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ORIGINAL ARTICLE

Shifting ranges of two tree weta species (*Hemideina* spp.): competitive exclusion and changing climate

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ABSTRACT

Aim Species' responses to climate change are likely to depend on their ability to overcome abiotic constraints as well as on the suite of species with which they interact. Responses to past climate change leave genetic signatures of range expansions and shifts, allowing inferences to be made about species' distributions in the past, which can improve our ability to predict the future. We tested a hypothesis of ongoing range shifting associated with climate change and involving interactions of two species inferred to exclude each other via competition.

Location New Zealand.

Methods The distributions of two tree weta species (*Hemideina crassidens* and *H. thoracica*) were mapped using locality records. We inferred the likely modern distribution of each species in the absence of congeneric competitors with the software MAXENT. Range interaction between the two species on an elevational gradient was quantified by transect sampling. Patterns of genetic diversity were investigated using mitochondrial DNA, and hypotheses of range shifts were tested with population genetic metrics.

Results The realized ranges of *H. thoracica* and *H. crassidens* were narrower than their potential ranges, probably due to competitive interactions. Upper and lower elevational limits on Mount Taranaki over 15 years revealed expansion up the mountain for *H. thoracica* and a matching contraction of the low elevation limits of the range of *H. crassidens*. The observed nucleotide diversity in *H. thoracica* was consistent with a species that persisted in northern areas during Pleistocene glacial periods, from where it expanded at warmer times. In contrast, a two-tailed distribution of nucleotide diversity in *H. crassidens* was as expected for a species that expanded northwards during glacials and southwards during interglacials.

Main conclusions Range shifts resulting from climate change involve complex species interactions. Competition among related species is an important factor limiting realized ranges. In New Zealand, *H. thoracica* is likely to continue to displace *H. crassidens* as human-induced global warming proceeds.

Keywords

Biotic interactions, climate change, competition, *Hemideina*, mitochondrial DNA, New Zealand, phylogeography, range shifts, species range.

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INTRODUCTION

The spatial distribution of animal and plant species has long intrigued biologists (Wallace, 1876). Currently, the study of biogeography involves not only the recognition of distribution patterns but also the testing of hypotheses about the processes leading to these patterns (Crisp *et al.*, 2011). Most environments pose a variety of physical and biological challenges for organisms. When modelling species distributions, it is key to include the biotic factors that contribute to

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delimiting species' ranges, because biotic interactions shape species' distributions across all spatial scales (Acevedo *et al.*, 2012; Wisz *et al.*, 2013).

Since the start of the Pleistocene (2.6 Ma), global climate on Earth has cycled repeatedly through cool and warm extremes, influencing species distributions (e.g. range shifts in Europe; Taberlet *et al.*, 1998; Hewitt, 1999; Seddon *et al.*, 2001). As climate changes, so does regional biodiversity and the size of species' ranges. Although most easily attributable to abiotic factors, extinction, immigration and expansion are also influenced by biotic interactions, and studies of the responses of species to concurrent changes in physical (i.e. climate) and biological (i.e. competitors, predators) environmental parameters have resurged recently (e.g. Davis *et al.*, 1998; Gaston, 2003; Montoya & Raffaelli, 2010; Acevedo *et al.*, 2012; Hellmann *et al.*, 2012). This is mostly the consequence of the realization that species' responses to climate change are likely to depend not only on their ability to overcome abiotic constraints, but also on the suite of species with which they either interact now, or are likely to interact with, in the future. If viewed as elements embedded in complex networks of interactions, the patterns of species' interactions determine the stability of populations when recovering from perturbations, and the likely consequences of local species extinctions on those populations that remain (Montoya & Raffaelli, 2010). How these network properties and the ecosystems linked to them will be modified under climate change is poorly understood (Berg *et al.*, 2010; Walther, 2010). On the other hand, the genetic signatures of range expansions and shifts have been well explored (Excoffier *et al.*, 2009; Arenas *et al.*, 2012) and allow inferences to be made about species distributions in the past which can improve our ability to predict the future.

New Zealand provides a convenient environment in which to study biogeographical processes, with an elongated landscape on a north–south axis generating a subtropical to cool-temperate gradient, and a marine margin that imposes an abrupt environmental boundary. Previous studies on glacial refugia in New Zealand were developed from Northern Hemisphere models (Hewitt, 1996, 1999; Michaux *et al.*, 2003), but because glaciers only formed in part of western South Island, the idea of refugia relates primarily to shifts in broad vegetation types (Alloway *et al.*, 2007; Trewick *et al.*, 2011). Because most of New Zealand since the Last Glacial Maximum (LGM) was covered by forest, it was expected that animals and plants would show patterns of diversity consistent with the restriction of forest during glacial episodes. Evidence of this is not especially compelling (Wallis & Trewick, 2009; Trewick *et al.*, 2011): although some forest insects have a signature of expansion from northern New Zealand (e.g. stick insects, Buckley *et al.*, 2009; Morgan-Richards *et al.*, 2010), many other taxa have high levels of diversity throughout the country (e.g. Onychophora, Trewick, 1999; ferns, Shepherd *et al.*, 2007; fungus beetle, Marske *et al.*, 2009). If a recent (post-LGM) population expansion involving normal, short-distance dispersal occurred, we expect a wave-front with low genetic diversity (Excoffier *et al.*, 2009). Higher mean population nucleotide diversity is expected where large population sizes have been maintained for longer periods of time. Thus, we would expect contrasting patterns of diversity over species' ranges.

