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Humans, Megafauna and environmental change in tropical Australia

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Abstract

Debate concerning the environmental impact of human arrival in Australia has continued for more than a century. Here we review the evidence for human impact and the mechanisms by which humans may have affected the environment of tropical Australia. We limit our review to tropical Australia because, over three decades ago, it was proposed that the imposition of an anthropogenic fire regime upon human occupation of the Australian continent may have resulted in profound changes in regional vegetation and climate across this region. We conclude that ecological processes and vegetation-fire-climate-human feedbacks do exist that could have driven a significant shift in boundary conditions and ecosystem state at the sub-continental scale through the sustained imposition of an anthropogenic fire regime over tens of millennia. These potential feedbacks operate through the inhibition of forest expansion both directly, by targeted burning at established forest edges and newly irrupted forest patches, and indirectly, through lengthening of the dry season as a result of changes to the timing of burning. However, the impact of any such anthropogenic forcing may have been entirely overshadowed by the effects of natural climate change and variability, as well as the generally low nutrient status of Australian soils. A robust assessment of the degree to which the environment of tropical Australia at the large scale has been modified from its 'natural' state as a result of human occupation will require new, coordinated collaborations between indigenous traditional landowners, archaeologists, anthropologists, geochronologists, geoscientists, ecologists, climatologists and modellers.

1. Introduction

'Oh no, not again' was the last thought that went through the mind of a bowl of petunias as it fell to the ground on an alien planet in 'The Hitchhiker's Guide to the Galaxy' (Adams, 1979: 103). Whatever else the petunias thought, it is clear that they had been in the same position previously. And so it is with the debate surrounding the environmental impact of the arrival of humans in Australia.

Well over a century ago, it was known that a number of large, now extinct, marsupial species had once been extant in Australia, and so began the debate as to whether climate change or 'Australoid wielders of clubs and throwing sticks' (Owen, 1877: cited in Horton, 1980: 86) were responsible for their demise (see Horton, 1980 and Johnson, 2006 for reviews).

Over four decades ago, Merrilees (1968) and Jones (1968) independently postulated that humans were implicated in megafaunal extinction, and Jones (1968: 189) suggested that it was likely that humans had arrived in Australia much earlier than previously thought: 'For the present an antiquity of 30,000 years is a reasonable claim'. Jones (1969) elaborated on his earlier work proposing that humans had manipulated the environment since arrival through 'firestick farming'.

Over three decades ago, Kershaw (1974, 1986) first suggested that Aboriginal burning had led to a sustained decline in fire-sensitive gymnosperm taxa and an increase in sclerophyll and grass taxa. This conclusion was based on a pollen record from a single site: Lynch's Crater on the Atherton Tablelands of north Queensland. Also over three decades ago, Horton (1982: 238) noted that 'There have been a few criticisms of this general thesis [that humans caused megafaunal extinction]'. On reviewing the information available at the time, he found little evidence to support human agency in either megafaunal extinction (Horton, 1980) or modification of vegetation through anthropogenic manipulation of fire regime (Horton, 1982).

Over two decades ago, Flannery (1990) proposed that after megafaunal extinction brought about by 'blitzkrieg' over-hunting, humans responded to subsequent increased fuel loads by firestick farming, thereby assisting in the maintenance of biodiversity in medium-sized mammals and some plants. Release from this anthropogenic fire regime upon arrival of Europeans resulted in another 'trophic cascade' of extinctions. Thermoluminescence (TL) and optically stimulated luminescence (OSL) dating was used by Roberts *et al.* (1990, 1994) to push back the proposed date of human occupation of mainland Australia to between 50 and 60ka, while Nanson *et al.* (1992) used TL and uranium-series dating methods to document a number of wet and dry phases in central and south-eastern Australia over the last 300 ka. Miller and Magee (1992) went further and proposed that Lake Eyre is dry in the current interglacial as a result of substantial modification of vegetation across tropical Australia following the imposition of an anthropogenic fire regime.

Over a decade ago, combinations of more robust radiocarbon pretreatment techniques, OSL and other dating techniques continued to suggest occupation of Australia occurred considerably before 40ka (Turney *et al.*, 2001a, Bird *et al.*, 2002, Bowler *et al.*, 2003), with some claims of occupation close to 60ka (Roberts *et al.*, 1998, Thorne *et al.*, 1999). Roberts *et al.* (2001) used OSL and uranium-series methods to date articulated megafaunal remains and their burial sediments at a number of sites to infer that extinction occurred in the interval of 40-51ka. Miller *et al.* (1999) and Johnson *et al.*, (1999) suggested extinction of the large flightless bird *Genyornis newtoni* and large-scale vegetation change was a direct result of human arrival and the imposition of an anthropogenic fire regime at 45-55ka, perhaps underlain by natural climate change. We observe that, while there is abundant evidence for early human occupation across the tropical north, from the Kimberley to Cape York (Figure 1), there are comparatively few well-dated megafauna sites in tropical Australia. However, the widespread existence of notionally 'Late Pleistocene' megafaunal remains in the region (Field *et al.*, 2008: Figure 12) suggests that they were a significant component of the fauna encountered by humans on arrival.

At each stage of the debate in the twentieth century, claims for earlier arrival of humans on the Australian mainland, as well as the assertion that humans were responsible for megafaunal extinction and/or significant ecosystem modification through firestick farming, have been vigorously contested. Opposition has generally taken the form of disputing the reliability of the dating, the stratigraphic association between dated material and physical evidence, the selective use of evidence, conflicting evidence and/or insufficient evidence, coupled with the general observation that fire was a significant factor in tropical Australia prior to human arrival (Horton, 1980, 1982, O'Connell and Allen, 1998, Bowman, 1998, Mulvaney and Kamminga, 1999).

It is not our purpose to review in detail the development of the debate on the timing of human arrival and megafaunal extinction, though we do summarize debate from the last decade. Rather, we focus instead on the development of two divergent, testable, end-member hypotheses for the impact of human occupation on the landscape-scale ecology and climatology of tropical Australia. In particular:

(i) that human dispersal through and occupation of tropical Australia had little or no impact on regional ecosystems and climate; or

(ii) that human dispersal through and occupation of tropical Australia either rapidly or cumulatively over many millennia, resulted in a profound change to regional ecosystems and climate.

We focus on the literature that bears on the development of these hypotheses rather than on making a detailed assessment of the burgeoning literature surrounding the timing of human arrival and human impact on the environment following arrival. We constrain our area of interest to the Australian monsoon tropics as defined by Bowman *et al.* (2010): those areas of Australia that (currently) receive more than 85% of rainfall between November and April.

2. Timing of human colonization

Early human occupation at sites in tropical Australia such as Ngarrabullgan, Nauwalabila 1, GRE-8, Riwi and Carpenter's Gap has been established since the 1990s, although exactly how early remains the subject of debate (e.g. O'Connell and Allen, 2012). In the last decade, further sites with dates interpreted as suggesting human occupation at or before 40ka have been identified across tropical Australia: Nawarla Gabarnmang (David *et al.*, 2011), Parnkupirti (Veth *et al.*, 2009) Nonda Rock (David *et al.*, 2007), and GRE-8 (Slack *et al.*, 2004) (Figure 1) – as well as Papua New Guinea (e.g. Summerhayes *et al.,* 2010). While the absolute antiquity of initial colonization remains contested, there appears to be emerging consensus that humans had arrived in Australia and had expanded 'archaeologically instantaneously' across much of mainland Australia and Papua New Guinea by not later than 44-46ka (Hiscock, 2008, O'Connell and Allen, 2012).

There is little evidence upon which to base inferences as to the number or size of colonization events or the likely population after colonization. Nevertheless, O'Connell and Allen, (2012: 12) contend that after arrival and 'despite their inherent capacity for growth, Sahul populations remained surprisingly small and spatially concentrated in persistent 'sweet spots'. Williams (2012) used 2996 radiocarbon dates from 800 archaeological sites in Australia to explore occupation trends from 40ka to the present. While subject to considerable uncertainty, the results from that study suggest approximately constant levels of occupation from the beginning of the record, with occupation levels increasing into the Holocene (see also Johnson and Brook, 2011).

For the purposes of this paper, we conclude simply that humans had arrived on the Australian mainland by at least ~45ka (Hiscock, 2008, Hiscock and Wallis, 2005), a date now consistent with the timing of migration through mainland and island SE Asia (Higham *et al*., 2009, Demeter *et al*., 2012) and Papua New Guinea (Summerhayes *et al*., 2010). We further conclude that within a few millennia, humans had dispersed throughout mainland Australia (O'Connell and Allen, 2012), with the possible exception of parts of the arid interior (Smith *et al*., 2008).

3. Megafaunal extinction: The Rasputin Syndrome 7

Recognizing that claims for earlier arrival may be correct, the apparent consensus that humans had arrived on mainland Australia by ~45ka has marginally narrowed the range of debate concerning the timing and cause of megafaunal extinction: humans and megafauna clearly co-existed for a period of time, and hence humans could potentially have been responsible for at least a component of megafaunal extinction. Gunn *et al.* (2011) report the existence of rock art in Arnhemland that appears to depict the extinct giant bird *Genyornis* *newtoni* (Figure 2) and Flannery (2012) reports rock art in the Kimberley region that has been interpreted as depicting the extinct marsupial lion (*Thylacoleo carnifex*). Both imply direct co-existence (for other rock art examples see Murray and Chaloupka, 1984). If humans and megafauna did overlap in time, it is difficult to envisage a situation where humans and megafauna could co-exist on the same continent without any form of interaction.

Correlative evidence in the last decade supporting rapid extinction coincident with human arrival has come from Tasmania (Turney *et al.*, 2008, Gillespie *et al.*, 2012) and north Queensland, the latter inferred from the abrupt decline in *Spororomiella* fungal spores – indicative of mega-herbivores – in the Lynch's Crater record at around 41ka, coincident with an abrupt increase in charcoal (Rule *et al.*, 2012). At the site of Cuddie Springs in western New South Wales, claims for survival of megafauna for at least 10 ka after human arrival (Field *et al.*, 2008) have been countered by Grün *et al.* (2010), who concluded from direct electron spin resonance (ESR) and uranium-series dating of megafauna teeth and bones that the Cuddie Springs material had been reworked from older deposits. This evidence is consistent with earlier suggestions of sediment disturbance (Roberts *et al.*, 2001, Gillespie and Brook, 2006).

Arguments against a human-induced extinction 'event' have continued to appear in the last decade (Wroe and Field, 2006, Field and Wroe, 2012). Price *et al.* (2011) used OSL and uranium-series dating techniques to constrain the ages of multiple taxa in the Darling Downs in southeastern Queensland and concluded that 15 taxa disappeared from the local record over a staggered time interval between 122 and 83ka ago. The authors considered that megafaunal extinction was a process underway for some time prior to the arrival of humans, in response to a long-term trend to greater aridity. Faith and O'Connell (2011) re-examined the data of Prideaux *et al.* (2010) from Tight Entrance Cave in southwest Western Australia and concluded that the evidence was consistent with environmentally-mediated extinction, with uncertainties in the dating making it impossible to exclude the possibility that the majority of megafauna were extinct by the penultimate glacial maximum (MIS-6), but that uncertainties in the dating made it impossible to discriminate between gradual attenuation over the last few glacial cycles and synchronous extinction between about 50 and 40ka. By contrast, Prideaux *et al.* (2010) noted that the MIS-6 had no lasting impact on the regional fauna, which argued against climate change as the sole or primary driver of the extinction. The latter interpretation is also consistent with the only other faunal sequence in Australia with a paired climate record extending back 300ka – namely, Cathedral Cave in South Australia (Prideaux *et al.*, 2007).

