RESEARCH ARTICLE

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Resolving Australian analogs for an Eocene Patagonian paleorainforest using leaf size and floristics[1]

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PREMISE OF THE STUDY: The diverse early Eocene flora from Laguna del Hunco (LH) in Patagonia, Argentina has many nearest living relatives (NLRs) in Australasia but few in South America, indicating the differential survival of an ancient, trans-Antarctic rainforest biome. To better understand this significant biogeographic pattern, we used detailed comparisons of leaf size and floristics to quantify the legacy of LH across a large network of Australian rainforest-plot assemblages.

METHODS: We applied vein scaling, a new method for estimating the original areas of fragmented leaves. We then compared leaf size and floristics at LH with living Australian assemblages and tabulated the climates of those where NLRs occur, along with additional data on climatic ranges of "ex-Australian" NLRs that survive outside of Australia.

KEY RESULTS: Vein scaling estimated areas as accurately as leaf-size classes. Applying vein scaling to fossil fragments increased the grand mean area of LH by 450 mm^2, recovering more originally large leaves. The paleoflora has a majority of microphyll leaves, comparable to leaf litter in subtropical Australian forests, which also have the greatest floristic similarity to LH. Tropical Australian assemblages also share many taxa with LH, and ex-Australian NLRs mostly inhabit cool, wet montane habitats no longer present in Australia.

CONCLUSIONS: Vein scaling is valuable for improving the resolution of fossil leaf-size distributions by including fragmented specimens. The legacy of LH is evident not only in subtropical and tropical Australia but also in tropical montane Australasia and Southeast Asia, reflecting the disparate histories of surviving Gondwanan lineages.

KEY WORDS biogeography; Gondwana; leaf size; rainforests; paleobotany; paleoclimate; paleoecology; vein scaling

Many plant lineages with Gondwanan histories have maintained ancestral ecological traits and associations, despite tectonic and climatic change over geologic time. Late Cretaceous and Cenozoic paleofloras from Gondwanan areas preserve many genera that are extant, frequently in association, in subtropical and tropical rainforests of Australasia and Southeast Asia (Hill, 2004; Wilf et al., 2009; Carpenter, 2012; Wilf, 2012; Carvalho et al., 2013; Knight and Wilf, 2013). The Gondwanan floristic signature has been quantitatively tracked, from the fossil records of South America, Antarctica, Australia, and New Zealand, to modern-day Australia, New Caledonia, Fiji, New Guinea, and Borneo, among many other areas (Kooyman et al., 2014). Further, the majority of the southern hemisphere plant lineages have retained their connections to ancestral biomes over geologic time (Crisp et al., 2009). These patterns have primarily been described at coarse spatial and temporal scales or on a limited, taxon-by-taxon basis alongside new fossil discoveries.

Detailed comparisons of living ecosystems and their ancient counterparts are needed to better understand the remarkable persistence of Gondwanan lineages and associations. Quantitative approaches are now possible due to the steady growth in both systematic paleobotanical reports and plot-scale data from living rainforests. Here, we focus on one outstanding Gondwanan flora that is located far from most of its living analogs: the early Eocene Laguna del Hunco (LH) paleoflora of Chubut, Patagonia, Argentina (Berry, 1925, 1938; Wilf et al., 2005). We use leaf-size and floristic data to compare the LH assemblage with an extensive network of living assemblages from rainforest plots in Australia.

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Leaf size has established value in fossil-modern ecological comparisons (e.g., MacGinitie, 1969; Christophel and Greenwood, 1987; Jacobs, 1987). The seminal work of the late L. Webb (1959, 1968; Webb et al., 1984) is responsible for the recognized importance of leaf size in Australian rainforest ecology. Webb distinguished Australian rainforest types using the dominant canopy-angiosperm leaf size, in addition to structural features such as crown shapes, canopy evenness, and the presence and abundance of buttresses, epiphytes, vines, and lianas. Furthermore, Webb's observations catalyzed ecological comparisons between paleorainforests and their living equivalents. For example, Greenwood (1992, 1994) classified several Australian paleofloras into Webb's rainforest categories by comparing the leaf sizes of fossils with those of extant leaf litter at specific locations.

Greenwood's approach and others like it (Christophel and Greenwood, 1987; Jacobs, 1987; Specht, 1992; Greenwood and Christophel, 2005) require accurate measurements of fossil leaf size. The compaction and dewatering associated with fossilization are thought to have negligible effects on leaf-size preservation (Blonder et al., 2012). However, several other taphonomic filters can bias leaf size, especially by reducing the signal of large, complete leaves, and fossil leaf size is conventionally considered an underestimate of that of the source forest. First, the mean sizes of leaves collected from the forest floor are typically smaller than those of the overlying canopy (Raunkiaer, 1934; Webb, 1959; Greenwood, 1992; Steart et al., 2002). Additionally, stream-transported leaf litter shows a bias against large leaves that increases with transport distance (Greenwood, 1992). Leaf litter collected from lakes also tends to over-represent smaller, tougher sun leaves (Burnham, 1989; Greenwood, 1992), and this bias increases with distance from shore (Roth and Dilcher, 1978; Spicer, 1981; Hill and Gibson, 1986).

Another complicating factor in assessing fossil assemblage leaf-area is the difficulty of measuring fragmented leaves. The Raunkiaer–Webb leaf-size classes (Raunkiaer, 1934; Webb, 1959) accommodate some uncertainties in leaf dimensions by categorizing leaves into discrete, broad groups. Alternatively, the Cain and Castro (1959) formula is often used, where leaf area = 2/3 × leaf length × leaf width. However, both methods require fossil leaves to be somewhat intact, excluding the majority of moderately to highly fragmented specimens that are common in paleofloras. Area underestimates for assemblages are especially likely because large leaves tend to fragment more frequently than small leaves (Roth and Dilcher, 1978; Spicer, 1981; Hill and Gibson, 1986; Greenwood, 1992; Steart et al., 2002).

A new vein-scaling technique, based on the global relationship between dicot leaf area and secondary (2°) vein density (Sack et al., 2012), could ameliorate the general difficulty of estimating fossil leaf area. This relationship corresponds to a model of leaf development in which 2° veins form at high density in the leaf primordium, then are pushed apart as leaf growth switches from a period dominated by cell division to one dominated by cell expansion. It follows that further increases in leaf size must decrease 2° vein density, therefore linking 2° vein density to leaf area in a nearly consistent manner across taxa (Sack et al., 2012). If the same scaling relationship exists in fossil leaves, it can be used to estimate the original areas of otherwise unmeasurable leaf fragments. This promising method for reconstructing leaf size has not previously been tested on fossils.

The early Eocene, 52.2 Ma Laguna del Hunco (LH) paleoflora, from Chubut, Argentina (Berry, 1925; Wilf et al., 2003, 2005) is ideal both for testing the vein-scaling method and for exploring the legacy of Gondwanan paleofloras in living ecosystems. Collections from LH include several thousand exceptionally well-preserved leaves, of which many have complete areas and clearly visible venation. The assemblage is noteworthy for its high diversity, including over 154 species and morphotypes (henceforth "species" throughout for simplicity) of angiosperm leaves (Wilf et al., 2005; this study). Furthermore, LH has a growing number of systematically well-defined taxa whose nearest living relatives (NLRs) inhabit tropical and subtropical Australasia and Southeast Asia (Tables 1, 2).

Laguna del Hunco's Old World NLRs give it a central role in clarifying trans-Antarctic biogeographic connections during the global warmth that coincided with the last stages of Gondwana (Wilf et al., 2013). The LH paleoflora is, by far, the most complete record of South American vegetation during the Early Eocene Climatic Optimum (defined by Zachos et al., 2001). At that time, Antarctica had not yet fully separated from South America nor Australia (Scher and Martin, 2006; Lawver et al., 2011). Abundant plant and animal fossil evidence indicates that biotic interchange occurred among South America, Antarctica, and Australia until at least the early middle Eocene (e.g., Wilf et al., 2013; Kooyman et al., 2014). Many of the Gondwanan fossil species from LH also occur in the middle Eocene Río Pichileufú paleoflora (RP; 47.7 Ma, Río Negro, Argentina), suggesting that the LH and RP biotas were parts of a once-extensive, wet biome that mostly went extinct in South America but survived elsewhere (Berry, 1938; Petersen, 1946; Wilf et al., 2005; Wilf, 2012).

Australian rainforests are informative living ecosystems for comparison with LH because they are well described (Webb, 1959, 1968; Kooyman et al., 2011, 2012), have similar family composition (Wilf et al., 2009; Kooyman et al., 2014), and contain a high number of NLRs, including several genera endemic to Australia (Tables 1, 2). In particular, the Simple Notophyll Vine Forests (SNVFs; Webb, 1959) of New South Wales and southern Queensland are often compared with LH based on floral composition, species richness, and leaf areas (Romero and Hickey, 1976; Wilf et al., 2009; Carvalho et al., 2013). The SNVFs often have widely spaced trunks, an even canopy with emergents, occasional vines and epiphytes, and a dominant leaf size of microphyll to notophyll. Many Australian SNVFs include *Araucaria cunninghamii* (Hoop Pine), which, as a member of *Araucaria* section *Eutacta*, is a close relative of the abundant Laguna del Hunco fossil *A. pichileufensis* (Berry, 1938; Florin, 1940b; Wilf et al., 2005). Comparing the fossil assemblage at Laguna del Hunco with a larger and more detailed range of Australian rainforest assemblage samples would better define SNVFs as potential living analogs.

