

RESEARCH ARTICLE

Holocene climate–fire–vegetation feedbacks in tropical savannas: Insights from the Marura sinkhole, East Arnhem Land, northern Australia

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Abstract

Aims: Informed management of savanna systems depends on understanding determinates of composition, structure and function, particularly in relation to woody-plant components. This understanding needs to be regionally based, both past and present. In this study, Holocene plant patterns are explored at a site within the eucalypt savannas of northern Australia. Australian savannas are the least developed globally and uniquely placed to track ecological change.

Location: Northern Territory, Australia.

Methods: Palynological analyses were undertaken on a 5-m sediment core, spanning the last 10,700 calendar years. Pollen was categorised to capture vegetation type, classified further according to plant function and/or environmental response. Detrended Correspondence Analysis was used to quantify ecological dissimilarities through time.

Results: At the Pleistocene transition, grasses were abundant then declined and remained low relative to increased woody cover from the mid-late Holocene. Savanna composition gradually transitioned from *Corymbia* to *Eucalyptus* dominance until significantly disturbed by a phase of repeated, extreme climate events. Highest non-savanna variability in terrestrial and wetland plant types formed mixed vegetation communities through the mid-Holocene.

Conclusions: Savannas are not homogeneous but the product of plant changes in multiple dimensions. In the Northern Territory, dynamic though restricted non-eucalypt shifts are embedded within larger, slower eucalypt change processes. Primary climate–vegetation relationships determine the long-term fire regime. The role of large but infrequent disturbance events in maintaining savanna diversity are significant, in degrees of impact on tree–grass turnover, its form and the extent of

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vegetation recovery. People's landscape interactions were found to be interwoven within this feedback hierarchy.

KEYWORDS

charcoal, disturbance events, fire-regime, late quaternary, monsoon, northern Australia, pollen, tree:grass

1 | INTRODUCTION

Tropical savannas are defined by a continuous C_4 grass layer, with a discontinuous stratum of disturbance-tolerant woody species (Lehmann et al., 2014). They are highly dynamic, complex, and rich in biota (Williams et al., 2017), though commonly perceived as a homogeneous entity (Lehmann et al., 2014). The world's three largest savanna estates are located in the wet-dry tropics of Australia, South America and Africa (Anderson & Vasconcelos, 2022). Although structurally and physiognomically similar between continents, tropical savannas are compositionally and functionally different between regions (Ratnam et al., 2020). Lehmann et al. (2014, p. 551) refer to global savanna vegetation as 'analogous but not identical', particularly regarding woody strata, whose distribution and cover varies greatly in space and time. No one global framework encapsulates tropical savanna woody dynamics (Doughty et al., 2016). Lehmann et al. (2008) make the case for regionalism in investigating environmental controls and associated woody plant response. Hutley and Setterfield (2019) link savanna plant dynamics and spatial heterogeneity to landscape scale histories. Savanna dynamics may be considered between continents, but ultimately more localised analyses underpin plant patterns, including more-or-less wooded states. Tropical savannas are gaining international prominence as an endangered biome (Tng, 2019) with 'regional lessons for global challenges' recommended as the way forward by Russell-Smith et al. (2003, p. 7).

In Australia, tropical savannas occupy the northernmost third of the continent. They occur across the monsoonal biogeographic regions of the Kimberley (north Western Australia), the Top End Northern Territory (NT), and Queensland's Gulf Country-Cape York Peninsula (mapped, the vegetation and phytogeography compared by Wannan, 2014). From a global perspective, Australian savannas are relatively intact ecologically (Bowman et al., 2010; Lewis et al., 2021; Woinarski et al., 2007). In turn, the NT contains the majority unfragmented savanna in good ecological condition, thus holding significance for the conservation of savanna environments more generally (Woinarski, 2004). Australian savannas allow for analyses of landscape heterogeneity and nature of the vegetation as a complex system composed of subsystems (Gillson, 2004). Given Australian savannas are little modified, they hold greater capacity to record plant community-level assembly and reorganisation over time.

Comprehensive records of past vegetation change are scarce for the NT. Lehmann et al. (2008) explicitly refer to the NT savannas

as having remained an ecological conundrum because of a paucity of palaeoecological studies. While the immediate effects of local changes to disturbance regimes on woody-grass cover and plant diversity are largely understood, little NT data exists on patterns of change at landscape and regional scales, as well as over multiple time-scales (Lehmann et al., 2008 and references therein). The age and geological stability of the north Australian landscape, together with seasonal contrasts in rainfall, have created poor conditions for sediment accumulation and organic preservation (Bowman et al., 2010). This has restricted the distribution of sites suitable for late Quaternary research. Sinkholes, however, occur in the Top End NT and offer permanently inundated sites of sediment infill. Entire, well-stratified sediments accumulate in a sinkhole's closed lake, which is typically deep relative to its catchment area (Twidale, 1987).

This paper makes use of the Marura sinkhole for a palaeoecological savanna study in the East Arnhem Land region of the NT. Long-term environmental data are missing from Arnhem Land and are needed to understand fully the underlying environmental drivers that come into play in NT savanna dynamics (including resilience and stability, Hutley & Setterfield, 2019; Ma et al., 2013), and thereby contextualise modern observations (Rull, 2012; Rull et al., 2013). How disturbance agents (herbivory, fire, and stochastic events such as cyclones), soils, and climate (all operating at different scales of influence, Lehmann et al., 2008) interact to influence tree-grass interactions and determine savanna floristics and productivity (Hutley & Setterfield, 2019) have been long-standing questions in Australia (Ma et al., 2013; Williams et al., 2017) and internationally (Ratnam et al., 2020; Sankaran et al., 2008). Owing to global interest in tropical savanna woody variability (Doughty et al., 2016; Ratnam et al., 2020; Stevens et al., 2016), our study seeks to understand tree component dynamics and structural variation within the eucalypt savannas of northeastern NT. These eucalypt savannas are also the matrix within which other tropical ecosystems occur (monsoonal forest, vine thicket, shrubland, floodplain and riverine complexes; Williams & Douglas, 1995, 2017). Past non-eucalypt and wetland plant assemblages are therefore also of interest, as an aid to recognising long-term diversity patterning in savanna environments, while exploring what factors may separate savanna from other vegetation types.

The emphasis in this paper is on palaeoecological detail. Discussion of the results is divided into two parts: (i) Holocene wetland-associated habitats and (ii) terrestrial ecosystems at and around the site. Only by gaining a detailed palaeoecological insight from within the north NT, can comparison between the

NT and other north Australian savanna biomes (Gulf–Cape York Peninsula, Queensland, and the Kimberley–Western Australia) begin, thereby enabling access to answers to a finer scale of questions in relation to ecological dynamics across tropical Australia, ultimately enabling comparison to the drivers of savanna dynamics on other continents.

2 | SITE & ENVIRONMENT

2.1 | Landscape setting

The Marura sinkhole (13.409°S, 135.774°E, Figure 1) is one of several sinkhole features within the Central Arnhem bioregion of the NT. This bioregion stretches from the Arnhem Plateau to the Gulf of Carpentaria and covers the McArthur Basin geological unit (Ahmad et al., 2013). Cretaceous sandstones–siltstones, lateritised Tertiary material, and yellow earthy sands dominate. Elevation ranges from 400m in the west on the Arnhem Plateau to sea level in the east, and most of the region is below 200m (Baker et al., 2005). Marura sits at 50m a.s.l., 10 km west of Blue Mud Bay. The site is in an overlapping zone between the Laynhapuy and South East Arnhem Land Indigenous Protected Areas (IPAs), both divided into estates, each defined by the sacred sites and songlines of the Yolŋu (Yugul or Yolngu) Traditional Owners (Gambold, 2015; LHAC, 2017). Both IPAs form part of the Arnhem Land Fire Abatement Project area (ALFA NT Ltd, <https://www.alfant.com.au/>).

