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THE DIVERSITY AND BIOGEOGRAPHY OF THE ALPINE FLORA OF THE SIERRA NEVADA, CALIFORNIA

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ABSTRACT

The alpine zone of the Sierra Nevada of California, defined as non-forested areas at or above 3500 m, includes 385 species (409 taxa) of native vascular plants. Were the alpine boundary defined as at or above 3300 m, the alpine flora would grow to 536 species (570 taxa). There are 97 species that reach elevations of 4000 m and 27 species that reach to 4200 m. Over half of the alpine species occur in just six families, led by the Asteraceae (55 species, 59 taxa), Poaceae (39 species, 47 taxa), Brassicaceae (34 species), and Cyperaceae (31 species). The largest genus present is *Carex* with 29 species, and 18 more species would be added by lowering the alpine boundary to 3300 m. Next in size are *Draba* (14 species) and *Lupinus* (11 species, 16 taxa). Life forms of the flora are heavily dominated by broad-leaved erect perennials (50%), followed in importance by graminoid perennials (21%) and mats and cushions (11%). Annuals and woody shrubs each account for about 6% of the flora. Only nine species are obligate alpine taxa with a range restricted to elevations of 3500 m or above. An additional 67 species (17% of the flora) occur in both subalpine and alpine habitats but not lower. More than a quarter of the alpine species have elevational ranges that extend as low as foothill habitats defined as occurring below 1200 m. In terms of biogeographic affinities, the broad relationships of the flora include the cordillera of western North America (35%), Intermountain region of the Great Basin (20%), Sierra/Cascade axis (16%), and widespread distributions (14%). There are 36 species in the alpine flora endemic to the Sierra Nevada, and another 31 species that are Californian endemics.

Key Words: Alpine, arctic-alpine flora, cushion plant, Sierra Nevada, treeline.

How large and diverse is the alpine flora of the Sierra Nevada in California and what are its biogeographic relationships? There has been a long history of floristic and ecological studies of the alpine region of the Sierra Nevada addressing this and related issues, but a clear answer to the question has not been achieved. Unlike the majority of alpine regions in the northern hemisphere that share extensive elements of a circumboreal arctic-alpine flora, the Sierra Nevada has developed a unique component to its alpine flora under the influence of mediterranean-climate conditions with relatively dry summers added to other alpine environmental factors of stress. Also significant in the evolution of this alpine flora has been the relative isolation of the range from other high mountain floras of the western United States. Moreover, the Sierra Nevada possesses a complex mosaic of substrate, glacial history, and soil variation superimposed over broad patterns of climatic and topographic heterogeneity.

Interest in the alpine flora dates back to early descriptions by Coville (1893) and Harshberger (1911), who recognized the distinctiveness of the Sierran alpine flora. Hall and Grinnell (1919) gave a very brief description of the alpine zone in the context of a broader description of California life zones, and provided a short list of characteristic species. More significant, however, have been five studies over the past 80 years that have provided an analysis of the diversity and floristic affinities of the high elevation flora of the Sierra Nevada. The earliest of these was the work of Smiley (1921), whose definition of the boreal region of the Sierra Nevada comprised the Canadian, Hudsonian, and Arctic-Alpine zones as characterized in the Merriam system of life zones (Daubenmire 1938). These life zones roughly correspond to the upper montane, subalpine and alpine zones under current concepts (Fites-Kaufman et al. 2007). Smiley's work was followed by the classic investigation of Sharsmith (1940), and in more recent decades with analyses by Chabot and Billings (1972), Major and Taylor (1977), and Stebbins (1982). Early speculations on the origin of the Sierran alpine flora were contributed by Went (1948, 1953). Beyond these broad floristic surveys, there have been numerous studies of the floristics and vegetation of regional areas of subalpine and alpine vegetation in the Sierra Nevada (Howell 1944, 1951; Klikoff 1965; Pemble 1970; Taylor 1976b; Major and Taylor 1977; Tatum 1979; Benedict and Major 1982; Burke 1982; Ratliff 1982; Benedict 1983; Porter 1983; Constantine-Shull 2000; Sawyer and Keeler-Wolf 2007).

None of the existing literature has provided a satisfactory answer to the fundamental question. How many species are there in the alpine flora of

the Sierra Nevada? The objective of this paper is to present a broad overview of the alpine flora of the Sierra Nevada by providing a detailed and updated analysis of the floristic richness, ecological diversity, and biogeographic relationships of the species present within the alpine zone. The paper takes a conservative approach following Sharsmith (1940) by defining the alpine zone using a lower elevational limit of 3500 m. Climatic treeline typically occurs from 3300–3500 m in the central and southern Sierra Nevada where the great majority of alpine habitat in California is located (Fig. 1). Although the northern Sierra Nevada lacks high elevation areas, it nevertheless has a good representation of alpine species that reach above 3500 m in the central or southern areas of the range. To provide a broader context examining the significance of elevation in the definition of the alpine zone, analyses have been made for all species occurring at or above 3300 m within California.

Beyond an intrinsic interest in the evolution of biodiversity of alpine biota, there are very significant reasons to support Sierran alpine studies that can serve as baseline studies for important early warning systems of potential environmental impacts of climate change. Climate change models for California suggest that there will be significant effects on environmental conditions of subalpine and alpine habitats of the Sierra Nevada (Hayoe et al. 2004; Shafer et al. 2001), and historical data on vertebrate distribution demonstrates that these effects are ongoing today in influencing the distributions of vertebrate species (Moritz et al. 2008; Tingley et al. 2009).

Materials and Methods

The Jepson Manual, 2nd Edition (Baldwin et al. 2012) was used to identify California species with an elevational distribution up to or above 3300 m within the state, and which occurred in the Sierra Nevada. This reference is the sole source and reference for binomials used in this article. Species at or above 3500 m in California were considered to comprise the alpine flora. The upper and lower elevational ranges of each of these species were recorded, along with their biogeographic distribution and occurrence within the geographic regions of California (Hickman 1993). These geographic regions included records of species presence in the montane and higher elevations of the northern, central, and southern subregions of the Sierra Nevada, as well as the high Cascade Range, the Klamath/Siskiyou mountains, Transverse and Peninsular ranges of southern California, and ranges east of the Sierra Nevada including the Sweetwater and White-Inyo mountains (Fig. 1). The elevational limits and geographical ranges listed in Baldwin et al. (2012) are specimen-based records and thus considered reliable. Only native species were included in this analysis, however, alien species recorded as occurring at high elevations in the Sierra Nevada are very few. *Poa pratensis* L. is recorded as reaching 3500 m and *Taraxacum officinale* F. H. Wigg. reaches 3300 m.

Each taxon occurring at elevations of 3300 m or above was categorized into a series of growth forms, based on a modified scheme of Raunkiaer (1934). These categories were broad-leaved herbaceous perennials (tussocks, rosettes, and biennials), graminoid perennials, mats and cushion plants, geophytes, aquatics, annuals, subshrubs, woody shrubs (deciduous and evergreen), and trees.

The lower elevational limit of occurrence in California was used to separate alpine species into categories of lowest elevational zone of occurrence on the following basis: 1) foothill habitats of woodland and chaparral— <1199 m; 2) lower montane habitats dominated by mixed conifer and yellow pine forests— 1200–1999 m; 3) upper montane habitats of red fir and lodgepole pine forests— 2000–2699 m; 4) subalpine habitats of open conifer stands near treeline— 2700–3499 m; and 5) alpine habitats— >3500 m. Because elevational boundaries of these major vegetation zones change with latitude, as well as locally with slope exposure, these elevational ranges represent averaged boundaries across the west slope of the central and southern Sierra Nevada.

The biogeographic range of each alpine species was classified into one of six categories. These were: 1) widespread species present in many habitats or regions across North America and/or throughout the world; 2) cordilleran species broadly distributed in mountain regions of the western United States; 3) Sierra/Cascade species with a Pacific Northwest distribution; 4) Intermountain Region species present in the Great Basin; 5) species endemic to the Sierra Nevada; and 6) species endemic to California, broadly defined to include adjacent Great Basin ranges extending into western Nevada (i.e., Sweetwater, Wassuk, and White-Inyo mountains) and southern Oregon. Dividing species into such simple biogeographic categories is inherently arbitrary for some species, and expanded field studies in the future may well change these classifications and alter the list of Sierran endemics based on new records or taxonomic revisions.

Results

The Geography of California Alpine Habitats

The elevational contour interval of 3500 m is highly irregular in the Sierra Nevada, as it defines a relatively continuous area along the crest of the

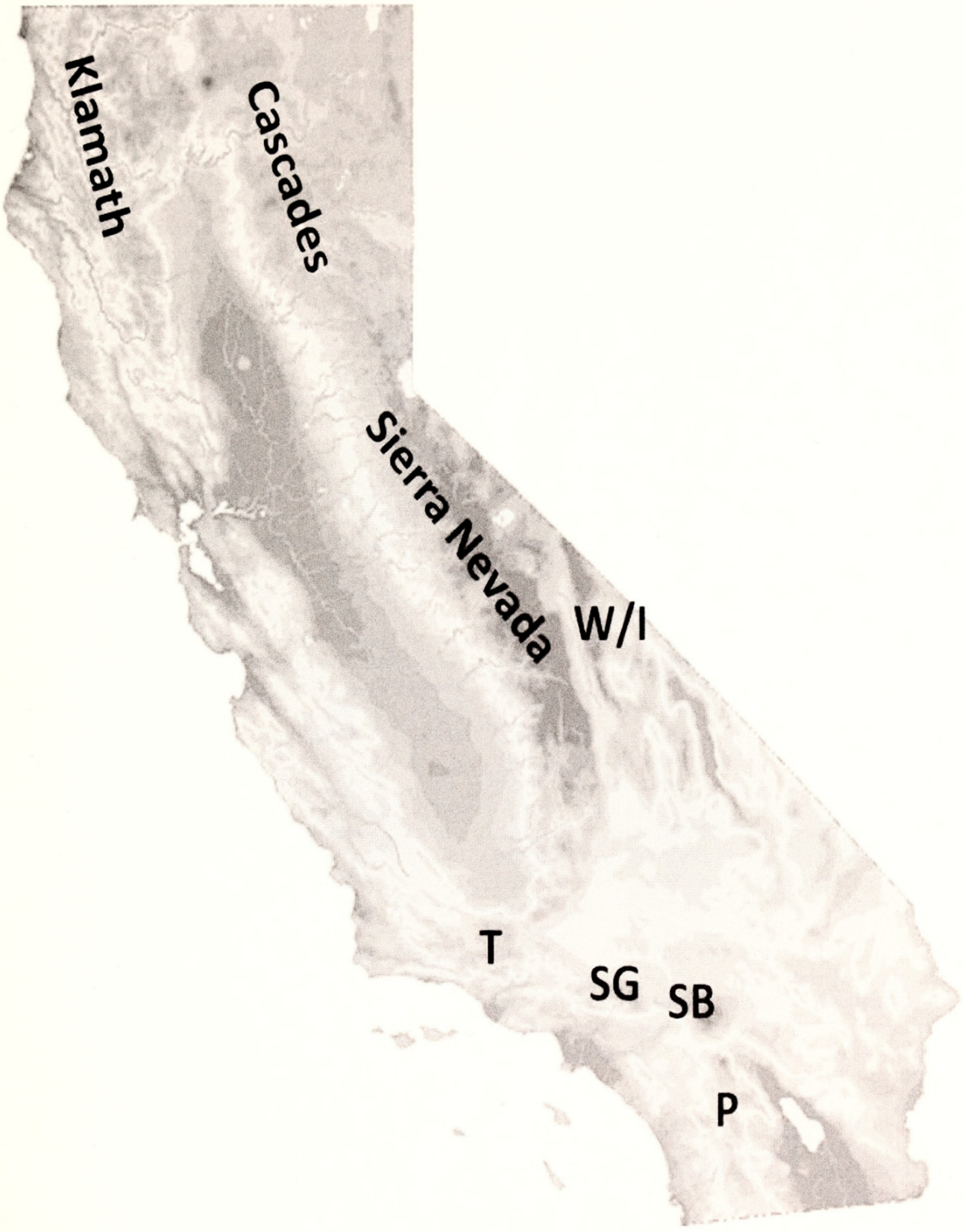

FIG. 1. Topographic map of California showing the major areas of mountain systems. W/I = White-Inyo Mountains, T = Tehachapi Mountains, SG = San Gabriel Mountains, SB = San Bernardino Mountains, and P = Peninsular Ranges.

central and southern crest of the range extending from northern Tuolumne and Mono counties in the area of Leavitt Peak (3527 m) near Sonoran Pass and south across Yosemite National Park where the highest peak is Mount Lyell (3999 m; Fig. 2). Further south this belt of alpine habitat continues into Kings Canyon and Sequoia National parks where there are extensive areas of alpine habitat with ten peaks that reach above 4000 m. Mount Whitney at 4421 m is the highest

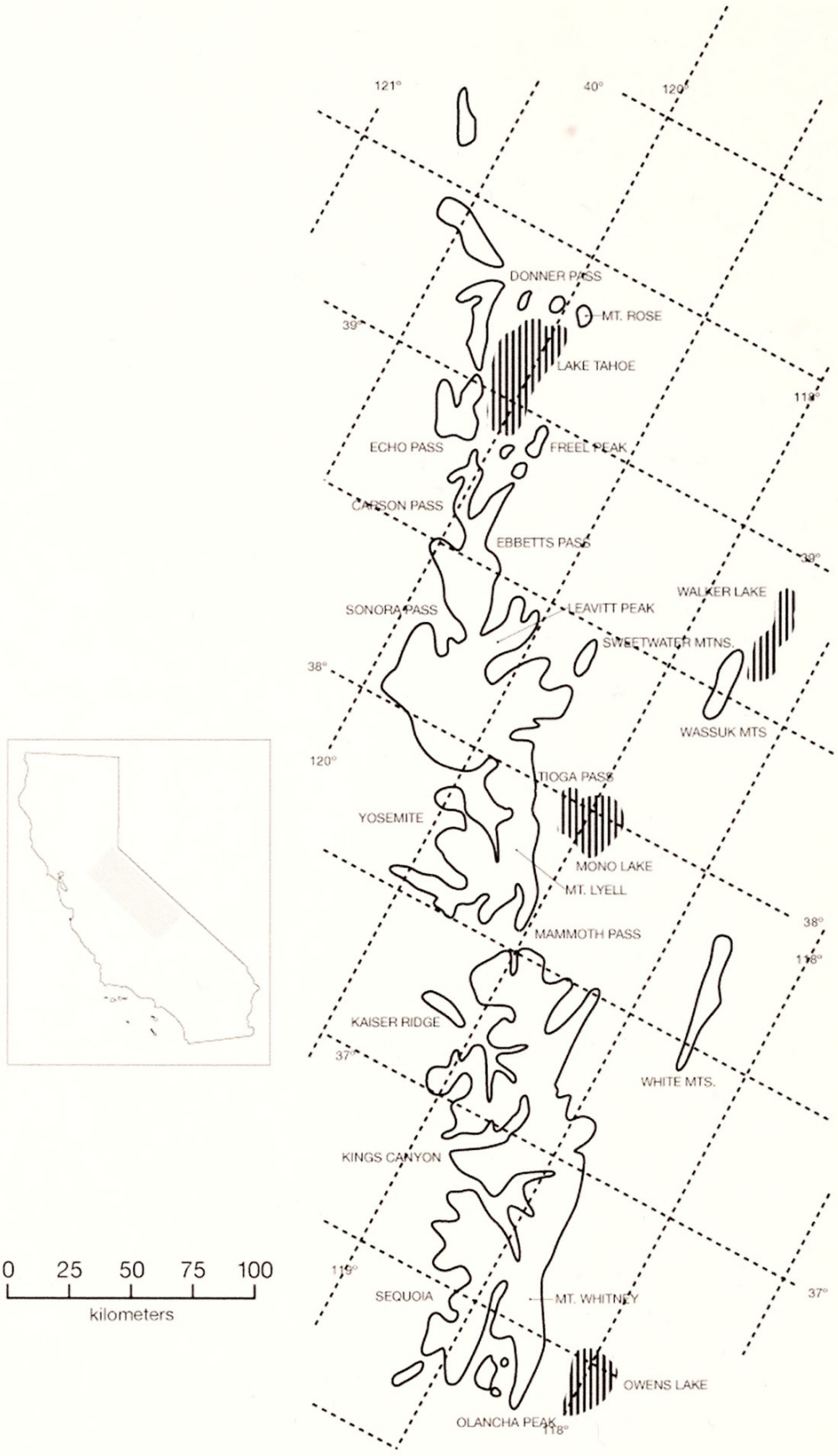

FIG. 2. Geographic distribution of high elevations of the Sierra Nevada and adjacent ranges. The solid line marks a rough position of the 3000 m contour. Adapted from Hovanitz (1940).

point in the contiguous United States. The southern limit of this extensive and virtually contiguous alpine zone occurs at Cirque Peak (3932 m) in Sequoia National Park at the southern end of the continuous chain of glaciated peaks in the Sierra Nevada. To the south, the alpine zone reappears on Olancha Peak (3698 m; Fig. 2), the southernmost glaciated summit of the range lying

on the Tulare-Inyo county line (Howell 1951; Tatum 1979). Two major breaks with subalpine elevations but not true alpine provide the only major discontinuity for this primary Sierran alpine region. These are Tioga Pass in Yosemite National Park (3031 m) and Mammoth Pass (Minaret Summit) (2824 m), which is the route for California Highway 203.

