IVG FOREST CONSERVATION REPORT 5B

GIANT EUCALYPT FORESTS – A GLOBALLY UNIQUE FIRE-ADAPTED RAIN FOREST

Note: This report forms part of the reference material utilized in Chapter 1 of IVG Report 5A, "Tall Eucalypt Forests as World Heritage".

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Summary

Tree species exceeding 70m in height are rare globally. Giant gymnosperms are concentrated near the Pacific coast of the USA, but the tallest angiosperms are eucalypts in eastern Australia. In eucalypts, probable drivers of gigantism are intense intra-specific competition following severe fires, and inter-specific competition amongst adult trees. Giant eucalypts co-exist with rain forest trees in eastern Australia, but occur where rain forest is now extinct in SW Western Australia. Given ideal growth conditions, the local abundance of giant eucalypts is controlled by interactions between fire activity and landscape setting. Giant eucalypts have features that increase fire risk (eg. oil-rich foliage and open crowns, etc.) relative to other rain forest trees but debate remains whether these features are adaptations or exaptations. 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. The resulting syndrome of a fire-dependent forest above a fire-intolerant forest is only known in the associations between eucalypts and Australian rain forest. These unique ecosystems are of high conservation value, in light of substantial clearing and logging over the last 150 years.

I. Introduction

Although conifers have long been recognized as including most of the world's tallest trees (Eckenwalder, 2009), a few angiosperm species also attain comparable heights (Fig. 1). The tallest of these are some species of *Eucalyptus* growing in relatively fertile, mesic areas of Australia (Sillett *et al.,* 2010). Giant eucalypts (for the purposes of this review restricted to species recorded as being over 70m) are often associated with rain forest (Jackson, 1968; Ashton & Attiwill, 1994), a vegetation type which is pyrophobic in nature (Bowman, 2000). However, eucalypts are generally considered as being pyrophyllic, and dominate most of the highly flammable vegetation that occurs across the non-arid regions of Australia (Bowman, 2000). This juxtaposition of pyrophyllic giant emergents with pyrophobic forest canopies raises a series of evolutionary and ecological questions: Is a giant eucalypt a rain forest tree? Are there global analogues to giant eucalypts in other environments? What was the selection pressure for eucalypts to become giant trees? Is the association of giant eucalypts and rain forest competitive?

The ecology of giant eucalypt forests has been of prime importance for the development of theories about how fire influences Australian forest dynamics and landscape patterns (Bowman, 2000). Australian ecosystems, including the giant eucalypt forests, have also featured prominently in global thinking about the evolutionary coupling of fire and plants (Bond & van Wiglen, 1994). Due to the ubiquity of fire-dependent vegetation, combined with the presence of localized patches of fire sensitive vegetation embedded within the former, Australia provides an outstanding natural testing ground for evolutionary and ecological theory (Bowman, 2000). The presence of this mosaic of pyrophyllic and pyrophobic vegetation across such a wide geographic range and in climates ranging from tropical to temperate alpine and from arid to humid is consistent with a fire-driven alternative stables state model (Bowman, 2000; Prior *et al.,* 2011; Wood *et al.,* 2011). Forests dominated by giant eucalypt trees (often called 'tall open forests', 'wet sclerophyll forests' or 'mixed forests') occur in environments that are suitable for the development of humid tropical, subtropical and temperate rain forest (Adam, 1992, Ashton & Attiwill, 1994; Bowman, 2000). Regeneration of the giant eucalypts requires intense fire that kills other competitors, a fact that has been incorporated into silvicultural practices (Hickey & Wilkinson, 1999). Without fire, eucalypts are eventually replaced by tree species that can continuously regenerate (Jackson, 1968).

Giant eucalypts are also of considerable social significance. These trees dominate highly productive and extremely carbon dense forests (Keith *et al.,* 2009), and therefore have been important for commercial forestry. Because of high fuel loads, fires in giant eucalypt forests are some of the most intense on earth, and the juxtaposition of human habitation with these systems has resulted in catastrophic disaster, the most recent occurring in 2009 near Melbourne in South-Eastern Australia. Remaining unburnt old growth forests are of both high conservation and economic value resulting in ongoing political dispute about their future. Long-term conservation of these systems must incorporate cycles of intense fires essential for their regeneration. However, thinking remains rudimentary about how this can be achieved in landscapes fragmented by land clearance and forestry, and that are exposed to a background of natural fires (e.g. Lindenmayer *et al.,* 2011). This is further complicated by the risks associated with intense fires, social distaste for burnt landscapes, and the political focus on placing existing old growth stands into protected areas such as national parks.

While there is substantial literature considering the ecology of various giant eucalypt forest types (see Ashton & Attiwill, 1994; Harrington *et al.,* 2000; Wardell-Johnston, 2000), there have been few attempts to understand the evolutionary advantages of their gigantism, to compare the ecology of giant eucalypts forests across their geographic range, or even to compare these systems to giant forests elsewhere. It also remains unclear whether giant eucalypts are ecological engineers that have created a globally specialized plant community that is an alternate state 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 ideas is the purpose of this review.

II. Giant eucalypts– definition, distribution and taxonomic variation

The 15 giant species of *Eucalyptus* (Table S1) form a small proportion of the 700 or so described species of the genus (Brooker, 2000). In southeastern Australia, *Eucalyptus delegatensis*, *E. obliqua* and *E. regnans* routinely achieve statures in excess of 70m, and other species, such as *E. viminalis* and *E. globulus*, will occasionally reach these heights (Boland *et al*., 2006). Indeed, the tallest living *E. regnans* measured at 99.6m clearly qualifies as the tallest flowering plant on Earth (Fig. 1, 2a). There is also a convincing historical record of 114.3m in this species in

Victoria (Mifsud, 2002) (Table S1). In the humid subtropical and tropical zone of eastern Australia, *E. grandis* attains heights of over 70m (Boland *et al*., 2006) (Fig. 2b). In highest rainfall parts of southwestern Australia, *E. jacksonii* and *E. diversicolor* attain comparable heights (Boland *et al*., 2006). The only extra-Australian giant eucalypt is *E. deglupta*, which can exceed 70m and occurs in Malesia (Whitmore, 1998).

The molecular phylogeny with best representation of species of *Eucalyptus* (Steane *et al*., 2002; Bayly & Ladiges, 2007) suggests that giant eucalypts have evolved at least seven times - three times within subgenus *Eucalyptus* (in *E. jacksonii*, in *E. delegatensis*, and in the group closely related species, *E. regnans, E. obliqua* and *E. pilularis*) and four times within subgenus *Symphyomyrtus* (with independent evolution in *E. diversicolor*, *E. deglupta, E. grandis* and at least once in tribe *Maidenaria - E. viminalis*, *E. nitens*, *E. nobilis* and *E. globulus*) (Fig. 3). Cross matching this phylogeny with the dated phylogeny presented by Crisp *et al.* (2011) suggests that all of these evolutionary events occurred in the last 20 million years, and it is credible that many, or even all of them, are much more recent. While not achieving heights in access of 70m, some species in other genera of Myrtaceae (*Corymbia*, *Lophostemon* and *Syncarpia*) sometimes achieve statures of over 60m (Boland *et al.,* 2006).