The sinkhole itself is circular, 190m in diameter with a water depth of 11.5 m and overflows to the east at a water depth of ~11.9 m. Marura's catchment area is small, ~0.25km² (Figure 2). The terrain slopes at a greater angle (5%–10%) along the southern to western edges of the site. To the northeast, where the lake can

overflow, the slope is very low-gradient and nowhere are the slopes so steep as to restrict aerial input of pollen and charcoal.

2.2 | Climate

Present-day regional climate is tropical monsoonal (Australian Summer Monsoon, ASM). Inter-annual variability is influenced by the El Niño–Southern Oscillation (ENSO), with monsoon onset later and rainfall below average during El Niño years. Monsoonal winds are west to northwesterly, whereas east to southeasterly in the dry season (Charles et al., 2016). Temperatures are uniformly high (annual average 32°C) and mean annual rainfall is 1252 mm. The region is subject to tropical cyclones, with data in the NT northern region from 1969 to 2019 recording 22 cyclone landfalls within 100km of the site (BoM, 2020).

2.3 | Vegetation and fire

Eucalypt forests and woodlands form the major element of the northern half of the NT. These eucalypt formations include extensive floristic and structural variation, though generally gradational and developed over very large distances. *Eucalyptus miniata* and *E. tetradonta* open-forest with a *Sorghum* grassland understorey is most characteristic (Woinarski, 2004). Various non-eucalypt tree–shrub genera may occur in the upper–mid storeys (Baker et al., 2005). In the Marura catchment, *Callitrix*, *Calytrix*, *Erythrophleum* and *Petalostigma* were observed. Relative to the extent of eucalypt vegetation, the north NT includes small areas of *Melaleuca* forest and woodland, typically on seasonally waterlogged or inundated areas. Similarly, a monsoonal forest network

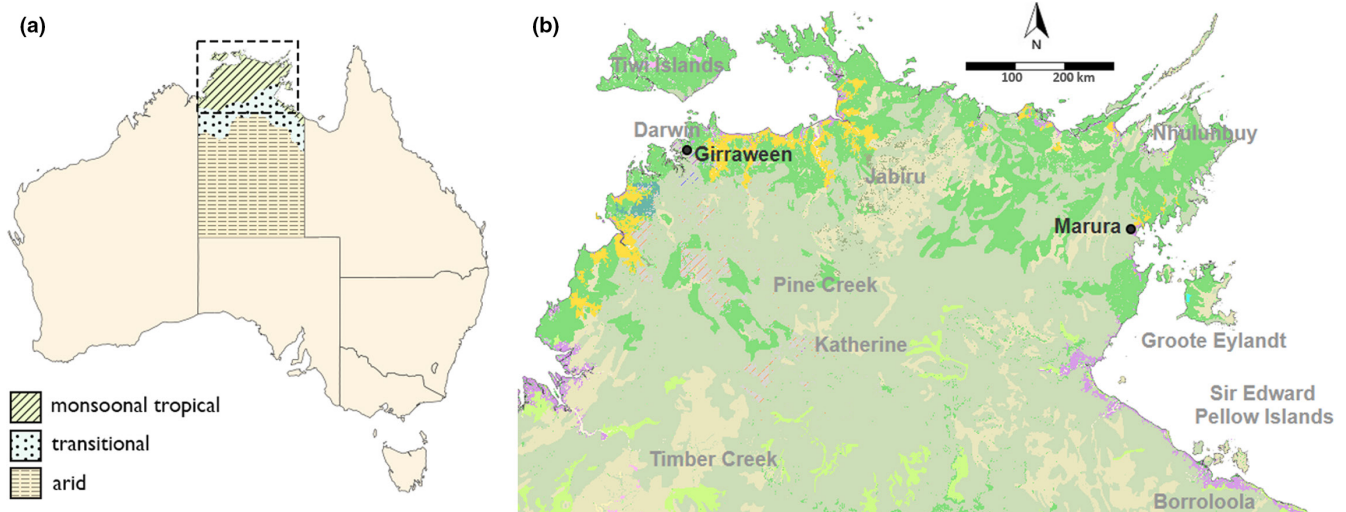


FIGURE 1 (a) Broad climate zones for the Northern Territory displayed north-to-south as monsoonal tropical, transitional and arid, and (b) location of the Marura study site in relation to major townships, places mentioned in the text, the Girraween sinkhole study (Rowe et al., 2019), and regional vegetation (after natural resource maps NT incorporating the National Vegetation Information System, <https://nrmmaps.nt.gov.au/>).

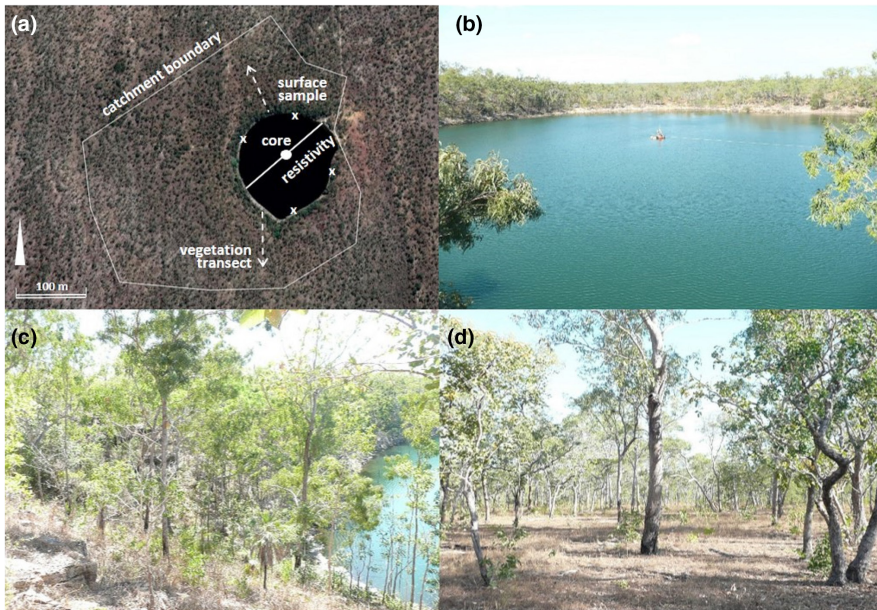


FIGURE 2 The Marura study site: (a) satellite view (Google earth) showing fieldwork locations and approximate sinkhole catchment boundary, (b) sinkhole and waterbody view looking northeast (the coring raft shown), (c) example vegetation occupying sinkhole slopes, and (d) example surrounding savanna-woodland vegetation.

occurs mainly in the north, currently highly restricted in area (Baker et al., 2005; Woinarski, 2004). Marura's immediate sloping sinkhole terrain includes *Melaleuca*, with clustered *Pandanus*, *Persoonia*, *Acacia*, palm types and unidentified lianas. No aquatic plants (floating or submerged) were recorded during fieldwork. A thin, very patchy fringe of Cyperaceae lined the waterbody, mixed with taxa such as *Eriocaulon*.

A fire history spanning 2000–2019 based on the Northern Australian Fire Information (NAFI) data set is presented in Rehn et al. (2021). Across a ca. 10-km² area surrounding Marura, fire frequency averages 2–4 years (NAFI, 2020), typical of the region (Russell-Smith & Yates, 2007). No recent fire events were evident while visiting the site.