The crest of the Sierra Nevada lies at lower elevations to the north of the Tioga Pass area, with only scattered areas of good alpine habitat present. A notable ecological change occurs north of this pass where volcanic substrates replace the granites of the central and southern Sierra Nevada. Fragmented communities of alpine species are present at elevations below 3500 m, particularly along exposed ridgelines and on steep north-facing slopes that were heavily glaciated. However, there are no elevations in the northern Sierra Nevada that reach the 3500 m limit used here to define the alpine zone. Alpine habitats are weakly developed in Alpine Co. (with Sonora Peak reaching 3493 m) and eastern El Dorado Co. (with Freel Peak reaching 3318 m), extending to their northern limit on Mount Rose (3285 m) in the Carson Range east of Lake Tahoe in Nevada (Fig. 2). Nevertheless, there are scattered communities of alpine-like habitat existing at upper elevations in the northern Sierra Nevada, positioned above local edaphically-controlled treelines, and the alpine flora is well represented (Smiley 1915). Despite the floristic relationships of high elevation Sierran species all along the range, Stebbins and Major (1965) linked the Sierra Nevada north of Lake Tahoe with the Cascade Range rather than with the region of the central and southern Sierra Nevada on the basis of the dominance of volcanic substrates.

To the north of the Sierra Nevada, Mount Shasta in the southern Cascade Range reaches an elevation of 4322 m, while Lassen Peak is lower at 3187 m. The highest peaks in the Klamath Mountains of northwestern California and adjacent Oregon are Mount Eddy (2750 m) in Siskiyou Co., Thompson Peak (2744 m) in Trinity Co., and Mount Ashland (2296 m) in Jackson Co., Oregon. These high peaks contain areas with permanent or long-lasting snowfields on north-facing slopes with associated alpine species (Howell 1944; Major and Taylor 1977).

There are several high mountain ranges to the east of the Sierra Nevada at the western margin of the Great Basin. The Sweetwater Mountains, located just 33 km east of the Sierra Nevada, reach 3552 m on Mount Patterson (Hunter and Johnson 1983). The Wassuk Range in west-central Nevada lie 48 km east of the Sweetwater Mountains and 88 km north of the White Mountains, reaching 3427 m on Mount Grant (Bell and Johnson 1980). The White Mountains have an extensive alpine area and reach to 4344 m on White Mountain Peak, the third highest peak in California (Rundel et al. 2008). To the south, Mount Waucoba forms the high point at 3390 in the Inyo Mountains. The Panamint Mountains lying east of the White-Inyo Mountains reach a maximum elevation of 3366 m on Telescope Peak. Further south, the Spring Mountains in southwestern Nevada divide the Pahrump Valley and Amargosa River basins from the Las Vegas Valley watershed and define part of the southwestern boundary of the Great Basin. The highest point is Charleston Peak at 3633 m.

High elevations are also present in the Transverse and Peninsular ranges of southern California (Fig. 1) where a subset of Sierran alpine species is present in weakly developed alpine-like communities (Hall 1902; Parish 1917; Horton 1960; Hanes 1976; Major and Taylor 1977; Meyers 1978). Mount San Gorgonio in the San Bernardino Mountains reaches 3506 m, while other high points are Mount San Jacinto in the San Jacinto Mountains at 3302 m and Mount Baldy in the San Gabriel Mountains at 3068 m. Alpine species are present in both xeric and mesic habitats at high elevation, but alpine communities, defined as extended areas dominated by assemblages of alpine species, are only poorly developed.

The alpine zone of the Sierra Nevada experiences mediterranean-type climate conditions that differ significantly from those that characterize the Rocky Mountains and most of the continental alpine habitats of the world where summer rainfall predominates. The fraction of annual precipitation that falls as winter snow in the Sierra Nevada is about 95% at upper treeline (Stephenson 1998). Deep snow packs and cool temperature at higher elevations mean that snowmelt extends into the spring, but the length and magnitude of the summer drought period experienced by plants is significant. Patterns of rainfall decline gradually from north to south in the Sierra Nevada, and summer drought decreases as elevation increases because of both increased levels of precipitation and cooler temperatures with lower evaporative demand at higher elevations (Stephenson 1998; Urban et al. 2000).

Winter mean monthly low temperatures are moderate in the Sierra Nevada compared to the Rocky Mountains, and soils only rarely freeze to even moderate depth. While, the mean minimum temperature above treeline is below freezing for ten months of the year, with nighttime lows that typically reach only -3 to -6°C, although extremes can reach temperatures of -15°C or lower on the high peaks. Nevertheless, these moderate low temperatures as well as other limiting factors for survival at high elevations sharply reduce the diversity of species able to tolerate such conditions (Körner 2003).

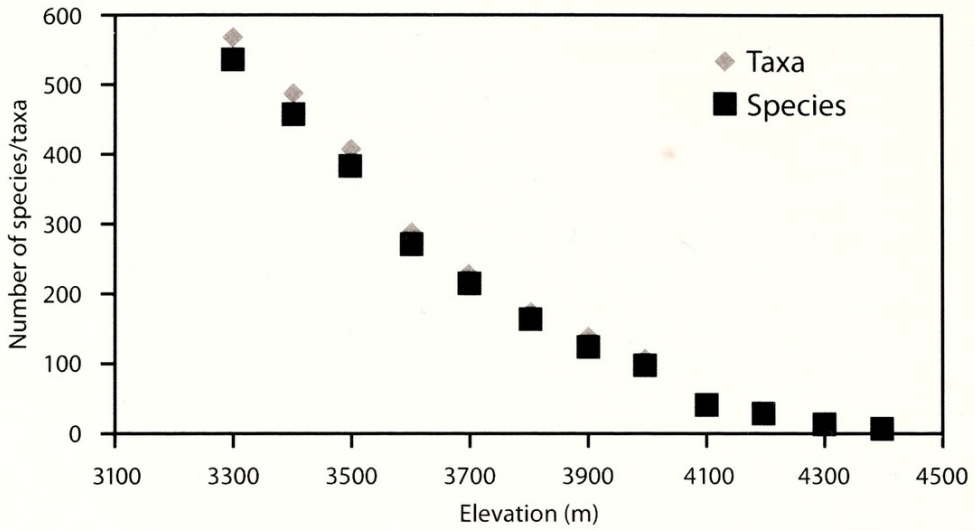

FIG. 3. Elevational distribution of species in the high mountain flora of the Sierra Nevada.

Floristic Richness

The alpine flora of the Sierra Nevada, defined as species reaching 3500 m or more at their upper limit of distribution, comprises 385 vascular plant species. The species total includes 10 ferns and fern relatives (2.6%), five conifers (1.3%), 85 monocots (22.1%), and 285 eudicots (74.0%). With the inclusion of an additional 24 named varieties and subspecies, the total number of alpine taxa is 409.

Of course, the predetermined elevational boundary has a very strong influence on the size of the flora (Fig. 3). If the alpine flora were defined as those species reaching to 3400 m, then 76 additional species would be added for a total of 460 species (488 taxa). Were the limit defined as 3300 m, there would be a flora of 536 species (570 taxa), with the relative proportions of monocots and eudicots virtually unchanged and the addition of five ferns and one conifer.

There are 97 species (101 taxa) with an elevational range that extends as high as 4000 m, an elevation reached by only the highest Sierran peaks (Fig. 3). This number declines to 27 species that reach 4200 m in elevation. These 27 high elevation species do not display dominance by a few families as is the case with the full alpine flora but are rather spread among 15 different families (Appendix 1). Three species have been recorded as reaching to 4400 m. These are *Epilobium anagallidifolium* Lam. (Onagraceae), *Saxifraga hyperborea* R. Br. (Saxifragaceae), and *Erigeron vagus* Payson (Asteraceae). Additional taxa that occur up to or above 4300 m are *Erigeron compositus* Pursh (Asteraceae), *Boechera lemmonii* (S. Watson) W. A. Weber (Brassicaceae), *Cerastium beeringianum* Cham. & Schltdl. (Caryophyllaceae), *Calyptridium umbellatum* (Torr.) Greene (Montiaceae), *Festuca brachyphylla* Schult. & Schult. subsp. *breviculmis* Fred., *Poa keckii* Soreng. and *P. lettermannii* Vasey (Poaceae), *Phlox pulvinata* (Wherry) Cronquist (Polemoniaceae), *Ranunculus eschscholtzii* Schltdl. var. *oxynotus* (A. Gray) Jeps. (Ranunculaceae), and *Potentilla pseudosericea* Rydb. and *Sorbus californica* Greene (Rosaceae).

There are six families that contribute 20 or more taxa to the alpine flora. The largest of these is the Asteraceae with 55 species (59 taxa), followed in size by the Poaceae (39 species, 47 taxa), Brassicaceae (34 species), Cyperaceae (31 species), Rosaceae (21 species, 23 taxa), and Fabaceae (18 species, 27 taxa). These six families together comprise 52% of the alpine flora.

At the generic level, *Carex* stands out prominently with 29 species in the alpine flora, with an additional 18 species present at elevations between 3300 and 3500 m. Next in order of size are *Draba* (Brassicaceae, 14 species), and *Lupinus* (Fabaceae, 11 species, 16 taxa). There are 10 species of *Boechera* (Brassicaceae) and nine species each of *Epilobium* (Onagraceae), *Eriogonum* (Polygonaceae), and *Potentilla* (Rosaceae). There are three genera with eight species—*Penstemon* (Plantaginaceae), *Poa* (Poaceae), and *Salix* (Salicaceae).

Growth Form Distribution

Herbaceous perennial growth forms, broadly defined, comprise the great majority of taxa reaching to or above 3500 m in the Sierra Nevada. This growth form with all of its subgroups includes 343 taxa, or 84% of the 409 taxa that comprise the flora. These herbaceous perennials can be broken down into subgroups of erect herbaceous perennials, perennial graminoids, prostrate mats and cushion plants, biennials, and geophytes. The largest numbers of herbaceous perennials form the category of erect herbaceous perennials, with 186 species (206 taxa; Fig. 4). The most important families for the erect herbaceous perennials are the Asteraceae, Brassi-

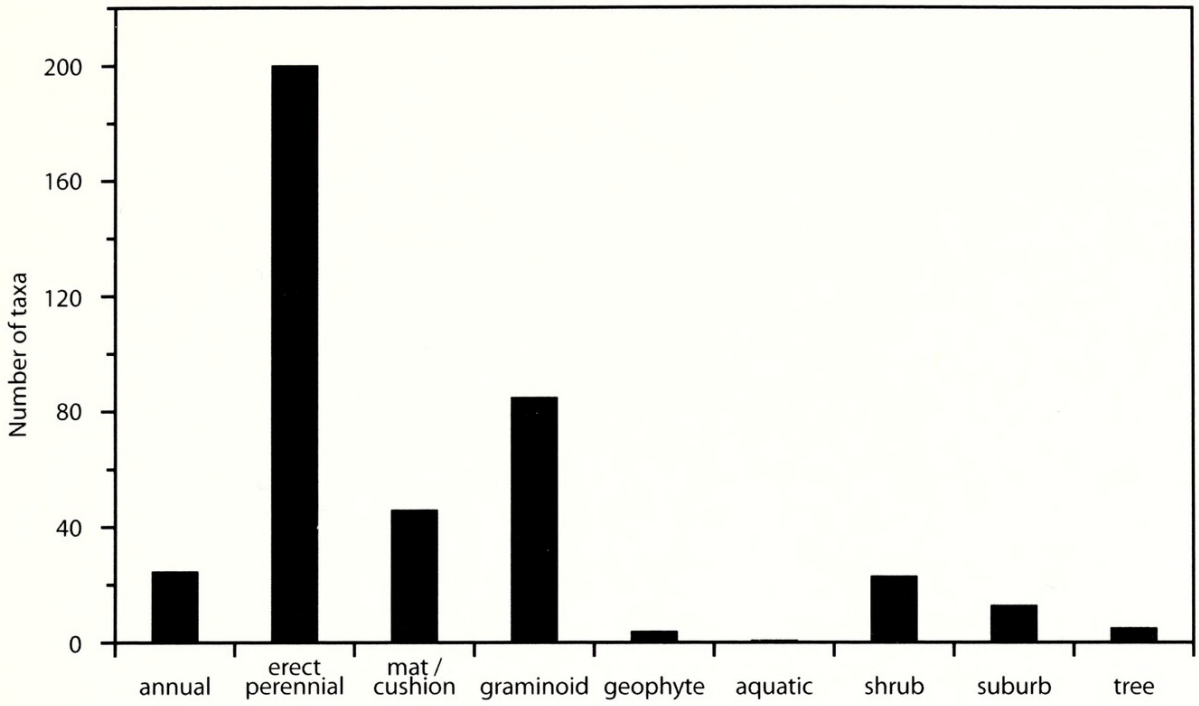

FIG. 4. Growth form distribution of alpine taxa in the alpine flora of the Sierra Nevada.

caceae, Fabaceae, Rosaceae, Polygonaceae, and Onagraceae. Among the erect herbaceous perennials are four species that are reported to have the potential to survive as facultative annuals. Although these have not been studies in detail, it is expected that these species have biennial or short-lived perennial life histories in the alpine zone, and they are included here in the totals for erect herbaceous perennials. Three of these are members of the Brassicaceae, each representing a different genus. Among these facultative annuals, only *Androsace septentrionalis* L. (Primulaceae) with an elevation range of 2700–3600 m can be considered as a subalpine and alpine specialist.

There are several additional groups classified broadly as erect herbaceous perennials. The 10 species of ferns and fern relatives included here within the alpine flora represent four families (Pteridaceae, Ophioglossaceae, Woodsiaceae, and Selaginellaceae). Four of these species reach elevation at or above 4000 m—*Botrychium lineare* W. H. Wagner, *B. paradoxum* W. H. Wagner, *Cystopteris fragilis* (L.) Bernh., and *Selaginella watsonii* Underw. Lowering the characterization of the alpine zone lower limit to 3300 m would add five additional fern species (Appendix 2). Also classified as erect perennials are seven species of hemiparasites, all members of the Orobanchaceae, with four species (five taxa) of *Castilleja* and three species of *Pedicularis*. Six more species from this family would be added by lowering the alpine boundary to 3300 m, including five more species of *Castilleja*.

Next in diversity among the herbaceous perennials is the subgroup of graminoids (Cyperaceae, Juncaceae, Juncaginaceae, and Poaceae) with 83 species (85 taxa, Fig. 4). All of the members of these four families within the alpine flora are perennials, with *Agrostis, Bromus, Carex, Elymus, Juncus, Luzula, Poa,* and *Stipa* forming genera with five or more taxa (Appendix 1). These perennial graminoids include one species of C_4 grass, *Muhlenbergia richardsonis* Rydb. (Sage and Sage 2002). Two other C_4 members of this genus, the perennial *M. montana* Hitchc. and the annual *M. filiformis* Rydb., just miss inclusion, reaching to elevations of 3420 m and 3350 m, respectively. Lowering the alpine boundary to 3300 m would add significantly to the diversity of graminoid perennials, with 43 additional taxa present (Appendix 2).

Prostrate mats and cushion forms of growth are common in some of the herbaceous perennials of the Sierran alpine flora (Fig. 4). These species are low in stature and form a heterogeneous group that shares the characteristic of a prostrate growth form with either a central taproot or multiple points of rooting through layering. Mats and cushions often form an ecologically significant component of plant cover on exposed ridges and fellfield. There are 46 species classified here as mats or cushions, with 19 of these high subalpine and alpine specialists not occurring below 2700 m elevation The growth form characteristics of mats and cushions may be genetic in some cases but in others is environmentally induced, with mat forms of growth only occurring at higher elevations (personal observations). Alpine mat and cushion species are well represented in the Asteraceae with 13 species (notably taxa of *Antennaria* and *Erigeron*), Polygonaceae (*Eriogonum*) with eight species,

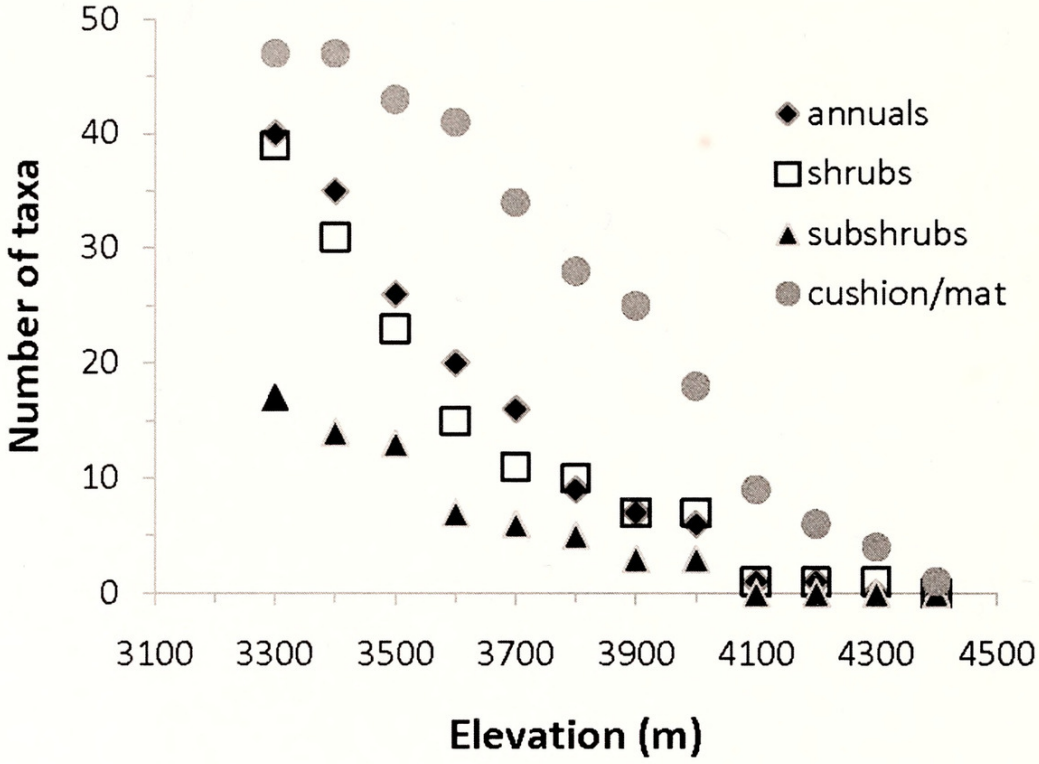

FIG. 5. Elevational distribution of taxa of annuals, shrubs, subshrubs, and mats/cushions in the alpine flora of the Sierra Nevada.

