



Battling the Elements:

Environmental Determinants of North

Kimberley Rainforests

by

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An aerial view of the north Kimberley in the wet season. The landscape is dominated by savannas, with small rainforest patches predominantly found in topographically sheltered locations (bottom left).

Declaration

This thesis contains no material which has been accepted for the award of any other degree or diploma in any tertiary institution, and to the best of my knowledge and belief, contains no material previously published or written by another person, except where due reference is made in the text of the thesis, nor does the thesis contain any material that infringes copyright.

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Chapter 2 is published:

Ondei S., Prior L.D., Williamson G.J., Vigilante T., and Bowman D.M.J.S. 2017. Water, land, fire, and forest: landscape-level determinants of rainforests in the Australian monsoon tropics. *Ecology and Evolution* 7(5), 1592-1604.

Candidate was the primary author, undertook all remote sensing analyses and most data analyses. The Candidate as well as author 2, 3, and 5 contributed to developing the idea. Author 4 assisted during field work. Authors 4 and 5 contributed to some data analysis. The candidate as well as authors 2, 3, and 4 assisted with refining the text.

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Statement of ethical conduct

The research associated with this thesis abides by the international and Australian codes on human and animal experimentation, the guidelines by the Australian Government's Office of the Gene Technology Regulator and the rulings of the Safety, Ethics and Institutional Biosafety Committees of the University.

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Abstract

Rainforests and savannas are floristically and structurally distinct vegetation types which, within an intermediate rainfall range (1000-2000 mm·year⁻¹), can coexist in the same landscape. In those areas the relative importance of bottom-up factors, like geology and water availability, or top-down controls, such as fire and megaherbivores, as drivers of rainforest distribution is still controversial. In this thesis I aim to assess the influence of environmental factors on rainforest density and boundary change in the Wunambal Gaambera Country (north Kimberley, Western Australia), where rainforests are represented by small patches surrounded by a savanna matrix, and are potentially under threat due to climatic changes, alteration of fire regimes, and the recent introduction of cattle. I then provide management guidelines for the Indigenous land managers, taking into account western science and Aboriginal knowledge.

First, I used a GIS-based approach to investigate variations in rainforest density in the north-western Australian monsoon tropics by blending existing maps, and in the north Kimberley by creating *ex novo* a detailed map of rainforest patches (30-m accuracy). I showed that at a regional scale climatic factors associated with water availability, such as mean annual rainfall and moisture index, were the main drivers of rainforest density. At a landscape scale geology and topography strongly affected rainforest density, supporting the hypothesis that bottom-up controls influence rainforest distribution. Nonetheless, rainforest density was higher in locations characterised by low fire frequency, implying that top-down controls may also be involved.

To further investigate the role of top-down controls, I conducted a natural experiment to test the effects of disturbance on historical rainforest expansion trends and current structure of rainforests and adjacent savannas, using historical aerial photographs and vegetation transects. I selected two study locations characterised by similar climate and geology, to remove the effect of bottom-up controls, but strikingly different levels of disturbance (fire activity and cattle). Disturbance negatively affected rainforest expansion, and was associated with sharp rainforest-savanna boundaries. In

disturbance-free areas savannas displayed abundance of rainforest elements, with gradual transition from rainforest to savanna.

Despite the importance of fire in determining rainforest distribution, growing evidence shows that some rainforest species are able to survive a single fire event. To test this hypothesis, I compared survival rate and resprouting strategies of rainforest saplings burnt with an experimental treatment that mimicked a low-intensity savanna fire with savanna saplings burnt by an ambient early dry season fire. The results suggested that, despite low stem survival rates that restricted resprouting to basal buds, a proportion of the rainforest species found in the north Kimberley is able to survive a fire event. Basal resprouting however negatively affects growth rates, yet this does not necessarily prevent rainforest expansion under low-intensity fire regimes.

Finally, I tested whether the fire management currently in place is leading to a positive change in fire regimes. I also examined the implications of vegetation management for the local fauna, with particular focus on threatened species, by using camera traps to record animal presence across the vegetation transects described above. Fire management successfully led to a shift from late dry season to early dry season fires, which are typically less intense. However, both high fire frequencies and unmanaged cattle had a negative effect on native animal distribution. Fire management should then focus on reducing fire frequency in areas exposed to prevailing wildfires through planned burning, while of in fire-protected areas a relatively low frequency of patchy prescribed fires would suffice to keep the sizes of single fuel age patches at manageable levels.

In conclusion, I found that disturbance regimes have a strong influence on rainforest distribution, which is determined by the interplay of both bottom-up and top-down controls. Land management should thus be adaptive, and evolve based on changing environmental conditions between different locations and in time.

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Chapter 1

General introduction

1.1 RAINFOREST AND SAVANNA DISTRIBUTION

Globally, the geographic distribution of rainforests is predominantly determined by climate. Rainforests are generally found in high precipitation, warm regions; where annual rainfall is lower, they are replaced by savannas (Whittaker, 1975). However, it has been observed that the current global distribution of rainforests does not entirely reflect their potential extent (Bond, 2005). Extensive tropical regions where, based solely on climate, rainforests should be dominant, are in fact covered by savannas, especially in South America and Africa (Bond and Keeley, 2005). When mean annual rainfall falls within an intermediate range (1000-2000 mm/year) and rainfall seasonality is mild, savannas can coexist with rainforests under the same climate and can even be the dominant vegetation type (Sankaran *et al.*, 2005, Staver *et al.*, 2011b). An example is represented by the seasonal tropics, composed of a mosaic of savanna and closed-canopy rainforest. In these environments, rainforests and savannas are described as alternative stable states, since they tend to coexist while maintaining the contrasting different floristic composition and vegetation structure that characterised them: rainforests typically occur in rarely burnt environments, where dense canopy cover and the consequent lack of grass prevents flammable fuel accumulation (Ratnam *et al.*, 2011, Little *et al.*, 2012); conversely, savannas are fire-prone environments defined by a continuous grass layer and variable tree cover (Whittaker, 1975). According to the Alternative Stable State theory, when different vegetation types coexist in the same environment they are maintained in a stable state by a complex network of feedbacks involving climatic and local factors. The interactions between factors and vegetation produce strong biological feedbacks (Beckage *et al.*, 2009, Staver *et al.*, 2011b, Bowman *et al.*, 2015), which tend to maintain the existing rainforest-savanna pattern (Sankaran *et al.*, 2005). Disruption of these feedback networks can shift vegetation from one type to the other (Murphy and Bowman, 2012, Hoffmann *et al.*, 2012a). Support for the hypothesis that rainforest and savannas represent alternative stable states comes from a range of field and remote sensing observations. Analyses of satellite imagery have detected bimodality in canopy cover distribution, with peaks corresponding to a savanna or rainforest state and intermediate states scarce or non-existing (Hirota *et al.*, 2011, Staver *et al.*, 2011b). Field data have

also highlighted the presence of sharp structural and climatic transitions across the rainforest-savanna boundary (Dantas *et al.*, 2013a, Bowman, 1992).

1.2 FACTORS INFLUENCING RAINFOREST-SAVANNA DYNAMICS

1.2.1 Bottom-up factors: resources

Factors modulating growth rates strongly influence the ability of a rainforest to establish (Murphy and Bowman, 2012). A primary factor influencing plant growth is water availability, which is mostly determined by climate, particularly mean annual rainfall and rainfall seasonality. In addition, at a landscape scale, soil permeability and topography also affect the proportion of water retained in the soil and available for plants (Ash, 1988). Palynological and isotopic analyses showed that savanna and rainforest have shifted in the palaeoecological past in response to climate changes. For example, pollen and carbon isotopes data from Gabonese lakes highlighted a strong correlation between changes in rainforest structure and climatic fluctuations (Ngomanda *et al.*, 2007). In the Congo, carbon isotope analyses identified fast rainforest encroachment into savannas, with the latter predicted to disappear from the area within the next 1000-2000 years, should the current conditions persist (Schwartz *et al.*, 1996). In the Amazon basin, pollen data supported the association between wetting trends and rainforest expansion (Behling and Hooghiemstra, 2000). Reduced precipitation during the Early-Mid-Holocene caused significant shifts in rainforest-savanna boundaries, with rainforest contraction (Desjardins *et al.*, 1996), while during the Late Holocene increased precipitation reversed this trend and rainforests expanded once again (Mayle *et al.*, 2004).

Enhanced levels of atmospheric CO₂ are also thought to favour woody plant dominance (Higgins and Scheiter, 2012). CO₂ enhances trees' growth rate, allowing them to recover fast after a disturbance, and increases the carbon assimilation in plants possessing the C3 pathway (which includes most rainforest woody plants), while

species using C4 pathway (including most savanna grasses) are less affected (Bond and Midgley, 2000). However, this hypothesis is still controversial. Recent studies failed to identify a link between CO₂ levels and plant growth rates (e.g. van der Sleen *et al.*, 2015, Manea and Leishman, 2015, Silva and Anand, 2013), although some found that CO₂ enhances water use efficiency in plants, reducing transpiration by shallow-rooted species and increasing percolation of soil water to deeper soil layers, favouring establishment and persistence of deep-rooted woody plants (van der Sleen *et al.*, 2015). Elevated levels of CO₂ have also been associated with faster post-fire resprouting in savanna trees (Hoffmann *et al.*, 2000).

Soil fertility is often a limiting growth factor in rainforests (Silva *et al.*, 2013), and fertility thresholds have been detected across rainforest-savanna boundaries (Dantas *et al.*, 2013a). It has been hypothesised that soil fertility is the main driver, together with climate, of rainforest distribution, and other factors such as fire activity are a consequence of the vegetation type established rather than one of its drivers (Veenendaal *et al.*, 2015, Lloyd and Veenendaal, 2016). However, nutrient stock analyses showed that most savannas are able to sustain rainforests (Bond, 2010), despite their low levels of P and Ca (Silva *et al.*, 2013) and rainforests have shown to be able to colonise adjacent savannas (e.g. Bowman *et al.*, 2001, Russell-Smith *et al.*, 2004). It is also important to note that soil fertility is locally subject to the dynamic interaction between vegetation and abiotic factors (Pellegrini, 2015). For example, nutrient input via litterfall is higher in rainforests than in savannas, due to the greater canopy productivity (Paiva *et al.*, 2015), which results in soil enrichment over time and contributes to sharpening the differences between rainforests and savannas.

1.2.2 *Top-down factors: disturbance*

Recognised as a natural element of many ecosystems (Bond and Keeley, 2005), fire is ascribed as a crucial factor determining the presence of either rainforests or savannas (Dantas *et al.*, 2016, Staver *et al.*, 2011b, Pausas, 2015a). Savanna species, adapted to a fire-prone environment, possess a suite of traits associated with fire resistance, such as thick bark (Lawes *et al.*, 2011c, Pausas, 2015b) and the ability to resprout after fire from aerial buds (Clarke *et al.*, 2013). Conversely, rainforests species are characterised

by a thinner bark (Lawes *et al.*, 2013), which leads to higher rates of top-kill after a fire (Hoffmann *et al.*, 2009). As a consequence of top-kill, rainforest trees require longer fire-free intervals to reach the threshold height that allows them to escape the ‘fire trap’ by accumulating enough bark to avoid stem death during fire (Hoffmann *et al.*, 2012a). Once a rainforest has had the chance to establish, the lack of grasses in the understorey substantially limits the amount and ignitability of surface fuels, and thus the capacity of a fire to spread in the rainforest (Just *et al.*, 2015). Alterations in fire regimes, both natural and anthropogenic, can consequently shift the balance toward one vegetation state or the other (Murphy and Bowman, 2012). An alternative view is that fire is, rather than a driver of vegetation, a consequence of it (Veenendaal *et al.*, 2015), a ‘sharpening factor’ reinforcing soil-driven mechanisms at best (Lloyd and Veenendaal, 2016).

Megaherbivores, both grazers and browsers, are also thought to have an impact on rainforest-savanna dynamics. Browser activity prevents large trees establishment (Staver and Bond, 2014), with a consequent reduction in tree density in favour of a grass layer (Staver *et al.*, 2009), leading to more extensive and less patchy fires (Waldram *et al.*, 2007). Conversely, the presence of grazers reduces fuel load, decreasing fire intensity and facilitating increases in woody cover (Van Langevelde *et al.*, 2003) as well as fire heterogeneity (Holdo *et al.*, 2009, Kerby *et al.*, 2006). Large fires restrain heavy grazing, thereby maintaining the balance between graze-tolerant and graze-intolerant grasses (Archibald *et al.*, 2005). The effects of pyric-herbivory feedbacks on vegetation are scale-dependent (Kerby *et al.*, 2006). Grazer-vegetation models of African savannas detected minor effect of grazers on distribution of biomes at a continental scale (Pachzelt *et al.*, 2015), whereas in the United States the effects of fire-herbivore interactions were scale-dependent (Collins and Smith, 2006). Both browsers and grazers can also have a direct negative effect on rainforests through trampling and wallowing on moist soil (Russell-Smith and Bowman, 1992).

1.2.3 Human management

Land use and management have a strong influence on rainforest distribution. Models indicated that tropical rainforests are amongst the habitats most affected by land use

changes during this century, with the conversion of rainforests to grasslands resulting in substantial loss of tree species and associated animals (Sala *et al.*, 2000). Nonetheless, appropriate rainforest management can have positive effects on rainforest distribution and biodiversity. Many rainforests across the globe have in fact been managed by Indigenous people for generations and their current conditions are, in many cases, the result of centuries, if not millennia, of human interaction with those environments (Ellen, 1998). Traditional rainforest management can occur at different levels. A simple approach consists of intentionally planting useful species, as practiced by the rainforest dwellers in the Amazon (Bennett, 1992); over time even small groups of hunter-gatherers can cause habitat changes through dropping seeds of species collected for food (Ellen, 1998). Complex management systems can involve more substantial habitat changes. The Kayapo Indians of Brazil, for example, are known to preserve and enhance rainforest biodiversity by creating ‘artificial’ forest islands, *apete*, containing a high number of medicinal plants, palms and vines that produce drinking water (Gadgil *et al.*, 1993). Indigenous rainforest management can also include practices aimed to protect rainforests from potential threats. In northern Australia, for instance, Traditional Aboriginal rainforest management involves the skilful use of fire to reduce fuel load near rainforest patches, preventing potential wildfires from damaging the fire-sensitive rainforests (Russell-Smith *et al.*, 1997, Mangglamarra *et al.*, 1991).

1.3 THE STRANGE CASE OF AUSTRALIA

Satellite-based analyses did not detect bimodality in tree cover in Australia, due to the absence of high tree cover rather than due to the presence of intermediate states (Staver *et al.*, 2011b). Rainforest distribution is also more restricted in Australian tropical regions when compared with South American or African regions with similar rainfall (Hirota *et al.*, 2011). This is possibly caused by climatic factors, such as the long duration of the dry season (Staver *et al.*, 2011b), or biogeographic factors, like the presence of eucalypts in the Australian savannas, which are believed to allow fire to

invade rainforests (Murphy and Bowman, 2012). The relative importance of local factors may then be higher in Australia, to the point of partially overriding the influence of climate. Nonetheless, rainforest expansion (Bowman *et al.*, 2010a, Banfai and Bowman, 2007, Wigley *et al.*, 2010) and savanna thickening (Fensham and Fairfax, 2003) have been documented in the Australian tropics, apparently associated with wetting trends, together with raised CO₂ levels.

In Australia, even the definition of ‘rainforest’ is controversial. Several attempts have been made to clearly define them, based either on canopy cover, species composition, light environment, fire susceptibility, or even on what they are not (Bowman, 2000). Defining these environments is challenging because Australian rainforests include a broad variety of environments with different floristic and structural characteristics, and they are usually classified based on the climatic regimes under which they occur (Fig. 1.1). The term ‘rainforest’ itself, rather than ‘rain forest’, was adopted to avoid a definition based solely on precipitation (Baur, 1968), since Australian rainforests can be found in areas with mean annual precipitation as low as 600 mm · year⁻¹ (Bowman, 2000). Lynch and Nelder (2000) proposed a definition of rainforest as environments with above ground biomass dominated by trees, the tallest of which are unable to regenerate in undisturbed closed canopy. However, some giant eucalypt species, such as *Eucalyptus regnans* or *Eucalyptus grandis*, have been found to be common elements of rainforests in their early stages and have several functional traits in common with rainforest species (Tng *et al.*, 2013). These observations suggest that, despite their dependence on fire for regeneration, giant eucalypts should be considered rainforest pioneers (Tng *et al.*, 2012b). Because of the arbitrarily chosen climatic and structural parameters adopted to define rainforests, Bowman (2001) recommended continuing to use the term *ad hoc*, requiring scientists to justify their definition. For the purpose of this study, I defined ‘rainforest’ as closed canopy vegetation, not dominated by eucalypts (*Eucalyptus* spp. and *Corymbia* spp.) or paperbark (*Melaleuca* spp.) species (Russell-Smith, 1991). For the classification of individual species as rainforest elements, I relied on the floristic classification performed by Kenneally *et al.* (1991).

1.3.1 Australian monsoon rainforests

The Australian monsoon tropics are an example of the coexistence of rainforests and savannas in a vegetation mosaic. In these landscapes, mostly dominated by savannas, rainforests are found as small patches of closed canopy vegetation often confined to specific landscape settings and occupying a small portion of their potential climatic range (Bowman, 2000). Rainforest expansion has also been detected in the Australian monsoon tropics during the last decades (Banfai and Bowman, 2006, Brook and Bowman, 2006), despite the recent increase in fire frequency and intensity (Russell-Smith *et al.*, 2010a). In spite of their limited extent, they substantially contribute to floristic biodiversity (Russell-Smith, 1991) and represent important refugia and food sources for animal species (Woinarski *et al.*, 2004). In this study, I investigated rainforest-savanna dynamics in the Wunambal Gaambera Country (north Kimberley, Western Australia), the traditional country of the Wunambal Gaambera Aboriginal people. The rainforests found in this area, located toward the driest climatic end of the Australian tropical rainforest range (Fig. 1.1; Bowman, 2000), are classified as monsoon rainforests, ranging from evergreen wet forests to dry semi-deciduous vine thickets (Russell-Smith, 1991). These rainforests are of great ecological and cultural value (McKenzie *et al.*, 2009, Wunambal Gaambera Aboriginal Corporation, 2010). There is concern that climatic changes, alteration of fire regimes, and the recent introduction of cattle may pose a threat to these rainforests. In this study, I investigated the relative importance of bottom-up and top-down factors, in order to clarify the impact of disturbance on rainforest distribution and boundary dynamics and evaluate management options to protect rainforests in the light of regional and global environmental changes.

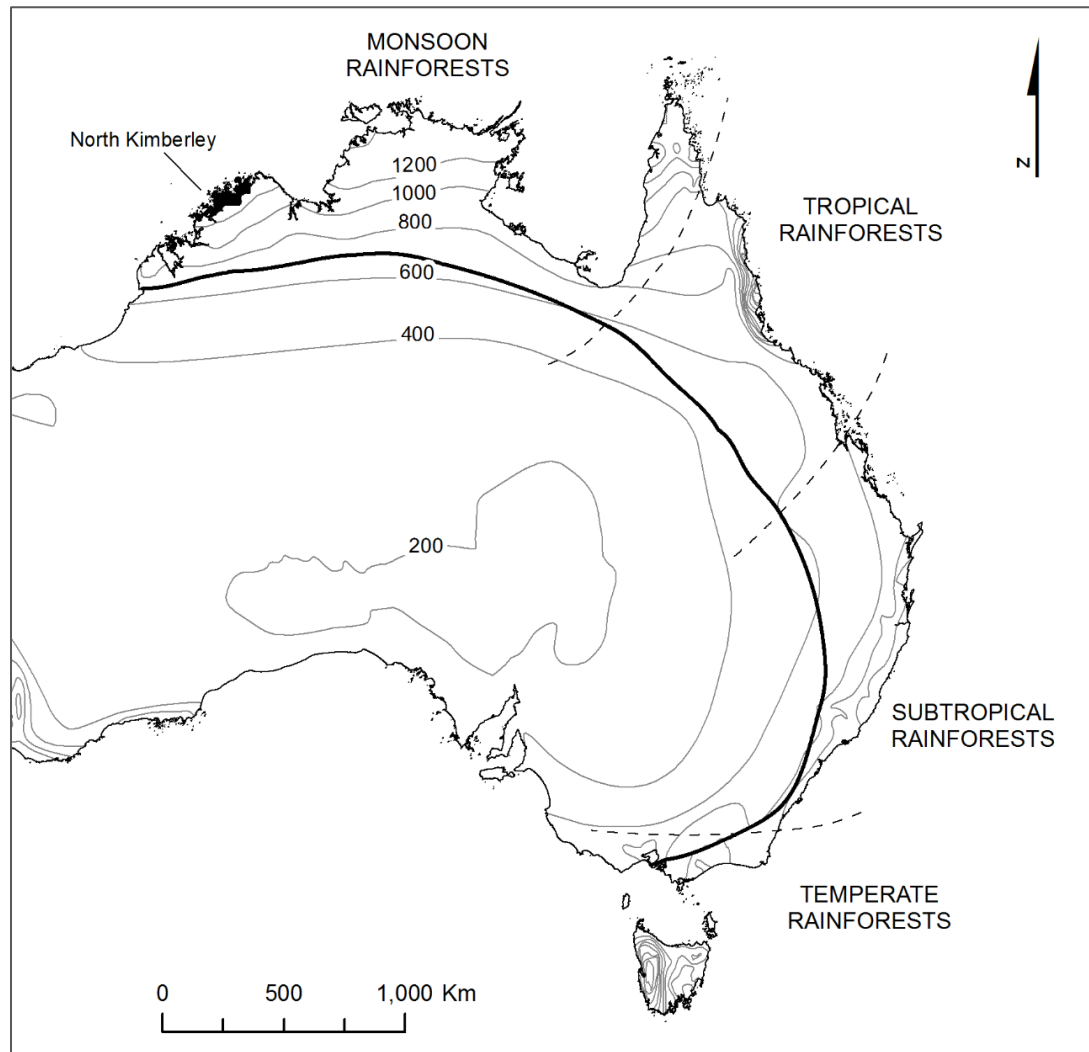


Figure 1.1 Approximate climatic range of rainforests in Australia (bold line) and location of the north Kimberley (Western Australia), situated toward the driest end of the monsoon rainforest climatic range (adapted from Bowman *et al.*, 2000).

This study was performed in collaboration with the Wunambal Gaambera Aboriginal Corporation and was covered by a cooperative research agreement. The project included participatory research with Unguu Rangers and Traditional Owners were involved in field work planning and implementation and the results of this thesis will inform future management and monitoring of monsoon rainforests (Wulo) in the Wunambal Gaambera Country.

1.4 THESIS OUTLINE

1.4.1 Aims

The aims of this project were to:

- Investigate the climatic factors influencing rainforest density at a sub-continental scale and the local factors affecting it at a regional scale in the Australian monsoon tropics;
- Quantify the historical rainforest expansion rates and associate them with disturbance, current vegetation structure and rainforest-savanna boundary dynamics;
- Test the importance of fire intensity by assessing ability of rainforest saplings to survive and regenerate after a low-intensity fire;
- Evaluate the implications of vegetation structure and disturbance levels for the local fauna, and the effectiveness of local management plans in reducing disturbance.

1.4.2 Overview of chapters

My thesis consists of 6 chapters. The experimental chapters of this thesis (Chapters 2 – 5) have been written in paper style and Chapters 2 – 4 are published or in the process of publication. Chapter 2 and Chapter 4 have been published as peer-reviewed articles (Ondei *et al.*, 2016b, 2017 attached in Appendices 4-5). Chapter 3 has been submitted and is currently in review (Ondei *et al.*, 2016a). In all cases I was lead author, and developed and conducted the research under the guidance of my supervisors. Due to the paper style structure of this thesis, some repetition of concepts and ideas was unavoidable, particularly in the Introduction and Study area sections. The published or in review papers have been reformatted (including figure and table numbering), and the references have been combined into a single section.

Prior to this study, the exact distribution of rainforest patches in the north Kimberley was unknown, and so was the importance of different environmental factors as drivers of this distribution. In Chapter 2, I adopted a sub-continental scale approach to investigate the correlations between rainforest density and climatic factors in the north-western Australian monsoon tropics. I then assessed the importance of local

factors, such as geology, topography, and fire activity through a regional-scale analysis, based on a highly detailed map of the north Kimberley rainforests created *ex novo*.

During the last decades, rainforest expansion has been detected in several areas of the Australian tropics. Is this phenomenon also occurring in the small patches of monsoon rainforests of the north Kimberley? Do fire and cattle influence expansion rates? In Chapter 3 I combined the analysis of historical aerial photographs and vegetation transects to answer these questions through a natural experiment.

Despite their lack of protection, some rainforest species are thought to be able to regenerate after a low-intensity fire. To test this hypothesis, in Chapter 4 I undertook a burning experiment by burning rainforest saplings, all found on a rainforest edge, with a gas burner, controlling for duration and intensity to replicate the intensity of a mild savanna fire. One year later I assessed survival rates and resprouting strategies and compared them with those recorded for savanna species.

In Chapter 5 I addressed the management implications of my results. To do so, I identify the most vulnerable rainforest patches, based on their characteristics and fire activity, and analyse the effectiveness of the recently reintroduced Aboriginal-led burning program in proximity of rainforests. To provide a broader ecological view I also performed an exploratory study to associate vegetation and disturbance with relative differences in faunal abundance, with particular attention to small/medium mammals, currently declining in the Australian tropics.

In Chapter 6 I summarised the key findings and discuss their relevance to my chief question of whether monsoon rainforest distribution is influenced by disturbance, in particular fire activity. I then placed the results in the context of global rainforest distribution and management. Finally, I suggested possible directions for future research

Chapter 2

Water, land, fire and forest: multi-scale determinants of rainforests in the Australian monsoon tropics

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2.1 ABSTRACT

The small rainforest fragments found in savanna landscapes are powerful, yet often overlooked, model systems to understand the controls of these contrasting ecosystems. We analysed the relative effect of climatic variables on rainforest density at a sub-continental level, and employed high-resolution, regional-level analyses, to assess the importance of landscape settings and fire activity in determining rainforest density in a frequently burnt Australian savanna landscape. Estimates of rainforest density ($\text{ha} \cdot \text{km}^{-2}$) across the Northern Territory and Western Australia, derived from pre-existing maps, were used to calculate the correlations between rainforest density and climatic variables. A detailed map of the north Kimberley (Western Australia) rainforests was generated and analysed to determine the importance of geology and topography in controlling rainforests, and to contrast rainforest density on frequently burnt mainland and nearby islands. In the north-western Australian tropics rainforest density was positively correlated with rainfall and moisture index, and negatively correlated with potential evapotranspiration. At a regional scale, rainforests showed preference for complex topographic positions and more fertile geology. Compared to mainland areas, islands had significantly lower fire activity, with no differences between terrain types. They also displayed substantially higher rainforest density, even on level terrain where geomorphological processes do not concentrate nutrients or water. Our multi-scale approach corroborates previous studies that suggest moist climate, infrequent fires, and geology are important stabilizing factors that allow rainforest fragments to persist in savanna landscapes. These factors need to be incorporated in models to predict the future extent of savannas and rainforests under climate change.

2.2 INTRODUCTION

The global extent of closed canopy tropical rainforests and savannas is determined by climate, especially mean annual precipitation (Lehmann *et al.*, 2014, Murphy and Bowman, 2012). However, at around $1000\text{--}2000 \text{ mm} \cdot \text{year}^{-1}$ rainforest and savanna form vegetation mosaics (Hirota *et al.*, 2011, Staver *et al.*, 2011a, Staver *et al.*, 2011b).

Tropical savannas are characterised by a low tree cover and a high biomass of C4 grasses, which supports frequent fires in the dry season (Bond *et al.*, 2005, Hoffmann *et al.*, 2012b). By contrast tropical rainforests have a species rich tree flora that form dense canopies, little grass and infrequent fire activity.

The mechanisms that control patterning of rainforest and savanna mosaics are disputed, with debate polarised between the importance of fire and soils. One view is that edaphic factors like soil nutrients are the main control of rainforest - savanna mosaics, and fire is not a cause but rather a consequence of vegetation patterns (Lloyd *et al.*, 2008, Veenendaal *et al.*, 2015). Although savanna soils may have sufficient nutrient stocks to support rainforest trees (Bond, 2010, Vourlitis *et al.*, 2015), rainforests are generally found on more nutrient-rich soils compared with savannas (Dantas *et al.*, 2013a, Silva *et al.*, 2013). Infertile savanna soils are known to limit expansion of rainforest (Silva *et al.*, 2013), while deeper and more fertile substrates allow rainforest to grow in drier climates (known as 'edaphic compensation'; Ash, 1988, Webb, 1968). However, it is not clear whether these patterns result from a direct edaphic effect or from local feedbacks. Soils underneath rainforests are often more rich in nutrients, compared with savannas, regardless of the inherent fertility of soil parent material (Dantas *et al.*, 2013a, Silva *et al.*, 2013), because of nutrient acquisition and cycling (Silva *et al.*, 2008). Tree canopy cover and canopy productivity increase soil nutrient content (Paiva *et al.*, 2015), particularly N concentration and availability (Schmidt and Stewart, 2003). Consequently, there are substantial practical difficulties in making ecologically meaningful measurements of soil fertility variation, particularly across rainforest ecotones, where forest boundaries wax and wane (Silva *et al.*, 2013, Warman *et al.*, 2013).

The alternative view is that rainforest and savanna are 'bi-stable' in regions with intermediate productivity, and the realisation of vegetation depends on landscape fire history (Bond *et al.*, 2005, Dantas *et al.*, 2016, Hoffmann *et al.*, 2012a, Murphy and Bowman, 2012, Staver *et al.*, 2011a, Warman and Moles, 2009). This view is based on alternative stable state (ASS) theory, whereby stabilising feedbacks hold rainforest or savanna in specific 'basins of attraction' (Hirota *et al.*, 2011). Resolving the role of

edaphic factors in controlling rainforest boundaries directly or indirectly via feedbacks is complex and demands multiple lines of evidence, including direct measurements of soils, modelling and experiments (Bowman *et al.*, 2015). Analysis of remote sensing estimates of canopy cover at a global scale has been presented as evidence for the bimodal distribution of rainforests and savannas (Staver *et al.*, 2011b). It has been argued that the intensity of the bimodality may be a statistical artefact associated with the use of regression tree (CART) analyses, which impose discontinuities in satellite tree-cover estimates (Hanan *et al.*, 2014, Staver and Hansen, 2015, Hanan *et al.*, 2015), although global canopy height analyses, based on products derived from LiDAR measurements, confirmed the bimodality detected through satellite data (Xu *et al.*, 2016).

Regional-level analyses based on remote sensing have been employed in studies investigating the environmental controls of different types of vegetation (e.g., Dahlin *et al.*, 2014, Fensham *et al.*, 2005, Murphy *et al.*, 2010). However, there has been surprisingly limited analysis of rainforest-savanna mosaics at a regional level. In an important pioneering study, Ash (1988) synthesised data from topographic maps, aerial photography and field data to create a model of the environmental controls of rainforests and savanna vegetation in the wet tropics of North Queensland (Australia), to assess the relationship between rainforest location and environmental characteristics. Ash (1988) concluded that the distribution of rainforest boundaries can be empirically predicted based on water availability and topography, and substrate fertility might allow rainforests to expand into otherwise unfavourable environments. This research was supported by Fensham (1995), who employed aerial photography and satellite imagery to investigate the relation between dry rainforest and environmental variables in North Queensland. To the best of our knowledge, there are no other map-based analyses of rainforest-savanna mosaics at a regional scale anywhere else in the tropics. These rainforest patches are known to be biodiverse and important for a broad cross section of fauna (e.g. Price, 2006, Tutin *et al.*, 1997), yet they have been poorly researched compared with the more extensive wet rainforests (Sánchez-Azofeifa *et al.*, 2005).

North-western Australia is an attractive model system because it spans a wide rainfall gradient at the driest extreme of the Australian tropical rainforest estate (Bowman 2000). The global analysis of Staver et al. (2011b) suggests the region is deterministically savanna; yet tiny patches of rainforest exist, embedded in the savanna matrix. These environments rainforests are more exposed to fire due to their higher boundary/core ratio, nonetheless, in some locations rainforest expansion has occurred (Banfai and Bowman, 2006, Bowman et al., 2001, Clayton-Greene and Beard, 1985). Studies from northern Australia and elsewhere in the tropics have identified the importance of landscape setting in determining rainforest distribution in areas subject to high fire activity. For example, rainforests can be more abundant on islands that have lower fire activity than adjacent mainland savannas (Clayton-Greene and Beard, 1985). Rainforests can also be confined to steep gullies or valleys (Bowman, 2000, Ibanez et al., 2013a, Warman and Moles, 2009) because of the fire protection they provide (Murphy and Bowman, 2012), although additional effects of higher nutrient and water availability could also be important (Ash, 1988).

We employed a macroecological approach to determine the effect of climatic and geomorphological factors (topography and geology) on rainforest abundance at a large spatial scale. Geology was used as a proxy for the nutrient stock provided by the parent material, to exclude the effect of vegetation on soil fertility. To assess the correlations between climate and rainforest distribution in the entire north-western Australian monsoon tropics, we analysed existing sub-continental scale vegetation maps. We then assessed the importance of topography and geology at a regional scale, since the effects of these factors on rainforest distribution are detectable at this scale, compared with climate (Murphy and Bowman, 2012). To do so, we generated a detailed map of rainforests in the north Kimberley (Western Australia), which is characterised by a limited rainfall range (200mm · year⁻¹), and a variety of geologies and topographic settings. Within this region we undertook a local-scale ‘natural experiment’, comparing the influence of topography and fire activity on rainforest density on mainland and adjacent islands with similar rainfall, geology and distance from the coastline. We addressed the following hypotheses:

- At a sub-continental scale, factors associated with water availability are the main climatic drivers determining rainforest density;
- At a regional scale, topography and geology affect rainforest distribution;
- At a local scale, the importance of insularity and topography is directly related to fire activity. In locations with high fire activity (mainland), rainforests are predominantly confined to fire-sheltered settings, whereas in areas with lower fire activity (islands), rainforests will also be able to grow in more exposed settings.

Collectively this study investigates the drivers of rainforest distribution across multiple spatial scales in northern Australia, thereby illuminating the capacity for climate change and fire management to affect rainforest coverage and providing insights for both theoretical ecology and applied land management.

2.3 METHODS

2.3.1 Geographic context

The Australian monsoon tropics are characterised by a pronounced wet and dry season associated with the Australian summer monsoon (Bowman *et al.*, 2010b). This region includes the whole of northern Australia except the Australian wet tropics in North Queensland (Bowman, 2000) (Fig. 2.1a). In contrast to the wet tropics, where tropical rainforests dominate, the monsoon tropics support vast eucalypt savannas (Bowman, 2000) (Fig. 2.2a, c). Embedded in these savannas are very small patches of monsoon tropical rainforest, ranging from a few trees to 100 ha in area (McKenzie *et al.*, 1991). These rainforests have floristic and biogeographic affinities with wet tropical rainforests in both Asia and Australia. They have been intensively studied given their unusual biogeography and ecology, particularly their ability to persist in a highly flammable tropical savanna environment (Bowman, 2000). Some rainforests are known to grow on aquifers (Kenneally *et al.*, 1991; Russell-Smith, 1991), which insulate them from regional climate, but our mapping could not differentiate these

types from the more widespread and drought adapted rainforests (Bowman et al., 1991, Russell-Smith, 1991). The locus of the sub-continental study was the Australian monsoon tropics west of the Carpentarian Gap biogeographic divide, which separates the biota of the Northern Territory and Western Australia from Cape York Peninsula (Bowman et al., 2010b). Annual rainfall in this area varies from approximately 1900 mm in the north east to 700 mm in the south west (Fig. 2.1c), that would be expected to exert a strong influence on the abundance of rainforest. This analysis was made possible by combining vegetation maps produced by the Northern Territory and Western Australian government land management agencies, noting that the border between the two states broadly aligns with the Ord Arid Intrusion, a major biogeographic boundary that separates the biota of the Kimberley region of Western Australia from that of the ‘Top End’ of the Northern Territory (Fig. 2.1; Bowman et al., 2010b; Eldridge et al., 2011), and that likely affects rainforest species diversity.

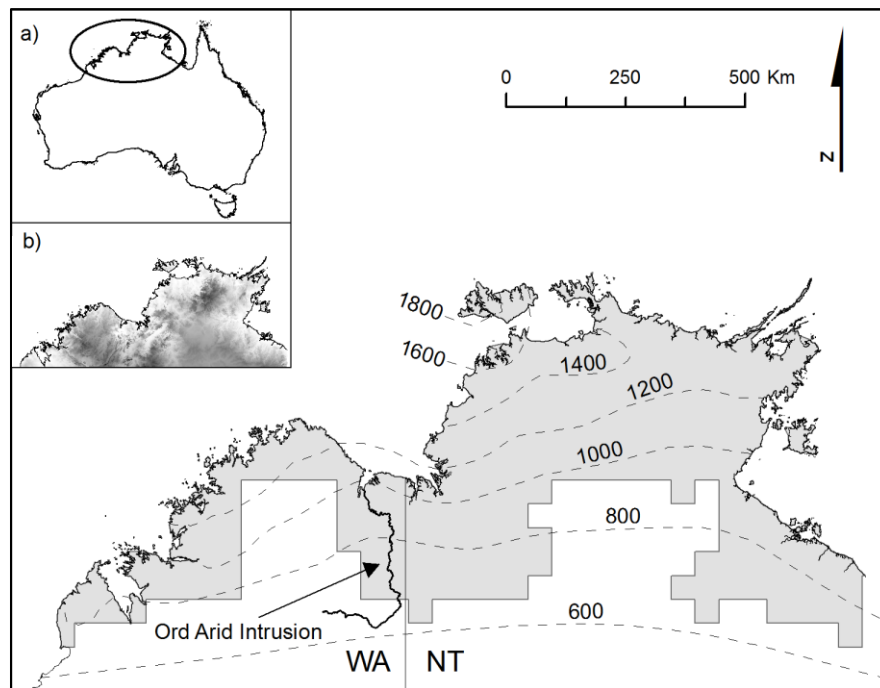


Figure 2.1 The monsoon rainforest domain in north-western Australia. The grey area represents the monsoon rainforest domain in the north of Western Australia (WA; Kimber et al. 1991) and the Northern Territory (NT). The Ord Arid Intrusion, the main biogeographic barrier between the two states, is indicated. Dashed lines indicate rainfall isohyets (mm). The insets show (a) the study area within Australia and (b) elevation (minimum, 0 m, white; maximum, 960 m, black).

In addition to this coarse-scale sub-continental study, we undertook a more detailed analysis of the rainforests to the west of the Ord Arid Intrusion. This region, located at the extreme end of the precipitation gradient where rainforest occurs in northern Australia, has limited spatial variability in rainfall (1200 to 1400 mm), which allowed us to identify ecological factors, other than precipitation, that shape rainforest distribution. This was based on fine-scale mapping of the traditional lands of the Wunambal Gaambera people, henceforth called the Wunambal Gaambera Country.

The Wunambal Gaambera Country occupies an area of 9144 km², dominated by biodiverse tropical savannas occurring on deeply weathered sandstones and basaltic base rocks of Precambrian age, often capped by Cainozoic laterites. In this region average annual rainfall occurs almost entirely during the summer wet season (November to April), while the rest of the year is almost rain-free (Beard, 1976). The landscapes are shaped by geology; the dominant substrates are infertile sandstone, where the Holocene sea-level rise has created rugged coastlines, and the moderately fertile basalt country, characterised by gentle slopes and hills (Speck *et al.*, 1960, Beard, 1979) (Fig. 2.2b). The vegetation is predominantly eucalypt savanna. *Eucalyptus tetradonta* – *E. miniata* savannas are found on the laterite mesas and hills, while *E. tectifera* – *E. grandifolia* savannas are common on deeper, clay soils on plains. Small patches of semi-deciduous rainforests are interspersed in the savanna (Fig. 2.2c, e), typically located in fire-protected locations (Vigilante *et al.*, 2004).

Fire regimes in the north Kimberley are strongly shaped by anthropogenic ignitions, and have been for over 40,000 years (O'Connor, 1995). This ancient tradition of Aboriginal fire management is likely to have maintained biodiverse open savanna habitats and protected small isolated rainforest fragments (Mangglamarra *et al.*, 1991, Trauernicht *et al.*, 2015, Vigilante *et al.*, 2009). The cessation of Aboriginal fire management in many northern Australian environments has been associated with degradation of some rainforests and other fire sensitive plant communities (Russell-Smith and Bowman, 1992, Trauernicht *et al.*, 2012), although in rarely burnt areas there can be expansion of rainforest (Bowman and Fensham, 1991, Clayton-Greene and Beard, 1985).

