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## RARITY IN *ASTRAGALUS*: A CALIFORNIA PERSPECTIVE

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### ABSTRACT

*Astragalus* (Fabaceae), the largest genus of plants in the world with an estimated 3270 species, is known for large numbers of rare endemic species. An inventory of patterns of climatic, topographic, and edaphic diversity of *Astragalus* taxa in California (98 native species and 144 named taxa) provides a means to understand the occurrence of rarity in relation to climatic equitability and regional species richness of congeneric taxa. Most taxa in the genus have relatively small ranges of distribution, with 50% restricted geographically to a single Jepson Bioregion. The California Native Plant Society lists 51 *Astragalus* taxa (35% of the native *Astragalus* taxa) as rare, threatened, or endangered (RTE). Climate characteristics of geographic regions such as rainfall and temperature extremes show no obvious relationship to species richness or the proportion of listed taxa. Species richness is highest in the arid Great Basin (35 species and 53 taxa) combining both its components, followed by 29 species and 39 taxa in the Sierra Nevada East region that includes the White and Inyo Mountains. The Mojave Desert is also high in diversity with 32 species and 39 taxa, but in contrast the Sonoran Desert region is low with only 12 species and 14 taxa. Despite ranking highest in the number of *Astragalus* taxa present, the Great Basin regions are low in their proportion of RTE taxa (17%) compared to the South Coast Region (39.5%) and Mojave Desert (32%). Strong edaphic specialization is associated with the majority but not all RTE taxa. While no single ecophysiological adaptation can explain this pattern, it is significant that *Astragalus* taxa have the potential ability to develop symbiotic nitrogen fixation, and this trait is key to success in soils not conducive to growth of many potential competitors. Land use changes, alien grass invasion and grazing, among other threats, are increasing fragmentation of habitats for many rare taxa with consequent impacts on gene flow. The continued survival of rare and locally endemic taxa will require improved knowledge of their individual demographic traits and long-term population dynamics.

Key words: *Astragalus*, California biodiversity, edaphic specialization, nitrogen fixation, rarity.

### INTRODUCTION

An understanding of rare plants and their relation to specific habitats of occurrence form a fundamental component of biodiversity management. Although considerable effort has gone into cataloguing rare taxa using a variety of criteria, we nevertheless lack the unifying principles and underlying critical data for the practical management of rare taxa and an understanding of the traits that separate them from common taxa (Kunin and Gaston 1997; Médail and Verlaque 1997; Bevil and Louda 1999; Domínguez Lozano and Schwartz 2005). While there is a large body of published literature describing individual rare taxa, there is far less research on the nature of microhabitats and microclimates that support rare local endemics. The high frequency of rarity in regional floras leads to the question of how these naturally rare species have persisted through evolutionary time and avoided extinction in spite of what are often three-way problems of small geographic ranges, low population numbers, and specific habitat conditions (Rabinowitz 1981). Recent studies have suggested that benign climates with spatially extensive specialized habitats, rather than specific

life history traits or membership in rapidly speciating lineages, are positively associated with the persistence of naturally rare species (Harrison et al. 2008). Issues of conservation management of rare species are particularly critical in California, a global hotspot of biodiversity (Norman 2003), where the large flora contains a high proportion of endangered, threatened, and rare species.

The legume genus *Astragalus* L. with an estimated 3270 species of largely herbaceous perennials is the largest genus of vascular plant in the world (Frodin 2004) and presents classic examples of rarity. The distribution of *Astragalus* is widespread in semi-arid, arid, and cool temperate regions of the northern hemisphere, with very high species diversity in a band extending across the mountain steppes of the eastern Mediterranean Basin across south-central Asia to the western Himalayan Plateau, where there are estimated to be about 1500–2000 species. Examples of this extreme diversity can be seen in Afghanistan with 380 species (Breckle and Rafiqpoor 2010), Turkey with 391 species (Günar et al. 2001), China with 401 species (Xu et al. 2010), and Iran with 451 species (Mahmoodi et al. 2009). However, western North America is a secondary center of evolution of *Astragalus* with about 400–450 species (Barneby 1964). There is a small disjunct species complex in tropical East Africa (Gillett 1964). South America is home to about 100 species, with their diversity centered in the southern and central Andean region. These South American species represent two distinct clades that arrived independently by long-distance dispersal from North America (Scherson et al. 2008).

The geographic center of diversity and presumed origin of *Astragalus*, as with most of its close relatives in the tribe Galegeae Dumort., lies in arid and semi-arid regions of south-central Asia (Polhill 1981). The Galegeae clade is entirely an Old World group with the exception of the genera *Astragalus* and sister group *Oxytropis* DC. which also became established in North America. Although species-rich in northern temperate latitudes, *Astragalus* has relatively few arctic species, a trait that it shares with other large temperate genera such as *Carex* L., *Senecio* L., and *Vaccinium* L. (Hoffmann and Röser 2009).

One of the characteristic biogeographic features of *Astragalus* over its range of occurrence is a remarkable level of edaphic specialization, often leading to highly restricted geographic ranges of distribution and rarity. This population trait is not only characteristic of the Irano-Turkish region and Himalayan Plateau in floras from those regions, but is also expressed in the *Astragalus* flora of the western United States. The Great Basin and Mojave Desert are notable for diverse examples of local endemism in *Astragalus* associated with edaphic specialization. These geographic patterns of isolated populations coupled with limited dispersal ability of seeds have been hypothesized to promote rapid local differentiation and geographic speciation over the Quaternary (Sanderson and Wojciechowski 1996).

