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ORIGINAL ARTICLE

Local ecology and geographic ranges of plants in the Bishop Creek watershed of the eastern Sierra Nevada, California, USA

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ABSTRACT

Aim The physiological requirements and tolerances of a species partially determine both its habitat preferences within a community and its broader geographic range. Therefore, we predicted that local ecology should be correlated with geographic distribution. We tested for a correlation between local ecology and range size, and we attempted to account for this correlation by the climate of the range.

Location Bishop Creek Watershed, on the eastern side of the Sierra Nevada, California.

Methods We recorded all plant species growing in each of 263 plots in the montane to alpine zones of the watershed. The local habitat preferences of 282 species were described in terms of wetness, elevation, soil, and amount of shade. The size and centre of the geographic range for each species were determined from regional floras.

Results Wetness preference within the watershed was significantly correlated with range size. Specifically, plants of wet sites had larger ranges that extend to the north, whereas plants of dry sites tended to have smaller ranges centred to the east. The correlation between local wetness preference and range size was entirely explained by the location of the range centre of the species.

Main conclusions A possible reason for the large ranges of mesophilic plants in our study area is that mesic habitats are continuous throughout the western Cordillera, while dry alpine habitats are isolated by valleys to the east. The correspondence between local ecology and geographic distributions implies evolutionary stasis in the niches of these plant species.

Keywords

Alpine plants, endemism, niche, range size, Sierra Nevada, species distributions.

INTRODUCTION

All species have ecophysiological requirements and tolerances, and both their local niche occupancy and their geographic distribution depend on the availability of suitable habitat (Gaston, 1990). Range sizes have been correlated with a number of variables, including niche breadth, local abundance, body size, growth form, pollination syndrome, and dispersal mode (Bock & Ricklefs, 1983; Brown, 1984; Gaston & Lawton, 1990; Novotny, 1991; Gaston, 1996; Kelly & Woodward, 1996; Pyron, 1999). Most studies have demonstrated a positive relationship between local abundance and geographic range (Bock & Ricklefs, 1983; Gaston, 1990; Pyron, 1999). This correlation may depend on niche breadth, with species that are able to withstand a diversity of environments being successful at achieving high densities in many sites and at occurring throughout a large geographic area (Brown, 1984). Gaston & Lawton (1990) suggest that the correlation between local density and range size depends on the degree to which the habitat sampled, ‘the reference habitat’, resembles the habitat of the surrounding geographic area. Thus, it would be interesting to determine the degree to which physiologically important aspects of the reference habitat are correlated with characterizations of species’ ranges.

The characteristics of the geographic range of a species are partially determined by macrotopography and climate. The west side of the Cascades has an abundance of wet habitat with great connectivity, whereas the mountains that rise out of the Great Basin are drier and more insular. The abundance and connectivity of habitats partially determine the distribution of species that require those habitats. At a geographic scale, a species range ends where there is not enough habitat of a specific type for the species to be maintained. When a patch of suitable habitat is very small, a species is less likely to occur there because the chance of dispersal is decreased and the population may be too small to maintain itself (Brown, 1984). The edge of any species range is where that species can no longer survive or disperse to, i.e. where its density reaches zero. Spatial changes in habitat may be gradual (such as with incremental changes in latitude) or abrupt (such as where ocean meets land). Abrupt changes in elevation may represent abrupt changes in habitat for many species, such that mountain ranges may represent 'sky islands' whose shapes will determine the connectivity of habitat at a geographic scale.

Generalist species that can withstand a diversity of habitat types may become both locally abundant and widespread, resulting in a positive correlation between density and range size. This correlation can depend on the quality of the habitat (Novotny, 1991). In disturbed habitats, local abundance is positively correlated with range size because the most successful species are *r*-selected generalists. In contrast, local abundance is negatively correlated with range size and with niche breadth in undisturbed habitats, where *K*-selected species are most successful. Another possibility is that negative correlations between range size and abundance are cases in which the reference habitat differs from the surrounding geographic region, allowing specialists on the reference habitat to become abundant locally without occurring in other areas (Gaston & Lawton, 1990). The resulting communities are the product of species sorting themselves out according to their abiotic requirements and preferences as well as their biotic interactions with competitors, facilitators, and herbivores.

High altitude plant species on the eastern side of the Sierra Nevada have abrupt range discontinuities to the east because of the sudden drop in altitude. Similarly, altitude changes almost as rapidly to the west. However, high altitude habitat is continuous along the length of the Sierra and to the north up through the Cascade mountain range and beyond. We relate the size of the geographic range of plants to the way the species sort themselves out among habitats at a small scale. Our local study area was on the eastern side of the Sierra Nevada, in the upper reaches of the Bishop Creek watershed. We expected that the local site conditions in which a species is found within the watershed (the niche) should resemble the habitat of the range of the species. Stebbins (1982) found that mesophilic plants in the High Sierra were of the north, while xerophilic plants were of the east. Stebbins (1952) stated that semiarid areas are regions of rapid speciation due to isolation and specialization. The existence of many widespread species to the north, along with the specialized nature of dry-site plants led us to hypothesize that plants in wet sites would have large ranges, while dry-site plants would have small ranges.

Many of the classic floristic studies of the Sierra Nevada have attempted to describe the migratory routes of phytogeographic elements into the Sierra (Axelrod & Raven, 1985; Raven & Axelrod, 1978; Chabot & Billings, 1972; Klikoff, 1965). We will place our study on the local ecology and ranges of plants in this context by describing current knowledge of the geologic history of the western Cordillera. New geologic evidence suggests that high mountains have existed in the location of the Sierra Nevada for much longer than previously thought (Millar, 1993; Small & Anderson, 1995; House *et al.*, 1998; Chamberlain & Poage, 2000). The present geologic framework demands an updated interpretation of the origin of the Sierran flora.

MATERIALS AND METHODS

Study area

The Bishop Creek watershed, like the entire eastern slope of the Sierra, is very steep. The mean catchment slope, calculated from a digital elevation model based on a 30 by 30 m grid, is 48.6%. Wetness is also highly variable. There is little summer rain, so dry sites become very dry, while prolonged snowmelt allows sites near drainages to stay continuously wet. The watershed is composed of three large and several smaller basins that were glaciated during the Pleistocene. The highest peak is Mount Agassiz at 4234 m (13,891 ft.) elevation. Nearby is Mount Darwin at 4216 m (13,831 ft.), and it along with other high peaks and ridges was not glaciated due to wind exposure (Sharsmith, 1940; Hill, 2000). Our study includes the area above the sagebrush vegetation, which ends at an elevation of *c.* 2740 m (9000 ft). The study area encompasses *c.* 164 km^2 (64 mi^2) on parts of the Mt Darwin, Mt Thompson, and North Palisade USGS 7.5″ quadrangles.

Botanical inventory and taxonomic coverage

Over the last 20 years, an attempt has been made to record all vascular plants within the watershed, from the Sierran crest to the Owens River in the valley floor (Crowther & Crowther, 2002). At present the count is at 872 varieties (hereafter referred to as 'species'); 481 have been found above 2740 m (9000 ft). We will not report on the distributions of all of these plants. Grasses, sedges and rushes will not be treated here because they were too difficult to distinguish in field plots. Species that are usually from below 9000 ft. and that were never found in a plot were also excluded even if they have been occasionally recorded above 9000 ft. Alien species were excluded. Appendix 1 lists the 282 'species' included in the analysis. In a few cases, our taxonomic skills were imperfect or multiple names exist for plants of dubious distinction. When this was the case, we pooled two or three taxa before analysis. We also pooled *Gentianopsis holopetala* (A. Gray) Iltis and *Gentiana newberryi* A. Gray var. *tiogana* (A. A. Heller) J. Pringle because they bloom so late that it was impossible to distinguish them during the field season. Finally, during our first year of plot data we failed to distinguish *Cystopteris fragilis* (L.) Bernh. from *Woodsia scopulina* D. Eaton var. *scopulina*, although this was rectified the following year. Taxa that we pooled are shown in Appendix 1 as indented groups. Vouchers of taxa in Appendix 1 have been deposited in the herbarium at California State University, Northridge (SFV), except for a few rare taxa that we have not collected ourselves but studied at the herbarium of Rancho Santa Ana Botanical Garden (RSA). Information on species, subspecies, and varietal ranges was tabulated from regional floras, particularly Hickman (1993), Cronquist *et al.* (1972–97), and Hitchcock & Cronquist (1973). For the Brassicaceae, we used Rollins (1993).

Plot census

All the included plants were recorded in 263 plots of 100 m^2. We chose many of the plots merely to represent a variety of moisture conditions and elevations scattered across as many reaches of the watershed as feasible. Wet sites were surveyed beyond their representation in the landscape in order to have as many sites of differing moisture as possible. Plots were set down on top of unusual plant species that we came across, so rare species are included in plots more often than would be expected if plot locations had been chosen at random. This method enabled us to include many more species in our study than would have otherwise been possible. In general, the plots were circular and were delineated as the area within 5.64 m of a centre point. However, in some cases we adjusted the shape of the plot to conform to natural patchiness in the environment; for instance, along stream banks, we made the plot long and narrow to sample only that particular moisture regime. Wetness class, rockiness, slope, and shadiness were estimated for each plot. Wetness followed Stebbins (1982) as 1, usually dry; 2, often dry; 3, often wet; or 4, continually wet. Rockiness was categorized as 1, well developed soil; 2, gravel; 3, rock with gravel; or 4, essentially bedrock. Shadiness was 1, full sun; 2, mostly sun; 3, partial shade; 4, full shade.

Variables under study

For each 'species' included in our study, we compiled the following information. (i) Range centre was the direction of the centre of the range, i.e. north, east, south, or west of our study area. For many species, one direction was clearly appropriate because the central Sierra Nevada is near the edge of the range. When this was not the case, we sometimes knew the plant to be much more common in one direction (e.g. north) than others where it also occurs (south and east). Some plants, nevertheless, had to be given more than one direction, either because the Sierra Nevada is at the centre of its range or because we could not determine the direction in which the species was the most common. In addition, species with very limited ranges, such as those endemic to the Sierra Nevada, could not be categorized directly. For these species, we based the direction on the distribution of the closest relatives. In two cases, *Draba sierrae* Sharsm. and *Arabis pygmaea* Rollins, the closest relatives were uncertain, so we did not attribute geographic affinity. (ii) The range centre was used to describe the range tendency of the species, in which the climate of each region was categorized by moisture. The range tendency of plants whose range centres are to the north and northwest were classified as wet, while the range tendency of plants with ranges centred to the east, south, and northeast up to the eastern slope of the Cascades were classified as dry. Some plants whose ranges extended in more than one direction were assigned a range tendency of 'both', and were treated as missing cases in our analyses. (iii) We recognized four categories for range size: 1, endemic to only a portion of the Sierra Nevada and sometimes the adjacent White Mountains; 2, mainly restricted to the Sierra Nevada and parts of adjacent mountain ranges in the southern Cascades, Whites, Inyos, or Tehachepi Mountains; 3, with major extensions into areas not immediately adjacent to the Sierra Nevada, such as into the main part of the Cascades, the Transverse Ranges of southern California, or the mountains of the Great Basin; and 4, with ranges extending farther, into Canada, the Rockies, or Mexico. Pluses and minuses were sometimes assigned in borderline cases. (iv) Elevational preference was the median elevation of the plots in which we found a species in the watershed. We also have data on the maximum and minimum elevations at which we have found each species over the last 20 years (Crowther & Crowther, 2002), but we will use the median for statistical analyses. (v) For wetness preference within the watershed, we used the mean wetness of the plots in which a species was found, unless it was found in three or fewer plots, in which case we subjectively categorized its wetness preference on our 4-point scale. (vi) Rockiness preference was similarly treated as the mean of the rockiness of plots in which a species was found. (vii) Shade preference was the mean shadiness of plots in which the species was found.

Statistical analysis

Range sizes and tendencies were correlated against local habitat preferences by Spearman's rank correlations r_s. We treated each 'species' as having independently had the opportunity to move throughout the watershed into its preferred habitat. We then determined if the local preferences were related to geographic variables such as the size of the species' range. We treated each species as a separate independent data point. Lack of independence could be due to species interactions or because there are phylogenetic clusters of species with similar niche requirements. Thus, when we reject a null hypothesis, there are several possible explanations to be discussed. *P*-values will be reported using the *t*-test approximation for large sample sizes (equation 18.4 in Zar, 1996). Throughout the paper, we will note the results of significance tests as follows: $^{NS}P > 0.1$; $\dagger P < 0.1$; $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$. We have not adjusted for doing numerous tests. For each test, we are taking a separate risk of making a type I error (Zar, 1996).

