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# BRIDGING THE ''BEECH-GAP'': NEW ZEALAND INVERTEBRATE PHYLOGEOGRAPHY IMPLICATES PLEISTOCENE GLACIATION AND PLIOCENE ISOLATION

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*Abstract.*—The existence of areas of lower endemism and disjunction of New Zealand biota is typified by *Nothofagus* beech trees (hence ''beech-gap'') and have been attributed to a variety of causes ranging from ancient fault-mediated displacement (20–25 million years ago) to Pleistocene glacial extirpation (<1.8 million years ago). We used cytochrome oxidase I and 12S mtDNA sequence data from a suite of endemic invertebrates to explore phylogeographic depth and patterns in South Island, New Zealand, where the ''beech-gap'' occurs. Phylogeographic structure and genetic distance data are not consistent with ancient vicariant processes as a source of observed pattern. However, we also find that phylogeographic patterns are not entirely congruent and appear to reflect disparate responses to fragmentation, which we term ''gap,'' ''colonization,'' and ''regional.'' Radiations among congenerics, and in at least one instance within a species, probably took place in the Pliocene (2–7 million years ago), possibly under the influence of the onset of mountain building. This orogenic phase may have had a considerable impact on the development of the biota generally. Some of the taxa that we studied do not appear to have suffered range reduction during Pleistocene glaciation, consistent with their survival throughout that epoch in alpine habitats to which they are adapted. Other taxa have colonized the beech-gap recently (i.e., after glaciation), whereas few among our sample retain evidence of extirpation in the most heavily glaciated zone.

*Key words.*—Alpine Fault, Insecta, invertebrates, mitochondrial DNA, Onychophora, vicariance.

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The last two decades have witnessed the renaissance of biogeography in the form of phylogeography (Avise et al. 1987) and placed it once more at the center of evolutionary debate (Riddle 1996; Avise 1998). Phylogeographic data have proven effective in the development of biogeographic scenarios (e.g., Thorpe et al. 1994; Schneider-Broussard et al. 1998), testing geologically based hypotheses (e.g., Barendse 1984; Bowen et al. 1989; Holder et al. 1999; Lessios et al. 1999) and revealing hitherto cryptic pattern (e.g., Avise 1992; da Silva and Patton 1998; Barrowclough et al. 1999).

Several northern hemisphere phylogeographic studies have focused upon the role of Pleistocene climate change on organismal distribution (Zink 1996; Soltis et al. 1997; Taberlet et al. 1998; Hewitt 1999; Demboski and Cook 2001). This work has demonstrated that the assembly of modern biotas to a large extent results from range expansion into denuded areas from refugia at the start of the current interglacial (~14,000 years ago). These biologically recent patterns overlie those deriving from ancient tectonic activity (Ball 1976; Nelson and Rosen 1981), seen by many vicariance biogeographers as the principal explanation for major distribution patterns (Wiley 1988; Craw et al. 1999). In particular, Southern Hemisphere intercontinental distribution patterns are often attributed to tectonic break-up of Gondwana, and this thesis has been extended to regional patterns where biotic distributions are, it is argued, congruent with fault-mediated displacement of terranes (Craw 1988; Heads 1989, 1999).

New Zealand's oceanic isolation (>70 million years (my)), relatively large land area (269,000 km$^2$), and dynamic geological history (including volcanism, tectonics, marine inundation, climate change) render it an interesting but challenging system in which to study the relationship of distribution pattern and process (Fleming 1979). It provides an excellent forum in which to contrast the roles of ancient and recent processes and to undertake comparisons with northern hemisphere systems.

Areas within New Zealand are characterized by markedly different levels of biodiversity and endemicity of the extant biota, and the origin of this diversity has long been the subject of speculation (Cockayne 1926; Willet 1950; Wardle 1963; Burrows 1965; Dumbleton 1969; McGlone 1985; Craw 1988; Rogers 1989). Endemicity is high in northern North Island (NI), northern South Island (SI) and southern SI, and low in southern NI and central SI (Wardle 1963) (approximate boundaries shown in Fig. 1). In SI, the central zone of low endemicity coincides with a gap (disjunction) in the distribution of many species (Burrows 1965; Heads 1998). This zone is particularly evident from the distribution of species of southern beech (*Nothofagus*), hence the general term: ''beech-gap.'' Alternative explanations for this biogeographic feature are exemplified by two contrasting hypotheses. Early commentators (e.g., Cockayne 1926; Willet 1950) proposed that Pleistocene climate extremes, glaciation, and glacial outwash extinguished many taxa in the narrow waist of SI (Fig. 2). Although on a different spatial scale, the glacial hypothesis is analogous to glaciation in the Northern Hemisphere, the biological effects of which have been well documented (e.g., Taberlet et al. 1998; Hewitt 1999, 2000). More recently, a panbiogeographic explanation for biogeographic patterns has been advanced which relates distributions of biota to tectonic movement of geological terrains (Heads 1989, 1998) (Fig. 1). These paradigms have been applied to North Island, although the delineation of zones is less precise (Rogers 1989).

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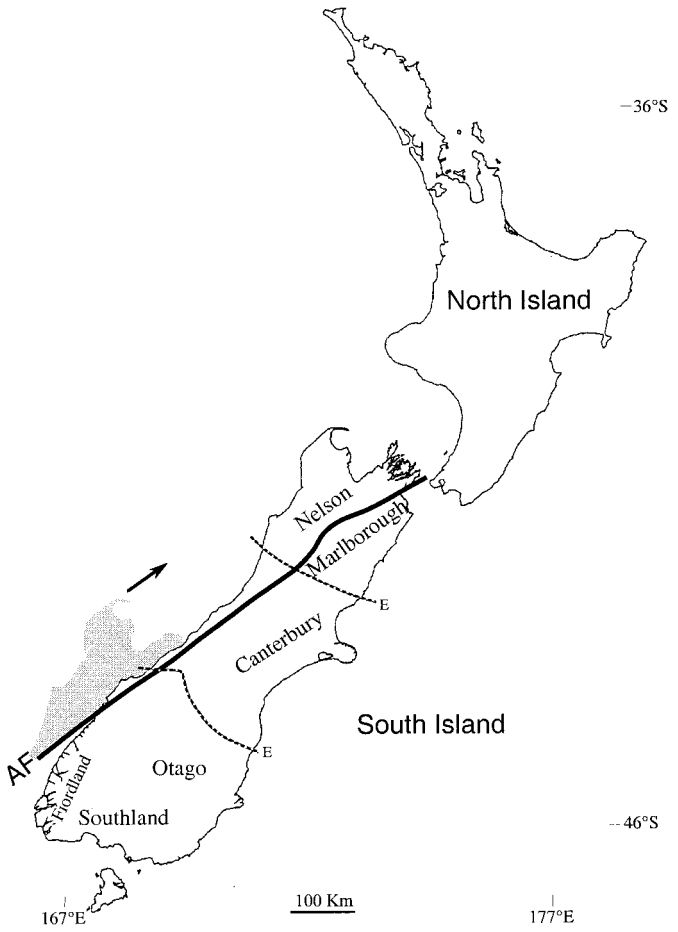


FIG. 1. Map of New Zealand showing the two principal islands, biogeographic regions of South Island, approximate position of the Alpine Fault (AF, bold line). The dashed lines (E) indicate the northern and southern limits of the central zone of low endemicity as identified by Wardle (1963). A ''shadow'' of the Nelson region indicates approximate relative positions of the Australian and Pacific tectonic plates about 25 mya (after Kamp 1992).

