Rampant Rainforests:
An Assessment of Rainforest Boundary Dynamics in Kakadu National Park based on Aerial Photography, Field Surveys and Multi-Scale Modelling

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Declaration:

I hereby declare that the work herein, now submitted as a thesis for the degree of Doctor of Philosophy of the Charles Darwin University, is the result of my own investigations, and all references to ideas and work of other researchers have been specifically acknowledged. I hereby certify that the work embodied in this thesis has not already been accepted in substance for any degree, and is not being currently submitted in candidature for any other degree.

Signed:

Date:
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Abstract

Understanding the extent and causes of savanna-forest dynamics in tropical regions is vital as small but widespread changes to tropical forests can have a major impact on global climate, biodiversity and human well-being. Changes to the boundaries of 50 monsoon rainforest patches in Kakadu National Park were assessed using temporal sequences of digitised aerial photography between 1964 and 2004. Wet and dry rainforest boundaries were manually classified for each year using a 20 x 20 m point lattice in a GIS. This revealed an overall expansion of rainforest patches by an average of 28.8%. A reassessment of the rate of change using bootstrapping of all available aerial photography supported the existence of an overall expansion of rainforest, but suggested that the rate of change was overestimated for dry rainforest. Floristic, structural, environmental and disturbance attributes of the changes were investigated by sampling 588 survey plots across 30 rainforest patches. The abundance of rainforest trees and grass were consistent with the trend of rainforest expansion. The view that the rainforest boundaries had been highly dynamic at a decadal scale was supported by (i) the overall floristic composition of newly established rainforest and stable rainforest being similar, and (ii) the rapid rates of change observed for a subset of nine rainforest patches with detailed aerial photographic histories. Generalized linear modelling supported an effect of late dry season fire frequency, historical buffalo impact and rainforest type in mediating the rate of change. The effect of fire in driving the changes was also supported by an effect of topographic fire protection and flammable weeds in GIS mapping of three rainforest case studies. However disturbance factors were unable to account for the overall expansion of rainforest. We conclude that the boundary expansion is likely to have been primarily driven by factors that have shown similar increases during the study period, such as annual rainfall and atmospheric CO₂. Nonetheless, fire and buffalo impact have mediated the rate of change. This study provides a unique historical perspective on rainforest dynamics and will contribute to ‘adaptive management’ programs, particularly with respect to fire management.
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Preface

The chapters presented in this thesis have been published or accepted for publication in various journals. Consequently, there is some repetition of material. However, editing has been conducted to keep repetition to a minimum.
Chapter 1 - Introduction
The macroecological approach

Despite great progress in specialized disciplines such as ecology, biogeography and paleontology, it is increasingly acknowledged that answers to many scientific questions lie beyond - and across - the boundaries of traditional disciplines. An approach that attempts to address this issue is that of ‘macroecology’. Macroecology is a way of studying relationships between organisms and their environment that involves characterizing and explaining statistical patterns of abundance, distribution and diversity (Brown and Maurer 1989). The prefix ‘macro’ is used, as to characterize patterns in the individuals, populations or species, it is usually necessary to work at relatively large spatial and temporal scales to obtain sufficiently large samples. Additionally, macroecology expands the scale of ecological research to incorporate the techniques of several disciplines such as biogeography and systematics. There is an emerging understanding that multidisciplinary studies are needed to gain the full picture, as each technique used has limitations as to the kind of information that can be derived (Bowman 2002).

It is often not possible or practical to perform experiments at the spatial and/or temporal scale required to answer some applied questions. The reductionist approach to research, pulling systems apart and examining their components in great detail has also proved unable to grasp the complexities of entire, complex systems. This is partly due to the fact that the results of small-scale studies usually cannot be extrapolated to larger scales. Most ecological experiments have been conducted at relatively small scales due to the high cost of techniques such as quadrat based field sampling. Many large scale variables such as climatic and geological factors are also impossible to manipulate experimentally.

Much research is also conducted at spatial and temporal scales that are not of practical use to land managers. Land managers of many Australian environments critical to conservation, such as national parks, are faced with the challenge of managing huge areas with relatively little resources. Studies conducted at the landscape scale are therefore critical. Additionally, the temporal scale of much research is either too short
(such as those conducted at only one point in time) or too long (such as paleological studies) to be of practical use for land managers (Brown and Maurer 1989).

There is also a practical need for macroscopic studies in the Australian context. Over the last two centuries since European invasion there have been unprecedented changes in the natural environment brought about by shifts in a variety of social and environmental factors. For example most of Australia has experienced the breakdown of traditional Aboriginal systems of fire management and the introduction of European management. This is thought to have had profound effects on a variety of ecological processes, with resultant major shifts in vegetation patterns across the continent. Such changes have threatened the integrity of many biological processes and the survival of vast numbers of species. The challenge of understanding these changes is heightened further by interactions with global environmental change phenomena, such as rising temperatures and elevated greenhouse gasses (Lewis et al. 2004a).

Here we investigate the nature and causes of changes to rainforest boundaries in Kakadu National Park (KNP). The study adopts the macroecological approach in that it (i) is conducted at a large spatial scale with samples taken across the c. 20,000 km² that the Park covers, (ii) examines a relatively large temporal scale, making use of aerial photography to assess changes over several decades and (iii) combines a number of different approaches including field sampling, GIS analyses, and modelling in order to gain a greater understanding of the system studied.

**Australian rainforests**

There is no consensus as to the precise definition of rainforest in Australia. The term ‘rainforest’ is used to define a broad variety of atypical Australian forest types (Bowman 2000a). These include a variety of structural and floristic types and are broadly classified by the climatic regime in which they occur as either tropical, subtropical, monsoonal and both cool and warm temperate rainforest types. The current distribution of rainforests in Australia occurs as an arc of rainforest fragments along the east and northern coastlines
(Figure 1). The monsoonal rainforests, which are the subject of this study, are adapted to a climate which is characterized by seasonally wet and dry conditions (Bowman 2000a).

Figure 1. The distribution of the four major types of rainforest in Australia (adapted from Bowman, 2000). The dash line indicates the approximate inland extent of rainforest (includes the whole of Tasmania).

The pioneering work on describing and classifying Australian rainforests was carried out by Webb and Tracey (1981). More recently, extensive surveys of 1219
Rainforest patches by Russell-Smith (1991) allowed the classification of rainforests of northern Australia into 16 floristic types.

For the purposes of this study, rainforests in KNP were defined as vegetation with a closed canopy which were not dominated by species such as eucalypts (*Eucalyptus* and *Corymbia* spp.) or paperbarks (*Melaleuca* spp.). Rainforest patches were identified based on previous mapping by Russell-Smith (1991). The two basic types of rainforest sampled were ‘wet monsoon rainforest’ which occurs on sites with perennial moisture supplies such as springs, and ‘dry monsoon rainforest’ which occurs on freely drained sites that are often associated with topographic fire protection such as rocky areas, cliff lines and hill tops (Bowman et al. 1991, Russell-Smith 1991). For simplicity these vegetation types are referred to here as ‘wet rainforest’ and ‘dry rainforest’. *Allosyncarpia ternata* S.T.Blake dominated rainforest also occurs on the Arnhem Land plateau region of KNP, but were not included in this study as they are a unique system and were the subject of a parallel study (Bowman and Dingle 2006).

**Rainforest boundary dynamics in northern Australia**

Rainforest boundaries are known to be highly dynamic on both long and short time scales, and these changes appear to have been driven by shifts in climatic variables as well as disturbance events (Bowman 2000a). Information on early rainforests in Australia comes from a wide variety of fossil types. Although there are many gaps and uncertainties, there is sufficient evidence to show that a large part of the continent was covered with rainforest for much of the late Cretaceous and Tertiary period (Truswell 1990). Greater uncertainty exists regarding the history of monsoonal rainforests such as those sampled in this study, due to the absence of relevant paleorecords in the region where this rainforest type occurs. However, the current distribution of monsoon rainforests as an archipelago of islands separated by drier vegetation such as savanna, supports the view that this forest type was once much more widespread (Russell-Smith and Dunlop 1987).
The fossil record for eastern Australia suggests that a dramatic reduction in rainforest area occurred in the late Tertiary period, and was most likely primarily driven by climatic cooling and drying (Truswell 1990). There is debate as to the relative contribution of Aboriginal burning to the retreat of rainforest vegetation in Australia, however it is almost certain that such fire practices would have accelerated the process of forest fragmentation over the last c. 50,000 years (Bowman 2000a).

Further evidence of rainforest boundary dynamics in northern Australia in the late Holocene is provided by abandoned Orange-footed Scrubfowl (*Megapodius reinwardt*) nests. Scrubfowl create large mounds (>1 m high) of soil and leaf litter in which to incubate their eggs. Scrubfowl are thought to only create these nests under a closed canopy, so nests found in savanna areas surrounding rainforest patches are inferred to indicate historical rainforest boundary retreat. Such exposed mounds have been observed in several areas across northern Australia including around rainforest patches near Darwin (Panton 1993) and within Kakadu National Park (Russell-Smith 1985).

Number of studies have also indicated a high degree of dynamism in the rainforest boundaries in northern Australia at the decadal scale. A field based survey of 1,219 rainforest patches by Russell-Smith and Bowman (1992) suggested monsoon rainforests had contracted at a regional scale as a result of unfavorable fire regimes and feral animal disturbance. However, localized studies using aerial photography have revealed rainforest expansion at the expense of more open vegetation types. These include rainforests in Litchfield National Park near Darwin (Bowman et al. 2001), on the Arnhem Land Plateau (Bowman and Dingle 2006) and in the Gulf of Carpentaria (Brook and Bowman 2006). The changes observed in these studies parallel rainforest expansion observed on the east coast of Australia (Harrington and Sanderson 1994, Russell-Smith et al. 2004a).

A biological mechanism for such expansion has also been previously established through detailed field studies of stand structures. For example, Banfai and Bowman (2005) conducted ground truthing of the rainforest expansion recorded in Litchfield National Park based on aerial photography between 1941 and 1994. The size class distributions of rainforest and non-rainforest tree species were consistent with the
observed changes, with a higher density of rainforest saplings and poles in savanna where rainforest expansion had occurred, compared to stable savannas.

**Causes of boundary dynamics**

*Fire*

Previous research throughout the tropics has highlighted that fire regimes can have a major impact on rainforest boundary dynamics. Fire can lead to rainforest contraction by killing seedlings and consuming live foliage, thus reducing tree growth and survival on rainforest boundaries (Bowman 2000a). The generally high intensity of late dry season fires are thought to be particularly threatening to the integrity of rainforest boundaries (Russell-Smith and Bowman 1992). However, rainforest seedlings are usually able to survive the effects of at least a single fire (Russell-Smith and Dunlop 1987, Bowman and Panton 1993). Fire frequency is therefore thought to be of critical importance in determining the rate of boundary dynamics.

A reduction in fire frequency has often been attributed as the cause of rapid expansion of tropical forests globally (Hopkins 1992, Swaine et al. 1992, King et al. 1997). In northern Australia, an important driver of rainforest expansion is thought to be a reduction in the frequency of fire following the transition from Aboriginal to European management (Bowman et al. 1990, Crowley and Garnett 1998, Bowman et al. 2001). Under traditional Aboriginal management, rainforest patches in northern Australia were commonly afforded habitat-specific fire management. Examples include the careful burning of rainforest boundaries to protect food resources such as yams (Russell-Smith et al. 1997a). There has been a substantial disruption of traditional fire regimes over the last century due to a dramatic reduction in the Aboriginal population in many areas and the establishment of European management practices. However, traditional fire management practices continue in many localized regions (Press and Lawrence 1995).

While it is often assumed that there has been a reduction in the frequency of fire following the transition from Aboriginal to European management, this is uncertain as
fire frequencies remain very high in northern Australia. For example, an average of 57% of the lowlands of KNP burnt each year between 1980 and 1995 (Edwards et al. 2003).

Feral animals

Feral animals such as Asian water buffalo (*Bubalus bubalis*) are also known to have dramatic impacts on rainforests. A study in KNP showed that rainforest patches that were more intensively used by buffalo had a lower density of vegetation <3 m during the dry season and a higher foliage height diversity because buffalo knocked down many young trees (Braithwaite et al. 1984). Soil compaction was also thought to have led to the death of large trees due to poor recharge of groundwater.

The feral pig (*Sus scrofa*) can also cause damage to rainforest by upturning soil while foraging and by rubbing trees, wallowing and trampling. Regional surveys by Russell-Smith and Bowman (1992) indicated that extensive rooting activity was present in 10.3% of rainforests, with wet rainforests being particularly susceptible. In the short term, pigs do far less structural damage to rainforest than buffalo, however, pig disturbance could have a major impact in the long term as they limit recruitment of rainforest seedlings. The feral pig has been implicated in contributing to the decline of the palm *Ptychosperma bleeseri* in the Darwin area (Barrow et al. 1993).

Rainfall

Climate is a primary factor determining the location of forest boundaries, and shifts in rainfall patterns can alter the balance between forests and more open vegetation types (Cramer et al. 2004, Vanacker et al. 2005). An increase in rainfall has occurred in the Northern Territory over the last century. Between 1910 and 1995 the total annual rainfall increased by 15-18% (Hennessy et al. 1999). The increasing trend has been considerably steeper for the second half of the 20th Century (Smith 2004).

Increased rainfall may have facilitated expansion of rainforest by increasing supply of water to tree roots through influencing catchment scale soil moisture patterns (Cook et al. 1998). Soil moisture has been shown to be important for establishment of rainforest seedlings in north Australian savannas (Bowman and Panton 1993). In
addition to the increase in rainfall, there was an increase of almost 20% in the number of rain days in the last 100 years (Hennessy et al. 1999), which may have extended the growing season for rainforest trees limited by water availability.

\( CO_2 \)

Atmospheric \( CO_2 \) has shown a steady rise over the last few decades, increasing from 320 ppm in 1964 to 377 ppm in 2004 (Keeling and Whorf 2004). Increased levels of atmospheric \( CO_2 \) may facilitate the expansion of forest into more open vegetation types, as it favors the growth of trees (predominantly \( C_3 \) photosynthetic pathway) over grasses (predominantly \( C_4 \)) (Bond et al. 2003, Berry and Roderick 2006). Controlled experiments have consistently shown an increase in plant growth rates under elevated \( CO_2 \), known as the ‘\( CO_2 \) fertilization effect’. For example, seedlings of \textit{Maranthes corymbosa} Blume, a rainforest species that occurs in KNP, showed a marked increase in growth in a doubled \( CO_2 \) environment with total shoot dry weight increasing by 163% (Berryman et al. 1993). Faster growth rates may therefore have allowed rainforest trees to more readily escape the ‘fire trap’ posed by regular fires (Bond et al. 2003). Increased atmospheric \( CO_2 \) also increases the water use efficiency of trees, which may have allowed rainforest to establish in areas that were previously water limited.

However, increases in atmospheric \( CO_2 \) may not have contributed substantially to the expansion of rainforest where other factors are limiting. Such factors may include mycorrhizas and soil fertility, which have been shown to be important determinants of rainforest seedling establishment into savannas (Bowman and Panton 1993). Considerable uncertainty remains as to the effect of elevated \( CO_2 \) on vegetation change in Australia (Hughes 2003).
The study site - Kakadu National Park

Landforms and soils

KNP is located on the north coast of the Northern Territory of Australia (Figure 1), 250km east of Darwin. The lowlands cover two thirds of the Park (Figure 1) and consist of rolling plains sloping gently northward to the sea. They are primarily a late Tertiary depositional surface derived from erosion of Mesozoic sediments and earlier cover rocks. Resistant rocks form outcropping low strike ridges or hills in certain areas (Williams 1969). The surface consists of a complex of repeatedly weathered gravels, sands, silts and clays. Toward the south, soils are typically uniform to deep, well drained red sands to sandy loams. Further north, soils are usually gradational, yellowish sandy loams, often with poor drainage. The lower slopes vary from deep sands in depressions to shallow sandy mantels in alluvial environments (Russell-Smith et al. 1995).

The lowlands are abutted by two other major landforms; the Arnhem Land plateau and escarpment complex and the coastal riverine plains (Figure 1). The Arnhem Land plateau and escarpment complex forms the dominant feature of the Kakadu landscape with sheer cliffs fringing the lowlands and a quartz sandstone plateau dissected by deep gullies. Soils are absent from large parts of the plateau. Some areas have skeletal veneers of shallow sand and there are deep sand plains in sedimentary basins (Russell-Smith et al. 1995). The coastal riverine plains are associated with the lower reaches of several large rivers that flow northward. The plains are of recent origin and were formed by deposition of estuarine-deltaic sediments. Soils comprise saline to hypersaline clays and mudflats as well as shelly beach ridges, or cheniers, on some coastal plains. There are also large areas of floodplain with black, organic cracking clays which are usually inundated for months in the wet season (Russell-Smith et al. 1995).

Vegetation

The vegetation of the KNP area has been described in a large number of studies, including descriptions based on ‘land systems’ (Story et al. 1976) and more recent
studies based on mapping of faunal habitats (Schodde et al. 1987). On the lower reaches of the rivers there are extensive freshwater flood plains that grade into mangrove swamps and salt flats along the coastline. Eucalypt savannas occur on the deeply weathered plains that flank the floodplains and abut the rugged western edge of the Arnhem Land Plateau. *Melaleuca* forests occur on seasonally inundated floodplain margins and form gallery forests along rivers and creeks, often grading into rainforest. The rainforest types present in KNP have been described above (see Australian Rainforests).

**Climate**

The region has a monsoonal climate with over 90% of the c.1.5 m annual rainfall occurring in the wet season (October to March). Day time air temperatures remain high throughout the year (~30°C) with cooler nocturnal temperatures (~25°C) occurring during the dry season (Bureau of Meteorology 2003).

**Human history**

The archaeological record suggests that the Alligator Rivers region has been continuously occupied by Aboriginal people for somewhere between 50,000 and 60,000 years (Roberts et al. 1993, Russell-Smith et al. 1997a). It is estimated that the Aboriginal population of the Kakadu region was about 2000 when Europeans arrived in the mid 19th Century (Press and Lawrence 1995). By the first few decades of the 20th century the regional Aboriginal population was probably only a couple of hundred people, a decline primarily attributable to introduced diseases and social dislocation (Lucas et al. 1997). The Kakadu region continued to be sparsely populated throughout the mid 20th century with most residents engaged in economic pursuits such as the pastoral industry and the shooting of crocodiles.

The area was purchased by the federal government and declared a national park in 1979. Further major sections were added to the park in 1984 and 1987. In 1979 probably less than 100 Aboriginal people resided in the park, however the numbers have
increased steadily since that time (Press and Lawrence 1995). The non-Aboriginal population has also increased due to localized developments such as mining and tourism. The area is now jointly managed by the traditional owners and a federal conservation agency (Parks Australia North) via a lease arrangement, and is divided into five management districts. Aboriginal people currently reside in the Park in approximately ten communities and continue traditional management practices such as gathering, hunting and burning, albeit in a substantially reduced way relative to pre-contact levels.

**Feral animals**

The Asian water buffalo was introduced into northern Australia from South-east Asia in the 1820s (Letts 1962). Large populations became established in the Kakadu region in the late 1800s. Buffalo were hunted for their hides from the 1880s until 1956 when the industry failed. Their population began to increase dramatically after this time. In the absence of reliable historical estimates of population size, it is not possible to determine precisely when the population reached peak levels (Skeat et al. 1996). However evidence from aerial photography and anecdotal evidence from local residents (e.g. David Lindner *pers. comm.*) suggests that peak levels were reached in the 1970s. The Brucellosis and Tuberculosis Eradication Campaign (BTEC) commenced in the early 1980s and between 1983 and 1988 buffalo densities in KNP reduced from 5.6 to 1.2 animals km\(^{-2}\) (Skeat et al. 1996). However higher numbers may have occurred in rainforest patches as buffalo preferentially used rainforest habitat. For example, Ridpath (1983) estimated the density in forest vegetation along floodplain margins as 34 animals km\(^{-2}\). Buffalo are still present in the Park, at low density. The populations of other feral animals such as pigs and horses were also dramatically reduced by the BTEC campaign and small numbers continue in the Park.

**Fire regimes**

Little is known of the frequency and extent of burning in KNP prior to the record of fire scars from satellite imagery, which are available from 1980 onwards (Bowman et al. in
The available ethnographic, historical and contemporary data about Aboriginal burning in northern Australia suggests that, prior to European settlement, Aboriginal people used fire in a skilful manner for a diverse range of both cultural and ecological (i.e. resource management) applications (Bowman 1998, Russell-Smith 2001, Preece 2002). Burning tended to be highly patchy, creating a fine-grained habitat, and was primarily undertaken in the second half of the year (Bowman et al. 2004a, Bowman et al. in press-a). Such practices were widespread in northern Australia at least until the end of the 19th century (Preece 2002). Current management in KNP is primarily focused on reducing the incidence of destructive late season fires, with a focus on burning early in the year to reduce fuel loads and create fire breaks. In recent years, Aboriginal residents and Traditional Owners have recommenced many traditional burning practices in localized areas (Edwards et al. 2003).

Fire scar records from satellite imagery suggest that fire frequencies have remained high over the last few decades. Between 1980 and 1994 an average of 46% of KNP was burnt each year, with 25% burnt early (prior to July) and 21% burnt late in the dry season (Russell-Smith et al. 1997b). An average of 57% of the lowlands burnt each year. The extent of burning appears to have decreased slightly between 1996 and 2000 where an average of 40% of the Park, and 49% of the lowlands burnt each year (Edwards et al. 2003).