Brassicaceae (*Draba* and *Anelsonia*) with six species, and Fabaceae (*Astragalus, Lupinus, Oxytropis,* and *Trifolium*) with five species. Also notable in their ecological dominance are mats of Caryophyllaceae (*Cerastium, Eremogone, Minuartia*) and Polemoniaceae (*Phlox*).

The alpine flora includes just four species of geophytes, which represent the Alliaceae (*Allium obtusum* Lemmon var. *obtusum*), Liliaceae (*Calochortus leichtlinii* Hook. f.), Melanthiaceae (*Veratrum californicum* Durand var. *californicum*), and Themidaceae (*Triteleia dudleyi* Hoover). The highest elevation species among these is *C. leichtlinii*, which reaches up to 4000 m. None of these geophytes can be considered to be high elevation specialists as all reach lower elevational limits of 1200–1500 m in California. There are six species of geophytes that just miss reaching the lower alpine limit, as defined here, but occur at or above 3300 m (Appendix 2). These include *Allium validum* S. Watson (Alliaceae), *Iris missouriensis* Nutt. (Iridaceae), *Lilium kelleyanum* Lemmon (Liliaceae) and three Orchidaceae (*Platanthera dilatata* (Pursh) Lindl. ex L. C. Beck var. *leucostachys* (Lind.) Luer, *P. sparsiflora* Schltr., and *Spiranthes romanzoffiana* Cham.

Only a single species of aquatic plant, *Callitriche palustris* L. (Plantaginaceae), reaches the alpine zone of the Sierra Nevada. This is perhaps not surprising given the relatively small area of oligotrophic lakes that are present above 3500 m. *Potamogeton robbinsii* Oakes (Potamogetonaceae) and *Limosella acaulis* Sessé & Moc. (Scrophulariaceaeae) have a range that extends as high as 3300 m, and a number of aquatic species including *Isoetes* (Isoetaceae) reach elevations of 3000 m.

Plants with an annual life history comprise a small but significant component of the alpine flora of the Sierra Nevada, with 24 species (26 taxa) reaching to elevations of 3500 m (Fig. 4). The annual species occurring at the highest elevation is *Gayophytum decipiens* F. H. Lewis & Szweyk. (Onagraceae), which ranges up to 4200 m. Five other species of annuals reach 4000 m in elevation—*Gentianopsis holopetala* (A. Gray) Iltis (Gentianaceae), *Phacelia hastata* Douglas ex Lehm. subsp. *compacta* (Brand) Heckard (Boraginaceae), *Mimulus suksdorfii* A. Gray (Phrymaceae), *Gayophytum racemosum* Torr. & A. Gray (Onagraceae), and *Collinsia torreyi* A. Gray var. *wrightii* (S. Watson) I. M. Johnst. (Plantaginaceae). The number of annual species present increases sharply below the limit set here for inclusion in the alpine flora. Including the above taxa, there are 33 annual species (36 taxa) with a range reaching to or above 3400 m and 38 species (41 taxa) occurring at or above 3300 m (Fig. 5).

Most of the annuals reaching into the alpine zone are species with wide elevational ranges that extend down to lower foothill habitats. Only 13 of the alpine annual species have ranges limited to elevations at or above 1200 m, a distribution that would indicate adaptation to montane and higher elevation habitats. Five annual taxa can be

considered as subalpine and alpine specialists having a lower elevation limit of 2700 m or above and/or a median elevational range above 3000 m. These species, none of which ranges as high as 4000 m or above, are *Comastoma tenellum* (Rottb.) Toyok. (Gentianaceae), *Cryptantha circumscissa* (Hook. & Arn.) I. M. Johnst.var. *rosulata* J. T. Howell (Boraginaceae), *Streptanthus gracilis* Eastw. (Brassicaceae), and *Leptosiphon oblanceolatus* (Brand) J. M. Porter & L. A. Johnson and *Gymnosteris parvula* A. Heller (Polemoniaceae). Just missing this criteria, but certainly also a high elevation specialist, is *Phacelia orogenes* Brand (Boraginaceae). Four of these six, with *Comastoma tenellum* and *Gymnosteris parvula* as exceptions, are Sierra Nevada endemics.

The most important family in contributing to the annual flora of high elevations is the Boraginaceae, with 11 species (12 taxa) representing five genera. Next in importance are the Polemoniaceae with five species (comprising five genera), and the Onagraceae with four species (five taxa) representing just a single genus. There are four genera that contribute three or more species to the annual flora. These are *Gayophytum* (Onagraceae, four species, five taxa), *Phacelia* (Boraginaceae, four species), *Cryptantha* (Boraginaceae, three species, four taxa), and *Mimulus* (Phrymaceae, three species).

Subshrubs, defined as semi-woody species that maintain living perennial tissue in winter above the ground surface, include 13 species occurring at elevations of 3500 m or above (Fig. 4). The Asteraceae contribute more than 60% of the alpine flora of subshrubs, with eight species. Four species of *Ericameria* (Asteraceae) and three species each of *Penstemon* (Plantaginaceae), and one *Monardella* (Lamiaceae) form subshrubs that reach alpine elevations. Five species are considered to be subalpine and alpine specialists based on a lower elevational limit of 2700 m or a mean elevational range above 3000 m. Four of these are members of the Asteraceae—*Sphaeromeria cana* (D. C. Eaton) A. Heller, *Ericameria parryi* (A. Gray) G. L. Nesom & G. I. Baird var. *monocephala* (A. Nelson & P. B. Kenn.) G. L. Nesom & G. I Baird, *E. bloomer* (A. gray) J. F. Macbr., and *Chrysothamnus viscidiflorus* (Hook.) Nutt. var. *viscidiflorus*. The two latter species have very broad elevational occurrence from 800–4000 m.

There are 23 species of woody shrubs that extend into the alpine zone of the Sierra Nevada (Fig. 4). Just four families account for the majority of the high elevation shrubs. The largest of these is the Salicaceae (eight species of *Salix*), followed by the Ericaceae (five species, each in a different genus), Grossulariaceae (three species of *Ribes*), and Rosaceae (three species, each in a different genus). The highest elevation reached is reported for *Sorbus californica* at 4300 m. However, this elevation record appears to not be supported by specimen records in the Consortium of California Herbaria (ucjeps.berkeley.edu/consortium), and therefore needs confirmation. There are six additional shrub species that reach elevations of 4000 m—*Salix orestera* C. K. Schneid., *S. planifolia* Pursh, *S. petrophila* Rydb., *Gaultheria humifusa* (Graham) Rydb., *Holodiscus discolor* (Pursh) Maxim. var. *microphyllus* (Rydb) Jeps., and *Ribes montigenum* McClatchie. Only three shrub species can be considered as subalpine and alpine specialists based on a lower elevational limit at or above 2700 m or median range of occurrence above 3000 m. These are *Salix planifolia, S. brachycarpa* Nutt. var. *brachycarpa,* and *S. nivalis* Hook. Three more shrub species just miss this definition of high elevation specialist. *Arctostaphylos uva-ursi* (L.) Spreng. has an elevational range of 2400–3300 m, while *Jamesia americana* Torr. & A. Gray (Hydrangeaceae) and *Ribes cereum* Douglas var. *inebrians* (Lindl.) C. L. Hitchc. are alpine species that extend down to lower elevations of 2070 m and 2100 m, respectively. Including the above species, there are a total of 39 shrub species that occur at elevations of 3300 m or above in the Sierra Nevada. This group includes two more species of *Salix*, one additional *Ribes*, five Ericaceae, three Rosaceae, two species of Caprifoliaceae, and a scattered diversity of species from other families (Appendix 2).

Five species of coniferous trees in the Pinaceae have scattered populations that extend well above typical treeline elevation on favorable sites. The treeline pines, *Pinus albicaulis* Engelm., *P. flexilis* E. James and *P. balfouriana* Grev. & Balf., all have local populations that reach as high as 3700 m in elevation in the Sierra Nevada, while *P. contorta* Loudon subsp. *murrayana* (Grev. & Balf.) Critchf. and *Tsuga mertensiana* (Bong.) Carrière reach 3500 m. Just missing the elevation of the alpine zone are scattered trees of *Pinus monticola* Douglas ex D. Don that reach up to 3400 m.

Elevational Amplitude

Separating alpine taxa into categories of elevational ranges over which they occur provides some insight into their ecological amplitude and thus a crude measure of potential niche breadth. There are nine obligate alpine taxa in the Sierra Nevada restricted in occurrence to elevations at or above 3500 m. These are *Boechera depauperata* (A. Nelson & P. B. Kenn.) Windham & Al-Shehbaz (Brassicaceae), *Botrychium paradoxum* and *B. tunux* Stensvold & Farrar (Ophioglossaceae), *Carex incurviformis* Mack. (Cyperaceae), *Draba sierra* Sharsm. (Brassicaceae), *Eriogonum wrightii* Torr. ex Benth. var. *olanchense*

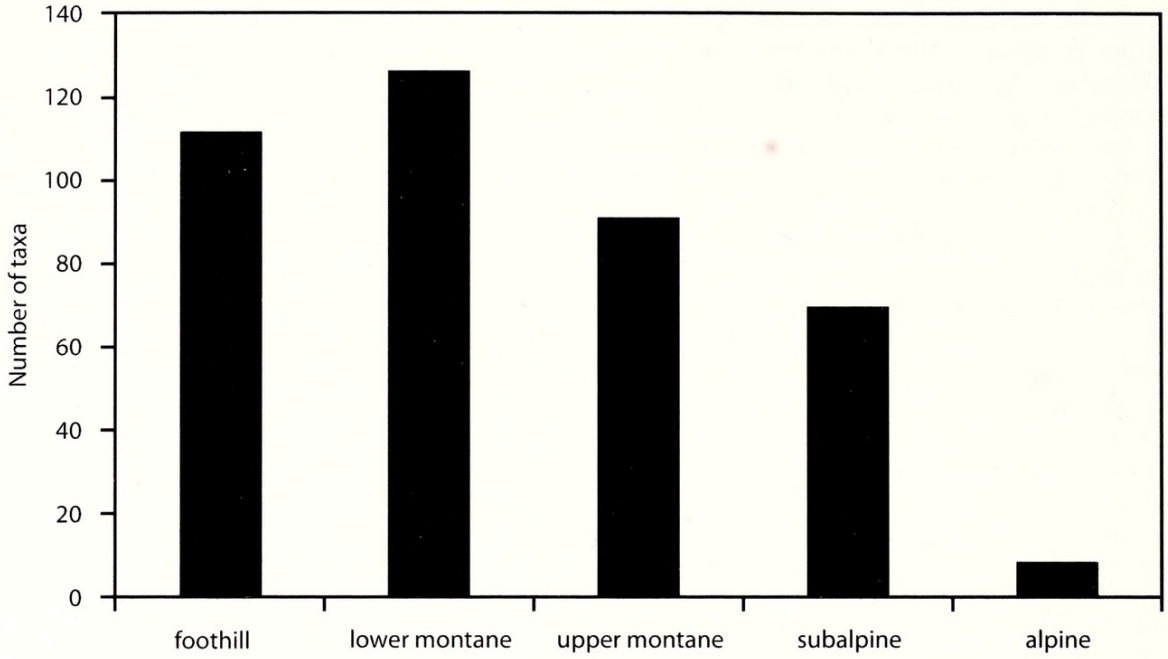

FIG. 6. Lower elevational zone of occurrence for taxa in the alpine flora of the Sierra Nevada. The elevational limits of these zones are 0–1190 m for the foothill zone, 1200–1990 m for the lower montane zone, 2000–2699 m for the upper montane zone, 2700–3490 m for the subalpine zone, and 3500 m and above for the alpine zone.

(J. T. Howell) Reveal (Polygonaceae), *Minuartia stricta* (Sw.) Hiern (Caryophyllaceae), *Phlox dispersa* Sharsm. (Polemoniaceae), and *Poa lettermanii* (Poaceae).

There an additional 67 alpine species (70 taxa, 17.2% of all taxa) with ranges restricted to the elevations of subalpine and alpine habitats at or above 2700 m (Fig. 6). Examining the floristic composition of all 76 species (79 taxa) with a range restricted to subalpine and alpine elevations, just four families comprise more than half of these. These are the Asteraceae (11 species), Brassicaceae (nine species), Rosaceae (eight species, nine taxa), and Poaceae (eight species). Three additional species would be added to the obligate subalpine and alpine flora if the elevational limit were reduced to 3300 m. These are *Astragalus ravenii* Barneby (Fabaceae), *Carex tiogana* D. W. Taylor & J. D. Mastrog. (Cyperaceae), and *Chaenactis douglasii* (Hook.) Hook. & Arn. var. *alpina* A. Gray (Asteraceae).

Looking at the level of all alpine taxa, 22.4% have a lower elevational limit in the upper montane zone (2000–2699 m) and a further 31.0% have a lower limit in the lower montane zone (1200–1999 m). Finally 27.5% of the alpine taxa have a broad elevational amplitude of occurrence extending upward from the foothill zone below 1200 m up into the alpine (Fig. 6).

Plotting the elevational amplitude of all of the alpine taxa shows a peak at about 2300 m, with relatively fewer species exhibiting very broad or very narrow elevational amplitudes (Fig. 7). Nevertheless, there are many taxa with surprising broad ranges of elevational occurrence. There are 77 species that have an elevational amplitude of 3000 m or more, and six species that have 4000 m or more of amplitude in California. These latter species, each in a different family, are *Callitriche palustris* (Plantaginaceae), *Calyptridium umbellatum* (Montiaceae), *Cystopteris fragilis* (Woodsiaceae), *Draba cana* Rydb. (Brassicaceae), *Epilobium ciliatum* Raf. subsp. *ciliatum* (Onagraceae), and *Erysimum capitatum* (Hook.) Greene var. *capitatum* (Brassicaceae). Were the elevational definition of the alpine zone lowered to 3300 m, a large number of species with broad elevational amplitudes would be added to the flora. There are 42 species in this group of added taxa that have 3000 m or more of elevational amplitude in their range of occurrence.

Biogeography and Endemism

Within the Sierra Nevada itself, the distributions of the high elevation flora are relatively well spread between the northern, central and southern subregions of the Sierra Nevada. Assessing species reaching an elevational boundary of 3300 m, 70% of the 567 taxa occur in all three subregions. The northern subregion has 76% of the alpine flora present, while the central and southern Sierra Nevada have 90% and 88% of the alpine flora present, respectively. A number of alpine species have their southern limit of distribution in the central Sierra Nevada. These include *Carex whitneyi* Olney (Cyperaceae), *Podistera nevadensis* (A. Gray) S. Watson (Apiaceae), *Claytonia megarhiza* (A. Gray) S. Waston (Montiaceae), *Thalictrum alpinum* L. (Ranunculaceae), *Galium grayanum* Ehrend. var. *grayanum* (Rubiaceae), and *Salix nivalis* (Salicaceae).

