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Ecological and Genetic Variation Among Populations of *Boechera caeruleamontana* sp. nov. (Brassicaceae) from Blue Mountain and Dinosaur National Monumentin Eastern Utah and Western Colorado

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ABSTRACT

Ecological and Genetic Variation Among Populations of *Boechera caeruleamontana* sp. nov. (Brassicaceae) from Blue Mountain and Dinosaur National Monument in Eastern Utah and Western Colorado

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Boechera is a large genus of flowering plants whose taxa are found primarily in North America. *Boechera vivariensis* (S.L. Welsh) W.A. Weber (the Park rockcress) is restricted to the Uintah Basin on Weber sandstone substrates in the vicinity of Dinosaur National Monument and Blue Mountain. The nomenclature of Park rockcress is significantly impacted by the discovery that the type collections of the taxon represent a rare, apomictic diploid resulting from the hybridization between *B. thompsonii* and an undescribed sexual diploid (to be called *Boechera caeruleamontana* sp. nov. Allphin and Windham). As a result, greater information is needed regarding how *B. vivariensis* and *B. caeruleamontana*. are distributed geographically in the region of Dinosaur National Monument and surrounding areas. Thus, we performed genetic analyses on leaf samples taken from over 50 individuals at known sites of *B. vivariensis* throughout its geographic range. Individuals from each site were also compared morphologically. We also compared associated plant communities at each site and characterized the soils. In our thorough sampling, we did not pick up *B. vivariensis*. All individuals sampled belonged to *B. caeruleamontana*, suggesting that most individuals previously assigned *to B. vivariensis*, are actually representative of *B. caeruleamonanta*. Populations of *B. caeruleamontana* were genetically diverse compared to other *Boechera* species, most likely indicative of its insect pollination strategy. However, all populations had lower heterozygosity than expected based upon Hardy-Weinberg expectations. Reproductive and genetic data indicated that populations are showing signs of inbreeding. The population at Jones Hole Fish Hatchery was most unique genetically, morphologically, and reproductively.

Keywords: *Boechera*, Brassicaceae, systematics, Dinosaur National Monument, plant ecology, conservation biology, genetic diversity, inbreeding, rare and endangered species

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INTRODUCTION

Dinosaur National Monument was founded in 1915, in order to preserve the fossil beds discovered by paleontologist Earl Douglass. The monument was originally a small 80 acres that only covered the Dinosaur bone quarry, but in 1938 the value of the surroundings was seen and the land expand to over 200,000 acres.

In addition to extensive fossil beds, Dinosaur National Monument and surrounding areas are known for many unusual and unique rock formations. There are twenty-three rock strata, with layers from as far back as 1.2 billion years. Within this time period, it is believed that the area has been through many geologic changes, from an ancient sea, to plains, to deserts. The geology gives rise to many unique soil properties, some of which are only found in the region, that allow for the diversity of plants and animals that thrive in this region.

Dinosaur National Monument and the Blue Mountain region sit on the boundary of the eastern edge of Utah and the western edge of Colorado. As it is a national monument, Dinosaur National Monument is managed and cared for by the National Park Service, in the US Department of Interior. The lands surrounding Dinosaur National Monument are also primarily public federal lands, managed by the Bureau of Land Management in the Department of Interior.

Within Dinosaur National Monument, there are approximately 700 confirmed vascular plant species, with a possibility of up to 1259 species (this number includes confirmed species that are known in the surrounding area but have not necessarily been identified within the monument). This diversity of plant species might be attributed to the diversity of geologic formations that are found in the Monument. In addition, with approximately 250 mm of precipitation a year (Colorado state averages 350 mm and Utah state averages 480 mm according to usclimatedata.com), the species found in the monument are known for being very hardy.

However, many of these plant species in Dinosaur National Monument are considered to be rare, according to criteria of Rabinowitz (1981).

Rare plant studies are extremely important because they address not only the immediate practical concerns of species conservation, but also offer insight on questions of fundamental importance in ecology and evolutionary biology that are relevant to the development of management strategies for rare and endangered plant species (Falk and Holsinger 1991). While many weedy and domestic species life history strategies have been studied extensively, these rare, isolated, small endemic species have been largely ignored. It is necessary to enlarge our understanding of how these rare species, at risk for extinction, respond to disturbance. Life history strategies for rare species must be determined in order to understand why they lack optimal reproduction and survival as a population after a disturbance and be able to predict the long-term results of such disturbances on a population.

One of the goals in conservation biology is to preserve a species evolutionary potential by maintaining its natural levels of genetic diversity (Hamrick et al. 1991). Thus, studies on the distribution and levels of genetic variability in rare species are extremely useful to managers of rare and endangered taxa. Because reduced genetic variability is common in small populations and makes them more vulnerable to extinction, it is pertinent to understand the effect that greater or lesser genetic variability exerts on fitness parameters such as reproductive success.

Studies on the reproductive capacity of rare species are also an integral part of conservation programs, because reproductive success often equates with fitness in these species. Therefore, the development and implementation of management strategies for any rare species requires a detailed knowledge of its reproductive biology and population genetics.

Boechera is a genus in the family *Brassicaceae*, named after the Danish botanist, Tyge W. Böcher, a researcher of alpine mustards. *Boechera*, or the rockcresses, are taxonomic group found primarily in North America, but can also be found in Greenland and the far north eastern stretches of Russia. Little is known about the genus. The species within the genus are often difficult to separate morphologically, in part because of the tendency for the species to hybridize (Al-Shehbaz and Windham 2010).

Eighteen (16.5%) of 109 *Boechera* species included in the recent Flora of North America (Al-Shehbaz and Windham 2010) treatment are identified as being "of conservation concern." Sixteen others (14.7%) are either considered "sensitive" by the one or more agencies of the federal government, or are very rare but only recently named and therefore just beginning to garner attention for conservation. With ca. 30% of its species considered globally rare and new rare species being continually discovered, *Boechera* is a prime subject for integrative studies of the factors contributing to rarity and extinction. Conservation of rare taxa in *Boechera* has been limited by our incomplete understanding of the evolutionary processes at work in this group. A more detailed understanding of factors contributing to rarity in specific species is warranted.

The Park rockcress, *Boechera vivariensis* (S.L. Welsh) W.A. Weber, is a rare perennial member of the genus *Boechera* that is restricted to Weber sandstone substrates in the vicinity of Dinosaur National Monument and surrounding BLM lands in the Blue Mountain area along the Colorado-Utah Border. Historically the species was described as *Arabis vivariensis* S.L. Welsh. Research showed that this taxon more appropriately belonged in the genus *Boechera* (Al-Shehbaz 2003).

The Park rockcress has been treated as both a distinct species and as a subspecies of *Boechera fernaldiana* known to inhabit the Great Basin. Welsh et al. (2008) treated the Park

rockcress as a subspecies of *B. fernaldiana [B. fernaldiana subsp. vivariensis* (S.L. Welsh) Wyndham & Al-Shehbaz], even though another allopatric segregate found in the Southern Sierra Nevada mountains was treated as a distinct species called *B. evadens* (Welsh et al. 2008).

The most recent phylogeny (Alexander et al 2013) illustrated that *B. fernaldiana subsp. vivariensis* had been inaccurately included in the *B. fernaldiana* species complex and represented its own species. This phylogeny showed 100% bootstrap support for a sister relationship between *B. fernaldiana* and *B. evadens*, while the position of Park Rockcress, though unresolved with respect to the phylogenetic backbone, was clearly more distant. If *Boechera evadens* represents a distinct species separate from *B. fernaldiana*, then *subsp. vivariensis* must be also be elevated to species status (as *B.vivariensis*), because it is phylogenetically even more distant.

With the growing number of techniques being developed in molecular biology, population biologists are using nuclear DNA markers to measure genomic variability. Because DNA is directly analyzed, genetic variation can be directly measured instead of estimated by phenotype locality (Schaal et al. 1991). Microsatellites, or simple sequence repeats (SSRs), are a class of DNA markers located throughout the genome that yield molecular data from distinguishable loci with discrete, co-dominant alleles that can be unambiguously scored similarly to allozyme data (Love et al. 1990; Schlotterer et al. 1991; Akkaya et al. 1992; Queller et al. 1993). These microsatellites are short tandem repeats of motifs (1-6 bases), each representing a highly variable locus with multiple alleles.

A preliminary analysis of a 15-locus micro-satellite dataset (Beck et al. 2011) with broad geographic sampling of *B. fernaldiana* and related taxa revealed additional details that were relevant to the taxonomy of this group (Allphin et al., unpublished data). The nomenclature of Park rockcress was significantly impacted by the discovery that the type collections of *Boechera*

vivariensis include two different taxa: (1) the isotype at Rocky Mountain Herbarium is a sexual diploid representative of the majority of collections previously assigned to this taxon, and (2) the isotype at Garrett Herbarium and the holotype at the Stanley L. Welsh Herbarium, Brigham Young University, represent a rare, apomictic diploid resulting from the hybridization between the (1) sexual diploid and related species *B. thompsonii*. If the parents of (2) are considered distinct species (as they currently are), then *B. vivariensis* is appropriately recognized at species level.

Under this scenario, however, the sexual diploid taxon comprising most herbarium specimens assigned to *B. vivariensis* would need a new name. Allphin and Wyndham are proposing, *B. caeruleamontana* (Allphin and Windham, manuscript in preparation). As a result, greater information is needed regarding how *B. vivariensis* and *B. caeruleamontana* sp. nov. are distributed geographically in the region of Dinosaur National Monument and surrounding BLM lands in the Blue Mountain are of Utah and Colorado.

