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Global warming leads to habitat loss and genetic erosion of alpine biodiversity

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Abstract

Aim: Species living on steep environmental gradients are expected to be especially sensitive to global climate change, but little is known about the factors influencing their responses to contemporary warming. Here, we investigate the influence of climate on the biogeography of three alpine species with overlapping ranges.

Location: Te Waipounamu (South Island) Aotearoa–New Zealand.

Taxon: Endemic alpine adapted Catantopinae grasshoppers.

Methods: We used niche modelling to estimate and project the potential niche of three focal species under past and future climate scenarios. Vulnerability assessments were performed using niche factor analyses. Demographic trends and phylogeographic structure were investigated using samples from 15 mountain tops to generate mitochondrial DNA haplotype networks and population genetic statistics.

Results: Niche models and genetic data suggest suitable habitat for all three alpine species was more widespread and contiguous in the past than today. Demographic analyses indicate in situ survival rather than post-Pleistocene colonisation of current habitat. Population structuring and genetic divergence suggest that mountain uplift during the Pliocene and environmental barriers during Pleistocene glacial and interglacial stages shaped contemporary population structure of each species. Although geographically overlapping, niche analyses suggest these alpine species are not ecologically identical, each showing distinct responses to environmental change, but all will lose intraspecific diversity through population extinction.

Main Conclusions: Climatic, biological and geophysical factors controlled population structuring of three cold-adapted species during the Pleistocene with a legacy of spatially separate intraspecific lineages. Ecological niche models for each species emphasise distinct combinations of environmental proxies, but all are expected to experience severe habitat reduction during climate warming. Increased global temperatures drive available habitat to higher elevation resulting in population contractions, range shifts, habitat fragmentation, local extinctions and genetic impoverishment. Despite alpine species not being ecologically identical, we predict all mountain biota will lose significant genetic diversity due to global warming.

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KEYWORDS

alpine species, Aotearoa New Zealand, biogeographic barriers, climate change, environmental envelope, habitat availability

1 | INTRODUCTION

Across the biogeographic spectrum, species range shifting (usually poleward and upward) has been proposed as a general ecological response to contemporary planetary heating (Bellard et al., 2012; Chen et al., 2011; Freeman et al., 2018; Lenoir & Svenning, 2015; Walther et al., 2002). In keeping with inferences of variable prehistoric range shifts gleaned from phylogeographic (e.g. Taberlet et al., 1998) and fossil data (e.g. Lyons, 2003), contemporary range changes show considerable disparity in response pattern and rate (Chen et al., 2011; Lenoir et al., 2010; Moritz & Agudo, 2013). Critically, studies of past range shifts usually deal with much larger time-scales than we now know are relevant to extant populations (IPCC, 2022). Variation among species range shifts likely reflects the extent to which a species is exposed to climate change across its range, its phenotypic and genetic diversity and the capacity of local populations to disperse into newly available habitat (Bellard et al., 2012; Moritz & Agudo, 2013; Rinnan & Lawler, 2019).

The elevational gradient on mountains results in a decrease in mean air temperature with increasing elevation due to reduced atmospheric pressure. This means that vulnerability to global climate change is expressed over a narrow spatial scale, and recent analyses indicate a nonlinear relationship with enhanced rates of warming at high elevation (MRI, 2015). In addition, the extent of alpine habitat tends to be attenuated with elevation due to the shape of mountains (Pauli & Halloy, 2019). Therefore, the upward shift of alpine populations also isolates them in progressively smaller and more scattered high-elevation habitat patches (Chinn & Chinn, 2020; Galbreath et al., 2009; Gifford & Kozak, 2012), leading to population fragmentation, local extinction of intraspecific lineages and loss of intraspecific diversity (e.g. Pavlova et al., 2017; Rehnus et al., 2018; Rizvanovic et al., 2019).

Past climate change, and in particular Plio–Pleistocene climate cycling is inferred to have imposed changes in habitat availability for populations, hallmarked by latitudinal range shifts of warm climate species documented in Europe and North America (Davis & Shaw, 2001). Cold adapted species experienced analogous changes in fortune culminating in retreat of habitat at the start of the present interglacial as warming forced optimal climatic envelopes to higher elevation and latitude (e.g. Carmelet-Rescan et al., 2021; Endo et al., 2015; Galbreath et al., 2009; Trewick et al., 2000), a trend that continues today at an increased rate (Bellard et al., 2012; Chen et al., 2011; Freeman et al., 2018; Walther et al., 2002). In contrast, during glacial phases, cold-adapted organisms could have experienced population and range expansion and connectivity via valley corridors (Carmelet-Rescan et al., 2021; Endo et al., 2015; Hewitt, 2004; Trewick et al., 2000), although valleys can also act as barriers (Trewick et al., 2000).

The dynamics of alpine glaciers reflect regional and temporal differences in precipitation, temperature and orography and models of palaeoglacier dynamics reflect this (Groos et al., 2021; James et al., 2019). During the last glacial maximum (LGM) on Kā Tiritiri o te Moana (Southern Alps) of Aotearoa (New Zealand), montane glaciers with as much as 6800 km³ of ice covered up to 30% of Te Waipounamu (South Island; James et al., 2019), but do not appear to have formed extensive ice fields overtopping mountain peaks. Instead, glaciers were predominantly valley-constrained (James et al., 2019; Figure 1). If there was sufficient snow melt on peaks during the glacial summer, it is plausible that an alpine-adapted biota persisted through glacial stages on nunataks of the Southern Alps. Although originally proposed for Scandinavia (Dahl, 1987), the nunatak hypothesis is relevant to New Zealand biogeography as it was not directly influenced by polar ice and associated periglacial climate (Gowan et al., 2021). Today vegetation grows directly beside active montane glaciers and in some cases even on the edge of the ice itself (Fickert et al., 2022), and this appears to have been the case during glacials (e.g. Marra & Thackray, 2010; Moar, 1980; Vandergoes et al., 2008).

The configuration of Pleistocene glaciers in the Southern Alps allowed the persistence of plant and animal populations on mountain tops, supporting high, spatially structured intraspecific genetic diversity in alpine habitats (e.g. Carmelet-Rescan et al., 2021; Trewick et al., 2000; Trewick & Wallis, 2001). As the degree of population isolation in the past underpins the distribution of variation today, the biodiversity consequences of future climate change are implicated. Here, we investigated whether environmental processes driving distributional changes among endemic sympatric flightless alpine grasshoppers (Orthoptera: Acrididae) resulted in similar phylogeographic outcomes in separate species. This monophyletic group radiated before Pleistocene climate cycling began (Koot et al., 2020), so their current distributions could reveal responses to glacial and interglacial conditions (e.g. Carmelet-Rescan et al., 2021). We couple phylogeography, ecological niche modelling and climatic niche comparisons to investigate how climate change across the latitudinal and elevational gradients of the Southern Alps influences three endemic, alpine grasshopper species with overlapping ranges that span 670 linear km.

