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Author statements

Credit author statement:

Viviana D. Barreda: Design the manuscript and main goals, write the initial draft and coordinate the research activity. **Luis Palazzesi**: Design the manuscript and main goals, apply statistical techniques to analyze data and write the initial draft. **Roberto R. Pujana**: Reassess palaeobotanical data. **Carolina Panti**: Reassess palaeobotanical data. **Mariano Tapia**: Reassess fossil spore-pollen data. **Damián A. Fernández**: Reassess fossil spore-pollen data. **María Sol Noetinger**: Reassess fossil spore-pollen data. All authors contributed to the final version of the manuscript.

The Gondwanan heritage of the Eocene–Miocene Patagonian floras

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Abstract

The breakup of Gondwana and the associated climatic changes led to the fragmentation of floras that were once connected across the Southern lands. The diversity of the Gondwanan remnants has long been assumed to have fluctuated in Patagonia across the Cenozoic, although it has never been quantified so far. Here we address when the major floristic members of the Gondwanan legacy (*e.g.,* southern beeches, proteas, podocarps, gumtrees) expanded, contracted, or became extinct during the Patagonian biogeographic isolation (Eocene–Miocene) on the basis of the re-assessment of the fossil record (*i.e.*, woods, leaves, and spore-pollen grains). We found that the Patagonian floras experienced moderate to severe shifts in the diversity of the Gondwanan component —relative to the total flora— with the highest estimates in the late Eocene–early Oligocene (~50%) and the lowest estimates in the late Miocene (~20%) according to the fossil pollen record. The most important floristic changes include two major replacements: 1) tropical Gondwanan taxa (*e.g., Akania, Eucalyptus, Gymnostoma*) by typically cool-temperate taxa (*e.g.,* Nothofagaceae) in the Eocene, and 2) humid taxa (*e.g.,* Podocarpaceae) by arid-adapted floras, mostly of non-Gondwanan affinity, across the Miocene. The variation in diversity of the Gondwanan component from Patagonia shows a striking resemblance to that from Australia for the same period, probably indicating a global-scale driver of floristic turnover (*e.g.*, global cooling conditions). Today, the Patagonian subantarctic forests harbor only about ~15% of the Gondwanan diversity, representing a three-fold decrease from its climax in the late Eocene–early Oligocene.

Keywords: Gondwana, Diversity, Fossils, Paleoflora, Patagonia

1. **Introduction**

From the earliest days of botanical exploration in the 19th century, affinities between the living floras of the high southern continents were noticed by botanists and explorers. Joseph D. Hooker visited Australia, New Zealand, southern South America (Patagonia) and various sub-Antarctic islands on his expeditions with James Clark Ross, commanding HMS Erebus and HMS Terror, during 1839–1843. In his descriptions of the floras, Hooker recognized a close botanical affinity, even at a generic level, among the Southern lands (Brundin, 1966; Crisp et al., 1999). He also speculated that these floras —now separated by oceanic barriers— were the remains of a once more continuous tract of land (Brundin, 1966). Each of these lands developed a distinct flora when southern Gondwanan landmasses became apart from each other, yet there were similarities and parallel changes in all of their evolutionary histories.

The floras from Patagonia include today a combination of ancient dispersals and radiations of Gondwanan taxa that have persisted through drastic climatic changes since the split of southern South America from Antarctica in the Eocene. The shift towards cooler temperatures caused by the expansion of ice-sheets in Antarctica and the gradual aridification by the Andean uplift led to a major floristic change in Patagonian landscapes. The Gondwanan forests became replaced by a vast desert (*i.e.*, Patagonian steppe) during the Miocene (*e.g.*, Palazzesi et al., 2014), except in the Andean region (Fig. 1) where rainfall has been high enough to support Nothofagaceae (*Nothofagus*), Proteaceae (*Lomatia*, *Embothrium*, *Orites*), Podocarpaceae (*Podocarpus*, *Saxegothaea*), Winteraceae (*Drimys*), Gunneraceae (*Gunnera*), among other families of Australasian affinity (Veblen et al., 1996). During the Paleogene and early Neogene, however, these taxa were not only more diverse but also more widespread across southern South America. The context and timing of this large-scale floristic contraction have been relatively well studied in Patagonia on the basis of the fossil record (*e.g.*, Palazzesi et al., 2014). However, the diversity of the Gondwanan component —now represented by more than twenty plant families— have never been explored quantitatively so far; for example, we still do not fully understand when the Gondwanan component flourished or became highly reduced during the most important period of biogeographic isolation (Eocene–Miocene) in Patagonia. In this study, we re-assess the Patagonian plant fossil record (*i.e.*, woods, leaves, and spore-pollen grains) for that period to quantify the loss of the Gondwanan legacy.

2. **Materials and Methods**

We surveyed the plant fossil record for the Eocene–Miocene sedimentary units in Patagonia based on the available palynological and paleobotanical information. We examined more than 70 palynological and paleobotanical studies providing fossil data from the Eocene–Miocene of Patagonia, the southernmost region of South America, which extends between latitudes 38°S and 55°S (Fig. 1). We excluded from our analysis assemblages vaguely dated and taxa imprecisely assigned. We used the term tropical to denote those taxa growing today in the tropical terrestrial ecoregions independently of their past geographic distribution (*i.e., Cupania*, Malpighiaceae, Arecaceae). We used the term Gondwana to denote the southern part of this landmass that remains bio-geographically connected even during the early Cenozoic (*i.e.,* Australia, New Zealand, Antarctica and southern South America). In this context, we used key Gondwanan plant families (or genera) that represent typical components of extant southern forests and occur widely in the fossil record from southern Gondwana, following the criteria of Kooyman et al. (2014) and Lee et al. (2016). These are: Cyatheaceae (*Cnemidaria*, *Cyathea*), Dicksoniaceae (*Dicksonia*, *Lophosoria*), Lygodiaceae (*Lygodium*), Araucariaceae, Podocarpaceae (*e.g.*, *Podocarpus*, *Lagarostrobos*, *Dacrycarpus*, *Dacrydium*), Cupressaceae, Aextoxicaceae, Akaniaceae (*Akania*), Atherospermataceae (*Laurelia*), Casuarinaceae (*Casuarina*, *Gymnostoma*), Cunoniaceae (including Eucryphiaceae), Gunneraceae (*Gunnera*), Lauraceae, Myrtaceae (*e.g.*, *Eucalyptus*), Nothofagaceae (*Nothofagus*), Onagraceae (*Fuchsia*), Paracryphiaceae (*Quintinia*), Proteaceae (*e.g.*, *Embothrium*), and Winteraceae (*Drimys*). Apart from these genera/families we also included Osmundaceae (*Todea*), Gomortegaceae (*Gomortega*), and Ripogonaceae (*Ripogonum*).

We quantified the floristic response of the Gondwanan component in the context of the major global climatic events for the Eocene–Miocene. For that, we selected seven temporal phases: 1) **Phase 1** (*ca*. 52–48 Ma) with the Early Eocene Climatic Optimum (EECO); 2) **Phase 2** (*ca*. 48–38 Ma) with the Middle Eocene Climatic Optimum (MECO); 3) **Phase 3** (*ca*. 38–28 Ma) with the late Eocene presence of ephemeral Antarctic ice-sheets and early Oligocene Glaciation; 4) **Phase 4** (*ca*. 28–23 Ma) with the late Oligocene warming; 5) **Phase 5** (*ca*. 23–16 Ma) with the Early Miocene Glaciation; 6) **Phase 6** (*ca*. 16–12 Ma) with the Mid-Miocene Climatic Optimum; 7) **Phase 7** (*ca*. 12–6 Ma) with the establishment of the Late Miocene Antarctic ice-sheet, and the Andean uplift (Fig. 1). We stratigraphically arranged the Patagonian fossil records of the selected taxa within these seven phases (Tables 1 and 2). In these tables, we documented the first appearance of some Gondwanan taxa even after the split of Patagonia from the remaining southern Gondwanan landmasses (post-Eocene event). These records must be either due to a detection issue (*e.g.,* reappearance from refugia or Lazarus taxa) or arrival via long-distance dispersal from Australasia. Moreover, given the spatial and temporally coverage of our dataset is not uniform, our phases can potentially be biased towards a particular floristic type.

We estimated “within-flora floristic diversity” as the percent of the Gondwanan species relative to the diversity of total flora of each phase, following Lupia et al. (1999). We plotted this “within-flora floristic diversity” as spindle diagrams using the ggplot2 package (Wickham, 2011), in R Software, version 3.6.1 (R Core Team, 2019), on the basis of the spore-pollen records. Macrofossil data complement the palynological evidence at a number of sites. For comparison purposes, we estimated within-flora diversity from Australia based on the same Gondwanan components and time (Eocene–Miocene). For these Australian estimates, we used the spore-pollen database provided by Kooyman et al. (2014, Supplementary Data 2), with additional information from Phase 1 (Carpenter et al., 2012) and Phase 7 (Martin, 1990; Macphail and Truswell, 1993).

3. **Results**

We compiled a matrix including 82 fossil-species of pollen and spores, 102 of leaves, 2 of fruit, and 34 of woods assigned to Gondwanan taxa across the Eocene–Miocene (Tables 1 and 2). A list of the selected formations along with the temporal constraint of the fossil-bearing sediments is also given in Tables 1 and 2. We found that the percentages of the major groups of plants (*i.e.*, angiosperms, gymnosperms and ferns), with few exceptions, remain relatively constant across the selected phases (Fig. 2, Table 3). However, the Gondwanan component, with several diversifications as well as extinctions, underwent evident shifts across the selected phases (Fig. 3, Table 4, Supplementary Tables 1 and 2):

1) Phase 1 (early Eocene, ~52–48 Ma): Moderate diversity of Gondwanan components (~35% of the total flora diversity, Fig. 3, Table 4). This is widely considered to represent a period of high moisture and warm climates under which rainforests flourished in Patagonia (Wilf et al., 2003, 2005). Fossils show floristic links to Australasian floras, with most taxa representing groups now associated with subtropical or tropical environments. Among these, we emphasize the occurrence of

angiosperms (*Gymnostoma* (Casuarinaceae), *Akania* (Akaniaceae), and *Ceratopetalum* (Cunoniaceae)) and gymnosperms (*Acmopyle* (Podocarpaceae), *Retrophyllum* (Podocarpaceae), *Agathis* (Araucariaceae), and *Papuacedrus* (Cupressaceae)) that have largely been recorded in this phase (Tables 1, 2). *Nothofagus* was a minor component in the vegetation. Gondwanan ferns are diverse, with the occurrence of *Dicksonia* (Dicksoniaceae) and *Todea* (Osmundaceae), among others.