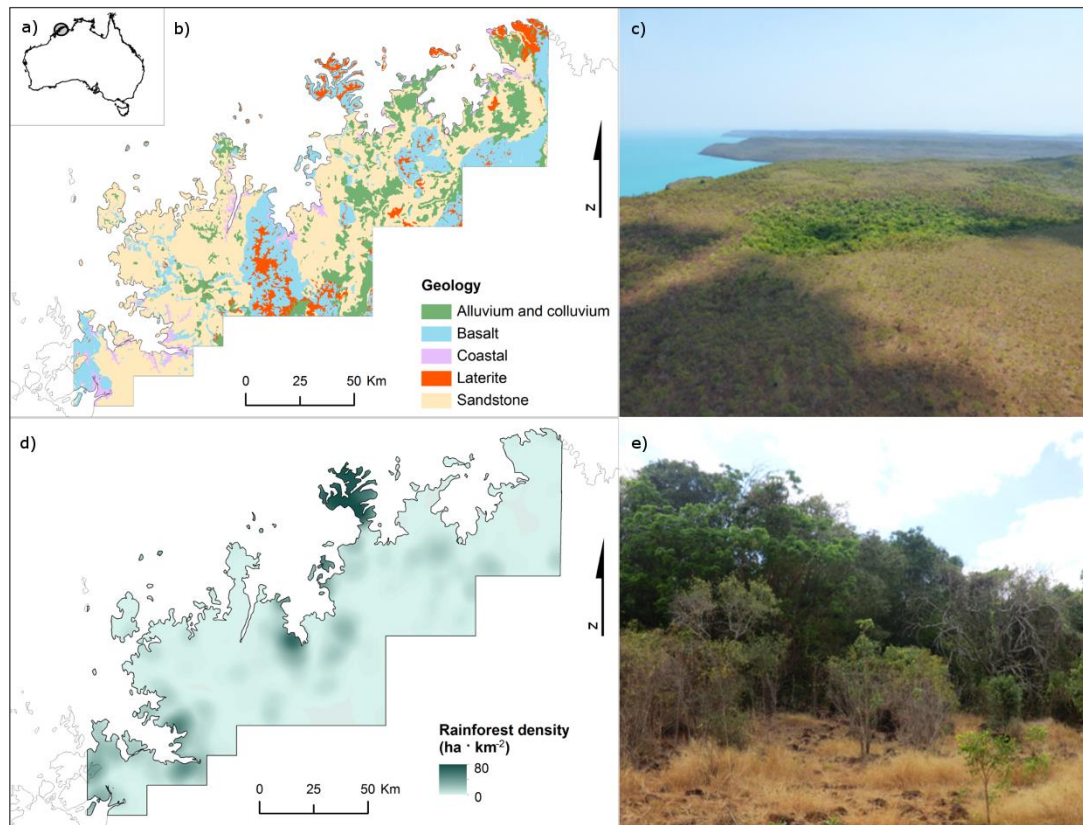


Figure 2.2 (a) Extent of the mapped area in the north Kimberley, including (b) the main geology types in the area and (d) rainforest density, calculated in ha per km² of land. In this area rainforests are typically represented by (c) small patches surrounded by savanna (Beard *et al.* 1990), with (d) sharp boundaries between the two vegetation types.

2.3.2 Rainforest mapping and analyses

Sub-continental scale – climatic drivers of rainforest density

The distribution and areal extent of the rainforests in the north-western Australian monsoon tropics was determined by blending existing vegetation maps. Total coverage of rainforest in Western Australia and Northern Territory was calculated for a lattice of grid cells 50 x 50 km in area. The Western Australia map (1: 200000) was derived from Kimber *et al.* (1991), who used semi-automated classification of Landsat imagery taken in 1986 and did not differentiate floristics or structure variation amongst rainforests. The Northern Territory vegetation data (1: 80000), based on interpretation of aerial photography classified according to Russell-Smith (1991), were supplied by

the Department of Land Resource Management, © Northern Territory of Australia. In calculating rainforest coverage in the Northern Territory lattice cells we selected both dry and wet rainforest types because they are structurally and floristically similar to the Western Australian rainforests (Kenneally *et al.*, 1991, Bowman, 1992). We combined the Western Australia and Northern Territory data to create a map of the north-western rainforest domain, extending from 11.00 °S to 18.00 °S in latitude and from 122.14 °E to 138.00 °E in longitude (Fig. 2.1). This resulted in 192 and 63 grid cells in the Northern Territory and Western Australia respectively. For each grid cell, mean annual rainfall, precipitation seasonality (coefficient of variation of monthly rainfall expressed as a percentage), potential evapotranspiration, moisture index (mean annual precipitation over potential evapotranspiration; Thornthwaite, 1948), and annual mean temperature were calculated for the centre point of each cell. Rainfall, precipitation seasonality and temperature data were obtained from WorldClim Global Climate Data (Hijmans *et al.*, 2005) and moisture index and potential evapotranspiration were downloaded from the Global Aridity and PET database (Zomer *et al.*, 2008). Minimum, maximum and median values of the climatic variables were calculated separately for the Western Australia and Northern Territory grid cells.

Regional scale – local drivers of rainforest density

We generated a map of the rainforests in the north Kimberley, covering the entire Wunambal Gaambera Country and expanding the analysis to the adjacent coastal areas (total surface 12,572 km²), as follows. Orthophotos (scale 1:8,000) taken during the dry season (May-August) of the years 2005-2007 were used create a map of the rainforest patches located in the study area. A lattice of 30 m x 30 m cells was overlaid on the orthophotos and every cell was manually classified as “rainforest”, “savanna” or “other”. The vegetation type of each cell was considered to be the one occupying the highest proportion of the cell. A map of the rainforest patches was produced by merging the contiguous cells classified as “rainforest” (Fig. 2.2d). A helicopter survey was conducted to validate the map. The flight path, designed to include locations with both high and low rainforest cover, included coastal and inland areas as well as islands. It covered the main geologic substrates, in particular basalt, sandstone and laterite. We

flew along the selected path at an average height of 300 m above the ground for a total length of 550 km on 22 September 2013. Waypoints, collected every 10 seconds, were visually identified as “rainforest” or “savanna”. The points were then buffered 30 m and intersected with the rainforest map. A confusion matrix was generated to calculate map accuracy, omission and commission errors, and kappa coefficient of agreement (Congalton, 1991).

Patch size, distance from the coastline and distance from the nearest drainage line were calculated for every rainforest polygon on the regional scale map. Rainforest density was calculated as ha of rainforest per km² of land, based on a grid of 1 km x 1 km size cells for computational reasons. For each cell we also calculated: (i) the geology category, based on the predominant geology type in each 1 km x 1 km cell, and (ii) the topographic category, based on the predominant topographic position index (TPI; Jenness, 2006) in the cell. The TPI was calculated for every pixel in the mapped area from a 30-m resolution digital elevation model (DEM), based on the difference in elevation between each pixel and the average elevation of the eight neighbouring pixels; values lower than -1 were classified as “valley”, and values higher than +1 as “ridge”. Intermediate values were classified as “flat” or “slope” depending on the slope of the pixel ($\leq 4^\circ$ for flat areas, $>4^\circ$ for slopes), obtained from the 30-m DEM. (iii) Each grid cell was further classified as having ‘complex’ or ‘level’ terrain, noting that complex terrain is often associated with rockiness. Cells in which the categories ‘valley’ + ‘ridge’ + ‘slope’ occupied more than 50% of the cell were classified as ‘complex’, the others as ‘level’. The average rainforest density in the north Kimberley was then calculated for each geologic substrate and TPI based on the rainforest density grid.

2.3.3 Local scale natural experiment - Mainland Vs Islands

We expected there would be differences in fire activity and rainforest distribution between islands and mainland, because islands have been subject to fewer human ignitions due to infrequent visitation in recent times (Vigilante *et al.*, 2013) and the sea provides a natural fire break from surrounding landscape fires. To test this, we compared rainforest density grid cells on islands and the mainland. We selected areas

that were geographically, floristically, and ecologically similar by extracting from the ‘regional scale dataset’ only grid cells with the following attributes: mean annual rainfall between 1250-1382 mm · year⁻¹, distance from the coastline <5 km (equivalent to the radius of the biggest island, hence the maximum distance from the coastline on islands), and geology developed on basalt, laterite or coastal sediments. Islands and coastal areas of the north Kimberley are floristically similar, with only a very small group of taxa recoded only from islands (Lyons *et al.*, 2014). Grid cells located on the Bougainville Peninsula were included in the category ‘islands’, due its narrow neck which makes it functionally equivalent to an island in terms of isolation from the mainland.

Fire activity was calculated from a 15-year fire history map (2000-2014), created at a pixel resolution of 250 m based on MODIS satellite imagery, accesses via North Australian Fire Information website (<http://www.firenorth.org.au/nafi3/>). Due to the coarse resolution of the fire history map it was impossible to accurately locate every fire scar, so the data were used to provide coarse-scale information about differences in fire activity between the mainland and islands. For every cell of the rainforest density grid the area-weighted proportion of years burnt was calculated by dividing the average number of years in which the cell was burnt by 15, the total number of years investigated. The average fire activity per year and rainforest density were calculated for cells classified as ‘island’ or ‘mainland’ and, within each category, ‘complex’ or ‘level’ terrain.

2.3.4 Statistical analyses

At a sub-continental scale, we employed the Pearson product moment correlation coefficient to examine correlations amongst rainforest density and the climatic variables, and presented the results in a constellation diagram. For presentation (but not in the analysis), we aggregated the grid cells into 200 mm- mean annual rainfall bins and calculated the average rainforest density for each bin.

At a regional scale, we first tested for spatial autocorrelation in rainforest density and assessed minimum sampling distance, estimated by plotting the semi-variance as a

function of distance, using the software R (R Core Team, 2013) and the R package *geoR* (Ribeiro and Diggle, 2001) (Fig A1.1 in Appendix 1). We then tested whether the factors terrain and geology are related to rainforest density. We also checked whether rainforest density was associated with geology within level and complex terrain types. To do this, we used generalised linear models (GLMs) and complete subset regression and model selection based on Akaike's Information Criterion (AIC; Burnham and Anderson, 2002), calculated using the R package 'MuMIn' (Bartoń, 2009). We used the compound Poisson-gamma distribution, included in the tweedie family of distributions, which allows regression modelling of zero-inflated positive continuous data (R packages 'tweedie' (Dunn, 2014) and 'statmod' (Smyth *et al.*, 2015)). To assess the importance of each variable, we calculated Akaike weights (w_i), which represent the probability that a given model is the best in the candidate set (Burnham and Anderson, 2004). We then calculated variable importance (w_+) as the summed w_i of the models in which the variable occurs. w_+ values higher than 0.73 were considered to indicate that the variable is a statistically important predictor (Murphy *et al.*, 2010). Model summaries are provided in Table 1.1a-c in Appendix 1.

When comparing mainland vs islands, we examined differences in rainforest density and fire activity between locations, testing for the factors insularity (island or mainland) and terrain (complex or level). To do so, we employed GLMs, using the compound Poisson-gamma distribution for both rainforest density and fire activity, complete subset regression, and model selection based on AIC as described above. Variable importance was assessed by calculating w_+ , as described above. Model summaries are provided in Table 1.1d, e in Appendix 1.

2.4 RESULTS

2.4.1 Sub-continental scale

The north-western Australian rainforest domain covered an area of 640,000 km², ranging from the coastline to a maximum of 350 km inland. Rainforest density was

lower west of the Ord Arid Intrusion: in Western Australia rainforest density ranged from 0 to 8.7 ha of rainforest per km² of land (average 1.1 ± 0.2 ha · km⁻²), while in the Northern Territory the range was 0 to 19.0 ha per km² of land (average 1.4 ± 0.2 ha · km⁻²). The Northern Territory showed higher median values and a broader range of both mean annual rainfall and moisture index (Fig. 2.3a, b). Mean annual temperature and precipitation seasonality showed higher median and maximum values in Western Australia and minimum in the Northern Territory (Fig. 2.3c, d), while annual potential evapotranspiration had a similar range in the two states but higher median values in the Northern Territory (Fig. 2.3e).

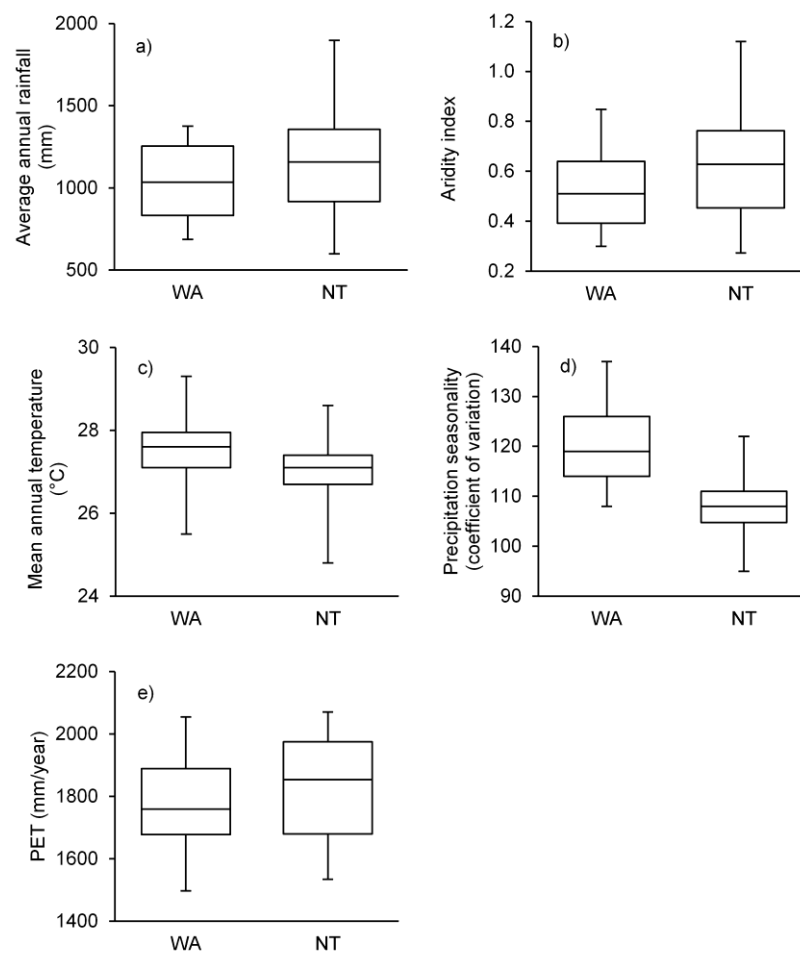


Figure 2.3 Comparison of (a) average annual rainfall, (b) moisture index, (c) mean annual temperature, (d) precipitation seasonality, and (e) potential evapotranspiration (PET) within the monsoon rainforest domain in Western Australia (WA) and Northern Territory (NT). Boxes indicate median value and upper and lower quartiles, bars the 10th and 90th percentiles.

There was a positive correlation between rainforest density and both mean annual rainfall and moisture index (Figs 2.4, 2.5), which were also positively correlated. Potential evapotranspiration was negatively correlated with rainforest density, moisture index and rainfall, while precipitation seasonality was negatively correlated with rainfall and moisture index. Mean annual temperature was not correlated with any of the climatic variables investigated nor with rainforest density.

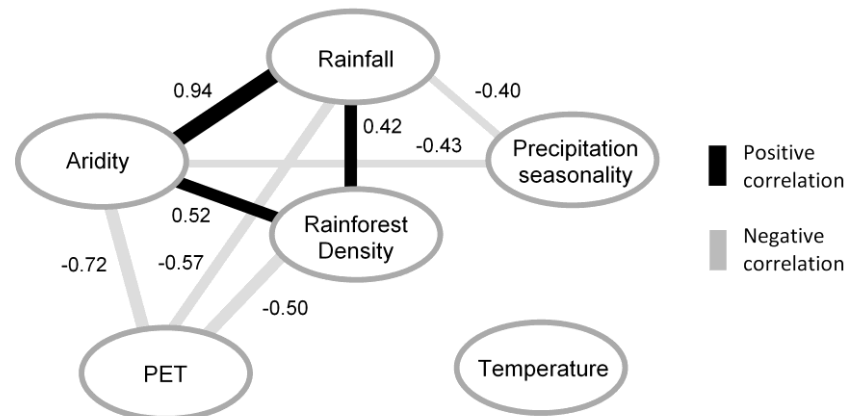


Figure 2.4 Constellation diagram showing the strength and direction of correlations amongst rainforest density and the climatic variables average annual rainfall, moisture index, potential evapotranspiration (PET), precipitation seasonality, and mean annual temperature in the monsoon rainforest domain in north-west Australia. Positive correlations are represented by black lines, negative correlations by grey lines. Correlations stronger than 0.4 or -0.4 are indicated; wider lines indicate stronger correlations, narrower lines weaker correlations.

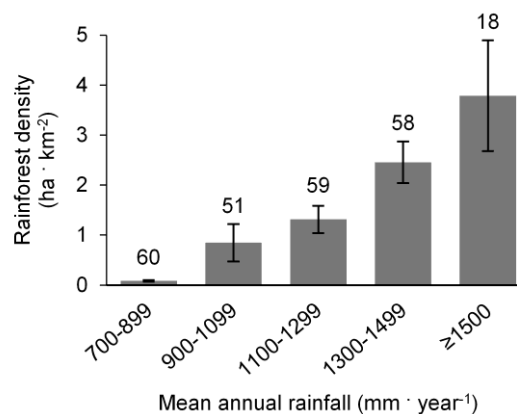


Figure 2.5 Average rainforest density by average annual rainfall, calculated within the rainforest domain in the Australian monsoon tropics. The numbers above each column represent the number of grid cell included in that rainfall interval. Error bars represent standard errors.

2.4.2 Regional scale

In total, 2902 points were assessed during the aerial survey. There was a strong concordance between the rainforest map and the aerial assessment, with a resulting overall map accuracy of 93% (Kappa coefficient 0.78; Table 2.1). A high accuracy was obtained for savanna points (95% for both producer's and user's accuracy), meaning few savanna points were mistaken for rainforest. We attribute the lower producer's and user's accuracy for rainforests (83% and 82% respectively) to the floristic composition of the monsoon vine thickets, where semi-deciduous species can dominate (Beard, 1979), making portions of the forest patches undetectable from orthophotos taken during the dry season.

Table 2.1 Accuracy of the north Kimberley rainforest map, assessed through aerial survey.

	Habitat	
	Rainforest	Savanna
Producer's accuracy (omission)		
In class (%)	83	95
Not in class (%)	17	5
User's accuracy (commission)		
In class (%)	82	95
Not in class (%)	18	5
Overall accuracy (%)	93	
Kappa coefficient	0.78	

Savanna was by far the most common vegetation, covering 98.9% of the area. We detected a total of 6460 rainforest patches covering 10300 ha, equivalent to 0.82% of the mapped land. Patch size ranged from 0.1 to 220 ha, and averaged $1.6 \text{ ha} \pm 0.1$ (SE). Seventy-five percent of patches were smaller than 1 ha, and only 2.5% were larger than 10 ha (Fig. 2.6a). More than 40% of the mapped rainforest patches were located

within 1 km of the coastline (Fig. 2.6b), but patches were detected up to 47 km inland (average $4.7 \text{ km} \pm 0.1 \text{ (SE)}$). A similar pattern was identified for distance from drainage lines, with 64% of the patches located within 1 km of the nearest drainage line (Fig. 2.6c), but some up to 32 km distant (average $1.7 \text{ km} \pm 0.0 \text{ (SE)}$).

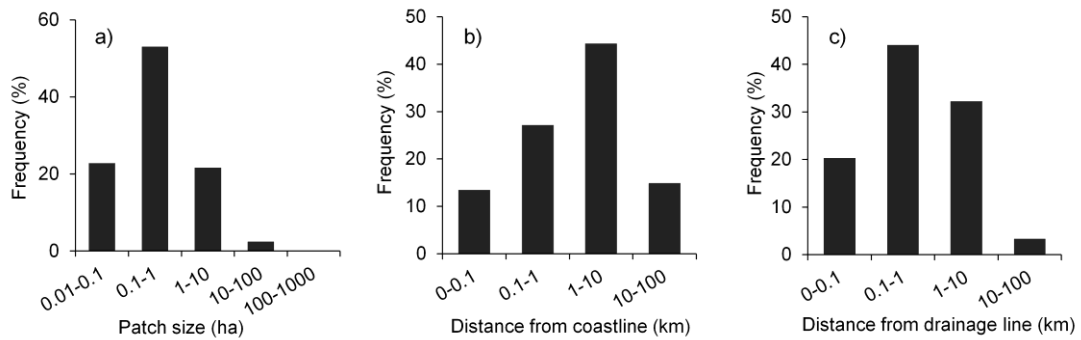


Figure 2.6 Frequency distribution of rainforest patches in the north Kimberley region according to (a) size, (b) distance from the coastline, and (c) distance from the nearest drainage line. Note the logarithmic scale for the x axes.

Rainforest density was strongly dependent on both terrain ($w+ = 1.00$) and geology ($w+ = 1.00$); average rainforest density was higher on relatively fertile substrates (laterite, coastal sediments and basalt), and lower on alluvium and colluvium and infertile sandstone (Fig. 2.7a). Average rainforest density was also higher in complex terrain such as ridges, slopes and valleys and lower on level areas (Fig. 2.7b). The model including geology and terrain explained 32.1% of the deviance. The preference for relatively nutrient-rich geology was independent on terrain, as on both level and complex terrain rainforest density was strongly associated with geology ($w+ = 1.00$ in both cases). Geology explained 13% of deviance on complex terrain and 10% of deviance on level terrain.

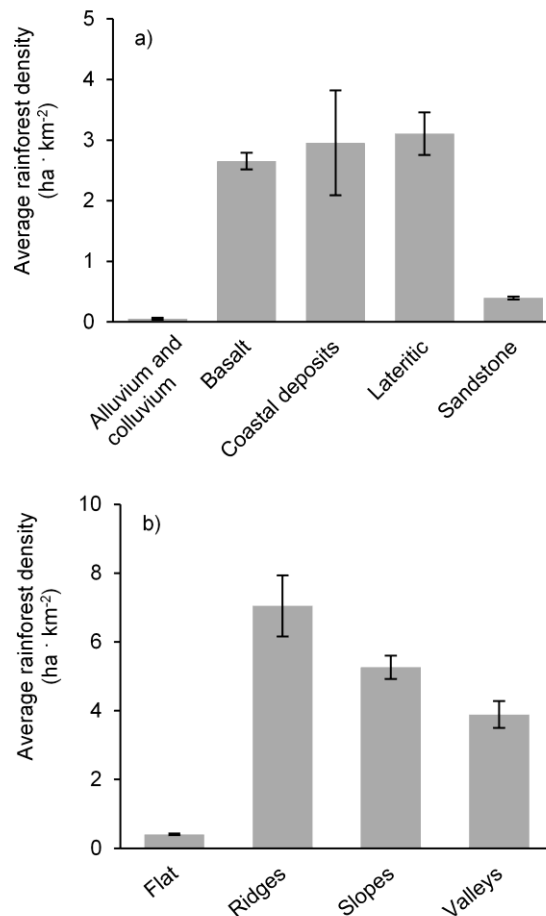


Figure 2.7 Rainforest density in relation to (a) geological substrate and (b) topographic position in the north Kimberley (regional analysis). Rainforest density was highest on coastal sediments, basalt, and lateritic substrates. It was also higher on ridges, slopes and valleys, and almost absent in flat areas. Error bars represent standard errors.

2.4.3 Local Scale - Mainland vs Islands

The grid cells on basalt, laterite and coastal substrates and within 5 km of the coast covered an area of 332.4 km^2 on islands and 693.1 km^2 on the mainland. The total area covered by rainforests was 47.0 km^2 on the islands, compared with 13.6 km^2 on the mainland, so that rainforest density was 7 times higher on the islands (Table 2.2). Islands were more topographically complex than the mainland. There was statistical support for an influence of both insularity ($w+ = 1.00$) and terrain ($w+ = 1.00$) on rainforest density (Table 2.3), and the model including both explained 35% of

deviance. There was less fire activity on islands (average 0.061 ± 0.003 times burnt per year) than on the mainland (average 0.266 ± 0.004 times burnt per year; $w+ = 1.00$), and insularity alone accounted for 39.1% of deviance. Contrary to expectations, there was no statistical support for an effect of terrain on fire activity ($w+ = 0.48$; Table 2.3).

Table 2.2 Extent, rainforest cover, average rainfall and extent of the geologic substrates and terrain type on the selected grid cells used to compare rainforest density on islands and the mainland in the north Kimberley.

		Islands	Mainland
Total land (km ²)		332.4	693.1
Rainforest area (km ²)		47.0	13.6
Average rainfall (mm · year ⁻¹)		1348 ± 1	1307 ± 1
Geology type	Basalt	64.4%	81.2%
	Coastal sediments	0.5%	2.7%
	Laterite	35.1%	16.1%
Terrain type	Complex	62.8%	55.6%
	Level	37.2%	44.4%

Table 2.3 Average fire activity, measured as times burnt per year, and average rainforest density, measured as ha · km⁻², for complex and level terrain located on the selected grid cells on islands and mainland in the north Kimberley.

Location	Terrain	Fire activity (average times burnt per year ± SE)	Rainforest density (ha · km ⁻² ± SE)
Islands	Complex	0.05 ± 0.00	19.69 ± 0.88
	Level	0.08 ± 0.01	6.81 ± 0.73
Mainland	Complex	0.27 ± 0.01	4.29 ± 0.42
	Level	0.26 ± 0.01	0.30 ± 0.06

2.5 DISCUSSION

We found that in north-western Australian monsoon tropics rainforest patches are tiny and scattered across a vast savanna matrix. Due to their small size, these rainforest fragments are essentially undetectable at the resolution employed by global-level assessments (Murphy and Bowman, 2012, Staver *et al.*, 2011b). At a subcontinental

scale, the strong correlation between rainforest density and annual rainfall, potential evapotranspiration, and moisture index highlighted the primacy of water supply compared to mean annual temperature and precipitation seasonality, and supported our first hypothesis. This correlation is congruous with the observation that a trend of increasing rainfall in northern Australia since the 1940s is the key driver of rainforest patch expansion (Bowman *et al.*, 2001, Banfai and Bowman, 2007). These findings are also consistent with the global trend of increasing proportion of rainforest (and decreasing savanna) as mean annual precipitation increases (Hirota *et al.*, 2011, Murphy and Bowman, 2012). In the drier landscapes west of the Ord Arid Intrusion, rainforest species diversity is also lower than to the wetter east and most of the species in Western Australia are a subset of those in the Northern Territory (Kenneally *et al.*, 1991). However, the presence of rainforests in the north-western Australian monsoon tropics showed that the region cannot be defined as deterministically savanna based solely on climate (Murphy and Bowman, 2012). Similarly, rainforest patches exist throughout much of the tropics globally, which suggests that in all but arid tropical regions, climate alone is not the only factor controlling rainforest distribution (Staver *et al.*, 2011b). In Brazil, for example, small patches of deciduous and semi-deciduous rainforests are interspersed in a matrix of savanna plants (Cerrado) or thorn scrubs (Caatinga), and are restricted to slopes and moist, nutrient-rich sites (Oliveira-Filho and Ratter, 2002, Leal *et al.*, 2005). Likewise, in Ivory Coast the dominant savanna vegetation is scattered with small patches of dry rainforest (Goetze *et al.*, 2006).

We also found support for our second hypothesis, that topography and geology affect rainforest distribution. The influence of topography on rainforest density was manifest in the higher rainforest density on complex compared with level terrain. Rainforest density was also higher on nutrient-rich basalt compared with the nutrient-poor sandstone, despite the higher fire frequency and intensity recorded on basalt (Vigilante *et al.*, 2004). This pattern is consistent with the edaphic compensation hypothesis (Ash, 1988, Webb and Tracey, 1981), whose underlying mechanism is probably the effect of increased fertility in enhancing plant growth, allowing trees to reach the threshold size that triggers the switch from savanna to rainforest through grass shading (Hoffmann *et al.*, 2012a, Murphy and Bowman, 2012). It is important to note that

geology and terrain are typically not independent. For example, in the north Kimberley rounded hills are more common on basalt, while steep gorges are frequently found on sandstone (Vigilante *et al.*, 2004). However, in our analysis we were able to demonstrate an effect of geology alone by comparing areas on the same terrain, showing that there are more rainforests on basalt than on less fertile geologies.

There was only partial support for our third hypothesis, that insularity and topographic effects are directly related to fire activity. Clearly, there were more rainforests on islands, where there was also less fire activity compared with the mainland. The importance of fire in restricting rainforests has been demonstrated by rainforest expansion in other savanna landscapes where fire has been excluded, in northern Australia (Scott *et al.*, 2012, Fensham and Butler, 2004) and elsewhere (Bond *et al.*, 2003). Rainforest species are typically less fire tolerant than savanna species due to thinner bark and less developed post fire recovery mechanisms (Lawes *et al.*, 2013, Ondeï *et al.*, 2016, Pausas, 2015b). However, we failed to detect a corresponding difference in fire activity between terrain types on the mainland, and found only a minor difference on islands. There are two possible reasons for this lack of correspondence, which are not mutually exclusive. One is that terrain, or associated rockiness, did exert an influence on fire activity, but this was obscured by the coarse scale of the grid cells in our analysis (1 km x 1 km). Another possible reason is that the higher rainforest density on complex terrain is the result of water and nutrient accumulation (Daws *et al.*, 2002, Ash, 1988), rather than topographic fire protection. Nonetheless, the presence of rainforest on level terrain on islands, but not on the mainland, suggests that fire is an important controller of rainforest distribution in the region.

We suggest that rainforest density is determined by the interplay of fire activity and plant growth rates (Fig. 2.8a). Fire activity is shaped by insularity and possibly terrain complexity, while plant growth rates are known to be controlled by water availability and the nutrient stock provided by the geological substrate control (Murphy and Bowman, 2012), with an effect of terrain in enhancing water and soil accumulation (Ash, 1988). Growth rates affect the capacity of rainforest trees to grow rapidly and

escape the ‘fire trap’, thereby developing a closed canopy which shades out grass biomass, reducing fire frequency which in turns reinforces rainforest expansion (Murphy and Bowman, 2012, Hoffmann *et al.*, 2012a, Dantas *et al.*, 2013a). Our findings are summarised in Fig. 2.8b, which shows characteristic patterns of rainforest fragments in the landscape, and how these fragments are likely to expand in response to a wetting climate under contrasting fertility and fire regimes. Rainforest expansion should be proportionally greater in lower rainfall areas that currently have low rainforest density, like the north Kimberley, because there are more landscape niches available for occupancy, such as nutrient-rich and fire protected sites. A prediction of our work is that, under the current wetting trend, there will be continuing rainforest expansion in the Kimberley, as has been observed elsewhere in the Australian tropics (e.g. Russell-Smith *et al.*, 2004).

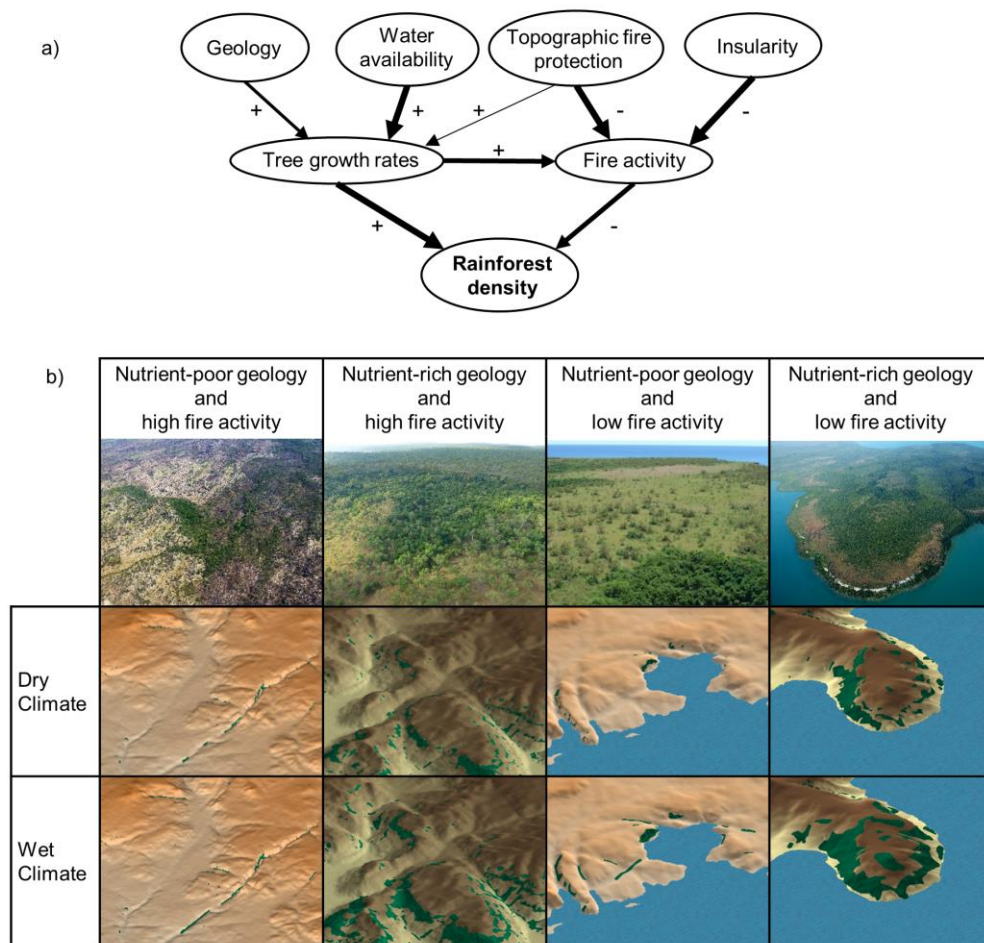


Figure 2.8 Synthesis of the environmental determinants of monsoon forest fragments in the north Kimberley. (a) Diagram showing the positive (+) and negative (-) effects of environmental factors on rainforest density based on the results of this study. The thickness of the arrows scales to the magnitude of the effects. (b) Top row: oblique aerial photos showing examples of the density of rainforest fragments on sites with contrasting geology (sandstone vs. basalt) and fire activity in the north Kimberley. Second row: 3D renderings of rainforest distribution (dark green) on sandstone (nutrient-poor) and basalt (nutrient-rich) landscape under current dry climate. Bottom row: 3D renderings of plausible rainforest density under a climate as wet as coastal regions of the Northern Territory. In this study we demonstrated that insular sites have substantially lower fire activity than environmentally comparable mainland savanna areas. Under the current climate rainforest density is highest on fertile infrequently burnt areas, and in frequently burnt landscapes is confined to topographically fire protected settings, particularly on nutrient-poor geology. Under a wetter climate we expect the rainforest patches to expand and new patches to establish in suitable landscape niches, with the greatest expansion on basalt landscapes. The exact amount of expansion is unpredictable because of the influence of fire activity and fire management.

2.6 CONCLUSION

We have shown that the density of monsoon rainforest in the north-western Australian savanna is affected by moisture availability, substrate and fire. The effects of these drivers appear to involve complicated feedbacks and interactions, such as the combined effects of potential fire protection and increased productivity in topographically complex terrains. We acknowledge that our correlative analysis cannot separate cause and effect, or test the fire driven alternative stable state model in explaining the distribution of rainforests. To do this demands analysis of vegetation boundary dynamics coupled with contrasts of substrate type and fire history. This can be achieved through carefully designed regional scale analysis of rainforest boundaries trends, such as field surveys and historical sequences of aerial photography (Banfai and Bowman, 2006, Butler *et al.*, 2014, MacDermott *et al.*, 2016), and is the subject of a subsequent paper. Despite its limitations, our approach is an important step in understanding the effect of climate change and anthropogenic disturbances on naturally fragmented rainforests elsewhere in the tropical savanna biome.

Chapter 3

Fire and cattle disturbance as potential drivers of vegetation structure and limiting factors of rainforest expansion in the Australian monsoon tropics

This chapter is in review in *Journal of Biogeography*

3.1 ABSTRACT

Rainforest expansion into savannas has been detected in several tropical locations, including the Australian tropics, but little is known about rainforest boundary dynamics in the north Kimberley. To assess rainforest expansion and the effects of climate change and disturbance on vegetation dynamics in that region, we used sequences of geo-rectified aerial photographs of the Mitchell Plateau and the Bougainville Peninsula, locations characterised by similar geology and mean annual rainfall but different disturbance (fire activity and cattle) levels. We generated maps of rainforest patches in 1949 and 1969, and compared them a map of rainforest patches from 2005. To ground-truth rainforest expansion we established 20 transects, each containing five plots, running across rainforest-savanna boundaries. The plots were associated to the corresponding vegetation type mapped in 1949, 1969 and 2005. Generalised linear models were used to detect differences in species, stand basal area, canopy cover, grass and rock cover, cattle impact, and fire activity between vegetation types and locations. On the Bougainville Peninsula average fire frequency was low (0.11 per year) and cattle entirely absent, while on the Mitchell Plateau average fire frequency was high (0.58 per year), and cattle were common and associated with lower seedling density in savannas. Rainforest expanded more on the Bougainville Peninsula (69%), where patches were bigger and more convoluted, than on the Mitchell Plateau (9%). Rainforest expansion was positively associated with rainfall and topographic complexity, and on level terrain, it occurred only on the Bougainville Peninsula. Rainforests were floristically and structurally similar in the two locations, while savannas on the Bougainville Peninsula had denser vegetation and more abundant rainforest elements. The frequency distribution of canopy cover was bimodal on the Mitchell Plateau, signalling the presence of two distinct vegetation states, and unimodal on the Bougainville Peninsula, consistent with the blending of the two states. Wetting trends are likely strong drivers of rainforest expansion, but at a landscape scale their effect is probably modulated by fire activity and the presence of megaherbivores, which may also be pivotal in maintaining sharp floristic and structural distinctions between rainforests and savannas.

3.2 INTRODUCTION

Top-down disturbances, such as fire and mega-herbivory, have been postulated to shape vegetation structure and in some cases cause departure from climate-constrained potential vegetation (Bond, 2005). A prime example of this concerns the distribution of rainforests and savannas. Globally, the geographic distribution of these biomes is strongly controlled by climate, with rainforests, characterised by high canopy cover and an absence of grass, dominant in high rainfall areas, and savannas, distinguished by a continuous grass layer and sparse trees, found in lower rainfall regions (Lehmann *et al.*, 2011). However, in landscapes with intermediate rainfall (1000-2000 mm year⁻¹), rainforests and savannas can coexist in the same landscape, forming complex mosaics (Staver *et al.*, 2011). Contrasting fire regimes are considered key factors influencing these vegetation types and maintaining sharp boundaries between the two (Dantas *et al.*, 2016). Rainforests are rarely burnt, because the dense canopy cover creates a moist microclimate and little flammable grass is present (Little *et al.*, 2012), limiting the incursion of fire (Just *et al.*, 2015). When fires do occur, they are typically mild surface fires in leaf litter (Cochrane, 2003). By contrast, savannas are characterised by high degree of disturbance, such as frequent fires (Huntley and Walker, 2012). Compared to rainforest species, savanna plants are better adapted to tolerate (e.g. thick bark) and recover (aerial buds) from fire (Lawes *et al.*, 2013, Ondeï *et al.*, 2016, Pausas, 2015b). Dynamic global vegetation models suggest that some tropical savannas have the climatic potential to become forests in the absence of fire (Bond *et al.*, 2005). Several small-scale experiments have demonstrated substantial changes in species diversity and stem density in response to fire exclusion, although this was not necessarily associated with conversion to rainforest (e.g. Bowman and Panton, 1995, Woinarski *et al.*, 2004).

Another common disturbance is grazing by megaherbivores. In the Australian monsoon tropics, introduced cattle, pigs and buffalo can damage rainforest patches through trampling vegetation and wallowing in moist soils (Russell-Smith and Bowman, 1992, Petty *et al.*, 2007). Experimental exclosures of medium and large herbivores in Mexican and Brazilian rainforests resulted in higher seedling recruitment

and survival (Camargo-Sanabria *et al.*, 2015, Fleury *et al.*, 2015), due to the removal of the direct negative effects of browsing on plant biomass and the indirect effects of trampling (Fleury *et al.*, 2015). While herbivory can affect woody vegetation floristics and structure (Midgley *et al.*, 2010), it is unclear if mega-herbivore disturbance substantially influences rainforest-savanna boundaries at a landscape-level (Petty *et al.*, 2007). Furthermore, a strong interaction between megaherbivores and fire has been posited by palaeoecological studies. Following the extinction of Australian megafauna, the consequent increase in fire activity could have led to a shift from broadleaf to more flammable vegetation (Rule *et al.*, 2012).