The absence of clear evidence of human predation on, or consumption of megafauna, also continues to be advanced as an argument against human involvement in megafaunal extinction (Davidson, 2012), although this issue had earlier been addressed by Brook and Johnson (2006), Roberts and Brook (2010) and, more recently, by Surovell and Grund (2012) who conclude that such evidence in Australia is likely to be very rare even in comparison to evidence from parts of the world occupied by humans more recently (e.g. North America and New Zealand).

Miller *et al.* (2005b), building on their earlier work, concluded that *Genyornis* became extinct as a result of anthropogenic burning between 50 and 45ka. On the other hand, Murphy *et al.* (2010), using the same stable isotope analyses of *Dromaius* eggshell reported by Miller *et al.* (2005b), concluded that ecosystem change began before the arrival of humans and could be better modelled as a gradual change in response to overall decreasing water availability between 80 and 30ka. Hence, ecosystem change due to the imposition of an anthropogenic fire regime was not necessarily the primary cause of the extinction of *Genyornis*.

Gregori Rasputin, a monk and a controversial member of the court of the Russian Tzar through the early part of the twentieth century, was variously poisoned, shot and clubbed to death in 1916. Which of these violent actions caused his ultimate demise remains a subject of debate and it is also possible that he survived the initial attempts on his life, lingering on for a period before finally succumbing to drowning after being dumped through a hole in the ice on the Neva River. And so it is with megafaunal extinction. The potential drivers of extinction can be summarized as direct human impact in the form of direct predation or selective predation of juveniles (Brook and Johnson, 2006), indirect anthropogenic ecosystem change through modifications to fire regimes, introduced disease or natural climate change (for a review see Johnson, 2009). It has been argued that extinction followed rapidly on the heels of human occupation (Roberts *et al.*, 2001, Miller *et al.*, 2007, Turney *et al.*, 2008, Gillespie *et al.*, 2012) but the possibility cannot yet be excluded that some of the megafauna that were extant at human arrival lingered on for some time (Johnson, 2005, 2006, Field and Wroe, 2012). In that context, it is worth noting that for communities subject to non-pluvial climate regimes there is a strong correlation between precipitation, plant productivity and both total herbivore biomass (Coe *et al.*, 1976) and large herbivore diversity (Olff *et al.*, 2002); Thus it is likely that megafaunal populations were already in decline due to increasing aridity at the time of the first human occupation. Such declining populations would be also be expected to have been more sensitive to anthropogenically-induced changes in environment (or direct hunting pressure) than would have been the case for a more stable or expanding megafaunal population (Hubbell, 2001). Thus, the two hypotheses are not necessarily exclusive.

Field and Wroe, (2012: 69) conclude 'that the megafaunal extinction debate in Australia has a long way to go before even the most fundamental of questions are convincingly resolved'. For the purposes of this paper, the details of the mechanism and timing of extinction are not important, except insofar as determining whether human agency was involved. This is because mega-herbivores in modern tropical environments are capable of a significant degree of 'engineering' of the ecosystems they inhabit (Asner *et al.*, 2009, Staver *et al.*, 2009, Midgley *et al.*, 2010, Tanentzap and Coomes, 2012). Mega-herbivore browsers are partly responsible, along with fire and other edaphic controls, for the maintenance, and in some cases extension, of open vegetation types. The removal of megafauna from Australian tropical ecosystems is therefore likely to have resulted in some degree of ecological transformation (Johnson, 2009), and this would be considered anthropogenic if humans were responsible, in part or in whole, for megafaunal extinction.

We conclude that the results of Roberts *et al.* (2001), which were based on dating of articulated extinct megafaunal remains only, do indicate that megafauna were dramatically reduced in numbers from, to use the terminology of Johnson (2005), 'palaeontological visibility' to 'archaeological visibility' during a period of a few millennia following human arrival. As a result, and regardless of whether they became literally extinct at that time, megafauna were thereafter unlikely to be able to exert a significant influence on vegetation structure in tropical Australia. We do not speculate in detail on the likely cause of this reduction in numbers, other than to note that, of the mechanisms identified, climate change as the sole driver of extinction represents the least likely possibility; a conclusion that has previously been reached by several authors (Owen-Smith, 1987, 1989, Miller *et al.*, 2007, Brook and Bowman, 2004, Prideaux *et al.*, 2007, 2009, 2010, Murphy *et al.*, 2012).

While we acknowledge a long-term trend to increasingly arid conditions in some parts of Australia over the last 300ka (Nanson *et al.*, 1992, Magee *et al.*, 2004, Wroe and Field, 2006, Webb, 2008), there is no evidence for 'sharp, intra-decadal through millennial-scale fluctuations in temperature and precipitation' (O'Connell and Allen, 2012: 7) during the period of interest through Marine Isotope Stage 3 (MIS-3: 28-59ka). High latitude northern hemisphere ice core records and temperate northern hemisphere speleothem records do indicate significant millennial-scale variability associated with Dansgaard-Oeschger (D/O) cycles (e.g. Weninger and Jöris, 2008). However, the expression of D/O events is very muted in the southern hemisphere ice core climate records from Antarctica and the signal associated with D/O events is likely to be even more muted in low latitude locations such as tropical Australia. Hesse *et al.* (2004) concluded that the 'largest changes in circulation patterns [in Australia] over the glacial cycle probably occurred in the location and/or intensity of summer tropical convergence in northern Australia', but there is no evidence to suggest that climate variability in MIS-3 on any temporal scale was more extreme than at any time prior or subsequent to the interval during which extinction occurred.

The discussion above leads us to conclude that human occupation of the continent did play a direct and decisive, if currently unquantified, role in the rapid reduction of megafaunal populations to levels at which they could no longer exert an influence on the vegetation structure of tropical Australia. The possibility cannot be excluded, however, that other environmental factors may have played a role - as yet unquantified - in eventual megafaunal extinction (Roberts *et al.*, 2001, Koch and Barnosky, 2006, Prideaux *et al.*, 2010, Lorenzen *et* *al*., 2011, Prescott *et al*., 2012). In the absence of other human impacts, extinction of the megafauna may have itself led to modifications to ecosystem function through changes to the nature and abundance of fuel loads and changes in the density of woody vegetation through release from browsing pressure.

4. Ecological and climatological impacts of occupation

Much of eastern tropical Australia has been argued to fall into the category of 'ecosystem uncertain', where the present-day climate is such that a range of vegetation states are potentially possible (Bond and Keeley, 2005; Staver *et al*., 2012; Hirota *et al.,* 2012). Although such results have been interpreted as supporting the notion of forest and savanna representing alternative steady states in such climates, with the latter induced and then maintained by fire (e.g., Hoffmann *et al*., 2012; Murphy and Bowman, 2012), it is important to recognise that factors such as soil cation status which are known to sometimes be substantially higher for forest and savanna vegetation formation types (e.g. Cochrane, 1989) are not accounted for in such 'climate only' simulations. Similarly, soils underlying more open savanna formation types also tend to have a lower cation status than for nearby woodier savanna formations (Lopes and Cox, 1977) and given the low fertility of Australian tropical soils in general (McKenzie *et al*., 2004) edaphic factors may account for much of the region currently being savanna rather than forest. Nevertheless, significant large-scale anthropogenic modification to vegetation cover sustained over many millennia to the present day is at least a possibility. Human occupation could potentially have modified the vegetation cover of tropical Australia in three ways, with all potential mechanisms operating through an influence on the dynamics of tree–grass competition.

First, the removal of any browsing megafauna would improve opportunities for establishment of trees and shrubs (Bond and Keeley, 2005, Staver *et al.*, 2009). Second, and alternatively, if the bulk of the megafauna were browsers rather than grazers, then an increased standing crop of herbaceous biomass may have resulted, with increased fire frequencies/intensities ensuing (Flannery, 2012). Third, any deliberate change in intensity, number or timing of fires would also be expected to modify the recruitment opportunities for trees and shrubs relative to grasses (Bond, 2008, Bond and Midgley, 2012, Lehmann *et al.*, 2011, Nano and Clarke, 2011, Prior *et al.*, 2009, 2010, Russell-Smith *et al.*, 2010, Scott *et al.*, 2012). A shift towards more trees, for example, is thought to potentially result in a positive feedback, leading to further vegetation thickening as a result of the suppression of grass growth and, hence, the ability to carry fire, and vice versa (Sankaran *et al.*, 2005, Bond and Midgley, 2012, Higgins and Scheiter, 2012, Murphy *et al.*, 2012).

It is important to note that a change in the timing of fires does not necessarily imply a change in the total burnt area, and hence a change in fire regime may not be reflected in a simple change in charcoal abundance in sedimentary records (Mooney *et al.*, 2011). It is also important to note that any anthropogenic modification to fire regime and land cover would necessarily have occurred against a background of changes due to natural forcing primarily associated with changes in atmospheric CO_2 (Bond and Midgley, 2012, Higgins and Scheiter, 2012) and climate from the time of human occupation to the present (Mooney *et al.*, 2011).

There is no doubt that the ‘indigenous’ (anthropogenic) fire regime in tropical Australia is not the same as a ‘natural’, pre-human fire regime (e.g. Burrows and van Didden, 1991). In the monsoon tropics of north Australia, a natural fire regime would likely have been low frequency due to an absence of significant natural ignition sources (lightning) over most of the seasonal cycle, but of higher severity due to fuel accumulation between the more infrequent fire returns. Most recently, Bliege Bird *et al.* (2012) clearly demonstrated substantial differences in fire regime between areas subject to indigenous fire management and areas that are not subject to management, in the spinifex grasslands of northern Western Australia. Areas under indigenous fire management are subject to more but smaller fires, buffering climate-driven variability in fire size and resulting in increased patch richness, diversity and evenness (Yibarbuk *et al.*, 2001, Yates *et al.*, 2008). Price *et al.* (2012) note that the depopulation of indigenous land custodians from northern Australia in the early to mid-twentieth century resulted in a shift from a larger number of small, early dry-season fires to fewer but larger, more intense wildfires in the late dry season. Release from an indigenous fire regime has also seen considerable additions to forest area across tropical Australia, although this interpretation is complicated by the likelihood that increasing CO_2 or changes in precipitation regime are also contributing to forest expansion (Brook and Bowman, 2006, Donohue *et al.*, 2009, Bowman *et al.*, 2010, Tng *et al.*, 2012).

Archibald *et al.* (2012) have recently suggested that humans in Africa successively acquired the ability to manipulate fire frequency and season prior to 100ka and, finally, fuel connectivity with the advent of agriculture/pastoralism around 10ka. They conclude that, as in Australia, a lightning fire regime was characterized by seasonal fire distributions different from modern anthropogenic fire regimes, with major effects on the size and intensity of fires. They also conclude that substantial human impact on total burned area was probably not initiated until the middle Holocene in open landscapes, whereas humans could have altered fire regimes in closed/dissected landscapes by around 40ka.

