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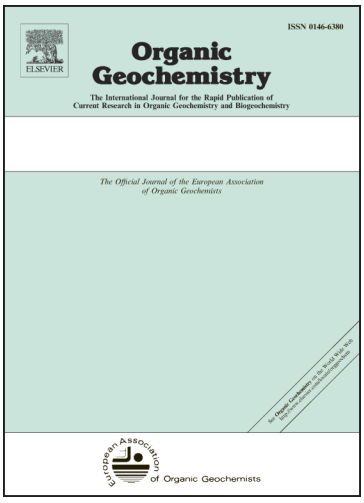

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TARAXEROL ABUNDANCE AS A PROXY FOR IN SITU MANGROVE SEDIMENT

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ABSTRACT

Mangrove sediments are valuable archives of relative sea-level change if they can be distinguished in the stratigraphic record from other organic-rich depositional environments (e.g., freshwater swamps). Proxies for establishing environment of deposition can be poorly preserved (e.g., foraminifera) in mangrove sediment. Consequently, differentiating mangrove and freshwater sediment in the stratigraphic record is often subjective. We explore if biomarkers can objectively identify mangrove sediment with emphasis on their utility for reconstructing relative sea level. Our approach is specific to identifying in situ sediment, which has received less attention than identifying allochthonous mangrove organic matter. To characterize mangrove and non-mangrove (freshwater) environments, we measured *n*-alkane, sterol, and triterpenoid abundances in surface sediments at three sites in the Federated States of Micronesia. Elevated taraxerol abundance is diagnostic of sediment accumulating in mangroves and taraxerol is particularly abundant beneath monospecific stands of *Rhizophora* spp. Taraxerol was undetectable in freshwater sediment. Other triterpenoids are more abundant in mangrove sediment than in freshwater sediment. Using cores from Micronesian mangroves, we examine if biomarkers in sediments are indicative of in situ deposition in a mangrove, and have utility as a relative sea-level proxy. Taraxerol concentrations in cores are comparable to surface mangrove sediments, which indicates deposition in a mangrove. This interpretation is supported by pollen assemblages. Downcore taraxerol variability may reflect changing inputs from *Rhizophora* spp. rather than diagenesis. We propose that taraxerol is a proxy that differentiates between organic sediment that accumulated in mangrove vs. freshwater environments, lending it utility for reconstructing relative sea level.

Highlights:

- Taraxerol is abundant in modern mangrove sediment, particularly below *Rhizophora.*
- Taraxerol is near-absent in supratidal sediment.
- Taraxerol is a proxy for mangrove sediment with utility for reconstructing sea level.
- Micronesian cores have taraxerol concentrations consistent with modern mangroves.

1. INTRODUCTION

Sequences of mangrove sediment are valuable archives of past environmental change. Unique to (sub-)tropical intertidal zones, mangrove depositional environments provide information on relative sea-level change (RSL; Woodroffe et al., 2015; Tam et al., 2018; Khan et al., 2022), climate change (Joo-Chang et al., 2015; Decker et al., 2021), paleoecology (Li et al., 2012; França et al., 2019), and blue carbon dynamics (Ezcurra et al., 2016; Rogers et al., 2019). Mangrove research often relies on confirmation that the sediment under examination accumulated in a mangrove rather than another depositional setting. Organic-rich mangrove sediment is readily distinguishable from inorganic sediment that accumulated in adjacent sub-tidal settings (e.g., coralline sand), but it can be difficult to visually differentiate from other organic-rich sediments that accumulated in nearby freshwater environments such as swamps. Identifying mangrove sediment is particularly important for reconstructing RSL because mangroves have a relationship to tidal elevation (i.e., they are a proxy for sea level; Woodroffe et al., 2015; Chua et al., 2021; Khan et al., 2022), but freshwater environments do not (i.e., they only indicate that RSL was below the elevation of the paleo surface). Field-based sedimentological descriptions (e.g., Bloom, 1970) often differentiate mangrove and freshwater sediment, but confirmation of these interpretations is challenging for (at least) four reasons: (1) plant macrofossils are rarely preserved, can be allochthonous, and may not be diagnostic of mangroves; (2) some key mangrove plants produce relatively modest amounts of pollen (for insect and bird pollination), which can be overprinted by wind-blown pollen from surrounding non-mangrove environments or poorly preserved in sediments (Sefton and Woodroffe, 2021); (3) microfossils such as foraminifera or diatoms are often poorly preserved despite forming assemblages in modern settings that are characteristic of specific depositional environments and with adequate numbers of tests for statistical analysis (Woodroffe et al., 2005; Berkeley et al., 2007); and (4) stable isotopes (e.g., $\delta^{13}C$) in bulk sediment do not readily distinguish inputs of mangrove and freshwater plant matter (Khan et al., 2019). Consequently, there is a need for alternative proxies to objectively identify mangrove sediment preserved in the stratigraphic record.

Biomarkers are lipid compounds that are synthesized by organisms and can be posthumously incorporated into the sedimentary record and preserved on millennial timescales (Ranjan et al., 2015; He et al., 2018; Kumar et al., 2019). Since some biomarkers are diagnostic of the botanical community that synthesized them, their recognition in sedimentary sequences can be used to infer depositional environments. Similar to other higher plants, mangroves produce *n*-alkanes, sterols, and pentacyclic triterpenoids (Ghosh et al., 1985; Misra et al., 1987; He et

al., 2020). Notably, mangroves produce some compounds (β-amyrin, lupeol, and germanicol, and especially taraxerol) in unusually high amounts compared to non-mangrove plants (Koch et al., 2003). Consequently, elevated taraxerol in offshore sediment cores has been used to identify allochthonous organic matter that accumulated in mangroves before being mobilized, transported, and redeposited in shallow and deep marine environments (Johns et al., 1994; Scourse et al., 2005; Xu et al., 2007; He et al., 2014; Chu et al., 2020), including studies that refer to sea-level change (Versteegh et al., 2004; Kim et al., 2005; van Soelen et al., 2010; Yu et al., 2023). The recognition of in situ (rather than allochthonous) mangrove sediment has received less attention, but is particularly important for RSL reconstructions because the spatial proximity of mangrove and freshwater environments in modern settings indicates that they can also be associated through time (i.e., subtle spatial and temporal transitions between mangrove and freshwater sediment may be preserved in the in situ stratigraphic record). Leaves of mangrove taxa such as *Rhizophora* spp. have particularly high concentrations of taraxerol compared to other parts of mangrove trees and non-mangrove taxa (Ghosh et al., 1985; Killops and Frewin, 1994; Koch et al., 2011), and since leaf litter is an important source of organic material to the mangrove sediment surface, relatively high taraxerol concentrations (measured in an appropriate stratigraphic context) in sediment likely indicates accumulation beneath a canopy of mangrove trees. Using compounds such as taraxerol as a proxy for depositional environments requires that their modern, in situ distribution is quantified from environments that are likely to be analogous to those encountered in core material (i.e., mangroves and organic-rich freshwater settings). In particular, efforts to reconstruct RSL using mangrove sediment may benefit from exploration of variability in biomarker abundances between floral zones that occupy distinct tidal elevations.

We test if biomarkers (specifically the relative abundance of sterols and pentacyclic triterpenoids normalized against *n*-alkanes) can distinguish between mangrove and freshwater sediment in the tropical western Pacific Ocean. We first quantify the relative abundance of several compounds in modern (surface) bulk sediment collected from known environments at three sites on the islands of Pohnpei and Kosrae in the Federated States of Micronesia. We then compare modern values to compound abundances in four sediment cores to evaluate whether downcore sediments were deposited in mangrove or freshwater environments. Downcore compound abundances are also compared to mangrove pollen, plant macrofossil, and foraminifera content to test the suitability and possible advantages of using biomarker abundance as a proxy for identifying in situ mangrove sediment.

