Antarctic Science 36(4), 231–250 (2024)

doi:10.1017/S0954102024000129

Evidence for a floristically diverse rainforest on the Falkland archipelago in the remote South Atlantic during the mid- to late Cenozoic

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Abstract: We report the discovery of an ancient forest bed near Stanley, on the Falkland Islands, the second such ancient deposit identified on the South Atlantic island archipelago that is today marked by the absence of native tree species. Fossil pollen, spores and wood fragments preserved in this buried deposit at *Tussac House* show that the source vegetation was characterized by a floristically diverse rainforest dominated by *Nothofagus*-Podocarpaceae communities, similar to cool temperate *Nothofagus* forests/woodlands and Magellanic evergreen *Nothofagus* rainforests. The age limit of the deposit is inferred from the stratigraphic distribution of fossil pollen species transported by wind, birds or ocean currents from southern Patagonia, as well as similar vegetation types observed across the broader region. The deposit is suggested to be between Late Oligocene and Early Miocene, making it slightly older than the previously analysed Neogene West Point Island forest bed (200 km west of *Tussac House*). The combined evidence adds to our current knowledge of the role of climate change and transoceanic dispersal of plant propagules in shaping high-latitude ecosystems in the Southern Hemisphere during the late Palaeogene and Neogene.

Received 26 July 2023, accepted 25 February 2024

Keywords: biodiversity, forest bed, fossil pollen, lignite deposit, Miocene, Neogene, Oligocene, Palaeogene

Introduction

The Falkland Islands (Malvinas) are some of a number of remote islands and archipelagos at high to polar latitudes in the Atlantic, Indian and Southern oceans that once supported rainforest and rainforest scrub (woody spp. <5 m tall) in the pre-Quaternary period (Cantrill & Poole 2012). Evidence for the former presence of tree-dominated vegetation includes *in situ* tree stumps, wood, leaves and fossil pollen and spores (Edwards 1921, Cookson 1947, Birnie & Roberts 1986, Poole & Cantrill 2007, Seward & Conway 1934, Stone *et al.* 2005, Truswell *et al.* 2005). In almost all cases, the palaeofloras are assumed to have colonized the islands via transoceanic dispersal of seeds and spores by wind, ocean currents and birds from adjacent larger

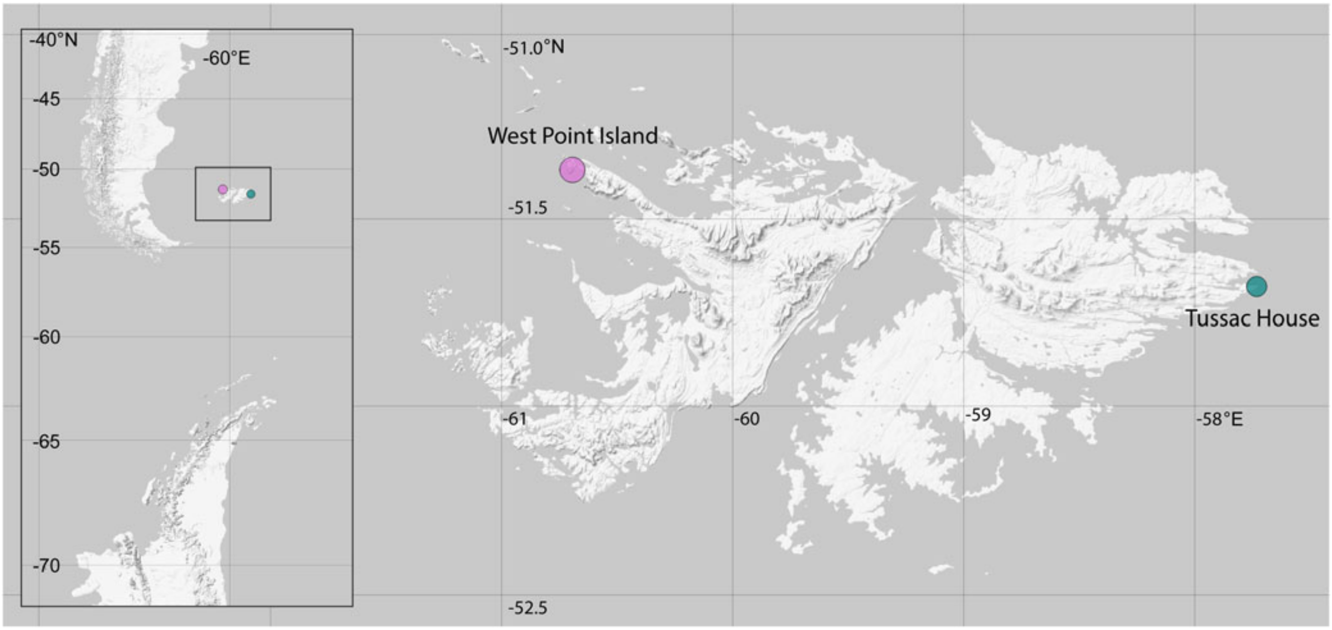

Figure 1. Location of *Tussac House* (green dot) and West Point Island (purple dot) on the Falkland Islands (inset, map of the South Atlantic region). Map produced using Generic Mapping Tools (GMT).

landmasses during globally warm periods (e.g. Late Cretaceous or Eocene; Zachos *et al.* 2001, Macphail & Cantrill 2006, Ortiz-Jaureguizar & Cladera 2006).

Here, we report the discovery of a buried lignitic deposit during excavations for the foundations of the *Tussac House* aged care centre on the foreshore at Stanley, the capital city on the eastern island of the Falkland Islands (Fig. 1). This is the second of two lignitic deposits (forest beds) found in the Falkland Islands that preserve evidence of forest or woody plant communities growing on this now-treeless archipelago (Macphail *et al.* 1994). The first discovery in 1899 comprised a lignitic deposit with tree trunks > 1.5 m in diameter found outcropping on the foreshore of West Point Island, a small island on the western side of the archipelago (Halle 1911). While it was initially proposed that this deposit may have been an accumulation of driftwood (Baker 1924), analysis of its stratigraphic relationships confirmed that the lignite was *in situ*, while the associated fossil pollen and spores suggested that the deposit was Late Neogene in age, representative of a time period when climate conditions allowed the growth of forests (Birnie & Roberts 1986). More recent palynological investigation by Macphail & Cantrill (2006) and an investigation of the wood assemblage (Poole & Cantrill 2007) of the West Point Island deposit narrowed its age limits to Middle Miocene to Early Pliocene. Here, we document the microfloras and wood fragments preserved in the *Tussac House* deposit. We infer the age limits by a combination of stratigraphic distribution of fossil pollen species transported by wind/birds from southern Patagonia and by comparing coeval floras present in Patagonia-Tierra del Fuego, the South Shetland Islands and West Antarctica.

Setting

The Falkland Islands lie at 52°S, 540 km east of the coast of South America. Unlike many volcanic islands off the Chilean coast, the Falkland Plateau is considered to be a rifted part of the African Plate associated with the break-up of Gondwana and the opening of the Atlantic Ocean during the Mesozoic (Stanca *et al.* 2022). The modern climate is made of up two main zones: subpolar oceanic climate (Köppen classification: Cfc) in lowland areas and polar tundra climate (Köppen classification: ET) in upland areas (Beck *et al.* 2018), being highly influenced by the surrounding cool South Atlantic waters. There are some isolated areas of cold desert (BWk) and cold steppe (BSk) in lowland areas influenced by rain shadows. The mean annual temperature is 5.5°C, with high mean monthly and annual wind speeds of ~8.5 m s^{-1} (with prevailing westerly winds) and relatively low annual precipitation of ~600 mm, distributed uniformly throughout the year (Lister & Jones 2014). Although the Falkland archipelago is ~8° latitude north of the southern limits of tree growth in southern South America, trees do not now grow naturally on the islands, and vegetation is dominated by acid grasslands, including whitegrass (*Cortaderia pilosa*) and diddle-dee (*Empetrum rubrum*), with tussac grass (*Poa flabellata*) found in coastal areas.

