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Vegetation changes through stadial and interstadial stages of MIS 4 and MIS 3 based on a palynological analysis of the Girraween Lagoon sediments of Darwin, Australia

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ABSTRACT

A palynological record from Girraween Lagoon sediments (Darwin region of the Northern Territory, Australia) provides detailed long-term insight into tropical savanna vegetation community patterns, climatic and fire relationships, through Marine Isotope Stage 4 (MIS 4: 71–57 thousand years ago, ka) and Marine Isotope Stage 3 (MIS 3: 57–29 ka). Owing to a lack of data in reconstructing northern Australian environments, this paper looks to define and describe to a greater degree the nature and scope of these stadial and interstadial stages for the region. Girraween Lagoon simultaneously provides proximal palaeoecological data for the time and region of Aboriginal people's first arrival into Australia, also encompassing the late Pleistocene continental decline of megafauna. This study provides a dataset enabling full exploration of long-term people-landscape and faunal-floral interactions. Sea levels and associated variations imposed on the transportation of moisture and heat, held implications for MIS 4 and MIS 3 monsoon strength, which was particularly consequential for Girraween regional ecology. Results reveal a prolonged transition from wooded- to grassy-savanna, into a cool drier semi-arid savanna. Increasingly episodic delivery of moisture influenced the permanency of freshwater in the landscape.

1. Introduction

In the Australian region, there are some periods of time which garner more interest than others. Marine Isotope Stage 4 (MIS 4, ~71–57 thousand years ago, ka; De Deckker et al., 2019) and Marine Isotope Stage 3 (MIS 3, ~57–29 ka; Kemp et al., 2020) are two such periods.

MIS 4 was a stadial phase, subject to glaciation (De Deckker et al., 2019) and its inception marked by an insolation minima and rapid cooling at ~72–70 ka. Draw down of atmospheric carbon dioxide (CO_2) occurred, resulting in further and extensive global cooling with the build-up of ice sheets (Menking et al., 2022), sea level decline, and changes in deep ocean circulation (Shackleton et al., 2021). As well as in-phase environmental conditions across Hemispheres, MIS 4 is further identified by a lack of millennial-scale variability and climatic instabilities (Jouzel et al., 2007). MIS 4 was, in summary, 'cool and stable' (Shackleton, 2021: 2281).

MIS 3 was warmer than MIS 4, associated with higher insolation values and therefore shifts in ice-mass balance and changing modes of thermohaline circulation. It was characterised by repeated fluctuations out of MIS 4 into its warmer state, followed by a slower return to cooler conditions (Zuraida et al., 2009; Van Meerbeeck et al., 2009). MIS 3 is not considered a prominent (intense) Quaternary interglacial (PAGES, 2016) and is referred to as a low magnitude interstadial (Tzedakis et al., 2009; MIS 3 therefore was not necessarily just 'the opposite' of MIS 4). Greater interhemispheric climatic contrasts were also evident at this time (Zuraida et al., 2009). MIS 3 was in summary 'mild and variable' (Van Meerbeeck et al., 2009: 33).

MIS 4 is often studied in order to evaluate the relative severity of MIS 2 (~29–14 ka; Reeves et al., 2013) full glacial climates (Peltier et al., 2021), notably the magnitude and structure of the Last Glacial Maximum (LGM; ~26–19 ka; Clark et al., 2009). Similarly, MIS 3 is targeted to gauge climatic warming, the nature of abrupt warming episodes, including efforts to determine when in the past the best analogue for the Holocene occurred (MIS 1, from ~14 ka; Kemp et al., 2020), and in the forecasting of future Anthropocene conditions (Fritz, 2013; Tzedakis et al., 2009; Zuraida et al., 2009). Improved understanding of

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stadial-interstadial transitions in how glacials and interglacials operate serves to highlight marine isotope stage intensity and internal variability, differences that ultimately impact vegetation dynamics and fire regimes (Peltier et al., 2021; Tzedakis et al., 2009).

In Australia, MIS 4 and MIS 3 attract attention for two contextual reasons (c.f. Kemp et al., 2019): (1) because the timing of Aboriginal people's first arrival centres on 65,000 years ago (a MIS 4 70.7–59.3 ka age frame, Clarkson et al., 2017), and (2) that MIS 3 encompasses continental decline of megafauna, with peak extinction occurring around 55–45 ka years ago (Saltré et al., 2016, and see Hocknull et al., 2020 as a north-eastern Australian example, ~40.1 ka). What is interesting about Aboriginal peopling, as well megafaunal decline is that each topic has transcended academic exploration into public interests and discourse (e.g. Griffiths and Russell, 2018; Paine et al., 2018; Brisbane Writers Festival, 2021; Lu, 2022; Westaway, 2022; Rademaker, 2022).

The spotlight on MIS 4 and MIS 3 in Australia has been interdisciplinary. Foundational information is derived from palaeontology (faunal fossil deposits, e.g. Price et al., 2021; Fraser and Wells, 2006) and archaeology (excavations, e.g. Roberts et al., 1994; David et al., 2019; Balme, 2000). In turn (and increasingly), models are applied to test scenarios describing when and how people moved across Australia, as well as the mechanisms leading to megafaunal loss (Bradshaw et al., 2021; Saltré et al., 2016). David et al. (2019; Aboriginal colonisation) and David et al. (2021; megafaunal extinction) analyse debates regarding the development of chronological frameworks that support interpretation across these time periods. In comparison, ecological examinations are far more fragmentary. In the status of MIS 4 and MIS 3 as context, the majority of insight is climatological and geomorphological, rather than ecological in nature.

For Australia, climatological and geomorphological parameters have been able to highlight the role of topographical attributes, hydrological networks, climatic advantages as well disruptions; conveyed as the 'landscape rules' (Crabtree et al., 2021: 1303). However within such a picture, the ecological framework represents a critical knowledge gap in understanding this window of time, no matter the disciplinary approach. Bird et al. (2013: 445) suggests the relative lack of consideration of dynamic ecological processes is 'striking'. Crabtree et al. (2021), in modelling first people's movement through Australia, evaluated findings against archaeological data, but not palaeoecological data; not incorporating the types of ecosystems people encountered into models was an acknowledged limitation for Crabtree et al. (2021; 1307) at the time of publication, in seeking to understand the 'underlying baseline landscape'.

Bird et al. (2018) propose palaeoenvironmental considerations as one element determining the dynamics movement of people across the continent, forming *theory* that suggests a key role for savanna woodlands in conjunction with coastal resources. Megafauna were considered vulnerable to plant community changes, including reductions in habitat area and/or primary productivity. Identifying vulnerability, the ultimate causes and consequences of extinctions, relies heavily on being able to understand megafaunal interactions within an ecological community, where shifts in vegetation can lead to bottom-up ecological cascades (Llewelyn et al., 2021). Choquenot and Bowman (1998) model megafauna abundance in relation to Aboriginal population density but have had to do so within a *hypothetical* tract of north Australian eucalypt savanna. The model further *assumes* that the eucalypt savannas prevailing in northern Australia during the late Pleistocene were relatively constant environments.

It is De Deckker et al. (2019: 203) who make the call 'toward a better definition of MIS 4 in the Australasian region', alongside Kemp et al. (2019): 101) emphasis that 'the most fundamental problem in reconstructing Australian MIS 3 environments is the lack of data'. These recent review papers collated research and Australasian climate reconstructions for MIS 4 and MIS 3 (respectively). Valuable indications are made toward understanding spatial variations in environments across the landscape; Kemp et al. (2019) in particular discuss hydroclimates and associated drivers in formulating a north-south geographic divide during this time, separating southern south-westerly wind influenced Australia from northern monsoon impacted regions (see also Croke et al., 2011). Other environmental review papers include Hope et al. (2004), Reeves et al. (2013), and Mooney et al. (2011).

Following on from Kemp et al. (2019); and Hope et al., 2004), this paper assesses biogeographical patterns through MIS 4 and MIS 3, in monsoonal northern Australia (Woinarski et al., 2007; Bowman et al., 2010). Given the global climatic backdrop for MIS 4 and MIS 3 is relatively well established (as summarised above), and climatic parameters for the Australian region effectively reviewed, this paper assesses the ecological response to climatic change during these periods 'on the ground'. What was the nature of MIS 4 and MIS 3 in monsoonal northern Australia, as revealed through vegetation change? In the context of Aboriginal arrival and megafaunal decline, the simple question is 'what was the plant ecology like?' at these times.