Factors affecting tree growth rates, particularly water availability and nutrient availability, influence the rate of forest expansion (Murphy and Bowman, 2012), because fast-growing plants require shorter disturbance-free time to grow tall enough to resist the negative effects of fire disturbance (Hoffmann *et al.*, 2012a). A trend in increasing precipitation, possibly amplified by enhanced CO₂, has been postulated as the cause for the expansion of rainforests into savannas north-western Australia (Banfai and Bowman, 2007, Bowman *et al.*, 2010a). Significant soil fertility gradients are also found across most rainforest-savanna boundaries (Dantas *et al.*, 2013a). Indeed, a controversial alternative perspective is that disturbance-based feedbacks on rainforest-savanna boundaries are a consequence of the established vegetation type, rather than a primary determinant (Veenendaal *et al.*, 2015, Lloyd and Veenendaal, 2016). Hence controlling for edaphic factors and climatic trends is essential when evaluating the effect of fire and megaherbivore disturbance on rainforest-savanna dynamics.

Classical experiments designed to determine the effects of exclusion of fire and herbivores on rainforests and savannas at the landscape level are often impractical, given the spatial and temporal scales involved and the difficulty in having adequate replication (Andersen *et al.*, 1998). A realistic alternative to tackle large-scale ecological problems is to take advantage of conditions naturally occurring in a landscape by performing natural experiments (Diamond, 1983). This approach requires careful site selection, to ensure locations share a common or known

environmental history (Johnson and Miyanishi, 2008), and some treatment combinations can be absent, due to the rarity of naturally long-unburnt areas (Andersen *et al.*, 1998). Nonetheless, natural experiments can successfully test the effects of disturbance on vegetation in fire prone environments (e.g. Vigilante *et al.*, 2004, Woinarski *et al.*, 2004).

We used a natural experiment to investigate rainforest expansion and vegetation structure in two extensive locations of the north Kimberley (Western Australia): the Bougainville Peninsula and the Mitchell Plateau. These two locations share similar climate and geologic substrate, but experience strikingly different levels of disturbance: the Mitchell Plateau has a high frequency of extensive savanna fires and a large, unmanaged population of cattle, whereas the Bougainville Peninsula is rarely burnt and is cattle-free. This contrast allows us to determine the combined effects of fire and cattle on rainforest-savanna dynamics while controlling for climate and geology. We used historical aerial photography (1949, 1969 and 2005), which provided time depth in forest boundary dynamics across the entire study areas. We then ground-truthed these analyses using transects that recorded variation in tree species populations across selected boundaries. Specifically, we hypothesised that rainforest expansion has occurred in the north Kimberley in response to the wetting trend in northern Australia over the last century (Bowman *et al.*, 2010a), together with increasing atmospheric CO₂, but that the expansion is strongly influenced by the combined effects of fire and megaherbivores. We also predicted that areas subject to high disturbance are characterized by smaller and more compact rainforest patches, separated from the surrounding savanna by sharp boundaries, whereas in cattle- and fire-free locations we expected to find bigger and more convoluted patches, with wider ecotones containing a mix of rainforest and savanna species, signs of ongoing rainforest expansion. This natural experiment therefore contributes to the broader debates about tropical savanna-forest boundaries, by testing the role of fire and megafauna disturbance as drivers of rainforest change in time and space.

3.3 METHODS

3.3.1 Study area

The study was conducted on the Wunambal Gaambera (WG) Country in the north Kimberley, Western Australia, which occupies an area of 9,144 km². It is defined by the Wanjina Wunggurr Unguu Native Title Determination, and represents the traditional lands of the Wunambal Gaambera Aboriginal people. The geology of the region is characterised by deeply weathered sandstones and basaltic base rocks of Precambrian age, often capped by Cainozoic laterites (Beard, 1976). Rainfall occurs almost entirely during the summer wet season (November to April), while the rest of the year is almost rain-free (Beard, 1976). Current average annual rainfall across the region ranges from 1200 to 1400 mm. A wetting trend has been detected since the beginning of the 20th century, with an increment in average annual rainfall of 40-50 mm every 10 years since the late 1940s (Bureau of Meteorology, 2016). The vegetation is predominantly biodiverse tropical savannas: *Eucalyptus tetrodonta*-*E. miniata* savannas are found on the laterite mesas and hills, while *E. tectifica*-*E. grandifolia* savannas are common on deeper, clay soils on the plains. Small patches of semi-deciduous rainforests are interspersed in the savanna, typically found in fire-protected locations (Beard, 1976, Vigilante *et al.*, 2004).

The study was centred on two of the locations with the highest density of rainforests in the north Kimberley: the Mitchell Plateau and the Bougainville Peninsula (Fig. 3.1). These locations have similar geology (basalt and laterite) and mean annual rainfall (range 1300-1400 mm year⁻¹), but contrasting management histories. The Mitchell Plateau (754 km²) has a high fire frequency (average times burnt: 0.5 year⁻¹; data from North Australia Fire Information, based on the 15-year time period from 2000-2014). The Bougainville Peninsula (298 km²), connected with the mainland only by a narrow strip of sand, has a much lower fire frequency (average times burnt: 0.08 year⁻¹). The fire regime of the entire study area has undergone dramatic shifts in the last 100 years. Wunambal Gaambera people practiced landscape scale burning as part of their hunter-gatherer lifestyle up until the 1940s and 1950s, when they moved off their country to settlements. The next 50 years were dominated by unmanaged wildfires moving in

from adjacent areas or started by lightning. Since 2010, Aboriginal land management programs have initiated prescribed burning programs. While pastoral leases have been established in parts of the north Kimberley since the 1950s, the study area has never been formally used for pastoral purposes. A 1976 biological survey of the Mitchell Plateau did not record any cattle in the area (Wilson, 1981). However, a biological survey of Kimberley rainforests in 1987 found evidence of cattle on the Mitchell Plateau, but not in the Bougainville Peninsula (Mckenzie and Belbin, 1991).

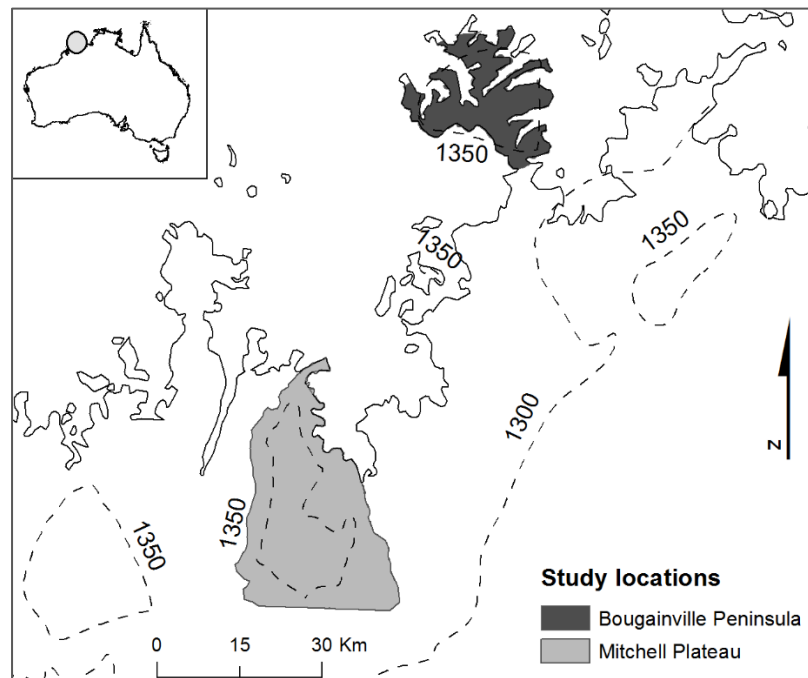


Figure 3.1 Location of the two study sites in the north Kimberley. The Mitchell Plateau extends in latitude from 14.457 °S to 14.893 °S and in longitude from 125.722 °E to 125.949 °E. The Bougainville Peninsula stretches from 13.897 °S to 14.146 °S in latitude and from 125.975 °E to 126.225 °E in longitude. Dashed lines represent isohyets (mm · year⁻¹). The inset shows the location of the study sites within Australia.

3.3.2 Rainforest-savanna boundary change

Digitized aerial photographs of the study locations were obtained for the years 1949 (black and white; 1: 50,000) and 1969 (black and white; 1: 83,300) and georectified, using the spline tool in ArcGIS 10 Georeferencing Toolbox to correct for obvious misalignments. Rainforests were mapped at a common scale of 1:2,500, adapting the

method described in Bowman *et al.* (2001), based on grid cell classification. We overlaid a 30 x 30 m lattice grid to the aerial photographs and, for each investigated year, grid cells were manually classified as “rainforest” or “other”, based on the vegetation type occupying the highest proportion of the cell. To compare the historic rainforest extent with a more recent distribution (dry season of 2005), we used a pre-existing, validated map of the north Kimberley rainforests produced using the same methods and resolution (30 x 30 m) in Ondeï *et al.* (2017) (Fig. 3.2).

3.3.3 Patch characteristics and location

A map of the rainforest patches was produced for the years 1949, 1969 and 2005, obtained by merging the contiguous cells classified as “rainforest”. For each patch we calculated area, perimeter, distance from the coastline, and topographic position index (TPI). The latter was calculated as described in Ondeï *et al.* (2017), classifying the land in four different topographic categories: valleys, slopes, ridges and flat areas. We analysed the effect on expansion of both patch size and shape, and defined the degree of patch convolution by calculating patch fractal dimension ($2 * \ln(0.25 * \text{perimeter}) / \ln(\text{area})$), which ranges from 1 (compact) to 2 (highly convoluted) (Hargis *et al.*, 1998).

3.3.4 Correlates of rainforest expansion

To investigate the environmental drivers of rainforest expansion in the time periods 1949-1969 and 1969-2005, we selected all savanna grid cells located within 60 m (equivalent to two times the map resolution) of the patch perimeter at the first year of each time period (1949 or 1969). For each selected grid cell, we calculated distance from the coastline, TPI, and the distance from and the size, convolution, and location of the nearest patch. We also calculated aspect, obtained from a 30-m Digital Elevation Model (DEM), and the bearing angle, defined as the angular direction of the cell relative to the patch of origin. Both bearing angle and aspect were decomposed into their North-South (cosine of angle) and East-West (sine of angle) components.

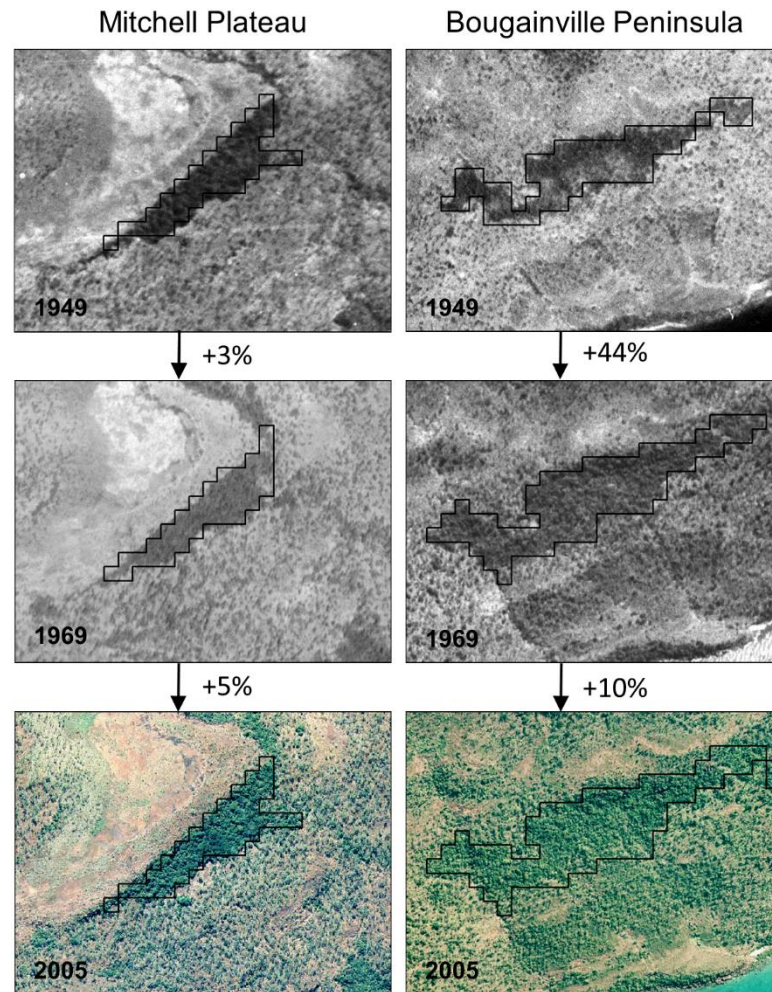


Figure 3.2 Example of aerial photography of the Mitchell Plateau and Bougainville Peninsula used in the analyses. Polygons obtained from merging grid cells classified as 'Rainforest' are shown. Percentage of change between each pair of photographs is indicated.

3.3.5 Vegetation structure

To determine vegetation structure and composition across the rainforest-savanna transition zones we established a total of 20 transects, 10 placed on the Mitchell Plateau and 10 on the Bougainville Peninsula. Transects were all located on different patches and at a minimum distance of 500 m. Each transect was 300 m long, and consisted of five 10 x 20 m plots placed at regular intervals along it. The first plot was located 60 m inside the rainforest, to measure structure and floristic composition of the forest core; the second was at the patch boundary, capturing, when present, the characteristics of the ecotone, while the remaining three were placed in the vegetation outside the rainforest. The patch boundary was visually determined as by Hennenberg *et al.* (2005), based on discontinuities in floristic composition and canopy cover. For each plot we recorded grass cover, rock cover, canopy cover, number of seedlings, and signs of cattle presence. Canopy cover was measured by taking hemispherical photographs using a fish-eye lens (Nikon AF Fisheye NIKKOR 10.5mm), taking pictures at 1 m height and calculating the percentage of closed canopy using the software CAN-EYE (www.avignon.inra.fr/can_eye). The number of seedlings was counted on a 1 x 20 m sub-plot. The presence of cattle was ranked on a qualitative scale, from '0' indicating no sign of cattle, to '3', high cattle impact, based on the presence of tracks and excrements on the ground and partially browsed plants. For each adult tree, operationally defined as having a diameter at breast height (DBH) > 5 cm and being taller than 2 m, we recorded species name, height, and DBH. Total basal area was calculated for each plot. We also recorded the species identity of every tree and shrub in the plot. When species identification was not possible in the field, voucher samples were collected and identified at the Northern Territory Herbarium, where they have been lodged. To determine whether a species was a rainforest element we relied on the floristic classification of Kenneally *et al.* (1991) for the north Kimberley rainforests. Each plot was then assigned to one of the following vegetation classes based on the mapping for 1949, 1969 and 2005: 'stable rainforest' plots were those mapped as 'rainforest' during all the investigated years; 'converted to rainforest in 1969' were plots mapped as 'savanna' in 1949 and 'rainforest' in 1969; 'converted to rainforest in 2005' plots were mapped as 'savanna in 1969' and 'rainforest' in 2005;

‘stable savanna’ plots were mapped as ‘savanna’ during the entire length of the study. Fire frequency was calculated for each plot based on 15-year data obtained from North Australia Fire Information (NAFI; available at www.firenorth.org.au), based on MODIS products displayed at a resolution of 250m.

3.3.6 *Statistical analyses*

All analyses were performed using the software R (R Core Team, 2013). To assess variation in patch size and convolution we employed generalized linear models (GLMs), using the Gamma family of distribution (link = “log”). Patch size and convolution were response variables and year and location were explanatory variables. For each location we calculated differences in the proportion of rainforests located on different topographic settings in the years 1949, 1969 and 2005.

To evaluate how environmental variables affected the conversion from savanna to rainforest in each time period, we randomly selected a subset of 5,000 grid cells within 60 m of a rainforest patch (selected as described above), stratified for vegetation type. We employed GLMs, considering the response variable as binary: 1 - savanna converted to rainforest, or 0 - savanna remained savanna, and using binomial models (link ‘logit’). We tested the relationship between the response variable and TPI, distance from the coastline, location, area, and convolution of the nearest patch, distance from the nearest patch, and North-South and East-West components of both aspect and bearing angle. Spatial autocorrelation was assessed by plotting semi-variograms of model residuals. As only few cells underwent a conversion from rainforest to savanna, no analyses on that vegetation change were performed.

To determine differences in fire activity between the two study locations, we employed GLMs and the Gaussian distribution. Differences in cattle impact between vegetation classes located on the Mitchell Plateau were tested using ordinal logistic regression (package ‘MASS’, Venables and Ripley, 2002) and the influence of cattle impact on the number of seedlings was investigated using the Poisson distribution.

GLMs were also used to test whether the disturbance levels, and environmental and vegetation characteristics recorded in each plot and listed below varied between

locations (Mitchell Plateau or Bougainville Peninsula) for plots within the same vegetation class (e.g. ‘stable savanna’). For these analyses the two classes ‘converted to rainforest in 1969’ and ‘converted to rainforest in 2005’ were merged due to the limited number of plots. When required, data were log transformed to meet the assumption of normality. Within the GLMs, the Poisson distribution (log link) was used for count data such as the number of seedlings, number of trees, species richness. The binomial distribution (logit link) was used to assess differences between locations in the proportion of rainforest and savanna species per plot, while the Gaussian distribution (identity link) was used for the response variable basal area. Differences in grass cover and rock cover were assessed using ordinal logistic regression.

For all the modelling we employed complete subset regression and Akaike’s Information Criterion (AIC; Burnham and Anderson, 2002) to evaluate models. To do this, candidate sets were constructed with models containing all possible combinations of explanatory variables, without interactions. Akaike weights (w_i) were calculated for each model to indicate the probability that a given model is the best in the candidate set (Burnham and Anderson, 2004). The importance of single variables (w_+) was calculated as the sum of w_i of the models within the set in which the variable occurred. Variables were considered important predictors if w_+ exceeded 0.73, as per Murphy *et al.* (2010). Summaries of all analyses are reported in Tables A2.1 and A2.2 in Appendix 2.

To compare variation in canopy across the rainforest-savanna boundary in the Mitchell Plateau and the Bougainville Peninsula, we calculated the average canopy cover profile for each location. To detect the presence of distinct vegetation states we also tested differences in canopy cover modality employing latent class analysis (Hirota *et al.*, 2011). To do this, we analysed the frequency distribution of canopy cover data, pooled for all plots within the vegetation transects at each location. We compared the fit of models with 1, 2 or 3 modes using the Bayesian Information Criterion (BIC). More details are given in Appendix 2 (Table A2.3).

3.4 RESULTS

3.4.1 Rainforest expansion/contraction

During the 20-year time period 1949-1969, the north Kimberley experienced expansion of rainforest cover. The extent of expansion varied depending on the location: rainforests expanded by 52%, equivalent to 4.25 km ha^{-1} , on the Bougainville Peninsula, and only by 9%, corresponding to 0.12 km ha^{-1} , on the Mitchell Plateau (Figs. 3.3a, b).

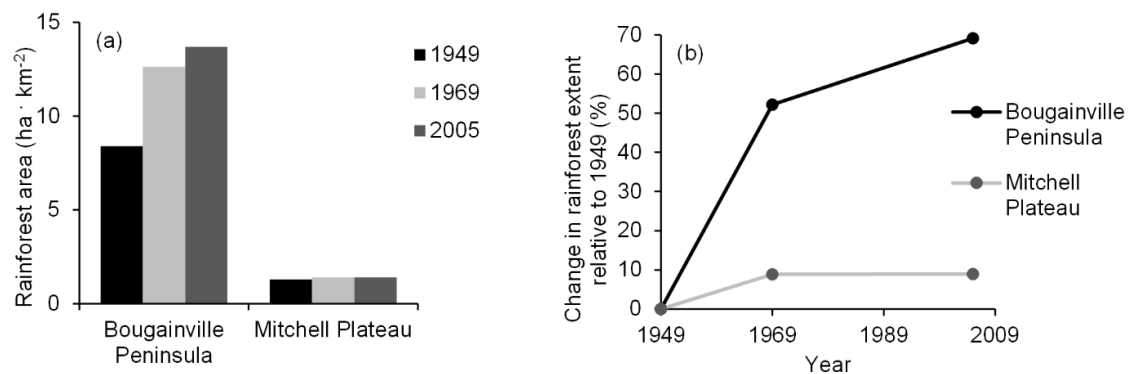


Figure 3.3 Rainforest extent over time in the studied locations. The graphs show a) rainforest area during 1949, 1969 and 2005, expressed as proportion of total land, and b) proportion of change in rainforest extent, relative to the baseline year 1949.

During the 36-year time period 1969-2005 the expansion continued at a lower rate on the Bougainville Peninsula, reaching an overall expansion of 69%, whereas on the Mitchell Plateau rainforest extent remained stable. On the Bougainville Peninsula, areas of contraction were recorded during both time periods, although always compensated by an overall higher proportion of expanded rainforest. At both sites rainforests consistently preferred slopes, valleys and ridges (Fig. 3.4).

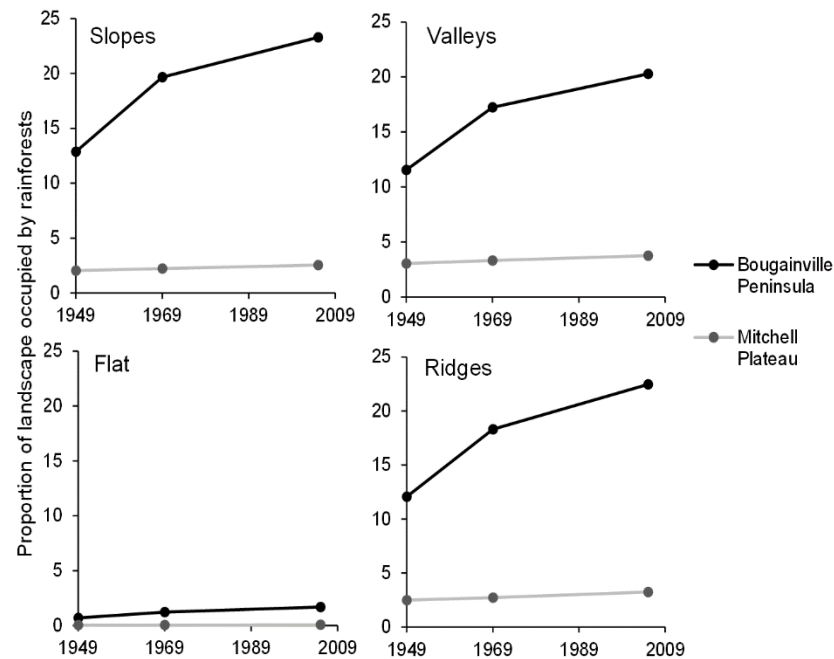


Figure 3.4 Proportion of landscape occupied by rainforest in slopes, valleys, flat areas, and ridges in the studied locations over time, from 1949 to 2005.

3.4.2 Patch characteristics

In 1949 a total of 1668 patches, covering 3% of the land, were mapped, and this area increased during the 20-year period to 1969, with a smaller increase between 1969 and 2005 (Table 3.1). There were marked differences in trends between the Mitchell Plateau and the Bougainville Peninsula in terms of patch density, individual patch size and convolution. At all three observation times, patches on the Mitchell Plateau were smaller ($w_+ = 1.00$) and more compact ($w_+ = 1.00$) than those on the Bougainville Peninsula. Patch size and density increased on the Bougainville Peninsula, while on the Mitchell Plateau there was no substantial change in average patch size over the entire 56-year time frame (Fig. 3.5a, b), but a small increase in patch density was detected between 1949 and 1969. Rainforests on the Bougainville Peninsula were bigger in 1969 and less convoluted in 2005 compared with 1949 (Fig. 3.5b, c).

Table 3.1 Total number of rainforest patches, rainforest extent, and proportion of land covered by rainforest for the years 1949, 1969 and 2005 in the Bougainville Peninsula (BP), Mitchell Plateau (MP) and the entire study area.

Year	Number of patches			Rainforest extent (ha)			Rainforest cover (ha · km ⁻²)		
	BP	MP	Total	BP	MP	Total	BP	MP	Average
1949	759	776	1668	2504	968	3786	8.4	1.3	3.5
1969	908	831	1891	3770	1053	5230	12.6	1.4	4.8
2005	989	869	2053	4085	1054	5713	13.7	1.4	5.2

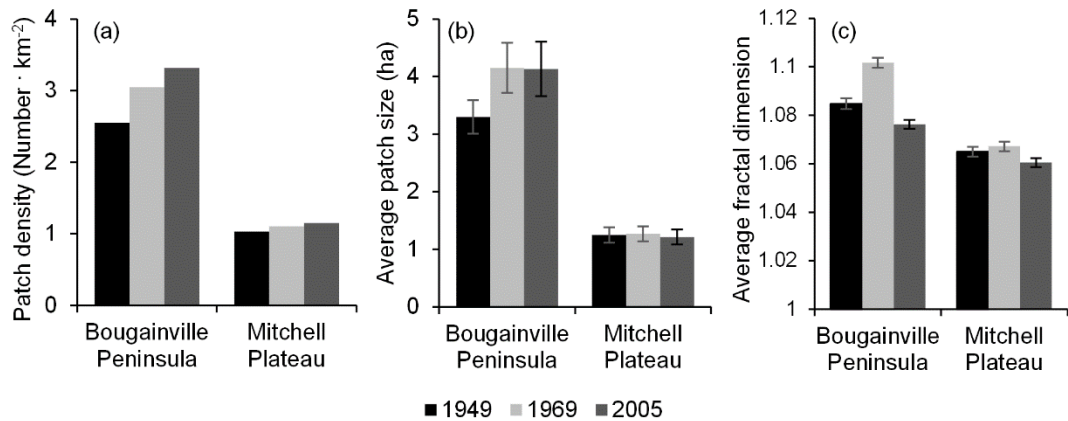


Figure 3.5 Patch characteristics in the Bougainville Peninsula and Mitchell Plateau in the years 1949, 1969, and 2005. (a) patch density, expressed as number of rainforest patches normalized by the location area, (b) average patch size, and (c) average fractal dimension of rainforest patches. Error bars represent standard errors.

3.4.3 Correlates of rainforest expansion

Model selection showed that between 1949 and 1969, the local variables that affected rainforest expansion were: convolution and area of the original patch, distance from patch edge, and TPI (Table 3.2). Areas on the Bougainville Peninsula, and those close to the edge of bigger and more convoluted patches, were more likely to convert from

savanna to rainforest. The same variables affected the expansion of rainforests between 1969 and 2005. During this period, rainforests were also more likely to establish on the northern side of already existing patches and close to the coast (Table 3.2). On the Bougainville Peninsula there was substantial expansion on flat locations during both periods, but this was not evident on the Mitchell Plateau (Fig. 3.4). The best models for both periods explained 22% of the deviance.

Table 3.2 Explanatory variables included in the models assessing the likelihood of a savanna cell, located within 60 m to a rainforest patch, to convert in a rainforest cell. The importance of each variable is expressed as $w+$, the probability of the factor to be included in the best model. The direction of the effect is indicated within brackets: + positive, or – negative for continuous variables; for categorical factors the categories positively affecting the conversion to rainforest are shown. Variables with $w+$ values > 0.73 (in bold) are considered important predictors.

Variable	$w+$	
	Time period	Time period
	1949-1969	1969-2005
Location (Bougainville Peninsula)	1.00	1.00
Fractal dimension (+)	1.00	1.00
Patch area (+)	1.00	0.98
Distance from rainforest edge (-)	1.00	1.00
TPI (slopes, ridges, and valleys)	1.00	1.00
Distance from the coastline (-)	0.27	1.00
Expansion North-South (North)	0.40	0.97
Expansion East-West (West)	0.44	0.32
North-South component of aspect (North)	0.31	0.40
East-West component of aspect (West)	0.30	0.28

3.4.4 Disturbance

No sign of cattle was found in any of the plots on the Bougainville Peninsula. On the Mitchell Plateau, cattle presence was detected in 62% of the plots, with no substantial differences in the intensity of cattle impact among vegetation classes ($w+ = 0.51$; Table A2.4). The intensity of cattle grazing was negatively correlated with tree seedling density in savannas ($w+ = 1.00$), but not in rainforests ($w+ = 0.63$). Fire frequency was lower on plots located on the Bougainville Peninsula ($w+ = 1.00$).

3.4.5 Floristics and vegetation structure

We identified 82 species belonging to the rainforest flora in plots on the Bougainville Peninsula, and 71 in those on the Mitchell Plateau. Most records were of species commonly found in Kimberley rainforests, with the exception of *Pouteria richardii* (F. Muell.) Baehni, found on the Bougainville Peninsula and never recorded before in Western Australia. Species composition was uniform within rainforest patches; of the species sighted at least five times, only four rainforest species were found exclusively on the patch edge (*Bridelia tomentosa* Blume, *Ficus aculeata* Miq., *Flueggea virosa* (Willd.) Voig, and *Trema tomentosa* (Roxb.) Hara), and only two were limited to the patch core (*Diospyros maritima* Blume and *Meiogyne cylindrocarpa* (Burck) Heusden). The savanna flora had similar richness in the Bougainville Peninsula and Mitchell Plateau (29 and 31 species respectively). However, while all the savanna species identified on the Mitchell Plateau are common throughout the north Kimberley, on the Bougainville Peninsula we detected uncommon species recorded in only a few sites in Western Australia, such as *Eucalyptus oligantha* Schauer, and *Xanthostemon psidioides* (Lindl.) Peter G. Wilson & J.T. Waterh. The latter is considered near threatened in Western Australia. We also recorded two species thought not to grow in the north Kimberley *Acacia drepanocarpa* subsp. *latifolia* Pedley and *Vachellia ditricha* (Pedley) Kodala (Atlas of Living Australia website at <http://www.ala.org.au>; Western Australian Herbarium, 1998-). Some of the savanna elements detected only on the Bougainville Peninsula, such as acacias (*Acacia hemignosta* F. Muell. *A. stigmatophylla* Benth, *A. drepanocarpa* subsp. *latifolia* Pedley),

are known to be sensitive to frequent fires (Russell-Smith *et al.*, 2010b). The full list of species is reported in Table A2.5 in Appendix 2.

Abrupt changes in vegetation characteristics were detected across rainforest-savanna boundaries on the Mitchell Plateau, while on the Bougainville Peninsula the differences were less apparent (Table A2.6, Fig. 3.6). The floristic composition and vegetation structure of stable and expanded rainforests were very similar at the two study locations, with the exception of higher tree and seedling density on the Bougainville Peninsula ($w+ = 0.92$ and $w+ = 1.00$ respectively, Table A2.7). Stable rainforests also had more seedlings ($w+ = 0.84$) and a higher proportion of rainforest species ($w+ = 1.00$) compared with recently expanded rainforests. For the savannas, there were clear differences between the two location, with signs of rainforest invasion on the Bougainville Peninsula. Indeed, every savanna quadrat on the Bougainville Peninsula contained rainforest species in the understorey, compared with only 27% on the Mitchell Plateau. Consequently, savannas on the Bougainville Peninsula displayed greater species richness ($w+ = 1.00$), due to more rainforest species per plot ($w+ = 1.00$). The Bougainville Peninsula's savannas also had higher densities of adult trees and seedlings ($w+ = 0.88$ and $w+ = 1.00$ respectively), and greater grass cover ($w+ = 0.87$).

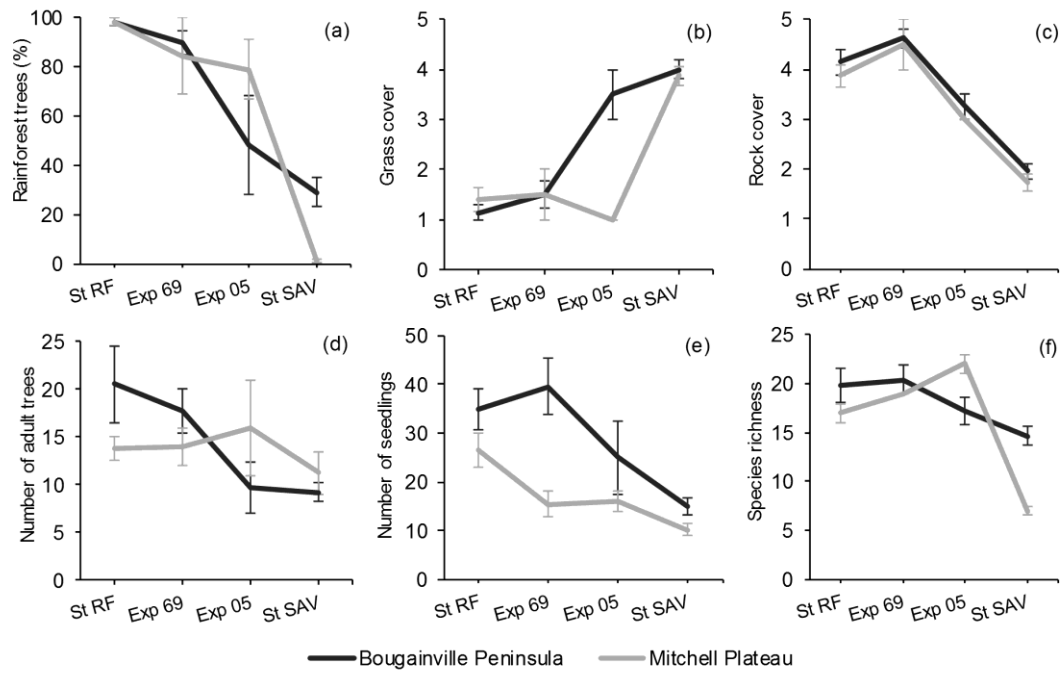


Figure 3.6 Average plot values of a) proportion of rainforest plants amongst the adult trees, b) grass cover, c) rock cover, d) number of adult trees, e) number of seedlings, and f) species richness in the two study locations for each vegetation class: (St RF) stable rainforests, (Exp 69) converted to rainforest in 1969, (Exp 05) converted to rainforest in 2005, (St SAV) stable savannas. Error bars represent standard errors.

The invasion of rainforest species into the savanna on the Bougainville Peninsula resulted in contrasting profiles of tree canopy cover across the rainforest-savanna boundaries at the two locations. There was a gradual change in canopy cover across boundaries on the Bougainville Peninsula compared with abrupt boundaries on the Mitchell Plateau (Fig. 3.7). Furthermore, frequency distribution of canopy cover on the Mitchell Plateau transects displayed the bimodality characteristic of two distinct vegetation states (Fig. 3.8, Table A2.3). By contrast, the unimodal canopy cover model, corresponding to blending of vegetation, was the best model for the Bougainville Peninsula.

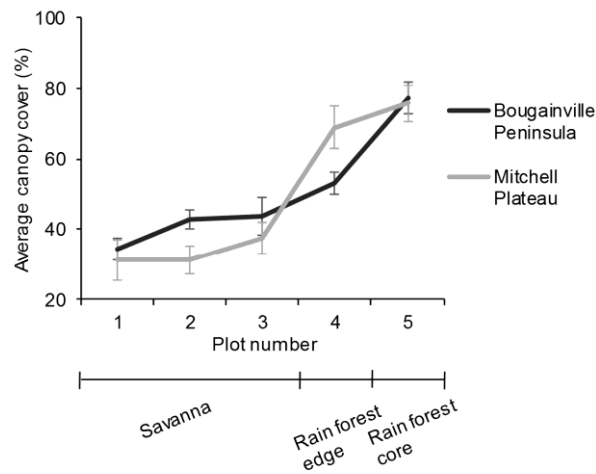


Figure 3.7 Average canopy cover recorded in the vegetation transects running across the rain forest-savanna boundary. In the Mitchell Plateau there was a steep increase in canopy cover in at the edge of the rain forest, while on the Bougainville Peninsula canopy cover increased gradually. Error bars represent standard errors.

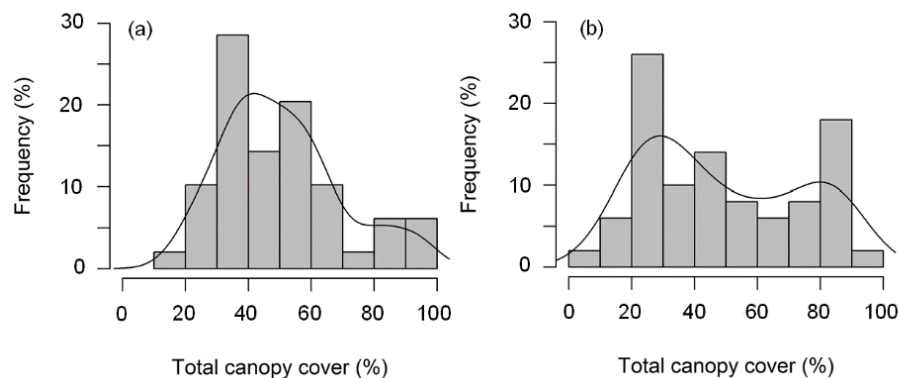


Figure 3.8 Probability density distribution of total canopy cover (trees and shrubs) in our study transects, illustrating a) unimodal distribution on the Bougainville Peninsula and b) bimodal distribution in the Mitchell Plateau, as indicated by the lowest BIC value. These patterns reflect the distinct vegetation boundary in the Mitchell Plateau, and blurring of the boundary due to rainforest expansion on the Bougainville Peninsula.

3.5 DISCUSSION

Our natural experiment in the north Kimberley, based on two geographically similar areas with contrasting disturbance regimes, revealed significant differences in vegetation structure and in the rate, magnitude, and environmental correlates of rainforest expansion in time. Specifically, the study design combined historical aerial photography and field measurements to address three predictions: (a) rainforest expansion has occurred in the north Kimberley concurrently with the trend of increasing precipitation and/or atmospheric CO₂ (b) this trend was locally influenced by the combined effects of fire and megaherbivores and (c) areas subject to high disturbance have different boundaries and patch shapes from less disturbed areas. Below we discuss our findings with respect to the current theories on rainforest-savanna dynamics.

The two study locations have similar climates, with mean annual precipitation towards the lower limit of rainforests in Australia and globally (Bowman, 2000). In the area, annual rainfall increased from an estimated 1080 mm to 1280 mm during the period 1949 and 2005, consistent with increasing precipitation and longer wet seasons observed in north-western Australia in the past decades (Feng *et al.*, 2013, Bureau of Meteorology, 2016). The positive correlation between wetting trends and rainforest expansion in the north Kimberley is consistent with findings of previous studies in the Australian tropics, which associated increased rainfall with rainforest expansion (Banfai and Bowman, 2006, Bowman *et al.*, 2010a) or savanna woody thickening (Lehmann *et al.*, 2009). However, we used space-for-time substitution and data for current rainforest cover in monsoonal Australia (Ondei *et al.*, 2017) and estimated that this increase in rainfall corresponds to a 41% relative increase in the 95th percentile of rainforest cover (Fig. A2.1). It is therefore improbable that wetting trends are solely responsible for the 69% increase in rainforest cover observed on the Mitchell Plateau. Elevated CO₂ has also been associated with enhanced tree growth and recruitment (Kgope *et al.*, 2010) and resprouting of seedlings after defoliation, potentially contributing to shift savannas towards a tree-dominated state (Bond and Midgley,

2000, Hoffmann *et al.*, 2000, Buitenwerf *et al.*, 2012). We also cannot rule out relaxation of disturbance regimes contributing to the rainforest expansion.