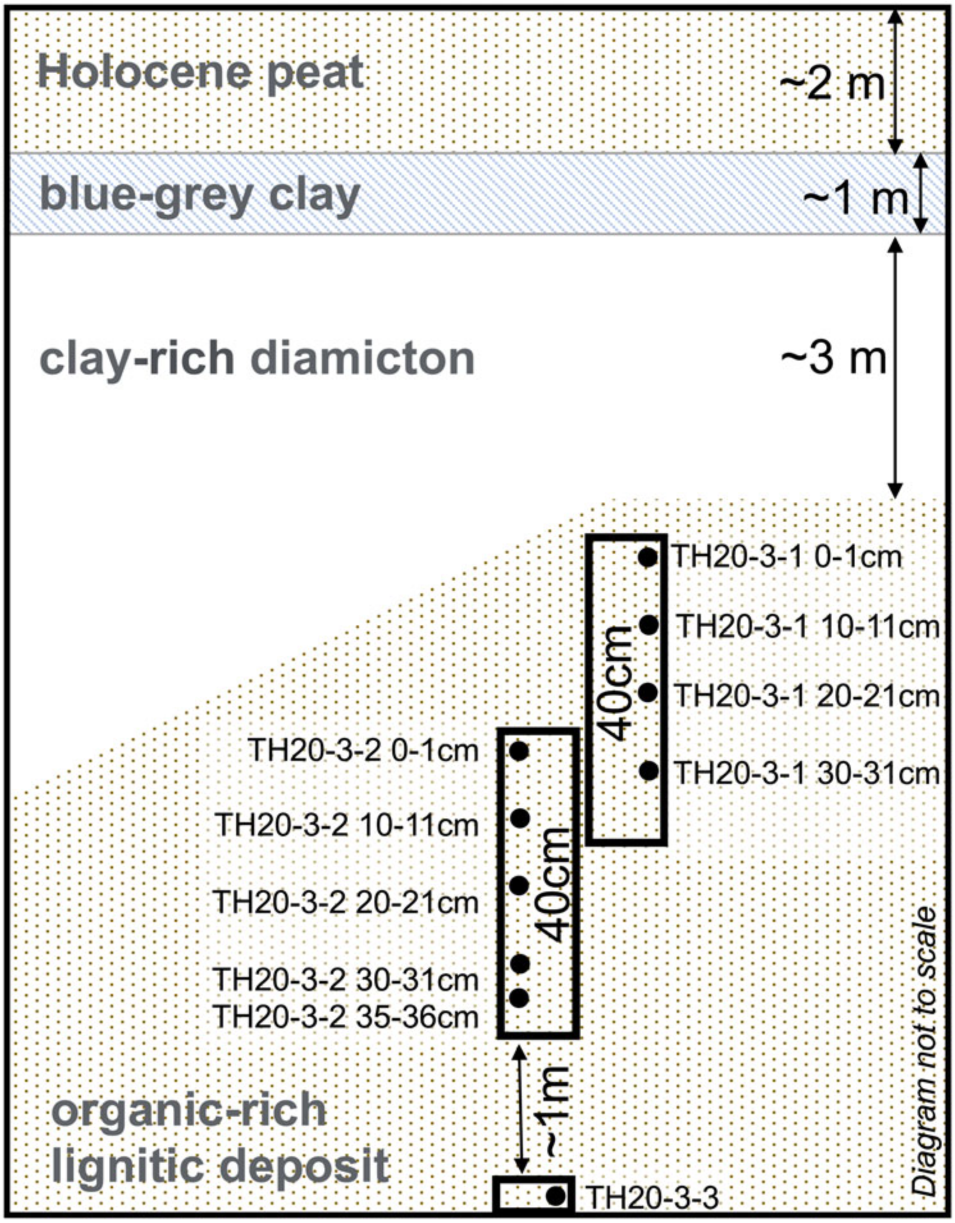

Figure 2. Lithostratigraphy of the *Tussac House* site.

Woody shrubs, such as native boxwood (*Veronica elliptica*), are relatively uncommon and confined to topographically sheltered areas. Reasons for the lack of timber-sized trees (and tree species) include the subdued topography, very extensive periglacial activity but limited glacier formation during Pleistocene glacial stages and prevalence of gale-force winds (Clark & Wilson 1992, Rosenbaum 1996, Hamson *et al.* 2008).

The *Tussac House* site is located on the foreshore of Stanley Harbour (51.6949°S, 57.8315°W). Geotechnical boreholes drilled on the site indicate that the subsurface geology consists of ~2 m of Holocene peats sequentially underlain by periglacial sediments comprising a 1 m-thick blue-grey clay and ~3 m thick clay-rich diamicton, which unconformably overlie the lignitic organic deposit. The total thickness of this organic deposit is unknown due to it meeting water table depth, but it is likely to be > 2 m thick.

Methods

A geotechnical excavation in March 2020 uncovered a lignitic wood-rich matrix at ~6 m depth. During a subsequent geotechnical dig in May 2020, the section was sampled, with the recovery comprising a 60 cm lignitic section (Fig. 2) and several large wood fragments (Supplemental Table 1a), probably representing tree-sized parent plants.

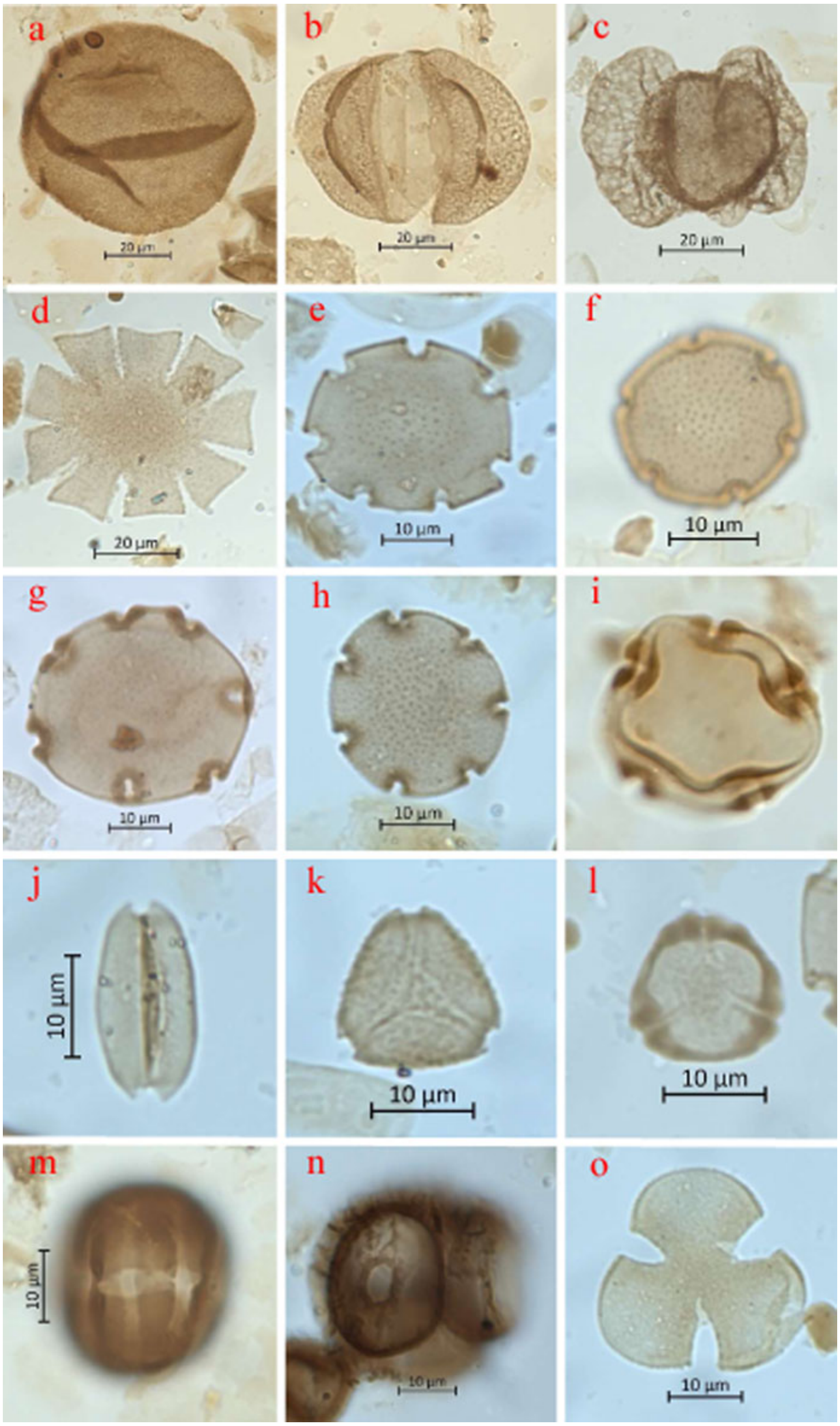

Figure 3. Selected photomicrographs of fossil pollen produced by gymnosperm and angiosperm living relatives in the rainforest of southern South America (nearest living relatives in parentheses): **a.** *Araucariacites australis* (*Araucaria*), **b.** *Podocarpidites* sp. (cf. *P. microreticuloidata*) (*Podocarpus*-*Prumnopitys*), **c.** *Podocarpidites* type 2 (*P. marwickii* complex) (*Podocarpus*-*Prumnopitys*), **d.** *Nothofagidites americanus* type (*Nothofagus* subgenus *Lophozonia*), **e.** *Nothofagidites acromegacanthus* complex (*Nothofagus* subgenus *Brassospora*?), **f.** *Nothofagidites brachyspinulosus* (*Nothofagus* subgenus *Fuscospora*), **g.-i.** *Nothofagidites flemingii-rocaensis-saraensis* complex (*Nothofagus* subgenus *Nothofagus*), **j.** *Dicolpites* sp. (*Tepualia stipularis* type), **k. & l.** *Myrtaceidites verrucosus* complex (includes *Myrceugenia*, *Temu*, *Ugni*), **m.** *Polycolporopollenites esobalteus* (*Polygonaceae*), **n.** *Pseudowinterapollis cranwellae* (*P. couperi*) (*Drimys*) and **o.** *Tricolpites reticularis* (*Gunnera*).