**Justification for study**

Tropical forests cover only *ca.* 10% of the land surface, but are of significant importance globally as they store and cycle large amounts of carbon in the atmosphere, contain more than 50% of the world’s species, and in many cases directly sustain human livelihoods and culture (Goombridge and Jenkins 2003, Malhi and Grace 2000). Small changes in the extent of tropical forests can therefore have major impacts on climate, biodiversity and human well-being.
Understanding the mechanisms of changes to tropical forests is particularly important in light of the risk of potentially dangerous positive feedbacks with the climate system that could dramatically accelerate and intensify climate changes (Lewis 2006). For example, while rainforests are currently sinks for carbon, by the middle of the 21st century they may become carbon sources under global ‘business as usual’ emissions of CO₂. Understanding the extent and causes of global savanna-forest dynamics is thus vital as changes in tropical forest extent can have a major impact on global climate, biodiversity and human well-being.

The rainforest of KNP are also of great importance at the regional scale. This forest supports a high diversity of plant species (Russell-Smith 1991) as well as providing an important refugia for savanna-adapted mammals to avoid climatic extremes, predators and fires (Bowman and Woinarski 1994). They are also critical to the conservation of frugivorous birds which move between patches of rainforest and thus depend on the existence of a network of patches. A spatial analysis of six bird species by Price et al. (1999) demonstrated that the destruction of individual patches can have far-reaching regional effects by increasing the distance between patches.

Changes to rainforests also have substantial implications for the Aboriginal cultural values of the Park. For example, traditional harvesting of a variety of rainforest plant species such as yams (Dioscorea spp.) for fruit and tuberous roots by local Aboriginal groups continues to the present day (Lucas et al. 1997, Russell-Smith et al. 1997a). Some rainforest patches are also of great spiritual significance being associated with Dreaming stories.

**Problem statement**

While the rainforests in northern Australia are clearly of great natural and cultural value, a number of processes are thought to be threatening the integrity of rainforest boundaries. There has been concern from traditional owners and rangers within KNP due to the occurrence of fire damage to the boundaries of some rainforest patches.
Additionally, surveys by Russell-Smith and Bowman (1992) indicated that monsoon rainforests are contracting at the regional scale due to the combined effects of an increase in late dry season fires, feral animal damage and weed invasion. These authors found that one-third of rainforest sites surveyed had boundaries severely degraded by fire.

However, the conclusions of this study were inferred from field observations at a single ‘time-slice’ rather than on reliable historical records of change. They thus may not have adequately captured the true nature of the dynamics, which are occurring at much larger spatial and temporal scales. As no broad-scale assessment of rainforest boundary change had been undertaken, the rate and even direction of boundary change has remained uncertain. The relative importance of the various possible drivers of change, such as historical shifts in fire, buffalo and climate were also poorly understood. The lack of a historical context of the extent and causes of changes in rainforest boundaries has made it difficult to make informed decisions regarding the management of these systems.

**Aims**

This study aims to assess:

1. **How have the rainforest boundaries in KNP changed over the last few decades?**

2. **What factors have caused these changes?**
Overview of chapters

Chapter 2 addresses the first aim of this study. Changes to the boundaries of 50 rainforest patches are assessed using temporal sequences of digitized aerial photography. Boundaries are compared for each of the years 1964, 1984, 1991 and 2004. Ground truthing was conducted to assess the error in the mapping. The possible causes of the observed changes are also introduced.

Chapters 3 to 5 address the second aim of this study, assessing the relative strength of evidence for each of the hypotheses for the causes of the observed changes proposed in Chapter 2. A different approach to the problem is adopted in each of these chapters.

In Chapter 3 a field assessment of the causes of change is conducted. Floristic, structural, environmental and disturbance attributes of the changes are investigated by sampling 588 plots across 30 rainforest patches. This included (i) assessment of the abundance of trees and grasses, (ii) ordination analyses comparing overall floristic composition between newly established rainforest and longer established rainforest, as well as (iii) generalized linear modelling of the relationship between the boundary dynamics and contemporary levels of disturbance and environmental variables as measured in the field.

In Chapter 4 generalized linear models and model selection techniques are used to assess the role of fire, buffalo impact and patch characteristics in determining the rate of boundary change over the study period. Predictor variables were derived via GIS analyses of historical data sources. The analysis is conducted at both the patch scale and within-patch scale to capture the different processes operating.

Chapter 5 constitutes a reassessment of the extent and causes of the observed boundary dynamics, through investigating the influence of the number of aerial photographs used. The rate of change is investigated for a subset of nine patches with detailed aerial photographic histories. Overall rate of change is reassessed based on all available photography. The effect of fire is also reassessed using case studies and a different method of calculating fire frequency in generalized linear models.
Finally, Chapter 6 provides a synthesis of the findings of the project and discusses their implications for both the literature and the management of rainforest in KNP. Avenues for further research are also suggested.
Chapter 2 - Forty years of rainforest expansion and boundary dynamics

This chapter has been published as: Banfai, D. S., and D. M. J. S. Bowman. 2006. Forty years of lowland monsoon rainforest expansion in Kakadu National Park, northern Australia. Biological Conservation 131:553-565.
Introduction

Within the lowlands of KNP, substantial changes to the natural and cultural landscape have altered the disturbance regime and resultant vegetation pattern over the last 150 years. These changes include the breakdown of traditional management practices following a dramatic reduction in the Aboriginal population due to disease and expatriation from their traditional lands (Press and Lawrence 1995) and massive fluctuations in the abundance of feral animals such as Asian water buffalo (Skeat et al. 1996). Given the field-based evidence for regional monsoon rainforest boundary contraction (Russell-Smith and Bowman 1992) and the numerable processes that may have threatened the ecological integrity of KNP, a historical context is clearly needed to provide land managers with an appreciation of recent landscape-scale changes to rainforest boundaries. Change in forest area is also of increasing importance in light of international climate change agreements as it is a dominating factor in the long-term net flux of carbon between terrestrial ecosystems and the atmosphere (Houghton 2005).

Aerial photography provides a powerful data source for the investigation of historical landscape change as it allows assessment of large areas over a wide geographic range, which would be impossible with a purely plot-based approach. It also has significant advantages over satellite based data sources due to its high resolution and the long time period the record spans (Fensham and Fairfax 2002). Despite its potential, the use of digitized aerial photography is a relatively recent development. This technique allows for accurate quantification of decadal-scale vegetation boundary dynamics (Kadmon and Harari-Kremer 1999, Augustin et al. 2001, Kennedy and Spies 2005). The utility of aerial photography to assess changes to rainforest distribution has been demonstrated in several studies in tropical regions outside Australia (Endress and Chinea 2001, Lawes et al. 2004) as well as within Australia (Bowman et al. 2001, Russell-Smith et al. 2004a).

This study provides the first large-scale assessment of the rate and magnitude of decadal-scale changes to rainforest boundaries in Australia by comparing temporal sequences of digitized aerial photography from KNP since the mid 20th century. Ground truthing was used to characterize the different vegetation types mapped and thereby
determine the reliability of the mapping. The variation in the patterns of rainforest
dynamics and their geographic distribution is then described. As well as providing a
historical context of change, this will allow appraisal of competing views of the relative
importance of various factors driving the dynamics.

**Methods**

*Site selection*

Previous broad-scale mapping of monsoon rainforest types used for site selection in a
previous study (Russell-Smith 1991) was used with a GIS to identify and stratify
lowland rainforest patches into ‘wet’ and ‘dry’ rainforest types. These habitat types are
useful in understanding the differing processes affecting the various elements of this
vegetation. The operational definition of rainforest was (i) closed canopy forests (ii) not
dominated by *Eucalyptus/ Corymbia spp.* or *Melaleuca spp.* and (iii) greater than 50m in
diameter to allow for aerial photography analysis. Sites not meeting these criteria were
discarded in the selection process. Based on stratification by rainforest type, 30 sites
were haphazardly chosen to encompass the full geographic range of KNP as well as the
variability in soil type and fire history based on thematic GIS layers. The proportion of
dry rainforest and wet rainforests selected was based on the proportion of each type in
the study area (ratio Dry to Wet c. 3 : 2). Effort was also made to stratify sampling by
each of the five management districts. An additional 20 sites of particular interest to the
local residents and other land managers were chosen making a total of 50 sample sites
(Figure 2).

Approximately 10% of the lowland rainforest patches in KNP were sampled for
each rainforest type. This is, however, a conservative estimate of the proportion of
closed canopy forests sampled, as the mapping by Russell-Smith (1991) on which the
selection was based used a much broader classification of rainforest which often
Figure 2. (a.) Location of study site in the Northern Territory of Australia, (b.) location of KNP at the regional scale and (c.) location and percentage change (1964-2004) of rainforest patches sampled overlayed on the different landforms present in the study site. ‘D’ indicates two patches excluded from analyses due to substantial disturbance due to infrastructure. Asterisks (*) indicate two patches on Field Island where percentage change 1950-2004 is indicated as 1964 photographs were not available.
included scattered rainforest trees and vegetation dominated by *Melaleuca spp.* (Jeremy Russell-Smith, pers. comm.).

*Vegetation mapping*

Aerial photography was sourced for each rainforest patch as contact prints. The years chosen for analysis were those that had a complete photographic coverage of KNP within two years at a scale suitable for the analysis; 1964/5, 1983/4, 1991 and 2004. All photographs used color film at a scale of 1 : 25,000 apart from the years 1964/5 which were black and white and at 1 : 16,000. For two rainforests on Field Island 1964/5 photographs were not available (Figure 2). These sites were therefore excluded from analyses involving that year.

The imagery were scanned to achieve a common pixel resolution of 1 m² and stored as standard tiff files. The 1991 photographs were georectified to 1:50 000 topographic maps using ArcGIS 8 (Environmental Systems Research Institute (ESRI)). All other photographs were registered to the 1991 images using image-to-image registration and ensuring the root mean square errors were <15 m (Average 8.48 m). The method of vegetation mapping used was adapted from Bowman et al. (2001) and has been shown to produce reliable estimates of boundary dynamics (Banfai and Bowman 2005). A 20 m x 20 m point lattice with fixed geo-coordinates was overlaid on each aerial photograph using Arcview 3.3 (ESRI). The extent of the dot grid was proportional to the size of the closed rainforest patch allowing for a 100 m buffer around the edge. Each dot grid point was manually classified for each year using ArcGIS 8 (ESRI) at a common scale of 1:3000 with reference to the area within 10m radius of the point. The rule-based dot grid method to classify vegetation was used to minimize the error associated with defining boundaries across ecotones. Categories used were as follows: (i) Open vegetation = no trees present; (ii) Savanna = trees present but not closed canopy; (iii) Paperbark forest = even light colored closed canopy; and (iv) Rainforest = uneven dark colored closed canopy. Rainforest vegetation was then further divided into wet and dry rainforest depending on the classification of each rainforest patch in previous mapping by Russell-Smith (1991). Examples of rainforest classification are
Figure 3. Examples of aerial photography for a dry and wet rainforest for each year used in analysis. Only dots classified as rainforest are shown. Percentage change in rainforest area between each pair of photographs is indicated.
provided in Figure 3. Points that corresponded to roads or settlements were classified as ‘Disturbed’. Points that remained unclassified were placed in an ‘Other’ category.

**Ground truthing**

A subset of 30 rainforest patches were selected for field sampling from the rainforest patches undergoing aerial photograph analysis. Effort was made to ensure that sites were surveyed across the full geographic range of lowland rainforest in the study site and that both rainforest types were sampled in proportion to their abundance. Surveys were conducted in the dry season between May and October 2004. Field survey plots were 20 m x 20 m and centered on grid points used in the vegetation mapping, which were relocated in the field with a Global Positioning System (GPS). Individual rainforest patches were stratified into four equal parts (vertical and horizontal divisions) in order to spread the samples over the patch. Where possible, four random points (one from each quarter) of each vegetation type based on the 2004 aerial photography were sampled. Extra sample points were added to sample areas where the vegetation had transitioned from monsoon rainforest to another vegetation type or *vice versa* based on the aerial photography record (maximum of 10 per site). A total of 588 points were sampled. Traditional owners were employed to assist with the surveys where possible.

At each sample point the basal area of trees was estimated with a Bitterlich wedge and the taxonomic identity of each tree recorded was noted. Dominant understorey plants (> 20% cover) were also recorded. Voucher specimens of all species were collected and their identity confirmed at the Northern Territory Herbarium. At the centre of each plot a 5 m x 5 m quadrat was used to measure total projective foliage cover > 2m and cover of trees in each structural height class on a Braun-Blanquet scale (Height classes: 20-30 m, 15-20 m, 10-15 m, 5-10 m, 2-5 m, < 2 m).

To assess the accuracy of the georeferencing and mapping process, GPS tracks with data points spaced every 5 m were recorded along 20 rainforest boundaries. Tracks were recorded only where there was a clear transition from rainforest to surrounding vegetation.

Helicopters were used to survey aerially a further 16 of the selected patches in November 2004. Two transects perpendicular to each other and intersecting at the centre
of each patch were flown at low speed. These surveys provided confirmation that the patches were dominated by rainforest species and notes were taken on the other vegetation types present as well as disturbance history.

**Data Analysis**

Although the site selection was partially based on their being of particular interest to stakeholders, this did not substantially bias the site selection as the direction of change was unknown and sites were well spread geographically. All 50 sites were therefore analyzed together.

Tree species were analyzed with a Two-way Indicator Species Analysis (TWINSPAN) procedure (McCune and Mefford 1999) to classify ‘rainforest’ and ‘non-rainforest’ species groups. Pseudo species cut off levels were 2, 5, 10 and 20. The resultant groups were classified as either rainforest or non-rainforest based on field experience and relevant literature (Liddle et al. 1994, Dunlop et al. 1995, Brock 2001). Benefits and limitations of this approach are discussed in Banfai and Bowman (2005).

Descriptive statistics of the measured structural and environmental data were calculated for each vegetation type. Where data were able to meet the assumptions of parametric statistical tests, one-way ANOVAs were undertaken and means compared using Tukey’s *post hoc* test. Non-parametric data were analyzed using Kruskal-Wallis tests. Structural complexity index was calculated as the number of different height classes in which cover was recorded.

To assess the accuracy of the mapped boundaries further, the average distance of GPS tracks to the nearest rainforest boundary were calculated. As the mapping was based on dot grids, the actual position of the mapped boundary was estimated by buffering each dot classified as rainforest to become a circle with 10m radius using ArcGIS 9 (ESRI). Ten random points on each GPS track were then selected and the distance to the edge of the nearest buffered rainforest point was measured. An overall average distance was then calculated based on the average for each patch.
Extent of change
Polygons representing each rainforest patch were created using ArcGIS 9 (ESRI) by converting points mapped as rainforest to 20m x 20m grid cells which were then joined. These polygons were used to calculate percentage change in patch size and absolute area change for each year, with 1964 as the baseline.

The average percentage of the 1964 boundary that expanded, contracted and remained stable was calculated using the Nearest Feature tool in ArcGIS 9 (ESRI). This was based on the distance from points on the outside edge of the rainforest patch in 2004 to the nearest point on the outside edge of the patch in 1964. Edges that were defined by the edges of photographs were excluded.

The variation in extent of change between patches was investigated via a map of patches showing their percentage change. A semivariogram was used to investigate further the spatial autocorrelation between patches as a plot of the difference in the percentage change squared against the separation distance between each pair of rainforests sampled. This was repeated for absolute area change.

Patch characteristics
Perimeter and patch size were calculated based on polygons as for absolute area change. The fragmentation was calculated as $2\ln(0.25P)/\ln(A)$, where $P = \text{total perimeter}$ and $A = \text{total patch size}$ (Hargis et al. 1998, Donovan and Welden 2002). This index ranges between 1 and 2 and gives an indication of how convoluted in shape a patch is. The perimeter and area are logged to reduce the influence of patch size. Fragmentation was compared between rainforests types for each year, and between years for each rainforest type, using one-way ANOVA.

Transition matrix
A transition matrix was created based on the percentage of points that changed from one vegetation type to another to assist in understanding the dynamics of individual points. This method allows for the investigation of losses and gains in each vegetation category beyond changes in the proportional area. For example, a vegetation type may have remained stable (i.e. be in a steady state) in total area while still exhibiting dynamic
behavior by having losses and gains from other vegetation categories (Johnson 1994). In order to avoid biasing the results toward larger sites, transition probabilities were calculated individually for each site and then averaged. The transition matrix was created to show the probability of each vegetation type in 2004 having been formed from the various vegetation types in 1964.

Rainfall

Average yearly rainfall was plotted for Oenpelli (12°19'35"S, 133°03'29"E) based on data sourced from the Bureau of Meteorology (2003). Oenpelli was used as it is the closest gauging station to the study site with a near complete rainfall record for the last century. It is located just outside the boundary of KNP to the northeast (Figure 2).

Results

Mapping and ground truthing

Twenty-nine dry rainforests and 21 wet rainforests were sampled (Figure 2) in a variety of landscape settings. Most of the dry rainforests (20) were on floodplain edges, with five patches located on hills or ridgelines, three on coastal islands and one in open savanna. Nearly all (18) of the wet rainforests were in open savanna, with the others occurring mostly on floodplain edges.

Savanna accounted for 74% of the mapped area in the 100 m buffer area surrounding the patches, being much more common than the other groups (Paperbark forest 5%; Open vegetation 15%; Other 4%). Area classified as ‘Other’ included small areas of mangrove forest along coastlines, water and unvegetated rock or sand. Less than 2% of the total area mapped was classified as ‘Disturbed’ in 2004. However, two dry rainforest patches experienced an exceptional amount of disturbance from the building of roads and settlements, decreasing in size by greater than 20% (Figure 2). These two sites were excluded from further analyses.
There was a strong concordance between the mapped vegetation types and the floristic attributes measured in the field surveys. The broad vegetation types separated well based on percentage cover as well as a number of other attributes such as vine cover (Table 1). While paperbark forest was not significantly different from rainforest or savanna in terms of percentage cover, it was distinct in that it had the highest average basal area of *Melaleuca* spp.

The results from the GPS tracks also supported the accuracy of the mapping of rainforest boundaries. The average distance between the track points and the mapped rainforest boundaries was 9.9 m (1.1 s.e.) which includes a c. 5 m error associated with the GPS in recording the tracks.

### Table 1. Mean (and standard error) of a variety of descriptive variables for each vegetation type.

**BA** = basal area. Significant differences between individual means (*p*<0.05) are shown as different letters.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Dry rainforest</th>
<th>Wet rainforest</th>
<th>Paperbark Forest</th>
<th>Savanna</th>
<th>Open Vegetation</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Total cover &gt;2m (%)</strong></td>
<td>46.1 (2.12)</td>
<td>53.8 (3.10)</td>
<td>38.0 (0.00)</td>
<td>25.0 (1.48)</td>
<td>1.4 (1.15)</td>
</tr>
<tr>
<td><strong>Total BA (m².hec⁻¹)</strong></td>
<td>9.0 (0.26)</td>
<td>12.6 (0.56)</td>
<td>12.6 (3.02)</td>
<td>7.8 (0.24)</td>
<td>2.4 (1.24)</td>
</tr>
<tr>
<td><strong>Proportion Rainforest spp.</strong></td>
<td>0.8 (0.02)</td>
<td>0.9 (0.03)</td>
<td>1.0 (0.03)</td>
<td>0.5 (0.02)</td>
<td>1.0 (0.00)</td>
</tr>
<tr>
<td><strong>Melaleuca sp. BA (m².hec⁻¹)</strong></td>
<td>0.5 (0.15)</td>
<td>1.4 (0.33)</td>
<td>8.8 (3.51)</td>
<td>0.6 (0.12)</td>
<td>0.2 (0.09)</td>
</tr>
<tr>
<td><strong>Grass cover (%)</strong></td>
<td>9.6 (1.60)</td>
<td>18.8 (3.15)</td>
<td>9.0 (4.96)</td>
<td>28.5 (1.99)</td>
<td>53.8 (5.31)</td>
</tr>
<tr>
<td><strong>Vine cover (%)</strong></td>
<td>7.7 (1.08)</td>
<td>2.9 (1.00)</td>
<td>0.8 (0.49)</td>
<td>4.0 (0.71)</td>
<td>0.3 (0.13)</td>
</tr>
<tr>
<td>Structural Complexity index</td>
<td>3.5 (0.10)</td>
<td>3.6 (0.14)</td>
<td>2.5 (0.42)</td>
<td>2.6 (0.08)</td>
<td>0.4 (0.11)</td>
</tr>
<tr>
<td><strong>N</strong></td>
<td>173</td>
<td>97</td>
<td>8</td>
<td>277</td>
<td>33</td>
</tr>
</tbody>
</table>

*Patch characteristics*

In 2004 dry rainforests had an average size of 35.9 ha (8.6 s.e.), while wet rainforest had an average size of 13.1 ha (2.6 s.e.). Although dry rainforests were generally much larger than wet rainforests, their size was also more variable. The size class distribution of patches (Figure 4) have a ‘J’ shaped distribution with the most frequent patch size being less than 10 ha for both dry rainforest and wet rainforest. Only dry rainforests are
in the largest size classes recorded. There was no substantial change in the size class distribution between 1964 and 2004.

The fragmentation of rainforest patches ranged from their being single almost circular patches to having highly convoluted boundaries with a number of sub-patches. Dry rainforests had a larger amount of variation in fragmentation than wet rainforests, encompassing both the lowest and highest index values (Figure 5). However, there was no significant difference in fragmentation index between the rainforest types for any year at the p<0.05 level. There was a small decrease in the average fragmentation index between 1964 and 2004, however there were no significant differences at the p<0.05 level between any of the years for either rainforest type. There was also no major change in the distribution of fragmentation for either rainforest type between 1964 and 2004 (Figure 5).