Three common characteristics for determining whether a species is endangered and in need of protection is limited geographic range, habitat specificity, and population size (Rabinowitz 1981). Because little is known about some rare taxa, it is often impossible to guess a taxon's susceptibility to extinction, making it incredibly difficult to manage the populations. Because little is known about the Park rockcress of Dinosaur National Park, it faces similar problems.

It is believed that the geographic range of the Park rockcress includes the Weber sandstone substrates in Dinosaur National Monument and surrounding areas that also include Weber sandstone substrates in lands administered by the Bureau of Land Management. Because of the narrow geographic range for the species, it meets one of the criteria for rarity (Rabinowitz

1981). In addition, the Park rockcress now includes two different taxa, making each of these taxa even rarer. Thus, ample sampling needs to occur across the geographic range of these taxa, in order to get a better idea of the extent and distribution of the known populations of each of the two taxa currently described as, *B. vivariensis* sensu lato,. Using ArcGIS to understand the current known population patterns, it may be possible to use these conditions and discover other potential habitat localities within in the Dinosaur National Park and surrounding BLM lands.

The Park rockcress is also thought to be a habitat specialist on Weber sandstone substrates in the Blue Mountain area. However, little is known regarding the habitat requirements of *B. vivariensis* and its new segregate, *B. caeruleamontana*. Ecological sampling across all populations of each of these taxa needs to be done to determine habitat requirements for each taxon. These species also uniquely grow in large mats that might help protect the endemic sandstone substrates from erosion, making it an important stabilizing factor within its habitat. Thus, it is also important to determine each taxon's role in its representative community.

OBJECTIVES

Where so little is known about *B. caeruleamontana* or *B. vivariensis* populations in the Dinosaur National Monument region, it is pertinent to discover how two separate taxa are distributed within and among populations geographically. Thus our specific objectives were:

1) Determine the extent and distribution of populations of *B. vivariensis and B. caeruleamontana*.
2) Determine the extent and distribution of genetic variation within and among populations of each taxon.
3) Determine morphologic differences between each of the taxa. Can the species be distinguished morphologically within and among populations?
4) Determine the habitat characteristics and describe the associated vegetative communities for both *B. vivariensis* and *B. caeruleamontana*.

Detailed analysis of morphology, habitat and distribution will determine if *B. caeruleamontana* and *B. vivariensis* can be distinguished by more than just their genetics. Greater understanding of the species biology of these taxa will better inform management decisions to help conserve these geographically restricted, habitat specialists.

METHODS

Study Area:

After conversations with personnel at Dinosaur National Monument, several sites were selected for analysis across the geographic extent of *B. vivariensis* senu lato in the Dinosaur National Monument boundaries. Herbarium collections were also used to determine additional collection locations across the Weber sandstone substrates within both Dinosaur National Monument and Bureau of Land Management lands in the Blue Mountain region of Utah and Colorado. Sampling was accomplished in the spring when it was believed, from past collections in herbaria that the Park rockcress would be flowering. Sampling also occurred one month after initial collections for collection of seed.

Mapping:

Locality data were obtained using a GPS unit for each sampling location and entered into ArcGIS. These data were used to generate distribution maps for each taxon. This was used to determine the extent and distribution of all sampled populations currently included within *B. vivariensis* sensu lato.

Genetic Analyses:

Leaf samples for at least 50 individuals at known populations of *B. vivariensis* senus lato were randomly taken (Fig. 1; Table 1). Because the taxa are clump forming (one plant growing an extensive root system forming one larger plant), careful sampling occurred to prevent the double sampling of any genetic individual.

DNA was extracted from leaf samples using a modified version of the CTAB protocol (Doyle and Dickson, 1987; Beck et al. 2011). DNA samples were analyzed using 15 previously developed microsatellite (SSR) loci following the PCR methods of Beck et al. 2011. Amplicons were sized using the 500 ROX standard on an Applied Biosystems 3730xl DNA Analyzer. Allelic determinations were made using GeneMarker 1.9 (SoftGenetics, State College, PA). Population genetic data were analyzed using *Genepop* 4.2 (Raymond M. & Rousset F, 1995, GENEPOP 4.2).

Genpop 4.2 was used to compute genetic parameters from genotype frequency data (Hartl 1988, Weir 1990). These genetic parameters included mean observed heterozygosity (H_o – direct estimate), expected heterozygosity (H_e, based on Hardy-Weinberg equilibrium model), mean proportion of polymorphic loci (*P*), mean number of alleles per locus (A), mean number of alleles per polymorphic loci (A_p), and number of private alleles across all loci for each population ($A_{private}$; Slatkin and Barton 1989). Deviations from Hardy-Weinberg (H-W) expectations were determined using a H-W U-test for heterozygote deficiency (Genepop 4.2). To analyze population structure, F-statistics were computed across all populations following Wright (1951,1965) and Weir and Cockerham (1984). Deviations of F-statistics from H-W equilibrium was determined based on the Markov chain method (Guo and Thompson, 1992). Gene flow (Nm- number of migrants per generation) was determined across all populations using the private alleles method of Slatkin and Barton (1989). Statistical differences for genetic means among sites were determined using Kruskal-Wallis tests with Dwass-Steel-Chrichlow-Flinger tests for pairwise comparisons using *Systat* 13.1. A cluster phenogram was generated from Wright's (1951, 1965) pairwise F_{ST} values using the unweighted pair group method with

arithmetic mean (UPGMA; Romesburg 1984) to allow hierarchical classifications of relationships among populations based on genetic distances among sampled populations.

Morphological and Reproductive Sampling:

Voucher specimens were taken at each sampled population of each taxon (Fig. 1; Table 1). Morphological measurements were taken from these specimens at each population. The holotype and an isotype of *B. vivariensis* from Brigham Young Herbarium (BRY) were also included in morphometric analysis. Morphologic measurement included: leaf size, caudex length, and floral size. Morphometric analyses were used to determine if distinguishing characteristics exist between the sexual diploid, *B. caeruleamontana* and its hybrid relative, *B. vivariensis*.

For samples where fruits were present, the number of inflorescences were measured. On each inflorescence, the length of fruits was recorded and the number of fruits per an inflorescence was also obtained. In cases where the plant was not flowering or the inflorescence was damaged or destroyed in collection, the inflorescence was recorded as absent since no fruits could be identified as belonging to the sample. The length of the fruits, when available was measured for the sample and then averaged for the plant. Finally, we measured leaf lengths on each specimen.

Morphological and reproductive data were also taken from 20 tagged individuals at each study population. Tagged individuals were selected by stretching a 40 m transect through the center of the population at sampling site. At every two meters along the transect, the closest individual to the two meter point was tagged and measured for clump (mat) diameter (two perpendicular measurements were taken), average leaf length (three leaves), number of rosettes,

number of inflorescences, number of flowers per inflorescence, average number of fruits per inflorescence, and fruit to flower ratio. We also collected any pollinators that we saw foraging on flowers in study populations.

Mature fruits were collected from each study population and tagged individuals where available, immediately prior to dehiscing, and taken back to the lab to be analyzed for seed set. In the laboratory, these fruits were opened and observed under a dissecting microscope. Number of ovules, number of viable seeds, and percent of abortion at four different developmental stages (no development, early abortion, partial development abortion and late development abortion) were assessed for each fruit.

Statistical differences among populations were assessed for each morphological and reproductive characteristic measured. Statistical analyses were performed using one-way ANOVA and Tukey multiple means comparisons in *Systat* 13.1 (Systat Software, San Jose, CA).

Soil Sampling:

At each plant sampling location soil samples were obtained from a depth of 0 - 10 cm (Fig. 1; Table 1). A total of five composite soil samples were taken across each of the study populations. At two locations, some of the plants were growing in mulch or duff. At these localities, 800 ml of mulch was obtained instead. All samples were sent to the Environmental Analytical Laboratory at Brigham Young University for analysis. For all soil samples, specific elemental nutrients were measured. These nutrients included: calcium, copper, iron, potassium, magnesium, manganese, sodium, zinc, total nitrogen, and total carbon. In addition, we measured texture pH, organic matter, nitrate-nitrite, and electrical conductivity of the soil. Texture of all samples was accomplished using a standard Bouyoucos hydrometer (Bouyoucos, 1962). pH was

measured via the pH saturated paste method (Soil Survey Staff. 2014). All analytical methods were based on those recommended by Black et al (1965) and as outlined in the NRCS Kellogg Soil Survey Laboratory Methods Manual (Soil Survey Staff 2014). Statistical differences among populations were assessed for each soil characteristic measured. Statistical analyses were performed using one-way ANOVA and Tukey multiple means comparisons in *Systat* 13 (Systat Software, San Jose, CA).

Vegetative Community Sampling:

At each site, a 40 m transect was stretched through the population in a random cardinal direction (Fig. 1; Table 1). Every 2 m along the transect line, a100 cm^2 nested frequency quadrat frame (Grieg-Smith 1983) was placed. From these data, frequency and cover of species in the associated plant community were obtained (Greig-Smith 1983). These data were used to develop a list of the prevalent associated species at each sampled locality of each taxon.

Frequency and cover data obtained from the plant community were also used to compute heterogeneity and biodiversity measures. Using Young's (2016) biodiversity calculator, we computed Simpson's and Shannon's diversity indices (Simpson 1949, Shannon 1949). These indices of species diversity provide a quantitative measure that reflects the heterogeneity in the community. Species richness and species dominance were also determined using this software to characterize the communities where these taxa occur (Young 2016).