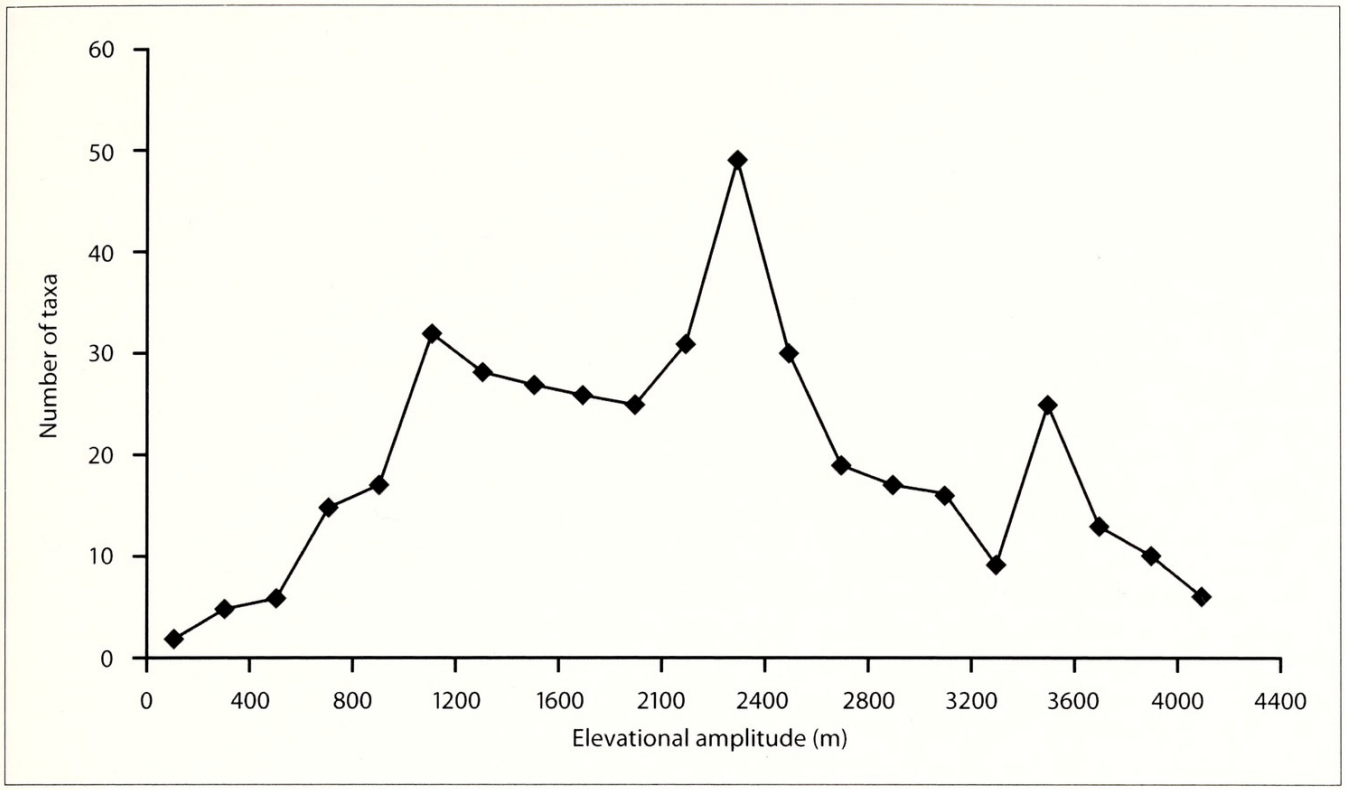

FIG. 7. Elevational amplitude of alpine taxa in the Sierra Nevada. These values are based on the range expressed from upper and lower limits of elevational distribution in California as presented in Baldwin et al. (2012).

The broader biogeographic relationships of the alpine flora at or above 3500 m indicate its diverse origins (Fig. 8). Widespread species distributed across North America and beyond as boreal or arctic-alpine taxa comprise 13.6% of the flora (Table 1). The largest group of taxa (34.3%) shows patterns of distribution as cordilleran species widespread in mountain regions of the western United States. Next in importance are taxa with a range in the Intermountain Region of the Great Basin, comprising 20.5% of taxa. A group consisting of 15.8% of the taxa has ranges extending along the Sierra Nevada axis to the Cascade Range and often on to the Pacific Northwest.

The alpine flora of the Sierra Nevada includes 36 endemic taxa restricted in their distribution to the Sierra Nevada (Table 2). These endemic taxa

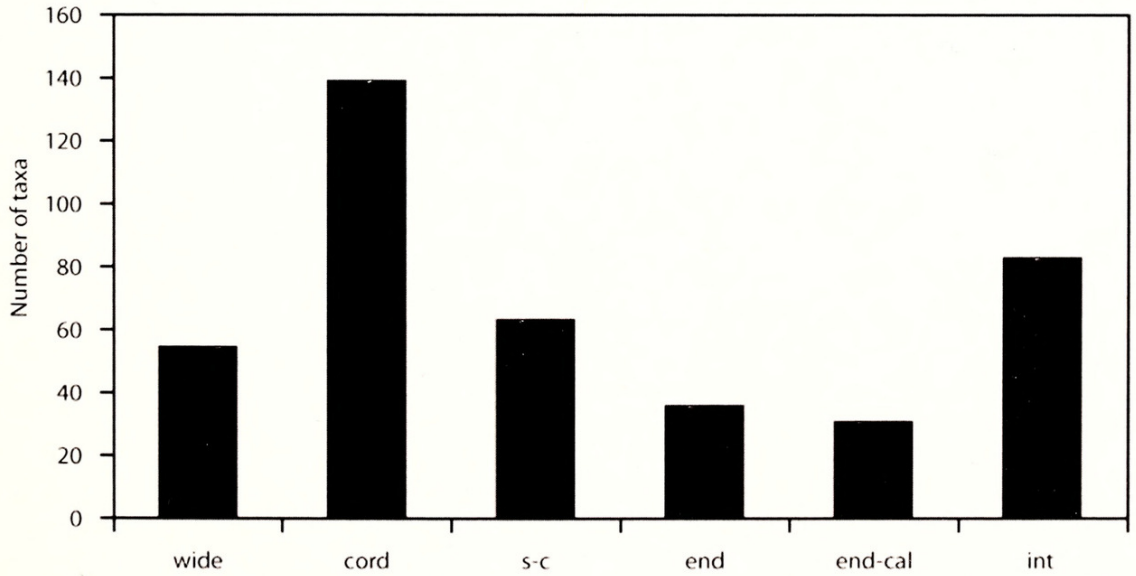

FIG. 8. Biogeographic relationships of the alpine flora of the Sierra Nevada. WIDE = widespread taxa present in many habitats or regions across North America and/or throughout the world; CORD = cordilleran taxa widespread in mountain regions of the western United States; S-C = Sierra/Cascade taxa with a Pacific Northwest distribution; END = taxa endemic to the Sierra Nevada; and END-CAL = taxa endemic to California, as broadly defined; INT = intermountain taxa present in the Great Basin. See text for discussion.

TABLE 1. EXAMPLES OF THE BROADER BIOGEOGRAPHIC RELATIONSHIPS OF THE ALPINE FLORA OF THE SIERRA NEVADA.

Biogeographic range category	Examplar taxa
Widespread taxa distributed across North America and beyond as circumboreal or arctic-alpine taxa	*Anemone drummondii* (Ranunculaceae), *Carex capitata* (Cyperaceae), *Crepis nana* (Asteraceae), *Cystopteris fragilis* (Woodsiaceae), *Deschampsia cespitosa* (Poaceae), *Oxyria digyna* (Polygonaceae), *Phleum alpinum* (Poaceae), *Rhodiola integrifolium* (Crassulaceae), *Salix nivalis* and *S. petrophila* (Salicaceae), *Sibbaldia procumbens* (Rosaceae), *Trisetum spicatum* (Poaceae)
Cordilleran taxa widespread in mountain regions of the western United States	*Antennaria media* (Asteraceae), *Carex phaeocephala* (Cyperaceae), *Erigeron vagus* (Asteraceae), *Gentiana calycosa* (Gentianaceae). *Lewisia pygmaea* (Montiaceae), *Phlox condensata* (Polemoniaceae), *Poa glauca* subsp. *rupicola* (Poaceae), *Ribes cereum* (Grossulariaceae), *Stipa pinetorum* (Poaceae)
Intermountain Region taxa distributed across the Great Basin	*Cryptantha nubigena* (Boraginaceae), *Cymopterus cinerarius* (Apiaceae), *Eriogonum incanum* (Polygonaceae), *Ivesia shockleyi* (Rosaceae), *Jamesia americana* (Hydrangeaceae), *Podistera nevadensis* (Apiaceae), *Selaginella watsonii* (Selaginellaceae), *Trifolium monanthum* subsp. *monanthum* (Fabaceae)
Taxa extending from the Pacific Northwest and Cascade Range	*Anelsonia eurycarpa* (Brassicaceae), *Astragalus whitneyi* (Fabaceae), *Boechera howellii* (Brassicaceae), *Carex breweri* (Cyperaceae), *Eriogonum lobbii* (Polygonaceae), *Gentiana newberryi* (Gentianaceae), *Potentilla breweri* and *P. flabellifolia* (Rosaceae), *Ranunculus alismifolius* var. *alismellus* (Ranunculaceae), *Senecio fremontii* var.*occidentalis* (Asteraceae), *Silene sargentii* (Caryophyllaceae)

are heavily weighted toward subalpine and alpine specialists, with 29 of these restricted in distribution to elevations of 2700 m or above, or with median elevational range above 3000 m. Two generic lineages are prominent among these endemics, with five taxa each of *Draba* and *Eriogonum*. Five of the alpine endemics are annual species—*Orochaenactis thysanocarpha* (A. Gray) Coville (Asteraceae), *Cryptantha circumscissa* var. *rosulata* (Boraginaceae), *Streptanthus gracilis* (Brassicaceae), and *Leptosiphon oblanceolatus* (Polemoniaceae).

The southern Sierra Nevada is the most significant subregion for endemics, with 15 of the 36 endemic taxa (42%) are restricted in distribution to the area from the Kings River drainage south that includes Kings Canyon and Sequoia National parks (Table 2). These are *Draba cruciata* Payson, *D. longisquamosa* O. E. Schulz, *D. sharsmithii* Rollins & R. A. Price, *Eriogonum polypodum* Small, *E. spergulinum* A. Gray var. *pretense* (S. Stokes) J. T. Howell, *E. wrightii* var. *olanchense, Galium hypotrichium* A. Gray subsp. *subalpinum* (Hilend & J. T. Howell) Ehrend., *Leptosiphon oblanceolatus, Monardella beneolens* Shevock, Ertter & Jokerst, *Oreonana clementis* (M. E. Jones) Jeps., *Orthochaenactis thysanocarpha, Phlox dispersa, Pinus balfouriana* var. *austina* R. J. Mastrog. & J. D. Mastrog., *Streptanthus gracilis,* and *Trifolium kingie* S. Waston subsp. *dedeckerae* (J. M. Gillett) D. Heller.

Another 13 taxa are restricted to the central and southern Sierra Nevada. Five of the endemics are present across the northern, central and southern subregions of the Sierra Nevada, and three endemic taxa are restricted in occurrence to the central Sierra Nevada. These are *Draba sierrae, Eriogonum ovalifolium* Nutt. var. *caelestinum* Reveal, and *Lupinus gracilentus* Greene (Table 2). Although the absence of peaks above 3500 m in the Sierra Nevada north of Yosemite National Park explains the lack of endemics restricted to this subregion, the scattered lower elevation alpine communities of the northern Sierra Nevada retain moderately high richness of species.

In addition to the members of the alpine flora that are endemic to the Sierra Nevada, there are an additional 31 alpine taxa that are Californian endemics, allowing for a broad interpretation of the floristic region to include the westernmost ranges of the Great Basin lying close to the Sierra Nevada and the southern Cascade Range in Oregon. Many of the Californian endemics have ranges that extend to the Sweetwater and/or White Inyo mountains, while others extend into the high Transverse and Peninsular Ranges of southern California and a small number extend into the southern Cascade Range. The pattern of dominant endemism centered in the southern Sierra Nevada is not seen among these taxa. Twelve of these occur throughout the Sierra Nevada and an additional 12 are restricted to the central and southern areas of the range, while only four species are limited to the southern Sierra Nevada.

If the lower limit of the alpine zone were dropped to 3300 m, 11 additional Sierra Nevada endemics would be added (Table 2). Four of these are restricted to the southern Sierra Nevada (*Astragalus ravenii, Boechera pygmaea* (Rollins) Al-Shehbaz, *Castilleja praeterita* Heckard & Bacig., and *Phacelia orogenes*), with three each present in the central and southern Sierra Nevada and in all three regions. One species is restricted

to the central Sierra Nevada. Five additional Californian endemics would be added if the lower alpine limit was dropped to 3300 m (Table 2).

Discussion

Defining the Alpine Zone of California

Critically defining what species should be included in an alpine flora is an imperfect task given the lack of a simple operational definition, as discussed below. The high elevation areas of the Sierra Nevada broadly classified as subalpine and alpine, or upper Hudsonian and Arctic-Alpine in the Merriam life zone classification (Daubenmire 1938), would roughly include those areas lying above about 3000 m elevation (Fig. 2). Such subalpine and alpine habitats cover extensive areas of the central and southern Sierra Nevada, but only scattered areas of the northern Sierra Nevada lying north of Sonora Pass. The higher elevation area of this northern Sierran region, however, supports mosaics of subalpine forest, shrublands, and low alpine-like vegetation (Smiley 1915, 1921).

A simple definition of alpine habitat is that area occurring above treeline, with the caveat that most alpine species are not obligate in inhabiting habitats above treeline and typically occur to varying degrees at lower elevations (Packer 1974). While this approach sounds logical, timberline itself can be highly variable even in a local area depending on slope exposure, erosional history, parent material, disturbance history, and local microclimate (Billings 2000).

Sharsmith (1940) recognized the alpine flora as a distinct subdivision of the overall California flora, characterized by its geographic range, growth forms, species composition, and constancy with which the alpine association of species is maintained. Although he described the alpine zone as reaching its lower limit at an average elevation of 3500 m, the limit used in this paper, nowhere in his dissertation is there a clear statement of criteria for his inclusion of species. He stated,

> While certain species are absolute indicators of the alpine flora, it is the particular association of species which gives it its characteristic. Although many species occur elsewhere, this special assemblage is not met until the alpine area is reached. Everywhere the flora presents the impression of unity, an impression reinforced by increased field experience.

The combined subalpine and alpine flora of the Sierra Nevada as defined by Smiley (1921) included 633 species, with 41 listed as indicators of the Arctic-Alpine zone. He considered 158 species to be Sierra Nevada endemics and another 20 species to be restricted in distribution to the Sierra Nevada and the southern California mountains. Sharsmith (1940) included 189 species in his alpine flora of the Sierra Nevada, with 31 of these considered to be endemic. This flora was composed of 183 herbaceous perennials and six annual species, but did not include any woody species. A similar estimate was made by Stebbins (1982) who stated that there were 207 species in the Sierra Nevada alpine flora. Finally, a much higher estimate came from Major and Bamberg (1967) who used the species descriptions in Munz (1959) to estimate a Sierran alpine flora of about 600 species, a number similar to that reported here for taxa reaching 3300 m or above.

Growth Forms

The relative dominance of a herbaceous perennial growth forms present in the alpine flora of the Sierra Nevada is typical of other alpine floras worldwide and does not change dramatically in a gradient from the Rocky Mountains west across the Great Basin (Billings 1978, 2000; Rundel et al. 2008). Herbaceous perennials have the characteristic of maintaining large proportions of total biomass belowground where they play an important role in carbohydrate storage over the winter months (Mooney and Billings 1960; Billings 1974). The herbaceous perennials include species with a variety of ecological forms and life history strategies of carbon allocation to belowground and aboveground vegetative, and reproductive tissues (Rundel et al. 2005), and many of these are relatively long-lived plants surviving for decades (Billings 1974; Pollak 1991).

As in other alpine regions, perennial graminoids in alpine habitats of the Sierra Nevada commonly dominate plant communities of wet meadows that dry earlier than fellfield communities. In contrast, fellfield habitats exhibit a mixed dominance of broad-leaved erect perennials, perennial graminoids, and mats and cushions (Rundel et al. 2005). Mat and cushion growth forms of herbaceous perennials are widespread in the high elevation Sierra Nevada, where the 46 taxa listed here represent 12% of the alpine flora. These are most prominent ecologically on windswept rocky slopes or other exposed areas that remain snow-free during the winter.

Because of limiting stress factors of short and severe growing conditions, annual plants are generally rare in the typical circumboreal arctic-alpine floras of the Northern Hemisphere, comprising no more than 1–2% of the flora (Billings 2000). Although not abundant, annuals, nevertheless, are more common in alpine flora of the Sierra Nevada and White Mountains where they comprise about 6–8% of the floras (Jackson and Bliss 1982; Jackson 1985; Rundel et al. 2008). The species richness of alpine annual taxa, however, drops rapidly at elevations above 3300 in the Sierra Nevada (Fig. 5). Went (1948, 1953)

TABLE 2. ENDEMIC TAXA OF THE ALPINE FLORA OF THE SIERRA NEVADA, CALIFORNIA WITH THEIR UPPER RANGE OF OCCURRENCE AND GROWTH FORMS. For range: n = northern Sierra Nevada, c = central Sierra Nevada, and s = southern Sierra Nevada. For growth forms: A = annual, G = geophyte, P = erect herbaceous perennial, P-G = perennial graminoid, P-MAT = mat or cushion, SS = subshrub, T = tree. Species names follow Baldwin et al. (2012).

