

# Biological memory of the first Pleistocene glaciation in New Zealand

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## ABSTRACT

**Living species retain memories of their evolutionary history in their DNA, and that evolutionary history commonly reflects distinct geological events, such as mountain building and glaciation. We synthesize previously documented genetic data for freshwater fishes and a wide range of upland insect and bird species to document the Pliocene and early Pleistocene topographic and glacial history of the Southern Alps of New Zealand. Genetic data for fish suggest that a long, linear mountain chain was established in the Pliocene. At that time, the mountain chain had a tectonically constructed narrow topographic neck in the middle, with wider uplift zones at either end. Separation of populations of upland insects and birds into faunal zones at the wider ends was caused by a major glacial advance at the narrow tectonic neck at  $2 \pm 0.5$  Ma. The composite biological memory constrains the relative timing of uplift of the Southern Alps as a linear mountain chain, with subsequent imposition of temperate glaciation during Pliocene-Pleistocene cooling in the Southern Hemisphere.**

## INTRODUCTION

The late Pliocene and early Pleistocene were times of periodic expansion of the Antarctic ice sheets as part of general cooling of global climate that led ultimately to Southern Hemisphere Pleistocene glaciations (e.g., Patterson et al., 2014). While the waxing and waning of the Antarctic ice in the late Pliocene and early Pleistocene has been well documented, the effects of global cooling on temperate regions of the Southern Hemisphere are less well defined. Subsequent major glacial advances have removed onshore evidence of early glaciation events from many temperate regions, where the record is primarily of the most recent Pleistocene events. The mountainous South Island of New Zealand, located halfway between the equator and the South Pole, is ideally located to act as a temperate “glacial thermometer,” although the onshore geological record of the rise of mountains and imposition of early glaciation is sparse and poorly dated (Sugate, 1990; Newnham et al., 1999; Rattenbury et al., 2006; Heenan and McGlone, 2013). In this paper, we present a novel biological approach to estimate the timing of the first temperate glaciation, as an example of reciprocal illumination between geology and zoology.

We have previously identified glacially mediated genetic discontinuities of terrestrial biota along the Andes, Himalaya, Pyrenees, and Southern Alps (New Zealand) in a predominantly biological context (Wallis et al., 2016). In this paper, we extend a New Zealand example to relate the established biology and genetic (DNA) data to specific tectonic, geological, and climatological aspects of the evolution of a mountain chain. We show that underlying crustal structure

has affected the tectonic and topographic evolution of the mountains, controlled glaciation, and caused major divergences in biological evolution. In particular, we focus on the geological evolution of a narrow tectonic neck in the mountain chain and subsequent development of a distinct faunal discontinuity at that neck.

Genetic and biogeographical data constitute a form of biological “memory” of geological events, and can provide information on (1) geographic development of distinct genetic lineages, (2) the time that has elapsed since these lineages diverged from their common ancestors, and (3) the general location of the geological events that drove biological speciation. There are two end-member scenarios for development of glaciation in active mountains: rise of mountains into an already-cool climate (Fig. 1A), and imposition of a cold climate on mountains that were already high enough for glaciation to occur (Fig. 1B). We use biological data to distinguish these hypotheses in New Zealand mountains where available geological data are equivocal.

## APPROACH AND METHODS

First, to define the age, shape, and continuity of the rising mountains, we use well-established biogeographical and genetic data for four different species from two genera of freshwater fish. These data are sourced from a wide range of endemic species based on their relevance to development of key topographic features in this study (Waters et al., 2010; Burrige et al., 2011; Craw et al., 2016). These fish are restricted to their natal river systems, so their genetic relationships are constrained by river drainage divides. Genetic comparisons of isolated river

populations can provide age estimates for their initial divergence across drainage divides. This temporal component has been calibrated for a wide range of fish species in the Pleistocene using geological events of known age, with extrapolation to the Pliocene and Miocene, by Craw et al. (2008), Waters et al. (2010), and Burrige et al. (2011).

Second, we estimate the age of initial glaciation in the Southern Alps using north-south genetic comparisons of 35 species from 13 genera of terrestrial organisms. These species have been selected from a large endemic fauna because of their upland habitats and susceptibility to geographic isolation (Wallis et al., 2016). Most of these species (33) are insects, all with limited dispersal ability, and 20 are flightless. We also include two bird genera, including a recently extirpated flightless moa, and a wren that has limited flying ability coupled with strict alpine habitat constraints. Our timing estimates for genetic divergences in these species are based on previously published molecular clock calibrations appropriate for each biological grouping (e.g., Wallis et al., 2016, and references therein). While individual age estimates are subject to errors arising from incomplete genetic and biological sampling and from evolutionary rate variation among lineages, the collation of congruent age estimates from multiple co-distributed biological lineages allows broad-scale establishment of geological divergence timing (e.g., O’Dea et al., 2016).

