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Phenotypic variation is greater in the absence of gene flow in three alpine grasshoppers

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Alpine organisms distributed on mountain ranges with broad latitudinal and elevational gradients provide an appropriate setting to explore clinal phenotypic variation and the role of gene flow. We used Bayesian generalized linear mixed models to investigate body size variation along genetically connected (elevation) and disrupted (latitude) gradients in three flightless alpine grasshopper species endemic to the Southern Alps (Kā Tiritiri o Te Moana) of New Zealand (Aotearoa), and test whether variation relates to geographic differences in environmental conditions. We found latitudinal size clines in all species, but little phenotypic variation was explained by elevation. Size clines are consistent with theoretical expectations of local adaptation, with minor roles for plasticity and drift. Size variation in each species has distinct climatic association, potentially reflecting microhabitat selective pressures and distinct evolutionary histories. Latitudinal size clines suggest that phenotypic differences may result from barriers to gene flow among mountaintop populations, while gene flow on steep elevational clines homogenizes body size. Rapid environmental change imposes selection that could result in local adaptation, but we have shown here that selection pressure cannot be considered in isolation from gene flow when predicting how populations will respond to climate change.

1. Introduction

Environmental conditions vary across species' ranges, often generating phenotypic clines due to selection gradients [1–3]. This is very evident in adult body size among populations adapted to local conditions and between males and females of a population in response to sex-specific selection [3]. Temperature is a central feature of any environmental gradient that correlates with clinal variation in body size in most, if not all, animal groups [4]. Bergmann's rule describes this pattern where larger individuals of a species occur at colder, higher latitude and elevation [5,6]. In endotherms, differential heat conservation in response to environmental temperature provides an adaptive explanation for the phenomenon [5–7]. Although this mechanism is not applicable to ectotherms, parallel trends are seen in many insects [8,9], even under laboratory conditions [10].

Comparison of species and populations among sites with different thermal conditions provides insight into the evolutionary mechanisms structuring phenotypic diversity [11]. Temperature and growing season length decrease gradually with latitude but more rapidly with elevation [11,12], and both can influence insect growth rate and body size [8,12,13]. Anthropogenic climate change is altering alpine insect distributions [14] and could have implications for the size of individuals if local populations are to persist. As different species living in shared landscapes are subjected to the same environmental regimes, convergent clinal variation can be interpreted as evidence of adaptation [15,16].

Separating genetic and plastic responses is challenging as they are not mutually exclusive, can interact, and both may be subject to natural selection [17]. Furthermore, traits that confer local adaptations are often polygenic involving numerous loci with small effects that complicate identification of influential loci [15,18]. Beyond the uncertainty surrounding direct genetic phenotypic change versus existing plasticity, we know that adaptive clines emerge and persist through the interplay of gene flow and natural selection across environmental gradients [1,2,19,20]. Selection can also vary between males and females across different environments, promoting the evolution of clinal patterns in sexual dimorphism [3]. However, it remains unclear whether environmental variability typically generates similar or distinct patterns of selection on each sex.

Cline theory predicts that sufficient gene flow among populations counters the effects of natural selection, promoting phenotypic uniformity [1–3,20]. However, gene flow across a species' range depends on demographic processes regulating population densities, and landscape features disrupting their continuity [1,2,21,22]. Populations that remain geographically and genetically isolated are expected to gradually accumulate phenotypic differences over time due to both neutral and selective processes [23,24]. Just as adaptive clines reflect species-specific responses to selective forces across environmental gradients [1,3,19,20], clinal sexual dimorphism can signal sex-specific selection and adaptation [3,13,25,26]. Thus, clinal studies provide an indirect means of inferring the directionality of adaptive phenotypic divergence within and between populations distributed across environmental gradients [1,3,19].

Here, we examined body size variation along genetically connected (elevation) and disrupted (latitude) gradients in three widespread, flightless *Sigaus* grasshopper species (Orthoptera: Acrididae) endemic to the Southern Alps (Kā Tiritiri o Te Moana) of New Zealand (Aotearoa) [27]: *S. australis* (Hutton), *S. nitidus* (Hutton) and *S. nivalis* (Hutton). These species are the product of an endemic radiation (13 species) associated primarily with alpine habitats and freeze tolerance that diversified around 13–15 Ma [28]. Across their overlapping ranges, these species show distinct microhabitat preferences: *S. nivalis* is more abundant on scree/rock habitat, whereas *S. australis* and *S. nitidus* are prevalent in tussock and herbfields [29–31]. Despite distinct range limits and evolutionary histories [32], these species are broadly sympatric with distributions that encompass wide temperature ranges across latitude and elevation. If body size is mainly shaped by contemporary thermal effects, convergent clines are expected, with species and sexes responding similarly to temperature gradients across latitude and elevation. Conversely, differences in magnitude and/or direction of clines could reflect the historical interplay among dispersal, sex-specific selection and environmental change. We know that even closely related species are not ecologically identical and so may differ in tolerance, vagility, evolutionary history, plasticity and adaptive potential; all of which can mediate responses to environmental stressors and ultimately dictate the degree of spatial phenotypic concordance [24].

