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Ice-age persistence of *Fitzroya cupressoides*,
a Southern Hemisphere conifer

Abstract Fossil evidence from *Metasequoia*-dominated forests continue to inform us as to how forests have responded to past climate change. As such, these *Metasequoia* findings and those of other high-latitude Northern Hemisphere forest tree species set rigorous standards for considering the case study of a Southern Hemisphere conifer, *Fitzroya cupressoides*. Tree ring analyses, fossils, glacial geology, and molecular evidence together piece together a remarkable case study. *Fitzroya cupressoides*, a site-specific endemic, persisted within its current range in Chile throughout the Late Pleistocene, surviving glaciers, volcanoes, and earthquakes. Here, we present a review for this *Fitzroya* case study, which is followed by a synthesis of research questions which could elucidate how forest species persisted locally over the course of Quaternary climate change.

Introduction

During late Quaternary glaciation, *Fitzroya cupressoides* populations in southern Chile and Argentina have persisted locally over the past 50,000 yr BP. This endemic species has persisted in a region prone to storms, glaciers, volcanic debris, and earthquakes – and now anthropogenic land-use changes. As such, *Fitzroya cupressoides* presents a remarkable contrast to the massive migrations typical of Northern Hemisphere forests during glaciation. *Fitzroya*'s local persistence and that of its associated forest tree species are the rule, not the exception, for South America's temperate forests.

Late Quaternary climate change in the Southern Hemisphere

The Arctic glaciers of the late Pleistocene melted over 10,000 yr BP, but they left a lasting mark on North American flora and fauna. Each glacier pushed vast sheets of ice southward, so glaciation was harsh. Boreal forest tree species such as *Pinus banksiana* responded by shifting their ranges south of these continuous ice sheets. When glaciers melted, these species re-colonized northward. This rapid re-colonization, or migration, of these Northern Hemisphere forest tree species relied on long-distance seed dispersal (Clark et al., 1998).

Massive migration left its mark on survivors: present-day DNA patterns of variation is unevenly

distributed among extant populations. This is well-documented for *Pinus banksiana* (i.e., Godbout et al., 2005). In simplest terms, those *Pinus banksiana* populations which retreated southward, away from Arctic glaciers, contributed more genetic diversity to present-day descendants than those populations which arose from recent colonization. Still other *Pinus banksiana* populations shrunk until nearly all genetic variation within these populations was lost. Their present-day descendants are genetically depauperate (Godbout et al., 2005). Such north-south migration patterns in present-day DNA variation are typical (Hewitt, 2000) although some North American species have east-west range shifts (Davis & Shaw, 2001).

Massive migration in the Northern Hemisphere has been so well-documented that it has become the prevailing paradigm. A notable exception to the prevailing paradigm is local persistence: a few refugial populations persisted locally despite glaciation. Of particular note are several North American hardwood species (McLachlan and Clark, 2004; McLachlan et al., 2005) and *Picea glauca* in Alaska (Anderson et al., 2006).

Do Southern Hemisphere trends parallel those of the Northern Hemisphere? If so, then one would expect Southern Hemisphere forest populations to have greater genetic diversity northward, away from Antarctica. This would correspond to the typical genetic diversity patterns for Northern Hemisphere populations which

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moved southward, away from the Arctic Circle. But this is not the case (Premoli et al., 2000; Moore, 2000). South American temperate forests have no parallel to the Northern Hemisphere paradigm (Markgraf et al., 1995; Moore, 2000). To show this, we present the case study of *Fitzroya cupressoides*, its taxonomy, life history, and Quaternary records, then end with a brief synthesis of future research direction. This case study brings fresh insights into how forests responded to climate change in the past.

