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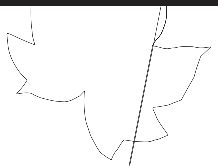

delimiting species' ranges, because biotic interactions shape species' distributions across all spatial scales (Acevedo et al., 2012; Wisz et al., 2013).

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 micro-

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In accordance with our prediction (Fig. 2), we found that mean population nucleotide diversityp)(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,p [illegible] *H. c a de*

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 types nt

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