Our objectives in this study are to examine the biogeographic and ecological patterns of rarity in the diverse taxa of *Astragalus* present in the California flora as a stimulus to future research. Are there patterns in the climatic, topographic, and edaphic diversity of California ecosystems that provide a useful template to predict the occurrence of rarity across these gradients? Do higher precipitation levels with less climatic stress favor the presence of rare species (Harrison et al. 2008)? A better understanding of geographic, and more specifically climatic correlates of rarity in *Astragalus*, could be significant in setting conservation strategies for rare species. In addition, this knowledge would provide a stimulus for expanding investigations of the associated genetic structure, life history, and demography of rare species.

#### MATERIALS AND METHODS

The second edition of the Jepson Manual (Baldwin et al. 2012) was used to determine the species biogeography of *Astragalus* taxa with a natural distribution in California, based on the Jepson bioregions of California. One new record for California, *A. nyensis*, was added. The Jepson Manual divides California into ten bioregions (Fig. 1): the northwest coast and Klamath Ranges (NW), Cascade Range (CaR), Sierra Nevada (SN), Great Valley (GV), Central Coast Ranges (CW), Southwest Coast and Ranges (SW), Modoc Plateau (MP), Great Basin/Sierra Nevada East (SNE), Mojave Desert (DMoj), and Sonoran Desert (DSon). Distribution was recorded for each *Astragalus* taxon within these geographic regions of California and their major subregions. The two floristically and climatically related Great Basin regions were merged into a single unit to produce nine regions for analysis.

The Natural Diversity Database of the California Department of Fish and Wildlife provides a classification system for vascular plants of special concern in the state (CNDDDB 2015). This broad list categorizes taxa of concern on the basis

of several scales of rarity, including those taxa listed either federally or by the state of California as Rare, Threatened, or Endangered (RTE). The database also includes a Rare Plant Rank, with a designation of 1B signifying taxa that are rare, threatened, or endangered (RTE) in California and elsewhere. Plants listed in category 1B are further divided into three threat ranks. Plants constituting California Rare Plant Rank 1B meet the definitions of California Endangered Species Act and are eligible for state listing. It is mandatory that they be fully considered during preparation of environmental documents relating to the California Environmental Quality Act (CEQA).

Available information on RTE species was gathered from our own field experience, the published literature, gray literature in government reports including Federal Register publications, and the California Native Plant Society's online Inventory of Rare and Endangered Plants (CNPS 2015). This inventory includes considerable information on habitat, geographic and elevational distribution, population numbers, and threats, as available.

#### RESULTS

##### *Biogeography and Diversity of California Astragalus*

The California flora includes 98 native *Astragalus* species with a total of 144 described taxa (Baldwin et al. 2012, plus one new record as described above). Following the Jepson Manual's designations of bioregions, the greatest richness of *Astragalus* is found in the combined Great Basin Bioregion with 35 species and 53 taxa (Table 1). Much of this diversity was present in the Sierra Nevada East Bioregion with 29 species and 39 taxa. Diversity was also high in the Mojave Desert with 33 species and 41 taxa. The high species richness of these arid regions does not extend to the Sonoran Desert which is relatively low in diversity with 12 species and 14 taxa. This low diversity reflects in part its smaller size compared with the Mojave Desert and also its more limited distribution of azonal edaphic habitats. Only six taxa are shared with the Mojave Desert.

The next-richest geographic regions are the South Coast Bioregion, including the Transverse and Peninsular Ranges (30 species and 38 taxa), and the Sierra Nevada (23 species and 30 taxa). There is a clear pattern showing the higher-elevation areas of the Sierra Nevada to be home to a higher diversity of *Astragalus* than lower-elevation areas. The Sierra Nevada foothills have only eight species and nine taxa, compared to the higher montane, subalpine, and alpine areas with 19 species and 24 taxa. There are eight *Astragalus* taxa that reach to alpine habitats of 3300 m or more in the range (Rundel 2011).

Taxa of *Astragalus* in California are largely restricted in their geographic distribution. Of the 144 taxa present, 86 taxa (60%) are restricted to a single bioregion (lumping the two Great Basin Bioregions). Another 39 taxa are present in only two bioregions. Only five *Astragalus* taxa have moderately broad ranges of distribution within California such that they occur in four or more of the major bioregions. *Astragalus purshii* Douglas var. *tinctus* M.E. Jones is present throughout eight of the nine bioregions of California treated here, missing only from the Central Valley, and extends into Oregon and Nevada. The species with all of its varieties occurs widely across the western US and Canada.



