The enigma of *Eucalyptus grandis* (Rose Gum)/rainforest ecotones in the Australian Wet Tropics – the plot thickens

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Abstract

Australian tall eucalypt forests have been the subject of awe and admiration since early colonial days. In the Wet Tropics of North Queensland, such forest occurs in transitional or ecotonal patches between rainforests and open woodland savannas. Rainforest species are commonly interpreted to be encroaching into the understorey of these tall eucalypt forests, namely those with statuesque Rose Gum (*Eucalyptus grandis*) dominants. This has led to concerns for the long term persistence of *E. grandis* forests, and ongoing debates over their need for active fire management. In this essay, I highlight the enigmatic ecology of these ecotonal forest habitats, and make the case that the management of these habitats should be grounded in ecological principles within a broader perspective of patterns in global vegetation change.

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Introduction

In the Wet Tropics of Queensland, a curious phenomenon has been occurring for the last half a century or longer – rainforest has expanded out into open-canopied vegetation (Harrington & Sanderson 1994; Harrington *et al*. 2000; Lawson *et al*. 2007; Tng *et al*. 2010, 2012a), with similar reports from numerous other tropical (Russell-Smith *et al.* 2004; Bowman & Dingle 2006; Bowman *et al*. 2001; Vigilante *et al*. 2017) and subtropical (Krishnan *et al*. 2019) locations in Australia. Far from being a phenomenon restricted to Australia, similar incursions of woody vegetation into savanna woodlands have also been documented in other locations globally (Murphy & Bowman 2012). Various explanations have been proposed as to the cause of this expansion, but increases in atmospheric CO_2 concentrations have been implicated as the leading driver (Bond & Midgley 2000; Murphy & Bowman 2012).

Rather than being a cause for more detailed study and analysis, the observation of rainforest expansion has led to distress on the part of some land managers and conservationists who consider that another forest type, wet sclerophyll forest (also variously called wet eucalypt forest, tall open forests, mixed forest, etc.) is at risk of disappearing.

The bulk of the attention has been focused on a subset of these forests that are dominated by Rose Gum (*Eucalyptus grandis*), which are charismatic and statuesque trees 40-60m tall (Fig. 1). The distribution of *E. grandis*-dominated forests falls within the climatic envelope that can potentially support rainforest, and thus rainforest species are often observed to form a closed canopy beneath

Figure 1. The management of statuesque Rose Gum (*Eucalyptus grandis*) forests has been the subject of ongoing debates in the Australian Wet Tropics. Note the developing canopy layer of rainforest trees beneath the Rose Gum canopy. Photo by David Tng.

the emergent canopy of *E. grandis* trees. On the basis of this observation, some consider these forests to be especially at risk from rainforest incursion. This sentiment is well expressed in the concluding passage in Harrington and Sanderson's (1994) classic paper: "*In addition to possible species extinction, it would be a significant loss if the aesthetically magnificent Wet Sclerophyll Forests of north Queensland were to be largely engulfed by rainforest*." Additional concern has also been raised for the survival of certain endangered mammals believed to be intimately dependent on these habitats (Bradford and Harrington 1999). For this reason, some authors are in support of using frequent low intensity burns as a tool to manage what is perceived as an "invasion" of rainforests into the understorey of *E. grandis* forests (Stanton *et al.* 2014a; Bradford 2018).

However, successful ecosystem management needs to take into account the complexity of ecosystems and economies of scale (Nanda *et al*. 2018). While there is a general consensus that eucalypt-dominated forests require fire to regenerate (Peeters & Butler 2014; Tng *et al*. 2014b; Bradford 2018), citing an exact fire return time in years is not straightforward and forms the basis of most disagreements between land managers. Prescribed burning is a management tool to achieve a desired management outcome, but the frequency, intensity and weather history between burns as well as prevailing environmental conditions will result in different ecological responses (Bowman *et al*. 2013). Different temporal and spatial patterns will also trigger different successional pathways and species associations (Smith *et al*. 2016). Thus, management policies for wet sclerophyll forest habitats in the Wet Tropics need to be placed into a broader ecological and landscape context, with a careful review of spatial and temporal variables.

