00	1.21	27.07	33.72	60.79
Total	**531.14**	1.49	26.93	67.89	0.24	3.45	28.42	31.87
Xeric Succulent Thicket (XST))								
97. Spekboom	2443.05	0.18	3.25	96.22	0.05	0.29	3.43	3.73
Total	**2443.05**	0.18	3.25	96.22	0.05	0.29	3.43	3.73
Afromontane Forest								
100. Knysna	2078.73	2.53	35.46	58.53	0.36	3.12	37.99	41.11
101. Swellendam	18.09	0.00	17.69	74.58	1.25	6.48	17.69	24.17
Total	**2096.82**	2.51	35.31	58.66	0.37	3.15	37.82	40.97
Indian Ocean Forest								
102. Alexandria	357.38	3.92	11.44	71.74	1.56	11.35	15.36	26.71
Total	**357.38**	3.92	11.44	71.74	1.56	11.35	15.36	26.71
Grand Total	**87891.6**	**1.56**	**25.86**	**69.14**	**1.02**	1.59	27.41	29.00

Commercially-important trees as invasive aliens – towards spatially explicit risk assessment at a national scale

Abstract

Alien species that are desirable and commercially important in parts of the landscape, but damaging invaders in other parts, present a special challenge for managers, planners and policy-makers. Objective methods are needed for identifying areas where control measures should be focussed. I analysed the distribution of forestry plantations and invasive (self-sown) stands of *Acacia mearnsii* and *Pinus* spp. in South Africa; these two taxa account for 60 % of the area under commercial plantations and 54 % of the area invaded by alien trees and shrubs. The distribution of commercial forestry plantations and invasive stands of these taxa were mapped and the data was digitized and stored on GIS (Arc/Info) layers. A series of environmental parameters were derived from GIS layers of climate, topography, geology, land use, and natural vegetation. The current distribution of the two taxa was subdivided into three groups according to the degree of invasion, the forestry history and the precision of the data collection. I used regression-tree analysis to relate, for each taxon, the distribution of invasive stands with environmental variables, and to derive habitat suitability maps for future invasion.

At a sub-continental scale, the current distribution of invasive stands was influenced more by climatic factors than by the distribution of commercial plantations for both taxa. Using environmental factors identified by the regression tree, I found that 6.6 and 9.8% of natural habitats currently untransformed by urbanisation or agriculture are suitable for invasion by *Pinus* spp. and *A. mearnsii* respectively. I then derived guidelines for policy on alien plant management based on vegetation type, degree of transformation, extent of invasion, and the risk of future alien spread. These factors were used to identify demarcated areas where these alien species can be grown with little risk of invasions, and areas where special measures are needed to manage spread from plantations.

Introduction

Biological invasions have major economic and ecological impacts. The formulation of effective, long-term strategies for managing invasive alien organisms requires perspectives from different spatial and temporal scales. Detailed studies on the ecology of invasive species are essential for planning control programs. For example, landscape-scale assessments of alien spread can show when and where mechanical control could be effectively used (Higgins et al., 2000). Regional or biome-scale assessments have shown the relative susceptibility of certain larger units within a region (e.g. climatic zones) to invasion (Reichard and Hamilton, 1997). Insights from all these scales are needed to understand the ecology of invasions, but such knowledge has limited value for policy makers. At a national scale, policy-makers face two main types of problems: 1) to implement legislation and other measures to keep potential invasive alien organisms out of the region; and 2) to manage those alien species already present in the region to curtail their spread and reduce actual and potential impacts. Screening systems for predicting invasive plants have been developed for some regions to address the first problem (e.g. Tucker and Richardson, 1995; Pheloung et al., 1999; Daehler and Carino, 2000). The second problem demands (among other things) a more spatially-explicit approach to identify risk areas and allocate limited resources where they are most needed.

The task of allocating priorities and focussing control efforts for invasive species is especially challenging when the target species are commercially important, and therefore desirable, in parts of the landscape. Commercial forestry trees that are also invaders are a good example of this problem (Richardson, 1998). South Africa probably faces more severe problems from invasive forestry trees than any other country (Richardson, 1998). The biology of invasive alien trees has been fairly well-studied in South Africa (for reviews, see Richardson et al., 1992; Richardson et al., 1997, Richardson and Higgins, 1998), and there is a reasonable understanding of the dynamics of invasion for many of the most widespread invasive species (e.g. seed biology, dispersal dynamics, the role of fire and other forms of disturbance in initiating and sustaining invasions). Such information is useful for management at the scale of landscapes (e.g. for tree invasion in fynbos, van Wilgen et al., 1992; Higgins et al., 2000, Higgins et al., 2001), but is not particularly helpful for planning long-term strategies at regional and sub-continental scales.

This chapter addresses the issue of what information is required by policy makers to implement appropriate national strategies for dealing with invasive alien plant problems. Invasions associated with plantation forestry activities in South Africa provide an informative case study. This study was prompted by the recent promulgation of legislation stipulating that the forestry industry should manage invasive alien plants to minimise their negative impacts on the environment. In terms of this legislation, certain species (including *Pinus* spp. and *Acacia mearnsii*) are categorised as invasive, but their commercial value is taken into account. Such species can only be grown in demarcated areas, where a permit is required; the species will be considered weeds outside these areas and landowners will be obliged to control such species on their property. Landowners with permits to grow invasive species will also be required to take reasonable steps to prevent them from spreading onto adjacent land. This legislation will place a major onus on landowners to prevent the spread of invasive species. But to what extent are invasions of species that are also grown in commercial plantations driven by the current plantations? And to what extent should commercial forestry companies be held responsible for managing invasions?

Such legislation represents a major step in implementing strategies for managing invasive alien plant species. However, the spatial dimensions of demarcated areas where alien species could be grown have yet to be precisely defined, and there is much uncertainty on how this could be done. Criteria are lacking for the objective classification of areas with regard to their susceptibility to invasion, and consequently the identification of areas where special measures are needed to manage invasions. Such predictive understanding is required at the scale of management decisions and policy-making -at a national scale in this case.

The aim of this study was thus to analyse the current and likely future patterns of alien plant invasion at a sub-continental scale to provide inputs to the development and implementation of the policy described above. I concentrated on two commercially-important tree taxa: *Acacia mearnsii* and *Pinus* spp. The study has three parts: 1) an assessment of the determinants of current and future distribution of invasive populations in South Africa; 2) an assessment of the importance of the current configuration of commercial forestry plantations in determining the distribution of invasive stands; and 3) the provision of guidelines for managing commercial plantations and invasive stands to minimise the negative impacts due to the invasiveness of these taxa.

Methods

Distribution of invasive stands and plantations

Data on distribution of invasive stands of *Acacia mearnsii, Eucalyptus* spp. and *Pinus* spp. were gathered in 1996 as part of a national assessment of the extent of the invasive alien plants that affects the water resources of South Africa (Versfeld et al., 1998). The extent of self-sown stands of these taxa was mapped using expert knowledge of local landowners and managers within each province. This was supplemented by information from existing databases. Alien-invaded areas were mapped as polygons with species and percentage cover data (7 categories, from rare to dense, see Versfeld et al., 1998). All data were captured in a Geographic Information System (Arc/Info). Versfeld et al. (1998) provide a complete description of the mapping approach. The quality of the data gathered was variable, depending on the level of information available in each province. To limit the risk of overestimating the extent of invasion, a conservative approach was taken by restricting the study to

Table 1. Potential predictors used in the analysis of determinants of distribution. For each variable, its importance presented (i.e. number of times the variable was used in theanalysis). Bold numbers relate to primary factors in the first analysis. *: used once, * *: used less than five times, * * *: used more than 5 times.

Variables	**Code**	**Type**	**Importance**
Biome	BIOME	Categorical (7)	* *
Vegetation	VEG	Categorical (16)	*
Geology	GEOL	Categorical (16)	* *
Land cover	LANDCOV	Categorical (12)	* *
Mean annual precipitation	MAP	Continuous	
Mean annual temperature	MAT	Continuous	* *
Minimum mean temperature	MINTEMP	Continuous	*
Mean temperature (hottest month)	MTHOT	Continuous	* *
Mean temperature (coldest month)	MTCOLD	Continuous	* *
Growth days	GDAYS	Continuous	* * *
Growth temperature	GTEMP	Continuous	
Mean number of days of heavy frost	FROST	Continuous	
Mean Minimum Soil-water stress (% stress days)	SWS-MIN	Continuous	*
Mean Maximum Soil-water stress (% stress days)	SWS-MAX	Continuous	* * *
Distance to the nearest plantation (km)	DISTPLANT	Continuous	

areas mapped as invaded at 5 %cover or higher. Preliminary maps using this cut-off closely matched data from a wider range of other sources and my own field experience throughout South Africa. The original polygons (captured at the scale of 1:250 000) were converted to a grid with a cell size of one decimal minute. A cell was considered to be invaded if alien plants occured in more than 10% of the cell. I then reclassified the invaded areas into two percentage cover classes: scattered (5-20%), and dense (> 20 %).

The data for *Eucalyptus* species was problematic for several reasons, e.g. large areas in the northern parts of the region mapped as invaded at low density where no invasions occur. Once invasive stands of *Eucalyptus* spp. with < 5% cover were removed, the *Eucalyptus* data set was too small for modelling purposes. *Eucalyptus* spp. are much less invasive than *Acacia mearnsii* and *Pinus* spp. So the ommision of data for this taxon did not compromise the aims of my study. Data for *A. mearnsii* and *Pinus* spp. were much more accurate, and I focussed on these taxa for modelling their future distribution. I did, however, include the extent of invasive stands of *Eucalyptus* spp. in the biplots (see below). Many species of *Pinus* have been planted in South Africa, but only five species (*P. elliottii, P. patula, P. pinaster, P. radiata,* and *P. taeda*) are currently widely grown in commercial plantations (Le Maitre, 1998, p. 423). Clearly, different species of *Pinus* have different responses to environmental conditions and display different degrees of invasiveness in different habitats (Richardson and Higgins, 1998). However, available maps of plantations and invasion at a national scale do not distinguish adequately between species of *Pinus.* I was thus forced to model the determinants of distribution for several species combined. Despite the differences in the ecology of the species, and the different disturbance regimes and other environmental factors in the vegetation

Table 2. Vegetation types from Low and Rebelo (1996). It was reclassified into 16 groups based on similar climatic and geologic attributes for the FIRM analysis. Habitats entirely modified by humans (cultivated and urban areas, water bodies, and mines) were excluded.

Code	Vegetation type	Group	Area (km^2)	% transformed	% protected
1	Coastal Forest	Forest	656.03	3.96	9.51
2	Afromontane Forest	Forest	4499.73	10.60	17.64
3	Sand Forest	Forest	199.41	17.39	44.62
4	Dune Thicket	Thicket	3661.63	31.49	14.49
5	Valley Thicket	Thicket	22232.77	12.08	2.14
6	Xeric Succulent Thicket	Thicket	8594.86	2.42	8.01
7	Mesic Succulent Thicket	Thicket	1991.21	13.35	5.33
8	Spekboom Succulent Thicket	Thicket	5170.21	1.68	1.76
9	Mopane Shrubveld	Mopane Shrubveld	2387.14	0.00	99.99
10	Mopane Bushveld	Mopane Shrubveld	19273.41	6.79	38.29
11	Soutpansberg Arid Mountain Bushveld	Mountain Bushveld	4358.12	4.84	12.59
12	Waterberg Moist Mountain Bushveld	Mountain Bushveld	11418.39	8.25	8.55
13	Lebombo Arid Mountain Bushveld	Sweet Bushveld	4176.05	8.65	37.96
14	Clay Thorn Bushveld	Thorn Bushveld	15198.51	33.33	0.93
15	Subarid Thorn Bushveld	Thorn Bushveld	7707.63	7.72	0.22
16	Eastern Thorn Bushveld	Thorn Bushveld	9398.28	13.13	0.45
17	Sweet Bushveld	Sweet Bushveld	15782.29	12.58	2.34
18	Mixed Bushveld	Sweet Bushveld	59681.39	15.44	3.05
19	Mixed Lowveld Bushveld	Sweet Bushveld	16328.5	18.99	28.25
20	Sweet Lowveld Bushveld	Sweet Bushveld	5407.19	15.13	67.26
21	Sour Lowveld Bushveld	Lowveld Bushveld	18305.26	20.22	9.65
22	Subhumid Lowveld Bushveld	Lowveld Bushveld	1306.28	6.64	21.49
23	Coastal Bushveld/Grassland	Coastal Bushveld	11678.49	39.64	14.03
24	Coast-Hinterland Bushveld	Coastal Bushveld	9886.69	25.93	3.56
25	Natal Central Bushveld	Natal Bushveld	16334.28	14.76	1.56
26	Natal Lowveld Bushveld	Natal Bushveld	9661.27	15.70	17.81
27	Thorny Kalahari Dune Bushveld	Kalahari Bushveld	2129.93	2.58	99.76
28	Shrubby Kalahari Dune Bushveld	Kalahari Bushveld	35312.91	0.88	19.45
29	Karroid Kalahari Bushveld	Kalahari Bushveld	17686.8	1.93	0.13
30	Kalahari Plains Thorn Bushveld	Kalahari Bushveld	47976.89	7.66	0.47
31	Kalahari Mountain Bushveld	Kalahari Bushveld	12493.47	0.12	0.03
32	Kimberley Thorn Bushveld	Kalahari Bushveld	25877.06	20.29	3.12
33	Kalahari Plateau Bushveld	Kalahari Bushveld	22267.45	4.01	0.00
34	Rocky Highveld Grassland	Highveld Grassland	22617.14	31.23	1.38
35	Moist Clay Highveld Grassland	Highveld Grassland	9693.06	27.55	0.00
36	Dry Clay Highveld Grassland	Highveld Grassland	2051.9	65.77	0.00
37	Dry Sandy Highveld Grassland	Highveld Grassland	54381.13	35.45	0.28
38	Moist Sandy Highveld Grassland	Highveld Grassland	14588.72	26.53	0.67
39	Moist Cool Highveld Grassland	Highveld Grassland	46635.93	37.25	0.29
40	Moist Cold Highveld Grassland	Highveld Grassland	21877.3	41.78	0.63
41	Wet Cold Highveld Grassland	Highveld Grassland	9146.85	7.55	6.72
42	Moist Upland Grassland	Mountain Grassland	43532.07	16.01	2.52
43	North-eastern Mountain Grassland	Mountain Grassland	39809.75	10.21	7.42
44	South-eastern Mountain Grassland	Mountain Grassland	22463.97	0.73	0.33
45	Afro Mountain Grassland	Mountain Grassland	15409.48	10.71	0.00

Table 2 (ctd.)

Code	Vegetation type	Group	Area (km^2)	% transformed	% protected
46	Alti Mountain Grassland	Mountain Grassland	11586.01	3.32	12.53
47	Short Mistbelt Grassland	Mountain Grassland	4693.36	25.62	2.37
48	Coastal Grassland	Coastal Bushveld	2898.67	10.07	1.13
49	Bushmanland	Nama Karoo	81211.89	1.76	0.03
50	Upper Nama Karoo	Nama Karoo	39275.1	0.46	0.03
51	Orange River Nama Karoo	Nama Karoo	51918.85	1.66	1.47
52	Eastern Mixed Nama Karoo	Nama Karoo	76402.93	3.68	1.08
53	Great Nama Karoo	Nama Karoo	18305.26	0.13	0.17
54	Central Lower Karoo	Nama Karoo	24747.07	0.56	0.04
55	Strandveld Succulent Karoo	Succulent Karoo	3757	7.54	0.40
56	Upland Succulent Karoo	Succulent Karoo	37911.02	1.44	4.39
57	Lowland Succulent Karoo	Succulent Karoo	30532.85	2.81	1.30
58	Little Succulent Karoo	Succulent Karoo	9184.42	6.73	2.34
59	North-western Mountain Renosterveld	Renosterveld	1592.39	4.72	0.00
60	Escarpment Mountain Renosterveld	Renosterveld	5875.37	0.64	0.13
61	Central Mountain Renosterveld	Renosterveld	7678.73	17.01	3.63
62	West Coast Renosterveld	Renosterveld	6178.82	90.83	1.76
63	South and South-west Coast Renosterveld	Renosterveld	14322.84	59.87	1.42
64	Mountain Fynbos	Fynbos	27694.87	7.11	26.14
65	Grassy Fynbos	Fynbos	6291.53	9.05	16.14
66	Laterite Fynbos	Fynbos	630.02	36.70	0.47
67	Limestone Fynbos	Fynbos	2181.95	4.50	13.84
68	Sand Plain Fynbos	Fynbos	5239.57	58.19	1.05

types in which the species are planted, the invasion dynamics of the five species are reasonably similar (Richardson and Higgins, 1998, p. 463).

Data on the distribution of commercial forestry plantations were mapped from 1:250 000 LANDSAT TM images of 1993 (Fairbanks et al., 2000). Only plantations greater than 25 ha were mapped; this layer therefore excludes small woodlots where *Pinus* and, especially, *Acacia mearnsii*. were also planted. Forestry stands were mapped as polygons with species data (*Acacia mearnsii* and *Pinus* spp.), and the distance from the nearest plantation was computed using a grid with cell size of one decimal minute.

Environmental variables

Climatic variables were obtained from the Computing Centre for Water Research (CCWR; University of Natal, Pietermaritzburg). These climatic parameters were derived from regression analysis or other simulation models (Schulze et al., 1997), and were available as GIS layers (Arc/Info) at a one by one-minute grid resolution. Climatic factors used in the analysis are listed in Table 1. Two additional bioclimatic variables - growth days and growth temperature - were added. These ecologically meaningful variables take into account the potential for plant growth. Growth days represents the number of days when sufficient moisture is available for plant growth; it is defined as the sum of the monthly ratios of precipitation to potential evaporation (where precipitation is always assumed greater than evaporation). Growth temperature gives the mean daily temperature of the growth days (see Fairbanks and Ben, 2000 for further details of these bioclimatic indexes). Soil-water Stress is linearly related to median monthly precipitation and separate equations were derived for each major rainfall regions within South Africa (see Schulze et al., 1997). The following variables were also included: vegetation types and biome (Low and Rebelo 1996), land cover (Fairbanks et al., 2000), geology, and province. Because of the limitations of the FIRM programme (see below), the original 68 vegetation types were reclassified into 16 broad vegetation types based on climatic and geologic similarities (see Table 2 and Fig. 1). Geology was classified into 16 categories based on the frequency distributions for planted and invaded areas (the top fifteen geology types were kept separate, and the others, all with trivial areas, were clumped into one category). The variable "province" was included to take into account the disparity in data collection (some provinces were better surveyed than others) and the different histories of afforestation (oldest plantations in the west, youngest plantations in the east).

Statistical analysis

The analysis comprised three steps: 1) split the data into subsets according to the province subdivisions to account for different invasion patterns, history of afforestation and methods applied in data collection; 2) derive maps of areas likely to be invaded in the near future (20 to 50 years) using regression-tree analysis; and 3) assess priorities for management and policy guidelines using correlation biplots.

Splitting the data

Each province in South Africa has a different afforestation history– many plantations in the Western Cape are several hundred years old, whereas those in Eastern Cape or Mpumalanga were established much more recently (Richardson et al., in press). Furthermore, the data collection was collated during workshops within each province, resulting in strong differences in data mapping between provinces (Versfeld et al., 1998). Because of the points mentioned above, I analysed patterns of alien plant invasion at a provincial level. I thus subdivided the data into three "province groups" for *Acacia mearnsii* and *Pinus* spp. based on plantation history, invasion patterns, and data collection. Changes in percentage cover of invasive species was analysed by FIRM (see below) using province as an explanatory variable.

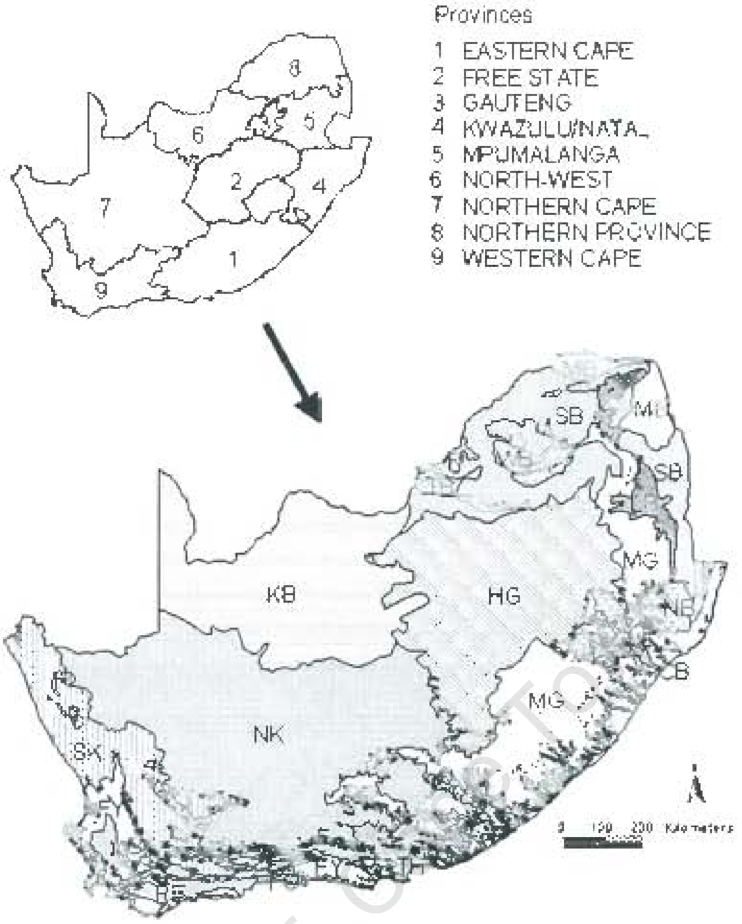


Figure 1. Province boundaries and vegetation map of South Africa showing the 16 vegetation types used (see Table 2 for more details on the vegetation types). CB: Coastal Grassland, FO: Forest, FY: Fynbos, HG: Highveld Grassland, KB: Kalahari Bushveld, LB: Lowveld Bushveld, MB: Mopane Bushveld, MG: Mountain Grassland, NB: Natal Bushveld, NK: Nam Karoo, RE: Renosterveld, SB: Sweet Bushveld, SK: Succulent Karoo, TB: Thorn Bushveld, TH: Thicket, WB: Mountain Bushveld.

Mapping areas likely to be invaded in future

I used Formal based Inference Recursive Modelling (FIRM) (Hawkins, 1995), a regression-tree analysis technique to relate distribution of invaded areas to environmental characteristics. Recursive partitioning is an attractive statistical technique for analysing large datasets, and it has shown to yield more accurate predictions than standard linear models (Hawkins, 1995; De'ath and Fabricius, 2000; Vayssieres et al., 2000). This method has been successfully applied to modelling alien plant species distribution at sub-continental (Reichard and Hamilton, 1997), regional (Chapter 4), and local (Rouget et al. 2001) scales. A full description of the methodology is given in Rouget et al. (2001) and in Chapter 2. Advantages of this non-parametric method are that both categorical and continuous variables can be incorporated in the analysis, and that it uncovers structure in data with variables that can be hierarchical, nonlinear or categorical. It also captures nonadditive behaviour, where the relationships between some predictors and the response variable depend on the values of other predictors.

In the FIRM approach the data set is successively split into smaller subsets, based on the values of the predictor variables. Each split is designed to separate the cases in the node being split into a set of successor nodes that are maximally homogeneous. The output of FIRM is a dendrogram that provides an intuitive pictorial interface to understanding the structuring of the problem as well as an effective way of making further predictions.

First, I determined the factors affecting the distribution and percentage cover of invaded areas for each taxon. For each cell containing invasive trees, I derived a series of 17 environmental predictors (including the distance to the nearest plantations, see Table 1). This constituted the set of "presence" observations. A coverage of 5000 random points (then converted to a grid of 1minute resolution) was generated outside the invaded area. The same series of environmental predictors was derived as for the grid of invaded areas. This constituted the set of "absence" observations. The percentage cover of invaded cells versus non-invaded cells was analysed in FIRM to identify which environmental characteristics are suitable for spread of the two invasive groups considered. The null hypothesis was that the distribution of invaded areas was primarily influenced by their distance from the commercial forestry plantations. To test this hypothesis, I ran a FIRM analysis for each species using only one factor, distance to the nearest plantation. Separate analyses were run for each set of provinces (see Table 3).

Next, I derived maps of the potential extent of future invasion for each taxon from the dendrograms generated by the FIRM analysis. Dendrograms show areas predicted to be invaded using appropriate combinations of environmental variables (e.g., growth days > 160 in Fig. 5). For each node of the dendrogram (i.e. for each combination of environmental factors), the category (medium or high % cover of invasive stands) was predicted to occur if this category was over-represented

Table 3. Subdivision of the invasion patterns according to provinces boundaries. Sample size, mean percentage cover and standard deviation relate to a FIRM analysis of all invaded areas vs. 3000 random locations uninvaded. Province subdivision was the single most important factor to explain the spatial distribution of alien plants at a broad scale. A separate analysis of invasion pattern was thus was made for each subset (see Methods). Province groups are sorted by decreasing degree of invasion.

