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Rapid biological speciation driven by tectonic evolution in New Zealand

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Collisions between tectonic plates lead to the rise of new mountain ranges that can separate biological populations and ultimately result in new species[1]. However, the identification of links between tectonic mountain-building and biological speciation is confounded by environmental and ecological factors[2–4]. Thus, there are surprisingly few well-documented examples of direct tectonic controls on terrestrial biological speciation. Here we present examples from New Zealand, where the rapid evolution of 18 species of freshwater fishes has resulted from parallel tectonic landscape evolution. We use numerical models to reconstruct changes in the deep crustal structure and surface drainage catchments of the southern island of New Zealand over the past 25 million years. We show that the island and mountain topography evolved in six principal tectonic zones, which have distinct drainage catchments that separated fish populations. We use new and existing[5,6] phylogenetic analyses of freshwater fish populations, based on over 1,000 specimens from more than 400 localities, to show that fish genomes can retain evidence of this tectonic landscape development, with a clear correlation between geologic age and extent of DNA sequence divergence. We conclude that landscape evolution has controlled on-going biological diversification over the past 25 million years.

Geologic events are known to drive biological processes, with notable examples including evolution on developing volcanic island chains[7] and rifting apart of continental crust[8] (Supplementary Table 1). While mountain-building events are similarly thought to drive biological evolution, landscape uplift also generates environmental change, including development of rainfall and temperature gradients, which in turn dominate terrestrial biological diversification processes[4,9,10]. Indeed, numerous studies have shown that environmental heterogeneity can underpin biological evolution, irrespective of any underlying tectonic processes[9,11], and timescales of this biological evolution are generally shorter than the geologic processes (Supplementary Table 1). Furthermore, most active mountain belts are growing on pre-existing land surfaces that had pre-established terrestrial biota[12,13], so biological diversity that predated uplift can obscure the effects of tectonic processes[4].

Our study uses New Zealand's South Island as an example of an actively growing mountain belt in which evolution of freshwater fish species is occurring at similar rates to evolution of the tectonic landscape, and separate species have formed in as little as 500,000 years as a direct result of tectonic processes[5,6,14–17]. Species distributions are strongly controlled by the several different tectonic landscapes in which they have evolved (Fig. 1a–f). This example is constrained by New Zealand's rise from the sea since the Miocene epoch, with freshwater fish having evolved from marine-migratory ancestors during this period[5,6] (Fig. 2a). We have reconstructed the biological and tectonic histories into parallel evolutionary 'trees', for both the tectonic landmass and the freshwater fish, after both emerged from the sea in the Miocene (Fig. 2a,b).

Riverine fish populations in New Zealand are generally widespread[15] and relatively unaffected by environmental factors that influence distributions and evolution of terrestrial taxa. Thus, isolation of populations of freshwater fish by growing mountains is almost entirely a tectonically driven process[6,14,16], unconfounded by environmental heterogeneity. Further, freshwater-limited fish populations typically occupy a single catchment, and evolve within that catchment. Consequently, it is possible to use genetic relationships of populations of these low-dispersal species to trace histories of river drainage reorientation and landscape evolution[14,17].

South Island straddles a major tectonic boundary between the Pacific and Australian plates, which occurs on land as the Alpine Fault (Fig. 1a). The diverse basement rocks that make up South Island were formed into a broad continental landmass, Zealandia, during the Mesozoic era[18]. Cretaceous crustal thinning resulted in the submergence of Zealandia by the middle Cenozoic era[19]. Any small relict island(s) had negligible effect on subsequent landscape evolution, and present freshwater fish fauna reflects post-Oligocene colonization and diversification[5]. The Alpine Fault was initiated in the Miocene as a strike-slip structure and this evolved into an obliquely convergent structure through the Pliocene epoch to the present[20] (Fig. 1a). A major mountain chain, the Southern Alps, developed on the Pacific Plate side of the Alpine Fault, and these mountains and associated ranges to the east dominate topography (Fig. 1a). The mountains cause abundant orographic rainfall ($>10\,\mathrm{m\,yr^{-1}}$) on the western side, with a rainshadow ($<1\,\mathrm{m\,yr^{-1}}$ precipitation) to the east.

