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ORIGINAL ARTICLE

Non-congruent fossil and phylogenetic evidence on the evolution of climatic niche in the gondwana genus *Nothofagus*

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ABSTRACT

Aim We used fossil and phylogenetic evidence to reconstruct climatic niche evolution in *Nothofagus*, a Gondwana genus distributed in tropical and temperate latitudes. To assess whether the modern distribution of the genus can be explained by the tropical conservatism hypothesis, we tested three predictions: (1) species from all *Nothofagus* subgenera coexisted under mesothermal climates during the early Eocene; (2) tolerance to microthermal climates evolved during the Eocene–Oligocene cooling from an ancestor that grew under mesothermal conditions; and (3) the climatic niche in *Nothofagus* is phylogenetically conserved.

Location Australia, New Zealand, New Caledonia, Papua-New Guinea and South America.

Methods We estimated the palaeoclimate of the Early Eocene, fossil-bearing Ligorio Marquez Formation (LMF, Chile), using coexistence and leaf physiognomic analysis. We reconstructed ancestral climatic niches of *Nothofagus* using extant species distributions and a time-calibrated phylogeny. Finally, we used the morphological disparity index and phylogenetic generalized least squares to assess whether climatic variables follow a Brownian motion (BM) or an Ornstein–Uhlenbeck (OU) model of evolution.

Results Our palaeoclimatic estimates suggest mesothermal conditions for the LMF, where macrofossils associated with subgenera *Lophozonia* and possibly *Fuscospora*, and fossil pollen of *Brassospora* and *Fuscospora/Nothofagus* were recorded. These results are not supported by our phylogenetic analysis, which instead suggests that the ancestor of *Nothofagus* lived under microthermal to marginally mesothermal conditions, with tolerance to mesothermal conditions evolving only in the subgenus *Brassospora*. Precipitation and temperature dimensions of the realized climatic niche fit with a gradual BM or constrained OU model of evolution.

Main Conclusions Our results suggest that the use of phylogenetic reconstruction methods based only on present distributions of extant taxa to infer ancestral climatic niches is likely to lead to erroneous results when climatic requirements of ancestors differ from their extant descendants, or when much extinction has occurred.

Keywords
Eocene, Gondwana, into the tropics, niche modelling, Nothofagaceae, palaeoclimate, phylogenetic signal, tropical conservatism hypothesis.

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INTRODUCTION

Over the course of geological time, lineages either adapt to new conditions, track their ancestral habitats or become extinct (Hoffmann & Sgro, 2011). In the case of plants, phylogenetic and evolutionary studies suggest that related species tend to grow in similar climates, latitudes and biomes, indicating that ecological requirements are phylogenetically conserved (Crisp *et al.*, 2009; Hawkins *et al.*, 2011; Pérez *et al.*, 2014). Consequently, habitat tracking, associated with niche conservatism, is the main explanation for the persistence of lineages through geological climate change (Wing & Greenwood, 1993). The hypothesis that lineages track favoured climates has strong support, to the extent that it tends to be assumed that ancestral climatic conditions are similar to those under which extant species of a lineage thrive (Wing & Greenwood, 1993; Mosbrugger & Utescher, 1997). Furthermore, it is assumed that ancestral climate niches may be inferred from a consideration of the ecological and climatic characteristics of modern taxa (Yesson & Culham, 2006; Evans *et al.*, 2009). However, comparisons between phylogenetic inferences and those obtained from fossil records are scarce (Quental & Marshall, 2010). The fossil record provides evidence about the past ecological and abiotic conditions under which species lived and thus can contribute to our understanding of the constraints associated with a phylogenetic approach.

Climatic niche conservatism has been invoked to explain the well-documented global trend, whereby species diversity in most groups declines from the tropics to the poles [e.g. tropical conservatism hypothesis (TCH; Wiens & Donoghue, 2004; Donoghue, 2008)]. TCH links both historical and evolutionary assumptions (Kerkhoff *et al.*, 2014). Historical explanations assume that lineages from low latitudes originated and underwent diversification under tropical climatic conditions (Donoghue, 2008), while evolutionary explanations suggest that dispersal into the temperate zone is limited by the capacity of organisms to adapt to new, colder and more seasonal climates, due to niche conservatism (Donoghue, 2008; Kerkhoff *et al.*, 2014). Palaeoclimatic reconstructions have shown that near-tropical conditions dominated at high latitudes (i.e. 60° S) in the Early Eocene (Carpenter *et al.*, 2012; Pross *et al.*, 2012), when global temperatures were 12 °C warmer than today (Zachos *et al.*, 2001). During the Eocene–Oligocene glaciation and presence of ice-sheets over the poles, global temperatures decreased by 7 °C (Zachos *et al.*, 2001). Therefore, TCH predicts that the vast majority of temperate lineages should be derived from tropical lineages (Wiens & Donoghue, 2004; Donoghue, 2008). Indeed, at a global scale, it has been shown that plant lineages currently occurring at low latitudes are older than those occurring at high latitudes (Hawkins *et al.*, 2011; Kerkhoff *et al.*, 2014). However, this pattern is less clear in the Southern Hemisphere (Segovia *et al.*, 2013), where there are many plant genera of Gondwana origin that are currently distributed in tropical and temperate latitudes (e.g.

Nothofagus, Drimys, Weinmannia) (Arroyo *et al.*, 1995; Villagrán & Hinojosa, 1997; McGlone *et al.*, 2001).

Nothofagus is considered an emblematic plant genus for understanding biogeographical processes of Gondwana lineages with modern distributions in both tropical and temperate regions (Linder & Crisp, 1995). *Nothofagus* comprises 43 species grouped into four monophyletic subgenera (Hill & Read, 1991; Hill, 2001a). The tropical subgenus *Brassospora* (25 species), endemic to New Guinea and New Caledonia, is sister to the temperate subgenus *Nothofagus*, endemic to southern South America, and together they are sister to the other two temperate subgenera, *Lophozonia* and *Fuscospora* (Romero, 1986; Swenson *et al.*, 2000; Hill, 2001a; Sauquet *et al.*, 2012). The majority of the literature on fossil and extant *Nothofagus* uses the taxonomy erected by Hill & Read (1991), but Heenan & Smissen (2013) recently suggested that morphological and molecular differences between the four subgenera are sufficient for these to be recognized as separate genera. We do not adopt this revision in the present work, in order to avoid confusion between the modern taxonomy and the fossil record.