Ecological niche modelling and niche analyses provide information about vulnerability of potential habitat based on climate proxies, and genetic data allow inference of past population connectivity that likely reflects local environmental traits. We sampled grasshoppers at 15 mountain tops spanning the latitudinal gradient (~4.5°) of the Southern Alps and proximity to LGM glaciers (Figure 1). We expect that glacial stages generally allowed range expansion compared to interglacials, but propose that the

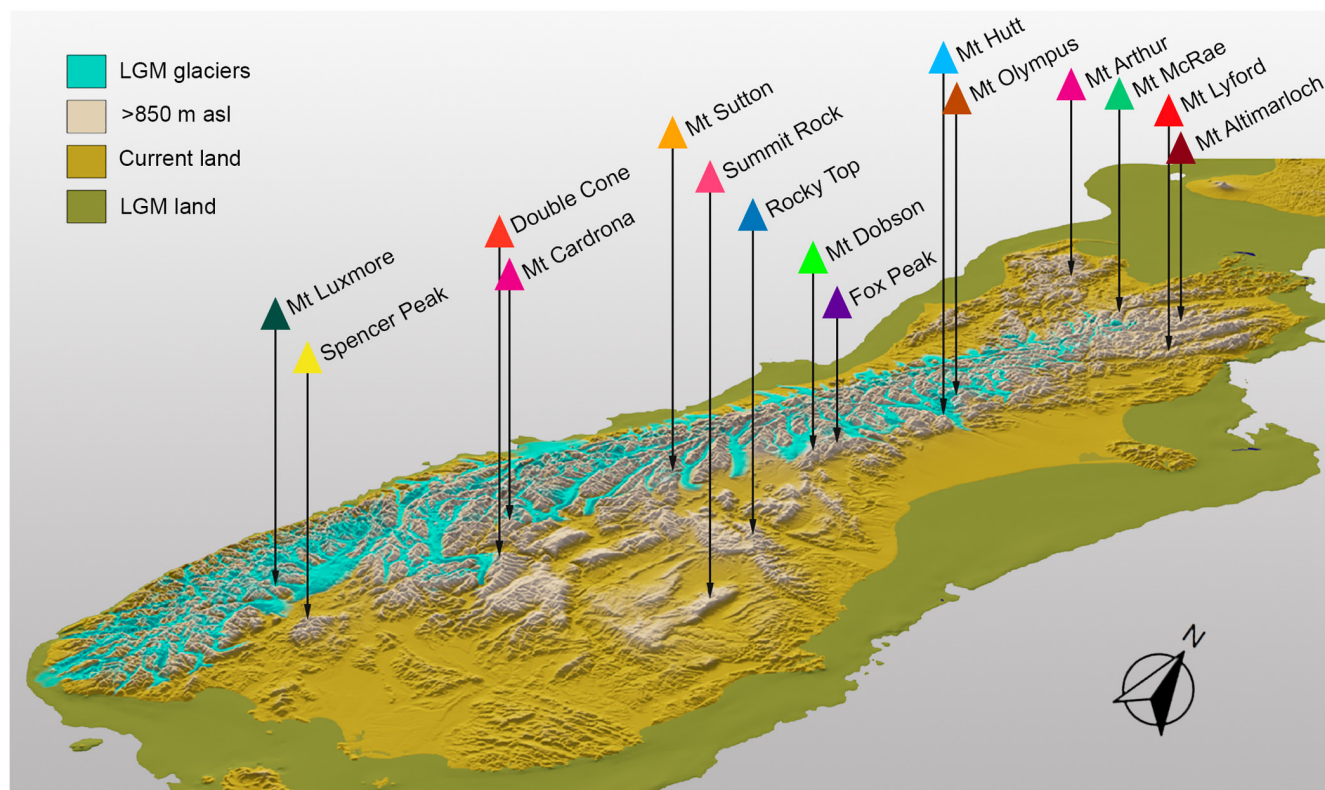


FIGURE 1 Oblique three-dimensional projection of South Island, New Zealand depicting inferred land extent, topography and glaciation during the last glacial maximum of the Pleistocene (after James et al., 2019). Sampling locations on 15 mountains, for grasshopper specimens used for genetic analyses (*Brachaspis nivalis*, *Paprides nitidus* and *Sigauss australis*), are indicated. Map projection: NZGD2000, with vertical scale emphasised for clarity.

pattern of glaciation would tend to isolate populations in the west more than those to the east given the thickness and extent of glaciers in the Southern Alps during LGM (Figure 1). The latitudinal gradient of the Southern Alps is expected to result in cooler conditions to the south compared to the north, and this correlates with the elevation of the forest–alpine transition that tends to be higher in the north and lower in the south of New Zealand (Wardle, 2008). If, as we expect, LGM conditions influenced the spatial distribution of intraspecific diversity, then anthropogenic warming over the next 50 years could result in uneven genetic erosion even among sympatric and closely related species.

2 | MATERIALS AND METHODS

2.1 | Taxon sampling

We surveyed populations of *Brachaspis nivalis* (Hutton), *Paprides nitidus* Hutton and *Sigauss australis* (Hutton) on 15 mountain tops in Southern Alps, spanning the documented range of each species (Figure 1). Grasshoppers were collected during summer when they are active (December to March 2015–2020) and frozen before being preserved in 95% ethanol. Species were identified using morphological traits following Bigelow (1967).

2.2 | Ecological niche modelling

To estimate and project the potential niche of each focal species, we acquired location records with geodetic datum WGS84 for 14 endemic New Zealand grasshopper species, spanning 1967–2016 (Koot et al., 2022). Additional records were retrieved from recent collections by the Phoenix group (<http://evolves.massey.ac.nz>), including target-group absences (Mateo et al., 2010). Duplicates were removed ensuring one data point per pixel (~1 km² habitat). A fundamental assumption of niche models is that species' current ranges are in equilibrium: matching the full extent of environmental conditions so they can persist indefinitely (Sax et al., 2013; Soberón & Peterson, 2005). This assumption might be void if occupancy is subject to anthropogenic land-use change (e.g. Carmelet-Rescan et al., 2021; Koot et al., 2022; Trewick, 2008). Mismatches between niche and range arise when individuals of a species can survive but not persist through time in places where environmental conditions exceed those realised in their native ranges (Sax et al., 2013). To minimise the influence of non-climatic, anthropogenic activity (Faurby & Araújo, 2018), we filtered presence records from areas unavailable to grasshoppers before humans reached Aotearoa about 800 years ago (Wilmshurst et al., 2008). Here, tall forest (Leathwick et al., 2004) was incompatible with native temperate grasshoppers (Sivyer et al., 2018; Figure S1.1). The resulting database consisted

of 1138 site records, including 80 presences for *B. nivalis*, 65 for *P. nitidus* and 187 for *S. australis* representing the native realised niche of these species (Figure S1.2; Table S1.1).

For potential niche proxies, we accessed 19 bioclimatic variables (averaged from 1960 to 1990) from WorldClim v1.4 (<http://www.worldclim.org>; Hijmans et al., 2005) for three periods (MIROC-ESM global climate model): current (averaged from 1960 to 1990), past (LGM ~22 kyr) and future (averaged from 2061 to 2080). Two future global warming scenarios were projected: a greenhouse gas stabilisation pathway (RCP4.5) and a high concentration pathway (RCP8.5), with mean temperature increases in New Zealand of at least 1.4°C (RCP4.5) and 3.0°C (RCP8.5) by 2090 (New Zealand Ministry for the Environment, 2018). We included four additional variables describing geodiversity (soil type) and topography (slope, aspect and roughness), which are important for plant growth and treeline position in New Zealand (Case & Buckley, 2015; Wardle, 1965), and might be constraints on grasshopper habitat availability (Carmelet-Rescan et al., 2021; Koot et al., 2022). All layers were at 30 arc-seconds resolution (~1 km²), except LGM layers which were at 2.5 arc minutes (~5 km²). Layer files were cropped to the extent of New Zealand (Latitudes: -49, -32; Longitudes: 165, 180), which represents the potential accessible area for these species during the relevant time period (Soberón & Peterson, 2005) since New Zealand's major islands were connected during Pleistocene glacial phases (Trewick & Bland, 2012). Selection of relevant variables used the R (R Core Team, 2019) package 'fuzzySim' v.3.0 (Barbosa, 2015) such that variables retained for modelling did not show multicollinearity (VIF < 3; Table S1.2). Data processing used QGIS 3.16.1 (QGIS Development Team, 2020).

