

PALEO-ANTARCTIC RAINFOREST INTO THE MODERN OLD WORLD TROPICS: THE RICH PAST AND THREATENED FUTURE OF THE “SOUTHERN WET FOREST SURVIVORS”¹

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- *Premise of study:* Have Gondwanan rainforest floral associations survived? Where do they occur today? Have they survived continuously in particular locations? How significant is their living floristic signal? We revisit these classic questions in light of significant recent increases in relevant paleobotanical data.
- *Methods:* We traced the extinction and persistence of lineages and associations through the past across four now separated regions—Australia, New Zealand, Patagonia, and Antarctica—using fossil occurrence data from 63 well-dated Gondwanan rainforest sites and 396 constituent taxa. Fossil sites were allocated to four age groups: Cretaceous, Paleocene–Eocene, Neogene plus Oligocene, and Pleistocene. We compared the modern and ancient distributions of lineages represented in the fossil record to see if dissimilarity increased with time. We quantified similarity–dissimilarity of composition and taxonomic structure among fossil assemblages, and between fossil and modern assemblages.
- *Key results:* Strong similarities between ancient Patagonia and Australia confirmed shared Gondwanan rainforest history, but more of the lineages persisted in Australia. Samples of ancient Australia grouped with the extant floras of Australia, New Guinea, New Caledonia, Fiji, and Mt. Kinabalu. Decreasing similarity through time among the regional floras of Antarctica, Patagonia, New Zealand, and southern Australia reflects multiple extinction events.
- *Conclusions:* Gondwanan rainforest lineages contribute significantly to modern rainforest community assembly and often co-occur in widely separated assemblages far from their early fossil records. Understanding how and where lineages from ancient Gondwanan assemblages co-occur today has implications for the conservation of global rainforest vegetation, including in the Old World tropics.

Key words: Antarctica; assemblage; Australia; biogeography; Gondwana; New Zealand; Old World tropics; paleobotany; Patagonia; rainforest.

The recognition of similar plant communities on isolated landmasses played an important role in the development of modern biogeography (Raven and Axelrod, 1974). Hooker (1853) first recognized elements of a circum-Antarctic flora in the forest and alpine habitats of Australia, New Zealand, and

South America. An iconic example is the *Nothofagus* (Antarctic Beech)–conifer rainforest assemblages that occur today in cool, high-rainfall areas of those regions (Hill, 1994). The rich paleobotanical history of the *Nothofagus* assemblage—and many others like it—classically suggests persistence of Gondwanan rainforest associations from deep time to the present and provides strong support for the concept of phylogenetic biome conservatism (Crisp et al., 2009). For example, fossil discoveries from the Paleogene of Patagonia and Australia include many shared genera that are now extinct in Patagonia but are extant, often in association, in Australasian and southeast Asian rainforests (e.g., Hill et al., 1999, 2008; Wilf et al., 2013).

Differences in plant traits and climate tolerances that reflect abiotic gradients determine the success of plants under different environmental conditions (Schimper, 1903; Westoby and Wright, 2006). The timing of the Gondwanan breakup, the

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movement and isolation of the various landmasses, and subsequent shifts in global climate shaped Southern Hemisphere plant evolution, distribution, assembly, and extinction (Raven and Axelrod, 1974; Wilford and Brown, 1994; Sanmartín and Ronquist, 2004; Lawver et al., 2011; Weston and Hill, 2013; Wilf et al., 2013; Bowman et al., 2014). The loss of suitable habitat in middle to high latitudes since the early Paleogene, and subsequent (Neogene) movement into newly emerging moist upland habitats (often in lower latitudes), resulted in major shifts in the distributional ranges of rainforest components in the paleo-Antarctic Gondwanan flora. Survival was dependent on the positions of major continents in relation to suitable versus aridifying climatic zones, and the timing of opportunities that included the emergence of land (Lawver et al., 2011). New land emerged in orogenic events associated with the formation of volcanic arcs and trains of emerging islands, and with plate collisions and uplifts (Lawver et al., 2014). These geological forces have controlled the always changing distributions of less extreme (i.e., warm-cool, and generally frost-free), wet (perhumid) habitats, across a substantial range of global latitude and longitude.

Close geographic proximity between South America and Antarctica was still evident during the Late Cretaceous and continued until at least the early Eocene, after which isolation by formation of the Drake Passage began. Like Patagonia, Australia was still proximal to, but began to separate from, Antarctica during the middle to late Eocene (Wilford and Brown, 1994; Lawver and Gahagan, 1998; Lawver et al., 2011, 2014; Dalziel, 2014). After the Eocene, the Australia–Antarctica–South America corridor was severed, deep seaways formed (but see Dalziel, 2014), and Antarctic glaciation and the global transition from greenhouse to icehouse conditions were underway (e.g., Zachos et al., 2001; Francis et al., 2009).

Despite those abiotic changes, elements of the Gondwanan rainforest flora can now be found, usually at great distance from the fossil sites that document their early history, on both old and more geologically recent terrains. These include Australia, New Zealand, Patagonia, New Guinea, New Caledonia (Burbidge, 1960; Webb and Tracey, 1981; Hill, 2004), remote locations in the southwest Pacific such as Fiji and Vanuatu (Enright and Jaffré, 2011), and recently uplifted areas of Southeast Asia, including Mt. Kinabalu in northern Borneo (Kitayama et al., 2011). Each of those separate and geologically diverse regions contains areas with mesic climates that harbor plant communities with surviving Gondwanan lineages, thus hypothetically approximating the ancestral biome.

Some of the strongest signals for shifts in distribution of Gondwanan lineages come from the fossil and living southern conifers, which were among the first living Australasian taxa recognized in Patagonian fossil floras (Berry, 1938; Florin, 1940a, b; Brodribb and Hill, 1999). Recent studies have identified physiological traits in many of the broad-leaved southern conifers related to water balance, and shade and freezing tolerance, which are thought to have strongly influenced deep-time shifts in their distributions and relative abundance (Hill and Carpenter, 1991; Brodribb et al., 2005; Biffin et al., 2012; Brodribb et al., 2014). Because those conifer lineages are regarded, for well-understood physiological reasons, as drought intolerant today, they are presumed to have been so in the past (Brodribb and Hill, 1998, 1999; Brodribb, 2011; Brodribb et al., 2012; Wilf, 2012).

The survival of Gondwanan rainforest lineages is critically important to conservation in the modern world. Their history shows that they adapted to, or tracked, global climate change,

were subjected to large-scale extirpation events, and continued to contribute to rainforest assembly across the Southern Hemisphere. Today, they remain important to the survival, diversity, and function of many rainforest areas, including montane parts of the modern Asian tropics (e.g., Kitayama, 1992). However, human activities are now exposing those survivors to significant and rapid global and local disturbances, including logging, clearing, and climate change (e.g., Laurance et al., 2014), that is unlike anything known from the fossil record. The rates of disturbance and change are widely thought to be too rapid for these lineages to adapt, or to track suitable habitat across large areas of unsuitable terrain.

In recent years, fossil discoveries at sites across the Southern Hemisphere have dramatically expanded our direct knowledge of paleorainforests on the former Gondwanan landmasses (Hill, 1994; Brodribb and Hill, 1999; Zamaloa et al., 2006; Barreda et al., 2012; Wilf et al., 2013). This increase in paleontological knowledge provides an exciting opportunity to use site-assemblage data to quantify the patterns of distribution and co-occurrence of southern lineages from deep time to the present.

We here present a large compendium of fossil rainforest sites and their constituent taxa from Patagonia, Antarctica, Australia, and New Zealand, and we compare the fossil assemblages to the extant distributions of the same lineages, using data from Australia, New Zealand, Patagonia, Papua New Guinea, New Caledonia, Fiji, and Mt. Kinabalu. We analyze these data to quantify and identify: (1) Gondwanan rainforest composition; (2) the signal of the ancient in modern assemblages; and (3) the floristic fidelity of Gondwanan rainforest assemblages through time and space. We use these analyses to test the ideas that floristic dissimilarity among regions increased with time, and that Gondwanan rainforest associations have persisted within regions. In addition, we ask whether the strengths of contribution by particular southern rainforest lineages shifted through time, and what influence those genera and families have on patterns of floral assembly.

MATERIALS AND METHODS

Fossil data compilation—An ARC-NZ Vegetation Network Working Group meeting at Macquarie University allowed the initial gathering of the authors in Sydney, Australia, August 2010, to undertake: (1) a compilation of suitable Late Cretaceous to Pleistocene Gondwanan fossil sites and the well-identified components of their macrofloras and microfloras, plus geochronologic data (see Supplemental Data with the online version of this article; Appendices S1 and S2); (2) data assessment and cleaning; and (3) taxonomic resolution and updates.