Here, we focus on the orthopteran genus *Hemideina* (tree weta), which comprises seven species endemic to New Zealand. Three largely parapatric species are found in the North Island: *Hemideina crassidens*, *H. trewicki* and *H. thoracica* (Fig. 1). *Hemideina trewicki* has the narrowest range, in eastern North Island. *Hemideina thoracica* is widely distributed in the northern two-thirds of the North Island, whereas *H. crassidens* is found in the southern third of the North Island and also in the north-west of the South Island. There is an area of intersection between *H. crassidens* and *H. thoracica* (Trewick & Morgan-Richards, 1995). At a number of sites in central North Island, *H. crassidens* populations are marooned in a sea of *H. thoracica*, suggesting competitive exclusion of *H. thoracica* by *H. crassidens* in colder microhabitats, with the reverse (*H. thoracica* excludes *H. crassidens*) in warmer areas (Trewick & Morgan-Richards, 1995). Mixed-species harems have sometimes been observed in the narrow contact zone where the two species meet, but there is no evidence of introgression (Morgan-Richards *et al.*, 1995). Differences in karyotype might explain the lack of successful interbreeding (Morgan-Richards, 1995).

We explore the events governing the current distribution of *H. crassidens* and *H. thoracica* using a combination of phylogeographical, spatial, climatic and ecological data. First, using a species distribution model (SDM), we investigated the potential range of *H. thoracica* and *H. crassidens* if other *Hemideina* species were not present. Second, we examined the effects of current climate warming experienced globally (Houghton *et al.*, 2001; Dillon *et al.*, 2010) on species' elevational limits where the two tree weta species meet on a steep environmental gradient (Mount Taranaki). Third, we predicted that mean nucleotide diversity in *H. thoracica* populations would show a cline from high in the north to low in the south (Charlesworth, 2009), whereas higher mean nucleotide diversity is expected in the centre of the range of *H. crassidens* if populations persisted in this region during glacial phases (Fig. 2).

MATERIALS AND METHODS

Background and rationale

Hemideina tree weta are primarily associated with forest and scrub, where they feed on leaves, fruits and invertebrates (Griffin *et al.*, 2011). They are flightless and nocturnal, concealing themselves in tree holes during the day (Gibbs, 1998). Adult tree weta are relatively large, with impressive spines on their hind legs, and marked sexual dimorphism (Field & Deans, 2001). The studied species have broad diets and occur in contiguous habitat with no evidence of partitioning associated with forest type. Only

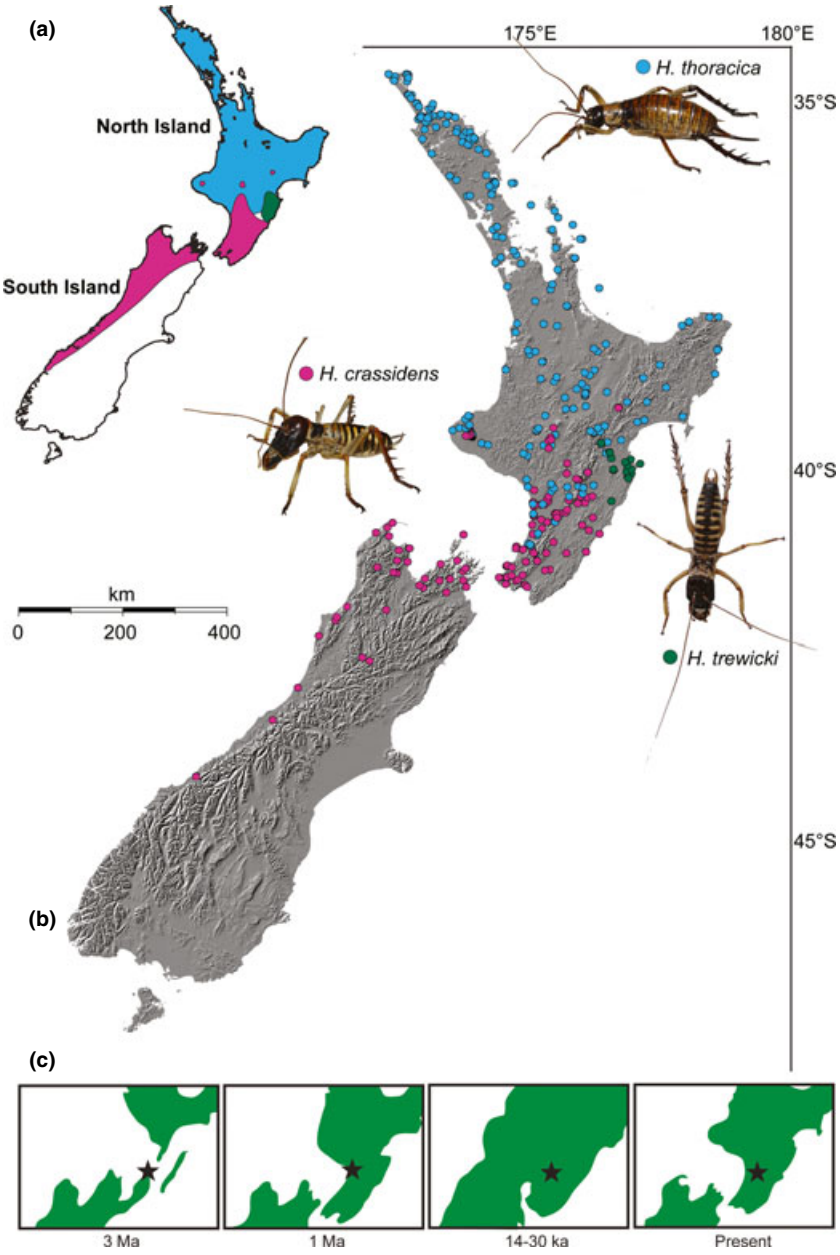

Figure 1 (a) The approximate distribution of three species of tree weta in New Zealand: *Hemideina crassidens* (in fuchsia), *H. thoracica* (in turquoise) and *H. trewicki* (in green). (b) The presence of *H. crassidens* (n = 176), *H. thoracica* (n = 267) and *H. trewicki* (n = 15) at 458 sampled point locations in New Zealand. (c) Palaeogeography of central New Zealand indicates habitat availability for terrestrial animals (redrawn from Trewick & Bland, 2012). The star marks the approximate position of Palmerston North for reference.