**Overall change**

Overall change in rainforest area from 1964 to 2004 was an average increase of 28.8%, with an average absolute area change of 4.0 ha per patch. These results conceal the fact that eight rainforest patches decreased in size over this time (average -8.4%). Additionally, the averages are skewed by a few patches that had dramatic increases. The
median percentage increase for the study period was 11.8%, while the median absolute area change was an addition of 1.9 ha.

Investigation of the spatial autocorrelation of the changes showed a high level of variability between patches. The trajectory and rate of change often differs for sites situated close together geographically (Figure 2). Thus there are no clear regional trends in expansion or contraction. Inspection of the semivariograms also showed no clear trends in the way that changes are spatially related.

**Dry rainforest vs. wet rainforest change**

There were clear differences in the changes observed for the different rainforest types (Figure 6). The average change for dry rainforests from 1964 to 2004 was an increase of 42.1%, whereas for wet rainforests was one third of this at 13.1%. For dry rainforest there is an almost linear increase in rainforest area over the study period. Wet rainforests experienced their greatest increase in rainforest area between 1983/4 and 1991, with only a slight increase between the other years sampled. The trends in absolute area were very similar to percentage change (Figure 6). The average absolute increase in rainforest area for dry rainforest between 1964 and 2004 was 5.7 ha, while for wet rainforest it was 1.93 ha.
The variability in the change was also much higher for dry rainforest. This is primarily due to a few dry rainforests experiencing dramatic increases. The median increases over the study period for the different rainforest types were much more similar (dry rainforest 15.3%; wet rainforest 10.9%).

Approximately 30% of the 1964 patch boundaries expanded over the 40 years (Figure 7), while an average of around 20% of the boundary contracted for both rainforest types.

Figure 6. (a) Average percentage change in rainforest area relative to 1964 and (b) Average absolute change in rainforest area per patch relative to 1964 comparing dry rainforest (solid line) and wet rainforest (dashed line). Standard errors are indicated.
**Transition matrices**

Most of the increase in rainforest size has been the result of the transition from savanna to rainforest (Table 2). For example, the percentage probability that a dry rainforest point in 2004 was originally savanna is 29.4%, whereas the probability that it was originally either of the other non-rainforest vegetation types adds to only 1.4%. Similar trends were observed for wet rainforest. The probability that a savanna point had been formed from a rainforest point was 6.2% and 3.7% for dry rainforest and wet rainforests respectively. These data suggests that this is a dynamic system involving substantial changes in the opposite direction to the overall trend of expansion.

![Figure 7. Average percentage of the 1964 boundary that contracted, remained stable, or expanded between 1964 and 2004, comparing dry rainforest (white bars) to wet rainforest (diagonal hash). Standard errors are indicated.](attachment:image.png)

**Table 2. Transition matrix of average percentage probability of vegetation types in 2004 having been formed from each vegetation type in 1964. Bold print denotes the highest probability of change for each vegetation type in 2004.**

<table>
<thead>
<tr>
<th>Rainforest type</th>
<th>Vegetation type 2004</th>
<th>Vegetation type 1964/5</th>
<th>Rainforest</th>
<th>Paperbark</th>
<th>Savanna</th>
<th>Open</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dry Rainforest</td>
<td>69.2</td>
<td>1.0</td>
<td><strong>29.4</strong></td>
<td>0.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Paperbark Forest</td>
<td>1.8</td>
<td>54.1</td>
<td><strong>40.4</strong></td>
<td>3.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Savanna</td>
<td>6.2</td>
<td>2.2</td>
<td>87.4</td>
<td>4.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Open vegetation</td>
<td>0.6</td>
<td>1.3</td>
<td><strong>17.2</strong></td>
<td>80.9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wet Rainforest</td>
<td>74.8</td>
<td>0.5</td>
<td><strong>24.7</strong></td>
<td>0.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Paperbark Forest</td>
<td>6.9</td>
<td>67.3</td>
<td><strong>19.0</strong></td>
<td>6.9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Savanna</td>
<td>3.7</td>
<td>0.7</td>
<td>95.1</td>
<td>0.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Open vegetation</td>
<td>0.0</td>
<td>0.1</td>
<td><strong>59.6</strong></td>
<td>40.2</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Rainfall

Although highly variable, the rainfall data for Oenpelli showed a clear increasing trend in average yearly rainfall for most of the last century with peak rainfall periods around the 1970s and in recent years (Figure 8).

Figure 8. Five-year running average yearly rainfall in Oenpelli. The least squares regression line is shown.

Discussion

Extent of change

Assessment of changes to rainforest boundaries revealed a previously undetected overall expansion of rainforest vegetation in the lowlands of KNP. The rate of expansion for dry rainforests was generally higher and much more variable, primarily due to cases where the expansion was of a substantially greater magnitude than wet rainforests. The observed expansion of rainforest is not consistent with previous regional studies that had suggested rainforests in northern Australia have been under threat from an increase in late dry season fires following European settlement, damage from feral animals such as buffalo, and the combined effects of both (Russell-Smith and Bowman 1992). This
result was also surprising to land managers of the study area given the general perception that rainforests were either stable or contracting.

However, the observed expansion of rainforest is consistent with previous smaller-scale studies in northern Australia based on aerial photography (Bowman et al. 2001, Bowman et al. in press-b). For example, mapping by Bowman et al. (2001) demonstrated that forest patches had nearly doubled in size between 1941 and 1994 in a 30 km$^2$ area of Litchfield National Park near Darwin. Subsequent ground truthing of this area has also established a biological mechanism for rainforest expansion in northern Australia through detailed analysis of stand structures (Banfai and Bowman 2005).

The observed expansion of rainforest is also consistent with other research within KNP. The few permanent survey plots on rainforest boundaries that were established to monitor the impact of fire throughout the Park showed a 51% increase in rainforest trees between 1995 and 2000 (Edwards et al. 2003). Additionally, a recent study of the endemic *Allosyncarpia ternata* dominated rainforest in upland areas of the Park have also shown similar trends of thickening (Bowman and Dingle 2006).

The authenticity of the observed expansion is supported by the strong concordance of the mapping with the field survey based on the 2004 images. The vegetation types were clearly distinguishable using the field survey data. There were some errors associated with the recording of GPS tracks such as the positional error of the GPS and the fact that tracks were only able to be recorded where there was a clear distinction between rainforest and surrounding vegetation. Nonetheless, the GPS track results provided further evidence for the overall accuracy of the georeferencing and mapping process.

It is also acknowledged here that there is inevitably some error in the photographic analysis process. Such errors may be generated by variation in scale, film type and season of photography (Fensham and Fairfax 2002). Comparing photographs with a variety of scales can be problematic as a small canopy gap is more likely to be evident on large-scale than small-scale photographs (Avery 1958). However the difference in scale between years was not great and errors were minimized by viewing the images at a common scale on-screen. Error associated with film type resulting from comparing black-and-white to colour photography was minimised by basing the
classification primarily on the distance between tree crowns. As all photographs were taken in the dry season, errors due to variation in season are likely to have been minimal. This study makes a substantial contribution to the weight of evidence supporting the expansion of rainforest throughout northern Australia. The rate of expansion observed is akin to that of the tropical rainforests in northern Queensland (Harrington and Sanderson 1994, Russell-Smith et al. 2004a), which also challenges previous experimental studies suggesting rainforest expansion occurs at much slower rates than that observed in KNP (Bowman and Panton 1993).

Causes of change
The observed expansion of rainforest in KNP raises the question of ‘what are the drivers of this change?’ Determining the cause of change is complicated by the fact that, as with many other areas in Australia (Pickard 2002), Kakadu is a confounded experiment with a number of factors varying simultaneously. However, the nature of the observed expansion does provide insight into the relative importance of the various factors driving the changes.

Feral animals
KNP has had an intensive history of fluctuations in feral animals such as Asian water buffalo and feral pigs (*Sus scrofa*) which are both known to cause substantial damage to rainforests (Braithwaite et al. 1984, Russell-Smith and Bowman 1992). In the absence of reliable historical estimates of population size, it is not possible to determine the precise years that the populations reached peak levels (Skeat et al. 1996). However aerial photography and anecdotal evidence from local residents (David Lindner *pers. comm.*) suggests that peak levels were reached in the 1970s. The Brucellosis and Tuberculosis Eradication Campaign commenced in the 1980s and between 1983 and 1988 buffalo densities for the Park were reduced from 5.6 to 1.2 animals km$^{-2}$ (Skeat et al. 1996). Feral pigs are thought to have followed similar population trends to buffalo.

A striking feature of the rainforest expansion is that despite the highly dynamic boundaries at any particular location there has been a consistent increase in rainforest area over time. This change is therefore unlikely to be related to factors such as feral
animals that have varied substantially in their intensity over this period. Nonetheless, the abrupt increase in wet rainforest area between 1984 and 1991 may reflect a decrease in feral animal disturbance due to the eradication program.

*Fire*

Previous research throughout the tropics has highlighted that fire regime can have a direct effect on rainforest boundary dynamics (Eden and McGregor 1992, Hopkins 1992, Swaine et al. 1992, King et al. 1997, Bowman 2000a). The importance of fire in driving the changes to rainforest boundaries in KNP is supported by the fact that the boundaries have been highly dynamic. A substantial proportion of patches declined in size over the study period and patches have generally experienced contraction of a substantial proportion of their boundary. Additionally, the rate of change often differed markedly for sites situated close together geographically. The spatial variability of the changes across the landscape is consistent with their having been mediated by differences in local fire regimes.

The rainforest boundaries were often highly fragmented and convoluted. This observation is also consistent with fire mediated vegetation dynamics as fire damage causes invagination of the boundary. A reduction in fire disturbance can also cause expanding boundaries to become ragged as the savanna habitats that support the highest growth rates are the first to be occupied, enabling rainforest tree regeneration to escape the fire trap. The observed fragmentation is also likely to be partly due to ‘nucleation’ whereby rainforest propagules are dispersed some distance from rainforest margins where they develop into mature rainforest groves, as has been observed with tropical rainforest on the east coast of Australia (Russell-Smith et al. 2004a).

This pervasiveness of fire in driving the vegetation dynamics in the study site is further supported by the following case studies of individual rainforest patches:

- The dry rainforest site that experienced one of the greatest reductions in percentage area (-22% from 1964 to 2004) is claimed by Park staff to have received regular late dry season fires (Greg Miles, pers. comm.).
• The three sites situated on islands, locations largely protected from fire, all experienced an increase in rainforest area.

• The two rainforest patches that had the highest rates of expansion (+352% and +256% from 1964 to 2004) have experienced a substantial reduction in the frequency of fire following a lessening in the intensity of Aboriginal management. Both these sites are likely to have had a history of intensive Aboriginal management as they are adjacent to historical Aboriginal camps and were important sites for traditional food resources (Lucas et al. 1997).

These observations provide evidence that fire is a powerful force in driving rainforest boundary dynamics in the study area. A decrease in the frequency and/or intensity of fire is therefore likely to have contributed to the expansion of rainforest observed in KNP, while recurrent fires have resulted in localized contraction of rainforest boundaries. However, the observed overall expansion of rainforest boundaries in KNP means that the establishment and survival of rainforest seedlings in the rainforest boundary zone has continued throughout periods of apparently unfavorable fire regimes. Frequent and intense fires are observed to have occurred prior to the establishment of the National Park (Edwards et al. 2003), and regular fires have continued ever since. For example, an average of 57% of the lowlands burnt each year between 1980 and 1995 (Russell-Smith et al. 1997b). A substantial proportion of these fires were late in the dry season, which tend to be of high intensity and damaging to vegetation. The continued rapid establishment and growth of rainforest trees in the boundary zone in the face of recurrent fires suggests that reduced fire frequency is not the primary factor driving the observed expansion process.

Rainfall and CO₂
The consistently increasing trend of expansion of rainforest boundaries observed suggests that the changes may have been caused by factors that have shown similar gradual changes over time. Possible candidates include variation in rainfall and atmospheric CO₂.
The average yearly rainfall has shown an increasing trend in Australia over the last century. Between 1910 and 1995 the total annual rainfall in the Northern Territory has risen by 15-18% (Hennessy et al. 1999). The increasing trend has been considerably steeper for the second half of the 20th Century (Smith 2004). These increasing trends in rainfall were reflected in the analyses for Oenpelli gauging station near the study site.

Soil moisture is important for establishment of rainforest seedlings in savanna (Bowman and Panton 1993). Increases in rainfall may therefore have increased the water available for use by rainforest trees by influencing catchment scale soil moisture patterns (Cook et al. 1998). This is likely to have had a differential effect on wet and dry rainforest as dry rainforests source their moisture from the unsaturated zone, whereas wet rainforests source their water from groundwater. The rate of expansion for dry rainforests may therefore depend on the length of the wet (growing) season, when water is easily available in the unsaturated zone. Between 1910 and 1995 there was a 41% increase in rainfall in the Northern Territory in autumn (Hennessy et al. 1999) which may have contributed to dry rainforests showing a greater expansion rate than that of wet rainforests. For wet rainforest, the sharp increase in area between 1983/4 and 1991 may have been the result of increased recharge of groundwater from the peak in rainfall around 1980 (Figure 8).

The observed expansion of rainforest boundaries is also correlated with changes in atmospheric CO₂, which has increased linearly over the study period (Keeling and Whorf 2004). Controlled experiments have consistently shown an increase in plant growth rates under elevated CO₂, known as the ‘CO₂ fertilization effect’. Enhanced atmospheric CO₂ also has the potential to alter the balance across forest-savanna boundaries as it advantages trees and shrubs (predominantly C₃ photosynthetic pathway) over (predominantly C₄) grasses (Berry and Roderick 2002).

While the observed rainforest expansion is consistent with having been driven by an increase in rainfall and atmospheric CO₂, the exclusive importance of these factors is not consistent with the evidence for fire driving boundary dynamics as noted above.
Synergistic effects

Determining the relative importance of the various factors driving the rainforest boundary dynamics is complicated by the likelihood of interactions amongst the putative causes discussed above. Table 3 ranks the foremost likely causes of the observed rainforest contraction and expansion. This list does not claim to be exhaustive, rather it is evidenced-based building on the results presented in this and previously published studies. Below we briefly outline why such interactions are likely to be important using three case studies.

While buffalo do not appear to have had a major direct impact on rainforest boundary dynamics, they may have had a greater impact on boundaries indirectly through their interaction with fire. The large numbers of buffalo from about 1950 to about 1980 are likely to have reduced the frequency and intensity of fires by reducing

Table 3. Summary of the foremost plausible causes of expansion and contraction of rainforest boundaries in KNP, with an explanation of the effect and hypothesized relative strength based on available evidence.

<table>
<thead>
<tr>
<th>Causes of expansion</th>
<th>Hypothesised Strength</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Variable(s)</strong></td>
<td><strong>Explanation</strong></td>
</tr>
<tr>
<td>Rainfall</td>
<td>Direct effects of increased water availability</td>
</tr>
<tr>
<td>CO₂</td>
<td>Direct effect of increased water use efficiency and competitive advantage to C₃ over C₄ plants</td>
</tr>
<tr>
<td>CO₂ X fire</td>
<td>Increased growth through enhanced water use efficiency allows seedlings to escape recurrent fires</td>
</tr>
<tr>
<td>Fire</td>
<td>Direct effect of reduced fire frequency</td>
</tr>
<tr>
<td>Fire X rainfall</td>
<td>Increased soil moisture enhances growth rates and allows rainforest seedlings to escape recurrent fires</td>
</tr>
<tr>
<td>Fire X buffalo</td>
<td>Reduced fuel loads on rainforest boundaries leading to less frequent and intense fires</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Causes of contraction</th>
<th>Hypothesised Strength</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Variable</strong></td>
<td><strong>Explanation</strong></td>
</tr>
<tr>
<td>Fire</td>
<td>Direct tree mortality</td>
</tr>
<tr>
<td>Fire X weeds</td>
<td>Weeds increase fuel loads, more frequent and intense fires</td>
</tr>
<tr>
<td>Fire X rainfall</td>
<td>Increased rainfall increases fuel loads, more frequent and intense fires</td>
</tr>
<tr>
<td>Feral animals</td>
<td>Direct damage through wallowing, trampling etc.</td>
</tr>
</tbody>
</table>
fuel loads throughout KNP (Skeat et al. 1996). As buffalo preferentially use rainforest habitat, it is likely that a reduction in fuel would have afforded substantial protection from fire, allowing the rainforest boundaries to expand.

Rainfall can also interact with fuel loads and thus fire. Rainfall is one of the factors that determines fuel loads in the savanna, which has a resultant effect on fire frequency (Williams et al. 1999). An increase in rainfall can therefore increase the frequency and intensity of fires. This effect may thus lead to contraction of rainforest boundaries, which runs counter to the view that increased rainfall is driving the observed expansion.

Additionally, there are also a variety of higher order interactions between CO₂ levels, temperature, fire and soil (Archer et al. 2000, Berry and Roderick 2002). For example, increased growth rates from elevated CO₂ may have enabled tree seedlings to escape the savanna ‘fire trap’ posed by regular fires (Bond et al. 2003). However, the fertilization effect may not occur in cases where growth is limited by other factors such as soil nutrient levels (Ghannoum et al. 2001).

**Conclusion**

This study has provided land owners and managers of KNP with an appreciation of the extent and possible causes of landscape-scale rainforest dynamics over the last 40 years. However, the relative importance of the various drivers of change remains uncertain due to the presence of complex interactions. Nonetheless, the increasing trends in rainfall and CO₂ are consistent with the observed expansion. Fire is clearly a powerful force in limiting rainforest expansion and is likely to be the primary cause of localized boundary contraction. Available evidence therefore suggests that the observed rainforest expansion is likely to have been primarily driven by increases in variables such as rainfall and atmospheric CO₂, but has been strongly mediated by fire regime. Historical fluctuations in feral animal numbers may also have influenced the rate of change, particularly for wet rainforest. To further investigate how the rate of change has been mediated by different variables, an appropriate methodology will be spatially-explicit modelling that incorporates information from a number of different thematic layers (Augustin et al. 2001, Bowman et al. in press-b).
Chapter 3 – A field assessment of the drivers of rainforest boundary dynamics

**Introduction**

Experimental attribution of the causes to changes in tropical forests is extremely difficult due to physical, financial and ethical constraints (Osmond et al. 2004). One approach shown to help narrow down hypotheses for the causes of forest dynamics is to examine the ecological ‘fingerprint’ of the changes. Different causes of change have different signatures that are evident in their field attributes (Banfai and Bowman 2005, Lewis et al. 2004a). Investigating the field attributes of areas with different histories of vegetation change can therefore help to interpret the dynamics.

KNP provides a model system to apply this methodology at a spatial scale large enough to capture heterogeneity in factors such as landscape setting, fire regime and soil type. A study of 50 rainforest patches found that the rainforest patches increased in size from 1964 to 2004 by an average of 28.8% (Chapter 2, Figure 9). Expansion was observed in both wet and dry rainforest types, thus spanning the hydrological range of this vegetation formation. This general response was suggestive of a geographically widespread driver such as climate (i.e. increased rainfall and/or CO₂, Figure 9) or disturbance history (e.g. fire regime or feral animals) (Chapter 2). However, substantial uncertainty remained as to the relative importance of these various potential causes of change. It is extremely difficult to substantiate that global change is driving vegetation dynamics, and thus before embarking on such a quest it is prudent to ensure that more localized factors are not responsible for the observed change.

The purpose of this paper is therefore to investigate these competing hypotheses by determining the nature of the observed changes in terms of floristics, structure, environmental and disturbance correlates as measured in the field. Specifically we assess the hypotheses that rainforest expansion: (1) Occurs across a range of the geomorphic settings as measured by soil type and slope angle. (2) Is not restricted to any particular species or assemblage of species. (3) Is not strongly related to specific levels of recent fire disturbance or feral animal impacts. We argue that if all of the above hypotheses are consistent with the field attributes then this invites more serious consideration of global change phenomena and we suggest possible landscape modelling approaches to advance
this problem. The results are also discussed in relation to the long-term stability of the rainforest boundaries and the regional management of rainforests.

Figure 9. Changes in area of rainforest in KNP compared to trends of various climate variables. Percentage change (± SE) in rainforest area over study period relative to 1964 (Banfai & Bowman 2006) (a). Five-year running average rainfall for Oenpelli, the closest rainfall station to KNP with a complete record (Bureau of Meteorology 2003). The least squares regression line is also shown (b). Annual mean maximum and minimum temperatures recorded at Oenpelli (Bureau of Meteorology 2003) (c). Atmospheric CO₂ concentrations collected at Mauna Loa Observatory, Hawaii (Brook & Bowman in press) (d).
Methods

Aerial photography
Rainforest boundaries were mapped by the author (Chapter 2) for each of the years 1964, 1984, 1991 and 2004 using a 20 × 20-m lattice grid. All photographs used color film at a scale of 1:25,000 apart from 1964 which were black and white and at 1:16,000. The imagery was scanned from contact prints to achieve a common pixel resolution of 1 m². Each lattice grid point was manually classified into vegetation types for each year using ArcGIS 8 (ESRI) at a common scale of 1:3000, primarily based on the distance between tree crowns. Stereo view was not used.

Here field survey plots were centered on these grid points to compare the attributes of areas with different histories of vegetation change. For the purposes of this study we operationally define ‘stable’ plots as those that did not change vegetation type in any of the four photographic time-slices from 1964 to 2004. ‘Transitional’ plots were defined as those that changed between 1964 and 2004 from savanna to rainforest or vice versa. Analysis of the various combinations and permutations of change that occurred between these two endpoints would require an enormous sample size in order to be statistically robust and was therefore beyond the scope of this study. In any case consideration of the individual change trajectories would only be warranted if the current analysis indicated that site-specific factors were important in understanding the landscape variation in the floristic composition of the boundaries.