To estimate the environmental niche for each grasshopper, we used three methods to build ensemble models: Generalised Boosting, Random Forest and Maximum Entropy. The best set of tuneable hyperparameters was inferred using the R package 'SDMtune' v.1.1.4 (Vignali et al., 2020) with the most relevant predictors (Tables S1.3 and S1.4). We refitted final models in the R package 'Biomod2' v.3.4.6 (Thuiller et al., 2020), using the most relevant predictors and the best performing parameters through a spatial-blocking cross-validation approach (Figure S1.3) with the R package 'blockCV' v.2.1.1 (Valavi et al., 2019). Five runs were completed for each modelling method, resulting in 15 models per species. We assessed the performance of individual models with the True Skill Statistic (TSS) and area under the curve values (AUC) of receiver operator characteristic (ROC) curves. Models with TSS and AUC values > 0.8 were retained for building the final ensemble forecast output using a weighted average approach. Spatial projections under current conditions (1960–1990) were generated using the final mean-weighted ensemble models (EMmw). Variable importance for the final EMmw was calculated by applying the weightings used for the ensemble forecasting to the variable importance scores for individual models, summing values by variable and then dividing by the number of modelling methods applied.

Extrapolation risk associated with modelling past and future projections was assessed through a multivariate environmental

similarity surface (MESS) analysis (Elith et al., 2010) using the R package 'dismo' v.1.3-3 (Hijmans et al., 2020). To designate areas as suitable or not suitable, binary projections for each period (past, current and future) were generated from the final EMmw models using the cut-off value that maximised the proportion of presences and absences correctly predicted by the model. Output values higher than the predetermined threshold were considered 'presences'; otherwise, 'absences'. Binary vectors were used to estimate range metrics for past, present and future projections. Past (LGM) vectors were disaggregated to correspond with a 30-arc sec resolution using the R package 'raster' v.3.4-5 (Hijmans, 2020). Range change analyses were implemented using the *RangeSize* function in the R package 'Biomod2' v.3.4.6 (Thuiller et al., 2020) and QGIS.

2.3 | Niche factor analyses

We used ecological-niche factor analyses (ENFA; Hirzel et al., 2002) to quantify two different aspects of each species' niche: (1) marginality, a measure of the position of a species' niche in the available environmental space (i.e. the global area), and (2) specialisation, a metric of the size of a species' niche relative to the global area (Hirzel et al., 2002; Rinnan & Lawler, 2019). The higher the marginality, the greater the ecological distance of habitat occupied by a species from the average habitat available; the higher the specialisation, the narrower a species niche (Hirzel et al., 2002). We also estimated three metrics reflecting different aspects of the species' potential responses to climate change: (1) sensitivity, a measure of a species persistence ability given the climatic conditions of its habitat; (2) exposure, a metric of the extent to which a species will experience climate change across its range; and (3) vulnerability, a measure of a species susceptibility to climate change given its sensitivity and exposure. In general, the higher the sensitivity of a species, the narrower the climatic niche it inhabits; the higher its exposure, the greater the departure of its habitat from current to future climate; and the higher its vulnerability, the more susceptible to climate change (Rinnan & Lawler, 2019). We used the binary vector resulting from our niche modelling as a proxy for the current ranges of the grasshopper species. The global study area was defined as the combined range of the three species (Rinnan & Lawler, 2019), that is, the extent of the South Island. To determine the global climatic conditions, we used the subset of climate variables used for niche modelling, as they are not strongly correlated and are important in predicting suitable environments for these grasshoppers. Analyses in this section were conducted using the R package 'CENFA' v.1.1.0 (Rinnan, 2018).

2.4 | DNA extraction, sequencing and alignment

Whole genomic DNA was extracted from leg muscle of 155 specimens (*B. nivalis* = 61, *P. nitidus* = 94) using a solvent-free Proteinase K and salting out method (Sunnucks & Hales, 1996) as described

by Sivyer et al. (2018). DNA samples were subject to PCR amplification of the mitochondrial NADH-dehydrogenase 2 (ND2) gene under standard conditions, using the primers HopND2_147F and HopND2_1286R (Carmelet-Rescan et al., 2021). In these grasshoppers, ND2 has a higher capacity to accumulate haplotype diversity when compared with the commonly analysed COI locus (Carmelet-Rescan et al., 2021). Cycle sequencing reactions used BigDye Terminator v.3.1 (Life Technologies) with signal capture on an ABI-3500 Genetic Analyser (Life Technologies), and resulting sequences were edited and aligned in GENEIOUS R10 (Kearse et al., 2012). Published DNA sequence data for *S. australis* ($n = 132$) were included (Carmelet-Rescan et al., 2021).

2.5 | Population genetic structure

Genealogical relationships among ND2 haplotypes were inferred with haplotype median-joining (Bandelt et al., 1999) networks in PopART v.1.7 (Leigh & Bryant, 2015). Statistical support for distinct mitochondrial lineages was evaluated with a Bayesian phylogenetic analysis in MrBAYES v.3.2.6 (Ronquist et al., 2012) with *Alpinacris crassicauda* Bigelow as the outgroup taxon (Koot et al., 2020). The best partition scheme for all three codon positions was HKY+ Γ (LnL = -2379.62; BIC = 5664.86) as inferred using PARTITIONFINDER version 2.1.1 (Lanfear et al., 2017). Analyses used four chains on two runs for 10^6 generations, with sampling frequency of 10^3 generations and a burn-in of 0.10. Convergence of the posterior distribution parameters was examined by monitoring the effective sample size (ESS > 800) and trace plots in TRACER v1.6 (Rambaut et al., 2018). Pairwise genetic distances between populations were estimated using MEGA X (Kumar et al., 2018) based on the Kimura 2-parameter (K2P; Kimura, 1980) and Tamura-Nei (TN; Tamura & Nei, 1993) models with a bootstrap procedure (1000 replicates).

Matrilineal genetic variability was estimated in population samples ($n \geq 5$) using DNASP v.5.10 (Librado & Rozas, 2009) to compute haplotype diversity (h), which represents the probability that two randomly sampled alleles are different (Nei & Tajima, 1981), and nucleotide diversity (π), which is defined as the average number of nucleotide differences per site between two sequences (Nei, 1987). Pairwise Φ_{ST} values (Excoffier et al., 1992) were computed in ARLEQUIN v.3.5.2.2 (Excoffier & Lischer, 2010) to infer mtDNA differentiation among population samples, and a significance statistic permuted using 10,000 replicates. To identify whether the predicted loss of suitable habitat under climate change could result in changes of extant genetic diversity, we identified which of our sampled populations could be lost under warming scenarios and estimated haplotype diversity (h) and nucleotide diversity (π), excluding sequence data from those locations.

