Yosemite National Park

An Analysis of the Vegetation in Tuolumne Meadows

Division of Resources Management and Science

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Cover Photo: California Conservation Corps member removing sapling lodgepole pines from Tuolumne Meadows 2007

AN ANALYSIS OF THE VEGETATION IN TUOLUMNE MEADOWS

ELIZABETH BALLENGER AND LISA ACREE

REVIEWED BY N.S. NICHOLAS AND J. WEASER

BACKGROUND

Meadows (and associated riparian areas) are critical landscape elements in the Tuolumne River ecosystem. Meadows link the main Tuolumne River channel with neighboring terrestrial systems and regulate the entry of water, nutrients, and organic material into the river channel (Gregory et al. 1991). Efforts to sustain the integrity of the Tuolumne River ecosystem are likely to be more effective over the long term when they address the integrity of the meadow and associated riparian areas. Past studies in Tuolumne suggested that the biological integrity of meadow communities in Tuolumne may be compromised (Cooper 2006). This study examines selected vegetation features related to the biological integrity of meadows and compares these features in Tuolumne with similar subalpine meadows, in an effort to appraise the degree of meadow degradation in Tuolumne.

The concept of biological integrity was defined by Frey as "the capability of supporting and maintaining a balanced, integrated, adaptive community of organisms having a species composition, diversity, and functional organization comparable to that of natural habitat of the region" (1975). This study focuses on several measures of meadow integrity – community level plant diversity, the forb: graminoid ratio, the percentage of areas without functioning vegetation (bare ground), and levels of small mammal activity. Botanists also documented other features of habitat structure including vegetation height, vegetation form, and the diversity of dominant plant species. Data gathered in Tuolumne Meadows was compared with data from eight comparable subalpine meadows in the park.

These vegetation measures were selected for study for a variety of reasons. It is important to examine the diversity of plant communities (or associations) in Tuolumne in relation to other subalpine meadows to understand whether the basic plant community composition of Tuolumne Meadows is comparable to others in Yosemite. The forb: graminoid ratio is important because it offers a glimpse into the sustainability of the meadow system and links the vegetation structure with meadow soils. High levels of organic matter in meadow soils are generally derived over many centuries from plants with high underground productivity such as deep-rooted sedges, rushes, and clonal grasses. Areas that have a high organic content in the soil, but are missing the deep-rooted dense plants, suggest that the vegetation species composition has changed. High levels of bare ground can indicate degraded community structure and overall community functions. The activity of small mammals (such as pocket gophers) in meadows has been found to alter soil characteristics such as nitrogen content, organic matter, and soil porosity (Laycock and Richardson 1975, Sherrod and Seasteadt 2001). Mammal activity has also been found to create disturbances that allow for invasion of sagebrush in meadows (Burke and Grime 1996, Berlow et al. 2002), and it has been suggested that pocket gophers may maintain a continual state of disturbance that does not allow for the formation of a thick root mat (Cooper et al. 2006).

METHODS

The Tuolumne Meadows survey area was defined with GIS software using meadow polygons from the 1997 Parkwide Vegetation Map for Yosemite National Park. Using ArcMap, 590 survey points were generated on a 50m grid across the meadow. Each plot location was visited using Trimble Juno GPS units and all data were recorded in the unit's data dictionary. All 590 points on the grid were assigned to a plant association from the 1997 Yosemite floristic vegetation classification (Natureserve 1997). At 300 of those points, data were collected at 5x5m square plots to assess vegetation cover of dominant species, substrate characteristics, small mammal activity, litter depth and vegetation canopy height. All data were collected mid-August through the end of September, 2008.

Data from the eight comparable subalpine meadows closest in elevation (within 800 ft) to Tuolumne were used for comparative analyses in this study (Table 2-1). These meadows are likely not in optimal condition themselves because they receive some visitor use and may have been grazed in the past, though they currently receive no packstock grazing. Data from these meadows were collected as part of a parallel study evaluating effects of packstock use on meadows; these meadows receive little to no current packstock use.

Meadow name	Elev. (ft)	Size (ha)	Slope (deg.)	Aspect (deg.)	#Gridpoint plots	Plot spacing (m)	Comments
Dog Lake	9170	3.21	2	240	65	20	Extensive day use by hikers
Dog Lake East	9240	1.93	2	119	35	20	
E of Gaylor Pit	9320	2.82	2	190	60	20	
Echo Lake	9356	6.87	2	176	51	30	
Lower Lyell	8720	6.63	3	0	77	25	Extensive day use by hikers
Snow Flat	8760	3.94	1.5	76	82	20	Near road to May Lake trailhead
South of Matterhorn	8440	2.2	1	182	16	20	Portion of meadow not sampled due to time constraints
West of Tilden	8340	5.9	2	200	65	25	Portion of meadow not sampled due to time constraints
Tuolumne	8600	149.63	1-3 (var)	variable	300	50	290 observations of plant community type were collected at alternating gridpoints

Table 1-1. General attributes of the eight subalpine meadows used for comparison with Tuolumne Meadows.

The following data were collected at each 5x5m plot in Tuolumne Meadows:

- Total vegetation cover: Bird's eye view of all vascular vegetation cover in the plot (could not exceed 100%, does not account for layered vegetation).
- Graminoid Cover: Total cover of all grass, sedge, and rush species in the plot.
- Forb cover: Total cover of all non-grasslike herbaceous species in the plot.
- Shrub cover: Total cover of shrub species in the plot (*Artemisia tridentata* and *Salix* species).
- Subshrub cover: Total cover of subshrubs in the plot (*Vaccinium caespitosum*).
- Tree cover: Total cover of *Pinus contorta* (seedlings, saplings or trees). Overhanging cover of trees rooted outside the plot was included.
- Dominant species cover: The species with the highest percent cover was listed as Dominant Species 1. Two other dominant species (and their cover) were recorded if they had at least half the relative cover of the most dominant species.
- Association name: The vegetation community of the plot and area surrounding it (usually 20m in all directions) was assigned a name from the 1997 Yosemite vegmap classification. This field characterized a larger area than the 5x5m plot, to minimize the effect of plots falling on an anomalous point. When a plot and the area surrounding it did not fit the 1997 floristic vegetation map classification, "Other association" was recorded for the association name and a new name was recorded in the next field.
- Association comments: If the community was a mix of different associations, or if it did not fit any of the association names, information was recorded in this field.
- Moss cover: Cover of all moss species in the plot. Cover for dormant moss was estimated as if it was in a fully green condition.
- Bare ground cover: All bare ground (including that created by rodent burrowing activity) was included in this estimate.
- Rock cover: All rocks with a diameter greater than a quarter (coin) at any point were included in this estimate.
- Litter cover: Litter was defined as plant material that was dead before this year's growing season, that was either detached or present in the form of thatch (as in perennial graminoid communities). In *Ptilagrostis kingii*, the curly dead blades attached to the culms, which give this species its characteristic look, were counted as litter.
- Burrow cover: Only fresh burrow holes and exudium (created or used last winter and this year) were included in this estimate.
- # Burrow holes: Any distinct small mammal burrow entrances, recent or old, were counted in the plot.