1. Environmental envelope

In Australia giant eucalypts typically occur where rainfall is between 1500-2000mm per year with at least 50mm of rainfall in the driest month, but can grow at rainfalls as low as 1000mm on fertile soils (Ashton, 1981ab) (Fig. 4a,b; Table 1). Some giant eucalypts, such as *E. obliqua* and *E. viminalis*, have ecotypes tolerant of a wide range of edaphic or other environmental conditions and can occur in diminutive forms in drier forest (Wells & Hickey, 2005). In eastern Australia, the distributions of giant eucalypts overlap with the climatic envelope that can potentially support rain forest (Fig. 4a,b; Table 1) (Adam, 1992). However, two giant eucalypt species, Karri (*E. diversicolor*) and Red Tingle (*E. jacksonii*) occur in southwestern Australia where no rain forest is currently present (Wardell-Johnston, 2000). 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 1).

Extreme fire weather occurs infrequently in giant eucalypt forests (Fig. 4b), but on these rare occasions high fuel loads result in extreme intensity fires. These forests have the highest fire intensities (>50,000 kWm^{-1}) of any vegetation type in Australia (McCarthy *et al.,* 1999), comparable to some Canadian and Alaskan boreal coniferous forests (van Wagner, 1983). Extreme fire often results in massive regeneration and results in even-aged stands across large expanses of landscape (Ashton, 1975, 1981a; Florence, 1996; Wardell-Johnston *et al*., 1997; Wood *et al*., 2008). However, some fires may not kill all adults (Vivian *et al*., 2008), resulting in multiple age stands (Lindenmayer *et al*., 2000; Simkin & Baker, 2008; Turner *et al.,* 2009). Fire frequency and local environmental conditions influence the understoreys, which in turn influences fire risk. Sites that are frequently burnt, have infertile soils or both, are typically dominated by sclerophyllous shrubs, grasses, forbs 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, have more fertile soils or both favour mesic shrubs and trees or rain forest understoreys creating the juxtaposition of fire-dependent and fire-intolerant floras. Little *et al.* (2012, *in press*) (Fig. 5) have shown that humid tropical rain forest understoreys have a microclimate that is less flammable than the adjacent and more open canopied *E. grandis* forests, highlighting how vegetation can modify prevailing climate and change fire risk.

2. Landscape Ecology and Historical Biogeography

The landscape pattern of giant eucalypt forests differs markedly in extent in different climate zones. Tropical and subtropical giants are typically restricted to narrow bands, whereas giant eucalypt forests span broader areas in the temperate zone. For instance, in Far North Queensland, *E. grandis* forms a thin strip (<4km) of marginal forest on the western edge of major tropical rain forest formations (Harrington *et al.,* 2000; Tng *et al.*, 2012) but in Tasmania *E. obliqua* and *E. regnans* tall open forest extend widely in association with cool temperate rain forest (Fig. 6). Interestingly, forestry provenance growth trials where seed collections of mainland and Tasmanian *E. regnans* show negligible genetic variation in growth rates, suggesting that the

ecological niches occupied by these giant trees are narrow (Raymond *et al*., 1997). Thus the cause of the abrupt and gradual gradients from rainforest to sclerophyll vegetation is probably shaped by environmental variation including edaphic factors (Florence, 1964), fire frequency (Jackson, 1968), mesoclimate associated with topography (Wells & Hickey, 2005), moisture gradients (Ashton 1981ab) and historical factors shaping the realised niche of giant eucalypts. Indeed, there is no question that the current distributions of the same eucalypts differ considerably from their historical distributions. Pollen analyses from volcanic crater lakes in Far North Queensland show that rain forest boundaries, and undoubtedly the occurrence of giant eucalypt forest, have been oscillating throughout geological history (Kershaw, 1976; Haberle, 2005). Molecular phylogeographic data implies that during the last glacial maximum, both *E. regnans* and *E. obliqua* were limited to various refugia that also allowed the survival of rain forest species (Nevill *et al.*, 2009; Worth *et al.,* 2009; Bloomfield *et al.*, 2011). Phylogeographic studies of *E. grandis* show that *E. grandis* populations in Far North Queensland may be of a more recent origin compared to those populations in Southeast Queensland and New South Wales (Jones *et al.*, 2006).

III. Giant eucalypts in a global context

Giant trees (> 70m tall) are known to occur in approximately 50 species of trees, and although these species include angiosperms and gymnosperms, in both tropical and temperate regions (Table S1), they are very restricted phylogenetically and geographically (Fig. 1). The giant conifers are members of three families (Cupressaceae, Pinaceae and Araucariaceae), whereas almost all of the giant angiosperms are species of the mainly Australian genus, *Eucalyptus* (Myrtaceae), or of subfamily Dipterocarpoideae of Dipterocarpaceae, which ranges from India to New Guinea. All but four of the species occur in three mesic regions: western North America from California to British Columbia, Southeast Asia (especially Borneo) and eastern Australia (Fig. 1) (Table S1). The four remaining species are also from mesic temperate zones in New Zealand, southern Russia, and Southwestern Australia. Average heights of the ten tallest tree species in each of these regions provide a 'Rucker index' (Frank, 2008) and on this count Australia bears the distinction of being third on the world scale as a result of the presence of giant eucalypts.

The world's tallest living tree is the conifer *Sequoia sempervirens* (coastal redwood) that occurs on the Pacific northern west of the USA, while the tallest angiosperm is *Eucalyptus regnans*. These two species highlight the differences in life history strategies associated with growth and gigantism between angiosperms and gymnosperms (Sillett *et al.,* 2010). The large size attained by conifers provides a buffer against environmental stress (especially for nutrients and moisture) and the extreme rarity of and thus long intervals between destructive fires and storms, permits conifers to outgrow co-occurring hardwoods with more limited stature and life spans (Waring & Franklin, 1979). *Sequoia sempervirens* regenerates in tree fall gaps, grows very slowly and lives for over 2000 years (Busing & Fujimori, 2002). Southern hemisphere forests with tall conifers (eg. *Agathis australis* in New Zealand; *Araucaria araucana* and *Fitzroya cupressoides* in Southern South America; *Araucaria bernieri* in New Caledonia; *Araucaria hunsteinii* in Papua New Guinea, etc.) follow similar strategies of attaining greater height by virtue of great longevity (Lane-Poole, 1925; Jaffré, 1995; Ogden & Steward, 1995; Veblen *et al.,* 1995).

The growth strategy of giant eucalypts contrasts strongly with that of the giant conifers. For example, *E. regnans* regenerates prolifically after intense fires, has extremely rapid growth in the first 100 years of life outcompeting co-occurring rainforest trees and then senesces after ~ 500 years (Wood *et al.,* 2008, 2010). A giant conifer that has a similar dependence on fire for regeneration as giant eucalypts is the shade-intolerant and fast-growing *Pseudotsuga menziesii* (Douglas fir) (Bušina, 2007). This life history allows this species to compete with the shade tolerant and slower growing *Tsuga heterophylla* (western hemlock). *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). The competitive interaction between rapid growing light-demanding trees and slower shade tolerant trees results in a two-tiered forest of towering emergent trees above lower closed forest canopy (Bušina, 2007). However, within angiosperm-dominated forest systems, the syndrome of a fire dependent forest above a fire intolerant forest is known only in the associations between eucalypts and rain forest.

