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RESEARCH

Evolutionary and ecological controls over leaf-level traits in New Zealand's tussock grasses

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Abstract: Removal of a strong selective pressure allows for modification of traits previously requisite for survival, which may enable species to take advantage of new ecological opportunities. Globally many traits shared by grasses are a byproduct of strong selection due to mammalian herbivores and fire, including non-dehiscence of senesced leaves. We used two genera of grasses (Danthoniiae), *Chionochloa* and *Rytidosperma*, that have radiated in New Zealand in the absence of mammalian herbivory and low fire frequency and have unusually high proportions (>50%) of species with dehiscent leaves to examine the ecological consequences of novel growth strategies. We integrate phylogenetic, niche modelling, and common garden studies to understand the evolutionary, biogeographic, and physiological consequences of leaf dehiscence. The *Chionochloa* and *Rytidosperma* phylogenies show a complex pattern of the development of dehiscence, with multiple lineages developing leaf dehiscence and several species or subspecies showing reversion to non-dehiscent states. Ecologically, the non-dehiscent species have broader physiological and geographical niches, likely representing continued adaptations to ancestral New Zealand habitats, while dehiscent species have narrower and distinctive niches in colder and wetter habitats. Both modelling and laboratory studies show that dehiscent species are more low temperature adapted than non-dehiscent species. Additionally, dehiscent species have lower quality leaves for herbivores, based on stoichiometry and silica content, suggesting that invertebrate and avian herbivory may have also been an important evolutionary factor in leaf-level traits in these genera. Both dehiscent and non-dehiscent species have similar sensitivity to shading. Our results indicate that dehiscence evolved as species changed their defence strategies and allowed species to respond to the new ecological opportunity presented with the appearance of cold, wet alpine environments in the Pliocene-Pleistocene.

Keywords: ecological opportunity, Jmax, physiological niche modelling, stoichiometry, Vcmax

Introduction

The biogeography of adaptive radiations can provide insights into the ecological or evolutionary role of key traits during lineage diversification (Losos et al. 1997; Warheit et al. 1999; Algar et al. 2013; Linder & Bouchenak-Khelladi 2017). Opportunities that develop with mountain orogeny or founder events allow species to diversify ecologically, with some traits becoming over- or under-expressed due to different selection factors in these novel contexts (Stroud & Losos 2016). After the initial expansion phase, diversification rates often slow, with post-radiation biogeography reflecting the ecological adaption of new species to novel environments and the distribution of a specific trait reflecting its potential role in ecological adaptation (Warheit et al. 1999; Losos 2011). This is particularly well established in plants where traits like height, sclerophylly, flammability, and dehiscence have all been connected to adaptation to ecological conditions (Hanley et al. 2007; Pachzelt et al. 2015; Linder & Bouchenak-Khelladi 2017). Many of these traits in grasses appear to have co-evolved to address adaptive pressure from grazing, fire, and drought-prone environments (Monteiro et al. 2011; Scheiter et al. 2012; Hoetzel et al. 2013; McGlone et al. 2014; Pachzelt et al. 2015; Charles-Dominique et al. 2016). Several traits, including quantitative traits such as sclerophylly, specific leaf area, leaf non-dehiscence, tissue chemistry, and other anti-nutritive traits, play an important role in protecting plants from herbivores (Agrawal 2007, 2011; Hanley et al. 2007).

Non-dehiscence in grasses is nearly universal with leaves persisting long after senescence. The dropping of dead leaf lamina tissue via abscission (dehiscence) is globally a rare trait, with only 3.6% of non-bamboo grasses shedding

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senescent leaves (Antonelli et al. 2011). In New Zealand, over 18% of grass species have dehiscent leaves, with dehiscence particularly prevalent in Danthonioidae in the genera *Chionochloa* and *Rytidosperma.* These two genera have 74% of the 34 dehiscent grass species in New Zealand (McGlone et al. 2014). A number of studies have examined how species derived under strong herbivory pressure develop more complex defence traits than ancestral species (Wink 2003; Wink & Mohamed 2003; Liscombe et al. 2005), however, it remains less clear what ecological and physiological opportunities emerge when grasses are released from mammalian herbivory pressure or when they are found in limited fire environments. Therefore, understanding the physiological and ecological consequences of dehiscence in these two genera will provide insights into the evolutionary processes that drive trait development.

The adaptive radiation of danthonioid grasses in New Zealand provides an ideal system in which to examine the role of plant traits in ecological adaptation (Pirie et al. 2010; Humphreys & Linder 2013; Wuest et al. 2015; Linder & Bouchenak-Khelladi 2017). First, two genera of danthonioid grasses, *Chionochloa* and *Rytidosperma*, experienced extensive radiations in New Zealand during the Pliocene, coinciding with the uplift of the Southern Alps (Pirie et al. 2010; Antonelli et al. 2011; McGlone et al. 2014; Leopold et al. 2015; Tanentzap et al. 2015). Interestingly, these two genera are outliers among grasses globally, overexpressing the trait of leaf dehiscence (Antonelli et al. 2011; McGlone et al. 2014) where at senescence the leaf lamina separates from the basal sheath. This provides a unique system in which to examine the role of leaf dehiscence in determining niche breadth and adaptation to biophysical environments. While there is an ongoing debate about the relative importance of New Zealand's evolutionary history of mammalian grazing and the role of fire in promoting leaf dehiscence (Antonelli et al. 2011; McGlone et al. 2014), there is a specific need to identify how leaf dehiscence has influenced the physiological and geographic niche space of species in these two genera during their radiation in New Zealand.

Development of dehiscence could influence leaf-level traits physiologically, structurally, and chemically, and key interactions between traits (Fig. 1). For example, physiologically the loss of senesced tissue may increase light transmission into the canopy of tussock grasses and change the responsiveness of photosynthesis to light conditions (A-light curves; Knapp & Seastedt 1986; McGlone et al. 2014). If dehiscence accompanied establishment into novel niche spaces upslope during the orogeny of the Southern Alps, dehiscence could also be associated with changes in the relationship between photosynthesis and CO_2 concentrations (A-C_i curves) or sensitivity to temperature (frost tolerance; Mark 1975; Reitsma 1994; Bannister 2005). Likewise, if dehiscence developed due to a release from mammalian grazing, there may be shifts in other defence mechanisms including tissue chemistry (carbon to nitrogen ratio [C/N], carbon to phosphorus ratio [C/P], or silica concentrations) or structure (specific leaf area) to provide protection from avian browsing (Fig. 1; Mark et al. 2000; Wardle et al. 2002; Lee et al. 2010; Antonelli et al. 2011; Burns 2014).

To identify whether the evolution of leaf dehiscence alters habitat preferences, physiology, and defence strategies, we performed three analyses in this study. First, we developed cladograms for *Chionochloa* and *Rytidosperma* on which we could evaluate the co-evolutionary history of traits associated with dehiscence. Second, we use a physiologically based niche model to explore whether dehiscent and non-dehiscent grass species occupy distinctive niche spaces to infer the adaptive advantages of these traits. This modelling approach allows us to examine geographic range, environmental range, and key environmental niche dimensions that describe how growth and resource uptake are influenced by temperature, soil nitrogen, water availability, and solar radiation. We hypothesise that if dehiscence is principally associated with the need to increase

