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Holocene savanna dynamics in the seasonal tropics of northern Australia.

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Abstract

An environmental history is presented from Girraween Lagoon, Darwin region of the Northern Territory, Australia. Pollen and charcoal analysis of a 5-meter sediment core provides a record of vegetation change, fire history and climate spanning 12,700 cal BP to the present day. This study focusses on tree-grass vegetation dynamics, eucalypt to non-eucalypt plant interactions, and climate-fire-human relationships in an area where few long-term savanna records exist. The dataset suggests wetlands experienced alternating episodes of ephemeral waterlogging and seasonal inundation due to post-glacial monsoon variability up until permanent inundation from approximately 6000 cal BP. The surrounding catchment transformed from a terminal Pleistocene-early Holocene wooded-savanna to a later Holocene open forest. This increase in woody cover was a prominent site feature, primarily driven

by climate-moisture availability. In turn, the extent of fire and fire impact, is a function of climate-vegetation feedbacks. Such interplay between fire history, climate change and vegetation pattern was also influenced by more intense human management of the area, in the last 4000 years of the record. It is proposed Girraween may have become a much-socialised and managed human landscape in this late Holocene phase. Results provide essential baseline data describing savanna dynamics linked to contemporary ecological observation, understanding and management goals, and serves as an important resource for the Quaternary sciences and archaeology of northern Australia.

Keywords

Eucalypt, Poaceae, pollen, fire, Northern Territory, monsoon

1. Introduction

Savannas are environmentally and socioeconomically important in Australia, spanning some 1.93 million km², covering the majority of the northern quarter of the continent and 12% of global savanna (Beringer et al., 2015). By global standards, Australian savannas are relatively intact ecologically however, among 22 nominated Australian ecosystems, tropical savannas are included in the top ten most vulnerable to tipping points, facing disproportionately large changes in ecosystem properties as a result of a range of anthropogenic impacts, including threats to biodiversity from unfavourable fire regimes, clearing, and influence of invasive plant and animal species (Laurance et al., 2011; Setterfield et al 2018). This vulnerable status is compounded by the potential impacts of climate change. It is because of their importance and geographic extent, yet also their vulnerability, that we need to revise how we view the savanna and how we research, understand and ultimately manage these north Australian landscapes. Climate and landscape processes and the nature of human-environment interactions through time require greater emphasis.

Savanna consists of mixed tree-grass communities, and the fact that these contrasting plant life-forms co-dominate distinguishes savanna structure from grasslands or forest (Scholar and Archer, 1997).

Processes allowing this tree-grass coexistence have 'long intrigued ecologists' (Murphy et al. 2015, 1),

and the mechanisms driving changes in tree-grass cover in savanna through time and space remains a largely unresolved issue in ecology (Lehmann et al., 2008, 2014). Factors including climate, fire, herbivory, plant competition, topographic and/or edaphic variation interact and operate at different scales of vegetation influence (Lehmann et al., 2011; 2014). Many studies differentiate these as primary determinants (e.g. climate, soils and geology) or secondary determinants (e.g. disturbance) (Wiegand et al., 2006). The mesic savanna (>1000 mm/yr of rainfall, Russell-Smith et al., 2010) of Australia's Northern Territory has received significant research attention focused on drivers of woody biomass, and the relative importance of water (as mediated by climate) and disturbance (fire) (Hutley et al., 2001; Cook et al 2002; Russell-Smith et al., 2003; Fensham and Kirkpatrick, 1992; Bowman and Panton, 1993; Bowman and Minchin, 1987; Sharp and Bowman, 2004; Lehmann 2008). Much of the focus has been on fire effects (e.g. Prior et al., 2010). But here, Wiegand et al. (2006) believe research into savanna structure has disproportionately centred on secondary determinants and overlooked primary determinants. Murphy et al. (2015) further propose that fire regulation has been overemphasised in northern Australia, suggesting savanna tree abundance is more strongly controlled by water availability and potentially tree grass-competition. Whether, and/or how, eucalypt composition has an influence on savanna tree dynamics, and the extent to which non-eucalypt woody cover responds to eucalypt dynamics, fire, precipitation, or all of these, are questions not yet resolved (Lawes et al., 2011; Ward et al., 2013). The tropical savannas of northern Australia have high plant diversity (Haque et al., 2017; Lawes et al., 2011; Woinarski et al., 2007), so floristic composition is an equally significant attribute in addition to wood-grass structural attributes (Williams et al., 1996) and also key to understanding spatio-temporal patterning in savannas.

These 'conundrums' relating to understanding contemporary spatial and temporal patterns of savanna distribution, as described by House et al. (2003), persist today. House et al. (2003) suggest studies to date have been small-scale, short-term and site specific; that research has not been sufficiently long-term to capture the important effects of interannual variation in climate and disturbance, and/or often measuring either the tree or grass component in isolation. Staver (2017) and Wiegand et al. (2006) agree. Lehmann et al. (2008) highlight the limited available data to describe patterns of savanna tree

cover change at landscape scales and over different time-scales across north Australia. This paper argues that to focus on tree-grass coexistence and to ask what controls the dynamics of current northern Australian vegetation, contemporary ecological observation and experiment would benefit from an independent palaeoecological perspective. It is as Kruger (2015, 121) describes 'explaining a contemporary savanna state is an exercise in history'.

Palaeoecology is able to provide long-term insight into vegetation structural and compositional transformations, yet the savanna region of northern Australia remains little studied in this context (but see Field et al., 2017; Proske, 2016; Head and Fullager, 1992; Schulmeister, 1992). Fine scale palaeoecology and palynology, including detailed chronologies of vegetation change are scarce, particularly for the Northern Territory. For northern Australia, proxy records from offshore ocean deposits only provide a broad framework for discussion of long-term Quaternary environmental patterns (Kershaw and van der Kaars, 2012). Offshore records are complemented by coastal palaeoecology (see maps in Reeves et al., 2013), and evidence of landscape change across the inland north largely derived from sediments of once extensive lakes, together with palaeosols and the studies that have provided measures of the relative activity of dune systems (Fitzsimmons et al., 2013; Hesse, 2010). Marine records are coarse in spatial and temporal scales with limited plant-taxonomic resolution. That non-coastal pollen interpretations derived near-shore are masked by mangrove dynamics and sea-level variations (e.g. Woodroffe et al., 1985), confounds the situation. As such, there is diminished capacity to document the magnitude of savanna landscape-ecological change, factors determining plant interactions beyond the coastal fringe, and the range of possible vegetation assemblages. Discussing inland environmental patterns in terms of broad glacial versus interglacial phases (van der Kaars et al., 2000) further fails to resolve detailed variations for time periods punctuated by phases of relatively rapid change, including the terminal Pleistocene into Holocene period, and in the Holocene to modern day transition (see recommendations in Williams et al., 2013; Bowman et al., 2010).

This paper is the first in a series of palaeoecological investigations stemming from Girraween Lagoon (12.517°S, 131.081°E). Girraween is the first in a series of Quaternary study sites from across the 'Top

End' of Australia's Northern Territory (Bird et al., 2019). These new sites are focused on the development of a high-resolution network of terrestrial records of vegetation and environmental change in Australian savannas. We seek to document changes before, during and after the arrival of humans (Indigenous and European) and aim to disentangle natural and human drivers of change in northern Australia's climate and biodiversity (Bird et al. 2013). We query the extent to which the northern Australian savanna biome is natural or anthropogenic in form and function, and/or represents a region in transition or a region in a stable ecosystem state.

This paper is also the first to provide a detailed palynological account of a Northern Territory Holocene savanna. Core data reported here provides a significant palaeoecological resource for northern Australia that informs contemporary ecology by presenting pollen results according to plant function in the savanna, resource use, and environmental responses. In so doing, this paper is more able to explore tree-grass coexistence and dynamics, the defining attribute of a savanna (Scholes and Archer, 1997), as opposed to pollen types examined as a series of individual plant taxa. Where long-running questions in the Quaternary Sciences are increasingly discussed (e.g. the post Last Glacial Maximum initiation and operation of the Australian Summer Monsoon, Denniston et al., 2013a; McRobbie et al., 2015), the next step is to examine and describe landscape palaeoecological changes more closely, to refine discussions further through disentangling cause-and-effect at sites such as Girraween. Where other questions remain debated (e.g. late Quaternary human-environment interactions, Williams et al., 2015a; Bird et al., 2013), locally determined long-term comprehensive vegetation analysis is required, and is the aim of this paper. A 'Top End' multi-site methodology is also an important approach. Girraween, as representative of mesic Australian tropical savanna, represents a first step in this endeavour.

2. Study site

Girraween is one of 137 'lagoons' identified by Schultz (2004) in an inventory of freshwater wetlands across the Darwin region, Northern Territory. Located within the Howard River sub-catchment of Darwin Harbour in the municipality of Howard Springs, Girraween forms part of a privately-owned estate, in the

peri-urban fringe of Darwin where land uses include rural settlements, tourism, and horticulture. Three recent Northern Territory (NT) governmental, resource and research institutional reports acknowledge the ecological importance of local wetlands but admit Darwin's lagoons are not well understood compared to other freshwater systems (Schult and Welch, 2006); Lamache (2008) describes the situation as a lag in information, and Woodward et al. (2008) mention Girraween specifically as lacking in descriptive biophysical and biological data. The climate and biophysical attributes of Girraween are described below.

2.1. Climate

The region experiences a strongly seasonal climate, encompassed within Köppen-Geiger's 'Tropical Savanna' classification subtype Aw (Peel et al., 2007). Temperatures are uniformly high, with fluctuating rainfall regimes and wind-flow reversal. The mean annual temperature maximum is 32.6°C (minimum 23.2°C). Average annual rainfall is 1720 mm (Bureau of Meteorology, Darwin Airport, station 014015, 1941-2017, 24 km northwest), with the majority falling between December and April (monsoonal 'wet season'). The 'dry season' period extends May to October. Monsoon conditions incorporate west to north-westerly winds whereas winds in the dry season are dominated by east to south-easterlies. The region is subject to Tropical Cyclones with records in the NT northern region from 1964 to 2015 including 32 severe cyclone landfalls (categories 3, 4 or 5 on the Australian scale, BoM, 2017).

2.2. Geology and Hydrology

Girraween Lagoon is a perennial waterbody, with a surface area of 45 hectares (ha) and a maximum depth of 5 m. Water drains into the lagoon from a catchment of 917 ha and can overflow westward via a diffuse channel network that drains north into the Howard River. The lagoon is immediately underlain by the Cretaceous Darwin member (sandstones/siltstones), in turn overlying metamorphosed Proterozoic Dolomite. Water bore records surrounding the lagoon and within 1 km of the lake centre (RN038195; RN039018; RN006365; RN004933; RN004933; RN004433; data available at <http://nrmaps.nt.gov.au/>) indicate the lake is immediately underlain by lateritized and heavily weathered sandy to clayey

Cretaceous sediments. These sediments are underlain at 30-50 m depth by a Proterozoic dolomite aquifer. Bore RN038195 300m NE of the lagoon encountered a 5m void in the dolomite. This is consistent with Girraween and other lagoons originating as sinkholes due to collapse into voids created by dissolution of the underlying dolomite (McFarlane et al. 1995).

The lagoon surface is coincident with the water table in the wet season, based on water levels monitored in bore RN004433 (Figure 1). Prior to groundwater extraction in the rural area, the water table depth decreased by an average 4 m over the course of a dry season before being replenished during the following wet season. Pumping now reduces the water table depth in the dry season by 10-15 m, but the lagoon remains perennial likely due to the sediments on the lake floor impeding deep drainage. Evaporation and some infiltration lead to a 1-2 m fluctuation in lagoon water depth between the wet and dry seasons. Lake waters are fresh, never exceeding 0.12 mS/cm conductivity. The water temperature at 1 m depth cycles over 1-2°C diurnally and annually from daily maxima of 32-35°C in the wet season to minima of around 25°C in the dry season. Schult and Welch (2006) report that pH of Girraween water varies between 5.5 and 6.0 over an annual cycle, dissolved oxygen is uniformly high (60-90%) and turbidity is uniformly low (1-10 NTU).

2.3. Land use

Traditionally, the Darwin region was occupied by the Larrakia people spanning the Cox and Darwin Peninsulas, including adjacent Islands, and stretching to Shoal Bay to the north and Adelaide River in the southeast. The Larrakia were also known to be closely allied and intermarried with the Wulna peoples who occupied territories further east (Wells, 2001; Burns 1999). Today, the Larrakia maintain regional customary associations, including in the Howard River area and Girraween catchment (Wells, 2001; Burns 1999). The name 'Girraween' is of traditional origin meaning 'the place of flowers' (<http://www.ntlis.nt.gov.au/placenames/>).