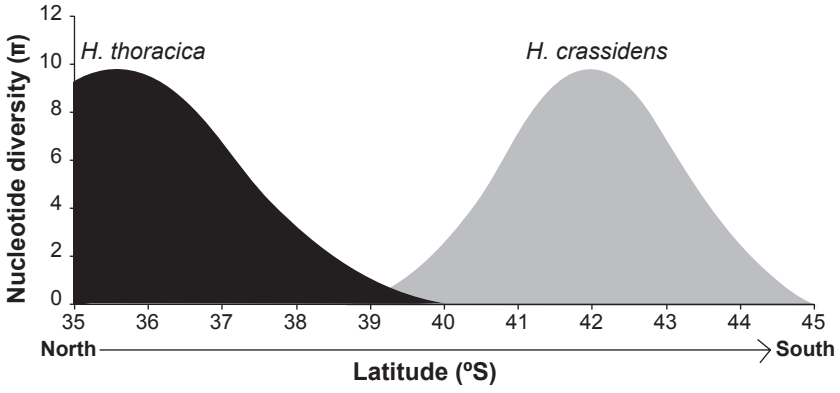

Figure 2 Predicted latitudinal distribution of nucleotide diversity for the New Zealand tree weta species *Hemideina crassidens* and *H. thoracica*, based on hypothesized past distributions and range expansion associated with Pleistocene climate cycling. Expanding populations (at range margins) have relatively low nucleotide diversity compared to stable larger populations.

climate appears to influence their distributions. Based on the mean temperatures of their current habitats (Minards, 2011) and their different cold tolerance (Sinclair *et al.*, 1999), we infer that, during Pleistocene glacial cycles, the range of *H. thoracica* was limited to the northern part of the North Island. At that time, *H. crassidens* could have extended its range northwards. Palynological evidence suggests that well-developed forests were also range-limited during the LGM (Wardle, 1963; Alloway *et al.*, 2007). *Hemideina crassidens* could have been restricted to forest remnants in the north-west region of the South Island – as suggested for cicadas (Marshall *et al.*, 2009) – or may have made use of the patchy coastal forest and scrub vegetation that was probably widespread in most other areas (Shepherd *et al.*, 2007). We hypothesize that Holocene climate warming following the LGM enabled *H. thoracica* to advance south and attain its current range (Morgan-Richards *et al.*, 2001). As *H. thoracica* advanced, competitive exclusion would explain the restriction of *H. crassidens* to the south. The range of *H. crassidens* is therefore inferred to have contracted from the north, and expanded into higher elevation/latitude environments, leaving remnant populations of a once-wider distribution. Current distributions are unlikely to depend only on the local climatic conditions that influence some invertebrates (e.g. Williams *et al.*, 2012); our observations of captive weta over many years show that they can tolerate a wide range of temperatures.

Localities and species information

Hemideina crassidens and *H. thoracica* were collected and surveyed throughout New Zealand (see Appendix S1 for specimen and locality information) under Department of Conservation collection permits (WE-31465-FAU, NM-32444-FAU, TW-32116-FAU and WA-22197-RES) where appropriate.

Current distribution and climatic data

The distributions of *H. crassidens*, *H. thoracica* and *H. trewicki* were mapped using all available locality records. We used global positioning system (GPS) coordinates in the New Zealand Map Grid (NZMG) format with the software ArcMap from ArcGIS 10.1 (ESRI, Redlands, CA, USA).

A finer-scale analysis of distribution where *H. crassidens* and *H. thoracica* replace each other on Mount Taranaki was carried out in 2008. Two mountain roads were used as elevational transects – Manaia (transect 1) and Pembroke (transect 2) – as in a previous study (Trewick & Morgan-Richards, 1995). The search area was divided into 50-m sections using GPS between 600 and 900 m a.s.l. on each transect. The forest within each section was searched in daylight for tree weta 10 m either side of the transect. The species and location of each individual found was recorded.

Inferring potential distribution of *Hemideina* species

We inferred the distributions of *H. crassidens* and *H. thoracica* in the absence of closely related ecological competitors (other *Hemideina* spp.) using climate data from the Land Environments of New Zealand (LENZ) database (Leathwick *et al.*, 2002). Preliminary analyses indicated that five climate layers were the most influential for tree weta, and these were incorporated into the modelling: mean annual temperature (°C); mean minimum temperature of the coldest month (July, representing winter minimum temperature, °C); October vapour pressure deficit (when persistent westerly winds result in strong geographical variation in vapour pressure deficits across New Zealand, kPa); annual water deficit (mm); and monthly water balance (ratio; Leathwick *et al.*, 2002, 2003). All climate layers used in LENZ are derived from mathematical surfaces (thin-plate splines) that use information from observed meteorological data (climate, location and elevation, from 1950 to 1980; Leathwick *et al.*, 2002, 2003). These climate data are held in a geographical information system as ESRI grids using NZMG coordinates. The minimum and maximum values of the five climate layers for both species are summarized in Appendix S2.

We generated species distribution models (SDMs) with Maxent 3.3.3k (Phillips *et al.*, 2006; Phillips & Dudík, 2008), which uses the maximum entropy method for modelling presence-only distribution data, by distinguishing presence from random. The model was based on 176 georeferenced localities for *H. crassidens* and 267 for *H. thoracica*. The default convergence threshold was used in Maxent, maximum iterations were increased to 5000 to allow the model time to converge, and regularization values and functions of environmental variables were selected automatically. We modelled the modern distributions of each species 15 times, using 90% of the localities to train the model and 10% to test the model. Model performance was evaluated using the area under the receiver operating characteristic curve (AUC) and the threshold-dependent binomial omission tests calculated by Maxent. The AUC varies between 0.5 (localities equally likely to be designated presence or absence) to 1 (perfect assignment of presence and absence), although AUC is below 1 in practice (Phillips *et al.*, 2006); values above 0.7 indicate adequate determination (Swets, 1988). Model predictions were visualized in ArcGIS.

