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RESEARCH ARTICLE

Has global environmental change caused monsoon rainforests to expand in the Australian monsoon tropics?

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Abstract A large research program in the Australian monsoon tropics has concluded that monsoon rainforests have expanded within the savanna matrix, a trend that has been emulated throughout the tropics worldwide. The driver of the northern Australian trend was not resolved, but it was suggested to be linked to a long-term trend towards wetter climates, atmospheric CO_2 enrichment, and changed fire regimes. We review these findings with particular consideration of its analytical and evidentiary basis and plausibility of the global change hypothesis. Field validation has largely demonstrated that the aerial photographic technique that underpinned the previous research is reliable enough to detect rainforest expansion. Statistical modelling demonstrated that the expansion is related to sites with regionally low fire activity, although models are of low explanatory power reflecting the sketchy historical records of fire and feral animal impacts. Field studies show that current fire regimes adjacent to expanding rainforest patches are causing populations of the native conifer *Callitris intratropica,* an obligate seeder, to crash. Therefore, it is unlikely that changes in fire regimes, which have been deleterious to other fire-sensitive taxa and plant communities in the region, are responsible for the rainforest expansion. We conclude that the expansion of monsoon rainforests is most plausibly linked to the current wetting trend or elevated CO_2 concentration. Increases in either water availability or CO_2 concentration can potentially overwhelm the negative feedback between fire and rainforest cover that is responsible for the meta-stability of monsoon rainforest boundaries. However, further research at the continental scale, using aerial photography, tree rings and other proxies, is required to evaluate this hypothesis.

Keywords Aerial photography · *Allosyncarpia ternata* · Climate change · Closed forest · CO_2 · Eucalypt · Fire · Monsoon rainforest · Rainfall · Tropical savanna

Introduction

Rainforest boundary dynamics are likely to be strongly affected by accelerating global environmental change, especially changes in water availability (Laurance and Williamson 2001), atmospheric CO_2 concentration (Bond and Midgley 2000), fire regime (Cochrane 2003), and their synergistic effects (Cochrane 2001; Laurance and Williamson 2001; Mitchard et al. 2009).

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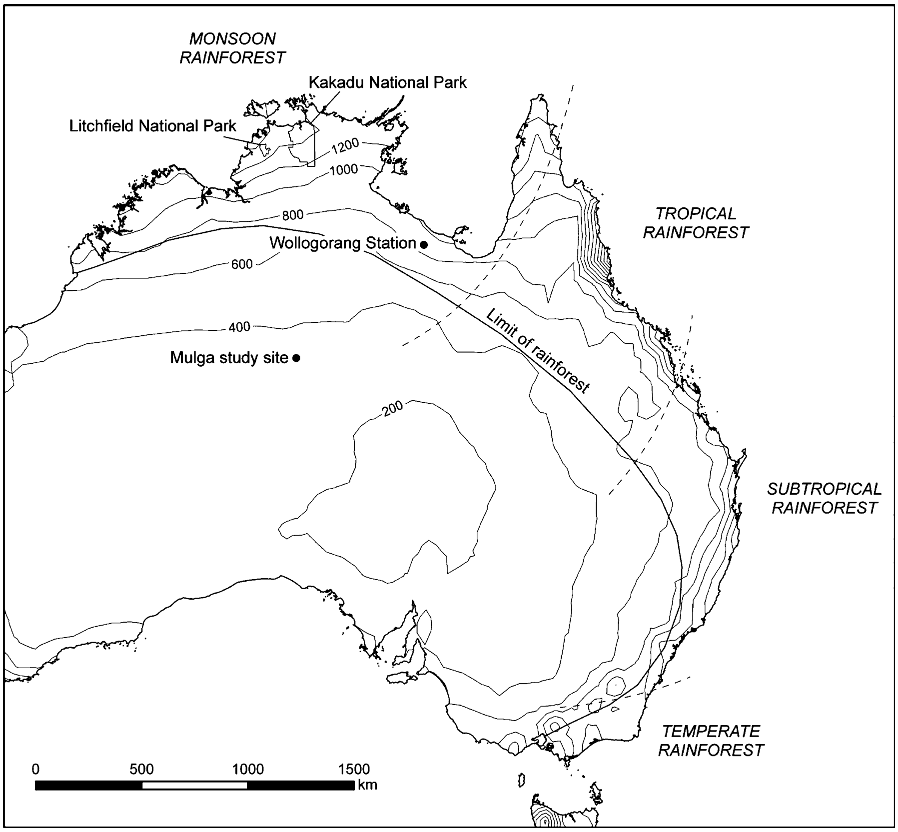
Understanding how the distribution of rainforests will change is critically important because of the high values associated with them, especially those relating to carbon storage (Loarie et al. 2009) and biodiversity (Bradshaw et al. 2008), but also a range of other environmental services (e.g. Bradshaw et al. 2007; Sheil and Murdiyarso 2009). One of the critical factors assumed to control rainforest boundaries is landscape fire, and there is the potential for increases in fire frequency and intensity, associated with climate and landuse change, to cause rainforests to contract. Indeed, increases in the frequency of fires in Southeast Asia and South America in recent decades, in synergy with other anthropogenic disturbance, are destroying or degrading large tracts of rainforest (Cochrane 2003; Field et al. 2009).