Our earlier work on these three grasshopper species demonstrated the genetic distinctiveness of populations on mountaintops (figure 1) consistent with a Pleistocene history of isolation [32], and we predict this will have fostered local directional selection on phenotype [1,2,24]. Local adaptation is expected to take the form of clinal rather than abrupt variation given that environmental conditions across latitudinal and elevational gradients tend to be clinal [11,12]. However, the expanded genetic sampling presented here shows that, despite steep elevational gradients, intraspecific gene flow is widespread along elevation (figure 1, electronic supplementary material, figure S1.1), and this is expected to limit evolution of adaptive clines [1,2,20]. Thus, predicted latitudinal trends in size may not to be accompanied by elevational trends [34].

Specifically, we tested the following predictions. (i) Body size will show congruent clines across three sympatric grasshopper species as expected of adaptation to shared selective pressures. (ii) Gene flow on an elevation gradient will impede body size adaptation within mountain populations but not among populations on a latitude gradient. (iii) Body size variation will correlate with spatial variation of environmental variables. We also examined whether size clines differ between sexes, as this will show the degree to which sexual size dimorphism varies with geography and such variation is linked to environmental factors.

2. Methods

2.1. Taxon sampling

We sampled populations of our three focal grasshopper species (*S. australis*, *S. nitidus* and *S. nivalis*) across their overlapping ranges spanning 670 km of latitude. These species are not sister taxa, each being more closely related to other congenerics [27], and are not known to hybridize with one another. Sampling took place above the treeline on six mountaintops (figure 1) arrayed along the latitudinal gradient of the Southern Alps (approx. 4.5°): Mt McRae, Mt Temple, Hamilton Peak, Mt Hutt, Fox Peak and Mt Cardrona. These mountains embrace most of these species' ranges, capturing distinct aspects of their environmental envelopes. The three grasshopper species studied here have narrow native elevational ranges from the treeline up to, 2020 m for *S. australis*, 1830 m for *S. nitidus* and 2000 m for *S. nivalis* [27]. However, these limits vary with mountain height and geographic location, as habitat availability is influenced by the elevation of the forest–alpine transition, that is lower in southern regions and higher in the north of New Zealand [35]. Adult grasshoppers were collected during summer when they are active (late January to early March 2015–2023), along six transects (one per mountain) divided into elevation intervals of 66–291 m (hereafter, sampling sites, mean = 118 ± 48.5 m) that ranged in ground length between 383 and 761 m. Transect length varied depending on mountain height, terrain steepness and accessibility, as well as on local spatial variation in species presence and abundance (electronic supplementary material, table S2.1 and figure S2.1). This resulted in uneven sampling among mountains, sites and years. Species, sex and maturity were identified using morphological traits [30].

2.2. Body size proxies

Adult body size was quantified on structural and mass components. We explored three non-independent linear metrics as proxies of overall structural size (electronic supplementary material, figure S3.1): left hind femur length (FL), maximum left femur width (FW) and mid-line pronotum length (PL). Measurements were made on 873 adult grasshoppers (*S. australis* = 163♀, 118♂; *S. nitidus* = 198♀, 189♂; *S. nivalis* = 113♀, 92♂) using an Olympus SZX7 stereomicroscope with Olympus SC100 image capture (Olympus Corporation, Japan). Repeatability scores indicated high reproducibility (electronic supplementary material, figure S3.2). Body mass was recorded as fresh mass (FM) from live specimens (± 0.001 mg) using a Sartorius Quintix35-1S scale (Sartorius Lab Instruments GmbH & Co, Germany). For grasshoppers collected before 2020 that lacked FM data, we measured ethanol-preserved mass, which was then converted to FM using an accurate mass-to-mass conversion equations derived for the focal grasshoppers [36]. Acridid grasshoppers are income breeders, allocating resources for reproduction from feeding intake during the growing season [37], which is usually expressed as residual variation when regressing body mass on structural size [36]. The length of the hind jumping leg is of interest given its functional role for locomotion and predator avoidance in the flightless grasshoppers studied here. Thus, heavier individuals are expected to have larger jumping legs, as increased mass without proportional leg growth would be disadvantageous. Unlike FM, femur length does not carry variance due to intra-seasonal changes in body condition and is closely related to other size components and thus to overall body size [36]. This relationship was evident in our dataset (electronic