## SOUTH ISLAND TECTONIC TOPOGRAPHY

South Island straddles the obliquely convergent Pacific–Australian plate boundary (Fig. 1C), and the topography results from tectonic processes associated with that plate boundary superimposed on inherited crustal structure (Figs. 1D–1G; Figs. DR1a and DR1b in the GSA Data Repository<sup>1</sup>; Cox and Sutherland, 2007; Upton et al., 2009). This tectonic topography has been evolving since the island emerged from the sea in

<sup>1</sup>GSA Data Repository item 2017196, Figure DR1 and DR2 (structure, topography, and evolution of the tectonic neck), and Figure DR3 (summary distribution of terrestrial biota), is available online at <http://www.geosociety.org/datarepository/2017/> or on request from [editing@geosociety.org](mailto:editing@geosociety.org).

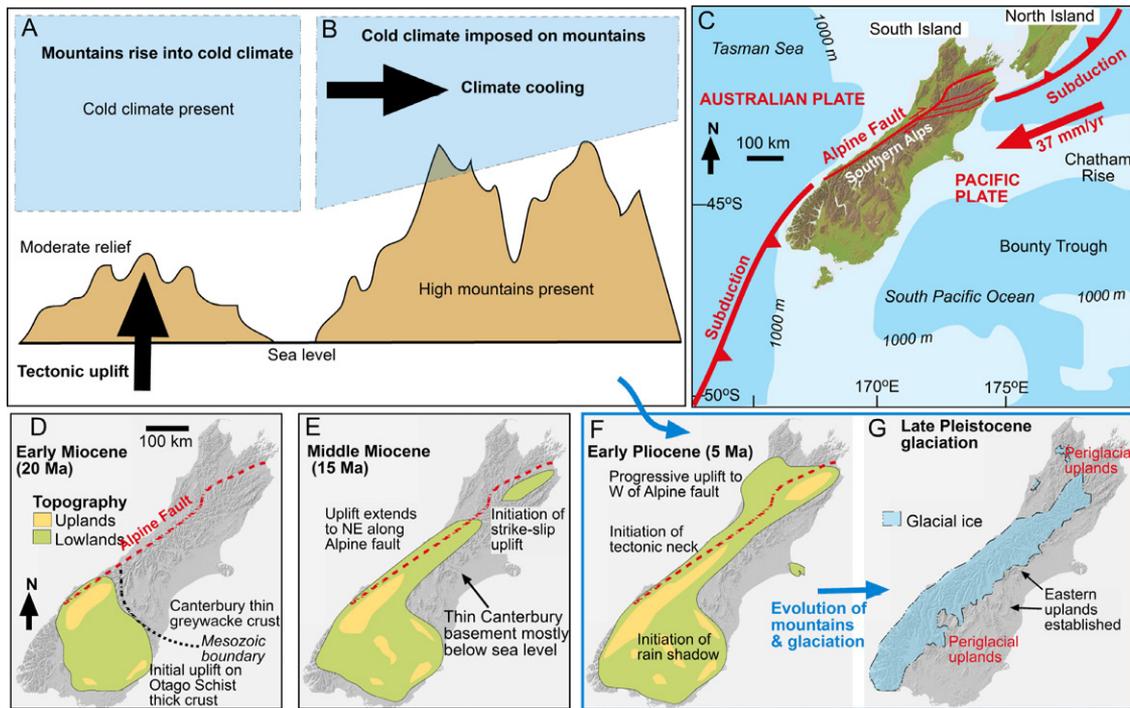


Figure 1. A,B: Cartoons showing two end-member scenarios for initiation of glaciation in actively rising mountains. A: Rise of mountains to form high altitude areas after the onset of cold climate. B: Imposition of cold climate on mountains that already had high-altitude areas. C: Plate tectonic setting of New Zealand in South Pacific Ocean. D-G: Geological evolution of South Island of New Zealand. Onset of glaciation in mountains, via mechanism in A or B, occurred between time periods represented by F and G.

