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HABITAT SUITABILITY AS A LIMITING FACTOR FOR ESTABLISHMENT IN A NARROW ENDEMIC: *ABRONIA ALPINA* (NYCTAGINACEAE)

Meredith D. Jabis[1] and Tina J. Ayers[2]

ABSTRACT.—Understanding the causes of narrow endemism is crucial to conservation, particularly in biodiversity hotspots like the California Floristic Province. The loss of rare species as a consequence of climate change could result in substantial reductions in biodiversity, especially in high-elevation systems. We investigated causes of range restriction by using the narrow alpine endemic *Abronia alpina* (Ramshaw Meadows sand verbena) as a case study. This study examined habitat suitability as a limiting factor for the establishment of *Abronia alpina,* an endemic native to only 2 meadow systems in the Sierra Nevada Mountains, Inyo National Forest, California, USA. We tested habitat suitability by (a) using vegetation community composition and diversity as a proxy; (b) measuring key physical environmental characteristics (i.e., soil moisture, pH, soil texture, and surface soil temperature); and (c) establishing experimental field and greenhouse germination tests that exposed seeds to soils from several potentially suitable meadows. These 10 apparently suitable meadow systems were compared to the currently occupied meadow. Our results suggest that though there is some difference in suitable habitat among the 10 meadows studied, most meadows are relatively similar, for the rest of the measured parameters, to the native meadow. Vegetation community composition in the occupied meadow differed significantly from 8 of the surveyed meadows but was similar to 2 meadows. However, species diversity and richness in the native meadow did not generally differ from other surveyed meadows. Seven of 10 meadows were significantly colder than the occupied meadow, but 3 meadows with similar elevation ranges were equivalent. Range restriction does not appear to be a result of physical soil conditions, but cooler minimum temperatures may play a role. Although seeds only germinated in 2 of the tested meadows in field trials, dispersal limitation may be important in the species' restricted range, as seed germination was not significantly different among any meadow soils. Thus, nonhabitat factors, such as seed dispersal or recent speciation, may be the cause for the narrow range of *A. alpina.* Given stable climatic conditions, we recommend 3 meadow systems for establishment if recent population declines continue and relocation is deemed necessary. We also identify 7 other meadows that may be suitable, given a changing climate.

RESUMEN.—El comprender las causas de la limitación endémica es crucial para la conservación, particularmente en puntos calientes de biodiversidad como la Provincia Floral de California. La pérdida de especies poco comunes, como producto del cambio climático, podría resultar en una reducción sustancial de la biodiversidad, especialmente en sistemas de alta elevación. Investigamos las causas de la restricción de rango usando la especie alpina endémica *Abronia alpina* como estudio de caso. Este estudio examinó la idoneidad del hábitat como un factor restrictivo para el establecimiento de la *Abronia alpina,* una especie endémica de sólo dos praderas en las Montañas Sierra Nevada, Inyo NF, California, Estados Unidos. Analizamos la idoneidad del hábitat del siguiente modo: (a) usando la composición y la diversidad de la comunidad vegetal como representante; (b) midiendo características físicas medioambientales clave (tales como: humedad de la tierra, niveles de pH, textura de la tierra y temperatura de la superficie de la tierra); y (c) estableciendo pruebas de campo experimentales y de germinación en invernadero, exponiendo las semillas a tierras de varios prados potencialmente idóneos. Estos 10 sistemas de praderas aparentemente idóneos fueron comparados con el prado actualmente ocupado. Nuestros resultados sugieren que, aunque hay algunas diferencias en la idoneidad del hábitat entre los 10 prados estudiados, la mayoría de los prados eran relativamente similares a la pradera nativa, según el resto de los parámetros medidos. La composición de la comunidad vegetal en el prado ocupado difería significativamente de la composición de 8 de los prados analizados, pero era similar a 2 praderas. Sin embargo, la diversidad de las especies y la riqueza del prado nativo no diferían de otros prados medidos. Siete de los 10 prados eran significativamente más fríos que el prado ocupado, pero 3 prados con valores similares de elevación eran equivalentes. La restricción de rango no parece ser el resultado de las condiciones físicas del terreno, pero las temperaturas mínimas podrían jugar un papel importante. Aunque las semillas sólo germinaron en 2 de los prados analizados en las pruebas de campo, la limitación de dispersión puede ser importante en el rango de restricción de la especie, ya que la germinación de las semillas no era significativamente diferente de la del resto de los prados. Así, los factores no relativos al hábitat, como la dispersión de semillas o la reciente especiación, podrían ser la causa de la distribución limitada de *A. alpina.* Dadas las condiciones climáticas estables, recomendamos 3 sistemas de prados para su establecimiento si el reciente declive de la población continúa y se considera necesario un traslado, y hemos identificado otros 7 prados que podrían ser aptos, si hubiera un cambio en el clima.

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The cause of range restriction in both rare and endemic species has been intensively studied. Characterization of the life history traits of these often-threatened species is important to both the conservation of biodiversity and the effective management of such biodiversity, particularly in biodiversity hotspots such as the California Floristic Province (CFP), which includes 2124 endemics out of 3488 native vascular plant species (Myers et al. 2000). Several empirical studies have quantified predictable characteristics of endemic species, such as deficiency in resource acquisition or competitive ability (Lloyd et al. 2003, Lavergne et al. 2004), reduced reproductive rates (Byers and Meagher 1997, Kunin and Shmida 1997), or reduced genetic variability (Karron 1987, Barrett and Kohn 1991, Ellstrand and Elam 1993, Hamrick and Godt 1996, Gitzendanner and Soltis 2000, Cole 2003). These species also exhibit narrow environmental tolerance (Lesica 1992, Lloyd et al. 2003). For example, endemics are associated with higher elevation habitats, infertile soils, and more stressful environments (Kruckeberg and Rabinowitz 1985, Cowling et al. 1994, McDonald and Cowling 1995, Kessler 2000, Odeja et al. 2001, Wolf 2001, Lavergne et al. 2004). There is an almost equally large body of literature that suggests that particular physiological or reproductive traits may contribute to rarity. Rare plants are self-compatible or pollinator limited and have lower reproductive investment, slower growth rates, smaller seed size, lower seed set, shorter growth forms, and shorter flowering seasons compared to closely related common species (Wilson 1976, Harper 1979, Hodgson 1986, Fiedler 1987, Aizen and Patterson 1990, Lahti et al. 1991, Kunin and Gaston 1997, Cowling et al. 1994, Byers and Meagher 1997, Kunin and Gaston 1993, Lloyd et al. 2003, Lavergne et al. 2004). Narrow endemics, such as *Abronia alpina* (Ramshaw Meadows sand verbena), that exhibit some or all of the above characteristics may be especially prone to extinctions caused by a changing climate (Primack and Miao 1992). To effectively manage and conserve these most vulnerable species, it is necessary to clarify which of these listed characteristics or mechanisms are relevant and identify suitable habitat where each species exists.

To identify suitable habitat, plant associations between 2 locations can be compared to indicate similar environmental filters acting at a site (Keddy 1992). Successful plant colonization requires overcoming the selection pressures of abiotic stress, disturbance, and competition (Grime 1977). In addition, as the environment becomes more stressful, positive interactions such as facilitation are thought to be particularly important to survival and may be especially relevant in harsh alpine environments (Bertness and Callaway 1994, Callaway et al. 2002). These interacting forces of site and biotic elements undoubtedly structure plant composition. Though measuring physical site characteristics, such as soil moisture, pH, texture, and temperature, is important, it can be difficult to quantify all of the necessary environmental variables that may determine whether a site will provide suitable habitat. Therefore, a comparison of species assemblages themselves or diversity indices may assist in determination of site equivalence.