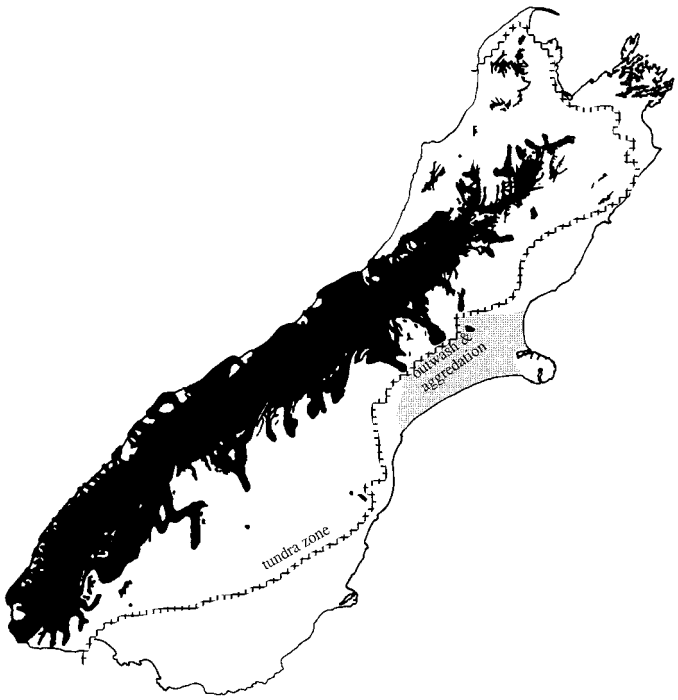


FIG. 2. South Island indicating in black the approximate maximal extent of Pleistocene glaciers (redrawn from Pillans et al. 1992). Stippling indicates the area most significantly affected by glacial outwash and aggredation (after Fleming 1979) and the crosshatched line indicates the hypothesized boundary of the tundra zone (after Willett 1950).

### *Contrasting Hypotheses*

The two hypotheses (glacial and Alpine Fault) make quite different predictions about the phylogeographic relationships of New Zealand taxa. Under the glacial hypothesis, disjunct sister taxa ought to be young (i.e., closely related, recent coalescence), perhaps as little as 100,000 years ago (the approximate start of the last glaciation). Splits between Nelson and Southland/Otago taxa might be marginally older than 1.8 my if they resulted from an early glacial cycle or if they reflected clinal diversity that existed prior to the Pleistocene by virtue of geographic distance. Genetic divergences between sister taxa in the neighboring Nelson and Marlborough areas would not be expected to be consistently deeper, than divergences between Nelson and Southland/Otago. With this time scale (~1.8 my), it is feasible that disjunct taxa (lineages) would be paraphyletic, or even polyphyletic, through retention of ancestral molecular diversity. Recolonization of the gap could follow the retreat of glaciers from one or both major refugia (north and south).

Under the Alpine Fault scenario, disjunct and endemic organismal distributions should be much older. Heads (1998) proposed that shearing of rock terrains at the contact of the Pacific and Australasian continental plates (along the Alpine Fault) displaced incumbent biotic assemblages. If the displacement of terrains, amounting to about 480 km in 20–25 my (Kamp 1992) as given by Heads (1998), caused a vicariant event in the biota, we would expect genetic divergences and very probably taxonomy to reflect this deeper time. This situation would still apply even if a large proportion of the movement occurred over the last 11–16 my, as has been suggested recently (Sutherland 1994, 1999). Regional biotas should be monophyletic, taxa in the disjunct regions (i.e., Nelson vs. Southland/Otago) should be sisters, and taxa on either side of the fault in northern South Island (i.e., Nelson and Marlborough) should be the most deeply diverged (>25 million years ago (mya)), as these would have been separated the longest (see Fig. 1). Such patterns should be congruent among taxa and would suggest that biological dispersal was insufficient to counter the pace of geological movement (Heads 1998; Wallis and Trewick 2001).

Our molecular phylogeographic approach to examining patterns of organismal distribution and relationships enables us to identify, and estimate the timing of, phylogenetic splitting events among regional samples (Avise 1992). Information of this type enables us to test predictions about phylogenetic patterns made a priori and derived from the alternative hypotheses. The use of pairs of taxa with disjunct distributions (in the manner of Heads 1998) provides genetic distances to estimate likely times of divergence and thus goes

some way towards testing the alternative hypotheses. The difference in timing between the two events is between one and two orders of magnitude, allowing distinction using even a sloppy molecular clock. However, important information is also gained by examining phylogenetic pattern, therefore we have sampled taxa widely in South and North Islands. To do otherwise could also result in paralogous comparisons with consequent overestimation of divergence. Our approach is to construct phylogenies using molecular data obtained from a suite of endemic invertebrate taxa comprising a range of taxonomic affinities (congenerics and conspecifics), distribution patterns, and ecological characteristics. These taxa are an essentially random sample that provide taxonomic replicates to assess phylogenetic congruence and timing of coalescence to distinguish recent glacial events from ancient tectonic displacement.

## Methods

### *Approach*

We consider contrasting predictions derived from two alternative hypotheses for the distribution patterns reported from South Island New Zealand: (1) Pleistocene glacial extirpation and (2) Alpine Fault vicariance. (1a) Taxa in Nelson and Otago/Southland not necessarily disjunct (northwest and south) or sisters; (1b) Taxa in Nelson (northwest) and Marlborough (northeast) usually sisters; (1c) Molecular clock indicates northwest/south splits less than 1.8 mya (much less than 25 mya); and (2a) Taxa in Nelson and Otago/Southland disjunct (northwest and south) and always sisters; (2b) Taxa in Nelson (northwest) and Marlborough (northeast) not sisters. Marlborough lineages a sister group to all others; (2c) Molecular clock indicates northwest/south splits up to 25 mya.