This study is based in the 'top-end' Northern Territory (NT, Darwin region, Girraween Lagoon, Fig. 1) so is representative of both tropical-savanna Australia and the region of Aboriginal arrival (Bird et al., 2018), as well as diverse discussions on megafauna (skeletal, Price et al., 2021; rock art, Taçon and Webb, 2017; eggshell, Miller and Fogel, 2016). In addressing MIS 4 and MIS 3 environments, and broadly surrounding Girraween Lagoon, are north-central Australian geomorphic studies (lacustrine, fluvial, aeolian indicators responding to the abundance of water in the landscape. These include records from the Gregory Lakes basin, Fitzsimmons et al., 2012, Bowler et al., 2001; Cabbage Tree Creek, Wende et al., 1997), Queensland wetland sequences (geochemical, microfloral based climate and ecological change; Lynch's Crater, Kershaw et al., 2007; Welsby Lagoon, Cadd et al., 2018, Tibby et al., 2017), Gulf of Carpentaria investigations (sedimentological, microfaunal climatic/sea-level proxies; Reeves et al., 2008), and marine core records (palynological; east-Indonesian region, van der Kaars, 1991, van Der Kaars et al., 2000; Wang et al., 1999). Combining direct top-end NT palaeoecological research with this set of studies is of prime importance.

2. Site setting

Girraween is one of 137 lagoons within the Darwin region of the Northern Territory (inventory by Schultz, 2004). The waterbody established within a sinkhole, itself formed by deep weathering of the underlying lateritic sediments and dolomitic bedrock, leading to collapse and formation of a closed basin (Bird et al., 2019; McFarlane et al., 1995). Girraween Lagoon is perennial, with a surface water area of 45 ha (ha) and a maximum depth of 5 m (m). Water drains into the lagoon from a catchment of 917 ha.

An extensive overview of Girraween's regional environmental setting has been provided by Rowe et al. (2019, 2021). Darwin's climate is distinctly monsoonal, encompassed within Köppen-Geiger's 'Tropical Savanna' classification subtype Aw (Peel et al., 2007). Temperatures are uniformly high, with strong rainfall seasonality and wind-flow reversal. The region is also subject to tropical cyclones (for climate statistics: Bureau of Meteorology, Darwin Airport, station 014015, 24 km northwest of the site).

Modern catchment vegetation is dominated by tropical mesic open-forest savanna and/or savanna woodland (Moore et al., 2016; Hutley et al., 2011; Brock, 1995). *Eucalyptus tetrodonta*, *E. miniata*, and *Corymbia polycarpa* dominate the overstorey. In the understorey, *Sorghum* and *Heteropogon* grasses are abundant. Variable transitional plant zones occur on approach to the water (*Terminalia*, *Lophostemon*, *Planchonia*, *Banksia* and *Pandanus* species are characteristic, with mixed monsoonal and/or riparian forest associates such as *Ficus, Syzygium, Buchanania, Ampelocissus*). Saplings, shrubs and broad-leaf herbs differ in density and height, dependent on seasonal rainfall alterations and local fire history. Lagoonal plant communities are determined by depth of open water or onshore waterlogging. *Melaleuca* (notably *M. symphyocarpa* and

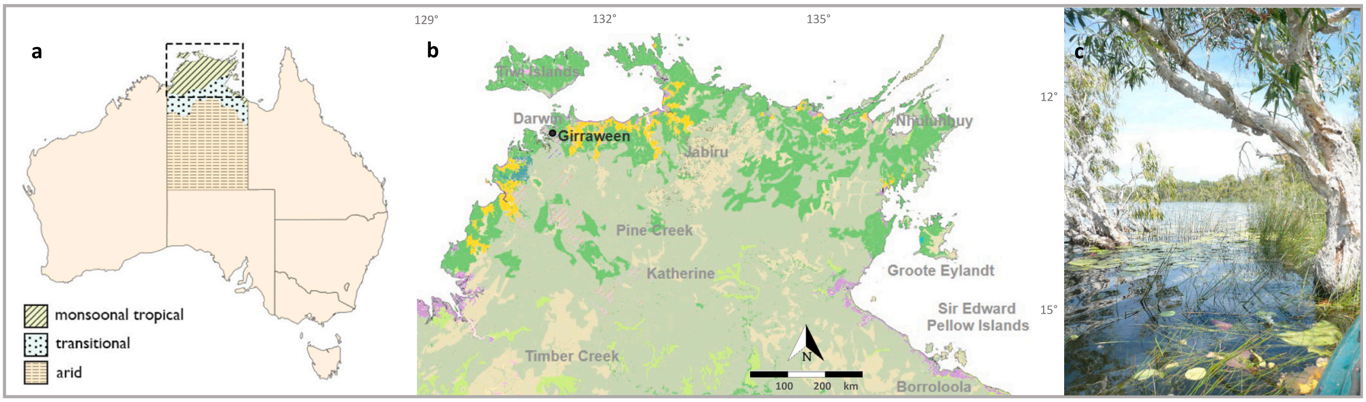

Fig. 1. a) Broad climate zones for the Northern Territory (NT) displayed north-to-south as monsoonal tropical (hashed green), transitional (spotted blue) and arid (dashed darker orange), b) The Girraween Lagoon study site in relation to major north NT locations and diversity in regional vegetation based on the Australian National Vegetation Scheme (displayed after Natural Resource Maps NT, https://nrmaps.nt.gov.au/), and c) Girraween Lagoon image incorporating shoreline vegetation (photo CR). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

M. viridiflora), with sedgeland (e.g. *Cyperus*, *Eleocharis* species) form swamp zones. Aquatic groups are well represented by *Nymphaea* and *Nymphoides*, as well as *Eriocaulon* and *Xyris*. Areas within a 2 km radius of Girraween have burnt every year since 2000, but the site's immediate surrounds have burnt ≤6–7 times (a fire return regime of 2–3 years, typical for north NT savanna, Russell-Smith and Yates, 2007; http:

Fig. 2. Photo series showing coring methodology at Girraween Lagoon: a) floating platform, b) hydraulic coring-rig, c) core extraction, and d) final core collection inside plastic tubing. Photos CR.

//www.firenorth.org.au/nafi3/).

The Larrakia Nation and Wulna people maintain traditional customary associations with Darwin Country, including the Girraween catchment (Wells, 2001; Burns, 1999). Jackson (1998) and Calnan (2006) describes the cultural significance of wetlands and the associated relationships upheld by the Larrakia and Wulna people.

3. Methods

3.1. Palynological techniques

Girraween Lagoon was cored using a hydraulic coring-rig mounted on a floating platform. A 19 m core in 1.0 m sections was collected to the point of bedrock (refer to Fig. 2 for demonstrative images). Each section was sealed during fieldwork in a plastic core liner tube for transport. Core sections were then split in half in the laboratory, described and subsampled at 5–10 cm intervals. Palynological sample preparations are detailed in Rowe et al. (2019, 2021). Briefly, chemical treatments incorporated $Na_4P_2O_7$, KOH, HCl, acetolysis and C_2H_5OH washes, with glycerol as the final storage medium. Sieving took place at 7 μm and 125 μm and a *Lycopodium* spike (Lunds University batch 3862) was added prior to preparations to aid pollen-charcoal concentration calculations. Pollen counts are a minimum of 200 grains per sample. Where samples did not reach this minimum count standard, nearest-neighbour samples were merged.

Pollen identifications are based on floral reference collections held at James Cook University, and online resources including the Australasian Pollen and Spore Atlas (http://apsa.anu.edu.au/). Sources such as FloraNT (eflora.nt.gov.au) provided insight into plant ecologies. Pollen was divided into groups to capture plant form and/or vegetation type, classified further into plant-function and/or environmental response categories as a measure of fire tolerance and to evaluate wet-dry continuums. Rowe et al. (2019) provide additional discussions on these pollen allocations. All pollen types were identified to the most refined taxonomic level possible and morphological descriptors are included to highlight differing grain types (thus ensuring diversity within the record is not overlooked, Rowe et al., 2019). Microcharcoal particles (black, opaque, angular, >10–125 μm in length) were counted alongside pollen. For an evaluation and discussion surrounding charcoal as a proxy for landscape fire occurrence, see Rowe et al. (2022). All data were plotted using TGView (Grimm, 2004). A dendrogram was produced by CONISS to guide the pollen's stratigraphic zonation (Grimm, 1987, 2004). Pollen rarefaction analysis was undertaken according to Holland (2003).

3.2. Chronology

Chronology for the MIS 4 and MIS 3 sedimentary sequence at Girraween is based on optically stimulated luminescence dating (OSL, Huntley et al., 1985; eight samples represent the MIS 4-MIS 3 period). OSL provides a measure of time since sediment grains were deposited and therefore last exposed to sunlight (Murray et al., 2021), with all Girraween samples prepared and measured using methods and equipment described and tested previously (e.g. Jacobs et al., 2019 and see Bird et al., 2024). Samples were collected from one-half of the split core in subdued red light. Each sample represents a 10 cm-depth interval with midpoint depths provided in Table 1.

Bayesian age modelling was applied to the full 19 m Girraween record, utilising the R package rbacon91 to calibrate radiocarbon ages (calibration SHCal20, Hogg et al., 2020), and to combine these with OSL ages for determination of depth probability distributions of age in R 4.0.093 (Blaauw and Christen, 2011; R core team, 2022). In total, 12 radiocarbon ages and 24 OSL ages constitute the full Girraween sequence.