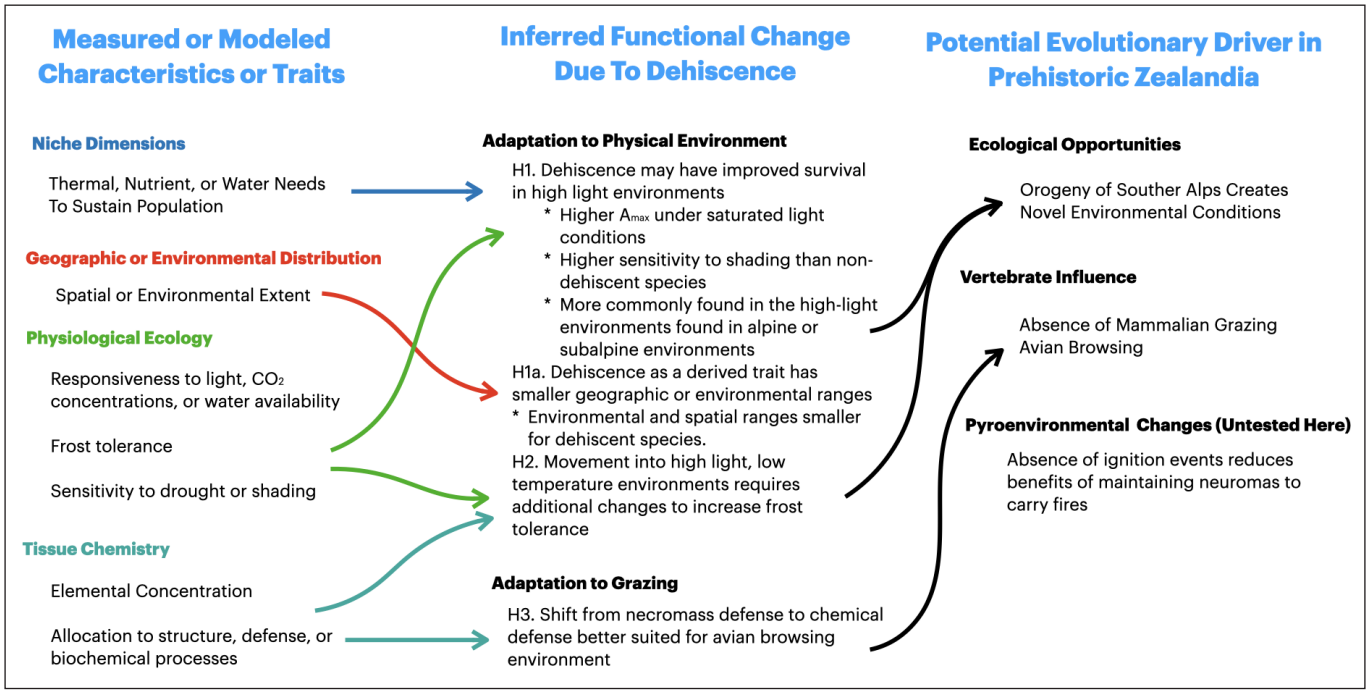

Figure 1. Concept diagram that links measured plant traits to hypothesised functional change with possible evolutionary drivers that favour or select against a particular function.

light transmission into the canopy in environments where there is shading, dehiscent species will be found disproportionately in warmer, ancestral habitats dominated by trees while non-dehiscent species will be found in the high light environments of the alpine zone. Finally, we tested whether dehiscence results in differences in ecophysiological and tissue chemistry traits using common garden experiments. Specifically, we examined light and CO_2 response curves and the sensitivity of individuals to freezing and long-term shading to see whether dehiscent and non-dehiscent species differ in their response to environmental variation, as well as measuring trait differences related to specific leaf area, leaf construction cost, and leaf stoichiometry and silica concentrations. We hypothesised that if dehiscence was primarily associated with shade avoidance, dehiscent species would be less sensitive to a shading treatment than non-dehiscent species or dehiscent species would have higher light compensation points than non-dehiscent species. Alternatively, we hypothesise that if dehiscence is principally associated with release from mammalian grazing, we will observe alternative anti-grazing, leaf-level traits in dehiscent species, including greater C/N or C/P ratios or increases in silica. These traits allow us to infer if maintaining dead tissue allows for the maintenance of higher quality live leaves within the tussock.

Methods

Time-calibrated phylogeny construction

Phylogenies for taxa of *Chionochloa* and *Rytidosperma* indigenous to mainland New Zealand were constructed using DNA sequence data aggregated from GenBank (primarily from Pirie et al. 2008; Humphreys et al. 2010; Pirie et al. 2010), or newly generated for this study. Genomic coverage included 10 loci from the chloroplast: the *rbc*L, *mat*K and *ndh*F coding regions, the *trn*L and *rpl*16 introns, and the *atp*B-*rbc*L, *trn*D-*psb*M, *psb*M-*ycf*6, *ycf*6-*trn*C and *trn*L-*trn*F intergenic spacers. Taxonomic coverage included 22 of 22 *Chionochloa* species (100% sampling) with 30 of 33 infraspecific taxa (90.9% sampling), and 21 of 21 *Rytidosperma* species (100% sampling, with no relevant infraspecific taxa). We were unable to acquire sequence data for *Chionochloa crassiuscula* subsp. *directa*, *Chionochloa flavescens* subsp. *flavescens*, or *Chionochloa pallens* subsp. *pallens*.

Time-calibrated phylogenetic analyses were conducted using BEAST 1.8.4 (Drummond & Rambaut 2007; Drummond et al. 2012), from sequence alignments generated in MAFFT 7.402 (Katoh et al. 2002; Katoh & Standley 2013). The final DNA sequence matrices included a total of 10 494 aligned base pairs for *Chionochloa*, and 10 543 base pairs for *Rytidosperma*. Each gene region was assigned the best fitting substitution model as selected by Smart Model Selection (Lefort et al. 2017) using the Akaike information criterion. A birth-death speciation prior (Gernhard 2008) was implemented in combination with an uncorrelated relaxed molecular clock model (Drummond & Rambaut 2007). Secondary calibration points were derived from the Poaceae plastid timetrees produced in Christin et al. (2014). Markov chain Monte Carlo (MCMC) tree searches were run for 200 000 000 generations, with a sampling frequency of 20 000 generations, and 20% of the initial trees discarded as burn-in. The adequacy of the MCMC convergence and burn-in period was confirmed using Tracer 1.7 (Rambaut et al. 2018).

Niche modelling

We used the Thornley transport resistance species distribution model (TTR-SDM) to model the physiological niche space of all *Chionochloa* and *Rytidosperma* species in New Zealand for which we have distribution data (Higgins et al. 2012). The TTR-SDM is based on the Thornley transport resistance (TTR) model of plant growth (Thornley 1972, 1998; Higgins et al. 2012; Buitenwerf & Higgins 2016). In the TTR-SDM parameters in the TTR model are influenced by environmental variables. Specifically, C-uptake is influenced by solar radiation, shoot N, soil moisture, and mean temperature, whereas N-uptake is related to soil N and mean temperature. Biomass growth is controlled by minimum temperature while respiration is controlled by mean temperature.

We estimate the parameters of TTR-SDM using distribution data for all *Chionochloa* and *Rytidosperma* species in New Zealand. For environmental factors we used soil N from (Shangguan et al. 2014); soil water and monthly net radiation were taken from Trabucco and Zomer (2019); monthly T_{mean}, T_{min}, and T_{max} were taken from Hijmans et al. (2005). In the TTR-SDM the TTR model is run on a discrete monthly time step as forced by the environmental forcing factors listed in the previous sentence. This allows the model to simulate how the co-limitation of environmentally forced physiological processes varies through the growing season. Simulations were run for 300 time steps which is long enough to reach stable biomass and access substrate pools (Higgins et al. 2012). For further details and model equations of the TTR-SDM see Higgins et al. (2012). We obtained species distribution data for all *Chionochloa* and *Rytidosperma* species present in New Zealand from New Zealand Herbarium records (http://www.virtualherbarium.org.nz/home), the New Zealand National Vegetation Survey Databank (https://nvs.landcareresearch.co.nz/) and unpublished field records (e.g. Kelvin Lloyd, Wildland Consultants, Ltd, Dunedin, NZ pers comm).

Using the TTR model output, we calculated normalised niche breadth for all nine niche axes considered by the TTR-SDM. In addition, we projected the potential range of each species using the TTR-SDM and interpret this range size as niche size since species with broader TTR-SDM niche axes will have larger ranges. We calculate the range size as the potential geographic range size in New Zealand as projected by the TTR-SDM. However, the assumption that geographic range sizes is an indicator of physiological niche sizes only holds if all environment types are equally common in geographic space. To ensure this we used a resampled range that ensures that each New Zealand's environmental types are equally common in the sample used to calculate range size (see Higgins & Richardson 2014).

Ecophysiology

In Spring 2015, five to seven individuals from 24 species were collected and transplanted into pots that were transported to a common garden located in Dunedin, New Zealand (Table 1). Nine of these species were from the genus *Rytidosperma* and 15 were from the genus *Chionochloa.* Species were selected to ensure a near even distribution of dehiscent and non-dehiscent species for each genus. Plants were potted into commercial potting soil and were kept near field capacity using irrigation. Measurements were made March–April 2016 and January–March 2017. Elevational range estimates were determined using published accounts of species distributions (Connor & Edgar 1979; Connor 1989, 1991, 2004).

Table 1. Ecological traits of Rytidosperma and Chiochloa species in common garden experiment.