Endemic species could be range restricted due to habitat specificity, but they can also be localized due to other processes, such as recent speciation, creation of relict populations by glaciation (i.e., vicariance), or long-distance dispersal (Hodgson 1986, Lahti et al. 1991, Thompson et al. 1999, Fenner et al. 2001, Lloyd et al. 2002, 2003). Reduced dispersal abilities in some rare plants have been suggested by their absence from apparently suitable sites (Kruckeberg and Rabinowitz 1985, Shaw and Burns 1997, Wiser et al. 1998). Broad dispersal into unsuitable or highly competitive habitat would not confer a fitness advantage (Gaston 1994)—a possible explanation for observed low dispersal capacity. Thus, the hypothesis of directed dispersal suggests that seed dispersal is adapted to allow seeds to reach suitable habitat (Howe and Smallwood 1982, Venable and Brown 1993). This form of dispersal is thought to be particularly important for edaphic endemics like *A. alpina.* In a comparative study of 9 species of *Abronia* in California, Wilson (1976) suggested dispersal as a potential factor limiting the breadth of the species' range. *Abronia alpina* seeds lack the winged appendages found in many members of the genus, and seeds fall directly below the mother plant, which often touches or covers the ground and may prohibit movement of seeds by wind or runoff. Narrowly endemic plants with seed dispersal limitations may be especially sensitive to a changing climate.

Abronia alpina inhabits the southern Sierra Nevada of California, a region of the CFP that
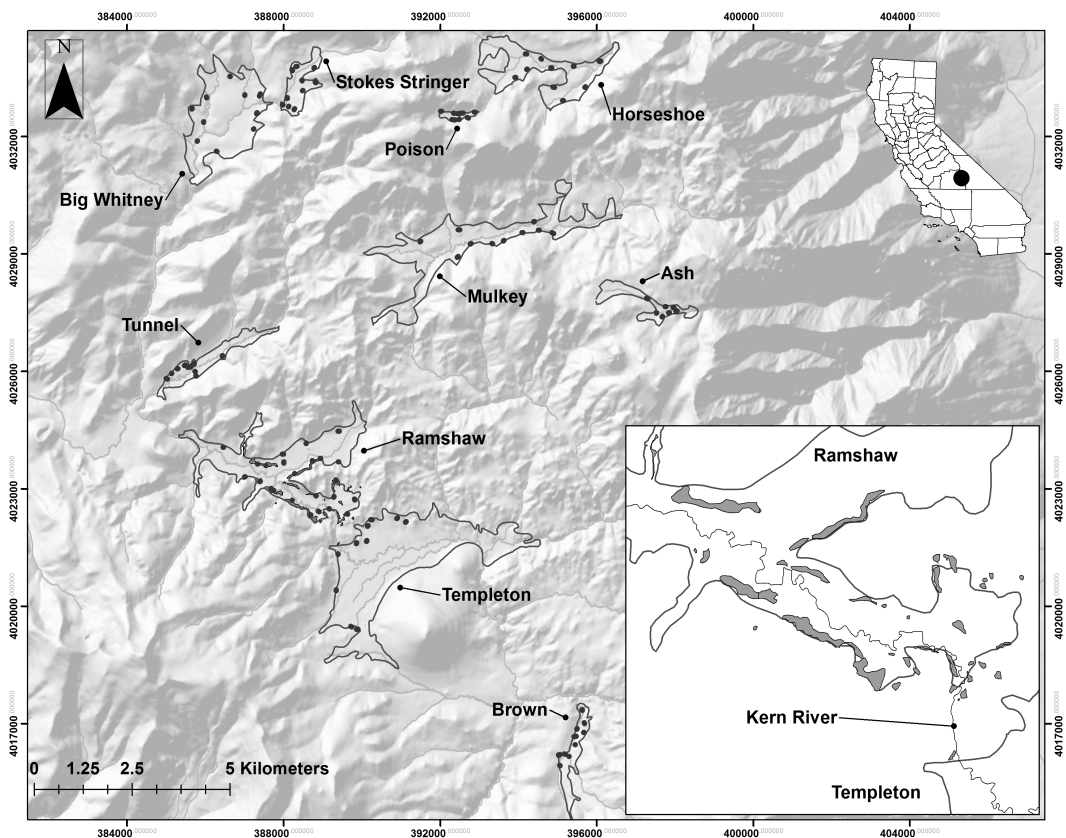
Fig. 1. Study region within the Golden Trout Wilderness, including the 10 meadow systems sampled in this study. Black dots indicate transect locations, meadows are outlined in black, and *Abronia alpina* subpopulations (gray polygons) are visible in the inset along with the South Fork of the Kern River, connecting the single Templeton subpopulation.

is species rich (Shevock 1996, Davis et al. 1997). The species was first documented by Brandegee in 1899, and whether its range was once larger is unclear, because of potential discrepancies between the original geographic reference and the current place names. The species is currently restricted to sandy, arkosic gravel margins between sagebrush scrub and lodgepole pine forest on the edges of 2 meadows, Ramshaw and Templeton, at an elevation of approximately 2680–2740 m (Fig. 1). The total population covers a combined area of approximately 6 ha. Because of its limited range, the plant is a Candidate 1 species for the Endangered Species List. Although endemic to this narrow habitat type (Wilson 1970), *A. alpina* has a relatively large population that ranges from a high of 132,000 individuals in 1987 to a low of 55,410 individuals in 2003 (Fig. 2). The single population is

divided into 34 subpopulations based on breaks in suitable habitat. Previous studies have indicated that the species is an obligate outcrosser that maintains substantial genetic diversity (Jabis et al. 2011), although it is still unclear why the species is so range restricted.

Abronia alpina does not exhibit many of the typical life history characteristics associated with rarity or endemism. Its relatively large population size, mating system, and high genetic diversity (Jabis et al. 2011) suggest that the species has the potential to colonize new sites, so it is unclear why the species is not found in several nearby meadows with apparently similar habitat. Perhaps the nearby meadows have subtle habitat differences that preclude population establishment. We examined 3 questions: (1) whether biotic structure, measured as vegetation community composition, species richness, and diversity, differs between occupied
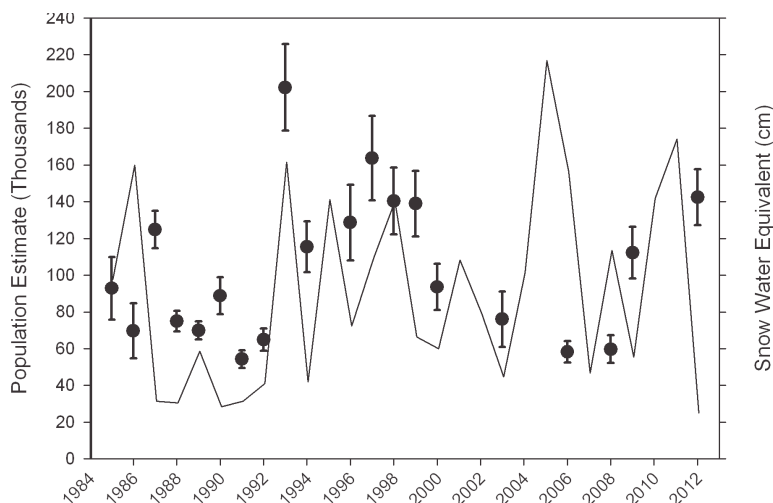
Fig. 2. *Abronia alpina* population estimates from 1985 to present (black circles) plotted with precipitation data in the form of snow water equivalents (black line). Missing data points are from years during which the population was not sampled; whisker bars represent the 95% confidence interval.

sites and nearby unoccupied meadows; (2) whether environmental variables, including soil moisture, pH, texture, and surface soil temperature, differ between the occupied meadow (Ramshaw Meadow) and 10 similar meadow systems (because the subpopulation sizes of *A. alpina* are prone to large interannual fluctuations, we also investigated whether precipitation variability could predict population variability); and (3) whether dispersal is a limiting factor in *A. alpina* establishment. We addressed this question indirectly with a field and a controlled greenhouse germination trial to remove dispersal constraints and isolate any potential site filtering or limitations. If dispersing seeds can reach habitat in these other meadow systems, we would expect germination and growth if the habitat were truly suitable.

Understanding the causes of range restrictions for narrow endemics like *A. alpina* will enable successful management, particularly given the potential for climate change to force alpine species upward in elevation (Parmesan and Yohe 2003). Isolating other potential sites for assisted migration will be crucial for species with limited ranges, for those species may be threatened with extinction in a changing climate (Primack and Miao 1992, Parmesan and Yohe 2003, Thomas et al. 2004). Finding potential sites is particularly important because in the California Floristic Province, up to 66% of species are expected to experience 80%

reductions in climatically suitable range size (Loarie et al. 2008).