- Litter depth: Depth from the soil surface to the surface of the litter/thatch, measured at two randomly-selected locations in the plot.
- Vegetation height: Height of the tallest structure (vegetative, reproductive, or dead) of one of the three dominant species listed for the plot. This was measured within a one-meter radius of the two randomly selected litter depth locations in the plot.
- Gridpoint comments: Any supplemental information about the plot (such as presence of cut *Pinus contorta* stumps, compacted soil, etc.) was recorded in this field.

The same plot data were collected at the eight other subalpine meadows, with the exception of life form cover (graminoid cover, forb cover, shrub cover, etc.) All cover class data were collected using the classification breaks shown in Table 2-2.

Cover Class	Percent Cover
T	Trace (<1%)
P	1-5%
1a	6-10%
1b	11-15%
02	16-25%
03	26-35%
04	36-45%
5a	46-50%
5b	51-55%
06	56-65%
07	66-75%
08	76-85%
09	86-95%
10	96-100%

Table 1-2. Cover class breaks used for gridpoint plot collection.

To ensure consistency of the data, the field crew was carefully trained in cover estimations and calibrated at the start of each work week and/or meadow. In addition, the same crewmembers collected data throughout the summer, so the effects of observer bias should be minimal. Cover was estimated for all vegetation that was alive during this growing season, and since data were collected through the end of the growing season, cover for all vegetation that was shriveled and dried was visualized in its fully alive condition.

If a gridpoint fell on an area considered to be anomalous according to the protocols (in the river, on the transition between two distinct plant communities, or on rocks that were >1a cover class), the data collector would move the plot by pacing 5m directly away from the anomalous location. This situation probably occurred in less than 10% of the plots visited.

Data were downloaded from the GPS units and differentially corrected in Pathfinder Office, then exported to ArcMap, MS Access, MS Excel, and JMP for summary and analysis.

Results

Vegetation communities

Twenty plant associations from the 1997 Parkwide Vegetation Map were found in Tuolumne Meadows (Figure 2-1). Plant associations that contained less than five gridpoints were grouped into "Other associations" and all Salix associations were grouped into "*Salix* sp". A complete list of plant associations found in Tuolumne Meadows and the number of points keyed to each type are found in Appendix A. All the dominant species recorded in plots, and the number of plots where they were found, are listed in Appendix B.

The most dominant plant associations in Tuolumne Meadows were also common in the eight subalpine reference meadows, although the proportions of these associations varied widely (Table 2-3). The most widespread associations in Tuolumne Meadows were *Ptilagrostis kingii* (Sierra false needlegrass) and *Carex filifolia* (Shorthair sedge) herbaceous vegetation, which together comprised over 35% of the 590 points surveyed. Associations characterized by *Calamagrostis breweri* (Brewer's reedgrass) alone or with co-dominant species *Aster alpigenus* (Alpine aster) and *Vaccinium caespitosum* (Dwarf bilberry) were also prevalent, with over 18% of the plots falling into these types. *Artemisia tridentata* (Mountain sagebrush) – *Carex filifolia* shrublands (7.4% of plots) were common in drier areas of the meadow, particularly on the north end.

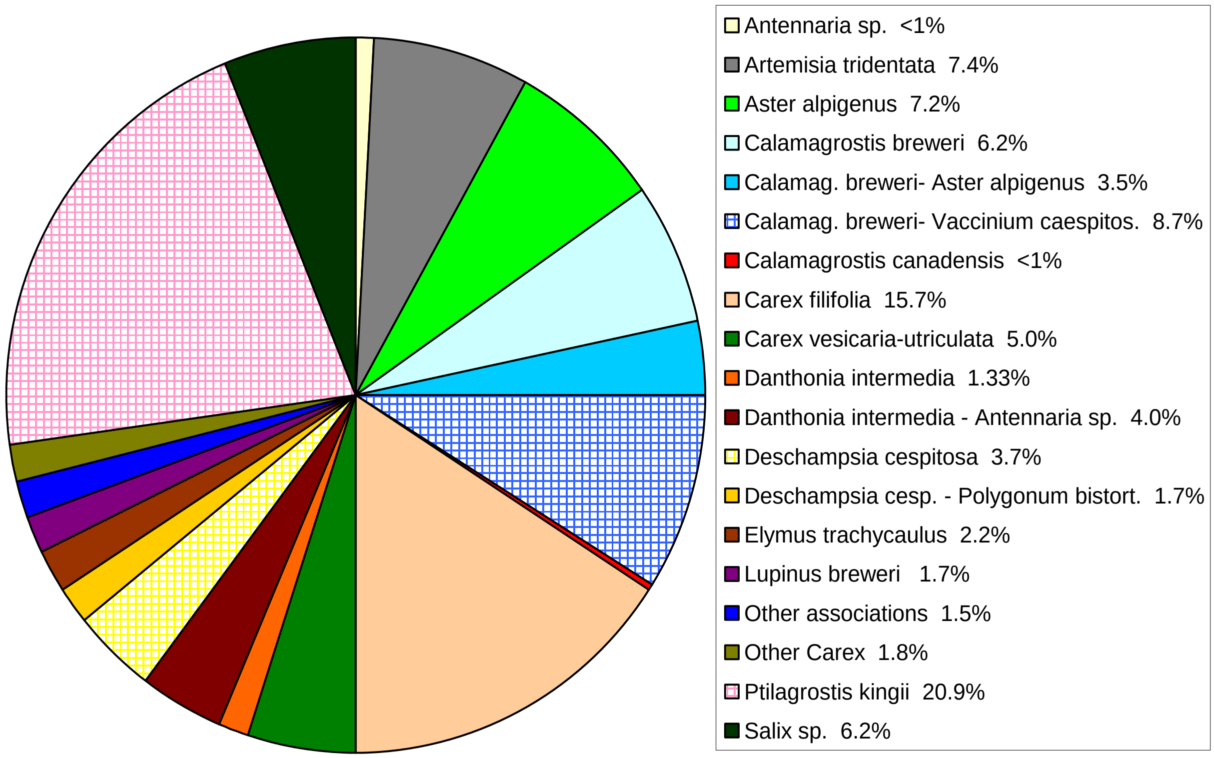

Figure 1-1. Plant communities in Tuolumne Meadows, with percentage of plots listed for each community type

The *Aster alpigenus* association was found almost exclusively in the western quarter of the survey area, just east of Pothole Dome. *Calamagrostis breweri / Vaccinium caespitosum* is common on the dry meadow edges, and is most common along the treeline in the southwestern part of the survey area. *Carex filifolia* occupies meadow edges where soil is more coarse and gravelly from decomposed granite, but may occupy any part of the meadow where these coarse, gravelly soils exist. *Calamagrostis canadensis*, *Lupinus breweri*, and *Salix* associations are all common to the river corridor on the first and second terraces, though *Salix* was strikingly absent along the river in the northern part of the survey area. *Carex vesicaria* – *Carex utriculata* communities require inundated soil conditions for at least part of the growing season and are present in most of the shallow ponds, depressions, and old oxbows mainly in the western half of the survey area. *Artemisia tridentata* shrublands (with *Carex filifolia* understory) are found almost exclusively on the north side of the Tuolumne River, on dry meadow edges in the eastern and northeastern-most part of the survey area.