One complication when using Australian rainforest assemblages as analogs for LH is that there are several "ex-Australian" genera in the LH assemblage. These are taxa that have fossil records in Australia but are now restricted to other regions of Australasia or Southeast Asia; the genera of interest here are the conifers *Acmopyle*, *Dacrycarpus, Retrophyllum*, and *Papuacedrus* (Tables 1, 2). Decreasing rainfall during the Cenozoic is thought to have played a critical role in the extinction of these drought-sensitive lineages in Australia and their survival elsewhere (Brodribb and Hill, 1998; Brodribb and Holbrook, 2005; Greenwood and Christophel, 2005; Kooyman et al., 2014).

In this study, we first test the hypothesis that the vein-scaling method can be used to accurately estimate the intact areas of

TABLE 1. Laguna del Hunco fossil taxa and nearest living relatives used in floristic analyses.

Fossil species	Organ(s)	Sources	Nearest living relative(s)
Acmopyle engelhardti (Berry) Florin	L	Florin, 1940a; Wilf, 2012	*A. pancheri* (Brongn. & Gris) Pilg. *A. sahniana* Buchholz & N. E. Gray
Agathis zamunerae Wilf [a]	L, PC, S, SC	Wilf et al., 2014	*A. atropurpurea* Hyland[a] *A. lenticula* de Laub. *A. microstachya* J. F. Bailey & C. T. White[a] *A. robusta* (C. Moore ex F. Muell.) F. M. Bailey[a]
Akania patagonica Gandolfo, Dibbern, and Romero[a]	L	Romero and Hickey, 1976; Gandolfo et al., 1988	*A. bidwillii* (Hend. ex Hogg) Mabb.[a]
Araucaria pichileufensis Berry[a]	L, SC, S	Berry, 1938; Florin, 1940b	*A. cunninghamii* Mudie[a]
Atherospermophyllum guinazui C. L. Knight[a]	L	Knight and Wilf, 2013	*Daphnandra apatela* Schodde[a] *D. repandula* (F. Muell.) F. Muell.[a] *D. tenuipes* G. Perkins[a]
Ceratopetalum sp.	F	Gandolfo and Hermsen, 2012	*C. apetalum* D. Don *C. corymbosum* C. T. White *C. succirubrum* C. T. White *C. virchowii* F. Muell.
Caldcluvia sp.[a]	L	Wilf et al., unpublished data	*C. australiensis* (Schltr.) Hoogland[a] *C. paniculata* (Cav.) D. Don[a]
Cochlospermum previtifolium Berry	F	Berry, 1935, 1938; Wilf et al., 2005; González, 2009	*C. gillivraei* Benth.
Dacrycarpus puertae Wilf	L, SC, PC	Wilf, 2012	*D. cinctus* (Pilg.) de Laub. *D. compactus* (Wasscher) de Laub. *D. dacrydioides* (A. Rich.) de Laub. *D. imbricatus* (Blume) de Laub. *D. kinabaluensis* (Wasscher) de Laub. *D. vieillardii* (Parl.) de Laub.
Eucalyptus frenguelliana Gandolfo and Zamaloa[a]	L, F, Fl	Gandolfo et al., 2011; Hermsen et al., 2012	*E. acmenoides* Schauer *E. campanulata* (R. T. Baker & H. G. Sm.) L. A. S. Johnson & Blaxell *E. grandis* W. Hill[a] *E. microcorys* F. Muell.[a] *E. pellita* F. Muell.[a] *E. pilularis* Sm.
Monimiophyllum callidentatum C. L. Knight[a]	L	Knight and Wilf, 2013	*Wilkiea angustifolia* (F. M. Bailey) Perkins *W. austroqueenslandica* Domin *W. hugeliana* (Tul.) A. DC.[a] *W. macrophylla* (A. Cunn.) A. DC. *Wilkiea* sp. Barong (L. W. Jessup)[a] *Wilkiea* sp. McIlwraith[a] *Wilkiea* sp. Mt Hemmant *Wilkiea* sp. Mt Molloy (L. S. Smith) *W. wardellii* (F. Muell.) Perkins
Orites bivascularis Romero, Dibbern and Gandolfo	F	Romero et al., 1988; González et al., 2007	*O. excelsus* R. Br. *O. megacarpus* A. S. George & B. Hyland
Papuacedrus prechilensis Wilf	L, SC	Wilf et al., 2009	*P. papuana* (F. Muell.) H. L. Li
Podocarpus andiniformis Berry[a]	L	Berry, 1938; Wilf, 2012	*P. dispermus* C. T. White[a] *P. elatus* R. Br. ex Endl.[a] *P. grayae* de Laub.[a]
Retrophyllum sp.	L	Wilf, 2012	*R. comptonii* (J. Buchholz) C. N. Page *R. vitiense* (Seem.) C. N. Page

Abbreviations: F, fruits, Fl, flowers; L, leaves; PC, pollen cones; S, seeds, SC, seed cones.
[a] Leaf areas shown in Fig. 4.

fragmented fossil leaves. Second, we compare the Laguna del Hunco paleoflora with hundreds of Australian rainforest-plot assemblages in terms of leaf size and floristics to test if subtropical Australian SNVFs are the closest living analogs. Finally, we assess to what extent the modern assemblages with Laguna del Hunco NLRs are located in similar or disparate environments, potentially reflecting biome conservatism vs. adaptation through time, respectively. To do so, we compare the climate parameters of the living subtropical and tropical Australian assemblage samples that contain the NLRs, as well as the more coarsely estimated climatic ranges of ex-Australian genera.

MATERIALS AND METHODS

***Laguna del Hunco paleoflora*—**We studied the Laguna del Hunco flora from recent collections (e.g., Wilf et al., 2003, 2005, 2014) curated at MEF (Museo Paleontológico Egidio Feruglio), Trelew, Chubut, Argentina. Fossils (Appendix S1, see Supplemental Data with online version of this article) came from 27 quarries in a 170-m section of the Tufolitas Laguna del Hunco, Middle Chubut River volcanic-pyroclastic complex, northwest Chubut, Patagonia, Argentina (Berry, 1925; Aragón and Romero, 1984; Aragón and Mazzoni,

TABLE 2. Climate and elevation ranges of Laguna del Hunco nearest living relatives (Table 1) and number of records used.

Nearest living relatives	Records	MAT (°C)	MAP (mm)	Elevation (m a.s.l.)	Range
Australian species					
Agathis atropurpurea[a]	2	19	2408 ± 576	1085 ± 21	T
Agathis microstachya[a]	1	20	1912	790	T
Agathis robusta[a]	16	22 ± 1	1813 ± 473	609 ± 239	T
Akania bidwillii[a]	41	17 ± 1	1659 ± 192	394 ± 218	ST
Araucaria cunninghamii[a]	78	17 ± 2	1461 ± 309	418 ± 227	ST, T
Caldcluvia australiensis[a]	11	22 ± 2	2156 ± 545	778 ± 250	T
Caldcluvia paniculata[a]	127	16 ± 2	1541 ± 318	583 ± 283	ST
Ceratopetalum apetalum[a]	72	16 ± 2	1714 ± 304	591 ± 234	ST
Ceratopetalum corymbosum[a]	3	23	2356	627 ± 87	T
Ceratopetalum succirubrum	11	20 ± 1	2008 ± 638	925 ± 189	T
Ceratopetalum virchowii[a]	3	19 ± 1	3177 ± 628	1067 ± 58	T
Cochlospermum gillivraei[a]	10	25 ± 1	1329 ± 270	49 ± 26	T
Daphnandra apatela[a]	96	17 ± 1	1451 ± 308	507 ± 235	ST
Daphnandra repandula[a]	27	21 ± 1	2399 ± 809	625 ± 358	ST
Daphnandra tenuipes[a]	10	18 ± 1	1861 ± 60	351 ± 202	ST
Eucalyptus acmenoides	43	17 ± 1	1537 ± 279	334 ± 192	ST
Eucalyptus campanulata	20	16 ± 1	1410 ± 299	706 ± 122	ST, T
Eucalyptus grandis[a]	58	17 ± 1	1630 ± 270	285 ± 201	ST
Eucalyptus microcorys[a]	107	17 ± 1	1572 ± 281	419 ± 233	ST
Eucalyptus pellita[a]	2	25 ± 1	1679 ± 115	253 ± 350	T
Eucalyptus pilularis	42	17 ± 2	1701 ± 174	356 ± 224	ST
Orites excelsus[a]	92	16 ± 2	1622 ± 512	723 ± 263	ST, T
Orites megacarpa[a]	2	23	2356	691 ± 86	T
Podocarpus dispermus[a]	1	22	2645	680	T
Podocarpus elatus[a]	21	18 ± 2	1561 ± 323	422 ± 215	ST, T
Podocarpus grayae[a]	45	24 ± 2	2135 ± 558	275 ± 291	T
Wilkiea angustifolia[a]	15	21 ± 2	2507 ± 535	828 ± 326	T
Wilkiea austroqueenslandica	33	18 ± 1	1772 ± 218	355 ± 212	ST
Wilkiea Barong	24	22 ± 1	2279 ± 721	485 ± 382	T
Wilkiea hugeliana[a]	156	17 ± 1	1596 ± 284	464 ± 281	ST
Wilkiea macrophylla[a]	3	17 ± 1	1832 ± 21	324 ± 230	ST
Wilkiea McIlwraith	2	24	1781 ± 258	360 ± 28	T
Wilkiea Mt Hemmant	4	23 ± 1	2201 ± 712	473 ± 283	T
Wilkiea Mt Molloy	5	22	1813 ± 571	611 ± 105	T
Non-Australian species					
Acmopyle pancheri[a]	72	20 ± 1	1792 ± 292	566 ± 190	New Caledonia
Acmopyle sahniana[a]	4	22 ± 1	2820 ± 348	530 ± 204	Fiji
Agathis lenticula[a]	—	19 ± 2	2900 ± 900	1375 ± 325	Malaysia: Sabah
Dacrycarpus cinctus	55	15 ± 3	2736 ± 511	2391 ± 734	New Guinea
Dacrycarpus dacrydioides	490	11 ± 2	2913 ± 1373	318 ± 248	New Zealand
Dacrycarpus imbricatus[a]	170	18 ± 4	2569 ± 630	1729 ± 873	SE Asia/Australasia
Dacrycarpus kinabuluensis	3	12 ± 2	2092 ± 5	2934 ± 406	Malaysia: Sabah
Dacrycarpus vieillardii	33	21 ± 1	1655 ± 357	360 ± 254	New Caledonia
Dacrycarpus compactus	49	13 ± 3	2940 ± 766	2860 ± 510	New Guinea
Papuacedrus papuana[a]	352	15 ± 5	2950 ± 1050	2050 ± 1450	New Guinea
Retrophyllum comptonii	50	20 ± 1	1825 ± 319	603 ± 250	New Caledonia
Retrophyllum vitiense	21	23 ± 3	3285 ± 912	767 ± 679	Malesia