4. Results

The following section provides a sedimentary description and chronological summary, with explanation of pollen zonations to accompany the pollen diagram figures. This explanation is followed by the paleoecological reconstructive results, divided into wetland and dryland environments, addressing vegetation structure and composition, and arranged into the MIS 4 and MIS 3 time phases. Significant palynological indicators of ecological change are highlighted throughout, to be utilised in discussion.

4.1. Stratigraphy and chronology

Sediments through the MIS4 and MIS3 intervals of the core (from 931 cm depth to 570 cm depth) are uniform, composed of mottled heavy clay throughout, lacking sand and with a firm, plasticine texture (diffuse transitions between Gley 2, 4/5BG dark greenish gray; Gley 2, 3/5BG very dark greenish gray; 2.5Y 6/1 Gy). All data associated with the calculation of OSL ages for MIS 4 and MIS 3 samples are presented in Table 1. To assist with documentation, the Girraween age-depth model, with stratigraphic diagram, are provided in Supplementary Section 1.

4.2. Pollen and microcharcoal analysis

Summary MIS4 and MIS 3 palynological records for the Girraween Lagoon record are presented in Figs. 3 and 4 respectively, with corresponding pollen data presented in Tables 2 and 3. Complete pollen diagrams and full data details are presented in Supplementary Sections 2 and 3.

For MIS 4, 37 pollen taxa were identified. Due to low pollen recovery, samples were merged between 902 and 866 cm and again from 859 to 792 cm (67.9–64.6 ka BP, and 64.05–57.6 ka BP, charcoal samples remain unchanged, and see Bird et al., 2024 for additional sediment discussion). Using these consolidated samples, three pollen zones were calculated; a lower zone labelled GIR 4/1 (917–904 cm below sediment surface, bss; 70.9–69.5 ka BP), middle zone GIR 4/2 (904–860 cm bss; 69.5–65.3 ka BP), and upper zone GIR 4/3 (860–784 cm bss; 65.3–57.3 ka BP). Zonation is determined largely by variations in Poaceae relative

Table 1

Dose rate data, single-grain equivalent doses and quartz OSL ages for MIS 4 and MIS 3 samples from Girraween Lagoon. Estimated long-term water content is expressed as % dry mass of the mineral fraction. De values for samples with an asterisk were calculated using the conventional SAR approach, and De values for all others calculated using the 'LnTn' method (Forbes et al., 2021). Two estimates of age uncertainty are provided for the 68.3% probability (1σ). The first combines all systematic and random sources of error, and the second (bracketed) only unshared (random) sources of error and is the term used in the Bayesian age model (Fig. S1).

Sample code	Depth (cm)	Water (%)	Environmental dose rate, total (Gy/ka)	no. grains	CAM De (Gy)	Over-dispersion (%)	Age (ka)
GIR3-F-75	579	50	1.49 ± 0.09	694/1000	48.6 ± 0.6*	47 ± 1	32.6 ± 2.0 (1.4)
GIR3-G-60	656	50	1.64 ± 0.10	586/1000	53.3 ± 0.7*	49 ± 1	32.5 ± 2.1 (1.6)
GIR3-H-30	703	50	1.59 ± 0.10	410/1500	68.0 ± 1.4*	60 ± 2	42.7 ± 2.9 (2.1)
GIR3-H-70	743	50	1.68 ± 0.10	411/1000	82.2 ± 2.3*	50 ± 2	49.1 ± 3.3 (2.2)
GIR3-I-5	767	50	1.77 ± 0.09	542/1000	95.9 ± 1.7*	58 ± 2	54.3 ± 3.2 (2.3)
GIR3-I-30	792	50	1.98 ± 0.11	564/1000	115.4 ± 3.3	53 ± 2	58.3 ± 3.9 (3.0)
GIR3-I-65	825	50	1.86 ± 0.11	520/1000	108.2 ± 1.7*	39 ± 1	58.3 ± 3.6 (2.6)
GIR3-J-13	873	50	1.88 ± 0.12	347/1000	117.4 ± 4.9	50 ± 2	62.4 ± 4.8 (3.5)

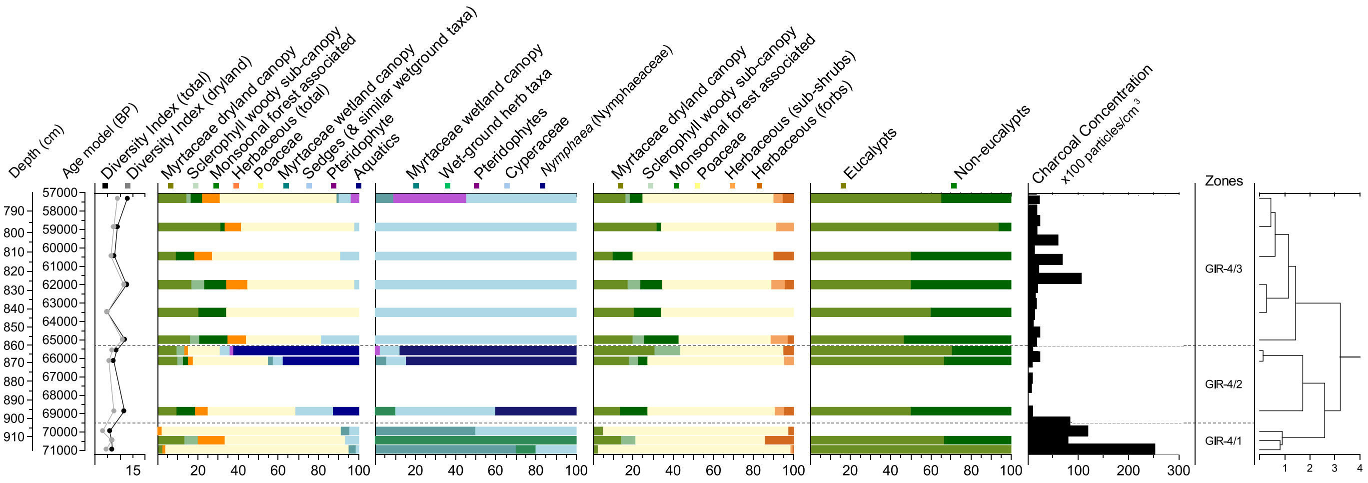

Fig. 3. Girraween MIS 4 percentage pollen diagram. Summary data include diversity indices, pollen vegetation group summaries (wetland pollen-plant types, terrestrial pollen-plant types and broad tree function), and micro-charcoal concentration. All percentages are derived from the total pollen sum including spores. Data are plotted against depth, calibrated age range, and distance from the coastline (calculated using the average of the bathymetry on transects north and northwest from the coast adjacent to Girraween Lagoon to the continental shelf edge).

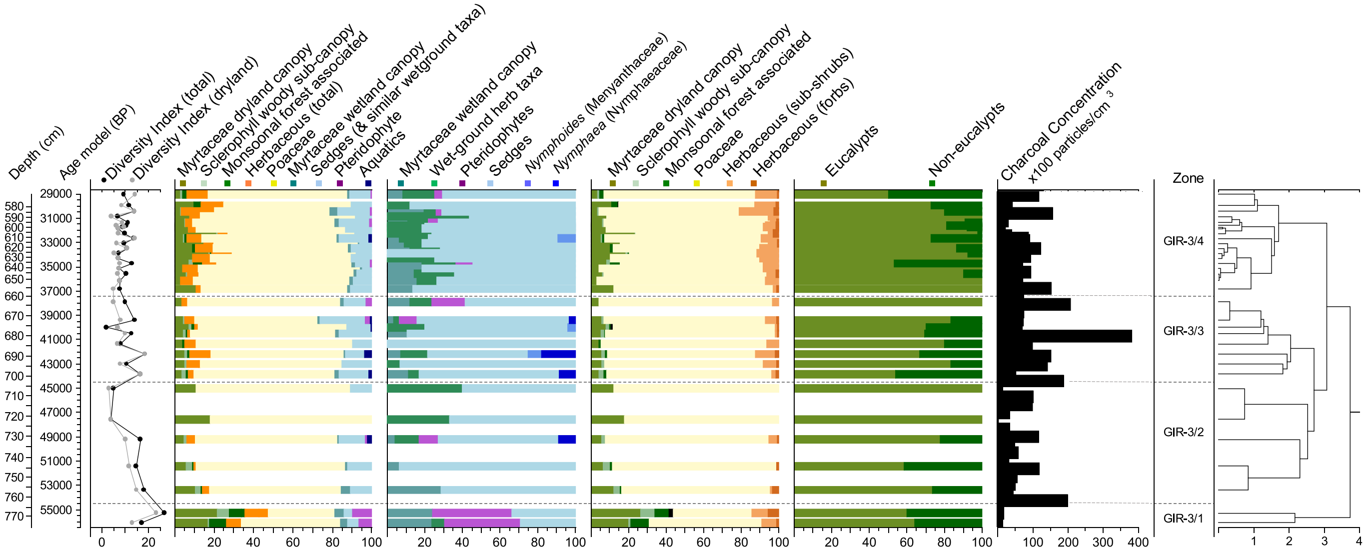

Fig. 4. Girraween MIS 3 percentage pollen diagram. Summary data include diversity indices, pollen vegetation group summaries (wetland pollen-plant types, terrestrial pollen-plant types and broad tree function), and micro-charcoal concentration. All percentages are derived from the total pollen sum including spores. Data are plotted against depth, calibrated age range, and distance from the coastline (calculated using the average of the bathymetry on transects north and northwest from the coast adjacent to Girraween Lagoon to the continental shelf edge).

to dryland pollen, and distinction in the presence of wetland pollen across the zone boundary. Secondary influences include shifts toward an increased presence, and a greater range in, woody pollen types (dryland). Pollen diversity measures are initially lower, show a degree of fluctuation between approximate 67–62 ka BP, and levelling by 57 ka BP. Charcoal concentrations decline substantially from GIR zones 4/1 into 4/2.

