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Southern-most *Nothofagus* trees enduring ice ages: Genetic evidence and ecological niche retrodiction reveal high latitude (54°S) glacial refugia

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ABSTRACT

Hypotheses of tree survival in refugia or long-distance postglacial migration can be disentangled combining genetic polymorphisms and ecological niche modeling. This is particularly relevant for ecologically distinct taxa which are undistinguishable by pollen morphology in fossil records. We hereby test the long-term persistence of the cold-hardy *Nothofagus pumilio* at high latitudes in southern South America during glacial cycles. Modern and past (LGM) ecological niche modeling (ENM) for *N. pumilio* was developed using current climate data and including 19 bioclimatic variables and topography. We collected fresh tissue for isozyme analysis from 14 locations within Tierra del Fuego selected on the basis of their location relative to LGM glacier extent: ice-free, ice-margin, and formerly glaciated areas. We resolved 11 isozyme loci and calculated within-population genetic diversity and among-population divergence parameters. Glacial effects on population structure were analyzed by UPGMA and Bayesian models. ENM yielded distinct areas in eastern and interior Tierra del Fuego exceeding >0.3 probability values that would have been suitable for *N. pumilio* during the LGM. Populations within formerly glaciated areas hold lower genetic diversity and thus were affected by genetic drift during colonization from refugia. Our data provided no evidence for wide-ranging postglacial colonization from warmer northern locales and suggested local survival of *Nothofagus* forests at southern-most South America.

1. Introduction

Paleoecological records, specifically pollen records, offer key information for evaluating species' responses to past climatic changes. However, their utility can be undermined by the fact that low-density plant populations and even locally surviving scattered individuals, which are particularly relevant in genetic terms, may remain undetected by the fossil records. This problem is augmented by the fact that many ecologically distinct species cannot be differentiated by their pollen morphology. As a result, conclusions about local persistence or recent arrival for a given species cannot be teased apart. The combined use of genetic markers (e.g. Anderson et al., 2006) and ecological niche modeling predictions (e.g. Waltari et al., 2007) would complement paleoenvironmental reconstructions in the detection of past presence of local populations that may have acted as key refugia for repopulation after deglaciation. Although uncertainties and concerns exist about the implementation and interpretation of species distribution modeling this approach has been successfully applied to northern hemisphere taxa (e.g. Svenning et al., 2008). Such a combined approach of genetic analysis, ecological niche modeling, and independent paleoecological data would have profound implications in the understanding of the existence and location of glacial refugia, tree migration rates, and resilience to climatic forcing.

Although extensive paleoecological work has been performed in southern South America, it remains controversial if the largely unglaciated coastal areas in northeastern Tierra del Fuego and contiguous, nowadays submerged continental shelves harbored local *Nothofagus* forests during the last glaciations (Markgraf, 1993; Markgraf and Huber, 2010). A steppe-tundra vegetation would have expanded in proglacial environments during the Last Glacial Maximum (LGM) at ca. 18 to 20 ka BP (Rabassa et al., 2000; Mancini et al., 2008; Markgraf and Huber, 2010).

The classic interpretations of Caldenius (1932) located the eastern limit of the two oldest glaciations in Tierra del Fuego beyond the coast onto the present Atlantic submerged continental shelf. More recently, consensus established that portions of land remained ice-free during major Pleistocene glaciations at least since 1.5 Ma BP (Rabassa et al., 2000; Bujalesky and Isla, 2006). These unglaciated terrains were surrounded by large outlet glaciers originating from the Cordillera Darwin ice cap in western Tierra del Fuego that flowed north and eastwards as the Magellan, Bahía Inútil, Fagnano, and Beagle lobes, from N to S, respectively, some of them onto the present Atlantic submerged shelf (Mercer, 1983; Meglioli et al., 1990; Porter, 1990; Clapperton, 1993; Isla and Schnack, 1995; Rabassa et al., 2000; Coronato et al., 2004; Rabassa et al., 2005; Sugden et al., 2005; Rabassa, 2008).

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In contrast to the wealth of support for a coastal eastern ice-free area in Tierra del Fuego, it has remained unclear whether the dominant tree species survived LGM as well as former glacial intervals at these and other suitable locations within the island. In addition, ecologically distinct species within subgenus *Nothofagus* inhabiting high latitudes (*N. antarctica*, *N. betuloides*, and *N. pumilio*) share *fusca* (b) pollen type (Hill, 2001) and thus are undistinguishable from records. Although *Nothofagus pumilio* forests are widely distributed throughout the southeastern lowlands of the island and on both sides of the Andes, it is yet unclear if full glacial climate conditions allowed the survival of small populations of *Nothofagus*. Markgraf (1993) suggested that tree taxa must have grown in suitable coastal locales or areas that became exposed when sea level was lower during the full glacial. Two main sources of evidence are presented by Markgraf (1993). On one hand, evidence based on pollen and fossil beetle records from different latitudes shows that tree taxa and flightless forest beetles did not show substantial migration lags, thus suggesting that they remained locally present throughout the full glacial (Ashworth and Markgraf, 1989; Ashworth et al., 1991). Local persistence of *Nothofagus* is suggested by one record from the steppe/forest boundary near the eastern Atlantic coast (Viamonte 54°11′S, 66°21′W, 5 m elevation; Auer 1956 recalculated by Markgraf 1993, Fig. 2b), showing continuous representation of c. 20–40% *Nothofagus* pollen since an earlier interstadial (>41 kyr BP). On the other hand, dominance of non-arboreal taxa, Poaceae, Asteraceae, herbaceous taxa, and traces of *Nothofagus* in high latitude pollen records suggests resemblance with present-day steppe and steppe-scrub with continued presence of local tree populations (Markgraf, 1993). In addition, the mire at Puerto Hambre (53°36′21″S, 70°55′53″W), 100 m inland from the Straits of Magellan in southern Patagonia contained *Nothofagus* pollen at an estimated 14,700 14 C yr BP (c. 17,500 cal. yr BP) at a time when eustatic sea level was at least 120 m lower than today (Kaplan et al., 2008). This result was interpreted as local presence of forests (Heusser et al., 2000) or long-distance transport (McCulloch and Davies, 2001).