Notes: Data from Kooyman et al. (2012) plot network for Australia (see text); see Materials and Methods for non-Australian occurrences. Uncertainties are ± one standard deviation or absent when only one value was available. Australian species that may occur elsewhere are only represented by their Australian occurrences. MAP, mean annual precipitation; MAT, mean annual temperature; ST, subtropics; T, tropics.

[a] Climate ranges shown in Fig. 6.

1997; Wilf et al., 2003). Based on the ^{40}Ar-^{39}Ar ages of three primary ash-fall tuffs and several paleomagnetic reversals within the section, the working age of the entire flora is 52.2 Myr (early Eocene, Ypresian) as detailed elsewhere (most recently by Wilf, 2012). Primary stratigraphic data and quarry locations were published by Wilf et al. (2003). The inferred paleolatitude of Laguna del Hunco is ca. 47°S, slightly higher than the present-day latitude of 42.5°S (Wilf et al., 2005).

The depositional environment of LH is interpreted as a caldera lake (Aragón and Mazzoni, 1997). Most specimens were found within a densely fossiliferous, 60-m stratigraphic section (Wilf et al., 2003). The fossil assemblage includes many examples of exceptionally preserved, delicate organs, including fern fronds with in situ sori (Carvalho et al., 2013); an articulated compound cycad leaf (P. Wilf, unpublished data); possible *Papuacedrus* seedlings (Wilf et al., 2009); large, intact angiosperm leaves (up to 12500 mm^2 in area); and *Eucalyptus* flower buds (Gandolfo et al., 2011; Hermsen et al., 2012). The associated fauna includes fish, frogs, insects, and diverse insect-feeding damage on leaves (e.g., Casamiquela, 1961; Fidalgo and Smith, 1987; Azpelicueta and Cione, 2011; see Wilf et al., 2009 for summary). The paleoflora is also unusually diverse, with >215 leaf and reproductive organ species, including six newly discovered

(Wilf et al., 2005; Appendix S1). The presence of these fragile and diverse fossils indicates low-energy taphonomic conditions. Neither floristic composition nor leaf size change significantly through the stratigraphic section (Wilf et al., 2005), and we increased statistical power by pooling fossil species from all collected quarries in the analyses.

Fossil leaf area measurements—We analyzed fossils digitally from high-resolution photographs, using a light microscope on site at MEF to confirm details as needed. Photographs were taken with a Nikon D90 camera or chosen from the image library of LH leaves that were digitally extracted from the matrix by B. Cariglino (2007) and later used by Peppe et al. (2011). When necessary, Camera Raw (Photoshop CS6 v. 13.0; Adobe, San Jose, California, USA) was used to adjust whole-image contrast and brightness.

For the fossil conifers with Australian NLR genera (*Agathis*, *Araucaria*, and *Podocarpus*; ex-Australian taxa were not analyzed for leaf area), we estimated fossil leaf area using the Cain and Castro (1959) formula. *Agathis zamunerae* leaf length and width data are from Wilf et al. (2014). *Araucaria pichileufensis* leaves are small and imbricate, usually occluding neighboring leaf bases. When this occurred, we averaged *A. pichileufensis* leaf lengths and widths across several leaves of the same branch.

Dicot leaf-area measurements (or leaflets in the case of compound leaves) are summarized in Table 3 and detailed in Appendix S1. The total data set describes 1147 specimens of 154 species, plus 522 unidentified leaves. We defined intact leaves as having no more than 1 cm of missing margin and nearly intact leaves as having measurable length and width. Fragmented specimens were characterized as having unmeasurable length and width.

We made new high-resolution area estimates of 322 identified dicot specimens (Table 3). Intact and nearly intact specimens were measured by digitally tracing the blade margin to the point of petiole attachment (Image J; National Institutes of Health, Bethesda, Maryland, USA). If a specimen had both a part and counterpart, only one of these was measured. We compiled new measurements with previously published data for identified dicots from LH (Wilf et al., 2003, 2005; Table 3); those leaf areas were estimated by using the Cain and Castro formula on leaves with measurable lengths and widths and Raunkiaer–Webb leaf-size classes otherwise. Leaf-size classes were used to estimate leaf area following Wilf et al. (1998), i.e., by taking the average of the natural log-transformed upper and lower size-class bounds of each specimen.

Laguna del Hunco species-mean leaf areas were calculated as the average of the natural log of the largest and smallest leaf of each species, including the estimated areas of fragmented leaves. The leaf size index (LSI) for LH was also calculated using the following formula: LSI = $(m + 2n + 3M - 100)/2$, where m = % of dicot species that are microphyll or smaller, n = % notophyll, and M = % mesophyll or larger (Wolfe and Upchurch, 1987; Burnham, 1989; Greenwood, 1992, 1994).

Because the vein-scaling method had not yet been applied to fossils, we first verified whether the LH fossils exhibit scaling relationships similar to living dicots (Sack et al., 2012). We analyzed 159 intact, identified dicot specimens, chosen for good 2° vein preservation and no more than 1 cm of missing or damaged margin. These specimens included pinnately and palmately veined leaves for 76 fossil species. The directly measured areas ranged widely, from 67 to >8000 mm^2 (nanophyll to mesophyll). Additionally, we used the Cain and Castro (1959) formula and Raunkiaer-Webb size classes to estimate the areas of intact leaves for comparison to vein-scaling results.

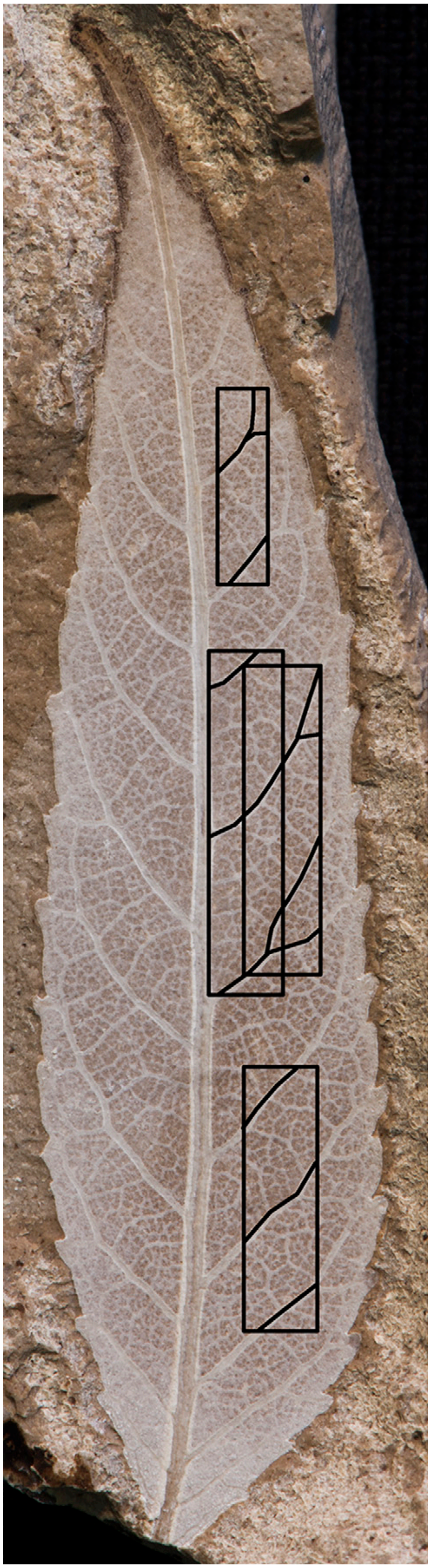
For this test set, we recorded primary (1°) vein diameter, the densities of 1° and 2° veins (vein length mm/leaf area mm^2), and leaf area. Primary vein diameter was averaged from measurements at the leaf base and the centers of the basal, middle, and apical thirds of the blade. The basal diameter measurement was made just above the petiole insertion point, or, if the petiole was absent, at the basalmost preserved portion of the midvein. Secondary veins were identified with reference to the *Manual of Leaf Architecture* (Ellis et al., 2009). We measured density for all 2° veins, including intersecondaries, minor secondaries, and interior secondaries. If the leaf was symmetrical, 2° vein length measurements were conducted on one medial side of the midvein and doubled.

