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BIODIVERSITY RESEARCH

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Persistence of genetic diversity and phylogeographic structure of three New Zealand forest beetles under climate change

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Abstract

Aim: Contemporary climate change is predicted to impact all levels of biodiversity, including intraspecific genetic diversity, the evolutionary basis for future adaptation. While numerous studies use species distribution models (SDMs) to predict species' future distributions, relatively few investigate potential climatic impacts on the spatial structure of genetic diversity, and how it varies across species ranges. We revisited phylogeographic data for three New Zealand forest beetles to predict the effects of climate change on the geographic distributions, genetic diversity and phylogeographic structure for each species.

Location: New Zealand

Methods: We used ensemble SDMs to predict potential distributions for *Agyrtodes labralis* (Leiodidae), *Brachynopus scutellaris* (Staphylinidae) and *Epistranus lawsoni* (Zopheridae) in 2035, 2065 and 2100. To assess the impact of predicted range loss on genetic diversity and phylogeographic structure, we estimated haplotype and nucleotide diversity, Φ_{ST}, Average Taxonomic Distinctness (AvTax), Phylogenetic Diversity (PD) and Net Relatedness Index (NRI) under current and future climatic scenarios, excluding sequences from localities predicted to become unsuitable. We tested whether predicted population loss was spatially clustered and how losses were distributed across the phylogenies of each species.

Results: *Agyrtodes labralis* is predicted to lose parts of its current distribution by 2100, with the loss of 50% of unique haplotypes and a significant reduction in PD, while *Brachynopus scutellaris* and *Epistranus lawsoni* will likely experience an expansion in climatically suitable area and little change in genetic diversity. *Brachynopus scutellaris* populations are predicted to be more phylogenetically clustered than expected by 2100, but changes in AvTax were negligible for all species.

Main conclusions: We demonstrate that the loss of genetic diversity under climate change is significant; however, intraspecific lineages with deep genetic divergences are widely distributed, buffering against greater change in phylogeographic structure. For species with strong geographic clustering of genetic diversity, climate change impacts may be quite different.

KEYWORDS
biodiversity scenarios, climate change biogeography, conservation phylogeography, genetic diversity, phylogenetic diversity, species distribution modelling

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1 | INTRODUCTION

Global climate is changing, and its impacts upon biodiversity are anticipated to be profound (Moritz & Agudo, 2013). Species confronted with significant change have a limited suite of potential responses: They can disperse to follow suitable climates, persist via phenotypic plasticity or adapt to the changing conditions within their current distribution (Hoffmann & Sgrò, 2011; Parmesan & Yohe, 2003). Numerous systems provide evidence that species are already on the move, with geographic range shifts (Giersch et al., 2015; Moritz et al., 2008; Morueta-Holme et al., 2015) resulting in changes to community composition and richness patterns (Dornelas et al., 2014; Gottfried et al., 2012; Thomsen et al., 2016). Furthermore, there is evidence that climate-driven range shifts and reduction have already led to detectable genetic erosion in some species (Jordan et al., 2016; Rubidge et al., 2012). While the likelihood of the persistence of genetic diversity has been investigated for species from a variety of geographic regions, less is known about how different configurations of range dynamics may buffer or exacerbate the impacts of climate change on genetic diversity. Also, surprisingly, few studies assess the effects of predicted genetic erosion in a phylogenetic context to test how this basic diversity loss may potentially eradicate the evolutionary history of these species (e.g., Bálint et al., 2011).

Genetic diversity and events of population divergence are not evenly distributed across space; rather, they are a product of how species have responded to geographic variation in climatic change, landscape evolution, biotic interactions and other factors in both the past and the present. For example, a wealth of evidence indicates that species persisted through the climate change of the Late Quaternary in glacial refugia, from which they later expanded their ranges, leaving characteristic distributions of genetic richness (Hewitt, 2000). The genetic consequences of this movement are increasingly well known, with the erosion of genetic diversity in leading edge populations during range shifts and postglacial expansion (Arenas, Ray, Currat, & Excoffier, 2012; Hewitt, 2000; Waters, Fraser, & Hewitt, 2013). For many species which experienced significant range shifts during the Late Quaternary, genetic diversity in recently colonized areas is still a subset of that at the trailing edge (Johansson, Stoks, Nilsson-Örtman, Ingvarsson, & Johansson, 2013; Pellissier et al., 2016). Thus, the magnitude of genetic diversity loss and pruning of evolutionary relationships over the coming century is highly contingent upon which part of the range disappears, as well as how much and how fast.

Given these findings, coupled with the significant number of species globally which are predicted to lose parts of their current ranges over the next few decades (Loyola, Lemes, Brum, Provete, & Duarte, 2014; Thomas et al., 2004), there is growing concern regarding the genetic consequences of anthropogenic climate change (Moritz & Agudo, 2013; Pauls, Nowak, Bálint, & Pfenninger, 2013). Species distribution models (SDMs) have long been instrumental in predicting the effects of climate change on species geographic ranges, and applying them to assess the future distribution of genetic diversity is a natural next step (e.g., Bálint et al., 2011; Inoue & Berg, 2017). Results of these studies have yielded significant insights into how the landscape of intraspecific divergence shapes species' risk of genetic erosion under climate change. For example, one study of nine European aquatic insect species found that the most imperilled parts of their ranges were the low-latitude margins and low mountain ranges—regions which harbour a high proportion of endemic intraspecific lineages (Bálint et al., 2011). Another European study found a similar pattern, that the oldest and most genetically diverse parts of the range of a bat species were those at highest risk from climate change (Razgour et al., 2013). Finally, a study of 27 northern Holarctic plant species indicated that those species not adapted to long-distance dispersal will likely to lose genetic diversity at twice the rate of species with such adaptations, given similar levels of range loss, and that this is related to the uneven distribution of diversity across their ranges (Alsos et al., 2012). Rarely have the results of these studies painted an optimistic picture of the future (however, see Alsos, Alm, Normand, & Brochmann, 2009).

