Title
Contemporary pack stock effects on subalpine meadow plant communities in Sequoia and Yosemite National Parks

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Contemporary pack stock effects on subalpine meadow plant communities in Sequoia and Yosemite National Parks

A Thesis submitted in partial satisfaction of the requirements for the degree
Master of Science

in

Environmental Systems

by

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Committee in charge:

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Abstract

Title: Contemporary pack stock effects on subalpine meadow plant communities in Sequoia and Yosemite National Parks
Student: Steven Randall Lee
Degree: Master of Science, Environmental Systems
School: University of California, Merced 2013
Committee Co-Chairs: Stephen C. Hart and Eric L. Berlow

Sierra Nevada meadow plant communities are influenced by multiple multi-scale environmental processes ranging from elevation and climate to local soil moisture regimes. In recent years, land managers have faced concerns over potential impacts of recreational pack stock use to these meadow communities. Detecting the effects of such a stressor amongst a large amount of inherent natural variability requires taking into account variation due to environmental processes across multiple temporal and spatial scales. I evaluated the influence of pack stock use within Sequoia and Yosemite National Parks on three meadow plant community responses: 1) total vegetation cover and bare ground, 2) multivariate species composition and abundance, and 3) local-scale spatial variability in plant community structure. The study design accounted for inherent natural variability across multiple scales by: 1) controlling for among-meadow variability by using remote sensing data to select non-stock ('control') sites, 2) accounting for within-meadow variation in the local hydrology using in-situ soil moisture readings and 3) controlling for variation in stock use patterns by sampling across the entire available gradient of stock use. Increased cover of bare ground was detected only within "dry" meadow areas at the two most heavily used stock meadows. No difference in species composition or abundance was detected for any level of soil moisture or stock use. Increased local-scale spatial variability in plant community structure was detected in "wet" meadow areas at the two most heavily used meadows. These results suggest that at the meadow scale plant communities are generally resistant to the contemporary levels of recreational pack stock use studied. However, within-meadow responses such as increased bare ground can be context-dependent as a function of local-scale hydrological conditions and the ability to detect such effects may be dependent on short term (1–2 years) antecedent site conditions and use levels.

Introduction

Separating the effects of anthropogenic stressors[1] from inherent variability in natural systems is a challenge to land managers, particularly when it is impossible or impractical to conduct controlled experiments. Difficulty arises because natural systems are influenced by multiple environmental processes that can interact with each other, operate across multiple spatial scales, and vary over time (Cushman & McGarigal 2002). This results in a hierarchy where large-scale environmental factors and processes often constrain environmental factors operating at local scales (da Silva et al. 2012). In turn fine-scale heterogeneity of local site factors is often responsible for spatial and temporal variability within local communities (Cushman & McGarigal 2002, da Silva et al. 2012). Such intrinsic complexity results in a high degree of variability in the diversity, structure and function of biological communities, which can complicate evaluations of whether or not effects are truly occurring from anthropogenic stressors (Peterman 1990). Addressing this challenge requires taking into account variation in environmental processes across multiple spatial and temporal scales.

Meadows in Sierra Nevada Mountains of California offer an ideal case system for such an approach. Occupying approximately 3% of the Sierra Nevada, meadows occur nested within a topographically complex mountainous landscape (National Park Service 2009, Keeler-Wolf et al. 2012). This contributes to meadow ecosystems being influenced by a hierarchy of environmental processes ranging from regional patterns of precipitation to steep gradients of within-meadow soil moisture. As a result, Sierra Nevada meadows supply essential habitat for a diverse array of plant and animal species (Graber 1996, Jones 2011); however, they also serve as popular destinations for visitor pack stock (i.e., horses and mules) groups. This leads to a potential conflict for land managers trying to balance ecological integrity and visitor access. The use of pack stock to carry people and supplies through the rugged Sierra Nevada is a long standing tradition (McClaran and Cole 1993) that has continued into contemporary times through recreational use by park visitors and administrative use by the National Park Service (NPS). Over the last several years there been increased concern by the NPS, the United States Forest Service, as well as special interest groups over possible adverse effects of pack stock on mountain meadows. However, attempts at meaningful evaluations of stock use impacts on plant communities will be unsuccessful if the challenge presented by multi-scaled natural variability is not also addressed.

[1]Anthropogenic stressors are human-caused factors or processes that may induce a response in a biological entity such as an individual, population or community (Crowe et al. 2000).

Specific concerns are that pack stock may directly impact meadows through the defoliation of plants, trampling of vegetation, and compaction of soil (McClaran and Cole 1993). Studies evaluating similar impacts to other grassland systems suggest such activities could lead to severe indirect effects as well, by influencing structure and functional processes within the plant community. For example, selective grazing of palatable species can drive shifts in plant communities towards less palatable species via competitive release (Furbish & Albano 1994, Anderson & Briske 1995). Trampling can damage the physical structure of vegetation, causing altered growth forms of perennial plant species and changes to local micro-climate conditions, which may drive re-organization of community assemblages (Cole 1995, Kobayashi et al. 1997, Striker et al. 2011). Soil compaction can increase soil bulk density and reduce water holding capacity (Taboada & Lavado 1988, Altesor et al. 2006), which in turn can change the local hydrology and expose the system to potential invasion by species that typically occur in drier communities (Berlow et al. 2003).

While these studies indicate potentially strong impacts to meadow plant communities, results from the few studies assessing pack stock use have been mixed. Monitoring over a 25-year period in Sequoia & Kings Canyon National Parks (SEKI) found greater differences in species composition across meadow pairs than between paired stock and non-stock meadows (Hopkinson et al. 2013). In contrast, a study evaluating pack stock effects in meadows in the nearby Inyo National Forest suggests that indirect effects from stock use, such as meadow moisture draw down, may have driven shifts in community composition (Shryock 2010).

The difficulty in detecting a consistent effect may arise from the point that pack stock use as a stressor occurs against a background of large amounts of natural variability inherent to meadow ecosystems. Meadows are hierarchically nested within the mountainous landscape, where among-meadow variability in plant communities may be due to strong large-scale environmental factors (e.g., elevation, climate, hydrology; Wood 1975), while within-meadow variation is largely driven by natural heterogeneity in soil moisture regimes (Allen-Diaz 1991). Complicating processes at each scale is the high inter-annual variability in climatic conditions that occurs across the Sierra Nevada landscape (Lundquist & Cayan 2007). Adopting an approach that accounts for this natural complexity to evaluate pack stock use is particularly appropriate when manipulative experimental approaches are impractical. Many of the meadows used by pack stock occur within national parks where experimental manipulations are generally restricted, or are limited to scales much smaller than actual pack stock use scenarios (Cole et al. 2004). Additionally, the intensity of stock use in meadows is not allocated with consideration of an a priori experimental design to maximize detection of impacts. However, contemporary levels of stock use intensity do span a large gradient, lending to a natural or quasi experimental design for evaluating potential pack stock effects.

In this light, I assessed meadow plant community responses to pack stock use while accounting for multi-scale drivers known to promote variability of subalpine meadows. Specifically, I asked whether current levels (2004-2009) of pack stock use influence: 1) total vegetation cover and bare ground, 2) multivariate species composition and abundance and 3) local-scale spatial variability in plant community structure. These questions were assessed using a multi-step approach that included:

1. Controlling for large-scale, among-meadow variability by matching subalpine pack stock use meadows with non-pack stock ‘controls’ from a comprehensive database of all subalpine meadows in the region, coupled with remotely sensed estimates of meadow hydro-climatic and geospatial attributes.

2. Controlling for within-meadow variation in local hydrology by measuring in-situ soil moisture in every sampling plot and stratifying analyses by vegetation grouped to specific moisture classes that emerged from the data.

3. Controlling for variation in pack stock use patterns by sampling across a large gradient in reported use.

Methods

Study Area

I used subalpine meadows within Sequoia National Park (SEKI, abbreviated to include the management unit Sequoia and Kings Canyon National Parks) and Yosemite National Park (YOSE) in the Sierra Nevada Mountains, California. The Sierra Nevada subalpine zone varies in elevation with respect to latitude, aspect, and local climate, but generally occurs between 2,450–3,600 m. Like much of the Sierra Nevada, soils in the subalpine zone are poorly developed originating from a solid granite parent material that has received repeated glaciation during the recent Pleistocene epoch (Fites-Kauffman et al. 2007). The zone can be described as a continuous complex of mixed conifer forests (predominately *Pinus contorta),* rocky outcrops, and scrub vegetation types interspersed with highly diverse and productive meadow habitats (Fites-Kauffman et al. 2007). The Sierra Nevada experiences a Mediterranean-type climate with cool, wet winters (October-April) and a dry, warm summer season, with most of the water input to the subalpine and higher elevations falling as snow in the winter months. The growing season for the meadows varies dependent on timing of snowmelt, but typically runs from late May through August.