We additionally subsampled 2° vein density in four rectangular areas along the best preserved medial half of the lamina (Fig. 1), namely, the centers of the basal, middle, and apical thirds of the leaf half and the middle third adjacent to the midvein. Subsampling areas were sized to include at least two 2° veins and had a mean area of 1.4 ± 0.11 cm^2 (1 SD). Areas with poor preservation were not measured. We averaged the 2° vein density of each specimen across all subsampling areas and scaled the result to estimated leaf area using the Sack et al. (2012) regression: $\log_{10}$ (leaf area cm^2) = 1.96 − 2.04 × $\log_{10}$ (subsampled 2° vein density cm/cm^2). Additionally, we derived an ordinary linear regression that was fitted only to the 159 intact fossil leaves: $\log_{10}$ (leaf area cm^2) = 1.51 − 1.31 × $\log_{10}$ (subsampled 2° vein density cm/cm^2). An *F* test comparing the two scaling equations for variation in slope found no significant difference ($F_{1, 314} = 0.41$, $P = 0.52$). However, in comparison with the Sack et al. (2012) regression, the fossil-based model produced smaller area estimates in small leaves and larger area estimates in large leaves. This tendency had undesirable effects when applied to fragmented fossil leaves from Laguna del Hunco, producing estimates that were smaller than original fragmented areas in more than half (68) of the 120 fragmented specimens measured. Because the original regression of Sack et al. produced fewer definite underestimates

TABLE 3. Summary of Laguna del Hunco fossil dicot leaf-area measurements.

Status (*N*)	Completeness (*N*)	Source	Method (*N*)
Identified specimens (1147)	Intact (161)	This study	Direct (161)
	Nearly intact (41)	This study	Direct (41)
	Fragmented (120)	This study	Vein scaling (98); size classes (22)
	Fragmented to intact (825)	Wilf et al., 2003, 2005	Cain and Castro (553); size classes (272)
Indeterminate specimens (522)	Fragmented to nearly intact (522)	This study	Vein scaling (508) Size classes (14)

Note: See Appendix S1 for all leaf-area measurements by specimen.



and was based on a geographically and phylogenetically broader sample with a greater range of leaf areas, we chose to use it for vein scaling instead of the fossil-based model. The choice of vein-scaling model had no effect on our main conclusions.

After testing the vein-scaling method on intact leaves, we applied it to 120 identified, fragmented leaves from Laguna del Hunco. These specimens varied in preserved size from 90 to 31 571 mm^2 (4.50 to 10.36 ln mm^2). We followed the same measurement protocol as in intact leaves, using the scaling model of Sack et al. (2012) for 2° vein density, averaged across all preserved subsampling regions (Fig. 1). We calculated the 95% prediction limits of vein-scaling estimated areas and restricted the lower limit of each specimen to its original area.

Like most paleofloras, the Laguna del Hunco collection contains hundreds of leaves of indeterminate species, of which many are fragmented. To test for taphonomic filtering of large leaves in this fraction, we analyzed 522 indeterminate specimens using vein scaling (Table 3; Appendix S1). These specimens had preserved areas from 80 to 17 662 mm^2, and their vein-scaling reconstructed areas ranged from 253 to 20 025 mm^2 (nanophyll to mesophyll).

For 22 identified (18%) and 14 indeterminate (3%) specimens, vein scaling yielded area estimates that were smaller than the actual preserved areas. These specimens included two leaves whose preserved areas (> 22 000 mm^2) exceeded any of the intact leaves studied. To avoid including known underestimates, we estimated leaf area for these specimens using the Raunkiaer–Webb leaf size classes, based only on the preserved leaf portions.

Australian rainforest data set—We used a detailed ecological assemblage data set (Kooyman et al., 2012) of Australian rainforest plots for comparisons to Laguna del Hunco. The data set records identifications, leaf sizes, and many additional traits of mature woody plant species, excluding vines, palms, ferns, and any plants <1 m in height. A total of 1137 species from 95 families are identified from the 596 plot-based assemblage samples. The plot areas vary from 0.1 to 0.5 ha (1000–5000 m^2), as defined by the local area of one tree and its ca. 30 nearest neighbor trees from the canopy or subcanopy. The limited spatial scales of the plots allow observation of differences in forest structure, keeping in mind that the individual coverage areas are much smaller than that of the Laguna del Hunco paleolake catchment.

To provide a larger spatial scale, we binned the Australian plots into five geographic regions (Table 4), the first two tropical and the rest subtropical: Cape York, Wet Tropics, Nightcap-Border Ranges, Washpool, and Dorrigo. Cape York is in the northeast of the continent and here represents the area north of Cooktown on the Endeavor River; the Wet Tropics are located close to the coast, in the area south of Cooktown extending to Townsville; Nightcap-Border Ranges includes the border region between northeast New South Wales and southeast Queensland; Washpool describes the rainforest

FIGURE 1 Example of regional subsampling in the vein-scaling method. Secondary vein density was sampled on one medial side of the lamina in four regions (small rectangles): the centers of the basal, middle, and apical thirds of the half leaf; and adjacent to the midvein in the middle third of the half leaf. The fossil shown is a *Caldcluvia* sp. leaflet (specimen field number LH02-1086) with a length of 5.7 cm.

TABLE 4. Statistics for Australian rainforest regions studied.

Region	Plots	MAT (°C)	MAP (mm)	Elevation (m)	Species richness
Cape York	140	25.3 (22–26)	1603 (1022–2041)	87.2 (1–500)	35.12 (9–60); 650
Wet Tropics	146	22.0 (18–24)	2432 (913–4170)	452.6 (3–1500)	39.23 (4–80); 436
Nightcap–Border Ranges	140	17.1 (14–19)	1562 (966–2197)	427.2 (65–1036)	45.25 (24–117); 288
Washpool	43	15.3 (13–17)	1159 (1080–1236)	786.3 (285–1125)	29.21 (12–55); 113
Dorrigo	127	16.2 (12–18)	1616 (1024–1914)	434.1 (9–1044)	32.56 (19–99); 200

Notes: Values in order are means (ranges); totals. Data from Kooyman et al. (2012). MAP, mean annual precipitation; MAT, mean annual temperature.

areas of the Gibraltar Range to Washpool National Park; and Dorrigo includes the rainforests of the Dorrigo National Park and nearby reserves that extend to the New England Tableland escarpment. There was only limited climatic overlap in these data between the tropics and subtropics, regardless of elevation (Table 4). Tropical regions were on average 5–10°C warmer in mean annual temperature than subtropical regions and included the wettest climates. Only 61 plots had mean annual precipitation values over 2500 mm, and these were all from the Wet Tropics.

Similarly to the fossils, the Australian leaf-size data represent mature simple leaves or the lateral leaflets of compound leaves. Because the Australian leaf areas had been estimated as leaf length × leaf width × 0.70, we multiplied the data by the necessary conversion factor to be compatible with the Cain and Castro (1959) formula's coefficient (2/3). We calculated the grand mean leaf area of each plot from the natural-log transformed species-mean areas per Wilf et al. (1998).

Fossil–modern floristics and climates—We focused on 15 genera of dicotyledons and conifers from Laguna del Hunco with identified nearest living relatives in Australasia and Southeast Asia (Tables 1, 2; see Table 1 for references supporting this summary). These taxa included five dicots known from leaves, three dicots known only from fruits and not leaves, three Australian conifers, and four ex-Australian conifers. In addition, one dicot could only be considered qualitatively (*Gymnostoma*). We note that several of the living-relative genera have Australian fossil records and remain extant there, whereas others have no Australian fossil record (see Kooyman et al., 2014 for details).