We compared all study localities using Ruzicka's (1958) pair wise index of similarity based upon relative frequency values for associated species. We performed a cluster analysis of these pairwise similarity values using the unweighted pair group method of arithmetic mean

(UPGMA; Romesburg 1984). This analysis allowed us to look at hierarchical relationships among the sampled populations with respect to their vegetative communities.

RESULTS

Genetic Results:

We measured genetic variation of the sampled plants across 15 microsatellite (SSR) loci. Allelic variation at these loci was used to generate genetic diversity statistics for all sampled populations (Table 2). It is important to note that based on our microsatellite results all samples were identified molecularly as the sexual diploid, *B. caeruleamontana*. In all our sampling across a wide geographic range, none of our samples were genetically identified as the hybrid taxon *B. vivariensis*. Thus, from this point forward, results will be focused upon *B. caeruleamontana.*

Mean observed heterozygosity for sampled *B. caeruleamontana* populations varied among sampling locations (ranging from 0.210-0.343; Table 2). Jones Hole was more genetically diverse than the other sites at all fifteen loci. Jones Hole had the largest sample size, with 69 sampled. It also exhibited the highest heterozygosity compared to all other sites, with a H_o of 0.343 (Table 2) and the highest proportion of polymorphic loci, *P,* with a value of 0.933 (Table 2).

All populations had a large number of alleles per locus (mean 4.76; Table 2). Although all sites had high allelic diversity, observed heterozygosity was lower than expected at most sites (Table 2). All sites, except the one locality, showed significant Hardy-Weinberg heterozygote deficits (*P*- values ≤ 0.05; Table 2). These values are consistent with inbreeding. The F-statistic, F_{IS} is the average deviation from Hardy-Weinberg proportions for loci in populations, or increase in homozygosity, due to inbreeding (Weir and Cockerham 1984). Thus, F_{IS} is also called the

inbreeding coefficient. Values of F_{IS} range from 0-1, and positive values indicate that individuals in the population are more homozygous than one would expect based on random mating and negative values indicate heterozygote excess (Wright 1965). A value of one would indicate complete inbreeding (Wright 1965). Based upon F_{IS} estimates generated from our population samples, most of the 15 loci deviated from H-W equilibrium at several sites (Table 3). The type locality at Blue Mountain showed the least deviation, only one locus deviated from H-W expectations (Table 3). Other sites had more than six loci that deviated from H-W equilibrium, consistent with inbreeding (Table 3).

Genetic divergence estimates (F_{ST}) are given in Table 4. The F-statistic, $F_{ST,}$ is a measure of population substructure and population divergence (Wright 1965). F_{ST} values range from 0-1, where 0 represents complete interbreeding (panmixia) between populations and 1 indicates complete divergence (Wright 1965; Weir and Cockerham 1984). Based upon F_{ST} estimates, our sampled populations were not that divergent from one another (Table 4). However, our pair-wise population F_{ST} values were highly variable. We estimated gene flow to be relatively low (Nm = 1.572 migrants per generation). We also showed large numbers of private alleles per population (Table 2).

A UPGMA cluster diagram based on pairwise F_{ST} estimates (Table 4; Fig. 2) illustrated the genetic relationships among sites. Blue Mountain type locality and other herbarium samples from Blue Mountain were the most genetically similar, with the lowest pairwise F_{ST} value (0.0106; Fig. 2). Jones Hole and the site along Blue Mountain Road were the most genetically distant from other sites (0.09-.0.27; Table 4; Fig. 2).

Soil Results:

All sites had soils that were sandy loams (Table 5). All soils were very sandy (67.8% - 77.5% sand). Organic matter at each site was highly variable (between 1.5% and 14.2%). Jones Hole had significantly more organic matter in the soil compared to all other sites (Table 5).

Salinity of the soils was low, (EC dS/m), measurements were between 0.42 - 0.88, and no significant differences were found among sites (Table 5). Carbonate, $CaCO_3$, levels were highly variable, 1.8% - 7.6%. Echo Road had the highest carbonate levels of all sites (Table 5). pH ranged from 6.3 to 7.4. Jones Hole had a significantly lower pH compared to all other sites (Table 5). Elemental nutrient values are summarized in Table 6. Sites showed much variation with respect to elemental nutrient levels. Once again, Jones Hole had significantly higher levels of nitrates, phosphorus, potassium compared to all other sites Table 5).

Morphological and Reproductive Results:

Sites showed a wide range of variation for morphological characteristics (Table 7). Clump size ranged between 11.513 cm - 29.45 cm and clump areas varied from 124.457 mm^2 - 1041.7 mm^2 across study sties. Mean number of rosettes varied across sampled populations (51.9 - 128.9) and mean leaf length measurements were also highly variable among sites (5.84 cm - 12.05 cm; Table 7). Individual plants at Jones Hole were significantly larger ($P \leq 0.05$) than all other sites with the exception of the type locality at Blue Mountain.

The mean number of flowering stalks ranged between 4.3 - 18.9 across study populations (Table 7). The Type locality had the highest number of flowering stalks of the sites measured. The ratio of fruits to flowers was between 0.571-0.687, with no significant differences among sites. The mean number of fruits on a stalk varied from 2.3 - 4.5, with no significant differences

among sites, and the fruit to flower rations were between 0.60-0.70, with no significant differences among study locations (Table 7).

Seed to ovule ratio varied from 0.37 - 0.57. The type locality, Blue Mountain road, Jones Hole, and Split Mountain were statistically similar ($P > 0.05$; Table 8). The overall seed to ovule ratio across all sites was 0.50. However, Split Mountain and Jones Hole had the lowest S/O ratios, both with a mean seed/ovule of 0.37 (Table 8).

The number of ovules all significantly varied among populations and ranged between 39.9 - 50.4 ovules per fruit (Table 8). The overall mean number of ovules for the sites was 45.19. The number of filled ovules varied from 14.14 - 29.18. Ovule abortion rates varied among sites. The mean proportion of ovules aborting for the sites was 0.12 (Table 8). Jones Hole and Split Mountain had the lowest seed set, significantly lower than the other sites, and highest abortion rates of developing ovules (Table 8).

At each site, we made observations of any potential pollinators visiting flowers. The type locality site on Blue Mountain was the only population that we sampled while in early to full flower. During our visit, we saw two different species of pollinators moving from flower to flower consistently. We collected one to two samples of each of these pollinators. They were each identified as Hymenoptera. The two bees that were visiting flowers were an *Andrena* sp. and a *Bombus* sp.

Vegetative Community Results:

Plant species richness at our sites varied between 9 species at Jones Hole to 19 species at Echo road (Table 9). Echo Road and the type locality were the most heterogeneous sites (Table

9). Jones Hole was the least diverse with respect to associated species (Table 9). Our average, species richness values at the sites were between 11.31- 17.5 species.

Simpson's diversity index (Simpson 1949) values ranged from 0.1347 and 0.2135 with three of the sites were statistically similar (the type locality, Echo road, and Split Mountain; Table 9). Simpson's index values range from 0-1 and represent the probability that two individuals selected from random sample in the community with belong to different species (Simpson 1949). Thus, our populations were not highly diverse and showed signs of being dominated by one or more species. We also computed species dominance, by subtracting the value of Simpsons from 1, across all the study the sites. Our sites showed high proportion of species dominance with values ranging from 0.7865 and 0.8653. Jones Hole exhibited the overall lowest degree of species dominance (Table 9).

The Shannon diversity index (H, Shannon 1948) is another measure of heterogeneity in the associated plant community. These values represent the number of equally abundant species in a community. If a community is becoming dominated by one to a few species, this value would be much less than species richness. Our Shannon diversity values were consistently smaller than species richness (Table 9). Our study sites varied with diversity values ranging from 1.7 and 2.3 species (Table 9). Jones Hole exhibited the lowest Shannon species diversity, as well as the lowest species richness (Table 9).

Because many of the sampled populations had low abundance (low percent frequency of occurrence in sampling and low percent cover of ground) of associated species, we used a relative abundance that allowed for direct comparisons among sites. There was significant variability in the associated plant communities across all sites (Table 10). The Type locality on Blue Mountain, our highest elevation site, had very different species composition than the other

sites and no evidence of cheatgrass, *Bromus tectorum* invasion. However, all other sites had high relative frequency and cover of cheatgrass. For most sites, *B. tectorum* was the most abundant species encountered, next to *B. caeruleamontana* (Table 10).

Only two tree species were found in our vegetative sampling of associated plant communities, pinyon (*Pinus edulis*) and juniper (*Juniperus osteosperma*). *Juniperus osteosperma* was the most abundant tree species at each of the sites, with a relative frequency of occurrence that ranged from 0 - 3.26 % (Table 10). *Pinus edulis* was also found at the type locality and Echo road locations with a relative frequency of occurrence between 0.43 - 1.40%.

Five different shrub species were observed within our sampling areas (Table 10). *Artemesia vaseyana* was found at the type locality with a relative frequency of 1.30% and relative cover 3.11%. *Amelanchier alnifolia* was present at sites the type locality and Blue Mountain road with low abundance, a relative frequency of occurrence between 0.43 - 0.93%. *Ephedra virdis* occurred at sites Blue Mountain road, Echo road and Jones Hole sites with a relative frequency of 0.47 - 2.00%. *Symphoricarpus oreophilus var. utahensis* was found at the type locality on Blue Mountain, Blue Mountain road, and Jones Hole with relative frequency of occurrence values of 0.71 - 6.09%. *Chrysothamnus visidiflorus* was only found at Echo road in relatively high abundance, with a relative frequency of occurrence of 5.58%. (Table 10).

