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Neogene plant macrofossils from West Antarctica reveal persistence of *Nothofagaceae* forests into the early Miocene

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The extinction of woody vegetation in Antarctica remains difficult to constrain due to its fragmented macrofossil record. Despite its long-standing polar position, Antarctica hosted extensive vegetation throughout the Paleogene. This changed near the Eocene-Oligocene Transition (ca. 34 Ma) as glaciation led to vegetation decline. Sparse evidence suggests tundra-like forests persisted until the Pliocene in East Antarctica, but the Neogene record from West Antarctica is largely restricted to palynoflora data. Here, we report early Miocene plant macrofossils from West Antarctica, consisting of *Nothofagus* leaves. U-Pb zircon geochronology confirms tundra-like vegetation existed in this region during the early Miocene (ca. 22–20 Ma), representing the youngest macrofossil record of West Antarctica. These findings suggest that *Nothofagus* either persisted through Antarctica's harsh Late Cenozoic Ice Age conditions or recolonised during intermittent warm periods. This substantially advances our understanding of West Antarctica's vegetation history and extends the known record of *Nothofagus* in Antarctic ecosystems.

One of the most enigmatic aspects of Antarctica's history is its transition from terrestrial ecosystems dominated by thriving forests in the early Cenozoic to its current configuration, with no tree or shrub layers and terrestrial biota limited to a few invertebrates, lichens, mosses, diatoms and microbial groups^{1–3}. The present combination of low temperatures, lack of humidity and winter darkness results in a limited distribution and diversity of plant species⁴. However, throughout the Mesozoic and early Cenozoic, Antarctica was home to a wide variety of plant life⁵, despite already being situated at polar latitudes⁶. Although plant macrofossils

are very sparse, it has been inferred that Antarctica may have been capable of supporting woody plants well into the Neogene^{7–11}. A major challenge in assessing the evolution of vegetation dynamics in Antarctica is that nearly 98% of the continent is covered by ice¹², resulting in a highly spatially and temporally fragmented fossil record. Consequently, the timing of the extirpation of woody vegetation across Antarctica remains poorly understood and is often interpreted through methods other than direct macrofossil evidence, such as palynological and molecular studies.

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Although ephemeral ice sheets appeared in Antarctica during the late Mesozoic¹³, driven by a gradual decrease in global temperatures^{14–16}, a permanent ice sheet did not develop until the Eocene–Oligocene Transition^{17,18} (EOT; *ca.* 34 Ma), which marked the initiation of the Late Cenozoic Ice Age¹⁹. The plant macrofossil record in Antarctica postdating the EOT suggests that some woody vegetation may have persisted in low-diversity *Nothofagus*-dominated tundra ecosystems^{20–23}. *Nothofagus* is a genus of southern beech trees (family Nothofagaceae) that may have been able to inhabit latitudes up to 85°S^{5,8,9,11} in East Antarctica until as late as the Pliocene. This implies that areas at lower latitudes were probably able to support this vegetation during the Neogene as well, although direct macrofossil evidence remains elusive. However, this idea remains controversial, as ice-cap models are not consistent with the presence of Antarctic vegetation after the EOT, particularly from the Miocene onwards^{24–26}. The study of *Nothofagus* fossils in Antarctica is therefore fundamental for understanding when and how forests became extinct on the continent.

The study of how woody vegetation disappeared from Antarctica is further complicated by marked differences in the fossil record between East and West Antarctica²¹. East Antarctica has yielded sporadic macrofossil discoveries that provide a broader basis for reconstructing past vegetation dynamics^{4,5}. In contrast, in West Antarctica, the macrofossil record is far more limited and primarily restricted to deposits dating to shortly after the EOT^{5,21}. Furthermore, the evidence for the presence of tundra-like vegetation in West Antarctica during and after the Oligocene is largely drawn from palynological studies. The nature of pollen evidence is such that there is substantial uncertainty as to whether this vegetation was physically present in the same location as the fossil pollen finds, since (i) anemophilic pollen may be able to travel considerable distances and (ii) tundra-like vegetation was present in proximal southern Patagonia during the mid- and late Cenozoic^{27,28}, providing a potential source.

In this study, we present *Nothofagus* leaf macrofossils from the Miocene-aged glaciomarine sedimentary rocks of the Cape Melville Formation, exposed on King George Island in the northeastern Antarctic Peninsula (Fig. 1). These represent the youngest macrofossil evidence of

woody vegetation on record for West Antarctica. Our results are further supported by U–Pb zircon geochronological data (LA-ICP-MS) collected from an ash-layer intercalated within the Cape Melville Formation, providing robust chronological control for the age of the fossils. Combined, this evidence provides unequivocal proof of tundra-like vegetation in West Antarctica during the Late Cenozoic Ice Age and enhances our understanding of how long these forests managed to persist during Antarctic glaciation.

The geology of Melville Peninsula, King George Island

Melville Peninsula is located at the northeast extremity of King George Island (Fig. 2), which is the largest island in the South Shetland Islands. Although King George Island is mostly covered by an ice cap, the rocks that are exposed host an exceptional Cenozoic stratigraphic record^{29,30} and therefore hold critical exposures for studies addressing the Cenozoic evolution of Antarctica. The South Shetland archipelago extends parallel to the northern Antarctic Peninsula on the western side (Fig. 1), separated from the peninsula by the Bransfield Strait, which is a relatively young back-arc rift basin formed during the last 4 Myr³¹. The archipelago of the South Shetland Islands is mainly composed of the products of the active margin developed as a result of the eastward subduction of the Phoenix Plate beneath the continental crust of the Antarctic Peninsula^{32–37}. This active margin was tectonically active from at least the late Palaeozoic to early Mesozoic^{38–40}, until approximately 20–19 Ma⁴¹, when arc magmatism ceased as a result of trench–ridge collisions along the margin.

The archipelago of the South Shetland Islands records tectonic, global sea-level and climate change throughout the Mesozoic and Cenozoic³², which has been divided into three main stages: (i) deep marine sedimentation during the Jurassic and Early Cretaceous^{33,42}; (ii) subaerial arc volcanism and sedimentation with a proliferation of plants and fauna from *ca.* 140–34 Ma^{33,33,35,43–45}; and (iii) glacial and interglacial deposits from *ca.* 34 Ma^{29,30,32}. While Jurassic and Early Cretaceous rocks are exposed in the southwest of the South Shetland Islands^{32,36}, Cenozoic formations are confined to the northeast of the archipelago^{46,47}. The exposures of King George