We integrate SDMs, population genetic and phylogenetic comparative methods for three New Zealand forest beetles to estimate how much existing genetic diversity is likely to remain by the end of this century, and the extent to which its loss will erode evolutionary relationships among surviving populations. The distribution of genetic divergence for these species reflects New Zealand's dynamic geological history, including persistence in multiple distinct forest refugia during the Last Glacial Period. Mitochondrial lineages are spatially structured relative to that climatic history and to the recent topographic evolution of New Zealand, particularly the uplift of the Southern Alps, which transect New Zealand's South Island (Marske, Leschen, Barker, & Buckley, 2009; Marske, Leschen, & Buckley, 2011, 2012). Saproxylic beetles represent an important component of forest biodiversity in New Zealand and elsewhere, and studies predict complex responses of these communities to climate change and habitat disturbance (Müller et al., 2015; Thom et al., 2017). End-century temperature increase in New Zealand is predicted to be slightly below the global average, but seasonal changes in precipitation may be dramatic, and there is substantial variation among climate models in their predictions of future precipitation patterns (Ministry for the Environment, 2016; Mullan et al., 2008; Reisinger, Mullan, Manning, Wratt, & Nottage, 2010). In particular, strong variation in winter and summer precipitation may affect the forested areas of the northern South Island which harbour unique genetic lineages across multiple arthropod species (Boyer, Baker, & Giribet, 2007; Marshall, Hill, Fontaine, Buckley, & Simon, 2009; Marske et al., 2012). Due to this phylogeographic structure underlying each species range, we investigate the extent to which the predicted loss of genetic diversity will be spatially clustered or widely distributed across the ranges of our focal species, and whether these losses will be sufficient to affect phylogeographic structure.

2 | METHODS

2.1 | Taxon sampling and intraspecific phylogenies

Focal taxa included *Agyrtodes labralis* (Broun, 1921) (Leiodidae), *Brachynopus scutellaris* (Redtenbacher, 1868) (Staphylinidae) and *Epistranus lawsoni* (Sharp, 1876) (Zopheridae). *Agyrtodes labralis* and *E. lawsoni* are endemic to the New Zealand archipelago, while *B. scutellaris* also occur on the outlying Chatham Islands. These species are widely distributed in the South (*A. labralis*) or North and South Islands (*B. scutellaris*, *E. lawsoni*), despite *E. lawsoni* being wingless. All species feed on saprophytic fungi such as polypores and corticoids and are found in dead wood and leaf litter of native southern beech and podocarp forests (Leschen, Buckley, Harman, & Shulmeister, 2008; Marske et al., 2009, 2011). Geographic localities and mitochondrial CO1 sequence data for *A. labralis*, *B. scutellaris* and *E. lawsoni* were the same as in Marske et al. (2012) and Buckley and Leschen (2013), excluding individuals from offshore islands and some coastal regions which were outside the extent of our climatic data (see Supporting information Appendix S1 for GenBank Accession codes).

Intraspecific phylogenies of the three species were generated using Bayesian methodology in BEAST 1.8.0 (Drummond & Rambaut, 2007; Drummond, Suchard, Xie, & Rambaut, 2012), in association with the beetle-specific CO1 divergence rate of 3.54% per MY (Papadopoulou, Anastasiou, & Vogler, 2010) and the parameters of sequence evolution, population growth and molecular clock model specified by Marske et al. (2012) and Buckley and Leschen (2013) (see Supporting information Appendix S1 for details). These analyses replicate those previously published because we needed a selection of trees from the posterior distribution for subsequent comparative analyses. The sequence alignments of each species were analysed under these settings five times independently, with the MCMC chains for *A. labralis* and *B. scutellaris* run for 50 million generations, and those of *E. lawsoni* for 20 million generations. The resulting trees were sampled every 2,000 or 1,000 generations, respectively. The log files of these runs were inspected with Tracer 1.6 (Rambaut, Suchard, Xie, & Drummond, 2014) to ensure that the models had reached a stable distribution, and that chain mixing and convergence were adequate. For each species, posterior trees from all five runs were combined and reduced in size using LogCombiner, with burn-in and resampling frequency as indicated in Supporting information Appendix S1. Subsequently, we summarized this distribution of phylogenies in TreeAnnotator as a Maximum Clade Credibility (MCC) tree (Drummond et al., 2012). The resulting MCC trees had topologies and nodal support consistent with those previously published (see Marske et al., 2009, 2011, 2012).

2.2 | Climate data and variable selection

Climate data for species distribution modelling were obtained from the NIWA National Climate Centre, Wellington, New Zealand, at a spatial resolution of 5 km. Baseline data included mean seasonal temperature (Kelvin) and mean daily precipitation (mm) for the period 1986–2005 (Andrew Tait, NIWA, pers. comm.). Future climate change projections, given as absolute change in mean monthly temperature and percentage of monthly precipitation averaged over the periods 2016–2035 (near-future), 2046–2065 (mid-century) and 2081–2100 (end-century), were obtained for three General Circulation Models (GCMs): GFDL-CM3, HadGEM2-ES and NorESM1-M. These were selected because they captured the wide variation in predicted changes in precipitation for New Zealand (see https://ofcnz.niwa.co.nz/#/nationalMaps for images of the different scenarios). All GCMs incorporated three different Representative Concentration Pathways (hereafter RCPs), including two greenhouse gas stabilization pathways (RCP 4.5 and 6.0) and one high concentration pathway (RCP 8.5) (IPCC, 2013). All climate change scenarios were fitted specifically to New Zealand using a combination of statistical and dynamical downscaling (Ministry for the Environment, 2016, and sources therein). From these data, we derived seasonal (winter, spring, summer, autumn) variables for mean temperature (°C) and mean daily precipitation (mm) for all time periods for use in SDMs.