Genetic data

Previously published mitochondrial cytochrome *c* oxidase subunit I (*COI*) DNA sequences (550 bp, $n = 442$) were available for *H. thoracica* (Morgan-Richards *et al.*, 2001; Morgan-Richards & Wallis, 2003). We expanded this dataset by including individuals from six new populations ($n = 494$). For *H. crassidens*, we amplified a 925-bp mitochondrial DNA (mtDNA) fragment that spans part of cytochrome *b* (cyt *b*), tRNASer and part of NADH dehydrogenase 1 (*ND1*). For most individuals, we sequenced

only the cyt *b* portion of this. The primers designed for this study are described in Appendix S3.

MtDNA sequence data (cyt *b*) were obtained from 257 *H. crassidens* individuals and also from two *H. trewicki* individuals for comparison. The sampling spans the geographical range of *H. crassidens* and includes newly discovered locations. We also obtained additional gene sequence data (i.e. *ND1*–cyt *b* for *H. thoracica* and *COI* for *H. crassidens*) for 21 representatives of these species to allow phylogenetic analysis with maximum homologous data. DNA extraction, polymerase chain reaction (PCR) and sequencing were performed following standard protocols (Trewick & Morgan-Richards, 2005).

For populations of tree weta that had not previously been used in cytogenetic studies (Morgan-Richards, 1995, 1997, 2002; Morgan-Richards & Wallis, 2003), chromosome spreads were prepared on microscope slides from freshly fixed testes of male weta, air-dried and stained with Giemsa stain. Mitotic cells were examined to infer diploid number and identify chromosome race as previously described (Morgan-Richards, 1995, 1997).

Genetic analysis

DNA sequence reads were verified for accuracy using Sequencher 4.7 (Gene Codes, Ann Arbor, MI, USA). We aligned concatenated *COI*, cyt *b* and *ND1* sequences for 21 representative *H. crassidens*, *H. thoracica* and *H. trewicki* individuals using the Geneious 5.6 (Drummond *et al.*, 2012) alignment algorithm with default parameter settings, and then checked these alignments by eye. We excluded the difficult-to-align tRNASer region, resulting in an alignment of 1128 bp (540 bp *COI*, 411 bp cyt *b* and 177 bp *ND1*). Population samples for *H. thoracica COI* and *H. crassidens ND1*–cyt *b* were aligned separately. All sequences have been deposited in GenBank (accession numbers are given in Appendix S1).

We implemented maximum-likelihood (ML) bootstrap analysis with the software PhyML (Guindon *et al.*, 2010) in Geneious 5.6. Our analysis employed a GTR+I+G model (general time-reversible with invariant sites, gamma-distributed among-site rate variation) with parameters estimated during the run with 2000 resampled datasets.

For haplotype analysis of the population data, we used the 481-bp alignment of the cyt *b* gene fragment for *H. crassidens*, and the 550-bp of *COI* for *H. thoracica*. To determine the extent of haplotype sharing among *H. crassidens* individuals, we constructed a haplotype network using the median-joining algorithm in the software network 4.1 (Bandelt *et al.*, 1999).

We defined a 'population sample' as a minimum of four weta collected from localities that were separated by less than 5 km (linear distance), with an average sample size of 8.3 for *H. crassidens* and 14.1 for *H. thoracica*. We calculated nucleotide diversity (π) for each population sample of *H. crassidens* (29 populations) and *H. thoracica* (35 populations) using Arlequin 3.5 (Excoffier & Lischer, 2010), and estimated base frequencies and genetic distances using paup* 4.0b10 (Swofford, 1998).

RESULTS

Spatial distribution

The current known distributions of *H. crassidens*, *H. thoracica* and *H. trewicki* were mapped with a total of 458 data points (Fig. 1). The latitudinal geographical range of *H. crassidens* has been extended northwards by the recent discovery of an isolated population at Whirinaki Forest Park (38.89211° S, 176.66178° E). The range of *H. thoracica* is as previously reported (Morgan-Richards, 1995; Morgan-Richards & Wallis, 2003), but new localities for *H. trewicki* include Cape Kidnappers (39.67222° S, 177.03585° E) and Boundary Stream (39.11889° S, 176.80747° E).

The modelled distribution for *H. crassidens*, based on Maxent and assuming the absence of interspecific competitors, encompasses a larger area than its current distribution (Fig. 3a). The test AUC for the SDM, averaged across all 15 runs, is moderately high (0.866, SD = 0.018). The average relative contributions of the environmental variables to the Maxent model are: mean annual temperature, 45.3%; minimum temperature of the coldest month, 22.7%; October vapour pressure deficit, 15.3%; annual water deficit, 11.3%; and monthly water balance, 5.4% (Appendix S2). Mean annual temperature was the variable with highest gain when used in isolation, according to jackknife tests of variable importance, suggesting that this variable contained the most useful information by itself. The variable that decreased the gain the most when omitted was annual water deficit. The modelled distribution for *H. crassidens* includes the southern two-thirds of the North Island but not Northland, where temperatures are on average higher than current populations experience. The inferred range includes the top half of the South Island, except for high-elevation areas of the Southern Alps, and includes areas currently occupied by the congeneric species *Hemideina femorata*, *H. ricta* and *H. maori*.

The SDM for *H. thoracica* without congeneric competitors includes most of the North Island and limited areas in the South Island (Fig. 3b). The average test AUC for the replicate runs was 0.845 (SD = 0.023). The relative contributions of the variables to the Maxent model are: mean annual temperature, 56.3%; minimum temperature of the coldest month, 28.7%; annual water deficit, 9.6%; monthly water balance, 4.8%; and October vapour pressure deficit, 0.6% (Appendix S2). Jackknife tests of variable importance indicate that minimum temperature of the coldest month was the variable with highest gain when used in isolation. The variable that had the most information that is not present in the other variables was annual water deficit. Despite extensive collections of *Hemideina* spp., *H. thoracica* has never been found south of 41° S, although suitable forest appears to exist there.