Species	**Leaf Abscission** (Type) L=Disarticulating at Ligule F=Fracturing of Sheath	**Specific Leaf Area (mg cm^{-2})**	**Average Plant Height (cm)**	**Elevational Range (m)**	**Habitat**	**Included in Frost Tolerance Study**
Rytidosperma austral	Dehiscent	5.70	6	900–1350	Variable grassland	NO
Rytidosperma buchananii	Dehiscent	3.33	25	300–1000	Rocky and alluvial grasslands	NO
Rytidosperma clavatum	Nondehiscent	6.05	25	20–500	Open well drained dry grasslands	NO
Rytidosperma corinum	Dehiscent	4.98	17	450–1200	Dry well-drained grasslands	NO
Rytidosperma gracile	Nondehiscent	5.29	23	0–1200	Dry grassland and scrubland	NO
Rytidosperma maculatum	Dehiscent	6.73	10	0–700	Dry well drained grassland	NO
Rytidosperma setifolium	Dehiscent	10.30	32	0–900	Well drained grassland	NO
Rytidosperma telmaticum	Nondehiscent	5.57	7	300–1100	Moist grassland	NO
Rytidosperma unarede	Nondehiscent	6.78	33	0–500	Well drained grassland	NO
Chionochloa beddiei	Nondehiscent	17.40	23	0–850	Coastal cliffs and bluffs	YES
Chionochloa bromoides	Nondehiscent	11.25	25	0–200	Coastal cliffs and bluffs	YES
Chionochloa cheesemanii	Nondehiscent	10.83	26	900–1500	Forest and grasslands	YES
Chionochloa conspicua subsp. *conspicua*	Dehiscent (L)	16.20	87	0–1500	Forest and scrub	YES
Chionochloa crassiuscula subsp. *crassiuscula*	Dehiscent (L)	20.24	71	700–1400	Poorly drained grassland	YES
Chionochloa flavescens subsp. *flavescens*	Dehiscent (F)	20.07	116	50–1550	Well drained grassland and scrub	YES
Chionochloa flavicans f. flavicans	Nondehiscent	9.09	63	0–975	Coastal cliffs and Bluffs	YES
Chionochloa macra	Nondehiscent	12.09	48	500–1700	Well drained mature soil in grassland	YES
Chionochloa pallens subsp. *pallens*	Nondehiscent	13.65	51	500–1650	Well drained recent soil in grassland	YES
Chionochloa rigida subsp. *amara*	Dehiscent (F)	16.31	69	500–1450	Mature soil in grassland and scrub	YES
Chionochloa rigida subsp. *rigida*	Dehiscent (F)	16.52	69	0–1700	Well drained mature soil in grassland and scrub	NO
Chionochloa rubra subsp. *cuprea*	Nondehiscent	22.05	96	0–1500	Poorly drained grassland and scrub	YES
Chionochloa rubra var. *rubra*	Dehiscent (F)	24.12	96	550–1400	Variable soils supporting grassland and scrub	NO
Chionochloa rubra var. *occulta*	Dehiscent (F)	15.55	36	600–1700	Poorly drained grassland and scrub	NO
Chionochloa spiralis	Dehiscent (F)	17.56	50	300–1000	Limestone cliffs and bluffs	YES
Chionochloa teretifolia	Dehiscent (L)	24.38	34	300–1300	Poorly drained grassland	YES

Leaf level physiology

Gas exchange measurements were made on attached, fully emerged, green leaves when possible. For *Rytidosperma australe* and *Rytidosperma telmaticum* leaves were clipped immediately prior to making gas exchange measurements to accommodate the geometry of the cuvette. Others have found no difference in gas exchange measurements made within 2-h of detaching leaves from a plant (Tissue et al. 2002; Monson et al. 2007). Plants were randomly assigned to one of two portable photosynthesis systems (LI-6400XT, LI-COR, Lincoln, NE, USA) and measurements were made in late March and early April 2016. Plants were brought into the laboratory from the common garden for measurements. Individual leaves were laid in parallel and not overlapping to fill the gas exchange cuvette. Conditions in the cuvette were set to a temperature of 20°C and relative humidity of 40–60%. Response curves of assimilation (A) versus light and A versus intercellular CO_2 (C_i) concentrations were measured. The light response curves were made with an atmospheric CO_2 concentration of 400 ppm. The A-C_i curves were made with 1500 mmol m^{-2} s^{-1} photosynthetically active radiation. The light response curves were conducted using a declining light regime (1500, 1200, 1000, 500, 300, 150, 100, 65, 50, 25, 15, 0 mmol m^{-2} s^{-1}), while the A-C_i curves were constructed using an increasing CO_2 regime after an initial measurement at 400 ppm (400, 50, 100, 150, 250, 350, 500, 700, 900, 1200, 1500 ppm). Using these curves we estimated maximum Rubisco activity, V_{cmax}, and maximum electron transport rate, J_{max}, as well as light and CO_2 compensation points, dark respiration, apparent quantum yield, and maximum net assimilation rate using a consistent set of photosynthesis model equations (Medlyn et al. 1999; Warren et al. 2015). Only response curves with an $R^2 > 0.95$ were used in our analysis and those falling below this threshold were rerun.

Environmental responsiveness

To examine the sensitivity of gas exchange to light and water availability, we grew four individuals of each species in one of two light treatments in a glasshouse. The first light treatment was shade free, with average maximum daily illumination of 1422 mmol m^{-2} s^{-1}. The second treatment condition was created with shade cloth, with an average maximum daily illumination of 345 mmol m^{-2} s^{-1}. All plants were at field capacity at the beginning of the experiment. Half the plants were watered every two weeks of the experiment and other half were watered to field capacity every three days. Grasses were grown for six weeks between April and May 2016 in these conditions. Maximum photosynthesis and stomatal conductance for all plants was measured during week six. Photosynthesis and stomatal conductance were measured when stable at 20°C, 400 mmol mol^{-1} CO_2, and illuminated at 1500 mmol m^{-2} s^{-1} using a Licor 6400XT portable photosynthesis system (Licor Biosciences, Lincoln, NE, USA) and reported as A_{max} (mmol C m^{-2} s^{-1}). A_{max} and g were averaged between all individuals of the same species in the same light and water treatments for statistical purposes. Instantaneous water use efficiency was measured as A_{max} g^{-1}.

Frost tolerance

Frost tolerance was measured as loss of function of light harvesting pigments after leaf exposure to freezing conditions (Schreiber 2004). We conducted this experiment on a subset of our common garden plants, choosing twelve *Chionochloa* species (Table 1). Fluorescence was measured using pulse amplitude modulation (PAM). PAM allows the measurement of stress placed on the plant by measuring the Fv/Fm or the maximum photochemical quantum yield of photosystem II. A light inductive setting was used to both saturate the chlorophyll with light and allow for a recovery period to maximise fluorescent yield. Live leaf samples were collected from the leaves of two plants of each species. Measurements were taken using PAM on leaves that were not exposed to freezing temperature (Pre-freeze), a control at low, non-freezing temperature (3°–4 °C), and increasingly cold temperatures (−5°C, −10°C, −15°C, and −20 °C). The rate of temperature change was 4–5 °C $h^{-1}$and maintained target temperature for 1 hour. After the period at target temperature, the leaves were returned gradually to room temperature. Loss of function was measured as the difference between the pre-freeze PAM measurements and the PAM measurements on leaves after they were exposed to the treatment temperature.

Structural and chemical leaf traits

Plant traits are reported as an average of all individuals for a single species. Height was measured as the distance from the soil surface to tip of the longest fully expanded leaf on the individuals in the common garden experiment. Specific leaf area (SLA) was calculated as leaf area, measured using a flatbed scanner and ImageJ software (Schneider et al. 2012), divided by sample dry mass (@ 60 °C). Foliar nutrient content was determined on one composite sample of dried, live leaf tissue collected from 3–4 individuals using combustion analysis. Each sample was ground (0.85 mm mesh screen) and analyzed for total C and N by combustion using a Leco TrueSpec CN Determinator (Leco Corporation, St. Joseph, MI, USA). Minerals were determined by nitric acid–hydrogen peroxide microwave digestion (Ethos EZ, Milestone, Shelton, CT, USA) followed by ICP-OES analysis (iCAP 7400, Thermo Electron, Madison, WI, USA).

Analysis

Niche model

To evaluate the species distribution model, we created a confusion matrix to summarise the number of true positives, true negatives, false positives, and false negatives for each model projection estimated from the species distribution data. A Bayesian linear regression model (Gelman & Su 2013) was used to describe the effects of dehiscence state on potential and resampled range sizes (Appendix S1). We plot the posterior estimates of the mean estimated range sizes of these groups. The significance of the regression coefficients were tested using a z test (Gelman & Su 2013).

Trait analysis

Differences between genus and dehiscence state were determined using a two-way analysis of variance using SigmaPlot 14.0 (Systat Software, San Jose, CA, USA). All comparisons were evaluated using the Shapiro-Wilk normality test and the Brown-Forsythe equal variance test. If assumptions of normality failed, we conducted a Kruskal-Wallis analysis of variance on ranks, comparing medians. Comparison of slopes was conducted to evaluate differences between the relationship between V_{cmax} and J using the test for equality of slopes using SigmaPlot 14.0 (Systat Software, San Jose, CA, USA). Parameters for the A-Ci curve was estimated using A/Ci response curve fitting 10.0 downloaded from

Landflux.org on 1 March 2016. Parameters are reported for the fitting using the Ellsworth function. Parameters for the light response curves were estimated using the light response curve fitting package 1.0 downloaded from Landflux.org on 1 March 2016. Parameter estimates for the light response curves were based on fitting a non-rectangular hyperbola following Marshall and Biscoe (1980) and Thornley and Johnson (1990). To assess the relationship between habitat and trait, we conducted an analysis of covariance where dehiscence state was the factor and maximum elevation was the covariate. In all analyses, significance was determined based on a p-value of 0.05.