the Miocene (Fig. 1D; Landis et al., 2008). Basement topography of the southern portion of the island developed during differential uplift mediated by crustal structure inherited from Mesozoic terrane amalgamation (Fig. 2A). In particular, the rheologically weak and thick Otago Schist crust abuts stronger, thinner crust of Canterbury greywacke (Fig. 1D; Figs. DR1a and DR1b; Upton et al., 2009, 2014). Late Cenozoic reactivation of this rheological boundary has formed a wide zone of moderate relief on the Otago Schist belt, which was initiated in the Miocene and developed a topographically induced rain shadow in the Pliocene (Figs. 1D and 1E; Craw, 1995; Chamberlain et al., 1999; Horton et al., 2016). In contrast, uplift from below sea level of the thin Canterbury crust occurred only in a narrow zone near the Alpine fault, starting in the middle Miocene (Fig. 1E; Figs. DR1a and DR1b). Most of the greywacke basement is still below sea level, and is covered with a thick sequence of fluvial gravels derived from the rising land to the west (Figs. 1E–1G). Uplift at the northern end of the island began in the middle Miocene and spread to the west of the plate boundary above the west-dipping subduction zone to form a wider basement zone than in Canterbury (Figs. 1C, 1E, and 1F; Figs. DR1a and DR1b; Rattenbury et al., 2006; Ghisetti et al., 2016).

A topographically narrow neck in the center of the island (Fig. 1F; Figs. DR1a, DR1b, DR2a, and DR2b) has resulted from this tectonic evolution. The tectonic neck coincides with the present highest mountains (up to 4 km) on Canterbury greywacke crust near the Alpine fault. The timing of initial development of the high mountains is poorly constrained, although scattered remnants of fluvial sediments attest to the presence of

erodible relief in the Pliocene (Upton et al., 2004; Cox and Barrell, 2008; Figs. DR2a–DR2d). The continuity and geometry of that relief is not well known from the geological record. However, the biological memory described herein allows us to provide some constraints.

### FISH SPECIATION DURING MOUNTAIN GROWTH

Tectonic topography and associated biological evolution have proceeded in concert for many non-dispersive New Zealand species since the

Miocene uplift began (Craw et al., 2016). For instance, freshwater fish in New Zealand rivers have evolved from ancestral seagoing species that have colonized the rising islands, probably from Australia, since the Miocene (Waters et al., 2010; Burridge et al., 2011). Once these established lineages became freshwater limited, their inter-drainage dispersal has relied on river capture events, mingling of rivers on coastal plains, and periods of low sea level. Uplift of the Southern Alps led to clear separation of the South Island into distinct eastern and western

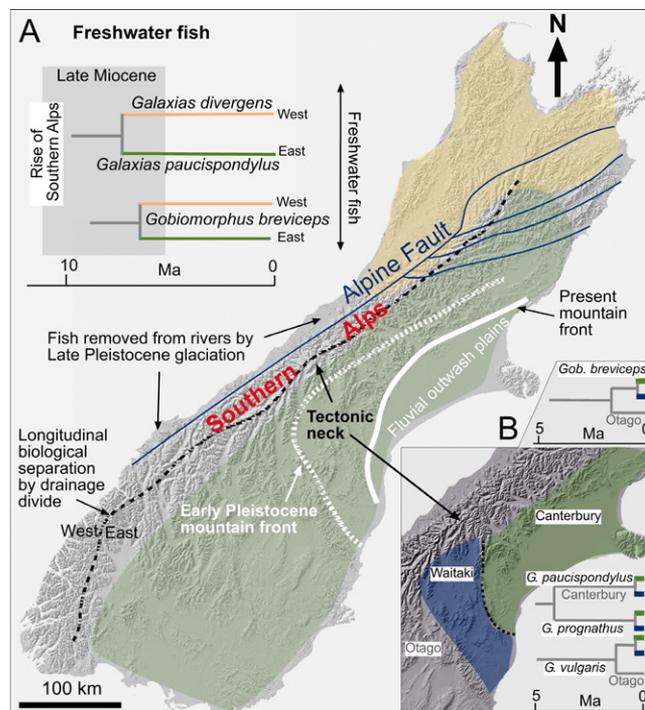
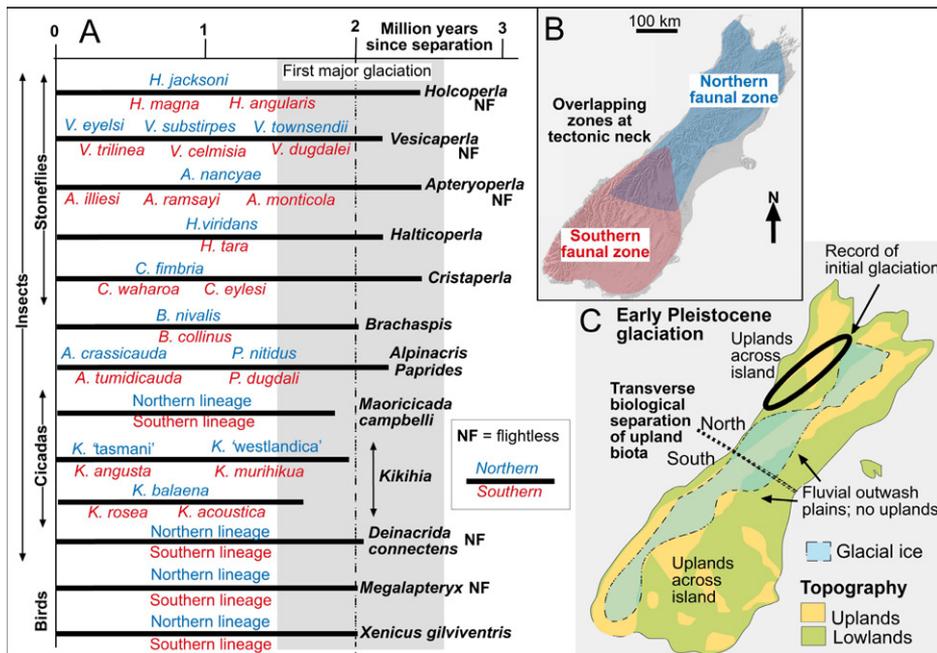