A small proportion (6.6%) of the plot areas could not be keyed to any of the existing plant associations, and when at least five of these plots were similar, they were given a new association name for this study. Three new association names were created for Tuolumne Meadows vegetation: *Lupinus breweri* herbaceous vegetation, *Elymus trachycaulus* herbaceous vegetation, and *Antennaria* sp. herbaceous vegetation.

Lupinus breweri was prevalent on the wide, sand or cobble terraces of the Tuolumne River and was nearly always the only species dominant in the area, often with scattered clumps of *Salix sp*. present. *Elymus trachycaulus* herbaceous associations were usually located on the higher terraces of the Tuolumne River. They were dominated by the tall rhizomatous grass *Elymus trachycaulus*, with an often strong presence of *Carex filifolia*. *Antennaria* sp., *Muhlenbergia filiformis*, *Danthonia intermedia*, *Pucinella nutalii* and *Achnatherum lettermanii* were also codominant in some areas. *Antennaria* sp. (usually not identified to species since phenology was too advanced, though *Antennaria media*, *Antennaria corymbosa*, and *Antennaria rosea* were all found) was often co-dominant in *Ptilagrostis kingii* communities, but areas which were overwhelmingly dominated by *Antennaria* sp. were given this new association name. *Antennaria* sp. was also strongly present in many *Danthonia intermedia* communities, and these areas were given the *Danthonia intermedia – Antennaria rosea* (or sp.) association name.

Meadow	*Ptilagrostis kingii*	*Carex filifolia*	*Calamagrostis breweri*	Other dominant communities
Dog Lake	23.1%	9.2%	55.3%	*Carex vesicaria/utriculata* 5%, *Deschampsia cespitosa* 5%
Dog Lake East	48.6%	0%	17.1%	*Carex vesicaria/utriculata* 5%, *Deschampsia cespitosa* 5%
E of Gaylor Pit	28.3%	13.3%	40%	*Danthonia intermedia* 6.7%
Echo Lake	15.7%	5.7%	62.7%	
Lower Lyell	1.3%	50.7%	16.9%	*Danthonia intermedia* 18%
Snow Flat	12.2%	0%	43.9%	*Deschampsia cespitosa* 28%
S of Matterhorn	0%	0%	0%	*Carex vesicaria / utriculata* 69%, *Carex scopulorum* 25%
W of Tilden	43.1%	0%	3.1%	*Deschampsia cespitosa* 36.8%, *Carex vesicaria/utriculata 9.2%*
Tuolumne	20.9%	15.7%	17.4%	*Aster alpigenus* 7.2%, *Carex vesicaria/ utriculata* 5%.

Table 1-3. Proportions of common plant communities in Tuolumne Meadows and eight other subalpine meadows

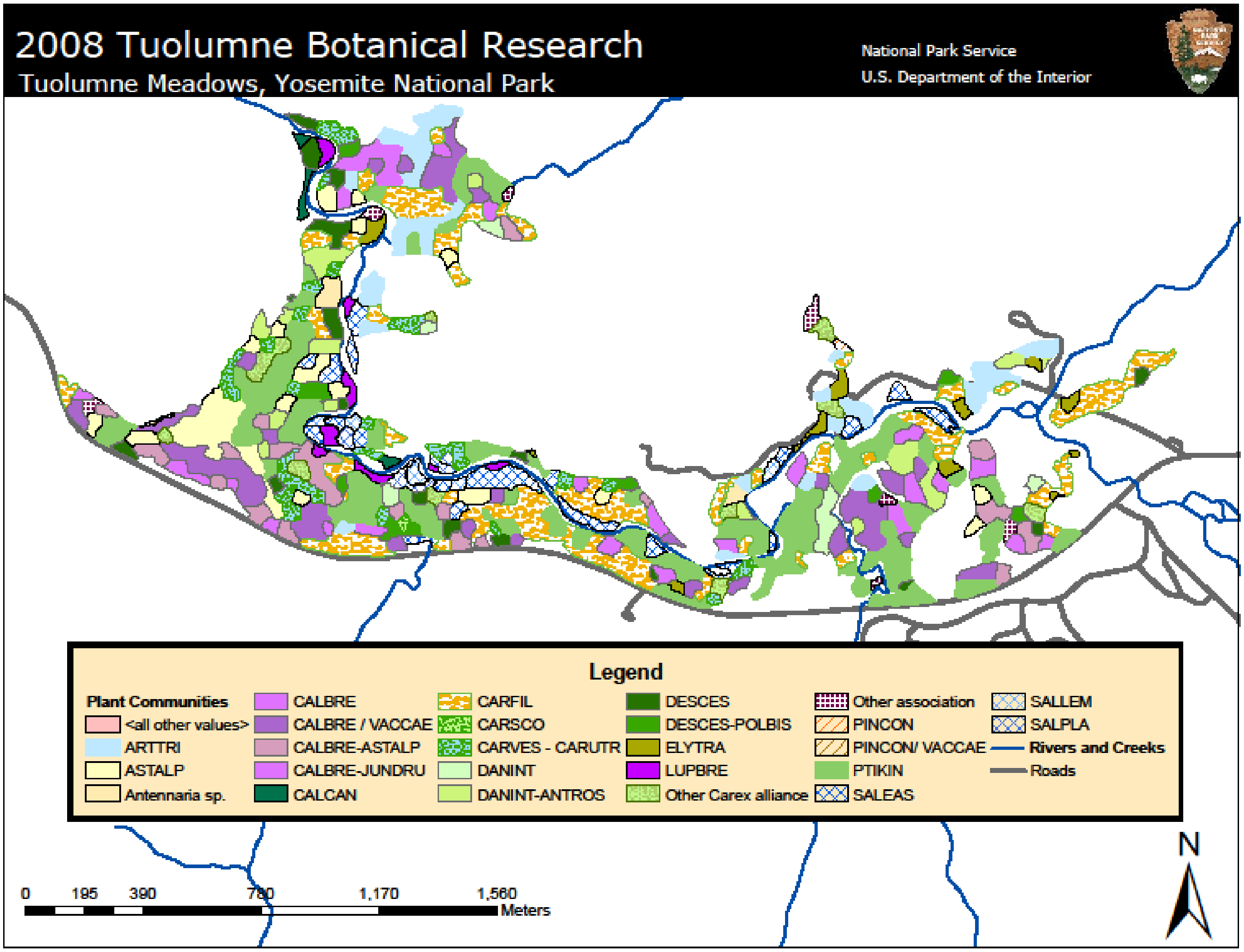

Figure 1-2. Plant communities in Tuolumne Meadows. Plant names are abbreviated using a six-letter code (the first 3 letters of the genus and species). See Appendix A for a crosswalk of six letter codes to association names.

A vegetation map was created from the gridpoint study plot data (Figure 2-2). Polygons were drawn using data from the 590 vegetation plots and images from the National Agricultural Imagery Program. Each polygon encompasses 1 to 16 study plots of the plant association identified by the polygon. Polygon boundaries are approximate.

