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Comprehensive survey of Early to Middle Triassic Gondwanan floras reveals under-representation of plant–arthropod interactions

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Plants and arthropods are primary drivers of terrestrial ecosystem function. Trace fossils of plant–arthropod interactions (PAIs) provide a unique window into assessing terrestrial ecosystem states through geological time and evaluating changes in herbivorous arthropod feeding guilds in the wake of global biotic crises. The end-Permian event (EPE; c. 252 Ma) resulted in the loss of keystone plant species from humid tropical and high-latitude ecosystems and the extinction of several major insect groups. The subsequent Early to Middle Triassic evinced diminished terrestrial productivity, punctuated by a series of second-order biotic crises that hindered recovery. Here, we survey records of Gondwanan Early to Middle Triassic floral assemblages for evidence of PAIs as an indication of ecosystem recovery following the EPE. We compiled a comprehensive dataset of fossil plant taxa and PAIs for lower Mesozoic strata of Gondwana, revealing an increase in specific and generic floral diversity from the Early to Middle Triassic. We noted a lack of PAIs reported from many localities with abundant fossil leaves, which might be interpreted to be a consequence of a post-EPE delay in the recovery of arthropod feeding guilds compared to the flora. However, by comparing floral assemblages between regions of Gondwana, our results also partly attribute the absence of PAIs to the relative paucity of palaeoichnological and palaeobotanical studies of this interval. To test for potential under-reporting of PAIs in the Triassic, we present a case study of the well-described Australian Middle Triassic Benolong Flora. In contrast to existing Australian Early to Middle Triassic PAI reports on only three plant specimens, this systematic investigation revealed 44 PAI traces comparable to published examples, hosted by 40 fossil plant fragments (7.77% of fragments assessed; $N = 591$). Margin-feeding traces constituted the dominant Functional Feeding Group (FFG) identified (23 examples: 3.72% of fragments assessed). Our review highlights several Early and Middle Triassic Gondwanan plant fossil-rich successions and existing collections that require further

examination. We predict that investigations of these assemblages will greatly elucidate the relationships between rapidly changing environments during the Early and Middle Triassic and their effects on the plant and arthropod communities in the Southern Hemisphere.

KEYWORDS

End-Permian extinction, fossil, Gondwana, palaeobotany, palaeoecology, plant-herbivore interactions, post-extinction recovery, Triassic

1 Introduction

1.1 Plant–arthropod interactions in the fossil record

Plants (c. 380,000 extant species; [Christenhusz and Byng, 2016](#)) and terrestrial arthropods (c. 7 million extant species; [Stork, 2018](#)) constitute the most significant proportion of the lower trophic levels on which all higher levels of life on land depend, with their interactions playing a crucial role in terrestrial ecosystem nutrient cycling. Understanding and quantifying the relationships between arthropods and the plants with which they are associated can, therefore, be used to indicate the condition and evolution of terrestrial ecosystems ([Labandeira, 2013](#)). Today, arthropods can be observed directly interacting with plant organs, and specialized associations between particular plant and arthropod taxa can be identified. In fossil plant assemblages, traces of herbivory (consumption of live plant tissue), detritivory (feeding on dead tissues) and oviposition (egg-laying) left on or within plant organs provide evidence of fundamental behavioral interactions that formed the basis of ancient terrestrial food webs and ecosystem function ([Labandeira and Currano, 2013](#)).

Plant–arthropod interactions (PAIs), captured as trace fossils on plant tissues, record behaviors of arthropods that may not be deducible from their body fossils. Moreover, plants are relatively common in the fossil record and an arthropod may interact with many plants during its lifetime. So, the likelihood of a plant fragment exhibiting a PAI being preserved is greater than the likelihood of preserving an arthropod body fossil. Consequently, PAIs are important indicators of the richness and abundance of arthropods and herbivore guilds present in an ancient ecosystem ([Labandeira and Wappler, 2023](#)). Furthermore, fossil leaves are utilized in many palaeoecological studies as they are consistently more abundant and widespread than most other plant organs, such as wood and seeds and, therefore, provide more accessible records ([Wilf, 2008](#)). Morphological deterrents against arthropod herbivory, such as spines and hairs, have a much higher potential for preservation in the fossil record than chemical defenses. Their presence on plant fossils is evidence that arthropod interactions provided sufficient evolutionary pressure on plant taxa to favor

selection of those plants investing resources in physical defenses ([War et al., 2018](#)).

Although detritivory is interpreted to have occurred since the initial establishment of complex terrestrial ecosystems in the late Silurian to Early Devonian ([Kenrick et al., 2012](#); [Garwood et al., 2020](#)), the progression to herbivory is not extensively documented in the fossil record ([Labandeira and Currano, 2013](#); [Labandeira and Wappler, 2023](#)). Probable arthropod coprolites (fossilized fecal pellets) containing spores and other fragments associated with late Silurian (412 Ma) and Early Devonian (390 Ma) land plants have been identified as the earliest documented evidence for the consumption of live tissues alongside dead plant matter ([Edwards et al., 1995](#); [Hagström and Mehlqvist, 2012](#); [Labandeira and Wappler, 2023](#)). The extraction of nutrients from plants via piercing and sucking of cortical stem tissues has been reported in Early Devonian vascular plants displaying lesions resulting from repeated insertion of stylet mouthparts ([Banks and Colthart, 1993](#)). By the Middle Devonian, several types of herbivory were represented on simple land plants: external tissue feeding, galling, and piercing and sucking ([Labandeira et al., 2014](#)).

[Labandeira et al. \(2007\)](#) published a guide focused primarily on trace fossil evidence of damage to foliage, consisting initially of 150 distinct Damage Types (DTs) almost all of which are probably linked to arthropods. The latest available updated compendium (as yet unpublished; C. Labandeira, pers. comm.) defines over 420 distinct damage types. These DTs are classified into a series of Functional Feeding Groups (FFGs): 1, hole feeding; 2, margin feeding; 3, skeletonization; 4, surface feeding; 5, oviposition; 6, piercing and sucking; 7, mining; 8, galling; 9, seed predation; 10, pathogenic damage; 11, boring; and 12, domatia construction. To these feeding and other interactive behaviors can be added palynophagy and nectarivory, which can be difficult to detect in the fossil record.

With a standardized classification scheme, the quantification of fossil leaves with invertebrate traces through time can be utilized to infer the state of health of the lower trophic levels, e.g., terrestrial ecosystem development and recovery before and after major environmental changes ([Labandeira et al., 2018](#)). The majority of mass extinction events were associated with worldwide changes in the climate, the most common and lethal of which were rapid

warming episodes, or ‘hyperthermal events’ (Bond and Grasby, 2017). An understanding of how plant–arthropod interactions have responded to cases of past environmental destabilization will elucidate how terrestrial ecosystems evolve (Wilf et al., 2001; Labandeira, 2006; Wilf, 2008; Labandeira and Currano, 2013; Currano et al., 2016; Labandeira and Wappler, 2023; Zambon et al., 2023). Moreover, assessing the traits common to mass extinction survivors, and observing the progression of ecosystem inhabitants over time, enables the identification of potential patterns of recovery between plants and their dependent invertebrates throughout evolutionary history (Labandeira, 2006; Cariglino et al., 2021). This may then inform our predictions of how extant terrestrial ecosystems may be affected by modern rapid climate changes (Currano et al., 2016; Zambon et al., 2023).

1.2 Latest Permian to Middle Triassic climatic events

The transition from the Paleozoic to Mesozoic eras was punctuated by a series of climate-driven ecosystem shifts (Figure 1). The first of these was the end-Permian event (EPE, c. 252.2 Ma) that has been clearly linked to a major magmatic episode of the Siberian Traps Large Igneous Province (Burgess et al., 2017; Joachimski et al., 2019; Shen et al., 2023). The EPE hyperthermal event involved increases in atmospheric CO₂ (Cui et al., 2021; Wu et al., 2023), temperature (Sun et al., 2012; Cui and Kump, 2015), wildfires (Vajda et al., 2020; Lu et al., 2022; Mays and McLoughlin, 2022), freshwater microbial blooms (Mays et al., 2021) and enhanced seasonality in precipitation (Fielding et al., 2019; Frank et al., 2021). A combination of these (and related) kill mechanisms during the EPE led to the highest biodiversity loss of any mass extinction within both the marine and continental realms (Stanley, 2016; Viglietti et al., 2021) including a globally significant floral and insect turnover (Anderson et al., 1999; Labandeira, 2005; Cascales-Miñana et al., 2016; Gastaldo et al., 2020; Schachat and Labandeira, 2021). Therefore, the Triassic fossil flora, entomofauna and their associated interactions can be used to inform patterns of recovery and continental ecosystem evolution in the aftermath of Earth’s greatest extinction event.

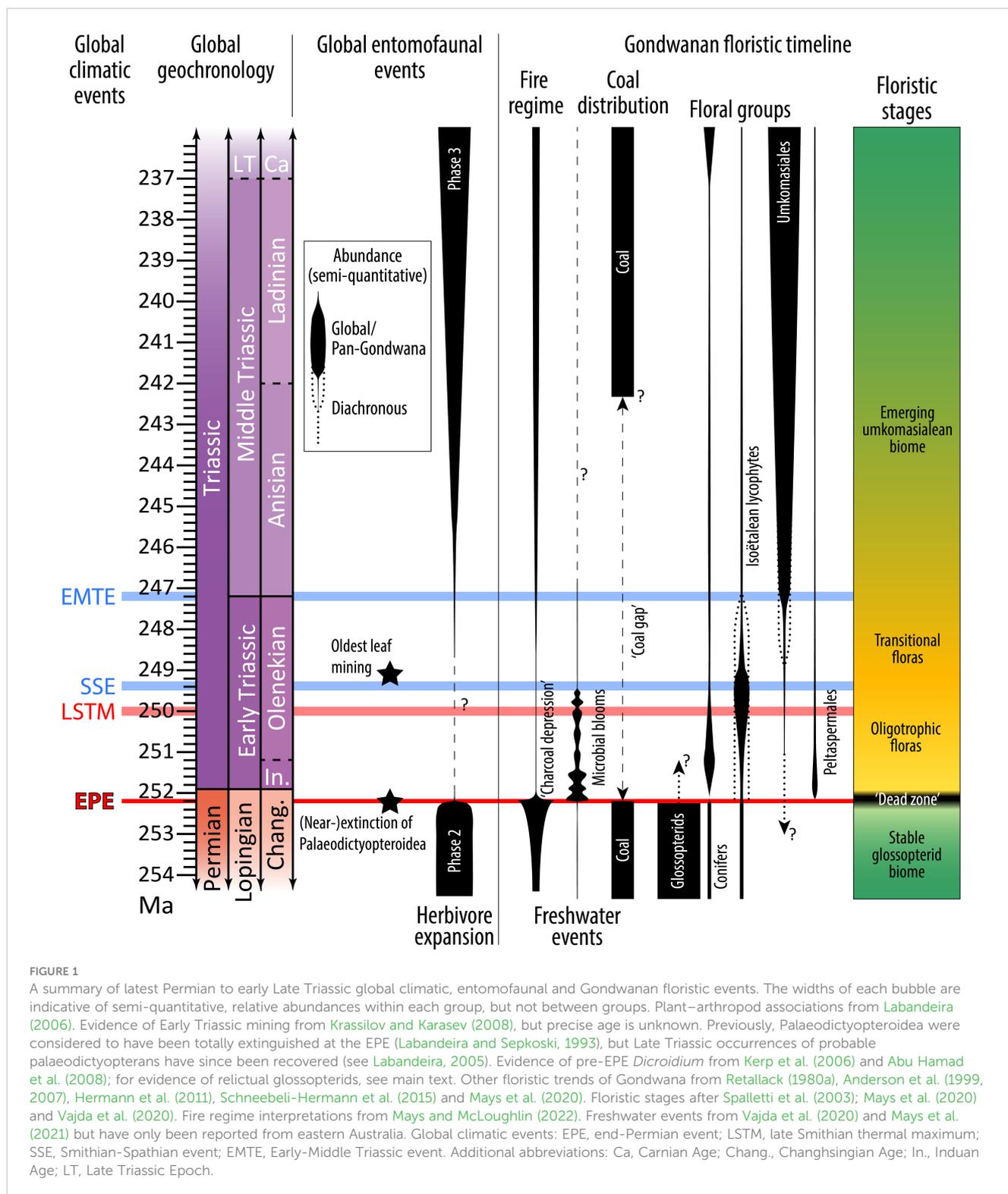
The post-EPE recovery of ecosystems is complicated by a series of Early Triassic climatic events (Figure 1). Three of these events have demonstrated major biotic impacts (in chronological order): 1, the late Smithian thermal maximum (c. 250 Ma; Sun et al., 2012; Du et al., 2022); 2, the Smithian–Spathian event (c. 249.2 Ma; Hermann et al., 2012a; Lindström et al., 2020); and 3, the Early–Middle Triassic event (c. 247.2 Ma; Hermann et al., 2012b). At least one of these (the late Smithian thermal maximum) has been linked to enhanced global warming (Du et al., 2022), possibly as a result of renewed Siberian Traps Large Igneous Province magmatism (Shen et al., 2019) although this is contested (Widmann et al., 2020). The latter two events (the Smithian–Spathian event and the Early–Middle Triassic event), however, seem to be associated with cooling trends (Romano et al., 2013; Widmann et al., 2020). Although magmatism has been indicated as the ultimate cause of both (Du et al., 2022; Saito et al., 2023), the precise mechanisms remain obscure. Regardless of the causes, it is highly likely that the