The importance of fire is particularly conspicuous on the Australian continent, where rainforests have a highly fragmented distribution within a matrix of highly flammable vegetation (Bowman 2000a). Indeed, an operational definition of Australian rainforest is woody vegetation types that are more susceptible to recurrent fire disturbance than the ubiquitous, archetypical fire adapted vegetation dominated by eucalypts (Bowman 2000b, 2001). It is important to note that unlike the rest of the world, the term ‘rainforest’ is used in Australia to define a broad variety of atypical rainforest types (Bowman 2000a). The current distribution of Australian rainforests occurs as an arc of patches along the eastern and northern coastlines (Fig. 1) and includes a variety of structural and floristic types that are typically grouped by the climatic regime (e.g. temperate, subtropical, tropical, monsoonal).

Monsoon rainforests are adapted to a climate that is characterised by seasonally wet and dry conditions (Bowman 2000a). In coastal regions of the monsoon tropics, 90% of annual rainfall occurs in the wet season (October to March) and daytime air temperatures remain high throughout the year (~30°C) with cooler nocturnal temperatures (~20°C) occurring during the dry season (Bureau of Meteorology 2009). Monsoon rainforests are very small patches of closed canopy vegetation in tracts of frequently burnt

Fig. 1 The distribution of the four major types of rainforest in Australia (adapted from Bowman 2000a). The *bold line* indicates the approximate inland extent of rainforest (includes the whole of Tasmania) and the *contour lines* indicate mean annual rainfall (Australian Bureau of Meteorology, Canberra). The locations where monsoon rainforest expansion has been demonstrated are indicated, as well as the location of the study of mulga dynamics of Bowman et al. (2008a)



savanna dominated by eucalypts (*Eucalyptus* and *Corymbia* spp.) or paperbarks (*Melaleuca* spp.). The monsoon rainforests support a high diversity of plant species (Russell-Smith 1991) and are important refugia for savanna-adapted mammals to avoid climatic extremes, predators and fires (Bowman and Woinarski 1994). They are also critical to the conservation of frugivorous birds that move between patches of rainforest and thus depend on the existence of a network of patches. A spatial analysis of six bird species by Price et al. (1999) demonstrated that the destruction of individual patches could have far-reaching regional effects on habitat availability for frugivorous birds, by dramatically increasing the distance between patches.

An extensive survey of 1219 rainforest patches by Russell-Smith (1991) allowed the classification of northern Australian monsoon rainforests into 16 floristic types. The two basic types of rainforest that occur are 'wet rainforest' which occurs on sites with perennial moisture supplies such as springs, and 'dry rainforest' which occurs on freely drained sites that are often associated with topographic fire protection such as rocky areas, cliff lines and hill tops (Bowman et al. 1991; Russell-Smith 1991). An important monsoon rainforest community (that can be either wet or dry type) is dominated by *Allosyncarpia ternata,* a myrtaceaous tree that is endemic to the Arnhem Land Plateau that forms the eastern border of Kakadu National Park (Russell-Smith et al. 1993; Bowman and Dingle 2006).

While monsoon rainforest trees can recover following a single fire (Bowman 1991), they are susceptible to recurrent fires (Fensham et al. 2003a; Bowman 2005) and are therefore vulnerable to increases in fire frequency. Conversely the tolerance of savanna trees to fire is thought to explain why they dominate the monsoon tropical landscape despite having lower growth rates and assimilation rates compared to monsoon rainforest trees (Prior et al. 2003, 2004a, b). In northern Australia, it is commonly accepted that the historically recent breakdown of Aboriginal fire management, which is characterised by numerous small, low intensity fires (Bowman et al. 2004b), has resulted in a regime of frequent and intense landscape fires that is hostile to rainforests (Russell-Smith and Bowman 1992; Bowman and Panton 1993; Russell-Smith et al. 2002) and other fire sensitive vegetation such as the endemic conifer *Callitris intratropica* that forms groves in eucalypt savannas (Bowman et al. 2001a). In this context, the recent discovery of rainforest expansion since the middle of the last century at four locations in the Northern Territory (Fig. 1) (Bowman et al. 2001b; Banfai and Bowman 2006; Bowman and Dingle 2006; Brook and Bowman 2006) is remarkable, being contrary to the widely accepted view that fire limits the extent of rainforests. The expansion of rainforests in northern Australia is paralleled by a similar expansion elsewhere in the tropics (e.g. Schwartz et al. 1996; Guillet et al. 2001; Puyravaud et al. 2003; Wigley et al. 2009).

The reported rainforest expansion in northern Australia, based on analysis of historical sequences of aerial photography, is at odds with regional permanent plot studies pointing to ecological degradation associated with uncontrolled fires (Prior et al. 2009; Murphy et al. 2010a; Russell-Smith et al. 2010). Indeed, there has been a region-wide population crash of cypress-pine (*Callitris intratropica*) in response to current hostile fire regimes in sharp contrast to the widespread expansion of rainforests (Bowman and Panton 1993; Bowman et al. 2001a). It is important to note that the discovery of rainforest expansion in northern Australia does not necessarily discount the role of fire in controlling rainforest distribution if some other process is causing rainforests to expand. Indeed, the authors of these four studies from the Northern Territory (Bowman et al. 2001b; Banfai and Bowman 2006; Bowman and Dingle 2006; Brook and Bowman 2006), have claimed that global environmental change is the ultimate cause of the reported expansion of monsoon rainforests, a view that has been incorporated into the recent Intergovernmental Panel on Climate Change report (Hennessy et al. 2007).