Meadows generally occur at perennially wet locations where ground water is at or near the surface (Wood 1975) and plant species compositions are closely linked to the underlying local soil hydrology (Allen-Diaz 1991, Weixelman et al. 2011). Subalpine meadows in the region are dominated by perennial herbaceous plant species including graminoids (e.g., *Carex scopulorum, Calamagrostis muiriana*) and forbs (e.g., *Oreostemma alpigenum, Gentiana newberryii*) interspersed with understory moss at the ground level. Subalpine meadows are also used by native herbivores including mule deer (*Odocoileus hemionus californicus),* voles (*Microtus* spp.) and pocket gophers (*Thomomys monticola*.).

Meadow Selection

To control for known variability among meadow plant communities due to differences in major environmental factors, "stock meadows" (defined here as meadows that have received reported pack stock use within the past decade) were paired with "non-stock meadows" (defined here as meadows that had no reported use from any time period) using a suite of geospatial and hydro-climatic remote sensing data. This included newly available park-wide meadow Geographic Information System (GIS) layers that incorporate many previously unidentified meadows in each park (Berlow et al., *In Review).* Meadow pack stock use records were obtained from NPS pack stock monitoring programs from each park and assigned to corresponding meadow polygons. Pack stock use records were based on the number of animals per night in a given meadow (e.g., five animals in a meadow for three nights equals 15 stock nights). All stock meadows with at least 10 reported stock nights during at least one of the most recent six years (2004–2009) of available data leading up to the start of the 2011 sampling period were considered. Stock meadows were then constrained by meadow size (< 25 ha) in order to: (1) allow for feasible sampling of multiple meadows within the short growing season, and (2) avoid uncertainty of stock use patterns in very large meadows where reported use does not identify locations where stock tend to graze or aggregate. To ensure accuracy, stock use records for candidate meadows were then crosschecked by both the local NPS Wilderness Specialist and the Biologist in charge of pack stock monitoring in YOSE, and by the local NPS Plant Ecologist also in charge of pack stock monitoring in SEKI.

Paired non-stock meadows were selected from a potential pool that included all identified non-stock meadows within each park (3,606 in SEKI and 2,440 in YOSE) using remote sensing data and a multivariate matching technique. The top 20 candidate stock meadows from each park were matched to non-stock meadows with no previously recorded stock use, using the package 'Matching' (Sekhon 2011) in the statistical program R, version 2.13.0 (R Core Development Team 2011). Matches are based on

Mahalanobis generalized distances, which take into account the correlation among the various descriptors (i.e., covariates) for comparing groups (i.e., meadows; Legendre & Legendre 2012). Twenty-seven geospatial, hydro-climatic, and vegetation covariates derived from remote sensing were used for the matching process (Table 1), and the top three matches were selected as potential non-stock meadows to be used as controls. Meadows were then visited and assessed qualitatively to find the single best match, based on similarities in meadow size, landscape position (i.e., hill slope or basin), elevation and proximity to the matched stock meadow. This resulted in 22 matched meadow pairs (one stock and one non-stock control), with 14 pairs sampled between the 2011 and 2012 growing seasons in YOSE and 8 pairs sampled during the 2012 growing season in SEKI. YOSE meadows ranged in size from 1.15 to 2.14 ha with an average meadow size of 5.90 ha, and SEKI meadows ranged in size from 0.42 to 10.62 ha with an average meadow size of 2.60 ha. The maximum number of stock nights in a single year during the 2004–2009 period ranged from 10 to 577 stock animal nights in YOSE, with an average maximum stock nights of 134 per year; and from 82 to 271 stock nights in SEKI, with an average maximum stock nights of 155 per year.

Table 1. Twenty-seven geospatial, hydro-climatic, and vegetation covariates derived from remote sensing used for multivariate matching of non-stock meadows to selected stock meadows in Yosemite (YOSE) and Sequoia (SEKI) National Parks.

Data	Description
Meadow Area	Meadow Area (ha) of meadow polygon
Elevation	Elevation at meadow centroid derived from 10-m Digital Elevation Models (DEM)
Short Hair Sedge Cover (%)	Percent of meadow polygon composed of vegetation alliance 7120 - Short Hair Sedge
Semi-permanent Flooded Meadow Cover (%)	Percent of meadow polygon composed of vegetation alliance 9000 - Semi-permanent Flooded Meadow
Distance to Nearest Lake	Euclidian distance (m) to nearest lake
Distance to Nearest Meadow	Euclidian distance (m) to nearest meadow
Distance to Nearest Road	Euclidian distance (m) of meadow to nearest road
Distance to Nearest Trail	Distance (m) to nearest trail
Estimated Minimum Travel Time From Trailhead	Estimated travel time from trailhead (only used in YOSE)
Nearest Meadow Cumulative Elevation Change	Elevation change (m) between each meadow and nearest meadow
Nearest Meadow Maximum Slope	Maximum slope between meadow and nearest meadow
Ranked Mean Precipitation	Rank of meadow in mean precipitation (1980-2010) www.daymet.ornl.gov
Ranked Standard Deviation of Precipitation	Rank of meadow in standard deviation of precipitation
Ranked Standard Deviation of Average Temperature	Rank of meadow in standard deviation of Average Temperature
Ranked Mean Meadow Melt Date	Rank of meadow in mean meadow melt data. Melt dates derived from MODIS snow cover data (2002-2007; Dozier and Frew 2009)

Table 1. (continued)

Data	Description
Ranked Standard Deviation for Meadow Melt Date	Rank of meadow in melt data standard deviation
Ranked Standard Deviation for meadow 50 % Snow Cover Date	Rank of meadow in snow melt data when meadow is 50% covered by snow
Ranked Mean Meadow 50% Snow Cover Date	Rank of meadow in mean data for when meadow is 50% covered by snow
Ranked Mean Tasseled Cap Greenness Index	Rank of meadow from mean Tasseled Cap Greenness data Landsat-5 (1986-2006) (http://earthexplorer.usgs.gov/)
Ranked Standard Deviation for Tasseled Cap Greenness Index	Rank of meadow from standard deviation of Tasseled Cap Greenness data from Landsat-5
Ranked Average of Standard Deviation for Tasseled Cap Greenness	Rank of meadow from the average standard deviation for Tasseled Cap Greenness data from Landsat-5
Ranked Mean Tasseled Cap Wetness	Rank of meadow in mean Tasseled Cap Wetness
Ranked Standard Deviation for Tasseled Cap Wetness	Rank of meadow in standard deviation of Tasseled Cap Wetness Landsat-5
Ranked Average of Standard Deviation for Tasseled Cap Wetness	Rank of meadow in standard deviation of Tasseled Cap Wetness Landsat-5
Ranked NDVI	Rank of meadow in Normalized Difference Vegetation Index (NDVI) Landsat-5
Ranked Standard Deviation for NDVI	Rank of meadow in standard deviation of NDVI
Ranked Average of Standard Deviation for NDVI	Rank of meadow in mean standard deviation of NDVI Landsat-5

Field Sampling

Each meadow was sampled once during the summer growing season (June–August) and observations were made by United States Geological Survey field crews (teams of 3–6 people). Sampling occurred along 5-m wide belt transects spaced 40 m apart, running across the meadow width and perpendicular to the main meadow drainage and/or meadow length. Along the centerline of each belt transect, 2 x 2 m (4 m^2) sampling plots were established at 20-m intervals (Appendix I). Ocular aerial estimates of the total vegetation cover (%), litter cover (%) and exposed mineral soil cover (%; i.e., bare ground) were recorded within each plot. Plant species composition was sampled at every third sampling plot along each transect (Appendix I). Ocular aerial estimates of cover for all species were collected in eight 25 x 25 cm sub-plots spaced systematically within each 4 m^2 plot. Cover was used as a proxy for abundance of each species.

In order to account for hydrologic variation both within and among meadows, field crews measured soil volumetric water content (VWC; 0 – 12 cm depth) within every 4 m^2 plot using a Field Scout TDR 100 soil moisture probe (Spectrum Technologies, Plainfield, IL). A probe depth of 12 cm was chosen because it falls within the rooting zone for many of the meadow species (Baldwin et al. 2012). Readings were taken within 10 cm of the inside of each corner and at the approximate center of each plot. Values within a plot were averaged to get a plot mean.

