A female green foliage cicada, Kikihia ochrina. Photo by Dr. Chris Simon
711x976mm (72 x 72 DPI)

Word count for the MS (inclusive of abstract, text, and references): 6833

Estimate of the number of journal pages required by figures: 5

Figure 1: 8cm

Figure 2: 11cm

Figure 3ab: 17cm

cd: 17cm

e: 17cm

f: 17cm

Figure 4: 11 cm

Figure 5: 17 cm

Original Article: Phylogeography of six co-distributed New Zealand cicadas and their relationship to multiple biogeographic boundaries suggests a re-evaluation of the Taupo Line.

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Comparative Phylogeography of New Zealand's North Island

ABSTRACT

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Aim Comparative biogeographers question the extent to which co-distributed species respond similarly to environmental change. Such responses should create similar, appropriately timed patterns of cladogenesis among co-distributed taxa. Evolutionary independence—where taxa respond differently to environmental stimuli—limits the predictions that can be made for unstudied species. During the Pleistocene, forest species are hypothesized to have contracted into refugia during glacial phases and expanded into previously uninhabitable territory during interglacials, but non-forest dwellers may have experienced increased habitable areas. For all taxa, these shifts are hypothesized to be strongly influenced by regional variation in physiography and climate. Here we compare phylogeographic patterns across ecologically divergent, co-distributed taxa in the light of NZ's palaeohistory and test the significance of several proposed biogeographic boundaries.

Location North Island, New Zealand

Methods Mitochondrial DNA from six co-distributed cicada species (*Kikihia ochrina, K. cutora, K. laneorum, K. cauta, K. scutellaris* and *K. dugdalei*) were analysed using phylogenetic methods and molecular dating techniques. We analysed phylogeographic distributions using AMOVA to determine the significance of hypothesized biogeographic boundaries.

Results Five species (*Kikihia ochrina, K. cutora, K. laneorum, K. cauta,* and *K. scutellaris*) show various degrees of intraspecific concordance with biogeographic boundaries found in previously studied taxa – the Kauri Line, the Northland Line, and the NW-SE Line (identified here). Clade splits of forest species correlate with the Kauri Line and/or Northland Line, while splits of scrub/hill species correlate with the NW-SE Line. Four species (*Kikihia ochrina, K. cutora, K. laneorum,* and *K. cauta*) diversified before the last glacial maximum (LGM, 20,000 ya), while two species (*K. scutellaris,* and *K. dugdalei*) show only post-LGM diversification.

Main Conclusions Despite species idiosyncrasies, we see the imprint of shared palaeoclimatic/geological events. We distinguish between the importance of biogeographic lines as the demarcation between older genetically diverse and newer genetically depauperate populations versus the importance of lines as biogeographic boundaries between sister-clades. We also stress the importance of dating clade splits to ensure consistency with explanations for biogeographic lines in question. We suggest that

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the Taupo Line has been overemphasized as a biogeographic boundary while the importance of the NW-SE mountain axis has been overlooked.

Keywords

Cicadidae, Kauri Line, Last Glacial Maximum, New Zealand, Northland Line, Phylogeography, Taupo Line

INTRODUCTION

The existence of common phylogeographic boundaries for co-distributed species suggests that similar historical and/or ecological factors have determined their divergence and distribution. However, contact zones and phylogeographic clade splits within or among species do not always occur at the same geographic locations. Even closely related species can exhibit discordant distributional patterns suggesting different responses to a common geological history. For this reason, many taxa need to be explored to make valid predictions (e.g. Soltis *et al*., 2006; Spencer *et al*., 2006).

Here, we analyse mitochondrial phylogeographic patterning in six co-distributed species of North Island, New Zealand (NI, NZ) cicadas of the genus *Kikihia* and evaluate proposed biogeographic boundaries for this region (Fig. 1). We compare our results to previously published studies, and we discuss the interpretation and testing of biogeographic lines. Although many species are indeed idiosyncratic (Trewick *et al*., 2011), shared patterns can be found (Marske *et al.*, 2009). Previous NZ cicada work has mainly focused on specific species or species complexes with an emphasis on the SI (e.g. Buckley & Simon, 2007; Marshall *et al*., 2009; 2011). The current study is the first to tackle the phylogeography of the many co-distributed NI endemic *Kikihia* forest and shrub cicada species.

North Island forest and scrub cicadas of the genus *Kikihia*

Progenitors of two cicada lineages arrived in NZ in the mid Miocene (~14 Ma) (Arensburger et al., 2004) and began to diversify (Buckley *et al.*, 2002; Buckley & Simon, 2007; Marshall *et al.,* 2008; 2012). The six NI species examined here belong to the genus *Kikihia*, which is the largest NZ cicada genus and part of the larger of the two independent radiations.

Two of the focal species are known as “shade singers” because they often sing in the forest understorey [*Kikihia cauta* (Myers 1921)*, K. scutellaris* (Walker 1850)]. The remaining four species [*K.*

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ochrina (Walker 1858), *K. dugdalei* (Fleming 1984), K. *cutora* (Walker 1850), and *K. laneorum* (Fleming 1984)], known as the "green foliage" species, inhabit forest edges or shrub habitat. The *K. cutora* species complex has three described subspecies: *K. c. cutora* (Walker 1850), *K. c. cumberi* (Fleming 1973), and *K. c. exulis* (Hudson 1950) (the latter restricted to the Kermadec Islands) (Fleming, 1975). *Kikihia convicta* (Distant 1892), restricted to Norfolk Island, was described as a separate species but falls within the cutora species complex with high support [(Arensburger *et al.*, 2004); this study].

Geological history of NZ and mid-Miocene colonization

In the late Miocene, after the NZ cicada lineages had become established, substantial structural changes took place on NI including volcanism and the creation of mountains and basins and volcanism during the late Miocene (McGlone, 1985; Lewis *et al*., 1994). Strike-slip movement occurring throughout the Pliocene (5-2.6 Ma) eventually led to flooding from the north into the Taupo region (Lewis *et al.,* 1994; Bunce *et al*., 2009), creating a sea strait covering much of the southern half of the NI. The northern boundary of the strait moved progressively south during this epoch (Fig. 2). Mountain building continued throughout the Pliocene and Pleistocene (2.6-0.1Ma), with later uplift of the southern NI Axial Ranges about 340 Ka (TePunga, 1954; Rogers, 1989), accelerating in northern NI around 345 Ka, and again 50 Ka (Claessens *et al*., 2009). NZ cooled in the late Pliocene by 5-10°C (Lee *et al.*, 2001) from late Pliocene to Pleistocene. The late Pleistocene was characterized by extreme cycles of warm and cold periods, occurring about every 100,000 years (Carter & Gammon, 2004). Accompanying low temperatures, increased aridity, and dramatic vegetational shifts resulted in uninhabitable areas of the NI for many lineages during each glacial advance (Burge & Shulmeister, 2007; McGlone *et al.*, 2010). In addition, the central NI (centred at the Taupo Volcanic Zone, TVZ) was affected by major volcanic eruptions in the late Pleistocene (Bunce *et al*., 2009) causing habitat destruction and creating disjunct populations (McDowall, 1996). The geological and climatic events of these time periods are likely to have affected species present in NZ causing allopatric speciation and/or extinction. In this study, we use this detailed knowledge of NZ geology to phytogeographically analyse six species of NZ. We then examine our results with respect to recognized and unrecognized biogeographic regions and compare our results to previous studies of NZ organisms.

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MATERIALS AND METHODS

Collecting

Cicadas were collected throughout their ranges by D.C.M., K.B.R.H., C.S. and associates (see Acknowledgements) over more than 15 years and identified to species using courtship songs and morphology. Unlike South Island (SI) *Kikihia*, hybrid individuals (where mtDNA does not match song or morphology) are rare. Tissue samples were stored in 95% EtOH, kept cold, and later stored in freezers. GPS coordinates were recorded for individual cicadas that are identified by an eleven-character code (Appendix S2).

Mitochondrial DNA extraction, amplification and sequencing

Genomic DNA was extracted from 0.1g of leg muscle tissue using a Qiagen DNeasy Tissue Kit (Valencia, CA, USA). Standard polymerase chain reaction (PCR) methods were used to amplify 750 bp of the 3' end of cytochrome oxidase subunit I (COI) using primers C1-J-2195 and TL2-N-3014 (Simon et al., 1994) and the entire cytochrome oxidase subunit II (COII), 750 bp, using primers TL-2-J-3034 (Simon et al., 1994) and TK-N-3786 (Sueur et al., 2007). PCR products were purified using ExoSAP-IT (Affymetrix, Santa Clara, CA, USA).

Specimens were sequenced in 5' and 3' directions for both gene regions using a standard PCR cycle-sequencing reaction (BigDye version 1.1: Applied Biosystems, Foster City, CA, USA). Sequencing was performed using an ABI 3100xl capillary sequencer with ABI Prism Sequence Analysis 3100 software (Applied Biosystems). Sequencher (DNAStar Inc., Madison, WI, USA) software was used for alignment and editing.

Phylogenetic analyses

Phylogenetic analyses were performed using maximum likelihood (ML) implemented in Garli version 2.0 (Zwickl, 2006) and reversible jump Bayesian Markov chain Monte Carlo (rjMCMC) analyses using Phycas1.2.0 (Lewis *et al.,* 2010). All taxa were included in one midpoint-rooted phylogenetic tree. Midpoint rooting was chosen due to the large genetic distances to outgroup NZ cicada genera, relative to

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short ingroup branches. The Akaike information criterion (AIC) was implemented in jModelTest (Posada, 2008) to determine the best-fit model (two partitions-- 1^{st} + 2^{nd} positions, 3^{rd} positions; both GTR+I+G). Support for nodes was estimated using the nonparametric bootstrap for 1000 replicates.

Initial Bayesian analyses were performed using a variety of partitioning schemes and priors, and were run for 400,000 cycles. [Phycas adjusts each parameter in each cycle, and one Phycas cycle is equivalent to about 100 MrBayes generations (Lewis *et al.*, 2010)]. Phycas was chosen for its accommodation of polytomies, which are likely in hypothesized radiations. We compared trials with various priors chosen using Tracer v1.5 (Rambaut & Drummond, 2003). Branch support was estimated using Bayesian posterior probabilities (PP).

Divergence time estimation and choice of priors

Divergence time estimates were obtained using Bayesian relaxed clock dating (BEAST version 1.7; Drummond & Rambaut, 2007). The *K. cutora* tree was calibrated using the approximate date of uplift of the Axial Ranges, which we hypothesize caused the gradual cessation of gene flow between the ancestor of the two major clades of *K. c. cumberi* (Fig. 3f). The age of the most recent common ancestor (MRCA) of the *K. c. cumberi* clades was calibrated using a normal distribution with 95% of the distribution between 0.2-1.2 Ma with a mean of 0.7 +/- 0.037. Proposed insect mitochondrial molecular clocks, spanning the range of insect rate estimates, from the fastest [0.035 estimated substitutions per site (pairwise divergence) per million years (Papadopoulou *et al.*, 2010)], to the slowest [0.015 pairwise divergence per million years (Quek *et al.,* 2004)] were used as priors on substitution rates for the mtDNA by using a normal distribution (mean=0.0115; standard deviation=0.1). To avoid circularity, we estimated substitution rates and divergence times for all combinations of these priors (MRCA of the two *K.c. cumberi* clades, mitochondrial molecular clock rates, and both combined). We again compared trials with Tracer v1.5 to assess stable parameters with adequate effective sample sizes (Rambaut & Drummond, 2003). Ten million generations were run with a burn-in of 1 million. The chain was sampled every 1000 generations, 10,000 times.

The mean clock-rate obtained from the *K. cutora* analyses were used to calibrate the final BEAST phylogeny that used a pruned selection of study taxa (representing all major clades) including the out-

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group taxa *Rhodopsalta leptomera* and *R. microdora* (Arensburger *et al.*, 2004). We also included the previous calibration of the axial ranges to constrain the age of the MRCA of the two *K. c. cumberi* clades.