Field sampling
Thirty rainforest patches were selected for field sampling from the 50 rainforest patches that were the subject of aerial photographic analysis (Figure 10). Full details of the sampling design of the 50 patches are provided in Chapter 2. Effort was made to ensure that field surveys were conducted across the full geographic range of lowland rainforest in the study site and that variation in fire regime and soil type was captured. Surveys were conducted in the dry season between May and October 2004.
Field survey plots were 20 × 20 m and centered on grid points used in the vegetation mapping, which were located in the field with a Global Positioning System (GPS). Individual rainforest patches were stratified into four equal parts (north-south and east-west divisions) in order to spread the samples over the patch. Where possible, four random points (one from each quarter) of each vegetation type based on the 2004...
aerial photography were sampled. Extra sample points were added to sample transitional sites based on the aerial photography record (maximum of 10 per site). A total of 588 points was sampled. Traditional owners were employed to assist with the surveys where possible.

Table 4 summarizes the variables recorded within each 20 × 20-m survey plot and the field measures used. Soil texture categories were adapted from McDonald et al. (1990). Flammable weed species recorded were *Sorghum* spp., *Pennisetum polystachion* (L.) Schult., *Urochloa mutica* (Forssk.) T.Q.Nguyen and *Andropogon gayanus* Kunth. Voucher specimens of all species were collected and their identity confirmed at the Northern Territory Herbarium.

**Table 4. Field measures for all variables recorded.**

<table>
<thead>
<tr>
<th>Variable</th>
<th>Field measure</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tree basal area</td>
<td>Sweep with Bitterlich wedge from centre of plot</td>
</tr>
<tr>
<td>Dominant species</td>
<td>Identity of each tree recorded with the Bitterlich wedge</td>
</tr>
<tr>
<td>Buffalo (<em>Bubalus bubalis</em>) impact;</td>
<td>Proportion of plot covered as either &lt;1%, 1-5%, 6-25%, 26-50%, 51-75%,</td>
</tr>
<tr>
<td>Pig (<em>Sus scrofa</em>) impact</td>
<td>76-99% or 100%</td>
</tr>
<tr>
<td>Cover &gt;2 m; grass cover; flammable weed cover</td>
<td>Projective foliage cover measured on the same ordinal scale used for buffalo impact. Cover &gt;2 m was recorded within a 5 × 5 m quadrat in the centre of each plot</td>
</tr>
<tr>
<td>Time since fire</td>
<td>0 = fire since last wet season, 1 = fire less than 5 y ago, 2 = fire more than 5 y ago, 3 = no evidence of fire. Visual assessment based on fire scars on trees.</td>
</tr>
<tr>
<td>Soil texture</td>
<td>Surface (10 cm) as 1 = sand, 2 = sandy loam, 3 = loam, 4 = clay loam, 5 = clay</td>
</tr>
</tbody>
</table>

**Framework for data analysis**

It has been previously demonstrated that there was a clear floristic separation between dry and wet rainforests in the study site (Bowman et al. 1991, Russell-Smith 1991). All analyses were therefore performed separately for these two rainforest types. As the vast majority of vegetation changes occurred between savanna and rainforest (Chapter 2), only transitions between these two vegetation types were considered. Where possible,
analyses were based on patch averages; survey plots of the same vegetation change trajectory within a rainforest patch were averaged to avoid bias toward patches with more samples. This also controls for the spatial autocorrelation of multiple samples within rainforest patches. The following statistical tests were undertaken to address the various hypotheses regarding the expansion of rainforest.

*Structural and floristic attributes*

The average basal areas of rainforest and non-rainforest tree species were calculated for each vegetation transition based on a previous classification of species groups with a Two-way Indicator Species Analysis (TWINSPIAN) procedure (Chapter 2). Benefits and limitations of this approach are discussed by Banfai and Bowman (2005). The average abundance of rainforest trees, non-rainforest trees and grass cover was calculated for each of the four possible vegetation changes between rainforest and savanna, and were compared with Kruskall-Wallis tests. To control for variation in grass cover due to recent burning, plots that were burnt since the last wet season were excluded from analyses of grass cover.

Blocked MRPP (MRBP) is a variant of the Multi-Response Permutation Procedure (MRPP) (Mielke 1991) that is able to account for floristic variation between rainforest patches. MRBP was used to test the hypothesis that there was no difference in overall tree species composition between stable and transitional plots and whether there was an effect of proximity to the rainforest and savanna boundary. Edges were defined as being within two grid points (c.40 m) of the mapped rainforest boundary. Edge and core plots were identified using Arcview 3.3 (ESRI). MRBP requires a balanced design with only one sample unit for each combination of block and treatment. To accommodate this, where several samples were taken of a particular transition at a rainforest patch, one sample was randomly selected. This procedure was repeated five times and the median P value was calculated.

To investigate whether expanding rainforest areas were dominated by particular species the proportion of the total basal area of the species in plots that changed from savanna to rainforest between 1964 and 2004 was ranked and averaged. Average basal
area and average frequency was also calculated for the most abundant species. These rankings were repeated for stable rainforest plots.

**Effect of environmental and disturbance variables**

The proportion of plots in each soil texture and time-since-fire category was calculated for each vegetation transition. Kruskall-Wallis non-parametric tests were used to assess differences in environmental and disturbance variables between different vegetation change trajectories. Plots that were burnt since the last wet season were excluded from analyses of flammable weeds, as it was not possible to assess the presence of weeds at these sites.

Generalized linear models (GLMs) were used to further investigate the hypothesis that environmental and disturbance variables were not strongly related to vegetation transitions. GLMs are a generalization of linear regression models and have the advantage of allowing for a variety of distributions for the response and error terms in the model (McCullagh and Nelder 1989). Mixed-effect GLMs were used so that rainforest patch could be coded as a random effect to account for the variance between patches. Predictor variables included in the models were chosen *a priori* in accordance with the Information Theoretic paradigm (Burnham and Anderson 2001). The fixed effects included were time since fire (factor), feral animal impact and soil type (factor). These particular variables were chosen as previous research had suggested that they may be good predictors of historical changes to rainforest boundaries in the context of KNP (Chapter 2). Interactions were not included in the models as we were primarily interested in the main effects at this stage in the investigation. The inclusion of interaction terms would also have made the number of parameters fitted by the models excessively large, inflating the amount of deviance explained by the models.

Different models were developed for savanna-to-rainforest and rainforest-to-savanna transitions, as the ecological processes involved in these transitions are fundamentally different (Brook and Bowman 2006): (1) Savanna change model. The dependent variable of a binomial mixed-effects GLM (logit-link) was whether a savanna point changed to rainforest between 1964 to 2004 (coded as a 1), or remained savanna throughout (coded as a 0). (2) Rainforest change model. This had the same structure as
the savanna change model, except that the dependent variable was whether a rainforest point changed to savanna between 1964 to 2004 (coded as a 1), or remained rainforest throughout (coded as a 0). The amount of deviance explained by the global models was then calculated for both rainforest types.

**Results**

**Structural and floristic attributes**

Stable wet rainforests had a much higher average basal area than stable dry rainforests (15.2 vs. 9.1 m$^2$ ha$^{-1}$) but were similar in terms of canopy cover (Figure 11). Basal area and cover were consistent with the mapped changes because the transitional plots had average values intermediate between the stable states for both rainforest types. Similarly, the average abundance of rainforest and non-rainforest trees was also were intermediate for the transitional plots (Figure 12). For example, in wet rainforests the density of rainforest trees in stable savanna was 5.3 m$^2$ ha$^{-1}$, stable

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**Figure 11.** Percentage cover >2 m is shown against basal area (with SE) for different trajectories of vegetation change between 1964 and 2004. a) Dry rainforests; b) Wet rainforests. Diamonds = Stable rainforest (RF); Squares = Stable Savanna (Sav); Circles = Sav to RF; Triangles = RF to Sav (N patches averaged for Dry rainforest RF-Sav = 7, Sav-RF = 15, Stable RF = 18, Stable Sav = 19; Wet rainforest RF-Sav = 7, Sav-RF = 6, Stable RF = 10, Stable Sav = 10).
rainforest had 13.3 m² ha⁻¹ while savannas that had changed to rainforest had an intermediate value of 10.9 m² ha⁻¹. Savannas that became rainforests had a higher abundance of rainforest trees relative to stable savannas for both wet and dry rainforest types based on Kruskall-Wallis tests (Dry rainforest H = 33.528, P < 0.001; Wet rainforest H = 4.443, P = 0.035), while there was no significant difference in non-rainforest trees. At least 10% of the basal area was non-rainforest trees in sites classified as stable rainforest, and stable savanna plots notably had >50% rainforest trees (Figure 12).

Grass cover showed the opposite trend to tree abundance for both rainforest types (Table 5). For example, stable savannas surrounding dry rainforests had 22.1% grass cover which was significantly greater than savannas that had changed to dry rainforest which had 9% grass cover (H = 7.457, P = 0.007 in Kruskall-Wallis test). For the transition from rainforest to savanna, the opposite differences were observed, with...
average grass cover being greater in transitional plots relative to stable rainforests, although these differences were not statistically significant (Table 5).

Table 5. Mean (± SE) for field attributes comparing different trajectories of vegetation change. Dry and wet rainforest types are shown separately. Sav = Savanna; RF = rainforest.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Vegetation change</th>
<th>Stable Sav</th>
<th>Sav to RF</th>
<th>Stable RF</th>
<th>RF to Sav</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Dry rainforest</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grass cover (%)</td>
<td>22.1 ± 4.92</td>
<td>9.0 ± 3.69</td>
<td>10.8 ± 2.61</td>
<td>29.5 ± 8.97</td>
<td></td>
</tr>
<tr>
<td>Flammable weed cover (%)</td>
<td>2.0 ± 1.96</td>
<td>0.1 ± 0.08</td>
<td>0.1 ± 0.07</td>
<td>2.8 ± 1.55</td>
<td></td>
</tr>
<tr>
<td>Pig impact (%)</td>
<td>38.3 ± 3.12</td>
<td>15.6 ± 5.29</td>
<td>16.7 ± 4.36</td>
<td>11.9 ± 16.6</td>
<td></td>
</tr>
<tr>
<td>Buffalo impact (%)</td>
<td>0.1 ± 1.34</td>
<td>0.2 ± 0.23</td>
<td>2.1 ± 1.96</td>
<td>1.5 ± 0.11</td>
<td></td>
</tr>
<tr>
<td>Total feral animal impact (%)</td>
<td>38.5 ± 3.31</td>
<td>15.8 ± 5.26</td>
<td>18.8 ± 4.57</td>
<td>12.9 ± 16.5</td>
<td></td>
</tr>
<tr>
<td>Slope (°)</td>
<td>0.8 ± 0.44</td>
<td>0.9 ± 0.24</td>
<td>2.1 ± 0.87</td>
<td>1.6 ± 0.41</td>
<td></td>
</tr>
<tr>
<td>N (plots)</td>
<td>161</td>
<td>68</td>
<td>103</td>
<td>11</td>
<td></td>
</tr>
<tr>
<td><strong>Wet rainforest</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grass cover (%)</td>
<td>56.2 ± 6.85</td>
<td>15.9 ± 12.5</td>
<td>26.2 ± 6.10</td>
<td>32.4 ± 18.8</td>
<td></td>
</tr>
<tr>
<td>Flammable weed cover (%)</td>
<td>0.3 ± 6.18</td>
<td>0.4 ± 0.38</td>
<td>1.3 ± 0.67</td>
<td>11.3 ± 0.33</td>
<td></td>
</tr>
<tr>
<td>Pig impact (%)</td>
<td>12.1 ± 2.17</td>
<td>13.4 ± 6.90</td>
<td>17.9 ± 8.50</td>
<td>5.3 ± 8.75</td>
<td></td>
</tr>
<tr>
<td>Buffalo impact (%)</td>
<td>0 ± 0.84</td>
<td>0 ± 0.00</td>
<td>0.4 ± 0.27</td>
<td>1.5 ± 0.00</td>
<td></td>
</tr>
<tr>
<td>Total feral animal impact (%)</td>
<td>12.1 ± 2.89</td>
<td>13.4 ± 6.90</td>
<td>18.3 ± 8.43</td>
<td>6.8 ± 8.75</td>
<td></td>
</tr>
<tr>
<td>Slope (°)</td>
<td>2.7 ± 0.56</td>
<td>2.1 ± 0.82</td>
<td>4.1 ± 1.03</td>
<td>2.2 ± 0.83</td>
<td></td>
</tr>
<tr>
<td>N (plots)</td>
<td>47</td>
<td>11</td>
<td>58</td>
<td>10</td>
<td></td>
</tr>
</tbody>
</table>

Rainforest plots showed a consistent overall floristic difference to savanna plots at the P < 0.05 level for dry rainforest, but not for wet rainforest (Table 6). There were no significant floristic differences between edge and core samples for rainforest or savanna for both rainforest types (Table 6). There were also no significant differences in the floristic composition between transitional plots and their stable counterparts.
Table 6. Blocked MRPP results comparing floristic composition of rainforest and savanna, edge and core samples, as well as comparing transitional samples to their stable counterparts. The two rainforest types are shown separately.

<table>
<thead>
<tr>
<th>Comparison</th>
<th>N (patches)</th>
<th>Median P</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Dry rainforest</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rainforest vs. Savanna</td>
<td>19</td>
<td>0.003</td>
</tr>
<tr>
<td>Rainforest (edge vs. core)</td>
<td>18</td>
<td>0.899</td>
</tr>
<tr>
<td>Savanna (edge vs. core)</td>
<td>18</td>
<td>0.137</td>
</tr>
<tr>
<td>Stable RF vs. Sav-RF</td>
<td>7</td>
<td>0.787</td>
</tr>
<tr>
<td>Stable Sav vs. RF-Sav</td>
<td>14</td>
<td>0.126</td>
</tr>
<tr>
<td><strong>Wet rainforest</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rainforest vs. Savanna</td>
<td>10</td>
<td>0.170</td>
</tr>
<tr>
<td>Rainforest (edge vs. core)</td>
<td>7</td>
<td>0.158</td>
</tr>
<tr>
<td>Savanna (edge vs. core)</td>
<td>10</td>
<td>0.332</td>
</tr>
<tr>
<td>Stable RF vs. Sav-RF</td>
<td>7</td>
<td>0.230</td>
</tr>
<tr>
<td>Stable Sav vs. RF-Sav</td>
<td>6</td>
<td>0.072</td>
</tr>
</tbody>
</table>

Most of the dominant species in plots that changed from savanna to rainforest are classified as rainforest species (Table 7). A few species were identified as having a particularly high average basal area and frequency in plots that changed from savanna to rainforest, however they only comprised a small proportion of the total basal area. For dry rainforest, these species included *Strychnos lucida* and *Erythrophleum chlorostachys* (Table 7). For wet rainforest, dominant species included *Lophostemon lactifluus*, *Xanthostemon eucalyptoides* and *Pandanus spiralis* (Table 7). The assemblage of dominant species was consistent with the ordination analysis that indicated transitional rainforest areas had a similar floristic composition to stable areas.

**Effect of environmental variables**

Average slope was very low for all vegetation transitions (Table 5), with 90% of survey plots having a slope below 5°. No significant differences were observed between vegetation change trajectories for either rainforest type. Both stable and transitional plots...
both rainforest types. Asterisks (*) indicate classified as rainforest species. N patches averaged for savanna to rainforest = 15; stable rainforest = 18.

<table>
<thead>
<tr>
<th>Species</th>
<th>Prop. BA (%)</th>
<th>BA (m² ha⁻¹)</th>
<th>Freq. (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Savanna to dry rainforest</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Strychnos lucida R.Br. *</td>
<td>8</td>
<td>0.7</td>
<td>42</td>
</tr>
<tr>
<td>Erythrophleum chlorostachys (F.Muell.) Baill.</td>
<td>7</td>
<td>0.9</td>
<td>24</td>
</tr>
<tr>
<td>Corymbia polysciada (F.Muell.) K.D.Hill &amp; L.A.S.Johnson*</td>
<td>6</td>
<td>0.4</td>
<td>24</td>
</tr>
<tr>
<td>Syzygium suborbiculare (Benth.) T.G.Hartley &amp; L.M.Perry*</td>
<td>6</td>
<td>0.5</td>
<td>22</td>
</tr>
<tr>
<td>Corymbia bella K.D.Hill &amp; L.A.S.Johnson</td>
<td>5</td>
<td>0.5</td>
<td>17</td>
</tr>
<tr>
<td>Barringtonia acutangula (L.) Gaertn.*</td>
<td>5</td>
<td>0.2</td>
<td>14</td>
</tr>
<tr>
<td>Alstonia actinophylla (A.Cunn.) K.Schum. *</td>
<td>5</td>
<td>0.3</td>
<td>31</td>
</tr>
<tr>
<td>Acacia auriculiformis A.Cunn. *</td>
<td>4</td>
<td>0.3</td>
<td>15</td>
</tr>
<tr>
<td><strong>Stable dry rainforest</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Strychnos lucida R.Br. *</td>
<td>9</td>
<td>0.9</td>
<td>41</td>
</tr>
<tr>
<td>Erythrophleum chlorostachys</td>
<td>8</td>
<td>0.4</td>
<td>23</td>
</tr>
<tr>
<td>Syzygium suborbiculare*</td>
<td>5</td>
<td>0.3</td>
<td>11</td>
</tr>
<tr>
<td>Acacia auriculiformis*</td>
<td>4</td>
<td>0.4</td>
<td>15</td>
</tr>
<tr>
<td>Canarium australianum F.Muell. *</td>
<td>4</td>
<td>0.3</td>
<td>23</td>
</tr>
<tr>
<td>Alstonia actinophylla*</td>
<td>4</td>
<td>0.4</td>
<td>25</td>
</tr>
<tr>
<td>Terminalia microcarpa Decne. *</td>
<td>3</td>
<td>0.4</td>
<td>17</td>
</tr>
<tr>
<td>Vitex acuminata R.Br.</td>
<td>3</td>
<td>0.2</td>
<td>13</td>
</tr>
<tr>
<td><strong>Savanna to wet rainforest</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lophostemon lactifluus (F.Muell.) Peter Wilson &amp; J.T.Waterh.*</td>
<td>26</td>
<td>3.0</td>
<td>50</td>
</tr>
<tr>
<td>Xanthostemon eucalyptoides F.Muell. *</td>
<td>11</td>
<td>0.7</td>
<td>33</td>
</tr>
<tr>
<td>Pandanus spiralis R.Br.*</td>
<td>9</td>
<td>1.5</td>
<td>56</td>
</tr>
<tr>
<td>Melaleuca leucadendra (L.) L.*</td>
<td>6</td>
<td>2.1</td>
<td>8</td>
</tr>
<tr>
<td>Eucalyptus tetrodonta F.Muell.</td>
<td>5</td>
<td>1.1</td>
<td>25</td>
</tr>
<tr>
<td>Erythrophleum chlorostachys</td>
<td>5</td>
<td>0.9</td>
<td>17</td>
</tr>
<tr>
<td>Eucalyptus miniata A.Cunn. ex Schauer</td>
<td>4</td>
<td>0.8</td>
<td>17</td>
</tr>
<tr>
<td>Lophostemon grandiflorus (Benth.) Peter Wilson &amp; J.T.Waterh.*</td>
<td>4</td>
<td>0.4</td>
<td>8</td>
</tr>
<tr>
<td><strong>Stable wet rainforest</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Xanthostemon eucalyptoides*</td>
<td>17</td>
<td>2.1</td>
<td>49</td>
</tr>
<tr>
<td>Melaleuca leucadendra*</td>
<td>10</td>
<td>2.7</td>
<td>41</td>
</tr>
<tr>
<td>Syzygium nervosum DC.*</td>
<td>10</td>
<td>2.0</td>
<td>37</td>
</tr>
<tr>
<td>Pandanus spiralis*</td>
<td>6</td>
<td>1.1</td>
<td>28</td>
</tr>
<tr>
<td>Lophostemon lactifluus*</td>
<td>6</td>
<td>1.3</td>
<td>28</td>
</tr>
<tr>
<td>Erythrophleum chlorostachys</td>
<td>6</td>
<td>0.8</td>
<td>25</td>
</tr>
<tr>
<td>Gmelina schlecteri H.J.Lam*</td>
<td>5</td>
<td>1.1</td>
<td>28</td>
</tr>
<tr>
<td>Eucalyptus alba Reinw. ex Blume*</td>
<td>3</td>
<td>0.4</td>
<td>14</td>
</tr>
</tbody>
</table>
occur across a range of soil types (Figure 13). The majority (>68%) of dry rainforest plots were on sandy loam soils, with a small proportion (<15%) on sand or clay. In contrast, wet rainforests had more variable soil types. For both rainforest types, the different vegetation change trajectories were generally similar in their proportions of plots with different soil types. However, notably over 80% of wet rainforests that changed from savanna to rainforest were on sandy loam soils, with the rest being on clay loam soils (Figure 13).

Figure 13. Proportion of plots with different soil texture for each vegetation transition. Dry and wet rainforest types are shown separately. RF = rainforest; Sav = Savanna (Total N plots averaged for dry rainforest RF-Sav = 11, Sav-RF = 68, Stable R = 103, Stable S = 161; wet rainforest RF-Sav = 10, Sav-RF = 11, Stable R = 58, Stable S = 47).
**Effect of disturbance variables**

Evidence of fire was recorded in >70% of plots for all four vegetation change trajectories (Figure 14). It was particularly notable that most stable rainforest plots had evidence of past fire. For all transitions, the majority of plots were evidently burnt less than 5 y ago. There also was no systematic relationship between time since fire and vegetation change transition, with only minor differences in the proportions of the different categories of time since fire between the different vegetation transitions for both wet and dry rainforest. This indicates that the probability of recent fire was not substantially different for the four vegetation transitions (Figure 14).