In addition to studying correlations among species, we also examined relationships among plots. We will present multiple regressions of number of species in a plot and the mean range size of species in a plot as a function of plot wetness and elevation. Both number of species in a plot and the mean range size of species in a plot had residuals that were approximately normally distributed.

We go on to quantify for each common species the degree to which environmental variables determined its occurrences using multiple logistic regressions. We restricted these analyses to species found in nine or more plots. We modelled presence vs. absence as a function of wetness and the elevation of the plots in which it was found (Appendix 1). There are some problems with our use of logistic regression. The method is good at detecting relationships when a species' preferences are extreme, but it is poor at showing relationships for species that prefer sites with intermediate wetness or elevation. This is because logistic regression detects monotonic trends in the probability of finding a species. Although a unimodal model might have been more realistic, it would have had much less power, and significance tests would have to be implemented through randomizations. Second, the use of multiple logistic regressions holds one variable constant while looking at the effect of the other variable. Thus, when elevation is footnoted as significant, the presence of the species non-randomly depends on elevation while holding wetness constant (assuming both are monotonic and additive in their contribution to affecting the probability of occurrence).

Finally, we will present an ordination, implemented with PC-ORD (McCune & Mefford, 1999). The ordination was calculated only on the associations of the plants with one another. First, we use Beals' smoothing on a plot-by-species matrix to estimate the probabilities of species occurring in plots based on their associations with other species (whether they did or did not actually occur in the plots). This technique avoids the problem of many plots being equally dissimilar from one another in the form of not actually sharing any species. Using the Beals' smoothed matrix, we ran non-metric multidimensional scaling on Bray–Curtis distances to find a two-dimensional ordination in which the graphic distances from one plot to the next represent the dissimilarities in the plant associations. We rotated the output so that axis 1 was maximally correlated with plot wetness. The graphic to be displayed has wetness, elevation, rockiness and shadiness overlain on an ordination that was based only on the distributions of the plants.

RESULTS

After pooling we identified 277 terminal taxa (species, subspecies, or varieties); 231 of these 'species' were found in at least one plot. Appendix 1 lists the species included, characterizes their local ecological preferences, and describes several aspects of their geographic ranges. The most species-rich genera in the watershed were *Senecio* (nine species), *Potentilla* (nine), *Arabis* (nine), *Erigeron* (eight), *Draba* (seven), *Epilobium* (seven), *Eriogonum* (seven), *Mimulus* (seven), *Arnica* (seven), and *Saxifraga* (six).

There were 263 plots: 97 were categorized as usually dry, 55 often dry, 40 often wet, and 74 continuously wet. The plots were fairly evenly spread over the elevational range with 25% of plots below 3176 m (10,420 ft), 50% of plots below 3351 m (10,993 feet), and 75% below 3503 m (11,493 ft). Wet plots had a tendency to be of slightly lower elevation ($r_s = -0.147^*$). Extremely high plots had rocky soils ($r_s = 0.231^{***}$). Wet plots had well-developed soils ($r_s = -0.723^{***}$). Since about half of the elevational range of the study was above tree line, the amount of shade decreased with increasing elevation ($r_s = -0.484^{***}$). Shady plots tended to be wet ($r_s = 0.189^{**}$) with less rocky soils ($r_s = -0.226^{***}$). We focused our analysis on wetness and elevation, although these variables may also represent rockiness and shade, as well as other unmeasured aspects of the environment.

The local habitat preferences of species within the watershed

Wetness and substrate were strongly related to species presence vs. absence. Figure 1 shows a map of the plots, indicating their wetness and the occurrence of 10 species that have strong moisture preferences (five chosen as wet-site indicators and five chosen as dry-site indicators). The dry plots (white circles) tend to have more of the dry-site indicators, and the wet plots (black circles) have more of the wet-site indicator species. Species that live in wet sites also live in sites with well-developed soil ($r_s = -0.749^{***}$, $n = 227$). This is because moisture drains quickly from rocky boulders, while sites with well-developed soil retain moisture. Preference for shady sites was positively correlated with preference for wet sites ($r_s = 0.406^{***}$, $n = 227$). Plots that were wetter tended to have more species (mean = 16.8 vs. mean = 13.8). For number of species in a plot, the standardized partial regression coefficients were $b' = 0.171^{**}$ for wetness and $b' = -0.316^{***}$ for elevation (multiple $R = 0.383$).

Figure 2 shows a map of the study area that emphasizes indicator species with strong elevational preferences. The species that live at high elevations tend to live in dry places ($r_s = -0.285^{***}$, $n = 230$). Many of the species that live at high elevations prefer very rocky spots ($r_s = 0.401^{***}$, $n = 226$). These include some of the most abundant species, such as *Antennaria media* E. Greene, *Leptodactylon pungens* (Torrey) Rydb., *Monardella odoratissima* Benth. ssp. *pallida* (A. A. Heller) Epling, *Erigeron algidus* Jepson, and *Arenaria kingii* (S. Watson) M. E. Jones var. *glabrescens* (S. Watson) Maguire. The species found in many plots live in rocky places rather than in well-developed soil ($r_s = 0.207^{**}$, $n = 227$). Shade preference and elevation preference are negatively correlated ($r_s = -0.644^{***}$, $n = 226$). Plots at higher elevations contain fewer species than plots at lower elevations ($r_s = -0.329^{***}$, $n = 263$).

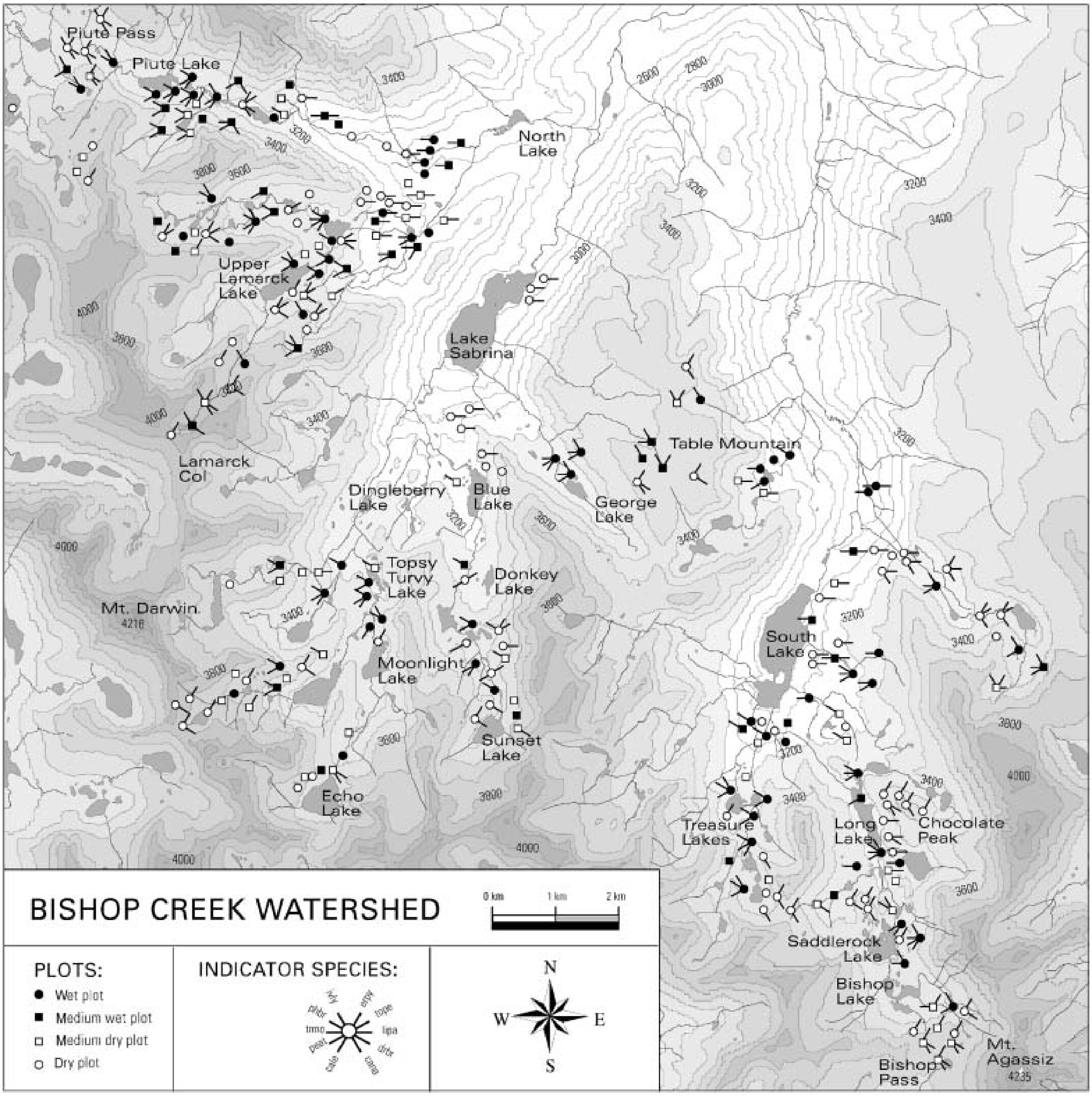

Figure 1 Map of the study area, with plots coded according to their wetness. The black plots are wet and the white plots are dry. Circles indicate extremes and squares indicate medium wet or dry preferences. The presence of mesophilic species is indicated with whiskers to the left of the plots: *Ivesia lycopodioides* A. Gray ssp. *scandularis* (Rydb.) Keck (ivly on map legend), *Phyllodoce breweri* (A. Gray) Maxim. (phbr), *Pedicularis attollens* A. Gray (peat), *Trifolium monanthum* A. Gray. var. *monanthum* (trmo) and *Castilleja lemmonii* A. Gray (cale). The presence of xerophilic species is indicated with whiskers to the right: *Erigeron pygmaeus* (A. Gray) E. Greene (erpy), *Tonestus peirsonii* (Keck) G. Nesom & R. Morgan (tope), *Linanthus pachyphyllus* R. Patterson (lipa), *Draba breweri* S. Watson (drbr), and *C. nana* Eastw. (cana). Elevation (m) is written on the isoclines, which are at intervals of 100 m.

Appendix 1 gives the wetness and elevational preference of each species. The niche occupancies of 32 species are displayed in more detail in Fig. 3. The figure shows four panels for species with different wetness preferences. Within each panel, the cumulative occurrence of eight species shows their elevational preferences. The slope of the curves shows how specialized they are to a narrow elevational band, with steep curves indicating specialization and shallow curves indicating generalization. These cumulative curves are the equivalent of the gradient analysis curves of Whittaker (1975, Chapter 4). Clearly, in the Bishop Creek watershed, there are species that prefer virtually all levels of wetness and elevation. Many species significantly prefer one extreme or another. This is evident from the logistic regressions done on each common species