Province group	Provinces	Sample size	Mean % cover	Standard deviation
Invasion by *Pinus* spp.				
1	Western Cape	1518	20.9	19.8
2	Eastern-Cape, Kwazulu-Natal, Free-State, Gauteng	1308	7.1	12.2
3	Mpumalanga, Northern Province	477	2.6	5.4
Invasion by *Acacia mearnsii*				
1	Eastern-Cape, Kwazulu-Natal, Gauteng, Mpumalanga	1748	23.6	29.4
2	Western Cape	938	19.6	21.3
3	Free-State, North-West Province	494	3.7	14.1

in the node (likelihood of occurrence higher than 0.5). Since all environmental variables were available in GIS format for the whole country, I identified areas likely to be invaded by selecting appropriate

environmental conditions (according to the respective dendrogram) for the occurrence of medium and high density stands. The area identified was considered as the potential distribution of the invasive taxa, and thus are under future risk of invasion (if not already invaded). The model accuracy was calculated as the percentage of the dataset correctly classified.

Analysing potential impacts on vegetation using biplots

Biplots are very useful techniques for visualising multivariate data (Gabriel, 1971; Underhill, 1990). They can be considered as the multivariate analogue of bivariate scatter diagrams. Biplots show a scatter of n points, representing the n samples, and superimpose information on the original variables, generally represented by vectors starting from the origin. As the scatter of points is derived by multidimensional scaling, some degree of approximation must be accepted to display the information in two dimensions (Gower and Hand, 1996). In this study, I used correlation biplots, which display best correlation between variables.

I briefly describe the major properties of biplots and how to interpret them. Figure 2 shows a hypothetical correlation biplot for 10 vegetation types (labelled from 1 to 10) and 4 environmental variables. The cosine between the vectors of two variables represents the coefficient of correlation between these two variables. Monthly precipitation and mean temperature are thus uncorrelated (angle close to 90°), while precipitation and altitude are strongly positively correlated (acute angle), and altitude and percentage transformed are negatively correlated (obtuse angle) (Fig. 2). The scalar product between a sample point and a variable (Y) gives information on the relation between the Y-value for the sample point and the mean of Y (Gower and Hand, 1996). In the case of the percentage of transformation, vegetation types 1, 5 and 7 are more transformed than in average, vegetation types 3, 4, and 10 did not differ from the average, and vegetation types 2, 8, and 9 are less transformed than average (Fig. 2).

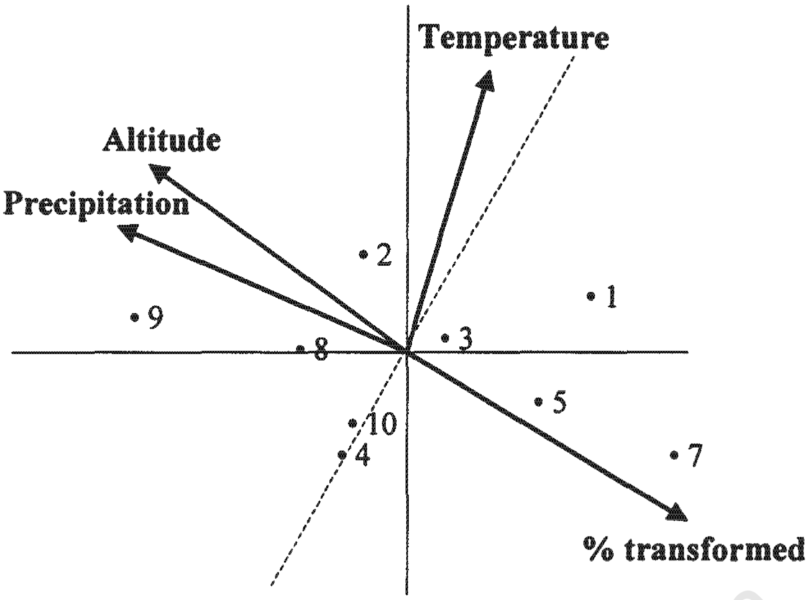


Figure 2. Hypothetical biplot for illustrating its main property and how to interpret it. Four environmental variables and 10 sample points (representing 10 different vegetation types) are displayed. The cosine between the vectors of two variables represents the coefficient of correlation between these two variables. The scalar product between a vegetation type and a variable (Y) gives information on the relation between the Y-value for this vegetation type and the mean of Y. All vegetation types falling on the left of the dashed line have this less transformed than in average, and all vegetation types falling on the right are more transformed than in average (shaded area).

I analysed each vegetation type in relation to four variables: 1) the mean % cover of the invasive taxon of concern; 2) the mean % cover of other invasive species (*Acacia mearnsii* and *Eucalyptus* spp. for *Pinus* spp., and *Pinus* and *Eucalyptus* spp. for *A. mearnsii*); 3) the % of the vegetation type suitable to be invaded in future -based on maps of potential distribution of invasive taxa, and 4) the % of habitat transformed. These factors are likely to be the most important criteria for setting policies and management guidelines. I used vegetation types as they were the only system of land classes available at a sub-continental scale, and are appropriate mapping unit for national-scale conservation planning (e.g. Reyers et al., in press). Separate analyses were made for each subset of provinces. For each invasive taxon and each province group, I derived biplots based on the vegetation types present within the province group, and the four variables mentioned above. I did not include vegetation types where no invasive occurs and where no risk factor was identified, as it considerably reduces the percentage of the total variation explained in two dimensions by the biplot.

Results

Current distribution of invasive species

Three distinct groups of invasion patterns were identified for *Pinus* spp. according to provinces (Table 3 and Fig. 3). Most of the invasive *Pinus* stands occur in the Western Cape (Fig. 3; mean % cover of 20%), the province with the longest history of forestry plantations in South Africa (762 km^2 currently afforested). This constitutes the first group (Table 3 and Fig. 3). The second group consists of recent to fairly recent forestry plantations (3 922 km^2) with few stands of invasive species recorded (mean % cover of 7%). This group comprises the Eastern Cape, Kwazulu-Natal, Free State and Gauteng provinces. The last group consists of Mpumalanga and Northern Province where forestry plantations started very recently and where invasion is not widespread (Fig. 3; mean % cover of 2.6%).

The invasion pattern of *Acacia mearnsii* was slightly different and I was able to distinguish three groups (Table 3 and Fig. 4). The first group relates to dense invasive stands and large extent of forestry plantations. This group includes Eastern Cape, Kwazulu-Natal, Gauteng, and Mpumalanga provinces (mean % of cover 23.6%). The second group is the Western Cape province (long history of planting) with some densely invaded areas (mean % cover of 19.6%). The last group consists of the Free State and the North-West province where the plantation extent and the spread of *A. mearnsii* is still limited (Fig. 4).

Distribution of invaded areas in relation to forestry plantations

Distance to the nearest commercial plantation was moderately significant in explaining the distribution of invasive stands. In all FIRM analyses that explored the determinants of the distribution for the two taxa, distance to the nearest plantation was never used as a primary factor (Table 1). It was sometimes included as a secondary factor (Table 1). When this factor was analysed separately, it reveals different relationship between percentage cover of invaded areas and distance from plantations for both taxa. No pattern was found in the case of *Acacia mearnsii* percentage cover (Table 4). However, I found that the percentage cover of *Pinus* spp. decreases with increasing distance from the nearest plantations (Table 4). The effect was stronger for the third province group (most recent pine plantations) where invasion percentage cover decreases sharply after 3.6 km from the nearest plantation. In the Western Cape (much older plantations), this effect was still present but the percentage cover decreased only 50 km away from the plantations.

Table 4. Effects of distance from forestry plantations on invasion patterns of *Pinus spp* and *Acacia Mearnsii*. A FIRM analysis (series of chi-square tests adjusted with Bonferroni procedures) was done using distance from plantations only. The hypothesis was that percentage cover of invasive aliens decreases when the distance from plantations increases.

Province group	**Invasion by *Pinus spp.***		**Invasion by *Acacia mearnsii***	
	p-value	Effect	p-value	Effect
1	<0.0001	Decreasing	-	No pattern
2	-	No pattern	-	No pattern
3	<0.0001	Decreasing	-	No pattern

Potential distribution of invasive stands

The dendrograms derived from the FIRM analysis correctly classified 91.5% of the *Pinus* data set and 83% of the *Acacia mearnsii* data set. Eleven environmental factors were used to derive suitable habitats for invasive spread (Table 1). Most important environmental factors used in the models were maximum soil-water stress (especially for *A. mearnsii*) and growth days (Table 1). Figure 5 illustrates the results of one FIRM analysis for the distribution of invasive *Pinus* spp. in the Western Cape. Only three factors were necessary to model accurately 90% of the presence/absence of the invasive taxon. Dense stands of *Pinus* spp. were predicted for areas where number of growth days > 80 with limited soil moisture stress. Distance from the nearest plantation was used as a secondary factor (Fig. 5). Similar dendrograms were generated for each province group and each taxon, but are not shown here. Figures 3b and 4b show the potential distribution map of *Pinus* spp. and *A. mearnsii* in South Africa (generated from the FIRM dendrograms). These areas have identical environmental characteristics as the areas currently invaded.

Spread of invasive taxa was only modelled in remaining natural vegetation (currently untransformed by agriculture, urbanisation, forestry plantations and mining). According to these models, *Pinus* spp and *A. mearnsii* could potentially invade 6.6% and 9.8% of untransformed land respectively. These two taxa appear to invade different habitats as there was only 35% overlap between their potential distributions.

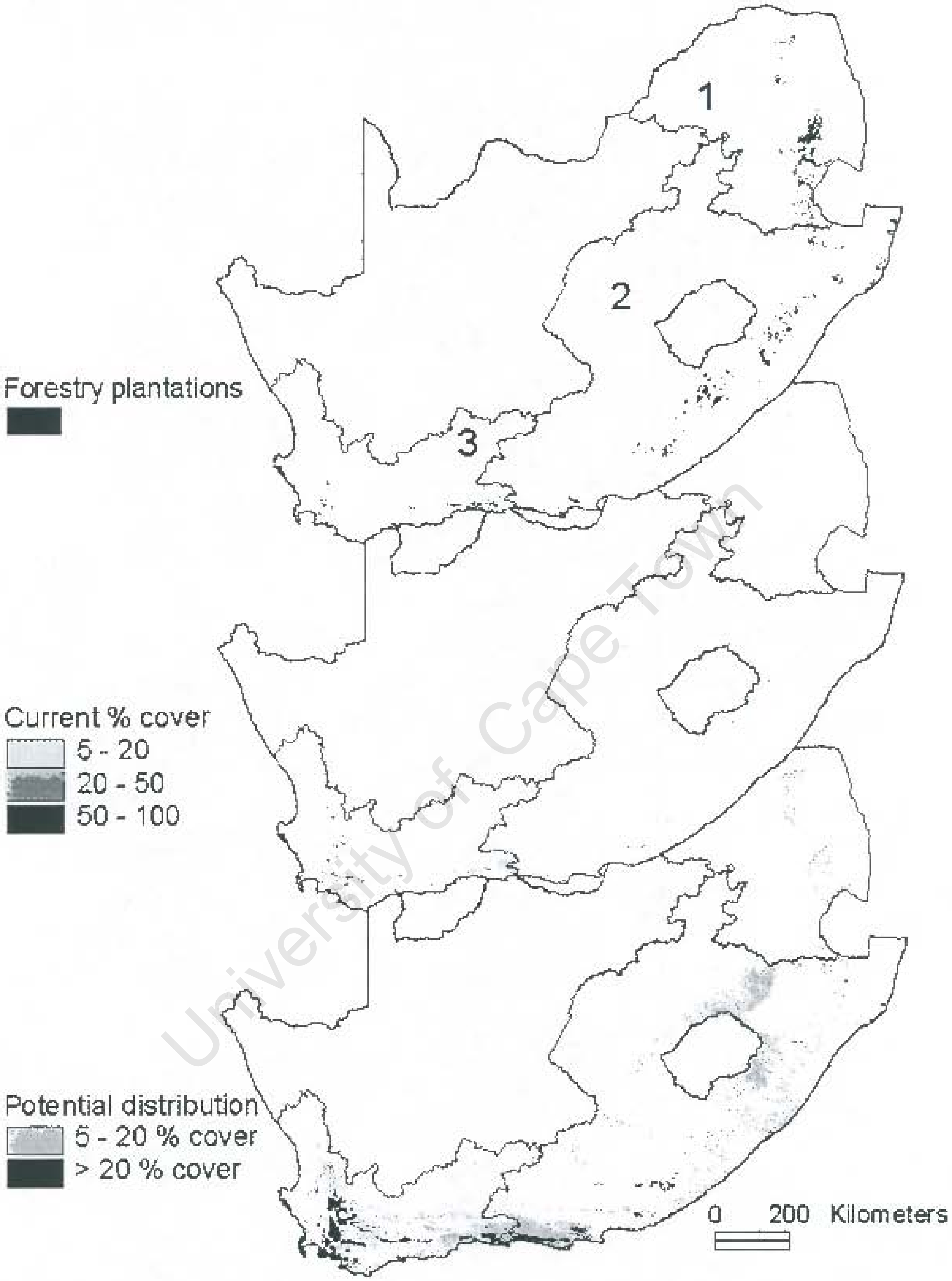


Figure 3. Current and potential distribution maps of *Pinus* spp. Fig. 3a shows the location of the main forestry plantations; Fig. 3b illustrates the current invasion pattern; and Fig. 3c shows the area suitable for future spread generated from FIRM analysis. The numbers refer to the province groups. 1: Western Cape; 2: Eastern Cape, Kwazulu-Natal, Free State and Gauteng; 3: Mpumalanga and Northern Province

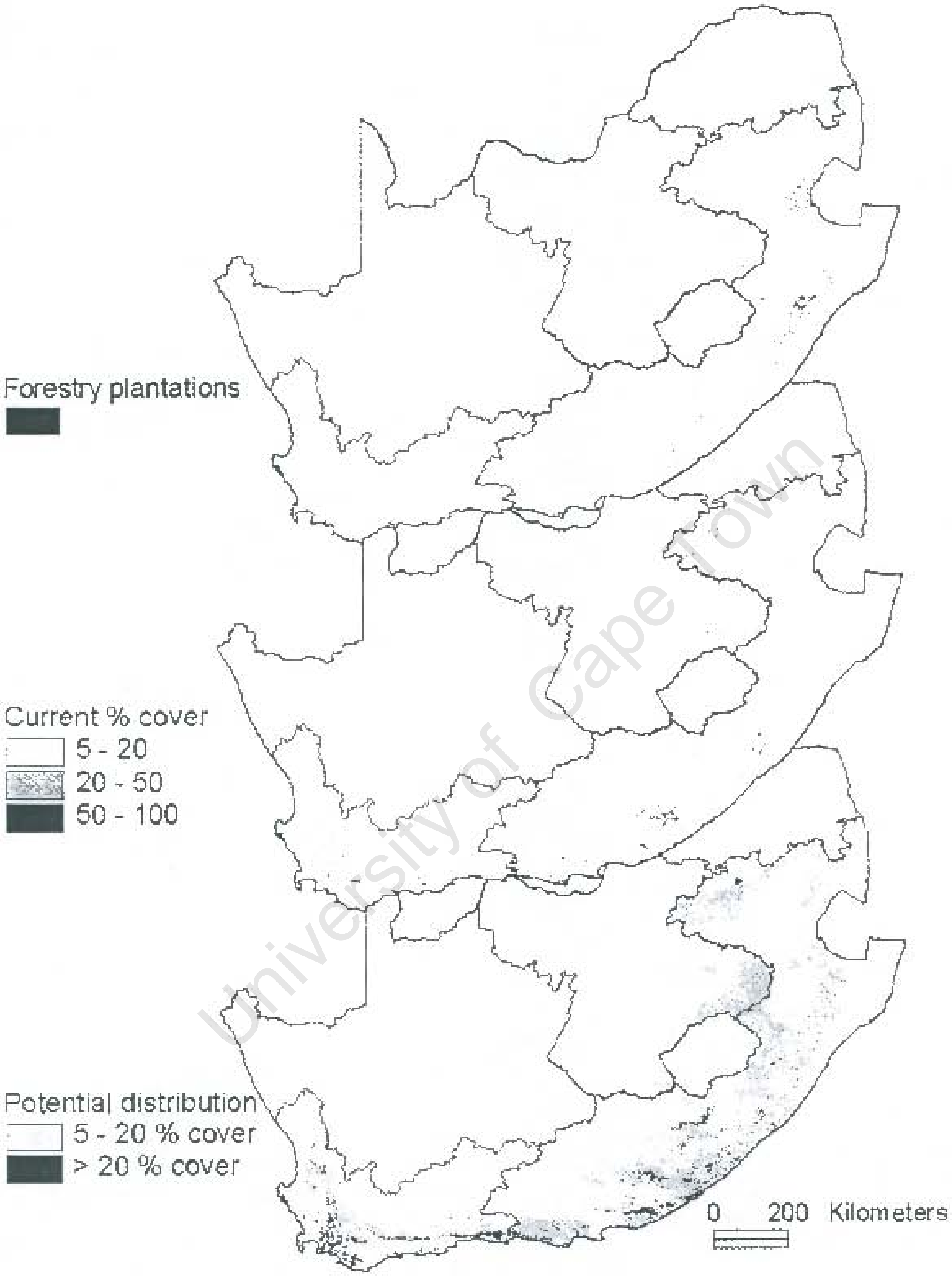


Figure 4. Current and potential distribution maps of *Acacia mearnsii*. Fig. 3a shows the location of the main forestry plantations; Fig. 3b illustrates the current invasion pattern; and Fig. 3c shows the area suitable for future spread generated from FIRM analysis. The numbers refer to the province groups. 1: Eastern-Cape, Kwazulu-Natal, Gauteng and Mpumalanga; 2: Western Cape; 3: Free-State and North-West Province.

Current and future invasion patterns in relation to vegetation types

Figures 6 and 7 show the invasion pattern of *Pinus* spp. and *Acacia mearnsii* respectively within each province groups in relation to vegetation types and four key environmental factors: percentage currently transformed, currently afforested, mean percentage cover of *Pinus* spp., and mean percentage cover of other invasive taxa. These biplots display accurately in two dimensions between 69 and 82% of the total variation. While specific information for each vegetation type can be retrieved from the biplots, here I discuss the general pattern.

The risk factor, which relates to the habitat suitability for future invasion, was generally positively correlated with the current mean percentage cover of invasive taxa. The correlation was stronger in the first province group (i.e. where most of the invasive stands occur) of each invasive taxa (Fig. 6a and Fig. 7a). In some instances, the mean percentage cover of invasive taxa were positively correlated, like the percentage cover of *Pinus* spp. and the percentage cover of other invasive spp. in the second province group (Fig. 6b). The degree of transformation was generally not correlated with any other factor except in the Western Cape Province where it was strongly positively correlated with the mean percentage cover of *A. mearnsii* (Fig. 7a).

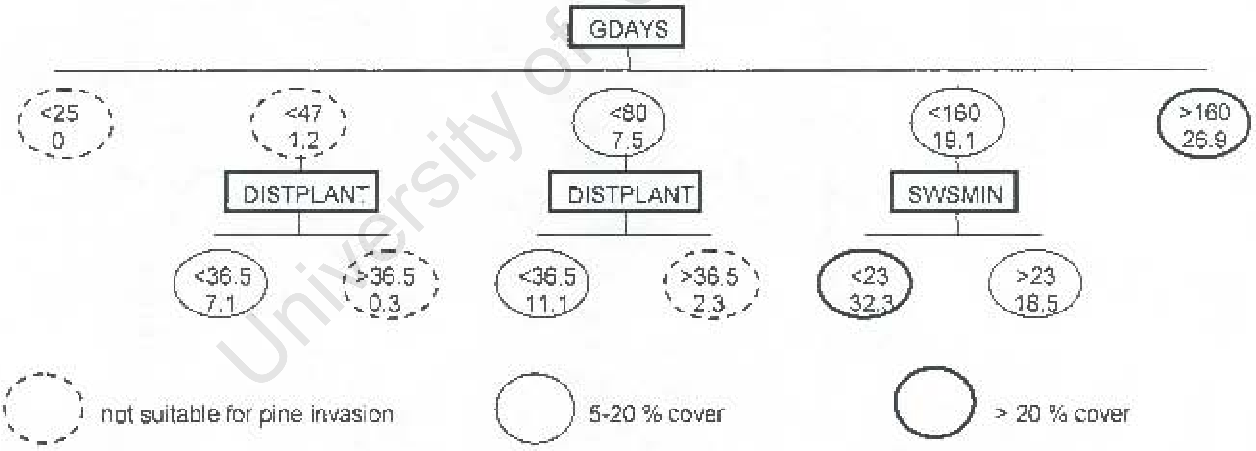
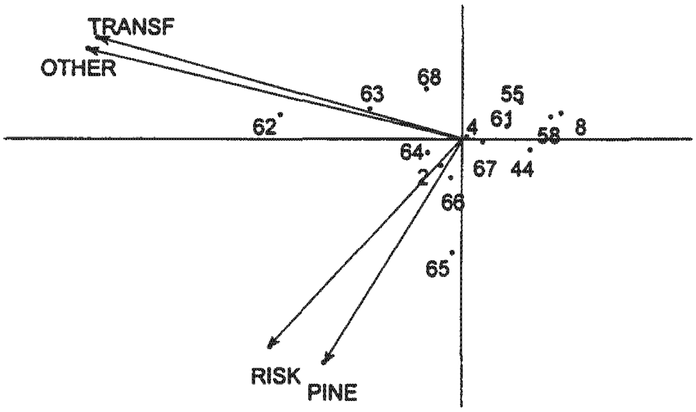
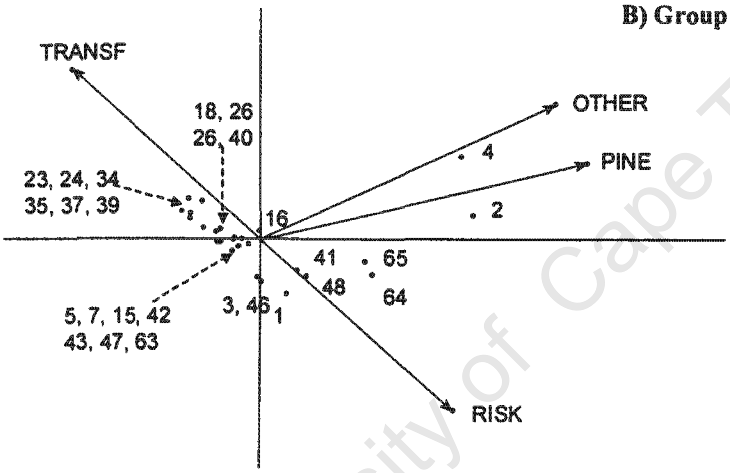


Figure 5. Dendrogram depicting environmental determinants of the distribution of *Pinus* spp invasive stands in the Western Cape (group 1). The dendrogram was generated by FIRM analysis. Significant variables are indicated inside boxes (see Table 1 for variable coding). The first value in the circles relates to the variable grouping, the second is the mean percentage cover of *Pinus* spp. stands. If the circle appears in bold, this condition favours invasion of high percentage cover (more than 20%), if it appears in thin line, medium percentage cover (between 5 and 20%). GDAYS (growth days) are expressed in number of days, DISTPLANT (distance to the nearest plantation) in km, and SWSMIN (minimum soil-water stress) in percentage.