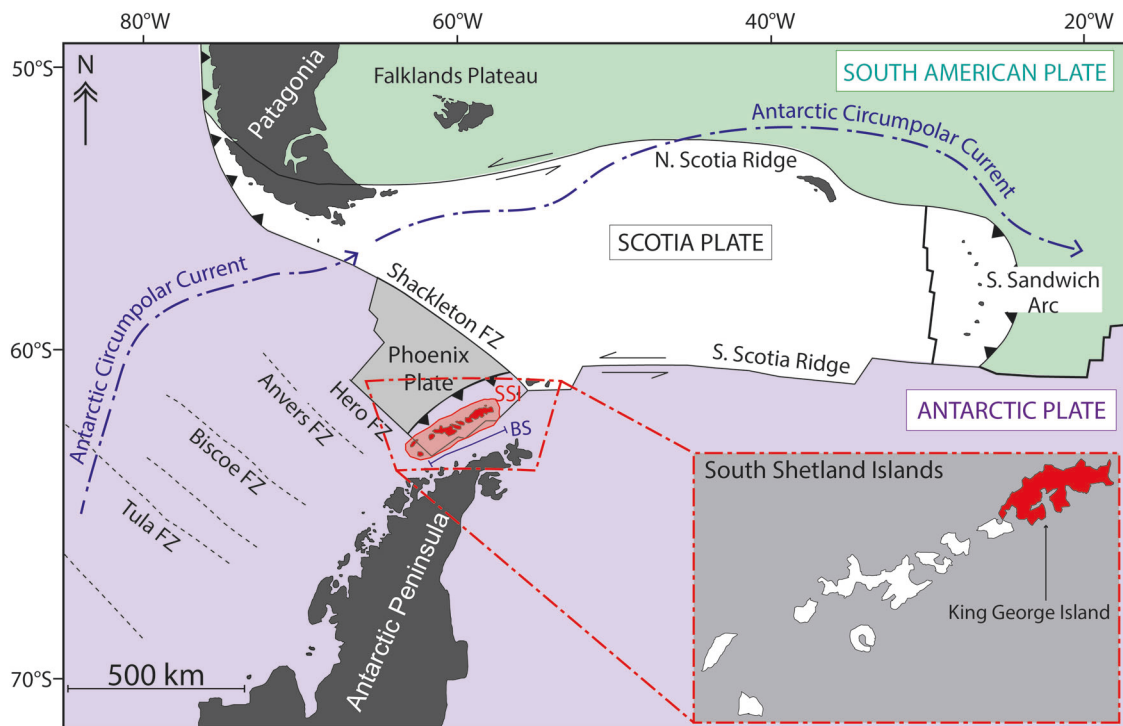
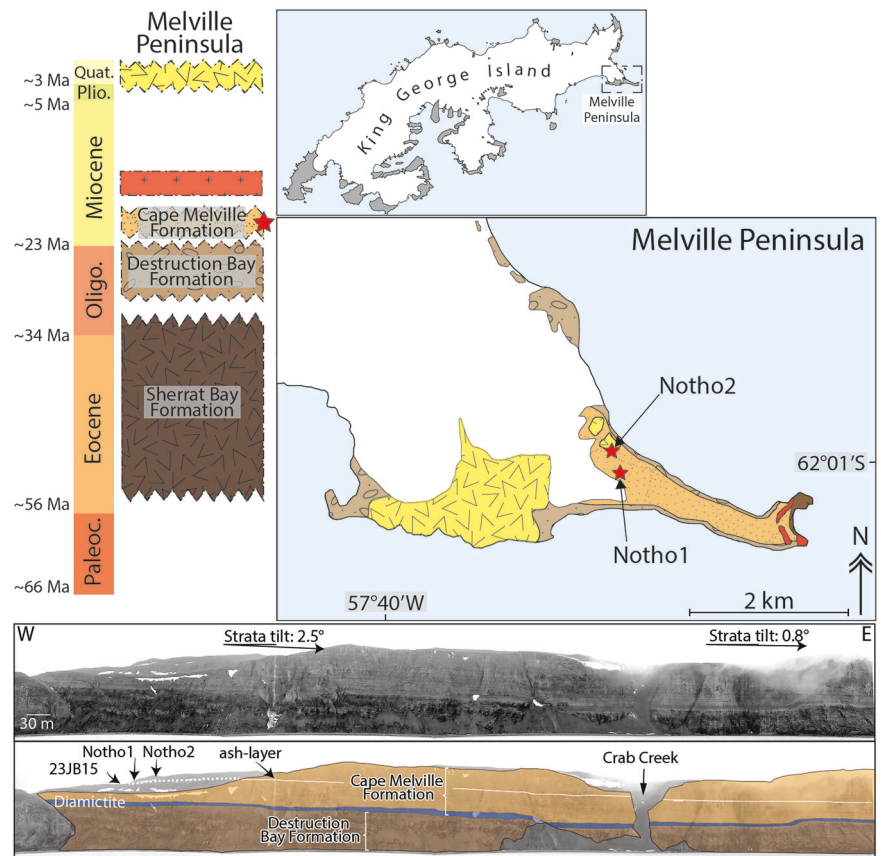


Fig. 1 | Present-day tectonic configuration of the Scotia Plate, Patagonia, and the Antarctic Peninsula. The locations of the South Shetland Islands (SSI) and the Bransfield Strait (BS) are highlighted. Figure modified from³². Red box in the inset

figure shows the location of the South Shetland Islands archipelago with King George Island in red. FZ fault zone.

Fig. 2 | Geological map and stratigraphic log of the Melville Peninsula, King George Island. Fossil localities are indicated by stars. Modified from refs. 32,47,48.



Island are dominated by Cenozoic volcanic and sedimentary strata^{32,36,48,49}. Notably, in the southwestern region hosts the Moby Dick Group, an Eocene to Miocene volcano-sedimentary succession^{50,51} (Fig. 2) composed of three formations: (i) Sherratt Bay Formation, (ii) Destruction Bay Formation and (iii) Cape Melville Formation.

The Sherratt Bay Formation consists of an andesitic-basaltic succession which is exposed on the eastern edge of the Melville Peninsula (Fig. 2). While this unit has been interpreted as a terrestrial plateau-basalt sheet at the base of the Moby Dick Group⁴⁹, it has been argued that it may be instead be a doleritic sill⁴⁸. Its age remains poorly constrained. A K-Ar date of ca. 18 Ma⁸, previously attributed to the Sherratt Bay Formation, is likely associated with the early Miocene dike intrusions that are widespread on the Melville Peninsula rather than the Sherratt Bay rocks themselves⁴¹.

A stratigraphic hiatus separates the Sherratt Bay Formation from the overlying Oligocene fossiliferous Destruction Bay Formation. Although the presence of fossil wood has been mentioned for the Destruction Bay Formation⁴⁶, no further details have been presented or documented. This formation consists of a ca. 40–100 m thick succession of volcanoclastic rocks, dominated by reworked basaltic material with horizons (mostly siltstones) rich in marine invertebrates⁴⁶ (Fig. 2). The sedimentary features of this unit suggest a nearshore depositional environment under non-glacial conditions⁴⁶. The age of the Destruction Bay Formation is loosely bracketed between 25.3 ± 0.8 Ma (brachiopods, ⁸⁷Sr/⁸⁶Sr⁵²) and 23.6 ± 0.7 Ma (basaltic tuff, K-Ar⁵³).