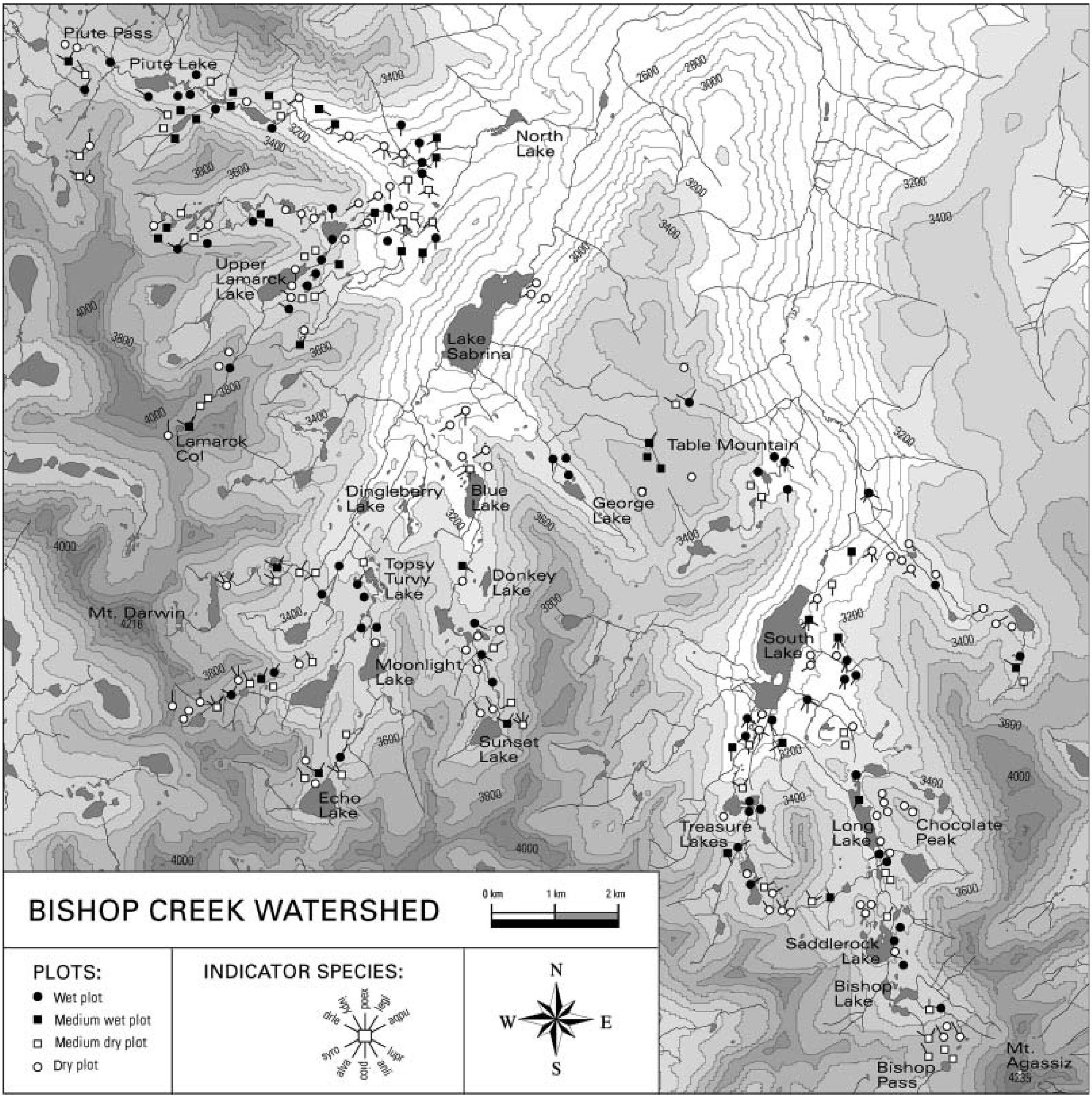

Figure 2 Map of the study area, showing the presence of elevational indicator species. High elevation species are indicated with whiskers pointing upward: *Draba lemmonii* S. Watson var. *lemmonii* (drle), *Ivesia pygmaea* A. Gray (ivpy), *Polemonium eximium* E. Greene (poex), *Ledum glandulosum* Nutt (legl), and *Aquilegia pubescens* Cov. (aqpu). The low elevation species are indicated with whiskers pointing downward: *Symphoricarpos rotundifolius* A. Gray var. *rotundifolius* (syro), *Allium validum* S. Watson (alva), *Pinus contorta* Loudon ssp. *murrayana* (Grev. & Balf.) Critchf. (pico), *Angelica lineariloba* A. Gray (anli), and *Lupinus pratensis* A. A. Heller var. *pratensis* (lupr).

(Appendix 1). For most species, presence vs. absence was related to wetness or elevation, or often to both.

Species varied in their degree of specialization, i.e. the degree to which they had niche preferences. For example, *Polemonium eximium* E. Greene is only found in the dry rocky zone above 3536 m (11,600 ft) elevation. In contrast, *Solidago multiradiata* Aiton occurs throughout the elevational range of the study, in all wetness classes and soil types. *Dodecatheon redolens* (H. M. Hall) H. J. Thompson specializes on wet areas but can exist at a variety of elevations. *Salix arctica* Pallas occurs in continuously wet areas above 3353 m (11,000 ft). None of the species occur in wet and dry plots within a narrow elevational range.

Our ordination (Fig. 4) revealed that species associations sort plots along axes of variation that strongly correspond to wetness ($r = 0.887$ with axis 1, $r = -0.034$ with axis 2) and elevation ($r = -0.317$ with axis 1, $r = -0.812$ with axis 2). The physical factors these axes represent drive much of the variation in plant associations within the watershed.

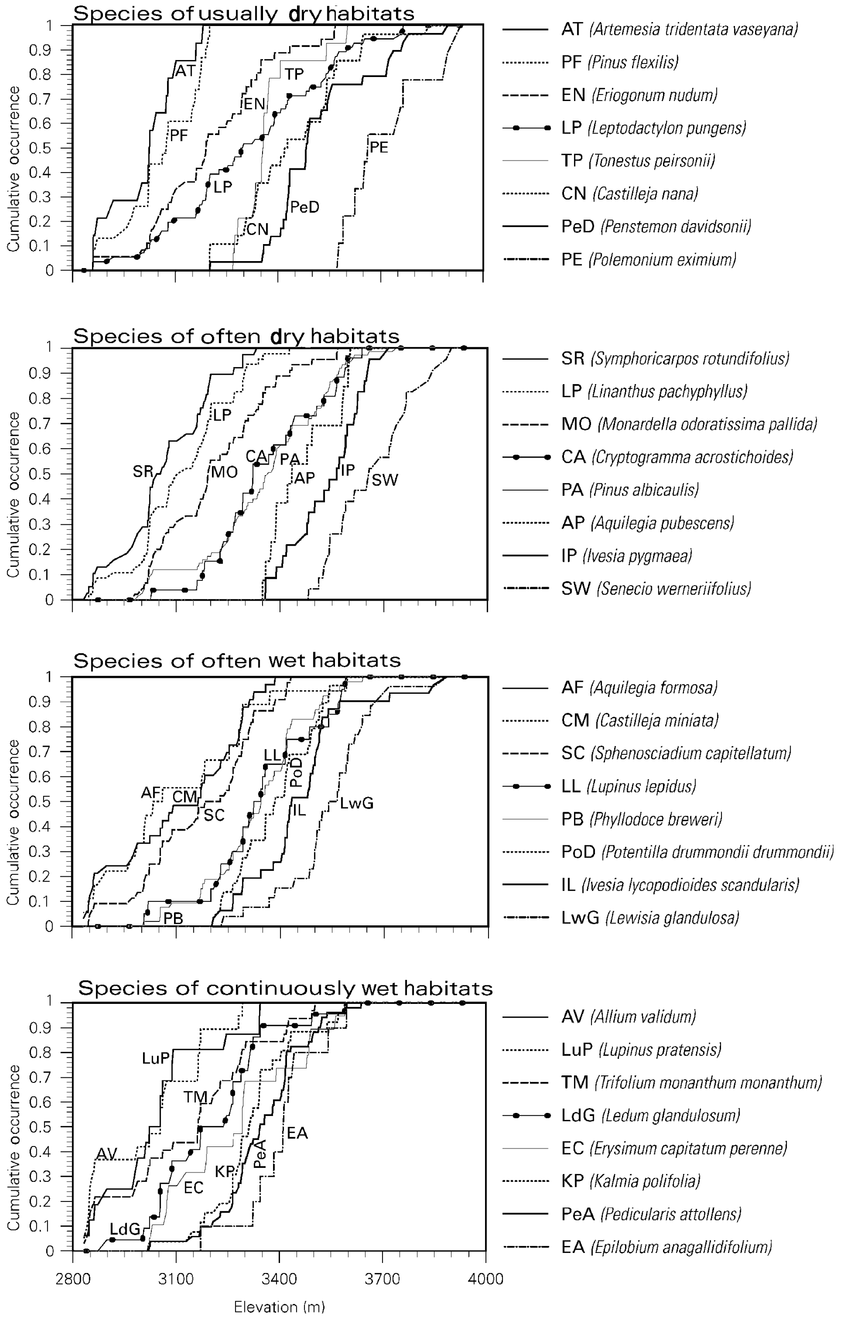

Figure 3 The distribution of occurrence of 32 species of plants in the Bishop Creek watershed by elevation and wetness preference. Cumulative occurrence is the number of plots in which a species occurs from the lowest elevation up to the elevation indicated (expressed as a proportion of the number of plots in which it occurred in the whole study). Lines to the left are low-elevation species; lines to the right are high-elevation species. Steep lines are elevational specialists; shallow lines are elevational generalists.

Relationships to broader geographic ranges

There were many species with large ranges and there were relatively few endemics: 58.1% had a range size of 4 or 4–; 17.0% had a range size of 3+, 3 or 3–; 16.6% had a range size of 2+, 2 or 2–; and only 8.3% had a range size of 1+ or 1 ($n = 277$). Wetness preference was positively correlated with range size ($r_s = 0.338^{***}$, $n = 277$; Fig. 5). Species such as *S. arctica*, *Epilobium anagallidifolium* Lam., *Arnica mollis* Hook., *Ledum glandulosum* Nutt., *E. peregrinus* (Pursh) E. Greene var. *callianthemus* (E. Greene) Cronq., *Orthilia secunda* (L.) House, and *Equisetum arvense* all occur in continuously wet places within the watershed and have very large ranges centred to the north of the study area. Species with smaller ranges, like *Chaenactis alpigena* Sharsm., *Castilleja nana* Eastw., *Astragalus lentiginosus* Hook. var. *ineptus* (A. Gray) M. E. Jones, *Tonestus peirsonii* (Keck) G. Nelsom & R. Morgan, *Sphaeromeria cana* (D. C. Eaton) A. A. Heller, *Penstemon papillatus* J. Howell, and *C. applegatei* Fern. ssp. *pallida* (Eastw.) Chuang & Heckard, prefer dry sites within the watershed and have small ranges centred to the east.

Range size is not necessarily directly responsible for wetness preference or vice versa. Instead, the range's centre and climatic tendency seems to explain the correlation between range size and wetness (Fig. 6). There were 103 'species' with ranges centred to the north, 95 to the east, seven to the south, and none

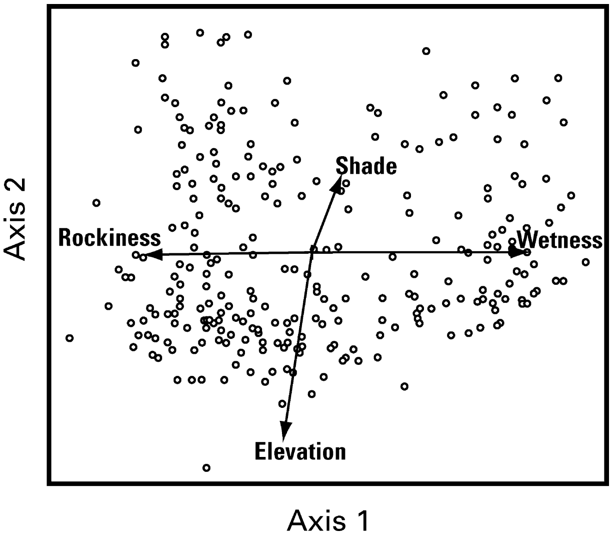

Figure 4 Ordination of plots based only on species with four environmental variables overlain after the analysis. Plots-by-species matrix was Beals smoothed. The transformed matrix was ordinated using non-metric multidimensional scaling of Bray–Curtis distances. The graph was rotated so that axis 1 corresponded maximally to wetness. Vectors represent correlations between the four environmental variables and the axes of the ordination. The length of the vector represents the strength of the correlation.