A) Group 1: WC



B) Group 2: KW, GP, FS & EC



C) Group 3: NP, MP

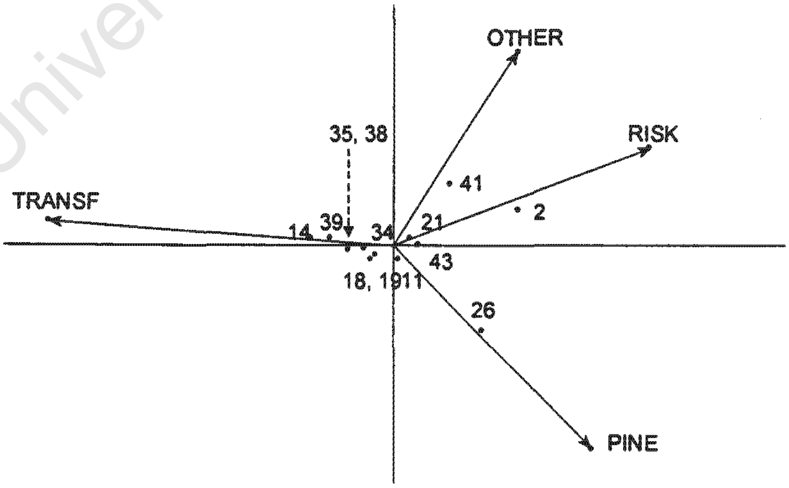


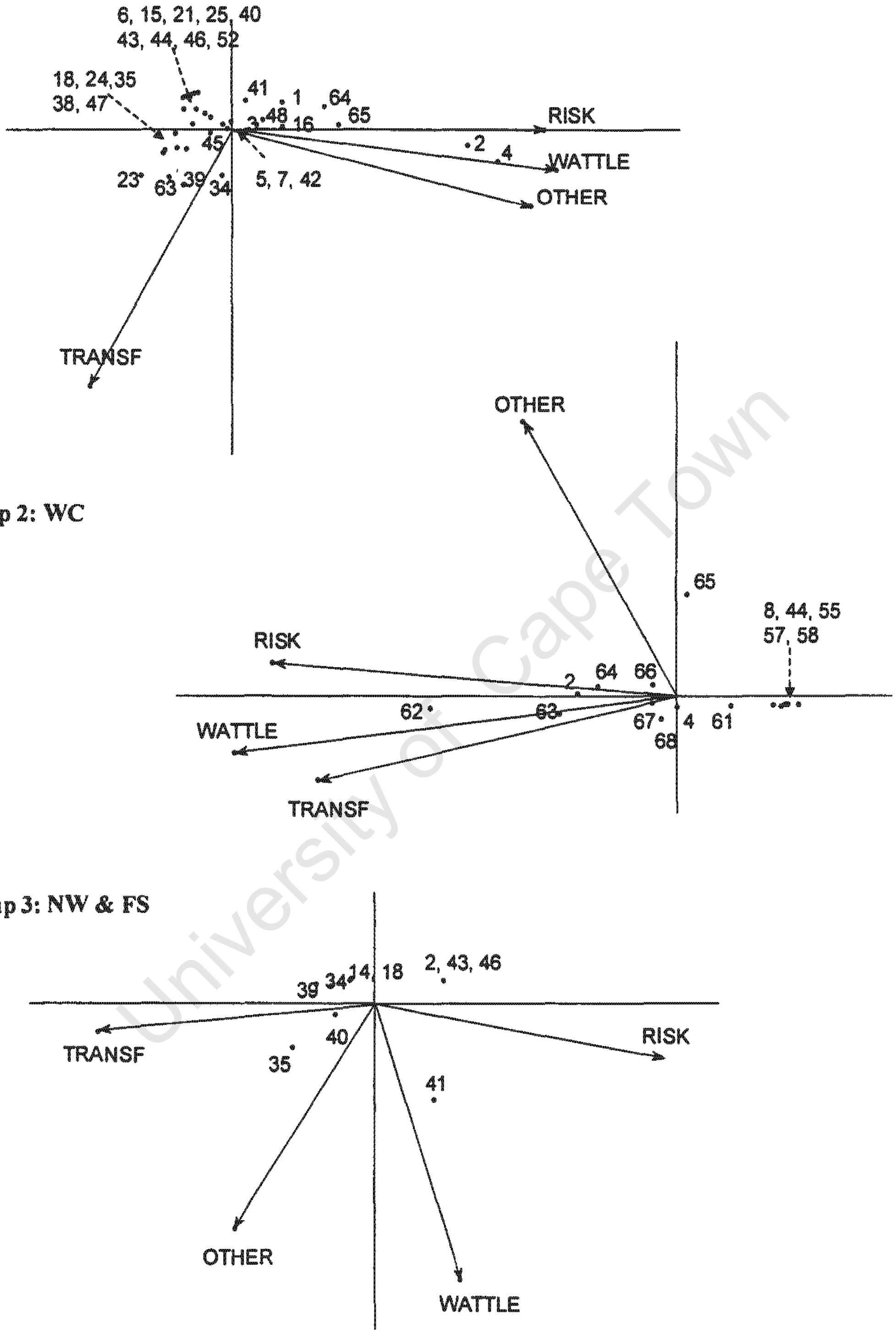
Figure 6. Biplots displaying the extent of *Pinus* spp. invasion within each vegetation type in relation to four variables: mean % cover of *Pinus* spp. (PINE), mean % cover of other invasive taxa (OTHER), % suitable for future invasion (RISK), and % currently transformed (TRANSF). The numbers relate to vegetation types (see Table 2 for coding). A separate analysis was done for each province group.

Vegetation types largely invaded by *Pinus* spp. were Grassy Fynbos and Laterite Fynbos (also at high risk of future invasion) in the Western Cape (Fig. 6a), Afromontane Forest and Dune Thicket in the second province group (Fig. 6b), and Natal lowland Bushveld (but at low risk of future invasion) in the third province group (Fig. 6c). Vegetation types largely invaded by *Acacia mearnsii* were Afromontane Forest and Dune Thicket in the first province group (Fig. 7a), West Coast Renosterveld and South-West Coast Renosterveld in the Western Cape (Fig. 7b), and Wet Cold Highveld Grassland in the last province group (Fig. 7c). Vegetation types currently invaded by *Pinus* spp. in the first province group were highly suitable for future invasion (Fig. 6a), and the same pattern was found for *A. mearnsii* (Fig. 7a). Few vegetation types were currently invaded at a low percentage cover and highly suitable for future invasion. This was the case for all forest types for *Pinus* spp. (Fig. 6b and 6c); and for Coastal Forest (Fig. 7a) and Mountain Grassland types (Fig. 7c) for *A. mearnsii.* Regarding the invasion pattern of *Pinus* spp., there were several vegetation types currently transformed to a large extent but that appeared to be at low risk of future invasion (e.g. Coastal vegetation types and Highveld Grassland, Fig. 6b). I found the opposite pattern in few vegetation types for *A. mearnsii*, where, for example, coastal Renosterveld was highly transformed, invaded, and at high risk of future invasion (Fig. 7b).

Discussion

The dynamics of invasion by Acacia mearnsii and Pinus spp.

I modelled the habitat suitability for future invasion using recursive modelling. This method successfully identified the main environmental determinants of the current distribution patterns as more than 80% of the original data was accurately classified. However, like every static modelling approach, it assumes a pseudo-equilibrium between the environment and observed species patterns (Guisan and Zimmermann, 2000). This assumption probably does not hold for invasive species that have been recently introduced, as such species have not had time to colonise every suitable habitat. This was confirmed by the lack of correlation between the mean percentage cover of invasive species and the proportion suitable for future invasion for vegetation types where the species has been recently planted (Fig. 6c and Fig. 7c). In places where forestry plantations have been present for much longer, there was a strong positive correlation between those two factors (Fig. 6a and Fig. 7a). This indicates that most of the area suitable for invasion is already invaded.



A) Group 1: EC, KW, MP, GP

B) Group 2: WC

C) Group 3: NW & FS

Figure 7. Biplots displaying the extent of *Acacia mearnsii* invasion within each vegetation type in relation to four variables: mean % cover of *Acacia mearnsii* (WATTLE), mean % cover of other invasive taxa (OTHER), % suitable for future invasion (RISK), and % currently transformed (TRANSF). The numbers relate to vegetation types (see Table 2 for coding). A separate analysis was done for each province group.

The maps of potentially invaded areas are based on the actual distribution of the invasive species, which cannot be considered at equilibrium. It is likely that, with time, more areas will become suitable for invasion if the spread is not controlled. Moreover, due to limitations of the data, the predictions should be used with care. Areas identified by the model as unsuitable for future invasion could be interpreted in at least three ways: 1) area really not suitable, 2) area not classified as suitable because of omission of the species distribution, 3) area currently identified not suitable because the species has not yet spread in all environments.

These models rely largely on indirect factors (like climate, topography) that influence the growth of species and few direct factors like growth days (Table 1). These factors are generally good predictors of species and vegetation distribution at a broad scale (Woodward, 1987). Because of the scale of the study, I was not able to quantify disturbance and other human-induced factors that greatly affect the distribution and the spread of invasive species at finer spatial scales (Hobbs and Huenneke, 1992). At a local scale, the spread of *Pinus* spp. has been found to be influenced by factors such as fire regime, agriculture practices, and as soil pH (Rouget et al., 2001). The consideration of disturbance and fine-scale land-use is therefore required to gain a better understanding of the dynamics and the spatial patterns of biological invasions.

Limitations of the dataset

This study was constrained by the quality of the data for the distribution of invasive taxa. As expert knowledge was incomplete and unreliable in some areas, the extent of invasion appears overestimated where invaded trees occur at low percentage cover, and underestimated in other areas. The methodology used for mapping invasive stands also differed between provinces. I believe however that this is a rather common problem for large ecological data sets, and that new approaches should be developed to counter such problem. Because of these factors, I excluded from the analysis all areas invaded at low percentage cover (< 5%) and subdivided the analysis according to province (Table 3).

The distribution of commercial forestry plantations was generally insignificant to explain the current invasion pattern of *Pinus* spp. and *Acacia mearnsii* (Table 4). An earlier study (Nel et al., 1999) conducted at a finer scale found a significant spatial correlation between the distribution of dense stands of invasive species and plantation forestry. At the scale of this study, it would be very difficult to demonstrate a significant relationship between commercial forestry and invasions. The real impact of forestry plantations has probably been underestimated for several reasons. Firstly, the current extent of plantations (used in this study) does not include many plantations (especially for *A. mearnsii*) that have been abandoned or cleared (seeds from such stands would have initiated invasions before they were cleared). Secondly, plantations have been in place in some areas for much longer than others – plantations in the Western Cape are hundreds of years old, while those in other parts of the country have only been there for several decades or less. The areas around older plantations would therefore have had much more time to become invaded. Thirdly, the dispersal characteristics of the different species lead to completely different patterns of invasion. For example, *Pinus* spp. have wind-dispersed seeds and will establish in a random pattern, sometimes with isolated invasion foci appearing kilometres away from the source (Higgins and Richardson, 1999). *Acacia mearnsii*, on the other hand, has water-dispersed seeds and spread primarily down water courses, displaying linear invasion patterns that will radiate downstream from the invasion source (Richardson et al., 1992). In such cases, "distance to plantations" will be a poor predictor of invasion success. Finally, many of the species used in plantations have been widely planted outside of plantations, often in isolated situations with one or a few individuals, and these isolated plantings will add to the seed source for invasion, but I was not able to consider them, as they were not mapped at the scale of this study.

Many factors influence the current (and future) distribution of invasive species. While this study might have underestimated the effect of plantation forestry, the influence of environmental factors was clearly identified. Considering the rate of alien spread and its negative impacts, one cannot wait for "error-free" ecological data sets. I thus believe that, despite the limitations posed by the dataset, the results generated in this study suggest guidelines for setting objective policies for dealing with invasions from commercial plantations at a national scale.

Implications for a national policy on managing invasive species

Plantations of alien trees cover 1.52 million ha in South Africa (FOA, 1998), and have brought many benefits. Plantation forestry contributes US$300 million, or 2%, to the GDP and employs over 100,000 people in South Africa. Downstream industries, based on forestry, realize products worth a further US$1.6 billion, much of which is exported, earning valuable foreign exchange (FOA, 1998). Commercial forestry based on alien trees is a well-established feature of the South African landscape and economy, but the invasions that are associated with it will need to be managed to minimize conflicts around scarce resources, especially water (Le Maitre et al., in press).

One way in which the South African government plans to deal with invasive species with commercial value is to allow landowners to grow the trees for profit, provided that they apply for a permit to demarcate the areas where such trees will be allowed to grow. The landowners will then also have to accept responsibility for preventing the spread of the species outside of the demarcated area, through taking "reasonable steps" to prevent spread. The actual implementation of this policy will be subject to

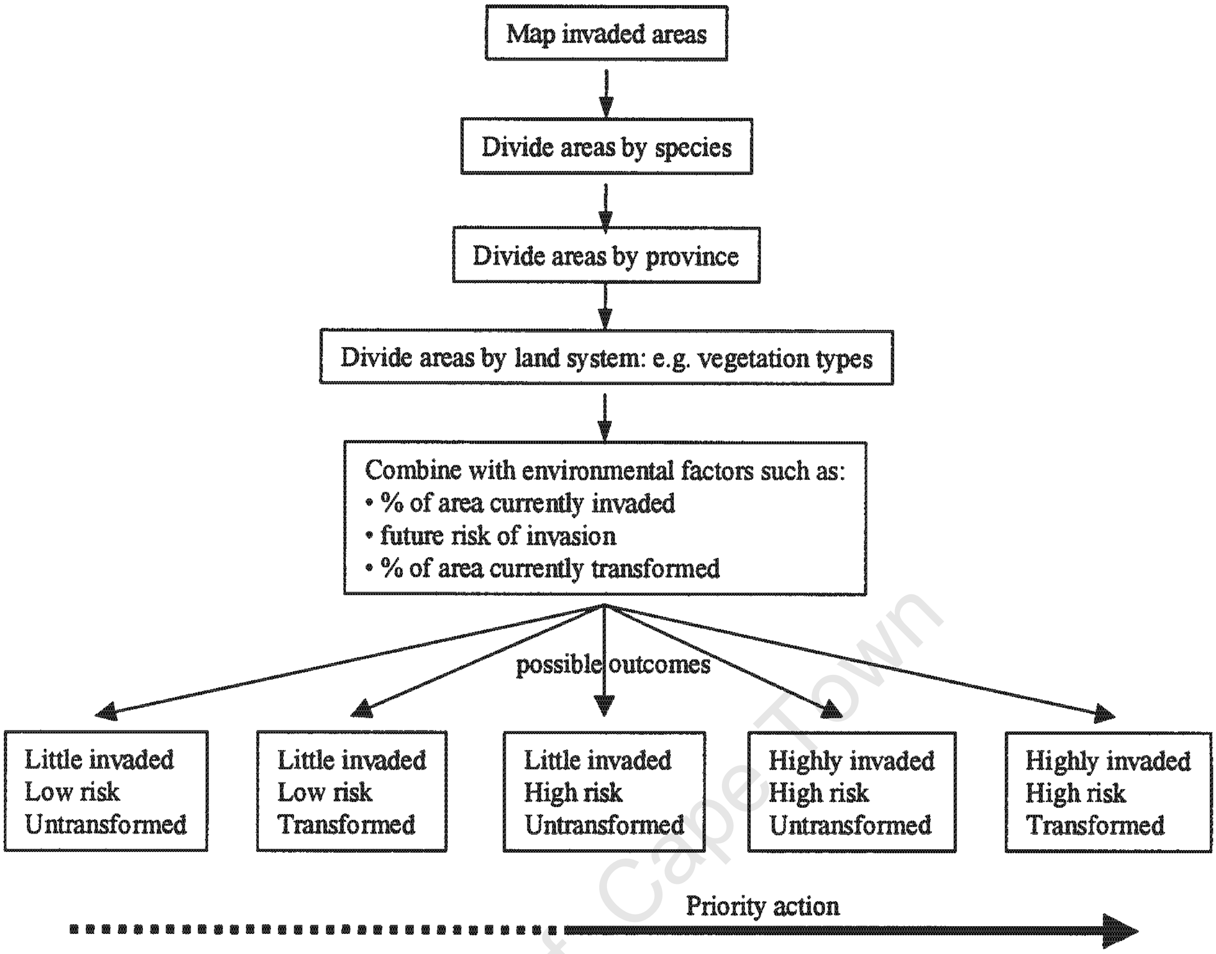


Figure 8. Protocol suggested for implementing environmental policy on alien plant management. The different factors considered are indicated; these factors enable the identification of demarcated areas (i.e. areas where alien plants can be grown) and areas for priority actions.

practical problems, and the definition of "reasonable steps" will no doubt be tested, probably in a court of law, at some stage. This study has shown that distance to the nearest plantations is not the only factor to consider when implementing policy for invasive aliens that have commercial value. A more proactive and integrated approach is needed for assessing the risk of habitats being invaded. I provide the basis for an approach that will go some way towards facilitating that implementation.

The proposed approach is outlined in Figure 8. The first step would be to map invaded areas within a management unit, for example a province or part of a province. The factors that characterise the landscape will be mapped and the areas at risk from invasion will be derived for each species within subdivisions of the management unit, for example vegetation types or cadastral units. I suggest that at least three major categories within each land class will be evident – uninvaded areas at low risk, uninvaded areas at high risk, and invaded areas at high risk. These categories can be identified using biplots (Fig. 6 and 7). Decisions on whether or not to allow the demarcation of areas, and on what categories within each land class will be evident – uninvaded areas at low risk, uninvaded areas at high risk, and invaded areas at high risk. These categories can be identified using biplots (Fig. 6 and 7). Decisions on whether or not to allow the demarcation of areas, and on what conditions to attach to demarcation permits, could differ within each of these subdivisions. In uninvaded areas at low risk, permits for demarcation could be readily granted, as invasion would not be predicted from current patterns and understanding. It would nonetheless be prudent to monitor the population dynamics of the species concerned, and if invasion is detected then the requirements under the permit for landowners to take "reasonable steps" to prevent spread could be invoked. Uninvaded areas at high risk of invasion may include priority areas for conservation, or they could be important watersheds. In such areas, planting permits should stipulate the need for intensive management to prevent invasions. In invaded areas at high risk of invasion, the focus of management should be on integrated control. Such areas would typically include many areas already heavily planted to forestry, where the refusal of permits would not be expedient due to the existing investments in such plantations and the regional economic dependence on them. For example, in the case of *Pinus* spp., Grassy Fynbos has all the characteristics of a vulnerable system: it is already invaded to a large extent by *Pinus* spp. (and also by *A. mearnsii*), 100% is considered suitable for future invasion (Fig. 6b), and forestry plantations are already present.

This approach also suggests including the extent of current habitat transformation (the degree to which urbanisation and agriculture threaten natural habitats) as an additional criterion for decision-making for setting priorities for invasive alien plant management and land demarcation. Information on vulnerability (the likelihood of one habitat being lost by some transformation agent) has been increasingly used over the recent years to prioritise and implement conservation actions (see Cowling et al. 1999; Rouget et al. submitted a). I recommend to focus management of invasive species on habitats of high conservation value and already transformed by some other factors because they are most likely to be lost in the near feature. This is clearly the situation for West Coast Renosterveld where 90% of its original extent has been transformed (mainly by agriculture), and where the remaining vegetation is invaded by *Pinus* spp. and *Acacia mearnsii* (Fig. 7a).

References

Cowling, R.M., Pressey, R.L., Lombard, A.T., Heijnis C.J., Richardson, D.M., Cole, N., 1999. Framework for a conservation plan for the Cape Floristic Region. Institute for Plant Conservation, Cape Town.

Daehler, C.C., Carino, D.A., 2000. Predicting invasive plants: prospects for a general screening system based on current regional models. Biological Invasions 2, 93-102.

De'ath, G., Fabricius, K.E., 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. Ecology 81, 3178-3192.

Dye, P.J., 1996. Climate, forest and streamflow relationships in South African afforested catchments. Commonwealth Forestry Review, Pretoria.

Fairbanks D.H.K., Benn, G.A., 2000. Identifying regional landscapes for conservation planning: a case study from Kwazulu-Natal, South Africa. Landscape and Urban Planning 50, 237-257.

Fairbanks, D.H.K, Thompson, M.W., Vink, D.E., Newby, T.S., van der Berg, H.M., Everard, D.A., 2000. The South African land-cover characteristics database: a synopsis of the landscape. South African Journal of Science 96, 69-85.

FOA., 1998. Abstract of South African forestry facts for the year 1996/97. Forest Owners Association, Johannesburg.

Gabriel, K.R., 1971. The biplot graphic display of matrices with application to principal components analysis. Biometrics 58, 453-467.

Gower, J.C., Hand, D.J., 1996. Biplots. Chapman and Hall, London, 277 pp.

Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135, 147-186.

Hawkins, D.M., 1995. Formal Inference-based Recursive Modelling. Department of Applied Statistics, University of Minnesota, St Paul.

Higgins, S.I., Richardson, D.M., 1999. Predicting plant migration rates in a changing world: the role of long-distance dispersal. The American Naturalist 153:464-475.

Higgins, S.I., Richardson, D.M., Cowling, R.M., 2000. A dynamic spatial model for managing alien plant invasions at the landscape extent. Ecological Applications 10, 1833-1848.

Higgins, S.I., Richardson, D.M., Cowling, R.M., 2001. Validation of a spatial simulation model of a spreading alien plant population. Journal of Applied Ecology 38, 571-584.

Higgins, S.I., Richardson, D.M., Cowling, R.M., Trinder-Smith, T.H., 1999. Predicting the landscape scale distribution of alien plants and their threats to biodiversity. Conservation Biology 13, 303-313.

Hobbs, R.J., Huenneke, L.F., 1992. Disturbance, diversity, and invasion: implications for conservation. Conservation Biology 6, 324-337.

Iverson, L.R., Prasad, A.M., 1998. Predicting abundance of 80 tree species following climate change in the eastern United States. Ecology Monographs 68, 465-485.

Le Maitre, D.C., 1998. Pines in cultivation. In: Richardson, D.M. (Ed.), Ecology and Biogeography of Pinus. Cambridge University Press, Cambridge, pp 407-431.

Le Maitre, D.C., van Wilgen, B.W., Gelderblom, C.M., Bailey, C., Chapman, R.A., Nel, J.A., in press. Invasive alien trees and water resources in South Africa: Case studies of the costs and benefits of management. Forestry Ecology & Management.

Low, A.B., Rebelo, A.G., 1996. Vegetation of South Africa, Lesotho and Swaziland. Department of Environmental Affairs & Tourism, Pretoria.

Nel, J.L., van Wilgen, B.W., Gelderblom, C.M., 1999. The contribution of plantation forestry to the problem of invading alien trees in South Africa: a preliminary assessment. Report ENV/S-C 99003, CSIR, Stellenbosch, 26 pp.

Pheloung, P.C., Williams, P.A., Halloy, S.A., 1999. A weed risk assessment model for use as a biosecurity tool evaluating plant introductions. Journal of Environmental Management 57, 239-251.

Reichard, S.H., Hamilton, C.W., 1997. Predicting invasions of woody plants introduced to North America. Conservation Biology 11, 193-203.

Reyers, B, Fairbanks, D.H.K., van Jaarsveld, A.S., Thompson, M., (in press) South African vegetation priority conservation areas: a coarse-filter approach. Diversity and Distributions.

Richardson, D.M., 1998. Forestry trees as invasive aliens. Conservation Biology 12, 18-26.

Richardson, D.M, Cambray, J.A., Chapman, R.A., Dean, W.R.J., Griffiths, C.L., Le Maitre, D.C., Newton, D.J., Winstanley, T., (in press) Vectors and pathways of biological invasions in South Africa – past, present and future. In: Carlton, J.T, Ruiz, G. (eds), *Pathways of biological invasions*, Island Press, Washington, D.C.

Richardson, D.M., Higgins, S.I., 1998. Pine as invaders in the southern hemisphere. In: Richardson, D.M. (Ed.), Ecology and Biogeography of Pinus. Cambridge University Press, Cambridge, pp 450-473.

Richardson, D.M., Macdonald, I.A.W., Hoffmann, J.H., Henderson, L., 1997. Alien plant invasions. In: Cowling, R.M., Richardson, D.M., Pierce, S.M. (Eds.), Vegetation of southern Africa. Cambridge University Press, Cambridge, pp 535-570.

Rouget, M., Richardson, D.M., Milton, S.J.M., Polakow, D., 2001. Predicting the dynamics of four invasive *Pinus* species in a fragmented semi-arid shrubland in South Africa. Plant Ecology 152, 79-92.

Schulze, R.E., Maharaj, M., Lynch, S.D., Howe, B.J., Melvil-Thomson, B., 1997. South African atlas of agrohydrology and -climatology. Water research commission, Pretoria.

Sisk, T.D., Launer, A.E., Switky, K.R., Ehrlich, P.R., 1994. Identifying extinction threats: global analyses of the distribution of biodiversity and the expansion of the human enterprise. BioScience 44, 592-604.

Tucker, K.C., Richardson, D.M., 1995. An expert system for screening potentially invasive alien plants in South African fynbos. Journal of Environmental management 44, 309-338.

Underhill, L.G., 1990. The coefficient of variation biplot. Journal of Classification 7, 241-256.

van Wilgen, B.W., Bond, W.J., Richardson, D.M., 1992. Ecosystem management. In: Cowling, R.M. (Ed.), The ecology of fynbos: nutrients, fire and biodiversity. Oxford University Press, Cape Town, pp 345-371.

Vayssieres, M.P., Plant, R.E., Allen-Diaz, B.H., 2000. Classification trees: an alternative non-parametric approach for predicting species distributions. Journal of Vegetation Science 11, 679-694.

Versfeld, D.B., Le Maitre, D.C., Chapman, R.A., 1998. Alien invading plants and water resources in South Africa: A preliminary assessment. WRC, Pretoria.

Woodward, F.I., 1987. Climate and plant distribution. Cambridge University Press, Cambridge.

Measuring conservation value at fine and broad scale: implications for diverse and fragmented regions

Abstract

This chapter explores the implications of spatial scale for conservation planning in the Agulhas Plain, South Africa. Regional planning relies on broad-scale data but fine-scale data are usually required for implementation at local level. This study addresses the implications of broad-scale planning for fine-scale implementation. Two systems of notional reserves were developed for this region using C-Plan, a decision support system for systematic conservation planning. The first conservation plan was derived using broad scale data (1:250 000) and consisted of nine Broad habitat units (land classes based on topography, geology, and climate), remote sensing mapping of habitat transformation and 1/16th degree square as planning units (average size 3 900 ha). The second system was identified at a finer scale (1:10 000) using 36 vegetation types (mapped in the field), ground survey mapping of habitat transformation and cadastral boundaries as planning units (average size 252 ha). All analyses were done using a Geographic Information System. Using classification trees and correlation biplots, I compared reserve-design efficiency (the area required to achieve conservation targets), the spatial patterns of conservation value (the relative contribution of one area to conservation targets), biodiversity, and habitat transformation at both scales.