Overlying the Destruction Bay Formation is the Cape Melville Formation (Fig. 2), which is composed of glacio-marine sediments including sandstones, conglomerates, clay-shales and silty shales with occasional iceberg-rafted dropstones⁴⁶. The dropstones often show glacial striae and glacially polished facets, thus giving primary evidence for the presence of a continental ice-sheet in Antarctica^{46,47}. This glacial event has been correlated with the Mi-1 and Mi-1a glaciations^{47,48}, which are the most relevant glaciation events following the establishment of the ice-cap in Antarctica

during the EOT⁵⁴. However, it is possible that West Antarctica developed a comparatively smaller ice cap relative to East Antarctica⁵⁵. An abundant fossil record is present in the Cape Melville Formation, with (i) a thriving community of marine invertebrates, which includes Bivalvia, Gastropoda, Anthozoa, Decapoda, Scaphopoda, Bryozoa, Brachiopoda, Echinodermata, and Polychaeta⁵⁶, and (ii) reworked palynomorphs (spores and pollen), which include pollen morphogenus *Nothofagidites* sp. type fusca and brassi⁴⁷. The benthic foraminifera of the Cape Melville Formation suggest an early Miocene age⁵⁷ and an inferred Sr age of 22.6 ± 0.4 Ma was obtained from skeletal carbonate⁵². Recently, a tuff interbedded in the Cape Melville Formation has been dated (⁴⁰Ar/³⁹Ar on hornblende) to an age of 21.3 ± 3.1 Ma⁴⁸. These two geochronological constraints have been used to suggest an early Miocene age for the Cape Melville Formation⁴⁸.

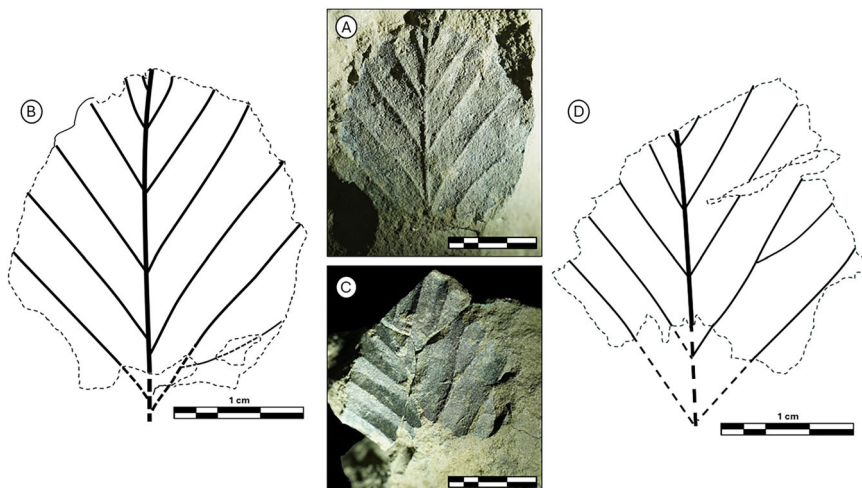
Methods

Fieldwork and fossil preparation

The fieldwork campaign took place on the Melville Peninsula during January and February 2023 as part of the Chilean Antarctic Institute's ECA-59 expedition aboard the Betanzos Vessel. Plant macrofossils were found preserved as impressions at two localities, Notho1 (62.019°S, 57.633°W) and Notho2 (62.018°S, 57.632°W) (Fig. 3). These fossils are housed in the Palaeontological Collection of Antarctica and Patagonia at the Chilean Antarctic Institute (INACH) in Punta Arenas, Chile. They were examined under a Zeiss Stemi 2000-C stereo microscope, and photographic records were captured using a Sony Alpha 7 III camera with a macro lens. The systematic description followed standardised guidelines⁵⁸. For the palynological preparation, the standard acetolysis method was followed (Erdtman, 1960). Thirty grams of rock containing the macrofossil CPAP 9105 were processed. The procedure involved crushing the rock with a mortar, treating it with hydrochloric and hydrofluoric acids, filtering the residue through a microscopic mesh, mounting it on a slide, and examining it under a Karl Zeiss Axioscope microscope.

Fig. 3 | Fragmentary leaf imprints of *Nothofagus* from the early Miocene Cape Melville Formation.

A *Nothofagus* sp.1 fossil leaf (CPAP 9105) showing the primary and second veins; **B** drawing with detail of secondary opposite venation; **C** *Nothofagus* sp.2 foliar imprint (CPAP 9106) showing the primary and second veins; **D** drawing with detail of craspedodromous, evenly spaced venation.



LA-ICP-MS zircon U-Pb geochronology

Zircon grains were separated from an ash-layer (23JB15) collected in the Cape Melville Formation using standard crushing, hydraulic, magnetic and heavy liquid procedures. They were then mounted and imaged by cathodoluminescence (CL) using a scanning electron microscope (SEM) at the ETH Zürich. Laser ablation inductively coupled plasma mass spectrometry (LA-ICPMS) techniques were used to determine trace element abundances and U-Pb ages. A 193 nm Resonetics Resolution S155 laser ablation system was used coupled to a Thermo Element XR, Sector-field single collector ICP-MS⁵⁹. Laser parameters include a 19 μm spot size, a repetition rate of 5 Hz and an energy density of ca. 2 J cm^{-2} . The ablation aerosol was mixed in the fast washout S-155 ablation cell (Laurin Technik) with carrier gas consisting of helium (ca. 0.25 L min^{-1}) and make-up gas consisting of argon (ca. 1 L min^{-1}) and nitrogen (2 mL min^{-1}). The ablated aerosol was then homogenised by flushing through a squid device before introduction into the plasma torch. The single collector sector-field MS is equipped with a high-capacity (80 $\text{m}^3 \text{h}^{-1}$) interface pump to improve sensitivity. Before each analytical session the instrument was optimised with NIST SRM612 glass to achieve a detection efficiency in the range of 1% (on Pb, Th, U) while keeping a low oxides production ($^{248}\text{ThO}^+ / ^{232}\text{Th}^+ \leq 0.25\%$) and a U/Th ratio of ca. 1. Intensities were recorded for the following isotopes: ^{27}Al , ^{29}Si , ^{31}P , ^{89}Y , ^{91}Zr , ^{93}Nb , ^{137}Ba , ^{139}La , ^{140}Ce , ^{141}Pr , ^{146}Nd , ^{147}Sm , ^{153}Eu , ^{157}Gd , ^{159}Tb , ^{163}Dy , ^{165}Ho , ^{167}Er , ^{169}Tm , ^{173}Yb , ^{175}Lu , ^{178}Hf , ^{181}Ta , ^{202}Hg , ^{204}Pb , ^{206}Pb , ^{207}Pb , ^{208}Pb , ^{232}Th , ^{235}U , and ^{238}U . The full dataset can be found in the associated supplementary dataset (10.5281/zenodo.16738353), following the community-derived guidelines⁶⁰.