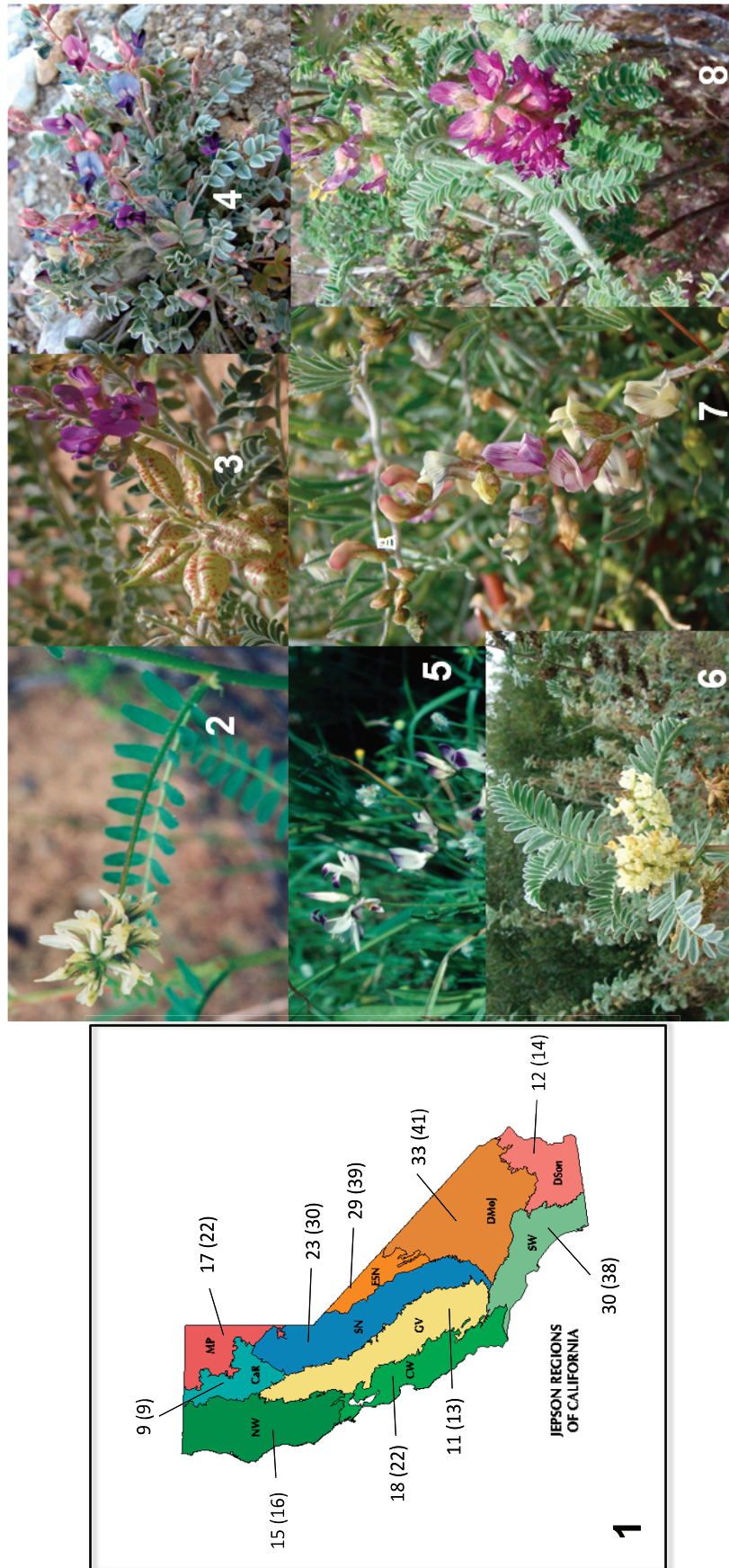


Fig. 1–8. California *Astragalus*.—1. Distribution of *Astragalus* species and taxa (in parentheses) in the Jepson Manual Bioregions of California (Baldwin et al. 2012).—2–8. Rare taxa of California *Astragalus*.—2. *Astragalus agnicidus* (photo by Jennifer L. Kalt).—3. *Astragalus lentiginosus* var. *coachellae* (photo by Brent Miller).—4. *Astragalus albens* (photo by Chris Wagner, SBNF).—5. *Astragalus claranus* (photo by Jake Ruygt).—6. *Astragalus pycnostachyus* var. *lanosissimus* (photo by Nicholas Jensen).—7. *Astragalus jaegerianus* (photo by Duncan Bell).—8. *Astragalus brauntonii* (photo by Michael Charters).

Table 1. Occurrence of *Astragalus* species and described taxa within the major Jepson bioregions and subregions of California. The number and proportion of listed rare, threatened and endangered taxa (RTE) based on classification by the California Native Plant Society (CNPS 2015). Totals include one species added since Baldwin et al. (2012). The column for dominant vegetation gives a broad characterization of each bioregion and subregion.

Biogeographic region	Species	Taxa	RTE taxa	% listed taxa	Dominant vegetation
Northwest Coast/Klamath	15	16	3	18.8	Wet conifer forest
Cascade Range	9	9	1	11.1	Conifer forest
Sierra Nevada	23	30	8	26.7	Conifer forest
Foothills	8	9	0	0	Woodland, chaparral
High Sierra	19	24	8	33.3	Conifer forest, alpine
Central Coast	18	22	4	18.2	Woodland, chaparral
South Coast and Southern California Ranges	30	38	15	39.5	Chaparral, conifer forest
Transverse Ranges	20	24	5	20.8	Conifer forest
Peninsular Ranges	14	16	4	25.0	Conifer forest
South Coast	10	13	4	30.8	Chaparral, woodland
Channel Islands	8	8	2	25.0	Chaparral, sage scrub
Great Basin	35	53	9	17.0	Cold Desert
Modoc/Warner Mountains	17	22	4	18.2	Sagebrush, pinyon/juniper
Sierra Nevada East	29	39	6	15.4	Conifer forest
Mojave Desert	33	41	13	31.7	Warm desert
Sonoran Desert	12	14	3	21.4	Warm desert