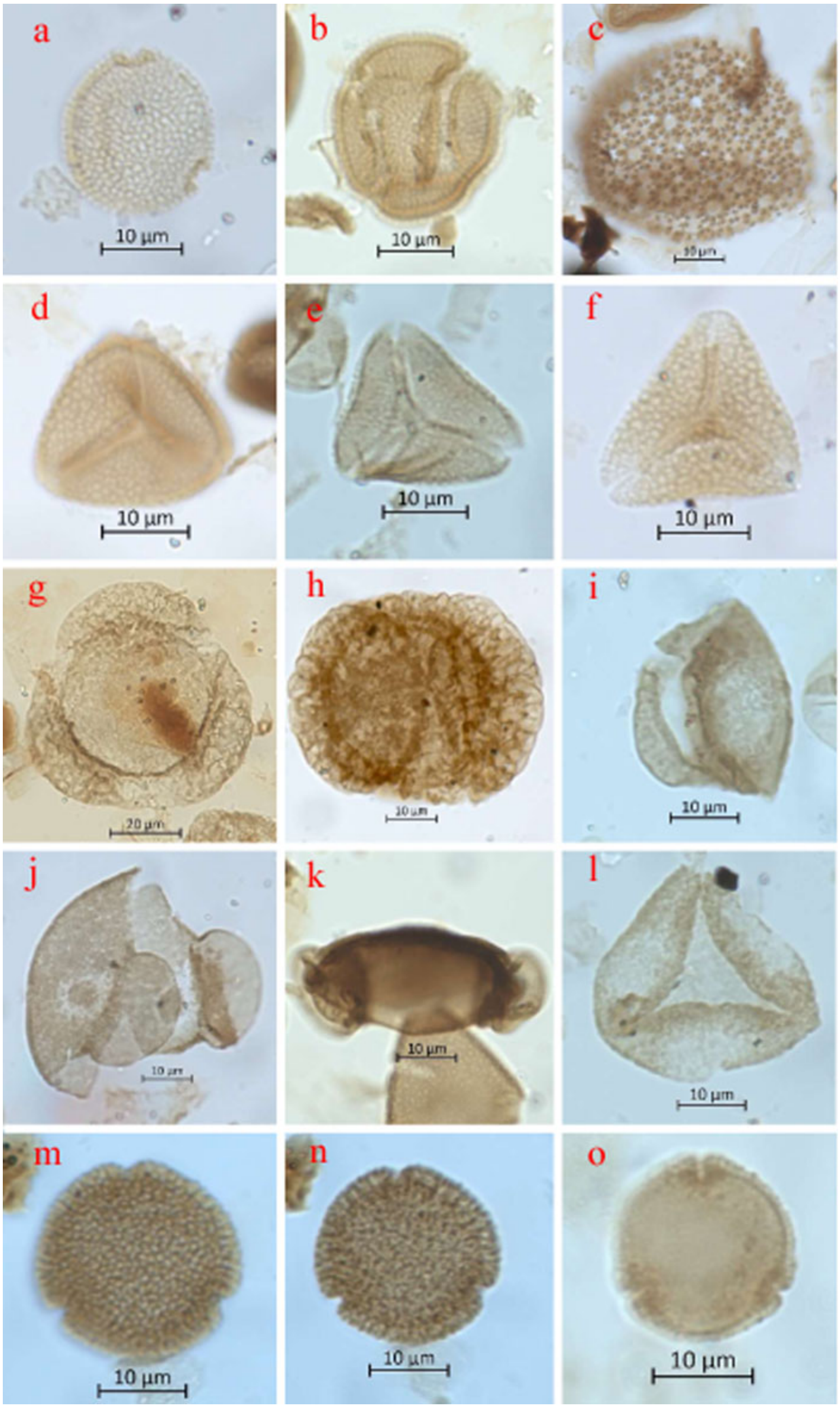

Figure 4. Selected photomicrographs of pollen of age-diagnostic and phytosociologically significant taxa (nearest living relatives in parentheses; all morphogenera and species are now extinct in southernmost South America and on the Falkland Islands: **a.** *Canthiumidites* cf. *bellus* (*Randia* type), **b.** *Clavatipollenites glarius* (*Hedyosum*), **c.** *Thymelaepollis* sp. of Macphail & Cantrill (*Ovidia* type), **d.-f.** *Cupanieidites reticularis* (Sapindaceae tribe Cupanieae), **g.** *Dacrycarpidites australiensis* (*Dacrycarpus*), **h.** *Dacrydiumites florinii* (*Dacrydium*), **i.** *Microalatidites palaeogenicus* (*Phyllocladus*), **j.** *Phyllocladidites mawsonii* (*Lagarostrobos franklinii*), **k.** *Phyllocladidites elongatus* (extinct *Lagarostrobos* sp.), **l.** *Trichotomosulcites subgranulosus* complex (extinct Podocarpaceae) and **m.-o.** Gen. et sp. nov. of Macphail & Cantrill (2006).

Ten samples of 1 cc of sediment spaced along the 60 cm section were prepared for palynostratigraphic investigation (Macphail 2021). Concentrating the oxidation-resistant fossil pollen and spores (miospores) and fungal spores preserved in cultural deposits and soils requires the removal of the inorganic matrix and organic matrix (see Wood *et al.* 1996). Sample process included 1) treatment with 10% potassium hydroxide, 2) sieving residue through a 100 μm mesh sieve, 3) addition of a lycopodium tablet and 10% hydrochloric acid, 4) sodium polytungstate heavy liquid separation at a specific density of 1.8 g/cm^2 to remove mineral matrix and finally 5) treatment with acetolysis solution (sulphuric acid and acetic anhydride). Aliquots of the organic extracts were set on permanent strew mounts using Petropoxy 154.

The plant microfossil component in each sample was counted using a Zeiss™ Photomicroscope II fitted with Plan-Neofluar™ and Planapo™ objectives, which provide magnifications up to 2000×. Specimens of fossil pollen and spores were counted until statistically robust numbers of fossil pollen and spores were recorded (> 250 specimens), and then the remainder of the strew mounts and additional strew mounts for each sample were scanned for additional rare morphospecies; in the case of low-yield samples, the pollen count comprises the total numbers of fossil pollen and spores present on the microscope slide.

Samples of wood from the section were taken for radiocarbon measurements at the University of New South Wales Chronos ^{14}Carbon-Cycle Facility to determine whether the material returned infinite radiocarbon ages (i.e. > 50 000 years). Each sample type was pre-treated following the protocols outlined in Turney *et al.* (2021). The wood specimens were also examined by light microscopy to determine their taxonomic class. To investigate the anatomical characteristics, the material was fractured to expose the three planes of section (transverse and radial and tangential longitudinal) mounted on aluminium stubs. Specimens were not treated/coated prior to imaging. Backscattered electron imaging was conducted using a Hitachi TM4000Plus scanning electron microscope at 15 kV in standard vacuum mode (~30 Pa). Wood specimens are described using the terminology of the IAWA Committee (1989, 2004) wherever possible. We compared samples with the published literature on wood samples from West Point Island (Poole & Cantrill 2007) to facilitate identification.

To provide further context for our plant proxy evidence, we performed a brief comparison of the Falklands climate with palaeoclimate modelling scenarios of the Miocene and Oligocene. Here, we used the simulations of Farnsworth *et al.* (2019), who ran palaeoclimate simulations for each of the periods of interest: namely, the Langhian (13.8–16.0 Ma), Burdigalian (16.0–20.4 Ma), Aquitanian (20.4–23.0 Ma), Chattian (23.0–27.8 Ma) and Rupelian (27.8–33.9 Ma), as well as a pre-industrial control simulation. These simulations were performed using the HadCM3BL model, using palaeogeography reconstructions generated by Getech. The model simulations were coarse resolution (2.50° latitude × 3.75° longitude) to cover many geological periods within the computational resources available. This means that each simulation typically had no land grid cell assigned to the Falkland Islands, or in some cases only a single grid cell, depending on the configuration. Thus, the model can produce a good representation of South American topography and climate through time, whereas the Falkland Islands generally fall below the model resolution.

To overcome the resolution limits, we used the palaeoclimate simulations to reconstruct anomalies of temperature and precipitation at the Falkland Islands geographical coordinates rather than absolute values. These anomalies were then used to adjust a modern high-resolution (30 arc-seconds) climatology of temperature and precipitation (WorldClim version 2; Fick & Hijmans 2017) to create palaeoclimatologies. These palaeoclimatologies were reconstructed using an additive anomaly for temperature and a multiplicative anomaly for precipitation (following Beck *et al.* 2018).

Results

Palynostratigraphic analysis

All samples yielded large to very large numbers of mostly well-preserved terrestrial palynomorphs in organic extracts dominated by cuticle fragments and organic fines. Cysts of marine algae (dinoflagellates) and miospores of freshwater aquatic or semi-aquatic plants are absent except for occasional *Botryococcus* and a single specimen of *Sparganiaceaepollenites* (*Sparganium*, *Typha*) at 20–21 cm in TH20-3-1. Whether or not frequent to common 'amorphous spheres' (cf. *Leiosphaeridia*) in the samples represent freshwater algae is unknown.

Taxonomy

The majority of commonly occurring and some rare miospores in the *Tussac House* samples (Figs 3 & 4) can be assigned to fossil morphospecies formally described from Palaeogene-Neogene deposits in southern Australia, New Zealand and South America (references in Macphail *et al.* 1994, Barreda & Palazzesi 2007, Palazzesi & Barreda 2007, Raine *et al.* 2011). However, the morphological diversity exhibited by some morphospecies and genera is unusually high, particularly within

Table I. Modern affinity of selected fossil morphospecies and genera with Eocene to Miocene time distributions in Patagonia.