Among other angiosperms, dipterocarps (Dipterocarpaceae) are the group most comparable to eucalypts. Both groups have species that can compete with broadleaf understorey species in

unburnt settings (thus forming closed forests) and can also persist in frequently burnt communities with grassy understoreys (thus forming savanna) (Martin, 1973; Stott, 1984). Further, some Southeast Asian rain forest dipterocarps in Borneo have been observed to attain heights comparable to eucalypts (Ashton, 1964). The tallest measured tropical tree, *Shorea faguetiana*, stands at 88.1m (Roman Dial, *pers. comm.*) but across the distributional range of dipterocarps, such heights are the exception rather than the rule. In other parts of Southeast Asia, the canopies of dipterocarp forest are rarely more than 60m high (Wyatt-Smith, 1964; Whitmore, 1998). Like giant eucalypts the rain forest, dipterocarps tend to occur in the emergent or canopy stratum (Ashton & Hall, 1992), but in contrast to giant eucalypts, the giant dipterocarps are shade tolerant. Other giant angiosperms (*Koompassia* and *Ceiba*) are all scattered emergents in tropical rain forest, dependent on gap-phase regeneration (Richards, 1996) and, unlike giant eucalypts (Ashton 1981a), do not become canopy monodominant.

IV. Functional ecology of giant eucalypts

Height plays a central role in plant ecological strategy because it can determine a plant's competitive ability to compete for light. In angiosperms, height is also broadly correlated with a large number of plant functional traits such as leaf mass fraction, leaf area ratio, leaf nitrogen per area, leaf mass per area and canopy area (Falster & Westoby, 2003). Plant height is also an important part of a maximum population density (Enquist *et al.,* 1998) and thereby affects important ecosystem variables such as carbon sequestration capacity (through its relationship with plant biomass). The functional ecology of giant eucalypts has not received comprehensive treatment, although there are numerous idiosyncratic studies of various species. We draw heavily on literature relating to the tallest eucalypt, *E. regnans*. This species is well studied, largely because it is commercially important (Ashton, 1975; Wardlaw *et al.*, 2009).

1. Anatomy and physiology of gigantism

Debate surrounds the constraints on tree height. Koch *et al.* (2004) argues that the fundamental control of maximum tree height is water supply to the treetop, with the maximum height of 110m resulting in significant stress resulting from the corresponding decrease of 1.1 MPa in leaf water

potential. This stress contributes to the restriction of giant trees to mesic environments - in dry climates this gravitationally induced decrease in water potential increases the water stress imposed by dry soils (Koch *et al.*, 2004). Eucalypts tend to be considerably taller than their co-occurring species - that is, they are emergents even in short forest types (Groves, 1999). This would argue that eucalypts in general may have features that allow them to tolerate greater water potential gradients than their co-occurring species. The mechanisms underlying this are poorly understood, but such tolerance would imply that the occurrence of giant eucalypts relates to the evolution of specific characteristics that allow them to compete in rainforest environments. The anatomical basis underpinning the great heights in giant eucalypts has been studied by Petit *et al*. (2010), who measured the vertical profiles of conduit (i.e. vessel) dimensions and density of *E. regnans* trees of varying heights. The xylem of *E. regnans* tapers rapidly at the stem apex, with a plateau lumen size towards the tree base. Petit *et al.* (2010) interpreted that this form of conduit tapering should be a highly effective strategy for compensating for the hydraulic limitations caused by increased tree height, and concluded that *E. regnans* has evolved a xylem design that ensures a high hydraulic efficiency. This feature enables the species to rapidly attain heights of 50–60 m, beyond the maximum height of most other hardwood trees (Petit *et al.,* 2010). It remains unclear if this type of vessel architecture is common amongst other giant eucalypts.

Few studies have compared the functional ecology of giant eucalypts with their co-occurring rain forest species. In the humid tropics, Duff (1987) studied the growth of a suite of nine species across a tropical rain forest-tall open forest boundary and found that *Eucalyptus grandis* exhibited faster growth and acquired more biomass than both pioneer and climax rain forest taxa when grown under glasshouse conditions. Duff (1987) showed that *E. grandis* exhibited patterns of resource allocation that were broadly similar to fast growing rain forest pioneers like *Alphitonia* and *Toona*. He also demonstrated that given sufficient light and nutrients, *E. grandis* seedlings 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.

2.   Growth phases and self-thinning

Giant eucalypts have three distinct growth phases: crown-lifting, crown-deepening and crown-retraction (Wardlaw *et al*., 2009). Crown-lifting occurs in the first 100 years of development and is associated with an intense race to overtop neighbours. For example *E. regnans* can grow as quickly as 2m per year in the first decade (Ashton, 1981a) and attain half of its mature height within the first 25-35 years (Jackson, 1968). During this phase, a straight, branch free trunk develops as branches at the crown base are shaded out and shed through an effective abscission system (Jacobs, 1955). This phase is also associated with intense self-thinning of the initial high seedling densities (Ashton, 1976; Jackson, 1968), resulting in the intense density dependent selection pressure for height (Hardner & Potts, 1997) that has presumably driven the evolution of gigantism. In corroboration, eucalypts are notoriously shade intolerant (Ashton, 1981b), and Herbert (1929) suggested that the resulting lack of ability to survive suppression explains why so few species of eucalypts have managed to survive in rain forest. Undoubtedly, the height advantage in giant eucalypts relative to most rain forest trees allows giant eucalypts to persist in the overstorey while a rain forest canopy develops beneath.

The second phase, crown-deepening occurs in the next 100-200 years, when growth slows substantially (Wood *et al.,* 2008). During this phase light is no longer limiting for the eucalypts, and slower but continual growth results in deep crowns and thick branches. The third stage (crown-retraction) occurs from about 200 years onward, when trees have reached their maximum height (Ashton, 1976, Wardlaw *et al*., 2009). Barring catastrophic damage from fire or falling, non-suppressed trees may enlarge steadily in girth (Ashton, 1975) and maintain high leaf area well into old age even after height growth has nearly ceased (Sillett *et al*., 2010). This phase continues till the end of the tree's natural lifespan, which may be in excess of 500 years in *E. regnans* (Wood *et al*., 2010) and at least 400 years in other giant eucalypts (Wardell-Johnson & Coates, 1996). During this final two phases, the open crown of mature eucalypts allows for the development of a closed canopy rain forests.

3. Fire tolerance and fire promoting features

The success of eucalypts in the Australian landscape is thought to hinge on a combination of the capacity for fast growth with a diverse array of specialized features (lignotubers, thick fibrous bark, epicormic buds and woody serotinous capsules) (Fig. 2c,d,e) to withstand fire or to allow seedling regeneration after fires (Ashton, 1981a; Jackson, 1968). The expression of these traits varies both among eucalypts species and within species, particularly amongst giant eucalypts (Whittock *et al*., 2003). For example, lignotuber development becomes less pronounced in ecotypes of *E. viminalis* that occur in wet environments (Ladiges, 1974). Furthermore, it is possible that fire risk varies with the developmental stage of individual trees (McCarthy *et al.,* 2001). Jackson (1968) believed that mixed *Nothofagus – E. regnans* forest had a lower fire risk than the younger regrowth eucalypt, although it is not clear whether such differences are due to differences in flammability of the understorey or to the of flammability of the eucalypts. Lindenmayer *et al.* (2011) claimed that the balance of the life stages of *E. regnans* influences fire activity, and that logging of old growth has increased fire risk substantially.