Our experiment was designed to compare locations with similar climate and geology, and thus amounts of nutrients derived from the parent material. Yet, remarkable differences in rainforest expansion were detected between the Mitchell Plateau and the Bougainville Peninsula, suggesting that rainforest distribution is not determined by resources alone. Furthermore, our results showed that on the Bougainville Peninsula, rainforest expanded into infrequently burnt savannas across all landscape settings, while on the Mitchell Plateau rainforest expansion was constrained to slopes, valleys and ridges. These differences highlight the importance of disturbance history in modifying the expansion of rainforest. The frequently burnt savannas on the Mitchell Plateau had structurally abrupt and floristically distinct rainforest-savanna boundaries, consistent with the view that fire maintains a sharp transition between these two vegetation types (Dantas *et al.*, 2013a, 2016). Elevated fire activity may also explain the very restricted patches and their limited convolutions. By contrast, on the Bougainville Peninsula the lower fire activity resulted in large, convoluted patches that occurred across a range of landforms. Grass cover was higher in savannas on the Bougainville Peninsula than the Mitchell Plateau, and a striking feature of the Bougainville Peninsula's savannas was the admixture of savanna and rainforest trees. Because of the low fire frequency in the savanna on the Bougainville Peninsula, rainforest trees, including some species not found elsewhere in the Kimberley, were able to grow even where the canopy was not yet closed sufficiently to exclude grasses (Lawes *et al.*, 2011b). The rarity of anthropogenic ignitions on the Bougainville Peninsula and its fire-protected position have possibly caused this anomaly. Here, the main limitation to rainforest tree growth appears to be competition with savanna trees and grasses for resources (Bond, 2008). By contrast, on the Mitchell Plateau, frequent disturbance also imposes a constraint on rainforest tree growth.

The invasion of cattle on the Mitchell Plateau during the time period 1969-2005 is likely to have accentuated the differences in rainforest expansion between the Mitchell Plateau and the Bougainville Peninsula, through direct and indirect effects. Cattle may

have limited the expansion of patches on the Mitchell Plateau, because trampling and browsing of juveniles likely contributed to lower seedling density. Cattle may also have increased grass cover by opening up understories on rainforest boundaries, thereby increasing fire activity (Mckenzie and Belbin, 1991, Staver *et al.*, 2009, Camargo-Sanabria *et al.*, 2015, Fleury *et al.*, 2015).

Because our natural experiment was based on only two locations (and hence $n = 1$), we cannot rule out the possibility that factors other than those we tested contributed to differences in rainforest structure, distribution, and expansion, as the study is pseudoreplicated, due to the lack of multiple disturbed and undisturbed locations. Nonetheless, by removing climatic and geological differences from our study design, we showed that fire activity probably has a primary role in driving vegetation dynamics (Hoffmann *et al.*, 2012a, Lawes *et al.*, 2011b, Murphy and Bowman, 2012), with cattle herbivory perhaps playing a subsidiary role. On fertile substrates and when freed from disturbance, rainforests can occupy a larger range of landscapes than is typically observed. We found that the expansion of rainforests into unburnt savannas resulted in ecotonal vegetation that blends the floristic and structural elements of both vegetation types. This highlights the importance of fire regimes in shaping vegetation structure and floristic composition in regions where savanna and rainforest co-exist (Dantas *et al.*, 2013a). It is possible that, prior to Aboriginal colonisation and the marsupial megafaunal extinctions, there would have been a less pronounced dichotomy between savannas and rainforests, and long-lasting transitional states such as those that now occur on the Bougainville Peninsula may have been present. Analysis of pollen, charcoal and *Sporormiella* records in north-east Australia have been interpreted as showing that the extinction of marsupial megafauna following human colonisation led to a transition from relatively open and mixed rainforest-sclerophyll forest to pure sclerophyll vegetation and an increase in fire activity (Rule *et al.*, 2012). Aboriginal fire management possibly sharpened boundaries between savanna and rainforests, maintaining fire sensitive vegetation in a matrix of flammable savanna (Trauernicht *et al.*, 2015).

Across northern Australia, contemporary disturbance regimes, which include frequent landscape burning and widespread cattle grazing, are thought to be contributing to the decline of many small to medium sized mammals due to loss of shelter and food resources (Legge *et al.*, 2011a, Woinarski *et al.*, 2015). In this context, the cattle-free and rarely burnt Bougainville may be important for biodiversity, by offering more long-unburnt habitats for large numbers of threatened small to medium sized mammals and fire-sensitive floristic elements rarely found elsewhere in northern Australia (Radford *et al.* 2015, Woinarski *et al.* 2004).

Chapter 4

Post-fire resprouting strategies of rainforest and savanna saplings along the rainforest-savanna boundary in the Australian monsoon tropics

This chapter is published in *Plant Ecology*

4.1 ABSTRACT

In tropical areas where climatic conditions support both rainforests and savannas, fire is considered one of the main factors determining their distribution, particularly in environments where growth rates are limited by water availability. The observed expansion of some rainforests into savannas suggests that rainforest saplings could have traits that enable them to survive in the savanna environment, including recovering from infrequent fires. We applied the Clarke *et al.* (2013) buds-protection-resources (BPR) framework to the rainforest-savanna system of the north Kimberley (Western Australia), to compare the resprouting response of five savanna species saplings burnt by an ambient early dry season fire with seven rainforest species saplings burnt using an experimental treatment that mimicked a savanna fire. Most plants survived the fire, although plant mortality was higher for rainforest (19%) than savanna (2%) individuals, as was stem mortality (37% vs. 12%). All rainforest and savanna species expressed aerial resprouting; two of the savanna species and two of the rainforest species did not express basal resprouting. After one year most savanna individuals had more and longer shoots than the rainforest saplings and had regained their original height while rainforest plants were on average 43% shorter than their pre fire height. These results suggest that, although rainforest species are less able to escape the ‘fire trap’ than savanna species, they are able to recover from a low intensity fire.

4.2 INTRODUCTION

Boundaries between rainforest and savanna provide important insights into the feedbacks between vegetation type and fire activity under a common climate (Murphy and Bowman, 2012). Fire activity is higher in savannas because of the abundance of flammable C4 grass biomass, which supports frequent fires with a high rate of spread and long flame lengths compared to forests; the latter have less frequent and lower intensity fires, owing to dense litter fuels beds and a moister and more shaded microclimate (Hennenberg *et al.*, 2006, Hoffmann *et al.*, 2012b, Little *et al.*, 2012,

Ratnam *et al.*, 2011). Savanna fire regimes present a powerful filter of tree species, selecting for ensembles of traits relating to fire resistance and recovery. For example, savanna species have thicker bark compared to rainforest species (Brando *et al.*, 2012, Dantas *et al.*, 2013a, Hoffmann *et al.*, 2012a, Lawes *et al.*, 2013, Pausas, 2015b), rendering them less vulnerable to thermal shock (Lawes *et al.*, 2011c) and stem death ('top kill'). Nonetheless, rainforest species also show capacity to regenerate via aerial and basal shoots after a low-moderate intensity fire (Bowman, 1991, Bowman and Panton, 1993, Campbell and Clarke, 2006, Hoffmann *et al.*, 2004, Marrinan *et al.*, 2005, Müller *et al.*, 2007, Poorter *et al.*, 2010, Williams, 2000, Williams *et al.*, 2012, Zimmer *et al.*, 2015).

Frequent burning is recognised as one of the main constraints to rainforest seedling establishment, causing rainforest plants to suffer higher mortality compared with savanna plants (Bowman and Panton, 1993, Fairfax *et al.*, 2009, Fensham *et al.*, 2003, Gignoux *et al.*, 2009, Hoffmann *et al.*, 2000, Hoffmann *et al.*, 2004, Müller *et al.*, 2007, Rossatto *et al.*, 2009, Russell-Smith *et al.*, 2004). Nonetheless, rainforests have been reported expanding into savannas. Descriptive studies on the Bougainville Peninsula and nearby islands in the north Kimberley recognised rainforest elements colonising savanna (Beard *et al.*, 1984). Elsewhere in northern Australia, some encroachment of rainforests into the surrounding savanna has occurred (Banfai and Bowman, 2006, Bowman *et al.*, 2001, Clayton-Greene and Beard, 1985, Russell-Smith *et al.*, 2004, Tng *et al.*, 2012a) despite a recent increase in the extent, frequency and severity of savanna fires associated with regional declines in biodiversity (Radford, 2010, Trauernicht *et al.*, 2013). It has been asserted that rainforests are encroaching into frequently burnt savannas because of enhanced growth rates in response to increasing atmospheric CO₂ and mean annual precipitation over the last 50 years (Banfai and Bowman, 2006, Bowman *et al.*, 2010a). This expansion raises intriguing questions concerning the comparative fire tolerance and post-fire recovery of savanna and rainforest trees. Quantifying these differences is essential for understanding the potential of state shift between rainforest and savanna. There has been recent focus on the role of bark in affording fire protection (Brando *et al.*, 2012, Lawes *et al.*, 2011c, Pausas, 2015b), how this trait varies across forest-savanna

boundaries (Dantas *et al.*, 2013a, Hoffmann *et al.*, 2012a), and post fire recovery of temperate rainforest juveniles growing in nursery conditions (Zimmer *et al.*, 2015). However, to date there have been no comparative studies of the regeneration strategies of tropical savanna or rainforest saplings using experimental burning conditions in their natural environment.

We hypothesised that (i) there are marked differences in regeneration strategies amongst savanna and rainforest species, reflecting differences in both sensitivity to and recovery from fire. This influences the dynamics of the boundary between these contrasting vegetation types; (ii) rainforest plants can recover after a mild fire, although less efficiently than savanna plants. To test these hypotheses, we undertook a burning experiment on a rainforest-savanna boundary in the Mitchell Plateau (north Kimberley, Western Australia) to determine the responses of the rainforest trees to a simulated savanna fire. We did this by exposing rainforest saplings located along the forest boundary to flames that are comparable, in terms of temperature and intensity, to observed savanna fires. Seeking to explain differential responses in terms of bark thickness and the position of regenerative shoots, we recorded the mortality, and the type and extent of vegetative recovery of the rainforest species. We followed the classification designed by Clarke *et al.* (2013), which provides an important conceptual framework to understand the resprouting strategies of woody species in response to fire regime based on the position and protection of regenerative buds and the allocation of resources, known as the buds-protection-resources (BPR) framework. We made similar observations and analyses of savanna species burnt by an ambient low severity fire, which allowed qualitative comparisons of the responses of savanna and rainforest species.

4.3 METHODS

4.3.1 Study site

The Mitchell Plateau is located at the driest end of the Australian rainforest's climatic range (Bowman, 2000). The land surface is intensely weathered Precambrian basalt resulting in a landscape with rounded hills and low mesas capped by laterite (Beard, 1979). Average elevation is 200 m asl (range: 0 – 500m asl). The climate is monsoonal, with a pronounced austral summer wet season (November to April) with the remainder of the year rain-free. Average yearly rainfall is above 1300 mm, higher than the Kimberley average of about 700 mm per year (Craig, 1997); a trend to increasing precipitation has been observed since the middle of last century (Reisinger *et al.*, 2014). The average daily maximum temperature exceeds 30°C every month, but average daily minimum temperature ranges from 14°C in austral winter months to 25°C in austral summer months (Bureau of Meteorology, 2016).

Eucalypt savanna is the main vegetation of the area, with *Eucalyptus tetrodonta* – *E. miniata* savanna dominating the laterite mesas and hills and *E. tectifica* – *E. grandifolia* savanna common in deeper, clay soils on plains dominated by perennial tussock grasses with some annual sorghum (*Sarga timorensse*) on drier and shallower sites. Interspersed in these savannas are small patches of rainforests with a mix of deciduous and evergreen species, typically in fire-sheltered landscape settings (Beard, 1979, Beard, 1990). There is concern that some rainforests are being degraded by the current fire regime, which is characterised by extensive frequent fires (Vigilante *et al.*, 2004). Nonetheless, some rainforests in this region have been shown to invade into long unburnt savannas (Beard *et al.*, 1984).

The study was conducted in a rainforest patch at a place called *Yalgi* by the Wunambal Gaambera people, located within the Yalgi Aboriginal Reserve, 11 km far from Kandiwal Aboriginal Community in the valley of Camp Creek (Fig. 4.1).

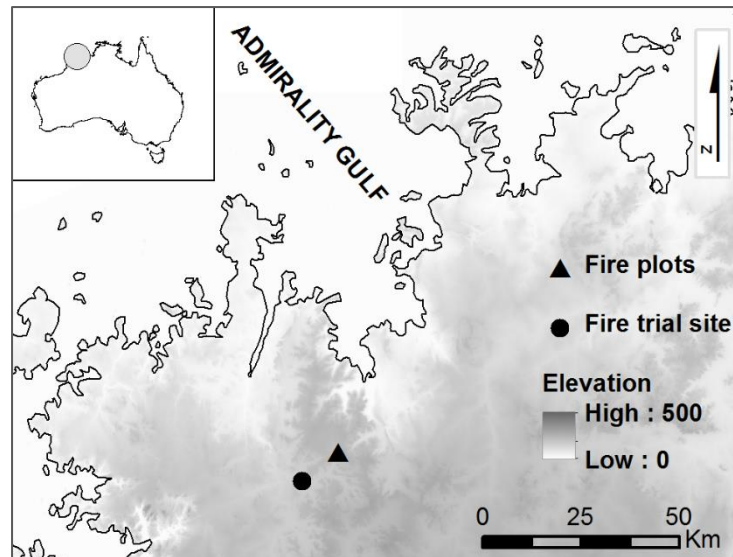


Figure 4.1 Location of the rainforest study site on the Mitchell Plateau in northern Australia (14.888° S, 125.770° E). Elevation is indicated.

The surrounding *E. tectifica* – *E. grandifolia* savanna has been burnt 8 times in the last 13 years (North Australian Fire Information; NAFI, 2016). The boundary that separates the two vegetation types is very sharp across a gradual slope, where the savanna occurs on soils with little surface rock cover and the rainforest occurs on soils with variable rock cover (Fig. 4.2).



Figure 4.2 Abrupt boundary between the monsoon rainforest (left) and the surrounding savanna (right) at Yalgi, on the Mitchell Plateau, northern Australia.

4.3.2 Definition of resprouting

We followed the Clarke *et al.* (2013) framework to record regeneration strategies of rainforest and savanna species. Amongst the described key regeneration types are ‘aerial resprouters’ and ‘basal resprouters’. The ‘aerial resprouters’ type is broken down into subtypes including ‘axillary resprouters’, characterised by survival of the main aerial stem with the regenerative process occurring through axillary buds protected by the leaf base, and ‘epicormic resprouters’, which possess accessory buds protected by the bark. Amongst the ‘basal resprouters’ type the ‘collar resprouters’ subtype is defined by death of the main stem with regeneration occurring from buds located at the stem base beneath the bark.

4.3.3 Savanna fire intensity

Practical and ethical issues concerning lighting fires in the rare, small and potentially threatened north Kimberley rainforests required the use of a gas burner to simulate a mild savanna fire rather than setting fires in the rainforest. The gas burner method has already been used to simulate fire effects in other savanna studies (e.g. Bowman *et al.*, 2014). In order to apply a representative treatment, we first measured the residence time, temperature and intensity of an actual savanna fire. To achieve this, we set fires in the early dry season on two plots 4000 m² in area outside Kandiwal community (Fig. 4.1). The fires were set at 4 p.m. on 27 June 2013. A portable meteorological station showed that during the controlled burn the wind speed was 10 km h⁻¹, humidity was 53% and air temperature 29.2°C. The average temperature of flames 1.5-2 m high, measured using a thermocouple mounted at the end of a rigid wire, was 387°C ±16 (SE). Fire intensity was estimated using Byram’s fire-line intensity (Byram, 1959):

$$I = Hwr$$

where I is fire intensity (kW m⁻¹), H is heat of combustion (17781 kJ kg⁻¹; Trollope, 1984), w the mass of fuel combusted (kg m⁻²) and r the rate of spread of the head fire front (m s⁻¹). Data were collected following the methods of Trauernicht *et al.* (2012): fuel load was assessed cutting and weighting the standing biomass of litter and dead

and live graminoids from five, randomly placed 1x1 m quadrats collected before and after the fires. Rate of spread was calculated from the time elapsed for the fire front to pass through two pair of points located 20 m apart (Pérez and Moreno, 1998). These measurements showed that the rate of spread was 0.11 m s^{-1} , and fuel consumption averaged $0.153 \text{ kg m}^{-2} \pm 0.087 \text{ SE}$, about 60% of the standing biomass. We thereby estimated the intensity of fire at 300 kW m^{-1} . Scorch heights were measured on the two plots to provide an alternative estimate for fire intensity, using the empirical relationship described between scorch height and fire intensity in Australian tropical savannas by Setterfield *et al.* (2010). Scorch height of the fire ranged from 0.9 to 4 m (average $2.42 \text{ m} \pm 0.22 \text{ SE}$), falling within the low intensity ($<1000 \text{ kW m}^{-1}$) range of savanna fires as defined by Russell-Smith and Edwards (2006). We also estimated the energy of these fires at ground level by using five aluminium drink cans filled with 50 g of water as open-calorimeters, and five cans were placed away from the fire to account for ambient evaporation. Water loss was used as a proxy for the energy released by the fires which was calculated using the following formula:

$$Q = mL_v$$

where Q is the latent heat, m is the mass of water lost and L_v is the latent heat of vaporization ($2.26 \times 10^6 \text{ J kg}^{-1}$ for water) (Pérez and Moreno, 1998). This showed the energy absorbed by the cans was $5.0 \text{ kJ} \pm 1.0 \text{ (SE)}$.

Informed by the above measurements we burnt the rainforest plants using a butane gas burner. The above ground portions of the plants were bathed in flames by evenly sweeping the burner up and down the axis of the stem for 60 seconds and using a thermocouple to ensure the flame was at 300 to 500 °C. We validated this treatment in two ways. First, ten replicate aluminium cans were placed on the ground and exposed to the gas burner flame using the same procedure and we recorded the mass of water lost at ground level, while accounting for ambient evaporation losses. This showed our burning treatment caused the cans to absorb $3.0 \text{ kJ} \pm 1.6 \text{ (SE)}$ from the gas flame, which is slightly lower than the values obtained from the savanna fires. Second, we calculated the fire intensity (kW m^{-1}) from the burner using the flow rate of the butane, the energy density of this gas (47 MJ per kg), and the width of the flame (11.5

cm). This showed that the gas burner treatment produced a fire intensity of 290 kW m⁻¹, similar to the intensity of the savanna fires.

4.3.4 Rainforest fire trial

Seven rainforest species were selected for the experiment: *Atalaya salicifolia* (A.DC.) Blume (Sapindaceae), *Canarium australianum* F.Muell. (Burseraceae), *Ficus aculeata* Miq. (Moraceae), *Sterculia quadrifida* R.Br. (Malvaceae), *Strychnos lucida* R.Br. (Loganiaceae), *Terminalia petiolaris* Benth. (Combretaceae), *Vitex acuminata* R.Br. (Lamiaceae). We focused on rainforest plants located along the boundary because some of these species are known to colonise unburnt savanna elsewhere in this region (Vigilante and Bowman, 2004). For each species, 10 individuals across a range of sizes were selected, from 50 cm to 300 cm height (i.e. combined juveniles and small saplings classes of Werner and Prior (2013); all would be beneath the mean typical flame height of a savanna fire), and stem height and basal diameter were measured. Following the guidelines in Perez-Harguindeguy *et al.* (2013), bark thickness was recorded as the average of two measurements obtained by peeling the bark at the stem base and measuring it with digital callipers (0.01mm). These callipers were sensitive enough to detect differences in the thin bark of rainforest saplings. Relative bark thickness was used for interspecies comparison and was calculated as the ratio of individual bark thickness to stem diameter (Lawes *et al.*, 2013).

The rainforest species were burnt in June 2013 using a gas burner. In August 2014 we recorded (i) whether the plants survived the treatment; (ii) the regenerating strategy of all surviving individuals according to the Clarke *et al.* (2013) framework (i.e. epicormic, axillary, and basal resprout); (iii) living stem height; (iv) number of shoots, which we operationally defined as having at least one fully expanded leaf; and (v) length of the longest shoot. Relative height difference pre- and post-fire was calculated as the difference between the initial stem height and the stem height after one year (August 2014), expressed as a percentage. Because of lost tags, the post-fire response of 6 stems could not be assessed.

4.3.5 Savanna species post-fire recovery

It was not possible to repeat for savanna species the same procedure adopted for rainforest plants, due to the high grass biomass and the associated risk of uncontrolled fire. A low severity (*sensu* Russell-Smith and Edwards, 2006), early dry season fire occurred in a portion of the savanna on the perimeter of the Yalgi rainforest two months before the rainforest fire treatment (NAFI, 2016), providing the opportunity to gather data from savanna plants for a qualitative comparison of the two vegetation types. The five savanna species selected for study were *Corymbia confertiflora* (F.Muell.) K.D.Hill & L.A.S.Johnson (Myrtaceae), *Erythrophleum chlorostachys* (F.Muell.) Baill. (Fabaceae), *Eucalyptus tectifica* F.Muell. (Myrtaceae), *Planchonia careya* (F.Muell.) R.Knuth (Lecythiadaeae), and *Terminalia canescens* (DC.) Radlk. (Combretaceae). The measurement protocol and time of sampling was the same as for rainforest plants except bark thickness data were collected from the portion of the stem that remained unburnt. Because of lost tags, post-fire responses of 8 stems could not be assessed. A table with the data recorded for both rainforest and savanna plants is provided in Table A3.1 in Appendix 3.

4.3.6 Statistical analyses

Variables were checked for normality and where necessary, data were log- or square root-transformed. The stem traits absolute bark thickness, relative bark thickness (ratio of individual bark thickness to stem diameter) and stem diameter – height ratio were compared between rainforest and savanna species using univariate analysis of variance (ANOVA) and the software R (R Core Team, 2013). For each species we calculated the equation describing the relationship between stem diameter and bark thickness and applied it, using the stem diameter recorded one year after the fire trial, to estimate the increment in bark thickness. Because of the differences in fire treatments (experimental vs. ambient) it was not valid to statistically compare survival and mode of resprouting for rainforest and savanna individuals, but we were able to compare responses of the various regeneration types within rainforest and savanna vegetation. For rainforest individuals, we tested whether the three response variables, whole plant survival (living vs. dead), stem survival (living vs. dead), and resprouter type (basal

vs. aerial) were correlated with bark thickness, species and plant height. For savanna plants we modelled only stem survival, because only one savanna individual died. We also tested whether the number and length of shoots and relative height difference differed among species and resprouter type (aerial vs. basal). We further investigated factors potentially affecting the number of shoots, assessing if the number of shoots of basal and aerial resprouters differed among species, controlling for stem diameter. To do this, we used generalised linear models (GLM), complete subsets regression and model selection based on Akaike's Information Criterion for small sample size (AIC_c) (Burnham and Anderson, 2002). Linear models were used for shoot length and relative height difference, Poisson models with a log link were applied for the number of shoots and binomial models with a logit link were used to test survival and resprouter type. Akaike weights (w_i) were calculated as a "weight of evidence" to evaluate the probability of a given model to actually be the best in the set (Burnham and Anderson, 2004). Importance of single variables (w_+) was calculated as the sum of w_i of the models within the set in which the variable occurs. w_+ values higher than 0.73 indicate that the variable is likely to be an important predictor (Murphy *et al.*, 2014). Full AIC_c results are provided in Table A3.2 in Appendix 3. For each species we computed the Pearson's product-moment correlation coefficient to assess the relationship between the average bark thickness and the percentage of aerial resprouters, as well as the relationship between the estimate bark thickness increment and the height increment.

4.4 RESULTS

4.4.1 Stem traits comparison

Stem diameter-height ratio values were significantly different ($P < 0.001$) between rainforest (average $1.00 \text{ cm m}^{-1} \pm 0.05 \text{ SE}$) and savanna trees (average $1.78 \text{ cm m}^{-1} \pm 0.09 \text{ SE}$), meaning that within our pre-selected height range rainforest species had smaller basal stem diameters than savanna trees for a given height (Fig. 4.3.a, b). For example, modelled basal stem diameter of a 2-m high rainforest tree was 2.4 cm while

that of a savanna tree was 4.0 cm. There was also a positive relationship between absolute bark thickness and stem diameter for both vegetation types (Fig. 4.3 c, d).

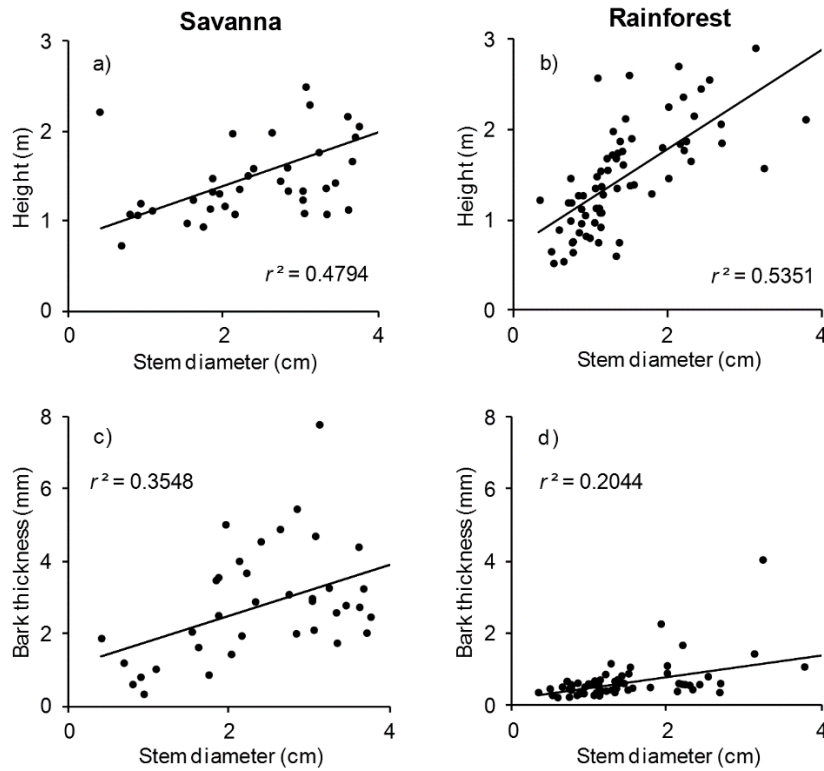


Figure 4.3 Relationship between diameter and height for (a) savanna and (b) rainforest species, and diameter and unburnt bark thickness for (c) savanna and (d) rainforest species. Regression lines and coefficients of determination (r^2) are shown.

Rainforest plants had thinner bark than savanna species of comparable size; ANOVA showed that savanna species had higher absolute and relative bark thickness ($P < 0.001$ and $P < 0.05$ respectively; Fig. 4.4 a, b).

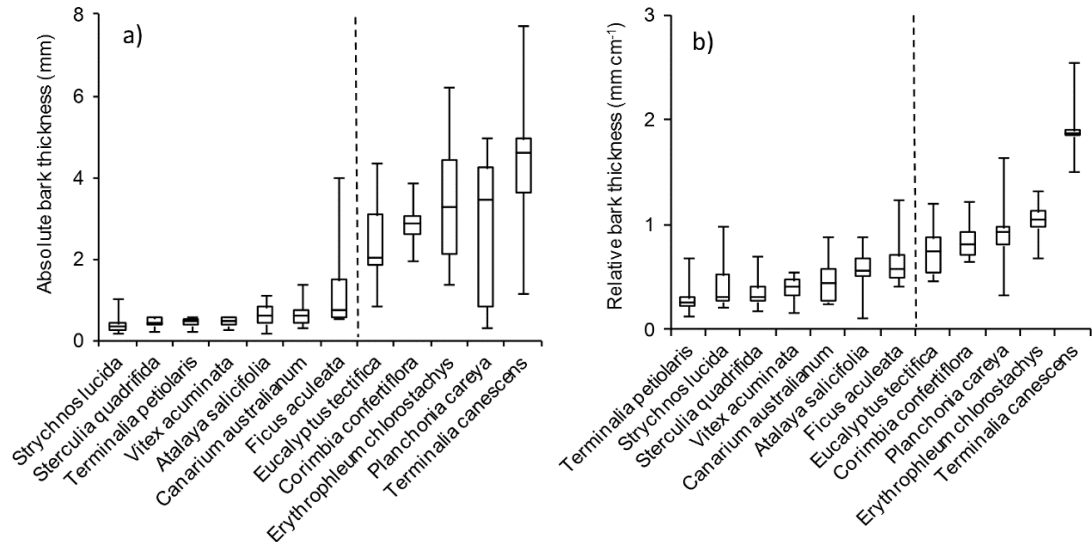


Figure 4.4 a) Absolute and b) relative unburnt bark thickness of the studied rainforest and savanna species. The species are ordered by median value; all the rainforest species fell on the left side of the dashed line and savanna species on the right side.

4.4.2 Post-fire regeneration of savanna plants

One year after the low intensity fire, whole plant mortality was observed in only one individual, a *Terminalia canescens* sapling (Table 4.1). For all five savanna species most of the main stems (88%) survived, with no stem death recorded in the two Myrtaceae species (*Corymbia confertiflora* and *Eucalyptus tectifica*), and thus these species did not have any basal shoots. AIC_c model selection showed no relationship between the few occurrences of main stem death and plant size, bark thickness or species (Fig. 4.5a).

Table 4.1 Individual survival, stem survival and mode of regeneration of rainforest and savanna species to a low intensity fire in northern Australia.
Rate of plant survival and stem survival are calculated considering all the studied plants, grouped by species.

Species	Phenology	Number of observed plants	Plant survival (%)	Stem survival (%)	% of plants		Relative height difference (%) (mean \pm SE)		Number of shoots (mean \pm SE)		Length of the longest shoot (cm) (mean \pm SE)	
					Basal	Aerial	Basal	Aerial	Basal	Aerial	Basal	Aerial
Rainforest <i>Atalaya salicifolia</i>	Evergreen	10	90	30	67	33	-23 \pm 17	18 \pm 40	3 \pm 0	7 \pm 4	89 \pm 23	60 \pm 21
<i>Canarium australianum</i>	Deciduous	10	60	40	33	67	-36 \pm 7	48 \pm 76	1 \pm 0	1 \pm 0	18 \pm 16	55 \pm 16
<i>Ficus aculeata</i>	Evergreen	9	100	44	56	44	-23 \pm 10	-23 \pm 6	2 \pm 1	3 \pm 0	95 \pm 15	84 \pm 18
<i>Sterculia quadrifida</i>	Deciduous	5	80	40	50	50	-70 \pm 13	-23 \pm 22	3 \pm 1	3 \pm 1	34 \pm 4	39 \pm 21
<i>Strychnos lucida</i>	Deciduous	10	100	40	60	40	-72 \pm 6	-50 \pm 15	2 \pm 0	3 \pm 1	44 \pm 17	62 \pm 11
<i>Terminalia petiolaris</i>	Deciduous	10	50	50	0	100	-	10 \pm 10	-	6 \pm 1	-	70 \pm 15
<i>Vitex acuminata</i>	Deciduous	10	80	80	0	100	-	-35 \pm 9	-	2 \pm 0	-	56 \pm 6
Total rainforest		64	81	47	41	59	-43 \pm 7	-12 \pm 11	2 \pm 0	3 \pm 1	66 \pm 10	62 \pm 5
Savanna <i>Corymbia confertiflora</i>	Deciduous	8	100	100	0	100	-	1 \pm 7	-	8 \pm 2	-	32 \pm 6
<i>Erythrophleum chlorostachys</i>	Semi-deciduous	8	100	75	25	75	-33 \pm 9	-19 \pm 11	5 \pm 3	9 \pm 3	89 \pm 4	35 \pm 5
<i>Eucalyptus tectifica</i>	Evergreen	8	100	100	0	100	-	8 \pm 3	-	17 \pm 2	-	44 \pm 3
<i>Planchonia careya</i>	Deciduous	8	100	75	25	75	-8 \pm 13	-13 \pm 10	5 \pm 1	13 \pm 3	85 \pm 55	50 \pm 11
<i>Terminalia canescens</i>	Semi-deciduous	10	90	80	11	89	-44 \pm 0	-4 \pm 6	5 \pm 0	10 \pm 1	110 \pm 0	31 \pm 8
Total savanna		42	98	86	12	88	-25 \pm 9	-5 \pm 3	5 \pm 1	12 \pm 1	92 \pm 18	38 \pm 3

After one year the savanna plants were on an average 93% of their pre fire height. Our modelling showed that the resprouter type was not correlated with any of the tested variables (Fig. 4.5a); the variation in relative height difference pre- and post-fire was not well correlated with either species or resprouter type, while resprouter type best predicted the number of shoots ($w+ = 0.77$; Fig. 4.5c). There was no correlation between the average bark thickness and the percentage of aerial resprouters ($r = -0.21$; Fig. 4.6a), while there was a negative correlation between the average estimated bark thickness increment and the average height increment ($r = -0.76$; Fig. 4.6c). Amongst aerial resprouters there was strong support for differences amongst species and a positive effect of stem diameter ($w+ = 1.00$ for both) on the number of shoots. All savanna individuals with surviving stems (i.e. aerial resprouters) resprouted epicormically, exclusively for all species except *T. canescens*, which also exhibited strong aerial axillary resprouting. With the exception of the two eucalypts, which were not topkilled, all of the species had some basal shoots. For savanna basal resprouters, neither species nor stem diameter was predictive of the number of shoots. Amongst all savanna individuals the length of the longest shoot was best predicted by resprouter type ($w+ > 0.99$; Fig. 4.5c), whereby basal shoots were longer than aerial shoots (Table 4.1).

4.4.3 Post-fire regeneration of rainforest plants

After one year 81% of the rainforest plants had survived the experimental fire. Stem and plant survival were not predicted by any of the investigated factors, while resprouter type was correlated with species ($w+ 0.91$; Fig. 5b). Of the surviving plants, 41% regenerated via basal resprouting, although neither *T. petiolaris* nor *Vitex acuminata* adopted this regeneration strategy (Table 4.1). All the main stems that recovered had axillary shoots, and none had epicormic shoots. The variation in relative height difference (pre- and post-fire) and the number of shoots were both strongly affected by species ($w+ 0.97$ and 1.00 respectively) and resprouter type ($w+ 0.88$ and 0.89 respectively; Fig. 5d). No correlation between bark thickness and the percentage of aerial resprouters was detected ($r = 0.34$; Fig. 4.6b), while there was a positive relationship between the estimated bark thickness increment and the height increment

($r = 0.64$; Fig. 4.6d). Basal resprouters lost relatively more height and had fewer shoots than aerial resprouters. For instance, the basal resprouter *S. lucida* had the largest height loss (-71.7 ± 6.2 SE %), while aerial resprouters of *Canarium australianum* substantially increased their relative height (by 48 ± 76 SE %). Amongst basal resprouters, neither stem diameter nor species clearly explained variation in the number of regenerative shoots; in contrast, the number of shoots produced by aerial resprouters was most affected by species ($w+ 0.81$). No variables were found to be associated with the length of the longest shoot.

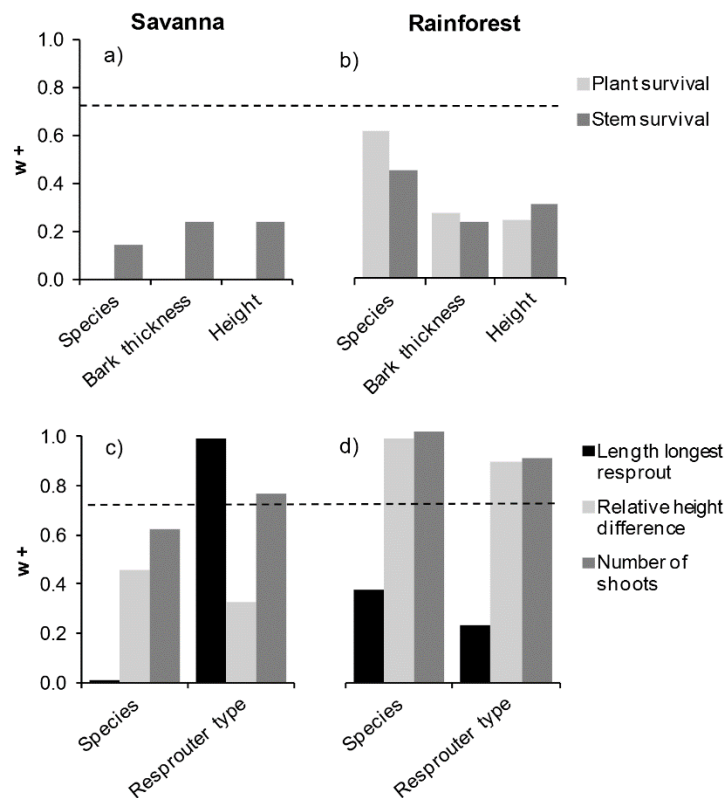


Figure 4.5 Importance of the variables examined in rainforest and savanna environments, expressed as $w+$, the probability of the variable being included in the best model. Species, bark thickness and plant height were included in models describing whole plant and stem survival and resprouter type, while models describing relative height difference, number of shoots and length of the longest shoot were based on the variables species and resprouter type. $w+$ values > 0.73 , indicated by the dashed line, were considered important.

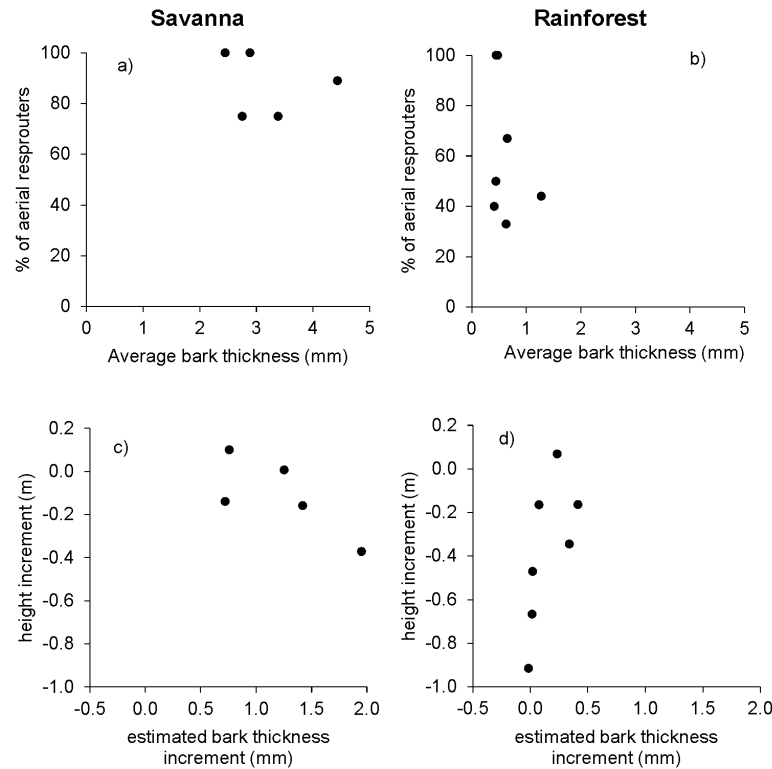


Figure 4.6 Relationship between average bark thickness and percentage of aerial resprouter for (a) savanna and (b), rainforest species, and estimated bark thickness increment and height increment for (c) savanna and (d) rainforest species.

4.5 DISCUSSION

We tested the survival and resprouting strategies of savanna and rainforest saplings burnt by low intensity fires typical of the early dry season, classifying regenerating strategies according to the framework designed by Clarke *et al.* (2013). We have shown that while both vegetation types have limited mortality, they have markedly different modes of recovery. The savanna species have thick bark, which protects stem tissue from fire, and following defoliation are able to replace their crowns and regain their pre-fire height via aerial resprouting within one year, predominantly via epicormic buds. In contrast, the rainforest species have limited investment in bark protection and, following a simulated low severity savanna fire, had high stem mortality and basal resprouting was common in 5 of the 7 species. These patterns

concord with the findings of Dantas *et al.* (2013a), who assessed the existence of threshold patterns in functional traits across the rainforest-savanna boundary in the Cerrado, and Clarke *et al.* (2015), who undertook a survey of regeneration strategies of the Australian tree and shrub flora. We found that savanna species produced more shoots, and savanna basal resprouters had longer shoots than those of rainforest basal resprouters. Amongst savanna species, basal resprouters had longer shoots than aerial resprouters, a pattern similar to that recorded by aerial and basal resprouts of *Eucalyptus tetrodonta* (Franklin *et al.*, 2010). After one year, recovering rainforest species regained only about 60% of their pre-fire height whereas savanna plants had almost fully recovered. Although the savanna plants were burnt two months before the rainforest plants, this is not likely to affect the dissimilarities in growth rate we detected, because the time difference occurred during the dry season and most of the annual growth of rainforest species occurs during the wet season (Prior *et al.*, 2004).