In a series of studies carried out between 2010 and 2014, I studied the ecology of *E. grandis* forests and other temperate forests dominated by an exceptional guild of large-statured eucalypts (Tng *et al*. 2012a,b, 2013). From the insights gleaned from these studies, I presented a contentious suggestion that *E. grandis* forests will naturally regenerate en-masse in the presence of large disturbances, and should be passively managed (Tng *et al*. 2014a). These conclusions have led to ongoing discussions (Stanton *et al*. 2014a,b; Little 2015), some of which appeared in a recent volume of the North Queensland Naturalist (Russell & Franklin 2018; Bradford 2018). The objective of this essay is, therefore, to add some additional perspectives and observations to the dialogue, potentially conciliating opposing ideas, and most of all to highlight the need for further research on these fascinating ecosystems.

A landscape view of Rose Gum forest ecology

In the Wet Tropics, *E. grandis* forest occurs between rainforests and savanna in thin bands varying from a few hundred metres to no more than 4 km in width, within a somewhat mesic zone where rainforest plants can also grow. Because *E. grandis* forests occur on the margins of rainforest, their natural regeneration would have been dependent on encroaching savanna fires. These would have to have been sufficiently severe to have spread into rainforest under circumstances that would provide a window of opportunity for *E. grandis* individuals to seed, whilst keeping rainforest regeneration at bay long enough for these individuals to establish. Spot fires in rainforest may also occasionally open patches up in otherwise continuous rainforest, and *E. grandis* may recruit in such patches if there are parent trees in the vicinity (Russell & Franklin 2018). A balanced view would hence be that an intermediate intensity and frequency fire may be the most appropriate natural fire regime for the species. However, prescribing an exact fire return time in years is not straightforward.

One problem that is central to this discussion on the management of *E. grandis* forest vegetation is the persistent view that these forests are a discrete ecosystem. Yet, the habitat between rainforest and savanna that *E. grandis* typically inhabits has all the ecological hallmarks of an ecotone (Tng *et al*. 2013). By their very nature, such habitats are zones of rapid change (Kark & van Rensburg 2006; Oliveras & Malhi 2016) because they are subjected to opposing environmental factors such as fire and water, creating a zone of ecological tension (Warman & Moles 2009). Rainforest species recruiting within a forest-savanna ecotone should not come as a big surprise, but on the same note, it should also be possible that disturbance will occur that causes a shift in favour of savanna species. It is therefore puzzling that natural plant-environment feedback phenomena such as rainforest regeneration within an ecotone is described with non-objective terms such as "invasion".

One point that deserves to be made is that the actual spatial width and location of ecotones can be expected to shift depending on prevailing environmental conditions (Warman & Moles 2009; Oliveras & Malhi 2016). Unsurprisingly, this difficulty in assigning stability to an inherently unstable ecosystem state confounds management and conservation perspectives which aim to maintain the status quo in a perceived vegetation state.

In an earlier landscape level analysis (Tng *et al*. 2012a), I compared aerial photos from the 1950s and photography from 2008 and quantified how much rainforest had expanded into open vegetation. This was conducted in an attempt to provide updates to earlier work by Unwin (1989) and Harrington & Sanderson (1994) who had first observed the rainforest expansion phenomenon. While this work added more confirmation that rainforest had expanded, and across all geologies, one conclusion I drew from the study was that rainforest expansion is not happening at an equal rate across the Wet Tropics. Indeed, some areas did not appear to have changed much over the course of 50 years (Tng *et al*. 2010, 2012a). That leads to a question of whether some *E. grandis* forests are actually in a state of ecological stasis, or arrested succession, due to previous fires, where rainforest plants may be continuously recruiting but not successfully establishing. Given the ecological affinity of both *E. grandis* and rainforest species for wet habitats, the Type 1 *E. grandis*-dominated forests with grassy understorey of Harrington & Sanderson (1994) are in many ways a rather atypical structural type. Unfortunately very little data is available before 1943 to suggest whether these specific patches were artificially maintained by aboriginal land owners or early colonists.