2. STUDY AREA

Pohnpei and Kosrae are basaltic islands in the western Pacific Ocean with large areas of mangroves fringing their coastlines (Figure 1). The mangrove forests are dominated by *Rhizophora apiculata*, *Sonneratia alba*, and *Bruguiera gymnorrhiza*, with minor populations of *Xylocarpus granatum, Rhizophora stylosa*, *Lumnitzera racemosa*, *Rhizophora mucronata*, *Rhizophora* x *lamarki*, *Barringtonia racemosa*, *Acrostichum* spp., and *Nypa fruticans.* (Fujimoto et al., 1995). The mangrove forests are considered relatively pristine and many individual trees and plants reach advanced ages and sizes (Allen et al., 2001). *Rhizophora stylosa* typically dominates the seaward, low-elevation fringe of the mangrove, and transitions into a mixed community of *Rhizophora apiculata*, *Sonneratia alba*, and *Bruguiera gymnorrhiza* in the higher-

elevation interior (Ellison et al., 2022). At the landward edge of the mangrove environment, *Xylocarpus granatum* appears, before transitioning into upland (non-mangrove) vegetation. On Pohnpei, the upland vegetation adjacent to the mangrove environment (i.e., the supratidal environment) is dominated by *Cocos nucifera*, *Nypa fruticans*, *Miscanthus floridulus*, and *Terminalia* sp. On Kosrae, upland vegetation adjacent to the mangrove environment is dominated by *Nypa fruticans*, *Terminalia carolinensis*, *Cyrtosperma merkusii*, and *Miscanthus floridulus*. Great diurnal tidal range (mean lower low water to mean higher high water) is 0.88 m at Pohnpei, 1.17 m at Kosrae, and does not vary among sites on either island (Willsman, 2012; Buffington et al., 2021; Sefton et al., 2022a). Some mangroves on Pohnpei and Kosrae are underlain by up to ~6 m of mangrove sediment that accumulated over the past ~5,000 years (Fujimoto et al., 1996, 2015), likely due to island subsidence (Sefton et al., 2022a). The origin of this sediment was established principally from sedimentological descriptions by researchers from multiple groups and disciplines (Bloom, 1970; Matsumoto et al., 1986; Fujimoto et al., 2015) and occasionally through palynology (Yamanaka and Kikuchi, 1995; Athens and Stevenson, 2012). These sedimentary archives are rapidly accreting (Krauss et al., 2010) and may yield long, near-continuous, and detailed histories of paleoenvironmental change (including RSL; Sefton et al., 2022a). The steep topography of the islands means there are few freshwater, peat-forming environments on Pohnpei and Kosrae today. However, high annual rainfall (~5000–6000 mm; Krauss et al., 2007) and thick upland vegetation means that such environments could have been more widespread in the past and may be challenging to visually distinguish from mangrove sediment in the coastal stratigraphic record.

3. METHODS

3.1. Sample collection and pre-treatment

3.1.1. Modern samples

We collected surface sediment samples at two sites on Pohnpei (Madolenihmw and Nihkewe) and one site on Kosrae (Utwe; Figure 1). These sites represent the geomorphic and botanical diversity of mangroves encountered in the Federated States of Micronesia and have adjacent freshwater environments where organic-rich sediment is accumulating. Along transects running from the seaward to landward edges of the mangrove and neighboring freshwater, supra-tidal locations at each site, we documented the species of mangrove plants present (other vegetation was grouped as broadly non-mangrove). Samples of bulk surface (0–1 cm) sediment were collected along each transect into plastic bags and refrigerated in darkness at ~4 °C. We did not sample shallow, sub-tidal sediment adjacent to the seaward edge of the mangrove because at all sites it is coarse-grained, pale-coloured, inorganic sand and shell/coral hash, which is easily distinguished from fine-grained, dark colored, organic mangrove or freshwater sediment. On return to the laboratory, sediment samples were freeze-dried and homogenized to a fine powder using a solvent-rinsed ball mill and stored in glass jars. The elevation of each sample relative to tidal datums was established by levelling with a theodolite and staff relative to an automated water logger, or timed water levels within the mangrove. These measurements were then related back to contemporary measurements made by the Pohnpei-C tide gauge for which tidal datums were established over the 1983–2001 epoch (Sefton et al., 2022a). On Kosrae, we deployed an automated water logger at the site where a tide gauge operated from 2011 to 2016 (Leluh; Willsman, 2012)). Tidal datums were established from this observational time series and

the logger was leveled directly to the same benchmarks used by the tide gauge (see Sefton et al., 2022a for details).

3.1.2. Core samples

At four sites (Nanitipw, Pwok, and Rohi on Pohnpei and Utwe on Kosrae; Figure 1) we collected sediment cores that were interpreted in the field as having likely accumulated in a mangrove. These sites were selected from existing literature (Fujimoto et al., 1996, 2015) to capture variability in site geomorphology and underlying substrate (e.g., estuarine sediment or coral). Core-top elevations were measured using the same approach and equipment as described for modern samples. Cores were collected in overlapping, 50-cm long sections using an Eijkelkamp peat sampler, placed in rigid plastic sleeves, wrapped in plastic, and stored in darkness at ~4 °C until further analyses. Each core was sliced into 1-cm thick samples, of which a subset (distributed approximately evenly down each core) were analyzed. One half of the chosen samples was freeze-dried and homogenized to a fine powder using a solvent-rinsed ball mill for biomarker measurements; the remaining half was used for pollen analyses (Section 3.3).

Upon examination of the cores in laboratory, we found sparse plant macrofossils, though none could be reliably identified as mangrove in origin. Additionally, we examined duplicate cores for foraminifera using standard methods (Edwards and Wright, 2015) and found that they are present in the cores, but at abundances so low (<5 specimens) that we deemed them unreliable for establishing an environment of deposition (quantitatively or qualitatively), although the presence of any foraminifera, given their propensity for poor preservation in mangroves (Woodroffe et al., 2005; Khan et al., 2019), does support an intertidal origin.

3.2. Determination of *n*-alkanes, sterol, and pentacyclic triterpenoidsabundance

3.2.1. Sample treatment & extraction

Samples (2 g), procedural blanks (2 g) and QC (Quality Control; 0.5 g) were each spiked with authentic standards tetracosane-d_{50} (2 µg), 5α-cholestane-d_6 (2 µg), androstanol (100 µg) and 5α-cholestanol-d_5 (100 µg) in 100 µL of toluene. They were then mixed with copper powder (2 g) and granular anhydrous sodium sulphate dispersant and transferred to an accelerated solvent extraction (ASE) cell. Sediments were extracted using an ASE 350 (Thermo Scientific) with dichloromethane/methanol (3:1v/v) at 100 °C, 5 min static period and 60% flush volume. Each extract was reduced to dryness using a TurboVap evaporator at 40 °C, reconstituted in acetone (10 mL) and agitated in a sonic bath to ensure disaggregation and dissolution. This solution was split into two equal aliquots, one for *n*-alkane analysis and the other for terpenoid analysis.