3 | METHODS

3.1 | Sedimentary collection and analysis

An electrical resistivity survey of the sinkhole was conducted to help identify areas of low-resistivity sediment, interpreted as lacustrine sediment, and to identify the thickest sequence for coring. Marura was then cored using a floating platform with hydraulic coring rig. A 5.85-m core in 1.0-m sections was collected to bedrock. Each section was sealed in its plastic core liner tube for transport. Vegetation surveys were undertaken along transect lines extending northwest (300 m) and south (200 m distance).

3.2 | Palynological techniques and analysis

Core sections were split in half, described and subsampled at 5 cm intervals. Palynological preparations are detailed in Rowe

et al. (2019, 2021) as per sites elsewhere in the NT). Chemical treatments included Na₄P₂O₇, KOH, HCl, acetolysis and C₂H₅OH washes (Bennett and Willis, 2002). Sieving took place at 7 μm and 125 μm. A *Lycopodium* spike (Lund University batch 3862) was added prior to preparations to determine concentrations of pollen and microcharcoal particles. Final residues were mounted in glycerol. Pollen counts targeted 200 grains (terrestrial and aquatic) per sample, a high total for northern Australian sediments.

Pollen identification utilised palynological reference collections held at James Cook University, and the Australasian Pollen and Spore Atlas (<http://apsa.anu.edu.au/>) online resource. FloraNT (eflora.nt.gov.au) provided insight into plant ecologies. Pollen was divided into groups to capture plant form and function and/or vegetation type. Rowe et al. (2019, 2021) provide additional discussions on these pollen allocations, where these serve to help evaluate fire tolerances as well as assess wet-dry habitat continuums. Microcharcoal particles (black, opaque, angular, >10–125 μm in length) were counted simultaneously with pollen as an indicator of landscape fire (Whitlock & Larsen, 2002).

All data were plotted using TGView (Grimm, 2004). A dendrogram was produced by CONISS and based on constrained cluster analyses as a method for quantitative definition of stratigraphic zones (Grimm, 1987, 2004). Detrended Correspondence Analysis (DCA), provided additional interpretative guidelines (Birks, 2007; Correa-Metrio et al., 2014; Urrego et al., 2009). Square-root transformation of the data was applied, first-axis scores plotted chronologically, and the Euclidean distance between sample scores calculated to derive their ecological dissimilarity. (Correa-Metrio et al., 2014; Urrego et al., 2009). Aquatics and sedge group pollen were excluded from the DCA to avoid masking dryland vegetation changes and because these taxa are considered heavily influenced by the physical nature of the sinkhole itself. All DCA data analyses were performed using R (Venables et al., 2003), notably the *vegan* package (Oksanen

TABLE 1 Lead-210 sample results used to develop the age model presented (table adapted from Rehn et al., 2021; age model graphed within Appendix S1)

Depth (cm)	Lab. no.	Method	Material	Unsupported Pb ²¹⁰ decay (corrected to Oct. 17)	Calculated Constant Initial Concentration (CIC) ages (years before collection)	Mean calibrated age from age-depth model (cal BP)
0-1	U526	²¹⁰ Pb	sediment organics	25 ± 7		
2-3	U527	²¹⁰ Pb	sediment organics	31 ± 5		
6-7	U528	²¹⁰ Pb	sediment organics	31 ± 5		
10-11	U087	²¹⁰ Pb	sediment organics	35 ± 5	47 ± 14	-12
15-16	U088	²¹⁰ Pb	sediment organics	24 ± 4	69 ± 21	13
20-21	U089	²¹⁰ Pb	sediment organics	9 ± 5	91 ± 28	55

Mixing across these depths and representing since ~1950 CE (0 cal BP)

et al., 2009). Pollen rarefaction analysis (n = 150) was undertaken according to Heck et al. (2003).

3.3 | Chronology

Six samples were taken from the uppermost 20 cm of sediment for lead-210 dating by alpha spectrometry. Below this depth, nine samples were collected for carbon-14 accelerator mass spectrometry (AMS) measurement, pre-treated using the ABA (Acid-Base-Acid) method. All lead-210 and radiocarbon sample preparation and analysis were undertaken at the Australian Nuclear Science and Technology Organization (ANSTO). Age reporting follows Rehn et al. (2021) for consistency. Lead-210 (converted to calendar years BP) and radiocarbon dates (calibrated to cal BP using SHCal20, Hogg et al., 2020) were combined to form a Bayesian age-depth model using the *rBacon* package within R (Rehn et al., 2021).

4 | RESULTS

4.1 | Chronology and stratigraphy

Table 1 shows the decreasing abundance with depth for unsupported lead-210 between 10 and 20 cm. Sediments above 10 cm display mixing (assigned as modern) and the samples below 20 cm reach background lead-210 levels. Samples analysed for radiocarbon show monotonically increasing age with depth (Table 2). The age-depth model (Appendix S1) indicates a steady sediment accumulation rate with final modelled age 10,705 calibrated years before present (cal BP). Sediments were visually homogeneous down-core, consisting entirely of black (7.5YR - 2.5/1) peats gradually increasing in clay content with depth. Sediment resistivity and monitoring of lake water parameters (depth, temperature and conductivity) are presented in Appendix S2.

4.2 | Pollen and microcharcoal analysis

Marura's fossil palynological record is summarised in Figure 3 and Table 3. The complete pollen diagram, as well as detailed data descriptions, are provided in Appendices S3 and S4. In total, 83 pollen taxa were identified, divided into four principal pollen zones and two subzones. The four lowermost samples in the core [477-462 cm below sediment surface (bss), 10.48-10.18 ka cal BP] were largely devoid of identifiable pollen, with poor charcoal recovery. These samples have not been included in Table 3 or Figure 3. In the same lowermost unit, high densities of sponge spicules were encountered.

Taxa associated with open canopy cover and/or drier conditions achieved higher DCA axis 1 scores (Figure 3). Such taxa were prominent before ca. 8.36 ka cal BP. Sample scores decline gradually after this point to show increasingly closed cover, interrupted between 2.58 and 1.92 ka cal BP with a return series of spiked positive

TABLE 2 Radiocarbon accelerator mass spectrometry (AMS) sample results used to develop the age model presented (table adapted from Rehn et al., 2021; age model graphed within Appendix S1)

Depth (cm)	Lab. no.	Method (AMS)	Material	$\delta^{13}\text{C}\text{‰}$ (± 0.2)	^{14}C age (years BP)	Mean calibrated age from age-depth model (cal BP)
44–45	OZW494	^{14}C	sediment organics	-23.7 ± 0.1	1105 ± 30	907
72–73	OZW495	^{14}C	sediment organics	-21.0 ± 0.1	1360 ± 35	1250
118–119	OZW496	^{14}C	sediment organics	-24.0 ± 0.2	2055 ± 35	1991
158–159	OZW497	^{14}C	sediment organics	-24.1 ± 0.1	2555 ± 40	2633
204–205	OZW498	^{14}C	sediment organics	-25.2 ± 0.1	3535 ± 35	3781
244–245	OZW499	^{14}C	sediment organics	-25.8 ± 0.3	4155 ± 50	4690
285–289	Wk-51084	^{14}C	sediment organics	-26.2 ± 0.4	5076 ± 25	5763
325–326	Wk-51085	^{14}C	sediment organics	-24.6 ± 0.4	5668 ± 26	6430
407–408	Wk-51086	^{14}C	sediment organics	-22.2 ± 0.4	8186 ± 28	9038