climatic fluctuations hindered ecological recovery for millions of years following the EPE (Grauvogel-Stamm and Ash, 2005; Friesenbichler et al., 2021). A demonstration of this hindrance is the global absence of thick, economic coal deposits until the Middle Triassic (Veevers et al., 1994; Retallack et al., 1996); the likely oldest post-EPE coals in Gondwana are in the c. upper Anisian (Dolby and Balme, 1976) lower Mungaroo Formation on the Australian northwest shelf (Retallack et al., 1996; Zeng et al., 2019). The absence of dense vegetation represented by the coal gap was a probable contributor to the Early Triassic ‘charcoal depression’, an interval of relatively low wildfire prevalence (Figure 1; Mays and McLoughlin, 2022). These signs indicate that, although the main plant constituents of Gondwanan Middle and Upper Triassic coals (Umkomasiales, e.g., *Dicroidium*) had spread across the continent soon after the EPE, their abundances remained low until long after the major climatic fluctuations of the Early Triassic.

1.3 Ecosystem evolution after the end-Permian event (EPE)

Permian floral assemblages of Gondwana are overwhelmingly dominated by the remains of one group of broadleaved, arborescent seed plants, the glossopterids, alongside subsidiary lycopsids, sphenopsids, ferns, cycadales, ginkgoaleans, cordaitaleans, conifers and several seed plants of uncertain affinity (Anderson and Anderson, 1985; McLoughlin, 1992, 1994a, b; Prevec et al., 2009, 2010). With the extinction of glossopterids near the end of the Permian, new terrestrial ecosystems were slowly established and dominated by peltaspermean, voltzialean conifer, pleuromeian/isoetalean lycophyte, and, eventually, umkomasialean (primarily *Dicroidium*) floras through the Early and Middle Triassic (Figure 1; Lele, 1974; Retallack, 1977; McLoughlin et al., 1997; Anderson et al., 1998). By the Middle Triassic, *Dicroidium* had filled the canopy plant niche left by the glossopterids until their own eventual extinction across Gondwana at the close of the Triassic, apart from a few potential relictual communities that persisted into the Early Jurassic in East Antarctica (Bomfleur et al., 2018).

Evidence for PAIs through the Permian of Gondwana has been broadly surveyed based on published literature (McLoughlin et al., 2021b) but there have been few quantitative studies of individual assemblages (Prevec et al., 2009, 2010). Labandeira (2006) identified four distinct phases of land plant–arthropod associations through deep time, with the EPE as the boundary between Herbivore Expansion Phases 2 and 3 (Figure 1). Most of the major functional feeding groups (FFGs) had evolved by the EPE, specifically during Herbivore Expansion 2, with the exception of mining and nectarivory (Labandeira, 2006; Schachat et al., 2014). Although putative evidence for leaf mining, has been reported on *Glossopteris* leaves from the Permian of South America (Adami-Rodrigues et al., 2004; Cariglino, 2018), these records are equivocal and, if present, mining was evidently extremely rare prior to the Triassic (McLoughlin and Santos, 2024). The oldest unequivocal leaf mining has been identified in leaves of the peltaspermean seed fern *Vjaznikopteris rigida* from Lower Triassic strata of the Volga Basin in central Russia (Figure 1; Krassilov and Karasev, 2008).



Parallel to the floral timeline, the late Permian to Early Triassic was a pivotal evolutionary interval for insects when the Paleozoic Evolutionary Fauna was largely replaced by the Modern Evolutionary Fauna (terms *sensu* Labandeira, 2005). The floral and faunal turnovers of the EPE resulted in novel plant–arthropod associations being established by the Middle Triassic that characterize Herbivore Expansion Phase 3, but recorded

instances of PAIs for the Early Triassic are sparse (Labandeira, 2006; Labandeira et al., 2018). Comparatively little is known about the transitional recovery flora and associated herbivores of the first five million years of the Triassic because there are relatively few well-preserved or well-documented fossil floras in continental deposits from the Early Triassic globally (Grauvogel-Stamm and Ash, 2005; Wappler et al., 2015). The Early Triassic spans a c. five-

million-year interval for which published records of PAIs are, consequently, scarce (Labandeira et al., 2016; Cariglino et al., 2021; Labandeira and Wappler, 2023). Furthermore, the majority of existing PAI data from the Early Triassic come from deposits of the Northern Hemisphere (Krassilov and Karasev, 2008; Kustatscher et al., 2014; Labandeira and Wappler, 2023).

With the numerous and extreme environmental changes through the late Permian to the Middle Triassic, the plant and invertebrate components of terrestrial ecosystems were altered accordingly, and this is predicted to be reflected in the interactions recorded in fossil plant assemblages. Extinction and turnover of plant and invertebrate lineages, and their corresponding trophic interactions, are likely to have resulted in a reduced frequency of associated trace fossils prior to the recovery of these groups (Labandeira and Currano, 2013).

Building upon recent detailed surveys of Gondwanan Permian (Prevec et al., 2009, 2010; McLoughlin et al., 2021b), Late Triassic (Scott et al., 2004; Labandeira et al., 2018; Cariglino et al., 2021) and Jurassic (McLoughlin et al., 2015) PAIs, this review aims to document and quantify our current knowledge of PAIs on fossil leaves during the post-EPE recovery interval of the Early and Middle Triassic in the Southern Hemisphere. To this end, we conducted a comprehensive survey of published literature on austral fossil plant assemblages, with special emphasis on leaf floras, given their relative abundance and suitability as substrates of PAIs. A comparison of this data compilation to the results of a case study on a well-described Middle Triassic floral assemblage provides an independent gauge of the rate of PAI reporting. The review of the literature, and additional new case study, will: 1, assess the reliability of the present state of the fossil record as a gauge of terrestrial ecosystem health; 2, summarize the broad ecological stages represented by the plant–arthropod trace fossil records of the Early and Middle Triassic of Gondwana (with regional comparisons); 3, assess PAI presence in the eastern Australian Middle Triassic Benolong Flora, for which no herbivore damage has yet been reported; 4, establish a series of hypotheses regarding terrestrial ecosystem collapse and replacement that are testable with the late Paleozoic to early Mesozoic fossil record of plant–arthropod interactions; and 5, identify fossil assemblages for further research to address the gaps in our collective knowledge of Early to Middle Triassic Gondwanan floras and arthropod interactions.

2 Materials and methods

2.1 Data selection and database taxonomy

The literature evaluation and database creation (Supplementary Table S1) involved the following inclusion criteria: 1, fossil assemblages yielding plant material; 2, Early and Middle Triassic interpreted ages (including those with ages that may extend into the late Permian or Late Triassic); and 3, localities from the Gondwanan supercontinent. Some temporally relevant stratigraphic units bearing fossil flora from across the Southern Hemisphere were initially identified from the reports of Retallack (1980a), Anderson and Anderson (1993a, b), Escapa et al. (2011), Cariglino et al. (2021)

and Moisan (2024). For every fossil plant assemblage identified, additional searches were conducted to identify any existing PAI records. The primary means of finding relevant papers was by using varied combinations of search terms in Google and Google Scholar. The search terms consisted of: “XX Formation” + “XX Basin” + “Triassic” + “fossil” + “plant” + “leaf”/“leaves” + “flora” + “palaeobotany” + “Dicroidium” + “insect”/“arthropod” + “damage”/“herbivory”; searches consisted of a combination of keywords with and without quotation marks.

Some of the identified fossil assemblages have poor age controls, and the chronostratigraphic boundaries of some lithostratigraphic units may extend beyond the target interval (Middle to Upper Triassic) but contain some beds of relevant age. These instances are indicated in the database (Supplementary Tables S1, S2). Some sources report Lower Triassic stratigraphic units containing specimens typical of pre-EPE late Permian plant assemblages, such as *Glossopteris* (in Australia, Jordan, Madagascar and South Asia). Although some of these recorded fossil assemblages are likely to be of Early Triassic age, the formations that contain these beds may: 1, have poor age constraints; 2, span the Permian-Triassic boundary; and/or 3, the identified fossils may be stratigraphically misplaced. Some specimens documented by previous authors may also have been misidentified. Resolving these possibilities is beyond the scope of the present study. Some records of plant assemblages have not been assigned to a particular lithostratigraphic unit; instead, they were listed according to their positions relative to identifiable units, or the localities at which they were found. For some units indicated by previous authors to contain plant macrofossils, it was not possible to locate all the primary literature. In such cases, non-peer reviewed conference abstracts, and unpublished doctoral and bachelor’s theses were utilized, and these were indicated in the database. Despite these efforts, some units included in the database host very few confirmed species- or genus-level records, and the authors that have indicated additional macrofossils have been cited.

Lithostratigraphic units were grouped into time bins: latest Permian (Lopingian)–Early Triassic (LP–ET), Early Triassic only (ET), Early to Middle Triassic (ET–MT), Middle Triassic only (MT) and Middle to Late Triassic (MT–LT). Assemblages of more uncertain age spanning the Early to Late Triassic (ET–LT) were not included in analyses (Supplementary Table S2).

In addition to leaves, all macrofossil plant materials reported in the compiled literature were entered into the database, including wood, reproductive organs, seeds, and unidentifiable fragments (Supplementary Table S1); plant microfossil records (micro-/megaspores and pollen) were not included. Owing to their prevalence in the fossil record, and their diverse and diagnostic forms, this study focused primarily on fossil leaf damage types. Records of Early to Middle Triassic woods and seeds are sparse, and these data were not compiled systematically herein. Similarly, this review deals with damage caused primarily by terrestrial invertebrate species and excludes any diagnostic herbivory, detritivory or incidental damage caused to plant remains by aquatic invertebrate taxa (Philippe et al., 2022).