Fossil rainforest sites were identified by comparing the constituent taxa of assemblages with an a priori list of primary Gondwanan rainforest indicator taxa. That list included certain co-occurring southern conifers and associated angiosperm taxa identified in the literature (e.g., Hill, 1994; Brodribb and Hill, 1999) and by the authors as the strongest indicators of rainforest (Table 1). Our focus was on the multiple and repeated co-occurrence of these rainforest indicator lineages, not rainforest structural definition *sensu stricto*, which is far more difficult to evaluate from fossil assemblages. The primary matrix includes separate fields for major fossil organ categories, including leaf, cuticle, reproductive (fruit, seed, flower), wood, and pollen (Table 2). The organ categories were merged for each taxon by region to genus (or family) level for the taxon-level analyses (Appendix S2). Species-level data, while noted in our compilation, were often not available, or comparisons between very similar fossil species were difficult to evaluate. Lists of woody taxa from extant rainforest floras in Australia, New Zealand, and Patagonia were compiled to compare extant taxon richness and taxonomic structure with fossil floras (Table 3a–d).

Our approach does not involve or assess the extensively discussed “vicariance versus dispersal” biogeographic scenarios or molecular “dating” techniques (e.g., Weston and Hill, 2013; Wilf and Escapa, 2014). Instead, we make

TABLE 1. Indicator taxa used to recognize fossil-rainforest sites of Late Cretaceous and younger age and their fossil occurrences in the four major regions studied.

	Aust	NZ	Pat	Ant
CONIFERS				
<i>Agathis</i>	1	1	1	0
<i>Araucaria</i>	1	0	1	1*
<i>Dilwynites</i>	1*	1*	1*	1*
<i>Acropyle</i>	1	0	1	0
<i>Dacrycarpus</i>	1	1	1	1*
<i>Dacrydium</i>	1	1	1*	1*
<i>Falcatifolium</i>	1	0	0	0
<i>Lagarostrobos</i>	1	1*	1*	1*
<i>Lepidothamnium</i>	1	0	0	0
<i>Microstrobos</i>	1	0	0	0
<i>Phyllocladus</i>	1	1	1*	1*
<i>Podocarpus</i>	1	1	1	1*
<i>Prumnopitys</i>	1	1	0	0
<i>Retrophillum</i>	1	0	1	0
<i>Athrotaxis</i>	1	0	0	0
<i>Fitzroya</i>	1	0	0	0
<i>Libocedrus</i>	1	1	0	0
<i>Papuacedrus</i>	1	0	1	0
ANGIOSPERMS				
Chloranthaceae	1*	1*	1*	1*
<i>Gymnostoma</i>	1	1	1	0
<i>Nothofagus_Brassospora</i>	1	1	1	1*
<i>Nothofagus_Fuscospora</i>	1	1*	1	1
<i>Nothofagus_Lophozonia</i>	1	1*	1	1*
<i>Nothofagus_Nothingus</i>	1	0	1	1*
Trimeniaceae	1*	0	1*	0

Notes: Aust = Australia; NZ = New Zealand; Pat = Patagonia; Ant = Antarctica. *Athrotaxis* is known from older fossil deposits in Patagonia (Menéndez, 1966; Del Fueyo et al., 2008). *Papuacedrus* (and potentially other conifers on this list) is known from the Eocene of Antarctic Peninsula (Zhou and Li, 1994; Wilf et al., 2009), but not from a site that meets our vetting criteria. List includes extant southern conifer and associated primary indicator angiosperm lineages. For simplicity, palynotaxa thought to correlate to particular extant taxa (e.g., the pollen type *Dacrycarpites*, corresponding to the living genus *Dacrycarpus*) are simply reported under those taxa; see Appendices S1 and S2. *Dilwynites* is listed separately because of its affinities to both *Agathis* and *Wollemia* (Macphail and Carpenter, 2014). *Microstrobos* is synonymous with *Pherosphaera*. * Pollen record only.

direct use of the burgeoning primary data and examine empirically where lineages are actually known to have occurred through time and space, based on their fossil occurrences and their geochronologic constraints (Gradstein et al., 2012). Our extensively vetted compilation of sites and occurrences, as described below, is fully presented online (see Supplemental Data with the online version of this article) for those who wish to explore further using other approaches.

We compiled a matrix of 63 sites and 396 taxonomic occurrences, representing 154 families of vascular plants, from locations in Patagonia, Malvinas/Falkland Islands, Antarctica, New Zealand, and Australia (Table 3a). We provide one additional site in the compendium that is from eastern Antarctica (Appendix S2; Pross et al., 2012) but do not include it in quantitative analyses because it is the only deep-sea core. Extant and extinct taxa were selected and coded to allow filtering of the data. Data sources are provided in full in the supplemental materials to this article as a reference list linked to sites (see Appendix S1). As described above, sites were included in the compendium on the basis of rainforest floristic affinities, so the list of localities per region is not exhaustive. Occurrences for some of the individual lineages described here were also excluded because these were not clearly associated with rainforest fossil sites or had limited supporting information, especially regarding geologic age (e.g., *Papuacedrus* in Antarctica: Zhou and Li, 1994; *Lactoris* in Australia: Macphail et al., 1999). We vetted all fossil occurrences carefully to modern standards based on their preservation of diagnostic features, and we accordingly rejected many doubtful occurrences in the literature. Taxonomic assignments were done at

TABLE 2. Summary of fossil datasets and bases for derived analyses.

Dataset	Derived from	Published
1. Macrofossil taxa records: 852	Primary, literature	Yes
2. Palynotaxa records: 1734	Primary, literature	Yes
3. Leaf component: 429	Dataset 1	Yes
4. Cuticle component: 319	Dataset 1	Yes
5. Reproductive organs: 83	Dataset 1	Yes
6. Wood: 22	Dataset 1	Yes
7. Fossil Locations: 63	Datasets 1, 2	Yes
8. Genera / Families (identified): 396	Datasets 1, 2	Yes
9. Conifers (all): 34	Datasets 1, 2	Yes
10. Conifers (indicator): 33	Datasets 1, 2	Yes
11. Angiosperms: 315	Datasets 1, 2	Yes
12. Ferns and lycopsids: 39	Datasets 1, 2	Yes
13. Cycads: 3	Datasets 1, 2	Yes
14. <i>Sphagnum</i> : 2	Datasets 1, 2	Yes
15. Hornworts: 1	Datasets 1, 2	Yes
16. Liverworts: 2	Datasets 1, 2	Yes
17. Extinct: 62 (total)	Datasets 1, 2	Yes
18. Extinct conifers: 8	Datasets 1, 2	Yes
19. Extinct angiosperms: 51	Datasets 1, 2	Yes
20. Extinct ferns: 2	Datasets 1, 2	Yes
21. Extinct Ginkgoaceae: 1/1	Datasets 1, 2	Yes

Notes: Associated literature and published sources are provided as a bibliography in the supplemental materials to this article (Appendix S1). Datasets (1) and (2), from which all the other datasets are derived, were merged into a single matrix (Appendix S2). In all cases, tallies represent identified fossil taxa by location(s) as records (occurrences), not total number of individual fossils. In most cases, and always for macrofossils, there is at least one museum specimen supporting the identification, usually of type, figured, and/or referenced material as listed in the source publications. This is not always the case for pollen.

two levels for subsequent analyses: genus and family. Most (61%) fossil taxonomic occurrences were identified to living genus by default. Where occurrences could be identified to family but not to genus (23%), we used the family name. The remainder represented mostly extinct genera (refer to Appendix S2). To simplify the text, we refer to taxa as “genera” throughout but acknowledge the inclusion of family-level data (described above). Also, several taxa that are strictly considered near equivalents of genera were analyzed as “genera.” One example of this is the four sections of *Nothofagus* (recently proposed as separate genera by Heenan and Smitsen, 2013), analyzed here under their historical section names.

The fossil rainforest compilation includes the most significant examples of the trans-Antarctic paleorainforest flora, in the broad sense, that is best known from the Late Cretaceous to late Eocene of the western Antarctic; Late Cretaceous to early Paleocene (Maastrichtian–Danian), early and middle Eocene, and early Miocene of Patagonia plus Malvinas/Falkland Islands; late Paleocene to late Pleistocene of Australia; and Paleocene and early Miocene of New Zealand. Details are provided in Appendix S2. Geochronology is based on Gradstein et al. (2012), as updated at <http://www.stratigraphy.org/ICSChart/ChronostratChart2014-02.jpg>.

Consistent with the known age of separation of the last Gondwanan landmasses from Antarctica during the Eocene and the associated global cooling events, we allocated sites to four broad time bins: K—Cretaceous; P—Paleocene and Eocene; Ne+O—Neogene plus Oligocene; and Pleistocene. We note that Australia and New Zealand had no Cretaceous rainforest fossil sites in our data, and only Australia had Pleistocene sites.