Average yearly rainfall has shown an increasing trend in northern Australia over the last century. Between 1910 and 1995 total annual rainfall in the Northern Territory rose by 15–18% (Hennessy et al. 1999), with the increasing trend considerably steeper for the second half of the 20th century (Smith 2004). There was also an almost 20% increase in the number of rain days between 1910 and 1995 (Hennessy et al. 1999). In contrast, annual rainfall decreased in eastern, southern, and southwestern Australia in the second half of the 20th century (Smith 2004). Thus, the observed expansion of rainforest boundaries throughout northern Australia may be driven by a wetting trend. In addition, atmospheric CO_2 concentration has been rapidly increasing for the last two centuries, with the increase dramatically accelerating in the 20th century (Keeling and Whorf 2004). Numerous controlled experiments have frequently shown an increase in tree growth rates under elevated CO_2 due to the CO_2 'fertilisation effect' (Ainsworth and Long 2005), including species of trees from Australian monsoon rainforest (Berryman et al. 1993). Elevated atmospheric CO_2 has the potential to shift forest-savanna boundaries as it advantages trees and shrubs (C_3 photosynthetic pathway) over (predominantly C_4) tropical grasses (Bond and Midgley 2000; Berry and Roderick 2002) with the consequence of changing the strongly contrasting fuel types between rainforest and savanna (grass vs. leaf litter) (Bowman and Wilson 1988). Thus, fire regimes may also change because woody plants can suppress grassy fuels, reversing the well known positive feedback between fire and grass cover (the 'grass/fire cycle' of D'Antonio and Vitousek 1992). Elevated CO_2 may also indirectly increase growth by improving plant water status (Ainsworth and Long 2005). Thus, rising atmospheric CO_2 may be the primary driver of the widespread woody vegetation expansion.

There is emerging evidence of profound changes to the structure and function of tropical rainforests, both in northern Australia and elsewhere (Lewis et al. 2004). The expansion of northern Australian monsoon rainforests parallels reports of expansion of tropical rainforest on the east coast of Australia (Harrington and Sanderson 1994; Russell-Smith et al. 2004a) and increased tree growth and biomass accumulation in tropical rainforests elsewhere in the world (Phillips and Gentry 1994; Lewis et al. 2009; Mitchard et al. 2009). Furthermore, there have been many reports of woody plant encroachment over the past century for a diverse range of grassland and savanna ecosystems in Australia, North and South America, Africa and Southeast Asia (Archer et al. 1995, 2000; Roques et al. 2001; Sharp and Whittaker 2003). Yet despite being a global phenomenon there is no unanimity as to the cause of these changes (e.g. Archer et al. 1995; Phillips 1995; Sheil 1995). Indeed, opinions and research findings are divided over whether there is a clear global, or even Australia-wide, trend towards increasing woody cover or if expansion and contraction is in response to local factors (e.g. Fensham et al. 2003b; Sharp and Whittaker 2003; Sharp and Bowman 2004; Lunt et al. 2010).

The spatial and temporal scale of the northern Australian monsoon rainforest expansion precludes landscape-scale controlled experiments. While longitudinal studies based on permanent plots are crucial to understanding future changes (e.g. Prior et al. 2009; Murphy et al. 2010a; Russell-Smith et al. 2010), the logistics and costs prohibit the establishment of a representative sample across the diversity of monsoon rainforest boundaries. Furthermore, the pace of climate change means that such landscape-scale studies can't provide insights into past processes that have caused the rainforest expansion. For these reasons, the evidence for changes to monsoon rainforest boundaries hinges on the analysis of historical sequences of aerial photography. Aerial photographic data tend to have spatial resolutions with longer time depth than most satellite imagery, however the frequency of repeat aerial photography is much lower, resulting in idiosyncratic 'snapshots' of landscape change. Such limited temporal resolution of the aerial photographic record is a serious disadvantage for understanding landscape ecology, as one or more cycles of an ecological process (such as pulses of tree establishment) may be rendered invisible or incomplete by the available imagery. Further, many ecological processes operate at different time scales: infrequent, rapid changes may occur, while over longer time scales, there may be continuous and gradual shifts occurring. A good example of such a multi-temporal ecological process is the encroachment of woody plants into more open vegetation types such as grasslands (Archer et al. 1995). The continuous dispersal, establishment and growth of trees can be abruptly interrupted, and sometimes reversed, following an unpredictable and infrequent disturbance event, such as landscape fire.

Analysis of aerial photography has been used to chronicle changes to rainforest coverage at four locations in monsoonal northern Australia: Litchfield National Park near Darwin (Bowman et al. 2001b); the rugged and infertile escarpment of the Arnhem Land Plateau in Kakadu National Park (Bowman and Dingle 2006); the lowlands of Kakadu National Park (Banfai and Bowman 2006); and a sandstone escarpment south of the Gulf of Carpentaria at the arid limit of monsoon rainforest (Brook and Bowman 2006) (Fig. 1; Table 1). The purpose of this paper is to review these studies, with particular consideration of the analytical and evidentiary basis of the unexpected direction of this landscape change and evaluate the plausibility of the global change hypothesis. Indeed, an emerging theme in landscape ecology is the need to synthesize and integrate diverse studies focused on particular problems such as the controls of rainforest boundary dynamics. Such studies need to capture the floristic, structural, geographic and environmental variability of the target systems and use multiple methodological approaches ranging from controlled and natural experimentation, using field survey and ecophysiological approaches, to interrogation of environmental proxies, such as stable isotopes, and historical archives including aerial photography and satellite imagery. Given practical and budgetary constraints, such synthetic research programs provide the most robust frameworks to understand the relative impacts of regional and global environmental change on landscapes, and attempt to manage them sustainably in the face of ongoing change.