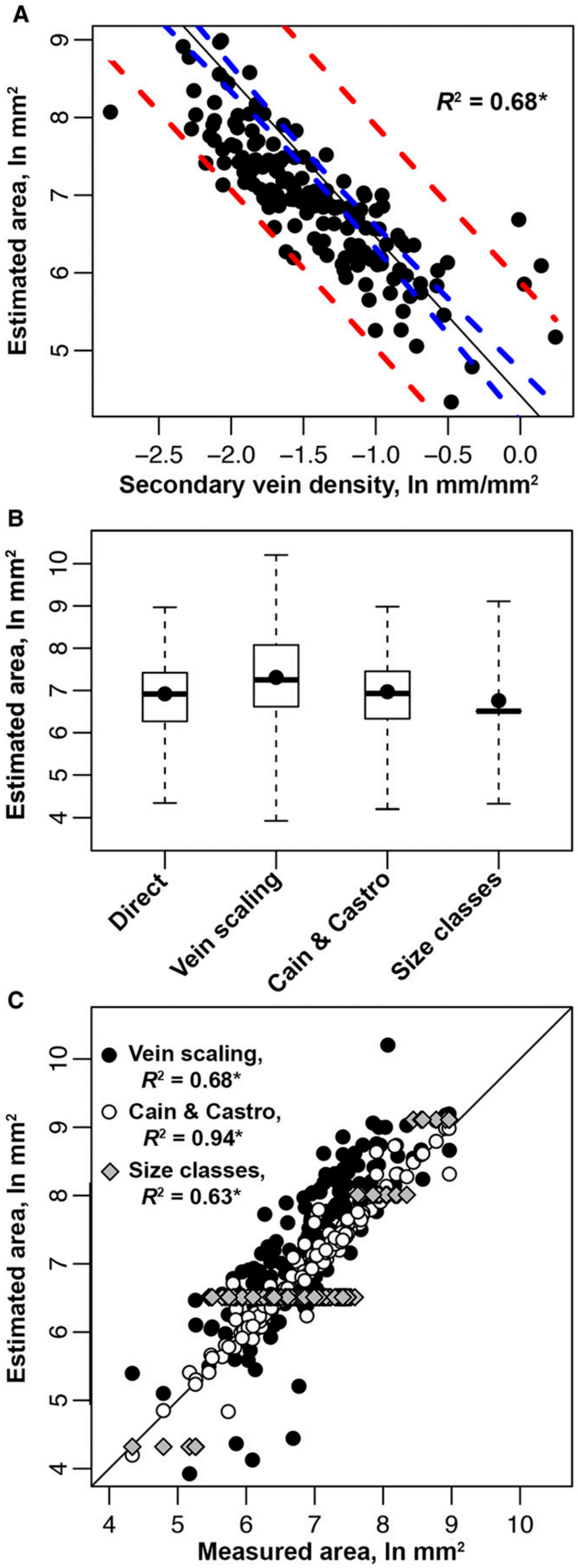
Fossil dicot species known from leaves, and occasionally other organs, include compound leaves and isolated leaflets of *Akania patagonica* (Akaniaceae), which belongs to a monotypic genus endemic to Australia. *Atherospermophyllum guinazui* (Atherospermataceae) is most similar to the Australian genus *Daphnandra* and the species *D. apatela*. Similarly, *Monimiophyllum callidentatum* (Monimiaceae) is most comparable to the Australian genus *Wilkiea* and the species *W. hugeliana*. The iconic Australian and Australasian genus *Eucalyptus* (Myrtaceae) is known from LH from over 100 leaf fossils of *E. frenguelliana*, along with abundant *Eucalyptus* infructescences, dispersed fruits, and rare flowers and flower buds. An unpublished species of *Caldcluvia* (Cunoniaceae, morphotype TY116 of Wilf et al., 2005) is recognized from a combination of features, including compound leaf arrangement, characteristic leaf architecture, and the presence of hairy domatia in 2° vein axils. *Caldcluvia* (*Ackama*) occurs in Australasia, South America, and Southeast Asia. Taxa known from fruits but not yet from leaves include the Australasian genus *Ceratopetalum* (Cunoniaceae), identified from winged fossil fruits. *Cochlospermum previtifolium* (Cochlospermaceae) is related to living, pantropical *Cochlospermum*, found in tropical Australia, Africa, and the Americas. *Orites bivascularis* (Proteaceae) belongs to a genus that occurs in both fossil and living floras of temperate Australia, as well as southern South America.

The three fossil conifers from living Australian genera include *Araucaria pichileufensis* (Araucariaceae) of *Araucaria* section *Eutacta,* which today inhabits Australia and New Caledonia. *Agathis zamunerae* (Araucariaceae) belongs to a genus that is extant from New Zealand to Sumatra, including Australia. However, the pollen cone morphology of *A. zamunerae* is most similar to the northern Borneo endemic *A. lenticula*, which we accordingly consider in the pool of NLRs (Table 2). *Podocarpus andiniformis* (Podocarpaceae) belongs to a genus that occurs today in wet habitats across Africa, Asia, and the Americas, with three species in tropical Australia.

Of the four fossil species from ex-Australian conifer genera, three are in Podocarpaceae: *Acmopyle engelhardti, Dacrycarpus puertae*, and an undescribed species of *Retrophyllum*. *Acmopyle* is extant only in Fiji and New Caledonia. *Dacrycarpus* is extant over large areas of Southeast Asia and Australasia, excluding Australia, and *Retrophyllum* is extant from Malesia to Fiji and in the Neotropics. The fourth, *Papuacedrus prechilensis* (Cupressaceae), belongs to a monotypic living genus that is endemic to montane Papua New Guinea and the Moluccas.

Finally, *Gymnostoma* (Casuarinaceae) is known from LH as leaves, male inflorescences with in situ pollen, and three infructescence species (Zamaloa et al., 2006). The genus could not be included in leaf area measurements because it has photosynthetic branchlets and highly reduced leaves that are unusual among angiosperms. In addition, the genus was not present in our plot-assemblage samples. Nevertheless, we include *Gymnostoma* in qualitative discussions because it has a rich fossil record in Australia (Christophel et al., 1992; Scriven and Hill, 1995; Guerin and Hill, 2003); *Gymnostoma* is extant in several regions with Laguna del Hunco NLRs, including Fiji, New Caledonia, and Borneo as well as tropical Australia (its Australian range is accessible elsewhere, e.g., through the Australian Virtual Herbarium [2015]).

We tabulated the occurrences, co-occurrences, and climate parameters (MAT, mean annual temperature; MAP, mean annual precipitation) of the Australian NLRs of 11 fossil taxa (Tables 1, 2) across the Australian assemblage plots (Kooyman et al., 2012). Nearest living relatives were identified as Australian species of the same genus or the most morphologically similar genus, and "NLR genera" are the respective, 11 extant genera as listed in Table 1. The one exception was the fossil *Araucaria pichileufensis*, which was only compared with *A. cunninghamii*, the one living Australian species of section *Eutacta* (i.e., *A. bidwillii* of section *Bunya* was excluded). We note that some Australian taxa have broader climatic distributions in relation to complete continental or distributional sampling (e.g., Kooyman et al., 2013). However, the aim of this



paper is to compare living and fossil assemblages and locations when possible, rather than making traditional species-by-species comparisons; inclusion of additional data from Australia would not affect our conclusions.

For the ex-Australian taxa, which are usually much less studied at the plot scale, we simply used available data on species climatic ranges. Data on *Acmopyle*, *Dacrycarpus*, and *Retrophyllum* species were sourced from Biffin et al. (2012). Climate values for *Agathis lenticula* and *Papuacedrus papuana* were estimated using georeferenced occurrence data from the Global Biodiversity Information Facility (GBIF; accessed through the GBIF Data Portal: data.gbif.org, 2014). For these two species, we used R statistical software version 3 (R Core Team, 2014) and the packages 'sp' and 'raster' to derive temperature ranges from reported elevation and precipitation ranges (e.g., Farjon, 2010) using WorldClim (Hijmans et al., 2005). We estimated climates for the two species as the averages of maximum and minimum values and uncertainty as the difference between the maximum and mean. Although we rely on potentially incomplete GBIF records and calculations that may overestimate the ranges of *A. lenticula* and *P. papuana*, these are the most detailed climate data available.

RESULTS

Vein scaling tested on fossils—For 159 intact leaves, area estimates predicted from vein scaling had individual standard errors from 0.72 to 0.74 ln mm^2 (Fig. 2A). On average, vein scaling tended to overestimate leaf area by 5% (in ln mm^2 units) and produced the widest range of estimated areas of the methods studied (Fig. 2B). The accuracy of vein scaling was similar to that of leaf size classes but much lower than that of the Cain and Castro formula (Fig. 2C). Vein-scaling areas were somewhat better correlated with measured areas for the 141 leaves whose 2° vein density could be subsampled from all four regions (as in Fig. 1; R^2 = 0.74 compared with R^2 = 0.68 for all 159 specimens, P < 0.001). Vein scaling yielded significantly underestimated areas (by 25–30%) for four specimens with 2° vein densities greater than 1 mm/mm^2 (Fig. 2A, right). All four were fossil *Eucalyptus*, characterized by numerous secondary and intersecondary veins.