![Dry rain forest](image)

![Wet rain forest](image)

**Figure 14.** Proportion of plots with different time since fire for each vegetation transition. Dry and wet rainforest types are shown separately. RF = rainforest; Sav = Savanna (N plots averaged is as in Figure 13).
The cover of flammable weeds was very low (<3%) for almost all vegetation change transitions in both rainforest types (Table 5). Only wet rainforest plots that changed from rainforest to savanna had a slightly higher average weed cover (11.3%).

The vast majority of feral animal impact was from pig rooting (Table 5). Buffalo impact was generally negligible with an average of less than 2.5% buffalo impact cover for all vegetation change trajectories. For dry rainforests, feral animal impact was highest for stable savannas (38.5%), while for wet rainforests it was highest for stable rainforest areas (18.3%). Average feral animal damage was lowest for the transition from rainforest to savanna for both rainforest types (Table 5).

Kruskal-Wallis tests showed no significant difference between vegetation change trajectories for any of the disturbance variables at P < 0.05 for either rainforest type. Additionally, the deviance explained by the models including both disturbance and environmental variables was very low for both dry and wet rainforest. In the case of dry rainforests, the savanna change model explained 6.8% of the deviance, while the rainforest change model explained 4.3%. For wet rainforest, the savanna change model explained 2.3% of the deviance, while the rainforest change model explained 11.4%.

**Discussion**

*Structural and floristic attributes*

Areas that changed from savanna to rainforest between 1964 and 2004 were associated with an increase in rainforest trees and a decrease in grasses, relative to stable savannas. This can be interpreted as suppression of grasses by woody species, which acts to reduce fire frequency and intensity (Stott 2000). The opposite relationship between rainforest tree abundances and grass cover was observed for the transition of rainforest to savanna when compared to stable rainforests. The reduction in grass cover in areas where rainforest expansion has occurred is expected given the general inability of grass to establish beneath a closed canopy, and is consistent with the inference of Hennenberg et al. (2006) who analyzed transects across forest-savanna boundaries in the Comoe
National Park, Ivory Coast. In this study we have been able to verify these relationships as we have knowledge of the recent boundary dynamics based on historical aerial photography.

Rainforests that established since 1964 were found to be very similar in their assemblage of species to longer established rainforest given (1) there was little overall difference in floristics between transitional plots and their stable counterparts and (2) the most abundant tree species in areas where rainforest expansion had occurred were similar to that of stable rainforest areas. Further, there was a substantial proportion of both rainforest and non-rainforest trees in plots classified as ‘stable’. For stable savanna this is most probably the result of historical fluctuations in the position of the rainforest boundary where large rainforest trees have become stranded in the savanna following rainforest boundary retreat. Likewise, the non-rainforest trees in the ‘stable’ rainforest may either be relics of forest expansion that occurred prior to 1964, or are the result of savanna incursion into the rainforest between 1964 and 2004 which has allowed non-rainforest species to become established.

In aggregate these observations support the view that rainforest boundaries in KNP are highly dynamic, with colonization of areas surrounding rainforests by a range of rainforest species occurring rapidly at the decadal scale. This is consistent with previous studies documenting that a large proportion of the rainforest species in northern Australia are highly vagile, with the ability to rapidly colonize new areas. For example, diverse rainforest assemblages occur frequently on recently evolved landforms such as stabilized beach dunes and riverine floodplains (Russell-Smith and Lee 1992, Bowman and Panton 1993).

Effect of environmental variables
The field attributes suggested that the expansion of rainforests over the last 40 y has been little influenced by environmental factors. The rainforest expansion occurred across a range of soil types and there was little systematic difference in soil texture between vegetation change trajectories. There was however a tendency for savanna to change into wet rainforest on sandy loam soils. Such a relationship is to be expected as this rainforest type is likely to have established on the wettest, most suitable soil types before
spreading to more marginal, freely draining soils. These results are consistent with transect studies in three dispersed regions ranging from Central America, the northern Amazon Basin and the central Brazilian plateau, were soil nutrient status was related to, but did not necessarily determine, the position of the forest-savanna boundary (Furley 1992).

Slope was also similar between vegetation change trajectories at the rainforest boundary. The low slope values recorded were expected given the lowlands of KNP consist of predominantly flat sedimentary plains (Williams 1969). This contrasts to other landscape settings with more topographic relief where slope and aspect are thought to be important determinates of rainforest habitat suitability (Puyravaud et al. 1994, Brook and Bowman 2006). In sum, the similarity of environmental attributes between different vegetation transitions reinforces the view that KNP provides a model system for investigating the relative importance of other factors driving landscape change.

Effect of disturbance variables
Disturbance factors measured in the field showed no ecologically consistent relationships with the rainforest boundary dynamics. For example, there was little systematic difference in the evidence of recent fire between the four vegetation change trajectories. This is inconsistent with studies where the local dynamics of the forest-savanna boundary zone were inferred to be primarily a function of fire incidence (Furley 1992, King et al. 1997, Ratter 1992). There were also a surprisingly high proportion of stable rainforest sites with evidence of past fires. These results reflect the ability of many rainforest species to survive at least a single fire (Bowman 1991). Thus fire frequency (which was not determined) rather than simply time since fire is probably of more importance in influencing the probability of vegetation change (Bowman 2000a).

Flammable weeds were recorded as their high biomass can greatly increase the frequency and intensity of fires (Stott 2000). However, the cover of flammable weeds was consistently very low across the different vegetation transitions, suggesting that they are not a major factor influencing the rainforest boundaries. Nonetheless it is notable that both patches that contracted in area greater than 5% between 1964 and 2004 both had flammable weeds present. The one patch that experienced the greatest overall
contraction (-18%) was the only site to have *Urochloa mutica* recorded, and also infestations of *Pennisetum polystachion*, which are both highly flammable introduced weeds. The other patch that contracted substantially had no introduced flammable weeds but had a large proportion of its boundary surrounded by the native annual grass *Sorghum* spp., which is also thought to be related to high fire frequency and intensity (Yibarbuk et al. 2001, Russell-Smith et al. 2003). These results signal that management of flammable weeds around rainforest boundaries should remain a priority for land managers.

There was also relatively little recent feral animal impact recorded in all vegetation change transitions, with the vast majority of the damage being from pig rooting. The fact that average feral animal impact was lowest in plots that had contracted from rainforest to savanna for both rainforest types is not consistent with the hypothesis that the contraction of rainforest is associated with high feral animal impact. The general lack of buffalo impact contrasts with regional surveys conducted in the 1980s by Russell-Smith and Bowman (1992) where severe damage attributable to buffalo and cattle impact was recorded at 20.4% of sites. The reduction in buffalo impact is probably related to the major drop in buffalo numbers from culling during the Brucellosis and Tuberculosis Eradication Campaign in the 1980s (Skeat et al. 1996).

The modelling confirmed that contemporary disturbance and environmental factors measured in the field are poor predictors of historical vegetation transitions on rainforest boundaries. However, this study has only focused on the biological endpoint of disturbance histories at the local (plot) scale. It must be admitted that a limitation of this analysis is insufficiently detailed historical information on fire impacts and feral animal distributions. Nonetheless, there is the opportunity to use a GIS approach to further examine variation in rainforest dynamics at the patch scale. For example, an index of buffalo impact on rainforest patches could be derived from buffalo tracks observed on historical aerial photography. Proxies for fire activity could also be used such as fire scar mapping from satellite imagery which dates back to 1980 (Russell-Smith et al. 1997b).
Conclusions

The similarity of newly established rainforest to more stable rainforest in KNP and the lack of environmental limits to change suggest that the current trend of rainforest expansion will continue if current climatic trends and disturbance regimes persist. This is supported by previous detailed floristic and biogeographical studies of rainforests in northern Australia indicating that these forests currently only occupy a fraction of their potential domain (Bowman 2000a).

It remains unclear as to whether the rapid expansion of rainforest boundaries in KNP represents a short-term fluctuation of boundaries that are stable on a longer time scale, as has apparently occurred on Croker Island near the boundary of the Park (Bowman et al. 2004b). Stable isotopes in soil at Croker Island led Bowman et al. (2004b) to argue that rainforest boundaries had been ‘stable’ at the millennial scale, yet tiny fragments of rainforest and abandoned ‘nests’ of *Megapodius reinwardt* were interpreted as evidence of short-term fluctuations in the location of the boundary. They hypothesized that the episodic expansion and contraction of rainforest was related to fluctuations in cyclonic disturbance and rainfall cycles where wetter periods allow rainforest species to grow at sufficient rates to colonize the savanna despite recurrent fire disturbance. The rainforest dynamics in KNP may also be responding to similar long-term climate driven cycles.

The limited effect of environmental and disturbance variables on the probability of rainforest boundary expansion in KNP is consistent with the ubiquitous effect of global change. Increased atmospheric CO$_2$ (Figure 9d) may have contributed to the observed changes as it is known to preferentially advantage trees (mostly C$_3$ photosynthetic pathway) over grasses (mostly C$_4$), shifting the balance toward trees on the savanna-forest boundary (Berry and Roderick 2002). For example, seedlings of *Maranthes corymbosa* Blume, a rainforest species that occurs in KNP, showed a marked increase in growth in a doubled CO$_2$ environment with total shoot dry weight increasing by 163% (Berryman et al. 1993). The rainforest expansion is also correlated with an increase in annual rainfall over the last few decades (Chapter 2, Figure 9b). Increased rainfall may have contributed to the rainforest expansion as increased soil moisture can promote rainforest species establishment in the surrounding savanna and is an important
determinant of the location of forest-savanna boundaries in tropical regions (Bowman and Panton 1993, Furley 1992).

Substantial uncertainty remains as to the relative importance of the various potential drivers of rainforest boundary dynamics in KNP. For example, although time since fire was a poor predictor of historical vegetation transitions in this study, there is a need to investigate the effect of fire frequency. Historical feral animal impacts may also have had a major effect on the rate of rainforest boundary change that could not be detected in contemporary field surveys. Additionally, the relationship between the rate of boundary dynamics and fluctuations in rainfall has not yet been explored. An appropriate methodology to tease out the relative importance of these factors will be spatially explicit modelling that incorporates information from a number of different thematic layers (Augustin et al. 2001, Brook and Bowman 2006).
Chapter 4 - Multi-scale modelling of the drivers of rainforest boundary dynamics

This chapter has been published as: Banfai, D. S., Brook, B. W. and D. J. M. S. Bowman. In press. Multi-scale modelling of the drivers of rainforest boundary dynamics in Kakadu National Park, northern Australia. Diversity and Distributions.
Introduction

Tropical forests are critical reservoirs of biodiversity, housing the majority of the Earth’s species (Heywood 1995). Tropical forests also play a major role in cycling atmospheric carbon, annually processing about six times as much carbon through photosynthesis as humans release to the atmosphere through fossil fuel combustion (Lewis 2006). Work over the last few decades has demonstrated that the boundaries between tropical forests and other vegetation types are highly dynamic. While there has been a major loss in tropical forest area due to factors such as logging (Nobre et al. 1991, Mertens and Lambin 2000), studies have also documented the expansion of forest into more open vegetation types (Eden and McGregor 1992, Harrington and Sanderson 1994, King et al. 1997, Bowman et al. 2001, Endress and Chinea 2001, Guillet et al. 2001).

Understanding the causes of these changes is critical as future changes in the position of savanna-forest boundaries may have profound implications for both the human and natural environment (Lewis 2006).

Climate is thought to be one of the primary factors determining the distribution of forests globally, and shifts in rainfall patterns can result in boundary changes (Cramer et al. 2004, Vanacker et al. 2005). Increased levels of atmospheric CO₂ may also act to shift the balance between trees and grasses on the rainforest boundary (Bond et al. 2003, Berry and Roderick 2006). Additionally, disturbances such as fire and feral animal impact are thought to be important in determining the dynamics of rainforest boundaries (Braithwaite et al. 1984, Russell-Smith and Bowman 1992). Despite the potential impact of shifts in forest boundaries on biodiversity and human well-being, the relative importance of the various drivers of the change are not well understood.

KNP provides a model system to investigate this problem at a spatial scale large enough to capture variation in factors such as soil type and fire regime. A previous study of 50 rainforest patches in KNP, based on historical aerial photography, showed that between 1964 and 2004 there has been a 28.8% average increase in patch size, although localized contraction of rainforest boundaries was also common (Chapter 2). Available evidence from GIS and field-based studies was consistent with the rainforest expansion having been driven primarily by shifts in global change phenomena, such as increases in
rainfall and atmospheric CO$_2$ (Chapters 2 and 3). However there was substantial uncertainty regarding the relative importance of factors such as fire frequency and historical buffalo impact. The relationship between geospatial patch characteristics (such as patch size and fragmentation) on the rate of boundary change had also not been investigated.

The purpose of this paper is to use model selection techniques to assess the relative importance of fire, buffalo impact and patch shape in determining the rate of historical changes to rainforest patch boundaries in KNP. Model selection techniques, such as information theory using Akaike’s information criterion (AIC), provide a robust methodology to investigate these issues. These methods provide an assessment of the relative support from data for multiple competing hypotheses, represented as statistical models (Burnham and Anderson 2002).

KNP provides a model system to investigate this important problem at a spatial scale large enough to capture variation in factors such as landscape setting, soil type and fire regime. A previous study of 50 rainforest patches in KNP, based on historical aerial photography, showed that between 1964 and 2004, patch size increased by an average of 28.8% (Banfai and Bowman 2006).

Our analysis was conducted at two different scales, to capture the different spatial processes likely to be involved. We examined: (i) what determines the probability of change for areas on the boundary within a patch? and (ii) what determines the variation in the rate of change in total patch size? If the observed boundary dynamics are not strongly related to local disturbance factors, we argue that this supports the view that the observed forest expansion is being driven by global change phenomena, such as rainfall and atmospheric CO$_2$. 
Chapter 4 - Multi-scale modelling of the drivers of rainforest boundary dynamics

**Methods**

*Statistical analysis framework*

Mapping of rainforest boundaries for 48 rainforest patches in KNP, spanning the years 1964 to 2004, was based on a previous study by the author (Chapter 2, Figure 15). Two rainforest patches in the original sample by the author (Chapter 2) were unique in that they experienced a major decline in rainforest area due to the building of infrastructure and roads, and were thus excluded from this analysis.

Modeling of changes to the rainforest boundaries was conducted at two scales: patch and plot. The patch-scale analysis considered factors affecting changes in the overall size of the rainforest patches. However this fails to capture factors influencing the probability of change on the boundary at a local scale, within a given patch. Modeling of dynamics at the scale of individual plots within rainforest patches and surrounding areas was therefore also conducted as a separate analysis. The plots used for this analysis were points in the 20m x 20m lattice grid used by the author (Chapter 2) to map the extent of rainforests. Predictor variables and models were selected *a priori* in accordance with the information theoretic paradigm (Burnham and Anderson 2002). The models used to represent hypotheses developed in previous research on historical changes to rainforest boundaries in KNP (Chapters 2 and 3). The predictor variables included in the plot-scale analysis were also based on those found to be important in previous finer scale studies of vegetation boundary dynamics (Augustin et al. 2001, Brook and Bowman 2006). These are summarized in Tables 1 and 2.

*Plot-scale analyses - Data sub-setting and spatial autocorrelation*

Spatial autocorrelation can produce misleading results in statistical analyses of spatially explicit data, due to the non-independence of error components of individual data points (Legendre et al. 2002). This violates an assumption of the maximum likelihood approach used to fit generalized linear models (McCullagh and Nelder 1989). To reduce the effect of spatial autocorrelation in this study, we sub-sampled the lattice points used in the
rainforest boundary mapping. For each rainforest patch, 25 lattice points corresponding to each vegetation change trajectory involving rainforest (R) and savanna (S) were randomly sampled, i.e. 25 points for each of the transitions R-R, S-S, R-S and S-R. The data analysis was only conducted on this subsample. Stratifying the sampling by rainforest patch also ensured that all patches were represented in the analysis, while a
random sample may have excluded some patches. Only changes between rainforest and savanna were investigated, rather than transitions involving other vegetation types, because (i) savanna is the dominant vegetation type surrounding the rainforest patches; and (ii) the majority of the changes to the boundaries had occurred between savanna and rainforest (Banfai and Bowman 2006).

*Plot-scale analyses - Model variables*

The model variables included in the plot-scale analysis are provided in Table 8. These were calculated using ArcGIS 9 (ESRI) for each of the lattice points mapped in 1964. All possible subsets of distance and aspect were included in the model set. Interactions between the variables were not assessed as they are not biologically meaningful in this context. The effect of contiguous rainforest grid points (neighbor) on boundary conversion was analyzed separately to the other predictor variables, because the number of rainforest neighbours was only relevant to points adjacent to the boundary.

<table>
<thead>
<tr>
<th>Hypothesis (determinant of probability of change)</th>
<th>Variable</th>
<th>Derivation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Distance from rainforest boundary, due to availability of propagules and susceptibility to disturbance</td>
<td>Distance</td>
<td>Based on the 1964 mapping. Rainforest boundaries were defined as the grid points mapped as rainforest on the margins of the patches.</td>
</tr>
<tr>
<td>Amount of surrounding rainforest, due to availability of propagules and susceptibility to disturbance</td>
<td>Neighbor</td>
<td>The number of neighboring points classified as rainforest, with neighborhood defined as the eight nearest points.</td>
</tr>
<tr>
<td>Aspect of rainforest boundary, due to directional effect of fire</td>
<td>Aspect</td>
<td>Index of ‘south-easterliness’ calculated as Aspect = ( \sin(\theta - \frac{\pi}{4}) ) where ( \theta ) is the angle of each point from the centroid of the largest sub-patch within each rainforest patch.</td>
</tr>
</tbody>
</table>

Previous studies also found that other variables such as slope, aspect (of ground surface) and distance to drainage can be important predictors of vegetation habitat suitability (Augustin et al. 2001, Brook and Bowman 2006). However these variables were not relevant to this study, because the lowlands of KNP consist predominantly of
flat sedimentary plains (Story et al. 1976), with clearly defined drainage channels in the vicinity of rainforest patches being rare.

*Plot-scale analyses - Generalized linear models*

Methodology for plot-scale modelling analyses was adapted from Brook and Bowman (2006). Using the information on historical vegetation transitions, we developed the following models: (i) A rainforest expansion model. The dependent variable of a binomial mixed effects GLM (logit-link) was whether a savanna point changed to rainforest between 1964 to 2004 (coded as a 1), or remained savanna throughout (coded as a 0). (ii) A rainforest contraction model. This had the same structure as (i) above, except that the dependent variable was whether a rainforest point changed to savanna between 1964 to 2004 (coded as a 1), or remained rainforest throughout (coded as a 0).

Mixed-effect GLMs with rainforest patch as the random effect were used to account for variation between patches. All GLMs and associated analyses were derived using the statistical package ‘R’ 2.0.1 (Ihaka and Gentleman 1996). Wet and dry rainforest types were analyzed separately to allow for comparison.

*Patch-scale analyses - Model variables*

The candidate set of models for the patch-scale analyses is given in Table 9. Although there is likely to be a number of higher order interactions present at the patch scale, these were not included in the set as they are difficult to interpret.
Table 9. Hypotheses for the causes of boundary dynamics for patch scale modelling analyses, with the corresponding variables included in the generalised linear mixed effects models. Patch was included as a random effect in all models.

<table>
<thead>
<tr>
<th>Hypothesis</th>
<th>Model</th>
</tr>
</thead>
<tbody>
<tr>
<td>Direct effect of fire on tree mortality</td>
<td>Fire frequency</td>
</tr>
<tr>
<td>Rainforest type is primary mediating factor due to water source and/or landscape setting</td>
<td>Rainforest type</td>
</tr>
<tr>
<td>Buffalo grazing and trampling limits tree recruitment and causes direct mortality</td>
<td>Buffalo impact</td>
</tr>
<tr>
<td>Landscape setting mediates changes due to topographic fire protection</td>
<td>Rainforest type X fire frequency</td>
</tr>
<tr>
<td>Buffalo impact varies between rainforest types due to hydrology and landscape setting affecting buffalo density and habitat preferences</td>
<td>Rainforest type X buffalo impact</td>
</tr>
<tr>
<td>Smaller patches more vulnerable to fire due to higher edge/core ratio</td>
<td>Patch size X fire frequency</td>
</tr>
<tr>
<td>More fragmented patches more vulnerable to fire due to higher edge/core ratio</td>
<td>Fragmentation X fire frequency</td>
</tr>
<tr>
<td>Smaller patches more vulnerable to buffalo impact due to higher edge/core ratio</td>
<td>Patch size X buffalo impact</td>
</tr>
<tr>
<td>More fragmented patches more vulnerable to buffalo impact due to higher edge/core ratio</td>
<td>Fragmentation X buffalo impact</td>
</tr>
<tr>
<td>Buffalo interacts with the impact of fire due to altering fuel loads from browsing and transport of flammable weeds</td>
<td>Fire frequency X buffalo impact</td>
</tr>
<tr>
<td>Variation in rate of boundary change is due to factors other than those captured by the models</td>
<td>Null, with random effect for patch</td>
</tr>
</tbody>
</table>

The model variables were derived for each rainforest patch as follows:

i) Rainforest type (RT) as ‘dry’ or ‘wet’, based on previous mapping by Russell-Smith (1991).

ii) Patch size (PS) as total area mapped as rainforest in 1964 for each site. Points mapped as rainforest were converted to 20m x 20m grid cells and then joined to form polygons representing each rainforest patch using ArcGIS 9 (ESRI). Area was then calculated for these polygons.

iii) Fragmentation (FG) was calculated as $2\ln(0.25P)/\ln(A)$, where $P =$ total perimeter and $A =$ total patch area (Hargis et al. 1998, Donovan and Welden 2002). This index ranges between 1 and 2 and gives an indication of how convoluted in shape a patch is. Perimeter and area was calculated based on polygons as for PS.
iv) Fire frequency (FI) as an index of fire frequency based on previous mapping of fire scars from LANDSAT imagery from 1984 to 2003 (Edwards et al. 2003). A fire was recorded as occurring at a rainforest patch if at least 20% of the rainforest boundary was within 100m of a mapped fire scar using ArcGIS (ESRI). The index was calculated as the total number of fires occurring at the boundary of each rainforest patch over the study period. Due to the spatial error inherent in the fire scar mapping process (Russell-Smith et al. 1997b, Bowman et al. 2004a), the fire scar was recorded as affecting the rainforest boundary if it was within 100m. The frequency of fires that occurred late in the dry season (post July) were also recorded.

v) Buffalo impact (BI) was recorded as average number of buffalo tracks visible in a 200m buffer around the rainforest margins on the aerial photographs for the beginning and end of each photographic interval. Values were standardized by patch size and averaged between the beginning and end of the time period. The boundary increment of each patch was calculated as the average change in the position of the boundary where rainforest expansion was given a positive value, while contraction was negative. This was based on the distance of each grid point on the boundary at time 2 ($T_2$) to the nearest point on the boundary at $T_1$ using the ‘nearest feature’ extension in ArcGIS (ESRI). Boundary increment was used as the response variable as other possible measures of changes to the patch boundary, such as percentage change in patch size, are strongly dependent on the original patch size, and thus would not allow independent assessment of patch size in influencing the rate of change.