Endemic group	Family	Range	Growth form
Sierra Nevada endemics >3500 m			
Aquilegia pubescens	Ranunculaceae	n,c,s	P
Calamagrostis muiriana	Poaceae	c,s	P-G
Carex congdonii	Cyperaceae	c,s	P-G
Cryptantha circumscissa var. *rosulata*	Boraginaceae	n,c,s	A
Dodecatheon subalpinum	Primulaceae	c,s	P
Draba cruciata	Brassicaceae	s	P
Draba lemmonii	Brassicaceae	n,c,s	P
Draba longisquamosa	Brassicaceae	s	P
Draba sharsmithii	Brassicaceae	s	P
Draba sierrae	Brassicaceae	c	P-MAT
Eriogonum nudum var. *scapigerum*	Polygonaceae	c,s	P
Eriogonum ovalifolium var. *caelestinum*	Polygonaceae	c	P-MAT
Eriogonum polypodum	Polygonaceae	s	P-MAT
Eriogonum spergulinum var. *pratense*	Polygonaceae	s	P
Eriogonum wrightii var *olanchense*	Polygonaceae	s	P-MAT
Galium hypotrichium subsp. *subalpinum*	Rubiaceae	s	P
Hazardia whitneyi var. *whitneyi*	Asteraceae	n,c,s	SS
Ivesia muirii	Rosaceae	c,s	P
Ivesia pygmaea	Rosaceae	c,s	P
Leptosiphon oblanceolatus	Polemoniaceae	s	A
Lewisia disepala	Montiaceae	c,s	P
Lupinus covillei	Fabaceae	c,s	P
Lupinus gracilentus	Fabaceae	c	P
Luzula orestera	Juncaceae	n,c,s	P-G
Monardella beneolens	Lamiaceae	s	SS
Oreonana clementis	Apiaceae	s	P
Oreostemma peirsonii	Asteraceae	c,s	P
Orochaenactis thysanocarpha	Asteraceae	s	A
Phlox dispersa	Polemoniaceae	s	P-MAT
Pinus balfouriana var. *austrina*	Pinaceae	s	T
Poa stebbinsii	Poaceae	c,s	P-G
Polemonium eximium	Polemoniaceae	c,s	P
Stipa kingii	Poaceae	c,s	P-G
Streptanthus gracilis	Brassicaceae	s	A
Trichophorum clementis	Cyperaceae	c,s	P-G
Trifolium kingii subsp. *dedeckerae*	Fabaceae	s	P
Sierra Nevada endemics 3300–3499 m			
Astragalus ravenii	Fabaceae	s	P
Boechera pygmaea	Brassicaceae	s	P
Castilleja praeterita	Orobanchaceae	s	P
Erigeron elmeri	Asteraceae	c,s	P
Hulsea vestita subsp. *vestita*	Asteraceae	c,s	P
Ipomopsis aggregata subsp. *bridgesii*	Polemoniaceae	c,s	P
Lilium kelleyanum	Liliaceae	c,s	G
Lomatium torreyi	Apiaceae	n,c,s	P
Phacelia eisenii	Boraginaceae	c,s	A
Phacelia orogenes	Boraginaceae	s	A
Trifolium monanthum subsp. *tenerum*	Fabaceae	n,c,s	P
Californian endemics >3500			
Astragalus kentrophyta var. *danaus*	Fabaceae	c,s	P-MAT
Carex mariposana	Cyperaceae	n,c,s	P-G
Castilleja nana	Orobanchaceae	n,c,s	P
Chaenactis alpigena	Asteraceae	n,c,s	P-MAT
Delphinium polycladon	Ranunculaceae	n,c,s	P
Draba breweri	Brassicaceae	n,c,s	P
Draba subumbellata	Brassicaceae	s	P-MAT
Eriogonum gracilipes	Polygonaceae	c,s	P-MAT
Eriogonum umbellatum var. *covillei*	Polygonaceae	c,s	P-MAT

TABLE 2. CONTINUED.

Endemic group	Family	Range	Growth form
Galium hypotrichium subsp. *hypotrichium*	Rubiaceae	c,s	P
Hulsea vestita subsp. *pygmaea*	Asteraceae	c,s	P
Ivesia lycopodioides subsp. *lycopodioides*	Rosaceae	n,c	P
Ivesia lycopodioides subsp. *scandularis*	Rosaceae	c,s	P
Ivesia santolinoides	Rosaceae	n,c,s	P
Lewisia glandulosa	Montiaceae	c,s	P
Lupinus breweri var. *breweri*	Fabaceae	n,c,s	P-MAT
Lupinus breweri var. *bryoides*	Fabaceae	s	P-MAT
Lupinus latifolius var. *parishii*	Fabaceae	c,s	P
Lupinus lepidus var. *ramosus*	Fabaceae	c,s	P
Lupinus padre-crowleyi	Fabaceae	s	P-MAT
Lupinus pratensis var. *pratensis*	Fabaceae	c,s	P
Phyllodoce breweri	Ericaceae	n,c,s	S
Poa keckii	Poaceae	n.c.s	P-G
Potentilla pseudosericea	Rosaceae	c,s	P
Potentilla wheeleri	Rosaceae	s	P
Primula suffrutescens	Primulaceae	n,c,s	P
Ranunculus eschscholtzii var. *oxynotus*	Ranunculaceae	n,c,s	P
Tonestus peirsonii	Asteraceae	c	P
Triteleia dudleyi	Themidaceae	c,s	G
Viola pinetorum subsp. *grisea*	Violaceae	n,c,s	P
Viola purpurea subsp. *mesophyta*	Violaceae	n,c,s	P
Californian endemics 3300–3499 m			
Eriogonum latens	Polygonaceae	c,s	P
Frasera puberulenta	Gentianaceae	c,s	P
Hordeum brachyantherum subsp. *californicum*	Poaceae	n,c,s	P-G
Penstemon caesius	Plantaginaceae	s	SS
Plagiobothrys torreyi var. *diffusus*	Boraginaceae	n,c,s	A

suggested that many of the high elevation annuals in the Sierra Nevada were related to desert species.

Severe winter conditions typically limit the occurrence of woody plants above treeline, with prostrate mats and cushions as prominent exceptions. The upright growth form of woody shrubs and krummholtz tree species exposes their tissues to extreme conditions of temperature and wind exposure (Körner 2003). This impact on shrub occurrence can be seen in Fig. 5 where shrub richness in the Sierra Nevada drops sharply with increasing elevation above 3300 m, similar to the pattern for annual species. Much of the alpine flora of woody species comes from species of *Salix* and members of the Ericaceae, groups which favor moist habitats with some level of protection.

Biogeography and Endemism

The alpine flora of mountain ranges on the western margin of the Great Basin of California and western Nevada exhibit very strong relationships to that of the Sierra Nevada (Rundel et al. 2008). The Sweetwater Mountains supports a flora of 173 species in 16 km^2 of alpine habitat, with 94% of this flora common to the Sierra Nevada (Hunter and Johnson 1983). The Wassuk Range has an alpine flora of 70 species in just 2.6 km^2 of alpine habitat (Bell and Johnson 1980). Again, this flora is has stronger floristic relationships to the Sierra Nevada than the Rocky Mountains.

As with the Sweetwater Mountains and Wassuk Ranges, the flora of the White Mountains exhibits much stronger floristic relationships to the Sierra Nevada than to the Rocky Mountains. About 90% of the species in the alpine flora of the White Mountains are also found in the Sierra Nevada (Rundel et al. 2008), compared with only 58% that occur in the ranges of the central Rocky Mountains (Scott 1995). These values are significantly higher for both ranges than earlier estimates made on incomplete data (Lloyd and Mitchell 1973).

Mountain ranges in the central Great Basin generally show strong floristic linkages to the Rocky Mountains and weaker links to the Sierra Nevada (Billings 1978). Loope (1969) reported 189 alpine species from the Ruby Mountains in northeastern Nevada, with this flora heavily linked to the Rocky Mountains. The isolated San Francisco Mountains in Arizona with only 5.2 km^2 of alpine habitat has 80 species, and likewise shows strong floristic relationships to the Rocky Mountains despite its separation of about 200 km (Schaak 1983).

The level of endemism in the alpine Sierra Nevada flora is a relatively small part of the overall endemism for the montane and higher parts of the range. Based on current information, there are 205 taxa endemic to what *The Jepson*

Manual (Hickman 1993) classifies as the northern, central, and southern high Sierra Nevada, i.e., the montane, subalpine and alpine zones above foothill habitats (R. Moe, Univ. of California, Berkeley, personal communication). The 36 Sierran endemics present in the alpine flora would thus comprise 18% of the endemic flora of the higher Sierra Nevada.

The unique California component of the alpine flora of the Sierra Nevada is considerably greater if one considers the endemic component of 31 species in the alpine flora that are not uniquely limited to the Sierra Nevada but are Californian endemics as defined earlier. Combining the endemic taxa with Sierran and Californian limits of distribution, the total of 66 taxa represents 16% of the alpine flora. This is a relatively high figure compared to other alpine ranges in continental North America and Europe, and reflects the environmental stress conditions associated with the summer-dry mediterranean-type climate present in the Sierra Nevada.

Stebbins (1982) analyzed the flora of the high Sierra Nevada, defined similarly to that of Smiley (1921) as the upper montane to alpine zones, and identified 119 endemic species, 13.5% of the total flora. He further noted that another 60% of the flora extended beyond the Sierra Nevada only as far as southern California, western Nevada, and southern Oregon.

Raven and Axelrod (1978) briefly discussed the diversity and evolution of the subalpine and alpine flora of the Sierra Nevada, listing 68 endemics for this region. Their table of endemics, however, is outdated by more recent information on distribution patterns and species concepts. Shevock (1996) gave a figure of 405 endemic taxa of vascular plants for the entire Sierra Nevada. The 36 alpine endemics reported here would comprise 9% of this total. Of the three geographical subregions (northern, central, and southern) of the entire range, the southern Sierra Nevada is the richest in endemics, rare species, and total floristic composition (Shevock 1996), a finding similar to that reported here.

The Evolution of the Sierran Alpine Flora

A detailed assessment of the biogeographic and evolutionary origin of the alpine flora of the Sierra Nevada is beyond the scope of this review. Broad interpretations of biogeographic relationships within alpine lineages have been discussed by previous authors (e.g., Smiley 1921; Sharsmith 1940; Chabot and Billings 1972; Taylor 1977; Major and Taylor 1977; Raven and Axelrod 1978; Stebbins 1982) but recent phylogenetic studies have made many of these earlier interpretations subject to re-evaluation.

Evidence for a north to south route of colonization of high mountain areas of the Sierra Nevada comes from a pattern of decreasing presence of Rocky Mountain floristic elements and an increasing number of endemics alpine species as one moves from the northern to southern crest of the range (Chabot and Billings 1972; Raven and Axelrod 1978). The southern limit of a number of alpine species on Mount Lassen suggests the possibility that some of these and other Cascade Range species may well have been present in the Sierra Nevada in the late Pliocene or early Pleistocene. Although the species composition of lower and middle elevation conifer forests of Lassen National Park are strongly related to that of the Sierra Nevada, the summits of the highest peaks in Lassen support an alpine flora that exhibits stronger floristic links to Mount Shasta and the Cascade Range to the north (Gillett et al. 1995). Alpine species with disjunct patterns of distribution from Mount Lassen to the Cascade Range volcanoes include *Cardamine bellidifolia* L. (Brassicaceae), *Carex illota* L. H. Bailey (Cyperaceae), *Collomia larsenii* (A. Gray) Payson (Polemoniaceae), *Draba aureola* S. Watson (Brassicaceae), *Erigeron elegantulus* Greene and *E. nivalis* Nutt. (Asteraceae), *Hulsea nana* A. Gray (Asteraceae), *Polemonium pulcherrimum* Hook. var. *pilosum* (Greenm.) Brand (Polemoniaceae), and *Silene suksdorfii* B. L. Rob. (Caryophyllaceae). The Klamath Mountains also mark the southern distribution limit of a number of boreal species that do not occur in the high elevations of the Sierra Nevada (Howell 1944).

Alpine and subalpine species characteristic of wet meadows and other moist sites typically have broad geographic ranges but become increasing habitat specific moving to the south in the Sierra Nevada as precipitation decreases (Kimball et al. 2004; Moore et al. 2007). The relative isolation of the Sierra Nevada from northern ranges and the summer-dry have clearly acted as a filter to exclude some widespread circumpolar arctic-alpine species such as *Dryas integrifolia* Vahl (Rosaceae) and *Silene acaulis* L. (Caryophyllaceae) which do not occur anywhere in California. Species growing in xeric rocky habitats show higher levels of endemism and smaller range size due to isolation and divergence from ancestral populations distributed in wetter habitats to the north.

More controversial, however, is the origin of disjunct Rocky Mountain species present in the central and southern Sierra Nevada, often growing in azonal soil conditions. There is both geological and paleobotanical evidence to suggest that the mean elevation of the Great Basin was as much as 1500 m higher in the Miocene and that the current Basin and Range topography is the result of subsidence rather than uplift (Wernicke et al. 1988; Wolfe et al. 1997). The presence of higher elevations in the Great Basin during the

Pleistocene could possibly have provided stepping stones to allow the dispersal of alpine organisms from the east (Major and Bamberg 1967; Taylor 1976a). Molecular evidence indicates that at least one lineage of butterflies entered the Sierra Nevada by this route (Nice and Shapiro 2001). However, other authors feel that the majority of these disjunct plant species reached the Sierra Nevada by the same dominant route from the Western Cordillera via the Cascade Range and south (Chabot and Billings 1972).

Modes of speciation in the development of the endemic alpine flora of the Sierra Nevada are clearly complex. Polyploidy and associated apomixis are widely recognized as major factors in plant evolution, and these factors have had a relatively recent impact on speciation in producing stable self-propagating lineages (Soltis et al. 2009). In the alpine region of the Sierra Nevada, as in other alpine regions, diploid lineages of polyploid complexes often occupy unglaciated areas and resist introgression due hypothetically to a significantly higher seed set. However, asexual apomictic populations are more widespread than their sexual relatives in glaciated areas. Sexual and asexual polyploids may become distinct stabilized species through hybrid origin.

Reproductive isolation and stability of tetraploids within their respective distribution as well as the value of uniparental reproduction provide the advantages of apomixis. Many important genera in the alpine flora of the Sierra Nevada are notable for the presence of apomixis, with *Boechera* (Schranz et al. 2005; Dobes et al. 2007), *Draba* (Jordon-Thaden and Koch 2008), and *Antennaria* (Bayer and Stebbins 1987) as examples. Additional speciose genera in the Sierra Nevada known to have complex apomictic populations include *Arnica* and *Crepis* (Asteraceae; Noyes 2007), *Poa* and *Calamagrostis* (Poaceae), and *Potentilla* (Rosaceae) (Asker and Jerling 1992).

Other modes of alpine speciation have also been described for the Sierra Nevada. Some speciation, for example, has hypothetically come from lowland arid-adapted taxa colonizing the glaciated terrain of the range at the end of the Pleistocene (Went 1948, 1953). Speciation has also been shown to be the result of population disjunction and reproductive isolation (Chase and Raven 1975).

Although the Transverse and Peninsular ranges are well separated from the higher elevations of the Sierra Nevada, more than one third of the Sierran alpine flora has a range of distribution that extends to these southern California ranges. While some of these species occur at lower elevations, others are typically subalpine and alpine species that must have crossed the Mojave Desert during the cold conditions of the Pleistocene. This latter group includes *Androsace septentrionalis* (Primulaceae), *Hulsea vestita* A. Gray subsp. *pygmaea* (A. Gray) Wilken (Asteraceae), *Oxyria digyna* (L.) Hill (Polygonaceae), and *Podistera nevadensis* (Apiaceae).

There are lessons to be learned from recent studies of the patterns of diversification in the European alpine flora. These strongly demonstrate that speciation have been promoted by diverse ecological, evolutionary, and life history traits related to population structure, phylogenetic relationships, breeding system, dispersal syndromes, ecophysiological ranges of habitat requirements, and competitive abilities (Comes and Kadereit 1998; Taberlet et al. 1998; Hewitt 2000; Gugerli and Holderegger 2001; Vargas 2003). The complex and dynamic climatic and geological history of the Sierra Nevada operating on such traits suggests that there have been a range of different colonization and extinction histories that are species specific. Much more work on the comparative phylogeography of alpine plants in the Sierra Nevada will be necessary before we understand all of the factors responsible for present distributions and predominant modes of speciation in the alpine flora of the range.

Research Needs

There is little doubt that the stability of the ecotone between alpine and treeline ecosystems in the Sierra Nevada and other high mountain regions has been and continues to be a function of complex interactions, with multiple drivers operating across diverse scales of time and space. This ecotone has been highly dynamic in the past and given the importance of temperature in controlling the elevation of treeline and higher alpine ecosystems, this ecotone and associated species are likely to be particularly sensitive to climate change in the future (Lloyd and Graumlich 1997; Graumlich et al. 2005; Grabherr et al. 2010). Beyond treeline studies, the expansion of woody shrub species into alpine habitats has been shown to also be a sensitive indicator of potential climate change, with significant feedbacks on microclimate and soil ecosystems (Hallinger et al. 2010), as well as species facilitation (Callaway et al. 2002). The potential sensitivity of alpine ecosystems to climate change has been the stimulus for establishing the worldwide research program Global Observation Research Initiative in Alpine Environments (GLORIA, http://www.gloria.ac.at) with the aim of providing long-term observations on the state and dynamics of alpine biota.

