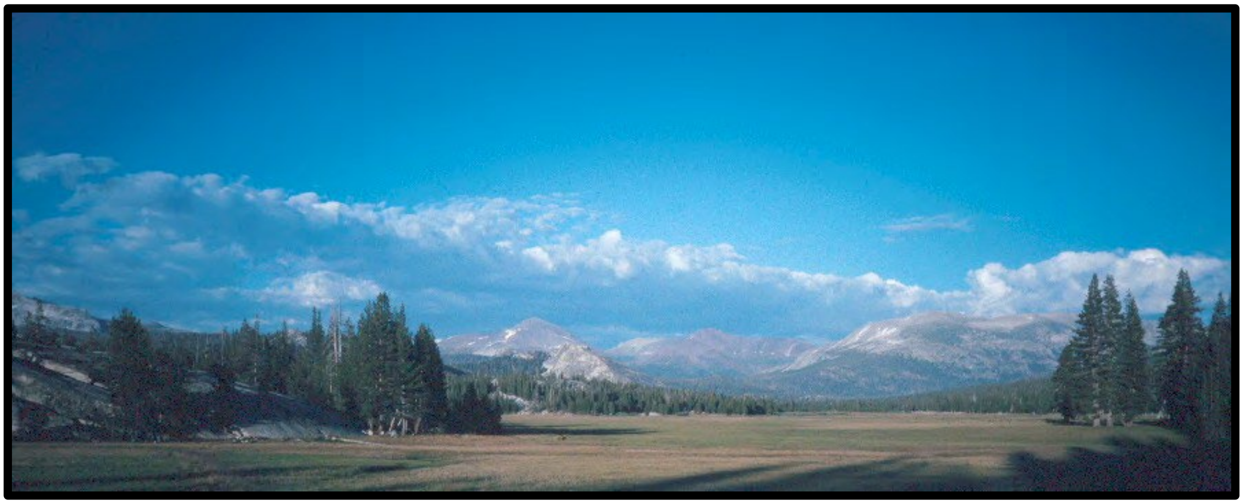
Effects of experimental trampling addition and reduction on vegetation, soils, and invertebrates and assessment of current conditions in Tuolumne Meadows



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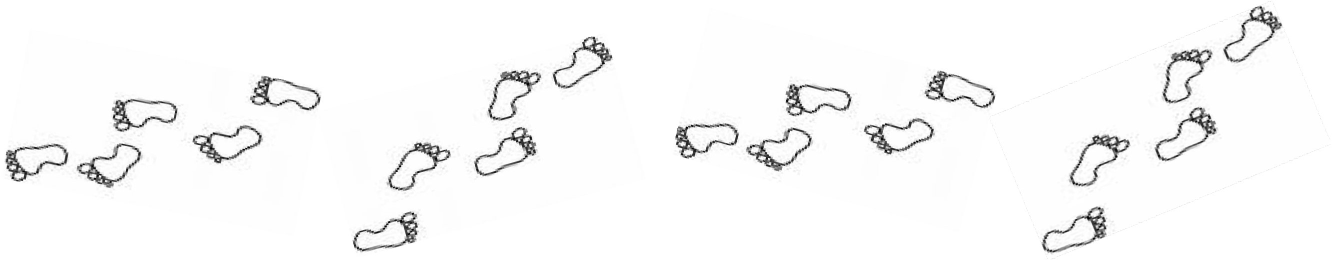


"[No experience] will be remembered with keener delight than the days spent sauntering on the broad velvet lawns by the river . . ."

John Muir, The Yosemite, 1912
reflecting upon Tuolumne Meadows

Summary

Tuolumne Meadows has a long history of heavy trampling, grazing, and other usage. This work seeks to answer the following questions: 1) Are the Meadows still sensitive to trampling pressure despite previous long-term impact? 2) Will meadow habitat recover quickly if trampling pressure is lessened? 3) What is the current ecological condition of heavily used areas of the Meadows in comparison with areas of lesser use? We addressed these questions with two parallel, but independent, manipulative experiments, one adding trampling pressure and the other experiment eliminating trampling, and one observational study comparing heavily and moderately used areas. Each of the two experiments included both experimental and control plots that were sampled for vegetation, soils, and invertebrates before, after, and for some metrics, during the manipulations. Both core experiments were conducted at the height of the 2006 growing season and were analyzed as 1x2 randomized block ANOVAs with repeated measures. Continued recovery, as indicated by a subset of vegetation and soil metrics, was also assessed on the exclosure plots

during the following year (2007) using the same analyses. The observational study compared the control plots from the two experiments, and analysis was via one-way repeated measures ANOVAs.

We established ten trampling addition replicates in areas of the meadow that normally receive moderate usage. We wished to have common vegetation assemblages represented among the replicates, so we used a stratified random approach to select multiple *Carex filifolia*, *Ptilagrostis kingii*, *Calamagrostis muiriana*, and *Oreostemma alpigenus*-dominated sites for inclusion as replicates. Trampling pressure was applied by walking back and forth over each "trampling lane" replicate.

We placed the ten experimental units for the exclosure experiment in heavily used portions of the Meadows. Experimental exclosure plots were 2x2m and were constructed with 40cm long, 5mm diameter dowels and nylon cord. The dowels were intentionally flimsy, so as to break rather than trip visitors or entangle animals. The light-duty materials also rendered the plots visually unobtrusive.

Vegetation and physical response variables sampled on each plot included standing crop, canopy height, litter depth, gross percent cover estimates, percent cover by common plant species, plant species richness, soil penetration pressure, and soil moisture. We sampled fauna with a vacuum net apparatus, and response variables included total, order, and family abundances, as well as species and family richness.

Although this study was primarily an ecological assessment of trampling impact and recovery, we also recorded data on number and location of visitors. We emphasized several areas of heavy usage.

Trampling addition resulted in rapid and severe impacts to most measured characteristics of meadow habitat, including vegetation, soils, and fauna. Further, trampling caused degradation of habitat across all plant assemblages in an almost equal fashion.

The exclosures were effective at modifying visitor behavior but produced only minimal effects on habitat and fauna over the two growing seasons of study. Effects were more substantial in late season, after vegetation was senescent. Late-season exclosures had more standing brown vegetation, and less bare ground, than the trampled control plots.

The observational study found that meadow habitat subject to the greatest amount of foot traffic demonstrated strikingly poorer ecological condition relative to the less trammeled portions of the Meadows. In particular, a massive loss of trophic diversity was apparent in the heavily trampled areas, as only a remnant of the typical subalpine meadow fauna was present on these sampling sites. The deterioration of habitat quality in heavily used areas within the growing season is also of concern.

Daily visitation patterns approximated a normal distribution with the apex of usage at mid-day. Highest usage was in the meadow habitat near the Soda Springs trailhead.

At the outset of the study, we thought that the long history of heavy usage in Tuolumne Meadows might have left highly resistant assemblages and that addition plots could be slow to respond to trampling pressure. However, impact was immediate and severe. The meadow environment, including higher trophic levels, is clearly still very sensitive to additional impact, and the threshold for impact appears to be remarkably low, as plots showed negative effects of trampling after only one or two weeks of added trampling pressure. This initial first year of study sought to determine general susceptibility to trampling by establishing a coarse threshold for impact. The actual threshold for damage is clearly much lower than the levels of disturbance applied in this first year, and further work will be needed to identify minimum levels of trampling that are likely to cause impact.