Trends in rainforest expansion

Analyses of sequences of aerial photographs have revealed that a diversity of monsoon rainforests across a wide rainfall gradient have increased their coverage since the mid-20th century. The rate of expansion per decade has varied between 13 and 97% (Table 1). However these estimates of the overall extent of boundary change in the previous studies have been based on only one observation interval, using two ‘snapshots’ of rainforest extent (i.e. the first and last in the photographic record) and therefore do not provide a true indication of the temporal variability of rainforest extent. Furthermore, we are unable to provide precise measurements of the rate of boundary expansion (e.g. in m year^{-1}). This is because aerial photography sequences are ortho-rectified to a relative geographic datum (a base map) rather accurately determined ground points using survey methods. The RMS error associated with the ortho-rectification was <25 m providing the capacity to only detect gross changes in the extent of rainforest patches. We instead express boundary change using proportional change relative to the

Table 1 Summary of recent studies of monsoon rainforest expansion in tropical savannas in the Northern Territory of Australia

Study location	Mean annual rainfall (mm)	Forest type	Change (%)	Time period (years)	Area sampled (km^2)	Reference
Northwestern Litchfield National Park	1650	*Melaleuca* forest and rainforest (lowland and sandstone plateau)	+97	53 (1941–1994)	31	Bowman et al. (2001b)
Lowland areas of Kakadu National Park	1280–1470	Dry rainforest	+42.1*	40 (1964–2004)	30 sites	Banfai and Bowman (2006)
		Wet rainforest	+13.1*		20 sites throughout ~15 000 km^2	
Western Arnhem Land Plateau, Kakadu National Park	1240–1490	*Allosyncarpia ternata* rainforest	+21	40 (1964–2004)	12 sites throughout ~4700 km^2	Bowman and Dingle (2006)
Wollogorang Station, south of the Gulf of Carpentaria	950	Dry rainforest	+42	50 (1947–1997)	5 sites throughout ~1800 km^2	Brook and Bowman (2006)

See Fig. 1 for location of study sites. An asterisk indicates a patch-averaged estimate of change, as opposed to total change initial patch size apparent on the first photography in a sequence. Proportional change is a useful measure to capture the response of highly variable shape and size of rainforest patches and the tendency for boundary change (both expansion and retreat) to occur irregularly on the perimeter.

Estimates of the rate of rainforest change (e.g. on a decadal basis), and its variability, will be influenced by the frequency of available 'snapshots'. To investigate how sensitive inferences are to the number of aerial photographic 'snapshots', we mapped boundary change at nine patches previously sampled by Banfai and Bowman (2006) that had detailed aerial photographic histories (6–10 dates). These photographs were digitised and mapped following the methods of Banfai and Bowman (2006). The mean rate of change for the entire study period 1964 to 2004 was calculated by averaging the rates of change in patch size for all possible photographic intervals (greater than 5 years) for all rainforest patches, and was compared to estimates based only on the photographic endpoints.

This analysis revealed that the rates of change were variable for both wet and dry rainforest types (Fig. 2). Generally, large rates of change in patch area were observed over short time intervals and smaller changes over longer time periods (Fig. 3). Wet rainforest consistently had positive rates of change while dry rainforest was much more variable with both positive and negative changes. The calculated rate of change per decade based on all combinations of photographs equates to a 23.2% expansion of the dry rainforest patches over the 40-year period, which is substantially lower than if the assessment were based solely on the endpoints (42.1%). For wet rainforests, the estimated overall rate of change was the same in the two analyses. These results are consistent with the inference of Banfai and Bowman (2006) that there has been an overall expansion of rainforest in Kakadu National Park, with dry rainforests expanding at the fastest rate. However the reassessment shows that the previous estimates based on a limited number of repeat aerial photographs provided an inaccurate estimate of the rate of change and masked the highly dynamic nature of the dry rainforest boundary. However this effect is diminished when longer photographic intervals are used, instilling confidence in the previous reports of rainforest expansion.