Family	Tribe/genus	Fossil morphospecies	Age range (Patagonia)
Amaranthaceae	-	*Chenopodipollis chenopodiaceoides*	Late Oligocene to Miocene
Anacardiaceae	-	*Striatotricolporites gamerroi*	Palaeocene to Late Miocene
Aquifoliaceae	*Ilex*	*Ilexpollenites* spp.	Eocene
Arecaceae	-	*Arecipites* spp.	Palaeocene to Late Oligocene
Asteraceae	Tribe *Mutisieae*	*Mutisiapollis* spp.	Late Oligocene to Early Miocene
	Subfamily *Tubuliflorae*	*Tubulifloridites* spp.	Miocene
Casuarinaceae	*Allocasuarina/Casuarina*	*Haloragacidites harrisii*	Palaeocene to Eocene
	Gymnostoma?	*Haloragacidites trioratus*	Middle Eocene to Early Miocene
Caesalpiniaceae	-	*Margocolporites van wijhei*	Late Oligocene to Miocene
Chloranthaceae	*Hedyosum*	*Clavatipollenites glarius*	Oligocene to Early Miocene
Convolvulaceae	*Cressa*, *Wilsonia*	*Tricolpites trioblatus*	Miocene
Cyperaceae	-	*Cyperaceaepollis neogenicus*	Miocene
Ericaceae	*Empetrum*, *Gautlheria*, *Pernettya*	*Ericipites* spp.	Palaeocene to Miocene
Euphorbiaceae	*Alchornea*	*Psilatricolporites operculatus*	Late Oligocene to Middle Miocene
	(*Austrobuxus/Dissilaria*)	*Malvacipollis diversus*	Eocene
	Cf. *Corynabutilon*	*Malvacipollis robustus* ms.	Oligocene to Miocene?
Goodeniaceae	(*Coprosma/Opercularia*)	*Poluspissusites* spp.	Late Oligocene to Early Miocene
Grossulariaceae	Cf. *Quintinia*	*Quintiniapollis*	Late Oligocene to Early Miocene
Gunneraceae	*Gunnera*	*Tricolpites reticulatus*	Palaeocene to Middle Miocene
Loranthaceae	-	*Gothanipollis bassensis*	Eocene
Malvaceae	-	*Baumannipollis*, *Malvacearumpollis*	Late Oligocene to Middle Miocene
Menyanthaceae	(*Liparophyllum* type)	*Striasyncolpites laxus*	Early to Middle Miocene
Mimosaceae	*Acacia*	*Acaciapollenites myriosporites*	Early Miocene
	(*Adenanthera* type)	*Polyadopollenites*	Early Miocene
Myrtaceae	(Includes *Metrosideros* type)	*Myrtaceidites parvus-mesonesus*	Palaeocene to Miocene
	Myrceugenia, *Temu*, *Ugni*, etc.	*Myrtaceidites verrucosus*	Eocene to Miocene
Nothofagaceae	*Nothofagus* (*Lophozonia*) spp.	*Nothofagidites americanus/tehuelchesii*	Eocene to Miocene
	Nothofagus (*Brassospora*) spp.	*Nothofagidites acromegacanthus*	Eocene to Miocene
	Nothofagus (*Nothofagus*) spp.	*Nothofagidites flemingii*	Eocene to Miocene
	Nothofagus (*Nothofagus*) spp.	*Nothofagidites rocaensis/Saraensis*	Oligocene to Miocene
Onagraceae	(*Epilobium* type)	*Corsinipollenites atlantica.*	Early to Middle Miocene
	Fuchsia	*Diporites aspis*	Late Oligocene
Poaceae	-	*Graminidites* spp.	Late Oligocene to Miocene
Polygonaceae	*Persicaria*	*Glencopollis ornatus*	Miocene
Proteaceae	*Embothrium*	*Granodiporites nebulosus*	Late Oligocene to Early Miocene
	-	*Peninsulapollis gillii*	Palaeocene to Eocene
	Proteacidites cf. *Telopea*	*Triporopollenites ambiguus*	Middle Eocene
Rubiaceae	*Randia*?	*Rubipollis oblatus*	Late Oligocene
	Randia type	*Canthiumidites* cf. *bellus*	Late Oligocene to Early Miocene
Sapindaceae	Tribe *Cupanieae*	*Cupanieidites reticularis*	Late Oligocene to Middle Miocene
Sparganiaceae	*Sparganium*	*Sparganiaceaepollenites sphericus.*	Middle Miocene
Thymelaeaceae	*Ovida*	*Thymelaepollis* sp.	Late Palaeogene-Neogene?
Trimeniaceae	-	*Periporopollenites demarcatus*	Eocene
Winteraceae	*Drimys*	*Pseudowinterapollis couperi*	Oligocene to Middle Miocene

morphotypes assigned to *Podocarpidites* (nearest living relative (NLR) *Podocarpus*-*Prumnopitys*) and *Nothofagidites* (*Nothofagus*). In both cases, individual pollen grains can vary markedly in size and shape. Reasons for this include deposition of both immature and mature pollen grains representing plants whose remains form the lignitic deposit or were growing close to the site (M.K. Macphail, personal observation 2023). In addition, curtailed pollen development may have occurred due to the short growing season at high latitudes and the associated climate stress on flower development.

In this study, the *Podocarpidites* component has been assigned to two broad groups based on the size and mode of attachment of the sacci to the corpus of the pollen grain, not to species identified in the Neogene flora of Tierra del Fuego by Zamaloa & Romero (2005). The *Nothofagidites* component is assigned to three broad morphospecies groups comprising *Nothofagidites acromegacanthus* (NLR *Nothofagus* subgenus *Brassospora*), *Nothofagidites americanus/tehuelchesii* (*Nothofagidites* subgenus *Lophozonia*) and *Nothofagidites flemingii/rocaensis/saraensis* (*Nothofagidites* subgenus *Nothofagus*). Unidentified triporate, tricolpate and tricolporate pollen grains have been grouped into *Proteacidites* spp. (Proteaceae), *Tricolpites* spp. and *Tricolporites* spp., respectively.

Table II. Relative abundances of commonly occurring and selected uncommon to rare morphospecies recovered from the *Tussac House* samples. Rare taxa (< 1%) within the spore-pollen count are indicated by '+'; very rare taxa recorded outside the spore-pollen count are indicated by '×'.

Fossil taxon	TH20-3-1 (depths in cm)				TH20-3-2 (depths in cm)					TH20-3-3
	0–1	10–11	20–21	30–31	0–1	10–11	20–21	30–31	35–36	-
Cryptogams										
Baculatisporites turboensis	+	×	×	+	+	1%		+	×	
Cyathidites australis/minor	×	×	×	×	×	×	×	×	×	×
Deltoidospora sp.	×				×		×	+	+	×
Foveotriletes palaequetrus		×	×	×						
Ischyosporites areapunctatis	+	×		+		+	×	+	×	×
Polypodiisporites inanguahuensis			×	×	×	×				
Unassigned trilete spores	+	×		×	+		+		×	
Total count	*1%*	*1%*	+	*2%*	*2%*	*1%*	+	*2%*	*1%*	+
Gymnosperms										
Araucariacites australis	+	+	+	+	×	+	+	+	×	+
Cupressacites					+		+			
Dacrycarpites australiensis	+	×	+				+			
Dacrydiumites florinii	3%	4%	6%	3%	4%	2%	5%	4%	2%	1%
Equisetosporites sp.	×				+					
Microalatidites palaeogenicus	1%		+	+	+	+	+		+	+
Phyllocladidites mawsonii complex	42%	44%	45%	45%	34%	45%	42%	45%	48%	48%
Phyllocladidites verrucosus	+	+					×		×	+
Podocarpidites type 1 complex	12%	6%	8%	10%	6%	7%	11%	9%	7%	10%
Podocarpidites type 2 complex	9%	4%	8%	5%	3%	6%	4%	6%	5%	6%
Podosporites parvus				+	×	×	×			×
Trichotomosulcites subgranulosus	3%	2%	1%	2%	6%	1%	1%	1%	+	+
Unassigned gymnosperms	+	+	+	1%	+				+	+
Total count	*72%*	*61%*	*69%*	*65%*	*55%*	*62%*	*63%*	*65%*	*62%*	*66%*
Angiosperms (monocotyledons)										
Sparganiaceaepollenites			×							
Liliacidites type 2	+	×	+	×		×	+	+	+	+
Luminidites cf. *phormoides*			×	×	×					
Total count	*2%*	*1%*	*1%*	+	*1%*	*1%*	*2%*	+	+	
Angiosperms (dicotyledons)										
Clavatipollenites glarius		×	×	×	+		×	×		
Compositoipollenites cf. *tarragoensis*	×	×	+				1%	×	+	
Cupanieidites orthoteichus		×				×	×			×
Ericipites spp.		×	×	+	+		+	×	+	×
Gen. et sp. nov.		×								
Gothanipollis cf. *bassensis*			+	×		×	+	+	+	+
Granodiporites nebulosus	×									
Malvacipollis robustus ms		×								
Myrtaceidites verrucosus type 1	3%	1%	4%	6%	7%	6%	6%	5%	4%	5%
Myrtaceidites verrucosus type 2	+	+	×				×	×		
Myrtaceidites verrucosus type 3	×				×				×	+
Myrtaceidites sp. (dicolpate)	×	+		+	+	+	+	+	+	
Nothofagidites americanus/tehuelchesii	+	2%	+	+	1%	2%	1%	+	+	+
Nothofagus acromegacanthus	7%	9%	4%	2%	5%	6%	6%	6%	6%	4%
Nothofagidites flemingii/saraensis	10%	19%	14%	18%	20%	16%	14%	14%	15%	15%
Total *Nothofagidites* count	17%	30%	18%	20%	26%	24%	21%	20%	23%	19%
Polycolporopollenites esobalteus		×	×	×		×	×	×	×	×
Proteacidites cf. *symphyonemoide*s		+	×	×						
Proteacidites type 1	+	×	+	+	+	+		×	+	+
Proteacidites type 2	×	×	2%	+	+	×		×	+	+
Total *Proteacidites* count	1%	1%	3%	3%	4%	2%	2%	3%	2%	2%
Pseudowinterapollis couperi	×	+	×	×	×	×	×	+	×	×
Unassigned *Rhoipites* spp.	+	×	+	+	+	+	+	×	×	+
Striatotricolporites gammeroi			×				cf.			
Thymelaepollis sp. (*Ovidia* type)	×	×	×	+	×	×	×	×	+	×
Tricolpites reticulatus	+			×	+	+	×	+	+	×
Tricolpites sp. A	×	×	×		×	×	×	×		

(*Continued*)

Table II. (*continued*).

Fossil taxon	TH20-3-1 (depths in cm)				TH20-3-2 (depths in cm)					TH20-3-3
	0–1	10–11	20–21	30–31	0–1	10–11	20–21	30–31	35–36	-
Canthiumidites cf. *bellus*						×				
Unassigned *Triporopollenites* spp.	+	×				+				
Inassigned angiosperms	+	+	+	+	+		+	+	+	+
Total dicotyledon count	*26%*	*36%*	*31%*	*33%*	*42%*	*36%*	*34%*	*33%*	*36%*	*31%*
Pollen sum	*591*	*513*	*590*	*609*	*495*	*613*	*634*	*507*	*556*	*555*
				Fungi						
Unassigned spores	+	+	1%	+	+	1%	2%	5%	59%	23%

Table III. *Tussac House* wood anatomical characteristics.