Topography on the dry eastern side is primarily constructional, so that mountains and valleys are formed by differential tectonic uplift, with only minor erosion[21]. In contrast, topography on the narrow western zone is primarily erosional[21]. Tectonic uplift has evolved six principal tectonic zones that reflect the interactions of plate boundary tectonic processes with differing crustal structures inherited from Mesozoic Zealandia (Figs 1a and 2a,b and Supplementary Table 2). The different tectonic zones have evolved characteristic orientations of mountain ridges and intervening valleys (Fig. 1a and Supplementary Table 2). Each tectonic zone has river drainage systems that are now largely confined to that zone, as a result of uplift of marginal mountain ranges. Of particular importance, the Otago Schist belt is a geomorphologically distinctive zone of thick and relatively weak schistose crust inherited from Mesozoic Zealandia, sandwiched between the rheologically stronger greywacke terranes of Canterbury and Southland[22,23]

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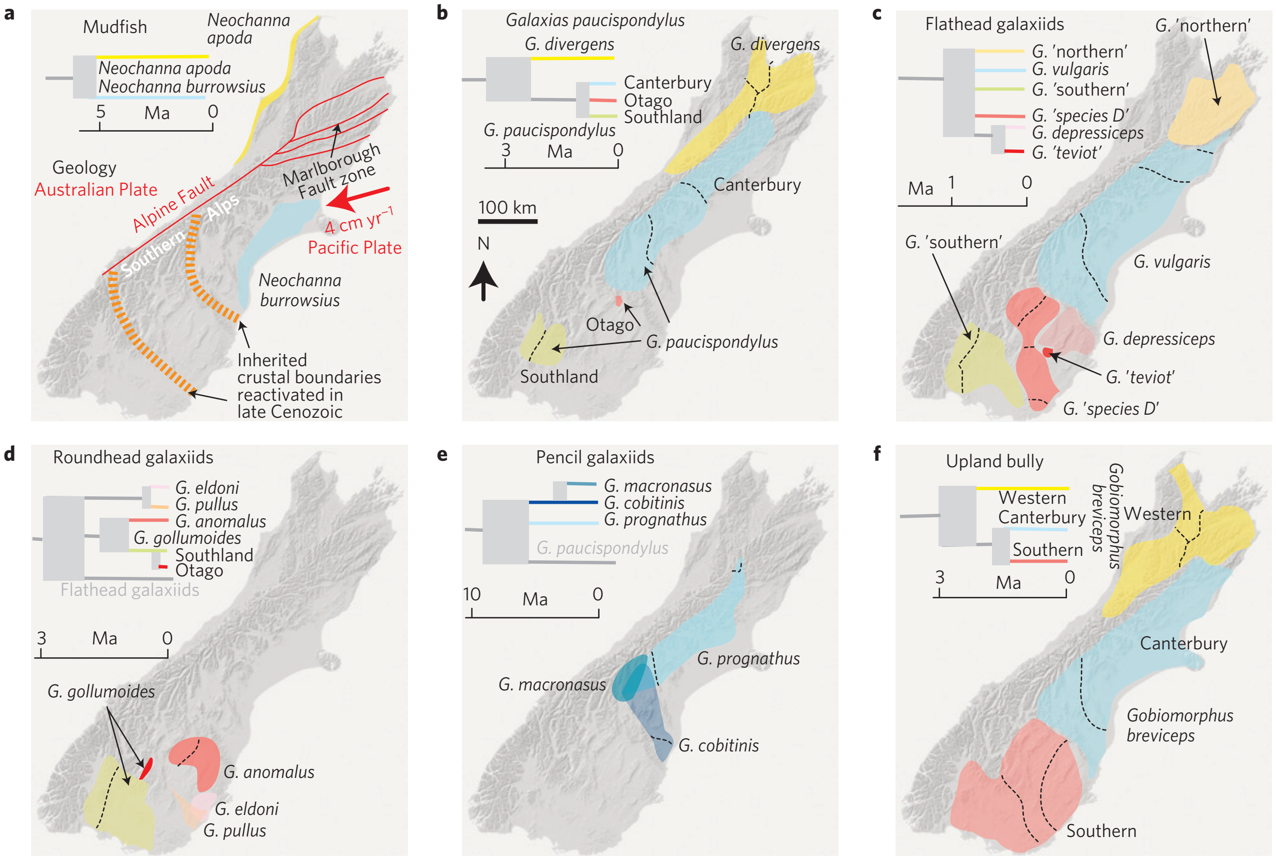

