Are Giant Eucalypt Forests

Rain Forests?

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Declaration

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Chapter 2 is published:

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Candidate was the primary author. The Candidate as well as author 2 and 3 contributed to developing the idea. Author 4 undertook some data analysis. The candidate as well as authors 2 and 3 assisted with refining the text.

Chapter 3 is published:

Tng DYP, Murphy BP, Weber E, Sanders G, Williamson G, Kemp J, Bowman DMJS. 2012. Humid tropical rain forest has expanded into eucalypt forest and savanna over the last 50 years. *Ecology and Evolution* **2:** 34–45.

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Abstract

Forests dominated by giant eucalypts (eucalypt species with the potential to attain heights exceeding 70m) occur along the Australian east coast in association with rain forest. These forests contribute significantly to the global carbon budget but their ecological classification suffers from ambiguities around the definition of rain forest. The belief that eucalypts are 'sclerophyllous' and therefore not rain forest is a subjective view that has led to problems with conservation policies and management strategies of giant eucalypt forests. Understanding these forests from a global and functional viewpoint is paramount for their effective management. *Eucalyptus grandis*-dominated giant eucalypt forests in the Wet Tropics of Australia serve as a case study. Observing that rain forest species continuously regenerate in the understories of these eucalypt forests and believing that rain forest incursion will lead to the local elimination of the giant eucalypts, land managers prescribe frequent, low intensity fires. This management strategy is contentious and not underpinned by robust ecological understanding. To resolve these classificatory problems around eucalypts occurring in rain forest, I take a multidisciplinary approach to address the specific question: Are giant eucalypt forests rain forests?

To obtain an in depth understanding of the ecology of giant eucalypts and the forests they dominate, and to provide a global context for these systems, I synthesise over a century's worth of literature on these systems (Chapter 2). Based on these data I propose that giant eucalypts are ecologically akin to rain forest emergent pioneers with a unique dependence on fire for regeneration, and that their habitat should be considered a type of secondary rain forest.

Using a GIS-based approach I investigate the landscape scale vegetation dynamics of rain forest and *E. grandis* forest in the Wet Tropics, where *E. grandis* forests are considered to be threatened (Chapter 3). Using a environmentally stratified sample of sites, I show that rain forest has expanded over the past 50 years, and that this expansion is most likely a response to a global driver such as increased atmospheric CO_2 rather than with local environmental factors. Projective modelling of this rain

forest expansion predicts that, even at the fastest estimated rate known for the region, it will be more than 2000 years before rain forest fully engulfs giant eucalypt forests.

In Chapter 4, I present a seedling growth experiment to examine if the regeneration niche of *E. grandis* exhibits ecological convergence with that of well-studied temperate giant eucalypts. I show that *E. grandis* seedlings grow poorly in unburnt rain forest soils because of the unavailability of phosphorus. The addition of phosphorus lifts phosphorus-deficiency symptoms in seedlings in rain forest soils, and accords well with the idea of *E. grandis* being a rain forest pioneer with the unique requirement of fire as a disturbance mechanism to create suitable open habitats for regeneration.

To contextualize the rain forest – giant eucalypt forest – savanna transitions in Australia from a functional and macroecological perspective, I present a plant functional trait analysis of representative plants across these vegetation transitions in both tropical and temperate Australia (Chapter 5). I show that both tropical and temperate giant eucalypt forest are functionally convergent with rain forest and not with savanna. These results suggest that a classification of giant eucalypt forest based on functional attributes of the whole forest will be more useful for management policy than the established classification based on canopy dominants

In conclusion (Chapter 6), the synthesis of my landscape ecology and functional biology data supports my overarching hypothesis that giant eucalypt forests are functionally and ecologically rain forests and should be managed as such. I discuss the implications of my research for the management of Wet Tropics giant eucalypt forest and recommend that *E. grandis* forest should be managed under a regime of total fire suppression. Given that rare natural fires can be expected to occur under this management, the resulting regime will mimic the inherently long fire return times of these systems.

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Chapter 1

General introduction

1.1 Rain forest – savanna boundaries

Globally, the rain forest biome and its boundary zone or ecotone vegetation
communities have immense biological significance. Not only do they contain some
of the world's highest levels of animal and plant biodiversity, ancient lineages,
species endemism and complex species interactions (Richards, 1996; Smith *et al.*,
1997), they are also key systems for understanding forest ecology. Deforestation,
rain forest fragmentation and global climate change bring into focus the increased
importance of ecotones between rain forest and adjacent open canopied vegetation
(woodland or savanna vegetation types). As ecotones are zones of rapid spatial
change they may be expected to respond rapidly to shifts in global climate (Nielson,
1993; Hutyra *et al.*, 2005; Staver *et al.*, 2011). Ecotones have also been central to the
development of ecological and evolutionary theory (Risser, 1995; Smith *et al.*, 1997;
Fagan *et al.*, 1999; Kark & van Rensburg, 2006), and can serve as model systems for
testing contemporary ecological theories (Cadenasso *et al.*, 2003; Hirota *et al.*,
2011). Specifically, one could investigate how environmental factors (e.g. fire, soils
and climate) (Russell-Smith *et al.*, 2004a; Warman *et al.*, 2013) and biological
feedbacks (Russell-Smith *et al.*, 2004b; Mayer & Khalyani, 2011; Ibanez *et al.*,
2013) contribute to the dynamics of ecological communities.

By international standards, the ecological and evolutionary biology of ecotones
between rain forests, savannas and related vegetation from tropical to temperate
latitudes in Australia are well studied, positioning Australian rain forest – savanna
transitions as potential global models. However, while the potential benefits of
making cross-continental comparisons between these systems and ecologically or
functionally analogous systems worldwide is huge (e.g. Corlett & Primack, 2006),
the lack of a globally unified classification system for these vegetation transitions

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make such comparisons difficult (e.g. Blasco *et al.*, 2000; Ratnam *et al.*, 2011; Torello-Raventos *et al.*, 2013). For Australia, an additional difficulty is encountered in the use of strictly local vegetation classifications by Australian ecologists, as reflected in sometimes confusing appellations for the vegetation types they study (e.g. 'mixed forest' of Gilbert, 1959, 'dry rainforest' of Baur, 1965, and 'wet sclerophyll forest' of Keith, 2004; Harrington *et al.*, 2005; Wells & Hickey, 2005) (Table 1.1) and also inconsistencies in criteria used to delineate vegetation types. For instance, to deal with the occurrence of eucalypts in rain forest, Floyd (1990) considered forests as rain forest when the cover of eucalypts is less than 40% in New South Wales. In Victoria, this threshold was between 10 and 50%, and as low as 5% (AFC, 1975), and 10% (Kirkpatrick & Dickinson, 1984) in Tasmania (Hickey *et al.*, 1993). Importantly, even if there was agreement on the threshold, the accurate measurement of crown cover in the field is very difficult and time consuming.

Consequently, there are considerable difficulties and contentions in defining what rain forest constitutes in Australia, and understanding how these vegetation types relate to rain forests elsewhere in the world (Bowman, 2000; Webb & Tracey, 1981a). For the purpose of this thesis and to provide a global context for the Australian vegetation types examined, I will accept a range of definitions for rain forest that encompass the full range of recognised types from tropical to temperate zones (Table 1.1).

1.2 The paradox of emergent eucalypts in rain forest and the Australian Wet Tropics of Australia as a field case

A significant roadblock to arriving at a clear and functional definition of rain forest in Australia is that many rain forest regions of Australia contain a suite of members from plant families and genera now more typical of open, sclerophyllous vegetation. Some, such as many rain forest Proteaceae (Johnson & Briggs, 1975) and *Gymnostoma* (Casuarinaceae) (Prider & Christophel, 2000) are clearly true rain forest species that are remnants of ancient mesic floras from which dry climate

Table 1.1 – Summary of schemata used to define and classify rain forest in Australia. These schemata are variously based on climate or forest physiognomy or structure or the dominance of certain plant traits.

Authors	Rain forest definition/schema and notes
*Schimper (1903)	First global definition of rain forests with a climatological basis - dense vegetation of high-rainfall regions in both tropical and temperate areas was classified as 'Regenwald', which was then translated into English as rain forest. Tropical rain forest occurs in environments with at least 180cm of annual rainfall and is is described as being 'evergreen, hygrophilous in character, at least 30m high but usually taller, rich in thick-stemmed lianes, and in woody as well as herbaceous epiphytes'. For temperate regions with mild winters and summer rainfall, Schimper delineated temperate rain forest as an impoverished rain forest formation. This scheme included giant eucalypt forest (i.e. tall open forest, wet eucalypt forest, wet sclerophyll forest) of southeastern Australia. However, Schimper did not discuss whether such a scheme would extend to subtropical and tropical regions where giant eucalypt forest also occur.
Beadle & Costin (1952)	A closed community dominated by usually mesomorphic meso- or megaphanerophytes forming a deep densely interlacing canopy in which lianes and epiphytes are invariably present, with mesomorphic subordinate strata of smaller trees, shrubs, and ferns and herbs. Four rain forest subformations were defined: temperate, subtropical, tropical and monsoonal.
Gilbert (1959)	Described 'mixed forest' for temperate Australia – a forest with a species composition characteristic of a recognised rain forest community, but including eucalypt emergents or dominants, may be representative of a seral community transitional to rainforest.
Webb (1959)	Defined and classified rain forest based on a combination of leaf sizes, physiognomic and structural characters, (e.g. "Complex mesophyll vine forest" refers to lowland tropical rain forest). Webb argued that rain forest in Australia is best defined in negative terms, and viewed 'sclerophylly' as a primary character to separate rain forest from other Australian forest types with predominantly sclerophyllous species. Webb therefore excluded from his rain forest definition forests containing emergent eucalypts.
Baur (1965)	A closed, moisture-loving community of trees and shrubs; frequently mixed in composition; the species typically but not invariably broad-leaved and evergreen; heavy vines (lianes), vascular and non-vascular epiphytes, stranglers and buttressing often present and sometimes abundant; floristic affinities mainly with the relic Gondwanan flora; eucalypts typically absent except as relicts of an earlier community. Baur recognized all of Beadle & Costin's (1952) rain forest subformations but opted for calling monsoonal rain forest 'dry rainforest' instead. Baur's definition also includes vine thickets.
Specht (1970)	Classified vegetation based on canopy closure. Most rain forest in Australia would fall under Specht's description of "Closed forest".
UNESCO (1973)	Rain forest definition based on a priori description of its structure similar to Beadle and Constin (1952). Rain forest is defined based on features such as its closed canopy and evergreen nature (e.g. 'Tropical ombrophilous forest' and 'Temperate evergreen ombrophilous forest'). Some Australian rain forest types do not fit well with this system.
Dale *et al.*, (1980)	Included under their rain forest scheme all transitional and seral communities with a similar floristic composition to mature rain forest.
Jarman & Brown (1983)	Defined cool temperate rain forest in Tasmania based on the occurrence of pools of vascular plant species that are able to regenerate independently of catastrophic disturbances such as fire. This definition included high altitude vegetation of modest height and relatively open structure (montane rain forest). Excluded forest with emergent eucalypts in their rain forest definition.
Johnston and Lacey (1984)	A classification system for tree-dominated vegetation in Australia based on various structural and floristic attributes. This system introduces new and complex terminologies where the term 'rain forest' is sidestepped and replaced with 'hyptiophyll closed forest' based on the predominant leaf orientation of the plants making up the vegetation type.
Ash (1988)	Dichotomized rain forest and other forest types as being pyrophobic (i.e. fire-sensitive) and pyrophytic (i.e. fire-loving).
Russel-Smith	Like Webb (1959), Russel-Smith defined rainforest for the Northern Territory of Australia in negative terms, and thus excluded woody vegetation dominated by

(1991)	mangroves or sclerophyllous species such as *Eucalyptus*, *Melaleuca* and *Callitris*.
*Cameron (1992)	Included in his definition of cool temperate rain forest in Victoria the presence of emergent eucalypts.
Bowman (2000, 2001)	Suggested an *ad hoc* usage of the term 'rain forest', arguing that the strict dichotomization of rain forest and drier forest types will require truncating floristic continua that range from arid to alpine environments.
Lynch & Neldner (2000); Neldner & Lynch (2001)	Made allowance for the inclusion of eucalypt emergents in rain forest but maintained the etymology of 'mixed forest' for some forests with eucalypt emergents exceeding 70% projective cover in the vegetation.

*These authors consider forest with emergent eucalypts to be rain forest, a classification stance which this thesis seeks to test.

sclerophyll floras evolved. However, there is also a suite of species of sclerophyll origins which appear to have invaded the rain forest habitat. These include *Acacia*, *Allocasuarina*, *Banksia*, *Grevillea*, *Lophostemon* and *Syncarpia*. However arguably the most conspicuous and ecologically significant of these are the giant eucalypts (here defined as any species of *Eucalyptus* that is known to attain height equalling or exceeding 70m) (Table 1.1; see also Chapter 2). For some of these species such as *E. regnans* and *E. grandis*, all or most populations are likely to be capable of such heights. However, some of the species, such as *E. globulus* and *E. obliqua*, also include populations that occur in dry or cold habitats that are unlikely to sustain giant height growth. In some cases, the trees in such populations have genetically controlled low growth (Jordan et al., 2000).

These giant eucalypts, which include the tallest flowering plants globally (e.g. *Eucalyptus regnans* F.Muell.; Chapter 2; Fig. 2.1), have long been perceived to be sclerophyllous and therefore not belonging to rain forest (Cameron, 1992; Dale *et al.*, 1980; Jarman & Brown, 1983). The nomenclatural problems of classifying forest dominated by these species have a strong bearing on their management and economical politics (Gell & Mercer, 1992; Lynch & Neldner, 2000; Bowman 2001; Neldner & Lynch, 2001; Kirkpatrick & DellaSalla, 2011). Since the early 1980s for instance, various forests with eucalypt or 'sclerophyll' emergents in Tasmania, Victoria and New South Wales were the subjects of conservation battles where

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politicians, foresters and conservationists have sought to use conflicting definitions of rain forest to back their arguments (Cameron, 1992; Adam, 1994).
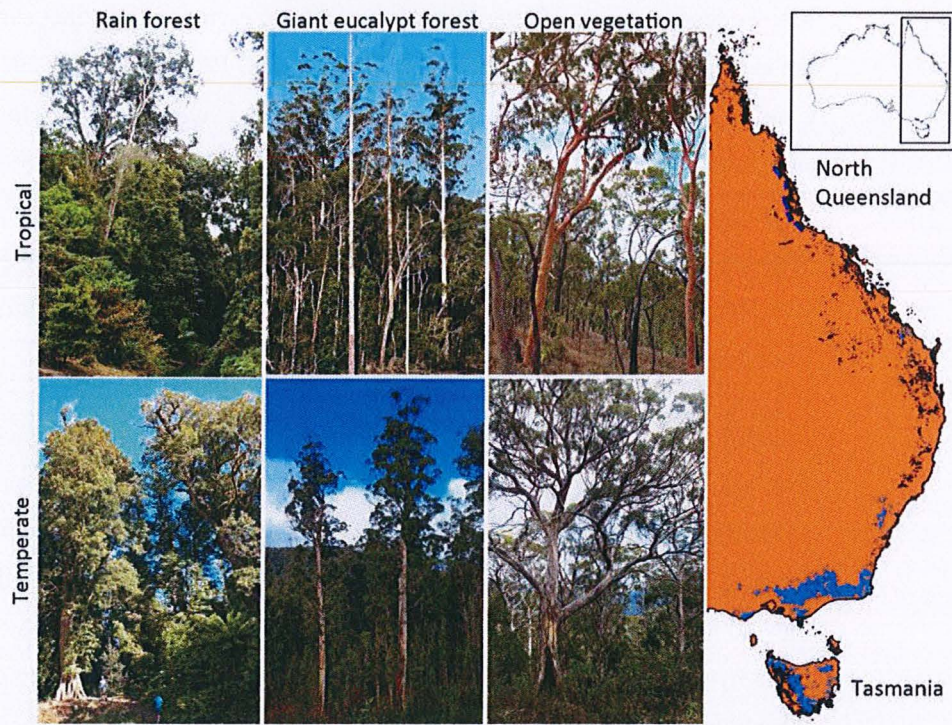
Fig. 1.1 - The distribution of rain forest (black) and giant eucalypt forest (blue) along the east coast of the Australian continent. The orange-coloured regions are open vegetation (including savanna and open eucalypt woodland). The ecotonal nature of giant eucalypt forest is most pronounced in tropical north Queensland, where these forests form narrow bands between rain forest and savanna (spatial extent exaggerated for clarity). In cool temperate Tasmania, giant eucalypt forests form a broad transition between the west and the eastern parts of the island. The inset images feature representative rain forests, giant eucalypt forest and open vegetation of the tropical and temperate zones. Note the taller stature and open canopy of giant eucalypts relative to rain forest in the understoreys. Giant eucalypts are defined as *Eucalyptus* spp. documented to achieve heights of at least 70m (see Chapter 2).

As a focal point for my thesis, the giant eucalypt dominated ecotones in the humid tropics of Australia exemplify the nomenclatural problems and management conundrums surrounding the giant eucalypt forests of Australia. In the Wet Tropics Bioregion, giant eucalypt forests dominated by *Eucalyptus grandis* W. Hill ex Maiden reach a height of over 60 metres and form narrow but distinct bands that do not exceed 4 km in width (Harrington & Sanderson, 1994; Tng *et al.*, 2012d; see Chapter 2, Fig. 2.3a). These forests are locally called "wet sclerophyll forest" (Harrington *et al.*, 2005) and are habitats for a suite of habitat-specialized birds and endangered mammal species such as the Yellow Bellied Glider (*Petaurus australis* Shaw subsp. *reginae*) and the Northern Bettong (*Bettongia tropica* Wakefield) (Chapman *et al.*, 1999; Vernes, 2003; Goldingay & Quin, 2004; Department of Environment and Resource Management, 2011).

Eucalyptus grandis is an obligate seeder because it is among the few eucalypt species that lack lignotubers: fire-resistant, underground stems structures that sprout new shoots if the main trunk is killed (Nicolle, 2006). The species is vulnerable to frequent low intensity fires because young *E. grandis* saplings can be killed because they do not have thick bark and their short stature means that their crowns will be burnt by ground fires (i.e. they have not reached the height necessary to escape the "fire trap") (e.g. Bond *et al.*, 2012). Mature *E. grandis* trees, on the other hand, can tolerate multiple small fires due to their thicker bark and greater height, although frequent burning may reduce the bark's protective capacity (e.g. McArthur, 1968). Moreover, the impacts of fire appear to be more adverse on trees with hollows and cavities than on undamaged trees (Eyre, 2005). This is important because many fauna depend on these hollows or cavities.

Land Management Agencies (e.g. Queensland National Parks, Wet Tropics Management Authority) tasked with conserving the Wet Tropics World Heritage Area face a perplexing management conundrum. Rain forests have been expanding throughout the Wet Tropics region (Harrington & Sanderson, 1994; Tng *et al.*, 2010, 2012d; Stanton *et al.*, 2014a), and the establishment of understorey rain forest species is perceived to threaten the continual persistence of the giant *E. grandis*

forests (Harrington & Sanderson, 1994; Fig. 1.2). *E. grandis* forests in the Wet

Tropics have therefore been listed as a threatened vegetation community under the

state of Queensland (Sattler & Williams, 1999; Queensland Herbarium, 2011).
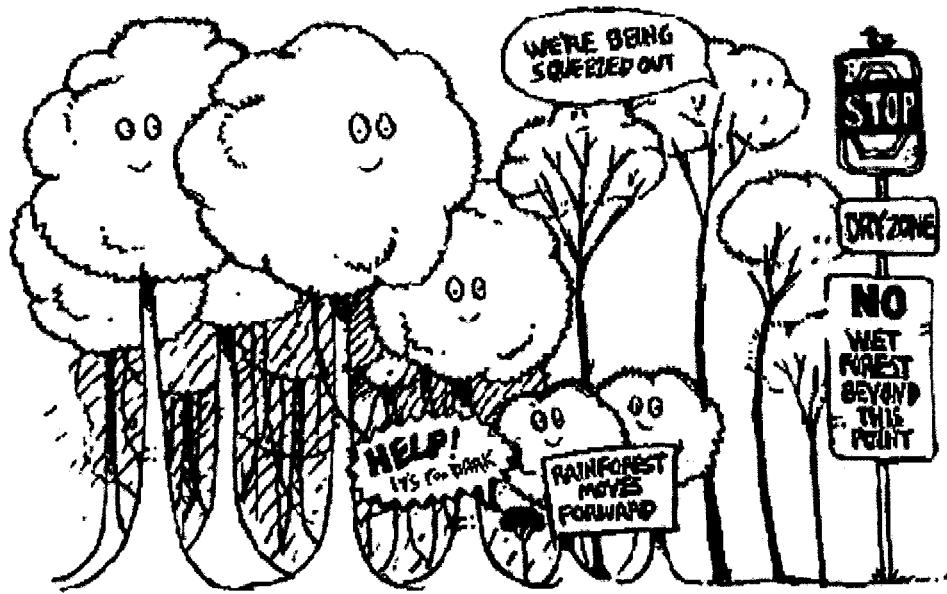
Fig. 1.2 - A caricature of the relationship between rain forest and eucalypt forest in tropical north Queensland (after Anonymous, 1993; reproduced with permission of the Wet Tropics Management Authority). Rain forest here is depicted as being invasive with the ability to smother eucalypt forest.

Some land managers believe that the survival of *E. grandis* trees and endangered

animals such as the northern bettong requires a forest with a permanent grassy

understorey (Harrington & Sanderson, 1994; QPWS, 2013; Stanton *et al.*, 2014b).

This view associates a healthy or high integrity *E. grandis* forest with a grassy

understorey, and that the management actions necessary to achieve this outcome is to

implement a program of high frequency burning to reduce the incidence of tree,

shrub or herb life-forms in the understorey. However, such management objectives

and prescription burning practices are highly contentious because of: the destruction

of rain forest species; loss of early regenerating stages in the life cycle of *E. grandis*; longer-term impacts on *E. grandis* forest successional dynamics; and concerns about anthropogenic CO_2 emissions and the global carbon budget (Bowman *et al.*, 2013). Such a debate demands evaluation of the ecology and evolution of the giant forests, and their ecological relationship to rain forest. Specifically, it will be important to investigate the the ecological relationships between eucalypts and other species in conditions that are ecologically suitable for the development of rain forest.

The key to disentangling the nomenclatural and perceptual issues I have outlined therefore depends on providing an ecologically informed answer to a tantalizingly simple question: Are giant eucalypt forests rain forests? As a significant body of literature has amassed on the ecology and biology of giant eucalypt-dominated vegetation, I therefore seek to answer this question by undertaking a critical review of this literature as a first step to providing new insights and a global context for this frequently misunderstood vegetation type. From an experimental angle, recent developments in landscape ecology systems theory and plant functional trait studies show promise as potential frameworks for defining biomes and understanding the ecological paradoxes that surround the issue of 'sclerophyllous' taxa occurring in rainforest. In combination with the critical review, a multi-disciplinary approach integrating geospatial science, species regeneration biology, and plant functional biology may provide further insights to these theoretical-ecological problems.

1.3 Aims

In this thesis I:

1. Provide a critical review of the literature regarding giant eucalypts and giant eucalypt forests to gain some insight as to their functional significance and landscape ecology
2. Characterise landscape-scale rain forest change in Far North Queensland
3. Test the edaphic controls on the regeneration of a tropical giant eucalypt

4. Provide a plant functional trait basis to the understanding of the landscape ecological theory which underpins rain forest – ecotone – savanna transitions

5. Synthesize trends in contemporary landscape ecology theory and functional biology to inform the fire management of Wet Tropics giant eucalypt forest.

1.4 Overview of chapters

My thesis consists of six chapters. Three of these chapters (chapters 2, 3, 5 and 6) have been published as peer-reviewed articles (Tng et al., 2012c, 2012d, 2013; 2014a attached in Appendix 3), one (Chapter 4) has been submitted (Tng et al., 2014b), chapter 1 and 2 is partly comprised of the content of a consultancy report (Tng et al., 2012ab). My contributions to each of the published or submitted articles is noted at the beginning of relevant chapters, but in all cases I was lead author, and developed and conducted the research under the guidance of my supervisors. All of these publications have been modified slightly for integration into this thesis.

In Chapter 2 is an extensive review of the literature on giant eucalypts written since the early 20th century (Schimper, 1903). Giant eucalypts are dominant components of the ecotonal vegetation between rain forest and other open vegetation types, and a globally contextualized critical examination of their ecology would be a good basis to understand the central question of this thesis. I therefore compile an exhaustive checklist of all the tree species that have been recorded to exceed 70m in height globally, and discuss the unique ecological strategies that enable giant eucalypts to inhabit the rain forest/open vegetation ecotone.

In Chapter 3 I adopt a landscape-scale approach using geospatial modelling to answer questions about the dynamism of rain forest boundaries and its effect on ecotonal vegetation. Literature within the last decade has shown woody vegetation thickening in many parts of the world (Silva et al., 2008; Wigley et al., 2010). As such it appears likely that global, rather than local drivers are the cause of these phenomena. In Australia also, recent GIS studies also report rain forest expansion (see Chapter 3; Table 3.5), which can be considered a similar phenomenon to woody

vegetation thickening. Shifting rain forest boundaries create an imperative for significant changes in the way rain forest in Australia is classified and delineated for management purposes. Also, the fate of giant eucalypt forests may be uncertain, due to the possibility that expanding rain forest may totally engulf giant eucalypt forests. Therefore in Chapter 3 I use GIS and spatial statistics to examine the landscape level changes of rain forest cover in tropical north Queensland over a period of 50 years. To inform management, I also model the rate of giant eucalypt forest understoreys being encroached by rain forest.

In Chapter 4, I adopt an experimental approach to examine the regeneration niche of a tropical giant eucalypt species, *Eucalyptus grandis*. Our understanding of the regeneration ecology of giant eucalypt forest comes primarily from experiments on temperate systems, in particular Chambers & Attiwell's (1994) classic study of *E. regnans*, the world's tallest flowering plant. Chambers & Attiwell (1994) examined the chemical properties of sterilized soil, and concluded that the effects of fire on soil constituted an "ash-bed effect", which is important for the regeneration of *E. regnans*. In Chapter 4 therefore, I present a seedling growth experiment on *Eucalyptus grandis* to confirm if similar processes operate in this tropical species.

In Chapter 5, I present an experiment that linked plant functional biology to landscape ecology theory. "Alternative Stable States" is a key concept in contemporary landscape ecology. From this macroecological perspective, vegetation types governed by different climatic or environmental regimes will often appear to be ecologically stable in time and space. Thus, rain forest and savanna can be thought to be two alternative stable states. However, the position of giant eucalypt forest in this macroecological scheme is uncertain. Warman & Moles (2009) suggested that the giant eucalypt forest is an unstable state wedged between rain forest and savanna. Given that rain forest and savanna plants should have very contrasting functional biology, elucidating the functional biology of representative plants in the giant eucalypt forest can reveal where this forest type stands functionally relative to rain forest and savanna. Functional trait-mediated assembly processes also reflect successional changes in community diversity in forest systems

(Lasky *et al.*, 2014). In Chapter 5 I therefore measure plant functional traits of woody tree and shrub species across rain forest – giant eucalypt forest – savanna transitions to examine the idea that rain forest and savanna are alternative stable states while giant eucalypt forest is an unstable state between the two.

Finally, in Chapter 6 I synthesize my findings and discuss their relevance to my chief question of whether giant eucalypt forests are rain forests. I then use this and other evidence as a basis for a section dedicated to the management of giant eucalypt forest in Far North Queensland. Finally, I make some recommendations for the general classification of giant eucalypt forests and suggest avenues for further research.

Chapter 2

Chapter 2 Giant eucalypts – globally unique fire-adapted rain forest trees?

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These papers were conceived by DYPT, who carried out the literature review and wrote the manuscript. Extensive supervision, guidance and corrections were provided by DMJS and GJJ. GJW carried out the statistically analysis and fire modelling.

2.1 Summary

Tree species exceeding 70 m in height are rare globally. Giant gymnosperms are concentrated near the Pacific coast of the USA, while the tallest angiosperms are eucalypts (*Eucalyptus* spp.) in southern and eastern Australia. Giant eucalypts co-occur with rain forest trees in eastern Australia, creating unique vegetation communities comprising fire-dependent trees above fire-intolerant rain forest. However, giant eucalypts can also tower over shrubby understoreys (e.g. in Western Australia). The local abundance of giant eucalypts is controlled by interactions between fire activity and landscape setting. Giant eucalypts have features that increase flammability (e.g. oil-rich foliage and open crowns) relative to other rain forest trees but it is debatable if these features are adaptations. Probable drivers of eucalypt gigantism are intense intra-specific competition following severe fires, and inter-specific competition among adult trees. However, we suggest that this was made possible by a general capacity of eucalypts for 'hyper-emergence'. We argue that, because giant eucalypts occur in rain forest climates and share traits with rain forest pioneers, they should be regarded as long-lived rain forest pioneers, albeit with a particular dependence on fire for regeneration. These unique ecosystems are of high conservation value, following substantial clearing and logging over 150 yr.

2.2 Introduction

Gigantic trees arouse fascination and awe given their great age, size and global rarity (Griffiths, 2001; Spies & Duncan, 2009). These trees have been heavily exploited for forestry and there is political friction about the management of remaining old-growth forests given their high conservation, carbon storage and commercial timber values (Luyssaert *et al.*, 2008; Keith *et al.*, 2009; Dean & Wardell-Johnson, 2010; Lindenmayer *et al.*, 2011). Gigantism also provides insights into biological constraints on tree growth. Surprisingly, there are few global synopses of giant trees, and particularly comparative analyses of the biology of giant conifers and angiosperms.

While conifers from western North America have long been recognized as including most of the world's tallest trees (Eckenwalder, 2009), it is less widely known that some angiosperm tree species in Australia and Borneo attain comparable heights (Fig. 2.1; Supporting Information Table S1). Australia is a centre of giant trees as a consequence of the presence of exceedingly tall eucalypts (members of the genus *Eucalyptus sensu stricto*: excluding *Corymbia* and *Angophora* spp.; Slee *et al.*, 2006) in relatively fertile, mesic areas of the continent (Hickey *et al.*, 2000; Sillett *et al.*, 2010). Such giant trees are at the extreme tail of the distribution of tree heights. Although any definition of gigantism is necessarily arbitrary, a practical threshold of 70 m maximum height captures this tail because it delimits c. 50 species (Appendix 1; Table A1), representing < 0.005% of an estimated total of 100 000 tree species (Oldfield *et al.*, 1998). Conifer and eucalypt species exceeding 70 m represent 6% and 2% of maximum potential height distribution within their respective taxonomic groups (Fig. 2.2).
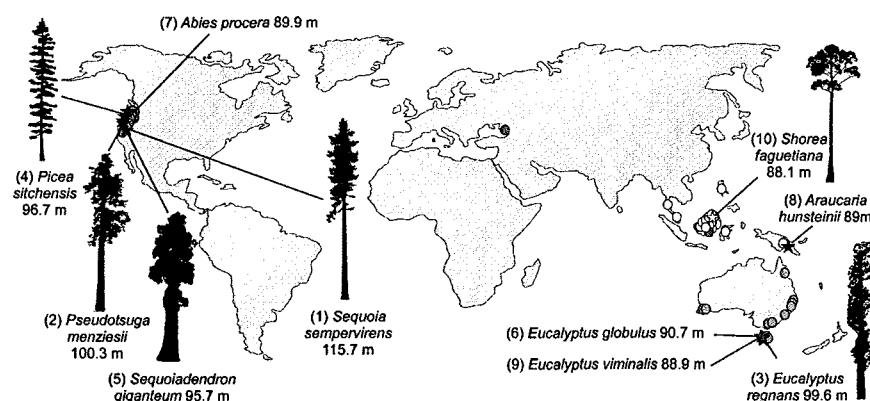
Figure 2.1 – Global distribution of the tree species know to reach 70m in height (See also Appendix 1, Table A1). Most of the tallest species are either conifers from the west coast of North America (represented by blue stars for the top five species and light blue dots for the remainder) or eucalypts in Tasmania (red stars for the three tallest species and light red dots for the remainder), although one dipterocarp species from Borneo (yellow star) and one conifer from New Guinea (blue star) rank among the top ten. Other angiosperm species that can exceed 70m (pale yellow dots) are found in southeast Asia, especially Borneo. One tall conifer (pale blue dot) occurs in Eurasia.
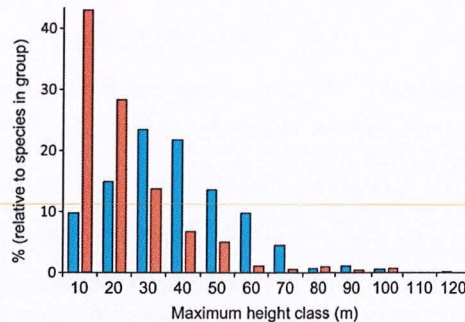
Figure 2.2 – Maximum height class distributions of conifer (n = 603 taxa) and *Eucalyptus* spp. (n = 783 taxa). All known taxa of conifer and eucalypt (including *Eucalyptus* subspecies) were included. Height data for conifers was compiled from Farjon (2010) and The Gymnosperm Database (http://www.conifers.org) and eucalypts from EUCLID (Slee *et al.*, 2006) and supplemented from data sources listed for Table S1. Two conifer taxa (*Abies hildalgensis* Debreczy, Rácz & Guízar and *Dacrydium leptophyllum* (Wasscher) de Laub.) were excluded due to lack of height information.

Despite extensive literature on the ecology of various giant eucalypt forest types (see Ashton & Attiwill, 1994; Harrington *et al.*, 2000; Wardell-Johnson, 2000), few studies compare the ecology of giant eucalypt forests across their geographic range. The preponderance of giant eucalypts in Australia is puzzling, given that Australia is the driest vegetated continent and, while giant eucalypts inhabit the mesic parts of Australia, there are similar mesic habitats in the Southern Hemisphere that have not evolved comparably tall angiosperm trees. Solving this apparent paradox might illuminate the evolutionary advantages of tree gigantism. This demands understanding of giant eucalypts in a global context, yet this quest is frustrated by terminological issues surrounding the classification of Australian rain forest (Adam, 1992; Bowman, 2000a; Lynch & Neldner, 2000).

Although giant eucalypts typically regenerate following fire disturbance (Jackson, 1968; Ashton & Attiwill, 1994), they are often emergent from a tree layer made up of

rain forest species able to regenerate without disturbance (Bowman, 2000a). Several theories have been proposed to explain the co-occurrence of these pyrophobic and pyrophilic tree species (Gilbert, 1959; Jackson, 1968; Warman & Moles, 2009; Wood & Bowman, 2012), yet it remains unclear whether giant eucalypts form plant communities that are alternative states to rain forest, or are simply 'fire weeds' (Cremer, 1960) on the margins of rain forests and therefore functionally a pioneer rain forest plant. Exploring these issues in a global context is the primary motivation of this review. To do this, we focus on the ecological and phylogenetic distributions of giant trees, how eucalypts fit into this group of plants, what allows eucalypts to be giants, and their intimate relationship with fire, and finally we integrate this information to consider the unique ecological relationships of eucalypts with rain forest.

2.3 Giant eucalypts in a global context

We were able to identify reliable records of 46 angiosperm and gymnosperm species with heights over 70 m in natural vegetation (Table S1; includes taxonomic authorities). Anecdotal evidence suggests that a few other species (such as *Cupressus cashmeriana* Royle ex Carrière (Farjon, 2010) and possibly *Ceiba pentandra* (L.) Gaertn.) may also reach such heights. Some of the species with giant trees can grow very tall across much of their range (e.g. *Sequoia sempervirens* and *Eucalyptus regnans*), but others show large variation in stature depending on environment and genotype (e.g. *Eucalyptus globulus* (Jordan *et al.*, 2000) and *Pseudotsuga menziesii* (Farjon, 2010)). This review will focus on the giant forms.

Although giant trees grow in both tropical and temperate regions, they are very restricted geographically and phylogenetically (Fig. 2.1). All the known giant trees occur in mesic climates, but nearly all of them (members of 43 species) are found in three regions: western North America from California to British Columbia, Southeast Asia (especially Borneo) and eastern Australia (Fig. 2.1; Table S1). The remaining three species with giant trees are from temperate zones in southern Russia and

southwestern Australia. The 17 species of conifers with giant trees are members of three families (Cupressaceae, Pinaceae and Araucariaceae), whereas almost all of the 29 angiosperm species with giant members are eucalypts or emergent tropical rain forest trees of the family Dipterocarpaceae (i.e. dipterocarps; Ashton & Hall, 1992).

Eucalyptus regnans is the tallest flowering plant on Earth (Figs 2.1, 2.3a) with a living Tasmanian tree measured at 99.6 m and a convincing historical record of 114.3 m for a tree in Victoria (Mifsud, 2002; Table S1). In fact, these cool temperate regions of Tasmania and eastern Victoria are centres for giant eucalypts, containing the six tallest recorded species of the genus (Fig. 2.1; Table S1). Several other eucalypt species with giant trees are found in the mesic, subtropical zone of eastern Australian, and one of these species, *Eucalyptus grandis* (Fig. 2.3b), extends into the humid tropical forest zone of northern Queensland. In the highest rainfall parts of southwestern Australia, which has a mediterranean-type climate, *Eucalyptus jacksonii* and *Eucalyptus diversicolor* (Fig. 2.3c) attain comparable heights (Boland *et al.*, 2006). *Eucalyptus deglupta* is the only extra-Australian giant eucalyptus species. This species occurs naturally in Mindanao, Indonesia and Papua New Guinea (Carr, 1972; Whitmore, 1998). Several eucalypt species also attain heights of over 70 m in plantations outside Australia, and have become the tallest recorded angiosperm trees in some regions. Thus, the tallest recorded angiosperm in Europe is a 72-m *E. diversicolor* in the Caucasus Mountains (Nicolle, 2011); the tallest tree in New Zealand is an *E. regnans* that was 69 m in 1984 (Burstall & Sale, 1984), and is still growing, and the tallest known tree in Africa is an 81.5-m-tall specimen of *Eucalyptus saligna* Sm. (Trabado, 2008). The tallest measured tropical angiosperm (*Shorea faguetiana*; Dipterocarpaceae) stands at 88.1 m (R. Dial, pers. comm.) but among dipterocarps such heights are the exception, with emergent dipterocarps typically < 60 m tall (Wyatt-Smith, 1964; Cao & Zhang, 1997; Whitmore, 1998). In addition to great heights, there are some other commonalities among eucalypts and dipterocarps, including the species richness of these clades, and the presence of species (e.g. *Eucalyptus obliqua* and *Shorea* spp.) that can both compete with broadleaf understorey species in unburnt settings (thus forming closed forests) and

Figure 2.3 - Characteristics of giant eucalypts. (a) The Centurion at 99.6m (*Eucalyptus regnans*), the world's tallest flowering plant, Arve Valley, Tasmania. This tree overtops the main canopy by over 60m; (b) *Eucalyptus grandis*, Mt Paluma, Queensland; (c) Mature even-aged stand of *Eucalyptus diversicolor* tall forest with sclerophyllous understorey, Porongorup National Park, Western Australia. Rain forest existed in Western Australia until ~3 million years ago (Dodson & Macphail, 2004); (d) Serotinous woody capsules of *E. globulus*, Hobart, Tasmania; (e) Radial longitudinal section of the outer part of the epicormic strand in the bark of *E. regnans*, an obligate seeding species. A meristematic strip which may function as an epicormic strand is arrowed at the right of the image. Several other meristem strips are partially shown on the left; (f) *Eucalyptus grandis* plantation in Cameron Highlands, Malaysia. Note the dense regeneration of native rain forest in the understorey.

persist in frequently burnt communities with grassy understoreys (thus forming savanna; Stott, 1984).

A global analysis of plant height identified the rainfall of the wettest month as the main predictor of height in plants, with plants generally being taller in the tropics (Moles *et al.*, 2009). However, this predictor fails to explain the distribution of giant trees. Elucidating the climatic determinants of tree height is beyond the scope of this review, but a basic climatic analysis on annual potential evapotranspiration and annual precipitation axes show that giant trees occupy a broad climatic envelope (Fig. 2.4) that is also occupied by many forest types with no giant trees.
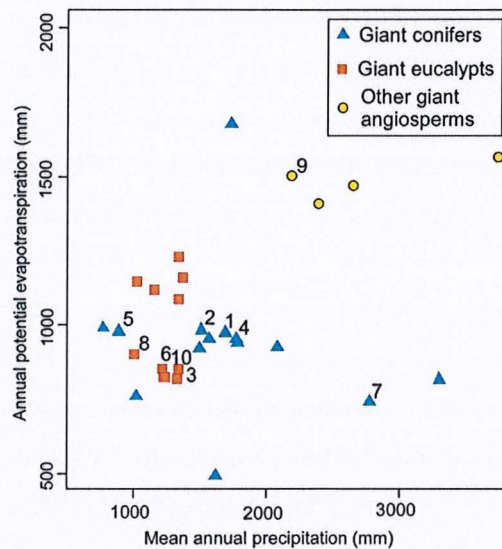
Figure 2.4 - Distribution of 35 of the tallest tree species in the world along annual potential evapotranspiration and annual precipitation axes. The ten species labelled are: 1 - *Sequoia sempervirens*; 2 - *Pseudotsuga menziesii*; 3 - *Eucalyptus regnans*; 4 - *Sequoiadendron giganteum*; 5 - *Abies procera*; 6 - *Eucalyptus viminalis*; 7 - *Araucaria hunstenii*; 8 - *Eucalyptus delegatensis*; 9 - *Petersianthus quadrialatus*; 10 - *Eucalyptus obliqua*. Tropical angiosperms (*Petersianthus*, *Shorea* and others) and temperate angiosperms (*Eucalyptus* spp.) clearly occupy different positions along evapotranspiration-precipitation axes, and *Araucaria hunstenii* is also climatically segregated from both groups. The remaining species that have been used in this analysis are indicated in Appendix 1, Table A1.

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The giant trees also occur across a wide range of thermal regimes, ranging from the tropical lowlands to cool temperate regions (Table S1). The tallest temperate conifers and eucalypts appear to be clustered within a relatively narrow-range climate envelope centred on 1000 mm annual potential evapotranspiration and 1000 mm mean annual precipitation, perhaps signifying convergence in habitat requirement (Fig. 2.4). Indeed, *Sequoia sempervirens* (coastal redwood), the tallest coniferous tree, and *E. regnans*, the tallest angiosperm, have been considered to be ecological analogues (Box, 2002). However, this view ignores the large differences in life history strategies between these species (Sillett *et al.*, 2010).