Taxonomy, present-day range, life history, and ecology

1. Taxonomy

Fitzroya cupressoides (Molina) I. M. Johnst. belongs to a monotypic genus within Cupressaceae *sensu lato*, the same family as *Metasequoia*. Charles Darwin chose its scientific name in honor of Captain Robert Fitzroy of the HMS *Beagle*, but its common name is *lahuán* in the Mapuché language or *alercé* in the Spanish language. More recently this tree has become known as South American redwood because its rot-resistant wood has a beautiful grain resembling that of redwood. Like some of the redwood species, *Fitzroya cupressoides* is polyploid.

Polyploidy is unusual among conifers. Most conifers, including *Metasequoia glyptostroboides*, are diploid, yet *Fitzroya cupressoides* is reportedly polyploid ($2n = 4x = 44$ chromosomes) (Hair & Beuzenberg, 1958). Its polyploidy status needs to be confirmed using a larger sample from the entire species' range (Ahuja, 2009), because this condition can vary among populations. Polyploidy can affect seed and pollen viability, but also bears on how to correctly interpret molecular marker data.

2. Present-day range

Fitzroya cupressoides has a narrow distribution which runs across the three parallel north-south landforms of Chile into Argentina. The first landform is the Cordillera de la Costa, a densely forested cloud-covered range of low mountains which parallels the Pacific Ocean. Here, *Fitzroya* occurs at latitudes of 39°50' to 42°35'S, especially within the Valdivian rain forest. Next is the Central Valley Depression, where *Fitzroya* occurs between 41°30' and 41°50'S; this is a low-lying region characterized by volcanic ash and glacial moraines. Third is the Andes Mountains range which runs parallel to the Pacific Ocean along the other side of the Central Valley Depression. Here, *Fitzroya*'s range occurs between 41°30' and 43°30'S. The Andes Mountains range is the nexus for glacier formation, volca-

noes, and seismic activity; many of the highest mountains are volcanoes. Below them, northeast of Puerto Montt, is Chile's Lake District. The Lake District has a well-defined glacial geology along with a wealth of late Pleistocene fossil data (Heusser, 1966; Parker & Donoso, 1993; Veblen et al., 1999), which have led to late Quaternary reconstruction. From here, the range of *Fitzroya cupressoides* extends over the other side of the Andes, into Argentina, where it extends only between 40°57' and 42°45'S (Kitzberger et al., 2000).

3. Life history

Fitzroya's reproductive biology is poorly understood. This is not surprising given the difficulty of studying large, reproductively mature organisms which have tiny strobili and even smaller pollen grains. Both female cones and male strobili are only 5 mm in length (Grosfeld & Barthelemy, 2001), while its spheroidal pollen is only 26 to 36 μm in diameter (Heusser, 1966).

Despite this difficulty, *Fitzroya* reproduction was recently tallied within a 3-ha area of Nahuel Huapi National Park in Argentina (Grosfeld & Barthelemy, 2001). The species is decidedly dioecious. Of those classified as either male- or female-bearing, only one tree out of 533 produced both male and female strobili in each of the three years of observation (Grosfeld & Barthelemy, 2001). All of these *Fitzroya cupressoides* adults had low reproduction rates across the three years of observation. Roughly 75% of the female-bearing trees had low numbers of strobili and ovulate cones, while 79.5% of the male-bearing trees also had low numbers of strobili (Grosfeld & Barthelemy, 2001).

Seed and pollen viability were not determined in this study. Viability is the link between reproduction and poor natural regeneration of *Fitzroya cupressoides* (i.e., Veblen et al., 1999; Smith-Ramirez, 2007). Regeneration is not related to the method of timber harvest (Smith-Ramirez, 2007), but *Fitzroya* seedlings seem to thrive after a major disturbance. *Fitzroya* seedlings appear after a major disturbance such as volcanic ash deposition, lava flows, and landslides (Donoso et al., 1993; Parker & Donoso, 1993).