Similar amount of land was required to fulfil all conservation targets (identified using minimum sets) using broad and fine scale data sets. There was considerable overlap between both conservation plans as most of fine-scale conservation targets could be achieved under the broad-scale scenario. Large planning units were less efficient (i.e. more land required) in achieving conservation targets than cadastral units. However, irreplaceability values, which measure the contribution of planning units for achieving representation targets, were much higher at the fine-scale. The use of broad-scale biodiversity features underestimated conservation value in heterogeneous and fragmented portions of the landscape. The implications of moving from broad-scale to fine-scale conservation planning, as well as their respective benefits are discussed. Maximising biodiversity conservation while minimising cost and resources might be achieved by a combination of broad-scale assessments for relatively homogeneous and untransformed areas and fine-scale ones for heterogeneous and fragmented areas.

Introduction

In past decades, biodiversity was perceived largely in terms of species richness, and conservation attention was often directed at hotspots rich in total species or rare species (Noss, 1987). More recently, there has been a shift in conservation planning, and protection strategies are increasingly based on broad-scale approaches, conserving biodiversity at the ecosystem level across whole regions (Franklin, 1993; Mittermeier et al., 1998; Soulé and Terborgh, 1999; Schwartz, 1999; Poiani et al., 2000). This emphasis on broad-scale conservation is highlighted by recent ecosystem-based management policies by federal agencies in the USA (Christensen et al., 1996; Soulé and Terborgh, 1999). An important aspect of this approach is the use of a "coarse-filter" of targeted features (Noss, 1987) such as communities, habitats, ecosystems or landscapes to serve as surrogates for the distribution of biodiversity.

Although coarse-filter conservation has several conceptual advantages, such as the preservation of ecosystem linkages and processes, its implementation is not straightforward. There is no *a priori* basis for prioritising ecosystem attributes, and various methods have been suggested (Heywood, 1995). No accepted classification for communities or ecosystems exists and questions remain about appropriate levels of the classification hierarchy for recognition, inventory and protection of natural communities (Ferrier, in press).

The emergence of remote-sensing systems and Geographic Information System procedures for identifying and measuring habitat structure or landscape types provides important opportunities for conservation planning, more particularly for coarse-filter conservation (Davis, 1995; Burke, 2000). The spatial scale at which conservation decisions are taken is, however, a crucial issue. The scale of data collection, habitat classification, or selection units (used for the design of conservation areas) can greatly affect the outcomes of conservation planning (Pressey and Logan, 1998; Fuller et al., 1998). Information collected at one scale might be completely inappropriate to answer management questions at another scale (Chapter 7). The spatial scale used in the habitat classification (i.e. the units of conservation) will depend on the level of detail desired, but the choice of scale is generally determined and constrained by the availability of data and resources (mainly time and finance). So, although fine-scale data on biodiversity surrogates such as vegetation types is desirable, maps of coarse-filter surrogates for large regions are generally produced at a broad scale (coarse resolution).

The constraints on fine-scale mapping across large regions introduce a problem for conservation planning. Regional assessments of conservation priority are important to place individual areas in the context of natural processes and interactions. Consistent data on coarse-filter surrogates across whole regions are usually available only at broad scales (e.g. 1:1 000 000 or 1:250,000). But conservation plans produced at these scales must be implemented at finer scales, often below the resolution of the regional data sets. In some parts of regions, there will be localised, fine-scale data sets available for implementation. In these situations, planners and managers will have to consider whether the assessment of conservation values derived in the regional plan with broad-scale data matches the assessment of values that would emerge from analysis of the fine-scale data. They might also have to consider replacing the values from the big picture with more localised ones based on the fine-scale surrogates. This transition from broad-scale planning to fine-scale implementation has received little attention.

The Cape Action Plan for the Environment (CAPE), a systematic conservation and implementation process for South Africa's Cape Floristic Region (CFR) (see Cowling and Pressey, in press; Younge and Fowkes, in press) provided a rare opportunity for assessing the effects of spatial scale on systematic conservation planning. Cowling and Heijnis (2001) mapped broad habitat units at 1:250,000 to support a conservation plan for the whole CFR. In a region in the south of the CFR, finer-scale mapping of vegetation types at 1:10,000 and a development of a conservation plan for achieving targets for these types were completed to provide insights for implementing conservation action on the ground (Cole et al., 2000). In this paper, I apply the same planning protocol to both data sets and compare the patterns of conservation values that emerge. Several measures have been suggested to quantify the conservation value of an area and to assess the efficiency of reserve systems. Conservation value of any area, and therefore its prioritisation, can be quantified by its relative contribution to the conservation target (Ferrier et al., 2000).

Specifically, this study has three aims: (i) to compare the efficiency of broad-scale conservation planning in achieving conservation targets derived at a fine-scale; (ii) to compare differences in patterns of conservation values at broad and fine scales; and (iii) to assess how the spatial scale of primary data layers (broad habitat units, vegetation types, and transformation of native vegetation) affect the outcomes of conservation planning.

Methods

Study area

The Agulhas Plain (2 160 km^2) is part of the Cape Floristic Region (CFR), one of the global hotspots of plant diversity and endemism (Myers et al, 2000). The Agulhas Plain is a low coastal peneplain with a complex mosaic of edaphic types and has a typical mediterranean-type climate (mean annual rainfall of 500 mm). It is home to at least 1751 vascular plant species and most local endemic species (ca. 100) are edaphic specialists, occurring in small and scattered populations (Cowling and Holmes, 1992). The predominant vegetation types on the Agulhas Plain are fynbos (on nutrient-poor soils) and renosterveld (on more fertile soils), both sclerophyllous, fire-prone shrublands (Cowling, 1992). The area is extensively impacted and fragmented by agricultural practices, and some 40% of the original natural vegetation has already been thus transformed (Cole et al., 2000). Recently, the South National

Parks Board initiated the establishment of a national park to conserve the lowland fynbos and wetland ecosystems of the southern Agulhas Plain (Heydenrych et al., 1999). The park configuration largely follows the reserve system identified by Lombard et al. (1997).

The data

I used the protocol and the data developed in the CAPE and Agulhas Plan projects as baseline data (see Cowling et al., 1999b; Cole et al., 2000; Cowling et al., in press). Two systems of notional reserves were designed for the study area: one at a broad scale (1:250 000) derived from the CAPE project (Cowling et al., 1999b), and the other at a finer scale (1:10 000) derived from the Agulhas project (Cole et al., 2000). Both systems were developed using the same procedure. All the data were digitised in a Geographic Information System where the analysis was completed. The two notional systems were derived from the data sets presented in Table 1. The characteristics of each data set are summarised here. Broad-scale data (used for the CAPE project, see CAPE data set in Table 1) and fine-scale data (used for the Agulhas project, see Agulhas data set in Table 1) are presented for each category (biodiversity, habitat transformation, and planning units). Data and methods are described in more details by Cole et al. (2000) for the fine-scale study and by Cowling et al. (1999b) for the broad-scale study.

Biodiversity surrogates

A system of land classes was developed to act as broad-scale biodiversity surrogates for the CFR. Although floristic and botanical knowledge is substantial for the Cape Floristic Region, no system of land classes at a sufficiently fine scale was available for the entire area that could be used for regional conservation planning (Cowling and Heijnis, 2001). In the CFR, plant biodiversity is largely driven by

Table 1. Framework for analysing the effect of spatial scale on conservation planning. For each factor (biodiversity, habitat transformation mapping, and planning units) I used data from fine and broadscale mapping while holding the two other factors as fixed (based on the Agulhas data set). Results from data sets 1, 2, and 3 were compared with results from the Agulhas data set. Changes in the factor analysed are shown in bold.

Data sets	**Factor analysed**	**Biodiversity features**	**Habitat transformation mapping**	**Planning units**
Original				
Agulhas		vegetation types (36)	ground survey	cadastral units
CAPE		BHUs (9)	remote sensing	1/16th degree square
Derived				
Data set no 1	Biodiversity	**BHUs**	ground survey	cadastral units
Data set no 2	Habitat transformation	vegetation types	**remote sensing**	cadastral units
Data set no 3	Planning units	vegetation types	ground survey	**1/16th degree square**

climate, geology and topography (Cowling, 1992), therefore land classes were identified on the basis of these three factors as well as expert knowledge. Broad habitat units (BHUs) were derived on the basis of unique combinations of geology, climate and topography. One hundred and two BHUs were derived for the CFR planning domain, of which nine occur on the Agulhas Plain (Fig. 1).

Fine-scale biodiversity surrogates were developed by mapping vegetation types in the field for the entire Agulhas Plain (2 160 km^2). Vegetation units identified by Cowling et al. (1988) were used as the basis for vegetation groups for the study area. These vegetation units were further divided during field mapping by an expert botanist. Vegetation types were defined on the basis of dominant and differential plant species. Thirty-six vegetation types were mapped and these were used as biodiversity features for fine-scale (1:10 000) conservation planning (Fig. 1).

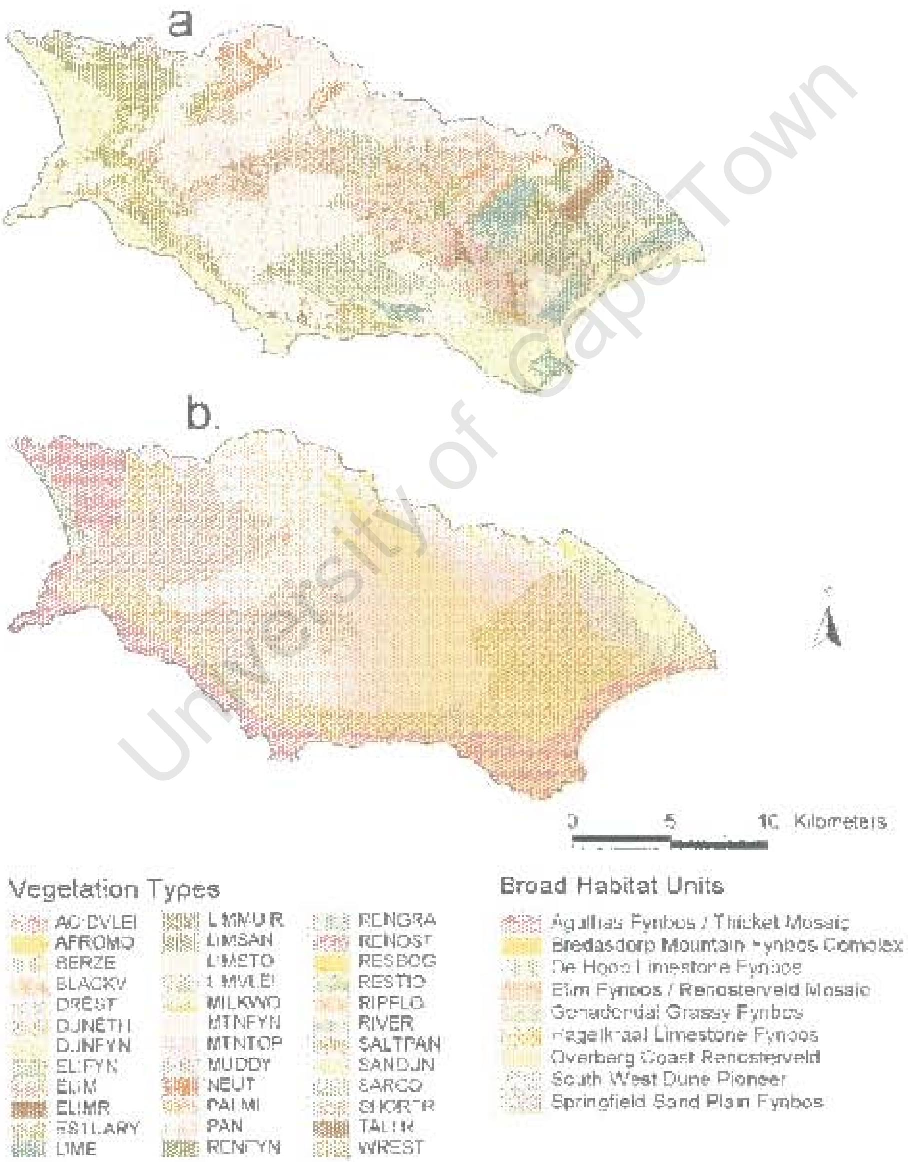


Figure 1. Differences in biodiversity pattern arising from the scale of mapping biodiversity features. a. Thirty six vegetation types (1:10 000, on top) were identified at fine-scale (Agulhas data set); b. nine Broad habitat units (1:250 000, bottom) were used for broad-scale conservation planning (CAPE data set).

Habitat transformation pattern

Assessing the spatial extent and configuration of transformed areas (i.e. agriculture, urbanisation, and invasive alien plants) is crucial for conservation planning. The spatial dimensions of habitat transformation identifies the area available for planning (i.e. area still considered as "natural") and play a role in setting conservation targets for biodiversity features (Pressey et al., in press; see below). Current (1996) patterns of habitat transformation were assessed at broad scale for the entire CFR by means of satellite imagery (Chapter 4). A Landsat image was classified using supervised classification. Because of the scale of the CAPE project, the minimum mapping unit was 25 ha (i.e. no patch of natural vegetation was distinguished below 25 ha). Fine-scale mapping of transformed and untransformed areas was derived based on aerial photographs (1: 10 000) and complemented by extensive, expert-based ground survey for the Agulhas Plain (Cole et al., 2000). Owing to habitat fragmentation, most of the remaining vegetation occurs on small fragments. In both the broad- and fine-scale studies, areas covered in dense stands of invasive species (wattles, pines, and eucalyptus) were not considered for achieving conservation targets.

Planning units

Planning units (also called selection units) consist of *a priori* subdivisions of the landscape and are used for developing a system of reserves (Pressey and Logan, 1998). They are usually different in size and configuration from the biodiversity features to protect. Reserve selection algorithms, such as those embedded in C-Plan, assess the importance of each planning unit for achieving pre-defined conservation targets (see below). In many conservation planning studies, planning units usually comprised arbitrary subdivisions of grid cells (such as quarter degree squares) but cadastral boundaries, and property boundaries were also used (Pressey and Logan, 1998). The size and configuration of planning units can importantly influence the outcome of reserve selection algorithms (Pressey and Logan, 1998).

In order to derive a systematic conservation planning for the CFR, planning units were based on sixteen-degree squares (SDS, approximately 3900 ha). For a better representation of existing protected areas, the exact configuration of protected areas was used as planning units. Thus, in this case, broad-scale planning units consisted of sixteen-degree squares wrapped around boundaries of protected areas. Because the fine-scale (Agulhas Plain) study was aimed at identifying implementation opportunities and constraints associated with land tenure and incentives (Pence et al., in press), cadastral units, which are largely coincident with farm boundaries under single ownership, were used for fine-scale conservation planning in the Agulhas Plain (Table 1).

Data sets were compiled which recorded the occurrence of unique biodiversity features (area of BHUs or vegetation types) per planning unit (sixteenth degree square or cadastral unit). Only the area currently untransformed (i.e. available for planning) was recorded. Reserve selection algorithms, such as those embedded in C-Plan, select sets of planning units to represent pre-defined conservation targets for each biodiversity feature (expressed as percentage area targets).

Spatial analysis of conservation value and priority

Conservation targets interpret the broad, qualitative conservation goal for a planning domain. In both the broad- and fine-scale studies, this goal was to identify and implement a system of conservation areas that would ensure adequate representation of the region's biodiversity (Cole et al, 2000; Cowling et al., 1999). Targets were set for each biodiversity features (9 BHUs in the broad-scale study and 36 vegetation types in fine-scale study). They were expressed as a percentage of the extant area (i.e. currently untransformed) of each biodiversity feature. Targets for each feature should not be equal but should vary according to the need for conservation (Pressey and Taffs, 2001). For both systems (broad and fine scale), conservation targets were allocated with the formula:

$$TARGET = B + R$$

where B is a baseline target, which accommodates differential patterns of plant species turnover and R is a retention target included to retain a proportion of the extant habitat in relation to future biodiversity threats and extent of current habitat transformation. In the fine-scale Agulhas data set, baseline targets were 10% of original area for vlei and forest vegetation types, 15% for lowlands vegetation types and 25% for montane vegetation types. In the broad-scale CAPE data sets, baseline targets were 10% of original area for lowland BHUs, and 15% for upland BHUs. Retention targets were allocated as follows:

$$R = H \times (1 + [t - e] / e)$$

where H is a threat weighting component, t the original area of the biodiversity feature, e the extant area (i.e. currently untransformed). Spatially-explicit predictions of future urbanisation, agriculture and invasive alien plants were derived (see Chapter 4; Cole et al., 2000) to assess the potential of future habitat transformation for each biodiversity feature. If the highest potential was high, then H was 30% of extant habitat, if the highest potential was medium, then H was 15%, and if the highest potential was low, then H was 0% of the extant habitat (see Pressey et al., in press for a complete description on how the targets were set). Biodiversity features likely to be transformed in future thus received higher conservation targets. Final conservation targets ranges from 11.7% to 100% of the extant area (i.e. untransformed area) of vegetation types, and from 55 to 100% of the extant area of BHUs. Pressey et al. (in press) provide additional discussion on the rationale for target setting.

Reserve selection algorithms select a set of areas (based on planning units) to achieve nominated conservation targets. Such selection of planning unit has been termed "minimum set" and many conservation planning exercises have used minimum sets in the past (e.g. Kirkpatrick, 1983; Possingham et al., 2000). However, a minimum set tells us very little about the contribution of unselected areas and the relative contribution of each planning unit to the conservation targets. There may be many alternative minimum sets for achieving the same target (Pressey et al., 1997). To counter the limitations of minimum sets, a measure has been developed which reflects the relative importance of any area in contributing to the conservation target. This measure has been termed "irreplaceability" (Pressey et al., 1994). Irreplaceability values range from 0 (not needed) to 1 (irreplaceable, necessary to achieve conservation goal). Previous studies have shown that the choice of planning units as well as the biodiversity features influence minimum sets and irreplaceability measures (Pressey and Logan, 1998; Pressey et al., 1999).

I used C-Plan for deriving minimum sets and irreplaceability values across the Agulhas Plain using two data sets, namely the CAPE and the Agulhas projects (described above, see Table 1). Differences in minimum set identified and irreplaceability patterns between fine and broad scale conservation planning could thus emerge from three factors:

- the use of different biodiversity features (BHUs vs. vegetation types),
- the use of different methods for mapping habitat transformation (remote sensing vs. ground surveys), and
- the use of different planning units (sixteenth degree squares vs. cadastral units).

These differences could translate into inadequate implementation priorities when moving from the broad- to fine-scales. For example, broad-scale assessment could fail to select high-priority areas that would only be identified using fine-scale data. In this paper, I explore situations where differences in minimum sets and irreplaceability values would arise. As differences could emerge form three factors (see above) and in order to assess the relative importance of each factor, I analysed each factor separately (Table 1) while holding the other constant. I therefore compiled three other data sets that combine fine-scale data from the Agulhas project and one broad-scale component derived from the CAPE project (see "derived" data sets in Table 1). Data set 1 consisted of fine-scale pattern of habitat transformation (derived from ground-survey), fine-scale planning units (cadastral units) but used broad-scale biodiversity data (9 BHUs). Data 2 consisted of fine-scale biodiversity features (36 vegetation types) and planning units, but used broad-scale pattern of habitat transformation (derived from remote-sensing). Finally, data set 3 consisted of fine-scale biodiversity and habitat transformation pattern but used broad-scale planning units (sixteenth degree squares) (Table 1). Minimum sets and irreplaceability values obtained from these three derived data sets were compared with the original fine-scale data, the Agulhas data set (Table 1).

The analysis was subdivided into two sections: 1) the extent to which conservation planning using broad-scale components (biodiversity, transformation mapping, and planning units) achieve fine-scale conservation targets (identified for the 36 vegetation types); and 2) the factors driving patterns of irreplaceability at fine and broad scale.

Minimum sets

For each data set (see Table 1), minimum sets were generated to achieve all conservation targets. Minimum sets are likely to differ because either planning units or conservation targets or both differ for each data set. Conservation targets vary between data sets (Agulhas, CAPE, 1, and 2) as these data sets are based on different biodiversity features and/or mapping of habitat transformation. Planning units differ between data sets (Agulhas, CAPE and 3). Five minimum sets were generated. I then computed the percentage of the untransformed area of each vegetation type that was selected in each resulting minimum set and quantify the extent to which this minimum set contribute to conservation targets defined for the Agulhas Plain at the fine-scale level (Agulhas data set in Table 1). For each minimum set, I calculated the number of vegetation types for which conservation targets (as calculated in the original Agulhas data set) were achieved. An index of reserve design efficiency was compiled as follows:

$$EFFICIENCY = CONTRIB \,/\, MIN\ SET$$

where *CONTRIB* is the total area of selected untransformed vegetation contributing to conservation targets as defined in the Agulhas data set, and *MIN SET* is the total area selected for each minimum set.

Irreplaceability pattern

Irreplaceability pattern was generated by C-Plan for each data set (see Table 1) and compared to irreplaceability values found using fine-scale data (Agulhas data set). I used classification trees in S-Plus (Chambers and Hastie, 1992) to identify which variables influence irreplaceability pattern. Classification trees are very suitable for such analysis because they can incorporate both categorical and continuous factors, and because of their ability to detect interactions and non-additive behaviour among variables (Breinam et al, 1984; Hastie et al., 2001). These non-parametric methods are also distribution-free. Previous studies have shown that classification trees generate more accurate results for analysing determinants of distribution than traditional regression techniques (De'ath and Fabricius, 2000; Rouget et al., 2001).

This study focussed more on understanding the data structure then predicting the outcomes with high accuracy; therefore classification trees were kept simple and with relatively few terminal nodes (less than 8). Trees were pruned after 6 nodes in each case.

Effect of scale of biodiversity mapping on irreplaceability pattern

Two maps of irreplaceability were derived using the Agulhas data sets and data set no 1 (Table 1). Biodiversity features consisted of BHUs (data set no 1) and vegetation types in the Agulhas data set (Table 1). Habitat transformation mapping and planning units did not vary between data sets. They were those derived in the finer-scale Agulhas project (Agulhas data set, Table 1). I then analysed differences in irreplaceability values at the cadastral level using classification trees in S-Plus (Chambers and Hastie, 1992). All planning units less than 25 ha were ignored to account for the mapping accuracy of the broad-scale data (mapped at 1:250 000). Irreplaceability values were grouped in 5 categories: <0.2, 0.2-0.4, 0.4-0.6, 0.6-0.8, and > 0.8.

The data set consisted of 670 cadastral units. The dependent variable, the difference in conservation value (irreplaceability), was categorised as follows:

- 0 (match between two scales, i.e. same irreplaceability category in both data sets)
- +1 (over-estimate of conservation value from the data set no 1 using broad-scale biodiversity features)
- -1 (underestimate of conservation value from the data set no 1 using broad-scale biodiversity features).

The following factors were considered as potential predictors of differences in irreplaceability: the total area of the cadastral unit, the area of untransformed vegetation within a cadastral unit, the presence/absence of all BHUs and vegetation types occurring in the cadastral unit, and the number of vegetation types present in the cadastral unit. Because the planning units (cadastral units here) are not homogenous in size, such unweighted analysis would give similar importance to differences in irreplaceability value for small or large cadastral units. Preliminary weighted analysis (weight proportional to area of cadastral unit) generated regression trees with similar significant factors as unweighted analysis; therefore unweighted analysis was performed throughout the study.

Effect of the scale of habitat transformation mapping on irreplaceability pattern

I compared irreplaceability pattern obtained from the Agulhas data set and the data set no 2 (Table 1). The calculation of targets for biodiversity features and the area available for conservation planning were derived from two estimates of habitat transformation (remote sensing and ground surveys). Biodiversity features and planning units were as for the Agulhas project; i.e. vegetation types and cadastral units, respectively (Table 1). Two maps of irreplaceability were produced and I analysed difference in irreplaceability values at the cadastral level using a classification tree as above. The data set consisted of 670 cadastral units and the same dependent and independent variables were used as above.

Effect of the size of planning units on irreplaceability pattern

I compared irreplaceability pattern generated from the Agulhas data set and the data set no 3 (Table 1). These data sets were derived using cadastral units (Agulhas data set) and sixteenth degree squares (data set no 3) as planning units. Biodiversity features and threat mapping were as for the Agulhas project (Table 1). Irreplaceability values were generated for each data set. Because these two data sets are based on different planning units, they did not share any spatial directly comparable entities. Both layers of planning units (cadastral units for data set Agulhas, sixteenth degree squares for data set no 3) were intersected to obtain comparable units. This resulted in 961 new polygons for which the irreplaceability values derived from the Agulhas data set and the data set no 3 were retained. Therefore, each of the new 961 polygons had irreplaceability values from the cadastral unit and from the sixteenth degree square to which they belong. Each new polygon also retained the original attributes (such as vegetation types present) of the cadastral unit and sixteenth degree square they originated from. Differences in conservation value for all polygons (n=961) could then be related to differences in biodiversity representation within the original cadastral unit and sixteenth degree square. The analysis was done using classification tree as described above.