Research into the interactions between fire, indigenous or natural, on ecosystems in northern Australia can directly examine a time window encompassing the last half-century or so (for review see Bowman, 1998). The ecosystems that were present at the time of European arrival are generally considered to be the benchmark for what is 'natural'. The extent to which indigenous fire regimes that had been in place for tens of millennia prior to European arrival had led to the modification of land cover in tropical Australia is currently unknown, but is of critical importance because of the potential feedbacks between land cover and climate that operate on a range of spatial scales and of timescales, from annual to millennial and longer (Beerling and Osborne, 2006, Bond and Midgley, 2012).

It has been argued that extensive regional scale tree cover can exert a direct influence on meso-scale climate (Shiel and Murdiyarso, 2009), with tropical forests recycling water by transpiration at higher rates compared to grasslands (Zhang *et al.,* 2001) and extracting water from greater depths within the soil (Hayden, 1998, Beerling and Osborne, 2006). Vegetation–climate feedbacks have been suggested to exist for regions ranging from the Amazon Basin (D'Almeida *et al.*, 2007) to the Sahel (Los *et al.*, 2006). Spracklen *et al.* (2012) found that for 60% of the tropical land surface, including much of central Australia, air that had previously passed over areas of extensive vegetation produced at least twice as much rain as air that had passed over little vegetation in the few days prior to the rainfall. In similar vein, recent studies in Australia have attributed regional reductions in rainfall to vegetation clearing, where conversion of forest to croplands that could function similarly to shallow-rooted grasslands (Pitman *et al.*, 2004, Deo, 2011).

Miller and Magee (1992) first proposed that the imposition of an anthropogenic fire regime in northern Australia could have reduced tree/shrub cover across tropical Australia, to the extent that the degree of penetration of monsoonal rains into the continental interior was reduced, resulting in the anomalous comparatively dry state of Lake Eyre in the Holocene (Magee *et al.*, 2004). Miller *et al.* (2005a) later used a modelling approach to explore the potential feedbacks between vegetation and climate in tropical Australia assuming the extreme scenarios of a pre-human landscape of "broadleaf deciduous trees on sandy loam soils and landscape after occupation of "desert vegetation on sandy soil". The study concluded that tree cover in tropical Australia exerts a significant control on monsoon penetration, with higher amounts of tree cover leading to deeper penetration of monsoon rains into the continental interior. In contrast, Pitman and Hesse (2007), found little response of the monsoon to changes in vegetation, a result subsequently criticized by Miller *et al.* (2007) on the basis that Pitman and Hesse (2007) specified modern insolation for Holocene simulations.

In another modelling study, Marshall and Lynch (2006) inferred only a muted response of the monsoon to vegetation change, whereas the modelling results of Lynch et al. (2007) suggested that late, high intensity fires could increase monsoon precipitation in modern northern Australia by up to 31%, (although this response was obtained from an artificially high burnt area of 90% and high severity fire events). The most recent and comprehensive simulations to date, (Notaro *et al.*, 2011), assuming only a 20% reduction in vegetation cover, found a non-significant effect of this vegetation change on peak monsoon period precipitation (January to March) but a significant 40mm reduction in rainfall in the pre-monsoon (October to December) season, thus effectively lengthening the dry season.

Nevertheless, even a 20% reduction in total vegetation cover as assumed by Notaro *et al.*, (2011) may be not be realistic, as the real driver of change in rainfall is change in latent and sensible heat fluxes associated with the anthropogenically-induced vegetation change (e.g., Grace *et al.,* 1998). And here we note that, contrary to some claims (e.g., Flannery, 2012), savanna fires tend to accelerate rates of nutrient cycling (van de Vevjer *et al.,* 1999) with net fire-induced nutrient losses usually minimal at a regional scale due to the subsequent return of emitted nutrients through wet- and dry-atmospheric deposition (Delon *et al*., 2012; Kugbe *et al*., 2012). Thus, with a stimulation of vegetative growth, if anything, latent heat fluxes may actually be greater for invigorated savanna vegetation regrowing after low to moderate severity fire events (Santos *et al.,* 2003) and even where large effects of long-term fire regime on woody vegetation cover have occurred stand-level evaporation rates are minimally affected (Quesada *et al.*¸ 2008).

The major source of natural ignition is lightning and Kilinc and Beringer (2007) found that lightning strikes in the Northern Territory are concentrated in the wet season and during transition periods between seasons. Very few dry season lightning strikes were observed. They also found that lightning strikes were more common in grasslands relative to woodier ecosystems. This was argued, at least in part, to be due to the higher sensible heat flux from grasslands than surrounding vegetation types within the landscape mosaic and hence a greater potential for convective activity directly above. Bowman *et al.* (2007) noted a link between late dry season fires and rainfall with one explanation being the dynamic effects of aerosols released by burning invigorating convection, with the formation of an enhanced and higher cloud cover than would otherwise be the case: this leading to higher rainfall (Andreae *et al.,* 2004; Lin *et al*., 2006).

On balance, the studies cited above provide some support for the possibility that anthropogenic fire regimes could have, over an extended period and through a number of fire-biosphere-atmosphere feedbacks, resulted in an appreciably different climate and land cover across northern Australia than would be the case had humans not occupied the continent. We explore the mechanisms in the following section, but note the following, inconclusive, evidence supporting this possibility:

(i) the most cited evidence for a change in fire regime following human arrival leading to a change in vegetation comes from the record of Lynch's Crater (Kershaw *et al.*, 2007). In this record, a sustained increase in charcoal flux at around the time of human arrival (Turney *et al.*, 2001b, Rule *et al.*, 2012) is accompanied by a dramatic decrease in gymnosperm taxa and concomitant increase in sclerophyll and grass taxa. It is also the case that fire-sensitive *Callitris* species disappear from the record, probably before human arrival, but never to reappear at similar levels of abundance despite having been abundant in the penultimate glacial and last interglacial (Kershaw *et al.*, 2007),. This observation has also been made for the Lake Frome region by (Luly, 2001).

The interpretation of the Lynch's Crater record as indicative of a broad change in fire regime in northern Australia is complicated by an observation originally made by Kershaw (1976: 492): 'This area is climatologically sensitive and it may be that the vegetation changes, and the climatic shifts implied by them, were exaggerated there as compared with the rest of north-eastern Australia'. The rainforest or rainforest fringe areas that are typical of the Atherton Tablelands are climatically atypical of northern Australia, which is dominated by lowland sclerophyll woodlands and shrublands occurring on vast sand-sheets of low relief (Ash, 1983, Shulmeister, 1992). It is therefore undesirable to extrapolate northern Australian palaeoenvironments solely on the basis of the Atherton Tablelands pollen record as a significant impact on vegetation cover at Lynch's Crater may not equate to a significant impact on vegetation across the majority of tropical Australia.

A potentially more representative pollen record for tropical Australia is provided from the marine sediment core (SHI-9014) of van der Kaars *et al.* (2000). This record, from the Banda Sea and therefore sampling a broad area of northern Australia and the Sahul shelf (but also including a southeast Asian component), is interpreted as indicating a significant expansion of grassland and a concomitant decline in *Eucalyptus* in northern Australian and the Sahul Shelf region from 37ka ago, sustained to the present-day. Further evidence for a sustained change comes from the disappearance of *Olea* pollen, indicative of vine thickets, from marine core MD98-2167 at around 45ka (Kershaw *et al.*, 2011). In neither of these cases are changes in charcoal abundance closely associated with the changes in pollen abundance, nor are there abrupt changes in charcoal abundance coinciding with initial human arrival.

(ii) As discussed above, the dominantly dry modern condition of Lake Eyre is anomalous in the context of its record of previous episodes of filling under analogous climate conditions (Magee *et al.*, 2004). More recent work on Lake Mega-Frome, which was last connected to Lake Eyre 50-47ka ago and is also currently dry, has suggested a greater importance for Southern Ocean sources, but still posits a significant influence from tropical moisture sources in the Holocene in determining its state (Cohen *et al.*, 2011).

(iii) The carbon isotope estimates of the proportion of C_4 grass in the diet of both emus and wombats, which suggested a mixed C_3 and C_4 diet prior to ~45ka and including the last interglacial and penultimate glacial periods, indicate a permanent shift to a lower proportion of C_4 biomass in the diet from 45ka until the present time (Miller *et al.*, 2005b, 2007). While these results derive from more southerly latitudes than tropical Australia, they do imply a large and permanent shift in environmental conditions across tropical Australia at some time after 45ka.

(iv) In tropical Australia, tropical dry forest types, with no perennial access to water but often with a measure of fire protection, extend in patches into regions of <600mm rainfall (Fensham, 1996, Miles *et al.*, 2006) and are common but widely dispersed in regions that receive >600mm (Figure 1). These patches have been shown to have both expanded and contracted over adjacent areas in the recent past, suggesting there is no general soil-imposed limit on their potential (local) distribution above 600mm rainfall (Bowman *et al.*, 1994). Murphy *et al.* (2010) conclude that both fire and soil fertility control the relative distribution of mulga and spinifex in the more arid interior.

Sankaran *et al.* (2005) has argued that in African savannas areas above 650mm are 'disturbance' savannas, where fire and/or herbivory are required to prevent canopy closure, although Lloyd *et al.* (2008) have pointed out that there are other explanations for their observations. Nevertheless, if we accept Sankaran *et al.'s* (2005) thesis, then the observation of Archibald *et al.* (2009) is pertinent – that fires become uncommon in Africa when rainfall exceeds ~800mm and canopy cover exceeds 40%. This is because, in the tropical Australian context, Bond (2008; Figure 1) has demonstrated that, in contrast to African savannas, modern Australian savannas fail to reach an African-type rainfall-determined maximum cover below 650mm. Above this threshold, where closed canopy vegetation should (based on the conclusions of Sankaran et al. (2005) for Africa), represent a much woodier stable state in the absence of disturbance.

Thus Australian savanna continues to persist to a much higher mean annual rainfall than Africa with one explanation being that long-standing indigenous fire regimes have resulted in large areas of savanna in northern Australia maintained by fire-mediated feedbacks preventing the return of the vegetation to an alternative, forest type, vegetation formation (Warman and Moles, 2009; Lawes *et al.*, 2011; Murphy and Bowman, 2012). Nevertheless, we add a note of caution that whilst the notion of forest and savanna representing two alternative steady states is conceptually attractive but is contested (House *et al.,* 2003, Lehmann *et al.,* 2011). We also note that Fensham *et al.* (2005) examined changes in woody cover in the 500-800mm rainfall zone of central Queensland and found that neither fire nor grazing exerted significant control, with variations in woody cover driven largely by variations in relative rainfall since the 1940s.

In summary: (i) it has been suggested by some modelling studies that forest vegetation can potentially exist over a larger area of tropical Australia than is currently the case, where local soil conditions allow; (ii) current climate and fire regime clearly favour the maintenance of open vegetation across much of tropical Australia; (iii) a number of potential feedbacks, some highly non-linear, have been suggested to operate between vegetation and climate, potentially resulting in alternative states of climate and vegetation; (iv) a change in fire regime theoretically provides one mechanism by which one state may be advantaged over another; and (v) there is evidence that fire regime has been manipulated by humans to some degree since their arrival in tropical Australia and across Sahul.