As in living leaves, fossil 1° vein diameter scaled positively with leaf area, and 1° vein density scaled negatively with leaf area (Sack et al., 2012; Appendix S1). Of all vein characters studied, total 2° vein density (i.e., when vein density could be scored over the entire leaf lamina) had the strongest correlation with fossil leaf area

FIGURE 2 Results of testing three methods for estimating leaf area on 159 intact Laguna del Hunco specimens. Asterisks indicate significance at P < 0.001. (A) Relationship between subsampled 2° vein density and estimated leaf area, all data converted to natural log units for comparability. Thin black line indicates the Sack et al. (2012) scaling equation with 95% confidence (blue dashed) and 95% prediction (red dashed) limits. (B) Box plot comparisons of measured and estimated areas. Bold points are means, bold lines are medians, boxes contain second and third quartiles, and box plot tails show full ranges. No box is given for the size-class boxplot because there were only four categories; consequently, the second and third quartiles are equivalent to the median. (C) Estimated vs. measured fossil leaf areas, plotted on a 1:1 line.

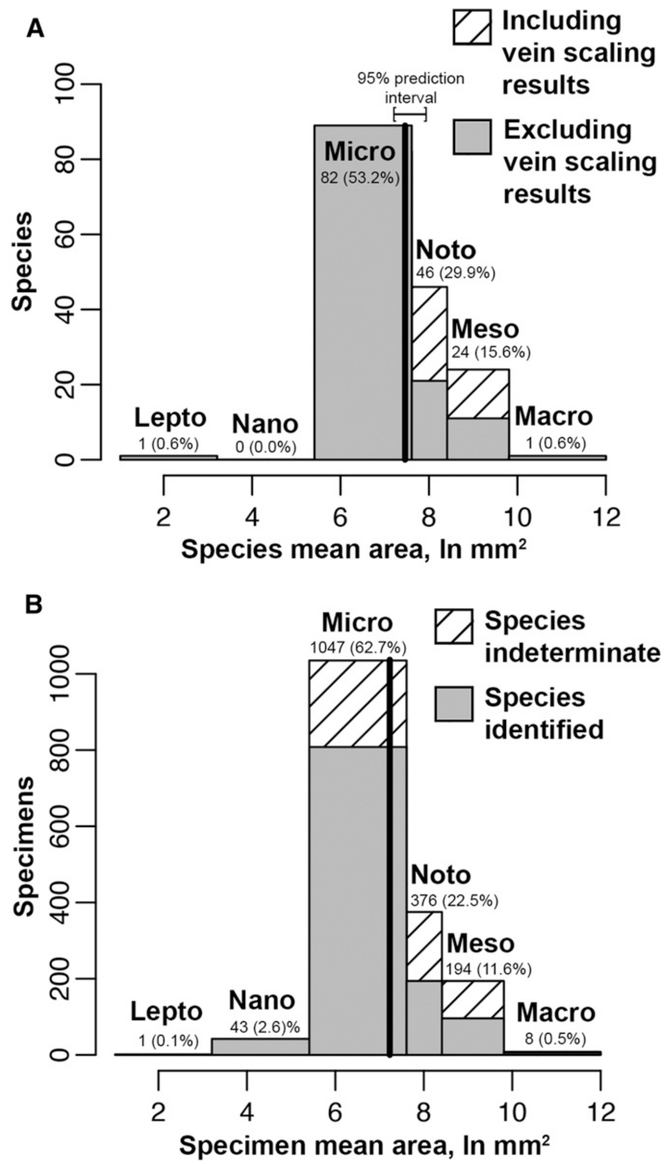


FIGURE 3 Reconstructed leaf-size distributions for Laguna del Hunco, binned by size class ("-phyll" suffix removed for brevity) with bin counts and percentages. See Table 3 for the breakdown of fossil area measurements by method. (A) Leaf-size distribution by species, shown with and without vein-scaling estimates from fragmented specimens. Bold line indicates the grand mean of 7.46 ln mm^2 (1737 mm^2, large microphyll). (B) Leaf-size distribution by specimen (i.e., without regard to identification), shown with and without vein-scaling estimates of 522 specimens from indeterminate species. Bold line indicates the mean of 7.22 ln mm^2 (1366 mm^2, large microphyll), including indeterminate specimens.

(R^2 = 0.75, P < 0.001, for 112 specimens). This correlation is comparable to that found in living leaves (Appendix S1; Sack et al., 2012).

Leaf area reconstruction—Including the vein-scaling reconstructed areas of 94 fragmented leaves, the grand mean leaf area of the Laguna del Hunco paleoflora was 1737 mm^2 (7.46 ln mm^2), with a 95% prediction interval between 1380 and 2752 mm^2 (large microphyll to small notophyll; Fig. 3A). The modal size class was microphyll. Seventy-seven species (50%) were represented by more than one area measurement. The best-sampled fossil species also showed the greatest variation in leaf area, ranging from 75 to 15 063 mm^2 ("*Celtis*" *ameghenoi*, Appendix S1).

Laguna del Hunco fragmented leaves had vein-scaled reconstructed areas of 53 to 49 513 mm^2 (leptophyll to macrophyll). By including fragmented specimens in our results, we added 31 species that previously had no size data and significantly increased the grand mean leaf area of the paleoflora (T_{195} = 6.73, P < 0.001) by 101 mm^2 to 1465 mm^2 at 95% prediction limits (Fig. 3A). Many previously unmeasured species had reconstructed areas of large notophyll or mesophyll (Appendix S1).

Indeterminate specimens were larger on average than identified species (Fig. 3B). When analyzed by specimen rather than by species, the mean leaf area of the identified fraction was 1097 mm^2 (7.00 ln mm^2). With the 522 indeterminate specimens included (Table 3), the specimen mean significantly increased, to 1366 mm^2 (7.22 ln mm^2; T_{2472} = 5.61, P < 0.001).

Leaf size comparisons—Laguna del Hunco leaf areas were consistently smaller than those of their Australian NLRs (Fig. 4; Appendix S1). *Podocarpus* and *Monimiophyllum* had the greatest size differences with their NLRs, but there is only one known specimen of the latter. Fossil *Agathis*, *Caldcluvia*, *Atherospermophyllum*, and *Eucalyptus* leaf areas were closer to, or overlapped, those of their NLRs. There was no correlation between a fossil taxon's sample size and its size similarity to Australian NLRs (Appendix S1). The leaf size index (LSI) for LH was 31, within the characteristic range of leaf litter from living Australian Simple Notophyll Vine Forests and no other Australian forest type (Greenwood, 1994).

For Australian plots, the grand mean (species-based) leaf areas by region varied from 2038 to 15063 mm^2 (7.62 to 9.62 ln mm^2), all larger than the value for LH of 1737 mm^2 (7.46 ln mm^2; Fig. 5A).

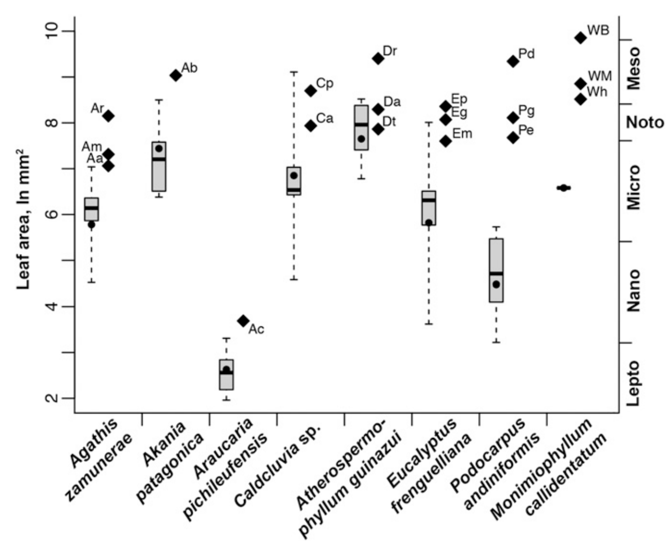


FIGURE 4 Leaf-size comparisons for eight Laguna del Hunco species (boxplots) and Australian NLRs (diamonds, some overlaps omitted). Table 1 (see footnote) indicates the Australian NLR species corresponding to the abbreviations. Bold points are means, bold lines are medians, boxes contain second and third quartiles, and box plot tails show full ranges. Leaf size classes labeled at right (abbreviated as in Fig. 3).