FORB:GRAMINOID RATIO

Typically, high levels of organic matter in meadow wetland soils are derived from plants with dense deep-rooted rhizomatous or clonal plants such as sedges, rushes, and grasses. Meadows with a high proportion of forbs may not be producing as much soil organic matter as those with a lower forb:graminoid ratio.. The forb:graminoid ratio in Tuolumne Meadows was determined by comparing the total cover of all grass, sedge, and rush species in each plot with the total cover of all non-grasslike herbaceous species in the plot.

A graminoid:forb ratio was computed for each of the 300 full plots from the life form cover class data. In Tuolumne Meadows, 28% of the plots had a graminoid:forb ratio < or =1, indicating a high dominance of forb species. The most prevalent forbs in Tuolumne were *Antennaria* sp. (a dominant in 29.7% of plots) and *Aster alpigenus* (a dominant in 16.7% of plots). *Polygonum bistortoides, Solidago multiradiata*, *Senecio scorzonella*, and *Dodecatheon jeffreyi* were occasionally dominant in some areas. No direct comparisons with the eight other meadows on the life form data was available because life form cover class data were not collected in the these meadows.

In order to make forb:graminoid ratio comparisons with the eight other meadows, the proportion of Tuolumne plots with a forb as the most dominant species in the meadow was calculated and compared with this proportion from the eight other meadows. The percent of plots which had a forb present as a subdominant in the species list was also calculated (Figure 2-3). For the purposes of this analysis, the grass *Muhlenbergia filiformis* was treated as a forb, since it does not have the root mass and soil stabilizing properties of other grasses and sedges and does not contribute to soil organic matter (Cooper et al. 2006). Shrub and subshrub-dominated plots were excluded from this analysis.

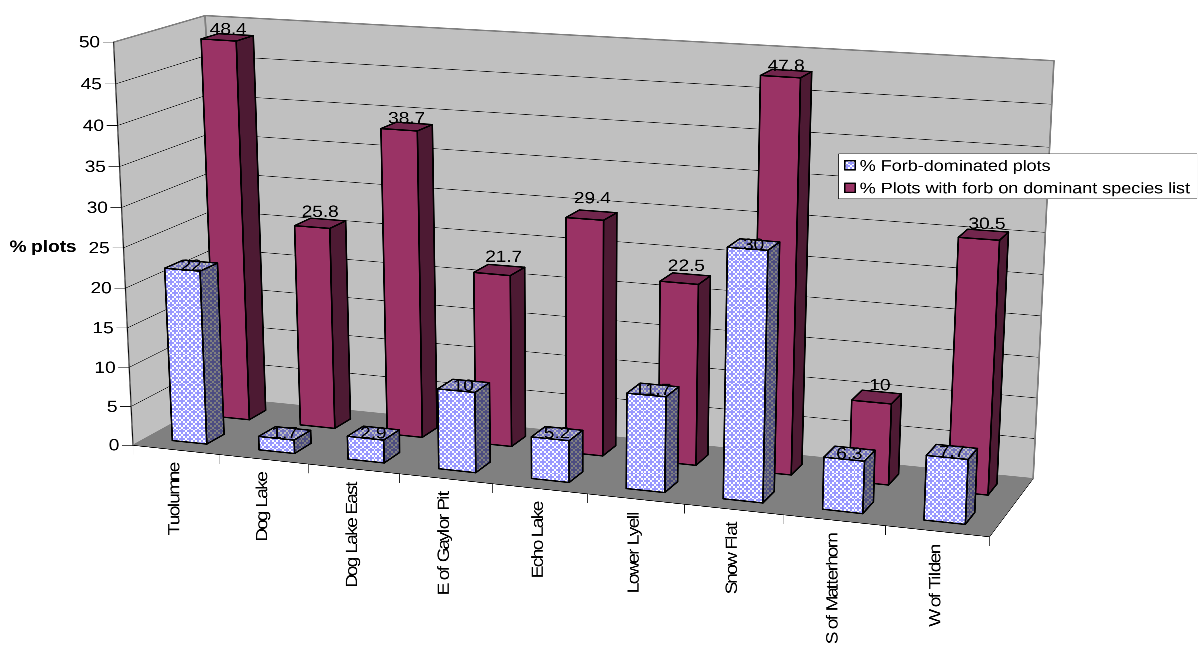

Figure 1-3. Forb dominance in Tuolumne Meadows and eight other subalpine meadows, showing the percentage of plots in which a forb was the most dominant species and the % of plots in which forb species were present on the dominant species list for the plot.

Tuolumne Meadows had higher forb dominance than all the other meadows except for Snow Flat, which had high concentrations of *Aster alpigenus* (most dominant in 25.6% of plots) and *Polygonum bistortoides* (second and third most dominant in 15.9% of plots), but no dominance of *Antennaria* sp. The biggest difference between Tuolumne and the other meadows was seen in the percent of plots where forbs were the most dominant species. Twice as many plots (proportionately) in Tuolumne were forb-dominated compared to Lower Lyell and East of Gaylor Pit, and 4-8 times the proportion of plots were forb dominated in Tuolumne compared to the four remaining meadows.

Bare Ground and Total Vegetation Cover

Fig. 1-4. Large barren patch in Tuolumne Meadows

Bare ground values in Tuolumne Meadows plots ranged from <1% to 85%, and plots with high bare ground values (>50%) were scattered throughout the survey area (Figure 2-5).

Patches of barren/gravel soil were observed anecdotally in Tuolumne Meadows. These patches were scattered throughout the meadow (Figure 2-4) and varied in size (usually 20-50m across). Bare patches of this size were not seen in any of the eight other reference meadows.