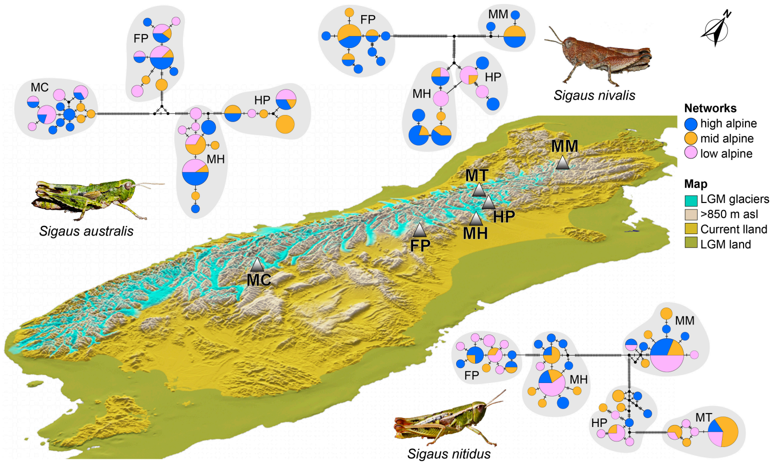

Figure 1. Sampling locations of three grasshopper species (*Sigaus australis*, *Sigaus nitidus* and *Sigaus nivalis*) on six mountains in South Island, New Zealand: Mt McRae (MM), Mt Temple (MT), Hamilton Peak (HP), Mt Hutt (MH), Fox Peak (FP), Mt Cardrona (MC). Genealogical relationships within (elevation) and among (latitude) mountaintop populations are networks of mitochondrial NADH-dehydrogenase 2 haplotypes with relative elevation of samples indicated by colour (see electronic supplementary material 1 for complete information on DNA extraction, amplification and sequencing methods and electronic supplementary material, figure S1.1 for details on elevation). Note that not all species were sampled at every mountain, nor at every elevation within each mountain. The base map (NZGD2000) is an oblique three-dimensional projection of South Island, New Zealand depicting current and past topography and glaciation during the last glacial maximum (after [33]).

supplementary material, figure S3.3), so we used femur length as an index of overall body size for downstream analyses, and results based on FM are presented as electronic supplementary material (see §3).

2.3. Environmental predictors of body size

Mountaintop insects in temperate regions experience relatively brief periods of favourable conditions due to pronounced seasonal environmental fluctuation, so body size would be expected to respond to climate seasonality and isothermality [38]. The duration of the growing season, which coincides with New Zealand summer, and temperature and precipitation regimens during growth are also likely influential for final body size in the studied species [39]. Here, we explored six variables (Pearson's r from –0.70 to 0.60, indicating low to moderate correlations) capturing distinct aspects of these environmental factors as potential predictors of size variation in the grasshoppers: isothermality, temperature seasonality, temperature of the driest quarter, precipitation seasonality, precipitation of driest quarter and growing season length (electronic supplementary materials, table S4.1 and figure S4.1). Environmental layers (averaged 1981–2010) were obtained from the Chelsa database [40] at 30 arc-sec resolution (approx. 1 km^2). We acknowledge that there may be fine-grain variation within a 30 arc-sec grid cell, but given the geographical and temporal scale of our sampling, these layers are expected to capture the relative magnitude of current climate trends better than older climate series (1970–2000). Each of the six environmental predictors exhibits a distinct clinal relationship with latitude and elevation, differing in both the strength and direction of association across the study region (electronic supplementary material, figure S4.2), suggesting a role in shaping local adaptation.

2.4. Statistical modelling

We fitted Bayesian generalized linear mixed models with the R package brms [41], using a Gaussian distribution (link = identity) with weakly informative priors for population-level coefficients [normal(0, 2.5)], intercept [student-t(3, 0, 5)], and group-level standard deviations [exponential(1)], and brms's default priors for residual standard deviation (sigma). Continuous predictors were standardized by centring and dividing by two standard deviations [42]. Models used four chains of 40 000 iterations, discarding the first half as burn-in and saving every 10th generation and adapting deltas of 0.99. Chain convergence and autocorrelation were checked by examining trace plots and ensuring Rhat ($\hat{R}$) values were close to 1.0. We examined model assumptions and performance using the R packages performance [43] and loo [44]. We reported posterior medians and 95% Bayesian high-density intervals (HDI) for each parameter of interest. We considered predictors to have a meaningful effect on the response variable (i.e. body size) if the 95% HDI did not overlap with zero. Alternatively, we estimated Bayesian indices of effect existence (probability of direction, Pd) and significance (full region of practical equivalence, full ROPE) using the R package bayestestR [45]. Predictors with $\mathrm{Pd} \geq 99\%$ (positive or negative), and full ROPE values $\leq 1\%$ were regarded as indicating significant [45] meaningful effects on size.

2.4.1. Spatial clines in body size and sexual size dimorphism

We tested whether grasshopper populations along latitudinal and elevational gradients exhibit clinal variation in size by fitting a random-intercept and random-slope model for each species, as preliminary plots suggested that the effect of elevation on size might vary among mountains. These plots also indicated potential non-linear effects of latitude on size, but not of elevation, so competing models including both linear (1.1) and quadratic (1.2) terms for latitude were considered:

$$BS_{ijklmn} = \beta_0 + \beta_1 L_i + \beta_2 E_j + \beta_3 S_k + \beta_4 L_i \times S_k + \beta_5 E_j \times S_k + b_{0l} + b_{1l} E_j + b_{0m} + b_{0n} + e_{ijklmn}, \tag{1.1}$$