For every stratigraphic unit, each distinct report of a plant taxon was entered as one record in the database. Duplicate reports

attributed to the same formation (e.g., reports of the same species collected in separate sampling expeditions) were combined into one record (Supplementary Table S1). In an attempt to standardize the database with other eastern Australian Early to Middle Triassic floras and minimize the potential for taxonomic inflation, classifications of taxa higher than genus rank follow the scheme used for description of the Nymboida flora (eastern Australia), which has been documented extensively (Holmes, 2000, 2001a, 2003; Holmes and Anderson, 2005a, b, 2007; 2008, 2013a, 2022; Holmes et al., 2010). Other plant species, genera and higher rank taxa were included in the database with the original designations utilized by the cited authors; however, designations were updated in cases where typographical errors were identified. Consequently, there is some potential for taxonomic inflation as some genera and species may have been reassigned in subsequent studies. For example, Holmes and Anderson (2005a) designated the following genera as junior synonyms of *Dicroidium*: *Dicroidiopsis*, *Diplasiophyllum*, *Johnstonia*, *Tetraptilon*, *Xylopteris* and *Zuberia*. Misidentifications of specimens and leaf features (incorrect taxa or pseudotraces) by previous authors may also be included.

For temporal and spatial comparison of floral composition, records were organized into fourteen groups in accordance with the aforementioned taxonomic designations: bryophytes, lycophytes, ferns and sphenophytes (spore producers); bennettitaleans, conifers, cordaitaleans (*sensu* the original authors), cycads, ginkgophytes, gnetopsids, ‘seed ferns’ (i.e., Umkomasiales, Peltaspermales and affiliated groups), gymnosperm *incertae sedis* (seed producers); and other taxa of uncertain affinity *incertae sedis*. In contrast to the “*incertae sedis*” group that was defined by uncertainty in higher taxonomic affinity of the genera by the original authors, higher taxonomic affinities for 61 plant records, reported only as a genus or genus + species by the cited sources, were not able to be identified using the search protocol outlined above and were placed into an additional group denoted by a question mark “?”.

In many cases, the plant fossils were not identifiable to species level and, instead, are only reported to genus or even higher taxonomic levels (referred to as suprageneric records herein). Records containing indications of uncertainty in the genus or species identifications, or taxa in open nomenclature (“sp.,” “spp.,” “cf.,” “aff.,” “?,” etc.) were included in the database and subsequent analyses where they were informative of floral diversity. There are 191 plant fossil records where the number of species discussed was unclear and thus were not included in analyses of counts of species reports from each locality (Supplementary Table S3): 129 suprageneric records (including three records where two genera were indicated as equally probable), and 62 records only specified to genus level, 11 of which were reported as “spp.” indicating the presence of at least one distinct fossil-species from a given genus.

2.2 PAI case study

To determine whether the currently reported levels of arthropod herbivore damage are representative of Triassic

assemblages across Gondwana, we also conducted a case study of the Middle Triassic Benolong Flora of the Napperby Formation in the Gunnedah Basin, Australia (Supplementary Table S4). The Benolong Flora is from a site at Ugothery, near Benolong, New South Wales. All specimens investigated in this study ($N = 591$) are housed in the Australian Museum Palaeontological Collection, Sydney, Australia. For data collection, all hand specimens $c. \leq 40$ cm long were photographed using a Canon 80D camera with a 50 mm Canon macro lens. Dust and loose particles were removed from the specimens prior to imaging using an air blower brush tool. Photography of each sample was conducted under three light conditions: one ‘ambient’ high-angle light condition, and two conditions of low-angle light with orthogonal light directions. For each light condition, a series of photos were taken at slightly different focal lengths. Each photo series was then merged into a composite focused image using Helicon Focus v.8.2.2. Individual hand specimens were typically imaged with a consistent field of view and, hence, focal length (notwithstanding the minor length changes for the composite image-stitching outlined above). However, average focal length varied between samples ($c. 30\text{--}100$ cm), thus resulting in an inconsistent spatial resolution.

All fossils identifiable as individual plant fragments were included in the analyses. For each rock surface, the number of distinct plant fragments was counted, and assessed for PAIs using the DT/FFG categories described by Labandeira et al. (2007) and later unpublished additions (C. Labandeira, pers. comm.). Physical herbivore defenses, such as hairs or spines, were also documented.

Artefacts that could be misidentified as PAIs include abiotic or non-herbivore biotic damage to the plant prior to fossilization, the effects of taphonomic processes, extraction marks, overlying sediment, and adhering dust. The presence of reaction tissue—produced by the living plant around the damaged area to limit tissue infection—was utilized to more confidently identify biotic damage inflicted on living plant tissue. In this way, traces of herbivory were distinguishable from detritivore damage on dead plant material and subsequent taphonomic artefacts. Furthermore, stereotypy, the repeated pattern of size, shape and position of damage, was used to distinguish PAI evidence from abiotic environmental damage to the plant (Labandeira et al., 2016; Currano et al., 2021). Imaging the fossil using low-angle light from orthogonal directions highlighted low-relief, positive and negative topographic features on the rock surfaces, allowing for areas where fossil layers were absent or covered by overlying sediment to be distinguished from plant fossil areas removed by herbivory.

Additional potential confounding variables include the difficulty in accurately counting specimens on rock surfaces with multiple overlapping plant fragments. Moreover, over the course of examining 591 plant fragments, it is possible that the accuracy of the assessment improved due to increased familiarity with the DT guide and assessors’ skills in recognizing more subtle PAIs and in excluding pseudotraces. As noted by Thomas and Hill (2023), none of the images used to assign a PAI to the DT categories of Labandeira et al. (2007) is of an Australian specimen. Moreover, most of the specimens illustrated by Labandeira et al. (2007) are: 1, of much younger material than the Middle Triassic Benolong Flora; and 2, consist almost exclusively of angiosperms, a group of

plants for which there is no unequivocal Middle Triassic evidence. Hence, some variation in the expression of these FFGs is expected and a significant proportion of PAIs identified were not confidently assignable to a DT, but were referred only to an FFG.

3 Results

3.1 Database: localities and stratigraphic units

Eighty-nine stratigraphic units yielding 1559 plant records were included in the Gondwanan Early–Middle Triassic fossil database (Figure 2; Supplementary Tables S1, S2): six from Africa, three from Antarctica, two from Jordan, fifty from Oceania, twenty-three from South America, and five from South Asia.

3.1.1 Late Permian to Early Triassic assemblages

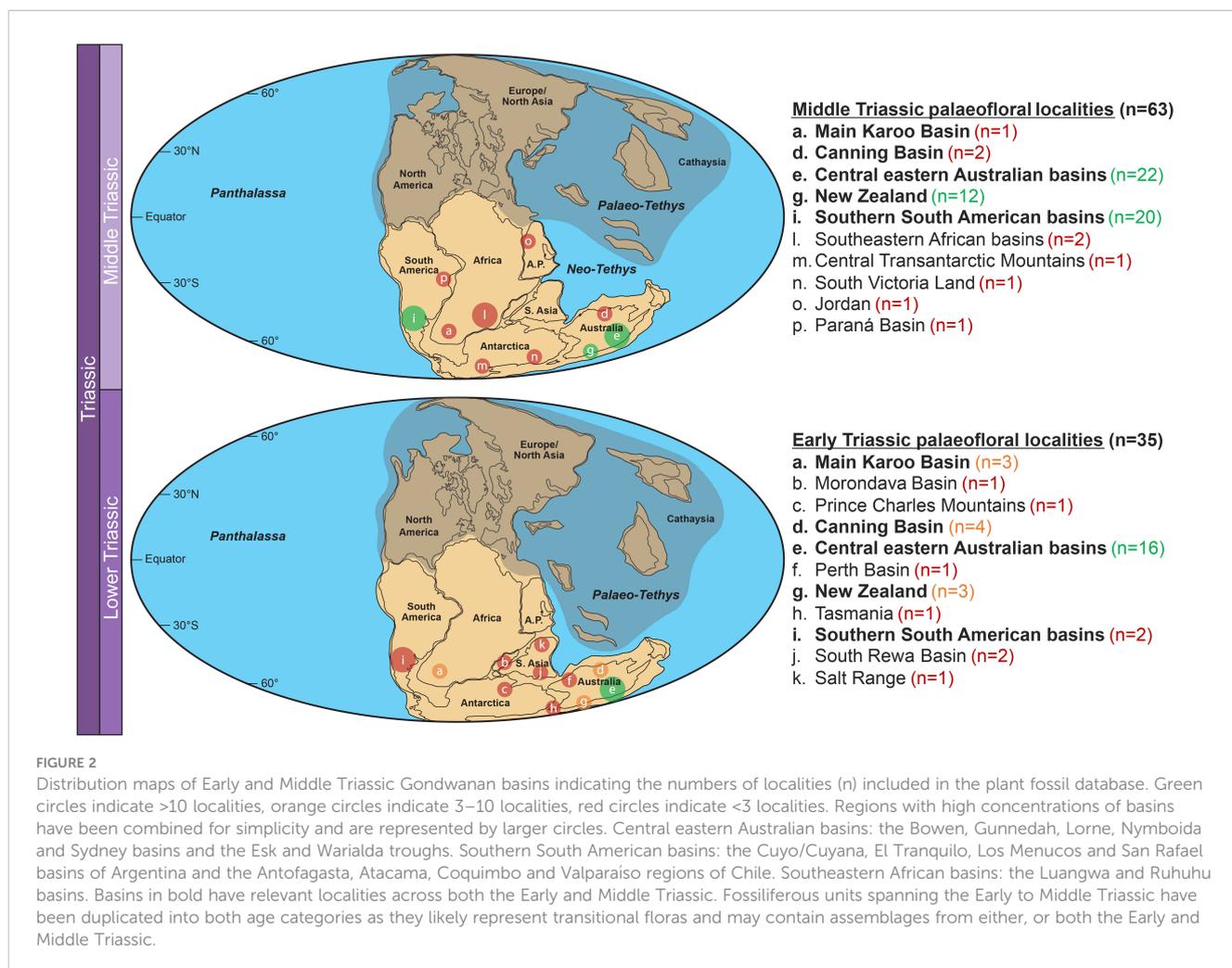
Fossil leaves of latest Permian to earliest Triassic age (i.e., close in age to the EPE) are represented in South Asia from the Mianwali Formation (Schneebeil-Hermann et al., 2015) and the Nidpur beds and adjacent strata (Bose and Srivastava, 1971; Banerji et al., 1976; Srivastava, 1988; Bhowmik and Parveen, 2014). Stratigraphic units

of other Gondwanan regions that span this interval are: the Puesto Tschering Formation (Argentina) and the Sakamena Formation (Madagascar) (Carpentier, 1935, 1936; Artabe, 1985a, b; Spalletti et al., 1999; Falco et al., 2020). This time bin contains 96 records (including seven genus-only/“spp.” records and eight suprageneric records).

The Jordanian Umm Irna Formation, of putative latest Permian age (LP; Supplementary Table S2), hosts abundant *Dicroidium* and the floral records and PAI reports were included in the plant fossil database for comparison (57 plant records including one suprageneric record) (Abu Hamad et al., 2008, 2017; Blomenkemper et al., 2018, 2019, 2020, 2021; Kerp et al., 2021, 2024). However, there are no strata that extend into the specified Early to Middle Triassic age range and so the floral records were not included in any further analyses.