2) Phase 2 (middle Eocene, ~48–38 Ma): Moderate diversity of Gondwanan components (~34% of the total flora diversity, Fig. 3, Table 4). Since the middle Eocene, the onset of a long-term global cooling was widely identified, although some short periods of greenhouse conditions (*i.e.*, Mid Eocene Climatic Optimum or MECO) occurred. A major floristic replacement of the Gondwanan elements took place, largely because of the rise to dominance of Nothofagaceae (with at least three subgenera, *i.e.*, *Fuscospora*, *Lophozonia* and *Nothofagus*) and the demise of several previously recognized genera (*e.g.*, *Gymnostoma*, *Akania*, *Ceratopetalum*) distributed today in (sub)tropical Australasia (Tables 1 and 2). This has traditionally been linked to the onset of global cooling conditions, although tropical species still occurred (*e.g.*, malpighs, Cupanieae (Sapindaceae)) even at the highest Patagonian latitudes.
3) Phase 3 (late Eocene–early Oligocene, ~38–28 Ma): Highest diversity of Gondwanan components (~50% of the total flora diversity, Fig. 3, Table 4). A global climatic shift occurred near the Eocene–Oligocene boundary with the first glaciation in Antarctica. The global cooling trend appears to have pushed tropical elements northwards and favored the dispersion of some cool-tolerant floras. Paleofloras became represented by a large percentage of Gondwanan angiosperms (~40%, Fig. 2, Table 3). Among

these, Nothofagaceae and Proteaceae were the most diverse families during this phase (Tables 1 and 2). *Drimys* (Winteraceae) is recorded for the first time.

4) Phase 4 (late Oligocene, ~28–23 Ma): Moderate diversity of Gondwanan components (~33% of the total flora diversity, Fig. 3, Table 4). A global warming pulse during the late Oligocene promoted the expansion of tropical elements (*e.g.*, Cupanieae (Sapindaceae), Malpighiaceae, Arecaceae) while Gondwanans became reduced in diversity. However, there are important occurrences of some typically Gondwanan genera such as *Laurelia* (Atherospermataceae) and *Gillbeea* (Cunoniaceae) (Table 2). The Australasian *Quintinia* (Paracryphiaceae) occurred for the first time in this phase and persisted until the late Miocene in Patagonia (Table 1). Among gymnosperms, we detected the first appearances of fossils assigned to the South American *Saxegothaea* and the Australasian *Phyllocladus*, both of the Podocarpaceae.
5) Phase 5 (early Miocene, ~23–16 Ma): Moderate diversity of Gondwanan components (~29% of the total flora diversity, Fig. 3, Table 4). The climatic consequences triggered by the early Miocene Antarctic glaciation and the Andean uplift have both led to major floristic turnovers. First records of specimens assigned to Aextoxicaceae (Table 2), a common family in the subantarctic forest in southern South America. The diversity of the most common Gondwanan families continued to be high across Patagonia (*e.g*., Myrtaceae, Proteaceae, Nothofagaceae), although the fragmentation of forests became evident as patches of open vegetation began to develop (Barreda and Palazzesi, 2014). The gymnosperms *Araucaria* and Cupressaceae (probably related to the South American *Austrocedrus*) frequently occurred while the dry-intolerant *Microcachrys* became extinct during this phase (Table 1).
6) Phase 6 (middle Miocene, ~16–12 Ma): Moderate diversity of Gondwanan components (~25% of the total flora diversity, Fig. 3, Table 4). The Mid Miocene

Climatic Optimum interrupted the long-term cooling trend of the Neogene. A number of important wet-demanding Gondwanan taxa became extinct from Patagonian landscapes such as the podocarps *Phyllocladus*, *Lagarostrobos*, *Dacrycarpus* and *Dacrydium* (Table 1). Angiosperms became highly reduced, including Proteaceae, Myrtaceae, and Nothofagaceae. The retraction of these Gondwanan elements occurred concomitantly with the expansion of tropical (*e.g.*, *Cupania* (Sapindaceae), *Alchornea* (Euphorbiaceae)) and arid-adapted (*e.g.*, Asteraceae, Amaranthaceae) families (Palazzesi and Barreda, 2012).

7) Phase 7 (late Miocene, ~12–6 Ma): Low presence of Gondwanan components (~18% of the total flora diversity, Fig. 3, Table 4). During this phase, the establishment of the Antarctic ice-sheet and the Andean uplift both promoted increasing cooling and aridity across eastern Patagonia. The majority of the key Gondwanan taxa became locally extinct from non-Andean Patagonia including humid-demanding ferns (Dicksoniaceae, Cyatheaceae) as well as Myrtaceae and Proteaceae (Table 1). Gondwanan forest became highly fragmented during this phase while arid-adapted taxa dominated the assemblages (Palazzesi and Barreda, 2004; Barreda et al., 2008).

4. **Discussion**

Patagonia began to break from its closest Gondwanan landmass (Antarctica) during the Eocene (Scher and Martin, 2006), leading to the fragmentation of biotas that were once connected across the southern lands. Since then, the composition of the Gondwanan floristic remnants fluctuated in Patagonia across the Cenozoic. Here we quantified the timing of the main Gondwanan floristic turnovers (expansion, contraction or extinction) following the major climatic phases recognized during and after the break up of Antarctica from southern

South America. Although the Paleogene marks the onset of the paleogeographic isolation of Patagonia from Antarctica, there were frequent long-distance dispersal events from Australasia even during the Neogene (Renner et al., 2010).

Periods of global cooling have been traditionally associated with the increasing diversity of Gondwanan components in the fossil record (Romero, 1993). This is partly because some plant species occurred in Antarctica during the Late Cretaceous (*e.g.,* Nothofagaceae, Podocarpaceae) and flourished in South America simultaneously with the oldest Antarctic glaciation in the late Eocene–earliest Oligocene. However, the Gondwanan component also includes a number of taxa today restricted to tropical regions of Australasia; for example, *Agathis* (Araucariaceae), *Papuacedrus* (Cupressaceae), *Ceratopetalum* (Cunoniaceae), *Gymnostoma* (Casuarinaceae), *Akania* (Akaniaceae), *Todea* (Osmundaceae) occur today in New Guinea, New Caledonia and other low-latitude regions. These taxa were common in Patagonia during the early Eocene (Phase 1), supporting the equable climatic context independently inferred from other proxy data (Huber and Caballero, 2011), yet they disappeared shortly afterwards. Other Gondwanan elements more frequently associated with temperate climates (*e.g*., Nothofagaceae) took over, even though the climatic context appears not to have changed dramatically. The sudden diversification of Nothofagaceae during Phase 2 played a role in the reduction of some Gondwanan taxa; members of this family, once established and diversified, tend to form a continuous monospecific canopy and probably competitively excluded other well-represented plant species, as postulated by Australia (Macphail et al., 1994). Overall, we do detect a major floristic replacement from Phase 1 to Phase 2 (Tables 1, 2), although Gondwanan diversity remains quite steady (Fig. 3) probably because extinctions and diversifications may have been balanced.

The establishment of ice sheets in Antarctica and the drop in the concentration of carbon dioxide led to a global climatic cooling at about 34 Ma (Phase 3) (Carter et al., 2017). This context favored the representation of cool-temperate tolerant Gondwanan families (*e.g.*, Nothofagaceae, Proteaceae, Winteraceae), which peaked in diversity during this phase, while non-Gondwanan tropicals (*e.g.*, palms, juglans of the subfamily Engelhardioideae) dispersed northwards. Whereas the increase in diversity of the Gondwanan component can be partly an artifact because of the fewer palynological/paleobotanical data from the late Eocene and early Oligocene, there is a widespread belief that this expansion across Patagonia was a real phenomenon. The fossil record from Australia, with a comparatively higher study effort, witnessed a similar increasing trend in the Gondwanan component, even peaking at our Phase 3 (Fig. 4, Supplementary Table 3), as we will discuss later on. Subsequent global warming pulses (*i.e.*, Phase 4) promoted the immigration of Neotropical elements from low to high South American latitudes; the tropical Gondwanans no longer dispersed from Australasia via Antarctica due to the presence of physical barriers.

From the Miocene, a progressively cool-temperate and dryer scenario (Herbert et al., 2016) began to establish (Phases 5 to 7). These conditions forced the major geographic restriction, or even extinction, of some typically temperate Gondwanan forest components. Among the most reduced Gondwanan members in Patagonia, we highlight the Podocarpaceae and Nothofagaceae. These key Gondwanan lineages share a comparable evolutionary history in Patagonia; this is understandable if we assume that both families also share a comparable eco-physiological response in this region, growing in areas that typically receive high amounts of rainfall. Both Podocarpaceae and Nothofagaceae include taxa with characteristic fossil morphologies that can be easily distinguished from each other (Fig. 5). We detected a zenith of Podocarpaceae diversity during the Paleogene (particularly from Phases 1 to 4) with the presence of *Microcachrys*, *Dacrydium*, *Dacrycarpus*, *Phyllocladus*, *Lagarostrobos*, *Podocarpus* and *Saxegothaea*. Most of them became gradually extinct during the Miocene (Phases 6 and 7) except *Podocarpus* and *Saxegothaea*, which still occur today, although highly reduced geographically in Patagonia, confined only to the subantarctic forests. Most of the fossil morphotypes of Nothofagaceae are detected in the Paleogene (Phases 2 to 4) and the initial part of the Neogene (Phase 5), assigned to the four extant subgenera (*i.e.*, *Fuscospora*, *Brassospora*, *Lophozonia*, *Nothofagus*). The subgenus *Brassospora* is restricted today to tropical Australasia (*i.e.*, New Guinea, New Caledonia). It appears to have been present in Patagonia (*Nothofagidites dorotensis*, Dettmann et al., 1990), occurring sparsely in the palynological record until Phase 6 (Fig. 3, Table 1). However, neither fossil woods nor leaves of this subgenus have been recorded so far (Pujana et al., in press). Among the Nothofagaceae occurring today in the region, the subgenus *Nothofagus* is the most widespread with five species (*N. antarctica, N. pumilio, N. betuloides, N. nitida*, *N. dombeyi*) while the subgenus *Lophozonia* includes two species (*N. glauca*, *N. oblicua*), all of them distributed in the subantarctic forests in Patagonia. The subgenus *Fuscospora*, represented by only one species in South America (*N. alessandrii*), is restricted to central Chile. The Proteaceae, Winteraceae, and Araucariaceae, also became reduced during and after Phase 7 along with those two previously mentioned Gondwanan families (Podocarpaceae and Nothofagaceae). All these families occurred as isolated forest patches across Patagonia during the late Miocene, yet they became restricted to the slopes of the Andean Mountains in western Patagonia sometime during the Pliocene. This retraction mirrored the expansion of arid-adapted floras (*e.g.*, Amaranthaceae, Ephedraceae, Asteraceae), largely caused by the Andean uplift (Blisniuk et al., 2005). The gradual retraction of the Gondwanan component across the Miocene, as previously pinpointed, appears to have occurred not only in Patagonia; using the same approach, we found that the diversity of Gondwanan components shows a striking resemblance between Patagonia and Australia (Figs. 3, 4). According to our comparison, this trend appears to have taken place more or less synchronously, with the zenith (Phase 3) and the impoverishment (Phase 7) of the Gondwanan component occurring at the same time. Gondwanan diversity estimates from Australia exceed those from Patagonia across the Eocene–Miocene, probably as a result of the higher diversity of Gondwanan plant families in the Australian fossil record (*e.g.*, Proteaceae (~30 fossil-species), Myrtaceae (~15 fossil-species)), which could also be strengthened by an increased sampling effort.