5. Towards testable hypotheses

What is striking in the discussion to date concerning the impact of human arrival is the relative lack of consideration of the dynamic ecological processes that would necessarily underlie any impact associated with human arrival (but see Bowman, 1998, Johnson, 2009). It is clear that many of the landscapes and ecosystems encountered upon European arrival were 'naturalized' rather than 'natural' (e.g. Bliege Bird *et al.*, 2012). However, the degree to which humans may have affected vegetation and/or climate at more than the local scale in Australia – 'The Biggest Estate on Earth' (Gammage, 2011) – remains unresolved after decades of debate.

Based on the discussion in the preceding sections, we elaborate below on two testable 'end-member' hypotheses concerning the broad-scale impact of an anthropogenic fire regime in the tens of millennia following human arrival, recognizing that a continuum of possible scenarios lies between them.

5.1 One minus one equals zero: no change

This scenario represents the null hypothesis and is straightforward to articulate. The removal or dramatic diminution of megafauna, and particularly browsing megafaunal herbivore populations, removed an impediment to tree recruitment and survival. The increased potential recruitment and survival of trees in tropical Australia was offset by the introduction of an anthropogenic fire regime. The net effect of an anthropogenic fire regime was to more or less maintain the status quo, with changes in the 'spatial grain' of ecosystem processes favouring enhanced biodiversity and resource availability at the local scale (Bliege Bird *et al.*, 2008). Whilst, over an extended period of time, this fire regime may have been instituted across a large area, a population probably never numbering more than one million people (Butlin, 1983), and possibly considerably fewer (Atkinson *et al.*, 2008, Eriksson *et al.*, 2012), was not capable of significant large-scale influence on ecosystems.

The relative areas of ecosystems at the broad scale were determined entirely by natural changes in regional climate, in turn forced by global changes in sea-level and insolation, modulated by the dynamics of the Asian monsoon and regional oceanic and atmospheric variability, overprinted by a long-term trend to greater aridity in Australia (Magee *et al.*, 2004, Webb, 2008, Cohen *et al.*, 2011, Field and Wroe, 2012). A 300ka record of vegetation change from the Timor Sea, northwest and downwind of tropical Australia, provided by Wang *et al.* (1999), shows no evidence of a significant change in the balance between tree and grass pollen, or in charcoal abundance, coincident with human arrival or at any time subsequent to human arrival. Indeed, the records of early explorers suggest that in the arid and semi-arid tropics, indigenous fire may have been infrequent and restricted to intermittent favourable seasons (Silcock et al., 2013).

Peaks in charcoal abundance prior to human arrival in core ODP-820 from off northeast Queensland (Moss and Kershaw, 2007) and core GC-17 off Western Australia (van der Kaars and De Deckker, 2002) indicate that this proxy cannot be reliably interpreted as indicative of anthropogenic fire. Indeed, in their review of charcoal records from the region, Mooney *et al.* (2011) found no 'distinct change' in charcoal abundance after human arrival in Australasia, though a possible trend to increased biomass burning between 50 and 40ka is one possible interpretation of the composite record. They note, however, the 'considerable uncertainty' associated with the chronology of records that lie beyond the limit of radiocarbon dating, and their composite record for Australasia as a whole may also conceal significant trends at finer spatial scales.

Modern tree and grass distributions in tropical Australia are largely explained by low nutrient soils, high natural climate variability (Fensham *et al.*, 2003, Lehmann *et al.*, 2009, Fisher *et al.*, 2012) and by the dominance of fire-adapted eucalypts (Lawes *et al.*, 2011, Crisp *et al.*, 2011). Increased atmospheric CO_2 and rainfall on their own can explain the observed forest encroachment and thickening of savannas over the twentieth century (Bond *et al.*, 2003, Bowman *et al.*, 2010, Fensham *et al.*, 2005, Lawes *et al.*, 2011, Tng *et al.*, 2012).

5.2 One plus one equals three: profound change

Significant human influence on vegetation in tropical Australia could have resulted from the effects of an anthropogenic fire regime on climate–vegetation feedbacks through two mechanisms. The first is indirect, operating through a change in the timing of burning, while the second is direct, from targeted burning at forest boundaries and of newly irrupted forest patches. Both mechanisms operate cumulatively on centennial to millennial timescales, with landscape-scale change not readily observable across several human generations, although local changes would be observable on decadal timescales, as is currently the case (Banfai and Bowman, 2005). Neither mechanism requires 'more' fire than a natural fire regime, simply a change in the frequency, timing and focus of burning. Hence, there is no requirement for a discernible change in biomass burning proxies accompanying human arrival (Mooney *et al.*, 2011).

Neither mechanism requires a large population. This is because an area under an active anthropogenic fire regime by definition shares a boundary with areas not under active management. Thus, human-lit fires could be expected, under favourable conditions, to carry over into areas not actively managed, thereby leading to change in the timing of burning in areas not actively managed and a more constant source of ignition than provided by lightning alone. In glacial and early post-glacial times, arid conditions may have also served to focus a comparatively small population around forest edges, which would have provided access to a wider resource base and accessible surface water in riparian areas.

Bond *et al.* (2003) modelled the impact of low CO_2 and fire and found that, at the CO_2 concentrations pertaining at the LGM, seedling growth rates were too slow to ensure growth to a 'fire-escape' height. Over the 25–30ka from human arrival to the LGM, incremental introduction of fire at a higher recurrence interval, early in the dry season and at low CO_2, may have exacerbated a natural trend to stem thinning in open environments and a reduction in forest area in response to drying and cooling of the continent (Hesse *et al.*, 2004).

After the LGM, climate began to warm, CO_2 began to rise and the monsoon re-established across tropical Australia by ~14ka (Wyrwoll and Miller, 2001). In the absence of humans, this combination of factors, coupled with the absence of browsing megafauna, would have improved the establishment and persistence potential for trees in northern Australia. Given the vast expanse of woodlands across this region, an increase in tree cover would have initiated a positive feedback, increasing the evapotranspirative movement of moisture into the continental interior and enabling tree establishment further towards the centre of the continent (Miller *et al.*, 2005a). Late dry-season lightning fires had the effect of reducing dry season length (Notaro *et al.*, 2011) and/or increasing wet season precipitation (Lynch *et al.*, 2007), further favouring tree establishment. Examination of the current degree of seasonality in precipitation across tropical Australia (Figure 1) indicates that even a 5% change in the proportion of rain falling outside the wet season would dramatically change the climate of much of northern Australia. Once tree cover passed a threshold, equivalent to ~40% canopy cover in Africa (Archibald *et al.*, 2009), the incidence of fire would be reduced, further promoting the establishment of woody vegetation formations across a much broader area than is currently the case.

The above scenario was not, however, realised because the anthropogenic fire regime operating in the post-LGM times was characterized by increased frequency of ignitions, decreased return interval and a shift to more common early dry-season fires. This could have had the indirect result of instituting a negative feedback, constraining tree establishment through the maintenance of a longer dry season as well as constraining both the intensity of the monsoon and its penetration into the continental interior. As a result, canopy closure was inhibited and fire, mediated by humans, maintained the system in a relatively open state across a larger area than would otherwise have been the case (Murphy and Bowman, 2012).

This indirect negative feedback, hindering forest establishment, could have been further amplified by targeted anthropogenic burning along forest boundaries. Certainly, some forest environments in northern Australia were difficult to exploit, with limited or no occupation of forests in the wet tropics until the Holocene (Cosgrove *et al.*, 2007). This suggests that indigenous populations may have preferred to maintain an open vegetation type in the face of forest encroachment. In the Northern Territory, monsoon forest patches are currently valued for a number of resources, particularly yams in the wet season, and both Haynes (1985) and Russell-Smith *et al.* (1997) found that such forest patches are actively protected by early dry-season burning outwards from their edges. While such a strategy may be effective in protecting existing forest areas, in post-LGM times it may also have limited the expansion of forest area by inhibiting tree seedling maturation beyond forest boundaries (Woinarski *et al.*, 2004). Frequent low intensity fires in open vegetation may also have deterred forest establishment through inhibition of irruption of new forest patches in the landscape, as has been demonstrated in the modern environment (Russell-Smith *et al.*, 2004a, b). Indeed, given the relatively slow rates of forest advance by edge progression, generally no more than a few metres per year (e.g. Favier *et al.*, 2004b; Tng *et al.,* 2012), inhibition of the formation of new forest patches across the landscape might be the dominant mechanism by which forest advance could be limited by anthropogenic fire.

The net effect of an anthropogenic fire regime applied for tens of millennia on the observed modern vegetation cover, under this scenario, would be a more highly seasonal climate with lower penetration of the monsoon into the continental interior. This may in turn have fed back into (i) a more limited distribution of dry/monsoon forest cover over northern and northeastern Australia, (ii) savannas with comparatively low-density tree cover over much of the tropical north, (iii) the expansion of spinifex grasslands at the expense of shrublands in the arid interior (Miller *et al.*, 2007) and, ultimately, (iv) to the anomalously dry condition of modern Lake Eyre (Magee *et al.*, 2004). This scenario is consistent with results from the long pollen record from core SHI-9014 in the Banda Sea (van der Kaars *et al.*, 2000), which shows a significant expansion of grassland and concomitant decline in eucalypts in northern Australia and the Sahul Shelf region from 37ka, sustained to the present-day. Indeed, it is possible that the present link between increased savanna woodiness and increased rainfall in Queensland savannas in the second half of the twentieth century (Fensham *et al.*, 2005) is partly the result of release from an anthropogenic fire regime in the early twentieth century – a trend that may continue for centuries to millennia.

6. Conclusions: What is natural in tropical Australia?

There is abundant evidence that the vegetation patterns and biodiversity across tropical Australia at the time of European arrival were, to some degree, anthropogenic (Jones and Bowler, 1980, Johnson, 2006, Gammage, 2011), so the question 'what is natural?' is one of spatial and temporal scale. We conclude that mechanisms do exist (supported by limited evidence) to support the hypothesis that human occupation resulted in profound modification to broad-scale vegetation patterns and climate across tropical Australia at the millennial scale. However, human activity, primarily expressed through megafaunal extinction and modifications to natural fire regime, occurred against a background of significant natural climate change and generally nutrient-poor soils that may ultimately have mitigated against any more than local expression of this potential for significant broad-scale anthropogenic change.

It is not possible to discriminate unequivocally between the two hypotheses proposed above, or any intermediate between the two, because the data required to undertake a rigorous assessment do not exist. Obtaining the data required to draw a defensible conclusion will require closer collaborations between indigenous traditional land owners, archaeologists, anthropologists, geoscientists, climatologists and ecologists than has been the case to date. The evidence required to discriminate between these hypotheses can potentially come from several avenues:

(i) geosciences – the Lynch's Crater record has existed for almost 40 years, but is not suited to assessing broad-scale human impact across tropical Australia. There is a need for terrestrial records spanning the last interglacial period to the present in the savannas of northern Australia, to examine in detail the trajectory of environmental change across the tropics. The obvious location for such records is in the regions that currently receive >600mm of rainfall each year (Figure 1) – regions that could potentially support a higher forest cover, but which are currently dominated by woodland and open-forest savanna of between 20% to 60% cover with scattered patches of closed forest, including currently flooded continental shelf areas.