Sixty-five pollen taxa were identified for MIS 3 with four diagram zones apparent: the lower-most zone GIR 3/1 (774.5–762 cm bss; 56.1–54.5 ka BP), middle zones GIR 3/2 (762–704.8 cm bss; c. 54.5–44.6 ka BP) to GIR 3/3 (704.8–662 cm bss; c. 44.6–37.4 ka BP) and upper zone GIR 3/4 (662–573 cm bss; c. 37.4–29.1 ka BP). Zonation reflects the distribution of non-eucalypt woody and herbaceous taxa. These patterns are also reflected in the lowering before stabilization of total woody pollen proportions (and as reflected in the diversity index). Charcoal concentrations incorporate periodic peaks in value (the highest at 35.7 ka BP) but are otherwise relatively steady.

4.3. Wetland and lagoon environments

4.3.1. MIS 4

During MIS 4 Girraween lacked continual wetland plant presence and wetland woody taxa were more occasional than non-woody. Patchy wetland plant appearances in time occurred without demonstrating successive sequences in hydrology, sedimentation, or assemblages of taxa. No cyclic wetland regeneration and recolonization took place.

Three wetland episodes occurred: between 69.9 and 68.3 ka BP, *Melaleuca* was present with a small suite of sedges (*Cyperus*, *Eleocharis/Schoenus*) and wetter-habitat herbs (*Caldesia*, *Dapsilanthus*). Early MIS 4, *Melaleuca* existed locally, but likely not to the extent of a wetland woodland formation. Sedges and herbs therefore were not present as an understory, but emergent plants occurred within the sinkhole. *Caldesia*

Table 2
Girraween MIS 4 pollen zones as determined by CONISS (Grimm, 1987, 2004). Contains descriptions of pollen assemblages and microcharcoal trends found within each zone (bss refers to below sediment surface). Fig. 3 displays the summary diagram and Supplementary Sections 2 and 3 show the complete dataset, 71–57 ka.

Zone division	Pollen assemblage and charcoal concentration
GIR 4/1 (917–904 bss; 70.9–69.5 ka cal BP)	Highest percentage Poaceae (values ≥90% alternate with an upper-zone reduction to 60%). The mid-zone (68.7 ka cal BP) is marked by greater proportion herbaceous taxa (dryland and wetland affiliated; Lamiaceae, Convolvulaceae and Fabaceae types), and with Eucalypt and *Callitris* tree pollen. Minor herbs Malvaceae, Chenopodiaceae/Amaranthaceae and Euphorbia are otherwise recorded. No monsoonal forest associated pollen has been captured. Wetland pollen categories incorporate *Melaleuca* with undergrowth Cyperaceous types and *Caldesia*, all at values <5%. Charcoal concentrations progressively decline. Values are high compared with the upper zone, reaching over 10-fold abundance in the record's lowermost sample.
GIR 4/2 (904–860 cm bss; 69.5–65.3 ka cal. BP)	Differentiated in part by higher proportion dryland woody and appearance of non-eucalypt types (sclerophyll sub-canopy and forest pollen, noting *Podocarpus*). Cyperaceous and Hydrocotyle (single record) initially increase before high input of *Nymphaea* pollen (peaking 64.2 ka cal BP). *Nymphaea* then declines (to absence). *Cyperus* pollen typically averages 5%. Single sample *Melaleuca* is recorded at 66.14 ka cal BP (2.5%). Poaceae pollen declines to 45–40% and herb type are minor. Charcoal differs substantially from zone 4/1 into 4/2, reaching its lowest concentrations for the entire sequence (68.8–65.3 ka cal BP).
GIR 4/3 (860–784 cm bss; 65.3–57.3 ka cal. BP)	*Cyperus* pollen reaches 18% (63.7 ka cal BP) then declines to near half this value. Poaceae pollen decline then rise (reducing to 45% as dryland tree pollen increase, 63.7 ka cal BP), but do not reach proportions seen in zone 4/1. Mixed, sporadic herb pollen is incorporated (minor, each <5%), and with Amaranthaceae/Chenopodiaceae the most repeated herb type.Eucalypt pollen rises, but fluctuates. Sclerophyll types Arecaceae, *Dodonaea*, *Acacia*, *Terminalia* and Fabaceae occur more sporadically than monsoonal-forest affiliates *Podocarpus* and *Trema* (the latter is no longer recorded after 62 ka cal BP). Charcoal concentration maintain low similar values up until c.62 ka then start to rise, with a series of high phases between 61.4 and 59.3 ka cal BP. Values then decline, consistent to the conclusion of MIS 4.

and *Eleocharis* characterize the presence of water as up to 30–40 cm deep (Cowie et al., 2000). *Cyperus*' marginal ecology (Cowie et al., 2000) suggests a peripheral wet-dry habitat related to gradation in water across the site's floor.

Spanning 67.2–64.2 ka BP (and concentrated after 65 ka cal BP) sedges (predominantly *Cyperus*) co-occurred with *Nymphaea*, the latter indicative of open water inclusion in some portion of the swamp across the sinkhole floor. Fringing plant gradation declined with the shift in water distribution, and seemingly in favour of a pond. Submerged and rooted floating-leaved plants occupy habitats which hold water deep enough and long enough for their development (i.e. near permanent or at least cross-seasonal, Brock, 1995). The aquatic *Nymphaea* is known to occupy water up to 2.5 m deep (Cowie et al., 2000; Stephens and Dowling, 2002).

Wetland plant combinations shifted again, across the MIS 4/MIS 3 boundary (61.0–54.3 ka BP), where *Cyperus* (now reduced, and as the only representative sedge) was present with pteridophytes and a small return of *Melaleuca*. Approaching MIS 3, the sinkhole lost surface water. Wetting frequencies only maintained a moist habitat, to co-support ferns with *Cyperus*. Ferns likely also benefited from shaded protection, whether provided by the sinkhole depression and/or the occurrence of

Table 3
Girraween MIS 3 pollen zones as determined by CONISS (Grimm, 1987, 2004). Contains descriptions of pollen assemblages and microcharcoal trends found within each zone (bss refers to below sediment surface). Fig. 4 displays the the summary diagram and Supplementary Sections 2 and 3 show the complete dataset, 57–29 ka.

Zone division	Pollen assemblage and charcoal concentration
GIR 3/1 (774.5–762 cm bss; 56.1–54.5 ka cal BP)	Characterised by a mixed suite of pollen, with a greater proportion of combined woody and herbaceous categories comparative to Poaceae. Poaceae values are lowest for the sequence (50–34%). Eucalypt types dominate (up to 22%), recorded with *Pandanus*, Arecaceae, *Dodonaea,* Fabaceae and *Terminalia* (all <5%). *Podocarpus* is the highest represented monsoonal-forest associate (6.5%, 56.1 ka cal BP), over Euphorbiaceae (*Macaranga*), *Barringtonia/Planchonia*, Urticaceae (c. f. *Pipturus*), Moraceae, and vine-creeper pollen types (all <2%). Eleven herbaceous pollen taxa are incorporated. Wetland pollen comprise *Melaleuca* and *Cyperus*. Fern spores are at their highest for the sequence Microcharcoal particles are at their lowest concentrations.
GIR 3/2 (762–704.8 cm bss; 54.5–44.6 ka cal. BP)	Poaceae values rise to >60% (averaging 75%) and maintained close to this proportion for the remainder of the sequence. Zone 2 includes one of two Poaceae pollen peaks (82%) and by upper samples (ranging 47–44 ka cal BP) eucalypts are the only other dryland pollen category to co-occur with grasses. Herb pollen show sizable decline from zone 3/1. Monsoonal-forest pollen also shows considerable decrease and an absence in the majority of this zone. Small value *Trema* and *Bombax* pollen occur 52–50 ka cal BP. Sclerophyll sub-canopy *Terminalia*, Areaceae and *Dodonaea* are temporarily joined by *Acacia* and Fabaceae pollen types. Wetland pollen proportions remain similar from the previous zone but include wetland herb representation. *Melaleuca* pollen and fern spores decline. Microcharcoal values start to fluctuate; higher sample concentrations occur at 50, 47.1 and 44.1 ka cal BP.
GIR 3/3 (704.8–662 cm bss; 44.6–37.4 ka cal. BP)	Further decline in the proportion of total woody pollen, largely driven by ongoing reduction in eucalypts. Sclerophyll woody sub-canopy (nine taxa) and monsoonal-forest pollen (five taxa) return following upper zone 3/2 absences and taxa diversify. Herb representation increases, with Amaranthaceae/Chenopodiaceae pollen highest, co-recorded with *Gonocarpus* and *Euphorbia* pollen, as well as the family groups Convolvulaceae/ Lamiaceae and Liliaceae. Patterns in wetland pollen are maintained. Cyperaceae (and similar wet ground taxa) rise further in proportion as *Melaleuca* pollen and ferns spores remain comparatively low. *Nymphaea* pollen re-occurs throughout this zone in small values (<2.5%). Pollen changes are accompanied by increases in microscopic charcoal
GIR 3/4 (662–573 cm bss; 37.4–29.1 ka cal BP)	Poaceae pollen dominates and peaks again (82%, 34.4 ka cal BP). Highest herbs occur for the record (ongoing increase to 16%, 30.2 ka cal BP, Amaranthaceae/Chenopodiaceae pollen remains prominent and consistent). Pollen such as Asteraceae are added to the assemblage. Eucalypt pollen rises mid-zone (32–31.3 ka cal BP) only to decline toward the top of the sequence. Sub-canopy sclerophyll and monsoonal forest pollen remain minor. Pollen-plant types such as *Terminalia*, *Pandanus*, *Dodonaea* and *Bombax* are lost from the record. Other tree pollen such as Brachychiton and *Timonius* are gained. Wetland pollen is characterised by a greater consistency in *Melaleuca* and the presence of undergrowth types such as *Caldesia*. These remain secondary to Cyperaceae pollen.