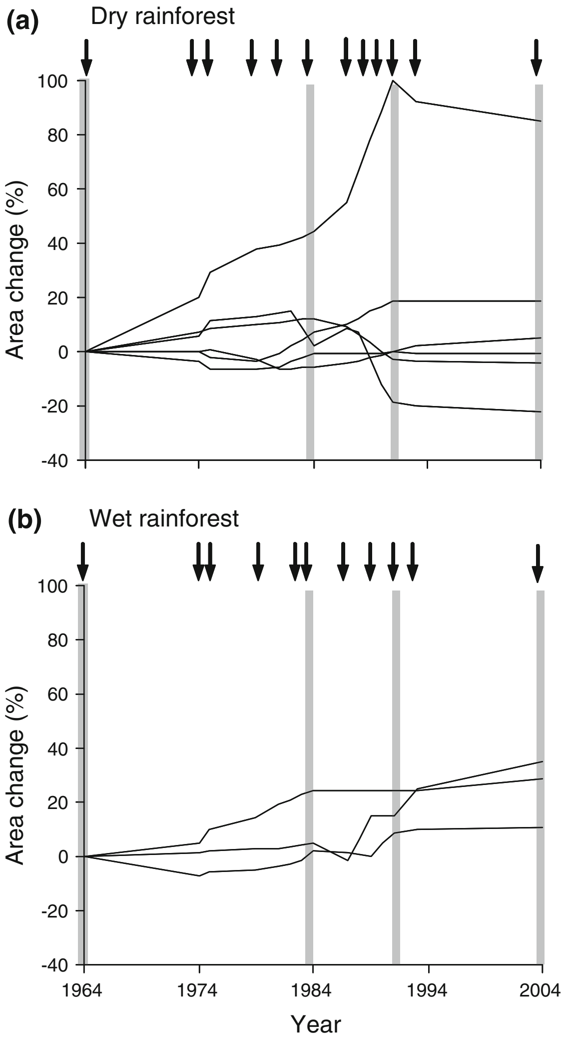


Fig. 2 Changes in area of lowland rainforest patches in Kakadu National Park, 1964–2004, using detailed photographic histories. Proportional change in patch area, relative to 1964, is shown for each rainforest patch with a detailed aerial photographic history, with (**a**) dry rainforest and (**b**) wet rainforest shown separately. *Arrows* indicate years for which aerial photographs were available for at least one patch. *Shaded bars* indicate the four sampling occasions used by Banfai and Bowman (2006), for a much larger number of sites

Field validation and the reality of the expansion

Monsoon rainforests and savanna vegetation are easily discriminated on aerial photographs given the differences in canopy closure and canopy texture. For example Bowman and Dingle (2006) demonstrated a high congruence between the mapped perimeter of Round Jungle using 2004 aerial photography and

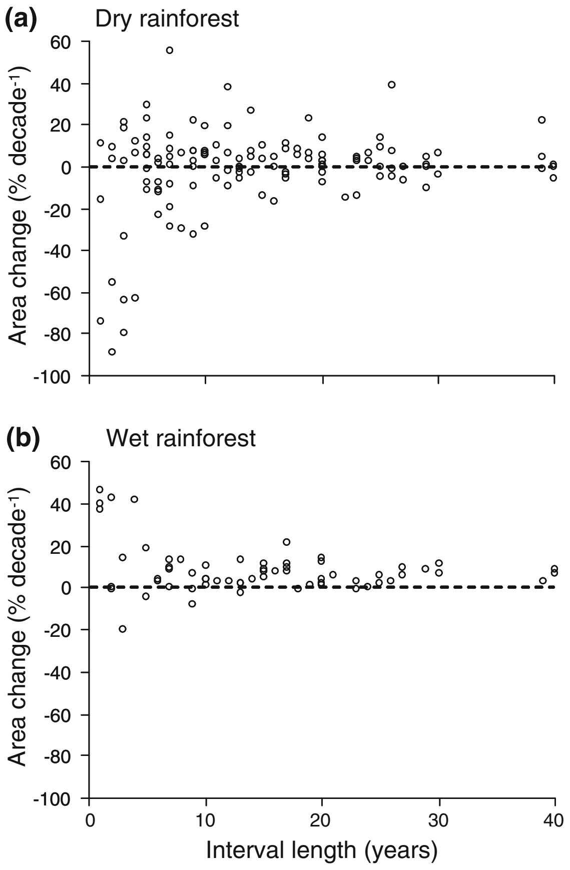


Fig. 3 Proportional change in area (per decade) for all possible photographic intervals, for each lowland rainforest patch in Kakadu National Park with a detailed aerial photographic history. **a** Dry rainforest and (**b**) wet rainforest are shown separately

GPS waypoints taken on the rainforest perimeter in 2005.

Banfai and Bowman (2005) undertook a field validation of the mapping in Litchfield National Park by Bowman et al. (2001b), by determining the stand structures of savanna and rainforest trees (based on an a priori classification) at locations with different trajectories: for example, savannas that had remained stable over 40 years vs. savannas that had converted to rainforest. Reassuringly they found that the floristic composition of the stands were concordant with the mapped trajectories. A similar field validation was undertaken by Banfai and Bowman (2007) for wet and dry lowland rainforests in Kakadu National Park. They were also able to discriminate between stable rainforest and recently formed rainforest (since 1964) on the basis of floristics, basal area and canopy cover. In sum, ground validation has supported the inference of rainforest expansion drawn from analysis of aerial photographs.

While some studies of size class distributions in expanding rainforest areas in northern Australia have been conducted (e.g. Russell-Smith et al. 2004b; Banfai and Bowman 2005), further detailed studies are required. We would expect recently formed rainforest to have a characteristically ‘young’ rainforest tree size class distribution, with very few older rainforest trees (e.g. Mitchard et al. 2009). Confirmation of such a pattern would strongly validate the widespread rainforest expansion based on aerial photography, and is probably best achieved in areas where there is a detailed photographic record, and evidence of very recent transition from savanna to rainforest. The characteristics of size class distributions may also provide valuable insights into the causes of the expansion, such as whether it is a gradual process (supporting the climate change or CO_2 hypotheses) or the result of the rapid establishment of a single cohort of rainforest trees within the savanna (supporting the disturbance hypothesis).

Environmental correlates of expansion

Environmental correlates of observed monsoon rainforest expansion have been examined with varying levels of analytical sophistication. The most basic approach has been to compare the rate of expansion across different landscape settings. For example, Bowman et al. (2001b) found that the probability of savanna to rainforest conversion varied according to landscape setting across an abrupt sandstone escarpment in Litchfield National Park. These authors found that there was a moderate probability (about 20%) of savanna being converted to forest on lowland creek lines but a very low probability (about 1%) of this occurring in plateau catchments.