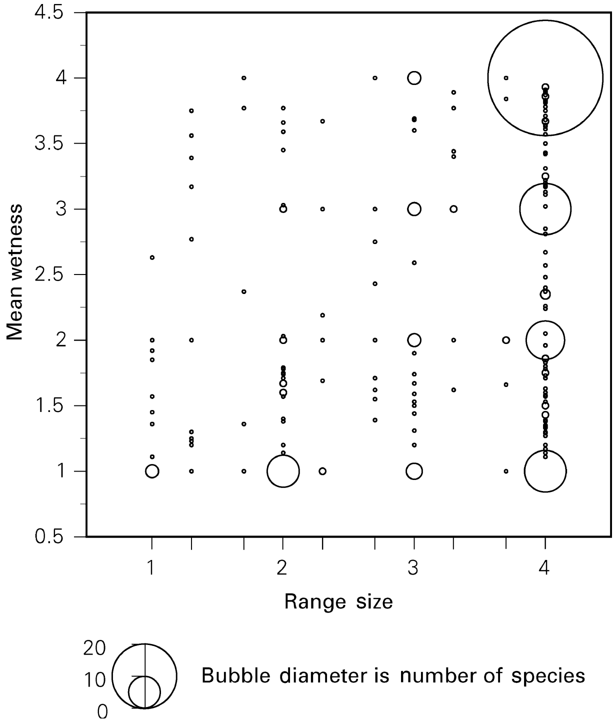

Figure 5 The relationship between the wetness preference of species and their range size.

to the west. Twenty-one had ranges centred to the north and east, eight to the south and east, and five to the north and west. Species with ranges extending to wetter places (e.g. the Cascades and the Arctic) tend to be widespread, and species with ranges extending to drier places (e.g. the mountains of the Great Basin) tend to have smaller ranges. We were unable to judge range tendency for 54 species, but of the remaining 223, 49.8% have range centres in drier regions, and 50.2% have range centres in wetter regions. Species with ranges in wet areas were found in wet plots ($r_s = 0.498^{***}$, $n = 223$) and have larger ranges ($r_s = 0.549^{***}$, $n = 223$). For example, *Botrychium simplex* Hitchc., which was found in wet places within the watershed, has a huge range centred in the wet Arctic. *Kalmia polifolia* Wangenh. ssp. *microphylla* (Hook.) Calder & Roy Taylor and *L. glandulosum* were both found in wet meadows within the watershed and have large ranges centred in the wet Cascades. *Swertia puberulenta* (Davidson) Jepson, found in dry plots, only occurs in the central and southern Sierra highlands and the White and Inyo Mountains to the east. *Astragalus whitneyi* A. Gray var. *whitneyi* also has a small range centred to the east, and occurred in dry sites within the study area. Partial correlation showed that the correlation between local wetness preference and range size disappeared when the range centre was held constant ($r_{\mathrm{wetness\backslash rsize \cdot rtend}} = 0.070^{\mathrm{NS}}$). There was a persistent correlation between local wetness preference and

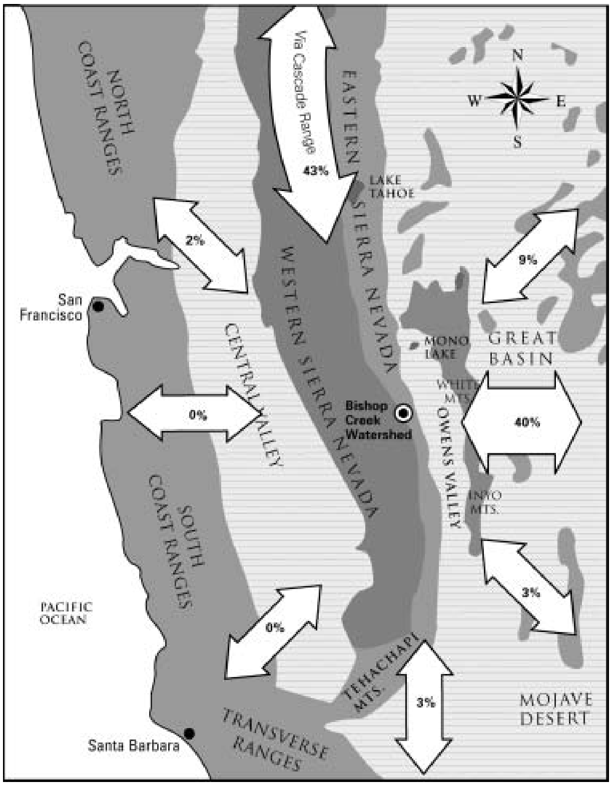

Figure 6 Map of Sierra Nevada and adjacent regions, showing the portions of the upper Bishop Creek flora with geographic affinities in each direction. Species ranges were categorized based on the direction in which the species is most common, e.g. a species common to the east but occasionally found to the north was coded as E. Percentages are out of 239; excluded were 40 species whose ranges extend in opposing directions, including cosmopolitan species.

range tendency even when range size was held constant ($r_{\text{wetness}\backslash\text{rtend} \cdot \text{rsize}} = 0.421^{***}$; $n = 223$).

Of course, wetness may not be the environmental variable *per se* that the species are responding to. Similar correlations could be presented for other variables that are correlated with wetness. The species with large ranges live in meadows, which have well-developed soil, while the endemics live in rocky well-drained substrate ($r_s = -0.219^{***}$, $n = 227$). Rockiness preference is correlated with range tendency ($r_s = -0.405^{***}$, $n = 184$). Wetness, the variable, may represent a combination of water availability, soil development, protected topography, and other factors. Similarly, elevation represents a combination of temperature, length of growing season, exposure to wind and sunlight, and atmospheric pressure.

The elevational preferences of species within the watershed were correlated with the size of their range ($r_s = -0.282^{***}$, $n = 230$) but not with their range tendency ($r_s = -0.080^{\mathrm{NS}}$, $n = 186$). This pattern is due to low-elevation dry-site species having large ranges to the east and south. Species found only at very high elevations, like *P. eximium* and *Cryptantha nubigena* (E. Greene) Payson, tend to have small ranges, while species found at low elevations, like *Cercocarpus ledifolius* Nutt. var. *intermontanus* N. Holmgren and *Pyrola minor* L., tend to have large ranges. The lack of correlation between elevational preference and range tendency is a bit surprising, since most high-elevation species are from dry areas. However, at mid- and low-elevations, species are from both wet and dry areas. *Chamaebatiara millefolium* (Torrey) Maxim. and *C. linariifolia* Benth. are found at low elevations and have large ranges, but they occur in dry areas to the east. Other low-elevation wide-ranging species, like *Trifolium longipes* Nutt. var. *nevadense* Jepson and *Mimulus guttatus* DC., occur in all directions from the watershed, so they were excluded from the analysis.

The abundance of species (number of plots in which each species was found) was negatively correlated with range size ($r_s = -0.130^{*}$, $n = 277$). *Salix orestera* C. Schneider, *Silene sargentii* S. Watson, *Linanthus pachyphyllus* R. Patterson, *P. heterodoxus* A. Gray var. *heterodoxus*, *E. pygmaeus* (A. Gray) E. Greene, *Lewesia glandulosa* (Rydb.) Dempster, *Pyrrocoma apargioides* (A. Gray) E. Greene, *D. lemmonii* S. Watson var. *lemmonii*, and *C. applegatei pallida* are all examples of species with small ranges that were found in many plots. *Pyrola asarifolia* Michaux ssp. *asarifolia*, *M. suksdorfii* A. Gray, *Potentilla flabellifolia* Hook., *Oxytropis borealis* DC. var. *viscida* (Nutt.) Welsh, *P. speciosus* Lindley, *Saxifraga nidifica* E. Greene var. *nidifica*, and *Fritillaria atropurpurea* Nutt. are all examples of species found in few plots that have large ranges.

We did a series of analyses attempting to relate degree of 'niche specialization' to range size and range tendency. Our three measures of a species' niche specialization were the standard deviation in the wetness of plots, the interquartile range in the elevation of plots, and McFadden's ρ^2 from the logistic regression of presence vs. absence on wetness and elevation. This was done on a data set consisting of species found in nine or more plots ($n = 97$ species). Generally, there were no strong correlations between the degree of specialization and range tendency or range size. There was one significant correlation, a positive one between ρ^2 values and range size ($r_s = 0.200^{*}$). The more that elevational and wetness preference explain the distribution of a species within the watershed, the larger its range size is likely to be. In other words, specialists have large geographic ranges. Range size, however, was not significantly related to the standard deviation in wetness ($r_s = -0.027^{\mathrm{NS}}$) or the interquartile range in elevation ($r_s = 0.041^{\mathrm{NS}}$). Similarly, range tendency for wet vs. dry regions was not significantly related to standard deviation in wetness ($r_s = -0.101^{\mathrm{NS}}$), interquartile range in elevation ($r_s = -0.053^{\mathrm{NS}}$), or ρ^2 ($r_s = 0.107^{\mathrm{NS}}$). Thus, it would appear that the degree of specialization is not (much) correlated with the size of a species' range or the tendency to extend to wetter vs. drier regions.

Among plots for mean range size, the standardized partial regression coefficients were $b' = 0.255^{***}$ for wetness and $b' = -0.480^{***}$ for elevation (multiple $R = 0.579$). Plots that were wetter tended to have plants with larger range sizes. Continuously wet plots had a mean range size of 3.29, while usually dry plots had a mean range size of 3.04. The mean range size of the species in higher elevation plots tended to be less than the mean range size of species in lower elevation plots.

Response to the suggestion of a phylogenetic analysis

In interpreting the correlations between ecological preferences and geographic ranges, one might wish for a phylogenetic analysis (Brooks & McLennan, 1991; Kelly & Woodward, 1996). Imagine that we are dealing with only two genera that each contain many species. Let one genus have species that are mesophilic, and for completely unrelated reasons, let its members also have great dispersal abilities that prevent ranges from becoming fragmented thereby giving its species large ranges. Let the other genus have species that are xerophilic, and for genetically and physiologically unrelated reasons, let it have poor dispersal abilities that result in smaller ranges. This would yield a correlation that is due to common ancestry, not to wetness preference affecting large ranges or to large ranges being associated with species from wet places that prefer wet habitats within the watershed.

One might suggest an analysis that controls for phylogeny, to look for a correlation between changes in ecological preferences and changes in range size. This is not feasible with the current data set. The usual methods for taking into account phylogeny focus on differences between closely related species in order to study correlated convergence (Felsenstein, 1985; Grafen, 1989; Rohlf, 2001). The species in this study are spread over many genera and families that contain species with all sorts of ecological preferences and geographic ranges, so except at the tips of the (poorly resolved) phylogeny one would only remove the effects of deep and irrelevant phylogeny.

Luckily, our study includes many genera, so the possibility seems remote that the patterns are merely phylogenetically confounded happenstance. We tested to see if the correlations hold up without pseudoreplicating within genera. We took our original data set (Appendix 1), and shortened it so that each genus was represented by only one species. We selected the species in each genus with the smallest range so as to counteract the disproportionate number of species with range sizes of 3 and 4. When two or more species tied in range size, we kept the one that was found in the most plots. This preserved as much power as possible. We deleted species without considering local wetness preference, which we believe has been free to vary as the community in the watershed has developed. After doing this, we found that among genera as represented by the species with the smallest range, wetness preferences was still positively correlated with range size ($r_s = 0.293^{***}$, $n = 143$) and as before even more so with range tendency ($r_s = 0.451^{***}$, $n = 118$). It seems safe to assume that essentially all the genera have histories that are separate enough to be phylogenetically independent. If one considers the whole diversity in each genus (not just the species in the watershed), then essentially all the genera contain species with many different range sizes, elevational affinities, and ecological preferences.

DISCUSSION

Wetness and elevation represent two very important axes of variation in the plant community of the Bishop Creek watershed. Furthermore, the behaviour of plants within the watershed reflects their broader geographic distributions. Nearly all plants have ranges that extend to comparably high elevation regions, not to nearby lowlands. Additionally, there was a persistent correlation between wetness preference within the watershed and features of the geographic range. These results are easily understood under the proposition that both the local ecology and the geographic range are partially determined by the species' ecophysiological requirements and tolerances. Species found locally in wet areas have ranges that extend to wet regions in the north. Species found locally in dry areas have ranges that extend to dry regions in the east. Local adaptation has not overwhelmed the ecological characteristics of the species.

The mystery that remains is why mesophilic species have large ranges while species with small ranges live in dry rocky places. Three possible explanations come to mind. (1) The pattern is a result of the decrease in species diversity with increasing latitude. Species of the north have larger ranges. There are wet regions to the north. These mesophilic widespread species have filled the wet niches in the eastern Sierra. (2) The pattern is a result of the geographic role of the Sierra Nevada as a sky peninsula of mountains. Species from the 'continent of mountains' to the north naturally have large ranges. Plants of dry sites are more isolated from dry mountains and have diverged due to this isolation. (3) Life in a wet alpine meadow is the same over large geographic ranges. Plants in wet places experience more intense competition than plants of dry habitats, and the structure of that competition may be largely the same throughout the mountains of western North America. Plants of dry habitats presumably have more abiotic difficulties to overcome, and these abiotic factors may vary geographically promoting local endemism (Stebbins, 1952). There may be other explanations as well.

We will structure the rest of our discussion around two topics. First, we will discuss the floristic history of the eastern Sierra Nevada and the floristic elements it shares with other provinces. Second, we will explore the causes and consequences of differences in range size and how range size correlates with niche factors.

Geographic affinities

Botanists have generally thought of the Sierra Nevada as a young Pliocene mountain range into which floristic elements have migrated (Klikoff, 1965; Chabot & Billings, 1972; Raven & Axelrod, 1978). Geologists now think that high mountains have been in the region as far back in time as the Cretaceous (House *et al.*, 1998). There seems to have been some isostatic uplift during the late Cenozoic, resulting in an increase in the elevation of the highest peaks of the Sierra, but the uplift was probably caused by erosion of the western flank and a *decrease* in the mean elevation (Small & Anderson, 1995). The age of (T–Th)/He apatite along rivers on the western side of the Sierra suggests very high topography as long ago as 50–60 Myr (Wernicke *et al.* 1996; House *et al.*, 1998), and stable isotopic data of oxygen and hydrogen originating from rainwater and incorporated into volcanic ashes on the east side indicate that a very major rain-shadow has existed back to 16 Ma and presumably to even more remote ages (Chamberlain & Poage, 2000; Poage & Chamberlain, 2002). The change in thinking about the geologic age of the Sierra Nevada calls for a change in thinking about Sierran plants as well. The Sierra was once described as a place with little *in situ* speciation, making it possible to trace the phytogeographic derivation of many of the plants (e.g. Chabot & Billings, 1972; Taylor, 1977; Raven & Axelrod, 1978; Stebbins, 1982). Now, the province must be considered as a possible source of alpine plants to surrounding mountain areas.