In the case of some of the largest giant eucalypts, like *E. delegatensis* and *E. regnans*, there is limited expression of fire regenerative characters (Waters *et al*., 2010). Thus, *E. regnans* is vulnerable to fire kill and dependent upon seeding (i.e. it is an obligate seeder) because it produces no lignotubers, has thin bark, and limited epicormic regrowth (Nicolle, 2006). Although mechanisms for individual survival are prominent mechanisms in fire prone environments, obligate seeding can be an evolutionary strategy to survive fires (Bond & van Wilgen, 1996). Thus, obligate seeding can provide a competitive advantage by allowing faster growth and earlier maturity than resprouters that must develop and maintain protective structures and storage organs and regenerative tissues (Bond & van Wilgen, 1996; Knox & Clarke, 2005). Some giant eucalypts, such as *E. delegatensis*, *E. grandis* and *E. regnans*, conform well to this evolutionary model. Obligate seeding eucalypts have aerial seed bank in the form of woody capsules (i.e Fig. 2d) that protect seeds from the heat of a fire (Ashton, 1981a). The masses of viable seed released after a crown-scorching fire saturates seed predation, allowing the survival of huge numbers of seedlings (Ashton, 1979; O'Dowd & Gill, 1984). Growth of seedlings is

enhanced because of the death of the canopy and emergent trees releases seedlings from intraspecific competition for environmental resources with adult trees (Bowman & Kirkpatrick, 1986; Dignan *et al*., 1998; Van Der Meer *et al.,* 1999). In contrast to this strategy, some giant species (such as *E. obliqua*) have well developed vegetative recovery mechanisms such as thick bark, epicormic buds and lignotubers (Bowman, 2000). Such species tend to occur in more fire prone sites, but as shown by the comparison of the obligate seeder, *E. regnans*, with its resprouting relative, *E. obliqua*, this comes at the cost of slower growth rate (Ashton, 1981a). Differences in growth are no doubt affected by the cost/benefit trade-offs of investing in bark and/or lignotubers (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 gain additional photosynthetic area from chloroplasts in the bark (Cernusak *et al.,* 2006). Thus, giant eucalypts can occur on either side of the obligate-seeder – vegetative resprouter regeneration strategy divide.

The applications of phylogenetic analyses are crucial for charting the evolution of putative fire adaptation, although this approach has to date only had limited application in eucalypts. The recent analysis of Crisp *et al.* (2011) suggests that the unique anatomical feature (i.e. cambium strands capable of generating stems) that enables prolific vegetative regeneration has an ancient pedigree dating back to the early Cainozoic. Their analysis implied that the obligate seeding response in the *E. regnans* is a derived feature (Fig. 3). This species is deeply nested within the eucalypts (Ladiges *et al.,* 2010) but still possesses specialised protected meristem strips involved in epicormic resprouting throughout the genus (Waters *et al.,* 2010) (Fig. 2e).

There is an intense and unresolved debate about whether or not eucalypts have specific adaptations to increase flammability or if these are exaptations (eg. 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). Many claims about characters that increase fire risk, such as decorticating bark strips that spread spotfires hinge on unsubstantiated 'group selection' arguments (see Bowman, 2000; Bowman *et al.,* 2012 *in press*).

4. Stand dynamics and ecological niche of giant eucalypts

Landscape ecology perspectives that emphasise landscape dynamics between rain forests and the contrasting need of fire to initiate regeneration in these systems have framed thinking about the stand dynamics of giant eucalypts. In high rainfall areas of Tasmania, 'mixed forests' (Gilbert, 1959) are made up of giant eucalypts emerging from rain forest understoreys occur in large areas (Fig 4b). Jackson (1968) suggested that mixed forests form a distinct stage in a fire driven successional series from frequently-burnt treeless vegetation to rain forest. Jackson argued that each stage in this succession was a distinctive community, with a characteristic fire regime that would tend to perpetuate the community: only significant deviation in fire frequency would cause a switch to another community. Thus 'mixed forests' were unlikely to be converted to rain forest, and this would occur if the fire-free interval exceeded the lifespan of the eucalypts. This model prefigured the alternative stable states concept of Beisner *et al.* (2003). In the humid tropics of north Queensland, *E. grandis* forests form narrow ecotones along rain forest edges (Adam, 1992; Ash, 1988; Unwin, 1989). Warman & Moles (2009) suggest that these ecotones are not actual plant communities, but rather that the giant eucalypt has specialised to exist sandwiched between the two alternative stable states of pyrophobic rain forest and pyrophilic savanna.

V. ARE GIANT EUCALYPTS RAIN FOREST TREES?

There is enormous confusion about the concept of 'rain forest' in Australia (see Bowman, 2000, Lynch & Neldner, 2000). In his original conception of rain forest, Schimper (1903) included giant eucalypts because they occurred in mesic environments. However, most Australian ecologists have disagreed with this view, suggesting that giant eucalypts are not rain forest trees because of their dependence on extensive disturbance. Problematically, this argument ignores the fact that *E. deglupta*, the extra-Australian giant eucalypt, is already accepted as pioneer species in Melasian rain forests (Carr, 1972; Swaine & Whitmore, 1988). To determine if giant eucalypts are rain forest trees we (1) compare obligate seeding giant eucalypts with recognised rain forest pioneer (or secondary) species, and (2) consider if giant eucalypts facilitate rainforest development.

1. Are giant eucalypts rain forest pioneers?

Turner (2004) states that two characteristics are diagnostic for rain forest pioneer species: (1) seed germination that is dependent on the exposed conditions present in canopy gaps and (2) shade-intolerance. *E. regnans* and other giant eucalypts conform to both of these features, albeit that the seedbeds and forest gaps are created by intense fires (Ashton, 1975, 1981ab; Wardlaw *et al*., 2009). Moreover, numerous studies also show that several giant eucalypts can regenerate in the absence of fire, through exposure of mineral soil by mechanical disturbance combined with the removal of the overstorey (Raison 1980).

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 (Richards, 1996). Giant eucalypts employ similar *r*-selected reproductive strategies, with early reproductive maturity, prolific and often continuous production of small seeds (Ashton, 1981a) and extremely rapid height growth that allows them to overtop conspecifics in height by ~50%. Interestingly, such 'hyper-emergence' is also apparent in heath, mallee, dry sclerophyll, subalpine and savanna communities (Groves, 1999).

Another feature of many pioneer species is a long lived seed bank (Turner, 2004). In rain forest pioneers this seed bank is commonly held in the soil, but the aerial seed bank of eucalypts provides an analogous function. Given that the long life spans of giant eucalypts (~ 400-500 years: Wood *et al.,* 2010) is often equivalent, or even greater than that of climax 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). Like giant eucalypts, such species persist as emergents in rain forest (eg. *Ceiba pentandra, Hura crepitans* etc) and rely on large infrequent disturbances for regeneration (Condit *et al*., 1998). Another key component of the question of the ecological status of giant eucalypts is whether giant eucalypts inhibit or facilitate rain forest development.