	TH20-3	TH20-5a	TH20-5b	TH20-5c	TH20-6	TH20-8
Anatomical affinity	Podocarpaceae xylotype 3	Podocarpaceae xylotype			Xylotype 7	Podocarpaceae xylotype 3
Growth rings	Distinct	Indistinct	Distinct	Distinct	Distinct	Distinct
• Number of rings	31	-	101	110	56	58
• Average growth rate	0.369 mm/year	-	0.407 mm/year	0.516 mm/year (high variability)	0.514 mm/year	0.256 mm/year
Resin canals	Not observed	Present (rare)	Not observed	Not observed	Present (rare)	Not observed
Parenchyma						
• Contents						
• Strand length						
Tracheids						
• Spiral thickenings	? absent	? absent	? absent	? absent	? absent	? absent
• Pitting tangential longitudinal section	Uniseriate, contiguous, 15–20 μm diameter	Uniseriate, non-contiguous, 10–15 μm diameter	?	?	Rare	Uniseriate, non-contiguous, 10–15 μm diameter
• Pitting radial longitudinal section	Uniseriate, contiguous	Uniseriate, non-contiguous, 10–15 μm diameter	?	?	rare	Uniseriate, non-contiguous
Rays	Homocellular	Homocellular	Homocellular	Homocellular	Homocellular	Homocellular
• Width; height (cells)	Uniseriate	Uniseriate (number of cells between 2 and 12, $n = 72$)	?	Uniseriate (number of cells between 2 and 4, $n = 12$)	Uniseriate (number of cells between 2 and 3, $n = 14$)	Uniseriate (number of cells between 3 and 12, $n = 33$)
• Indentures	? absent	? absent	? absent	? absent	? absent	? absent
Cross-field pits	1–4	?	?	?	1–2	1–2
• Diameter					5–10 μm	5–12 μm
• Apertures	Cupressoid	Cupressoid			Cupressoid	Cupressoid
Ray tracheids	? absent	? absent	? absent	? absent	? absent	? absent

More generally, the usage of Australian and New Zealand names for morphologically similar pollen and spore morphotypes in South America has led to a *de facto* broadening of the original fossil species diagnosis as used in the South American literature, and it is probable that the fossil taxon represents more than one

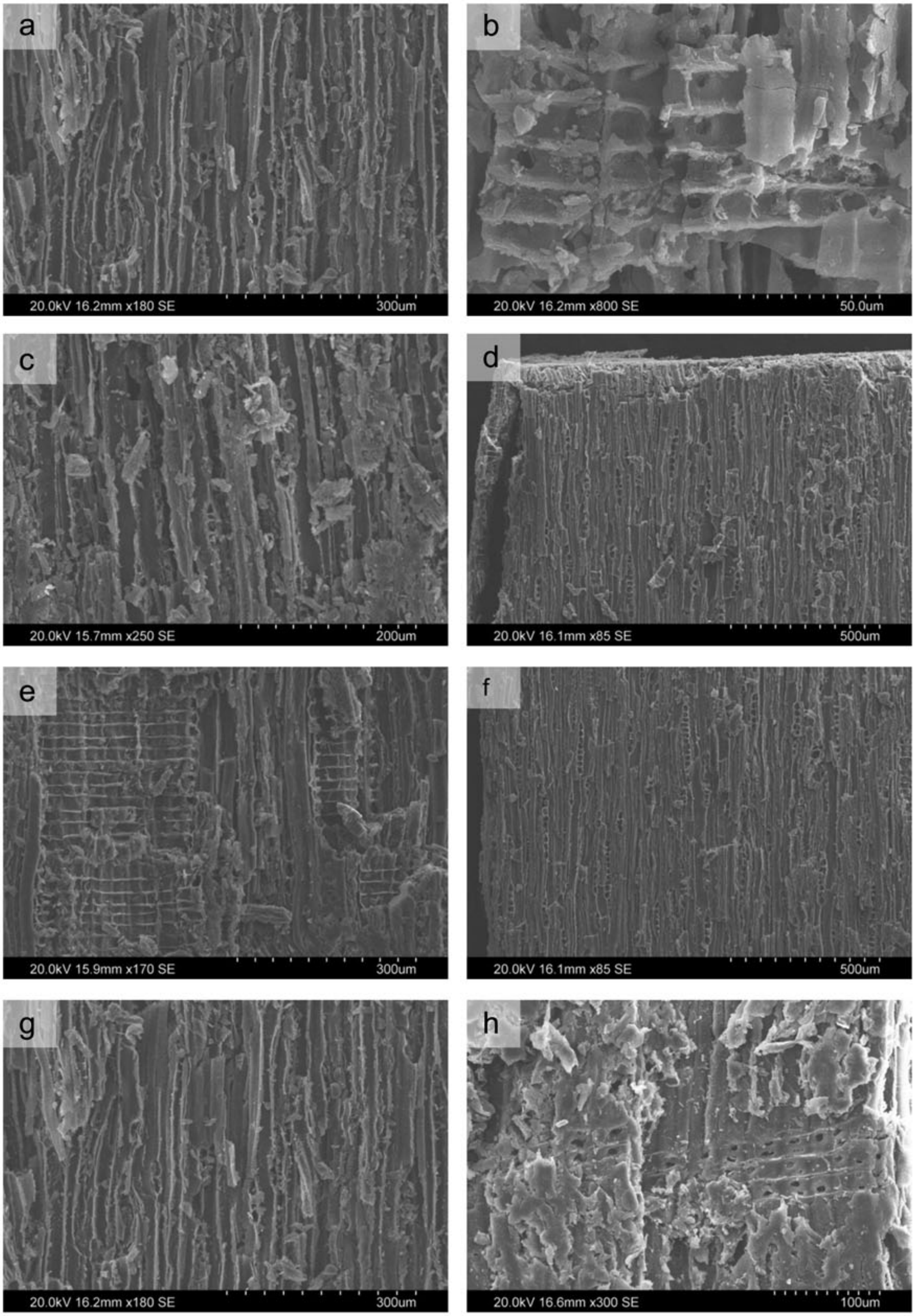

Figure 5. Scanning electron microscopy images of wood fragments. **a.** TH20-3 radial section - homocellular rays, **b.** TH20-3 radial section - smooth cell end wall, **c.** TH20-3 tangential longitudinal section - low-height uniseriate rays, **d.** TH20-5a tangential longitudinal section - low- to medium-height uniseriate rays, **e.** TH20-5a tangential longitudinal section - smooth end walls, **f.** TH20-5a tangential longitudinal section, **g.** TH20-6 tangential longitudinal section - low-height uniseriate rays and **h.** TH20-6 radial section - cross-field pits.

ecotype, species or genus, some of which are extinct and potentially had different ecological tolerances to their NLRs (Macphail *et al.* 1994, Macphail & Cantrill 2006).

Many of these and less commonly occurring taxa have NLRs in Argentina and/or Chile (Table I), although the taxonomic resolution is mostly low (to genus and family levels), or they are ancestral members of the living clades in South America at least to the family level (cf. Heusser 1971, Markgraf & D'Antoni 1978, Palazzesi & Barreda 2007). At least one novel morphotype (Gen. et sp. nov., this study) appears to be unique to the Falkland archipelago (Macphail & Cantrill 2006).

Dominance and diversity

All fossil assemblages are dominated by fossil species of Podocarpaceae, Nothofagaceae and Myrtaceae (NLRs in parentheses) in which *Phyllocladidites mawsonii* (*Lagarostrobos franklinii*) is the dominant morphospecies and *Podocarpidites* (*Podocarpus*/*Prumnopitys*/ *Retrophyllum*), *Nothofagidites acromegacanthus*, *Nothofagidites flemingii*/*rocaensis*/*saraensis* (*Nothofagidites* subgenus *Nothofagus*), *Myrtaceidites verrucosus* (numerous South American Myrtaceae genera) and *Proteacidites* (Proteaceae) occur in frequent to common numbers (Table II). Estimates of relative abundance are based on statistically robust counts of > 450 fossil pollen and spores (excluding fungal spores) for each sample. Percentages < 1% and morphospecies recorded outside the pollen sum are indicated by '+' and '×' in Table II, respectively.

Wood analysis

Samples of wood from the section were taken for radiocarbon dating at the University of New South Wales Chronos ^{14}Carbon-Cycle Facility. All gave infinite radiocarbon ages of > 50 ka (Table III & Supplemental Table 1b), confirming the geological antiquity of the deposit.

Widespread compression made it difficult to diagnose anatomical characteristics of many of the wood fragments (Table III & Supplemental Tables 1a & 1b). Where possible, xylotype was inferred from available diagnostic characteristics and compared directly to the xylotype classification of Poole & Cantrill (2007).

The material observed is assigned to xylotype 3 (Podocarpaceae) documented from the West Point Island deposit (Poole & Cantrill 2007). Although widespread compression makes identification of certain features difficult, some anatomical characteristics are observable (Fig. 5). Samples TH20-3, TH20-5 and TH20-8 appear to have consistent anatomical characteristics where these are observable. Rays are exclusively uniseriate and range between 2 and 12 cells. Cell end walls, when observed, tend to be smooth. In the radial section view, cross-field pits are generally cupressoid. This xylotype appears to have anatomical similarities to podocarpaceous wood. Xylotype 7 appears to be represented by only one sample: TH20-6. This xylotype is characterized by rare or absent pitting and the presence of resin canals. More material with better preservation is needed for further taxonomic assessment.

Discussion

Most of the fossil pollen and spores preserved in the *Tussac House* forest bed (Macphail 2021) closely resemble pollen (gymnosperms, angiosperms) and spores (ferns, fern allies) produced by plants in the modern floras of South America and other landmasses in the Southern Hemisphere, although time distributions in southern South America (cf. Tables I & II; Macphail 1999, Partridge 1999, Raine *et al.* 2011) may vary from, for example, New Zealand and Australia. Some herbs and shrubs remain extant on the Falkland Islands (e.g. *Huperzia fuegianum*, Amaranthaceae, Asteraceae, *Gunnera*, Ericaceae (*Empetrum*, *Gaultheria*) and Myrtaceae (*Myrteola*); Broughton & McAdam 2005). Other taxa almost certainly are ancestral members of the living clades at least to the family level. In many instances, it is probable that the fossil taxon represents more than ecotype, species or genus, some of which are extinct and potentially had different ecological tolerances to their NLRs (Macphail *et al.* 1994).

