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Testing the niche-breadth–range-size hypothesis: habitat specialization vs. performance in Australian alpine daisies

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Abstract. Relatively common species within a clade are expected to perform well across a wider range of conditions than their rarer relatives, yet experimental tests of this "niche-breadth–range-size" hypothesis remain surprisingly scarce. Rarity may arise due to trade-offs between specialization and performance across a wide range of environments. Here we use common garden and reciprocal transplant experiments to test the niche-breadth–range-size hypothesis, focusing on four common and three rare endemic alpine daisies (*Brachyscome* spp.) from the Australian Alps. We used three experimental contexts: (1) alpine reciprocal seedling experiment, a test of seedling survival and growth in three alpine habitat types differing in environmental quality and species diversity; (2) warm environment common garden, a test of whether common daisy species have higher growth rates and phenotypic plasticity, assessed in a common garden in a warmer climate and run simultaneously with experiment 1; and (3) alpine reciprocal seed experiment, a test of seed germination capacity and viability in the same three alpine habitat types as in experiment 1. In the alpine reciprocal seedling experiment, survival of all species was highest in the open heathland habitat where overall plant diversity is high, suggesting a general, positive response to a relatively productive, low-stress environment. We found only partial support for higher survival of rare species in their habitats of origin. In the warm environment common garden, three common daisies exhibited greater growth and biomass than two rare species, but the other rare species performed as well as the common species. In the alpine reciprocal seed experiment, common daisies exhibited higher germination across most habitats, but rare species maintained a higher proportion of viable seed in all conditions, suggesting different life history strategies. These results indicate that some but not all rare, alpine endemics exhibit stress tolerance at the cost of reduced growth rates in low-stress environments compared to common species. Finally, these findings suggest the seed stage is important in the persistence of rare species, and they provide only weak support at the seedling stage for the niche-breadth–range-size hypothesis.

Key words: Australian alpine region; Brachyscome*; common garden; endemism; habitat preference; rare species; reciprocal transplant experiment; seed; seedling; widespread species.*

Introduction

What determines whether a species is widely distributed or narrowly distributed? The niche-breadth–range-size hypothesis states that species able to tolerate a broad range of environmental conditions (i.e., have a broad niche breadth) tend to have more suitable habitats to occupy, and consequently have larger geographic ranges than narrowly distributed species (Brown 1984). Niche-breadth–range-size associations may also be artefacts of historical effects (e.g., species age differences or catastrophic range reductions) or may simply reflect the incidence of habitats to which a species is adapted (Slatyer et al. 2013). To test the niche-breadth–range-size hypothesis, experimental tests are ideally needed but these are exceedingly rare (Slatyer et al. 2013), especially in field conditions (Sexton et al. 2017).

There are several experimentally testable reasons why species may have a narrow niche breadth that can be tested experimentally. Species with a narrow breadth may have a home site performance advantage in their preferred habitat driven by trade-offs in specialization to local stressors (Grime 1977, Callaway et al. 2002, Griffith and Sultan 2012, Porter and Rice 2013), although trade-offs need not evolve because of specialization (Fry 1996, Whitlock 1996, Stanton and Galen 1997). Niche breadth may be reduced by decreased genetic variation or plasticity (Gugger et al. 2015) as well as lower growth and competitive rates accompanied by higher stress tolerance (Boulangeat et al. 2012*a*,*b*). In the case where species perform poorly away from their home sites, they may be expected to be more susceptible to

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environmental change, including climate change (Klanderud and Birks 2003) and novel, no-analog ecosystems (Williams and Jackson 2007).

Here we use an experimental approach that examines these issues in a set of daisies found in Australian alpine environments, with both in situ and ex situ common garden experiments. Widely distributed daisy species are hereafter referred to as "common," although we acknowledge that having relatively large range sizes by definition does not mean local dominance (Rabinowitz 1981, Gaston 2003); conversely, locally restricted daisies are hereafter referred to as "rare," but will often have high abundance at one habitat type within a mosaic of habitats (Andrieu et al. 2007). If niche-breadth–range-size reflects environmental tolerance, we expect common daisy species to show higher survival and grow more vigorously than rare species in a greater range of environments, including novel environments not previously experienced. There is some experimental evidence for this in other species groups (Sheth and Angert 2014, Dangremond et al. 2015). However, it is still mainly unclear why rare species are narrow in their distribution (Kruckeberg and Rabinowitz 1985, Lavergne et al. 2003); some experiments even suggest that, under controlled conditions, there may be little difference in plant performance between paired narrow endemics and widespread congeners (Imbert et al. 2012, Lacher and Schwartz 2016), perhaps due to the absence of biotic stressors that impede growth in the field (Verdú and Traveset 2005).

The alpine environments from which these daisies originate are known for their high level of plant endemism as well as their mosaic of habitat types. Alpine endemism is not just related to elevation, but also tied to the distinct mosaic of environments within alpine areas, dictated by strong gradients in abiotic conditions such as edaphic and topographic heterogeneity and periodic snow cover (McGlone et al. 2001, Boulangeat et al. 2012*a*,*b*). Endemic alpine species may be particularly prone to climate change, which can lead to a decline of alpine refugia (Klanderud and Birks 2003) as a consequence of direct climate effects and indirect effects such as competition in novel plant communities (Alexander et al. 2015). These are relevant concerns (Hennessy et al. 2003, Williams et al. 2014, Camac et al. 2015).

We focus on members of the Australasian genus *Brachyscome* Cass, which are common in alpine treeless communities (McDougall and Walsh 2007). Of the 14 recognized *Brachyscome* species in the Australian Alps (Short 2014), we compared seven species that co-occur in the Bogong High Plains: a "rare set," consisting of a Victorian alpine endemic and two species restricted to the treeless Australian alpine communities (alpine endemics); and four "common" widespread species that extend beyond the alpine region. The four common species include one found across many alpine habitats and three with more restricted alpine habitat affinities, but a geographic range that extends beyond the alpine zone. Our experiments focused on seed germination and seedling performance, because these early stages are demographically important within the alpine environment (Venn and Morgan 2009) yet are prone to high rates of failure due to harsh microclimatic conditions (Williams et al. 2014).

Using a reciprocal transplant approach, we investigated whether performance in different environments was predicted by distribution. We hypothesized that rare species would have higher performance in terms of seedling survival and growth, and seed germination/viability, in habitats where they occur naturally than in novel environments. As an adaptation to stressful alpine conditions (c.f. Boulangeat et al. 2012*a*,*b*) we anticipated rare species to show extended seed viability and as seedlings show slow growth rates when compared to common species that co-occur in a rare species natural habitat. We predicted common species would exhibit higher performance (in terms of seedling growth and survival) than rare species on average, but lower performance than each rare species in its home environment. In terms of phenotypic plasticity, for growth, we predicted common species, at the population level, to be higher than rare species under the assumption that this allows species to adjust their growth form to varying environments. Because of previous evidence of local adaptation in co-occurring species in these habitats (Byars et al. 2007, M'Baya et al. 2013), we included two source populations for common and rare species, unless only one population was known. In addition to using a reciprocal transplant design, seedlings were planted into a common garden in a warmer, drier environment near sea level, far from the alpine area. We predicted that common species would outperform rare species in this environment, both in terms of survival and seedling growth rate (Table 1).

METHODS

Study species and experimental set up

Alpine *Brachyscome* are perennial outcrossing herbaceous daisies with no specialist pollinator requirements, flowering and setting seed across the Bogong High Plains in the warmer months. Seven species from the genus *Brachyscome* were used in this study: *Brachyscome spathulata*, *B. scapigera*, *B. rigidula*, *B. decipiens*, *B. nivalis*, *B. foliosa*, and *B. tadgellii*. Species vary in their habit, morphology, geographic range, and habitat preference (Table 2).

We chose three habitat types, open heathland, tussock grassland, and rocky grassland, to match the habitat associations of the three rare species (r) in this study; *B. foliosa* (r) in open heathlands, *B. tadgellii* (r) in tussock grasslands, and *B. nivalis* (r) in rocky grasslands. Each habitat type is classified by topography, soil moisture, and community assemblage, and represented by two or three replicate sites within the broader Bogong High Plains area (Fig. 1). We followed habitat definitions and descriptions from McDougall and Walsh (2007).

TABLE 1. The niche-breadth–range-size hypothesis, showing the experiments, the traits scored (germination/viability and survival/growth), expected findings, observed findings, and whether there is support, partial support, or no support in the overall findings of this study.

Hypothesis, experiment, and traits tested	Expected	Observed	Support
Rare species have a higher performance in habitats where they naturally occur than in novel environments			
Seedling			
Survival	rare > novel	two of three rare species showed high survival in their habitat of origin	partial
Growth	rare > novel	one of three rare species showed high growth in their habitat of origin	partial
Seed			
Germination	rare > novel	rare species did not germinate readily regardless of habitat/planting site	no
Rare species have extended seed viability			
Seed			
Viability	rare > common	all rare species showed a longer period of seed dormancy than common species	yes
Rare species show specialization trade-off			
Common garden			
Growth	rare > common	opposing patterns were detected for survival and growth	partial
Common species exhibit higher performance in habitats they share with rare species			
Seed			
Germination	common > rare	common species showed higher germination	yes
Viability	common > rare	common species showed lower seed viability	no
Seedling			
Survival	common > rare	common species did not show any clear patterns in terms of their relative survival in habitats where they were found	no
Growth	common > rare	common species did not show consistently strong growth across all habitat types when compared to rare species	no
Common species show higher levels of plasticity			
Seedling			
Growth	common > rare	plasticity at the species level was not detected	no
Common garden			
Growth	common > rare	rarity effects were not detected in the plasticity tests	no
Populations of species show local adaptation†			
Seedling			
Survival and growth	away < home > foreign	variance components for population by habitat interactions were 0 or small	no
Common species outperform rare species in a warmer drier environment			
Common garden			
Survival	common > rare	survival differed among the species and was generally lower for common species compared to rare species	no
Growth	common > rare	common species generally showed greater relative growth and biomass	partial

Note: Experiments are seedling, alpine reciprocal seedling; seed, alpine reciprocal seed; and common garden, warm environment common garden.