METHODS

Study Sites

Ramshaw Meadow, occupied by *A. alpina,* is a high-elevation meadow (~2680–2740 m) located in the Golden Trout Wilderness, Inyo National Forest, Tulare County, California, USA. Also occupied is a small portion of Templeton Meadow adjacent to the entry of the south fork of the Kern River from Ramshaw Meadow (Fig. 1). Other meadows sampled were located within a 32-km radius of Ramshaw, and they range from 2590 to 2990 m in elevation. The sandy margin habitat on which *A. alpina* grows is thought to be maintained by the decomposition of granite rock outcroppings upslope (Wilson 1970). Subpopulations are located between wet meadow or sagebrush scrub habitats and upslope lodgepole pine forest. The soil is porous and very well drained. Average annual precipitation in the region is approximately 76.2 cm (CDWR 2014), with most falling in the winter as snow. These meadows can experience winter snowpacks of up to 2 m during heavy precipitation years (CDWR 2014).

Vegetation and Environmental Sampling

To determine the vegetation composition of suitable habitat for *A. alpina,* we randomly

chose 10 sandy margin sites within Ramshaw Meadow where the species occurs and established 2 random transects within each site. To compare the habitat of *A. alpina* with other potential sites, we chose 9 other unoccupied meadows with habitat similar to Ramshaw Meadow (Fig. 1). Since the second meadow where *A. alpina* occurs (Templeton Meadow) maintains only one subpopulation that is not replicated, this meadow was also treated as unoccupied and was included with all other meadows sampled. In addition, within the native Ramshaw Meadow, both "occupied" sites (sandy margin sites with *A. alpina* subpopulations) and "unoccupied" sites (sandy margin sites that do not support subpopulations) were included for a total of 220 transects in 11 "meadows."

Along each transect, three 1 × 1-m quadrats were established at 0 m (adjacent to the sagebrush/meadow edge), 10 m, and 20 m (moving toward lodgepole pine forest). Percent cover of biotic and abiotic elements were recorded in each quadrat. Abiotic factors sampled included sand, rock, and litter. Cover of each plant species was recorded as a percent of total area. Unknown species were vouchered and identified to species level at the Deaver Herbarium, Northern Arizona University, Flagstaff, Arizona (Appendix).

Of the abiotic factors that could limit seedling establishment, we measured soil moisture, slope, texture, pH, and temperature. Soil moisture and temperature are especially important for germination and subsequent growth; slope and texture can influence soil moisture content; and pH can limit plant development via nutrient availability (Singh and Agrawal 2008). We sampled soil moisture in the center of each quadrat in June and July 2007, using a Moisture Point 917 (Environmental Sensors, Inc., Sidney, Canada), which employs time-domain reflectometry to measure average volumetric water content (Sun et al. 2000). We measured slope using a Suunto Tandem Compass Clinometer (Suunto, Vantaa Finland). At the first quadrat of each transect we recorded slope and collected soil samples for the germination study, soil pH, and textural analyses. We recorded soil temperature using one Log-Tag temperature data logger (LogTag Recorders, Aukland, New Zealand) placed in each meadow under 2.5 cm of soil. Data loggers were located in sites with an eastern-facing aspect and were set to take 11 readings per day for 365 days.

To test soil pH, we processed samples using a calcium chloride protocol (Carter 1993) that used an ORION 720A pH meter (Thermo Scientific, Waltham, MA). We performed soil texture analyses by using the hydrometer method (S. Hart personal communication), which resulted in a percentage of sand, silt, and clay for each soil sample.

Field and Greenhouse Germination Trials

Abronia alpina fruits, one-seeded anthocarps enveloped in the base of perianth tissue, were collected during the summer of 2007 and 2008 and were used for both field and greenhouse trials. Fruits were collected from dry, mature, brown anthocarps and from dry, green, but potentially slightly immature anthocarps. Seeds were randomly collected from 18 of 34 subpopulations and were combined in equal proportions to ensure sampling from a variety of plants and locations. Approximately 20 seeds were collected from each individual plant, resulting in a total of approximately 136 mother plants and approximately 5 plants per subpopulation.

The field germination trial involved sowing seeds into each of 6 meadows and sowing an additional set into unoccupied sites in Ramshaw. All seeds were monitored using 2.5 × 16-cm plug cells filled with native soil and placed in the ground. Soil was extracted using a 38 × 5-cm PVC tube pounded into the ground to remove soil while maintaining soil horizons and minimizing disturbance to the natural structure. Four seeds were placed in each cell, and 3 cells were placed in each of the 6 meadows. The field trial was established in August 2007, and all cells were examined for germinants in July and August 2008. Four of these meadows, in addition to Ramshaw unoccupied sites, were replenished with seeds and monitored again for germination in June and July 2009.

A greenhouse trial was used to isolate whether soils alone, irrespective of climate, were different enough to affect germination. Seeds were dried in paper envelopes and stored in a freezer at –2.2 °C for 3.5 months. Seed viability was tested on 60 random seeds collected in 2007 and 144 random seeds collected in 2008. The viability testing procedure used a 1% solution of tetrazolium chloride and

followed a protocol modified from the Tetrazolium Testing Handbook (Peters 2000). Following preliminary germination trials, the remaining 1320 seeds were cold stratified at 2.8 °C for one month between 2 pieces of thoroughly wet paper towel sprayed with Consan20 fungicide (Voluntary Purchasing Group, Bonham, TX). When at least 5 of the seeds were observed germinating in cold stratification, it was assumed that all seeds were prepared to initiate germination, and the greenhouse trial commenced. Seeds from brown anthocarps were kept separate from seeds with green anthocarps to assess the importance of this difference for future seed collection and germination. Two greenhouses were used in the study. The first was kept within a relatively constant temperature range of 21–24 °C during spring germination—March through July. To determine whether extreme daily fluctuations (which the species would experience under natural conditions) were important for germination, the second greenhouse was maintained at ambient temperatures that ranged from approximately 26 to 38 °C daily highs and –3 to 12 °C evenings. Thirty soil samples were collected in the field. Each sample was used to fill 4 plug cells. Two of these plugs were placed in each greenhouse, and each plug was given a seed from one of 2 anthocarp types. Because we tested 2 greenhouse environments and 2 types of anthocarps, 120 soil plugs were filled with soil from each meadow. One seed was placed in each plug container. The greenhouse trial was checked each week for new *A. alpina* germination.

Data Analysis

Abiotic and biotic data were averaged across quadrats for each transect, and the 2 transects were also averaged for a total of 10 independent samples per meadow. Species accumulation curves were generated for each meadow to determine sampling effectiveness. Population estimates of *A. alpina* were obtained from the USDA Forest Service (S. Weis personal communication; Fig. 2).

Nonmetric multidimensional scaling (NMDS) ordination was used to visually compare community composition among meadow transects. For this community data set, we chose Sørensen (Bray–Curtis) distance, a proportional cityblock distance measure capable of handling data sets with multiple zero values (McCune and Grace 2002). We used the slow and thorough autopilot NMDS ordination method, which allows a maximum of 400 iterations, sets an instability criterion of 0.00001, and uses a potential of 6 axes to plot the data to minimize stress among the data points in reduced space.

Statistical analyses of community composition were performed in PCORD5 (McCune and Mefford 2006) using a permutational multivariate analysis of variance (PERMANOVA). An overall test and pairwise tests were conducted to compare unoccupied to occupied sites. Bonferroni corrections were applied to pairwise tests. Both the ordination and the PERMANOVA are nonparametric and suited to community data, which are often nonnormal and contain many zero values (Peterson and McCune 2001, McCune and Grace 2002). PERMANOVA allows partitioning of the variance of the distance matrix while preserving the distribution-free qualities of nonparametric tests. The test statistic is calculated directly from the distance matrix, and *P* values are obtained using random permutations of the data (Anderson 2001). In addition, the correlation coefficients between dominant vegetation and the ordination axes were scrutinized to determine which species could be influencing the assemblages in ordination space. To analyze species diversity across meadows, Shannon's diversity index was calculated in PCORD5 based on percent cover values for each meadow. Species diversity and richness measures from each meadow were compared with Ramshaw occupied sites by using PERMANOVA.