Multivariate analyses—The multivariate analyses were based on three site-by-genus occurrence matrices, described in sequence below. All multivariate analyses were done using Primer version 6 (Clarke and Gorley, 2006). Sites in ordinations were labeled by geographic region (location) and age (see above; Figs. 1 and 2).

First, to compare all fossil assemblages in relation to age and region, we used the “full” matrix (Table 3a) based on the presence of genera ($n = 396$) at all identified fossil sites ($n = 63$; Fig. 1). Dissimilarity among sites was measured using Sorensen distances and nonmetric multidimensional scaling (NMDS) based on the underlying distance matrix. Lineage (genera) contributions

TABLE 3. Summary by region of number of known rainforest fossil taxa for three matrices used in multivariate analyses and for extant floras.

3a.	Full fossil data	Australia	New Zealand	Patagonia	Antarctica	Totals
	Number of families	125	66	93	45	154
	Number of genera	334	99	151	60	396
3b.	Reduced fossil data	Australia	New Zealand	Patagonia	Antarctica	Totals
	Number of families	62	59	80	40	95
	Number of genera	112	85	116	52	153
3c.	Survivor woody genera					
	Number of woody families	31	24	43	14	49
	Number of woody genera	68	39	63	23	87
3d.	Extant woody data	Australia	New Zealand	Patagonia	Antarctica	Totals
	Extant families	136	57	50	NA	162
	Extant genera	667	70	81	NA	759
	Extant woody species	2308	222	163	NA	2693

Notes: 3a. Full fossil data—families and genera in the full fossil data compendium (396 genera by 63 sites and 4 locations); 3b. Reduced fossil data—the 153 genera by 56 sites and 4 locations remaining after removal of: sites 1, 4, 5, 20, 13, 54, and 56; extinct lineages; and singleton taxa, by location (see text); 3c. Survivor woody genera—the 87 living woody genera representing known fossils; and 3d. Extant woody data—overview of the total extant woody rainforest floras from three regions (Australia, New Zealand, and Patagonia) for comparison to 3c.

to multivariate (Sorensen) similarity within, and dissimilarity among, groups of sites representing regions (Antarctica, Patagonia, Australia, and New Zealand) were quantified using the Simper routine (in Primer). This routine decomposes similarities within pairs of samples of a group (e.g., among samples of a single region at different times), and dissimilarities among groups (regions), into percentage contributions from each genus, and lists the taxa in decreasing order of contribution for every pairwise comparison.

Second, the same procedure was applied to a “reduced” matrix of 56 sites and 153 genera (Table 3b; Fig. 2). The data from the full matrix (Table 3a) were filtered to remove the following: Pleistocene locations in Australia, because these had no analogues in other regions; outlier sites without rainforest indicator conifers; one site (S56-Balcombe Bay) with only three genera recorded and described to date; extinct genera; and all taxa that occurred at only one site (singletons). The reduced matrix allowed us to (1) test the influence of outliers and singletons on the data analysis; (2) improve the basis for comparison among regions by aligning ages and removing the disproportionate amount of Pleistocene data from Australia; and (3) assess any shifts in site position in the ordinations in relation to pairwise comparisons and groupings with the reduced information. The Simper routine described above was repeated on the reduced matrix.

To measure the strength of influence of genera on the position (similarity) of assemblages in the ordination, we used the column-wise (site–region) aligned presence data (0–1) in the matrix to provide a binary ranking from which the standard product-moment correlation (Pearson) is computed. Because we used 0–1 presence data only, this defaults to a Spearman rank coefficient (Legendre and Legendre, 1998) that uses the taxa as variables. Values range from 0 to 1, where 0 = no influence and 1 = strongest possible influence. The results do not show causality, nor do they account for the problem of rare species interactions. However, they do highlight the complex relationships between genera and regions in a broad sense. We note that influence can include increasing or decreasing presence, and local extinction, across regions through time.

The third “age-by-region” matrix was used to compare the contributions of genera occurring as fossils to both fossil and modern assemblages. The matrix was produced by merging the fossil sites by the four regions (Australia, Patagonia, New Zealand, and Antarctica) into three age categories (bins), K, P–E, and Ne+O, and including only the woody genera occurring in the four locations. The rationale for excluding other life forms was that trees and vines represent the main structural features of any rainforest assemblage, and nonwoody plants are rarely and unevenly represented as fossils. We refer to the 87 woody fossil genera remaining in the matrix (Tables 3c and 4) as “survivor” taxa. This matrix included nine age-by-region fossil assemblages: P–E and Ne+O for Australia; K, P–E, and Ne+O for Patagonia; P–E and Ne+O for New Zealand; and K and P–E for Antarctica. We then added the extant distributions of the genera in the fossil matrix based on their occurrences in seven areas: Australia, New Zealand, Patagonia, Papua New Guinea, New Caledonia, Fiji, and Mt. Kinabalu. These included all fossiliferous regions in our dataset where rainforest is still extant (Australia, Patagonia, and New Zealand), and both old and relatively recent terrains. The additional regions included the northern uplift and older southern areas of New Guinea; Mt. Kinabalu, a recently uplifted granitic monolith associated with old Gondwanan fragments in South East Asia (Cottam et al., 2013); New Caledonia from the northern tip of Zealandia, the now largely submerged landmass that also included New Zealand (Schellart et al., 2006); and Fiji. Fiji represents an island

group in the southwest Pacific associated with continental crust of possible Gondwanan origin that includes both older (late Eocene) island–arc volcanics and more recent (Miocene) plutonic intrusions (Neall and Trewick, 2008).

We note that applicable fossil sites for comparison are not yet available from these additional areas. However, there are palynological data that show relatively late (post-Eocene, particularly Neogene) penetration for most relevant southern lineages into areas north of Australia, and a corresponding lack of southern-derived taxa during the early Eocene and earlier Cenozoic (Muller, 1966; Khan, 1976; van der Kaars, 1991; Morley, 1998, 2002; Jin, 2009; Yao et al., 2009). For example, *Dacrydium* reached Southeast Asia by the Oligocene, and *Dacrycarpus* and *Phyllocladus* probably dispersed into New Guinea (from adjoining Australia) during uplift in the Miocene, then “island-hopped” to Borneo during the mid-Pliocene (Morley, 2011). By contrast, fossil pollen of *Podocarpus* and some other taxa first appear in Southeast Asia in the Eocene, either sourced from India as it docked with Asia or via long-distance dispersal from Australia (Morley, 1998, 2011).

The age-by-region matrix was the basis for the combined neo- and paleo-analyses, comparisons, and interpretations presented, including NMDS ordinations (Figs. 3 and 4) and measures of taxonomic structure (Fig. 5). This matrix allowed us to track the survivors across geographic regions through time (i.e., a “where did they begin” and “where are they now” analysis). To visualize the co-occurrences of genera and provide a directional measure of the strength of their influences on the position (similarity) of assemblages in the ordination, vectors representing the genera were added to the NMDS ordination using Pearson correlation (Fig. 4). The length of the vector axis of a genus is set by the circle (radius 0–1) and represents the strength of contribution to the ordination (Fig. 4). We preface the quantitative results with a qualitative synthesis, and also provide details of the broad-scale location of survivors in both fossil and extant rainforest floras in Table 4. Presence–survival in Australasia and eastern Antarctica was identified as E (= eastern); in West Antarctica and Patagonia as W (= western); and shared as EW (= both). Table 4 includes vector lengths (from the second and third matrices described above) as an overall measure of the strength of contribution by survivors to the multivariate relationship of regions in the ordinations. Actual percentage contributions by survivors to similarity (Simper routine) among regions are provided in the online Supplemental Materials (see Supplemental Data with the online version of this article; Appendix S3) for all three matrices. Appendix S3 allows detailed pairwise comparisons of taxon (including survivor) contributions across all combinations of regions, in relation to both the full and reduced datasets.

It was not our intention, nor was it feasible, to run comparative analyses for the full “living” tropical floras of Australia, Indo-Malesia including New Guinea, New Caledonia, and Oceania. Initial attempts to do so for Australia, New Zealand, and Patagonia (Table 3d) shed minimal light on analyses of surviving fossil lineages because most taxa lack fossil records.