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APPENDIX 1. Annotated checklist of the alpine flora of the Sierra Nevada, including all taxa reaching an elevation of 3500 m. Lower and upper elevations limits are those for all of California and taken from Baldwin et al. (2012). Growth form abbreviations are: P = erect broad-leaved perennial; G = geophytes; P-G = graminoid perennial; P-MAT = mat or cushion; A = annual; Q = aquatic perennial; SS = subshrub; S = woody shrub; and T = tree. Biogeographic relationships are abbreviated as follows: WIDE = widespread taxa present in many habitats or regions across North America and/or throughout the world; CORD = cordilleran taxa widespread in mountain regions of the western North America; S-C = Sierra/Cascade taxa with a Pacific Northwest distribution; INT = intermountain taxa present in the Great Basin; END = taxa endemic to the Sierra Nevada; and END-CAL = taxa endemic to California, as broadly defined in the text. Species names follow Baldwin et al. (2012).

Higher level taxon	Specific or infraspecific taxon	Lower elevation (m)	Upper elevation (m)	Growth form	Biogeographic relationship
PTERIDOPHYTA					
Ophioglossaceae	*Botrychium crenulatum*	1500	3600	P	CORD
Ophioglossaceae	*Botrychium lineare*	2500	4000	P	CORD
Ophioglossaceae	*Botrychium paradoxum*	4000	4200	P	CORD
Ophioglossaceae	*Botrychium simplex* var. *compositum*	1500	3800	P	WIDE
Ophioglossaceae	*Botrychium tunux*	3600	3600	P	WIDE
Pteridaceae	*Pellaea breweri*	1500	3700	P	INT
Selaginellaceae	*Selaginella watsonii*	1350	4100	P	INT
Woodsiaceae	*Athyrium distentifolium* var. *americanum*	1700	3700	P	WIDE
Woodsiaceae	*Cystopteris fragilis*	50	4100	P	CORD
Woodsiaceae	*Woodsia scopulina*	1300	3500	P	WIDE
CONIFERAE					
Pinaceae	*Pinus albicaulis*	2135	3700	T	CORD
Pinaceae	*Pinus balfouriana* var. *austrina*	2700	3700	T	END
Pinaceae	*Pinus contorta* subsp. *murrayana*	1525	3500	T	S-C
Pinaceae	*Pinus flexilis*	2600	3700	T	CORD
Pinaceae	*Tsuga mertensiana*	1200	3500	T	S-C
MONOCOTYLEDONAE					
Alliaceae	*Allium obtusum* var. *obtusum*	1500	3500	G	INT
Cyperaceae	*Carex albonigra*	3000	4200	P-G	CORD
Cyperaceae	*Carex breweri*	2000	3900	P-G	S-C
Cyperaceae	*Carex capitata*	1200	3900	P-G	WIDE
Cyperaceae	*Carex congdonii*	2600	3900	P-G	END
Cyperaceae	*Carex deflexa* var. *boottii*	0	3800	P-G	CORD
Cyperaceae	*Carex douglasii*	300	3800	P-G	CORD
Cyperaceae	*Carex filifolia* var. *erostrata*	1500	3700	P-G	CORD
Cyperaceae	*Carex haydeniana*	2400	4200	P-G	CORD
Cyperaceae	*Carex helleri*	2400	4100	P-G	S-C
Cyperaceae	*Carex heteroneura*	1300	4000	P-G	INT
Cyperaceae	*Carex hoodii*	650	3600	P-G	CORD
Cyperaceae	*Carex incurviformis*	3700	4000	P-G	CORD
Cyperaceae	*Carex jonesii*	900	3500	P-G	CORD
Cyperaceae	*Carex lenticularis* var. *lipocarpa*	0	3600	P-G	CORD
Cyperaceae	*Carex leporinella*	1900	4000	P-G	CORD
Cyperaceae	*Carex mariposana*	750	3600	P-G	END-CAL
Cyperaceae	*Carex multicostata*	1900	3500	P-G	CORD
Cyperaceae	*Carex nigricans*	1900	3700	P-G	CORD
Cyperaceae	*Carex phaeocephala*	2500	4000	P-G	CORD
Cyperaceae	*Carex praeceptorium*	2200	3500	P-G	CORD
Cyperaceae	*Carex proposita*	3000	4100	P-G	S-C
Cyperaceae	*Carex rossii*	0	3800	P-G	CORD
Cyperaceae	*Carex scirpoidea* var. *pseudoscirpoidea*	2800	3700	P-G	CORD
Cyperaceae	*Carex specifica*	1200	3500	P-G	INT
Cyperaceae	*Carex spectabilis*	1800	3700	P-G	CORD
Cyperaceae	*Carex straminiformis*	1700	4100	P-G	S-C
Cyperaceae	*Carex subfusca*	700	3800	P-G	INT
Cyperaceae	*Carex subnigricans*	2600	3800	P-G	CORD
Cyperaceae	*Carex tahoensis*	3200	3700	P-G	CORD

APPENDIX 1. CONTINUED.

Higher level taxon	Specific or infraspecific taxon	Lower elevation (m)	Upper elevation (m)	Growth form	Biogeographic relationship
Cyperaceae	*Carex vernacula*	1800	4000	P-G	CORD
Cyperaceae	*Eleocharis quinqueflora*	40	3600	P-G	WIDE
Cyperaceae	*Trichophorum clementis*	2400	3600	P-G	END
Juncaceae	*Juncus bryoides*	600	3600	P-G	CORD
Juncaceae	*Juncus drummondii*	200	3500	P-G	CORD
Juncaceae	*Juncus mertensianus*	1200	3500	P-G	CORD
Juncaceae	*Juncus mexicanus*	0	3800	P-G	WIDE
Juncaceae	*Juncus orthophyllus*	1200	3500	P-G	CORD
Juncaceae	*Juncus parryi*	2000	3800	P-G	CORD
Juncaceae	*Luzula divaricata*	2100	3700	P-G	S-C
Juncaceae	*Luzula orestera*	2700	3600	P-G	END
Juncaceae	*Luzula spicata*	2900	3700	P-G	WIDE
Juncaceae	*Luzula subcongesta*	2000	3500	P-G	S-C
Juncaginaceae	*Triglochin palustris*	2400	3500	P-G	WIDE
Liliaceae	*Calochortus leichtlinii*	1300	4000	G	S-C
Melanthiaceae	*Veratrum californicum* var. *californicum*	0	3500	G	CORD
Poaceae	*Agrostis idahoensis*	0	3500	P-G	CORD
Poaceae	*Agrostis pallens*	200	3500	P-G	CORD
Poaceae	*Agrostis scabra*	100	3500	P-G	WIDE
Poaceae	*Agrostis thurberiana*	1300	3500	P-G	CORD
Poaceae	*Agrostis variabilis*	1600	4000	P-G	CORD
Poaceae	*Alopecurus aequalis* var *aequalis*	50	3500	P-G	WIDE
Poaceae	*Bromus carinatus* var. *carinatus*	0	3500	P-G	S-C
Poaceae	*Bromus carinatus* var. *marginatus*	0	3500	P-G	S-C
Poaceae	*Bromus orcuttianus*	560	3500	P-G	S-C
Poaceae	*Bromus porteri*	550	3500	P-G	CORD
Poaceae	*Bromus richardsonii*	1200	3600	P-G	CORD
Poaceae	*Calamagrostis muiriana*	2480	3900	P-G	END
Poaceae	*Calamagrostis purpurascens*	1300	4000	P-G	WIDE
Poaceae	*Deschampsia cespitosa* subsp. *cespitosa*	0	3820	P-G	WIDE
Poaceae	*Elymus elymoides* subsp. *californicus*	275	4200	P-G	CORD
Poaceae	*Elymus multisetus*	0	3800	P-G	CORD
Poaceae	*Elymus scribneri*	2900	4200	P-G	CORD
Poaceae	*Elymus sierrae*	1800	3530	P-G	INT
Poaceae	*Festuca brachyphylla* subsp. *breviculmis*	2800	4300	P-G	WIDE
Poaceae	*Festuca minutiflora*	2850	4050	P-G	CORD
Poaceae	*Hordeum jubatum* var. *jubatum*	20	3500	P-G	WIDE
Poaceae	*Koeleria macrantha*	0	3840	P-G	WIDE
Poaceae	*Muhlenbergia richardsonis*	1220	3670	P-G	CORD
Poaceae	*Phleum alpinum*	0	3700	P-G	WIDE
Poaceae	*Poa abbreviata* subsp. *pattersonii*	3300	3660	P-G	CORD
Poaceae	*Poa cusickii* subsp. *epilis*	2400	3600	P-G	CORD
Poaceae	*Poa cusickii* subsp. *purpurascens*	2100	3500	P-G	S-C
Poaceae	*Poa glauca* subsp. *rupicola*	3300	4100	P-G	CORD
Poaceae	*Poa keckii*	3300	4340	P-G	END-CAL
Poaceae	*Poa lettermanii*	3500	4300	P-G	CORD
Poaceae	*Poa secunda* subsp. *secunda*	0	3900	P-G	CORD
Poaceae	*Poa stebbinsii*	2700	3700	P-G	END
Poaceae	*Poa wheeleri*	1300	3800	P-G	CORD
Poaceae	*Stipa hymenoides*	60	3500	P-G	CORD
Poaceae	*Stipa kingii*	2000	3650	P-G	END
Poaceae	*Stipa nelsonii* subsp. *dorei*	450	3500	P-G	CORD
Poaceae	*Stipa occidentalis* subsp. *pubescens*	1200	3500	P-G	CORD

APPENDIX 1. CONTINUED.

Higher level taxon	Specific or infraspecific taxon	Lower elevation (m)	Upper elevation (m)	Growth form	Biogeographic relationship
Poaceae	*Stipa pinetorum*	2000	3900	P-G	INT
Poaceae	*Stipa webberi*	1450	3500	P-G	INT
Poaceae	*Torreyochloa erecta*	2000	3500	P-G	INT
Poaceae	*Torreyochloa pallida* var. *pauciflora*	0	3500	P-G	CORD
Poaceae	*Trisetum spicatum*	1370	3900	P-G	WIDE
Themidaceae	*Triteleia dudleyi*	1200	3500	G	END-CAL
EUDICOTS					
Adoxaceae	*Sambucus racemosa* var. *melanocarpa*	1800	3600	S	CORD
Apiaceae	*Cymopterus cinerarius*	2100	3500	P	INT
Apiaceae	*Oreonana clementis*	1500	4000	P	END
Apiaceae	*Podistera nevadensis*	3000	4000	P	INT
Apiaceae	*Sphenosciadium capitellatum*	0	3500	P	CORD
Asteraceae	*Achillea millefolium*	0	3650	P	WIDE
Asteraceae	*Ageratina occidentalis*	0	3700	P	CORD
Asteraceae	*Agoseris aurantiaca* var. *aurantiaca*	1500	3500	P	CORD
Asteraceae	*Agoseris monticola*	2500	3800	P	S-C
Asteraceae	*Antennaria media*	1800	3900	P-MAT	CORD
Asteraceae	*Antennaria pulchella*	2800	3700	P-MAT	INT
Asteraceae	*Antennaria rosea* subsp. *confinis*	1200	3700	P	WIDE
Asteraceae	*Antennaria rosea* subsp. *rosea*	1200	3700	P-MAT	CORD
Asteraceae	*Antennaria umbrinella*	1800	3900	P-MAT	WIDE
Asteraceae	*Arnica chamissonis*	1800	3500	P	WIDE
Asteraceae	*Arnica lanceolata* subsp. *prima*	2200	3500	P	CORD
Asteraceae	*Arnica longifolia*	1300	3500	P	CORD
Asteraceae	*Arnica mollis*	2500	3500	P	CORD
Asteraceae	*Arnica ovata*	1800	3600	P	CORD
Asteraceae	*Artemisia arbuscula* subsp. *arbuscula*	1500	3800	S	CORD
Asteraceae	*Artemisia ludoviciana* subsp. *incompta*	0	3500	P	INT
Asteraceae	*Artemisia norvegica* subsp. *saxatilis*	2300	3800	P	WIDE
Asteraceae	*Artemisia spiciformis*	2100	3700	P	CORD
Asteraceae	*Chaenactis alpigena*	220	3900	P-MAT	END-CAL
Asteraceae	*Chaenactis douglasii* var. *douglasii*	400	3500	P	CORD
Asteraceae	*Chrysothamnus viscidiflorus* var. *viscidiflorus*	900	4000	SS	INT
Asteraceae	*Cirsium arizonicum* var. *arizonicum*	2300	3500	P	INT
Asteraceae	*Cirsium occidentale* var. *venustum*	0	3600	P	INT
Asteraceae	*Cirsium scariosum* var. *americanum*	1600	3500	P	CORD
Asteraceae	*Crepis nana*	2000	4000	P-MAT	CORD
Asteraceae	*Ericameria bloomeri*	900	4000	SS	INT
Asteraceae	*Ericameria discoidea*	2300	3800	SS	INT
Asteraceae	*Ericameria nauseosa* var. *speciosa*	50	3500	S	INT
Asteraceae	*Ericameria parryi* var. *monocephala*	2800	3700	SS	INT
Asteraceae	*Ericameria suffruticosa*	2100	3800	SS	INT
Asteraceae	*Erigeron algidus*	2600	3700	P	INT
Asteraceae	*Erigeron compositus*	2000	4300	P-MAT	WIDE
Asteraceae	*Erigeron lonchophyllus*	1800	3550	P-A	WIDE
Asteraceae	*Erigeron pygmaeus*	2900	4100	P-MAT	S-C
Asteraceae	*Erigeron vagus*	3300	4400	P-MAT	INT

APPENDIX 1. CONTINUED.

Higher level taxon	Specific or infraspecific taxon	Lower elevation (m)	Upper elevation (m)	Growth form	Biogeographic relationship
Asteraceae	*Eriophyllum lanatum* var. *integrifolium*	1400	3500	P	CORD
Asteraceae	*Hazardia whitneyi* var. *whitneyi*	1200	3500	SS	END
Asteraceae	*Hieracium nudicaule*	1800	3500	P	S-C
Asteraceae	*Hieracium triste*	1650	3550	P	CORD
Asteraceae	*Hulsea algida*	3000	4000	P	INT
Asteraceae	*Hulsea vestita* subsp. *pygmaea*	3200	3900	P	END-CAL
Asteraceae	*Hymenoxys hoopesii*	1500	3650	P	CORD
Asteraceae	*Oreostemma alpigenum* var. *andersonii*	1200	3500	P	S-C
Asteraceae	*Oreostemma peirsonii*	3000	3800	P	END
Asteraceae	*Orochaenactis thysanocarpha*	1600	3800	A	END
Asteraceae	*Packera cana*	1200	3500	P	S-C
Asteraceae	*Packera werneriifolia*	3000	3650	P	S-C
Asteraceae	*Pyrrocoma apargioides*	2200	3800	P	S-C
Asteraceae	*Raillardella argentea*	1800	3900	P	S-C
Asteraceae	*Raillardella scaposa*	2000	3500	P	S-C
Asteraceae	*Senecio fremontii* var. *occidentalis*	2800	4000	P-MAT	S-C
Asteraceae	*Senecio integerrimus* var. *major*	100	3600	P	CORD
Asteraceae	*Senecio pattersonensis*	3000	3700	P	INT
Asteraceae	*Senecio scorzonella*	1600	3500	P	S-C
Asteraceae	*Senecio spartioides*	1000	3500	SS	CORD
Asteraceae	*Solidago multiradiata*	1250	3950	P	CORD
Asteraceae	*Sphaeromeria cana*	1800	4000	SS	CORD
Asteraceae	*Stenotis acaulis*	1800	3600	P-MAT	INT
Asteraceae	*Tonestus peirsonii*	2900	3700	P	END-CAL
Boraginaceae	*Cryptantha circumscissa* var. *circumscissa*	150	3650	A	CORD
Boraginaceae	*Cryptantha circumscissa* var. *rosulata*	2950	3650	A	END
Boraginaceae	*Cryptantha glomeriflora*	1800	3750	A	S-C
Boraginaceae	*Cryptantha humilis*	1700	3600	P	INT
Boraginaceae	*Cryptantha nubigena*	2400	3900	P	INT
Boraginaceae	*Hackelia micrantha*	1200	3500	P	CORD
Boraginaceae	*Hackelia sharsmithii*	3150	3700	P	INT
Boraginaceae	*Nama densum*	880	3560	A	INT
Boraginaceae	*Phacelia hastata* subsp. *compacta*	1500	4000	A	S-C
Boraginaceae	*Phacelia mutabilis*	900	3500	P	S-C
Boraginaceae	*Phacelia ramosissima*	0	3800	P	CORD
Brassicaceae	*Anelsonia eurycarpa*	1600	4100	P-MAT	S-C
Brassicaceae	*Boechera depauperata*	3650	3900	P	INT
Brassicaceae	*Boechera howellii*	1500	3800	P	S-C
Brassicaceae	*Boechera inyoensis*	1200	3500	P	INT
Brassicaceae	*Boechera covillei*	2200	3500	P	S-C
Brassicaceae	*Boechera inyoensis*	1200	3500	P	INT
Brassicaceae	*Boechera lemmonii*	2000	4350	P	INT
Brassicaceae	*Boechera lyallii*	2000	3900	P	CORD
Brassicaceae	*Boechera paupercula*	2500	3700	P	CORD
Brassicaceae	*Boechera repanda*	1400	3600	P	INT
Brassicaceae	*Boechera tiehmii*	3000	3600	P	INT
Brassicaceae	*Cardamine cordifolia*	600	3600	P	CORD
Brassicaceae	*Descurainia incana*	100	3500	P	CORD
Brassicaceae	*Draba albertina*	900	3700	P-A	CORD
Brassicaceae	*Draba breweri*	3100	4100	P	END-CAL
Brassicaceae	*Draba cana*	0	4100	P	CORD
Brassicaceae	*Draba cruciata*	2500	3963	P	END
Brassicaceae	*Draba densifolia*	1900	3650	P-MAT	INT
Brassicaceae	*Draba lemmonii*	3050	4000	P	END

APPENDIX 1. CONTINUED.