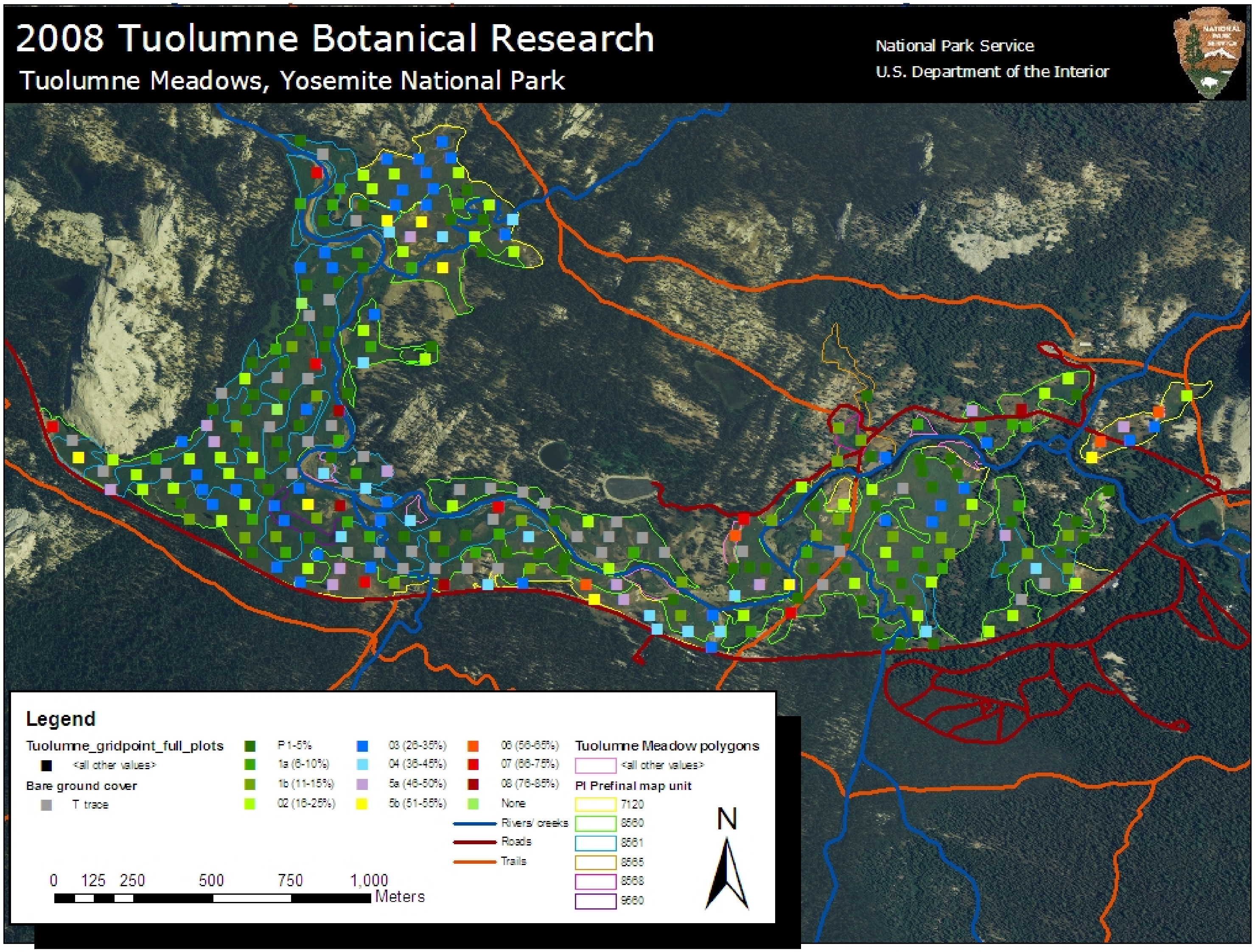

Figure 1-5. Aerial photo map of Tuolumne Meadows, showing locations of full plots and their bare ground values. Plots with extreme bare ground (greater than 50%) are orange, yellow, and red.

Certain meadow plant communities naturally have more bare ground than others. For example bare ground cover is higher in *Carex filifolia* communities, which grow on dry gravelly areas, compared to more mesic communities like *Calamagrostis breweri* or *Aster alpigenus*. To account for these natural differences, average percent bare ground cover was calculated for the most dominant plant communities in Tuolumne Meadows and plotted with bare ground values for the same plant communities in the other meadows (Figure 2-6). All values for bare ground were higher in Tuolumne Meadows plant communities than the other meadows, though the differences were greatest in *Aster alpigenus*, *Calamagrostis breweri*, and *Carex filifolia* communities.

ANOVA with LSMeans Tukey tests were run to determine the relationship of dominant species and meadow (Tuolumne or non-Tuolumne) to bare ground cover. This interactions effect was statistically significant (p= 0.023), and the difference between Tuolumne Meadows and the other meadows in *Aster alpigenus* communities was statistically significant. Reanalyses of the data using reseampling methods (permutation tests or bootstrapping) at the meadow level is necessary to validate the statistical differences in bare ground between Tuolumne Meadows and the eight other meadows sampled.

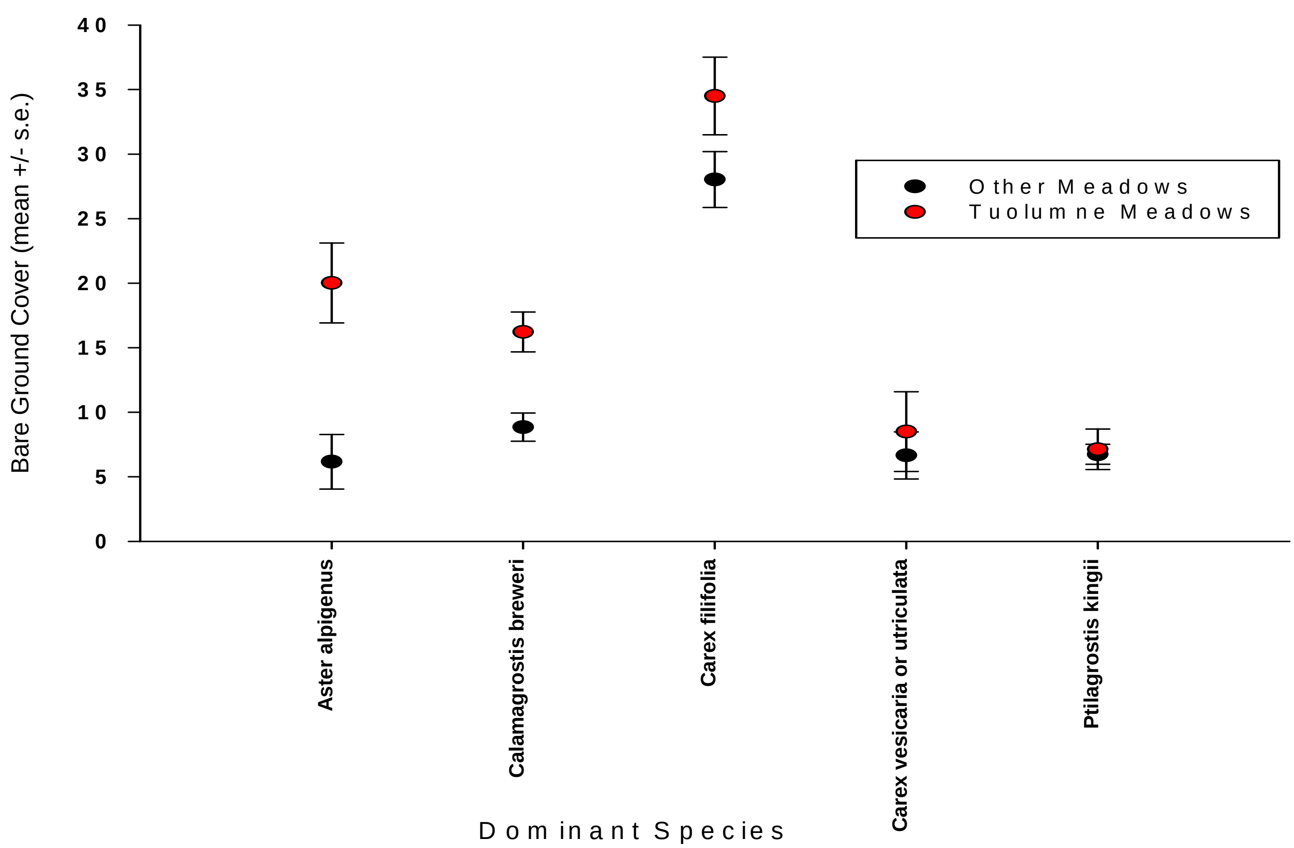

Figure 1-6. Average bare ground values for the most common plant communities in Tuolumne Meadows compared to the eight other meadows sampled.