2.3 | Species distribution models

Ensemble species distribution models were generated using R Version 3.2.0 (R Core Team, 2015) and the package *biomod2* (Thuiller, Georges, & Engler, 2014). Ensemble forecasting integrates the results of multiple SDM algorithms into a single geographical projection for each time period, reducing the uncertainties associated with the use of a single model algorithm (Araújo & New, 2007; Garcia, Burgess, Cabeza, Rahbek, & Araújo, 2012). Models were calibrated using the GBM, GLM, GAM, RF, CTA, ANN, MARS and FDA algorithms (Supporting information Appendix S2) and 84 localities for *A. labralis*, 123 for *B. scutellaris* and 174 for *E. lawsoni*. Models were calibrated using a unique set of randomly drawn pseudoabsences (5 × the number of presence localities) and a different randomly selected 70% of localities to train the model and 30% to test the model for each of the 20 cross-validation runs. Models were also calibrated using the full data set for each pseudoabsence set. We assessed the performance of individual models using the Area under the Curve (AUC) of the Receiver Operating Characteristic (ROC) plot (Fielding & Bell, 1997). For each cross-validation run with AUC ≥ 0.7, we retained the corresponding full-data run for the final ensemble, for a maximum of 160 possible models for each GCM, RCP and period combination. These were assembled as a weighted mean ensemble (Marmion, Parviainen, Luoto, Heikkinen, & Thuiller, 2009).

To predict the extent of suitable climatic conditions for each species at 2035, 2065 and 2100 for each RCP, we first forecast each GCM-weighted mean ensemble separately for the three species, implementing a clamping mask in *biomod2* to limit our projections to the set of climate conditions encountered by the models during testing; areas which fell outside of these projections were excluded from future predictions. To designate areas as suitable/not suitable for subsequent phylogenetic analyses, we applied a threshold of

AUC ≥ 0.7 to each GCM ensemble. Given the variability in predicted future precipitation patterns (Ministry for the Environment, 2016,), our thresholded consensus prediction for each species, period and RCP included all areas considered as suitable in at least one GCM. GCM-weighted mean ensembles were also averaged to attain a continuous-suitability consensus model for each species per period for each RCP.

2.4 | Present and future genetic/phylogenetic diversity

To estimate the effects of the different climate change scenarios on extant population genetic diversity and structure, we identified localities (and associated sequences) predicted to be present or absent under each climatic scenario. For all sequences and for those in localities predicted to remain climatically suitable, we estimated nucleotide diversity (Nei, 1987), haplotype diversity (Nei & Tajima, 1981) and Φ_{ST} (Excoffier, Smouse, & Quattro, 1992). Genetic statistics were calculated using the R packages *pegas* (nucleotide diversity; Paradis, 2010) and *strataG* (haplotype diversity and Φ_{ST}; Archer, Adams, & Schneiders, 2017); note that *strataG* only estimates the between-population component of Φ_{ST}, in this case individual localities. Because *pegas* and *strataG* are sensitive to missing data, 21 and 27 base pairs were removed from the ends of the alignment for *A. labralis* prior to running these analyses.

To identify whether the predicted loss of populations under climate change could result in significant changes in evolutionary relatedness and phylogenetic diversity, we computed Average Taxonomic Distinctness (AvTax; Clarke & Warwick, 1999), Faith's D (PD; Faith, 1992; Moritz & Faith, 1998) and the Net Relatedness Index (NRI; Webb, 2000). AvTax estimates the average phylogenetic distances, in terms of branch lengths, between all species pairs within a given community or site. Here, we compared the intraspecific phylogenies of each beetle species (in which sequenced individuals are the terminal taxa) to 'future' phylogenies in which taxa from populations predicted to occur in areas that become climatically unsuitable have been pruned. Differences in AvTax values between present and future climate scenarios do not describe the potential loss of phylogenetic diversity per se, but a change in the average branch length among taxa (here individual sequences), such that a systematic loss of either closely or distantly related intraspecific lineages results in a decrease or increase in relatedness. PD calculates the sum of the branch lengths of a given phylogeny (Faith, 1992), which we estimated on both the contemporary phylogeny and on our climatically pruned trees; changes in phylogenetic diversity, in this case, represent changes in genetic diversity. Finally, NRI assesses whether a set of taxa (here, sequences predicted to remain under the various climate scenarios) are more closely or distantly related on the phylogeny than expected by chance (Webb, 2000).

To ensure that observed reductions in genetic or phylogenetic diversity were not simply the result of analysing a smaller sample size, we evaluated our climate change results for each metric against one or two null models. First, for the population genetic statistics, AvTax and PD, we drew 1,000 subsets of taxa independently that maintained the same number of localities predicted to remain suitable under each climate change scenario, sampling all associated sequences from those localities. This null model tests for a geographical bias in the localities lost, while accounting for the reduced number of localities. For each null subset, we recalculated our metrics of genetic and phylogenetic diversity, comparing the empirical test values against the distribution of these values, using a two-tailed *t*-test. Second, for AvTax and PD, we compared our pruned trees against 1,000 unpruned random draws across the posterior distribution of post burn-in phylogenies, to determine whether differences between present and future scenarios exceed the variation in phylogeographic structure expected from phylogenetic uncertainty in the branch length estimation. Finally, for NRI, we drew 1,000 subsets of taxa independently for each climate change scenario that maintained the same number of sequences predicted to remain, irrespective of the localities at which they are found. This tested the extent to which future losses are scattered or clustered across the phylogeny. As some island and coastal populations for all three species fall outside the extent of our climate data, we provided estimates of PD and AvTax for both the full alignment and the modelled current distribution for each species. All tips not present in the current modelled distribution were pruned from the phylogenies prior to performing all randomizations for AvTax, PD and NRI. Phylogenetic analyses were performed in R using a custom script.