Quality control was achieved by performing repeated intra-batch analyses of a combined single mangrove sediment core (British Geological Survey identification code PRC24) from Puerto Rico. These were both included as replicates at the beginning and end of each batch of ASE extractions at a minimum of every 19 sample intervals and analysed in duplicate using the same method as for the samples. A procedural blank was prepared from the sodium sulphate / copper powder dispersant.

3.2.2. *n-Alkane analysis*

Each aliquot for n-alkane analysis was reduced to dryness using a gentle steam of dry nitrogen, reconstituted in n-hexane (1 mL), and agitated in a sonic bath (0.5 min) to ensure disaggregation and dissolution. The resultant solution was introduced at the top of a glass Pasteur pipette mini-column containing 5% deactivated silica gel 60 (2 g, 0.2–0.5 mm) that was pre-conditioned with n-hexane, eluted with three column volumes of n-hexane, and reduced in volume to 0.5–0.8 mL using a gentle steam of dry nitrogen. An internal standard of squalane was added (1 µg in 0.1 mL toluene) and the solution made-up to 1.0 mL with n-hexane in a 1.5 mL septum top vial. The prepared sample extracts were stored in a fridge at 4 °C prior to analysis.

n-Alkanes concentrations were determined by gas chromatography-mass spectrometry (GC-MS) using a Thermo Scientific Trace 1300-TSQ9000 triple quadropole MS operated in scan mode (ionization energy 70 eV, 40-600 Da). Sample application (1 µL) was by programable temperature vaporiser injection, split mode (1:5, 60 °C to 330 °C at 10 °C/s). The GC was fitted with a fused silica Agilent DB-1 capillary column (60 m length × 0.25 mm i.d. × 0.10 µm film thickness). The GC oven-temperature program was 60 °C (1 minute isothermal) to 320 °C at 8 °C/min (12 min isothermal). Helium was used as the carrier gas (1 mL/min). Data processing was performed using Chromeleon software (version 7.2.10). Analytes and internal standard concentrations were determined using ions m/z 85 (qualifying ions m/z 57 and m/z 71). The surrogate (tetracosane-d_{50}) concentration was determined using m/z 98 (qualifying ions m/z 66 and m/z 82). A 6-level calibration from 0.17 to 9.00 µg/µL was performed using a commercially available certified standard containing thirty *n*-alkanes (C_{10} to C_{40}), pristane and phytane.

3.2.3. *Mangrove sterol and pentacyclic triterpenoid GC-MS analysis*

Each aliquot for measurement of mangrove biomarkers was transferred to a 50 mL Pyrex glass screw-top bottle and reduced to dryness using a gentle steam of dry nitrogen. The extract was then saponified using 1M methanolic KOH (10 mL), the vessel screwed closed and agitated in a sonic bath (0.5 min) to ensure disaggregation and dissolution. The mixture was placed in an oven at 70 °C for 1 hour and allowed to cool. 30 mL of MilliQ-grade water was then added and liquid-liquid extracted by shaking with 10 mL of dichloromethane (DCM). The DCM was removed, and the process repeated with a further 10 mL of DCM. The DCM extracts were combined, and any trace or dissolved water removed the addition of a minimum quantity anhydrous sodium sulphate. The extract was reduced to dryness using a gentle steam of dry nitrogen prior to the column chromatography clean-up stage. Extracts were quantitatively transferred to a pre-conditioned an solid phase extraction cartridge (Bond Elut, HF Mega BE – SI, 10 gm 60mL, Agilent Technologies). The cartridge was eluted with two fractions using gravity: Fraction A (40 mL, hexane:toluene, 3:1); and Fraction B (40 mL, hexane:ethylacetate, 4:1). Fraction B was reduced to dryness using a TurboVap evaporator at 40 °C and reconstituted in pyridine (1 mL) containing 50000 µg of the internal standard cholesterol-d_6. A 20 µL aliquot was added to a 200 µL glass insert containing 140 µL of pyridine, 40 µL of N,O-bis(trimethylsilyl)trifluoroacetamide with 1% trimethylchlorosilane. The insert was placed in a 2 mL GCMS vial, sealed with a septum cap and mixed by inversion. It was placed in an oven at 70 °C for 1 hour and allowed to stand for >12 hours prior to analysis.

Mangrove biomarker concentrations were determined by gas chromatography-mass spectrometry (GCMS) using a Thermo Scientific Trace 1300-TSQ9000 triple quadropole MS in

scan mode (ionization energy 70 eV, 60-650 Da). Sample application (1 µL) was by PTV injection, split-splitless mode (splitless for 0.7 min, the split 1:5, 60 °C to 300 °C at 10 °C/s). The GC was fitted with a fused silica Agilent DB-5 capillary column (30 m length × 0.25 mm i.d. × 0.25 µm film thickness). The GC oven-temperature program was 60 °C (1 minute isothermal) to 300 °C at 6 °C/min (10 min isothermal). Helium was used as the carrier gas (1 mL/min). Data processing was performed using Chromeleon software (version 7.2.10). Ions used are presented in the Supplementary Table 3. A 5-level quadratic calibration from 1.50 to 20.00 ng/µL was performed containing analytes: stigmasterol, taraxerol, β-amyrin, lupeol; surrogates: 5α-androstanol, 5α-cholestanol-d_5 and internal standard cholesterol-d_6. Due to spectral interference, a separate calibration was made for β-sitosterol. Germanicol was determined using the calibration of β-amyrin and the ions used were based on the mass spectrum of germanicol presented by Killops and Frewin (1994).

Since (1) the rate of sediment accumulation (including the flux of organic material and biomarkers) varies among modern depositional environments and through time; (2) coastal sediment may include organic inputs from sources other than higher plants (e.g., marine algae); and (3) taraxerol can be derived from non-mangrove plants, we normalized measured compound abundances (µg/g) against the measured abundance of the C_{29} alkane (µg/g) that is a marker for the input of lipids from higher plants (i.e., µg compound per gram dry sediment divided by µg C_{29} alkane per gram dry sediment). Values presented in text and figures follow this convention and are presented unitless (unless stated otherwise; i.e., where units are reported, values are not normalized). The Pearson correlation between the abundance of the C_{29} and C_{31} alkanes in the modern dataset is 0.958, which indicates that our results would not materially change if either the C_{29} or C_{31} alkane (or their sum) was used in normalization. For clarity of presentation, normalized abundances are rounded to one decimal place.

3.2.4. n-Alkane indices

To evaluate the origin of organic matter in bulk sediment, we express the degree of odd-over-even predominance in the long-chain *n*-alkane distribution using the carbon preference index ($CPI_{(24–34)}$; Bray and Evans, 1961):

$$CPI = \frac{1}{2}\left[\left(\frac{C25 + C27 + C29 + C31 + C33}{C24 + C26 + C28 + C30 + C32}\right) + \left(\frac{C25 + C27 + C29 + C31 + C33}{C26 + C28 + C30 + C32 + C34}\right)\right]$$

Values greater than 1 indicate that the organic material has a non-degraded plant origin, and values less than 1 indicate an algal, bacterial, or degraded plant origin (Bray and Evans, 1961). To estimate the relative contribution of organic material in bulk sediment from higher (terrestrial) plant versus aquatic plants, we used the P_{aq} index (Ficken et al., 2000):

$$Paq = \frac{(C23 + C25)}{(C23 + C25 + C29 + C31)}$$

A high value (>0.7) indicates a dominant input from aquatic plants (in which the C_{23} and C_{25} alkanes are more common), and lower values indicate a dominant input from higher plants (in which the C_{31}, C_{33}, and C_{35} alkanes are more common; Ficken et al., 2000).