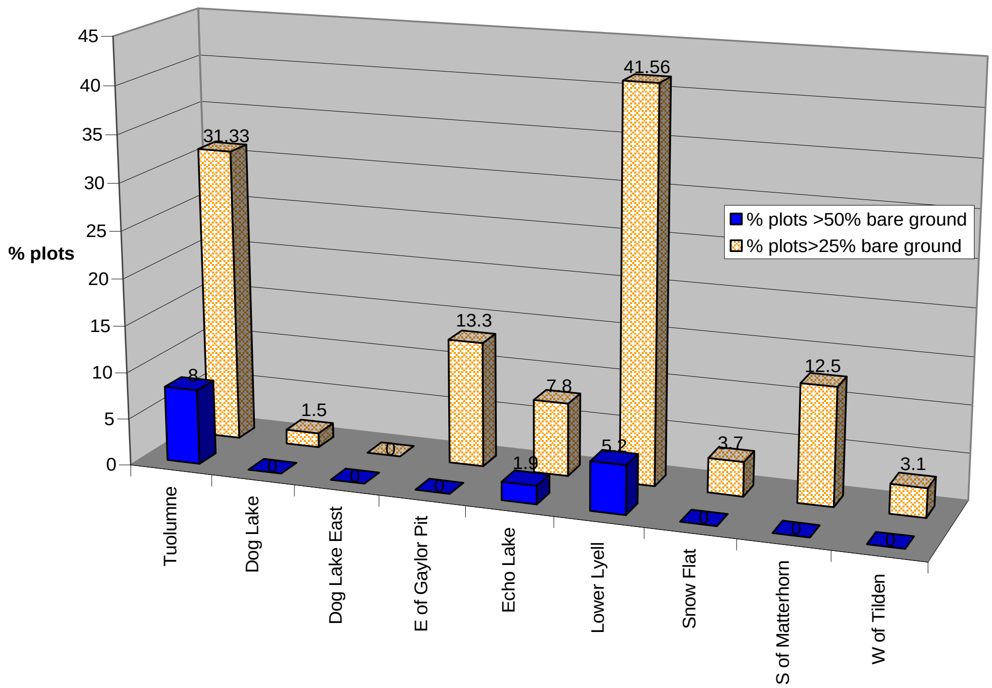

Figure 1-7. Percent of plots with greater than 50% bare ground and greater than 25% bare ground for Tuolumne Meadows and eight other meadows.

Another way to look at the difference in bare ground cover between Tuolumne and the other meadows is to compare the proportion of plots per meadow with high bare ground cover values (Figure 2-7). Most of the other meadows have no plots with bare ground cover greater than 50%, whereas 8% of the plots in Tuolumne have greater than 50% bare ground cover. Nearly a third of Tuolumne's plots had greater than 25% cover of bare ground, whereas most of the other meadows had 0-13% of plots in this state. Lower Lyell is the one meadow which exhibits bare ground cover similar to Tuolumne Meadows, though this meadow still has a lower proportion of extremely bare plots (>50% bare ground) compared to Tuolumne Meadows.

A low cover of bare ground in a meadow community does not necessarily imply high vegetative cover, since the ground may be covered by litter or moss. Therefore total vegetation cover was also compared among the most dominant plant communities in Tuolumne and the other meadows (Figure 2-8). For most plant communities, Tuolumne Meadows had lower vegetative cover than the other meadows, except for the very wet *Carex vesicaria/ utriculata* community. Again, ANOVA with LSMeans Tukey tests were performed to determine the effect of plant community and meadow (Tuolumne or non-Tuolumne) on total vegetation cover. The interactions effect was statistically significant (p= 0.010), and the difference between Tuolumne Meadows and the other meadows in *Calamagrostis breweri* communities was statistically significant. However, reanalyses using reseampling methods (permutation tests or bootstrapping) at the meadow level is necessary to validate the results presented here.

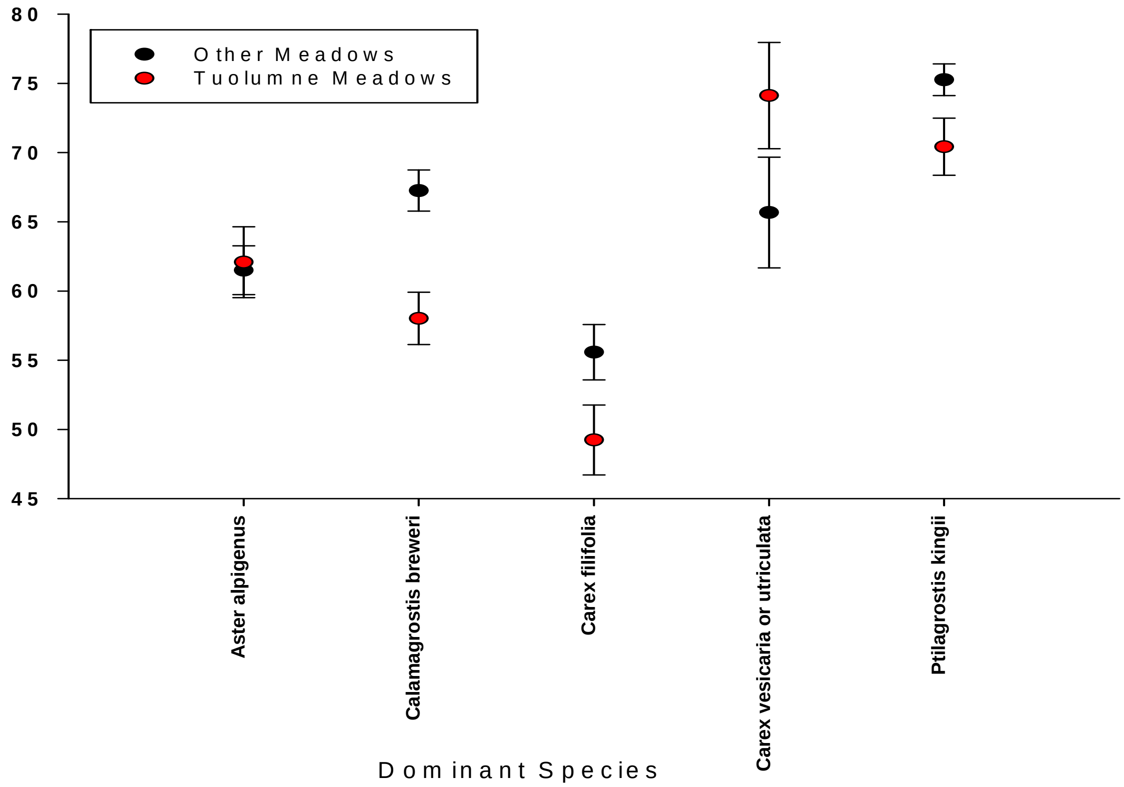

Figure 1-8. Average total vegetation cover values for the most dominant plant communities in Tuolumne Meadows and eight other meadows.