Ethnohistoric accounts indicate extensive Larrakia knowledge of the environment and a landscape incorporating birthing to burial sites, sites connected with ceremonial activity, and land marks representative of Dreaming locations (Wells, 2006; see also Burns, 1999 and Bourke et al., 2005). The

Larrakia people themselves describe having moved constantly about their country, hunting and fishing in accordance with cultural requirements, seasonal patterns of resource use and the availability of freshwater. People depended heavily on fish and shellfish from coastal areas as well as fish, duck, geese and waterlilies from permanent water bodies. The latter were also important camping places (Woodward et al., 2008; Wells, 2001). Wells (2001) further documents how Larrakia people harvested numerous plants from their country. Wells' (2001) book provides an account of Darwin from a Larrakia perspective.

Howard Springs' European settlement dates from the first surveys of 1864. Initial settlement and land uses were primarily agricultural and pastoral, with the spring providing water for Darwin. Growth first took place in the 1870-80s following construction of the Overland Telegraph Line, but it was not until the 20th Century post World War II years that marked population expansions particularly after the 1970s. Since 1996, Howard Springs has experienced further increases in population, a result of new residential developments and interests in horticultural use (Lamache, 2008; Woodward et al., 2008). The site is currently surrounded by residential development, bordered by a c.500-1200 m wide zone of intact savanna.

2.4. Vegetation and fire

Modern vegetation is *Eucalyptus* dominated tropical open forest savanna and/or savanna woodland (Moore et al., 2016; Hutley et al., 2013). Wilson (1991) classifies the area as a regional *Eucalyptus tetradonta* - *Eucalyptus miniata* - *Corymbia polycarpa* alliance. Darwin surveys of remnant vegetation describe *E. tetradonta* - *E. miniata* with mixed species woodland at the site (Brock, 1995). Within the Girraween catchment *Eucalyptus* dominate better-drained (sandy, sandy loam) soils, extending greater distances from the lagoon than *Corymbia* as well as other secondary and/or mid-layer trees. Variable transition communities dominated by *Lophostemon* spp. and *Melaleuca* spp. and broad-leaf herbs occur on approach to the water, including areas with species allied to 'forest' (see Russell-Smith (1991) for discussions on broadleaf taxa, allied to monsoonal rainforest, thicket and/or riparian communities).

The lagoon itself incorporates a wetland fringe. Zonations in vegetation close to the lagoon edge are determined by depth of open water and extent of onshore soil waterlogging. *Melaleuca* form woodlands in the shallow waters to waterlogged soils, from outer sedge boundaries and inland to grassland. Site vegetation communities are mapped in Figure 1 and detailed in Tables 1 and 2 (map associated table, and vegetation structural definitions used in text). From the Girraween catchment, woodlands continue coastward to merge with the Darwin Harbour embayment, associated riverine environments and lower-lying coastal plains (c. 10km distance). Here, mudflats and mangrove forests line the shorelines, rivers and creeks.

For the wider Darwin region, the modern-day fire regime reflects fuel loads arising from the dominance of annual C4 spear grass species (Bowman et al., 2007) and over the decade, rapid invasion of exotic grasses, notably *Andropogon gayanus* (Gamba Grass) (Rossiter et al., 2003). Areas within a 2 km radius of Girraween have burnt every year since 2000 (an annual fire return interval) but the site's immediate private estate has burnt $\leq 6-7$ times, equating to a fire return interval of 2-3 years, a typical regime of Top End savanna (Russell-Smith and Yates, 2007). Fires closely surrounding Girraween have tended to occur earlier in the fire-season, with minimal repeat location burns (<http://www.firenorth.org.au/nafi3/>).

3. Methods

Girraween Lagoon was cored using a floating platform with hydraulic coring-rig. A 19.4 m core in 1 m sections was collected (to the point of bedrock). The focus of this paper is the upper 5 m of this core. Each 1 m section was collected in plastic tubing and sealed in the field for transport. Vegetation surveys, including floral reference collections, were undertaken at the time of coring and a topographical survey traversed the site from approximately southwest to northeast.

Core sections were split in half, described and sub-sampled at 5 or 10 cm intervals (dependent on the changing nature of sediments). Two cubic centimeter sediment samples were processed for pollen and microcharcoal analysis. Sample preparation followed standard techniques as outlined in Bennett and Willis (2001) and detailed in Brown (2008). Chemical preparations were selected to initially disperse the

organic-mineral matrix then progressively remove humic-acids, calcium carbonates, bulk (in)organics and cellulose, silicates, as well as to render pollen ornamentations more visible (including $\text{Na}_4\text{P}_2\text{O}_7$, KOH, HCL, Acetolysis and $\text{C}_2\text{H}_5\text{OH}$ washes). Sieving took place at 7 μm and 125 μm . A *Lycopodium* spike (Lunds University batch 3862, tablet concentration 9666 with an error $\pm 2.2\%$) was added during laboratory preparations, to determine concentrations of pollen and microcharcoal particles.

Pollen identification was based upon regionally representative floral reference libraries in development by the lead author (CR). Online resources including the Australasian Pollen and Spore Atlas (<http://apsa.anu.edu.au/>) were also utilised. The Northern Territory has a large and diverse flora. This, in combination with current reference collection and scarce published material for the region, can limit the level of identification possible. In certain cases pollen are categorised to family and/or tribe, incorporating grain morphological descriptors. Accounting for pollen types in this way at least ensures diversity within the record is not lost. Associations between plant types and therefore pollen types further assists grain classifications. The 'unknown' types within a family are different to the unidentified category that is composed of damaged and/or deteriorated grains (c.f. Stevenson et al., 2010). Pollen sums averaged 300 grains (including spores) per sample.

Microcharcoal incorporated within the final sample concentrate (black, opaque, angular particles, $>10 \mu\text{m}$ in length) was counted simultaneously with pollen. Charcoal size, as a proxy for fire occurrence, is guided by the advice of Whitlock and Larson (2001). Notably, the exclusion of particles $<10 \mu\text{m}$ eliminates charcoal most likely to have been transported from outside the catchment (917 ha). All data were plotted using TGView (Grimm, 2004) and pollen assemblages divided into zones based on the stratigraphically constrained classification undertaken by CONISS (Grimm, 1987; 2004). To further explore the relationships within, as well as between, pollen zones, an unconstrained Principal Components Analysis (PCA) was undertaken using C2 (Juggins 2007). The PCA is used to help illustrate variation between zones and samples, rather than similarity (as in the CONISS cluster analysis), and to display the data in terms of a few dominant gradients of variation.

Samples of bulk sediment for radiocarbon dating were pre-treated by hydrogen pyrolysis to remove labile carbon and decontaminate the charcoal component. They were then combusted to CO₂ and reduced to a graphite target for measurement at ANSTO, as reported in Bird et al. (2014). Age reporting follows Stuiver and Polach (1977), converted into calibrated ages using CALIB REV7.1.0 (Stuiver and Reimer, 1993, Hogg et al., 2013; calibration curve SHCal13). A Bayesian age-depth model was constructed for the core using Bacon 2.2 (Blaauw and Christen, 2011).

4. Results

4.1. Chronology and sedimentology

The core interval of relevance to this paper spans 0 - 504 cm. The core chronology is based on seven radiocarbon measurements. Sample depths, percent modern carbon (pMC), conventional radiocarbon ages (BP) and calibrated ages (cal BP) are listed in Table 3.

Sediments forming the lowermost core section are highly variable, composed of strongly mottled fine-clays with interlayered sand, small clay aggregates and thin bands of heavier compact clay. Fine clays are present until 440 cm depth, thereafter the sediments abruptly change into dark fibrous, organic mud containing sand and grit. This in turn transitions (420 cm depth) into black organic consolidated peat material, visually decomposed with uniform texture lacking sand or grit. Black organic peat continues for the remainder of the core, with a notable band of sand spanning 287-266 cm depth, and incorporating algal remains in the upper 38 cm.

Sedimentation and mass accumulation rates (corrected for compaction) are incorporated into Figure 2a. Four relatively steady-rate sedimentation phases are punctuated by periods of decline and increase. Sedimentation rates fall after 9250 cal BP (345 cm) and stabilize to remain consistent between 7100-4600 cal BP (287-234 cm, 0.21 m/ka). They increase until c.3300 cal BP, hold steady (0.49 m/ka), and rise again 1950-1300 cal BP (125-85 cm, to 0.70 m/ka). The upper 100 cm includes a sharper degree of change. Overall, mass accumulation decreases toward the surface. Fluctuations are more evident to approximately 5500 cal BP (245 cm). Mass accumulation subsequently steadies before oscillating in

the surface samples (<50 cm, under 800 cal BP). Total values range from 1.76 g/cm²/ka (12,150 cal BP) to 0.10 g/cm²/ka (350 cal BP).

4.2. Palynology

The Holocene pollen record for Girraween is presented in Figure 2a, b, c and d. A total of 117 pollen taxa were identified, with unidentified pollen accounting for an average of 11% of sample pollen sums. Identifiable pollen was divided into 12 groups to capture plant form and/or vegetation type; dryland (10 taxa) and wetland associated Myrtaceae (8 taxa), other sclerophyll pollen (20 taxa), monsoonal forest associates (22 taxa), liana and mistletoes (6 taxa), mangroves (3 taxa), Poaceae (two grain-size classes), herbaceous sub-shrubs (15 taxa) or forbs (14 taxa), sedges (and similar wet-ground taxa, 7), aquatics (3 taxa) and pteridophytes (7 taxa). These groups were then condensed further, and pollen allocated into plant-function and/or environmental response categories. Woody taxa versus grasses were grouped to evaluate woody dominance and fire. Woody taxa were further split into eucalypts (*Eucalyptus* and *Corymbia*) and non-eucalypts as two functionally distinct groups with significant differences in fire tolerance, with non-eucalypts considered more sensitive to fire (Lawes et al. 2011). To assess a wet to dry continuum, *Melaleuca*, *Corymbia* and *Eucalyptus* are also graphed comparatively. Herbs are considered an additional environmental indicator group for ground moisture (Ward and Kutt, 2009) and aquatics/sedges have been graphed as a ratio to serve an approximate localised precipitation proxy. Pollen into plant-function, environmental-response categories are included in the PCA. Bi-plot variation is described, and taxa driving zonal (and/or sample) distribution along environmental gradients, are assessed in Appendix A. Eight pollen zonations are apparent in Figure 2, each representing distinct changes in dominant taxa, GIR 1 (504-458 cm below sediment surface (bss) to GIR 8 (0-30 cm bss). As a complete palynological reference piece Figure 2 is described in full within the supplementary information Appendix B. An outline is provided below with charcoal results.

4.2.1. Pollen

The PCA (Appendix A) provides a useful assessment of inter-zone relationships. Degrees of vegetation openness and moisture fire/gradients between zones are also evident, and the PCA illustrates the

period of least variability within the record has been over the last c.3000 years. Zone GIR-1 identifies on the basis of non-eucalypts, separate from GIR-2, GIR-3 and GIR-4 as zones defined more strongly by grasses and herbaceous taxa. Zone GIR-5 is characterised by eucalypts. The upper three zones are similar, also in association with eucalypts, but incorporating non-eucalypts to a greater degree. Zones GIR-6 and GIR-7 are more closely associated with each other than with GIR-8.

Within the lowermost zone GIR-1 (504-458 cm bss, 12,670–11,820 cal BP) all plant groups fluctuate substantially in relative abundance. Woody taxa are primarily sclerophyll and co-exist with Poaceae in most samples. Herbaceous taxa are minor. Wetland taxa are characteristically the sedge group and Pteridophyte spores are prominent (similarly zone GIR-2).

GIR-2 (458-420 cm bss, 11,820–10,965 cal BP) is characterized by a rise and fall pattern in Poaceae. Sedge pollen show the opposite pattern and covary inversely with the grasses. Low-consistent values of herbaceous taxa are also recorded (maintained up-core). Woody representatives fall through this interval; within these groups all Myrtaceous pollen fluctuate, whereas sub-canopy sclerophyll and monsoonal-forest pollen (non-eucalypts) begin to increase. Aquatic pollen appears but is not consistently present. Mangrove pollen is minor.

The next two zones, GIR-3 (420-372 cm bss, 10,965–9870 cal BP) and GIR-4 (372-320 cm bss, 9870–8670 cal BP), incorporate reduced sample-to-sample variability and develop consistently high Poaceae pollen abundance. In response, dryland and wetland myrtaceous pollen are at their lowest for the record. Relative to the eucalypts, non-eucalypts are more abundant. Sedge pollen does not fluctuate to the extent seen in earlier zones. Mangrove pollen increases.

Zone GIR-5 (320-175 cm bss, 8670–2975 cal BP) is defined by gradual decreases in Poaceae and a steady rise in woody taxa, notably the Myrtaceae. Non-eucalypts consist of a broad range of pollen types, but values start to decline mid-zone. Indications of wetland expansions are combined rises in sedges and aquatics (aquatic pollen maintains constant pollen percentages from this zone onwards). Mangrove pollen peaks in the early part of this zone.