3 | RESULTS

3.1 | Present and future geographic ranges

Ensemble models of the distributions for all species showed good predictive ability, with average AUC scores of 0.959 (*A. labralis*; range 0.956–0.961), 0.941 (*B. scutellaris*; range 0.940–0.943) and 0.937 (*E. lawson*; range 0.931–0.939). Predicted contemporary distributions are consistent with previous SDMs for these species (Marske et al., 2012), with *A. labralis* and *B. scutellaris* predicted to be widely distributed throughout the South Island, and *E. lawsoni* projected to have a more northerly distribution encompassing the North Island (Figure 1; Supporting information Appendix S2, Figures S2.1–6). Future projections indicate a complex response to climate change by *A. labralis*, with the southern and eastern parts of this species' distribution growing, shrinking and shifting between periods for all RCPs (Figure 1a; Supporting information Figure S2.4). An eastward shift of suitable area for *A. labralis* is projected by 2100 under all RCPs, with increasing patchiness and eventual loss of range along the west coast most pronounced in RCP 2100. Expansion in suitable Southland area projected under RCPs 4.5 and 6.0 is not indicated for RCP 8.5 for *A. labralis*. In contrast, the climatic distribution of *B. scutellaris* is projected to increase under all climate scenarios, particularly in the south-eastern South Island and north-eastern North Island (Figure 1b; Supporting information Figure S2.5). No major regions of its current climatic distribution are predicted to be lost, although its range within central Nelson

(a) *Agyrtodes labralis*

(b) *Brachynopus scutellaris*

(c) *Epistranus lawsoni*
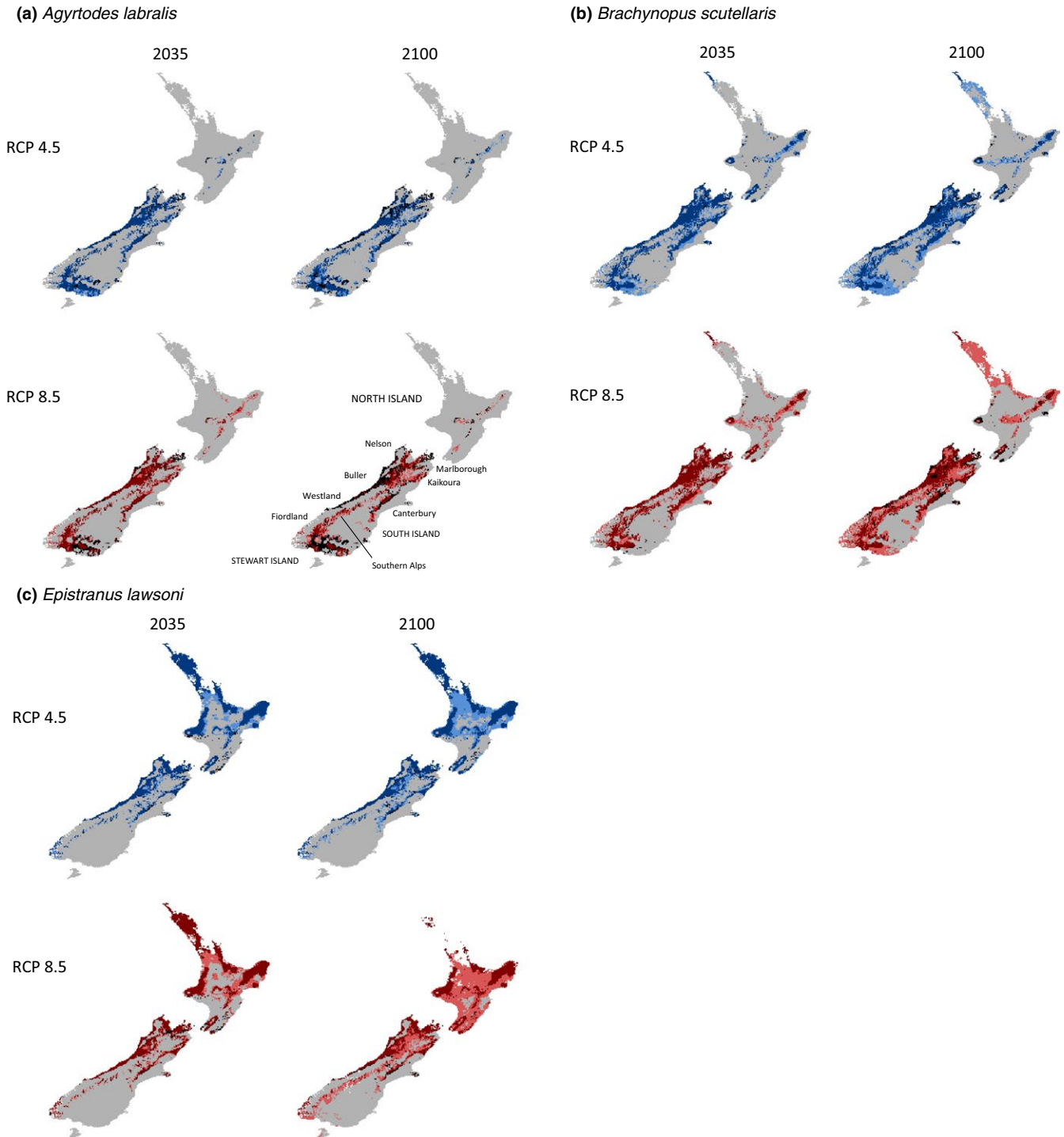
FIGURE 1 Species distribution models for (a) *Agyrtodes labralis,* (b) *Brachynopus scutellaris* and (c) *Epistranus lawsoni.* Projected contemporary distributions are shown in black, with predicted future distributions for 2035 and 2100 overlayed in blue (RCP 4.5) or red (RCP 8.5) so that darker shades indicate overlap between present and future (full results for all RCPs are available in Supporting information Appendix S2, Figures S2.1–6). By 2100 the current distribution of *Agyrtodes labralis* is predicted to shift eastward, while *B. scutellaris* and *E. lawsoni* are predicted to gain climatically suitable area. Regions referenced throughout the manuscript are indicated in Figure 1a. The truncated North Island distribution of *E. lawsoni* at 2100 (RCP 8.5) is due to climatic conditions outside of those used to test the model [Colour figure can be viewed at wileyonlinelibrary.com]