We found three different grass species across our five sampled sites (Table 10). The most commonly occurring grass species across all sites was the annual weedy species *Bromus tectorum*. This taxon occurred at sites Blue Mountain road, Echo road, Jones Hole and Split Mountain with a relative frequency between 25.23 - 28.57%. *Oryzopsis hymenoides* was a common native grass species found, occurring at Echo road and Split Mountain with a relative

frequency ranging from 0.93 - 8.84%. *Poa secunda* was another native grass species found at all sites with a relative frequency ranging from 3.40 - 23.91% (Table 10).

The sampled sites were rich in forb species (Table 10). However, there was significant variation among sites with respect to relative frequency and cover of forb species. The species, considered in this manuscript, *Boechera caeruleamontana*, was the most abundant forb species in our sampled communities, with a relative frequency of occurrence ranging from 4.08 - 28.57%. *Gilia inconspicua* complex was also present at all sites, except the Type locality with a relative frequency of 0.47 - 18.57% (Table 10). Other forbs were observed at one or more sites, but varied significantly with respect to relative frequency and/or cover at these localities (Table 10).

Moss was found at all sites with a relative ground cover ranging between 3.10 - 28.07%. Leaf and other vegetative litter was found at all sites with a relative ground cover of 18.52 - 44.10%. Bare rock was found at all sites with a relative cover of 0.62 - 29.14%. Bare soil was found at all sites with a relative cover of 6.21 - 24.50%.

A UPGMA cluster analysis of sites based upon relative frequency values compared among sites shows Echo road (Sand Canyon) and Blue Mountain road to be most similar sites, with respect to the associated vegetative community at ~46.8 % similarity (Fig. 3). However, none of the sites were very similar. The Type locality on Blue Mountain was least similar site to all other sites, based on vegetative community at only 12.8% similarity to all other sites (Fig. 3). This site is at the highest elevation (Table 1) and thus, is characterized by species associated with higher elevations that were not found at other sites (Table 10).

DISCUSSION

Most interesting was the find that all of our samples belonged to *B. caeruleamontana.* In our thorough sampling of all known sites of *B. vivariensis* sensu lato*,* we did not actually pick up *B. vivariensis.* Thus, most of the individuals and populations thought to belong to *B. vivariensis* actually represent *B. caeruleamontana.* This suggests that *B. vivariensis* is either much rarer than was prior known (possibly now extinct from our sites), or a rare (possibly recurring) spontaneous emergence that happens in the presence of co-occurrences of *B. caeruleamontana* and *B. thompsonii* populations. More sampling and searching for *B vivariensis* should be done. Most certainly long term evaluation of sites and additional DNA analysis could add to our understanding of the frequency of *B. vivariensis*.

Because *B. caeruleamontana* is a new species, much remains to be discovered about its biology. In addition, more information is needed on the taxon's ability to outcross and hybridize with other taxa (as in the formation of *B. vivariensis*). Long term monitoring of both taxa is suggested for all sites, and if any other sites are located they should be evaluated to see their genetic and morphological uniqueness. Nonetheless, managers should manage *B. caeruleamontana* as a distinct entity from *B. vivariensis*.

Sexual diploid species of *Boechera* typically exhibit very low levels of heterozygosity (Beck et al. 2011). Observed and expected heterozygosity values for *B. caeruleamontana* were much higher than those found for other sexual diploid species in *Boechera* (Table 2; Beck et al. 2011). *Boechera caeruleamontana* has one of the larger flowers seen in the genus (Al-Shehbaz and Windham 2010). Large flower size is often indicative of outcrossing in this group. We found two pollinator species visiting our large flowers and the populations exuded a strong aroma when the flowering. Higher levels of outcrossing could explain the higher heterozygosity

values in *B. caeruleamontana* compared to its other sexual diploid congeners (most have self-pollination or mixed mating systems; Beck et al. 2011). The seed to ovule ratios (mean = 0.50) that we observed in *B. caeruleamontana* were also characteristic of an outcrossing plant species. Outcrossing species of plants from many different taxonomic groups have been shown to be about 0.50, on average (Wiens 1984, Wiens et al. 1987).

Outcrossed species with high levels of heterozygosity have also been suggested to have an increased the number deleterious recessive lethals that accumulate in the heterozygous state (segregational load) (Wiens et al. 1987, Charlesworth 1989). Low seed set can occur in these outcrossed species, if populations are forced to inbreed (i.e. loss of pollinators or less gene flow). Inbreeding will reduce seed set due to more of these lethals being expressed in the homozygous state (Wiens et al. 1987, Wiens et al. 1989, Allphin 2002). We found significant heterozygote deficits (Tables 2 & 3) for most of our study populations of *B. caeruleamontana*. In addition, the two populations with the highest heterozygote deficits also had the lowest seed sets (Split Mountain and Jones Hole; Table 3 & 8). Low seed/ovule ratios and heterozygote deficits are consistent with inbreeding in most populations of *B. caeruleamontana*. Managers should also consider implications of the signs of inbreeding and look for ways to maintain genetic diversity and gene flow among populations of this taxon.

Populations of *B. caeruleamontana* appear to be restricted to sandy soils under pinyon and junipers in the Weber sandstone substrates. This species forms large mats and is the most dominant species at most of the sites where it occurs (Table 10). For this reason, it may play an important role in stabilizing the sandy soils in these plant communities. Thus, it is critical that the taxon be conserved. For those currently doing research into erosion control methods, this taxon might be a plant of interest. The tendency of *B. caeruleamontana* to grow in large mats that can

easily be removed may be of use in controlling erosion on similar soil types (sandy loam) as found in the study area.

The second most abundant species in all but one of the associated communities was the invasive weed, cheatgrass or *Bromus tectorum.* Cheatgrass is known to be a terrible weed affecting ecosystems in western North America (Mack 1981, Knapp 1996, Brooks et al. 2004). Therefore populations of *B. caeruleamontana* should be monitored for continued impact of invasive species, such as *B. tectorum*. At some of the sites, cheatgrass appeared to be "choking out" much of the *B. caeruleamontana* individuals, preventing clump spread. Many of our study sites were directly along roadways which makes it difficult to control weedy species. Jones Hole had the lowest species richness, but was also farther away from roads than most of the other sites, which is the most likely reason it had a lower occurrence of *Bromus tectorum*. We did not pick up *Bromus tectorum* at the type locality on Blue Mountain, a site that is also a long distance from roads. We recommend that actions be taken to prevent further invasion or spread of cheatgrass into populations of this rare taxon.

Jones Hole was our most unique population when compared with the others sampled in this study. Jones Hole had lower seed to ovule ratios, along with differences in number of filled and undeveloped ovules. This population also showed significant deviation from H-W equilibrium and greatest signs of inbreeding. Because this population was the most unique genetically, ecologically and morphologically, it might be high priority for conservation. The Jones Hole is also the type locality for *B. vivariensis*, although we did not pick it up in our thorough sampling at this site. We suggest that Jones Hole should warrant conservation priority for its uniqueness.

Low seed/ovule ratios and heterozygote deficits are consistent with inbreeding in these populations. Although populations have not diverged significantly from one another, gene flow estimates were low and populations had high numbers of private alleles indicative of little genetic exchange among populations. Moreover, populations may be smaller than we think due to the large mats and may have fewer genetic individuals. The populations may be exhibiting signs of inbreeding due to reductions in population size. Continued monitoring of sites for population trends is critical. Maintenance of large clumps may be less important than total number of genetic individuals for maintaining genetic diversity in this taxon. In addition, managers should also consider implications of the signs of inbreeding in most of the sampled populations and look for ways to maintain genetic diversity and gene flow among its populations.

Overall, *B. caeruleamontana* is a locally abundant rare plant species that is endemic to the Weber sandstone substrates in the Blue Mountain area of Dinosaur National Monument and surrounding BLM lands. This taxon should be subject to continued monitoring. We set up long term monitoring sites at the five sites sampled ecologically, providing a baseline for continued research. Continued monitoring of the populations is important but should be done with consideration of habitat monitoring as well. Continued habitat monitoring of the plants found in the immediate area may be helpful for determining if sites are likely to be invaded by weeds in the future. It is also suggested that a pollination study be done to see if we can determine how and when pollination is occurring. We observed two species during sampling in daylight, but with the large white flowers it is possible that these plants have another pollinator (i.e. moths) visiting them in the evening or at night. Moreover, because we were unable to obtain all the soil nutrient information at Jones Hole, it would be prudent to resample soils in this area.

Because *B. caeruleamontana* is rare and endemic, restricted to only to the Blue Mountain area, it is critical that it be protected. All active management activities, that might impact this taxon, should be planned carefully by local management agencies in order to ensure they are done with minimal disruption to this species. Impacts from local grazing populations of ungulates should also be monitored as they could cause damage to the plant habitat and promote further weed invasion. Because most sites are within Dinosaur National Monument, managers should monitor tourist activities, such as hiking, to ensure prime locations of *B. caeruleamontana* are not disturbed.

LITERATURE CITED

Akkaya, M.S., A.A. Bhagwat, and P.B. Cregan. 1992. Length polymorphisms of simple sequence repeat DNA in soybean. Genetics 132:1131-1139.