Historical demography was inferred based on the observed mismatch distribution under the constant population size model using DNASP. A smooth, unimodal distribution is expected when populations have undergone recent demographic expansion, while multimodal and ragged distributions suggest a stable population

(Rogers & Harpending, 1992). Harpending's raggedness index (Harpending, 1994) was used to evaluate the fit of the observed distribution to the constant population size model, and its statistical significance was assessed with 10,000 coalescence simulations. A significant index indicates a stable population typically showing 'ragged', multimodal mismatch (Harpending, 1994). Tajima's D (Tajima, 1989), Fu's F_S (Fu, 1997) and Ramos-Onsins' R_2 (Ramos-Onsins & Rozas, 2002) neutrality tests were performed in DNASP to detect departures from the mutation-drift equilibrium indicative of population size changes. Statistical significance was assessed with 10,000 coalescence simulations. Significantly negative Fu's F_S and Tajima's D values and significantly positive R_2 values were taken as evidence of recent population expansion (Galbreath et al., 2009).

3 | RESULTS

3.1 | Ecological niche modelling

Ensemble models showed high predictability, with average AUC scores of 0.966 for *B. nivalis*, 0.981 for *P. nitidus* and 0.978 for *S. australis*. True-positive rate (i.e. percentage of presences correctly predicted) and true-negative rate (i.e. percentage of absences correctly predicted) of predictions were also high, above 92.50% and 90.62%, respectively, for all species (Table S1.5). Evaluation scores for individual models indicated good to excellent performance (Figure S1.4). Temperature-related predictors had the largest influence on the environmental envelope estimated for all species. Annual mean temperature was in all cases the most important predictor variable (importance score > 70% in all cases), but the proximate importance of the other variables differed (Figure S1.5).

Current predictions support a wide distribution of *B. nivalis* (9720 km²) and *P. nitidus* (12,757 km²) throughout the northern portion of the Southern Alps, while *S. australis* is predicted to have a wide distribution (16,651 km²) across the southern half of South Island (Figure 2; Figure S1.6). Past projections indicate, for all three species, areas of suitable climate were less fragmented and more widespread during the LGM than today: 14,205 km² for *B. nivalis*, 20,441 km² for *P. nitidus* and 45,545 km² for *S. australis*. Areas of strict extrapolation for past conditions occur mainly in the southern portion of the Southern Alps, within the native distributional range of *S. australis* (Figure 2). Accounting for areas of strict extrapolation reduced inferred suitable area for this species during the LGM by 21% to 35,763 km². Suitable habitat for this species is predicted to have existed in North Island during past glacial periods, but *S. australis* is not found there (Koot et al., 2022). In general, our models showed a good performance in predicting the extent of deep valley glaciers during the LGM (Figure S1.6).

For all species, future projections indicate that the spatial distribution of suitable conditions will move poleward and upslope, in most cases accompanied by dramatic area reductions (Figure 2; Figure S1.7). Suitable habitat for *B. nivalis* and *P. nitidus* is expected to undergo a southward shift under future scenarios, with progressive

contraction of their current northern ranges. Habitat loss with respect to current habitat, however, is projected to be more severe for *B. nivalis* (RCP4.5 = 62% loss and RCP8.5 = 0.75% loss) than for *P. nitidus*, where even a slight increase was predicted under the most optimistic climate change scenario (RCP4.5 = 5% gain and RCP8.5 = 20% loss). Suitable habitat for *S. australis* is expected to

undergo marked reduction under future climate change, with increasing patchiness and eventual loss of most native environmental space (RCP4.5 = 80% loss and RCP8.5 = 90% loss). Areas of strict extrapolation for future conditions occur mostly across the lowlands of northern South Island, which are outside the projected suitable areas for the species (Figure 2).

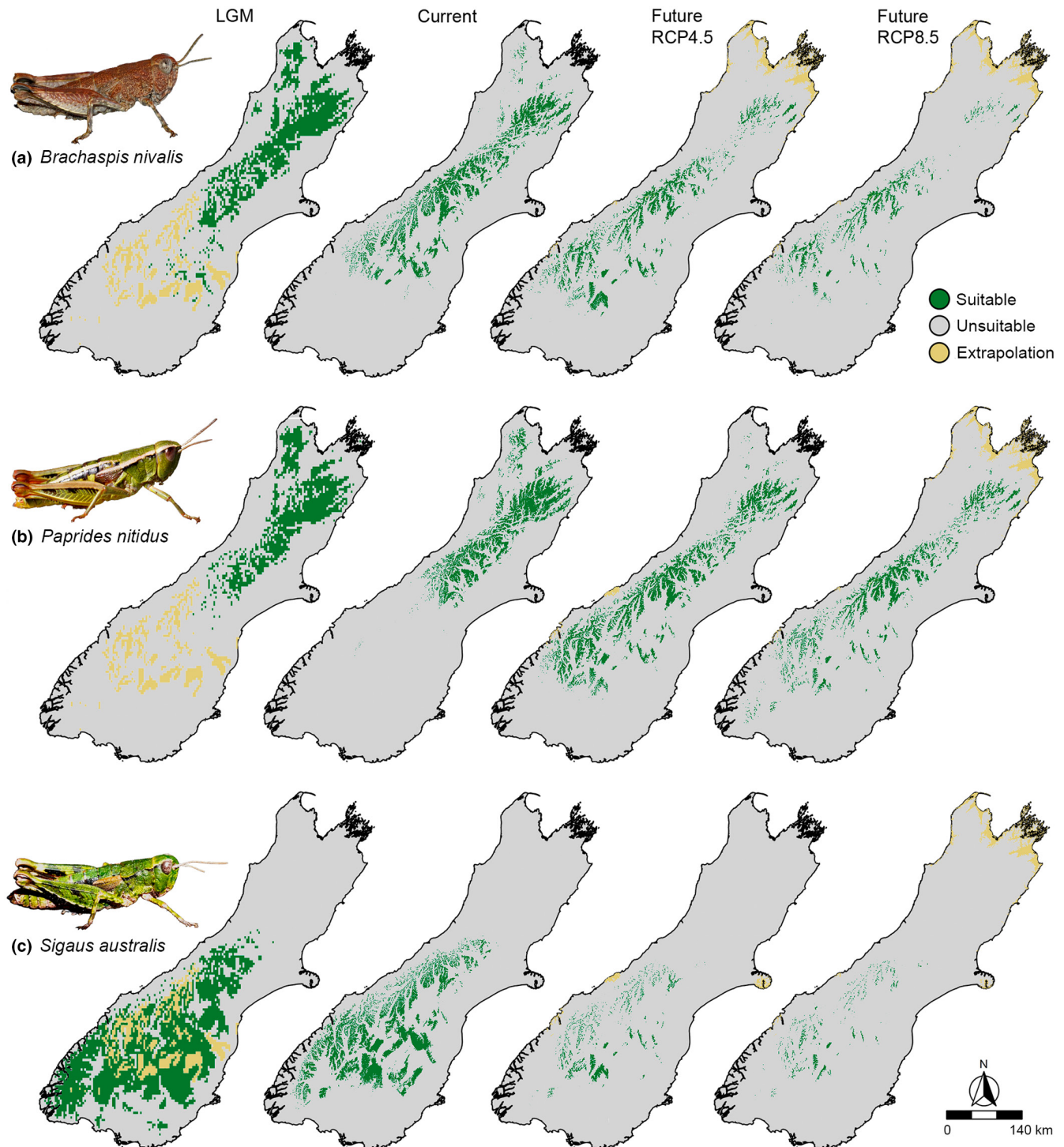


FIGURE 2 Predicted shifts in the suitable niche space for (a) *Brachaspis nivalis* (cut-off = 354.5), (b) *Papirides nitidus* (cut-off = 209.5) and (c) *Sigaus australis* (cut-off = 462.5) in South Island, New Zealand under past (LGM), current and two future scenarios. Areas of strict extrapolation indicate climate conditions that differ from those in the calibration area used to develop the model. Map projection: NZGD2000.