For U-Pb geochronology, GJ-1 was used as the primary calibration reference material (CRM). Validating reference materials (VRMs) included Plešovice (337 Ma⁶¹), Temora (417 Ma⁶²) and 91500 (1062 Ma⁶³) zircons. The VRMs results show the achievable precision and accuracy of the method, which is in the range of 1.0%. The data was reduced using the software Iolite 4.5^{64,65} with VizualAge⁶⁶. No common-Pb correction was applied but integration intervals were set to exclude inclusions, common Pb and discordant parts of the signal. The long-term external uncertainty is in the range of 1.5% for $^{206}\text{Pb}/^{238}\text{U}$ ages and is composed of the uncertainty from the applied corrections, uncertainty of the decay constants, lacking common-Pb correction, the uncertainty on the true $^{206}\text{Pb}/^{238}\text{U}$ ratio of the primary standard GJ-1, and possible uncertainty from matrix effects. For trace element quantification we used Si as internal standard at 15.2 wt% SiO_2 in zircons, and SRM NIST610 as external CRM. Ti was quantified by zircon 91500 (Ti: $4.73 \pm 0.15 \text{ mg g}^{-1}$)⁶⁷.

Results

Systematic *Nothofagus* description

Two angiosperm leaf impressions were recovered from in situ siltstone layers at two separate sites, both within the Cape Melville Formation of the

early Miocene. These rocks are interpreted as part of a glacio-marine depositional environment, offering a rare and valuable insight into the Neogene vegetation of West Antarctica. The samples provide the basis for the systematic description of *Nothofagus*.

Class EUDICOTYLEDONEA

Order FAGALES

Family NOTHOFAGACEAE Kuprianova 1962⁶⁸

Genus *Nothofagus* Blume 1850⁶⁹

Type species *Nothofagus antarctica* Örsted, 1873⁷⁰

Nothofagus sp.1

Figure Fig. 3A, B.

Material. Palaeontological Collection of Antarctica and Patagonia CPAP 9105.

Locality. Notho1, Cape Melville, King George Island, Antarctica.

Description. Incomplete leaf impression corresponding to a microphyll, measuring 3.0 cm in length and 2.5 cm in width (L/W ratio = 1.2), ovate to suborbicular in shape. The primary vein is straight and prominent. Secondary venation is pinnate, opposite, consists of 5–6 pairs of straight, well-defined craspedodromous veins per side. The divergence angle of the secondary veins ranges from $\sim 50^\circ$ at the base to $\sim 40^\circ$ toward the apex, indicating a moderate and gradually decreasing pattern. Tertiary venation is not preserved, but thin, divergent basal agrophic veins are present, extending toward the margin. The margin is partially preserved and lobed, with broad, rounded shallow lobes. The apex and base are not preserved.

Floristic comparisons. The specimen described here is morphologically comparable to fossil leaves assigned to *Nothofagus subferruginea*, taxon documented from the Oligocene to early Miocene of Chile and Argentina⁷¹, as well as from strata in West Antarctica on King George Island^{72–75}. The similarities are primarily based on its ovate to orbiculate shape, craspedodromous venation, and lobed margin. However, it differs in its smaller overall size, greater number of secondary veins, and distinctly dentate margins. It also exhibits morphological similarities with *Nothofagus variabilis*, originally described by Dusén from Patagonia and widely recorded from the Eocene to the Miocene in formations such as Río Guillermo, Loreto, Río Turbio, Ñirihuau, Cullen, and Barrancas Carmen Silva²⁸. *Nothofagus variabilis* exhibits an elliptic to broadly ovate or suborbiculate lamina and 6–10 pairs of craspedodromous secondary veins emerging at a moderately acute angle⁷¹. However, in contrast to the present material, *Nothofagus variabilis* possesses a serrate composite margin, with convex–convex primary teeth and straight–straight secondary teeth. The fossil leaf also bears resemblance to *Nothofagus*

cunninghamii and other species of the subgenus *Brassospora* from the Miocene of New Zealand and Australia, particularly in its lobed margin and straight craspedodromous venation. *Nothofagus cunninghamii* typically displays 5–6 pairs of secondary veins arranged at a moderately acute angle relative to a straight, pinnate midvein⁷⁶. Comparative analysis reveals morphological similarities between *Nothofagus sp. 1* and *Nothofagus gunnii*, the tanglefoot or deciduous beech endemic to the highlands of Tasmania, Australia. Both species fall within the microphyll size class and exhibit pinnate primary venation, with a broadly ovate to suborbicular lamina and a comparable length-to-width ratio (~1.2). Additionally, both taxa display craspedodromous secondary venation, and, despite differences in lobation depth, they share the presence of marginal lobes. In *Nothofagus gunnii*, the lobes are markedly deep with well-defined sinuses, whereas in *Nothofagus sp. 1*, the lobes are broader, more rounded, and shallow—possibly reflecting a plesiomorphic or less specialised condition. Notable distinctions include the number of secondary veins: *Nothofagus sp. 1* has 5–6 pairs per side, exceeding the typical 3–5 pairs observed in *Nothofagus gunnii*. Furthermore, basal agrophic veins are present in the fossil specimen from King George Island but are absent in *Nothofagus gunnii*, indicating further divergence in venation architecture.

Another morphotype displaying similar morphology is *Nothofagus australis*, synonymised with *Nothofagus simplicidens*⁷¹. *N. australis* shares a similar geographic and stratigraphic range with *Nothofagus variabilis* in Patagonia and is characterised by small, leptophyllous to microphyllous ovate leaves with craspedodromous venation and 5–6 straight secondary vein pairs entering the tooth apex medially. However, *Nothofagus australis* differs in its rounded apex, cuneate to obtuse base, and dentate margin, which contrasts with the lobed margin and specific venation patterns observed in the morphotype described here.

Although the absence of a preserved apex or tertiary venation limits definitive assignment, the overall morphological and venational structure shows the strongest resemblance to southern temperate rainforest species within Nothofagaceae. The finding of *Nothofagidites* pollen grains with affinities to subgenus *Fuscospora*, with an equatorial diameter of 23.26 microns, a circular outline, five colpi, a curved mesocolp, an average colpus aperture length of eight microns, ornamentation was not visible under optical microscope, and the exine thickness measured 0.62 µm. in the same beds, would help confirm the taxonomic placement. Furthermore, the late Oligocene–early Miocene was apparently the time of maximum spatial distribution of Nothofagaceae worldwide⁷⁷.

Class EUDICOTYLEDONEA

Order FAGALES

Family NOTHOFAGACEAE Kuprianova 1962⁶⁸

Genus *Nothofagus* Blume 1850⁶⁹

Type species *Nothofagus antarctica* Ørsted, 1873

Nothofagus sp. 2

Figure Fig. 3 C–D.

Material. Palaeontological Collection of Antarctica and Patagonia - CPAP 9106.

Locality. Notho2, Cape Melville, King George Island, Antarctica.