Alexander, P., M. D. Windham, J.B. Beck, I.. Al-Shehbaz, L.Allphin and C. D. Bailey. 2015. Weaving a Tangled Web: Divergent and Reticulate Speciation in Boechera fendleri Sensu Lato (Brassicaceae: Boechereae) Systematic Botany 40 (2): 572–596.

Allphin L, D. Wiens, and K.T. Harper. 2002. The relative effects of resources and genetics on reproductive success in the rare Kachina daisy, *Erigeron kachinensis* (Asteraceae). Int. J. Plant Sci. 163(4):599-612.

Al-Shehbaz, I. and M. Windham. 2010. Boechera. Flora of North America Editorial Committee, eds.,Flora of North America North of Mexico. Vol. 7, pages 226-367; New York and Oxford.

Al-Shehbaz, I., 2003. Transfer of most North American species of *Arabis* to *Boechera* (Brassicaceae). Novon 13(4):381-391.

Beck, J.B., P.J. Alexander, L. Allphin, I.A. Al-Shehbaz, C. Rushworth, C. D. Bailey, and M.D. Windham. 2011. Does hybridization drive the transition to asexuality in diploid *Boechera*? Evolution 66:985-995.

Black, C.A., D.D. Evans, J. L. White, L.E. Ensminger, and F.E. Clark. 1965. *Methods of Soil Analysis, Part 1: Physical and Mineralogical Properties, Including Statistics of Measurement and Sampling,* American Society of Agronomy, Inc., Madison, WI.

Bouyoucos, G.J.. 1962. Hydrometer method improvement for making particle size analysis of soils. Agron. J. 54: 179-186.

Brooks, M.L., C.M D'Antonio, D. M. Richardson, J.B. Grace, J.E. Keeley, J.M. DiTomaso, R.J. Hobbs, M.Pellant, and D. Pyke. 2004. The effects of invasive alien plants on fire regimes. Bioscience 54:677-688.

Charlesworth, D. 1989. Evolution of low fertility in plants: pollen limitation, resource allocation, and genetic load. Trends Ecol. Evol. 4:289-292.

Doyle, J. D., and E. E. Dickson. 1987. Preservation of plant samples for DNA restriction endonuclease analysis. Taxon 36:715–722.

Elith, J., Steven J. Phillips, Trevor Hastie, Miroslav Dudík, Yung En Chee, and Colin J. Yates. 2011. A statistical explanation of MaxEnt for ecologists. Diversity and Distributions, 17:43-5.

Digital Geologic Map of Dinosaur National Monument and Vicinity, Colorado and Utah (GRI MapCide DINO) nrdata.nps.gov/geology/gri_data/gis/dino/dino_geology.pdf

Falk, D. A. and Holsinger, K. E. 1991. Genetics and Conservation of Rare Plants. Oxford University Press, New York.

Federal Register.1993. Endangered and Threatened Wildlife and Plants; Review of Plant Taxa for Listing as Endangered or Threatened Species. Vol. 58, No. 188.

Greig-Smith, P. 1983. *Quantitative plant ecology*. Blackwell Scientific Publications, Oxford. 3rd ed. p. 9.

Hamrick JL, Godt MJW, Murawski DA and Loveless MD. 1991. Correlations between species traits and allozyme diversity: in implications for conservation biology. In: Genetic and conservation of rare plants (Falk DA and Holsinger KE, eds.). Oxford University Press, New York, 75-86.

Hartl, D.L. 1988. *A Primer of Population Genetics.* Sinauer Associates, Inc., Sunderland, MA.

Hirzel, A. H. 2008. Using relative capacity to measure habitat suitability. Israel Journal of Ecology and Evolution 54: 421-434.Knapp, P.A. 1996. Cheatgrass (*Bromus tectorum* L.) dominance in the Great Basin Desert: history persistence, and influences on human activities. Global Environmental Change 6:37-52.

Lewis, P.O. and D. Zaykin.2001. Genetic Data Analysis: Computer Program for the Analysis of Genetic Data. Version 1.0 (d16c). http://lewis.eeb.uconn.edu/lewishome/software.html.

Love J. M., A. Knight, M. A. Mcaleer and J. A. Todd, 1990 Towards construction of a high resolution map of the mouse genome using PCR-analysed microsatellite. Nucleic Acid Res. 18 4 123-4 130.

Mack, R.N. 1981. Invasion of *Bromus tectorum* L.in western North America: and ecological chronicle. Agro-Ecosystems 7:145-165.

Phillips, Steven J., Robert P. Anderson, and Robert E. Schapire. 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling, 190:231-259.

Queller, D.C., J. E. Strassmann, and C. R. Hughes. 1993. Microsatellites and kinship. Trends in Ecology and Evolution 8:285-288.

Rabinowitz, D. 1981. Seven forms of rarity. pp. 205-217 in The Biological aspects of rare plant conservation. Ed. by H. Synge. Wiley.

Raymond M. & Rousset F, 1995. GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. J. Heredity, 86:248-249

Romesburg, H.C. 1984. *Cluster analysis for researchers,* Lifetime Learning Publications, Blemont, CA.

Rousset, F., 2008. Genepop'007: a complete reimplementation of the Genepop software for

Windows and Linux. Mol. Ecol. Resources 8: 103-106.

Ruzicka, M. 1958. Anwendung Mathematisch-Statisticher Methoden in Der Geobotanik (Synthetische Bearbeitung Von Aufnahmen). Biologia, Bratisl 13: 647–661.

Schaal, B. A., Leverich, W. J., and S. H. Rogstad. 1991. A comparison of methods assessing genetic variation in plant conservation biology. In D. E. Falk & D. E. Holsinger, eds., Genetics and Conservation of Rare Plants. Oxford University Press, New York. pp. 123-134.

Schlötterer C, Amos B, and D. Tautz. 1991. Conservation of polymorphic simple sequence loci in cetacean species. Nature 354: 63–65.

Shannon ,C. 1948. A mathematical theory of communication. Bell Syst. Tech. J. 27:379–423.

Simpson, E.H. 1949. Measurement of diversity. Nature 163:688.

Slatkin, M. and N.H. Barton. 1989. A comparison of three indirect methods for estimating average levels of gene flow. Evolution 43:1349-1368.

Soil Survey Staff. 2014. Kellogg Soil Survey Laboratory Methods Manual. Soil Survey Investigations Report No. 42, Version 5.0. R. Burt and Soil Survey Staff (ed.). U.S. Department of Agriculture, Natural Resources Conservation Service.

SYSTAT (Systat Software, San Jose, CA) version 13.1(SYSTAT version 13.1, from Systat Software, Inc., San Jose California USA, www.sigmaplot.com).

Utah Rare Plant Field Guide. 2003. http://www.utahrareplants.org/

Weir, B.S. 1990. *Genetic Data Analysis,* Sinauer Associates, Inc., Sunderland, MA.

Weir, B.S. 1996. *Genetic Data Analysis II,* Sinauer Associates, Inc., Sunderland, MA.

Weir, B.S., and C.C. Cockerham. 1984. Estimation of F-statistics for analysis of population structure. Evolution 38:1358-1370.

Welsh, S. L. 2008. *A Utah Flora*, 4th edition. Brigham Young University Press, Provo, UT, USA.

Wiens, D. 1984. Ovule survivorship, brood size, life history, breeding system, and reproductive success in plants. Oecologia 64:47-53.

Wiens, D., C.L. Calvin, C.A. Wilson, C. I. Davern, D. Frank, and S.R. Seavey. 1987. Reproductive success, spontaneous embryo abortion, and genetic load in flowering plants. Oecologia 71;501-509.

Wiens, D., C.L. Calvin, C.A. Wilson, C. I. Davern, D. Frank, and S.R. Seavey. 1989. Developmental failure and loss of reproductive capacity in the rare paleoendemic shrub *Dedeckera eurekensis.* Nature*,* 338: 65-67.

Wright, S. 1951. The genetical structure of populations. Annals of Eugenics 15:323-354.

Wright, S. 1965. The interpretation of population structure by F-statistics with special regard to systems of mating. Evolution 19:395-420.