2.   Do giant eucalypts inhibit or facilitate rain forest regeneration?

Deciding whether giant eucalypts are rain forest pioneers requires an understanding of any antagonistic or facilitative effects of these trees on regenerating rain forest species. The potential arguments for antagonism are two fold. If the eucalypts have more flammable foliage and generate greater fuel loads than the rain forest that would otherwise occupy a site, then eucalypts may increase the fire risk compared to unblemished primary rain forest. While rain forest is pyrophobic, fires do occur naturally in these forests, albeit at low frequencies (Cochrane & Laurance, 2002), and many rain forest plants have mechanisms to recover from fire (Floyd, 1989; Chesterfield *et al.,* 1991). Thus, changes in fire regimes resulting from the presence of giant eucalypts may not have large local impacts on rain forest. Indeed, the existence of narrow bands of giant eucalypts in the humid tropics suggests that these giant eucalypts are unable to increase fire occurrence to such a degree to override other environmental controls rainforest (Little *et al.*, 2012) or inhibit the current expansion of rainforest (Tng *et al.*, 2012) in this environment. However, it remains plausible that under some climates, such as those occurring in Tasmania, eucalypts can these alter fire regimes to reduce the extent of rain forest at the landscape-level. For instance, Jackson (1968) proposed that the presence of giant eucalypts increases the frequency and/or severity of fire. However, several aspects of this concept remain poorly tested (Wood & Bowman, 2012).

Another argument for antagonism pertains to interspecific competition. If eucalypts decrease soil water, and are efficient extractors of nutrients, this could also be antagonistic to rain forest. However, the presence of extensive co-existence of giant eucalypts with rain forest argues that any antagonistic effects are likely to be weak at the individual site level. This may be contrasted with cases of allelopathic effects attributed to eucalypts of other drier habitats (Moral & Muller, 1970; May & Ash, 1990). It is also likely that given the high rainfall where giant eucalypts occur, potential allelopathic agents may be diluted or leached from the soil. On the whole, giant eucalypts in mature eucalypt 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.* (2012) document the expansion for humid tropical rain forest into *E. grandis* forest in Far North

Queensland over the last 50 years, and a similar process has been observed in *E. grandis* plantation within 27 years on central coast of New South Wales (Turner & Lambert, 1983). Similarly, the temperate rain forest dominant *Nothofagus cunninghamii* rapidly colonizes the understoreys of unburnt *Eucalyptus* forests across a range of soil types (Ellis, 1985; Needlam, 1960). In Central Victoria, the understoreys of *E. regnans* forest are being invaded by *Pittosporum undulatum*, a broad-leaved rain forest tree (Gleadow & Ashton, 1981).

The argument for giant eucalypts as pioneer species is reinforced by evidence that eucalypts can facilitate rain forest development, at least in tropical and subtropical regions. There are many possible ways such facilitation could occur. 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). An ambient amount of shade in the overstorey that minimises photostress for regenerating plants, and also reduces evaporative demand at times of water deficit (Messier *et al.,* 1998) may also be important. In terms of below-ground interactions, pre-existing trees could also be a source of mycorrhizal inoculum for developing rain forest seedlings. For instance, the persistence of ectomycorrhiza on relict *E. grandis* trees in rain forests may provide ectomycorrhizal propagules for rain forest taxa (Adams *et al.,* 2006). Additionally, 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 giant eucalypts may act as facilitators of rain forest regeneration. The clumped distribution of rain forest seedlings under pre-existing trees is a process is known as nucleation (Yarrangton & Morrison, 1974) and has been documented for rain forests in North Queensland (Fensham & Butler, 2004; Russell-Smith *et al*., 2004). Bird-dispersed rain forest taxa are also very common in far north Queensland *E. grandis* forest (Tng, unpublished data).

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 plantation eucalypt trees can have facilitative or nurse effects on the regeneration of natural forest. Other studies document uninhibited regeneration of rain forest species under eucalypt plantations. Native rain forest species have

been observed to regenerate in the understoreys of *Eucalyptus grandis* plantations in both Brazil (da Silva Junior *et al.,* 1995), and the Cameron Highlands in Peninsula Malaysia (Tng *pers. obs.*; Fig. 2f). 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 like teak (*Tectonia grandis*) can inhibit native vegetation regeneration (Healey & Gara, 2003).

In summary, we argue that the high seedling density and intense competition of space and resources following disturbance results in inhibition of rain forest (as reviewed in Section IV) but facilitate rain forest development during the middle and later growth phases of the eucalypts. 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 there is a strong case for treating giant eucalypts as rain forest pioneer trees, albeit one with unique features relating to fire disturbance.

VI. Conclusions

The giant eucalypts stand out as the tallest of flowering plants, and form a globally unique set of ecosystems of giant pyrophyllic angiosperms over a pyrophobic rain forest canopy and understorey. These ecosystems include multiple eucalypt lineages and range from the tropics to cool temperate zone. Giant eucalypts 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 occupy a climate envelope suitable for rain forests in Victoria and SW Western Australia. Underscoring the nexus between rain forests and eucalypts are other species that also survive in rain forest environments but do not attain great heights (eg *Eucalyptus pellita, E. macta, Corymbia torelliana*, *C. intermedia*), although little is known about the regeneration niche dynamics of these smaller species.

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, 2000; Lynch & Nelder, 2002) 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 as a globally unique pioneer species, or ecotonal specialists.

The giant eucalypt syndrome occurs in at least seven clades within eucalypts, amongst species occurring from tropical to temperate environments. However, given the 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). The underlying capacity for gigantism may therefore have evolved once, with convergent evolution of other traits (eg rapid growth, 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. In the tropics and subtropics *E. grandis* only occurs in narrow bands while the cool temperate species, *E. regnans*, forms large tracts of forests. The available data show that past climates have influenced the extent of giant eucalypt forests. For example, under glacial climates *E. regnans* was less widespread (Nevill *et al.,* 2009). Climate has a very strong effect on fire activity (Fig. 3), and it remains unclear how much the potential increase flammability with the arrival of eucalypts changed the competitive balance with other rain forest trees. For example, the Pleistocene extinction of rain forest species of a more mesic nature in Southwest Australia may simply reflect the development of a drier and more fire-prone climate inimical for those taxa (Dodson & Macphail, 2004), rather than the impact of increased fire activity associated with dominance of eucalypts. Factoring out 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 fire risk created by eucalypts would have long term implication for rain forest habitats in regions such as Brazil where eucalypt plantations are becoming increasingly important. Alternatively, 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 eucalypts forests is a key step in understanding these temporal trends.

