



Geology shapes biogeography: Quaternary river-capture explains New Zealand's biologically 'composite' Taieri River



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ABSTRACT

Geological processes are hypothesised to strongly affect species distributions. In particular, a combination of geological and biological data has suggested that tectonic processes can drive vicariant isolation and speciation in freshwater-limited taxa. Here we synthesise geological and biological evidence to demonstrate a composite geological and biological history for New Zealand's 290-km long Taieri River. Specifically, we assess evidence from structural geology and petrology, combined with phylogenetic and biogeographic analysis of galaxiid fishes, to show that the modern Taieri River was formed via capture of the ancestral Kye Burn during the mid-late Quaternary. Molecular dating analyses support a late-Quaternary timeframe for the geologically-mediated divergence between formerly-connected sister taxa *Galaxias depressiceps* and *G. 'teviot'*. Fish biogeography lends further support to the geological hypothesis, as there is a substantial biogeographic disjunction between the lower- (ancestral) and upper (captured) portions of the Taieri River. Geological and biological data are assessed independently yet yield consilient patterns and timeframes for the evolutionary events inferred. Broadly, this study highlights the interplay between physical and biological processes in a geologically dynamic setting.

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1. Introduction

One of the primary goals of biogeography is to understand the biological and physical processes underpinning the evolution and distribution of species around the globe (Briggs, 1995; Lomolino et al., 2005; Gillespie et al., 2012). Freshwater systems represent particularly fertile systems for studying interactions between geological processes (Bishop, 1995) and biological evolution (Mayden, 1988; Bănărescu, 1990). Specifically, freshwater-limited populations tend to have relatively restricted geographic ranges (McDowall, 1990; Berra, 2001; Leathwick et al., 2008), are particularly prone to vicariant isolation (Mayden, 1988; Matthews, 1998; Near and Keck, 2005; Burridge et al., 2006; Kozak et al., 2006) and often exhibit contrasting levels of genetic divergence within and among catchments (Avise et al., 1987; Ward et al., 1994; Avise, 2000; DeWoody and Avise, 2000). Indeed, genetic analyses from several parts of the globe have recently revealed tight links

between landforms and associated freshwater biotas [e.g. (White et al., 2009; Goodier et al., 2011; Schwarzer et al., 2011; Gottscho, 2015)].

New Zealand is a geographically isolated and geologically dynamic region that presents a particularly informative setting for assessing relationships between geological history and biological evolution (Fleming, 1979; Goldberg et al., 2008; Wallis and Trewick, 2009; Heenan and McGlone, 2012). The country's recent history of tectonic uplift has had particularly profound evolutionary effects on freshwater-limited taxa (Wallis and Trewick, 2009). In particular, phylogeographic studies of New Zealand's freshwater species have revealed numerous cases of population fragmentation, with strong regional cladogenesis within and among taxa (Waters et al., 2001; Burridge et al., 2006; Apte et al., 2007; Craw et al., 2007a).

The evolution and biogeography of New Zealand's distinctive galaxiid fish fauna has interested scientists for decades (McDowall, 1970, 1990). In particular, the species-rich *Galaxias vulgaris* complex has an intriguing widespread biogeographic distribution in South Island, spanning no fewer than 40 distinct catchments. While the group was once considered to represent a paraphyletic assemblage formed via multiple convergent losses of marine dispersal ability (Allibone and Wallis, 1993; Waters and Wallis, 2001a), it now seems

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likely that this radiation has a monophyletic freshwater origin (Waters et al., 2010), and that its biogeographic history has been shaped by river drainage evolution (Waters et al., 2001; BurrIDGE et al., 2008b).

Phylogenetic and statistical phylogeographic methods present powerful tools for reconstructing histories of recent-evolved species assemblages (Avisé, 2000; Lemey et al., 2009). Such approaches can potentially be used to unravel biogeographic histories [e.g. (Funk et al., 1995; Shaw, 1996; Hewitt, 2000; Juan et al., 2000; Picard et al., 2008; Wallis and Trewick, 2009)], including inferences of ancestral taxon ranges, and the timings of dispersal and vicariant events. In the case of New Zealand's species-rich *G. vulgaris* complex, links between earth-history and freshwater biogeography are compelling (Waters et al., 2001; BurrIDGE et al., 2008b). While detailed phylogeographic reconstructions of ancestral ranges for this assemblage have yet to be undertaken, extant species distributions alone suggest that the complex likely has an origin in southern South Island (Fig. 1), as the region boasts relatively high species-diversity (Allibone et al., 1996; McDowall and Wallis, 1996; McDowall, 1997; Wallis et al., 2001; Waters and Wallis, 2001b). McDowall and Wallis (McDowall and Wallis, 1996), for instance, suggested that the Canterbury lineage (to the north) "may be derived from one of the southern forms ... by dispersal north from the Taieri or Clutha". This 'out of the south' scenario is also supported by regional contrasts in levels of allozyme (Wallis et al., 2001) and mtDNA (Waters and Wallis, 2001b) variation, with consistently higher genetic diversity found in southeastern South Island (Otago) populations.