Analysis of spatial patterns of biodiversity and habitat transformation at fine and broad-scale

Irreplaceability pattern is likely to be driven by few highly irreplaceable biodiversity features for which all extant fragments are required to achieve conservation target. I used correlation biplots (Gower and Hand, 1996) to identify the characteristics of the broad-scale biodiversity features (9 BHUs) and the fine-scale ones (36 vegetation types). Biplots illustrate the relationships between biodiversity features (BHUs and vegetation types) and the factors likely to influence irreplaceability value or conservation targets. For each biodiversity entity, the following factors were considered: extent (expressed as % of total area), extant portion (expressed as % of original extent of vegetation), conservation target (in % of extant area of the biodiversity entity considered), mapping accuracy of untransformed vegetation (between broad-scale remote sensing and fine-scale ground survey mapping), habitat diversity (number of vegetation types per BHU - used for BHUs only), and nestedness (% of vegetation area nested within one BHU - used for vegetation types only).

Biplots are very useful techniques for visualising multivariate data (Gabriel, 1971; Underhill, 1990). They can be considered as the multivariate analogue of bivariate scatter diagrams. They show a scatter of *n* points, representing the *n* samples, and superimpose information on the original variables, represented by vectors starting from the origin. As the scatter of points is derived by multidimensional scaling, some degree of approximation must be accepted to display the information in two dimensions (Gower and Hand, 1996). In this study, I used correlation biplots, which display best correlation between variables. Biplots were created with the software SVDD (Greenacre and

Table 2. Contribution to fine-scale conservation targets in relation to different data sets. This represents the extent to which conservation targets set for vegetation types were achieved using minimum set identified for the following data sets. Data set are described in Table 1. **Area required**: total area (in ha) necessary to achieve conservation targets; **No of veg. types conserved**: number of vegetation types for which conservation targets have been achieved; **Targeted area**: Total area of untransformed vegetation contributing to fine-scale conservation targets (as defined in the Agulhas data set); **Efficiency**: ratio of targeted area and total untransformed area selected in the minimum set (a ratio of 100% means that all conservation targets has been achieved in the minimum amount of land).

Data sets	Factor analysed	Area required (ha)	No of veg types conserved	Targeted area (ha)	Efficiency (%)
Original					
Agulhas		154 014	36	67 137	81.6
CAPE		158 718	27	64 748	71.2
Derived					
Data set no 1	Biodiversity	167 089	26	63 814	67.1
Data set no 2	Habitat transformation	161 220	31	65 981	73.9
Data set no 3	Planning units	179 124	36	67137	70.6

Underhill, 1981). The cosine between the vectors of two variables represents the coefficient of correlation between these two variables. The scalar product between a sample point and a variable (Y) gives information on the relation between the Y-value for the sample point and the mean of Y (Gower and Hand 1996).

The spatial characteristics of biodiversity features (BHUs and vegetation types) and land cover (agriculture and remaining natural vegetation) were also compared at both scales. Both biodiversity layers were spatially intersected and I derived frequency distribution of each vegetation type in relation to the nine BHUs. This was then used to assess the extent to which vegetation types were nested within broader biodiversity units (BHUs). The spatial match of habitat transformation pattern was also compared at both scales. Each layer of transformed/untransformed vegetation was converted to a 25m grid and I derived confusion matrix (cross-tabulation of untransformed/transformed areas) to assess the level of correspondence between the two scales.

Results

Efficiency of minimum sets at fine and broad-scale

The fine-scale conservation planning, identified by a minimum set algorithm based on the Agulhas data set, achieved all conservation targets (36 vegetation types, 67 137 ha required) in 154 014 ha (66% of the whole Agulhas Plain). This represents an efficiency of 81.6% (67 137 ha targeted in 82 293 ha of untransformed vegetation selected, Table 2). The broad-scale conservation planning, based on the CAPE data set, achieved all conservation targets for the nine broad habitat units in 158 718 ha (68% of the total area). Although, these two minimum sets (based on Agulhas and CAPE data sets) were derived independently, there was relatively good spatial overlap between the two conservation plans. The area selected based on sixteenth degree squarea planning units for broad-scale conservation targets also captured a substantial amount of the area required for achieving fine-scale conservation

Table 3: Characteristics of fine-scale biodiversity features of the Agulhas Plain. **Target:** the % of the extant of each vegetation type required; **Nestedness**: % of each vegetation type occurring in one BHU, **Mapping accuracy**: accuracy between habitat transformation mapping at fine and broad scale, **Failed target** refers to the conservation plan in which this target could not be achieved (C: CAPE data set (broad-scale plan), B: data set 1 (biodiversity features), T: data set no 2 (habitat transformation), see Table 2).

	Vegetation type	**Area (ha)**	**% extant**	**Target (%)**	**Nestedness**	**Mapping accuracy**	**Failed target**
1	Acid Vlei (ACIDVLEI)	97.4	100.0	25.0	98.7	28.5	
2	Afromontane Forest (AFROMO)	107.8	85.7	45.9	75.8	100.0	T
3	Berzelia Riparian (BERZE)	4360.4	65.4	63.2	44.0	96.2	
4	Black Vlei (BLACKV)	146.3	81.0	30.1	34.2	92.8	
5	Dry Restioid Fynbos (DREST)	2355.8	36.3	65.8	93.1	65.7	C
6	Dune Thicket (DUNETH)	90.7	97.5	25.6	41.0	76.9	
7	Dune Fynbos (DUNFYN)	29644.8	79.9	36.7	80.0	96.2	
8	Elim Fynbos (ELIFYN)	13270.0	39.3	86.3	92.0	84.0	T
9	Elim Asteraceous Fynbos (ELIM)	23256.2	15.3	100.0	81.1	78.9	C, B
10	Elim Riparian (ELIMR)	3340.9	41.7	83.4	74.1	70.4	
11	Estuary (ESTUARY)	268.2	98.9	25.2	61.9	97.4	
12	Limestone Fynbos (LIME)	10360.3	81.8	18.3	61.9	96.6	
13	Limestone dominated by *Leucospermum muirii* (LIMMUIR)	727.3	90.2	16.6	54.7	97.1	
14	Limestone and Sand (LIMSAN)	15918.7	59.3	67.4	38.7	96.1	C, T
15	Limestone Outcrop Fynbos (LIMSTO)	2023.8	71.5	40.2	47.5	94.9	
16	Limestone Vlei (LIMVLEI)	2.1	90.8	43.7	100.0	100.0	C, B
17	Milkwood Thicket (MILKWO)	991.7	82.6	47.3	48.7	91.0	
18	Mountain Fynbos (MTNFYN)	52299.4	79.1	49.7	50.9	97.9	
19	Mountain Top Fynbos (MTNTOP)	7919.0	94.8	26.3	72.3	99.9	
20	Muddy Vlei (MUDDY)	1009.7	95.3	26.1	77.9	99.3	
21	Transitional Fynbos (NEUT)	4944.9	33.9	94.0	43.6	83.8	C, T, B
22	Palmiet Riparian (PALMI)	3144.0	58.1	68.3	55.6	87.9	
23	Pans (PAN)	45.0	52.7	41.0	57.2	0.0	
24	Renoster Fynbos (RENFYN)	8376.7	14.4	100.0	73.2	23.0	C, B
25	Renoster Grassland (RENGRA)	5236.7	27.0	100.0	50.4	2.2	T, B
26	Renosterveld (RENOST)	4298.7	21.4	100.0	59.1	21.2	C, B
27	Restio Bog (RESBOG)	33.0	100.0	45.0	100.0	100.0	
28	Restioid Wetland (RESTIO)	3462.8	81.8	53.7	49.4	61.0	B
29	Riparian Flood Plain (RIPFLO)	394.5	51.7	73.5	90.4	93.7	
30	Rivers (RIVER)	251.1	68.9	53.8	64.3	65.8	C
31	Salt Pan (SALTPAN)	354.5	85.2	11.7	72.7	97.8	
32	Sand Dune (SANDUN)	2460.7	99.4	25.1	88.8	99.1	
33	*Sarcocornia* Wetland (SARCO)	381.9	57.2	38.8	69.2	70.3	C
34	Short Reed (SHORTR)	1998.2	70.0	60.4	54.7	53.8	B
35	Tall Reed (TALLR)	3907.5	68.6	61.2	41.8	65.1	B
36	Wet Restioid Fynbos (WREST)	8517.1	59.0	67.6	63.3	84.9	

targets. The CAPE minimum set achieved fine-scale targets for 27 vegetation types with an efficiency of 71.2% (Table 2). The effects of varying biodiversity features, transformation mapping and planning units on minimum set efficiency are summarised in Table 2. The choice of biodiversity features seems to have the greatest effect on achieving fine-scale targets. The area selected by a minimum set using BHUs as biodiversity features would adequately protect 26 of the 36 vegetation types (i.e. target met) with the lowest efficiency (67.1%, Table 2). A minimum set using remote-sensing mapping of habitat transformation (as opposed to ground survey) will meet conservation targets for 31 vegetation types; the missing one are listed in Table 3. A conservation plan based on larger planning units (sixteenth degree square) required more land than a conservation plan based on cadastral planning units for the same level of conservation target achievement (Table 2). Large planning units were less efficient than smaller ones for achieving the nominated conservation targets.

What drives patterns of irreplaceability at fine and broad-scale?

Although fine-scale conservation targets could be achieved to a certain extent by minimum sets using any broad-scale component (biodiversity features, transformation mapping, or planning units), the spatial pattern of irreplaceability (the conservation value of each planning unit) differs considerably.

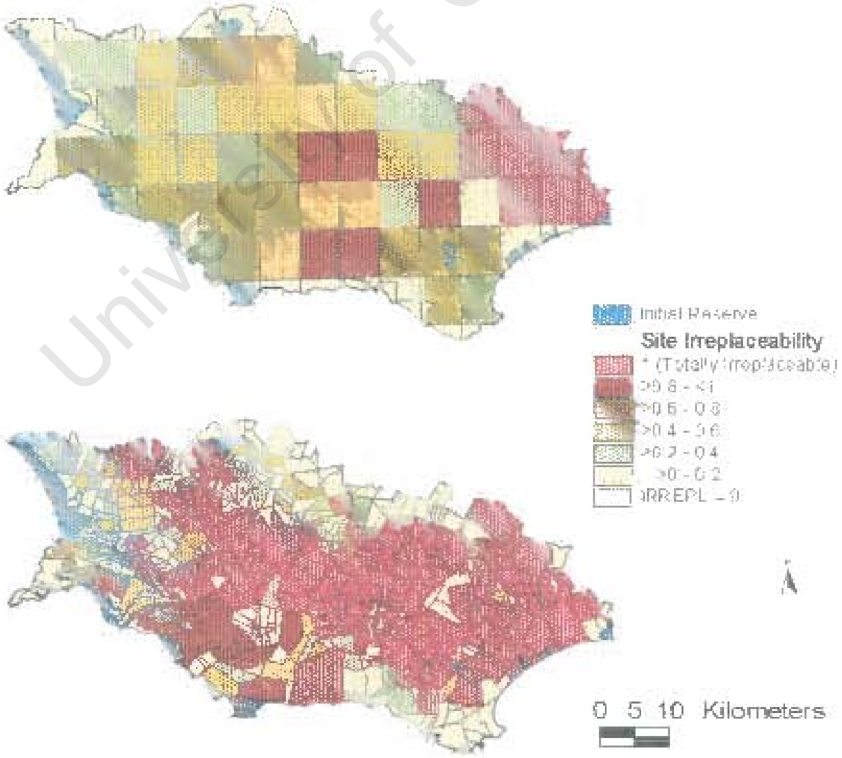


Figure 2: Spatial pattern of conservation value (irreplaceability) from broad-scale (1: 250 000 scale, on top) and fine-scale (1: 10 000, bottom) conservation planning. Broad-scale data consisted of nine broad habitat units (BHUs), habitat transformation mapped by remote-sensing and planning units comprising 1/16th degree squares. Fine-scale data consisted of 36 vegetation types, habitat transformation mapped by ground survey, and cadastral boundaries as planning units.

Table 4: Differences in conservation value (irreplaceability) in relation to the spatial scale of biodiversity features, habitat transformation mapping and size of planning units. Irreplaceability values obtained from Agulhas data (fine-scale) were compared to broad-scale data for the factor of concern (see Table 1). Values are shown in % of total area.

Comparison	Data sets	Similar values	Broad-scale overestimation	Broad-scale underestimation
Overall	CAPE vs. Agulhas	18.3	27.7	54.0
Biodiversity	1 vs. Agulhas	36.3	2.9	60.8
Habitat transformation	2 vs. Agulhas	79.1	12.2	5.8
Planning units	3 vs. Agulhas	56.1	33.6	10.3

Fig. 2 shows the differences in irreplaceability patterns across the Agulhas Plain obtained from the CAPE data set (1:250 000 scale) and from the Agulhas data set (1:10 000 scale). Almost 50% of the total area was considered as irreplaceable (i.e. absolutely necessary to achieve conservation targets) using fine-scale data (Agulhas data set, Table 1) compared to 11% when using broad-scale data (CAPE data set, Table 1). Only 18.3% of the area had similar irreplaceability value between broad-scale (regional) and fine-scale (local) conservation planning (overall comparison, Table 4). The conservation value of 54% of the area was regionally underestimated, while 27.7% was overestimated compared to conservation values found at fine-scale conservation planning (overall comparison, Table 4).

A classification tree was used to understand which factors explained the differences between irreplaceability values at fine scale (Agulhas data set) and broad-scale (CAPE data set). Almost 80% of these differences could be explained by the presence of one vegetation type, the number of vegetation types per planning unit and the area of four BHUs per planning units (Fig. 3). Differences in irreplaceability values were largely influenced by the presence of the vegetation type Elim Asteraceous Fynbos (first factor in the classification tree model, Fig. 3). Irreplaceability value derived from fine scale data was higher in areas where this vegetation type occurs. Elim Asteraceous Fynbos had a fine-scale conservation target of 100% of its extant habitat; therefore, every planning unit where it occurs was required for the fine-scale conservation plan. At broad-scale, this vegetation type was predominantly mapped as BHU Elim Fynbos/Renosterveld Mosaic, which has a lower conservation target. Irreplaceability value derived from fine scale data was also higher in planning units where more than four vegetation types occur. There was a significant positive relationship between irreplaceability value and number of vegetation types per cadastral unit ($R^2 = 0.31$, $p < 0.001$). Heterogeneous planning units (i.e. with high number of vegetation types) tend to contain highly transformed vegetation types (with high conservation targets) and therefore have higher irreplaceability values than homogeneous planning units. Irreplaceability values derived from broad-scale data were higher in areas where the BHUs Elim Fynbos/Renosterveld Mosaic, Springfield Sand Plain Fynbos, and Agulhas Fynbos/Thicket Mosaic (medium to high priority BHUs based on targets) occur over

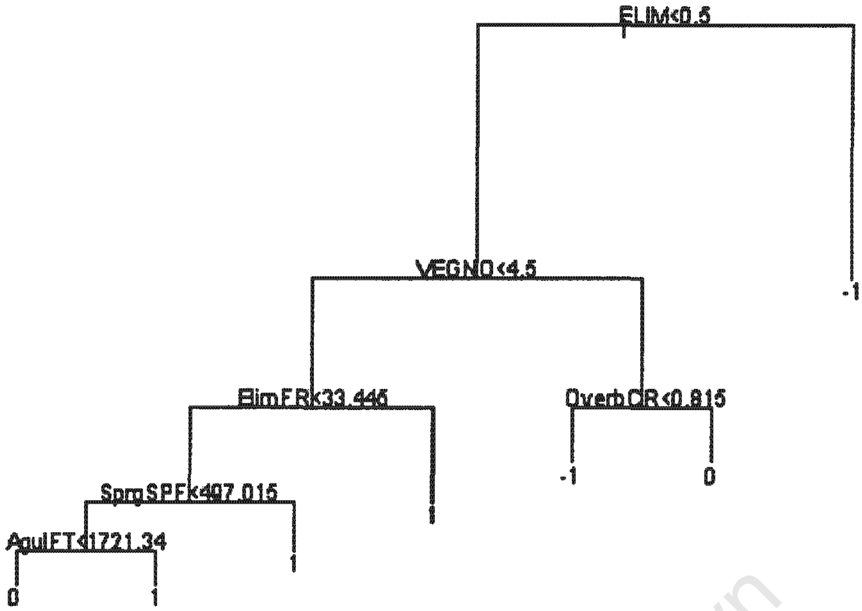


Figure 3. Differences in conservation value between broad-scale and fine-scale conservation plans. The classification tree was generated in S-Plus. The model is based on 961 planning units (see methods). Areas of the vegetation type Elim asteraceous Fynbos (ELIM), and the BHUs Elim Fynbos Renosterveld Mosaic (ElimFR), Overberg Coast Renosterveld (OverbCR), Springfield Sand Plain Fynbos (SprgSPF), and Agulhas Fynbos Thicket Mosaic (AgulFT) are indicated in ha. VEGNO: number of vegetation types present in broad-scale planning units. The condition on top of the branch applies for the left side of the branch. Outcomes are predicted as follows: 0 (match between two scales, i.e. same irreplaceability category in both data sets), +1 (over-estimate of conservation value from the broad-scale data), -1 (underestimate of conservation value from the broad-scale data).

relatively large areas (Fig. 3). At fine-scale (i.e. using Agulhas data set), planning units where these three BHUs predominate scored lower irreplaceability values partly because, in these planning units, "pockets" of low priority vegetation types occur among the large areas of medium to high priority BHUs.

Below I present in more details how changes in scale for biodiversity features, threat mapping and planning units affect pattern of conservation value.

BHUs vs. vegetation types

There were significant differences in conservation value between conservation plans using fine-scale and broad-scale biodiversity features (biodiversity comparison, Table 4). Although similar conservation values were found in 36.3% of the Agulhas Plain, the use of BHUs (broad-scale biodiversity features) underestimated conservation value in 60.8% of the area. In less than 3% of the area, the use of vegetation types (fine-scale biodiversity features) underestimated conservation value.

A classification tree using five variables could accurately explain 85% of the differences in conservation value between the two data sets (Fig. 4). The presence of three vegetation types, the remaining untransformed area and the number of vegetation types present in each cadastral unit were

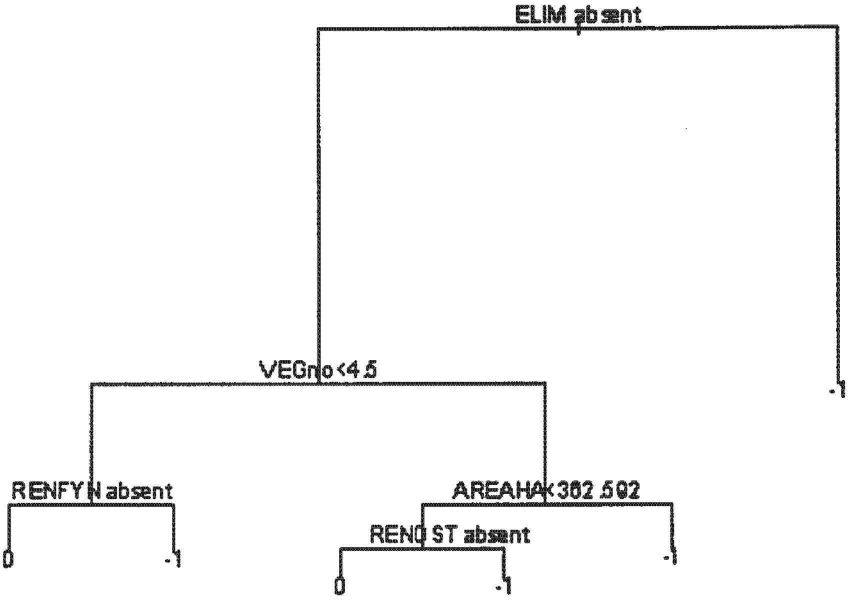


Figure 4. Differences in conservation value between conservation plans using broad-scale and fine-scale biodiversity features. The model is based on 670 cadastral units. The presence of the vegetation types Elim Asteraceous Fynbos (ELIM) Renoster Fynbos (RENFYN), and Renosterveld (RENOST) within the planning units is indicated. AREAHA: area of the planning unit (in ha); VEGno: number of vegetation types present. The condition on top of the branch applies for the left side of the branch. Outcomes are predicted as fdlows: 0 (match between two scales, i.e. same irreplaceability category in both data sets), +1 (overestimate of conservation value from broad-scale data), -1 (underestimate of conservation value from broad-scale data).

the most important factors (Fig. 4). Three considerably transformed vegetation types that were only identified at fine-scale mapping (namely Elim Asteraceous Fynbos, Renosterveld, and Renoster Fynbos) contributed to high irreplaceability values for cadastral units in which they were present. At broad-scale, these vegetation types were mapped as widespread common BHUs with lower conservation targets relative to extant areas. These cadastral units therefore did not score high irreplaceability values by using broad-scale biodiversity features (BHUs). Conservation value was also underestimated using broad-scale biodiversity data in large cadastral units containing more than four vegetation types (Fig. 4).

Habitat transformation from remote sensing vs. ground survey

Conservation value was relatively unaffected by fine or broad-scale mapping of habitat transformation (habitat transformation comparison, Table 4). Similar values of irreplaceability were found in almost 80% of the total area, while the use of remote sensing mapping overestimated irreplaceability in 12% of the area (Table 4). Broad-scale mapping of habitat transformation was found to slightly increase the amount of land needed to achieve all conservation targets (Table 2). Using classification tree model, the remaining difference in irreplaceability value within cadastral units could not be explained by any factor. The scale of habitat transformation mapping however did influence conservation targets. The

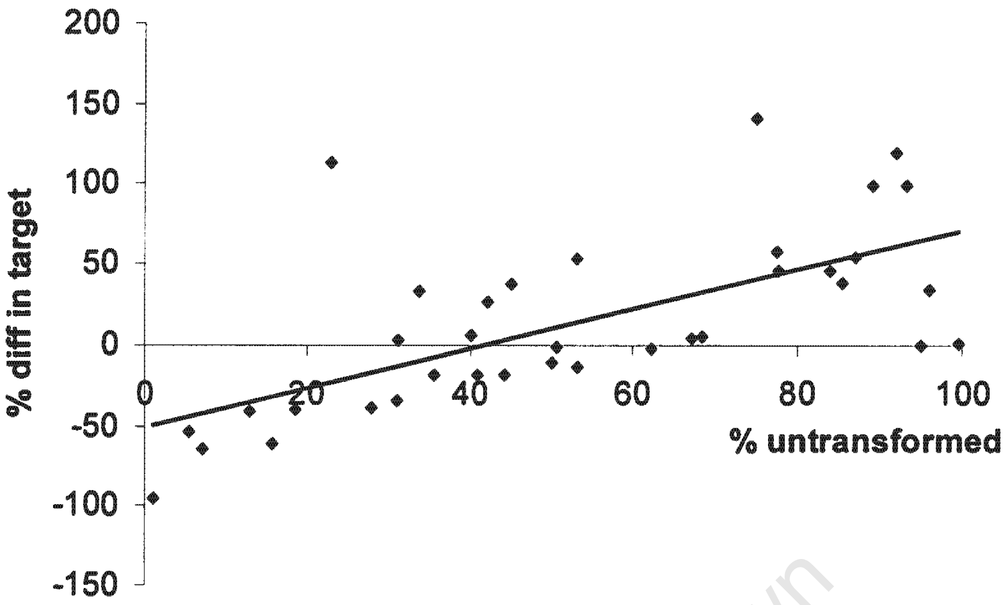


Figure 5. The effect of habitat transformation mapping in setting conservation targets for vegetation types. For each vegetation type, the difference (in %) between target derived using remote sensing mapping of habitat transformation (broad-scale) and target derived using field-mapping (fine-scale) was calculated.

use of broad-scale mapping generated higher targets for untransformed vegetation types (compared to the original fine-scale targets in the Agulhas data set) and lower targets for transformed ones (Fig. 5).

Sixteenth degree square vs. cadastral units

Broad-scale planning units were less efficient (i.e. more land was required) than fine-scale units for achieving all conservation targets for vegetation types (76.8% of the total area required compared to 66%, Table 2). Conservation value was similar in 56% of the area, but the use of sixteenth degree squares generated higher irreplaceability values for 33.6% of the area (comparison of planning units, Table 4).