may become increasingly patchy. *Epistranus lawsoni* is also predicted to experience a net expansion in climatically suitable area by 2100, including expansion into nearly all of the North Island (Figure 1c; Supporting information Figure S2.6) and losing relatively few localities that contributed phylogeographic information to this study (Figure 2c). However, for RCP 8.5, climatic conditions across much of the northern North Island at 2100 are beyond the training conditions for *E. lawsoni*, and this region is excluded from the 2100 projection (Figure 1c; Supporting information Figure S2.3 and S2.6).

3.2 | Future changes in genetic and phylogenetic diversity

Despite predicted losses in the number of unique haplotypes for each species (up to 50% for *A. labralis*, 15% for *B. scutellaris* and 22% for *E. lawsoni*; Figure 2a-c), there is almost no difference in either haplotype or nucleotide diversity between the current and projected future populations (Table 1). Notably, sequences and haplotypes are not progressively lost towards 2100 for any RCP except for *A. labralis* (RCP 8.5 only), and the fewest unique haplotypes were recovered for all species at 2065, RCP 4.5. However, for all species, end-century nucleotide or haplotype diversity is significantly different from expected given the number of localities for at least one RCP, indicating a significant effect of geographical orientation of these populations (Table 1). *Agyrtodes labralis* and *B. scutellaris* are predicted to see an increase in Φ_{ST} by 2100 under most scenarios, while *E. lawsoni* is predicted to decrease in population structure under the two more extreme RCPs, and for all species, there is significant geographical bias to this change beyond the null expectation based on the same number of randomly drawn localities (Table 1).

Results for the three metrics of phylogenetic diversity indicate that most climate change scenarios will have limited effects on phylogeographic structure for all three species (Table 2). All species experienced a net reduction in PD; however, only for *A. labralis* is PD predicted to be significantly reduced when evaluated against 1,000 random draws from the posterior distribution (Table 2), indicating that this difference is beyond the variation expected due to uncertainty in branch length estimation. These differences are not recovered for AvTax, given that many short terminal branches are retained in all future climate scenarios for all species (Figure 2a-c). PD and AvTax were also compared against phylogenies with the same number of randomly drawn localities, and for all species, there is significantly more PD maintained in all climate change scenarios than when randomly drawing the same number of localities (Table 2). There was no difference between observed and expected AvTax given the number of localities included in each scenario. Finally, for *E. lawsoni* and all but one scenario for *A. labralis* (RCP 4.5 near-future), values of NRI were not considered significant when contrasted against a random distribution of sequences drawn across the phylogeny, indicating that loss of intraspecific phylogenetic diversity is predicted to occur in an even manner across the tree. In contrast, for *B. scutellaris*, the remaining tree tips are predicted to be significantly more clustered than expected by 2100, under all RCPs.

4 | DISCUSSION

We investigated the potential for climate change to erode the geographical distributions, intraspecific genetic diversity and evolutionary relationships among populations of three saproxylic forest beetles from New Zealand within the next few decades. Our results warrant cautious optimism: Only one species, *A. labralis*, is predicted to experience a reduction in genetic diversity (as indicated by PD). However, despite the projected loss of important parts of its South Island distribution and up to 50% of unique haplotypes, *A. labralis* is not expected to undergo many significant changes in haplotype or nucleotide diversity or phylogenetic structure (AvTax or NRI). In contrast, *B. scutellaris* and *E. lawsoni* may realize significant gains in climatically suitable area, particularly in the North Island, although *B. scutellaris* will likely to experience some changes in phylogenetic structure by 2100, with NRI indicating that populations projected to remain under climate change will be more phylogenetically clustered than if losses were randomly scattered across the tree. The lack of significant changes in average phylogenetic distances (AvTax) for all species indicates the tree structure will remain relatively unchanged, allowing important regional differences among lineages which may contribute to species' adaptive potential to be preserved.

These initially surprising results highlight the importance of the geographic configuration of genetic divergence in limiting the loss of genetic diversity and reduction in phylogeographic structure expected under climate change. First, our SDM projections indicate that range loss, particularly for *B. scutellaris* and *E. lawsoni*, is likely to be limited, patchy and scattered across the length of the South Island (Figure 1a-c). Even for *A. labralis*, which is restricted to the South Island and is predicted to lose much of the west coast portion of its range, none of the previously identified mitochondrial lineages (Marske et al., 2009, 2011, 2012) are predicted to completely disappear. Second, unique haplotypes within each lineage are widely distributed where those lineages occur, and this broad distribution of genetic diversity is likely why all three species are predicted to have a higher PD in all future scenarios than expected from a random draw of localities, despite the overall reduction in PD for *A. labralis*. This is also why we predicted changes in population structure (Φ_{ST}) for all species and scenarios, but only scattered differences in nucleotide or haplotype diversity relative to a random draw of localities. Thus, the fragmented pattern of range loss projected for these species is not sufficient to drive concerted or systematic patterns of change in our estimates of genetic diversity or phylogeographic structure.