Environmental variables were analyzed in 3 main ways. First, all environmental variables except for temperature were combined in a single analysis across meadows by using a PERMANOVA to compare each meadow to the control. Second, soil moisture, texture, pH, and slope were then analyzed individually using PERMANOVA to determine whether some environmental variables were offsetting otherwise statistically significant differences in others. Finally, we used PCORD5 to determine which environmental variables were correlated with at least 9% of the variation of an ordination axis (Laughlin and Abella 2007).

Temperature was analyzed separately from other environmental variables because only one data logger was placed in each meadow. The analyses were performed on meadows by month using a 2-factor PERMANOVA in PCORD5.

TABLE 1. Number of species, mean percent cover, species accumulation curve final slope (SPAC), and the community composition and diversity results for each meadow system. Average distance values (Sørensen's distance) are given for community composition comparing all meadows with native Ramshaw Meadow (*C*). Also given are average Shannon's diversity index values (*H*) and average richness values (*S*); significance was evaluated using PERMANOVA. Bonferroni corrected α = 0.005. Values for the native meadow (Ramshaw occupied) are set in bold, italicized text

Meadow	Species	% Cover	SPAC	*C*	*H*	*S*
Ramshaw occupied	*17*	*16.3*	*0.7*	*0*	*1.56*	*7.6*
Ash	19	15.4	0.3	*0.59	1.64	7.9
Big Whitney	18	19.3	0.4	*0.64	1.62	7.8
Brown	23	20.4	1	0.30	1.52	7.9
Horseshoe	13	13.6	0.5	*0.67	1.44	6.3
Mulkey	18	16	0.6	*0.58	1.71	7.9
Poison	23	18.1	0.7	*0.53	1.78	9
Ramshaw unoccupied	13	16.9	0.4	0.22	1.45	6.2
Stokes Stringer	16	16.4	0.3	*0.74	1.57	7.1
Templeton	15	13.5	0.5	0.27	1.28	5.8
Tunnel	14	13.5	0.4	*0.51	1.40	*5.4

*Indicates meadows that are significantly different from the native meadow (Ramshaw occupied).

Each month was analyzed across meadows by using a single-factor PERMANOVA to determine whether temperatures of particular months were important for germination, dormancy, or establishment.

We tested whether population estimates collected over a 23-year period were correlated with precipitation in the form of winter snow by using simple linear regression on snow water equivalents (JMP, Version 8; SAS 1989–2008). We also analyzed time lags using 1- and 2-year prior snow water. Precipitation data were obtained from the California Department of Water Resources historical data set for Ramshaw Meadow (CDWR 2014).

Counts and percentage of seed germination and viability were calculated for each germination trial (field and lab) and by meadow. Seed germination was compared by meadow using a chi-square test and by greenhouse using PERMANOVA. Nonparametric tests were used because the data set contained a large number of zeros due to low overall germination rates.

RESULTS

Site Composition

Forty-one species from 20 families were recorded in the study (Appendix). Many of the species accumulation curves for each meadow approach a slope of zero (Table 1), indicating that most of the species present at each site had been adequately sampled, with the possible exception of Poison, Brown, and Ramshaw occupied sites (final slopes 0.7, 1.0, and 0.7, respectively). The first and second-order jackknife estimates, respectively, predict the pres-

ence of 50.9 and 57.8 species in all meadows. Between 31% and 56% of all recorded species were found in each meadow, and mean cover ranged from 13.5% to 20.4%, with decomposed granite occupying most of the rest of the ground surface (Table 1).

Community Composition and Diversity Indices

In pairwise comparisons, Ramshaw Meadow plant community composition was significantly different from that in 7 meadows ($F_{10, 99}$ = 6.09, $P < 0.005$ in all pairwise comparisons; Fig. 3) but was not different than Brown, Templeton, and unoccupied sites within Ramshaw ($F_{10, 99}$ = 6.09, P = 0.12, 0.11, and 0.03, respectively). The final ordination represented 79% of the information in the original distance matrix with 30.5% loaded on axis 1, 28.5% on axis 3, and 20.2% axis 2. (final stress = 16.61546, final instability = 0.00366). A 3-dimensional solution was selected beyond which additional dimensions provide only a small reduction in stress. The 2 axes that explained most of the variation (1 and 3) were chosen for graphing. Seventy-nine percent of the total variation in community composition was captured in the ordination analysis, with 7 primary species explaining a large fraction of the variation (Table 2). *Lupinus breweri* was most closely associated with Ramshaw occupied sites followed by *Eriogonum spergulinum* and *Orochaenactis thysanocarpa.* Diversity measures show a different pattern from the community data. No meadows were significantly different from Ramshaw Meadow when examined using
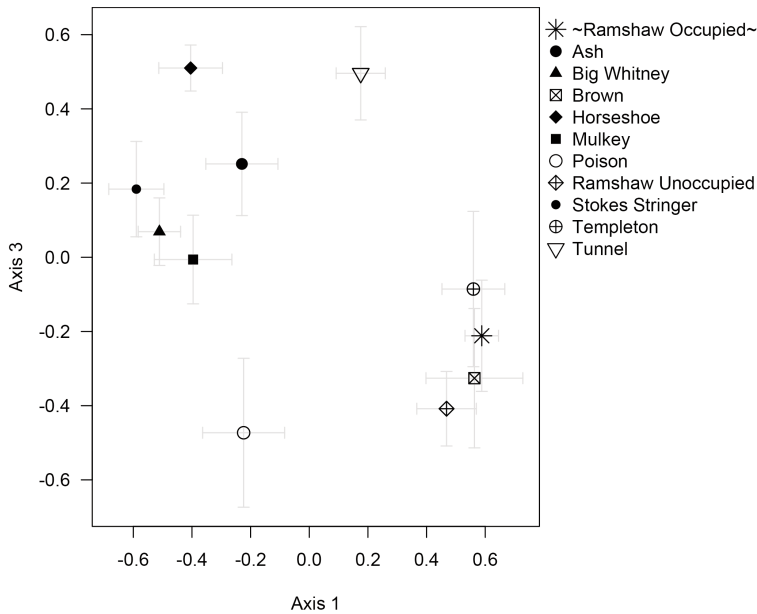
Fig. 3. In this NMDS ordination, each point represents the average location for each meadow, and standard error bars represent the variability of transects within a meadow. Meadows with similar community composition are represented as points that are in close proximity, whereas communities that are less similar are represented by points that are farther apart. A clear grouping of points in the lower right quadrant depicts 4 areas with similar community composition: Ramshaw occupied, Ramshaw unoccupied, Brown meadow, and Templeton meadow (P = 0.1240 and 0.0144, respectively, using PERMANOVA; all other comparisons had a probability of >0.005).

TABLE 2. Correlation coefficients for the species and ordination axes that explained most of the variation in the original distance matrix. Bold text indicates cells with the strongest correlation.

Species	r, Axis 1	r, Axis 3
Cistanthe umbellata	**0.70**	0.15
Oreonana clementis	**−0.72**	0.43
Hulsea vestida	**−0.55**	0.33
Achnatherum occidentale	0.32	−0.21
Lupinus breweri	**0.55**	**−0.85**
Eriogonum spergulinum	0.02	−0.25
Orochaenactis thysanocarpa	0.03	−0.20

Shannon's diversity index ($F_{10,99}$ = 0.0078, P > 0.002 for all meadows, Bonferroni corrected α = 0.005), and only Templeton Meadow (P = 0.0004) was different with respect to richness ($F_{10,99}$ = 0.0004, P > 0.002 for all other meadows, Bonferroni corrected α = 0.005; Table 1).

Environmental Variables

We found only minor environmental differences among most meadows and the native meadow. The combined analysis of environmental variables, including soil moisture, pH, texture, and slope, indicated that no meadows were significantly different from the native meadow ($F_{10,99}$ = 2.1, pairwise P > 0.007, Bonferroni corrected α = 0.005; Table 3). When environmental variables were tested separately, 3 meadows—Ash, Horseshoe, and Big Whitney—were different from Ramshaw for only one or 2 variables each: pH/texture, slope, and soil moisture, respectively (Table 3). No correlation was found between any environmental variable and the ordination axes, indicating that none of the environmental variables measured were driving community composition patterns (r^2 = 0.120 or lower for each axis). The ordination was driven primarily by community differences, not environmental variables.