Absolute and probable age limits of the Tussac House *forest bed*

Unlike Argentina (see Barreda 1996a,b, Barreda & Palamarczuk 2000a,b,c, b, Barreda & Palamarczuk 2000a,b,Barreda *et al.* 2009, Amenabar *et al.* 2023), no formal pollen and spore-based palynostratigraphy has been developed to date and correlate Palaeogene and Neogene sediments on the Falkland Islands or independently dated marine sediments on the submerged Falkland Plateau or Malvinas Basin (Amenabar *et al.* 2023 and references therein). Accordingly, the age limits of the West Point Island forest bed and the *Tussac House* forest bed (Macphail & Cantrill 2006, Macphail 2021) have been inferred using the time distribution of fossil pollen species (morphospecies) whose NLRs occur in mega- and meso-thermal rainforest in Patagonia, commonly defined as encompassing the Argentinean provinces of Neuquén, Río Negro, Chubut, Santa Cruz and Tierra del Fuego (Quattrocchio *et al.* 2011, Palazzesi *et al.* 2021 and references therein).

The present study focuses on the time distribution of fossil pollen of three rainforest thermophiles preserved in marine sedimentary formations in Patagonia, viz. *Canthiumidites* cf. *bellus* *Clavatipollenites* and

Cupanieidites, whose NLRs, respectively, are *Randia* (now found in dry forest communities in northern South America), *Hedyosmum* (Chloranthaceae; now found in lowland to montane rainforest, including disturbed areas at low elevations, from 18°N to 25°S) and *Cupania* (Sapindaceae; now found north of 30°S in southern South America; see Marchant *et al.* 2002). Isotopic (^{86}Sr/^{87}Sr, Ar/Ar, U-Pb) foraminifer and marine dinoflagellate dinocysts of these formations provide independent age control for the time distributions of the morphospecies in Patagonia (Guler *et al.* 2021 and references therein, Parras & Cuitino 2021).

Supporting evidence is provided by 1) objective (Jaccard coefficient) comparisons of Oligocene-Miocene palynofloras in Patagonia and Tierra del Fuego, 2) the presence or absence of pollen from wind-pollinated plants dominating Patagonian steppe vegetation (e.g. Nanez *et al.* 2009, Cornu *et al.* 2012, 2014) and 3) stratigraphic distributions of taxa that are now prominent in Patagonian steppe (Amaranthaceae, Asteraceae, Poaceae) and *Randia* type (*Canthiumidites* cf. *bellus*), which may be evidence for sourcing of pollen from northern Argentina in the Oligocene-Miocene.

Complicating the palynostratigraphic record of the establishments, extirpations and extinctions of these and other mesotherm taxa are (Barreda & Palazzesi 2007, Barreda *et al.* 2008, Quattrocchio *et al.* 2011, Vizcaíno *et al.* 2013, Estebenet *et al.* 2014, Sachse *et al.* 2015, Warny *et al.* 2019, Parras *et al.* 2020, Palazzesi *et al.* 2021, Amenabar *et al.* 2023): 1) geographical, geomorphic and climatic factors such as the progressive tectonic uplift of the Andes during the Palaeogene-Neogene,) opening of Drake Passage and development of the Antarctic Circumpolar Current in the Late Eocene and earliest Oligocene *c.* 34–23 Ma, 3) two marine inundation events (*c.* 22–15 Ma) during the latest Oligocene and Early to Middle Miocene represented by marginal and shallow- to deep-water marine deposits, 4) extinction in Patagonia by the mid-Eocene of previously established mega- and meso-therm taxa followed by the associated emergence of *Nothofagus*-Podocarpaceae communities in the Middle Eocene to Early Oligocene and by the expansion of arid-adapted Patagonian steppe communities in the Late Oligocene and Miocene and 5) marked differences between the palaeofloras occupying coastal and hinterland regions.

Much of the published age-range data from Argentina come from outcrops deposited during the Late Oligocene to Early Miocene *Patagoniense* transgression. Representative sections occur from the Andean Foothills in the north-west to Tierra del Fuego in the extreme south of Argentina, although these represent significantly different periods within the Oligocene to Middle Miocene time (Guerstein *et al.* 2004, Blisniuk *et al.* 2005, Parras *et al.* 2012, Cornou *et al.* 2014, Estebenet *et al.* 2014, Kohn *et al.* 2015, Guler *et al.* 2021, Parras & Cuitino 2021). For example, the palynostratigraphically well-studied Santa Cruz Formation (Parras *et al.* 2020) began accumulating at *c.* 17.5 Ma in the south-west, *c.* 19.8 Ma in the north-west and *c.* 19. 3 Ma in the south-east in Santa Cruz Province and at *c.* 16 Ma in the Golfo San George Basin in the adjacent Chubut Province but is absent further to the north and west in the Valdes and Neuguén basins. Underlying Eocene to Early Miocene formations are mostly confined to specific basins in Patagonia (e.g. the Monte Leon, Río Leona, Río Turbio and San Julien formations (Austral-Magallanes Basin), the Chenque and Centinela formations (Golfo San Jorge Basin) and Slogget Formation (Tierra de Fuego); cf. Guerstein *et al.* 2004, Parras *et al.* 2020, Parras & Cuitino 2021, Amenabar *et al.* 2023). Palynostratigraphic data from marine cores on the Argentine continental shelf are limited to two wells, as are data from confirmed Middle and Late Miocene and Pliocene continental outcrops in Patagonia.

For this reason, and due to the possibility that other relevant records are unpublished, the age limits of samples from the *Tussac House* forest bed are assigned to broad periods of geological time only. The inferred age limits assume that pollen of mesotherm taxa have been transported long distances by wind, birds or insects prior to their extinction or extirpation in continental Patagonia (see Macphail & Cantrill 2006, Macphail 2021). This approach includes caveats that are difficult to test given that the morphospecies are mostly preserved in lignitic sediments where much of the associated palynoflora represents plants growing in or around the site. The reasons for this are as follows:

1) The Falklands flora show a strong affinity with Patagonian South America and Tierra de Fuego and more limited links with the sub-Atlantic Islands, New Zealand and, especially in the past, Australia (see McDowell 2005). However, any colonization of the Falkland archipelago by mega- and meso-thermal plants in the early Palaeogene is most likely to have occurred during periods of global warmth, particularly the Early Eocene hyperthermals. Nevertheless, we recognize that rainforest thermophiles with broad ecological tolerances might have survived after they became extinct in Patagonia (due to increasing aridity) or West Antarctica (due to cold conditions; cf. Zachos *et al.* 2008, Hyland & Seldon 2018, Fernandez *et al.* 2021, Srivastava *et al.* 2023). Nevertheless, given the biologically profound impact of the major global cooling event at the Eocene-Oligocene boundary (Mi-1) elsewhere at mid- to high latitudes in the Southern Hemisphere (cf. Macphail *et al.* 1994, 2014), we consider it improbable that any thermophiles survived this event

Table IV. Chronostratigraphic distribution of trace records of fossil *Cupania*-type, *Hedyosmum*-type and *Randia*-type pollen in Patagonia, Argentina. (+) indicates species is present; (-) indicates species was not recorded, (cf.) indicates comparable pollen.

Basin/province	Formation (offshore well)	Age limits		Mesotherm taxa			Steppe taxa			Reference
		Published	Revised[a]	*Randia* type	*Cupania* type	*Hedyosmum* type	Amaranthaceae	Asteraceae	Poaceae	
Central Chile (Region V1, ~33°S)	(Lauca Basin	Mio-Pliocene boundary	NA	-	-	-	-	+	+	Feitl *et al.* (2019)
	Subtropical Andes)	Latest Miocene	NA	-	cf.	-	-	-	-	Tronosco & Encinas (2006)
Salta Basin	Salto Group	Palaeocene-Early Eocene	NA	-	-	-	-	-	+	Quattrocchio & Volkheimer (1990)
	Metan Subgroup	Undifferentiated Miocene	NA	--	-	-	-		+	Quattrocchio *et al.* (2003)
	Cerro Morado	Early-Middle Miocene	NA	-	cf.	-	+	-	-	Barreda *et al.* (2003)
Neuquen and Nirihuau basins	Salto del Macho	Undifferentiated Palaeogene	NA	-	-	-	-	-		Cornou *et al.* (2012)
	Salto del Macho	Eocene-Early Oligocene	NA	-	-	-			+	Cornou *et al.* (2014)
	(YPE.SE.LH x-2)	Middle(?) Miocene	NA	-	-	-	+		+	Ottone *et al.* (2013)
Colorado Basin	(Cx-1)	Late Miocene	NA	-	-	-		+		Guler *et al.* (2001)
Catamarca	Chiquimil	Late Miocene	NA	-	-	-	-	+	+	Mautino & Anzotegui (1998, 2002a,b)
Chubut Basin	Chenque	Late Oligocene-Middle Miocene	Middle Miocene	+	+	-	+	+	+	Barreda (1996a)
	Porto Madryn	Middle-Late Miocene	Late Miocene(?)	-	-	-	+	+	+	Palazzesi & Barreda (2004)
Golfo San Jorge Basin	Chenque	Oligocene(?)-Miocene(?)	Middle Miocene	-	-	-	+	+	+	Barreda (1993)
	Perfiles Mazarredo	Late Oligocene-Miocene	Miocene(?)	-	+	+	-	-	-	Barreda & Palamarczuk (2000b)
	Chenque (top)	Early Miocene	Miocene(?)	-	+	+	+	-	-	Barreda & Palamarczuk (2000b)
Austral-Magallanes Basin	Río Turbio	Early(?) Eocene	Middle Eocene	-	-	-	-	-	-	Romero & Zamaloa (1985)
	Río Turbio	Middle Eocene	Middle Eocene	-	-	+	--	-	-	Fernandez *et al.* (2021)
	Río Leona	Early Late Oligocene	Early Late Oligocene	-	-	+		+	+	Barreda *et al.* (2009)
	Continental shelf	Late Oligocene-Middle Miocene	NA	+	-	-	+	+	+	Barreda & Palamarczuk (2000a)
	San Julian	Undifferentiated Oligocene	Oligocene	+	-	-		+		Barreda (1997)
	San Julian	Late Oligocene	Late Oligocene	-	+	+	+	+	+	Heredia *et al.* (2012)
	San Julian	Late Oligocene	Late Oligocene	-	-	-	+	-	+	Nanez *et al.* (2009)
	Continela	Late Oligocene	Late Oligocene-Early Miocene	-	-	-	+	-	+	Guerstein *et al.* (2004)
	Monte Léon	Early(?) Miocene	Early Miocene	-	-	-	+		+	Barreda & Palamarczuk (2000c)

(*Continued*)

TABLE IV. (*continued*).