The diversity of the Gondwanan component, as we quantitatively assessed, became highly fragmented and reduced in Patagonia during the last 50 Ma. Today, the Patagonian subantarctic forests harbor only about ~15% of the Gondwana diversity in the pollen assemblages (Vilanova et al., 2019), representing a three-fold decrease in diversity from its climax in the early Oligocene. Improved conservation and management measures will be required to meet the challenge of preserving this heritage for future generations.

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Figure legends

Figure 1. Location map with selected paleobotanical and palynological sites used for each phase. **Phase 1**: **1**- Huitrera Fm. (Laguna del Hunco locality, Chubut Province), **2**- Huitrera Fm. (Nahuel Huapi Este/Pampa de Jones locality, Neuquén Province), **3-** Arroyo Lyn Fm. (Chubut Province), **4-** Ligorio Márquez Fm. (Santa Cruz Province). **5**- La Barca Fm. (Tierra del Fuego Province). **6-** Punta Torcida Fm.(Tierra del Fuego Province). **Phase 2**, **7-** Huitrera Fm. (Confluencia locality, Neuquén Province), **8-** Huitrera Fm. (Río Pichileufú locality, Río Negro Province), **9-** Río Turbio Fm., Lower member (Santa Cruz Province). **Phase 3**, **10**- Río Turbio Fm., Upper member (Santa Cruz Province). **11**- Sloggett Fm. (Tierra del Fuego Province), **12**- "Estratos Ea. La Correntina" (Tierra del Fuego Province). **13**- Puesto San José Fm. (Tierra del Fuego Province). **14**- Loreto Fm. (Chile). **Phase 4**, **15**- San Julián Fm. (Santa Cruz Province), **16**- "Margosa Inferior" (Aries well, Tierra del Fuego continental platform). **Phase 5**, **17**- Lileo Fm. (Neuquén Province), **18**- Río Foyel Fm. (Neuquén Province). **19-** Ñirihuau Fm. (Río Negro Province), **20**- Chenque Fm., Sequences I and II (Chubut Province), **21**- "Sierra La Colonia" outcrops (Chubut Province), **22**- Gaiman Fm. (Chubut Province), **23-** Río Guillermo Fm. (Santa Cruz Province), **24**- Río Leona Fm. (Santa Cruz Province), **25-** Mina Chilena Fm. (Chile), **26-** Chichinales Fm. (Río Negro Province), **27-** Rancahué Fm. (Neuquén Province), **28-** Monte León Fm. (Santa Cruz Province), **29**- Centinela Fm. (Santa Cruz Province), **30**- El Chacay Fm. (Santa Cruz Province), **31**-Carmen Silva (Tierra del Fuego), **32**- Cullen Fm. (Tierra del Fuego Province). **Phase 6**, **33**- Salto del Macho Fm. (Neuquén Province), **34**- Collón Cura Fm. (Neuquén Province), **35**- Chenque Fm. Sequences III to V (Chubut Province), **36-** Río Correntoso Fm. (Santa Cruz Province), **37-** Santa Cruz Fm. (Santa Cruz Province), **38-** Arroyo de los Ciervos strata (Santa Cruz Province). **Phase 7**, **39**- Barranca Final Fm. (Río Negro Province), **40**- Puerto Madryn Fm. (Chubut Province).

Figure 2. Plots showing changes in diversity of major Gondwanan and non-Gondwanan plant groups (ferns, gymnosperms, angiosperms) through time (Table 3). Note the peak in diversity of Gondwanan angiosperms in Phase 3, and the marked decrease of all Gondwanan groups towards the latest phases.

Figure 3. Spindle diagram showing diversity fluctuations of the Gondwanan component — relative to the total flora— through the seven temporal phases (1 to 7) in Patagonia (Tables 1, 4 and Supplementary Table 1). The top of the diagram represents the recent diversity of the Gondwanan components in the Patagonian subantarctic forest (Vilanova et al., 2019).

Figure 4. Spindle diagram showing diversity fluctuations of the Gondwanan component — relative to the total flora— through the seven temporal phases (1 to 7) in Australia (Supplementary Table 3). Note the resemblance with the Patagonian trend in diversity (Fig. 3). This analysis was based on the spore-pollen database of Kooyman et al. (2014, Data Supplement S2), with additional information for Phase 1 (Carpenter et al., 2012) and Phase 7 (Martin, 1990; Macphail and Truswell, 1993).

Figure 5. Selected spore-pollen grains (A–H), leaves (I–L) and wood remains (M–O) of Gondwanan fossil species from Patagonia. A- *Araucariacites australis* (*Araucaria*, Araucariaceae), B- *Cyatheacidites annulatus* (*Lophosoria*, Dicksoniaceae), C- *Granodiporites nebulosus* (*Embothrium*, Proteaceae), D- *Myrtaceidites verrucosus* (Myrtaceae), E- *Nothofagidites acromegacanthu*s (*Nothofagus*, Nothofagaceae), F- *Phyllocladidites mawsonii* (*Lagarostrobos*, Podocarpaceae), G- *Propylipollis pseudomoides* (*Lomatia*, Proteaceae), H- *Pseudowinterapollis couperi* (*Drymis*, Winteraceae), I- *Araucaria paraaraucana* (*Araucaria*, Araucariaceae), Fig. J- *Elatocladus* sp. (Podocarpaceae), Fig. K- **Embotriophyllum* sp. (Proteaceae), Fig. L- *Nothofagus subferruginea* (*Nothofagus*, Nothofagaceae), M- *Myrceugenellites oligocenicum* (*Luma*, Myrtaceae), N-*Nothofagoxylon*

scalariforme (*Nothofagus* (*Nothofagus*), Nothofagaceae), O- *Scalarixylon grandiradiatum* (Proteaceae). Fig. A, J–K, M–O, from the Rio Leona Fm. (early Miocene, Phase 5); Figs. B, E, F and H, from the Chenque Fm. (early–middle Miocene Phases 5, 6); Figs. C, D and G, from the Río Turbio Fm. (middle–late Eocene, Phases 2, 3); Fig. I, from the Sloggett Fm. (late Eocene–early Oligocene, Phase 3), Fig. L, from the Río Turbio Fm. upper section (late Eocene, Phase 3). Scale from Figs. A–H: 10 µm; Figs. I, K–L: 1 cm; Fig. J: 0.5 cm; Figs. M–O: 500 µm. *Ambiguous assignment.

Tables

Table 1. Temporal distribution of the selected fossil key Gondwanan spore pollen species (or genera), across the seven temporal phases: **Phase 1**, Huitrera Fm.: Nahuel Huapi Este/Pampa de Jones locality, Neuquén Province (Melendi et al., 2003; Wilf et al., 2010); Laguna del Hunco locality, Chubut Province (Barreda et al., 2020). Ligorio Márquez Fm., Santa Cruz Province (Macphail et al., 2013). La Barca Fm., Tierra del Fuego Province (Quattrocchio, 2017). Punta Torcida Fm., Tierra del Fuego Province (Quattrocchio, 2017). **Phase 2**, Huitrera Fm.: Confluencia locality, Neuquén Province (Melendi et al., 2003; Báez et al., 1991); Río Pichileufú locality, Río Negro Province (Barreda et al., 2010). Río Turbio Fm. Lower member, Santa Cruz Province (Archangelsky 1972; Romero 1977; Romero and Zamaloa, 1985; Fernández 2018; Fernández et al., 2012). **Phase 3**, Río Turbio Fm. Upper member, Santa Cruz Province (Archangelsky 1972; Romero 1978; Romero and Zamaloa, 1985; Fernández 2018; Fernández et al., 2012). Sloggett Fm., Tierra del Fuego Province (Olivero et al., 1998). “Estratos Ea. La Correntina”, Tierra del Fuego Province (Rossello et al., 2004). Puesto San José Fm., Tierra del Fuego Province (Quattrocchio, 2017). Loreto Fm., Chile (Fasola, 1969). **Phase 4**, San Julián Fm., Santa Cruz Province (Barreda, 1997c; Barreda and Palamarczuk, 2000b; Náñez et al., 2009; Heredia et al., 2012). “Margosa Inferior” Aries well,

Tierra del Fuego continental platform (Palamarczuk and Barreda, 2000). **Phase 5**, Lileo Fm., Neuquén Province (Leanza et al., 2002). Río Foyel Fm., Neuquén Province (Barreda et al., 2003; Quattrocchio et al., 2012). Chenque Fm. Sequences I and II, Chubut Province (Barreda, 1993, 1996, 1997a, b). “Sierra La Colonia” outcrops, Chubut Province (Archangelsky and Zamaloa, 2014). Gaiman Fm., Chubut Province (Palazzesi, 2008). Río Leona Fm., Santa Cruz Province (Barreda et al., 2009). Monte León Fm., Santa Cruz Province (Barreda and Palamarczuk, 2000a). Centinela Fm., Santa Cruz Province (Guerstein et al., 2004). El Chacay Fm., Santa Cruz Province (Tapia, 2019). Cullen Fm., Tierra del Fuego Province (Vergel and Durango de Cabrera, 1988; Zamaloa and Romero, 1990, 2005; Zetter et al., 1999; Zamaloa, 2000, 2004). **Phase 6**, Salto del Macho Fm., Neuquén Province (Cornou, 2012, Cornou et al., 2012, 2014 —age assignment based on Bechis et al., 2014—). Collon Cura Fm., Neuquén Province (Baldoni, 1987 —age assignment based on Bechis et al., 2014—). Chenque Fm. Sequences III to V, Chubut Province (Barreda, 1993, 1996, 1997a, b). **Phase 7**, Barranca Final Fm., Río Negro Province (Palazzesi et al., 2014). Puerto Madryn Fm., Chubut Province– (Barreda et al., 2008; Palazzesi and Barreda, 2004; Palazzesi, 2008; Palazzesi et al., 2014). Black circle: presence, White circle: absence. *Haloragacidites harrisii* (=*Haloragacidites trioratus*). *Ambiguous assignment.