Comparisons across vegetation assemblages indicated remarkable consistency of trampling effect. We cannot recommend special treatment for some assemblages and less for others. Instead, there is substantial evidence that all common vegetation types are very sensitive to trampling.

The plots used in our 2006 trampling additions will recover, at some unknown rate, regardless of whether or not follow-up assessment is done. This information will be lost if an assessment is not conducted through the following growing seasons. We advocate follow-up work in 2009 and 2010, in order to gain a precise understanding of how much time is required for recovery from a *known* level of moderate trampling pressure.

We initially thought that it would be difficult to exclude visitors from heavily-used areas, but our low profile exclosures were very effective. This support from visitors is encouraging, and our success suggests that minimal, unobtrusive techniques can be used to virtually eliminate access to recovering habitat.

The addition experiment indicated that the subalpine habitat in Tuolumne Meadows is still exquisitely sensitive to trampling impact, and the exclosure experiment indicated that, once severely damaged, habitat is slow to recover. The late season loss of standing brown vegetation, and possible wind transport of litter away from trampled areas, suggests that a positive feedback mechanism may exist, ultimately causing trampled areas to suffer further degradation. We advocate longer exclosure experiments to determine whether or not exclosures can lead to significant recovery over a three-five year period.

The Soda Springs trailhead area appears to receive the greatest use of any meadow habitat in Tuolumne Meadows, and the observational study demonstrated the impacts to this area. It is unfortunate that visitors encounter such degraded habitat at what will in many cases be their only stop away from the car in the Meadows. Interventions to appropriately channel visitors and protect habitat may be advisable for this area as well as the meadow across Tioga Road from the store.

Introduction

Park visitors are urged to "take nothing but photos, leave nothing but footprints", but are those footprints always innocuous? Trampling, i.e., walking upon a natural substrate, can inadvertently reduce both plant and animal populations (e.g., Woodland and Hooper 1977, Cole 1995, Eckrich and Holmquist 2000). Tuolumne Meadows, with its open expanses and nearby Tuolumne River, is a treasure that beckons visitors from Highway 120. Many motorists stop their vehicles to stroll across the meadow to the river, and visitors can generally be observed in all portions of the meadow. Is this intense usage capable of directly deteriorating the condition of Tuolumne Meadows? Human trampling could also, via soil compaction, contribute to the lodgepole invasion so apparent in the Meadows (Vale and Vale 1994; Cooper et al. 2006).

Both flora and fauna in the Meadows may have been affected by trampling. Although there clearly is significant ongoing trampling by visitors at Tuolumne, the meadows also have a long history of grazing and associated trampling, particularly by sheep (Le Conte 1875; O'Neill 1984; Cooper et al. 2006). The plant and animal assemblages currently present may be resistant to further trampling damage, and our work seeks to determine 1) if the Meadows are still sensitive to trampling pressure, 2) if this meadow habitat will recover quickly if trampling pressure is lessened, and 3) if heavily used portions of the meadow are in worse condition than other areas. We addressed these questions with two parallel manipulative experiments, one adding trampling pressure and the other experiment eliminating trampling, and one observational comparison of portions of the meadow with varying levels of usage.

Rapid degradation of plant and/or animal assemblages in response to experimental increases of trampling pressure would indicate continued vulnerability of this important and highly visible Park resource. Rapid recovery of plant and animal populations following reduction of trampling on experimental plots would be hopeful, because this result would indicate that widespread recovery would be possible via modification of visitor behavior. This study also identifies unobtrusive methods of reducing visitor trampling and seeks to determine if specific areas of the Meadows could benefit from further protection.

Methods

Each of the two manipulations included both experimental and control plots that were sampled for vegetation, soil characteristics, and invertebrates both before and after the manipulations, i.e., a before-after-control-experimental (BACI; e.g., Green 1979) design. Some response variables were obtained more frequently as well (see below).

We established ten trampling addition plots, each with a paired control, and ten trampling exclusion plots, each with a paired control. Three of the reduction plots also had an associated exclosure control (see below). There were thus a total of 43 plots established in Tuolumne Meadows (Table 1; see Holmquist and Schmidt-Gengenbach 2006 for an overview of invertebrate and plant assemblages in the Meadows). There were 86 full sampling events and another 86 partial sampling events. Both experiments were 1x2 randomized block designs with repeated measures. The observational study compared the two sets of control plots, i.e., the addition controls in moderately impacted portions of the meadow and the exclosure controls in heavily used portions of the meadow. The two experiments address causation, whereas the comparison of the two sets of control plots documents current conditions in a comparative fashion, thus a mensurative "experiment," as per Hurlbert (1984).

Table 1. Sampling site numbers and UTM coordinates (WGS84, Zone 11) for trampling addition and reduction plots. Experimental plot locations are given. Associated controls are within 5m of each experimental plot.

Trampling addition plots

1-2-2-1-1	292537mE	4194577mN
1-2-2-1-2	292531mE	4194542mN
1-2-2-1-3	291783mE	4194560mN
1-2-2-1-4	291822mE	4194534mN
1-2-2-1-5	291726mE	4194411mN
1-2-2-1-6	291785mE	4194455mN
1-2-2-1-7	292421mE	4194639mN
1-2-2-1-8	291659mE	4194318mN
1-2-2-1-9	291722mE	4194487mN
1-2-2-1-10	291741mE	4194533mN

Trampling reduction plots

1-2-4-1-1	292591mE	4194531mN
1-2-4-1-2	292584mE	4194534mN
1-2-4-1-3	291579mE	4194269mN
1-2-4-1-4	291569mE	4194330mN
1-2-4-1-5	291515mE	4194276mN
1-2-4-1-6	291554mE	4194317mN
1-2-4-1-7	292598mE	4194453mN
1-2-4-1-8	292603mE	4194457mN
1-2-4-1-9	290993mE	4194465mN
1-2-4-1-10	290973mE	4194491mN

Trampling addition experiment

The level of applied trampling pressure was based on literature values and observations of visitor use patterns in Tuolumne Meadows. Cole and Bayfield (1993) report that 500 passes is often sufficient to cause a 50% reduction in cover. However, this level of cover loss may not be obtained until 1,000 passes have been applied, and Cole and Bayfield (1993) recommend increasing initial trampling pressure accordingly if a plant assemblage is likely to be resistant to disturbance. Based upon the long history of trampling and/or grazing in Tuolumne Meadows, we decided to use 800 passes over the growing season in this first year of study, because we believed that this level of trampling was likely to identify a coarse threshold for damage across most assemblage types.

We applied trampling pressure during the apex of the growing season as recommended by Cole and Bayfield (1993). We trampled plots over a six-week period, from 23 June 2006 through 4 Aug 2006.

Temporal concentration of trampling appears to cause no more damage than trampling distributed evenly in time (Bayfield 1979, Cole 1985, Cole and Bayfield 1993). However, we sought to reproduce visitor trampling pressure as closely as possible (as per Eckrich and Holmquist 2000), so we applied 125 passes per addition plot over the course of each of the six weeks of study.