Harrington & Sanderson (1994) also classified under their forest-open woodland ecotone scheme, other types of "wet sclerophyll forest" that seem to represent a gradient extending out towards the savanna woodlands, grading from tall eucalypt forest with a rainforest understorey to medium-statured dry eucalypt forests, and also some other forest types dominated by *Allocasuarina torulosa* (Rose She-oak). Some of these forests do not even include *E. grandis* (Harrington & Sanderson 1994).

A broader ecological question that arises is: how can we actually define this ecotone? Under ecological theory, the different vegetation types encompassed under the wet sclerophyll vegetation of Harrington & Sanderson (1994) may represent a series of different unstable vegetation states arrayed along a gradient of humidity and fire return times (Warman & Moles 2009). If this is the case, would it be reasonable to apply a broad brush recommendation for the wet sclerophyll vegetation on the drier end which burns readily (Harrington & Sanderson 1994) to the vegetation on the wetter end?

Managing *Eucalyptus grandis* forests based on a single species?

On the regenerative biology of the species, I have previously cited *E. grandis* to be an obligate seeding eucalypt species (Tng *et al*. 2012b). I have since observed, as have Williams *et al*. (2012) and Bradford (2018), that young *E. grandis* trees are able to resprout basally after fire. With the assertion that *E. grandis* is a facultative seeder, Bradford (2018) recommends frequent low-intensity fires to maintain *E. grandis* populations. Yet, the use of fire as a management tool for *E. grandis* forests on a whole is still debatable, because the management of a forest habitat by fire should not be based solely on stand structures or regeneration strategies of a single species (Franklin 1993).

Indeed, my argument for recommendation of passive management for *E. grandis* forests was not based simply on the perceived inability of *E. grandis* to resprout (Tng *et al*. 2014a), but also took into consideration the overall ecological and habitat context within which the species lives, and its relationship with adjoining rainforest and savanna habitats (Warman & Moles 2009; Tng *et al*. 2013).

There are also some important qualifications to be added to the discussion. Although Williams *et al*. (2012) made observations that even small-stemmed *E. grandis* saplings have some ability to resprout when damaged by fire, they had studied *E. grandis* regeneration under a very specific set of experimental conditions. Specifically, they had selected wet sclerophyll forest patches which they deemed had sufficient grass and sedge fuels to carry fires. They subsequently experimentally burned these patches with low intensity fires to examine the post-fire regeneration of both sclerophyll and rainforest species. The response of *E. grandis* saplings to these fires should therefore be interpreted with this experimental context in mind.

While Williams *et al*. (2012) found 9% basal coppicing of two-year old *E. grandis* saplings after a small fire, this represented only 3 out of 35 saplings. By any measure, this would represent a very low success rate over repeated fires. Additionally, 35 saplings is a small sample size on which to base an entire recovery plan for a species, let alone that of a habitat type. With this in mind, the use of repeated fire regimes on forest patches with young *E. grandis* should in fact be discouraged, practiced only in certain priority areas under careful monitoring, or recommended only after results from more controlled experiments become available.

To present a more balanced discussion on the topic of resprouting that includes other species within the habitat, it should be noted that Williams *et al*. (2012) reported that rainforest species had similarly survived these experimental fires by epicormic coppicing or by seeding, and that there was no difference in stem regeneration densities of sclerophyll and rainforest species. Also, Williams *et al*. (2012) documented that a number of obligate seeding eucalypt forest species such as *Acacia celsa* (Brown Salwood), *Allocasuarina torulosa*, and *Dodonaea triquetra* (Large-leaved Hop-bush) were killed and subsequently reseeded after fire (but they did not report further the effects of repeated fires on these species). These results of Williams *et al*. (2012) could also be interpreted as an inability for repeated low-intensity fires to prevent the regeneration of rainforest species, or that both sclerophyll and rainforest species can persist equally within these ecotonal habitats.