Table 2. Temporal distribution of the selected fossil key Gondwanan leaf and wood species (or genera), across the seven temporal phases: **Phase 1**, Huitrera Fm.: Nahuel Huapi Este/Pampa de Jones locality, Neuquén Province (Wilf et al., 2010) and Laguna del Hunco locality, Chubut Province (Berry, 1925; Carvalho et al., 2010, 2013; Carpenter et al., 2014; González et al., 2007; Hermsen et al., 2012; Knight and Wilf, 2013; Pujana et al., 2020a; Rossetto-Harris et al., 2020; Wilf et al., 2009, 2014, 2017; Wilf, 2012, 2020; Zamaloa et al., 2006). Arroyo Lyn Fm., Chubut Province (Pujana et al., 2018). Ligorio Márquez Fm., Argentina/Chile (Carpenter et al., 2018; Troncoso et al., 2002). **Phase 2,** Huitrera Fm: Río

Pichileufú locality, Río Negro Province (Berry, 1938; González et al., 2007; Rossetto-Harris et al., 2020; Wilf et al., 2009, 2017; Wilf, 2020). Río Turbio Fm. Lower Member, Santa Cruz Province (Hünicken, 1967; Panti, 2010, 2014, 2018, 2019; Pujana and Ruiz, 2019; Vento and Prámparo, 2018). **Phase 3,** Río Turbio Fm. Upper member, Santa Cruz Province (Panti, 2010, 2014, 2018, 2019; Pujana and Ruiz, 2019; Vento and Prámparo, 2018). Slogget Fm., Tierra del Fuego Province (Panti et al., 2008). Loreto Fm., Chile (Dusén, 1899; Ohsawa et al., 2016; Otero et al., 2012; Terada et al., 2006a). **Phase 5,** Ñirihuau Fm.: Pico Quemado locality, Río Negro Province (Frenguelli, 1943; González et al., 2007; Caviglia and Zamaloa, 2014). Río Guillermo Fm., Santa Cruz Province (Panti, 2011; Pujana, 2008; Vento et al., 2016). Río Leona Fm., Santa Cruz Province (Césari et al., 2015; Pujana 2007, 2008, 2009a, 2009b); Mina Chilena Fm., Chile (Boureau and Salard, 1960; Nishida et al., 1988, 1989; Salard, 1961; Terada et al., 2006b). Chichinales Fm., Río Negro Province (Ragonese, 1977). Rancahué Fm., Neuquén Province (Brea et al., 2015). Carmen Silva locality, Tierra del Fuego Province (Caviglia, 2017); Cullen Fm., Tierra del Fuego Province (Caviglia, 2019). **Phase 6,** Río Correntoso Fm., Santa Cruz Province (Pujana et al, 2020b). Santa Cruz Fm., Santa Cruz Province (Brea et al., 2012). Arroyo de los Ciervos strata, Santa Cruz Province (Pujana et al., 2015). **Phase 7**, no megafossil record. Black circle: presence, White circle: absence, Dashed-line: non applicable. *Ambiguous assignment.

Table 3. Diversity estimates of the major Gondwanan plant groups (Ferns, Gymnosperms, Angiosperms) relative to the total flora for each temporal phase from Patagonia (Table 1, Supplementary Table 1).

Table 4. Gondwanan diversity estimates relative to the total flora for each temporal phase in the Eocene–Miocene from Patagonia (Table 1, Supplementary Table 1).

Supplementary Table 1. Combined list of palynomorph species (total flora) used in the estimations of Gondwanan diversity for each temporal phase. *Stereisporites antiquasporites* (=*Cingutriletes australis*), *Haloragacidites harrisii* (=*Haloragacidites trioratus*). Species authorities in Table 1 and Supplementary Table 2. *Ambiguous assignment.

Supplementary Table 2. Complete list of palynomorph species (plus Gondwanan megafossils) used in the present work for each sedimentary unit (for references see captions of Tables 1 and 2). Locality numbers of the sampling units as in Fig. 1. *Stereisporites antiquasporites (=Cingutriletes australis), Haloragacidites harrisii* (=*Haloragacidites trioratus*). *Ambiguous assignment.

Supplementary Table 3. Gondwanan diversity estimates relative to the total flora for each temporal phase in the Eocene–Miocene from Australia. This analysis was based on the spore-pollen database of Kooyman et al. (2014, Data Supplement S2), with additional information for Phase 1 (Carpenter et al., 2012) and Phase 7 (Martin, 1990; Macphail and Truswell, 1993). We selected the same Gondwanan taxa used in the diversity analysis from Patagonia. TAS = Tasmania.

Phases	Phase 1	Phase 2	Phase 3	Phase 4	Phase 5	Phase 6	Phase 7
% Ferns over total flora of each phase	24.7	22.6	23.6	30.1	26.9	31.1	9.9
% Gymnosperms over total flora of each phase	17.2	10.5	13.6	12.3	11.3	11.8	9.9
% Angiosperms over total flora of each phase	58.1	66.9	62.7	57.7	61.8	57.0	80.3
% Gondwanan ferns over total ferns	21.7	13.3	11.5	12.2	16.0	11.9	0.0
% Gondwanan gymnosperms over total gymnosperms	93.7	92.9	93.3	85.0	85.7	81.2	71.4
% Gondwanan angiosperms over total gymnosperms	22.2	31.5	40.6	33.0	25.2	23.4	15.8

Phases	Phase 1	Phase 2	Phase 3	Phase 4	Phase 5	Phase 6	Phase 7
% Ferns over total flora of each phase	24.7	22.6	23.6	30.1	26.9	31.1	9.9
% Gymnosperms over total flora of each phase	17.2	10.5	13.6	12.3	11.3	11.8	9.9
% Angiosperms over total flora of each phase	58.1	66.9	62.7	57.7	61.8	57.0	80.3

Botanical affinities and Patagonian Gondwanan fossils				**Phases**											
Extant Divisions/Families/Genus/Species		**Fossil species**		Phase 1		Phase 2		Phase 3		Phase 4		Phase 5		Phase 6	
		Leaf	Wood	Leaf	Wood	Leaf	Wood	Leaf	Wood	Leaf	Wood	Leaf	Wood	Leaf	Wood
Pteridophyta [monilophytes] [Subclass Polypodiidae]															
Dicksoniaceae	*Dicksonia*	*Dicksonia* sp. in Carvalho et al. 2013		●	—	○	—	○	—	○	—	○	—	○	—
Osmundaceae	*Todea*	*Todea amissa* Carvalho et al. 2013		●	—	○	—	○	—	○	—	○	—	○	—
Gymnospermophyta [Subclass Pinidae]															
Araucariaceae	*Araucaria*	*Araucaria paraaraucana* Panti et al. 2007		○	—	○	—	●	—	○	—	○	—	○	—
	Araucaria	*Araucaria* cf. *A. pichileufensis* Wilf et al. 2010		●	—	○	—	○	—	○	—	○	—	○	—
	Araucaria	*Araucaria huncoensis* Rossetto-Harris 2020		●	—	○	—	○	—	○	—	○	—	○	—
	Araucaria	*Araucaria pichileufensis* Berry 1938		○	—	●	—	○	—	○	—	○	—	○	—
	Araucaria	*Araucaria nathorstii* Dusén 1899		○	—	○	—	●	—	○	—	○	—	○	—
	Araucaria	*Araucaria sp.* in Ohsawa et al. 2016		○	—	○	—	●	—	○	—	○	—	○	—
	Araucaria	*Araucarites alatisquamosus* Ohsawa et H. Nishida 2016		○	—	○	—	●	—	○	—	○	—	○	—
	Araucaria		*Araucaria marenssii* Brea et al. 2012	—	○	—	○	—	○	—	○	—	●	—	○
	Araucaria		*Araucarioxylon kellerense* Lucas and Lacey 1981	—	●	—	○	—	○	—	○	—	●	—	○
	Araucaria		*Araucarioxylon pichasquense* Torres and Rallo 1981	—	●	—	○	—	●	—	○	—	●	—	○
	Araucaria		*Agathoxylon* cf. *antarcticus* (Poole and Cantrill 2001) Pujana et al. 2014	—	○	—	○	—	●	—	○	—	○	—	○
	Araucaria		*Agathoxylon* sp. in Pujana et al. 2015	—	○	—	○	—	○	—	○	—	○	—	●
	Agathis	*Agathis zamunerae* Wilf et al. 2014		●	—	●	—	○	—	○	—	○	—	○	—
Podocarpaceae	*Dacrycarpus*	*Dacrycarpus puertae* Wilf 2012		●	—	○	—	○	—	○	—	○	—	○	—
	Dacrycarpus	*Dacrycarpus* sp. in Panti et al. 2008		○	—	○	—	●	—	○	—	○	—	○	—
	Dacrycarpus	*Dacrycarpus chilensis* (Engelhardt) Wilf nov. comb. 2012		●	—	○	—	○	—	○	—	○	—	○	—
	Podocarpus	*Podocarpus andiniformis* Berry 1938		●	—	○	—	○	—	○	—	○	—	○	—
	Podocarpus	*Podocarpus* sp. in Wilf et al. 2010		○	—	○	—	○	—	○	—	●	—	○	—
	Rethrophyllum	*Retrophyllum oxyphyllum* (Freng. and Parodi) Wilf comb. nov. 2020		●	—	●	—	○	—	○	—	○	—	○	—