### *Taxa*

Our sample comprises flightless, endemic invertebrate taxa that inhabit a broad range of environments, from decaying forest logs to alpine scree. Ten endemic genera were surveyed: eight insects and two onychophorans. The eight insect genera included five orthopterans, two coleopterans, and one blattoidean across six families. At least 43 species were included in the analyses.

*Ooperipatellus* (Onychophora: Peripatopsidae). Egg-laying peripatus with two species described (Ruhberg 1985); most common in South Island where it inhabits decaying forest logs and moss predominantly west of the axial mountain ranges.

*Peripatoides* (Onychophora: Peripatopsidae). Live-bearing peripatus found in North and South Islands. The South Island fauna includes one described species that also occurs in North Island (Trewick 1998) and at least three other taxa (Trewick 1999, 2000). These peripatus have been found in decaying logs, under stones, and among detritus of forest/scrub and grassland but are scarce in the axial mountains and the west.

*Lyperobius* (Coleoptera: Molytinae). Weevils: 16 species mostly occurring with speargrasses and other endemic Apiaceae (Craw 1999). All but two of the species have relatively restricted ranges in South Island. The exceptions are an offshore island endemic and *L. huttoni* that occurs primarily in northeastern South Island plus a site in south North Island.

*Mecodema* (Coleoptera: Carabidae). Carabid beetles: about 58 endemic species (Britton 1949; Townsend 1971) distributed in a wide range of habitats. The majority of species (~41) occur only in South Island. Some species are localized but others are widespread and sympatry of several species is common.

*Celatoblatta* (Blattariae: Blattidae). Cockroaches: 13 described endemic species, with the genus represented through most of New Zealand (Johns 1966). Most are habitat specific and localized (e.g., *C. quinqemaculata* among stones in the subalpine-alpine zone); some are widespread (e.g., *C. vulgaris*).

*Alpinacris* (Orthoptera: Acrididae). Grasshoppers: two endemic species that are disjunct with respect to one another and present on both sides of the fault (Bigelow 1967). *Alpinacris tumidicauda* occurs in Otago and Fiordland and *A. crassicauda* in Nelson. Both occupy subalpine and alpine tussock grasslands. *Alpinacris* was given as an example of Alpine Fault disjunction by Heads (1998).

*Paprides* (Orthoptera: Acrididae). Grasshoppers: two endemic species that are disjunct with respect to one another. *Paprides dugdali* is known from Otago and Southland, and *P. nitidus* occurs on both sides of the fault and some way into the beech-gap from mid-Canterbury north (Bigelow 1967). Both species occupy subalpine tussock grasslands.

*Deinacrida* (Orthoptera: Anostostomatidae). Giant weta (king crickets): species occupy distinct habitats and most have very localized distributions in modern New Zealand, although the scree weta, *D. connectens*, occurs in alpine sites throughout South Island (Trewick et al. 2000). A recently described pair of species occurs on either side of the Alpine Fault with *D. pluvialis* distributed along the axial southern alps to the east of the fault and *D. talpa* restricted to a mountain range on the north west of the fault (Gibbs 1999). This distribution has been cited as a possible example of Alpine Fault disjunction (Gibbs 2001).

*Hemideina crassidens* (Orthoptera: Anostostomatidae). Tree weta: one of several species of large, tree-hole dwelling crickets. Distributed throughout lower North Island, and in Nelson, northern Marlborough, and the west coast of South Island.

*Talitropsis sedilloti* (Orthoptera: Raphidophoridae). Cave weta: a small, widespread species found throughout North and South Islands living in tree-holes and logs in forested areas.

### *Molecular Techniques*

Following euthanasia with ether, muscle tissue (generally from a leg) was removed and stored at −80°C or used immediately. DNA was extracted using a salting-out method (Sunnucks and Hales 1996). Tissue was macerated and incubated with 5 μl of 10 mg/ml proteinase-K in 600 μl of TNES buffer (20 mM EDTA, 50 mM Tris, 400 mM NaCl, 0.5% SDS) at 50°C; 10% 5 M NaCl was added and the extractions shaken vigorously for 20 sec followed by spinning at 14,000 rpm for 5 min. The supernatant was removed and precipitated with an equal volume of cold 100% ethanol.

DNA was collected by spinning and washed with 70% ethanol, then dried and dissolved in water.

Molecular analysis used DNA sequences obtained using primers that target part of the mitochondrial gene cytochrome oxidase I (COI). These primers are known to be highly conserved and applicable to a wide range of invertebrate taxa (Lunt et al. 1996). COI has been successfully utilized in intra- and interspecific studies of many invertebrates (e.g., Szymura et al. 1996; Zhang and Hewitt 1996; Funk 1999, Trewick et al. 2000). Either of two pairs of primers were used to amplify fragments of COI: C1-J-1718 and C1-N-2191 or C1-J-2195 and L2-N-3014 (Simon et al. 1994). Part of the mt 12S rRNA gene was also amplified in cases of ambiguity (see Results) using SR-N-14588 and SR-J-14233 (Simon et al. 1994). PCRs were performed in 25 μl volumes (200 μM dNTPs, 2.5 mM $MgCl_2$, 0.25 U Qiagen Taq) with 40 cycles of 94°C for 15 sec, 50°C for 30 sec, and 72°C for 90 sec with an initial denaturation of 94°C for 60 sec. PCR products were either gel-purified using Qiaquick spin columns (Qiagen, Venlo, The Netherlands) or cleaned directly using High Pure purification columns (Roche Diagnostics, Mannheim, Germany). Cycle sequencing used Bigdye chemistry (Perkin Elmer, Wellesley, MA) following the manufacturer's protocols using primer C1-N-2191, C1-J-2195, or SR-N-14588, as appropriate. Sequences were aligned manually using SeqEd. Vers. 1.0.3 (ABI, PE). Distance estimation and phylogenetic analysis were performed using PAUP* 4.0b4 (Swofford 1998). Character evolution was assessed using McClade Vers. 3.07 (Maddison and Maddison 1997). All primers used were sourced from the insect primer set (John Hobbs, Univ. of British Columbia).