3.2 | Niche factor analyses

Specialisation was higher for *B. nivalis* ($S = 3.208$) and *P. nitidus* ($S = 2.672$) than for *S. australis* ($S = 2.171$), suggesting that these two species have narrower climate niches, hence, more specialised environmental requirements. Marginality values were similar for all species (*B. nivalis* = 2.172, *S. australis* = 2.176 and *P. nitidus* = 1.974), indicating that they inhabit environments substantially different from the mean climate conditions in South Island. Deviations from current climatic conditions are expected to be most pronounced for these species under the RCP8.5 scenario, as indicated by higher departure values than the RCP4.5 scenario. In general, *B. nivalis* had the greatest vulnerability while *S. australis* had the highest departure under future conditions (Table S1.6). These species are most sensitive to mean temperature of driest quarter and isothermality (*B. nivalis* and *P. nitidus*); and annual mean temperature and precipitation seasonality (*S. australis*). Moderate departures in mean temperature of driest quarter resulted in increased vulnerability for *B. nivalis* and *P. nitidus*, while substantial deviations in annual mean temperature and precipitation seasonality led to increased vulnerability for *S. australis* (Table S1.7).

Predicted spatial ranges of the three grasshopper species consistently exhibit high departures from current conditions in almost every variable under both climate change scenarios (Table S1.7). Areas with moderate to high exposure values typically coincide with the most vulnerable current native habitat for all species. For *B. nivalis*, this appears in the northeast (Marlborough and Kaikōura) and southeast (Mackenzie and Waitaki) mountains. For *P. nitidus*, areas of moderate to high vulnerability are scattered across the north (Marlborough) and central west of its current suitable envelope. The most vulnerable current native habitat for *S. australis* appears along the western mountains (Westland) and margins of Central Otago. Areas with low vulnerability to climate change are on the periphery of the central distributions of each species (Figure 3).

3.3 | Population genetic structure

Mitochondrial DNA protein-coding gene ND2 sequences were obtained from 155 individuals. A 708 bp alignment with missing data for some sequences was used for Bayesian phylogenetic analyses. Trimming missing data for other analyses produced an unambiguous aligned region of 603 bp containing 163 unique mtDNA haplotypes detected among the 287 individuals (Table S2.1): 39 in *B. nivalis* ($n = 61$), 55 in *P. nitidus* ($n = 94$) and 69 in *S. australis* ($n = 132$; data from Carmelet-Rescan et al., 2021). Haplotype networks and phylogenetic analyses revealed significant spatial genetic structure in all three grasshopper species (Figure 4). In all species, each haplotype was unique to a single mountain population sample; no haplotypes were shared among mountain samples.

Phylogenetic analyses of ND2 haplotypes recovered three well-supported major lineages (posterior probabilities ≥ 0.95) for *B. nivalis*,

five for *S. australis* and six for *P. nitidus* (Figure 4). Most lineages presented well-supported subdivisions reflecting intermediate levels of geographic structure; however, shallow divisions were generally not well resolved. Median-joining haplotype networks for each species showed similar clustering patterns as those produced by phylogenetic analyses (Figure 4; Figure S2.1). Pairwise Φ_{ST} showed large and significant departures from zero among populations, indicating little gene flow among mountain populations ($\Phi_{ST} > 0.409$; $p < 0.001$; Tables S2.2–S2.4). The most similar haplotypes among population samples were seen at Mt Fox and Mt Dobson (*B. nivalis*; *S. australis*), and Mt Fox and Mt Hutt (*P. nitidus*). Phylogeographic splits correlate with the north–south orientation of the Southern Alps for all species and average genetic distances among the deepest intraspecific lineages exceeded 10.3% (K2P) and 10.8% (TN). Within lineage distances were on average lower than 7.0% (K2P) and 7.5% (TN) in northern lineages, and below 6.2% (K2P) and 6.5% (TN) in southern lineages (Tables S2.2–S2.4).

The level of genetic polymorphism in the ND2 matrilineal marker was similar in all three grasshoppers (Table S2.5). Haplotype diversity (h) and nucleotide diversity (π) values were marginally higher in the species with the largest sample sizes; *S. australis* ($h = 0.984$; $\pi = 0.066$), compared to *P. nitidus* ($h = 0.972$; $\pi = 0.055$) and *B. nivalis* ($h = 0.964$; $\pi = 0.057$). Mismatch distributions for each grasshopper species were multimodal, suggesting large, sustained populations. Neutrality statistics (D , F_S and R_2) of the drift–mutation equilibrium were non-significant, supporting the hypothesis of stable population sizes for all three species. Values of Harpending's r lacked statistical significance for all species. Taken together, these results (mismatch graphs and neutrality tests) were consistent with constant population size (Table S2.6), except for the Mt McRae population of *P. nitidus*, for which population expansion was indicated by the results from mismatch distributions and neutrality test.

To illustrate the potential for intraspecific genetic erosion, we projected current niche models onto future climate scenarios and identified local population extinction that would result in loss of some components of sampled genetic diversity (Figure 5; Table S2.7). A substantial proportion of our sampled haplotypes will be lost in the warmest scenario (RCP8.5): up to 36% for *B. nivalis* and 49% for *S. australis*. Similarly, sampled nucleotide diversity (π) would reduce by 14% for *B. nivalis* and 10% for *S. australis*. Results for *P. nitidus* suggest limited loss of genetic diversity, but the populations predicted to be lost for this species were under-sampled in our analyses ($n = 2$).

4 | DISCUSSION

Montane environments have distinctive ecological characteristics and specialised biology that are sensitive to global climate change (Ikeda, 2022). As in the Andes (Hazzi et al., 2018), Himalayas (Muellner-Riehl, 2019) and European Alps (Schönschetter & Schneeweiss, 2019), Pleistocene climate cycles in New Zealand promoted dramatic changes in the distribution of alpine habitat (Newnham et al., 1999) and cold-adapted organisms are inferred to have attained larger