Description. The specimen represents an incomplete, simple leaf, estimated to be microphyllous in size. The approximate leaf width 2.5 cm, estimated length ~3.0–3.5 cm (based on contour extrapolation) yielding a length-to-width ratio of ~1.2–1.4. The preserved lamina exhibits an overall broadly ovate to suborbicular shape, with a weakly lobed margin. The base and apex are not preserved, limiting detailed characterisation of these regions. The primary venation is pinnate, marked by a robust, straight midvein. No clear evidence of secondary or tertiary venation is observed, likely due to preservation constraints. The leaf margin is moderately undulate, with shallow sinuses and rounded projections, potentially indicative of broad lobes. The overall contour of the leaf is

consistent with morphotypes attributed to *Nothofagus sensu lato*, particularly members of the subgenus *Brassospora*, based on the broad lamina, lobed margins, and absence of pronounced dentition. While the absence of visible venation limits a full taxonomic comparison, the gross morphology and marginal patterning bear resemblance to fossil species such as *Nothofagus sulferruginea* and *Nothofagus australis* as described in *Nothofagus sp. 1*.

Geochronology

The ash layer 23JB15, of andesitic composition, was sampled within a section of the sequence dominated by sandstones, approximately 70 m above the formation boundary with the Destruction Bay Formation (Fig. 4a). CL imaging of zircon grains revealed either (i) oscillatory zonation with distinct cores, or (ii) patchy and homogeneous zoning, with an absence of rim-core relationship, both textural varieties are typical of zircons crystallised in magmatic environment^{37,40} (Fig. 4b). Ablation of zircons yielded concordant analyses spanning ²⁰⁶Pb/²³⁸U ages from 19.3 ± 1.0 to 68.1 ± 3.1 Ma. From these, two main populations are observed: an older cluster that yielded ages between 63.1 ± 2.6 and 68.1 ± 3.1 Ma, and a younger group with concordant dates between 19.3 ± 1.0 and 22.3 ± 1.3 Ma (Fig. 4c). The latter yields a weighted mean age of 20.97 ± 0.22 Ma (n = 27, MSWD = 1.2, Fig. 4d). Late Cretaceous magmatism is present in several parts of the Antarctic Peninsula⁷⁸ and may represent part of the basement underlying King George Island⁷⁹, making it the most likely source of the 68–63 Ma inherited zircon grains. The younger zircon ages are closely associated with the late-stage arc magmatic pulses, which are particularly well documented in this sector of King George Island⁴¹. The full dataset is available in associated supplementary dataet (<https://doi.org/10.5281/zenodo.16738353>).

Discussion

Age of the *Nothofagus* leaves

The *Nothofagus* leaves discovered in the early Miocene Cape Melville Formation are stratigraphically closely associated with the ash layer 23JB15 (Fig. 4). The latter contains zircon grains exhibiting internal oscillatory zoning and homogeneous U–Pb ages, indicating direct magmatic sourcing with minimal, if any, reworking or sedimentary input. Thus, the weighted mean age of 20.97 ± 0.22 Ma provides the best estimate for the depositional age of the ash layer and constrains the age of the Cape Melville Formation. No substantial stratigraphic discordance or hiatus was identified between the ash layer and the fossiliferous horizon, nor within the entire Cape Melville Formation. Unfortunately, no ash bed has been found above the fossilised leaves to further bracket their age. However, the available evidence suggests that the leaves were deposited between 20 and 22 Ma, making this the youngest plant macrofossil record from West Antarctica.

Post-EOT vegetation evolution of Antarctica: east versus west

Despite being located in a polar position since at least the Cretaceous^{34,80}, East Antarctica maintained vegetation dominated by floristically rich forests prior to the EOT²¹ (Fig. 5). This vegetation was diverse in both composition and stature⁸¹, with forests dominated by *Nothofagus*, *Araucaria* and podocarps, including large trees⁸². This suggests that the climate was not extreme, and vegetation resembled the forests currently found in Patagonia, known vernacularly as ‘Valdivian Forest’^{83–85}. Temperatures fell at the end of the Eocene, leading to the collapse of these forests as a viable ecosystem⁸⁶. The Oligocene pollen records suggest that southern beech forests grew locally, with minor components of podocarps, Proteaceae and other shrubby angiosperms²¹. This vegetation type is similar to the present-day Patagonian steppe of bunchgrasses and shrubs or the *Nothofagus*-podocarp forests of New Zealand. These Oligocene forests were dominated by *Nothofagus*⁸⁷, which had become reduced in both stature and diversity compared to the pre-EOT vegetation^{88,89}. Among these Oligocene vegetational assemblages, the extensive fossil record of *Nothofagus* subgenus *Fuscospora* suggests that it may have been the only species^{21,90}. The fossil leaves described herein, characterised by their microphyllous size, lobed margin, and craspedodromous secondary venation, display a suite of