(*continued on next page*)

Table 3 (*continued*)

Zone division	Pollen assemblage and charcoal concentration
	Microscopic charcoal fluctuates at an increased zone average, with additional high points at 34.4 ka cal BP and 33.7 and 30.1 ka cal BP.

Melaleuca (Short et al., 2003 provide an overview of ferns and fern allies of the Northern Territory).

4.3.2. MIS 3

From a punctuated wetland through MIS 4, Girraween transitioned to ongoing water retention. The site gained effective moisture with more persistent plant presence in MIS 3. Out of MIS 4, Girraween's wetland shifted in two stages.

Initiated from 56.8 ka BP, a *Melaleuca-Cyperus* community was present. *Eleocharis/Schoenus* reoccupied the lagoon margin from early MIS 4 and *Fimbristylis* appeared. The wetland habitat therefore resumed a zoned sedge coverage, responding to an extended period of wetness and sediment build-up. *Melaleuca* remained minor in presence as in MIS 4, but expanded in taxon types from the early period MIS-3 (51.9 ka BP).

Phased in from 48.2 ka BP, and more definitively after 41.8 ka BP, were episodic open-water ponds (*Nymphaea*, *Nymphoides*) and mosaics of ferns and herbs (*Caldesia, Utricularia, Dapsilanthus, Pogostemon*) within the sedge growth. Both features would have diversified the shallow water zone in particular. Increased proportions of *Melaleuca* occurred 43.2–40.3 ka BP, adding to community complexity. This dynamic of macro consistency (emergent sedge vegetated swamp), yet flux in internal micro components (taxon rich herb pockets, ponding areas, *Melaleuca* stands) continued through the remainder of MIS 3, to 28.7 ka BP. Recurring ponds were a point of contrast between MIS 3 and MIS 4, featured as a single fluctuation through the earlier stage, notably more common (though smaller) for MIS 3.

4.4. Dryland environments

4.4.1. The savanna dynamic

Ma et al. (2013) define savannas as wooded communities with a conspicuous perennial or annual grass component. The full savanna spectrum ranges from almost pure grassland to closed woodland. The savanna dynamic around Girraween incorporated differing phases in the encroachment of grass versus woody components throughout MIS 4 and MIS 3, but all the while maintained an open vegetation structure. There was no wholescale turnover in the relative proportions of trees-plus-shrubs and grasses toward one or the other end-spectrum savanna.

By 70.9 ka BP grasses were extensive, widely maintained up until 68.8 ka BP, from which time woody abundance progressively increased. Girraween MIS 4 wooded presence peaked 65.5–64.9 ka BP. Wooded-grassy co-dominance largely continued through the remainder of MIS 4 and up until 55.3 ka BP in MIS 3. Grass expansion had re-initiated by 53.4 ka BP and in MIS 3, large tracts of grassy-savanna were present in the surrounding region. Grass representation continued to rise gradually to 45.0–43.8 ka BP, thereafter maintaining a structurally stable grassy-savanna (comparative to MIS 4's wooded-savanna). An increase in trees and shrubs featured within the catchment between approximately 33.1–31.7 ka BP.

Three broad fire regimes characterised MIS 4 and MIS 3 within an overall increase in the prevalence of burning to a variable degree: 1) 70.9–69.9 ka BP, 2) 68.8–55.0 ka BP, and 3) 54.7–29.9 ka BP. Fire declined through the initial 1000 years of MIS 4 (period 1), and maintained minor presence to 55 ka BP with charcoal recorded at its lowest accumulation across the two stages (period 2). In the third period, burning expanded and incorporated highest incidence of fire for this study. No regularity in fire events occurred but burning spiked at 37.5 ka BP.

Burning correlated primarily with grass abundance, suggesting fire extent was linked to grass biomass and continuity of the grass layer. Fire played a role in maintaining the catchment in an open condition, although the hierarchy of feedbacks are to be explored amongst climatic and topographic discussions, as below. The more structurally stable grassy-savanna phase of MIS 3 was the environment that was subject to an increased incidence of fire. Charcoal values during MIS 3 rise above those observed by Rowe et al. (2021) for MIS 2, including the LGM, while charcoal fluxes in MIS 4 are similar to MIS 2. All three marine isotope stages record significantly less charcoal than observed during the Holocene (Rowe et al., 2019) including the present day (Bird et al., 2019).

4.5. Woody indicators

4.5.1. MIS 4

Within the MIS 4 wooded-savanna, eucalypts were the dominant trees. Secondary mid-storey tree taxa and/or shrubs were not abundant. Sub-canopy eucalypt associations appeared only as periodic 'flushes' throughout the course of MIS 4 and each differed in composition. At 70.4 ka BP *Callitris* formed an associate, clustered amongst the eucalypts (a growth pattern based on Radford et al., 2013; clumped, according to Bowman et al., 1988 and/or in groves, Bowman et al., 2022). Though burning was repetitive, the presence of *Callitris* pollen indicates a low-severity fire regime for early MIS 4 (Bowman et al., 1988). *Callitris intratropica* is fire intolerant, able to survive low-intensity incomplete combustion litter fires, but that intense burning typically defoliates trees, degrading stands leading to adult and juvenile mortality and recruitment bottlenecks (Bowman et al., 2022; Crisp et al., 2019). Spanning 66.1–65.0 ka BP, *Pandanus*, Arecaceae and *Dodonaea* were present in the sub-canopy. This suite is suggestive of wetter, lower tree stands. However, their co-occurrence with *Nymphaea* potentially places these taxa within the sinkhole slopes in closer association with the ponded open water. A mid-storey again occurred at 62.0 ka BP, but the composition shifted to incorporate *Acacia* and *Terminalia*, and subsequently combining *Erythrophleum* and Fabaceae (57.3 ka BP). Beadle (1981) refers to *Erythrophleum* and *Terminalia* as mesomorphic, implying a degree of savanna moisture even away from the sinkhole.

The interesting feature of MIS 4 is the gymnosperm *Podocarpus*, present after 68.8 ka BP and in its majority from 65.0 to 60.4 ka BP. *Podocarpus grayae* currently maintains isolated modern NT populations on the Arnhem Land plateau, associated with *Allosyncarpia*-dominated-closed forest types but restricted due modern high fire frequencies (Russell-Smith et al., 1993; Brophy et al., 2004; Dixon, 2004; *Podocarpus* coincided with minor/low severity fires inMIS 4 and MIS 3). Mellick et al. (2012) places this taxon more specifically along ecotonal gradients bordering these forest types, potentially related to light availability. *Podocarpus* co-occurs with *Trema* from 65.0 to 62.0 ka BP, a pioneer taxon amongst tropical vegetation types and an important component of successional vegetation following disturbances (Yesson et al., 2004). A non-eucalypt dominated vegetation association may have therefore been in place, possibly fragmented in canopy cover and/or undergoing a high turnover of taxa. The presence of *Podocarpus* and *Trema* may be used as ecological indicators of a wider 'community of plants' in this regard, particularly given inconsistent pollen preservation at this depth, and known poor pollen production and/or dispersal from rain-forest associated taxa (Moss et al., 2005). Owing to floristic relationships, *Podocarpus* may notably serve as an indicator of NT *Allosyncarpia* forest biogeography and floristic patterning through the late Quaternary.