Testing support for biogeographic lines

Biogeographic lines were described from multiple species where there was strong Maximum Likelihood and Bayesian support for a split (denoted in red, Fig. 3a-f) along a particular geographic boundary. Less-well supported, but still non-conflicting splits at the same geographic location were used as supporting evidence for these biogeographic lines. In the case of East Cape, no taxa had both strong ML and BI support for splits involving this area, so we call this a zone of interest rather than a biogeographic line and merely point out when unique haplotypes exist in this area. AMOVA (Arlequin v3.5; Excoffier *et al.,* 2005) was run with 10,000 generations to test the amount and significance of variation across each proposed biogeographic boundary (Fig. 1a,b).

RESULTS

A total of 180 specimens were used in this study: 77 of the *K. cutora* complex (including two *K. convicta*), ten *K. dugdalei*, 16 *K. laneorum,* 36 *K. ochrina*, 16 *K. cauta*, and 25 *K. scutellaris* (Appendix S2). The phylogenetic tree estimated for all six species studied (Appendix S1) is divided into subsections (Fig. 3a-f), corresponding to the six species clades. We placed the root along the branch leading to *K. scutellaris* (Fig. 3a) and *K. cauta* (Fig. 3b) following Marshall *et al.* (2008). Our data also identified a clade within *K. c. cumberi* that was identified by John Dugdale and nicknamed *K.* "integra" (Archives of the NZ Arthropod Collection, Landcare Research, Auckland), but not published. Unfortunately, no record remains of characters used to recognize this subspecies, so we identify this clade as the "eastern *K.c. cumberi* clade".

Insect Mitochondrial Molecular Clocks

BEAST estimated the uncorrelated log-normal relaxed clock to have a mean rate of 1.21×10^{-2} – 1.39×10^{-2}, corresponding to a between-lineage divergence of 0.024 – 0.028 estimated substitutions per site per million years. From our analyses of six NI *Kikihia* species studied, we find phylogenetic relationships (Appendix S1) similar to Marshall *et al.* (2008), with the exception of a rearrangement of the weakly

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supported deepest nodes joining *K. ochrina, K. dugdalei,* and *K. laneorum* to the Cutora subspecies. This suggests that these lineages diversified between two and six million years ago (Fig. 4).

Biogeographic boundaries

Kauri Line. Based on AMOVA, the Kauri Line explains 67.45%, 35.28%, and 28% of the variation in the *K. cutora*-complex*, K. ochrina*, and *K. scutellaris* lineages, respectively with statistically significant p-values (Appendix S3). Two of the *K. cutora* subspecies*, K. c. cutora* and *K. c. cumberi,* meet at this line (Fig. 3e). In our sampling, Coromandel includes *K. c. cutora* exclusively, contrary to Fleming (1973). Localities marked TK.LUC/CWW and WO.WTC/WTJ (Fig. 3e) are areas where *K. c. cutora* and *K. c. cumberi* mitochondrial haplotypes appear together along the western coast. The individual labeled TNW.05 (dark blue clade) appears to be the sister lineage to all other *K. c. cutora* and *K. c. exulis* clades and had a divergent song (DCM and KBH, unpublished data). Diversification dates throughout *K. c. cutora* suggest survival in separate refugia through multiple glacial cycles (Fig. 4).

Northland Line. Nearly every taxon sampled in this study exhibits unique haplotypes in the Far North region. AMOVA results corroborate the boundary within the *Kikihia cutora*-complex, *K. ochrina,* and *K. scutellaris* lineages with statistically significant p-values. Two sequential sister clades are present in *K. ochrina* (Fig. 3c) and molecular dating suggests they have been separate for multiple glacial cycles (Fig. 4). In *K. laneorum* (Fig. 3f) individuals collected from the ND.TNW locality possess a unique Far North haplotype. A second clade (purple) is more widely distributed but has a unique Northland population located ~80 kilometres south of the dark blue clade and appears to have been separate through at least one glacial cycle (Fig. 4). *K. cauta* (Fig. 3b) has a unique Northland haplotype that is sister to all other *K. cauta* populations, with the split dating from 0.4-2.0 Ma (Fig. 4). Signal for the Northland Line is also present in the more recently diversified species (Fig. 4) *K. scutellaris* (Fig. 3a) and *K. dugdalei* (Fig. 3d).

NW-SE Line. *Kikihia cutora* phylogeography (Fig. 3e) shows three major clades, one restricted to the hills surrounding the axial ranges. These ranges are separated from the higher elevation TVZ by the Rangitaiki and Whakatane Rivers and their alluvial plains. This finding is corroborated by AMOVA anal-

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yses, with 42.06% of the variation within the *K. cutora*-complex associated with this line (Appendix S3). Soil types differ drastically between the TVZ (volcanic soil and rock) and the Axial Ranges (sedimentary rock) (Molloy & Smith, 2002).

East Cape Zone. *Kikihia ochrina* (MTN.01, Fig. 3c), *K. cutora* (MRC.01, Fig. 3e), *K. laneorum* (MTP.02, Fig. 3f) and *K. scutellaris* (TRY.04, Fig. 3a) show evidence of a unique haplotype in the northern region of the Eastern peninsula, often forming a divergent sister-lineage. These individuals may be indicative of populations in East Cape persisting through glacial cycles longer than in other NI locations. While unique haplotypes were found in single individuals in *K. ochrina* and *K. laneorum* in East Cape, *K. cutora* shows more extensive southwestern diversification.

DISCUSSION

Throughout this discussion we contrast two interpretations of biogeographic lines: 1) as divisions between sister clades isolated by dispersal barriers (either ecological or physical), and 2) as boundaries between older, genetically diverse populations and newer, less diverse populations. In New Zealand, and likely elsewhere, the distinction between these two interpretations has been blurred. We describe how this confusion is particularly relevant to the most widely discussed NZ biogeographic line, the Taupo Line. We also stress the importance of confirming that estimated dates of splits are consistent with biogeographic explanations related to the line in question.

Kauri Line

The Kauri Line is named for the southern limit of the Kauri, *Agathis australis* (Wagstaff & Clarkson, 2012). It has been suggested that continuous NI forest habitat was largely restricted to the Northland+Auckland region during the Last Glacial Maximum (LGM) (Fleming, 1962; Alloway *et al.*, 2007; McGlone *et al.*, 2010). Many NZ phylogeographic studies report a genetic break and/or pattern of northern richness and southern purity across the Kauri Line (for examples, see Wallis & Trewick, 2009). The latter pattern--the antipodean equivalent to Hewitt's (1996) northern hemisphere pattern—may have been caused by repeated cold, dry glacial periods over the last 100,000 years that fragmented northern forest habitats and

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broadly extinguished southern habitats, leading to allopatric diversification in northern regions (Trewick & Morgan-Richards, 2005; Spencer *et al.*, 2006; Wagstaff & Clarkson, 2012) and genetic uniformity in the south following rapid southward dispersal and population re-establishment (with accompanying diversity-destroying bottlenecks) after each cycle. Alternatively, volcanic eruptions of the TVZ may have caused population extinctions south of the Kauri Line (Wilson *et al.*, 1995), but this process would not account for genetic uniformity of the entire southern NI (Trewick *et al.*, 2011).

Kikihia ochrina (Fig. 3c) is a good example of the pattern of Northern Richness-Southern Purity. Three different clades/haplotypes are found above the Kauri line and just one with only moderate genetic structure below it dating to less than 250 Ka. This suggests that much of the habitat south of the Kauri Line was not suitable for survival of *K. ochrina* during the LGM and that the species subsequently moved south with the advancing forest edge similar to *Kikihia* "flemingi" on SI (Marshall *et al.*, 2009). Our dating analyses are consistent with this hypothesis (Fig. 4).

Although the Cutora-group possesses distinct clades on either side of the Kauri line, it does not show the pattern of northern richness-southern purity. *Kikihia cutora cutora* shows moderate genetic structuring within all three geographic regions it occupies. We suggest this because these species inhabit scrub and forest edge, rather than forest, allowing population survival during one or more glacial ages in various parts of the NI. Divergence-time estimates are consistent with the hypothesis that *K. cutora cutora* and *K. cutora cumberi* diversified due to Pleistocene tectonic uplift and subsequent adaptation of *K. cutora cumberi* to higher elevations and cooler temperatures, a pattern found in other NZ cicadas (Buckley *et al.,* 2001; Buckley & Simon, 2007).

Northland Line

The region north of the Northland Line differs from the larger northern area bounded to the south by the Kauri Line in its unique ultramafic rock soil rich in iron and magnesium (Molloy & Smith, 2002), that supports an unusual floral and faunal ecology. During the Pliocene, higher sea levels reduced Northland to two small islands in the north and one larger island to the south separated from mainland NZ by a strait near the Manukau Harbour [pictured in Trewick & Bland (2012) and reviewed in Wallis & Trewick (2009) and Buckley *et al.* (2014)]. Some Pleistocene glacial cycles were more severe than others with the most

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extreme occurring around 0.4 Ma (Zachos *et al.*, 2001; Carter & Gammon, 2004). This drastic cycle may have caused more extreme vegetational shifts into this far northern area seen in many taxa with divergences dating to less than 400 ka but older than the ages of the two later glacial maxima (e.g., this study, and others, see Wallis & Trewick (2009). Very recent northern clade diversifications as in the cicada *Amphipsalta cingulata* (Marshall *et al.,* 2012) are attributed to more recent climate cycles. This area is known to contain many unique organisms, not only because of its Pliocene history, but also recent endemic speciation (Spencer *et al.*, 2006), making it a priority area for conservation management (Buckley *et al.*, 2010; 2014).

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Taupo Line

The Taupo Line has been drawn at various locations between 38.5º and 39.5º S latitude (Fig. 1b). Hypotheses for the existence of this ill-defined line include Pliocene Sea Strait flooding (McGlone, 1985; Lewis *et al.,* 1994; Chapple *et al.,* 2009), tectonic uplift throughout the Pleistocene (McGlone, 1985), volcanic activity (Wilson *et al.*, 1984; 1995), and Pleistocene glacial cycles (Buckley *et al.*, 2010). Discrepancy in placement may be due to the idiosyncratic responses of different species to these factors, the migration of the Pliocene sea strait gradually southward (Fig. 2) and/or the speed of recolonization of different taxa southward. With over fifty years since its description and the publication of many relevant phylogeographic studies, it is time to re-evaluate the Taupo Line.

The Taupo Line was first proposed by Wardle (1963) – though not given that name until the mid 1980's (Henderson, 1985, Gibbs, 1989) – to describe regional levels of endemism, not a biogeographic boundary. He noted a greater number of endemic vascular plants found above versus below the Taupo Line. As summarized by McGlone (1985), there are 125 species of endemic woody trees above this line, and only 36 below. However, closer inspection shows that most endemic species (95) are found only above the Kauri Line and that only an additional 10 endemic species are added by including the area between the Kauri and Taupo Lines (see McGlone, 1985). To lump these two zones is to hide this striking difference. The Kauri Line seems to be a more significant biogeographic boundary. The lesser biodiversity of the Taupo region versus the Northland and Auckland Regions is likely related to altitudinal and other ecological differences in addition to the frequent volcanic and glacial disturbances.

The expectations for phylogeographic patterns associated with Taupo Line(s) depend on the causal mechanism (Trewick *et al.,* 2011). If the Pliocene Sea Strait is hypothesized to be a biogeographic barrier, then splits associated with it would date to > 5 Ma (Fig. 2). None of the species in this study are this old (Fig. 4). If colonization of newly emerged land following either the retreat of the Pliocene Sea Strait, or each glacial cycle was assumed to be the causal mechanism, the expected result would be not a clade split at the Taupo Line, but rather comparatively lower genetic diversity below the line due to recent population expansion and predicted divergence times would be younger than 2 Ma.