Sequences were grouped and aligned by genus or species and checked for frame shifts, stop codons, and amino acid substitutions (COI, Lunt et al. 1996), and patterns of base substitution frequency and inferred secondary structure (12S, Hickson et al. 1996). Sequences were analyzed group by group using maximum-parsimony (MP) and neighbor-joining (NJ) as implemented by PAUP* 4.0b4 (Swofford 1998). In each case, bootstrap resampling using 500 replicates was employed to assess the degree of support for nodes. For each group, analyses were repeated using various weighting regimes (ti:tv, codon position). However, the networks presented are those derived from MP bootstrap analyses using unweighted data, because support for the nodes of interest was not improved by the use of other schemes. Unweighted MP has the added advantage that the edge lengths and scale bars are proportional to absolute numbers of substitutions. Permutations of alternative nucleotide substitution and among-site rate variation models (I—invariable sites and Γ—gamma distribution) were assessed by comparing likelihood scores for a suite of models in order to achieve the best compromise between parameter richness and likelihood scores as in Trewick et al. (2000). However, most distance estimates presented here are based on the widely used Kimura 2-parameter (K2p) model. Where necessary we include details of distance estimates based on substitution models that are expected to be more accurate for deeper divergences. In networks, deeply divergent lineages (e.g., *Deinacrida*) are retained in order to provide comparison with species pairs of particular relevance (e.g., *D. talpa* and *D. pluvialis*). Details of numbers of haplotypes sequenced and taxonomy are given in networks (Fig. 3). All sequences have been deposited at Genbank.

## Results

Cytochrome oxidase I (COI) sequences were obtained from multiple individuals within each taxon, collected from a range of sites. In addition, 12S sequences were obtained from *Alpinacris* and *Paprides* grasshoppers. As is typical with COI sequences, our data showed high AT bias (in particular at 3rd codon positions) and a strong bias in the distribution of substitutions among codon positions (Table 1). Third codon positions accrued the majority of all inferred substitutions (80–88% in our interspecific comparisons), similar to levels reported from other insects (e.g., 86% in phasmida, Sandoval et al. 1998; 80% in coleoptera, Caccone and Sbordoni 2001). However, we found that only between 43% (*Lyperobius*) and 55% (*Mecodema*) of all 3rd codon positions were variable, compared to higher proportions in other studies (e.g., >85% in collembola, Frati et al. 2000). This suggests that although some of our datasets will contain 3rd codon sites that have had multiple substitutions, there are others that are unchanged but are free to vary. As has previously been reported from studies of invertebrate cytochrome oxidase (e.g., Brown et al. 1994), we found that ti:tv ratios were relatively low in several of our datasets, but down-weighting transitions in phylogenetic analyses did not improve resolution. Similarly, removing 3rd codon positions from phylogenetic analyses severely reduced signal. Even among those groups in our study that had low ti:tv ratios (see Table 1), the sequence divergences we encountered were markedly lower than those reported in many other interspecies studies (e.g., 16% in Lepidoptera, Brown et al. 1994; 18% in Coleoptera, Juan et al. 1995; 30% in Coleoptera, Stauffer et al. 1997; 20% in Phasmida, Sandoval et al. 1998). Comparisons of intergeneric data suggest that the effects of saturation become evident beyond divergences of about 13% (Szymura et al. 1996), and all of our K2p values were below this (Table 1). Thus, our data show the expected variation in substitution patterns among samples of different taxonomic range, but none appear to show characteristics indicative of extensive saturation.

*Ooperipatellus* (480 bp, 43 parsimony informative sites). Although statistically not well supported, there is phylogenetic evidence of north-south bipartition. The most extensively sampled lineage occurs across the Alpine Fault at its southern end. The average genetic distance among all lineages is 6.9% (max 11%). Genbank accessions AY042353–042359.

*Peripatoides* (540 bp, 77 parsimony informative sites). The South Island fauna comprises three well-supported clades. The geographic distribution of these taxa is consistent with Alpine Fault vicariance. However, the fact that genetic distances are as high among the Southland-Otago taxa as between either of these and the Nelson taxon is not predicted by fault vicariance. The average genetic distance among these lineages is 6.7% (max 11%). The highest genetic distances are between lineages of the Piano and Dunedin clades (Southland/Otago). Genbank accessions AF188222, 188223, 188241, 188244, 188245, 188247, 188248, 188250–188252, 188258, 18826–188262, 221452, 221454, 221458.