Two unexplored possibilities exist. The first are large sinkholes, up to 100m in depth that exist across the Top End of the Northern Territory in various stages of infilling, generally in limestone or dolomitic terranes. The second comprises the many swamps created by basaltic volcanism in northeast Queensland over the last several million years (Stephenson, 1989, Whitehead *et al.*, 2007). There are a large number of untested potential targets that are currently in savanna that could, prior to human occupation, have featured a higher woody cover and potentially of non-eucalypt species (Pole and Bowman, 1996). The deposits in the sinkholes and basalt-dammed swamps contain both charcoal and quartz, making them amenable to numerical dating by radiocarbon and OSL. There are new geochemical techniques that can provide carbon isotope fingerprints for both terrestrial carbon and charcoal, to assess any long-term changes in the balance between C_3 trees and C_4 grasses in the surrounding environment (Bird and Ascough, 2012, Wurster *et al.*, 2012). Pollen grains and *Sporomiella* spores can provide information on vegetation and megafaunal abundance over time (Roberts and Brook, 2010, Rule *et al.*, 2012).

The most important periods for detailed examination are not the time intervals shortly before and after human arrival, but the comparatively wet periods of MIS-5 and MIS-4, prior to human arrival, and the post-glacial period after human colonization, when climate was broadly similar. The long-term maintenance of savanna vegetation would imply little impact of human occupation, whereas the existence of forest at such sites prior to human arrival would provide further evidence of substantial human impact.

A further source of high-resolution climate proxy information is speleothems, and such records might be brought to bear on the issue of climate variability and megafaunal extinction in MIS-3, in particular. Speleothem records have proved remarkably valuable in palaeoclimate studies in southern Australia (e.g. Ayliffe *et al*., 1998) and elsewhere (e.g. Weninger and Jöris, 2008), but the potential for long-term climate records from tropical Australian speleothems has yet to be extensively investigated.

(ii) archaeology and anthropology – testing the two hypotheses presented above requires a more complete understanding of the evolution and distribution of population numbers in prehistory to determine the plausibility of the 'profound impact' hypothesis, in particular. It could also require the revisiting of available archaeological information and the material excavated from sites to, for example, determine local vegetation and climate from the geochemical analysis of biotic discard materials (e.g. bones, mollusc shell). There is considerable space for further research into the use of forest edges across tropical Australia in the past, the dynamics of and rationale behind the indigenous fire regime applied at forest edges, as well as the perception of, and response to, decadal-scale change in stem density and tree recruitment in savannas. This implies collaboration with contemporary traditional owners to explore the meaning, uses and value of modern forest and savanna areas across the tropical north (Bliege Bird *et al*., 2008).

(iii) environmental biology – understanding the response of tropical vegetation types to changing climatic conditions on millennial timescales will require a better understanding of plant, animal and ecosystem responses to fire and water stress, the historical biogeography of Australia's tropical flora and fauna, and a better understanding of the role of soil physical and chemical properties in influencing the structure and function of tropical vegetation formations and how soil properties interact with climate to determine vegetation type.

(iv) modelling – there have been significant, but largely separate, efforts across several disciplines to model the interactions between vegetation, climate and fire in savannas, both globally and in Australia (e.g. Archibald *et al.*, 2012, Murphy and Bowman, 2012). There have also been efforts to model the evolution of the monsoon in Australia in the Quaternary, to identify the controls underlying monsoon variability in the past, including the impact of vegetation (e.g. Notaro *et al.*, 2011). The work of Archibald *et al.* (2012), in particular, has, for the first time, explicitly included humans as an agent capable of influencing the fire–vegetation–climate system in prehistory. Africa has been occupied by humans for a much greater length of time than Australia and saw the incremental development of human ability to control fire frequency and season over the last million years with the continued existence of mega-herbivores (Koch and Barnosky, 2006). The human ability to manipulate fire frequency and season was imposed 'instantaneously' upon arrival in Australia. Combined with the ensuing rapid loss of megafauna, the resulting trajectory of change in Australia may have been substantially different from that in Africa.

Archibald *et al.* (2012) note that anthropogenic fire may have affected forest expansion and contraction in Africa in the past, but, as yet, there have been no integrated attempts to include the potential millennial-scale feedbacks between anthropogenic fire, vegetation and climate in ecosystem models. This would be a challenging undertaking for tropical Australia, but would potentially enable an assessment of the sensitivity of the vegetation–climate system to perturbations, particularly in those boundary conditions potentially capable of modification through the imposition of an anthropogenic fire regime.

In conclusion, we are not able, on the basis of the data currently available, to determine which of the two broad hypotheses outlined above better define the actual trajectory by which we arrived at the vegetation distribution we observe across tropical Australia. The degree to which anthropogenic fire regimes in prehistory may have shaped the modern environment is critical to understanding its trajectory under future anthropogenic climate change. The possibility that human occupation resulted in profound environmental change at the very least suggests that phenomena observed to be operating in the modern environment cannot necessarily be extrapolated into the past, as significant anthropogenic impacts on regional climate and vegetation may have considerably more time depth than is currently supposed. As Midnight Oil (1987) noted, '40,000 years can make a difference to the state of things …'.

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References

Adams D. 1979. *The Hitchiker's Guide to the Galaxy*. Pan Books: London.

Archibald S, Roy DP, Wilgen V, Brian W, Scholes RJ. 2009. What limits fire? An examination of drivers of burnt area in Southern Africa. *Global Change Biology* **15:** 613–630.

Archibald S, Staver AC, Levin SA. 2012. Evolution of human-driven fire regimes in Africa. *Proceedings of the National Academy of Sciences* **109:** 847–852.

Ash JE. 1983. Rainfall patterns in northeastern Queensland: 7 ± 2 ka. *Proceedings of the first CLIMANZ conference.*

Asner GP, Levick SR, Kennedy-Bowdoin T, Knapp DE, Emerson R, Jacobson J, Colgan MS, Martin RE. 2009. Large-scale impacts of herbivores on the structural diversity of African savannas. *Proceedings of the National Academy of Sciences* **106:** 4947–4952.

Atkinson QD, Gray RD, Drummond AJ. 2008. mtDNA variation predicts population size in humans and reveals a major Southern Asian chapter in human prehistory. *Molecular Biology and Evolution* **25:** 468–474.

Ayliffe LK, Marianelli PC, Moriarty KC, Wells RT, McCulloch MT, Mortimer GE, Hellstrom JC. 1998. 500 ka precipitation record from southeastern Australia: Evidence for interglacial relative aridity. *Geology* **26:** 147–150.

Banfai DS, Bowman DMJS. 2005. Dynamics of a savanna-forest mosaic in the Australian monsoon tropics inferred from stand structures and historical aerial photography. *Annual Review of Ecology, Evolution, and Systematics* **53:** 185–194.

Beerling DJ, Osborne CP. 2006. The origin of the savanna biome. *Global Change Biology* **12:** 2023–2031.

Bird MI, Ascough PL. 2012. Isotopes in pyrogenic carbon: a review. *Organic Geochemistry* **42:** 1529–1539.

Bird MI, Turney CSM, Fifield LK, Jones R, Ayliffe LK, Palmer A, Cresswell R, Robertson S. 2002. Radiocarbon analysis of the early archaeological site of Nauwalabila I, Arnhem Land, Australia: implications for sample suitability and stratigraphic integrity. *Quaternary Science Reviews* **21:** 1061–1075.

Bliege Bird RB, Bird DW, Codding BF, Parker CH, Jones JH. 2008. The “fire stick farming” hypothesis: Australian Aboriginal foraging strategies, biodiversity, and anthropogenic fire mosaics. *Proceedings of the National Academy of Sciences* **105:** 14796–14801.

Bliege Bird RB, Codding BF, Kauhanen PG, Bird DW. 2012. Aboriginal hunting buffers climate-driven fire-size variability in Australia’s spinifex grasslands. *Proceedings of the National Academy of Sciences* **109:** 10287–10292.

Bond WJ. 2008. What limits trees in C_4 grasslands and savannas? *Annual Review of Ecology, Evolution, and Systematics* **39:** 641–659.

Bond WJ, Keeley JE. 2005. Fire as a global ‘herbivore’: the ecology and evolution of flammable ecosystems. *Trends in Ecology & Evolution* **20:** 387–394.

Bond WJ, Midgley GF. 2012. Carbon dioxide and the uneasy interactions of trees and savannah grasses. *Philosophical Transactions of the Royal Society B: Biological Sciences* **367:** 601–612.

Bond WJ, Midgley GF, Woodward FI. 2003. The importance of low atmospheric CO_2 and fire in promoting the spread of grasslands and savannas. *Global Change Biology* **9:** 973–982.

Bowler JM, Johnston H, Olley JM, Prescott JR, Roberts RG, Shawcross W, Spooner NA. 2003. New ages for human occupation and climatic change at Lake Mungo, Australia. *Nature* **421:** 837–840.

Bowman D. 2002. The Australian summer monsoon: a biogeographic perspective. *Australian Geographical Studies* **40:** 261–277.

Bowman D, Woinarski JCZ, Russellsmith J. 1994. Environmental relationships of Orange-footed Scrubfowl *Megapodius reinwardt* nests in the Northern Territory. *EMU* **94:** 181–185.

Bowman DMJS. 1998. The impact of Aboriginal landscape burning on the Australian biota. *New Phytologist* **140:** 385–410.

Bowman DMJS, Dingle JK, Johnston FH, Parry D, Foley M. 2007. Seasonal patterns in biomass smoke pollution and the mid 20th ‐ century transition from Aboriginal to European fire management in northern Australia. *Global Ecology and Biogeography* **16:** 246–256.

Bowman DMJS, Murphy BP, Banfai DS. 2010. Has global environmental change caused monsoon rainforests to expand in the Australian monsoon tropics? *Landscape Ecology* **25:** 1247–1260.

Brook BW, Bowman DMJS. 2004. The uncertain blitzkrieg of Pleistocene megafauna. *Journal of Biogeography* **31:** 517–523.

Brook BW, Bowman DMJS. 2006. Postcards from the past: charting the landscape-scale conversion of tropical Australian savanna to closed forest during the 20th century. *Landscape Ecology* **21:** 1253–1266.

Brook BW *et al*. 2007. Would the Australian megafauna have become extinct if humans had never colonised the continent? Comments on "A review of the evidence for a human role in the extinction of Australian megafauna and an alternative explanation" by S.Environmental rela. *Quaternary Science Reviews* **26:** 560–564.

Brook BW, Johnson CN. 2006. Selective hunting of juveniles as a cause of the imperceptible overkill of the Australian Pleistocene megafauna. *Alcheringa: An Australasian Journal of Palaeontology* **1:** 39–48.

Butlin NG. 1983. *Our Original Aggression: Aboriginal Populations of Southeastern Australia 1788-1850*. G. Allen & Unwin Sydney: Sydney.

Cohen TJ, Nanson GC, Jansen JD, Jones BG, Jacobs Z, Treble P, Price DM, May JH, Smith AM, Ayliffe LK. 2011. Continental aridification and the vanishing of Australia's megalakes. *Geology* **39:** 167–170.