Taxonomic structure—To test whether, and how, taxonomic structures vary across sites and regions, we used average taxonomic distinctness (AvTD) to measure pairwise taxonomic distances between the lineages in a sample, to family and genus level (Clarke and Gorley, 2006). Average taxonomic distinctness is known to be orthogonal to richness and, importantly, is unaffected by either sample size or sampling effort. The measure (AvTD) describes the relatedness



Fig. 1. NMDS ordination of 63 fossil assemblages based on full floristics, representing all identified genera ($n = 396$) from all life forms for each of the four fossiliferous regions grouped by age: K = Cretaceous; P-E = Paleocene and Eocene; Ne+O = Neogene plus Oligocene; and Pleis = Pleistocene. Two Eocene Patagonian sites (larger squares; LH = Laguna del Hunco and RP = Río Pichileufú) nested with the Australian Paleocene to Eocene sites. Antarctica groups with Patagonia. The ordination used the Sorensen distance measure. Stress: 0.2.

of taxa (genera in this case) within a sample at a given richness and uses a simple taxonomic (relatedness) tree with equalized branch lengths, based on the background list of genera and families. Expected values at a given richness represent a null (no taxonomic structure) derived from 1000 random draws from the available pool. Lower values (outside the 95% confidence intervals [CIs] for average taxonomic distinctness in relation to random draws from the full pool) occur when genera have lower taxonomic breadth at a level of richness than expected under a null model (i.e., genera are more related or clustered). Higher values reflect greater taxonomic breadth at a given richness in relation to the null and equate with overdispersion or evenness (i.e., genera are less related).

To compare taxonomic structure across the paleo- and neo-representation of genera in regions, we focus on the age-by-region matrix described above, which included the survivor genera in nine age–location fossil assemblages and seven extant regional assemblages (Figs. 3 and 4). The pool of available taxa is based on the 87 survivors. Taxonomic structure results at site level from the full matrix ($n = 63$ sites; $n = 396$ genera) and the reduced matrix ($n = 56$ sites; $n = 153$ genera) are provided online (see Supplemental Data with the online version of this article; Appendix S4; Figs. S1 and S2).

Continental phylogenetic structure—To quantify the contribution of the Gondwanan rainforest survivor taxa to continental community phylogenetic structure in Australia, we calculated net relatedness index (NRI; Webb et al.,

2002) for a full continental dataset. This was done both with and without the survivor genera included (see Supplemental Data with the online version of this article; Appendix S5; Fig. S3 and Table S1), using the software program Biodiverse (Laffan et al., 2010). A correlation coefficient (r value) was generated to test the hypothesis of “no difference” in continental phylogenetic structure after removal of Gondwanan lineages. The dataset included the distribution records of all Australian woody rainforest taxa (freestanding and climbing plants) but excluded marginal taxa from wet sclerophyll, heath, and mangrove habitats (see Kooryman et al., 2013). We used Australia as a working example because there is access to full continental-scale distribution data previously allocated to 10×10 km grid cells (Kooryman et al., 2013); the continent provides a range of environmental gradients and filters across more than 30° of latitude; and, as reaffirmed here, its fossil record shows continuous occupation by classical Gondwanan lineages despite significant floristic exchange with Indo-Malesia (Sniderman and Jordan, 2011).

RESULTS

Taxonomic patterns—We present the following qualitative synthesis of taxonomic patterns in our data as a framework for interpretation of the quantified measures that follow (Figs. 1–4;

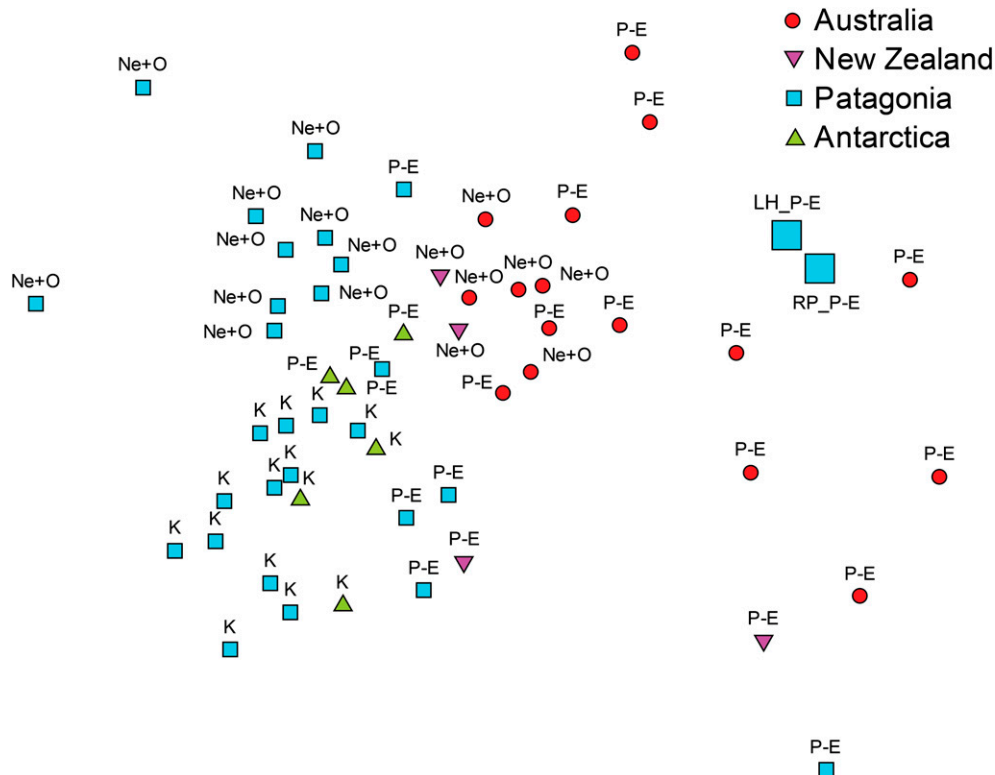


Fig. 2. NMDS ordination of 56 fossil assemblages ($n = 153$ genera) with sites 1, 4, 5, 20, 13, 54, and 56 removed (see text); plus extinct lineages and singleton taxa removed by location. Abbreviations and labeling as in Figure 1. The ordination used the Sorensen distance measure. Stress: 0.19.

Table 4). See Appendix S1 for the primary bibliography that supports this discussion.

Araucariaceae—Fossil Araucariaceae, including *Araucaria*, are known from all land areas in this compilation, and they occur across (and well before) the full temporal range covered here. *Araucaria* Section *Eutacta* occurred in Western and Eastern Gondwana, but it survives only in Australasia (eastern survival), whereas Section *Araucaria*, once present in Australasia and much earlier (Early Cretaceous) in Patagonia, is extant only in South America (western survival). *Agathis*, previously known from the fossil record only from Australia and New Zealand (Hill et al., 2008; Pole, 2008), is now known in Patagonia from early Paleocene and early and middle Eocene macrofossils of both vegetative and reproductive organs (Escapa et al., 2013; Wilf et al., 2014). The extant distribution of the genus is in New Zealand, Australia, Southeast Asia, and Oceania (eastern survival). It is present as fossils in Australia from at least the late Paleocene and in New Zealand since the early Miocene. Pollen assigned to *Dilwynites* can represent both *Agathis* and *Wollemia* (Macphail et al., 2013; Macphail and Carpenter, 2014). It appears in our data during the Eocene of Antarctica and Patagonia and the Paleocene to Pleistocene of Australia, where both *Agathis* and *Wollemia* remain extant (eastern survival).

Podocarpaceae—Records for Podocarpaceae in these data commence in the Late Cretaceous, in Antarctica and Patagonia. We acknowledge many earlier records of extinct podocarp genera, including from the Early Cretaceous of Patagonia (Archangelsky, 1966; Archangelsky and Del Fueyo, 1989; Del

Fueyo et al., 1991), but these cannot be inferred to come from rainforest assemblages. Important genera that are extinct in Patagonia but extant in Australasia and Oceania (eastern survival) include *Microcachrys* (Carpenter et al., 2011), *Dacrycarpus*, *Lagarostrobos*, *Dacrydium*, *Phyllocladus*, and *Acmopyle*. *Lepidothamnium* is extant in New Zealand and South America; *Retrophillum* is extant in both Oceania and northern South America and extinct in Australia; while *Falcatifolium* has no fossil record from southern South America or Antarctica and is extant in Oceania and Australasia. Similarly, *Halocarpus* occurs during the middle Eocene of central Australia and the early Miocene of New Zealand, where it is extant. Both *Dacrycarpus* and *Acmopyle* are noted for their drought intolerance and affinities with extremely wet habitats (Brodribb and Hill, 1998, 1999, 2004). *Dacrycarpus* survived in Australia until the early Pleistocene, while *Acmopyle* is present in these data from the early and middle Eocene of Patagonia and the late Paleocene to early Oligocene of Australia. It is extant today only in the Pacific, as one species each in Fiji and New Caledonia. In our data, *Microcachrys*, *Dacrycarpus*, *Dacrydium*, *Lagarostrobos*, and *Podocarpus* are present in Antarctica and Patagonia during the Late Cretaceous, and in Australia (and a little later in New Zealand) from the late Paleocene. *Prumnopitys* and *Phyllocladus* occur first during the late Paleocene of Australia. While both are known from the fossil record in New Zealand, *Phyllocladus* is not evident there until the early Miocene, whereas *Prumnopitys* is present from the late Paleocene. *Prumnopitys* is extant today in South America, Oceania, Australasia, and New Zealand. *Phyllocladus* is extant in New Zealand, Australia (Tasmania), and Malesia, but extinct in South America (eastern survival).