where BS_{ijklmn} is the body size for the i-th latitude, j-th elevation, k-th sex, l-th mountain, m-th site and n-th year. β_0 is the intercept, $\beta_1\mathrm{L}_i$ is the effect of latitude, $\beta_2\mathrm{E}_j$ is the effect of elevation, $\beta_3\mathrm{S}_k$ is the effect of sex, $\beta_4\mathrm{L}_i \times \mathrm{S}_k$ is the two-way latitude×sex interaction, $\beta_5\mathrm{E}_j \times \mathrm{S}_k$ is the two-way elevation ×sex interaction, b_{0l} is the random mountain effect, $b_{1l}\mathrm{E}_j$ is the mountain-specific slope for elevation, b_{0m} is the random sampling site effect, b_{0n} is the random year effect and e_{ijklmn} are residuals. This model tested whether size is influenced by latitude, elevation, sex and their interactions (to test for sex-specific clines and infer latitudinal and elevational trends in size dimorphism), while accounting for size variability due to unaccounted differences among mountains, sites and years, with the random-slope term capturing mountain-specific responses to elevation. The quadratic model is the same as before (1.1), except for the inclusion of quadratic terms to test for non-linear latitudinal effects:

$$\begin{aligned} BS_{ijklmn} = {} & \beta_0 + \beta_1 L_i + \beta_2 L_i^2 + \beta_3 E_j + \beta_4 S_k + \beta_5 L_i \times S_k + \beta_6 L_i^2 \times S_k + \beta_7 E_j \times S_k + b_{0l} + b_{1l} E_j \\ & + b_{0m} + b_{0n} + e_{ijklmn} \end{aligned} \tag{1.2}$$

where $\beta_2\mathrm{L}_i^2$ is the quadratic effect of latitude and $\beta_6\mathrm{L}_i^2 \times \mathrm{S}_j$ is the interaction effect between quadratic latitude and sex. Linear and quadratic models were ranked based on their predictive accuracy using Watanabe–Akaike information criterion (WAIC) and pseudo-Bayesian model averaging (pseudo-BMA) weights with Bayesian bootstrap as implemented in the R packages performance [43] and loo [44]. Models with lower WAIC and higher pseudo-BMA weights were inferred to have higher predictive performance and weights, meaning the model is better at explaining the data while avoiding overfitting.

2.4.2. Environmental determinants of body size

To test for contemporary environmental effects on body size, we followed a two-step process. Given the relatively large number of predictors (six), we first applied a Bayesian variable selection procedure using projection predictive feature selection (PPFS) with the R-package projpred [46]. For this, we fitted random intercept-only reference models including only additive main effects (2.1) without sex interactions or random slopes to avoid increasing model complexity beyond the limits of our datasets:

$$S_{ijklm} = \beta_0 + \sum_{i=1}^{6} \beta_i Y_i + \beta_7 S_j + b_k + b_l + b_m + e_{ijklm}, \tag{2.1}$$

where $\sum_{i=1}^{6} \beta_i \mathrm{Y}_i$ is the sum of the effects of all six environmental predictors and $\beta_7\mathrm{S}_j$ is the effect of sex; other terms are the same as in equation (1.1). We then used PPFS to find the submodel with fewer predictors that showed similar predictive performance as the reference model, using cross-validation (see electronic supplementary material, table S4.2 for details). This analysis indicated that excluding sex, one predictor usually provided similar performances as the reference models (see §3 for details), thus in the next step, we used the top-ranked predictors to fit random intercept-only models for each species (2.2):

$$BS_{ijklm} = \beta_0 + \beta_1 L_i + \beta_2 S_j + \beta_3 L_i \times S_j + b_k + b_l + b_m + e_{ijklm}, \tag{2.2}$$

where $\beta_1 Y_i$ is the effect of the selected environmental factor, $\beta_2 S_j$ is the effect of sex, and $\beta_3 Y_i \times S_j$ is their two-way interaction (to infer sex-specific responses to environmental change). This model structure does not include a random-slope term, as preliminary plots do not suggest varying responses to environmental factors across mountains, likely due to the coarse-resolution of our predictors. Quadratic terms were omitted as data did not suggest curvilinear trends.

3. Results

Despite collecting all three grasshopper species at numerous sites, we did not detect any evidence of hybridization. The distribution of mitochondrial haplotypes revealed no sharing among species or mountains, but widespread sharing among conspecifics at different elevations on the same mountain (figure 1, electronic supplementary material, figure S1.1). All body-size models ran smoothly with no post-sampling warnings, and diagnostic statistics indicated good model predictive performance and convergence for all parameters. Conditional R^2 scores ranged from 0.926 to 0.978 (mean = 0.956 ± 0.023 s.d., standard deviation), indicating that most of the variance in our datasets was explained by the models. While the examined geographic and climatic predictors explained a reasonable amount of variation in body size, sex had the strongest effect (tables 1 and 2), as expected from a system with large females and small males [30,36].