MAMMAL BURROWING ACTIVITY

Small mammal burrow entrances (holes) and evidence of burrowing activity (burrow exudium) was used as an indicator of small mammal density. For the purposes of this study, a high level of small mammal activity was defined as being >5% cover of burrowing evidence in a plot. The proportion of plots having burrow entrance holes was calculated for each meadow, as well as the proportion of plots having a high level of small mammal activity (Figure 2-9). Lower Lyell showed the highest levels of burrowing activity, though nearly all the meadows had one-quarter to one-half of their plots with burrow holes present. Tuolumne had a higher proportion of plots (10% of all plots) with high levels of small mammal activity compared with the seven remaining meadows, although the proportion of plots with burrow holes was not greatly different.

Evidence of small mammal activity was found in nearly all vegetation types in Tuolumne Meadows, but was most commonly seen in *Carex filifolia*, *Calamagrostis breweri*, *Calamagrostis breweri* / *Vaccinium caespitosum*, *Ptilagrostis kingii*, and *Artemisia tridentata* communities. It should be noted that these are also some of the most common plant communities in Tuolumne Meadows. However, there was proportionately more small mammal evidence in *Carex filifolia* and *Artemisia tridentata* communities compared to the abundance of these communities in Tuolumne. Approximately one quarter of all Tuolumne plots that had small mammal burrowing evidence were in *Carex filifolia* communities, but only 15% of all plots were *Carex filifolia*. Likewise, 10% of plots with burrow holes were in *Artemisia tridentata* communities but only 7% of all plots were in *Artemisia tridentata*.

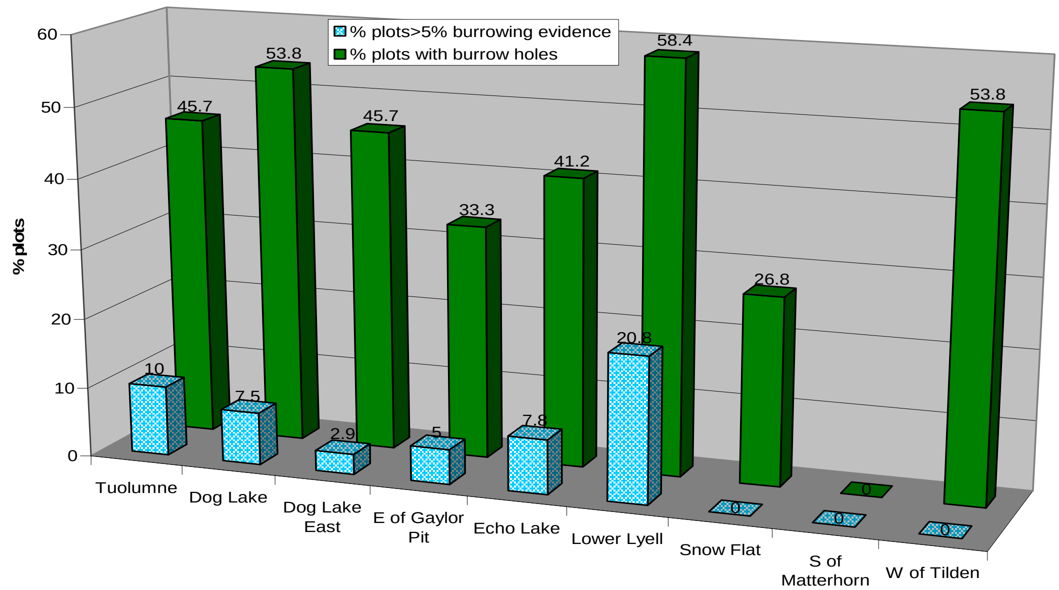

Figure 1-9. Percent of plots with burrowing activity for Tuolumne Meadows and eight other meadows.

Discussion

While the dominant plant communities in Tuolumne Meadows were consistent with the eight other subalpine meadows, specific vegetation and habitat attributes related to biological integrity differed between Tuolumne Meadows and the other meadows. In particular, bare ground levels and the ratio of forb to graminoid species were higher in Tuolumne Meadows than most of the reference meadows. Tuolumne Meadows was the only meadow surveyed with areas dominated by *Artemisia tridentata* shrubs, which may be indicative of past grazing-related disturbance.

In terms of bare ground values, about 8% of the reference plots in Tuolumne had greater than 50% bare ground, where most of the other meadows had no plots with a bare ground cover of greater than 50%. Nearly a third of Tuolumne's plots had greater than 25% cover of bare ground, whereas most of the other meadows had 0-13% plots with greater than 25% cover. This suggests that in general, bare ground levels in Tuolumne Meadows are outside the normal range of variability. Future reanalysis of the dataset at the meadow level using resampling techniques (at the meadow level) is necessary to validate the statistical differences in bare ground between Tuolumne Meadows and the eight other meadows sampled.

In terms of the forb:graminoid ratio, study plots in Tuolumne Meadows had four to eight times the proportion of plots dominated by forbs compared to four of the other meadows, and twice the proportion of forb-dominated plots as two of the other meadows. Areas in Tuolumne Meadows that have a high forb:graminoid ratio are of particular importance, especially in areas with high organic content in the soil. (for example, the large polygon of Aster alpigenus east of Pothole Dome in Fig 2-2). High organic content levels in meadow soils were likely generated by centuries of organic matter contributed from deep-rooted graminoids. If graminoids are missing from the floral composition, the plant composition may have changed. In addition, shallow- or tap-rooted forbs do not grow as densely as long-lived rhizomatous and clonal plants, and they do not grow into and reduce the areas of bare ground in the same manner as the graminoid species. Because tap- or shallow-rooted forbs lack the soil stabilizing characteristics of graminoids and do not contribute significantly to soil organic matter, areas with a high proportion of forbs are also at higher risk of soil erosion and loss of soil organic matter (Cooper et al. 2006). Areas with high forb:graminoid ratios and high levels of bare ground are not likely to revegetate on their own, and soils may be losing organic matter.

Tuolumne Meadows was the only meadow surveyed with areas dominated by*Artemisia tridentata* shrubs. In related meadow studies, expansion of sagebrush into meadows has been thought to be caused by livestock grazing-related disturbances which can compact soil, increase the aridity of soils, and cause changes in meadow hydrologic processes from stream incision (Vavra et al. 1994, Magilligan and McDowell 1997). Berlow et al (2002) found that intact moist meadow vegetation effectively prevents sagebrush germination and subsequent seedling survival, and that small disturbances (such as gopher activity) can decrease competition with other vegetation and promote sagebrush invasion (Burke and Grime 1996). The fact that Tuolumne Meadows has areas dominated by *Artemisia tridentata* is another symptom that the biological integrity of this meadow is in a compromised state.