4. Ecology

The species thrives only in waterlogged sites which have mean annual precipitation of 2000 to 4000 mm. As such, it is regarded as a sensitive indicator of climate change (Roig et al., 2001). Among these wet areas is the dense Valdivian evergreen rain forest (40°40' to 43°20'S), where the oldest specimens of *Fitzroya cupressoides* reach a diameter of 4 to 5 m and a height

exceeding 50 m (e.g., Heusser, 1966). The Valdivian rain forest corresponds to the path of eastward-moving storms coming ashore from the Pacific Ocean. Most of this precipitation comes during winter, arriving as rainfall rather than as fog, snow, or ice (Heusser, 1966; Roig et al., 2001). Here *Fitzroya* is found growing in a dense forest of trees, lianas, epiphytes, ferns, and herbaceous species.

5. Associated forest tree species

These include evergreen Southern Hemisphere beeches, *Nothofagus*, and a few Southern Hemisphere conifers (Boninsegna et al., 2009) such as *Araucaria* spp. (Araucariaceae) and *Austrocedrus chilensis* (Cupressaceae) (Arana et al., 2010). These all occur across a wide range of site types, but a third conifer, *Pilgerodendron wuiferrum* (Cupressaceae), has the same range as *Fitzroya*: it too requires wet, boggy soils.

Present-day condition of *Fitzroya cupressoides*

Fitzroya cupressoides is gradually declining. The principal reason for the species' decline is climate change (Heusser, 1966; Veblen et al., 1999). While other causes are difficult to untangle from human-mediated disturbances (e.g., Armesto et al., 2010), its decline does parallel the increasingly drier climate for the coastal range of Chile. This trend is supported by fossil pollen records which pre-date human disturbance (Heusser, 1966).

The species is sensitive to fire (Veblen et al., 1999), so another contributor to its decline is increased fire incidence. Increased fire incidence came with early human arrival in ca. 12,500 to 14,500 yr BP, but it became more prevalent after the Spanish conquest (1550–1600 AD). With time, colonial timber exports, copper smelting, and pasture conversion became major contributors to forest cover losses (Armesto et al., 2010).

Protective measures for this narrow endemic are numerous. Logging of *Fitzroya* ceased after 1850 in Chile (Heusser, 1966), but logging continued in Argentina until 1920 (Veblen et al., 1999). National preserves such as Los Alerces National Park in Argentina's Chubut province and Alerce Andino National Park in Chile's Los Lagos region were established to slow loss of this difficult-to-regenerate species. Logging prohibitions were introduced in Argentina by 1973 and in Chile by 1976. Also, *Fitzroya cupressoides* is protected as an endangered species on the IUCN Red List, and it is protected by the Convention on International Trade in Endangered Species (CITES). *Fitzroya*'s valuable wood still commands high prices in international markets, so the challenge to halt its logging continues

in spite of protective measures (Armesto et al., 2010). Only 15% of the original *Fitzroya* forests still remain.

Late Quaternary records for Chile

Reconstructing the late Quaternary response of *Fitzroya cupressoides* to climate change brings a number of surprises. Evidence comes from five sources: 1) tree ring analyses, 2) fossil pollen records, 3) subfossil evidence, 4) glacial geology, and 5) molecular data from living populations sampled in Chile and Argentina.

1. Tree ring analyses for recent millennia

Perhaps the most remarkable life history trait of *Fitzroya cupressoides* is its long lifespan. The oldest specimens to date have been 3622 years old (Lara & Villalba, 1993). These specimens led to definitive climate reconstructions for South America. Four climatic episodes are identified from tree ring analyses: a) the period from 900–1070 AD was cool, moist; b) 1080–1250 AD was warm, dry period; c) 1270–1670 AD was cool, moist again, coinciding with the Little Ice Age events in the Northern Hemisphere; d) warmer conditions resumed between 1720–1790 AD. These tree-ring data were corroborated by Patagonia glacier data (Boninsegna et al., 2009) and, given the soundness of these findings, led to tree ring analyses for other long-lived Southern Hemisphere forest species such as *Austrocedrus chilensis* (age 1000 years) as reviewed by Boninsegna et al. (2009). *Fitzroya cupressoides* is so long-lived that its living specimens can provide near-term reconstructions which align well with millennial climatic records and fire history.