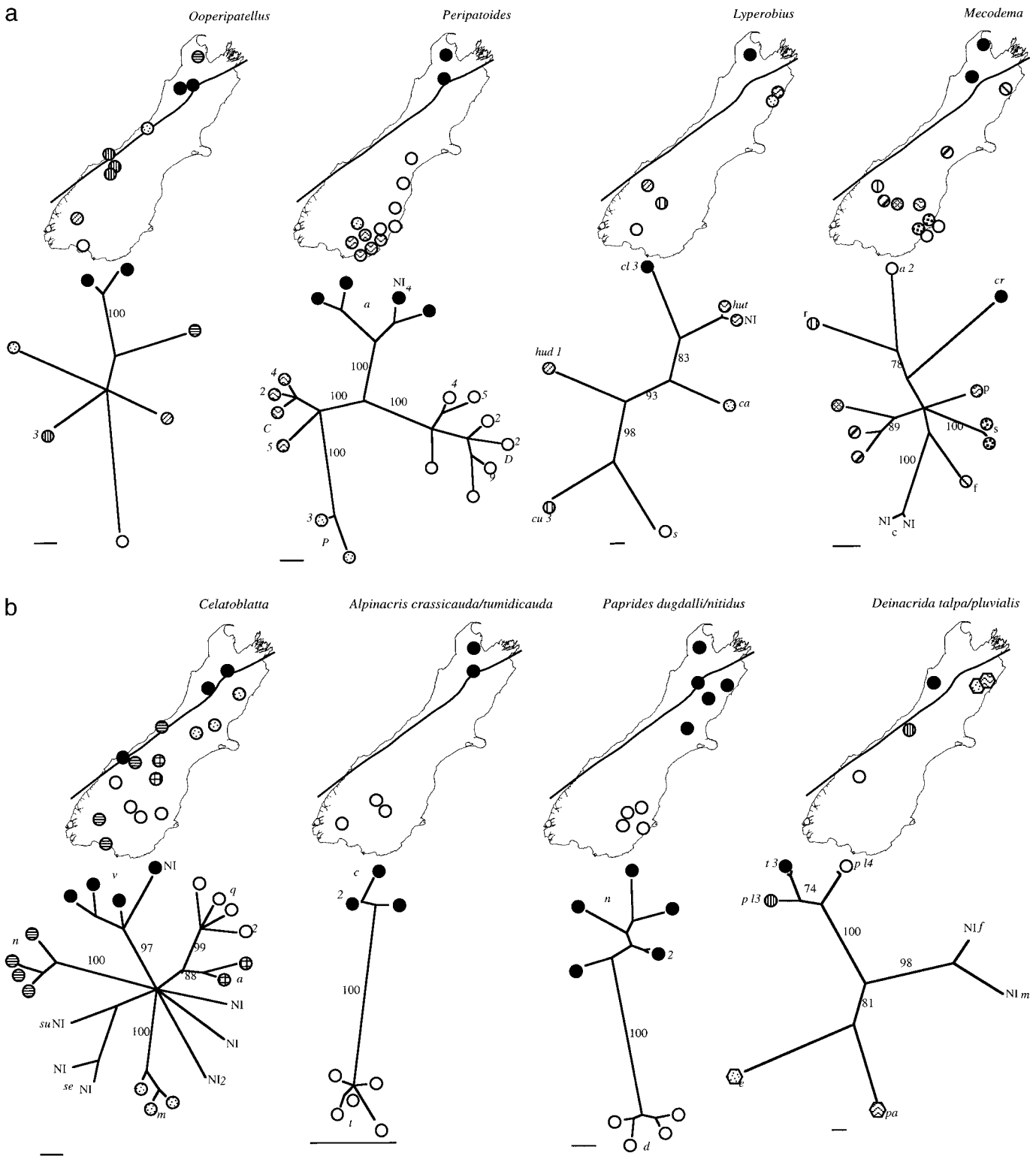


FIG. 3. MP networks and South Island distributions of endemic New Zealand invertebrates. Scale bar with each network indicates five changes. North Island taxa/populations are indicated by NI with no pattern code unless the taxon has also been sampled in South Island. Hexagons indicate outgroup taxa where applicable. In interspecies comparisons, each species is indicated by the first letters of its name, if known. Numbers at termini indicate haplotype frequency where more than one. Numbers on internal edges indicates percent support from 500 MP bootstrap replicates. *Peripatoides* (*aurorbis*, *C*atlins, *D*unedin, *P*iano); *Mecodema* (*alternans*, *crenicole*, *fulgidum*, *occiputale*, *punctatum*, *rugriceps*, *sculpturatum*); *Lyperobius* (*carinatus*, *clarkei*, *cupiendus*, *hudsoni*, *huttoni*, *spedenii*); *Celatoblatta* (*anisoptera*, *montana*, *notialis*, *quincemaculata*, *sedilotti*, *subcorticaria*, *vulgaris*); *Alpinacris* (*crassicauda*, *tumidicauda*); *Paprides* (*dugdali*, *nitidus*) lineages are coded by taxon. *Ooperipatellus* (*nanus*, *viridimaculatus*) and *Deinacrida* (*carinatus*, *connectens*, *elegans*, *fallai*, *mahoenui*, *pluvialis*, *parva*, *talpa*, *tibiospina*), *Hemideina* (*crassidens*, *trewicki*) and *Talitropsis sedilloti* are coded by lineage.

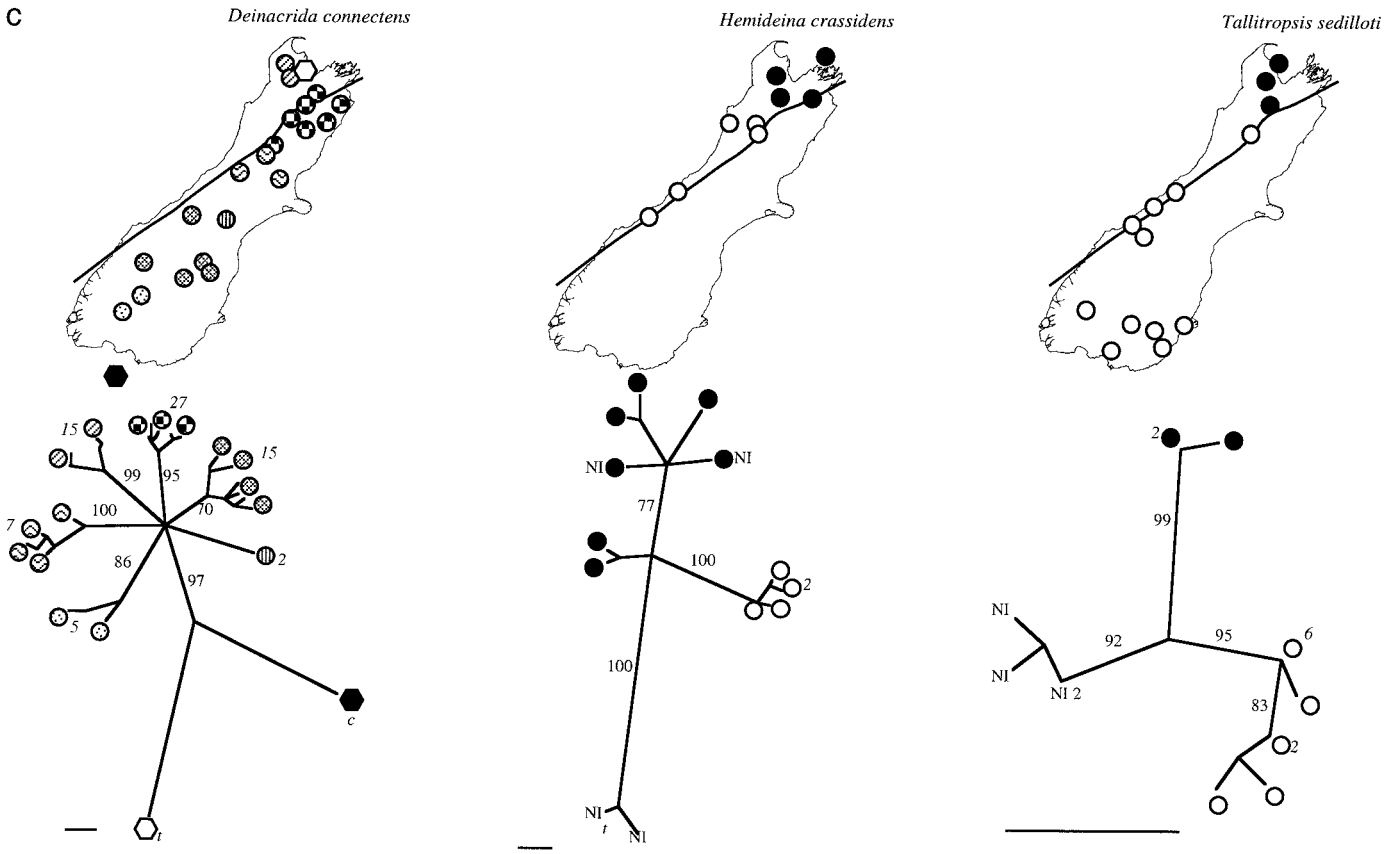


FIG. 3. Continued.