*Astragalus gambelianus* E. Sheld. var. *gambelianus* (Gambel milkvetch) is present in all six of the non-desert bioregions of California and extends into southwestern Oregon and northwestern Baja California. *Astragalus pachypus* Greene var. *pachypus* (thick-pod milkvetch) is present in six bioregions, skipping only the northern bioregions and Great Basin. *Astragalus didymocarpus* Hook. & Arn. var. *didymocarpus* (dwarf white milk vetch) is reported in five bioregions of the state, including the Mojave Desert Bioregion and adjacent Nevada, but like *A. pachypus* it is absent from the northern bioregions and Great Basin. Adding in the range of the other three varieties does not expand its range into other bioregions.

At the species level, the most widespread species present in California is *Astragalus canadensis* L. (Canadian milkvetch), which occurs throughout the United States and Canada in many habitats from wetlands to woodlands and prairies. California has *A. canadensis* var. *brevidentis* (Gand.) Barneby, which occurs only in Great Basin areas and the northern high Sierra Nevada. Also very widespread over its range of varieties is *A. lentiginosus* which occurs across the western United States, north into Canada, and south into northern Mexico. Lumping all of the varieties of this polymorphic species together, it is present in seven of the bioregions of California, being absent from only the northern two regions (North Coast/Klamath and Cascade). *Astragalus lentiginosus* var. *variabilis* Barneby is the most widely distributed variety in California with a range that includes the Central Valley, Sierra Nevada, Great Basin, and Mojave Desert Bioregions.

#### Rarity in California *Astragalus*

On a national basis of designated rarity, the genus *Astragalus* appears prominently with 21 taxa that are federally listed as endangered or threatened and an additional five candidate taxa. Ten of these federally listed taxa, eight endangered and two threatened, are present in California. Formal state designations of protection in California extend to nine taxa, with five listed as endangered, one threatened, and

three rare. Interestingly, only four taxa of *Astragalus* are designated on both the federal and state lists of protected species—*A. claranus*, *A. magdalenae* var. *peirsonii*, *A. pycnostachyus* var. *lanosissimus*, and *A. tener* var. *titi*.

Rare (RTE) taxa are disproportionately represented in California *Astragalus* compared to the flora as a whole. Of the 144 taxa present, 51 taxa (35%) are listed in the California Rare Plant Ranking as rare, threatened, or endangered (RTE). This designation is defined by those species in categories 1B.1 (18 taxa), 1B.2 (27 taxa), and 1B.3 (6 taxa). Another 12 taxa are listed as rare in California but more common elsewhere, and 19 listed species have limited distribution and are classified as deserving of monitoring.

There are no obvious patterns linking the proportion of RTE taxa and their diversity with bioregion and associated climate regime or geographic position. Although the Great Basin Bioregion of California has the highest number of *Astragalus* taxa present, it ranks relatively low in proportion of RTE taxa with 17.0% (Table 1). The Mojave Desert Bioregion was higher at 31.7%, while the Sonoran Desert Bioregion relatively low at 21.4%. The highest proportion of RTE species was found in the South Coast Bioregion (39.5%). However, the Central Coast Bioregion had only 18.2% RTE taxa. Within the Sierra Nevada Bioregion the proportion of RTE taxa was relatively high for the montane and higher elevations at 33.3%, but no RTE taxa were present in the foothills. Low rates of RTE taxa were present in the Cascade Range Bioregion (11.1%) and Northwest Coast/Klamath Bioregion (18.8%).

Table 2 lists known edaphic specialization for the 51 RTE *Astragalus* taxa in California. This edaphic specialization takes many forms, indicating that no single ecophysiological adaptation to specialized soil conditions can explain this pattern. Edaphic conditions point to a tolerance of diverse substrates within *Astragalus* including carbonate soils, volcanic clays, sedimentary clays, serpentines, alkaline wetlands, vernal pools, pebble plains, pumices, granite barrens, desert dunes, coastal dunes, and volcanic hot spring sites.

## DISCUSSION

*Rarity and Life History Traits*

As described by Rabinowitz (1981), there are multiple components of rarity. Rarity can be determined on the basis of geographic range (wide vs. narrow), habitat requirements (generalist vs. specialist), and population size (large vs. small). Thus, rarity can be classified into seven categories representing the combinations of the three components, with the eighth category of widespread, generalist species with large population size classified as common. Most rare taxa in *Astragalus* have special conservation significance in that they fit the category of the most extreme rarity in having limited geographic range, highly specialized habitat requirements, and small population sizes.