3.1.2 Early Triassic assemblages

The majority of records of Early Triassic leaves are from Australian strata: the Bald Hill Claystone, Bulgo Sandstone, Munmorah Conglomerate, Tuggerah Formation, a single species from the Banks Wall Sandstone, and two plant assemblages with imprecise stratigraphic provenance, are all from the Sydney Basin (Raggatt, 1969; Helby, 1970; Balme and Helby, 1973; Retallack, 1980a). In addition to the Sydney Basin localities, there is also the Camden Head Claystone and Grants



Head Formation (one reported species) from the Lorne Basin, the Arcadia Formation from the Bowen Basin, the Blina Shale and Millyit Sandstone from the Canning Basin, the Kockatea Shale from the Perth Basin, and the Knocklofty Formation from Tasmania (White and Yeates, 1976; Ash, 1979; Holmes and Ash, 1979; Chaloner and Turner, 1987; Retallack, 1995, 1997; Cantrill and Webb, 1998; Haig et al., 2015). Non-Australian Early Triassic assemblages include those from the Flagstone Bench Formation (Ritchie Member) in Antarctica and the Katberg and Verkykerskop formations from South Africa (McLoughlin et al., 1997; Gastaldo et al., 2005; Gastaldo and Bamford, 2023). This investigation did not identify any records of plant macrofossil assemblages of definitive Early Triassic age from the Arabian Peninsula, South America or South Asia.

This time bin contains 139 records (including 16 genus-only records and 27 suprageneric records).

3.1.3 Late Early to early Middle Triassic assemblages

The fossil-bearing stratigraphic units that may span the Lower to Middle Triassic boundary in Gondwana are largely from Australia: the Buralow, Garie, Gosford and Terrigal formations of the Sydney Basin, the Clematis Sandstone and Glenidal Formation of the Bowen Basin, and the Culvida and Erskine sandstones from the Canning Basin (White, 1965; Goldberg, 1969; Raggatt, 1969; White, 1971; White and Yeates, 1976; Retallack, 1977; Ash, 1979; Retallack, 1980a; Chaloner and Turner, 1987; Holmes, 2001b; McLoughlin, 2011a). The Murihiku Supergroup from New Zealand includes the Potiki Siltstone and the Wairuna Peak Beds of this age, along with some leaf fossil occurrences not allocated to a stratigraphic unit (Retallack, 1985). The palaeoflora-bearing Burgersdorp Formation (South Africa) and the Puesto Vera Formation (Argentina) have also been attributed to the Early to Middle Triassic (Anderson and Anderson, 1985; Artabe, 1985b, a; Bamford, 1999; Spalletti et al., 1999; Hancox et al., 2002; Bamford, 2004; Gastaldo et al., 2005; Falco et al., 2020; Hancox et al., 2020).

This time bin contains 159 records (including seven genus-only/"spp." records and 15 suprageneric records).

3.1.4 Middle Triassic assemblages

Fossil leaves confidently ascribed to the Middle Triassic are also described predominantly from Australian sedimentary basins. Fossiliferous units of this interval include the Gragin Conglomerate and Gunnee Beds from the Warialda Trough, the Napperby Formation from the Gunnedah Basin, the Ashfield Shale, Bringelly Shale, Brookvale Shale, Hawkesbury Sandstone and the Newport Formation from the Sydney Basin, the Moolayember and Teviot formations from the Bowen Basin, the Basin Creek Formation from the Nymboida Basin, and the Bryden and Esk formations, together with a single record from the Nera Volcanics in the Esk Trough (Walkom, 1924, 1928; White, 1965; Branagan, 1969; Jell, 1969; Lovering and McElroy, 1969; White, 1969, 1971; Bourke et al., 1977; Rigby, 1977; Retallack, 1980a; Holmes, 1982; Playford et al., 1982; Webb, 1982; Webb and Holmes, 1982; Webb, 2001). Also from the Sydney Basin, another small assemblage reported as "Mittagong Formation or basal Ashfield Shale" by Retallack (1980a, p. 426), and

one unit yielding only one species, the Minchinbury Sandstone, were included (Lovering and McElroy, 1969). From New Zealand, the Black Jacks Formation and the Tank Gully Coal Measures are assigned to the Middle Triassic (Retallack, 1980b, 1983), along with the remaining Murihiku Supergroup units and unspecified assemblages (Retallack, 1985): The North Etal Group, the North Peak (Jacobs River Member) and Pears formations, an assemblage "southeast of Mautaurau island" (p. 11), an assemblage "above the Franklin Conglomerate" (p. 9) and the 'Tauringatura Group' (p. 13), the latter two with only one species reported each. The remaining Middle Triassic strata are: 1, the Mukheiris Formation from Jordan (Abu Hamad et al., 2019), and; 2, the Barreal, Cerro de Las Cabras, Corral de Piedra, Monina, Montaña, Paramillos, and Quebrada de los Fósiles formations from Argentina (Brea et al., 2008; Cariglino et al., 2016, 2018; Bodnar et al., 2019; Pedernera et al., 2019; Drovandi et al., 2020; Pedernera et al., 2022).

This time bin contains 582 records (including 19 genus-only/"spp." records and 39 suprageneric records).

3.1.5 Middle to Late Triassic assemblages

Formations with strata indicated to extend from the Middle Triassic into the Upper Triassic are located predominantly in South America, the vast majority of which have uncertain age controls: 1, the Cañadón Largo Formation from the El Tranquilo Basin (Herbst, 1988; Jalfin and Herbst, 1995; Gnaedinger and Herbst, 1998a, b, 1999; Troncoso et al., 2000; Herbst et al., 2001; Herbst and Gnaedinger, 2002; Adami-Rodrigues et al., 2008; Villalva, 2017; Gnaedinger et al., 2023; Villalva et al., 2023); 2, the Agua de la Zorra, Cortaderita (Don Raúl Member), Agua de Los Pajaritos and Potrerillos formations from the Cuyo/Cuyana Basin in Argentina (Ottone et al., 2011; Cariglino et al., 2016; Lara et al., 2017; Bodnar et al., 2019; Pedernera et al., 2019); 3, the El Bordo and El Mono beds, and the Pular, Tuina, Guanaco Sonso, Las Breas and El Puquén formations of Chile (Azcarate and Fasola, 1970; Breitkreuz et al., 1992; Lutz et al., 1999; Troncoso and Herbst, 1999; Herbst, 2000; Herbst and Troncoso, 2000; Melchor and Herbst, 2000; Troncoso et al., 2000; Gnaedinger and Herbst, 2001; Herbst and Gnaedinger, 2002; Gnaedinger and Herbst, 2004a, b; Niemeyer et al., 2008; Moisan, 2024); and 4, the Santa Maria Formation of Brazil (Guerra-Sommer and Cazzulo-Klepzig, 2000; Cenci, 2013; Barboni and Dutra, 2015; Barboni et al., 2016; Cenci and Adami-Rodrigues, 2017; Cenci et al., 2019). Very few plant species have been identified from the Tuina Formation and El Mono beds in this review. Similarly, only four species were reported from the Ntawere Formation in Zambia, and only one plant species was identifiable from the Manda Formation of Tanzania, which is poorly dated but suggested to be within this age range (Dixey, 1937; Lacey and Smith, 1970). The rich plant assemblages from the permineralized peat (and associated beds) of the upper Fremouw Formation of the Transantarctic Mountains (Schopf, 1978; Stubblefield and Taylor, 1986; Perovich and Taylor, 1989; Taylor et al., 1989; Millay and Taylor, 1990; Pigg, 1990; Delevoryas et al., 1992; Meyer-Berthaud et al., 1993; Taylor et al., 1994; Del Fueyo et al., 1995; Yao et al., 1995, 1997; Axsmith et al., 1998; Phipps et al., 2000; Klavins et al., 2002; Rothwell et al., 2002; Cúneo et al., 2003; Klavins et al., 2003; Kellogg

and Taylor, 2004; Klavins et al., 2004; Retallack et al., 2005; Hermsen et al., 2006, 2007a, b; Decombeix et al., 2010; Schwendemann et al., 2010; Bergene et al., 2013; Decombeix et al., 2014) have commonly been assigned to the Middle (or even Lower) Triassic (Taylor et al., 1986, 1993). However, palynoassemblages from these beds are preferable to the *Alisporites* Assemblage Zone C or Australian APT4 zone, indicating a possible Carnian (Late Triassic) age (Farabee et al., 1990). The Antarctic Lashly Formation and the Long Gully Formation of New Zealand have also been assigned to this geochronological interval (Retallack, 1981; Escapa et al., 2011; Bomfleur et al., 2013b).

This time bin contains 444 records (including ten genus-only/“spp.” records and 33 suprageneric records).

3.1.6 Assemblages of Early to Late Triassic or uncertain age

There are three remaining formations in the database, indicated to be in the range of Lower to Upper Triassic without more precise stratigraphic resolution: the Chilean San Felix Formation (Mohr and Schöner, 1985; Bell and Suarez, 1994; Troncoso et al., 2000; Salazar et al., 2013) and the Indian Panchet and upper Kamthi formations (Bose and Banerji, 1974; Banerji et al., 1976; Banerji and Bose, 1977; Pal and Ghosh, 1997; Pal et al., 2010, 2014; Saxena et al., 2019; Ghosh et al., 2021). As plant fossil records from these formations (82 records, including three genus-only/“spp.” records and six suprageneric records) cannot be grouped into any particular time bin or used for comparison across the Early to Middle Triassic, they were not included in the analyses.

Additional units in India are possibly referable to the Middle Triassic (e.g., the Pali, Parsora, and Panchmarhi formations) but age constraints are currently insufficient for confident assignment of fossil assemblages from these units to any particular time bin (Joshi et al., 2014).

3.2 Floral composition

Gondwanan terrestrial ecosystems were dominated by glossopterid gymnosperms throughout most of the Permian (McLoughlin, 2011b). The end-Permian event in Gondwana was marked by the demise of glossopterids (Figure 1) and many associated free-sporing and gymnospermous plants (Anderson et al., 1998; Retallack et al., 2005; Lindström and McLoughlin, 2007; Fielding et al., 2019; Gastaldo and Bamford, 2023). Reports of glossopterids surviving the end-Permian extinction event and persisting into the earliest Triassic are equivocal. Records of glossopterids in units close to or spanning the Permian-Triassic boundary collated in the present database derive from: 1, the Umm Irna Formation (LP; Jordan; Kerp et al., 2021); 2, the Sakamena Formation (LP-ET; Madagascar; Carpentier, 1935, 1936); 3, the Munmorah Conglomerate, Blina Shale, Millyit Sandstone (ET; Australia) the Erskine Sandstone (ET-MT; Australia) (Raggatt, 1969; White and Yeates, 1976); and 4, several units in India, including the Nidpur beds and associated strata, the Mianwali Formation (all LP-ET), and the Panchet and Kamthi formations (ET-LT) (Supplementary Table S1; Banerji et al., 1976; Banerji and Bose,

1977; Srivastava, 1988; Pal and Ghosh, 1997; Pal et al., 2010; Schneebeli-Hermann et al., 2015; Saxena et al., 2019). Additional Indian strata hosting putative *Glossopteris* of possible Triassic age are the Pali, Hinjir, Maitur, Parsora, and Hirapur/“Upper Kamthi” formations (Maheshwari, 1992; Shah, 2000; Ghosh et al., 2016; Shah, 2021); however, these records may represent misidentifications of typical Triassic taxa, such as *Gontriglossa*. With the exception of the Munmorah Conglomerate and Blina Shale, *Dicroidium* has also been reported from these same strata (Carpentier, 1935, 1936; Raggatt, 1969; Bose and Srivastava, 1971; Bose and Banerji, 1974; Banerji et al., 1976; White and Yeates, 1976; Srivastava, 1988; Maheshwari, 1992; Retallack, 1995; Pal and Ghosh, 1997; Shah, 2000; Pal et al., 2014; Schneebeli-Hermann et al., 2015; Saxena et al., 2019; Kerp et al., 2021). Srivastava et al. (2010) also reported *Dicroidium* associated with *Glossopteris* from Lower Permian strata of the Barakar Formation, however, the putative *Dicroidium* specimens were later reinterpreted as peltaspermalean foliage (Srivastava et al., 2011). Other putative co-occurrences of *Dicroidium* and *Glossopteris* recorded in this database may include confluences of pre-EPE Permian and post-EPE Permian or Triassic plant assemblages that have been grouped into the same formation or have become stratigraphically misplaced by faulted juxtapositioning of beds of different ages (Tiwari and Ram-Awatar, 1990). Although we cannot exclude the possibility that some glossopterids persisted as post-EPE survivors, this conclusion awaits verification. No *Glossopteris* has yet been identified in any of the Antarctic or South American Triassic units included in this database, although Rigby and Schopf (1969) report the co-occurrence of these taxa in an Antarctic assemblage they determined to be equivalent to the Panchet Stage (no formation indicated).