Higher level taxon	Specific or infraspecific taxon	Lower elevation (m)	Upper elevation (m)	Growth form	Biogeographic relationship
Brassicaceae	*Draba lonchocarpa*	2800	4000	P	WIDE
Brassicaceae	*Draba longisquamosa*	3000	3900	P	END
Brassicaceae	*Draba novolympica*	1500	3700	P-MAT	CORD
Brassicaceae	*Draba oligosperma*	2000	3900	P-MAT	CORD
Brassicaceae	*Draba praealta*	2500	4100	P	WIDE
Brassicaceae	*Draba sharsmithii*	3300	3800	P	END
Brassicaceae	*Draba sierrae*	3500	4114	P-MAT	END
Brassicaceae	*Draba subumbellata*	3300	4100	P-MAT	END-CAL
Brassicaceae	*Erysimum capitatum* var. *capitatum*	0	4000	P	WIDE
Brassicaceae	*Erysimum perenne*	2000	4000	P	S-C
Brassicaceae	*Lepidium densiflorum*	0	3500	P-A	WIDE
Brassicaceae	*Rorippa curvipes*	100	3500	P-A	CORD
Brassicaceae	*Rorippa curvisiliqua*	0	3500	A	CORD
Brassicaceae	*Streptanthus gracilis*	2600	3600	A	END
Brassicaceae	*Streptanthus tortuosus*	200	4100	P	S-C
Caryophyllaceae	*Cerastium beeringianum*	2900	4300	P-MAT	WIDE
Caryophyllaceae	*Ereomogone kingii* var. *glabrescens*	2100	4050	P-MAT	S-C
Caryophyllaceae	*Minuartia nuttallii* var. *gracilis*	2600	3800	P-MAT	S-C
Caryophyllaceae	*Minuartia obtusiloba*	3150	3700	P-MAT	CORD
Caryophyllaceae	*Minuartia rubella*	2400	3800	P	CORD
Caryophyllaceae	*Minuartia stricta*	3500	3900	P	CORD
Caryophyllaceae	*Sagina saginoides*	1000	3800	P	WIDE
Caryophyllaceae	*Silene bernardina*	1350	3600	P	CORD
Caryophyllaceae	*Silene sargentii*	2400	3800	P	S-C
Caryophyllaceae	*Stellaria calycantha*	1700	3800	P	WIDE
Chenopodiaceae	*Chenopodium atrovirens*	300	3500	A	CORD
Chenopodiaceae	*Monolepis nuttalliana*	0	3700	A	CORD
Crassulaceae	*Rhodiola integrifolia*	1800	4000	P	WIDE
Crassulaceae	*Sedum obtusatum* subsp. *obtusatum*	1200	3700	P	S-C
Ericaceae	*Cassiope mertensiana*	1800	3505	S	CORD
Ericaceae	*Gaultheria humifusa*	1350	4000	S	CORD
Ericaceae	*Kalmia polifolia* subsp. *microphylla*	1000	3500	S	CORD
Ericaceae	*Phyllodoce breweri*	1200	3500	S	END-CAL
Ericaceae	*Pterospora andromedea*	60	3700	P	WIDE
Ericaceae	*Rhododendron columbianum*	0	3630	S	CORD
Fabaceae	*Astragalus kentrophyta* var. *danaus*	2900	4000	P-MAT	END-CAL
Fabaceae	*Astragalus kentrophyta* var. *tegetarius*	2700	3600	P	CORD
Fabaceae	*Astragalus lentiginosus* var. *ineptus*	1250	3700	P	INT
Fabaceae	*Astragalus platytropus*	2350	3500	P	INT
Fabaceae	*Astragalus purshii* var. *lectulus*	1500	3650	P	INT
Fabaceae	*Astragalus whitneyi* var. *whitneyi*	1550	3500	P	S-C
Fabaceae	*Lupinus adsurgens*	1000	3500	P	S-C
Fabaceae	*Lupinus angustiflorus*	1000	3500	P	INT
Fabaceae	*Lupinus argenteus* var. *meionanthus*	1500	3500	P	INT
Fabaceae	*Lupinus argenteus* var. *montigenus*	2500	3500	P	INT
Fabaceae	*Lupinus breweri* var. *breweri*	1000	4000	P-MAT	END-CAL
Fabaceae	*Lupinus breweri* var. *bryoides*	2500	4000	P-MAT	END-CAL
Fabaceae	*Lupinus breweri* var. *grandiflorus*	2000	3500	P-MAT	INT
Fabaceae	*Lupinus covillei*	2500	3500	P	END
Fabaceae	*Lupinus gracilentus*	2500	3500	P	END

APPENDIX 1. CONTINUED.

Higher level taxon	Specific or infraspecific taxon	Lower elevation (m)	Upper elevation (m)	Growth form	Biogeographic relationship
Fabaceae	*Lupinus latifolius* var. *columbianus*	1000	3500	P	S-C
Fabaceae	*Lupinus latifolius* var. *parishii*	0	3500	P	END-CAL
Fabaceae	*Lupinus lepidus* var. *lobbii*	2000	3500	P	S-C
Fabaceae	*Lupinus lepidus* var. *ramosus*	3000	4000	P	END-CAL
Fabaceae	*Lupinus obtusilobus*	2500	3500	P	S-C
Fabaceae	*Lupinus padre-crowleyi*	2500	4000	P-MAT	END-CAL
Fabaceae	*Lupinus pratensis* var. *pratensis*	1000	3500	P	END-CAL
Fabaceae	*Oxytropis borealis* var. *australis*	3300	3900	P	INT
Fabaceae	*Oxytropis borealis* var. *viscida*	3300	3900	P	CORD
Fabaceae	*Oxytropis parryi*	3100	3800	P-MAT	INT
Fabaceae	*Trifolium kingii* subsp. *dedeckerae*	2100	3500	P	END
Fabaceae	*Trifolium monanthum* subsp. *monanthum*	1700	3900	P-MAT	INT
Gentianaceae	*Comastoma tenellum*	3200	3900	A	WIDE
Gentianaceae	*Gentiana calycosa*	1300	3900	P	CORD
Gentianaceae	*Gentiana newberryi* var. *tiogana*	1500	4000	P	S-C
Gentianaceae	*Gentianella amarella* subsp. *acuta*	1500	3500	A	WIDE
Gentianaceae	*Gentianopsis holopetala*	1800	4000	A	S-C
Grossulariaceae	*Ribes cereum* var. *inebrians*	2100	3850	S	INT
Grossulariaceae	*Ribes montigenum*	800	4000	S	CORD
Grossulariaceae	*Ribes velutinum*	700	3500	S	CORD
Hydrangeaceae	*Jamesia americana*	2070	3700	S	INT
Lamiaceae	*Monardella beneolens*	2500	3600	SS	END
Lamiaceae	*Monardella linoides* subsp. *sierrae*	1000	3500	SS	INT
Lamiaceae	*Monardella odoratissima* subsp. *glauca*	1000	3500	SS	INT
Linaceae	*Linum lewisii*	400	3657	P	INT
Montiaceae	*Calyptridium monospermum*	300	3970	P	INT
Montiaceae	*Calyptridium roseum*	1500	3800	A	CORD
Montiaceae	*Calyptridium umbellatum*	240	4300	P	CORD
Montiaceae	*Claytonia nevadensis*	2200	3500	P	S-C
Montiaceae	*Lewisia disepala*	1300	3500	P	END
Montiaceae	*Lewisia glandulosa*	3000	4000	P	END-CAL
Montiaceae	*Lewisia nevadensis*	609	3596	P	S-C
Montiaceae	*Lewisia pygmaea*	1700	4020	P	CORD
Montiaceae	*Lewisia triphylla*	1300	3500	P	CORD
Montiaceae	*Montia chamissoi*	1100	3700	P	S-C
Onagraceae	*Epilobium anagallidifolium*	1500	4500	P	WIDE
Onagraceae	*Epilobium ciliatum* subsp. *ciliatum*	0	4000	P	CORD
Onagraceae	*Epilobium ciliatum* subsp. *glandulosum*	0	3500	P	WIDE
Onagraceae	*Epilobium clavatum*	1200	4200	P	CORD
Onagraceae	*Epilobium glaberrimum* subsp. *fastigiatum*	1200	3800	P	CORD
Onagraceae	*Epilobium hallianum*	100	3700	P	CORD
Onagraceae	*Epilobium hornemannii* subsp. *hornemannii*	1200	3900	P	WIDE
Onagraceae	*Epilobium obcordatum*	1700	4000	P	S-C
Onagraceae	*Epilobium oregonense*	1200	3500	P	CORD
Onagraceae	*Epilobium saximontanum*	1400	3500	P	CORD
Onagraceae	*Gayophytum decipiens*	1800	4200	A	INT
Onagraceae	*Gayophytum diffusum* subsp. *diffusum*	800	3700	A	S-C

APPENDIX 1. CONTINUED.

Higher level taxon	Specific or infraspecific taxon	Lower elevation (m)	Upper elevation (m)	Growth form	Biogeographic relationship
Onagraceae	*Gayophytum diffusum* subsp. *parviflorum*	800	3700	A	INT
Onagraceae	*Gayophytum racemosum*	1000	4000	A	CORD
Onagraceae	*Gayophytum ramosissimum*	500	3500	A	INT
Orobanchaceae	*Castilleja applegatei* subsp. *pallida*	1900	3600	P	INT
Orobanchaceae	*Castilleja applegatei* subsp. *pinetorum*	300	3600	P	INT
Orobanchaceae	*Castilleja lemmonii*	1550	3700	P	S-C
Orobanchaceae	*Castilleja miniata* subsp. *miniata*	1500	3500	P	INT
Orobanchaceae	*Castilleja nana*	2400	4200	P	END-CAL
Orobanchaceae	*Pedicularis attollens*	1200	4000	P	S-C
Orobanchaceae	*Pedicularis groenlandica*	1000	3600	P	S-C
Orobanchaceae	*Pedicularis semibarbata*	1500	3500	P	S-C
Parnassiaceae	*Parnassia palustris*	0	3600	P	WIDE
Phrymaceae	*Mimulus suksdorfii*	1100	4000	A	INT
Plantaginaceae	*Callitriche palustris*	0	4000	Q	WIDE
Plantaginaceae	*Collinsia parviflora*	800	3500	A	WIDE
Plantaginaceae	*Collinsia torreyi* var. *wrightii*	800	4000	A	INT
Plantaginaceae	*Penstemon davidsonii*	2000	3750	P-MAT	INT
Plantaginaceae	*Penstemon heterodoxus* var. *heterodoxus*	2700	3900	P-MAT	S-C
Plantaginaceae	*Penstemon newberryi* var. *newberryi*	1000	3700	P-MAT	INT
Plantaginaceae	*Penstemon procerus* var. *formosus*	2100	3600	P-MAT	INT
Plantaginaceae	*Penstemon roezlii*	300	3500	SS	INT
Plantaginaceae	*Penstemon rostriflorus*	500	3500	SS	INT
Plantaginaceae	*Penstemon rydbergii* var. *oreocharis*	1000	3600	P	INT
Plantaginaceae	*Penstemon speciosus*	850	3800	P	INT
Plantaginaceae	*Veronica wormskjoldii*	1500	3500	P	WIDE
Polemoniaceae	*Collomia linearis*	600	3650	A	WIDE
Polemoniaceae	*Gymnosteris parvula*	2400	3700	A	CORD
Polemoniaceae	*Ipomopsis congesta* subsp. *montana*	1500	3700	P	S-C
Polemoniaceae	*Leptosiphon oblanceolatus*	2800	3700	A	END
Polemoniaceae	*Linanthus pungens*	1700	4000	P	CORD
Polemoniaceae	*Phlox condensata*	2000	4000	P-MAT	CORD
Polemoniaceae	*Phlox diffusa*	1100	3600	P-MAT	CORD
Polemoniaceae	*Phlox dispersa*	3600	4200	P-MAT	END
Polemoniaceae	*Phlox pulvinata*	3300	4300	P-MAT	CORD
Polemoniaceae	*Polemonium eximium*	3000	4200	P	END
Polemoniaceae	*Polemonium pulcherrimum* var. *pulcherrimum*	2400	3700	P	S-C
Polygonaceae	*Eriogonum gracilipes*	2900	3900	P-MAT	END-CAL
Polygonaceae	*Eriogonum incanum*	2100	4000	P-MAT	INT
Polygonaceae	*Eriogonum lobbii*	1600	3800	P-MAT	S-C
Polygonaceae	*Eriogonum nudum* var. *scapigerum*	2800	3800	P	END
Polygonaceae	*Eriogonum ovalifolium* var. *caelestinum*	3000	3600	P-MAT	END
Polygonaceae	*Eriogonum ovalifolium* var. *nivale*	1700	4200	P-MAT	INT
Polygonaceae	*Eriogonum polypodum*	2800	3500	P-MAT	END
Polygonaceae	*Eriogonum rosense* var. *rosense*	2300	4000	P-MAT	INT
Polygonaceae	*Eriogonum spergulinum* var. *pratense*	1300	3500	P	END
Polygonaceae	*Eriogonum umbellatum* var. *covillei*	3000	3600	P-MAT	END-CAL
Polygonaceae	*Eriogonum wrightii* var. *olanchense*	3500	3600	P-MAT	END

APPENDIX 1. CONTINUED.

Higher level taxon	Specific or infraspecific taxon	Lower elevation (m)	Upper elevation (m)	Growth form	Biogeographic relationship
Polygonaceae	*Oxyria digyna*	1800	4000	P	WIDE
Polygonaceae	*Rumex californicus*	0	3500	P	CORD
Polygonaceae	*Rumex paucifolius*	1500	4000	P	S-C
Polygonaceae	*Rumex salicifolius*	0	3500	P	INT
Polygonaceae	*Rumex utahensis*	1000	3500	P	CORD
Primulaceae	*Androsace septentrionalis*	2700	3600	P-A	WIDE
Primulaceae	*Dodecatheon redolens*	2400	3600	P	INT
Primulaceae	*Dodecatheon subalpinum*	2100	4000	P	END
Primulaceae	*Primula suffrutescens*	2000	4200	P	END-CAL
Pteridaceae	*Pellaea breweri*	1500	3700	P	INT
Ranunculaceae	*Aconitum columbianum* subsp. *columbianum*	300	3500	P	CORD
Ranunculaceae	*Aquilegia pubescens*	2600	3650	P	END
Ranunculaceae	*Delphinium polycladon*	2200	3600	P	END-CAL
Ranunculaceae	*Ranunculus alismifolius* var. *alismellus*	1400	3600	P	S-C
Ranunculaceae	*Ranunculus eschscholtzii* var. *eschscholtzii*	2200	3600	P	S-C
Ranunculaceae	*Ranunculus eschscholtzii* var. *oxynotus*	2700	4300	P	END-CAL
Ranunculaceae	*Ranunculus glaberrimus*	1200	3600	P	CORD
Ranunculaceae	*Thalictrum alpinum*	2900	3700	P	WIDE
Ranunculaceae	*Thalictrum sparsiflorum*	1400	3500	P	CORD
Rosaceae	*Dasiphora fruticosa*	2000	3600	S	WIDE
Rosaceae	*Drymocaulis lactea* var. *lactea*	1800	3700	P	INT
Rosaceae	*Drymocaulis pseudorupestris* var. *crumiana*	3200	3900	P	CORD
Rosaceae	*Drymocaulis pseudorupestris* var. *saxicola*	2300	3500	P	CORD
Rosaceae	*Holodiscus discolor* var. *microphyllus*	1159	4000	S	CORD
Rosaceae	*Ivesia gordonii* var. *ursinorum*	1800	3500	P	INT
Rosaceae	*Ivesia lycopodioides* subsp. *lycopodioides*	3000	4000	P	END-CAL
Rosaceae	*Ivesia lycopodioides* subsp. *scandularis*	3000	4115	P	END-CAL
Rosaceae	*Ivesia muirii*	2900	4000	P	END
Rosaceae	*Ivesia pygmaea*	2700	4000	P	END
Rosaceae	*Ivesia santolinoides*	1500	3600	P	END-CAL
Rosaceae	*Ivesia shockleyi*	2700	4000	P-MAT	INT
Rosaceae	*Potentilla breweri*	1500	3700	P	S-C
Rosaceae	*Potentilla flabellifolia*	1700	3700	P	S-C
Rosaceae	*Potentilla bruceae*	1200	3700	P	INT
Rosaceae	*Potentilla glaucophylla* var. *glaucopylla*	2600	3500	P	WIDE
Rosaceae	*Potentilla gracilis* var. *fastigiata*	800	3500	P	INT
Rosaceae	*Potentilla jepsonii*	2700	3800	P	INT
Rosaceae	*Potentilla pensylvanica*	2700	3800	P	WIDE
Rosaceae	*Potentilla pseudosericea*	3200	4300	P	END-CAL
Rosaceae	*Potentilla wheeleri*	1800	3500	P	END-CAL
Rosaceae	*Sibbaldia procumbens*	1820	3700	P	WIDE
Rosaceae	*Sorbus californica*	1200	4300	S	INT
Rubiaceae	*Galium bifolium*	1500	3700	A	CORD
Rubiaceae	*Galium grayanum* var. *grayanum*	1830	3500	P	S-C
Rubiaceae	*Galium hypotrichium* subsp. *hypotrichium*	3000	4200	P	END-CAL
Rubiaceae	*Galium hypotrichium* subsp. *subalpinum*	2650	3880	P	END
Salicaceae	*Salix brachycarpa* var. *brachycarpa*	3200	3500	S	CORD

APPENDIX 1. CONTINUED.