This prediction of resilience of species ranges, genetic diversity and phylogeographic structure for *A. labralis*, *B. scutellaris* and *E. lawsoni* is related to NZ's dramatic topography, with high spatial heterogeneity allowing pockets of suitable conditions to remain scattered across the landscape—as they did in the past. Anthropogenic climate change is unlikely to erase all suitable habitat from the regions predicted to have maintained climatic refugia for these beetles during the Last Glacial Maximum (Kaikoura, Marlborough, Nelson and Buller; Marske et al., 2012), and even *A. labralis*, for whom those former refugia are most at risk, is predicted to retain more phylogenetic diversity than expected given the extent of range loss. We would expect quite different results for other spatial configurations of genetic diversity, such as the classical 'southern richness, northern purity' pattern (Hewitt, 2000), where unique haplotypes and lineages are strongly clustered by latitude. Indeed, previous studies
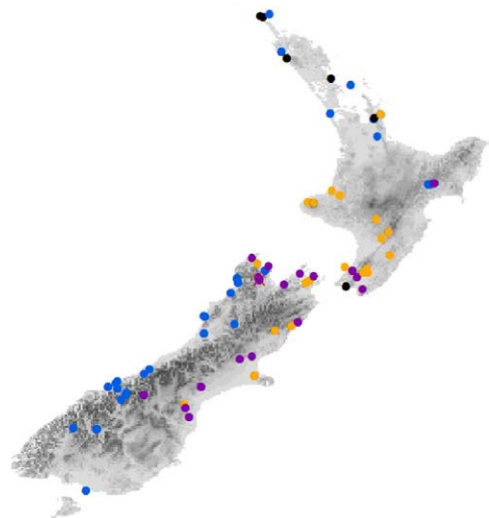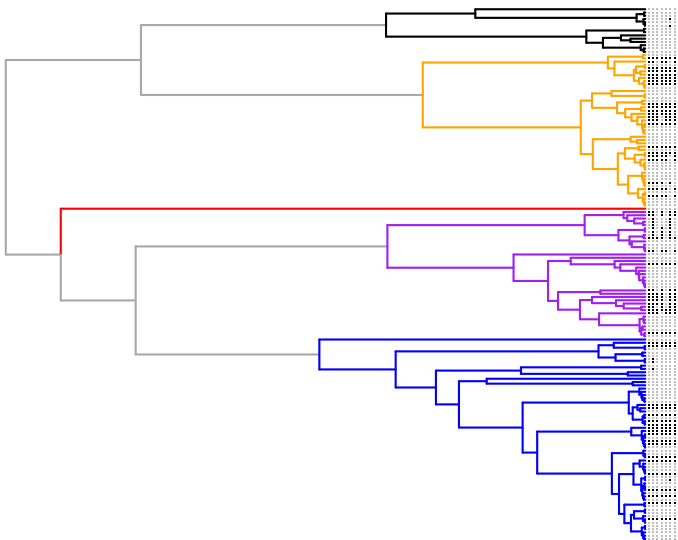
(a) *Agyrtodes labralis*
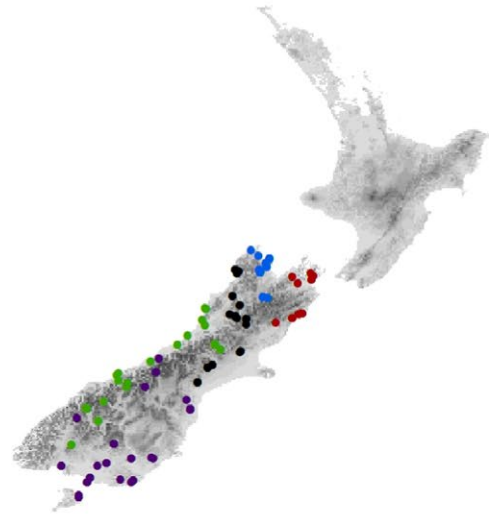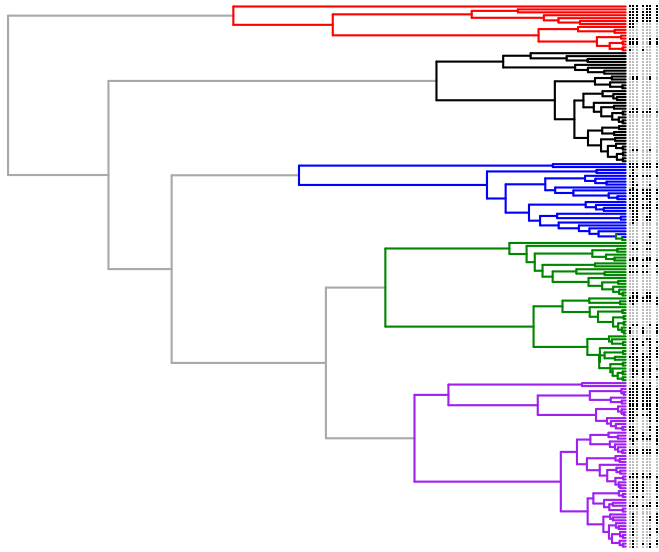
(b) *Brachynopus scutellaris*
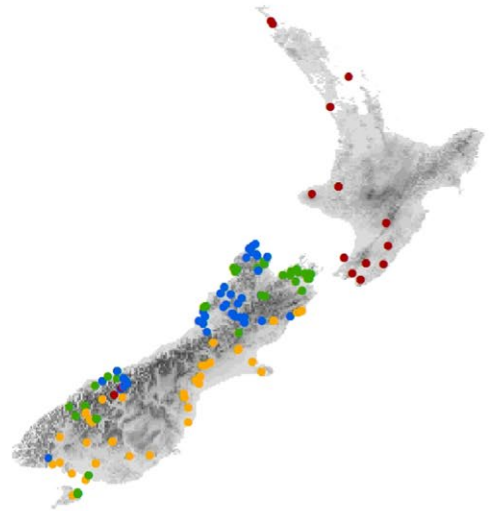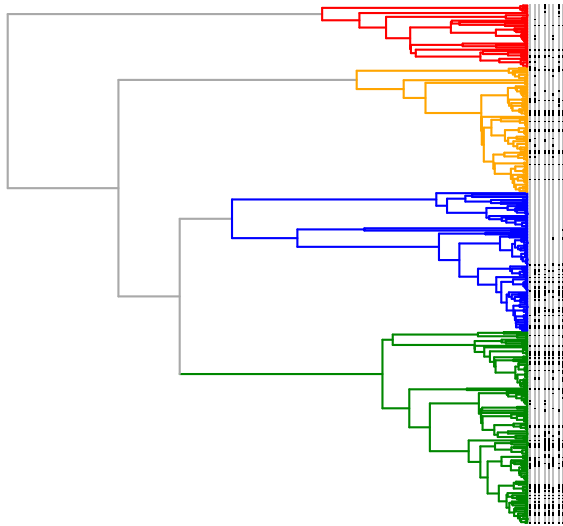
(c) *Epistranus lawsoni*