Acknowledgements

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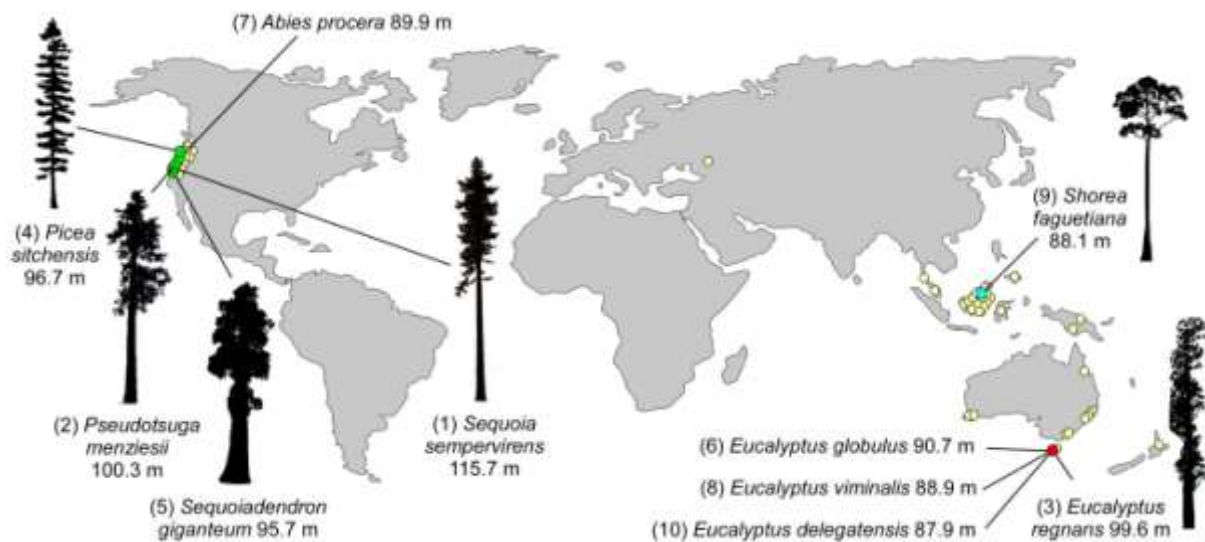
Figure 1. Global distribution of the top ten extant tallest tree species (See also Table S1). Most of the tallest species are either conifers from the west coast of North America (green dots) or eucalypts in Tasmania (red dot), although one dipterocarp species from Borneo (blue dot) ranks among the top ten. Other species that can exceed 70m (pale yellow dots) are mostly found on the west coast of North America, in eastern Australia and in Borneo.