*Lyperobius* (640 bp, 69 parsimony informative sites). There is phylogeographic evidence for a north-south bipartition that crosses the fault and is therefore inconsistent with the fault hypothesis. Genetic distances are relatively high but are lower among northern and southern species respectively (average 6.7% and 8.7%) than between north and south species (12%). Genbank accessions AY042347–042352.

*Mecodema* (650 bp, 57 parsimony informative sites). Although only a small portion of this speciose genus was sampled (7–8 species), it is evident that this group radiated quite recently. There is no clear phylogeographic pattern among the haplotypes obtained. Genetic distance among these morphologically diverse beetles averaged 4.9% (max 7.7%). Genbank accessions AF320667–320674.

*Celatoblatta* (610 bp, 95 parsimony informative sites). This genus shows strong phylogeographic structure indicative of allopatric differentiation. Montane/scree species (e.g., *C. quincemaculata*) appear to be the most restricted, occupying

TABLE 1. Mitochondrial DNA sequence divergence (K2p) of ingroup haplotypes, estimated maximum time to coalescence based on a divergence rate of 2.3% per million years, and inferred phylogeographic pattern. Details of sequence length (Seq. bp), numbers of transitions and transversions (ti/tv), and estimated numbers of steps by codon position (codon) are given. Genus abbreviations: *D.*, *Deinacrida*; *H.*, *Hemideina*; *T.*, *Tallitropsis.*

| Taxon | Gene | Seq. bp | Ti/tv | Codon | Mean K2p % | Max. K2p % | ~Max. age my | Pattern |
|---|---|---|---|---|---|---|---|---|
| *Ooperipatellus* | COI | 480 | 60/26 | 12,2,105 | 6.9 | 11.0 | 4.8 | regional |
| *Peripatoides* | COI | 540 | 82/48 | 95,1,154 | 6.7 | 11.0 | 4.8 | regional |
| *Mecodema* | COI | 640 | 73/41 | 24,4,113 | 4.9 | 7.7 | 3.3 | regional |
| *Lyperobius* | COI | 650 | 103/35 | 21,4,169 | 9.9 | 12.7 | 5.5 | regional |
| *Celatoblatta* | COI | 610 | 136/50 | 51,3,217 | 5.9 | 8.5 | 3.7 | regional |
| *Alpinacris* | 12S | 370 | 16/7 | — | 3.6 | 6.0 | 2.6 | gap |
| *Paprides* | COI | 540 | 54/21 | 15,0,85 | 6.2 | 10.1 | 4.4 | gap |
| *Paprides* | 12S | 370 | 11/6 | — | 2.9 | 5.1 | 2.2 | gap |
| *D. talpa/pluvialis* | COI | 510 | 31/1 | 1,0,41 | 3.7 | 6.6 | 2.7 | colonization |
| *D. connectens* | COI | 540 | 122/15 | 13,1,44 | 4.8 | 8.1 | 3.5 | regional |
| *H. crassidens* | COI | 510 | 36/10 | 8,1,75 | 4.3 | 7.7 | 3.4 | colonization |
| *T. sedilloti* | COI | 480 | 15/4 | 5,0,16 | 1.2 | 2.8 | 1.2 | colonization |

particular mountain ranges. Lowland/forest species (e.g., *C. notialis*) occur more widely, including locations on both sides of fault. Average genetic distance among all taxa is 5.9% (max 8.5%). Maximum genetic distances within the species with the broadest sampled ranges were 2.7% (*C. notialis*) and 4.4% (*C. vulgaris*, including North Island). Genbank accessions AF320646–320656.

*Alpinacris tumidicauda*/*A. crassicauda*. We identified genus-specific nuclear copies of the COI gene in our data set of *Alpinacris* sequences. Phylogenetic analysis was performed including ambiguous (*N*) sites, but to confirm this phylogeny we also sequenced a portion of 12S. The 12S phylogeny had the same well-supported bipartition as COI. Genetic distances between *A. tumidicauda* and *A. crassicauda* averaged 3.6% (12S). The phylogeographic structure identified is consistent with separation by glaciation and movement on the fault (Heads 1998), but genetic distances indicate splitting occurred much too recently for the latter hypothesis. Genbank accessions AY042334–042338.

*Paprides dugdali*/*P. nitidus* (COI, 540 bp, 55 parsimony informative sites). Monophyletic *P. nitidus* bridge the Alpine Fault in Nelson/Marlborough, which is inconsistent with the fault hypothesis. The distribution of *Paprides* is disjunct north and south suggesting glacial separation. Mean genetic distances between the two species are 4.1% (12S) and 9.4% (COI). As expected, 12S appears to be evolving more slowly than COI. Genbank accessions AY041360–042369.

*Deinacrida pluvialis*/*D. talpa* (510 bp, 74 and 38 parsimony informative sites with and without outgroups respectively). The distribution of these two species is consistent with their separation by the Alpine Fault in that they occur on either side of it (Gibbs 2001). However, the presence of *D. pluvialis* in the gap and the low overall genetic distances suggest recent dispersal and speciation. Genetic distance between the two species is low (4.9%), and *D. pluvialis* is paraphyletic with respect to *D. talpa*. The geographically closest populations of the two species are also the genetically closest, 3.5% compared to 5.5% between the two *D. pluvialis* populations. This phylogeographic pattern suggests recent isolation of these populations with rapid adaptation to distinct habitats. Genbank accessions AY042339–042341.

*Deinacrida connectens* (540 bp, 87 and 76 parsimony informative sites with and without outgroups respectively). Pronounced phylogeographic pattern is evident from COI data with several regions of South Island bearing distinct lineages. Genetic distances among the lineages are low, example, 6.3% (Nelson vs. Marlborough) and 7.1% (Nelson vs. Southland/Otago; Trewick et al. 2000). No gap is apparent and lineages occupying the beech-gap area appear to share coalescence time with other lineages. Genbank accessions AF202586–AF202621.

*Hemideina crassidens* (510 bp, 68 and 42 parsimony informative sites with and without outgroup respectively). Two clades are supported comprising individuals distributed widely but contiguously west of the axial ranges. The northern clade includes NI individuals. The southern, west coast clade has very low intraclade genetic distances (averaging 0.8%), compared to those between this clade and other conspecifics which average 6%. Phylogeographic structure and genetic distances suggest recent colonization of the gap, and this ''colonizer'' status is consistent with *H. crassidens* distribution in southern North Island and north and western South Island (Trewick and Morgan-Richards 1995). Genbank accessions AY042342–042346.