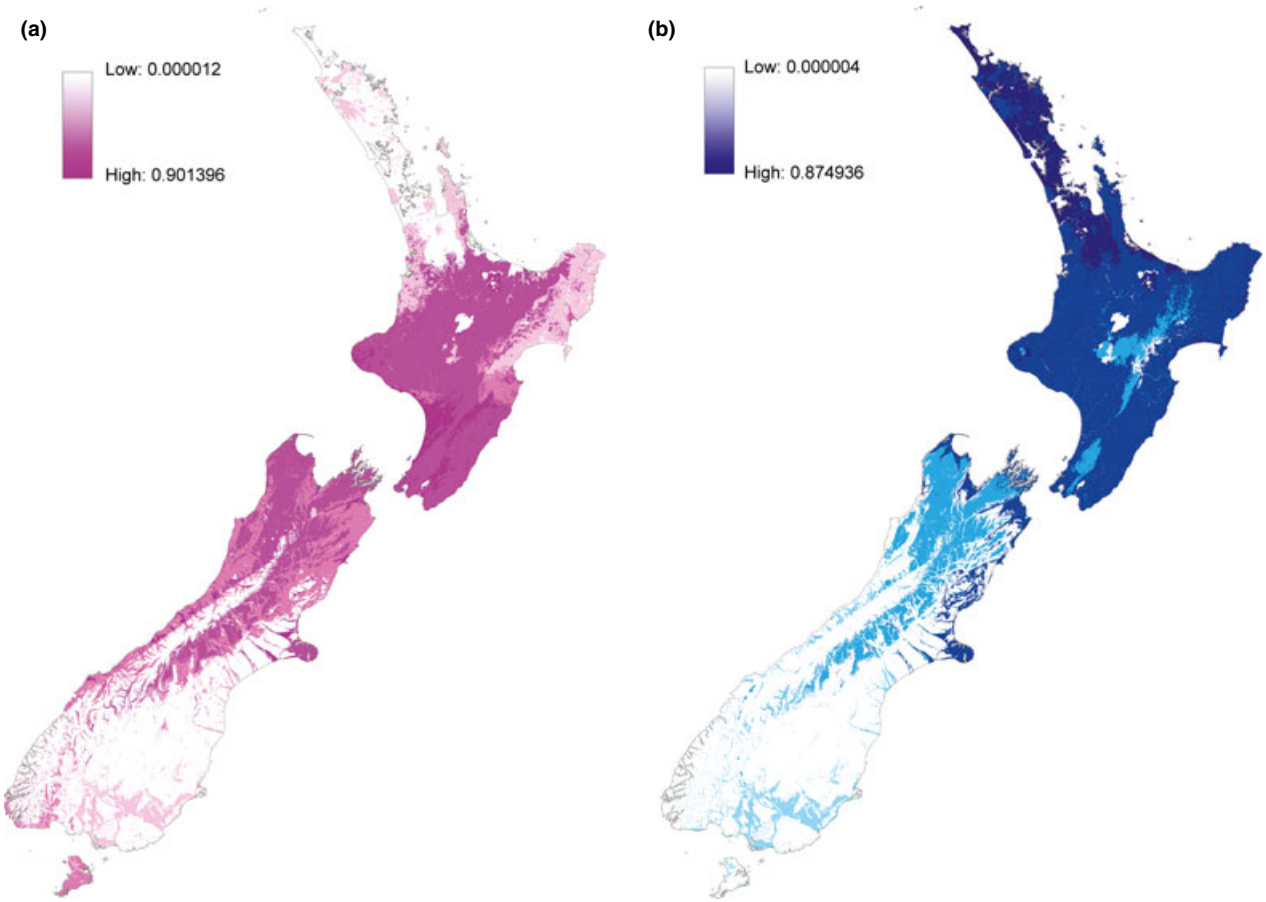

Figure 3 Ecological niche model projections of the current distributions of two New Zealand tree weta species (a, *Hemideina crassidens*; b, *H. thoracica*) when competition or other range-limiting factors are not included. Environmental variables for the MAXENT model are: mean annual temperature; minimum temperature of the coldest month; October vapour pressure deficit; annual water deficit; and monthly water balance. Dark colours indicate land inferred to be within the niche and pale represents land outside the niche. The intensity of shading is proportional to the probability of presence in a given area. The maximum probability of presence in (a) is 0.901396 and in (b) is 0.874936.

Changes in distribution on an elevational gradient: Mount Taranaki

In 2008, 73 tree weta were located along two Mount Taranaki transects. The maximum number of individuals found within any 10 m × 50 m section was 20, but in some sections no weta were located. Both species of tree weta were found at the same search section once on each transect. In one instance, the two species were sharing the same tree-hole refuge. Estimates of the elevational overlap of the two species were 14 m (transect 1) and 6 m (transect 2). The lower range limit for *H. crassidens* on both transects of this study was higher than recorded in 1993 and, concordantly, the upper range limit at which *H. thoracica* was found was higher than recorded in 1993, on both transects (Table 1).

Table 1 Lower and upper elevational limits on Mount Taranaki, New Zealand, for *Hemideina crassidens* and *H. thoracica*, respectively.

		Elevation (m a.s.l.)	
	Transect	1993*	2008
Lower range limit	1	650	789
for *H. crassidens*	2	810	822
Upper range limit	1	680	803
for *H. thoracica*	2	780	828

*Data for 1993 from Trewick & Morgan-Richards (1995).