The fossil record of *Nothofagus* pollen dates back to the Late Cretaceous (80 Ma) at high latitudes in Antarctica (Dettman *et al.*, 1990; Hill & Dettman, 1996), but the lineage only became widespread and diverse after the Mid-Eocene, under a mesothermal climate with little thermal seasonality and high precipitation throughout the year (Romero, 1986; Hill & Dettman, 1996; McGowran *et al.*, 2000; Hinojosa & Villagran, 2005; Macphail, 2007; Read *et al.*, 2010). The low percentage of pollen and absence of macrofossils of *Nothofagus* in the fossil record for the warm Early Eocene suggests that the genus was mostly restricted to high latitudes or high-altitude areas during that period (McGowran *et al.*, 2000; Read *et al.*, 2010). However, recent micro- and macrofossils of *Nothofagus* found at mid-latitudes in southern South America from the Early Eocene suggest that *Nothofagus* lived at mid-latitudes during the Eocene (Suárez & de la Cruz, 2000; Okuda *et al.*, 2006). This fossil record can be used to reconstruct the past climatic conditions under which *Nothofagus* species from different subgenera coexisted, and thus to assess whether *Nothofagus* was capable of growing under a warm climate during the Early Eocene.

We examined the climatic history of *Nothofagus* using phylogenetic models and fossil evidence obtained from the mid-latitude, Early Eocene, Ligorio Marquez Formation (hereafter LMF) in Chile. We first described the unequivocal presence of *Nothofagus* in the LMF, and then using both coexistence and physiognomical analysis, we estimated the palaeoclimate of the LMF fossil flora. In order to assess whether the TCH hypothesis can explain the modern distribution of *Nothofagus*, we modelled the realized climatic niches of extant *Nothofagus* species and estimated the ancestral states and phylogenetic signal of climatic variables, using a previously published phylogeny (Sauquet *et al.*, 2012). Specifically, we tested three predictions: (1) species from all

Nothofagus subgenera coexisted under mesothermal climates during the early Eocene; (2) tolerance to microthermal climates evolved during the Eocene–Oligocene cooling from an ancestor that grew under mesothermal conditions; and (3) the climatic niche in the genus *Nothofagus* is phylogenetically conserved.

METHODS

Local presence of *Nothofagus* during the Early Eocene: the Ligorio Marquez Formation

The LMF (Suárez & de la Cruz, 2000) is a terrestrial clastic deposit consisting of fluvial channels, flood plains and marsh deposits, with abundant plant megafossils and pollen remains (Yabe *et al.*, 2006). It is exposed in the eastern central region of Patagonia, in Chile, at a palaeolatitude of 51.68° S, 69.81° W. It is older than 47.6 ± 0.78 Ma (K/Ar date, Yabe *et al.*, 2006) and, according to our U–Pb zircon analysis, younger than 59.9 ± 1.1 Ma. Based on chronostratigraphic charts in both Palynodata & White (2008) and Ruiz *et al.* (1999), the presence of pollen grains from *Psilatricolporites inargutus*, *Retitricolporites medius* and *Nothofagidites kaitangataensis* in the microflora (Carvajal, 2013) allowed us to restrict the age of the LMF to the Early Eocene. To confirm the presence of *Nothofagus* in the LMF, we analysed leaf impressions and pollen fossils from the study site 'Mina Ligorio Marquez'. The material was described and identified by comparisons with Southern Hemisphere palaeobotanical records and modern leaves from plants within the genus.

Palaeoclimate of the Ligorio Marquez Formation

To estimate the palaeoclimate of the LMF, we conducted a coexistence analysis (Mosbrugger & Utescher, 1997) based on the families that we identified from pollen fossils from the same formation. This analysis considers the climatic interval of coexistence between a group of taxa as the best estimate of the climate under which the fossil assemblage lived. The climatic niche for each family was modelled using the maximum entropy algorithm Maxent (Phillips *et al.*, 2006) and the 19 bioclimatic variables contained in the WorldClim global database (Hijmans *et al.*, 2005), with a resolution of 5 km^2. For each family, we used a total of 50 replicates, 25% of the data as a training set, a regularization multiplier of 1 and bootstrap replicated run type Maxent parameters. To measure the degree to which the ecological niche model differed from random, we used the area under the receiving operating characteristic curve (AUC). To obtain the predicted niche occupancy (PNO) profiles with respect to the 19 climatic variables, we used the raw probability (RP) distribution of each family, derived from Maxent (Evans *et al.*, 2009). The interval of coexistence between those families identified in the LMF was built separately for each climatic variable, using the 20th–80th percentile range obtained from

the PNO results. These analyses were conducted using the R package Phyloclim (Heibl, 2011).

To obtain an independent estimate of the LMF palaeoclimate, we conducted leaf margin analysis (LMA; Wolfe, 1979), using samples extracted from the same strata as the pollen fossils. Leaf margin analysis is based on the relationship between the proportion of plant species with entire leaf margins (pE) in a plant community and current mean annual temperature (MAT). This relationship allowed us to infer past MATs from fossil pEs. In this study, we used the pE obtained from the LMF flora [65% on 55 morphotaxa; Hinojosa *et al.* (2006) and the equations published by Peppe *et al.* (2011) and Hinojosa *et al.* (2011)]. Finally, we used the following categories of the bioclimatic thermal regime nomenclature proposed by Nix (1991): megathermal climate (MAT ≥ 22 °C, mean annual precipitation (MAP > 549 mm); mesothermal climate (MAT range: > 14–22 °C, MAP > 549 mm); microthermal climate (MAT ≤ 14 °C, MAP range: 719–3000 mm).

Realized Climatic Niche of extant *Nothofagus* species

We modelled the modern realized climatic niche of 27 of the 35 extant *Nothofagus* species using Maxent (Phillips *et al.*, 2006) and the 19 WorldClim bioclimatic variables, with a resolution of approximately 1 km^2 (Hijmans *et al.*, 2005). We used a total of 20,000 valid occurrences obtained from the online global database GBIF (Global Biodiversity Information Facility), regional herbaria records (CONC, Universidad de Concepción; MEL, National Herbarium of Victoria and HO, Tasmanian Herbarium) and field records stored in the Palaeoecology Laboratory of the Universidad de Chile. PNOs (Evans *et al.*, 2009) for each species were built for each climatic variable in the Phyloclim R package (Heibl, 2011), following the same protocol as described above. Finally, we estimated the weighted mean (wmean) for each of the 19 bioclimatic variables, to be used in comparative analyses.

Evolution of climatic niche and comparative methods

To reconstruct the evolution of the climatic niche in *Nothofagus,* we used the maximum clade credibility beast tree topology published by Sauquet *et al.* (2012). Specifically, we used the chronogram scenario 4, which explicitly incorporates the fossil record (fig. 3 in Sauquet *et al.*, 2012). The PNO profiles were used to calculate the maximum likelihood estimate and 95% confidence intervals (95% CI) for each climate variable at each interior node of the phylogeny, assuming Brownian motion evolution (Evans *et al.*, 2009). Confidence intervals were calculated using an unbiased estimate of the variance of the Brownian motion. Analyses were conducted using the R packages Phyloclim (Heibl, 2011), Ape (Paradis *et al.*, 2004) and Phytools (Revell, 2012).