*Tallitropsis sedilloti* (480 bp, 11 parsimony informative sites). This species shows minimal phylogeographic structure with lineages distributed across the fault. Maximum genetic distances among haplotypes (North and South Islands) are 3.5%. Genetic distances among haplotypes in the lower three-fourths of South Island average 0.4% (max 1.0%). Genbank accessions AF320679–320687.

## Discussion

### *Timing*

Estimates of mtDNA molecular divergence rates vary (1.4% per my, Knowlton and Weigt 1998; 2.0%, Brown et al. 1979; 2.3%, Brower 1994. Generalized rates average among genes and parts of genes (e.g., domains, loops and helices, codon position) and it is recognized that rates may vary among taxa (e.g., Crozier et al. 1989). However, the principle of a local molecular clock is well founded and estimations based on it provide a valuable, if crude, indicator of divergence times (Fleischer et al. 1998). The rate of 2.3% sequence divergence per million years was derived from arthropod taxa (mostly insects) and applied to COI and COII data from butterflies (Brower 1994). It is therefore arguably the most appropriate rate for the present study. We applied the 2.3% divergence rate to our data using the maximum K2p genetic distances obtained for each taxon (Table 1). The oldest estimated coalescence time we found was 5.5 mya using K2p or about 7.2 mya using GTR+I (among the *Lyperobius* weevils). Alternatively, when we applied a nonlinear calibration (as in previous studies of insects with cytochrome oxidase data; Juan et al. 1995, 1996; Sandoval et al. 1998) to our *Lyperobius* K2p distance, a coalescence time of about 7 mya was indicated. Only one taxon (*Tallitropsis*, 1.2 mya) gave divergences younger than Pliocene age (range of others 2.2–5.5 mya). However, molecular divergence between some lineages occupying the beech-gap and their sisters outside the gap were very low (*H. crassidens* $<1.2\%$, *T. sedilloti* $<0.9\%$, *C. notialis* $<2.7\%$). In these instances, genetic distances coupled with evidence from location and wide geographic ranges are consistent with colonization during or after the Pleistocene. Allowing for rate variation among taxa, and recognizing that coalesence of haplotypes precedes vicariance because of polymorphism, the consistent signal is for Plio-Pleistocene radiation and disjunction.

### *Phylogeographic Congruence*

We expect the timing and nature of historic processes that shaped the distribution of organisms to be manifest in the phylogeographic patterns observed in the invertebrate taxa we surveyed. Our predictions, based on the glacial and Alpine Fault hypotheses were for distinct phylogeographic patterns and depth, and congruence among these taxa. Congruence of pattern has generally been observed in studies over limited geographic areas (Avise 1992; Joseph et al. 1995), but not in continentwide studies (Zink 1996; Taberlet et al. 1998).

Three broad patterns were evident from the taxa surveyed, and we summarize these as ''gap,'' ''colonization,'' and ''regional'' (Table 1). These categories have the following features: gap, disjunction of northern and southern populations/species which have failed to reunite (e.g., *Paprides*); colonization, recently dispersing taxa that have closed the gap (e.g., *Talitropsis sedilotti*); regional, taxa with regionally distinct lineages whose phylogenetic relationships and genetic diversity do not appear to reflect any history of a gap corresponding to Pleistocene glaciation (e.g., *Deinacrida connectens*). None of the phylogeographic patterns that we observed were wholly consistent with ancient tectonic separation.

The existence of differing patterns may well reflect differences in life-history characteristics (ecology, vagility, fecundity) and thus gene flow among taxa, as well as persistence of heterogeneous environments throughout the Pleistocene. Inconsistency in the level of sampling among taxa has probably emphasized the perceived variation. For instance, we do not know whether the intraspecific phylogeography of *Mecodema* is indicative of the gap or colonization patterns. But, we note that the type of pattern observed is not restricted by taxonomic level (e.g., *Deinacrida connectens* and *Mecodema* spp. are both regional).

### *Alpine Fault Hypothesis*

The examples cited in support of the Alpine Fault hypothesis are mostly pairs of conspecific taxa (Heads 1998). This level of taxonomic distinction appears to us to be inconsistent with the time frame indicated by geology (as are a number of other aspects of the idea, Wallis and Trewick 2001). We would expect a greater number of sister species to have evolved into morphologically distinct taxa following such a prolonged independent history since the Oligocene ($\sim$25 mya). We feel that most of the examples given by Heads (1998) are more likely to represent more recently disrupted distributions or clines, either by alpine uplift 2–7 mya or by glaciation less than 1.8 mya. Our molecular data support that expectation. Phylogenetic patterns consistent with an ancient time frame (i.e., late Oligocene) have been identified in New Zealand birds (wrens, moa, and kiwi; Cooper and Cooper 1995) and may well be paralleled by some invertebrates (e.g., *Deinacrida*; SAT, unpubl. data), but no phylogeographic pattern has been identified at this depth.

Although there are instances where taxa in our sample have distribution patterns that fit with the Alpine Fault hypothesis (e.g., *Alpinacris*, which was cited as evidence for this by Heads 1998), the majority do not, and many strongly contradict the hypothesis (e.g., *Paprides*, *Lyperobius*). In no cases are genetic distances consistent with the Alpine Fault hypothesis, which would result in coalescence 20–25 mya. It is probable that the rate of lateral movement on the fault has not been constant since its inception ($\sim$25 mya), and allowing for acceleration indicates that most displacement occurred in the last 11–16 my (e.g. $\sim$38mm per year, Sutherland 1999). However, this date is still earlier than any of the coalescence times estimated from our dataset.

### *Glacial Refugia Hypothesis*

As noted above, the array of patterns observed in South Island and their lack of congruence is more similar to observations in continental situations (Europe, Comes and Kadereit 1998; Taberlet et al. 1998; Hewitt 1999; North America, Zink 1996) than regional systems (Gulf of Mexico, Avise 1992; Australian wet tropics, Joseph et al. 1995). Despite its comparatively small size, New Zealand maintained a broad habitat range throughout the Pleistocene. Pollen profiles indicate vegetational changes of a magnitude similar to continental regions (McGlone et al. 1993). Cooling (and in eastern areas drying) of the climate is thought to have resulted in general northward retreat of forest (Fleming 1979; Wardle 1963; McGlone et al. 1993). Grasslands expanded but forest remained in the north and remnants are thought to have persisted in many areas and on coasts (McGlone 1985). However, this relatively mild impact was offset where the steep slope and high precipitation ($>$10 m per year; Griffiths and McSaveney 1983) of the Southern Alps resulted in intense glaciation. This included the extension of west coast glaciers to the sea (Pillans et al. 1992), which even today extend to lower altitudes than any others in temperate regions. This diversity of physical conditions may explain the range of phylogeographic patterns we observe.