Sequoia sempervirens regenerates in tree-fall gaps, grows very slowly and lives for over 2000 yr (Busing & Fujimori, 2002). The large size attained by *S. sempervirens* is believed to provide a buffer against environmental stress (especially for nutrients and moisture) and the extremely long average intervals between destructive fires and storms permit this conifer to outgrow co-occurring hardwoods with more limited stature and life spans (Waring & Franklin, 1979). By contrast, *E. regnans* does not depend on extreme longevity to gain great height. This species regenerates prolifically after intense fires, has extremely rapid growth in the first 100 yr of life and then senesces after c. 500 yr (Wood *et al.*, 2010). After the first few months of growth, this species overtops its co-occurring community, which typically becomes progressively more dominated by rain forest species (Gilbert, 1959). Within angiosperm-dominated forest systems, the two-tiered syndrome of a fire-dependent forest towering above a fire-intolerant forest is known only in the associations between eucalypts and rain forest. Dipterocarps typically germinate and establish below a closed forest canopy and maintain seedling banks below closed forest (Whitmore & Brown, 1996). Although many giant dipterocarps, such as *Parashorea malaanonan* and *Shorea johorensis* (Whitmore & Brown, 1996), require the high light intensities of canopy gaps for growth, these species differ from eucalypts in being able to persist under shade (Meijer & Wood, 1964). All other large angiosperms (e.g. *Koompassia* and *Ceiba*) are scattered emergents in tropical rain forest, dependent on gap-phase regeneration (Whitmore, 1998) and, unlike giant eucalypts or dipterocarps (Ashton, 1981a), do not become canopy monodominants.

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Some giant conifers show a similar dependence on fire for regeneration to giant eucalypts. For instance, *Pseudotsuga menziesii* (Douglas-fir) is shade-intolerant and shows very rapid growth after landscape-scale fires induce regeneration. This species is therefore considered to be a pioneering species relative to the shade-tolerant and slower growing *Tsuga heterophylla* (western hemlock), with which it co-occurs (Bušina, 2007). *Picea sitchensis* (Sitka spruce) is also fast-growing and responds well to fire, but does not require fire to initiate regeneration to the same degree as eucalypts (Alaback, 1982). Some Southern Hemisphere forests with tall conifers (e.g. *Agathis australis* (D. Don) Loudon in New Zealand; *Araucaria araucana* (Molina) K. Koch and *Fitzroya cupressoides* I.M. Johnston. in southern South America; *Araucaria bernieri* Buchh. in New Caledonia; and *Araucaria hunsteinii* in Papua New Guinea) regenerate after large and infrequent landscape-level disturbances such as tectonic instability and volcanism but are not specialized to regenerate following fire. These species attain great height by virtue of great longevity, thereby persisting as emergents above close-canopied vegetation that subsequently develops beneath them (Lane-Poole, 1925; Jaffré, 1995; Ogden & Stewart, 1995; Veblen *et al.*, 1995).

2.4 Giant eucalypts – distribution and taxonomic variation

The molecular phylogeny with best representation of species of *Eucalyptus* (Steane *et al.*, 2002; Bayly & Ladiges, 2007) shows that giant eucalypts occur in at least seven different clades – three within subgenus *Eucalyptus* (*E. jacksonii*, *Eucalyptus delegatensis*, and the clade containing *E. regnans*, *E. obliqua* and *Eucalyptus pilularis*) and four within subgenus *Symphyomyrtus* (*E. diversicolor*, *E. deglupta*, *E. grandis* and section *Maidenaria*: *Eucalyptus viminalis*, *Eucalyptus nitens*, *Eucalyptus nobilis* and *E. globulus*; Fig. 2.5). While not attaining heights exceeding 70 m, a number of other tall eucalypts (e.g. *Eucalyptus dunnii* Maiden, *Eucalyptus macta* L.A.S. Johnson & K.D. Hill, and *Eucalyptus subcrenulata* Maiden & Blakely) and some species in closely related genera (*Corymbia*, *Lophostemon* and *Syncarpia*) exhibit maximum heights of 50–70 m and occur as emergents in rain forests (Benson

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& Hager, 1993; Harrington *et al.*, 2000; Keith, 2004; Harris & Kitchener, 2005; Boland *et al.*, 2006).
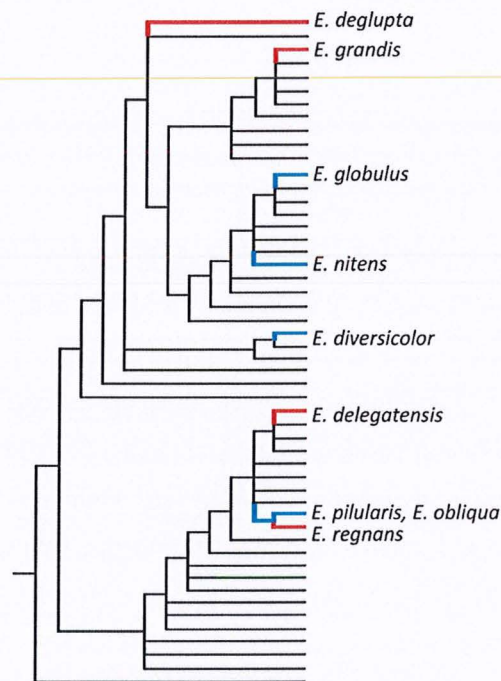
Figure 2.5 - Eucalypt phylogeny showing the phylogenetic position of various giant eucalypts (>70m max height), based on nuclear ribosomal interspacer (ITS) sequences (simplified from Steane *et al.*, 2002). Red lines indicate giant eucalypt species that exhibit obligate seeding (Nicolle, 2006). Gigantism appears to have arisen independently at least seven times, and obligate seeding in giant trees has arisen independently from resprouting taxa at least four times.

Giant eucalypts are unable to cope with prolonged periods of drought and are therefore restricted to areas that receive at least 50 mm of rainfall in the driest month (Ashton, 1981a; Fig. 2.6; Table 2.1). Some giant eucalypts have very narrow environmental ranges requiring both high rainfall and fertile soils. For example, the most site-sensitive giant eucalypts, such as *E. regnans*, require deep and well-drained

soils (Ashton, 1981a) and typically occur on very wet sites with high and reliable rainfall (in excess of 1200 mm per annum). Underscoring the narrow niche of this species are results from forestry growth trials that revealed little genetic variation in growth rates among provenances (Raymond *et al.*, 1997). Some species with giant members, such as *E. obliqua* and *E. viminalis*, have ecotypes tolerant of a wide range of edaphic or other environmental conditions, and can also occur in diminutive forms in areas with drier climates, infertile soils, or both (Wells & Hickey, 2005).
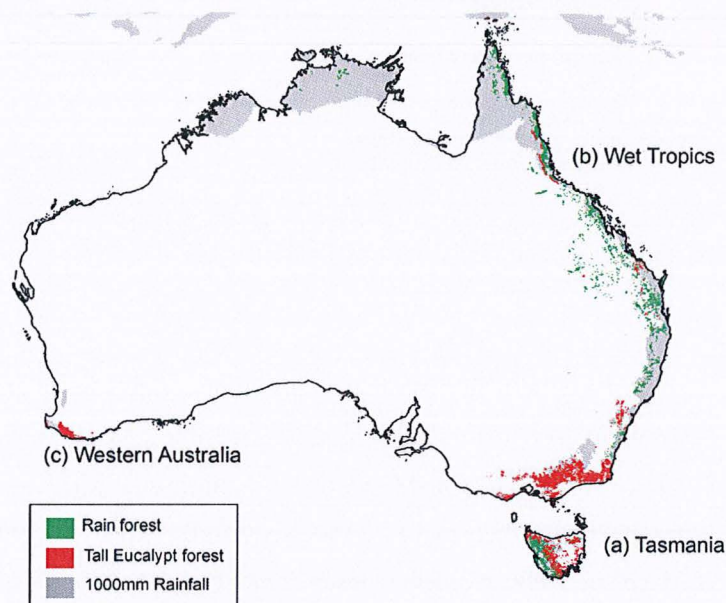
Figure 2.6 - The distribution of tall eucalypt forest and rain forest in Australia. Areas exceeding 1000m annual precipitation (data from Bureau of Meteorology, 2011) is indicated in grey. The main areas of tall eucalypt forest discussed in the text represent: (a) cool temperate Tasmania, where tall eucalypt forest extends widely in association with rain forest; (b) the north Queensland Wet Tropics where tall eucalypt forest occurs only as a marginal strip on the western edge of rain forests, and; (c) the mediterranean climate Western Australia where rain forest does not currently occur. Note that the boundaries between rain forest and tall eucalypt forest in eastern Australia are approximate. In reality, large areas of tall eucalypt forest may contain a rain forest understorey. (Sources: Queensland – Department of Environment and Resource Management, 2011; Tasmania – Department of Primary Industries and Water, 2009; Western Australia – Western Australian Herbarium, 1998).

Table 2.1 – Rainfall envelope and altitudinal range of selected giant eucalypts and co-occurring rain forest trees (except SW Australia).

*Climatic zone/Species	Mean annual rainfall (mm)	Altitude (m a.s.l.)
Tropics (Papua New Guinea)		
Eucalyptus deglupta Blume	2500-5000	0-1800
Pometia pinnata J.R.Forster & G.Forster f.	1500-5000	0-1700
Tropics (Far North Queensland)		
Eucalyptus grandis W. Hill ex Maiden	1000-3500	0-1100
Flindersia pimenteliana F. Muell.	1100-3800	0-1200
Subtropics (Central Coast Queensland and New South Wales)		
Eucalyptus pilularis Sm.	900-1750	0-700
Ceratopetalum apetalum D. Don	1000-2000	100-900
Temperate (Eastern Australia and Tasmania)		
Eucalyptus regnans F. Muell.	750-1700	150-1100
Eucalyptus obliqua L'Hér	500-2400	0-750
Nothofagus cunninghamii (Hook.) Oerst.	1100-2500	0-1570
Atherosperma moschatum Labill.	1000-2000	0-1375
Mediterranean (Southwestern Australia)		
Eucalyptus diversicolor F. Muell.	900-1300	0-300
Eucalyptus jacksonii Maid.	1150-1250	50-150

*Sources of rainfall envelop data for: Australia species: Boland *et al.* (2006); *E. deglupta*: http://www.worldagroforestrycentre.org; *Pometia pinnata*: http://www.agroforestry.net

In eastern Australia, the distribution and climatic envelope of giant eucalypts overlap with rain forest (Adam, 1992; Figs 2.6, 2.7; Table 2.1). However, two giant eucalypt species, *E. diversicolor* and *E. jacksonii*, occur in southwestern Australia (Wardell-Johnson, 2000), where rain forest became locally extinct c. 3 million yr ago (Dodson & Macphail, 2004; Wardell-Johnson, 2000; Figs 2.6, 2.7). Most *E. diversicolor* forests occur in drier climates compared with *E. regnans* and *E. grandis* forests (Fig. 2.7). The only extra-Australian giant eucalypt, *E. deglupta*, occurs in rain forest in New Guinea, Indonesia and the Philippines (Carr, 1972) under a hot tropical ever-wet climate of 2500–5000 mm of precipitation per year (Table 2.1).

The geographical distribution of giant eucalypts has varied considerably through time. Molecular phylogeographical data imply that, during the last glacial maximum, *E. regnans*, *E. obliqua* and associated rain forest species were limited to multiple refugial areas scattered across the current ranges of these species (Nevill *et al.*, 2009; Worth *et al.*, 2009; Bloomfield *et al.*, 2011). Likewise, pollen analyses from volcanic

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crater lakes in humid tropical Queensland show that rain forest boundaries, and undoubtedly co-occurring giant eucalypt forest, oscillated during the Quaternary (Kershaw, 1976; Haberle, 2005). This is consistent with the comparative genetic uniformity of populations of *E. grandis* in humid Queensland compared with the more differentiated populations in southeastern Queensland and New South Wales (Jones *et al.*, 2006).
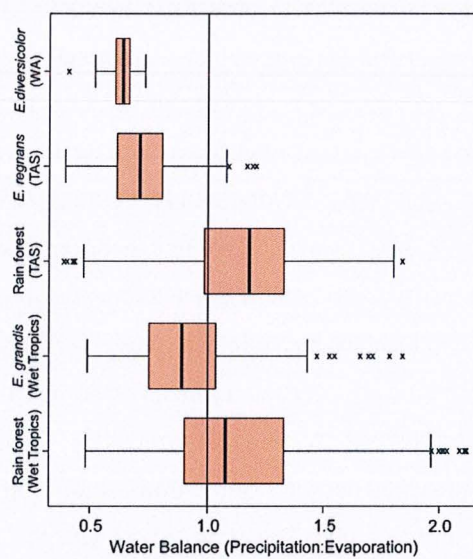
Figure 2.7 - Occurrence of *Eucalyptus diversicolor*, *E. regnans*, *E. grandis* tall forest and associated rain forest types in Tasmania (TAS) and north Queensland (Wet Tropics) along a water balance expressed as precipitation:evaporation (Evaporation data: Donohue *et al.*, 2010). Higher values indicate wetter environments. In both north Queensland and Tasmania, the vegetation data used included all vegetation types mapped under wet eucalypt forest (which would include the giant eucalypts in this review) and rain forest. Rain forest is not currently present in Western Australia (WA) but was present in the region up to ~ 3 million years ago (Dodson & Macphail, 2004). (Sources: as per Fig. 2.6).

In southwestern Australia, there is evidence of rain forest occurring in the region as recently as c. 3 million yr ago (Dodson & Macphail, 2004). The extinction of rain

forest species in southwestern Australia may simply reflect the development of drier and more fire-prone climates inimical for those taxa (Dodson & Macphail, 2004). Thus, it is conceivable that *E. diversicolor* forest has replaced rain forest and now fills the role of an alternative stable state to more pyrophylic vegetation types in the region (Bowman, 2000b; see also Figs 2.6, 2.7).

Fire frequency and local environmental conditions influence the understoreys, which in turn influence the flammability of giant eucalypt forests. Sites that are frequently burnt, have infertile soils, or both are typically dominated by sclerophyllous shrubs, grasses, graminoids or ferns that have phylogenetic and floristic links with the understorey species of dry eucalypt forest (Florence, 1964; Adam, 1992). Sites that are less frequently burnt and/or have more fertile soils favour mesic shrubs and, if they occur in the regional flora, rain forest trees. However, the spatial extent and understorey type of giant eucalypt forests differ markedly in different climate zones. In the southwestern and southeastern temperate zones of mainland Australia, giant eucalypts can form extensive forests above a shrub layer, or, in parts of the southeast, intergrade with *Nothofagus* rain forest (Keith, 2004; Harris & Kitchener, 2005). Tropical and subtropical giants are typically restricted to narrow bands (< 4 km width) sandwiched between humid tropical rain forest and eucalypt savanna (Harrington *et al.*, 2000; Tng *et al.*, 2012), whereas in Tasmania these often intergrade with *Nothofagus* rain forest (Gilbert, 1959; Fig. 2.6).

An important control of the landscape-scale pattern of giant eucalypt forests and rain forest is fire intensity. Temperate rain forests sustain surface fires of very low intensity (Hill, 1983), yet *E. regnans* forests have the highest fire intensities (> 50 000 kW m−1) of any vegetation type in Australia (McCarthy *et al.*, 1999), comparable to some Canadian and Alaskan boreal coniferous forests (Van Wagner, 1983). Such fires occur as a result of infrequent severe fire weather and antecedent droughts, as indicated by the high forest fire danger index (FFDI) values (Noble *et al.*, 1980) of giant eucalypt forests (Fig. 2.8). While tropical *E. grandis* forests have a higher mean FFDI, these forests are exposed to less extreme FFDI events than their temperate equivalents in southeastern and southwestern Australia (Fig. 2.8). This is a

potential explanation as to why *E. grandis* does not penetrate tropical rain forest habitats to the same extent as *E. regnans* infiltrates cool temperate rain forest environments. Similarly, it is also plausible that the higher frequency of high to severe FFDI events of *E. diversicolor* forest compared with both *E. regnans* and *E. grandis* (Fig. 2.8) may be related to the occurrence of *E. diversicolor* in drier habitats (Fig. 2.7) and/or the lack of rain forest in the region. Indeed, there is evidence that the microclimate of humid tropical rain forest understoreys renders the vegetation type less flammable than the adjacent and more open canopied *E. grandis* forests (Little *et al.*, 2012), and this is probably the case for *E. regnans* forests (Jackson, 1968). It is possible that flammability of *E. regnans* varies with age of the trees (McCarthy *et al.*, 2001); for instance Jackson (1968) believed that younger regrowth eucalypt forest had higher flammability than older mixed *Nothofagus–E. regnans* forest.
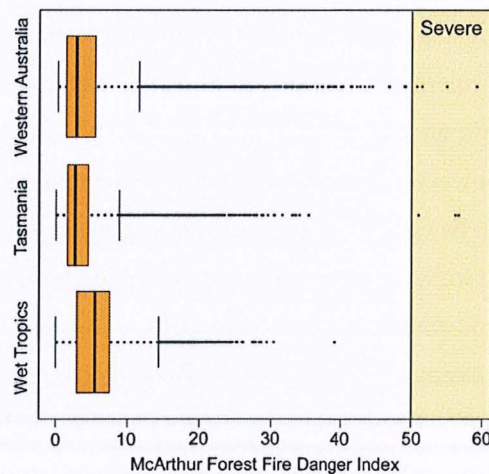
Figure 2.8 - Forest fire danger index of three regions where tall eucalypt forest occurs (Tasmania, Wet Tropics and southwest Western Australia: Fig. 2.6), calculated using daily weather records (Bureau of Meteorology, 2011). The McArthur forest fire danger index is a widely used measure of fire risk in Australia and can be calculated for any given area. The index is measured using climatic data such as maximum temperature, mean wind speed, minimum relative humidity, total rainfall and mean soil moisture. A fire danger index is over 50, as indicated by the line in the graph, is considered severe.

2.5 Growth of giant eucalypts

Understanding the evolution of gigantism in eucalypts requires a consideration of the characteristics of eucalypts that allow them to exceed the heights of their co-occurring species, and the specific features of giant species that allow them to reach such extreme heights. Eucalypts and some closely related genera (*Corymbia*, *Lophostemon* and *Syncarpia*) form all of the canopy or emergent trees of many vegetation types in Australia (Groves, 1999), and are considerably taller than all or almost all other species in these communities. This trend of 'hyper-emergence' extends across climates and clades, with eucalypts and related genera exceeding the heights of other co-occurring species in many other vegetation types, including heath, mallee, dry sclerophyll, subalpine and savanna communities (Groves, 1999). Some giant eucalypt trees are > 60 m taller than the underlying rain forest canopy (Fig. 2.3a). This characteristic of hyper-emergence involves not only the capacity to deal with the mechanical and hydraulic limitations of height per se, but also the need for rapid growth to attain this height before the tree senesces or succumbs to disease. The nearly ubiquitous nature of hyper-emergence in eucalypts suggests that the trait of hyper-emergence is an ancestral feature of the eucalypt lineages, and if this is true, would have arisen > 60 million yr ago (see the dated phylogeny of Crisp *et al.*, 2011). However, cross-matching the eucalypt phylogeny (Fig. 2.5) with the molecular dates of Crisp *et al.* (2011) suggests that all of the evolutionary transitions into giant trees occurred in the last 20 million yr, and it is possible that many, or even all of them, are much more recent. Most of the last 20 million yr has been associated with increasing aridification of the Australian continent (Bowler, 1982) which appears to have resulted in significant increases in the frequency of fire in rain forests habitats (Kershaw *et al.*, 1994). Thus, we propose that gigantism in eucalypts evolved opportunistically when members of this group of hyper-emergent plants were exposed to an environment that contained both the fire essential for regeneration and the environmental conditions that allowed the rapid growth necessary for a species to reach extreme height without extreme longevity.

The mechanisms that allow eucalypts to be much taller than other species in a wide range of habitats are poorly understood, and represent a fertile field of potential research. Such mechanistic explanations could consider how eucalypts deal with a series of problems relating to the difficulties of creating a trunk and root system that is biomechanically (Niklas, 1994) and hydraulically (Koch et al., 2004) adequate. The explanations could also consider what characteristics give the eucalypts (and other angiosperms) the high relative growth rates necessary to construct this trunk within the short lifespan of these trees compared with giant conifers (Stephenson & van Mantgem, 2005). Furthermore, evolutionary explanations of hyper-emergence in eucalypts should consider the adaptive costs and benefits of far exceeding the heights of competitors (Falster & Westoby, 2003). Little is known about these aspects of eucalypt biology, but some evidence has been presented regarding growth rates and hydraulics.

Although the physiological basis for rapid growth in eucalypts is unknown, there are at least two plausible theories for an adaptive advantage for very rapid height growth. Bond (2008) argued that very rapid early growth of trees, including savanna eucalypts, may allow them to escape a 'fire trap' such that this growth would allow saplings to reach heights that allow them to avoid the effects of high-intensity ground fires. Such processes could apply to eucalypts in general, but may be less applicable to giant eucalypt species, for which fire return intervals are typically very long (decades to centuries). In the giant eucalypts, shade intolerance combined with intense intraspecific and interspecific competition provides a strong selection pressure for rapid growth (Ashton, 1981b; Hardner & Potts, 1997; Falster & Westoby, 2003). For example, E. regnans can grow as quickly as 2 m yr−1 in the first decade (Ashton, 1981a) and attain half of its mature height within the first 25– 35 yr (Jackson, 1968). During this phase there is intense self-thinning of the initial high seedling densities (Ashton, 1976; Jackson, 1968) and surviving stems form straight, branch-free trunks as a result of shedding of shaded branches (Jacobs, 1955). Hardner & Potts (1997) demonstrated that this selection had strong genetic effects by showing that inbred genotypes of E. regnans were rapidly eliminated, leaving only outbred individuals with rapid growth.

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The few comparative studies of the functional ecology of giant eucalypts have suggested that eucalypts overtop their co-occurring rain forest species. In the humid tropics, Duff (1987) studied a suite of nine species spanning a tropical rain forest–tall eucalypt forest boundary and found that *E. grandis* grew faster and acquired more biomass than both pioneer and climax rain forest taxa when grown under glasshouse conditions. *Eucalyptus grandis* exhibited patterns of resource allocation that were broadly similar to those of fast-growing rain forest pioneers such as *Alphitonia* and *Toona*, and, given sufficient light and nutrients, could capitalize on the available resources more efficiently than the rain forest species. Similar findings were reported by Barrett & Ash (1992), who compared the growth and carbon partitioning of rain forest and eucalypt species occurring along a vegetation transitional sequence in south coastal New South Wales. They found that, under high irradiance, the mean plant biomass of eucalypts exceeded that of ecotonal species and rain forest species, and concluded that the eucalypts maximized leaf area in proportion to plant mass for a given level of irradiance, presumably to maintain high growth rates.

Ryan & Yoder (1997) argued that hydraulics were major determinants of tree height, because greater height resulted in greater xylem resistance as a result of the greater distance over which water must be conducted and increased gravitational potential opposing the ascent of water in taller trees. Tall trees can deal with these effects (equal to 1 MP in water potential for 100 m in height) by some combination of constructing highly conductive xylem and operating at very low leaf water potentials. Furthermore, the risk of embolism in water-conducting tissue (Tyree & Sperry, 1989) increases not only with whole-plant water deficit but with tree height (Koch *et al.*, 2004). These factors provide a possible explanation of why giant trees are restricted to mesic environments. There is some evidence that giant eucalypts have specific features that may help overcome hydraulic limitations associated with great height.

Compared with other hardwoods, *E. regnans* (England & Attiwill, 2007) and *E. delegatensis* (Mokany *et al.*, 2003) have comparatively wide sapwood vessels (up to 278 and 270 μm, respectively). Likewise, *E. regnans* (Legge, 1985) and *E. obliqua* (Skene & Balodis, 1968) have comparatively long vessels (1.8 and 4 m). The pipe

model theory proposes that, for a given tree species, the ratio of sapwood area (A_s) to foliage area (A_f) should remain constant (Waring *et al.*, 1982) or in fact increase as trees grow taller to compensate for the increased path length that water must travel to reach the leaves (Magnani *et al.*, 2000). This mechanism of increasing A_s:A_f ratios to cope with increasing heights has been demonstrated for a range of trees and specifically for the giant conifer *Pseudotsuga menziesii* (McDowell *et al.*, 2002) and the tall eucalypt *E. saligna* (Barnard & Ryan, 2003). However, giant eucalypt species such as *E. regnans* (Vertessy *et al.*, 1995), *E. delegatensis* (Mokany *et al.*, 2003) and the related *Eucalyptus sieberi* L.A.S. Johnson (Roberts *et al.*, 2001) exhibit decreasing A_s:A_f ratios with increasing height, largely as a result of an increase in the specific conductivity of sapwood (Mokany *et al.*, 2003; England & Attiwill, 2007). As *E. regnans*, *E. pilularis*, *E. globulus* and *E. nitens* trees mature, increased sapwood conductivity is achieved initially through increased vessel diameter, after which subsequent increases in conductivity result from increases in vessel density (Bamber & Curtin, 1974; England & Attiwill, 2007; Hudson *et al.*, 1998). Petit *et al.* (2010) measured the vertical profiles of the conduit (i.e. vessel) dimensions and density of *E. regnans* trees of varying heights. They found that the way in which the xylem tapers in *E. regnans* is unusual and constitutes a highly effective strategy for compensating for the hydraulic limitations caused by increased tree height. They concluded that, relative to other fast-growing trees, *E. regnans* has evolved a xylem design that ensures a high hydraulic efficiency, enabling the species to rapidly attain heights beyond the maximum height (50–60 m) of most other hardwood trees (Petit *et al.*, 2010).

2.6 Fire and regeneration of giant eucalypts

In their natural range, giant Australian eucalypts are generally known to be dependent on fire for regeneration (Ashton & Attiwill, 1994). In eucalypts, as with woody plants in general, there are two broad fire regeneration syndromes: obligate seeders and resprouters. Obligate seeders are usually killed by fire, but can have a competitive advantage over resprouters by growing more rapidly and maturing

earlier than resprouters because they do not invest in protective structures and storage organs and regenerative tissues (Bond & van Wilgen, 1996; Knox & Clarke, 2005). Although almost all eucalypts exhibit strong resprouting responses after fire, several giant eucalypts, notably *E. regnans*, *E. grandis*, *E. delegatensis* and *E. deglupta*, are obligate seeders (Nicolle, 2006). Thus, *E. regnans* has an aerial seed bank in the form of woody capsules (i.e. Fig. 2.3d) that protect seeds from the heat of a fire (Ashton, 1981a), limited epicormic regrowth and no lignotubers (Nicolle, 2006; Waters *et al.*, 2010). The large quantity of viable seed released after a crown-scorching fire saturates seed predators, allowing the survival of huge numbers of seedlings (Ashton, 1979; O'Dowd & Gill, 1984). Fire also releases nutrients and ameliorates soil conditions which would otherwise be unfavourable for seed germination and seedling growth of eucalypts such as *E. regnans* (Chambers & Attiwill, 1994). Growth of seedlings is further enhanced because the death of canopy and emergent trees releases seedlings from short-term competition for environmental resources (Dignan *et al.*, 1998; Van Der Meer *et al.*, 1999). However, intraspecific competition rapidly comes into play, further enhancing height growth (see section 2.7, "Are giant eucalypts different from other rain forest trees?").

Although severe fire typically results in the death of obligate seeding eucalypts, triggering massive regeneration and development in even-aged stands across large expanses of landscape (e.g. Fig. 2.3c; Ashton, 1975, 1981a; Wardell-Johnson *et al.*, 1997), adults quite often survive in patches where fire is less intense (Gilbert, 1959; Vivian *et al.*, 2008), creating mixed-aged stands (Simkin & Baker, 2008; Turner *et al.*, 2009). Thus, Turner *et al.* (2009) found that almost half the stands of *E. regnans* in Tasmania were mixed-aged.

Nevertheless, obligate seeders such as *E. regnans* are less likely to form mixed-aged forests than resprouting species such as *E. obliqua* (Turner *et al.*, 2009). These resprouting species can possess combinations of well-developed vegetative recovery mechanisms such as thick bark, epicormic buds and lignotubers, although some ecologically diverse species (e.g. *E. viminalis*) have less pronounced lignotubers in environments suitable for gigantism (Ladiges, 1974). Resprouter giant eucalypts also

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exhibit slower growth rates than obligate seeders such as *E. regnans*, probably as a consequence of the cost/benefit trade-offs of investing in lignotubers and/or thick bark (Ashton, 1981a). Smooth-barked eucalypt species have less fire protection than species with thick bark, but need to invest less in bark growth and can achieve small photosynthetic gains from chloroplasts in the bark (Cernusak *et al.*, 2006).

The analysis of Crisp *et al.* (2011) suggests that an anatomical feature (deeply embedded cambial strands capable of generating epicormic stems) that enables prolific vegetative regeneration throughout the genus is an ancient adaptation allowing recovery from fire dating back to c. 60 million yr ago. Their analysis therefore implies that obligate seeding in *E. regnans* is a derived feature (Fig. 2.5) given that this species is deeply nested within the eucalypts (Ladiges *et al.*, 2010) but still possesses the specialized cambial strands (Waters *et al.*, 2010; Fig. 2.3e). The evolution of other fire-related traits in eucalypts is less clear. Thus, it remains unclear if eucalypts have specific adaptations to increase flammability, and hence increase their regeneration niche (e.g. Bradshaw *et al.*, 2011; Keeley *et al.*, 2011). For example, although oil-rich foliage is often claimed to be an adaptation to increase flammability, there is strong evidence that it acts as a chemical defence against invertebrate and vertebrate herbivores (O'Reilly-Wapstra *et al.*, 2004). It is true that decorticating bark strips spread spotfires (Mount, 1979), but whether this feature is an adaptation for this purpose remains unproven (see Bowman *et al.*, 2012).

2.7 Are giant eucalypts different from rain forest trees?

We have demonstrated in the preceding review that Australian giant eucalypts are globally distinctive given (1) their dependence on fire to regenerate in rain forest environments and (2) the development of an emergent canopy overtopping rain forest. Although Schimper (1903) included giant eucalypts as rain forest trees because they occurred in mesic environments, most Australian ecologists consider that giant eucalypts are not rain forest trees because of their dependence on fire for regeneration. This has created ongoing controversy about the definition of 'rain

forest' amongst ecologists and environmentalists (e.g. Adam, 1992; Bowman, 2000a;
Lynch & Nelder, 2000). Flammable eucalypt forests are accepted as being ecological
distinct from pyrophobic rain forests, rendering the vast majority of Australian
forests as having no global analogue, thereby frustrating international comparisons.
Logging and burning a cut stand of giant eucalypts have been widely regarded as
acceptable practices because these systems regenerate after fire disturbance, and
because giant eucalypt forests are not classified as 'rain forest' they were not affected
by the phasing out of rain forest logging that has occurred in New South Wales and
Queensland.

Rain forest classifications excluding giant eucalypts on the basis of their fire
dependence also run into a number of logical issues. First, lower statured and fire-
sensitive rain forest types in dry areas (oxymoronically described as 'dry rain forest')
often have scattered eucalypt emergents (Sattler & Williams, 1999), commensurate
with those in mesic rain forests with giant eucalypts. Secondly, non-forest fire-
sensitive vegetation, such as alpine coniferous heaths, has ecological relationships
with flammable vegetation analogous to those between rain forests and eucalypt
forests (Bowman, 2000b). Thirdly, the extra-Australian giant eucalypt *E. deglupta*
has always been accepted as a rain forest tree (Carr, 1972). Gandolfo *et al.* (2011)
also recently described *Eucalyptus* macrofossils dated at ~52 million years ago
located in present-day Argentina. These Patagonian eucalypts dominated
volcanically disturbed areas surrounded by rain forest, thus indicating that fire-
adapted taxa could occur in places where rain forest was the dominant vegetation.
Likewise, no consensus has been reached regarding the question of whether a suite of
other tall eucalypts (e.g. *E. dunnii*, *Eucalyptus pellita* F. Muell. and *E. macta*) and
other analogous Myrtaceae (e.g. *Lophostemon*, *Corymbia intermedia* (R.T. Baker)
K.D. Hill & L.A.S. Johnson and *C. torelliana* (F. Muell.) K.D. Hill & L.A.S.
Johnson) which co-occur with rain forests are true rain forest trees (Benson & Hager,
1993; Sattler & Williams, 1999).

Vegetation with co-occurring giant eucalypts and *Nothofagus* rain forest has been
described as a specific plant community called 'mixed forests' (Gilbert, 1959; Lynch

& Neldner, 2000). Jackson (1968), while acknowledging these forests to be successional, also considered them to be sufficiently stable to persist as a distinct vegetation type across the landscape (Wood & Bowman, 2012). In contrast, Warman & Moles (2009) suggested that giant eucalypt forests in northern Queensland are not actual plant communities, but rather a eucalypt-dominated unstable ecotone sandwiched between the two alternative stable states of pyrophobic tropical rain forest and pyrophilic savanna. In terms of function, giant eucalypts could then be considered rain forest pioneers (Smith & Guyer, 1983). To address whether giant eucalypts should be considered as rain forest species, we will consider how they fit into global views on what constitutes a rain forest pioneer species, and where giant eucalypts fit along the pioneer–climax species spectrum.

Within a rain forest, the pioneer–climax species spectrum refers to a continuum of species which have different tolerance to light or gap sizes (Turner, 2004). Climax species are typically extremely shade-tolerant, have the ability to regenerate continuously and subsequently grow or persist in a suppressed state under the dense shade of the forest canopy until released from this suppression by the influx of light caused by a tree-fall gap or other disturbances. By contrast, two characteristics are diagnostic of rain forest pioneer species: seed germination that is dependent on the exposed conditions present in canopy gaps; and shade intolerance (Turner, 2004). Giant eucalypts conform to both of these features, albeit that the seedbeds and forest gaps are typically created by fires (Ashton, 1975; Ashton & Attiwill, 1994). Furthermore, rain forest pioneers show r-selected reproductive strategies, with high reproductive output and rapid growth enabling them to complete their life cycle before being suppressed by slower-growing and more shade-tolerant trees (Swaine & Whitmore, 1988; Whitmore, 1998; Turner, 2004). Giant eucalypts employ similar r-selected reproductive strategies, with early reproductive maturity, prolific and often continuous production of small seeds and extremely rapid height growth that allows them to overtop slower-growing and more shade-tolerant trees in height by c. 50% (Ashton, 1981a). Another feature of many pioneer species is a persistent seed bank (Turner, 2004). In rain forest pioneers this seed bank is commonly held in the soil, but the aerial seed bank of eucalypts can be argued to provide an analogous function.

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Given that the life spans of giant eucalypts (c. 400–500 yr: Wood *et al.*, 2010) are often equivalent to, or even greater than, those of co-occurring rain forest species, the best analogue in the pioneer–climax paradigm that would apply to these eucalypts would be a subset of pioneer species known as long-lived secondary species (see Condit *et al.*, 1998), or 'large pioneers' (Swaine & Whitmore, 1988). Examples of this guild of species include various Southern Hemisphere conifers discussed in Section 2.3, "Giant eucalypts in a global context", and some angiosperms such as *Ceiba pentandra* and *Dipteryx panamaensis* (Pittier) Record & Mell from tropical South America, and *Weinmannia trichosperma* Ruiz & Pav. from temperate Chile. While some of these species do not grow to extreme heights, they resemble eucalypts in being shade-intolerant and reliant on large infrequent disturbances (Condit *et al.*, 1998; Lusk, 1999).

On the whole, giant eucalypts in mature forest show little or no sign that they actively inhibit the growth of developing rain forest or late successional species in either the tropics or the temperate zone, consistent with the view that giant eucalypts are rain forest pioneer trees. Thus, Tng *et al.* (2010, 2012d) documented the expansion of humid tropical rain forest into *E. grandis* forest in northern Queensland over the last 50 yr, and a similar process has been observed in *E. grandis* plantation within 27 yr on the central coast of New South Wales (Turner & Lambert, 1983). Similarly, the temperate rain forest dominant *Nothofagus cunninghamii* colonizes the understoreys of unburnt Eucalyptus forests across a range of soil types (Ellis, 1985). In the absence of fire, the understoreys of *E. regnans* forest in central Victoria are being invaded by *Pittosporum undulatum* Vent., a broad-leaved rain forest tree (Gleadow & Ashton, 1981).

While there is no experimental evidence showing that giant eucalypts facilitate rain forest succession in natural settings, there are many possible ways that such facilitation could occur. For instance, overstorey trees in a regenerating rain forest can improve soil water balance and give shallow-rooted plants such as rain forest seedlings access to water through hydraulic lift (Phillips & Riha, 1994; Emerman & Dawson, 1996). Shade from the overstorey that can minimize photostress for

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regenerating plants, and reduce evaporative demand at times of water deficit (Messier *et al.*, 1998), may also be important. Guevara *et al.* (1986) highlighted the importance of trees as perches for avian dispersers of rain forest plants, and this is perhaps the most immediate and easily observable way in which giant eucalypts may act as facilitators of rain forest regeneration. This mechanism of ecological facilitation is known as nucleation (Reis *et al.*, 2010), whereby rain forest trees, in particular bird-dispersed taxa, regenerate and exhibit a clustered distribution under pre-existing trees in the landscape. In northern Queensland, nucleation of rain forest trees has been documented in eucalypt woodlands (Russell-Smith *et al.*, 2004) and, likewise, bird-dispersed rain forest taxa are also very common in the understoreys of *E. grandis* forest (D. Y. P. Tng, unpublished).

Ironically, the most detailed evidence for giant eucalypts facilitating the regeneration of rain forest trees comes from extra-Australian studies of eucalypt plantations. Feyera *et al.* (2002) summarized data showing that the canopies of established plantation eucalypt trees can have facilitative or nurse effects on the regeneration of natural rain forest. Other studies document uninhibited regeneration of rain forest species under eucalypt plantations. For instance, native rain forest species have been observed to regenerate in the understoreys of *Eucalyptus grandis* plantations in both Brazil (da Silva *et al.*, 1995) and the Cameron Highlands in Peninsular Malaysia (D. Y. P. Tng, *pers. obs.*; Fig. 2.3f). Similar observations of native forest regeneration have also been documented in South Africa in the understorey of *E. saligna* plantations (Geldenhuys, 1997). This can be contrasted with cases where other exotic trees such as teak (*Tectona grandis* L.f.) can inhibit native vegetation regeneration (Healey & Gara, 2003).

In summary, we argue that, under optimal giant eucalypt regeneration, high eucalypt seedling density and intense competition for space and resources immediately following disturbance are inhibitive to rain forest (as reviewed in Section 2.5, "Growth of giant eucalypts"). During the middle and later growth phases of the eucalypts, however, rain forest regeneration is facilitated. This pattern is consistent with Finegan's (1984) schema where pioneer trees are defined by the ability to

colonize, grow and produce seed in early successional environments. We therefore assert that there is a case for treating giant eucalypts as rain forest pioneer trees, albeit with unique features relating to fire disturbance.

2.8 Conclusions

Giant eucalypts are among the tallest plants on Earth, and include the tallest angiosperm. The giant eucalypt syndrome occurs in at least seven clades within eucalypts, among species occurring from tropical to temperate environments. Giant eucalypts can coexist with rain forest trees on the margins of tropical rain forests in Queensland, form large expanses of mixed *Nothofagus* rain forest with emergent eucalypts in Tasmania and are the sole canopy tree in forests with shrubby understoreys in areas suitable for rain forests in Victoria and southwestern Western Australia (Ashton, 1981a; Sattler & Williams, 1999; Wardell-Johnson, 2000; Harris & Kitchener, 2005). Although giant eucalypts require intense fire to regenerate and outcompete other rain forest species, once established, adults do not significantly suppress, and possibly even facilitate, the development of continuously regenerating understorey made up of the same rain forest species. The dependence of giant eucalypts on fire for regeneration, in contrast to rain forest trees, has led Australian ecologists, with some exceptions (e.g. Smith & Guyer, 1983; Warman & Moles, 2009), to treat these forests as a distinct ecosystem. This approach to vegetation classification has created ongoing controversy about the definition of rain forest in Australia (e.g. Bowman, 2000a; Lynch & Nelder, 2000) that has dogged Australian ecology and environmental politics for years. Further, it has stymied international comparative studies because of difficulties in relating Australian vegetation types to those on other continents. However, such problems disappear if we adopt the paradigm that giant eucalypts are functionally rain forest trees, albeit globally unique pioneer species that depend on fire for regeneration.

Giant eucalypts conform to a general trend for eucalypts to act as hyper-emergents wherever they occur; the tallest eucalypt species may simply be those that can

compete and/or survive in their habitat (i.e. the rain forest habitat). An underlying capacity for gigantism may therefore have evolved once, with convergent evolution of other traits (e.g. rapid growth and obligate seeding) allowing the expression of extreme heights by providing these species with the capacity to occupy the relevant (rain forest) habitats. The success of the giant eucalypts under contemporary conditions is variable and the available data show that past climates have influenced the distribution of giant eucalypt forests. For example, under glacial climates *E. regnans* was more restricted in range (Nevill *et al.*, 2009). Climate has a very strong effect on fire activity, and it remains unclear how much the potential increase in flammability with the arrival of eucalypts changed the competitive balance with other rain forest trees. A functional trait-based approach to understanding the ecological niche of giant eucalypts and the role of climate and eucalypt traits on fire activity is of considerable theoretical and applied significance. Phylogenetic research is required to explore whether there has been a co-evolutionary relationship between fire and eucalypts. Such knowledge is important because any significant increase in flammability created by eucalypts would have long-term implications for natural habitats in extra-Australian regions (e.g. Brazil, China and Portugal; da Silva *et al.*, 1995; Malvar *et al.*, 2011; Zhang *et al.*, 2012) where eucalypt plantations are becoming increasingly important. If climate is the main arbiter of the competitive balance between rain forest, giant eucalypts and fire activity, then warmer climate may see a further dominance of eucalypts. Monitoring the dynamics of giant eucalypt forests is a key step in understanding these temporal trends.

Chapter 3

Humid tropical rain forest has expanded into eucalypt forest and savanna over the last 50 years

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Some of the material was also presented in the report:

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These papers were conceived by DMJSB. DYPT conducted the study and wrote the manuscripts. GS, EW and JK conducted part of the study. BPM and GJW analysed the data. who carried out the literature review and wrote the manuscript.. GJW carried out the statistically analysis and fire modelling.

3.1 Summary

Tropical rain forest expansion and savanna woody vegetation thickening appear to be a global trend, but there remains uncertainty about whether there is a common set of global drivers. Using geographic information techniques, we analyzed aerial photography of five areas in the humid tropics of northeastern Queensland, Australia, taken in the 1950s and 2008, to determine if changes in rain forest extent match those reported for the Australian monsoon tropics using similar techniques. Mapping of the 1950s aerial photography showed that of the combined study area (64,430 ha), 63% was classified as eucalypt forests/woodland and 37% as rain forest. Our mapping revealed that although most boundaries remained stable, there was a net increase of 732 ha of the original rain forest area over the study period, and negligible conversion of rain forest to eucalypt forest/woodland. Statistical modelling, controlling for spatial autocorrelation, indicated distance from pre-existing rain forest as the strongest determinant of rain forest expansion. Margin extension had a mean rate across the five sites of 0.6 m per decade. Expansion was greater in giant eucalypt forest types but also occurred in shorter, more flammable woodland vegetation types. No correlations were detected with other local variables (aspect, elevation, geology, topography, drainage). Using a geographically weighted mean rate of rain forest margin extension across the whole region, we predict that over 25% of giant eucalypt forest (a forest type of high conservation significance) would still remain after 2000 years of rain forest expansion. This slow replacement is due to the convoluted nature of the rain forest boundary and the irregular shape of the giant eucalypt forest patches. Our analyses point to the increased concentration of atmospheric CO_2 as the most likely global driver of indiscriminate rain forest expansion occurring in northeastern Australia, by increasing tree growth and thereby overriding the effects of fire disturbance.