Figure 2. Freshwater fish faunal divisions of South Island, New Zealand. A: Distributions of freshwater fish species, with timing of their longitudinal separation by formation of drainage divide. B: Pleistocene tectonically mediated evolution of separated populations (green—Canterbury; blue—Waitaki) of three species of *Galaxias*, and *Gobiomorphus breviceps* in eastern foothills of tectonic neck zone (Figs. DR1a–DR1b and DR2a–DR2d [see footnote 1]).



**Figure 3. Distributions of some upland and subalpine species and their genetic relationships (South Island, New Zealand). A:** Northern (blue) and southern (red) species and timing of their separation, as deduced from DNA divergences. Abbreviated genus names are spelled out to the right. **B:** Summary of distributions of northern and southern faunal zones, with transverse faunal boundary (as in Figs. DR3a–DR3d [see footnote 1]) that include species indicated in A. **C:** Inferred distribution of ice during first glaciation in early Pleistocene.

sets of catchments. This isolation in turn led to longitudinal distribution patterns for related fish species, with the backbone of the island forming an important topographic boundary starting in the Pliocene or even late Miocene (Fig. 2A; Craw et al., 2016). Hence, fish genetic data provide evidence that the proto–Southern Alps had formed a well-defined and continuous linear topographic barrier by the Pliocene (Figs. 1B and 1F).

### PLEISTOCENE EVOLUTION OF THE TECTONIC NECK

Four fish species that evolved to the east of the rising Southern Alps still inhabit streams emanating from the mountains (Fig. 2B). Populations of all four of these fish species in the southernmost river catchment of these plains, the Waitaki catchment, became isolated in the late Pleistocene as a result of basement uplift to form foothills in the tectonic neck (Figs. 2A and 2B; Figs. DR2a–DR2d; Waters and Craw, 2007). Uplifted remnants of Pliocene and early Pleistocene well-rounded fluvial gravels occur within these eastern uplands (Upton et al., 2004; Figs. DR2a–DR2d). These gravels are remnants of the lowland fluvial plains that preceded the late Pleistocene rise of foothills that caused the isolation of populations of fish species (Figs. 1G and 2B). The biological memory and the fragments of geological evidence both show that the eastern mountain front was closer to the main drainage divide in the early Pleistocene, and the tectonic neck in the main Southern Alps chain was narrower than it is now (Fig. 2A; Figs. DR1a, DR1b, and DR2a).

### SEPARATION OF UPLAND TERRESTRIAL FAUNA

Tectonic uplift in the Pliocene provided extensive novel montane and alpine habitat for species that could adapt to this zone. Terrestrial animals are not constrained by river drainages, as fish are. Some insects spend a portion of their life cycle in streams, but these have flying and/or walking stages as well. Hence, terrestrial fauna can migrate widely within the limits of their environmental tolerance. In this study, we have focused on terrestrial species that inhabit upland environments and are therefore tolerant of subalpine or even alpine environments.