	gen. indet.	*Elatocladus* sp. in Césari et al. 2015		○	—	○	—	○	—	○	—	●	—	○	—
	gen. indet.	Podocarpaceae indet in Wilf et al. 2010		●	—	○	—	○	—	○	—	○	—	○	—
	gen. indet.	Podocarpaceae indet in Otero et al. 2012		○	—	○	—	●	—	○	—	○	—	○	—
		Podocarpaceae indet. in Panti el al. 2008		○	—	○	—	●	—	○	—	○	—	○	—
	gen. indet.	*Coronelia molinae* Florin 1940		●	—	○	—	○	—	○	—	○	—	○	—
	basal		*Phyllocladoxylon antarcticum* Gothan 1908	—	●	—	●	—	●	—	○	—	○	—	○
	gen. indet.		*Podocarpoxylon* sp. in Pujana et al. 2018	—	○	—	●	—	○	—	○	—	●	—	○
	gen. indet.		*Podocarpoxylon/Phyllocladoxylon* sp. in Pujana and Ruiz 2017	—	●		○	—	○	—	○	—	○	—	○
	extinct		*Protophyllocladoxylon francisiae* Pujana et al. 2014	—	●	—	○	—	●	—	○	—	○	—	○
Cupressaceae	*Papuacedrus*	*Papuacedrus prechilensis* (Berry) Wilf et al. 2009		●	—	●	○	—	○	—	○	—	○	—	○
Magnoliophyta [Subclass Monocotyledoneae]															
Ripogonaceae	*Ripognum*	*Ripogonum americanum* Carp, Wilf, Conran and Cúneo 2014		●	—		○	—	○	—	○	—	○	—	○
Magnoliophyta [Subclass Magnoliidae]															
Aextoxicaceae	*Aextoxicon*		*Aextoxicoxylon haramburi* Nishida et al. 1988	—	○	—	○	—	○	—	○	—	●	—	○
Akaniaceae	*Akania*	*Akania patagonica* Gandolfo et al. 1988		●	—	○	—	○	—	○	—	○	—	○	—
	Akania	*Akania americana* Romero and Hickey 1976		●	—	○	—	○	—	○	—	○	—	○	—
	Akania *		*Akanioxylon santacrucensis* Brea et al. 2017	—	○	—	○	—	○	—	○	—	○	—	●
Atherospermataceae	*Laurelia*		*Laurelites doroteansis* Nishida et al. 1988	—	○	—	○	—	○	—	○	—	●	—	○
	gen. indet.	*Atherospermophyllum guinazui* (Berry) C.L. Knight 2013		●	—	○	—	○	—	○	—	●	—	○	—
	*Daphnandra**	cf. *Daphnandra* sp. in Troncoso et al. 2002		●	—	○	—	○	—	○	—	○	—	○	—
Casuarinaceae	*Gymnostoma*	*Gymnostoma patagonicum* (Frenguelli) comb. nov. Zamaloa 2006		●	—	○	—	○	—	○	—	○	—	○	—
	Gymnostoma	*Gymnostoma archangelsky* Zamaloa and Romero 2006		●	—	○	—	○	—	○	—	○	—	○	—
	Gymnostoma	*Gymnostoma argentinum* Zamaloa and Gandolfo 2006		●	—	○	—	○	—	○	—	○	—	○	—
Cunoniaceae	*Ceratopelalum*	*Ceratopetalum edgardoromeroi* Gandolfo and Hermsen 2016		●	—	○	—	○	—	○	—	○	—	○	—

	Weinmania		*Weinmanioxylon multiperforatum* Petriella 1972	—	○	—	○	—	○	—	○	—	●	—	○
	Weinmania		cf. *Weinmannioxylon* in Pujana and Ruiz 2019	—	●	—	○	—	○	—	○	—	○	—	○
	Eucryphia		*Eucryphiaceoxylon eucryphioides* (Poole et al.) Poole et al. 2003	—	○	—	○	—	○	—	○	—	●	—	○
	gen. indet.		*Caldcluvioxylon torresiae* Pujana and Ruiz 2019	—	○	—	●	—	○	—	○	—	○	—	○
Gomortegaceae	*Gomortega*		*Gomortegoxylon patagonicum* Nishida et al. 1989	—	○	—	○	—	○	—	○	—	○	—	○
Lauraceae	*Acrodiclidium*	*Acrodiclidium flavianum* Hünicken 1967		○	—	●	—	○	—	○	—	○	—	○	—
	Camphoromoea	*Camphoromoea speciosa* Engelhardt 1891		●	—	○	—	○	—	○	—	○	—	○	—
	Goeppertia	*Goeppertia ovalifolia* Engelhardt 1891		●	—	○	—	○	—	○	—	○	—	○	—
	Notaphoebe	*Notaphoebe neogaea* Berry 1938		●	—	○	—	○	—	○	—	○	—	○	—
	Ocotea	*Ocotea menendezi* Hünicken 1967		○	—	●	—	○	—	○	—	○	—	○	—
	Ocotea	*Ocotea* sp. in Hünicken 1967		○	—	●	—	○	—	○	—	○	—	○	—
	gen. indet.	*Laurophyllum* sp. in Césari et al. 2015		○	—	○	—	○	—	○	—	●	—	○	—
	gen. indet.	*Laurophyllum* sp. 1 in Panti 2018		○	—	●	—	●	—	○	—	○	—	○	—
	gen. indet.	*Laurophyllum* sp. 2 in Panti 2018		○	—	●	—	○	—	○	—	○	—	○	—
	gen. indet.	*Laurophyllum* sp. 3 in Panti 2018		○	—	○	—	●	—	○	—	○	—	○	—
	gen. indet.	*Laurophyllum* sp. 4 in Panti 2018		○	—	●	—	●	—	○	—	○	—	○	—
	gen. indet.	*Laurophyllum* sp. 5 in Panti 2018		○	—	●	—	○	—	○	—	○	—	○	—
	gen. indet.	*Laurophyllum* sp. 6 in Panti 2018		○	—	●	—	○	—	○	—	○	—	○	—
	gen. indet.	*Laurophyllum* sp. 7 in Panti 2018		○	—	●	—	○	—	○	—	○	—	○	—
	gen. indet.	Lauraceae indet. 1 in Troncoso et al. 2002		●	—	○	—	○	—	○	—	●	—	○	—
	gen. indet.	Lauraceae indet. 2 in Troncoso et al. 2002		●	—	○	—	○	—	○	—	○	—	○	—
	gen. indet.	Lauraceae indet. 3 in Troncoso et al. 2002		○	—	○	—	○	—	○	—	○	—	●	—
	gen. indet.	Lauraceae sp. 1 in Carpenter et al. 2012		●	—	○	—	○	—	○	—	○	—	○	—
	gen. indet.	Lauraceae sp. 2 in Carpenter et al. 2012		●	—	○	—	○	—	○	—	○	—	○	—
	gen. indet.	Lauraceae sp. 3 in Carpenter et al. 2012		●	—	○	—	○	—	○	—	○	—	○	—
	Persea	*Persea* sp. in Troncoso et al. 2002		○	—	●	—	○	—	○	—	○	—	○	—

	Persea	*Persea* sp. in Vento and Prámparo 2018		○	—	○	—	●	—	○	—	○	—	○	—
	Persea		*Paraperseoxylon* sp. in Brea et al. 2012	—	—	—	○	—	○	—	○	—	●	—	○
	gen. indet.		*Laurinoxylon atlanticum* Brea et al. 2012	—	○	—	○	—	○	—	○	—	●	—	○
Monimiaceae	gen. indet.	*Monimiophyllum callidentatum* Knight and Wilf 2013		●	—	○	—	○	—	○	—	○	—	○	—
Myrtaceae	*Eugenia*	*Eugenia rioturbioensis* Hünicken 1967		○	—	●	—	●	—	○	—	○	—	○	—
	Eugenia	*Eugenia* sp. 1 in Panti 2014		○	—	●	—	○	—	○	—	○	—	○	—
	Eugenia	*Eugenia* sp. 2 in Panti 2014		○	—	●	—	●	—	○	—	○	—	○	—
	Eugenia	*Eugenia comparabilis* Hollick 1924		○	—	○	—	○	—	○	—	●	—	○	—
	Myrcia	*Myrcia bagualensis* (Dusén) Hünicken 1967		○	—	●	—	●	—	○	—	●	—	○	—
	Myrcia	*Myrcia deltoidea* (Berry) González 2009		○	—	●	—	○	—	○	—	○	—	○	—
	Myrcia	*Myrcia* cf. *reticulato-venosa* Engelhardt 1891		●	—	●	—	○	—	○	—	○	—	○	—
	Myrcia	*Myrcia chubutensis* Berry 1938		○	—	○	—	○	—	○	—	●	—	○	—
	Myrcia	*Myrcia* sp. in Hünicken 1967		○	—	○	—	○	—	○	—	●	—	○	—
	Myrcia	*Myrcia nitens* Dusén 1899		○	—	○	—	○	—	○	—	●	—	○	—
	Myrciaria	*Myrciaria acuminata* Engelhardt 1891		○	—	○	—	○	—	○	—	●	—	○	—
	Myrcianthes	*Myrcianthes* sp. in Panti 2014		○	—	●	—	○	—	○	—	○	—	○	—
	Psidium	*Psidium araciformis* Berry 1938		○	—	●	—	○	—	○	—	○	—	○	—
	Psidium	*Psidium* sp. in Panti 2014		○	—	●	—	●	—	○	—	○	—	○	—
	Eucalyptus	*Eucalyptus frenguelliana* Gandolfo and Zamaloa 2012		●	—	○	—	○	—	○	—	○	—	○	—
	Eucalyptus	*Eucalyptus lynchiae* Gandolfo and Hermsen 2012		●	—	○	—	○	—	○	—	○	—	○	—
	Eucalyptus	*Eucalyptus caldericola* Hermsen, Gandolfo and Zamaloa 2012		●	—	○	—	○	—	○	—	○	—	○	—
	Eucalyptus	*Eucalyptus* sp. in Panti 2014		○	—	●	—	●	—	○	—	○	—	○	—
	gen. indet.	*Myrtiphyllum* sp. in Césari et al. 2015		○	—	○	—	○	—	○	—	●	—	○	—
	gen. indet.	*Myrtiphyllum bagualense* Dusén 1899		○	—	○	—	○	—	○	—	●	—	○	—
	gen. indet.	Myrtaceae sp. in Panti et al. 2008		●	—	○	—	●	—	○	—	○	—	○	—
	Myrceugenia		*Myrceugenia chubutense* Ragonese 1980	—	○	—	○	—	○	—	○	—	●	—	○
	Luma		*Myrceugenellites oligocenum*	—	○	—	○	—	○	—	○	—	●	—	○