Mammal burrowing activity did not differ greatly between Tuolumne and the eight other meadows. Although Tuolumne had proportionately more plots with high levels of mammal activity (except Lower Lyell), the proportion of Tuolumne plots with any burrow activity falls in the normal range of variability of the other meadows. *Carex filifolia* and *Artemisia tridentata* communities appear to have more burrowing activity than other plant communities in Tuolumne, but this difference may not indicate a real difference in activity levels. *Carex filifolia* and *Artemisia tridentata* communities occur in drier soils and are comprised of slow-growing, sparse vegetation which would likely not rebound from the disturbances of small mammals as readily as mesic *Calamagrostis breweri* or *Aster* *alpigenus* communities. Therefore, the evidence of small mammals may remain longer in these communities, giving the impression of greater abundance.

These findings support the importance of more investigation into the root causes of differing vegetation and habitat features in Tuolumne. High levels of bare ground in areas that likely have rich organic soil suggest that the dense deep-rooted sedges and grasses that formed these soils over centuries of time may not be self-sustaining, and these areas may even be losing organic matter. When coupled with high forb:graminoid ratios, revegetation may not occur on its own. Research into the root causes of vegetation differences, the make-up of historic vegetation, and whether carbon is being lost in the soil could confirm these hypotheses. Integrity is reflected in both biotic elements and the processes that generate and maintain those elements such as ground water flows (Angermeier 2005). Investigations into the presence of high water tables at the end of the growing season would indicate whether this important physical driver of the meadow ecosystem is still in place.

Perhaps the biggest difficulty in this study was the selection of the benchmark state. The eight subalpine meadows that were chosen for comparison to Tuolumne are likely not in optimal condition themselves because they receive some visitor use and may have been grazed in the past, though they currently receive no packstock grazing. The fact that differences in measures of biological integrity exist between Tuolumne and these less-than-pristine reference meadows suggests that more attention should be given to the condition of Tuolumne and methods for improving the health of this important meadow ecosystem. Should research into the root causes reveal that the differences found in the biological and physical attributes in Tuolumne Meadows were caused by human-related adverse actions, ecological restoration may be warranted.

APPENDIX A. PLANT ASSOCIATIONS FOUND IN TUOLUMNE MEADOWS DURING 2008 FIELDWORK

Associations are from the 1997 Yosemite vegetation map classification (NatureServe 2007).

Association name	6 Letter Code	# plots
Antennaria sp. (new)	Antennaria sp.	5
Artemisia tridentata / Carex filifolia	ARTTRI	44
Aster alpigenus	ASTALP	43
Calamagrostis breweri	CALBRE	36
Calamagagrostis breweri- Aster alpigenus	CALBRE - ASTALP	21
Calamagrostis breweri- Juncus drummondii	CALBRE- JUNDRU	1
Calamag. breweri- Vaccinium caespitosum	CALBRE / VACCAE	52
Calamagrostis canadensis	CALCAN	3
Carex filifolia	CARFIL	94
Carex scopulorum	CARSCO	1
Carex vesicaria-utriculata	CARVES_CARUTR	30
Danthonia intermedia	DANINT	8
Danthonia intermedia - Antennaria sp.	DANINT-ANTROS	24
Deschampsia cespitosa	DESCES	22
Deschampsia cespitosa - Polygonum bistortoides	DESCES - POLBIS	10
Elymus trachycaulus (new)	ELYTRA	13
Lupinus breweri (new)	LUPBRE	10
Other associations or unclassifiable	Other associations	7
Other Carex	Other Carex	10
Pinus contorta	PINCON	1
Pinus contorta / Vaccinium caespitosum	PINCON / VACCAE	1
Ptilagrostis kingii	PTIKIN	125
Salix eastwoodiae	SALEAS	29
Salix lemmonii	SALLEM	5
Salix planifolia	SALPLA	3

APPENDIX B. PLANT SPECIES FOUND IN TUOLUMNE MEADOWS DURING 2008 FIELDWORK

List includes only those species that were most dominant in each gridpoint plot. Dominant 1 would be the most dominant species in a plot. Dominants 2 and 3 would have at least half the relative cover of Dominant 1.

Tuolumne Meadows Dominant Species List

Species	# Gridpoints Dominant 1	# Gridpoints Dominant 2	# Gridpoints Dominant 3	Total Gridpoints as a dominant	Life form
Achillia millefolium			1	1	Forb
Achnatherum nelsonii			1	1	Graminoid
Achnatherum lemmonii	1		1	2	Graminoid
Antennaria corymbosa		5	2	7	Forb
Antennaria media	1	3	1	5	Forb
Antennaria rosea	1	5	5	11	Forb
Antennaria sp.	13	35	18	66	Forb
Artemisia tridenta	6	10	2	18	Shrub
Aster alpigenus	28	15	7	50	Forb
Aster integrifolius	1			1	Forb
Aster occidentalis	1	2	6	9	Forb
Aster sp.			1	1	Forb
Calamagrostis breweri	52	14	3	69	Graminoid
Calamagrostis canadensis	1	2		3	Graminoid
Carex athrostachya	2			2	Graminoid
Carex filifolia	59	10	4	73	Graminoid
Carex lanuginosa	1	3		4	Graminoid
Carex lenticularis			1	1	Graminoid
Carex scopulorum	1	1		2	Graminoid
Carex sp.	3		1	4	Graminoid
Carex subnigricans	1	1	1	3	Graminoid
Carex vesicaria or utriculata	17	3	2	22	Graminoid
Danthonia intermedia	11	18	15	44	Graminoid
Deschampsia cespitosa	8	11	6	25	Graminoid
Dodecatheon jeffreyi		3	2	5	Forb
Eleocharis quinqueflora			1	1	Graminoid
Elymus sp.	1			1	Graminoid
Elymus trachycaulus	6	6	5	17	Graminoid
Gentiana newberyii			1	1	Forb

Species	# Gridpoints Dominant 1	# Gridpoints Dominant 2	# Gridpoints Dominant 3	Total Gridpoints as a dominant	Life form
Ivesia lycopoidiodes		3		3	Forb
Juncus balticus		1	3	4	Graminoid
Juncus balticus var. *mexicanus*	1	3		4	Graminoid
Juncus mertensianus		1	1	2	Graminoid
Juncus parryi		1	1	2	Graminoid
Juncus sp.			1	1	Graminoid
Lupinus breweri	6			6	Forb
Lupinus sp.	1			1	Forb
Luzula orestera	1			1	Graminoid
Luzula sp.		1	1	2	Graminoid
Muhlenbergia filiformis	6	18	7	31	G (Forb, For analysis)
Muhlenbergia richardsonis			1	1	Graminoid
Penstemon heterodoxus		1		1	Forb
Penstemon rydbergii		1	2	3	Forb
Perederidia bolanderi		1	1	2	Forb
Pinus contorta	2		3	5	Tree
Polygonum bistortoides			5	5	Forb
Potentilla flabellifolia			1	1	Forb
Ptilagrostis kingii	49	11	3	63	Graminoid
Puccinela nuttalii	1		1	2	Graminoid
Pyrrocoma apargiodes		2		2	Forb
Salix eastwoodiae	10	2	2	14	Shrub
Salix lemonii		1		1	Shrub
Salix planifolia	4			4	Shrub
Senecio scorzonella	1	4	2	7	Forb
Senecio sp.	1	1		2	Forb
Solidago multiradiata		7	5	12	Forb
Vaccinium caespitosum	4	26	10	40	Subshrub

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