Through zones GIR-6 (175-130 cm bss, 2975–2042 cal BP) and GIR-7 (130-30 cm bss, 2042–442 cal BP) Myrtaceae-eucalypt pollen dominate, and reach maximum values for the core. Wetland woody taxa also expand. Low proportion (yet diverse) non-eucalypts are maintained. Poaceae percentages fall to values less than woody taxa. Sedge pollen decrease in a step-like pattern before maintaining roughly even presence.

The uppermost zone GIR-8 (30-0 cm bss, 442 – c.20 cal BP) is marked by a reversal in mid- to late-Holocene pollen trends, defined by a decline in Myrtaceous pollen (dryland and wetland canopy taxa), with corresponding increases in non-eucalypts, Poaceae and sedges.

4.2.2. Charcoal

Girraween's charcoal record permits discussion of changes in catchment fire occurrence and/or abundance. Fire characteristics (fire intensity and fire or burn severity) are more difficult to document, however changes in pollen that can be tied to vegetation flammability may be interpreted as reflecting fire intensity (c.f. Higgins et al., 2000; Govender et al., 2006; Lentile et al., 2006). Grass-led fires, for example, promote an increase in fire frequency and severity (Lehmann et al., 2014; although as Whitlock and Larsen 2001 highlight, fire regimes characterized by frequent and efficient ground fires may not produce much charcoal).

Disturbed, changeable sediments at the base of the section are likely to have reduced charcoal deposition-preservation in zones GIR-1 and GIR-2 (low charcoal accumulation rate aligns with low pollen recovery). What charcoal has been recovered prior to 11,000 cal BP is interpreted to indicate a low incidence of fire just prior to the Holocene. Rising charcoal preservation and pollen accumulation rates then correlate with increased organic accumulation. Commencing 11,000-10,800 cal BP, burning within Girraween's environment is more prevalent, but a strong rise-and-fall charcoal pattern from zone GIR-3 suggests considerable variation in the occurrence and character of early Holocene fire. Raised and more sustained inputs of charcoal begin early zone GIR-3 (c. 9700 cal BP and higher again c.7700 cal BP), implying the start of a period of increased and ongoing burning. Greater charcoal continues into zone GIR-5 to peak at approximately 3100 cal BP, incorporating several high charcoal events

(charcoal spikes every 1000-2000 years). This type of fire activity then decreases in the late Holocene and toward the present day. Downward trends in total charcoal accumulation occur after 3100 cal BP suggest fire gradually became less extensive (zones GIR-6 to GIR-8). This milder burning incorporates more frequent smaller peak charcoal events (Figure 2a, every 300-700 years). Fire remains a continual feature in the landscape after 3100 cal BP but with two recent reductions in burning, between 1400-1150 cal BP and after 600 cal BP.

5. Discussion

The purpose of this paper is to provide a detailed palynological and palaeoecological account of a north Australian tropical savanna. We present the discussion as a series of reconstructive vegetation descriptions and climate-fire responses, divided into three environments (coastal, wetland and dryland) and arranged into time phases (late Pleistocene-early Holocene, early- into mid-Holocene, and late Holocene). The discussion ends by exploring the influences of human activity.

5.1. Mangrove encroachment and contraction

Rhizophora, *Brugueria/Ceriops* and *Casuarina* pollens are wind distributed (Rowe, 2012 and references therein). These taxa are not present on-site at Girraween during the Holocene. Rather, their pollen tracks the main phases of post glacial marine transgression documented for the north Australian coast (Chappell, 2001; Mulrennan and Woodroffe, 1998; Wasson, 1992).

Rhizophora, *Brugueria/Ceriops* and *Casuarina* are presented in Figure 2c. Mangroves approached Girraween between 11,700-10,800 cal BP, and established at their closest proximity 9700-7100 cal BP. After 7100 cal BP mangroves contracted seaward, but remained stable in the broader Girraween area until 2150 cal BP. They declined further beginning c.1950 cal BP, but recovered within the previous 1000 years to present-day Darwin-coastal coverage. *Casuarina* also encroached on Girraween in the early Holocene but disappeared as mangrove forests expanded. From the late Holocene, *Casuarina* maintained a fluctuating on-off long-distance presence in the pollen record.

Similar mangrove forest developments (dated >9000-7000 cal BP) during marine transgressive stages have been recorded from the NT's Mary, Daly and Alligator Rivers (the 'big swamp phase', Chappell, 1993; Mulrennan and Woodroffe, 1998; Woodroffe et al., 1986), consistent with Woodroffe et al. (1986) who suggested it is not until 9000 years ago that the sea began to invade inland NT channels. This is also comparable to mangrove changes across the King River region of north-west Australia (Proske et al., 2014). In turn, Girraween's pollen is consistent with subsequent so-called mid Holocene 'transition phases' of mangrove contraction in these adjacent regions of the NT (e.g. 3900-2000 yr BP, Woodroffe et al., 1985). Present day sea levels were attained in the previous 3000-2000 years resulting in the establishment of modern Darwin coastal conditions (Fredericksen et al., 2005). Archaeological documentations of coastal change in Darwin Harbour report shorelines of open beaches with only scattered stands of mangrove c.1400 years ago (Hiscock, 1997; Bourke, 2004). Hiscock (1997) interprets the more continual mangrove communities found across the Harbour today as having an antiquity of 1000-700 years. The pollen from Girraween supports this regional late-Holocene fluctuation and mangrove return.

5.2. Wetland development

Figure 2d reveals changing areas of permanent inundation (open water), seasonal inundation (swamp) and ephemeral waterlogging (referred to as 'dampland' by Semeniuk and Semeniuk, 2004). Holocene variability in wetland vegetation was associated with forms of disturbance incorporating substrate erosion-deposition phases, as well as due to hydrology and Australian Summer Monsoon (ASM) intensity. The developing lagoon and its immediate dampland surrounds did not support and/or promote fire, nor were they significantly affected by burning.

5.2.1. Late Pleistocene-early Holocene: fluctuating wet-dry conditions

During the transition to the Holocene (12,700-10,900 cal BP), Girraween was a fluctuating wet-dry system, characterized by active site surfaces and temporary local habitats occupied by reactive plants and those favouring disturbed sites. Mottling in sediments deposited at this time suggests phases of impeded drainage and prolonged saturation (McKenzie et al., 2004). Oxidation of pollen, poor

preservation and low concentrations with poorer grain identifications also suggests alternate periods of dryer surface exposures (Brown, 2008; Head and Fullagar, 1992).

Alternate wetting and drying events can trigger processes of ground-surface sealing (Zejun et al., 2002; Greene, 2006), and related 'hardsetting', a widespread phenomenon in Australian soils, particularly in relation to clay mineral assemblages that tend toward natural cementation (McKenzie et al., 2004).

Sealing occurs when surface aggregates breakdown on wetting, then dry in their smaller particle state to form a hard mass. This in turn reduces infiltration/drainage (Greene, 2006; Mullins et al., 1990). A Last Glacial Maximum (LGM) initiated, and late Pleistocene-early Holocene sealed, Girraween surface is suggested to have facilitated the development of lake-like permanent inundation (with peat accumulations) recorded more recently in the core.

In Australasia, the LGM was a significant climatic event (the globally defined glacial period 30,000-18,000 yr BP, peaking at the LGM c.21, 000-18,000 yr BP) and diverse proxy data reveal prolonged low temperatures and phases of extreme dryness. The ASM is considered to have been regionally inactive or greatly weakened at this time (see Reeves et al 2013 for a synthesis of climate data). Bowler et al. (2001) refer to the LGM monsoon has having collapsed. Other studies signal localised rainfall variations. Northern NT geomorphic evidence through the past 30,000 years reveal episodic flood records of high (e.g. 30,000-20,000 yr BP) and low (e.g. 16,000-14,000 yr BP) magnitudes (Nott and Price, 1996). North Western Australian (WA) stalagmite records pin-point centennial to millennial-scale pulses of glacial-phase rainfall variability (e.g. within 24,000-22,000, yr BP, 17,000-14,000 yr BP and after 12,800-11,500 yr BP, Denniston *et al.*, 2013b). Under glacial conditions, a periodically exposed Girraween lake floor would crack and fragment, generating aggregates available for breakdown, as well as those observed whole in the core. Dust is also more likely to have become available and trapped by rough ground surfaces (McKenzie et al., 2004), thereby contributing additional fine particles. Sediment textural and compositional layering (sand to gravel sized particle inlays, to an extent not seen elsewhere in the record) further suggests physical processes around the site. Periodic sheet wash from

the surrounding margins is a possibility with discrete rainfall and/or flood-like events, magnifying the sealing effects of wetting and drying.

From c.12,700 cal BP Girraween was a patchy marsh (a singular hydrological zone), and pollen diversity values are low. Palaeo-precipitation studies indicate a change in moisture regime and deglacial transition to humid conditions tied to renewal of the ASM, ranging from 14,000-12,000 cal BP, consistent with 'enhanced' and/or 'intensified' monsoon activity that has been recorded in marine core records (Kuhnt et al., 2015), lake levels and river discharge (Wyroll and Miller, 2001), speleothems (Denniston et al., 2013a, b), peat deposits (Field et al., 2017) and alluvial deposition (Wende et al., 1997). Denniston et al (2013) describe more specifically the character of monsoonal redevelopment, demonstrating the Australian Summer Monsoon (ASM) strengthened, weakened, and then strengthened again (16,000-13,000 yr BP). Field et al (2017) similarly show the monsoon slowly strengthened (from 14,000 yr BP).

Girraween provides further evidence of an intermittent climate transition approaching the Holocene boundary. Dampland mixed sedge growth expanded and contracted with terrestrial grasses under shifting rainfall conditions. Aquatic plants were absent suggesting an initial irregular wet seasonality. Extra-local tree growth was sparse, and only *Melaleuca* is recorded (more widely tolerant of wet-dry habitats than *Asteromyrtus* and *Leptospermum*, Cowie et al., 2000; Short and Cowie, 2010). When moist, Cyperaceae (foremost *Cyperus*) combined with taxa such as *Caldesia* and an array of ferns. The latter are common colonisers of disturbed habitats in the tropics (Walker, 1994), confirming the early fluctuating nature of the site. Walker (1994) further suggests ferns are more competitive on low-nutrient substrates. The sub-shrub *Solanum* (12,650 cal BP) similarly prefers disturbed moist habitats, lacking canopy cover (CSIRO, 2010). When present, *Caldesia* indicates shallow waters 20-30 cm deep (Stephens and Dowling, 2002). Alternating drier Poaceae expansions notably incorporated Amaranthaceae/Chenopodiaceae, and taxa from the pioneer-species Fabaceae family.

Local plant growth from 12,700 cal BP (whether across the site floor or immediately peripheral) would trap and bind sediment, with root growth and turnover contributing in-situ organic deposits directly to

the LGM hardset surface (c.f. Semeniuk and Semeniuk, 2004). Sedges and ferns would play notable roles in this process. The importance of ferns in tropical succession, as highlighted by Walker (1994) and Slocum (2000), facilitate the establishment and growth of other taxa by increasing site stability and improving microclimates. Such influence is evident in an increase in diversity measures from c.11,800 cal BP (pollen zone GIR-2, also noting improved pollen preservation), with a richer suite of herbs accompanying Poaceae, including more perennials. Sedges, with their creeping, mat-forming rhizomes, would also not only help retain new sediments and thus nutrients, but retard water flow and evaporation. The development of still water, even if shallow, promotes the anaerobic conditions required for the accumulation of decomposing organics and eventual formation of peat (Andriess, 1988). This too encouraged new species. For example, Cowie et al. (2000) describe the reed *Typha* as preferring stable water levels, and *Typha*'s appearance 12,200-11,600 cal BP indicates these wetter incursions gradually formed perennial ponded water. Haloragaceae's presence (as a wet and dryland herb family) from 11,700 cal BP provides further evidence for developing perennial ponded water. At this time, at least two *Melaleuca* taxa combine with *Asteromyrtus* in an emerging wet-woody community.

Therefore, from 12,700 cal BP, each spike in sedges (and similar taxa) represents a stage in the establishment of swamp conditions responding to monsoon redevelopment, and each more successful than the last in transitioning Girraween from a patchy, singular hydrological system to dual dampland-swamp site. Two extreme, yet short-lived (dual sample) expansions in sedge-swamp coverage center on 11,200 and 10,000 cal BP (dominated by *Cyperus*), consistent with Denniston et al's (2013b) concept of rainfall pulses at this time. These represent the last of the late Pleistocene-early Holocene transition steps; they reduce the abundance of terrestrial grasses and herb pollen locally across the core site, while also starting to interact with expansions in wetland tree growth and initial areas of permanent inundation.