The upland terrestrial species (Fig. 3A) are all endemic to New Zealand and have apparently evolved with the rising Southern Alps. Present distributions of these species indicate ancestral separation of populations between the northern and southern parts of South Island (Wallis et al., 2016; Figs. DR3a–DR3d). The contrasting distributions have a transverse boundary, with minor overlap, that is perpendicular to the longitudinal division that proto–Southern Alps uplift imposed on the freshwater fish (Figs. 2A and 3B; Figs. DR3a–DR3d). The estimates of timing of the separation of these species from their common ancestors, as deduced from the divergence of their DNA, ranges from ca. 1.5 Ma to 2.5 Ma (Fig. 3A). Temporal modeling of genetic separation of five of the genera strongly support a single divergence event, consistent with simultaneous fragmentation of numerous widespread subalpine insect lineages (McCulloch et al., 2010).

### DISCUSSION AND CONCLUSIONS

Freshwater fish distribution and genetic data support the existence of a well-defined linear mountain chain, the proto–Southern Alps, in the Pliocene (Fig. 2A). This mountain chain had a long linear drainage divide in a similar position to the present divide (Fig. 2A). At the same time, common ancestors of a large number of upland terrestrial species were apparently present continuously along the length of this mountain chain, prior to their glacier-driven isolation (Figs. 3A and 3B). On this basis, we conclude that there was already a significant mountain chain present, with upland and even subalpine habitat, during the cooling of the climate in the late Pliocene (scenario in Fig. 1B). The biological data preclude development of a long high mountain chain after imposition of a cold climate in the late Pliocene (scenario in Fig. 1A), but we cannot discount a general increase in elevation during the late Pliocene–early Pleistocene cold climate.

The continuity of distribution of terrestrial species was disrupted by a major event in the early Pleistocene, at  $2 \pm 0.5$  Ma, which we infer to have been the first major glaciation (Figs. 3A–3C; Suggate, 1990). This event caused separation and subsequent isolation of populations of upland terrestrial species, so that they evolved into genetically distinctly different taxa in the northern and southern parts of South Island (Figs. 3A and 3B). An alternative scenario involving independent and parallel dispersal of these lineages from one end of the mountains to the other would not have yielded such uniform separation time estimates for isolation. The limited recolonization and distributional overlap by separated taxa (Fig. 3B) has probably resulted from competitive exclusion (Waters et al., 2013) and has been further facilitated by repeated glaciation of the transverse contact zone.

The transverse boundary between the northern and southern faunal zones occurs in the region of the tectonically induced neck that developed because of a combination of inherited crustal structure and modern tectonics (Figs. 1C–1F and 2A; Fig. DR1a). The first Pleistocene glaciation imposed on the mountains had the strongest effect on biological distributions because the tectonic neck was narrow, with high mountains, at that time (Fig. 3C). Glaciers extended to the sea on the western side and to the fluvial plains on the eastern side, creating a wide ice barrier (Fig. 3C). To the north and south of this glacial barrier there were unglaciated upland areas where the island is wider at both ends, and these uplands provided continuous refugia for northern and southern populations of terrestrial fauna.

The mountains are still highest and narrowest in this part of the island, but the subsequent growth of foothills to the east of the mountains in this area (Fig. 2A; Figs. DR2a–DR2d) has

created potential refugia during major glaciations such as the Last Glacial Maximum (Fig. 1G). Hence, a faunal discontinuity as significant as that documented at 2 Ma (Figs. 3A–3C) became less likely through the Pleistocene as these eastern foothills evolved (Fig. 2A). Further, at least some hybridization of separated species can occur when they are reunited after short periods (<2 m.y.; Marshall et al., 2008). The first glaciation was sufficiently extensive to ensure that the resultant major faunal discontinuity survived to the present. The biological memory of that event, combined with the fish genetic evidence of a pre-existing mountain chain, contribute to the geological understanding of the tectonic evolution of the Southern Alps, the Pliocene–Pleistocene cooling of the Southern Hemisphere, and the interactions of these two processes. A similar approach could be used elsewhere, such as in the Andes of South America where similar biogeographical discontinuities occur (Wallis et al., 2016) and where the onshore geological records of early glaciations have been removed by subsequent ice advances (e.g., Rodbell et al., 2009).

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