3.2 Introduction

Determining the dynamics of tropical rain forest and savanna boundaries is a prerequisite for a comprehensive understanding of a major feedback system within the global carbon cycle, as these two geographically and ecologically linked biomes constitute substantial above- and belowground carbon stocks and fluxes on a global scale. Brazilian rain forests, for instance, store around 250–300 t C ha–1 and the adjacent tropical savanna stores 135 t C ha^{-1} (Behling 2002). Numerous reports on the expansion of rain forest (Puyravaud *et al.*, 1994, 2003; Schwartz *et al.*, 1996; Happi, 1997; Delègue *et al.*, 2001; Banfai & Bowman, 2006; Banfai *et al.*, 2007; Silva *et al.*, 2008) and increasing biomass in both rain forest (Lewis *et al.*, 2009) and savanna worldwide (Bowman *et al.*, 2001; Briggs *et al.*, 2005; Lehmann *et al.*, 2008; Wigley *et al.*, 2010) signal that these biomes are potentially important global carbon sinks. The physiological mechanisms causing these sinks are related to more efficient nutrient and water use by trees in response to increased atmospheric CO_2 concentrations (Drake *et al.*, 1997; Poorter, 1998). Increases in atmospheric CO_2 concentrations have also been correlated to increased growth rates of trees (Bond & Midgley, 2000), possibly contributing to the expansion of forests (Bond *et al.*, 2003; Behling *et al.*, 2005).

However, whether rain forest expansion or general vegetation thickening is driven by local or global drivers is a contentious issue. Many studies show that local factors (e.g., fire regimes, geology and topography) can play an important role in rain forest expansion or woody vegetation increases (Archer *et al.*, 1995; Bond *et al.*, 2003; Russell–Smith *et al.*, 2004b). A difficulty in such studies lies in disentangling the importance of global drivers from the "noise" of local variation (Wigley *et al.*, 2010). Moreover, many such landscape-scale studies (Russell–Smith *et al.*, 2004b; Banfai & Bowman, 2006) also suffer from the confounding effects of spatial autocorrelation (Murphy *et al.*, 2010).

Advances in geospatial techniques in the past decade have enabled the study of tropical rain forest systems at a landscape scale, and the use of geographic information systems (GIS) are increasingly valuable in ecological studies of

vegetation dynamics (e.g., Banfai & Bowman, 2005; Brook & Bowman, 2006; Wigley *et al.*, 2010). Indeed, Bowman *et al.* (2010) have summarized a range of aerial photographic studies undertaken in the Australian monsoon tropics that disclose a regional increase in forest cover, despite fire regimes that are damaging components of the region's savanna biodiversity.

Here, we determine the rates of landscape change and landscape conditions associated with rain forest expansion in the humid tropics of Australia to see if there is a trend similar to that in the Australian monsoon tropics. We assess change in rain forest boundary locations in a 644.3 km^2 study area within in the Wet Tropics World Heritage Area of northeastern Queensland using aerial photography taken in the 1950s (1951–1955) and 2008. We use geospatial statistics to determine to what extent rates of rain forest change were mediated by environmental conditions (geology, elevation, topographic position, slope, aspect). Using our estimated rates of change in rain forest extent, we also project the effects of expanding rain forests on the spatial extent of giant eucalypt forests, a forest type commonly with rain forest in the region, and which is considered to be under threat (see Chapter 1, Section 1.2). We expected that if global drivers were also driving rain forest expansion in the Australian humid tropics, the expansion would occur indiscriminately across all environmental conditions.

3.3 Materials & methods

The study area was situated in the Wet Tropics Bioregion, a humid tropical zone in northeastern Queensland, Australia (Fig. 3.1), covering approximately 1.8 million hectares. The area is characterized by a mosaic of naturally and artificially fragmented areas of tropical rain forest interspersed with fire-prone vegetation (e.g. grassland, open eucalypt woodland, and forest (Hopkins *et al.*, 1993; Hilbert *et al.*, 2001)) and pasture and agricultural fields. Rain forest in this region is physionomically and floristically diverse, ranging from species-rich, complex vine forest developed on relatively nutrient-rich, moist but well-drained soils, to

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structurally simple rain forest types on oligotrophic moist soils (Webb, 1959; Webb & Tracey, 1981b).
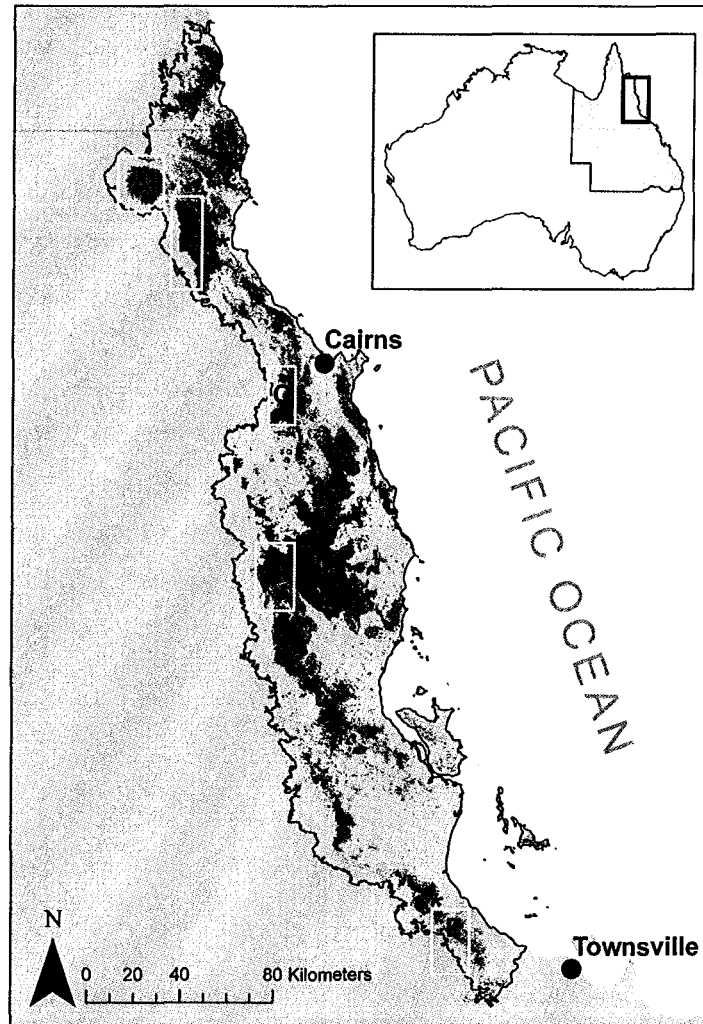
Figure 3.1 – **Selected sites for mapping of rain forest change, denoted by rectangles representing: Mt. Windsor (A), Mt. Carbine (B), Clohesy (C), Koombooloomba (D), and Paluma (E).** Shaded areas denote the mapped extent of rain forest and Wet Tropics Bioregion is represented by a black outline. Weather stations used in the current study are indicated with asterisks, the northern-most being the Mossman Central Mill weather station and the southern-most being the Paluma Ivy Cottage weather station. The inset shows the outline of Australia with the state of Queensland shaded and the bounded rectangle denotes the whole study area.

Prior to European settlement in the 19th and 20th centuries, rain forest covered an estimated 965,000 ha. Subsequent human impacts resulted in a reduction in the area of rain forest to approximately 750,000 ha. Some small areas of rain forest are privately owned, although most of the remaining rain forest areas in northeastern Queensland were secured by the declaration of the Wet Tropics World Heritage Area in 1988 (Lane & McDonald, 2000).

A distinctive feature of uncleared rain forest tracts in the Queensland humid tropics is the occurrence of physiognomically abrupt boundaries between rain forest and eucalypt-dominated vegetation (Unwin, 1989; Harrington & Sanderson, 1994). Giant eucalypt forest formations dominated by tall (>40 m) eucalypts (e.g., *Eucalyptus grandis* and *E. macta*) typically forms a narrow fringe ranging in width from around 300 m to 4 km along the rain forest margins on the western side of the Wet Tropics Bioregion (Harrington & Sanderson, 1994; Harrington *et al.*, 2000). It has been suggested that this forest formation is in danger of being replaced by expanding rain forest (Harrington & Sanderson, 1994; Goosem *et al.*, 1999) making some elements of the biodiversity vulnerable to local extinction. The remainder of the terrestrial vegetation comprises a variable mosaic of low to medium height eucalypt-dominated open forests and woodlands occupying a broad range of freely draining substrates, heaths restricted to shallow, infertile soils, and *Acacia, Lophostemon*, or *Syncarpia* dominated forests.

The sites selected for the current study lie within the upland regions of Mt. Windsor, Mt. Carbine, Clohesy, Koombooloomba, and Paluma (Fig. 3.1; Table 3.1). Vegetation in the five study sites comprises a representative subset of the uncleared vegetation mosaics found within the Wet Tropics Bioregion, which includes rain forest and a range of vegetation types on drier areas. The geology of the five areas was highly variable, but granite and mudstone made up the bulk of the sites, with localized areas of basalt, that has been the predominant target of land clearing (Table 3.1).

Table 3.1 — Details of study sites in the Wet Tropics of Australia.

Study sites	Date(s) of first time period aerial photography	*Area (ha)	Altitude range (m. a.s.l.)	Geology
Mt. Windsor	1951-1955	12137	300-1328	Palaeozoic granite batholiths, Hodgkinson Formation metamorphics and Devonian mudstone
Mt. Carbine	1955	14882	311-1348	Palaeozoic granite batholiths, Hodgkinson Formation metamorphics and Devonian mudstone
Clohesy	1949	11003	350-1310	Lower Permian granites and Devonian mudstone and metamorphic
Koombooloomba	1951	18175	672-1182	Carboniferous acid volcanics, Late Tertiary basalts, Middle Carboniferous granite complexes and Quaternary Colluvium and Alluvium
Paluma	1950	8232	240-1003	Lower Permian to Middle Carboniferous granites and Middle Palaeozoic metamorphic

* denotes the total area of grid cells for each site used in the final analysis

3.3.1 Mapping rain forest change

Available 1950s black and white aerial photos (scales ranging from 1:24,000 to 1:30,000) for the five areas (Fig. 3.1; Table 3.1) were scanned at 1690 dots per inch, orthorectified and stitched to create an orthomosaic. A 30-m horizontal resolution digital elevation model (DEM) (Shuttle Radar Topographic Mission Level 2 data, licensed for use by Geoscience Australia) provided the rectification surface. A color 2008 orthomosaic covering the entire Wet Tropics Bioregion was used as a comparison image for vegetation change, and provided a 0.5-m resolution control layer for spatial referencing and adjustment of the 1950s photography. Features such as drainage lines, rocky outcrops, buildings, and occasionally the center point of a single tree canopy were aligned to corresponding features in the 2008 orthomosaic.

To estimate temporal change, we employed a grid approach and layered 50 m × 50 m cells over each of the five areas for both time periods and attributed each cell for vegetation type. Collectively, all five grid areas encompassed an area of 644.3 km^2. These grid cells were positioned to include both rain forest and eucalypt forest/woodland vegetation across vegetation boundaries. The vegetation for each grid cell was attributed by assigning a status of being either rain forest or "savanna" (defined here as eucalypt forest and other open woodland types), based on canopy openness (closed canopy = rain forest; open canopy = savanna) and discernable understorey components. Individual eucalypts (genera *Eucalyptus* and *Corymbia*), *Lophostemon* and *Syncarpia* can readily be recognized on aerial photographs by a fuzzy canopy, or by the general color in the 2008 orthomosaic. To facilitate the process of vegetation attribution from non-stereo image interpretation, and as an added measure of accuracy, we overlaid a 2008 vegetation map provided by the Wet Tropics Management Authority as an additional guideline for determining vegetation type. Grid cells in which both rain forest and savanna occurred were attributed based on the dominant vegetation type. Grid cell areas that covered bare rock, roads, water bodies, built-up areas, or plantations were excluded from the subsequent analysis.

To determine the linear distance of vegetation change, we selected, for each of the five sites, 100 points on the 1950s rain forest boundary. For each of the 500 points, the distance to the nearest 2008 rain forest boundary was measured.

3.3.2 Correlates of rain forest change

The grid cells used for attributing vegetation type were also attributed for environmental variables including elevation, geology, proximity to water bodies or drainage systems, and distance to rain forest (Table 3.2). We excluded rainfall as it was strongly correlated with elevation. Elevation was calculated from the same DEM used for aerial photo rectification. A topographic position index (TPI; Jenness, 2005) was calculated from the same DEM, using a search radius of 500 m. TPI provides a measure of the difference in elevation of a location and the mean elevation of the

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surrounding area, and is therefore useful for classifying locations as ridges, valleys, etc. The distance from pre-existing rain forest was extrapolated from the grid cells attributed for rain forest in the 1950s.

Table 3.2 - Local environmental correlates deemed to have an influence on rain forest change.

Variable	Description	Hypothesised effect
Aspect	Aspect was incorporated as a composite variable consisting of 'northness' [cosine(aspect)*%slope] and 'eastness' [sine(aspect)*%slope]. Thus, 'northness' and 'eastness' were indices ranging from -1 (steep south or west-facing slope) to 1 (steep north or east-facing slope).	Lower probability of expansion on steeper slopes due to increased fire intensity and reduced moisture trapping, and greater probability of expansion on steeper slopes correlated with topographic protection.
Distance from pre-existing rain forest	Distance (m) from the nearest rain forest patch margin as mapped in the earlier time period (1950s) from the five sites using the first time period orthomosaic.	Declining probability of invasion at points distant from pre-existing rain forest due to limitations on seed dispersal.
Elevation	Elevation (m) above sea level from 30 m resolution DEM.	Greater probability of expansion at higher elevations due higher rainfall and lower evaporation rates.
Geology	Broad classes extracted from Australian Geological Survey 1:250,000 map for the region.	Expansion rates will vary with geology due to differences in fertility and water holding capacity.
Slope	In degrees, calculated from a 30m digital elevation model (DEM).	Lower probability of expansion on steeper slopes, due to higher fire intensity, greater water run off.
TPI	Topographic Position Index (Jenness, 2005) determined for each grid cell of a 30m DEM by calculating the difference between the elevation of the grid cell and the mean elevation calculated from all grid cells in a circular window of radius 500m centred on the cell of interest.	Lower probability of expansion on ridges, due to higher fire activity and lower water availability.
Distance to drainage systems/water bodies	Proximity (m) to water bodies or drainage systems.	Greater probability of expansion close to water due to higher water availability, fire protection and propagule dispersal in water.

3.3.3 Modelling rain forest change

We treated our response variable as binary (i.e., 0 = savanna remained savanna; 1 = savanna changed to rain forest). Models representing all combinations, without interactions, of the seven environmental correlates (Table 3.2) considered to be relevant to rain forest change were constructed as generalized autoregressive error models (GAR_{err}), using a binomial error family with logit link. This type of model was recently developed by Murphy *et al.* (2010) to analyze spatially autocorrelated nonnormal data. It is similar to the simultaneous autoregressive error model for normal data (Cressie, 1993) but can cope with nonnormal data types such as a generalized linear model. This type of spatial model is limited to 4000 observations, so we chose a random sample of our total dataset. Because virtually no conversion from savanna to rain forest occurred >1 km from a rain forest boundary, we selected 4000 points from within this distance. We confirmed that the GAR_{err} models successfully accounted for residual spatial autocorrelation using correlograms based on Moran's I (Dormann *et al.*, 2007).

Models were evaluated using the Bayesian Information Criterion (BIC), a model selection index favoring both model fit and model simplicity (Burnham & Anderson, 2002). BIC is analogous to the more widely used Akaike Information Criterion (AIC), but tends to penalize complex models more heavily than AIC. Hence, it tends to be more appropriate for large datasets where the main underlying drivers are of primary interest (Link & Barker, 2006). Lower values of BIC indicate greater support for a model, relative to other models in the same candidate set. From BIC, evidence weights (w_i) were calculated for each model and these are equivalent to the probability of a given model being the best in the candidate set. The importance of each variable was evaluated by calculating w_+, the sum of w_i for all models in which that variable occurred. For each variable, w_+ is equivalent to the probability of the best model containing that variable, and is a useful expression of the weight of evidence for the importance of the variable. We considered that w_+ values of < 0.73 were indicative of substantial model selection uncertainty, and that a relationship between the response and the explanatory variable in question was not well

supported by the data. A w_+ value of 0.73 is equivalent to a BIC difference of two units between the models containing the variable under examination and those not containing it. A difference of two units is a common "rule of thumb" used in ecological studies to assess evidence of an effect (Richards, 2005).

We also performed a *post hoc* test to determine the effect of vegetation type (i.e., giant eucalypt forest vs. dry eucalypt forest: Queensland Herbarium, (2009)) on the probability of conversion to rain forest. Using BIC, we compared the best model from the a priori candidate set, with the same model incorporating a term representing vegetation type.

3.3.4 Projected rain forest expansion into giant eucalypt forest

Using standard GIS functions, a 100-m square lattice of points was generated across the entire extent of giant eucalypt forest in the Wet Tropics Bioregion, as per Queensland Regional Ecosystems vegetation mapping (Queensland Herbarium, 2009), and the distance from preexisting rain forest was calculated for each point. Using a geographically weighted estimate of the rate of boundary expansion from the five study sites, we estimated the proportion of giant eucalypt forest remaining over various time periods up to 2000 years. Using a weighted average of the linear boundary change allows for a more realistic analysis, as it takes into account the variation in mean linear boundary change across the five study sites. We considered this modelling exercise conservative and representative of a "worst-case-scenario" in terms of giant eucalypt forest loss, as it assumes: (i) there will be no landscape scale perturbances at the rain forest margins (e.g., droughts, natural fires, or cyclonic damage) that might affect the rate of rain forest expansion, (ii) rain forest expansion will advance across the landscape unchecked by preexisting geographical or climatic barriers, and (iii) giant eucalypt forest – eucalypt woodland boundaries are static and giant eucalypt forest does not advance ahead of the advancing rain forest.

3.4 Results

3.4.1 Changes in rain forest area and linear spread

At all five study sites our results show that most boundaries remained stable, but where change occurred, rain forest expanded into surrounding savanna (Fig. 3.2; Table 3.3) with a net rain forest expansion of 732 ha. The extent of rain forest expansion was greatest at Mt. Windsor (8.5%) and least at Paluma (0.8%). Conversion of rain forest to savanna was negligible.

In terms of linear boundary shifts, 25% of the 500 paired sampling points across the five sites exhibited change in the location of rain forest boundaries (Fig. 3.2). Across all sites, most of the boundaries showed that rain forest expansion was less than 30 m since the 1950s (Fig. 3.2), and at an average rate of 0.6 m per year. Comparatively, savanna expansion was very limited (Fig. 3.2).

3.4.2 Correlates of change

There was a very strong effect of distance from the original rain forest boundary on the probability of conversion of savanna to rain forest. The probability (w_+) of "distance to rain forest" appearing in the best model of savanna conversion was >0.99 (Fig. 3.3; Table 3.4). Little savanna situated more than 200 m from a rain forest boundary became rain forest. No other variables had any clear effect on the probability of conversion from savanna to rain forest (Table 3.4). Out of 256 models generated, the best model of savanna conversion ($w_i = 0.91$) explained 32% of the residual deviance at the five sites combined.
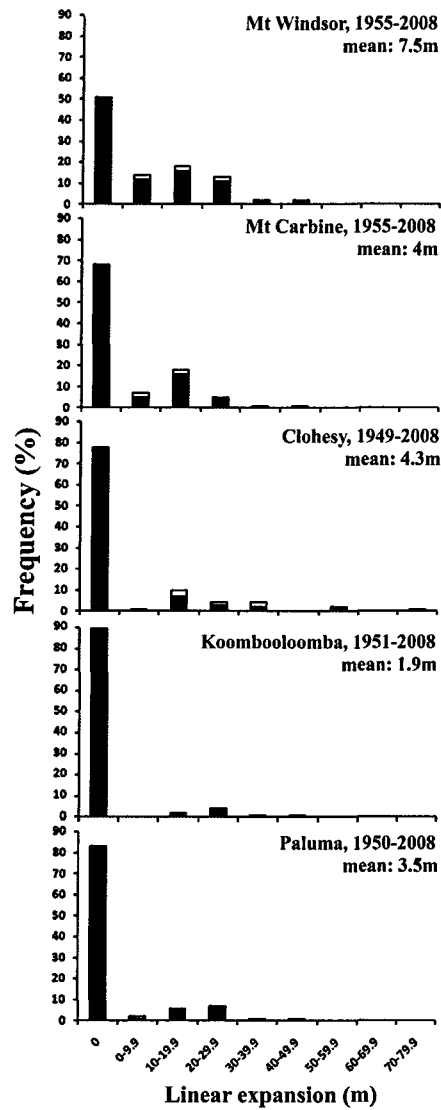
Figure 3.2 - Linear expansion of the rain forest margins on the five study sites as measured from 100 random paired points from each site. Black bars denote points where the rain forest boundary had expanded in 2008; and white bars denote points where the savanna boundary has expanded. The mean decadal linear rain forest expansion (m) over the study period is indicated for each site.
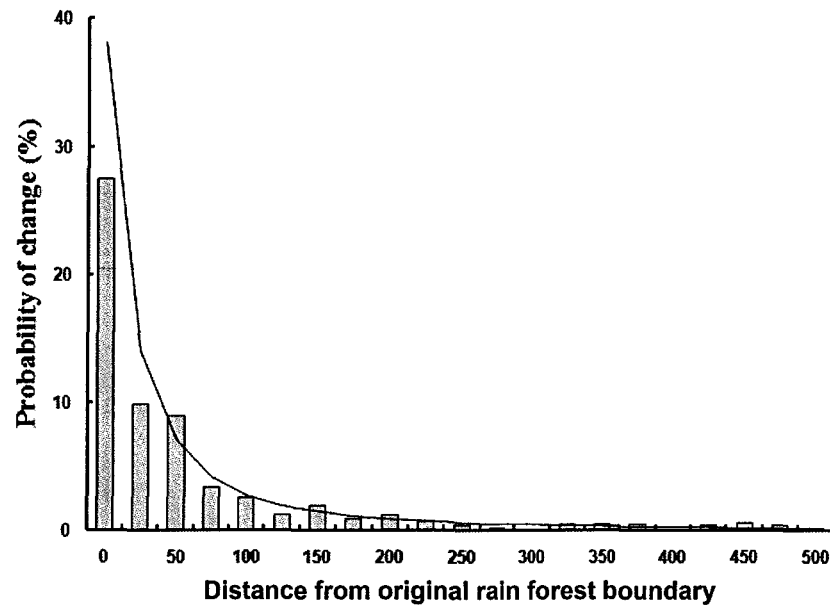
Figure 3.3 - The observed (bars) and predicted (line) probabilities of conversion of savanna to rain forest in relation to distance to the original rain forest boundary. The model predictions are based on multimodel averaging of the entire candidate set of models, weighted according to w_i and assuming mean values for all other variables.

Table 3.3 - Change in area extent of rain forest and savanna in the five study sites from the 1950s to 2008.

	Year	Rain forest area (ha)	Savanna area (ha)	Proportional change (Rain forest to Savanna) (%)	Proportional change (Savanna to Rain forest) (%)	Net change in rain forest area (%)
Mt. Windsor	1950s	4356	7781	0.8	5.2	8.5
	2008	4724	7413			
Mt. Carbine	1955	5232	9650	0.8	1.3	1.6
	2008	5313	9569			
Clohesy	1949	5075	5929	0.1	1.6	1.8
	2008	5165	5839			
Koombooloomba	1951	5159	13016	2.6	2.3	3.1
	2008	5319	12856			
Paluma	1950	4224	4008	0	0.8	0.8
	2008	4257	3975			
Combined	1950s	24046	40384	0.9	2.2	3.2
	2008	24778	39652			

Table 3.4 - Importance values (w_+) of environmental predictors of combined rain forest expansion at the five study sites, based on the Bayesian Information Criterion (BIC). 'w_+' can be interpreted as the probability of that variable being in the best model. As a 'rule of thumb', values of w_+ ≥0.73 (shown in bold) can be interpreted as clear evidence of an effect (Richards, 2005).

Variable	$w+$
Distance to pre-existing rain forest	**>0.99**
Topographic position index	0.04
Elevation	0.02
Slope	0.02
Geology	0
Distance to drainage	0.02
Aspect	0

Our analyses on the effect of vegetation type on the probability of rain forest expansion show that rain forest was more likely to expand into adjacent giant eucalypt forest than into other woodland types. The difference between rain forest expansion into giant eucalypt forest and other woodland types was significant (ΔBIC > 2), although the magnitude of the difference was not large (Fig. 3.4).
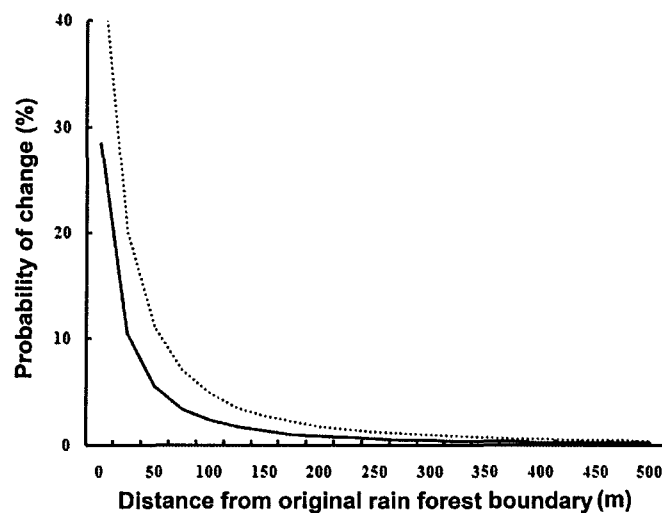
Figure 3.4 - The probabilities of conversion of giant eucalypt forest (dashed line) and other dry forest types (unbroken line) into rain forest in relation to distance to the original rain forest boundary.

3.4.3 Projected rain forest expansion into giant eucalypt forest

We project that after 100 years of rain forest expansion, there would be over 85% of giant eucalypt forest area remaining (Figs. 3.5, 3.6). The sharpest decrease in giant eucalypt forest extent is predicted to occur within the first 250 years, during which 30% of giant eucalypt forest area would be engulfed by rain forest. Expansion of rain forest into giant eucalypt forest is predicted to slow after the first 250 years, and after 2000 years there is still more than 25% of the original area of giant eucalypt forest remaining (Fig. 3.6).
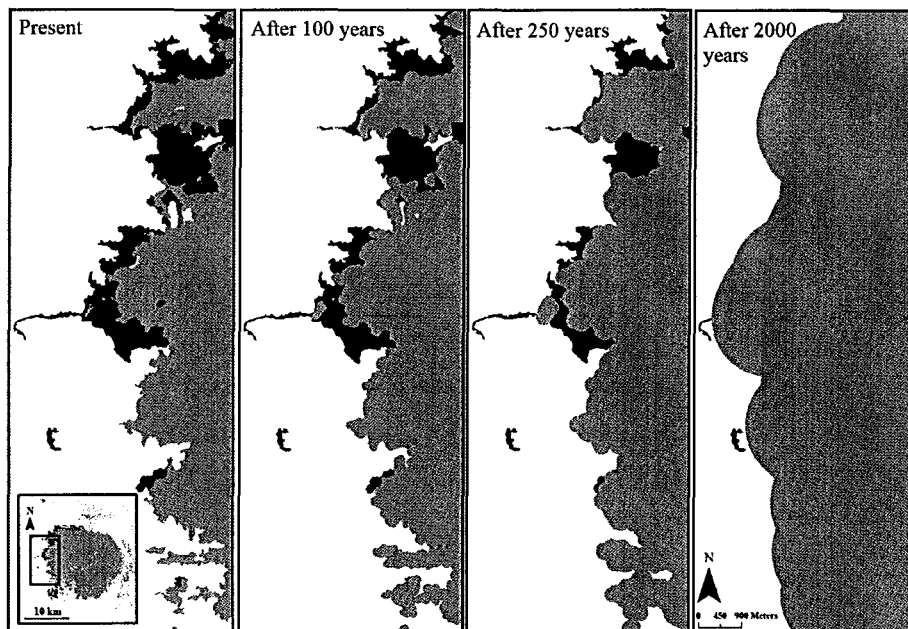
Figure 3.5 - Projection of the engulfment of giant eucalypt forest (dark grey) by rain forest (light grey) at Mt. Windsor after 100, 250 and 2000 years, based on an average rain forest expansion rate of 6 m decade^{-1}. Inset shows the Mt. Windsor study site (Fig. 3.1) and the bounded area is the selected area for illustrating the time series. Note how the irregular shape of the giant eucalypt forest patches slows the rate of rain forest engulfment.
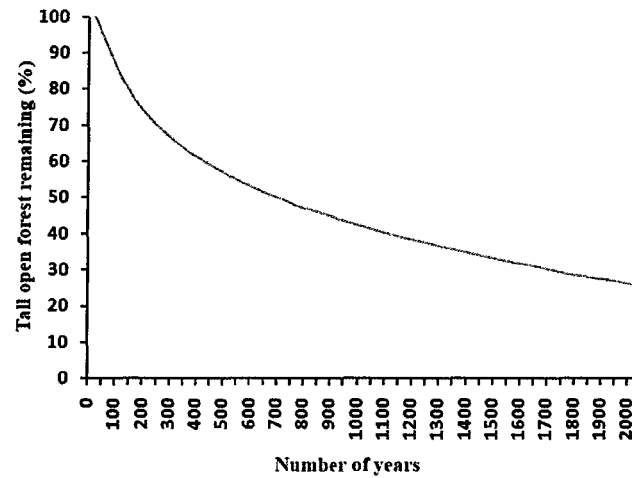
Figure 3.6 - The extent of giant eucalypt forest predicted to be engulfed by rain forest over time. Predictions are based on an average rain forest expansion rate of 6 m decade^{-1}.

3.5 Discussion

Although most rain forest boundaries in our study were stable over a 60-year period, those that did change all expanded into surrounding eucalypt forest and savanna resulting in a regional increase in rain forest. Such rain forest expansion has been documented in other studies throughout the tropics of Australia (Table 3.5). Indeed, visual comparison of the historical aerial photographs showed that there was also a general increase in cover throughout our study region (data not shown). This is in agreement with the findings of Johansen & Phinn (2005), who reported increased woody vegetation cover in the Wet Tropics Bioregion inferred from Landsat TM/ETM+ imagery from 1988 to 1999, and with reports of savanna thickening in other parts of Australia (Burrows *et al.*, 2002; Fensham & Fairfax, 2003; Lehmann *et al.*, 2008) and worldwide (Singh & Joshi, 1979; Cabral *et al.*, 2003; Britz & Ward, 2007; Wigley *et al.*, 2010).

Unwin (1989) measured rain forest boundary dynamics on a transect in the Herberton highlands (near the Clohesy study site in the current study) over a 10-year study period, and estimated that rain forest was expanding at 1 m year^{-1}, which is

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similar to our upper estimate (45 m in 53 years, equivalent to 0.8 m year^{-1}).

However, our results suggest that on a broader landscape scale, rain forest expansion typically occurs at a much slower rate (Fig. 3.2; Table 3.3).

Table 3.5 - Summary of literature on rain forest expansion in Australia.

Location	Reference
Kakadu, Northern Territory	Banfai & Bowman (2005, 2006, 2007); Bowman & Dingle (2006)
Litchfield National Park, Northern Territory	Bowman et al. (2001)
Gulf of Carpentaria, Northern Territory	Brook & Bowman (2006)
Cape York Peninsula, Queensland	Russell-Smith et al. (2004b)
Atherton, Queensland	Harrington & Sanderson (1994)
Herberton, Queensland	Unwin (1983, 1989)
Kirrama, Queensland	Harrington & Sanderson (1994)
Mossman, Queensland	Lawson et al. (2007)
Mt Spurgeon, Queensland	Harrington & Sanderson (1994)

Our spatially explicit modelling approach showed that expansion occurred indiscriminately on all geologies and at all elevations, although the rate and amount of expansion varied among the five sites. The reasons for the different extent of rain forest expansion between the five sites could not be explained by the set of environmental variables used in our analyses. Past logging of giant eucalypt forest and rain forest (Crome et al., 1992) does not appear to have influenced rain forest expansion, given that rain forest expansion was found on all sites regardless of logging history. For instance, the Mt. Carbine site has not been logged but still exhibited rain forest expansion. Nonetheless, rain forest was found to exhibit a higher probability of expansion into giant eucalypt forest (Fig. 3.4) than into more open forest and woodland types. This was expected, as the environment in giant eucalypt forest is probably more amenable to rain forest regeneration (Unwin, 1989). That rain forest expanded into both giant eucalypt forest and other woodland types, albeit more slowly than into woodland types, bolsters our conclusion that this process occurs indiscriminately throughout the study area.

Our statistical modelling showed that the only significant correlate of rain forest expansion was distance to preexisting rain forest. This finding is concordant with Banfai *et al.* (2007) who demonstrated that monsoonal rain forest expansion in Kakadu was most strongly correlated with distance to preexisting rain forest. Contrastingly, field surveys undertaken by Russell–Smith *et al.* (2004a) suggests that rain forest in the Iron Range region of Cape York also expands via a process of "nucleation" around focal trees in the savanna leading to an eventual rain forest "irruption" via coalescence of nuclei. It is possible that successional processes such as nucleation and irruption are difficult to quantify using GIS methods, particularly when such successional processes are in the early stages.

Our findings are broadly consistent with a diversity of localized studies in northern Australia (Table 3.5). Ash (1988) argued that rain forest boundaries in the Wet Tropics are strongly controlled by environmental factors, such as geological disjunctions and precipitation gradients, which results in their stability. Topography can also provide "fire shadows" to protect rain forest from frequent fires that occur in eucalypt savannas (Webb, 1968; Bowman, 2000). Russell-Smith *et al.* (2004b) found rain forest expansion in the Iron Range on eastern Cape York Peninsula across all geologies sampled, but they also detected a higher probability of rain forest expansion on more fertile geologies. Harrington & Sanderson (1994) reported rain forest expansion in the Mt. Spurgeon area (part of the Mount Carbine region in the current study) using visual interpretation and manually delineating vegetation types from aerial photography taken in the 1940s to the 1990s.

Harrington & Sanderson (1994) suggested that the expansion of rain forest into giant eucalypt forest is a threatening process to native mammals such as the Yellow-bellied Glider (*Petaurus australis*) and Brush-tailed Bettong (*Bettongia tropica*) that occur in giant eucalypt forest habitats. Their work sparked concern for the fate of these forests and led to calls for managers to use fire to limit rain forest expansion. However, our projections of rain forest expansion show that these giant eucalypt forests will largely remain intact within the next century, and will still persist within the next 2000 years (Fig. 3.5, 3.6). The initial steep rate of rain forest engulfment in

the first 250 years (Fig. 3.5, 3.6) represents the infilling of embayments of giant eucalypt forest existing near the rain forest margins. It is important to note that our analysis was based on the very unlikely scenario that the region would remain undisturbed by landscape fires, and therefore represents an exaggeration of the actual trajectory of rain forest expansion. There is no doubt that some combination of tropical cyclones, droughts, and landscape fires within the next 2000 years will push back at least some rain forest margins, and stimulate large-scale natural regeneration of giant eucalypt forest that is generally thought to depend on disturbance for regeneration (Ashton, 1981, Adam, 1992). Further, even if all the giant eucalypt forest understoreys currently have a rain forest understorey, the decline of the overstorey eucalypts, particularly those dominated by *E. grandis*, may take another couple of centuries, given the inherent longevity of giant eucalypt forest eucalypts (e.g., 500 years in *E. regnans* (Wood *et al.*, 2010), a eucalypt species similar to *E. grandis* in habit and regenerative strategies). Moreover, it is possible that *E. grandis* forests are unstable ecotonal states that will shift spatially as the rain forest expands outwards (Warman & Moles, 2009).

It has been suggested that European colonization and related pastoral activities may have altered the fire regimes previously affected by aborigines and lightning strikes (Unwin, 1983, 1989; Ash, 1988). If fire suppression since European colonization was a key driver of rain forest expansion, we would expect a clear signal of expansion from fire-protected areas near drainage systems, or topographically protected areas (e.g. Brook & Bowman, 2006), rather than the trend of indiscriminate expansion. Further, the palynological record shows that Aboriginal landscape burning was unable to stop the climate-driven expansion of rain forest at the commencement of the Holocene (Haberle, 2005), supporting our view that changed fire regimes are not the explanation for the expansion of rain forest.

Several global drivers of vegetation change have recently been proposed: increased temperature, rainfall, atmospheric nitrogen deposition, and atmospheric CO_2 concentrations. In savannas, rainfall, rather than temperature, is more likely to influence tree cover, particularly during extreme events such as prolonged droughts

(Fensham *et al.*, 2005). Likewise, humid tropical forests depend on abundant and regular water supply and drying trends can result in forest retraction (Behling, 2002; Pennington *et al.*, 2004; Silva *et al.*, 2009). Mean annual rainfall for northeastern Queensland in the last decade fell by more than 2% compared to the previous 30 years (Queensland Government, 2011), suggesting that a wetting trend is not responsible for the rain forest expansion.

Atmospheric nitrogen deposition is another candidate driver of vegetation change (Pearson & Steward, 1993). However, the magnitude of atmospheric nitrogen deposition, and the effects, if any, on the terrestrial vegetation has not been studied in Australia and there is no regional source for this pollution, unlike many regions in the northern hemisphere. Also, atmospheric nitrogen deposition has been found to have a more significant effect on species composition within ecosystems, rather than large increases in biomass (Matson *et al.*, 2002; Bobbink *et al.*, 2010).

With the exclusion of rainfall, temperature effects, and nitrogen deposition, the most parsimonious explanation for the indiscriminate rain forest expansion in the current study is the increase in atmospheric CO_2, consistent with earlier explanations of landscape-scale rain forest expansion in the Australian monsoon tropics (Banfai & Bowman, 2005, 2006, 2007) and elsewhere (Wigley *et al.*, 2010). Bowman *et al.* (2010) suggest that rain forest expansion is a signal of global environmental change that is so strong that it is overwhelming any retardant effect fire might have on rain forest. The implications of this vegetation shift from flammable savanna and eucalypt forest to rain forest are significant not only at a local scale for biodiversity and management, but may constitute an important carbon cycle feedback at a global scale. Continued rain forest expansion in tropical regions worldwide could possibly instigate a cascade of feedbacks resulting in further land cover changes due to changes in carbon sequestration, albedo, evapotranspiration, fire incidence, cloud nucleation among others (Wigley *et al.*, 2010), and has the potential to significantly alter the earth system within a relatively short time frame.

Chapter 4

Phosphorus limits *Eucalyptus grandis* seedling growth in an unburnt rain forest soil

4.1 Summary

Rain forest is characterized as pyrophobic. Paradoxically, pyrophilic giant eucalypts in Australia grow in association with rain forest. In temperate Australia, giant eucalypts that co-occur with rain forest depend on extensive, infrequent fires to produce suitable edaphic conditions for regeneration. Little is known, however, about the regeneration of giant eucalypts co-occurring with tropical rain forest. We tested whether regeneration of a tropical giant eucalypt species was constrained edaphically similar to its temperate counterparts, and we hypothesized that phosphorous fertilization would alleviate edaphic constraints. We grew *Eucalyptus grandis* seedlings in a factorial experiment combining fumigation (to simulate soil pasteurization by fire without modifying chemical composition), soil type (rain forest versus *E. grandis* forest soil) and phosphorus fertilization as factors. We found that: (i) phosphorus is an important limiting factor *E. grandis* seedling survival and growth in rain forest soil; and (ii) fumigation enhances survival and phosphorus nutrition of seedlings in both *E. grandis* forest and rain forest soils. Similar to temperate giant eucalypts, mineral nutrient and biotic attributes of an ambient tropical rain forest soil can hamper *E. grandis* seedling establishment. *E. grandis* regeneration requires conditions akin to a fire-generated ashbed (i.e., an "ashbed effect").

4.2 Introduction

Fire is an important phenomenon that influences the dynamics and evolution of many vegetation systems worldwide (Whelan, 1995; Bond *et al.*, 2005; Bowman *et al.*, 2009). In a number of ecosystems such as some coniferous forests of circumpolar regions (Stocks, 2004; Body *et al.*, 2010), various giant coniferous forests of the Pacific Northwest of the United States (Franklin & Hemstrom, 1981; Agee, 1993), and giant eucalypt forests in temperate Australia (Ashton & Attiwell, 1994; Tng *et al.*, 2012c), regeneration depends primarily on high intensity fires resulting from high fuel loads and rare episodes of severe fire weather. As well as removing dense

understories and reducing plant competition such fires can modify the physical, chemical and biological properties of the soil (Certini, 2005) in ways that promote the early growth of the regenerating forest. This potential growth-promoting effect of fire has been documented for several forest types throughout Australia (Hatch, 1960; Pryor, 1963; Humphreys & Lambert, 1965; Renbuss *et al.*, 1973).

Regeneration promotion by fire – an 'ashbed effect' – typically is characterised by an ash-rich germination medium high in plant-available nutrients together with an abundance of safe sites for germination and establishment (Pryor, 1963; Loneragan & Loneragan, 1964; Humphrey & Lambert, 1965). The burning of established vegetation and litter potentially increases the number of safe sites by: (i) altering soil characteristics, for example, reducing bulk density and thereby increasing water availability (Certini, 2005; Boerner *et al.*, 2009); (ii) denaturing residual plant toxins or inhibitory compounds (Christensen & Muller, 1975; May & Ash, 1990); (iii) removing potentially competing surrounding vegetation (Ashton, 1986); (iv) eliminating other biological opposition to recruitment, such as that by soil-litter microorganisms and pathogens (e.g. Florence & Crocker, 1962; Ellis & Pennington, 1992); and (v) potentially disrupting common mycorrhizal networks (Janos *et al.*, 2013). Elimination of inhibitory soil factors may be especially important as suggested by soil from an old-growth *Eucalyptus regnans* forest retarding the growth of *E. regnans* seedlings (Ashton & Willis, 1982) and soil from temperate rain forest inhibiting *Eucalyptus delegatensis* R.T.Baker seedlings (Ellis & Pennington, 1992).

In Australia, most studies of the effects of intense fires on forest regeneration have been conducted in temperate ecosystems, mostly in mesic regions, but also in seasonally dry, mediterranean-climate communities such as that of the Karri (*Eucalyptus diversicolor* F.Muell.) (Loneragan & Loneragan, 1964) and the Tuart (*Eucalyptus gomphocephala* DC.) (Ruthrof *et al.*, 2002). *E. regnans*, the world's tallest angiosperm, provides a classic example of the importance of intense fires for producing conditions suitable for regeneration (Gilbert, 1959; Cunningham, 1960; Chambers & Attiwell, 1994). *E. regnans* inhabits highly productive mesic environments in southeast Australia, and is a fast-growing, obligate seeder which can

achieve half its final mature height within 25–35 years (Jackson, 1968; Ashton, 1976). As *E. regnans* forest matures, the understorey becomes dominated by closed-canopy rain forest which is inimical to subsequent regeneration by the shade-intolerant *E. regnans* (Ashton, 1981a). Thus, in both natural and silvicultural settings, *E. regnans* is highly dependent for regeneration on infrequent, high intensity fires which produce an ashbed and removes the closed forest canopy (Van der Meer *et al.*, 1999; Bauhus *et al.*, 2002). In mesic, temperate regions, massive regeneration by other giant eucalypts (*sensu* Tng *et al.*, 2012c) such as *E. delegatensis*, *E. obliqua* L'Hér. and *E. pilularis* Sm., similarly relies on ashbeds produced by intense fires (Floyd, 1962; O'Dowd & Gill, 1984; Ashton & Attiwell, 1994).