We established ten trampling addition replicates in areas of the meadow that normally receive light to moderate usage (Table 1). We wished to have common vegetation assemblages represented among the replicates, so we used a stratified random approach to select three *Carex filifolia*, three *Ptilagrostis kingii*, two *Calamagrostis muiriana*, and two *Oreostemma alpigenus*-dominated sites (Fig. 1; see also Ratliff 1982, 1985, Cooper et al.. 2006, Holmquist and Schmidt-Gengenbach 2006). Paired trampling lanes and associated controls were co-located with no more than 5m of separation so as to minimize inter-plot differences (Fig. 2). We wished to minimize impact, so we established

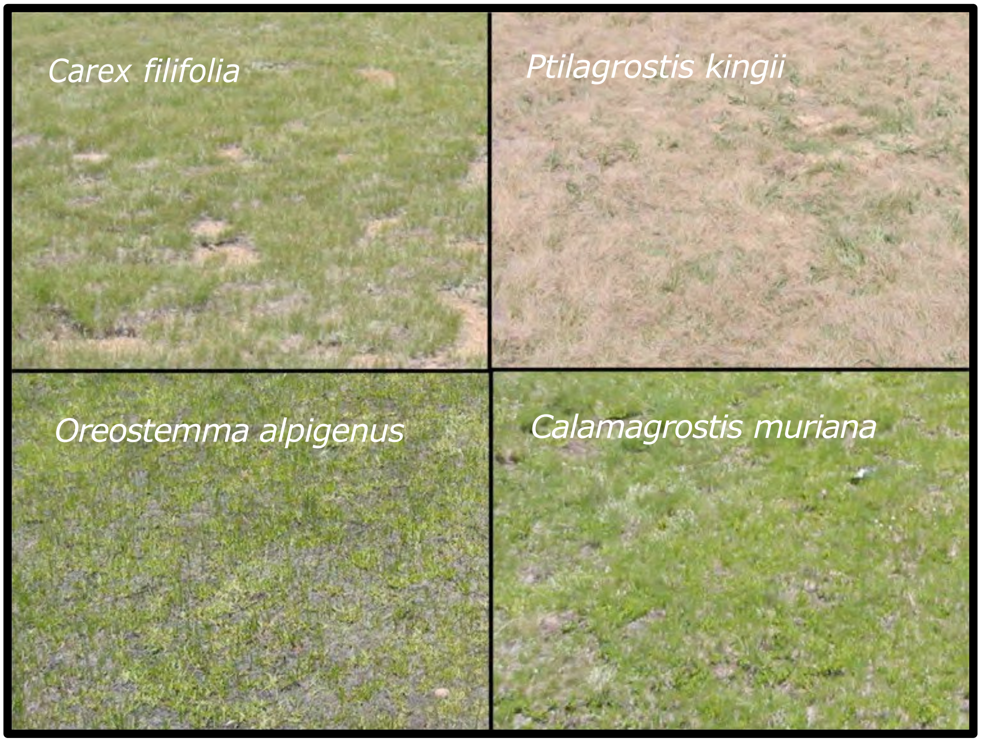


Fig. 1 . Common vegetation types used in the study. Note also the coarse, exposed, and low organic content soil associated with *Carex filifolia* (Cooper et al. 2006) and *Polygonum bistortoides* associated with *Ptilagrostis kingii*.

Fig. 2 . Trampling in progress on trampling addition plot. Note small artificial "lodgepoles" at each end of the trampling plot and bracketing the control plot (visible in foreground in front of sampling apparatus).

lanes that were only 0.5m wide (Fig. 2), just over the minimum width of 0.4m recommended by Cole and Bayfield (1993). Lanes were 3m in length and oriented randomly. We wished to mark plots in an unobtrusive way so as not to impair the visual experience of visitors and to avoid artifacts caused by attracting visitors to the plots. Each lane was marked at each end with 15cm tall plastic "lodgepole pines" constructed from Christmas garland material (Fig. 2). We have had excellent success with this method as part of other projects in Tuolumne Meadows (Holmquist and Schmidt-Gengenbach 2006). A 0.25x0.25m subplot was centered in each trampling lane and marked by pounding nails into the four corners with the heads flush with the substrate.

The nails served as a backup marking system for the entire plot, in case the “lodgepoles” were lost or removed, because the nails could be located with a metal detector. The nails also served to more precisely mark the location of the sampling area to be used throughout the study. A second 0.25x0.25m plot was similarly identified and marked for use with the controls (Fig. 2).

Our trampling technique was consistent with the standardized methods proposed by Cole and Bayfield (1993). We used lightly-lugged boots on tramplers of 55 and 75kg (Fig. 2). Each one-way walk down a trampling lane was counted as a single pass, and we used three start points at each end of the lanes so as to ensure good coverage of the entire lane (see also Eckrich and Holmquist 2000). Turns create additional damage, and therefore all turns were made outside of the sampling area. After trampling damage became visually apparent, the lodgepole markers were removed from the addition plots, because plots could then be located without markers. Lodgepole markers were removed from the control plots in August 2006. However, the nails were left in place in anticipation of additional years of study at these locations.

Exclosure experiment

We placed the ten experimental units for the exclosure experiment in heavily used portions of the Meadows: north of (across the highway from) the store, near the Soda Springs trailhead, and north of (across the highway from) the visitor center at a pullout. Experimental exclosure plots were 2x2m, and paired controls were established in the same manner as in the trampling addition experiment. We also established exclosure controls with three of the experimental units to detect artifacts associated with the exclosures.

The 2x2m exclosures were constructed with 40cm long, 5mm diameter dowels and nylon cord (Fig. 3). We affixed 8x15cm labels at ground level that explained the purpose of the exclosures. The dowels were intentionally flimsy, so as to break rather than potentially trip visitors or entangle animals. The light-duty materials also rendered the plots visually unobtrusive (Fig. 3)

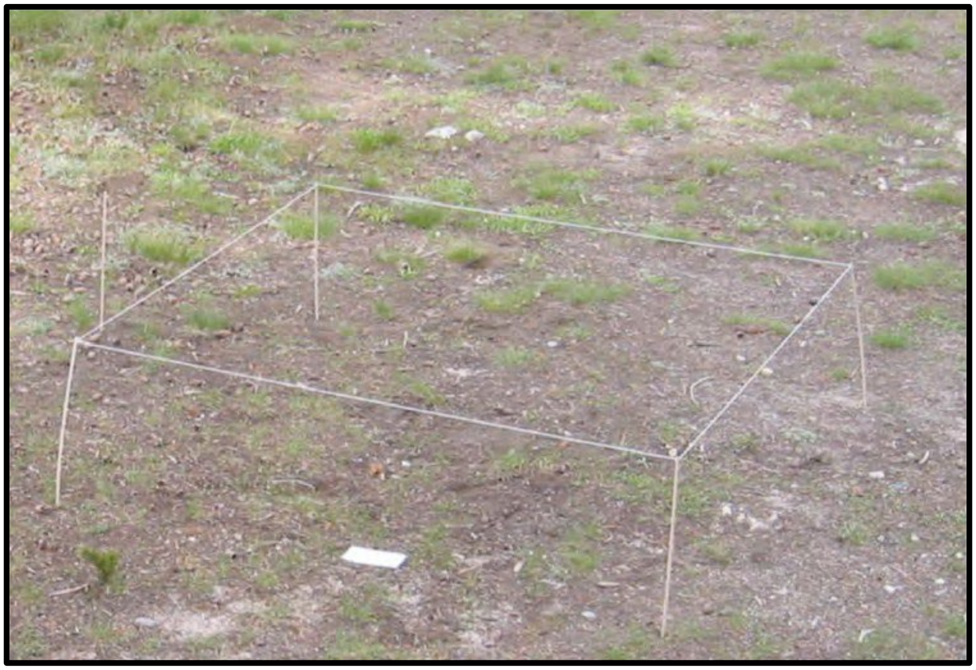


Fig. 3. Trampling exclosure plot (2x2m).

compared to more robust post and rail or post and rope approaches. A repeat sampling plot was located in the center of each exclosure and was marked with nails.