To evaluate phylogenetic niche conservatism (PNC), defined as the retention of ecological traits over time among
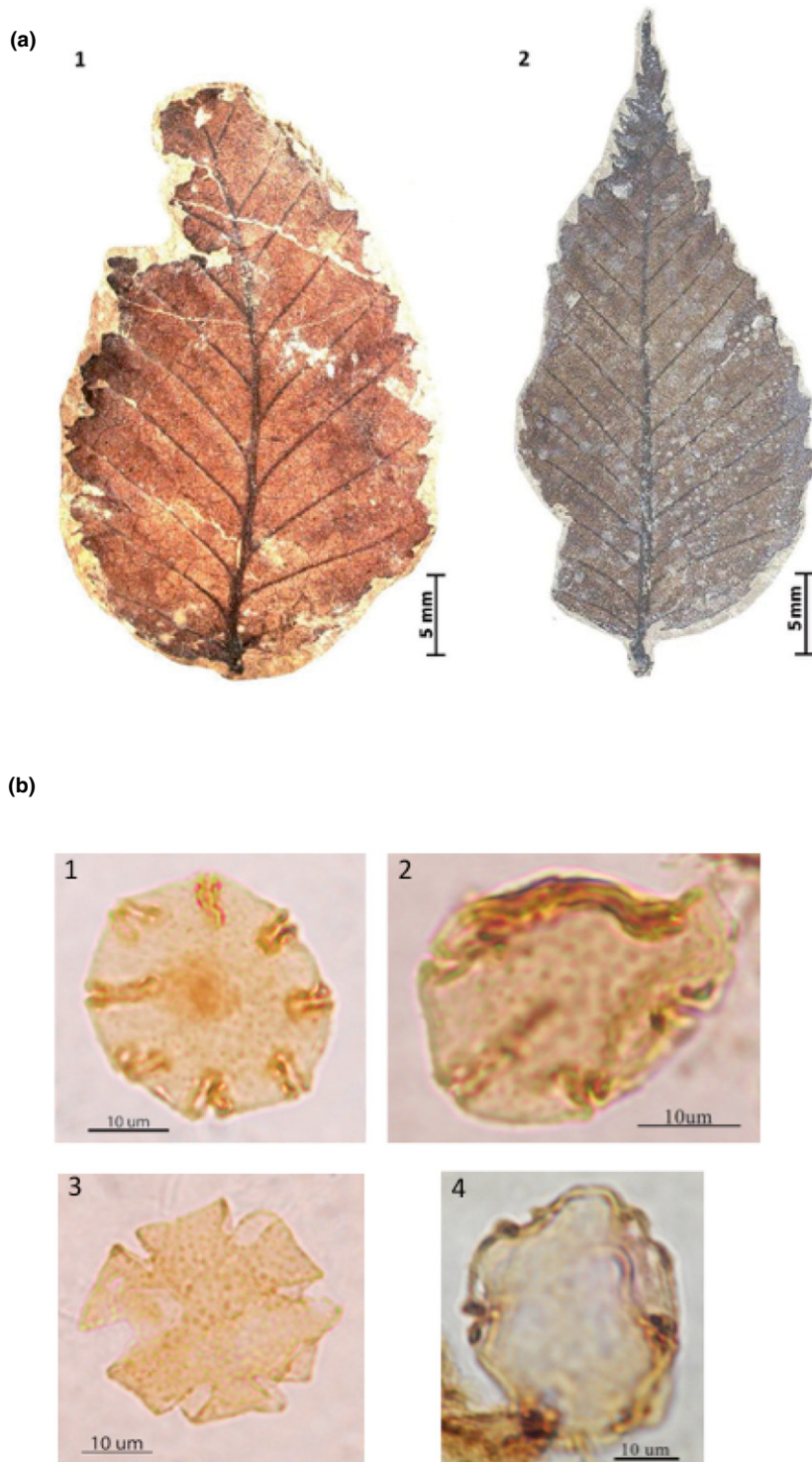
(a)

(b)

Figure 1 Leaf remains and fossil pollen grains of *Nothofagus* recovered from the Ligorio Marquez Formation. (a) Leaf imprint of *Nothofagus serrulata*. 1) Morphotype SGO 1571, Chile. 2) Morphotype NSM-PP-12349, Japan). (b) Pollen type associated with *Nothofagus*. 1) *Nothofagidites kaitangataensis*, 2) *Nothofagidites acromegacanthus*, 3) *Nothofagidites dorotensis* and 4) *Nothofagus* Fusca group.

related species (Wiens *et al.*, 2010), we used two approaches. First, we measured the phylogenetic signal of the climatic niche of *Nothofagus* using the morphological disparity index (MDI) described by Harmon *et al.* (2003). The MDI compares the observed disparity to that expected under an evolutionary model that assumes unconstrained Brownian motion (BM). Disparity is based on the average pairwise Euclidean distance between taxa with respect to the mean predicted climate occupancy (Evans *et al.*, 2009). Positive MDI values indicate that the disparity is distributed mostly within subclades due to niche evolution within subclades, while negative MDI values suggest that the disparity is distributed mostly among subclades due to niche conservatism within subclades (Evans *et al.*, 2009). According to Losos (2008), niches should be more similar than expected under BM to demonstrate PNC, but for other authors, BM is

considered the simplest macroevolutionary model of PNC (Cooper *et al.*, 2010). In general, no phylogenetic signal means that the trait varied randomly across phylogeny, but as highlighted by Wiens *et al.* (2010), it can also indicate stasis, which is consistent with strong PNC. To examine this possibility, we calculated the log-likelihood of the phylogenetic generalized least squares fit of three models of evolution to each bioclimatic variable ($_w$mean values), including (1) a Brownian motion (BM) model of gradual and continuous drift, (2) a stabilizing selection Ornstein–Uhlenbeck (OU) model with one optimum; and (3) a white noise (WN) model of random variation, in which the similarity of species is independent of their phylogenetic relationships (Hansen *et al.*, 2008; Hawkins *et al.*, 2014). We used the Akaike information criterion (*w*AIC) to compare the relative fit of each model, using the Geiger package in R (Harmon *et al.*, 2008). The phylogenetic dependence of the realized climatic variation between related species, combined with the comparison of BM and OU evolutionary models, provides an assessment for testing PNC (Losos, 2008; Wiens *et al.*, 2010) and was thus suitable for our study.