†*Populations of species show local adaptation* is not a core component of the niche-breadth–range-size hypothesis but an important aspect in detecting trade-offs in species and specialization.

TABLE 2. The root structure, approximate adult plant height and width reached, Australian states species occurs in, study terms, and the seven *Brachyscome* study species.

						Bogong High Plains, Victoria Habitat and species occurrence		
Species	Root structure	Plant height (cm)	Plant width/ diameter (cm)	Australian State/ Territory	Study terms	Open heathland	Tussock grassland	Rocky grassland
B. spathulata	stoloniferous	60	20	NSW, VIC, TAS	common	†, ‡	**x**	**x**
B. scapigera	rhizomatous	30	30	QLD, NSW, VIC	common	†, ‡	**x**	**x**
B. rigidula	tap root	30	30	VIC, TAS	common	**x**	**x**	†, ‡
B. decipiens	tap root	20	25	NSW, VIC, TAS	common	†	†, ‡	†, ‡
B. nivalis	stoloniferous	30	30	NSW, VIC	rare	**x**	**x**	†, ‡
B. foliosa	stoloniferous	20	10	NSW, VIC	rare	†, ‡	**x**	**x**
B. tadgellii	stoloniferous	15	30	VIC,	rare	**x**	†, ‡	**x**

Notes: States are QLD, Queensland; NSW, New South Wales (includes Australian Capital Territory); VIC, Victoria; TAS, Tasmania. Symbols depict occurrence within Bogong High Plains only: † species naturally occur in this habitat; ‡ species sampled from this habitat, **x** species do not occur in this habitat. Values are means.

The three rare alpine endemics are all stoloniferous, with basal leaves and a clumping habit. *Brachyscome foliosa* (r) is considered threatened under the State Flora and Fauna Guarantee Act 1988. *Brachyscome nivalis* (r) and *B. tadgellii* (r) are closely related (Appendix S1: Fig. S1), with possible hybridization occurring in natural populations (M. Hirst, *unpublished data*). The other four study species (designated as c, common) have a wider distribution extending beyond the alpine zone within the eastern states of Australia, and occur in one of the habitat types where one of the rare species also occurs. *Brachyscome spathulata* (c) and *B. scapigera* (c) occur in the

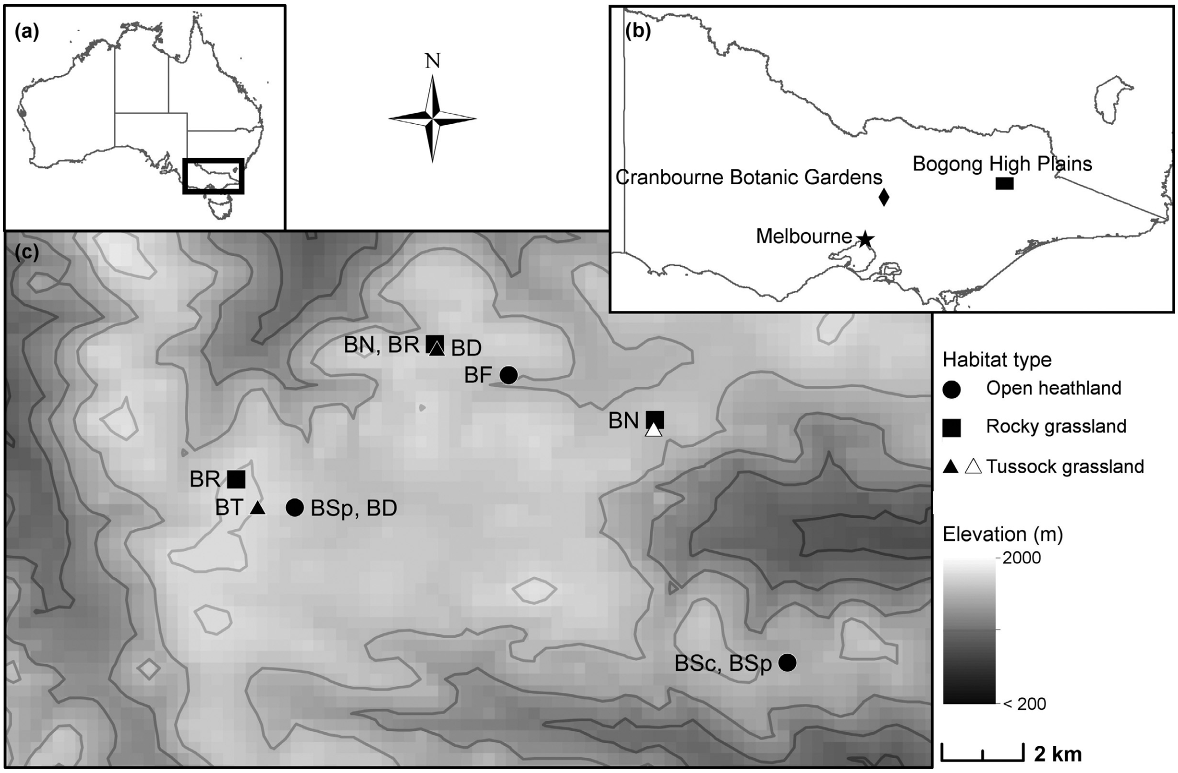

FIG. 1. (a) Map of Australia with black outline indicating southern state of Victoria. (b) State of Victoria, depicting the Bogong High Plains (where the field based experiments were conducted) and Cranbourne Botanic Garden (where the common controlled garden was conducted) in relation to the major city of Melbourne. (c) Map of the Bogong High Plains indicating where the reciprocal transplants were situated. The seven species are as follows: BD, *Brachyscome decipiens*; BF, *Brachyscome foliosa*; BN, *Brachyscome nivalis*; BR, *Brachyscome rigidula*; BSc, *Brachyscome scapigera*; BSp, *Brachyscome spathulata*; and BT, *Brachyscome tadgellii*. Black symbols show the site of origin and the reciprocal sites. The white symbol shows site of origin only. Contours are 200 m elevation.

alpine open heathlands like *B. foliosa* (r). Both are stoloniferous species with a wide geographic and altitudinal range. *Brachyscome rigidula* (c) occurs in a rocky grassland habitat like *B. nivalis* (r) and is a non-stoloniferous sprawling herb found at lower elevation in subalpine shrub land and open eucalypt forests. *Brachyscome decipiens* (c) is a rosette forming herb found growing in multiple alpine habitats (open heathlands, tussock grasslands, and rocky grasslands; see Table 2), as well as subalpine and montane woodlands, grasslands, and swamps.

To test whether the common vs. rare characterization was confounded by phylogenetic history, sequences were obtained for the nuclear ITS and chloroplast *mat*K marker for at least one representative of each of the 14 informal taxon groups that comprise the *Brachyscome* genus (Short 2014) with outgroups also included in the analysis. The methods and results of this analysis are provided in the supplementary material, and confirmed that the rare species are not all clustered together phylogenetically (see Appendix S1: Fig. S1).

The warm environment common garden was situated in the eastern site of The Royal Botanic Gardens Victoria, located at Cranbourne, 45 km south east of the City of Melbourne, Australia. This is a wholly landscaped outdoor research area consisting of aboveground experimental plots situated 77 m above sea level (Fig. 1). Climate data for both localities (Falls Creek Bogong High Plains and Cranbourne Botanic Garden) are *available online*.[6] Over a 27-yr average, the difference in the maximum temperature of these experimental sites in spring and autumn is ~9.9°C, while in winter it is ~1.9°C and in summer it is ~8.1°C. Higher rainfall occurs over the summer months in the alpine experiment site, which receives ~50 mm more precipitation than the common garden site at Cranbourne.

Alpine reciprocal seedling experiment

Three to five seeds from each site were sown into individual plugs (Jiffy 30 mm pellet packs, (Jiffy Products International BV, Moerdijk, The Netherlands) under ambient nursery conditions, December 2011. Germination and early cotyledon growth occurred over a six-week period and seedlings were thinned to allow only one seedling per plug. A weak solution of seaweed-based plant fertilizer, Seasol (Seasol International, Bayswater, Victoria, Australia), was applied to the seedlings two weeks' post-germination. At the four-leaf stage or when seedlings were approximately 4 cm in height, seedlings were placed outdoors for a further 14 d to harden prior to field planting, which was performed in March 2012.

The alpine reciprocal seedling experiment involved a total of 2,544 mixed seedlings planted in autumn, 2012 in a completely randomized design. At each site (see Table S1 locality), 280 mixed seedlings were divided into two experimental plots (140 seedling per plot) per site locality, with 10 × 8 cm spacing. Seedling numbers of each species (and, in some cases, each population) varied across the eight sites; *B. spathulata* (varied between 48 and 53 seedlings per site); *B. scapigera* (19–24 seedlings per site), *B. rigidula* (53–58 seedlings per site), *B. decipiens* (23–42 seedlings per site), *B. nivalis* (22–38 seedlings per site), *B. foliosa* (24–32 seedlings per site), and *B. tadgellii* (19–24 seedlings per site). Vegetation was cleared from each plot prior to planting out, but no hessian covering was used (unlike in the alpine reciprocal seed experiment). Seedlings were hand watered once only to reduce potential transplantation shock. We undertook the following measurements 17 d after transplantation and then in the following spring and autumn, 14 months after seedlings were put outside, using digital calipers: plant height, plant width, and length of longest leaf. We also recorded plant mortality. After the study, we harvested all remaining plants using a sharp metal trowel and placed each individual sample into a labelled paper bag and stored them in a cool box while in the field. Soil, if present, was removed by light washing after samples were returned to the lab, and the aboveground shoots and root sections were patted dry, weighed, and bagged separately. All material was then dried in an oven at 60°C for 72 h before plants were reweighed.