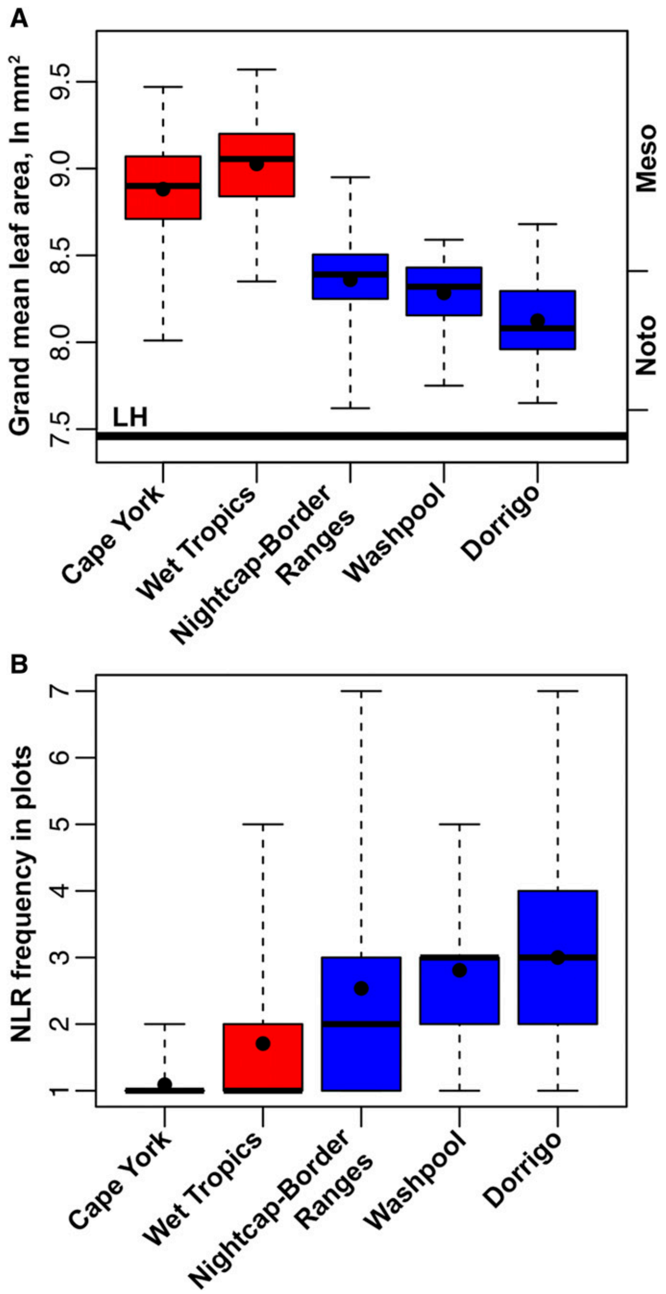


FIGURE 5 Laguna del Hunco leaf size (A) and composition (B) compared with extant Australian plots. Red, Australian tropics; blue, Australian subtropics. Bold points are means, bold lines are medians, boxes contain second and third quartiles, and box plot tails show full ranges. (A) Distribution of plot grand mean (by species) leaf areas by Australian region; bold line shows LH grand mean (see also Fig. 3A). (B) Regional plotwise frequencies of 11 NLR genera (Tables 1, 2).

The subtropical plots have smaller leaf areas that are more similar to LH: the 10 plots with the lowest leaf areas are cool (mean MAT 16.7°C), moderately wet (mean MAP 1656 mm), and located in lowland to upland elevations (mean 311.2 m; Table 5). The majority of these plots had metasedimentary bedrock, and their average richness (24.1 species/plot) was lower than that of the typical subtropical plot (Tables 4, 5).

***Floristic and climatic comparisons*—**Most Laguna del Hunco genera that are extant in Australia have both tropical and subtropical ranges; the exceptions are *Akania* (subtropical, monotypic), *Cochlospermum* (tropical, one Australian species), and *Gymnostoma* (tropical, one Australian species; Wilson and Johnson, 1989). Australian *Agathis* only occurs in tropical plots in our data set, but we note that *A. robusta* also has a subtropical distribution (Farjon, 2010).

Subtropical plots have more Laguna del Hunco NLR genera than do tropical plots (Fig. 5B, Table 6). All the Australian plots studied have at least one NLR genus, as follows: *Eucalyptus* (26% of plots), *Caldcluvia* (23%), *Daphnandra* (22%), *Orites* (16%), *Ceratopetalum* (15%), *Araucaria* (13%), *Podocarpus* (11%), *Akania* (7%), *Agathis* (3%), *Cochlospermum* (2%). Two plots have seven NLR genera each; one of these is in Moonpar State Forest, Dorrigo, and the other is in Whian Whian State Forest (now Nightcap National Park), Nightcap-Border Ranges (Table 6). Both plots have the rare, endemic genus *Akania*. Of the 10 Australian plots with the highest numbers of NLR genera, five are from the Nightcap-Border Ranges region. The climates of these 10 plots (Table 6) are cool (mean MAT 16.9°C), moderately wet (mean MAP 1596 mm), and at upland elevations (mean 549 m). All 10 plots have metasedimentary or igneous bedrock and relatively high species richness (mean 71.9 species/plot; Tables 4, 6).

Including ex-Australian taxa, Laguna del Hunco NLRs occur in three distinct climate spaces (Fig. 6, Table 2) that correspond to the respective ranges of subtropical Australian, tropical Australian, and ex-Australian genera. Most subtropical Australian NLRs have cooler climate spaces than tropical Australian NLRs, including those from higher elevations. Several ex-Australian NLRs inhabit higher elevation, wetter climate spaces than Australian NLRs.

DISCUSSION

***Fossil leaf area from vein scaling*—**Laguna del Hunco fossil leaves have secondary vein densities and vein-scaling relationships to area that are compatible with a broad spectrum of living dicots (Fig. 2A; Sack et al., 2012). This finding supports the hypothesis that leaf size and major venation had similar developmental constraints in the early Cenozoic to today. We found that the vein-scaling method predicted intact fossil areas as accurately as traditional leaf size classes. Our results show the substantial potential of this new method for reconstructing the areas of fragmented leaves that cannot be assigned to a leaf-size class.

Although fragments made up only 8.1% of the Laguna del Hunco specimens that we analyzed, including their vein-scaling reconstructed areas increased the grand mean leaf area of the paleoflora by 101 mm², to 1465 mm² (at 95% prediction limits; Fig. 3A), keeping in mind that vein scaling may slightly overestimate leaf area (Fig. 2C). Applying vein scaling allowed us to recover many large leaf areas that would otherwise have been unrepresented (Fig. 3A) and to use 31 species that previously could not be measured. This finding is noteworthy because observed species richness has a significant effect on the precision of leaf-physiognomy data (Wilf, 1997). In sum, the vein-scaling method has considerable promise, especially for more typical paleofloras with much greater leaf fragmentation than Laguna del Hunco.

***Assessing taphonomic bias in leaf area*—**Although this study probably does more to mitigate taphonomic bias in fossil-leaf

TABLE 5. The 10 Australian plots with the smallest leaf areas.

Plot	Mean LA (ln mm²)	NLR genera	Species richness	Elevation (m a.s.l.)	MAT (°C)	MAP (mm)	Bedrock	Region
N77	7.62	1	24	247	18	1965	r	NB
D180	7.65	3	19	647	15	1900	m	D
N133	7.65	1	24	453	17	1168	s	NB
D210	7.67	2	19	28	18	1684	m	D
D233	7.69	2	26	433	16	1602	m	D
N76	7.73	2	25	226	18	1965	r	NB
W289	7.75	3	25	377	16	1159	m	W
D190	7.75	2	24	115	18	1654	m	D
D251	7.78	1	27	412	15	1569	m	D
D205	7.79	4	28	174	16	1889	m	D
Mean	7.71	2.1	24.1	311.2	16.7	1655.5		
Range	7.62–7.79	1–4	19–28	28–647	15–18	1159–1956		

Notes: Data from Kooyman et al. (2012). D, Dorrigo; LA, leaf area; m, metamorphic; NB, Nightcap-Border Ranges; NLR, nearest living relative (Table 2); r, rhyolite; s, sandstone; W, Washpool.

area than any prior analysis, Laguna del Hunco leaf sizes must still be considered minimum estimates. The unreconstructed, preserved areas of some identified fragmented leaves were larger than those of intact leaves, supporting the consensus that large leaves are especially prone to fragmentation (Roth and Dilcher, 1978; Spicer, 1981; Hill and Gibson, 1986; Burnham, 1989; Greenwood, 1992). Also, indeterminate leaf specimens were reconstructed as larger, on average, than those of identified fossil species (Fig. 3B). Our results provide a new motivation to identify fossil specimens that are represented by fragments of once-large leaves because they are likely to have a significant impact on paleoecological reconstructions.

The mean leaf areas of all eight Laguna del Hunco fossil species studied were smaller than those of their Australian NLRs (Fig. 4). This trend was present in both conifers and angiosperms and, therefore, most likely reflects a shared taphonomic bias against large leaves rather than a general evolutionary increase in leaf area. However, the large difference in leaf size between fossil *Araucaria pichileufensis* and living *A. cunninghamii* (Fig. 4) appears to require a different explanation. The fossils have minuscule (mean area 14 mm²), scale-like leaves that are always found attached to branches and not fragmented, suggesting little possibility of taphonomic bias. A possible solution is that several of the New Caledonian species of *Araucaria* section *Eutacta* have small leaves whose sizes are closer to *A. pichileufensis*. For example, *A. columnaris* (very similar to *A. pichileufensis*: Florin, 1940b) has a mean leaf area ca. 16.7 mm² (2.73 ln mm²; compare with Fig. 4), based on the Cain and Castro formula and length and width data from Silba (1986).