Intraspecific genetic variability

Maximum-likelihood (ML) analysis of data from three mitochondrial genes for the three North Island *Hemideina* species confirmed their reciprocal monophyly and the presence of three distinct clades within *H. crassidens* (Fig. 4). Analysis of population-level sampling of mtDNA sequences from *H. crassidens* revealed 95 unique haplotypes among 257 individuals. The same three well-differentiated clades, identified using neighbour-joining and ML analyses, were recovered in the haplotype network (Fig. 5). Genetic distances between

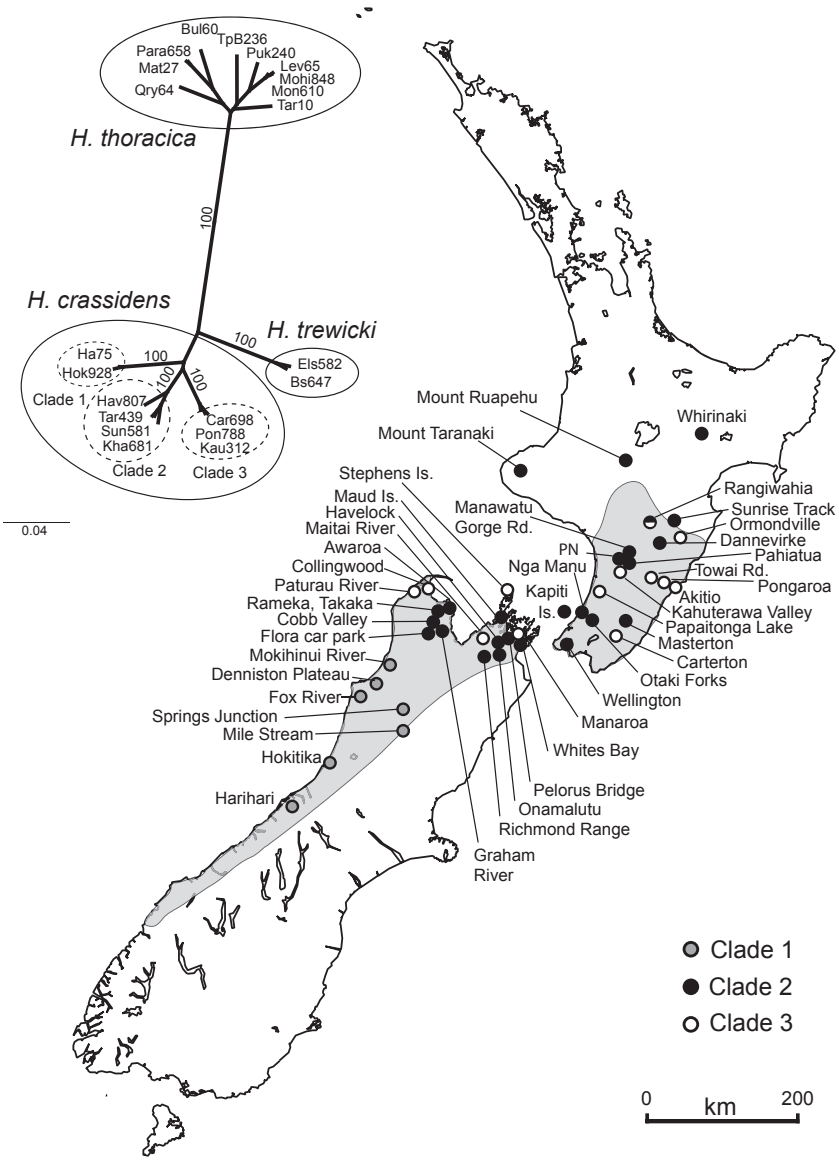

Figure 4 Distribution of the three mitochondrial DNA haplotype clades identified within *Hemideina crassidens* in New Zealand. The shaded areas indicate the range of *H. crassidens* (redrawn from Gibbs, 1998). The names correspond to collection localities. Clade 1 is concordant with the 19-chromosome race, whereas the 15-chromosome race is represented by clades 2 and 3. The inset shows a phylogenetic tree inferred for the three *Hemideina* species found in the North Island using maximum-likelihood analysis of concatenated data from three mitochondrial gene fragments (*COI*, cyt *b*, *ND1*; 1128 bp). Values on branches represent the level of support (%) for that node as indicated by maximum-likelihood bootstrap resampling.

the three clades calculated using a GTR model (variable base frequencies; symmetrical substitution matrix) were relatively high for within an insect species. Clades 2 and 3 were separated by an average distance of 0.07 (SD = 0.007), clades 1 and 2 by a distance of 0.08 (SD = 0.009), and clades 1 and 3 by a distance of 0.09 (SD = 0.009). Similar genetic distances were returned using uncorrected *p* (pairwise distances).

Clade 1 comprised all South Island *H. crassidens* that belong to the 19-chromosome race [$2n = 19$ (male, XO) or 20 (female, XX); Morgan-Richards, 2002]. This chromosome race was thought to be restricted to an area south of the Buller River, but individuals from the Denniston Plateau and Mokihinui River (Fig. 4) were found to have this karyotype. Clades 2 and 3 belonged to the 15-chromosome race and came from South Island and North Island localities with no discernible pattern. Gene flow seems to be low enough to allow population differentiation, with almost every location having a novel haplotype (of 95 haplotypes, only 7 were shared among populations; Fig. 5).

Of particular interest were the three isolated *H. crassidens* populations in the central North Island. *Hemideina crassidens* from Mount Ruapehu had two unique haplotypes that were closely related to the haplotypes from the Mount Taranaki population sample. Mount Taranaki weta had two haplotypes, one of which was found in 93% of the Mount Taranaki individuals and another of which was found in only one individual from Manaia Road. The commonest haplotype in Mount Taranaki was also found in four individuals from elsewhere in the North Island (Pahiatua and Dannevirke; Fig. 5). All individuals from Whirinaki Forest Park had the same unique haplotype that was most similar to *H. crassidens* haplotypes from White's Bay, Marlborough Sound, South Island (about 400 km away).

We found 90 different haplotypes in the 35 *H. thoracica* populations sampled. An unusually high GC (guanine+cytosine) content of 41.6% was found for *COI*, a bias previously reported by Morgan-Richards *et al.* (2001).