Warm environment common garden

To compare seedling survival and growth under a warmer climate well away from the alpine area, we established a common garden experiment involving raised outdoor planter boxes. As noted above, the environment at the Cranbourne site is quite different than in the alpine area, with temperatures around 10°C higher and no snow cover. Seeds were collected and grown to seedling stage as per the alpine reciprocal seedling experiment. A total of 1,448 seedlings were planted in autumn, 2012 in the raised planter boxes, consisting of 10 completely randomized blocks, two per planter box. In each block, 133–145 mixed seedlings were planted. The soil in the planter boxes was a mix of one part brown coal, one part double-composted mulch, and eight parts sand (as in Hirst et al. 2016). We did not apply any fertilizer. The drip irrigation in the garden beds was set to release 0.185 L of water per second for three minutes. After the first watering, a 10-minute waiting period ensured absorption of the water into the soil, after which time another three minutes of water was delivered. Initially, the water cycle occurred once a day in the afternoon. As the project progressed, and seasonal rain increased, it was found through soil moisture measurements (Theta ML2 hand held probe; Delta-T Devices, Cambridge, UK) that natural rainfall adequately soaked the garden beds and irrigation was not required. We undertook the following measurements using digital calipers at similar seasonal intervals (after transplant, spring, summer, late autumn) as in the alpine reciprocal transplants (excluding plant height at the transplant phase): height, width, longest leaf, and

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[6] www.bom.gov.au/climate/data/

mortality. After the experiment finished, surviving individuals were harvested, and assessed for biomass as described above. The alpine reciprocal seedling experiment and the warm common garden experiment ran simultaneously over 14 months, concluding in late autumn 2013. We did not control soil (and associated nutrient) differences between the in situ alpine soil and the sand-based media in the common garden experiment.

Seedling experiments: data analysis

In the alpine reciprocal seedling experiment and the warm environment common garden experiment, the average performance of a species/population within a plot (within a site in the case of the alpine reciprocal transplant) was used as the response variable, with species nested within rarity (common and rare). For both experiments, we initially examined the average growth rate of seedlings that survived to autumn, plotting changes in width and height of the plants for each of the planted sites (alpine reciprocal experiment) or common garden site at multiple time points. We focused on these time points (spring and autumn) because selection in alpine areas involves very different conditions across these periods. We were also mindful of the potential to bias results if we only considered plants that survived throughout the experiment. Nevertheless, we also ran repeated measures analyses on plants that survived across the two time points.

We analysed survival at each time point using generalized linear models with a log link, treating survival in a plot as a binomial variable. We used general linear models (GLMs) to consider the quantitative traits. These analyses were undertaken with IBM SPSS Statistics 23 (IBM, Armonk, New York, USA) and tested for the impact of rarity (common/rare status), species, site of origin, site of planting, and their interaction on survival and measured traits. In the initial analysis, we included population as a factor and considered population effects for those species where two source populations were tested. We then used these analyses to determine the size of the population term relative to species differences and included an interaction effect with site. For this purpose, population and species were treated as random variables and the percentage of variance accounted for by these terms and interaction effects was estimated. Because our focus was on species comparisons, we plotted species averages (the average of replicate populations). Note that we also ran GLMs that included a nested population term for those species with two populations, but this did not affect the conclusions. Because repeat measurements were made, we corrected probabilities for multiple comparisons by the Bonferroni approach where appropriate. We also ran repeated-measure GLMs on growth traits for plants that survived the entire experimental period.

To estimate phenotypic plasticity for each species in the transplant experiment at the population level, we computed the coefficient of variation over the planting sites (environments) based on trait (width, height, leaf length, and biomass) means (CVm) and also computed a phenotypic plasticity index (PI_v), based on the difference between maximum and minimum means for the fur traits across environments divided by the maximum value (Valladares et al. 2006). We treated each plot (alpine reciprocal and warm common garden) separately to get replicate measures of plasticity (i.e., plasticity computed from one random plot at each site was treated as one replicate, and plasticity computed from the remaining plot as another replicate). We then compared species with ANOVAs for plasticity in spring and autumn, and used MANOVAs to assess species differences in plasticity overall across traits. This was followed by post hoc tests (Tukey b) to identify differences between species pairs.

One of the patterns that emerged from the warm common garden experiment was a negative association between growth and survival at the species level (see *Results*). To see if this pattern was also evident within species, we visualized the association between a plant trait (plant width) taken at a census point on subsequent survival at the ensuing census point, by plotting trait means for individuals of surviving plants from each species against trait means of the same group that did not survive, treating plots separately. If trait values were not associated with subsequent survival, we expected plotted points to fall on a line with unit slope. We also ran a GLM on these width data with survival, species, and plot as factors to test if there was a significant effect of survival on width.

Alpine seed reciprocal experiment

To determine if the common species followed different seed germination strategies from the rare species, we assessed seed in the field for viability prior to collection. This was undertaken with a cut test of ~50 seed per potential collection in the field (Offord and Meagher 2009) to assess overall quality and ensure the majority of dissected seed are full (not shriveled), and the embryo and surrounding tissue are firm and white. Following this on-site viability assessment, seed for each species was collected from within two or three sites for each habitat type: open heathland, rocky grassland, and tussock grassland. At each location, seed was randomly collected from ~80 plants within 100 m radius of each experimental site (total of eight sites). One additional seed collection was made at a rocky grassland site that was not an experimental site and so referred to as a site of origin only (rocky grassland habitat, Basalt Hill site, see Table S1). Seed of each species collected from each site where they occurred naturally, were combined to create a representative single species seed mix of that site (eight sites) and habitat type (three habitat types).

All seed for the alpine reciprocal seed, alpine reciprocal seedling, and the warm environment common garden were collected between January and March 2011 within ~100 m radius of the experimental site representing each species site of origin. For example, *Brachyscome foliosa* only occurs at one site (Sun Valley) and so seed was collected from this vicinity, which represents *B. foliosa'*s site of origin, and represents one of three open heathland habitats. Seed for the alpine reciprocal seed experiment was stored in a dehumidifying cabinet (15°C and 15% relative humidity) until preparation and sowing for the experiment commenced in spring 2013, and concluded in the spring of the following year.

The seed mix was used to test for germination and seed viability in two experimental plots located at each of eight experimental sites: three open heathlands, three tussock grasslands, and two rocky grasslands (see Table S1 for site localities and coordinates). To prepare the seed, we positioned approximately 5–10 seed per individual collection (depending on seed numbers available) in biodegradable filter paper (like a tea bag; Yireen Group, Jiangdong District, China) and secured the contents with a photographic slide mount (size of slide, 24 × 36 mm; Matin International, Seoul, South Korea). To prepare the plots, vegetation was cleared from a small area (2 × 4 m). We used a total of 326 slide mounts, consisting of four slides placed at each of the 16 plots per species (two plots × eight sites). All collection details and replicate numbers were marked on the slide mount (see example illustration in Rasmussen 1993:1375). All individual slide mounts were placed in the experimental plots in a completely randomized design, between 80 and 100 mm apart. Slide mounts were buried 5 mm from the soil surface and were covered with the existing topsoil and plant debris at each planting site, and a covering of hessian was secured over each grid. Slide mounts were placed in plots in spring 2013 and removed in autumn 2014 (n = 158, 1–2 removed per plot per species accounting for missing/damaged slides) or in the following spring 2014 (n = 168, 1–2 per plot per species accounting for missing/damaged slides). Once a slide mount was removed from the soil, it was placed into a labelled plastic zip lock bag, and held in a cool box until inspection under magnification (20×) in the laboratory. All missing and/or damaged slides were removed from analyses, subsequently leading to uneven totals in the number of slides across species and sites.

For the seed measurements, each individual slide mount was inspected, and we defined germination (G) as the emergence of a radicle, viable seed (V) as seed containing firm, white embryos upon dissection, and non-viable seed (NV) as seed that was very soft upon dissection, and with an embryo (if present) having a light brown color. We used the total number of seed (initially sown) per slide mount (TS) to calculate germination capacity as (G/TS) × 100 and viability as (V/TS) × 100. We compared germination and viability by environments, rarity, and species (nested within rarity) through a generalized linear model with traits treated dichotomously.

RESULTS

Do rare species have a higher performance in habitats where they naturally occur than novel environments?

Alpine reciprocal seedling experiment: survival.—A generalized linear model indicated no effect of rarity on survival between transplantation and the spring census periods (G_1 = 1.371, P = 0.242), but a significant effect of species nested within rarity (G_5 = 63.484, P < 0.001) as well as an effect of planting site (G_7 = 125.040, P < 0.001), with an interaction between rarity and planting site (G_7 = 15.952, P = 0.026). Regarding the three rare species in spring; *B. tadgellii* (r) showed high relative survival in the tussock grassland (habitat of origin), particularly at the tussock BH site (Fig. 2a) and in the rocky grassland, but low relative survival in the open heathland sites (Fig. 2a). This species ranked first overall in performance when averaged across the tussock sites but lowest in the open heathland sites. The relative survival of *B. foliosa* (r) in its home habitat (open heathland) was also high overall although this varied between sites (Fig. 2a). This species ranked second overall in performance. Unlike the other two rare species that performed relatively well in their home habitat sites, *B. nivalis* (r) had low survival in the rocky grassland habitat where it originated, as did *B. decipiens* (c) and *B. spathulata* (c) (Fig. 2).

Seedling death occurred throughout this experiment; 17 d after transplantation, 91.1% (n = 2,318) of plants survived, while after the winter snow had cleared in spring, survival had dropped to 43.8% (n = 1,004). By autumn, 71.8% of the alpine plants that survived the previous summer remained (n = 695); this meant that 36% of the seedlings planted at the start of the experiment were still alive. Species differences evident in autumn, contrast with the lack of large differences at the transplant stage (see Table S4) where differences are averaged across sites and expressed in terms of habitat. Survival at the autumn census showed rarity did not have an effect overall (G_1 = 0.001) but there was an interaction between rarity and planting sites (G_7 = 12.708, P < 0.001). Survival differed significantly among species (G_5 = 46.635, P < 0.001) and planting sites (G_7 = 90.527, P < 0.001). At this stage, few plants remained alive in the rocky sites, with only the narrow endemic *Brachyscome tadgellii* (r) and two widespread species, *B. spathulata* (c) and *B. rigidula* (c), persisting there (Fig. 2b). The rare *B. tadgellii* and *B. foliosa* showed higher relative survival in their habitat of origin sites than most other species (Fig. 2b). *Brachyscome tadgellii* (r) performed particularly well at one tussock site (habitat of origin).