2. Fossil pollen records from Chile's Lake District from 12,000 yr BP to present

Heusser (1966) sampled at three sites, all bogs or former lakes, in Chile's Lake District, an area which has present-day stands of *Fitzroya*, *Pilgerdendron*, and *Nothofagus*. The pollen from the first two species are so similar in size that they cannot be distinguished. Given this limitation, one can only state that fossil *Fitzroya-Pilgerdendron* pollen was present continuously at two of the three sites during the Late Glacial (ca. 12,000–10,000 yr BP), then later all three sites had fossil pollen. This suggests that one or both species spread during the postglacial period. Pollen count rose and ebbed repeatedly from the Late Glacial period onward through the postglacial period. This supports the idea that soon after the Late Glacial period, *Fitzroya* forests expanded and spread into pure stands or *alercal* (Heusser, 1966).

The decline in *Fitzroya-Pilgerdendron* pollen count

begins before the Spanish conquest in 1550–1600 AD. This decline corresponds to drier climatic conditions in Chile rather than to human-mediated disturbance. More to the point, this study registers the first evidence for local persistence of *Fitzroya*, *Pilgerdendron*, and *Nothofagus* forests during the Last Glacial period. Subfossil remains provide more definitive evidence for this unusual finding.

3. Subfossil remains in Chile's Lake District for 50,000 yr BP

These fossil stumps provide strong evidence for *Fitzroya*'s local persistence during glaciation. The subfossil tree remnants come from the same region as the fossil pollen, the southern Lake District of Chile. These subfossils were well-preserved *Fitzroya cupressoides* stumps, which were unearthed along with those of *Pilgerdendron wuiferum* by an earthquake in 1960; these stumps were originally buried by volcanic debris (Roig et al., 2001). Using carbon dating, the minimum age of the wood samples were estimated at $49,770 \pm 2,040$ ^{14}C yr BP (Roig et al., 2001).

4. Glacial history shows milder glaciation and incomplete ice sheets

Of particular interest here is the Lake District's Late Quaternary glacier history. The fossil records clearly show that *Fitzroya* has remained here, within its present-day range for more than 50,000 yr BP. Did this region have glacial cover? Geological records are affirmative on this point.

Glacial cycles in southern Chile and other parts of the Southern Hemisphere typically had milder oscillations than those associated with the Northern Hemisphere (Heusser, 1966; Markgraf et al., 1995; Rodbell et al., 2009). The Pacific Ocean currents ameliorate glacier formation. Other factors were the orogeny of the Andean Mountains and insolation. As Heusser (1966) describes, Andean glaciers formed long tongues which extended from the high Cordillera down into principal valleys, following water flow patterns. These tongues, or incomplete ice sheets, left pockets of forested areas.

Andean glaciers did not respond in lockstep with one another over the entire Last Glacial period: glacial timing was not synchronous (Rodbell et al., 2009). Instead, Andean glacial history is so localized and so complex that it shows little, if any, parallel to vast, yet relatively uniform Pleistocene glaciers typical of the Northern Hemisphere (Heusser, 1966; Markgraf et al., 1995; Rodbell et al., 2009).

Glacial geology is even more specific for Chile's Late District. Andean glaciers flowed westward onto the

coastal plain on numerous occasions throughout the late Quaternary (i.e., Heusser, 1966; Rodbell et al., 2009). The last glacial advance occurred shortly after 14,600–14,900 ^{14}C yr BP, with a retreat back to the Andes by 12,300 yr BP (Rodbell et al., 2009). This Last Glacial Maximum event occurs well after subfossil record dates, lending support to *Fitzroya*'s local persistence during glaciation. *Fitzroya*'s local persistence is not the rare exception. As such, Quaternary history for the Southern Hemisphere has no parallel to the massive range shifts typical of Northern Hemisphere forest species during glaciation.