Cosgrove R, Field J, Ferrier Å. 2007. The archaeology of Australia's tropical rainforests. *Palaeogeography, Palaeoclimatology, Palaeoecology* **251:** 150–173.

Crisp MD, Burrows GE, Cook LG, Thornhill AH, Bowman DMJS. 2011. Flammable biomes dominated by eucalypts originated at the Cretaceous-Palaeogene boundary. *Nature Communications* **2:** 193.

D'Almeida C, Vörösmarty CJ, Hurtt GC, Marengo JA, Dingman SL, Keim BD. 2007. The effects of deforestation on the hydrological cycle in Amazonia: a review on scale and resolution. *International Journal of Climatology* **27:** 633–647.

David B *et al*. 2011. Nawarla Gabarnmang, a 45,180±910 cal BP site in Jawoyn Country, southwest Arnhem Land plateau. *Australian Archaeology* **73:** 73–77.

David B, Roberts RG, Magee J, Mialanes J, Turney C, Bird M, White C, Fifield LK, Tibby J. 2007. Sediment mixing at Nonda Rock: investigations of stratigraphic integrity at an early archaeological site in northern Australia and implications for the human colonisation of the continent. *Journal of Quaternary Science* **22:** 449–479.

Davidson I. 2012. Peopling the last new worlds: the first colonisation of Sahul and the Americas. *Quaternary International*. DOI: 10.1016/j.quaint.2012.09.023.

Demeter F, Shackelford LL, Bacon AM, Duringer P, Westaway K, Sayavongkhamdy T, Braga J, Sichanthongtip P, Khamdalavong P, Ponche JL. 2012. Anatomically modern human in Southeast Asia (Laos) by 46 ka. *Proceedings of the National Academy of Sciences* **109:** 14375–14380.

Deo RC. 2011. Links between native forest and climate in Australia. *Weather* **66:** 64–69.

Donohue RJ, McVicar TR, Roderick ML. 2009. Climate ‐ related trends in Australian vegetation cover as inferred from satellite observations, 1981–2006. *Global Change Biology* **15:** 1025–1039.

Eriksson A, Betti L, Friend AD, Lycett SJ, Singarayer JS, von Cramon-Taubadel N, Valdes PJ, Balloux F, Manica A. 2012. Late Pleistocene climate change and the global expansion of anatomically modern humans. *Proceedings of the National Academy of Sciences* **109:** 16089–16094.

Faith JT, O'Connell JF. 2011. Revisiting the late Pleistocene mammal extinction record at Tight Entrance Cave, southwestern Australia. *Quaternary Research* **76:** 397–400.

Favier C, Chave J, Fabing A, Schwartz D, Dubois MA. 2004. Modelling forest–savanna mosaic dynamics in man-influenced environments: effects of fire, climate and soil heterogeneity. *Ecological Modelling* **171:** 85–102.

Fensham RJ. 1996. Land clearance and conservation of inland dry rainforest in north Queensland, Australia. *Biological Conservation* **75:** 289–298.

Fensham RJ, Fairfax RJ, Archer SR. 2005. Rainfall, land use and woody vegetation cover change in semi ‐ arid Australian savanna. *Journal of Ecology* **93:** 596–606.

Fensham RJ, Fairfax RJ, Butler DW, Bowman D. 2003. Effects of fire and drought in a tropical eucalypt savanna colonized by rain forest. *Journal of Biogeography* **30:** 1405–1414.

Field J, Fillios M, Wroe S. 2008. Chronological overlap between humans and megafauna in Sahul (Pleistocene Australia–New Guinea): A review of the evidence. *Earth-Science Reviews* **89:** 97–115.

Field J, Wroe S. 2012. Aridity, faunal adaptations and Australian Late Pleistocene extinctions. *World Archaeology* **44:** 56–74.

Fisher JB, Badgley G, Blyth E. 2012. Global nutrient limitation in terrestrial vegetation. *Global Biogeochemical Cycles* **26:** GB3007.

Flannery TF. 1990. Pleistocene faunal loss: implications of the aftershock for Australia's past and future. *Archaeology in Oceania* **25:** 45–55.

Flannery, TF. (2012) After the Future: Australia's New Extinction Crisis. *Quarterly essay No 48*. Black Inc., Melbourne, 80pp.

Gammage B. 2011. *The Biggest Estate on Earth*. Allen and Unwin: Melbourne.

Gillespie, R, Brook, BW. (2006) Is there a Pleistocene archaeological site at Cuddie Springs? *Archaeology in Oceania* **41**: 1–11.

Gillespie R, Camens AB, Worthy TH, Rawlence NJ, Reid C, Bertuch F, Levchenko V, Cooper A. 2012. Man and megafauna in Tasmania: closing the gap. *Quaternary Science Reviews* **37:** 38–47.

Grün R, Eggins S, Aubert M, Spooner N, Pike AWG, Müller W. 2010. ESR and U-series analyses of faunal material from Cuddie Springs, NSW, Australia: implications for the timing of the extinction of the Australian megafauna. *Quaternary Science Reviews* **29:** 596–610.

Gunn RG, Douglas LC, Whear RL. 2011. What bird is that? Identifying a probable painting of *Genyornis newtoni* in western Arnhem land. *Australian Archaeology* **73:** 1–12.

Hayden BP. 1998. Ecosystem feedbacks on climate at the landscape scale. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **353:** 5–18.

Haynes CD. 1985. The pattern and ecology of munwag: traditional Aboriginal fire regimes in north-central Arnhem Land. *Proceedings of the Ecological Society of Australia* **13:** 203–214.

Hesse PP, Magee JW, Van Der Kaars S. 2004. Late Quaternary climates of the Australian arid zone: a review. *Quaternary International* **118:** 87–102.

Higgins SI, Scheiter S. 2012. Atmospheric CO_2 forces abrupt vegetation shifts locally, but not globally. *Nature* **488:** 209–212.

Higham TFG, Barton H, Turney CSM, Barker G, Ramsey CB, Brock F. 2009. Radiocarbon dating of charcoal from tropical sequences: results from the Niah Great Cave, Sarawak, and their broader implications. *Journal of Quaternary Science* **24:** 189–197.

Hiscock P. 2008. *Archaeology of Ancient Australia*. Routledge: London.

Hiscock P, Wallis LA. 2005. Pleistocene settlement of deserts from an Australian perspective. *Desert peoples: archaeological perspectives*, Smith M, Hiscock P (eds). Blackwell: Oxford; 34-57.

Horton DR. 1980. A review of the extinction question: man, climate and megafauna. *Archaeology & Physical Anthropology in Oceania* **15:** 86–97.

Horton DR. 1982. The Burning Question: Aborigines, Fire and Australian Ecosystems. *Mankind* **13:** 237–252.

House JI, Archer S, Breshears DD, and Scholes R. 2003. Conundrums in mixed woody-herbaceous plant systems. Journal of Biogeography 30: 1763–1777.

Hubbell SP. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press: Princeton.

Johnson BJ, Miller GH, Fogel ML, Magee JW, Gagan MK, Chivas AR. 1999. 65,000 years of vegetation change in central Australia and the Australian summer monsoon. *Science* **284:** 1150–1152.

Johnson C. 2006. *Australia's Mammal Extinctions: a 50,000 year history*. Cambridge University Press: New York.

Johnson CN. 2005. What can the data on late survival of Australian megafauna tell us about the cause of their extinction? *Quaternary Science Reviews* **24:** 2167–2172.

Johnson CN. 2009. Ecological consequences of Late Quaternary extinctions of megafauna. *Proceedings of the Royal Society B: Biological Sciences* **276:** 2509–2519.

Johnson CN, Brook BW. 2011. Reconstructing the dynamics of ancient human populations from radiocarbon dates: 10 000 years of population growth in Australia. *Proceedings of the Royal Society B: Biological Sciences* **278:** 3748–3754.

Jones R. 1968. The geographical background to the arrival of man in Australia and Tasmania. *Archaeology & Physical Anthropology in Oceania* **3:** 186–215.

Jones R. 1969. Fire-stick farming. *Australian Natural History* **16:** 224–228.

Jones R, Bowler J. 1980. Struggle for the savanna: northern Australia in ecological and prehistoric perspective. *Northern Australia: Options and Implications* 3–31.

Kershaw AP, Bretherton SC, van der Kaars S. 2007. A complete pollen record of the last 230 ka from Lynch's Crater, north-eastern Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology* **251:** 23–45.

Kershaw AP. 1974. A long continuous pollen sequence from north-eastern Australia. *Nature* **251:** L16402.

Kershaw AP. 1976. A late Pleistocene and Holocene pollen diagram from Lynch's Crater, northeastern Queensland, Australia. *New Phytologist* **77:** 469–498.

Kershaw AP. 1986. Climatic change and Aboriginal burning in north-east Australia during the last two glacial/interglacial cycles. *Nature* **322:** 47–49.

Kershaw A, Van Der Kaars S, Flenley JR. 2011. The Quaternary history of Far Eastern rainforests. *Tropical Rainforest Responses to Climatic Change Second Edition*, Bush M, Flenley J, Gosling W (eds). Springer Praxis Books: Berlin; 85-123.

Kilinc M, Beringer J. 2007. The spatial and temporal distribution of lightning strikes and their relationship with vegetation type, elevation, and fire scars in the Northern Territory. *Journal of climate* **20:** 1161–1173.

Koch PL, Barnosky AD. 2006. Late Quaternary extinctions: State of the debate. *Annual Review of Ecology, Evolution, and Systematics* **37:** 215–250.

Lawes MJ, Murphy BP, Midgley JJ, Russell-Smith J. 2011. Are the eucalypt and non-eucalypt components of Australian tropical savannas independent? *Oecologia* **166:** 229–239.

Lehmann CER, Ratnam J, Hutley LB. 2009. Which of these continents is not like the other? Comparisons of tropical savanna systems: key questions and challenges. *New Phytologist* **181:** 508–511.

Lehmann CER, Archibald SA, Hoffmann WA, Bond WJ. 2011. Deciphering the distribution of the savanna biome. *New Phytologist* **191:** 197–209.

Lloyd J, Bird MI, Vellen L, Miranda AC, Veenendaal EM, Djagbletey G, Miranda HS, Cook G, Farquhar GD. 2008. Contributions of woody and herbaceous vegetation to tropical savanna ecosystem productivity: a quasi-global estimate. *Tree physiology* **28:** 451–468.

Lorenzen ED *et al.* 2011. Species-specific responses of Late Quaternary megafauna to climate and humans. *Nature* **479:** 359–U195.

Los SO, Weedon GP, North PRJ, Kaduk JD, Taylor CM, Cox PM. 2006. An observation-based estimate of the strength of rainfall-vegetation interactions in the Sahel. *International Journal of Climatology* **33:** L16402.

Luly JG. 2001. On the equivocal fate of Late Pleistocene Callitris Vent. (Cupressaceae) woodlands in arid South Australia. *Quaternary International* **83-5:** 155–168.