Basin/province	Formation (offshore well)	Age limits		Mesotherm taxa			Steppe taxa			Reference
		Published	Revised[a]	*Randia* type	*Cupania* type	*Hedyosmum* type	Amaranthaceae	Asteraceae	Poaceae	
Tierra del Fuego	Monte Léon	Early Miocene	Early Miocene	-	-	-	+	+	+	Barreda & Palamarczuk (2000c)
	Monte Léon	Early Miocene	Early Miocene	-	+	-	+	-	+	Nanez *et al.* (2009)
	Loreto	Middle Tertiary	NA	-	-	-	-	-	-	Fasola (1969)
	Sloggett	Palaeogene (Late Eocene?)	NA	-	-	-				Olivero *et al.* (1998)
	(Drake Passage)	Mid-Late Eocene	NA	-	-					Amenabar *et al.* (2023)
	(Aries x-1)	Late Oligocene	NA	-	-	-	+	-	+	Palamarczuk & Barreda (2000)
	(Aries x-1)	Early Miocene	NA	-			+	-	+	Palamarczuk & Barreda (2000)

[a] After Parras & Cuintino (2021) and Amenábar *et al.* (2023).
NA = not applicable.

given the exposed habitats on the topographically subdued Falkland archipelago. Whether any recolonization of the Falklands by thermophiles growing in northern Argentina occurred during the Middle Miocene Climatic Optimum (MMCO) at *c.* 15–17 Ma is unknown.

2) Transoceanic dispersal of seeds by wind or water from South America into the Atlantic Ocean is well documented (cf. Renner 2004, Turney *et al.* 2016, Thomas *et al.* 2018, Zwier *et al.* 2022), but successful establishment on remote oceanic islands such as the Falklands is markedly reduced if the 'target' environment(s) differ significantly from those occupied by the parent plants (see McDowell 2005, Ali 2017). Most of these constraints do not apply to pollen or spores of temperate and subtropical plants in South America that are dispersed into the south-west Atlantic or Pacific oceans, although the marine depositional conditions tend to favour long-term preservation more than many terrestrial environments (Kappen & Straka 1988, Montade *et al.* 2011).
3) The rarity of *Canthiumidites* cf. *bellus*, *Clavatipollenites* and *Cupanieidites* and the absence of other South American thermophile pollen types in the *Tussac House* forest bed is likely to reflect deposition in an environment where much of each microflora is derived from locally growing plants (see Barreda *et al.* 2009).
4) There is an unknown likelihood that some earlier or later occurrences of *Canthiumidites* cf. *bellus*, *Clavatipollenites* and *Cupanieidites* in Patagonia are unpublished.

Records of *Cupania* type (*Cupanieidites*), *Hedyosmum* type (*Clavatipollenites*) and *Randia* type (*Canthiumidites* cf. *bellus*) obtained from review surveys of the published palynostratigraphic literature for Patagonia and adjacent regions in southern South America (see Barreda *et al.* 2008) are given in Table IV. The fossil record of *Randia* type (*Canthiumidites* cf. *bellus*) in Patagonia is notable as this thermophile is an important element in dry forests in northern South America (Marchant *et al.* 2002).

Maximum age limits of the Tussac House *forest bed*

On the data available, the parent source(s) of *Clavatipollenites* but apparently not *Cupanieidites* or *Canthiumidites* cf. *bellus* were present in Patagonia in or by the Middle Eocene. Assuming the former became extinct during the Mi-1 global cooling event, the maximum age limit of the *Tussac House* forest bed is inferred to be Late Oligocene based on records of *Clavatipollenites*, *Cupanieidites* and *Canthiumidites* cf. *bellus* in the Austral-Magallanes, Chubut and Golfo San Jorge basins in (or by) the Late Oligocene sediments

(Río Leona, Monte Léon and San Julian formations; Barreda 1997, Barreda *et al.* 2009, Heredia *et al.* 2012). Whether any of the parent sources had reached as far south as Tierra del Fuego by this time is uncertain.

Minimum age limit of the Tussac House *forest bed*

The minimum age limit of the *Tussac House* forest bed is no older than Middle Oligocene based on multiple records of *Cupanieidites* and *Clavatipollenites* in the Austral-Magallanes Basin (Monte Leon and San Julian formations) and, less certainly, Golfo San Jorge Basin (Perfiles Mazarredo Formation), but it might be as young as Middle Miocene (*Cupanieidites*, *Canthiumidites* cf. *bellus*) based on ^{86}Sr/8^{7}SR dates for the Chenque Formation in the Golfo San Jorge (cf. Barreda 1996a, Parras *et al.* 2020). Whether or not the latter age limit is supported by the trace records of pollen representing the wind-pollinated/dispersed families Amaranthaceae (*Chenopodipollis chenopodiaceoides*) and Poaceae (*Graminidites media*) in the *Tussac House* microfloras is uncertain as the parent plants are recorded in Nothofagaceae-Podocarpaceae communities prior to the Late Miocene expansion of steppe vegetation in Patagonia. The absence of Asteraceae (*Tubulifloridites* spp.) pollen is less easily explained unless this is due to its lower pollen production and more limited dispersal by wind and animals.

Depositional environment

Relative level data indicate that the top depth of the *Tussac House* lignitic deposit is ~1.5 m above mean high water mark and that the base of the deposit extends below present-day mean sea level and therefore may have accumulated during a period of low relative sea level. The local depositional environment is more likely to have been a damp depression given the virtual absence of obligate or semi-obligate algal cysts or pollen of herbs such as Sparganiaceae (Sparganiaceaepollis) and Menyanthaceae (*Striasyncolpites laxus*), which occur in 'marsh' deposits in Patagonia during the Oligocene-Miocene. One possibility, suggested by the strong east to west alignment of the basement rocks and ongoing tectonic uplift of the archipelago (Stanca *et al.* 2022), is a depression on the back slope on a tilted fault block.

Palaeoflora and vegetation

As the microfloras represent essentially the same Podocarpaceae-*Nothofagus* rainforest or rainforest shrub community (Table II), the data more compelling suggests that the lignites were deposited over a short period of geological time under perhumid cool or, less likely, cold conditions. The closest modern analogues are Magellanic evergreen *Nothofagus* rainforest (see table 10.1 in Veblen *et al.* 1996). Shared characteristics include the rarity of *Araucaria* and the prominence of *Nothofagus* spp., whose NLRs may be ancestral to extant species in the subgenus *Fuscospora* (e.g. *Nothofagus antarctica*, *Nothofagus betuloides* and *Nothofagus pumilo*) given the high-latitude position of the Falkland Islands throughout the Late Palaeogene and Neogene. The parent plants of *Nothofagidites americanus* and *Nothofagus teheulchesii* may be extinct, as subgenus *Lophozonia* spp. in South America (*Nothofagus alpina*, *Nothofagus obliqua*) are restricted to latitudes above ~40°S in southern Chile and Argentina.

This palaeo-community, however, has no clear modern analogue, as the NLRs of most Podocarpaceae morphospecies are endemic to Tasmania (*Lagarostrobos franklinii*), New Zealand and/or Southeast Asia (e.g. *Dacrycarpus* (*Dacrycarpites australiensis*), *Dacrydium* (*Dacrydiumites florinii*) and *Phyllocladus* (*Microalatidites palaeogenicus*)). Two podocarp clades are extinct (*Podosporites parvus*, *Trichotomosulcites subgranulosus*). The NLRs of most rare ferns and angiosperm shrubs represent humid-demanding species with broad geographical distributions in South America. Examples are the probable tree fern *Cyathidites australis* (Cyatheaceae), the club-moss *Foveotriletes palaequetrus* (*Huperzia fuegianum*) and *Embothrium* (*Diporites granulosus*), all of which occur as far south as Tierra del Fuego, and tree ferns in Andean 'cloud forests' at lower latitudes (Broughton & McAdam 2005). The same is likely to be true of the herb flora whether the unassigned *Tricolpites*/*Tricolporites* counts represent herbaceous or woody plants. The absence of *Lophosoria* (*Cyatheacidites annulatus*) is surprising given that this ground fern became established elsewhere on sub-Antarctic islands (e.g. the Kerguelen Islands; Cookson 1947) during the Miocene.