3.1. Spatial clines in body size and sexual size dimorphism

The three grasshopper species varied in body size across latitude with species and sex dependant relationships (table 1 and figure 2). Latitudinal variation in size was most often explained by models incorporating quadratic terms (electronic supplementary material, table S5.1). Fixed effects explained most of the variance in size in our datasets, with marginal R^2 scores ranging from 0.844 to 0.971 (mean = 0.915 ± 0.065 s.d.).

Parameter estimates (table 1) and Bayesian indices of effect existence (Pd) and significance (ROPE) from the best-fitted latitudinal models indicated no significant main effects of latitude on *S. australis* size, neither linear (Pd = 68.6, ROPE = 8.19) nor quadratic (Pd = 69.67, ROPE = 8.38). Significant latitude × sex interactions (linear: Pd = 100; ROPE = 0.00; quadratic: Pd = 100, ROPE = 0.00) revealed only female size changed quadratically with latitude yielding increased size dimorphism at mid-latitudes (table 1; figure 2*a*). Likewise, we found no evidence of main effects of latitude on *S. nitidus* size (linear: Pd = 82.35, ROPE = 6.85; quadratic: Pd = 94.09, ROPE = 2.46), but a significant quadratic interaction with sex (Pd = 100, ROPE = 0.00) suggested that size in males and females follows different trajectories. Steeper quadratic curves in female *S. nitidus* led to increased size dimorphism in southern latitudes (table 1a; figure 2*b*). In contrast, latitude had a significant but weak linear effect on *S. nivalis* size, consistent with Bergmann's rule (Pd = 99.06, ROPE = 0.71), and a significant linear latitude × sex interaction (Pd = 99.62, ROPE = 0.99) showed that females exhibit slightly steeper clines than males. Thus sexual size dimorphism increases accordingly with latitude in *S. nivalis* (table 1a; figure 2*c*). We found no evidence for a significant effect of elevation on body size across species, neither as a main effect nor in interaction with sex (table 1). Similar results were obtained when analysing FM as a proxy of overall body size, and the conclusions were not affected (electronic supplementary material, figure S6.1).

3.2. Environmental determinants of body size

Model size selection plots indicated that apart from sex (which always ranked first), one environmental predictor was enough to obtain a predictive performance close to that of the reference models for *S. australis* and *S. nitidus*, though three predictors were required for *S. nivalis* (electronic supplementary materials, figure S4.2 and table S4.3). Variables capturing seasonal shifts in temperature were ranked highest most often, yet the top-ranked predictors varied among species: temperature variation (isothermality) was the most important predictor of size for *S. australis*, rainfall variation (precipitation seasonality) for *S. nitidus* and temperature of the driest quarter for *S. nivalis*. Fixed effects explained most of the variance in size in our datasets (table 2), with marginal R^2 scores ranging from 0.641 to 0.926 (mean = 0.826 ± 0.161 s.d.).

Table 1. Effects of latitude and elevation on body size (femur length) of three flightless alpine grasshopper species endemic to South Island, New Zealand: *Sigaus australis*, *Sigaus nitidus* and *Sigaus nivalis*. Median [95%-HDI] = median point estimate [95% Bayesian highest density interval]. Estimates for random effects are reported as standard deviations, as estimated by brms: random intercept (τ_{00}) and random slope (τ_{11}). Bold face type indicates fixed parameters with significant effects (see main text for values on indices of effect existence and significance).

	S. australis	***S. nitidus***	***S. nivalis***
parameter	**median [95%-HDI]**	**median [95%-HDI]**	**median [95%-HDI]**
(intercept)	17.30 [16.17, 18.30]	15.70 [15.31, 16.10]	15.16 [13.72, 16.22]
latitude	−1.24 [−6.04, 3.70]	1.52 [−2.13, 4.26]	**2.73 [0.73, 4.34]**
latitude^2	−1.32 [−6.12, 3.65]	2.53 [−0.80, 5.16]	
elevation	0.27 [−0.48, 0.94]	0.02 [−0.26, 0.30]	0.43 [−0.46, 1.36]
sex	**−5.98 [−6.12, −5.84]**	**−4.77 [−4.85, −4.70]**	**−3.69 [−3.88, −3.50]**
latitude × sex	**4.66 [2.70, 6.63]**	1.04 [−0.42, 2.50]	**−0.88 [−1.53, −0.21]**
latitude^2 × sex	**7.77 [5.56, 9.98]**	**−4.08 [−5.50, −2.64]**	
elevation × sex	−0.49 [−0.76, 0.12]	0.07 [−0.10, 0.24]	−0.19 [−0.55, 0.19]
random effects			
mountain (τ_{00})	0.82	0.23	0.83
mountain (τ_{11})	0.52	0.19	0.42
site (τ_{00})	0.18	0.09	0.49
year (τ_{00})	0.29	0.21	0.30
residual (σ^2)	0.30	0.14	0.31
$R^2_{\text{conditional/marginal}}$	0.967/0.930	0.978/0.971	0.928/0.844

Table 2. Effects of environmental factors on adult body size (femur length) of three flightless alpine grasshopper species endemic to South Island, New Zealand: *Sigaus australis*, *Sigaus nitidus* and *Sigaus nivalis*. Median [95%-HDI] = median point estimate [95% Bayesian highest density interval]. Estimates for random effects are reported as standard deviations, as estimated by brms: random intercept (τ_{00}) and random slope (τ_{11}). Bold face type indicates fixed parameters with significant effects (see main text for values on indices of effect existence and significance).