Recent phylogeographic studies of taxa with respect to the Taupo line

Our studies of NZ cicadas from a wide variety of habitats (forests, open dry habitats, dense forest, forest edge, scrub (Marshall *et al.* (2012), this study) have failed to find strong support for the Taupo Line as a biogeographically significant break between clades or the demarcation of a shift in patterns of diversity. Of the three Taupo Lines proposed (Fig. 1b), the placement by Wardle (1963) is the most meaningful and most often discussed. In all but one of our study taxa, a more northern latitudinal line marks a genetic dividing line between clades (i.e. Northland or Kauri Lines, Appendix S3). The AMOVA of *K. cauta* did find statistically significant support for the Wardle (1963) placement of the Taupo Line, but sampling remains poor throughout the Taupo region (Fig. 3b). A previously studied cicada, *Amphipsalta cingulata*, shows a genetic split between clades above and below the Taupo Line (save for one individual found North of Auckland), but this differentiation is far too recent to have been caused by the sea strait and there are not large differences in genetic diversity above and below the line (Marshall *et al.*, 2012). Another cicada, *Notopsalta sericea* is restricted to the NI and does show a genetic break near the Taupo Line but this split is also recent (~1 Ma) and more likely attributable to the NE-SW line and tectonic uplift (Marshall *et al.*, 2012).

Similarly, studies of fungus beetles show only a few clades with phylogeographic patterns consistent with the Taupo Line. The beetle *Pristoderus bakewelli* has a genetic break with one clade (D-2) found above the Taupo Line and multiple clades below it, all of which inhabit both the southern half of the NI and most of the SI; the date of the split is consistent with the Taupo Line/Pliocene Sea Strait (4.43-7.32 Ma) (Marske *et al.,* 2011). This same study examined genetic patterning in the beetle *Epistranus*

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lawsoni and found a less clear influence of the Taupo Line; one clade (A-1) was found to the north of the line, was missing from the southern NI, and then was present again on the SI. A third beetle species, *Hisparonia hystrix*, possessed one clade (black dot) that occurred only south of the Taupo Line and another that was distributed both above and below the line (Marske *et al.*, 2012). However, it — like other examples we discuss below — may be better described by the NW-SE Line.

Northwest-Southeast Line

The Axial Mountain Ranges (extending from Wellington Harbour to East Cape) split the southern NI into east and west portions. The highest peaks (close to 1800m) are in the southernmost--Tararua and Ruahine--ranges. . Altitudes decrease as the mountains progresses north, becoming less likely to affect dispersal patterns (Cockayne, 1911). Uplift began around 2 Ma (Bunce *et al.,* 2009) followed by Pliocene erosion and re-emergence during the Pleistocene (Erdman & Kelsey, 1992), with most recent mountain-building occurring during the last half-million years (TePunga, 1954; Rogers, 1989). During the Pliocene, a long narrow island existed along what is now the southeast coast (Fig. 2).

Like *K. cutora*, the grass species *Kikihia "aotea"* (a mid-elevation foothill-dwelling cicada In the Muta Group) shows a clear genetic break across the NW-SE line (Marshall *et al.,* 2011). *Kikihia* "aotea east" (Fig. 5), is co-distributed with eastern *K. c. cumberi* clade (Fig. 3e) and is made up of two well-defined clades: one southern and one northern. Each of these clades has geographically structured subclades suggesting gradual subdivision and little migration. The sister-clade, *K.* "aotea west" (Fig. 5c) occurs to the northwest of the NW-SE Line and is made up of three subclades: one northern, one western, and one central lineage (Marshall *et al.,* 2011).

The NW-SE Line could be explained in both the *Kikihia cutora* and *K.* "aotea" groups in a scenario related to uplift. The southeastern Pleistocene island (Fig. 2, 2 Ma) connected by a small landbridge to the main NI may have harboured the ancestor of *K. c. cumberi* and eastern *K.* "aotea" that is hypothesized to have occupied the entire NI below the Kauri Line. Gene flow may have decreased between the southeastern population and the northwestern populations due to the increase in uplift of the axial ranges (Fig. 2, 1Ma) and a concomitant increase in volcanic activity in the area to the west. This could explain the relatively recent genetic break within subspecies. Selection due to differences in soil type and vegetation in the two areas may have also encouraged differentiation. These shrub- and grass-adapted species may have been well adapted to persist locally through Pleistocene cold and dry periods.

Uplift creating both an ecological and physical biogeographic barrier could have isolated the two other cicadas studied by (Marshall *et al.,* 2011) — lowland-dwelling *Kikihia muta* clades (Fig. 5b), which show a 1Ma break that is contemporaneous with the two *K.c. cumberi* clades (Fig. 4,5a). We suggest that the eastern and western *K. muta clades* inhabited lowland areas from the eastern shore of what is now Hawkes Bay and extending along the northern shore of the Pliocene Sea Strait (Fig. 2, 2 Ma). Gene flow was then stopped due to the uplift and subsequent disjunction of the shoreline (Fig. 2, 1 Ma).

The NW-SE Line (described in the past as simply an east-west division in the central NI) appears in a wide variety of other taxa, including: *Haplodactyylus* and *Naultinus* geckos (Nielsen *et al.,* 2011), *Dactylanthus taylorii* parasitic plants (Holzapfel *et al.,* 2002), *Pachyornis mappini* moa (Baker *et al.,* 2005), *Clitarchus hookeri* stick insects (Buckley *et al.,* 2010), and *Notopsalta* cicadas (Marshall *et al.,* 2012). A more weakly correlated east-west pattern is found in *Asplenium hookerianum* ferns (Shepherd *et al.*, 2007). An interesting observation is that Wellington mtDNA haplotypes sometimes cluster with western populations [as in *Asplenium hookerianum* ferns, (Shepherd *et al.*, 2007)] and sometimes with eastern populations [as in *Dactylanthus taylorii* parasitic plants (Holzapfel *et al.*, 2002), *Clitarchus hookeri* stick insects (Buckley *et al.*, 2010), and *Kikihia cutora* and *Kikihia* "aotea east" (this paper)]. This widespread NW-SE Line should be distinguished from potential recent central-NI patterns related to recolonization after multiple post-LGM Taupo volcanic explosions (e.g., Shepherd & Lambert, 2008; Trewick *et al.*, 2011). The NW-SE Line appears to explain NI biogeography of some taxa better than the Taupo Line, especially species occupying the hill country as opposed to the relatively restricted coastal lowlands (See for example, Buckley *et al.* (2010), figure 2).

East Cape Zone

Glacial refugia in the northern portion of the East Cape region have been previously predicted (Marske *et al.*, 2009; Buckley *et al.*, 2010) and several NI cicadas provide corroboration (Figs. 3a,c,e,f). This pattern was also found in *Meterosideros* trees (Gardner *et al.*, 2004) and a species of *Leiopelma* frog (Fouquette, 1975). The appearance of deeply divergent clades in a wide variety of taxa, including four of six *Kikihia* species in this study, further suggests that the East Cape region is a significant, possibly relictual biogeographic subdivision. Northern East Cape has soil that differs from others in that it includes a mixture of basaltic lava, pillow lava, and tuff (the result of a seafloor volcano, Molloy & Smith, 2002), in addition to a warmer, hill, and coastal climate. Topographic complexity and resulting habitat diversity, a factor influencing diversification of many groups [other *Kikihia* species (Marshall *et al.,* 2009; 2011; 2012), in *Maoricicada* (Buckley & Simon, 2007), and likely in carabid beetles of the genus *Duvaliomimus* (Townsend, 2010)] combined with lower latitude, may have resulted in better maintenance of mesic refuges during the Pleistocene in this region.

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CONCLUSIONS

We have reviewed five main NI biogeographic lines/regions (Kauri Line, Northland Line, Taupo Line, NW-SE Line, and East Cape Zone), evaluated them for six species of New Zealand *Kikihia* cicadas, and compared these results to previous studies of NZ cicadas and other organisms. Forest species are most likely to show phylogeographic breaks or distributional limits associated with the Northland and Kauri Lines. Species that occupy shrub/hill habitats respond to the NW-SE Line. In two cicada species that have been sampled in fine detail, a primary NW-SE division is present, with the eastern NW-SE clade divided into northern and southern subclades probably related to the Pleistocene uplift of the axial ranges. In four cicada species, a unique East Cape haplotype is found. Two of the NI *Kikihia* species show little population structure indicating a recent, rapid spread from a single Pleistocene refuge. The other NI *Kikihia* provide evidence for multiple Northern Peninsula refugia during Pleistocene glacial cycles due to the presence of two or more well-supported clades dating to various, different pre-LGM times in each tree. Only one NI cicada species shows a pattern of “Northern Diversity, Southern Purity” genetic differentiation about the Kauri Line, although many show unique far north haplotypes. We find no compelling evidence of the widely discussed Taupo Line despite sampling a variety of elevations and habitat types (grass, scrub, and dense forest). Instead, we suggest post-Pliocene uplift along a NW-SE axis is more important in determining clade boundaries in the southern NI, especially for non-forest taxa.

ACKNOWLEDGEMENTS

We thank Elizabeth Wade, Geert Goemans, John Cooley, Paul Lewis, Patrick Gero, Russ Meister, Sarah Banker, Thomas Buckley, and the Oakley lab for thoughtful input and/or field assistance. We also thank reviewers Melodie McGeoch, Adrian Paterson, and Richard Leschen for their helpful comments. Financial support was provided by NSF DEB 0422386, 0529679 (REU), 0720664, and 0955849, as well as grants from the University of Connecticut and the NZ Marsden Fund. Computational resources for the phylogenetic analyses were provided by the Bioinformatics Facility of the Biotechnology/Bioservices Center, University of Connecticut, Storrs, CT, USA. We thank the Department of Conservation, especially Ian Millar and Bev Freer, for assistance in obtaining permits, and good colleagues too numerous to name for assistance with field collecting/advice over the last 20 years.

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Data Accessibility

Readers may access mtDNA sequences via NCBI Genbank accession numbers listed in Appendex S2 (will supply after MS acceptance).

Biosketch

Author contributions: D.M, K.H, and C.S. collected the specimens. E.A.E. collected the data with assistance from C.O. and K.H. P.K. contributed to the geological interpretations. E.A.E., D.M., and C.O. conducted the analyses. E.A.E. and C.S. wrote the manuscript. All authors edited and/or approved the manuscript. Members of the Simon lab (http://hydrodictyon.eeb.uconn.edu/projects/cicada/simon_lab/simonlab.php) focus on biodiversity discovery and understanding the origin, spread, maintenance, natural history, and taxonomy of biodiversity. They use cicadas worldwide as their model organism. They have a special interest in the cicadas of New Zealand, Australia, and North America. Peter Kamp (http://sci.waikato.ac.nz/about-us/people/pjjk) studies tectonic development of New Zealand through the Cretaceous and Cenozoic by application of basin analysis, low temperature thermochronology, and geochronology and contributed geological maps and assisted with geological interpretations.

Editor: Melodie McGeoch

Figure 1 North Island, New Zealand biogeographic boundaries referenced in this study. Placement of biogeographic boundaries described in this study: Northland Line, Kauri Line (after Wagstaff and Clarkson 2012), NW-SE Line, East Cape Zone. Cicada species influenced by each boundary are indicated on the map (a). Historical placements of the Taupo Line by Wardle (1963), McGlone (1985), and Rogers (1989) (b).

Figure 2 Paleogeographic maps illustrating particularly how the geography of North Island changed during the Pliocene and Pleistocene. These maps are part of a larger set showing the Cenozoic paleogeographic development of New Zealand, which are constrained by the present stratigraphy and structure as mapped, and by a numerical model (P. Kamp in prep.) that accounts for the Neogene plate boundary deformation through New Zealand and palinspastic relocation of stratigraphic units displaced within the plate boundary zone. Note how the west-east marine seaway in central-southern North Island became more restricted through 5 Ma to present, ultimately becoming land.

Figure 3 North Island phylogeography and clade distribution maps for *Kikihia* Shade- Singer and Cutora-Group taxa examined in this study. Phylogeographic trees are clipped from the "All *Kikihia*" ML phylogeny modelled with GTR+I+G, two partitions (1^{st},2^{nd}/3^{rd}) shown in Appendix S1. Colours on the maps correspond to colours of clades on each phylogram. Locality codes as in Appendix S2. Phylograms and clade distributions are shown for *Kikihia scutellaris* (a); *K. cauta* (b); *K. ochrina* (c); *K. dugdalei* (d); *K. cutora* subspecies (dark blue = *K. cutora cutora*, light blue= *K. cutora* cumberi east, and purple = *K. cutora cumberi* west) (e); and *K. laneorum* (f).