Several features of the life history and population genetics of *Astragalus* have been hypothesized to promote high rates of diversification and speciation in other plants. These include the herbaceous growth form and associated short generation time (Doyle and Donoghue 1993), isolated population structure with restricted gene flow (Niklas et al. 1985), short seed dispersal distances (Morris et al. 2002; Becker 2010), and large amounts of chromosomal variability (Levin and Wilson 1976). However, Sanderson and Wojciechowski (1996) dismiss the last of these as a likely factor by demonstrating that the causal factors of high rates of diversification in *Astragalus* may be related to basal traits associated with the entire astragalean clade, which lacks much of this chromosome variability. This clade has notably radiated in arid and semi-arid regions and is largely composed of herbaceous perennials that exhibit high levels of local endemism. *Oxytropis* (300 species, Eurasian and North American temperate) and *Colutea* L. (200 species, Eurasian temperate) are other diverse genera within this lineage (Lewis et al. 2005).

The recurring pattern of ecological restriction and/or edaphic specialization present in the astragalean clade suggests that there may be key adaptive innovations associated with this specialization (Barneby 1964; Spellenberg 1976). However, vegetative traits of growth form and leaf morphology show no such obvious innovation. Instead, they are common features that have evolved countless times in parallel through evolutionary time, presenting a large but finite number of variations on the same structural plan (Polhill 1981 et al.).

There have long been studies comparing the breeding systems, levels of inbreeding depression, and genetic structure in widespread and local species of many lineages, with the hypothesis that taxa with restricted ranges and small population sizes will more likely exhibit self-compatibility, low levels of inbreeding depression, low levels of genetic polymorphism than widespread abundant species (Lande and Schemske 1985; Schemske and Lande 1985). The results of research on *Astragalus* have shown uneven support for these hypotheses, as self-compatibility and low inbreeding may be present in widespread as well as restricted range species (Karron 1989), and the organization of genetic variation may not differ between these groups (Karron et al. 1988; Walker and Metcalf 2008).

While it is not sufficient to explain the pattern of endemism and rarity, *Astragalus* and most other genera of Papilionoideae have the potential to fix atmospheric nitrogen in root tissues through a symbiotic relationship with rhizobium bacteria. This

trait facilitates establishment and survival of nodulated plants on oligotrophic soils and habitats with regular disturbance that promote primary succession. There are examples in both Europe and the western United States of extremely rare species of *Astragalus* found to be restricted in occurrence to disturbed and heavily grazed sites (e.g., Sauer et al. 1979; Nordhag 1991). This trait is also present in California, with *A. agnicidus* Barneby as a prominent example (see below), and many species are best known from roadside verges where road maintenance is thought to present a threat (Table 2). It is worth noting that two other genera of California legumes with diverse species and local endemics, *Lupinus* and *Acmispon* (formerly *Lotus*), also are highly successful on oligotrophic soils and disturbed sites. There are 103 *Lupinus* taxa and 37 *Acmispon* taxa in California, with many more unresolved taxa of the former (Jepson eFlora, <http://ucjeps.berkeley.edu/IJM.html>). These genera, however, lack the frequency of rarity present in *Astragalus* taxa. There are 21 taxa of *Lupinus* and 7 taxa of *Acmispon* with RTE status in California (CNPS 2011).

It has been hypothesized that rarity and local endemism may be associated with the most climatically favorable sites within a region having unusual soil conditions. Rarity in California serpentine endemics is positively associated with regions with higher mean annual precipitation, suggesting that less competitive taxa may be more likely to survive where climatic stress is reduced (Harrison et al. 2008). However, the patterns of local endemism and rarity in *Astragalus* do not support this hypothesis. There is no obvious pattern of relationship between climate regime and the proportions of *Astragalus* rarity present across the diversity bioregions of California. High proportions of rarity are present in a range of climatic regimes throughout California ranging from arid desert bioregions, coastal regions of moderate climate conditions, high mountains, or the humid northwestern coast and Klamath Ranges.

*Examples of Local Endemism*

The notable pattern of rarity in *Astragalus* can be seen in many California endemic taxa that are restricted to unusual substrates in local areas. The following examples show the diversity of geographic regions and edaphic conditions which may be associated with the evolution of these rare taxa.

*Astragalus agnicidus* (Humboldt County milkvetch, Fig. 2), known from only a small number of sites in the outer North Coast Ranges of Humboldt and Mendocino counties in northwestern California, is an early successional species that prefers disturbed sites such as logged ridges, open canopy wooded areas, and scarified ground. Although never common, it was subjected to a deliberate program of eradication in the 1930s and 1940s when it was considered to be poisonous to livestock. It was thought to be extinct until it was rediscovered in 1987 on a recently logged and highly disturbed site. It is listed as endangered by the State of California.

One of the most interesting examples of taxonomic divergence and rarity in *Astragalus* can be seen in *Astragalus lentiginosus* (freckled milkvetch). This species has 34 named subspecific taxa, more than any other species in the entire flora of the United States (Knaus 2010). The overall species distribution of *A. lentiginosus* extends throughout the arid regions of western North America where it occupies both pristine and disturbed soils, saline sites, dunes, and other



Table 2. Vegetation association, edaphic specialization, and major threats to *Astragalus* taxa listed as rare, threatened, or endangered by the California Native Plant Society (CNPS 2015). See text for explanation of rare plant rank categories. Formal listings of rank include FE (federal endangered), SE (state endangered), FT (federal threatened), ST (state threatened), and SR (state rare). Threat information based on CNPS (2015).