The Great Basin region has been undergoing extension for at least the last 15 Myr (Sonder & Jones, 1999). The area of Nevada was once narrow, and the high Sierra may have once been better connected to a high-elevation plateau to the east. Fossil leaves from several sites in western Nevada suggest that the area was around 2900 m (9514 ft) and moister than the current mountains of the Great Basin (Wolfe *et al.*, 1997). Over millions of years, the underlying crust was stretched thin, resulting in subsidence of the region as a whole, while expansion and faulting caused grabens and half-grabens to drop in elevation between the ranges (DeCourten, 2003). Sedimentation in the basins indicates that they have been lower than the surrounding mountains for 3–12 Myr (Trexler *et al.*, 2000). During much of the Miocene, the basins are thought to have been more mesic than they are currently, with aridity increasing in the Pliocene as the region fell relative to the Sierra's rain-shadow (Grayson, 1993, Wolfe *et al.*, 1997, Trexler *et al.*, 2000). During the Pleistocene, there were cycles of warm-dry climates and cold-wet times. During the glacial intervals, large pluvial lakes, like the Great Salt Lake, occupied the bottoms of many of the basins. We suppose that alpine plants in the Sierra have been isolated from the high mountains of the Great Basin (e.g. Toiyabe mountains) about to the extent that they are now for several million years although the vegetation of the lowlands has undergone great fluctuations, perhaps allowing for easy migration of species we think of as being of the montane zone.

The subduction that created the Cascades was active as early as the Eocene (Reiners *et al.*, 2002). The western Cascade Mountains began to form *c.* 25 Ma (Alt & Hyndman, 1991). During the early Miocene, volcanic activity in Oregon shifted to the east. Volcanism resumed in the Cascade Range at the end of the Miocene, and has continued through the present. In the northern Cascades, Miocene uplift produced high elevations (Reiners *et al.*, 2002). Pollen and whole plant fossils indicate a warm and mesic early Miocene climate throughout eastern Washington and Idaho, suggesting that the Cascade Range was not yet tall enough to create a rain-shadow (Wolfe, 1981). By the late Miocene, there was a fairly continuous band of high altitude habitat in western North America from the Sierra Nevada up through the Cascades into northern Alaska, although there were short breaks in the continuity of the mountains, as between the current Mount Lassen, Mount Shasta, and Mount Ashland.

Many ecologists have attempted to divide the flora of the High Sierra into floristic elements based on geographic affinities. Stebbins (1982) divided the flora into four categories, Chabot & Billings (1972) divided the flora into three units, and Sharsmith (1940) identified nine. On a broader scale, McLaughlin (1989) used local floras to describe floristic provinces throughout the western USA. His Sierra Nevada floristic element is a narrow belt extending into Oregon but separate from the northern Cascades. In this study, the range centres of the plants fall into categories similar to phytogeographic elements. However, we view the range centres as the direction between which genetic material is exchanged presently or has been exchanged in the past. We do not presume that all plant species migrated *to* the Sierra Nevada *from* their range centres.

Stebbins (1982) considered 19% of the Sierra's flora to be from lowland California, with the preponderance of those species living in dry sites within the Sierra. Stebbins' concept of a species' derivation took into account the range of other species in the genus as well as the species' own range. None of the plants we found in the Bishop Creek watershed on the eastern side of the Sierra had species ranges centred to the west. There were a few species with ranges centred to the south, but these are species that extended to the high Transverse Ranges, so they are not lowland California species. McLaughlin (1989) also noted an abrupt transition between the Sierra Nevada floristic element and the Californian element to the west. Clearly elevation represents a largely static aspect of many plants' niches.

Botanists often comment on the high numbers of annuals in the alpine flora of the Sierra Nevada in comparison with the Cascades and Rockies. The Sierra's annuals have usually been considered to derive from the Great Basin flora (Chabot & Billings, 1972; Axelrod & Raven, 1985). Within the elevational limits of our study, we found 12 annual taxa and 11 weak perennial taxa. Some of these, however, were species that just made it above our 2740 m (9000 ft) elevational cut-off. Eleven of the 23 were found above 3353 m (11,000 ft) elevation. The reason often given for the high numbers of annual alpine plants is that the alpine Sierra Nevada has drier summers than other North American mountain ranges, which allows for desert annuals to occur in the alpine zone (Chabot & Billings, 1972; Axelrod & Raven, 1985). Chabot & Billings (1972) state that the high elevation plants are primarily lower elevation species that only ephemerally occur in the alpine zone. We believe that this is not the case for the truly montane annual species we found in multiple plots: *Collinsia parviflora* Lindley, *Polygonum minimum* S. Watson, *P. polygaloides* Meissner ssp. *kelloggii* (E. Greene) J. Hickman, and *M. breweri* (E. Greene) Cov. *Collinsia* as a genus may be characteristic of lowland California, but *C. parviflora* itself ranges widely in high mountains. The *Polygonum* species have ranges extending to the north, and *M. breweri* ranges to the north and east. There may be a connection to plants of low elevation if deeper phylogenetic relationships are considered, but this is not evident in the species-level ranges of our plants.

The plants with ranges extending to the east of the study area occur in the high mountain ranges of the Great Basin rather than in the lowlands. Evidently, it is very difficult to become adapted to growing at high elevations, and it is a relatively rare phylogenetic innovation. In contrast, others seemed to think that Great Basin plants in the Sierra are from the lowland deserts (Taylor, 1976; Stebbins, 1982; Axelrod & Raven, 1985). Taxa from families whose representation in the alpine flora increases to the south (Scrophulariaceae, Polemoniaceae, and Ranunculaceae) are suggested to have colonized the Sierra from lowland areas (Taylor, 1977). In general, the alpine plants of the region are described as having migrated from the north during the Pleistocene glaciation or as differentiating from drought-adapted lowland taxa (Axelrod & Raven, 1985). For example, Chabot & Billings (1972) suggest that *Calyptridium umbellatum* (Torrey) E. Greene is from the lowland desert because there are many species of the genus *Calyptridium* in the deserts of the Great Basin. We see *C. umbellatum* as a species with affinities in the mountains to the north, with its alpine nature probably predating the Great Basin deserts. *C. nubigena* and *Ivesia pygmaea* A. Gray have also been given as examples of species derived from the Great Basin lowland flora (Chabot & Billings, 1972). We believe that these species arose in the Sierra Nevada but not necessarily from lowland species.

The Sierra Nevada experienced repeated periods of glaciation during the Pleistocene, which caused changes in the distributions of most plant species known from pollen records and packrat middens (Koehler & Anderson, 1995; Woolfenden, 1996). Glaciation must have disturbed the habitat of many alpine plants, causing some to become locally extinct, some to move down-slope where conditions became like the alpine habitat to which they were adapted, and others to be restricted to the high wind-swept peaks in refugia, or 'nunataks' (Sharsmith, 1940). For example, *P. eximium* and *Hulsea algida* A. Gray survived glaciation in special unglaciated sites (Chabot & Billings, 1972). These species still occupy high unglaciated ridges and peaks. *Penstemon davidsonii* E. Greene var. *davidsonii* and *Aquilegia pubescens* Cov., both high elevation species that hybridize with their low-elevation relatives, may have differentiated by being isolated on nunataks (Chabot & Billings, 1972). The very high species in our study have small ranges, indicating a possible Sierran origin, but this does not confirm or refute the nunatak theory.

Vegetation in the surrounding lowlands was semi-arid during the Pleistocene. For example, the late Pleistocene Owens Valley flora was probably quite different from that of the High Sierra, including *Yucca whipplei* Torrey, *Y. brevifolia* Engelm., and *Juniperus osteosperma* (Torrey) Little (Grayson, 1993). In the Alabama hills just to the east of the Sierra, packrat middens provide a 31,500-year record of woody plants suggesting that throughout the Pleistocene the lowlands were occupied by a series of desert vegetation types. The community first included *J. osteosperma* and *Y. brevifolia*, then *Purshia glandulosa* Curran and *Ephedra viridis* Cov., and eventually *Opuntia echinocarpa* Engelm. & J. Bigelow and *Lycium andersonii* A. Gray (Koehler & Anderson, 1995). Very few of the species in our study were recorded from these middens, and all are species characteristic of the lower end of our elevational coverage, like *P. tridenta* (Pursh) DC.

With the shrinking of the glaciers, expanded Sierran alpine habitat would have been re-colonized by the species that had moved down-slope or were isolated in nunataks. Additional species may have migrated from surrounding mountainous regions to occupy the unglaciated habitat. So far as is known from limited fossils, the composition of the Sierran plant communities has not changed dramatically since the Pliocene, indicating that glacial periods caused extinction in glaciated areas and recolonization of deglaciated areas without much change in community composition (Millar & Woolfenden, 1999). The Western Cordillera pre-dates the Pleistocene glaciation. North–south migration may or may not have been disrupted during glacial periods, but gene flow resumed during the Holocene.

In summary, the Cascade Mountains have long provided a migration corridor between the Sierra Nevada and areas to the north for alpine species to colonize high elevation sites (Chabot & Billings, 1972; Taylor, 1977; Stebbins, 1982). Lowland plants have remained restricted to low elevations. Mountain ranges to the east allow for some east and westward migration of alpine plants, but the Great Basin desert has served as a barrier restricting colonization at least since the Pliocene (Chabot & Billings, 1972; Morefield, 1992; Trexler *et al.*, 2000) and possibly as early as the Eocene (Wolfe *et al.*, 1997). Within the eastern Sierra Nevada, dry sites exist that are too xeric for the northern plants, and these sites contain high elevation species that also occur in dry areas to the east. The east–west migration route is less facile, and the resulting isolation has led to some differentiation. Thus, the dry-site species include narrow endemics whose closest relatives occur in the east, and the wet-site species have large ranges centred to the north.

Range size

The majority of species in our study area have relatively large ranges. The narrow endemics in our study area are *A. pubescens*, *C. applegatei pallida*, *A. pygmaea* Rollins, *A. repanda* S. Watson var. *greenei* Jepson, *A. lentiginosus ineptus*, *C. glomeriflora* E. Greene, *D. lemmonii lemmonii*, *D. sierrae*, *I. muirii*, *I. pygmaea*, *Phlox dispersa* Sharsm., *P. eximium*, and *T. peirsonii*. With the exception of *C. glomeriflora* (essentially a sagebrush species that just makes it into our study area), these are all high elevation species that form woody caudices. *Draba lemmonii lemmonii* and *P. eximium* are particularly high elevation specialists. The Sierra Nevada is characterized by a relatively large number of endemic species, although the percentage of endemism is low in comparison with the rest of the state (14% for the Sierra Nevada according to Stebbins, 1982, as opposed to around 30% for the state as a whole). This is because the Sierra is connected to mountain ranges in the north (Shevock, 1996). Genera with species endemic to the High Sierra include *Lupinus*, *Castilleja*, *Draba*, *Ivesia*, and *Hackelia* (Stebbins, 1982). *Eriogonum*, *Astragalus*, and *Mimulus* are the genera containing the most endemic taxa in the entire Sierra Nevada (Shevock, 1996). The High Sierra is definitely the centre of distribution for *Ivesia* (Stebbins, 1982).

The density of rare species often appears to be inflated, because they are interesting and of political importance, so people look out for them and record every sighting (Gaston, 1990). Similarly, our abundance data could be criticized because plots were not placed randomly throughout the landscape. We made a special effort to include rare plants in our study, but their abundance is probably not inflated enough to distort the correlations of abundance with other variables. The number of plots in which a species was found was negatively correlated with range size. This suggests that there were many specialists in our study area and that the reference habitat was different from the surrounding habitat. Brown (1984) notes that the 'jack of all trades, master of none' hypothesis predicts that specialists should become more abundant locally because they are more successful than generalists in their own habitat, but he states that such a trade-off has not been documented. The relationship between range size and degree of specialization needs to be examined more closely. Often, plants that specialize on a specific soil type have large ranges. For example, *O. borealis viscida*, found on small metamorphic outcrops in our study was locally rare and has a huge range. Negative correlations between abundance and range size may indicate that specialists need not have small ranges.