Figure 2. Characteristics of giant eucalypts. (a) The Centurion at 99.6m (*Eucalyptus regnans*), the world's tallest flowering plant, Arve Valley, Tasmania; (b) *Eucalyptus grandis*, Mt Paluma, Queensland; (c) Young even-aged stand of *Eucalyptus obliqua* tall open forest with sclerophyllous understorey, Huon Rd, Tasmania. This species has thick fibrous bark and exhibits epicormic resprouting and extends to drier areas than its close relative *E. regnans*; (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 meristemic 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. Scale bar = 500 μm; (f) *Eucalyptus grandis* plantation in Cameron Highlands, Malaysia. Note the dense regeneration of native rain forest in the understorey.
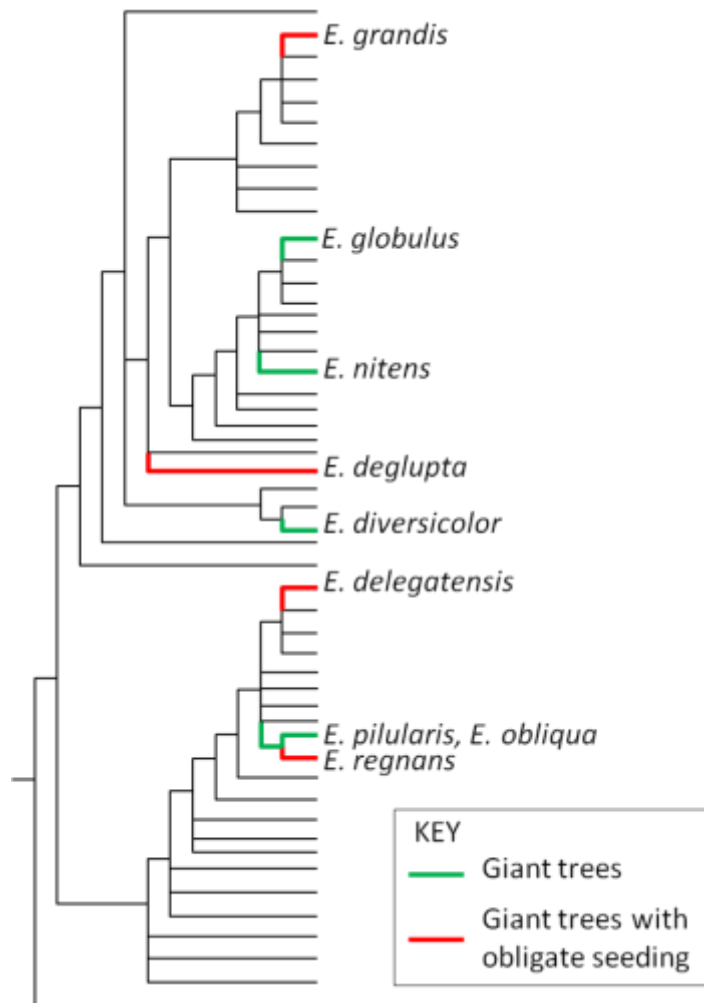
Figure 3. Eucalypt phylogeny showing the phylogenetic position of various giant eucalypts (<70m max height), based on nuclear ribosomal interspacer (ITS) sequences (Simplified from Steane *et al.*, 2002). Red lines indicate giant eucalypt species that exhibit obligate seeding. Gigantism appears to have arisen independently at least seven times, and obligate seeding in giant trees has arisen independently from resprouting taxa at least four times.
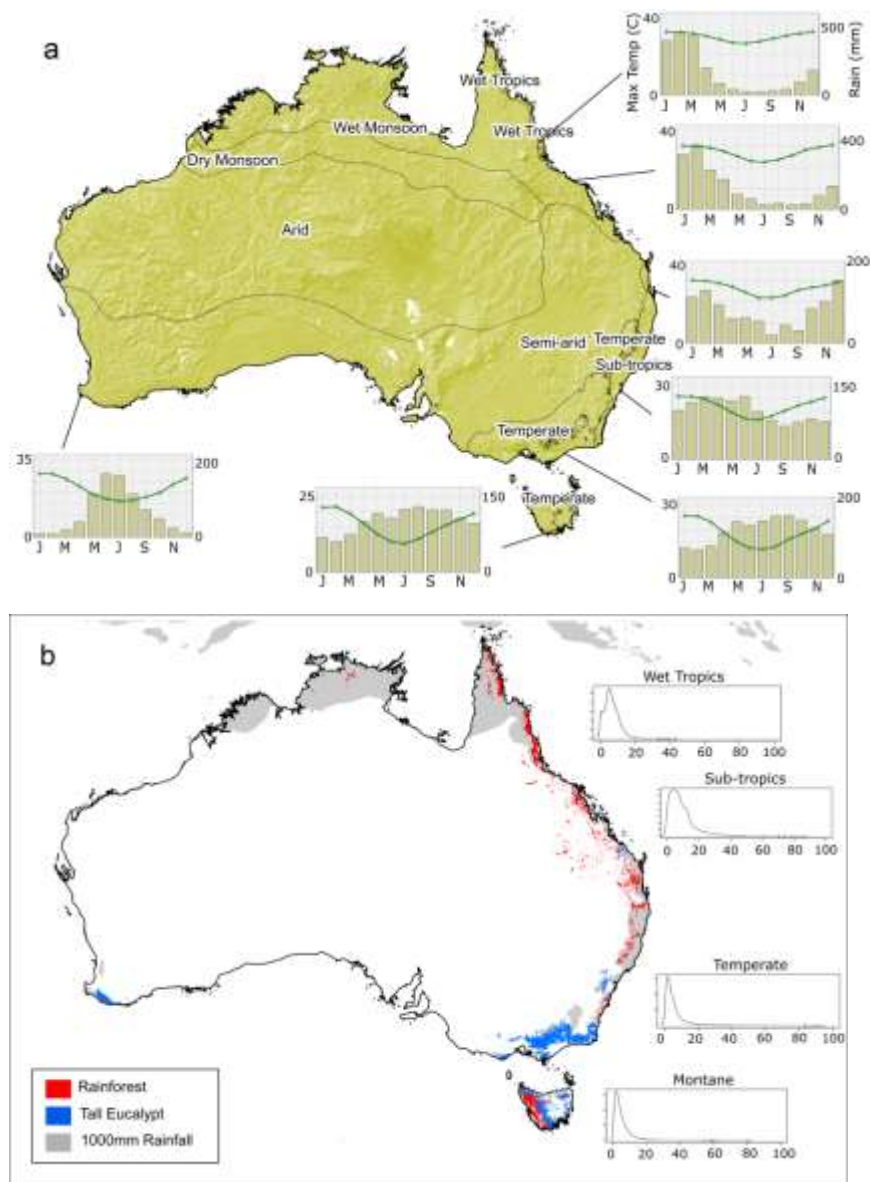
Figure 4. (a) Hutchinson's Climatic Regions for Australia (Hutchinson *et al.*, 2005). Embedded graphs show the monthly mean maximum temperature (green lines) and precipitation (vertical bars) for regions where giant eucalypts occur (Bureau of Meteorology, 2011); (b) the distribution of tall eucalypt forest and rain forest in Australia. Embedded graphs show the forest fire danger index of each climatic zone, calculated using daily weather records (Bureau of Meteorology, 2011).
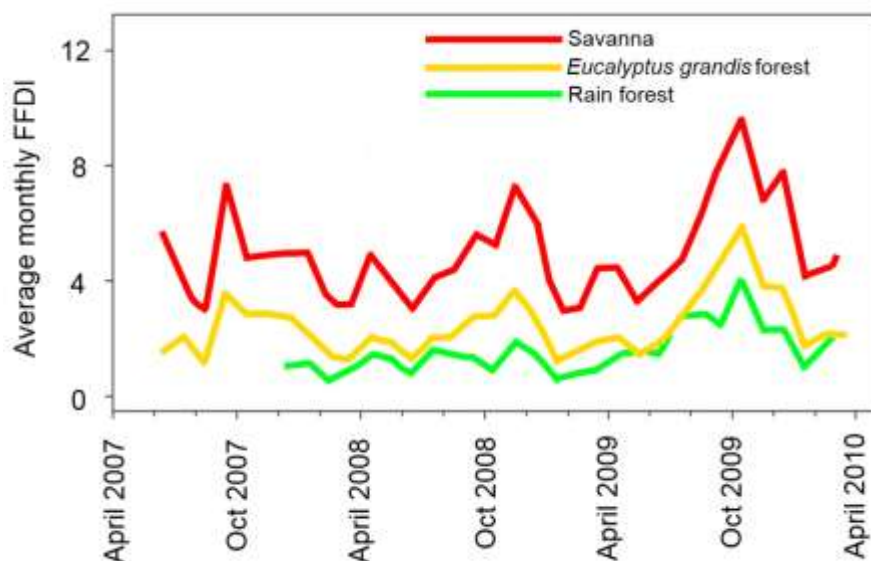
Figure 5. Average monthly Forest Fire Danger Index (FFDI) of savanna, *Eucalyptus grandis* tall open forest and rain forest in Far North Queensland, Australia between 2007 and 2010 (modified from Little *et al.*, 2012 in press). The data was computed from microclimatic observations from eight sites over the study period. The forest fire danger is typically higher in *E. grandis* forest than in rain forest but at certain times approximates that of the latter vegetation type.
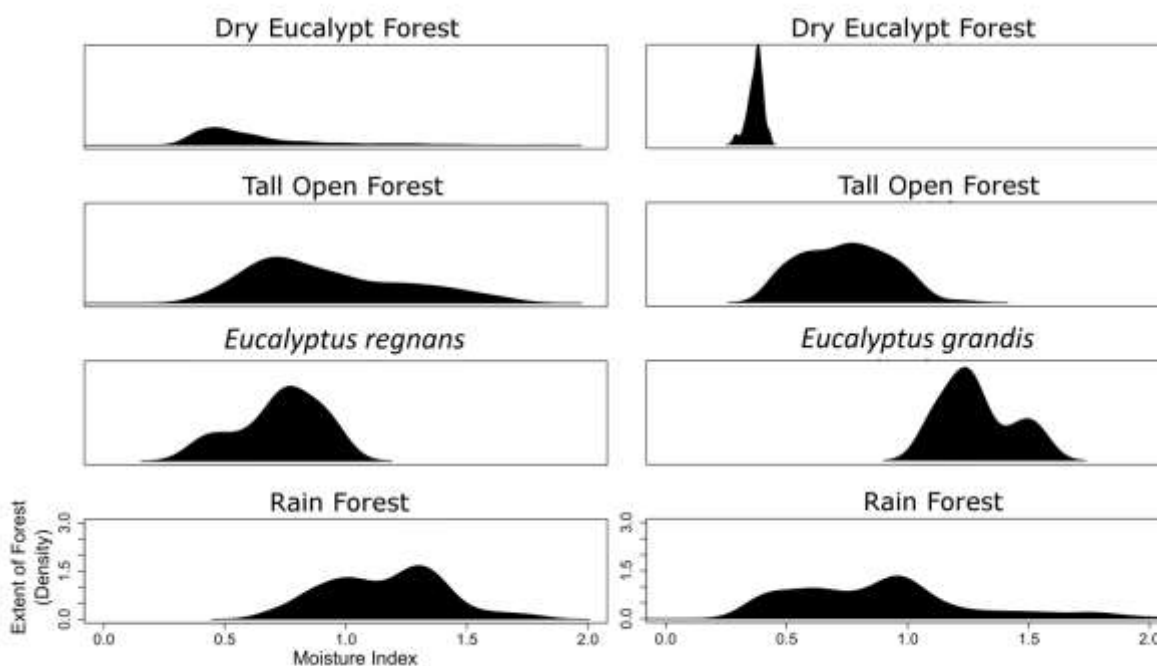

Figure 6. The mapped extent of dry eucalypt forest, tall open forest and rain forest in Tasmania (left column) and Far North Queensland (right column) and their occurrence along

a moisture index. The mapped extent of *Eucalyptus regnans* (Tasmania) and *E. grandis* (Far North Queensland) forest is shown (on an enlarged scale) as an indication of the niche position these forest types occupy along the dry eucalypt forest to rain forest continuum. The moisture index is the ratio of precipitation to Thornthwaite potential evaporation (Evaporation data: Donohue *et al.*, 2010). Higher values indicate wetter environments. In both Far North Queensland and Tasmania, the vegetation data used included all vegetation types mapped under their respective categories of dry sclerophyll, wet sclerophyll (which would include the giant eucalypts in this review) and rain forest. For *Eucalyptus grandis* and *E. regnans* graphs the area was derived specifically from GIS polygons mapped under tall open forest types dominated by that specific species (Sources: Queensland – Department of Environment and Resource Management, 2011; Tasmania - Department of Primary Industries and Water, 2009).