Figure 1 | Maps showing distributions of key freshwater fish species and divergent populations. a–f, The fish distributions are colour-coded for the tectonic and geomorphic zones they occupy (Fig. 2a,b). The present tectonic setting and the key underlying geologic features are indicated in **a**. Dashed lines indicate further, younger, genetic distinctions. Approximate timings of genetic divergence of various groups are indicated, with thick grey zones showing the broad uncertainties. Ma, Myr ago.

(Figs 1a and 2a,b and Supplementary Table 2). The high Southern Alps are being constructed across this inhomogeneous Mesozoic crust, resulting in contrasting topography on rheologically different crustal blocks[22] (Figs 1a and 2a,b and Supplementary Table 2).

For the biological component of this study, we have compiled freshwater fish distributions across South Island, and reconstructed phylogeographic relationships of lineages using a variety of mitochondrial and nuclear DNA sequences[5,6] (Fig. 1a–f). We focus on freshwater-limited galaxiid fishes whose genetic relationships we have elucidated (Fig. 1b–e; refs 5,6). The galaxiids include several widespread species groups that are ecologically differentiated from one another, encompassing a range of habitat types: for example, shallow pools and bogs (mudfish), major rivers (river galaxiids), and subalpine, glacially fed, streams (pencil galaxiids).

Within each fish species group, there is clearly a strong relationship between fish species distributions and the tectonic and geomorphic zones that dominate South Island (Figs 1a–f and 2b). In addition, we have determined the magnitude of genetic differentiation of related populations or species in adjacent catchments. These data allow us to define river drainage-reorientation events (river capture), and estimate the time since species/populations were reproductively isolated by such events[6,14,17,24,25]. While these molecular estimates of divergence timing can be imprecise due to sampling error and violation of molecular clock assumptions, relative divergence-time estimates have nevertheless been obtained for the Miocene–Holocene period of interest to this study[6,14] (Figs 1a–f and 2a,b). To avoid a circular approach to inferring timeframes of biological evolution, we have calibrated fish phylogenies using a variety of fossil data, drainage-reorientation events, and non-tectonic calibration points[13]—phenomena that are distinct from the tectonic events presented here.

Geographically disjunct western (*Galaxias divergens*), and eastern (*G. paucispondylus*) sister species evolved from galaxiid populations that became separated by the rise of the Southern Alps in the Pliocene (Fig. 1b). Post-Pliocene tectonic events have further isolated populations of *G. paucispondylus* in the different tectonic and geomorphic zones of Canterbury, Otago and Southland (Fig. 1b). The flathead galaxiids show high levels of diversity associated with tectonic and geomorphic zonation[17] (Fig. 1c). Roundhead galaxiids diverged from the flathead lineage in the late Pliocene in Otago and Southland[5] (Fig. 1d). The pencil galaxiid clade is largely confined to the topographic transition between the geomorphic zones of Canterbury and Otago[22] (Fig. 1e).

Lowland or coastal populations of mudfish (*Neochanna* spp.) were also separated by uplift of the Southern Alps in the Pliocene[6] (Fig. 1a). A single freshwater-limited 'upland-bully' species, *Gobiomorphus breviceps*, is distributed throughout South Island, with several genetically distinct phylogeographic groupings[26] (Fig. 1f). These regional clades of *G. breviceps* are mainly confined to particular tectonic and geomorphic zones, with distributions mirroring those of *Galaxias paucispondylus* and *G. divergens* (Fig. 1b,f).