Only one of our measures of niche specialization was weakly positively correlated with range size and not with range tendency. Widespread high-alpine specialists are probably responsible for the positive correlation, but there are many species that seem to contradict the pattern. Endemics may also be specialized but not necessarily to the most extreme conditions revealed by logistic regression. Correlations between density and range size may be weak when the reference habitat differs from the surrounding area enough to prevent some generalists with large ranges from colonizing the area, while only allowing for limited specialization (Gaston & Lawton, 1990). The wet areas within our study area are similar to surrounding areas to the north. The dry patches of our reference habitat are similar to the sky islands to the east and to the Transverse Ranges to the south. The Great Central Valley to the west and the deserts to the south and east are completely different because they are low in elevation. These patterns may explain the correlation between local habitat preference and geographic range size within the Bishop Creek Watershed.

Understanding the determinants and correlates of the geographic range sizes of species leads to an understanding of community structure (Gaston, 1990). In this study, we examined the relationship between local habitat preference and range size, integrating the historical development of phytogeographic elements. There are many different methods of calculating range size, and our method is a crude one (Gaston, 1991). Ideally, we would study all the closely related species in a series of groups and take phylogenetic relatedness into account when determining range size correlates (Kelly & Woodward, 1996). This would lead us toward a more regional analysis, and one that would be improved by detailed mapping of species ranges and climatic variables. Our methods of determining range centre and range tendency were coarse, but the correlation between range size and tendency and local habitat preferences is a persistent one. It is sensible to expect that the species occur in areas of the globe with conditions that resemble their local habitat.

Most studies on correlates of range size have been on animals (Gaston & Blackburn, 1996; Lawton, 1990; Brown & Maurer, 1987). Range size is sometimes related to other factors, like trophic level and body size. Studies on plants may correlate growth form, pollination syndrome, and methods of dispersal with range size (Kelly & Woodward, 1996). Some correlates of range size may be important to all species. For example, species with small ranges are at a greater risk of extinction (Gaston, 1990). Additionally, ranges of different sizes have different likelihoods of giving rise to new species. The range sizes of species may provide information on whether the species is in its early phases, rapidly expanding, or declining (Gaston, 1996). From these data, one may be able to locate habitats in which new species are arising.

Competition, along with niche breadth, may explain the correlations we found between range size and wetness preferences. Water is perhaps the most important limiting resource for plants, so plants that live in wet places are probably good competitors. They may range widely due to their superior competitive abilities. Morefield (1992) found that wet areas support widespread (even alien) plant taxa in the White Mountains. In the Bishop Creek watershed, the alien plants (which we excluded from our analysis) had the largest ranges, and they were all plants of wet habitats. The widespread arctic–alpine species that occur in the Sierra Nevada grow in wet sites and are not drought-tolerant. This leaves the dry sites open for drought-tolerant species, which under this hypothesis would be poor competitors (Chabot & Billings, 1972; Klikoff, 1965). It is very difficult to live in a dry site, especially at high elevations. Plants in these rough conditions must be able to withstand long cold winters and short dry summers. They must all be specialists to some degree. The endemics in our study area are the high-elevation drought-tolerant taxa. They would not be able to compete with plants in other areas, and they live in high dry rocky areas that may be sites of relatively rapid speciation.

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BIOSKETCHES

Sarah Kimball is studying for her PhD at the University of California, Irvine, in the Department of Ecology and Evolutionary Biology. Her dissertation is on the maintenance of the species boundary between *Penstemon davidsonii* and *P. newberryi*. Her MS thesis was on the effects of grazing on native vs. alien plants. She found that grazing in a California Valley Grassland favors aliens that are superior at compensating for herbivory.

Paul Wilson earned his PhD in Ecology and Evolution from the State University of New York at Stony Brook. His postdoctoral work was in vegetation ecology at Harvard University. He is currently an Associate Professor of biology at California State University, Northridge. He teaches evolutionary biology, field ecology, plant morphology, and biometry. His primary research is on plant–pollinator interactions.

Jack Crowther is a retired history teacher and basketball coach who with his wife Pat Crowther has botanized the Sierra Nevada for 20 years, and hiked it for several decades previous to that. He learned much of his botany in the field from Mary Dedecker and Carl Sharsmith.

Appendix 1 The ecological preferences and range characterizations of plants found in the Bishop Creek watershed. The species are ordered first by their wetness preference and then by their elevational preference. ***n*** is the number of plots in which the species was found. **Wetness preference** for plants occurring in more than three plots is the mean wetness of those plots; for plants occurring in three or fewer plots, it is our subjective impression of its wetness preference. **Elevation preference** for plants occurring in plots is the median elevation of those plots; for plants not occurring in plots it is the mid-range of known locations. Superscripts on wetness preference and elevation preference relate to P-values from a multiple logistic regression that modelled presence/absence as a function of plot wetness and elevation (^{NS} $P > 0.1$; † $P < 0.1$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$). ρ^2 is McFadden's rho squared from the logistic regression; in general ρ^2-values are less than the more familiar R^2 values. Logistic regressions were only done for species occurring in nine or more plots. **Range Size**, 1 indicates that the taxon is endemic to only a portion of the Sierra Nevada and sometimes adjacent White and Inyo Mountains, 2 indicates that the species is mainly restricted to the Sierra Nevada and parts of adjacent mountain ranges in the southern Cascades, Whites, Inyos, and Tehachepe Mountains, 3 indicates that the species has major extentions into areas not immediately adjacent to the Sierra Nevada such as into the main part of the Cascades or the Ranges of the Great Basin, and 4 indicates that the species is even more broadly distributed. Range centre is the direction of the main part of the range relative to Bishop Creek (with other major extensions in parentheses). **Range tendency** tells whether the centre of the range is in a wet region (e.g., the Cascades) or a dry region (e.g., east of the Cascades or the Great Basin)

	n	Wetness preference	Elevation preference	ρ^2	Range size	Range centre	Range tendency
Species of usually dry habitats							
Hulsea algida A. Gray	6	1.5	3728	–	3	E (N)	Dry
Minuartia obtusiloba (Rydb.) House	0	1	3697	–	4	N	Wet
Polemonium eximium E. Greene	9	1.1*	3664***	0.529	1	E(S)	Dry
Cryptantha nubigena (E. Greene) Payson	13	1.2*	3645**	0.215	1+	ES	Dry
Oxytropis parryi A. Gray	0	1	3597	–	3	E	Dry
Arabis davidsonii E. Greene	4	1	3548	–	2+	EN	Dry
Raillardella argentea (A. Gray) A. Gray	18	1.4*	3532**	0.153	3	E(NS)	Dry
Erigeron pygmaeus (A. Gray) E. Greene	55	1.4***	3527***	0.365	2	E	Dry
Eriogonum ovalifolium Nutt. var. *nivale* (Canby) M. E. Jones	70	1.4***	3516***	0.388	4	NE	Both
Draba breweri S. Watson	30	1.4**	3509***	0.241	2	EN	Dry
Artemisia arbuscula Nutt. ssp. *Arbuscula*	0	1	3498	–	4	E	Dry
Eriogonum lobbii Torrey & A. Gray var. *lobbii*	7	1.1	3483	–	2	NE	Both
Penstemon davidsonii E. Greene var. *davidsonii*	29	1.3***	3483***	0.247	3	N	Wet
Eriogonum rosense Nelson & Kenn.	4	1	3482	–	2	E	Dry
Galium hypotrichium A. Gray ssp. *Hypotrichium*	10	1.3*	3472^{NS}	0.133	1+	E	Dry
Chaenactis alpigena Sharsm.	4	1.3	3464	–	1+	E	Dry
Draba oligosperma or *sierrae*	22	1.3***	3460**	0.217	–	–	–
D. oligosperma Hook. var. *oligosperma*	–	–	–	–	4	N	Wet
D. sierrae Sharsm.	–	–	–	–	1	–	–
Castilleja nana Eastw.	28	1.4***	3424*	0.156	2−	E	Dry
Oxytropis borealis DC. var. *viscida* (Nutt.) Welsh	1	1	3424	–	4	N	Wet
Arenaria kingii (S. Watson) M. E. Jones var. *glabrescens* (S. Watson) Maguire	41	1.4***	3422^{NS}	0.157	3−	E(N)	Dry
Arabis lemmonii varieties	44	1.5***	3397†	0.126	–	–	–
Arabis lemmonii S. Watson var. *depauperata* (Nelson & Kenn.) Rollins	–	–	–	–	1	E	Dry
Arabis lemmonii S. Watson var. *lemmonii*	–	–	–	–	1	N(E)	Wet
Ericameria discoidea (Nutt.) G. Nesom	26	1.3***	3382^{NS}	0.135	4	E	Dry
Astragalus lentiginosus Hook. var. *ineptus* (A. Gray) M. E. Jones	5	1	3375	–	1	E	Dry
Tonestus peirsonii (Keck) G. Nesom & R. Morgan	14	1.4**	3357^{NS}	0.102	1	E	Dry
Senecio spartioides Torrey & A. Gray	0	1	3353	–	4	ES	Dry
Erigeron compositus Pursh	11	1.0^{NS}	3352^{NS}	0.268	4	NE	Both
Sedum lanceolatum Torrey	10	1.3*	3339^{NS}	0.106	4	N	Wet
Ivesia shockleyi S. Watson var. *shockleyi*	2	1	3308	–	2+	E	Dry
Minuartia nuttallii (Pax) Briq. ssp. *gracilis* (Robinson) McNeill	3	1	3304	–	2	E	Dry
Leptodactylon pungens (Torrey) Rydb.	56	1.2***	3296†	0.302	4	N	Wet
Senecio canus Hook., the smaller variety	4	1	3294	–	–	–	–
Sphaeromeria cana (D. C. Eaton) A. A. Heller	5	1.2	3292	–	2	E	Dry
Woodsia scopulina D. Eaton var. *scopulina*	*[7]*	1.4	3267	–	4	N(ES)	Wet
Astragalus purshii Hook. var. *lectulus* (S. Watson) M. E. Jones	4	1	3267	–	2−	S	Dry