Data Analyses

Classification and Regression Tree (CART) analyses were used (e.g., De'ath and Fabricus 2000) as a non-parametric approach for assessing the relative contribution of stock use versus other geospatial and hydro-climatic covariates in explaining differences in vegetation between paired stock and non-stock meadows. In order to utilize the paired study design, response variables used in each CART analysis were calculated as the difference between each paired stock and non-stock meadow. This allowed for direct interpretation of each response in the context of pack stock use. For example a positive value for the difference in bare ground between a matched meadow pair suggests that the stock location had more estimated bare ground than the paired non-stock meadow. Uncertainty in the estimates of meadow-scale differences between stock and non-stock meadows of each pair was quantified using a bootstrapping method (described under *Response Variables* below). CART was performed using JMP 10.0 (SAS Institute) and calculations to derive each response and explanatory variable were done using R version 2.15.1 (R Core Team 2012).

Response Variables

Three basic metrics derived from raw sample plot data were used to calculate each response variable: Bare ground, species dissimilarity, and species dispersion.

(1) Bare ground: Total cover of bare ground in each plot was used both as a direct measure of exposed soil and as an indirect measure of total vegetation cover since these plot attributes were strongly negatively correlated (vegetation cover vs. bare ground: Pearson's $r = -0.65$, and vegetation plus litter cover vs. bare ground: Pearson's $r = -0.84$).

(2) Species dissimilarity: Potential shifts in species composition and abundance due to stock use were assessed by calculating the multivariate Bray-Curtis dissimilarity in plant species cover between paired meadows using the VEGAN community ecology package for R (Oksanen et al. 2012).

(3) Species dispersion: A measure of multivariate species dispersion was used to evaluate differences among stock and non-stock meadows in the patterns of local-scale (4 m^2 plot-scale) spatial variability in plant community structure (Fraterrigo & Rusak 2008, Houseman et al. 2008). Such changes in spatial variability may occur even in the absence of clear differences in the multivariate community patterns averaged across all plots (Anderson et al. 2006, Houseman 2008, Muehlbauer 2011). Species dispersion was estimated within each 4 m^2 sampling plot by calculating the mean Bray-Curtis distance of each of the eight 25 cm x 25 cm sub-plots to an ordinated centroid of all eight plots

(Anderson 2006) using the 'betadisper' function in the VEGAN package in R. Thus, in this study, an increase in species dispersion can be interpreted as an increase in small-scale spatial heterogeneity of plant community structure within the 4 m^2 patch (plot) scale.

The nature of the gridded sampling effort created sample sizes (n) directly dependent on the size of the meadow. In order to ensure an adequate sample size, those moisture class pairs that had less than three plots for any meadow in the pair were dropped from the analyses. This resulted in different total numbers of matched pairs (N) used in each moisture class analysis (Figure 2). Mean values for each response as well as 95% confidences intervals were estimated using bootstrapping in order to quantify the uncertainty due to different sample sizes (n) used in the subsampling of each meadow moisture class. Differences in average bare ground and differences in species dispersion means were calculated by subtracting the bootstrapped means of a non-stock meadow from the bootstrapped means of the paired stock meadow. Each procedure was run 1000 times to produce an estimated mean difference in each meadow pair taken as the median value of the bootstrapped distribution. These were then used as the response variables in each CART analysis. Mean estimates and 95% confidence intervals for species dissimilarity between matched pairs were calculated based on bootstrapped estimates of mean values for each species within each meadow moisture class. Similar to the bare ground response, the procedure was run 1000 times and a median value from the resulting distribution was taken as a mean estimate to be used in the CART analysis.

Explanatory Variables

While the focus of this study is to relate differences observed in the plant communities to stock use, physical site attributes may also contribute to observed differences between stock and non-stock meadow pairs (e.g., dissimilar community composition at different elevations). In order to address potential variation in responses due to multiple factors, explanatory variables used in the CART analyses fell into three broad categories:

(1) Stock Use: Reported stock use for the grazed meadow of the matched pair: six measures of stock use based on NPS records from 2004-2009 were used: mean and maximum annual stock nights, mean and maximum annual stock density (i.e., stock nights per hectare-year), and the standard deviation and coefficient of variation of annual stock nights across the six year period.

(2) Within Pair: The difference in physical attributes between the meadows within each pair. Within Pair values were used to evaluate how much the difference in vegetation between stock and non-stock meadows within each pair is explained by simple

differences in their physical attributes (e.g., size, elevation, hydrology, snow regime). A large difference in each response due to within pair differences could relate to a poor pairing between stock and non-stock meadows.

(3) Between Pairs: The mean physical attributes of each meadow pair. Between Pairs values were used to evaluate how much the difference in vegetation between stock and non-stock is explained by differences in the overall environmental context of the meadow pair (e.g., a high elevation pair might show a different response than a low elevation pair).

For Within Pair and Between Pairs, 14 geospatial and hydro-climatic meadow covariates derived from remote sensing were used (Table 1, Appendix II). I excluded redundant covariates that were collinear ($r > 0.80$) and covariates that exhibited extremely low variation among the selected meadows (e.g., remotely sensed vegetation alliances). For the CART analyses, to avoid model over-fitting and potential problems of interpreting model coefficients, trees were pruned to include only splits that added more than 10% to the total R^2 and to eliminate the presence of 'ties' in the covariate choice.

Natural variability in broad soil moisture regimes that are known to drive coarse scale patterns of dominant vegetation within each meadow were addressed by stratifying all analysis across three moisture classes ('Wet,' 'Intermediate,' and 'Dry'). To do this, patterns in the distribution of the 12 most dominant plant species were explored using locally weighted non-parametric regression models (LOESS, smoothing parameter = 0.10). Moisture classes were then delineated based natural breaks and transitions in the distribution each of the species along a soil moisture gradient (see Results; Figure1). Potential effects from intra- and inter-annual variation in soil moisture between meadows was minimized by converting each plot mean VWC value to a Z-score standardized to individual meadow means (Gotelli & Ellison 2004).

Results

Moisture Classes

Trends for the top 12 most abundant plant species along the soil moisture gradient showed clear patterns of limited distributions (Figure 1). These distributions guided the delineations made for Dry, Intermediate and Wet moisture classes used in the subsequent analyses. Dry moisture class areas were dominated by *Carex filifolia*, a xeric vegetation type indicator species (Weixelman et al. 2011). *Carex vesicaria* and *Carex scopulorom*, both characteristic of wet meadow habitats (Weixelman et al. 2011) were highly abundant within the Wet moisture class, yet steadily decreased in abundance as plots transitioned into the Intermediate moisture class. Finally, the Intermediate moisture class showed the greatest cumulative cover of the three classes and supported the greatest number of dominant species assessed.