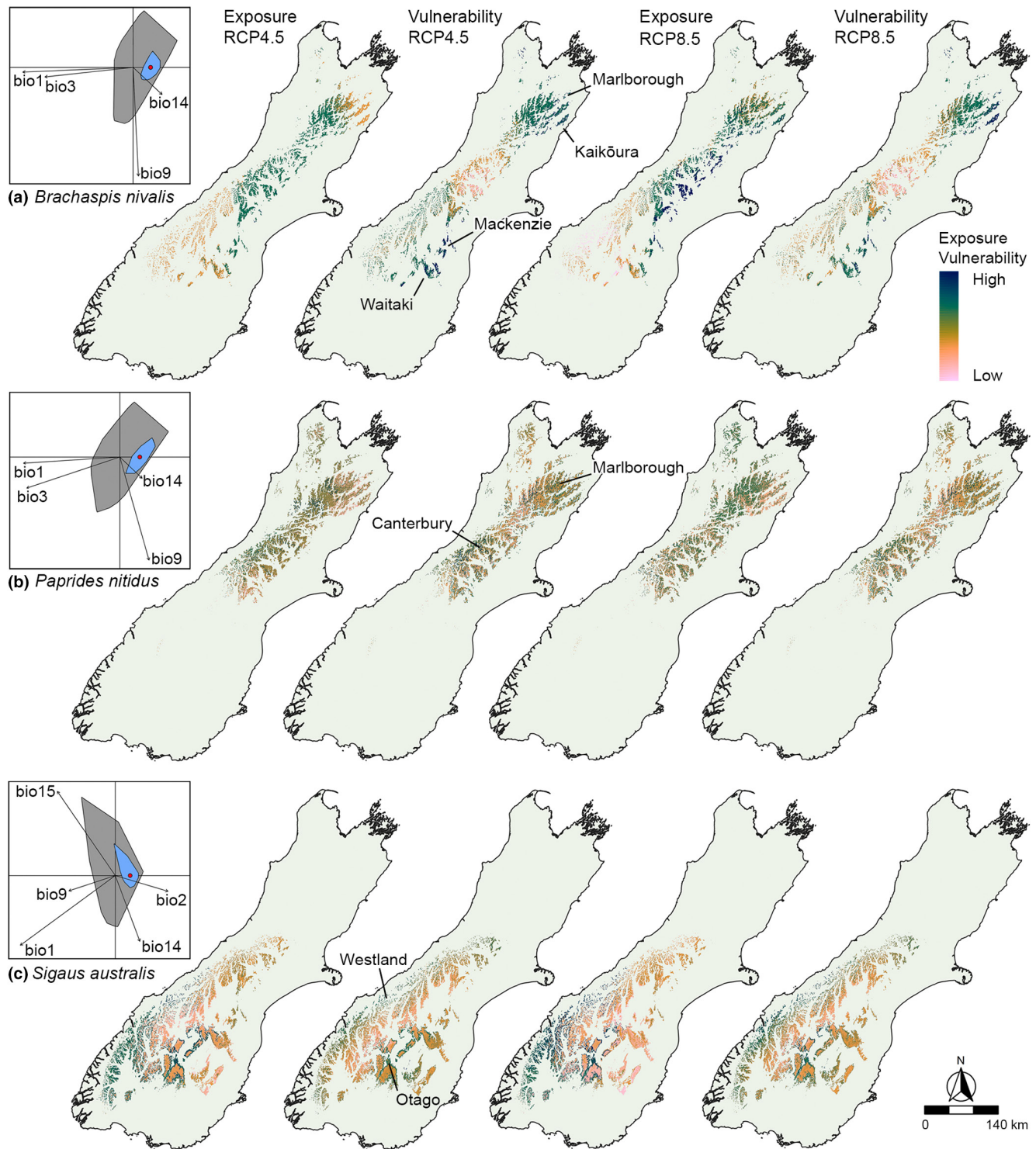


FIGURE 3 Future climatic exposure and vulnerability across the current native ranges of (a) *Brachaspis nivalis*, (b) *Paprides nitidus* and (c) *Sigaus australis* in South Island, New Zealand under two future climate scenarios (RCP4.5 and RCP8.5). Insets show the suitable space (blue) within the available background (grey) across the marginality (x) and specialization (y) axes. Red dots correspond to the centroid of the used habitat and arrows are the projections of the environmental variables: annual mean temperature (bio1), annual mean diurnal range (bio2), isothermality (bio3), mean temperature of driest quarter (bio9), precipitation of driest month (bio14) and precipitation seasonality (bio15). Map projection: NZGD2000.

distributions during lengthy glacial periods by tracking suitable environments (Carmelet-Rescan et al., 2021; Trewick, 2001a; Trewick et al., 2000, 2011). We developed niche models to examine this in detail for three sympatric alpine grasshoppers in the Southern Alps

and found their habitat was more extensive and contiguous during the LGM than today. Consistent with this, we found high intraspecific genetic diversity in these grasshoppers across their spatial ranges. As high genetic diversity is indicative of large, persistent

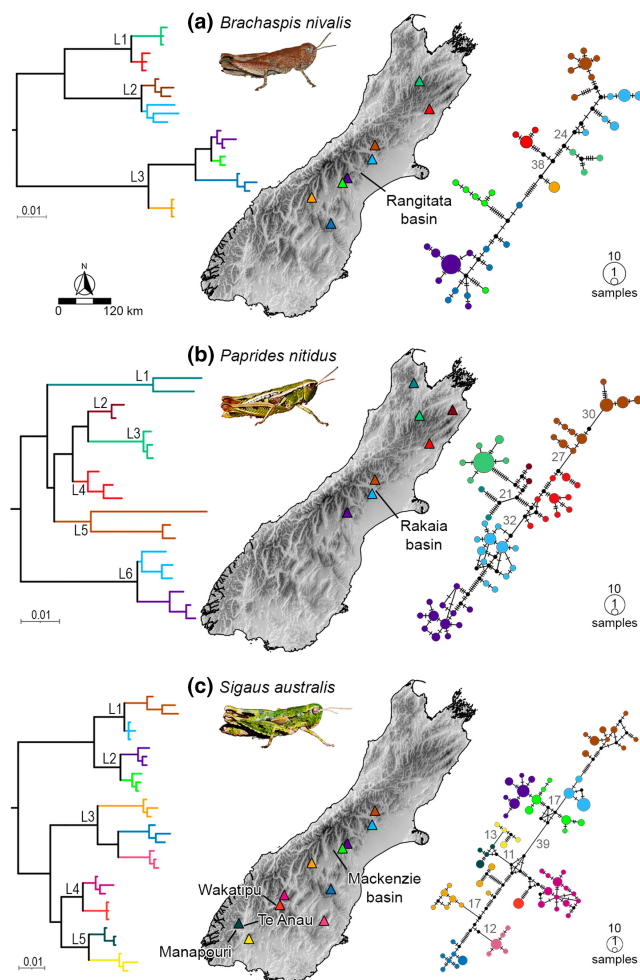


FIGURE 4 Mountains in South Island, New Zealand, sampled for genetic analyses of (a) *Brachaspis nivalis*, (b) *Papirides nitidus* and (c) *Siga australis*. Phylogenetic (left) and genealogical relationships (right) among major ND2 lineages for the studied species. Each mountain location has a different colour as shown on map and used to code haplotypes by sample location; the same colours are used for each of the three sympatric species. In the networks, > 10 inferred substitutions between haplotypes are shown in numbers. For visualisation purposes, only the most common ND2 haplotypes are shown in the phylogenetic trees. See Figure S2.1 for the complete information on relationships and node support. Map projection: NZGD2000.

population size (Charlesworth, 2009; Morgan-Richards et al., 2017), we can infer that the alpine adapted grasshoppers maintained dense populations through the Pleistocene. Similar high intraspecific diversity is known from other New Zealand alpine insects including wētā (King et al., 2020; Trewick et al., 2000) and stoneflies (McCulloch et al., 2009). Deep gene trees with major lineages of each grasshopper species in allopatry suggest long-term extrinsic barriers partitioning large populations.