In Ramshaw Meadow, summer temperature highs ranged from 32 to 35 °C and lows from 4 to 10 °C. Winter temperature highs ranged from −3 to −1 °C and lows from −12 to −4 °C. The overall analysis (PERMANOVA) of temperature by month indicated that 6 of 9 meadows were significantly different from the native Ramshaw Meadow; the 3 similar meadows had similar elevation ranges: Brown, Tunnel, and Templeton ($F_{9,81}$ = 52.3, P = 0.001; Fig. 4). Multiple one-way analyses of each month indicate that

Table 3. Mean soil environmental variables, including soil moisture, slope, pH, and texture, as well as results of one-way analyses. Average distance values are given for a combined multivariate test (Combined). All comparisons use a Bonferroni corrected α of 0.005. Values for the native meadow (Ramshaw occupied) are set in bold text.

Meadow	Soil moisture	Slope	pH	% Sand	% Silt	% Clay	Combined
Ramshaw occupied	**4.28**	**9.1**	**4.56**	**93.29**	**5.43**	**1.27**	**0**
Ash	4.67	8.75	*4.28	*85.52	*9.31	*5.17	0.070
Brown	4.47	10.85	4.44	88.35	7.03	4.62	0.050
Big Whitney	4.72	*5.6	4.65	89.15	7.28	3.57	0.053
Horseshoe	*4.70	6.55	4.56	90.39	6.43	3.18	0.038
Mulkey	4.41	8.35	4.57	90.42	6.56	3.02	0.028
Poison	4.57	9.85	4.28	90.57	6.35	3.08	0.029
Ramshaw unoccupied	4.27	9.75	4.62	92.27	8.09	−0.37	0.022
Stokes	4.32	6.35	4.51	93.401	4.9	1.69	0.017
Templeton	4.17	9.6	4.42	89.84	7.28	2.88	0.033
Tunnel	4.46	7.65	4.66	90.12	6.97	2.91	0.034

*Indicates meadows that are significantly different from the native meadow (Ramshaw occupied).

no more than 6 meadows differed from Ramshaw for any given month, and no meadows differed in June, July, or November. In addition, all meadows that differed from Ramshaw were slightly cooler in temperature overall, except for springtime when 2 of 6 were slightly warmer. Finally, regressions of population and precipitation indicated that precipitation, in the form of winter snow, was not strongly related to population fluctuations (P = 0.27, 0.16, 0.73 for prior year, 2 years prior, and 3 years prior, respectively; Fig. 2).

Field and Greenhouse Germination Trials

Abronia alpina seedlings were recorded in 3 meadows that were replenished with seeds and retained into 2009: 1 in Tunnel, 2 in Templeton, and 1 in the Ramshaw occupied site. However, all field trials in 2008 failed to produce any germinants that survived until the survey date, including the native meadow site. In the greenhouse, the overall germination rate was extremely low: 7% germination for 1320 seeds. Greenhouse survival was relatively high, at 78%, during the 7 months of the study. Seed viability, tested using tetrazolium chloride, was 63% in 2007 (n = 60) and 61% in 2008 (n = 141) overall. Seed germination was not significantly different by meadow soil overall (Fig. 5; χ^2 = 13.27, P = 0.21). In addition, seed germination did not differ by greenhouse ($F_{1,118}$ = 0.29, P = 0.59).

Discussion

Biotic and Environmental Constraints

Vegetation establishment is a product of particular biotic and abiotic conditions, and untangling the effects of each is often difficult. Species assemblages can provide information about the environment, as many species of plants are indicators of specific environmental states, and comparable plant composition can imply habitat similarity. Community composition is also a result of biotic interactions that may not be accounted for in a comparison of the environment alone. The ordination suggested that community composition revealed differences in habitat that environmental variables alone did not uncover, as composition explained more variation in the ordination than did the environmental variables. If community composition is a reliable indicator of habitat suitability, it appears that only 2 of the meadows, Brown and Templeton unoccupied sites, would be appropriate sites for establishment of *A. alpina* under current climatic conditions, because the 7 other meadows had significantly different community compositions from the occupied sites. Vascular plant diversity, however, was roughly similar among all sites. Community assemblage is likely more crucial in evaluating site suitability, as diversity indices do not elucidate differences in species identity. Like many other narrow endemic and alpine species, *A. alpina* appears to require particular biotic associations (Callaway et al. 2002). Because mother plants often appear to protect seeds in the wild, *A. alpina* may require a host-plant association to facilitate germination and survival of seedlings. In addition, natural germination appears higher near mature plants (Jabis personal observation), perhaps due to adult plants acting as seed traps. Alternatively, increased competition may limit establishment
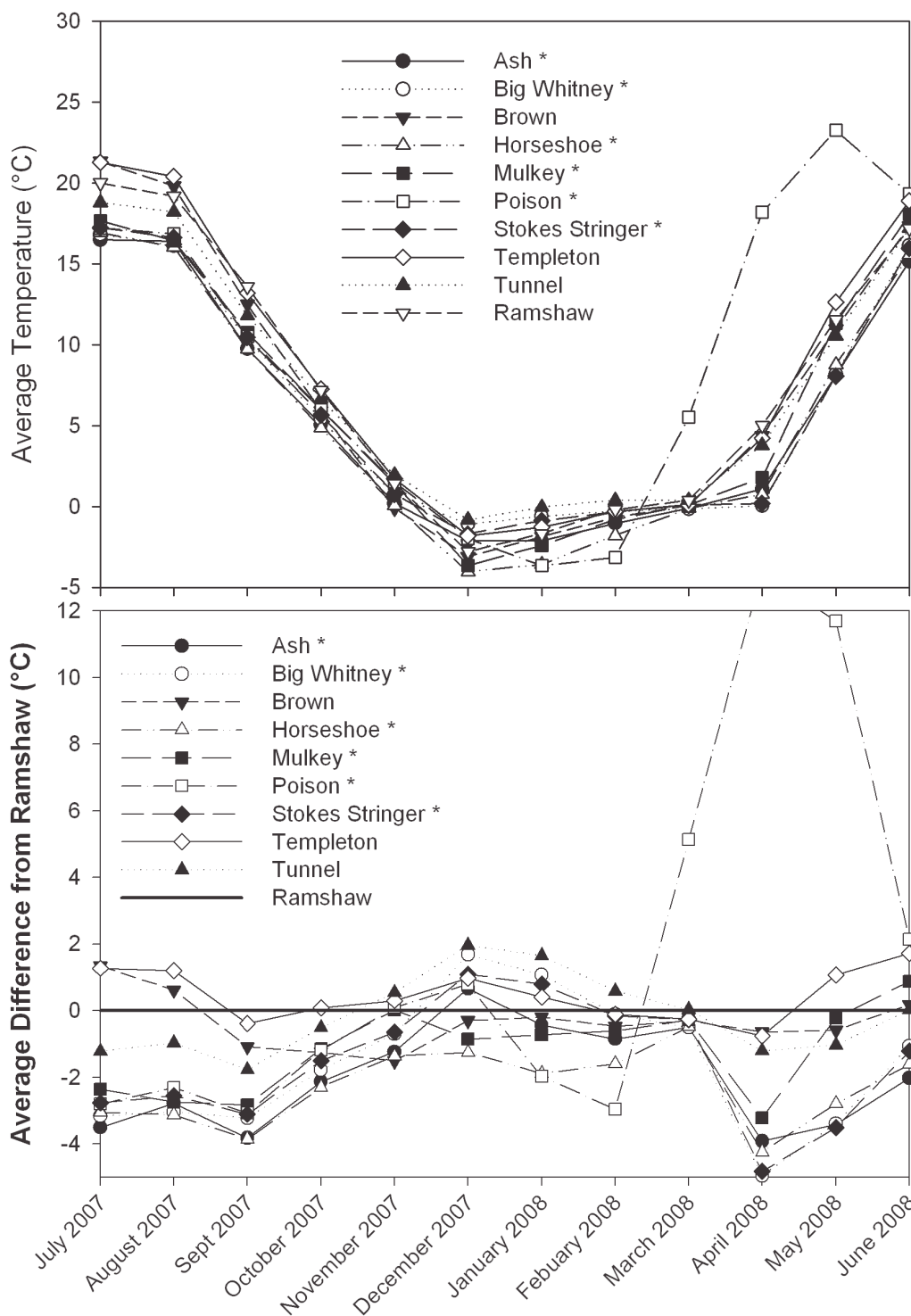
Fig. 4. Average monthly temperature (top panel) and differences in temperature from Ramshaw meadow (bottom panel) for one year, July 2007–June 2008. An asterisk (*) indicates that the meadow is significantly different in average monthly temperature from the native meadow. Measurements from Poison meadow from February to June 2008 may be incorrect due to surfacing of the data logger.
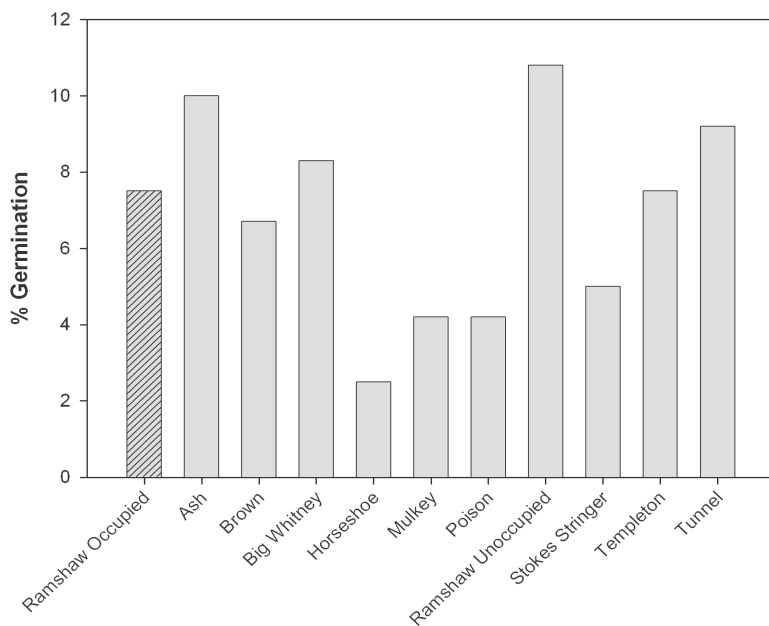
Fig. 5. Seed germination in each meadow soil in a controlled greenhouse experiment; $n = 120$ seeds for each meadow.