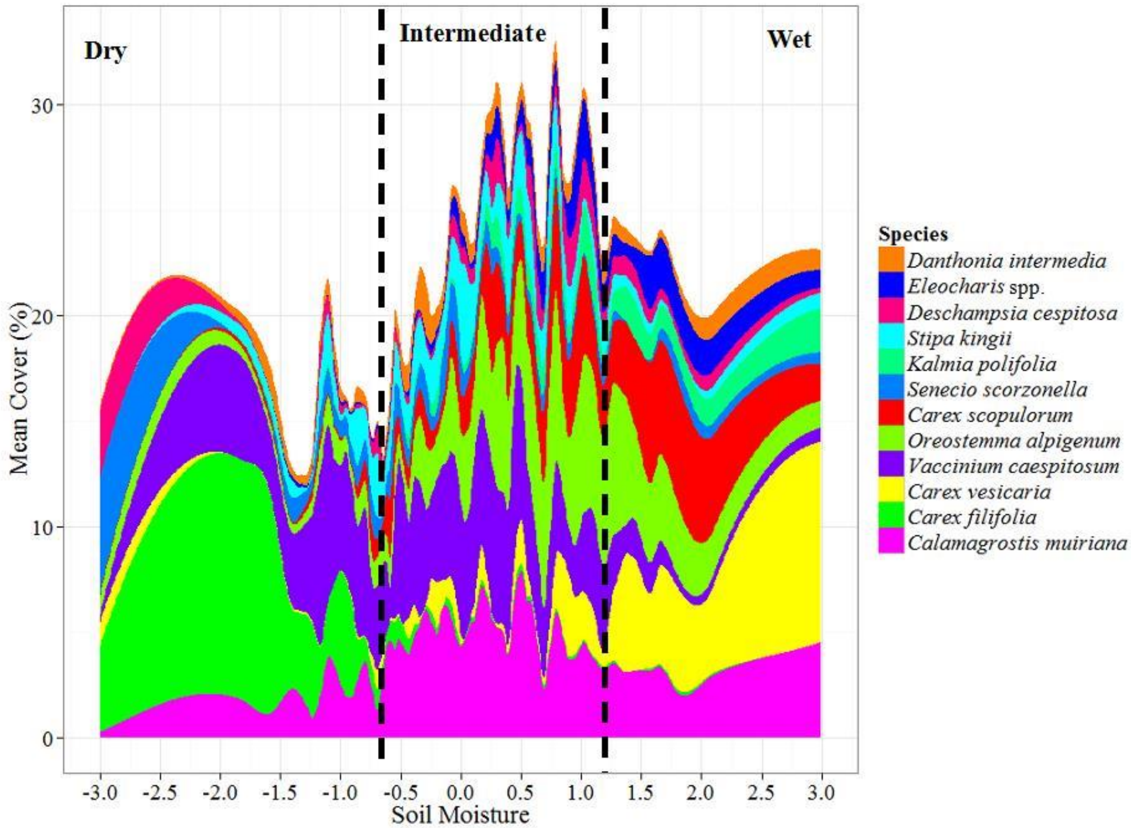

Figure 1. Locally weighted regression (LOESS) models of mean cover (%) for the top 12 most abundant species along a soil moisture gradient. X-axis (Soil Moisture) values are represented here as standardized volumetric water content values (Z-scores). Values run from driest plots on the left (-3.0) to wettest plots on the right (3). Vertical dashed lines indicate breaks used to delineate vegetation moisture classes (Dry, Intermediate and Wet). Breaks were subjectively based on the distributions of plant species.

Classification and Regression Tree (CART)

CART models explained 58 to 93% of the variation among meadow pairs in the difference between stock and non-stock meadows, however relative contributions of different classes of explanatory variables differed among responses and moisture classes (Figure 2, Appendix II). At the meadow scale, Stock Use covariates explained less variation than hydro-climatic and geospatial differences between meadows either within (Within Pair) or among meadow pairs (Between Pairs; Figure 2, Panels A, E, I). However, when the analyses were stratified by vegetation moisture class, Stock Use alone contributed the most in explaining differences in bare ground cover in the Dry moisture class (66% of the total sum of squares; Panel B) and differences in species dispersion in both Dry and Wet moisture classes (66% and 78% of the total sum of squares, respectively; Panels J, L). Thus, Stock Use explained differences in local-scale spatial variability in plant community structure, even though larger scale, multivariate patterns of species composition and abundance (species dissimilarity) were not influenced by Stock Use (Panels E, G, H). In general, mean physical attributes of the meadow pairs (Between Pairs) explained more variation in each response than did differences in physical attributes within each pair (Within Pairs; Figure 2, light gray vs. dark gray bars). These trends suggest that pairing of stock with non-stock 'control' meadows was successful at minimizing other sources of natural variation among meadows.

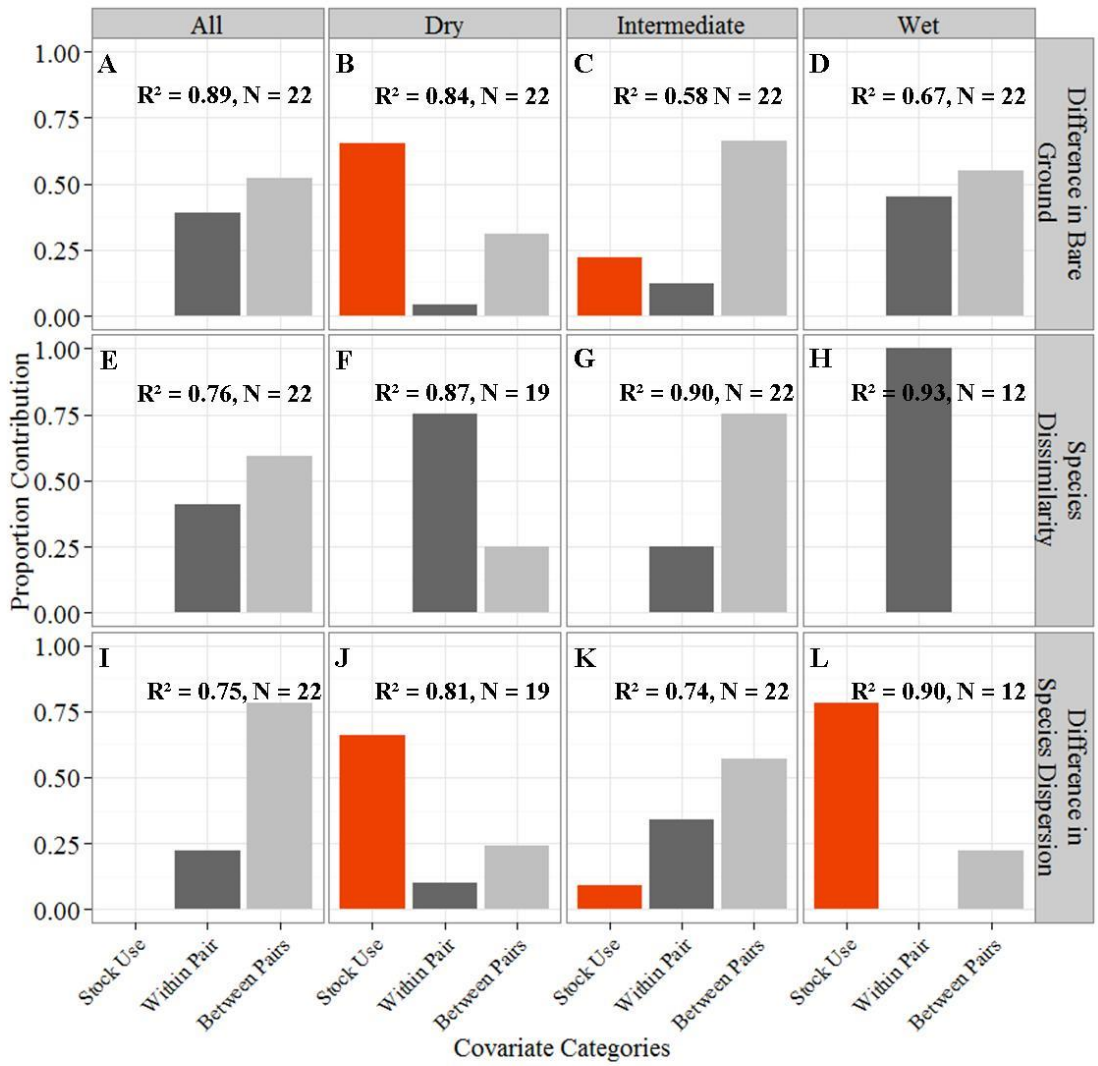

Figure 2. The relative contribution of different classes of covariates in explaining variation in the differences between stock and non-stock meadow pairs for CART models. Separate models were run for each moisture class (Dry, Intermediate, and Wet) and the entire meadow scale (All). Each panel shows the CART R^2 and sample size of meadow pairs (N). Covariate categories [shades]: Red (Stock Use) = Six measures of stock use for the grazed meadow of the pair; Medium Gray (Within Pair) = differences in physical attributes between meadows within each stock and non-stock pair' Light gray (Between Pairs) = differences among meadow pairs in their mean physical attributes (see text).

Detailed Bootstrapped Analysis

The previous analysis provides a big picture view of the relative contributions of pack stock use and a suite of coarse physical meadow attributes in explaining differences between stock and non-stock meadow pairs. Given the strong management interest in evaluating potential impacts of pack stock use, here I describe in more detail the patterns of meadow plant communities across a gradient of stock use intensity (mean stock nights/ha).

Bare Ground

Generally, most pairs showed no significant difference in bare ground between stock and non-stock meadow for any soil moisture class or stock use intensity (Figure 3, $y \approx 0$). In pairs with significant differences, non-stock meadows exhibited more instances of greater bare ground than did stock meadows (Figure 3, negative values) across all soil moisture classes. However, in agreement with the CART results, greater bare ground cover was significantly higher in stock than non-stock at the two highest stock use intensity meadows within the Dry moisture class (Figure 3, Panel A). These two meadows were located in SEKI. If the parks were assessed separately or if these meadows were treated as outliers and all other meadows pairs were assessed separately, no significant increase of bare ground would be detected with increased stock use intensities. Similarly both the Intermediate and Wet moisture classes showed no trends of increased bare ground with stock use, with each only having one meadow pair where bare ground was greater in the stock meadow (Figure 3, Panels B, C).