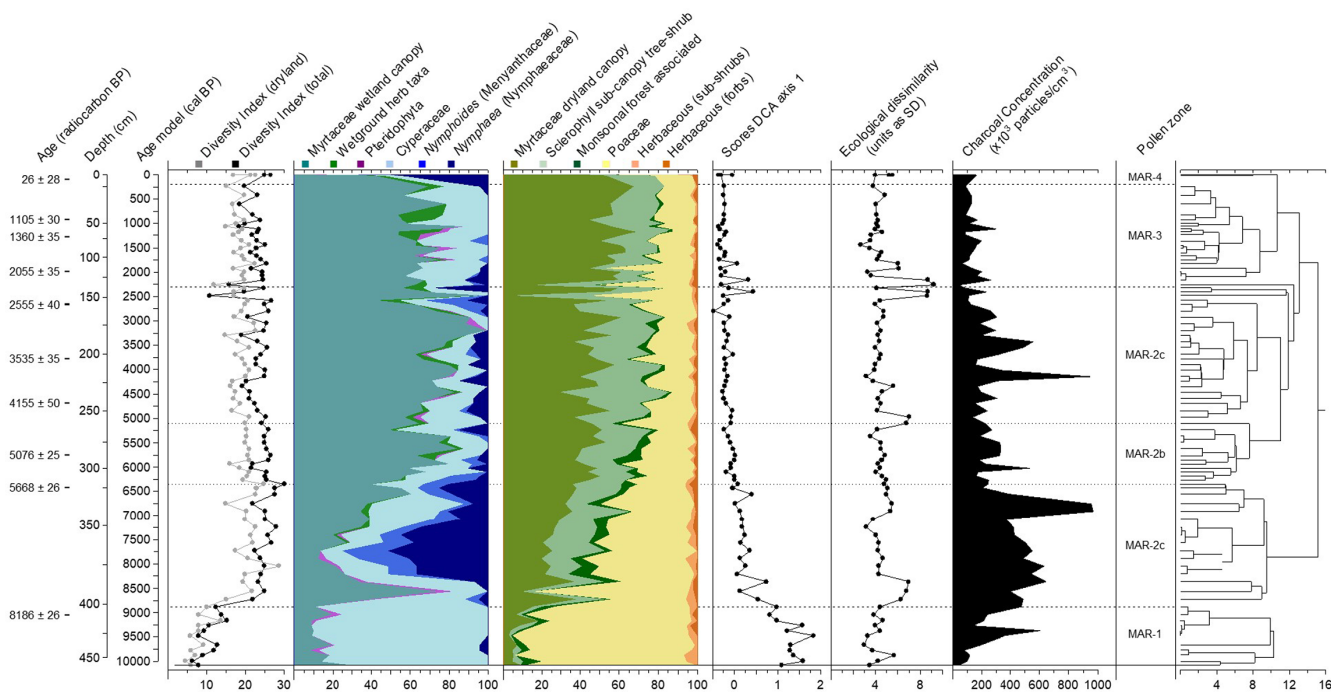


FIGURE 3 Marura percentage pollen diagram. Summary data include diversity indices, pollen vegetation group summaries (wetland pollen-plant types, terrestrial pollen-plant types), Detrended Correspondence Analysis (DCA) axis 1 scores with ecological change metrics, micro-charcoal. All percentages are derived from the total pollen sum including spores. Data are plotted against depth, radiocarbon results, and calibrated age range. Appendices S3 and S4 present the complete data set.

scores. The most prominent shift in ecosystem structure occurred between 9.56 and 8.72 kcal BP (Figure 3). Periods of greatest palynological dissimilarity span 8.56–7.4 kcal BP, 5.1–4.23 kcal BP and foremost 2.58–1.92 kcal BP. A series of lower ecological distance scores run between each peak, identifying more homogeneous periods, of relative ecological stability (Figure 3).

5 | INTERPRETATION AND DISCUSSION

5.1 | Wetland ecological reconstruction

From 10.71 kcal BP, the chemical and/or physical characteristics of the sinkhole floor were suited to the accumulation of freshwater



TABLE 3 Marura pollen zones as determined by CONISS (Grimm, 1987, 2004)

Zone division	Pollen assemblage
MAR-1 (457–402 cm bss, 10.08–8.88 kcal BP)	Highest Poaceae proportions and significant Cyperaceae representation. Woody categories at their lowest values for the sequence, largely comprised of undefined canopy eucalypts. Sclerophyll subcanopy types diversify in upper samples, <i>Timonius</i> combines with emerging <i>Syzygium</i> pollen in the monsoonal forest group. Seven herbaceous pollen types (minor) are recorded
MAR-2 (402–130 cm bss, 8.88–2.20 kcal BP)	Marked transition from MAR-1 in non-woody to woody pollen. Continual rise in dryland woody proportions and proportional representation of non-eucalypts to eucalypts woody wetland representatives increase, as one part of a prominent zonal sequence in Cyperaceae to aquatic to <i>Melaleuca</i> pollen. Poaceae and <i>Cyperus</i> progressively less represented as subzone 2a transitions into 2b and again into 2c
MAR-2a (402–320 cm bss, 8.88–6.35 kcal. BP)	Poaceae values drop and Cyperaceae abruptly declines. Cyperaceae loss followed by rise to peak aquatics (<i>Nymphaea</i> , <i>Nymphoides</i>), which then tail off into minor representation until MAR-4. All eucalypt pollen increase, with greater representation of <i>Corymbia</i> . Sclerophyll subcanopy taxa expand and monsoonal forest types increase (in proportion and composition). The herbaceous group does not vary in total percentage representation but diversifies in pollen types
MAR-2b (320–260 cm bss, 6.35–5.10 kcal. BP)	Pollen patterns initiated in MAR-2a are consolidated in MAR-2b. As part of an increase in Myrtaceae pollen, <i>Eucalyptus</i> types occur in proportions that are more equal to <i>Corymbia</i> . Additional minor pollen values in subcanopy taxa appear. Some herbaceous types are lost
MAR-2c (260–130 cm bss, 5.10–2.20 kcal. BP)	The majority of pollen-plant groups show relative consistency in MAR-2c. Similar proportions in <i>Corymbia</i> and <i>Eucalyptus</i> pollen are maintained. Greatest change from MAR-2b occurs in non-eucalypt subcanopy taxa (e.g. <i>Callitris</i> rise); as a group, pollen proportions increase and/or compositions switch. Across the zone 2–3 boundary, a phase of prominent data seesawing occurs
MAR-3 (130–20 cm bss, 2.20–0.16 cal BP)	High Poaceae samples occur at 2.48, 2.25 and 1.92 kcal BP. In Myrtaceae tree pollen, <i>Eucalyptus</i> values consistently surpass <i>Corymbia</i> . Discontinuation in many non-eucalypt pollen types is recorded; similarly, a decline in herb types occurs. <i>Callitris</i> values are less than their subzone MAR-2c peak. <i>Melaleuca</i> and <i>Lophostemmon</i> reduce whereas <i>Cyperus</i> sedge values regain slightly
MAR-4 (20–0 cm bss, 0.16 kcal BP to present)	Marked by reversals in mid- to late-Holocene trends; a decline in dryland Myrtaceous pollen occurs with increase in Poaceae. <i>Eucalyptus</i> types remain at a higher fraction than <i>Corymbia</i> . Non-eucalypt pollen is heavily sclerophyllous. Monsoonal forest pollen is near absent
Charcoal concentration and diversity indexes	
A rise-and-fall charcoal pattern occurs throughout, but overall charcoal concentrations decline toward the surface. Raised and sustained inputs of charcoal occur in subzone MAR-2a. Charcoal concentrations fall into subzone MAR-2b, these values are maintained but with variable high points through subzone MAR-2c, and then decrease further through zone MAR-3. In upper samples toward the present day, charcoal increases. Notable peaks in charcoal concentrations occur at 6.83, 4.14 and 3.42 kcal BP, and to a lesser extent 6.01 and 1.12 kcal BP. Pollen diversity indexes show marked difference between zone MAR-1 and the remainder of the record. These values are initially much lower	

Note: Descriptions of the main pollen and micro-charcoal trends are included. Appendices S3 and S4 provide the full dataset (bss refers to below sediment surface).

sponge spicules (formed from silicon dioxide and less susceptible to oxidation; Frost, 2001). Low-productivity, low-energy freshwater environments have been linked to high spicule concentrations (Bush et al., 1992; Owen et al., 1982), also associated with still water ponding and lacking siltation (Harrison, 1988; Parolin et al., 2007). Stanisc's (1987) Arnhem Land freshwater sponge survey describes common specimens as occupying shallow waters on varied substrates (e.g. rocks, logs). Alkaline conditions were also observed as favouring sponge growth (Stanisc, 1987), a pH range detrimental for the preservation of pollen grains (Moore et al., 1991).