Later in the Early Triassic, phases of alternating dominance by pleuromeian lycopsids, voltzialean conifers and *Dicroidium* (Umkomasiales), together with spikes in charcoal abundance, indicate repeated fluctuations in environmental conditions (Retallack, 1977; Helby et al., 1987; Mays et al., 2020; Mays and McLoughlin, 2022). By the end of the Early Triassic, Umkomasiales had become established as the dominant gymnosperm group across southern Gondwana (Figures 1, 3; Retallack, 1977; Anderson and Anderson, 2003).

Through the Middle Triassic, Umkomasiales diversified and retained dominance of the Gondwanan temperate vegetation (Retallack, 1977; Anderson and Anderson, 1985; Taylor et al., 1993). They were associated with a broad range of sphenophytes, ferns, broad-leaved conifers, cycads, bennettitids, peltasperms, voltzialean conifers and various gymnosperms of uncertain affinity (Figures 3, 4; Walkom, 1928; Anderson and Anderson, 1985; Taylor et al., 1993; McLoughlin et al., 2018b). Overall land-plant diversity continued to increase in the austral temperate zone (>35°S) through the Middle and Late Triassic (Anderson and Anderson, 1989, 2003), before suffering depletion and replacement of key taxa during the end-Triassic extinction event (Anderson et al., 1998; Kustatscher et al., 2018).

A floral transition is evidenced in the present database by the higher proportion of bryophytes, lycophytes, sphenophytes and conifers in the Early Triassic compared to the Middle Triassic, whereas ferns, bennettitaleans, cycads, ginkgophytes, gnetopsids and gymnosperms of uncertain affinity constitute a greater

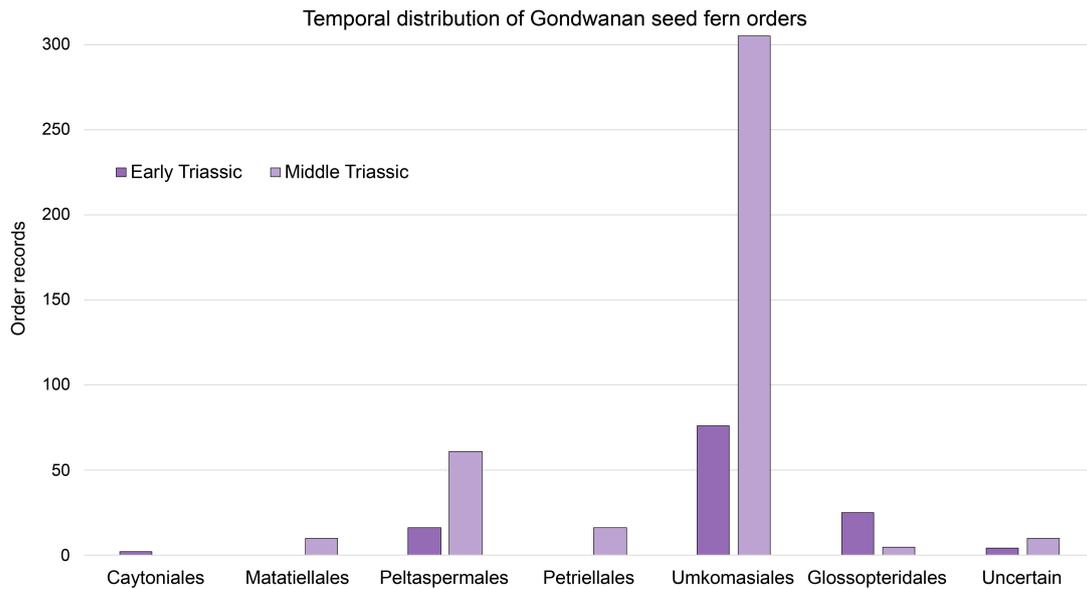


FIGURE 3 Gondwanan Early and Middle Triassic seed fern diversity. The number of records of each order in the plant fossil database is reported. The "uncertain" group consists of fossil records where authors have indicated affinity to seed ferns, but for which designations of order were not specified. Seed fern records from assemblages spanning Early to Middle Triassic age have been included in both age categories: Early Triassic (n=123); Middle Triassic (n=407).

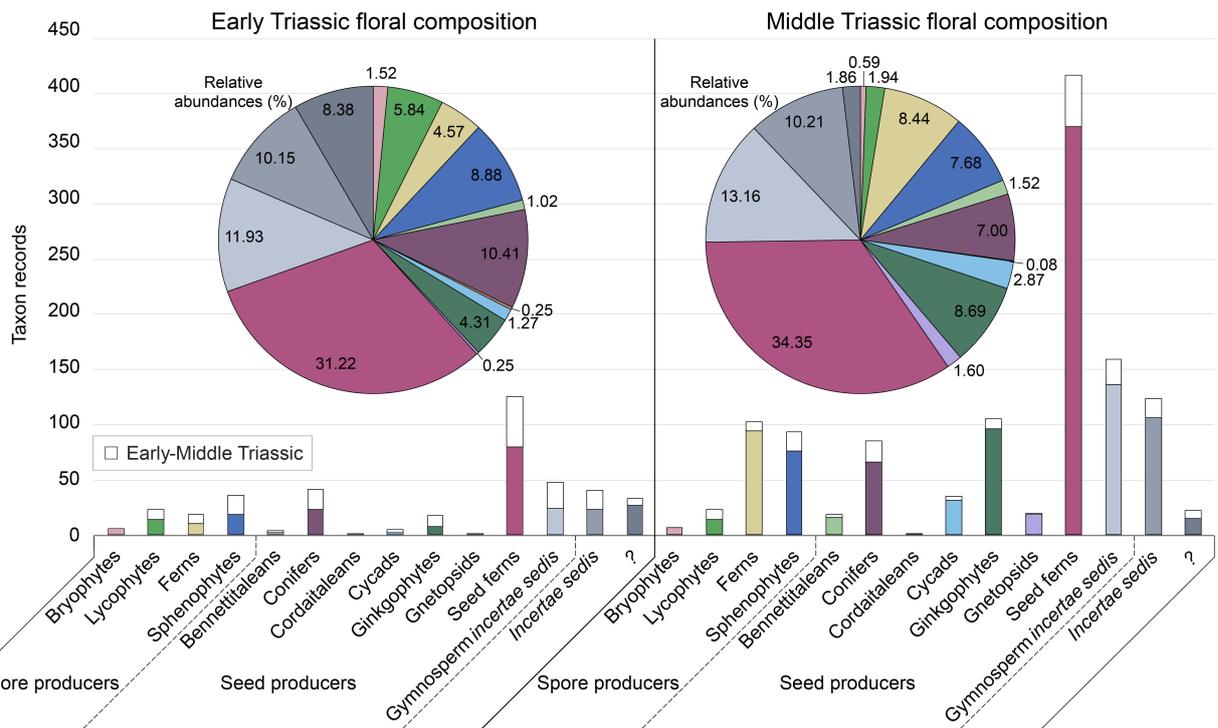


FIGURE 4 Comparison of Gondwanan Early and Middle Triassic floral composition. The number of records of each higher taxonomic group in the plant fossil database is reported. Uncoloured bars represent Early to Middle Triassic plant fossil records, with equal values above the data for both the Early Triassic and Middle Triassic age categories. Higher taxonomic groups follow the same sequence for all charts: bryophytes; lycophytes; ferns; sphenophytes; bennettitaleans; conifers; cordaitaleans; cycads; ginkgophytes; gnetopsids; seed ferns; gymnosperm *incertae sedis*; *incertae sedis*; "?". The "?" group consists of plant fossil genera for which higher taxonomic designations were unable to be identified in this review, in contrast to the *incertae sedis* group defined by uncertainty in higher taxonomic affinity of the genera. Pie chart values represent proportional contributions of each higher taxonomic group to the total floral records in that age category (in %). Plant fossil records from assemblages spanning Early to Middle Triassic age have been included in the pie charts of both age categories; total Early Triassic records (n=394); total Middle Triassic records (n=1185).

proportion of Middle Triassic diversity than in the Early Triassic assemblages (Figure 4). Seed ferns, including umkomasialeans and peltasperms, although dominant in both Early and Middle Triassic assemblages, constitute a greater proportion of Middle Triassic total species richness, demonstrating their continued diversification (Figures 3–5). The total number of plant species reported increases in the Middle Triassic, particularly in Oceania and South America (Figures 3–5, Supplementary Figure S1; Supplementary Table S3). This likely represents a combination of recovery in species diversity after the EPE, and increased collection and taxonomic identification efforts for Middle Triassic assemblages compared to those of the Early Triassic.

3.3 PAI record of Gondwana

Of the 85 stratigraphic units included in the Gondwanan Early–Middle Triassic analyses (Supplementary Table S1), only twelve (14.1%) yielded PAIs reported in the surveyed literature (Table 1).

3.3.1 Africa

We could find no reports of insect damage from Early to Middle Triassic African floral assemblages. Labandeira et al. (2018) noted

the conspicuous absence of galls from a collection of 1386 plant specimens of the Burgersdorp Formation (ET–MT).

3.3.2 Antarctica

The majority of PAI records from the late Middle to early Late Triassic of Antarctica derive from the Fremouw Formation, with several organ types affected, although no PAIs have yet been found on leaves. These trace fossils include evidence of boring—likely caused by oribatid mites—in 220 specimens of stems, petioles and roots including a petiole of the fern *Antarctopteris* (Kellogg and Taylor, 2004). This assemblage also yielded insect coprolites containing pollen located in the cycad pollen cone *Delemaya spinulosa* (Klavins et al., 2005). Additionally, Hermsen et al. (2006, 2009) identified feeding galleries in stems of the cycad *Antarcticycas schopfii* of the Fremouw assemblage, which was likely caused by wood-boring arthropod larvae. Fungal damage has also been observed in almost eighty specimens of *Araucarioxylon*-type wood and one specimen of the coniferous ovulate organ *Parasciadopitys* from this formation (Stubblefield and Taylor, 1986; Bomfleur et al., 2013a). Bomfleur et al. (2013a) also reported fungal hyphae on one coniferous leaf of *Heidiphyllum* from the Lashly Formation of the same age. However, as noted above, the ages of the upper Fremouw and Lashly formations may be Late Triassic.