Higher level taxon	Specific or infraspecific taxon	Lower elevation (m)	Upper elevation (m)	Growth form	Biogeographic relationship
Salicaceae	*Salix eastwoodiae*	1600	3800	S	CORD
Salicaceae	*Salix geyeriana*	1450	3600	S	CORD
Salicaceae	*Salix lemmonii*	1400	3500	S	CORD
Salicaceae	*Salix nivalis*	3100	3500	S	CORD
Salicaceae	*Salix orestera*	1100	4000	S	S-C
Salicaceae	*Salix petrophila*	1670	4000	S	CORD
Salicaceae	*Salix planifolia*	2500	4000	S	WIDE
Saxifragaceae	*Heuchera rubescens*	1000	4000	P	CORD
Saxifragaceae	*Lithophragma glabrum*	0	3750	P	CORD
Saxifragaceae	*Micranthes aprica*	1600	3600	P	CORD
Saxifragaceae	*Micranthes bryophora*	1600	3500	P	CORD
Saxifragaceae	*Micranthes nidifica*	1000	3500	P	CORD
Saxifragaceae	*Micranthes tolmiei*	1980	3596	P	CORD
Saxifragaceae	*Pectiantia breweri*	1500	3500	P	S-C
Saxifragaceae	*Saxifraga hyperborea*	3000	4500	P	WIDE
Valerianaceae	*Valeriana californica*	1500	3700	P	INT
Violaceae	*Viola adunca*	0	3570	P	WIDE
Violaceae	*Viola bakeri*	900	3800	P	INT
Violaceae	*Viola macloskeyi*	609	3600	P	WIDE
Violaceae	*Viola pinetorum* subsp. *grisea*	1981	3700	P	END-CAL
Violaceae	*Viola purpurea* subsp. *mesophyta*	1400	3598	P	END-CAL

APPENDIX 2. Annotated checklist of the flora of the Sierra Nevada with an upper elevational limit of 3300–3499 m. Abbreviations as in Appendix 1. Species names follow Baldwin et al. (2012).

Higher level taxon	Specific or infraspecific taxon	Lower elevation (m)	Upper elevation (m)	Growth form	Biogeographic relationship
PTERIDOPHYTA					
Aspleniaceae	*Asplenium septentrionale*	2500	3350	P	WIDE
Ophioglossaceae	*Botrychium lunaria*	2300	3400	P	WIDE
Pteridaceae	*Adiantum aleuticum*	0	3400	P	WIDE
Pteridaceae	*Aspidotis densa*	100	3400	P	CORD
Pteridaceae	*Cryptogramma acrostichoides*	1400	3400	P	INT
CONIFERAE					
Pinaceae	*Pinus monticola*	150	3400	T	S-C
MONOCOTS					
Alliaceae	*Allium validum*	1200	3400	G	CORD
Cyperaceae	*Carex abrupta*	1200	3450	P-G	S-C
Cyperaceae	*Carex aurea*	1100	3300	P-G	WIDE
Cyperaceae	*Carex buxbaumii*	0	3300	P-G	WIDE
Cyperaceae	*Carex davyi*	1400	3300	P-G	S-C
Cyperaceae	*Carex disperma*	1100	3400	P-G	WIDE
Cyperaceae	*Carex fissuricola*	1500	3300	P-G	CORD
Cyperaceae	*Carex fracta*	250	3300	P-G	S-C
Cyperaceae	*Carex illota*	2100	3400	P-G	CORD
Cyperaceae	*Carex integra*	800	3400	P-G	S-C
Cyperaceae	*Carex microptera*	1500	3400	P-G	CORD
Cyperaceae	*Carex pellita*	60	3300	P-G	WIDE
Cyperaceae	*Carex petasata*	600	3400	P-G	CORD
Cyperaceae	*Carex preslii*	1800	3400	P-G	CORD
Cyperaceae	*Carex simulata*	0	3300	P-G	CORD
Cyperaceae	*Carex tiogana*	3100	3350	P-G	S-C
Cyperaceae	*Carex utriculata*	0	3400	P-G	WIDE
Cyperaceae	*Carex vesicaria*	0	3300	P-G	WIDE
Cyperaceae	*Carex whitneyi*	1200	3400	P-G	S-C

APPENDIX 2. CONTINUED.

Higher level taxon	Specific or infraspecific taxon	Lower elevation (m)	Upper elevation (m)	Growth form	Biogeographic relationship
Cyperaceae	*Eleocharis acicularis* var. *acicularis*	0	3300	P-G	WIDE
Cyperaceae	Eleocharis acicularis var. gracilescens	0	3300	P-G	WIDE
Cyperaceae	*Eleocharis suksdorfiana*	0	3400	P-G	CORD
Cyperaceae	*Eriophorum criniger*	2000	3350	P-G	S-C
Iridaceae	*Iris missouriensis*	900	3400	G	CORD
Juncaceae	*Juncus hemiendytus* var. *abjectus*	1400	3400	P-G	INT
Juncaceae	*Juncus nevadensis* subsp. *nevadensis*	1200	3300	P-G	CORD
Juncaceae	*Luzula parviflora* var. *parviflora*	1000	3300	P-G	WIDE
Liliaceae	*Lilium kelleyanum*	2200	3300	G	END
Orchidaceae	*Platanthera dilatata* var. *leucostachys*	0	3400	G	CORD
Orchidaceae	*Platanthera sparsiflora*	100	3400	G	CORD
Orchidaceae	*Spiranthes romanzoffiana*	0	3300	P	WIDE
Poaceae	*Agrostis humilis*	1500	3350	P-G	CORD
Poaceae	*Bromus suksdorfii*	1250	3300	P-G	S-C
Poaceae	*Calamagrostis canadensis* var. *canadensis*	1500	3400	P-G	WIDE
Poaceae	*Calamagrostis canadensis* var. *langsdorfii*	1500	3400	P-G	WIDE
Poaceae	*Calamagrostis stricta* subsp. *inexpansa*	0	3400	P-G	WIDE
Poaceae	*Calamagrostis stricta* subsp. *stricta*	1500	3350	P-G	WIDE
Poaceae	*Danthonia intermedia* var. *intermedia*	1460	3450	P-G	WIDE
Poaceae	*Elymus trachycaulus* subsp. *trachycaulus*	0	3400	P-G	WIDE
Poaceae	*Hordeum brachyantherum* subsp. *brachyantherum*	0	3400	P-G	CORD
Poaceae	*Hordeum brachyantherum* subsp. *californicum*	0	3400	P-G	END-CAL
Poaceae	*Melica bulbosa*	0	3400	P-G	CORD
Poaceae	*Melica stricta*	1200	3350	P-G	INT
Poaceae	*Muhlenbergia filiformis*	150	3350	A	CORD
Poaceae	*Muhlenbergia montana*	1640	3420	P-G	WIDE
Poaceae	*Stipa nevadensis*	1000	3450	P-G	CORD
Poaceae	*Stipa occidentalis* subsp. *californica*	150	3450	P-G	CORD
Poaceae	*Stipa occidentalis* subsp. *occidentalis*	1200	3450	P-G	CORD
Poaceae	*Trisetum wolfii*	1740	3300	P-G	CORD
EUDICOTS					
Apiaceae	*Angelica lineariloba*	1700	3300	P	END-CAL
Apiaceae	*Ligusticum grayi*	1000	3300	P	CORD
Apiaceae	*Lomatium torreyi*	1100	3300	P	END
Apiaceae	*Perideridia parishii* subsp. *latifolia*	2000	3400	P	S-C
Asteraceae	*Agoseris parviflora*	1400	3400	P	CORD
Asteraceae	*Artemisia cana* subsp. *bolanderi*	1200	3300	S	S-C
Asteraceae	*Artemisia dracunculus*	0	3400	P	INT
Asteraceae	*Chaenactis douglasii* var. *alpina*	3000	3400	P-MAT	CORD
Asteraceae	*Crepis acuminata*	1000	3300	P	CORD
Asteraceae	*Crepis intermedia*	800	3300	P	CORD
Asteraceae	*Ericameria parryi* var. *aspera*	1900	3300	SS	INT
Asteraceae	*Erigeron barbellulatus*	2100	3300	P	END-CAL
Asteraceae	*Erigeron clokeyi* var. *pinzliae*	2200	3400	P	INT
Asteraceae	*Erigeron coulteri*	1900	3400	P	CORD
Asteraceae	*Erigeron elmeri*	1300	3300	P	END
Asteraceae	*Erigeron glacialis* var. *glacialis*	1300	3400	P	CORD
Asteraceae	*Erigeron tener*	2300	3400	P-MAT	CORD
Asteraceae	*Helenium bigelovii*	0	3400	P	S-C
Asteraceae	*Hieracium albiflorum*	0	3300	P	WIDE
Asteraceae	*Hieracium horridum*	1350	3300	P	S-C
Asteraceae	*Hulsea vestita* subsp. *vestita*	2400	3350	P	END
Asteraceae	*Microseris nutans*	1000	3400	P	CORD
Asteraceae	*Nothocalais alpestris*	1300	3400	P	S-C
Asteraceae	*Packera pauciflora*	1800	3300	P	WIDE
Asteraceae	*Senecio triangularis*	100	3300	P	CORD
Asteraceae	*Tetradymia canescens*	1000	3400	S	CORD
Asteraceae	*Tonestus eximius*	1800	3300	P	CORD
Asteraceae	*Wyethia mollis*	900	3400	P	S-C

APPENDIX 2. CONTINUED.

Higher level taxon	Specific or infraspecific taxon	Lower elevation (m)	Upper elevation (m)	Growth form	Biogeographic relationship
Boraginaceae	*Cryptanrtha watsonii*	1250	3300	A	CORD
Boraginaceae	*Cryptantha confertiflora*	1050	3350	P	INT
Boraginaceae	*Lappula redowskii*	1300	3300	A	WIDE
Boraginaceae	*Mertensia ciliata*	1310	3380	P	S-C
Boraginaceae	*Phacelia bicolor*	700	3400	A	INT
Boraginaceae	*Phacelia eisenii*	1300	3400	A	END
Boraginaceae	*Phacelia orogenes*	2060	3400	A	END
Boraginaceae	*Plagiobothrys hispidulus*	1200	3400	A	CORD
Boraginaceae	*Plagiobothrys torreyi* var. *diffusus*	1200	3400	A	END-CAL
Brassicaceae	*Barbarea orthoceras*	0	3400	B/P	WIDE
Brassicaceae	*Boechera calderi*	2050	3350	P	CORD
Brassicaceae	*Boechera davidsonii*	1200	3400	P	S-C
Brassicaceae	*Boechera pygmaea*	2600	3400	P	END
Brassicaceae	*Boechera stricta*	1800	3400	P	CORD
Brassicaceae	*Cardamine oligosperma*	50	3300	A/B	CORD
Brassicaceae	*Descurainia californica*	1700	3400	A/B	CORD
Brassicaceae	*Draba asterophora*	2600	3300	P	INT
Brassicaceae	*Physaria occidentalis*	600	3350	P	INT
Caprifoliaceae	*Lonicera conjugialis*	140	3300	S	S-C
Caprifoliaceae	*Symphicarpos rotundifolius* var. *parishii*	1100	3300	S	INT
Caryophyllaceae	*Ereomogone congesta* var. *subfrutescens*	1200	3300	P	INT
Ericaceae	*Arctostaphylos patula*	750	3350	S	CORD
Ericaceae	*Arctostaphylos uva-ursi*	2400	3300	S	WIDE
Ericaceae	*Vaccinium caespitosum*	0	3400	S	WIDE
Ericaceae	*Vaccinium uliginosum* subsp. *occidentale*	0	3400	S	WIDE
Fabaceae	*Astragalus bolanderi*	1400	3300	P	INT
Fabaceae	*Astragalus ravenii*	3400	3450	P	END
Fabaceae	*Trifolium monanthum* subsp. *tenerum*	1600	3300	P	END
Fagaceae	*Chrysolepis sempervirens*	700	3300	S	S-C
Gentianaceae	*Frasera puberulenta*	1700	3400	P	END-CAL
Gentianaceae	*Gentianopsis simplex*	1200	3400	P	INT
Grossulariaceae	*Ribes inerme var. inerme*	1200	3300	S	CORD
Lamiaceae	*Monardella breweri* subsp. *lanceolata*	0	3400	A	INT
Montiaceae	*Claytonia megarhiza*	2600	3300	P	CORD
Montiaceae	*Lewisia leana*	1300	3350	P	S-C
Onagraceae	*Chamerion angustifolium* subsp. *circumvagum*	0	3300	P	WIDE
Orobanchaceae	*Castilleja arachnoidea*	1300	3300	P	INT
Orobanchaceae	*Castilleja linariifolia*	1000	3350	P	INT
Orobanchaceae	*Castilleja peirsonii*	1500	3400	P	S-C
Orobanchaceae	*Castilleja pilosa*	1200	3400	P	INT
Orobanchaceae	*Castilleja praeterita*	2200	3400	P	END
Orobanchaceae	*Orobanche fasciculata*	0	3300	P	WIDE
Papaveraceae	*Dicentra uniflora*	1000	3300	P	CORD
Phrymaceae	*Mimulus breweri*	1200	3400	A	CORD
Phrymaceae	*Mimulus nanus* var. *mephiticus*	1520	3445	A	S-C
Phrymaceae	*Mimulus tilingii*	1400	3400	P	CORD
Plantaginaceae	*Penstemon caesius*	1800	3400	SS	END-CAL
Plantaginaceae	*Veronica americana*	0	3300	P	WIDE
Polemoniaceae	*Ipomopsis aggregata* subsp. *bridgesii*	1800	3300	P	END
Polemoniaceae	*Microsteris gracilis*	0	3300	A	WIDE
Polemoniaceae	*Navarretia breweri*	1000	3300	A	CORD
Polemoniaceae	*Polemonium occidentale* subsp. *occidentale*	900	3300	P	WIDE
Polygonaceae	*Eriogonum latens*	2600	3400	P	END-CAL
Polygonaceae	*Eriogonum microthecum* var. *alpinum*	2500	3300	SS	END-CAL
Polygonaceae	*Eriogonum microthecum* var. *ambiguum*	1100	3300	SS	INT
Polygonaceae	*Eriogonum saxatile*	800	3400	P-MAT	INT
Polygonaceae	*Eriogonum spergulinum* var. *reddingianum*	1300	3400	A	INT
Polygonaceae	*Eriogonum wrightii* var. *subscaposum*	200	3400	P-MAT	INT

APPENDIX 2. CONTINUED.

Higher level taxon	Specific or infraspecific taxon	Lower elevation (m)	Upper elevation (m)	Growth form	Biogeographic relationship
Polygonaceae	*Polygonum polygaloides* subsp. *kelloggii*	1500	3300	P	CORD
Polygonaceae	*Polygonum shastense*	2100	3400	P	S-C
Potamogetonaceae	*Potamogeton robbinsii*	1600	3300	Q	WIDE
Primulaceae	*Dodecatheon alpinum*	1700	3400	P	CORD
Ranunculaceae	*Anemone drummondii*	1200	3350	P	S-C
Ranunculaceae	*Aquilegia formosa*	0	3300	P	S-C
Ranunculaceae	*Caltha leptosepala* var. *biflora*	900	3300	P	CORD
Ranunculaceae	*Delphinium nuttallianum*	300	3300	P	CORD
Rhamnaceae	*Ceanothus cordulatus*	365	3365	S	INT
Rosaceae	*Amelanchier utahensis*	200	3400	S	INT
Rosaceae	*Fragaria virginiana*	1200	3300	P	WIDE
Rosaceae	*Geum macrophyllum* var. *perincisum*	1000	3300	P	WIDE
Rosaceae	*Horkelia fusca* subsp. *parviflora*	1400	3300	P	CORD
Rosaceae	*Ivesia gordonii* var. *alpicola*	2100	3300	P	INT
Rosaceae	*Ivesia saxosa*	900	3300	P	INT
Rosaceae	*Rosa woodsii* subsp. *gratissima*	800	3400	S	INT
Rosaceae	*Spiraea splendens*	548	3400	S	S-C
Salicaceae	*Salix jepsonii*	1000	3400	S	S-C
Salicaceae	*Salix scouleriana*	1	3400	S	CORD
Scrophulariaceae	*Limosella acaulis*	0	3300	A-Q	WIDE