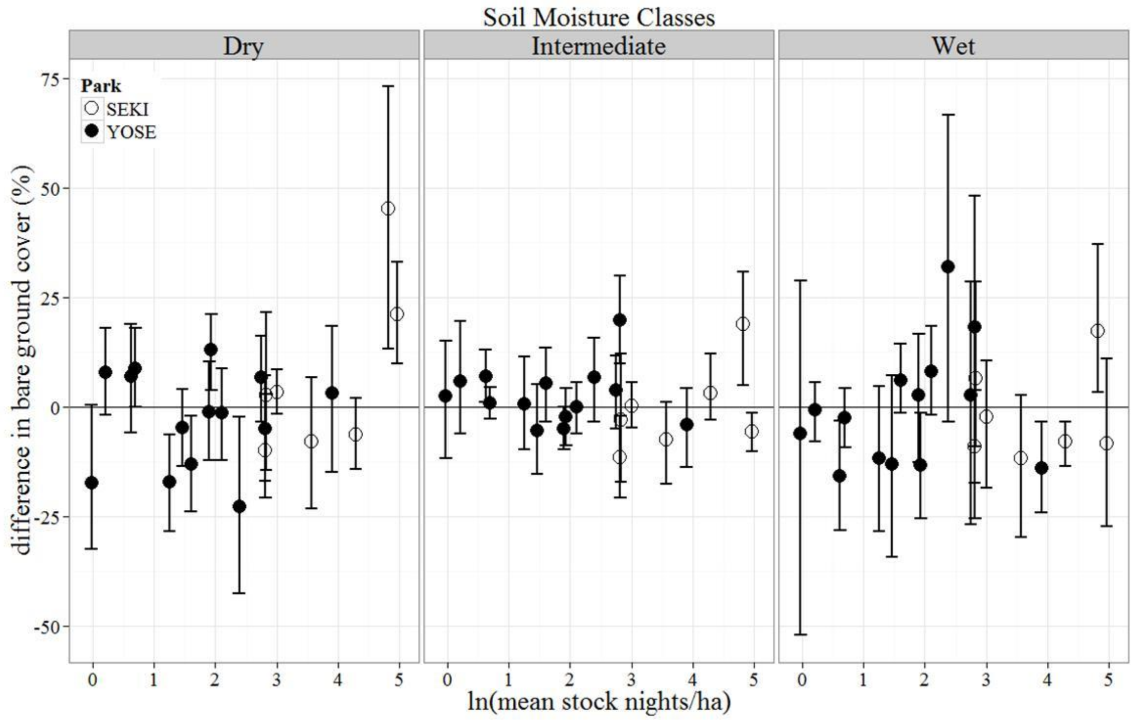

Figure 3. Difference in percent bare ground cover (bootstrapped mean + 95% Confidence Interval) in Yosemite (YOSE) and Sequoia (SEKI) National Parks between matched stock and non-stock meadows for each soil moisture class (Dry, Intermediate, Wet) . The range of 0-5 (ln) mean stock nights/ha corresponds to a range of 1-144 untransformed mean stock nights/ha.

<u>Species Dissimilarity</u>

Meadow pairs showed large amounts of variability in species composition and abundance. Both parks were similar in their differences in plant community composition and abundance and always exhibited some level of species dissimilarity between stock and non-stock pairs (Figure 4, y > 0) across all levels of stock use. Some of the meadow pairs with the largest species dissimilarities were those with very low stock use intensities, while conversely some meadows with the lowest dissimilarities were at relatively higher stock use levels (Figure 4). A slight apparent trend may be present within the Intermediate moisture class. However, CART analysis showed that precipitation was the strongest variable influencing differences in species dissimilarity within the Intermediate moisture class than any stock use metric (Appendix II).

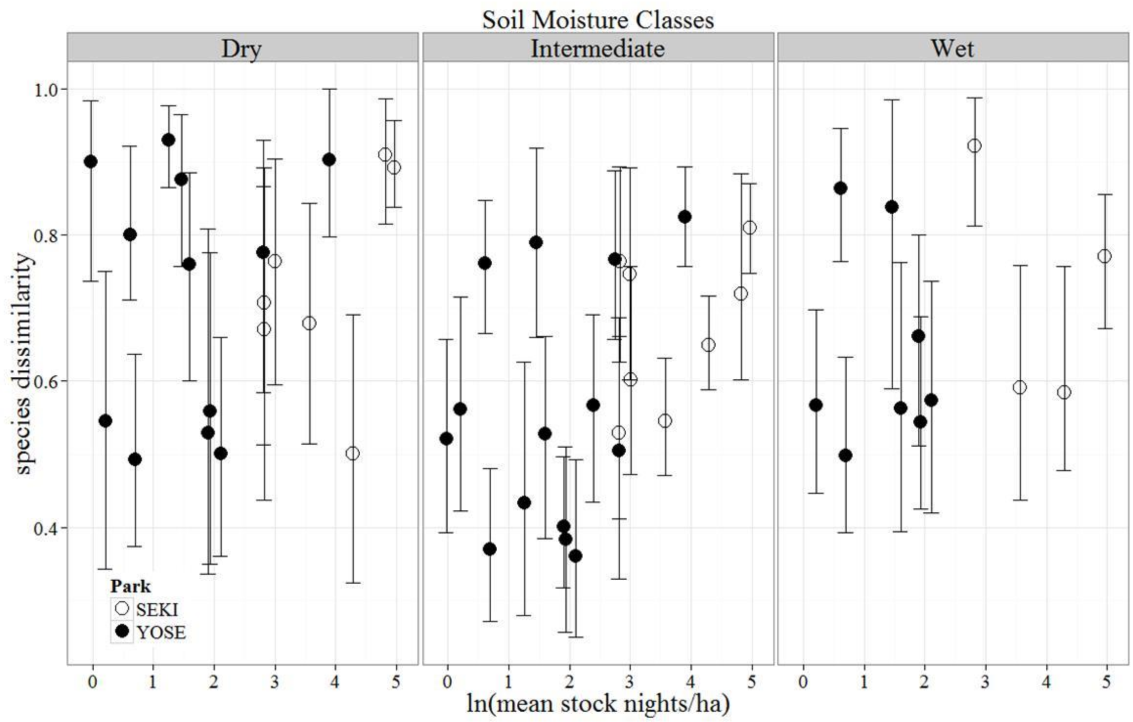

Figure 4. Difference in species dissimilarity (bootstrapped mean + 95% Confidence Interval) in Yosemite (YOSE) and Sequoia (SEKI) National Parks between matched stock and non-stock meadows for each soil moisture class (Dry, Intermediate, Wet) . The range of 0-5 (ln) mean stock nights/ha corresponds to a range of 1-144 untransformed mean stock nights/ha.

<u>Species Dispersion</u>

In general there was little difference in species dispersion between stock and non-stock meadows across all stock use intensities. The Dry moisture class showed greater local-scale spatial variability in plant community structure in non-stock than stock meadows at the two lowest stock use intensities (negative values; Figure 5). The only meadow pair within the Dry moisture class to show greater species dispersion within the stock meadow occurred at moderate stock use intensity levels. Within the Intermediate moisture class, species dispersion was consistently similar between stock and non-stock pairs across all stock use intensities. Within the Wet moisture class, only pairs at the two highest stock use intensity meadows showed greater species dispersion for stock use meadows than paired non-stock meadows. Similar to trends within the Dry moisture class for bare ground, these meadows were both located within SEKI with no trends of increased species dispersion observed from YOSE even at highest stock use intensities.