**Patch-scale analyses - Generalized linear models**

GLMs were used as in the point-scale analysis, but without patch as a mixed effect (because the unit of change in this case was at the level of the patch). The response variable in the GLMs was the patch boundary increment transformed with log link function to provide a Gaussian distribution.

While the study period was 1964 to 2004, the fire frequency data was only available for the photographic interval of 1984 to 2004. The modelling analyses were therefore conducted separately for the periods 1964 to 1984 and 1984 to 2004.
Two dry rainforest patches had very high boundary increments which made them extreme outliers. Achieving model diagnostics with no major deviations from the underlying regression assumptions was only possible by excluding these outlying data points. These two rainforest patches were therefore only included in the post hoc analyses. After excluding these two points, diagnostics of the final models showed no evidence of overdispersion, as measured by the variance inflation factor (Burnham and Anderson 2002).

**Results**

*Plot-scale analyses*

For dry rainforest the modelling showed that proximity to the rainforest edge was of prime importance for both expansion and contraction (albeit with less deviance explained for contraction; Table 10). The best-supported models according to AIC<sub>c</sub> included distance as the only predictor variable and had about twice the weight of the next best selected models. Models including aspect as well as distance to edge explained negligibly more of the deviance (< 0.1%), suggesting that aspect was irrelevant once distance had been accounted for.

Similar results were found for wet rainforest, with distance explaining the greatest amount of deviance (rainforest expansion model captured 40.5% of the deviance in the data; rainforest contraction model captured 16.8%), while aspect again explained very little of the deviance (< 1%). The relatively low amount of deviance explained by distance in the rainforest contraction model compared to the expansion model may be due to there being less variation in distance to rainforest edge within rainforest patches compared to within savannas.
Table 10. Rainforest expansion and contraction generalised linear mixed effects model results for dry rainforest, including the variables distance to rainforest boundary and aspect (AS). Patch was a random effect common to all models.

<table>
<thead>
<tr>
<th>Model</th>
<th>log(L)</th>
<th>K</th>
<th>AICc</th>
<th>Δ AICc</th>
<th>wi</th>
<th>Deviance explained (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rainforest expansion model</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Distance</td>
<td>-433.276</td>
<td>4</td>
<td>874.595</td>
<td>0.000</td>
<td>0.733</td>
<td>33.149</td>
</tr>
<tr>
<td>Distance + AS</td>
<td>-433.276</td>
<td>5</td>
<td>876.617</td>
<td>2.022</td>
<td>0.267</td>
<td>33.150</td>
</tr>
<tr>
<td>AS</td>
<td>-645.929</td>
<td>4</td>
<td>1299.901</td>
<td>425.306</td>
<td>0.000</td>
<td>0.338</td>
</tr>
<tr>
<td>Null</td>
<td>-648.120</td>
<td>3</td>
<td>1302.265</td>
<td>427.670</td>
<td>0.000</td>
<td>-</td>
</tr>
<tr>
<td>Rainforest contraction model</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Distance</td>
<td>-475.457</td>
<td>4</td>
<td>958.966</td>
<td>0.000</td>
<td>0.666</td>
<td>7.775</td>
</tr>
<tr>
<td>Distance + AS</td>
<td>-475.133</td>
<td>5</td>
<td>960.343</td>
<td>1.377</td>
<td>0.334</td>
<td>7.838</td>
</tr>
<tr>
<td>Null</td>
<td>-515.541</td>
<td>3</td>
<td>1037.113</td>
<td>78.147</td>
<td>0.000</td>
<td>-</td>
</tr>
<tr>
<td>AS</td>
<td>-515.457</td>
<td>4</td>
<td>1038.965</td>
<td>79.999</td>
<td>0.000</td>
<td>0.016</td>
</tr>
</tbody>
</table>

For both rainforest types there was a negative relationship between distance from rainforest edge and probability of change for both expansion and contraction (Figure 16). The decline with increasing distance in the probability of change for wet rainforests was steeper than for dry rainforests (Figure 16). The vast majority of rainforest expansion and contraction occurred within one grid point (< 30 m) from the boundary for both rainforest types (Figure 17).

Figure 16. Predicted values for models with distance to rainforest edge as the only fixed effect. Rainforest contraction distances are given negative values. Full lines = dry rainforest; dashed lines = wet rainforest.
Models with the number of neighboring rainforest grid points as the predictor variable had very strong support compared to the null models for both wet and dry rainforest (i.e., the ratio of AICc weights [evidence ratio], a measure of relative support for competing models, was greater than $1 \times 10^6$). There was a positive relationship between the number of rainforest neighbours and the probability of vegetation change for the rainforest expansion models, and a negative relationship for the rainforest contraction models. However, in both models, the number of neighboring rainforest grid points explained only a small amount of the deviance (dry rainforest $< 6\%$; wet rainforest $< 9\%$), suggesting it was not a good predictor of the probability of change.

**Patch-scale analyses**

For the period 1964 to 1984 the best-selected model for explaining the variation in rate of boundary change consisted of an additive effect, and interaction between, rainforest type and buffalo impact (Table 11). The model with rainforest type as the only predictor variable also had strong support, although it had only about half the weight of the best-selected model. The other models in the set were ranked lower than the null model and
had weak support, with $\Delta \text{AIC}_c$ values of greater than 6 (and hence low $\text{AIC}_c$ weights) compared to the best-selected model (Table 11).

Table 11. No fire: results of AIC analyses of generalised linear mixed effects models for period 1964 to 1984, during which time fire variables were not quantified. RT = Rainforest type; BI = Buffalo impact; FG = Fragmentation; FI = Fire frequency; PS = patch size.

<table>
<thead>
<tr>
<th>Model</th>
<th>log(L)</th>
<th>K</th>
<th>AICc</th>
<th>$\Delta$ AICc</th>
<th>$w_i$</th>
<th>Deviance explained (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>RT X BI</td>
<td>-112.325</td>
<td>4</td>
<td>233.702</td>
<td>0.000</td>
<td>0.571</td>
<td>24.730</td>
</tr>
<tr>
<td>RT</td>
<td>-115.371</td>
<td>2</td>
<td>235.042</td>
<td>1.340</td>
<td>0.292</td>
<td>13.273</td>
</tr>
<tr>
<td>BI</td>
<td>-117.316</td>
<td>2</td>
<td>238.932</td>
<td>5.231</td>
<td>0.042</td>
<td>5.059</td>
</tr>
<tr>
<td>Null</td>
<td>-118.432</td>
<td>1</td>
<td>238.962</td>
<td>5.261</td>
<td>0.041</td>
<td>5.059</td>
</tr>
<tr>
<td>PS</td>
<td>-117.973</td>
<td>2</td>
<td>240.246</td>
<td>6.544</td>
<td>0.022</td>
<td>2.114</td>
</tr>
<tr>
<td>PS X BI</td>
<td>-116.002</td>
<td>4</td>
<td>241.057</td>
<td>7.355</td>
<td>0.014</td>
<td>10.689</td>
</tr>
<tr>
<td>FG</td>
<td>-118.426</td>
<td>2</td>
<td>241.152</td>
<td>7.450</td>
<td>0.014</td>
<td>0.029</td>
</tr>
<tr>
<td>FG X BI</td>
<td>-117.306</td>
<td>4</td>
<td>243.666</td>
<td>9.964</td>
<td>0.004</td>
<td>5.102</td>
</tr>
</tbody>
</table>

Table 12. Fire: results of AIC analyses of generalised linear mixed effects models for period 1984 to 2004, with fire variable included. RT = Rainforest type; BI = Buffalo impact; FG = Fragmentation; FI = Fire frequency; PS = patch size.

<table>
<thead>
<tr>
<th>Model</th>
<th>log(L)</th>
<th>K</th>
<th>AICc</th>
<th>$\Delta$ AICc</th>
<th>$w_i$</th>
<th>Deviance explained (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>RT X BI</td>
<td>-120.022</td>
<td>4</td>
<td>249.019</td>
<td>0.000</td>
<td>0.401</td>
<td>17.041</td>
</tr>
<tr>
<td>Null</td>
<td>-124.319</td>
<td>1</td>
<td>250.729</td>
<td>1.709</td>
<td>0.171</td>
<td>-</td>
</tr>
<tr>
<td>FG X BI</td>
<td>-120.966</td>
<td>4</td>
<td>250.908</td>
<td>1.889</td>
<td>0.156</td>
<td>13.564</td>
</tr>
<tr>
<td>RT</td>
<td>-124.134</td>
<td>2</td>
<td>252.548</td>
<td>3.529</td>
<td>0.069</td>
<td>0.799</td>
</tr>
<tr>
<td>BI</td>
<td>-124.211</td>
<td>2</td>
<td>252.702</td>
<td>3.683</td>
<td>0.064</td>
<td>0.466</td>
</tr>
<tr>
<td>FI</td>
<td>-124.276</td>
<td>2</td>
<td>252.831</td>
<td>3.812</td>
<td>0.060</td>
<td>0.186</td>
</tr>
<tr>
<td>FG X FI</td>
<td>-122.410</td>
<td>4</td>
<td>253.796</td>
<td>4.777</td>
<td>0.037</td>
<td>7.963</td>
</tr>
<tr>
<td>RT X FI</td>
<td>-123.457</td>
<td>4</td>
<td>255.890</td>
<td>6.871</td>
<td>0.013</td>
<td>3.676</td>
</tr>
<tr>
<td>PS X BI</td>
<td>-123.503</td>
<td>4</td>
<td>255.981</td>
<td>6.961</td>
<td>0.012</td>
<td>3.487</td>
</tr>
<tr>
<td>PS X FI</td>
<td>-123.609</td>
<td>4</td>
<td>256.193</td>
<td>7.173</td>
<td>0.011</td>
<td>3.041</td>
</tr>
<tr>
<td>FI X BI</td>
<td>-124.030</td>
<td>4</td>
<td>257.035</td>
<td>8.016</td>
<td>0.007</td>
<td>1.249</td>
</tr>
</tbody>
</table>

The model with the highest $\text{AIC}_c$ support for the later period, 1984 to 2004, was the same as that of the earlier period: an additive and interactive effect between rainforest type and buffalo impact (Table 12). This model had moderate support, with about twice the weight of evidence than the null model. However, the deviance explained by this model was lower than for the former period, at only 17%. All other models were ranked lower than the null model. There was therefore very little support
for an effect of fire frequency, patch size and fragmentation on the rate of boundary change.

The model with the highest AIC<sub>c</sub> support for the later period, 1984 to 2004, was the same as that of the earlier period: an additive and interactive effect between rainforest type and buffalo impact (Table 12). This model had moderate support, with about twice the weight of evidence than the null model. However, the deviance explained by this model was lower than for the former period, at only 17%. All other models were ranked lower than the null model. There was therefore very little support for an effect of fire frequency, patch size and fragmentation on the rate of boundary change.

To further explore the impacts of buffalo and rainforest type on the rate of boundary change, the best-selected models (above) were used to predict the boundary increment across the range of buffalo impact, for both time periods. For 1964 to 1984, there was a negative relationship between boundary increment and buffalo impact in both rainforest types (Figure 18). Higher boundary increment values were also predicted for dry rainforests across the range of buffalo impact. The slope of the fit for the two rainforest types was similar, suggesting little interaction between the two variables. The 95% confidence intervals indicate that it is very unlikely for dry rainforest to contract, regardless of the level of buffalo impact. However, the width of the confidence intervals also highlights the large amount of uncertainty in the relationships, particularly for wet rainforests with high buffalo impact levels.

The predictions of the best selected model for the later period, 1984 to 2004, were almost identical to that of the former period, with a negative relationship between boundary increment and buffalo impact. The second best-selected model for the period 1964 to 1984, with only rainforest type as a predictor variable, predicted a considerably higher per decade boundary increment for dry rainforests (3.38m) compared to wet rainforests (0.60m).
Little deviance was explained by those models which included fire frequency, patch size and fragmentation (Tables 11 and 12). To further assess whether these variables were unrelated to the rate of boundary change, the separate effect of each variable was explored visually. The two outlying patches, with particularly high rates of boundary expansion, were also included in these exploratory analyses.

There were few clear patterns in the relationship between the fire indices and the decadal boundary increment between 1984 and 2004, with moderate rates of rainforest expansion occurring across the full range of both total and late fire frequency (Figure 19). The only ecologically consistent relationship was observed at the extreme values of late fire frequency: the two rainforest patches that experienced the greatest rate of contraction had relatively high late fire indices, while conversely, late fires were infrequent (indices of only 1 and 3) at the two patches that experienced the highest rate of expansion between 1984 and 2004 (Figure 19b).
Chapter 4 - Multi-scale modelling of the drivers of rainforest boundary dynamics

Figure 19. (a) Total and (b) late fire indices compared to decadal boundary increment between 1984 and 2004 for both rainforest types. Shaded circles = Dry rainforest; Open circles = Wet rainforest.

There was also no clear relationship between patch shape and boundary increment, with variable rates of rainforest expansion occurring across the range of patch size and fragmentation index (Figure 20). However the two patches with particularly high boundary increments over the study period both had very small patch sizes and high fragmentation indices.

Figure 20. Decadal boundary increment for the period 1964 to 2004 versus (a) patch size and (b) fragmentation index for both rainforest types. Shaded circles = Dry rainforest; Open circles = Wet rainforest. The two dry rainforest patches that were excluded from the modelling analyses as they had particularly high boundary increments are indicated with an asterisk (*).
Patch size and fragmentation were also graphed against total change in patch area to investigate the influence of these variables on the susceptibility of patches to change relative to their original patch size. The greatest changes in percentage area occurred for very small patch sizes (Figure 21a). There also appeared to be a threshold effect occurring for fragmentation in dry rainforests, with large increases in patch area observed beyond a fragmentation index of 1.23 (Figure 21b).

Figure 21. Percentage change in patch area for the period 1964 to 2004 versus (a) patch size and (b) fragmentation index for both rainforest types. Shaded circles = Dry rainforest; Open circles = Wet rainforest. The two dry rainforest patches that were excluded from the modelling analyses as they have particularly high percentage changes and are indicated with asterisks (*) on the graphs.

Discussion

Plot-scale drivers

At the plot scale, the distance from rainforest edge was found to be the most important determinant of vegetation change. For example, there was a high probability of the transition from savanna to rainforest occurring close to the rainforest boundary, which declined steadily with distance. This supports the view that the rainforest boundary dynamics in KNP has primarily been incremental, as has been observed in other regions of northern Australia such as at Weipa, northern Queensland (Bowman and Fensham
The rainforest expansion has therefore occurred primarily through the process of margin extension, rather than other successional processes such as nucleation and irruption (Russell-Smith et al. 2004b).

Expansion of the boundary was more likely to occur where there was more rainforest surrounding the area, which is consistent with other transition modelling studies (Augustin et al. 2001). This is likely to be due to an increased availability of rainforest propagules to become established in the savanna, and may also relate to boundary protection from disturbance by surrounding vegetation. However, the low amount of deviance explained by this variable suggests that the number of rainforest neighbours was not an important factor determining the probability of change.

Aspect also explained little of the deviance in the probability of vegetation change. Aspect was included in the models as the winds in the dry season around the KNP region are predominantly from the south-east (Gill et al. 1996). If fire disturbance was limiting the expansion of the rainforests we would expect the probability of contraction and expansion to be dependent on the aspect of the rainforest boundary. The lack of deviance explained by both aspect and neighborhood therefore does not support the fire hypothesis, *sensu stricto*. However, the effect of aspect may have been confounded, as the direction of approaching fires is dependent on the occurrence of topographic barriers and local effects of surrounding vegetation that were not accounted for in this analysis.

**Patch-scale drivers**

The rate of boundary change at the patch scale was best predicted by rainforest type and the level of buffalo impact. The generally higher rate of boundary expansion in the dry rainforests may have been related to this forest type having, by definition, a markedly different hydrology to wet rainforests. While wet rainforests source their water primarily from groundwater, dry rainforests rely on rainfall (Russell-Smith 1991). Given the general wetting trend over the last century (Smith 2004), it is possible that increased soil moisture in the surrounding savannas has allowed the more rapid expansion of previously moisture-restricted dry rainforest boundaries over the study period (Banfai
and Bowman 2006). However increased rainfall may have also promoted the expansion of wet rainforests due to greater discharge from springs.

Buffalo appear to have restricted the expansion of rainforest in KNP over the study period. Such an effect is consistent with previous studies were buffalo were found to have a major impact on rainforest vegetation. For example, a study in KNP by Braithwaite et al. (1984) showed that sites that were more intensively used by buffalo had a lower density of vegetation < 3 m in height during the dry season, because buffalo knocked down many young trees. Soil compaction was also thought to have led to the death of many large trees due to the restriction of discharging groundwater. These results also concord with observations made by resident Aboriginal landowners in the region. Jawoyn elders have noted that buffalo impacts had severely damaged some rainforest patches (Robinson et al. 2005).

There was no clear relationship between fire frequency and the rate of boundary change. For example, high fire frequencies were recorded at the two dry rainforest patches that also had the highest rates of boundary expansion over the study period. Additionally, rainforest expansion continued to occur even when patches experience regular late dry season fires. As such, these results are consistent with the plot-scale analyses, which showed little support for an effect of fire disturbance on the probability of vegetation change along the rainforest boundaries.

The lack of a demonstrable fire effect on rainforest change, at both the local and regional scale, are contrary to the restrictive hypothesis that regular fires alone limit rainforest expansion in Australia (Bowman 2000a). Our results are also inconsistent with studies of other tropical forests where the local dynamics of the forest-savanna boundary zone were inferred to be primarily a function of fire incidence (Furley 1992, Ratter 1992, King et al. 1997, Favier et al. 2004).

However, fire frequency may not have had a detectable impact on the rate of change because the impact of fire on the rainforest boundary is strongly determined by the fuel type present in the surrounding savannas (Stott 2000). This potential confounder could not be controlled for in this analysis. The poor spatial resolution of the fire scar mapping (Russell-Smith et al. 1997b, Bowman et al. 2003), combined with the coarse
temporal scale provided by the aerial photography (20 year time periods), may also make it difficult to identify the effect of landscape fire on rainforest boundary dynamics. Similarly to fire frequency, there was no simple relationship between patch size and the rate of boundary change. The rate of boundary expansion was also highly variable across the range of the fragmentation index. However, small and highly fragmented patches were susceptible to fast rates of change, particularly for dry rainforest. Under the current scenario of rainforest expansion, this has resulted in a few patches having very large increases in rainforest area relative to their original patch size. This was demonstrated by the two rainforest patches that had particularly high percentage increases in patch area. However, where contraction is occurring, a similar rate of change for a small patch would result in a rapid reduction in patch area. Small and highly fragmented rainforest patches therefore remain particularly vulnerable to destruction where threatening processes are occurring. This is of particular concern as the loss of individual patches can have potentially far-reaching effects on regional biodiversity (Turner and Corlett 1996, Price et al. 1999).

Other potential drivers, and interactive effects
While rainforest type and buffalo impact were the most important of the predictors of the rate of boundary change we considered, these factors are unable to explain the general trend toward rainforest expansion throughout the study period. If buffalo impact was a primary factor controlling the rate of change on the boundary we would have expected a contraction of rainforest boundaries between 1964 and 1984 when buffalo numbers were at their peak (Skeat et al. 1996). The relatively small proportion of the deviance explained by the variables included in the models also lends support to the view that the rate of boundary change has been strongly influenced by other unmodeled factors.

More pervasive regional or global factors appear to have driven the trend toward rainforest expansion. A plausible hypothesis is that the trend of rainforest expansion has been driven by a concomitant increase in rainfall over the study period (Banfai and Bowman 2006). Increased rainfall can facilitate rainforest establishment in savanna by
increasing the supply of water to tree roots (Bowman and Panton 1993). The effect of variation in rainfall between rainforest patches was not able to be assessed in this study due to the paucity of rainfall stations in the KNP region. However, rainfall has been found to be an important driver of vegetation change in the savannas of eastern Australia (Fensham et al. 2005) as well as globally (Roques et al. 2001, van Wijk and Rodriguez-Iturbe 2002, Kraaij and Ward 2006).