Cold-adapted species worldwide are inferred to have experienced range contraction as temperatures increased after the LGM (e.g. Guerrina et al., 2022; Ikeda, 2022; Muellner-Riehl, 2019; Trewick et al., 2011). This is the situation for the flightless, alpine

grasshoppers studied here (see also Koot et al., 2022), where postglacial contraction of alpine conditions isolated their populations to mountain ridges and summits, retaining or emphasising existing population segregation (e.g. Carmelet-Rescan et al., 2021; Trewick, 2001b). Associated with this contraction of open alpine habitat is the increased elevation of closed, forest habitat with a timberline (Wardle, 1965) forming a strong natural barrier to dispersal. Population genetics and niche modelling indicate that current grasshopper populations are not derived from a few glacial refugia but represent numerous populations that persisted in situ through the Pleistocene (e.g. Carmelet-Rescan et al., 2021; Trewick, 2001a). The high levels of mtDNA genetic diversity and partitioning of genetic variation among populations is consistent with large populations accumulating mtDNA diversity through many glacial stages that together represent the dominant environmental conditions (~80% of past 800 ka) of the Pleistocene (PIWG, 2016).

In all three grasshopper species, deep intraspecific splits are associated with population samples arrayed along the north-south orientation of the Southern Alps (Figure 4). The most divergent clusters of each species are broadly concordant in the central region of South Island implying a similar process and timing of divergence, but locations are not identical (Figure 1): the Rangitata (*B. nivalis*), Rakaia (*P. nitidus*) and Mackenzie basins (*S. australis*). Similar phylogeographic structure is known from other alpine animals in the Southern Alps (e.g. Hill et al., 2009; King et al., 2020; Trewick, 2001a; Trewick et al., 2000; Weston & Robertson, 2015), but these might reflect lineage sorting at different times (Trewick et al., 2011). The grasshoppers considered here each encompassed more than 10% sequence divergence (see also Trewick, 2001b, 2008), which for comparison, is an order of magnitude greater than found in well-studied *Chorthippus* grasshoppers across Europe (e.g. Lunt et al., 1998). Whereas phylogeographic structure in *Chorthippus* and other animals in western Europe reflect postglacial population expansion (Hewitt, 2000; Schmitt, 2007), divergence within the New Zealand species plausibly originated early in the establishment of alpine habitat in the Southern Alps (~3–5 Mya).

For many alpine animals, valleys represent barriers between populations if they contain inhospitable habitat that cannot be traversed (Figure 6). Forest, during interglacials, and ice, during glacials, are both likely to impede range shifts and gene flow among populations of flightless grasshoppers (Trewick et al., 2000). Thus, although shallower lineage splits (0.8%–2.6%) were associated with intraspecific grasshoppers samples from adjacent mountains (e.g. *B. nivalis* and *S. australis* on Fox Peak and Mt Dobson, and *P. nitidus* on Mt Hutt and Fox Peak), valley habitat might override geographic distance as the main evolutionary driver. For example, gene flow was apparently more restricted among southern populations of *S. australis* that exhibit genetic divergence greater than 3.1% (e.g. Mt Cardrona, Double Cone, Mt Luxmore and Mt Spencer; see also Carmelet-Rescan et al., 2021; Trewick, 2008). Deep incised glacial lakes (e.g. Te Anau, Wakatipu, Manapouri) appear to have limited

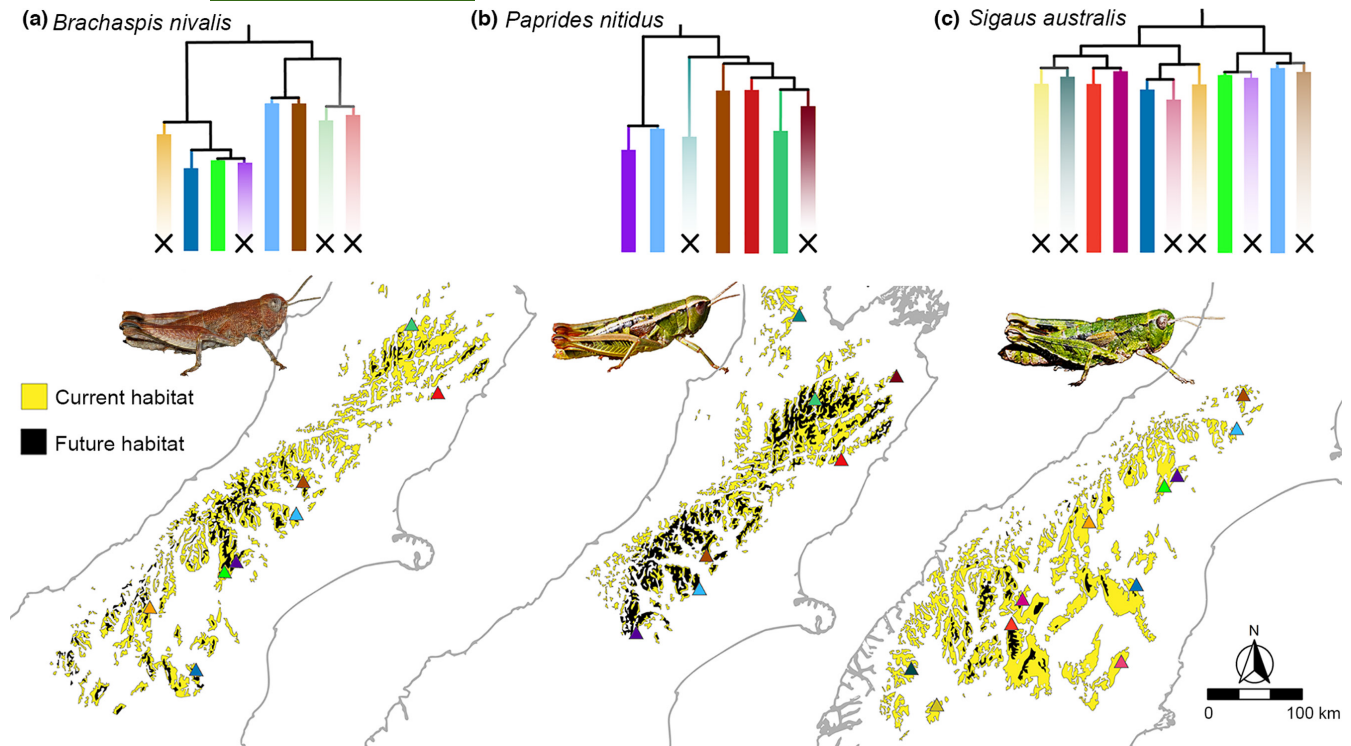


FIGURE 5 Predicted shifts in suitable native area and sampled intraspecific diversity for (a) *Brachaspis nivalis*, (b) *Paprides nitidus* and (c) *Sigauss australis* in South Island, New Zealand, under the warmest climate scenario (RCP8.5). Faded lineages in the phylogenies correspond to populations expected to be lost (X) under global warming. Colours for sampling locations as in Figure 1. Map projection: NZGD2000.