Because temperate giant eucalypt forests typically comprise understories of fire-sensitive rain forest species (Tng *et al.*, 2012c), these forests' dependence on intense fires for eucalypt regeneration is somewhat paradoxical. The association of rain forest species with giant eucalypts in mesic, temperate regions is thought to be a consequence of natural succession (Gilbert, 1959; Jackson, 1968): high intensity fires enable the giant eucalypts to regenerate after which rain forest species establish as an understorey beneath their emergent canopies (Bowman, 2000; Tng *et al.*, 2012c).Somewhat in contrast to the well documented, mesic, temperate zone patterns, in the humid tropics of North Queensland, *E. grandis* W.Hill ex Maiden occurs as a canopy dominant within an ecotonal band that separates rain forest from savanna (Unwin, 1989; Harrington *et al.*, 2000). Nevertheless, Bowman (2000) and Tng et al. (2012c) have suggested that the tropical *E. grandis* forests may be ecologically similar to temperate giant eucalypt forests in requiring high intensity fires for regeneration (Duff, 1987).

Regeneration of *E. grandis* forests is a matter of considerable current interest because of their uniqueness (Tng *et al.*, 2012c) and because they can contain threatened species of conservation importance. Interest is heightened by concern that *E. grandis* forests might be at risk of being replaced by rain forest. Contemporary trends of rain forest expansion often are at the expense of *E. grandis* forest (Harrington & Sanderson, 1994; Tng *et al.*, 2012d), perhaps because the natural high intensity fires

upon which *E. grandis* regeneration depends are rare in the tropics (Little *et al.*, 2012; Tng *et al.*, 2012c). Understanding the regeneration of *E. grandis*, however, currently is hampered by a lack of experimental evidence on the importance of ashbeds. In particular, it is not known whether tropical rain forest soil inhibits *E. grandis* seedlings in the absence of an ashbed.

The aim of this study was to compare the effects of one tropical rain forest soil versus a nearby *E. grandis* forest soil on the survival and growth of *E. grandis* seedlings. Because it is not practical to experimentally expose soils to high intensity fire, we used methyl-bromide soil fumigation to simulate partial sterilization and nutrient release by fire without modifying soil structure (Chambers & Attiwell, 1994; Bowman & Fensham, 1995). We examined the growth of *E. grandis* seedlings in fumigated and non-fumigated soils from both tropical rain forest and *E. grandis* forest. Because fumigation may release plant available nitrogen and phosphorus (Weston & Attiwell, 1990; Chambers & Attiwell, 1994; Serrasolsas & Khanna, 1995) and may eliminate soil pathogens (Ridge, 1976; Ebben *et al.*, 1983), we predicted that: (i) the survival and growth of *E. grandis* seedlings would be greater in fumigated *E. grandis* forest soil than in non-fumigated soil and would exceed that in rain forest soil, and (ii) inhibitory effects of rain forest soils can be alleviated by phosphorus addition.

4.3 Materials & methods

4.3.1 Soil preparation and analysis

We collected soil from two forest types, a *Eucalyptus grandis* forest and an adjacent tropical rain forest at Davies Creek, Far North Queensland (17°1'30" S, 145°35'46" E) in May, 2010, at the beginning of the dry season. This area also was sampled by Warman *et al.* (2013) for their comparison of Queensland forest soils, and thus their work provides a context within which the soils that we used for seedling performance comparisons can be placed.

Although both the *E. grandis* forest and the tropical rain forest were underlain by granite, the two forest types differed drastically in light environment, floristics and fire risk (Turton & Duff, 1992; Little *et al.*, 2012). The *E. grandis* forest was tall-statured, with an even but open canopy (~35 to 50 % canopy cover) ranging from 40 to 45 m in height, and an understorey dominated by a mix of grasses together with herbaceous and shrubby rain forest pioneers. The adjacent rain forest was simple notophyll vine forest (Webb, 1959) which principally comprised primary rain forest species. It had a closed canopy (~75 % canopy cover) ranging from 20 to 35 m in height, and was more species rich than the *E. grandis* forest.

Within each forest type, we collected 60 kilograms of the top 15cm of soil excluding leaf litter from three places approximately a meter apart and then thoroughly mixed the soil of each forest type separately to homogenize it. The soil was not sieved in order to minimize changes in texture. Half of the soil from each forest type was fumigated with methyl-bromide gas at a rate of 64 g/m^3 for 24 hours in porous sisal bags, each of which was approximately 30 cm high when filled and laid on its side. Fumigation by methyl-bromide was chosen because it can release plant-assimilable N and P (Eno & Popenoe, 1964), thereby mimicking that aspect of fire (Bowman & Fensham, 1995) in addition to killing both pathogenic and beneficial microbes. The soil was aired inside a shelter for one week before use.

To determine the mineral nutrient contents of each soil type both before and after fumigation, samples were sent to a commercial soil laboratory in Western Australia for analysis. There, ammonium and nitrate were extracted in KCl; P (Colwell) in sodium bicarbonate; soil pH and electrical conductivity were determined in a 1:5 soil:water extract; Cu, Fe, Mn and Zn in a DTPA extract; and Ca, Mg, K and Na in an ammonium chloride extract. Additional samples of each soil were sent to the School of Plant Biology, University of Western Australia for analyses of plant-available inorganic phosphorus (P_i) by anion exchange membrane (AEM) extraction (Nuernberg *et al.*, 1998).

To compare the effect of fumigation with that of burning, we opportunistically collected ambient and burnt soil for AEM P_i analysis from another *E. grandis* forest near Ravenshoe, Queensland (17°39'24" S, 145°30'35" E) that is physiognomically similar to the Davies Creek forest, but which was affected by a wildfire in September, 2012. At the Ravenshoe site, we collected a total of three kilograms of the top 15cm of soil excluding leaf litter from three places approximately a meter apart and then thoroughly mixed the soil from burned and unburnt *E. grandis* forest separately to homogenize it.

4.3.2 Seedling growth

Eucaly*ptus grandis* seeds from naturally occurring populations in North Queensland were not available for the experiment, so we obtained seeds from a plantation south of Grafton, on the east coast of New South Wales, Australia. Seeds were sown onto a shallow tray containing fumigated *E. grandis* forest soil on May 16, 2011. Germination occurred within a week. Two weeks after germination, seedlings were transplanted (one per pot) into 10 cm diameter pots containing 600 cm^3 of soil. Care was taken to ensure that seedling root systems were not damaged during transplant. Initially, four treatments of 60 plants each were established: fumigated *E. grandis* forest soil; non-fumigated *E. grandis* forest soil; fumigated rain forest soil; and non-fumigated rain forest soil. Subsequently, half of the surviving plants in each treatment were fertilized with phosphorus to constitute a fully-crossed, three-factor experiment with soil type (rain forest versus *E. grandis* forest soils), fumigation (or not), and P addition (or not) as factors.

At 86 days after transplant (DAT), we began P addition. In order to equalize seedling sizes between P-fertilized and not fertilized groups within treatments, the surviving plants from each initial soil type × fumigation treatment were rank-ordered by height, and every second seedling was assigned to be fertilized weekly with 15 ml of 0.8 mg/ml P. The P solution was prepared by diluting triple superphosphate in water. No other fertilizer was added.

After transplant, pots were arranged on a metal rack supported 70 cm above ground under ambient outdoor conditions in Cairns, Queensland (16°51'03" S, 145°44'53" E), and were watered daily during the dry season with tap water as needed to maintain the soil near field capacity. Pots containing fumigated and non-fumigated soils were arranged in separate blocks 100 cm apart to minimize potential movement between treatments of arbuscular mycorrhizal fungus spores by water splash. No microbial filtrate (Koide & Li, 1989; Allen *et al.*, 1993) was added to any of the soils. The pots were rearranged within blocks every three weeks to mitigate position effects. Weeds and invertebrate herbivores were removed manually upon detection. Native weeds only were found in pots of non-fumigated soil, attesting to successful fumigation.

Beginning immediately after transplant, we measured seedling height from the soil surface to the shoot apex, censused mortality, and also tabulated mineral nutrient deficiency symptoms based on leaf colour (Dell, 1996) at irregular, 20–33 d intervals. Final growth measurements and leaf colour assessments were made at 146 DAT when the experiment was harvested. We decided to harvest the experiment at that time because 13 seedlings exhibited symptoms of damping off or abnormal leaf development. All aboveground shoot tissues (shoots including all stems and leaves) were harvested, dried in an oven at 60° C for one week and weighed. After weighing, the shoots were ground to powder and analysed for total nitrogen and phosphorus at the School of Plant Biology, University of Western Australia. At least 0.2 g of ground shoot was needed, but because many small plants provided insufficient tissue individually, we combined plants within treatments by quantiles of seedlings rank-ordered by height within each treatment. This resulted in three composite samples from the non-fertilized, fumigated rain forest soil treatment, five from the non-fertilised, non-fumigated rain forest soil treatment, and eight from each of the other six treatments (in which the largest plants were found). Thirteen seedlings that exhibited pronounced symptoms of disease were excluded from the analyses. These seedlings were distributed relatively evenly among the eight treatments and therefore unlikely to bias comparisons between treatments.

4.3.3 Mycorrhiza assessment

After harvesting above ground shoot tissues at 146 DAT, we extracted the fine roots of six randomly-selected plants per treatment by gentle rinsing over a 2 mm sieve, and we preserved the roots in 50 % ethanol for later assessment of mycorrhizas. Subsequently, the preserved roots were cleared in 10 % KOH at room temperature for 48 h and then stained in 0.05 % trypan blue in lactoglycerol. For each plant sample, we mounted ten, 1–2 cm root pieces including lateral, ultimate rootlets on microscope slides and checked for the presence of ectomycorrhizas or, in their absence, arbuscular mycorrhizal fungi (typical hyphae and vesicles in the root cortex) with a compound microscope at 200-times magnification. We used the magnified gridline intersection method (McGonigle *et al.*, 1990) with assessment of 100 intersections per seedling as a basis for quantifying mycorrhizas.

4.3.4 Data analysis

Because we submitted only single samples of our homogenized, non-fumigated and fumigated *E. grandis* forest and rain forest soils for physicochemical analyses, we compared them by two-way analyses of variance (ANOVA) using the interaction terms as estimators of error. Because of the limited power of these analyses, we did not Bonferroni-correct for the number of soil parameters examined.

The onset of P addition at 86 DAT divided our experiment into two time segments that we analysed separately. The effects of soil type and fumigation were analysed from seedling transplant to 86 DAT, and the effects of soil type, fumigation and P addition were analysed from 86 DAT to harvest at 146 DAT. To test for differences in survival and foliar P-deficiency symptoms among treatments, we used two-way, factorial logistic regressions against soil type and fumigation for the initial 86 DAT, and three-way, factorial logistic regressions with soil type, fumigation and P addition as factors from 86 to 146 DAT. For the survival analysis, we used all seedlings that were surviving including those that were diseased. For foliar P deficiency symptoms, 209 surviving seedlings at 86 DAT and 193 surviving and non-diseased seedlings at

146 DAT were analyzed. For the 146 DAT analyses, we used the number of seedlings out of those 193 surviving and non-diseased seedlings which had changed from markedly purple to green as the response variable. These logistic regression results are reported as χ^2 values and their associated probabilities.

To analyse the effects on seedling height of soil type, fumigation and their interaction prior to fertilisation, we analysed height at 86 DAT with a two-way ANOVA by using the aov function of R (Version 2.7.1, R Development Core Team, 2004). For growth from 86 DAT to 146 DAT, we performed a three-way ANOVA on a log-transformed height ratio that was obtained by dividing the seedling height at 146 DAT by that at 86 DAT. Tukey's honestly significant difference (HSD) tests with $P \leq 0.05$ were used to identify differences among treatments.

For harvest data, the effects of soil type, fumigation, P addition and their interactions on aboveground shoot dry weight, aboveground shoot N and aboveground shoot P concentrations were analysed by three-way ANOVA. Tukey's HSD tests with $P \leq 0.05$ were used to compare treatment means. For the dry weight analyses there were 193 seedlings, but for the N and P concentrations 56 composited quantiles represented those 193 seedlings.

4.4 Results

4.4.1 Soil analysis

We detected no significant differences between *E. grandis* forest soil and rain forest soil when fumigated or not for ammonium, Colwell P, AEM P_i, conductivity, extractable Cu, Fe, exchangeable Al or Na (Table 4.1). In spite of the limited power of our statistical analyses, however, Mn was significantly higher in *E. grandis* forest soil than in rain forest soil, but was significantly diminished by fumigation. In contrast, both measures of pH were significantly higher for rain forest soil than for *E. grandis* forest soil, and fumigation elevated pH in both soils. Although not affected significantly by fumigation, exchangeable Mg and marginally significantly ($F_{1,3}$ =

70

137.3, $P = 0.0542$) exchangeable Ca were higher in rain forest than in *E. grandis* forest soil, consistent with the pH difference between the soils. Also marginally significantly higher in rain forest than in *E. grandis* forest soil were nitrate ($F_{1,3} = 112.36$, $P = 0.0599$), Zn ($F_{1,3} = 75.94$, $P = 0.0727$) and exchangeable K ($F_{1,3} = 86.22$, $P = 0.0683$). *E. grandis* forest soil at Ravenshoe that was affected by a wildfire had 10.88 mg/Kg AEM P_i, while unburnt soil had 6.98 mg/Kg

Table 4.1 - Attributes of soils collected from Davies Creek, Far North Queensland.

Attribute	Units	Fumigated E. grandis forest soil	Non-fumigated E. grandis forest soil	Fumigated Rain forest soil	Non-fumigated Rain forest soil
Ammonium (NH$_4$)	mg/Kg	66	49	215	66
Nitrate (NO$_3$)	mg/Kg	3	14	61	62
Phosphorus (Colwell) (P)	mg/Kg	10	9	11	16
Conductivity	dS/m	0.086	0.103	0.331	0.227
pH (CaCl$_2$)	pH	5.4	5.2	5.6	5.4
pH (H$_2$O)	pH	6.1	6.0	6.2	6.1
Copper (Cu)	mg/Kg	0.82	0.29	0.46	0.34
Iron (Fe)	mg/Kg	25.84	26.90	41.26	37.54
Manganese (Mn)	mg/Kg	101.23	137.77	36.30	78.81
Zinc (Zn)	mg/Kg	0.61	0.82	2.65	2.44
Exchangeable Aluminium (Al)	meq/100g	0.104	0.118	0.203	0.077
Exchangeable Calcium (Ca)	meq/100g	7.27	7.93	15.60	14.95
Exchangeable Magnesium (Mg)	meq/100g	2.11	2.18	2.82	2.81
Exchangeable Potassium(K)	meq/100g	0.36	0.37	0.65	0.73
Exchangeable Sodium (Na)	meq/100g	0.05	0.05	0.04	0.05

4.4.2 Mortality and foliar phosphorus deficiency symptoms

By 86 DAT, mortality of seedlings differed significantly between fumigated and non-fumigated treatments ($\chi^2 = 7.91$, $P = 0.0049$) with seedlings in non-fumigated soils of both types having significantly higher mortality than those grown in fumigated soil (Fig. 1). Between 86 and 146 DAT, fumigation alone ceased to have a significant effect ($\chi^2 = 0.19$, $P = 0.667$), but soil type ($\chi^2 = 8.215$, $P = 0.0042$), soil type × P addition ($\chi^2 = 4.47$, $P = 0.034$), and fumigation × P addition ($\chi^2 = 4.63$, $P = 0.031$) significantly affected survival. Overall, there was lower percentage survival in fumigated and non-fumigated rain forest soils than in any other treatment (Fig. 4.1). All treatments receiving P addition had higher survival percentages than their non-fertilized counterparts (Fig. 4.1).
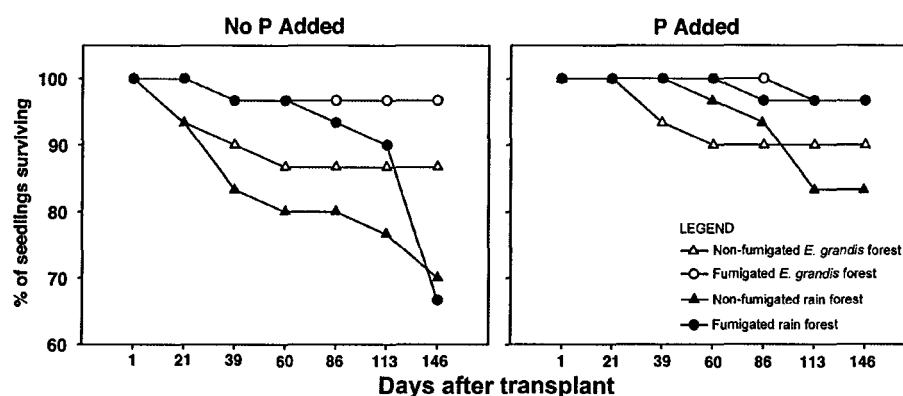
Figure 4.1 - Percentage of *Eucalyptus grandis* seedlings surviving when grown with no added P or with P added for 146 days after transplant (DAT). Open triangles represent non-fumigated, and open circles represent fumigated *Eucalyptus grandis* forest soil; filled triangles represent non-fumigated and filled circles represent fumigated rain forest soil. P addition began 86 DAT. Percentage survival is based on 30 replicate plants allocated to each of the eight treatments at 86 DAT.

Some seedlings of all treatments showed purple coloration of leaves (Fig. 4.2), symptomatic of phosphorus deficiency, by 86 DAT. Other deficiency symptoms

were not apparent. To 86 DAT, the percentage of seedlings with purple leaves (P deficiency) was higher for seedlings in rain forest soil than for those in *E. grandis* forest soil (χ^2 = 120.2, P < 0.0001) and also was higher for those in non-fumigated soils than in fumigated soils (χ^2 = 6.27, P = 0.0123; Fig. 3). At 146 DAT, fumigation (χ^2 = 7.73, P = 0.0054), P addition (χ^2 = 41.39, P < 0.0001) and fumigation × P addition (χ^2 = 5.28, P = 0.022) significantly affected the percentages of P-deficient seedlings. There was a steep decline in the percentage of P-deficient seedlings in all treatments after P fertilisation, and by the end of the study none of the fertilised seedlings showed symptoms of P deficiency (Fig. 4.3). In contrast, when not fertilized, the percentage of P-deficient seedlings in both the non-fumigated *E. grandis* forest soil and the non-fumigated rain forest soil treatments continued to increase over the course of the experiment, and in the latter treatment, all surviving seedlings were P-deficient by 146 DAT (Fig. 4.3).

Figure 4.2 - Examples of seedlings grown in non-fumigated rain forest soil without or with P fertilization at 146 days after transplant. P-deficiency in the non-fertilized seedling (left) is indicated by conspicuous purple leaf coloration (see Dell 1996) in comparison to the green leaves of the fertilized plant (right). Percentage survival is based on 30 replicate plants allocated to each of the eight treatments at 86 DAT.
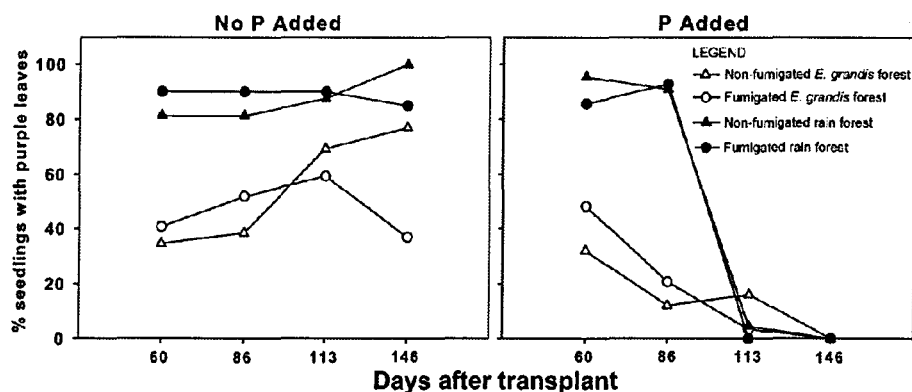
Figure 4.3 - Percentage of *Eucalyptus grandis* seedlings exhibiting purple leaf coloration (indicative of phosphorus deficiency; see Fig. 2) when grown with no phosphorus (P) added or with P added versus days after transplant (DAT). Open triangles represent non-fumigated, and open circles represent fumigated *Eucalyptus grandis* forest soil; filled triangles represent non-fumigated and filled circles represent fumigated rain forest soil. P addition began 86 DAT. Because of mortality, the number of replicates at 146 DAT no P added or with P added respectively in parentheses for each soil treatment are as follows: Non-fumigated *E. grandis* (n = 26, 25), Fumigated *E. grandis* (n = 27, 29), Non-fumigated rain forest (n = 16, 22) and Fumigated rain forest (n = 20, 28). Thirteen seedlings which exhibited symptoms of disease at 146 DAT are excluded from this graph.

4.4.3 Growth attributes, tissue N and P content and mycorrhizal colonization

Immediately before fertilisation at 86 DAT, seedlings grown in eucalypt forest soil irrespective of fumigation on average were almost three times taller than those grown in rain forest soil (Fig. 4.4). A two-way ANOVA confirmed that this difference was significant ($F_{1, 216} = 236$, $P < 0.0001$). The ANOVA detected no significant effect of fumigation ($F_{1, 216} = 1.88$, $P = 0.18$), however, nor any interaction between fumigation and soil type ($F_{1, 216} = 0.22$, $P = 0.63$).
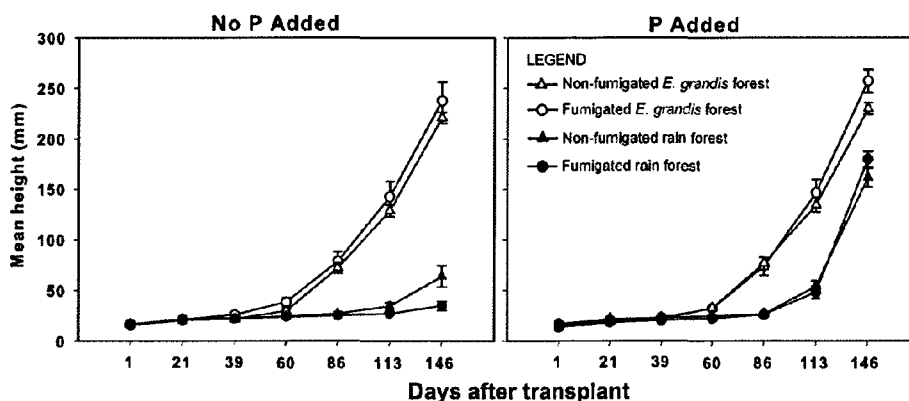
Figure 4.4 - Mean height (mm ± standard error) for 146 days after transplant (DAT) of *Eucalyptus grandis* **seedlings grown with no P added or with P added.** P addition began 86 DAT. Because of mortality, the number of replicates at 146 DAT no P added or with P added respectively in parentheses for each soil treatment are as follows: Non-fumigated *E. grandis* (n = 26, 25), Fumigated *E. grandis* (n = 27, 29), Non-fumigated rain forest (n = 16, 22) and Fumigated rain forest (n = 20, 28). Thirteen seedlings which exhibited symptoms of disease at 146 DAT are excluded from this graph.

After P addition commenced (between 86 and 146 DAT), the log-transformed height ratio analysed by three-way ANOVA was significantly affected by soil type, P addition, soil type × fumigation, soil type × P addition, and fumigation × P addition (Table 4.2). Tukey's HSD tests showed significant differences between fertilized rain forest seedlings and those not fertilized, and also between all groups of seedlings in rain forest soil and those in *E. grandis* forest soil. Seedlings in *E. grandis* forest soil consistently were the tallest (Fig. 4.4).

Mean aboveground dry weights of *E. grandis* seedlings at 146 DAT were affected significantly by soil type, P addition and soil type × P addition, but neither fumigation nor any of its interactions affected dry weight significantly (Table 4.2). Seedlings grown in rain forest soil without P addition had significantly lower mean aboveground dry weights than those in any other treatment (Fig. 4.5a).

Table 4.2 - Three-way ANOVA results for the effects of soil type, fumigation and P fertilization on *Eucalyptus grandis* seedling attributes at 146 days after transplant (DAT). The attributes are the log-transformed ratio of height 146 DAT to height 86 DAT, aboveground dry weight at harvest at 146 DAT, and shoot tissue N and P concentrations determined from composited plant tissues. Statistically significant effects ($P \le 0.05$) are shown in bold.

	Height ratio (Height 146 DAT/Height 86 DAT)	Aboveground dry weight	Aboveground tissue N concentration	Aboveground tissue P concentration
	$F_{7, 171}, P$	$F_{7, 186}, P$	$F_{7, 48}, P$	$F_{7, 48}, P$
Soil	**8.81, <0.0034**	**141.26, <0.0001**	**32.98, <0.0001**	**16.57, 0.0002**
Fumigation	2.51, 0.115	3.354, 0.069	2.83, 0.099	**5.94, 0.0185**
P fertilization	**225.3, <0.0001**	**93.37, <0.0001**	**11.02, 0.002**	**292.18, <0.0001**
Soil x fumigation	**4.86, 0.029**	0.19, 0.662	**17.44, 0.0001**	1.38, 0.246
Soil x P fertilization	**180.89, <0.0001**	**81.53, <0.0001**	**12.45, 0.0009**	**38.99, <0.0001**
Fumigation x P fertilization	**7.63, 0.0063**	0.2, 0.654	2.15, 0.149	**4.22, 0.045**
Soil x fumigation x P fertilization	2.24, 0.137	0.004, 0.951	1.52, 0.223	0.64, 0.429

Mean aboveground shoot N concentrations of *E. grandis* seedlings at 146 DAT were affected significantly by soil type, P addition, soil type × fumigation and soil type × P addition (Table 4.2). Seedlings of the non-fumigated, non-fertilized rain forest soil had significantly higher aboveground shoot N concentrations than those of any other treatment (Fig 4.5b). In contrast to N, mean aboveground shoot P concentrations were affected significantly by all main factors (soil type, fumigation, and P addition) as well as by soil type × P addition and fumigation × P addition interactions (Table 4.2). When seedlings were not fertilized, only those in fumigated rain forest soil had an elevated mean P concentration, but when fertilized, seedlings in *E. grandis* forest soil had the highest aboveground shoot P concentrations of all and significantly exceeded those of seedlings in rain forest soil which tended to be higher than those of seedlings in most non-fertilized treatments (Fig. 4.5c).
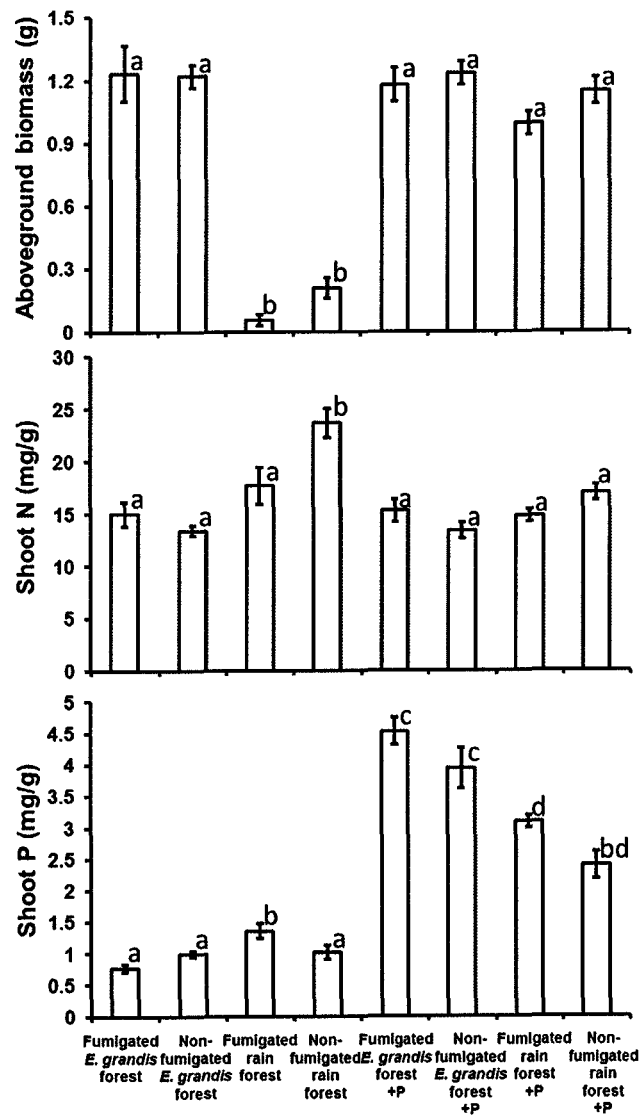
Figure 4.5 - Soil type, fumigation and P fertilization effects on *Eucalyptus grandis* seedling (a) aboveground dry weight, (b) aboveground tissue nitrogen concentration (mg/g), and (c) aboveground tissue phosphorus concentration (mg/g) at harvest, 146 days after transplant (DAT). Each box encompasses the 25th to 75th percentiles with the median indicated by the horizontal line within the box; the bars outside the box indicate the 10th and 90th percentiles, and dots indicate outliers. Boxes accompanied by the same letter do not differ significantly ($P \leq$ 0.05) by Tukey's honestly significant difference *post-hoc* tests.

Although we examined at least 10 cm root length for each of 48 seedlings (six seedlings per treatment × eight treatments) for a total length examined of approximately 5 m, we found no fully-formed ectomycorrhizas, nor did we find arbuscular mycorrhizal fungus colonization at any of the 4800 examined gridline intersections with roots. Away from gridline intersections, however, we very rarely did see typical glomeromycotan hyphae as well as a few vesicles in root cortices. Although we did not quantify them, septate hyphae were relatively common in seedlings of all treatments. Some septate hyphae had clamp connections and may have been incipient ectomycorrhizal colonization, but most lacked clamps and sometimes the melanised hyphae were accompanied by microsclerotia suggestive of "dark septate endophytes" (Mandyam & Jumpponen, 2005). We also found endobiotic, holocarpic chytrid sporangia in *E. grandis* seedling fine roots.

4.5 Discussion

We modelled aspects of the ashbed phenomenon for *E. grandis* by studying seedling growth in fumigated versus non-fumigated *E. grandis* forest and adjacent rain forest soils as well as response to P addition in those soils. Our non-fumigated rain forest soil fell within the ranges (means ± 1 SD) of parameters reported by Warman *et al.* (2013) for five Queensland rain forests, except for ammonium (1.5 times their reported mean), nitrate (8.8 times), and conductivity (only one-tenth of theirs) (see our Table 4.1). Hence, our rain forest soil might have been slightly more favourable for seedling growth than the average Queensland rain forest soil, especially with respect to nitrogen nutrition. Our non-fumigated *E. grandis* forest soil, however, appeared to differ from the three wet sclerophyll forests (i.e., *E. grandis* forests) studied by Warman *et al.* (2013) by having 3.5 times the ammonium, 7 times the nitrate, and nearly 20 times the Mn, slightly higher pH, and much lower conductivity and exchangeable Al. Nevertheless, all of those differing parameters of our *E. grandis* forest soil were similar to values reported for rain forest soils by Warman *et al.* (2013). Thus, our *E. grandis* forest soil might have been more favourable for *E. grandis* seedling growth than wet sclerophyll forest soils generally. High survival

and vigorous growth of seedlings in our non-fumigated *E. grandis* forest soil additionally suggests that the New South Wales provenance of our seeds did not constrain our results. Although some eucalypts such as *E. obliqua* have distinct ecotypes (Bloomfield *et al.*, 2011), ecotypic differences are not known for *E. grandis* (Jones *et al.*, 2006).

For both of the soils that we studied, even though the only significant effect of fumigation on soil chemistry was to diminish extractable Mn, fumigation enhanced early seedling survival (to 86 DAT) and reduced foliar symptoms of P deficiency throughout our 146 day experiment. In spite of generally more favourable chemical attributes of rain forest than *E. grandis* forest soil, without fumigation, seedlings survived poorly in rain forest soil — 100 % showed symptoms of P deficiency at harvest — and they had slower height increase and lower mean shoot dry weight than seedlings in *E. grandis* forest soil. Phosphorus addition in rain forest soil, however, improved seedling survival, completely eliminated P deficiency symptoms, produced high rates of height increase and similar shoot dry weights to seedlings in *E. grandis* forest soil.

These results accord with our predictions and suggest that as for *E. regnans* (Chambers and Attiwell, 1994), the provision of an ashbed, especially the release of phosphorus by fire, may be necessary for *E. grandis* regeneration on rain forest soil. Our results also are consistent with soil fumigation, like intense fires, potentially alleviating inhibitory effects of soil microbiota on seedling survival. Although fire may volatilize some N, intense fires kill microbes and thereby release microbially-sequestered N and P in addition to diminishing the P-immobilization capacity of soil (Weston & Attiwell, 1990; Chambers & Attiwell, 1994; Serrasolsas & Khanna, 1995). Release of assimilable N and P by fire is corroborated by wood cores of adult *E. grandis* having peaks of N and P that correspond to episodes of fire activity (Heinrich, 2006). We found AEM P$_i$ in *E. grandis* forest soil at Ravenshoe, Queensland was elevated by a burn. Unlike intense fires, however, in our experiment fumigation did not significantly alter ammonium, nitrate, Colwell P, or

AEM P_i of our soils, so its principal influence most likely was to have diminished soil microbial inhibition of *E. grandis* seedlings.

In spite of our inability to detect differences in phosphorus concentrations between soil types or in consequence of fumigation, our study strongly underscores the importance of phosphorus in the mineral nutrition of *E. grandis* seedlings as for other eucalypt species (Dell *et al.*, 1987). Phosphorus addition improved survival, eliminated deficiency symptoms and markedly accelerated seedling height increase in rain forest soil as well as increasing aboveground dry weight. Other investigators also have shown P addition to stimulate *E. grandis* seedling growth (Mulligan & Sands, 1988; Kirschbaum *et al.*, 1992). Even though seedling aboveground dry weight was not affected by P addition of *E. grandis* forest soil, P addition did increase aboveground shoot P concentrations significantly in both *E. grandis* and rain forest soils. High seedling P concentrations with little growth response suggest luxury accumulation of P (De Mazancourt & Schwartz, 2012) and growth limitation by another mineral nutrient in P-fertilized *E. grandis* forest soil.

It is somewhat perplexing that when not fertilized, even though seedling shoot P concentrations differed little between soil types, seedlings had higher aboveground dry weight in *E. grandis* soil than in rain forest soil. Little difference in shoot P concentrations, however, is consistent with similar Colwell P and AEM P_i in both soil types. Although both measures of P differed little between soil types, rain forest soil tended to have higher exchangeable calcium than *E. grandis* forest soil, which might indicate greater capacity for P immobilization. The only mineral nutrient conspicuously more abundant in *E. grandis* forest soil than in rain forest soil was Mn, and because Mn strongly influences electron transport and photosynthesis (Raven *et al.*, 2005), we hypothesize that high Mn availability in *E. grandis* forest soil may have contributed to greater seedling height growth than in rain forest soil when neither was P-fertilized. That Mulligan (1989) found no effect of a very low P supply on rate of net photosynthesis by *E. grandis* seedlings bolsters our interpretation. Nevertheless, this hypothesized effect of Mn might be peculiar to where we collected our soils because Warman *et al.* (2013) found median Mn

availability generally to be higher in rain forest than in *E. grandis* forest soil. Moreover, in our experiment, fumigation diminished extractable Mn in both soil types, but increased survival and diminished P deficiency symptoms suggesting that there may have been a slight, but analytically non-detectable increase of soil P with fumigation.

In our experiment, although nitrate and exchangeable potassium were marginally more abundant in rain forest than in *E. grandis* forest soil, neither had any evident effect on *E. grandis* seedling performance (and neither did pH, Mg, Ca or Zn which also tended to be higher in rain forest than in *E. grandis* forest soil). Seedling aboveground shoot N concentration was significantly highest in non-fertilized, non-fumigated rain forest soil, and seedlings in non-fertilized, fumigated rain forest soil had the second highest mean N concentration (but not significantly so). Thereby, high N concentrations were associated with the lowest seedling dry weights. Consequently, the low seedling shoot N concentrations of other treatments with statistically indistinguishable, high aboveground dry weights probably reflect a dilution effect (Johnson *et al.*, 1980) of plant size. Mulligan & Sands (1988) also found high foliar N concentrations in *E. grandis* grown under phosphorus limitation, and they suggested that accumulation of N might have resulted in ion imbalance and N toxicity that exacerbated poor growth.

While methyl-bromide fumigation of soil may not elevate available mineral nutrients to the same extent as heating of soil (Eno & Popenoe, 1964) or an actual fire, in our experiment, fumigation improved seedling survival in both soil types which might have reflected a reduction of parasitic and pathogenic microorganisms. In unburnt, temperate *E. regnans* forest for example, the fungus *Cylindrocarpon destructans* (Zinssm.) Scholten is a common pathogen that can affect seedling growth negatively (Ashton & Willis, 1982; Iles *et al.*, 2010). Bowman & Fensham (1995) found for the tropical eucalypt *Eucalyptus tetrodonta* F.Muell. that non-fumigated monsoon rain forest soil significantly inhibited seedling growth and that the inhibition was not alleviated by an NPK fertilizer. In our experiment at harvest, chytrids and dark

septate endophytes were relatively common in *E. grandis* seedling roots, and tree species tend to respond negatively to such endophytes (Mayerhofer *et al.*, 2013).

Not only may deleterious soil microorganisms be affected by soil fumigation, fire, or even air drying of soils, but so too may generally beneficial organisms such as mycorrhizal fungi. Launonen *et al.* (2005) grew *E. regnans* seedlings in air-dried and ambient soils from mature *E. regnans* forest and found that seedling dry weights were 3–6 times greater in air-dried than in ambient soil. In a related study, a higher percentage of *E. regnans* seedlings were P-deficient in ambient than in air-dried soil (Launonen *et al.*, 2004). Launonen *et al.* (2004, 2005) attributed these differences to changes in ectomycorrhizal fungus composition and/or other microbial associates in the soil upon air drying. Warcup (1983) showed that ectomycorrhizal fungi in sunbaked and steamed soils differed from those in ambient soil. In a glasshouse study, Ellis & Pennington (1992) showed that growth of *E. delegatensis* seedlings was increasingly inhibited by soils taken from different successional stages progressing towards rain forest, but that the inhibition could be overcome by inoculation with healthy *E. delegatensis* forest soil. They concluded that microbiological factors such as mycorrhizal fungi might influence seedling growth inhibition (Ellis & Pennington, 1992).

The roles of mycorrhizal fungi in the establishment and growth of eucalypt seedlings may be complex, because some species, such as *E. grandis*, can be colonized by both ectomycorrhizal and arbuscular mycorrhizal fungi, with arbuscular mycorrhizas most prominent at the seedling stage (Adams *et al.*, 2006). In our seedlings, however, we found very little root colonization by arbuscular mycorrhizal fungi (none at our root gridline intercepts) and no fully intact ectomycorrhizas. This suggests that when collected, our soils may have been very low in viable propagules of both types of mycorrhizal fungi, or that the conditions of our experiment (such as soil temperature in the relatively small, 10 cm diameter pots) were inimical to mycorrhiza formation.

Arbuscular mycorrhizas have been shown to benefit the growth of several *Eucalyptus* species, although generally less so than ectomycorrhizas benefit those species (Jones

et al., 1998; Chen *et al.*, 2000; Kariman *et al.*, 2012). In a survey of eleven *Eucalyptus* species, Adjoud *et al.* (1996) found that arbuscular mycorrhizas most benefited those species that had attained high leaf phosphorus concentrations (ca. 2.5 mg/g after 20 weeks of P addition with a total 8.2 mg P in a non-nutritive substrate) when without mycorrhizas. The potential benefits of arbuscular mycorrhizas to *E. grandis* have not been studied extensively, but the few reports together with our findings strongly suggest that *E. grandis* seedlings are highly facultatively mycotrophic (*sensu* Janos, 2007), well able to grow in the absence of any mycorrhizas provided that adequate P is available. Lapeyrie *et al.* (1992) cited a conference abstract and a manuscript in press (by Muchovej & Amorim, and Amorim & Muchovej, respectively) about *E. grandis*, but we could not find either. Lapeyrie *et al.* (1992) stated, however, that arbuscular mycorrhizal inoculation alone had no effect versus non-inoculated *E. grandis* seedlings, but when combined with ectomycorrhizal inoculation had a negative effect versus solely ectomycorrhizal plants. Fernandes *et al.* (1999) reported that inoculation of *E. grandis* seedlings with the arbuscular mycorrhizal fungus *Glomus etunicatum* W.N. Becker & Gerd. alone had no effect on the plants, but that dual inoculation reduced ectomycorrhiza formation. Pagano & Scotti (2008) studied arbuscular mycorrhizal and ectomycorrhizal colonization of one and two year-old *E. grandis* saplings in monoculture plantations in Brazil, and failed to find any arbuscular mycorrhizas on *E. grandis* (although they found relatively abundant arbuscular mycorrhizas on *Eucalyptus camaldulensis* Dehnh., and found ectomycorrhizas on both eucalypt species). In consequence, they concluded that *E. grandis* is not dependent on arbuscular mycorrhizas for growth (Pagano & Scotti, 2008).

That *E. grandis* might depend little if at all on arbuscular mycorrhizas is consistent with Adams *et al.* (2006) reporting less than 10 % root length colonized for field-collected adults, but raises the question of why those authors found *E. grandis* seedlings to have up to 40 % root colonization. Perhaps arbuscular mycorrhizas do benefit *E. grandis* seedlings under some conditions not yet investigated. In a study of another tropical Australian eucalypt, *E. tetrodonta*, however, Janos *et al.* (2013) found that common arbuscular mycorrhizal networks exacerbated belowground

competition between *E. tetrodonta* seedlings and an exclusively arbuscular mycorrhizal rain forest tree species, *Litsea glutinosa* (Lour.) C. Rob. Janos *et al.* (2013) concluded that the survival and growth of *E. tetrodonta* in rain forest soil was not a likely consequence of abiotic ashbed effects, but most likely resulted from fire-caused mortality of rain forest arbuscular mycorrhizal host plants that disrupted common arbuscular mycorrhizal networks and diminished inimical arbuscular mycorrhizal fungi.