3.3. Pollen analysis

Pollen was isolated using standard laboratory methods (Bernhardt and Willard, 2015), including digestion in hydrofluoric acid, acetolysis, alkali digestion, sieving, and were stained before mounting on microscope slides. Pollen counts represent the total processed residue from a 1 cm depth-thickness sample (approximately 8 cm^3). Pollen was identified and grouped as either mangrove (in this case, *Rhizophora* spp., *Sonneratia* spp., *Bruguiera* spp., and *Acrostichum* spp.), or non-mangrove (everything else) for further interpretation.

4. RESULTS

4.1. Modern transects

At two sites (Madolenihmw and Nihkewe; Figure 1D) on Pohnpei, we collected a total of 17 surface samples, of which 11 represent mangrove environments and six represent freshwater environments. At Utwe on Kosrae, we collected five surface sediment samples (Figure 1C), of which four represent mangrove environments and one was from an adjacent freshwater environment. Therefore, the combined modern dataset is 15 samples of bulk surface sediment from mangroves (representing four distinctive mangrove floral zones; Figure 3A–C) and seven freshwater samples representing settings where organic-rich material is accumulating in vegetated supratidal environments. Modern transect data are summarized in Table 1.

All surface sediment samples (irrespective of site or environment) exhibit odd-to-even predominance in the *n*-alkane series ranging from C_{13} to C_{37} (Figure 2A). The C_{27}, C_{29}, and C_{31} alkanes are the most abundant. In 21 out of 22 samples, C_{31} is the single most common alkane. In mangrove samples, the mean abundance of C_{31} is 1534 ng/g (range 1065–2213 ng/g), compared to 2150 ng/g (range 1172–2957 ng/g) in freshwater sediment. Surface sediment at Madolenihmw contains the highest amount of C_{31} (mean of 2023 ng/g across all environments) and Nihkewe the lowest (mean of 1456 ng/g for all samples).

The CPI for surface sediment samples ranged from 8.9 to 19.0 (Table 1) and mean P_{aq} was 0.1 (range 0–0.7).

We quantified the abundance of two sterols and four pentacyclic triterpenoids that are common in the tissue of mangrove plants (Killops and Frewin, 1994; He et al., 2018): β-sitosterol (stigmast-5-en-3β-ol); and stigmasterol (24E-stigmasta-5,22-dien-3β-ol); taraxerol (taraxer-14-en-3β-ol); β-amyrin (olean-12-en-3β-ol); germanicol (olean-18-en-3β-ol); lupeol (lup-20(29)-en-3β-ol). Broadly, the abundance of all identified compounds (normalized against C_{29}; see Section 3.2.3.) is greater in mangrove sediment than in freshwater sediments (Table 1; Figure 3D). β-sitosterol and stigmasterol are typically among the most abundant compounds in the tissue of higher plants from a wide range of ecosystems (Bot, 2019), and these compounds are therefore expected to be common in bulk surface sediment where the principal input of organic matter is from higher plants (as evidenced by the calculated CPI and P_{aq} values). The mean abundance of β-sitosterol was 9.4 (range 0–35.6) in mangrove sediment compared to 6.6 (range 0–38.2) in freshwater sediment (although we note that the maximum value from a sample at Utwe appears anomalous among freshwater samples; Figure 3D). The mean abundance of stigmasterol in mangrove sediment was 1.6 (range 0–11.4) compared to 0 (range 0–1.0) in freshwater

sediment (although we note two mangrove samples from Nihkewe had anomalously high values; Figure 3D). We conducted a Mann-Whitney-Wilcoxon Test to quantitatively determine the difference between the normalized abundance of β-sitosterol and stigmasterol in freshwater and mangrove sediment and obtained *p* values of >0.05 indicating no significant difference (Figure 3D). The lack of distinction between mangrove and freshwater sediment using β-sitosterol and stigmasterol reflects their widespread production in higher plants across depositional environments.

The remaining four compounds are associated with mangrove plants specifically (Koch et al., 2003) and our results support this inference (Table 1; Figure 3D). Germanicol is more abundant in mangrove sediment (mean 2.4, range 0.1–9.0) than in freshwater sediment (mean 0.5, range 0.5–1.4). Mangrove sediment also has more lupeol (mean 5.4, range 1.7–22.3) than freshwater sediment (mean 1.0, range 0.1–2.7). Similarly, β-amyrin is more abundant in mangrove sediments (mean 5.9, range 1.5–16.8) than freshwater sediments (mean 0.8, range 0–2.6). The results of the Mann-Whitney-Wilcoxon Test indicate that the normalized abundance of germanicol, lupeol, and β-amyrin is significantly different between freshwater and mangrove samples (*p* values <0.05; Figure 3D).

The disparity between environments is greatest for taraxerol (Figure 3D). In mangrove sediments, the mean abundance of taraxerol was 20.3 (range 2.2–84.1), while only one of seven freshwater samples included a detectable amount of taraxerol. The single freshwater sample with detectable taraxerol (1.9) was collected at Madolenihmw and is markedly less than the minimum taraxerol abundance in mangrove sediment (7.6) at this site. Notably the freshwater sample that yielded taraxerol came from a site immediately adjacent to the landward/highest elevation limit of mangroves (transition vegetation zone; Figure 3A). The results of the Mann-Whitney-Wilcoxon Test indicate the normalized abundance of taraxerol is significantly different between freshwater and mangrove samples (*p* values <0.05; Figure 3D).

The highest normalized abundances for the proposed mangrove markers occur at Nihkewe and mangrove samples from this site returned five of the six greatest abundances of taraxerol (Figure 3D). The mean abundance of taraxerol in mangrove samples at Nihkewe was 43.9, which is an order-of-magnitude difference compared to 11.3 at Madolenihmw and 4.1 at Utwe. The high abundance of taraxerol at Nihkewe was measured in samples where the dominant vegetation is monospecific stands of *Rhizophora apiculata* or *Rhizophora stylosa* (Figure 3B) and this vegetation zone was not sampled at other sites, where mangroves are more diverse (e.g., mixed *Rhizophora apiculata*, *Sonneratia alba*, and *Bruguiera gymnorrhiza*; Figure 3A–C).

4.2. Core samples

A total of 37 core sediment samples were analyzed from four sites for biomarker and mangrove pollen abundance (16 at Nanitipw, seven at Pwok, five at Rohi, and nine at Utwe; Table 2; Figure 4). The stratigraphy at all sites consisted of organic silt, silty peat, and humified peat that we interpreted in the field as having accumulated in a mangrove (Figure 4), overlying either coral rubble or shelly, pale-coloured silt. Among all cores and samples, the mean $CPI_{(24–34)}$ value was 12.8 (range 9.0–17.2) and mean P_{aq} was 0.2 (range 0–0.6).

Taraxerol is the most abundant compound in the core sediments (mean 22.9, range 6.6–55.5). When compared to modern values (Figure 4), all core samples display taraxerol concentrations greater than the minimum measured in surface mangrove sediment (2.2; Table 1). Additionally,

24 out of 37 core samples have concentrations within the range of modern samples from monospecific *Rhizophora* sp. zones (e.g., *Rhizophora apiculata* dominated zone has a mean value of 24.6; Tables 1, 2). Variability in taraxerol concentrations is greater within cores than it is among sites. The mean abundance of taraxerol ranges from 26.4 in the Rohi core to 17.5 in the Pwok core. In contrast, downcore variability can be large. Nanitipw and Utwe show relatively high variability (e.g., Nanitpw varies 8.5–55.5; Table 2), but Pwok and Rohi have more consistent, or small changes in downcore concentration (e.g., Pwok varies 9.9–22.9; Table 2).