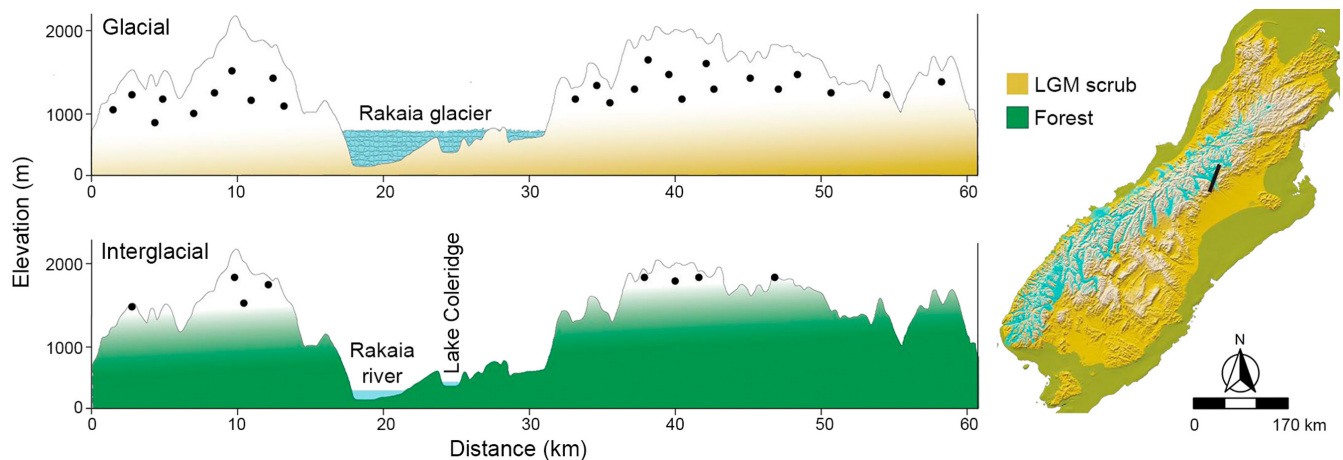


FIGURE 6 Valley habitats form dispersal barriers for flightless, alpine-adapted grasshoppers (black dots), where they contain montane glaciers during Pleistocene glacials, or dense forest during interglacials. The elevation profile represents a south-west section of the Southern Alps across the Rakaia (black line on map). Population segregation hypothesis for glacial conditions (top) and interglacial conditions (bottom). Map projection: NZGD2000.

genetic exchange between these nearby populations of *S. australis* (e.g. Trewick, 2001b; Trewick et al., 2000). Similarly, lineage sharing in *P. nitidus* on Mt Hutt and Fox Peak (~70 km apart) but not between the closer (~30 km) Mt Hutt and Mt Olympus populations implies isolation that could be explained by glaciers (Figure 1). Deeply split genetic lineages in all three grasshoppers correlate with LGM glaciers and proglacial lakes (Sutherland et al., 2019) and strongly suggest that these were extrinsic barriers to grasshopper populations

that persisted on nunataks (Figure 1) as proposed for alpine scree wētā in this landscape (Trewick et al., 2000). Nevertheless, in central South Island, the low lying, eastern Canterbury Plains developed from glacial alluvial outwash and likely provided opportunities for grasshopper range shifts during glacials.

Projecting forward and considering current climate change trends makes it clear that habitat availability for mountaintop species in the enhanced, protracted, anthropogenic 'interglacial' currently

developing around the globe (PIWG, 2016) will further diminish. If niche stability, conservatism and saturation operate, we can expect further contraction and emphasised population reduction and fragmentation (Freeman et al., 2018). However, upward range shift and/or shrinkage will occur at species-specific rates, implying non-identical responses to change among these grasshoppers, dependent on intrinsic features of each species (e.g. niche specialisation and ecological preferences) and uneven climate departures across their ranges under future conditions. Here, differences in the distribution of current habitat led to different projected habitat availability which in turn signals species-specific patterns of genetic erosion (Figure 5). Range loss under the worst-case scenario (RCP8.5) is predicted to be least for *P. nitidus* (20%), and substantially more for *B. nivalis* (75%) and *S. australis* (90%), but all three are likely to lose diversity because lineages are associated with distinct regions along the latitudinal gradient. Thus, a Pleistocene history of spatial isolation will culminate in local extinction. Future latitudinal tracking of climatically suitable habitat, as predicted by niche models (Figure 2), is unlikely to result in opportunities for these flightless grasshoppers; their limited capacity for long-range dispersal between habitat patches is evident from their phylogeography.

Temperature variation is a key predictor of these species' distributions and vulnerability patterns, but distinct bioclimatic factors suggest that the grasshopper species are subject to microhabitat segregation despite overlapping ranges. Likewise, deviations from current climatic conditions are projected to vary across the Southern Alps, and so strongly influence potential responses to global warming. Climate variables contributing to models are, however, better considered as proxies for combinations of environmental conditions and may not themselves be the direct drivers of species ranges, and correlative niche modelling and niche-factor analyses neglect other ecological processes shaping species' niches such as biotic interactions and population dynamics (e.g. Freeman et al., 2018; Suttle et al., 2007). Species of New Zealand alpine grasshopper co-occur throughout their ranges (Bigelow, 1967; Trewick & Morris, 2008) and interact with other biotic and abiotic elements that likely affect their ability to persist under environmental change (Thompson & Fronhofer, 2019). Accounting for these interactions might improve model predictions but gathering such data is challenging and the pace of environmental change may be overwhelming.

The existence of localised peripheral populations of these three flightless grasshoppers in non-alpine habitats (Trewick & Morris, 2008) suggests some capacity for survival in alternative conditions that enables range-shift into adjacent, novel habitat arising from anthropogenic activity (e.g. Sivyer et al., 2018). However, this opportunity relies on additional anthropogenic activity (removal of natural lowland forest vegetation) generating corridors from the alpine zone. As such, range adjustments into exotic habitat probably have only brief viability as lowland populations are likely to have low genetic diversity, small population size, diminished population cohesion (e.g. Pavlova et al., 2017; Rehnus et al., 2018; Rizvanovic et al., 2019), and might experience lag-extinction effects (e.g. Sax et al., 2013). Novel, anthropogenic open habitats are at high risk from continued land-use change (e.g.

Koot et al., 2022; Sivyer et al., 2018), are dominated by exotic plants, and their derived species assemblages are in disequilibrium (Blonder et al., 2015), subject to invasive predators and weeds (e.g. Smith et al., 2007). Location and taxon-specific introgression (e.g. Dowle et al., 2014; Morgan-Richards et al., 2021) will influence the evolutionary potential of populations in new locations.

Despite its relatively small land area, the persistence of many populations throughout the Pleistocene has yielded much higher intraspecific diversity in these New Zealand insects than typically encountered in the Northern Hemisphere. As a result, genetic erosion of alpine biodiversity by anthropogenic global climate change will be especially intense. An optimistic view is that biodiversity decline will be countered by evolution (Catullo et al., 2019). Whether populations of flightless, alpine grasshopper shift their range up mountains as they track dwindling suitable habitat, or find dispersal corridors to exotic habitats, we know fragmentation leads to small populations with reduced adaptive potential (Willi et al., 2006) that are unlikely to have the genotypic scope to respond to natural selection arising directly from rapid climate change and other anthropogenic threats (Bowler et al., 2020). Despite alpine species not being ecologically identical, we expect loss of genetic diversity for all alpine biota due to global warming.

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CONFLICT OF INTEREST STATEMENT

We declare we have no competing interests.

DATA AVAILABILITY STATEMENT

The mtDNA sequences supporting the findings of this study are openly available in Genbank at <https://www.ncbi.nlm.nih.gov/genbank>, accession numbers OQ267402–OQ267581. Sequence alignments and distribution data are available at Dryad Data Repository (<https://doi.org/10.5061/dryad.rfj6q57fp>).

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BIOSKETCH

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SUPPORTING INFORMATION

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

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