Results

Phylogeny

As has been reported previously by Antonelli et al. (2011) and McGlone et al. (2014), leaf abscission arises multiple times in both *Chionocholoa* (Fig. 2a) and *Rytidosperma* (Fig. 2b). There are several clades, including the southern *crassicula* clade in *Chionochloa* and the *petrosum* and *australe* clades in *Rytidosperma* where all species abscise their leaves. In *Rytidosperma*, the *exiguum* clade has all non-dehiscent species. However, the majority of clades are polymorphic for dehiscence state, with seven examples of sister taxa being polymorphic for this trait (Fig. 2: *Chionochloa juncea-rubra* subsp. *rubra*; *Chionochloa conspicua* subsp. *conspicua-australis*; *Chionochloa rigida* subsp. *rigida-rubra, Chionochloa rubra* subsp. *cuprea*, *Chionochloa macra-flavescens* subsp. *flavescens, Rytidosperma tenue-buchananii*, *Rytidosperma viride-gracile*).

Niche dimensions

The species distribution model fits our distributional data well, with very low false-negative rates (Appendix S1). The false negative rate, calculated as number of false negatives/(true positives + true negatives), averaged 3.5% across all species with *Chionochloa* having a slightly lower false negative rate (1.97%) than *Rytidosperma* (5.0%). No *Chionochloa* species had a false negative rate over 8%, while two *Rytidosperma* species had false negative rates over 15% (*Rytidosperma australe* 17.9%, *Rytidosperma penicillatum* 20.6%).

Across most niche dimensions, there are no significant differences between dehiscent or non-dehiscent species. However, there are two niche axes where average niche occupancy differs between dehiscence state (Fig. 3). First, contrary to our hypothesis, the minimum temperature niche dimension that identifies the lower temperature threshold for C uptake is colder for dehiscent species than non-dehiscent species suggesting that dehiscent species are found disproportionately in the colder environments of the subalpine and alpine compared to non-dehiscent species (Fig. 3a, $p < 0.001$). The median lower minimum temperature threshold (−14.9°C) and the median low temperature threshold where T no longer affected growth (−8.9°C) were much lower in dehiscent than non-dehiscent species (−8.35°C; −2.9°C respectively). Second, the model predicts that non-dehiscent species were able to take up N at lower water availability than dehiscent species (Fig. 3b, $p < 0.001$). This dimension is reported as a normalised value from 0–100. The median lower water limit was marginally significant ($p = 0.05$), with non-dehiscent species able to take up sufficient N at a normalised water content value of 42.9 while it was 78.6 for dehiscent species. The median threshold where water availability no longer had an impact on N-uptake was also significantly different ($p = 0.03$), with non-dehiscent species having a threshold of 61.3 while dehiscent species reach this threshold at 97.9.

Range size based estimates of niche size both for the New Zealand range sizes and the resampled range sizes were significantly different between genera ($p < 0.001$), with *Rytidosperma* species on average potentially occupying 31.3% of New Zealand geographic range and 34.5 % of resampled environmental space while *Chionochloa* has, on average, narrower potential niche spaces, occupying 19.0 % of the geographic area of New Zealand and 15.7% of resampled environmental space (Fig. 4). Dehiscent species were more specialised environmentally and had smaller environmental niche spaces than non-dehiscent species ($p = 0.01$). There were also significant differences in the New Zealand geographic range sizes ($p < 0.04$) and the resampled environmental range sizes ($p < 0.007$) of dehiscent and non-dehiscent species. Non-dehiscent species had broader geographic and environmental range sizes with non-dehiscent species occupying 29.3% of New Zealand geographic space compared to 21.0% for dehiscent species. Each non-dehiscent species occupied, on average, 29.9% of resampled environmental space while each dehiscent species only occupied 20.3% of resampled environmental space.

For the six cases where there are sister taxa differing in dehiscence state, five of the six pairs had the dehiscent species occupying a range with a lower temperature for growth than the non-dehiscent species. The one exception to this is *C. macra*, the non-dehiscent species, which has a lower temperature threshold for C uptake than *C. flavescens subsp. flavescens* (Fig 2). There was no consistent trend of geographic or environmental range size for sister taxa, with dehiscent or non-dehiscent species equally likely to have broader range sizes.

Physiological traits

Response curves

The key traits associated with CO_2-response (A-Ci) curves are A_{max}, V_{cmax}, J, and CO_2 compensation point (Table 2). Maximum photosynthetic rates (A_{max}) measured with A-Ci curves were not significantly different between *Chionochloa* and *Rytidosperma* (Table 2, $p = 0.185$), nor was dehiscence state an important predictor of A_{max} (Table 2, $p = 0.662$). Mean rates ranged from 6.1 μmol CO_2 m^{-2} s^{-1} for dehiscent *Chionochloa* species to 9.2 μmol CO_2 m^{-2} s^{-1} for non-dehiscent *Rytidosperma* species. Likewise, V_{cmax} and CO_2 compensation point were not influenced by genus or dehiscence state ($p > 0.05$). *Chionochloa* has higher *J* than *Rytidosperma*, but dehiscence state is a non-significant predictor of J (Table 2; $p < 0.05$).

The key traits associated with A-E (assimilation-irradiance) curves are quantum yield, light compensation, and dark respiration (R_{dark}). There were no significant differences in quantum yield or light compensation point between species or dehiscence state (Table 1; $p = 0.681$). Dark respiration is a trait where we do see a significant interaction between genus and dehiscence state (Table 2; $p = 0.017$). Within *Rytidosperma*, dehiscent species have a respiration rate over two times higher than non-dehiscent species (1.17 μmol m^{-2} s^{-1} vs 0.535 μmol m^{-2} s^{-1}), while within *Chionochloa* there are no significant differences associated with dehiscence state. In addition, nondehiscent *Chionochloa* have significantly higher respiration rates than non-dehiscent *Rytidosperma* species. We also saw a strong linear relationship between R_{dark} and the light compensation point (Table 2; Fig. 5; $p < 0.001$, $R^2 = 0.529$).

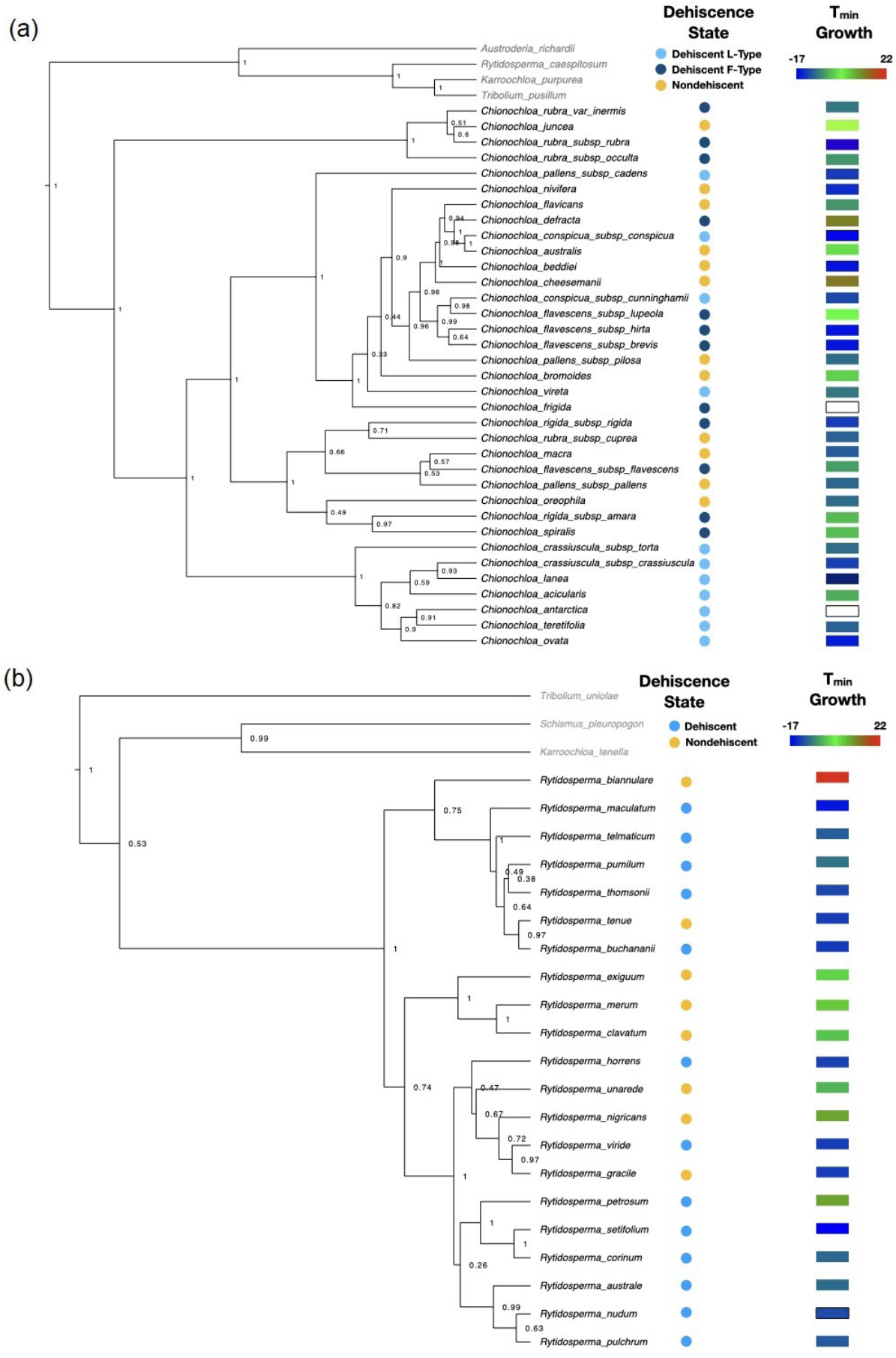

Figure 2. Phylogenetic reconstruction of New Zealand taxa of the genera *Chionochloa* and *Rytidosperma* with dehiscence state and modelled minimum temperature for growth indicated.