Scientific name	Rank	Vegetation	Edaphic specialization	Threats
<i>Astragalus agnicidus</i> Barneby	IB.1, SE	Northwest conifer	Disturbed soils	Logging, eradication
<i>Astragalus albens</i> Greene	IB.1, FE	Mojave desert scrub, pinyon-juniper	Carbonates	Mining
<i>Astragalus anxius</i> Meinke & Kaye	IB.3	Great Basin scrub, pinyon-juniper	Volcanic	Grazing in past
<i>Astragalus atratus</i> S. Watson var. <i>mensanus</i> M.E. Jones	IB.1	Great Basin scrub, Mojave, pinyon-juniper	Volcanic clay	Grazing
<i>Astragalus austini</i> A. Gray	IB.3	Alpine and subalpine rock fields	Boulder fields	?
<i>Astragalus bernardinus</i> M.E. Jones	IB.2	Joshua tree, pinyon-juniper	Granite or carbonate	Mining, urbanization, grazing
<i>Astragalus brauntonii</i> Parish	IB.1, FE	Chaparral	Calcareous	Urbanization, fire regime, non-native species
<i>Astragalus cimae</i> M.E. Jones var. <i>cimae</i>	IB.2	Great Basin scrub, pinyon-juniper	Clay	Grazing
<i>Astragalus cimae</i> var. <i>sufflatus</i> Barneby	IB.3	Great Basin scrub, pinyon-juniper	Calcareous	Grazing?
<i>Astragalus claranus</i> Jeps.	IB.1, FE, ST	juniper		
<i>Astragalus deanei</i> (Rydb.) Barneby	IB.1	Chaparral/woodland	Serpentine/volcanic	Urbanization, recreation, non-native plants
<i>Astragalus didymocarpus</i> Hook. & Arn. var. <i>milesianus</i> (Rydb.) Jeps.	IB.2	Chaparral/woodland Coastal scrub	Sandy wash Clay	Urbanization, fire regime, non-native plants
<i>Astragalus douglasii</i> (Torr. & A. Gray) A. Gray var. <i>perstrictus</i> (Rydb.) Munz & McBurney	IB.2	Chaparral/woodland, pinyon-juniper	Rocky	Urbanization, non-native plants
<i>Astragalus erteriae</i> Barneby & Shevock	IB.3	Pinyon-juniper	Granitic	?
<i>Astragalus funereus</i> M.E. Jones	IB.2	Mojave desert scrub	Calcareous	Grazing?
<i>Astragalus gilmanii</i> Tidestr.	IB.2	Great Basin scrub, pinyon-juniper	Gravel	Grazing, mining
<i>Astragalus hornii</i> A. Gray var. <i>hornii</i>	IB.1	Valley grassland	Alkaline wetlands	Eradication
<i>Astragalus jaegerianus</i> Munz	IB.1, FE	Desert scrub	Granite barrens	Military training, non-native plants
<i>Astragalus johannis-howellii</i> Barneby	IB.2, SR	Great Basin scrub	Hot spring soils	Grazing, mining, vehicles
<i>Astragalus lemmonii</i> A. Gray	IB.2	Great Basin scrub	Wet meadow, seeps	Habitat loss, pipeline
<i>Astragalus lentiformis</i> A. Gray	IB.2	Great Basin scrub, conifer	Volcanic	Road maintenance, logging
<i>Astragalus lentiginosus</i> Douglas var. <i>antonius</i> Barneby	IB.3	Conifer	Granitic	Urbanization, non-native plants, road maintenance
<i>Astragalus lentiginosus</i> var. <i>cochellae</i> Barneby	IB.2, FE	Sonoran desert scrub	Desert dunes	Urbanization, vehicles
<i>Astragalus lentiginosus</i> var. <i>kernensis</i> (Jeps.) Barneby	IB.2	Subalpine conifer	Wet sandy	?
<i>Astragalus lentiginosus</i> var. <i>micans</i> Barneby	IB.2	Mojave desert scrub	Desert dunes	Vehicles
<i>Astragalus lentiginosus</i> var. <i>piscinensis</i> Barneby	IB.1, FT	Great Basin scrub	Alkaline wetlands	Hydrology, non-native plants, grazing
<i>Astragalus lentiginosus</i> var. <i>sesquimetalis</i> (Rydb.) Barneby	IB.1, SE	Desert scrub	Alkaline wetlands	Trampling

Table 2. Continued.