5.2.2. Early into mid-Holocene: permanent lagoon with swamp margins

Standing ponded water at Girraween was initiated c.10,200 cal BP. This coincides with organic (peat) accumulation and greater pollen input. Across northern Australia warmer-wetter early Holocene climatic conditions are commonly recorded. Greatest regional precipitation and reduced annual seasonality ranges c. 9000-4000 cal BP (Field et al., 2017; Denniston et al., 2013b; Proske et al., 2014. Nott and Price (1996) specifically suggest peak NT rainfall 8000-4000 years ago), with a thermal maximum estimated at 6800-5500 cal BP (Reeves et al., 2013) (driven by marine transgression and high sea level stands; coastal flooding facilitating increased moisture and heat transfer/transport fuelling monsoon activity). Importantly, the Girraween wetlands reflect developments of 'reliable' and 'persistent' monsoonal moisture, where north Australia-Indonesia is characterized as 'steadily' becoming wetter through the early Holocene (Wyroll and Miller, 2001, 127; Reeves et al., 2013, 108). Girraween represents a refinement of northern Australian palaeoenvironmental monsoonal-landscape patterns and processes in this respect. Aquatics first appeared at Girraween c.11, 500 cal BP, but were not continuous, and likely first inhabited small ponded waters (as above, but see also Table 1; *Nymphoides* in particular, where Cowie et al (2000) observe depth preferences 20-30cm). As aquatics appeared, ferns declined, in succession toward Girraween incorporating (mid Holocene) larger permanent open water with a range of depths and with greater site stability.

From 10,220 cal BP both *Nymphoides* and *Nymphaea* were present, however conditions remained more suited to *Nymphoides* (still, shallower freshwater with steady infill rates) until c.6100 cal BP. These shallow waters momentarily expanded 9750-9500 cal BP, followed by more gradual increases in deeper water, with small rises in *Nymphaea* (growth range 2-2.5m deep, Cowie et al., 2000) beginning c.9000 cal BP. From c.6100-4000 cal BP, *Nymphaea* becomes well established. It is from this point onwards that sinkhole infilling and permanent water conditions comparable to the modern lagoon existed.

In summary, permanent water at Girraween drove the emergence of taxa characteristic of a dampland-swamp environment to form a fringing zone. *Leptospermum*, *Asteromyrtus* and *Pandanus* were initially more prominent (beginning 8000-7000 cal BP) as fringing woody taxa. Establishment of a woodland

fringe zone was then dominated by *Melaleuca* from 5500-5000 cal BP. In the sedge and herb fringes (6050-4050 cal BP) *Cyperus* was accompanied to a greater extent by *Eleocharis/Schoenus*. These combine with *Fimbristylis*, *Dapsilanthus* and herbs Haloragaceae and *Solanum*. Matching patterns in *Nymphaea* representation occurred at the monsoon peak, and the spatial footprint of wetlands at Girraween was at its widest and wettest.

5.2.3. Late Holocene: drying phases with wetland contraction.

Girraween's permanent, deeper water zones show some contraction through 3750-3500 cal BP, c.2850 and 1300-1250 cal BP (aquatic pollen decline). These contractions may be equivalent to the short-lived drying phases described for locations such as north WA (after 4000 cal BP, Field et al., 2017; Fitzsimmons et al., 2012; McGowan et al., 2012). They are, with changes at Girraween's swampy margins (see below), consistent with increasing late Holocene climatic variability (weakening of monsoon rainfall, Denniston et al., 2013b, heightened seasonality and emerging El Niño-Southern Oscillation (ENSO) relationships, McGowan et al., 2012), but are not considered to reflect the same pronounced aridity as suggested in these other studies.

The fringe sedge-swamp system similarly declined (narrowed) beginning 2850 cal BP. The *Melaleuca* woodlands did not. All Cyperaceae taxa reduced, as well as *Dapsilanthus*. *Fimbristylis* and *Dapsilanthus* alternated to a small degree with *Utricularia* and Haloragaceae, suggesting fluctuation and taxon change at the swamps' water margin into dampland. In a declining swamp, plant accommodation space may have reduced, driving taxon competition at ground level. Herbaceous swamp taxa can also vary in cover and floristic make-up according to the amount of shading imposed by tree canopies (Grindrod, 1988), as with the established *Melaleuca* woodland. *Cyperus* and *Eleocharis/Schoenus* remained co-dominant.

Evidence of monsoon re-expansions in north WA over the last few centuries (Field et al., 2017; Denniston et al., 2015; see also Head and Fullager, 1992) is also manifest at Girraween. The swamp fringe expanded slightly across the last 350 years, for example. This community remained in place through to the present day.

5.3. Dryland change

This section focusses on dynamics and trends in woody-grass plant-functional-groups, divided into broad time phases. Where appropriate, this section provides additional comment on dryland vegetation composition, notably non-eucalypt composition(s). Eucalypts were the dominant surrounding (and regional) dryland tree types through the 12,700 year record. Greater floristic variety is evident in Girraween's intermediate woody layers. Both sclerophyll and monsoonal forest affiliated taxa were present amongst the *Eucalyptus* and *Corymbia*, in varied combinations through the Holocene, and contributed significantly to changing ecologies in this capacity.

The pollen compositional detail provided in Figures 2a-d and Appendix B expands our understanding of woody dynamics by revealing taxa such as *Banksia*, *Grevillea*, as well as *Pandanus* and/or *Livistona*, are the more probable key indicator taxa of vegetation communities differing from the *Eucalyptus*-*Corymbia* systems. These are more likely to occur in concentrated pockets, and Beadle (1981) and Wilson et al. (1990) provide descriptions of *Banksia dentata* and *Grevillea pterifolia* low lying, wet-woodlands as well as wet-fringing woodlands of *Pandanus spiralis*, where *Arecaceae* groves are common components indicating poorly drained damplands. *Banksia*, *Grevillea*, as well as *Pandanus* and/or *Arecaceae* assist in revealing finer subdivisions in Girraween's drylands, the moisture gradients from dry to wetlands in particular (PCA, Appendix A). They are also important as likely harbors of monsoonal-forest affiliated diversity. Pollen records indicate a grass layer is the more prominent, characteristic Holocene lower layer, comparative to any formal shrub/scrub layer(s). A variety of annual and perennial subshrubs, forbs and lianas combined with *Poaceae*, but were largely outcompeted by the grasses.

At Girraween, dryland vegetation and fire changed together. Woody biomass was foremost associated with climate (water availability). Climate was the main driver of tree populations, which in turn determined the nature of fire, collectively shaping vegetation further. Climate-fire interactions differentially affected eucalypt and non-eucalypt dryland woody components (PCA, Appendix A), facilitating coexistence and potentially reducing direct tree-to-tree competition. Fire occurrence, and its

relationship with climate-vegetation feedbacks, is later influenced by human occupation, within the previous 6000-4000 years.

5.3.1. Late Pleistocene-early Holocene: changeable mixed mosaic

Dryland pollen has captured the remnants of a late last-glacial into early-Holocene mixed woodland. Eucalypts were dominant with non-eucalypts incorporated. Broad-leaf deciduous species (*Bombax*), a variety of (semi)deciduous (*Canarium*, *Glochidion*) and evergreen trees (*Alstonia*, *Elaeocarpus*, *Myristica*) and/or shrubs (*Melastoma*, *Trema*) were present. Sclerophyll sub-canopy trees such as *Acacia* and *Terminalia* were included. Importantly, and specifically, both Wilson et al. (1990) and Brock (1995) list these taxa as characteristic of NT monsoonal forest (or thicket) associated with seasonally dry habitats. Beadle (1981) indicates their distribution can include open to enclosed stands amongst eucalypts. Habitats may also include pockets within the sinkhole depression itself. For all authors, this is a distinct vegetation category comparative to any occupying perennially moist habitats. These indications of shifting, seasonal scarcity in woodland moisture supply and storage correspond with alternating peaks in *Eucalyptus*, *Corymbia* and *Melaleuca* canopies, a lack of herbs, and fluctuating establishment of ponded water and/or shifts in sedge-swamp coverage within the sinkhole space. They also coincided with discontinuous wetter *Banksia* habitat and limited *Pandanus* woodland. Forest taxon Urticaceae (*Pipturus*) and Meliaceae (*Melia*) include species favoured by disturbance and regrowth (Hyland et al., 2010), corroborating the disturbance evidence provided by ferns.

These mixed woodland pollen trends show the collective wetland and terrestrial environment was variable at Girraween in response to late glacial climate transitions, including rainfall pulses and intermittent monsoonal renewal, and that an assorted changeable 'mosaic' vegetation had developed. Low charcoal confirms strong climatic controls at this time, and that variability in rainfall pattern did not enhance fire potential. Although relatively woody, a mosaic distribution pattern may have restricted fire, where clumps of different woody plant communities hindered fire spread (Hoffmann et al., 2012a, 2012b; Scholes and Archer, 1997). The sinkhole depression would also provide protection from fire.

Discontinuous grass cover formed one part of the mosaic biomass, and fire was more likely to be limited to these patches at this time.

5.3.2. Early into mid Holocene: grasses expand

Beginning 11,900-11,700 cal BP, woody abundance declined. Decline takes place under strengthening monsoonal renewal, and was led by a reduction in eucalypts; with a greater fall in *Eucalyptus* comparative to *Corymbia*, and culminating in an extended phase of lowest eucalypt presence 11,700-5500 cal BP. As eucalypts decreased, the previous wooded mosaic thinned, grasses expanded and a more uniform open-woodland savanna was initiated. Grass cover was pronounced between approximately 10,800 cal BP and 5500 cal BP, and in the period 10,200-8900 cal BP achieved maximum extent. Grass for woody replacement was accompanied by an increase in burning after 11,000 cal BP and the appearance of fluctuating rises in charcoal. Through the early into mid-Holocene, such fire may have helped keep Girraween's biomass below what is expected to be higher woody-plant carrying capacity under increasingly aseasonal high annual precipitation and temperatures. Lawes et al. (2011) observe rainfall as setting the upper bounds to woody biomass in mesic savannas. So, as precipitation increases, the water demands of woody taxa (trees in particular) would presumably be more easily met, permitting a greater packing of woody biomass within a given space (*c.f.* Sankaran et al., 2004). However, soil depth, and its influence on soil drainage and water holding capacity, is an important determinant of savanna form and function in Australia (Williams et al., 1996). *Eucalyptus* species distribution in the NT is affected by subsurface soil moisture, including landscape inundation patterns and the water-table position during wet and dry seasons. The most common species at Girraween, *Eucalyptus tetradonta*, preferentially occurs on soils that remain well aerated throughout the wet season but suffer drought stress during the dry season (Prior, 1997). *Eucalyptus tetradonta* favours light, deep, well drained soils (Boland, 2002) and appears to have been beyond its upper moisture threshold during the early into mid Holocene. Conversely, *Corymbia* is a known 'tree of moist habitats' (Boland et al., 2006, 210). Ecological preferences toward seasonally

inundated areas with shallow soils (e.g. *Corymbia polycarpa*, Brock, 2001), accounts for *Corymbia*'s expansion 9000-4000 cal BP (Figure 2a summary).

Taxa such as *Eucalyptus tetradonta* would be disadvantaged and marginalized in an environment with lower potential evaporation and greater tendency to waterlogging. They would have likely contracted away from the lagoon to landscape positions capable of free drainage and deeper positioning of the water table. *Eucalyptus* canopies were therefore no longer sufficiently widespread and/or dense enough to competitively constrain grasses. In turn, grasses responded extensively to elevated temperatures and precipitation, competing strongly for light and nutrient resources. Under these circumstances, grasses maintained a fuel load able to carry fire. Vegetation openness then also assists fire spread (c.f. Lehmann et al., 2008). Unfavourable waterlogged growth conditions may also have rendered *E. tetradonta* vulnerable to what fire was present. Grasses, and the flame zone of grass-layer fires, are capable of reducing the emergence, growth and survival of woody seedlings also favouring the maintenance of open vegetation (Scholes and Archer, 1997; Bond et al. 2012). Studies into grass-fire feedbacks demonstrate grasses produce a fuel bed with low bulk density, resulting in relatively intense fires with higher burn severity (Hoffmann et al., 2012b). Such fire types may have been capable of persisting through wetter monsoonal climate phases that maintained a distinct dry season.

As eucalypts declined, non-eucalypts increased. Both sclerophyll and monsoonal-forest-affiliate non-eucalypts formed a greater proportion of woody taxa between 11,200-10,200 cal BP and again 9700-6000 cal BP. With *Eucalyptus* decline during these phases, reduced tree-to-tree competition also came into effect (Scholes and Archer, 1997; Lawes et al., 2011), reflected in increased representation of taxa such as *Acacia*, *Petalostigma* and *Terminalia*. A shift in mid-layer composition toward sclerophyll low trees-shrubs was further initiated, where a mixture of *Brachychiton*, *Cochlospermum*, *Atalaya*, *Dodonaea* and *Calytrix* were incorporated. *Brachychiton*, *Cochlospermum* and *Atalaya* prefer sparse cover (Brock, 1995; Short and Cowie, 2010), confirming the early- into mid-Holocene canopy openness and savanna structure primarily driven by the *Eucalyptus*-grass dynamics.