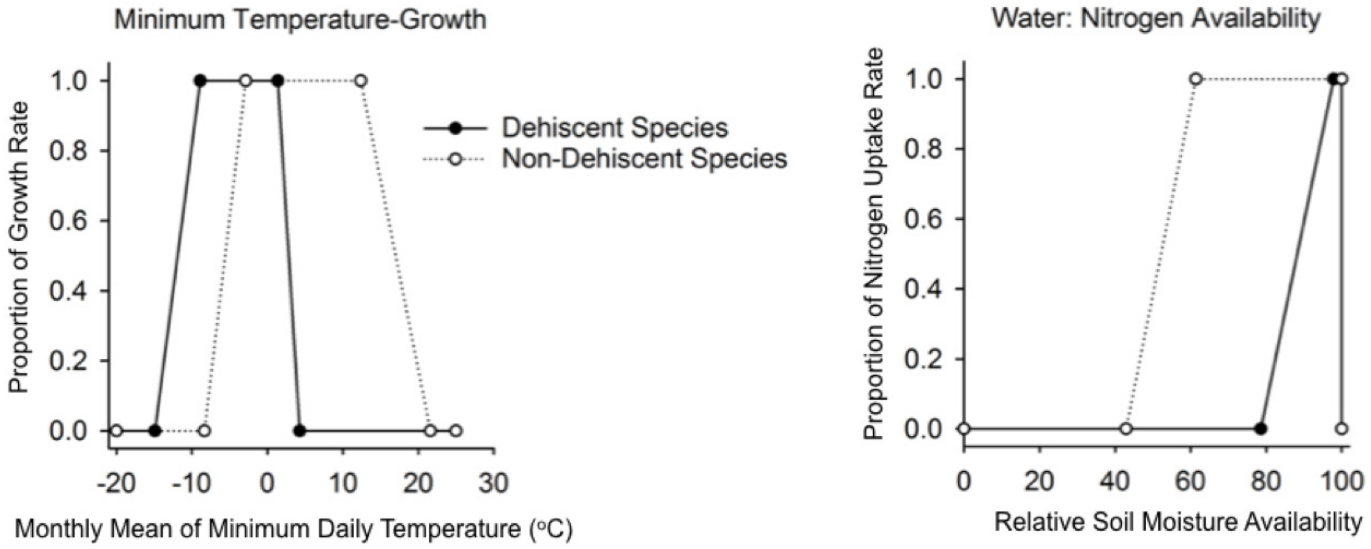

Figure 3. Niche dimensions for dehiscent (solid line, filled circle) and non-dehiscent species (dashed line, open circle) of the genera *Chionochloa* and *Rytidosperma* in New Zealand derived from the Thornley transport resistance model. (a) Effect of minimum temperature on growth; (b) Effect of soil water on the acquisition of nitrogen.

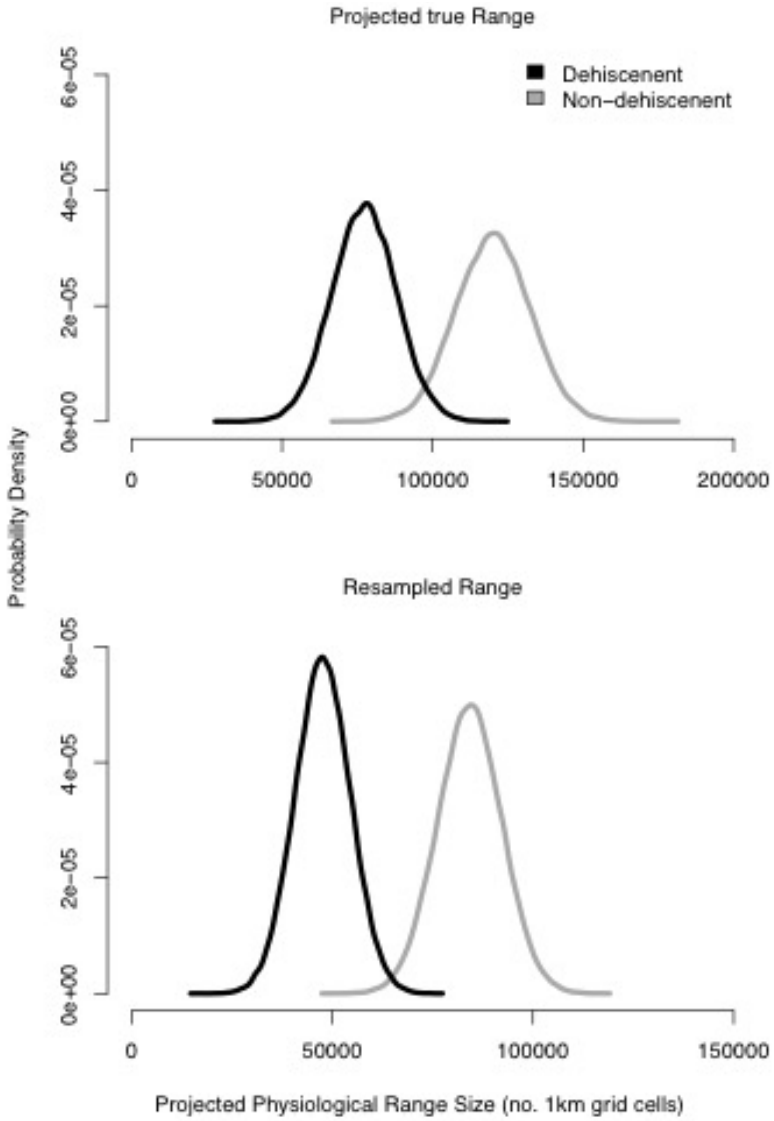

Figure 4. Posterior densities of potential range sizes of dehiscent and non-dehiscent species in (a) New Zealand and (b) a resampled range where all environmental zones are equally common. The posterior densities are calculated from regression coefficients of a bayesian regression model.

Table 2. Physiological characteristics of Rytidosperma and Chiochloa species in common garden experiment.

Species	A_{max} mmol m^{-2} s^{-1}	V_{cmax} mmol m^{-2} s^{-1}	J mmol m^{-2} s^{-1}	R_{dark} mmol m^{-2} s^{-1}	J/V_{cmax}	Quantum Yield (f)	Light Compensation Point mmol m^{-2} s^{-1}
Rytidosperma australe	3.34	29.9	57.3	1.31	1.9	0.042	35.91
Rytidosperma buchananii	8.67	31.3	58.6	1.2	2.1	0.036	34.71
Rytidosperma clavatum	17.62	45	66.9	0.4	1.4	0.069	5.94
Rytidosperma corinum	12.66	57.5	87.6	1.3	1.6	0.044	30.58
Rytidosperma gracile	9.48	28.7	54.7	0.83	1.9	0.06	14.16
Rytidosperma maculatum	9.03	77.2	60.4	1.34	0.7	0.03	51.68
Rytidosperma setifolium	7.00	120.7	122.8	0.71	1.1	0.038	20.15
Rytidosperma telmaticum	5.98	41.2	61.9	0.84	1.6	0.022	41.32
Rytidosperma unarede	3.77	24.4	49.7	0.07	2.1	0.03	2.3
Chionochloa beddiei	8.81	54.4	110	2.1	1.8	0.046	51.01
Chionochloa bromoides	2.43	64.7	94.6	0.03	1.4	0.018	1.63
Chionochloa cheesemanii	4.76	19.6	37.8	1.15	1.7	0.037	31.38
Chionochloa conspicua subsp. *conspicua*	5.45	38.7	88.2	0.23	2.3	0.034	6.71
Chionochloa crassiuscula subsp. *crassiuscula*	7.03	90.6	111.7	0.09	1.3	0.03	2.92
Chionochloa flavescens subsp. *flavescens*	5.34	22.9	61.3	1.31	2.6	0.05	34.87
Chionochloa flavicans f. flavicans	15.07	138.7	137.5	1.26	1.1	0.079	16.27
Chionochloa macra	5.4	68.3	132.1	1.49	1.8	0.039	38.3
Chionochloa pallens subsp. *pallens*	13.61	69.2	107.3	0.77	1.6	0.046	17.14
Chionochloa rigida subsp. *amara*	2.93	25	58	0.97	2.6	0.045	21.66
Chionochloa rigida subsp. *rigida*	5.94	20.8	58.7	0.73	2.7	0.063	-20.88
Chionochloa rubra subsp. *cuprea*	2.7	79.7	119.6	1.1	1.4	0.046	23.82
Chionochloa rubra var. *rubra*	3.8	14.1	44.8	1.12	2.8	0.021	54.64
Chionochloa rubra var. *occulta*	5.12	33.5	50.9	0.97	1.5	0.029	34.39
Chionochloa spiralis	3.59	56.2	92.5	0.98	1.6	0.039	26.86
Chionochloa teretifolia	7.77	83.6	116.6	1.13	1.4	0.071	17.78

Table 3. Leaf tissue chemistry traits of Rytidosperma and Chiochloa species in common garden experiment.