Young, Al. 2016. Biodiversity calculator for Simpson and Shannon Indexes. https://www.alyoung.com/labs/biodiversity_calculator.html?numberOfSpecies=18

FIGURES

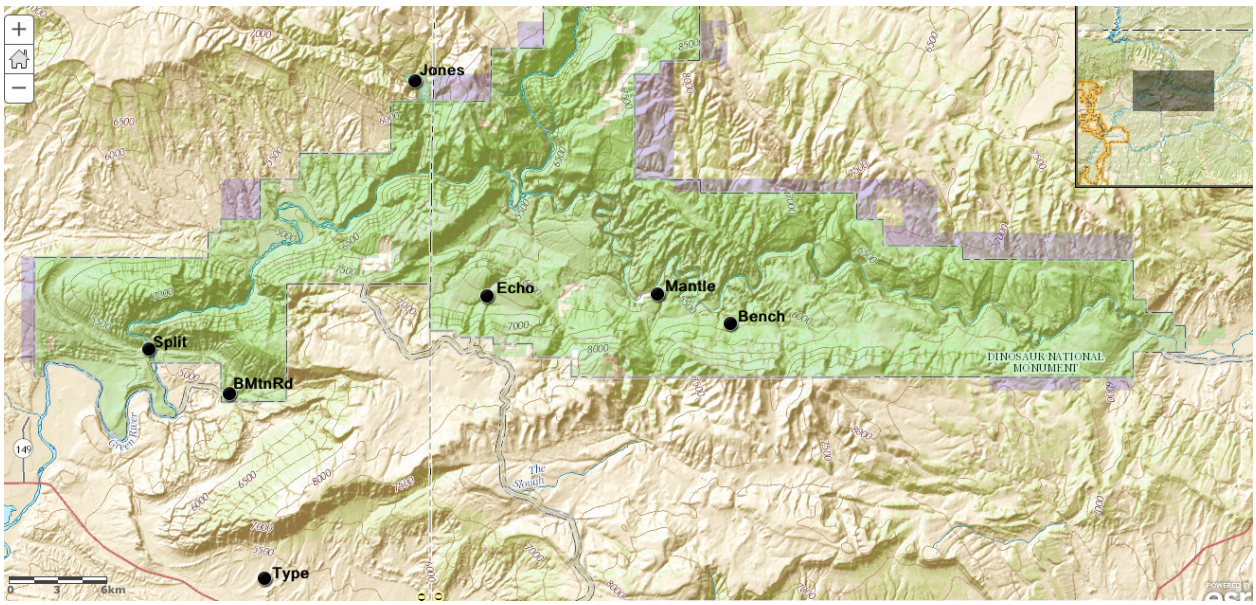

Figure 1. Locations of collecting sites for genetic and ecological sampling of *B. caeruleamontana* in Dinosaur National Monument and surrounding BLM lands in the Blue Mountain area of Utah and Colorado.

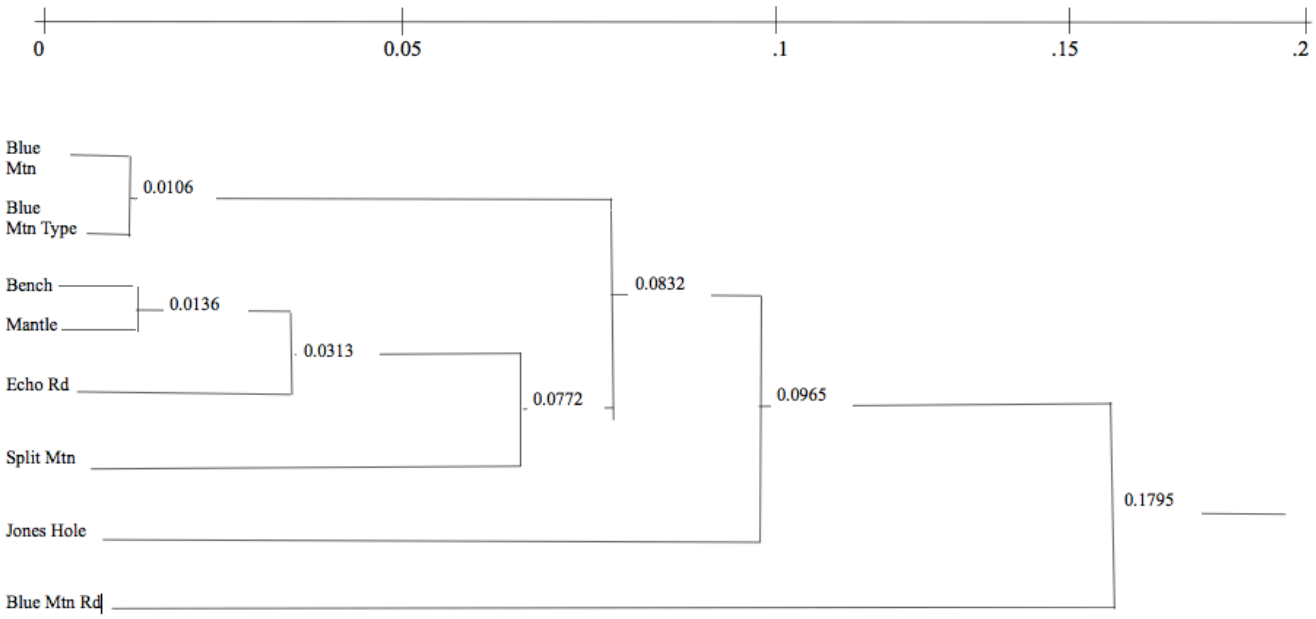

Figure 2. Phenogram of cluster analysis using the unweighted pair group method with arithmetic mean (UPGMA) based upon pairwise FST values among *B. caeruleamontana* study sites in Dinosaur National Monument and surrounding lands administered by the Bureau of Land Management.

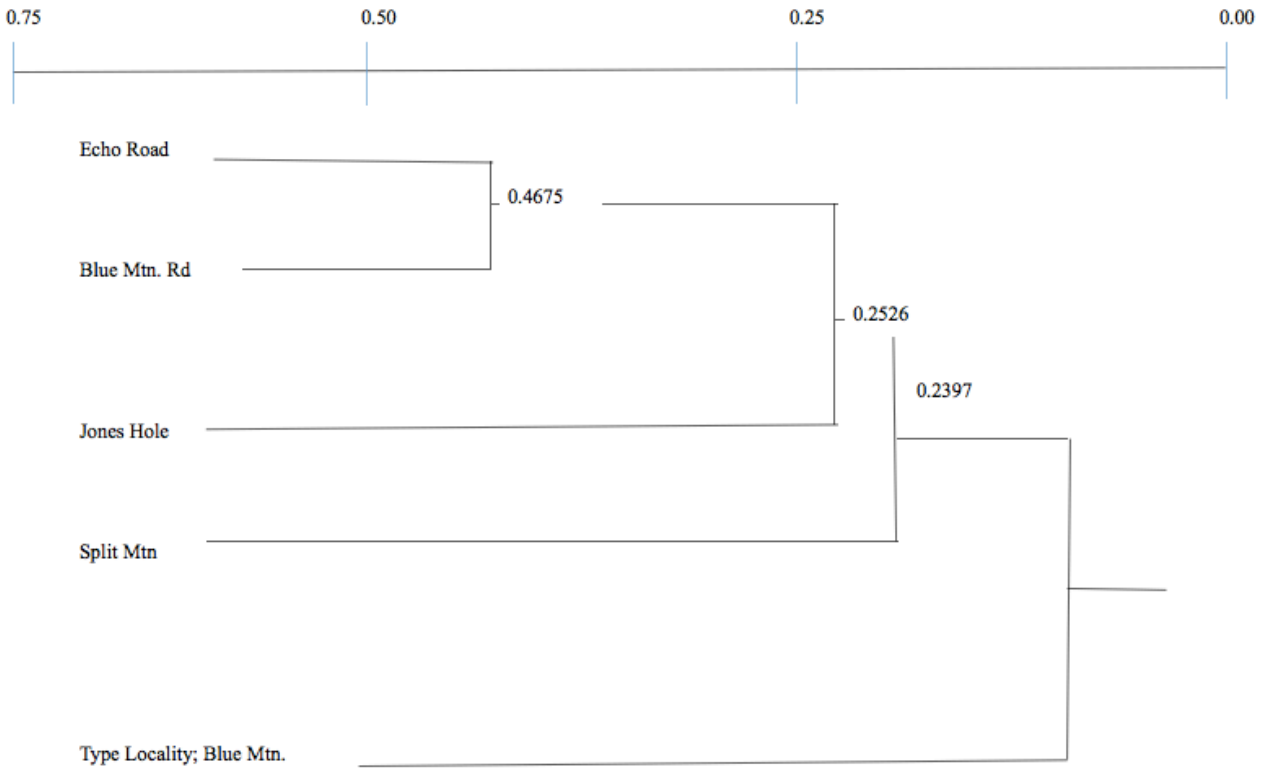

Figure 3. Phenogram of cluster analysis using the unweighted pair group method with arithmetic mean (UPGMA) based on relative frequency values of associated species at each study site using Ruzicka's (1958) pairwise index of similarity among *B. caeruleamontana* study sites in Dinosaur National Monument and surrounding lands administered by the Bureau of Land Management.

TABLES

Table 1. Site characteristics for the sampling localities of *B. caeruleamontana* used in this study from the Blue Mountain area in Utah and Colorado. * Indicates sites that we resampled at this site for this study.

Population (Sites)	**Land Ownership**	**Elevation**	**Latitude**	**Longitude**
Blue Mountain Type Locality (Type) *	DNM	7650 ft	40.35160° N	109.17340° W
Blue Mountain Road * (BMtnRd)	BLM	5200 ft	40.41405° N	109.19161° W
Echo Road-Sand Canyon (Echo) *	DNM	5800 ft	40.47639° N	109.00878° W
Jones Hole Fish Hatchery (Jones)*	BLM	5800 ft	40.58830° N	109.06040° W
Split Mountain Boat Ramp (Split) *	DNM	6200 ft	40.46930° N	109.05373° W
Bench Road (Bench)	DNM	5800 ft	40.45860° N	108.83200° W
Mantle Road (Mantle)	DNM	5800 ft	40.47430° N	108.88400° W

Table 2. Genetic diversity statistics among sampled populations of *B. caeruleamontana* in Dinosaur National Monument and surrounding lands administered by the Bureau of Land Management.. Values were determined using Genepop 4.2. Standard errors are shown in parentheses below each mean value. Means followed by the same letter are not significantly different at P≤ 0.10 (Statistics are generated using Kruskal-Wallis test with Dwass-Steel-Chrichlow-Flinger test for pairwise comparisons using Systat 13).