into other meadow systems, but this alternative explanation is unlikely because plant cover is low, approximately 16% on average in the harsh and infertile decomposed granitic habitat.

Most meadows were not different in environmental conditions overall, which may suggest that some other process not explored explicitly in this manuscript may be responsible for the limited range of the species. The absence of *A. alpina* in these meadows implicates physical mechanisms such as seed dispersal or past range contraction as potential causes of range limitation. Alternatively, biotic constraints such as herbivores, pathogens, and seed predators or lack of interspecific facilitators such as pollinators, soil microbes, or fungi could be responsible for the narrow range of this species. Previous work indicates that *A. alpina* is an obligate outcrosser dependent on pollinators for successful reproduction and seed set (Jabis et al. 2011); however, the observed floral visitors were relatively common insect species not necessarily limited in abundance, so *A. alpina* is not likely pollinator limited.

Ramshaw meadow was similar to most other meadows in the study with respect to soil characteristics that could permit seed establishment and germination (Table 3), with the potential exception of 3 meadows: Ash, Big Whitney,

and Horseshoe. This implicates that seed dispersal rather than soil characteristics may limit establishment. When soil temperature was considered, 6 of 9 meadows were apparently different from the native Ramshaw Meadow (Fig. 4). Of these 6 meadows, all were slightly cooler overall and higher in elevation. Though cooler conditions may not affect seed dormancy, or seedling establishment and growth, these meadows may be too cold to allow successful germination, except for Poison and Stokes Stringer meadows, which were warmer in the spring. In a climate-warming scenario, however, these cooler meadows may be excellent sites for potential relocation. Three meadows with similar elevation ranges—Brown, Tunnel, and Templeton (Fig. 4)—were not different from Ramshaw, and the *A. alpina* germination at Tunnel and Templeton suggests that both meadows would provide appropriate sites for relocation under current climatic conditions. This gradient of meadow systems with varying elevation ranges will therefore provide a host of opportunities for the species to be resilient to climate change, provided assisted migration is possible.

Like other rare species, *A. alpina* experiences large fluctuations in population size. Winter snowpack, which provides the bulk of precipitation to the system, does not appear to predict

these population fluctuations, although spring observation suggests that late snowmelt or early spring rain may enhance seedling germination. These nuances could not be tested due to a paucity of precipitation data for this remote field site. Because many endemics are found in disturbance-prone or early successional habitats (Lesica 1992, Lavergne et al. 2004), future work should investigate 2 potential sources of disturbance: temperature fluctuations that may cause severe frost-heave action or gopher disturbance, both of which may promote seed dispersal. Additionally, because *A. alpina* is an obligate outcrosser, changes in annual pollinator abundance or activity could cause population fluctuations (Fernandez et al. 2012).

Seed Germination and Dispersal Implications

The failure of most field seed germination trials reduces our ability to predict whether seed dispersal is a factor limiting the species' range; however, weak germination in Templeton and Templeton Meadows suggests this process is likely a constraint. Because the soils themselves do not appear to limit colonization of *A. alpina,* limitation via bacterial or mycorrhizal associations is not likely. However, these processes may explain low observed germination. Greenhouse germination rates were probably suboptimal because there was no protocol for this species. If future studies require propagated seedlings, we recommend longer cold stratification on the order of 3 to 4 months and germination in cold stratification prior to transplant. It does not appear to matter whether seeds are collected from green or brown anthocarps, as long as the anthocarps are dry on the plant when collected.

Many studies support seed dispersal as a mechanism for the limitation of a species range. Lloyd et al. (2002, 2003) suggest that within short-statured species, taller culm length is associated with a higher release of seed and greater dispersal distance; common species had greater culm length. Seeds without specialized dispersal structures achieve shorter dispersal distances, and according to dispersal theory, longer dispersal distances are associated with faster range expansion (Oakwood et al. 1993, Willson 1993, Kelly et al. 1994, Edwards and Westoby 1996, Levin et al. 2003). However, the importance of remaining on suitable habitat may outweigh benefits of long-distance dispersal (Levine and Murell 2003).

In a comparison of 9 species of *Abronia* in California, the only endemic species in the study, *A. alpina,* had the least specialized dispersal mechanisms and the poorest dispersal capability. Dispersal structures were reduced or absent in *A. alpina,* while many other species had winged appendages (Wilson 1976); reduced dispersal capacity apparently kept the species on suitable habitat and out of more fertile, competitive sites. Because the accessory costs of dispersing and maturing a seed are suggested to be 73% of total reproductive allocation (Lord and Westoby 2006), it is not surprising that rare species may have reduced investment in long-distance dispersal and greater investment in directed dispersal to local suitable habitats. This theory is consistent in this system in 2 ways. First, germinants were often observed adjacent to mature plants (Jabis personal observation), and second, the single subpopulation in Templeton Meadow may be the product of a rare long-distance dispersal event via the Kern River that drains from Ramshaw into Templeton Meadow (Fig. 1).

Endemic Species Predictions
and *Abronia alpina*

The Sierra Nevada provides a suitable study site within North America to investigate patterns of endemism because these mountains cover approximately 20% of the landmass in California and contain over 50% of the state's flora (Shevock 1996). Understanding the causes of range restriction in rare endemic species is important because proper management of these species is critical to mitigation of their increased extinction risk from climate warming (Parmesan and Yohe 2003, Thomas et al. 2004). Narrow endemism can be a result of habitat specificity, reduced competitive or colonization abilities, lower reproductive rates, reduced genetic variability, or limited dispersal. For *A. alpina,* genetic diversity and breeding system do not appear to cause reduced seed production. Therefore, the species' habitat preferences may result from low competitive ability, causing the species to colonize sites with relatively low fertility and fewer competitors. Directed dispersal is likely, and it has been suggested that lineages with limited long-distance dispersal capability will split into a larger number of species over time, each with a narrow geographic range (Oakwood et al. 1993). The genus *Abronia* has 2 other members, both of which

are endangered endemics and thus lend credence to this theory. Adaptation to stress or small-scale habitat differentiation has been implicated as a cause for speciation because both lead to isolation of populations (Chapin et al. 1993, Kessler 2000). It is possible that *A. alpina* is the result of this type of speciation event following long-distance dispersal.