An additional point is that the strict delineation of plant regeneration strategies into obligate seeders, and resprouters has come under criticism, as the ability to resprout is an inherently variable character that often depends on factors such as age and height and also previous disturbance (Vivian *et al*. 2008, 2010). It is also becoming increasing clear that plants may have multiple post-fire recovery strategies (Poulos *et al*. 2018). More critically, the ability of young individuals of a species to resprout epicormically says nothing about the responses of older individuals. Indeed, mature *E. grandis* individuals, and in particular, those older individuals valued for providing tree hollows for native fauna, may be disadvantaged by having to deal with frequent fires. Some observations also suggest that multiple low-intensity fires readily kill mature *E. grandis* trees (Little 2015). This could be because multiple fires degrade the protective bark of trees, and adult trees that are not strong resprouters may be at risk of dying after multiple fires (Fairman *et al*. 2016). Additionally, old trees that have ground level hollows may be at greater risk as these hollows may allow fire to enter and smoulder (Holland *et al*. 2017).

Threatened fauna in ecotones

One frequently used argument for managing *E. grandis* forest using frequent low-intensity fires is for the maintenance of habitat for fauna. Of particular concern is a regionally endemic subspecies of the Yellow-belled Glider (*Petaurus australis*, unnamed subspecies) (Brown *et al*. 2006).

The Yellow-bellied Glider of the Wet Tropics feeds on tree sap, and appears to rely exclusively on the *Eucalyptus resinifera* (Small-fruited Red Mahogany) as a feed tree (Bradford & Harrington 1999). They also inhabit dens formed in hollows of old *E. grandis* or potentially also *E. resinifera* trees (Little 2015). There is good quantitative data on the use of *E. resinifera* feed trees on Mt Baldy, and most are within a short distance from a potential nest tree (Bradford & Harrington 1999). However, movement tracking by Goldingay *et al*. (2001) shows that these gliders can travel at least 1 km between nest trees. In all, it seems that there is very little published work that either assesses the den use of gliders in tree hollows or the abundance of tree hollows in the landscape, or that ascertains the environmental conditions favourable to tree hollow formation.

As highlighted earlier, the effects of frequent fire on such nest trees also remains to be assessed, and so are the indirect effects such regimes may have on gliders. Probably more worryingly, continual logging of native forest is an ongoing threat to Yellow-bellied Gliders (Arup 2015), and specifically, Little (2015) has highlighted that continued selective extraction of large *E. resinifera* constitutes a more immediate threat to glider populations.

Perhaps also, the emphasis on a single, albeit threatened animal species, needs to be counterbalanced with a consideration of how prescription burning may affect other fauna that inhabit these forests. While some species may be advantaged after fire, others may be negatively impacted due to the loss of certain forest structural components such as logs or ground den sites (e.g. Doumas & Koprowski 2013; Holland *et al*. 2017). Concurrent monitoring and investigation of faunal communities should be integrated as part of monitoring programs after prescription burning to determine the long-term response of fauna to fire-induced changes.

Aboriginal burning, then logging in post-European times?

Another aspect used to support active fire management is the perception that these habitats are suffering from changes to fire regimes once maintained by Aboriginal people. However, this is a weak basis on which to base fire management because we simply do not have very good records of how fire was used in pre-colonial times over the entire region.

The Kuku Yalanji people used fire to maintain small areas of open forest at rainforest margins where food plants such as native cycads (*Cycas* spp.), yams (*Dioscorea* spp.) and other carbohydrate-rich resource species grew (Ens *et al*. 2017). Yet, such management would have only been possible on a local scale, and regional scale fires were determined by environmental factors (Hill & Baird 2003). In coastal regions at least, the view that recent trends in rainforest expansion are the result of the disappearance of Aboriginal people and their fire practices has been contested (Hill *et al*. 2000). Using aerial photos combined with records of early land use, Hill *et al*. (2000) argued that management of fire by the Kuku-Yalanji people prior to European occupation ensured the presence of extensive rainforest cover, and that current rainforest expansion in her study region represents recovery from logging. The regeneration from logging hypothesis is also highly likely for upland rainforest, given an estimate of more than 40% of the original area of rainforest on the Tablelands at the time of contact in the late nineteenth century had been cleared, mainly for cane farming and cattle grazing (Tracey 1982).