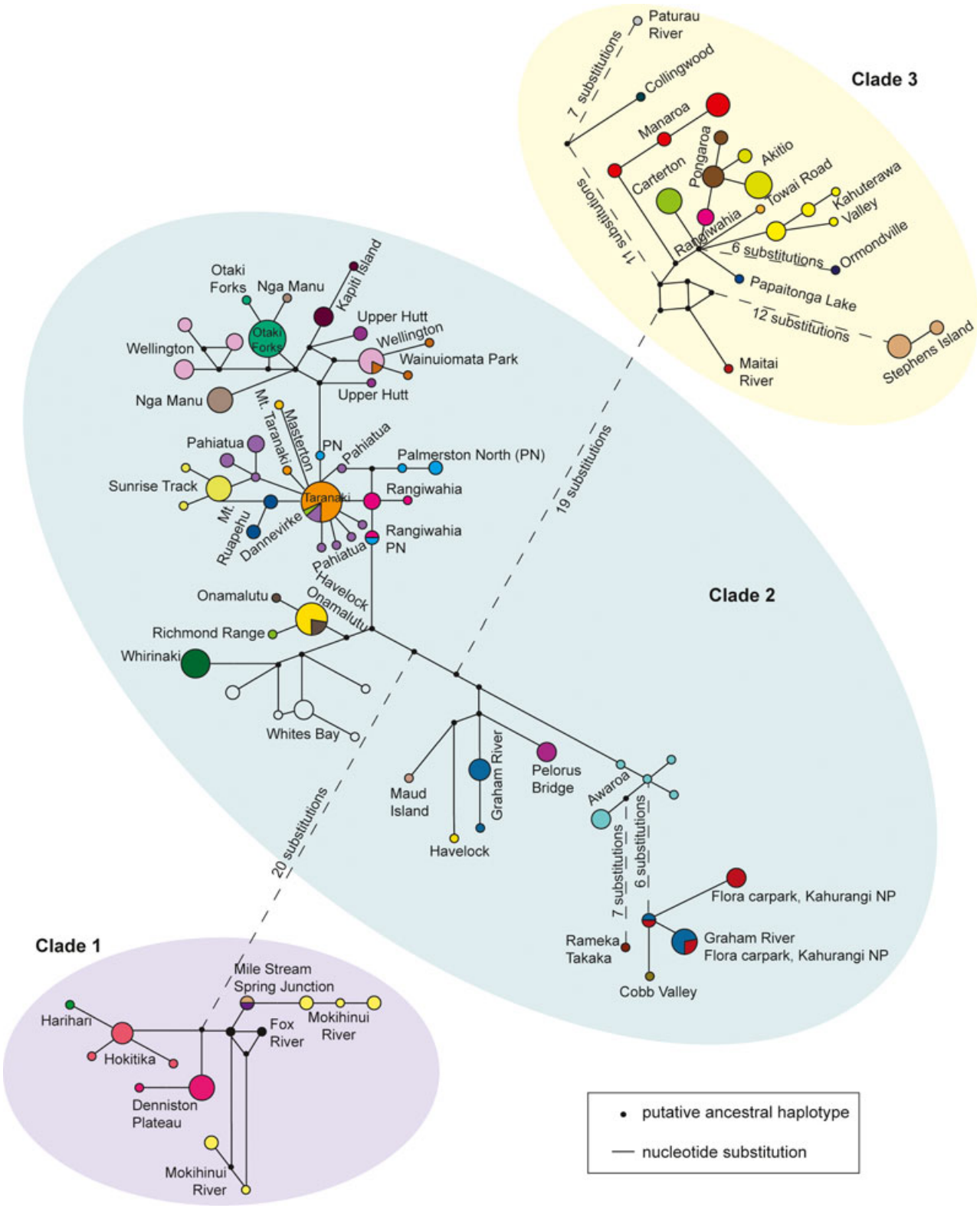

Figure 5 Unrooted parsimony network for *Hemideina crassidens* (n = 257) in New Zealand, showing the relationships of cyt *b* haplotypes. The areas of the circles are proportional to the number of haplotypes observed. PN, Palmerston North.

In accordance with our prediction (Fig. 2), we found that mean population nucleotide diversity (π) in *H. thoracica* formed a cline with the highest values in the north and the lowest in the south of its range (Fig. 6). In contrast, but as predicted, π was highest in the centre and northern extent of the range of *H. crassidens* (Fig. 6). The population sample

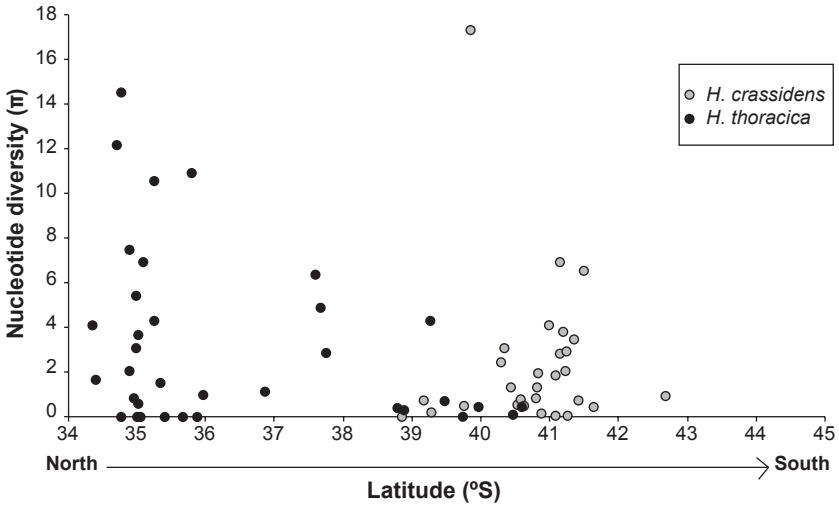

Figure 6 The distribution of nucleotide diversity (π) in population samples of two New Zealand tree weta across latitude. For *Hemideina crassidens*, π was estimated from 257 aligned sequences of 481 bp cyt *b* mtDNA (grey), and for *H. thoracica*, π was estimated from 442 aligned sequences of 550 bp *COI* mtDNA (black). Note the highest π observation for *H. crassidens* ($\pi = 17.3$) corresponding to weta from Rangiwahia Hut Track with haplotypes from both clades 2 and 3.

with the highest nucleotide diversity within *H. crassidens* was Rangiwahia Hut Track in the Western Ruahine Forest Park, where haplotypes from both clades 2 and 3 were found at the same locality (see outlier in Fig. 6).