A feature of our results is the uniformity of responses within vegetation types by species from a range of lineages, suggesting that the regenerative traits have evolved convergently, presumably in response to sharply contrasting fire regimes. In savanna there is strong selection pressure to escape the fire trap through rapid height growth, whereas the development of dense crowns by rainforest species is advantageous because they suppress grass, thereby reducing the risk of frequent fires (Hoffmann *et al.*, 2012a). Our findings showed the existence, amongst the studied savanna species, of a trade-off between increment in bark thickness and in height; the species that invested more in bark thickness had the lowest height recovery and vice-versa. While none of the rainforest plants resprouted epicormically, this strategy was common amongst savanna species. Despite their thin bark epicormic resprouting was the only strategy adopted by the two eucalypt species, *Eucalyptus tectifica* and *Corymbia confertiflora*, the thinnest recorded amongst the investigated savanna species. Previous research has shown that eucalypt clade has evolved radially oriented meristem strips through the cambium, an anatomy unique in the plant kingdom which provides an extraordinary capacity to recover after canopy defoliation (Burrows, 2013, Clarke *et al.*, 2013, Crisp *et al.*, 2011, Lawes *et al.*, 2011a). Basal resprouting in eucalypts is also well known: they have well developed lignotubers, and root suckering

occurs in some tropical species (Lacey, 1974). The lack of basal resprouting by the eucalypts in this study is probably explained by the absence of topkill. The only axillary resprouting species detected in the savanna, *Terminalia canescens*, belongs to a genus represented in both rainforest and savanna. The two *Terminalia* species investigated in our study were located at the extremes of the bark thickness range: the savanna tree *T. canescens* had the thickest bark of all the sampled species and showed basal resprouting capacity, whereas *T. petiolaris*, found in the rainforest, had very thin bark and no basal shoots, resulting in the high mortality of this species. Consistently with an evolutionary response to a biome switch from rainforest into the savanna (Crisp *et al.*, 2011), the thick bark and basal resprouting of *T. canescens* presumably enable this species to recover from fire, in contrast to its congener. This finding supports the theory that resprouting ability and stem defences belong to a suite of co-evolved traits associated with survival in a disturbed habitat (Keeley *et al.*, 2011, Poorter *et al.*, 2010).

Amongst rainforest species, basal shoots were recorded for about half of the individuals. None of the basal resprouters was able to fully recover the original height after one year; indeed, basal resprouters of the rainforest species *Sterculia quadrifida* and *Strychnos lucida* lost on average 70% of the original height. However, five of the rainforest species were able to resprout from aerial buds, enabling rapid height recovery. The species that best recovered their height were also those with the highest estimated increase in bark thickness; for example, the *Canarium australianum* individuals increased their height by almost 50% (Table 4.1), and this capacity to rapidly gain height and bark thickness following fire suggests this species may be able to invade savannas. Figs have also been identified as potential pioneers: they are important contributors in terms of seed bank (Russell-Smith and Setterfield, 2006) and in our study *Ficus aculeata*, a species which tolerates a broad range of environmental conditions, had comparatively thick bark, intermediate between the savanna species and other rainforest species. *Vitex acuminata* exhibited only aerial resprouting (by eight stems), with no basal resprouting from the two stems that were killed by fire.

It is important to note that basal resprouters occur in both savanna and rainforest habitats, and this strategy is also beneficial following disturbances other than fire, like cyclonic storms (Bowman and Panton, 1994). For example, Franklin *et al.* (2010) found that in the savanna, saplings or trees highly damaged by a tornado tend to resprout predominantly from basal shoots. In addition, some rainforest species have well developed aerial resprouting in response to disturbance other than fire (Marrinan *et al.*, 2005).

Our findings suggest substantial differences in resource allocation amongst rainforest and savanna species. Previous studies, from around the globe and including northern Australia, have stressed the greater investment of savanna species in bark protection compared to rainforest species (Charles-Dominique *et al.*, 2015, Dantas *et al.*, 2013a, Dantas *et al.*, 2013b, Hoffmann *et al.*, 2009, Hoffmann *et al.*, 2012a, Lawes *et al.*, 2013, Pausas, 2015b). North Australian savanna seedlings are better able to recover from multiple landscape fire events compared to rainforest seedlings (Bowman, 2005). A similar pattern in South American savanna and rainforest seedlings has been attributed to higher total non-structural carbohydrate (TNC) reserves in the roots of savanna seedlings (Hoffmann *et al.*, 2004) as a consequence of their high root:shoot ratio providing more resources per unit of above-ground biomass (Hoffmann *et al.*, 2003).

Because of contrasting regeneration strategies, rainforest and savanna saplings have different capacities to recruit into the canopy layer in frequently burnt savannas. Aerially resprouting savanna plants only need a few years without fire to escape from the effects of grass fires. In contrast, basally regenerating rainforest species are in direct competition with grass for light and are highly vulnerable to further top kill until they can suppress grass cover, requiring longer fire free periods. Our observed differences in regeneration strategy concords with the observations of Williams *et al.* (2012), which established the predominance of basal resprouters in wet tropical rainforest species in north-eastern Australia, in contrast to many aerial, particularly epicormic, resprouters in adjacent savannas. Our results therefore support the conceptual model of Hoffmann *et al.* (2012a), which explains the control of rainforest-

savanna boundaries as an interplay between fire frequency, differential mortality and recovery between savanna and rainforest species via interspecific variation in growth rate, resprouting and bark thickness.

Our study site had an abrupt boundary only partially associated with an increase in rock cover on the rainforest margin, pointing to the importance of frequent fires in controlling rainforest extent. Murphy and Bowman (2012) have proposed a model where increased tree growth rate can result in expansion of rainforest boundaries. Based on our results, the expansion of rainforests into the north Kimberley savannas seems unlikely under the current frequent-fire regime. However, this may change in response to climate change. Our system is at the driest end of the rainforest range, where the very limited occurrence of rainforests is restricted to the highest rainfall areas and in topographic settings that capture or supply moisture. It would hence be expected that this system is sensitive to variations in annual rainfall, given that water availability is a major factor limiting growth of rainforest trees in savanna habitat (Hao *et al.*, 2008). Together with increasing rainfall, rising CO₂ levels would enhance plant growth (Drake *et al.*, 1997, Lewis *et al.*, 2009) by increasing photosynthetic efficiency, in particular at the seedling and sapling stage (Bond and Midgley, 2012, Lloyd and Farquhar, 2008), and resprouting ability (Hoffmann *et al.*, 2000). These changes could affect trees-grass dynamics by facilitating C3 trees and shrubs over the savanna C4 grasses (Bond and Midgley, 2000, Bowman *et al.*, 2010a) with a consequent reduction of the flammable grass layer. That could allow rainforest trees to escape the fire-trap more quickly, despite their less effective regeneration strategies, and possibly expand into savannas, as has been argued by Bowman *et al.* (2010). Resolving the effect of CO₂ and precipitation on growth of rainforest species is important to understand the future dynamics of these systems, as well as to predict changes in wetter systems where a possible decrease in rainfall has been predicted (e.g. continental edges of north-eastern Australia; Reisinger *et al.*, 2014).

Chapter 5

A cross-cultural approach to rainforest management: changes in fire regimes, animal abundance, and management options

5.1 ABSTRACT

In northern Australia, severe late dry season fires have become widespread following the decline of Aboriginal Traditional fire management through the 20th century. A fire management program, designed to re-instate Aboriginal fire regimes according to customary principles, has been introduced in the Wunambal Gaambera Country (north Kimberley, Western Australia) since 2010. We analysed the effectiveness of the fire program in protecting rainforests from wildfires, as well as its potential consequences for wildlife. To do so, we investigated whether there were shifts in fire regimes, from high-intensity late dry season fires to early dry season fires, in the proximity of rainforests. We also identified the most vulnerable patches based on size, distance from neighbouring patches and fire frequency, and tested for changes in fire regimes in areas with clusters of vulnerable patches. Fire management performed by Aboriginal rangers effectively shifted fire regimes, decreasing the frequency of late dry season fires, particularly in areas with clusters of vulnerable rainforests. In addition, we compared native small/medium mammal abundance in rainforests and savannas with different fire disturbance levels using camera traps. Rainforests in frequently burnt areas had significantly lower small/medium mammal abundance than infrequently burnt areas, and savannas invaded by rainforest had more abundant and diverse native mammal fauna than frequently burnt savannas, suggesting that long unburnt areas might be critical for the survival of fire-sensitive species. We recommend ongoing monitoring and community consultation to evaluate the effects of current and long-term management interventions.

5.2 INTRODUCTION

The important role of Indigenous People in biodiversity conservation programs is becoming increasingly recognized internationally (e.g. Convention on Biological Diversity 2011, Berkes *et al.*, 2006, Gadgil *et al.*, 2003, Prado *et al.*, 2013, Bohensky *et al.*, 2013). This includes the declaration of Indigenous and Community Conservation Areas (ICCAs), whereby indigenous or other communities voluntarily

conserve their lands and waters as protected areas. In Australia, over 70 Indigenous Protected Areas (IPAs), formally recognised by the Australian Government and counted in the National Reserve System, have been declared by Indigenous groups in recent decades, and now cover 65 million hectares, which represents 7% of Australia and 40% of the National Reserve System (Australian Government, 2016, Altman and Whitehead, 2003). IPAs, like other protected areas, require management planning, monitoring and evaluation, and a variety of approaches have been adopted by practitioners (Davies *et al.*, 2013). Implementation of management on indigenous lands also requires the integration of the knowledge systems of Indigenous people (including Traditional Ecological Knowledge) and non-indigenous partner agencies and the development of participatory community-based approaches to monitoring and management (including Participatory Monitoring and Management) (Participatory monitoring and management partnership, 2016, Constantino *et al.*, 2012, Luzar *et al.*, 2011, Hill *et al.*, 2011b).

The strong relationship between Aboriginal people and the land they inhabit translates to deep knowledge of these environments, which comes from thousands of generations of direct experience (Horstman and Wightman, 2001). Such depth of ecological knowledge matches other studies elsewhere in the world that show the indigenous inhabitants of tropical rainforests carefully managed and utilised plant and animal resources such as food, medicine, and materials for boats, houses and tools (Ellen, 1998, Bennett, 1992). Often this knowledge is encoded in cultural stories and ceremonial sites (Ellen, 1998, Banfai and Bowman, 2006, McIntyre-Tamwoy, 2008). Karadada *et al.* (2011) compiled the ethno-ecological knowledge of rainforests by Wunambal Gaambara people, including the names and uses of several plant and animal species for food (e.g. yams (*Dioscorea spp.*), black flying-foxes, and birds and their eggs), canoes (e.g. *Bombax ceiba*) and medicine, some of which are associated with special Dreaming stories, songs and a style of rock art (*Gwion*) (Wunambal Gaambara Aboriginal Corporation, 2010).

Indigenous knowledge is based on long-term presence in an area and is the result of accumulated experience, experimentation and information exchange that can track

back to hundreds or even thousands of years (Gadgil *et al.*, 2003) and can complement scientific studies with time-depth (Prado *et al.*, 2013). In Australia Traditional Aboriginal knowledge has been successfully combined with western science to assess and monitor environmental issues (Bohensky *et al.*, 2013), such as feral buffalo impact (Ens *et al.*, 2010a), the decline in fruit production of bush tucker species (Ens *et al.*, 2010b), fire management (Vigilante *et al.*, 2009), mammal decline (Ziembicki *et al.*, 2013) and botanical data collection (Ens and Towler, 2011).

The Unguu Indigenous Protected Area was declared by Wunambal Gaambera Aboriginal Corporation (WGAC) in 2011 and now extends over 800,000 ha. The management plan for the Unguu IPA was developed using a local form of the Open Standards for the Practice of Conservation called ‘Healthy Country Planning’, and identified 10 important ‘Conservation Targets’ (assets) to be monitored and managed (Moorcroft *et al.*, 2012, The Nature Conservancy (TNC), 2010). Rainforests, known as Wulo in Wunambal and Gaambera languages, are one of the 10 ‘Targets’ identified as important to Traditional Owners in the Wunambal Gaambera Healthy Country Plan. These rainforests, classified as monsoon vine thickets, are found across northern Australia, occurring in regions with strongly seasonal climate at the driest end of the Australian rainforest climatic range. They are characterised by low stature trees, a high density of shrubs and vines, and are a type of tropical monsoon forest (Russell-Smith, 1991, Webb, 1959). Rainforests were not formally reported as occurring in Western Australia until 1965 (McKenzie, 1991), when the botanist John Beard and some associates provided the first descriptive studies (Beard, 1976, Beard *et al.*, 1984). These monsoon vine thickets and some other evergreen rainforest types associated with aquifers were also documented in a series of biological surveys in the region, some of which included parts of Wunambal Gaambera Country (WGC) (Miles and Burbidge, 1975, Wilson, 1981, Burbidge and McKenzie, 1978, Bowman, 1992). Despite their relative small extent, rainforests contribute to 25% of floristic biodiversity of the north Kimberley (McKenzie *et al.*, 2009), and a comprehensive survey of rainforests, undertaken from 1987-1989 as part of the National Rainforest Conservation Programme (McKenzie, 1991), recorded 453 species of vascular plants, 93 of which were rainforest specialist trees. *Hibiscus peralbus* Fryxell, a shrub

belonging to the Malvaceae family, was the only endemic species found. Unusually for that period, the survey team included an indigenous elder Geoffrey Mangglamarra (now deceased), who accompanied scientists to a number of rainforests in the WGC and contributed a paper to the study. It included the names of important animals and plants and a description of how rainforests were used and managed by his people in the past (Mangglamarra *et al.*, 1991).

Unmanaged wildfires are one of the key threats to the health of rainforests identified in the Healthy Country Plan. Likewise, wildfires are recognised as a threat to natural and cultural values elsewhere in the Australian monsoon tropics (Trauernicht *et al.*, 2015, Williams *et al.*, 1999, Legge *et al.*, 2011b, McKenzie and Belbin, 1991). Changes in fire regimes have been observed in Australia with the switch from Traditional Aboriginal burning to European colonisation. This led to a decrease in early dry season (EDS) fires, typically of low intensity, in favour of late dry season (LDS) fires, which are likely to pose a threat to rainforests due to their high intensity and extent (Russell-Smith *et al.*, 2012, Edwards and Russell-Smith, 2009). This is in spite of the rainforest expansion trends observed in the Australian monsoon tropics in the past years (Banfai and Bowman, 2006, Bowman *et al.*, 2001), which have been linked with regional wetting trends and possibly atmospheric CO₂ enrichment (Bowman *et al.*, 2010a, Banfai and Bowman, 2007, Buitenwerf *et al.*, 2012, Bond and Midgley, 2000). Intense fires can cause direct damage to entire rainforest patches or portions of them, since rainforest species generally present limited fire protection (thick bark) and ability to resprout after a fire compared with savanna species (Clarke *et al.*, 2013, Lawes *et al.*, 2013). Indirect effects include increased run-off and soil erosion at time of first rain (Townsend and Douglas, 2000). It can also influence the dynamics of woody vegetation in savanna adjacent to rainforest patches and affect the expansion and contraction of rainforests over time (Bowman *et al.*, 2001, Banfai and Bowman, 2006). Johnstone and Burbidge (1991) suggested that fire had affected a rainforest patch at the Mitchell Plateau; an abandoned Orange-footed Scrubfowl mound on the edge subject to burning was evidence that wildfire had caused the patch to recede, since Scrubfowl are thought to nest only under closed canopy, and that this degradation had resulted in fewer bird records (Bowman *et al.*, 1994, Bowman *et al.*,

1999). Of the 95 patches visited in the 1987 survey, 40 showed evidence of fire damage (McKenzie and Belbin, 1991). In an attempt to restore pre-European fire regimes in the WCG, in 2010 the WGAC initiated a fire management program, consisting in a combination of ground-lit fires and aerial burning performed during the EDS.

Altered fire regimes may be contributing to the alarming decline of mammal species observed in many parts of northern Australia over the past ~ 200 years (Woinarski *et al.*, 2015). This decline has been detected by scientific studies (Johnson, 2006, Woinarski *et al.*, 2011, Woinarski *et al.*, 2010, Fitzsimons *et al.*, 2010) and also in interviews conducted with Aboriginal people (Ziembicki *et al.*, 2013). However, in the comparatively high rainfall and most rugged areas of the north Kimberley, mammal populations are thought to be relatively stable (Turpin, 2015), although potentially affected by changes in fire regimes (Start *et al.*, 2007). Kimberley rainforests constitute the preferred habitat for a number of mammal species (Start *et al.*, 2007, Woinarski *et al.*, 2004). They also are important habitat for some bird species, including 22 species that are rainforest specialists, such as the Orange-footed Scrub-fowl and the Rainbow Pitta (Johnstone and Burbidge, 1991), and provide refuges for several endemic species of invertebrates, particularly land snails (Solem, 1991).

The aim of this chapter was to evaluate the effectiveness of the fire management program in protecting rainforests from high intensity LDS fires, and its likely consequences for wildlife. To do this, we compared fire regimes pre- and post-fire management in proximity of rainforest. We also designed an index to calculate the level of vulnerability to fire of each rainforest patch, based on patch connectivity and fire frequency, and assessed if differences in fire regimes occurred in areas where clusters of vulnerable patches were found. In order to discuss the potential benefits and disadvantages of the fire management program in a broader ecological context, we also employed camera traps to perform an exploratory wildlife survey. We compared the abundance of small/medium native mammals in rainforests and savannas characterised by contrasting fire regimes, testing whether areas with low fire

activity displayed higher small mammal abundance. Finally, we combined these results with some of the outputs of the previous chapters to consider implications and options for ongoing management and monitoring of the rainforest biodiversity by Traditional Owners.

5.3 STUDY AREA

The WGC occupies about 800,000 ha of land and sea in the north Kimberley region of Western Australia, which is located toward the driest portion of the rainforest range in the Australian tropics (Bowman, 2000), and listed as one of the 15 Australian National Biodiversity Hotspots (Australian Government, Department of Environment). WGC is defined by the Wanjina Wunggurr Uunguu Native Title Determination, and represents the traditional lands of Wunambal Gaambara Aboriginal people (Fig. 5.1).

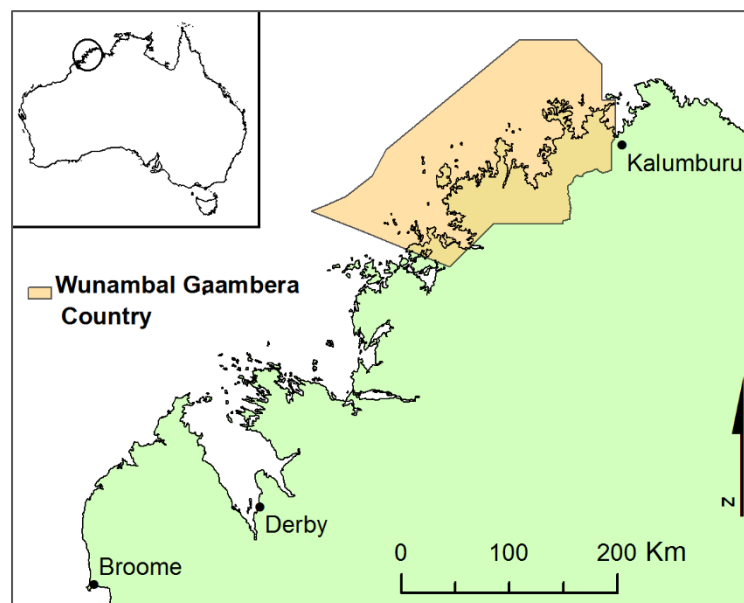


Figure 5.1 Extent of the Wunambal Gaambara Country, as defined by the Wanjina Wunggurr Uunguu Native Title Determination. Adapted from Wunambal Gaambara Aboriginal Corporation (2010).

5.3.1 Environment

WGC lies on the Kimberley basin, which forms a dissected plateau of deeply weathered sandstones of Precambrian age with interspersed areas of Precambrian basaltic base rocks, occasionally capped by mid-Cainozoic laterite (Beard, 1979, Vigilante, 2001). The climate is tropical monsoonal, characterised by a short summer wet season (November to April) during which most of precipitation occurs, while the rest of the year is virtually rain-free (Beard, 1979). Mean annual rainfall currently ranges from 1000 to 1400 mm and average maximum temperatures are equal or higher than 30°C all year, while average minimum temperatures vary from 20°C or more in summer to as low as 10°C in winter (Bureau of Meteorology, 2016). A wetting and warming trend has been detected since the beginning of the 21st century, with an increment in average annual rainfall of 40-50 mm/10 years, and a temperature rise of 0.15°C/10 years since the late 1940s (Bureau of Meteorology, 2016). WGC falls within the Gardner botanical district classification (Beard, 1979) and the Mitchell sub-region of the North Kimberley Bioregion (Thackway and Cresswell, 1995). Its vegetation is predominantly biodiverse tropical savannas: *Eucalyptus tetrodonta*-*E. miniata* savannas are found on the laterite mesas and hills, while *E. tectifica*-*E. grandifolia* savannas are common on deeper, clay soils on plains. Small patches of monsoon rainforests are interspersed in the savanna, typically found in fire-protected locations (Beard, 1979). These monsoon rainforests support a high diversity of plant species (Russell-Smith, 1991) and are important refugia for savanna-adapted mammals to avoid climatic extremes, predators and fires (Bowman and Woinarski 1994).

The analysis of fauna pattern was focused on two specific locations: the Mitchell Plateau and the Bougainville Peninsula, which share similar climate and geology, but different levels of disturbance. The Mitchell Plateau (754 km²) has a high fire frequency (average times burnt: 0.5 · year⁻¹, data from North Australian Fire Information (NAFI, 2016), based on a 15-year time period (2000-2014)) and unmanaged cattle are found throughout the area. By contrast, Bougainville Peninsula (298 km²) has a much lower fire frequency (average times burnt: 0.08 · year⁻¹) and

cattle have never been recorded (McKenzie and Belbin, 1991). These dynamics are likely to have persisted during the last decades; a study performed in 1985 found that half of the surveyed rainforest patches in Mitchell Plateau were damaged by fire and/or cyclones, while on Bougainville Peninsula cyclones were the only visible cause of damage (Clayton-Greene and Beard, 1985).

5.3.2 *Historical fire management*

Prior to European colonisation Traditional Owners practiced landscape-scale burning on an annual basis for a range of purposes including for hunting and gathering. These burning practices steadily declined during the colonial period, which commenced in the late 19th century, as traditional lifestyles were increasingly disrupted by European colonisation and Aboriginal people moved into settlements. By the 1950s Aboriginal burning had largely ceased in remote parts of the north Kimberley, but was practiced to a limited extent around communities (Vigilante, 2004). The cessation of Aboriginal burning led to the emergence of large destructive late dry season wildfires, set by both anthropogenic ignitions and lightning, that became a dominant feature of the fire regime of the region until recent times (Fisher *et al.*, 2003). As described earlier, prescribed burning began in 2010 through the Wunambal Gaambera Healthy Country Plan.

5.4 METHODS

5.4.1 *Changes in fire regimes*

The recent fire history of rainforest patches was examined using ‘firescar’ data created at a pixel resolution of 250 m based on MODIS satellite imagery, accessed from the North Australian Fire Information website (NAFI, 2016). A 250m buffer was created around each individual rainforest patch and the fire scar data for each year from 2000 to 2015 was analysed using the ‘spatial join’ function in ArcGIS. Each rainforest patch was considered to have experienced fire if one or more fire scars occurred within its area. This was intended to be an index of fire regime rather than an absolute measure

of fire impact on rainforest patches and their boundaries. Total fire frequency, frequency of EDS fires (January to July) and frequency of LDS fires (August to December) were calculated (Hunt, 2015). Fire scar years were organised into unmanaged ‘baseline’ years (2000-2009) and managed ‘project’ years (2012-2015), aligning with the Wunambal Gaambera Unguu Fire Project and the Savanna Burning Methodology (Hunt, 2015). The years 2010 and 2011 were excluded from the analysis as they were ‘transition’ years where WGAC was reaching management capacity. Differences in the frequency of EDS fires, LDS fires, and total fire frequency were then analysed with a paired t-test. Using the baseline period (2000-2009, for which fire scar data was accessible) as a sample of the pre-management period (1950s-2000s), the frequency of fires was calculated. Pearson product moment correlation coefficient (r) was employed to examine correlations of fire frequency with distance from the coastline and slope. Fire frequency was also compared for geology types using the Kruskal-Wallis test and the average fire frequency was calculated for each geology type.

5.4.2 Patch vulnerability

Based on the rainforest map generated in Ondeí *et al.* (2017), we identified the most isolated patches by calculating, for each rainforest patch, the average edge-to-edge distance of the nearest five neighbours, using the ‘average nearest neighbour’ tool in ArcMap. A simple connectivity index was then calculated as follows

$$\text{Patch connectivity} = \frac{A}{\text{Dist}}$$

Where A is the area of the focal patch (ha), and Dist is the distance to the nearest five patches (km) (Munguía-Rosas and Montiel, 2014). Patch isolation increases with the decrease of this index. Further analyses were then undertaken to analyse risk factors associated with isolation.

In order to identify which patches were most at risk of being completely destroyed by fire, with a lower chance of being recolonised, we calculated a vulnerability index,

taking into account patch size, distance from neighbouring patches and fire frequency. The ‘Vulnerability index’ was hence calculated for each rainforest patch as follows

$$\frac{\text{Patch connectivity}}{\text{Total Fire Freq}_{bas}}$$

where *Patch connectivity* includes information on patch size and distance from the nearest five patches, and total *Fire Freq_{bas}* is the total fire frequency in proximity of the patch recorded during the baseline years. We used total fire frequency because under unmanaged fire regimes, even EDS fires can be extensive and intense due to fuel accumulation. Note that lower index values indicate higher vulnerability to fire.

Based on the fire risk index values, we tested for the presence of clusters of patches potentially at risk, by using the Moran’s I test in ArcMap on (i) all patches and (ii) the 5% most vulnerable patches. We then evaluated the effectiveness of planned burning in protecting particularly vulnerable patches by comparing using a paired t test, changes in LDS fire frequency for the 5% most vulnerable patches.

5.4.3 *Examining fauna patterns in rainforests and adjacent savannas*

During my rainforest study, rainforest patches were sampled to investigate if plant and animal populations are influenced by patch distribution, other environmental factors and potential threatening processes. To do so, 20 vegetation transects, running across the rainforest-savanna boundary, were established in Mitchell Plateau and Bougainville Peninsula, as described in Chapter 3. Each transect included five 10 x 20m plots, and for each plot, data on canopy cover, grass cover, rock cover, floristics, stand basal area, and number of adult trees were collected. In the study documented in this current chapter, I associated vegetation structure in the established transects with animal abundance using camera traps. Vertebrate species were sampled using 40 camera traps (RECONYX HyperFire™ PC800 Professional) positioned along the vegetation transects for 8-9 months (from July/August 2014 to May/June 2015). For each transect, two cameras were positioned, one on the rainforest edge and the other

in the savanna, at a minimum distance of 500m. Cameras were set up to take 3 pictures per trigger, with a one-second pause between pictures and one-minute delay between triggers. For each species or animal group, sampling effort was calculated as the number of observations divided by the total camera effort for each location and vegetation type. We compared the number of small/medium mammals (excluding human-introduced predators such as dingoes and cats) detected by camera traps in savannas and rainforests in the Mitchell Plateau and the Bougainville Peninsula. Differences in the number of these mammals detected between rainforests and savannas in the same location (Mitchell Plateau or Bougainville Peninsula), and between locations for the same vegetation type (rainforest or savanna), were analysed using generalised linear models (GLM) and the Poisson family of distribution, controlling for differences in trapping effort between cameras by including trapping effort as offset. Analyses were conducted in R (R Core Team, 2013).

5.5 RESULTS

5.5.1 *Changes in fire regimes*

The fire history estimated for the baseline years (2000-2009), showed that total fire frequency around rainforest patches ranged from 0.000 to 0.900 times burnt \cdot year⁻¹ (average 0.295 ± 0.003 ; Fig. 5.2a), while during the project years total fire frequency ranged from 0.000 to 1.000 times burnt \cdot year⁻¹ (average 0.333 ± 0.004 ; Fig. 5.2b). Total fire frequency under unmanaged conditions (baseline years) was correlated with distance from the coastline ($r = 0.65$), but not with topographic slope ($r = -0.15$). It also differed significantly between geology types ($P < 0.001$), with alluvium and colluvium experiencing the highest average frequency (0.36 ± 0.03 times burnt \cdot year⁻¹) and coastal deposits the lowest (0.16 ± 0.02 times burnt \cdot year⁻¹), reflecting contrasting productivity of these substrate types.

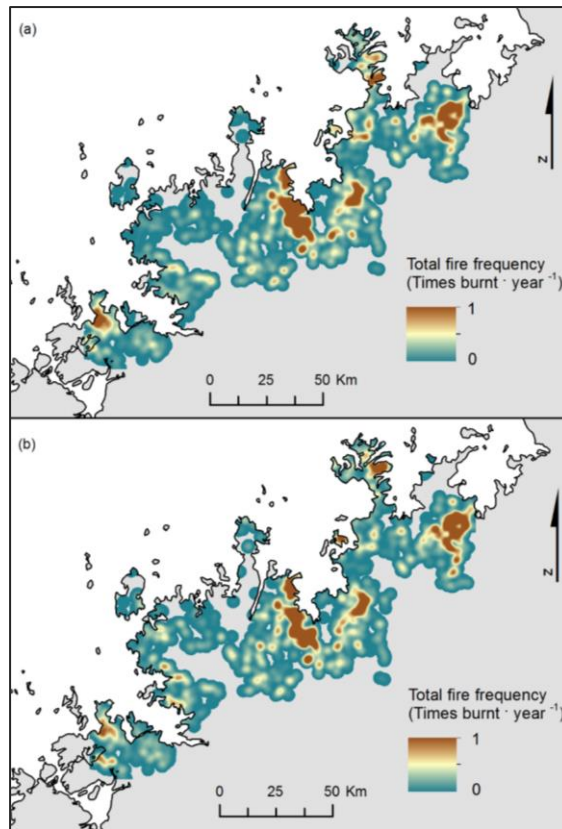


Figure 5.2 Maps showing total fire frequency in proximity of rainforests during (a) the unmanaged baseline years and (b) the project years.

Prescribed burning resulted in a significant reduction in LDS fires between the baseline years and the project years ($P < 0.001$), and a significant increase of EDS and total fire frequency ($P < 0.001$ for both; Fig. 5.3). Average frequency of EDS fires, LDS fires, and total frequency for the baseline years and the project years are reported in Table 5.1.

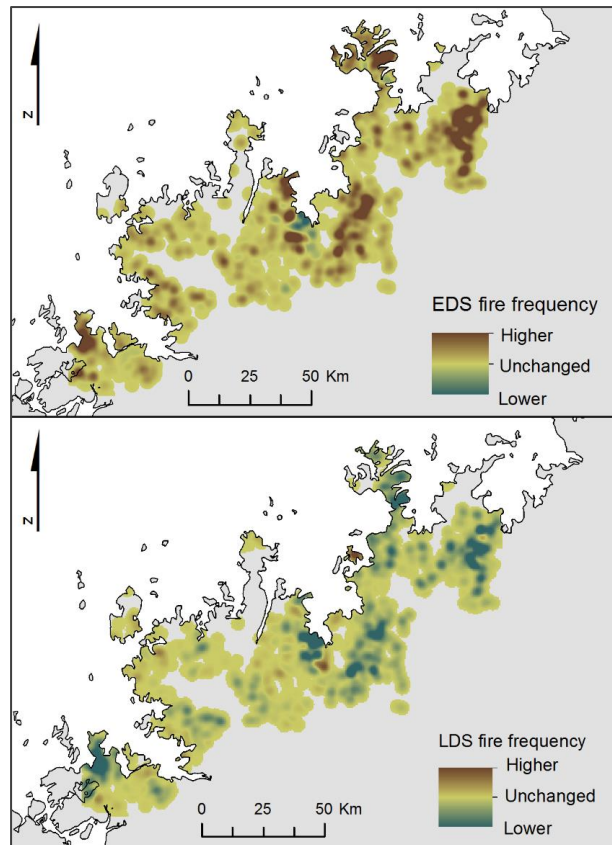


Figure 5.3 Maps displaying variations in the frequency of early dry season (EDS) fires and late dry season (LDS) fires in proximity of rainforests between the baseline years (2000-2009) and the project years (2012-2015).

Table 5.1 Average frequency (\pm standard error) of early dry season (EDS) fires, late dry season (LDS) fires and total fire frequency recorded for the baseline years (2000-2009) and the project years (2012-2015).

	EDS	LDS	Total
Baseline	0.091 (\pm 0.002)	0.213 (\pm 0.002)	0.295 (\pm 0.003)
Project	0.252 (\pm 0.003)	0.091 (\pm 0.002)	0.333 (\pm 0.004)

5.5.2 Patch vulnerability

The average distance from a rainforest to the five nearest patches ranged from 0.015 km to 10.879 km (average $0.659 \text{ km} \pm 0.011 \text{ km}$), and patch connectivity index ranged from 0.008 to 7327.150 (average 8.887 ± 1.774) (Fig. 5.4). The frequency of baseline

fires was correlated with distance from the coastline ($r = 0.65$), but not with slope ($r = -0.15$). It also differed significantly between geology types ($P < 0.001$).

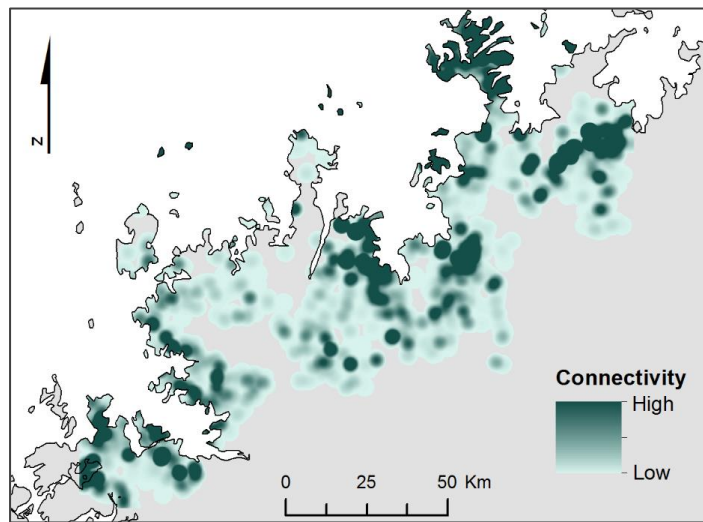


Figure 5.4 Patch connectivity of rainforests in WGC. showing areas with high connectivity, meaning patches are larger and close to each other (dark green), and areas with low connectivity, meaning patches are smaller and more sparse (light green).

Based on our vulnerability index, which considers patch size, distance from neighbouring patches and fire frequency, no clustering was detected when considering all rainforest patches. However, when only the 5% most vulnerable patches were considered, we detected significant clustering ($P < 0.001$; Fig. 5.5). The most vulnerable patches experienced a significant reduction in LDS fires, with an average reduction of 0.32 times burnt \cdot year⁻¹ during the LDS ($P < 0.001$), while total fire frequency did not significantly change.

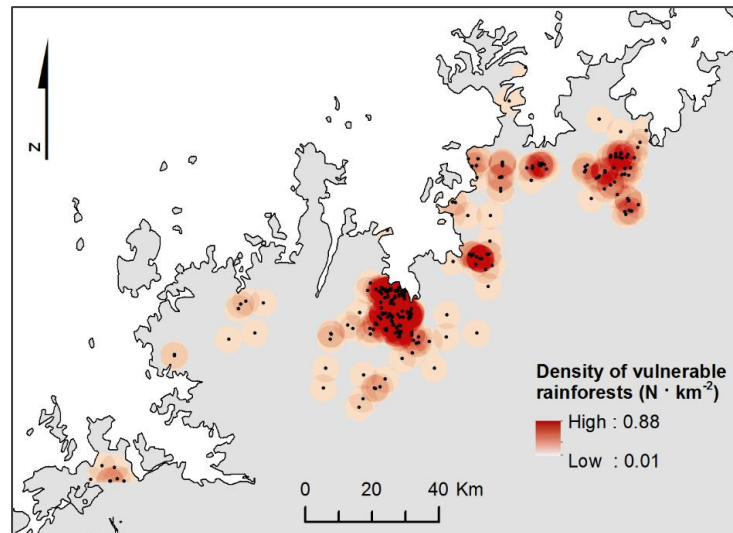


Figure 5.5 Location and density of the most vulnerable 5% of rainforest patches, based on their size, distance from neighbouring patches and fire frequency. The density map (red gradient) shows some clear clusters of vulnerable patches. Black dots represent single patches.

5.5.3 Fauna patterns

Total camera trapping effort was 9140 trap-nights between 10 July 2014 and 2 June 2015. In the Bougainville Peninsula trapping effort was 2,755 nights in rainforests and 2,561 nights in savannas. In the Mitchell Plateau, two cameras were burnt and two went missing. Thus trapping effort in this location was lower, at 2,643 nights in rainforests and 1,181 nights in savannas. In total 5,506 true-triggers were taken, resulting in 1,869 animal detections. Photos were taken of six native mammal species, ten bird species, one reptile species and three introduced mammal species (cattle, dingoes, and feral cats). For 18% of the photos, animals were identified only at a sub-order or family level, and 1% of the photos were unidentifiable (Table 5.2).

Small/medium native mammal species were not equally distributed throughout the study locations. We detected significantly more of these species in rainforests than savannas in both locations ($P < 0.001$ in both cases) and significantly more small/medium mammals on Bougainville Peninsula when separately comparing rainforests and savannas in the two locations ($P < 0.001$ for both vegetation types; Fig. 5.6a, b).

Table 5.2 Summary of the animal observations obtained from the camera traps deployed in the Mitchell Plateau and Bougainville Peninsula from July 2014 to May 2015.