The zone of Otago Schist in southern South Island seems to have had a major effect on the evolution of freshwater fish species (Figs 1b–e and 2b). To examine this key tectonic geometry further, we present results of two numerical mechanical models that were developed to test the range of values for various tectonic parameters and geometrical relationships[22,23]. The key parameters and geometry used in the models are summarized in

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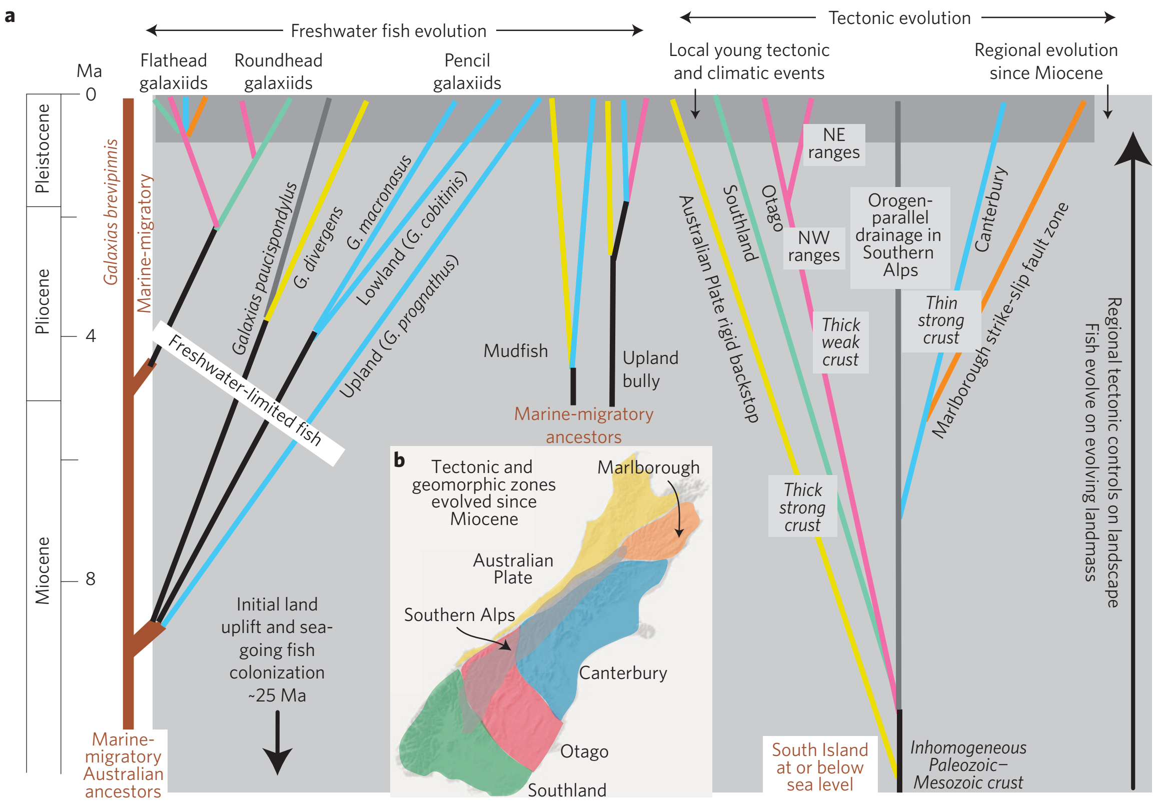

Figure 2 | Summary evolutionary trees for South Island's tectonic and geomorphic zones. a,**b**, Miocene–present tectonic evolution of the landmass (right; colour-coded in **b**, described in Supplementary Table 2), and associated freshwater fish lineages (left and centre) that evolved on that landmass. Light grey background indicates the timescale of the regional tectonic evolution discussed in this study, compared to local tectonic and climatic events (dark grey) that affected local fish populations relatively recently.

Supplementary Table 3. The modelled topographic evolution of Canterbury, Otago and Southland crustal blocks provides a clear tectonic basis for associated fish diversification (Figs 3 and 4).