Germanicol concentrations in the core samples (mean 2.4) are consistent with those measured in modern mangrove sediments (2.4; Tables 1, 2). β-amyrin concentrations in the core samples is less than the mean concentration of modern mangrove sediments (3.1 compared to 5.9, respectively; Tables 1, 2). β-sitosterol, stigmasterol, and lupeol have low concentrations in core sediments (e.g., Rohi; Figure 4), or decrease downcore (e.g., Utwe; Figure 4). There is a high degree of co-variance among β-amyrin, germanicol, and taraxerol, which are three compounds most commonly associated with mangroves in previous studies from mangroves across multiple regions (Koch et al., 2003).

In all sediment cores and samples, the mean relative abundance of mangrove pollen was 21.2% (range 4.4–45.8%; Figure 4). Pollen abundance within single cores also varies considerably (6–43.2% at Pwok for example). Mangrove pollen abundance covaries with β-sitosterol and stigmasterol (with *p* values of 0.023 and 0.00048, respectively), but shows no covariance with other compounds (taraxerol, lupeol, germanicol, and β-amyrin had *p* values >0.05).

5. DISCUSSION

5.1. Source(s) of sediment organic matter

Higher plants (including mangroves) are characterized by long-chain, odd-numbered alkanes (Eglinton and Hamilton, 1967; Jaffé et al., 2001), while aquatic plants and algae are characterized by mid- and short-chain, odd-numbered *n*-alkanes (Cranwell, 1984; Cranwell et al., 1987; Mead et al., 2005). The balance between these two sources of organic material is quantified using the P_{aq} index (Ficken et al., 2000; see Methods), where a low/high P_{aq} value indicates dominance of long-chain/short-chain alkanes and therefore organic material derived from terrestrial/aquatic plants. On Pohnpei and Kosrae, organic matter in modern mangrove and freshwater supratidal sediment is predominantly derived from higher plants (either deposited in situ or transported) as evidenced by low P_{aq} values (mean = 0.1; Table 1). While the specific expression used to calculate P_{aq} (and therefore threshold values) varies somewhat between studies, this result is consistent with studies from mangroves elsewhere. For example, in southern Florida, USA, mangrove and terrestrial plants had P_{aq} values <0.3 while submerged and emergent aquatic plants and seagrasses had P_{aq} values of 0.4–1.0 (Mead et al., 2005; He et al., 2020).

The dominance of organic material derived from higher plants in the Pohnpei and Kosrae surface mangrove sediments occurs despite regular tidal flooding which can deliver allochthonous marine organic matter (Bouillon et al., 2003). This higher plant dominance likely reflects a relatively high flux of organic matter from the in situ mangrove plant community coupled with the attenuation of waves, currents, and tides by roots which serve to limit delivery of organic matter (particularly large particulate material) into the mangrove (Wolanski et al., 1996). For example, seagrass communities are present on both Pohnpei and Kosrae (McKenzie et al., 2021), but surface sediment *n*-alkane distributions and P_{aq} values do not suggest that seagrass material reaches the mangrove surface in large quantities. The presence of a barrier reef around Pohnpei and a fringing reef at the Utwe site on Kosrae may further limit the supply of large aquatic organic matter (e.g., rafts of Sargassum; Kemp et al., 2019) since the exchange of water between the lagoon and open ocean is restricted to inlets.

The distribution of *n*-alkanes distinguishes between environments where the dominant source of organic matter is from higher, terrestrial plants (including mangrove and terrestrial sources) rather than aquatic plants and seagrasses (Sainakum et al., 2021). However, mangroves are not distinguishable from other terrestrial environments using *n*-alkane distributions alone (Johns et al., 1994; Bianchi and Canuel, 2011; He et al., 2020). We evaluate if sterols and pentacyclic triterpenoids can be a proxy for deposition in a mangrove.

5.2. Surface sediment compounds: mangrove versus terrestrial organic matter?

Modern mangrove samples across all three sites have taraxerol abundances at least two orders of magnitude higher than the supratidal freshwater samples (Table 1; Figure 3D). In all modern samples with non-mangrove vegetation, taraxerol was not detectable in surface sediment. Taraxerol was detectable in one sample at the 'transition' between the landward edge of mangroves and supratidal freshwater environments (1.9; Table 1; Figure 3A). The marked difference in the taraxerol abundance of surface sediment between mangrove and non-mangrove environments likely reflects the composition of plant material that is contributed from the dominant community to the sediment surface as leaf litter and downed wood (aboveground carbon), or via roots (belowground carbon). In the southeastern Atlantic, Versteegh et al. (2004) measured taraxerol and *n*-alkanes in *Rhizophora racemosa* leaves and recognized that they contained unusually high ("unprecedented") amounts of taraxerol. Similarly, *Rhizophora* spp. leaves from southern Florida, USA (Killops and Frewin, 1994; He et al., 2022), Okinawa, Japan (Basyuni et al., 2007), and Hainan, China (Chu et al., 2020) are observed to include high concentrations of taraxerol. Increased production of triterpenoids (such as taraxerol) in higher plants may be a physiological adaption to brackish and saline conditions (Basyuni et al., 2012), hence its higher abundance in mangrove plants compared to freshwater plants. The geographic consistency of this finding indicates that mangrove plant tissues contain high abundances of taraxerol across a range of environmental conditions (e.g., salinity, climate) and by extension, it is assumed to remain abundant through time even against a backdrop of changing environmental conditions. Importantly, Versteegh et al. (2004) noted that most taraxerol in mangrove leaves is found in the leaf interior rather than as a surface compound and concluded that it would therefore be fluxed as particulate litter rather than being evaporated and wind-blown. *n*-Alkanes are concentrated in the leaf surface and are more susceptible to wind transport, and could therefore influence alkane-normalized sterol and pentacyclic triterpenoid concentrations. However, in mangroves where in situ organic matter production is high and the expansive canopy dampens winds we do not expect *n*-alkane concentrations in surface sediments to be determined by aeolian deposition.

We propose that the high concentration of taraxerol in surface sediment from mangroves on Pohnpei and Kosrae reflects a direct flux of organic matter (largely from above-ground biomass such as leaves; Woltz et al., 2022) from the in situ mangrove community. The lack of detectable taraxerol in six of seven freshwater samples indicates that the supratidal settings contain plants that do not produce high abundances of taraxerol and do not receive a substantial allochthonous input of mangrove-derived organic matter. Attenuation of tides and currents by mangrove aerial roots likely inhibits upward and landward redistribution of plant litter, even during rare, high-energy events. The one freshwater sample with detectable taraxerol likely received direct input from mangrove plant litter falling from nearby trees since it was positioned at the transition from mangrove to non-mangrove floral zones. In addition, taraxerol-producing *Barringtonia racemosa* typically occupies the mangrove-to-freshwater transition on Pohnpei and Kosrae. The high concentration of taraxerol in modern mangrove sediment suggests that these environments do not receive enough allochthonous material from adjacent uplands to overprint the signature of in situ organic matter. The apparent lack of supratidal-derived organic matter may reflect the geomorphology of Pohnpei and Kosrae where steep topography results in small catchments and an absence of large rivers to move material in or out of mangrove areas. We conclude that taraxerol is a specific biomarker for in situ mangrove organic matter (Koch et al., 2003; Versteegh et al., 2004; He et al., 2022) in the western equatorial Pacific Ocean.