The exclosure controls, where constructed, were located within 5m of the exclosure plots and control plots. These exclosure controls consisted of dowels only, without nylon cord. The sampling plot was again marked with nails. Structure can produce artifacts, such as providing bird perches, which can result in altered levels of predation or nutrient addition via bird defecation (Holmquist et al. 1989, Powell et al. 1991). The exclosure controls were placed to detect gross artifacts of this nature.

Exclosures and exclosure controls were left in place after the six week study period (until 6 October 2006), in order to extend the period of trampling exclosure for assessment the following year. Lodgepole markers from the control plots were removed in August 2006, though the nails were again left in place in anticipation of additional years of study at these locations. Plots were reestablished on 18 May 2007 and maintained until 25 October 2007.

Faunal sampling

We sampled prior to either marking or trampling the plots. Fauna were sampled first, so that animals would not flee, followed by vegetation and soils.

We collected fauna with a vacuum net apparatus (Fig. 4). Vacuums with nets inserted in the intake tube generally offer an improvement in efficiency over other methods of sampling invertebrates in vegetation, and this technique has been used in a variety of studies (e.g., Richmond and Graham 1969, Hand 1986, Macleod et al. 1994), including at least one Park Service monitoring program (Fellers and Drost 1991) and several Sierra Nevada Network projects, including work evaluating effects of trails on montane and subalpine invertebrates (Holmquist and Schmidt-Gengenbach 2004, 2005, 2006). Vacuums are more efficient than visual censuses (Arnold et al. 1973) or sweep netting (e.g., Dietrick et al. 1960, Arnold et al. 1973, Buffington and Redak 1998, Holmquist and Schmidt-Gengenbach 2006), especially for ground dwellers (New 1998, Holmquist and Schmidt-Gengenbach 2006), because sweep netting underestimates ground-dwelling invertebrates (Whittaker 1952,

Fig. 4. Tossing the netted quadrat and vacuuming fauna from vegetation through the elasticized aperture in the net. L. Greene photos.

Hughes 1955, Holmquist and Schmidt-Gengenbach 2006). This increased efficiency incorporates both abundance and species richness (Buffington and Redak 1998; Holmquist and Schmidt-Gengenbach 2006). Vacuums are also superior to pitfall trapping, which not surprisingly is a poor technique for capturing flying taxa (Holmquist and Schmidt-Gengenbach 2005). Vacuums also cause less damage to invertebrates than sweep netting (Callahan et al. 1966) and are particularly efficient at removing animals in litter and lower vegetation (Stewart and Wright 1995, Holmquist and Schmidt-Gengenbach 2006). Vacuum sampling has been found to be most efficient when used with some form of enclosure box which is placed prior to suctioning (Henderson and Whittaker 1977, Hower and Ferguson 1972, Harper and Guynn 1998), although enclosures are often not used.

Despite the general efficiency of vacuum sampling, this method has not worked well in capturing rapidly-moving insects (Powell et al. 1996). The operator creates disturbance, and even if an enclosure box is used, flying and other vagile insects will flee the area before the enclosure is placed. In order to capture motile fauna and sample a known area of habitat, Holmquist and Schmidt-Gengenbach (2002) constructed a 0.5 m^2 steel quadrat with a conical mesh covering (Fig. 4). The mesh cone has an elasticized hole at the apex through which a vacuum intake tube can be inserted. This quadrat is thrown toward the target area from a distance and staked in place to form a seal with the substrate. The vacuum intake is then inserted through the mesh aperture for sampling (Fig. 4). This technique has been tested and shown to be both very efficient as well as particularly effective at capturing motile taxa (Holmquist and Schmidt-Gengenbach 2006).

We used a Craftsman 320 km/h gasoline vacuum modified with a nylon "no-see-um" mesh (0.25mm) collecting chamber inserted in the intake tube in conjunction with the netted quadrat (Fig. 4). After staking the thrown quadrat, we made multiple passes through the vegetation with the vacuum intake from different orientations over a four-minute period. The intake was then extracted from the quadrat, the integral mesh collecting bag was removed from the intake tube, and the fauna and litter were transferred to a re-sealable plastic bag and placed on ice or frozen as soon as possible.

After faunal sampling, plots were established. We sampled fauna again at the end of the six-week study 2006 period. We did not sample fauna in 2007.

Fauna were sorted and identified to family in the laboratory. Family-level taxonomy provides a good cost-benefit ratio, and there has been good success in using family-level identifications in monitoring and research programs (e.g. Hilsenhoff 1988). Response variables included total, order, and family abundances, as well as species and family richness.

Vegetation and physical parameters

Response variables sampled on each plot during 2006 included the following: gram dry mass of standing crop, canopy height, litter depth, gross percent cover estimates, percent cover by common plant species, soil penetration pressure, and soil moisture. Measures were taken before and after the 2006 experiments with the exceptions of canopy height, litter depth, and penetration pressure (a measure of soil compaction) which were measured every two weeks on the addition plots. In 2007, we recorded canopy height, litter depth, gross percent cover estimates, and soil penetration pressure on all plots of the exclosure experiment before and after the experiment as well in October 2007. A photo of each plot was also taken for reference before and after the experiment each year, plus in October 2007.

After each netted quadrat was thrown and sampled, we randomly established the following: two 12.5 cm^2 standing crop quadrats at each of two outside corners of the faunal sampling device and a 50 cm^2 quadrat for characterizing the vegetation assemblage at a third outside corner.

Standing crop and litter were clipped/removed from the two 12.5 cm quadrats and dried at 90^o C for 24 hours prior to weighing. Percent cover by plant genus or species was recorded for common vascular plant types in the 50 cm^2 quadrat. Litter depth was measured with a 1mm diameter spring steel wire.

We recorded soil penetration pressure (kg/cm^2) at all four corners of the netted quadrat with a Lang penetrometer with a 0.18 cm^2 tip. We determined soil moisture via gravimetrics as per American Society for Testing and Materials standards (1992). Each soil sample was composed of 40cc of soil derived in equal parts from surface material at each of the four corners of the fauna plot. Samples were dried at 90° C for 24 hours, and percent water content was determined as follows: *Percent water content=*

(1-((Mass of dry specimen)/(Mass of wet specimen))) X 100

Visitation patterns

Although this study was primarily directed towards an ecological assessment of trampling impact and recovery, we noted number and location of visitors whenever we were in the Meadows. In particular, we delineated three meadow areas of concern: north of (across the highway from) the store, the untrailed meadow habitat near the Soda Springs trailhead, and habitat adjoining the Soda Springs Trail between the trailhead and the Tuolumne River bridge. Counts of visitors were made at half-hour intervals and did not include persons on either maintained or social trails.