The first numerical model simulates the evolution of topography during Miocene strike-slip deformation of the simplified inherited inhomogeneous crustal structure of Canterbury, Otago and Southland (Fig. 3a–d and Supplementary Table 2). The deformation spreads out over the weaker block and, in doing so, results in convergence at the northern end of the weak material and stretching of material at the southern end of the weaker material. A key feature of the results of this model is the orogen-parallel topography, which permitted drainage connection from the strong impacting block (Canterbury), across the weak block (Otago), to the other strong block (Southland; Fig. 3d). The plate boundary evolved from strike slip to transpression during the Miocene and Pliocene, and our second model focuses more particularly on oblique convergence at the crustal boundary between the Canterbury and Otago zones (Supplementary Tables 2 and 3) from the middle Miocene to the Pleistocene (Fig. 4a–d). Orogen-parallel ridges and valleys form adjacent to the plate boundary on both crustal blocks, but the uplift zone is much narrower on the strong block (Canterbury) than the weak block (Otago), from the earliest stages of deformation (Fig. 4a). A robust result of both models is the prominent NW trending mountain ranges along the Canterbury–Otago boundary that grew substantially in the Pliocene[23] (Fig. 4b). This model is too generalized to define the NE trending ridges and valleys on the weak crustal block, and shows this as a broad zone of uplift through the Pleistocene (Fig. 4c,d).

Drainage reorientations are important processes shaping landscape evolution[27]. However, river valleys, and topography in general, can migrate laterally in tectonically active areas, and uplift and erosion can overprint former drainage patterns[21]. Hence, the genetic divergences of freshwater fish that evolved in the developing landscape can provide evidence of the tectonic landscape history. For example, the presence of *G. paucispondylus* along the full length of the Southern Alps (Fig. 1b) provides evidence not otherwise available for long-distance orogen-parallel drainage connections, as modelled in Fig. 3a–c, across what are now high mountain ranges (Fig. 3d). More recently, the sister species *G. divergens* has locally made secondary contact with *G. paucispondylus* in the Marlborough zone (Fig. 1b), at the same time as eastward migration of the western upland-bully population (Fig. 1f), across what is now a low topographic divide along the Alpine Fault[14].

We have previously documented numerous examples of processes and timings of minor drainage changes at the margins of the tectonic zones studied herein[14,24]. Most of these drainage changes resulted from glaciation/deglaciation and/or local tectonic events within the past million years, and were relatively minor in the parallel evolutionary history of the fish and South Island landscape that began in the Miocene (Fig. 2a). The strong relationships between fish species distributions and geomorphic zones show that longer-term tectonic processes have been the principal drivers for the spectacular speciation and distinctive biogeography of these species (Fig. 1a–f). Importantly, the current study shows strong relationships between fish species distributions and older geomorphic features, links extending back over much deeper timeframes, highlighting that longer-term tectonic processes have been the principal drivers for the distinctive speciation patterns and biogeographies of New Zealand's freshwater fish assemblages (Figs 1 and 2). While numerous studies have previously inferred links between tectonic orogenesis and biological divergence, New Zealand presents a

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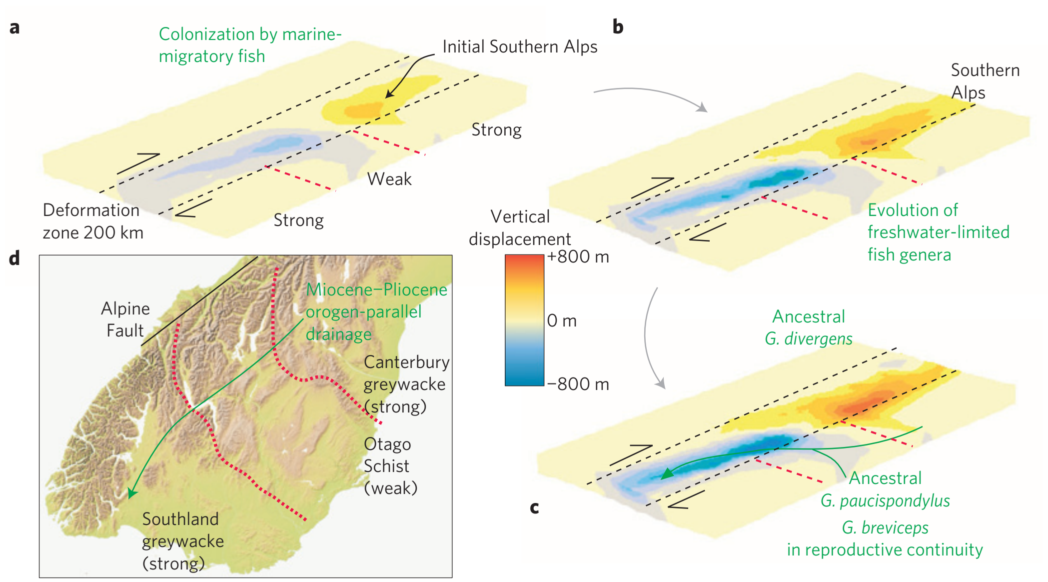