			Pujana 2009												
	gen. indet.		*Myrceugenlellites maytenoides* Nishida et al. 1988	—	○	—	○	—	○	—	○	—	●	—	○
	gen. indet.		*Myrceugenelloxylon pseudoapiculatum* Nishida 1981	—	○	—	○	—	○	—	○	—	●	—	○
Nothofagaceae	*N. Fuscospora*	*Nothofagus subferruginea* (Dusén) Tanai 1986		○	—	●	—	●	—	○	—	●	—	○	—
	N. Fuscospora	*Nothofagus dicksonii* (Dusén) Tanail 1986		○	—	○	—	●	—	○	—	●	—	●	—
	N. Fuscospora	*Nothofagus* sp. cf. *N. dicksonii* Vento and Prámparo 2018		○	—	○	—	●	—	○	—	○	—	○	—
	N. Fuscospora	*Nothofagus* sp. aff. *N. alessandri* Panti 2019		○	—	○	—	●	—	○	—	○	—	○	—
	N. Fuscospora		*Nothofagoxylon ruei* Salard 1961	—	○	—	○	—	○	—	○	—	●	—	○
	N. Fuscospora		*Nothofagoxylon boureaui* Salard 1961	—	○	—	○	—	○	—	○	—	●	—	○
	N. Nothofagus	*Nothofagus simpliciedens* Dusén 1899		○	—	●	—	●	—	○	—	●	—	●	—
	N. Nothofagus	*Nothofagus variablilis* Dusén 1899		○	—	○	—	●	—	○	—	●	—	●	—
	N. Nothofagus	*Nothofagus serrulata* Dusén 1899		○	—	○	—	○	—	○	—	●	—	●	—
	N. Nothofagus	*Nothofagus crenulata* Dusén 1899		○	—	○	—	○	—	○	—	●	—	●	—
	N. Nothofagus		*Nothofagoxylon scalariforme* Gothan 1908	—	○	—	○	—	●	—	○	—	●	—	●
	N. Lophozonia	*Nothofagus magelhaenica* (Engelhardt) Dusén 1899		○	—	●	—	●	—	○	—	●	—	●	—
	N. Lophozonia	*Nothofagus* cf. *N. obliqua* Panti 2019		○	—	○	—	●	—	○	—	○	—	○	—
	N. Lophozonia	*Nothofagus elongata* Dusén emend Romeron and Dibbern 1997		○	—	●	—	●	—	○	—	●	—	●	—
	N. Lophozonia		*Nothofagoxylon kraeuselii* Boureau and Salard 1960	—	○	—	○	—	○	—	○	—	●	—	○
	N. Lophozonia		*Nothofagoxylon triseriatum* Torres and Lemoigne 1988	—	○	—	○	—	○	—	○	—	●	—	○
	N. Lophozonia		*Nothofagoxylon aggregatum* Pujana 2009	—	○	—	○	—	○	—	○	—	●	—	○
	N. Lophozonia		*Nothofagoxylon menendezii* Ragonese 1977	—	○	—	○	—	○	—	○	—	●	—	○
	N. extinct	*Nothofagus* sp. in Panti et al. 2008		○	—	○	—	●	—	○	—	○	—	○	—
	N. extinct	*Nothofagus densinervosa* Dusén 1899		○	—	○	—	○	—	○	—	●	—	●	—
	N. extinct	*Nothofagus australis* Dusén 1899		○	—	○	—	○	—	○	—	○	—	●	—
	N. extinct	Nothofagaceae indet. 1 in Pujana et al. 2015		○	—	○	—	○	—	○	—	○	—	●	—

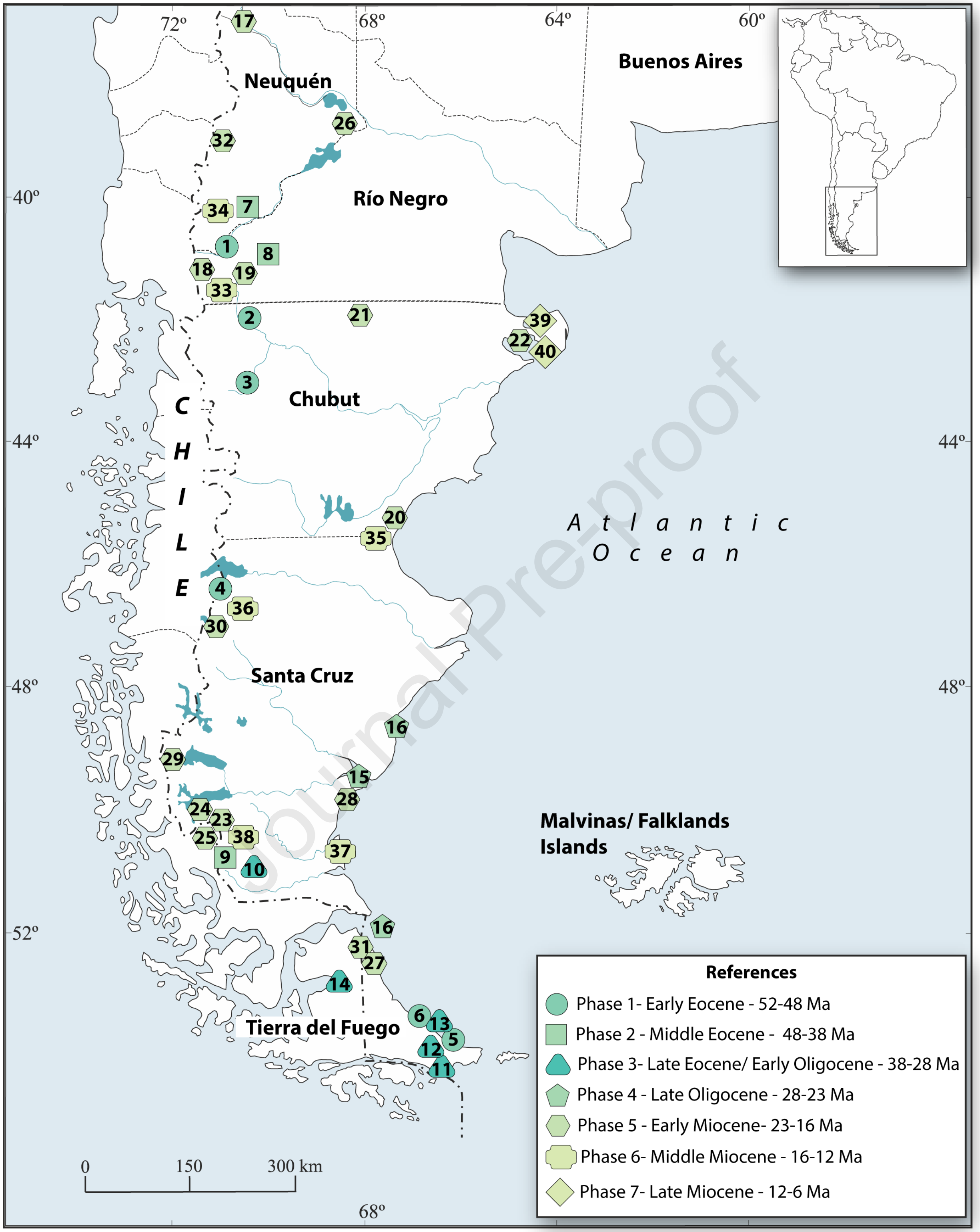
	N. extinct	Nothofagaceae indet. 2 in Pujana et al. 2015		○	—	○	—	○	—	○	—	○	—	●	—
	N. extinct	Nothofagaceae indet. 3 in Pujana et al. 2015		○	—	○	—	○	—	○	—	○	—	●	—
	N. extinct	Nothofagaceae indet. 4 in Pujana et al. 2015		○	—	○	—	○	—	○	—	○	—	●	—
	N. extinct	Nothofagaceae indet. 5 in Pujana et al. 2015		○	—	○	—	○	—	○	—	○	—	●	—
	Carpolithus	*Carpolithus* sp. (fruit) in Césari et al. 2015		○	—	○	—	○	—	○	—	●	—	○	—
Proteaceae	*?Embothrium**	*Embothriophyllum* sp. in Césari et al. 2015		○	—	○	—	○	—	○	—	●	—	○	—
	*?Embotrhium**	?*Embotrhium pregrandiflorum* Berry 1938		○	—	●	—	○	—	○	—	○	—	○	—
	*?Embotrhium**	?*Embotrhium precoccineum* Berry 1938		○	—	●	—	○	—	○	—	○	—	○	—
	*?Embotrhium**	*Embothriophyllum dubium* Dusén 1899		○	—	○	—	●	—	○	—	○	—	○	—
	*Roupala**	*Roupala patagonica* Durango de Cabrera and Romero 1988		●	—	○	—	○	—	○	—	○	—	○	—
	Orites	*Orites bivascularis* (fruit) (Berry) Romero et al. 1988		●	—	○	—	○	—	○	—	○	—	○	—
	Lomatia	*Lomatia preferruginea* Berry 1938		●	—	○	—	○	—	○	—	○	—	○	—
	Lomatia	*Lomatia occidentalis* (Berry) Frenguelli 1943		●	—	○	—	○	—	○	—	○	—	○	—
	Lomatia	*Lomatia patagonica* Frenguelli 1943		○	—	○	—	○	—	○	—	●	—	○	—
	gen. indet.		*Scalarixylon romeroi* Pujana and Ruiz 2019	—	○	—	○	—	●	—	○	—	○	—	○
	gen. indet.		*Scalarixylon grandiradiatum* Pujana 2007	—	○	—	○	—	○	—	○	—	●	—	○
	gen. indet.		*Scalarixylon patagonicum* Pujana 2007	—	○	—	○	—	○	—	○	—	●	—	○

Botanical affinities and Patagonian gondwanan fossils			**Phases**						
Extant Divisions/Families/Genus/Species		**Fossil species**	Phase 1	Phase 2	Phase 3	Phase 4	Phase 5	Phase 6	Phase 7
Pteridophyta [monilophytes] [Subclass Polypodiidae]									
Cyatheaceae	*Cnemidaria*	*Kuylisporites waterbolkii* Potonie 1956	○	●	○	○	●	○	○
	Cyathea	*Cyathidites australis* Couper 1953	●	●	●	●	●	●	○
	Cyathea	*Cyathidites paleospora* (Martin) Alley and Broadbridge 1992	●	○	○	●	●	○	○
	Cyathea	*Cyathidites subtilis* Stover and Partridge 1973	○	○	○	○	●	○	○
Dicksoniaceae	*Dicksonia*	*Ischyosporites areapunctatis* (Stuchlik) Barreda 1997	●	○	●	●	●	●	○
	Dicksonia	*Trilites tuberculiformis* Cookson emend. Dettmann1963	●	○	●	●	●	●	○
	Lophosoria quadripinnata	*Cyatheacidites annulatus* Cookson 1947	○	●	●	●	●	●	○
Lygodiaceae	*Lygodium*	*Verrucosusporites kopukuensis* (Couper) Stover 1973	○	○	○	●	●	●	○
	Lygodium	*Crassiretitriletes vanraadshoovenii* Germeraad et al. 1968	○	●	●	○	○	○	○
Osmundaceae	*Todea*	*Todisporites major* Couper 1958	●	○	○	○	○	○	○
Gymnospermophyta [Subclass Pinidae]									
Araucariaceae	*Araucaria*	*Araucariacites australis* Cookson 1947	●	●	●	●	●	●	●
	Agathis	*Dilwynites granulatus* Harris 1965	●	○	○	○	○	○	○
	Agathis	*Dilwynites* cf. *tuberculatus* Harris 1965	●	○	○	○	○	○	○
Cupressaceae	gen. indet.	*Inaperturopollenites hiatus* Thomson and Pflug 1953	○	○	○	●	●	●	○
Podocarpaceae	*Dacrycarpus*	*Dacrycarpites australiensis* Cookson and Pike 1953	●	●	●	●	●	●	○
	Dacrydium	*Lygistepollenites florinii* (Cookson and Pike) Stover and Evans 1973	●	●	●	●	●	●	○
	Lagarostrobos franklinii	*Phyllocladidites* sp.	○	○	○	○	●	○	○
	Lagarostrobos franklinii	*Phyllocladidites mawsonii* Cookson 1947 ex Couper 1953	●	●	●	●	●	●	○
	Lagarostrobos	*Phyllocladidites verrucosus* (Cookson) Stover and Evans 1973	○	○	●	●	○	○	○
	Microcachrys	*Microcachryidites antarcticus* Cookson 1947	●	●	●	●	●	○	○
	*Microcachrys?**	*Trisaccites microsaccatum* (Couper) Couper 1960	●	●	●	●	●	○	○