In the mesic savannas of the NT the non-eucalypt trees are the fire-sensitive plant group (Murphy et al., 2015; Brock, 2001). At Girraween, Holocene non-eucalypts responded positively to increases in water availability. Their dynamics were driven by the strength of the ASM in both the amount of rainfall delivered and its seasonality, and available plant moisture appears to have facilitated greater co-existence of different woody components, and also when confronted with increasing fire in the catchment (*c.f.* Lawes et al., 2011; Woinarski et al., 2004). For Girraween, it is proposed that standing open-water and lagoon expansions filling the sinkhole depression encouraged development of onshore soil-moisture gradients beyond the site and swamp zone (as above), and a sequence of concentric woody vegetation zones was the result. Wet to dry, *Melaleuca* woodlands bordered mixed riparian woodland (including *Corymbia*) which fringed the *Eucalyptus* open-woodland-savanna. Many of the signature seasonally dry thicket indicators and/or sub-canopy deciduous taxa declined beginning 9700 cal BP. Habitats within the sinkhole depression were gradually lost as standing water and peat accumulation filled the space. Drier thicket indicators and/or deciduous habits are largely replaced by taxa such as *Celtis*, *Ficus*, *Timonius* and Anacardiaceae (possibly *Bunchania*), *Ilex* (Aquifoliaceae) and *Barringtonia* (Lecythidaceae), described as occupants of evergreen monsoonal forests and/or riparian-type communities (Brock, 2001, 1995; Short and Cowie, 2010). Early *Pandanus* consistency from 9750 cal BP (notably incorporating *Arecaceae* 9350-9250 and 7100-6600 cal BP) further highlight these wetter woody habitats situated between lagoon fringe environments and the *Eucalyptus*-grassland community. Humid conditions, with reduced seasonality would limit moisture loss, creating microclimatic and soil conditions favourable for evergreen woody seedling recruitment. Closer canopies thereby excluded grasses and reduced the vulnerability of these habitats to fire. Early- into mid-Holocene fires would not significantly extend into these wetter vegetation types closer to the lagoon, further confining the impact of any fire that existed to the *Eucalyptus*-grass system away from the lagoon edge. Collectively, these wetter zonations acted as fire refugia for non-eucalyptus taxa, aiding subsequent expansions into the broader catchment.

5.3.3. Late Holocene: peak woody regrowth

Grass cover declined relative to woody cover in the mid-into late-Holocene. Burning increased and major peaks in charcoal abundance are recorded. *Eucalypt* abundance rose, initially expanding between 4100 and 3100 cal BP. Maximum sustained *Eucalyptus* pollen input spans 2850-600 cal BP, indicative of an open forest and peaking across the period 1150-600 cal BP. *Corymbia* remained stable during these times. Late Holocene climatic variability provides favourable catchment conditions for *Eucalyptus*, further enhanced by changes in fire regime.

Driven by overall drier climates and a likely increase in potential evaporation, *Eucalyptus* species recolonised the catchment. Weakening of the monsoon, and greater potential for seasonal drying (e.g. Denniston, 2013a, b) expanded the well-drained habitat preferences of taxa such as *E. tetradonta*. Contractions of the lagoon's open water and swamp zone suggests reduced water recharge and lowering of the water-table enhancing deeper drainage. As a developing open forest, the negative effects of *Eucalyptus* on grasses intensified, including effects resulting from shading of the shade-intolerant tropical grasses and to a lesser extent nutrient/water competition (Scholes and Archer, 1997; Sankaran et al., 2004). This change provided an opportunity for *Eucalyptus* seedlings and regrowth to escape previous grass competition.

Increases in woody-supported burning created a positive feedback loop; as *Eucalyptus* increased and became structurally stable, grass production was suppressed making repeated grass-led fires of the previous intensity required to maintain a more open canopy less likely (Bowman and Prior, 2004; Scholes and Archer, 1997). Fire in the late Holocene did not impact as an agent of disturbance; charcoal volumes are high, but the associated fire was not destructive, rather constructive, and the site appears to have supported high woody cover in the face of decreased available plant moisture. Milder but frequent burning type fire regimes encouraged biodiversity (Bowman et al., 2018) may also have buffered dryland vegetation from climate variability (Bird et al., 2013).

The same reduction in effective precipitation and lower soil-water storage at this time restricted the expansion of *Corymbia* and non-eucalypts. It is because of decreased and/or inconsistent moisture supply and retention that monsoonal-forest taxa in particular were not able to take advantage of less

abundant fire at certain phases in the last 1500 years. Wetter-loving taxa (*Barringtonia*, *Ilex*), renewed clusters of *Banksia-Grevillea*, and expanded *Pandanus-Arecaceae* show established woody transition communities approaching the lagoon remained into the late Holocene. Later Holocene intermittent *Brachychiton* and *Cochlospermum* reflects declining sclerophyll community openness, and *Acacia* was no longer a common component after 4000 cal BP (where Bowman et al. 1988 suggest *Acacia* also respond more positively to vegetation openness, and Hoffmann et al. 2012a highlight shade intolerances typical of savanna woody species). Woody-herbaceous Euphorbiaceae (*Euphorbia*, *Acalypha*) and Fabaceae taxa otherwise increased, adding to ground layer diversity amidst less grasses. Comparative to the early- and mid-Holocene, disturbance indicator taxa are absent (e.g. *Dodonaea*). Conversely, sclerophyll types *Callitris* and *Jaksonia* expanded as fire incidence was reduced, demonstrating landscape variability remained and available fire-protected habitats also existed away from the lagoon. The data suggest a structurally stable late Holocene system.

5.4. Human influences and site resources

Archaeology collated from the late Pleistocene (glacial phase) to early Holocene suggest a sparsely populated Top End region of highly mobile societies with extensive open social networks (Williams et al., 2015a, b). Small bands of hunter-gatherers exploiting riverine and savanna resources are described (Fredericksen et al., 2005; Bourke 2004; Brockwell, 2005). Populations remain low and isolated until 11,000-7000 yr BP, followed by an early to mid-Holocene characterized by exploration and expansion (9000-6000 yr BP). Significant technological, social and population changes then took place in the mid to late Holocene (4000 yr BP onwards, broadly referred to as 'intensification', see Brian, 2006, Williams et al., 2015a, b; Brockwell et al., 2009). In the area approximating the Larrakia estate (Cox Peninsula to Adelaide River) permanent Holocene occupation spans the previous 4000 years. Prominent expansions in human activity are estimated at 2300 yr BP and again between 1500-1000 yr BP.

Large water sources are repeatedly described as locations where hunter-gatherer populations concentrated during the Holocene (e.g. Williams et al. 2015a use the term 'converge', referring to waterbodies as resource-rich patches). In publications on the value of freshwater to Indigenous people

in northern Australia today, many waterbodies hold economic, ceremonial and social significance (Jackson, 2005; Toussaint et al., 2005). As not only a sizeable lagoon, but a site with permanent lake-like water from c.6000 cal BP, Girraween would have been a prominent feature for local people from this part of the Holocene, and particularly during variable monsoonal climatic conditions. Facilitated by permanent water, it is therefore possible human-fire resource management and/or social activities acted in conjunction with climatic and edaphic factors mid-Holocene, to influence Poaceae increases and hinder woody abundance. At times when other northern Australian sites (e.g. Proske, 2016; Head and Fullegar, 1992; Field et al., 2017) do not have sufficient freshwater to maintain wetland development (and undergo drying, to the point of aridity in these examples), Girraween was far less susceptible to disruption from climate change and remained a significant and reliable water supply.

The importance of Girraween as a water source is enhanced when at 3900 yr BP the mangrove transition phase resulted in a period of reduced (or variable) productivity on the NT coastal floodplains. With an intermingling of saline and freshwater zones, floodplain swamps were no longer a focus of settlement and exploitation. The unpredictable nature of the food-water resource base meant that coastal floodplain sites were not used as frequently, and populations became more widespread (Brockwell, 2005, 1996). Earth-mound cultural material recoveries show foraging strategies diversified; floodplain species (fish, turtle) declined and woodland resources (wallaby, possum) became more important (Brockwell, 2005; Burns, 1999).

Greater intensity local human movements and changes in resource-sourcing within the later Holocene are reflected in Girraween's dryland. It is at a near exact time that these changes in resource use are recorded (c.3750 cal BP), that Girraween experiences a change in fire regime and vegetation transformation. The ultimate expression of hunter-gatherer presence at Girraween is likely to be the stable open mixed forest. Ubiquitous charcoal-fire records are indicative of anthropogenic burning (Williams et al., 2015) and consistent with contemporary Aboriginal fire management of multi-mosaic burning with lower fuel loads (such as grasses), linked to structural woody complexity and plant diversity in Australian savannas (Trauernicht et al., 2016). Interestingly, Williams et al (2015) suggest

Aboriginal use of fire was higher during periods of climatic variability, when increases in landscape productivity were required. Ethnographic sources and NT information presented in Russell-Smith et al. (1997) indicate burning was particularly undertaken around water sources. Similarly, Bowman et al. (2004) highlight NT Indigenous burning patterns mirrored their tracking of resources. This included water, but that greater hunting effort of Aboriginal people targeted the higher densities of macropods supported by the more fertile mesic savannas (such as surrounding Girraween). Head (1994) applies such findings to the prehistoric period, stating that Aboriginal burning observed ethnographically in northern Australia, (embedded in patterns of seasonality) was a feature of the late Holocene. Head (1994) expands socially on the economical, adding that the concept of 'cleaning up the country' is also at least this old.

Girraween was therefore an attractive wet-dry resourced location. One of the 'markers of human intensification' is the increasing investment in, and handling of, such productive habitats (Williams et al., 2015a, b). Burning to encourage small game is one part of such behaviour. Fire use, as a translation of people's stewardship over country, is another (Head, 1994). Darwin regional archaeological evidence shows an increasing territorialism as a result of late Holocene population growth. This is what Williams et al. (2015b) refer to as demographic packing, where social and religious systems were formed to provide frameworks for negotiating ownership and/or maintenance of resources and property within a given area. After c.2500-2000 yr BP, 'packing' is seen in the increasing variety and diversification of archaeological sites around Girraween, notably the appearance of earth mound and cultural shell middens and open-artefact sites at locations such as the Alligator, Adelaide and Mary Rivers (Fredericksen et al., 2005, and references therein) as well as Darwin Harbour and Hope Inlet (Burns, 1999; Bourke, 2004). Dense occupation, a range of social, economic and environmental variables interacted in the Darwin region to peak in the last few thousand years, translating into peak relations with the Girraween catchment and management of fire and woody plants as an open forest and profitable mesic space. Suggestions of the introduction of disease from the Macassans (<750 years), resulting in significant population decline and break-down of estate borders across the Top End, may explain more recent declines in forest cover. Historical depopulation through European contact (<200

years) may also have been captured (Williams et al., 2015a; Brockwell, 2005). For archaeological research Girraween provides a comprehensive ecological context inland from the coastal fringe.

6. Conclusion

Understanding the functioning of Australia's tropical savannas is central to the management of these ecosystems, which face increasing population pressures, land use changes, shifts in disturbance regimes and climate change (Lehmann et al., 2008; Laurance et al., 2011). For contemporary ecology, the palaeoecology of sites such as Girraween have a role to play, in communicating long-term vegetation composition and the determinants of savanna structure. The Girraween record highlights change as a continuous process in the NT Top End, operating at a range of time-scales, with varied outcomes involving climate, fire and people. At the Holocene time-scale, moisture availability as determined by climate, has been the primary driver of Girraween's vegetation dynamics. In turn, the extent of fire and fire impact, were characteristics of climate and resultant vegetation. These feedbacks shift in the later Holocene, when Girraween may have become a more socialized and managed human landscape. The detail available in this study is based upon 117 identified pollen taxa, in a region where little savanna palaeoecological information has been available. In such aspects, this paper is a significant step forward.

The focus of this paper has been the upper 5 m of a 19.4 m core. This analysis of the Holocene now establishes a basis for the identification and interpretation of pollen and charcoal from the remainder of the core. In turn, having additional core material permits further examination of certain vegetation-environment relationships. Reduced woody abundances and high grasses are recorded in the early- to mid-Holocene, a time defined as warmer-wetter, with reduced annual seasonality. That modern-day seasonal climatic wet-dry cycles play a part in maintaining limited tree cover, keeping current canopies open and enabling grass persistence (House et al., 2003), leads to the question: to what extent was there still a dry season when the monsoon strengthened in the past? To what extent can the presence of a dry season, and/or magnitude in wet-dry monsoon cycles, be refined by the palaeoecological record of open savanna? Further, at no stage during the Holocene did fire-moisture conditions combine

to permit a competitive advantage and widespread expansion of non-eucalypt taxa at Girraween.