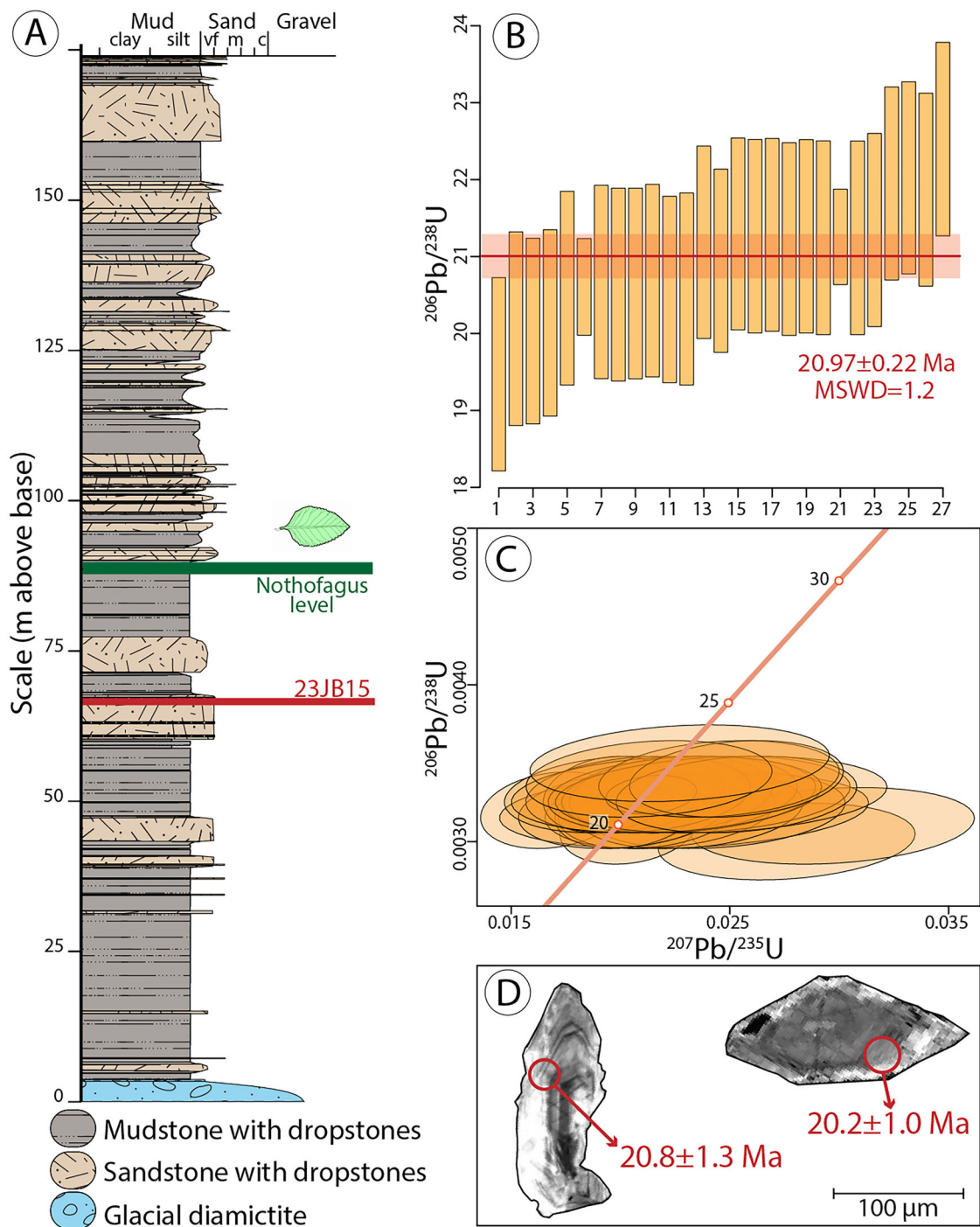


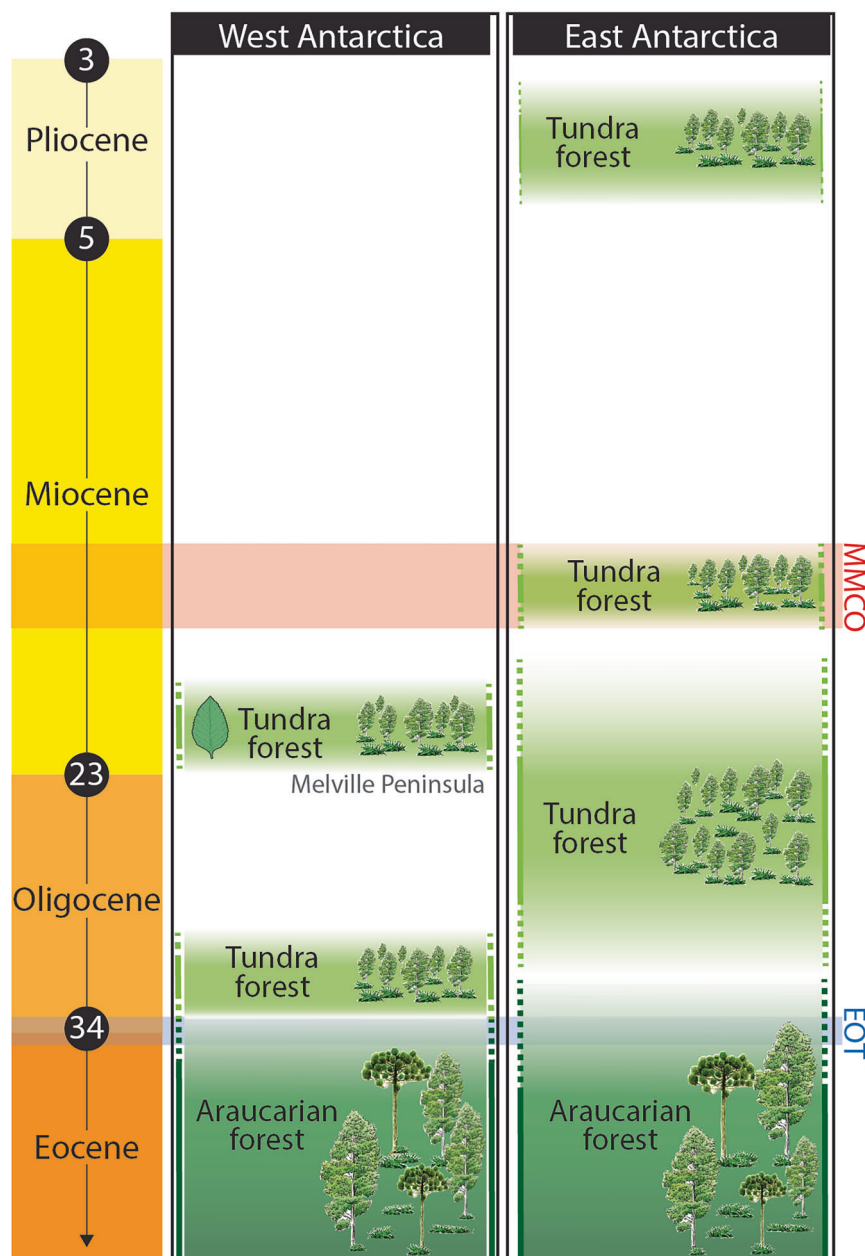
Fig. 4 | Stratigraphy (generalised) and geochronology of the Cape Melville Formation. **A** Composite stratigraphic section indicating the position of the sample analysed for U–Pb geochronology (23JB15) and the level where the leaf fossils were found. **B** Weighted mean $^{206}\text{Pb}/^{238}\text{U}$ dates of the volcanic ash-layer, sample 23JB15.

Bars represent single ablation spots and represent 2σ uncertainty. **C** Wetherill concordia plot of zircon U–Pb data for the sample 23JB15. **D** Representative SEM-based cathodoluminescence images of the dated zircons with location of analytical spots, including $^{206}\text{Pb}/^{238}\text{U}$ ages.

morphological features typically associated with mesic temperate forest environments. The combination of a straight, prominent midvein; 5–6 pairs of opposite, craspedodromous secondary veins; and broad, shallow lobes suggests an affinity with deciduous or semi-deciduous taxa inhabiting humid, temperate regions with seasonal climatic variability. Comparisons with extant and extinct members of *Nothofagus*, particularly species within the subgenera *Fuscospora* and *Brassospora*, also support this interpretation. Morphological affinities with *Nothofagus gummii*, a relict Tasmanian species adapted to cool temperate montane forests, and with fossil taxa such as

N. variabilis, *N. australis*, and *N. subferruginea*—widely distributed in Oligocene to Miocene strata of Patagonia, Antarctica, and Australasia—reinforce the hypothesis of a Nothofagaceae-dominated paleoflora in the studied assemblage. The presence of basal agrophic veins further supports assignment within Nothofagaceae and may indicate phylogenetic proximity to plesiomorphic lineages⁹¹. Although incomplete preservation precludes definitive taxonomic placement, the assemblage provides strong evidence for a paleovegetation type resembling modern southern temperate rainforests.