Scientific name	Rank	Vegetation	Edaphic specialization	Threats
<i>Astragalus lentiginosus</i> var. <i>sierrae</i> M.E. Jones	1B.2	Mojave desert scrub, pinyon-juniper	Moist gravelly flats	Urbanization, mining, fire regime
<i>Astragalus leucolobus</i> S. Watson ex M.E. Jones	1B.2	Conifer	Pebble plains	Urban, recreation, vehicles
<i>Astragalus magdalenae</i> Greene var. <i>peirsonii</i> (Munz & McBurney) Barneby	1B.2, FT, SE	Sonoran scrub	Desert dunes	Vehicles
<i>Astragalus mohavensis</i> S. Watson var. <i>hemigyrius</i> (Clovekey) Barneby	1B.1	Desert scrub, Joshua tree	Carbonates	Mining
<i>Astragalus monoensis</i> Barneby	1B.2, SR	Great Basin scrub, conifer	Pumice	Road maintenance, vehicles, grazing
<i>Astragalus nevadensis</i> A. Gray	1B.2	Coastal scrub	Coastal dunes	Grazing
<i>Astragalus nyensis</i> Barneby	1B.1	Mojave scrub	Alkaline soils	Solar development, non-native spp.
<i>Astragalus oocarpus</i> A. Gray	1B.2	Chaparral/woodland	?	Urbanization, road maintenance, recreation
<i>Astragalus oophorus</i> S. Watson var. <i>lavinii</i> Barneby	1B.2	Great Basin scrub, pinyon-juniper	?	?
<i>Astragalus pachyphus</i> Greene var. <i>jaegeri</i> Munz & McBurney	1B.1	Chaparral/woodland	Sandy/rocky	Urbanization
<i>Astragalus preussii</i> A. Gray var. <i>laxiflorus</i> A. Gray	1B.1	Desert chenopod scrub	Clay	Urbanization
<i>Astragalus pseudodanthus</i> Barneby	1B.2	Great Basin scrub	Stabilized desert dunes	Grazing
<i>Astragalus pulisiferae</i> A. Gray var. <i>pulisiferae</i>	1B.2	Pinyon-juniper, conifer, Great Basin scrub,	Granitic	Grazing, urbanization
<i>Astragalus pulisiferae</i> var. <i>suksdorfii</i> (Howell) Barneby	1B.2	Pinyon-juniper, conifer, Great Basin scrub,	Volcanic	Grazing mining, logging
<i>Astragalus pycnostachyus</i> A. Gray var. <i>lanosissimus</i> (Rydb.) Munz & McBurney	1B.1, FE, SE	Coastal scrub	Sand/coastal dunes	Urbanization, non-native plants
<i>Astragalus pycnostachyus</i> var. <i>pycnostachyus</i>	1B.2	Coastal scrub	Coastal dunes	Grazing, erosion, non-native plants
<i>Astragalus rattanii</i> A. Gray var. <i>jepsonianus</i> Barneby	1B.2	Chaparral/woodland	Serpentine	Road maintenance, energy development
<i>Astragalus ravenii</i> Barneby	1B.3	Alpine, subalpine conifer	Fellfield	?
<i>Astragalus shevockii</i> Barneby	1B.3	Conifer	Granitic	?
<i>Astragalus tener</i> A. Gray var. <i>ferrisiae</i> Liston	1B.1	Valley grassland	Vernal alkaline meadows	Agriculture non-native plants, urbanization
<i>Astragalus tener</i> var. <i>tener</i>	1B.2	Valley grassland	Alkaline wetlands	Agriculture
<i>Astragalus tener</i> var. <i>titi</i> (Eastw.) Barneby	1B.1, FE, SE	Coastal scrub	Coastal dunes	Urbanization, non-native plants
<i>Astragalus traskiae</i> Eastw.	1B.2, SR	Coastal scrub	Coastal dunes, bluffs	Military training
<i>Astragalus tricaratus</i> A. Gray	1B.2, FE	Sonoran desert scrub, Joshua tree	Sandy, gravelly	Pipeline, vehicles
<i>Astragalus webberi</i> A. Gray	1B.2	Conifer	Wet meadow	Mining, non-native plants, road maintenance



marginal habitats. Although many of the named varieties were originally described as species, further research found intermediate forms that led to the reduction of these species to varieties of a single morphologically plastic species. *Astragalus lentiginosus* has been viewed as a mosaic of taxa with morphological diversity representing a clinal response to the ecologically heterogeneous climates rather than to patterns of geographic occurrence (Knaus 2010).

The California flora includes 19 varieties of *Astragalus lentiginosus*, with six of these classified as RTE taxa by the state, and two federally listed as endangered. There is no simple pattern of habitat preference expressed by these RTE taxa. *Astragalus lentiginosus* var. *coachellae* (Coachella Valley milkvetch, federally listed as endangered, Fig. 3) and *A. lentiginosus* var. *micans* (shining milkvetch, Death Valley milkvetch) are specialists on local areas of desert dunes, while sandy soils of subalpine meadows are the favored habitat for *A. lentiginosus* var. *kernensis* (Kern Plateau milkvetch). Two rare varieties, *A. lentiginosus* var. *piscinensis* (Fish Slough milkvetch, federally listed as threatened) and *A. lentiginosus* var. *sesquimetalis* (Sodaville milkvetch, state-listed as endangered), occur only in alkaline desert wetlands and playas. The sixth RTE taxon, *A. lentiginosus* var. *antonius* (San Antonio milkvetch), is restricted to montane pine forests of the San Gabriel Mountains.

*Astragalus albens* Greene (Cushenbury milkvetch, Fig. 4), federally listed as an endangered species, is restricted in occurrence to a narrow belt of carbonate soils derived from decomposing limestone along rocky washes on the northern slopes of the San Bernardino Mountains. These soils occur at elevations of 1500–2000 m in Joshua tree and pinyon-juniper woodland habitat. *Astragalus albens* is known today from just 19 sites with a few thousand plants. Populations experience extreme fluctuations related to amounts of annual precipitation, with maximum numbers of no more than 5000–10,000 individuals. Nevertheless, isozyme research has shown a surprisingly high degree of heterozygosity for a local endemic species with small population size (Neel 2008). Threats to the survival of *A. albens* come principally from limestone mining, with off-road vehicles and rural developments as secondary concerns. This local belt of carbonate soils is also home to four other rare and endangered taxa—*Erigeron parishii* A. Gray, *Eriogonum ovalifolium* Nutt. var. *vineum* (Small) A. Nelson, *Lesquerella kingii* (S. Watson) S. Watson subsp. *bernardina* (Munz) Munz, and *Oxytheca parishii* Parry var. *goodmaniana* Ertter (Gonella and Neel 1995).