Overall, our results suggest that *E. grandis* seedling establishment in rain forest soils may be facilitated by high-intensity fires that increase phosphorus availability and remove rain forest overstorey plants which inhibit eucalypt regeneration by shading (Ashton, 1981a) or perhaps by detrimentally incorporating seedlings in common arbuscular mycorrhizal networks (Janos *et al.*, 2013). Moreover, high-intensity fires also may eliminate fast growing, arbuscular mycorrhizal grass, vine and shrub species which may compete strongly and thereby impede *E. grandis* regeneration. Phosphorus has been shown similarly to be the primary mineral nutrient limiting regeneration of the temperate, giant eucalypt *E. regnans* in unburnt soils (Ashton & Martin, 1982; Ashton & Kelliher, 1996), suggesting concordant regeneration niches for *E. grandis* and *E. regnans* (Tng *et al.*, 2012c).

4.5 Conclusion

We found that survival of *E. grandis* seedlings was significantly improved by fumigation of both *E. grandis* and rain forest soils, and that P deficiency symptoms were less and seedling growth was greater in *E. grandis* forest soil than in rain forest soil. Phosphorus addition, especially in rain forest soil, alleviated P deficiency symptoms and improved seedling survival and growth. These results support that in nature, high-intensity fires are likely to diminish inhibitory soil microorganisms and to increase P availability. This inference accords with effects of fire reported for temperate giant eucalypts such as *E. regnans*, and suggests concordance between tropical *E. grandis* and temperate *E. regnans* regeneration niches.

Chapter 5

Plant traits demonstrate that temperate and tropical giant eucalypt forests are ecologically convergent with rain forest not savanna

5.1 Summary

Ecological theory differentiates rain forest and open vegetation in many regions as functionally divergent alternative stable states with transitional (ecotonal) vegetation between the two forming transient unstable states. However, this transition vegetation is of considerable significance, not only as a test case for theories of vegetation dynamics, but also because the forest is of major economic importance, and is home to a suite of species of conservation significance including the world's tallest flowering plants. We therefore created predictions of patterns in plant functional traits that would test the alternative stable states model of these systems. We measured functional traits of 128 trees and shrubs across tropical and temperate rain forest – open vegetation sequences in Australia, and the giant eucalypt forests sandwiched between these vegetation types. We analysed a set of functional traits: leaf carbon isotopes, leaf area, leaf mass per area, leaf slenderness, wood density, maximum height and bark thickness, using univariate and multivariate methods. For most traits, giant eucalypt forest was similar to rain forest, while rain forest, particularly tropical rain forest, was significantly different from the open vegetation. In multivariate analyses, tropical and temperate rain forest diverged functionally, and both segregated from the open vegetation. However, the two types of giant eucalypt forests showed greater overall functional similarity to each other than to any of the rain forest or open vegetation types. Furthermore, the giant eucalypt forests overlapped in function with their respective rain forests. We conclude that tropical and temperate giant eucalypt forests are ecologically and functionally convergent. The lack of clear functional differentiation from rain forest suggests that giant eucalypt forests and are unstable states within the basin of attraction of rain forest. Our results have important implications for giant eucalypt forest management.

5.2 Introduction

Alternative Stable States models are becoming increasingly useful in explaining ecological dynamics, with empirical evidence for their existence at scales ranging

from species assemblages (Konar & Estes, 2003; van Nes & Scheffer, 2007) to biomes (Folke *et al.*, 2004). These models suggest that many ecosystems are intrinsically stable, but can be transformed into a different stable ecosystem by sufficiently large changes in extrinsic environmental factors (Angeli *et al.*, 2004). These models are often depicted as three-dimensional 'stability landscapes' with the ecosystems depicted as "balls" on the surface of this landscape, and the stability of these ecosystems determined by whether they lie in "basins" or domains of attraction (Beisner *et al.*, 2003; Scheffer & Carpenter, 2003) (Fig. 5.1). The depth of the "basins" denotes the stability of the ecosystem. These models therefore differ from classical succession models in which ecosystems slide along a continuum of steady states (Angeli *et al.*, 2004).

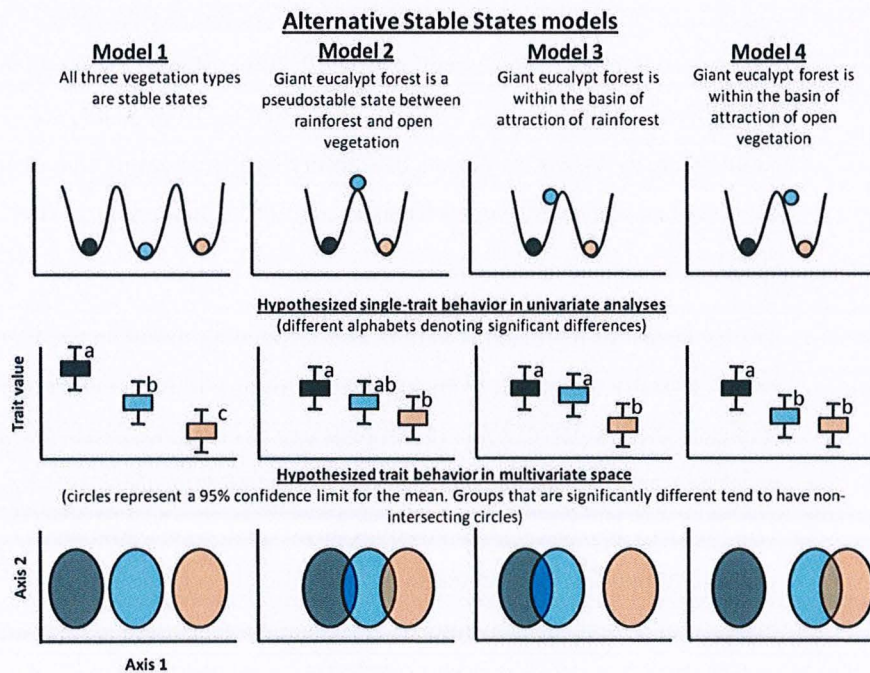Figure 5.1 - **Idealised Alternative Stable States 'ball and cup' scenarios for rain forest (dark grey), giant eucalypt forest (blue) and open vegetation (orange) and their corresponding hypothesized trait behaviour in univariate and multivariate analysis outputs.** In each case, the overlap between to the confidence limits of each functional profile will denote the functional affinities between habitats.

Alternative Stable States systems therefore arise from interactions between extrinsic and intrinsic factors. Changes in extrinsic factors, such as climate and fire (Beckage & Ellingwood, 2008; Odion Moritz & DellaSala, 2010; Bowman *et al.*, 2013), tend to drive changes in ecosystems, including transitions from one stable state to another. However, the stable states only exist when intrinsic characteristics of the ecosystem create negative feedbacks that create and maintain stability (Fukami & Lee, 2006; Beckage *et al.*, 2009; Díaz-Sierra *et al.*, 2010; Nicholas *et al.*, 2011). For example, alternative stable state ecosystems may co-occur in fire-susceptible regions because of different fire regimes caused by differences in fuel load, flammability, microclimate or other factors in each ecosystem. In most instances the characteristics of the organisms in each ecosystem create the different fire regimes. Thus, the obvious place to look for the drivers of stable states is the functional traits of the component organisms of each ecosystem. For instance, various leaf and bole traits can be of great significance in plant function, community assembly and ecological processes (Chapin, 2003; Cornelissen *et al.*, 2003; McGill *et al.*, 2006; Lasky *et al.*, 2014). One can test whether systems represent alternative stable states, and simultaneously assess the drivers of stability by investigating the functional traits of the component species (e.g. Hoffman *et al.*, 2005; Quétier *et al.*, 2007; Dantas *et al.*, 2013).

The east coast of mainland Australia and Tasmania present an excellent geographical setting to study forest-open vegetation transitions within a single continent. From the tropics to the temperate zone, rain forests exist as disjunct patches within a matrix of eucalypt-dominated savanna or open woodland (Adam, 1992, Bowman, 2000a) (Fig. 1.1). In many localities, giant eucalypt forest (also locally known as tall open forest, wet sclerophyll forest or mixed forest) are often observed wedged in the ecotone between rain forest and savanna or open canopy vegetation (Tng *et al.*, 2012c). In the tropics, these giant eucalypt forests are dominated by *Eucalyptus grandis* and range from a few hundred meters to a few kilometres wide in extent (Unwin, 1989; Harrington *et al.*, 2000) while in temperate zones, similar forests dominated by a range of species (e.g. *E. regnans* F. Muell., *E. obliqua* L'Hér.) may predominate over several kilometres (Harris & Kitchener, 2005; Tng *et al.*, 2012c). These forests

include the world's tallest angiosperms (Tng *et al.*, 2012c), are home to several important threatened species (Harrington *et al.*, 2000), and represent major carbon sinks (Keith *et al.*, 2009, 2010). Furthermore, these forests have been the focus of major conflicts between ecological and economic interests because they are major forestry resources (Musselwhite & Herath, 2005). In temperate Australia, logging of these forests is ongoing.

Warman & Moles (2009) hypothesized that the tropical *E. grandis* forests are unstable states between rain forest and savanna (Fig. 5.1), whereas Wood & Bowman (2012) inferred that temperate giant eucalypt forests in Tasmania are stable states, but of lower stability (i.e. occupying a shallower basin of attraction; Fig. 5.1) than the adjacent temperate rain forest and open vegetation. However, it remains unclear whether these tropical and temperate systems are functionally convergent, and whether it is possible to create a unified Alternative Stable States model for these geographically distant, but ecologically similar systems (Tng *et al.*, 2012c). Several authors have argued that the eucalypt dominants of these forests are essentially rain forest successional species (Cremer, 1960; Smith & Guyer, 1983; Tng *et al.*, 2012bc). However, these forests have largely been viewed as discrete vegetation types distinct from rain forest due to the subjective vegetation classifications based on the eucalypt dominants (i.e. Model 1; Fig. 5.1). A sound landscape ecology theory augmented by functional trait based understanding of the ecology of these giant eucalypt forests is necessary for effective management of these dynamic ecosystems. If these forests are functionally convergent with each other across tropical and temperate regions, and if they are indeed unstable ecological states (*sensu* Warman & Moles, 2009), the traditional approaches to their ecological management and conservation will need revision.

We tested Alternative Stable States theories in the rain forest/open vegetation transitions in both tropical and temperate regions using functional traits of woody trees and shrubs. We also tested whether the giant eucalypt forests of the tropical zone and the temperate zone are functionally convergent. First, we define state scenarios under an Alternative Stable States context, for the rain forest, giant

eucalypt forest and open vegetation (Fig. 5.1). Within both temperate and tropical regions, we expect that giant eucalypt forest fall under one of four possible models: (Model 1) it forms a third discrete stable state; (Model 2) it is an unstable state intermediate between the stable states of rain forest and open vegetation; (Model 3) it is unstable and falls within the basin of attraction of rain forest, or; (Model 4) it is unstable and falls within the basin of attraction of open vegetation (Fig. 5.1). Second, we use univariate analyses to compare each functional trait across vegetation types and multivariate analyses to visualize and compare of the functional profile for each vegetation type (Fig. 5.1). In addition, the proximity of giant eucalypt forest species from both regions in multivariate space will indicate the degree of functionally convergence. This is the first study to implicitly link functional trait behaviour and Alternative Stable States models.

5.3 Materials & methods

5.3.1 Study sites and sample collection

We sampled rain forest, and the surrounding giant eucalypt forest and open vegetation, in two regions: tropical north Queensland and cool temperate Tasmania (Fig. 1.1). North Queensland experiences a humid tropical climate with a typical site (Herberton: $17°38'S$, $145°39'E$) having a mean maximum annual temperature of $27.1°C$ and a mean annual rainfall of 2240 mm. The climate is thermally aseasonal, but has a summer-rainfall bias (Bureau of Meteorology, 2013). The regions of Tasmania studied here experience a cool temperate climate with a mean maximum annual temperature of $18.4°C$ and a mean annual rainfall of 2070 mm for a typical site (Arve Valley: $43°14'S$, $146°79'E$). The climate is thermally seasonal and has winter-dominated precipitation (Bureau of Meteorology, 2013). In each region the three vegetation types are readily recognised, allowing for *a priori* allocation of vegetation samples and species; (i) rain forests have closed canopies and an absence of eucalypts; (ii) giant eucalypts forests are emergent above either rain forest, or a mix of shrubby and grassy understoreys, and; (iii) open vegetation is dominated by

shorter eucalypts and has shrubs and herbaceous (including grass) species tolerant of high light environments. Tropical open forest/woodlands have a well developed grassy understorey and are classified as tropical savannas. Open vegetation in the temperate region is referred to here as savanna, as they can have some structural similarities with tropical eucalypt savannas. In both regions, the species measured for functional traits were selected because they were relatively abundant in at least one of the localities. This approach captured a representative spread of species in all three vegetation types. The trait data for any given species were taken from specimens collected from only one locality.

At the following three localities near the western edge of the Wet Tropics World Heritage Area we sampled the three vegetation types: Davies Creek (17°08'S, 145 °22'E), Mt Baldy (17°17'S, 145 °25'E) and Paluma (18°56'S 146°10E). At each site *Eucalyptus grandis* dominated the giant eucalypt forest, and the rain forest was the simple notophyll vine forest type (Tracey, 1982). However, the savanna was dominated in different localities by different eucalypt species (*Eucalyptus crebra* F. Muell., *E. mediocris* L.A.S. Johnson & K.D. Hill, *E. tereticornis* Sm., *E. tindaliae* Blakey) with grassy or shrubby understoreys (Goosem *et al.*, 1999). We sampled 32, 22 and 16 species from rain forest, giant eucalypt forest, and savanna respectively (see Appendix 2; Table A2.2). Most species were more-or-less restricted to one vegetation type.

Field sampling in Tasmania was undertaken in cool temperate rain forest and giant eucalypt patches from the northeast (41°14'S 147°44'E), southeast (42°56'S 147°17'E) and southern localities (43°05'S 146°43'E). This widespread sampling allowed us to sample the full structural range of cool temperate rain forest types (*sensu* Jarman *et al.*, 1991) associated with the two dominant giant eucalypt species (Kirkpatrick *et al.*, 1988). These rain forests are dominated by some combination of *Nothofagus cunninghamii* (Hook.) Oerst., *Atherosperma moschatum* Labill. and *Anodopetalum biglandulosum* (Hook.) Hook.f. The more patchy distribution and lower species richness of cool temperate rain forest and the broad extent of giant eucalypt forest necessitated a slightly different protocol than used in tropical

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Queensland. For the giant eucalypt forests, we restricted our sampling to areas dominated by *Eucalyptus regnans* or *E. obliqua* L'Hér. Open woodland was less common in the northeastern and southern sampling sites adjacent to rain forest and giant eucalypt forest. However, a similar suite of savanna species and their dominant overstorey eucalypts are common and geographically widespread in Tasmania and sampling species of this vegetation type from southeastern localities was sufficient to obtain a representative sample. This savanna vegetation was dominated by *Eucalyptus pulchella* Desf. with *E. viminalis* Labill. co-dominants and a shrubby understorey. We sampled 15, 23 and 20 species from temperate rain forest, giant eucalypt forest and savanna, respectively (Appendix 2; Table A2.1).

For each species sampled, we measured and compiled data on mature (> 60% potential height) individuals per species. We measured a set of four leaf traits and three bole traits (Table 5.1), following methods outlined by Cornelissen *et al.* (2003). For leaf carbon isotope ratio (δ13C) determination, the leaves of four to five individuals were bulked, ground finely and δ13C assessed by the School of Plant Biology, University of Western Australia. For leaf area and leaf mass per area, two to 20 replicates of sun-exposed leaves were obtained from the tree or shrub mid-canopy. For shrubs and short trees, an extension cutter was used to obtain the leaves but for trees taller than 10 meters, canopy branches were collected using a slingshot and weighted line. Only fully expanded leaves were used and these were scanned with a flatbed scanner and the leaf scans were processed by imaging software ImageJ to obtain leaf areas. Leaf slenderness was measured as the ratio of the leaf length to leaf breadth. These leaves were then dried to a constant weight at 60°C and weighed. Leaf mass per area was then determined by dividing leaf dry weight by the leaf area. For wood density, we followed a protocol similar to Falster & Westoby (2005). For trees, branches of at least two individuals per species were used and from each of these branches, two to five 5cm segments of the branch was obtained approximately 1m from the branch tip, whereas for shrubs, we collected wood segments by destructive sampling from the base of the shrub. The bark was removed from the wood segments and the displacement method was used to obtain the branch segment fresh volume. The branch segments were then dried at 60°C for a week, weighed, and

the wood density calculated as dry weight divided by fresh volume. Max height

(Ht_{max}) was obtained from literature sources (Francis, 1951; Curtis, 1963, 1967;

Curtis & Morris, 1975; Boland et al., 2006). Bark thickness was only measured on

trees, and was obtained using a bark gauge at breast height. As bark thickness

increases with bole diameter, we expressed bark thickness relative to stem diameter

(e.g. Lawes et al., 2013) by multiplying bark thickness by two and dividing this

figure by the recorded diameter. We therefore sampled bark thickness from 26, 16

and 9 tree species from tropical north Queensland, and 8, 16 and 6 tree species from

temperate Tasmania from their respective rain forests, giant eucalypt forests and

savannas.

Table 5.1 – Functional traits selected for the current study and their functional significance relevant to the current study. A reference set for each trait is compiled.

Functional Trait	Unit	Functional significance of relevance to current study	Refs
Leaf Traits			
Delta 13 C ($\delta^{13}C$)	‰	Correlated to plant water use efficiency and may also segregate plants of different successional status.	1
Leaf Area	mm^2	Consequential for leaf energy and water balance. Interspecific variation in leaf size has been connected with climatic variation, where heat stress, cold stress, drought stress and high radiation all tend to select for relatively small leaves.	2
Leaf mass per area	$g\ m^{-2}$	Correlated with potential relative growth rate. Higher values correspond with high investments in structural leaf defences and leaf lifespan, but also slower growth.	3
Leaf Slenderness	Unitless	Involved in control of water and temperature status. Slender leaves have a reduced boundary layer resistance and are can thus regulating their temperature through convective cooling more effectively.	4
Bole Traits			
Wood density	$g\ cm^{-3}$	Positively correlated with drought tolerance and tolerance of mechanical or fire damage; related to stem water storage capacity, efficiency of xylem water transport, regulation of leaf water status and avoidance of turgor loss.	5
Max height	M	Correlated to the competitive ability of plants.	6
Bark thickness	Unitless	Correlated to fire resistance with thicker bark expected in fire prone areas.	7

1 (Farquhar et al., 1989; Huc, Ferhi & Guehl, 1994; Bonal et al., 2007)
2 (Parkhurst & Loucks, 1972; Givnish, 1987; Royer et al., 2005)
3 (Westoby, 1998; Reich et al., 1999; Milla & Reich, 2007)
4 (Givnish, 1983; Lebrija-Trejos et al., 2010)
5 (Hacke et al., 2001; Meinzer, 2003; Bucci et al., 2004; Romero & Bolker, 2008; Chave et al., 2009; Pineda-García et al., 2011)
6 (Westoby, 1998; Westoby et al., 2002; Falster & Westoby, 2005)
7 (Pinard & Huffman, 1997; Brando et al., 2012; Lawes et al., 2013)

5.3.2 Data analysis

All variables were checked for normality and where required were log-transformed. For each region, univariate one-way ANOVAs were performed for each trait. Significant differences between habitats were determined by Tukey HSD tests using a confidence level of 0.05. All univariate analyses were performed in R. We also undertook univariate phylogenetic ANOVAs on each functional trait (see Appendix 2). The results were essentially similar to the normal set of ANOVAs (Appendix 2, Table A2.2) and so we report only the former. Two-way factorial ANOVAs using regions (tropical and temperate), vegetation type (rain forest, giant eucalypt forest and savanna) and their interaction were also performed. We excluded bark thickness for the two-way ANOVA as data for this trait was only available for trees.

For the multivariate analyses, we used canonical variate analysis to visualize overall trait position within and among habitats. This method is a weighted ordination method in which axes are weighted to maximise the difference between *a priori* groups of multivariate observations (Darlington *et al.*, 1973; Campbell, 1984). MANOVA is the multivariate analogue of ANOVA, and tests for differences among groups. We performed both one-way and two way MANOVAs and *post-hoc* pair-wise tests using a confidence level of 0.05 were used to test for differences between groups. These multivariate analyses were performed using the discriminant analysis function in JMP 10.0.0 (SAS Institute, Inc., Cary, NC). As with the two-way factorial ANOVAs, bark thickness was excluded from the multivariate analysis as we only had measurements for tree species.

5.4 Results

5.4.1 Univariate analyses

The two-way ANOVAs all showed significant differences, often with significant interaction effects, so we performed one-way ANOVAs. These showed a number of differences, and a number of similarities in trait behaviour in both regions (Table 5.2; Fig. 5.2, 5.3). In the tropical system, rain forest and savanna were significantly

different in all traits, with the latter having a significantly higher δ13C ratio, leaf

mass per area, leaf slenderness, wood density and bark thickness, but lower leaf area

and maximum height than the former (Fig. 5.2, 5.3). For most traits giant eucalypt

forest was not significantly different from rain forest, with the exception of greater

bark thickness.

Table 5.2 – One-way ANOVA results for of carbon isotopes ratios (δ13C), leaf area, leaf mass per area, leaf slenderness, wood density, maximum height, and bark thickness index comparisons between rain forests, giant eucalypt forests and savannas of tropical and temperate regions. Leaf area, leaf slenderness, Maximum height, and bark thickness were log transformed before analysis. N.S denotes non-significance. Bark thickness was left out in the analysis with both regions combined as data for this trait was only available for tree species.

Functional Trait	Tropical Queensland		Temperate Tasmania		Both Regions	
	$F_{2,67}$	P	$F_{2,55}$	P	$F_{5,122}$	P
Leaf traits						
δ13C	6.97	0.0018**	2.45	0.09 (N.S)	4.73	0.0005***
Leaf area	16.31	<0.0001***	10.13	0.0002***	34.04	<0.0001***
Leaf mass per area	20.56	<0.0001***	9.04	0.0004***	14.98	<0.0001***
Leaf slenderness	11.48	<0.0001***	2.58	0.08 (N.S)	7.54	<0.0001***
Bole traits						
Wood density	7.77	0.0009***	10.29	0.0002***	9.71	<0.0001***
Maximum height	4.88	0.011*	15.11	<0.0001***	9.67	<0.0001***
*Bark thickness	17.31	<0.0001***	9.15	0.0009***	NA	NA

*Bark thickness measurements were only performed on trees, hence the different degrees of freedom (Tropical Queensland: $F_{2,48}$; Temperate Tasmania: $F_{2,27}$) from the other traits.

In the temperate system, δ13C ratios and leaf slenderness was not significantly

different across vegetation types, but leaf area and maximum height were

significantly greater, while wood density and bark thickness were significantly lower

for rain forest than savanna species (Fig. 5.2, 5.3). However, temperate rain forest

and savanna were not significantly different in leaf mass per area. Temperate giant

eucalypt forest was not significantly different from rain forest in any of the measured

traits.

Figure 5.2 - Boxplots showing the leaf trait behaviour of rain forest (grey), giant eucalypt forest (blue) and savanna (orange) species from the tropical north Queensland (left block) and the cool temperate Tasmania (right block). Shown are carbon isotope composition ($\delta13C$), leaf area (LA), leaf mass per area (LMA) and leaf slenderness (LS). Each box encompasses the 25th to 75th percentiles; the median is indicated by the boldest vertical line and the other vertical lines outside the box indicate the 10th and 90th percentiles. Dots indicate outliers. One-way ANOVAs were performed on the data (log-transformed for LA and LS) and significant differences between vegetation types are indicated by different letters based on Tukey HSD tests at a 0.05 confidence level (see Materials and methods; Table 5.2). N.S denotes non-significance.
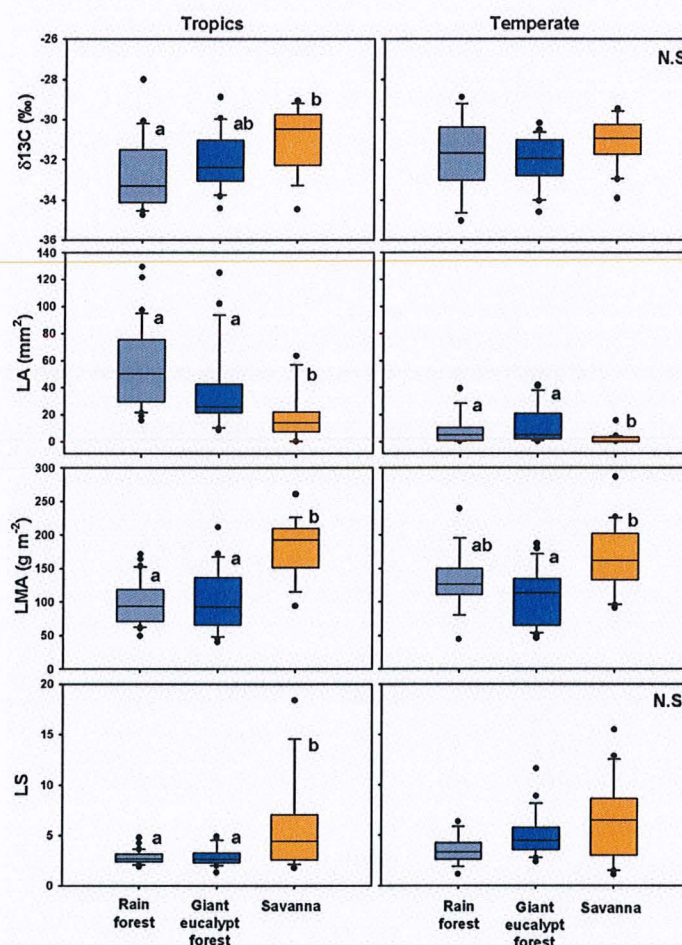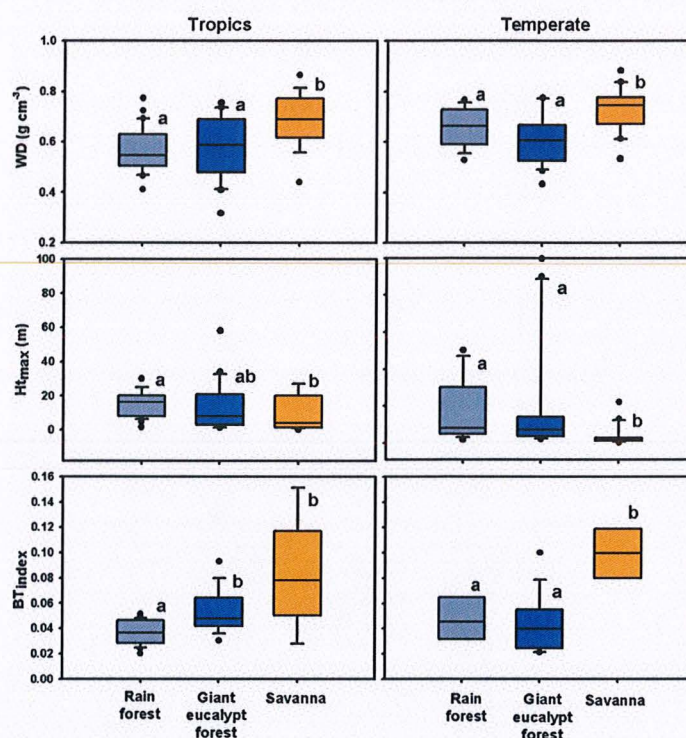
Figure 5.3 - Boxplots showing the bole trait behaviour of rain forest (grey), giant eucalypt forest (blue) and savanna (orange) species from the tropical north Queensland (left block) and the cool temperate Tasmania (right block). Shown are wood density (WD), maximum height (Ht_{max}), and bark thickness index (BT_{index}). Each box encompasses the 25th to 75th percentiles; the median is indicated by the boldest vertical line and the other vertical lines outside the box indicate the 10th and 90th percentiles. Dots indicate outliers. One-way ANOVAs were performed on the log-transformed data (except WD) and significant differences between vegetation types are indicated by different letters based on Tukey HSD tests at a 0.05 confidence level (see Materials and Methods; Table 5.2).

5.4.2 Multivariate analyses

Two-way MANOVAs show that region (Wilks' Lambda: $F_{6,117} = 19.53$, $P < 0.0001$), vegetation type (Wilks' Lambda: $F_{12,234} = 13.45$, $P < 0.0001$), and region x vegetation type interactions (Wilks' Lambda: $F_{12,234} = 1.87$, $P < 0.038$) were significant. We therefore performed one-way MANOVAs which showed highly significant

differences among vegetation groups within the tropics ($F_{2,67} = 27.33$, $P < 0.0001$) and the temperate zone ($F_{2,55} = 6.54$, $P = 0.003$), and in the combined analysis ($F_{5,122} = 14.5$, $P < 0.0001$). *Post-hoc* pairwise-tests show that the major differences occurred between rain forest and savanna in both regions, and also across regions (Fig. 5.4). Tropical rain forest was also significantly different from temperate rain forest, and tropical savanna from temperate savanna (Fig. 5.4). However, tropical and temperate giant eucalypt forest were not significantly different (Fig. 5.4).
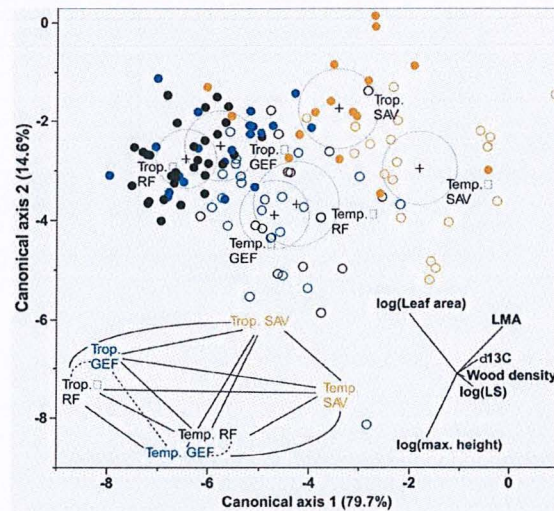
Figure 5.4 - Canonical variate analyses of functional trait means of 128 species from tropical and (closed circles) temperate (open circles) rain forest (black), giant eucalypt forest (blue) and savanna (orange). Six functional traits were used: carbon isotopes ($\delta 13C$); leaf area; leaf mass per area (LMA); leaf slenderness (LS); wood density, and; maximum height plotted into multivariate space. Each dot represents a species. On the bottom right the trait weightings (transformed where required) are plotted onto the graphs as vectors whose length and direction of which represent the contribution of the variable in explaining the clustering pattern. For each vegetation group, each multivariate mean is visualized as large grey circles encircling a black cross, the size of which corresponds to the 95% confidence limit for the mean. Groups that are significantly different tend to have non-intersecting circles. The proximities and overlaps of these circles are used to corroborate trait behaviour with Alternative Stable States model scenarios (Fig. 5.1). The bottom left inset is the results of pairwise *post-hoc* tests of a one-way MANOVA where unbroken lines represent significant differences between vegetation types, and dashed lines represent non-significance.

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Likewise in canonical variate analyses for the individual regions, significant differences were found between vegetation groups within both the tropical (Wilks' Lambda: $F_{12,124} = 6.85$, $P < 0.0001$) and temperate regions (Wilks' Lambda: $F_{12,100} = 7.92$, $P < 0.0001$). When all six habitats are analysed together, the canonical variate analyses was also significant (Wilks' Lambda: $F_{30,470} = 8.88$, $P < 0.0001$). As the trends of the individual regional analyses are captured in the combined analysis, we present only the plot for the combined ordination (Fig. 5.4). In multivariate space, the spread of species show clear clustering of rain forest and giant eucalypt forest species and this is visualized by the overlapping 95% confidence limit circles (Fig. 5.4). $\delta 13C$, leaf mass per area, leaf slenderness and wood density appears to be the major variables segregating the tropical and temperate savannas from the rain forest and giant eucalypt forest as a whole (Fig. 5.4). However, by virtue of their positioning in multivariate space, the temperate rain forest cluster, whilst being most functionally akin to giant eucalypt forest, also exhibits a mild clustering with the savanna cluster. The overlap of the rain forest and giant eucalypt forest clusters are stronger within each region, and the tropical giant eucalypt forest appear to be converging with the temperate giant eucalypt forest and temperate rain forest clusters. In contrast, the tropical and temperate rain forest regions are diverging, largely on the basis of tropical rain forest species having greater leaf area and temperate rain forest exhibiting higher leaf slenderness. Leaf mass per area, and to a lesser extent $\delta 13C$ and wood density, are responsible for the segregation of the two savannas from the rain forest-giant eucalypt forest cluster, but both savannas are also clearly segregated.

5.5 Discussion

Our univariate and multivariate analyses of leaf and bole functional traits effectively discriminated contrasting vegetation types in temperate and tropical Australia, supporting the hypothesis that that rain forest and savanna are alternative stable states (Hoffman et al., 2012; Murphy & Bowman, 2012). This provides direct support that the giant eucalypt forests are unstable successional states in the basin of

attraction of rain forest (model 3 in Fig. 5.1). The basis and significance of these hypotheses are outlined below.

5.5.1 Tropical and temperate rain forest and savanna

Tropical and temperate rain forests were functionally divergent (Fig. 5.4). Leaf area was generally larger in tropical systems than in temperate systems as expected (Webb, 1959; Givnish, 1987; Carpenter *et al.*, 1994; Royer *et al.*, 2005; Wright *et al.*, 2005). This is consistent with well known differences in physiognomy (Webb, 1959) and phylogenetic origins (Sniderman & Jordan, 2011) of the rain forest types. Experimental work by Lusk *et al.* (2013) and Xiang *et al.* (2013) show trade-offs for traits like leaf mass per area, leaf area and other leaf traits between tropical and temperate rain forest, and this might explain the tropical-temperate rain forest functional divergence. Collectively this suggests that rain forest is not a cohesive functional entity across the Australian continent, apart from the unifying factor of having a closed canopy (Specht, 1981).

There were marked leaf and bole trait differences between rain forest and savanna vegetation. Our results supported the concept that savanna plants will have relatively thicker bark than rain forest trees (Lawes *et al.*, 2013). Leaf mass per area was higher in both temperate and tropical savanna indicating intrinsic biological differences because this leaf trait correlates strongly with various leaf physiological and structural functions (Westoby, 1998; Cornelissen *et al.*, 2003; Wright *et al.*, 2004). Consistent with this interpretation is the finding of Hoffman *et al.* (2005) that leaf mass per area is a key functional trait explaining the differences between forest-savanna congeneric species pairs in central Brazilian ecosystems.

In the tropics three traits related to water relations ($\delta 13C$, leaf slenderness and wood density) showed strong difference between rain forest and savanna, but $\delta 13C$ and leaf slenderness were not significantly differentiated across temperate rain forest boundaries. Consistent both with the literature (Orchard *et al.*, 2010; Crowley *et al.*, 2012) and the concept that water use efficiency is related to water availability, was

our finding that tropical savanna species have more positive δ13C, and therefore higher water use efficiency (Farquhar *et al.*, 1989) than rain forest species. Tropical savanna species had slender leaves probably because narrow leaf width is related to radiative cooling in dry climates (Parkurst & Loucks, 1972; Nicotra *et al.*, 2011). Higher savanna wood density relative to rain forest is probably due to the higher potential for drought stress (Hacke *et al.*, 2001).

5.5.2 Giant eucalypt forests

The multivariate analyses of variance and canonical variates analyses show that overall, temperate and tropical giant eucalypt forest are functionally convergent and are closer in function to their respective rain forest types than to the savanna habitats (Fig. 5.4).

For all traits except bark thickness, univariate analyses showed that giant eucalypt forest were not significantly different from their respective rain forests. Significantly, giant eucalypt forest leaf mass per area did not differ from rain forest but was markedly different from the savanna, suggesting that the trees and shrubs of giant eucalypt forest on a whole are more functionally akin to rain forest in their leaf functioning. However, leaf mass per area in temperate rain forest was not significantly different from savanna unlike in the tropics (Fig. 5.2). This could be an inherent effect of thermal differences between the two regions, which may also explain why δ13C and leaf slenderness was not significantly different across rain forest boundaries in the temperate zone, unlike in the tropics (Fig. 5.2) (Xiang *et al.*, 2013).

Bark thickness was the only trait in the tropics that deviated from our hypothesized model that giant eucalypt forest are functionally different from rain forest but not from savanna (Fig. 5.1). This indicates that the trees in the tropical giant eucalypt forest show some affinity to savanna in their degree of fire-tolerance and contrasts with the temperate system which supports model scenario 3. The narrower spatial extent of the ecotone in tropical Queensland relative to the temperate one

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(Harrington *et al.*, 2000; Harris & Kitchener, 2005) (Fig. 1.1) could be a plausible explanation, as plants in the narrower tropical ecotone might be more prone to frequent low-intensity fires and therefore exhibit a greater degree of fire-adaptation.

The co-occurrence of rain forest and giant temperate eucalypt forests species to create distinctive vegetation types ('mixed forests') has long been recognised (Jackson, 1968), but the status of tropical communities dominated by giant eucalypt has been controversial (Warman & Moles, 2009). Our findings demonstrate that giant eucalypt forests in both the temperate and tropical regions lie within the basin of attraction of rain forest (Model 3 in Fig. 5.1). The convergence of the functional trait profiles of tropical and temperate giant eucalypt is consistent with insights from restoration ecology, which show that within a successional sequence, trait composition exhibits a clear decrease in multivariate distance with increasing restoration age, indicating trait convergence through time, regardless of whether species convergence occurs (Helsen *et al.*, 2012). For these reasons giant eucalypt forest species can be considered early to mid successional rain forest species (i.e. secondary forest species) corroborating both Schimper's (1903) early view that giant eucalypt forests are essentially rain forest, and our proposition that giant eucalypts are rain forest trees (Chapter 2; Tng *et al.*, 2012bc). The view that giant eucalypt forests are successional to rain forests would also explain the well documented tendency for their understoreys to accumulate rain forest species (Kirkpatrick *et al.*, 1988; Harrington *et al.*, 2000; Tng *et al.*, 2012d), thereby resulting in a two-tiered rain forest where the successional species form the overstorey (Adam, 1992; Tng *et al.*, 2012bc).

Despite of the great stature of the giant eucalypts in both regions, the functional profile of the giant eucalypt forest species suite on the whole was essentially the same as that of much smaller rain forest trees (Fig. 5.3). This suggests that while giant eucalypts (*E. grandis* and *E. regnans*) are often the focal point for classifying these forests (e.g. Kirkpatrick *et al.*, 1998; Harrington *et al.*, 2000), their heights contribute little to the overall functional profile of the forest. However, the contribution of height to the ability of these individual species to compete

successfully against other plants and dominate these transitional zones is consistent with the view that these plants are true ecotonal specialists (Tng *et al.*, 2012bc).

While our study examined giant eucalypt forests in tropical and temperate regions, forests of the giant eucalypt *E. diversicolor* F. Muell. exist in the Mediterranean-climate zone of western Australia. These giant eucalypt forests differ from giant eucalypt forests on the Australian east coast in the total absence of rain forest species, due to the extinction of rain forest from that region over the last 10 million years (Bowman, 2000b; Tng *et al.*, 2012c). In the context of our study, the transitory nature or instability of giant eucalypt forests associated with rain forest will likely continue as long as rain forest species are extant, or after the regional extinction of rain forests within mesic climatic zones suitable for rain forest trees. Thus *E. diversicolor* forest may be interpreted as a stable state alternative (and hence rain forest analogue) to other open woodland types (e.g. dominated by *Eucalyptus marginata* Donn ex Sm.) in this region, albeit detailed functional trait work will be needed to test this hypothesis.

5.6 Conclusion

Our study bridges landscape ecology theory and plant functional biology by examining the functional traits of representative tree and shrub species from tropical and temperate rain forest – giant eucalypt forest – savanna transitions. Functional leaf and bole trait segregation between rain forest and savanna were clear, especially in the tropics. The giant eucalypt forests however were functionally more akin to rain forest than to savanna in both tropical and temperate regions. These results augment the suggestion that giant eucalypts such as *E. grandis* and *E. regnans* are essentially rain forest trees (Tng *et al.*, 2012c) and calls for a functional, rather than floristic classification of these giant eucalypt forests. Our results also explain why rain forests can establish beneath giant eucalypt forests creating a globally-unique vegetation type. We expect this work to have important implications for the management and conservation of these unique giant eucalypt forests.

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Chapter 6

General Discussion and Synthesis

This chapter contains in part material from a manuscript that has been published as:

6.1 General discussion on key study findings

The overall aims of this thesis was to understand the ecology of giant eucalypts and giant eucalypt forest in a global context, and in doing so garner insights to inform the management of these forests, and also provide a functional and landscape ecological perspective on the classification of rain forest classification in Australia. To do this I examined rain forest, giant eucalypt forest and savanna at scales ranging from the macroecological to the species level, to reach a "top-down" and "bottom-up" synthesis.

As reviewed in Chapter 2, the ecology of giant eucalypts, and their close association with rain forest species seems to suggest that they are a specialized suite of rain forest pioneers. The occurrence of a suite of eucalypts as emergents in rain forest environments ranging from the tropical to the temperate zone compels me to propose that the overall context of giant eucalypt forests is consistent with the concept of them being rain forests, specifically a successional rain forest or a secondary forest (i.e. Corlett, 1994). However, further evidence on forest function is needed for this concept to be compelling. This is provided by experimental evidence from Chapters 3, 4 and 5.

In Chapter 3 I examined the rate of rain forest expansion in Far North Queensland and performed a "worst-case-scenario" modelling of how long it would take for rain forests to fully engulf giant eucalypt forest, which is the target vegetation for management in the region. Thus I found that rain forest was expanding across all geologies and environmental settings, but at a slower rate than previously thought. Local factors did not drive this expansion but instead, a global driver like increased atmospheric CO_2 was the most likely. Rain forest is more likely to expand into the understoreys of giant eucalypt forest than into other drier forest types. However, at the fastest predicted rate, it will be more than 2000 years before rain forest fully engulfs giant eucalypt forest assuming that the latter forest is spatially static and that there are no natural disturbances events that will bring about giant eucalypt regeneration within that period. These findings, in particular the finding that rain forest is more likely to expand into the understoreys of giant eucalypt forest, are

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consistent with the idea that giant eucalypt forests are a kind of secondary forest, albeit one occurring in marginal areas. It also supports the idea I proposed in Chapter 2 that the presence of giant eucalypts do not antagonize but could in fact facilitate rain forest regeneration in their understories.

As a corollary, I also suggested in Chapter 2 that giant eucalypts are rain forest pioneers. In temperate regions, this has been evident although not explicitly described as such in the literature on *Eucalyptus regnans* regeneration niche, but whether the same ecological thinking can be extended to tropical giant eucalypts remained to be investigated in more detail. In Chapter 4 therefore, I investigated the growth of *Eucalyptus grandis* seedlings in a three factorial treatment consisting of fumigated and non-fumigated rain forest and giant eucalypt forest soil, with and without phosphorus supplementation, to see if the "ash-bed" effect reported for temperate eucalypts is also valid for a tropical eucalypt. I found reduced survival and growth of *E. grandis* in rain forest soils. This growth inhibition was reversed by the addition of phosphorus, suggesting that the ash-bed effect, which chiefly involves the release of plant-available phosphorus after fire, is an important factor in the regeneration of tropical giant eucalypts. This finding supports the idea that the tropical *E. grandis* is ecologically very similar to the temperate *E. regnans* in regeneration niche requirements, and lends support to the view that temperate and tropical giant eucalypt forests are ecological convergent. However, a more targeted study taking into consideration the landscape ecology of these forests, and examining the ecology of their component species of these forests will be required to test such a hypothesis

In Chapter 5, I therefore presented an experiment using species functional biology to test landscape ecology theory, hence bridging the crevasse between species biology and macroecology. I achieved this by collecting leaf and bole functional traits of representative species in rain forest, giant eucalypt forest and savanna to generate a functional profile of these three putative vegetation types and then comparing their relative functional profiles in the context of alternative stable states hypotheses (Fig. 5.1). I found that tropical and temperate giant eucalypt forest are functionally

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convergent with each other while tropical and temperate rain forest are functionally divergent. Furthermore, both tropical and temperate giant eucalypt forest are functionally convergent with their associated rain forest. These findings provide empirical evidence for my hypothesis that giant eucalypts are rain forest trees that should be considered components of rain forest. It also explains my findings in Chapter 3 as to why rain forests are more likely to expand into the understories of giant eucalypt forests.