TABLE 4. Rainforest southern conifers, woody angiosperms, and ferns grouped by family and including survivor genera that occur in our fossil rainforest compendium (Appendix S1). Distributions of survivors in both fossil and extant rainforest floras: E = eastern; W = western (West Antarctica, Patagonia); EW = both. P1 and P2 represent the length (as strength of contribution by genera represented as positive values) of the Pearson correlation vectors from the reduced fossil matrix ($n = 56$ sites) and the age-by-region matrix (Fig. 4), respectively, in relation to the enclosing circle (0–1).

Family	Genus	Fossil	Extant	P1	P2
Conifers					
Araucariaceae	<i>Agathis</i>	EW	E	0.53	0.52
Araucariaceae	<i>Araucaria</i>	EW	EW	0.37	0.14
Araucariaceae	<i>Dilwynites</i>	EW	E	0.17	0.62
Araucariaceae		EW	EW	0.28	—
Podocarpaceae	<i>Acmopyle</i>	EW	E	0.40	0.29
Podocarpaceae	<i>Dacrycarpus</i>	EW	E	0.50	0.46
Podocarpaceae	<i>Dacrydium</i>	EW	E	0.31	0.41
Podocarpaceae	<i>Falcatifolium</i>	E	E	0.24	0.41
Podocarpaceae	<i>Lagarostrobos</i>	EW	E	0.49	0.58
Podocarpaceae	<i>Lepidothamnus</i>	E	EW	—	—
Podocarpaceae	<i>Phyllocladus</i>	EW	E	0.36	0.35
Podocarpaceae	<i>Microcachrys</i>	EW	E	0.52	0.60
Podocarpaceae	<i>Microstrobos</i> ^a	E	E	0.29	0.44
Podocarpaceae	<i>Halocarpus</i>	E	E	0.28	0.33
Podocarpaceae		EW	EW	0.13	—
Podocarpaceae	<i>Podocarpus</i>	EW	EW	0.36	0.69
Podocarpaceae	<i>Prumnopitys</i>	E	E	0.25	0.20
Podocarpaceae	<i>Retrophyllum</i>	EW	EW	0.46	0.24
Cupressaceae	<i>Athrotaxis</i>	E	E ^b	0.37	0.48
Cupressaceae	<i>Austrocedrus</i>	EW	W	0.15	0.43
Cupressaceae		EW	EW	0.26	—
Cupressaceae	<i>Callitris</i>	E	E	—	—
Cupressaceae	<i>Fitzroya</i>	EW	W	0.32	0.20
Cupressaceae	<i>Libocedrus</i>	E	E	0.39	0.34
Cupressaceae	<i>Papuacedrus</i>	EW	E	0.31	0.39
Ephedraceae	<i>Ephedra</i>	EW	W ^c	0.48	0.29
Cheirolepidiaceae	<i>Classopollis</i>	EW	—	—	—
Angiosperms					
Akaniaceae	<i>Akania</i>	W	E	0.34	0.16
Amaranthaceae		EW	EW	0.36	0.63
Anacardiaceae		EW	EW	0.06	0.61
Apocynaceae	<i>Alyxia</i>	E	E	0.11	0.67
Aquifoliaceae	<i>Ilex</i>	EW	E	0.18	0.68
Arecaceae	<i>Arecaceae</i>	EW	EW	0.39	0.40
Arecaceae	<i>Nypa</i>	EW	E	0.30	0.20
Atherospermataceae		EW	EW	0.18	0.38
Casuarinaceae	<i>Gymnostoma</i>	EW	E	0.55	0.51
Casuarinaceae	<i>Casuarina/Allocauarina</i>	EW	E ^d	0.20	0.63
Chloranthaceae	Chloranthaceae	EW	E	0.24	0.47
Cochlospermaceae		W	E	0.34	0.41
Convolvulaceae		EW	EW	0.36	0.61
Cunoniaceae	Cunoniaceae	EW	EW	0.34	0.79
Cunoniaceae	<i>Eucryphia</i>	EW	EW	0.35	0.08
Cunoniaceae	<i>Ceratopetalum</i>	EW	E	0.39	0.36
Cunoniaceae	<i>Caldcluvia (Ackama)</i>	EW	EW	—	—
Cunoniaceae	<i>Callicoma</i>	E	E	0.18	0.48
Cunoniaceae	<i>Gillbeea</i>	E	E	0.09	0.48
Cunoniaceae	<i>Weinmannia</i>	EW	EW	0.13	0.62
Elaeocarpaceae	<i>Elaeocarpus</i>	E	EW	0.28	0.71
Elaeocarpaceae		E	EW	0.18	0.72
Ericaceae	Ericaceae	EW	EW	0.23	0.80
Ericaceae	<i>Richea</i>	E	E	0.20	0.47
Euphorbiaceae	Euphorbiaceae	EW	E	0.27	0.51
Fabaceae	Fabaceae	EW	EW	0.21	0.67
Fabaceae	Caesalpiniaceae	EW	EW	0.30	0.62
Fabaceae	<i>Acacia</i>	E	E	0.18	0.67
Goodeniaceae		EW	EW	0.15	0.58
Gyrostemonaceae		E	E	0.17	0.45
Juglandaceae	Juglandaceae	W	EW	0.09	0.20
Lactoridaceae	<i>Lactoris</i>	W ^e	W	0.20	0.25
Lauraceae	Lauraceae	EW	EW	0.67	0.50
Malpighiaceae		W	EW	0.08	0.56
Malvaceae	<i>Brachychiton</i>	E	E	0.39	0.48
Malvaceae	Malvaceae	EW	EW	0.35	0.81
Meliaceae	<i>Dysoxylum</i>	E	E	0.15	0.74

TABLE 4. Continued.

Family	Genus	Fossil	Extant	P1	P2
Menispermaceae	Menispermaceae	W ^f	E	0.12	0.49
Myricaceae	Myricaceae	W	EW	0.27	0.20
Myrtaceae	Myrtaceae	EW	EW	0.35	—
Myrtaceae	<i>Eucalyptus</i>	EW	E	0.21	0.46
Nothofagaceae	<i>Nothofagus</i> _Brassospora	EW	E	0.69	0.41
Nothofagaceae	<i>Nothofagus</i> _Fuscospora	EW	EW	0.45	0.58
Nothofagaceae	<i>Nothofagus</i> _Lophozonia	EW	EW	0.63	0.10
Nothofagaceae	<i>Nothofagus</i> _Nothofagus	EW	W	0.40	0.13
Olacaceae	<i>Anacalosa</i>	EW	E	0.32	0.32
Onagraceae	<i>Fuchsia</i>	EW	EW	0.25	0.55
Picrodendraceae	Picrodendraceae	E	E	0.20	0.61
Paracryphiaceae	<i>Quintinia</i>	EW	E	0.26	0.38
Paracryphiaceae	<i>Sphenostemon</i>	E	E	0.15	0.48
Polygalaceae		EW	EW	0.18	0.51
Proteaceae	<i>Beauprea</i>	EW	E	0.36	0.61
Proteaceae	Proteaceae	EW	EW	0.33	—
Proteaceae	<i>Banksia</i>	E	E	0.26	0.59
Proteaceae	<i>Embothrium</i>	EW	W	0.16	0.41
Proteaceae	<i>Lomatia</i>	EW	EW	0.17	0.27
Proteaceae	<i>Telopea</i>	E	E	0.13	0.47
Proteaceae	<i>Orites</i>	EW	EW	0.28	0.24
Rhamnaceae		EW	EW	0.34	0.68
Rosaceae		EW	EW	0.13	0.63
Rutaceae		EW	E	0.07	0.57
Sapindaceae	<i>Cupania</i> and others	EW	E	0.16	0.60
Sapindaceae	<i>Dodonaea</i>	E	E	0.11	0.58
Sapotaceae		E	E	0.13	0.71
Symplocaceae	<i>Symplocos</i>	W ^g	E	0.27	0.52
Trimeniaceae		EW	E	0.09	0.62
Ulmaceae	Ulmaceae	W ^h	E	0.16	0.55
Vitaceae	<i>Cissus</i>	EW	EW	0.06	0.75
Winteraceae	<i>Drimys</i>	W	W	0.27	0.59
Ferns and other					
Cyatheaceae	Cyatheaceae	EW	E	0.63	—
Lycopodiaceae	<i>Lycopodium</i>	EW	EW	0.49	—
Sphagnaceae	Sphagnaceae	EW	EW	0.15	—
Sphagnaceae	<i>Sphagnum</i>	EW	EW	0.46	—
Gleicheniaceae	Gleicheniaceae	EW	EW	0.48	—
Gleicheniaceae	<i>Gleichenia</i>	EW	E	0.18	—
Lophosoriaceae	<i>Lophosoria</i>	EW	W	0.50	—
Dicksoniaceae	Dicksoniaceae	EW	EW	0.32	—
Dicksoniaceae	Dicksonia	EW	EW	0.37	—
Blechnaceae	Blechnaceae	EW	EW	0.11	—
Osmundaceae	Osmundaceae	EW	E	—	—
Osmundaceae	<i>Todea</i>	W	E	0.30	—
Polypodiaceae	Polypodiaceae	EW	EW	0.28	—
Selaginellaceae	<i>Selaginella</i>	EW	EW	0.29	—
Schizaeaceae	<i>Lygodium</i>	EW	EW	0.36	—
Anthocerotaceae	Anthocerotaceae	EW	EW	0.14	—

^a *Microstrobos* is synonymous with *Pherosphaera*.