Holocene water body development progressed from a swampy wetland, to shallow lake, to relatively stable permanent deep lake system. *Cyperus* (foremost) and *Eleocharis/Schoenus* swamp growth initiated (c. 10ka cal BP) and expanded (9.47–8.88 kcal BP). These taxa characterise hydrological regimes involving periodic inundation or waterlogging, classified as 'fluctuation-tolerant emergents'

and 'drivers of lake ecology' (Catford et al., 2017, p. 495). As these plants grow, occupy space, and decompose, they retain sediment, generate nutrients, and retard water flow (including evaporation). Waterlogging and accumulation of plant detritus can produce small dams which further modify site hydrology in favour of sediment formation and water retention (Catford et al., 2017; Moseley, 2018). Thus Marura in the early Holocene presented an exposed, low-productivity sinkhole floor with *Cyperaceae* cover promoting wetland developmental processes. This is viewed as a plant-based example of Twidale's (Twidale, 1987) modern NT sinkhole observations, where a propensity to site sealing, enabling lake filling, was observed via silts from lateritic A-horizons washed into the sinkhole depressions.

From waterlogged swamp sediments, to open permanent surface water, sedge presence declined from 8.88 kcal BP as waterlilies (*Nymphaea*, *Nymphoides*) appeared and increased from 7.88 to 6.91 kcal BP. Waterlilies are termed 'responders' – plants that

prefer a certain water depth, rather than tolerate variable water levels. (Catford et al., 2017). *Nymphaea*'s growth range (2.0–2.5 m depth, Cowie et al., 2000) indicates the extent of water accumulation from the early Holocene, the sedges drowned out and forced into a fringe zone. After 8.88 kcal BP, *Melaleuca* (Myrtaceae wetland canopy pollen), *Lophostemon* and palms (Arecaceae) suggest a mixed woody community grew to occupy the sinkhole slopes.

After 6.35 kcal BP sedges were further restricted and waterlilies diminished; mid-Holocene water levels continued to increase beyond the depth range of both plant groups. From 6.35 kcal BP onwards relatively stable inputs and outflows of water maintained the site as a deep lake, comparable to that seen today. A *Melaleuca*-dominated community was maintained as part of the lake–sinkhole system from this time. This study follows Quaternary investigations from the Girraween sinkhole (Darwin region, 520 km west; Bird et al., 2019; Rowe et al., 2019, 2021; Figure 1). These studies found that after a prolonged amelioration out of the last glacial maximum (LGM), permanent water conditions and fringing wet woodlands similarly established from 6.10 kcal BP at Girraween Lagoon (Rowe et al., 2019). Permanent waterbodies within the north NT landscape may therefore have been a widespread feature from ca. 6.0 kcal BP onwards (see also Shulmeister, 1992). With wooded slope cover, sedimentation does not appear to have contributed enough to significantly reduce water depth at Marura since the mid-Holocene, and not until ca. 2.20 kcal BP and again in the past 230 years did water levels (at least seasonally) drop, as evidenced by a rise in sedges and waterlilies, respectively.

5.2 | Terrestrial vegetation reconstruction

The Holocene terrestrial landscape around Marura incorporated grassy savanna, wooded savanna (with stages in *Eucalyptus* woodland, *Corymbia* woodland and co-dominant woodland), *Callitris* stands, and *Syzygium* monsoonal forest. Highest floristic diversity was observed through the mid-Holocene (ca. 8.5 to 3.0 kcal BP) indicating a variable vegetation mosaic. Savanna tree–grass dynamics are explained through transitions, whether progressive, irreversible or abrupt (Accatino et al., 2010). The savannas in the area were not static in form (structurally or in composition) and underwent both progressive and abrupt transformation. The following recounts Holocene tree–grass vegetation structure, followed by a description of plant composition, and how different vegetation communities may have co-existed.

5.3 | Vegetation structure

Grasses were prominent early in the record. Across the Pleistocene–Holocene boundary, large tracts of open grassy savanna occupied the landscape (see Rowe et al., 2021 for grassy savanna as a LGM legacy). Grass cover started to decline relative to a sharp rise in eucalypt woody growth from 9.0 to 8.5 kcal BP (Figure 3 and

Appendix S3), followed by progressive woodland development into the mid-Holocene. As woody cover increased and became structurally stable, a productive advantage of trees over grasses developed.

Trees, relative to grasses, increased from ca. 6.7 kcal BP with highest proportional tree cover achieved ca. 5.0 kcal BP, maintained until ca. 3.0 kcal BP. Tree cover did not thicken to the extent of exerting a negative effect on grass or herb growth. This trajectory toward high, sustained woody cover was disrupted through highly changeable, short-lived expansions in grass coverage, concentrated between 2.58–1.92 kcal BP. An excessive and rapid ‘seesaw’ in vegetation structure is evident not only in the pollen abundances but also in DCA measures (Figure 3). Following 1.92 kcal BP, woody cover reverted to mid-Holocene proportions, but did not re-establish an equivalent stable state. Trees were displaced in favour of grass abundance within the past 200 years, the characteristics of this most recent post-European (?) tree–grass switch unprecedented in the record. The interplay between woody and grassy plants changed at Marura in a parallel way to Girraween (Figure 4, and Rowe et al., 2019). For the north NT, a progressive Holocene transition toward an abundant wooded structure is an emerging signature savanna trend. At both Marura and Girraween, a similar wooded decline occurred in the uppermost part of the record (as is evident in Shulmeister, 1992).

5.4 | Plant composition and the mix of vegetation

Changes in tree proportion incorporated changes in savanna composition, as well as shifts in association with other vegetation communities. The Northern Territory's monsoonal forest network incorporates discrete community patches as well as affiliated taxa interspersed as eucalypt understories (Woinarski et al., 2007). The monsoon forest assemblage in Figure 3 (and Appendix S3) shows a discrete community, with *Syzygium* as the canopy tree (Brock, 1993; Fox & Garde, 2018). *Syzygium* played a keystone role at Marura, whereby the pollen of other forest affiliates simultaneously decline (or cease) with the decrease of *Syzygium* into the late Holocene. *Syzygium*'s known association with freshwater (Brock, 1993) indicates a monsoon forest was most probably positioned on the sinkhole slopes.