Australian analogs—Our study affirms and quantifies the remarkable similarities of living Australian rainforests, especially from the subtropics, to the Eocene Laguna del Hunco flora of Eocene Patagonia. Subtropical Australia has nine of the 10 plots with the highest numbers of NLR genera; both of the plots that had seven NLR genera each, including the rare endemic *Akania*; and all 10 of the plots with the smallest leaf sizes (Fig. 5B; Tables 5, 6). In addition, the LH paleoflora shows several characteristics of Australian Simple Notophyll Vine Forests (SVNF), which tend to be subtropical in distribution. The paleoflora has a majority of large-microphyll leaves with fewer notophylls and mesophylls, and its leaf size index of 31 is within the range of SNVF leaf litter (Greenwood, 1991, 1994). Laguna del Hunco also contains taxa that commonly have vine life forms and are found in SNVFs, such as *Ripogonum* (Carpenter et al., 2014) and Menispermaceae (Wilf et al., 2005). Another noted characteristic of SNVFs is the presence of emergents, and abundant evidence supports an emergent canopy layer at LH. The conifers *Agathis*, *Araucaria*, *Dacrycarpus*, *Podocarpus*, and *Papuacedrus* (Table 1) can reach heights of 50 m or more today (Paijmans, 1970; Farjon, 2010).

Tropical Australian plots also showed significant floristic similarities with LH. Tropical Australia contains some NLR genera that are not present in the subtropics, including *Cochlospermum* and *Gymnostoma* (Wilson and Johnson, 1989). In the Australian plots, *Cochlospermum* is deciduous and occurs in areas that are relatively hot (average MAT 25 ± 1°C) and dry (average MAP 1329 ± 270 mm; Table 2). In contrast, some LH genera with tropical Australian NLRs show physiological susceptibility to drought. For example, extant *Gymnostoma* has unprotected stomata (Johnson

TABLE 6. Australian plots with highest frequencies of Laguna del Hunco nearest living relative genera (Table 1).

Plot	NLR genera	Mean LA (ln mm²)	Species diversity	Elevation (m)	MAT (°C)	MAP (mm)	Bedrock	Region	Location
D144	7	8.21	97	646	16	1622	m	D	Moonpar SF
N61	7	8.28	92	189	19	1846	r	NB	Whian Whian SF
N10	6	8.49	103	160	18	1808	b	NB	Whian Whian SF
D141	6	8.24	75	611	14	1876	m	D	Dorrigo NP
N32	5	8.61	49	744	16	1795	b	NB	Border Ranges NP
N99	5	8.48	84	225	18	1849	g	NB	Mt Warning NP
N19	5	8.47	67	717	16	1120	b	NB	Beaury SF
D159	5	8.38	54	799	16	1566	b	D	Bellinger River NP
P45	5	8.76	61	790	21	1317	g	WT	Bakers Blue Mt
W273	5	8.26	37	604	15	1166	m	W	Washpool NP
Mean		8.41	71.9	548.5	16.9	1596			
Range		8.21–8.75	37–103	160–799	14–21	1120–1876			

Notes: Data from Kooyman et al. (2012). b, basalt; D, Dorrigo; g, granite; LA, leaf area; m, metamorphic; NB, Nightcap-Border Ranges; NP, National Park; r, rhyolite; SF, State Forest; W, Washpool; WT, Wet Tropics.

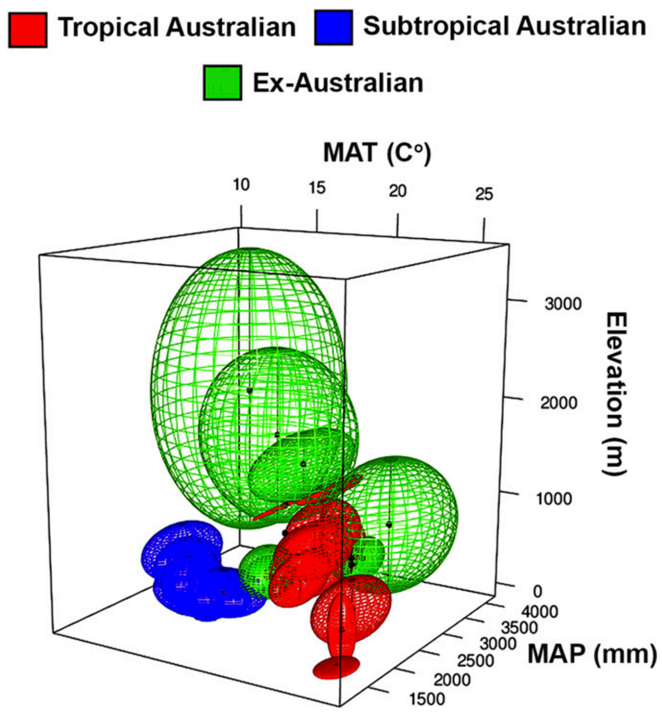


FIGURE 6 Climate and elevation spaces of Laguna del Hunco NLRs; Table 2 (see footnote) indicates the NLR species and corresponding data plotted here. Each species' climate space is depicted with an ellipsoid (radius ±1 SD) centered on its average mean annual temperature (MAT), mean annual precipitation (MAP), and elevation (Table 2; Australian species that may occur elsewhere are represented only with their Australian ranges). Ex-Australian taxa from Southeast Asia and Australasia usually have much less precise climate data.

and Wilson, 1989), and *Agathis* possesses foliar transfusion tissue (Kausik, 1976).

Climate and elevation—Our results suggest that there is no single climate and elevation zone that is suitable for all surviving lineages from LH. Occurrences of Laguna del Hunco NLRs show well-marked separation among Australian subtropical, tropical, and ex-Australian biomes (Table 2, Fig. 6). Ex-Australian NLRs mostly inhabit wetter and higher areas than Australian NLRs, except for the New Caledonian endemics *Acmopyle pancheri*, *Retrophyllum comptonii*, and *Dacrycarpus vieillardii*. Furthermore, within Australia, tropical NLRs are found in assemblages whose climates are mostly wetter and always warmer (by at least 2°C MAT) than those of the subtropical NLRs (Table 2, Fig. 6). Our results reinforce the idea that many Cenozoic conifer extinctions in Australia resulted from rainforest fragmentation and loss of cool, high-rainfall habitats (Brodribb and Hill, 1998; Brodribb and Holbrook, 2005; Kooyman et al., 2014).

Outside Australia, there are many Australasian and Southeast Asian regions that merit closer studies regarding their similarities to LH and other Gondwanan paleofloras. For example, the montane forests of Mt. Kerigomna and Mt. Wilhelm, Papua New Guinea, have Australian NLRs like *Podocarpus* and *Caldcluvia* as well as ex-Australian NLRs such as *Dacrycarpus* and *Papuacedrus* (Grubb and Stevens, 1985). Both locations also have a majority of microphyll or notophyll leaves that are similar to the sizes found for LH (Fig. 3A). These areas are relatively cool (7.8–14.3°C MAT), wet (>3985 mm MAP), and elevated (2500–3550 m a.s.l.; Grubb and Stevens, 1985), unlike any modern Australian region. Potential analogs for LH also exist off the Australian plate. On Mt. Kinabalu, northern Borneo, there are comparably cool, wet montane rainforests with microphyll and notophyll leaf areas (Kitayama et al., 2015). Further, the Mt. Kinabalu and Crocker Range region contains many Gondwanan taxa (Kooyman et al., 2014), including two Laguna del Hunco NLRs that are dominant and emergent (*Agathis lenticula* and *Dacrycarpus imbricatus*: Table 2).

The three distinct climate and elevation spaces of the NLRs (Fig. 6) imply that the LH lineages survived through different histories. In Australia, some taxa tracked or adapted to somewhat drier, cooler subtropical climates and others to wetter, hotter tropical climates. Outside of Australia, lineages survived in equatorial areas like New Guinea and Borneo by tracking or adapting to cool, wet climates of generally higher elevations. Some lineages, like *Dacrycarpus*, expanded even farther north, into mainland Southeast Asia. At the fine scale of one spectacular fossil site and its modern legacy, our results indicate that the ancient floras that once associated in Patagonia did not maintain a perfectly coherent, unified response to climatic and tectonic change over geologic time. On the other hand, it remains remarkable that so many Gondwanan associations are extant in numerous locations. The distributions of Laguna del Hunco survivors will continue to provide important input for classic questions regarding biome conservatism vs. adaptation in the context of historical events.

CONCLUSIONS

Fossil–modern comparisons presented here demonstrate the living legacy of the Laguna del Hunco paleoflora at a much higher level of resolution than was previously known. We improved fossil leaf area measurements by using the vein-scaling method. Applying this method to 98 fragmented specimens recovered large leaf areas that were previously unmeasured and increased the grand mean leaf area of the paleoflora. Vein scaling may be especially advantageous for the study of fossil floras that have many fragmentary leaf specimens, although it needs to be tested in more fossil floras for possible overestimation of large leaf sizes.

We found living analogs for the Laguna del Hunco paleoflora in three discrete, complementary areas: subtropical Australia, tropical Australia, and outside of Australia in cool, wet montane Southeast Asia and Australasia. Our detailed floristic assemblage and leaf-area comparisons affirm previous qualitative suggestions that, within Australia, Laguna del Hunco was most similar to Simple Notophyll Vine Forests. Nevertheless, tropical Australia contains a distinct fraction of the Laguna del Hunco NLRs known to date. Outside of Australia, cool, wet montane rainforests also have many NLRs from the paleoflora, including several genera that are extinct in Australia. These results suggest that surviving Gondwanan lineages known from Laguna del Hunco tracked or adapted to different climates, resulting in their diverse modern distributions and complex legacy in living ecosystems. Investigating the roles of biome conservatism vs. adaptation in the histories of these ancient lineages comprises a ripe area for future study.

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