Conclusions and Future Work

The results of this study indicate that 3 meadows (Brown, Templeton, and Tunnel) are suitable sites for *A. alpina* establishment given current climatic conditions. Competition in these relatively infertile soils appears to be low; instead, facilitation from plant associates via habitat amelioration is a more likely mechanism explaining occupancy. Since a previous study indicates the species is quite genetically variable (Jabis et al. 2011), it is not likely that its current narrow range results from a recent range contraction. The absence of *A. alpina* in Brown and Templeton meadows and the occurrence of the species at only one site in Templeton suggest 2 possibilities for its current restriction: (1) dispersal is a limiting factor for *A. alpina* range size or (2) the taxon results from a relatively recent speciation event and has not yet colonized other suitable sites. The latter is unlikely as the closest sister taxon is located in the Owens Valley, approximately 80 km distant. The species can germinate and grow on soils from all meadows, indicating redistribution is a viable alternative given future changes in currently suitable habitat. *Abronia alpina* can be propagated and relocated to 6 other meadows with cooler climates that may be more suitable, given population reductions due to climate warming.

Several questions remain for future study and we identify 3. First, to identify whether dispersal or biotic associations such as competition or facilitation are in fact limiting range expansion, 3 types of transplant experiments could be applied: (1) transplant to other meadows containing the 3 species most closely associated with *A. alpina*–occupied habitat; (2) transplant to sites with intraspecific associates; and (3) transplant to more fertile locations amid greater competition within Ramshaw Meadow. Second, to resolve whether dispersal is a limiting process, trials could quantify the maximum distance the seed is capable of moving via wind or water. And third, to determine whether early

spring rain or late snowmelt do in fact aid seedling germination, regular localized precipitation measurements could be collected. Such examinations in combination may identify the causes of narrow endemism for *A. alpina* and assist in future conservation and introduction attempts.

Literature Cited

AIZEN, M.A., AND W.A. PATTERSON. 1990. Acorn size and geographical range in the North American oaks (*Quercus* L.). Journal of Biogeography 17:327–332.

ANDERSON, M.J. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology 2:32–46.

BARRETT, S.C.H., AND J.R. KOHN. 1991. Genetic and evolutionary consequences of small population size in plants: implications for conservation. Pages 3–30 *in* D.A. Falk and K.E. Holsinger, editors, Genetics and conservation of rare plants. Oxford University Press, Cary, NC.

BERTNESS, M.D., AND R.M. CALLAWAY. 1994. Positive interaction in communities. Trends in Ecology and Evolution 9:191–193.

BRANDEGEE, T.S. 1899. New species of western plants. Botanical Gazette 27:444–457.

BYERS, D.L., AND T.R. MEAGHER. 1997. A comparison of demographic characteristics in a rare and a common species of *Eupatorium*. Ecological Applications 7:519–530.

[CDWR] CALIFORNIA DEPARTMENT OF WATER RESOURCES. 2014. California Data Exchange Center [online]. Available from: http://cdec.water.ca.gov/cgi-progs/snow/.

CALLAWAY, R.M., R.W. BROOKER, P. CHOLER, Z. KIKVIDZE, C.J. LORTIEK, R. MICHALET, L. PAOLINI, F.I. PUGNAIREQ, B. NEWINGHAM, E.T. ASCHEHOUG, ET AL. 2002. Positive interactions among alpine plants increase with stress. Nature 417:844–848.

CARTER, M.R. 1993. Soil sampling and methods of analysis. Canadian Society of Soil Science, Boca Raton, LA.

CHAPIN, F.S., III, K. AUTMN, AND F. PUGNAIRE. 1993. Evolution of suites of traits in response to environmental stress. American Naturalist 142:S78–S92.

COLE, C.T. 2003. Genetic variation in rare and common plants. Annual Review of Ecology, Evolution and Systematics 34:213–237.

COWLING, R.M., E.T.F. WITKOWSKI, A.V. MILEWSKI, AND K.R. NEWBEY. 1994. Taxonomic, edaphic and biological aspects of narrow plant endemism on matched sites in Mediterranean South Africa and Australia. Journal of Biogeography 21:651–664.

DAVIS, S.D., V.H. HEYWOOD, O. HERRERA-MACBRYDE, J. VILLA-LOBOS, AND A.C. HAMILTON. 1997. Centres of plant diversity: a guide and strategy for their conservation. IUCN, Oxford, United Kingdom.

EDWARDS, W., AND M. WESTOBY. 1996. Reserve mass and dispersal investment in relation to geographic range of plant species: phylogenetically independent contrasts. Journal of Biogeography 23:329–338.

ELLSTRAND, N.C., AND D.R. ELAM. 1993. Population genetic consequences of small population size: implications for plant conservation. Annual Review of Ecology, Evolution and Systematics 24:217–242.

FENNER, M., W.G. LEE, AND E.H. PINN. 2001. Reproductive features of *Celmisia* species (Asteraceae) in relation to altitude and geographical range in New Zealand. Biological Journal of the Linnean Society 74:51–58.

FERNANDEZ, J.D., J. BOSCH, B. NIETO-ARIZA, AND J.M. GOMEZ. 2012. Pollen limitation in a narrow endemic plant: geographical variation and driving factors. Oecologia 170:421–431.

FIEDLER, P.L. 1987. Life history and population dynamics of rare and common mariposa lilies (*Calochortus* Pursh: Liliaceae). Journal of Ecology 75:977–995.

GASTON, K.J. 1994. Rarity. Chapman and Hall, London, United Kingdom.

GITZENDANNER, M.A., AND P.A. SOLTIS. 2000. Patterns of genetic variation in rare and widespread congeners. American Journal of Botany 87:783–792.

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.

HAMRICK, J.L., AND M.J.W. GODT. 1996. Conservation genetics of endemic plant species. Pages 281–304 *in* J.C. Avise and J.L. Hamrick, editors, Conservation genetics: case histories from nature. Chapman and Hall, New York, NY.

HARPER, K.T. 1979. Some reproductive and life history characteristics of rare plants and implications of management. Great Basin Naturalist Memoirs 3: 129–137.

HODGSON, J.G. 1986. Commoness and rarity in plants with special reference to the Sheffield Flora Part I: the identity, distribution, and habitat characteristics of the common and rare species. Biological Conservation 36:199–252.

HOWE, H.F., AND J. SMALLWOOD. 1982. Ecology of seed dispersal. Annual Review of Ecology and Systematics 13:201–228.

JABIS, M.D., T.J. AYERS, AND G.J. ALLAN. 2011. Pollinator-mediated gene flow fosters genetic variability in a narrow alpine endemic, *Abronia alpina* (Nyctaginaceae). American Journal of Botany 98:1583–1594.

KARRON, J. 1987. A comparison of levels of genetic polymorphism and self-compatibility in geographically

restricted and widespread congeners. Evolutionary Ecology 1:47–58.

KEDDY, P.A. 1992. Assembly and response rules: two goals for predictive community ecology. Journal of Vegetation Science 3:157–164.

KELLY, D.L., E.V.J. TANNER, E.M. NICLUGHADHA, AND V. KAPOS. 1994. Floristics and biogeography of a rain forest in the Venezuelan Andes. Journal of Biogeography 21:421–440.

KESSLER, M. 2000. Elevational gradients in species richness and endemism of selected plant groups in the central Bolivian Andes. Plant Ecology 149:181–193.

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

KUNIN, W.E., AND K.J. GASTON. 1993. The biology of rarity: patterns, causes and consequences. TREE 8:298–301.

_____. 1997. The biology of rarity: causes and consequences of rare-common differences. Chapman and Hall, London, United Kingdom.

KUNIN, W.E., AND A. SHMIDA. 1997. Plant reproductive traits as a function of local, regional and global abundance. Conservation Biology 11:183–192.