Lynch AH, Abramson D, Goergen K, Beringer J, Uotila P. 2007. Influence of savanna fire on Australian monsoon season precipitation and circulation as simulated using a distributed computing environment. *Geophysical Research Letters* **34:**

Magee JW, Miller GH, Spooner NA, Questiaux D. 2004. Continuous 150 ky monsoon record from Lake Eyre, Australia: Insolation-forcing implications and unexpected Holocene failure. *Geology* **32:** 885–888.

Marshall AG, Lynch AH. 2006. Time-slice analysis of the Australian summer monsoon during the late Quaternary using the Fast Ocean Atmosphere Model. *Journal of Quaternary Science* **21:** 789–801.

Merrilees D. 1968. Man the destroyer: late Quaternary changes in the Australian marsupial fauna. *Journal of the Royal Society of Western Australia* **51:** 1–24.

Midgley JJ, Lawes MJ, Chamaille-Jammes S. 2010. Savanna woody plant dynamics: the role of fire and herbivory, separately and synergistically. *Australian Journal of Botany* **58:** 1–11.

Miles L, Newton AC, DeFries RS, Ravilious C, May I, Blyth S, Kapos V, Gordon JE. 2006. A global overview of the conservation status of tropical dry forests. *Journal of Biogeography* **33:** 491–505.

Miller G, Mangan J, Pollard D, Thompson S, Felzer B, Magee J. 2005a. Sensitivity of the Australian Monsoon to insolation and vegetation: Implications for human impact on continental moisture balance. *Geology* **33:** 65–68.

Miller GH, Magee JW, Fogel ML, Gagan MK. 2007. Detecting human impacts on the flora, fauna, and summer monsoon of Pleistocene Australia. *Climate of the Past* **3:** 463–473.

Miller GH, Fogel ML, Magee JW, Gagan MK, Clarke SJ, Johnson BJ. 2005b. Ecosystem collapse in Pleistocene Australia and a human role in megafaunal extinction. *Science* **309:** 287–290.

Miller GH, Magee JW, Johnson BJ, Fogel ML, Spooner NA, McCulloch MT, Ayliffe LK. 1999. Pleistocene extinction of *Genyornis newtoni*: human impact on Australian megafauna. *Science* **283:** 205–208.

Miller GS, Magee JW. 1992. Drought in the Australian outback: Anthropogenic impacts on regional climate. *American Geophysical Union, fall meeting* 104.

Mooney SD *et al.* 2011. Late Quaternary fire regimes of Australasia. *Quaternary Science Reviews* **30:** 28–46.

Moss PT, Kershaw AP. 2007. A late Quaternary marine palynological record (oxygen isotope stages 1 to 7) for the humid tropics of northeastern Australia based on ODP Site 820. *Palaeogeograpy, Palaeoclimatology Palaeoecology* **251:** 4–22.

Mulvaney DJ, Kamminga J. 1999. *The Prehistory of Australia, Second Edition.* Penguin Books: Ringwood, Victoria.

Murphy BP, Bowman DMJS. 2012. What controls the distribution of tropical forest and savanna? *Ecology Letters* **15:** 748–758.

Murphy BP, Paron P, Prior LD, Boggs GS, Franklin DC, Bowman DMJS. 2010. Using generalized autoregressive error models to understand fire-vegetation-soil feedbacks in a mulga-spinifex landscape mosaic. *Journal of Biogeography* **37:** 2169–2182.

Murphy BP, Williamson GJ, Bowman DMJS. 2012. Did central Australian megafaunal extinction coincide with abrupt ecosystem collapse or gradual climate change? *Global Ecology and Biogeography* **21:** 142–151.

Murray P, Chaloupka G. 1984. The Dreamtime animals: extinct megafauna in Arnhem Land rock art. *Archaelogy in Oceania* **19:** 105–116.

Nano CEM, Clarke PJ. 2011. How do drought and fire influence the patterns of resprouting in Australian deserts? *Plant Ecology* **212:** 2095–2110.

Nanson GC, Price DM, Short SA. 1992. Wetting and drying of Australia over the past 300 ka. *Geology* **20:** 791–794.

Notaro M, Wyrwoll KH, Chen G. 2011. Did aboriginal vegetation burning impact on the Australian summer monsoon? *Geophysical Research Letters* **38:** L11704.

O'Connell JF, Allen J. 1998. When did humans first arrive in Greater Australia and why is it important to know? *Evolutionary Anthropology: Issues, News, and Reviews* **6:** 132–146.

O'Connell JF, Allen J. 2012. The restaurant at the end of the Universe: Modelling the colonisation of Sahul. *Australian Archaeology* **74:** 5–17.

Oil M. 1987. *The Dead Heart.* Columbia Records: New York, New York.

Owen-Smith N. 1987. Pleistocene extinctions: the pivotal role of megaherbivores. *Paleobiology* **77:** 351–362.

Owen-Smith N. 1989. Megafaunal extinctions: the conservation message from 11,000 years BP. *Conservation Biology* **3:** 405–412.

Owen R. 1877. *Researches on the Fossil Remains of the Extinct Mammals of Australia: With a Notice of the Extinct Marsupials of England.* J. Erxleben: London.

Pitman AJ, Hesse PP. 2007. The significance of large-scale land cover change on the Australian palaeomonsoon. *Quaternary Science Reviews* **26:** 189–200.

Pitman AJ, Narisma GT, Pielke RA, Holbrook NJ. 2004. Impact of land cover change on the climate of southwest Western Australia. *Journal of Geophysical Research Atmospheres* **109:** D18109.

Pole MS, Bowman DMJS. 1996. Tertiary plant fossils from Australia's' Top End'. *Australian Systematic Botany* **9:** 113–126.

Prentice IC, Harrison SP. 2009. Ecosystem effects of CO_2 concentration: evidence from past climates. *Climate of the Past* **5:** 297–307.

Prescott GW, Williams DR, Balmford A, Green RE, Manica A. 2012. Quantitative global analysis of the role of climate and people in explaining late Quaternary megafaunal extinctions. *Proceedings of the National Academy of Sciences* **109:** 4527–4531.

Price GJ, Webb GE, Zhao J, Feng Y, Murray AS, Cooke BN, Hocknull SA, Sobbe IH. 2011. Dating megafaunal extinction on the Pleistocene Darling Downs, eastern Australia: the promise and pitfalls of dating as a test of extinction hypotheses. *Quaternary Science Reviews* **30:** 899–914.

Price OF, Russell-Smith J, Watt F. 2012. The influence of prescribed fire on the extent of wildfire in savanna landscapes of western Arnhem Land, Australia. *International Journal of Wildland Fire* **21:** 297–305.

Prideaux GJ, Ayliffe LK, DeSantis LRG, Schubert BW, Murray PF, Gagan MK, Cerling TE. 2009. Extinction implications of a chenopod browse diet for a giant Pleistocene kangaroo. *Proceedings of the National Academy of Sciences* **106:** 11646–11650.

Prideaux GJ, Gully GA, Couzens AMC, Ayliffe LK, Jankowski NR, Jacobs Z, Roberts RG, Hellstrom JC, Gagan MK, Hatcher LM. 2010. Timing and dynamics of Late Pleistocene mammal extinctions in southwestern Australia. *Proceedings of the National Academy of Sciences* **107:** 22157–22162.

Prideaux GJ, Roberts RG, Megirian D, Westaway KE, Hellstrom JC, Olley JM. 2007. Mammalian responses to Pleistocene climate change in southeastern Australia. *Geology* **35:** 33–36.

Prior LD, Murphy BP, Russell-Smith J. 2009. Environmental and demographic correlates of tree recruitment and mortality in north Australian savannas. *Forest Ecology and Management* **257:** 66–74.

Prior LD, Williams RJ, Bowman DMJS. 2010. Experimental evidence that fire causes a tree recruitment bottleneck in an Australian tropical savanna. *Journal of Tropical Ecology* **26:** 595–603.

Quesada, CA. Hodnett , MG, Breyer, LE, Santos, JB, Andreae, S, Miranda, HS, Miranda, AC, Lloyd, J, 2008. Seasonal variations of soil moisture in two woodland savannas of central Brazil with different fire history. *Tree Physiology* **28**: 417-424.

Roberts R, Yoshida H, Galbraith R, Laslett G, Jones R, Smith M. 1998. Single-aliquot and single-grain optical dating confirm thermoluminescence age estimates at Malakunanja II rock shelter in northern Australia. *Ancient TL* **16:** 19–24.

Roberts RG, Flannery TF, Ayliffe LK, Yoshida H, Olley JM, Prideaux GJ, Laslett GM, Baynes A, Smith MA, Jones R. 2001. New ages for the last Australian megafauna: continent-wide extinction about 46,000 years ago. *Science* **292:** 1888–1892.

Roberts RG, Jones R, Smith MA. 1990. Thermoluminescence dating of a 50,000-year-old human occupation site in northern Australia. *Nature* **345:** 153–156.

Roberts RG, Jones R, Spooner NA, Head MJ, Murray AS, Smith MA. 1994. The human colonisation of Australia: optical dates of 53,000 and 60,000 years bracket human arrival at Deaf Adder Gorge, Northern Territory. *Quaternary Science Reviews* **13:** 575–583.

Roberts RG, Brook BW. 2010. Turning back the clock on the extinction of megafauna in Australia. *Quaternary Science Reviews* **29:** 593–595.

Rule S, Brook BW, Haberle SG, Turney CSM, Kershaw AP, Johnson CN. 2012. The Aftermath of Megafaunal Extinction: Ecosystem Transformation in Pleistocene Australia. *Science* **335:** 1483–1486.

Russell-Smith J, Stanton PJ, Edwards AC, Whitehead PJ. 2004a. Rain forest invasion of eucalypt-dominated woodland savanna, Iron Range, north-eastern Australia: II. Rates of landscape change. *Journal of Biogeography* **31:** 1305–1316.

Russell-Smith J, Stanton PJ, Whitehead PJ, Edwards A. 2004b. Rain forest invasion of eucalypt-dominated woodland savanna, iron range, north-eastern Australia: I. Successional processes. *Journal of Biogeography* **31:** 1293–1303.

Russell-Smith J, Lucas D, Gapindi M, Gunbunuka B, Kapirigi N, Namingum G, Lucas K, Giuliani P, Chaloupka G. 1997. Aboriginal resource utilization and fire management practice in western Arnhem Land, monsoonal northern Australia: notes for prehistory, lessons for the future. *Human Ecology* **25:** 159–195.

Russell-Smith J, Price OF, Murphy BP. 2010. Managing the matrix: decadal responses of eucalypt-dominated savanna to ambient fire regimes. *Ecological Applications* **20:** 1615–1632.

Sankaran M, Hanan NP, Scholes RJ, Ratnam J, Augustine DJ, Cade BS, Gignoux J, Higgins SI, Le Roux X, Ludwig F. 2005. Determinants of woody cover in African savannas. *Nature* **438:** 846–849.

Scott K, Setterfield SA, Douglas MM, Parr CL, Schatz J, Andersen AN. 2012. Does long-term fire exclusion in an Australian tropical savanna result in a biome shift? A test using the reintroduction of fire. *Austral Ecology* **37:** 693–711.

Sheil, D, Murdiyarso, D. 2009. How forests attract their rain: an examination of a new hypothesis, *Bioscience*, **59**: 341–347.

Shulmeister J. 1992. A Holocene pollen record from lowland tropical Australia. *The Holocene* **2:** 107–116.