FIGURE 2 Predicted genetic consequences of climate change for (a) *Agyrtodes labralis*, (b) *Brachynopus scutellaris* and (c) *Epistranus lawsoni*. Maps indicate localities sampled for genetic sequencing, with colours corresponding to intraspecific lineages in the phylogeny (identified in Marske et al., 2012). Map background indicates elevation, with darker grey indicating mountainous regions. The three panels of three dots at the tips of the phylogeny indicate tips retained (grey) or lost (black) under each climate change scenario. From left to right, the panels are RCP 4.5–8.5 and the dots within each panel are arranged from near-future to end-century. For each species, all mitochondrial lineages are predicted to retain some localities under all scenarios. [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Present and projected future nucleotide and haplotype diversity and population structure

	Climate scenario	N sequences/haplotypes	Nucleotide diversity	Haplotype diversity	Φ_{ST}
	Agyrtodes labralis				
	Full alignment	186/121	0.027	0.986	0.886
	Model current	172/111	0.028	0.986	0.886
4.5	2016–2035	138/88	0.028	0.980	**0.883**
	2046–2065	81/55	0.028	0.982	**0.919**
	2081–2100	113/77	0.029	0.981	**0.911**
6.0	2016–2035	127/82	0.029	0.983	**0.900**
	2046–2065	142/90	0.029	0.981	**0.895**
	2081–2100	102/68	0.029	0.979	**0.912**
8.5	2016–2035	114/76	0.029	0.985	**0.875**
	2046–2065	100/67	0.031	0.981	**0.910**
	2081–2100	84/57	**0.030**	0.983	**0.909**
	Brachynopus scutellaris				
	Full alignment	340/205	0.027	0.985	0.797
	Model current	288/167	0.027	0.983	0.792
4.5	2016–2035	268/157	**0.026**	0.982	**0.796**
	2046–2065	237/141	0.030	0.982	**0.786**
	2081–2100	258/152	0.030	**0.980**	**0.792**
6.0	2016–2035	251/145	0.028	0.981	**0.786**
	2046–2065	270/155	0.030	**0.980**	**0.788**
	2081–2100	253/148	0.030	0.981	**0.805**
8.5	2016–2035	245/142	0.028	0.983	**0.782**
	2046–2065	245/146	0.031	0.980	**0.796**
	2081–2100	242/145	**0.031**	0.980	**0.799**
	Epistranus lawsoni				
	Full alignment	164/134	0.162	0.997	0.691
	Model current	131/112	0.166	0.998	0.649
4.5	2016–2035	109/93	0.167	0.997	**0.652**
	2046–2065	100/87	0.166	0.997	**0.614**
	2081–2100	115/99	0.167	0.997	**0.649**
6.0	2016–2035	109/94	0.166	0.997	**0.624**
	2046–2065	119/103	0.167	**0.998**	**0.680**
	2081–2100	106/92	0.164	**0.997**	**0.596**
8.5	2016–2035	110/94	0.167	0.997	**0.652**
	2046–2065	112/96	0.166	0.997	**0.622**
	2081–2100	103/87	**0.162**	0.997	**0.605**

Note. Results in bold are significantly different than expected based on a null model of random loss of sampling locations under each climate scenario; a significant result indicates spatial bias in the geographic orientation of lost populations. As some island and coastal populations for all three species fall outside the extent of our climate data, we provide population genetic information for the full alignment and the current distribution as modelled for each species.