Appendix 1 *continued*

	n	Wetness preference	Elevation preference	ρ^2	Range size	Range centre	Range tendency
Ribes cereum Douglas, varieties	34	1.5***	3235**	0.138	–	–	–
R. c. cereum	–	–	–	–	4	SEN	Both
R. c. inebrians (Lindley) C. Hitchc.	–	–	–	–	4	E	Dry
Ageratina occidentalis (Hook.) R. King & H. Robinson	3	1	3227	–	4–	N(E)	Wet
Eriogonum cespitosum Nutt.	0	1	3223	–	3	E	Dry
Astragalus whitneyi A. Gray var. *whitneyi*	3	1	3202	–	2	SE	Dry
Trifolium andersonii A. Gray. var. *beatleyae* (J. M. Gillett) Isely	0	1	3200	–	2	E	Dry
Penstemon speciosus Lindley	3	1	3200	–	4	N	Wet
Erigeron clokeyi Cronq.	8	1	3199	–	2	E	Dry
Erigeron breweri A. Gray var. *breweri*	2	1	3194	–	2	ES	Dry
Swertia puberulenta (Davidson) Jepson	5	1.2	3193	–	1+	E	Dry
Eriogonum nudum Benth., varieties indistinct	36	1.3***	3191***	0.262	4	NS	Both
Chaenactis douglasii (Hook.) Hook & Arn. var. *douglassii*	4	1	3187	–	4	EN	Dry
Holodiscus microphyllus Rydb. var. *microphyllus*	32	1.3***	3184***	0.272	4	SE	Dry
Castilleja applegatei Fern. ssp. *pallida* (Eastw.) Chuang & Heckard	40	1.5***	3184***	0.305	1	E	Dry
Arabis pygmaea Rollins	0	1	3170	–	1	–	–
Arabis holboellii Hornem. var. *retrofracta* (Graham) Rydb.	7	1.1	3128	–	4	N	Wet
Arabis holboellii Hornem. var. *pinetorum*	8	1.4	3127	–	4	N	Wet
Purshia tridentata (Pursh) DC. var. *tridentata*	6	1.2	3112	–	4	ES(N)	Dry
Chrysolepis sempervirens (Kellogg) Hjelmq.	5	1.2	3102	–	3	S(WNE)	Dry
Chrysothamnus viscidiflorus (Hook.) Nutt. ssp. *viscidiflorus*	2	1	3096	–	4	E(SN)	Dry
Pinus flexilis James	23	1.4***	3074***	0.43	4	E(S)	Dry
Ericameria suffruticosa (Nutt.) G. Nesom	0	1	3071	–	4	E	Dry
Arabis repanda S. Watson var. *greenei* Jepson	3	1	3044	–	1	SE	Dry
Cercocarpus ledifolius Nutt. var. *intermontanus* N. Holmgren	9	1.1*	3025***	0.522	4	E(SN)	Dry
Artemisia tridentata Nutt. ssp. *vaseyana* (Rydb.) Beetle	14	1.3***	3024***	0.513	4	E(SN)	Dry
Silene bernardina S. Watson	1	1	3023	–	3	E(N)	Both
Stephanomeria tenuifolia (Torrey) H. M. Hall *tenuifolia*	1	1	3017	–	4	E(N)	Dry
Phoenicaulis cheiranthoides Torrey & A. Gray	0	1	3010	–	4	EN	Dry
Lupinus argenteus Pursh var. *montigenus* (A. A. Heller) Barneby	2	1	3001	–	2	E	Dry
Streptanthus tortuosus Kellogg	0	1	2896	–	3	WN	Wet
Penstemon papillatus J. Howell	3	1	2860	–	1+	E	Dry
Chamaebatiara millefolium (Torrey) Maxim.	1	1	2859	–	4	E	Dry
Cryptantha echinella E. Greene	0	1	2789	–	3	E(SN)	Dry
Species of often dry habitats							
Erigeron vagus Payson	0	2	4100	–	3+	E	Dry
Senecio fremontii Torrey & A. Gray *occidentalis* A. Gray	9	1.8$^{\mathrm{NS}}$	3716**	0.13	2	SE	Dry
Senecio werneriaefolius A. Gray	23	1.7$^{\mathrm{NS}}$	3659***	0.448	3	E	Dry
Antennaria umbrinella Rydb.	0	2	3627	–	4	E(N)	Dry
Potentilla pseudosericea Rydb.	4	1.8	3594	–	2	E	Dry
Androsace septentrionalis L. ssp. *subumbellata* G. Robb.	6	1.8	3583	–	4	N	Wet
Ivesia pygmaea A. Gray	23	1.6*	3564***	0.179	1	S	Dry
Anemone drummondii S. Watson	1	2	3545	–	4	N	Wet
Oxyria digyna (L.) Hill	49	2.3†	3542***	0.188	4	N	Wet
Draba densifolia Nutt.	8	1.6	3523	–	4	NE	Both
Saxifraga tolmiei Torrey & A. Gray	4	1.8	3521	–	4	N	Wet
Phlox	61	1.7***	3513***	0.186	–	–	–
P. dispersa Sharsm.	–	–	–	–	1	S	Dry
P. condensata (A. Gray) E. Nelson	–	–	–	–	1	ES	Dry
P. pulvinata (Wherry) Cronq.	–	–	–	–	1	E	Dry
Arabis lyallii S. Watson *lyallii*	17	1.7†	3501†	0.07	4	NE	Both
Calyptridium umbellatum (Torrey) E. Greene var. *umbellatum*	47	1.7***	3491***	0.187	4–	E(NW)	Dry
Ivesia muirii A. Gray	13	1.9$^{\mathrm{NS}}$	3485†	0.046	1	S	Dry
Primula suffrutescens A. Gray	9	2.0$^{\mathrm{NS}}$	3481†	0.045	2	NE	Both
Silene sargentii S. Watson	43	1.8**	3478**	0.085	2	E	Dry
Erigeron algidus Jepson	57	2.4$^{\mathrm{NS}}$	3474***	0.075	2–	E	Dry

Appendix 1 *continued*

	n	Wetness preference	Elevation preference	ρ^2	Range size	Range centre	Range tendency
Pyrrocoma apargioides (A. Gray) E. Greene	34	2.0^{NS}	3455**	0.051	2	E	Dry
Aquilegia pubescens Cov.	13	1.8^{NS}	3435†	0.055	1	S	Dry
Eriogonum incanum Torrey & A. Gray	19	1.7†	3434†	0.061	2	N	Wet
Epilobium obcordatum A. Gray	20	2.0^{NS}	3428†	0.036	3	E(N)	Dry
Anelsonia eurycarpa (A. Gray) J. F. Macbr. & Payson	1	2	3417	–	2	NE	Both
Selaginella watsonii L. Underw.	93	1.6***	3407†	0.159	3+	ESN	Both
Polygonum minimum S. Watson	2	2	3400	–	4	N	Wet
P. davidsonii × *newberryi*	6	1.8	3399	–	–	–	–
Solidago multiradiata Aiton	88	2.5†	3399^{NS}	0.013	4	N	Wet
Potentilla fruticosa L.	7	1.9	3390	–	4	N	Wet
Phacelia hastata Lehm. ssp. *compacta* (Brand) Heckard	27	1.6**	3389†	0.084	3	N	Wet
Athyrium alpestre (D. H. Hoppe) Clairv. var. *americanum* F. K. Butters	3	2	3389	–	4	N(E)	Wet
Pinus albicaulis Engelm.	75	2.0**	3368^{NS}	0.03	4	N	Wet
Penstemon heterodoxus A. Gray var. *heterodoxus*	77	2.2^{NS}	3356^{NS}	0.003	2+	NE	Dry
Arabis platysperma A. Gray var. *howellii* (S. Watson) Jepson	6	2	3350	–	3	NE	Both
Hieracium horridum Fries	11	1.5*	3349^{NS}	0.057	3–	SEN	Dry
Dicentra uniflora Kellogg	0	2	3345	–	4	N(WE)	Wet
Cystopteris fragilis (L.) Bernh.	*[30]*	2.4	3330	–	4	NESW	Both
Arabis platysperma A. Gray var. *platysperma*	14	1.7†	3330^{NS}	0.044	2	E	Dry
Cryptogramma acrostichoides R. Br.	26	2.3^{NS}	3322^{NS}	0.002	4	N	Wet
Spiraea densiflora Torrey & A. Gray	5	1.8	3308		4	N	Wet
Arnica nevadensis or *diversifolia*	10	1.9^{NS}	3297^{NS}	0.023	–	–	–
Arnica nevadensis A. Gray	–	–	–	–	3	N	Wet
Arnica diversifolia E. Greene	–	–	–	–	4	N(E)	Wet
Antennaria rosea E. Greene ssp. *rosea*	67	1.8***	3294*	0.082	4	ENSW	Both
Aquilegia formosa × *pubescens*	24	2.1^{NS}	3292^{NS}	0.006	–	–	–
Erysimum capitatum (Douglas) E. Greene ssp. *perenne* (Cov.) R. A. Price	19	1.5**	3292^{NS}	0.091	3	N	Wet
Cirsium scariosum Nutt.	19	2.3^{NS}	3292^{NS}	0.019	4	EN(SW)	Both
Agoseris glauca laciniata	2	2	3287	–	4	E	Dry
Achillea millefolium L.	40	2.1†	3270**	0.055	4	N(WSE)	Wet
Jamesia americana Torrey & A. Gray var. *rosea* C. Schneider	9	1.7†	3253^{NS}	0.05	2	E	Dry
Heuchera rubescens Torrey var. *alpicola* Jepson	20	1.6**	3247**	0.109	2	ES	Dry
Descurainia californica (A. Gray) O. Schulz	1	2	3197	–	3	E	Dry
Cymopterus terebinthinus (Hook.) M. E. Jones var. *petraeus* (M. E. Jones) Goddrich	12	1.7*	3194*	0.105	3	E	Dry
Monardella odoratissima Benth. ssp. *pallida* (A. A. Heller) Epling	45	1.6***	3193***	0.181	2	EN(W)	Both
Gayophytum, mostly *racemosum*	22	1.7**	3192**	0.1	–	–	–
Gayophytum racemosum Torrey & A. Gray	–	–	–	–	4	NES	Both
Gayophytum decipiens Harlan Lewis & J. Szweykowski	–	–	–	–	4	ES(N)	Dry
Potentilla glandulosa Lindley ssp. *nevadensis* (S. Watson) Keck	35	2.4^{NS}	3190***	0.105	3–	SE	Dry
Senecio canus Hook., the larger variety	7	1.6	3188	–	4	EN	Dry
Cryptantha glomeriflora E. Greene	0	2	3185	–	1	E	Dry
Eriophyllum lanatum (Pursh) James Forbes var. *integrifolium* (Hook.) F. J. Smiley	1	2	3181	–	3	E(N)	Dry
Ribes montigenum McClatchie	23	2.3^{NS}	3171***	0.089	4	SEN	Dry
Pellaea breweri D. Eaton	17	1.5**	3167***	0.193	4	E(N)	Dry
Penstemon newberryi A Gray var. *newberryi*	38	1.7***	3166***	0.171	3–	N	Wet
Linanthus pachyphyllus R. Patterson	46	1.6***	3115***	0.41	2	E	Dry
Eriogonum umbellatum Torrey var. *nevadense* Gand.	13	1.6*	3102**	0.131	3–	E	Dry
Lithophragma glabrum Nutt.	4	1.8	3092	–	4	NE	Both
Polygonum douglasii E. Greene ssp. *johnstonii* (Munz) J. Hickman	0	2	3079	–	4	ENS	Both
Scrophularia desertorum (Munz) Shaw	1	2	3072	–	3–	E	Dry
Artemisia ludoviciana Nutt. ssp. *incompta* (Nutt.) Keck	10	2.4^{NS}	3053***	0.166	4	ES(N)	Dry
Symphoricarpos rotundifolius A. Gray var. *rotundifolius*	38	1.6***	3052***	0.517	4	SNE	Dry
Penstemon rostriflorous Kellogg	6	2	3044		4–	ES	Dry
Fritillaria atropurpurea Nutt.	1	2	3044		4–	EN	Dry
Angelica lineariloba A. Gray	9	1.7*	3024***	0.253	2	E	Dry
Apocynum androsaemifolium L.	5	1.6	3020	–	4	ENSW	Both

Appendix 1 *continued*

	n	Wetness preference	Elevation preference	ρ^2	Range size	Range centre	Range tendency
Populus tremuloides Michaux	25	2.2†	3017***	0.442	4	NESW	Both
Artemisia norvegica Fries ssp. *saxatilis* H. M. Hall & Clements	0	2	3002	–	4	N(SWE)	Both
Castilleja linariifolia Benth.	7	1.9	2919	–	4	E(SN)	Dry
Species of often wet habitats							
Lewisia glandulosa (Rydb.) Dempster	26	2.8***	3552***	0.22	1+	E	Dry
Saxifraga rivularis L.	4	3.3	3528	–	4	N	Wet
Draba lemmonii S. Watson var. *lemmonii*	24	2.6*	3527***	0.183	1	NE	Dry
Ivesia lycopodioides A. Gray ssp. *scandularis* (Rydb.) Keck	31	3.4***	3434***	0.274	1+	E	Dry
Antennaria media E. Greene	89	2.9***	3431***	0.23	4	N(E)	Wet
Sedum roseum (L.) Scop. ssp. *integrifolium* (Raf.) Hultén	43	3.0***	3431***	0.147	4	N	Wet
Sibbaldia procumbens L.	64	2.8***	3428***	0.164	4	N(SE)	Both
Saxifraga aprica E. Greene	16	2.8^{NS}	3419^{NS}	0.027	3–	NE	Dry
Potentilla diversifolia Lehm. var. *diversifolia*	0	3	3399	–	4	NE	Wet
Lewisia pygmaea or *nevadensis* (mostly *P*)	28	3.2***	3399^{NS}	0.098	–	–	–
Lewisia pygmaea (A. Gray) Robinson	–	–	–	–	4	NS	Both
Lewisia nevadensis (A. Gray) Robinson	–	–	–	–	4	NS	Both
Potentilla drummondii Lehm. ssp. *drummondii*	29	3.3***	3386*	0.154	4	N	Wet
Ranunculus eschscholtzii Schldl. var. *oxynotus* (A. Gray) Jepson	10	3.0†	3371^{NS}	0.048	3	NE	Wet
Potentilla drummondii Lehm. ssp. *breweri* (S. Watson) B. Ertter.	16	3.4***	3363*	0.161	3+	N	Wet
Cassiope mertensiana (Bong.) Don	10	3.2*	3351^{NS}	0.069	4	N	Wet
Phyllodoce breweri (A. Gray) Maxim.	53	3.5***	3344^{NS}	0.244	2	SN	Both
Rumex paucifolius S. Watson var. *paucifolius*	30	2.6^{NS}	3340^{NS}	0.009	4	N	Wet
Lupinus lepidus Douglas, mostly *sellulus*	20	3.0*	3334^{NS}	0.05	–	–	–
L. l. var. *lobbii* (S. Watson) C. Hitchc.	–	–	–	–	3	E	Dry
L. l. var. *ramosus* Jepson	–	–	–	–	1+	E	Dry
L. l. var. *sellulus* (Kellogg) Barneby	–	–	–	–	3+	NE	Both
Senecio scorzonella or *integerrimus*, mostly *s*	30	3.0**	3290^{NS}	0.077	–	–	–
Senecio scorzonella E. Greene	–	–	–	–	2	E(N)	Dry
Senecio integerrimus Nutt. var. *exaltatus* (Nutt.) Cronq.	–	–	–	–	4	EN	Both
Mimulus breweri (E. Greene) Cov.	9	2.7^{NS}	3264^{NS}	0.018	4	NSE	Both
Raillardella scaposa (A. Gray) A. Gray	2	3	3233	–	2	N	Wet
Sphenosciadium capitellatum A. Gray	44	3.4***	3205***	0.289	4	SE(N)	Dry
Crepis intermedia A. Gray	0	3	3200	–	4	WNE	Wet
Delphinium polycladon Eastw.	6	3.2	3181	–	1+	E	Dry
Saxifraga nidifica E. Greene var. *nidifica*	1	3	3167	–	4	N	Wet
Polygonum polygaloides Meissner ssp. *kelloggii* (E. Greene) J. Hickman	3	3	3164	–	4	NSE	Both
Castilleja miniata Hook. ssp. *miniata*	33	3.4***	3164***	0.345	4	N(E)	Wet
Arnica parryi A. Gray ssp. *sonnei* (E. Greene) Maguire	2	3	3148	–	4	N(E)	Wet
Smilacina stellata (L.) Desf.	6	3.2	3127	–	4	N(WSE)	Wet
Epilobium glaberrimum Barbey ssp. *fastigiatum* (Nutt.) P. Hoch & Raven	4	3.3	3127	–	4	N(WS)	Wet
Dugaldia hoopesii (A. Gray) Rydb.	5	3.4	3092	–	3+	E(N)	Dry
Thalictrum fendleri A. Gray var. *fendleri*	23	3.1**	3061***	0.251	4	SE(WN)	Dry
Epilobium angustifolium L. ssp. *circumvagum* Mosq.	35	3.1***	3054***	0.333	4	N	Wet
Pinus contorta Loudon ssp. *murrayana* (Grev. & Balf.) Critchf.	49	2.6^{NS}	3054***	0.397	3	NS	Both
Aquilegia formosa Fischer	18	3.2*	3048***	0.211	4	N(ESW)	Wet
Hackelia micrantha (Eastw.) J. Gentry	2	3	3028	–	4	N(E)	Wet
Salix planifolia Cham. ssp. *planifolia*	9	3.0^{NS}	3024**	0.179	4	N	Wet
Draba albertina E. Greene	3	3	3019	–	4	N(ES)	Wet
Collinsia parviflora or *torreyi*	3	3	3017	–	–	–	–
Collinsia parviflora Lindley	–	–	–	–	4	WN	Wet
Collinsia torreyi A. Gray var. *wrightii* (S. Watson) I. M. Johnston	–	–	–	–	3	WNS	Both
Salix scouleriana Hook.	0	3	2976	–	4	NWS	Both
Arnica cordifolia Hook. var. *cordifolia*	3	3	2972	–	4	NW(E)	Wet
Abies magnifica Andr. Murray var. *magnifica*	0	3	2865	–	3–	N	Wet
Antennaria corymbosa E. Nelson	0	3	2865	–	4	N(E)	Wet
Fragaria virginiana Duchesne	4	3.5	2848	–	4	N	Wet