4.5.2. MIS 3

Eucalypts remained the canopy dominant in MIS 3. However, as the dryland savanna structure transitioned from wooded to grassier, three adjustments in mid-storey tree-shrub composition (sclerophyll sub-canopy and monsoonal-forest groups) were incorporated.

In extension of MIS 4 (56.1–49.2 ka BP) eucalypts combined with *Terminalia*, *Grevillea* and *Acacia*, as well as the wetter set of *Pandanus*, Arecaceae and *Dodonaea*. With improved pollen preservation, the monsoonal-forest community to which *Podocarpus* and *Trema* bordered is more in evidence in early MIS 3. *Barringtonia, Bombax, Pipturus* and Moraceae (likely *Ficus*) trees were present. It is worth noting *Pipturus* is a characteristic component of rain-forest regrowth, favoured by disturbance (Zich et al., 2020). *Pipturus* underpins suggestions from the presence of *Trema*, to indicate a high turnover, unstable forested habitat. *Bombax* is deciduous (Zich et al., 2020), reinforcing a seasonally drier rather than humid-wetter forested nature. Floristic (and probably structural) contrasts to the savanna may be enough to position monsoonal-forests as isolated stands rather than an interspersed understorey, leading to lower local grass abundance and reduced burning. Given the ecological profile of *Podocarpus*, it was unlikely to be a savanna generalist and amongst the eucalypts, therefore placing it, and the community it signals, as a discrete landscape feature. Between 49.2 ka BP up to 43.8 ka BP the Girraween catchment lacked sub-canopy and/or monsoonal-forest non-eucalypt woody associations and the savanna returned to a eucalypt-Poaceae association. This in turn incorporated rising charcoal and periodic fire spikes.

Though stratification of the vegetation into canopy layers was re-established, after 43.8 ka BP and in the period up to 34.5 ka BP, numerous non-eucalypts started to disappear from the MIS 3 landscape, and the monsoonal forest was rendered to remnant taxa. In composition, *Pandanus, Terminalia, Dodonaea* and *Grevillea* co-occupied with eucalypts, but were eventually replaced by drier adapted (Short and Cowie, 2013) *Petalostigma* and Malvaceae savanna shrubs. Arecaceae was rare, even with wetland ponding. Remaining monsoonal-forest plant combinations were more distinctively seasonal (e.g. *Celtis*).

After 34.5 ka BP the savanna proportionally (competitively) gains eucalypts, altogether losing inter-mixing with other tree types. By this stage of MIS 3, the savanna no longer accommodated blended wetter-drier plant growth. Non-eucalypt taxa became confined to shrubs for the remainder of MIS 3, (dry taxa such as *Petalostigma* and *Brachychito*n), similar to the key vegetation responses at Girraween during the Last Glacial Maximum (LGM; Rowe et al., 2021). Little similarity in the composition of monsoonal forest taxa exists between the initiation and conclusion of MIS 3 (the *Pipturus-Trema* combination remained, although minor; from its peak in MIS 4, *Podocarpus* sporadically declined through MIS 3). Monsoonal-forest ‘treeness’ has also been affected, with greater vine and/or climber presence (*Stephania, Flaggelaria*). Moore (2005) discusses the ability of *Timonius* to extend into drier inland NT areas, and *Timonius* was found to have remained at Girraween into the LGM (Rowe et al., 2021).

4.6. Herbaceous indicators

The vegetation around Girraween lagoon incorporated a ground stratum of grasses, forbs and sub-shrubs. On the interaction between these different growth forms, Mott and Groves (1994) discuss the difficulty in applying successional concepts, suggesting that grass-associated vegetation exists in multiple states at any one time. With this, the herbaceous group may have formed its own small plant associations (Moore, 2005). Across MIS 4, grasses did not extensively co-exist with herbs. Individual herb taxa were sporadic and lacked an extensive long-term (multi-sample) presence. Herbs may only have been capable of episodic, rapid growth.

The grass understories of MIS 3 incorporated a greater presence, and more mixed suite, of herbs. These herbs show no strong relationship to upper and mid canopy tree-shrub compositions, but varied in two ways: The rise in grass proportions 53.4 ka BP to approximately 45.0 ka BP was largely at the expense of herbaceous taxa, and before and after this phase, herb composition differed. *Tacca, Spermacoce, Tricodesma, Solanum*, and Asteraceae were more prominent in early MIS 3 (a suite of woodland-forest taxa, including thicket margins and disturbed areas, Zich et al., 2020).

After 45.0 ka BP, herbs are dominated by Amaranthaceae/Chenopodiaceae types, broadly the ‘saltbushes’ (Leigh, 1994). The xeromorphic ecology of Amaranthaceae/Chenopodiaceae (Kadereit et al., 2005) means they are well represented within modern semi-arid environments of the NT (Hammer et al., 2021; Newsome, 1999; and see maps in ALA, 2021). As such, this pollen group serves an indicator for drier developing environmental conditions in MIS 3, reflected in changing community composition and associations. These taxa situate the grassy savanna of MIS 3 as increasingly semi-arid and water limited. The representation of Amaranthaceae/Chenopodiaceae pollen in the Girraween record continues through MIS 2 and the LGM (Rowe et al., 2021). In turn, Wiegand et al. (2006) observe patterns of tree distribution in arid savanna types, and highlight that woody patterns operate in a patch-dynamic. Amaranthaceae/Chenopodiaceae are not adapted to regeneration by fire, being succulent-like with low flammability. They are fire-sensitive (Moore, 2005), and that this herb group increased as charcoal deposition increased, yet were not replaced by fire-adapted grasses and shrubs, further supports a low intensity MIS 3 fire regime.

5. Discussion

5.1. Extrinsic drivers of change

5.1.1. Climate and sea level

Taking data from the Antarctic Dome C ice core (EPICA Project, Jouzel et al., 2007, quoted in De Deckker et al., 2019 for northern Australia), a maximum temperature decrease of 4.5 °C coincides with the MIS 4 interval, and CO_2 records show a gradual reduction after 72 ka to lower values (~197 ppmv) around 64 ka, with a fluctuating rise thereafter. *Podocarpus* populations (68.9–53.5 ka BP) are consistent with distinct cooling across the Girraween region during MIS 4 and early MIS 3. The genus does not occur at Girraween today and is an important climatic indicator. For palynologists working in South America, a critical manifestation of glacial-like cooling is the spread of *Podocarpus* (the distribution of podocarps across lowland Amazonian palaeoecological sites, for example, Colinvaux et al., 1996; Behling, 1998). During interglacial periods in the Queensland Wet Tropics, occurrences of *Podocarpus* were dramatically reduced when compared to glacial periods, indicating a preference for cooler-drier environments (Mellick, 2012; Kershaw et al., 2007).

Kershaw et al. (1993) and Moss et al. (2017) suggest glacial-age drier rainforests, incorporating *Podocarpus*, probably dominated the terrestrial vegetation in east coast areas that experienced less than −1500 mm annual mean rainfall. Such a rainfall estimate helps place the Girraween MIS 4 region as drier than today (Bird et al., 2019), but wetter than through MIS 2 and the LGM (Rowe et al., 2021; at least during the 68.9–53.5 ka BP window). Although *Podocarpus* experienced glacial-interglacial cyclicity, pollen evidence highlights an overall gradual late Quaternary-last glacial disappearance or reduction in range of gymnosperms from the east coast of Australia (Kershaw et al., 1993; Moss and Kershaw, 2007; Shimeld, 1995). Moss and Kershaw (2000) suggest eventual ‘relictual’ distribution, responding to increased climate variability, including phases of greater El Niño-Southern Oscillation activity within the last few hundred thousand years, with more recent superimposition of human activities (Moss and Kershaw, 2007). Based on this study, a trend toward a sustained regional reduction of *Podocarpus*, and its associated *Allosyncarpia* forested community, also occurred in the northern NT. Southern Hemisphere near-surface air temperature increases of 1–3 °C relative to MIS 4 have been suggested for MIS 3 (Zuraida et al., 2009). That a step-wise sharp then continual decline in *Podocarpus* at Girraween begins c.53.5 ka BP corresponds to the initiation of the ‘mild and variable’ interstadial MIS 3.

During the MIS 4 interval relative sea level dropped to a low stand of −98 m at 64.2 ka, rising rapidly 64.2–59.7 ka followed by a more subtle increase at the end of MIS 4. Changes in sea level were paralleled by sea surface temperatures (De Deckker et al., 2019). These shifting land-sea configurations changed proximity and consistency of the moisture source area for the Girraween region. During MIS 4 and to a lesser extent MIS 3, the coast was no longer adjacent, with less regional oceanic surface and heat content to generate high convective clouds and ensuing high seasonal rainfall and cyclonic activity (De Deckker et al., 2014; Shackleton et al., 2021). Monsoon activity continued to some degree, but was weaker during MIS 4, as inferred by van der Kaars et al. (2010) using core materials taken offshore from south-Sumatra. Miller et al. (2018) discuss the decreased ability of monsoonal rain to penetrate into the Australian interior, further reducing rainfall at in the Girraween region during this period.