Figure 4 North Island Shade Singer and Cutora Group *Kikihia* chronogram from BEAST. Dark blue bars show 95% confidence intervals. Locality codes as in Appendix S2.

Figure 5 North Island *Kikihia* Muta Group chronogram, phylogram, and distributions re-drawn using data and data analyses from Marshall *et al*. 2008, 2011; Colours on maps correspond to colours on the phylo-

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grams but colours are not meant to be consistent among figures a, b, c, and d. *Kikihia* species chronogram and map showing distributions of *Kikihia* Muta Group taxa. Dotted lines provide 1- and 2-Myr time guides. Note that the Muta Group is divided into two subgroups "Muta" and "Aotea" each of which formed eastern and western clades approximately 1 Ma. Ker = Kermadec Islands, NFL = Norfolk Island (a); *K. muta* "muta" map & phylogram. Note that the four plum-coloured dots on the shore of Hawke Bay indicate populations of *K.* "muta east" that are not part of the *K.* "muta west" phylogeographic tree (see text) (b); *K.* "aotea west" distribution and phylogram (c), *K. muta* "aotea east" distribution and phylogram (d).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 MtDNA phylogenies (Maximum Likelihood and Bayesian Inference) of all *Kikihia* species used in this study. Maximum Likelihood phylogram produced by Garli; Bayesian Inference phylogram produced by Phycas. Both phylograms have two partitions (1st, 2nd/3rd), each with GTR+I+G models. Zoom to see taxon names.

Appendix S2 Distribution (1992-2012), collection information, and accession codes for samples of the genus *Kikihia* used in this study. The specimen code contains the last two digits of the collection year, the two-letter district from Crosby *et al.* (1998), a three-letter site code, and a specimen number as databased at **http://hydrodictyon.eeb.uconn.edu/projects/cicada/databases/new_zealand/nz_search.php**. Taxon names are provided on each map that follows. Filled circles = specimens collected; hollow circles = aural records.

Appendix S3 Table of Analysis of Molecular Variance results calculated in Arlequin v3.5 of each hypothesized biogeography listed in Figure 1a,b

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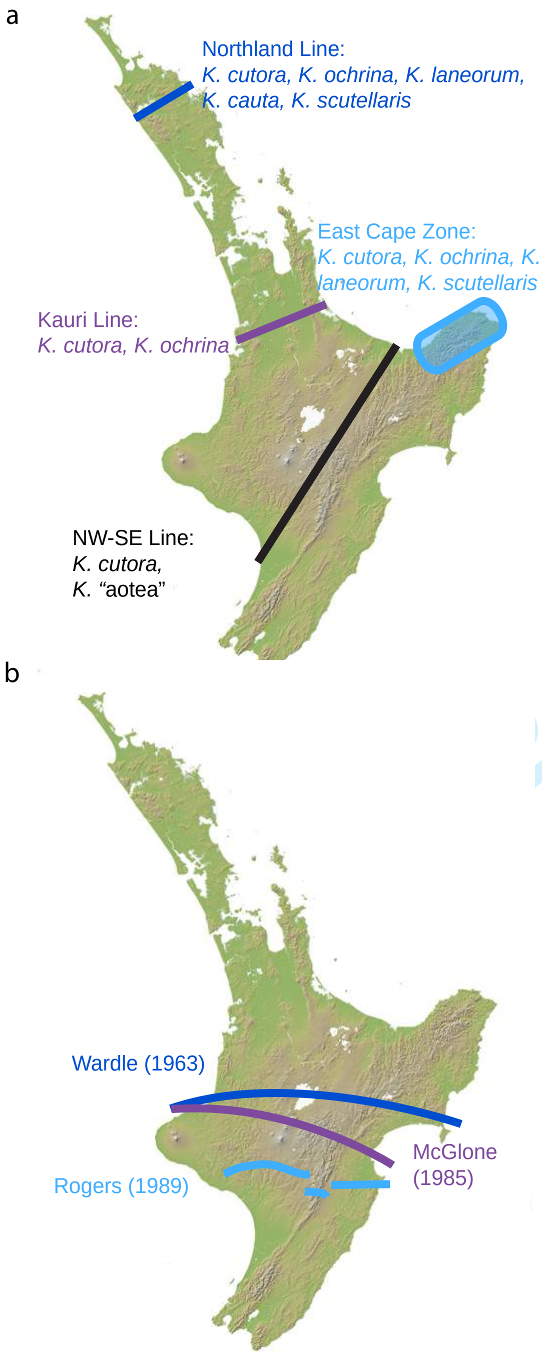
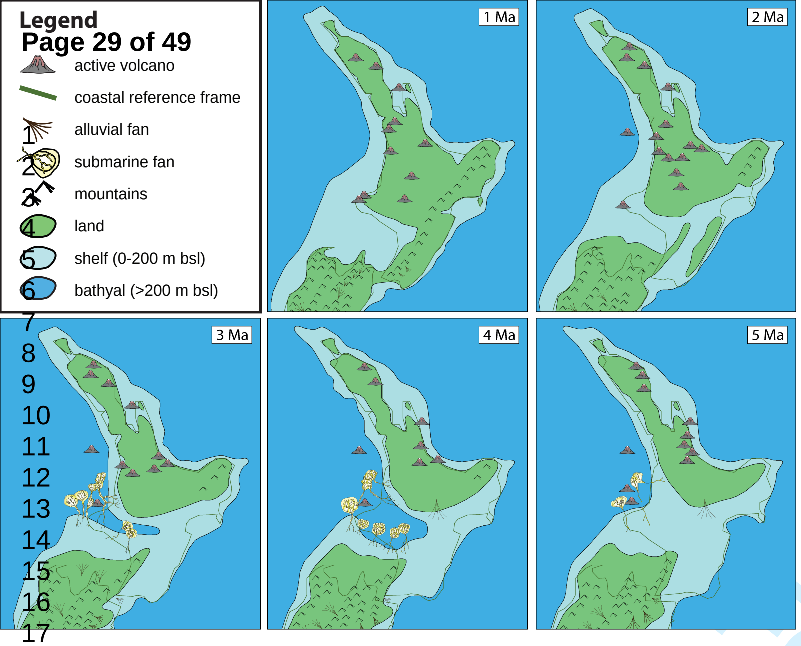


For Peer Review



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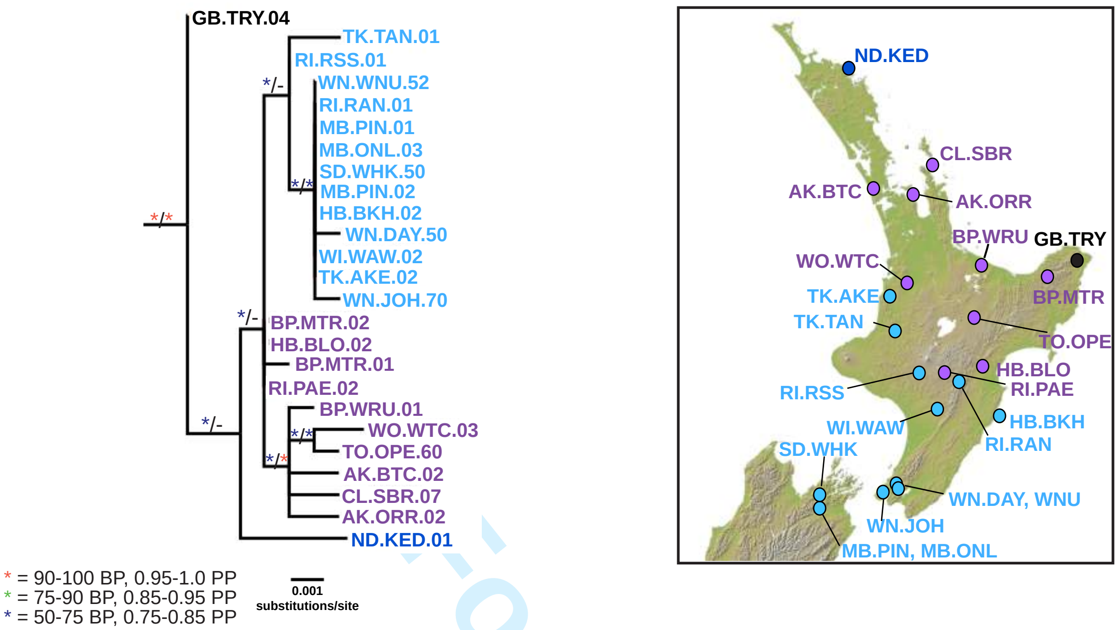
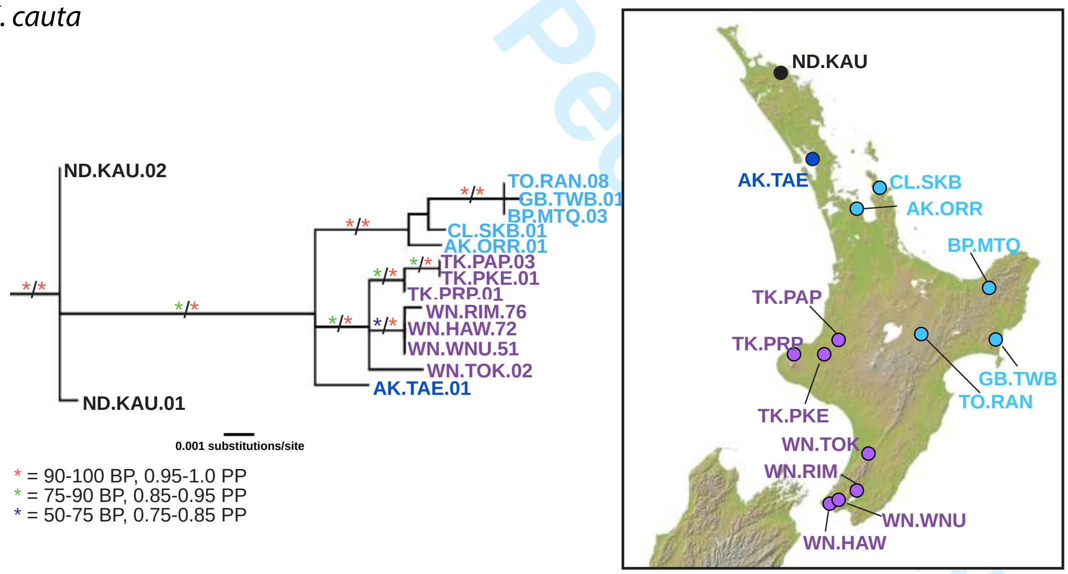
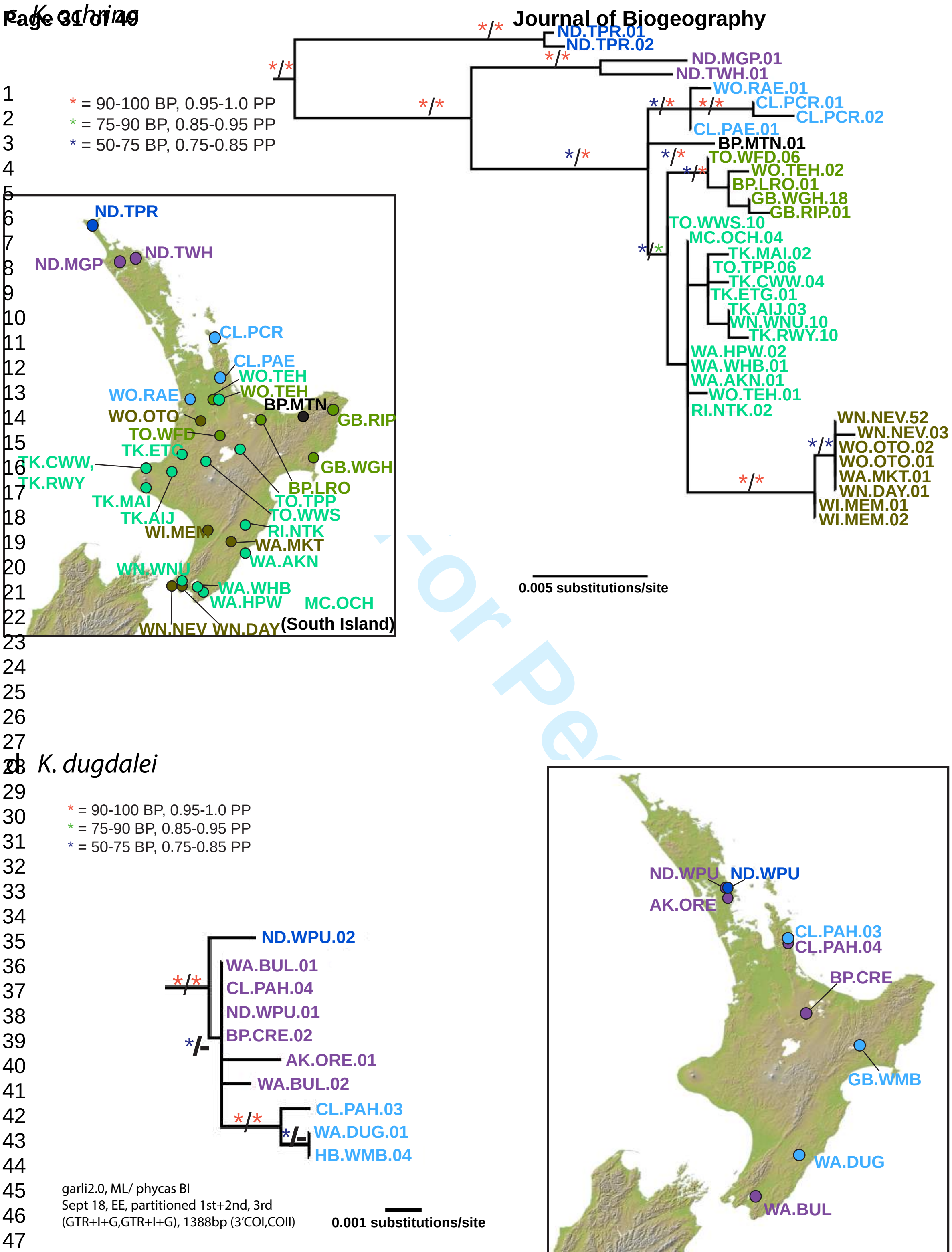
a. *K. scutellaris*