Analysis

Both experiments were analyzed as 1x2 randomized block ANOVAs with repeated measures. Treatments were control versus experimental in both experiments, blocks were pairs of control and experimental plots, and there were either two or four repeated measures in each analysis, depending on the metric. Faunal metrics were log + 1 transformed prior to analysis in order to meet assumptions of normality and homogeneity of variance. The three exclosure controls were considered separately. Analyses were performed in SYSTAT using general linear model procedures. The observational study comparing the two sets of controls was analyzed similarly but with a one-way repeated measures ANOVA. We also used sign and one-way paired t-tests for some vegetation, faunal, and visitation analyses.

Results

Addition experiment

In general, trampling degraded habitat quality (Fig. 5). Canopy height on the control and addition plots diverged rapidly, and throughout, the season, increasing on the control plots but decreasing on the experimental plots (Fig. 6; TREATMENTxTIME p = 0.00058). Similarly, percent green cover increased on the control plots, but decreased on the addition plots (Fig. 7; TREATMENTxTIME p= 0.0030). Percent bare ground doubled on the addition plots, while remaining unchanged on the controls (Fig. 8; TREATMENTxTIME p = 0.0029).

Fig. 5. Trampling damage on *Ptilagrostis kingii* plot. Note "lodgepole" markers.

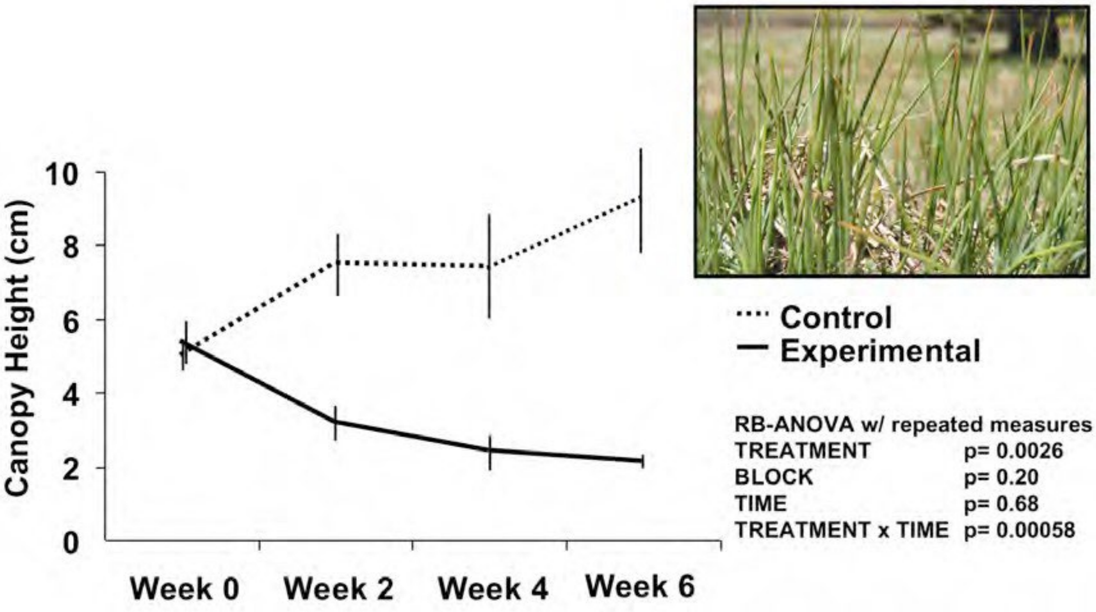


Fig. 6. Mean (SE) canopy height on control and addition plots during experiment. BLOCK represents plot effects. n= 10.

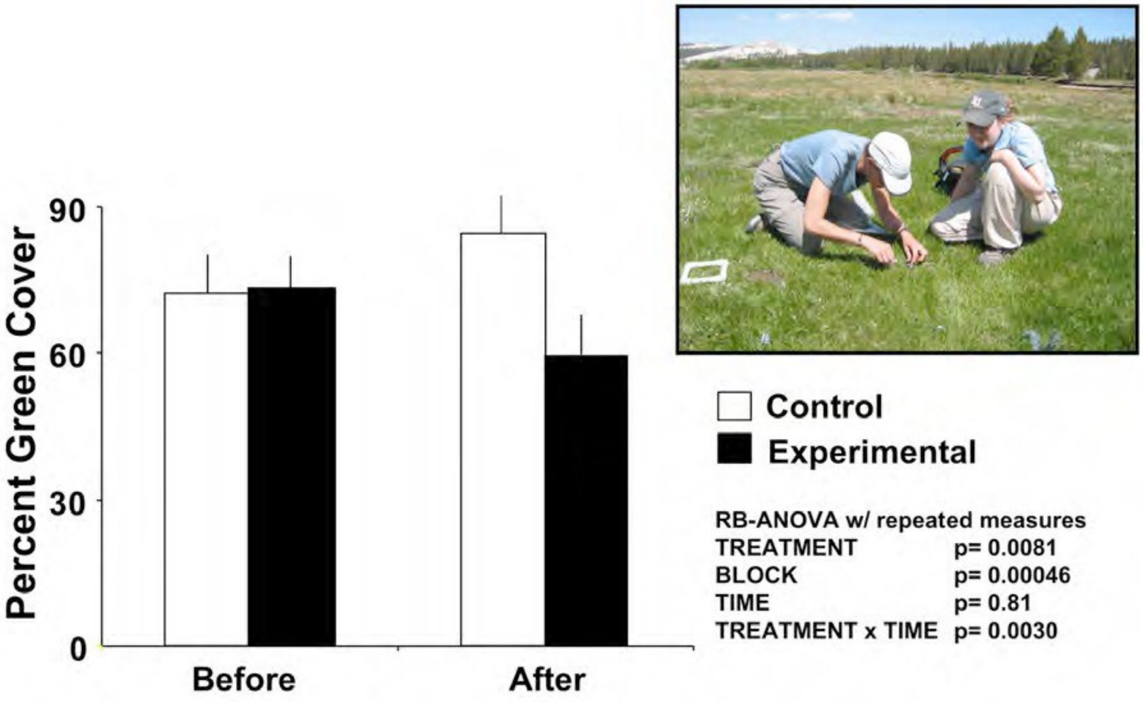


Fig. 7. Mean (SE) percent green cover on control and addition plots before and after experiment. BLOCK represents plot effects. n= 10.