*Astragalus claranus* (Clara Hunt's milkvetch, Fig. 5) is found on thin, rocky clay soils derived from volcanic or serpentine substrates in grasslands and openings of manzanita-blue oak woodlands in Napa and Sonoma counties. Only six historical occurrences were known, and two of these have been extirpated by urbanization and vineyard expansion. The four remaining disjunct populations are restricted to about 28 ha in total extent. Threats to *A. claranus* come from habitat destruction and modification, urbanization, recreational activities, and competition from invasive non-native plants. It is federally listed as endangered and state-listed as threatened.

Arguably one of the most extreme examples of rarity in California taxa of *Astragalus* can be seen in *A. pycnostachyus* var. *lanosissimus* (Ventura marsh milkvetch, Fig. 6). This taxon was first described in 1884 and subsequently known

from a few scattered collections from coastal sites in Los Angeles and Ventura counties, a limited area but broader than its single site of occurrence today. More recently it was thought to be extinct until 1997 when a population was rediscovered in a degraded coastal dune system near Oxnard. This rediscovered population consisted of fewer than 300 individual plants located within an area of less than 0.2 ha, and in subsequent years has dipped in population to as low as 29 plants. Habitat destruction over an already limited range is the cause of its extreme rarity today, and it is both federally and state-listed as endangered. The type variety *pycnostachyus* has a non-overlapping and broad range along the central and northern California coast but is also classified as rare.

*Astragalus jaegerianus* (Lane Mountain milkvetch, Fig. 7) is a federally listed endangered species restricted in distribution to small fragmented populations occurring over an area of less than 24 km<sup>2</sup> in the central Mojave Desert northwest of Barstow. Its habitat is an area of granite barrens with relatively low plant cover. Individual plants are herbaceous perennials that resprout annually from their base and develop trailing stems that clamber into the canopy of a low-growing host plant. Populations numbers have declined dramatically due to drought from a high of more than 5000 thousand plants surveyed a decade ago (Huggins et al. 2010; Sharifi et al. 2011).

*Astragalus brauntonii* (Braunton's milkvetch, Fig. 8), a federally endangered species, occurs in a small number of scattered populations in coastal ranges and foothill areas of Ventura, Los Angeles, and Orange counties, generally on carbonate soils. It is a tall perennial that can reach a subshrub form up to 1.5 m in height, but with a short lifespan of 2–3 years (Fotheringham and Keeley 1998). Soil seed pools are known to germinate after fires, indicating that altered fire regimes and perhaps invasive species as well as urbanization may be critical issues in its survival.

### Conservation of Rarity in *Astragalus*

The forms of threats to rare taxa are as diverse as the habitats in which they occur, and relate in particular to the protection of critical habitat. Urbanization is the most commonly cited threat to rare taxa (Table 2), as might be expected of taxa in the more heavily populated areas of coastal and southern California. Arguably second in importance as a threat is the expansion of invasive alien annual grasses, typically species from the Mediterranean Basin. They compete for space and resources in the open disturbed habitats that are often favored by *Astragalus*. Mining is a threat to local populations of a number of taxa, most notably those that occur on carbonate soils. At least two taxa, *A. agnicidus* (Humboldt County milkvetch) and *A. tener* var. *ferrisiae* (Ferris' milkvetch), have limited ranges today that may be due at least in part to deliberate eradication efforts in the past when they were thought to be toxic to livestock. Although there are numerous *Astragalus* taxa across the western United States that are known to be toxic because of the alkaloid swainsonine, nitrotoxins, or accumulated selenium (Welsh et al. 2007), many taxa are palatable. As a result, grazing by stock animals in semi-arid and arid regions forms a major threat to the survival of some taxa. Finally, off-road vehicles form a major threat to rare *Astragalus* taxa (*A. lentiginosus*

var. *coachellae*, *A. lentiginosus* var. *sierrae*, and *A. magdalenae* var. *peirsonii*) with desert dunes as their habitat.

#### CONCLUSIONS

It remains clear that despite considerable effort in recent years, our knowledge of the causal factors of rarity in *Astragalus* remains poor. There are certainly indications that the survival of rare and locally endemic herbaceous species likely depends heavily on demographic traits and population dynamics (Schemske et al. 1994; Fox et al. 2006) as well as genetic structure (see Lande 1988). There is cause for concern that land use changes and continued fragmentation of rare populations are leading to low levels of gene flow, even between geographically close populations (Walker and Metcalf 2008; Breinholt et al. 2009). We know little about the genetic makeup of most extant populations of rare taxa, although such information should be considered in management decisions such as new population establishment. The informed management and the persistence of these taxa will require not only a mitigation of major threats, but also a greater understanding of individual life history traits and long-term demography. The conservation of rarity requires better means of assessing risk, with these biological traits as well as geography and history as important factors (Knapp 2011).

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