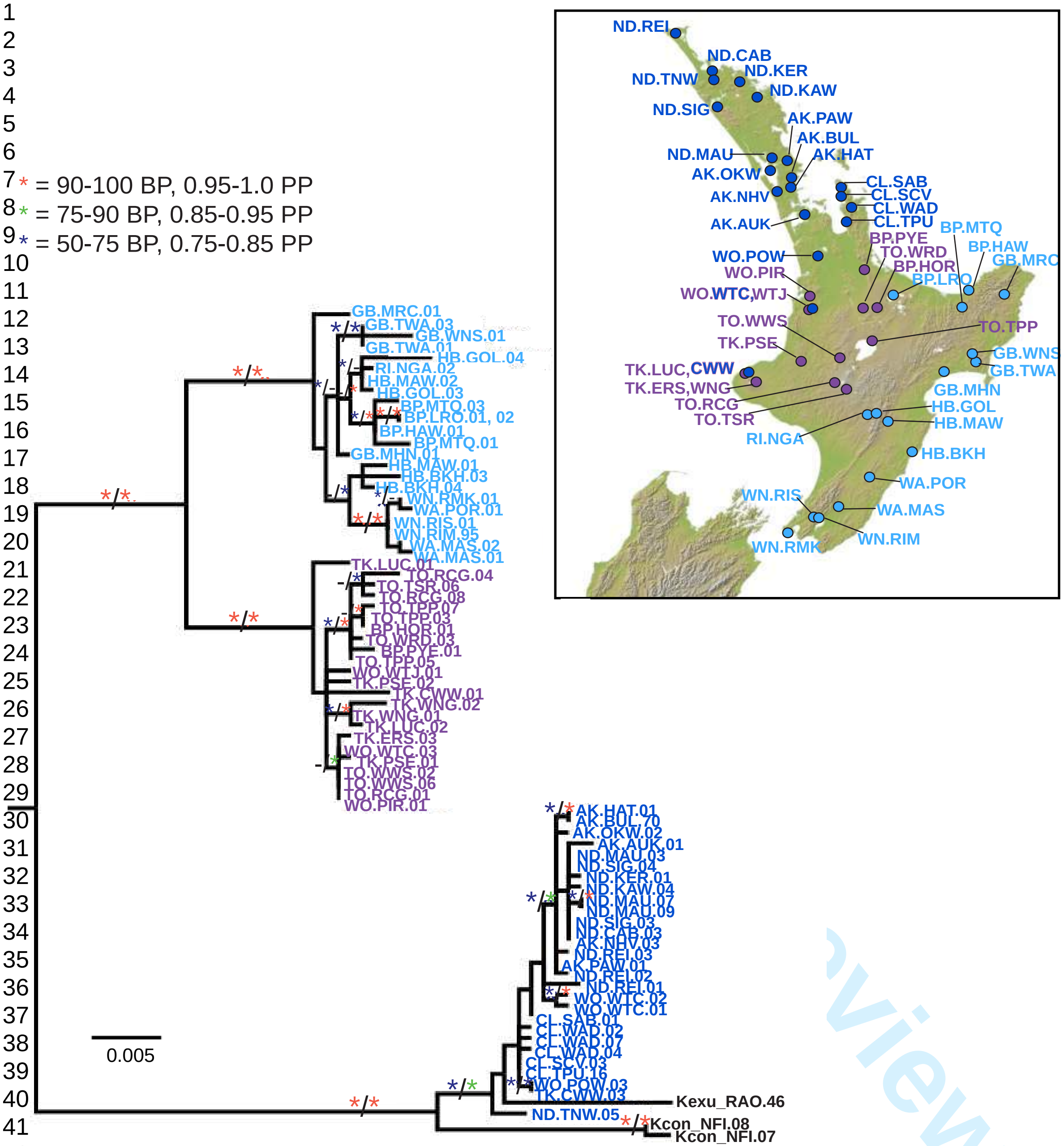


b. *K. cauta*




K. ochrina
* = 90-100 BP, 0.95-1.0 PP
* = 75-90 BP, 0.85-0.95 PP
* = 50-75 BP, 0.75-0.85 PP
ND.TPR.01
ND.TPR.02
ND.MGP.01
ND.TWH.01
WO.RAE.01
CL.PCR.01
CL.PCR.02
CL.PAE.01
BP.MTN.01
TO.WFD.06
WO.TEH.02
BP.LRO.01
GB.WGH.18
GB.RIP.01
TO.WWS.10
MC.OCH.04
TK.MAI.02
TO.TPP.06
TK.CWW.04
TK.ETG.01
TK.AIJ.03
WN.WNU.10
TK.RWY.10
WA.HPW.02
WA.WHB.01
WA.AKN.01
WO.TEH.01
RI.NTK.02
WN.NEV.52
WN.NEV.03
WO.OTO.02
WO.OTO.01
WA.MKT.01
WN.DAY.01
WI.MEM.01
WI.MEM.02
0.005 substitutions/site
ND.TPR
ND.TWH
ND.MGP
CL.PCR
CL.PAE
WO.TEH
WO.TEH
WO.RAE
BP.MTN
WO.OTO
GB.RIP
TO.WFD
TK.ETG
TK.CWW,
TK.RWY
GB.WGH
BP.LRO
TO.TPP
TK.MAI
TO.WWS
TK.AIJ
WI.MEM
RI.NTK
WA.MKT
WA.AKN
WN.WNU
WA.WHB
WA.HPW
MC.OCH
WN.NEV
WN.DAY
(South Island)
d K. dugdalei
* = 90-100 BP, 0.95-1.0 PP
* = 75-90 BP, 0.85-0.95 PP
* = 50-75 BP, 0.75-0.85 PP
ND.WPU.02
WA.BUL.01
CL.PAH.04
ND.WPU.01
BP.CRE.02
AK.ORE.01
WA.BUL.02
CL.PAH.03
WA.DUG.01
HB.WMB.04
garli2.0, ML/ phycas BI
Sept 18, EE, partitioned 1st+2nd, 3rd
(GTR+I+G,GTR+I+G), 1388bp (3'COI,COII)
0.001 substitutions/site
ND.WPU
ND.WPU
AK.ORE
CL.PAH.03
CL.PAH.04
BP.CRE
GB.WMB
WA.DUG
WA.BUL

e. *K. cutora*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* = 75-90 BP, 0.85-0.95 PP
* = 50-75 BP, 0.75-0.85 PP
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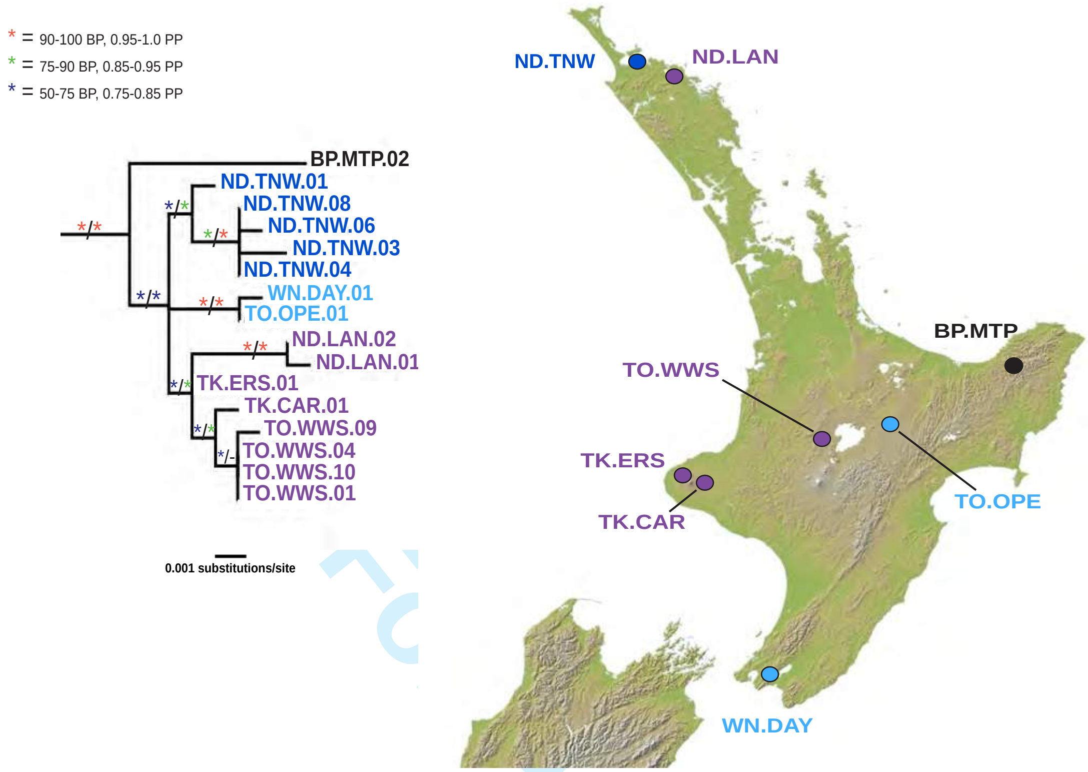
Kexu_RAO.46
Kcon_NFI.08
Kcon_NFI.07