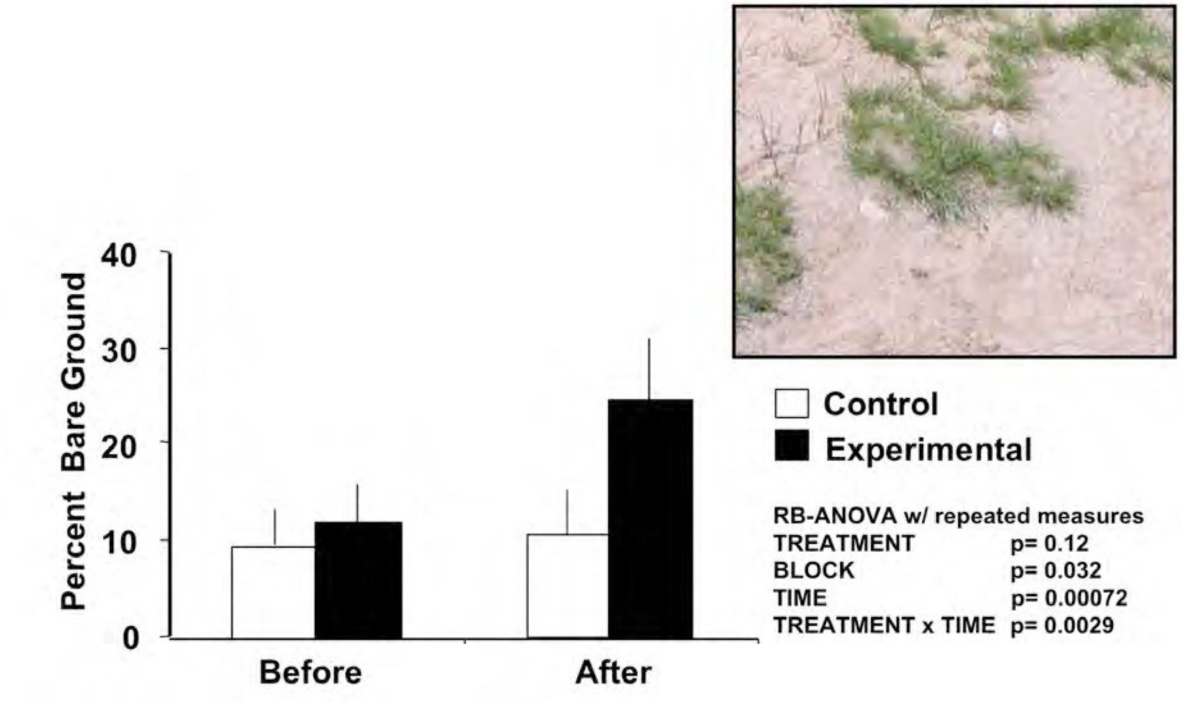


Fig. 8. Mean (SE) percent bare ground on control and addition plots before and after experiment. BLOCK represents plot effects. n= 10.

Standing crop increased on the controls but did not increase on the additions, although the interaction term was not significant (Fig. 9; TREATMENTxTIME p = 0.11). However, there was a significant TREATMENT term (p= 0.023) despite almost identical standing crops at the start of the experiment (Fig. 9). The only vegetation type with measurable litter depth was *Ptilagrostis*. These three replicates were too few for statistical tests, but mean litter depth on addition plots quickly fell below levels seen on the control plots (Fig. 10). Penetration pressure increased through the season on both control and addition plots (Fig. 11; TIME p< 0.00001). However, the rate of increase was much greater on the

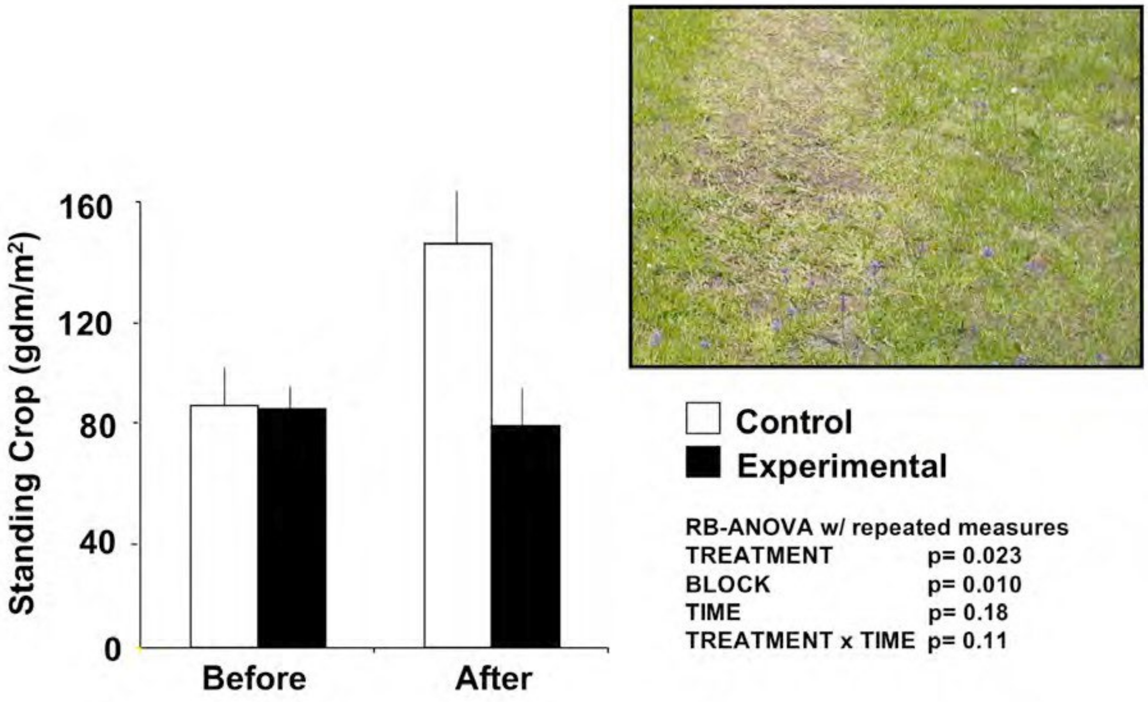


Fig. 9 . Mean (SE) standing crop on control and addition plots before and after experiment. BLOCK represents plot effects. n= 10. Inset photo shows habitat degradation in the *Oreostemma*-dominated assemblage.

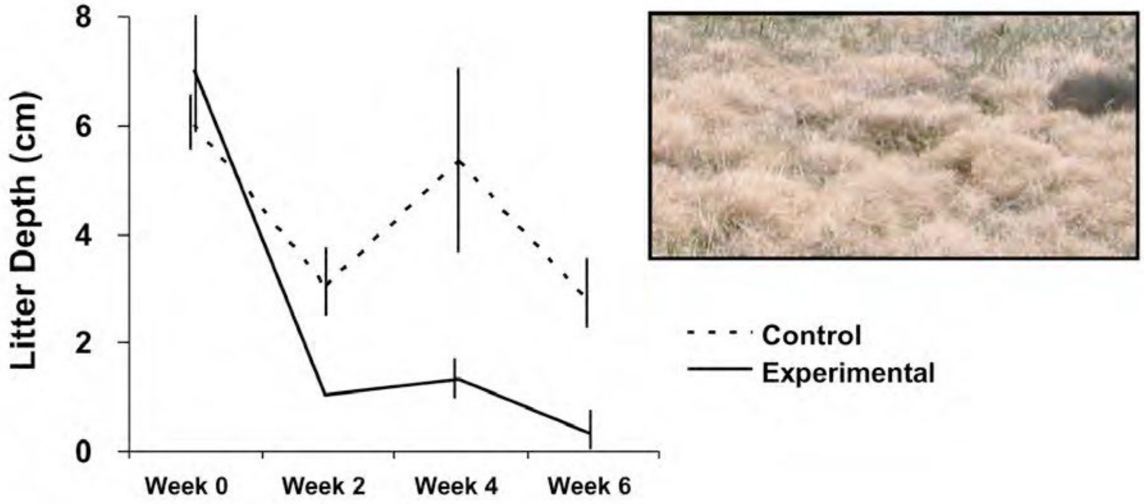


Fig. 10 . Mean (SE) litter depth on control and addition *Ptilagrostis* plots during experiment. BLOCK represents plot effects. n= 3.