^b *Athrotaxis* is known from older fossil deposits in Patagonia.

^c *Ephedra* occurs in both northern and southern hemispheres, but for the latter only in South America.

^d *Casuarina littoralis* is pan-tropical.

^{e,f,g,h} Known from the Australian fossil record but not from locations included in the final analyses (refer to full compendium in Supplemental Data). See additional taxonomic notes on Table 1.

Cupressaceae—In the Cupressaceae, *Libocedrus* is present as fossils from Australia and New Zealand during the late Paleocene to early Miocene, and it is extant in New Zealand and New Caledonia. *Austrocedrus* represents western survival in Patagonia of a genus that occurred in Tasmania during the Oligocene, and possibly in the Malvinas/Falkland Islands (grouped here with southern South America) during the middle to late Miocene. Similarly, *Fitzroya* is extant only in Patagonia (western survival) and occurs in these data in Tasmania during the early Oligocene and

Miocene. *Papuacedrus* is present in Patagonia during the early and middle Eocene (Wilf et al., 2009) and in Tasmania (Australia) during the early to late Oligocene and early Miocene (Hill and Carpenter, 1989); it is extant in New Guinea and nearby in the Moluccas. *Athrotaxis* has its entire fossil record in the Southern Hemisphere, including Patagonia (Menéndez, 1966; Del Fueyo et al., 2008). However, in probable rainforest sites in our data, it occurs only during the early Oligocene of Tasmania, where it persists (eastern survival).

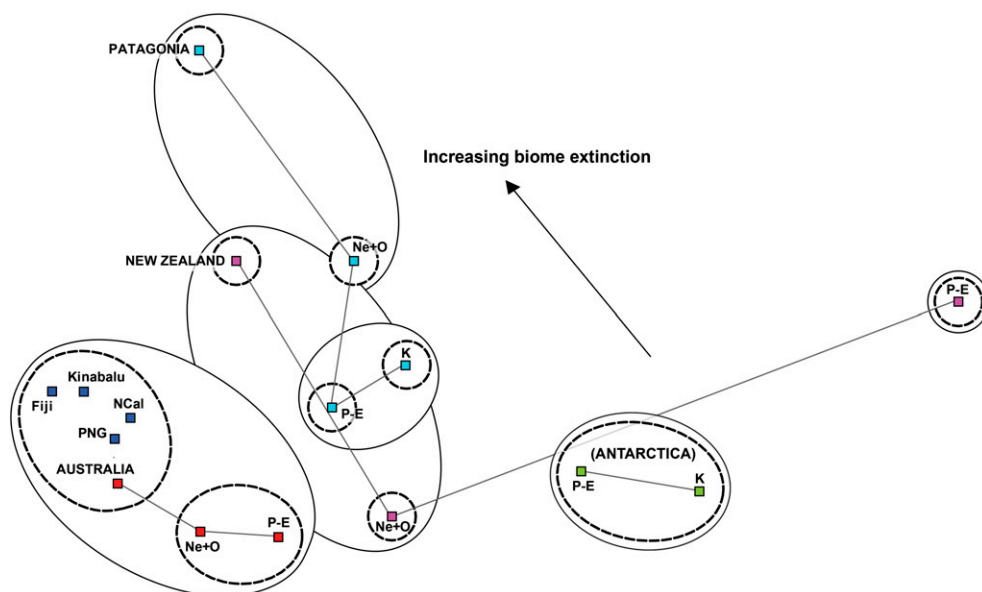


Fig. 3. NMDS ordination of 87 survivor genera (see text) from four fossiliferous and seven extant sample regions. Survivors represent woody fossil lineages that persisted through the long biogeographic history of the Gondwanan rainforest biome, and continue to contribute to biome persistence, lineage diversity, and community assembly. Age abbreviations for fossil samples as in Figure 1. Seven extant samples are from Australia (caps), New Zealand (caps), Patagonia (caps), Papua New Guinea (PNG), New Caledonia (NCal), Mt. Kinabalu, and Fiji. Antarctica is labeled in parentheses because it has no extant sample. Gray lines link the temporal sequence of each region. Gray ellipses/circles represent the groupings of age-regions with 55% similarity; broken black ellipses/circles show 65% similarity; black arrow shows the direction of increasing loss of the ancient rainforest biome.

Casuarinaceae—The family *Casuarinaceae* includes the wet-adapted lineage *Gymnostoma*, which is extant in the Australasian and Melanesian region. *Gymnostoma* macrofossils are present in these data from the Eocene of Patagonia, late Paleocene to Eocene of Australia, and the Miocene of New Zealand.

Casuarinaceae pollen occurs from the Paleocene to Pleistocene of Australia, the Cretaceous to Eocene of Patagonia, and the Paleocene to Oligocene of Antarctica. We note that *Gymnostoma* cannot be differentiated from other *Casuarinaceae* solely on the basis of pollen morphology.

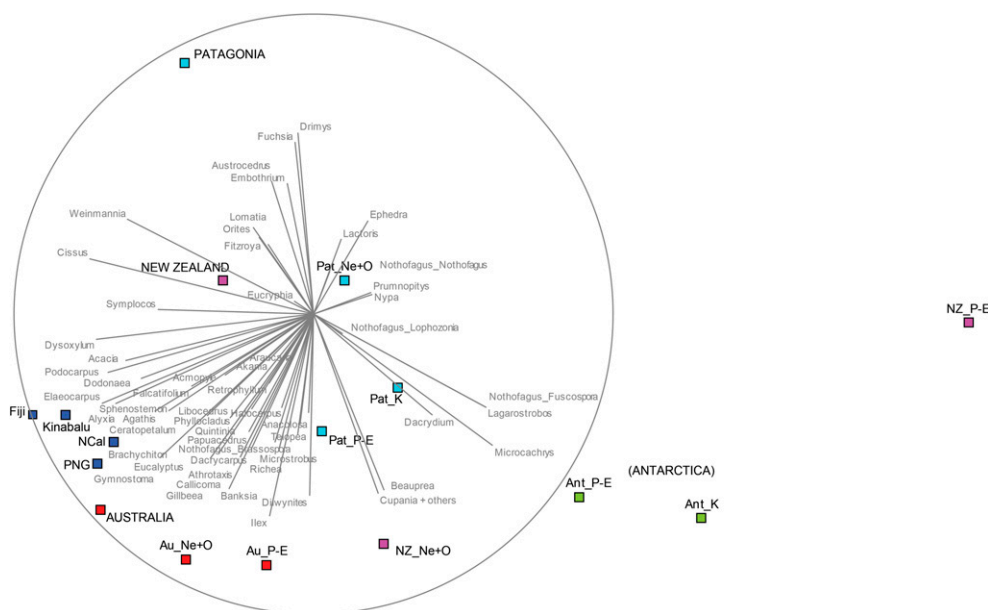


Fig. 4. NMDS ordination of 87 survivor genera from four fossiliferous and seven extant sample regions. Abbreviations and labeling as in Figure 3, plus labels for fossil samples: Au = Australia, NZ = New Zealand, Pat = Patagonia, and Ant = Antarctica. Gray vectors provide a directional measure of influence (strength) and co-occurrence of survivor genera on ordination of regions as Pearson Correlation values, where 0 = no influence and 1 = strongest possible influence. Enclosing gray vector circle is set at radius 1.0. Sorensen distance measure. Stress: 0.12.