Species	Rainforest		Savanna	
	Mitchell Plateau	Bougainville Peninsula	Mitchell Plateau	Bougainville Peninsula
MAMMALS				
Bandicoot (<i>Isoodon</i> sp.)	19	45	9	67
Echidna (<i>Tachyglossus aculeatus</i>)	0	2	0	1
Kangaroo – unidentified	13	180	14	19
Northern quoll (<i>Dasyurus hallucatus</i>)	4	2	0	0
Pale field rat (<i>Rattus tunneyi</i>)	0	1	0	0
Rodent – unidentified	56	31	0	26
<i>Melomys burtoni</i>	0	12	0	2
Short-eared rock wallaby (<i>Petrogale brachyotis</i>)	0	15	0	24
BIRDS				
Bar-shouldered dove (<i>Geopelia humeralis</i>)	9	8	0	39
Bird – unidentified	3	3	1	3
Emerald dove (<i>Chalcophaps indica</i>)	9	3	0	20
Great bowerbird (<i>Chlamydera nuchalis</i>)	9	2	0	2
Orange-footed Scrubfowl (<i>Megapodius (Megapodius) reinwardt</i>)	41	2	0	0
Pheasant coucal (<i>Centropus (Polophilus) phasianinus</i>)	0	1	0	15
Rainbow pitta (<i>Pitta (Pitta) iris</i>)	2	3	0	0
Sand goanna (<i>Varanus gouldii</i>)	0	1	0	0
Silver-crowned friarbird (<i>Philemon (Philemon) argenticeps</i>)	0	4	0	2
Sulphur-crested cockatoo (<i>Cacatua (Cacatua) galerita</i>)	7	0	0	0
Wedge-tailed eagle (<i>Aquila (Uroaetus) audax</i>)	0	0	5	0
REPTILES				
Friated lizard (<i>Chlamydosaurus kingii</i>)	0	0	4	0
Snake – unidentified	0	2	0	0
TOTAL NATIVE	199	329	45	265
AVERAGE PER 100 TRAP NIGHTS	6.5	11.5	2.3	8.6
INTRODUCED				
Cattle (<i>Bos (Bos) taurus</i>)	739	0	354	0
Dingo (<i>Canis lupus dingo</i>)	27	12	12	45
Feral cat (<i>Felis catus</i>)	4	0	5	0
TOTAL INTRODUCED	743	0	359	0
AVERAGE PER 100 TRAP NIGHTS	27.9	0.4	30.5	1.8
Unknown	17	0	1	0

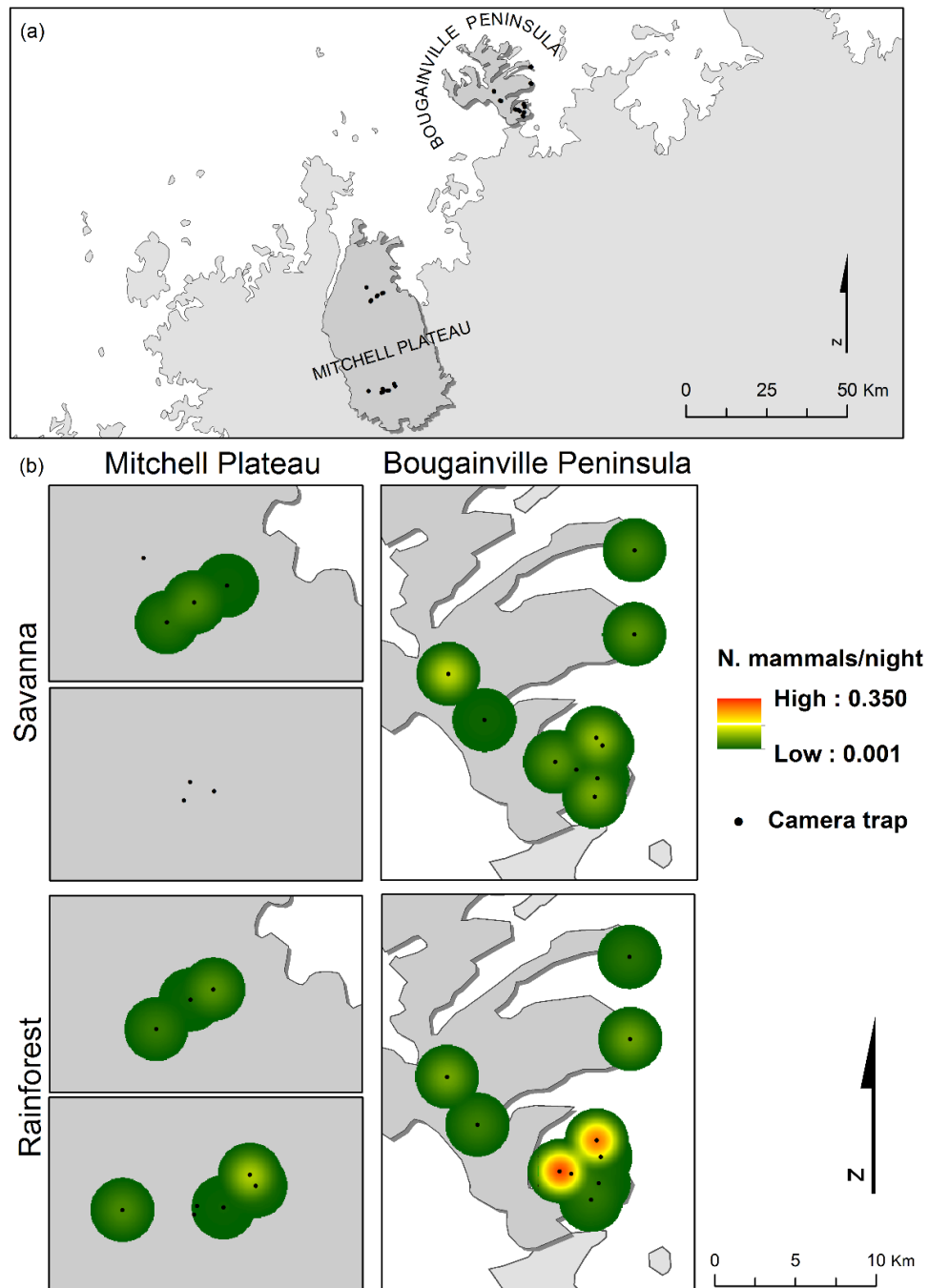


Figure 5.6 Maps showing (a) location of the camera traps in Mitchell Plateau and the Bougainville Peninsula and (b) average number of small/medium mammals detected per night in rainforests and savannas in the two sites.

5.6 DISCUSSION

5.6.1 *Fire regimes*

Our analysis showed that the combination of aerial and ground-based ignitions by Aboriginal Rangers has caused a shift from LDS fires to EDS fires. This approach seeks to emulate traditional Aboriginal fire management (Mangglamarra *et al.*, 1991), which protected rainforests from destructive wildfires in the past. EDS burning limits the build-up of fuel that can lead to large, and destructive wildfires (Vigilante *et al.*, 2004). The observed reduction of LDS fires in proximity of the most vulnerable 5% of rainforest patches suggests that this method can be effective in areas with clusters of those rainforests that would likely be severely damaged by an intense fire (Fig. 5.5). Savannas may also benefit from the reintroduction of EDS burning through the creation of fine-grained burn mosaics that are vital for wildlife (Bowman and Legge, 2016), and that are thought to characterise Aboriginal fire management (Trauernicht *et al.*, 2016).

5.6.2 *Small mammal abundance*

The greater small mammal abundance detected on the Bougainville Peninsula, combined with previous observations from Aboriginal rangers, suggests that the area may be a refuge for small mammals, allowing threatened species to avoid the decline associated with the recent range contractions observed elsewhere in the Australian tropics (Woinarski *et al.*, 2015). These results harmonise with the concept that long unburnt habitats are crucial for small mammal diversity (Woinarski *et al.*, 2004), due to the sensitivity of some animal species to fire frequency (Woinarski *et al.*, 2015). This highlights the need to carefully manage long unburnt areas such as the Bougainville Peninsula. It is also possible that the greater abundance of rainforest plant species detected on the Bougainville Peninsula, which provide a critical food source (particularly fruit) for the local fauna, contribute to the high habitat quality for small/medium mammals (McKenzie *et al.*, 2009). On mainland areas, it is impractical to create large unburnt patches, so the provision of long unburnt habitat is best achieved by fine-scale patch burning (Trauernicht *et al.*, 2015).

5.6.3 *Management options*

The results from the rainforest study raise some interesting management questions that Traditional Owners need to consider for the future. The archipelago of rainforest patches found in the WGC has been traditionally utilized by Aboriginal People. Such rainforest patches are crucial to maintaining landscape biodiversity and habitat islands for volant taxa (especially bats and fruit eating birds) in northern Australia (Price, 2006, Woinarski and Legge, 2013, Moran and Catterall, 2014, Palmer *et al.*, 2000) and ensuring the survival of low-dispersal animal taxa (Graham *et al.*, 2006). Thus the entire WGC estate needs to be carefully managed, to prevent individual patches from contracting below the minimum size that can support the animal species currently inhabiting them (Bierregaard *et al.*, 1992). Particular attention needs to be paid to small, isolated rainforests.

Prior to colonization, Traditional Owners burned some savanna areas on the Bougainville Peninsula to facilitate walking and hunting and gathering. This particularly took place in the open woodland on the laterite plateau and some of the larger savanna areas in the valleys and slopes, including the areas with cycads. Nowadays, the Traditional Owners and Aboriginal Rangers involved in fieldwork during this study express concern about some unburnt savanna that is overgrown with vines and shrubs, making walking difficult, and are inclined to burn such areas to restore savanna to a more open condition. Nonetheless, lower fire frequencies on the fire-protected Bougainville Peninsula over the last 50 years have enabled rainforest patches to expand into adjacent savanna (Chapter 3). Crucially, more small/medium native mammals were also found in that location than on the Mitchell Plateau. The question now arises as to whether more frequent fires should be returned to this area to maintain a healthy savanna, or whether rainforest expansion should be facilitated by excluding fire as much as possible.

Large, long unburnt areas can contain high and continuous fuel loads of grass, litter and woody debris, which presents a risk of late dry season wildfire. In other cases, long-unburnt areas do not always have higher amounts of grass and litter fuel than frequently burnt sites (Scott *et al.*, 2009, Elliott *et al.*, 2009), and their fuel composition

is characterized by more litter and less flammable grasses (Woinarski *et al.*, 2004). However, under severe fire weather, even moderate loads of continuous fuels can support wildfires. Should lightning hit a fire-protected area it could cause extensive and potentially destructive fires, as occurred on Bigge Island in 2012 and Middle Osborn Island in 2015 (NAFI, 2016). WGC is subject to frequent lightning, with an average of 8-12 flashes on the ground $\cdot \text{km}^{-2} \text{yr}^{-1}$, amongst the highest in Australia (Bureau of Meteorology, 2016). Unburnt areas may disadvantage some plant species such as the cycad population on Bougainville Peninsula, which could benefit from frequent fires to reduce competition with other species colonizing the savanna, such as rainforest trees.

The argument for increasing the frequency of fire in long unburnt savannas needs to be weighed against the biodiversity values of these habitats. Rainforests and rainforest-savanna mosaics in naturally fire-protected areas substantially enhance plant and animal biodiversity. Long unburnt areas are very rare in the Australian tropics, with approximately 3.1% of land remaining unburnt for at least five years and only 0.098 % for at least ten years (Woinarski *et al.*, 2004). These areas are increasingly recognised as important for key components of the savanna biota (Andersen *et al.*, 2005). To re-establish frequent fire regimes on the Bougainville Peninsula could irreversibly change vegetation structure and cause the loss of some of the rarest environments in the Australian tropics, along with the wildlife they host. From this perspective, fire management needs to be carefully planned, applied on a fine scale, and subject to long-term assessments to monitor its effects on vegetation and on wildlife, given that these fires may adversely affect some small mammals if they are too frequent (Perry *et al.*, 2016).

Chapter 6

Conclusions: reflections on theory and practice

6.1 SYNTHESIS

The overall aims of this thesis were to identify the ecological factors that influence rainforest distribution and expansion, focusing on tropical areas where rainforests are represented by small patches in a savanna-dominated landscape. To achieve this, I adopted a multi-scale approach, investigating the importance of climate, terrain, geology, and disturbance. Results from spatial analyses were validated and further explored through ground-based assessments and experiments.

The importance of bottom-up factors (resources) as drivers of rainforest distribution and boundary dynamics was confirmed by the results of both my sub-continental and regional analyses. The sub-continental analysis of rainforest distribution, described in Chapter 2, was the first to identify the rainforest domain in north-western Australia and to analyse the importance of climate on rainforest distribution when considering the entire north-western Australian monsoon tropics. I found that water availability was the most important climatic driver of rainforest density, as showed by the correlation between rainforest density with mean annual rainfall, moisture index, and potential evapotranspiration. At a regional scale, the importance of bottom-up factors was confirmed by the analysis of rainforest distribution in the north Kimberley, based on the first high resolution map of rainforests ever created for that area (Chapter 2). While rainforests were found on a wide range of landscape settings, rainforest density was significantly higher on nutrient-rich geologic substrates such as basalt and topographic positions like valleys, which provide higher amount of nutrients due to soil accumulation and water retention. Furthermore, the rainforest expansion trends detected in the Mitchell Plateau and Bougainville Peninsula using aerial photography from 1949 to 2005 (Chapter 3) occurred in conjunction with a wetting trend (Bureau of Meteorology, 2016). This suggests that increased annual rainfall facilitated the expansion of rainforests into surrounding savannas, as hypothesised for other locations in the Australian monsoon tropics (e.g. Banfai and Bowman, 2006, Bowman *et al.*, 2010a). It is also possible that the increase in atmospheric CO₂ levels contributed to this phenomenon, through increased photosynthetic rates (Lloyd and Farquhar, 2008), from which C3 trees would benefit more than C4 savanna grasses (Bond and Midgley,

2000), or via enhanced water-use efficiency of tropical trees (van der Sleen *et al.*, 2015). These results confirm the importance of bottom-up factors in determining rainforest distribution at different scales, but do not disprove the hypothesis that top-down factors (consumers), in particular fire regimes and cattle, may also strongly influence rainforest-savanna dynamics. Topographic positions such as slopes or valleys, for example, not only provide higher amount of nutrients due to soil accumulation and water retention, but also protection from fire (Ash, 1988). Similarly, geologic substrates richer in nutrients could support higher rainforest density because rainforests species require deep and not leached soils to establish (Bond, 2010), or because higher soil fertility enhances growth rates, increasing the chances of rainforest trees growing fast enough to escape the fire trap (Hoffmann *et al.*, 2012a), or both.

The presence, in the north Kimberley, of ecologically similar locations characterised by different levels of disturbance allowed us to perform the first analysis of rainforest distribution in disturbed and naturally undisturbed areas at a regional scale (Chapter 2). This was a rare opportunity, as fire is a ubiquitous feature of the north-western Australian tropics and the few fire-free areas are generally the result of artificial, small-scale fire exclusions (e.g. Woinarski *et al.*, 2004). The comparison of rainforest distribution on islands and the mainland (Chapter 2) showed a significantly higher presence of rainforests in undisturbed locations, such as islands, suggesting a strong influence of disturbance. This was further confirmed by the historical analysis of rainforest boundary dynamics in the Mitchell Plateau and Bougainville Peninsula (Chapter 3). Rainforest expansion into adjoining savannas was most pronounced in areas with low fire frequency and absence of cattle, such as the Bougainville Peninsula. By contrast, patches located in the Mitchell Plateau, and hence exposed to elevated disturbance levels, were found to have more stable boundaries, probably because they are restricted to topographically fire protected settings (Chapters 2 and 3). Small patches were less likely to expand compared with bigger patches, possibly because their perimeter to core ratio is higher, rendering them more vulnerable to intense fires (Russell-Smith and Bowman, 1992). This result is of particular importance considering that 75% of rainforest patches mapped in the north Kimberley are smaller than 1 ha (Chapter 2).

Rainforests in disturbed and undisturbed locations did not present substantial floristic differences, but the absence of disturbance facilitated tree recruitment, as shown by the higher tree and seedling density in rainforests on the Bougainville Peninsula, where we also detected the presence of rare species identified in the north Kimberley – or in some cases in the entire Western Australia - for the first time (Chapter 3). Disturbance not only influenced distribution and expansion rates of rainforests, but also the structure of the adjacent savannas and the rainforest-savanna boundaries. Savannas on the Bougainville Peninsula were characterised by higher proportions of rainforest adult trees and the widespread presence of rainforest species in the understorey, signalling that rainforest expansion is still occurring (Russell-Smith *et al.*, 2004). The structure of rainforest-savanna boundaries varied depending on the levels of disturbance. In the Mitchell Plateau they were characterised by abrupt transitions in vegetation characteristics, such as tree and seedling density and grass cover, similar to what has been observed in previous studies in Australia (Banfai and Bowman, 2007) and other in tropical areas in the world (e.g. Ibanez *et al.*, 2013b, Dantas *et al.*, 2013a). The analysis of canopy cover bimodality presented in Chapter 3 was the first to be based on transects running across the rainforest-savanna boundary, rather than satellite-based assessments or independent plots. It provided ground-based evidence to the hypothesis that rainforests and savannas exist as two distinct states (Staver *et al.*, 2011b, Hirota *et al.*, 2011). However, on the cattle free and fire protected Bougainville Peninsula rainforest-savanna boundaries were more blurred, with gradual transitions in vegetation structure, and canopy cover was unimodal. The results of this natural experiment pointed to disturbance as the major factor determining the presence of rainforests and savannas as alternative stable states (Dantas *et al.*, 2016).

Rainforest plants are damaged and killed by recurrent high intensity fires (Fensham *et al.*, 2003), probably due to their thin bark, which provides little fire protection (Lawes *et al.*, 2013, Pausas, 2015b). However, in some cases they displayed the capacity to survive and resprout after a fire (Clarke *et al.*, 2013). Fire intensity is likely to be a critical factor determining the post-burn recovery capacity of rainforest species, but previous field-based studies did not control for this factor (e.g. Williams *et al.*, 2012).

Conversely, in controlled studies that accounted for fire intensity, rainforest plants were burnt and left to recover in artificial environments, where they were not subject to natural conditions, such as competition and drought (e.g. Zimmer *et al.*, 2015). My field experiment combined for the first time controlled burning conditions with plant recovery in a natural environment (Chapter 4). It found that rainforest saplings displayed the capacity to survive a single low intensity savanna fire and recover through regenerative buds, suggesting that not only fire frequency, but also fire intensity is important. Rainforests plants would therefore benefit from a shift from the current fire regimes, characterised by late dry season intense and extensive fires (Vigilante *et al.*, 2004), toward less intense fire regimes, such as those typical of Aboriginal fire management, which facilitate the creation of habitat patchiness. Such patchiness would help protect fire-sensitive habitats, including rainforests (Trauernicht *et al.*, 2016, Woinarski *et al.*, 2004). In the Wunambal Gaambera Country, I demonstrated that the reintroduction of early dry season prescribed burning successfully reduced the number of high intensity, late dry season fires, particularly in locations with clusters of rainforest patches classified as vulnerable (Chapter 5). The ability of rainforest plants to survive at least a single low intensity fires suggests that this shift in fire regimes could facilitate rainforest tree survival. However, elevated fire frequency could still constrain rainforests to fire-protected locations. Regeneration of rainforest plants occurred predominantly through basal buds due to the high stem death rates, preventing rainforest plants from regaining their original height after one year. Frequent fires could then prevent them from reaching the height that allow them to develop enough protection to escape the ‘fire trap’ (Hoffmann *et al.*, 2012a).

I quantified the presence of cattle in rainforests and savannas in the Mitchell Plateau, as well as their impact on seedling number and grass cover, in rainforests and savannas of the north Kimberley (Chapter 3), previously only qualitatively observed by McKenzie and Belbin (1991). Cattle impact was not associated with reduced grass cover (Chapter 3), signalling that in the north Kimberley cattle presence does not reduce fuel load, contrary to what has been observed elsewhere in the tropics for other herbivores (Werner, 2005, Staver and Bond, 2014), perhaps because of the low cattle numbers. High cattle presence was instead associated with lower tree seedling density

in savannas (Chapter 3), suggesting that megaherbivores may cause a population bottleneck for tree species by substantially reducing tree recruitment, especially when combined with high fire activity and thus limiting the capacity of rainforests to expand into savannas. These results are comparable with the findings of Staver *et al.* (2009) for African savannas. I also provided the first ground-based evidence that the Bougainville Peninsula is free from cattle, highlighting the importance of maintaining the deterring methods currently in place, such as the cattle-proof fence built by the Wunambal Gaambera rangers at the base of that location.

The emerging pattern is that rainforest-savanna dynamics are driven by the interplay of water and nutrient availability (bottom-up factors) and fire activity and presence of megaherbivores (top-down factors), which can affect rainforests directly, or indirectly by influencing each other (Fig. 6.1) (Murphy and Bowman, 2012, Hoffmann *et al.*, 2012a). Due to their capacity to affect several of these factors, human activities and land management are also important.

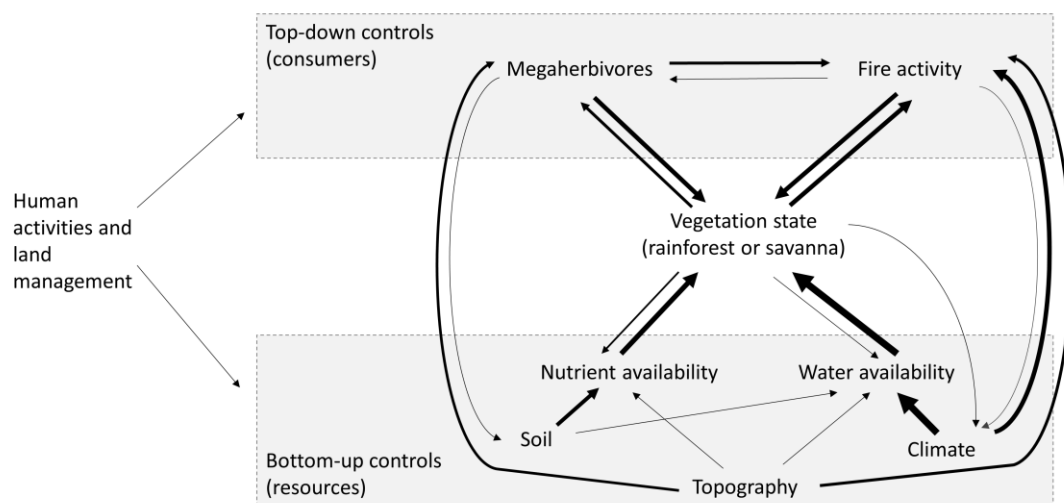


Figure 6.1 Feedbacks regulating the presence of rainforests or savannas. I adapted the diagram from Murphy *et al.* (2012) to show only the factors investigated in this study, and have included megaherbivores as a determinant of vegetation states. Factors were also classified as bottom-up controls (resources) or top-down controls (consumers). Vegetation acts as a consumer of resources such as water and nutrients, and as a resource for the consumers of biomass (megaherbivores and fire). Top-down and bottom-up controls influence each other via direct effect or by facilitating the establishment of one vegetation type or the other. The approximate strength of each relationship is indicated by the width of the arrows.

Severe decline of native mammal fauna has occurred in the last 20 years Northern Australia (Woinarski *et al.*, 2011). The north Kimberley is considered one of the few locations in the Australian tropics where mammal decline is occurring at a lower rate (Start *et al.*, 2007), although it is not exempt from the threat represented by frequent and high intensity fire regimes (Radford *et al.*, 2015). The exploratory study on animal abundance, performed using camera traps, was the first to investigate small/medium mammals in the remote and disturbance-free Bougainville Peninsula, enabling a comparison with the results from the fire-prone Mitchell Plateau (Chapter 5). Overall, I detected high presence of small/medium mammals, particularly in rainforests and savannas on the Bougainville Peninsula relative to the more disturbed Mitchell Plateau. These results suggest that in the north Kimberley the reduction in small/medium mammal abundance is still limited. The low level of threats such as predation and disturbance, and the high food availability due to the abundance of rainforest elements have probably contributed enhance the resilience of these mammal populations (Frank *et al.*, 2014, Legge *et al.*, 2011a, Woinarski *et al.*, 2011).

6.2 CULTURAL CONSIDERATIONS

Combining Aboriginal knowledge and management with the approaches and aims of western science can be challenging. Firstly, the specific objectives of Aboriginal land management and western science may not necessarily overlap. While most of the ecological targets considered important in Aboriginal culture find a parallel in western science (Moorcroft *et al.*, 2012), some specific objectives may differ, such as, for example, the protection of individual species for cultural reasons. It is then important that decision-making processes are participatory and represent Aboriginal law and traditions in area where Aboriginal people retain connection to country (Hill *et al.*, 2011b), and are considered in addition to western science in areas subject to co-management. In other settings, Aboriginal people are land owners with the primary land management responsibility and will manage land according to their own cultural principles. Second, monitoring and managing extensive remote areas is resource demanding. Aboriginal people and the organizations that represent them need to seek

external funding to manage these areas, which requires the recognition of the ecological and cultural value of their land (Hill *et al.*, 2011a) and careful planning in order to meet national management standards (Hill *et al.*, 2011b). Finally, it is necessary to ensure Traditional Aboriginal knowledge and customs are transferred from one generation to the next. This is increasingly difficult to achieve, due to the lack of Aboriginal people living on country and the tendency of young generations to adopt more western lifestyles (Moorcroft *et al.*, 2012); the lack of intergenerational transfer of knowledge may quickly lead to loss of Traditional knowledge (Horstman and Wightman, 2001).

In spite of these difficulties, restoring Aboriginal management is desirable for long-term conservation of both traditional ecological knowledge and for biodiversity, as well as contributing to livelihoods and well-being of Aboriginal people (Prado *et al.*, 2013, Burgess *et al.*, 2005). The results from Chapter 5 suggest that to protect rainforests it is necessary to (i) maintain the human component with which they evolved over the last thousands of years, (ii) adapt management strategies to local conditions to maintain both habitat stability and diversity, and (iii) frame management in light of global and regional environmental changes such as increasing climate variability, wetting trends, loss of long unburnt vegetation, and a small mammal extinction crisis. This demands community consultation to develop sustainable management regimes (Hill *et al.*, 2010). Ongoing monitoring is essential to evaluate the effects of management strategies and adapt to changing local and global socio-ecological circumstances.

6.3 FUTURE AVENUES FOR RESEARCH

The natural experiment performed in this study took advantage of the existence of a large, disturbance-protected area (the Bougainville Peninsula). Long unburnt areas are rare in the Australian tropics (Woinarski *et al.*, 2004). The comparison of vegetation dynamics in the Bougainville Peninsula and Mitchell Plateau offered the uncommon opportunity to investigate rainforest-savanna dynamics in the presence and absence of

cattle and fire, providing a better understanding of the effects of disturbance. More studies should be performed in these locations, to take further advantage of the existence of a vast fire-protected area. Although not designed to describe the totality of floristic diversity of the area, this study captured regionally interesting floristic elements in both rainforests and savannas of the Bougainville Peninsula (Chapter 3). These results suggest that intensive floristic studies would increase our knowledge of the local flora. To include, if at all possible, more geographically representative undisturbed and disturbed locations in the study would also increase the explanatory power of the analyses testing the influence of local and climatic factors on rainforest-savanna boundary dynamics.

Further animal studies also would be beneficial to investigate what habitats still support dense small mammal populations and what environmental changes would put them at risk. Long-term studies in rainforests and savannas of the Bougainville Peninsula, using both camera traps and animal capture data, would avoid the risk of multiple detections of the same individuals and facilitate species identification and range detection. Thanks to the presence of ecologically similar disturbed (Mitchell Plateau) and undisturbed (Bougainville Peninsula) areas, such studies would also benefit from a sampling framework that incorporates the effects of time as well as disturbance, such as BACI design (Before-After, Control-Impact, Stewart-Oaten *et al.*, 1986). This would provide important information on threatened or endangered species, such as the Nabarlek (*Petrogale concinna* Gould), the black-footed tree-rat (*Mesembriomys gouldii* Gray), or the brush-tailed phascogale (*Phascogale tapoatafa* Meyer) (<http://www.iucnredlist.org>; Woinarski *et al.*, 2011), and consequently useful insights for land managers to help limit further extinctions.

In this thesis I combined spatial analyses, performed at different scales, field observations of both flora and fauna, and field experiments to investigate the drivers of rainforest distribution, historical boundary change, and vegetation structure in the north Kimberley, focusing in particular on the impact of disturbance levels on rainforests and savannas. The outcomes of this study improved our understanding of rainforest-savanna boundary dynamics in locations where climatic and local factors

support the existence of both vegetation types, and showed the importance of both bottom-up and top-down in determining rainforest distribution. These results, as well as the methods developed, will be of use for ecologists working in similar environmental settings in Australia or elsewhere in the tropics (e.g. MacDermott *et al.*, 2016) and for land management planning.

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Appendix 1

Supplementary material to Chapter 2

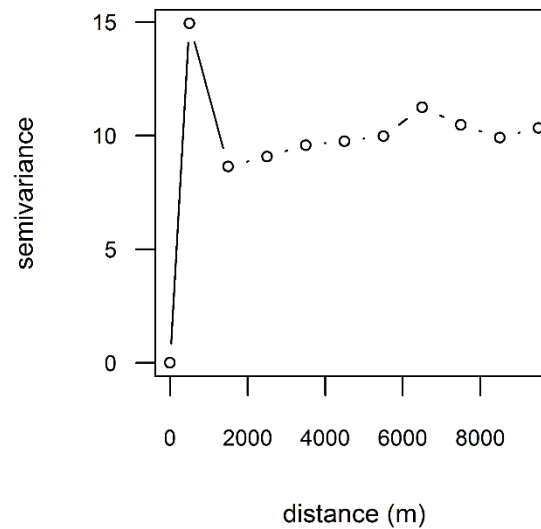


Figure A1.1 Semi-variogram describing the spatial pattern of rainforest density observations, obtained from the north Kimberley rainforest map. To measure the degree of spatial dependence between samples we plotted the semi-variance as a function of distance between pairs of observations. The graph shows that the semi-variance decreases when the lag distance exceeds 1000 m, which corresponds to the minimum distance between observations in our dataset

Table A1.1. Summary of regional and local scale models testing a) the importance of geology and terrain for rainforest density at a regional scale, and the importance of geology alone on b) complex terrain and c) level terrain; the effects of insularity (mainland vs islands) and terrain (complex vs level) at a local scale on d) rainforest density, and e) fire activity. K represents the number of parameters, AIC the Akaike value, Delta the difference between the AIC of the model and the AIC of the best model in the set, Weight the Akaike weight (defined as the relative likelihood of the model), and Deviance is the percentage of deviance explained by the model.

a) Rainforest density (Regional scale)

Model	K	AIC	Delta	Weight	Deviance
Geology and terrain	6	27898.0	0.00	1.00	32.0%
Terrain	2	28949.6	596.31	0.00	26.3%
Geology	5	28949.6	1051.52	0.00	19.4%
Null	1	30133.7	2235.65	0.00	NA

b) Rainforest density on complex terrain (Regional scale)

Model	K	AIC	Delta	Weight	Deviance
Geology	5	13085.8	0.00	1.00	13.0%
Null	1	13537.8	452.00	0.00	NA

c) Rainforest density on level terrain (Regional scale)

Model	K	AIC	Delta	Weight	Deviance
Geology	5	15164.8	0.00	1.00	10.0%
Null	1	15427.9	263.10	0.00	NA

d) Rainforest density (Local scale)

Model	K	AIC	Delta	Weight	Deviance
Insularity and terrain	3	7001.4	0.00	1.00	35.0%
Insularity	2	7278.2	276.82	0.00	21.7%
Terrain	2	7451.1	449.75	0.00	12.6%
Null	1	7669.5	668.15	0.00	NA

e) Fire activity (Local scale)

Model	K	AIC	Delta	Weight	Deviance
Insularity	2	-1402.0	0.00	0.52	39.1%
Insularity and terrain	3	-1401.8	0.12	0.48	39.2%
Terrain	2	-581.7	820.26	0.00	0.4%
Null	1	-576.9	825.04	0.00	NA

Appendix 2

Supplementary material to Chapter 3

Table A2.1 Summary of the models testing the importance of the factor location (Mitchell Plateau or Bougainville Peninsula) and vegetation type (stable rain forest or expanded rain forest) on a) the number of seedlings, b) number of trees, c) number of species, d) proportion of rain forest species, e) basal area, f) grass cover, g) rock cover in rain forest plots. Df represents the number of parameters, logLik the maximum likelihood, AIC the Akaike value, delta the difference between the AIC of the model and the AIC of the best model in the set, and weight the Akaike weight (defined as the relative likelihood of the model).

a) Number of seedlings

Model	Df	logLik	AIC	delta	weight
Vegetation type and Location	3	-201.399	408.8	0.00	0.84
Location	2	-204.047	412.1	3.30	0.16
Null	1	-221.804	445.6	36.81	0.00
Vegetation type	2	-221.715	447.4	38.63	0.00

b) Number of trees

Model	Df	logLik	AIC	delta	weight
Vegetation type and Location	3	-136.173	278.3	0.00	0.64
Location	2	-137.959	279.9	1.57	0.29
Null	1	-140.703	283.4	5.06	0.05
Vegetation type	2	-140.441	284.9	6.54	0.02

c) Number of species

Model	Df	logLik	AIC	delta	weight
Null	1	-105.418	212.8	0.00	0.33
Location	2	-104.602	213.2	0.37	0.28
Vegetation type	2	-104.69	213.4	0.54	0.26
Vegetation type and Location	3	-104.334	214.7	1.83	0.13

d) Proportion of rainforest species

Model	Df	logLik	AIC	delta	weight
Vegetation type	2	-64.707	133.4	0.00	0.59
Vegetation type and Location	3	-64.085	134.2	0.76	0.41
Location	2	-93.07	190.1	56.73	0.00
Null	1	-94.279	190.6	57.14	0.00

e) Basal area

Model	Df	logLik	AIC	delta	weight
Location	3	-39.61	85.2	0.00	0.37
Vegetation type	3	-40.068	86.1	0.92	0.23
Null	2	-41.172	86.3	1.12	0.21
Vegetation type and Location	4	-39.257	86.5	1.29	0.19

f) Grass cover

Model	Df	logLik	AIC	delta	weight
Vegetation type	5	-33.667	77.3	0.00	0.48
Vegetation type and Location	6	-33.428	78.9	1.52	0.22
Location	5	-34.832	79.7	2.33	0.15
Null	4	-35.836	79.7	2.34	0.15

g) Rock cover

Model	Df	logLik	AIC	delta	weight
Null	4	-41.644	91.3	0.00	0.40
Location	5	-40.885	91.8	0.48	0.32
Vegetation type	5	-41.557	93.1	1.83	0.16
Vegetation type and Location	6	-40.883	93.8	2.48	0.12

Table A2.2 Summary of the models testing the importance of the factor location (Mitchell Plateau or Bougainville Peninsula) on a) the number of seedlings, b) number of trees, c) number of species, d) proportion of rain forest species, e) basal area, f) grass cover, g) rock cover in savanna plots. Df represents the number of parameters, logLik the maximum likelihood, AIC the Akaike value, delta the difference between the AIC of the model and the AIC of the best model in the set, and weight the Akaike weight (defined as the relative likelihood of the model).

a) Number of seedlings

Model	Df	logLik	AIC	delta	weight
Location	2	-272.416	548.8	0.00	1.00
Null	1	-285.116	572.2	23.40	0.00

b) Number of trees

Model	Df	logLik	AIC	delta	weight
Location	2	-293.248	590.5	0.00	0.88
Null	1	-296.278	594.6	4.06	0.12

c) Number of species

Model	Df	logLik	AIC	delta	weight
Location	2	-164.732	333.5	0.00	1.00
Null	1	-205.583	413.2	79.70	0.00

d) Proportion of rain forest species

Model	Df	logLik	AIC	delta	weight
Location	2	-124.472	252.9	0.00	1.00
Null	1	-200.881	403.8	150.82	0.00

e) Basal area

Model	Df	logLik	AIC	delta	weight
Null	2	-85.793	175.6	0.00	0.73
Location	3	-85.774	177.5	1.96	0.27

f) Grass cover

Model	Df	logLik	AIC	delta	weight
Location	5	-72.036	154.1	0.00	0.87
Null	4	-74.916	157.8	3.76	0.13

g) Rock cover

Model	Df	logLik	AIC	delta	weight
Null	4	-70.275	148.6	0.00	0.57
Location	5	-69.546	149.1	0.54	0.43

Table A2.3 Analysis of canopy cover multimodality in the Plateau and the Peninsula.

Results of the analysis of multimodality, conducted to detect the number of modes in total canopy cover. We employed latent class analysis on arcsine square-root transformed total canopy cover (Hirota *et al.*, 2011) and compared the fit of the models with 1, 2, or 3 modes using Bayesian Information Criterion (BIC). The lowest BIC values, corresponding to the best fitting mode, are highlighted in bold. Analyses were performed using the ‘flexmix’ package in R (Grun and Leisch, 2008; R Core Team, 2013).

Location	1 mode	2 modes	3 modes
Bougainville Peninsula	-7.89	-6.22	5.45
Mitchell Plateau	18.44	14.44	22.41

Table A2.4 Disturbance levels recorded in plots classified as stable rainforest, rainforest expanded in 1969 (‘Expanded 1969’), rainforest expanded in 2005 (‘Expanded 2005’), and stable savanna. Data are shown separately for the Bougainville Peninsula (Boug) and Mitchell Plateau (Mitch). Standard errors are reported for average values.

Disturbance	Stable rainforest		Expanded 1969		Expanded 2005		Stable savanna	
	Boug	Mitch	Boug	Mitch	Boug	Mitch	Boug	Mitch
Cattle impact	0 ± 0	1 ± 0	0 ± 0	2 ± 1	0 ± 0	1 ± 1	0 ± 0	1 ± 0
Fire frequency	0.1 ± 0.0	0.6 ± 0.0	0.1 ± 0.0	0.4 ± 0.0	0.1 ± 0.0	0.5 ± 0.0	0.1 ± 0.0	0.6 ± 0.0

Table A2.5 List of trees, shrubs, and vines identified in the vegetation transects and number of plots in which they were recorded in rainforests (RF) and savannas (SAV) in the Mitchell Plateau and the Bougainville Peninsula.