RESULTS

Local presence of *Nothofagus* during the Early Eocene: the Ligorio Marquez Formation

Two leaf morphotaxa were identified from the LMF, *Nothofagus subferruginea* (Dusen) Tanai and *N. serrulata* Dusen (Fig. 1a). Both taxa were present in outcrops ranging from the Late Eocene to the Miocene age in southern South America (Romero & Dibbern, 1985; Tanai, 1986). *Nothofagus subferruginea* is associated with the modern subgenus *Fuscospora*, while *N. serrulata* is possibly associated with the modern subgenus *Lophozonia* (for systematic descriptions see Appendix S1 in Supporting Information). The pollen record of Nothofagaceae in the LMF includes *Nothofagidites kaitangataensis*, *Nothofagidites dorotensis*, *Nothofagidites acromegacanthus* and the '*Nothofagus* Fusca group' (Fig. 1b). *Nothofagidites kaitangataensis* corresponds to an ancestral pollen type that has no association with any extant subgenus and *N. dorotensis* and *N. acromegacanthus* are associated with subgenus *Brassospora*. The *Fusca* group pollen type can be associated with both the subgenera *Fuscospora* and *Nothofagus* (Dettman *et al.*, 1990).

Palaeoclimate of the Ligorio Marquez Formation

On the basis of the fossil pollen assemblage, we identified 11 families that could be used in the coexistence approach analysis (see Fig. S1, Table S1 in Appendix S2). The MAT coexistence interval was 17.2–20.9 °C and the MAP interval was 1080–1511 mm (Table 1). These results suggest that species from the different *Nothofagus* subgenera lived in mesothermal climates and this is further confirmed by our LMA results. Using the equation given in Peppe *et al.* (2011), we

Table 1 Bioclimatic variables estimated for the fossil flora of the Ligorio Marquez Formation using leaf margin analysis and a coexistence approach. Bio1*, estimate of mean annual temperature based on the proportion of species with entire leaf margin. Bio 1 to Bio 10, estimates of bioclimatic variables using coexistence approach. %I, percentage of families within coexistence interval. Bioclimatic variables according to Hijmans *et al.* (2005).

Variable		Estimate	%I
Temperature (°C)			
Bio1*	Mean annual temperature	17.3–17.4	–
Bio1	Mean annual temperature	17.2–20.9	81.8
Bio2	Mean diurnal range	9.6–10.9	90.9
Bio3	Isothermality	5.6–6	81.8
Bio4	Temperature seasonality	32.9–37	81.8
Bio5	Max temperature of warmest month	27.8–29	100
Bio6	Min temperature of coldest month	4.1–10.8	81.8
Bio7	Temperature annual range	19–20.4	90.9
Bio8	Mean temperature of wettest quarter	18.9–21.6	90.9
Bio9	Mean temperature of driest quarter	13.5–20.5	90.9
Bio10	Mean temperature of warmest quarter	21.6–22.6	100
Bio11	Mean temperature of coldest quarter	11.1–15.9	72.7
Precipitation (mm)			
Bio12	Mean annual precipitation	1079.3–1511	90.9
Bio13	Precipitation of wettest month	198.9–248.7	90.9
Bio14	Precipitation of driest month	42.7–56.9	90.9
Bio15	Precipitation seasonality (%)	48.7–54.1	100
Bio16	Precipitation of wettest quarter	403.2–672	81.8
Bio17	Precipitation of driest quarter	142–189.3	90.9
Bio18	Precipitation of warmest quarter	308.6–411.4	100
Bio19	Precipitation of coldest quarter	280.4–373.9	90.9

obtained MAT = 17.3 °C (SE = ± 4.0 °C) and using that of Hinojosa *et al.* (2011), MAT = 17.4 °C (SE = ± 2.3 °C). These two results indicate that the MAT was 11.3–11.4 °C warmer than present-day conditions in Ligorio Marquez area.

Phylogenetic climatic niche

Climatic niche models obtained with MAXENT performed consistently well. The average training AUC for 50-replicate runs ranged from 0.87 to 1.00 and all were > 0.9 (Table 2). Extant species of the *Nothofagus* genus are primarily found in microthermal and mesothermal climatic conditions, with a $_w$mean MAT ranging from 6.6° to 20.5°C and a $_w$mean MAP ranging from 902 to 3229 mm (Fig. 2, Table 2, Table S2 in Appendix S2).

According to the reconstruction of ancestral climatic variables, the common ancestor of the genus *Nothofagus* lived at a MAT of 11 °C (95% CI = ± 3.7 °C) and MAP of

Table 2 Modern distribution (MD), subgenera (Sub) and climatic niche of 25 extant *Nothofagus* species. Modern Distribution: SA, South America; NZ, New Zeland; AU, Australia; TZ, Tasmania; NC, New Caledonia; PNG, Papua-New Guinea. Subgenera: L, *Lophozonia*; F, *Fuscopora*; N, *Nothofagus*; B, *Brassospora* and (Sub) is also shown. Bio1 to Bio19, Bioclimatic variables (please see description of each bioclimatic variable in Table 1). Values are the weighted mean of each bioclimatic variable derived from predicted niche occupancy profiles. AUC, area under the receiver operating characteristic curve; SD, one standard deviation.