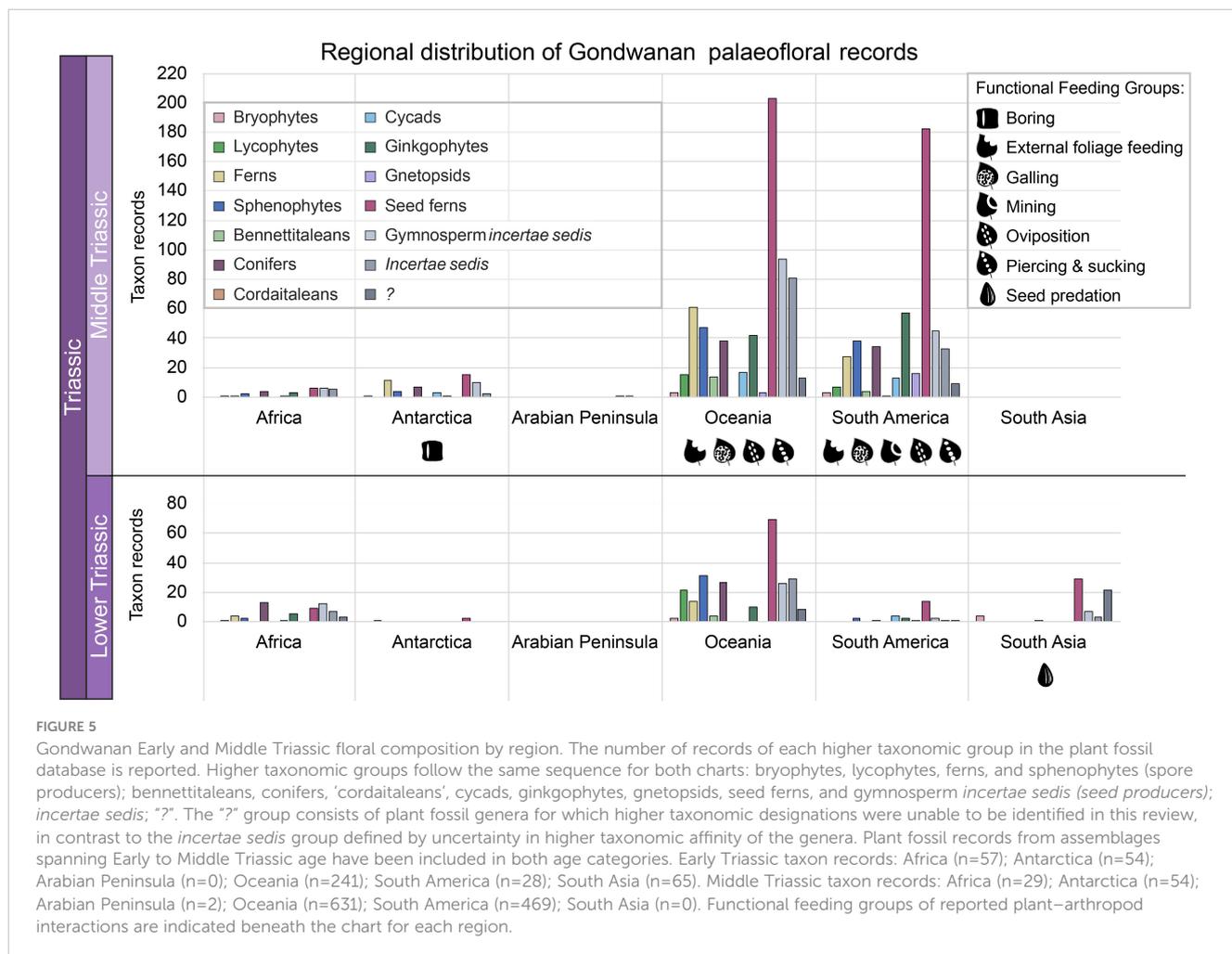


TABLE 1 Records of plant–arthropod interactions (PAIs) from formations in the Gondwanan plant fossil database.

Gondwanan region	Age group	Formation	Margin Feeding	Hole Feeding	Skeletonisation	Surface Feeding	Piercing & Sucking	Mining	Galling	Oviposition	Boring	Pollinivory	Pathogen	Uncertain PAI	References
Antarctica	MT-LT	Fremouw									>220	≥1	~80		a, b, c, d, e, f
Antarctica	MT-LT	Lashly											1		f
Oceania	MT	Basin Creek	1												g
Oceania	MT	Esk								1				1	h
Oceania	MT	Napperby	23	2			3		6	10				11	*
Oceania	MT	Newport							1						h
South America	MT	Quebrada de los Fósiles							≥1	≥1					i
South America	MT-LT	Cañadón Largo	(X)		(X)		(X)	(X)	(X)	1 (X)					i, j, k
South America	MT-LT	Las Breas								2					l
South America	MT-LT	Potrerrillos	6	2		1	1	2		1				1	m, n
South America	MT-LT	Santa Maria	>1			>1		>7	>164	>4				3	o, p, q
South Asia	LP-ET	Nidpur Beds												1	r

PAI traces have been identified on fossil plants from formations in the Late Permian–Early Triassic (LP-ET), Middle Triassic (MT), and Middle Triassic–Late Triassic (MT-LT) age categories. Reported numbers of affected plant fossils are indicated. (X) indicates records from a combination of the Cañadón Largo and Laguna Colorada (LT) formations. References: a, Stubblefield and Taylor (1986); b, Hermsen et al. (2006); c, Hermsen et al. (2009); d, Klavins et al. (2005); e, Kellogg and Taylor (2004); f, Bomfleur et al. (2013a); g, Holmes and Anderson (2007); h, McLoughlin (2011a); i, Cariglino et al. (2021); j, Adami-Rodrigues et al. (2008); k, Gnaedinger et al. (2023); l, Gnaedinger et al. (2014); m, Cariglino et al. (2022); n, Lara et al. (2017); o, Cenci (2013); p, Cenci and Adami-Rodrigues (2017); q, Cenci et al. (2019); and r, Bhowmik and Parveen (2014); *Benolong Flora case study presented herein (bold text).

3.3.3 Arabian peninsula

Hole feeding on three *Dicroidium irnensis* cuticles from the late Permian Umm Irna Formation (Jordan) was identified by McLoughlin et al. (2021a). However, no definitive Triassic PAIs have yet been reported.

3.3.4 Oceania

This review identified three Middle Triassic Australian formations hosting examples of PAI traces on fossil plants. Holmes and Anderson (2007) identified margin feeding on a leaf apex of the ginkgoalean *Sphenobaiera densinerva* from the Basin Creek Formation (MT). McLoughlin (2011a) recognized oviposition scars, possible margin feeding and either hole feeding or surface feeding on a leaf of *Taeniopteris parvilocus* from the Esk Formation (MT) and galling on a *Dicroidium odontopteroides* leaf from the Newport Formation (MT). The present study describes several newly identified PAIs from the Benolong Flora (Napperby Fm, MT); see section 3.4 below for more details.

3.3.5 South America

Permian and Triassic PAI records from South America were extensively compiled and reviewed by Gnaedinger et al. (2014), Cariglino et al. (2021) and Romero-Lebrón et al. (2022). An updated summary of these occurrences is provided below (in stratigraphic order).

The Argentinian Quebrada de los Fósiles Formation (MT) yielded gall-bearing leaves of the seed fern *Ptilozamites longifolia* (possibly = *Kurtziana* sp.) and oviposition traces on the frond of another seed fern of uncertain affinity (Cariglino et al., 2020, 2021).

Adami-Rodrigues et al. (2008) identified PAIs from the Argentinian El Tranquilo Group, including the Cañadón Largo Formation (MT–LT), and the Late Triassic Laguna Colorada Formation. That study listed several types of external foliage feeding, together with piercing and sucking, mining, galling and oviposition. PAIs were identified on sphenophytes, ginkgoaleans, conifers, gymnosperms of uncertain affinity and umkomasialean seed ferns, with fossils of the latter group hosting the majority of documented PAIs (Adami-Rodrigues et al., 2008; Cariglino et al., 2021). However, it was not clear which floral remains and their associated PAIs were recovered from strata of definitively Middle versus Late Triassic age. Gnaedinger et al. (2023) identified oviposition scars on a stem of the sphenopsid *Equisetites lateralis*, also from the Cañadón Largo Formation.

Two occurrences of oviposition traces were reported from two *Taeniopteris* sp. leaves of the Las Breas Formation, Chile (MT–LT; Gnaedinger et al., 2014).

The flora of the Potrerillos Formation from Argentina (MT–LT) hosts several PAIs. Lara et al. (2017) assessed 56 plant specimens, reporting 11 specimens hosting PAI traces: margin feeding on leaves of the umkomasialeans *Dicroidium argenteum*, *D. odontopteroides*, *Johnstonia stelzneriana* and the matatiellalean *Kurtziana brandmayri*, hole-feeding traces on leaves of *Johnstonia* sp. and *Yabeiella wielandii*, surface feeding and piercing-and-sucking traces on leaves of uncertain affinity, and oviposition traces on an indeterminate sphenophyte stem. Cariglino et al. (2022) identified mines on leaves

of the conifer *Heidiphyllum cacheutense* and the gnetalean *Yabeiella wielandii*, with possible oviposition or a fungal spot identified alongside the mine in one *Y. wielandii* leaf.

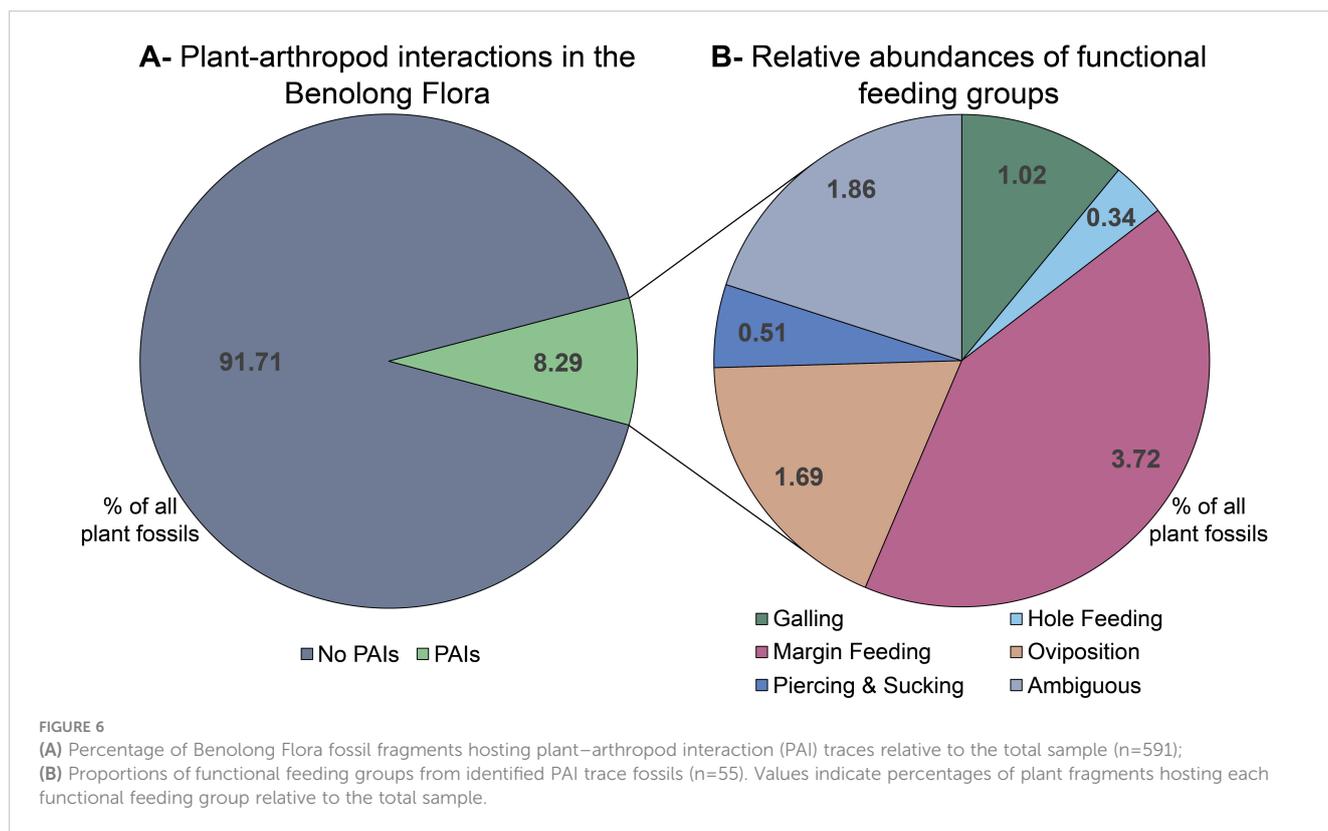
The leaf floras of the Santa Maria Formation of Brazil (MT–LT) have been the most extensively investigated assemblages of any Gondwanan locality, with the most PAI records in the database herein (Cenci, 2013; Cenci and Adami-Rodrigues, 2017; Cenci et al., 2019). Cenci (2013) noted that, of a total of 414 plant samples from the Santa Maria Formation, 149 (36%) hosted evidence of PAIs: 135 umkomasialean leaves (52 external foliage feeding (EFF) traces, seven mines, 578 galls), 11 ginkgoalean leaves (three mines, 49 galls), one voltzialean leaf (one mine), eight equisetalean stems (one mine, 22 galls) and nine *incertae sedis* (one EFF, two mines, 10 galls). Cenci and Adami-Rodrigues (2017) also found galls to be especially common in this unit, with 164 gall-bearing specimens from their sample of 414 (39.6%), apparently representing the same dataset as that employed by Cenci (2013). The vast majority of the galls were identified on umkomasialean leaves. Six-hundred and fifty-nine individual galls were identified across umkomasialean, ginkgoalean, equisetalean and *incertae sedis* taxa, including leaves of *Dicroidium odontopteroides*, *Dicroidium* sp., *Sphenobaiera* sp. and *Taeniopteris* sp., an umkomasialean seed, and a stem of the sphenophyte *Neocalamites*. Cenci et al. (2019) assessed 550 plant specimens, and reported oviposition (six DTs), surface feeding (three DTs), piercing and sucking (four DTs), mining (two DTs), margin feeding (one DT) and hole feeding (one DT). They found that the majority of PAI traces identified were hosted by the dominant umkomasialeans of the Santa Maria Formation, though the ginkgoaleans displayed the greatest proportion of affected specimens.