Therefore, for the north Australian tropical savannas, when and under what circumstances were non-eucalypts pronounced in the landscape? Expanding Indigenous populations as an alternative explanation to keeping woody biomass at Girraween below that expected in the mid-Holocene also requires further investigation. Cross-site data syntheses will help with such questions. The Girraween record is the first stage in the establishment of a comprehensive regional north Australian long-term data-set demonstrating the complex nature of savanna ecology and palaeoecology. What also remains is to merge Girraween within a series of Quaternary study sites from across the Northern Territory 'Top End'.

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Appendix A Supplementary Material: Principle component analysis of the Girraween Lagoon

Holocene pollen data.

An unconstrained Principle Component Analysis (PCA) was undertaken to explore relationships between Girraween's pollen zones and examine their organisation along ecological gradients. The first two axes of the PCA are shown in Figure A.1, and explain 52% of the variation within the data. How the plant functional-environmental response groups drive sample and zone distribution across the bi-plot

space is also shown. Sample distributions along the first axis (the x axis) appear to represent degrees of openness within the vegetation. The distribution of samples along the second axis (y axis) is considered to reflect a moisture/fire gradient.

From oldest to youngest, the pollen zones plot in an approximate clockwise progression. The oldest zone (GIR-1, 12,700-11,000 cal BP) is positioned in the top right of the bi-plot. Only one other sample is incorporated into this space. This quadrat of data reflects the presence of non-eucalypts, with the position of some samples further influenced by grasses and/or herbs. Woody versus non-woody taxa, and wider spread sample proximity, demonstrate the variable nature of this time period. Zones dating 11,800-8700 cal BP (GIR-2, GIR-3 and notably GIR-4) then cluster together in the lower right, defined more strongly by the presence of grasses and to a lesser extent herbaceous taxa. Zone GIR-5 (8700-3000 cal BP) largely separates and dominates across the lower left, dictated by eucalypts but also crossing the y-axis. Zones encompassing the previous 3000 years also cluster together in association with eucalypts as well as non-eucalypts (less predominantly). However, zones GIR-6 and GIR-7 (3000-450 cal BP), occupy the top left more distinctly than GIR-8 (previous 450 years), which transitions back into the space occupied by GIR-5 and the eucalypts. The PCA also illustrates that the period of least variability within the record has been over the last 3000 years.

Figure A.1: Principle components analysis (PCA) of the Girraween Lagoon pollen data. Samples distinguishing each pollen zone are coloured and outlined. The bi-plot shows the driving position between the four main plant functional groups, and inferred ecological gradients. The first two axes explain 52% of variation in the dataset.

Appendix B Supplementary Material: Complete data description, Girraween Lagoon Holocene record.

The pollen and charcoal Holocene record for Girraween Lagoon is divided into eight zones. Detailed descriptions of the pollen, charcoal, and sedimentological data are provided below. An outline of data has been presented in the main article text.

B1.1. GIR-1 (504-458 cm below sediment surface (bss), 12,670–11,820 cal BP).

The lowermost post glacial section of the core is highly variable, and composed of fine clays (strongly mottled, grey to dark grey 2.5Y 6/1-2.5Y 4/1) with interlayered sand and small clay aggregates (from 500-492 cm and 489-481 cm bss), and two thin bands of heavier compact clay (492-489 and 481-477 cm bss, very dark grey 2.5Y 3/1). Sediment boundaries in this unit are not distinct and the variable nature of sediments has impacted pollen concentrations. Very low pollen counts, with poorest preservation, occurs at depths 490, 467 and 461 cm. In this zone, charcoal accumulations are at their lowest for the record.

Poaceae initially makes up a large proportion of the pollen sum (67-69%, 12,675 – 12,590 cal yr BP), declining toward 13% before rising again to 50% at the zones 1-2 boundary. Sedges (and similar wet-ground indicators) show the opposite pattern; these jump to 29% as Poaceae declines (e.g. 467 cm bss, 12,010 cal yr BP), and incorporate three Cyperaceae taxa as well as *Caldesia*, *Typha* and *Dapsilanthus*. Pteridophytes are also important (and peak) in this zone. Other herbs show low values throughout, consisting of Amaranthaceae, *Spermacoce*, Solanaceae and Fabaceae types.

Dryland associated Myrtaceae form the bulk of woody taxa, averaging 20% of total pollen, but with a sharp spike in the upper zone to 76% of the pollen sum (473 cm bss, 12,130 cal yr BP). As preservation has affected distinguishing grain features undifferentiated Myrtaceous taxa dominate this category. However, grain sizes $\geq 15\mu\text{m}$ do suggest Eucalypteae (see Thornhill et al., 2012; Stevenson et al., 2015 consistent with *Eucalyptus* and *Corymbia* modern pollen collections). Other sclerophyll woodland taxa occur in low abundance; slight rises adjoin the Myrtaceous peak and 11 taxa are recorded (particularly *Terminalia*, *Petalostigma* and Proteaceae types, with repeat occurrences of *Acacia*, *Casuarina* and *Pandanus*). Wetland Myrtaceae comprise *Melaleuca* types only and largely appear mid-zone (478cm bss, 12,230 cal yr BP), increasing to 14%. There is no significant presence of monsoonal-forest group taxa; the liana *Stephania* is recorded, an occupier of forest edges providing some evidence of the local presence of a monsoon forest group. Mangroves show only trace value.

B1.2. GIR-2 (458-420 cm bss, 11,820–10,965 cal BP)

Transition from zone 1 into 2 correlates with an additional sand layer in the fine clay (460-446 cm bss). This fine clay continues until depth 441 cm, abruptly changing into dark (2.5Y 2.5/1, black) fibrous, organic mud containing sand and grit. Pollen and charcoal inputs remain very low and do not begin to increase until the uppermost samples. At this point rises are substantial.

Sample-to-sample variability as seen in zone GIR-1 continues. Poaceae forms an early important proportion of the pollen sum (41-46%), then shows a decline in abundance (26 to 9%), with corresponding increases in sedge categories. Sedges (and similar) which peak strongly at 84% toward the top of the zone (431 cm bss, 11,215 cal yr BP; best represented by *Cyperus*, with low consistent *Eleocharis/Schoenus* plus small rises in *Fimbristylis* and *Typha*). Aquatics primarily *Nymphoides* (5%), appear for the first time (c. 11,750-11,480 cal yr BP), just prior to the sedge peak, but are not maintained. The largest range of Pteridophytes occurs and there is an increased representation of herbaceous taxa. Eight sub-shrubs and eight forbs now are recorded (particularly Solanaceae, Goodeniaceae and Amaranthaceae types, with *Spermacoce*, c.f. *Jacksonia* and *Tricodesma* sub-shrubs. Fabaceae and Haloragaceae, Apiaceae/Platysace, Asteraceae, *Euphorbia*, *Polycarpaea* and *Tribulus* forbs are incorporated).

Woody representation is lower and marked by reduced Myrtaceous dominance. Dryland Myrtaceae fluctuate to a greater extent (3-15%) than wetland associated Myrtaceae (2-8%), the latter now incorporating Leptospermaceae (*Asteromyrtus*). *Eucalyptus* and *Corymbia* values are comparatively even. Other sclerophyll taxa average 7% (in total) of the pollen sum. *Casuarina*, the Fabaceae types, *Acacia*, *Pandanus* and *Petalostigma* show slight increases and *Dodonaea* is introduced into the record. These combine with minor *Banksia*, *Arecaceae* and *Terminalia*. There is an increase and developing consistency in the range and presence of monsoonal-forest taxa (10 taxa, up to 6% of the pollen sum from the base of the zone), including *Bombax*, *Elaeocarpaceae*, *Ilex*, *Melastoma*, *Myristica* as well as some composite identifications. No lianas or mistletoe are recorded. A small expansion in mangroves is seen, comprising *Rhizophora* and *Ceriops/Bruguiera*.

B1.3. GIR-3 (420-372 cm bss, 10,965–9870 yr BP)

A clear shift in sedimentation takes place into GIR-3. Dark (2.5Y, 2.5/1, black), organic consolidated peat material occurs. This is visually decomposed, with uniform spongy texture lacking sand or grit, is coincident with pollen zonation, and continues through zone GIR-4. Greater pollen concentrations and improved pollen preservation is associated with this sediment type. Pollen concentrations are variable, reaching above 10,000 grains/cm³ at the top of this zone. In a similar pattern, charcoal abundance varies over a wide range between samples.

GIR-3 features a rise in Poaceae (>60%) until presence of the sedge group increases sharply toward the top of the zone. This peak in sedges is dominated by *Cyperus* (77%). *Eleocharis/Schoenus* and *Fimbristylis* remain secondary taxa with limited distributions. Other minor wet-ground taxa such as *Dapsilanthus* and *Typha*, the Pteridophyta are also present, and combine with a low abundance of aquatics (*Nymphoides* is the primary aquatic). Contributing to this community are two lianas (*Flagellaria* and *Ampelocissus*), commonly associated with freshwater and/or riparian vegetation (Short and Cowie, 2011). The Cyperaceous undergrowth expands markedly (but momentarily) at 377 cm bss (9990 cal yr BP). Herbaceous taxa are eliminated from the record across this same depth and time. The wetland Myrtaceae woody fringe increases in representation, at 398 cm (10,470 cal yr BP) and 377 cm depth (9990 cal yr BP, to 13% of the pollen sum); *Melaleuca* percentages rise slightly from the previous zone while Leptospermeae (*Asteromyrtus*) remains stable. Leptospermeae (*Leptospermum*) is newly recorded at the top of the zone.

Reduced dryland Myrtaceous values are maintained for most of the zone (<10%). *Eucalyptus* and *Corymbia* are recorded, with the first appearance of *Calytrix* combining with *Acacia*, *Dodonaea*, *Banksia*, *Casuarina*, *Pandanus* and *Petalostigma* as sub-canopy taxa. *Cochlospermum* and Sapindaceae (c.f. *Atalya*) are introduced into this mixed woodland at this point. Dryland Myrtaceae rise (to 17%) at 377cm to dominate other sclerophyll taxa. Monsoonal forest associations are not a widespread vegetation feature (<2% each). Small (but increasing *Rhizophora*) numbers are incorporated into this zone.

B1.4. GIR-4 (372-320 cm bss, 9870–8670 cal BP)

Four details stand out in GIR-4; (1) consistently high Poaceae (>65%), and (2) reduced sample-to-sample variation. Further, (3) mangrove taxa increase (*Rhizophora*, coinciding with a *Ceriops/Bruguiera* return). In response, (4) dryland and wetland Myrtaceae are at their lowest in the record ($\leq 5\%$) to this point. Relative to the Myrtaceae, other sclerophyll taxa are slightly higher ($\leq 7\%$). The individual values of *Dodonaea*, *Acacia*, *Pandanus*, *Petalostigma* and *Terminalia* are greater or on par with those for *Eucalyptus* and *Corymbia*, *Melaleuca* and Leptospermeae, and intermingle with minor Arecaceae, *Bracychiton*, *Cochlospermum*, *Calytrix* and Fabaceae. Loranthaceae is also a part of this community. Monsoonal forest taxa show small but increasing abundances toward the top of the zone; beginning c.9450 cal yr BP, incorporating nine taxa, best represented by the Cannabaceae types *Trema* and *Celtis* but also reflected in the lianas. Small volumes of herbs are present amidst the Poaceae; forbs outnumber sub-shrubs and include Asteraceae, *Euphorbia*, Fabaceae types and Laminaceae-*Pogostemon*. Sedge (and similar) taxa do not fluctuate to the extent seen in earlier zones (maintaining 6-10%) and remains dominated by *Cyperus*. Aquatics (*Nymphoides* prominent) are initially higher. Conversely, Pteridophytes are absent at first then return in low numbers.

By around 9710 cal yr BP (365 cm bss) charcoal accumulations have increased to one of the highest values recorded. Charcoal accumulation rate declines thereafter (but remains above previous levels), through to ~9250 cal yr BP (345 cm bss), then rise again. A similar trend in pollen concentration is less pronounced.

B1.5. GIR-5 (320-175 cm bss, 8670–2975 cal BP)

Sediments in this zone comprise dark, organic and consolidated peat materials, continuing up-core into GIR-6 and GIR-7. This zone features a band of sand, spanning 287-266 cm bss (7125 – 6075 cal yr BP). The approximate depth of this sand corresponds with a series of changes in the pollen assemblage. Charcoal shows sustained increases via a series of spikes, reaching highest values in the record at 223cm bss (4080 cal yr BP) and 180cm bss (3070 cal BP; around 1 million particles/cm³ each).