Species	%C	%N	%P	%S	%K	Si (ppm)	C/N	C/P
Rytidosperma australe	50	0.93	0.11	0.13	0.78	651.225	53.7	456.5
Rytidosperma buchananii	48.3	1.32	0.18	0.13	1.54	716	36.7	274.7
Rytidosperma clavatum	47	1.27	0.2	0.14	1.51	332	37	229.6
Rytidosperma corinum	47.7	1.12	0.17	0.11	1.26	391	42.6	276.7
Rytidosperma gracile	46.7	1.55	0.24	0.16	1.46	342	30.2	198
Rytidosperma maculatum	46.5	1.79	0.2	0.19	1.52	742	26	236.3
Rytidosperma setifolium	48.7	0.69	0.14	0.1	1.07	852	70.1	346.8
Rytidosperma telmaticum	48.6	1.57	0.28	0.15	1.1	763	30.9	176
Chionochloa beddiei	50.4	1.28	0.32	0.18	1.7	276	39.5	156.8
Chionochloa bromoides	50	1.31	0.41	0.17	2.04	425	38.2	123.2
Chionochloa cheesemanii	49.6	1.13	0.18	0.17	1.17	385	44	272.1
Chionochloa conspicua subsp. conspicua	50.2	0.62	0.11	0.09	0.93	657	81	466.7
Chionochloa crassiuscula subsp. crassiuscula	49.2	0.96	0.16	0.24	1.24	444	51.2	312.7
Chionochloa flavescens subsp. flavescens	50.1	0.92	0.12	0.09	1.06	558	54.4	421.8
Chionochloa flavicans f. flavicans	46.7	1.20	0.23	0.24	1.82	389	38.9	200.1
Chionochloa macra	47.6	1.39	0.19	0.15	1.5	376	34.2	249.5
Chionochloa rigida subsp. amara	48.7	1.72	0.21	0.21	2.43	439	28.2	233.2
Chionochloa rigida subsp. rigida	50.2	0.96	0.14	0.12	1.38	407	52.3	369.4
Chionochloa rubra subsp. cuprea	49.2	0.91	0.15	0.18	1.45	282	54.4	328.5
Chionochloa rubra var. rubra	49.9	0.61	0.11	0.08	0.97	681	81.2	457.4
Chionochloa rubra var. occulta	48.8	1.15	N/A	N/A	N/A	N/A	42.4	N/A
Chionochloa spiralis	48.5	1.13	0.23	0.2	1.43	325	42.8	207.9
Chionochloa teretifolia	50.6	1.05	0.1	0.14	0.91	494	48	507.6

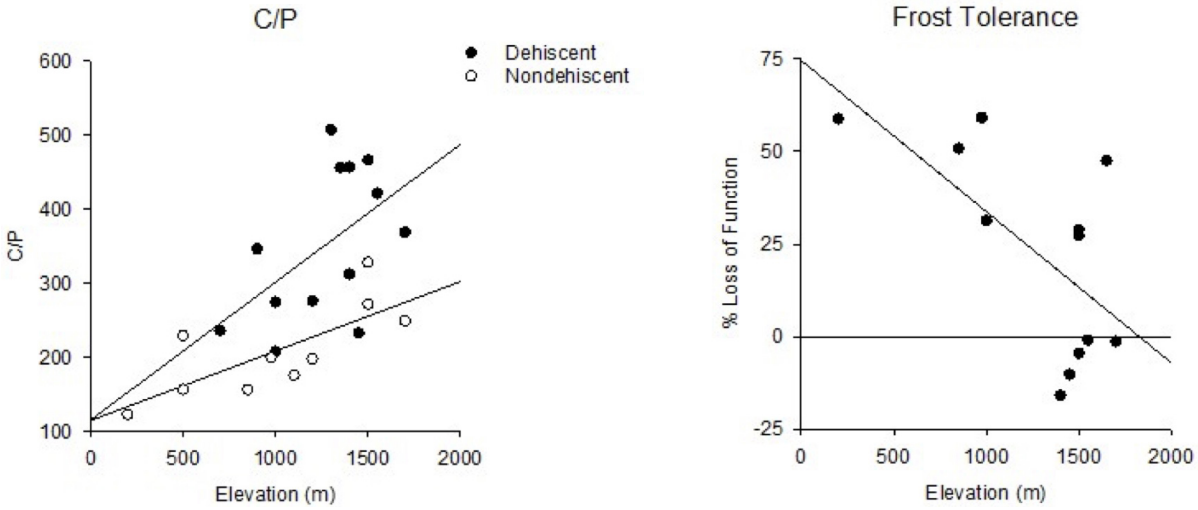

Figure 5. (a) Relationship between leaf C/P and maximum growth elevation for dehiscent (solid) and non-dehiscent species, which both show a positive association between elevation and C/P, with dehiscent species having higher C/P than non-dehiscent species, particularly in high-elevation zones. (b) relationship between change in fluorescence at −10°C and maximum growth elevation, showing that high elevation species are less sensitive to freezing than low elevation species in twelve species of the genera *Chionochloa*.

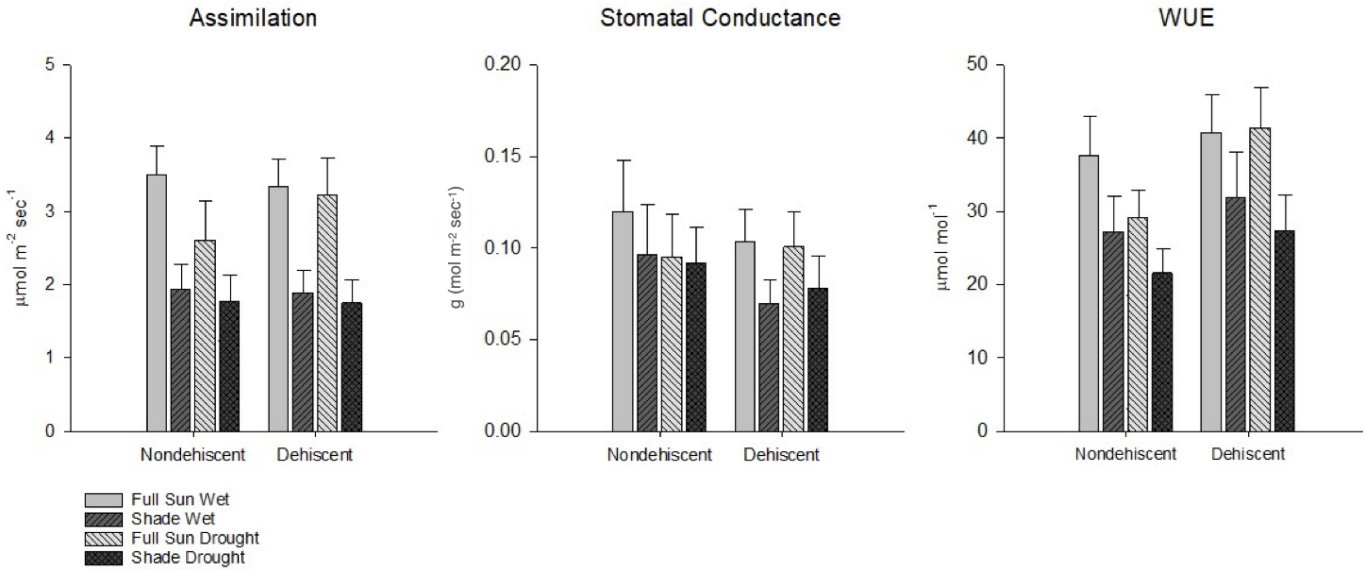

Figure 6. Photosynthetic responses to a 6-week exposure to shading and drought in dehiscent and nondehiscent species of the genera *Chionochloa* and *Rytidosperma*. (a) Maximum net assimilation rates (mmol m^{-2} s^{-1}), showing that shade significantly reduced photosynthesis, but there were no differences between dehiscent and nondehiscent species. (b) Stomatal conductance in *Chionochloa* and *Rytidosperma* showing no statistically significant differences due to the shading or drought treatments. (c) Water use efficiency for dehiscent and nondehiscent grasses exposed to shading and drought. Shading reduced water use efficiency but drought had no effect, nor did dehiscence status.