Table 1. Rainfall envelop and altitudinal of selected giant eucalypts and co-occurring rain forest trees (except SW Australia).

*Climatic zone/Species	Rainfall (mm)	Altitude (m asl.)
Tropics (Papua New Guinea)		
Eucalyptus deglupta	2500-5000	0-1800
Pometia pinnata	1500-5000	0-1700
Tropics (Far North Queensland)		
Eucalyptus grandis	1000-3500	<0-1100
Flindersia pimenteliana	1100-3800	<0-1200
Subtropics (Central Coast Queensland and New South Wales)		
Eucalyptus saligna	900-1800	<0-1100
Eucalyptus pilularis	900-1750	<0-700
Ceratopetalum apetalum	1000-2000	100-900
Temperate (Eastern Australia and Tasmania)		
Eucalyptus regnans	750-1700	150-1100
Eucalyptus obliqua	500-2400	<0-750
Nothofagus cunninghamii	1100-2500	<0-1570
Atherosperma moschatum	1000-2000	<0-1375
Temperate (Southwestern Australia)		
Eucalyptus diversicolor	900-1300	<0-300
Eucalyptus jacksonii	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

Table S1. Tree species known to reach 70m in height. The maximum height refers to tallest individual of the species measured to date and previous taller measurements of non-extant individuals given in parentheses. Sources for distributions and heights are given as footnotes

Taxon	Family	Maximum Height (m)	Distribution
[6]*Sequioa sempervirens*	Cupressaceae	115. 7 (115.9)	NW California, SW Oregon

[6]*Pseudotsuga menziesii*	Pinaceae	100.3 (126.5)	SW Canada, SW Oregon, Northern California
[4]*Eucalyptus regnans*	Myrtaceae	99.6 (132.2)	Australia (Tasmania, Eastern Victoria)
[6]*Picea sitchensis*	Pinaceae	96.7	Oceanic climates from Alaska to California
[6]*Sequioadendron giganteum*	Cupressaceae	95.7 (100.9)	West Coast of North America
[4]*Eucalyptus globulus*	Myrtaceae	90.7	Australia (Tasmania, Victoria)
[6]*Abies procera*	Pinaceae	89.9 (99.1)	West Coast of North America
[3]*Araucaria hunsteinii*	Araucariaceae	*(89)	Papua New Guinea
[4]*Eucalyptus viminalis*	Myrtaceae	88.9	Australia (New South Wales, South Australia, Tasmania, Victoria)
[3]*Shorea faguetiana*	Dipterocarpaceae	88.14	Borneo
[4]*Eucalyptus delegatensis*	Myrtaceae	87.9 (89)	Australia (Tasmania, Eastern Victoria)
[10]*Petersianthus quadrialatus*	Lecythidaceae	87.8	Philippines
[4]*Eucalyptus obliqua*	Myrtaceae	87 (98.8)	Australia (New South Wales, Queensland, South American, Tasmania, Victoria)
[3]*Koompassia excelsa*	Fabaceae	85.6	Borneo
[3]*Shorea superba*	Dipterocarpaceae	85.1	Borneo
[3]*Shorea argentifolia*	Dipterocarpaceae	84.8	Borneo
[11]*Eucalyptus nitens*	Myrtaceae	84.3	Australia (Eastern Victoria, SE New South Wales)
[6]*Tsuga heterophylla*	Pinaceae	82.9	Alaska to Northern California, extending into the Rocky Mountains

[3]*Hopea nutans*	Dipterocarpaceae	82.8	Borneo
[3]*Shorea smithiana*	Dipterocarpaceae	82.3	Borneo
[6]*Pinus lambertiana*	Pinaceae	82.2	Oregon to NW Mexico
[6]*Pinus ponderosa*	Pinaceae	81.9	SW Canada to NW Mexico
[9]*Eucalyptus saligna*	Myrtaceae	(81.5)	Australia (NE New South Wales, SE Queensland)
[6]*Abies grandis*	Pinaceae	81.4	SW Canada to NW California
[6]*Chamaecyparis lawsoniana*	Cupressaceae	81.1	SW Oregon, NW California
[3]*Shorea gibbosa*	Dipterocarpaceae	81.1	Borneo
[3]*Eucalyptus diversicolor*	Myrtaceae	80.5 (100.6)	Australia (SW West Australia)
[3]*Parashorea tomentella*	Dipterocarpaceae	80.2	Borneo
[3]*Eucalyptus nobilis*	Myrtaceae	79.5	Australia (NE New South Wales, SE Queensland)
[8]*Abies nordmanniana*	Pinaceae	78	Southern Russia to Turkey
[2]*Eucalyptus deglupta*	Myrtaceae	78	Indonesia, Philippines, Papua New Guinea
[5]*Eucalyptus grandis*	Myrtaceae	77	Australia (New South Wales, Queensland)
[6]*Abies magnifica*	Pinaceae	76.8	California, Western Nevada, SW Oregon
[3]*Shorea falciferoides*	Dipterocarpaceae	76.4	Borneo
[3]*Dryobalanops aromatica*	Dipterocarpaceae	76.2	Borneo
[3]*Dyera costulata*	Apocynaceae	76.2	Peninsula Malaysia
[12]*Agathis australis*	Araucariaceae	75	northern New Zealand

[6]*Pinus monticola*	Pinaceae	73.8	SW Canada to California
[3]*Shorea smithiana*	Dipterocarpaceae	72.9	Borneo
[3]*Parashorea malaanonan*	Dipterocarpaceae	72.8	Borneo
[3]*Shorea johorensis*	Dipterocarpaceae	72.5	Borneo
[6]*Abies ammabilis*	Pinaceae	71.9	SE Alaska to Northern California
[1,5]*Eucalyptus deanei*	Myrtaceae	71	Australia (NE New South Wales, SE Queensland)
[3]*Shorea parvifolia*	Dipterocarpaceae	70.9	Borneo, Peninsula Malaysia, Sumatera, Thailand
[6]*Agathis dammara*	Araucariaceae	70.1	Sulawesi
[8]*Pinus merkusii*	Pinaceae	*70	South-east Asia, Malesia, China
[1]*Eucalyptus denticulata*	Myrtaceae	>70	Australia (SE New South Wales, NEVictoria)
[1]*Eucalyptus jacksonii*	Myrtaceae	>70	Australia (SW West Australia)
[1]*Eucalyptus pilularis*	Myrtaceae	>70 (85)	Australia (NE New South Wales, SE Queensland)

[1]Boland *et al.* (2006); [2]Carder (1995, 2005); [3]Dial *et al.* (2005 unpublished report); [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 & Steward, (1995).