TABLE 2 Present and projected future Phylogenetic Diversity (PD), Average Taxonomic Distinctness (AvTax) and Net Relatedness Index (NRI)

	Climate scenario	PD	AvTax	NRI
	Agyrtodes labralis			
	Full alignment	27.24	2.41	–
	Model current	26.63	2.41	–
4.5	2016–2035	**21.75***	2.28	**3.89**
	2046–2065	**16.43***	2.34	1.04
	2081–2100	**19.01***	2.34	1.33
6.0	2016–2035	**20.81***	2.44	−0.59
	2046–2065	**21.27***	2.35	1.95
	2081–2100	**18.39***	2.36	0.85
8.5	2016–2035	**21.09***	2.42	−0.16
	2046–2065	**18.58***	2.40	0.23
	2081–2100	**16.89***	2.45	−0.53
	Brachynopus scutellaris			
	Full alignment	39.52	3.32	–
	Model current	38.43	3.32	–
4.5	2016–2035	**35.05**	3.17	**6.66**
	2046–2065	**33.54**	3.18	**4.22**
	2081–2100	**35.76**	3.18	**5.27**
6.0	2016–2035	**35.00**	3.27	1.95
	2046–2065	**35.85**	3.20	**5.77**
	2081–2100	**34.66**	3.20	**4.36**
8.5	2016–2035	**34.58**	3.23	3.01
	2046–2065	**35.05**	3.21	3.61
	2081–2100	**33.82**	3.14	**6.07**
	Epistranus lawsoni			
	Full alignment	196.58	26.69	–
	Model current	195.58	26.69	–
4.5	2016–2035	**187.94**	26.80	−0.49
	2046–2065	**184.72**	26.85	−0.60
	2081–2100	**190.82**	26.85	−0.78
6.0	2016–2035	**190.36**	26.80	−0.50
	2046–2065	**191.50**	26.80	−0.63
	2081–2100	**185.34**	26.69	−0.01
8.5	2016–2035	**188.08**	26.84	−0.70
	2046–2065	**187.35**	26.89	−0.92
	2081–2100	**184.29**	26.63	0.20

Notes. For PD and AvTax, * indicate results significantly different from a random draw of 1,000 posterior trees from the post burn-in Bayesian sample, while bold values indicate results significantly different from 1,000 random draws of the number of localities predicted to remain under each climate scenario. For NRI, bold values indicate results significantly different from a random draw of the same number of tree tips predicted to remain under each scenario. As some island and coastal populations for all three species fall outside the extent of our climate data, we provide estimates of PD and AvTax for the full alignment and the modelled current distribution for each species.

have shown that the part of the range predicted to be lost is critical for future projections of genetic diversity (Alsos et al., 2009; Bálint et al., 2011; Razgour et al., 2013).

Another potential explanation for our results—that these species are likely to undergo only moderate change in phylogeographic structure—may be that our tests for changes in phylogeographic structure are quite conservative. Our application of PD, AvTax and NRI differ from the community level studies of Clarke and Warwick (1999) and Webb (2000), where each tip is a species and most species occur in more than one population. In intraspecific phylogenies, tree tips represent a subset of sequences from the full population, and so there is no assumption that the tree includes all terminal taxa (which in this case are individual beetles). Intraspecific phylogenies may also include identical sequences, and the relationships among the short branches connecting individuals which share the same haplotype or differ by only a few base pairs are usually not strongly supported. Thus, changing the number or geographic orientation of sequences will naturally change estimates of PD and AvTax, and phylogeographic sampling should therefore encompass both the underlying spatial distribution and phylogeny for these species. Our null models attempt to account for this inherent variability by identifying systematic geographic or phylogenetic loss, above and beyond what would be expected from sampling fewer populations or variation in coalescent tree estimation. However, given that AvTax, in particular, is strongly affected by the short branch lengths connecting tips (as pairwise distances are averaged), comparison against a selection of Bayesian posterior trees is likely a conservative test of the impacts of change for this statistic. This is in contrast to PD, which indicates a significant reduction in diversity for *A. labralis*, in line with the large reduction in unique haplotypes.

Linking species distribution models with phylogenetic and phylogeographic methods provides a powerful framework for estimating how the consequences of climate change might ripple across the tree of life (Fordham, Brook, Moritz, & Nogués-Bravo, 2014; Loyola et al., 2014). These methods do not address the extent to which dispersal might facilitate range shifts, and like many other SDM studies, we implement the conservative assumption of no dispersal, where sequences are removed as localities become climatically unsuitable, even where they are close to areas projected to remain or become suitable. Given the high proportion of locality-specific haplotypes for *A. labralis* and the deep intraspecific divergences in the flightless *E. lawsoni* (Marske et al., 2009, 2011), together with New Zealand's mountainous terrain, an assumption of little to no dispersal within the next few decades may be realistic. However, the nondirectional changes we estimated for population structure, with Φ_{ST} fluctuating among periods even within the same RCPs, suggest that with rapidly shifting ranges, even short-distance dispersal may be enough to preserve genetic and phylogenetic patterns more in line with current distributions than we have predicted here.

Phylogeography has long been a key tool in understanding diversification and the generation of biodiversity, yet it is possible that

phylogeographic patterns already reflect some human influence over the distribution of genetic diversity within species (Miraldo et al., 2016). While it is difficult to say what absolute levels of genetic diversity are required to confer climatic resilience, conserving a broad selection of genotypes from across the phylogeny is likely key to preserving a representative subset of this diversity (Moritz & Faith, 1998). How this translates into real space is highly contingent on the history of the region and species therein. For these beetles, which are characteristic members of the New Zealand forest flora, the geographic configurations of haplotypes and lineages allows us to take an optimistic view of these species' chances of withstanding genetic and phylogenetic erosion under climate change; other taxa may not be so fortunate. We argue that biodiversity scenarios based on SDM projections of species' vulnerability to climate and land use change will benefit from including the geographical structure of intraspecific genetic diversity and illustrate how phylogenetic comparative methods used widely at the community level could be applied more broadly to explore the genetic consequences of environmental change.

DATA ACCESSIBILITY

All sequence alignments, intraspecific phylogenies and presence/absence matrices used to generate the results in Tables 1 and 2 are available at osf.io/bp2gs.

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BIOSKETCH

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Authors' contributions: M.R. and K.A.M designed the study; M.R., J.D.K. and K.A.M. performed the analyses; K.A.M, J.D.K and M.R. interpreted the results, and all authors contributed to writing the manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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