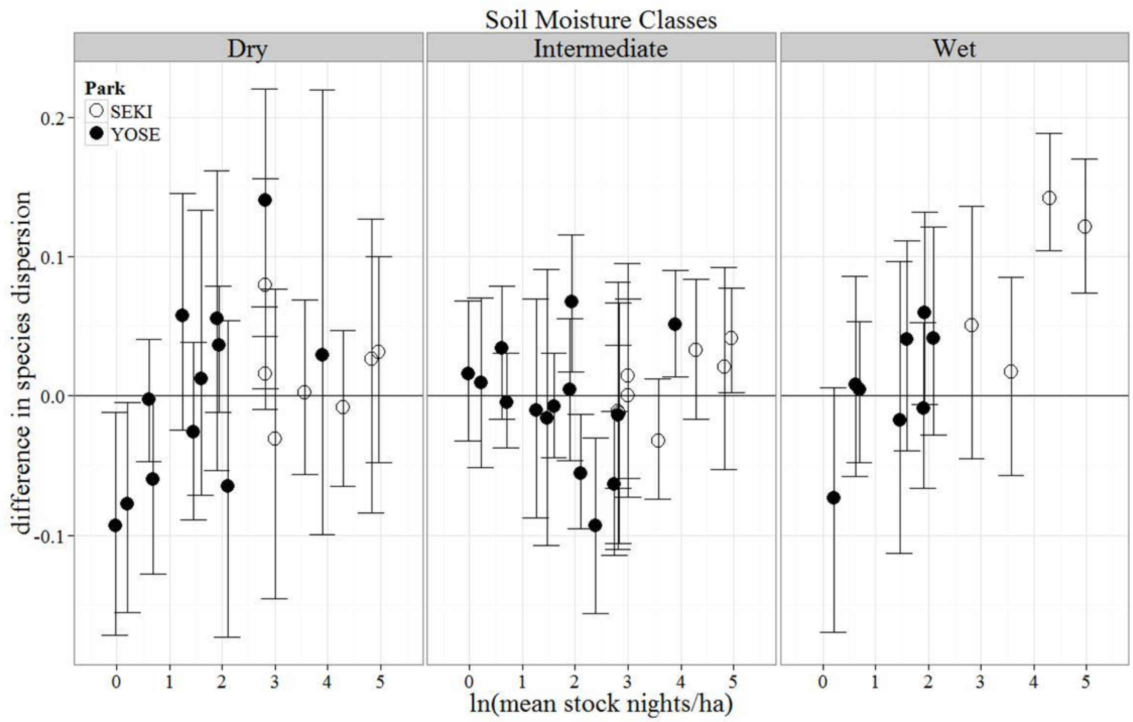

Figure 5. Difference in species dispersion (bootstrapped mean + 95% Confidence Interval) in Yosemite (YOSE) and Sequoia (SEKI) National Parks between matched stock and non-stock meadows for each soil moisture class (Dry, Intermediate, Wet) . The range of 0-5 (ln) mean stock nights/ha corresponds to a range of 1-144 untransformed mean stock nights/ha.

Discussion

Even with good pairing of non-stock meadows with existing stock meadows, an effect of stock use was never detected in plant communities at the meadow scale when within-meadow soil moisture gradients were not considered or if stock use was treated as a binary (yes/no) variable (Figure 2, Appendix III). By conducting analyses on multiple responses within soil moisture classes across a large gradient of stock use, significant differences in meadow vegetation between paired stock and non-stock meadows were observed under specific environmental and stock use conditions. More specifically, a potentially strong stock use effect was generally detected at only the highest current reported use levels in the Dry and Wet moisture classes. These moisture classes tend to have lower species richness than the Intermediate class and as a result could be comparatively less resilient or resistant to stressors (Yachi & Loreau 1999). The largest vegetation responses were increases in Bare Ground and small-scale ($4m^2$) spatial heterogeneity in community structure. Differences in spatially averaged, plant community composition and abundance (species dissimilarity) did not exhibit clear trends with stock use intensity at either the meadow scale or when plots were assigned to specific soil moisture classes.

Bare Ground

The detection of greater bare ground in the two highest stock use intensity meadow pairs within the Dry moisture class suggests that meadow areas with different soil moisture regimes may respond independently. Drier meadow areas generally have more naturally occurring bare ground cover (and less vegetation cover; Appendix III) and the detection of an increase in bare ground may indicate less resistance or resilience to grazing and/or trampling due to low productivity and slow recovery rates (Vogel et al. 2013). However, these results do not indicate that a clear threshold has been crossed to promote increased bare ground. Only two meadow pairs are driving the trend, one of which had the largest confidence intervals within the moisture class, indicating a large amount of variability. These results also suggest that different moisture classes may respond differently to stock use in regards to bare ground. Contrary to the pattern in the Dry moisture class, there was a general lack of any difference in bare ground between stock and non-stock meadows within the Intermediate moisture class, with only one of the 22 meadow pairs showing greater bare ground in a stock meadow (Figure 3). The Intermediate moisture class supports the greatest number of species of any other classes and may follow patterns observed in other grazed systems where areas with high species richness tend to display more temporal stability in biomass production in the face of ecological stressors (Tilman et al. 2006). The Wet class was the only case where meadow pairs exhibited a potential pattern of less bare ground cover in stock meadows than non-stock meadows. This may be a result of compensatory growth under moderate levels of stock use (Noy-Meir 1993), yet more likely may be a result of differences in physical attributes of the meadow pairs indicated by the CART analysis (Figure 2).

Despite the detection of greater bare ground at the highest stock use intensity in the Dry moisture class, overall results showed no differences in bare ground between stock and non-stock meadows and are inconsistent with previous studies and monitoring efforts. Ballenger et al. (2010) in YOSE observed greater mean bare ground cover in stock use meadows than non-stock meadows during the 2008 growing season (Appendix III). Holmquist et al. (2013) in SEKI also observed significantly greater bare ground in pack stock meadows during the 2010 growing season, but not in 2011, an unusually wet year where total stock use in both parks was low (see Figure 6). This suggests that antecedent conditions in both stock use and climate leading up to the sampling may play an important role in whether or not stock use has a detectable effect on bare ground. Here I do a simple comparison between the NPS monitoring results from YOSE (Ballenger et al. 2010) and the results from YOSE for the current study (2011,2012) in order to shed light on more basic dynamics in the relationship between stock use and meadow vegetation.

Monitoring in YOSE (Ballenger et al. 2010) took place in 2008 and sampled 14 stock and 14 non-stock meadows, of which 6 of the stock meadows were sampled with this study. The year prior to the 2008 YOSE sampling included higher than average stock use and extremely low snow pack (Figure 6, 63.7% below the 50-year mean), whereas the years preceding sampling for the current study had comparatively lower stock use and higher snow pack. These patterns suggest the response of bare ground cover to stock use may vary inter-annually, with the largest effects observed after dry years that experienced heavy stock use. These results suggest that even in a wet year, stock use may increase bare ground, but only in dry vegetation communities. Based on these results, I have developed a conceptual model relating single year primary productivity levels and stock use intensity to when an increase in bare ground due to stock use may be detected (Figure 7). Such a model could be tested with long term monitoring of bare ground and vegetation cover. On years that stock use is heavy and productivity is low (e.g., drought year) it may be expected that a significant increase in bare ground during that and the succeeding year might be detected, while if stock use is light and productivity is high (e.g., heavy snow year) an observable effect might not occur.

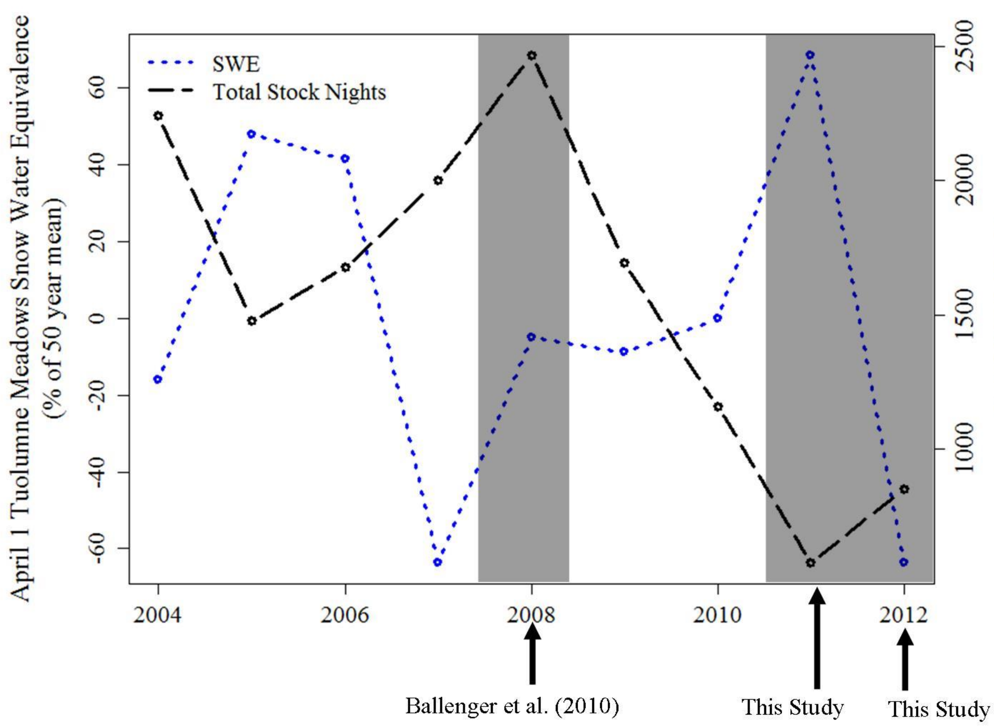

Figure 6. 2004–2012 April1 snow water equivalence (SWE) expressed as % of 50 year mean for Tuolumne Meadows and reported pack stock night totals for Yosemite National Park. Snow data is from Department of Water Resource, California Cooperative Snow Survey.
Available: http://cdec.water.ca.gov/cgi-progs/snowQuery_ss