The overall trend of expansion may also have been driven by an increase in atmospheric CO₂, which has risen by 18% over the study period (Brook and Bowman 2006). Increased atmospheric CO₂ can act to shift the balance toward trees (predominantly C₃ photosynthetic pathway) rather than grasses (predominantly C₄) at the rainforest boundary (Lewis et al. 2004b, Berry and Roderick 2006, Brook and Bowman 2006).

The effect of increased rainfall and atmospheric CO₂ on the rate of boundary change may also account for the differences in the rate of change between rainforest types, due to differences in landscape setting. While wet rainforests usually occur in edaphically isolated areas within the fire-prone open savannas (such as springs), dry rainforests generally occur in landscape settings largely protected from fire, such as on the margins of seasonally inundated floodplains or islands (Bowman 2000a). Thus, potential habitat for wet rainforests is far more restricted by inherent environmental factors, such as soil type and hydrology, than dry rainforests. Dry rainforest expansion is likely to be more strongly controlled by the balance between tree recruitment and fire damage. Therefore, factors that increase seedling growth – such as increased rainfall or atmospheric CO₂ – may be able to counteract hostile fire regimes that present a barrier to tree recruitment and regeneration. Such a process is a variant of the ‘fire trap’ and CO₂ enrichment hypothesis proposed by Bond et al. (2003) for savanna tree dynamics.

Conclusions
Here we have modeled the rate of change of rainforest patch boundaries in KNP over a four decade period, 1964 to 2004. The general trend of rainforest expansion in KNP is consistent with having been primarily driven by increases in rainfall and atmospheric
CO₂. Changes in rainforest extent have been mediated by the effects of historical buffalo impact and rainforest type. With buffalo numbers increasing in KNP, and throughout other areas of northern Australia, control of buffalo numbers remains a priority for land managers (Robinson and Whitehead 2003). It appears that current fire regimes are not sufficiently destructive to limit the overall expansion of the rainforest patches. However, smaller and more fragmented rainforest patches remain particularly vulnerable to being eliminated. Management efforts should therefore be focused on protecting these patches from potential threats.

Some uncertainty remains as to the relative importance of the various drivers of the rainforest boundary dynamics in KNP. The assessment of the effect of fire on the rainforest boundary may have been confounded by the coarse temporal scale of the analysis relative to the high frequency of landscape fire. Assessment of the relationship between fluctuations in rainfall and variation in the rate of boundary change has also not been conducted. One approach to advance this problem will be studies of the dynamics of rainforest patches with detailed photographic histories using time series modelling analyses (Minnich et al. 2000, Goetz et al. 2006).
Chapter 5 – A reassessment of the extent and causes of rainforest boundary dynamics
Chapter 5 - A reassessment of the extent and causes of rainforest boundary dynamics

Introduction

High resolution multi-temporal spatial data can greatly assist in understanding the drivers of landscape change. It is increasingly being recognized that historical aerial photographs provide a critically important archive to understand how landscapes have changed since the mid 20th century (Fensham and Fairfax 2002). Yet, whilst having relatively longer time depth and higher spatial resolution than most satellite imagery, the frequency of repeat aerial photography is much lower, resulting in ‘snap shots’ of landscape change. Such limited temporal resolution of the aerial photographic archive is a serious disadvantage for understanding landscape ecology, as one or more cycles of an ecological process may be rendered invisible or incomplete by the available imagery. Further, many ecological processes operate at different time scales: infrequent, rapid changes may occur while, over longer time scales, there may be continuous and gradual shifts occurring. A good example of such a multi-temporal ecological process is the encroachment of woody plants into more open vegetation types such as grasslands (Archer et al. 1995). The continuous dispersal, establishment and growth of trees can be abruptly interrupted, and sometimes reversed, following an unpredictable and infrequent disturbance event, such as landscape fire.

It is widely assumed that the most important factor in controlling rainforest boundaries throughout Australia is landscape fire (Bowman 2000a). Indeed, an operational definition of Australian rainforest are woody vegetation types that are relatively more susceptible to recurrent fire disturbance than the ubiquitous, archetypical fire adapted vegetation dominated by eucalypts (Bowman 2000b, 2001). In northern Australia, it is widely argued that the recent breakdown of Aboriginal fire management, which was characterized by numerous small fires, has resulted in a regime of frequent and intense landscape fires that is hostile to rainforests and other fire sensitive vegetation (e.g. Russell-Smith and Bowman 1992). In this context it is surprising that analyses of recent aerial photographic and supporting field based studies revealed a regional expansion of rainforests (Bowman et al. 2001, Chapters 2 and 3, Brook and Bowman 2006).
One such study used aerial photography from 1964 to 2004 to examine the boundary dynamics of 50 rainforest patches in KNP and found that the rainforest patches had expanded by an average of 28.8% (Chapter 2). The biological mechanism for such expansion has been previously established through detailed field studies of stand structures (Chapter 3, Banfai and Bowman 2005). Field assessments and statistical modelling have suggested that global change phenomena such as increases in rainfall and atmospheric CO$_2$ best explain the overall expansion of rainforest in KNP (Chapters 2 and 3). These studies also indicate that the occurrence of landscape fire is of limited explanatory power in controlling rainforest patch dynamics. However, this inference may be spurious because of a substantial mismatch between the infrequent temporal availability of repeat aerial photography (1964, 1984, 1991 and 2004) and the occurrence of very high frequency landscape fires (annual to biennial).

Additionally, the estimate of the overall extent of boundary change in Chapter 2 was based only on the two endpoints of the aerial photography (1964 and 2004). If there were rapid changes in the boundaries occurring over short time scales then this estimate may have been strongly influenced by the particular ‘snapshots’ provided by the aerial photography available, and may thus be an inaccurate assessment of the actual rate of change. The importance of consideration of such effects has also been demonstrated by a study of rainforest boundary dynamics in the Gulf of Carpentaria, northern Australia, where the number of aerial photographs used was shown to influence the accuracy of predicted boundary changes (Brook et al. 2005).

The objective of this paper is therefore to reassess the extent and causes of the rainforest boundary dynamics in KNP, by investigating how sensitive inferences are to the number of aerial photographic ‘snapshots’ used on the analysis. To achieve this objective we assess: (i) the temporal variation in the rate of boundary change of a subset of rainforest patches that have detailed aerial photographic histories; (ii) the overall rate of change based on sub-sampling of all available aerial photography, and (iii) whether the explanatory power of fire is influenced by the temporal scale used in generalized linear models.
**Methods**

*Aerial photography and site selection*
Changes in percentage area of 50 rainforest patches was derived from previous mapping by the author (Chapter 2) for years 1964, 1984, 1991 and 2004 using a 20 × 20-m lattice grid. Two patches were excluded that were unique in having experienced substantial contraction due to infrastructure, and a further two were excluded where the 1964 photographs were not available. Of the remaining 46 patches, a subset of nine patches were selected where at least two extra photographs were available (Figure 22). Effort was made to ensure that sites were selected across the full geographic range of KNP. The total number of photographs available for these patches varied from 6 to 10. All photographs used color film at a scale of 1: 25,000 apart from 1964 which were black and white film at 1 : 16,000. The imagery was scanned from contact prints to achieve a common pixel resolution of 1 m². Each lattice grid point was manually classified into vegetation types for each year using ArcGIS 8 (ESRI) at a common scale of 1:3000, primarily based on the distance between tree crowns. For full details of sampling and mapping see Chapter 2.

*Variation in the rate of boundary change*
The variability in the rate of change relative to 1964 was assessed visually for each of the subset of rainforest patches with detailed photographic histories. The change in patch size was calculated based on the number of grid points mapped as rainforest in each year based on the mapping outlined above. To assess the variation in the rate between different time intervals, the rate of change between all possible photographic pairs for each site was also calculated.

The mean rate of change for the entire study period 1964 to 2004 was calculated by averaging the rates of change in patch size for all possible photographic intervals (greater than 5 years) for all rainforest patches, and were compared to estimates based only on the photographic endpoints (e.g. only years 1964 and 2004 for the entire study
Figure 22. Location of study site in the Northern Territory of Australia (a), location of KNP at the regional scale (b) and location of rainforest patches sampled overlayed on the different landforms present in the study site (c). Asterisks (*) indicate subset of patches selected for detailed photographic analysis. Case studies 1, 2 and 3 are labelled numerically.

period). Confidence intervals for estimates based on endpoints and all combinations of photographic pairs were derived by bootstrapping using the statistical package ‘R’ 2.0.1 (Ihaka and Gentleman 1996). Dry and wet rainforest types were analyzed separately. This procedure was repeated for the first and second halves of the study period (1964 to 1984 and 1984 to 2004) to allow comparison.
Fire modelling

Given the high variability in the rates of boundary dynamics over short time intervals (Figures 2 and 3), and the fact that fire can cause rapid ecological responses to rainforest boundaries, the fires occurring in the few years preceding the end of the photographic interval may be critical in determining the overall rate of boundary change over the whole photographic interval.

The variability in the frequency of fire for shorter intervals preceding the end of the two sample periods (1984 to 1991 and 1991 to 2004) was described by determining the probability that a site remained unburnt or was not burnt by a late dry season fire. The number and season of fires were calculated for each successive year prior to the endpoint of the aerial photographic period for all available sites. The occurrence of early and late dry season fires for each year was estimated using ArcGIS 9 (ESRI) based on previous mapping of fire scars from satellite imagery for the period 1980 to 2003 (Edwards et al. 2003). The boundary was classified as burnt if a fire scar occurred within 100m, to account for the spatial error inherent in the fire scar mapping process (Russell-Smith et al. 1997b, Bowman et al. 2004a). A comparison is made of dry and wet rainforest types. The data were summarized by predicting the probability of fire for the years preceding the photographic endpoints using generalized linear models (GLMs). GLMs are a generalization of linear regression models and have the advantage of allowing for a variety of distributions for the response and error terms in the model (McCullagh and Nelder 1989). The predictor variable of binomial GLMs (logit-link) was whether the patch had been burnt for each consecutive year in the decade preceding the photographic endpoint (coded as 1) or remained unburnt (coded as 0). For example, to predict the probability of a rainforest patch having been burnt in the seven years before the photograph was taken, the fire scar mapping for each rainforest patch was assessed as to whether fire occurred near the rainforest boundary over that seven-year period. Patches where a fire had occurred were given a predictor variable of 1, while patches where no fire had occurred were given a predictor variable of 0. This
methodology was also repeated using only the occurrence of late dry season fires to allow comparison.

GLMs were also used to reassess the effect of fire frequency on the rate of change in patch size. Predictor variables included in the models were chosen a priori in accordance with the Information Theoretic paradigm (Burnham and Anderson 2002). To assess the interval prior to the photographic endpoint for which the fire frequency was the best predictor of the rate of change, models with a range of intervals were included in the model set (1, 2, 5 and 10 years). For the photographic interval 1984 to 1991, the 10 year fire frequency was not used as it exceeds the length of the photographic interval. The dependent variable of Gaussian GLMs (identity-link) was the percentage change in patch size over each time interval. Separate models were used to compare the effect of total and late dry season fire frequency. Total and late fire frequency for each interval was calculated using ArcGIS 9 (ESRI) as above. Given the differences observed in the predicted probability of fire between rainforest types as well as between the two photographic endpoints, a separate analysis was conducted for each of these combinations to allow for comparison.

The relative strength of evidence for the models was assessed based on Akaike’s Information Criterion adjusted for small sample sizes (AICc, Burnham and Anderson 2002). All GLMs and associated analyses were derived using the statistical package ‘R’ 2.0.1 (Ihaka and Gentleman 1996).

Case studies
Three patches from the subset of patches with detailed photographic histories were chosen as case studies. These were the dry rainforest patches which had the highest rate of contraction (Case Study 1) and expansion (Case Study 2) over the study period, as well as a randomly selected wet rainforest patch (Case Study 3).

To assess the spatial pattern of expansion and contraction of each patch boundary, maps indicating the changes that occurred over the entire study period were created using ArcGIS 9 (ESRI). Here the points in the lattice grid were converted to 20
m x 20 m pixels. Topography, drainage and infrastructure were based on 1:50000 topographic maps.

The variability in the occurrence of fire on the rainforest boundary was investigated by calculating the percentage of the boundary burnt each year for each site using ArcGIS 9 (ESRI) as above. The frequency of different proportions of the boundary being burnt was then compared visually using histograms. Early and late dry season fires were considered separately.

Results

Variation in the rate of boundary change for the subset of nine rainforest patches with detailed aerial photographic histories, large changes in patch size between the years of the record indicated that rates of change were highly dynamic for both rainforest types (Figure 23). Rapid changes were also observed between the years of aerial photography previously used to assess the rate of change (Chapter 2).

The rates of change in patch area differed depending on the length of the interval between the aerial photographic snapshots. Generally, there were large rates of change observed over short time intervals and smaller changes over longer time periods (Figure 24). There was also a difference in the short term changes between the rainforest types; wet rainforest predominantly had positive rates of change while dry rainforest had more episodes of negative boundary change. The rates of change for dry rainforest were also much more variable, particularly over longer time intervals.
Figure 23. Percentage change of rainforest patch area relative to 1964 for each patch in the subset with detailed aerial photographic histories. a) Dry rainforest; b) Wet rainforest. Arrows indicate years for which aerial photography was available for at least one patch. Shaded bars indicate years previously sampled for all sites by Banfai and Bowman (2006).

Figure 24. Percentage change in rainforest patch area per decade for all possible photographic intervals for the subset of sites with detailed photographic histories. a) Dry rainforest; b) Wet rainforest.
Reassessment of rates of change

The estimate of the rate of change per decade based on all combinations of photographs equates to a 23.2% expansion of the dry rainforest patches over the 40 year period (Table 13), which is substantially lower than the estimate based solely on the endpoints (42.1%). For wet rainforests the estimated overall rate of change was the same in the two analyses. There was less uncertainty around the estimate using all combinations of photographs for both rainforest types (Table 13). The reassessment of the rate of change based on all combinations of photographs supports the view that there has been an overall increase in rainforest patch area for both rainforest types over the total study period 1964 to 2004, given the lower limits of the 95% confidence intervals were positive values. Consistent with the endpoint analysis, the reassessment of the rate of change also supported the view that dry rainforests are expanding faster than wet rainforests, although there was a slight overlap in the confidence intervals between the two rainforest types (Table 13).

Table 13. Reassessment of the rate of change in the size of 46 rainforest patches in KNP. Sampling of photographic endpoints is compared with sampling all possible combinations of photographic pairs within each period. Bootstrapped confidence intervals are given. Dry rainforests N patches = 25; Wet rainforests N patches = 21.

<table>
<thead>
<tr>
<th>Rainforest Type</th>
<th>Sampling method</th>
<th>Period</th>
<th>Endpoints (% 10y⁻¹)</th>
<th>All combinations (% 10y⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dry</td>
<td></td>
<td>64-04</td>
<td>10.5 (3.8-19.6)</td>
<td>5.8 (3.8-8.3)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>64-84</td>
<td>12.9 (5.0-24.7)</td>
<td>10.8 (4.6-19.7)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>84-04</td>
<td>5.7 (0.4-13.4)</td>
<td>2.4 (0.6-4.8)</td>
</tr>
<tr>
<td>Wet</td>
<td></td>
<td>64-04</td>
<td>3.3 (1.8-4.7)</td>
<td>3.3 (2.6-4.1)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>64-84</td>
<td>0.8 (-1.3-3.0)</td>
<td>1.2 (-0.8-3.3)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>84-04</td>
<td>5.9 (2.9-8.7)</td>
<td>3.2 (1.9-4.4)</td>
</tr>
</tbody>
</table>

Fire modelling

For both rainforest types the probability of long fire free intervals was low, approaching zero in the decade prior to the photographic end point (Figure 25). The probability of an absence of late dry season fire was consistently much higher and declined at a slower
rate over time. There were also substantial differences in the probability of an absence of fire between the rainforest types as well as between the two different aerial photographic endpoints (Figure 25). For example, the case of the 2004 photography for wet rainforest was unique in that the probability of fire occurrence reduced to almost zero for only two years prior to the photographic endpoint.

![Graph showing probability of no fire over number of years for dry and wet rainforest types.](image)

**Figure 25.** Probability of no fire (full lines) and no late dry season fire (dashed lines) predicted via generalised linear models for varying numbers of years previous to endpoints of aerial photography sampled for all rainforest sites available (N = 46). A comparison is made of dry and wet rainforest types, as well as the different endpoints of photography available.

The incidence of late dry season fires in the year immediately prior to the end of the photographic interval was the best supported model identified by AIC<sub>c</sub> to explain
variation in rate of change of dry rainforests boundaries during the period 1984 to 1991 (Table 14). This model explained about 10% of the deviance and had a very similar amount of support as the null model, which was the next best selected model in the set. The other models in the set had less support and explained a negligible amount of deviance. For wet rainforests, the model including fire frequency based on late dry season fires for five years before the end of the photographic interval had the strongest support based on $AIC_c$ for the same period (Table 14). As with dry rainforests, this model explained only about 10% of the deviance and was closely followed by the null model in terms of relative support.

**Table 14. Modelling results of the effect of fire on the rate of change in rainforest patch areas**

(N=46) between 1984 and 1991. Predictor variables were the total number of fires (Total) and number of late dry season fires (Late) at 1, 2, 5 years prior to 1991. The models are ranked based on the model selection criterion, $AIC_c$. The log(L) is the log-likelihood of the model. K is the number of parameters. $\Delta AIC_c$ is the difference between the model’s $AIC_c$ value and the minimum $AIC_c$ value. $w_i$ is the probability of the model being the best in the candidate set.

<table>
<thead>
<tr>
<th>Rainforest type</th>
<th>Model</th>
<th>log(L)</th>
<th>K</th>
<th>$AIC_c$</th>
<th>$\Delta AIC_c$</th>
<th>$w_i$</th>
<th>% deviance explained</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dry 1y</td>
<td>Late 1y</td>
<td>-56.533</td>
<td>2</td>
<td>117.547</td>
<td>0.000</td>
<td>0.277</td>
<td>9.748</td>
</tr>
<tr>
<td></td>
<td>Null</td>
<td>-57.969</td>
<td>1</td>
<td>118.092</td>
<td>0.546</td>
<td>0.211</td>
<td>-</td>
</tr>
<tr>
<td>Late 2y</td>
<td>-57.036</td>
<td>2</td>
<td>118.553</td>
<td>1.006</td>
<td>0.168</td>
<td>6.446</td>
<td></td>
</tr>
<tr>
<td>Late 5y</td>
<td>-57.502</td>
<td>2</td>
<td>119.484</td>
<td>1.937</td>
<td>0.105</td>
<td>3.282</td>
<td></td>
</tr>
<tr>
<td>Total 1y</td>
<td>-57.595</td>
<td>2</td>
<td>119.671</td>
<td>2.124</td>
<td>0.096</td>
<td>2.636</td>
<td></td>
</tr>
<tr>
<td>Total 2y</td>
<td>-57.867</td>
<td>2</td>
<td>120.215</td>
<td>2.668</td>
<td>0.073</td>
<td>0.725</td>
<td></td>
</tr>
<tr>
<td>Total 5y</td>
<td>-57.908</td>
<td>2</td>
<td>120.295</td>
<td>2.749</td>
<td>0.07</td>
<td>0.439</td>
<td></td>
</tr>
<tr>
<td>Wet 5y</td>
<td>Late 5y</td>
<td>-39.752</td>
<td>2</td>
<td>84.209</td>
<td>0.000</td>
<td>0.252</td>
<td>11.821</td>
</tr>
<tr>
<td></td>
<td>Null</td>
<td>-41.010</td>
<td>1</td>
<td>84.241</td>
<td>0.032</td>
<td>0.248</td>
<td>-</td>
</tr>
<tr>
<td>Total 1y</td>
<td>-40.489</td>
<td>2</td>
<td>85.684</td>
<td>1.475</td>
<td>0.121</td>
<td>5.072</td>
<td></td>
</tr>
<tr>
<td>Late 2y</td>
<td>-40.556</td>
<td>2</td>
<td>85.818</td>
<td>1.609</td>
<td>0.113</td>
<td>4.436</td>
<td></td>
</tr>
<tr>
<td>Total 2y</td>
<td>-40.717</td>
<td>2</td>
<td>86.139</td>
<td>1.93</td>
<td>0.096</td>
<td>2.887</td>
<td></td>
</tr>
<tr>
<td>Late 1y</td>
<td>-40.757</td>
<td>2</td>
<td>86.220</td>
<td>2.011</td>
<td>0.092</td>
<td>2.496</td>
<td></td>
</tr>
<tr>
<td>Total 5y</td>
<td>-40.921</td>
<td>2</td>
<td>86.547</td>
<td>2.338</td>
<td>0.078</td>
<td>0.887</td>
<td></td>
</tr>
</tbody>
</table>

For the photographic interval 1991 to 2004 for dry rainforest, the best selected model was the same as for the preceding photographic interval; including the variable with late dry season fires from one year previous (Table 15). This model explained 13.4% of the deviance and had moderate support compared to the null model based on
AIC$_c$, with an evidence ratio of 2.37. For wet rainforest, the null model was the best selected model based on AIC$_c$ (Table 15). The other models in the set had weak support and explained a negligible amount of the deviance (<4%).

In sum, there was reasonable support for an effect of late dry season fires on the rate of change in rainforest patch size for both rainforest types, however, the level of support was much higher for dry rainforest than for wet rainforest (Tables 14 and 15).