LAHTI, T., E. KEMPPAINEN, A. KURTTO, AND P. UOTILA. 1991. Distribution and biological characteristics of threatened vascular plants in Finland. Biological Conservation 55:299–314.

LAUGHLIN, D.C., AND S.R. ABELLA. 2007. Abiotic and biotic factors explain independent gradients of plant community composition in ponderosa pine forests. Ecological Modelling 205:231–240.

LAVERGNE, S., J.D. THOMPSON, E. GARNIER, AND M. DEBUSSCHE. 2004. The biology and ecology of narrow endemic and widespread plants: a comparative study of trait variation in 20 congeneric pairs. Oikos 107:505–518.

LESICA, P. 1992. Autecology of the endangered plant *Howellia aquatilis;* implications for management and reserve design. Ecological Applications 2:411–421.

LEVIN, S.A., H.C. MULLER-LANDAU, R. NATHAN, AND J. CHAVE. 2003. The ecology and evolution of seed dispersal: a theoretical perspective. Annual Review of Ecology and Systematics 34:575–604.

LEVINE, J.M., AND D.J. MURELL. 2003. The community-level consequences of seed dispersal patterns. Annual Review of Ecology and Systematics 34: 549–574.

LLOYD, K.M., W.G. LEE, AND J.B. WILSON. 2002. Growth and reproduction of New Zealand *Acaena* (Rosaceae) species in relation to rarity and commonness. New Zealand Journal of Ecology 26:149–160.

LLOYD, K.M., J.B. WILSON, AND W.G. LEE. 2003. Correlates of geographic range size in New Zealand *Chionochloa* (Poaceae) species. Journal of Biogeography 30:1751–1761.

LOARIE, S.R., B.E. CARTER, K. HAYOE, S. MCMAHON, R. MOE, C.A. KNIGHT, AND D.D. ACKERLY. 2008. Climate change and the future of California's endemic flora. PLOS ONE 3:1–10.

LORD, J.M., AND M. WESTOBY. 2006. Accessory costs of seed production. Oecologia 150:310–317.

MCCUNE, B., AND J.B. GRACE. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, OR.

MCCUNE, B., AND M.J. MEFFORD. 2006. PC-ORD. Multivariate analysis of ecological data. Version 5.10. MjM Software Design, Gleneden Beach, OR.

McDonald, D.J., and R.M. Cowling. 1995. Towards a profile of an endemic mountain fynbos flora: implications for conservation. Biological Conservation 72:1–12.

Myers, N., R.A. Mittermeier, C.G. Mittermeier, G.A.B. da Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853–858.

Oakwood, M.O., E. Jurado, M. Leishman, and M. Westoby. 1993. Geographic ranges of plant species in relation to dispersal morphology, growth form and diaspore weight. Journal of Biogeography 20:563–572.

Odeja, F., M.T. Simmons, J. Arroyo, T. Maranon, and R.M. Cowling. 2001. Biodiversity in South African fynbos and Mediterranean heathland. Journal of Vegetation Science 12:867–874.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42.

Peters, J. 2000. Tetrazolium testing handbook: contribution no. 29 to the handbook on seed testing. Association of Official Seed Analysts. Available from: http://www.aosaseed.com/Tzwebsite/Tzupdateinex.html

Peterson, E.B., and B. McCune. 2001. Diversity and succession of epiphytic machrolichen communities in low-elevation managed conifer forests in western Oregon. Journal of Vegetation Science 12:511–524.

Primack, R.B., and S.L. Miao. 1992. Dispersal can limit local plant distribution. Conservation Biology 6: 513–519.

SAS. 1989–2008. JMP, version 8. SAS Institute, Inc., Cary, NC.

Shaw, W.B., and B.R. Burns. 1997. The ecology and conservation of the endangered endemic shrub, Kowhai Ngutukaka *Cilianthus puniceus* in New Zealand. Biological Conservation 81:233–245.

Shevock, J.R. 1996. Status of rare and endemic plants. *In:* Sierra Nevada Ecosystem Project: final report to Congress. Volume II, Assessments and scientific basis for management options. Centers for Water and Wildland Resources, Davis, CA.

Singh, A., and M. Agrawal. 2008. Acid rain and its ecological consequences. Journal of Environmental Biology 29:15–24.

Sun, Z.J., G.D. Young, R.A. McFarlane, and B.M. Chambers. 2000. The effect of soil electrical conductivity on moisture determination using time domain reflectometry in sandy soil. Canadian Journal of Soil Science 80:13–22.

Thomas, C.D., A. Cameron, R.E. Green, M. Bakkenes, L.J. Beaumont, Y.C. Collingham, B.F.N. Erasmus, M.F. de Siqueria, A. Grainger, L. Hannah, et al. 2004. Extinction risk from climate change. Nature 427:145–148.

Thompson, K., K.J. Gaston, and S.R. Band. 1999. Range size, dispersal and niche breadth in the herbaceous flora of central England. Journal of Ecology 87: 150–155.

Venable, D.L., and J.S. Brown. 1993. The population-dynamic functions of seed dispersal. Vegetation 107/108:31–55.

Willson, M.F. 1993. Dispersal mode, seed shadows, and colonization patterns. Vegetatio 107/108:261–280.

Wilson, R.C. 1970. The rediscovery of *Abronia alpina,* a rare specialized endemic of sandy meadows in the southern Sierra Nevada, California. Aliso 7:201–205.

_____. 1976. *Abronia:* IV. Anthocarp dispersibility and its ecological implications for nine species of *Abronia.* Aliso 8:493–506.

Wiser, S.K., R.K. Peet, and P.S. White. 1998. Prediction of rare-plant occurrence: a southern Appalachian example. Ecological Applications 8:909–920.

Wolf, A. 2001. Conservation of endemic plants in serpentine landscapes. Biological Conservation 100:35–44.

APPENDIX. Vascular plant species list for all meadows sampled.

Family	Scientific name
Alliaceae	*Allium obtusum*
Apiaceae	*Oreonana clementis*
Asteraceae	*Agoseris glauca*
Asteraceae	*Antennaria umbrinella*
Asteraceae	*Artemisia rothrockii*
Asteraceae	*Chaenactis douglasii*
Asteraceae	*Chrysothamnus viscidiflorus* ssp. *viscidiflorus*
Asteraceae	*Erigeron pygmaeus*
Asteraceae	*Hulsea vestida*
Boraginaceae	*Cryptantha circumcissa*
Boraginaceae	*Cryptantha nubigena*
Brassicaceae	*Arabis pygmaea*
Brassicaceae	*Erysimum capitatum*
Brassicaceae	*Orochaenactis thysanocarpa*
Chenopodiaceae	*Chenopodium desiccatum*
Cyperaceae	*Carex douglasii*
Fabaceae	*Astragalus subvestitus*
Fabaceae	*Lupinus breweri* var. *bryoides*
Fabaceae	*Lupinus breweri* var. *grandiflorus*
Fabaceae	*Lupinus sellulus* ssp. *sellulus* var. *sellulus*
Gentinaceae	*Frasera tubulosa*
Juncaceae	*Juncus parryi*
Nyctaginaceae	*Abronia alpina*
Onagraceae	*Gayophytum diffusum* ssp. *parviflorum*
Onagraceae	*Oenothera xylocarpa*
Pinaceae	*Pinus contorta*
Poaceae	*Achnatherum occidentale* ssp. *occidentale*
Poaceae	*Elymus elymoides* ssp. *brevifolius*
Poaceae	*Koehleria macrantha*
Poaceae	*Muhlenbergia richardsonis*
Polemoniaceae	*Linathus pungens*
Polygonaceae	*Eriogonum incanum*
Polygonaceae	*Eriogonum nudum*
Polygonaceae	*Eriogonum ovalifolium*
Polygonaceae	*Eriogonum polypodium*
Polygonaceae	*Eriogonum spergulinum*
Polygonaceae	*Eriogonum umbellatum*
Portulacaceae	*Cistanthe umbellata*
Rosaceae	*Ivesia santolinoides*
Rosaceae	*Ivesia campestris*
Scrophulariaceae	*Mimulus memphiticus*
Violaceae	*Viola pinetorum* ssp. *grisea*