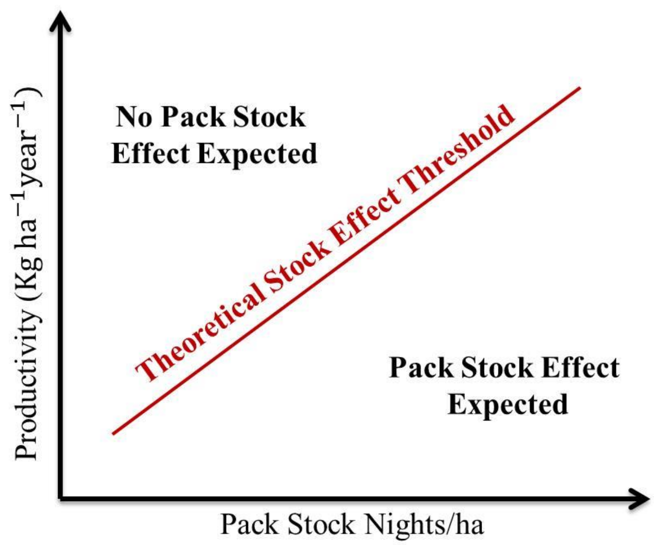

Figure 7. Conceptual model showing conditions that may lead to a detectable effect from stock use on bare ground. During years of low productivity the threshold of detectable stock effects is lower than years with high productivity.

Species Dissimilarity

The differences in species composition and abundance (species dissimilarity) between paired stock and non-stock meadows was highly variable showing no clear trend with stock use for any of the soil moisture classes (Figure 4). There is not enough replicate data across the various gradients of physical attributes to distinguish whether these lack of trends indicate no relationship between species composition and current stock use levels, or a relationship that is very context dependent. For example, some of the meadow pairs with the largest difference in species composition were those with relatively light stock use. These may represent meadow communities that are more sensitive than others to even light use, or they may simply reflect variation in environmental drivers other than stock use that could influence the plant community. The CART results suggest that the hydro-climatic and geospatial attributes of the meadow pair were often the best predictors of large differences between stock and non-stock meadows within a pair. Sampling more meadow pairs across a wider environmental gradient would help better explain variation in meadow response to stock use at given intensity levels. Grazing monitoring practices often focus on climax plant communities and seral trajectories of species composition (Dyksterhuis 1949, Weixelman et al. 1997). Our results suggest that simpler metrics of bare ground cover and spatial variability in community structure may be more sensitive indicators of stock use impacts than more costly and time intensive, traditional community comparisons.

Species Dispersion

Even though local-scale spatial variability in plant community structure (as species dispersion) showed a significant positive relationship with stock use within Wet areas of the meadows, no effect was found within either the Intermediate or Dry soil moisture classes. Based on initial field observations, I expected that increased species dispersion would be extended into the Intermediate soil moisture class because those areas tend to have higher species richness, and therefore a greater potential for spatial variability among the species present. The failure to detect changes in species dispersion within the Intermediate soil moisture class may be due to the resolution that was sampled. Intermediate soil moisture classes occupy a larger proportion of total meadows area compared to the Wet and Dry moisture classes. As a result this moisture class contains steep hydrologic gradients (Loheide & Booth 2011) with many different functional and hydrogeomorphic types of species (Weixelman et al. 2011), and strong biotic interactions, such as competition between high density species (del Moral 1983) adds to the dynamic properties of the plant community. The inherent natural variability within the Intermediate moisture class may be obscuring effects that are observable at finer spatial resolutions.

Despite no detection of overall changes in species composition and abundance, patterns of increased species dispersion within the Wet moisture class is a novel result and may be a useful metric for monitoring pack stock use. Local-scale spatial variability in plant community structure could be a more sensitive response to ecological stressors than mean shifts in species composition under certain conditions. Similar metrics of variability have been shown to be early warning signs of stress in other systems, for example grazing in arid environments (Kefi et al. 2007), and can have implications for ecosystem stability and transitioning states (Dakos et al. 2012). However, patterns of variability assessed as species dispersion have never been used in the context of transitioning plant communities, and it is not clear from the results of the current study that such a transition is occurring. Future studies that assess plant communities at a finer-scale resolution could help better understand the relationship between community variability, community stability and stressors within meadow systems. Our data imply species composition has not changed due to stock use within the Wet moisture class, and the pattern of increased species dispersion might be conditional on interactions with physical attributes that characterize the moisture class. Wet meadow areas remain saturated longer into the growing season and may be more susceptible to increased heterogeneity in microtopography from trampling, which could lead to increased variability in plant community structure (Sterling et al. 1984).

Conclusion

Meadow ecosystems are host to dynamic processes within the Sierra Nevada landscape. Meadows are routinely subjected to natural stressors such as seasonal flooding from snowmelt (Ratliff 1985), long-term decadal droughts (Graumlich 1993), and bioturbidation from small mammals (Laycock & Richardson 1975), and plant communities and environmental variables can vary greatly within and across meadows, watersheds, and latitudes. Using observational data alone, a statistically significant effect of pack stock use on meadow communities was observed by using a multi-scale approach that accounted for the environmental processes known to drive large natural variation in plant communities both among and within meadows. Landscape and regional scale environmental variables were addressed through multivariate pairing of non-stock meadows with use of remote sensing data. Within-meadow scale variability was addressed by stratifying the analysis within meadows across a soil moisture gradient – a dominant driver of plant community structure in these ecosystems (Allen-Diaz 1991). Variation in stock use was controlled for by actively sampling across a gradient of reported use and evaluating multiple metrics of stock use intensity. This approach allowed for direct comparison of stock and non-stock meadow communities while controlling for variation in both the environmental and anthropogenic drivers.

An important finding in this study was the relationship between local soil moisture regimes and where pack stock effects were detected. No effect was detected at the larger meadow spatial scale. This suggests that if landscape scale variables can be held constant, areas with dissimilar hydrologic characteristics (e.g., Dry and Wet moisture classes) may respond differently. Thus, future efforts for assessing potential impacts from anthropogenic stressors, like pack stock use, need to consider the dominant abiotic drivers across multiple scales with biological relevance for the particular system. In this way land managers may reach their goal of identifying ecological thresholds and maintaining ecosystem integrity in the face of ever-present anthropogenic stressors.

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Appendix I. Meadow Sampling Layout

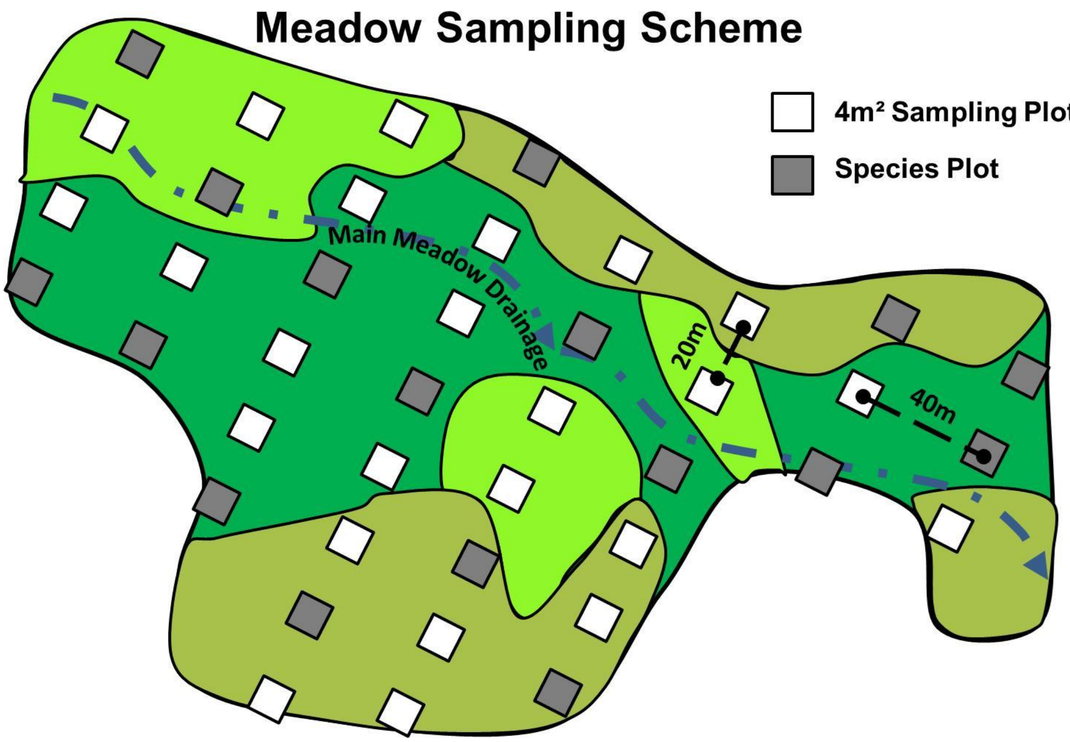

Figure AI-1. Meadow sampling scheme for 4m² sampling plots. Occular cover estimates for bare ground, vegetation, and litter were recored at every plot (White and Dark Gray). Occular cover estimates for all plant species were recoreded at every third plot (Dark Gray).