Environmental responses

In our six-week shade and drought experiment, we found that both *Chionochloa* and *Rytidosperma* species were highly susceptible to shading (Fig. 6; $p < 0.001$) but not the level of drought we produced in our experiment ($p = 0.262$) or dehiscence state (Fig. 6; $p = 0.762$). Shading reduced photosynthetic rates by 1.33 µmol CO_2 m^{-2} s^{-1}. None of our treatments produced a significant change in stomatal conductance (Fig. 6b; $p > 0.05$). Water use efficiency was influenced by shading, with shaded plants being less efficient with carbon capture per unit water loss than unshaded plants (Fig. 6c; $p = 0.009$).

Frost tolerance

Dehiscence state ($p = 0.014$) and temperature treatment ($p < 0.01$) are both significant predictors of frost-related loss of function, with a significant interaction between dehiscence and temperature ($p = 0.004$). Dehiscence protects against frost tolerance, with more than 9% more function retained compared to non-dehiscent species (Fig. 7a). Each stepwise change in temperature results in additional loss of function except between the control and −5°C treatment and the −15°C and −20°C. The interaction results in dehiscence state at −10°C producing significant differences, with dehiscent species having 29% greater function retained than non-dehiscent species. In

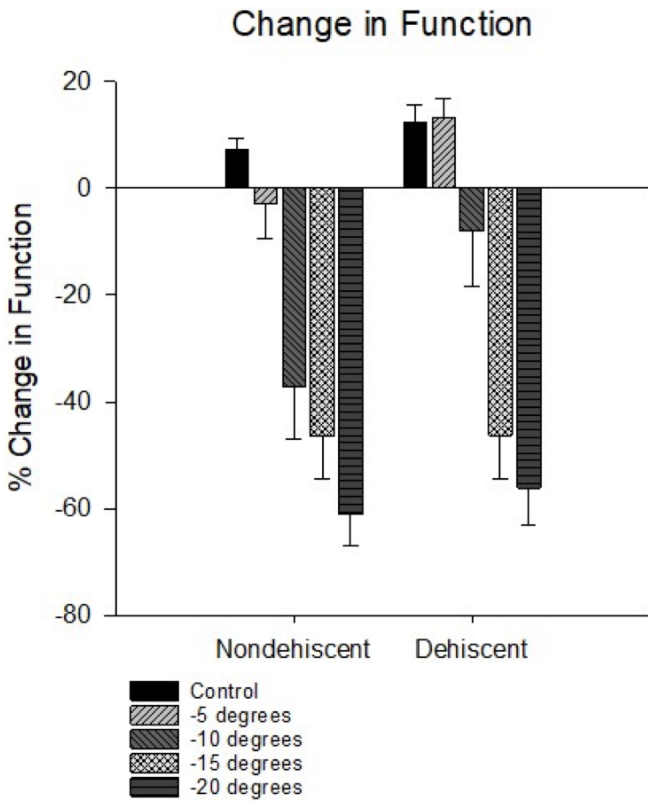

Figure 7. Change in PAM fluoresce between control leaves (filled black bar) and leaves exposed to −5°C (light grey, single hatch), −10°C (dark grey, single hatch), −15°C (light grey, cross hatch), and −20°C (dark grey, horizontal line) as a function of dehiscence state. There were significant differences between dehiscent and nondehiscent species at −10°C, with nondehiscent species having significantly reduced function compared to dehiscent species.

absolute fluorescence, dehiscence state does not influence mean values ($p = 0.098$), nor is there a significant interaction between temperature treatment and dehiscence state (Fig. 7b; $p = 0.325$). The mean fluorescence for nondehiscent species was 0.517 $Yield_{max}$ compared to dehiscent species having a 0.569 $Yield_{max}$. However, absolute yield did decline substantially due to temperature treatment ($p < 0.001$), with no significant difference in $Yield_{max}$ between from 0.769 in the control plants to 0.736 in those exposed to −5°C, but a significant decline to 0.541 in those exposed to −10°C, with another significant decline to 0.377 at −15°C and 0.291 at −20°C.

Structural and chemical traits

The clearest influence of genus and dehiscence on plant traits is seen in structural and chemical traits (Table 1, Table 3). The *Rytidosperma* species we studied are significantly shorter (19.8 cm on average) than our *Chionochloa* species (Table 1; 57.3 cm; $p < 0.001$). Likewise, specific leaf area (SLA) is significantly higher in *Chionochloa* than in *Rytidosperma* (Table 1; $p<0.001$), although there are no significant differences in height or SLA between dehiscent or non-dehiscent species. However, dehiscence was a significant factor in predicting phosphorus content, with nondehiscent species having nearly 60% more P than dehiscent species (0.243% vs 0.154%, $p = 0.006$; Fig. 8a). Associated with this are significant differences in C/P ratios, with dehiscent species having higher C/P than nondehiscent species (345 vs 211; $p = 0.004$). Both main effects (genus, dehiscence state) explained variation in silica content, with *Rytidosperma* having higher Si content (574 ppm vs 428 ppm; $p = 0.038$) and dehiscent species having higher Si than nondehsicent species (585.5 ppm vs 417 ppm; $p = 0.018$). Calcium and potassium were not influenced by dehiscence state but Ca concentration did differ between *Rytidosperma* (0.244%) and *Chionochloa* (0.135%, $p < 0.004$).

Elevation

The movement out of lowland forests and into montane and alpine systems is a key evolutionary innovation in tussock grasses and therefore there is a chance that some dehiscence associated traits may covary with elevation and habitat. The effect of dehiscence on R_{dark} depends on upper elevational distribution ($p = 0.024$), with R_{dark} nondehiscent species having a positive association with elevation, and R_{dark} in dehiscent species having a negative association (Fig. 5a; $p < 0.024$). Likewise, the effect of dehiscence on the light compensation point (LCP) also depends on the upper elevational distribution ($p = 0.024$), with LCP in nondehiscent species having a positive association with elevation and LCP in dehiscent species a negative association (Fig. 5b; $p < 0.015$). The C/P of live tissue has a significant covariance with upper elevational range, with dehiscent and non-dehiscent species having significantly different slopes. Dehiscent species C/P have a steeper, more positive slope than non-dehiscent species. Loss of function associated with low temperature at −10°C is significantly associated with maximum elevation distribution (Fig. 5b, $r^2 = 0.41$, $p = 0.026$), although dehiscence is not a significant factor ($p = 0.55$).

Discussion

The radiations of danthonioid grasses in New Zealand included the novel proliferation of leaf abscission in grasses (Antonelli et al. 2011; Linder & Bouchenak-Khelladi 2017). It is apparent that part of this radiation of abscising grasses was an ecological adaptation to the new ecological environments above treeline produced with the uplift of the Southern Alps, beginning in the Pliocene. First, it is clear from the phylogenies that dehiscence has emerged multiple times in both genera, indicating that it is a consequence of strong selection in the biophysical setting of ancestral New Zealand. Second, results from physiological niche modelling show that species with a dehiscent strategy are typically found in colder environments than non-dehiscent species and have narrower geographic and environmental ranges. Our modelling and direct measurement of frost tolerance showed that there are important thresholds between −10 ° and −5 °C where dehiscent species appear to be more robust and maintain physiological function. Overall, these results suggest that dehiscence was important in the radiation into the sub- and high- alpine, while non-dehiscent species are found more often occupying the geographically more expansive lowland and montane grasslands and shrublands of New Zealand. The final task was to evaluate changes in ecophysiology and tissue traits between dehiscent and nondehiscent species, particularly carbon assimilation during changes in the resources required for photosynthesis: light and CO_2. We found no evidence that there are systematic differences in how dehiscent and nondehiscent species respond to light availability, chronic shading, or even CO_2 availability. Finally, we found that