6.2 Synthesis and implications for management of Wet Tropics giant eucalypt forests and rain forest classification

Having studied giant eucalypt forest in both tropical and temperate regions as a case in point, my thesis suggests that the inclusion of emergent eucalypts within the definition of rain forest is ecologically and functionally sound. My thesis is therefore in support of a broad definition for rain forest in Australia harking back to the early definitions by Schimper (1903) but expands this definition to include giant eucalypt forests in the tropics. My thesis also supports Dale *et al.*, (1980) and Cameron (1992) who included under their rain forest scheme all transitional and seral communities with a similar floristic composition to mature rain forest (Table 1.1). However, my expanded definition of rain forest for Australia also views giant eeucalypt forest as a kind of 'secondary forest' – an ecological term that is globally used ecological lexicon. This ecological scheme is consistent in both tropical and temperate regions and could perhaps also be applicable for similar forest systems in subtropical regions.

Spercifically for the Wet Tropics region, the overall results of my thesis support the idea that *E. grandis* forest is most usefully considered as a secondary rain forest and that *E. grandis* behaves like a long-lived pioneer that regenerates *en masse* after infrequent large fire events (Fig. 6.1a). The establishment of rain forest species in the understorey of these forests can be seen as a process of succession occurring within the environmental regime of rain forest (Fig 6.1b). Conceiving of *E. grandis* forest as

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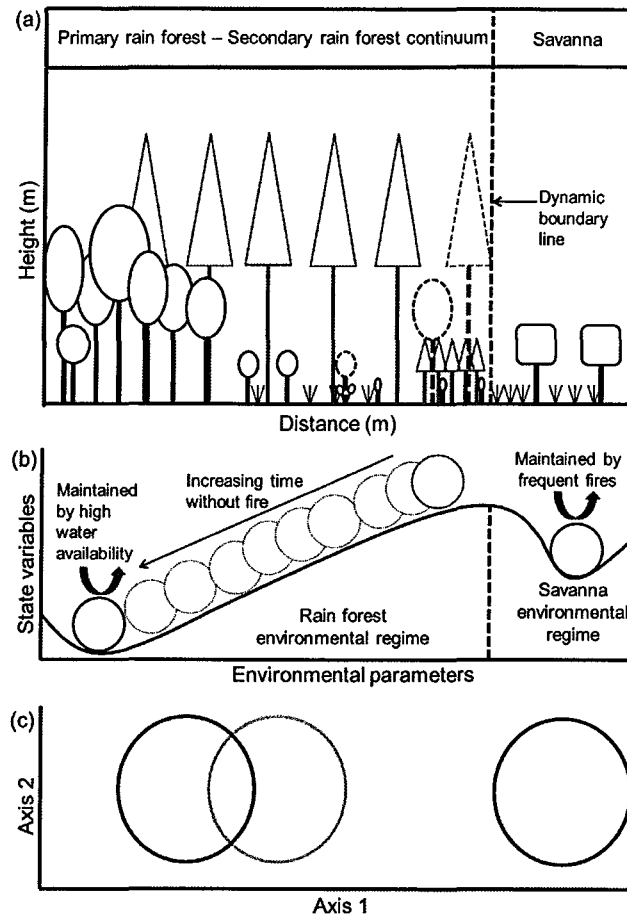
Figure 6.1 - The ecological characteristics and proposed classification schemes of rain forest – savanna vegetation transitions for the Australian wet tropics. (a) Proposed schematic vegetation classification and profile of a hypothetical rain forest (circles) – *E. grandis* forest (triangles) – savanna (squares) transition, showing the relative statures of canopy trees. Dead trees are denoted by dotted lines and the presence of grasses is depicted in the giant eucalypt forest and savanna understoreys. (b) An alternative stable state landscape ecology model explaining the state stability of rain forest and savanna. The vertical axis represents relative stability. Rain forest and savanna vegetation are in stable states maintained by water availability and fire, respectively, but *E. grandis* forests are within the "basin of attraction" of rain forest. (c) Functional profile of 70 representative trees and shrubs across the vegetation transition presented graphically. Each circle represents the functional profile for each vegetation type based on a set of traits from the leaf and wood economic spectrum (Tng *et al.*, 2013). The proximity of the circles denotes the functional relatedness.

a secondary rain forest also accords well with functional biology studies showing that rain forest and giant eucalypt forest form a functional continuum (Fig 6.1c).

Landscape ecology theory also predicts that the inherently more exposed conditions and higher fire risk associated with the interface between rain forest and savanna will provide favourable conditions for the establishment of rain forest pioneers like *E. grandis*. Therefore, rather than being threatened by it, the existence of *E. grandis* forest may be inextricably tied to natural successional processes occurring at these rain forest – savanna intergrading margins.

Such a framework integrating landscape ecology and functional biology provides a more functional classification of the rain forest – *E. grandis* forest – savanna transition which takes into consideration the dynamism of ecological boundaries (Fig. 6.1a). It also calls for a reappraisal of the need for prescription burning of these forests, and resolves the conundrum of having to burn rain forest. Moreover, it is well documented that many rain forest trees have the ability to recover from a single fire (Williams, 2000; Williams *et al.*, 2012). The most parsimonious and ecologically sensible way of managing giant eucalypt forests in the Wet Tropics therefore may be to let them be – to allow natural fuel loads to build-up and to rely on natural, stochastic fire events to shape the system, as Bowman *et al.*, (2013) suggested for similar giant eucalypt forests in southeast Australia.

Conserving a mosaic of habitats in the Wet Tropics World Heritage Area is undoubtedly important, but landscapes are inherently dynamic, and in the case of giant eucalypt forests, ecological processes operate on timescales far exceeding the lifespan of individual researchers or land managers. Effective conservation of landscapes must therefore be coupled with long-term monitoring of multiple permanent study sites throughout the region and interrogation of the palaeoecological record. The resources currently invested in trying to combat rain forest expansion into *E. grandis* forest may be better redirected in setting up long-term fire experiments in selected priority sites occupied by endangered animal populations (e.g. Laurance, 1997; Pope *et al.*, 2000). The national AusPlots project (White *et al.*

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2012) for instance, is currently setting up permanent plots in giant eucalypt forest across the Australian continent with the view of monitoring long-term vegetation dynamics. These permanent plots, in addition to fire experiments, will undoubtedly be highly informative for the future conservation of these forests. Current global phenomena such as woody vegetation thickening and rain forest expansion are part of complex global vegetation-climate feedbacks and are complementary to carbon emission reduction (Bond & Midgley, 2000; Murphy *et al.*, 2014; Chapter 3). Prescription burning, well-intentioned as it may be, may interfere with natural feedback mechanisms between the biota and the environment.

In reflection, it is ironic that while this thesis is primarily about giant eucalypts, I am forced to conclude that the often used schemata of using the dominant canopy tree to classify giant eucalypt forest as a discrete forest type (i.e. wet sclerophyll, tall open forest, wet eucalypt forest, mixed forest, etc) is inaccurate and confusing for land managers, policy makers and the general public, particularly when these forests have an understorey of rain forest trees and shrubs at varying stages of succession.

For the purposes of mapping such vegetation, I recommend a more consistent use of terms such as 'secondary rain forest complexes', 'young rain forest with emergent eucalypts' or 'mature phase rain forest with scattered eucalypt emergents' can serve as simple and less ambiguous mapping units. Such a classification scheme may also help with the adopting of more scientifically objective conservation polities that take into account the dynamism exhibited by such vegetation types. Additionally, as secondary forests is being increasingly recognized globally for their conservation significance (Martin *et al.*, 2013), considering giant eucalypt forest as a type of secondary forest creates a stronger imperative for their proper management and conservation. This in turn creates scope for much needed international comparisons, which will improve the global recognition of these systems.

6.3 Coda – giant eucalypts, Australian rain forest delimitation, and future directions

I have shown in Chapter 1 how the definition of rain forest in Australia has been fraught with controversy for over half a century: giant eucalypts have played a prominent role in these debates. Tied to this debate also, is a need to advance our understanding of the functional ecology of giant eucalypts, particularly given how big trees are gaining an increasingly prominent role in the forefront of conservation issues (Lindenmayer *et al.*, 2012) and the world's carbon budget (Stephenson *et al.*, 2014).

This thesis has attempted to add a functional component to how Australian rain forest may be delimited when giant eucalypts are involved. Unlike many systems that have trended towards the creation of complex terminology to add to a burgeoning ecological lexicon (Table 1.1), the system I have proposed is a simplification. For this purpose I have created the term 'giant eucalypt forest' in my Chapter 2 review paper referring to forests with eucalypts (>70m) dominating the overstorey layer.

Along with this terminology, I have presented experimental evidence to support the idea that these forests are within the environmental regime of rain forest and will consistently show signs of succession towards become pure rain forest (Tng *et al.*, 2014a and Fig. 6.1). In this fashion, giant eucalypt forests can also be considered a kind of secondary rain forest, whether they occur in tropical or temperate zones.

While the terminology I proposed in this thesis can be applied to vegetation classification in Australia as discussed in the previous section, my intention is not to replace tried and true terms that are already working well for vegetation mapping purposes. Rather, this terminology was devised to be easily understood by the general public, to provide a more global context for these forests, facilitate more international comparisons and to highlight the unique aspect of two-tiered forest structure of having a flammable overstorey tree layer in rain forest environment. These concepts have stimulated thinking about these tree and forest systems from a macroecological perspective, as evidenced by publications by other workers

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(Larjavaara, 2013; Prior & Bowman, 2014) that cite my review paper. In particular, Prior & Bowman (2014) show that inter-tree competition and response to tree size were particularly pronounced in species such as *E. regnans*, lending further support to the concept of Tng *et al.* (2012) that giant eucalypts such as *E. regnans* are adapted as rain forest emergent pioneers.

The idea that giant eucalypts are emergent rain forest pioneers rests on their competitive ability in rain forest environments. This is in turn underpinned by their ability to produce high levels of lignocellulosic biomass – the structural material that makes up their wood. Very recently, the genome of *Eucalyptus grandis* was sequenced, and the genes involved in wood production have been identified (Myburg *et al.*, 2014). Studying matching genes in other eucalypts could pave the way for understanding what regulates the expression of gigantism in eucalypts, and further our understanding of how eucalypts managed to penetrate the rain forest environment.

While this thesis has made a contribution to the debate on how Australian rain forest may be classified from a macroecological perspective, there is scope for much experimental work that can be done to clarify and augment the concepts proposed herein. As a start, there is a need for more information on the ecology of eucalypts and related taxa occupying rain forest or high productivity environments. In my preliminary investigations of such eucalypts, I found approximately 50 species of eucalypts from various regions of tropical to temperate Australia that fit this profile. While some of these species do not attain heights exceeding 70m, they are still of impressive stature often exceeding 50m (e.g. *Eucalyptus cyphellocarpa, E. microcorys*, etc) (Boland *et al.*, 2006; see also Fig. 2.2), and are observably always emergent over the rain forest species with which they co-occur. These species have received disproportionately less attention than giant species like *E. delegatensis, E. grandis, E. obliqua*, and *E. regnans*. It is expected that targeted experimental studies analysing the macroecology of these species will provide greater insights as to the ecological relationships between them and rain forest.

In Chapter 2, I also presented a brief analysis of the phylogeny of eucalypts and highlighted the derived positions that giant eucalypts occupy on this phylogeny (Fig. 2.5). Future work plotting all other rain forest emergent eucalypt species on a more updated eucalypt phylogeny could shed more light on the evolution of gigantism in eucalypts, historical rain forest dynamics and ultimately help shift the paradigm that eucalypts are strictly sclerophyllous or woodland species. As a corollary, the genus *Corymbia*, which is sister to *Eucalyptus*, also has members in rain forest. An example is *Corymbia torelliana*, a species typically restricted to rain forest margins which shows various morphological and ecological traits (e.g bee-dispersed seeds) (Wallace & Trueman, 1995; Wallace *et al.*, 2008) that imply that it is adapted to rain forest environments.

The recent finds of *Eucalyptus* fossils from the same subgenus as *E. grandis* (i.e. *Eucalyptus* subgenus *Symphyomyrtus*) in Patagonia, South America, has the potential to revolutionize our thinking about eucalypt evolution as a whole. These early Eocene (ca. 51.9 Ma) fossils are the oldest known *Eucalyptus* macrofossils, and indicate that *Eucalyptus* subgenus *Symphyomyrtus* is older than previously supposed (Gandolfo *et al.*, 2011; Hermsen *et al.*, 2012). Paleoecological data also indicate that the Patagonian *Eucalyptus* dominated volcanically disturbed areas adjacent to standing rainforest surrounding an Eocene caldera lake (Gandolfo *et al.*, 2011). Given the compelling paleoecological data, it is not inconceivable therefore that these early eucalypts may have been adapted to large-scale disturbances like the giant eucalypts described in this thesis. Future studies with are more robust fossil calibrated phylogeny and multiple molecular marker will augment our understanding of the eucalypt ecology in a phylogenetic context, and can be expected to improve our understanding of the adaptation of eucalypts to rain forest environments.

One avenue of research that can also be instructive to the topic of rain forest and giant eucalypts will be to conduct targeted studies of native plant regeneration under plantations of tropical giant eucalypts within Australia. Numerous observational studies of a similar nature already exist in the literature for regions where giant eucalypts such as *E. grandis* are planted as crops, and some observational studies

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also exist for *E. grandis* plantations in Australia (see Chapter 2). However, more hypothesis-driven studies looking at mycorrhizal relationships, and nutrient and water statuses of both regenerating rain forest plant and giant eucalypts in trial plots will be needed for answering the question of whether giant eucalypts have a facilitative effect on rain forest regeneration. In a similar vein, permanent monitoring plots in giant eucalypt forest, such as those being set up throughtout eastern Australia as part of the AusPlots project (White *et al.* 2012), will provide a basis for future studies on rain forest regeneration.

A greater application of functional trait analyses to the problem of rain forest boundaries can also be helpful, especially to test ecological theory and possibly to provide another dimension for consideration in conservation and management (e.g. functional diversity; Lohberg *et al.*, 2012). Functional trait analyses to such monitoring work has been used to study functional convergences throughout succession (Helsen *et al.*, 2012; Lasky *et al.*, 2014), and may provide further insights as to how rain forest can be functionally delimited along the rain forest to savanna continuum (Dantas *et al.*, 2013). Trait information for many species occupying giant eucalypt forest habitats in Australia is still lacking.

Reciprocal understandings gleaned from studies outside of Australia can also potentially bring insights for resolving the paradox of eucalypts in Australian rain forests. The extra-Australian giant eucalypt *Eucalyptus deglupta* for example, is an interesting case whose regeneration ecology deserves further study. This species occurs in rain forest environments in Papua New Guinea and has long been considered a rain forest pioneer, but comparative ecological studies of this species with Australian giant eucalypts are lacking. The regeneration ecology of *E. deglupta* is therefore expected to provide further insights for understanding giant eucalypt ecology and the delimitations of what can be called rain forest.

6.4 Conclusions

My thesis revolved around the question of whether giant eucalypts are rain forest trees, as this is pertinent not only to the conservation and management of forests

dominated by these species, but also to how rain forest is classified in Australia. My review of the biology and ecology of giant eucalypts (Chapter 2) suggests that they are specialized fire-adapted rain forest pioneers. My GIS studies (Chapter 3) showed that rain forest expands into giant eucalypt forest understoreys, which suggested that these understoreys are amenable to rain forest regeneration, i.e., that they are consistent with being secondary forests. My seedling growth experiment (Chapter 4), conducted and contextualized in the tradition of Chambers & Attiwell's (1994) study on temperate eucalypts, suggests that the regeneration niche of the tropical *E. grandis* is akin to that of temperate *E. regnans*. This provides evidence that tropical and temperate giant eucalypts in Australia are ecological convergents. The ecological convergence of giant eucalypts in both temperate and tropical regions is an ecological innovation *par excellence* on the part of eucalypts, in which a lineage of trees emblematic of open vegetation have evolved a means to survive in a rain forest environment.

Finally, the results of my functional trait studies (Chapter 5) on the representative trees and shrubs from tropical and temperate rain forest, giant eucalypt forest, and savanna leads me to conclude that the tropical and temperate giant eucalypt forest habitat is functionally convergent and more akin to rain forest than to savanna, answering the important nomenclatural question of whether giant eucalypt forest is rain forest. In the context of landscape ecology models, giant eucalypt forest falls under the regime of rain forest rather than that of savanna, and should be viewed as rain forest. I envision that the insights gleaned from my studies will contribute towards a more functional and less ambiguous classification scheme for these forests in Australia. My findings and conclusions have important implications for the conservation and management of giant eucalypts and their forests, as I discussed earlier for giant eucalypt forests in the Wet Tropics. If giant eucalypts are to be considered rain forest trees, burning or logging counters the basis of rain forest conservation.

As a whole, my thesis has used a combined "top-down" and "bottom-up" approach to understanding the ecology of giant eucalypts and their forest. On a broader scale,

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such an approach may also be effective for making intercontinental comparisons of rain forest – savanna boundaries. Synthesizing insights from species biology and landscape ecology allows for a more holistic picture of how the giant eucalypt forest system fits into landscape ecology theory, and how a suite of species has adapted to suit its unique niche. My work has set a framework for further research on tree gigantism (e.g. Larjavaara, 2013), and also set a global context for Australian rain forest, from which inter-continental comparisons may be built (e.g. Corlett & Primack, 2006). Importantly also, I envision that this format of inquiry will serve as a template for future studies on ecological convergence and species biology - ecosystems theory synthesis.

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Appendix 1
Supplementary material to Chapter 1

Table A1 - Tree species known to reach 70m in height in natural vegetation. The maximum height refers to tallest individual of the species measured to date and previous taller measurements of non-extant individuals given in parentheses. Group refers to high-level taxonomic affinity (i.e A=angiosperm; G=gymnosperm). * denotes species used in the climatic analysis presented in Fig. 2.2. Sources for distributions and heights are given as footnotes.

Taxon	Group	Family	Max. Height (m)	Distribution
*[*6]Sequoia sempervirens* (D. Don) Endl.	G	Cupressaceae	115. 7 (115.9)	NW California, SW Oregon
*[*6]Pseudotsuga menziesii* (Mirb.) Franco	G	Pinaceae	100.3 (126.5)	SW Canada to Central Mexico
*[*4]Eucalyptus regnans* F.Muell	A	Myrtaceae	99.6 (114.3)	Australia (Tasmania, Eastern Victoria)
*[*6]Picea sitchensis* (Bong.) Carr.	G	Pinaceae	96.7	Oceanic climates from Alaska to California
*[*6]Sequoiadendron giganteum* (Lindl.) J.Buchh.	G	Cupressaceae	95.7 (100.9)	West Coast of North America
*[*4]Eucalyptus globulus* Labill.	A	Myrtaceae	90.7	Australia (Tasmania, Victoria)
*[*6]Abies procera* Rehder	G	Pinaceae	89.9 (99.1)	West Coast of North America
*[*3]Araucaria hunsteinii* K. Schumann	G	Araucariaceae	89	Papua New Guinea
*[*4]Eucalyptus viminalis* Labill.	A	Myrtaceae	88.9	Australia (New South Wales, South Australia, Tasmania, Victoria)
[3]Shorea faguetiana Heim.	A	Dipterocarpaceae	88.14	Borneo
*[*4]Eucalyptus delegatensis* R.T.Baker	A	Myrtaceae	87.9 (89)	Australia (Tasmania, Eastern Victoria)
*[*10]Petersianthus quadrialatus* (Merr.) Merr.	A	Lecythidaceae	87.8	Philippines
*[*4]Eucalyptus obliqua* L'Hér.	A	Myrtaceae	87 (98.8)	Australia (New South Wales, Queensland, South American, Tasmania, Victoria)
*[*3]Koompassia excelsa* (Becc.) Taub.	A	Fabaceae	85.8	Borneo
*[*3]Shorea superba* Sym.	A	Dipterocarpaceae	85.1	Borneo
[3]Shorea argentifolia Sym.	A	Dipterocarpaceae	84.8	Borneo
*[*11]Eucalyptus nitens* H.Deane & Maiden	A	Myrtaceae	84.3	Australia (Eastern Victoria, SE New South Wales)
*[*6]Tsuga heterophylla* (Raf.) Sarg.	G	Pinaceae	82.9	Alaska to Northern California, extending into the Rocky Mountains
[3]Hopea nutans Ridley	A	Dipterocarpaceae	82.8	Borneo
*[*3]Shorea johorensis* Foxw.	A	Dipterocarpaceae	82.4	Borneo
*[*3]Shorea smithiana* Sym.	A	Dipterocarpaceae	82.3	Borneo
*[*6]Pinus lambertiana* Dougl.	G	Pinaceae	82.2	Oregon to NW Mexico
*[*6]Pinus ponderosa* Laws	G	Pinaceae	81.9	SW Canada to NW Mexico
*[*6]Abies grandis* (Douglas ex D. Don) Lindl.	G	Pinaceae	81.4	SW Canada to NW California
*[*6]Chamaecyparis lawsoniana* (A. Murray) Parl.	G	Cupressaceae	81.1	SW Oregon, NW California
*[*3]Shorea gibbosa* Brandis.	A	Dipterocarpaceae	81.1	Borneo
*[*3]Eucalyptus diversicolor* F.Muell.	A	Myrtaceae	80.5 (100.6)	Australia (SW West Australia)
*[*3]Parashorea tomentella* (Sym.) Meij.	A	Dipterocarpaceae	80.2	Borneo
*[*3]Eucalyptus nobilis* Johnson & Hill	A	Myrtaceae	79.5	Australia (NE New South Wales, SE Queensland)
[8]Abies nordmanniana (Steven) Spach	G	Pinaceae	78	Southern Russia to Turkey
[2]Eucalyptus deglupta Blume	A	Myrtaceae	78	Indonesia, Philippines, Papua New Guinea
*[*5]Eucalyptus grandis* W.Hill ex Maiden	A	Myrtaceae	77	Australia (New South Wales, Queensland)
*[*6]Abies magnifica* A.Murray	G	Pinaceae	76.8	California, Western Nevada, SW Oregon
[3]Shorea falciferoides Foxw.	A	Dipterocarpaceae	76.4	Borneo
[3]Dryobalanops aromatica Gaertn.f.	A	Dipterocarpaceae	76.2	Borneo
[3]Dyera costulata (Miq.) Hook.	A	Apocynaceae	76.2	Peninsula Malaysia
[6]Pinus monticola Dougl. ex D. Don	G	Pinaceae	73.8	SW Canada to California

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[3]*Parashorea malaanonan* (Blanco) Merr.	A	Dipterocarpaceae	72.8	Borneo
[6]*Abies ammabilis* Dougl. ex J.Forbes	G	Pinaceae	71.9	SE Alaska to Northern California
[*1,5]*Eucalyptus deanei* Maid.	A	Myrtaceae	71	Australia (NE New South Wales, SE Queensland)
[3]*Shorea parvifolia* Dyer.	A	Dipterocarpaceae	70.9	Borneo, Peninsula Malaysia, Sumatera, Thailand
[6]*Agathis dammara* (Lamb.) Rich.	G	Araucariaceae	70.1	Sulawesi
[8]*Pinus merkusii* Jungh. & de Vriese	G	Pinaceae	70	South-east Asia, Malesia, China
[*1]*Eucalyptus denticulata* I.O.Cook & Ladiges	A	Myrtaceae	>70	Australia (SE New South Wales, NEVictoria)
[*1]*Eucalyptus jacksonii* Maid.	A	Myrtaceae	>70	Australia (SW West Australia)
[*1]*Eucalyptus pilularis* Sm.	A	Myrtaceae	>70 (85)	Australia (NE New South Wales, SE Queensland)

[1]Boland *et al.* (2006); [2]Carder (1995, 2005); [3]Roman Dial (*pers. comm.*); [4]Giant trees (http://gianttrees.com.au); [5]National Register of Big Trees (http://www.nationalregisterofbigtrees.com.au/); [6]Native Tree Society (http://www.nativetreesociety.org); [7]van Pelt (2001); [8]The Gymnosperm Database (http://www.conifers.org); [9]Eucalyptologics (http://www.git-forestry.com); [10]Alcantara (2010); [11]Landmark Trees Archive (http://www.landmarktrees.net); [12]Ogden & Stewart (1995).

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Appendix 2
Supplementary material to Chapter 5

Method of phylogenetic correction for univariate traits, data analysis and trait data

As species descend hierarchically from common ancestors, statistical independence of the trait data cannot be assumed and we endeavoured to account for phylogenetic effects in our analyses. A phylogenetic tree for the study species (Table A2.1) was constructed using Mesquite ver. 2.75 based on the maximally resolved supertree for angiosperms (Bell *et al.*, 2010). As this tree was not fully resolved, genus- and species-level polytomies were resolved by obtaining additional phylogenetic information from (i) the user-supplied data repository in Phylomatic for the Ericaceae (Quinn *et al.*, 2003), Myrtaceae (Biffin *et al.*, 2010), and Proteaceae (Sauquet *et al.*, 2009) and (ii) from searches of the primary literature for the following clades: the genera *Acacia* (Murphy *et al.*, 2010), *Archirhodomyrtus* and *Rhodomyrtus* (Snow *et al.*, 2011), *Eucalyptus* (Steane *et al.*, 2011). As the phylogenetic tree was a composite from multiple sources and we lacked data on branch lengths, all branch lengths were set equal to 1.

A set of univariate one-way ANOVAs (Table A2.2) were performed for the dataset subject to phylogenetic corrections using the phylanova function in the phytools R package. To determine which groups were significantly different, *post hoc* tests were as part of the phylanova function, which performs a Bonferroni correction on the data. These results were similar to the normal ANOVAs which are presented in the manuscript.

Table A2.1 - Species mean trait values of carbon isotope ratios ($\delta13C$, ‰), leaf area (LA, mm^{-2}), leaf mass per unit area (LMA, g m^{-2}), leaf slenderness (LS), wood density (WD, g cm^{-3}), maximum height (Ht_{max}, meters) and bark thickness (BT_{index}) for 128 species collected from rain forest (RF), giant eucalypt forest (GEF) and savanna/open woodland (S/OW). For maximum height, some of the species values were reduced based on field observations in accordance with our, or published, field observations. For bark thickness, we only have data for 81 tree species.

Taxon	Veg.	δ13C	LA	LMA	LS	WD	Ht_{max}	BT_{index}
Acronychia acronychioides	RF	-33.20	44.24	116.03	3.16	0.58	15	0.050
Alangium villosum	RF	-33.39	27.20	67.84	2.70	0.54	20	0.027
Alphitonia whitea	RF	-31.52	74.91	163.81	2.84	0.58	20	0.040
Archirhodomyrtus beckleri	RF	-30.14	15.58	118.50	2.52	0.53	7	0.073
Brackenridgea australiana	RF	-33.77	49.88	114.84	3.53	0.77	6.5	0.031
Cardwellia sublimis	RF	-30.08	76.19	110.69	3.47	0.56	20	0.025
Casearia dallichiana	RF	-32.65	21.22	90.41	3.05	0.65	6	0.035
Castanospora alphandii	RF	-34.18	52.13	97.93	3.59	0.63	17	0.024
Croton triacros	RF	-32.37	44.88	99.17	2.43	0.57	10	0.043
Daphnandra repandula	RF	-34.24	40.33	48.98	3.64	0.50	9	0.047
Darlingia darlingiana	RF	-31.26	97.35	149.57	4.20	0.69	23	0.027
Doryphora aromatic	RF	-34.55	45.49	76.03	2.95	0.55	18	0.040
Eupomatia laurina	RF	-34.54	75.65	69.45	2.58	0.50	7	
Ficus leptoclada	RF	-33.32	18.95	76.94	2.50	0.48	13	0.030
Flindersia brayleyana	RF	-31.36	84.97	171.32	2.00	0.52	25	0.030
Flindersia pimenteliana	RF	-30.37	22.95	93.81	2.40	0.50	25	0.020
Geissois biagiana	RF	-33.38	129.51	103.30	2.07	0.46	25	0.025

Guioa lasioneura	RF	-33.49	23.59	128.83	2.75	0.72	9.5	0.041
Hedycarya loxocarpa	RF	-34.76	74.66	68.75	2.41	0.51	1.6	
Litsea connorsii	RF	-32.34	29.60	118.35	2.66	0.50	16	0.031
Macaranga subdentata	RF	-31.05	50.26	82.92	3.50	0.58	14	0.038
Myrsine porosa	RF	-34.75	36.31	80.65	2.72	0.68	8	0.046
Neolitsea dealbata	RF	-33.48	86.03	102.20	2.32	0.47	20	0.048
Pittosporum wingii	RF	-34.13	36.36	60.34	3.02	0.67	10	0.044
Polyosma alangiacea	RF	-32.05	59.94	90.62	2.67	0.63	20	0.051
Polyscias australiana	RF	-33.55	63.09	64.38	2.54	0.41	16	0.046
Sloanea langii	RF	-31.81	76.66	153.16	1.89	0.53	20	0.042
Steganthera laxiflora	RF	-34.49	64.02	71.09	2.46	0.50	7	0.047
Symplocos cochinchinensis	RF	-32.06	121.45	127.06	2.38	0.57	22	0.030
Tasmannia insipida	RF	-34.08	24.67	74.69	4.75	0.57	4.5	
Toona ciliata	RF	-28.02	66.40	61.96	2.12	0.53	30	0.029
Alstonia mullerana	GEF	-32.66	58.60	95.54	2.97	0.67	20	0.041
Breynia stipitata	GEF	-33.82	13.57	85.73	1.99	0.73	3.5	
Callicarpa pedunculata	GEF	-32.60	48.13	45.32	2.81	0.69	1.3	
Cryptocarya vulgaris	GEF	-32.14	27.04	125.89	2.37	0.70	12	0.046
Duboisa myoporoides	GEF	-34.42	22.74	56.12	4.11	0.32	6	0.093
Endiandra discolour	GEF	-31.19	23.37	131.48	2.30	0.58	8	0.064
Eucalyptus grandis	GEF	-30.06	26.28	156.09	4.70	0.59	58	0.030
Eucalyptus macta	GEF	-29.94	24.05	211.40	4.88	0.63	34	0.041
Euroschinus falcatus	GEF	-31.04	40.42	76.95	2.45	0.45	25	0.044
Glochidion sumatranum	GEF	-32.64	36.93	90.08	2.71	0.58	16	0.062
Guioa acutifolia	GEF	-32.16	31.13	137.28	3.03	0.74	8	0.064
Litsea leefeana	GEF	-33.17	74.28	95.30	2.02	0.49	14	0.049
Lophostemon suaveolens	GEF	-30.74	32.27	171.59	2.34	0.57	30	0.038
Macaranga involucrata	GEF	-31.51	102.12	66.89	1.31	0.42	3	
Melicope elleryana	GEF	-32.94	125.07	61.41	2.31	0.41	23	0.075
Pomaderris argyrophylla	GEF	-31.00	23.88	158.68	3.06	0.76	5	0.043
Psychotria loniceroides	GEF	-33.28	9.52	88.87	3.27	0.69	1	
Rhodomyrtus canescens	GEF	-33.64	12.34	99.12	3.23	0.69	1.7	
Schizomeria ovata	GEF	-31.32	21.26	135.62	2.49	0.54	8	0.044
Trema tomentosa	GEF	-33.02	21.79	59.04	2.60	0.46	2.5	0.071
Wikstroemia indica	GEF	-32.69	8.36	39.75	3.59	0.58	2.5	
Wilkiea pubescens	GEF	-28.88	25.62	90.67	2.09	0.60	4	
Acacia calyculata	SAV	-30.47	5.77	209.56	7.22	0.77	1.56	
Acacia flavescens	SAV	-32.82	63.54	137.88	3.40	0.80	9	0.146
Banksia aquilona	SAV	-32.62	13.82	213.62	13.60	0.72	20	0.078
Corymbia leptoloma	SAV	-29.06	24.24	192.81	4.59	0.63	19	0.064
Eucalyptus crebra	SAV	-31.89	14.62	260.48	6.75	0.70	27	0.085
Eucalyptus mediocris	SAV	-30.52	16.32	217.65	3.41	0.69	15	0.069
Eucalyptus tereticornis	SAV	-30.62	29.38	195.14	6.94	0.62	27	0.037
Eucalyptus tindaliae	SAV	-31.94	19.00	207.51	4.41	0.61	24	0.028
Ficus opposita	SAV	-33.00	55.65	120.86	2.25	0.44	4	
Hakea plurinervia	SAV	-29.35	19.81	195.81	5.80	0.72	1.6	
Hibbertia melhanioides	SAV	-30.27	3.99	164.54	3.06	0.59	1.2	
Hibbertia stirlingii	SAV	-29.65	0.17	139.46	11.60	0.61	0.35	
Persoonia falcata	SAV	-34.47	13.50	209.19	18.39	0.63	3.7	0.152
Petalostigma pubescens	SAV	-29.22	9.43	189.21	1.74	0.77	1.02	
Pomaderris canescens	SAV	-30.25	13.88	163.81	2.61	0.78	2.05	
Pultenaea millarii	SAV	-29.84	0.57	93.67	2.56	0.87	1.14	
Syncarpia glomulifera	SAV	-30.22	10.57	163.69	2.40	0.63	20	0.087

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Anodopetalum biglandulosum	RF	-31.69	4.58	105.95	2.76	0.64	15	0.043
Anopterus glandulosus	RF	-29.46	39.20	142.73	4.26	0.59	10	0.069
Aristotelia peduncularis	RF	-34.39	10.32	44.23	2.60	0.77	4	
Atherosperma moschatum	RF	-28.89	8.36	116.10	2.63	0.57	45	0.026
Cenarrhenes nitida	RF	-32.75	20.98	165.71	3.94	0.73	10	0.051
Eucryphia lucida	RF	-31.05	5.01	126.25	3.70	0.59	30	0.031
Leptospermum laenigerum	RF	-31.14	0.50	119.81	3.12	0.63	30	0.047
Nothofagus cunninghamii	RF	-30.39	1.16	130.00	1.14	0.53	50	0.032

Olearia persoonioides	RF	-32.03	3.53	153.75	2.67	0.73	4	
Orites diversifolia	RF	-33.71	10.46	149.40	5.55	0.75	8	
Tasmannia lanceolata	RF	-29.40	8.06	112.05	4.02	0.57	8	
Telopea truncata	RF	-31.84	11.21	238.80	6.36	0.67	8	
Trochocarpa cunninghamii	RF	-33.03	0.34	142.86	2.39	0.66	1.5	
Trochocarpa disticha	RF	-35.04	0.92	104.56	4.63	0.67	5	
Trochocarpa gunnii	RF	-31.64	0.47	111.38	3.32	0.67	7	
Acacia dealbata	GEF	-31.01	0.04	89.85	5.74	0.48	33	0.023
Acacia melanoxylon	GEF	-30.19	13.12	134.42	4.78	0.54	30	0.045
Acacia verniciflua	GEF	-32.16	4.67	93.74	7.22	0.62	8	0.041
Bedfordia salicina	GEF	-32.79	29.55	87.94	5.77	0.65	7	0.041
Cassinia trinervia	GEF	-33.91	2.76	46.21	11.59	0.52	7	
Coprosma quadrifida	GEF	-32.58	1.01	51.57	3.58	0.66	4	
Cyathodes glauca	GEF	-31.91	0.92	160.84	8.84	0.77	3.5	
Eucalyptus delegatensis	GEF	-31.96	29.63	186.86	3.88	0.53	87	0.030
Eucalyptus obliqua	GEF	-31.04	40.98	179.39	3.91	0.62	90	0.022
Eucalyptus regnans	GEF	-31.88	32.86	154.18	3.17	0.60	99.6	0.021
Gaultheria hispida	GEF	-32.67	4.93	113.81	4.55	0.50	2	
Melaleuca squarrosa	GEF	-31.49	0.53	93.24	2.37	0.59	11	0.038
Monotoca glauca	GEF	-32.88	1.73	132.50	4.31	0.63	6	
Nematolepis squamea	GEF	-31.26	5.71	122.03	5.93	0.77	10	0.061
Olearia argophylla	GEF	-30.81	41.67	114.65	2.73	0.67	10	0.021
Olearia lirata	GEF	-30.95	20.80	58.69	5.16	0.57	3	0.039
Oxylobium arborescens	GEF	-31.41	1.92	143.79	5.17	0.70	3.2	0.058
Pimelea cinerea	GEF	-34.05	2.12	92.13	2.97	0.52	2	
Pimelea drupacea	GEF	-34.61	4.23	56.65	4.10	0.43	3	
Pittosporum bicolour	GEF	-33.39	4.89	117.00	5.23	0.68	14	0.100
Pomaderris apetala	GEF	-32.03	20.51	124.12	2.81	0.60	13	0.044
Prostanthera lasianthos	GEF	-32.05	14.74	63.11	4.48	0.58	6	0.033
Zieria arborescens	GEF	-30.53	7.59	64.48	4.01	0.77	6	0.070
Acacia genistifolia	SAV	-30.29	0.23	286.95	7.16	0.69	1.2	
Acacia myrtifolia	SAV	-30.25	2.22	171.30	3.06	0.63	1	
Acacia stricta	SAV	-32.53	3.94	138.34	9.61	0.74	1.75	
Astroloma humifusus	SAV	-32.97	0.11	120.06	8.50	0.76	0.06	
Banksia marginata	SAV	-30.74	2.66	199.31	6.48	0.61	5	0.109
Bedfordia linearis	SAV	-31.09	2.68	166.91	12.86	0.77	3	0.091
Bursaria spinosa	SAV	-31.16	0.36	156.78	1.46	0.72	2.2	0.125
Callistemon pallidus	SAV	-30.54	3.53	202.14	6.00	0.75	4	0.117
Correa reflexa	SAV	-31.65	4.08	94.79	1.63	0.77	0.8	
Epacris impressa	SAV	-31.39	0.13	156.54	4.87	0.72	1.6	
Eucalyptus pulchella	SAV	-30.94	4.22	206.79	15.47	0.61	13	0.051
Eucalyptus viminalis	SAV	-30.23	15.48	226.69	9.26	0.67	22	0.090
Hibbertia riparia	SAV	-31.77	0.10	166.46	8.68	0.82	0.6	
Leptecophylla juniperina	SAV	-33.92	0.10	149.82	6.48	0.84	2	
Leucopogon collinus	SAV	-29.54	0.07	91.06	3.71	0.78	1.7	
Lomatia tinctoria	SAV	-30.97	0.31	188.72	8.35	0.78	0.55	
Philotheca verrucosa	SAV	-29.88	0.20	217.10	1.58	0.82	1.4	
Pimelea nivea	SAV	-30.27	0.59	144.09	1.06	0.53	1.5	
Pultenaea juniperina	SAV	-31.98	0.17	131.50	7.49	0.88	2.2	
Veronica formosa	SAV	-29.45	0.26	109.38	2.96	0.69	1.7	

Table A2.2 - Phylogenetic One-way ANOVA results for foliar and bole plant functional trait comparisons between rain forests, giant eucalypt forests and open woodland of tropical and temperate regions. Bark thickness was excluded from this analysis as it consisted of only a subset of the species in the phylogenetic tree.

Functional Trait	Tropical Queensland	Temperate Tasmania
Carbon isotopes determination	$F = 6.97, P = 0.03*$	$F = 4.11, P = 0.02*$
Leaf area	$F = 16.31, P = 0.002**$	$F = 7.31, P = 0.002**$
Leaf mass per unit area	$F = 20.56, P = 0.001**$	$F = 8.83, P = 0.0005***$
Leaf slenderness	$F = 11.48, P = 0.004**$	$F = 0.0987, P = 0.0906$
Wood density	$F = 6.63, P = 0.02*$	$F = 7.5959, P = 0.0012**$
Maximum height	$F = 4.31, P = 0.099$	$F = 17.7665, P < 0.0001***$

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Appendix 3
Publications from Ph.D candidature

Reprint attachments of papers published from this thesis, in the order corresponding to Chapters 3, 2, 5 and 6 respectively:

Tng DYP, Murphy BP, Weber E, Sanders G, Williamson GJ, Kemp J, Bowman DMJS. 2012. Humid tropical rain forest has expanded into eucalypt forest and savanna over the last 50 years. *Ecology & Evolution* **2:** 34–45.

Tng DYP, Williamson GJ, Jordan GJ, Bowman DMJS. 2012. Giant eucalypts – globally unique fire-adapted rain-forest trees? *New Phytologist* **196:** 1001–1014.

Tng DYP, Jordan GJ, Bowman DMJS. 2013. Plant traits demonstrate that giant eucalypt forests are ecologically convergent with rain forest not savanna. *PLoS ONE* **8:** e84378. doi:10.1371/journal.pone.0084378.

Tng DYP, Goosem S, Jordan GJ, Bowman DMJS. 2014. Letting giants be – rethinking active fire management of old-growth eucalypt forest in the Australian tropics. *Journal of Applied Ecology* **51:** 555–559.

Ecology and Evolution

Humid tropical rain forest has expanded into eucalypt forest and savanna over the last 50 years

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Abstract

Tropical rain forest expansion and savanna woody vegetation thickening appear to be a global trend, but there remains uncertainty about whether there is a common set of global drivers. Using geographic information techniques, we analyzed aerial photography of five areas in the humid tropics of northeastern Queensland, Australia, taken in the 1950s and 2008, to determine if changes in rain forest extent match those reported for the Australian monsoon tropics using similar techniques. Mapping of the 1950s aerial photography showed that of the combined study area (64,430 ha), 63% was classified as eucalypt forests/woodland and 37% as rain forest. Our mapping revealed that although most boundaries remained stable, there was a net increase of 732 ha of the original rain forest area over the study period, and negligible conversion of rain forest to eucalypt forest/woodland. Statistical modeling, controlling for spatial autocorrelation, indicated distance from preexisting rain forest as the strongest determinant of rain forest expansion. Margin extension had a mean rate across the five sites of 0.6 m per decade. Expansion was greater in tall open forest types but also occurred in shorter, more flammable woodland vegetation types. No correlations were detected with other local variables (aspect, elevation, geology, topography, drainage). Using a geographically weighted mean rate of rain forest margin extension across the whole region, we predict that over 25% of tall open forest (a forest type of high conservation significance) would still remain after 2000 years of rain forest expansion. This slow replacement is due to the convoluted nature of the rain forest boundary and the irregular shape of the tall open forest patches. Our analyses point to the increased concentration of atmospheric CO_2 as the most likely global driver of indiscriminate rain forest expansion occurring in northeastern Australia, by increasing tree growth and thereby overriding the effects of fire disturbance.