Within the subset of modern mangrove samples, taraxerol abundance is distinctly greater in samples collected from monospecific stands of *Rhizophora* spp. (mean 43.9 μg/g) than in mixed mangroves (mean 8.4 μg/g; Table 1; Figure 4). Previous studies suggested that while taraxerol is an indicator of mangrove organic matter more generally, unusually high taraxerol abundances in plant tissue are specific to *Rhizophora* spp. (Killops and Frewin, 1994; Koch et al., 2011; Chu et al., 2020), including those on Pohnpei (Ladd and Sachs, 2015). At our study site, taraxerol concentrations >0 indicate deposition in a mangrove environment because taraxerol is not detected in adjacent freshwater environments. In addition to this observation, we tentatively propose that taraxerol concentration >20 is indicative of sediment that accumulated in a monospecific *Rhizophora* spp. mangrove, while detectable taraxerol with abundance <20 suggests accumulation in a mixed mangrove community (Table 1; Figure 4). However, these threshold values are established from a small number of observations of monospecific *Rhizophora* sp. environments (and only one site; Nihkewe). We also acknowledge that taraxerol can be produced in non-mangrove plants and therefore may be present in some freshwater sediments (Pancost et al., 2002; Sharma and Zafar, 2015) including those adjacent to mangroves, although this is not the case in our dataset from Pohnpei and Kosrae. Expanding the number of samples from monospecific *Rhizophora* spp. environments to include additional sites would be valuable for understanding the spatial scale at which these threshold values are appropriate and could cause revision of thresholds.

Mangrove surface sediments also have higher abundances of β-amyrin, germanicol, and lupeol compared to supratidal freshwater samples (Table 1, Figure 3D). However, the difference in abundance of these compounds between depositional environments is less pronounced than it is for taraxerol. At all sites, there is overlap of abundances of these three compounds between mangrove and freshwater sediment (Figure 3D). This observation suggests that β-amyrin, germanicol, and lupeol have less utility in distinguishing between in situ mangrove and non-mangrove organic matter than taraxerol. However these compounds may provide supporting evidence of in situ organic deposition in a mangrove environment if their abundance is elevated simultaneously with taraxerol (Koch et al., 2003). Koch et al. (2011) suggested summing taraxerol, β-amyrin, and germanicol as a proxy for *Rhizophora mangle* derived organic matter. For Pohnpei and Kosrae, this approach yields little additional insight because the sum is

dominated by the contribution from taraxerol, and because taraxerol displays the greatest difference between depositional environments.

5.3. Identifying mangrove sediment in the stratigraphic record for RSL reconstructions

We use biomarker and mangrove pollen abundances to evaluate whether core sediments from Pohnpei and Kosrae accumulated in mangrove or organic supratidal environments, and therefore whether biomarker measurements have utility in RSL reconstructions. Taraxerol is the most abundant compound in all core samples and at concentrations consistent with the threshold derived from the modern surface sediments for deposition in a mangrove (i.e., >0 abundance; Table 1; Figure 4). Out of 37 core samples, 21 have taraxerol concentrations >20, which is the (tentative) modern threshold for deposition in a monogeneric *Rhizophora* spp. community (Figure 4), and the remaining 16 core samples are within the range for deposition in a mixed mangrove community (taraxerol concentration >0–20; Figure 4). From these observations, we propose that the sediment in the cores from Pohnpei and Kosrae accumulated in a mangrove environment, with two attendant conclusions.

First, the analogous abundance of taraxerol in mangrove surface sediment and in core sediments corresponding to ages of 100s to 1000s of years (Athens and Stevenson, 2012; Sefton et al., 2022a) indicates that post-depositional diagenesis and transport is likely insufficient to considerably alter interpretations of depositional environment. Taraxerol is less prone to microbial degradation in mangrove sediments over time in comparison to other pentacyclic triterpenoids (Koch et al., 2005). At both Pohnpei and Kosrae, the accumulation of mangrove sediment at multiple sites demonstrates sustained RSL rise over the past ~5,700 years (Bloom, 1970; Sefton et al., 2022a). RSL rise creates accommodation space that is subsequently filled by accreting mangrove sediment (e.g., modern accretion rates are shown to be 1.5–20.8 mm/year in Pohnpei and Kosrae mangroves; Buffington et al., 2021; Krauss et al., 2010), which may promote taraxerol preservation as burial minimizes the time that bulk sediment spends in the oxic zone where it is subject to diagenesis through alternating exposure to air and submergence during high tides, and bioturbation by roots and organisms (Khan et al., 2022; Sefton et al., 2022b).

Second, if taraxerol is refractory in mangrove sediment on centennial to millennial timescales, then downcore variability in its abundance may be interpreted as changes in vegetation community composition through time. On Pohnpei and Kosrae mixed mangrove communities of *Rhizophora apiculata*, *Bruguiera gymnorrhiza*, and *Sonneratia alba* are more common by surface area than monospecific *Rhizophora* spp. zones (Ellison et al., 2022; Figure 3A–C). *Rhizophora stylosa* — while less common relative to total mangrove area — has a distinct niche occupying the lower elevation seaward edge of the mangroves (Fujimoto et al., 1995; Buffington et al., 2021; Ellison et al., 2022). Therefore, changes in mangrove community composition may also represent changes in mangrove surface elevation relative to tidal datums. Downcore variability in taraxerol concentrations is inconsistent among our study sites suggesting that they reflect site-specific changes. For example, at the Pwok site, taraxerol concentrations vary little downcore and are at or close to the >20 threshold for a *Rhizophora* spp. dominated environment, and therefore may represent stability in the current vegetation composition (Figure 4). In contrast, the taraxerol concentrations in the Nanitipw core may represent an initial *Rhizophora* spp. dominated environment (between 241–389 cm; Supp Table 2), with gradual shifts to more a more diverse mangrove community over time (between 175–241 cm and 41–92 cm). Such downcore variations may represent site-specific changes to: (1) geomorphology (e.g.,

the migration of tidal creeks); and/or (2) forest disturbance and species succession (e.g., *Rhizophora stylosa* will occupy disturbed areas first, but will be replaced by more diverse mangrove communities as the stand matures), rather than a larger spatial-scale (regional) signal such as RSL change which would be common to all sites.

Due to poor preservation of diagnostic plant macrofossils and foraminifera in mangrove sediments (Woodroffe et al., 2005; Berkeley et al., 2007; Sefton et al., 2021), pollen is the most widely used proxy for establishing environments of deposition (Engelhart et al., 2007; Ellison, 2019). However, the relative contribution of mangrove pollen to sediments accumulating beneath mangroves is highly variable. Many mangrove species (e.g., *Xylocarpus* spp.) are pollinated by insects and birds, which results in relatively smaller amounts of pollen being transported shorter distances compared to wind-pollinated plants such as *Rhizophora* spp. (Tomlinson, 2016). In addition, allochthonous input of wind- and water-transported pollen from surrounding non-mangrove environments may reduce the relative abundance of mangrove pollen. These characteristics mean that mangrove pollen deposition can be highly localized, and therefore presence of mangrove pollen in sediments likely indicates deposition within or very close to mangrove environments (Grindrod, 1985; Ellison, 1989). A key exception is *Rhizophora* spp., which are wind pollinated and therefore produce relatively larger quantities of pollen which can be transported beyond the mangrove limits, particularly to marine environments (Grindrod et al., 1999; Versteegh et al., 2004). Ward (1988) examined pollen in modern sediments from 12 sites on Kosrae and concluded that pollen assemblages recognized localized (in situ) plant communities. Only occasional grains of mangrove pollen were identified in non-mangrove environments indicating that transport of mangrove pollen is likely insufficient for a freshwater environment to be wrongly identified as a mangrove on the basis of pollen content. In four sediment samples from mangrove forests, Ward (1988) reported that mangrove pollen (namely *Rhizophora* sp., *Sonneratia* sp., and *Bruguiera* sp.) comprised <~25% of the pollen assemblage and that some samples had low pollen concentrations, which required the preparation and counting of additional slides (a requirement that we also encountered).