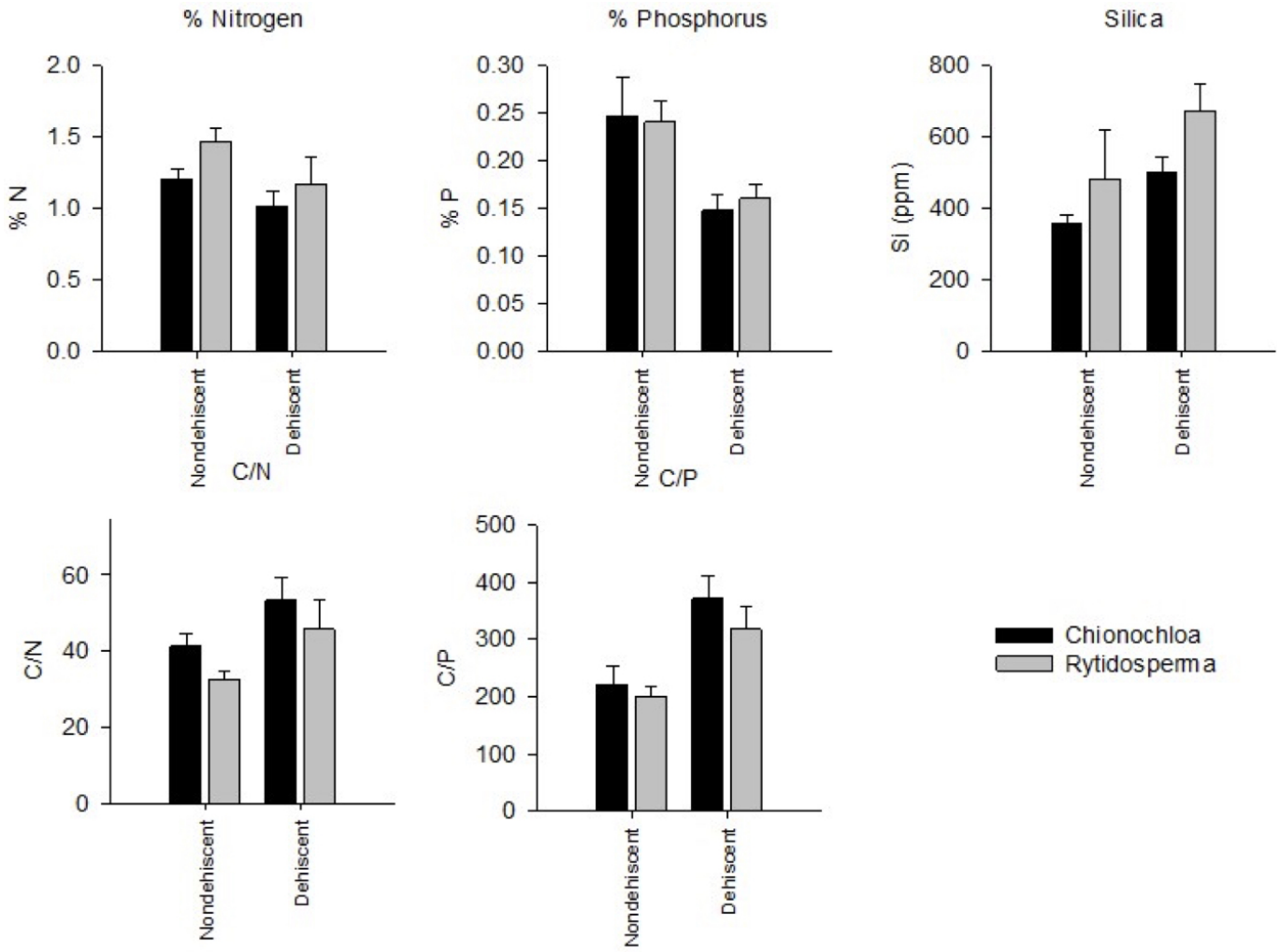

Figure 8. Live leaf tissue chemistry and stoichiometry for nondehiscent and dehiscent species of *Chionochloa* (solid black) and *Rytodosperma* (solid grey). (a) Percent Nitrogen, (b) Percent Phosphorus, (c) ppm Silica, (d) C/N and (e) C/P.

in areas of tissue chemistry associated with anti-nutritive strategies, dehiscent species often have lower quality tissue than nondehiscent species.

Subalpine and alpine adaptations

Our species distribution model results are consistent with other studies examining the frost-tolerance of New Zealand alpine grasses (Bannister 2005; Humphreys & Linder 2013). Bannister (2005) looked specifically at *Chionochloa rigida* (a dehiscent species) and found a midsummer frost tolerance to −11.1 ± 0.95°C, at which point the plants lost 50% of light harvesting capacity. Our species distribution model suggests that *Chionochloa rigida* begins growth at −8.0°C, which is consistent with a 1–2 K safety margin between minimum temperatures and frost resistance thresholds. Humphreys and Linder (2013) found that the dehiscent species *Rytidosperma buchananii* was the least frost-sensitive Danthonioidae grass that they grew in a common garden in Zurich, Switzerland, with near 100% survival in plots that experienced low temperatures of between −10 and −13°C. Our species distribution model predicts that cold temperature limitation on growth for *R. buchananii* occurs at −17.0°C, consistent with Humpreys and Linder (2013). In contrast, the non-dehiscent grass *R. unarede* had up to 30% mortality in their plots that had low temperatures of −10 °C and over 50% mortality in plots that had low temperatures of −12 to −13 °C (Humphreys & Linder 2013). Also fitting our species distribution model prediction, low temperature limitations for growth for *R. unarede* occurs at -7.9 °C.

The mechanistic connection between dehiscence and low-temperature tolerance is unclear from our data but is likely a consequence of either changes to within canopy microenvironment, changes in leaf architecture, or changes in leaf chemistry. Two dehiscent species, *C. rubra* var. *rubra* and *C. rigida* have been studied seasonally to see whether frost tolerance is induced or an inherent property. For *C. rubra*, there were no changes in frost tolerance with season, measured using electrical conductivity (Reitsma 1994). This would indicate that most of the frost tolerance is a product of leaf morphology or structural chemistry rather than changes in non-structural carbohydrates. However, for *C. rigida*, frost tolerance does change substantially seasonally when measured using fluorescence (Bannister 2005), indicating some induced frost hardiness as minimum tolerated minimum temperatures change from −11.1°C in midsummer to −17.5°C in late winter. The cold tolerance of tussock grasses is derived from the insulation provided by densely packed vegetation. In *Festuca orthophylla,* a tall tussock grass in the Andean

Altiplano, minimum temperatures were increased at the base of the grass by 8.7°C relative to bare ground (Monteiro et al. 2011). If dehiscence results in increased necromass at the base of the plant, they may produce greater depths of insolation at the plant base. Alternatively, dehiscence may have evolved in these extreme environments as a response to altered nutrient economy. By having programmed leaf loss, dehiscent species may be able to better control the resorption of nitrogen and phosphorus than non-dehiscent species that may lose tissue through fragmentation. Nutrient resorption may be particularly important in alpine environments where nutrient mineralisation and rock weathering rates are perennially slow (Li et al. 2016).

Self-shading

One of the fundamental hypotheses about the evolution of dehiscence is that it would allow for reduced self-shading (Knapp & Seastedt 1986; McGlone et al. 2014). We found that both dehiscent and non-dehiscent species were equally sensitive to six-week shading, with substantial decreases in the photosynthetic capacity after of shading. Our results suggest that there are substantial differences in gas exchange potential from species to species but not systematic differences due to dehiscence state. Quantum yield and light compensation point did not vary systematically with dehiscence state or elevation. The observed differences between genera would be expected as *Chionochloa* individuals tend to be larger with higher specific leaf area than *Rytidosperma* individuals.

Grazing

Our tissue chemistry results suggest that the transition to dehiscence also altered the resource allocation of tussock grasses. Mark (1975) first described differences in leaf anatomy between the dehiscent grass *C. rigida* and two non-dehiscent species *C. macra* and *C. oreophila,* noting the increase in hypodermal sclerenchyma and bundle sheath, with accompanying decreases in mesophyll tissue, in the dehiscent species. Our results suggest that, in general, dehiscent species have lower quality leaves based on silica content and nutrient stoichiometry.

The shift toward higher C/P, reduced P, and increased Si in leaf tissue likely represents the adoption of an alternative anti-nutritive defence mechanism that protects plants from the selective herbivory that is likely with grazing birds or insects (Strauss & Agrawal 1999; Agrawal 2007; Antonelli et al. 2011). There is abundant evidence that increasing C/P ratios can substantially reduce insect herbivory (Bishop 2002; Fagan et al. 2004; Gill et al. 2006) and silica phytoliths are a well-established anti-herbivory mechanism (Calandra et al. 2016; Stromberg et al. 2016). While there continues to be debate over the relative importance of release from grazing in driving the evolution per se of dehiscence (McGlone et al. 2014), it is clear that a consequence of dehiscence is a shift in anti-herbivory strategies.

Ultimately, we see that dehiscence in *Chionochloa* and *Rytidosperma* has resulted in an expansion of the genera-scale environmental space, allowing for the occupation of colder environments. Accompanying this change in leaf economy is a reduction in tissue quality and presumably increased protection from grazing. The relatively low grazing pressure in New Zealand may have allowed deciduousness to evolve, with changes in tissue chemistry sufficient protection to deter avian and insect grazing. By better controlling leaf death, dehiscent species were able to respond to the new ecological opportunity presented with the appearance of alpine environments in the Pliocene-Pleistocene.

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Additional information and declarations

Conflicts of Interest: The authors declare no conflicts of interest.

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Data and code availability: Data from this project are archived on DataDryad. Relevant code is available as an R package.

Ethics: Researches followed all proper procedures consistent with ANZCCART and government agency requirements while conducting this research.

Author contributions: RAG, SIH, MJL, and WGL conceived the idea and designed the study. RAG SIH, MJL did the species distribution modeling and analysis. BP and WGL conducted the phylogenetic analysis. RAG and WGL conducted the common garden and ecophysiological studies. RAG carried out the analysis and wrote the manuscript, with editorial contributions from SIH, MJL, and WGL.

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Supplementary Material

Additional supporting information may be found in the supplementary material file for this article:

Appendix S1. Confusion matrix of species distribution model.

The New Zealand Journal of Ecology provides online supporting information supplied by the authors where this may assist readers. Such materials are peer-reviewed and copy-edited but any issues relating to this information (other than missing files) should be addressed to the authors.