The common species did not show any clear patterns in terms of their relative survival in habitats where they were found. For instance, *B. spathulata* showed high survival in the rocky and tussock grassland habitats relative to its survival in the open heathland in which it naturally occurs. (Fig. 2). We also tested whether those species that were collected from two sites (i.e., *B. spathulata* (c), *B. rigidula*

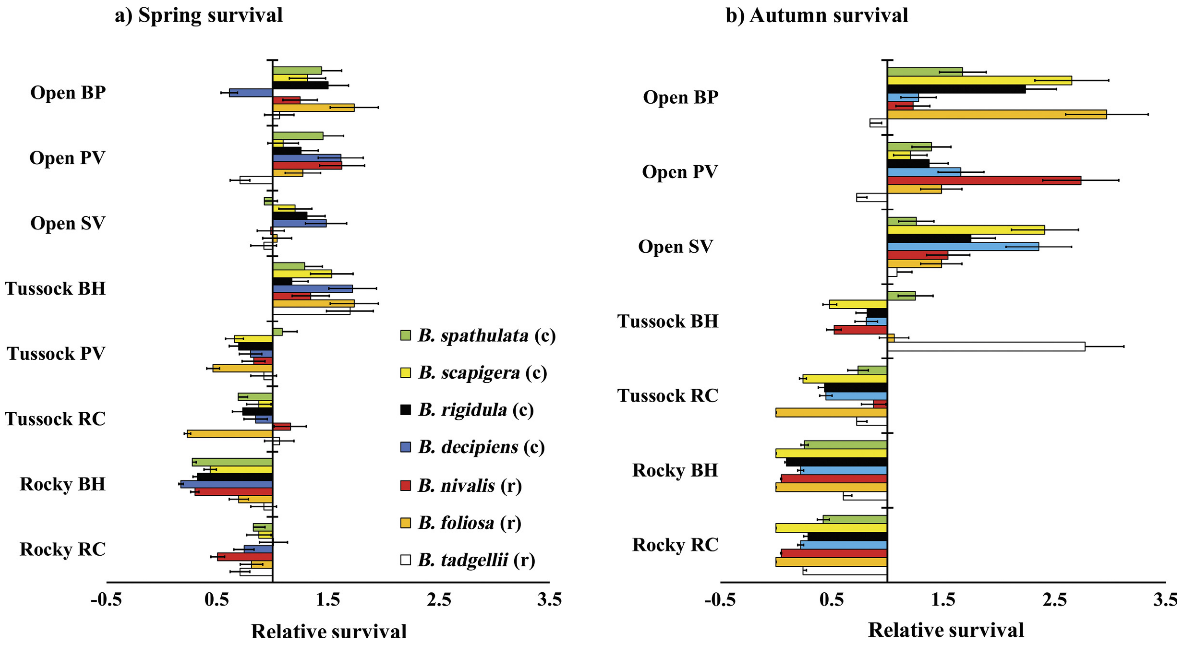

FIG. 2. Relative performance in each site of the seven species for survival in (a) spring and (b) autumn in the alpine reciprocal seedling experiment. Species are designated as rare (r) or common (c). Error bars indicate standard errors based on site values. Open refers to Open Heathland Habitat; Tussock refers to Tussock Grassland Habitat and Rocky refers to Rocky Grassland Habitat. The locality of each habitat type is as follows; BP = Buckety Plains; PV = Pretty Valley; SV = Sun Valley; BH = Basalt Hill; and RC = Ruined Castle.

(c), *B. decipiens* (c), and *B. nivalis* (r)) showed evidence for local adaptation in terms of survival. In a generalized linear model, there was no significant interaction between population tested as a nested term and site for survival ($P = 0.142$ in spring and $P = 0.132$ in autumn) providing no evidence for local adaptation (Table S4).

Alpine reciprocal seedling experiment: growth.—None of the common species showed consistently strong growth across all habitat types when compared to the rare species (Figs. 3,4). Rarity was only significant for autumn leaf length (see Table 3). While mean plant growth across the four census points (as measured by plant width and height) varied considerably between species, species were almost always wider when grown in the open heathland sites (Appendix S1: Fig. S3a–g). GLMs (Table 3) revealed strong site effects on growth rates but there were also some site-specific differences among the species. Width and height tended to be higher in the open heathland sites, particularly at the open BP site, when compared to other habitat sites in spring (Fig. 3a) and in autumn (Fig. 4a). This was also reflected in site biomass effects at the end of the experiment (Table 3).

Do rare species have extended seed viability?

Alpine reciprocal seed experiment.—Rare species showed a longer period of seed dormancy than common species by way of low germination but overall high seed viability, with viable seed present for all 24 species/site combinations in autumn (Fig. 5) and spring (Fig. 6). This contrasted with the common species, which had no viable seed in 3 of 32 site–species combinations in autumn and 12 of 32 combinations in spring. Seed viability for the rare species remained high in spring (percentage and standard error across sites for *B. tadgellii* (r) $\bar{x} = 68.9 \pm 2.2$; *B. foliosa* (r) $\bar{x} = 58.8 \pm 2.3$, *B. nivalis* (r) $\bar{x} = 51.2 \pm 2.4$), in contrast to the common species (percentage and standard error for *B. spathulata* (c), $\bar{x} = 36.2 \pm 2.5$, *B. scapigera* (c) $\bar{x} = 29.3 \pm 0.7$, *B. rigidula* (c) $\bar{x} = 15.5 \pm 1.6$, and *B. decipiens* (c) $\bar{x} = 3.5 \pm 0.5$).

Do rare species show specialization trade-off?

Warm environment common garden.—Opposing patterns were found for plant survival and growth at the species level (Fig. 7), while this possible trade-off was not evident at the plot level within species. We tested this by considering width in spring and testing whether smaller plants had higher survival at the subsequent census point (summer). However, the opposite pattern was found, in that there was a significant effect of whether plants that survived or died differed in width (generalized linear model, $\chi^2 = 238.783$, df = 1, $P < 0.001$) but wider plants within species had a greater likelihood of surviving over summer (Appendix S1: Fig. S4).

Do common species exhibit higher performance in habitats they share with rare species?

Alpine reciprocal seed experiment: germination and viability.—There was a significant effect of rarity on the

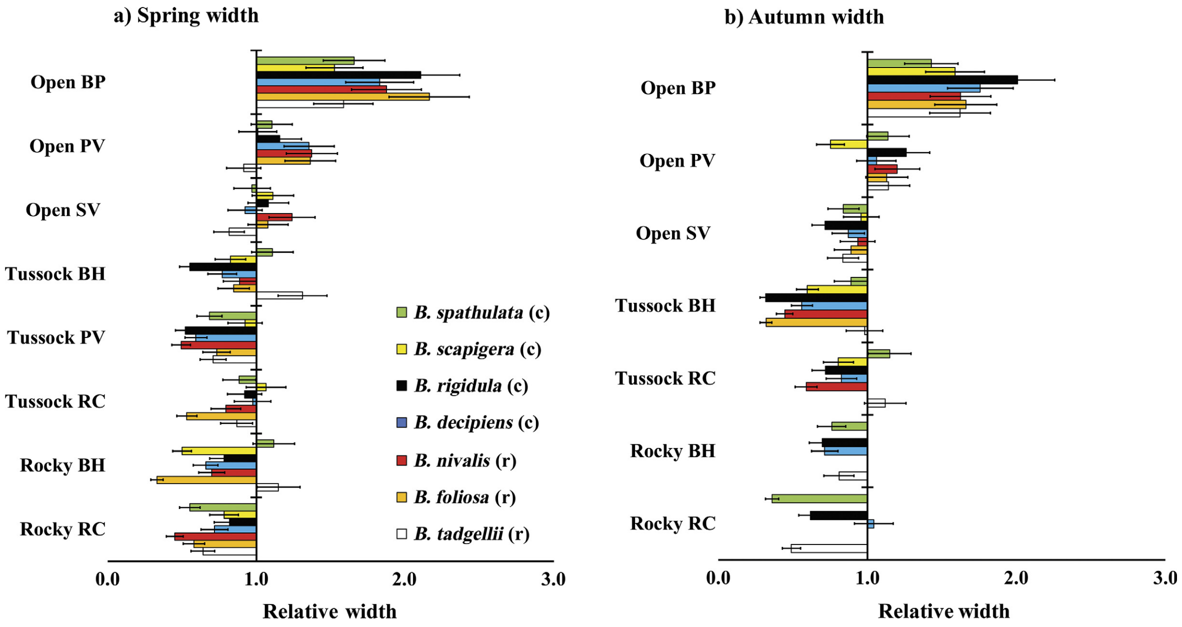

FIG. 3. Relative performance in each site of the seven species for plant width in (a) spring and (b) autumn in the alpine reciprocal seedling experiment. Data are presented for eight sites for spring measures and seven sites for autumn measures. Error bars indicate standard errors based on site values.