DISCUSSION

Range shifts

The effect of climate change on single species' distributions and regional biodiversity has been commonly predicted from a simple climate envelope model (e.g. Bakkenes *et al.*, 2002; Erasmus *et al.*, 2002) assuming that the observed distributions of species are in equilibrium with their current environment and can survive anywhere inside the defined conditions. Such models exclude the role of biotic interactions in determining species' distributions (Poloczanska *et al.*, 2008; Kissling *et al.*, 2012). Understanding how climate and biology interact is important if we are to forecast biological responses to climate change (Brooker *et al.*, 2007; Wisz *et al.*, 2013). Our approach incorporates current climate data from weta ranges and considers the role of interspecific interactions. The geographical ranges of *Hemideina* species almost certainly shifted in response to climatic conditions during the Pleistocene glaciations and post-glacials. The parapatry of *H. crassidens* and *H. thoracica* (by latitude and elevation) indicates a degree of competitive exclusion. Isolated populations of *H. crassidens* in central North Island within areas otherwise occupied by *H. thoracica* suggest past range contraction due to interactions with competitors and the environment. We tested this putative competitive exclusion interaction by inferring the suitable habitat currently available if the congeneric species were not present. Evidence that climatic conditions by themselves are not a barrier to colonization of the southern portions of the North Island by *H. thoracica*, and of the central North Island by *H. crassidens*, strengthen the inference of competitive exclusion.

Our fine-scale record of change in the distribution of the two *Hemideina* species on Mount Taranaki supports the hypothesis of competitive exclusion together with climate-driven range shifting. *Hemideina thoracica* is currently at the expanding edge while the range of *H. crassidens* seems to be contracting. Over the country as a whole, average temperatures were colder than normal in the early 1990s, but between 1993 and 2008, 10 of the 15 years were warmer than average, resulting in an approximate 0.2 °C increase in mean annual temperature (Wratt *et al.*, 2009). We observed short-term and short-range shifts in elevational distribution of the two species as expected from warmer temperatures over this time supporting a climate-driven range shift. With the current data, we cannot disentangle climate and competition as the determining factor of the range shifts.

Genetic diversity patterns

Populations in recently colonized areas are typically characterized by low levels of genetic diversity compared to older, more stable populations. Large populations retain alleles for longer, because drift removes alleles more slowly and more derived sequences are present due to the accumulation of mutations given the increased time to coalescent (Excoffier *et al.*, 2009). Thus, genetic diversity is positively correlated with population size (Charlesworth, 2009). We used mean pairwise nucleotide diversity in two *Hemideina* species to detect population expansion associated with range shifting. Population nucleotide diversity matched the predicted pattern, from which we infer recent southward expansion of both species. With continued global warming, we expect this expansion to continue southwards, with the likely displacement of *H. crassidens* from many lowland areas of central and southern North Island.

The low genetic diversity found in the southernmost populations of *H. crassidens* in the South Island is probably due to recent short-distance dispersal. Post-glacial range expansions in the South Island from one or more northern refugia have been documented in cicadas (*Kikihia subalpina*), leading to cicadas with the same mtDNA haplotypes being found on both sides of the Southern Alps (Marshall *et al.*, 2009).

Morgan-Richards (2002) concluded that a distinct *H. crassidens* karyotype in individuals from South Island's west coast might have had its origins during a recent southward expansion, but this does not explain the distinct mtDNA haplotypes (clade 1) in the 19-chromosome race. MtDNA data corroborate the karyotype data, but suggest an older origin than the post-LGM expansion.

Previous studies of putative Pleistocene refugia for New Zealand animal species have tended to assume that the documented range shifts of many forest plants (mostly from palynology; see McGlone *et al.*, 2010) would dictate the animals' ranges. Shepherd *et al.* (2007) found that for some plants (the fern *Asplenium hookerianum*), genetic diversity did not support this idea, but instead implied the persistence of populations even in the absence of forest. For animals too, as in the present case, it appears that past vegetation distribution cannot always be taken as a direct proxy for past animal distribution. Tree weta (*Hemideina* spp.) mainly eat leaves and usually live in tree holes, suggesting a reliance on forest. However, many extant tree weta populations occupy scrub habitats or even use rock refuges when trees are not available (Scott *et al.*, 2012).

Species' range shifts in the past and changes that continue today involve complex networks of species interactions, the results of which are influenced by local climatic conditions. Although climate is important, it must be viewed as part of a larger network of variables in determining the outcome of species' interactions and the changing environment. Here, competitive interactions are highlighted as key parts of these networks and predictions can be made that incorporate these factors (see also Kissling *et al.*, 2012). Our finding that tree weta populations on a steep environmental gradient are highly sensitive to short-range climate fluctuation indicates that they will be informative indicators of the effects of human-induced climate change.

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SUPPORTING INFORMATION

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

Appendix S1 Localities and sample sizes for all tree weta (*Hemideina*) specimens included in genetic analyses in this study.

Appendix S2 Mean, minimum and maximum values, and relative contributions to the MAXENT model of the five climate layers used for inferring the distributions of *H. crassidens* and *H. thoracica.*

Appendix S3 Primers used to amplify and sequence mtDNA from tree weta.

BIOSKETCH

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Author contributions: S.A.T., M.M.R. and M.B. conceived and brainstormed the ideas. M.M.R. and S.A.T. generated karyotype information and undertook genetic analyses. M.B. obtained most genetic and locality data, and led the writing. N.A.M. collated the distributional data points, and M.J.J. collected the Mount Taranaki data.

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