Brook and Bowman (2006) approached the question of environmental correlates of habitat expansion using generalised liner modelling and multi-model inference. They undertook retrospective habitat suitability modelling that was based on four landscape measures (drainage distance, slope angle, aspect and elevation) using photographs taken in 1947. The modelling correctly forecast the subsequent spatial distribution of the expansion, with expansion largely occurring in areas with topographic fire protection. Specifically, Brook and Bowman (2006) found that increasing habitat suitability index (HSI) values were related to a monotonic increase in the proportion of savanna converted to closed forest. For example, the observed proportion of converted points with the highest HSI values in 1997 was 5.3 times greater than the null expectation of a uniform 7.5% conversion across the entire distribution. They found that contraction of rainforest was also predictable by HSI, albeit with less precision. A key finding of their approach was that, for each of the four rainforest patches they studied, the independent predictors used in the HSI models developed based on the 1947 coverage of closed forest were not the same. For example, in 1947, drainage was the most important explanatory variable for three of the four sites, where areas closer to water were more likely to support closed forest. Further, the relative importance of the explanatory variables changed through time, likely reflecting the expansion of closed forest into more marginal landscape settings. Such variability lends support to a spatially and temporally variable process moderating the rainforest expansion, and the prime candidate being landscape fire activity. Indeed, Bowman and Dingle (2006) also used a index of fire activity between 1984 and 2004 in a habitat suitability model and showed that this variable had the strongest effect on *A. ternata* presence: most plots where *A. ternata* was present had a lower fire activity than those where it was absent [2.2 ± 0.1 (SE) vs. 4.1 ± 0.1 (SE) respectively]. Table 2 summarises the primary correlates with rainforest expansion reported by recent studies. Collectively this summary shows that despite variability all these correlates are broadly related to fire protection.

However high levels of fire frequency surrounding a rainforest does not necessarily result in contraction. This is apparent for an individual dry rainforest located in the southern part of Kakadu National Park (Fig. 4a), that lies along a strike ridge that rises more than 60 m above the surrounding lowland plains. This patch increased dramatically in size over the study period, by 84.9%, despite regular fires, with only 2 years between 1980 and 2003 having an absence of fire (Fig. 4b, c). The boundary expansion has occurred primarily on the northeastern side of the patch where the ridge may offer some fire protection, while the boundary contraction has occurred primarily on the southwestern side, which is not protected by the steep escarpment (Fig. 4b, c).

A problem with analysis of spatio-temporal trends derived from aerial photographic studies concerns the difficulty in analysing the episodic spatial coverage of photography given the scarcity of data on disturbance history (particularly feral animals and landscape fire) to correlate with the observed changes. Several approaches have been taken to deal with this issue. At the most basic level, the relationship between contemporary fire activity, landscape setting and observed rainforest change has been determined using available satellite fire mapping. For example, an analysis of existing fire scar mapping from satellite imagery by Banfai and Bowman (2005) showed that fire activity was systematically related to the observed direction of vegetation change for closed forests. Such a relationship is consistent with the primacy of fire in driving the observed vegetation dynamics, but it is confounded by the inherent interaction between fire and vegetation, thereby precluding statements of causality. Further, the satellite-derived fire history only overlapped with

Table 2 Summary of the environmental correlates, and direction of relationship, with monsoon rainforest boundary expansion

Study location	Important variables linked to rainforest expansion	Direction of relationship with change	Reference
Northwestern Litchfield National Park	Landscape settings across an escarpment	Catchments > creeklines	Bowman et al. (2001b)
Lowland areas of Kakadu National Park	Rainforest type	Dry > wet	Banfai and Bowman (2006)
	Distance to rainforest boundary	−ve	
Western Arnhem Land Plateau, Kakadu National Park	Fire frequency	−ve	Bowman and Dingle (2006)
Wollogorang Station, south of the Gulf of Carpentaria	Fire protection	+ve	Brook and Bowman (2006)

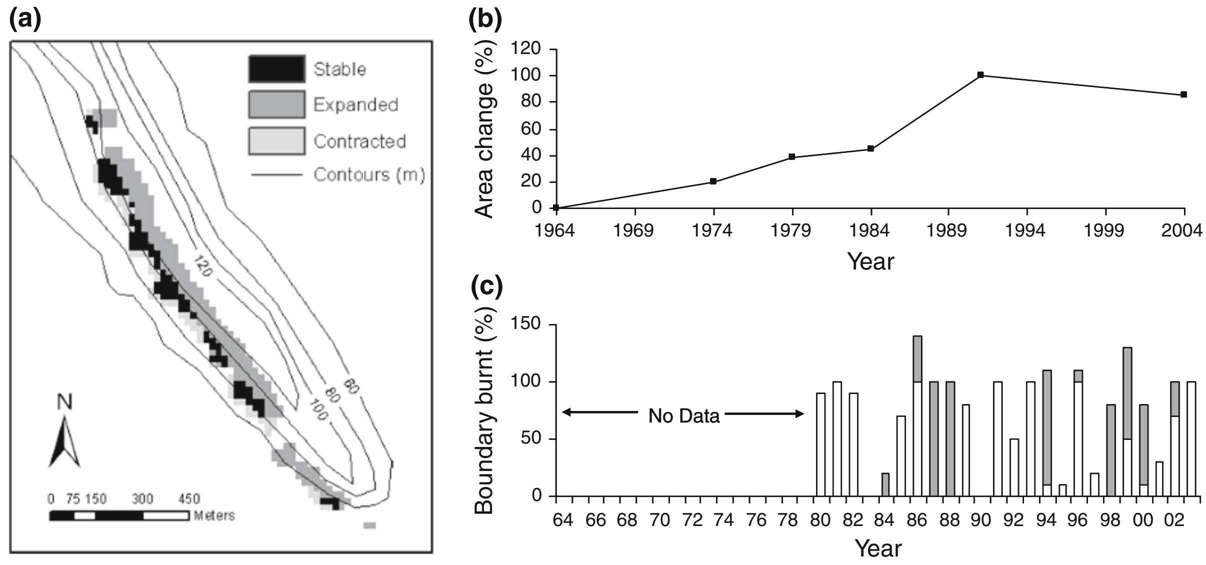


Fig. 4 The expansion of a dry rainforest patch in Kakadu National Park (13°24′2″ S, 132°13′6″ E) (**a**, **b**), despite high levels of fire activity (**c**). Note that the expansion is concentrated on the fire protected boundary on the northeastern side (**a**). The *shaded bars* in (**c**) indicate late dry season fires