3.3.6 South Asia

To our knowledge, records of PAIs from this region are almost entirely absent for the Early to Middle Triassic. Bhowmik and Parveen (2014) reported evidence of potential plant-insect interactions from the Indian Nidpur beds (LP–ET). They suggested that clumped pollen grains inside the pollen chamber of the pteridospermous seed *Gopadispermum papillatus*, indicate the possibility of fluid feeding, palynophagy and insect pollination in the seeds, although such pollen characters are also common in anemophilous plants (Benson, 1908; McLoughlin et al., 2018a). Ghosh et al. (2015) reported galls on *Dicroidium* leaves from the Parsora Formation (of unspecified Triassic age and, therefore, not included in the database).

3.4 Case study: Benolong Flora

Five hundred and ninety-one fossil leaf fragments were assessed from the Benolong Flora (Supplementary Table S4). Fifty-five potential traces of plant–arthropod interaction were identified on forty-nine plant fragments (8.29% of fragments assessed; Figures 6A, 7). Forty-four of these PAI traces (78.6%), hosted by 40 plant fragments (1.1 PAIs per affected fragment), matched the DT categories described by Labandeira et al. (2007). Margin feeding was the most common FFG, with 23 examples referable to



established DTs (identified on 3.72% of plant fragments; Figures 6B, 7A, B; Table 1); this was more than twice as common as oviposition (identified on 1.69% of plant fragments) and all other recognized (non-ambiguous) FFGs combined (Figures 6B, 7C–H; Table 1). However, margin-feeding traces may be more identifiable on compression fossils than other FFGs as they do not require relief to be observed and are especially visible where there is a high degree of contrast between the fossil and the host sedimentary matrix. Eleven traces were not consistent with any established DTs or had characters in common with DTs of multiple FFGs (e.g., resembling features of various hole feeding, oviposition or piercing and sucking DTs). In such cases, these were recorded as ‘ambiguous’.

Preservational artefacts resembling leaf mine traces (Supplementary Figure S2A) and leaf features with atypical textures and surficial patterns (Supplementary Figures S2B–D), potentially of biotic origin but not able to be categorized into any FFG using the guide images, were not included in the analysis. One fossilized structure resembled a gall with possible radiating partitions (Supplementary Figure S2E); however, this feature was not located on any observable plant remains and had the same color as the host sediment and so was also excluded from analyses. Other leaf features that highlighted the potential for the inflation of identified PAIs included a semicircular line of discoloration on the margin of another leaf fossil, suggestive of pathogenic, possibly fungal, damage (Supplementary Figure S2F resembles DT058) and the presence of pseudotraces, such as fern sori resembling the texture of a gall (Supplementary Figure S2G resembles DT106). Twenty-seven fossil fragments of leaves and stems displayed textural evidence of hairs or spines.

The data collection process in this case study, which involved systematic photography of an entire floral assemblage, is inherently limited by the resolution of the images. Even in cases where small specimens were imaged, evidence of smaller PAIs, such as piercing and sucking, was difficult to distinguish from preservational artefacts and adhering dust on the rock surface. Another potential source of error of this approach is the inconsistent focal length, hence spatial resolution, of images taken of separate specimens. At the maximum focal length, as used for the largest hand specimens, much less detail is captured on the image, resulting in lower levels of confidence in distinguishing PAIs from artefacts where these are not verified by microscopic inspection. For increased validity of inter-sample comparisons, we recommend a consistent, high-resolution field-of-view and stereomicroscopic evaluation of each specimen. Despite the limitations, we report abundant PAIs from this case study of a relatively small Middle Triassic fossil assemblage. These findings clearly demonstrate marked under-reporting of arthropod trace fossils from the post-EPE recovery phase, as discussed below.

4 Discussion

4.1 Patterns of Early to Middle Triassic plant–arthropod interactions in Gondwana

4.1.1 Temporal trends and gaps

With the inclusion of the 13 Early to Middle Triassic localities into the data of both age groups, only one of 35 localities from the

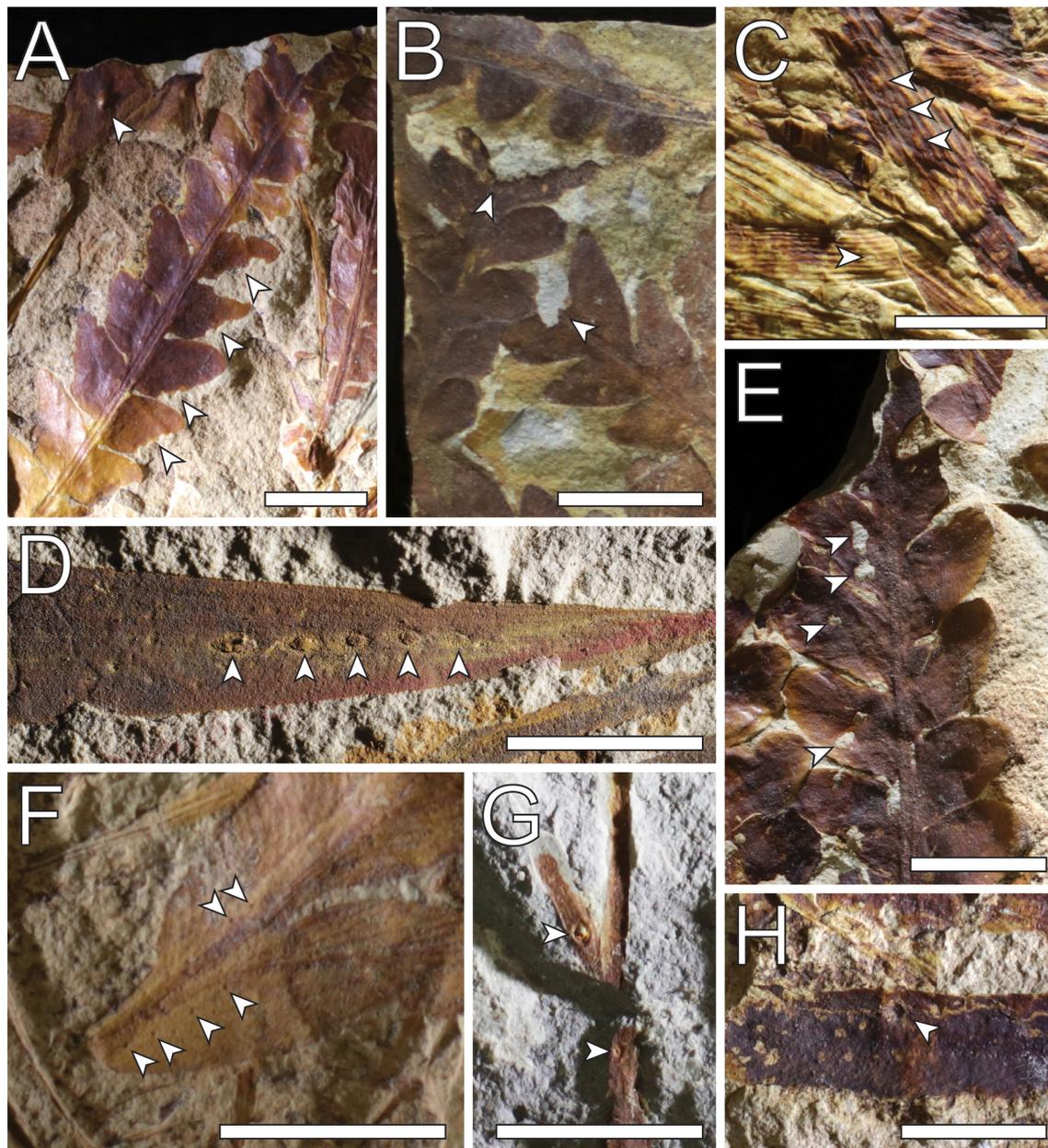


FIGURE 7

Plant–arthropod interaction traces on Benlong Flora fossil fragments. (A) gall (top arrow) and margin feeding on two fragments of *Dicroidium* sp. (F61131); (B) apical margin feeding on two fragments of *Dicroidium odontopteroides* (F61138); (C) oviposition scars on two fragments of *Heidiphyllum elongatum* (F61501); (D) oviposition scars on *Heidiphyllum elongatum* (F50237); (E) possible hole feeding on *Dicroidium odontopteroides* (F61140); (F) piercing and sucking on *Dicroidium* sp. leaf (F61143); (G) gall (top arrow) and an uncertain feature (F61129); and (H) gall on seed fern rachis (F61130). Scale bars: 1 cm.

Early Triassic group reported any PAIs (2.9% of localities), and eleven of 63 localities from the Middle Triassic group (17.5% of localities) yielded PAIs (Figure 2; Table 1; Supplementary Table S2). Our survey highlights the distinct paucity of arthropod trace fossil records from Early Triassic floras across Gondwana, with only one pteridospermous seed hosting putative arthropod traces reported from the Nidpur beds of India (Table 1; Supplementary Table S1). In contrast, at least 544 Middle and Middle-to-Late Triassic plant fragments from eleven localities have been confirmed to host PAI traces, from ten of eleven categories of FFG: margin feeding (5.70%

of quantifiable reports); hole feeding (0.74%); surface feeding (0.37%); piercing and sucking (0.74%); mining (1.65%); galling (31.62%); oviposition (3.68%); boring (40.44%); palynophagy (0.18%); pathogenic/fungal damage (14.89%). The remaining FFG, skeletonization, has been recognized but is possibly of Late Triassic age (Table 1; Supplementary Table S1).