	Saxegothaea	*Inaperturopollenites* sp.	○	○	○	●	●	●	●
	Podocarpus	*Podocarpidites elegans* Romero 1977	●	●	●	●	●	●	●
	Podocarpus	*Podocarpidites ellipticus* Cookson 1947	●	●	●	●	●	○	●
	Podocarpus/Prumnopitys	*Podocarpidites marwickii* Couper 1953	●	●	●	●	●	●	○
	Podocarpus	*Podocarpidites magnus* Romero 1977	●	●	○	○	○	○	○
	Podocarpus	*Podocarpidites microreticuloidatus* Cookson 1947	●	●	●	●	●	●	○
	Podocarpus	*Podocarpidites rugulosus* Romero 1977	●	●	●	●	●	●	●
	Podocarpus	*Podocarpidites exiguus* Harris 1965	○	○	●	●	●	○	○
	Podocarpus	*Gamerroites psilasaccus* (Archangelsky and Romero) Archangelsky 1988	●	●	●	●	●	●	○
	Phyllocladus	*Microalatidites paleogenicus* (Cookson and Pike) Mildenhall and Pocknall 1989	○	○	○	●	●	●	○
	gen. indet.	*Trichotomosulcites subgranulatus* Archangelsky 1973	○	○	○	●	●	○	○
Magnoliophyta [Subclass Magnoliidae]									
Casuarinaceae	*Gymnostoma/Casuarina*	*Haloragacidites harrisii* (Couper) Harris 1971	●	●	●	○	●	●	○
Cunoniaceae	*Eucryphia*	*Dicolpopollis* sp. 1 in Fernández 2018	○	●	●	○	○	○	○
	Gillbeea	*Concolpites leptos* Stover and Partridge 1973	○	○	○	●	○	○	○
	Weinmania	*Tricolpites communis* Archangelsky 1973	○	○	○	○	●	○	○
	Weinmania	*Tricolporites* sp. 2 in Barreda et al. 2020	●	○	○	○	○	○	○
Gunneraceae	*Gunnera*	*Tricolpites reticulatus* Cookson 1947	○	●	●	●	●	●	○
Myrtaceae	Myrteae	*Myrtaceidites verrucosus* Partridge 1973	○	●	●	●	●	●	○
	Myrtoideae	*Myrtaceidites eucaliptoides* Cookson and Pike 1954	○	○	●	○	○	○	○
	Myrtoideae	*Myrtaceidites mesonesus* Cookson and Pike 1954	○	●	●	●	○	○	○
	Myrtoideae	*Myrtaceidites parvus* Cookson and Pike 1954	○	●	●	○	○	●	○
	gen. indet.	*Myrtaceidites* sp.	●	○	○	●	●	●	○
Nothofagaceae	*Nothofagus (Brassospora?*)*	*Nothofagidites dorotensis* Romero 1973	○	●	●	●	●	●	○
	Nothofagus (Fuscospora)	*Nothofagidites saraensis* Menéndez and Caccavari 1975	●	●	●	●	●	●	●
	Nothofagus (Lophozonia)	*N. americanus* Zamaloa 1992	○	●	●	●	●	●	○
	Nothofagus (Lophozonia)	*N. tehuelchesii* Zamaloa and Barreda 1992	○	●	●	●	●	●	○
	Nothofagus (Nothofagus)	*Nothofagidites flemingii* (Couper) Potonié 1960	●	●	●	●	●	○	○

	Nothofagus (Nothofagus)	*Nothofagidites waipawaensis* (Couper) Fasola 1969	○	○	●	●	●	○	○
	Nothofagus (Nothofagus)	*Nothofagidites fortispinulosus* Menéndez and Caccavari 1975	●	●	●	○	○	●	○
	Nothofagus (Nothofagus)	*Nothofagidites rocaensis* Romero 1973	○	●	●	●	●	○	○
	Nothofagus (Nothofagus)	*Nothofagidites* sp. aff. *Nothofagus dombeyi* (Mirb.) Oerst.	○	○	○	○	●	○	●
	Nothofagus (Nothofagus)	*Nothofagidites* sp.	●	○	○	○	○	○	○
	Nothofagus extinct	*Nothofagidites acromegacanthus* Menéndez and Caccavari 1975	○	●	●	●	●	●	●
	*Nothofagus*extinct	*Nothofagidites anisoechinatus* Menéndez and Caccavari 1975	○	○	○	●	●	●	○
	Nothofagus extinct	*Nothofagidites fuegiensis* Menéndez and Caccavari 1975	○	○	●	●	●	●	○
	Nothofagus extinct	*Nothofagidites kaitangataensis* (Te Punga) Romero 1973	○	○	○	●	○	○	○
	Nothofagus extinct	*Nothofagidites nanus* Romero 1977	○	●	●	●	○	○	○
Onagraceae	*Fuschia*	*Diporites aspis* Pocknall and Mildenhall 1984	●	○	○	●	●	○	○
	Fuchsia	*Crassiorites australis* Zamaloa and Romero 1990	○	○	○	○	●	○	○
	*Fuchsia?**	*Corsinipollenites atlantica* Barreda 1997	○	●	○	●	●	●	●
	*Fuchsia?**	*Corsinipollenites* sp.	○	○	○	○	●	○	○
Paracryphiaceae	*Quintina*	*Quintiniapollis striatulosa* Barreda 1997	○	○	○	●	●	●	●
Proteaceae	*Beauprea*	*Peninsulapollis gillii* (Cookson) Dettmann and Jarzen 1988	●	●	●	●	○	○	○
	Franklandia, Aulax, Placospermun	*Cranwellipollis* sp. A in Fernández 2018	○	●	○	○	○	○	○
	Proteoidea not Leucadendrae	*Lewalanipollis senectus* Dettmann and Jarzen 1996	○	●	●	○	○	○	○
	Embothrium	*Granodiporites nebulosus* Stover and Partridge 1973	○	●	●	●	●	●	○
	Embothrium	*Propylipollis ambiguus* (Stover) Dettmann and Jarzen 1996	○	●	○	●	○	○	○
	Bleasdalea, Hicksbeachia	*Propylipollis reticuloscabratus* (Harris) Martin and Harris 1974	○	●	●	○	○	○	○
	Lomatia, Gevuina	*Propylipollis pseudomoides* (Stover) Dettmann and Jarzen 1996	●	●	●	●	●	○	○
	Xylomelum, Lambertia	*Propylipollis annularis* (Cookson) Martin and Harris 1974	○	●	○	○	○	○	○
	gen. indet.	*Propylipollis concretus* (Harris) Martin and Harris 1974	○	●	○	○	○	○	○

	gen. indet.	*Propylipollis rynthius* (Stover and Partridge) Quattrocchio and Ruiz 2009	○	○	○	●	●	○	○
	gen. indet.	*Propylipollis* sp.	●	○	○	○	○	○	○
	Agastachys, Telopea	*Proteacidites obscurus* Cookson 1950	○	●	●	●	●	○	○
	gen. indet.	*Proteacidites rectus* Pocknall and Mildenhall 1984	○	●	●	○	○	○	○
	gen. indet.	*Proteacidites parvus* Cookson 1950	○	○	○	●	○	○	○
	gen. indet.	*Proteacidites tenuiexinus* Stover 1973	○	○	○	●	○	○	○
	gen. indet.	*Proteacidites subscabratus* Couper 1960	○	●	●	●	●	○	○
	cf. *Orites*	*Proteacidites* sp. 1 in Olivero et al. 1998	○	○	●	●	●	○	○
	gen. indet.	*Proteacidites* sp.	●	○	●	○	●	●	●
Winteraceae	*Drymis*	*Pseudowinterapollis couperi* Krutzsch emend. Mildenhall 1979	○	○	●	●	●	●	●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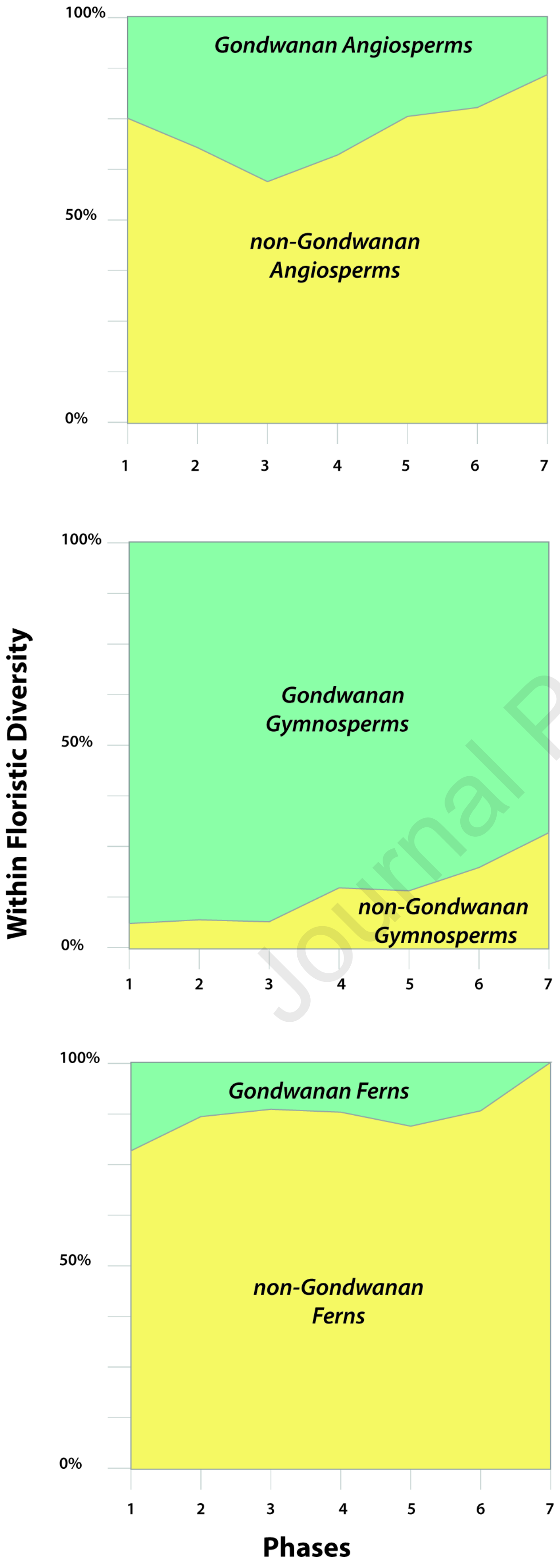
References
Phase 1- Early Eocene - 52-48 Ma
Phase 2 - Middle Eocene - 48-38 Ma
Phase 3- Late Eocene/ Early Oligocene - 38-28 Ma
Phase 4 - Late Oligocene - 28-23 Ma
Phase 5 - Early Miocene- 23-16 Ma
Phase 6- Middle Miocene - 16-12 Ma
Phase 7- Late Miocene - 12-6 Ma