Almost 75% of the differences in conservation value between the data set no 3 (using sixteenth degree squares planning units) and the Agulhas data set (using cadastral boundaries) could be explained by a classification tree (Fig. 6). The model was based on the four vegetation types and the area of untransformed vegetation in cadastral units. Conservation value was mostly driven by the occurrence of one vegetation type, Elim Asteraceous Fynbos. In cases where this type was present in both planning units (cadastral units and sixteenth degree squares), the irreplaceability value was similar, irrespective of other vegetation types also present (Fig. 6). The same applied for the vegetation type Renoster Fynbos. Conservation targets for these two vegetation types require all the remaining extant area, therefore each planning unit where they occur becomes irreplaceable (irreplaceability value of 1). In most cases where the vegetation types Mountain Top Fynbos and Wet Restioid Fynbos

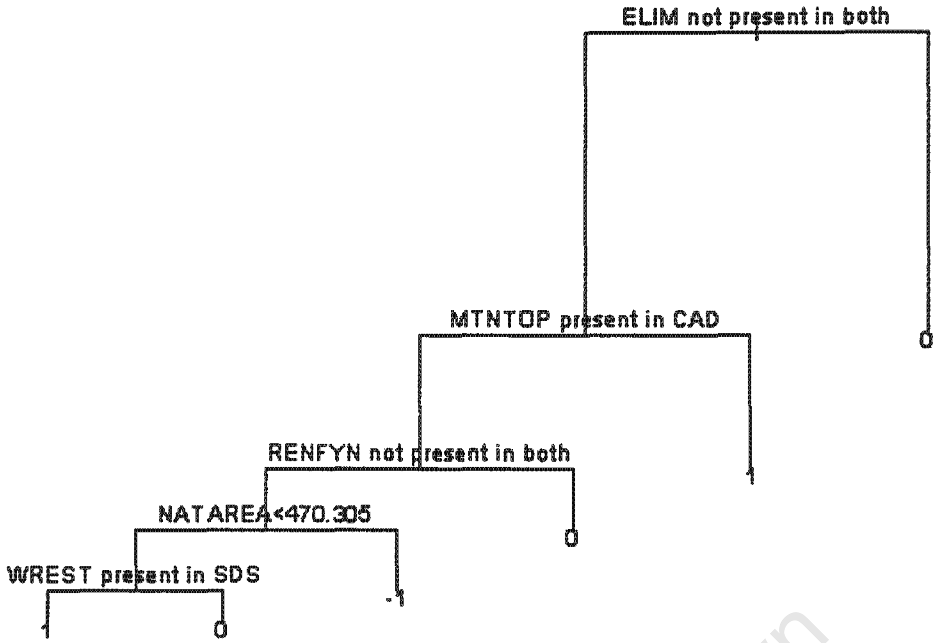


Figure 6. Differences in conservation value between conservation plans using broad-scale (1/16th degree square, SDS) and fine-scale (cadastral boundaries, CAD) planning units. The model is based on 961 planning units. Significant vegetation types were: Elim Asteraceous Fynbos (ELIM), Mountain Top Fynbos (MTNTOP), Renoster Fynbos (RENFYN), and Wet Restioid Fynbos (WREST). NATAREA: area of untransformed vegetation. The condition on top of the branch applies for the left side of the branch. Outcomes are predicted as follows: 0 (match between two scales, i.e. same irreplaceability category in both data sets), +1 (overestimate of conservation value from broad-scale data), -1 (underestimate of conservation value from broad-scale data).

occurs in sixteenth degree square planning units but not in cadastral units, their occurrence led to higher irreplaceability values in the sixteenth degree square planning units (Fig. 6).

Analysis of similarities and differences of basic features at broad and fine mapping scales

The two previous sections have shown the importance of the choice of biodiversity features in both determining pattern of irreplaceability and achieving conservation targets. Here I explore more generally how patterns of biodiversity and habitat transformation changed from fine to broad-scale, and how it relates to irreplaceability patterns and conservation targets.

Patterns of biodiversity and habitat transformation

Conservation targets were not achieved for 15 vegetation types by using either biodiversity features (BHUs), habitat transformation pattern or planning units from the broad-scale data set (see Table 3). These 15 vegetation types shared similar characteristics identified by a multi-variate analysis. A very simple classification tree based on the conservation target and the percentage of untransformed vegetation could correctly classify 32 of the 36 vegetation types into two categories: vegetation types for which conservation targets are achieved in all cases, and vegetation types for which conservation targets are not achieved when using broad-scale components (see Fig. 7). Targets were always

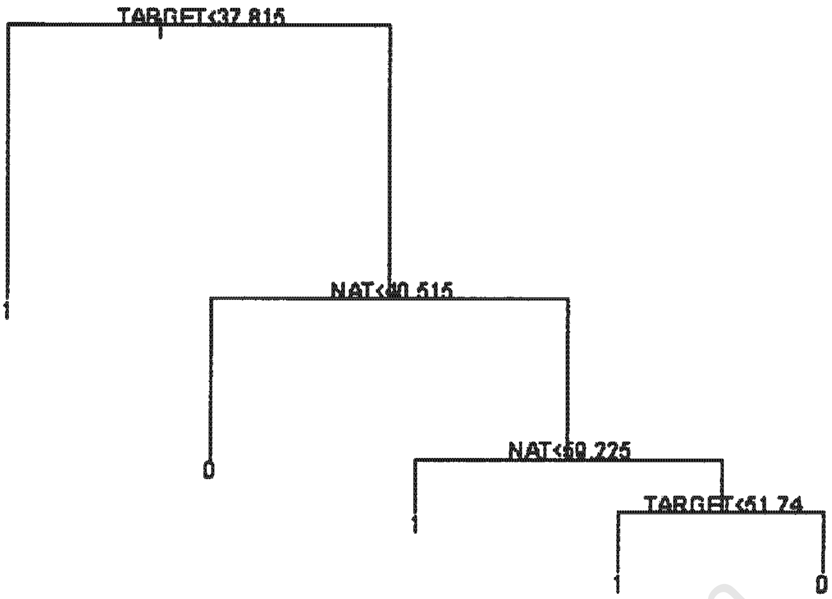


Figure 7. Efficiency of broad-scale conservation planning in achieving conservation targets for 36 vegetation types identified at fine scale. TARGET: original fine-scale conservation target (in % of extant area). NAT: extant area (in % of total area of vegetation type). The condition on top of the branch applies for the left side of the branch. Outcomes are predicted as follows: 0 (conservation target not achieved at broad-scale conservation planning), 1 (conservation target achieved at fine and broad-scale conservation planning).

achieved for vegetation types with low conservation targets (target <37.8% of extant area) while targets for highly-transformed vegetation types with high conservation targets could not be achieved in all cases (Fig. 7). Conservation planning based on broad-scale biodiversity features (BHUs) incidentally included extant portions of vegetation types "and indirectly achieved conservation targets for some of them (26 out of 36, see Table 2). However, conservation targets for some vegetation types are such that all the extant area of these vegetation types is required. This implies that targets for these vegetation types would not be achieved by a broad-scale conservation plan that incidentally selected vegetation types. Broad-scale mapping of habitat transformation underestimated the extant areas of highly-transformed vegetation types that mainly occur on small fragments (see below). The underestimation of extant areas led to a smaller area being selected at broad-scale and, therefore, fine-scale targets could not be achieved for these vegetation types in the broad-scale conservation plan. Conservation planning at the broad scale, therefore, generally fails to achieve conservation targets for highly transformed vegetation types with high conservation targets.

As mentioned earlier, overall differences in irreplaceability patterns could partly be explained by the distribution of four BHUs (see Fig. 3), namely Elim Fynbos/Renosterveld Mosaic (Elim), Springfield Sand Plain Fynbos (Springfield), Agulhas Fynbos/Thicket Mosaic (Agulhas), and Overberg Coast Renosterveld (Overberg). The characteristics of these BHUs are summarised in Fig. 8a. Elim, Springfield and Agulhas are among the most abundant BHUs (Elim covering the largest area), and

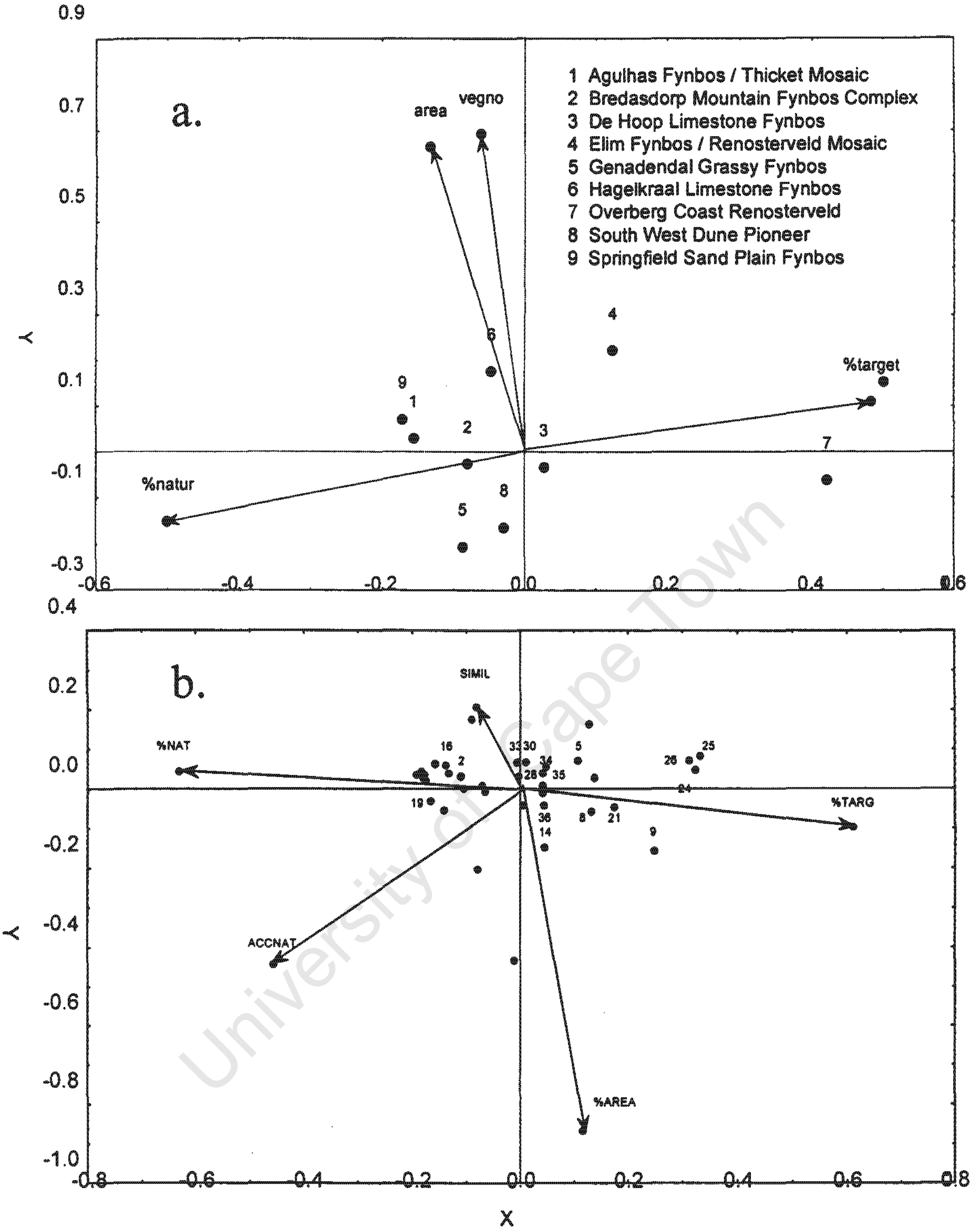


Figure 8: Correlation biplots for (a) broad habitat units and (b) vegetation types. Area: % of total area, %natur: % of extant vegetation, %target: conservation target in % of extant vegetation, vegno: number of vegetation types, ratio: edge/perimeter ratio, Simil: % of the total area of each vegetation type nested within one BHU; Accnat: spatial accuracy between habitat transformation derived at fine and broad scale. Codes for vegetation types are given in Table 3.

Elim and Overberg are also the most transformed BHUs (in percentage) and have the highest conservation targets (in % of extant area).

Similarly, a few vegetation types appeared to influence irreplaceability patterns (see Fig. 3 and 4), namely Elim Asteraceous Fynbos, Renoster Fynbos, Renosterveld, Mountain Top Fynbos, and Wet Restioid Fynbos. Their characteristics are illustrated in a correlation biplot (Fig. 8b). Three of them are the most transformed vegetation types with the highest conservation targets (100% of the remaining vegetation).

As expected, there were some substantial differences in the spatial pattern of biodiversity at both scales. The 36 vegetation types, mapped at the fine scale, were not entirely spatially nested within the 9 BHUs mapped at a coarser scale. For nine vegetation types, less than 50% of their spatial distribution fell within one BHU (Table 3). In other words, boundaries of fine- and broad-scale biodiversity features did not coincide for these vegetation types. However, 11 vegetation types are almost entirely distributed within one BHU. Vegetation diversity (simply expressed as number of vegetation types present) within each BHU, ranging from 2 to 30, could be expressed as a linear function of the BHU area ($R^2 = 0.84$, $p < 0.001$).

Patterns of agriculture and remaining natural vegetation.

Although the extent and the configuration of habitat transformation relative to biodiversity features generated pronounced differences in reserve design efficiency and irreplaceability patterns, the spatial distribution of land available for conservation planning (remaining natural vegetation not densely invaded) was not greatly affected by the scale of the analysis. Almost 80% of the untransformed land mapped at fine-scale (Agulhas data set) was classified as untransformed at broad-scale (CAPE data set). Looking at the spatial distribution of transformed areas, there was also a very good spatial match between the two data sets (86% agreement, Kappa value of 0.69).

Differences in habitat transformation patterns were not randomly distributed throughout the study area and among the 36 vegetation types. Differences were greater for transformed vegetation types. Fig. 8b shows that the variables accuracy of habitat transformation mapping (ACCNAT) and extent of untransformed vegetation (%NAT) are positively correlated ($r = 0.52$, $p < 0.01$). Greater differences in terms of extent of habitat transformation were found for highly transformed vegetation types. Habitat transformation was overestimated at the broad-scale for heavily transformed vegetation types such as renosterveld, as small remnants of natural vegetation were not captured by the broad scale study.

Discussion

This study attempts to demonstrate some of the implications when moving from fine-scale to broad-scale conservation planning and vice-versa. As conservation resources are generally limited, the need for fine-scale conservation planning should be seriously motivated against a generally more rapid conservation assessment at broader scales. Careful attention should be given to whether conservation decisions will benefit from additional information gained at finer scale (Conroy and Noon, 1996). Because of its expenses per unit area, fine-scale conservation planning is usually available only over limited areas, and regional planning therefore uses broad-scale data.

Conservation value, or irreplaceability, was here expressed as a function of the distribution of biodiversity features, the spatial patterns of current and future habitat transformation, and the size of planning units. In this paper I have attempted to tease out the effects of these interacting factors on irreplaceability value and reserve design efficiency at fine (1:10 000) and broad (1: 250 000) scale. Because of the interactive nature of these factors, the results can only be indications of possible consequences of taking conservation decisions at various spatial scales and should be interpreted cautiously.

Moving from broad to fine-scale conservation planning

The analysis of reserve design efficiency indicated that broad-scale conservation planning was relatively effective in achieving fine-scale conservation targets (Table 2). This raises the possibility that fine-scale data are not an absolute requirement for conservation planning since broad-scale assessments are efficient. However, the vegetation types for which conservation targets were not achieved are heavily transformed, consequently under threat, and are therefore priorities for conservation actions. Fine-scale conservation planning is the only way to identify these threatened habitats. Moreover, the efficiency of reserve selection exists only if the whole plan is implemented, meaning all selected areas being reserved. This is a serious drawback of using minimum sets since in practice implementation of conservation actions takes place over long period (Pressey and Taffs, 2001; Pence et al., in press). The use of minimum sets do not provide any information regarding the relative need of selected area for protection because they fail to identify areas as first priority for conservation (Pressey, 1997).

As opposed to reserve design efficiency, irreplaceability patterns (i.e. the relative contribution of one planning unit towards conservation targets) revealed strong differences between fine scale and broad scale conservation planning (Table 4). Although broad and fine-scale conservation plans differ in many aspects (biodiversity features, habitat transformation mapping and configuration of planning units), differences in conservation value could be explained by few factors, and the same vegetation types were found to govern irreplaceability patterns throughout the study.

Biodiversity

The fine-scale conservation plan generated overall higher irreplaceability values in planning units than the broad-scale plan. Fine- and broad-scale assessments of conservation value mostly differed in areas where highly transformed vegetation types (such as Elim Asteraceous Fynbos) occur. These habitats, occurring on small and isolated fragments were overlooked in the broad-scale analysis. They were incorporated into larger biodiversity features (BHUs) with lower conservation targets, thereby underestimating the real conservation value of these fragments. Conservation value was also underestimated in planning units with relatively high number of vegetation types (i.e. higher local diversity). In other words, conservation planning at the fine-scale shifts conservation value towards fragmented and/or diverse habitats. This was particularly clear in the Agulhas Plain, which is highly transformed and fragmented by agriculture (Cole et al., 2000) where 50% of the total area was considered irreplaceable at the fine scale as opposed to 10% at the broad-scale. This suggests that the adverse effects of broad-scale conservation planning would be more severe in fragmented and/or heterogeneous habitats but minimised in relatively intact and homogeneous habitats. Fine-scale conservation planning would therefore be more effective in preserving habitat diversity in fragmented and/or heterogenous areas. This was supported by the study of Stohlgren et al. (1997) where sampling plant diversity in heterogeneous habitats required finer spatial resolution (i.e. minimum mapping size) than for homogeneous habitats in order to better represent biodiversity pattern. The positive relationship between habitat fragmentation and habitat heterogeneity is however likely to be specific to the Agulhas Plain, where greatest vegetation type heterogeneity, comprising remnants of Elim types (7-9 in Table 4) Renoster types (24-26) and many wetland types, is found along catenae associated with agriculturally valuable soils (Thwaites and Cowling, 1988). The resultant transformation has left small pockets of these vegetation types, some on ferricrete outcrops unsuitable for cultivation (top of the catena; Elim Asteraceous Fynbos, Elim Fynbos), others on steep high quality midslopes soils that have escaped cultivation (Renoster Fynbos, Renoster Grassland, Renosterveld), and many wetland types on bottomlands unsuitable for cultivation (R.M. Cowling, personal communication).

Although fine-scale habitat heterogeneity is partially lost in broad-scale assessment of conservation value, the latter probably generate more consistent patterns of biodiversity for regional planning. Fine-scale biodiversity mapping is not error-free, especially when the original extant is estimated from field surveys. Field surveys do not consistently record features throughout the landscape (e.g. owing to landscape heterogeneity and inaccessibility) and are generally less objective than remote sensing classification (Fuller et al., 1998). Such uncertainty and subjectivity was probably minimised by defining land systems (BHUs in this study) mostly on the basis of similar topographic, geological and climatic features (Cowling and Heijnis, 2001). However, broad land systems tend to be more heterogeneous. Heterogeneity within and between classes has been rarely addressed for the setting of conservation targets in conservation planning (Ferrier et al., in press; Pressey et al., in press).

Habitat transformation

Recently, the consideration of threats to biodiversity in conservation planning has received increasing attention (Sisk et al., 1994; Richardson et al., 1996; Pressey, 1997; Flather et al., 1998; Chapter 4). Quantitative assessments of current and future land transformation improve the setting of conservation targets (Pressey et al., in press) and the identification of conservation priorities (Pressey et al., 1996; Pressey and Taffs, 2001). In this study, habitat transformation was quantified from remote-sensing interpretation (broad-scale) and ground survey (fine-scale). The spatial pattern of habitat transformation was very similar at both scales (80% in accuracy), but there was a strong negative interaction between spatial accuracy and extent of transformation for the 36 vegetation types (Fig. 8b). The most transformed vegetation types showed large discrepancies in their spatial patterns when habitat transformation was mapped from broad-scale or fine-scale data.

The consideration of habitat transformation was crucial when combined with biodiversity pattern. Patterns of irreplaceability at the fine-scale were driven by the presence of few highly transformed vegetation types; the conservation value of sites where these vegetation types occur was always underestimated at the broad-scale (Fig. 3). At the broad-scale, the apparent loss of conservation value in fragmented habitats will obviously depend on the degree of fragmentation (average size of fragments and connectivity between fragments). In this study, habitat transformation pattern was available at two different spatial scales only. By analysing the effects of various spatial scales (window size) on landscape characteristics in the Everglades region, Obeysekera and Rutchey (1997) found that islands of natural vegetation almost disappear beyond the 700m scale. Very few fragments of natural vegetation were identified using a window size of 700m. The critical mapping scale for which irreplaceability values considerably drop needs further investigation.

Planning units

Most systematic assessments of conservation systems rely on planning units with various size and shape configurations. This study confirms that broad-scale planning units (in this case, 1/16th degree square) are less efficient in achieving conservation targets than cadastral units (Pressey and Logan, 1998). The minimum set based on 1/16th degree squares selected more land than the minimum set based on cadastral units to fulfil the same conservation targets (Table 2). Large planning units are therefore more costly to implement (Pressey and Logan, 1998). Small units, such as cadastral units, can also be amalgamated with much more flexibility in choices of boundaries and configuration. When these small units are linked to land tenure, they greatly facilitate the implementation phase (Pence et al., in press).

Is there an appropriate spatial scale for conservation planning?

Because of its hierarchical nature, biodiversity can be estimated at several levels of spatial organisation (Franklin, 1993; Humphries et al., 1995). Several studies on biodiversity patterns have suggested that results obtained from one spatial scale might not be applicable to another scale (Levin, 1992; Collingham et al., 2000). This leads to the following question: Is there an appropriate scale (i.e. resolution) for conservation planning? From this study, one could easily argue that mapping biodiversity at 1:10 000 is still too coarse, and a finer mapping resolution is required to capture most of the biodiversity pattern. A finer mapping resolution will allow the capture of very rare habitat types, some of which are highly transformed. As the results of this study suggest, these highly transformed habitats of high conservation value are the most likely to be overlooked by the broad-scale assessment of conservation value. These habitats would be considered of high priority if conservation planning were undertaken at a finer resolution.

There is however no clear theoretical or practical answer on which scale to measure biodiversity (Heywood, 1995; Nagendra and Gadgil, 1999) and a multiple-scale approach is probably required (Conroy and Noon, 1996; Poiani et al., 2000). Any single-scale conservation assessment is likely to be flawed because of the hierarchical nature of biodiversity operating at various spatial scales (Fairbanks and Ben, 2000). This study has shown that fine-scale biodiversity patterns are not entirely nested within broader units and irreplaceability value of the same site differs between fine and broad scale conservation planning. The conservation value of few vegetation types was thus regionally underestimated (high priority areas in low priority regions) in 54% of the area of the Agulhas Plain while over-estimated in 27.7 % of the region (low priority areas in high priority regions).

It is generally stated that coarse-filter approaches encompass most of the biodiversity levels (Noss, 1987), but this has been tested in very few studies (Wessels et al., 1999; Araujo et al., 2001). Land classes (such as BHUs) are certainly good surrogates for biodiversity (Cowlings and Heijnis, 2001; Lombard et al, in press) but they are only surrogates and conservation planning based on BHUs or other surrogates should be completed by more fine-scale and detailed biodiversity assessment. In previous conservation study on the Agulhas Plain, Lombard et al (1997) found that reserve selection algorithms based on 11 vegetation types represented well populations of most endemic species. Appropriate systematic conservation planning should therefore aim at representing biodiversity patterns in its hierarchical form (from land classes to species) and incorporating biodiversity persistence (Cowling et al., 1999a). A good conservation plan should also look at combinations of land classes and the interactions between them.

Conclusion

Outcomes of conservation planning (conservation value and minimum set) are scale-dependent. They rely on the spatial scale at which biodiversity features and habitat transformation are mapped, and at which planning units are selected. Broad-scale conservation planning is probably suitable for homogenous and relatively intact landscapes. Such scale of analysis provides quick and consistent assessment of conservation value for entire regions. However, conservation value is likely to be underestimated in areas where localised and heavily transformed habitats do occur, these habitats being "missed" at broad scale. Fine-scale conservation planning is thus most important in fragmented and heterogeneous landscapes where the adverse effects of broad-scale mapping are likely to be severe.

References

Araujo, M.B., Humphries, C.J., Densham, P.J., Lampinen, R., Hagemeijer, W.J.M., Mitchell-Jones, A.J., Gasc, J.P., 2001. Would environmental diversity be a good surrogate for species diversity? Ecography 24, 103-110.

Breinam, L., Friedman, J.H., Olshen, R.A., Stone, C.J., 1984. Classification and Regression Trees. Wadsworth, Belmont.

Burke, V.J., 2000. Landscape ecology and species conservation. Landscape Ecology 15, 1-3.

Chambers, J.M., Hastie, T.J. 1992. Statistical models in S. Pacific Grove.

Christensen, N.L., Bartuska, A.M., Brown, J.H., Carpenter, S., D'Antonio, C., Francis, R., Franklin, J.F., MacMahon, J.A., Noss, R.F., Parsons, D.J., Peterson, C.H., Turner, M.G., Woodmansee, R.G., 1996. The report of the Ecological Society of America committee on the scientific basis for ecosystem management. Ecological Applications 6, 665-691.

Cole, N.S., Lombard, A.T., Cowling, R.M., Euston-Brown, D., Richardson, D.M., Heijnis, C.E., 2000. Framework for a conservation plan for the Agulhas Plain, Cape Floristic Region, South Africa. IPC report 0001, Cape Town.