Species	Family	Typical habitat	Mitchell Plateau		Bougainville Peninsula	
			SAV	RF	SAV	RF
<i>Abrus precatorius</i> L.	<i>Fabaceae</i>	R	2	6	5	11
<i>Acacia dimidiata</i> Benth.	<i>Fabaceae</i>	S	0	0	6	0
<i>Acacia drepanocarpa</i> sub. <i>latifolia</i> Pedley	<i>Fabaceae</i>	S	0	0	3	0
<i>Acacia hemignosta</i> F.Muell.	<i>Fabaceae</i>	S	0	0	1	0
<i>Acacia</i> sp. Mill.	<i>Fabaceae</i>	S	1	1	0	0
<i>Acacia stigmatophylla</i> Benth.	<i>Fabaceae</i>	S	0	0	1	1
<i>Adenia heterophylla</i> (Blume) Koord.	<i>Passifloraceae</i>	R	1	1	0	0
<i>Aglaia eleagnoidea</i> (A. Juss.) Benth.	<i>Meliaceae</i>	R	1	0	1	4
<i>Aidia racemosa</i> (Cav.) Tirveng.	<i>Rubiaceae</i>	R	2	4	1	3
<i>Ailanthus triphysa</i> (Dennst.) Alston	<i>Simaroubaceae</i>	R	0	0	0	1
<i>Albizia canescens</i> Benth.	<i>Mimosaceae</i>	R	0	0	1	0
<i>Albizia lebbek</i> (L.) Benth.	<i>Mimosaceae</i>	R	1	8	0	1
<i>Allophylus</i> sp. L.	<i>Sapindaceae</i>	R	1	0	0	0
<i>Alstonia actinophylla</i> (A.Cunn.) K.Schum.	<i>Apocynaceae</i>	R	2	0	0	0
<i>Alstonia spectabilis</i> R.Br.	<i>Apocynaceae</i>	R	0	1	1	0
<i>Antidesma ghaesembilla</i> Gaertn.	<i>Phyllanthaceae</i>	S	6	4	15	2
<i>Asparagus racemosus</i> Willd.	<i>Asparagaceae</i>	R	0	1	1	3
<i>Atalaya salicifolia</i> (A.DC.) Blume	<i>Sapindaceae</i>	R	3	10	1	10
<i>Bauhinia cunninghamii</i> Benth.	<i>Caesalpiniaceae</i>	R	0	0	3	6
<i>Bauhinia malabarica</i> Roxb.	<i>Caesalpiniaceae</i>	R	3	0	0	1
<i>Bombax ceiba</i> L.	<i>Malvaceae</i>	R	3	4	5	7
<i>Bossiaea bossiaeioides</i> (A.Cunn. ex Benth.) Court	<i>Fabaceae</i>	S	0	0	1	0
<i>Brachychiton diversifolius</i> R.Br.	<i>Malvaceae</i>	S	3	1	3	1
<i>Brachychiton xanthophyllus</i> Guymr	<i>Malvaceae</i>	R	0	5	11	13
<i>Breynia cernua</i> (Poir.) Mull.Arg.	<i>Phyllanthaceae</i>	R	3	6	11	4
<i>Bridelia tomentosa</i> Blume	<i>Phyllanthaceae</i>	R	0	0	10	3
<i>Brucea javanica</i> (L.) Merr.	<i>Simaroubaceae</i>	R	0	0	0	1
<i>Buchanania obovata</i> Engl.	<i>Anacardiaceae</i>	S	4	0	0	0
<i>Canarium australianum</i> F.Muell.	<i>Burseraceae</i>	R	4	4	0	2
<i>Capparis lasiantha</i> R.Br. ex DC.	<i>Capparaceae</i>	R	0	0	4	1
<i>Capparis sepiaria</i> L.	<i>Capparaceae</i>	R	2	16	10	9
<i>Capparis</i> sp. L.	<i>Capparaceae</i>	R	1	5	0	3
<i>Celtis philippensis</i> Blanco	<i>Ulmaceae</i>	R	1	7	18	17
<i>Clerodendrum</i> sp. L.	<i>Lamiaceae</i>	R	0	2	0	0
<i>Clerodendrum floribundum</i> R.Br.	<i>Lamiaceae</i>	R	0	0	1	0
<i>Clerodendrum tomentosum</i> (Vent.) R.Br.	<i>Lamiaceae</i>	R	0	1	0	0

Species	Family	Typical habitat	Mitchell Plateau		Bougainville Peninsula	
			SAV	RF	SAV	RF
<i>Cochlospermum fraseri</i> Planch.	<i>Bixaceae</i>	S	0	0	2	0
<i>Corymbia bella</i> K.D.Hill & L.A.S.Johnson	<i>Myrtaceae</i>	S	7	0	2	0
<i>Corymbia confertiflora</i> (F.Muell.) K.D.Hill & L.A.S.Johnson	<i>Myrtaceae</i>	S	13	2	1	0
<i>Corymbia latifolia</i> (F.Muell.) K.D.Hill & L.A.S.Johnson	<i>Myrtaceae</i>	S	1	0	10	6
<i>Corymbia nesophila</i> (Blakely) K.D.Hill & L.A.S.Johnson	<i>Myrtaceae</i>	S	14	0	13	0
<i>Corymbia polycarpa</i> (F.Muell.) K.D.Hill & L.A.S.Johnson	<i>Myrtaceae</i>	S	0	0	2	0
<i>Corymbia</i> sp. K.D.Hill & L.A.S.Johnson	<i>Myrtaceae</i>	S	3	0	2	0
<i>Croton habrophyllus</i> Airy Shaw	<i>Euphorbiaceae</i>	R	0	4	6	12
<i>Croton schultzei</i> Benth.	<i>Euphorbiaceae</i>	R	0	0	0	4
<i>Croton tomentellus</i> F.Muell.	<i>Euphorbiaceae</i>	R	0	0	2	4
<i>Cryptocarya cunninghamii</i> Meisn.	<i>Lauraceae</i>	R	0	0	0	1
<i>Cupaniopsis anacardioides</i> (A.Rich.) Radlk.	<i>Sapindaceae</i>	R	0	5	5	7
<i>Cyathostemma glabrum</i> (Span.) Jessup ex Utteridge	<i>Annonaceae</i>	R	0	8	1	2
<i>Cycas basaltica</i> C.A. Gardner	<i>Cycadaceae</i>	S	0	0	2	0
<i>Denhamia obscura</i> (A.Rich.) Meisn. ex Walp.	<i>Celastraceae</i>	R	0	2	2	1
<i>Dioscorea bulbifera</i> L.	<i>Dioscoreaceae</i>	R	1	0	0	0
<i>Diospyros calicantha</i> O.Schwarz	<i>Ebenaceae</i>	R	0	4	0	0
<i>Diospyros humilis</i> (R.Br.) F.Muell.	<i>Ebenaceae</i>	R	1	0	0	2
<i>Diospyros maritima</i> Blume	<i>Ebenaceae</i>	R	1	4	0	2
<i>Diospyros rugosula</i> R.Br.	<i>Ebenaceae</i>	R	0	0	1	1
<i>Dodonaea platyptera</i> F.Muell.	<i>Sapindaceae</i>	R	0	2	4	1
<i>Dolichandrone heterophylla</i> (R.Br.) F.Muell.	<i>Bignoniaceae</i>	S	0	1	15	4
<i>Drypetes deplanchei</i> (Brongn. & Gris) Merr.	<i>Putranjivaceae</i>	R	1	5	2	10
<i>Elaeodendron melanocarpum</i> F.Muell.	<i>Celastraceae</i>	R	1	5	1	5
<i>Erythrina vespertilio</i> Benth.	<i>Fabaceae</i>	S	1	0	0	0
<i>Erythrophleum chlorostachys</i> (F.Muell.) Baill.	<i>Fabaceae</i>	S	17	2	16	3
<i>Eucalyptus miniata</i> A.Cunn. ex Schauer	<i>Myrtaceae</i>	S	5	0	0	0
<i>Eucalyptus oligantha</i> Schauer	<i>Myrtaceae</i>	S	0	0	2	0
<i>Eucalyptus tectifera</i> F.Muell.	<i>Myrtaceae</i>	S	14	0	9	1
<i>Eucalyptus tetradonta</i> F.Muell.	<i>Myrtaceae</i>	S	2	0	0	0
<i>Exocarpos latifolius</i> R.Br.	<i>Santalaceae</i>	R	0	4	11	12
<i>Ficus aculeata</i> A.Cunn. ex Miq.	<i>Moraceae</i>	R	5	1	3	0
<i>Ficus hispida</i> L.f.	<i>Moraceae</i>	R	0	3	0	0
<i>Flagellaria indica</i> L.	<i>Flagellariaceae</i>	R	1	9	0	6
<i>Flueggea virosa</i> (Willd.) Voigt	<i>Phyllanthaceae</i>	R	1	4	17	2
<i>Ganophyllum falcatum</i> Blume	<i>Sapindaceae</i>	R	3	4	0	4
<i>Gardenia pyrifolia</i> Benth.	<i>Rubiaceae</i>	S	1	0	0	0
<i>Garuga floribunda</i> Decne.	<i>Burseraceae</i>	R	0	5	0	2

Species	Family	Typical habitat	Mitchell Plateau		Bougainville Peninsula	
			SAV	RF	SAV	RF
<i>Glochidion disparipes</i> Airy Shaw	Phyllanthaceae	R	0	2	0	0
<i>Glycosmis trifoliata</i> (Blume) Spreng.	Rutaceae	R	1	12	2	12
<i>Grevillea dimidiata</i> F.Muell.	Proteaceae	S	7	0	0	0
<i>Grevillea heliosperma</i> R.Br.	Proteaceae	S	2	1	0	0
<i>Grewia breviflora</i> Benth.	Malvaceae	R	4	5	10	13
<i>Grewia oxyphylla</i> Burret	Malvaceae	R	0	1	0	0
<i>Grewia retusifolia</i> Kurz	Malvaceae	S	10	2	11	2
<i>Hakea arborescens</i> R.Br.	Proteaceae	S	2	1	11	2
<i>Ichnocarpus frutescens</i> (L.) W.T.Aiton	Apocynaceae	R	2	5	0	0
<i>Ipomoea costata</i> Benth.	Convolvulaceae	S	0	0	2	1
<i>Jasminum didymum</i> G.Forst.	Oleaceae	R	0	2	6	7
<i>Lepisanthes rubiginosa</i> (Roxb.) Leenh.	Sapindaceae	R	0	2	0	0
<i>Litsea glutinosa</i> (Lour.) C.B.Rob.	Lauraceae	R	1	4	1	1
<i>Livistona eastonii</i> C.A.Gardner	Arecaceae	S	18	4	0	0
<i>Luffa aegyptiaca</i> var. <i>leiocarpa</i> (Naud.) Heiser & E.E.Schill.	Cucurbitaceae	R	1	0	0	0
<i>Luvunga monophylla</i> (DC.) Mabb.	Rutaceae	R	0	0	1	6
<i>Mallotus dispersus</i> P.I.Forst.	Euphorbiaceae	R	0	0	0	4
<i>Maytenus</i> sp. Molina	Celastraceae	S	3	1	0	0
<i>Meiogyne cylindrocarpa</i> (Burck) Heusdei	Annonaceae	R	0	6	0	3
<i>Melochia umbellata</i> (Houtt.) Stapf	Malvaceae	R	0	5	2	1
<i>Micromelum minutum</i> (G.Forst.) Wight & Arn.	Rutaceae	R	3	9	1	5
<i>Miliusa brahei</i> (F.Muell.) Jessup	Annonaceae	R	0	0	0	1
<i>Miliusa tracey</i> Jessup	Annonaceae	R	0	1	1	3
<i>Mimusops elengi</i> L.	Sapotaceae	R	1	3	5	14
<i>Murraya paniculata</i> (L.) Jack	Rutaceae	R	0	7	5	6
<i>Myristica insipida</i> R.Br.	Myristicaceae	R	0	0	0	1
<i>Myrsine kimberleyensis</i> Jackes	Primulaceae	R	1	1	0	1
<i>Operculina</i> sp. Silva Manso	Convolvulaceae	S	0	0	0	1
<i>Pachygone ovata</i> (Poir.) Hook.f. & Thomson	Menispermaceae	R	0	0	0	1
<i>Parsonsia velutina</i> R.Br.	Apocynaceae	R	1	1	1	2
<i>Passiflora foetida</i> L.	Passifloraceae	S	3	2	25	4
<i>Pavetta kimberleyana</i> S.T.Reynolds.	Rubiaceae	R	4	10	1	3
<i>Persoonia falcata</i> R.Br.	Proteaceae	S	1	0	0	0
<i>Petalostigma pubescens</i> Domin	Picrodendraceae	S	6	1	0	0
<i>Phyllanthus reticulatus</i> Poir.	Phyllanthaceae	S	0	1	0	0
<i>Pisonia aculeata</i> L.	Nyctaginaceae	R	0	0	0	1
<i>Pittosporum spinescens</i> (F.Muell.) L.Cayzer, Crisp & I.Telford	Pittosporaceae	R	1	2	2	6
<i>Planchonia careya</i> (F.Muell.) R.Knuth	Lecythidaceae	S	17	0	4	0
<i>Plumbago zeylanica</i> L.	Plumbaginaceae	R	0	3	0	0
<i>Polyalthia australis</i> (Benth.) Jessup	Annonaceae	R	1	6	0	2

Species	Family	Typical habitat	Mitchell Plateau		Bougainville Peninsula	
			SAV	RF	SAV	RF
<i>Pouteria richardii</i> (F.Muell.) Baehni	<i>Sapotaceae</i>	R	0	0	1	1
<i>Premna acuminata</i> R.Br.	<i>Lamiaceae</i>	R	0	0	0	2
<i>Psychotria nesophila</i> F.Muell.	<i>Rubiaceae</i>	R	0	1	0	1
<i>Secamone elliptica</i> R.Br.	<i>Apocynaceae</i>	R	0	0	0	1
<i>Sersalisia sericea</i> (Aiton) R.Br.	<i>Sapotaceae</i>	R	2	4	2	5
<i>Sterculia quadrifida</i> R.Br.	<i>Malvaceae</i>	R	2	2	2	3
<i>Strichnos lucida</i> R.Br.	<i>Loganiaceae</i>	R	2	8	15	14
<i>Tarenna dallachiana</i> (Benth.) S.Moore	<i>Rubiaceae</i>	R	0	4	1	2
<i>Terminalia canescens</i> (DC.) Radlk	<i>Combretaceae</i>	S	5	1	11	1
<i>Terminalia microcarpa</i> Decne.	<i>Combretaceae</i>	R	7	10	4	1
<i>Terminalia petiolaris</i> Benth.	<i>Combretaceae</i>	R	1	6	6	10
<i>Terminalia volucris</i> Benth.	<i>Combretaceae</i>	R	0	0	0	2
<i>Thespesia thespesioides</i> (Benth.) Fryxell	<i>Malvaceae</i>	S	2	0	0	0
<i>Tinospora smilacina</i> Benth.	<i>Menispermaceae</i>	R	0	0	1	1
<i>Trema tomentosa</i> (Roxb.) Hara	<i>Cannabaceae</i>	R	1	1	16	0
<i>Turraea pubescens</i> Hell.	<i>Meliaceae</i>	R	0	0	0	1
<i>Tylophora cinerascens</i> (R.Br.) P.I.Forst.	<i>Apocynaceae</i>	R	0	7	0	0
<i>Vachellia ditricha</i> (Pedley) Kodela	<i>Fabaceae</i>	S	0	0	1	0
<i>Vachellia suberosa</i> (Benth.) Kodela	<i>Fabaceae</i>	S	6	0	17	4
<i>Vavaea</i> sp. Benth.	<i>Meliaceae</i>	R	0	0	3	0
<i>Vitex acuminata</i> R.Br.	<i>Lamiaceae</i>	R	2	6	11	10
<i>Wrightia pubescens</i> R.Br.	<i>Apocynaceae</i>	R	0	8	1	0
<i>Xanthostemon psidioides</i> (Lindl.) Peter G.Wilson & J.T.Waterh.	<i>Myrtaceae</i>	S	0	0	1	0
<i>Xanthostemon</i> sp. F.Muell.	<i>Myrtaceae</i>	S	1	0	0	0
<i>Ziziphus quadrilocularis</i> F.Muell.	<i>Rhamnaceae</i>	R	0	2	9	12

Table A2.6 Number of plots and characteristics recorded in plots classified as stable rainforest, rainforest expanded in 1969 ('Expanded 1969'), rainforest expanded in 2005 ('Expanded 2005'), and stable savanna. Data are shown separately for the Bougainville Peninsula (Boug) and Mitchell Plateau (Mitch). Standard errors are reported for average values.

Plot characteristics	Stable rainforest		Expanded 1969		Expanded 2005		Stable savanna	
	Boug	Mitch	Boug	Mitch	Boug	Mitch	Boug	Mitch
N. plots	7	15	8	2	4	2	30	30
Grass cover	1 ± 0	1 ± 0	2 ± 0	2 ± 1	4 ± 1	1 ± 0	4 ± 0	4 ± 0
Rock cover	4 ± 0	4 ± 0	5 ± 0	5 ± 1	3 ± 0	3 ± 0	2 ± 0	2 ± 0
Number of seedlings	35 ± 4	27 ± 3	40 ± 6	16 ± 3	25 ± 7	16 ± 2	15 ± 2	10 ± 1
Number of trees	21 ± 4	14 ± 1	18 ± 2	14 ± 2	10 ± 3	16 ± 5	9 ± 1	11 ± 2
Basal area (m ² · ha ⁻¹)	13 ± 2	17 ± 4	10 ± 2	19 ± 6	6 ± 1	11 ± 5	8 ± 1	8 ± 1
Proportion of rainforest adult trees (%)	98 ± 2	98 ± 2	90 ± 5	84 ± 16	48 ± 20	79 ± 12	29 ± 6	1 ± 1
Savanna understorey (% of plots)	14	27	25	50	75	50	97	100
Rainforest understorey (% of plots)	100	100	100	100	100	100	100	27
Species richness (number/plot)	20 ± 2	17 ± 1	20 ± 1	19 ± 0	17 ± 1	22 ± 1	15 ± 1	7 ± 1
Tree canopy cover (%)	65 ± 9	62 ± 6	52 ± 6	72 ± 5	37 ± 3	73 ± 13	28 ± 3	26 ± 3
Full canopy cover (%)	75 ± 7	71 ± 5	66 ± 5	78 ± 3	48 ± 4	84 ± 3	41 ± 2	33 ± 3

Table S2.7 Importance (w_+) of a) the factors location (Mitchell Plateau or Bougainville Peninsula) and vegetation type (stable rain forest or expanded rain forest) as predictor of the listed response variables in rainforests and b) the factor location as a predictor in stable savannas. Factor importance is expressed as w_+ , with values > 0.73 (in bold) considered important predictors.

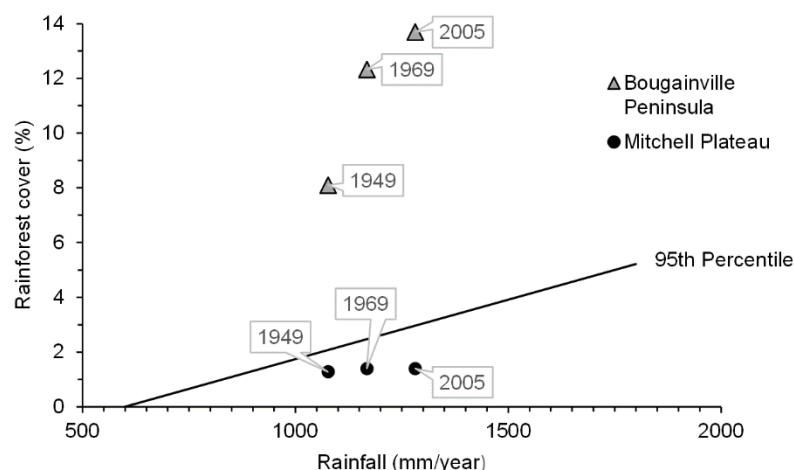
a) Rain forests (stable and expanded)

Response variable	w_+	
	Location	Vegetation type
N. seedlings	1.00	0.84
N. adult trees	0.92	0.66
N. species	0.41	0.39
Proportion of rainforest species	0.41	1.00
Basal area	0.56	0.42
Grass cover	0.37	0.70
Rock cover	0.43	0.28

b) Stable savannas

Response variable	w_+
	Location
N. seedlings	1.00
N. adult trees	0.88
N. species	1.00
Proportion of rainforest species	1.00
Basal area	0.27
Grass cover	0.87
Rock cover	0.43

Fig. A2.1 Percentile analysis of the correlation rainfall-rainforest cover. Using data for current rainforest cover and rainfall in northern Australia from Chapter 2, we employed the R package ‘quantreg’ (Koenker, 2016) to calculate the 95% percentile regression and compared the variation in rainforest cover and rainfall in the north-west Australian monsoon tropics with those obtained for the Plateau and Peninsula. This space-for-time substitution showed that an increase in rainfall from 1080 mm/year (as recorded in the study areas in 1949) to 1280 mm/year (as recorded in 1969) corresponded to a relative rainforest increment of 41%. The regression line represents variations in rainforest cover associated with differences in mean annual rainfall in the north-west Australian monsoon tropics. Rainforest cover detected in the two study locations in 1949, 1969, and 2005 are also reported.



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Appendix 3

Supplementary material to Chapter 4

Table A3.1 Main data collected, including species, bark thickness (2013), height (2013 and 2014), stem diameter (2013 and 2014) and resprouter type (2014).

Habitat	Species	Height (m) 2013	Stem diameter (cm) 2013	Bark thickness (mm) 2013	Condition 2014	Resprouter type 2014	Height (m) 2014	Stem diameter (cm) 2014
Rainforest	<i>Atalaya salicifolia</i>	0.89	0.58	0.19	Alive	Aerial - axillary	1.73	2.90
Rainforest	<i>Atalaya salicifolia</i>	0.76	0.76	0.40	Alive	Aerial - axillary	0.74	0.80
Rainforest	<i>Atalaya salicifolia</i>	0.75	0.75	0.55	Alive	Aerial - axillary	0.77	0.80
Rainforest	<i>Atalaya salicifolia</i>	1.72	1.27	1.13	Alive	Basal	1.06	1.70
Rainforest	<i>Atalaya salicifolia</i>	1.13	1.10	0.63	Alive	Basal	0.52	0.40
Rainforest	<i>Atalaya salicifolia</i>	1.61	1.41	0.79	Alive	Basal	0.64	0.50
Rainforest	<i>Atalaya salicifolia</i>	0.82	0.93	0.48	Alive	Basal	0.63	0.70
Rainforest	<i>Atalaya salicifolia</i>	1.90	1.52	1.03	Dead	-	-	-
Rainforest	<i>Atalaya salicifolia</i>	2.06	2.68	0.33	Alive	Basal	3.00	4.00
Rainforest	<i>Atalaya salicifolia</i>	1.68	1.20	0.83	Alive	Basal	0.86	1.80
Rainforest	<i>Canarium australianum</i>	2.36	2.19	0.56	Dead	-	-	-
Rainforest	<i>Canarium australianum</i>	1.13	1.06	0.65	Dead	-	-	-
Rainforest	<i>Canarium australianum</i>	0.65	0.48	0.43	Alive	Aerial - axillary	0.53	0.80
Rainforest	<i>Canarium australianum</i>	1.46	2.00	0.86	Alive	Basal	1.03	0.80
Rainforest	<i>Canarium australianum</i>	2.60	1.49	0.40	Missing	-	-	-
Rainforest	<i>Canarium australianum</i>	2.90	3.13	1.40	Alive	Aerial - axillary	1.30	3.70
Rainforest	<i>Canarium australianum</i>	2.55	2.53	0.77	Dead	-	-	-

Habitat	Species	Height (m) 2013	Stem diameter (cm) 2013	Bark thickness (mm) 2013	Condition 2014	Resprouter type 2014	Height (m) 2014	Stem diameter (cm) 2014
Rainforest	<i>Canarium australianum</i>	0.75	1.36	0.69	Alive	Aerial - axillary	0.70	2.30
Rainforest	<i>Canarium australianum</i>	0.54	0.64	0.48	Alive	Aerial - axillary	2.01	3.40
Rainforest	<i>Canarium australianum</i>	0.60	1.32	0.33	Alive	Basal	0.34	0.30
Rainforest	<i>Ficus aculeata</i>	1.68	1.32	0.64	Alive	Basal	0.82	0.90
Rainforest	<i>Ficus aculeata</i>	0.80	0.98	0.57	Alive	Basal	0.63	0.70
Rainforest	<i>Ficus aculeata</i>	1.08	1.11	0.54	Alive	Basal	0.97	0.90
Rainforest	<i>Ficus aculeata</i>	1.35	1.33	0.55	Alive	Basal	0.86	0.80
Rainforest	<i>Ficus aculeata</i>	1.57	3.24	4.01	Alive	Basal	1.61	3.20
Rainforest	<i>Ficus aculeata</i>	2.25	2.00	1.07	Alive	Aerial - axillary	1.80	2.80
Rainforest	<i>Ficus aculeata</i>	1.38	1.50	0.85	Alive	Aerial - axillary	1.14	2.50
Rainforest	<i>Ficus aculeata</i>	1.80	1.92	2.23	Alive	Aerial - axillary	1.54	3.00
Rainforest	<i>Ficus aculeata</i>	1.77	2.20	1.64	Missing	-	-	-
Rainforest	<i>Ficus aculeata</i>	1.37	1.13	0.68	Alive	Aerial - axillary	0.81	2.30
Rainforest	<i>Sterculia quadrifida</i>	0.86	0.84	0.59	Missing	-	-	-
Rainforest	<i>Sterculia quadrifida</i>	1.48	1.07	0.54	Dead	-	-	-
Rainforest	<i>Sterculia quadrifida</i>	2.15	2.33	0.41	Alive	Aerial - axillary	2.14	2.90
Rainforest	<i>Sterculia quadrifida</i>	2.45	2.42	0.55	Missing	-	-	-
Rainforest	<i>Sterculia quadrifida</i>	1.84	2.15	0.58	Alive	Aerial - axillary	1.02	2.90
Rainforest	<i>Sterculia quadrifida</i>	1.55	1.21	0.37	Alive	Basal	0.26	0.30
Rainforest	<i>Sterculia quadrifida</i>	0.96	0.87	0.35	Alive	Basal	0.41	0.50
Rainforest	<i>Sterculia quadrifida</i>	1.28	1.15	0.37	Missing	-	-	-
Rainforest	<i>Sterculia quadrifida</i>	1.27	0.83	0.25	Missing	-	-	-
Rainforest	<i>Strychnos lucida</i>	1.22	0.33	0.33	Alive	Basal	0.28	0.20
Rainforest	<i>Strychnos lucida</i>	1.54	1.12	0.24	Alive	Aerial - axillary	0.62	1.50
Rainforest	<i>Strychnos lucida</i>	1.12	0.87	0.30	Alive	Basal	0.14	0.20
Rainforest	<i>Strychnos lucida</i>	1.19	0.70	0.64	Alive	Basal	0.19	0.50

Habitat	Species	Height (m) 2013	Stem diameter (cm) 2013	Bark thickness (mm) 2013	Condition 2014	Resprouter type 2014	Height (m) 2014	Stem diameter (cm) 2014
Rainforest	<i>Strychnos lucida</i>	1.35	1.05	0.25	Alive	Aerial - axillary	0.33	1.50
Rainforest	<i>Strychnos lucida</i>	2.57	1.08	0.32	Alive	Basal	1.24	0.60
Rainforest	<i>Strychnos lucida</i>	1.98	1.28	0.40	Alive	Aerial - axillary	0.80	1.70
Rainforest	<i>Strychnos lucida</i>	2.11	3.78	1.04	Alive	Aerial - axillary	1.97	4.00
Rainforest	<i>Strychnos lucida</i>	1.46	0.73	0.43	Alive	Basal	0.36	0.50
Rainforest	<i>Strychnos lucida</i>	0.99	0.73	0.20	Alive	Basal	0.45	0.30
Rainforest	<i>Terminalia petiolaris</i>	1.74	1.34	0.44	Dead	-	-	-
Rainforest	<i>Terminalia petiolaris</i>	1.85	2.69	0.58	Alive	Aerial - axillary	1.90	4.40
Rainforest	<i>Terminalia petiolaris</i>	1.39	1.55	0.45	Dead	-	-	-
Rainforest	<i>Terminalia petiolaris</i>	3.12	4.64	0.60	Alive	Aerial - axillary	2.40	6.70
Rainforest	<i>Terminalia petiolaris</i>	1.87	2.23	0.55	Alive	Aerial - axillary	2.07	3.80
Rainforest	<i>Terminalia petiolaris</i>	1.29	1.78	0.47	Alive	Aerial - axillary	1.79	4.00
Rainforest	<i>Terminalia petiolaris</i>	1.65	2.29	0.53	Alive	Aerial - axillary	1.96	4.10
Rainforest	<i>Terminalia petiolaris</i>	0.92	1.12	0.28	Dead	-	-	-
Rainforest	<i>Terminalia petiolaris</i>	1.08	1.13	0.36	Dead	-	-	-
Rainforest	<i>Terminalia petiolaris</i>	0.52	0.51	0.25	Dead	-	-	-
Rainforest	<i>Vitex acuminata</i>	1.87	1.37	0.59	Alive	Aerial - axillary	0.96	2.10
Rainforest	<i>Vitex acuminata</i>	2.70	2.13	0.36	Alive	Aerial - axillary	2.50	2.90
Rainforest	<i>Vitex acuminata</i>	0.64	0.76	0.53	Alive	Aerial - axillary	0.65	1.30
Rainforest	<i>Vitex acuminata</i>	1.27	0.89	0.32	Alive	Aerial - axillary	0.92	1.50
Rainforest	<i>Vitex acuminata</i>	1.76	1.40	0.60	Alive	Aerial - axillary	1.28	2.00
Rainforest	<i>Vitex acuminata</i>	1.19	0.74	0.42	Dead	Aerial - axillary		
Rainforest	<i>Vitex acuminata</i>	2.12	1.44	0.58	Alive	Aerial - axillary	0.50	2.20
Rainforest	<i>Vitex acuminata</i>	0.97	1.04	0.58	Alive	Aerial - axillary	0.78	1.70
Rainforest	<i>Vitex acuminata</i>	1.05	0.92	0.30	Alive	Aerial - axillary	0.57	1.80
Rainforest	<i>Vitex acuminata</i>	0.75	1.09	0.53	Alive	Aerial - axillary	0.27	1.10

Habitat	Species	Height (m) 2013	Stem diameter (cm) 2013	Bark thickness (mm) 2013	Condition 2014	Resprouter type 2014	Height (m) 2014	Stem diameter (cm) 2014
Savanna	<i>Corimbia confertiflora</i>	2.07	4.23	3.86	Alive	Aerial - epicormic	1.98	5.20
Savanna	<i>Corimbia confertiflora</i>	2.57	4.65	3.03	Alive	Aerial - epicormic	2.60	6.00
Savanna	<i>Corimbia confertiflora</i>	1.50	2.33	2.86	Missing	-	-	-
Savanna	<i>Corimbia confertiflora</i>	1.59	2.84	1.98	Alive	Aerial - epicormic	1.75	40.00
Savanna	<i>Corimbia confertiflora</i>	2.05	3.77	2.44	Alive	Aerial - epicormic	1.85	4.90
Savanna	<i>Corimbia confertiflora</i>	1.36	3.34	2.56	Alive	Aerial - epicormic	1.60	5.00
Savanna	<i>Corimbia confertiflora</i>	1.42	3.46	2.76	Alive	Aerial - epicormic	1.70	4.90
Savanna	<i>Corimbia confertiflora</i>	1.44	2.75	3.06	Alive	Aerial - epicormic	0.85	3.50
Savanna	<i>Corimbia confertiflora</i>	1.23	3.04	2.88	Missing	-	-	-
Savanna	<i>Corimbia confertiflora</i>	2.18	4.04	3.41	Alive	Aerial - epicormic	2.40	5.00
Savanna	<i>Erythrophleum chlorostachys</i>	1.16	2.03	1.41	Missing	-	-	-
Savanna	<i>Erythrophleum chlorostachys</i>	1.33	3.04	2.95	Alive	Aerial - epicormic	0.50	4.50
Savanna	<i>Erythrophleum chlorostachys</i>	2.48	4.32	4.46	Alive	Aerial - epicormic	2.50	6.30
Savanna	<i>Erythrophleum chlorostachys</i>	2.89	5.46	6.22	Alive	Aerial - epicormic	3.00	7.90
Savanna	<i>Erythrophleum chlorostachys</i>	2.28	4.18	4.40	Missing	-	-	-
Savanna	<i>Erythrophleum chlorostachys</i>	2.75	4.27	3.58	Alive	Aerial - epicormic	1.70	
Savanna	<i>Erythrophleum chlorostachys</i>	2.72	4.29	4.71	Alive	Aerial - epicormic	2.50	5.90
Savanna	<i>Erythrophleum chlorostachys</i>	1.47	1.87	2.48	Alive	Basal	0.85	2.00
Savanna	<i>Erythrophleum chlorostachys</i>	0.97	1.54	2.03	Alive	Aerial - epicormic	0.89	2.10
Savanna	<i>Erythrophleum chlorostachys</i>	1.23	1.62	1.60	Alive	Basal	0.93	2.50
Savanna	<i>Eucalyptus tectifia</i>	1.12	3.63	2.71	Alive	Aerial - epicormic	1.15	4.00
Savanna	<i>Eucalyptus tectifia</i>	1.07	2.16	1.92	Alive	Aerial - epicormic	1.30	3.30
Savanna	<i>Eucalyptus tectifia</i>	1.08	3.06	2.08	Alive	Aerial - epicormic	1.20	3.00
Savanna	<i>Eucalyptus tectifia</i>	0.93	1.75	0.84	Missing	-	-	-
Savanna	<i>Eucalyptus tectifia</i>	1.07	3.35	1.72	Missing	-	-	-
Savanna	<i>Eucalyptus tectifia</i>	1.66	3.68	3.22	Alive	Aerial - epicormic	1.80	5.10

Habitat	Species	Height (m) 2013	Stem diameter (cm) 2013	Bark thickness (mm) 2013	Condition 2014	Resprouter type 2014	Height (m) 2014	Stem diameter (cm) 2014
Savanna	<i>Eucalyptus tectifica</i>	1.93	3.72	2.00	Alive	Aerial - epicormic	1.95	4.20
Savanna	<i>Eucalyptus tectifica</i>	2.21	0.41	1.85	Alive	Aerial - epicormic	2.30	4.80
Savanna	<i>Eucalyptus tectifica</i>	2.16	3.62	4.37	Alive	Aerial - epicormic	2.10	5.00
Savanna	<i>Eucalyptus tectifica</i>	1.62	4.82	3.75	Alive	Aerial - epicormic	1.85	6.00
Savanna	<i>Planchonia careya</i>	1.76	3.25	3.24	Alive	Basal	1.40	2.50
Savanna	<i>Planchonia careya</i>	2.17	4.72	4.62	Alive	Aerial - epicormic	2.10	5.80
Savanna	<i>Planchonia careya</i>	1.88	4.21	4.01	Alive	Aerial - epicormic	1.80	6.00
Savanna	<i>Planchonia careya</i>	2.29	5.08	4.98	Alive	Aerial - epicormic	2.00	6.90
Savanna	<i>Planchonia careya</i>	2.28	5.49	4.33	Alive	Basal	2.40	8.30
Savanna	<i>Planchonia careya</i>	1.35	2.22	3.65	Alive	Aerial - epicormic	1.60	3.80
Savanna	<i>Planchonia careya</i>	1.06	0.90	0.78	Alive	Aerial - epicormic	0.54	1.00
Savanna	<i>Planchonia careya</i>	1.07	0.80	0.58	Alive	Aerial - epicormic	0.75	1.00
Savanna	<i>Planchonia careya</i>	1.11	1.09	1.00	Missing	-	-	-
Savanna	<i>Planchonia careya</i>	1.19	0.94	0.31	Missing	-	-	-
Savanna	<i>Terminalia canescens</i>	1.30	1.96	4.99	Alive	Aerial - axillary	1.23	2.50
Savanna	<i>Terminalia canescens</i>	1.13	1.84	3.45	Alive	Aerial - epicormic	1.24	1.90
Savanna	<i>Terminalia canescens</i>	1.32	1.87	3.53	Dead	-	-	-
Savanna	<i>Terminalia canescens</i>	1.33	2.85	5.42	Alive	Aerial - epicormic	0.89	2.90
Savanna	<i>Terminalia canescens</i>	0.72	0.69	1.17	Alive	Aerial - axillary	0.73	1.30
Savanna	<i>Terminalia canescens</i>	2.29	3.13	7.75	Alive	Aerial - axillary	2.54	4.00
Savanna	<i>Terminalia canescens</i>	1.98	2.64	4.86	Alive	Aerial - axillary	2.20	3.90
Savanna	<i>Terminalia canescens</i>	1.97	2.13	3.98	Alive	Basal	1.10	1.00
Savanna	<i>Terminalia canescens</i>	1.58	2.40	4.52	Alive	Aerial - epicormic	1.21	2.00
Savanna	<i>Terminalia canescens</i>	2.49	3.08	4.67	Alive	Aerial - axillary	2.40	4.10

Table A3.2 Comparison of models describing the relationship between whole plant survival and bark thickness, species, and plant height for a) rainforest and b) savanna individuals.

	K	AIC_c	Δ_AIC_c	AIC_cWt	Cum.Wt	LL
a) Species	7	59.36	0	0.36	0.36	-21.66
Null Model	1	60.42	1.05	0.21	0.57	-29.18
Bark thickness + Species	8	61.88	2.52	0.1	0.68	-21.61
Height + Species	8	61.99	2.63	0.1	0.77	-21.66
Bark thickness	2	62.08	2.71	0.09	0.87	-28.94
Height	2	62.55	3.19	0.07	0.94	-29.18
Height + Bark thickness	3	64.22	4.85	0.03	0.97	-28.9
Height + Species + Bark thickness	9	64.58	5.22	0.03	1	-21.59
b) Null Model	1	11.55	0	0.47	0.47	-4.73
Height	2	13.07	1.52	0.22	0.69	-4.38
Bark thickness	2	13.67	2.12	0.16	0.85	-4.68
Height + Bark thickness	3	14.34	2.79	0.12	0.97	-3.85
Species	5	18.17	6.62	0.02	0.99	-3.25
Height + Species	6	20.54	8.99	0.01	0.99	-3.07
Bark thickness + Species	6	20.81	9.26	0	1	-3.21
Height + Species + Bark thickness	7	23.39	11.84	0	1	-3.05

Appendix 4

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ORIGINAL RESEARCH

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Water, land, fire, and forest: Multi-scale determinants of rainforests in the Australian monsoon tropics

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Abstract

The small rainforest fragments found in savanna landscapes are powerful, yet often overlooked, model systems to understand the controls of these contrasting ecosystems. We analyzed the relative effect of climatic variables on rainforest density at a subcontinental level, and employed high-resolution, regional-level analyses to assess the importance of landscape settings and fire activity in determining rainforest density in a frequently burnt Australian savanna landscape. Estimates of rainforest density (ha/km²) across the Northern Territory and Western Australia, derived from preexisting maps, were used to calculate the correlations between rainforest density and climatic variables. A detailed map of the northern Kimberley (Western Australia) rainforests was generated and analyzed to determine the importance of geology and topography in controlling rainforests, and to contrast rainforest density on frequently burnt mainland and nearby islands. In the northwestern Australian, tropics rainforest density was positively correlated with rainfall and moisture index, and negatively correlated with potential evapotranspiration. At a regional scale, rainforests showed preference for complex topographic positions and more fertile geology. Compared with mainland areas, islands had significantly lower fire activity, with no differences between terrain types. They also displayed substantially higher rainforest density, even on level terrain where geomorphological processes do not concentrate nutrients or water. Our multi-scale approach corroborates previous studies that suggest moist climate, infrequent fires, and geology are important stabilizing factors that allow rainforest fragments to persist in savanna landscapes. These factors need to be incorporated in models to predict the future extent of savannas and rainforests under climate change.

KEYWORDS

Australian monsoon tropics, fire, geologic substrates, rainfall gradients, rainforests, topographic fire protection

1 | INTRODUCTION

The global extent of closed canopy tropical rainforests and savannas is determined by climate, especially mean annual precipitation

(Lehmann et al., 2014; Murphy & Bowman, 2012). However, at around 1,000–2,000 mm/year rainforest and savanna form vegetation mosaics (Hirota, Holmgren, van Nes, & Scheffer, 2011; Staver, Archibald, & Levin, 2011a, 2011b). Tropical savannas are characterized by a low

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tree cover and a high biomass of C4 grasses, which supports frequent fires in the dry season (Bond, Woodward, & Midgley, 2005; Hoffmann, Jaconis, et al., 2012). By contrast, tropical rainforests have a species-rich tree flora that form dense canopies, little grass, and infrequent fire activity.

The mechanisms that control patterning of rainforest and savanna mosaics are disputed, with debate polarized between the importance of fire and soils. One view is that edaphic factors like soil nutrients are the main control of rainforest–savanna mosaics, and fire is not a cause but rather a consequence of vegetation patterns (Lloyd et al., 2008; Veenendaal et al., 2015). Although savanna soils may have sufficient nutrient stocks to support rainforest trees (Bond, 2010; Vourlitis et al., 2015), rainforests are generally found on more nutrient-rich soils compared with savannas (Dantas, Batalha, & Pausas, 2013; Silva et al., 2013). Infertile savanna soils are known to limit expansion of rainforest (Silva et al., 2013), while deeper and more fertile substrates allow rainforest to grow in drier climates (known as “edaphic compensation”; Ash, 1988; Webb, 1968). However, it is not clear whether these patterns result from a direct edaphic effect or from local feedbacks. Soils underneath rainforests are often more rich in nutrients, compared with savannas, regardless of the inherent fertility of soil parent material (Dantas et al., 2013; Silva et al., 2013), because of nutrient acquisition and cycling (Silva et al., 2008). Tree canopy cover and canopy productivity increase soil nutrient content (Paiva, Silva, & Haridasan, 2015), particularly N concentration and availability (Schmidt & Stewart, 2003). Consequently, there are substantial practical difficulties in making ecologically meaningful measurements of soils fertility variation, particularly across rainforest ecotones, where forest boundaries wax and wane (Silva et al., 2013; Warman, Bradford, & Moles, 2013).

The alternative view is that rainforest and savanna are “bi-stable” in regions with intermediate productivity, and the realization of vegetation depends on landscape fire history (Bond et al., 2005; Dantas, Hirota, Oliveira, & Pausas, 2016; Hoffmann, Geiger, et al., 2012; Murphy & Bowman, 2012; Staver et al., 2011a; Warman & Moles, 2009). This view is based on alternative stable state (ASS) theory whereby stabilizing feedbacks hold rainforest or savanna in specific “basins of attraction” (Hirota et al., 2011). Resolving the role of edaphic factors in controlling rainforest boundaries directly or indirectly via feedbacks is complex and demands multiple lines of evidence, including direct measurements of soils, modeling, and experiments (Bowman, Perry, & Marston, 2015). Analysis of remote sensing estimates of canopy cover at a global scale has been presented as evidence for the bimodal distribution of rainforests and savannas (Staver et al., 2011b). It has been argued that the intensity of the bimodality may be a statistical artifact associated with the use of regression tree (CART) analyses, which impose discontinuities in satellite tree cover estimates (Hanan, Tredennick, Prihodko, Bucini, & Dohn, 2014, 2015; Staver & Hansen, 2015), although global canopy height analyses, based on products derived from LiDAR measurements, confirmed the bimodality detected through satellite data (Xu et al., 2016).

Regional-level analyses based on remote sensing have been employed in studies investigating the environmental controls of different types of vegetation (Dahlin, Asner, & Field, 2014; Fensham, Fairfax, & Archer, 2005; Murphy et al., 2010). However, there has been

surprisingly limited analysis of rainforest–savanna mosaics at a regional level. In an important pioneering study, Ash (1988) synthesized data from topographic maps, aerial photography, and field data to create a model of the environmental controls of rainforests and savanna vegetation in the wet tropics of North Queensland (Australia), to assess the relationship between rainforest location and environmental characteristics. Ash (1988) concluded that the distribution of rainforest boundaries can be empirically predicted based on water availability and topography, and substrate fertility might allow rainforests to expand into otherwise unfavorable environments. This research was supported by Fensham (1995), who employed aerial photography and satellite imagery to investigate the relation between dry rainforest and environmental variables in North Queensland. To the best of our knowledge, there are no other map-based analyses of rainforest–savanna mosaics at a regional scale anywhere else in the tropics. These rainforest patches are known to be biodiverse and important for a broad cross section of fauna (Price, 2006; Tutin, White, & Mackanga-Missandzou, 1997), yet they have been poorly researched compared with the more extensive wet rainforests (Sánchez-Azofeifa et al., 2005).

Northwestern Australia is an attractive model system because it spans a wide rainfall gradient at the driest extreme of the Australian tropical rainforest estate (Bowman, 2000). The global analysis of Staver et al. (2011b) suggests the region is deterministically savanna; yet, tiny patches of rainforest exist, embedded in the savanna matrix. These environments rainforests are more exposed to fire due to their higher boundary/core ratio; nonetheless, in some locations rainforest expansion has occurred (Banfai & Bowman, 2006; Bowman, Walsh, & Milne, 2001; Clayton-Greene & Beard, 1985). Studies from northern Australia and elsewhere in the tropics have identified the importance of landscape setting in determining rainforest distribution in areas subject to high fire activity. For example, rainforests can be more abundant on islands that have lower fire activity than adjacent mainland savannas (Clayton-Greene & Beard, 1985). Rainforests can also be confined to steep gullies or valleys (Bowman, 2000; Ibanez et al., 2013; Warman & Moles, 2009) because of the fire protection they provide (Murphy & Bowman, 2012), although additional effects of higher nutrient and water availability could also be important (Ash, 1988).