Figure 3 | Results of numerical mechanical modelling of progressive evolution of topography in a strike-slip tectonic regime with inhomogeneous crust. **a**–**d**, These models (Supplementary Table 3) are representative of processes occurring after 3 Ma (**a**), 6 Ma (**b**) and 9 Ma (**c**), assuming 3 mm yr^{-1} of strike-slip motion across this distributed deformation zone adjacent to the developing Alpine Fault, in southern South Island (**d**) starting in the early Miocene.

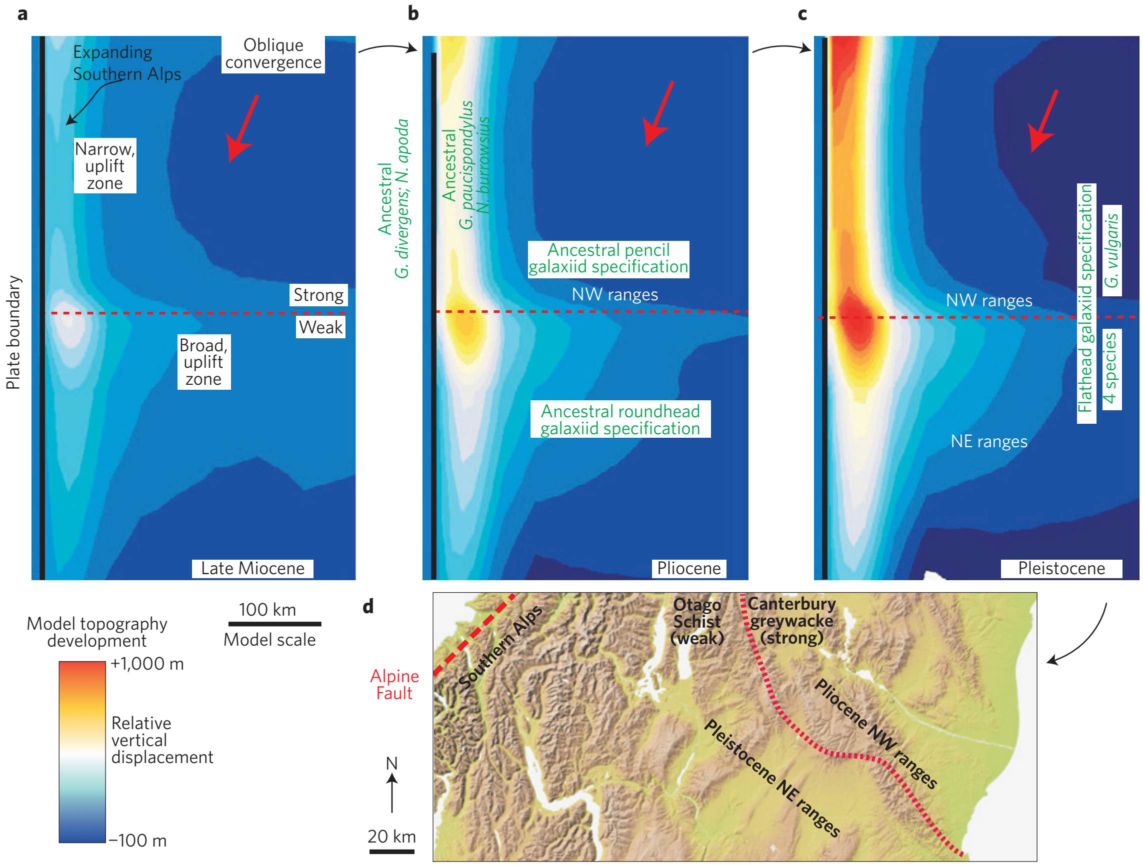

Figure 4 | Results of numerical mechanical modelling of progressive development of topography during oblique convergent deformation of inhomogeneous crust. a–**d**, These models (Supplementary Table 3) are representative of Canterbury and Otago in the late Miocene (**a**, 3 km distributed boundary parallel displacement), Pliocene (**b**, 6 km) and Pleistocene (**c**, 9 km), leading to the present (**d**).

unique situation whereby the same tectonic processes were directly responsible for both the initial formation and subsequent radiation of biological diversity from the Miocene to the present.