f. *K. laneorum*



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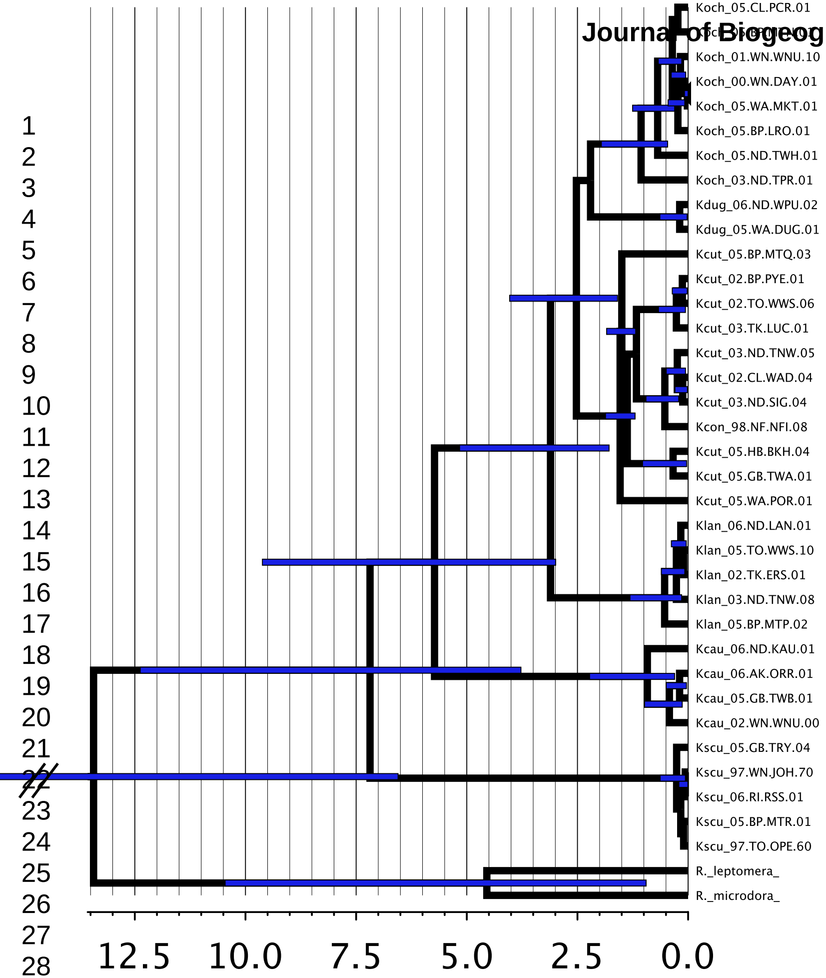
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Koch_05.BP.LRO.01
Koch_05.ND.TWH.01
Koch_03.ND.TPR.01
Kdug_06.ND.WPU.02
Kdug_05.WA.DUG.01
Kcut_05.BP.MTQ.03
Kcut_02.BP.PYE.01
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Kcut_03.TK.LUC.01
Kcut_03.ND.TNW.05
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Kcut_05.GB.TWA.01
Kcut_05.WA.POR.01
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Klan_05.TO.WWS.10
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Kcau_06.AK.ORR.01
Kcau_05.GB.TWB.01
Kcau_02.WN.WNU.00
Kscu_05.GB.TRY.04
Kscu_97.WN.JOH.70
Kscu_06.RI.RSS.01
Kscu_05.BP.MTR.01
Kscu_97.TO.OPE.60
R._leptomera_
R._microdora_
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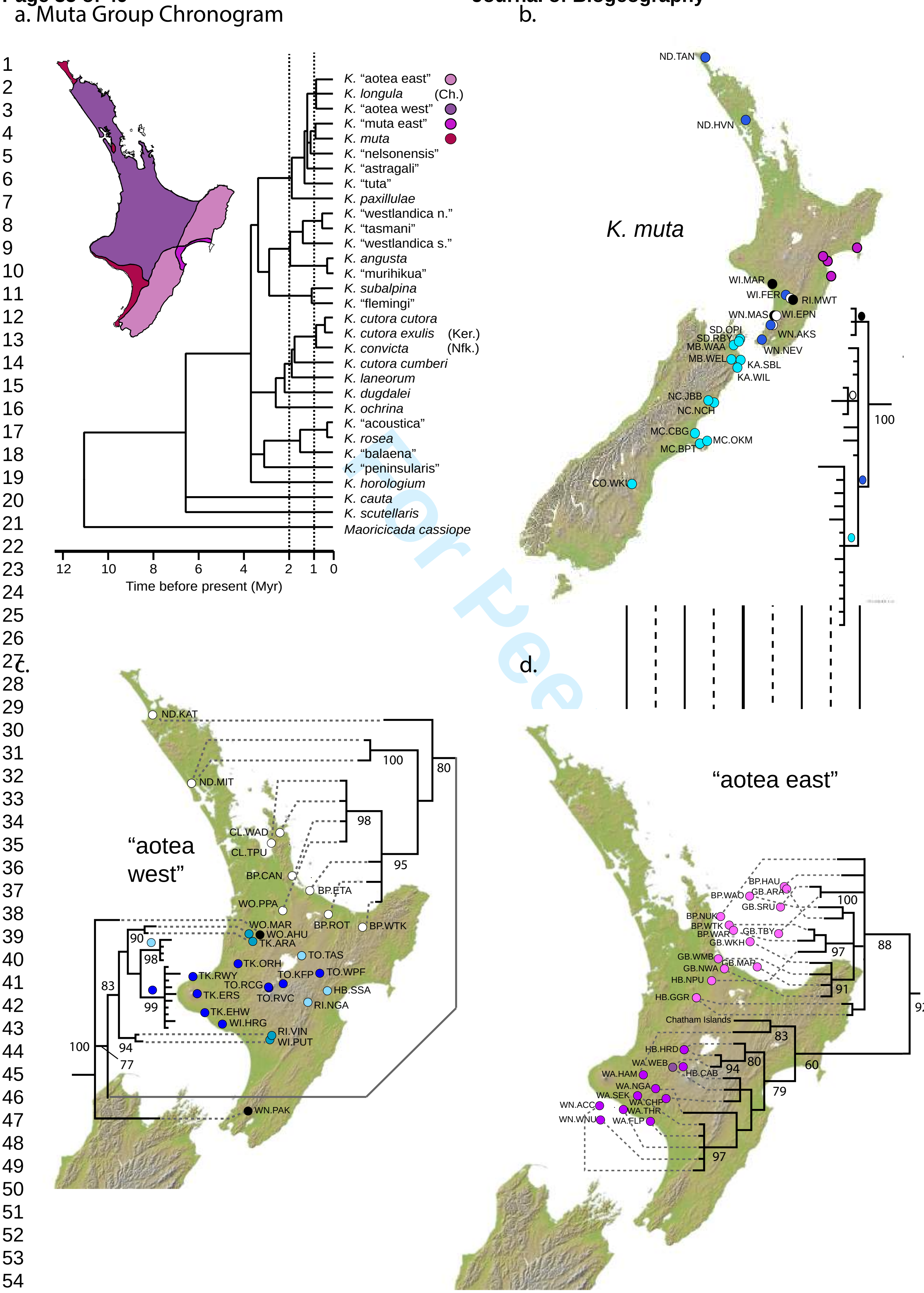
10.0
7.5
5.0
2.5
0.0


a. Muta Group Chronogram
K. "aotea east"
K. longula (Ch.)
K. "aotea west"
K. "muta east"
K. muta
K. "nelsonensis"
K. "astragali"
K. "tuta"
K. paxillulae
K. "westlandica n."
K. "tasmani"
K. "westlandica s."
K. angusta
K. "murihikua"
K. subalpina
K. "flemingi"
K. cutora cutora
K. cutora exulis (Ker.)
K. convicta (Nfk.)
K. cutora cumberi
K. laneorum
K. dugdalei
K. ochrina
K. "acoustica"
K. rosea
K. "balaena"
K. "peninsularis"
K. horologium
K. cauta
K. scutellaris
Maoricicada cassiope
12 10 8 6 4 2 1 0
Time before present (Myr)
b.
K. muta
ND.TAN
ND.HVN
WI.MAR
WI.FER
RI.MWT
WN.MAS
WI.EPN
SD.OPI
SD.RBY
WN.AKS
MB.WAA
WN.NEV
MB.WEL
KA.SBL
KA.WIL
NC.JBB
NC.NCH
MC.CBG
MC.OKM
MC.BPT
CO.WKI
100
c.
"aotea west"
ND.KAT
ND.MIT
CL.WAD
CL.TPU
BP.CAN
BP.ETA
WO.PPA
BP.ROT
BP.WTK
WO.MAR
WO.AHU
TK.ARA
TO.TAS
TK.ORH
TK.RWY
TO.KFP
TO.WPF
TO.RCG
TK.ERS
TO.RVC
HB.SSA
RI.NGA
TK.EHW
WI.HRG
RI.VIN
WI.PUT
WN.PAK
100
80
98
95
90
98
83
99
100
94
77
d.
"aotea east"
BP.HAU
BP.WAO
GB.ARA
GB.SRU
BP.NUK
BP.WTK
BP.WAR
GB.TBY
GB.WKH
GB.WMB
GB.MAR
GB.NWA
HB.NPU
HB.GGR
Chatham Islands
HB.HRD
WA.WEB
HB.CAB
WA.HAM
WA.NGA
WA.SEK
WA.CHP
WN.ACC
WA.THR
WN.WNU
WA.FLP
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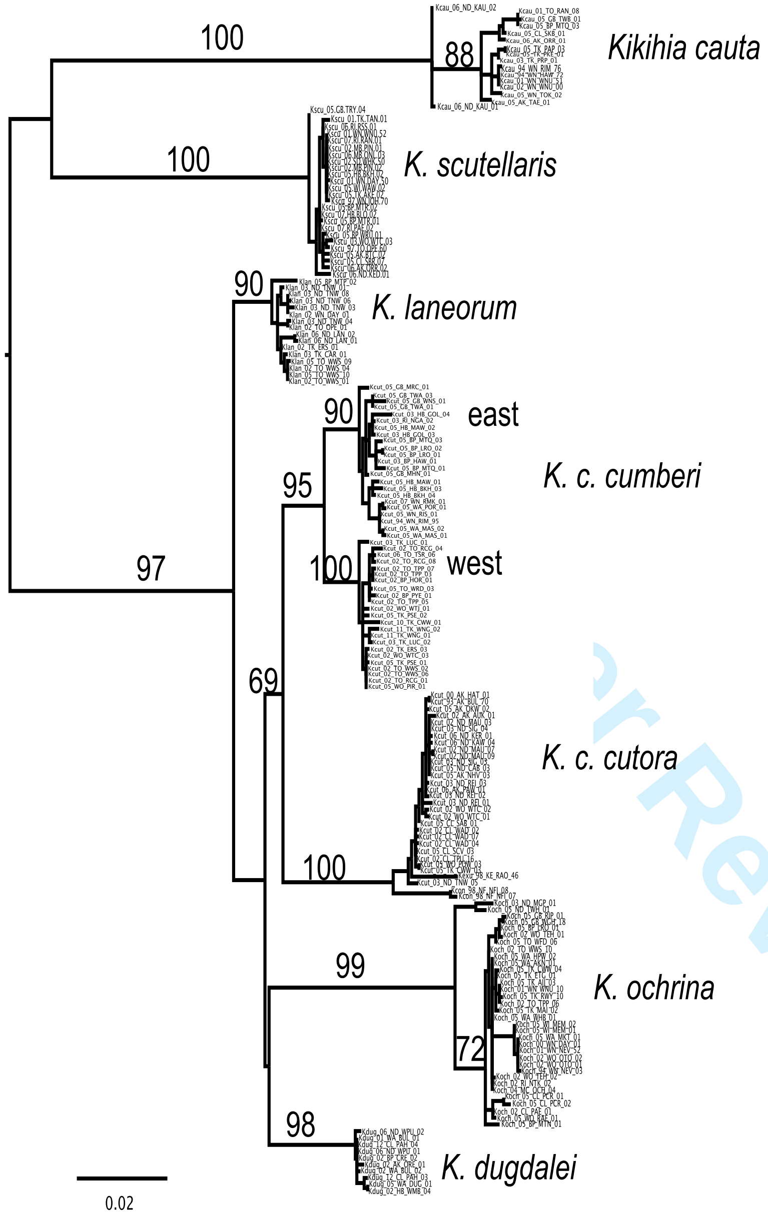
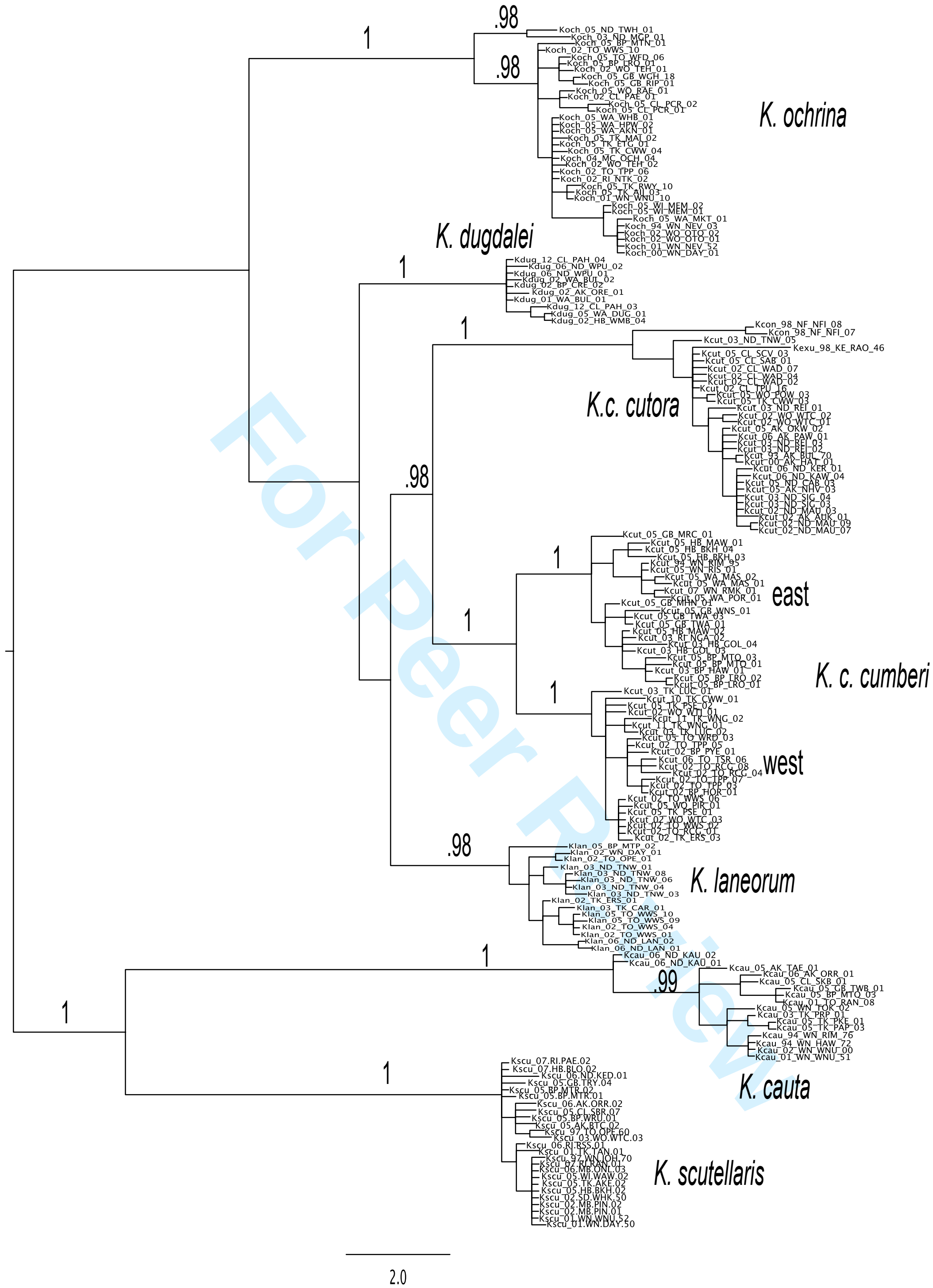
91
92
83
80
94
60
79
97