Introduction

Determining the dynamics of tropical rain forest and savanna boundaries is a prerequisite for a comprehensive understanding of a major feedback system within the global carbon cycle, as these two geographically and ecologically linked biomes constitute substantial above- and belowground carbon stocks and fluxes on a global scale. Brazilian rain forests, for instance, store around 250–300 t C ha^{-1} and the adjacent tropical savanna stores 135 t C ha^{-1} (Behling 2002). Numerous reports on the expansion of rain forest (Puyravaud et al. 1994, 2003; Schwartz et al. 1996; Happi 1997; Delègue et al. 2001; Banfai and Bowman 2006; Banfai et al. 2007; Silva et al. 2008) and increasing biomass in both rainforest (Lewis et al. 2009) and savanna worldwide (Bowman et al. 2001; Briggs et al. 2005; Lehmann et al. 2008; Wigley et al. 2010) signal that these biomes are potentially important global carbon sinks. The physiological mechanisms causing these sinks are related to more efficient nutrient and water use by trees in response to increased atmospheric CO_2 concentrations (Drake et al.

1997; Poorter 1998). Increases in atmospheric CO_2 concentrations have also been correlated to increased growth rates of trees (Bond and Midgley 2000), possibly contributing to the expansion of forests (Bond et al. 2003; Behling et al. 2005).

However, whether rain forest expansion or general vegetation thickening is driven by local or global drivers is a contentious issue. Many studies show that local factors (e.g., fire regimes, geology, topography) can play an important role in rain forest expansion or woody vegetation increases (Archer et al. 1995; Bond et al. 2003; Russell–Smith et al. 2004b). A difficulty in such studies lies in disentangling the importance of global drivers from the "noise" of local variation (Wigley et al. 2010). Moreover, many such landscape-scale studies (Russell–Smith et al. 2004b; Banfai and Bowman 2006) also suffer from the confounding effects of spatial autocorrelation (Murphy et al. 2010).

Advances in geospatial techniques in the past decade have enabled the study of tropical rain forest systems at a landscape scale, and the use of geographic information systems (GIS) are increasingly valuable in ecological studies of vegetation dynamics (e.g., Banfai and Bowman 2005; Brook and Bowman 2006; Wigley et al. 2010). Indeed, Bowman et al. (2010) have summarized a range of aerial photographic studies undertaken in the Australian monsoon tropics that disclose a regional increase in forest cover, despite fire regimes that are damaging components of the region's savanna biodiversity.

Here, we determine the rates of landscape change and landscape conditions associated with rain forest expansion in the humid tropics of Australia to see if there is a trend similar to that in the Australian monsoon tropics. We assess change in rain forest boundary locations in a 644.3-km^2 study area within in the Wet Tropics World Heritage Area of northeastern Queensland using aerial photography taken in the 1950s (1951–1955) and 2008. We use geospatial statistics to determine to what extent rates of rain forest change were mediated by environmental conditions (geology, elevation, topographic position, slope, aspect). Using our estimated rates of change in rain forest extent, we also project the effects of expanding rain forests on the spatial extent of other vegetation types. We expected that if global drivers were also driving rain forest expansion in the Australian humid tropics, the expansion would occur indiscriminately across all environmental conditions.

Materials and methods

Study area

The study area was situated in the Wet Tropics Bioregion, a humid tropical zone in northeastern Queensland, Australia (Fig. 1), covering approximately 1.8 million hectares. The area is characterized by a mosaic of naturally and artificially fragmented areas of tropical rain forest interspersed with fire-
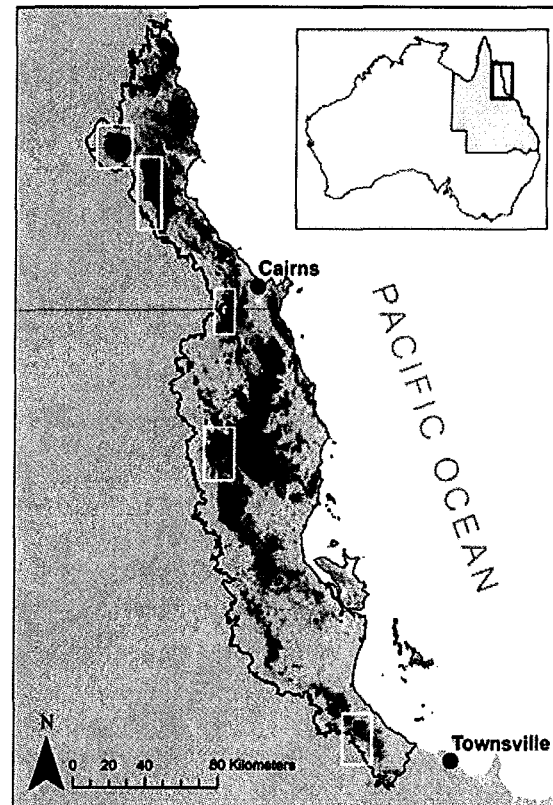

Figure 1. Selected sites for mapping of rain forest change, denoted by rectangles representing: Mt. Windsor (A), Mt. Carbine (B), Clohesy (C), Koombooloomba (D), and Paluma (E). Shaded areas denote the mapped extent of rain forest and Wet Tropics Bioregion is represented by a black outline. Weather stations used in the current study are indicated with asterisks, the northern-most being the Mossman Central Mill weather station and the southern-most being the Paluma Ivy Cottage weather station. The inset shows the outline of Australia with the state of Queensland shaded and the bounded rectangle denotes the whole study area.

prone vegetation (e.g., grassland, open eucalypt woodland, and forest [Hopkins et al. 1993; Hilbert et al. 2001]) and pasture and agricultural fields. Rain forest in this region is physionomically and floristically diverse, ranging from species-rich, complex vine forest developed on relatively nutrient-rich, moist but well-drained soils, to structurally simple rain forest types on oligotrophic moist soils (Webb 1959; Webb and Tracey 1981). Prior to European settlement in the 19th and 20th centuries, rain forest covered an estimated 965,000 ha. Subsequent human impacts resulted in a reduction in the area of rain forest to approximately 750,000 ha. Some small areas of rain forest are privately owned, although most of the remaining rain forest areas in northeastern Queensland were secured by the declaration of the Wet Tropics World Heritage Area in 1988 (Lane and McDonald 2000).

Table 1. Details of study sites.

Study sites	Date(s) of first time period aerial photography	*Area (ha)	Altitude range (m. a.s.l.)	Geology
Mt. Windsor	1951–1955	12,137	300–1328	Paleozoic granite batholiths, Hodgkinson formation, metamorphics and Devonian mudstone
Mt. Carbine	1955	14,882	311–1348	Paleozoic granite batholiths, Hodgkinson formation, metamorphics and Devonian mudstone
Clohesy	1949	11,003	350–1310	Lower Permian granites and Devonian mudstone and metamorphic
Koombooloomba	1951	18,175	672–1182	Carboniferous acid volcanics, Late tertiary basalts, Middle carboniferous granite complexes, and Quarternary Colluvium and Alluvium
Paluma	1950	8232	240–1003	Lower Permian to middle carboniferous granites and middle Paleozoic metamorphics

*The total area of grid cells for each site used in the final analysis.

A distinctive feature of uncleared rain forest tracts in the Queensland humid tropics is the occurrence of physiognomically abrupt boundaries between rain forest and eucalypt-dominated vegetation (Unwin 1989; Harrington and Sanderson 1994). A tall open forest formation dominated by tall (>40 m) eucalypts (e.g., *Eucalyptus grandis* and *E. resinifera*) typically forms a narrow fringe ranging in width from around 300 m to 4 km along the rain forest margins on the western side of the Wet Tropics Bioregion (Harrington and Sanderson 1994; Harrington et al. 2000). It has been suggested that this forest formation is in danger of being replaced by expanding rain forest (Harrington and Sanderson 1994; Goosem et al. 1999) making some elements of the biodiversity vulnerable to local extinction. The remainder of the terrestrial vegetation comprises a variable mosaic of low to medium height eucalypt-dominated open forests and woodlands occupying a broad range of freely draining substrates, heaths restricted to shallow, infertile soils, and *Acacia, Lophostemon,* or *Syncarpia* dominated forests.

The sites selected for the current study lie within the upland regions of Mt. Windsor, Mt. Carbine, Clohesy, Koombooloomba, and Paluma (Fig. 1; Table 1). Vegetation in the five study sites comprises a representative subset of the uncleared vegetation mosaics found within the Wet Tropics Bioregion, which includes rain forest and a range of vegetation types on drier areas. The geology of the five areas was highly variable, but granite and mudstone made up the bulk of the sites, with localized areas of basalt, that has been the predominant target of land clearing (Table 1).

Mean annual rainfall over the study period at the Mossman Central Mill weather station (Fig. 1) exceeded 2300 mm, mostly falling between December and April, with the highest rainfall occurring in January and the lowest in July. Mean annual rainfall at the Tully Sugar Mill weather station (Fig. 1) exceeded 4100 mm, mostly falling between December and

April, with the highest rainfall occurring in January and the lowest in August (Australian Bureau of Meteorology 2010).

Mapping rain forest change

Available 1950s black and white aerial photos (scales ranging from 1:24,000 to 1:30,000) for the five areas (Fig. 1; Table 1) were scanned at 1690 dots per inch, orthorectified and stitched to create an orthomosaic. A 30-m horizontal resolution digital elevation model (DEM) (Shuttle Radar Topographic Mission Level 2 data, licensed for use by Geoscience Australia) provided the rectification surface. A color 2008 orthomosaic covering the entire Wet Tropics Bioregion was used as a comparison image for vegetation change, and provided a 0.5-m resolution control layer for spatial referencing and adjustment of the 1950s photography. Features such as drainage lines, rocky outcrops, buildings, and occasionally the center point of a single tree canopy were aligned to corresponding features in the 2008 orthomosaic.

To estimate temporal change, we employed a grid approach and layered 50 m × 50 m cells over each of the five areas for both time periods and attributed each cell for vegetation type. Collectively, all five grid areas encompassed an area of 644.3 km². These grid cells were positioned to include both rain forest and eucalypt forest/woodland vegetation across vegetation boundaries. The vegetation for each grid cell was attributed by assigning a status of being either rain forest or "savanna" (defined here as eucalypt forest and other open woodland types), based on canopy openness (closed canopy = rain forest; open canopy = savanna) and discernable understorey components. Individual eucalypts (genera *Eucalyptus* and *Corymbia*), *Lophostemon* and *Syncarpia* can readily be recognized on aerial photographs by a fuzzy canopy, or by the general color in the 2008 orthomosaic. To facilitate the process of vegetation attribution from nonstereo image

interpretation, and as an added measure of accuracy, we overlaid a 2008 vegetation map provided by the Wet Tropics Management Authority as an additional guideline for determining vegetation type. Grid cells in which both rain forest and savanna occurred were attributed based on the dominant vegetation type. Grid cell areas that covered bare rock, roads, water bodies, built-up areas, or plantations were excluded from the subsequent analysis.

To determine the linear distance of vegetation change, we selected, for each of the five sites, 100 points on the 1950s rain forest boundary. For each of the 500 points, the distance to the nearest 2008 rainforest boundary was measured.

Correlates of rain forest change

The grid cells used for attributing vegetation type were also attributed for environmental variables including elevation, geology, proximity to water bodies or drainage systems, and distance to rain forest (Table 2). We excluded rainfall as it was strongly correlated with elevation. Elevation was calculated from the same DEM used for aerial photo rectification. A topographic position index (TPI; Jenness 2005) was calculated from the same DEM, using a search radius of 500 m. TPI provides a measure of the difference in elevation of a location

and the mean elevation of the surrounding area, and is therefore useful for classifying locations as ridges, valleys, etc. The distance from preexisting rain forest was extrapolated from the grid cells attributed for rain forest in the 1950s.

Modeling rain forest change

We treated our response variable as binary (i.e., 0 = savanna remained savanna; 1 = savanna changed to rain forest). Models representing all combinations, without interactions, of the seven environmental correlates (Table 2) considered to be relevant to rain forest change were constructed as generalized autoregressive error models (GAR_{err}), using a binomial error family with logit link. This type of model was recently developed by Murphy et al. (2010) to analyze spatially autocorrelated nonnormal data. It is similar to the simultaneous autoregressive error model for normal data (Cressie 1993) but can cope with nonnormal data types such as a generalized linear model. This type of spatial model is limited to 4000 observations, so we chose a random sample of our total dataset. Because virtually no conversion from savanna to rain forest occurred >1 km from a rain forest boundary, we selected 4000 points from within this distance. We confirmed that the GAR_{err} models successfully accounted for residual

Table 2. Local environmental correlates deemed to have an influence on rain forest change.

Variable	Description	Hypothesized effect
Aspect	Aspect was incorporated as a composite variable consisting of "northness" [cosine(aspect) × %slope] and "eastness" [sine(aspect) × %slope]. Thus, "northness" and "eastness" were indices ranging from −1 (steep south or west-facing slope) to 1 (steep north or east-facing slope).	Lower probability of expansion on steeper slopes due to increased fire intensity and reduced moisture trapping, and greater probability of expansion on steeper slopes correlated with topographic protection.
Distance from preexisting rain forest	Distance (m) from the nearest rain forest patch margin as mapped in the earlier time period (1950s) from the five sites using the first time period orthomosaic.	Declining probability of invasion at points distant from preexisting rain forest due to limitations on seed dispersal.
Elevation	Elevation (m) above sea level from 30-m resolution DEM.	Greater probability of expansion at higher elevations due higher rainfall and lower evaporation rates.
Geology	Broad classes extracted from Australian Geological Survey 1:250,000 map for the region.	Expansion rates will vary with geology due to differences in fertility and water-holding capacity.
Slope	In degrees, calculated from a 30-m digital elevation model (DEM).	Lower probability of expansion on steeper slopes, due to higher fire intensity, greater water run off.
TPI	Topographic Position Index (Jenness 2005) determined for each grid cell of a 30-m DEM by calculating the difference between the elevation of the grid cell and the mean elevation calculated from all grid cells in a circular window of radius 500 m centered on the cell of interest.	Lower probability of expansion on ridges, due to higher fire activity and lower water availability.
Distance to drainage systems/water bodies	Proximity (m) to water bodies or drainage systems.	Greater probability of expansion close to water due to higher water availability, fire protection, and propagule dispersal in water.

spatial autocorrelation using correlograms based on Moran's I (Dormann et al. 2007).

Models were evaluated using the Bayesian Information Criterion (BIC), a model selection index favoring both model fit and model simplicity (Burnham and Anderson 2002). BIC is analogous to the more widely used Akaike Information Criterion (AIC), but tends to penalize complex models more heavily than AIC. Hence, it tends to be more appropriate for large datasets where the main underlying drivers are of primary interest (Link and Barker 2006). Lower values of BIC indicate greater support for a model, relative to other models in the same candidate set. From BIC, evidence weights (w_i) were calculated for each model and these are equivalent to the probability of a given model being the best in the candidate set. The importance of each variable was evaluated by calculating $w+$, the sum of w_i for all models in which that variable occurred. For each variable, $w+$ is equivalent to the probability of the best model containing that variable, and is a useful expression of the weight of evidence for the importance of the variable. We considered that $w+$ values of < 0.73 were indicative of substantial model selection uncertainty, and that a relationship between the response and the explanatory variable in question was not well supported by the data. A $w+$ value of 0.73 is equivalent to a BIC difference of two units between the models containing the variable under examination and those not containing it. A difference of two units is a common "rule of thumb" used in ecological studies to assess evidence of an effect (Richards 2005).

We also performed a post hoc test to determine the effect of vegetation type (i.e., tall eucalypt forest vs. dry eucalypt forest: Queensland Herbarium 2009) on the probability of conversion to rain forest. Using BIC, we compared the best model from the a priori candidate set, with the same model incorporating a term representing vegetation type.

Projected rain forest expansion into tall open forest

Using standard GIS functions, a 100-m square lattice of points was generated across the entire extent of tall open forest in the Wet Tropics Bioregion, as per Queensland Regional Ecosystems vegetation mapping (Queensland Herbarium 2009), and the distance from preexisting rain forest was calculated for each point. Using a geographically weighted estimate of the rate of boundary expansion from the five study sites, we estimated the proportion of tall open forest remaining over various time periods up to 2000 years. Using a weighted average of the linear boundary change allows for a more realistic analysis, as it takes into account the variation in mean linear boundary change across the five study sites. We considered this modeling exercise conservative and representative of a "worst-case-scenario" in terms of tall eucalypt forest loss, as it assumes: (1) there will be no landscape scale perturbances

at the rain forest margins (e.g., droughts, natural fires, or cyclonic damage) that might affect the rate of rain forest expansion, (2) rain forest expansion will advance across the landscape unchecked by preexisting geographical or climatic barriers, and (iii) tall open forest eucalypt woodland boundaries are static and tall eucalypt forest does not advance ahead of the advancing rain forest.

Results

Changes in rain forest area and linear spread

At all five study sites our results show that most boundaries remained stable, but where change occurred, rain forest expanded into surrounding savanna (Fig. 2; Table 3) with a net rain forest expansion of 732 ha. The extent of rain forest expansion was greatest at Mt. Windsor (8.5%) and least at Paluma (0.8%). Conversion of rainforest to savanna was negligible.

In terms of linear boundary shifts, 25% of the 500 paired sampling points across the five sites exhibited change in the location of rain forest boundaries (Fig. 2). Across all sites, most of the boundaries showed that rain forest expansion was less than 30 m since the 1950s (Fig. 2), and at an average rate of 0.6 m per decade. Comparatively, savanna expansion was very limited (Fig. 2).

Correlates of change

There was a very strong effect of distance from the original rain forest boundary on the probability of conversion of savanna to rain forest. The probability ($w+$) of "distance to rain forest" appearing in the best model of savanna conversion was >0.99 (Fig. 3; Table 4). Little savanna situated more than 200 m from a rain forest boundary became rain forest. No other variables had any clear effect on the probability of conversion from savanna to rain forest (Table 4). Out of 256 models generated, the best model of savanna conversion ($w_i = 0.91$) explained 32% of the residual deviance at the five sites combined.

Our analyses on the effect of vegetation type on the probability of rain forest expansion show that rain forest was more likely to expand into adjacent tall open forest than into other woodland types. The difference between rain forest expansion into tall open forest and other woodland types was significant ($\Delta BIC > 2$), although the magnitude of the difference was not large (Fig. 4).

Projected rain forest expansion into tall open forest

We project that after 100 years of rain forest expansion, there would be over 85% of tall open forest area remaining (Figs. 5 and 6). The sharpest decrease in tall open forest extent is predicted to occur within the first 250 years, during which
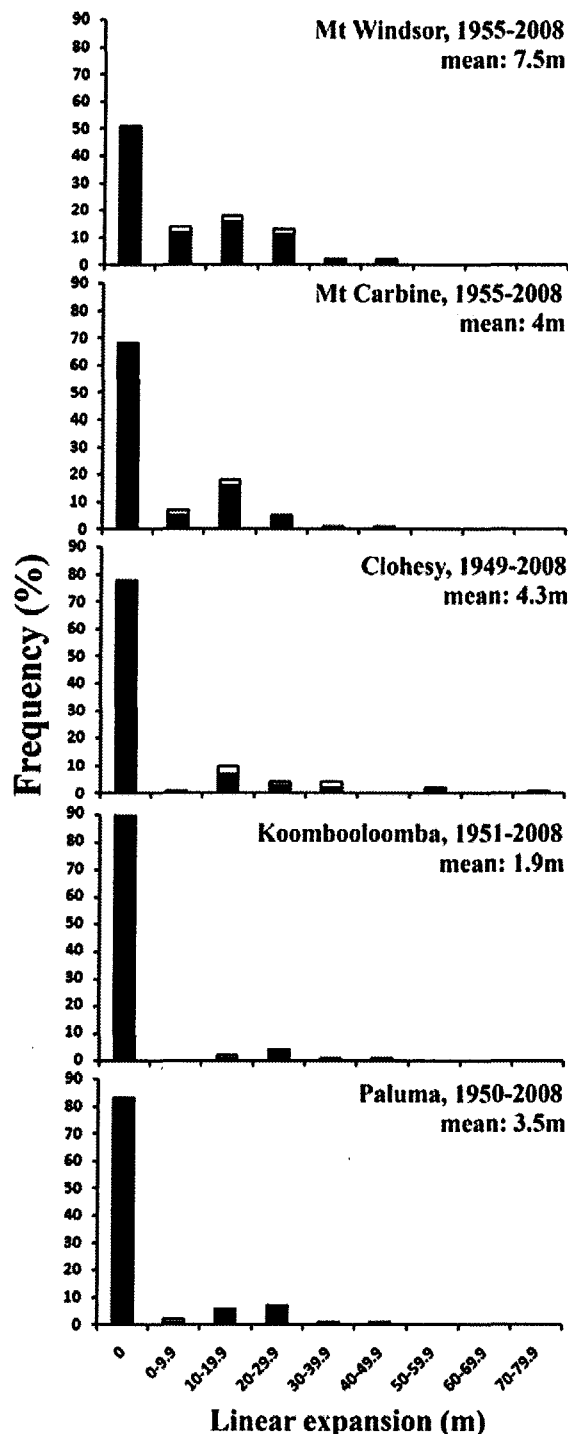
Figure 2. Linear expansion of the rain forest margins on the five study sites as measured from 100 random paired points from each site. Black bars denote points where the rain forest boundary had expanded in 2008; and white bars denote points where the savanna boundary has expanded. The mean decadal linear rain forest expansion (m) over the study period is indicated for each site.

30% of tall open forest area would be engulfed by rain forest. Expansion of rain forest into tall open forest is predicted to slow after the first 250 years, and after 2000 years there is still more than 25% of the original area of tall open forest remaining (Fig. 6).

Discussion

Although most rainforest boundaries in our study were stable over a 60-year period, those that did change all expanded into surrounding eucalypt forest and savanna resulting in a regional increase in rain forest. Such rain forest expansion has been documented in other studies throughout the tropics of Australia (Table 5). Indeed, visual comparison of the historical aerial photographs showed that there was also a general increase in cover throughout our study region (data not shown). This is in agreement with the findings of Johansen and Phinn (2005), who reported increased woody vegetation cover in the Wet Tropics Bioregion inferred from Landsat TM/ETM+ imagery from 1988 to 1999, and with reports of savanna thickening in other parts of Australia (Burrows et al. 2002; Fensham and Fairfax 2003; Lehmann et al. 2008) and worldwide (Singh and Joshi 1979; Cabral et al. 2003; Britz and Ward 2007; Wigley et al. 2010).

Unwin (1989) measured rain forest boundary dynamics on a transect in the Herberton highlands (near the Clohesy study site in the current study) over a 10-year study period, and estimated that rain forest was expanding at 1 m year^{-1}, which is similar to our upper estimate (45 m in 53 years, equivalent to 0.8 m year^{-1}). However, our results suggest that on a broader landscape scale, rain forest expansion typically occurs at a much slower rate (Fig. 2; Table 3).

Our spatially explicit modeling approach showed that expansion occurred indiscriminately on all geologies and at all elevations, although the rate and amount of expansion varied among the five sites. The reasons for the different extent of rain forest expansion between the five sites could not be explained by the set of environmental variables used in our analyses. Past logging of tall eucalypt forest and rain forest (Crome et al. 1992) does not appear to have influenced rain forest expansion, given that rain forest expansion was found on all sites regardless of logging history. For instance, the Mt. Carbine site has not been logged but still exhibited rain forest expansion. Nonetheless, rain forest was found to exhibit a higher probability of expansion into tall eucalypt forest (Fig. 4) than into more open forest and woodland types. This was expected, as the environment in tall eucalypt forest is probably more amenable to rain forest regeneration (Unwin 1989). That rain forest expanded into both tall open forest and other woodland types, albeit more slowly than into woodland types, bolsters our conclusion that this process occurs indiscriminately throughout the study area.

Table 3. Change in area extent of rain forest and savanna in the five study sites from the 1950s to 2008.

	Year	Rain forest area (ha)	Savanna area (ha)	Proportional change (Rain forest to Savanna) (%)	Proportional change (Savanna to Rain forest) (%)	Net change in rain forest area (%)
Mt. Windsor	1950s	4356	7781	0.8	5.2	8.5
	2008	4724	7413			
Mt. Carbine	1955	5232	9650	0.8	1.3	1.6
	2008	5313	9569			
Clohesy	1949	5075	5929	0.1	1.6	1.8
	2008	5165	5839			
Koombooloomba	1951	5159	13,016	2.6	2.3	3.1
	2008	5319	12,856			
Paluma	1950	4224	4008	0	0.8	0.8
	2008	4257	3975			
Combined	1950s	24,046	40,384	0.9	2.2	3.2
	2008	24,778	39,652			

Figure 3. The observed (bars) and predicted (line) probabilities of conversion of savanna to rain forest in relation to distance to the original rain forest boundary. The model predictions are based on multimodel averaging of the entire candidate set of models, weighted according to w_i and assuming mean values for all other variables.

Our statistical modeling showed that the only significant correlate of rain forest expansion was distance to preexisting rain forest. This finding is concordant with Banfai et al. (2007) who demonstrated that monsoonal rain forest expansion in Kakadu was most strongly correlated with distance to preexisting rain forest. Contrastingly, field surveys undertaken by Russell–Smith et al. (2004a) suggests that rain forest in the Iron Range region of Cape York also expands via a process of "nucleation" around focal trees in the savanna leading to an eventual rain forest "irruption" via coalescence of nuclei. It is possible that successional processes such as nucleation and irruption are difficult to quantify using GIS methods, particularly when such successional processes are in the early stages.

Our findings are broadly consistent with a diversity of localized studies in northern Australia (Table 5). Ash (1988) argued that rain forest boundaries in the Wet Tropics are strongly controlled by environmental factors, such as geological disjunctions and precipitation gradients, which results in their stability. Topography can also provide "fire shadows" to protect rainforest from frequent fires that occur in eucalypt savannas (Webb 1968; Bowman 2000). Russell–Smith et al. (2004b) found rain forest expansion in the Iron Range on eastern Cape York Peninsula across all geologies sampled, but they also detected a higher probability of rain forest expansion on more fertile geologies. Harrington and Sanderson (1994) reported rain forest expansion in the Mt. Spurgeon area (part of the Mount Carbine region in the current study)

Table 4. Importance values (w+) of environmental predictors of combined rain forest expansion at the five study sites, based on the Bayesian Information Criterion (BIC). "w+" can be interpreted as the probability of that variable being in the best model. As a "rule of thumb," values of w+ ≥0.73 (shown in bold) can be interpreted as clear evidence of an effect (Richards 2005).

Variable	w+
Distance to preexisting rain forest	>**0.99**
Topographic position index	0.04
Elevation	0.02
Slope	0.02
Geology	0
Distance to drainage	0.02
Aspect	0

using visual interpretation and manually delineating vegetation types from aerial photography taken in the 1940s to the 1990s.

Harrington and Sanderson (1994) suggested that the expansion of rain forest into tall open forest is a threatening process to native mammals such as the Yellow-bellied Glider (*Petaurus australis*) and Brush-tailed Bettong (*Bettongia tropica*) that are restricted to tall eucalypt forest habitats. Their work sparked concern for the fate of these forests and led to calls for managers to use fire to limit rain forest expansion. However, our projections of rain forest expansion show that these tall open forests will largely remain intact within the next century, and will still persist within the next 2000 years (Fig. 5 and 6). The initial steep rate of rain forest en-

gulfment in the first 250 years (Fig. 5 and 6) represents the infilling of embayments of tall open forest existing near the rain forest margins. It is important to note that our analysis was based on the very unlikely scenario that the region would remain undisturbed by landscape fires, and therefore represents an exaggeration of the actual trajectory of rain forest expansion. There is no doubt that some combination of tropical cyclones, droughts, and landscape fires within the next 2000 years will push back at least some rain forest margins, and stimulate large-scale natural regeneration of tall open forest that is generally thought to depend on disturbance for regeneration (Ashton 1981, Adam 1992). Further, even if all the tall open forest understoreys currently have a rain forest understorey, the decline of the overstorey eucalypts, particularly those dominated by *E. grandis*, may take another couple of centuries, given the inherent longevity of tall open forest eucalypts (e.g., 500 years in *E. regnans* [Wood et al. 2010], a eucalypt species similar to *E. grandis* in habit and regenerative strategies). Moreover, it is possible that *E. grandis* forests are unstable ecotonal states that will shift spatially as the rain forest expands outwards (Warman and Moles 2009).

It has been suggested that European colonization and related pastoral activities may have altered the fire regimes previously affected by Aborigines and lightning strikes (Unwin 1983, 1989; Ash 1988). If fire suppression since European colonization was a key driver of rain forest expansion, we would expect a clear signal of expansion from fire-protected areas near drainage systems, or topographically protected areas (e.g., Brook and Bowman 2006), rather than the trend of
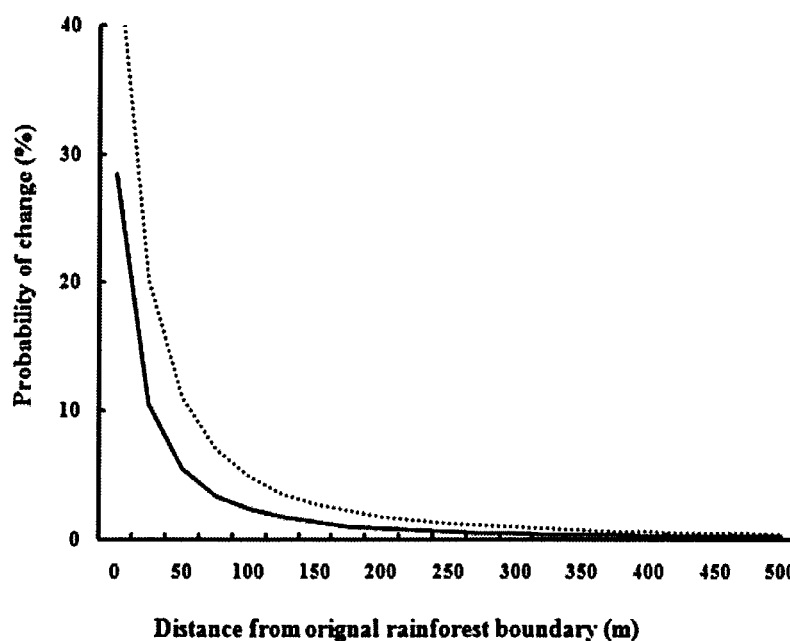
Figure 4. The probabilities of conversion of tall open forest (dashed line) and other dry forest types (unbroken line) into rain forest in relation to distance to the original rain forest boundary.

Y-axis: Probability of change (%) — 0, 10, 20, 30, 40
X-axis: Distance from orignal rainforest boundary (m) — 0, 50, 100, 150, 200, 250, 300, 350, 400, 450, 500

Figure 5. Projection of the engulfment of tall open forest (dark gray) by rain forest (light gray) at Mt. Windsor after 100, 250, and 2000 years, based on an average rain forest expansion rate of 6 m decade^{-1}. Inset shows the Mt. Windsor study site (Fig. 1) and the bounded area is the selected area for illustrating the time series. Note how the irregular shape of the tall open forest patches slows the rate of rain forest engulfment.
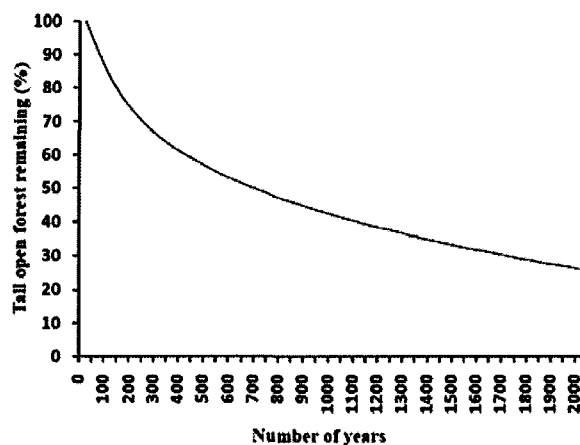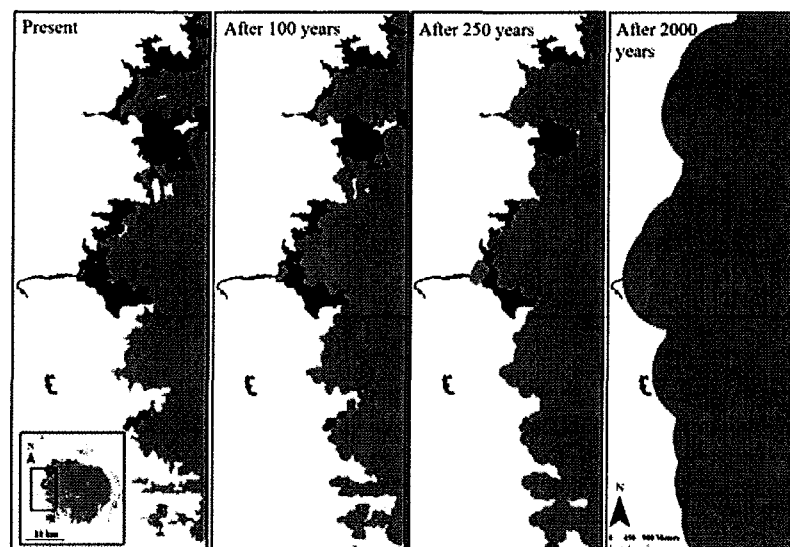

Figure 6. The extent of tall open forest predicted to be engulfed by rain forest over time.

indiscriminate expansion. Further, the palynological record shows that Aboriginal landscape burning was unable to stop the climate-driven expansion of rain forest at the commencement of the Holocene (Haberle 2005), supporting our view that changed fire regimes are not the explanation for the expansion of rainforest.

Several global drivers of vegetation change have been proposed in the recent literature, which include increased temperature, rainfall, atmospheric nitrogen deposition, and atmospheric CO_2 concentrations. In savannas, rainfall, rather than temperature, is more likely to influence tree cover, particularly during extreme events such as prolonged droughts (Fensham et al. 2005). Likewise, humid tropical forests depend on abundant and regular water supply and drying trends can result in forest retraction (Behling 2002; Pennington et al. 2004; Silva et al. 2009). Mean annual rainfall for northeastern Queensland in the last decade fell by more than 2% compared to the previous 30 years (Queensland Government 2011),

suggesting that a wetting trend is not responsible for the rain forest expansion.

Atmospheric nitrogen deposition is another candidate driver of vegetation change (Pearson and Steward 1993). However, the magnitude of atmospheric nitrogen deposition, and the effects, if any, on the terrestrial vegetation has not been studied in Australia and there is no regional source for this pollution, unlike many regions in the northern hemisphere. Also, atmospheric nitrogen deposition has been found to have a more significant effect on species composition within ecosystems, rather than large increases in biomass (Matson et al. 2002; Bobbink et al. 2010).

With the exclusion of rainfall, temperature effects, and nitrogen deposition, the most parsimonious explanation for the indiscriminate rain forest expansion in the current study is the increase in atmospheric CO_2, consistent with earlier explanations of landscape-scale rain forest expansion in the Australian monsoon tropics (Banfai and Bowman 2005, 2006,

Table 5. Summary of literature on rain forest expansion in Australia.

Location	Reference
Kakadu, Northern Territory	Banfai and Bowman (2005, 2006, 2007); Bowman and Dingle (2006)
Litchfield National Park, Northern Territory	Bowman et al. (2001)
Gulf of Carpentaria, Northern Territory	Brook and Bowman (2006)
Cape York Peninsula, Queensland	Russell–Smith et al. (2004b)
Atherton, Queensland	Harrington and Sanderson (1994)
Herberton, Queensland	Unwin (1983, 1989)
Kirrama, Queensland	Harrington and Sanderson (1994)
Mossman, Queensland	Lawson et al. (2007)
Mt. Spurgeon, Queensland	Harrington and Sanderson (1994)

2007) and elsewhere (Wigley et al. 2010). Bowman et al. (2010) suggest that rain forest expansion is a signal of global environmental change that is so strong that it is overwhelming any retardant effect fire might have on rain forest. The implications of this vegetational shift from flammable savanna and eucalypt forest to rainforest are significant not only at a local scale for biodiversity and management, but may constitute an important carbon cycle feedback at a global scale. Continued rain forest expansion in tropical regions worldwide could possibly instigate a cascade of feedbacks resulting in further land cover changes due to changes in carbon sequestration, albedo, evapotranspiration, fire incidence, cloud nucleation among others (Wigley et al. 2010), and has the potential to significantly alter the earth system within a relatively short time frame.

Acknowledgments

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Plant Traits Demonstrate That Temperate and Tropical Giant Eucalypt Forests Are Ecologically Convergent with Rainforest Not Savanna

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Abstract

Ecological theory differentiates rainforest and open vegetation in many regions as functionally divergent alternative stable states with transitional (ecotonal) vegetation between the two forming transient unstable states. This transitional vegetation is of considerable significance, not only as a test case for theories of vegetation dynamics, but also because this type of vegetation is of major economic importance, and is home to a suite of species of conservation significance, including the world's tallest flowering plants. We therefore created predictions of patterns in plant functional traits that would test the alternative stable states model of these systems. We measured functional traits of 128 trees and shrubs across tropical and temperate rainforest – open vegetation transitions in Australia, with giant eucalypt forests situated between these vegetation types. We analysed a set of functional traits: leaf carbon isotopes, leaf area, leaf mass per area, leaf slenderness, wood density, maximum height and bark thickness, using univariate and multivariate methods. For most traits, giant eucalypt forest was similar to rainforest, while rainforest, particularly tropical rainforest, was significantly different from the open vegetation. In multivariate analyses, tropical and temperate rainforest diverged functionally, and both segregated from open vegetation. Furthermore, the giant eucalypt forests overlapped in function with their respective rainforests. The two types of giant eucalypt forests also exhibited greater overall functional similarity to each other than to any of the open vegetation types. We conclude that tropical and temperate giant eucalypt forests are ecologically and functionally convergent. The lack of clear functional differentiation from rainforest suggests that giant eucalypt forests are unstable states within the basin of attraction of rainforest. Our results have important implications for giant eucalypt forest management.

Introduction

The study of ecotones between forest and open vegetation has been central to the development of ecological and evolutionary theory [1–5]. Such vegetation transition zones may provide insights into global change biology [6,7]. In particular, they provide model systems to investigate how extrinsic factors (e.g. fire, soils and climate) [8–10] and intrinsic processes such as biological feedbacks [11–13] contribute to the dynamics of ecosystems. They are therefore particularly important for testing contemporary ecological theories such as Alternative Stable States models [14,15].

Alternative Stable States models are becoming increasingly useful in explaining ecological dynamics, with empirical evidence for their existence at scales ranging from species assemblages [16,17] to biomes [18]. These models suggest that many ecosystems exist as stable states and are often depicted as "balls" that lie in "basins" or domains of attraction in a three-dimensional 'stability landscape'. The depth of the "basins" denotes the stability of the ecosystems [19–21] (Figure 1). These models differ from classical succession models in which ecosystems slide along a continuum of steady states [14].

Alternative Stable States systems therefore arise from interactions between extrinsic and intrinsic factors. Changes in extrinsic factors, such as climate and fire [22–24], tend to drive changes in ecosystems, including transitions from one stable state to another. However, the stable states only exist when intrinsic characteristics of the ecosystem generate positive feedbacks that create and maintain stability [25–29]. For example, in fire-susceptible regions different ecosystems may occur as alternative stable states because of different fire
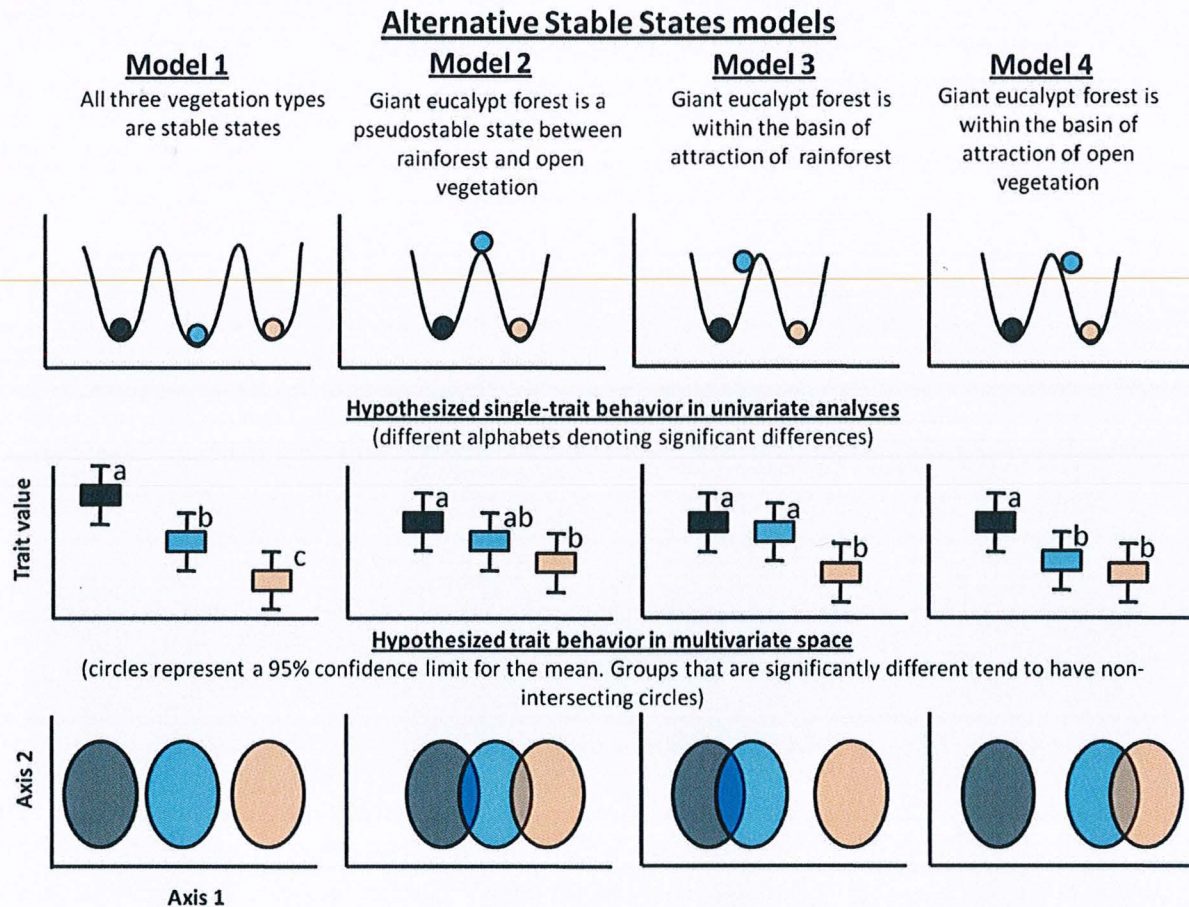
Alternative Stable States models

Figure 1. Idealised Alternative Stable States 'ball and cup' scenarios for rainforest (dark grey), giant eucalypt forest (blue) and open vegetation (orange) and their corresponding hypothesized trait behavior in univariate and multivariate analysis outputs. In each case, the overlap between to the confidence limits of each functional profile will denote the functional affinities between habitats.