Methods

Methods and any associated references are available in the online version of the paper.

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Author contributions

D.C. and J.M.W. conceived the project and prepared the original manuscript. J.M.W., G.P.W. and C.P.B. gathered and compiled the fish phylogenetic and phylogeographic data. P.U. conducted the numerical modelling. All authors refined the final manuscript.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to D.C.

Competing financial interests

The authors declare no competing financial interests.

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Methods

This study results from a multidisciplinary combination of separate research strands that have been developed in parallel, involving tectonic geomorphology, regional stratigraphy, crustal dynamics, numerical modelling, fish species distributions, and molecular phylogenetics (see references in Supplementary Table 2).

Freshwater fish were collected using pole nets or electric fishing apparatus[5,24]. Fish sampling was performed with the approval of the University of Otago Animal Ethics Committee, with collection permits from the Department of Conservation. DNA amplicons were sequenced[5,6,24] and all sequences have been deposited in GenBank (http://www.ncbi.nlm.nih.gov/genbank). Maximum likelihood and Bayesian phylogenetic analyses were carried out[13], with chronograms reconstructed using BEAST (ref. 28). Additional fish biogeographic and phylogeographic data were extracted from New Zealand's freshwater fish database (https://nzffdms.niwa.co.nz/search).

We have used data from multiple slow-evolving nuclear genetic markers to help resolve the deep evolutionary relationships of the galaxiid fishes, and these analyses primarily used fossil-derived calibrations[5,6,29]. On the basis of these analyses, New Zealand's galaxiid assemblages have apparently colonized the archipelago only within approximately the past 20 Myr (refs 5,6,29). On more recent (Pleistocene) evolutionary timescales, we have also used rapidly evolving mitochondrial DNA (mtDNA) sequences to demonstrate a clear chronosequence of mtDNA sequence divergence and geologic ages for a number of geologically constrained, tectonic and glacially mediated river-evolution events from the late Pleistocene to Holocene[14,24]. The Pleistocene-based molecular clock for mtDNA genetic divergence has been quantitatively calibrated, with genetic divergence (%) $= -2.2e^{-9t} + 2.5t + 2.2$, where t is isolation age in millions of years. These divergence rates become slower with age, and approach linearity beyond ~1 Myr, with a typical divergence rate of ~2.5% Myr^{-1}. The fast-evolving, non-recombining characteristics of mtDNA make this genetic marker a powerful tool for resolving biological evolution over short timeframes[30]. We have then combined deep-time inferences derived from multi-gene approaches, with the estimates based on the mtDNA calibration curve for galaxiid and bully mtDNA, to infer a detailed chronosequence in New Zealand from the Miocene to the present[5,6,14,16,24].

The numerical modelling was done using the numerical code FLAC^{3D}, a commercially available package (itascacg.com/software/flac3d/flac3d-sales) which utilizes a modified Lagrangian finite difference technique. The code treats rocks as continua represented by average values of mechanical properties. More details on the basis for the modelling, the geometry of the models, and specific relevant parameters for our models are provided in the Supplementary Information, including Supplementary Table 3 and Supplementary Fig. 1. Sensitivity analyses for various aspects of these model parameters within FLAC^{3D} have been evaluated[22,23]. All topography in the models results from differential uplift of model surfaces. Valleys form where the uplift amount and/or uplift rate is less than that for adjacent ridges, and are hence constructional, not erosional.

Computer code availability. The FLAC^{3D} code used to generate the numerical model of New Zealand's topographic evolution can be accessed here http://www.itascacg.com/software/flac3d/flac3d-sales.

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