What about rainforests? – some broader ecological and space-time perspectives

When visiting the Wet Tropics of Australia, it is easy to lose the perspective that rainforest actually occupies a miniscule portion of Australia (*c.* 0.5%), most of it occurring within the Wet Tropics (ABARES 2016). Set against this broader spatial perspective, any rainforest expansion that has been reported (Lawson *et al*. 2007; Tng *et al*. 2012a) is insignificant. Environmental niche modelling predicts that both rainforest and tall eucalypt forest have yet to occupy their predicted distribution in Australia (Hilbert & Fletcher 2012), and there is little doubt that fire is limiting the full development of these habitats (Bowman 2000).

On this note, some believe that forest advance is irreversible (Stanton *et al*. 2014a; Bradford 2018). However, there is overwhelming evidence from pollen and charcoal samples from lakes and soil cores in the region (e.g. Bromfield Swamp, Lynch's Crater, Lake Euramoo) that demonstrate that the shift between rainforest and open vegetation has occurred numerous times over the last >23,000 years (Kershaw 1970, 1971, 1975; Hopkins *et al*. 1993; Haberle 2005; Kershaw *et al*. 2007). In this context, rainforest advance cannot be considered irreversible.

When considering fire, the bigger concern should be the vulnerability of intact rainforest vegetation in the Wet Tropics. Climate change may already be causing unprecedented fire activity in the landscape, and current fire management problems are likely to be compounded by more frequent extreme fire-conducive weather conditions (Bowman *et al*. 2013). Even though rainforest is generally considered to be able to retard fires, the frequency of fires in rainforest can be expected to increase if droughts become more prevalent and severe across the landscape due to climate change (Bowman 2017). Studies already show that increases in forest fire danger on certain days of the year can magnify the risk of uncontrolled fires in rainforest (Little *et al*. 2012).

Even more pertinently, if the sole concern was the fate of *E. grandis* forests, Unwin (1989) has provided some evidence to show that *E. grandis* recruitment advances ahead of the expanding rainforest and I think that if we are to better understand the dynamics of these forests, the advancing edge of *E. grandis* forest should be where we must focus the bulk of our attention for future monitoring, by setting up more study transects and plots on this advancing edge.

There are more pressing threats in the short term to these forests than simply the lack of fire. Projected scenarios of rising temperatures, coupled with events of severe droughts or fire could have a negative impact on *both* rainforest and *E. grandis* forests, particularly if *E. grandis* forests are more adapted to cooler upland subtropical-type climates (Little 2015). One concern about frequent burning then would be that the open environments generally will be drier (De Frenne *et al.* 2013), and there will be less surrounding vegetation to buffer developing seedlings of *E. grandis* and other ecotone species from drought events.

Conclusion

Forests with *Eucalyptus grandis* as canopy dominants are charismatic habitats that have been the subject of much debate regarding their management. In this synthesis, I have brought together various lines of evidence to argue that these habitats are ecotonal, and that their management should take into account their dynamic quality, their relationship with adjacent habitats, and modern day trends in climate change.

As a rejoinder to my earlier suggestion to 'Let these giants be' (Tng *et al*. 2014a, 2019), I propose also that the sheer amount of resources needed to manage an inherently wet habitat throughout the whole of the Wet Tropics region using prescribed high frequency fires is prohibitive, not to mention the number of factors that will have to be taken into account to minimize the risk of fire spread into built up areas or to prevent collateral damage to rainforest. Taking a pragmatic view, fire management may only be feasible in certain localities and on a small scale (e.g. Russell & Franklin 2018). Additionally, I argue that an intensive monitoring program will be necessary for assessing the success of such endeavors and that significant resources would be needed to control for collateral damage that may occur.

Ultimately, I suggest that a top priority to maintain the integrity of these forests and their associated threatened fauna should be campaigning for the cessation of logging of native forests and extraction of large eucalypt trees. Additionally, our focus needs to be long term monitoring of species compositional change of these forest using permanent plots (Wood *et al*. 2015). Such monitoring should assist in understanding and appreciating the dynamic long term processes affecting these forests (Buettel *et al*. 2017). From the lines of evidence I have synthesized, I believe that *E. grandis* forests and the related wet sclerophyll forests are globally-unique ecotones, and thus my prediction regarding their longer term distributions would be, to use an illustrative metaphor, riding on the rainforest wave.

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