Genetic markers on tree species have been widely used to reconstruct historical events in Patagonia. In particular, genetic evidence is building up to suggest that cold-tolerant woody taxa survived locally in multiple glacial refugia along their current distributional range (Premoli et al., 2000). Some of the refugia of widespread taxa such as conifers including *Pilgerodendron uviferum* (Cupressaceae) (Premoli et al., 2002), *Podocarpus nubigena* (Podocarpaceae) (Quiroga and Premoli, 2010), and the broadleaf *Embothrium coccineum* (Proteaceae) (Souto and Premoli, 2007) were probably located towards the southern-most species' range where maritime influence is higher compared to northern Patagonia. A preliminary study on a reduced number of populations of *Nothofagus pumilio* using isozymes yielded levels of genetic diversity for the southern populations from Tierra del Fuego similar to those located further north, which was interpreted to indicate local survival in multiple refugia during the last glacial period (Premoli, 1998). DNA sequences using 13 universal primers of non-coding mitochondrial and chloroplast regions yielded no polymorphism within Tierra del Fuego (BIOCORES, 2003, p. 64). This was confirmed by a thorough screening of populations using sequences of three cpDNA regions throughout the entire range of *N. pumilio* that produced two reciprocal clades each containing populations north and south 43° S (Mathiasen and Premoli, 2010). Although the southern range of the species was genetically depauperate in chloroplast DNA this should not be taken as evidence for recent colonization of this region. Instead all the chloroplast genotypes (haplotypes) were endemic to this region, and were all more closely related to each other than to any other haplotypes. Given the very slow rates of evolution of the chloroplast genome, this provides evidence for long-term survival of the species at high latitudes in South America.

Ecological niche models (ENM) are increasingly being used in conjunction with paleoecological reconstructions and phylogeographic analyses to determine past species distributions. ENMs relate known present occurrences of species to physical data in a spatial context and thus allow to infer environmental requirements or potential distribution patterns (Guisan and Thuiller, 2005). Under the assumptions of niche conservatism (Wiens and Graham, 2005; Martínez-Meyer and Peterson, 2006) and equilibrium of species with environmental conditions, these models can be used to pinpoint possible areas that may have remained suitable for the species during glacial periods, and therefore identify potential refugia. While ENMs have long been used to reconstruct plant paleodistributions of Southern Hemisphere LGM scenarios (Williams, 1991; Kirkpatrick and Fowler, 1998; Eeley et al., 1999), only recently they have started to be combined and compared with genetic/phylogeographic evidence (Carnaval and Moritz, 2008; Jakob et al., 2009).

In this study we hypothesize that Atlantic coastal areas provided the appropriate conditions to sustain forest populations that may have survived throughout the Quaternary and may have served as colonization source during the interstadials. We use genetic measures based on isozyme polymorphisms and ecological niche modeling to analyze: 1. if and where ice-free areas may have remained suitable during glacial maxima for sustaining *Nothofagus pumilio* forests within the island of Tierra del Fuego and 2. if patterns of within-population genetic diversity and among-population divergence of the dominant tree taxon *N. pumilio* throughout Tierra del Fuego suggest a structuring that is concordant with the paleosuitability distribution. Although microsatellites were developed for *Nothofagus* species within the subgenus *Lophozonia*, (Jones et al., 2004; Marchelli et al., 2008) their transferability and polymorphism in *N. pumilio* is still being optimized (M. Arbetman, Universidad Nacional del Comahue, pers.com.). For this study, population sampling design encompassed an area within the continuous LGM ice boundary as determined by geomorphological evidence (Rabassa et al., 2000), a second area outside LGM ice boundary, and a third area located within terminal moraines corresponding to different Pleistocene glacial intervals. If viable populations persisted outside the continuous ice boundary during the full glacial we expect that those populations would harbor a higher genetic diversity than populations located in areas formerly covered by the ice sheet, because the latter may have become genetically impoverished as a result of genetic drift affecting populations during recolonization from refugia. In addition, if *N. pumilio* populations from Tierra del Fuego represented descendents from an ancient gene pool that had established before the onset of Quaternary climatic oscillations, we also predict that refugial areas would be genetically similar to each other due to long-term local persistence in climatically stable ice-free areas.

2. Materials and methods

2.1. Study species

Nothofagus pumilio is one of the most widespread South American *Nothofagus* species. It occurs throughout the southern Andes and in the high latitude lowlands encompassing *c*. 20° latitude (Fig. 1, left panel).

2.2. Ecological niche modeling

To develop the ecological niche modeling (ENM) for *Nothofagus pumilio*, we used current (pre-industrial) climate data at 30″ (~1 km) spatial resolution from the WordlClim database (Hijmans et al., 2005). This database provides 19 bioclimatic variables that represent summaries of means and variation in temperature and precipitation, and likely summarize dimensions of climate particularly relevant in determining species distributions (Hijmans et al., 2005). In addition we used elevation, slope, and aspect derived from the Digital Elevation Model Shuttle Radar Topography Mission (SRTM-90)