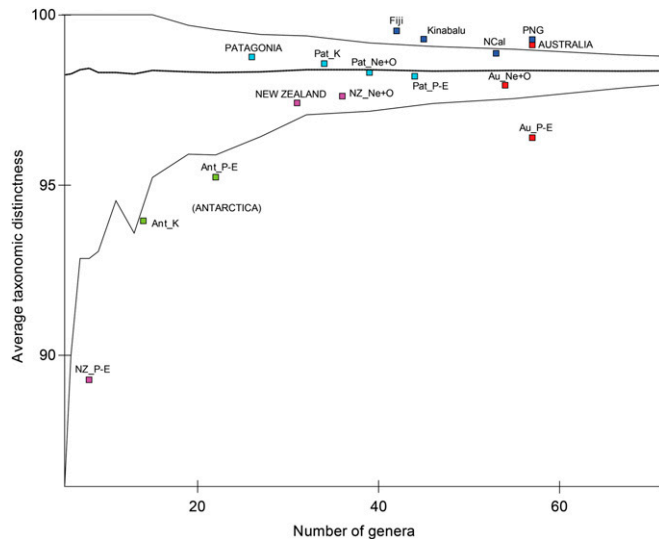


Fig. 5. Funnel plot of average taxonomic distinctness for 87 survivor genera representing four fossiliferous and seven extant sample regions. Abbreviations and labeling as in Figures 3 and 4. The funnel is bounded by 95% confidence intervals, and the central black line represents the expected position of regional samples in relation to average taxonomic distinctness at a given value of genus richness. Lower values than expected indicate less taxonomic breadth with genera more related than by chance, and higher values indicate more breadth and genera less related than by chance.

Proteaceae—The family Proteaceae is widespread but has a strong southern distribution of lineages that suggests Gondwanan origins (Johnson and Briggs, 1975; Weston, 2014). In these data, the rainforest members of the family show a continuous but surprisingly poorly differentiated record from the Cretaceous to Pleistocene (Sauquet et al., 2009), mostly from *Beauprea*-type and other, unattributed pollen. *Beauprea* itself is extant only in New Caledonia, representing eastern survival. *Embothrium* pollen is known from the Oligocene of Tasmania and Patagonia and the middle Miocene of the Malvinas/Falkland Islands. *Telopea* was recorded from the early Oligocene to Pleistocene of Australia, where it is extant (eastern survival). Records of *Telopea* from the Late Cretaceous of Patagonia were excluded from analyses because of ambiguity in relation to their assignment (Sauquet et al., 2009). Macrofossils of Proteaceae are best represented in these data from the Paleocene to Pleistocene of Australia (e.g., *Orites*, *Lomatia*, and *Banksia*), the Eocene of Patagonia (*Orites*; González et al., 2007), and the Oligo-Miocene of New Zealand (Carpenter et al., 2012).

Lauraceae and other Laurales—The family Lauraceae is globally widespread, but it differs from Proteaceae in being poorly represented in the palynological record (Macphail, 1980; Macphail et al., 2013). Macrofossils are present in our study from the Paleocene to Pleistocene in Australia, Cretaceous to Miocene in Patagonia, and the Paleocene in New Zealand. We note that older records for New Zealand are known (Cantrill et al., 2011; Bannister et al., 2012). The Laurales also include toothed-leaved genera in Atherospermataceae and Monimiaceae. Interestingly, recent fossil discoveries from the Eocene of Patagonia have strengthened the links between South American fossil Laurales and extant Australian genera, such as *Doryphora* and *Daphnandra* (Atherospermataceae) and *Wilkiea* (Monimiaceae) (Knight and Wilf, 2013).

Myrtaceae—Myrtaceae macrofossils in these data include *Eucalyptus* from the early Eocene of Patagonia, possibly sourced from volcanically disturbed areas adjacent to standing rainforest (Gandolfo et al., 2011; Hermesen et al., 2012). Other records include mostly undifferentiated taxa present from the Paleocene to Pleistocene in Australia, Late Cretaceous to Miocene of Patagonia, Late Cretaceous to late Eocene of Antarctica, and the Paleocene to early Miocene of New Zealand. Advances in systematic understanding of myrtaceous pollen promise improved biogeographic insights into this family (Thornhill and Macphail, 2012).

Nothofagaceae—The family Nothofagaceae is sister to all other Fagales and includes subgenera *Nothofagus*, *Fuscospora*, *Lophozonia*, and *Brassospora* (Hill, 1992; Hill and Jordan, 1993; Veblen et al., 1996). These distinctions are well supported by recent molecular systematic analyses (Sauquet et al., 2012; and see Heenan and Smissen, 2013) and allow relatively detailed exploration of the fossil record for this family. Juglandaceae (Fagales) is present in the record as pollen from the early Paleocene and Eocene of Patagonia, and Myricaceae (Fagales) is present from the Late Cretaceous to middle Eocene. Both families coexisted with *Nothofagus*. The first appearance of the Nothofagaceae in these data are from the Late Cretaceous of Patagonia, including pollen from both subgenera *Nothofagus* and *Fuscospora*, and from the western Antarctic, including subgenera *Lophozonia* and *Fuscospora*. By the Paleocene, all *Nothofagus* subgenera were present in western Antarctica at a single location (Seymour Island). Subgenera *Brassospora* and *Fuscospora* were present in Australia, and subgenus *Fuscospora* was present in New Zealand. During the middle to late Eocene, fossil assemblages from Patagonia included all *Nothofagus* subgenera. The late Eocene in Australia includes subgenera *Lophozonia*, *Brassospora*, and *Fuscospora*, and by the Oligocene also includes subgenus *Nothofagus*. Thereafter (in these data), all but subgenera *Lophozonia* and *Fuscospora* became extinct in Australia and New Zealand. Subgenus *Brassospora* is extant in New Guinea and New Caledonia (eastern survival), and subgenus *Nothofagus* is extant in South America (western survival) with subgenera *Lophozonia* and *Fuscospora*.

Cunoniaceae—The Cunoniaceae is another angiosperm family that is regarded as an important component of Gondwanan rainforest assemblages. Modern-day analogue vegetation types (notophyll vine forest or subtropical to warm temperate rainforest) that occur in Australia can be dominated by genera in Cunoniaceae such as *Ceratopetalum* and *Caldcluvia* (*Ackama*). These genera are evident in the record from the Eocene of Patagonia (Hermesen et al., 2010), and in Australia as *Ceratopetalum*- and *Weinmannia*-type pollen and macrofossils (Carpenter and Buchanan, 1993; Barnes et al., 2001). *Eucryphia* is extant in both South America and Australia. It is present in our compilation from the Paleocene to Pleistocene of Australia (Hill, 1991; Barnes and Jordan, 2000) and the Paleocene of Antarctica (Mirabelli et al., 2009).

Ferns and other life forms—Though not diagnostic for rainforest, *Lycopodium* (Lycopodiaceae) and *Sphagnum* (Sphagnaceae) are often associated with cool, moist habitats. In these data, they occur from the Cretaceous to late Eocene of Antarctica, the Cretaceous to Miocene of Patagonia, the Eocene to Pleistocene of Australia, and the Paleocene to Miocene of New Zealand.

Cyatheaceae, Gleicheniaceae (*Gleichenia*, *Sticherus*), Dicksoniaceae (*Dicksonia*), Polypodiaceae, and Blechnaceae (*Blechnum*) co-occur across the regions and throughout much of the temporal

record presented here. *Todea* (Osmundaceae) is extant in Australasia and South Africa, and it is known as macrofossils from the early Eocene of Patagonia (Carvalho et al., 2013). *Lophosoria* (Lophosoriaceae) is extant in Patagonia (western survival) and has fossil occurrences during the early Oligocene to Pleistocene of Australia, the Cretaceous to Miocene in Patagonia, and the Cretaceous to Paleocene of Antarctica (Hill et al., 2001). *Lygodium* (Schizaeaceae) is present here during the Eocene to Pleistocene of Australia, the Paleocene to Miocene of New Zealand, and the Cretaceous to late Oligocene of Patagonia.

Multivariate patterns and interpretations—For the full dataset, the grouping of fossil sites in relation to floristics was most strongly influenced by geographic location (Fig. 1). Antarctica grouped with Patagonia, including the Malvinas/Falkland Islands, and New Zealand was positioned between Australia and Patagonia. Interestingly, but not surprisingly given recent discoveries there, the diverse Eocene sites from Patagonia, Laguna del Hunco and Río Pichileufú, grouped with the late Paleocene and Eocene sites in Australia (Figs. 1 and 2).

The second analysis (Fig. 2) used the reduced fossil matrix ($n = 56$ sites, and $n = 153$ genera) and, importantly, showed a very similar result to the full matrix analysis (Fig. 1). Laguna del Hunco and Río Pichileufú remained with the Australian late Paleocene and Eocene group. Of the 36 taxa used here from Laguna del Hunco, 27 are extant in Australia, four represent extinct lineages, and three are extant in proximity to Australia (eastern survival or shared).