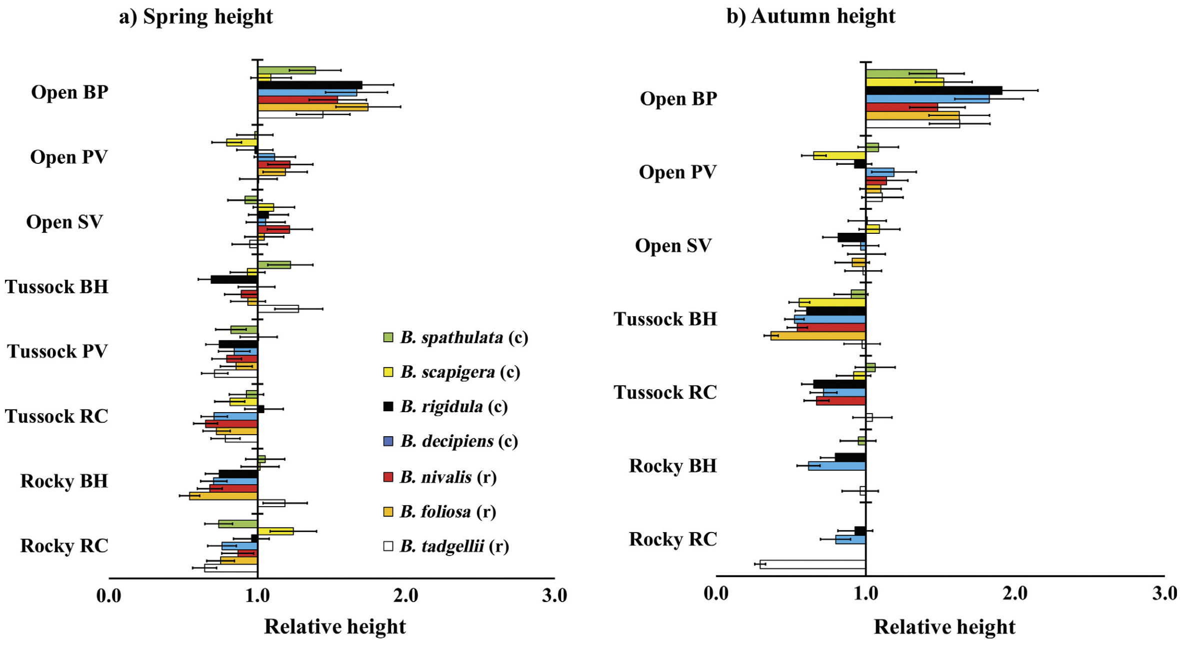

FIG. 4. Relative performance in each site of the seven species for plant height (a) spring and (b) autumn in the alpine reciprocal seedling experiment. Data are presented for eight sites for spring measures and seven sites for autumn measures. Error bars indicate standard errors based on site values.

germination and viability of species in both autumn and spring as common species exhibited relatively high germination capacity across most sites, although rare species maintained a higher proportion of viable seed (Figs. 5 and 6). In autumn, there was a significant effect of rarity on germination ($G_1 = 33.734$, $P < 0.001$) and viability ($G_1 = 70.004$, $P < 0.001$). There were also species differences (nested within rarity) for germination ($G_5 = 61.508$, $P < 0.001$) and viability ($G_5 = 58.227$, $P < 0.0001$). Site differences in autumn were also

TABLE 3. Analysis of growth measures in the alpine reciprocal seedling experiment. Results are presented of generalised linear models on quantitative traits (width, height, leaf length, fresh weight and dry weight) testing for the impact of rarity (common vs rare) site of planting, species (rarity), the interaction of site (rarity) × species and the interaction of site × rarity, in spring and autumn.

Trait	Time scored	Effect	F	df	P
Width	Spring	Rarity	1.91	1	0.167
		Site	34.69	7	<0.001
		Species (rarity)	14.71	5	<0.001
		Species (rarity) × site	1.70	35	0.007
		Site× rarity	2.38	7	0.021
		Error		755	
	Autumn	Rarity	0.02	1	0.899
		Site	23.63	6	<0.001
		Species (rarity)	2.65	5	0.023
		Species (rarity) × site	1.59	21	0.049
		Site× rarity	1.04	6	0.400
		Error		369	
Height	Spring	Rarity	4.20	1	0.041
		Site	17.22	7	<0.001
		Species (rarity)	36.25	5	<0.001
		Species (rarity) × site	2.63	35	<0.001
		Site× rarity	1.08	7	0.373
		Error		756	
	Autumn	Rarity	1.46	1	0.228
		Site	9.96	6	<0.001
		Species (rarity)	7.14	5	<0.001
		Species (rarity) × site	1.39	21	0.033
		Site × rarity	1.39	6	0.219
		Error		370	
Leaf length	Summer	Rarity	0.14	1	0.705
		Site	22.85	7	<0.001
		Species (rarity)	12.40	5	<0.001
		Species (rarity) × site	3.20	30	<0.001
		Site × rarity	1.78	7	0.090
		Error		473	
	Autumn	Rarity	7.08	1	0.008
		Site	18.66	6	<0.001
		Species (rarity)	25.79	5	<0.001
		Species (rarity) × site	2.97	21	<0.001
		Site × rarity	2.31	6	0.034
		Error		369	
Fresh weight	Autumn	Rarity	0.36	1	0.551
		Site	15.72	6	<0.001
		Species (rarity)	2.34	5	0.041
		Species (rarity) × site	1.45	21	0.091
		Site× rarity	0.10	6	0.996
		Error		371	
Dry weight	Autumn	Rarity	0.07	1	0.794
		Site	10.31	6	<0.001
		Species (rarity)	3.13	5	0.009
		Species (rarity) × site	1.20	21	0.248
		Site× rarity	1.00	6	0.427
		Error		349	

evident, but the interaction between site and rarity was not (see Table 4). In spring, there was an effect of rarity on germination ($G_1 = 14.196$, $P < 0.001$) and species differences within rarity ($G_5 = 39.378$, $P < 0.001$); there was also an effect of rarity on viability ($G_1 = 26.034$, $P < 0.001$) and among species nested within rarity ($G_5 = 16.197$, $P = 0.006$). There were differences among sites for both germination and viability as well as interactions between site and rarity (see Table 4). Germination in two rare species (*Brachyscome tadgellii* and

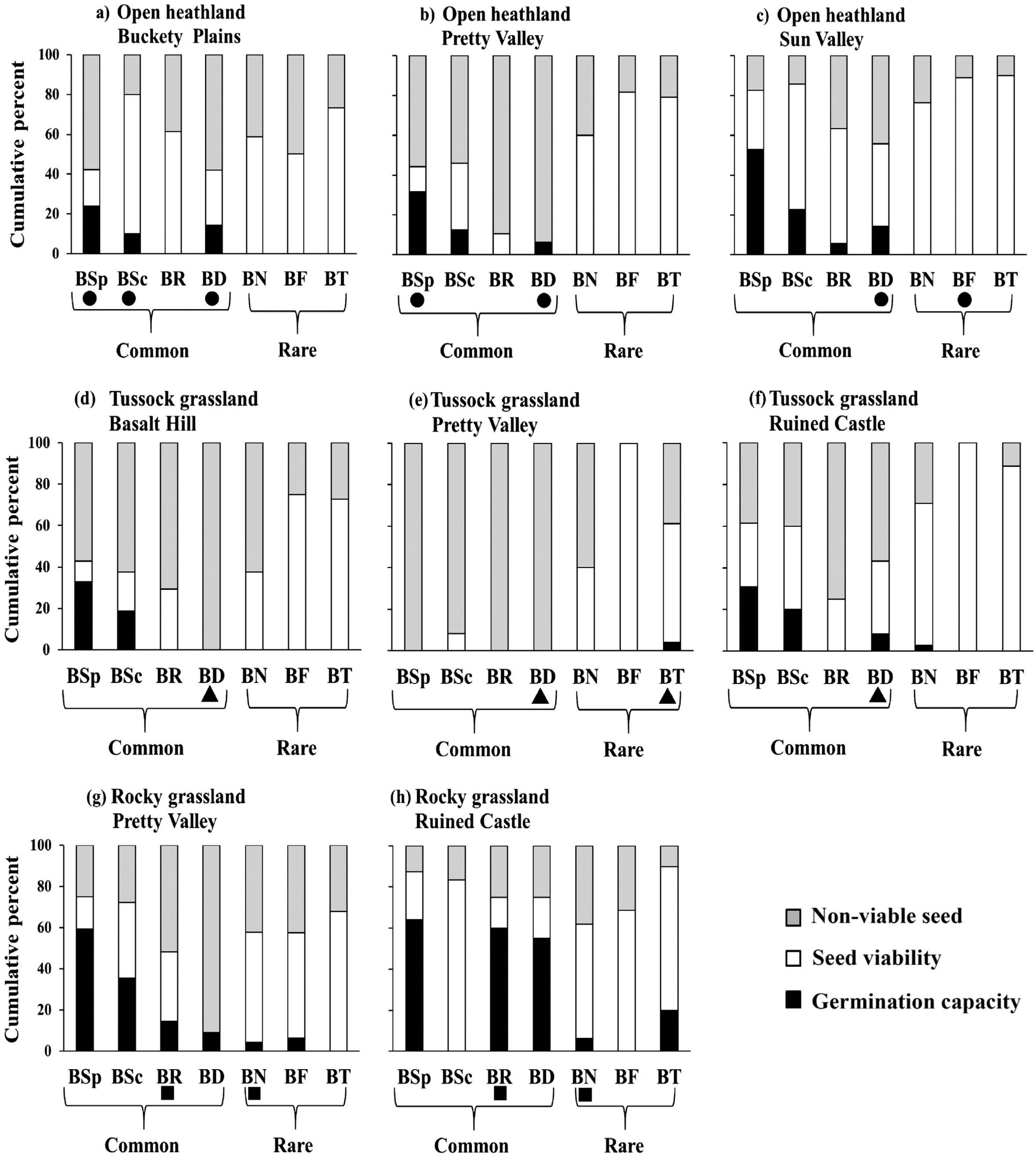

FIG. 5. Autumn germination and viability of unique slides sampled in the alpine reciprocal seed experiment. Stacked bar graphs show the germination capacity (black), seed viability (white), and non-viable seed (gray) of the seven alpine species in sites representing three different habitat types: (a–c) open heathland, (d–f) tussock grassland, and (g, h) rocky grassland. The four common species are BSp, *Brachyscome spathulata*; BSc, *Brachyscome scapigera*; BR, *Brachyscome rigidula*; and BD, *Brachyscome decipiens*. The three rare species are BN, *Brachyscome nivalis;* BF, *Brachyscome foliosa*; and BT, *Brachyscome tadgellii*. Black symbols show the site of origin.

B. foliosa) was very low at all sites in both seasons, occurring in only 3 of 16 site–species combinations in autumn and 2 of 16 in spring, in contrast to 21 of 29 and 14 of 21 site–species combinations in autumn and spring, respectively, for the common species where viable seed was present (see Figs. 5 and 6a–h). The other rare species, *Brachyscome nivalis* (r), only showed germination in autumn (Fig. 6f, g). On average (across species and sites), percent germination was higher in autumn ($\bar{x}$ = 11.7 ± 1.6) than spring ($\bar{x}$ = 6.8 ± 1.5), as was percent seed viability in autumn ($\bar{x}$ = 51.9 ± 2.0) than in spring ($\bar{x}$ = 35.5 ± 2.4).