Supplementary Figures

Appendix 1: Phylogenies of all specimens used in this study



S1. MtDNA phylogeny of all *Kikihia* species used in this study. Maximum Likelihood phylogram produced by Garli, two partitions (1^{st}, $2^{nd}/3^{rd}$) with GTR+I+G/ GTR+I+G models. Zoom in to see taxa names.



S2. MtDNA phylogeny of all *Kikihia* species used in this study. Bayesian phylogram produced in Garli, two partitions (1^{st}, $2^{nd}/3^{rd}$) with GTR +G/GTR+G models. Zoom in to see taxa names.

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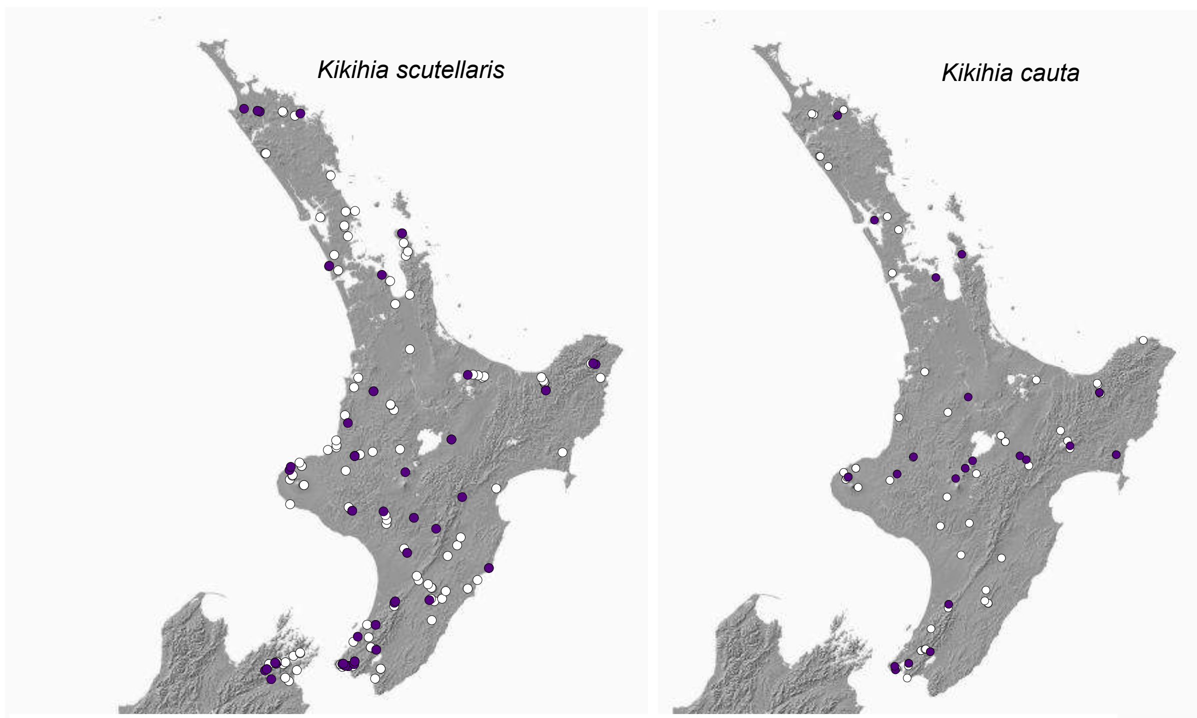
Appendix 2: Distribution and collection information


Kikihia scutellaris
Kikihia cauta

S3. Simon Lab distribution records (1992-2012) for Kikihia species used in the study. Taxon name is provided on each map. Filled circles = specimens collected; hollow circles = aural records. ? = uncertain aural record. X = Possible Hybrid.

Supplementary Table 1. Samples of the genus *Kikihia* used in this study. The specimen code contains the last two digits of the collection year, the two-letter district codes from Crosby et al. (1998), a three-letter site code, and a specimen number as databased at http://hydrodictyon.eeb.uconn.edu/projects/cicada/databases/new_zealand/nz_search.php.

Species	Specimen Code	District	Longitude	Latitude	Elevation (m)
K. cutora cutora	00.AK.HAT.01	Auckland	174.695	-36.5667	0
	93.AK.BUL.70	Auckland	174.688	-36.5	121
	02.AK.AUK.01	Auckland	174.788	-36.9998	45
	02.ND.MAU.03	Northland	174.301	-36.1139	72
	02.ND.MAU.07	Northland	174.301	-36.1139	72
	02.ND.MAU.09	Northland	174.301	-36.1139	72
	03.ND.SIG.03	Northland	173.373	-35.5401	82
	03.ND.SIG.04	Northland	173.373	-35.5401	82
	05.AK.NHV.03	Auckland	174.447	-36.6484	15
	05.ND.CAB.03	Northland	173.359	-34.9936	20
	06.ND.KAW.04	Northland	174.138	-35.3699	13
	06.ND.KER.01	Northland	173.956	-35.2351	47
	03.ND.REI.02	Northland	172.681	-34.4308	222
	03.ND.REI.03	Northland	172.681	-34.4308	222
	05.AK.OKW.02	Auckland	174.282	-34.346	7
	06.AK.PAW.01	Auckland	174.665	-36.2853	75
	02.WO.WTC.01	Waikato	175.101	-38.2622	84
	02.WO.WTC.02	Waikato	175.101	-38.2622	84
	03.ND.REI.01	Northland	172.681	-34.4308	222
	05.CL.SAB.01	Coromandel	175.457	-36.5254	5
	02.CL.TPU.16	Coromandel	175.508	-37.0039	0
	02.CL.WAD.02	Coromandel	175.664	-36.8431	23
	02.CL.WAD.04	Coromandel	175.664	-36.8431	23
	02.CL.WAD.07	Coromandel	175.664	-36.8431	23
	05.CL.SCV.03	Coromandel	175.46	-36.6694	129
	05.TK.CWW.03	Taranaki	174.071	-39.0578	11
	05.WO.POW.03	Waikato	175.153	-37.5403	20
	03.ND.TNW.05	Northland	173.452	-35.1846	310
K. cutora exulis	98.KE.RAO.46	Kermadec Islands	178.077	-29.2483	0
K. convicta	98.NF.NFI.07	Norfolk Island	167.95	-29.0333	115
	98.NF.NFI.08	Norfolk Island	167.95	-29.0333	115
K. cutora cumberi	02.BP.HOR.01	Bay of Plenty	176.173	-38.2506	380
	02.TO.TPP.03	Taupo	176.068	-38.6907	360

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	02.TO.TPP.07	Taupo	176.068	-38.6907	360
	02.BP.PYE.01	Bay of Plenty	176.125	-37.8631	371
	02.TO.RCG.04	Taupo	175.532	-39.1919	1068
	02.TO.RCG.08	Taupo	175.532	-39.1919	1068
	06.TO.TSR.06	Taupo	175.735	-39.2963	1028
	02.TO.TPP.05	Taupo	176.068	-38.6907	360
	05.TO.WRD.03	Taupo	175.81	-38.421	237
	02.TK.ERS.03	Taranaki	174.146	-39.3125	691
	02.TO.RCG.01	Taupo	175.532	-39.1919	1068
	02.TO.WWS.02	Taupo	176.068	-38.6907	669
	02.TO.WWS.06	Taupo	176.068	-38.6907	669
	02.WO.WTC.03	Waikato	175.101	-38.2622	84
	05.TK.PSE.01	Taranaki	174.932	-38.9636	271
	05.WO.PIR.01	Waikato	175.056	-38.0213	500
	05.WO.WTJ.01	Waikato	175.112	-38.2626	92
	03.TK.LUC.02	Taranaki	173.938	-39.1489	139
	11.TK.WNG.01	Taranaki	174.146	-39.3125	691
	11.TK.WNG.02	Taranaki	174.146	-39.3125	691
	05.TK.PSE.02	Taranaki	174.932	-38.9636	271
	10.TK.CWW.01	Taranaki	174.071	-39.0578	11
	03.TK.LUC.01	Taranaki	173.938	-39.1489	139
K. cutora ‘integra’	03.BP.HAW.01	Bay of Plenty	177.554	-37.8901	165
	05.BP.LRO.01	Bay of Plenty	176.558	-38.0498	330
	05.BP.LRO.02	Bay of Plenty	176.558	-38.0498	330
	05.BP.MTQ.01	Bay of Plenty	177.511	-38.178	565
	05.BP.MTQ.03	Bay of Plenty	177.511	-38.178	565
	03.HB.GOL.03	Hawkes Bay	176.382	-39.4123	771
	03.HB.GOL.04	Hawkes Bay	176.382	-39.4123	771
	03.RI.NGA.02	Rangitikei	176.312	-39.4002	715
	05.HB.MAW.02	Hawkes Bay	176.562	-39.6925	184
	05.GB.MHN.01	Gisborne	177.165	-39.0863	80
	05.GB.TWA.01	Gisborne	177.792	-38.8559	636
	05.GB.TWA.03	Gisborne	177.792	-38.8559	636
	05.GB.WNS.01	Gisborne	177.77	-38.8039	433
	05.GB.MRC.01	Gisborne	178.118	-38.103	534
	05.HB.BKH.03	Hawkes Bay	176.823	-40.1708	23
	05.HB.BKH.04	Hawkes Bay	176.823	-40.1708	23
	05.HB.MAW.01	Hawkes Bay	176.562	-39.6925	184
	05.WA.MAS.01	Wairarapa	175.662	-40.9498	112
	05.WA.MAS.02	Wairarapa	175.662	-40.9498	112