The earliest Holocene monsoon forest was characterised by *Timonius* (with *Syzygium*, *Podocarpus* and vines). Today, *Timonius* extends into drier inland NT areas along moist, protected corridors (Moore, 2005). This taxon also suggests an establishment of forest-affiliated plants on the sinkhole slopes, and discussed by Rowe et al. (2021) where *Timonius* remained at the Girraween sinkhole into the LGM. During initial total woody expansions (9.0–8.5 kcal BP, as above), *Timonius* was replaced by *Syzygium*, with monsoonal forest at its most expansive and diverse through to 5.1 kcal BP (*Syzygium*, with repeated *Canarium*, *Trema*, *Celtis*, *Ficus* and a range of vines). In the wooded savanna, *Corymbia* was more common than *Eucalyptus*, also until 5.3–5.1 kcal BP. Early, patchy shrub types *Calytrix* and *Dodonaea* were characteristic prior to 7.7–7.5 kcal BP, from which

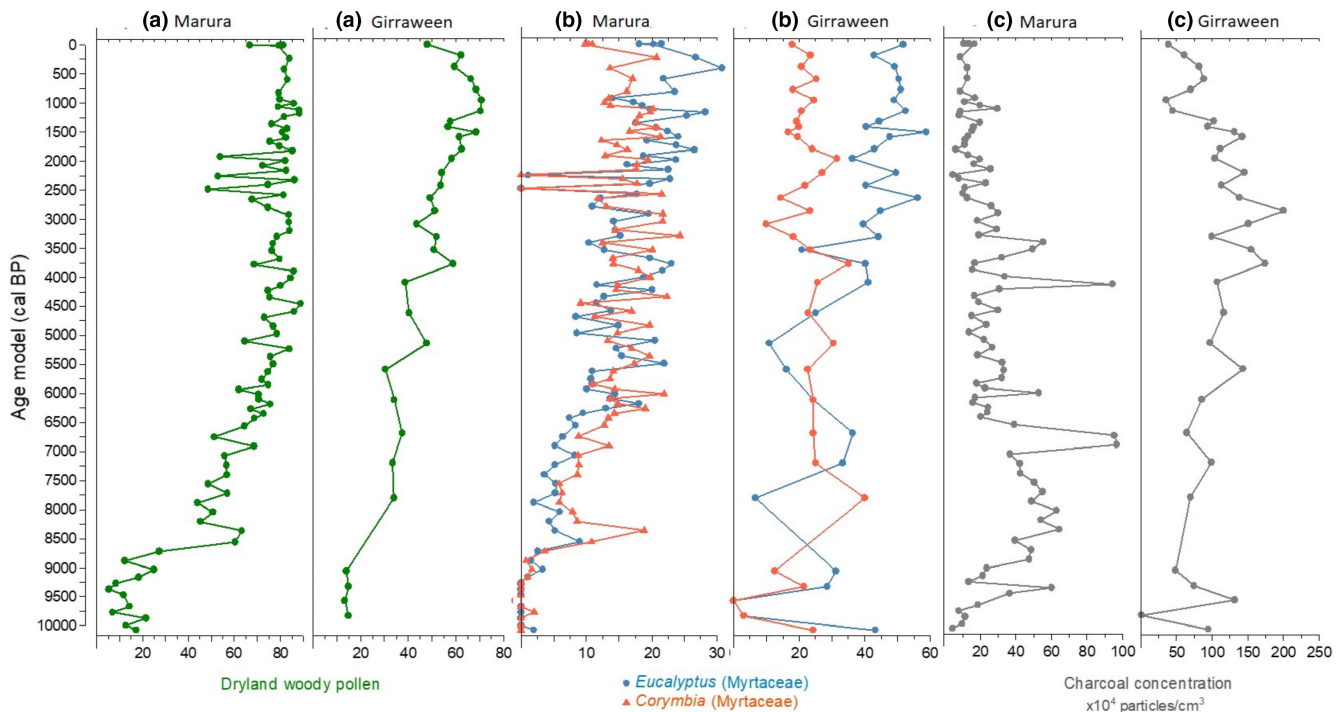


FIGURE 4 Comparative plot between selected pollen and charcoal values from the Marura and Girraween sinkholes, (a) dryland (terrestrial) woody pollen, (b) *Eucalyptus* and *Corymbia* pollen, and (c) charcoal concentrations.

time *Terminalia*, *Acacia*, *Pandanus* and *Callitris* increased and/or became continuously present subdominant trees. *Terminalia* was at its most widespread between 7.7 and 4.8 kcal BP and *Pandanus* more consistently present from 6.9 to 4.5 kcal BP. The presence of *Corymbia*, with such a suite of smaller trees, is indicative of a mesic savanna (Boland et al., 2006). The greater proportion of monsoonal forest taxa also implies moist vegetation.

Eucalyptus rose to co-dominate with *Corymbia*, and characterised high proportional tree cover, beginning 5.4–5.1 kcal BP. This *Eucalyptus*–*Corymbia* association continued to ca. 3.0ka cal BP. *Eucalyptus* species distribution in the NT is affected by subsurface soil moisture (inundation drainage patterns and water table depth). *Eucalyptus tetradonta* preferentially occurs on soils that remain well aerated throughout the wet season but undergo drought stress during the dry season (Prior, 1997). *Corymbia* species are comparatively more dependent on continuous moisture availability (Boland et al., 2006). Their co-occupation during the mid-Holocene suggests environments shifted into blended drier–wetter growth conditions across the local landscape. A similar *Eucalyptus*–*Corymbia* intermix at Girraween (Figure 4) suggests a widespread northern NT trend (Rowe et al., 2019). At Marura, *Eucalyptus*–*Corymbia* combined with subdominant *Acacia* and *Dodonaea*, *Calytrix*, and *Petalostigma*. A mesic wooded savanna therefore gradually transitioned to a drier wooded savanna. Drying is also reflected in declined proportion and complexity of monsoonal forest at 5.1–3.0 kcal BP, followed by local loss as a discrete vegetation community into the late Holocene.

Greater mid-Holocene tree cover included increased abundance of *Callitris* (from ca. 5.2ka cal BP). Preceding ca. 5.2ka cal BP, *Callitris* was common but less established (Appendix S3), proposed to have

tipped from sporadic co-occupier of the savanna into localised clusters (Bowman et al., 2014; Prior et al., 2007). Newsome's (1999) pollen deposition study concludes that *Callitris* pollen is important in revealing separate woodland formations, evident in *Callitris intratropica*'s ability to form large monospecific stands within a range of northern NT environments today (Bowman & Panton, 1994; Bowman et al., 2014; Prior et al., 2007). *Callitris* was not as strongly recorded at Girraween Lagoon. Rather, *Banksia*, *Grevillea* and *Pandanus* were used to subdivide wooded communities differing from the *Eucalyptus*–*Corymbia* system (Rowe et al., 2019). Bowman et al. (1988) further describe tree and grass competition as limiting *Callitris* seedling establishment. The genus may therefore have initially remained restricted at Marura under higher earlier Holocene abundances of *Corymbia*, *Terminalia*, *Pandanus*, and *Acacia*, as well as the higher (though overall declining) grass abundances.

Vegetation dynamics were driven by disturbance between ca. 3.0 and 2.0 kcal BP. Unstable, challenging conditions meant most taxa were only abundant for short durations, subject to high rates of 'switching'. *Eucalyptus*, *Corymbia* and *Callitris* fluctuated and alternated strongly with grasses. Non-eucalypt diversity in the sub-canopy declined. After 1.92ka cal BP, wooded-savanna recovery was led by *Eucalyptus*. *Corymbia* abundance reduced and it was no longer (co)dominant. *Callitris* populations also declined with respect to the mid-Holocene. Marura therefore resumed the pattern underway at Girraween (Rowe et al., 2019), with increase in *Eucalyptus* relative to *Corymbia* more pronounced at Girraween (Figure 4). Subcanopies were typified by dry shrubs *Petalostigma* and *Calytrix*, inconsistent intermediate trees and with *Acacia* in notable decline. Monsoon forest affiliates also became increasingly scattered; *Syzygium* was

replaced by *Bombax*. Since 500 years cal BP (and further in the last 200 years), monsoon forest taxa were effectively absent. Of the entire Holocene, herb abundance was particularly constrained in the ecological change of last 200 years.