Although the scanning electron microscopy analysis of the wood assemblage was able to identify two distinct xylotypes, poor sample preservation precluded a species-level identification and as such is unable to inform on the probable age limits of or genera presented in the *Tussac House* forest bed. An interesting characteristic observed in the West Point Island deposit was the preponderance of Podocarpaceae pollen (60%) compared to the wood, which is largely cf. *Austrocedrus*. Although the wood assemblages analysed from the *Tussac House* deposit were significantly lower in number, a similar trend is apparent. This is probably a reflection of the pollination strategy in Podocarpaceae (wind pollinated) as well as of taphonomic effects. The pollen grains are saccate and tend to float on surface water, so different concentrations of grains from the same vegetation are found depending on whether the grains were deposited from water or onto some sort of

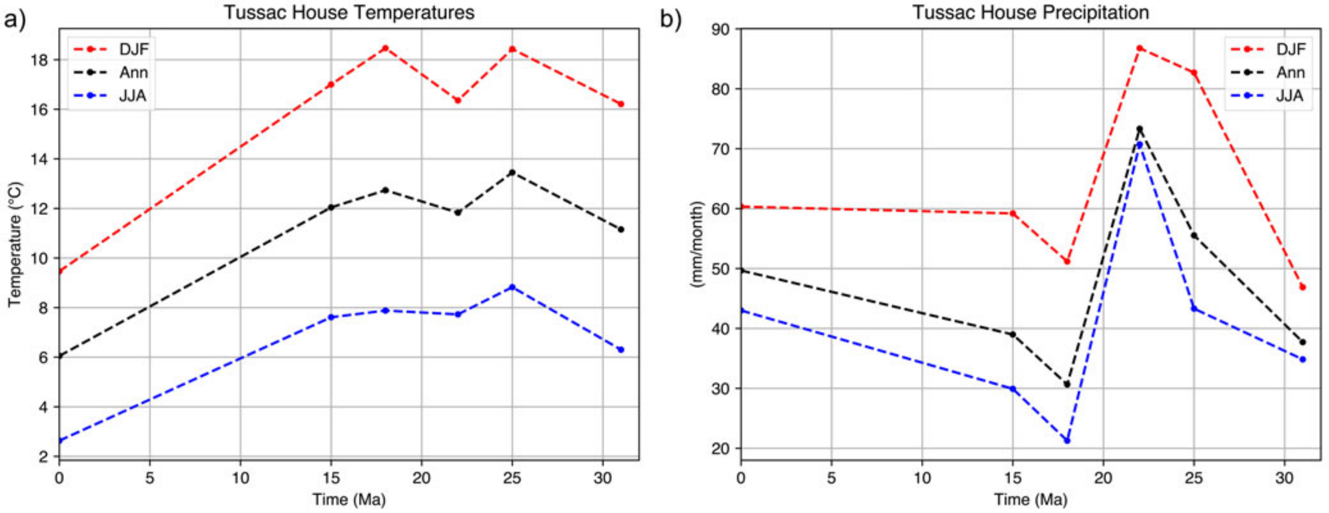

Figure 6. Reconstructed **a.** temperature and **b.** precipitation time series at *Tussac House* based on WorldClim v2 and anomaly-based temperature/precipitation reconstructions for the five palaeo-simulations of the Langhian, Burdigalian, Aquitanian, Chattian and Rupelian. Ann = annual; DJF = December, January, February; JJA = June, July, August.

peat surface (Traverse 2007). Even within standing water the deposition can fluctuate due to differential transport.

Comparison of the Tussac House *and West Point Island forest beds*

Comparisons between the West Point Island forest bed (Macphail & Cantrill 2006) and *Tussac House* forest bed microfloras suggest that the latter are slightly older than the former. With few exceptions, all common and most rare morphospecies recorded in the *Tussac House* forest bed also occur in the West Point Island forest bed. The only significant differences are that the relative abundance of *Phyllocladidites mawsonii* is lower in the West Point Island microfloras (15–25%) compared to the *Tussac House* microfloras (34–48%) and that *Chenopodipollis chenopodiaceoides*, *Graminidites* and *Myrtaceidites eucalyptoides* were not recorded in the *Tussac House* microfloras. *Cupanieidites reticularis* was not recorded in the West Point Island samples. Although trace occurrences of *Myrtaceidites eucalyptoides* in the West Point Island microfloras may represent contamination from drilling equipment, the significance of the other differences provides insights into probable age limits given the wide dispersal of Amaranthaceae and Poaceae pollen by wind around the Southern Hemisphere (Macphail 1979) *vs* the probable dispersal of Cupanieae pollen by insects.

On these data, the probable age limits of the West Point Island forest bed are more likely to be Late Oligocene to Early (Middle?) Miocene than the Middle(?) Miocene to Early Pliocene age limits (Table IV) based in part on *Sparganiaceaepollenites* and *Thymelaepollis* sp. (Macphail & Cantrill 2006). If correct, the revised age limits for the West Point Island forest bed indicate that *Lagarostrobos* populations on the Falkland Islands had undergone a significant contraction during the Early to Middle Miocene (i.e. during the warming period leading up to the MMCO at *c.* 15 Ma). This seems ecologically improbable given the broad distribution of extant *Lagarostrobos franklinii* from the lowlands to the subalpine/alpine zone in perhumid western Tasmania. Possible explanations are that the sources of *Phyllocladidites mawsonii* pollen on the Falkland Islands were now extinct, cold-demanding ecotypes or, less likely, that warming leading up to the MMCO was accompanied by a significant reduction in precipitation across the archipelago. In either case, the most probable period when *Lagarostrobos* and any other potentially tree-sized podocarps became extirpated from the Falkland Islands is the Late Miocene, a conclusion that is ecologically consistent with the earlier development of tundra on the South Shetland Islands during the Mi-1 glaciation (Warny *et al.* 2016).

Climate modelling and interpretation

Anomaly-based reconstructions of annual mean temperature and annual mean precipitation over the Falkland Islands were developed from palaeoclimate modelling scenarios of the Miocene and Oligocene generated by Farnsworth *et al.* (2019) using the HadCM3BL coupled climate model to provide further context for the palaeoflora evidence. Although the modern annual mean temperature of the Falklands is ~6°C, the reconstructed values are significantly warmer, ranging from ~12°C to 13°C in the Early to Middle Miocene (13.8–23.0 Ma), up to 14–15°C in the Late

Oligocene (23.0–27.8 Ma) and then cooler again (11–12°C) in the Early Oligocene (27.8–33.9 Ma; Supplemental Fig. 3). Precipitation varies significantly, from ~500 mm/year in the modern down to 300–400 mm/year for the Middle Miocene, becoming significantly wetter (~700–900 mm/year) in the Early Miocene (20.4–23.0 Ma) and Late Oligocene (23.0–27.8 Ma) and then trending lower again in the Early Oligocene (27.8–33.9 Ma; Supplemental Fig. 4). These patterns are consistent with a hypothesized decrease in precipitation from the Early to Middle Miocene, a possible cause of the changes in *Lagorostrobos* pollen discussed above.

We also use the temperature and precipitation climatologies to generate Köppen climate classifications for each of the Miocene and Oligocene time slices (Supplemental Fig. 5). Based on WorldClim version 2 data (Fick & Hijmans 2017), the modern Falklands climate is predominantly subpolar oceanic (Cfc), with areas of polar tundra (ET) at higher elevations. Going back in time, the Falklands are classified as predominantly cold steppe (BSk) for both the Langhian (13.8–16.0 Ma) and Burdigalian (16.0–20.4 Ma) due to relatively low precipitation and slightly warmer average temperatures. For the Aquitanian (20.4–23.0 Ma) and Chattian (23.0–27.8 Ma) the Falklands become predominantly temperate oceanic (Cfb; i.e. a similar zone to modern-day western Europe), in accordance with higher precipitation during those periods. Further back to the Rupelian (27.8–33.9 Ma) the Falklands are again dominated by cold steppe (BSk) climate.

Palaeoclimate time series for the closest grid point to *Tussac House* show summer (December–February), winter (June–August) and annual mean reconstructed temperatures and precipitation rates over the mid- to late Cenozoic (Fig. 6). These time series indicate the substantial variations in precipitation for the palaeo-reconstructions (with periods both wetter and drier than modern conditions), and the temperature reconstructions show that *Tussac House* was consistently 6–7°C warmer than modern in terms of the annual mean, and with greater seasonal variability, ranging from 6–8°C in winter to 16–18°C in summer. These climatic conditions would have been amenable for the development of the rainforest/scrub communities identified in the pollen spectra within the *Tussac House* lignite deposit.

Conclusion

The *Tussac House* deposit has a number of similarities to and differences from the West Point Island deposit that was first discovered in 1906. This study affirms that the South Atlantic region hosted diverse rainforests during the mid- to late Cenozoic period, perhaps in several episodic phases. All fossil pollen and spore assemblages (microfloras) recovered from *Tussac House* samples represent the same palaeo-community - *Nothofagus*-Podocarpaceae cool temperate rainforest or rainforest scrub - growing on the eastern Falkland Islands sometime between the Late Oligocene (maximum age limit) and the Middle Miocene (minimum age limit). In the absence of local independent age controls, these age limits rely on the time distribution of pollen from mesothermal rainforest plants found in southern Argentina, particularly *Cupanieidites reticularis* (NLR Sapindaceae tribe Cupanieae) and *Clavatipollenites glarius* (NLR *Hedyosum*). The minimum age limit is supported by palaeoclimate modelling and the absence of wind-transported pollen types from the arid-adapted steppe vegetation that developed in Argentina during the late Palaeogene-Neogene.

Acknowledgements

Special thanks to the South Atlantic Environmental Research Institute (SAERI) for facilitating this work. Thanks also to Sammy Hirtle, Daniel Ford and the construction team on the *Tussac House* site, who kindly paused their excavation to allow sampling. The authors acknowledge the facilities and the scientific and technical assistance of Microscopy Australia at the Electron Microscope Unit (EMU) within the Mark Wainwright Analytical Centre (MWAC) at UNSW Sydney. We would like to express our sincere gratitude to the two reviewers for their valuable comments and suggestions, which greatly improved the quality of this manuscript.

Financial support

This study was funded by the Australian Research Council Fellowship (DE200100907) awarded to ZAT. DKH is supported by DE220100279.

Competing interests

The authors declare none.

Author contributions

ZAT led the field expedition. ZAT, HC, CT and SC collected the samples. MM and HC undertook the Palaeogene palynostratigraphic and Quaternary pollen analyses and interpretation, respectively. DJC, HAH and KP undertook the wood analysis. DKH undertook the climate modelling. ZAT and MM drafted the manuscript, and all authors contributed to the preparation of the manuscript.

Climate data availability

The HadCM3BL climate data presented in this study were downloaded from an open access repository: https://www.paleo.bristol.ac.uk/ummodel/scripts/papers/Farnsworth_et_al_2019b.html. WorldClim version 2 climatologies were downloaded from https://www.worldclim.org/data/worldclim21.html.

Supplemental material

To view supplementary material for this article, please visit https://doi.org/10.1017/S0954102024000129.

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