MD	Sub	Species	Bio1	Bio10	Bio11	Bio12	Bio18	Bio19	AUC	SD
SA	L	*N. alpina*	9.8	14.7	5.3	1567.3	120.5	759.8	0.989	0.001
SA	L	*N. glauca*	12.2	17.5	7.2	971.9	42.1	538.7	0.994	0.001
SA	L	*N. obliqua*	10.8	15.7	6.2	1303.3	91.6	652.0	0.980	0.001
NZ	L	*N. menziesii*	8.9	13.4	4.0	2395.2	524.1	584.8	0.837	0.001
AU/TZ	L	*N. cunninghamii*	9.2	13.5	5.0	1538.4	92.4	497.4	0.878	0.025
AU	L	*N. moorei*	12.5	19.7	9.1	1354.9	489.3	231.3	0.997	0.0001
SA	F	*N. alessandri*	13.0	17.8	8.5	902.0	34.3	514.1	0.997	0.001
TZ	F	*N. gunii*	6.9	10.8	2.9	1763.2	289.9	545.2	0.972	0.016
NZ	F	*N. cliffortioides*	8.2	12.7	3.1	2189.7	476.3	537.8	0.870	0.002
NZ	F	*N. truncata*	11.1	15.3	6.7	2042.9	404.2	555.4	0.962	0.002
NZ	F	*N. fusca*	9.4	13.8	4.6	2069.6	434.7	560.9	0.888	0.002
NZ	F	*N. solandri*	10.4	14.7	5.8	1706.5	346.8	491.1	0.936	0.003
SA	N	*N. betuloides*	6.6	10.3	2.7	1457.0	302.3	441.2	0.963	0.005
SA	N	*N. nitida*	7.8	11.6	4.1	2082.6	350.9	741.1	0.982	0.002
SA	N	*N. antarctica*	7.3	11.6	2.9	1258.6	185.0	488.3	0.962	0.004
SA	N	*N. dombeyi*	9.6	14.1	5.3	1687.0	180.8	744.9	0.997	0.001
SA	N	*N. pumilio*	7.0	11.6	2.4	1144.8	139.8	485.4	0.981	0.003
NC	B	*N. codonandra*	19.9	23.0	16.8	1922.0	746.2	322.0	0.957	0.016
NC	B	*N. discoidea*	20.6	23.8	17.6	1834.3	673.5	313.6	0.964	0.023
NC	B	*N. baumanniae*	19.4	22.3	16.0	1935.3	729.7	345.0	0.992	0.005
NC	B	*N. aequilateris*	20.8	23.7	17.6	1977.4	746.2	340.2	0.974	0.008
NC	B	*N. balansae*	19.8	22.7	16.7	1803.9	741.6	280.0	0.932	0.024
PNG	B	*N. brassii*	15.1	16.0	14.4	2862.1	556.5	565.1	0.970	0.012
PNG	B	*N. resinosa*	17.3	18.0	16.6	3229.5	620.6	697.7	0.924	0.018
PNG	B	*N. perryi*	15.7	16.5	15.1	2580.7	401.1	390.7	0.987	0.003
PNG	B	*N. grandis*	16.4	17.3	15.7	2910.9	497.5	520.0	0.965	0.006
PNG	B	*N. carrii*	17.5	18.3	16.7	2854.4	504.1	523.9	0.968	0.008

1626 mm (95% CI = ± 294 mm), indicating microthermal to marginally mesothermal conditions (Fig. 2a,c, Table 3). Microthermal conditions were estimated for the common ancestors of the modern temperate subgenera: *Lophozonia* with a MAT of 10.6 °C (95% CI = ± 3.1 °C) and MAP of 1620 (95% CI = ± 249); *Fuscospora* with a MAT of 10.7° (95% CI = 3.2 °C) and MAP of 1610 (95% CI = ± 255 mm); and *Nothofagus* with a MAT of 10.1 °C (95% CI = ± 2.7 °C) and MAP of 1685 mm (95% CI = ± 216 mm; Table 3). In contrast, a broad realized niche that includes both mesothermal and microthermal conditions was estimated for the common ancestor of subgenus *Brassospora* (MAT = 15.3 °C ± 2.8 °C; MAP = 2145 ± 223 mm; Fig. 2a,c, Table 3).

In general, temperature variables show divergent evolution among clades and convergent evolution within clades (Fig. 2a,b), whereas precipitation variables exhibit more convergence among clades, causing the lines connecting putative ancestors with their descendants to cross (Fig. 2c,d). Thus, temperature variables had negative MDI values (except for maximum temperature), whereas precipitation variables had positive MDI values (Table 4). However, the MDI values of all 19 bioclimatic variables did not differ significantly from a BM model of evolution (Table 4). Our phylogenetic

generalized least squares analyses indicate that all bioclimatic variables fit a BM model better than a WN model (Table 4). This result is consistent with PNC. The OU model fits better than the BM model only for the variable BIO19 (precipitation in coldest quarter), suggesting that selection 'pulled' winter precipitation values towards an optimum (Table 4).

DISCUSSION

Predictions from the TCH are partially supported by our results in *Nothofagus*. Palaeoclimatic reconstructions based on coexistence and leaf margin analyses suggest mesothermal conditions for the LMF, where we identified macrofossils associated with the subgenera *Lophozonia* and possibly *Fuscospora,* as well as fossil pollen of subgenera *Brassospora* and *Fuscospora/Nothofagus*. The absence of *Brassospora* in the macrofossil record would indicate that these taxa were not present in the basin of deposition but nearby to the LMF, or that the morphological characteristics of the ancestor of this subgenus differed from those in modern *Brassospora* (Hill, 1991). Nonetheless, the presence of fossil records in the LMF of at least three *Nothofagus* subgenera, together with iconic tropical families such as Lauraceae
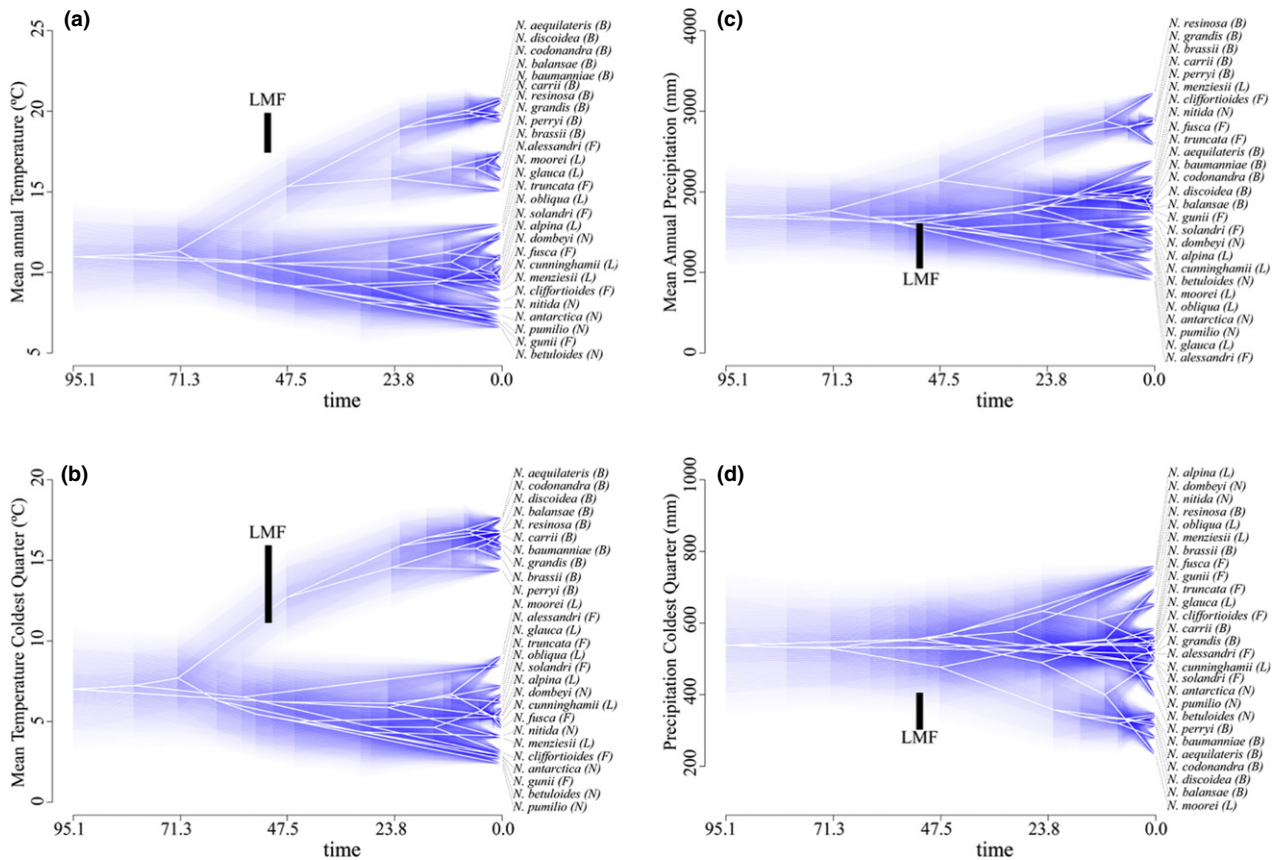
Figure 2 Traitgram of ancestral states of *Nothofagus* climatic niche. White lines correspond to a projection of the phylogenetic tree in a space defined by each bioclimatic variables. (a) Mean annual temperature (°C). (b) Mean temperature of coldest quarter (°C). (c) Mean annual precipitation (mm). (d) Precipitation of coldest quarter. Blue shade areas correspond to the 95% of confidence interval. Black bar in panels (a) to (d) represent the interval for each bioclimatic variable obtained from fossil pollen records in the Ligorio Marquez Formation (LMF). Dashed lines to the tips on the phylogenetic trees link the names of *Nothofagus* species. Subgenus of species are shown in parenthesis: B, *Brassospora*; F, *Fuscospora*; L, *Lophozonia*, N, *Nothofagus*.