	S. australis	***S. nitidus***	***S. nivalis***
parameter	**median [95%-HDI]**	**median [95%-HDI]**	**median [95%-HDI]**
(intercept)	17.55 [17.06, 18.02]	15.73 [15.35, 16.19]	15.20 [13.55, 16.93]
isothermality	**1.17 [0.75, 1.55]**		−1.60 [−4.22, 0.98]
precipitation seasonality		−0.37 [−0.79, 0.37]	−1.65 [−3.93, 1.44]
temperature driest quarter			**−2.01 [−3.79, −0.36]**
sex	**−6.17 [−6.33, −6.00]**	**−4.82 [−4.90, −4.74]**	**−3.77 [−3.95, −3.60]**
isothermality × sex	**−0.80 [−1.12, −0.48]**		0.58 [0.04, 1.11]
precipitation seasonality × sex		**0.32 [0.16, 0.47]**	0.51 [−0.05, 1.05]
temperature driest quarter × sex			0.72 [0.08, 1.35]
random effects			
mountain (τ_{00})	0.25	0.24	1.12
site (τ_{00})	0.20	0.13	0.49
year (τ_{00})	0.22	0.21	0.32
residual (σ^2)	0.37	0.14	0.12
$R^2_{\text{conditional/marginal}}$	0.960/0.944	0.977/0.957	0.926/0.641

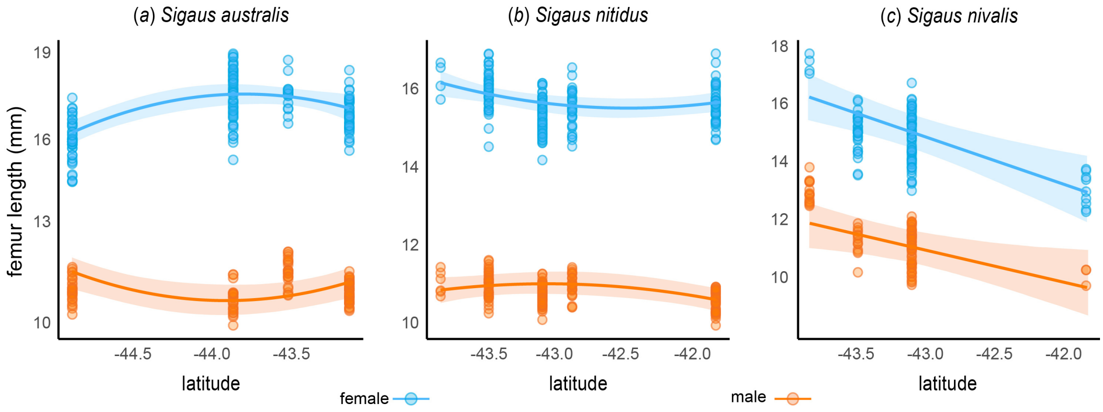

Figure 2. Body size (using femur length as a proxy for overall size) in relation to latitude in three flightless alpine grasshopper species endemic to South Island, New Zealand: (a) *Sigaus australis*, (b) *Sigaus nitidus* and (c) *Sigaus nivalis*. Females display the most difference in size leading to latitudinal shifts in size dimorphism. Shading indicates 95% Bayesian high-density intervals. Latitude in southern hemisphere from south (left) to warmer north (right). Patterns of femur length variation differ among species.

Parameter estimates (table 2) and Bayesian indices indicated a significant and positive effect of isothermality on *S. australis* size both as a main effect (Pd = 100, ROPE = 0.04) and in interaction with sex (Pd = 100, ROPE = 0.13), with females having steeper slopes than males (figure 3*a*). While precipitation seasonality remained the most informative predictor for *S. nitidus*, no main effect on size was detected (Pd = 92.33, ROPE = 19.72). Although we found a significant interaction with sex (Pd = 99.99, ROPE = 0.97), this effect was very weak and probably negligible in males (figure 3*b*). Despite three variables being selected as informative for *S. nivalis*, only temperature of the driest quarter had a significant and negative main effect on size (Pd = 99.65, ROPE = 0.99), without evidence of a significant interaction with sex (figure 3*c*). Other terms in the model were found negligible (Pd ≤ 98.72, ROPE ≥ 3.25). Comparable results were found when analysing FM as an index of overall body size, with no impact on the conclusions (electronic supplementary material, figure S6.1).