Fig. 5 | Macrofossil vegetation record in West and East Antarctica during the Eocene to Pliocene.
Based on this work and literature^{7,9,12,21,45,83,87,90,95,96,108,131}



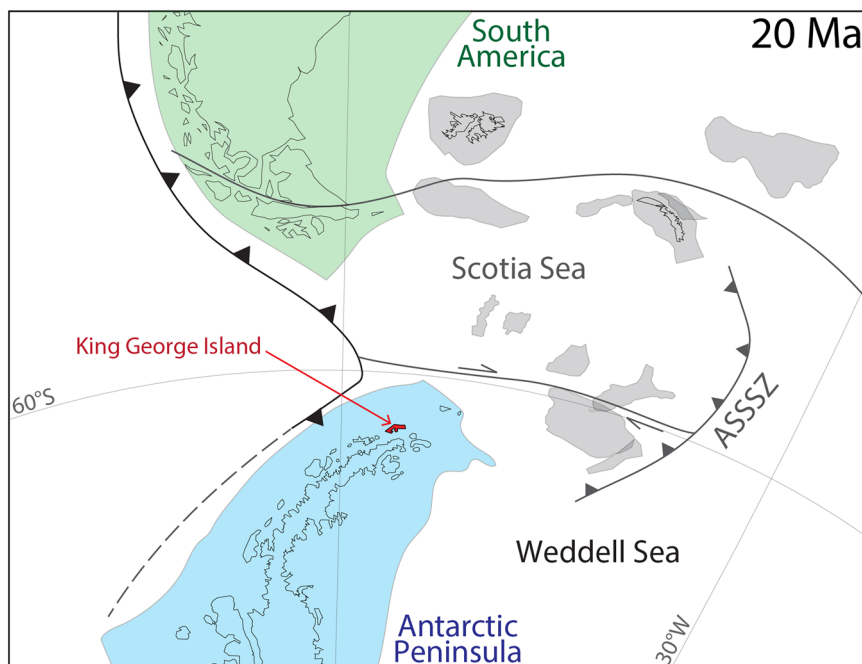
The co-occurrence of *Nothofagidites* pollen grains with affinities to *Fuscospora* or *Lophozonia* within the same stratigraphic context would provide additional support for this taxonomic interpretation. Taken together, these observations are consistent with established global biogeographic patterns. The transition from the late Oligocene to the early Miocene is marked by cooler climatic conditions compared to the earlier Miocene^{92,93}. Nonetheless, the palaeobotanical record from this interval, primarily composed of pollen and spores, with only limited occurrences of fossil wood and leaf impressions, suggests that tundra-like, low-diversity vegetation may have persisted beyond the EOT, likely restricted to climatically favourable or refugial microenvironments^{21,71,79,80}.

It is uncertain whether this vegetation persisted into the early Miocene, as most of the record is based on pollen evidence^{21,89,90}. The cold, glacial climate of the Miocene was briefly interrupted by a warm period *ca.* 17–15 Ma (the Middle Miocene Climatic Optimum; MMCO)⁹⁴. This warming resulted in a temporary increase in both the diversity and stature of East Antarctic vegetation^{22,95,96}, which facilitated the return of several *Nothofagus* taxa²¹. However, this was immediately followed by abrupt cooling⁹⁷, accompanied by the gradual disappearance of woody plants, although the

continued presence of *Nothofagus* pollen suggests that they may have persisted in glacial refugia in a manner analogous to the glacial refugia detected through Pleistocene glaciations in southern Patagonia^{28,99}, which explain the degree of endemism in this part of South America and the speed of subsequent recolonisation^{96,100}. After the MMCO, the ice sheet expanded in Antarctica throughout the Neogene and Quaternary, preventing the establishment of woody plants, with the exception of one notable site with tundra-like vegetation of mid-Pliocene age. The latter is found at less than 500 km from the South Pole^{5,21,101}, and had an assemblage similar to that in the modern-day southern Patagonia (Cape Horn)^{21,45}. This vegetation consisted of cushion-forming mosses and vascular plants with deciduous *Nothofagus* and rare podocarps^{9,21,102}. Notably, there is a lack of consensus on the age of the rocks that host these fossils^{7,21} and on how these tundra-like forests may have persisted in East Antarctica during the middle Pliocene.

To the west of the Transantarctic Mountains lies the West Antarctic region which, like East Antarctica, was already located in a polar position during the late Mesozoic^{38,40,80,103}. Our understanding of the Cenozoic vegetation evolution of the Antarctic Peninsula has been mostly constrained from the outcrops exposed in King George Island¹⁰⁴ and Seymour

Fig. 6 | Paleogeographic reconstruction of the Antarctic Peninsula and South America during the early Miocene. Redrawn from reference¹¹⁰. ASSSZ Ancestral South Sandwich Subduction zone.



Island^{75,105–107}. These outcrops also hold most of the evidence for woody vegetation in West Antarctica^{4,5}. Middle Eocene petrified forests are found in the centre-east of the island, revealing a once diverse ecosystem of *Nothofagus* and *Araucaria* conifers, among other species^{81,108}. This vegetation survived until the late Eocene⁴, when King George Island was on the locus of the arc axis in the Antarctic Peninsula^{32,36}. After the EOT, as the climate turned colder and drier¹⁰⁹, the woody vegetation transitioned to tundra-like forests dominated by *Nothofagus*²¹. Although it has been suggested that from the Oligocene onwards there may have been a relatively extensive ice cap in the Antarctic Peninsula, the lateral extent of such an ice cap remains unclear³⁰. Nevertheless, the development of an ice-cap during the Oligocene may have caused the tundra-like vegetation to succumb, at least temporarily⁴.

Evidence for woody vegetation is absent in West Antarctica after the early Oligocene, except for evidence from palynological studies on the early Miocene glacio-marine Cape Melville Formation on King George Island^{30,47}, which suggests the presence of a monotypic *Nothofagus* assemblage. Prior to our study, it was not possible to determine whether the source of the *Nothofagus* pollen was autochthonous or allochthonous, given the anemophilous nature of its grains. Because *Nothofagus* pollen is so widely wind-dispersed, it is difficult to use palynological evidence alone to reconstruct possible species co-occurrences within local vegetation. However, the macrofossil record does not suffer from this problem, since it is likely that most *Nothofagus* macrofossils are deposited very close to their source plants¹⁰⁰. While the *Nothofagus* leaves were found in the shallow marine Cape Melville Formation, suggesting transport before deposition, this does not preclude the presence of local vegetation, as they were recovered from a land-proximal marine environment⁵⁶.

Miocene tectonic models of the Antarctic Peninsula and the proximity of other *Nothofagus* communities

The Miocene tectonic history of the Antarctic Peninsula provides context for assessing the persistence of *Nothofagus* communities in West Antarctica during the early Miocene. The geological history of the Antarctic Peninsula is dominated by the development of a continental arc throughout the Mesozoic and part of the Cenozoic^{39,40}, which was the result of the eastward subduction of the oceanic lithosphere of the Phoenix Plate⁴¹. This subduction system waned during the Cenozoic to eventually cease at ca. 20 Ma^{34,41,110}. The sea floor remnants of the region and paleomagnetic studies

have been used to reconstruct this sector of Antarctica and South America and suggest that during the Jurassic and Cretaceous, Patagonia was in juxtaposition to the north of the Antarctic Peninsula^{103,110}. Therefore, during this period, there would have been a strong floral and faunal connection between these two regions⁸³. However, during the Cenozoic the Antarctic Peninsula drifted to the south with respect to South America as a response to the formation of the Scotia Plate, a sliver of oceanic lithosphere located between the Antarctic and the South American plates¹¹¹ (Fig. 6). This extension led to the opening of the Drake Passage, which effectively disconnected Antarctica from South America, causing the isolation of the Antarctic continent from any other landmass and setting up the Antarctic Circumpolar Current¹¹². This event, which occurred near to the EOT, marks the onset of the Late Cenozoic Ice Age¹¹¹ and is considered, at least in part, to have contributed to the initiation of this Earth period¹¹³. Throughout the Palaeogene, the Antarctic Peninsula experienced counterclockwise rotation, which caused it to progressively further separate from Patagonia¹¹⁰. During the early Miocene, when the Cape Melville Formation was deposited, it is estimated that the Antarctic Peninsula, and thus King George Island as well, was more than 500 km to the south with respect to Patagonia^{41,110} (Fig. 6). While anemophilic pollen may be able to travel considerable distances¹¹⁴ and tundra-like vegetation was present in southern Patagonia during the mid- and late Cenozoic^{27,28}, it is unlikely that leaves could have been transported and preserved more than 500 km south. This supports our argument that the *Nothofagus* leaf fossils originated from an autochthonous tundra-like forest.