(Troncoso *et al.*, 2002), supports the idea that the genus *Nothofagus* lived under warm humid, frost-free, mesothermal climates during the Early Eocene warming (Table 1). Warm and moist conditions (i.e. MAT *c.* 15 °C and MAP *c.* 3000 mm) have also been estimated for the Late Cretaceous in Antarctica (Poole *et al.*, 2005), where fossil pollen of all subgenera was found (Dettman *et al.*, 1990). These results therefore suggest that tolerance to mesothermal climates is an ancestral condition in the genus. However, in stark contrast with the fossil evidence, our phylogenetic reconstructions indicate that the ancestor of the genus *Nothofagus* lived at a MAT of 11 °C (± 3.7 °C) and MAP of 1626 mm (± 294 mm; Fig. 2), which corresponds to microthermal and marginally mesothermal climates. Biases in phylogenetic reconstructions of ancestral niches that are exclusively based on present-day distributions have been demonstrated to occur when climatic requirements of ancestors differ from their extant descendants (Meseguer *et al.*, 2015). In general, ecological requirements are highly conserved at short or middle time spans (up to thousands of years), but this assumption becomes improbable when

long time-scales are considered [millions of years; (Peterson, 2011), such as in the case of *Nothofagus*].

Most dimensions of the realized climatic niche of *Nothofagus* genus fit a Brownian motion (BM) model of evolution, indicating that species inherit their climatic niches from ancestors and slowly diverge as result of neutral drift. The only exception was winter precipitation (BIO 19), which followed an OU model of evolution, suggesting that this niche dimension is constrained to an optimum and evolved slower than the other ones. BM is usually considered the simplest macroevolutionary model for PNC (Cooper *et al.*, 2010; Wiens *et al.*, 2010), but for some authors niches must be more similar than is expected under Brownian motion to demonstrate PNC (Losos, 2008; discussed in Cooper *et al.*, 2010). Even so, our results show that there is a phylogenetic signal in the climatic niche of *Nothofagus*. We argue that the phylogenetic signal is principally influenced by the tropical subgenus *Brassospora*, which comprises two subclades differing slightly in climatic requirements from each other but strongly from the other three subgenera (Fig. 2). These latter three subgenera converge in the modern microthermal climate, suggesting

Table 3 Reconstruction of ancestral states and confidence interval at 95% of 19 bioclimatic variables for the common ancestor of *Nothofagus* genus and the common ancestor of subgenera *Lophozonia*, *Fuscospora*, *Nothofagus* and *Brassospora*. Var, Bioclimatic variable (please see description of each bioclimatic variable in Table 1).

Var	Genus *Nothofagus*	Subgenera *Lophozonia*	*Fuscospora*	*Nothofagus*	*Brassospora*
Bio1	11.0 ± 3.7	10.6 ± 3.1	10.7 ± 3.2	10.1 ± 2.7	15.3 ± 2.8
Bio2	10.1 ± 1.7	10.8 ± 1.5	9.9 ± 1.5	9.6 ± 1.3	9.1 ± 1.3
Bio3	5 ± 1	5 ± 1	5 ± 1	5 ± 1	6 ± 1
Bio4	31.5 ± 7.2	35.5 ± 6.1	32.5 ± 6.2	30.0 ± 5.3	20.6 ± 5.5
Bio5	21.7 ± 3.9	22.6 ± 3.3	21.5 ± 3.4	20.3 ± 2.9	23.3 ± 2.9
Bio6	2.7 ± 3.8	1.7 ± 3.3	2.3 ± 3.3	2.3 ± 2.8	8.5 ± 2.9
Bio7	19.0 ± 2.8	20.9 ± 2.4	19.2 ± 2.4	17.9 ± 2.1	14.8 ± 2.1
Bio8	9.3 ± 6.9	8.7 ± 5.9	8.2 ± 6.0	8.4 ± 5.1	15.9 ± 5.3
Bio9	13.3 ± 4.3	13.1 ± 3.7	13.6 ± 3.8	12.4 ± 3.2	15.6 ± 3.3
Bio10	15.1 ± 4.2	15.4 ± 3.5	14.9 ± 3.6	14.0 ± 3.0	18.0 ± 3.2
Bio11	7.0 ± 4.2	6.2 ± 3.5	6.5 ± 3.6	6.3 ± 3.1	12.7 ± 3.2
Bio12	1691 ± 294	1620 ± 249	1610 ± 255	1685 ± 216	2145 ± 223
Bio13	233 ± 209	233 ± 177	221 ± 182	232 ± 154	269 ± 159
Bio14	72 ± 199	63 ± 168	69 ± 172	74 ± 146	107 ± 151
Bio15	45 ± 58	50 ± 49	47 ± 51	42 ± 43	35 ± 44
Bio16	650 ± 294	648 ± 249	608 ± 255	651 ± 216	758 ± 223
Bio17	249 ± 294	223 ± 249	242 ± 255	251 ± 216	350 ± 223
Bio18	304 ± 294	259 ± 249	275 ± 255	306 ± 216	517 ± 223
Bio19	538 ± 294	556 ± 249	531 ± 255	545 ± 216	477 ± 223