Appendix II. Complete Classification and Regression Tree (CART) results

Table AII-1. Classification and Regression Tree (CART) model contributions (%) of specific stock use and physical covariates. Individual models are indicated by Moisture Class and Response Variable combinations. Moisture Class: A = All moisture classes; D = Dry moisture class; I = Intermediate moisture class; W = Wet moisture Class. Response Variables: 1 = difference in bare ground; 2 = species dissimilarity; 3 = difference in species dispersion.

	Response Variables:	**1**	**1**	**1**	**1**	**2**	**2**	**2**	**2**	**3**	**3**	**3**	**3**
Independent Variables	**Moisture Class:**	**A**	**D**	**I**	**W**	**A**	**D**	**I**	**W**	**A**	**D**	**I**	**D**
Stock Use Metrics													
Mean Stock Nights 2004-2009		0	2	0	0	0	0	0	0	0	0	0	0
Max Stock Nights 2004-2009		0	0	0	0	0	0	0	0	0	0	0	0
Standard Deviation Stock Nights 2004-2009		0	0	0	0	0	0	0	0	0	0	0	78
Coefficient of Variation Stock Nights 2004-2009		0	0	22	0	0	0	0	0	0	0	9	0
Mean Stock Nights per Hectare 2004-2009		0	0	0	0	0	0	0	0	0	0	0	0
Max Stock Nights per Hectare 2004-2009		0	63	0	0	0	0	0	0	0	66	0	0
Differences Between Meadows In Each Pair													
Difference in Size (ha)		0	0	12	0	0	0	0	0	0	0	9	0
Difference in Elevation		0	0	0	0	0	0	0	0	22	0	0	0
Difference in Elevation Change to the Nearest Meadow		0	0	0	45	0	0	0	0	0	0	0	0
Difference in Shortest Path to the Nearest Meadow		9	0	0	0	0	0	0	0	0	0	0	0
Difference in the Distance to the Nearest Lake		0	0	0	0	0	0	0	0	0	10	0	0
Difference in the Distance to the Nearest Trail		0	4	0	0	0	0	0	0	0	0	0	0
Difference in Mean Monthly Precipitation		0	0	0	0	0	0	0	18	0	0	0	0
Difference in Average Annual Days >50% Snow Cover		0	0	0	0	41	21	25	0	0	0	0	0
Difference in Summer Average Annual NDVI		0	0	0	0	0	54	0	0	0	0	0	0
Difference in Summer Annual CV NDVI		39	0	0	0	0	0	0	0	0	0	0	0

Table AII-1 (continued).

Independent Variables	Response Variables: / Moisture Class:	1 A	1 D	1 I	1 W	2 A	2 D	2 I	2 W	3 A	3 D	3 I	3 D
Differences Between Meadows In Each Pair (continued)													
Difference in Summer Average Annual Tasseled Cap Wetness		0	0	0	0	0	0	0	0	0	0	0	0
Difference in Summer Annual CV Tasseled Cap Wetness		0	0	0	0	0	0	0	0	0	0	25	0
Difference in Summer Average Annual Tasseled Cap Greenness		0	0	0	0	0	0	0	0	0	0	0	0
Difference in Summer Annual CV Tasseled Cap Greenness		0	0	0	0	0	0	0	82	0	0	0	0
Difference Between Meadow Pairs													
Mean Size		0	20	57	0	0	0	0	0	0	0	0	0
Mean Elevation		0	0	0	0	0	0	0	0	0	24	0	0
Mean Elevation Change to the Nearest Meadow		0	0	0	0	0	0	0	0	0	0	0	0
Mean Shortest Path to the Nearest Meadow		15	0	0	32	0	0	0	0	8	0	0	0
Mean Distance to the Nearest Lake		0	0	0	0	0	0	0	0	0	0	58	0
Mean Distance to the Nearest Trail		0	0	9	0	0	0	11	0	0	0	0	16
Mean Monthly Precipitation		0	10	0	0	59	0	64	0	0	0	0	0
Mean Annual Days >50% Snow Cover		37	0	0	0	0	0	0	0	0	0	0	0
Mean Late Summer Average Annual NDVI		0	0	0	0	0	0	0	0	70	0	0	5
Mean Late Summer Annual CV NDVI		0	0	0	0	0	0	0	0	0	0	0	0
Mean Late Summer Average Annual Tasseled Cap Wetness		0	0	0	23	0	0	0	8	0	0	0	0
Mean Late Summer Annual CV Tasseled Cap Wetness		0	0	0	0	0	25	0	0	0	0	0	0
Mean Late Summer Average Annual Tasseled Cap Greenness		0	0	0	0	0	0	0	0	0	0	0	0
Mean Late Summer Annual CV Tasseled Cap Greenness		0	0	0	0	0	0	0	0	0	0	0	0

Appendix III. Mean values for stock and non-stock bare ground

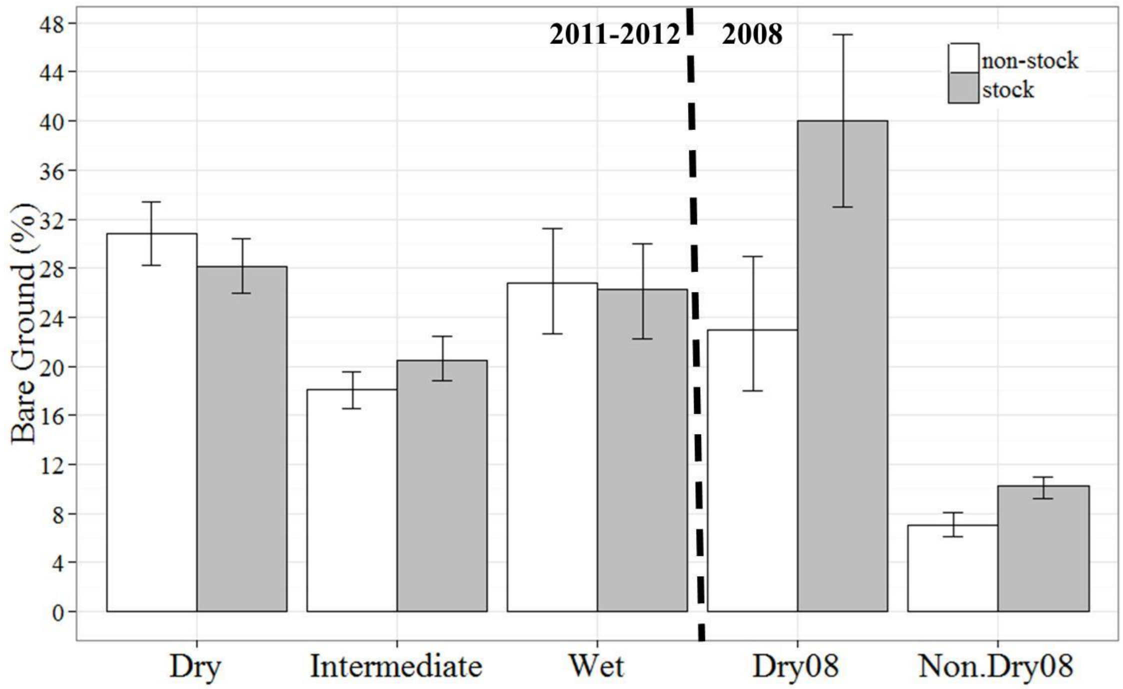

Figure AIII-1. Mean bare ground estimates (+/– standard error) for Yosemite National Park from the current study (2011-2012) and for 2008 as reported in Ballenger et al. (2010) . For the current study estimates are reported for individual soil moisture classes. For Ballenger et al. (2010) estimates are reported for *Carex filifolia* communities (Dry08) and non-*Carex filifolia* communities (Non.Dry08).