At Girraween lagoon, decreased and/or more episodic delivery of moisture during MIS 4 resulted in plant type and vegetation community impermanence (though landscape moisture-evaporative pressures were likely mediated by cooler temperatures). Reduced CO_2 would have diminished woody vegetation productivity and cover to some degree (Prentice et al., 2022; Ward et al., 2001), and lower CO_2 favours deciduous over evergreen leaf-traits (Harrison and Prentice, 2003; House et al., 2003). Woodland instability occurred, particularly evident in the sclerophyll sub-canopy's co-existence with eucalypts, alongside fragmentation of non-eucalypt communities. Herb representation was also episodic as a result. A similar initial increase in *Eucalyptus*, 'probably as a developing canopy above savanna grassland', is evident from the beginning of stage 4 in tropical north Queensland (Kershaw et al., 2007: 43, corroborated by Cadd et al., 2018 who noted a decline in rainforest pollen). Girraween was unable to build successive sequences in site hydrology, sedimentation, and assemblages of wetland taxa (especially woody). These relatively dry conditions locally are correlated with greater MIS 4 dust fall out in Antarctica, related to a combination of increased Southern Hemispheric drying and wind strength (De Deckker et al., 2019; Shackleton et al., 2021).

The record from Girraween is consistent with indications of drier conditions in the Gregory Lakes basin from late MIS 5 through MIS 4, where aeolian deposition and dune formation corresponds to lake regression having exposed sandy plains (Fitzsimmons et al., 2012). Water decline (though not absence) also formed a MIS 4 regressional shoreline at Kati Thanda-Lake Eyre (Cohen et al., 2022). Sedimentary records for MIS 4 are relatively rare for Kati Thanda-Lake Eyre, which may indicate a climate interval incorporating shorter-lived extremes (Fu et al., 2017). Of note here are De Deckker et al. (2019) and Schaefer et al. (2015) exploration in the possibility of a temporary southward shift of the Intertropical Convergence Zone (ITCZ) in MIS 4, with monsoon intensity and geographical extent having consequently peaked around 65 ka BP (paralleled by Heinrich Stadial 6, incorporating a CO_2 concentration increase and warming Antarctic temperatures, Menking et al., 2022). This event is signalled at Girraween through maximum wooded plant proportions over the catchment, trending to minimal charcoal deposition, and high representation of *Nymphaea* pollen, indicative of open water in the lagoon.

Sea level initially rose in MIS 3, reaching an average level of approximately −60 m for the first half of the stage with a subsequent uneven drop to −80 m. Sea level then fell to MIS 2 levels (Siddall et al., 2008). A global sea-to-land, rise-and-fall seesaw is in keeping with regional hydroclimate assessments, of Australia experiencing spatially variable climates from ~57 to 49 ka, becoming predominantly wet from ~49 to 40 ka, after which increasingly dry climates dominated (Kemp et al., 2019). Menking et al. (2022) and Bauska et al. (2021) discuss ocean heating and a CO_2 rise across the MIS 4–3 transition, as implicated in these changes. Environments were then influenced by an extended trend to lower CO_2. Schaefer et al. (2015) describe MIS 3 as having stalled in its interstadial state, before slipping back toward glacial conditions and the LGM in MIS 2.

Under renewed marine influence, convective feedback delivered early MIS 3 moisture to Girraween and shaped the intermediate tree layer into a configuration consistent with wetter conditions with more persistent individual taxa through time. Rain-forest regrowth benefited, though remained liable to turnover, and obligate deciduous taxa persisted (as CO_2 levels continued to decrease). Girraween transitioned to ongoing open water within the sinkhole and incorporated sediment build-up, resulting in the diversification of shallow water taxa. The existence of shallow water corresponds to an initial limited MIS 3 lake transgression within the Gregory Lakes basin (Fitzsimmons et al., 2012). NT wetland diversity at this time is in keeping with Kershaw et al.'s (2007) northeast Queensland observations; that a MIS 4 homogeneous cyperaceous swamp was replaced by a mixed herbaceous swamp in MIS 3, with *Leptospermum* the Myrtaceous woody feature in that case. Both vegetation records are consistent with Kemp et al.'s (2019) timing of a wetter MIS 3 climate, though no 'monsoonal maxima' was recorded for MIS 3 by Pei et al. (2021) as had been evident MIS 1, 5, 7 and 9. Zuraida et al. (2009) also suggest the heat and energy budget of MIS 3 was insufficient for a fully developed Australasian monsoonal system, with insolation peaking only in interglacials (i.e. during MIS 5 and the Holocene). Rainfall regularity rather than total amount is one of the most important factors differentiating types of wetlands in Australia (Finlayson, 1999). Early MIS 3 mixed-cover biomass and water availability at Girraween may therefore have been more about year-round moisture delivery rather than high annual totals limited to the monsoon season.

For monsoonal Australasia, Kershaw et al. (2003: 91) refer to 'a cluster of sustained vegetation changes from around the middle of MIS 3'. Poaceae increased relative to *Eucalyptus* (Banda Sea core SHI-9014), and canopy tree assemblages altered in an opening of Indonesian and northeastern Australian humid rainforests (van der Kaars et al., 2000; Kershaw et al., 2007; Moss et al., 2017). Approaching MIS 2, further shifts in north Queensland from drier rainforest to sclerophyll (myrtaceous) forest dominance (with very low complex rainforest and fern representation) strongly reflects reduced rainfall (Moss et al., 2017; Kershaw et al., 2003). Similarly, the Girraween catchment transitioned into a drier grassy-savanna (after 43.8 ka BP). By this second half of MIS 3, the savanna surrounding Girraween no longer accommodated blended wetter-drier plant growth; non-eucalypt sub-canopy trees were replaced by dry-adapted shrubs, and the distinguishing life form of the monsoonal forest community changed to vines. Changed structural and compositional attributes within eucalypt communities, and fragmentation of rainforest types, appears a common later-MIS 3 landscape feature for northern Australia.

Kemp et al. (2019: 95) also differentiate the second half of MIS 3's climate as progressively drying. Interestingly, statements are that northern Australia was not just drying, but undergoing 'aridification'. The presence of drought-resistant, (semi)arid Amaranthaceae/Chenopodiaceae are indicative of more acute drying at Girraween from 45 ka cal BP. Replacement of eucalypts by Chenopodiaceae in marine core GC-17 (offshore northwest Western Australia, WA, van der Kaars and De Deckker, 2002) is recorded, just as Chenopodiaceae/Amaranthaceae increased at Girraween, therefore suggesting an geographically extensive trend. Expanding MIS 3 aridity is specifically defined as both total rainfall reduction as well as increased seasonality. A northward shift of the boundary between areas with low winter rainfall and the region of higher summer rainfall occurred (van der Kaars and De Deckker, 2002). This correlates with Rowe et al.'s (Girraween MIS 2, Rowe et al., 2021) conclusions in relation to past rainfall gradients, corresponds to the end of mega-lake phases in the NT and WA, declines in fluvial system energy, and floodplain reorganisation (Croke et al., 2011; Wende et al., 1997). Kati Thanda-Lake Eyre mega-lakes were last recorded at 48 ± 2 ka, following which a major hydrological change occurred, resulting in the shift to playa-dominated conditions (Cohen et al., 2022, 2015). Elements of the 'aridification' in MIS 3 look to differentiate northern NT and WA from northeastern Australia. At Girraween, pollen evidence of greater arid-trending reactions in the catchment's dryland vegetation than in the local wetland, may signal a local sinkhole influence.

5.2. Intrinsic drivers of change

5.2.1. Sinkhole topography

Plants can respond to climate changes by shifting their range (Bátori et al., 2019), migrating with changes in coastline position for example, as sea-levels increase or decrease (Williams et al., 2009; and plant migrations are discussed in relation to Girraween Lagoon during MIS 2 and the LGM by Rowe et al., 2021). Plants may also persist in refugia. In this case, topographic complexity can create habitats that remain environmentally more stable through time (Bátori et al., 2019, 2021). It is worth considering that as an only partially filled sinkhole through MIS 4 and MIS 3, the Girraween depression may have incorporated microhabitats - warmer, drier, cooler and/or more moist than the prevailing regional climate, creating a mosaic of microclimates that allowed taxa to persist on site through environmental changes and maintain local diversity (Bátori et al., 2019). Darwin is a region of otherwise low coastal and floodplain relief. Sinkholes can show internal geo-climatic features (high humidity, lesser wind speeds, differing light availability), the ability to collect and retain water, to influence the composition of local vegetation (Battisti et al., 2017). Soil characteristics also vary within a sinkhole creating niche pockets (Ozkan et al., 2010). Sinkholes may also serve to reduce the impact of disturbances (e.g. fire, Battisti et al., 2017).