Table 4 Results of phylogenetic niche conservatism analyses. Var: Bioclimatic variables, Bio1-Bio19 (please see description of each variable in Table 1). MDI, morphological disparity index; PGLS, phylogenetic generalized least squares; W AIC, Akaike based on exp $(-0.5 \times \Delta AIC)$, expressing the probability that each model is the best among those compared. Avg. sq: Average squared Euclidean distance between all pairs of points. $2LR_{OU-BM}$ is twice the likelihood of the fit of an Ornstein–Uhlenbeck (OU) model against a Brownian motion (BM); $2LR_{OU-WN}$ is the comparison of the fit of an OU model against a white noise (WN) model. Bold numbers highlight the Precipitation of Coldest Quarter variable (Bio19), which fit an OU model of evolution.

Var	MDI Avg. sq	P	PGLS $2LR_{OU-BM}$	P	$2LR_{OU-WN}$	P	W AIC BM	OU	WN
Bio1	−0.19	0.48	1.4×10^{-14}	1.00	38.72	< 0.001	0.78	0.22	0.00
Bio2	0.00	0.70	4.3×10^{-14}	1.00	27.36	< 0.001	0.78	0.22	0.00
Bio3	−0.16	0.41	5.7×10^{-14}	1.00	50.11	< 0.001	0.78	0.22	0.00
Bio4	−0.21	0.41	2.8×10^{-14}	1.00	50.23	< 0.001	0.78	0.22	0.00
Bio5	0.03	0.74	1.1×10^{-1}	0.74	20.18	< 0.001	0.77	0.23	0.00
Bio6	−0.24	0.30	2.8×10^{-14}	1.00	46.01	< 0.001	0.78	0.22	0.00
Bio7	−0.22	0.44	2.8×10^{-14}	1.00	43.63	< 0.001	0.78	0.22	0.00
Bio8	−0.07	0.56	0.35	0.55	27.31	< 0.001	0.75	0.25	0.00
Bio9	0.06	0.70	1.43	0.23	15.37	< 0.001	0.64	0.36	0.00
Bio10	−0.04	0.59	0.20	0.65	24.19	< 0.001	0.76	0.24	0.00
Bio11	−0.21	0.37	2.8×10^{-14}	1.00	42.47	< 0.001	0.78	0.22	0.00
Bio12	0.03	0.67	0.98	0.32	18.91	< 0.001	0.69	0.31	0.00
Bio13	0.09	0.74	1.60	0.21	19.53	< 0.001	0.62	0.38	0.00
Bio14	0.03	0.74	0.53	0.47	18.48	< 0.001	0.73	0.27	0.00
Bio15	0.12	0.74	2.8×10^{-14}	1.00	27.11	< 0.001	0.78	0.22	0.00
Bio16	0.10	0.70	1.77	0.18	18.42	< 0.001	0.60	0.40	0.00
Bio17	0.08	0.70	0.75	0.39	17.01	< 0.001	0.71	0.29	0.00
Bio18	0.00	0.67	0.69	0.41	20.70	< 0.001	0.72	0.28	0.00
Bio19	**0.43**	**0.96**	**6.55**	**0.01**	**6.89**	**0.01**	**0.11**	**0.80**	**0.09**

that their climatic requirements are more labile than those of *Brassospora*. Accordingly, we found no significant differences when we compared MAT palaeoestimates from the LMF (i.e. 17.2–20.9 °C, Table 1) with the current climatic niche of the *Brassospora* subgenus ((w)mean MAT range: 15.1–20.8 °C, Table 2). This suggests that *Brassospora* has always lived

within the ancestral climatic conditions of the genus, and has tracked mesothermal climates. In contrast, we found strong differences between MAT palaeoestimates and current climatic niches of *Lophozonia, Fuscospora* and subgenus *Nothofagus* ($_w$mean: 6.6–13 °C; Table 2; Fig. 2). These differences may reflect a shift in the ecological requirements of these three subgenera or the extinction of their more warmth-loving members (Hill, 1991; Jordan, 1997). However, neither of these options are detected in phylogenetic analysis, leading to a mismatch between the ancestral climatic niche inferred by phylogenetic analysis and that inferred from fossil data (Meseguer *et al.*, 2015).

Overall, our results suggest that the genus *Nothofagus* was able to live under mesothermal climates during the Early Eocene, whereas the cool-tolerance of the modern temperate *Nothofagus* subgenera probably evolved during the Mid-Eocene–Oligocene cooling, or after the Mid-Miocene Climatic Optima (Zachos *et al.*, 2001). Reductions in global temperatures after the Mid-Eocene–Oligocene cooling, together with the contraction of the climatic belt towards equatorial zones, favoured the diversification and range expansion of *Nothofagus* towards low latitudes by tracking its ancestral mesothermal climate (Romero, 1986; Dettman *et al.*, 1990; Hill & Dettman, 1996; Hinojosa & Villagrán, 1997; Macphail, 2007; Carpenter *et al.*, 2014). Fossil records from Australia, including Tasmania and New Zealand, suggest that *Nothofagus* reached the north-east of Australia during the Oligocene and Miocene periods (Dettman *et al.*, 1990; Hill & Dettman, 1996; Carpenter *et al.*, 2014). Suitable climates for *Nothofagus* in tropical areas of New Guinea were available when this region emerged above sea level, and Australia reached its current latitudinal position, at the end of the Cenozoic (12 Ma) (Baldwin *et al.*, 2012). Similarly, *Nothofagus* may have reached New Caledonia from New Zealand during the Miocene, when islands and ridges connected those lands (Carpenter *et al.*, 2014). Mesothermal

climatic tracking should be independent of whether the arrival of *Nothofagus* in tropical regions occurred via long-distance dispersal (Hill & Dettman, 1996; McGlone *et al.*, 1996) or land-based range expansion (Swenson *et al.*, 2001; Carpenter *et al.*, 2014), as *Nothofagus* had to establish within the range of its original fundamental niche (Jackson & Overpeck, 2000; Pearman *et al.*, 2008) which, according to our reconstructions, was mesothermal.