In the Pohnpei and Kosrae sediment cores, mangrove pollen is present in all samples at relative abundances of 4.4–45.8% (Figure 4). The presence of mangrove pollen in all core samples likely indicates deposition in a mangrove environment despite the variable and sometimes low relative abundance exhibited (Ward, 1988; Figure 4). This result is consistent with downcore taraxerol abundance indicating deposition in a mangrove environment. However, the abundance of mangrove pollen does not positively correlate with taraxerol abundance, and therefore downcore variability may suggest: (1) mangrove pollen production varied over the period of deposition even if the community was unchanged; (2) the composition of the mangrove community varied through time; (3) mangrove pollen is variably (through time and space) diluted by non-mangrove pollen, or (4) mangrove pollen is variably preserved in sedimentary sequences.

5.4. Implications for RSL reconstructions

There are some important implications for paleoenvironmental research that arise from this work. Taraxerol abundance as an indicator of in situ mangrove accretion offers particular utility in reconstructing RSL and coastal change. Mangroves live exclusively in the intertidal zone, and therefore mangrove sediments are considered a quantitative proxy for RSL (Woodroffe et al., 2015; Khan et al., 2022). In organic-rich environments, where physical differences between supratidal (freshwater swamp) and intertidal (mangrove) deposits may be ambiguous, the

abundance of taraxerol may highlight intervals in a dated sediment sequence where the precise position of RSL can be identified in space and in time (i.e., sediment that accumulated in a mangrove living at elevations between mean tide level and mean higher high water), and intervals that qualitatively indicate RSL was below that point in space and time (i.e., sediment that accumulated in a freshwater swamp above the intertidal zone). If taraxerol additionally indicates increases or decreases in in situ *Rhizophora stylosa* (which occupies the seaward edge and lower elevations of the tidal frame; Figure 3b; Ellison et al., 2022), taraxerol abundance may indicate a rise or fall in RSL as monospecific *Rhizophora stylosa* environments migrate landwards or seawards. Identifying trends in species change over time using sedimentary archives may also provide information on: 1) the long term processes (centuries to millennia) of ecological succession (Lugo, 1980; Li et al., 2012); 2) which species lead to increased or decreased blue carbon sequestration (Rogers et al., 2019b) over time; and 3) the past distributions of mangrove species via natural or anthropogenic vectors (Woodroffe and Grindrod, 1991; Allen, 1998; Steele, 2006).

6. CONCLUSIONS

Our results from Pohnpei and Kosrae are consistent with previous studies that identify taraxerol as an indicator of mangrove-derived organic matter in modern and past environments, and that taraxerol abundance is particularly high in *Rhizophora* sp. communities (Versteegh et al., 2004; Koch et al., 2011; He et al., 2022). Notably, our results — which incorporate both geomorphological and ecological variables (i.e., elevation in tidal frame and vegetation zone) — demonstrate the utility of taraxerol identifying mangrove organic matter produced in situ, and in distinguishing other organic-rich sediments that occur above the reach of tidal influence. On Pohnpei and Kosrae, taraxerol concentrations from modern surface sediments of >0–20 and >20 indicate deposition in a mixed mangrove and *Rhizophora* spp. dominated environment respectively, while absence of taraxerol indicates deposition in a supra-tidal, freshwater environment. Presence of taraxerol in samples at all depths in all cores indicates continued mangrove accretion over centuries and millennia. In addition, we suggest that relative increases in taraxerol in cores from Pohnpei and Kosrae may represent a shift to *Rhizophora stylosa* dominated environments, and therefore demonstrate site-specific changes in local geomorphology or ecological succession over centennial and millennial timescales. Interpretation of core material as having accumulated in mangroves is supported by the presence of mangrove pollen, although changes in taraxerol concentrations are not mirrored the pollen assemblage. We show that taraxerol may be a useful proxy for in situ mangrove accretion, and potentially mangrove species change, in paleoenvironmental studies.

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FIGURE CAPTIONS

Figure 1: (A) Location of Pohnpei and Kosrae in the western Pacific Ocean. (B) Relative sea level change (at Pohnpei and Kosrae) as per Sefton et al. (2022a). (C) Map of Pohnpei and (D) Kosrae, with modern transect and core sites indicated.

Figure 2: Normal-alkane distributions (values presented are µg compound per dry gram sediment divided by µg C_{29} alkane per dry gram sediment; see Section 3.2.3. for normalization details; Table 1–2; Supplementary Table 1-2) for (A) all surface sediment samples, and (B) all core sediment samples.

Figure 3: (A–D) Surface transect geomorphological and general vegetation zone data for Madolenihmw, Nihkewe, and Utwe. Distance along transect 0 m = landward edge of transect, increasing towards the seaward edge. Terrestrial dominated denotes upland/non-mangrove vegetation, and transition denotes the short transition between mangrove into non-mangrove vegetation. Tidal datums for Pohnpei (Madolenihmw and Nihkewe) and Kosrae (Utwe) are dashed lines on each plot, MHHW = Mean Higher High Water and MTL = Mean Tide Level. (D) Surface sample abundance by compound (values presented are µg compound per dry gram sediment divided by µg C_{29} alkane per dry gram sediment; see Section 3.2.3. for normalization details). Mangrove or freshwater samples are plotted (jittered randomly to aid viewing) on the x-axis. Color denotes vegetation zone, and shape denotes surface transect site (Nihkewe, Madolenihmw, or Utwe). The *p* values presented are the results of the Mann-Whitney-Wilcoxon Test (see Section 4.1).

Figure 4: Downcore data for four core sites: Nanitipw, Pwok, Rohi, and Utwe with modern sediment mean values indicated, (values presented are µg compound per dry gram sediment divided by µg C_{29} alkane per dry gram sediment; see Section 3.2.3. for normalization details). Orange shading of the taraxerol data indicates values that lie within the 0–20 range that correspond to deposition in a mixed-species mangrove, and the purple shading indicates values >20 that correspond to deposition in a monospecfic *Rhizophora* sp. mangrove.

Table 1: Summarized modern surface sediment transect data (values presented are µg compound per dry gram sediment divided by µg C_{29} alkane per dry gram sediment; see Section 3.2.3. for normalization details) categorized by environment, site, and vegetation zone. Mean (range). CPI = Carbon Preference Index (see Section 3.2.4.), P_{aq} = P_{aq} index (see Section 3.2.4.).

Table 2: Core sample concentrations (values presented are µg compound per dry gram sediment divided by µg C_{29} alkane per dry gram sediment; see Section 3.2.3. for normalization details) , categorized by core. Mean (range). CPI = Carbon Preference Index (see Section 3.2.4.), P_{aq} = P_{aq} index (see Section 3.2.4.).

SUPPLEMENTARY DATA

Supplementary Table 1 Surface sediment biomarker concentrations (Table 1) and environmental variables (identifiers, elevation, distance along transect, vegetation zone, and general environment (mangrove or fresh). Normalized values (see Section 3.2.3.) and raw measurements presented in separate sheets.