5. Molecular evidence from extant *Fitzroya* populations

The next source of evidence, isozyme data from extant *Fitzroya* populations, complements fossil records. Population genetics analyses support the presence of past *Fitzroya cupressoides* stands within its current range along the eastern and western slopes of the Andes Mountains (Premoli et al., 2000). Its DNA variation patterns support the presence of multiple refugia which survived glaciation. Chances of its survival were enhanced by the incomplete ice sheets, which left open pockets of terrain suited to colonization (Markgraf et al., 1995; Premoli et al., 2000).

Whether or not *Fitzroya* populations formed a genetically connected network during glaciation is not yet clear. One view is that *Fitzroya cupressoides* stands had large population sizes and/or multiple refugial stands that re-colonized rapidly between periods of glacial cover (Premoli et al., 2000). The other view is that *Fitzroya* shows evidence of sharp population contractions, presumed to be a response to severe glacial displacement (Allnutt et al., 1999). Over 85% of the total genetic variation sampled in extant *Fitzroya* populations exists within populations (Allnutt et al., 1999), and these same data provide strong evidence of sharp contractions in effective population sizes (defined here as bottlenecks).

Our view is that both interpretations are true, that some populations could have been genetically connected, while more isolated populations could have suffered sharp contractions. This was the case for another Southern Hemisphere species, *Austrocedus chilensis*, in Chile, where both patterns of genetic variation were detected (Pastorino & Gallo, 2002; Arana et al., 2010). Testing all three views for *Fitzroya* requires a more finely drawn genetic analysis.

Available molecular evidence is too weak to test for bottlenecks. Isozyme data (Premoli et al., 2000) pro-

vide too few molecular markers for detecting bottlenecks, especially in this case where polymorphism levels for *Fitzroya* were 52%, far lower than what one usually sees for wind-pollinated forest tree species (Williams, 2009). On the other hand, RAPD markers (i.e., Allnutt et al., 1999) belong to a dominant marker system (i.e., band absent, band present scoring) which are not informative for the test of excess heterozygosity. Using DNA sequence data from a rangewide sampling or even DNA from fossil wood (see below) could provide more robust genetics data for determining past population structure of *Fitzroya* over the course of its Quaternary history. Determining whether *Fitzroya* persisted as networks of interconnected stands during glaciation is a significant finding, one which warrants in-depth study.

In short, the local persistence of *Fitzroya cupressoides* is supported by many independent temporal records. Its persistence has been attributed in part to mild Andean glaciation. The Southern Hemisphere's climate is ocean-dominated, and here glaciation was milder by comparison to the Northern Hemisphere. Glacial ice sheets also formed incompletely, and this enabled forest tree species to persist locally during glaciation.

Research needs

1. Past bottlenecks within *Fitzroya* populations?

Such a genetic analysis requires DNA variation assayed across a large number of codominant loci; a large sample of loci is absolutely essential to test for bottlenecks. The test is based on detecting an excess heterozygosity across all marker loci; this measures the difference between expected heterozygosity (H_e) and heterozygosity under mutation-drift equilibrium (H_{eq}) (Cornuet & Luikart, 1996). If there has been no bottleneck, then the estimates of H_e and H_{eq} will be equal under the null hypothesis of mutation-drift equilibrium. A genetic bottleneck causes a transient deviation from this mutation-drift equilibrium across all loci, generating a heterozygosity excess. For a population undergoing a genetic bottleneck and losing its rare alleles, H_e will be less than H_{eq} (Cornuet & Luikart, 1996). Conversely, an expanding population will have a heterozygosity deficiency across all loci so that the opposite trend will be detected. Testing for heterozygosity excess or deficiency across all loci in this way is appealing.