**Table 15. Modelling results of the effect of fire on the rate of change in rainforest patch areas (N=46) between 1991 and 2004.** Predictor variables were the total number of fires (Total) and number of late dry season fires (Late) at 1, 2, 5 and 10 years prior to 2004. The models are ranked based on the model selection criterion, AIC$_c$. The log(L) is the log-likelihood of the model. K is the number of parameters. Δ AIC$_c$ is the difference between the model’s AIC$_c$ value and the minimum AIC$_c$ value. $w_i$ is the probability of the model being the best in the candidate set.

<table>
<thead>
<tr>
<th>Rainforest type</th>
<th>Model</th>
<th>log(L)</th>
<th>K</th>
<th>AIC$_c$</th>
<th>Δ AIC$_c$</th>
<th>$w_i$</th>
<th>% deviance explained</th>
</tr>
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<tr>
<td>Dry</td>
<td>Late 1y</td>
<td>-45.902</td>
<td>2</td>
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<td>0.000</td>
<td>0.329</td>
<td>13.430</td>
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<tr>
<td></td>
<td>Null</td>
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<td>1</td>
<td>97.990</td>
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<td>-</td>
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<tr>
<td></td>
<td>Total 10y</td>
<td>-46.976</td>
<td>2</td>
<td>98.414</td>
<td>2.149</td>
<td>0.113</td>
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</tr>
<tr>
<td></td>
<td>Total 5y</td>
<td>-46.995</td>
<td>2</td>
<td>98.451</td>
<td>2.186</td>
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<tr>
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<td>2</td>
<td>98.966</td>
<td>2.701</td>
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<td>4.664</td>
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The coefficients of the fire variables in each of the best selected models were negative, indicating an inverse relationship between fire frequency and the rate of change in patch size. However, relatively little (maximum 13.4%) of the deviance was explained by the fire variables in the models.
Chapter 5 - A reassessment of the extent and causes of rainforest boundary dynamics

Case studies

The occurrence of fire was highly variable on the rainforest boundaries, both within sites and between sites, with different proportions of the boundary burnt in different years. This was demonstrated by the case studies (Figure 26). For example, in Case Study 1 the majority of fires only burnt a small proportion of the rainforest boundary, while in Case Study 3 many of the fires burnt a large proportion of the boundary.

![Figure 26. Frequency of percentage boundary burnt between 1984 and 2003 for each of the case studies for early dry season fires a) and late dry season fires b). Shaded bars = Case study 1; hatched bars = Case study 2; White bars = Case study 3.](image)

Case Study 1 is a dry rainforest and is located at Ubirr in the north-eastern corner of the study site (Figure 22). The northern and western aspects of the patch consist of a large expanse of open floodplains, while the other aspects face a mixture of rocky outcrops and dense savanna woodland. This patch had the highest rate of contraction of all patches mapped by the author, reducing in area by 22% between 1964 and 2004 (Chapter 2). This contraction occurred primarily in the second half of the study period, with a slight increase in area occurring in the previous two decades (2.4%). The majority of the contraction of the boundary has occurred on the northern and south-western aspects of the boundary which have little topographic fire protection (Figure 27).
Conversely, boundary expansion has occurred primarily on the eastern half of the patch, and particularly where there was fire protection from the rocky outcrops.

![Map of Case Study 1](image)

Figure 27. Map of Case Study 1 which is a dry rainforest patch that contracted over the study period 1964 to 2004. Stable, contracted and expanded parts of the rainforest boundary are shown, as well as rock outcrops which provide topographic fire protection.

Case Study 2 is located in the mid-west of the study site near old Goodparla Station (Figure 22), and lies along a strike ridge that rises more than 60 m above the surrounding lowland plains. This patch increased dramatically in size over the study period by a total of 84.9%. Fires have been very regular with only two years between 1980 and 2003 having an absence of fire. The boundary expansion has occurred primarily on the north-eastern edge of the patch where the ridge may offer some fire protection (Figure 28). The boundary contraction has occurred primarily on the south western side of the patch, which is not protected by the steep escarpment.

The wet rainforest in Case Study 3 is located on a spring in the southern half of the study site, and is adjacent to the Mary River ranger station and a sealed road (Figure 22). This patch increased in size over the study period by 11.9%, with the majority of expansion occurring in the second half of the study period. This patch experienced only two late dry season fires in 1980 and 1984, with the 1980 fire burning the entire boundary (Figure 26). Both boundary expansion and contraction occurred on all aspects
of the patch, with the greatest amounts of expansion occurring on the eastern side of the patch facing the road, and the southern end of the patch along the drainage line (Figure 29).

Figure 28. Map of Case Study 2 which is a dry rainforest on a strike ridge that expanded over the study period 1964 to 2004. Stable, contracted and expanded parts of the rainforest boundary are indicated, as well as topographic contours.

Discussion

The present study was consistent with the inference of Chapter 2 that there has been an overall expansion of rainforest in KNP, with dry rainforests expanding at the fastest rate. However our reassessment shows that the previous estimates based on a limited number of repeat aerial photographs provided an inaccurate estimate of the rate of change. This is because the rainforest boundaries in KNP were found to be subject to rapid fluctuations. Using only the photographic endpoints to quantify the rate of change over
time may be misleading, as the particular ‘snapshots’ chosen will have a large impact on the estimated rate. We therefore conclude that the number of aerial photographic snapshots influences the accuracy of estimates of boundary dynamics.

Figure 29. Map of Case Study 3 which is a relatively stable wet rainforest on a creekline. Stable, contracted and expanded parts of the rainforest boundary are indicated, as well as drainage lines and roads.

The rapid changes in rainforest patch size observed over small time intervals are likely to have been driven by factors that have shown a similar degree of variability over time. The site-specific nature of the observed boundary dynamics also suggests that the small-scale boundary dynamics have not been driven by factors that have varied at a regional scale, such as rainfall. Rather, the pattern of rapidly fluctuating boundaries which are not in step at a regional scale is consistent with the influence of disturbance factors.

A prime candidate in the context of KNP is fire, which is known to have major impacts on rainforest boundaries globally (Furley 1992, Ratter 1992, King et al. 1997, Favier et al. 2004). The high variability in the rainforest boundaries over time demonstrated a clear mismatch between the estimated frequency of fire and the data available (aerial photographic ‘snapshots’) to assess these changes, which presents a difficulty in deriving models of the drivers of change. We have attempted to overcome
this difficulty by only using the fire frequency data from the final few years previous to the end of the aerial photographic interval. Although only a small proportion of the deviance was explained by fire frequency, the modelling of the boundary dynamics supported an effect of late dry season fires on the boundary dynamics, particularly for dry rainforests. The importance of accounting for the difference in the temporal scales of the available data was underscored by the fact that the best predictors of change for dry rainforest were models which only included fire data from one year previous to the aerial photographic endpoint.

While the existence of a temporal mismatch between the aerial photographic intervals and the fire frequency is likely to have contributed to the low deviance explained by these models, there are several other factors that may have also contributed. Firstly, the vulnerability of rainforest patches to fire is very much dependent on the characteristics of the surrounding vegetation, especially understoreys (Russell-Smith and Dunlop 1987), which was not accounted for in these models. For example, the presence of flammable grassy weeds can greatly increase the fire intensity (Rossiter et al. 2003). The characteristics of the topography surrounding the rainforest patch may have also contributed to the variation in the response of the boundary to fire. Additionally, the fire scar mapping to derive the indices of fire frequency is at coarse spatial scale (30 m pixels) and is also prone to large spatial errors (Russell-Smith et al. 1997b, Bowman et al. 2004a).

Further evidence for the effect of fire on the boundary dynamics was provided by the dynamics of the three contrasting rainforest patches with detailed aerial photographic histories which were investigated as case studies. The spatial distribution of the changes on the patch boundaries was consistent with the effect of fire, with the boundary expansion and contraction being strongly related to topographic fire protection. The occurrence of fire was also highly variable on the rainforest boundary, which is consistent with the variable spatial distribution of the observed boundary dynamics. However, the complex nature of the effect of fire was demonstrated by the fact that rapid expansion of the rainforest patches can occur in spite of regular and frequently intense fires, as in Case Study 2.
Exotic weeds may have also influenced the distribution of the boundary dynamics within rainforest patches. This is demonstrated by Case Study 1, which had the highest rate of boundary contraction (-22%) of all 50 patches mapped by the author (Chapter 2). The areas where boundary contraction occurred corresponds to the general distribution of the highly flammable weed *Urochloa mutica* (Forssk.) T.Q.Nguyen which currently occurs along the northern and western sides of the rainforest patch in floodplain areas (Lyndel McLean, pers. comm., Figure 27). The combination of late dry season fires and weeds appears to have lead to very rapid boundary contraction. The detrimental effects of weeds on rainforest boundaries may also have been promoted by positive feedbacks associated with the grass-fire cycle (Rossiter et al. 2003).

The support for an effect of fire on the rate of boundary dynamics is consistent with studies of other tropical forests where the local dynamics of the forest-savanna boundary zone were inferred to be related to fire incidence (Furley et al. 1992, Ratter 1992, King et al. 1997, Favier et al. 2004). It seems that the gradual trend of rainforest expansion in KNP can be reversed at the local scale by the effect of late dry season fires, which in combination with flammable weeds can lead to rapid rainforest contraction. The rapid increase in flammable weed distributions across northern Australia is therefore a significant threat to the future integrity of these rainforests. Weed management at a regional scale remains a priority for land managers.

**Conclusion**

The reassessment of the landscape-wide rate of change supported the occurrence of an overall expansion of rainforest in KNP, and suggested that the rate of change had been largely overestimated in Chapter 2 for dry rainforest. This provides evidence that the number of aerial photographic snapshots used will affect the accuracy of estimates of boundary dynamics. This study also supported an effect of fire on the boundary dynamics, demonstrating that inferences regarding the effect of fire were influenced by the low frequency of aerial photography that is of high spatial resolution and the consequent mismatch with the high frequency of landscape fire that is of much lower spatial resolution. Caution is therefore needed when using data sources such as aerial photography, where there is often inconsistency between the temporal scales of the
photographic intervals and the processes driving the observed changes. Nonetheless, repeat aerial photography remains a powerful means to monitor changes in vegetation boundaries over time. Linking historical aerial photography to high resolution satellite imagery (e.g. Salami et al. 1999), which has much higher acquisition frequencies, may help to overcome this problem.
Chapter 6 - Conclusion


**Synthesis**

This study has used a macroecological approach to assess the extent and causes of rainforest boundary dynamics in KNP between 1964 and 2004. Understanding savanna-forest dynamics is vital as changes in tropical forest boundaries can have major impacts on global climate, biodiversity, and human well-being (Lewis 2006). At the regional scale, an appreciation of the extent and causes of change can also inform management decisions.

Comparison of aerial photography from 1964 to 2004 revealed an overall expansion of rainforest boundaries in KNP (Chapter 2). The biological mechanism for such expansion has been established through detailed field studies of stand structures (Chapter 3, Banfai and Bowman 2005, Russell-Smith et al. 2004b). The observed expansion of rainforest contrasts with previous field based studies at a regional scale, which suggested that rainforest boundaries are contracting in the contemporary environment due to factors such as late dry season fires (Russell-Smith and Bowman 1992). However, the observed rainforest expansion is consistent with other studies in northern Australia based on aerial photography (Bowman et al. 2001, Bowman and Dingle 2006, Brook and Bowman 2006) as well as global trends in vegetation thickening (Archer et al. 1995, Lewis et al. 2004a).

The trend of rainforest expansion in KNP was also supported by the field surveys. These found that those areas in which the aerial photography indicated that rainforest expansion had occurred were associated with a significantly higher abundance of rainforest trees and less grasses, relative to stable savanna areas (Chapter 3). A similar pattern was also observed in the nearby Litchfield National Park (Banfai and Bowman 2005).

Additionally, the field surveys suggested that the floristic composition was similar between newly established rainforest and longer established rainforest, supporting the view that the rainforest boundaries had been highly dynamic at a decadal scale (Chapter 3). This inference was consistent with the assessment of rainforest patches with detailed aerial photographic histories in which high rates of change were
observed over small time intervals (Chapter 5). Modeling of the boundary dynamics within patches suggested that this dynamic has occurred through incremental changes to the boundary rather than eruption of new patches (Chapter 3).

A reassessment of the rate of change based on all available photography supported the overall trend of rainforest expansion, but suggested that the rate of change had been greatly overestimated for dry rainforest (Chapter 5). Caution is therefore required when drawing inferences from widely spaced aerial photographic ‘snapshots’.

The observed changes in rainforest boundaries raised the question of what has driven the changes. Reaching any firm conclusions as to causality was made difficult by (i) the multiple simultaneous shifts in environmental variables and disturbance regimes, (ii) the many complex interactions between the possible drivers of change, and (iii) the lack of detailed historical information. Nonetheless, available data from aerial photography and previous studies allowed the relative strength of evidence for each of the possible hypotheses to be assessed.

The main possible factors that were thought to have contributed to the changes were fire, buffalo, rainfall, atmospheric CO₂ and weeds (Chapter 2). Field surveys of different vegetation transitions in the contemporary environment did not support an ecologically consistent relationship between the boundary dynamics and variables such as ‘time since fire’, weed abundances or buffalo impact (Chapter 3). However, these inferences were limited as the contemporary field surveys were unable to capture the historical impacts that these variables may have had.

The historical impact of buffalo on the rate of change in the rainforest boundaries was supported by the modelling analysis, which provided moderate evidence for an effect of buffalo impact for both rainforest types (Chapter 4). The major increase in the rate of expansion in the period 1984 to 1991 for wet rainforests may also have been a response to the reduction in buffalo impact following the removal of buffalo in the BTEC campaign (Chapter 2). These results are consistent with previous studies suggesting that buffalo have a profound impact on the integrity of rainforest patches in northern Australia (Braithwaite et al. 1984, Russell-Smith and Bowman 1992).

The effect of fire on the rate of boundary dynamics was supported by the large differences in the rate of change between patches that were situated nearby
Chapter 6 - Conclusion

driven geographically, as well as the rapid rates of change observed over small time intervals (Chapters 2 and 5). However, there was a lack of support for an effect of fire frequency on the rate of boundary dynamics in the initial analyses (Chapters 3 and 4), which contrasted with field-based studies suggesting that fire is a key driver of rainforest boundary change (Russell-Smith and Bowman 1992). However, the limited explanatory power of fire may have been due to a mismatch between the temporal scales of the frequent fires and the 20 year photographic intervals used. This was supported by the reassessment of the effect of fire, which suggested that late dry season fires towards the end of the photographic intervals were important determinants of the rate of change (Chapter 5). The effect of fire was further supported by evidence for an effect of topographic fire protection and flammable weeds in the case studies investigated (Chapter 5). The importance of fire in driving the boundary dynamics is consistent with studies of other tropical forests, where the local dynamics of the forest-savanna boundary zone were inferred to be related to fire incidence (Furley et al. 1992, Ratter 1992, King et al. 1997, Favier et al. 2004).

While buffalo and fire appear to have mediated the observed boundary dynamics, they are unable to account for the overall expansion of rainforest that has occurred in KNP. The expansion of rainforest boundaries continued throughout the period of peak buffalo numbers around the 1970s when their impact on rainforest boundaries is likely to have been greatest (Chapter 2). In relation to fire, a reduction in fire frequency is unlikely to explain the observed rainforest expansion, as fires continue to occur at very high frequencies and intensities at the rainforest boundaries (Chapter 4).

The overall expansion of rainforest is likely to have been primarily driven by factors that have varied on a regional scale, such as rainfall and atmospheric CO$_2$. Both these factors have shown increasing trends over the study period, and would have promoted the establishment of rainforest species in the surrounding savanna (Chapter 2). Interactions between fire and these factors may have been critical. For example, the increased growth rates caused by enhanced atmospheric CO$_2$ may have allowed the newly established rainforest trees to escape the ‘fire trap’ posed by regular fires (Chapter 4). This study adds to the emerging evidence for an effect of global change phenomena on tropical forests (Lewis et al. 2004a).
**Management implications**

This project has provided land managers with an appreciation of the extent and causes of landscape scale changes to rainforest boundaries in KNP. The rainforest boundaries have been highly dynamic over the last few decades. A rapid overall expansion of rainforest has occurred, however localised boundary contraction has also been common (Chapter 2). The similarity of newly established rainforest to more stable rainforest, and the lack of environmental limits to change, suggest that the current trend of rainforest expansion will continue if climatic trends and disturbance regimes persist (Chapter 3).

Fire management will be an important determinant of the extent and direction of future changes in rainforest boundaries in KNP. A continuation of the current fire regime is likely to allow the rainforest patches to continue to expand. Fire frequency in itself is not an important determinant of the rate of boundary dynamics, even if these fires occur in the late dry season. However a shift in the fire regime to regular late dry season fires will result in contraction of rainforest where high fuel loads are available on the boundary. Flammable weed management of introduced grass species such as *Pennisetum polystachion* and *Urochloa mutica* at a regional scale therefore remains a priority for land managers. Such weeds were recorded at many of the rainforest patches surveyed (Figure 30).

The rainforest boundary dynamics have also been mediated by buffalo impact (Chapter 3). Buffalo have acted to limit the expansion of rainforest and appear to have caused boundary contraction in extreme cases. The impact of buffalo on rainforest boundaries is likely to be low in the contemporary environment, as the numbers of buffalo in KNP were dramatically reduced between 1980 and 1991 during the Brucellosis and Tuberculosis Eradication Campaign (Skeat et al. 1996). However control of buffalo numbers remains a priority for land managers, as high numbers are still present in some parts of the Park and other areas of northern Australia (Robinson and Whitehead 2003).
Figure 30. Map of rainforest patches studied indicating priorities for management. Patches that are priorities for management are indicated with letters. C indicates that patch has contracted rapidly between 1984 and 2004. For these patches the percentage change over this period is also shown. S indicates patches that are of particularly small size (less than 3 ha). E indicates that exotic flammable weeds were recorded in the plant surveys.
Rainforest patches which have contracted by more than 5% over the last two decades should be given management priority, to limit the effect of threatening processes such as fire, weeds and buffalo (Figure 30). Small rainforest patches should also be given priority as they are also particularly vulnerable to being eliminated (Chapter 3, Figure 30).

The historical dynamics of rainforest boundaries observed in this study, and the potential for future changes driven by shifts in climatic variables, reinforces the view that stability cannot be assumed and conservation values cannot be maintained passively in these environments (Edwards et al. 2003).

Further avenues of research

This study has contributed to our understanding of the extent and dynamics of rainforest in northern Australia. However substantial uncertainty remains as to the extent and dynamics of tropical forests globally (Lewis 2006). The methodology of aerial photographic interpretation developed in this study could be applied to other regions. For example, the dynamics of rainforest patches on the east coast of Australia are poorly understood.

The reassessment of the extent and causes of the observed rainforest dynamics in this study suggested that the number of aerial photographic ‘snapshots’ used can affect the inferences drawn (Chapter 5). Given the high potential value of using aerial photography to understand historical landscape change (Fensham and Fairfax 2002), the paucity of research on this issue indicates a need for further investigation.

This study has focused on the changes to the boundaries of pre-existing rainforest patches. The birth of new patches could also be investigated. This could involve habitat suitability modelling of the occurrence of rainforest, combined with field checking.

Within KNP, the network of aerial photographic and survey plots established in this study provides a baseline for future monitoring of rainforest. Given the biological
and cultural importance of these systems and their susceptibility to rapid rates of change, an adaptive management approach is needed based on monitoring and evaluation of the impact of factors such as fire. Linking aerial photography to satellite imagery (e.g. Salami et al. 1999) may be a more economically viable way for this monitoring to continue in the future.

The occurrence of exotic flammable weeds on the rainforest boundary appears to be an important determinant of the rate of rainforest contraction. Further studies could be undertaken to investigate the impact of fires on rainforest boundaries with and without weeds.

The observed rainforest expansion in KNP was inconsistent with previous field studies such as that by Russell-Smith and Bowman (1992) which had suggested that rainforest boundaries were retreating due to factors such as unfavourable fire regimes. The occurrence of rainforest boundary expansion was also surprising given the high-frequency of landscape fire. Further research is needed in northern Australia to describe the mechanisms by which the expansion of boundaries is occurring (e.g. Russell-Smith et al. 2004b), particularly the survival and structure of rainforest tree recruitment in the surrounding savanna.

The analysis of the drivers of the boundary dynamics in this study was limited by a lack of detailed historical information on disturbance regimes. Useful historical data would include field records of fire and buffalo impacts on the rainforest boundary. Future collection of this data is critical to increasing the statistical power of future analyses, and would allow for the accurate prediction of the boundary dynamics under various potential management regimes.

An alternative approach to investigate the effect of fire would be to simulate fire occurrence on the rainforest boundary using cellular automata modelling (e.g. Favier et al. 2004). The growth of each rainforest patch over time could be simulated, with rules governing the impact of fire on the patch boundaries. Various scenarios of fire frequency and intensity could then be simulated on the rainforest boundaries. Historical modelling would allow assessment of the model predictions compared to the observed boundary dynamics in KNP, and allow the parameters to be calibrated. The model could then be used to assess various hypotheses regarding the potential impact of various future fire
frequencies and intensities on rainforest boundaries. The effect of topographic fire protection, initial patch size and fragmentation on these probabilities could also be investigated.

Developing our knowledge of the impact of fire on rainforest boundaries is critical given the importance of tropical forests to global biodiversity and climate, and the capacity of these systems to respond dramatically to shifts in their environment (Lewis 2006). At the regional scale, this will contribute to management by providing land managers with an appreciation of the potential impact of various fire frequencies and intensities on future changes in rainforest boundaries. This will allow land managers to make informed management decisions regarding the use of fire on rainforest boundaries.
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