Further mangrove expansions take place until c.6600 cal yr BP (c.277cm bss, >10%), after which percentages decline but are maintained for the remainder of the core (2-3%). *Rhizophora* is the principle taxon; *Ceriops/Bruguiera* show lower values and fluctuate to a greater extent. Poaceae decreases from GIR-4 and fluctuates between 23-46% of the pollen sum. The presence of herbs is small but consistent. Haloragaceae, Asteraceae and *Euphorbia* remain the major taxa, accompanied by Solanaceae/*Solanum*, Fabaceae (c.f. *Jacksonia*) and Amarathaceae types.

Sedges (and similar taxa) expand from GIR-4, building to a mid-zone high (~30%, centered on 245 cm bss, 5100 cal yr BP). *Cyperus* remains most common, however previously minor Cyperaceae increase. *Eleocharis*, *Fimbristylis* and greatest representations in *Dapsilanthus* and *Typha* are incorporated (the latter in separated peaks). Lianas may also be contributing to this wetland community (Vitaceae, for example, contains species known to occupy shallower parts of *Melaleuca* swamps, Cowie et al., 2000). Indications of wetland (and water depth) expansion are reinforced mid-zone with rises in aquatics. *Utricularia* is recorded for the first time and higher *Nymphaea* occurs (c. 255 cm bss, 5555 cal yr BP), maintaining constant percentages from this point onwards.

Total woody taxa increase through GIR-5. Dryland associated Myrtaceae strengthen towards the top of the zone (to 25%). Gradual increases in *Eucalyptus* pollen types are recorded (dominated by the *E. tetradonta* type). Total *Corymbia* pollen is more consistent through this zone, at lower values than the *Eucalyptus*, and *Calytrix* is present throughout (rising slightly from previous zones). Wetland Myrtaceae also increase toward the upper zone, jumping in value after the sedge group expansion (notably *Melaleuca-A*). The minor *Melaleuca* pollen types show rough alternation with *Leptospermum* and *Asteromyrtus*, suggestive of some flux in wetland secondary tree and/or shrub growth within a *Melaleuca-A* canopy. Non-Myrtaceous sclerophyll taxa consist of 19 pollen types (the highest recorded), incorporating the first appearance of three taxa (*Erythroleum*, Euphorbiaceae (*Excoecaria/Homolathus*), Malvaceae types). This group's stronger presence continues from GIR-4, higher at the base of the zone (to 14%, 287-277 cm, c. 7125-6610 cal yr BP), declining from then on, driven by falling *Acacia* and in particular *Pandanus* (from peak values 298-266 cm bss, c. 7676-6070

cal yr BP). Secondary and more stable taxa include *Petalostigma*, *Dodonaea* and *Terminalia*.

Casuarina and Fabaceae pollen are better represented early in the zone, *Banksia* and *Cochlospermum* later. Monsoonal forest taxa maintain ~5% of the pollen sum, but nonetheless comprise a broader range of 15 taxa. Trace values of *Trema*, *Urticaceae/Moraceae* and *Glochidion* are the most re-occurring. Other taxa such as *Barringtonia*, *Anacardiaceae* and *Celtis* are more intermittent. The remainder are sporadic.

B1.6. GIR-6 (175-130 cm bss, 2975–2042 cal BP)

Fluctuations between charcoal samples have become comparatively less dramatic in this unit. Values remain lower than zone five peaks, but higher than the early Holocene average. Pollen concentrations dip slightly mid zone, then maintain consistency. Pollen assemblages are comparable between samples. Dryland Myrtaceae and Poaceae become near even in representation (averaging 32.25 and 33.75% of the pollen sum, respectively) and together characterize this zone.

Eucalyptus, followed by *Corymbia*, increase in dominance as woodland arboreal taxa. *Calytrix* is present, maintaining similar values to the minor Eucalypteae pollen types (and in continuation from the upper half of GIR-5). These combine with a reduced range and abundances of secondary woody taxa (11 sclerophyll and 8 monsoonal-forest taxa). *Terminalia*, *Petalostigma* and *Dodonaea* are the best represented. Trace values in other sclerophyll taxa include *Acacia*, *Arecaceae*, *Banksia*, *Cochlospermum* and Fabaceae type. *Callitris* is new to the sclerophyll group. Very low forest representatives include *Celtis*, *Trema*, *Ficus*, *Anacardiaceae*, *Barringtonia* and *Premna*. In the wetland zone, *Melaleuca-A* is the primary tree. Lesser *Melaleuca* pollen types now overlap with minor *Leptospermum*, although *Asteromyrtus* has faded from the zone. The sedge group declines overall, driven by fallen Cyperaceae values (*Cyperus* to a greater degree) and where *Typha* is not recorded. Slight co-recorded increases in *Utricularia* and *Dapsilanthus*, alongside *Nymphoides*, occur at 158cm bss (2625 cal yr BP).

With the exception of a single upper-zone sample, herbaceous taxa consistently make up c.3 percent of the pollen sum. A greater range of sub-shrubs occurs comparative to forbs. Subshrubs consist of

Amaranthaceae, *Cariospermum*, Fabaceae (*c.f. Jacksonia*), Malvaceae (*c.f. Sida*), Solanaceae-*Solanum* and Spermaceae. Apiaceae (*Platysace*) and Haloragaceae are the only forbs recorded, the latter more common.

B1.7. GIR-7 (130-30 cm bss, 2042–442 cal BP)

Between 130-40cm the dark organic peats become progressively less consolidated and more fibrous. From 40cm bss, the peat is less decomposed, and incorporating algae and a higher water content (2.5Y, 3/1, very dark grey) toward the surface. With this change, pollen concentrations gently decline. Higher charcoal inputs are maintained until 91cm (1400 cal yr BP), with a prominent decrease mid-zone (73cm, 1150 cal yr BP). Burning expands again toward 40cm bss (600 cal yr BP, noting the bulk of charcoal concentrations remain comparable to GIR-6).

Across the zone boundary from GIR-6 Poaceae falls to values less than terrestrial woody taxa; dryland associated Myrtaceae dominate GIR-7 and the fall in grasses is constant (Poaceae ranges 21-30% and dryland Myrtaceae 37-47%). *Eucalyptus* and *Corymbia* reach their maximum extent in this zone and appear to co-dominate (where small peaks in one do not occur at the expense of another). *Calytrix* declines, but remains present. Sixteen non-Myrtaceous sclerophyll taxa are incorporated (3-7% for the group). Of these, *Pandanus*, *Petalostigma* and *Terminalia* are the highest recorded (elevated percentages spanning approximately 100-90cm bss, 1540-1390 cal yr BP). *Acacia*, Arecaceae, *Casuarina* and *Dodonaea* pollen are slightly less frequent, while *Banksia*, *Callitris* and the Fabaceae types are intermittent. *Grevillea/Hakea*, Malvaceae, Euphorbiaceae (*Excoecaria/Homolanthus*) return after absences of considerable depth. *Cochlospermum* and Rutaceae/Araliaceae disappear following an early presence, possibly in response to *Eucalyptus* competition. .

Wetland Myrtaceae also expand to maximum extent (20%). *Melaleuca-A* remains the principle taxon (to 12%) and *Melaleuca-B* is at its most abundant for the record (5.5%). Remaining Melaleuceae are variable but remain low, peaking at different stages. *Leptospermum* alternates between the melaleucas while *Asteromyrtus* appears in the majority of samples at trace values. Ten monsoon-forest associated taxa are distributed throughout the zone. *Trema* is the best represented pollen type, *Bombax* and

Glochidion/Nauclea also occurring more than once. A small mid zone rise in in the wetland Myrtaceae and other woody sclerophyll groups (97-91 cm bss, 1490-1400 cal yr BP) sees a corresponding decline in dryland Myrtaceae and forest affiliated taxa.

Herbaceous taxa roughly divide mid zone. A greater array of sub-shrubs occurs through the lower half of GIR-7, switching to majority (and an increased range) of forbs in the upper. Amaranthaceae, *Cardiospermum*, Solanaceae-*Solanum*, *Spermacoce*, the Euphorbiaceae and Fabaceae sub-shrubs give way to Apiaceae (*Platysace*), *Alysciarpus*, *Macroptilium*, Haloragaceae, Liliaceae and *Murdannia*. Asteraceae is the one exception, with strongest representation zone wide. Sedge and other wet ground taxa maintain similar group abundances to the previous zone (c.10%), but include maximum *Utricularia* and a temporary expansion in *Dapsilanthus*. Both deeper (*Nymphaea*) and shallow (*Nymphoides*) aquatics are ongoing (to 5% of the pollen sum) and moisture-favouring lianas are present. Pteridophytes are absent.

B1.8. GIR-8 (30-0 cm bss, 442 – c.20 cal BP)

This zone is marked by a decline in dryland Myrtaceae, with corresponding increases in Poaceae (down to 24%, up to 34%, respectively). This zone is also separated through increases in sedge (and similar) taxa. Herbaceous pollen and wetland Myrtaceae remain stable compared to GIR-7, with slight rises in the representation of non-Myrtaceous sclerophyll as well as monsoonal forest taxa. Aquatics increase in the uppermost sample.

A number of non-myrtaceous woody taxa (sclerophyll and forest) are lost in the transition from Gir-7, however many of those remaining increase in abundance. *Pandanus* and *Petalostigma* are common, and combine with increasing *Terminalia* (notably), *Acacia*, *Arecaceae* and *Casuarina*. Fabaceae types and *Dodonaea* are also present. Accompanying forest taxa include *Bombax*, *Celtis*, Euphorbiaceae (*Macaranga*), *Ficus*, *Podocarpus*, *Trema* and Urticaceae/Moraceae. *Eucalyptus* and *Calytrix* pollen initially decline but stabilize toward the surface. *Corymbia* decrease throughout the zone.

Leptospermum and *Asteromyrtus* are not recorded toward the surface. *Melaleuca-A* also falls (although remains dominant in the wetland zone); conversely minor *Melaleuca* taxa rise slightly. Small gains in

Cyperus (primarily), *Eleocharis/Schoenus*, and consistent low values in *Fimbristylis*, and *Dapsilanthus* also characterize the wetland environment. The aquatics *Nymphaea* and *Nymphoides* now combine with minor *Potamogeton*. Herbaceous cover consists of a similar proportion of sub shrubs to forbs, although the range of taxa has declined.

Pollen and charcoal curves initially decline before stabilizing at 15cm bss (125 cal yr BP), subsequently falling again toward the surface.

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Figure 1: Map and images of Girraween Lagoon showing location, core site, site vegetation communities (described in Table 1), water bores surrounding the lagoon, and the manner in which the lagoon surface is coincident with the water table in the wet and dry seasons (photograph by M. Bird).

Figure 2: Girraween Lagoon percentage pollen diagram plotted against depth, stratigraphy, radiocarbon results and calibrated age range. Data presentation divided into, 2a: Pollen group summaries and microcharcoal alongside core material sedimentation and mass accumulation rates, pollen diversity and precipitation estimates; 2b: Sclerophyll woody pollen taxa; 2c: Monsoonal forest associated woody taxa, liana and mistletoe, grasses, with long-distance coastal pollen, and 2d: Non-woody pollen taxa (herbaceous and aquatic). All percentages derived from total pollen sum inclusion.

Table 1: Girraween vegetation description

Map Code (Figure 1)	Vegetation Title	Vegetation Description
1	<i>Eucalyptus</i> woodland to open forest	<i>E. tetradonta</i> and <i>E. miniata</i> dominated. <i>Erythrophleum chlorostachys</i> and <i>Lophostemon lactiflorus</i> present in tree canopy. Secondary canopy includes <i>Terminalia ferdinandiana</i> , <i>Planchonia careya</i> , <i>Calytrix exstipulata</i> and <i>Buchania obovate</i> , incorporating <i>Acacia</i> , <i>Syzygium</i> and occasional <i>Pandanus</i> . Understorey shrubs and saplings vary in density and height, dependent on seasonal variation and fire history. Dominant grasses include species of <i>Sorghum</i> and <i>Chrysopogon</i>
2	<i>Melaleuca</i> seasonal swamp	<i>M. symphyocarpa</i> and <i>M. viridiflora</i> open to closed woodland subject to seasonal inundation. Forms temporary swamp communities. <i>Caldesia oligococca</i> , <i>Nymphoides indica</i> , species of <i>Utricularia</i> and herbaceous Fabaceae occur when waterlogged. Ground surfaces support minimal grasses and/or are bare when dry
3	Mixed species community	Mixed association with monsoonal forest and/or riparian inclinations. Dense woodland forming forest, with thicker mid-layers and <i>Eucalyptus</i> or <i>Corymbia</i> species as emergents. <i>Lophostemon lactiflorus</i> and <i>Pandanus spiralis</i> common. <i>Acacia</i> , <i>Syzygium</i> , <i>Alphitonia</i> and <i>Terminalia ferdinandiana</i> are present. Grass cover is reduced, with <i>Sorghum</i> absent. Lianas are noticeable (e.g. <i>Flagellaria indica</i>)
4	<i>Banksia</i> transition	Narrow transition vegetation. Dominant <i>Banksia dentata</i> with <i>Grevillea pteridifolia</i> low open woodland. <i>Lophostemon lactiflorus</i> , <i>Eucalyptus papuana</i> and <i>Acacia</i> sp. are occasional. Grassland ground cover with saplings of varied height. Community appears to be influence by wet soils.
5	Grassland	Open, mixed species grassland (annual and perennial species). Scattered trees include <i>Eucalyptus polycarpa</i> and <i>E. papuana</i> (saplings absent). Incorporates areas of track disturbance.
6	Sedgeland	Closed sedgeland. Seasonally flooded. Cyperaceae dominated (<i>Elaeocharis</i> , <i>Cyperus</i> and <i>Fimbristylis</i>), with species zonation (species presence, height and density determined by depth and duration of inundation). <i>Leptocarpus</i> , <i>Xyris</i> and small herbs present. Localised, low and thin <i>Melaleuca cajuputi</i> trees are incorporated. Pools of standing water interspersed throughout (occupied by <i>Nymphoides indica</i> and/or <i>Nymphaea</i> sp.).