2. Dispersal ecology of *Fitzroya* seed and pollen?

Dispersal ecology bears on multiple refugia or perhaps large populations which are likely to have been genetically connected during periods of glaciation. The

prevailing eastward winds across Chile are capable of transporting *Fitzroya* seeds and pollen far from source. Diminutive in size, both seeds and pollen are likely to show an unusual degree of buoyancy and thus a capacity for long-distance dispersal. Long-distance dispersal of viable seeds would have led to new colonies. Subsequent seed and pollen dispersal would lead to steady gene flow among populations. With such patterns of gene flow, even widely separated *Fitzroya* populations could have been genetically connected during periods of glaciation. Another possibility is that effective population sizes were historically large, not fragmented. Either case is purely hypothetical. Some inference can be drawn from measuring the aerodynamics properties of viable *Fitzroya* pollen and seeds. No real conclusions about how these populations persisted can be drawn without measuring the aerodynamics properties of *Fitzroya* seeds and pollen.

3. DNA extraction from wood?

In addition to using DNA from extant populations, DNA sequence data can also be extracted from wood samples. This DNA source would provide data complementary to the fossil record. DNA extraction protocols specific to wood are widely available (e.g., Finkeldey et al., 2010). If so, then this source of data can be used to test whether *Fitzroya* had large census (and effective) population sizes during the postglacial and Last Glacial Maximum.

4. How long has *Fitzroya cupressoides* persisted in southern Chile?

This is yet to be fully determined although Oligocene fossil evidence elsewhere have provided important insights. *Fitzroya* and *Austrocedrus* leaves and reproductive structures have been well-described at a number of sites in Tasmania (Paull & Hill, 2008, 2010). Of particular interest is *Fitzroya acutifolia* which grew in Tasmania's mixed forests during the early Oligocene-Early Miocene (Hill & Whang, 1996).

Finding Oligocene fossils in Tasmania is consistent with the concept of Antarctica as the original source of high-latitude Southern Hemisphere flora. Such flora are thought to have evolved rapidly before spreading to southern Chile, Tasmania, and parts of New Zealand (e.g., Hill & Scriven, 1995; Markgraf et al., 1995). Antarctica and southern South America were once connected as a single land mass in the Late Cretaceous, roughly 90 Ma, towards the end of Gondwana rifting. At this time, Antarctica had a flora which was angiosperm-dominated. *Nothofagus* species grew in sparse forests along with a low diversity of other vascular

plants including a few conifers (Hill & Scriven, 1995). No floristic migrations from equatorial latitudes have since occurred (Markgraf et al., 1995), which leads to the view that the Late Cretaceous flora spread from Antarctica via multiple pathways and that one of these pathways led to Chile's present-day temperate forests. If so, this raises the question of how long *Fitzroya* has been present in Chile and Argentina.

Summary

Latitude is a poor global predictor when it comes to predicting how southern South American forests responded to late Quaternary climate change. As shown by its well-documented geological and fossil records, *Fitzroya cupressoides* has persisted locally over the past 50,000 years despite its endemism and site-specificity. It has thrived in a region prone to storms, glaciers, volcanic debris, and earthquakes, and now human-mediated disturbance. As such, *Fitzroya cupressoides* presents a remarkable contrast to the massive migrations typical of Northern Hemisphere forests during glaciation. *Fitzroya*'s local persistence and that of its associated forest tree species are the rule, not the exception, for southern South American forests.

Do conifers, as the oldest living lineages of seed plants, have an undue advantage when it comes to climate change response? Some argue not (Markgraf et al., 1995) and state that the adaptive capacity of a species rather than the antiquity of conifers as living fossils is the better explanation. If so, then adaptive capacity of *Fitzroya cupressoides* is deserving of more research. These research needs draw from several disciplines: genetics, geology, paleoclimate, and ecology to name a few.

Continued research has global worth because the *Fitzroya* case study from the Southern Hemisphere has no parallel to the Northern Hemisphere record. Continuing its research would bring forth a more globally complete understanding of how forests once responded to climate change.

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