Supplementary Table 2 Core sediment biomarker concentrations (Table 2), mangrove pollen abundance (%), and identifiers. Normalized values (see Section 3.2.3.) and raw measurements presented in separate sheets.

Supp Table 3 List of compounds determined by GC-MS as their TMSi derivatives.

Compound (trivial name)	**type**	**Retention time (min)**	**Quantifier ion (m/z)**	**Qualifier ions (m/z)**
5α-androstanol	surrogate	32.01	243	333, 243
cholesterol-d_6	internal standard	41.64	219	333, 131
5α-cholestanol-d_5	surrogate	41.76	219	360, 131
stigmasterol	analyte	43.36	129	255, 394
taraxerol	analyte	44.18	204	269, 284
β-sitosterol	analyte	44.21	357	129, 396
β-amyrin	analyte	44.53	189	218, 203
germanicol	analyte	44.60	189	204, 190
lupeol	analyte	45.15	189	191, 369

Highlights:

- Taraxerol is abundant in modern mangrove sediment, particularly below *Rhizophora.*
- Taraxerol is near-absent in supratidal sediment.
- Taraxerol is a proxy for mangrove sediment with utility for reconstructing sea level.
- Micronesian cores have taraxerol concentrations consistent with modern mangroves.

966 **Table 1**: Summarized modern surface sediment transect data (values presented are µg
967 compound per dry gram sediment divided by µg C_{29} alkane per dry gram sediment; see Section
968 3.2.3. for normalization details) and categorized by environment, site, and vegetation zone.
969 Mean (range). CPI = Carbon Preference Index (see Section 3.2.4.), P_{aq} = P_{aq} index (see Section
970 3.2.4.).

	n	**CPI**	**P_{aq}**	**Stigmasterol**	**Taraxerol**	**Lupeol**	**Germanicol**	**β-sitosterol**	**β-amyrin**
All surface samples	22	13.3 (8.9–19.0)	0.1 (0.0–0.7)	1.1 (0–11.4)	13.9 (0–84.1)	4.0 (0.0–22.3)	1.8 (0.0–9.0)	8.5 (0–38.2)	4.3 (0–16.8)
Environment									
Mangrove	15	11.8 (8.9–16.0)	0.1 (0.0–0.7)	1.6 (0–11.4)	20.3 (2.2–84.1)	5.4 (1.7–22.3)	2.4 (0.1–9.0)	9.4 (0–35.6)	5.9 (1.5–16.8)
Fresh	7	16.4 (10.4–19.0)	0.0 (0.0–0.1)	0.1 (0–1.0)	0.3 (0–01.9)	1.0 (0.1–2.7)	0.5 (0.0–1.4)	6.6 (0–38.2)	0.8 (0–2.6)
Site									
Madolenihmw (Pohnpei)	9	12.7 (10.0–18.3)	0.0 (0.0–0.2)	0.5 (0–1.8)	7.8 (0–19.7)	3.8 (0.1–7.6)	1.4 (0.1–3.6)	4.3 (0–9.7)	4.0 (0.1–7.1)

Nihkewe (Pohnpei)	8	14.3 (8.9–18.6)	0.2 (0.0–0.7)	2.3 (0–11.4)	27.4 (0–84.1)	5.1 (0.3–22.3)	3.3 (0.2–9.0)	12.4 (0–35.)	5.6 (0–16.8)
Utwe (Kosrae)	5	12.9 (10.0–19.0)	0.1 (0.0–0.1)	0.4 (0–0.9)	3.2 (0–6.2)	2.8 (0.7–5.2)	0.2 (0.0–0.4)	9.7 (2.2–38.2)	2.6 (0.8–5.0)
Vegetation zone									
Ra dominated	3	12.0 (8.9–14.)	0.4 (0.2–0.7)	3.8 (0–11.4)	24.6 (13.5–38.1)	0.9 (0.2–2.2)	3.5 (2.0–4.5)	14.8 (0–35.6)	5.0 (3.1–6.5)
Rs dominated	2	14.5 (13.1–16.)	0.1 (0.–0.1)	3.7 (0–7.3)	72.8 (61.4–84.1)	0.6 (0.5–0.6)	6.5 (3.9–9.0)	26.7 (19.9–33.4)	14.2 (11.6–16.8)
Mixed Ra Bg Sa	7	11.3 (10.0–12.6)	0.1 (0.0–0.2)	0.3 (0–0.9)	6.7 (2.2–12.9)	3.7 (2.0–5.2)	1.4 (0.1–3.6)	3.1 (2.2–5.6)	3.4 (1.5–5.0)
Mixed Ra Bg Sa Xg	3	11.3 (10.3–12.3)	0.1 (0.0–0.1)	1.2 (0–1.8)	12.6 (7.7–19.7)	6.0 (5.0–7.6)	1.3 (0.8–2.0)	7.1 (2.2–9.7)	7.0 (7.0–7.1)
Transition	1	10.4	0.0	0.8	1.9	2.7	0.1	3.0	2.6

Terrestrial	6	17.4 (13.9 – 19.0	0.0 (0.0 – 0.1)	0 (0–0)	0 (0–0)	0.7 (0.1–2.0)	0.6 (0.0–1.4)	7.2 (0–38.2)	0.5 (0–1.4)

971

972 **Table 2**: Core sample concentrations (values presented are µg compound per dry gram
973 sediment divided by µg C_{29} alkane per dry gram sediment; see Section 3.2.3. for normalization
974 details), and categorized by core. Mean (range). CPI = Carbon Preference Index (see Section
975 3.2.4.), P_{aq} = P_{aq} index (see Section 3.2.4.).

	n	**CPI**	**P_{aq}**	**Stigmasterol**	**Taraxerol**	**Lupeol**	**Germanicol**	**β-sitosterol**	**β-amyrin**
All core samples	37	12.8 (9.0–17.2)	0.2 (0.0 – 0.6)	1.0 (0–6.9)	22.9 (6.6–55.5)	3.0 (0–16.0)	2.4 (0.5–5.9)	4.4 (0–37.2)	3.1 (0.8–8.8)
Nanitipw (Pohnpei)	16	13.1 (9.0–16.5)	0.1 (0.0 – 0.2)	0 (0–0)	25.6 (8.5–55.5)	1.0 (0–2.6)	2.9 (1.1–5.9)	0.4 (0–6.9)	3.5 (1.3–6.2)
Pwok (Pohnpei)	7	13.5 (10.5 – 17.2)	0.2 (0.1 – 0.6)	3.2 (0.6–6.9)	17.5 (9.9–22.9)	4.1 (1.1–11.6)	1.4 (0.7–2.5)	9.3 (2.5–19.1)	1.7 (0.8–2.7)
Rohi (Pohnpei)	5	12.2 (9.9–17.1)	0.2 (0.1 – 0.3)	0 (0–0)	26.4 (20.6–41.9)	4.3 (0.0–14.7)	3.0 (2.3–3.8)	8.6 (0–37.2)	4.5 (2.8–8.8)

Utwe (Kosrae)	9	12.1 (9.6–15.0)	0.2 (0.1–0.5)	1.6 (0–3.9)	20.1 (6.6–47.6)	5.1 (1.5–16.0)	2.0 (0.5–5.4)	5.2 (0–20.3)	2.7 (0.8–7.8)

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977

978 **Declaration of interests**

979

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

982

983 ☒ The authors declare the following financial interests/personal relationships which may be considered
984 as potential competing interests:

985

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