Silcock JL, Piddocke TP, Fensham RJ. 2013. Illuminating the dawn of pastoralism: Evaluating the record of European explorers to inform landscape change. *Biological Conservation* **159**: 321-331.

Slack MJ, Fullagar RLK, Field JH, Border A. 2004. New Pleistocene ages for backed artefact technology in Australia. *Archaeology in Oceania* **39:** 131–137.

Smith MA, Williams AN, Turney CSM, Cupper ML. 2008. Human-environment interactions in Australian drylands: exploratory time-series analysis of archaeological records. *Holocene* **18:** 389–401.

Spracklen DV, Arnold SR, Taylor CM. 2012. Observations of increased tropical rainfall preceded by air passage over forests. *Nature* **489:** 282–U127.

Staver AC, Archibald S, Levin SA. 2011. The global extent and determinants of savanna and forest as alternative biome states. *Science* **334:** 230–232.

Staver AC, Bond WJ, Stock WD, Van Rensburg SJ, Waldram MS. 2009. Browsing and fire interact to suppress tree density in an African savanna. *Ecological Applications* **19:** 1909–1919.

Stephenson P. 1989. East Australian volcanic geology: Northern Queensland. *Intraplate volcanism: in eastern Australia and New Zealand*, Johnson RW (eds). Cambridge University Press: Cambridge; 89-97.

Summerhayes GR, Leavesley M, Fairbairn A, Mandui H, Field J, Ford A, Fullagar R. 2010. Human adaptation and plant use in highland New Guinea 49,000 to 44,000 years ago. *Science* **330:** 78–81.

Surovell TA, Grund BS. 2012. The Associational Critique of Quaternary Overkill and Why It is Largely Irrelevant to the Extinction Debate. *American Antiquity* **77:** 672–687.

Tanentzap AJ, Coomes DA. 2012. Carbon storage in terrestrial ecosystems: do browsing and grazing herbivores matter? *Biological Reviews* **87:** 72–94.

Thorne A, Grün R, Mortimer G, Spooner N, Simpson JJ, McCulloch MT, Taylor L, Curnoe D. 1999. Australia's oldest human remains: age of the Lake Mungo 3 skeleton. *Journal of Human Evolution* **36:** 591–612.

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

Turney CSM, Bird MI, Fifield LK, Roberts RG, Smith M, Dortch CE, Grün R, Lawson E, Ayliffe LK, Miller GH. 2001a. Early human occupation at Devil's Lair, southwestern Australia 50,000 years ago. *Quaternary Research* **55:** 3–13.

Turney CSM *et al*. 2008. Late-surviving megafauna in Tasmania, Australia, implicate human involvement in their extinction. *Proceedings of the National Academy of Sciences, USA* **105:** 12150–12153.

Turney CSM, Kershaw AP, Moss P, Bird MI, Fifield LK, Cresswell RG, Santos GM, Di T, ML, Hausladen PA, Zhou Y. 2001b. Redating the onset of burning at Lynch's Crater (North Queensland): implications for human settlement in Australia. *Journal of Quaternary Science* **16:** 767–771.

van der Kaars S, De Deckker P. 2002. A Late Quaternary pollen record from deep-sea core Fr10/95, GC17 offshore Cape Range Peninsula, northwestern Western Australia. *Review of Palaeobotany and Palynology* **120:** 17–39.

van der Kaars S, Wang X, Kershaw P, Guichard F, Setiabudi DA. 2000. A late Quaternary palaeoecological record from the Banda Sea, Indonesia: patterns of vegetation, climate and biomass burning in Indonesia and northern Australia. *Palaeogeography, Palaeoclimatology, Palaeoecology* **155:** 135–153.

Veth P, Smith M, Bowler J, Fitzsimmons K, Williams A, Hiscock P. 2009. Excavations at Parnkupirti, Lake Gregory, Great Sandy Desert: OSL ages for occupation before the Last Glacial Maximum. *Australian Archaeology* **69:** 1–10.

Wang X, van der Kaars S, Kershaw P, Bird M, Jansen F. 1999. A record of fire, vegetation and climate through the last three glacial cycles from Lombok Ridge core G6-4, eastern Indian Ocean, Indonesia. *Palaeogeography, Palaeoclimatology, Palaeoecology* **147:** 241–256.

Webb S. 2008. Megafauna demography and late Quaternary climatic change in Australia: A predisposition to extinction. *Boreas* **37:** 329–345.

Weninger B, Jöris O. 2008. A ^{14}C age calibration curve for the last 60 ka: the Greenland-Hulu U/Th timescale and its impact on understanding the Middle to Upper Paleolithic transition in Western Eurasia. *Journal of Human Evolution* **55:** 772–781.

Whitehead PW, Stephenson PJ, McDougall I, Hopkins MS, Grahams AW, Collerson KD, Johnson DP. 2007. Temporal development of the Atherton Basalt Province, north Queensland. *Australian Journal of Earth Sciences* **54:** 691–709.

Williams AN. 2012. The use of summed radiocarbon probability distributions in archaeology: a review of methods. *Journal of Archaeological Science* **39:** 578–589.

Woinarski JCZ, Risler J, Kean L. 2004. Response of vegetation and vertebrate fauna to 23 years of fire exclusion in a tropical Eucalyptus open forest, Northern Territory, Australia. *Austral Ecology* **29:** 156–176.

Wroe S, Field J. 2006. A review of the evidence for a human role in the extinction of Australian megafauna and an alternative interpretation. *Quaternary Science Reviews* **25:** 2692–2703.

Wurster CM, Lloyd J, Goodrick I, Saiz G, Bird MI. 2012. Quantifying the abundance and stable isotope composition of pyrogenic carbon using hydrogen pyrolysis. *Rapid Communications in Mass Spectrometry* **26:** 2690–2696.

Wyrwoll KH, Miller GH. 2001. Initiation of the Australian summer monsoon 14,000 years ago. *Quaternary International* **83:** 119–128.

Yates CP, Edwards AC, Russell-Smith J. 2008. Big fires and their ecological impacts in Australian savannas: size and frequency matters. *International Journal of Wildland Fire* **17:** 768–781.

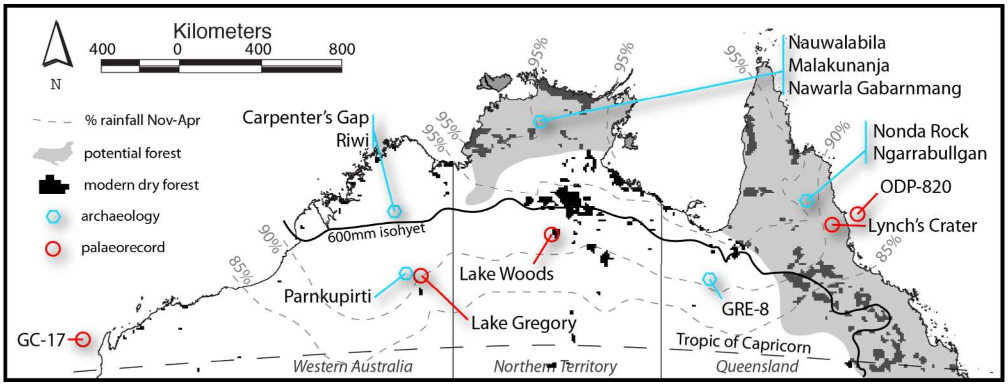
Yibarbuk D, Whitehead PJ, Russell ‐ Smith J, Jackson D, Godjuwa C, Fisher A, Cooke P, Choquenot D, Bowman D. 2001. Fire ecology and Aboriginal land management in central Arnhem Land, northern Australia: a tradition of ecosystem management. *Journal of Biogeography* **28:** 325–343.

Zhang L, Dawes, WR, Walker GW. 2001. Response of mean annual evapotranspiration to vegetation changes at the catchment scale. *Water Resources Research* **37:** 701-708.

Figure 1: Modern Tropical Australia. Percent of total annual precipitation falling between November and April shown as grey dashed lines (Bowman, 2002) along with the 600mm isohyet shown as a solid line. Modern dry forest area taken from Miles *et al.* (2006) based on 10km grid cells containing a minimum of 40% forest area. Light shading represents potential modern forest area based on the modelling of Bond and Keeley (2005). Also shown are archaeological sites and palaeoenvironmental sites mentioned in the text (locations of marine cores MD98-2167, SHI-9014 and G6-4, all from the seas off northwest Australia, are not shown).

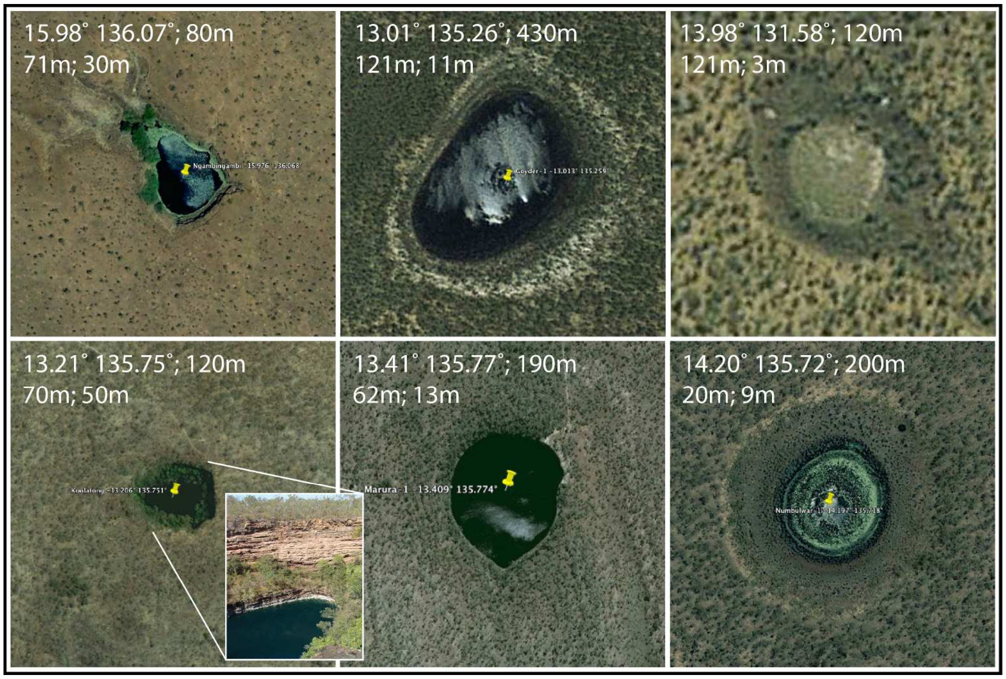
Figure 2: Rock art thought to be a representation of *Genyornis newtoni* from Jawoyn country, western Arnhemland (see Gunn *et al.* 2011 for discussion). Credit: Ben Gunn and Jawoyn Association.

Figure 3: Example sinkholes in the Northern Territory. Note that scale is variable. (in white: latitude ˚S, longitude ˚E; sinkhole maximum width; land surface elevation AMSL; vertical distance from land surface to water surface).



184x70mm (300 x 300 DPI)

199x132mm (300 x 300 DPI)



230x154mm (300 x 300 DPI)