Population (Site)	**N**	***P*†**	**H_O‡**	**H_E#**	**A***	**A_p****	**A_{priv}*****	**H-W H Deficit Test°**
Blue Mountain$	6	0.533	0.276 ab (0.090)	0.303 ab (0.890)	2.74 ac (0.65)	4.0 a (0.91)	2	0.1414
Blue Mountain Rd	25	0.600	0.210 b (.072)	0.250 b (0.074)	3.0 ac (0.60)	4.33 a (0.71)	4	0.0000°
Type Local	38	0.533	0.284 a (0.082)	0.322 ab (0.084)	3.6 a (0.90)	4.9 a (1.16)	1	0.0046°
Echo Road	66	0.867	0.303 a (0.080)	0.444 a (0.091)	6.6 b (1.59)	7.46 b (1.66)	14	0.0000°
Jones Hole	69	0.933	0.343 a (0.076)	0.439 a (0.081)	6.07 ab (1.17)	6.43 b (1.19)	12	0.0000°
Split Mountain	38	0.800	0.279 ab (0.077)	0.389 ab (0.075)	3.87 a (0.89)	4.31 a (0.97)	1	0.0000°
Bench Road$	3	0.733	0.214 b (0.066)	0.395 ab (0.093)	2.14 c (0.33)	2.78 c (0.36)	1	0.0006°
Mantle Road$	6	0.600	0.260 ab (0.082)	0.373 ab (0.091)	2.73 ac (0.52)	3.89 ac (0.061)	2	0.0014°
Mean	31.4	0.699	0.271	0.364	3.84	4.761	4.625	

$Samples taken from herbarium specimens where there were multiple available from given area.
†Proportion of polymorphic loci across 15 loci sampled
‡ Mean observed heterozygosity
#Mean expected heterozygosity based on HW equilibrium model
*Mean number of alleles per locus
**Mean number of alleles per polymorphic locus
***Number of private alleles across all loci
°P-values for Hardy-Weinberg (U) test for heterozygote deficiency. Those followed by symbol are significant at P≤0.05.

Table 3. F_{IS} estimates (Weir and Cochran 1984) for each locus and each population of *B. caeruleamontana* generated using Genepop 4.2. Estimates followed by symbols are significant deviations from H-W equilibrium based on the Markov chain method (Guo and Thompson, 1992). Some of the loci had no allelic variation at a site for that locus and so those were left blank.

Locus	Blue Mtn	Blue Mtn Rd	Blue Mtn Type	Echo Rd	Jones Hole	Split Mtn	Bench Rd	Mantle Rd
I3	-0.2121	0.1688	-0.0157	0.1265*	0.0731†	0.0079	0.3333	0.5152*
A1	--	--	--	--	-0.0229	0.5375*	--	--
B20	-0.1111	-0.1200	-0.0291	-0.0710	0.0110	0.0715	-0.1429	0.6000
B11	--	--	--	--	--	--	--	--
C8	0.7059†	-0.0000	0.0397	0.3239*	0.1800*	0.4127*	0.5000	0.6923*
I14	--	--	--	0.1772	-0.0510	-0.0734	--	--
B9	--	0.3544*	--	0.7912*	0.7809*	0.8136*	1.0000	--
E9	0.4118	-0.1302	0.2115†	0.0425	0.0790	-0.0659	1.0000	-0.2000
B18	--	--	--	--	0.1163	--	--	--
BF3	0.0741	0.6054*	0.1633*	0.1942*	0.0867*	0.2637*	0.5000	-0.0811
B6	--	--	-0.250	-0.0111	0.1601	-0.0440	--	--
BF19	-0.1321	-0.2701	-0.0319	0.1341*	-0.0702	-0.0695	0.6667†	-0.0323
BF15	--	--	-0.0165	-0.0019	0.3674*	0.7944*	0.1111	0.4074
A3	-0.0526	--	-0.0250	0.9031*	-0.0136	0.3101	--	--
B266	--	0.6000*	0.8689*	1.0000*	0.8090*	1.0000*	--	0.4545†

Table 4. Pairwise geographic distance (above the diagonal) in meters and pairwise F_{ST} estimates for all 15 microsatellite loci (below diagonal) following Weir and Cockerham (1984). FST estimates were generated using Genepop 4.2. Since Blue Mtn General was samples from herbariums the sites were across a very large area it was difficult to determine just one geographic coordinate and determine geographic distance. For this reason, geographic distanc was not available for Blue Mtn General.

Population	Blue Mtn General	Blue Mtn Rd	Blue Mt Type	Echo Rd	Jones Hole	Split Mtn	Bench Rd	Mantle Rd
Blue Mtn Rd	0.1862	----	7108.70	16942.32	22312.41	13178.22	30815.37	26861.76
Blue Mt Type	0.0106	0.2061	----	19653.94	27983.54	16540.41	31239.56	27996.13
Echo Rd	0.0395	0.1238	0.0775	----	13177.75	3880.54	15074.97	10550.09
Jones Hole	0.0903	0.1537	0.1367	0.0806	----	13235.54	24081.63	19530.38
Split Mtn	0.0660	0.1614	0.1204	0.0580	0.0995	----	18783.47	14324.83
Bench Rd	0.0950	0.2627	0.1346	0.0320	0.1045	0.0812	----	4761.07
Mantle Rd	0.0397	0.1599	0.0974	0.0306	0.0674	0.0924	0.0136	----

Table 5. Soil characteristics for the five ecologically sampled sites of *B. caeruleamontana* in the Blue Mountain area of Utah and Colorado. Standard errors are given below the means. Means in a column followed by the same letter do not differ significantly at $P < 0.05$. *Indicates no statistical difference among sites for that measurement.

Site	**% Texture**				**Ion exchange**		
Site	**Sand***	**Silt***	**Clay***	**OM**	**pH**	**EC***	**%$CaCO_3$**
Type	70.96 ±1.21	17.42 ±2.14	11.62 ±1.19	7.02 ±0.90 *a*	7.2 ±0.3 *ab*	0.48 ± 0.04	1.82 ±0.36 *a*
BMtnRd	76.90 ±0.55	14.98 ±0.75	8.10 ±1.29	2.72 ±0.92 *a*	7.4 ±0.7 *a*	0.42 ± 0.08	2.07 ±0.19 *a*
Echo	67.83 ±4.64	20.70 ±3.15	11.47 ±1.50	1.53 ±0.47 *a*	7.3 ±0.5 *a*	0.53 ± 0.07	7.65 ±1.41 *b*
Jones	71.57 ±1.33	17.37 ±0.67	11.07 ±0.67	14.24±3.50*b*	6.3 ±0.4 *b*	0.88 ± 0.22	ND
Split	77.50 ±3.50	12.70 ±3.50	9.80 ±0.001	1.55 ±0.45 *a*	7.2 ±0.3 *a*	0.55 ± 0.05	3.75 ±1.65

Table 6. Values of elemental nutrients (ppm or mg/kg) from composite soil samples taken at sampled sites across the geographic range of *B. caeruleamontana* in the Blue Mountain area of Utah and Colorado. Standard errors are given below the means. Means in a column followed by the same letter do not differ significantly at $P < 0.05$. *Indicates no statistical difference across sites.

	Nutrients ppm						
Site	**P***	**NO_3N**	**K***	**Zn***	**Fe**	**Mn***	**Cu**
Type	12.08 ±1.78	7.92 ±0.77 *ab*	201.80 ±21.90	1.30 ±0.24	21.39 ±2.71 *ab*	5.83 ±1.25	0.39 ±0.05 *b*
BMtnRd	16.32 ±4.26	5.30 ±1.70 *a*	113.00 ±23.98	0.76 ±0.08	17.32 ±6.29 *ab*	9.99 ±6.64	0.17 ±0.08 *a*
Echo	4.97 ±0.69	1.28 ±0.25 *a*	64.17 ±19.01	0.87 ±0.15	7.05 ±0.86 *a*	3.87 ±0.79	0.23 ±0.03 *a*
Jones	21.34 ±8.24	40.18 ±20.02 *b*	255.60 ±84.37	ND	ND	ND	ND
Split	6.00 ±1.90	2.55 ±0.25 *a*	89.00 ±35.00	1.07 ±0.12	5.88 ±0.65	6.60 ±0.58	0.26 ±0.04

Table 7. Mean values of morphological characteristics collected at study sites for 20 tagged individuals at each sampling site across the geographic range of *B. caeruleamontana* in the Blue Mountain area of Utah and Colorado Statistical differences among sites for selected abiotic variables using one way analysis of variance generated with Systat 13 followed by the same letter do not differ significantly at $P < 0.05$. *Indicates no statistical difference across sites. ND stands for no data.