We employed a macroecological approach to determine the effect of climatic and geomorphological factors (topography and geology) on rainforest abundance at a large spatial scale. Geology was used as a proxy for the nutrient stock provided by the parent material, to exclude the effect of vegetation on soil fertility. To assess the correlations between climate and rainforest distribution in the entire northwestern Australian monsoon tropics, we analyzed existing subcontinental-scale vegetation maps. We then assessed the importance of topography and geology at a regional scale, as the effects of these factors on rainforest distribution are detectable at this scale, compared with climate (Murphy & Bowman, 2012). To do so, we generated a detailed map of rainforests in the northern Kimberley (Western Australia), which is characterized by a limited rainfall range (200 mm/year), and a variety of geologies and topographic settings. Within this region, we undertook a local-scale “natural experiment” comparing the influence of topography and fire activity on rainforest density on mainland and

adjacent islands with similar rainfall, geology, and distance from the coastline. We addressed the following hypotheses:

- At a subcontinental scale, factors associated with water availability are the main climatic drivers determining rainforest density;
- At a regional scale, topography and geology affect rainforest distribution;
- At a local scale, the importance of insularity and topography is directly related to fire activity. In locations with high fire activity (mainland), rainforests are predominantly confined to fire-sheltered settings, whereas in areas with lower fire activity (islands), rainforests will also be able to grow in more exposed settings.

Collectively this study investigates the drivers of rainforest distribution across multiple spatial scales in northern Australia, thereby illuminating the capacity for climate change and fire management to affect rainforest coverage and providing insights for both theoretical ecology and applied land management.

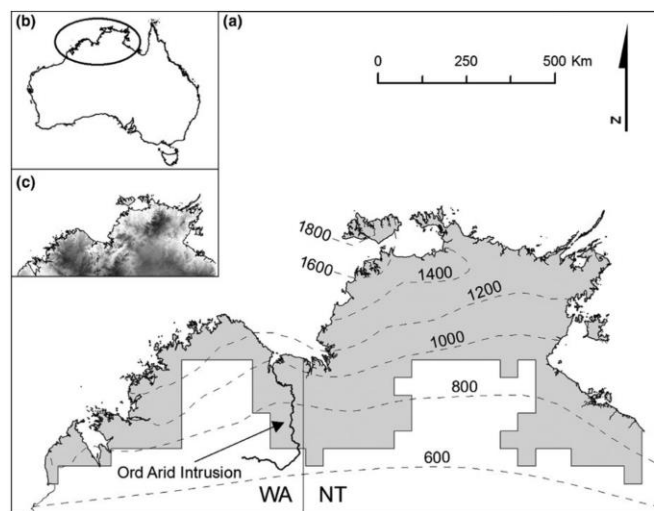
2 | METHODS

2.1 | Geographic context

The Australian monsoon tropics are characterized by a pronounced wet and dry seasons associated with the Australian summer monsoon (Bowman et al., 2010). This region includes the whole of northern Australia except the Australian wet tropics in North Queensland (Bowman, 2000; Figure 1a-c). In contrast to the wet tropics, where tropical rainforests dominate, the monsoon tropics support vast eucalypt savannas (Bowman, 2000; Figure 2a,c). Embedded in these savannas are very small patches of monsoon tropical rainforest, ranging from a few trees to 100 ha in area (McKenzie, Belbin, Keighery, & Kenneally,

1991). These rainforests have floristic and biogeographic affinities with wet tropical rainforests in both Asia and Australia. They have been intensively studied given their unusual biogeography and ecology, particularly their ability to persist in a highly flammable tropical savanna environment (Bowman, 2000). Some rainforests are known to grow on aquifers (Kenneally, Keighery, & Hyland, 1991; Russell-Smith, 1991), which insulate the patches from regional climate, but our mapping could not differentiate these types from the more widespread and drought-adapted rainforests (Bowman, Wilson, & McDonough, 1991; Russell-Smith, 1991). The locus of the subcontinental study was the Australian monsoon tropics west of the Carpentarian Gap biogeographic divide, which separates the biota of the Northern Territory and Western Australia from Cape York Peninsula (Bowman et al., 2010). Annual rainfall in this area varies from approximately 1,900 mm in the northeast to 700 mm in the southwest (Figure 1c), that would be expected to exert a strong influence on the abundance of rainforest. This analysis was made possible by combining vegetation maps produced by the Northern Territory and Western Australian government land management agencies, noting that the border between the two states broadly align with the Ord Arid Intrusion, a major biogeographic boundary that separates the biota of the Kimberley region of Western Australia from that of the "Top End" of the Northern Territory (Figure 1; Bowman et al., 2010; Eldridge, Potter, & Cooper, 2011), and that likely affects rainforest species diversity. In addition to this coarse-scale subcontinental study, we undertook a more detailed analysis of the rainforests to the west of the Ord Arid Intrusion. This region, located at the extreme end of the precipitation gradient where rainforest occurs in northern Australia, has limited spatial variability in rainfall (1,200–1,400 mm), which allowed us to identify ecological factors, other than precipitation, that shape rainforest distribution. This was based on fine-scale mapping of the traditional lands of the Wunambal Gaambera people, henceforth called the Wunambal Gaambera Country.

FIGURE 1 The monsoon rainforest domain in northwestern Australia. (a) The gray area represents the monsoon rainforest domain in the north of Western Australia (WA; Kimber et al., 1991) and the Northern Territory (NT). The Ord Arid Intrusion, the main biogeographic barrier between the two states, is indicated. Dashed lines indicate rainfall isohyets (mm). The insets show (b) the study area within Australia and (c) elevation (minimum, 0 m, white; maximum, 960 m, black)



The Wunambal Gaambera Country occupies an area of 9,144 km², dominated by biodiverse tropical savannas occurring on deeply weathered sandstones and basaltic base rocks of Precambrian age, often capped by Cainozoic laterites. In this region, average annual rainfall occurs almost entirely during the summer wet season (November–April), while the rest of the year is almost rain-free (Beard, 1976). The landscapes are shaped by geology; the dominant substrates are infertile sandstone, where the Holocene sea-level rise has created rugged coastlines, and the moderately fertile basalt country, characterized by gentle slopes and hills (Beard, 1979; Speck et al., 2010; Figure 2b). The vegetation is predominantly eucalypt savanna. *Eucalyptus tetrodonta*–*Eucalyptus miniata* savannas are found on the laterite mesas and hills, while *Eucalyptus tectifica*–*Eucalyptus grandifolia* savannas are common on deeper, clay soils on plains. Small patches of semi-deciduous rainforests are interspersed in the savanna (Figure 2c,e), typically located in fire-protected locations in the savanna (Figure 2c,e), typically located in fire-protected locations (Vigilante, Bowman, Fisher, Russel-Smith, & Yates, 2004).

Fire regimes in the northern Kimberley are strongly shaped by anthropogenic ignitions and have been for over 40,000 years (O'Connor, 1995). This ancient tradition of Aboriginal fire management is likely to

have maintained biodiverse open savanna habitats and protected small isolated rainforest fragments (Mangglamarra, Burbidge, & Fuller, 1991; Trauernicht, Brook, Murphy, Williamson, & Bowman, 2015; Vigilante, Murphy, & Bowman, 2009). The cessation of Aboriginal fire management in many northern Australian environments has been associated with degradation of some rainforests and other fire-sensitive plant communities (Russell-Smith & Bowman, 1992; Trauernicht, Murphy, Portner, & Bowman, 2012), although in rarely burnt areas there can be expansion of rainforest (Bowman & Fensham, 1991; Clayton-Greene & Beard, 1985).

2.2 | Rainforest mapping and analyses

2.2.1 | Subcontinental scale—climatic drivers of rainforest density

The distribution and areal extent of the rainforests in the north-western Australian monsoon tropics was determined by blending existing vegetation maps. Total coverage of rainforest in Western Australia and Northern Territory was calculated for a lattice of grid

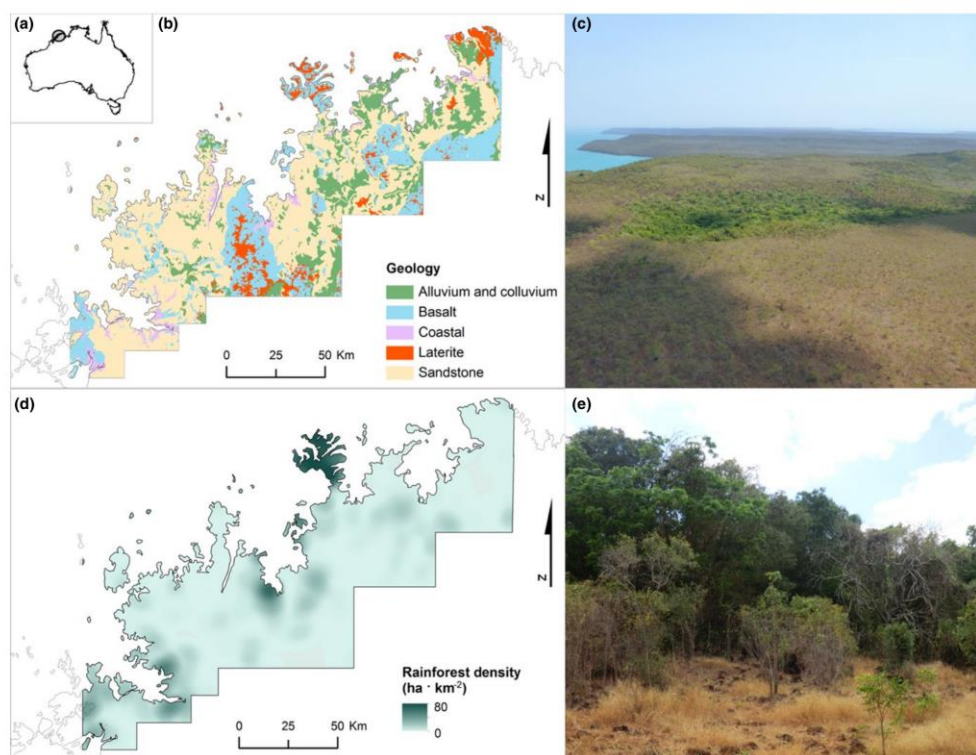


FIGURE 2 (a) Extent of the mapped area in the northern Kimberley; (b) the main geology types in the area, and (d) rainforest density, expressed as ha per km² of land. In this area, rainforests typically occur as (c) small patches (green) surrounded by savanna (brown), with (e) sharp boundaries between the two vegetation types

cells 50×50 km in area. The Western Australia map (1:200,000) was derived from Kimber, Forster, and Behn (1991), who used semi-automated classification of Landsat imagery taken in 1986 and did not differentiate floristics or structure variation among rainforests. The Northern Territory vegetation data (1:80,000), based on interpretation of aerial photography classified according to Russell-Smith (1991), were supplied by the Department of Land Resource Management, © Northern Territory of Australia. In calculating rainforest coverage in the Northern Territory lattice cells, we selected both dry and wet rainforest types because they are structurally and floristically similar to the Western Australian rainforests (Bowman, 1992; Kenneally et al., 1991). We combined the Western Australia and Northern Territory data to create a map of the northwestern rainforest domain, extending from 11.00°S to 18.00°S in latitude and from 122.14°E to 138.00°E in longitude (Figure 1). This resulted in 192 and 63 grid cells in the Northern Territory and Western Australia, respectively. For each grid cell, mean annual rainfall, precipitation seasonality (coefficient of variation of monthly rainfall expressed as a percentage), potential evapotranspiration, moisture index (mean annual precipitation over potential evapotranspiration; Thornthwaite, 1948), and annual mean temperature were calculated for the center point of each cell. Rainfall, precipitation seasonality, and temperature data were obtained from WorldClim Global Climate Data (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005), and moisture index and potential evapotranspiration were downloaded from the Global Aridity and PET database (Zomer, Trabucco, Bossio, & Verchot, 2008). Minimum, maximum, and median values of the climatic variables were calculated separately for the Western Australia and Northern Territory grid cells.

2.2.2 | Regional scale—regional drivers of rainforest density

We generated a map of the rainforests in the northern Kimberley, covering the entire Wunambal Gaambera Country and expanding the analysis to the adjacent coastal areas (total surface $12,572 \text{ km}^2$), as follows. Orthophotos (scale 1:8,000) taken during the dry season (May–August) of the years 2005–2007 were used to create a map of the rainforest patches located in the study area. A lattice of 30×30 m cells was overlaid on the orthophotos, and every cell was manually classified as "rainforest," "savanna," or "other." The vegetation type of each cell was considered to be the one occupying the highest proportion of the cell. A map of the rainforest patches was produced by merging the contiguous cells classified as "rainforest" (Figure 2d). A helicopter survey was conducted to validate the map. The flight path, designed to include locations with both high and low rainforest cover, included coastal and inland areas as well as islands. It covered the main geologic substrates, in particular basalt, sandstone, and laterite. We flew along the selected path at an average height of 300 m above the ground for a total length of 550 km on 22 September 2013. Waypoints, collected every 10 s, were visually identified as "rainforest" or "savanna." The points were then buffered 30 m and intersected with the rainforest map. A confusion matrix was generated to calculate map accuracy,

omission and commission errors, and kappa coefficient of agreement (Congalton, 1991).

Patch size, distance from the coastline, and distance from the nearest drainage line were calculated for every rainforest polygon on the regional scale map. Rainforest density was calculated as ha of rainforest per km^2 of land, based on a grid of 1×1 km size cells for computational reasons. For each cell, we also calculated: (1) the geology category, based on the predominant geology type in each 1×1 km cell; and (2) the topographic category, based on the predominant topographic position index (TPI; Jenness, 2006) in the cell. The TPI was calculated for every pixel in the mapped area from a 30-m resolution digital elevation model (DEM), based on the difference in elevation between each pixel and the average elevation of the eight neighboring pixels; values lower than -1 were classified as "valley," and values higher than $+1$ as "ridge." Intermediate values were classified as "flat" or "slope" depending on the slope of the pixel ($\leq 4^{\circ}$ for flat areas, $> 4^{\circ}$ for slopes), obtained from the 30-m DEM. (3) Each grid cell was further classified as having "complex" or "level" terrain, noting that complex terrain is often associated with rockiness. Cells in which the categories "valley" + "ridge" + "slope" occupied more than 50% of the cell were classified as "complex," the others as "level." The average rainforest density in the northern Kimberley was then calculated for each geologic substrate and TPI based on the rainforest density grid.

2.2.3 | Local-scale natural experiment—Mainland versus Islands

We expected there would be differences in fire activity and rainforest distribution between islands and mainland, because islands have been subject to fewer human ignitions due to infrequent visitation in recent times (Vigilante et al., 2013) and the sea provides a natural fire break from surrounding landscape fires. To test this, we compared rainforest density grid cells on islands and the mainland. We selected areas that were geographically, floristically, and ecologically similar by extracting from the "regional scale dataset" only grid cells with the following attributes: mean annual rainfall between 1,250 and 1,382 mm/year, distance from the coastline < 5 km (equivalent to the radius of the biggest island hence the maximum distance from the coastline on islands), and geology developed on basalt, laterite, or coastal sediments. Islands and coastal areas of the northern Kimberley are floristically similar, with only a very small group of taxa recoded only from islands (Lyons, Keighery, Gibson, & Handasyde, 2014). Grid cells located on the Bougainville Peninsula were included in the category "islands," due to its narrow neck which makes it functionally equivalent to an island in terms of isolation from the mainland.

Fire activity was calculated from a 15-year fire history map (2000–2014), created at a pixel resolution of 250 m based on MODIS satellite imagery, accessed via North Australian Fire Information website (<http://www.firenorth.org.au/nafi3/>). Due to the coarse resolution of the fire history map, it was impossible to accurately locate every fire scar, so the data were used to provide coarse-scale information about differences in fire activity between the mainland and islands. For every cell of the rainforest density grid, the area-weighted proportion of

years burnt was calculated by dividing the average number of years in which the cell was burnt by 15, the total number of years investigated. The average fire activity per year and rainforest density were calculated for cells classified as "island" or "mainland" and, within each category, "complex" or "level" terrain.

2.3 | Statistical analyses

At a subcontinental scale, we employed the Pearson product moment correlation coefficient to examine correlations among rainforest density and the climatic variables, and presented the results in a constellation diagram. For presentation (but not the analysis), we aggregated the grid cells into 200-mm mean annual rainfall bins and calculated the average rainforest density for each bin.

At a regional scale, we first tested for spatial autocorrelation in rainforest density and assessed minimum sampling distance, estimated by plotting the semi-variance as a function of distance, using the software R (R Core Team, 2013) and the R package *geoR* (Ribeiro & Diggle, 2001; Appendix S1). We then tested whether the factors terrain and geology are related to rainforest density. We also checked whether rainforest density was associated with geology within level and complex terrain types. To do this, we used generalized linear

models (GLMs) and complete subset regression and model selection based on Akaike's information criterion (AIC; Burnham & Anderson, 2002), calculated using the R package "MuMIn" (Bartoń, 2009). We used the compound Poisson-gamma distribution, included in the Tweedie family of distributions, which allows regression modeling of zero-inflated positive continuous data (R packages "tweedie" [Dunn, 2014] and "statmod" [Smyth, Hu, Dunn, Phipson, & Chen, 2015]). To assess the importance of each variable, we calculated Akaike weights (w_i), which represent the probability that a given model is the best in the candidate set (Burnham & Anderson, 2004). We then calculated variable importance (w_+) as the summed w_i of the models in which the variable occurs. w_+ values higher than 0.73 were considered to indicate that the variable is a statistically important predictor (Murphy et al., 2010). Model summaries are provided in Appendix S2.

When comparing mainland versus islands, we examined differences in rainforest density and fire activity between locations, testing for the factors insularity (island or mainland) and terrain (complex or level). To do so, we employed GLMs, using the compound Poisson-gamma distribution for both rainforest density and fire activity, complete subset regression, and model selection based on AIC as described above. Variable importance was assessed by

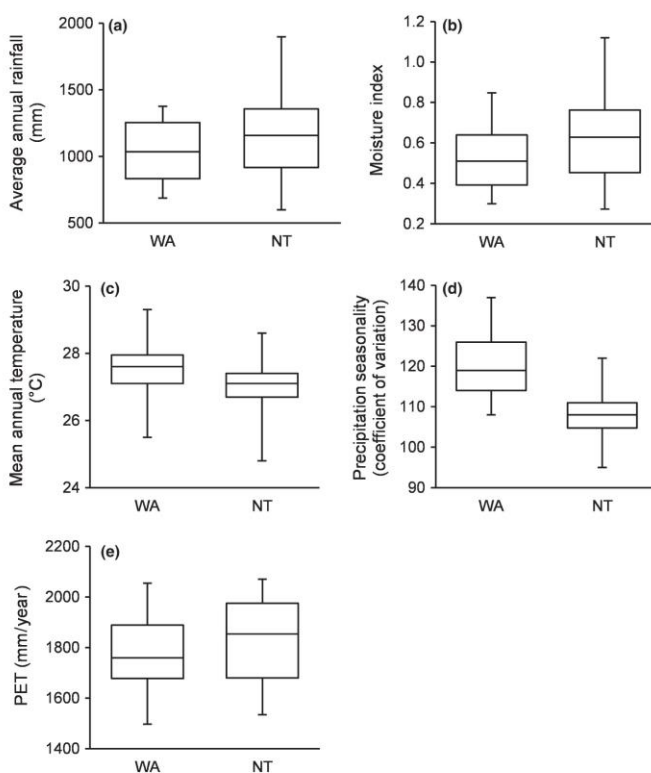


FIGURE 3 Comparison of the rainforest domain in Western Australia (WA) and Northern Territory (NT), showing (a) average annual rainfall, (b) moisture index, (c) mean annual temperature, (d) precipitation seasonality, and (e) potential evapotranspiration (PET). Boxes indicate median values and upper and lower quartiles, bars the 10th and 90th percentiles

calculating $w+$, as described above. Model summaries are provided in Appendix S2.

3 | RESULTS

3.1 | Subcontinental scale

The northwestern Australian rainforest domain covered an area of 640,000 km², ranging from the coastline to a maximum of 350 km inland. Rainforest density was lower west of the Ord Arid Intrusion: in Western Australia rainforest density ranged from 0 to 8.7 ha of rainforest per km² of land (average 1.1 ± 0.2 ha/km²), while in the Northern Territory the range was 0–19.0 ha/km² of land (average 1.4 ± 0.2 ha/km²). The Northern Territory showed higher median values and a broader range of both mean annual rainfall and moisture index (Figure 3a,b). Mean annual temperature and precipitation seasonality showed higher median and maximum values in Western Australia and minimum in the Northern Territory (Figure 3c,d), while annual potential evapotranspiration had a similar range in the two states but higher median values in the Northern Territory (Figure 3e).

There was a positive correlation between rainforest density and both mean annual rainfall and moisture index (Figures 4 and 5), which were also positively correlated. Potential evapotranspiration was negatively correlated with rainforest density, moisture index, and rainfall, while precipitation seasonality was negatively correlated with rainfall and moisture index. Mean annual temperature was not correlated with any of the climatic variables investigated nor with rainforest density.

3.2 | Regional scale

In total, 2,902 points were assessed during the aerial survey. There was a strong concordance between the rainforest map and the aerial

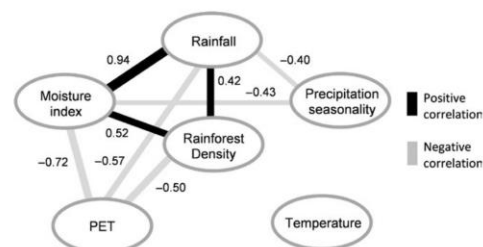


FIGURE 4 Constellation diagram showing the strength and direction of correlations among rainforest density and the climatic variables average annual rainfall, moisture index, potential evapotranspiration (PET), precipitation seasonality, and mean annual temperature in the monsoon rainforest domain in northwestern Australia. Positive correlations are represented by black lines, negative correlations by gray lines. Correlations stronger than .4 or -.4 are indicated; wider lines indicate stronger correlations, narrower lines weaker correlations

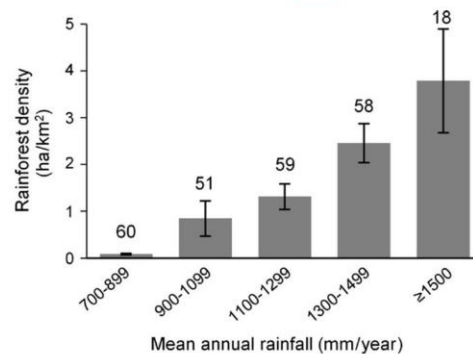


FIGURE 5 Average rainforest density by average annual rainfall, calculated within the rainforest domain in the Australian monsoon tropics. The numbers above each column represent the number of grid cell included in that rainfall interval. Error bars represent standard error

assessment, with a resulting overall map accuracy of 93% (Kappa coefficient .78; Appendix S3). A high accuracy was obtained for savanna points (95% for both producer's and user's accuracy), meaning few savanna points were mistaken for rainforest. We attribute the lower producer's and user's accuracy for rainforests (83% and 82%, respectively) to the floristic composition of the monsoon vine thickets, where semi-deciduous species can dominate (Beard, 1979), making portions of the forest patches undetectable from orthophotos taken during the dry season.

Savanna was by far the most common vegetation, covering 98.9% of the area. We detected a total of 6,460 rainforest patches covering 10,300 ha, equivalent to 0.82% of the mapped land. Patch size ranged from 0.1 to 220 ha and averaged $1.6 \text{ ha} \pm 0.1$ (SE). Seventy-five percent of patches were smaller than 1 ha, and only 2.5% were larger than 10 ha (Figure 6a). More than 40% of the mapped rainforest patches were located within 1 km of the coastline (Figure 6b), but patches were detected up to 47 km inland (average $4.7 \text{ km} \pm 0.1$ [SE]). A similar pattern was identified for distance from drainage lines, with 64% of the patches located within 1 km of the nearest drainage line (Figure 6c), but some up to 32 km distant (average $1.7 \text{ km} \pm 0.0$ [SE]).

Rainforest density was strongly dependent on both terrain ($w+ = 1.00$) and geology ($w+ = 1.00$); average rainforest density was higher on relatively fertile substrates (laterite, coastal sediments, and basalt), and lower on alluvium and colluvium and infertile sandstone (Figure 7a). Average rainforest density was also higher in complex terrain such as ridges, slopes, and valleys and lower on level areas (Figure 7b). The model including geology and terrain explained 32.1% of the deviance. The preference for relatively nutrient-rich geology was independent on terrain, as on both level and complex terrains rainforest density was strongly associated with geology ($w+ = 1.00$ in both cases; Appendix S4). Geology explained 13% of deviance on complex terrain and 10% of deviance on level terrain.

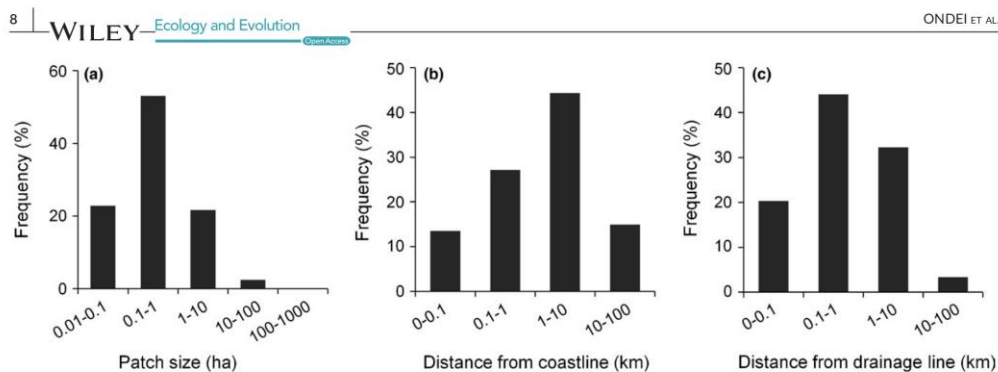


FIGURE 6 Frequency distribution of rainforest patches in the northern Kimberley region according to (a) size, (b) distance from the coastline, and (c) distance from the nearest drainage line. Note the logarithmic scale for the x axes

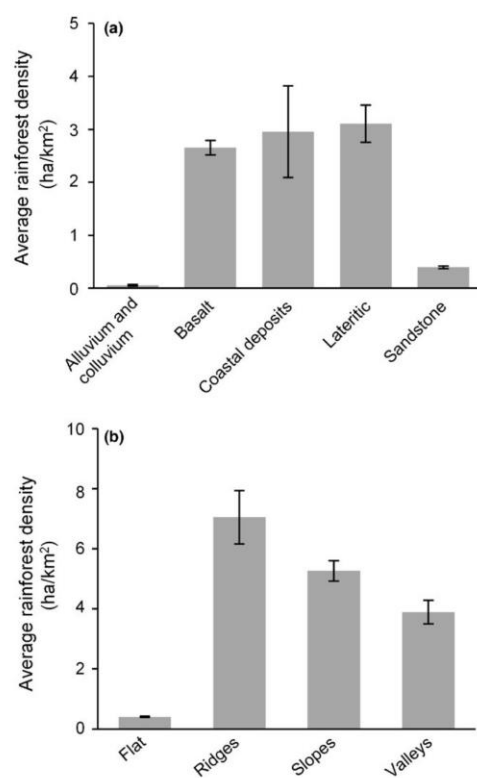


FIGURE 7 Rainforest density in relation to (a) geologic substrate, and (b) topographic position in the northern Kimberley (regional analysis). Rainforest density was highest on coastal sediments, basalt, and lateritic substrates. It was also higher on ridges, slopes, and valleys, and almost absent in flat areas. Error bars represent standard errors

3.3 | Mainland versus Islands

The grid cells on basalt, laterite, and coastal substrates and within 5 km of the coast covered an area of 332.4 km² on islands and 693.1 km² on the mainland. The total area covered by rainforests was 47.0 km² on the islands, compared with 13.6 km² on the mainland, so that rainforest density was seven times higher on the islands (Table 1). Islands were more topographically complex than the mainland (Table 1). There was statistical support for an influence of both insularity ($w+ = 1.00$) and terrain ($w+ = 1.00$) on rainforest density (Table 2), and the model including both explained 35% of deviance. There was less fire activity on islands (average 0.061 ± 0.003 times burnt per year) than on the mainland (average 0.266 ± 0.004 times burnt per year; $w+ = 1.00$), and insularity alone accounted for 39.1% of deviance. Contrary to expectations, there was no statistical support for an effect of terrain on fire activity ($w+ = 0.48$; Table 2).

4 | DISCUSSION

We found that in northwestern Australian monsoon tropics rainforest patches are tiny and scattered across a vast savanna matrix. Due to their small size, these rainforest fragments are essentially undetectable at the resolution employed by global-level assessments (Murphy & Bowman, 2012; Staver et al., 2011b). At a subcontinental scale, the strong correlation between rainforest density and annual rainfall, potential evapotranspiration, and moisture index highlighted the primacy of water supply compared with mean annual temperature and precipitation seasonality, and supported our first hypothesis. This correlation is congruous with the observation that a trend of increasing rainfall in northern Australia since the 1940s is the key driver of rainforest patch expansion (Banfai & Bowman, 2007; Bowman et al., 2001). These findings are also consistent with the global trend of increasing proportion of rainforest (and decreasing savanna) as mean annual precipitation increases (Hirota et al., 2011; Murphy & Bowman, 2012). In the drier landscapes west of the Ord Arid Intrusion, rainforest species diversity is also lower than to the wetter east and most of the

species in Western Australia are as subset of those in the Northern Territory (Kenneally et al., 1991). However, the presence of rainforests in the northwestern Australian monsoon tropics showed that the region cannot be defined as deterministically savanna based solely on climate (Murphy & Bowman, 2012). Similarly, rainforest patches exist throughout much of the tropics globally, which suggests that in all but arid tropical regions, climate alone is not the only factor controlling rainforest distribution (Staver et al., 2011b). In Brazil, for example, small patches of deciduous and semi-deciduous rainforests are interspersed in a matrix of savanna plants (Cerrado) or thorn scrubs (Caatinga) and are restricted to slopes and moist, nutrient-rich sites (Leal, da Silva, Cardoso, Tabarelli, & Lacher, 2005; Oliveira-Filho & Ratter, 2002). Likewise, in Ivory Coast the dominant savanna vegetation is scattered with small patches of dry rainforest (Goetze, Hörsch, & Porembski, 2006).

We also found support for our second hypothesis that topography and geology affect rainforest distribution. The influence of topography on rainforest density was manifest in the higher rainforest density on complex compared with level terrain. Rainforest density was also higher on nutrient-rich basalt compared with the nutrient-poor sandstone, despite the higher fire frequency and intensity recorded on basalt (Vigilante et al., 2004). This pattern is consistent with the edaphic compensation hypothesis (Ash, 1988; Webb & Tracey, 1981), whose underlying mechanism is probably the effect of increased fertility in

enhancing plant growth, allowing trees to reach the threshold size that triggers the switch from savanna to rainforest through grass shading (Hoffmann, Geiger, et al., 2012; Murphy & Bowman, 2012). It is important to note that geology and terrain are typically not independent. For example, in the northern Kimberley rounded hills are more common on basalt, while steep gorges are frequently found on sandstone (Vigilante et al., 2004). However, in our analysis we were able to demonstrate an effect of geology alone by comparing areas on the same terrain, showing that there are more rainforests on basalt than on less fertile geologies.

There was only partial support for our third hypothesis that insularity and topographic effects are directly related to fire activity. Clearly, there were more rainforests on islands, where there was also less fire activity compared with the mainland. The importance of fire in restricting rainforests has been demonstrated by rainforest expansion in other savanna landscapes where fire has been excluded, in northern Australia (Fensham & Butler, 2004; Scott et al., 2012) and elsewhere (Bond, Midgley, Woodward, Hoffman, & Cowling, 2003). Rainforest species are typically less fire tolerant than savanna species due to thinner bark and less developed post-fire recovery mechanisms (Lawes, Midgley, & Clarke, 2013; Ondei, Prior, Vigilante, & Bowman, 2015; Pausas, 2015). However, we failed to detect a corresponding difference in fire activity between terrain types on the mainland and found only a minor difference on islands. There are two possible reasons for this lack of correspondence, which are not mutually exclusive. One is that terrain, or associated rockiness, did exert an influence on fire activity, but this was obscured by the coarse scale of the grid cells in our analysis (1×1 km). Another possible reason is that the higher rainforest density on complex terrain is the result of water and nutrient accumulation (Ash, 1988; Daws, Mullins, Burslem, Paton, & Dalling, 2002), rather than topographic fire protection. Nonetheless, the presence of rainforest on level terrain on islands, but not on the mainland, suggests that fire is an important controller of rainforest distribution in the region.

We suggest that rainforest density is determined by the interplay of fire activity and plant growth rates (Figure 8a). Fire activity is shaped by insularity and possibly terrain complexity, while plant growth rates are known to be controlled by water availability and the nutrient stock provided by the geological substrate control (Murphy & Bowman, 2012), with an effect of terrain in enhancing water and soil accumulation (Ash, 1988). Growth rates affect the capacity of rainforest trees to grow rapidly and escape the "fire trap," thereby developing a closed canopy which shades out grass biomass, reducing fire frequency which in turn reinforces rainforest

TABLE 1 Extent, rainforest cover, average rainfall, and extent of the geologic substrates and terrain type on the selected grid cells used to compare rainforest density on islands and the mainland in the northern Kimberley

	Islands	Mainland
Total land (km ²)	332.4	693.1
Rainforest area (km ²)	47.0	13.6
Rainforest density (ha/km ²)	14.1	2.0
Average rainfall (mm/year)	1348 ± 1	1307 ± 1
Geology type (%)		
Basalt	64.4	81.2
Coastal sediments	0.5	2.7
Laterite	35.1	16.1
Terrain type (%)		
Complex	62.8	55.6
Level	37.2	44.4

TABLE 2 Average fire activity, measured as times burnt per year, and average rainforest density, measured as ha/km², for complex and level terrains located on the selected grid cells on islands and mainland in the northern Kimberley

	Level terrain		Complex terrain		w+	
	Mainland	Islands	Mainland	Islands	Terrain	Insularity
Fire activity (average times burnt per year ± SE)	0.26 ± 0.01	0.08 ± 0.01	0.27 ± 0.01	0.05 ± 0.00	0.48	1.00
Rainforest density (ha/km ² ± SE)	0.30 ± 0.06	6.81 ± 0.73	4.29 ± 0.42	19.69 ± 0.88	1.00	1.00

The w+ indicates the statistical support for the terms terrain and insularity when comparing mainland and islands (full results are presented in Appendix S2).

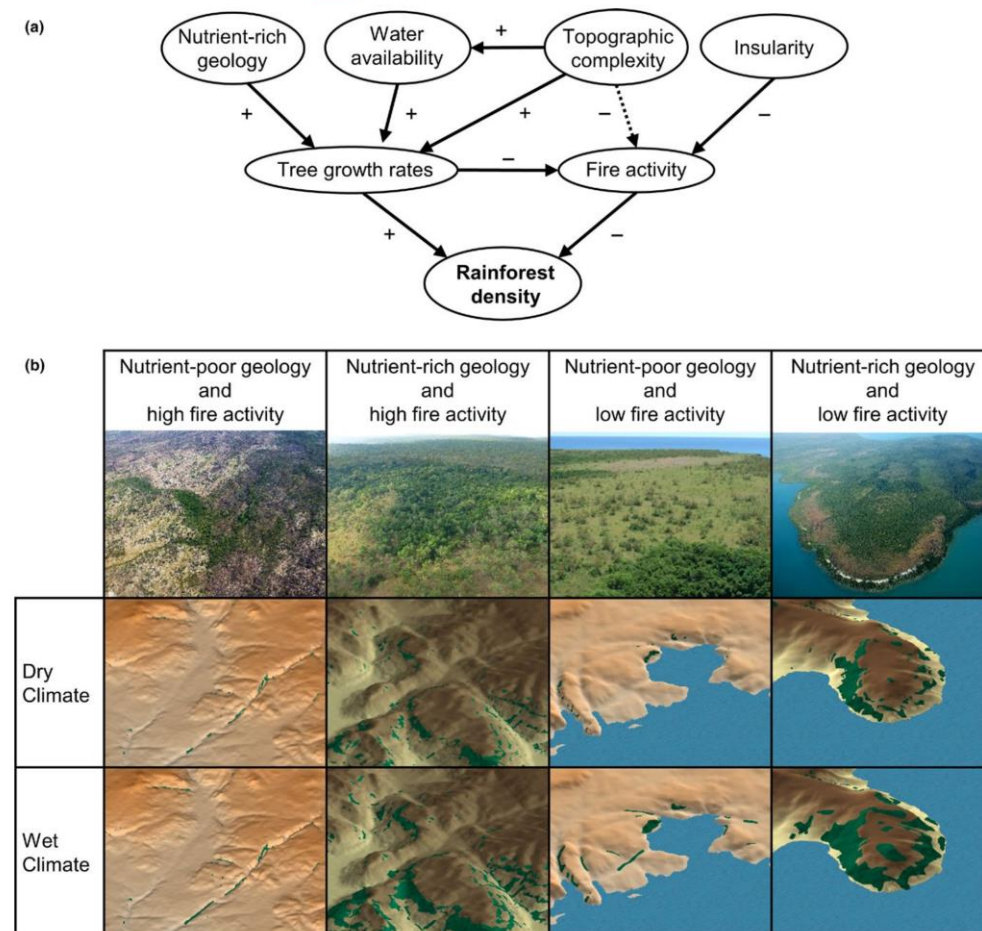


FIGURE 8 Synthesis of the environmental determinants of rainforest fragments in the northern Kimberley. (a) Diagram showing the positive (+) and negative (-) effects of environmental factors on rainforest density. Dotted lines represent probable effects. (b) Top row: oblique aerial photographs showing examples of the density of rainforest fragments on sites with contrasting geology (sandstone vs. basalt) and fire activity in the northern Kimberley. Second row: 3D renderings of rainforest distribution (dark green) on sandstone (nutrient-poor) and basalt (nutrient-rich) landscape under current dry climate. Bottom row: 3D renderings of plausible rainforest density under a climate as wet as coastal regions of the Northern Territory. In this study, we demonstrated that insular sites have substantially lower fire activity than environmentally comparable mainland savanna areas. Under the current climate, rainforest density is highest on fertile infrequently burnt areas, and in frequently burnt landscapes is confined to topographically fire-protected settings, particularly on nutrient-poor geology. Under a wetter climate, we expect the rainforest patches to expand and new patches to establish in suitable landscape niches, with the greatest expansion on basalt landscapes. The exact amount of expansion is unpredictable because of the influence of fire activity and fire management

expansion (Dantas et al., 2013; Hoffmann, Geiger, et al., 2012; Murphy & Bowman, 2012). Our findings are summarized in Figure 8b, which shows characteristic patterns of rainforest fragments in the landscape and how these fragments are likely to expand in response to a wetting climate under contrasting fertility and fire regimes. Rainforest expansion should be proportionally greater in lower-rainfall areas that currently have low

rainforest density, like the northern Kimberley, because there are more landscape niches available for occupancy, such as nutrient-rich and fire-protected sites. A prediction of our work is that, under the current wetting trend, there will be continuing rainforest expansion in the Kimberley, as has been observed elsewhere in the Australian tropics (Russell-Smith, Stanton, Edwards, & Whitehead, 2004).

5 | CONCLUSION

We have shown that the density of monsoon rainforest in the north-western Australian savanna is affected by moisture availability, substrate, and fire. The effect of these drivers appears to involve complicated feedbacks and interaction, such as the combined effects of potential fire protection and increased productivity in topographically complex terrains. We acknowledge that our correlative analysis cannot separate cause and effect, or test the fire-driven ASS model in explaining the distribution of rainforests. To do this demands analysis of vegetation boundary dynamics coupled with contrasts of substrate type and fire history. This can be achieved through carefully designed regional-scale analysis of rainforest boundaries trends, such as field surveys and historical sequences of aerial photography (Banfai & Bowman, 2006; Butler et al., 2014; MacDermott, Fensham, Hua, & Bowman, 2016) and is the subject of a subsequent paper. Despite its limitations, our approach is an important step in understanding the effect of climate change and anthropogenic disturbances on naturally fragmented rainforests elsewhere in the tropical savanna biome.

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CONFLICT OF INTEREST

None declared.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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