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regimes caused by differences in fuel load, flammability, microclimate or other factors. In such instances the characteristics of the organisms in each ecosystem contribute to creating different fire regimes. Measuring targeted functional traits [30] of the component organisms of ecosystems is therefore an obvious way to test whether these ecosystems represent alternative stable states, as these traits can be of great significance in plant function, community assembly and ecological processes [29–31]. For example, leaf mass per unit area (LMA), a commonly studied functional trait, is correlated with potential relative growth rate or mass-based maximum photosynthetic rate, leaf lifespan, leaf defences, etc. [30], and has been shown to be significantly different across the forest – savanna divide [32,33].

The east coast of mainland Australia and Tasmania presents an excellent geographical setting to macroecologically study forest-open vegetation transitions within a single continent.

From the tropics to the temperate zone, rainforests exist as disjunct patches within a matrix of eucalypt-dominated savanna or open woodland [34,35] (Figure 2). Giant eucalypt forests (also locally known as tall open forests, wet sclerophyll forests or mixed forests) dominated by eucalypt species that can attain heights exceeding 70m, are often observed wedged in the ecotone between rainforest and savanna or open canopy vegetation [36]. In the tropics, these giant eucalypt forests are dominated by *Eucalyptus grandis* W. Hill ex Maiden and range from a few hundred meters to a few kilometres wide in extent [37,38] while in temperate zones in Victoria and Tasmania, similar forests dominated by a range of species (e.g. *E. regnans* F. Muell., *E. obliqua* L'Hér.) may predominate over several kilometres [36,39]. Although these forests have no species in common, there are phylogenetic links between these geographical regions, evidenced by the presence of shared genera and subgenera. These forests include the world's tallest
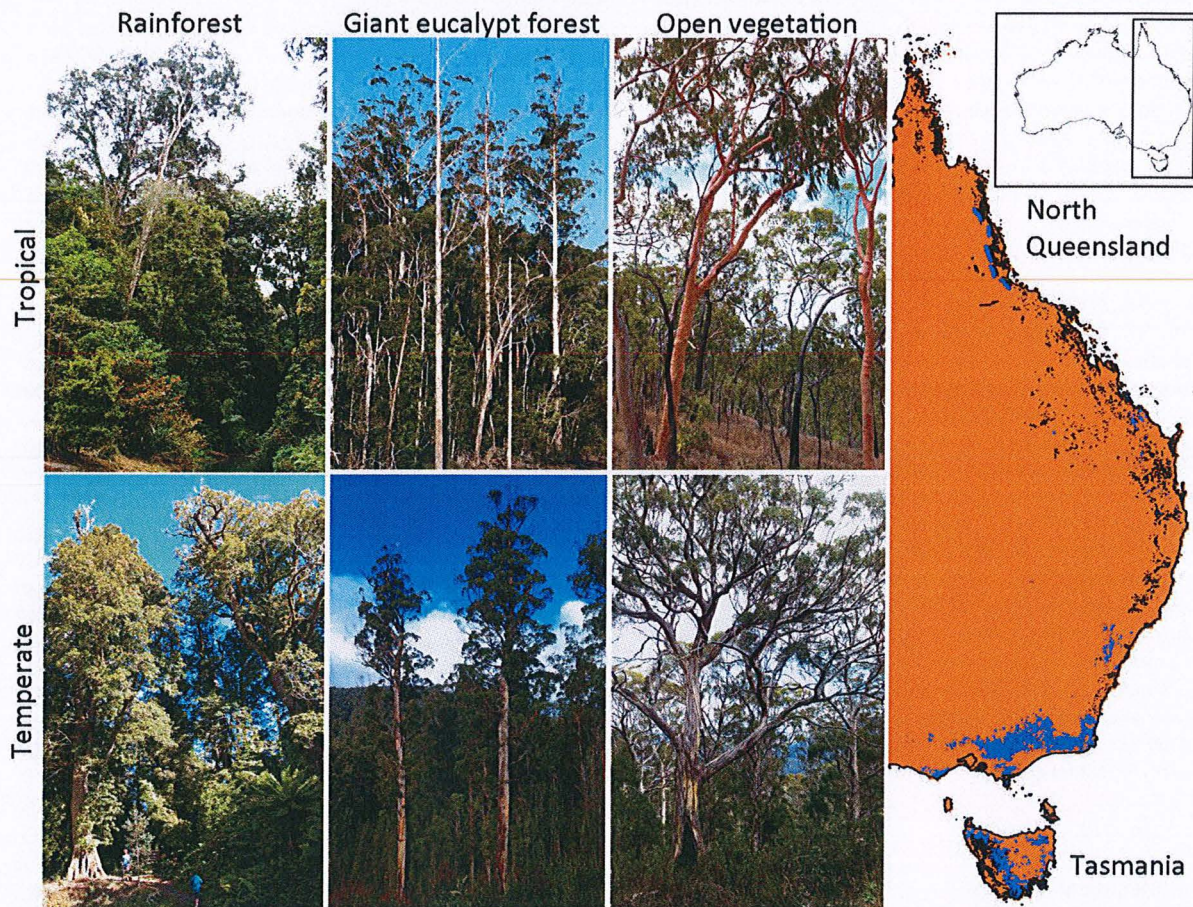
Figure 2. The distribution of rainforest (black) and giant eucalypt forest (blue) along the east coast of the Australian continent. The orange-coloured regions are open vegetation (including savanna and open eucalypt woodland). The ecotonal nature of giant eucalypt forest is most pronounced in tropical north Queensland, where giant eucalypt forests form narrow bands between rainforest and savanna (spatial extent exaggerated for clarity), and in cool temperate Tasmania, where giant eucalypt forests form a broad transition between the west and the eastern parts of the island. The inset images feature representative rainforests, giant eucalypt forests and open vegetation of the tropical and temperate zones. Note the taller stature and open canopy of giant eucalypts relative to rainforest in the understoreys.
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angiosperms [36], are home to several important threatened species [38], and represent major carbon sinks [40,41]. Together, giant eucalypt forests and rainforests have been the focus of major conflicts between ecological and economic interests because they are major forestry resources and extensive areas have been cleared for agriculture [42]. In temperate Australia, logging of these forests is ongoing.

Warman and Moles [14] hypothesized that the tropical *E. grandis* forests are unstable states forming an ecotone between rainforest and savanna (Figure 1). By contrast, Wood & Bowman [43] inferred that temperate giant eucalypt forests in Tasmania are stable states, but of lower stability (i.e. occupying a shallower basin of attraction; Figure 1) than the adjacent temperate rainforest and open vegetation. However, it remains

unclear whether these tropical and temperate systems are functionally convergent, and whether it is possible to create a unified Alternative Stable States model for these geographically distant, but ecologically similar systems [36]. Several authors have argued that the eucalypt dominants of these forests are essentially rainforest successional species [36,44,45]. However, these forests have largely been viewed as discrete vegetation types distinct from rainforest due to the subjective vegetation classifications based on the eucalypt dominants (i.e. Model 1; Figure 1). A sound landscape ecology theory augmented by functional trait based understanding of the ecology of these giant eucalypt forests is necessary for effective management of these dynamic ecosystems. If these forests are functionally convergent with each other across

tropical and temperate regions, and if they are indeed unstable ecological states (sensu Warman and Moles [14]), the traditional approaches to their ecological management and conservation will need revision.

Adopting a macroecological approach, we test whether the functional traits of trees and shrubs found in the rainforest/open vegetation transitions in both tropical and temperate regions are consistent with the patterns expected if Alternative Stable State theory applies to these vegetation (Figure 1). We also test whether the giant eucalypt forests of the tropical zone and the temperate zone are functionally convergent. First, we define state scenarios under an Alternative Stable States context, for rainforests, giant eucalypt forests and open vegetation (Figure 1). Within both temperate and tropical regions, we expect that giant eucalypt forest will fall under one of four possible models: (Model 1) it forms a third discrete stable state; (Model 2) it is an unstable state intermediate between the stable states of rainforest and open vegetation; (Model 3) it is unstable and falls within the basin of attraction of rainforest, or; (Model 4) it is unstable and falls within the basin of attraction of open vegetation types (Figure 1). Second, we use univariate analyses to compare each functional trait across vegetation types and multivariate analyses to visualize and compare the functional profile for each vegetation type (Figure 1). In addition, the proximity of giant eucalypt forest species from both regions in multivariate space will indicate the degree of functional convergence. This is the first study to explicitly link functional trait behavior and Alternative Stable States models in Australian terrestrial ecosystems (see also Dantas et al. [33]).

Materials and Methods

Ethics Statement

Permission to sample vegetation was obtained from the Queensland Government Environmental Protection Agency (permit number WITK07872410) for North Queensland sites, and the Department of Primary Industries, Parks, Water and Environment (permit number FL12268) for Tasmanian sites. The field studies did not involve threatened or endangered species.

Study Sites And Sample Collection

We sampled rainforest, and the surrounding giant eucalypt forest and open vegetation but did not sample treeless grasslands or sedgelands in two regions: tropical north Queensland and cool temperate Tasmania. North Queensland experiences a humid tropical climate with a typical site (Herberton: 17°38′S, 145°39′E) having a mean maximum annual temperature of 27.1°C and a mean annual rainfall of 2240 mm. The climate is thermally aseasonal, but has a summer-rainfall bias [46]. The regions of Tasmania studied here experience a cool temperate climate with a mean maximum annual temperature of 18.4°C and a mean annual rainfall of 2070mm for a typical site (Arve Valley: 43°14′S, 146°79′E). The climate is thermally seasonal and has winter-dominated precipitation [46]. In each region the three vegetation types are readily recognised, allowing for a priori allocation of vegetation samples and species; (i) rainforests

have closed canopies and an absence of eucalypts; (ii) giant eucalypt forests are emergent above either rainforest, or a mix of shrubby and grassy understoreys, and; (iii) open vegetation is dominated by shorter eucalypts and has shrubs and herbaceous (including grass) species tolerant of high light environments. Tropical open forests/woodlands have a well developed grassy understorey and are classified as tropical savannas. Open vegetation in the temperate region is referred to here as savanna, as they can have some structural similarities with tropical eucalypt savannas. In both regions, the tree and shrub species measured for functional traits (Table 1) were selected on the basis of their relative abundance in at least one of the localities, with the aim of capturing a representative spread of species in all three vegetation types. While many of the species sampled were widespread within their thermal zone, the trait data for any given species were taken from specimens collected from only one locality. The few species that occurred in more than one vegetation type were only sampled in the vegetation type where they occurred at the highest abundance. This selection process, based on extensive fieldwork to indentify species and assess their community affinities, was designed to minimise the confounding effect of giant eucalypt forest at different successional stages having varying components of rainforest species. Although vines were common in the tropical vegetation types, they were not sampled for trait measurements because of their low representativeness in temperate rainforest and giant eucalypt forest, and also because not all the functional traits used for our tree and shrub species will be applicable to vines.

At the following three localities near the western edge of the Wet Tropics World Heritage Area we sampled the three vegetation types: Davies Creek (17°08′S, 145°22′E), Mt Baldy (17°17′S, 145°25′E) and Paluma (18°56′S 146°10E). At each site the rainforest was the simple notophyll vine forest type [47]. Eucalyptus grandis dominated the giant eucalypt forest, and at all three localities, the understorey exhibited the full range of variability of being grassy-shrubby to being dominated by mesophytic broadleaved trees. The savanna was dominated in different localities by different eucalypt species (Eucalyptus crebra F. Muell., E. Mediocris L.A.S. Johnson & K.D. Hill, E. tereticornis Sm., E. tindaliae Blakey) with grassy or shrubby understoreys [48]. We sampled 32, 22 and 16 species from rainforest, giant eucalypt forest, and savanna respectively (Appendix S1 and Table S1 in Appendix S1). For the most part, species were exclusive to one vegetation type.

Field sampling in Tasmania was undertaken in cool temperate rainforest and giant eucalypt forest from the northeast (41°14′S 147°44′E), southeast (42°56′S 147°17′E) and southern localities (43°05′S 146°43′E). This widespread sampling allowed us to sample the full structural range of cool temperate rainforest types (sensu Jarman et al. [49]) associated with the two dominant giant eucalypt species, Eucalyptus regnans and E. obliqua [50]. These rainforests are dominated by some combination of Nothofagus cunninghamii (Hook.) Oerst., Atherosperma moschatum Labill. and Anodopetalum biglandulosum (Hook.) Hook.f. The more patchy distribution and lower species richness of cool temperate rainforest and the broad extent of giant eucalypt forest

Table 1. Functional traits selected for the current study and their functional significance relevant to the current study.

Functional Trait	Unit	Functional significance of relevance to current study	Refs
Leaf Traits			
Delta 13 C (δ^{13}C)	‰	Correlated to plant water use efficiency and may also segregate plants of different successional status.	1
Leaf Area	mm²	Consequential for leaf energy and water balance. Interspecific variation in leaf size has been connected with climatic variation, where heat stress, cold stress, drought stress and high radiation all tend to select for relatively small leaves.	2
Leaf mass per area (LMA)	g m⁻²	Correlated with potential relative growth rate. Higher values correspond with high investments in structural leaf defences and leaf lifespan, but also slower growth.	3
Leaf Slenderness	Unitless	Involved in control of water and temperature status. Slender leaves have a reduced boundary layer resistance and are can thus regulating their temperature through convective cooling more effectively.	4
Bole Traits			
Wood density	g cm⁻³	Positively correlated with drought tolerance and tolerance of mechanical or fire damage; related to stem water storage capacity, efficiency of xylem water transport, regulation of leaf water status and avoidance of turgor loss.	5
Maximum height	M	Positively correlated with competitive ability of plants.	6
Bark thickness	Unitless	Correlated to fire resistance with thicker bark expected in fire prone areas.	7

1 [73,80,81]
2 [61,63,74]
3 [69,82; 83]
4 [84,85]
5 [76,86–90]
6 [51,69,91]
7 [57,92,93]

necessitated a slightly different protocol than used in tropical Queensland. For the giant eucalypt forests, we restricted our sampling to areas dominated by *Eucalyptus regnans* or *E. obliqua*. Open woodland (savanna) adjacent to rainforest and giant eucalypt forest was geographically restricted at the northeastern and southern sampling sites. Because the suite of savanna species and their dominant overstorey eucalypts are common and geographically widespread in Tasmania, it was decided that sampling species of this vegetation type from southeastern localities was sufficient to obtain a representative Tasmanian sample. This savanna vegetation was dominated by *Eucalyptus pulchella* Desf. with *E. viminalis* Labill. co-dominants and a shrubby understorey. We sampled 15, 23 and

20 species from temperate rainforest, giant eucalypt forest and savanna, respectively (Appendix S1 and Table S1 in Appendix S1).

For each species sampled, we measured and compiled functional trait data on at least four to five mature (> 60% potential height) individuals per species. We measured a set of four leaf traits and three bole traits (Table 1), following methods outlined by Cornelissen et al. [30]. These traits are related to shade-tolerance, light use efficiency, water use efficiency, drought tolerance, nutrient use, growth rate, and fire resistance [30] (See also Table 1 and references therein). For leaf carbon isotope ratio (δ^{13}C) determination, the leaves of four to five individuals were bulked, ground finely and δ^{13}C assessed by the School of Plant Biology, University of Western Australia. For leaf area and leaf mass per area (LMA), two to 20 replicates per individual of sun-exposed leaves were obtained from the tree or shrub mid-canopy. For species with compound leaves, leaflets were taken to be the functional unit equivalent to leaves. For shrubs and short trees, an extension cutter was used to obtain the leaves but for trees taller than 10 meters, canopy branches were collected using a slingshot and weighted line. Only fully expanded leaves were used and these were scanned with a flatbed scanner and the leaf scans were processed by imaging software ImageJ to obtain leaf areas. Leaf slenderness was measured as the ratio of the leaf length to leaf breadth. These leaves were then dried to a constant weight at 60°C and weighed. LMA was then determined by dividing leaf dry weight by the leaf area. For wood density, we followed a protocol similar to Falster & Westoby [51]. For trees, we collected branches and obtained two to five 5cm segments of the branch approximately 1m from the branch tip, whereas for shrubs, we collected wood segments by destructive sampling from the base of the shrub. The bark was removed from the wood segments and the displacement method was used to obtain the branch segment fresh volume. The branch segments were then dried at 60°C for a week, weighed, and the wood density calculated as dry weight divided by fresh volume. Maximum height (Ht$_{max}$) was obtained from literature sources [52–56]. Bark thickness was only measured on trees, and was obtained using a bark gauge at a height of 1.3m above the ground. In trees with fissured bark, we took readings from 'ridges' inbetween fissures, and in individuals with buttresses, we took readings from the trunk above the buttresses. We excluded this trait for shrubs because it was not possible to obtain bark thickness values for this life form in the same standardized way that we could for trees. As bark thickness increases with bole diameter, we expressed bark thickness relative to stem diameter (e.g. Lawes et al. [57]) by multiplying bark thickness by two and dividing this figure by the recorded diameter. We therefore sampled bark thickness from 26, 16 and 9 tree species from tropical north Queensland, and 8, 16 and 6 tree species from temperate Tasmania from their respective rainforests, giant eucalypt forests and savannas.

Data Analysis

All variables were checked for normality and where required were log-transformed. For each region, univariate one-way ANOVAs were performed for each trait. Significant differences

between habitats were determined by Tukey HSD tests using a confidence level of 0.05. All univariate analyses were performed in R. We also undertook univariate phylogenetic ANOVAs on each functional trait (Appendix S1). The results were essentially similar to the normal set of ANOVAs (Table S2 in Appendix S1) and so we report only the latter. Two-way factorial ANOVAs using regions (tropical and temperate), vegetation type (rainforest, giant eucalypt forest and savanna) and their interaction were also performed. We excluded bark thickness for the two-way ANOVA as data for this trait was only available for trees.

For the multivariate analyses, we used canonical variate analysis to visualize overall trait position within and among habitats. This method is a weighted ordination method in which axes are weighted to maximise the difference between a priori groups of multivariate observations [58,59]. MANOVA is the multivariate analogue of ANOVA, and tests for differences among groups. We performed both one-way and two way MANOVAs and post-hoc pair-wise tests using a confidence level of 0.05 were used to test for differences between groups. These multivariate analyses were performed using the discriminant analysis function in JMP 10.0.0 (SAS Institute, Inc., Cary, NC). As with the two-way factorial ANOVAs, bark thickness was excluded from the multivariate analysis as we only had measurements for tree species.

Results

Univariate Analyses

The two-way ANOVAs all showed significant differences, often with significant interaction effects, so we performed one-way ANOVAs. These showed a number of differences, and a number of similarities in trait behavior in both regions (Table 2; Figure 3, 4). In the tropical system, rainforest and savanna were significantly different in all traits, with the latter having a significantly higher $\delta^{13}C$ ratio, LMA, leaf slenderness, wood density and bark thickness, but lower leaf area and maximum height than the former (Figure 3, 4). For most traits giant eucalypt forest was not significantly different from rainforest, with the exception of greater bark thickness.

In the temperate system, $\delta^{13}C$ ratios and leaf slenderness were not significantly different across vegetation types, but leaf area and maximum height were significantly greater, while wood density and bark thickness were significantly lower for rainforest than savanna species (Figure 3, 4). However, temperate rainforest and savanna were not significantly different in LMA. Temperate giant eucalypt forest was not significantly different from rainforest in any of the measured traits.

Multivariate Analyses

Two-way MANOVAs show that region (Wilks' Lambda: $F_{6,117}$ = 19.53, P < 0.0001), vegetation type (Wilks' Lambda: $F_{12,234}$ = 13.45, P < 0.0001), and region × vegetation type interactions (Wilks' Lambda: $F_{12,234}$ = 1.87, P < 0.038) were significant. We therefore performed one-way MANOVAs which showed highly significant differences among vegetation types within the tropics ($F_{2,67}$ = 27.33, P < 0.0001) and the temperate zone ($F_{2,55}$

Table 2. One-way ANOVA results for of carbon isotopes ratios ($\delta^{13}C$), leaf area, leaf mass per area (LMA), leaf slenderness, wood density, maximum height, and bark thickness index comparisons between rainforests, giant eucalypt forests and savannas of tropical and temperate regions.

Functional Trait	Tropical Queensland		Temperate Tasmania		Both Regions	
	$F_{2,67}$	P	$F_{2,55}$	P	$F_{5,122}$	P
Leaf traits						
$\delta^{13}C$	6.97	0.0018**	2.45	0.09 (N.S)	4.73	0.0005***
Leaf area	16.31	<0.0001***	10.13	0.0002***	34.04	<0.0001***
LMA	20.56	<0.0001***	9.04	0.0004***	14.98	<0.0001***
Leaf slenderness	11.48	<0.0001***	2.58	0.08 (N.S)	7.54	<0.0001***
Bole traits						
Wood density	7.77	0.0009***	10.29	0.0002***	9.71	<0.0001***
Maximum height	4.88	0.011*	15.11	<0.0001***	9.67	<0.0001***
*Bark thickness	17.31	<0.0001***	9.15	0.0009***	NA	NA

Leaf area, leaf slenderness, Maximum height, and bark thickness were log transformed before Analysis. S denotes non-significance. Bark thickness was left out in the analysis with both regions combined as data for this trait was only available for tree species. *Bark thickness measurements were only performed on trees, hence the different degrees of freedom (Tropical Queensland: $F_{2,48}$; Temperate Tasmania: $F_{2,27}$) from the other traits.
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= 6.54, P = 0.003), and in the combined analysis ($F_{5,122}$ = 14.5, P < 0.0001). Post-hoc pairwise-tests show that the major differences occurred between rainforest and savanna in both regions, and also across regions (Figure 5). Tropical rainforest was also significantly different from temperate rainforest, and tropical savanna from temperate savanna (Figure 5). However, tropical and temperate giant eucalypt forests were not significantly different (Figure 5).

Likewise in canonical variate analyses for the individual regions, significant differences were found between vegetation types within both the tropical (Wilks' Lambda: $F_{12,124}$ = 6.85, P < 0.0001) and temperate regions (Wilks' Lambda: $F_{12,100}$ = 7.92, P < 0.0001). When all six habitats are analysed together, the canonical variate analyses was also significant (Wilks' Lambda: $F_{30,470}$ = 8.88, P < 0.0001). As the trends of the individual regional analyses are captured in the combined analysis, we present only the plot for the combined ordination (Figure 5). In multivariate space, the spread of species show clear clustering of rainforest and giant eucalypt forest species and this is visualized by the overlapping 95% confidence limit circles (Figure 5). $\delta^{13}C$, LMA, leaf slenderness and wood density appear to be the major variables segregating the tropical and temperate savannas from the rainforest and giant eucalypt
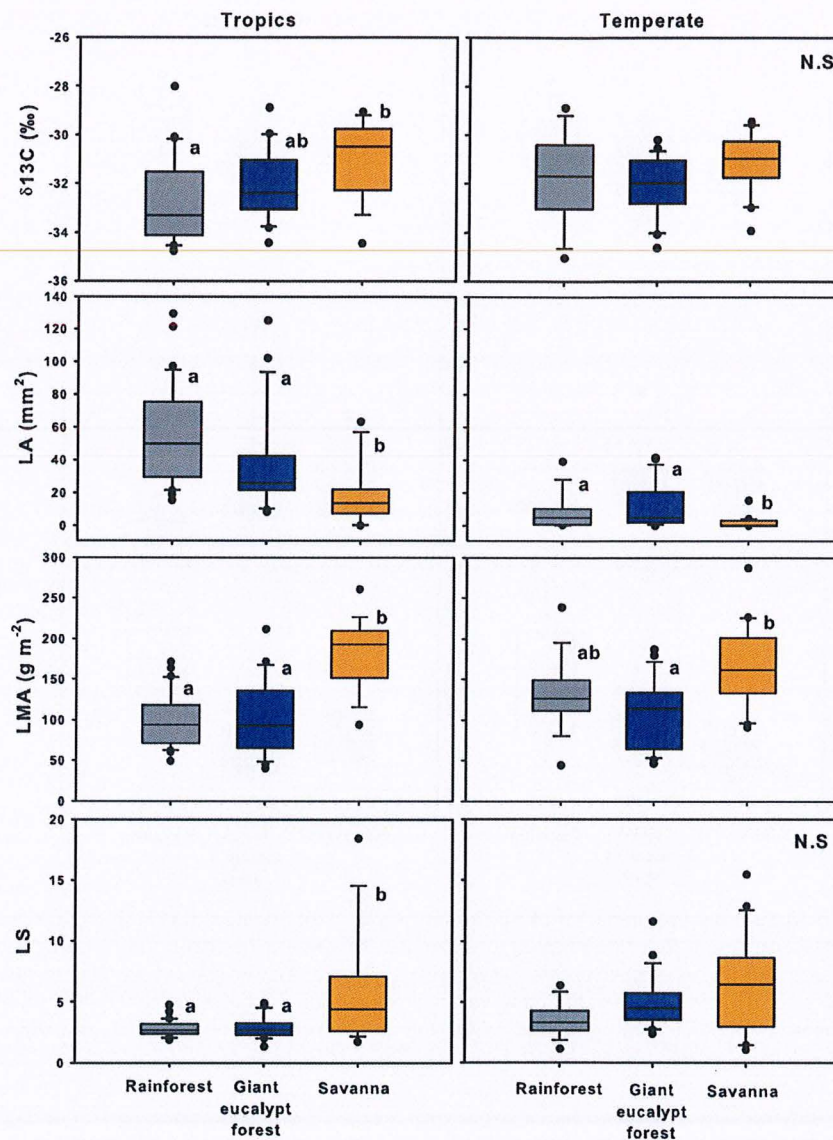
Figure 3. Boxplots showing the leaf trait behavior of rainforest (grey), giant eucalypt forest (blue) and savanna (orange) species from the tropical north Queensland (left block) and the cool temperate Tasmania (right block). Shown are carbon isotope composition ($\delta^{13}C$), leaf area (LA), leaf mass per area (LMA) and leaf slenderness (LS). Each box encompasses the 25th to 75th percentiles; the median is indicated by the boldest vertical line and the other vertical lines outside the box indicate the 10th and 90th percentiles. Dots indicate outliers. One-way ANOVAs were performed on the data (log-transformed for LA and LS) and significant differences between vegetation types are indicated by different letters based on Tukey HSD tests at a 0.05 confidence level (see Methods; Table 2). N.S denotes non-significance.
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forest as a whole (Figure 5). However, by virtue of their positioning in multivariate space, the temperate rainforest cluster, whilst being most functionally akin to giant eucalypt forest, also exhibits a mild clustering with the savanna cluster. The overlap of the rainforest and giant eucalypt forest clusters

was stronger within each region, and the tropical giant eucalypt forest appear to be converging with the temperate giant eucalypt forest and temperate rainforest clusters. In contrast, the tropical and temperate rainforest regions are diverging, largely on the basis of tropical rainforest species having greater
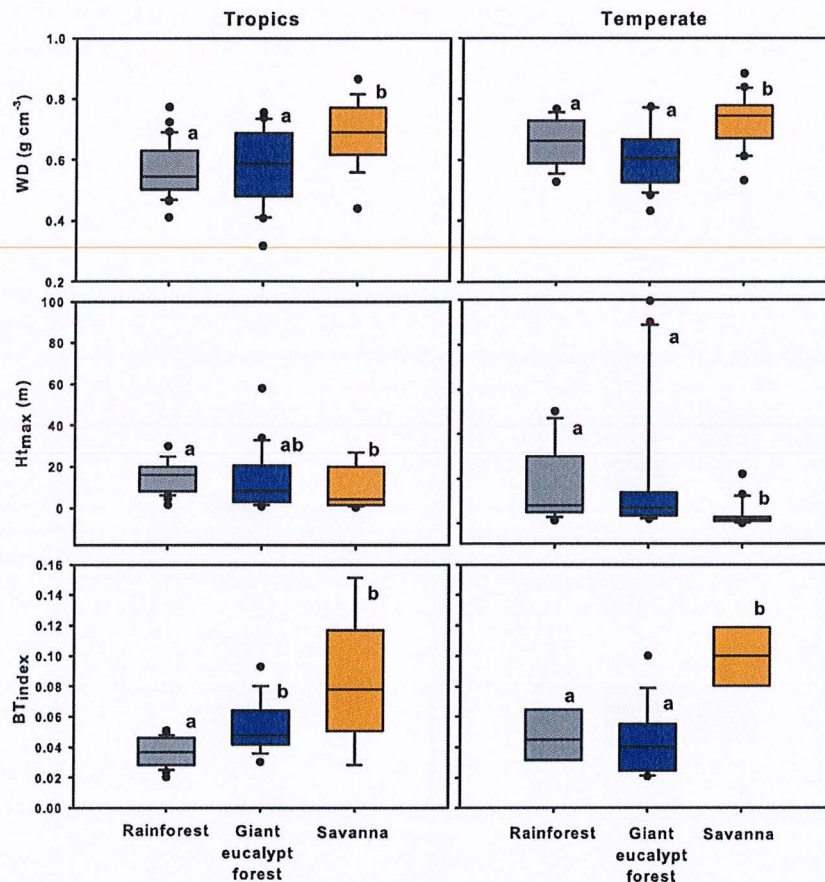
Figure 4. Boxplots showing the bole trait behavior of rainforest (grey), giant eucalypt forest (blue) and savanna (orange) species from the tropical north Queensland (left block) and the cool temperate Tasmania (right block). Shown are wood density (WD), maximum height (Ht_{max}), and bark thickness index (BT_{index}). Each box encompasses the 25th to 75th percentiles; the median is indicated by the boldest vertical line and the other vertical lines outside the box indicate the 10th and 90th percentiles. Dots indicate outliers. One-way ANOVAs were performed on the log-transformed data (except WD) and significant differences between vegetation types are indicated by different letters based on Tukey HSD tests at a 0.05 confidence level (see Methods; Table 2).

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leaf area and temperate rainforest exhibiting higher leaf slenderness. LMA, and to a lesser extent $\delta^{13}C$ and wood density, are responsible for the segregation of the two savannas from the rainforest-giant eucalypt forest cluster, but both savannas are also clearly segregated.

Discussion

Our univariate and multivariate analyses of leaf and bole functional traits of representative plants from rainforest and savanna in temperate and tropical Australia show differences consistent with what we would expect to find in the context of rainforest and savanna being alternative stable states [4,5]. Our results also provide direct support that the giant eucalypt

forests are functionally closer to rainforests than to savanna, and therefore better thought of as a successional stage towards rainforests. The basis and significance of these hypotheses are outlined below.

Tropical And Temperate Rainforest And Savanna

Tropical and temperate rainforests were functionally divergent (Figure 5), and this is augmented by the similar results obtained from both phylogenetic (Table S2 in Appendix S1) and normal ANOVAs (Table 2). Leaf area was generally larger in tropical systems than in temperate systems as expected [60–64]. This is consistent with well-known differences in physiognomy [60] and phylogenetic origins [65] of the rainforest types. Experimental work by Lusk et al. [66]
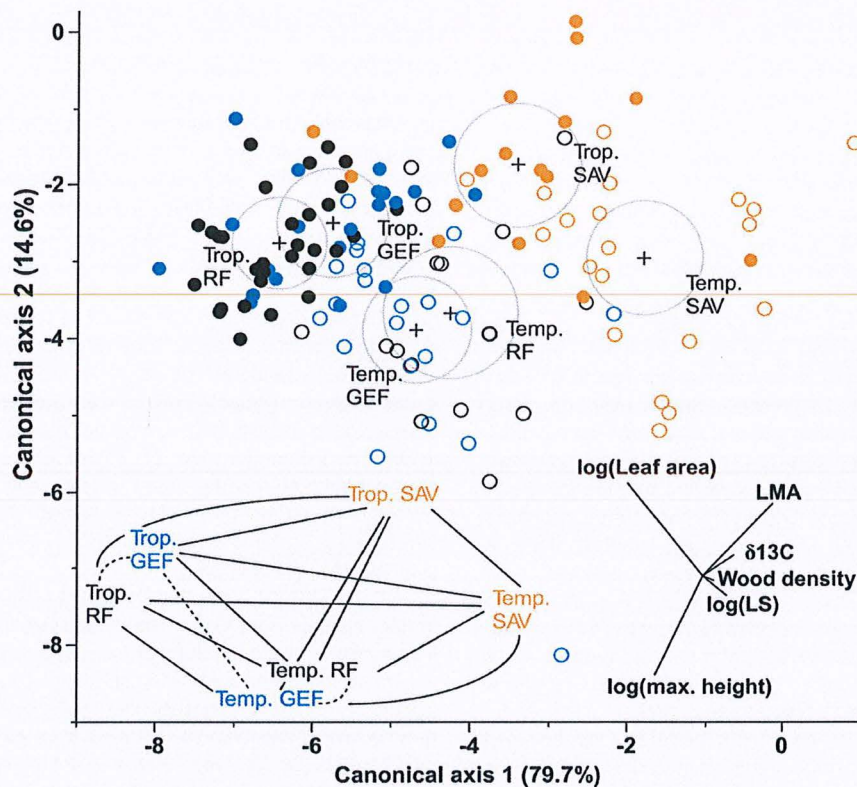
Figure 5. Canonical variate analyses of functional trait means of 128 species from tropical and (closed circles) temperate (open circles) rainforest (black), giant eucalypt forest (blue) and savanna (orange). Six functional traits were used: carbon isotopes ($\delta13C$); leaf area; leaf mass per area (LMA); leaf slenderness (LS); wood density, and; maximum height plotted into multivariate space. Each dot represents a species. On the bottom right the trait weightings (transformed where required) are plotted onto the graphs as vectors whose length and direction represent the contribution of the variable in explaining the clustering pattern. For each vegetation group, each multivariate mean is visualized as large grey circles encircling a black cross, the size of which corresponds to the 95% confidence limit for the mean. Groups that are significantly different tend to have non-intersecting circles. The proximities and overlaps of these circles are used to corroborate trait behavior with Alternative Stable States model scenarios (Figure 1). The bottom left inset is the results of pairwise *post-hoc* tests of a one-way MANOVA where unbroken lines represent significant differences between vegetation types, and dashed lines represent non-significance.
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and Xiang et al. [67] show trade-offs for traits like LMA, leaf area and other leaf traits between tropical and temperate rainforest, and this might explain the tropical-temperate rainforest functional divergence. Collectively this suggests that rainforest is not a cohesive functional entity across the Australian continent, apart from the unifying factor of having a closed canopy [68].

There were marked leaf and bole trait differences between rainforest and savanna vegetation. Our results supported the concept that savanna plants will have relatively thicker bark than rainforest trees [57]. LMA, which correlates strongly with important leaf physiological and structural functions such as growth rate, leaf lifespan, etc. [30,69,70] (Table 1), was higher in both temperate and tropical savanna than their rainforest counterparts, reflecting intrinsic biological differences between savanna and rainforest. Consistent with this interpretation is

the finding of Hoffman et al. [32] that LMA is a key functional trait explaining the differences between forest-savanna congeneric species pairs in central Brazilian ecosystems.

In the tropics three traits related to water relations ($\delta13C$, leaf slenderness and wood density) showed strong difference between rainforest and savanna, but $\delta13C$ and leaf slenderness were not significantly differentiated across temperate rainforest boundaries. Consistent both with the literature [71,72] and the concept that water use efficiency is related to water availability, was our finding that tropical savanna species have more positive $\delta13C$, and therefore higher water use efficiency [73] than rainforest species. Tropical savanna species had slender leaves probably because narrow leaf width is related to radiative cooling in dry climates [74,75]. Higher savanna wood density relative to rainforest is probably due to the higher potential of savanna species for tolerating drought stress [76].

Giant Eucalypt Forests

The multivariate ANOVAs and canonical variates analyses show that overall: (i) temperate and tropical giant eucalypt forests are functionally convergent, and; (ii) temperate and tropical giant eucalypt forests are closer in function to their respective rainforests than to their respective savannas (Figure 5). Even though there was high variability in species traits and overlaps in functional profile, the segregation between savannas and rainforests/giant eucalypt forests was significant (Figure 5). Augmenting these interpretations, we also obtained similar results for both phylogenetic (Appendix S1) and normal ANOVAs (Table 2) for most of the traits tested.

For all traits except bark thickness, univariate analyses showed that giant eucalypt forest were not significantly different from their respective rainforests. Significantly, in both temperate and tropical giant eucalypt forests, LMA did not differ from their respective rainforests but was markedly different from their respective savannas, suggesting that the trees and shrubs of giant eucalypt forest on a whole are more functionally akin to rainforest in their leaf functioning. However, LMA in temperate rainforest was not significantly different from savanna unlike in the tropics (Figure 3). This could be an inherent effect of thermal differences between the two regions, which may also explain why $\delta^{13}C$ and leaf slenderness were not significantly different across temperate rainforest boundaries, unlike in the tropics (Figure 3) [67].

Bark thickness was the only trait in the tropics that deviated from our hypothesized model that giant eucalypt forest is functionally different from savanna but not from rainforest (Figure 1). This indicates that the trees in the tropical giant eucalypt forest show some affinity to tropical savanna in their degree of fire-tolerance, and contrasts with the temperate system which supports model scenario 3. The narrower spatial extent of the ecotone in tropical Queensland relative to the temperate one [38,39] (Figure 2) could be a plausible explanation, as plants in the narrower tropical ecotone might be more prone to frequent low-intensity fires and therefore exhibit a greater degree of fire-adaptation. We acknowledge that more data, which was beyond our capacity to collect, on postfire recovery traits (e.g. resprouting, serotiny) would help further illuminate the relationship between savannas, giant eucalypts forests and rainforests.

The co-occurrence of rainforest and giant temperate eucalypt forest species to create distinctive vegetation types ('mixed forests') has long been recognised [44], but the status of tropical communities dominated by giant eucalypts has been controversial [14]. Our findings demonstrate that giant eucalypt forests in both the temperate and tropical regions are functionally more similar to rainforest than to savanna, which can lend support to the idea that these eucalypt forests lie within the basin of attraction of rainforest (Model 3 in Figure 1). The convergence of the functional trait profiles of tropical and temperate giant eucalypt is consistent with insights from restoration ecology, which show that within a successional sequence, trait composition exhibits a clear decrease in multivariate distance with increasing restoration age, indicating trait convergence through time, regardless of whether species convergence occurs [77]. For these reasons giant eucalypt

forest species can be considered early to mid successional rainforest species (i.e. secondary forest species) corroborating both Schimper's [78] early view that giant eucalypt forests are essentially rainforests, and our proposition that giant eucalypts are long-lived emergent rainforest pioneer trees [36]. The view that giant eucalypt forest is successional to rainforest would also explain the well documented tendency for their understoreys to accumulate rainforest species [9,38,50], thereby resulting in a two-tiered rainforest where the successional species (i.e. the giant eucalypts) form the overstorey [34,36]. The reason for the development of rainforest developing beneath eucalypts relates to differences in shade tolerance of species growing in these communities: eucalypts and rainforest pioneers are well known for being shade intolerant [34,36], while primary rainforest species are usually shade tolerant [34]. This major physiological difference results in the dominance of eucalypts in the high light environments of recently burnt stands, and the inability of eucalypts to regenerate in unburnt stands. Rainforest species are able to continually establish under dense regenerating giant eucalypt stands [36].

With the obvious exception that giant eucalypt forests have greater statures than rainforests in both regions, the functional trait profile of the sampled giant eucalypt forest species was essentially the same as that of the sampled rainforest species (Figure 4, 5). This suggests that while giant eucalypts (*E. grandis* and *E. regnans*) are often the focal point for classifying these forests [38,50], their heights contribute little to the overall functional profile of the forest. The contribution of height to the ability of these individual species to compete successfully against other plants and dominate these transitional zones is consistent with the view that these plants are true ecotonal specialists [36].

While our study examined giant eucalypt forests in tropical and temperate regions, forests of the giant eucalypt *E. diversicolor* F. Muell. exist in the Mediterranean-climate zone of western Australia. These western Australian giant eucalypt forests differ from those on the Australian east coast in the total absence of rainforest species, due to the extinction of rainforests from that region over the last 10 million years [36,79]. Functional trait studies could be used to investigate if these forests can be interpreted as a stable state alternative (and hence rainforest analogue) to other open woodland types (e.g. dominated by *Eucalyptus marginata* Donn ex Sm.) in this region. Forests dominated by other very large (exceeding 50m height) eucalypt species also occur in subtropical zones associated with rainforests in Southeast Queensland and New South Wales [34] and there is also scope for testing ideas related to functional traits in an alternative stable state context in these systems.

While our study has adopted a broad conceptual approach by constructing the functional profile of the sampled vegetation types from species that occur typically in those vegetation types across an entire region, there are inherent differences between the tropical and temperate systems that go beyond those that can be captured in our functional trait study (such as succession patterns, gap dynamics, and the role of functional groups that are not present in both areas). These differences

could be more effectively captured by including more functional traits [30] or by using an ecophysiological approach. At a more local scale, there is also scope for modelling the shifts in functional profiles with successional age and understanding the functional thresholds in the transition from rainforest to savanna. Such approaches could involve modelling trait profile discontinuities against a canopy closure index (i.e. Dantas et al. [33] to examine specific rainforest-savanna transitions under different environmental settings. In such studies we would recommend more consideration of traits relating to regeneration and growth strategies.

In conclusion, our study bridges landscape ecology theory and plant functional biology by examining the functional traits of representative tree and shrub species from tropical and temperate rainforest – giant eucalypt forest – savanna transitions. Functional leaf and bole trait segregation between rainforest and savanna were clear, especially in the tropics. The giant eucalypt forests however were functionally more akin to rainforest than to savanna in both tropical and temperate regions. These results augment the suggestion that giant eucalypts such as *E. grandis* and *E. regnans* are essentially rainforest trees [36] and calls for a functional, rather than floristic classification of these giant eucalypt forests. We expect this work to have important implications for the management and conservation of these unique giant eucalypt forests, and also encourage more landscape ecology – plant functional trait syntheses in terrestrial ecosystems.

Supporting Information

Appendix S1. Method of phylogenetic correction for univariate traits, data analysis and trait data.
Table S1. Species mean trait values of carbon isotope ratios ($\delta^{13}C$, ‰), leaf area (LA, mm^2), leaf mass per unit area (LMA, g m^2), leaf slenderness (LS), wood density (WD, g cm^3), maximum height (Ht_{max}, meters) and bark thickness (BT_{index}) for

128 species collected from rainforest (RF), giant eucalypt forest (GEF) and savanna (SAV) in Queensland and Tasmania. For maximum height, some of the species values compiled from literature but some were reduced in accordance with our field observations. For bark thickness, we only have data for 81 tree species.
Table S2. Phylogenetic One-way ANOVA results for leaf and bole plant functional trait comparisons between rainforests, giant eucalypt forests and savannas of tropical and temperate regions. Bark thickness was excluded from this analysis as it consisted of only a subset of the species in the phylogenetic tree.
(DOCX)

Author Contributions

Conceived and designed the experiments: DYPT GJJ DMJSB. Performed the experiments: DYPT. Analyzed the data: DYPT GJJ. Contributed reagents/materials/analysis tools: GJJ DMJSB. Wrote the manuscript: DYPT GJJ DMJSB.

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