Site	Clump	Clump Area	#Rosettes	Avg Leaf Length	#Flowering	Fruits/Flowers*	Fruits/Stalks*
Type	29.5 ± 4.8 *c*	104.7 ± 397.0 *b*	118.1 ± 18.1 *ab*	12.1 ± 0.7 *a*	18.9 ± 5.4 *a*	ND	ND
BMtnRd	14.5 ± 2.0 *a*	229.0 ± 51.7 *a*	53.9 ± 10.8 *a*	9.4 ± 0.8 *b*	8.9 ± 2.6 *b*	ND	2.3 ± 0.5
Echo	11.5 ± 1.2 *a*	124.5 ± 22.51 *a*	51.9 ± 9.9 *a*	1.1 ± 0.1 *c*	4.4 ± 0.8 *c*	0.6 ± 0.0	4.4 ± 0.8
Jones	25.9 ± 2.7 *bc*	635.5 ± 129.1 *ab*	128.9 ± 14.3 *b*	11.9 ± 0.7 *a*	9.9 ± 1.8 *b*	0.7 ± 0.3	4.5 ± 0.4
Split	13.8 ± 30.8 *a*	181.4 ± 28.6 *a*	71.5 ± 12.1 *a*	0.6 ± 0.3 *c*	4.3 ± 0.8 *c*	0.7 ± 0.2	3.4 ± 0.7

Table 8. Reproductive characteristics from tagged plants at ecological monitoring sites for *B. caeruleamontana* in the Blue Mountain area of Utah and Colorado Standard errors are given below the means. Means in a column followed by the same letter do not differ significantly at P < 0.05. *Indicates no statistical difference across sites.

Sites	Seed/Ovule Ratio	#Ovules	#Filled Seeds	Prop. Undev. Ovules	Prop. Early Abortions	Prop. Partial Abortions*	Prop. Late Abortions
Type	0.55 ± 0.26 *a*	41.2 ± 11.1 *b*	22.2 ±10.9 *a*	0.5 ± 0.3 *a*	0.1 ± 0.2 *a*	0.1 ± 0.1	0.3 ± 02 *a*
BMtnRd	0.50 ± 0.16 *a*	48.8 ± 13.1 *a*	25.0 ± 11.9 *a*	0.6 ± 0.2 *ab*	0.2 ± 0.2 *b*	0.1 ± 0.1	0.1 ± 0.2 *b*
Echo	0.57 ± 0.16 *b*	50.4 ± 10.2 *a*	29.2 ± 11.1 *a*	0.6 ± 0.3 *ab*	0.1 ± 0.2 *ab*	0.1 ± 0.2	0.2 ± 0.2 *ab*
Jones	0.37 ± 0.29 *a*	44.7 ± 11.9 *ab*	17.0 ± 13.6 *ab*	0.8 ± 0.2 *bc*	0.1 ± 0.1 *a*	0.04 ± 0.1	0.2 ± 0.2 *b*
Split	0.37 ± 0.31 *ab*	29.9 ± 14.4 *ab*	14.1 ± 11.5 *b*	0.9 ± 0.1 *c*	0.04 ± 0.1 *a*	0.03 ± 0.03	0.1 ± 0.1 *b*
Overall	0.50 ± 0.24	45.2 ± 12.1	22.7 ± 12.5	0.6 ± 0.3	0.1 ± 0.2	0.1 ± 0.1	0.2 ± 0.2

Table 9. Heterogeneity measures for all sampled sites of *B. caeruleamontana* based upon relative frequency and relative cover values obtained from community data generated using a nested frequency quadrat frame (Greig-Smith 1983) and generated using biodiversity calculator software (Young 2016) based upon Simpson (1949) and Shannon (1948).

	Type	BMtnRd	Echo	Jones	Split
Species Richness	18	14	19	9	14
Simpson Index	0.135	0.180	0.138	0.214	0.139
Shannon Index	2.284	1.906	2.329	1.671	2.221
Species Dominance	0.865	0.820	0.862	0.787	0.862
Average Population Size	12.780	15.850	11.940	17.500	11.310

Table 10. Percent relative frequency and percent relative cover of all associated plant species at each study site of *B. caeruleamontana* in Dinosaur National Monument and surrounding areas in the Blue Mountain region of Utah and Colorado generated using a nested frequency quadrat frame (Grieg-Smith 1983). Species are grouped by life history strategy (trees, shrubs, grasses, forbs, other).

	Type		**BMtnRd**		**Echo**		**Jones**		**Split**	
	% Rel Freq	% Rel Cover	% Rel Freq	% Rel Cover	% Rel Freq	% Rel Cover	% Rel Freq	% Rel Cover	% Rel Freq	% Rel Cover
Trees:										
Juniperus osteosperma	**0.43**	**.**	**.**	**1.85**	**3.26**	**0.02**	**1.42**	**0.58**	**2.04**	**1.99**
Pinus edulis	**0.43**	**.**	**.**	**.**	**1.40**	**.**	**.**	**.**	**.**	**.**
Shrubs:										
Artemesia vaseyana	**1.30**	**3.11**	**.**	**.**	**.**	**.**	**.**	**.**	**.**	**.**
Amelanchier anifolia	**0.43**	**.**	**0.93**	**3.09**	**.**	**.**	**.**	**.**	**.**	**.**
Chrysothamnus viscidiflorus	**.**	**.**	**.**	**.**	**5.58**	**0.02**	**.**	**.**	**.**	**.**
Ephedra virdis	**.**	**.**	**0.47**	**.**	**2.00**	**0.68**	**.**	**2.92**	**.**	**.**
Symphoricarpus oreophilus var. utahensis	**6.09**	**2.48**	**1.40**	**0.62**	**.**	**.**	**0.71**	**2.92**	**.**	**.**
Grasses:										
Bromus tectorum	**.**	**.**	**25.23**	**8.64**	**26.98**	**9.52**	**28.57**	**1.17**	**28.57**	**5.30**
Oryzopsis hymenoides	**.**	**.**	**.**	**.**	**0.93**	**.**	**.**	**.**	**8.84**	**1.99**
Poa secunda	**23.91**	**11.80**	**22.90**	**9.26**	**10.23**	**4.76**	**12.86**	**1.17**	**3.40**	**.**
Forbs:										
Achillea millefolium ssp. Lanulosa	**0.43**	**0.62**	**.**	**.**	**.**	**.**	**.**	**.**	**.**	**.**
Alyssum alyssoides	**.**	**.**	**17.75**	**4.94**	**8.37**	**0.68**	**.**	**.**	**.**	**.**
Allium sp.	**.**	**.**	**0.46**	**.**	**.**	**.**	**.**	**.**	**.**	**.**
Antennaria microphylla	**2.61**	**0.62**	**.**	**.**	**.**	**.**	**.**	**.**	**.**	**.**
Boechera caeruleamontana nov	**18.70**	**21.11**	**11.21**	**3.70**	**20.00**	**6.12**	**28.57**	**11.11**	**4.08**	**1.32**
Boechera selbyi?	**.**	**.**	**.**	**.**	**.**	**.**	**.**	**.**	**5.44**	**0.66**
Chrysopis villosa	**.**	**.**	**.**	**.**	**.**	**.**	**.**	**.**	**2.04**	**.**

	Type		BMtnRd		Echo		Jones		Split	
Commandra umbellata var. pallida	.	.	.	.	.	.	.	.	7.48	.
Cryptanta humilis	.	.	3.27	0.62	0.93	.	.	.	.	.
Crypthana flava	.	.	0.93	.	.	.	.	.	.	.
Cymopterus acaulis var. acaulis	.	2.17	.	.	.	.	.	.	.	.
Delphinium sp.	6.96	0.62	.	.	.	.	.	.	.	.
Descurania sophia	.	.	.	.	1.86	0.68	.	.	.	.
Eriogonum umbellatum	.	.	1.40	.	0.47	.	.	.	1.36	.
Erigeron eatonii	1.30	.	.	.	.	.	.	.	.	.
Galium aparine var. echinospermum	.	.	.	.	.	.	5.71	.	.	.
Geranium viscosissimum var. armeriodes	.	.	.	.	.	.	.	.	4.76	0.66
Gilia inconspicua complex	.	.	1.40	0.62	0.47	0.68	18.57	1.17	1.36	.
Haploppapus aremeriodies var. armeriodes	.	.	.	.	.	.	.	.	4.76	0.66
Heuchera parvifolia	3.48	.	.	.	2.33	.	.	.	.	.
Lepidium montanum var. jonesii	.	.	.	.	.	.	8.16	.	.	.
Lomatium juniperinum	.	.	.	.	.	.	3.57	.	.	.
Mertensia oblongifolia	16.52	5.59	.	.	.	.	.	.	.	.
Opuntia polycantha	.	.	0.93	0.62	.	.	.	.	.	.
Phlox austromontana var. austromontana	.	.	.	.	3.26	1.36	.	.	.	.
Ranunculus glaberrimus var. ellipticus	4.78	.	.	.	.	.	.	.	.	.
Senecio integerriumus var. exaltatus	1.74	.	.	.	1.40	0.68	.	.	.	.
Senecio multiobatus	.	.	.	.	4.65	2.72	.	.	.	.
Thelesperma megapotamicum	.	.	.	.	.	.	.	.	17.01	0.66
Sphaeralcea coccinea	.	.	.	.	1.40	.	.	.	.	.
Taraxacum offinale	.	.	.	.	3.26	.	.	.	.	.

	Type		BMtnRd		Echo		Jones		Split	
Townsendia mensana	.	.	.	.	.	.	.	.	6.80	0.66
Veronica americana	6.96	.	.	.	.	.	.	.	.	.
Misc.:										
Lichen	.	.	.	.	.	.	.	0.58	.	.
Moss	.	3.10	.	5.56	.	8.16	.	28.07	.	10.60
Algae	.	.	.	.	.	.	.	0.58	.	.
Litter	.	44.10	.	18.52	.	27.21	.	23.29	.	20.53
Rock	.	0.62	.	17.90	.	10.20	.	10.53	.	29.14
Bare Soil	.	6.21	.	24.07	.	23.82	.	15.79	.	24.50
Pavement	.	.	.	.	.	.	.	.	.	1.99