Collingham, Y.C., Wadsworth, R.A., Huntley, B., Hulme, P.E. 2000. Predicting the spatial distribution of non-indigenous riparian weeds: issues of spatial scale and extent. Journal of Applied Ecology 37: 13-27.

Conroy, M.J., Noon, B.R., 1996. Mapping of species richness for conservation of biological diversity: conceptual and methodological issues. Ecological Applications 6, 763-773.

Cowling, R.M., Bond, W.J., 1991. How small reserves can be? An empirical approach in the Cape fynbos. Biological Conservation 58, 243-256.

Cowling, R.M., Campbell, B.M., Mustart, P.J., McDonald, A.P., Jarman, M.L., Moll, E.J., 1988. Vegetation classification in a floristically complex area: the Agulhas Plain. South African Journal of Botany 54, 290-300.

Cowling, R.M., Heijnis, C.E., 2001. The identification of Broad Habitat Units as biodiversity features for a systematic conservation planning in the Cape Floristic Region. South African Journal of Botany 67, 15-38.

Cowling, R.M., Holmes, P.M., 1992. Endemism and speciation in a lowland flora from the Cape Floristic Region. Biological Journal of the Linean Society 47, 367-383.

Cowling, R.M., Pressey, R.L., Boshoff, A.E., Kerley, G.I.H., Lombard, A.T., Richardson, D.M., Rouget, M., in press. The identification of a system of conservation for terrestrial biodiversity. Biological Conservation.

Cowling, R.M., Pressey, R.L., in press. Context, characteristics and history of conservation planning. Biological Conservation.

Cowling, R.M., Pressey, R.L., Lombard, A.T., Desmet, P.G., Ellis, A.G., 1999a. From representation to persistence: requirements for a sustainable system of conservation areas in the species rich mediterranean-climate desert of southern Africa. Diversity and Distributions 5, 51-71.

Cowling, R.M., Pressey, R.L., Lombard, A.T., Heijnis, C.J., Richardson, D.M., Cole, N., 1999b. Framework for a conservation plan for the Cape Floristic Region. Institute of Plant Conservation, Cape Town. Available at http://www.panda.org.za/publications.php

Cowling, R.M.C., 1992. The ecology of Fynbos: nutrients, fire and diversity. Oxford University Press, Cape Town.

Davis, F.W., 1995. Information systems for conservation research, policy and planning. BioScience Supplement, S36-S42.

De'ath, G., Fabricius, K.E., 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. Ecology 81, 3178-3192.

Fairbanks, D.H.K., Benn, G.A., 2000. Identifying regional landscapes for conservation planning: a case study from KwaZulu-Natal, South Africa. Landscape and Urban Planning 50, 237-257.

Ferrier, S., in press. Mapping spatial pattern in biodiversity for regional conservation planning: where to from here? Systematic Biology.

Ferrier, S., Pressey, R.L., Barrett, T.W., 2000. A new predictor of the irreplaceability of areas for achieving a conservation goal, its application to real-world planning, and a research agenda for further refinement. Biological Conservation 93, 303-325.

Flather, C.H., Knowles, M.S., Kendall, I.A., 1998. Threatened and endangered species geography. BioScience 48, 365-376.

Franklin, J.F. 1993. Preserving Biodiversity - Species Ecosystems or Landscapes? Ecological Applications 3, 202-205.

Fuller, R.M., Wyatt, B.K., Barr, C.J., 1998. Countryside survey from ground and space: different perspectives, complementary results. Journal of Environmental Management 54, 101-126.

Gabriel, K.R., 1971. The biplot graphic display of matrices with aplication to principal components analysis. Biometrics 58, 453-467.

Gower, J.C., Hand, D.J., 1996. Biplots. Chapman and Hall, London.

Greenacre, M.J., Underhill, L.G., 1981. Scaling a data matrix in a low dimensional Euclidean space. In: Hawkins, D.M. (Ed.), Topics in applied multivariate analysis Vol. 2, CSIR, Pretoria.

Hastie, T., Tibshirani, R., Freidman, J., 2001. The elements of statistical learning: prediction, inference and data mining. Springer-Verlag. 536 pp.

Heydenrych, B.J., Cowling, R.M., Lombard, A.T., 1999. Strategic conservation interventions in a region of high biodiversity and high vulnerability: a case study from the Agulhas Plain at the southern tip of Africa. Oryx 33, 256-269.

Heywood, V.H. 1995. Global biodiversity assessment. Cambridge University Press, Cambridge.

Humphries, C., Williams, P.H., Vane-Wright, R.I. 1995. Measuring biodiversity value for conservation. Annual review of Ecology and Systematics 26, 93-111.

Kemper, J., Cowling, R.M., Richardson, D.M., 1999. Fragmentation of South African renosterveld shrublands: effects on plant community structure and conservation implications. Biological Conservation 90, 103-111.

Kirpatrick, J.B., 1983. An iterative method for establishing priorities for selection of nature reserves: An example from Tasmania. Biological Conservation 25, 127-134.

Levin, S.A., 1992. The problem of pattern and scale in ecology. Ecology 73, 1943-1967.

Lombard, A.T., Cole, N., Cowling, R.M., Pressey, R.L., Rebelo, A.V., in press. Efficiency of land class versus species locality data in conservation planning for the Cape Floristic Region. Biological Conservation.

Lombard, A.T., Cowling, R.M., Pressey, R.L., Mustart, P.J., 1997. Reserve selection in a species-rich and fragmented landscape on the Agulhas Plain, South Africa. Conservation Biology 11, 1101-1116.

Mittermeier, R.A., Myers, N., Thomsen, J.B., 1998. Biodiversity hotspots and major tropical wilderness areas: approaches to setting conservation priorities. Conservation Biology 12, 516-520.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots conservation priorities. Nature 403, 853-858.

Nagendra, H., Gadgil, M. 1999. Biodiversity assessment at multiple scales: linking remotely sensed data with field information. Proceedings of the national Academy of the United States of America 96, 9154-9158.

Noss, R.F., 1987. From plant communities to landscape in conservation inventories: A look at The Nature Conservancy (USA). Biological Conservation 41, 11-37.

Obeysekera, J., Rutchey, K., 1997. Selection of scale for Everglades landscape models. Landscape Ecology 12, 7-18.

Pence, G., Botha, M., Turpie, J.K., in press. From conservation planning to implementation: what lies between. A case study from the Agulhas Plain, South Africa. Biological Conservation.

Poiani, K.A., Richter, B.D., Anderson, M.G., Richter, H.E., 2000. Biodiversity conservation at multiple scales: functional sites, landscapes, and networks. BioScience 50, 133-146.

Possingham, H., Ball, I., Andelman, S., 2000. Mathematical methods for identifying representative reserve networks. In: Ferson, S., Burgman, M. (Eds.), Quantitative methods for conservation biology. Springer-Verlag, New York, pp 291-305.

Pressey, R.L, Taffs, K.H. 2001. Scheduling conservation action in production landscapes: priority areas in western New South Wales defined by irreplaceability and vulnerability to vegetation loss. Biological Conservation 100, 355-376.

Pressey, R.L., 1997. Priority conservation areas: towards an operational definition for regional assessments. In: Pigram, J.J., Sundell, R.C. (Eds.), National parks and protected areas: Selection, delimitation and management. Center for Water Research Policy, University of New England, Armidale, pp. 337-357.

Pressey, R.L., Cowling, R.L., Rouget, M., in press. Formulation of conservation targets for biodiversity pattern and process in the Cape Floristic Region. Biological Conservation.

Pressey, R.L., Ferrier, S., Hager, T.C., Woods, C.A., Tully, S.L., Weiman, K.M., 1996. How well protected are the forests of north-eastern New South Wales? - Analyses of forest environments in relation to formal protection measures, land tenure, and vulnerability to clearing. Forest Ecology and Management 85, 311-333.

Pressey, R.L., Johnson, I.R., Wilson, P.D., 1994. Shades of irreplaceability: towards a measure of the contribution of sites to a reservation goal. Biodiversity and Conservation 3, 242-262.

Pressey, R.L., Logan, V.S., 1998. Size of selection units for future reserves and its influence on actual vs targeted representation of features: a case study in western New South Wales. Biological Conservation 85, 305-319.

Pressey, R.L., Possingham, H.P., Day, J.R., 1997. Effectiveness of alternative heuristic algorithms for identifying indicative minimum requirements for conservation reserves. Biological Conservation 80, 207-219.

Pressey, R.L., Possingham, H.P., Logan, V.S., Day, J.R., Williams, P.H., 1999. Effects of data characteristics on the results of reserve selection algorithms. Journal of Biogeography 26, 179-191.

Richardson, D.M., van Wilgen, B.W., Higgins, S.I., Trinder-Smith, T.H., Cowling, R.M., McKell, D.H., 1996. Current and future threats to plant biodiversity on the Cape Peninsula, South Africa. Biodiversity and Conservation 5, 607-647.

Rouget, M., Richardson, D.M., Milton, S.J.M., Polakow, D., 2001. Predicting the dynamics of four invasive *Pinus* species in a fragmented semi-arid shrubland in South Africa. Plant Ecology 152, 79-92.

Schwartz, M.W., 1999. Choosing the appropriate scale of reserves for conservation. Annual Review of Ecology and Systematics 30, 83-108.

Sisk, T.D., Launer, A.E., Switky, K.R., Ehrlich, P.R., 1994. Identifying extinction threats: global analyses of the distribution of biodiversity and the expansion of the human entreprise. BioScience 44, 592-604.

Soule, M.E., Terborgh, J., 1999. Conserving nature at regional and continental scales - a scientific program for North America. BioScience 49, 809-817.

Stohlgren, T.J., Chong, G.W., Kalkhan, M.A., Schell, L.D., 1997. Multiscale sampling of plant diversity: effects of minimum mapping unit size. Ecological Applications 7, 1064-1074.

Thwaites, R.N., Cowling, R.M., 1988. Landscape vegetation relationships on the Agulhas Plain. Catena 15, 333-46.

Underhill, L.G. 1990. The coefficient of variation biplot. Journal of Classification 7, 241-256.

Wessels, K.J., Freitag, S., van Jaarsveld, A.S., 1999. The use of land facets as biodiversity surrogates during reserve selection at a local scale. Biological Conservation 89, 21-38.

Younge, A., Fowkes, S., in press. A sustainable conservation strategy for the cape floral kingdom: integrating socio-economic issues and conservation. Biological Conservation

Understanding actual and potential patterns of plant invasion at different spatial scales: quantifying the roles of environment and propagule pressure

Abstract

I explored the current and potential future patterns of invasive alien tree species (mainly *Acacia*, *Eucalyptus* and *Pinus* spp.) in South Africa at different spatial scales (landscape, regional, and sub-continental) ranging from 10 to 1 000 000 km^2. Data were collected from field mapping (landscape scale), aerial photographs and remote sensing (regional scale) and expert knowledge (sub-continental scale). All distribution data and information on biophysical characteristics were available in GIS format.

I first identified the determinants of the distribution of invasive stands using regression-tree analysis (Formal Inference-based Recursive Modelling, FIRM). I found that environmental factors best explained distribution at broad scales whereas propagule pressure explained most of the variation at finer (i.e. landscape) scale. A hierarchy in the environmental factors was observed. I then used the environmental determinants identified by FIRM to model the potential distribution of invasive alien species at each spatial scale investigated. FIRM accurately predicted between 60 and 90% of the distribution of invasive stands, but the accuracy of predictions was poorer at finer scales. I discuss how to integrate results when moving from landscape to broad scale assessments (and vice versa), and the implications for management and policy formulation for alien plant control.

Introduction

Biological invasions are one of the most important agents of land transformation and represent a major and growing threat to biodiversity worldwide (Wilcove et al., 1998). Increasing attention is being given to the study of invasions. Among the most pressing questions in invasion ecology are: 1) what makes some taxa successful invaders?; 2) what makes communities open to invasion?; and 3) what are the impacts of biological invasions and how can these be managed? Considerable progress has been made towards a predictive understanding of plant invasions (Rejmánek et al., in press).

The issue of scale is recognised as a central problem in ecology (Levin, 1992). Spatial scale is generally understood as having two components: extent (the size of the study area), and resolution (the precision of measurement) (Farina, 1998; Csillag et al., 2000). In this study, spatial scale is taken in its ecological rather than cartographic context (small scale meaning finer assemblage). The scale of observations influences the description of patterns and, of interest for this study, the understanding of plant distribution. There is no single obvious scale at which ecological phenomena should be investigated, since process that operate at many scales interact to affect distribution, diversity and all other properties of taxa and communities (Levin, 1992; Farina, 1998). Cross-scale studies are thus critical to complement single scale studies. Most ecological studies of plant distribution focus on one spatial scale. The feasibility of extrapolating perspectives from single-scale studies is very seldom tested and may be limited. This is a problem, since managers, planners, and policy makers operate at different scales, generally range from small patches of land (plot to landscape) to whole regions or countries. Good information on the drivers of processes at the local scale is probably most useful to managers responsible for manipulating individual organisms, populations or communities. The same information is generally much less useful to planners and policy makers responsible for setting priorities for management, and setting policies and legislation. Until recently, most information on processes and factors that drive invasions was applicable to landscapes or smaller units. Advances in remote-sensing techniques, computer technology and spatial analysis methods are facilitating easier access to perspectives on the drivers of invasion at much larger spatial scales. Managers, planners and policy makers now have access to information from very different scales. It is by no means clear how one could use information collected at one scale to define priorities at another scale.

The widespread occurrence of invasive alien trees and shrubs over very large parts of South Africa (Richardson et al., 1997), and a history of detailed studies of invasion dynamics at many different scales (Macdonald et al., 1986; Richardson et al., 1992; Richardson et al., 1997; Higgins, 1998), provides a good opportunity for exploring which factors are correlated with invasion at different spatial scales. Four different data sets recording the spatial distribution of invasive tree species were used. They span spatial scales ranging from landscape (tens of ha) to national boundaries (millions of ha). The aims were: 1) to test the ability to predict alien plant distribution at each scale; 2) to identify the main determinants of distribution at each scale; and 3) to assess the relevance of predictions derived at one scale for application at other scales.

Methods

Data collection

I assembled in a Geographic Information System (Arc/Info 7.2) four data sets for exploring the role of environmental factors and propagule pressure at different scales in determining the distribution of invasive trees and shrubs in South Africa. Data on the current distribution of invasive alien trees were collected in various ways from different localities (Fig. 1). Since details of each study have been already presented in previous papers and chapters, only brief summaries are provided here. Each data set consists of a different spatial scale (from landscape to nation-wide survey). Main characteristics and references for each study are summarised in Table 1.

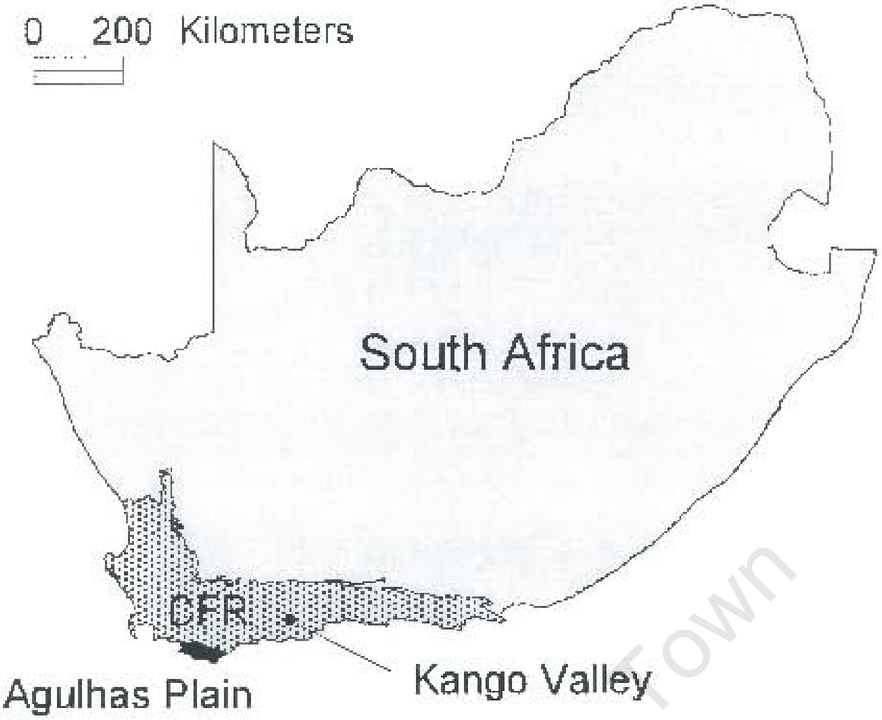


Figure 1. Map of four study areas. Features of the four areas are given in Table 1. CFR: Cape Floristic Region.

The **Kango Valley** (33.3° S, 22.1° E; 25 km^2) is located in the Western Cape province of South Africa (Fig. 1). The climate is semi-arid with winter rains (annual rainfall 420mm at 700m elevation). The vegetation consists of fire-prone shrubland (fynbos at higher altitudes, renosterveld in the lowlands). Four *Pinus* species have been planted in the area in various configurations and densities since 1926. Invasive trees (individuals and stands of the four *Pinus* species) were recorded with a GPS during field survey in the Kango Valley (see Rouget et al., 2001). Almost 1500 individuals were geo-referenced and the boundaries of over 1000 ha of self-sown stands were digitised (1:5 000 scale).

Aerial photographs and field surveys were used to quantify the extent and percentage cover of 36 alien tree species in the **Agulhas Plain**. This region lies at the southern part of the Cape Floristic Region and covers approximately 2 160 km^2 (Fig. 1). The area has a mediterranean-type climate, with a mean annual rainfall of 430 mm. Although the coastal peneplain has a relatively homogenous topography, there is a complex mosaic of geological substrata and soil types. Agriculture and alien plant invasions are the main threats to biodiversity in this hotspot of plant biodiversity. Extremely detailed field survey methods were used to map the distribution, composition and age (height) structure of stands of woody invasive species (chapter 3). Over 100 000 ha of self-sown stands were mapped throughout the Agulhas Plain (1:10 000 scale).

Table 1. Characteristics of the four case studies of invasive alien plant distribution in South Africa.

Study area	Extent (km^2)	Resolution (m)	no. of species	% cover	References
Kango Valley	25	25	4	continuous	Rouget et al., 2001
Agulhas Plain	2200	250	36	6 categories	Chapter 3, Cole et al., 2000
CFR	88000	1700	Combined	3 categories	Chapter 4
South Africa	$1.2\ 10^6$	1700	2 taxa	6 categories	Chapter 5; Versfeld et al., 1998

Remote sensing was used to map the extent of stands of invasive alien trees and shrubs (mainly *Acacia*, *Hakea*, and *Pinus* species) in three density classes across the entire **Cape Floristic Region** (CFR, Fig. 1). The CFR covers 88 000 km^2 and hosts some 9 000 plant species, 70% of them endemic to the region (Goldblatt and Manning, 2000). The CFR is extensively transformed by agriculture, alien plant invasion and urbanisation (Chapter 4). 2 200 km^2 of the CFR are covered by medium to dense stands of alien plants (1: 250 000 scale).

Finally, the extent and density of self-sown (invasive) stands of *Pinus* species and *Acacia mearnsii* were mapped for the **whole of South Africa** (1,219,090 km^2), using all available data supplemented by expert knowledge gathered at provincial workshops (Versfeld et al., 1998). I only used the distribution of self-sown *Pinus* species because of the difficulty to assess source populations for *Acacia mearnsii* (i.e. where the invasion started, see below). South Africa has a wide array of climates (from arid to tropical), landforms and topography (from sea level to 3375 m elevation) and vegetation (from desert to temperate forest) (Cowling et al., 1997). Species and densities were recorded for each invaded zone at the 1:250 000 scale (because of discrepancies in mapping methods between provinces, the data set is probably only accurate at 1: 500 000 scale).

Abiotic and biotic factors that could potentially explain the distribution of invasive species were also collected and stored in GIS format. The database contained information on climate, topography, vegetation, geology, sources of invasion (propagule pressure), land use, and disturbance (see Table 2). A series of environmental factors were derived separately for each study; the scale of environmental data thus varies between studies. The best factor for each predictor category (climate, topography, etc) was selected from the analysis performed for each separate case study (see references in Table 1).

Table 2. Abiotic and biotic factors used in exploring determinants of invasion patterns for alien tree species at four scales in South Africa (see Table 1 for details of the four areas). Within each category (climate, topography, etc), the best factor was chosen according to results of separate case studies. For each category, the factor included in the analysis is indicated, as is its relative rank of importance (1, most significant factor; 6, least significant).

Category	Kango Valley	Agulhas Plain	Cape Floristic Region	South Africa
Climate	-	Mean annual rainfall (4)	Growth days (1)	Growth days (2)
Topography	Aspect (4)	Altitude (3)	Distance to coast (3)	Altitude (6)
Vegetation	Vegetation density (2)	Vegetation groups (2)	Broad Habitat Units (2)	Vegetation types (1)
Geology, pedology	Soil pH (3)	Geology (6)	Geology (5)	Geology (4)
Land use	Proximity to field (6)	Land use (5)	Distance to roads (6)	Land use (5)
Disturbance	Fire (5)	-	-	-
Propagule pressure	Distance to source (1)	Distance to source (1)	Distance to plantations (4)	Distance to plantations (3)

Data Analysis

Data sets were first extracted from the GIS databases. For each study, I derived a sample of randomly distributed points (between 1434 and 8470 points, depending on the study). For each point, information on the distribution of invasive plant species (presence or absence) was available. Because categories of percentage cover recorded for each study differ, I was forced to use presence/absence data only. I also derived environmental attributes for each point based on the underlying environmental GIS data available in each study. This procedure generated a matrix of random observations containing values for the response variable (presence/absence of invasive species) and all the potential predictors (environmental factors).

Several statistical techniques are potentially suitable for exploring the determinants of species distribution (see Franklin, 1995; Guisan and Zimmerman, 2000 for reviews). The approach used here assumed that plant distribution patterns are correlated with environmental factors, and thus environmental factors can be used to identify areas suitable for plant establishment (in this case, invasion). I used regression-tree models (FIRM 2.1, Hawkins, 1995) to identify determinants of invasion patterns for each study. Regression-tree analysis is a very useful technique for exploring patterns in large data sets because the approach is distribution-free. It can also handle categorical (like geology) and non-categorical (like mean annual rainfall) predictors simultaneously. Classification trees can detect non-linear relationships between variables (Breinam et al., 1984). Further details of the analytical approach are given in Chapter 2.

In areas with low environmental heterogeneity but where the invasive plants are patchily distributed, one would expect environmental factors to be poor correlates of species distribution. In this situation, where plant species distribution is not driven primarily by environmental factors, dispersal or propagule pressure might be more important, at least in practical terms (Rejmánek et al., in press). To quantify the relative importance of environment versus propagule pressure for explaining invasion patterns, I also modelled species distribution as a function of the minimum distance to source populations. Source populations were defined as forestry plantations (in the South Africa-wide study of *Pinus* and in the Cape Floristic Region) or old stands at the origin of the invasion (the remaining studies). Minimum distance to source was considered to be a good surrogate for propagule pressure. Propagule pressure is widely recognized as a fundamental driver of invasions (D'Antonio et al., 2001; Rejmánek et al., in press). The quantification of its role in invasion is problematic, and this study seeks to develop a protocol for exploring this factor at different spatial scales.

For each study, I identified the major determinant of distribution using FIRM. Only one factor was used in the analysis. I compared the ability to understand and predict patterns of distribution using the most significant environmental factor as opposed to propagule pressure only. Comparisons were based on the prediction accuracy of invasive stands (% of presence data correctly classified by the model), and on the Kappa statistic. Kappa statistic measures the proportion of agreement between observed and predicted values while taking into account agreement obtained by chance only (Fielding and Bell, 1997).

To assess the relevance of predictions derived at one scale and applied to another scale, models were scaled up and down. The resolution was kept constant (1700 m) to separate the effects of spatial extent and resolution. Regarding scaling-down models, nation-wide predictions were assessed at regional (CFR) and local (Agulhas) scale, and regional predictions were assessed at the local scale. Regarding scaling up, the opposite approach was used. I only assessed the accuracy of the regional model (derived for the CFR) for predicting invasive species distributions at a sub-continental scale. Predictions were assessed based on three values: similarity, accuracy, and Kappa statistic. Similarity measures the overall spatial match between predictions based on different scales; Accuracy measures the percentage of correctly classified instances when applying models derived from another spatial scale; and the Kappa statistic reflects the overall significance of the match.

Table 3. A comparison of the main drivers of distribution of invasive alien trees at four scales in South Africa (see Table 1). For each spatial scale, I tested the importance of environment versus propagule pressure in explaining the distribution of invasive species. The rank of each factor is given (1 being the most significant factor). The predictive power of the model was assessed in terms of % presence correctly classified, % absence correctly classified, total accuracy (presence and absence correctly classified) and Kappa statistic.