4. Discussion

Environmental gradients provide powerful settings to infer ecological and evolutionary processes driving phenotypic change [1] and serve as analogues for predicting species responses under climate change [12]. We used Bayesian generalized linear mixed models to test for geographic clines in adult body size along genetically connected (elevation) and disrupted (latitude) gradients in each of three flightless alpine grasshopper species endemic to the Southern Alps of New Zealand. We found a positive relationship between latitude and body size (as predicted by Bergmann's rule) in only one of the three species (*S. nivalis*). Evidently, the shared environment has not resulted in convergence to the same latitudinal size cline in two other flightless grasshoppers. We saw in *S. australis* and *S. nitidus* contrasting non-linear associations between latitude and body size. Sex-by-latitude interactions suggest that female *S. australis* generally grow larger at mid-latitudes (soft concave cline), while female *S. nitidus* are smallest at mid-latitudes. In these two grasshopper species male body size varies little. There is no gene flow among mountain populations of each species [32], yet we have detected three significant phenotypic clines including signal for adaptation [1,2] of this polygenic trait [15,18]. We therefore suggest that the size clines found here primarily reflect genetic differences among spatially and reproductively isolated populations (e.g. [22,47,48]), even though ecological and sexual selection have not converged on the same size patterns. While decomposing a multi-dimensional trait such as body size to a single linear measure might be considered insufficient to capture overall size, in these grasshopper species femur length scales allometrically with body mass and other size proxies (see also [36]). Accordingly, common trends observed in femur length and FM in response to environmental variation likely reflect actual variation in overall body size.

Despite the steep environmental gradients associated with montane elevation, extensive gene flow could counter phenotypic differentiation [1,2], and we provided evidence of gene flow between population samples from different elevations of the same mountains, in all three grasshopper species (figure 1, electronic supplementary material, figure S1.1). As expected, we did not find size variation

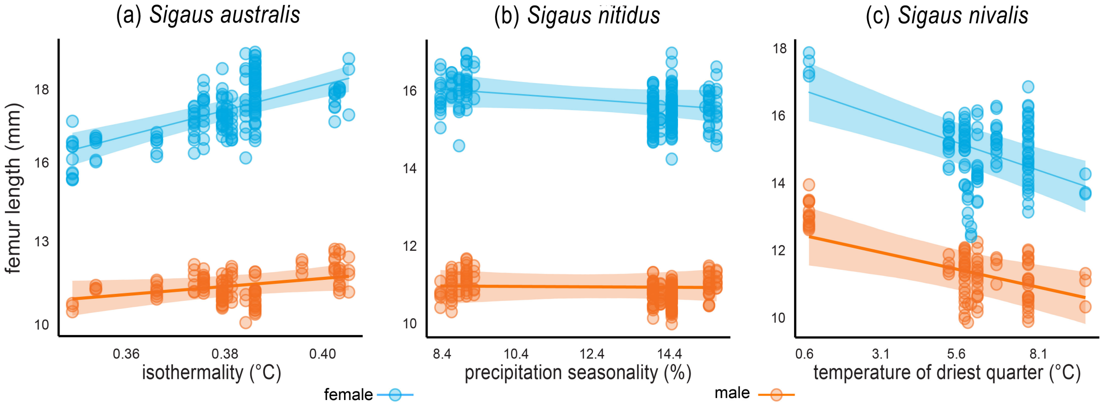

Figure 3. Effects of environmental factors on body size (using femur length as a proxy for overall size) of three flightless alpine grasshopper species endemic to South Island, New Zealand: (a) *Sigaus australis*, (b) *Sigaus nitidus* and (c) *Sigaus nivalis*. Shading indicates 95% Bayesian high-density intervals.

associated with elevation despite sampling transects spanning most of the elevational range of each species and replicated on four or five mountains. Thus, size overlap across elevations suggests that gene flow may impede the evolutionary processes driving phenotypic divergence, as proposed for montane grasshopper species differing in dispersal potential (e.g. [49,50]). Although the sampled mountains differ in topography and environmental settings, the narrow elevational ranges available to these flightless grasshoppers mean they each function as distinct mountain populations. However, rather than geographic distance *per se*, dispersal potential (hence gene flow) plays the more prominent role in phenotypic divergence, as observed in grasshopper species that occupy broader elevational ranges in other mountain systems (e.g. [49,50]). Alternatively, elevational selection on body size may be weak or inconsistent in the study system, such that neutral processes (e.g. genetic drift) predominate and no phenotypic cline emerges. Nevertheless, evidence of elevational size clines for other alpine grasshopper populations from New Zealand's Southern Alps [30,51] suggest that rate of gene flow and/or selection pressure vary among mountain slopes.