The third analysis used the 87 survivors in the age-by-region matrix and combined neo- and paleo-distribution data. The resulting ordinations (Table 3c; Figs. 3 and 4) showed high similarity for Australian fossil age samples (P–E and Ne+O; 65% similarity). Cretaceous (K) and P–E Patagonia samples grouped at 55% similarity but were isolated from Ne+O and extant Patagonia. Cretaceous (K) and P–E Antarctica grouped at 65% similarity. New Zealand P–E and Ne+O were highly dissimilar to each other. Australian extant and fossil samples grouped at 55% similarity. Extant New Zealand grouped with K and P–E Patagonia, and New Zealand Ne+O, at 55% similarity. Extant sample locations, including Papua New Guinea, New Caledonia, Mt. Kinabalu, and Fiji, grouped with extant Australia at 65% similarity, and with P–E and Ne+O Australia at 55% similarity. Figure 4 includes the survivors as vectors based on Pearson correlation values.

Taxonomic structure—We detected lower-than-expected estimates of taxonomic distinctness at four fossil age-locations in the combined analysis of 16 survivor samples. This result reflects phylogenetic clustering, or higher relatedness, among the genera in those four instances (Fig. 5). These included Cretaceous and Paleocene to Eocene Antarctica; and the Paleocene to Eocene of New Zealand and Australia. Higher-than-expected taxonomic distinctness, reflecting overdispersion or evenness and less relatedness of taxa within regions, was detected at four extant locations, including Australia, Papua New Guinea, Mt. Kinabalu, and Fiji. The remaining fossil and living floras showed expected levels of taxonomic distinctness in relation to richness (i.e., they occurred within the funnel bounded by 95% CIs). In terms of richness and taxonomic structure, the modern tropical floras adjacent to northern Australia were more similar to each other and to Australia itself than to modern New Zealand and Patagonia.

All fossil regions (Antarctica, Patagonia, Australia, and New Zealand) had some assemblages outside and lower than expectations defined by 95% CIs for taxonomic distinctness. This result was consistent at different levels of generic richness for fossil sites from the full ($n = 63$) and reduced ($n = 56$) data matrices (see Appendix S4: Figs. S1 and S2).

Continental phylogenetic structure—The correlation between NRI values for the Australian rainforest, both with and without the Gondwanan survivor genera identified in our compendium included, was $r = 0.43$, $P = 0.001$. A value of $r = 1.0$ equates with no difference following removal. Lower values (as here) suggest a measure of difference after removal, with (in this case) the retention of a strong positive relationship (see Appendix S5: Fig. S3).

DISCUSSION

Data compilation—The data compilation allowed us to track Gondwanan rainforest composition through time (Appendix S2; Figs. 1–4), identify the strength of the signal of the ancient in modern assemblages (Fig. 4; Table 4), and determine the stability of Gondwanan rainforest assemblages in regions (Figs. 1–4; Table 4).

Floristic patterns—The floristic analyses confirmed that dissimilarity within and among regions generally increased with time. However, despite major spatial movements, Gondwanan rainforest lineages apparently co-occurred continuously, both before and after final Gondwanan breakup. In addition, the direction of change, from ancient to modern, followed a similar trajectory among most of the regions, reflecting loss of diversity and local extinction (Fig. 3). However, the extent of floristic dissimilarity, reflecting change through time, differed markedly among the regions (Fig. 3).

Assembly through time—The strengths of contributions by genera in the survivor pool, to co-occurrence in regional assemblages, shifted most significantly in relation to regional extirpations and movement into newly emerging habitat. The results confirm that lineages continued to co-occur, but generally at locations far removed from their origins. Although the strength of contribution by some southern rainforest lineages shifted through time, for others it remained stable but included extirpation in different locations (Fig. 4 and Table 4). Despite the variation in assemblage composition among regions, it is clear that Gondwanan rainforest survivors continued to form assemblages reflecting ancient combinations.

In terms of contribution to modern floras, the correlation of continental phylogenetic structure values (NRI) for Australian rainforests (in grid cells) before and after removal of “survivor” genera showed a significant difference. However, the values remained positive, suggesting underlying similarity based on continuing contributions to rainforest assembly by other lineages, many of which lack fossil records (Sniderman and Jordan, 2011; Kooryman et al., 2013; see Appendix S5). Most notably, the NRI analysis showed that the fossil record is now sufficiently robust to record a statistically significant fraction of the lineages that influence the phylogenetic structure of living Australian rainforests.

By merging sites in regions, we identified the regional patterns of loss (extinction) of survivor genera, and we were able to quantify their continuing contribution to community assemblage

across the regions through time (Table 4). At the continental scale, Australia retained more of its ancient rainforest flora than Patagonia or New Zealand, despite losing vast areas of the biome to aridification. Loss of the biome was most severe in the south and west, whereas retention was highest in the east and northeast of the continent. Assemblage shifts in fossil locations through time, and the co-occurrences of survivors in modern floras (Figs. 3 and 4; Table 4), showed that genera extirpated from Australia because of the loss of cool-wet habitats survived by shifting into newly emerging highland, and other compatible habitats, in the nearby tropics (e.g., Papua New Guinea and New Caledonia). By contrast, Patagonia showed initial and increasing convergence (similarity) with Antarctica (K, P-E) and Australia (P-E), and then increasing extinction and loss of the ancient biome because of the transition from greenhouse to icehouse conditions and subsequent lineage filtering (from P-E to Ne+O to modern). Ancient Antarctica (K and P-E) showed only minor change, then lost the rainforest biome completely during the subsequent icehouse. Ancient New Zealand (P-E) was quite dissimilar from other land areas, though most similar to ancient (K) Antarctica (see Pole, 2014). New Zealand (Ne+O) was more similar to (P-E) Patagonia, Antarctica, and Australia (Fig. 3). The New Zealand trajectory then showed substantial extinction and loss of the accumulated elements of the ancient biome (Ne+O) followed by increasing similarity (into the present) with extant Patagonia.

The compositional similarity, taxonomic structure, and relatively high richness of samples from the extant Old World tropics confirmed that survivor genera from different lineages are well represented in those regions. These included *Agathis* and Podocarpaceae in Australia, New Guinea, Fiji, and Indo-Malesia (Wilf et al., 2013), and numerous other angiosperm lineages that occur in Australia and New Guinea (Sniderman and Jordan, 2011). At higher latitudes, the floristically simple cool-moist *Nothofagus* forest, with conifers and consistently co-occurring angiosperm lineages, remains a feature of southern Australia, Patagonia, and New Zealand (Veblen et al., 1996).

Regional extinction phases, and lineage movements, have previously been described and associated with major plate movements, volcanism, uplifts, subsidence, and shifts in climate (Crisp and Cook, 2013; Wilf et al., 2013; Lawver et al., 2014). A feature of those large-scale patterns is their close alignment with the movements of particular lineages (e.g., *Dacrycarpus* and *Acmopyle*) that are known to have greater sensitivity to factors such as water balance and freezing (Brodrribb and Hill, 1998, 2004; Brodrribb and Feild, 2010; Brodrribb et al., 2012; Wilf, 2012). The loss of mesic lineages from Patagonia–Antarctica and their persistence in Australia and Papua–Asia highlight the role of shifting distributions and increasing dissimilarity among locations through time.

The striking differences between the Paleocene–Eocene rainforest floras of New Zealand and their Oligocene to recent “replacements” reflect climate change and the catastrophic Oligocene inundation of most of Zealandia. This event was followed by the subsequent recolonization of reemergent New Zealand during the Neogene by long-distance dispersers, mostly from Australia (Campbell and Hutchings, 2007). The Neogene recolonization of New Zealand resulted in rainforests that were quite dissimilar from those in Australia and nearby regions, and from the ancestral associations, even though they do include a number of important ancient taxa (e.g., *Agathis* and many Podocarpaceae).

By contrast, the similarity of the Patagonian Eocene floras of Laguna del Hunco and Río Pichileufú to Australian fossil floras

quantified in this study (Figs. 1 and 2) highlights a period of floristic similarity between these now much more distant locations. This is thought to have been made possible by Eocene warmth that allowed the required trans-Antarctic distributions and a lack of significant oceanic barriers to biotic interchange. The floristic similarity between these fossil floras and the living floras of Australasia continues to grow with the inclusion of recently described and shared genera. Several of these taxa are not yet known as fossils in Australia (e.g., *Todea*, *Wilkiea*, *Daphnandra*, and *Akania*) but contribute substantially to modern Australian floras.

Conclusions—This study highlights the complex journey of survival of southern rainforest lineages and confirms their continuing co-occurrences in widely dispersed assemblages far from their fossil sources. The endurance, survival, and persistence of these rainforest lineages provide one of the earth’s greatest biological and evolutionary success stories. These assemblages from deep time remain ecologically important today. Their conservation will require targeted research to quantify the evolutionary, phylogenetic, ecological, and functional contributions of the ancient southern flora to global vegetation diversity and ongoing rainforest community assembly.

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