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	05.WA.POR.01	Wairarapa	175.982	-40.5495	220
	07.WN.RMK.01	Wellington	174.717	-41.2845	242
	05.WN.RIS.01	Wellington	175.211	-41.105	346
	94.WN.RIM.95	Wellington	175.232	-41.1146	561
K. cauta	01.TO.RAN.08	Taupo	176.432	-38.9174	743
	01.WN.WNU.51	Wellington	174.921	-41.2493	207
	03.TK.PRP.01	Taranaki	174	-39.1996	435
	05.AK.TAE.01	Auckland	174.32	-36.3536	78
	05.BP.MTQ.02	Bay of Plenty	177.511	-38.178	565
	05.BP.MTQ.03	Bay of Plenty	177.511	-38.178	565
	05.CL.SKB.01	Coromandel	175.528	-36.7098	78
	05.GB.TWB.01	Gisborne	177.794	-38.856	621
	05.TK.PAP.03	Taranaki	174.927	-38.9635	205
	05.TK.PKE.01	Taranaki	174.698	-39.1582	337
	05.WN.TOK.02	Wellington	175.482	-40.5854	351
	06.AK.ORR.01	Auckland	175.179	-36.9743	127
	06.ND.KAU.01	Northland	173.8	-35.2009	364
	06.ND.KAU.02	Northland	173.8	-35.2009	364
	07.GB.MAO.01	Gisborne	177.134	-38.7836	628
K. dugdalei	01.WA.BUL.01	Wairarapa	175.304	-41.3233	350
	02.AK.ORE.01	Auckland	174.693	-36.5801	18
	02.BP.CRE.02	Bay of Plenty	176.264	-38.1542	304
	02.GB.WMB.04	Gisborne	177.133	-38.749	632
	02.WA.BUL.02	Wairarapa	175.304	-41.3233	350
	05.WA.DUG.01	Wairarapa	176.166	-40.5292	176
	06.ND.WPU.01	Northland	174.665	-36.2853	75
	06.ND.WPU.01	Northland	174.665	-36.2853	75
	12.CL.PAH.03	Coromandel	175.875	-37.0312	200
	12.CL.PAH.04	Coromandel	175.875	-37.0312	200
K. laneorum	02.TK.ERS.01	Taranaki	174.146	-39.3125	691
	02.TO.OPE.01	Taupo	176.218	-38.7687	732
	02.TO.WWS.01	Taupo	175.496	-38.8949	669
	02.TO.WWS.04	Taupo	175.496	-38.8949	669
	02.TO.WWS.07	Taupo	175.496	-38.8949	669
	02.WN.DAY.01	Wellington	174.917	-41.2783	214
	03.ND.TNW.01	Northland	173.452	-35.1846	310
	03.ND.TNW.03	Northland	173.452	-35.1846	310
	03.ND.TNW.04	Northland	173.452	-35.1846	310
	03.ND.TNW.06	Northland	173.452	-35.1846	310
	03.ND.TNW.08	Northland	173.452	-35.1846	310
	03.TK.CAR.01	Taranaki	173.983	-39.2032	415

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	05.BP.MTP.02	Bay of Plenty	177.486	-38.0928	443
	05.TO.WWS.09	Taupo	175.496	-38.8949	669
	05.TO.WWS.10	Taupo	175.496	-38.8949	669
	06.ND.LAN.01	Northland	173.789	-35.1901	253
	06.ND.LAN.02	Northland	173.789	-35.1901	253
K. ochrina	00.WN.DAY.01	Wellington	174.917	-41.2783	214
	02.TO.WWS.10	Taupo	175.496	-38.8949	669
	01.WN.NEV.52	Wellington	174.829	-41.302	100
	01.WN.WNU.10	Wellington	174.921	-41.2493	213
	02.CL.PAE.01	Coromandel	175.679	-37.3885	41
	02.RI.NTK.02	Rangitaiki	176.354	-39.9343	216
	02.TO.TPP.06	Taupo	176.068	-38.6907	360
	02.WO.OTO.01	Waikato	175.255	-38.1739	85
	02.WO.OTO.02	Waikato	175.255	-38.1739	85
	02.WO.TEH.01	Waikato	175.595	-37.7881	155
	02.WO.TEH.02	Waikato	175.595	-37.7881	155
	03.ND.MGP.01	Northland	173.483	-35.1957	84
	03.ND.TPR.01	Northland	172.702	-34.4422	159
	03.ND.TPR.02	Northland	172.702	-34.4422	159
	04.MC.OCH.04	Christchurch	172.565	-43.5042	29
	05.BP.LRO.01	Bay of Plenty	176.558	-38.0498	330
	05.BP.MTN.01	Bay of Plenty	177.441	-38.0401	55
	05.CL.PCR.01	Coromandel	175.468	-36.5528	153
	05.CL.PCR.02	Coromandel	175.468	-36.5528	153
	05.GB.RIP.01	Gisborne	178.09	-37.8537	209
	05.GB.WGH.18	Gisborne	177.827	-38.7326	29
	05.ND.TWH.01	Northland	173.88	-35.1374	244
	05.TK.AIJ.03	Taranaki	174.597	-39.2296	188
	05.TK.CWW.04	Taranaki	174.071	-39.0578	11
	05.TK.ETG.01	Taranaki	174.921	-38.9698	284
	05.TK.MAI.02	Taranaki	174.124	-39.5509	83
	05.TK.RWY.10	Taranaki	174.058	-39.058	20
	05.TO.WFD.06	Taupo	175.675	-38.2872	189
	05.WA.AKN.01	Waikato	176.411	-40.5728	21
	05.WA.HPW.02	Waikato	175.226	-41.434	124
	05.WA.MKT.01	Waikato	176.016	-40.416	210
	05.WA.WHB.01	Waikato	175.172	-41.4097	13
	05.WI.MEM.01	Whanganui	175.488	-40.2402	134
	05.WI.MEM.02	Whanganui	175.488	-40.2402	134
	05.WO.RAE.01	Waikato	174.921	-37.8341	65
	94.WN.NEV.03	Wellington	174.829	-41.302	100
K.	03.WO.WTC.03	Waikato	175.101	-38.2622	84

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scutellaris					
	01.TK.TAN.01	Taranaki	174.858	-38.9822	691
	01.WN.DAY.50	Wellington	174.917	-41.2783	214
	01.WN.WNU.52	Wellington	174.921	-41.2493	213
	02.MB.PIN.01	Marlborough	173.638	-41.3483	46
	02.MB.PIN.02	Marlborough	173.638	-41.3483	46
	02.MB.WHK.04	Marlborough	173.758	-41.276	14
	05.AK.BTC.02	Auckland	174.452	-36.8863	13
	05.BP.MTR.01	Bay of Plenty	177.513	-38.1825	585
	05.BP.MTR.02	Bay of Plenty	177.513	-38.1825	585
	05.BP.WRU.01	Bay of Plenty	176.413	-38.0494	303
	05.CL.SBR.07	Coromandel	175.441	-36.5096	166
	05.GB.TRY.04	Gisborne	178.186	-37.8652	123
	05.HB.BKH.02	Hawkes Bay	176.823	-40.1708	23
	05.TK.AKE.02	Taranaki	174.753	-38.6186	41
	05.WI.WAW.02	Whanganui	175.641	-40.0363	336
	06.AK.ORR.02	Auckland	175.179	-36.9743	127
	06.MB.ONL.03	Marlborough	173.704	-41.4597	98
	06.ND.KED.01	Northland	174.028	-35.2096	9
	06.RI.RSS.01	Rangitaiki	175.286	-39.5859	248
	07.HB.BLO.02	Hawkes Bay	176.4	-39.4	659
	07.RI.PAE.02	Rangitaiki	175.722	-39.647	540
	07.RI.RAN.01	Rangitaiki	176.044	-39.7601	648
	97.TO.OPE.60	Taupo	176.218	-38.7687	732
	97.WN.JOH.70	Wellington	174.742	-41.2806	225

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Appendix 3: Support for Biogeographic Boundaries

	Northland Line	Oldest clade split	Most significant of all the lines	Kauri Line	NWSE Line	Is Wardle line significant?	Wardle Taupo Line	McGlone Taupo Line	Rogers Taupo Line
K. cutora	30.77 p-value = 0.01000 +/-0.00093	1.5 Ma	Kauri and NE/SW better than Wardle, Kauri best.	67.45 p-value = 0.0000 +/- 0.00000	42.06 p-value = 0.0000 +/- 0.00000	yes (most significant of the 3 Taupo lines)	29.08 p-value = 0.00300 +/- 0.00017	22.36 p-value = 0.0149 +/- 0.00041	28.07 p-value = 0.00287 +/- 0.00049
K. cauta	48.55 p-value = 0.07158 +/- 0.00301	1Ma then 0.5	Wardle	16.11 p-value = 0.06673 +/- 0.00252	3.33 p-value = 0.36040 +/- 0.00502	yes (most significant of the 3 Taupo lines)	36.00 p-value = 0.00079 +/- 0.00030	27.95 p-value = 0.00545 +/- 0.00076	20.30 p-value = 0.03030 +/- 0.00171
K. dugdalei	N/A	very recent < 0.25 Ma	none significant	17.01 p-value = 0.09277 +/- 0.00314	5.83 p-value = 0.23772 +/- 0.00399	NS	-21.87 p-value = 0.90762 +/- 0.00340	see Wardle	see Wardle
K. laneorum	-1.17 p-value = 0.56960 +/- 0.00497	very recent, 0.5	NW/SE fits best but just misses signf at .05 level.	see Northland	20.20 p-value = 0.06663 +/- 0.00265	NS	-0.68 p-value = 0.34436 +/- 0.00454	-15.56 p-value = 0.98297 +/- 0.00150	1.15 p-value = 0.37287 +/- 0.00515
K. ochrina	63.92 p-value = 0.00010 +/- 0.0001	1 Ma	Northland & Kauri equal in signif. and better than Wardle	35.28 p-value = 0.00010 +/- 0.0001	5.45 p-value = 0.11099 +/- 0.0033 (excluded MC.OCH)	yes (most significant of the 3 Taupo lines)	11.48 p-value = 0.00307 +/- 0.00054	9.83 p-value = 0.01129 +/- 0.00106	8.88 p-value = 0.03832 +/- 0.00184
K. scutellaris	54.80 p-value = 0.04099 +/- 0.00185	very recent < 0.25 Ma	Wardle best but Kauri is also significant (as is Northland)	28.00 p-value = 0.00545 +/- 0.00071	8.20 p-value = 0.05069 +/- 0.00196	yes (most significant of the 3 Taupo lines, tied with Rogers)	30.71 p-value = 0.00000 +/- 0.00000	28.21 p-value = 0.00050 +/- 0.00022	31.89 p-value = 0.00000 +/- 0.00000

Supplementary Table 2. Analysis of Molecular Variance calculated in Arlequin v3.5 of each hypothesized biogeographic boundary listed in Figure 1a,b

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