Most commonly, herbaceous species, grasses, ferns and Cyperaceae, are observed to grow in sinkhole slope crevices (Homoya and Hedge, 1982). Bátori et al. (2021) however suggest sinkholes facilitate the persistence of diverse plant functional groups (examining sinkhole refugia roles in the forest dynamics of Eastern Europe). In harbouring a range of plant types, a refugial capacity suggests the site could have provided taxa ready to re-expand locally (rather than only migrate regionally) as regional environments changed during climate oscillations. Continued sediment accumulation through MIS 4 into MIS 3 may also have diversified sinkhole habitats, to create more available niches, according to degree and duration of wetness, and from which marginal, crevice occupants spread. This could also have facilitated increases in varied *Melaleuca* (Arecaceae and/*or Pandanus*) species into the local environment. Homoya and Hedge (1982), in an examination of sinkhole wetlands in the United States, observed that most swamp species remained present on the periphery of any newly formed ponds, ready to establish more widely as suitable habitat became available. This process included peat accumulation on the border of ponds providing for the encroachment of woody species. It is proposed here that this 'invade-encroach' equivalent occurred at Girraween as predominantly dry and cold MIS 4 progressed into warmer and periodically wetter MIS 3.

5.2.2. Fire

Climate influences fire regime both directly, through lightening ignition, fuel moisture, and prevailing fire weather, and indirectly through changes in vegetation type and productivity (Daniau et al., 2010; Bradstock, 2010). The major control on trends in fire incidence at Girraween, were that colder-drier conditions reduced vegetation productivity through MIS 4 and thus the availability of fuel for burning. As the climate warmed, and the hydrological cycle became stronger, vegetation productivity increased in MIS 3 leading into an expansion of fuel and fire. Interwoven throughout, changed CO_2 altered the competitive performance of wooded plant functional types when confronted with fire. Overall, MIS 4 incorporated less burning than MIS 3, but variability in fire incidence was more pronounced under MIS 3 conditions than in MIS 4. Bird et al. (2024) provide insight into how fire indicators in MIS4–3 compare to those recorded in MIS 6–5 and MIS 2–1.

Increases in the charcoal flux (fire occurrence) are contemporaneous with greater grass pollen representation (availability of herbaceous fuel). The gradual shift in fire regime from MIS 4 into MIS 3 was associated with grass-layer dynamics. Grasses are the key savanna taxa (the so-called 'fuel species') as growth and curing of grasses respond rapidly to fluctuations in available moisture, and fuel connectivity is provided by grass material to maintain fire spread. C_4 grasses are particularly influential in both regards (Bradstock, 2010; Murphy and Bowman, 2007). Bradstock (2010) describes an interplay between woody litter and herbaceous fuels in sclerophyll woodland-like environments. At Girraween, woody litter fuel from trees/shrubs would have been increasingly discontinuous because of declining relative cover through MIS 4 (including clumped tree distribution). The degree to which fire was able to span grass-fuel discontinuities, may also have been reduced during MIS 4. The subsequent transition in MIS 3 into a semi-arid savanna, lead to an (irregular) increase in fire. In both MIS 4 and 3 fire sensitive taxa were able to maintain a presence. Fire was therefore incorporated into ecosystem dynamics as contributing to biodiversity, rather than as to the detriment of some plant functional types.

If lower-intensity fire was characteristic of fire regime across the Girraween region at these times, fire was likely restricted from monsoonal forest areas, associated *Podocarpus* margins, as well as *Callitris* stands. At a vegetation community scale, 'fire-suppression thresholds' exist. When tree canopy cover is sufficient (typically >40% tree cover), vegetation flammability is reduced by increasing atmospheric humidity and by inhibiting the growth of light-demanding grasses and resulting fuel loads, thereby reducing and disconnecting the distribution, intensity and propagation of fire (Oliveras and Malhi, 2016). Similar to broad-leaf forests, *C. intratropica* stands produce their own microhabitat, supressing understorey fuels (particularly grass biomass) to exclude, or substantially reduce the intensity of fires (Bradstock, 2010; Bowman et al., 1988, 2022; Trauernicht et al., 2012). Thresholds in woody canopy cover that influence fire behaviour do not appear to have been reached within the eucalypt communities in either MIS 4 or MIS 3. That is, eucalypt (or sclerophyll) canopy cover was insufficient for a shade-grass-fire suppression feedback to have taken place within this part of the catchment.

5.2.3. People and megafauna

To explore the long-term interaction between people and Australian ecosystems, palaeoecology looks for transitions; in situ change of biotas, landforms and hydrologies, often through fire (McNiven, 2008; Rowe et al., 2022; Bird et al., 2013). Transitions are part of what McNiven (2008) refers to as people's crafting of cultural landscapes. For plants, in situ transitions include altering the abundance, distribution and diversity of species (i.e. counter to climate). Through burning, people strategically promote certain plant species and suppress the growth of other species to create local environments of their own design. Engineered transitions include modifying sediment and hydrological regimes. (McNiven, 2008).

Contemporary megafauna (as megaherbivores) are observed as ecological keystones, a role translated back into the past. Survivors have been shown to influence plant community composition, vegetation structure and openness, seed dispersal, nutrient cycling, and fire regimes (Gill, 2014). Megafauna decline, and loss of their ecological interactions, also allows for detectable influences in palaeorecords. Outcomes of extinction can incorporate cascade effects on plant community composition, vegetation structure and ecosystem function, altered nutrient cycles, increased fire activity, novel communities and shifts in biomes. For late Quaternary savanna, whole regime shifts are proposed; extinctions may have disrupted tree-grass coexistence, vegetation openness was reduced and landscape heterogeneity decreased (Gill, 2014; Smith et al., 2016; Berzaghi et al., 2018).

Ecological feedbacks at Girraween were foremost consistent with climate, related to the MIS4-MIS 3 stadial–interstadial shift (evident in vegetation structure, composition, patterns in fragmentation, and enhancing the role of refugia). Weakened monsoonal mechanisms in particular drove a slow-sustained increase in grassy savanna. This gradual drying of savanna eventually peaked during the MIS 2 LGM (Rowe et al., 2021). Smith et al. (2016; 107) refer to how ecosystems 'unraveled' with megafauna decline or extinction (as above). Such impact extent is not detected within the Girraween MIS4 and MIS 3 data. Conceivably, extinction may not have occurred as a local sudden 'collapse', or the Girraween site exhibited little ecosystem shift after megafaunal loss because woody vegetation was already limited by low precipitation. Megafauna (likewise people) may have effectively moved from the inland areas to coastal regions on the emerging continental shelf, so creating a distance effect, diminishing the possibility of impact-proxies becoming incorporated within site sediments (Webb, 2008). Similarly, pinpointing climate does not exclude people from the earliest occupation of the northern NT as having been present and influential at Girraween. People likely utilised a wide range of local plant resources and land use strategies (see Florin et al., 2022 for MIS 4 and MIS 3), but that no palaeoecological transition signals were generated from within the catchment. Low-density populations are a possibility, until for example post-glacial MIS 2–1 around Girraween (Bird et al., 2024; Rowe et al., 2019), after which a cultural landscape was prominent and therefore evident in fossil records.

6. Conclusion

Stadial MIS 4 and interstadial MIS 3 can be misinterpreted as static, especially when viewed in comparison to MIS 5, MIS 2 and/or MIS 1 (overlooked, as suggested by De Deckker et al., 2019). Yet, as evident in this study, there were complex environmental scenarios, which are important to explore contextually, to study Australian long-term people-environment and fauna-flora interactions.

Girraween Lagoon is a site representative of the Australian tropical savanna region. MIS 4 and MIS 3 sea level changes and associated variations in moisture and heat transportation, held implications for monsoon delivery, which was particularly consequential for Girraween regional ecology. The woody-grassy dynamic, woody composition (notably sub-canopy non-eucalypts), and herbaceous associations, suggest the development of grassy eucalypt savanna through MIS 4 into MIS 3, likely patchy in its wooded structure, and where plant disturbance indicators are suggestive of unsteady vegetation communities throughout both time stages. The site ultimately transitioned into semi-arid savanna approaching MIS 2. This savanna sequence is representative of a prolonged cool-drying shift in north Australian vegetation change, likely involving gradual effects in ecological resources, for people as well as megafauna. Biomass fuel production does not appear to have been large enough to make fire a primary landscape driver. The frequency and/or intensity of burning was not high enough to exclude fire sensitive taxa at any point (though some may have occupied the sinkhole refugium). Wetland habitats, as essential landscape features for people and megafauna, were less continual and varied in MIS 4 than MIS 3.

This paper has taken the view to examine unique sinkhole-lagoonal sediments in order to learn what the plant-vegetation ecology was like in monsoonal northern Australia during MIS 4 and MIS 3, simultaneously expanding an understanding of what constituted the 'underlying baseline landscape' during Aboriginal people's first arrival into Australia and subsequent occupation. For researchers to be able to place megafauna within an ecological landscape – amongst changing vegetation habitats – assists in discussing their vulnerability. In its examination, this paper has built a high quality palaeoecological dataset, where a lack of late Quaternary vegetation information for the NT has been especially apparent.

CRediT authorship contribution statement

Cassandra Rowe: Conceptualization, Data curation, Investigation, Writing – original draft. **Christopher M. Wurster:** Writing – review & editing. **Michael I. Bird:** Investigation, Methodology, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2024.112150.

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