Analysis	Sample size	Rank	% presence	% absence	% total	Kappa
South Africa						
Vegetation types	4344	1	84.0	93.8	89.8	0.787
Distance to plantations	4344	3	53.0	92.8	76.6	0.486
Cape Floristic Region						
Growth days	2251	1	57.7	79.1	68.4	0.368
Distance to plantations	2251	4	39.3	82.8	61.0	0.221
Agulhas Plain						
Distance to sources	8470	1	55.8	79.1	66.9	0.345
Vegetation types	8470	2	62.1	60.7	61.5	0.229
Kango Valley						
Distance to sources	1434	1	75.3	57.4	65.1	0.314
Vegetation density	1434	2	38.9	88.3	67.2	0.289

Results

Determinants of invasion patterns

The spatial scale at which the analysis was performed influenced the accuracy of the models. Predictions (based on the best environmental factor and propagule pressure) were more accurate at large scale (Table 3, Fig. 2a). Kappa values were above 0.7 for the sub-continental data set and around 0.3 for the landscape study (Kango Valley, Fig. 2a). Based on presence accuracy (% of presence observations correctly classified), environmental factors were better predictors of invaded areas at large scale (regional to sub-continental) while propagule pressure was a better predictor at lower scale (landscape to local, Fig. 2b). Fig. 2b clearly shows the model response to environmental factors according to the spatial scale investigated. Similar model accuracy was obtained at fine (Kango valley) and broad (South Africa) scale but using two different sets of factors: propagule pressure (distance to sources) for Kango Valley and environmental variable (vegetation types) for South Africa.
The relative contribution of each factor in explaining the distribution pattern of invasive plant species is shown in Table 2. Among the six categories of predictors investigated, no category was identified as being the best factor to explain the distribution of invasive species at all spatial scales. Different environmental determinants govern the current invasion pattern. Propagule pressure was the most significant determinant of invasion pattern at fine scale (Kango and Agulhas data sets, Table 2).

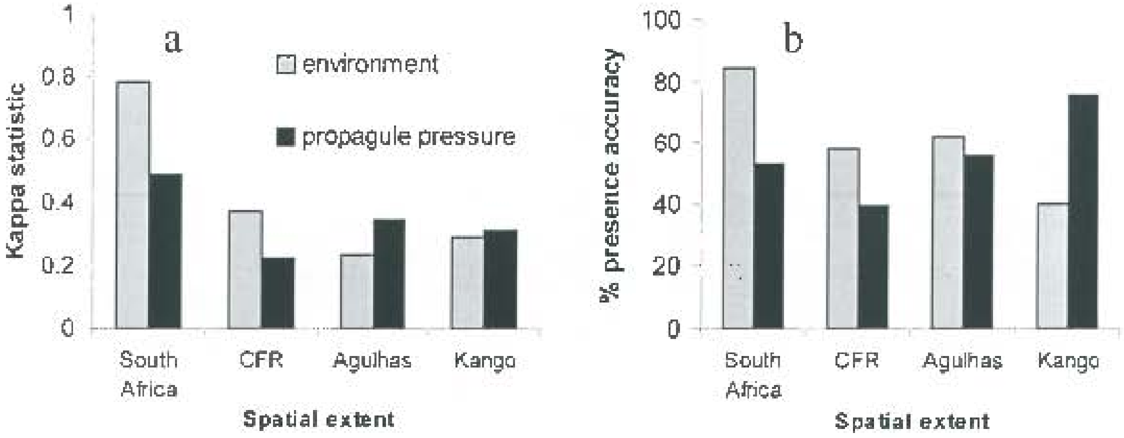


Figure 2. The importance of environmental factors and propagule pressure in predicting the distribution of invasive plants. a) Kappa Statistic, b) presence accuracy.

Annual number of growth days was the best determinant at regional scale for the Cape Floristic Region and vegetation types the best determinant at a sub-continental scale (Table 2). It however emerged that vegetation types were a good determinant of the distribution of invasive species at all scales (Table 2).

A closer analysis of the determinants of invaded areas for each scale is given in Table 4. This identified areas more likely to be invaded than expected by random, based on environmental factors and propagule pressure. Broad vegetation types were identified at a sub-continental level (such as fynbos and renosterveld, Table 4) which appears more suitable to plant invasion. These broad vegetation types also occur in the Agulhas Plain, and the use of data at a finer scale helped to identify fine-scale vegetation types suitable to plant invasion. In the Agulhas Plain, fynbos communities (such as limestone proteoid fynbos) and moist areas (like wetland and riverine habitats) were more invaded than what one would expect just by chance. At a finer scale (landscape study in the Kango Valley), the amount of bare ground was the best environmental predictor of the distribution of invasive species. Areas with less than 50% of bare ground were most likely to be invaded by pines (Table 4). Propagule pressure, the most significant factor at fine to medium scale, was perceived differently throughout the studies (Table 4). Propagule pressure influenced the distribution of invaded species up to 500-700 m in the Kango Valley and in the Agulhas Plain (fine scale) whereas it influenced the distribution of invaded species up to 8-15 km in the Cape Floristic Region and in South Africa (coarse scale).

Table 4. Determinants of distribution of invasive plant species identified at four different spatial scales. The best environmental factor among climate, geology, topography, land use, disturbance, and vegetation (see Table 2) was identified using classification trees. This was compared with the role of propagule pressure in determining the distribution. Only conditions where invasive species are predicted to occur are indicated.

Scale of study	Environmental factor	Propagule pressure
Landscape (Kango Valley)	Vegetation density <50% of bare ground	Distance to sources <687 m
Local (Agulhas Plain)	Vegetation groups Acid sand proteoid Fynbos Limestone proteoid Fynbos Forest and Thicket Riverine vegetation Wetland Sand dunes	Distance to sources <527 m
Regional (Cape Floristic Region)	Growth days > 125 days per year	Distance to plantations <7.6 km
Sub-continental (South Africa)	Vegetation types Fynbos Renosterveld Lowveld Bushveld Forest	Distance to plantations <15 km

Scaling up and down

Predictions from one model were extrapolated to another spatial scale. Attempts to scale-up or scale-down the models were not very successful.

The model based on the CFR data set performed poorly at a sub-continental scale (South Africa). By scaling up model, I failed to predict many invaded areas that occur outside the training model range in different environmental conditions. This resulted in low classification accuracy for presence data (Table 5). However, predictive models of invasive species distribution in South Africa, which were derived at a regional (CFR data set) and sub-continental (South Africa data set) were 86.5 % similar (Table 5).

Scaling down models also led to weak models. Predictive model based on South Africa performed poorly to predict invasive species distribution in the CFR and the Agulhas Plain. They generally failed to accurately predict sites where invasive species do not occur. These models however "missed" (i.e. failed to predict) relatively few sites where invasive species occur (Table 5). At a sub-continental scale, the entire Agulhas plain was predicted to be invaded (model based on South Africa).

Table 5. Scaling-up and down models of invasive distribution. For scaling-up, model based on CFR was extrapolated to predict invasive species distribution over South Africa. For scaling-down, each model was assessed with respect to a finer data set (test data set, e.g. sub-continental predictions based on South Africa were compared to the distribution of invasive species in the CFR and the Agulhas Plain). % similarity: degree of model similarity (i.e. same predictions at both scales); % presence: % of correctly classified presence in the test data set; % absence: % of correctly classified absence in the test data set; % total: % of correctly classified observations (presence and absence) in the test data set.

Model	Test	% Similarity	% presence	% absence	% total	Kappa
Scaling-up						
CFR	South Africa	86.5	39.4	89.8	89.6	0.049
Scaling-down						
South Africa	CFR	54.2	88.7	39.0	41.6	0.049
South Africa	Agulhas	71.7	99.6	0.8	52.6	0.005
CFR	Agulhas	69.6	71.2	43.1	57.4	0.15

Discussion

The ability to model the distribution of invasive species varied considerably according to the spatial scale of the analysis. Predictive power of models was greater at larger than at finer scale (Fig. 2a). This suggests that species response to the environment is better detected at large scale. This finding is partly due to the model approach used. Regression-like techniques rely on correlations between response variable (here, presence/absence of a species) and predictors (here environmental factors). Thus, it assumes that invasive species have reached a pseudo-equilibrium with the environment (Franklin, 1995). Although the range of invasive species, especially if they have been recently introduced, is still expanding, species distribution analysed at coarse scale can be considered to have reached stasis (Wiens, 1989; Collingham et al., 2000). A good correlation between species distribution and environmental factors is thus expected at coarse spatial scale. However, predictions of invasive species distribution based on environmental factors broke down at finer-scale. A loose species response to the environment was detected because invasive species have yet not spread into all suitable habitats. Moreover, the difficulty of building predictive models at the fine scale generally increases because observed patterns become less easy to generalise (Costanza and Maxwell, 1994). Modelling species distribution at a fine scale is also limited by the resolution of the environment data, which probably failed to capture fine-scale environmental heterogeneity.

A scale-dependent hierarchy of predictors was evident from the models I derived (Table 2). Environmental factors were better predictors of invasive species distribution at large scale whereas propagule pressure was more appropriate for modelling invasive species distribution at the fine scale. Climate and vegetation were the most important predictors at regional and sub-continental scales. Climate was a poor predictor of invasive species distribution at finer scale (Agulhas Plain, Table 2). This contrasts with the study by Collingham et al. (2000) where no hierarchy of environmental controls was observed in the distribution of riparian weeds. Since species-response to environment is poorly detected at fine-scale, propagule pressure, which represents species dispersal in a crude way, became the single most important predictor of invasion pattern at fine-scale. This suggests that biological attributes of invasive species need to be incorporated in fine-scale modelling of invasion (Higgins and Richardson, 1996). In a similar study, Higgins et al. (1999) used correlative models to predict the distribution of six invasive species in the Cape Peninsula (471 km^2). Elevation and annual rainfall were the most significant predictors but the total variance explained by the model was low (16-34%). Mechanistic models are likely to be better suited at this scale for modelling patterns of invasion because they integrate plant-environment interactions (Higgins et al., 1996).

There is not one ideal scale for analysing and modelling the many ecological phenomena that interact to mediate species distribution limits (Levin, 1992). Perspectives from different scales provide different layers of evidence. Attempts to scale-up and down models were generally not successful (Table 5). Outcomes based on one spatial scale should thus be applied with caution to another environment if the spatial extent or the resolution differs (Collingham et al., 2000). Scaling up the regional model to the sub-continental scale failed to predict invasive species distribution accurately because of the wider range of environmental conditions at the sub-continental scale. Although the predictions of coarse models in smaller areas (spatial extent decreased) were not satisfactory overall (Table 5), all invaded areas were correctly identified. This suggests that coarse-scale studies are appropriate for identifying broad priority areas. These priorities could be refined by analysis at a finer scale. For example, the sub-continental study identified fynbos and renosterveld as vegetation types that are highly prone to invasion (Table 4). A fine-scale study for the Agulhas Plain identified which vegetation communities within fynbos and renosterveld are likely to be invaded (Table 4). Coarse-scale studies are thus appropriate for policy on alien plant management and for defining regional conservation priorities (Chapter 4, Chapter 5) but their resolution is too coarse to be useful for management purposes. For management of invasive species, spread has to be better modelled, not just the susceptibility of the environment to invasion. This is likely to be achieved by combining spread models and plant-environment interactions (Chapter 3, Higgins and Richardson, 1998). Further studies of invasion pattern, which span over several spatial and temporal scales are required to infer process from pattern and gain a better understanding of invasive species spread.

References

Breinam, L., Friedman, J.H., Olshen, R.A., Stone, C.J., 1984. Classification and Regression Trees. Wadsworth, Belmont.

Costanza, R., Maxwell, T., 1994. Resolution and predictability: an approach to the scaling problem. Landscape Ecology 9,47-57

Collingham, Y.C., Wadsworth, R.A., Huntley, B., Hulme, P.E. 2000. Predicting the spatial distribution of non-indigenous riparian weeds: issues of spatial scale and extent. Journal of applied Ecology 37 (Suppl. 1), 13-27.

Cowling, R.M., Richardson, D.M., Pierce, S.M., 1997. Vegetation of southern Africa. Cambridge University Press, Cambridge.

Csilag, F., Fortin, M-J., Dungan, J.L., 2000. On the limits and extensions of the definition of scale. ESA Bulletin 81, 230-232.

D'Antonio, C.M., Levine, J., Thomsen, M., 2001. Ecosystem resistance to invasion and the role of propagule supply: A California perspective. Journal of Mediterranean Ecology 2, 233-246.

Farina, A., 1998. Scaling patterns and processes across landscapes. In Farina, A. (Ed.), Principles and Methods in Landscape Ecology. Chapman & Hall, London, pp. 35-49.

Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24, 38-49.

Franklin, J., 1995. Predictive vegetation mapping: geographic modelling of biospatial patterns in relation to environmental gradients. Progress in Physical Geography 19,474-499.

Goldblatt, P., Manning, J. 2000. Cape Plants: a conspectus of the Cape Flora of South Africa. National Botanical Institute and Missouri Botanical Garden, Cape Town.

Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135, 147-186.

Hawkins, D.M., 1995. Formal Inference-based Recursive Modelling. Department of Applied Statistics, University of Minnesota, St Paul.

Higgins, S.I., 1998. Predicting rates and patterns of alien plant spread. PhD thesis. University of Cape Town, Cape Town.

Higgins, S.I., Richardson, D.M., 1996. A review of models of alien plant spread. Ecological Modelling 87, 249-265.

Higgins, S.I., Richardson, D.M., 1998. Pine invasions in the southern hemisphere: modelling interactions between organism, environment and disturbance. Plant Ecology 135, 79-93.

Higgins, S.I., Richardson, D.M., Cowling, R.M., 1996. Modeling invasive plant spread: the role of plant-interactions and model structure. Ecology 77, 2043-2054.

Higgins, S.I., Richardson, D.M., Cowling, R.M., Trinder-Smith, T.H., 1999. Predicting the landscape scale distribution of alien plants and their threats to biodiversity. Conservation Biology 13,303-313

Hobbs, R.J., Humphries, S.E., 1995. An integrated approach to the ecology and managements of plant invasions. Conservation Biology 9, 761-770.

Levin, S.A., 1992. The problem of pattern and scale in ecology. Ecology 73, 1943-1967.

Macdonald, I.A.W., Kruger, F.J., Ferrar, A.A., 1986. The Ecology and Management of Biological Invasions in southern Africa. Cape Town, Oxford University Press.

Rejmánek, M., Richardson, D.M., Higgins, S.I. Pitcairn, M., Grotkopp, E., 2002. Plant Invasion Ecology: State of the art. In Mooney, H.A., Mc Neely, J.A., Neville, L., Schei, P.J., Waage, J. (Eds.), Invasive alien species: Searching for solutions. Island Press, Washington, D.C. (in press).

Richardson, D.M., Macdonald, I.A.W., Cowling, R.M., 1992. Plants and animal invasions. In Cowling, R.M. (Ed.), The Ecology of Fynbos: Nutrients, Fire and Biodiversity. Oxford University Press, Cape Town, pp. 450-473.

Richardson, D.M., Macdonald, I.A.W., Hoffmann, J.H., Henderson, L., 1997. Alien plant invasions. In Cowling, R.M., Richardson, D.M., Pierce, S.M. (Eds.), Vegetation of southern Africa. Cambridge University Press, Cambridge, pp. 535-570.

Rouget, M., Richardson, D.M., Milton, S.J., Polakow, D., 2001. Predicting the dynamics of four invasive Pinus species in a fragmented semi-arid shrubland in South Africa. Plant Ecology 152:79-92.

Scott, J.K, Panetta, F.D., 1993. Predicting the Australian weed status of southern African plants. Journal of Biogeography 20, 87-93.

Versfeld, D.B., Le Maitre, D.C., Chapman, R.A., 1998. Alien invading plants and water resources in South Africa: A preliminary assessment. CSIR contract report for Water Research Commission TT99/98. WRC, Pretoria.

Wiens, J.A., 1989. Spatial scaling in ecology. Functional Ecology 3, 385-397.

Wilcove, D.S., Rothstein, D., Dubow, D., Phillips, A., Losos, E., 1998. Quantifying threats to imperiled species in the United States. BioScience 48, 607-615.

Conclusions

This thesis was primarily aimed to provide a protocol for modelling the spatial patterns of plant species (particularly invasive species) at different spatial scales. This chapter briefly summarises the approach and reviews the major findings of this work.

Biological invasions as natural experiments

This work was based on a series of case studies of plant distribution at different spatial scales. Each case study represents a natural experiment. With the development of statistical techniques and Geographic Information Systems, such large-scale experiments are extremely valuable. Through the different chapters, I have demonstrated the value of natural experiments for quantifying the determinants of species distribution and for inferring process from pattern.

Modelling protocol

The protocol developed for modelling pattern of plant species distribution is described in Fig. 1. This figure relates the modelling objective, the model type, and the drivers of species distribution with the spatial scale investigated. I suggest that the first criterion to consider, irrespective of the spatial scale, is the modelling objective. In order to understand and model the spatial pattern of species distribution (i.e. presence/absence only), static modelling approaches are appropriate for modelling species distribution in their native range (Chapter 2), invasive species at local, regional, and sub-continental scales (Chapter 3, 4, and 5 respectively). Such approaches are easy to implement and provide a satisfactory level of accuracy. Determinants of species distribution are most likely to be environmental factors, the exact nature of which depends on the spatial scale analysed (Chapter 7).

In cases where the objective is modelling species abundance or invasive species spread, the type of modelling approach is probably scale-specific. At local scale, static approaches fail to accurately model species abundance because key-biological attributes (such as species dispersal) are not taken into consideration. Quasi-mechanistic or even purely mechanistic models are therefore required (Chapter 3). At this scale, propagule pressure was identified as the main driver of invasion spread (Chapter 3). At regional scale, species abundance (but not species co-existence) could be modelled using a static approach, which includes biotic factors, such as the abundance of other dominant species (Chapter 2). At this scale, species abundance (and regeneration) was found to be

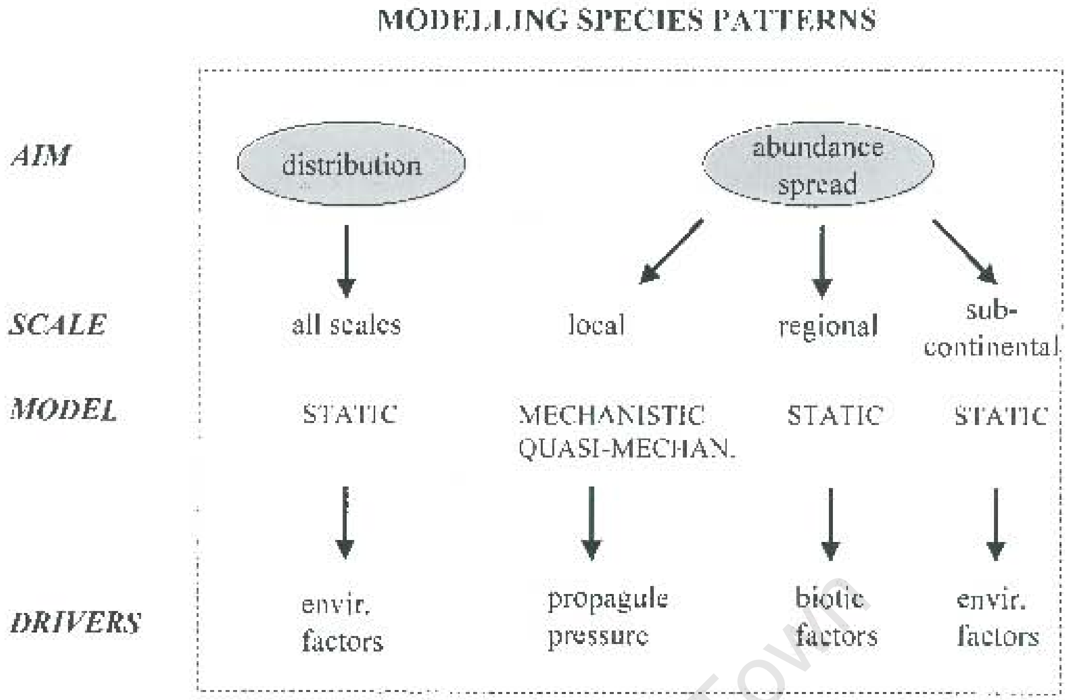


Figure 1. Protocol for modelling patterns of plant species distribution, abundance and invasion spread at different spatial scales. quasi-mechan.: quasi-mechanistic, envir.: environmental.

mediated mostly by biotic factors (Chapter 2). Finally, static approaches can be used to crudely model species abundance at sub-continental scale using abiotic factors (mostly climate, Chapter 5). However, the resolution from sub-continental studies might be broader than the resolution of the actual factors driving species abundance. This is especially the case for invasive species for which abundance is mostly determined by human-induced factors (such as disturbance or propagule pressure) (Chapter 5).

The effects of spatial scale on the determinants of distribution, model accuracy and application types

This study clearly illustrates the inter-dependence of determinants of species distribution, model accuracy, application types, and spatial scale. This is summarised in Fig. 2. The accuracy of static models to identify species determinants increases with the spatial scale analysed. General patterns are easily captured at broad-scale, whereas fine-scale patterns which tend to be context and species-specific, are therefore more difficult to predict (Chapter 7). However, "quasi-mechanistic" models, developed in Chapter 3, considerably improved the model predictions. Such models integrate species biological attributes through propagule pressure and environmental factors mediating the spread of invasive species.

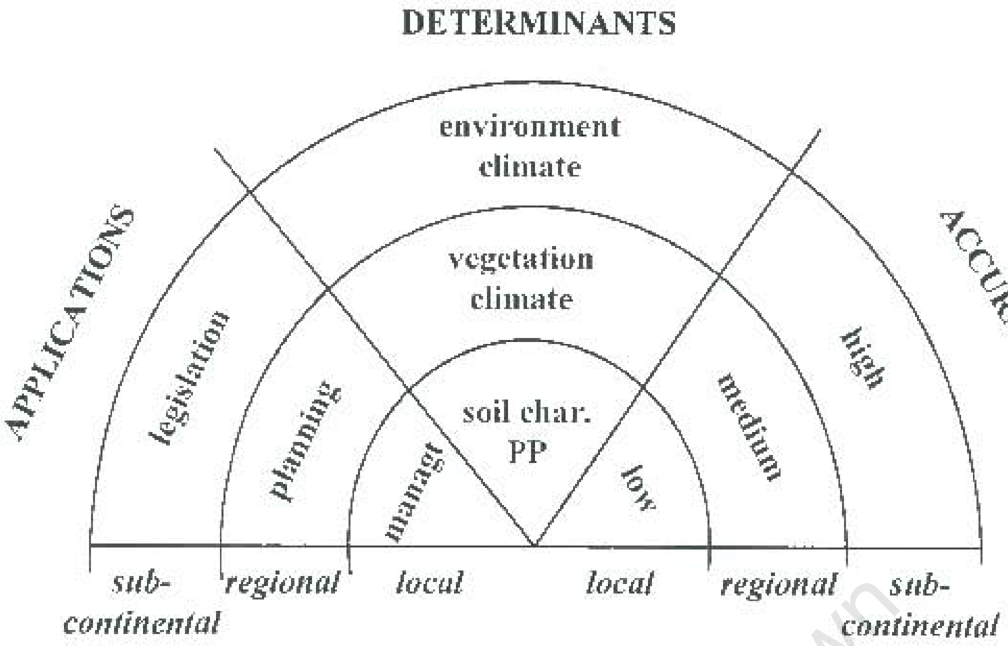


Figure 2. Inter-dependence of determinants of species distribution, model accuracy (static approach), application types, and spatial scale. managt: management; soil char.: soil characteristics; PP: propagule pressure).

A scale hierarchy in the environmental factors identified as determinants is observed. This hierarchy is however confused with the scale-dependence of mapping environmental factors. Climatic factors were the most important determinants of species distribution at regional (Chapter 2, 4) and sub-continental scale (Chapter 5). This study has shown that seasonal variability of climatic factors might play an important role in determining the distribution of some woody species (Chapter 2). The role of propagule pressure in determining the trajectory of invasions is more pronounced at fine-scale (Chapter 3) than broad-scale (Chapter 5).

Finally, the spatial scale of the information required by managers, planners, or policy-makers differs. Information collected at local scale is of little use to planners, or policy-makers (Chapter 5). A regional scale is probably more appropriate for planning purposes (e.g. Chapter 4), whereas countrywide assessments can provide guidelines for policy on alien plant management (Chapter 5).

Towards a predictive ecology

In order to respond to the major factors threatening biodiversity (such as global change, invasive species, land pressures), Ecology, as a scientific discipline, needs to be more predictive. Predictions of future changes, or impacts on biodiversity, ecosystem functioning, are required to anticipate threats and to prioritise conservation actions. This provides an interface between theory and applied science.

Predictions of future threats to biodiversity however remain a difficult task. This study has highlighted, with respect to invasive species, the importance of plant-environment interactions, but incorporating these interactions in modelling is challenging (Chapter 3). Through the different chapters, the scale-dependence of the results became clearer. For example, conservation value was higher at finer-scale than the one derived from broad-scale. This could imply that regional conservation plans fail to identify fine-scale priority-areas, especially in fragmented and diverse habitats (Chapter 6).

Novel modelling approaches are therefore required to predict the impact and the directions of future threats to biodiversity at multiple scales. Such approaches should include interactions between species dynamics and land use and should capture the spatial structure of landscape.