100%
50%
0%
Gondwanan Angiosperms
non-Gondwanan Angiosperms
1
2
3
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5
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7
100%
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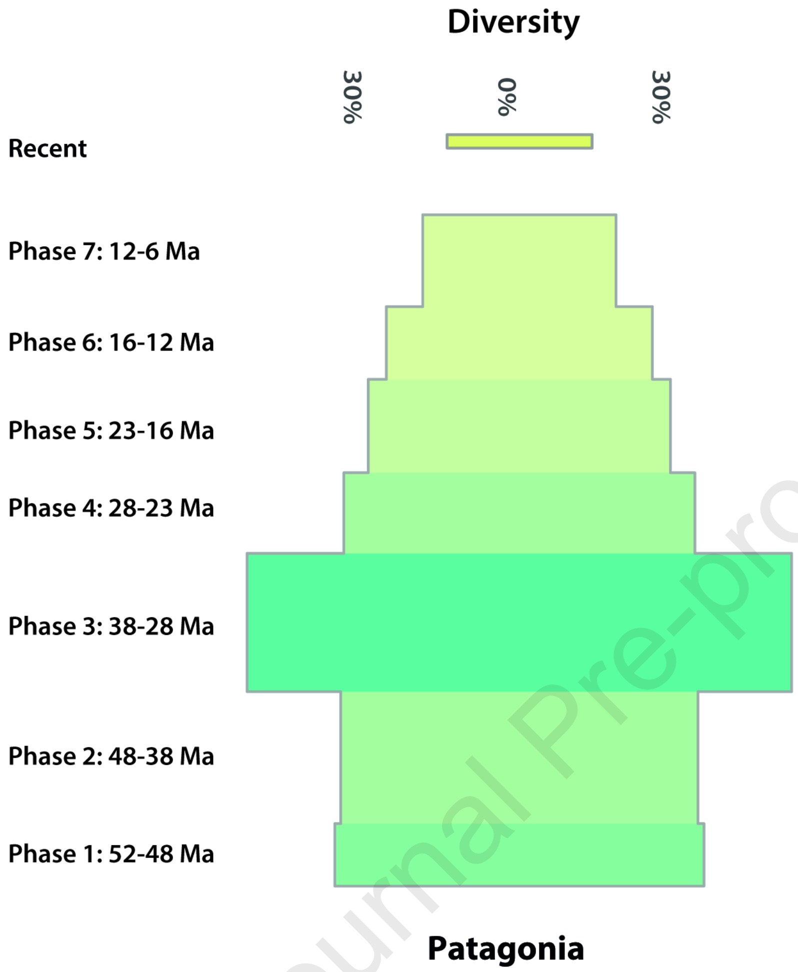
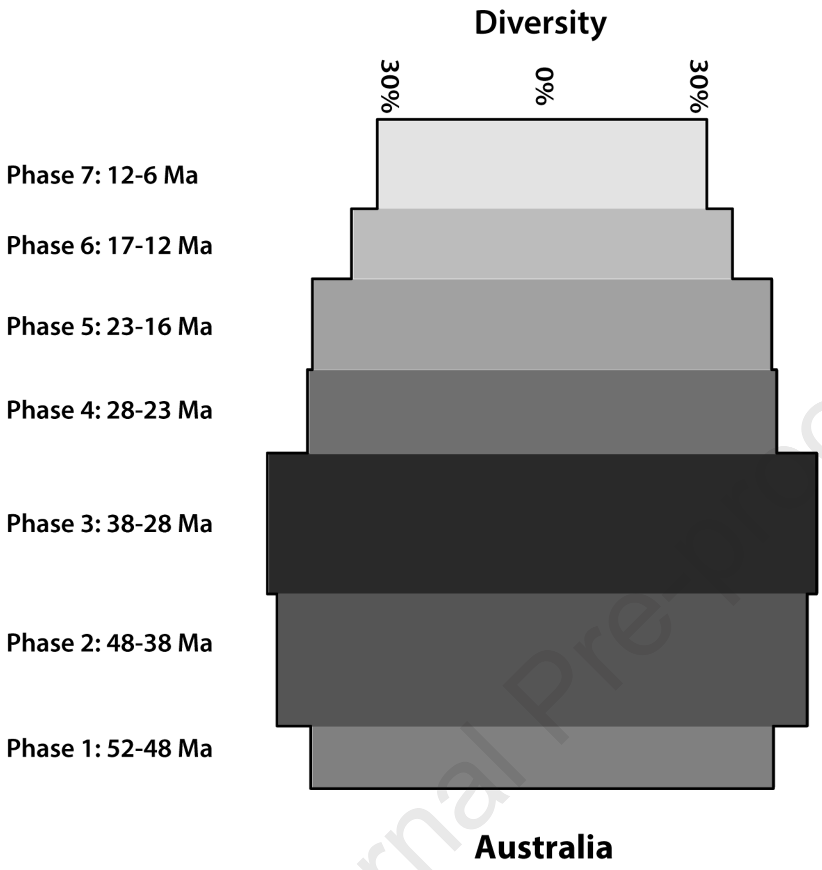
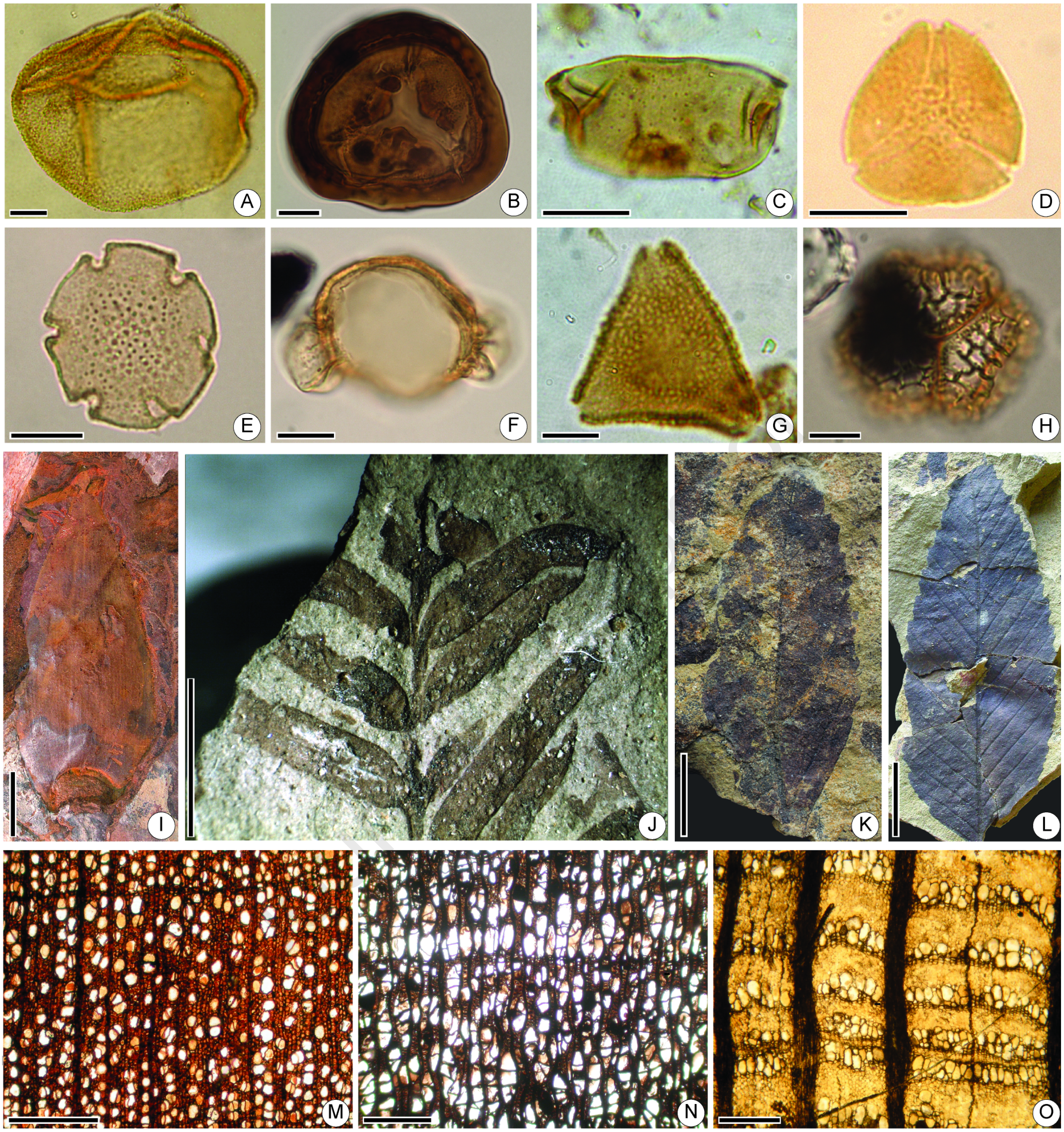
Gondwanan Gymnosperms
non-Gondwanan Gymnosperms
1
2
3
4
5
6
7
100%
50%
0%
Gondwanan Ferns
non-Gondwanan Ferns
1
2
3
4
5
6
7
Within Floristic Diversity
Phases


Diversity
30%
0%
30%
Recent
Phase 7: 12-6 Ma
Phase 6: 16-12 Ma
Phase 5: 23-16 Ma
Phase 4: 28-23 Ma
Phase 3: 38-28 Ma
Phase 2: 48-38 Ma
Phase 1: 52-48 Ma
Patagonia


Diversity
30%
0%
30%
Phase 7: 12-6 Ma
Phase 6: 17-12 Ma
Phase 5: 23-16 Ma
Phase 4: 28-23 Ma
Phase 3: 38-28 Ma
Phase 2: 48-38 Ma
Phase 1: 52-48 Ma
Australia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Highlights

Address the Eocene–Miocene expansion/contraction of Gondwanan plants in Patagonia

Found the highest diversity estimates of Gondwanans in the Eocene/Oligocene (~50%)

Found the lowest diversity estimates of Gondwanans in the late Miocene (~20%)

Today, the Patagonian subantarctic forests harbor only ~15% of the Gondwanan diversity

Declaration of interests

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

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