5.5 | Holocene vegetation and fire

Large proportions of the world's savanna are burnt each year (Hutley & Setterfield, 2019). Any savanna burning project needs to recognise the long-term, local interrelationships between biomass, flammability, fire weather, and ignition sources, natural or anthropogenic (Bradstock, 2010; Russell-Smith, 2021). In formulating an understanding of savanna fire regimes through time, patterns in burning at Marura are first discussed, then explored regarding the role of people and climatic influences, and how these may interact. Rehn et al. (2021) tracked the abundance of carbon-rich materials produced by fires at Marura over the past 4000 years, showing a steady decline in the amount of biomass burnt through time. The current study helps define fire ecology and clarify vegetation–fire–climate feedbacks for the entire Holocene. Trends in burning are consistent between the two studies where they overlap.

Higher early-Holocene microcharcoal (10.08–6.45 kcal BP), indicative of landscape fires, preceded a gradual decline across the mid- into late-Holocene phases (6.45–3.0 kcal BP and 3.0 kcal BP onwards with a recent increase in post-European times. Evidence of more fires is coincident with palynological evidence of grassy savanna. Reduced fire then correlates with reduced grass abundance, increased woody proportions and changeovers in woody composition (Figure 3, Appendix S3). Therefore, this suggests that as mixed tree–shrub abundance reached a threshold of cover, grass biomass was reduced and ultimately this reduced landscape flammability (Scholes & Archer, 1997). Hoffmann et al. (2012) and Bowman et al. (2007) discuss grasses responsible for the flammability of savanna ecosystems. Rehn et al.'s (2021) identification of abundant elongate macrocharcoal supports the notion of past grass-led fires at Marura. Grass layers are highly flammable (pyrogenic) as well as demographically and physiologically advantaged by fire (pyrophilous); they use fire disturbance as a mechanism in competition. Grasses form loosely packed fuel with a high surface:volume ratio that enhances burning to produce a flame zone damaging to tree seedling establishment (Beringer et al., 2007; Hoffmann et al., 2012).

Metastability in Marura's mid-Holocene (c. 6.45–3.0 kcal BP) *Eucalyptus*–*Corymbia* system is reflected in not only steady woody:grass proportions (pollen), but associated fire regime (charcoal abundance). Part of this stability may have been captured by Rehn et al. (2021), in the regularity of the intervals between recorded higher- to lower-intensity fire events, namely a 450-year return interval of high fire intensities prior to 3.0 kcal BP. The Marura landscape was rendered less flammable due to lower grass abundance, and between 5.5 and 3.0 kcal BP, supported a diverse suite of subdominant trees and shrubs, including fire-sensitive *Callitris*. Reduced

burning may also have assisted in creating a positive feedback loop for *Eucalyptus* (cf. Russell-Smith et al., 2010).

5.6 | Anthropogenic fire

Highest fire incidence at Marura occurs in the early Holocene, differing from neighbouring palaeoecological sites. The Marura charcoal record also deviates from trends at Girraween, where charcoal continues to rise and peaks at a much higher level in the late Holocene (Figure 4). The Walala Lake core on Vanderlin Island in the Sir Edward Pellew Islands (Gulf of Carpentaria) shows a continuing rise in charcoal accumulation, from 5.5 ka cal BP, toward peak fire occurrence at 4.5–3.0 kcal BP, declining thereafter (Prebble et al., 2005). On Groote Eylandt (Four Mile Billabong core), a prolonged Holocene fire regime of moderate burning occurred until ca. 3.8 ka yr BP, at which time charcoal abundance began to rise with burning becoming most extensive after 1.0 kyr BP (Shulmeister, 1992). On both islands, increased openness of the *Eucalyptus* vegetation is suggested as the reason for increased fire and discussed within the context of Aboriginal burning, related to either local population changes or shifts in resource usage.

Distinguishing a natural from an anthropogenic fire regime in the Marura record is difficult. Few archaeological surveys have been conducted in the east–southeast Arnhem Land region, and what exists is primarily coastal (e.g. Bourke, 2001; Faulkner, 2008, 2013). Aboriginal peoples living in eastern NT lowland areas in the Holocene practiced a mobile and flexible subsistence economy, utilising resources on the coastal margins, lowland plains and hinterlands, particularly in the last 4200 years (Faulkner & Clarke, 2004; Sim & Wallis, 2008). Such landform diversity matches that managed within the boundaries of today's IPAs (Gambold, 2015; Laynhapuy Homelands Aboriginal Cooperation, 2017–2022). Inland and south of Marura, ethno-archaeology fieldworks discuss movement and regional tool trade interactions between cultural groups from the mid-Holocene (Pickering, 1990; Riggs, 2015). West, on the Arnhem Plateau, increased intensities of rockshelter use and burning activities began 8000–6000 years ago (see Shine et al., 2015 and references therein). Shine et al. (2015) suggest rockshelter occupation and fire use enabled foraging in establishing mid-Holocene resource habitats, including peak site activity once hydrological environments stabilised (see also Hayes et al., 2021 for the Holocene use of habitats and plant taxa on the Arnhem Plateau).

Anthropogenic burning at Marura, based on cross-landform mobility and resource use, is a consideration based on regional archaeology. Differences in charcoal records between palaeoecological sites (as above) also points to the likelihood of an anthropogenic component to fire regime in the Holocene, although this is not conclusively demonstrated by the data presented in this study. Where Rehn et al. (2021) interpret declining fire incidence as restricted, managed ('cool burn') burning from ca. 3000 years ago, this pattern appears to have begun earlier in the longer record of this study. Deliberate control of fire, including a shift in the type of burning

around Marura, may have arisen ca. 6.0 kcal BP. That this change was brought about by imposition of an anthropogenic fire regime to constrain eucalypt thickening (for example), is a possibility. Stability in the mixed *Eucalyptus*–*Corymbia* ecosystem–fire feedback does coincide with the timing of initial lake development, but any managed burning activity linked to water permanency within the sinkhole is also unclear.

5.7 | Holocene vegetation and the influence of climate

Climate change was the primary driver of Holocene wetland and terrestrial site dynamics at Marura. Fire was secondary, with the extent of burning a function of climate–vegetation feedbacks. Foremost were variations in moisture delivery as determined by the Holocene ASM. Cyperaceous wetland formation and swampy infilling reflect the intermittently wetter, developing ASM climatic transition across the Pleistocene–early-Holocene boundary (Denniston et al., 2013; Kuhnt et al., 2015). The permanency of open water from ca. 6.0 ka cal BP onwards was a manifestation of the mid-Holocene climate optimum and the reliability of precipitation during that time (Sloss et al., 2018). That Marura, Girraween (Rowe et al., 2019), and Four Mile Billabong (Shulmeister, 1992) demonstrate very similar timing in their swamp-to-lake transition highlights the minimal east–west geographic extent of this past highly effective moisture regime across the northern NT. Although the water balance of the region tended drier in the later Holocene (Reeves et al., 2013; Sloss et al., 2018), the immediate sinkhole environment appears to have buffered the waterbody from extensive climatic impact.

From 9.0 to 8.5 kcal BP, ASM redevelopment (Denniston et al., 2013) facilitated the progressive spread of trees, promoting *Corymbia*, in particular, and drove the emergence of monsoonal forest as a specific plant community. The mid-Holocene climatic optimum triggered the bulk of savanna tree recruitment, which entrenched grass decline, which in turn determined the nature of the fire regime. Transitions from mesic to drier savanna, including increase to dominance of *Eucalyptus*, subsequently tracked monsoon weakening and increased seasonality (Bourke et al. 2007; Hope et al., 2004). This later Holocene promotion of taxa such as *Eucalyptus tetrodonta* was also observed at Girraween (Rowe et al., 2019). Shulmeister (1992, p. 112) similarly reports a mid-Holocene ‘collapse of grass pollen’ then expansion of *Eucalyptus* on Groote Eylandt.