most recent years of the study period and therefore may not have captured the fire regimes responsible for the observed vegetation changes. Adding to these limitations is the mismatch of the spatial resolution of the satellite imagery and aerial photography (pixel width of 30 m vs. 1 m), compounded by inherent errors in mapping fire scars (Russell-Smith et al. 1997; Bowman et al. 2004b).

Field evidence of fire disturbance

The inference that rainforests have expanded due to reduced fire activity is inconsistent with regional studies pointing to ecological degradation associated with uncontrolled fires (e.g. Russell-Smith and Bowman 1992; Russell-Smith et al. 2010). Indeed, there has been a region-wide population crash of cypress-pine (*Callitris intratropica*) in response to current hostile fire regimes in sharp contrast to the widespread expansion of rainforests (Bowman and Panton 1993; Bowman et al. 2001a). Analysis of historical aerial photography revealed that there has been a 21% expansion of *Allosyncarpia ternata* rainforests on the Arnhem Land Plateau, a region where pastoralism and feral herbivore densities have always been insignificant but fire regimes have changed (Bowman and Dingle 2006). At one *A. ternata* rainforest patch, that increased by 13%, a demographic analysis of tagged *A. ternata* and cypress-pine showed that there has been a substantial loss of older trees of both species due to fire damage (Prior et al. 2007). Yet, life-table calculations indicated there was sufficient recruitment of *A. ternata*, but not cypress-pine, to maintain population stability. *A. ternata* prolifically re-sprouts after fire, but cypress-pine is an obligate seeder that is thereby trapped in a fire-induced population bottleneck. It is therefore possible that the capacity of rainforest tree to resprout after fire is enabling sufficient recovery on fire damaged boundaries. But this does not answer the question of what has changed to cause the boundaries to expand. To resolve this conundrum, we have advanced the hypothesis that the current trend of increasing mean annual rainfall and atmospheric CO_2 concentration has stimulated woody growth (Bowman et al. 2001b; Banfai and Bowman 2006; Bowman and Dingle 2006; Brook and Bowman 2006), with localised changes in land management of secondary importance. This is consistent with the model of Bond and Midgley (2000), and has been proposed to explain expansion of forest patches elsewhere in the tropics (e.g. Wigley et al. 2009). Other northern Australian researchers have favoured the hypothesis that that recent rainforest expansion has been driven almost exclusively by changes in land management and associated fire regimes (Harrington and Sanderson 1994; Russell-Smith et al. 2004a). Resolving these competing hypotheses demands further observational and ecophysiological research, as well as contextualisation using palaeo-ecological and geographical approaches.

Palaeo-ecological contextualisation

Bowman et al. (2004a) analysed the stable carbon isotope signature and radio-carbon age of soil organic matter (SOM) from lateritic soil profiles across an abrupt monsoon rainforest-eucalypt savanna boundary on Croker Island, northern Australia. They found that soil organic carbon in 1.5 m profiles had a radiocarbon age of about 5000 years and that the carbon stable isotope composition of SOM from 10 cm deep layers from the surface, middle and base of three monsoon rainforest soil profiles was significantly different from the means for these layers in three adjacent savanna soil profiles, suggesting the isotopic ‘footprint’ of the vegetation boundary has been stable since the mid Holocene. Although there were no obvious environmental discontinuities associated with the boundary, the monsoon rainforest was found to occur on significantly more clay rich soils than the surrounding savanna, a fact they interpreted as being a consequence, rather than a cause, of the rainforest-savanna boundary. Indeed, there was evidence that the boundary was dynamic given the occurrence of tiny fragments of monsoon rainforest and abandoned nests (large earthen mounds) of the orange-footed scrubfowl (*Megapodius reinwardt*) in the surrounding savanna. Scrubfowl are an obligate monsoon rainforest species so the occurrence of abandoned nests in the savanna signals that the rainforest was once more extensive (see Bowman et al. 1994).

Bowman et al. (2004a) interpreted these results using the conceptual model that the rainforest boundary was meta-stable due to a fire-vegetation-soil feedback. The fertile rainforest soils enable monsoon rainforest tree species to grow rapidly following disturbance and achieve canopy closure, thereby excluding grass and reducing the risk of fire. Conversely, slower tree growth rates, grass competition and fire on the savanna soils would impede the expansion of the rainforest. Episodic rainforest expansion into the savanna, as evidenced by the extinct scrubfowl nests, is possibly due to changed climate conditions, such as high rainfall periods with shorter dry seasons, which reduce the frequency of fires and increase tree growth rates. It is possible that the observed rainforest dynamics in aerial photography may also be responding to similar longer-term climate variability.