In contrast to our expectation of convergent temperature-related size clines, we found distinct bioclimatic effects across species. Lack of congruent patterns of size variation among species in a common landscape suggests distinctive responses to environmental conditions [32]. *S. nivalis* are smallest where the temperature of the driest quarter is highest, in keeping with the temperature–size rule whereby ectotherms grow faster and mature at smaller sizes under warmer conditions [10]. The thermal environment this species encounters during its growing season is an important proximate predictor of Bergmann's rule, and this fits well with evidence that this rule is directly mediated by temperature [8,52]. *S. nivalis* are found primarily on scree slopes where mean ground temperature is likely to mainly reflect the thermal mass of the rock substrate. Although sympatric with *S. nivalis*, the other two alpine species, *S. australis* and *S. nitidus*, are more often found in herbfield/grassland habitat, where vegetation will moderate microhabitat conditions (e.g. transpiration and shading). Size variation in *S. australis* was positively related with isothermality, a proxy of thermal tolerance [53], with the largest *S. australis* found where daily temperature fluctuation through the year is lowest. In the same landscape, *S. nitidus* body size varies very little compared to the other two grasshopper species, but is weakly correlated with precipitation seasonality, resulting in smaller females where rainfall is more variable. In New Zealand, precipitation seasonality is a proxy of the west–east rain shadow gradient of the study region [54]. If uneven precipitation leads to more limited resources (e.g. food plants), this might explain slightly larger female *S. nitidus* where precipitation is more even throughout the year (e.g. [55]). However, this pattern was not apparent in males and our sampling of this species was biased towards drier, eastern mountains. Further research incorporating the microclimate variables would help relate large-scale climate to ecological attributes.

Sex-specific variation in size clines determines the degree to which size dimorphism varies across environmental gradients [13,25,26,56]. Consistent with this, we found that female grasshoppers (the larger sex) exhibit the greatest proportional size difference, resulting in distinct patterns of size dimorphism among species. This contradicts the prediction from Rensch's rule [57,58] that size increase typically reduces sexual size difference when females are the larger sex [57–59] and indicates that intraspecific allometric scaling patterns in the studied system may be linked to geographic variation in body size [13]. Strong directional selection for female fecundity and thus increased body size

[60,61] can result in female size increasing disproportionally more than male size when resource availability improves in unpredictable habitats [55,56]. Sexual selection for early sexual maturity of males, however, may also play a role in limiting their size under particular environmental conditions [62] as previously inferred for Australian alpine grasshoppers [61]. Many other ecological pressures could be contributing to shape the observed patterns in size dimorphism, via sex-specific selection or plastic effects [3,63,64]. Females of the species considered here also exhibited greater size variation in response to environmental factors, suggesting that the larger sex is less constrained or more sensitive to local selection pressures [60,63].

Rapid anthropogenic global warming is now imposing selection that could drive adaptation in local populations, but we have shown here that selection pressure cannot be considered in isolation from gene flow when predicting biotic responses to rising temperatures. Contemporary decline in animal body size has been proposed as a general response to global warming consistent with Bergmann's rule [65]. Only one grasshopper, *S. nivalis*, conforms with this pattern whereas weak non-linear clines were observed in *S. australis* and *S. nitidus*, and the opposite size trend exhibited by *S. piliferus* Hutton [66]. These results add to a growing list of exceptions to the hypothesized negative directional shift in size identified in most animal groups (e.g. [67,68]). Indeed, evidence for directional changes in body size due to global warming is limited [17,67], suggesting that selection for smaller bodies predicted by Bergmann's rule, is unlikely to be a general explanation for recent declines in size [69].

Despite this, directional size shifts can be expected for species with pronounced temperature–size relationships [68], modulated by differences in standing diversity and, most importantly, gene flow (see [7,70]). This might apply at both inter- and intraspecific levels. As the majority of variation in body size is female-biased, we predict this sexually dimorphic differentiation will be crucial to population viability under climate change (see [71]). Nevertheless, the lack of strong clines in body size up and down the same mountain suggests that some alpine populations might unable to fix phenotypic variation at an optimum with the speed necessary to match current climate warming.

5. Conclusion

Our study empirically tested cline theory regarding the interplay of gene flow and natural selection on body size using flightless alpine grasshoppers as a study system. Lack of convergent patterns of size variation in three species over a common landscape and distinct bioclimatic effects across species illustrates how the interplay between historical and contemporary events and processes leads to specific evolutionary outcomes, but did not negate the role of adaptation in the formation of this variation. Overall, we found that limited gene flow correlates with divergence in body size, suggestive of adaptive processes in isolated mountaintop populations. While we found support for the role of gene flow hindering the evolution of body size clines, our study highlights that body size can follow distinct evolutionary trajectories among closely related organisms, even at intraspecific level when comparing sexes. It remains unclear whether and how warming climates—and changes in other climate factors such as precipitation regimes—will affect the body size profiles of alpine insects at both inter and intraspecific levels. When predicting how local populations will respond to climate change selection, pressure cannot be considered in isolation from the homogenizing effect of gene flow.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee. New Zealand Department of Conservation granted access and approval to collect from the Conservation Estate (Authorization Number: 49878-RES and 97397-FLO).

Data accessibility. Data and R scripts for this study are freely available at Dryad Data Repository [72]. 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.

Supplementary material is available online [73].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. F.L.M.-J.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, validation, visualization, writing—original draft; M.M.-R.: conceptualization, funding acquisition, investigation, methodology, supervision, validation, writing – review and editing; S.A.T.: conceptualization, funding acquisition, investigation, methodology, supervision, validation, visualization, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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