7	Fringe <i>Melaleuca</i>	<i>Melaleuca cajuputi</i> dominated low open woodland forming a ring around open water zone. Width of woodland varies, but is commonly narrow. Borders with sedgeland are sharp. Permanently waterlogged.
8	Open water	Aquatic groups well represented by <i>Nymphaea</i> species and numerous submerged taxa.

Table 2: Vegetation structural terminology as used in the text (modified from Specht, 1981, and as used in the Northern Territory by Wilson et al., 1990, and Bowman and Minchin, 1987).

Life form and height	Percentage foliage cover of tallest plant layer			
	Dense (70-100%)	Open (30-70%)	Sparse (10-30%)	Very sparse (<10%)
Trees* 10-30m	Closed forest	Open forest	Woodland	Open woodland†
Trees <10m	Low closed forest	Low open forest	Low woodland	Low open woodland
Shrubs* >2m	Tall closed shrubland	Tall shrubland	Tall open shrubland	Tall sparse shrubland
Shrubs <2m	Closed shrubland	Shrubland	Open shrubland	Sparse shrubland
Grasses	Closed grassland	Grassland	Open grassland	Sparse grassland
Sedges	Closed sedgeland	Sedgeland	Open sedgeland	Sparse sedgeland
Herbs**	Closed herbland	Herbland	Open herbland	Sparse herbland
*A tree is defined as woody, usually with a single stem; a shrub is a woody plant with stems arising near the base				
** Flowering plants with no significant woody tissue above ground; includes forbs (broad-leaf) and sub-shrub (<1m perennial forb developing a woody lower base)				
† 'Savanna' applies to wooded vegetation with a pronounced grass component. Gillison (1983) and Walker and Gillison (1982) divide grass-savanna and wooded-savanna at 2% woody plant cover				

Table 3: ¹⁴C Radiocarbon AMS sample results. Age reporting follows Stuiver and Polach (1977) and Fink et al. (2004), converted into calibrated ages using CALIB REV7.1.0 (Stuiver and Reimer, 1993, Hogg et al., 2013; calibration curve SHCal13). A Bayesian age-depth model was constructed for the core using Bacon 2.2 (Blaauw and Christen, 2011). Hypy refers to hydrogen pyrolysis, used in the pre-treatment of samples for radiocarbon dated as reported in Bird et al. (2014).

Lab. Code	Sample code	Sample type	Depth (cm)	pMC (%)	?? ¹³ C (‰)	¹⁴ C Age (yr BP)	1σ error (yr BP)	Calibrated age 95% probability range (cal BP)	Calibrated age (median probability)
OZV436	A34-GIR3 SPAC-14	Hypy residue	41	90.75	-15.2	780	25	654 - 724	676
OZV437	B13-GIR3 SPAC-14	Hypy residue	115	88.94	-16.5	940	25	737 - 823	796
OZV438	C13-GIR3 SPAC-14	Hypy residue	214	64.38	-17.5	3535	25	3687 - 3852	3766
OZV439	C54-GIR3 SPAC-14	Hypy residue	258	53.27	-18.4	5060	35	5656 - 5798	5762

OZV440	D12-GIR3 SPAC-14	Hypy residue	313	37.96	-15.1	7780	35	8429 - 8590	8512
OZV441	D84-GIR3 SPAC-14	Hypy residue	390	32	-12.9	9150	35	10197 - 10302	10,252
OZV442	E45-50-GIR3 SPAC-14C	Hypy residue	455	19.9	-15.2	12,970	80	15188 - 15740	15,453

Highlights

- Palaeoecological insight in an area where few long-term savanna records exist.
- Increase in Holocene woody cover a prominent site feature.
- Moisture has been the primary driver of Holocene vegetation dynamics.
- Extent of fire and fire impact, is a characteristic of climate and resultant vegetation.
- Lagoon forms an important human freshwater source during variable Holocene climate.

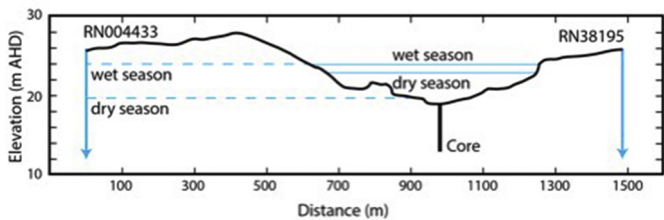
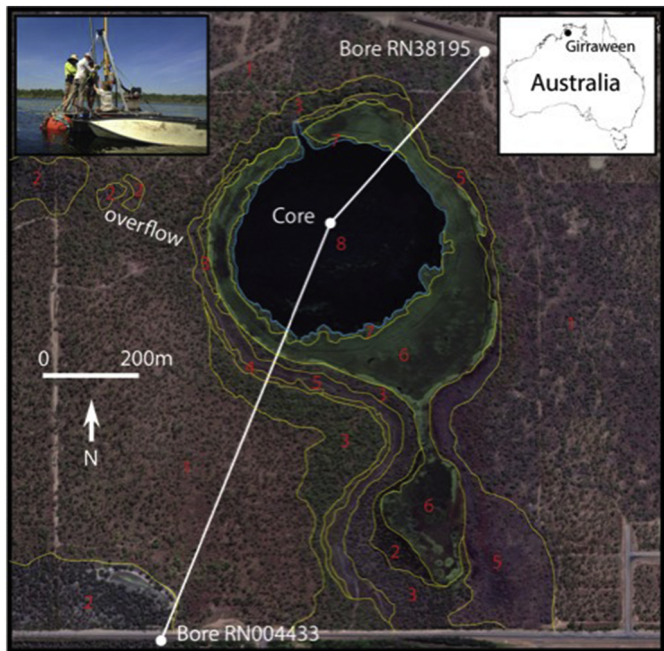


Figure 1

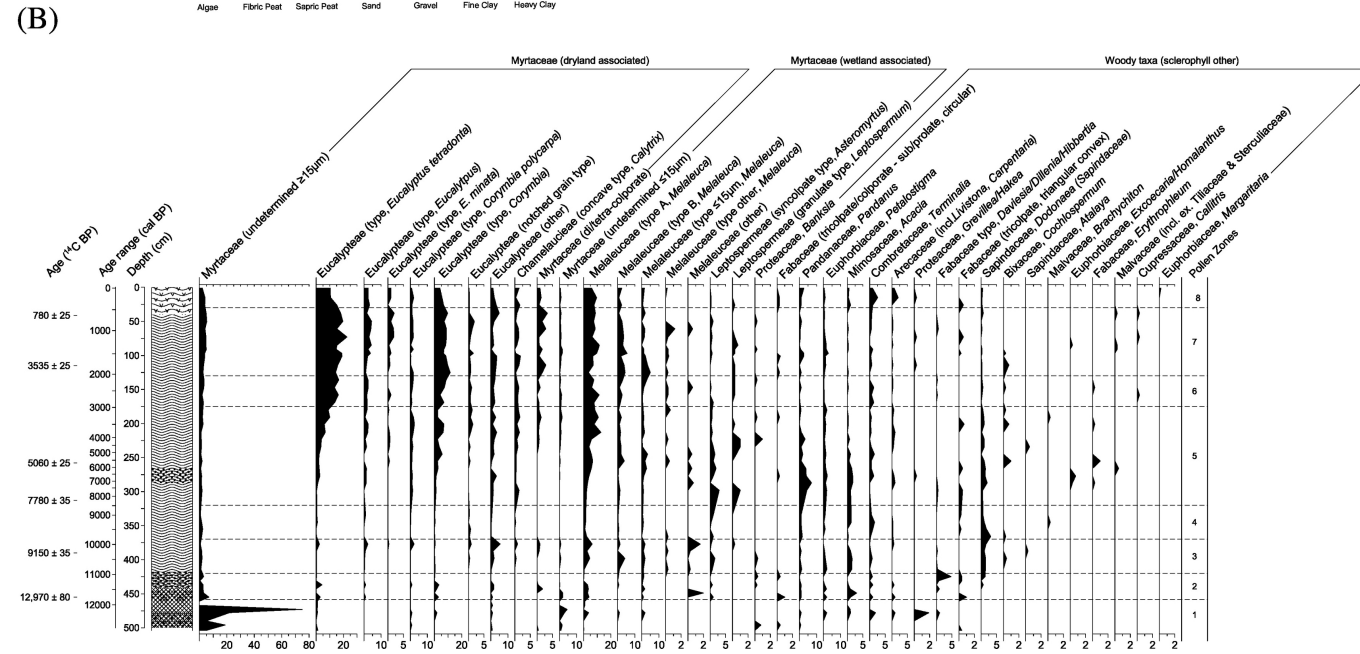
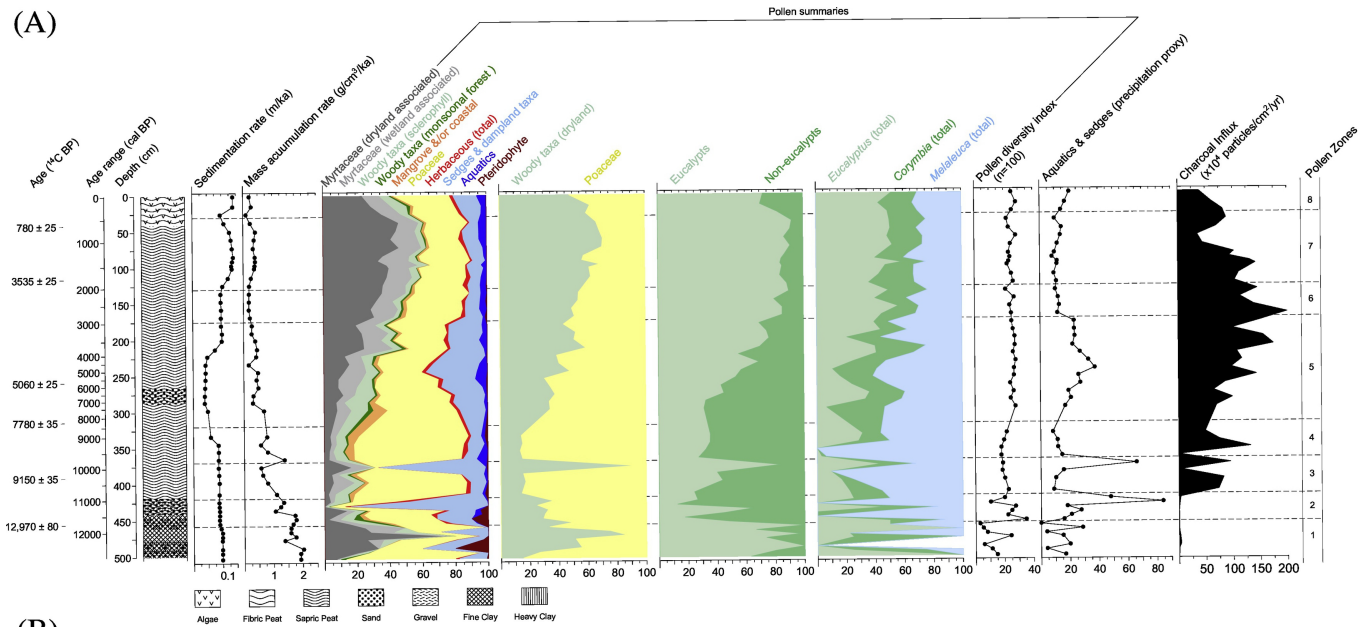


Figure 2A