Geographic contextualisation and global change hypothesis

Recent work in Kakadu National Park has revealed woody cover encroachment on freshwater flood plains (Bowman et al. 2008b) and increased canopy cover of eucalypt savannas (Lehmann et al. 2009) although these trends are confounded by fire regimes, feral animal densities and climate. However, a comparable woody expansion of mangroves into adjacent salt-flats near Darwin is particularly significant in the debate about woody vegetation expansion in the monsoon tropics because neither fire nor buffalo disturbance are plausible confounding factors in mangrove systems (Williamson et al. 2010). Williamson et al. (2010) were unable to explain the expansion of mangroves as a consequence of sea level rise. They noted that the landward expansion, especially onto salt flats, may be linked to the northern Australian wetting trend. They noted the striking parallel with the regional expansion of woody vegetation elsewhere in the region.

If the increased rainfall and/or CO_2 hypotheses are correct, it would be expected that closed canopy shrubland vegetation would have also expanded in arid central Australia, given that the wetting trend that has occurred in northern Australia also extends into that region. Nonetheless, woody expansion does not seem to be occurring there. A recent series of allied studies of the dynamics of *Acacia aneura* (mulga) shrublands in a *Triodia* (spinifex) grassland mosaic at the arid limit of the Australian monsoon tropics in central Australia provides a useful parallel to savanna-rainforest boundary dynamics (Bowman et al. 2007, 2008a; Murphy et al. 2010b; Nicholas et al. 2010; Fig. 1). Bowman et al. (2007), inferring changes in mulga-spinifex boundaries from the carbon isotope composition of soil, suggest that the mosaic they examined had existed for at least 1000 years. Bowman et al. (2008a) used historical aerial photography to conclude that mulga communities contracted by only 3% between 1950 and 2002, despite concerns that this community was undergoing widespread contraction following the cessation of traditional Aboriginal burning practices (Griffin et al. 1983; Latz 1995; Allan and Southgate 2002; Williams 2002). However, Bowman et al. (2008a) did find substantial movement of mulga boundaries at decadal time-scales (e.g. 13% reduction in mulga cover between 1950 and 1983), and that the expansion and contraction of mulga patches were associated with low and high fire frequencies, respectively. Yet drawing direct parallels between the monsoon tropics and arid ecosystems is problematic, particularly because fire occurrence in the arid zone is strongly predicated by above average antecedent rainfall (Allan and Southgate 2002), which also favours rapid woody growth. Further research is needed to understand the similarities and differences between fire ecology of the monsoon tropics, where rainfall is highly reliable, and the arid zone, where rainfall is highly erratic (Bowman et al. 2009).

Conclusion

A number of studies conducted in northern Australia have substantiated that monsoon rainforests have expanded, but the quest to understand the drivers of this change has been far less successful. The reason is partly that methodological issues have limited progress, notably issues associated with the temporally erratic aerial photographic record and the limitations of environmental data that can be meaningfully correlated with the observed patterns of change. Nonetheless, the research provides invaluable insights into landscape scale processes that would be otherwise unobtainable. It is clear that fire plays a critical role in determining rainforest boundaries in the monsoon tropics, a fact that may partly explain the high temporal variability of rainforest boundaries. However, there appears to be little evidence that changes in fire regimes have lead to the recent expansion of rainforest patches. Concurrent with the monsoon rainforest expansion has been a regional population crash of cypress-pine and other fire sensitive plants, small mammals, and bird populations (Franklin 1999; Bowman et al. 2001a; Woinarski et al. 2001). Thus the discovery of *expansion* of monsoon rainforests despite *hostile* fire regimes is perplexing and underscores serious gaps in knowledge of the drivers of landscape-scale vegetation dynamics. We consider it most likely that the expansion of rainforest patches is related to global climate change via increased rainfall and/or the CO_2 'fertiliser effect'. This is consistent with the recent finding from South Africa that strongly contrasting localised land management practices had little effect on the dramatic expansion of forest patches into the surrounding savanna in the latter half of the 20th Century, strongly implicating global environmental change.

We argue that advancing the question of the cause of the monsoon rainforest boundary expansion requires further research. First, geographic contextualisation is required to determine if Australian rainforests are uniformly expanding across their geographic range from the tropics to temperate zones. Even if rainforests are uniformly expanding, while discounting trends in rainfall, it does not necessarily demonstrate that the cause is global climate change. For example, it may reflect the past ubiquitous effect of Aboriginal landscape burning on restricting rainforests to fire sheltered environments. Therefore, a more mechanistic analysis of tree growth is required to test the hypothesis that global (such as CO_2) or sub-continental changes (such as rainfall) are linked to expansion of rainforests. Cypress-pines, in the genus *Callitris*, are also ideal subject species for the analysis of tree growth because they have clear growth-rings that can potentially provide a record of changes in growth patterns over time (e.g. Ash 1983; Baker et al. 2008; Cullen and Grierson 2009). Importantly, the genus is a component of humid rainforests (*C. macleayana*), dry rainforest, savanna and semi-arid woodland (*C. intratropica/glaucophylla*) and Tasmanian dry sclerophyll forest (*C. oblonga*) (Bowman and Harris 1995). Thus, *Callitris* growth and stand dynamics may provide a direct link between changes in rainforest boundaries and global climate change. The wide geographic range of *Callitris* is also of considerable significance because there is potential to separate the effects on growth of rising CO_2 from rainfall trends, given the southern Australian trend towards drier, hotter climates and the northern Australian trend towards wetter conditions. We suggest that Australia therefore provides a powerful 'model system' for landscape ecologists to understand, and rank the importance of, drivers of environmental change operating across temporal and spatial scales, and therefore provide invaluable insights into the trajectories, and thus prognosis for sustainability, of related biomes around the world.

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