Fossil plant and animal communities that are compositionally different from modern communities ('non-analogue communities') are usually associated with climatic conditions without a modern counterpart (Williams & Jackson, 2007). Accordingly, the formation and extinction of 'non-analogue' communities are explained by changes in climatic conditions that allow different subsets of taxa, with their different fundamental niches, to survive [i.e. potential niche *sensu* Jackson & Overpeck (2000)]. Therefore, shifts in the realized climatic niche of a given taxon can occur without changes in its climatic tolerance (Williams & Jackson, 2007). In the case of LMF fossil flora (which represent a non-analogue *Nothofagus* community), our palaeoclimatic reconstructions suggest that the palaeoclimate was mesothermal (MAT = 17.2–20.9 °C), with comparable amounts of precipitation in winter (BI019-coldest quarter: 280–373 mm) and summer (BI018-warmest quarter: 308–411 mm). These conditions are markedly different from modern climates of southern South America, but are only slightly warmer and drier than the realized climatic niche of *Nothofagus* species from New Guinea (*w*mean MAT: 15.1–17.3 °C, BIO18: 401–620 mm; BIO19: 390–697 mm (Fig. 3, Tables 1 & 2). Palaeoflora of all subgenera of *Nothofagus* has been recorded in the Tasmanian outcrops of Balfour and Little Rapid River and has also been associated with a mesothermal climate with low seasonality (Hill & Scriven, 1997; Hill, 2001b). We propose that shifts in the realized climatic niche of temperate *Nothofagus* subgenera were associated with changes in their climatic tolerances.
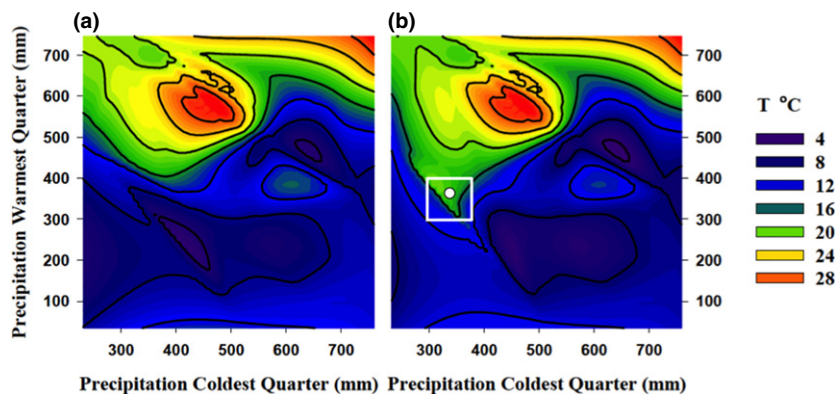

Figure 3 Contour plots of precipitation of coldest quarter, precipitation of warmest quarter, and mean annual temperature considering (a) only extant *Nothofagus* species and (b) including the palaeoclimatic estimates of the fossil flora of Ligorio Marquez Formation (LMF). The inclusion of LMF generates a potential climatic niche during the Eocene to *Nothofagus* (white square), slighter warmer and drier than the realized climate of extant *Nothofagus* species from New Guinea, but markedly different from southern South American species. White dot indicates the position of LMF. Contours plots are estimated using the weighted mean values of each variable derived from profiles of niche occupancy (Table 2).

Alternatively, extant species of these lineages (as well as their ancestors) would have the capacity to grow under both meso- and microthermal climates, but ecological characteristics other than climatic tolerances impede their subsistence in modern mesothermal climates, such as low competitive ability during the regeneration niche (Grubb, 1977).

Not always into the tropics

The question of why *Nothofagus* did not reach tropical latitudes in South America, as it did in Papua-New Guinea and New Caledonia, is an enigma in our understanding of the evolution and dynamics of the modern flora of South America. Fossil microflora from the Late Eocene–Early Oligocene from Colombian sites at present-day latitudes between 02° and 12° N, have fossil pollen grains of *Nothofagidites huertasii* (Jaramillo *et al.*, 2011), most likely of the *Fusca* pollen type (Dettman *et al.*, 1990). However, these low-latitude fossil pollen grains could have arrived by long-distance dispersal from more southerly populations, particularly considering that the Andes had not yet reached their current elevation (Gregory-Wodzicki, 2000). Indeed, *Nothofagus* pollen has a high dispersal capacity: modern pollen records have been found in areas as far as 1100 km away from the nearest *Nothofagus* populations in southern Chile and Argentina (Gassmann & Perez, 2006). Our phylogenetic results indicate that *Nothofagus* is highly sensitive to changes in winter precipitation in the coldest quarter (Bio 19 variable, Table 3), which followed a stabilizing selection OU model of evolution. Hence, we argue that long-standing aridity at subtropical latitudes in western South America (Hartley *et al.*, 2005) has historically been an effective barrier to the northward expansion of *Nothofagus* into tropical latitudes of South America. However, in order to firmly establish why *Nothofagus* was not able to reach tropical South America, more work is necessary in the transition area between the tropical and subtropical zones.

Finally, some assumptions of the TCH, such as the low-latitudinal origin of several plant lineages (Donoghue, 2008), together with high plant diversification under tropical ('Megathermal') climatic conditions (Kerkhoff *et al.*, 2014), contrast with our findings in *Nothofagus*. We argue that *Nothofagus* had a mid- to high-latitude origin and that its diversification occurred under mesothermal climatic conditions. So it is possible that lineages of temperate origin expanded into the tropics as species tracked mesothermal climates. Therefore, dispersal towards current tropical zones has been possible because species have tracked ancestral climatic niches from high or mid-latitudes towards lower latitudes, driven by both climatic and tectonic changes. Consequently, members of Gondwana lineages currently present in tropical regions will be younger and nested within the temperate clades. We suggest that this evolutionary process have occurred in other Gondwana lineages such as *Myrceugenia* or *Gunnera*, that are now present in the Neotropics.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Systematic descriptions of the fossils.
Appendix S2 Fossil pollen assemblage and weighted mean values of bioclimatic variables.

BIOSKETCH

Luis Felipe Hinojosa is an Associate Professor in the Ecology Department, Universidad de Chile, and at the Millennium Institute of Ecology and Biodiversity. He is interested in the historical biogeography of southern South American forests. In particular, he studies the palaeoecology of the Cenozoic using plant systematics, leaf physiognomy and pollen analysis.

The research interests of the team of authors are diverse, covering biogeography, ecology, functional ecology, evolutionary biology, systematics, evolution, palynology and palaeobotany of southern South American plant groups.

Author contributions: L.F.H., A.G. and M.F.P. conceived the ideas and study design; L.F.H., F.C., M.F.C., H.N., K.U. and A.Y. collected fossil material and contributed data; L.F.H., F.C. and M.Q. performed both palaeoclimate and pollen fossil analysis; L.F.H., M.F.C. and R.B. performed ecological niche modelling; L.F.H., M.F.C. and M.F.P. performed the phylogenetic reconstructions and analysed the data; L.F.H., A.G., M.F.P., R.B. and M.T.K.A. undertook the writing with the help of all co-authors.

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