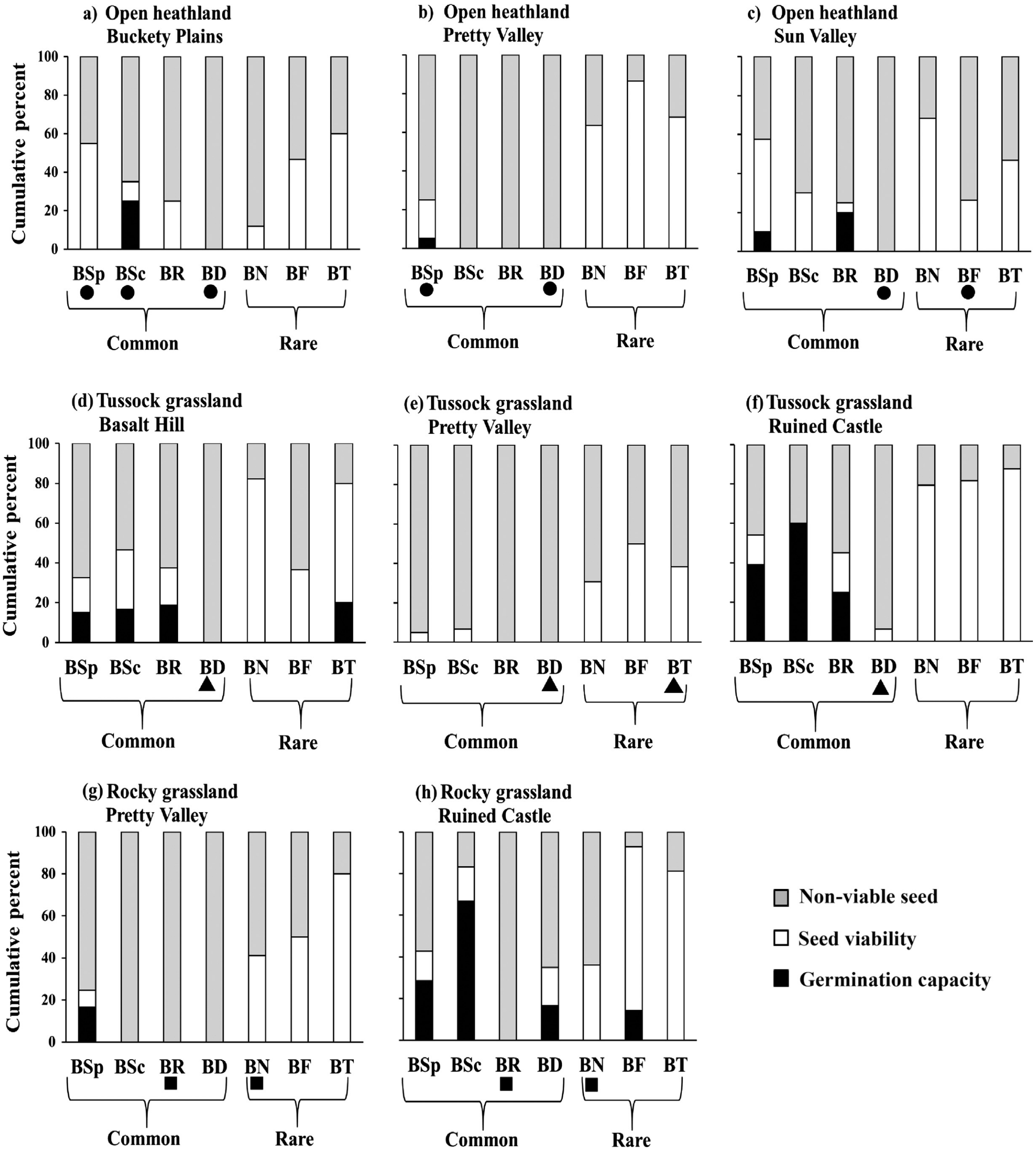

FIG. 6. Spring germination and viability of unique slides sampled in the alpine reciprocal seed experiment. Stacked bar graphs show the germination capacity (black), seed viability (white), and non-viable seed (gray) of the seven alpine species in sites representing three different habitat types: (a–c) open heathland; (d–f) tussock grassland, and (g, h) rocky grassland at eight sites. Species names are as in Fig. 5. Black symbols show the site of origin.

Do common species show higher levels of plasticity?

Alpine reciprocal seedling experiment.—Rarity effects were not detected in the plasticity tests in spring (height $F_{1,15}$ = 0.341, $P = 0.568$ and width $F_{1,15}$ = 0.855, $P = 0.370$), autumn (height $F_{1,15} = 2.352$, $P = 0.146$ and width $F_{1,15} = 0.197$, $P = 0.664$) or biomass (fresh mass $F_{1,15}$ = 1.275, $P = 0.277$ and dry mass $F_{1,15}$ = 0.234, $P = 0.636$). Weak differences in phenotypic plasticity at the population level as measured by PI_v among the species were detected. The GLM analysis indicated differences between species in plant width (Appendix S1: Fig. S2a) in spring ($F_{6,15} = 3.519$, $P = 0.022$) and autumn (Appendix S1: Fig. S2b; $F_{6,15} = 3.859$, $P = 0.016$) but not for spring height ($P = 0.144$) or autumn height ($P = 0.133$) (Appendix S1: Fig. S2c and d, respectively).

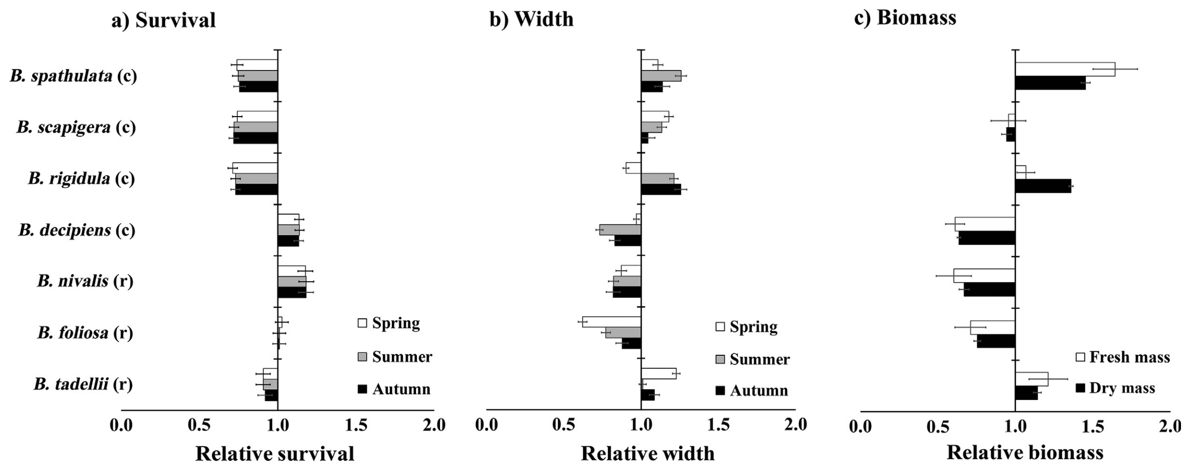

FIG. 7. Relative performance of the seven species over three census points for (a) survival, (b) plant width, and (c) biomass in the warm environment common garden. Error bars indicate standard errors based on plot values.

TABLE 4. Analysis of germination and viability measures in the alpine reciprocal seed experiment, by trait and time scored.

Effect	G	df	P
Germination			
Autumn			
Rarity	33.734	1	<0.001
Site	63.220	7	<0.001
Species (rarity)	61.508	5	<0.001
Species (rarity) × site	6.435	7	0.490
Spring			
Rarity	14.196	1	<0.001
Site	78.533	7	<0.001
Species (rarity)	39.370	5	<0.001
Species (rarity) × site	69.749	7	0.005
Viability			
Autumn			
Rarity	70.004	1	<0.001
Site	20.934	7	0.004
Species (rarity)	58.227	5	<0.001
Species (rarity) × site	8.652	7	0.279
Spring			
Rarity	26.034	1	<0.001
Site	16.288	7	0.023
Species (rarity)	16.197	5	0.006
Species (rarity) × site	38.845	7	<0.001

Note: Results are presented of generalized linear models testing for the impact of rarity, site (eight sites), species (rarity), the interaction of species (rarity) × site in autumn and spring. G represents the likelihood ratio.

Leaf length showed a species difference in spring ($F_{6,15} = 3.001$, $P = 0.039$). Fresh mass did not differ between species ($P = 0.095$), but did after drying ($F_{6,15} = 3.512$, $P = 0.023$; Appendix S1: Fig. S2g and h, respectively). It should be emphasized that most of these species differences were not significant for individual traits after Bonferroni correction. Nevertheless, the rare *Brachyscome tadgellii* (r) had a consistently low plasticity and ranked 6 of 7 in spring width (Appendix S1: Fig. S2a), and 7 of 7 for plant width in autumn (Appendix S1: Fig. S2b), plant height (Appendix S1: Fig. S2c, d), leaf length (Appendix S1: Fig. S2e, f), and biomass (Appendix S1: Fig. S2g, h). In contrast, the rare *Brachyscome foliosa* (r) ranked highest for plasticity (1 of 7) in autumn plant height (Appendix S1: Fig. S2d), leaf length (Appendix S1: Fig. S2e, f), and biomass (Appendix S1: Fig. S2g, h). *Brachyscome nivalis* (r), ranked 2 of 7 in spring height (Appendix S1: Fig. S4c), but dropped to 6 of 7 in the autumn height (Appendix S1: Fig. S2d). For all traits, *B. nivalis* plasticity was at the lower end of the among-species ranking. The two measures of plasticity ($\mathrm{PI_v}$ and $\mathrm{CV_m}$) showed similar patterns across species and sampling times (Table S3).

Do populations of species show local adaptation?

Alpine reciprocal seedling experiment.—We found interactions between species and site in spring for the size traits and to a lesser extent in autumn (Table S4). The rare *B. foliosa* grew relatively rapidly in its home habitat (open heathland) sites in spring, however this advantage was not apparent at the end of the experiment (Appendix S1: Fig. S3). The rare *B. tadgellii* grew well in one of its home tussock sites (tussock BH) in spring (Figs. 3a and 4a) and did well in terms of width and height at both the other tussock sites in autumn (Figs. 3b). Unfortunately, we were unable to assess growth of the rare *B. nivalis* in its home rocky site because of low survival.