Austral temperate floras were fundamentally restructured after the end-Permian extinction event. Earliest Triassic vegetation consisted of low-diversity open forests dominated by lepidopterid peltasperms and scale-leafed voltzialean conifers in the upper story,

and pleuromeian lycopsids, sphenopsids, and ferns in the understory (Retallack, 1980a; Mays et al., 2020; Vajda et al., 2020; McLoughlin et al., 2021a). There are 247 plant species across 118 genera reported from the Gondwanan Early Triassic, and 608 species from 200 genera identified from the Middle Triassic (Supplementary Table S1). Whereas the latest Permian to Early Triassic PAI was identified on a seed fern taxon, the Middle to Late Triassic PAIs are distributed across ferns, sphenophytes, conifers, cycads, ginkgophytes, seed ferns, and plants of uncertain taxonomic affinity (Supplementary Table S1). This disparity may be due to the relatively low productivity and slow recovery of the immediate post-EPE flora compared to the Middle Triassic. Low productivity and low diversity of vegetation would have contributed to fewer Early Triassic PAIs by: 1, producing fewer leaves for potential burial and 2, sustaining a smaller and less diverse population of arthropods. The difficulty in confidently identifying feeding traces on small needle- and scale-shaped leaves (e.g., voltzialean leaves and pleuromeian microphylls), owing to their diminutive size and commonly dense occurrence, may have implications for assessing damage frequency in the Early Triassic, when leaves of this type were proportionately more common (Figure 4). The absence of coals immediately post-EPE (Retallack et al., 1996) may provide another, economic, bias for the observed trends, as historic coal-mining efforts have produced a significant proportion of known plant fossil collections.

4.1.2 Geographic trends and gaps

Strata from South America and Oceania contain the vast majority of Lower and Middle Triassic palaeobotanical assemblages (Figure 2; Supplementary Table S2), floral diversity (Figure 5; Supplementary Figure S1; Supplementary Table S3) and PAIs (Figure 5; Table 1), constituting 75% of Gondwanan PAI-reporting localities and suggesting a major sampling bias towards these regions. Of the 23 South American localities included in the plant fossil database, five (21.7%) contain PAI traces attributable to at least seven FFG categories, whereas in Oceania only four of 50 localities (8%) host reported PAIs, in at least five FFGs. As both regions report sufficiently high numbers of plant species (Supplementary Table S3), this observed difference in the number of recorded FFGs from localities in Oceania versus South America likely represents a bias in effort towards South American arthropod trace fossil investigations. The PAI investigations of South America constitute the majority of quantitative PAI assessments included in the database (Potrerillos and Santa Maria formations in particular; all MT–LT; Table 1), however, there is a notable lack of Lower Triassic fossiliferous strata reported from South America (Supplementary Tables S2, S3). As discussed in section 4.1.1, the disparity in floral productivity between the Early and Middle Triassic is likely to impact the probability of finding PAIs over these two time intervals, and the greater proportion of Lower Triassic strata in Oceania suggests another potential reason for the observed South American PAI report abundance.

The Lashly Formation (Antarctica; MT–LT) yielded one leaf hosting fungal hyphae, the Fremouw Formation (Antarctica; MT–LT) and the Nidpur beds (India; LP–ET) do not report any PAIs on leaves at all, and the Umm Irna Formation (Jordan; late Permian)

reports only hole-feeding on one species of *Dicroidium* to make a combined total of four FFGs across these three Gondwanan regions (possibly five, as it was not clear what type of interaction was occurring on the Nidpur seed). There is clearly great potential in advancing research on the Early Triassic floras and PAIs of these broad regions.

To the authors' knowledge, the Benolong Flora investigation presented herein represents the first quantitative PAI assessment of an Early or Middle Triassic macrofloral assemblage from Oceania. More PAI traces were identified in the Benolong Flora than the majority of other assemblages in the database, except for the well-studied Santa Maria Formation fossil suites, and the quantitative investigations undertaken on wood specimens of the Fremouw Formation (Table 1); both of these assemblages are possibly Late Triassic in age. Furthermore, higher FFG diversity was identified in the Benolong Flora than any Antarctic, Arabian, Oceanian, and Indian localities, and three out of five of the South American stratigraphic units (Table 1). These findings indicate a high likelihood of under-reporting and under-investigation of PAIs for Triassic strata across the majority of Gondwana and clearly demonstrates how a concerted investigation can greatly increase the reported number of PAIs.

4.2 Future work and recommendations

Although there has been increased interest in PAI investigations in recent years, this compilation of data indicates large temporal and spatial gaps in our knowledge of plant–arthropod interactions during this interval of Gondwanan history. The pattern of gaps in the database can be informative, since they are not equally distributed in time or space, and our understanding of ancient plant–arthropod interactions is almost entirely dependent on the accuracy of identification and completeness of the plant fossil record.

The variation in floral composition between the Early to Middle Triassic resulted in major changes in the representation of shapes, sizes, and densities of leaves and other organs. The arthropod populations surviving in these evolving plant communities may have resulted in taxonomically specialized plant–arthropod interactions and spatiotemporal variations in FFG abundances. Taxonomic trends in FFG distribution on plants are difficult to discern from the current post-EPE PAI record, since specific plant–arthropod associations have not yet been reported in sufficient detail in most cases. Although some affected taxa and species were described in the reports included in this review, many PAIs/FFGs identified were not linked to specific plant taxa outside of individual instances in the figured specimens, and the numbers of affected leaves/organs per FFG were not clearly stated in many cases.

Thomas and Hill (2023) identified significant under-reporting of insect damage from plant fossils illustrated in the figures of Cenozoic publications, owing, in part, to the tendency for palaeobotanical researchers to preferentially illustrate undamaged leaves in their papers. This highlights the necessity for greater awareness of, and emphasis on, the reporting of PAIs by researchers conducting these plant taxonomic studies. Therefore, increased

efforts in describing new localities and floral assemblages, revisiting existing palaeobotanical collections and publications, and conducting PAI assessments would greatly increase available data and the reliability of any trends observed.

More extensive Early Triassic Gondwanan floral assemblage identification, collection, taxonomic description and PAI assessment would enable more accurate comparisons to Middle Triassic PAI records, and the determination of ecological recovery trends from this interval. Description of more floral assemblages from Middle Triassic strata of Africa, Antarctica, South Asia and the Arabian Peninsula would also provide a more representative pan-Gondwanan assessment of PAI spatiotemporal trends. Oceania hosts the majority of described palaeobotanical records in this database; however, PAIs from the Australasian flora are relatively understudied compared to South American assemblages. Eastern Australia in particular, hosts a thick succession of continental upper Permian to Middle Triassic stratigraphic units (Herbert, 1997; Fielding et al., 2021; McLoughlin et al., 2021a; Fielding et al., 2022) and an abundance of fossil plant-bearing strata (e.g., in the Bowen, Nymboida and Sydney basins and the Esk Trough; Walkom, 1924; White, 1965; Raggatt, 1969; White, 1969, 1971; Rigby, 1977; Retallack, 1980a; Playford et al., 1982; Cantrill and Webb, 1998; Holmes and Anderson, 2013b) that represent useful targets for tracking the evolution of Gondwanan Permian–Triassic plant and arthropod interactions.

Detailed quantification of arthropod damage (e.g., DT/FFG intensity and diversity; Schachat et al., 2022) is not currently practical for this time interval of Gondwana. With larger datasets resulting from detailed taxonomic assessment of more floral assemblages, and increased reporting of insect damage types, more quantitative analyses can then be conducted. A more accurate understanding of the changes in relative abundances of plant groups over time will contextualize implications for the PAI record (e.g., preferential or specialized arthropod interactions with specific plant groups, DT/FFG preservation biases between leaf types).

To this end, it is recommended that a standardized approach for the assessment and reporting of PAIs is implemented, necessitating approaches that accurately identify, record and report PAI data. Variation in preservational conditions between floral assemblages (e.g., impressions vs coalified compressions) may influence the detectability of various DTs and FFGs, potentially leading to reporting biases in DT frequency. Similarly, different PAI assessment techniques may be better for highlighting particular FFGs (e.g., analyzing images vs hand specimens, using microscopy, low-angle lighting, UV light, and X-ray tomography). Incorporating the DT code of Labandeira et al. (2007; unpublished additions) into PAI assessments will standardize records and increase confidence in DT identification. The ‘sampling unit’ per individual PAI recorded should be clearly defined as either one rock specimen, one plant fossil, or one plant organ (e.g., one leaf). Furthermore, a standard of quantitative reporting of findings should be established: for each DT, the average number of traces per plant sampling unit, the total number of sampling units involved, and the affected plant taxa should be reported; for each FFG, the DT diversity and distribution

across plant taxa could then be compared (see Labandeira et al., 2018).

Addressing these concerns will also enable researchers to contrast trends in plant–arthropod interactions from Gondwana to those of the Laurasian and Tethyan regions for a global perspective on the terrestrial ecological response to late Permian to Middle Triassic climatic instability.

5 Conclusions

This review summarizes our present understanding of an essential component of terrestrial ecosystem function following the most severe extinction event in Earth’s history. The compilation of Early and Middle Triassic fossil leaf floras of Gondwana and their associated arthropod traces presented herein demonstrates:

1. The present state of the published fossil record is temporally and spatially biased, providing an unreliable gauge of terrestrial ecosystem changes during the end-Permian event recovery in Gondwana. These spatial and temporal biases, particularly the patchiness and under-representation of PAI reporting, need to be addressed before the available data can be meaningfully assessed for quantitative ecological trends.
2. The reliability of the Gondwanan PAI record is compromised by two main biases. Firstly, observational biases, which include a geographical skew against Gondwanan collections in favor of those from Laurasia and the Tethys regions, and within Gondwana, a greater representation of assemblages from South America and Oceania. There is also a stratigraphic observational bias, particularly against Lower Triassic strata, which have historically received less attention owing to their scarcity of fossils and coal. Secondly, preservational biases will tend to facilitate the identification of PAIs in certain styles of fossilization and in specific types of leaves or plant organs over others (e.g., broad vs scale-like leaves). In addition to these biases, an absence of standardized data collection currently limits meaningful comparisons across the region.
3. By mitigating the limiting factors above, it may in the future be possible to utilize the PAI record of Gondwana to construct distinctive ecological and evolutionary trends during the recovery period following the end-Permian event.
4. In contrast to existing PAI reports from the Australian Early to Middle Triassic (that documented three fossil plant specimens hosting one PAI trace each), our systematic investigation of the Benolong Flora revealed 44 PAI traces consistent with published DTs, hosted by 40 fossil plant fragments. This demonstrates that a concerted quantitative investigation can greatly increase the number of PAIs identified on an assemblage and reaffirms the likelihood of under-reporting of PAIs for similarly overlooked Gondwanan sites.

5. We propose several key next steps to address the demonstrable gaps in our collective knowledge of Early to Middle Triassic Gondwanan floras and arthropod interactions. Specifically, we advocate for establishment of a standardized approach for assessing and reporting PAIs that will facilitate accurate identification, recording and reporting of PAI data. Finally, we highlight that the excellent Early and Middle Triassic macrofloral assemblages from age-controlled, and readily accessible localities in eastern Australia offer a remarkable opportunity to track the long-term patterns of recovery in plant and arthropod herbivores from before the end-Permian extinction through the environmental crises of the Early to Middle Triassic.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author/s.

Author contributions

H-AT: Conceptualization, Funding acquisition, Investigation, Methodology, Writing – original draft, Writing – review & editing. SM: Conceptualization, Funding acquisition, Methodology, Supervision, Writing – original draft, Writing – review & editing. CM: Conceptualization, Funding acquisition, Methodology, Software, Supervision, Writing – original draft, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2024.1419254/full#supplementary-material>

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