The glacial refugia hypothesis predicts that, to a greater or lesser extent, taxa will have colonized the 300 km gap since retreat of the ice. The gap has been closed by cave weta (*T. sedilloti*), which appears to have spread rapidly throughout SI and New Zealand generally, tree weta (*H. crassidens*), and lowland cockroaches (*C. notialis, C. vulgaris*) (low diversity). Relatively high sequence divergences in *H. crassidens* between west coast populations and those to the north, and between species pairs in *Paprides* and *Alpinacris*, probably result from sorting of lineages that predate the impact of Pleistocene glaciation (Hewitt 1999). Genetic diversity of beech (*Nothofagus*) itself also implies recent ($<$1 my) separation of Nelson and Southland populations (Stöckler and Lockhart 2000). In the absence of any environmental reason for lack of recolonization (Leathwick 1998), the genetic evidence suggests that the persistence of the gap relates to dispersal characteristics of beech, and this may be the case for other taxa. Other work on the montane/lowland *Galaxias vulgaris* suggests that this fish species has either closed the gap through the medium of unstable east-flowing braided rivers, or did not suffer complete glacial extinction (Wallis et al. 2001).

Other species have been less successful at dispersing widely. Most notable is *D. connectens* (on mountain tops) which shows high intraspecific diversity and pronounced phylogeographic structure (Trewick et al. 2000, Trewick 2001). In this case, haplotypes appear to have radiated in the Pliocene and persisted through the Pleistocene in discrete mountain range populations. Adaptation to the alpine zone presumably explains the high degree of phylogeographic structuring and is consistent with survival through the Pleistocene in rocky alpine environments in the vicinity of glaciers (arretes, ridges) and above glacier basins. Radiations of this type seem to have occurred in several plant groups (Wagstaff and Garnock-Jones 1998; Wagstaff and Wardle 1999; Breitwieser et al.

1999), and the notion of survival within glaciated regions through the Pleistocene has recently been advanced for Arctic flora (Abbot et al. 2000).

### *Patterns and Processes*

We made two contrasting sets of three predictions based on the (1) glacial and (2) Alpine-Fault hypotheses. Our data reveal that taxa in Nelson and Otago/Southland are *not* consistently sisters; taxa in Nelson and Marlborough *are* sisters, or equivocal; and dates of Nelson and Otago/Southland splitting events are *not* ancient. All of these are consistent with (1).

We therefore find no support for ancient Alpine Fault vicariance in the development of distribution patterns of endemic biota. The majority of examples given as evidence of Alpine Fault vicariance were intraspecific (Heads 1998), but it is among species, or even genera, that we would expect ancient vicariant disruptions to be apparent. Our data suggesting low genetic diversity within most species are consistent with our expectation.

Within genera and within at least one species, we find genetic diversity and phylogeographic pattern consistent with radiation during the Pliocene, perhaps in response to mountain building (Trewick et al. 2000). Older radiations do exist, for instance among *Deinacrida* (data not shown) but distributions of these taxa tend to show ecological rather than biogeographic patterns of distribution due in part to modern extirpation. Indeed, it is telling that the only species pair in this genus (*D. talpa, D. pluvialis*) that have a distribution that could be construed as consistent with the Alpine Fault hypothesis (Gibbs 2001) are the most closely related of all *Deinacrida*.

Glacial extirpation is a simple explanation for the absence of some taxa from the central region of South Island (Fig. 2). However, most of our date estimates are older than Pleistocene, falling within the Pliocene. This might be erroneous and result from marginal underestimation of the rate of molecular evolution or lineage sorting, or, it may reflect genuine timing of coalescence and thus indicate a third biogeographic explanation for the observed pattern. It is apparent that COI does have a higher mutation rate than 12S and other mitochondrial genes at some phylogenetic levels but we expect the use of the relatively high rate of 2.3% (Brower 1994) to compensate for this. Lineage sorting is likely to have featured in the history of at least some of the taxa that we studied, but if glacial extirpation were the major force in population structuring, it is more likely to have resulted in inconsistencies in timing estimates over the shorter time scale between glacials, as in some European examples (Hewitt 1999). Hence, our estimated coalescence times may corroborate the evidence of organismal distribution in correctly indicating that population structuring relates to Pliocene mountain building (Trewick et al. 2000).

A role in biogeographic structuring of mountain building has previously been mooted by McGlone (1985) who proposed that several aspects of New Zealand's post-Oligocene tectonic history were implicated in the development of biotic distribution patterns. In particular, he suggested that patterns of disjunction and endemism could be related to the persistence of diverse habitats at either end of South Island compared to extensive restructuring in the central area as mountains emerged. Our molecular data suggest that the most recent and extensive orogenic phase of the Pliocene (2–7 mya) probably did coincide with speciation and population structuring events. However, it cannot be determined whether absences in central South Island are the result of Pliocene or Pleistocene habitat destruction. The generation of novel habitats (notably the alpine screes) and potential barriers, following an extended period of altitudinal and climatic uniformity (Cooper and Millener 1993) appears to correlate with radiations in many groups of organisms (Winkworth et al. 1999). The presence of many of these taxa throughout the axial ranges of South Island suggests that glaciation did not destroy these habitats (Wardle 1963). From our study it appears that montane species such as *Deinacrida connectens*, *Celatoblatta quincemaculata*, and *C. montana* do, however, have strong phylogeographic pattern (at similar genetic distances) that reflect regional isolation on mountain ranges, whereas related lowland taxa (*Hemideina crassidens*, *Celatoblatta notialis*) have the colonizer pattern, suggesting the impacts of glaciation relate, not surprisingly, to ecology of the taxa concerned.

The ''beech-gap'' appears to be just one of several patterns and is most apparent from lowland intraspecific distributions. We expect the beech-gap to be most frequently evident among taxa with the least effective dispersal mechanisms. The tendency to identify and focus upon repeated pattern is an important feature of biological research, but one that has usurped the role of hypothesis testing among some biogeographers. It is clear that in South Island New Zealand, broad summaries of levels of endemism do indicate that there is a relative deficiency in the central zone and some taxa do show distinct disjunction across the same zone (notably *Nothofagus* beech). But, the listing of examples that show similar patterns (see Heads 1998) is of neither evidence of process nor perhaps even of a generalized pattern (Wallis and Trewick 2001). We would argue that the distribution of *Nothofagus* beech is an exemplar of just one of several types of pattern. The perceived importance of the beech-gap as a biogeographic feature may well reflect the relative congruence of such patterns in contrast to lack of congruence among many other taxa. Given the local intensity of glaciation in central South Island, it is striking that so many taxa do not show any evidence of lasting impact.

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