The common *B. rigidula* performed relatively poorly in tussock sites where it is not found. None of the common species showed consistently strong growth across all habitat types, including *B. decipiens*, which is found in all the habitats tested here. Variance components for population by habitat interactions, which would have reflected local adaptation in the four species where this could be tested, were 0 or small (Table S4) and not significant ($P > 0.05$) for any of the traits/sampling times.

We undertook a repeated-measures analysis for width and height in seedlings that survived to the end of the experiment (Table S5). No significant effects of rarity were found for either trait, consistent with the separate analyses at the two time periods and reflecting the inconsistent responses of species within the two groups. There was a significant interaction of species and planting site, reflecting species differences in growth at the sites, while the three-way interaction that also included sampling time approached significance for width. The planting site interaction with sampling time was significant for both traits, reflecting different effects of spring and autumn periods on growth at the planting sites.

Do common species outperform rare species in a warmer, drier environment?

Warm environment common garden: survival.—Survival differed among the species and was generally lower for the common species compared to the rare species. Rarity influenced autumn survival overall ($G_1 = 23.365$, $P < 0.001$) and there was no interaction between rarity and the raised garden plots ($P = 0.314$). The highest survival, across all census points, was for *B. nivalis* (r), followed by *B. decipiens* (c), *B. foliosa* (r), and *B. tadgellii* (r) (Fig. 7a). These analyses are presented for species because nested population terms were not significant for survival ($P > 0.05$). The highest seedling mortality in the common garden was observed in the late spring/summer months as opposed to the winter period in the field-based study. No mortality was observed in the common garden at the first census after transplanting ($N = 1{,}448$). By the autumn census, survival had decreased to 35.8% ($N = 519$). There was a significant difference between species nested within rarity ($G_5 = 88.976$, $P < 0.001$), and a difference between the raised experimental plots ($G_4 = 113.640$, $P < 0.001$).

Warm environment common garden: growth.—For the growth traits, we initially examined sites of origin within species in a nested GLM and found no significant differences between the replicate populations tested for the species (*B. spathulata* (c), *B. rigidula* (c), *B. decipiens* (c), and *B. nivalis* (r)) for any of the traits (all $P < 0.05$). In the GLMs focusing on species effects, rarity had a significant effect on plant width but not on biomass, while species differences (nested within rarity) were evident for all traits (see Table 5). The common species that showed lower survival (*B. spathulata*, *B. scapigera*, and *B. rigidula*) had a greater relative growth and biomass than species that showed higher survival (see Fig. 7a and b). Species differences for plant biomass (Fig. 7c) tended to follow those for plant width.

Discussion

The niche-breadth–range-size hypothesis was tested by including rarity (common/rare status) as a factor in models investigating survival and growth parameters in all three experiments. As predicted (refer to Table 1), we found clear support for different patterns of seed germination between common species and narrow endemics; common widespread species showed a greater capacity for germination while rare species retained more viable seed. However, we found mixed support when considering seedling survival and growth for the prediction that rare species should show higher performance in habitats where they naturally occur in comparison to novel environments. In the warmer environment, we found partial support for the expected opposing patterns of survival and growth in rare and common species. However, there was a notable exception, in that one of the rare species, *B. tadgellii*, showed the same survival/growth response as the common species. We also found no evidence for lower plasticity levels in the rare species from this group of daisies.

The rare species were characterized by high seed viability and low germination (or higher germination sensitivity), particularly in the open heathland habitat, which is known for its high species diversity. Previous research on germination in Australian alpine plants suggested that plants follow three strategies: postponed germination, immediate germination, and staggered germination (Hoyle et al. 2015). The *Brachyscome* species appear to follow the first and third of these strategies. Overall, the higher germination percentage of species in autumn than in the following spring may indicate these species germinate and develop under cooler temperatures before the onset of winter, possibly to invest in growth prior to the high temperatures and unfavorable dry conditions that can occur in this environment in summer (Griffin and Hoffmann 2012, Williams et al. 2014). Staggered germination across seasons (observed mainly in the common species in this study) may help to spread risk of seedling mortality under the variable alpine environmental conditions. Alternatively, the high seed viability and lack of germination exhibited by the three rare alpine endemics points to postponed germination involving dormancy. This strategy is common in alpine species (Schwienbacher et al. 2011), and physiological dormancy (Baskin and Baskin 1998) is found in alpine areas around the world (Schwienbacher et al. 2011, Hoyle et al. 2015).

The alpine reciprocal seedling experiment pointed to two alpine endemics (*B. tadgellii* (r) and *B. foliosa* (r)) and two widespread species (*B spathulata* (c) and *B. rigidula* (c)) performing relatively well in their habitat of origin. However, in the case of *B. rigidula* (c), performance in habitats depended on the trait being considered; for example, plants were wider in an open heathland, but taller in the rocky grassland from which the species originated. This contributed to *B. rigidula* (c) having a high plasticity for plant width. On the assumption that plasticity allows species to adjust growth forms appropriately to environments, we expected the common species to have a higher plasticity when compared to the rare set, including the widespread *B. decipiens* (c), which is found in a particularly wide range of habitats (Hirst et al. 2016). In a study examining perennial grassland species (including

TABLE 5. Analysis of growth measures in warm common garden environment. Results are presented of generalised linear models on quantitative traits (width and biomass) testing for the impact of rarity (common vs rare) plot, species (rarity), the interaction of plot (rarity) × species and the interaction of plot × rarity, in spring, summer and autumn.

Trait	Time scored	Effect	*F*	df	*P*
Width	Spring	Rarity	41.77	1	<0.001
		Plot	1.88	4	0.112
		Species(rarity)	31.42	5	<0.001
		Species (rarity) × plot	1.53	20	0.063
		Plot × rarity	3.55	4	0.007
		Error		1476	
	Summer	Rarity	14.31	1	<0.001
		Plot	6.37	4	<0.001
		Species(rarity)	10.86	5	<0.001
		Species (rarity) × plot	1.20	20	0.251
		Plot × rarity	1.90	4	0.109
		Error		523	
	Autumn	Rarity	11.86	1	0.001
		Plot	0.95	4	0.434
		Species(rarity)	5.80	5	<0.001
		Species (rarity) × plot	1.43	20	0.101
		Plot × rarity	0.58	4	0.677
		Error		509	
Fresh weight	Autumn	Rarity	2.16	1	0.143
		Plot	0.44	4	0.778
		Species(rarity)	4.89	5	<0.001
		Species (rarity) × plot	0.72	20	0.803
		Plot × rarity	0.44	4	0.780
		Error		479	
Dry weight	Autumn	Rarity	3.45	1	0.064
		Plot	0.22	4	0.927
		Species(rarity)	5.66	5	<0.001
		Species (rarity) × plot	0.90	20	0.588
		Plot × rarity	1.07	4	0.371
		Error		478	

Trifolium, *Ranunculus*, and *Briza*), a low level of morphological plasticity in alpine species compared to mid-elevation species was interpreted in terms of an increased level of canalization of traits in harsher conditions (Frei et al. 2014). However, the common *Brachyscome* we tested, which were also found in lowland environments, did not have consistently higher plasticity.

In the warm environment common garden, which was near sea level, we found a relatively high growth rate in three common species (*B. spathulata* (c), *B. scapigera* (c), *and B. rigidula* (c)), which may increase their competitive ability under such conditions. Additionally, and contrary to expectations for plants from harsh environments (Grime 1977), one of the rare species (*B. tadgellii* (r)) showed a relatively high growth rate. The low relative survival of the common species in this study accompanied with a high growth rate points to a general trade-off between these life history characteristics, with some exceptions. The low growth rate of *B. decipiens* (c) in contrast to its high survival in the novel garden was surprising, given that this common species occurs across a wide range of habitats. Perhaps the success of this species relates to its ability to survive and tolerate a wide range of conditions; in that sense, it may be opportunistic across a range of environments.

Despite evidence for habitat-related differences among species, there was no evidence of local adaptation within species, consistent with a more extensive comparison of nine populations of *B. decipiens* (Hirst et al. 2016), but in contrast to adaptive patterns found for some alpine species in this region (e.g., *Poa hiemata* [Byars et al. 2007]; *Carex* spp. [M'Baya et al. 2013]). Overall, interactions between habitat and population that would have indicated local adaptation accounted for a small proportion of the variance, whereas strong genetic × environment interactions were detected for *P. hiemata* (Byars et al. 2007). Gene flow may be high among the different habitat types and prevent local adaptation, although we do not have gene flow estimates for these species. Based on patterns often observed in alpine plants, we would predict seed dispersal to be relatively low (Scherff et al. 1994). In *Brachyscome,* seed appendages (i.e., pappus, bristles, or wings) are typically reduced or absent, which likely limits dispersal ability, as shown for *B. ciliaris* where mean dispersal distance is ≤1 m (Aleman et al. 2011). However, we note that this study only included populations from the common species that co-occurred with rare species in the Bogong High Plains. We anticipate that including a wider set of populations, and thus a greater amount of genetic variation, could reveal patterns of local adaptation. Field studies comparing performances with the full range of populations from common and rare species represent important knowledge gaps.

These results have implications for the maintenance of biodiversity across landscape mosaics such as alpine regions (Sedlacek et al. 2015). The low growth rate of some narrow alpine endemics outside their natural habitat may indicate vulnerability of these species to future environmental changes including the arrival of invasive competitors. In the Bogong High Plains, vegetation changes linked to climate change have already been noted (Wahren et al. 2013) and it is likely that the density of heath vegetation will increase under predicted increases in fire, whereas graminoid vegetation will increase in unburned areas (Camac et al. 2015), potentially decreasing habitat availability for many narrow endemics. If species decline, it may be possible to conserve some species ex situ, given their ability to survive and grow elsewhere as demonstrated in our common garden experiment. Low growth rate may nevertheless limit their persistence in novel communities responding to climate shifts (Alexander et al. 2015) unless these are carefully managed.