Survival or Recolonisation?

The presence of *Nothofagus*-dominated tundra-like forests as recently as the early Miocene in West Antarctica (this work) and the mid-Pliocene in East Antarctica raises the question of whether these species were resilient and adapted to survive in glacial refugia to changing climatic conditions throughout the Neogene, or briefly recolonised Antarctica under particularly favourable conditions during warm intervals. From an autoecological perspective, *Nothofagus* seed dispersal is by gravity and wind (anemochory), while germination is generally epigeal and occurs not far from the seed-producing tree crown¹¹⁵. Although some authors argue that *Nothofagus* seeds can disperse over long transoceanic distances¹¹⁵, there is still a considerable body of research that claims that their seeds are intolerant to seawater^{116–118}, and so would have been unable to recolonise the Antarctic

Peninsula from the southern tip of South America after the Drake Passage opened during the Paleogene¹⁹.

The base of the Cape Melville Formation is marked by a glacial diamictite, suggesting that the ice grounding line extended into the marine realm. This glacial advance is generally correlated with the Mi-1 and Mi-1a events, which occurred close to the Oligocene-Miocene boundary^{32,48}. Following this, the marine sedimentary succession evolved to ice-proximal and then ice-distal conditions prior to the deposition of the rocks hosting the *Nothofagus* leaf macrofossils^{9,12,30}. The presence of tundra-like forest thus coincides with evidence for a climate amelioration in this part of Antarctica. The evidence for extensive ice cover at the Oligocene-Miocene boundary indicates that this site is itself unlikely to have been a persistent glacial refugium.

The sparse occurrence of Neogene woody macrofossils in Antarctica may indicate that *Nothofagus* recolonised Antarctica during warmer intervals in suitable locations via long-distance dispersal^{120,121}, rather than persisting without interruption. This is based on the premise that continuous persistence would have yielded, albeit locally, a continuous record of woody plant fossils. Episodic recolonisation from tundra-like vegetational relicts would result in a more fragmented fossil record, which better fits the observed macrofossil data. Tundra-like forests existed in regions subjected to glacial conditions during this period, including Patagonia¹²², Falkland/Malvinas Islands¹²³ and Oceania^{124,125}, and potentially could have acted as seed sources for the resurgence of these forests in Antarctica. However, the absence of fossils does not necessarily disprove the presence of glacial refugia. Both the lack of appropriate sedimentation conditions and the inaccessibility of many sedimentary strata could produce a discontinuous and incomplete fossil record. In addition, the mechanism by which long-distance dispersal may have occurred remains unclear.

The record of tundra-like vegetation in East Antarctica after the early Miocene is limited to two episodes: the MMCO²² and the mid-Pliocene^{9,12} (Fig. 5). The fossiliferous site dated to the latter is located less than 500 km from the South Pole. If such latitudes were populated by *Nothofagus*-dominated forest relicts during these periods, it is reasonable to assume that this vegetation was also present at lower latitudes of Antarctica. However, direct macrofossil evidence is absent in West Antarctica after the early Miocene. Although the evidence presented here represents a substantial advance in our understanding of the Neogene vegetation history of West Antarctica, the question of persistence or recolonisation remains unresolved. Nevertheless, evidence presented herein supports refugia.

Stability of the Neogene ice-cap

The presence of low-diversity tundra-like vegetation either temporarily recolonising Antarctica during favourable conditions or persisting through the Late Cenozoic Ice Age has critical implications for understanding the stability of the Antarctic ice sheet. Although consecutive glaciations followed the EOT, during which the ice cap is conservatively estimated to have reached 80% to 110% of its modern volume¹²⁶, the presence of tundra-like forests suggests that at least some sectors remained ice-free during warm periods or possibly throughout the Neogene, lasting as late as the Pliocene. These findings challenge the assumption of a stable Antarctic ice sheet since the EOT. Furthermore, evidence indicates that ice sheets could have melted rapidly during brief warm periods^{127–130}, demonstrating their sensitivity to climate warming. This highlights the potential for rapid changes in the Antarctic ice cap under current global warming scenarios, where the return of woody vegetation could occur relatively quickly.

Conclusions

The *Nothofagus* leaf imprints from the Cape Melville Formation on King George Island presented here (Fig. 5), combined with our geochronological results (Fig. 4), provide the first robust evidence for the presence of tundra-like vegetation in West Antarctica during the early Miocene, suggesting that tundra-like forests were present in the region at least between 22 and 20 Ma and potentially even before this period, establishing it as the youngest woody macrofossil record from West Antarctica. This finding advances the debate

surrounding palynoflora-based interpretations of Neogene tundra-like forests in West Antarctica. Furthermore, it fills critical gaps in our understanding of how woody vegetation became extinct in Antarctica and underscores the remarkable adaptability of *Nothofagus* within Antarctic ecosystems.

Localised refugia with tundra-like vegetation in West Antarctica may have either survived numerous glaciations since the EOT or recolonised during warm interglacial periods. King George Island likely served as such an enclave during the early Miocene, suggesting a more complex climatic history than previously thought. This implies that Antarctic conditions may not have been uniformly harsh for woody vegetation, at least episodically. The biology of *Nothofagus* and its syndrome of reproduction argue against recolonisation from nearby areas (e.g. Patagonia). On the other hand, repopulation of tundra-like forests in Antarctica from glacial refugia is also uncertain, as the ice sheet should have reached volumes during the Late Cenozoic Ice Age that were similar to or greater than those of the present day. Therefore, whether tundra-like vegetation recolonised Antarctica or persisted under the harsh conditions of the Late Cenozoic Ice Age remains a challenging and open question, which should be the focus of future studies.

The presence of early Miocene tundra-like vegetation in West Antarctica suggests that the vegetation dynamics may have been more synchronised between East and West Antarctica than previously assumed, highlighting the complex stability of Antarctica's ice sheet.

Data availability

The authors declare that the data supporting the findings of this study are available within the paper and its supplementary information files, and are also accessible via the following repository: <https://zenodo.org/records/16738354>.

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Competing interests

The authors declare no competing interests.

Additional information

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