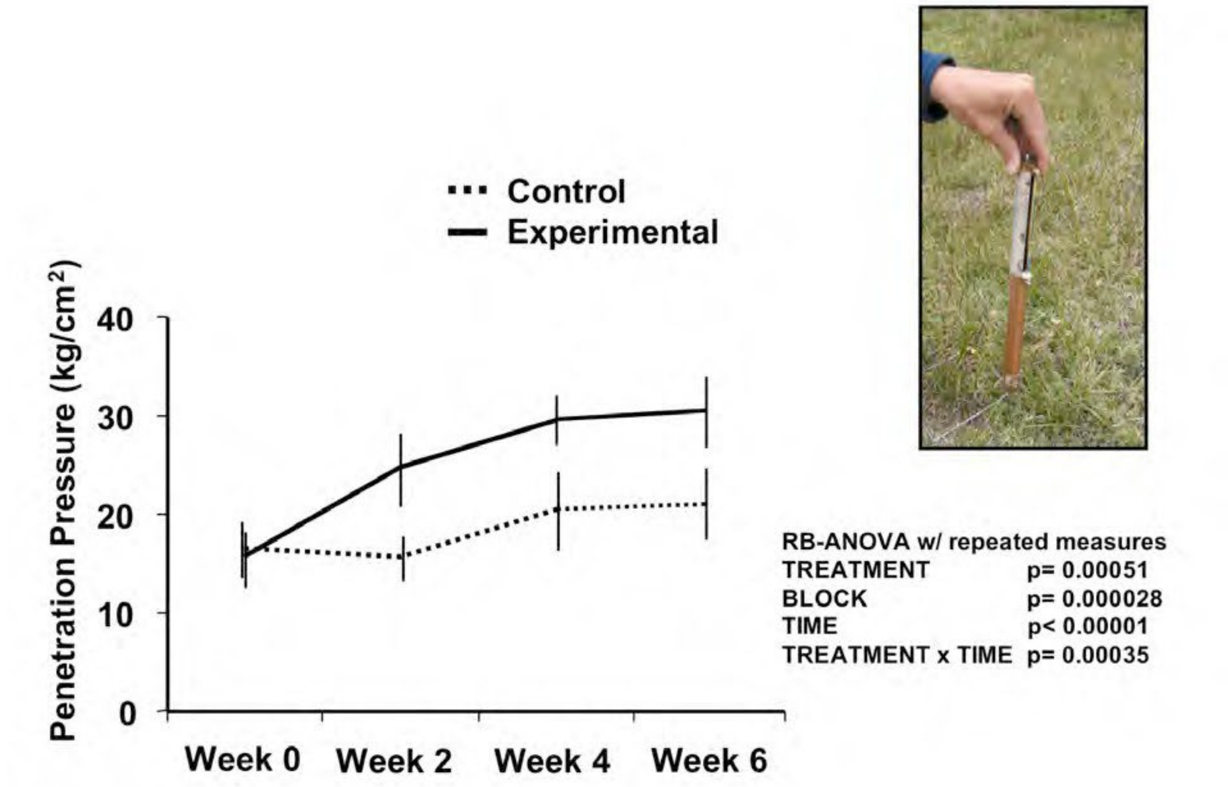


Fig. 11. Mean (SE) penetration pressure on control and addition plots during experiment. BLOCK represents plot effects. n= 10.

addition plots, doubling over the season (Fig. 11; TREATMENTxTIME p = 0.00035). Soil moisture decreased on both control and addition plots throughout the summer (Fig. 12; TIME p< 0.000001), but the manipulation did not cause added drying on the addition plots (Fig. 12; TREATMENTxTIME p = 0.85).

We stratified plot locations by vegetation type in order to include all major Tuolumne assemblages in the experiment and thus expand the generality

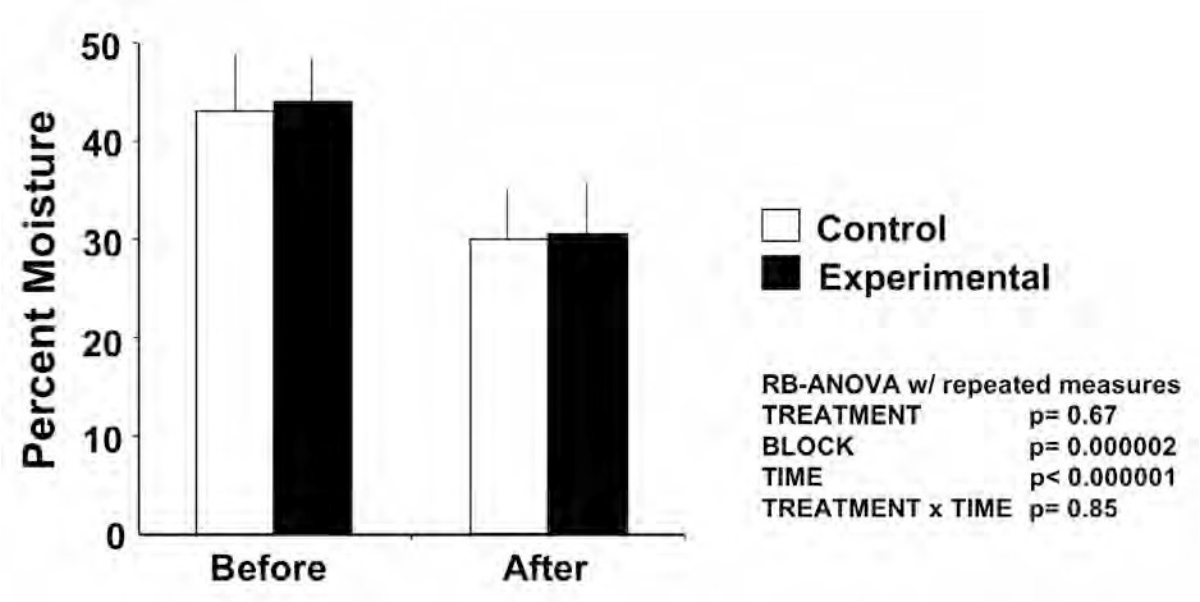


Fig. 12. Mean (SE) percent soil moisture on control and addition plots before and after experiment. BLOCK represents plot effects. n= 10.

of our results. Although we did not design the experiment to detect experimental effects as a function of vegetation type, it is possible to examine these data for trends despite the small sample sizes, i.e., two or three replicates per vegetation type.