Robust inferences regarding the role of geological processes in shaping biological phenomena rely on independent (non-circular) assessment of biological and geological evidence (Bishop, 1995). Previous structural geological analyses of central Otago have suggested that the region has a complex tectonic history that has driven substantial changes in drainage geometry from Miocene to present (Youngson et al., 1998; Craw et al., 2012; Upton et al., 2014). Similarly, the comparatively high species diversity of Taieri River *Galaxias* suggests a complex biogeographic history. We hypothesise that the 290 km-long Taieri River (Fig. 1a) has a composite history, reflecting mid-Quaternary uplift and associated river capture events. Here we synthesise existing geological and biogeographic data, and present new analyses, to elucidate the history of the Taieri River and test the hypothesis that drainage reversal has shaped fish biogeography and cladogenesis.

2. Geological setting

2.1. Initial development

The Otago region of southern South Island, New Zealand (Fig. 1a,b) has a dynamic geological history. The basement rocks are Mesozoic schist and greywacke, and the area of interest for this study occurs entirely on the schist (Fig. 1a,b). Regional uplift of the basement rocks from beneath the sea began in the late Cenozoic (~23 Ma) with the inception of a new tectonic plate boundary, the Alpine Fault (Fig. 1a inset; (Cooper et al., 1987; Sutherland, 1995; Landis et al., 2008)). Uplift of mountains and hills was initially accompanied by Miocene volcanism at the east coast (Figs. 1b and 2; (Coombs et al., 1986; Hoernle et al., 2006)). Localised subsidence resulted in development of a large lake complex, Lake Manuherikia, during the middle Miocene (Fig. 2; (Douglas, 1986; Marsaglia et al., 2011; Upton et al., 2014)).

In the Pliocene, debris from rising mountain ranges filled the lake to create a broad braided river plain that drained to the ancestral Clutha River (Fig. 2; (Douglas, 1986; Youngson et al., 1998; Craw et al., 2012; Upton et al., 2014)). This debris was dominated by greywacke

from ranges to the northeast (Figs. 1b and 2). Paleocurrent indicators within these remnants confirm the south to southwestward drainage of that time (Fig. 2; (Youngson et al., 1998)).

2.2. Quaternary drainage reorientation due to folded schist mountain uplift

The schist basement of the Otago region, including the Taieri River catchment, has a strongly developed planar schistosity that is generally nearly horizontal. This pervasive structural feature constitutes planes of weakness in the rock that permit the rock to fold during compressional deformation. Ongoing deformation associated with the Alpine Fault during the Quaternary has resulted in development of broad open folds of this schistosity to form anti-form (upfolded) mountain ranges with intervening synform (downfold) valleys, with a wavelength of ~20 km (Figs. 1a,b; 2; 3a; (Landis et al., 2008)). Faults have developed in tighter portions of these folds (Fig. 3a; (Jackson et al., 1996; Bennett et al., 2005, 2006)). Initiation of the rise of these mountain ranges has been dated to the middle Quaternary (~1 Ma) via cosmogenic analysis, allowing estimates of uplift rates (Bennett et al., 2005, 2006). These structures are still active, and several active faults occur along their margins (Turnbull, 2000; Forsyth, 2001).

2.3. Evolution of the Taieri River catchment

The most important features constraining the geometry of the Taieri River are the three antiformal fold ranges that define what is now the upper Taieri catchment: South Rough Ridge, Lammermoor Range, and Rock & Pillar Range (Figs. 1a; 2; 3a,b). The Rock & Pillar Range has developed at the edge of the pre-existing Miocene uplift zone, and the other two ranges have developed from beneath the Pliocene river plain. An additional antiformal range, North Rough Ridge, has grown and impinged on to South Rough Ridge, and an adjacent range is currently emerging through the sedimentary cover to the northeast of South Rough Ridge (Bennett et al., 2005, 2006). The Lammermoor Range, which is oriented at a high angle to the other ranges, has been controlled by a fault, the Teviot Fault, on its southwestern margin (Figs. 1b and 3a). This fault, which locally controls the Clutha River course, is an old basement structure that became reactivated in the late Cenozoic (Turnbull, 2000; Craw et al., 2012; Upton et al., 2014).

Growth of the antiformal fold mountains in the middle Quaternary was responsible for the formation of the present Taieri River drainage geometry. In particular, the rising South Rough Ridge, Lammermoor Range, and Rock & Pillar Range blocked the southward flow of a major Clutha River tributary, the Kye Burn (Figs. 1a; 2; 3a). As a result, this river was diverted to the southeast, into the ancestral Taieri River catchment, where it has since cut a deep gorge in that paleodivide, through a layer of Miocene lava flows and underlying schist basement (Fig. 3a). At the same time, the former middle reaches of the ancestral Kye Burn (now the upper Taieri) had their direction reversed, now flowing northeast along the edges of the growing Rock & Pillar Range before falling through the new gorge to the south (Fig. 3a). More locally, a previously southwest flowing stream at the southern end of South Rough Ridge became captured by northeast flowing Deep Creek (Taieri; Fig. 3a,b).

2.4. Taieri River catchment evolution in a wider context

A drainage reversal event similar to that of the Taieri River described in the previous section, occurred in the middle reaches of the ancestral Ida Burn (west of the Kye Burn) (Fig. 1a). This reversal occurred as a result of growing antiformal fold ranges to the west of

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