In conclusion, we found some support for the niche-breadth–range-size hypothesis. Common and rare *Brachyscome* exhibit some of the expected trade-offs in specialization vs. performance in a wider range of environments, but there are clear exceptions (e.g., a fast growth rate in the most restricted species, *B. tadgellii*), limiting our ability to make strong predictions about how species will generally fare under rapid environmental change within a given region. Nevertheless, the rare species in this study maintained a high level of seed viability, which may allow them to persist as variability in alpine climates increases.

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LITERATURE CITED

Aleman, R., P. Ainsley, J. Gibbs, F. Tiver, and M. Jusaitis. 2011. Germination requirements of *Brachyscome* species in South Australia. South Australian Naturalist 85:71.

Alexander, J. M., J. M. Diez, and J. M. Levine. 2015. Novel competitors shape species responses to climate change. Nature 525:515–518.

Andrieu, E., J. D. Thompson, and M. Debussche. 2007. The impact of forest spread on a marginal population of a protected peony (*Paeonia officinalis* L.): the importance of conserving the habitat mosaic. Biodiversity and Conservation 16:643–658.

Baskin, C. C., and J. M. Baskin. 1998. Seeds: ecology, biogeography, and evolution of dormancy and germination. Elsevier, San Diego, California, USA.

Boulangeat, I., D. Gravel, and W. Thuiller. 2012*a*. Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances. Ecology Letters 15:584–593.

Boulangeat, I., S. Lavergne, J. Van Es, L. Garraud, and W. Thuiller. 2012*b*. Niche breadth, rarity and ecological characteristics within a regional flora spanning large environmental gradients. Journal of Biogeography 39:204–214.

Brown, J. H. 1984. On the relationship between abundance and distribution of species. American Naturalist 124:255–279.

Byars, S. G., W. Papst, and A. A. Hoffmann. 2007. Local adaptation and cogradient selection in the alpine plant, *Poa hiemata*, along a narrow altitudinal gradient. Evolution 61: 2925–2941.

Callaway, R. M., et al. 2002. Positive interactions among alpine plants increase with stress. Nature 417:844–848.

Camac, J. S., R. J. Williams, C.-H. Wahren, F. Jarrad, A. A. Hoffmann, and P. A. Vesk. 2015. Modeling rates of life form cover change in burned and unburned alpine heathland subject to experimental warming. Oecologia 178:615–628.

Dangremond, E. M., I. C. Feller, and W. P. Sousa. 2015. Environmental tolerances of rare and common mangroves along light and salinity gradients. Oecologia 179:1187–1198.

Frei, E. R., J. Ghazoul, and A. R. Pluess. 2014. Plastic responses to elevated temperature in low and high elevation populations of three grassland species. PLoS ONE 9:1–13.

Fry, J. D. 1996. The evolution of host specialization: are trade-offs overrated? American Naturalist 148:S84–S107.

Gaston, K. J. 2003. The structure and dynamics of geographic ranges. Oxford University Press on Demand, Oxford University Press, New York, New York, USA.

Griffin, P. C., and A. A. Hoffmann. 2012. Mortality of Australian alpine grasses (*Poa* spp.) after drought: species differences and ecological patterns. Journal of Plant Ecology 5:121–133.

Griffith, T., and S. E. Sultan. 2012. Field-based insights to the evolution of specialization: plasticity and fitness across habitats in a specialist/generalist species pair. Ecology and Evolution 2:778–791.

Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. American Naturalist 111:1169–1194.

Gugger, S., H. Kesselring, J. Stocklin, and E. Hamann. 2015. Lower plasticity exhibited by high- versus mid-elevation species in their phenological responses to manipulated temperature and drought. Annals of Botany 116:953–962.

Hennessy, K., P. Whetton, I. Smith, J. Bathols, M. Hutchinson, and J. Sharples. 2003. The impact of climate change on snow conditions in mainland Australia. CSIRO Atmospheric Research, Aspendale, Victoria, Australia.

Hirst, M. J., J. P. Sexton, and A. A. Hoffmann. 2016. Extensive variation, but not local adaptation in an Australian alpine daisy. Ecology and Evolution 6:5459–5472.

Hoyle, G. L., K. J. Steadman, R. B. Good, E. J. McIntosh, L. M. E. Galea, and A. B. Nicotra. 2015. Seed germination strategies: an evolutionary trajectory independent of vegetative functional traits. Frontiers in Plant Science 6:731.

Imbert, E., S. Youssef, D. Carbonell, and A. Baumel. 2012. Do endemic species always have a low competitive ability? A test for two Mediterranean plant species under controlled conditions. Journal of Plant Ecology 5:305–312.

Klanderud, K., and H. J. B. Birks. 2003. Recent increases in species richness and shifts in altitudinal distributions of Norwegian mountain plants. Holocene 13:1–6.

Kruckeberg, A. R., and D. Rabinowitz. 1985. Biological aspects of endemism in higher plants. Annual Review of Ecology and Systematics 16:447–479.

Lacher, I., and M. W. Schwartz. 2016. Empirical test on the relative climatic sensitivity between individuals of narrowly and broadly distributed species. Ecosphere 7:e01227.

Lavergne, S., E. Garnier, and M. Debussche. 2003. Do rock endemic and widespread plant species differ under the leaf–height–seed plant ecology strategy scheme? Ecology Letters 6:398–404.

M'Baya, J., M. J. Blacket, and A. A. Hoffmann. 2013. Genetic structure of *Carex* species from the Australian alpine region along elevation gradients: patterns of reproduction and gene flow. International Journal of Plant Sciences 174:189–199.

McDougall, K. L., and N. G. Walsh. 2007. Treeless vegetation of the Australian Alps. Cunninghamia 10:1–57.

McGlone, M. S., R. P. Duncan, and P. B. Heenan. 2001. Endemism, species selection and the origin and distribution of the vascular plant flora of New Zealand. Journal of Biogeography 28:199–216.

Offord, C. A., and P. F. Meagher. 2009. Plant germplasm conservation in Australia: strategies and guidelines for developing, managing and utilising ex situ collections. Australian Network for Plant Conservation, Canberra, Australian Capital Territory, Australia.

Porter, S. S., and K. J. Rice. 2013. Trade-offs, spatial heterogeneity, and the maintenance of microbial diversity. Evolution 67:599–608.

Rabinowitz, D. 1981. Seven forms of rarity. Pages 205–217 *in* H. Synge, editor. The biological aspects of rare plant conservation. John Wiley & Sons, Chichester, UK.

Rasmussen, H. N., and D. F. Whigham. 1993. Seed ecology of dust seeds in situ:a new study technique and its application in terrestrial orchids. American Journal of Botany 80:1374–1378.

Scherff, E., C. Galen, and M. Stanton. 1994. Seed dispersal, seedling survival and habitat affinity in a snowbed plant: limits to the distribution of the snow buttercup, *Ranunculus adoneus*. Oikos 69:405–413.

Schwienbacher, E., J. A. Navarro-Cano, G. Neuner, and B. Erschbamer. 2011. Seed dormancy in alpine species. Flora-Morphology, Distribution, Functional Ecology of Plants 206:845–856.

Sedlacek, J., J. A. Wheeler, A. J. Cortés, O. Bossdorf, G. Hoch, C. Lexer, S. Wipf, S. Karrenberg, M. van Kleunen, and C. Rixen. 2015. The response of the alpine dwarf shrub *Salix herbacea* to altered snowmelt timing: lessons from a multi-site transplant experiment. PLoS ONE 10:e0122395.

Sexton, J. P., J. Montiel, J. E. Shay, M. R. Stephens, and R. A. Slatyer. 2017. Evolution of ecological niche breadth. Annual Review of Ecology, Evolution, and Systematics 48:183–206.

Sheth, S. N., and A. L. Angert. 2014. The evolution of environmental tolerance and range size: a comparison of geographically restricted and widespread *Mimulus*. Evolution 68:2917–2931.

Short, P. S. 2014. A taxonomic review of *Brachyscome* Cass.s.lat. (Asteraceae: Astereae), including descriptions of a new genus, *Roebuckia*, new species and new intraspecific taxa. Journal of the Adelaide Botanic Gardens 28:1–219.

Slatyer, R. A., M. Hirst, and J. P. Sexton. 2013. Niche breadth predicts geographical range size: a general ecological pattern. Ecology Letters 16:1104–1114.

Stanton, M. L., and C. Galen. 1997. Life on the edge: adaptation versus environmentally mediated gene flow in the snow buttercup, *Rannunculus adoneus*. The American Naturalist 150:143–178.

Valladares, F., D. Sanchez-Gomez, and M. A. Zavala. 2006. Quantitative estimation of phenotypic plasticity: bridging the gap between the evolutionary concept and its ecological applications. Journal of Ecology 94:1103–1116.

Venn, S. E., and J. W. Morgan. 2009. Patterns in alpine seedling emergence and establishment across a stress gradient of mountain summits in south-eastern Australia. Plant Ecology and Diversity 2:5–16.

Verdú, M., and A. Traveset. 2005. Early emergence enhances plant fitness: a phylogenetically controlled meta analysis. Ecology 86:1385–1394.

Wahren, C.-H., J. Camac, F. Jarrad, R. Williams, W. Papst, and A. Hoffmann. 2013. Experimental warming and long-term vegetation dynamics in an alpine heathland. Australian Journal of Botany 61:36–51.

Whitlock, M. C. 1996. The red queen beats the jack-of-all-trades: the limitations on the evolution of phenotypic plasticity and niche breadth. The American Naturalist 148: S65–S77.

Williams, J. W., and S. T. Jackson. 2007. Novel climates, no analog communities, and ecological surprises. Frontiers in Ecology and the Environment 5:475–482.

Williams, R. J., W. A. Papst, K. L. McDougall, I. M. Mansergh, D. Heinze, J. S. Camac, M. A. Nash, J. W. Morgan, and A. A. Hoffmann. 2014. Alpine ecosystems. Pages 167–212 *in* D. Lindenmayer, E. Burns, N. Thurgate, and A. Lowe, editors. Biodiversity and environmental change: monitoring, challenges and direction. CSIRO Publishing, Melbourne, Florida, USA.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.1964/suppinfo

DATA AVAILABILITY

Genbank references can be found in Supporting Information (see Table S2). Experimental reciprocal and common garden data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.1c045