Bowman et al. (1988) have suggested monsoon forest species were once more widespread, and that increased fire frequencies forced non-sclerophyll flora into refugia. Monsoon forest taxa were more prominent at Marura in the middle Holocene. However, given the location of monsoon forest on the sinkhole slopes, these plants were always occupying a ‘refugium’ habitat at the site, rather than being forced into containment as Holocene conditions changed. Even along the internal slopes of the sinkhole, climatic drying, irregularity in moisture delivery, and a drop in sinkhole water levels

(2.20 kcal BP), eventually forced the decline of this particular ecosystem towards the present.

The highest-amplitude Holocene climatic variability in the Gulf of Carpentaria occurred after 3000 years ago (Moss et al., 2015; Prebble et al., 2005; Riggs, 2015; Shulmeister, 1999). Prebble et al. (2005, p. 367) refer to an ‘intensified disturbance regime’, consistent with the marked, changeable switching in trees/grasses at Marura between 3.0 and 2.0 kcal BP. Marura may have been subject to a phase of repeated, short-interval extreme storm and/or cyclone events, invoked by increased ENSO strength and intensity (Riggs, 2015; Shulmeister & Lees, 1995). Extended or intense El Niño or La Niña events are both associated with extreme climatic conditions (Charles et al., 2016).

Storms and cyclones are important components of the natural disturbance regime of north Australian ecosystems. Hutley et al. (2013) estimate the recurrence interval of storms as one in 5–10 years and one in 500–1000 years for mega-cyclones. Quantified ecological impacts of cyclones are discussed by Hutley et al. (2013), Wilson and Bowman (1987), Williams and Douglas (1995) and Cook and Goyens (2008), particularly in relation to the aftermath of two NT large cyclone events, tropical cyclones Tracy and Monica (1974 and 2006 respectively). Emphasis was placed on the extent of tree mortality (or severe structural damage), and how reductions in woody cover were offset by enhanced grass growth. Such decline-and-offset patterns are evident in the Marura record. The influence on savanna woody size class distribution can last centuries (Hutley et al., 2013), similar to the sample resolution in this Holocene study.

Where wetland pollen and charcoal abundances between ca. 3.0 and 2.0 kcal BP remain relatively unchanged in Figure 3 (and Appendix S3), Erskine and Saynor (2016) observed that tropical cyclone Monica was characterized by extreme winds but relatively low rainfall and runoff. Hutley et al. (2013, p. 7) comment that the impact of this cyclone on fire was ‘less than anticipated’ and that significant tree damage did not dramatically shift the fire regime. Burning remained dominated by grass fuels rather than the rapid consumption of newly available dead wind-thrown woody fuels. Rehn et al. (2021, p. 9) generally note higher macrocharcoal variability between 2.8 and 0.90 kcal BP, potentially indicative of spatial shifts in regional fire frequency as also suggested by Hutley et al. (2013).

Large infrequent disturbances play a substantial role in structuring plant communities (Gillson, 2006). Simultaneously, it is recognised that the long-term effects of tropical cyclones on savannas are difficult to interpret (Cook & Goyens, 2008). Given that it is not clear whether the frequency of destructive storms and/or tropical cyclones may be rising in north Australia (Cook & Goyens, 2008), there is a value-add provided by studies such as this, which reveal the past occurrence of major disturbance events and allow the inference of the impacts of past extreme events. Moss et al. (2015) and Proske and Haberle (2012) make similar comments in relation to the role of palaeoecology in the understanding of environmental extremes through the provision of a longer temporal baseline of change.

6 | CONCLUSION

The Marura sinkhole has provided a continuous Holocene record with exceptional palynological detail. For the northern NT savanna biome, this paper reveals diverging palaeoecological patterns as well as shared Holocene histories. This paper also highlights what may be called Holocene 'signature events' for the region. Marura (northeastern NT) tracks the same course of savanna vegetation change over the Holocene as Girraween Lagoon (northwestern NT, Rowe et al., 2019), until significantly disturbed by a phase of repeated, extreme storm and/or cyclone events concentrated in the late Holocene (3.0–2.0 ka cal BP). Site similarities reveal the northern NT behaved as a unit in terms of the savanna's Holocene trajectory toward a more wooded structure and *Eucalyptus* canopy dominance. This hints at aspects such as rise of *Eucalyptus tetradonta* to biogeographic dominance in the NT through the Holocene as well as this plant community's process of expansion following contraction during the LGM period (Rowe et al., 2021). The north NT eucalypt community therefore demonstrates a larger-, slower- (meta-stable-) scale climate response signal, in contrast with the dynamic nature of non-eucalypt vegetation composition (plus proportion) and the heterogeneity this contributes to at local scales in terms of alternative states. The combined wetland records show that the magnitude of regional climate change overrode local-scale, individual sinkhole influences to initiate regional permanent lake development (ca. 6.0 ka cal BP).

The proposed impact of extreme storm events adds spatial insight into late-Holocene climatic variability experienced in the northern NT. Along with other Gulf of Carpentaria sites, this storm phase is suggestive of a heightened level of change in the northern NT's east versus west. It demonstrates not only the degree of impact, and the effect of such events on the interplay and adjustment between trees and grasses, but also the extent and trajectory of recovery from disturbance. Marura's 'event recovery' comprised a realignment into the NT regional trajectory of increasing woody cover. This study highlights the role of stochastic disturbance events in maintaining diversity between locations within the Australian savanna biome, where the influence of large infrequent disturbances may have been underappreciated.

A higher-level, primary climate–vegetation feedback determined the direction and extent of Holocene burning at Marura. When increased woody cover, as a result of increased effective moisture, began to impose constraints on grass abundance, so too was fire constrained. Fire therefore appears to have been part of a lower subsystem of change. Compared to Girraween Lagoon, Marura experienced a less variable fire regime after the mid-Holocene, potentially reflective of local Indigenous management of fire. The drier climate at Marura (currently 1252 mm), relative to the more mesic savanna of Girraween Lagoon (currently 1720 mm), may also have conferred a greater vulnerability to change at the introduction of non-Indigenous land management practices. Owing to European impacts, this vulnerability may speak to a reduced resilience of drier savanna ecosystems under future climate scenarios.

AUTHOR CONTRIBUTIONS

Michael I. Bird conceived the project and Michael I. Bird and Cassandra Rowe designed site methodological approach; Cassandra Rowe, Michael Brand, Christopher M. Wurster, Costijn Zwart undertook fieldwork and core collection; Rainy Comley coordinated all laboratory preparations; Cassandra Rowe analysed the data and lead the writing; Michael Brand and Lindsay B. Hutley provided specific ecological feedback, Emma Rehn insight into fire activities, with general interpretative contributions from all other authors; Vladimir Levchenko provided sample age determinations.

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DATA AVAILABILITY STATEMENT

At the conclusion of our Northern Territory research, all project site data sets will be made available (Research data JCU via Research Data Australia, <https://researchdata.edu.au/> and <https://research.jcu.edu.au/data/default/rdmp/home>). This is in agreement with funders, the Australian Research Council Centre of Excellence for Australian Biodiversity and Heritage (CABAH).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Age–depth model developed for the Marura pollen core (full core sequence, with image adapted from Rehn et al., 2021).

Appendix S2. Resistivity profile and lake monitoring data for Marura.

Appendix S3. Marura percentage pollen diagram. Complete data plotted against depth, radiocarbon results, and calibrated age range.

Appendix S4. Detailed pollen diagram description for the Marura core.

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