Appendix 1 *continued*

	n	Wetness preference	Elevation preference	ρ^2	Range size	Range centre	Range tendency
Iris missouriensis Nutt.	3	3	2847	–	4	ES(N)	Both
Species of continuously wet habitats							
Potentilla flabellifolia Hook.	1	4	3524	–	4	N	Wet
Montia chamissoi (Sprengel) E. Greene	3	4	3505	–	4	NE	Both
Potentilla pensylvanica L.	0	(1)-2	3505	–	4	E	Dry
Salix arctica Pallas	32	3.8***	3416***	0.468	4	N	Wet
Epilobium anagallidifolium Lam.	10	3.9**	3413*	0.312	4	N	Wet
Stellaria umbellata Karelin & Kir.	2	4	3411	–	4	N	Wet
Sagina saginoides (L.) Karsten	7	3.6	3411	–	4	NESW	Both
Agoseris glauca (Pursh) Raf. var. *monticola* (E. Greene) Q. Jones	0	(1)-3	3383	–	3+	N	Wet
Stellaria calycantha (Ledeb.) Bong.	3	4	3383	–	4	N	Wet
Pedicularis attollens A. Gray	51	3.7***	3344**	0.372	2+	N(E)	Both
Gentianopsis or *Gentiana*	48	3.8	3344	–	–	–	–
Gentiana newberryi A. Gray var. *tiogana* (A. A. Heller) J. Pringle	–	–	–	–	–	E	Dry
Gentianopsis holopetala (A. Gray) Iltis	–	–	–	–	–	E	Dry
Castilleja lemmonii A. Gray	15	4.0^{NS}	3342^{NS}	0.392	2–	N	Wet
Aster alpigenus (Torey & A. Gray) A. Gray var. *andersonii* (A. Gray) M. Peck	45	3.9***	3341*	0.493	3+	N(SEW)	Wet
Rumex salicifolius J. A. Weinm. var. *denticulatus* Torrey	0	4	3338	–	4	NWS	Both
Botrychium simplex Hitchc.	8	4	3333	–	4	N	Wet
Vaccinium caespitosum Michaux	30	3.9***	3332†	0.378	4	WN	Wet
Mimulus tilingii Regel	6	3.8	3318	–	4	SEN	Both
Kalmia polifolia Wangenh. ssp. *microphylla* (Hook.) Calder & Roy Taylor	26	4.0^{NS}	3314^{NS}	0.472	4	N	Wet
Saxifraga bryophora A. Gray	3	3-(4)	3293	–	2	N	Wet
Veronica wormskjoldii Roemer & Schultes	15	3.9**	3292^{NS}	0.309	4	N	Wet
Senecio pauciflorus Pursh	14	3.6***	3285^{NS}	0.177	4	N	Wet
Salix orestera C. Schneider	50	3.7***	3285^{NS}	0.336	2	E	Dry
Mimulus primuloides Benth. *primuloides*	44	3.8***	3285†	0.437	4–	N(SE)	Wet
Dodecatheon redolens (H. M. Hall) H. J. Thompson	69	3.8***	3281**	0.565	3+	SE	Dry
Arnica mollis Hook.	9	3.9*	3281^{NS}	0.245	4	N	Wet
Perideridia parishii (J. Coulter & Rose) Nelson & J. F. Macbr. ssp. *latifolia* (A. Gray) Chuang & Constance	16	3.7***	3246**	0.269	3	NS	Both
Lewisia triphylla (S. Watson) Robinson	0	3	3216	–	2+	N	Wet
Ledum glandulosum Nutt.	22	3.9***	3208†	0.332	4	N	Wet
Ribes inerme Rydb. var. *inerme*	1	4	3200	–	4	N	Wet
Rosa woodsii Lindley var. *ultramontana* (S. Watson) Jepson	1	4	3190	–	4	E(SN)	Dry
Gentianella amarella (L.) Boerner ssp. *acuta* (Michaux) J. M. Gillett	2	4	3186	–	4	N(ES)	Wet
Stellaria crispa Cham. & Schldl.	7	3.9	3183	–	4	N	Wet
Veratrum californicum Durand var. *californicum*	2	4	3177	–	4	NSE	Both
Erigeron peregrinus (Pursh) E. Greene var. *callianthemus* (E. Greene) Cronq.	23	3.6***	3171**	0.258	4	N	Wet
Epilobium hornemannii or *oregonense*	11	3.8**	3171†	0.256	–	–	–
Epilobium hornemannii Reichb. ssp. *hornemannii*	–	–	–	–	4	N(WSE)	Wet
Epilobium oregonense Hausskn.	–	–	–	–	3	N(WE)	Wet
Mitella breweri A. Gray	3	4	3171	–	4	N	Wet
Hypericum anagalloides Cham. & Schldl.	0	4	3170	–	4	NWS	Wet
Potentilla gracilis Hook. var. *fastigiata* (Nutt.) S. Watson	47	3.7***	3169***	0.438	4	SEN	Both
Trifolium monanthum A. Gray. var. *monanthum*	32	3.6***	3164***	0.349	2	E	Dry
Platanthera leucostachys Lindley	11	3.9*	3162***	0.415	4	N	Wet
Vaccinium uliginosum L. ssp. *occidentale* (A. Gray) Hultén	2	4	3156	–	4	WN	Wet
Amelanchier utahensis Koehne	3	(1)-2	3128	–	4	E(SN)	Dry
Dodecatheon jeffreyi Van Houtte	0	4	3124	–	4	N	Wet
Stellaria longipes Goldie var. *longipes*	7	3.7	3092	–	4	N	Wet
Trimorpha lonchophylla (Hook.) G. Nelsom	1	4	3092	–	4	N(SE)	Wet
Pyrola asarifolia Michaux ssp. *asarifolia*	1	4	3088	–	4	N(S)	Wet
Helenium bigelovii A. Gray	2	4	3082	–	3–	N(SW)	Wet
Mimulus suksdorfii A. Gray	1	4-(3)	3079	–	4	ESN	Dry
Crepis nana A. Richards	0	2(3)	3079	–	4	NSE	Both

Appendix 1 *continued*

	n	Wetness preference	Elevation preference	ρ^2	Range size	Range centre	Range tendency
Parnassia californica (A. Gray) E. Greene	2	4	3073	–	3	NE(W)	Wet
Pteridium aquilinum (L.) Kuhn var. *pubesecens* L. Underw.	1	4	3072	–	4	NESW	Both
Viola macloskeyi F. Lloyd	9	3.8*	3054**	0.293	4	N(SEW)	Wet
Senecio triangularis Hook.	15	3.9**	3054***	0.471	4	N(SE)	Wet
Orthilia secunda (L.) House	6	4	3054	–	4	N	Wet
Allium validum S. Watson	19	3.7***	3054***	0.506	3	N	Wet
Arnica chamissonis Less. ssp. *foliosa* (Nutt.) Maguire	0	(3)-4	3048	–	4	NSE	Both
Pellaea bridgesii Hook.	0	1-(2)	3048	–	2	E(N)	Dry
Lupinus pratensis A. A. Heller var. *pratensis*	16	3.6***	3038**	0.269	1+	E	Dry
Saxifraga odontoloma Piper	6	3.7	3025	–	4	N(SEW)	Wet
Thalictrum sparsiflorum Fischer & C. Meyer	1	4	3022	–	4	SNE	Both
Arabis × *divaricarpa* Nelson	1	4	3022	–	–	–	–
Spiranthes romanzoffiana Cham.	0	4	3018	–	4	NE	Both
Tofieldia occidentalis S. Watson ssp. *occidentalis*	0	4	3018	–	4	N	Wet
Cryptantha small annual of plot B5	3	2	3017	–	–	–	–
Aster breweri (A. Gray) Semple	1	2	3012	–	2+	NS	Both
Sorbus californica E. Greene	1	3-(4)	3012	–	3	NWE	Wet
Draba praealta E. Greene	0	3-(4)	2972	–	4	N	Wet
Agoseris aurantiaca (Hook.) E. Greene	2	4	2960	–	4–	N	Wet
Actaea rubra (Aiton) Willd.	2	3-(4)	2943	–	4	N(E)	Wet
Erigeron coulteri Porter	2	4	2943	–	3	E	Dry
Ceanothus velutinus Douglas var. *velutinus*	0	1-(2)	2941	–	2	N	Wet
Dodecatheon alpinum (A. Gray) E. Greene	6	4	2941	–	4	N(SEW)	Wet
Pyrola minor L.	4	3.8	2932	–	4	N(S)	Wet
Senecio pseudaureus Rydb. var. *pseudaureus*	0	4	2911	–	4	N	Wet
Lilium kelleyanum Lemmon	4	3.8	2881	–	1+	S	Dry
Equisetum arvense L.	8	3.6	2854	–	4	N	Wet
Polemonium occidentale E. Greene	2	4	2853	–	4	N(SE)	Wet
Trifolium longipes Nutt. var. *nevadense* Jepson	5	3.6	2850	–	3	NESW	Both
Arnica longifolia D. Eaton	1	4	2850	–	4	N(EW)	Wet
Sidalcea oregana (Torrey & A. Gray) ssp. *spicata* (Regel) C. Hitchc.	1	4	2850	–	3	NE	Dry
Aconitum columbianum Nutt.	6	3.7	2849	–	4	N(E)	Wet
Platanthera sparsiflora (S. Watson) Schltr.	2	4	2849	–	4	N	Wet
Epilobium halleanum Hausskn.	4	4	2849	–	4	NESW	Both
Betula occidentalis Hook.	1	4	2847	–	4	EN	Dry
Equisetum laevigatum A. Braun	1	4	2847	–	4	NESW	Both
Salix drummondiana Hook.	3	4	2846	–	4	NE	Both
Mimulus guttatus DC.	2	4	2841	–	4	NESW	Both