Canopy height on addition plots rapidly fell below levels seen on control plots across all vegetation types (Fig. 13). Canopy heights of all assemblages were about 5cm at the start of the experiment, but fell to about 3cm on addition plots. Control plots maintained a roughly 5cm canopy height across taxa, except in *Ptilagrostis*, where the canopy on controls grew to 20cm (Fig. 13).

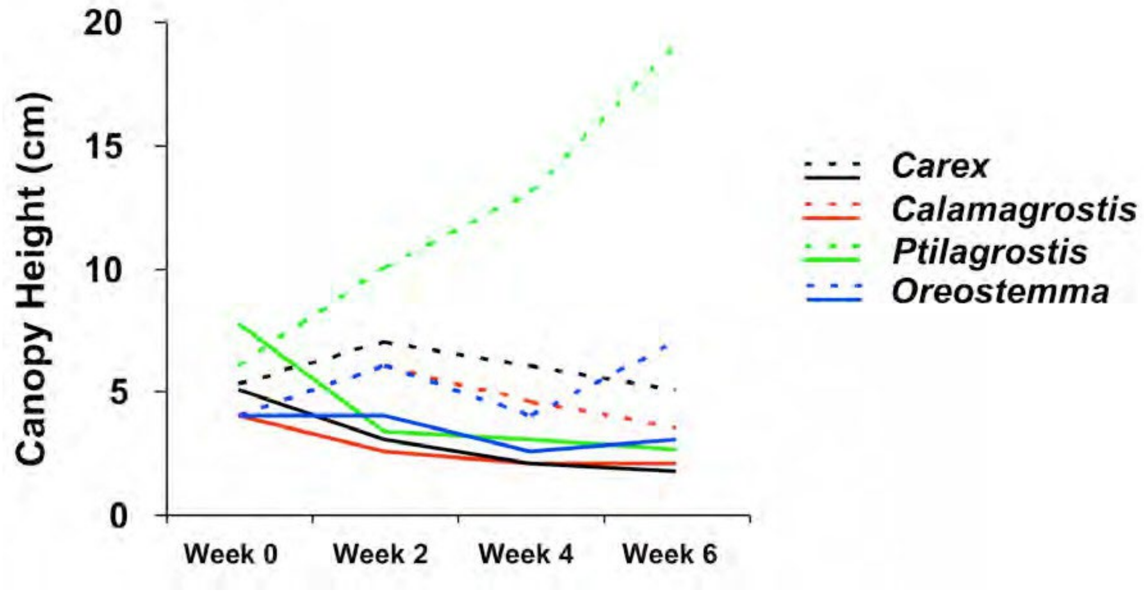


Fig. 13 . Mean canopy height on control and addition plots during experiment by vegetation type. Error estimates omitted for clarity. Dashed lines indicate controls; solid lines indicate additions. *Carex* n= 3; *Calamagrostis* n= 2; *Ptilagrostis* n= 3; *Oreostemma* n= 2.

Green cover varied at the start of the experiment, and results varied among vegetation types to some extent (Fig. 14). *Ptilagrostis* was the only dominant taxon with green cover below 50% at the start of the experiment, whereas *Oreostemma* and *Calamagrostis* had close to 100% green cover. After the experiment, green cover on the *Oreostemma* and *Calamagrostis* control plots was similar to that observed before the experiment (Fig. 14). In contrast, in *Ptilagrostis,* green cover on the *addition* plots remained similar to cover seen at the beginning of the experiment, but green cover on the controls doubled*.* The *Carex* plots had slightly more green cover on the additions than

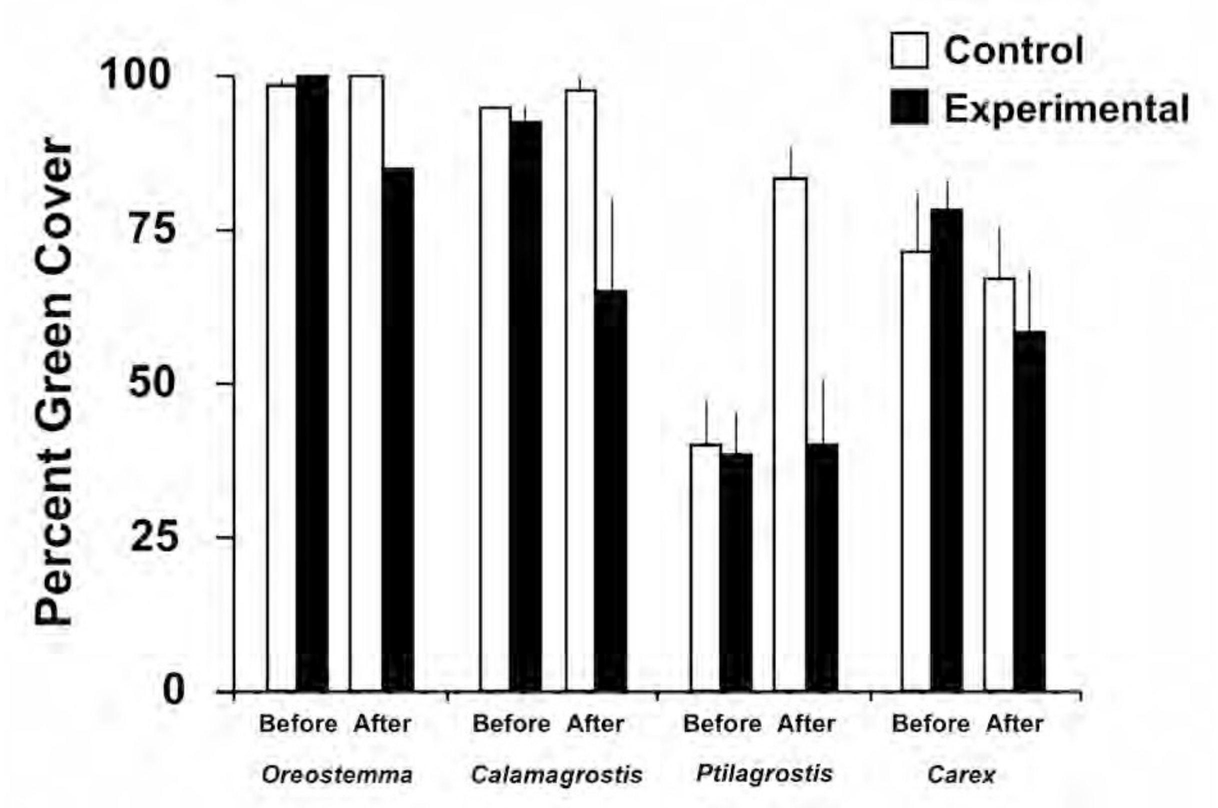


Fig. 14 . Mean (SE) percent green cover on control and addition plots before and after experiment by vegetation type. *Carex* n= 3; *Calamagrostis* n= 2; *Ptilagrostis* n= 3; *Oreostemma* n= 2.

on the controls before the manipulations, but this relationship reversed by the end of the experiment (Fig. 14). Thus, in all four of these vegetation assemblages, the controls had more green cover at the end of the experiment than the controls.

Bare ground also varied among plant assemblages at the start of the experiment (Fig. 15). Levels were very low for *Oreostemma* and *Calamagrostis* but over 20% for *Carex. Ptilagrostis* plots were unusual in that there was more bare ground on the addition plots *prior* to the experiment. After the

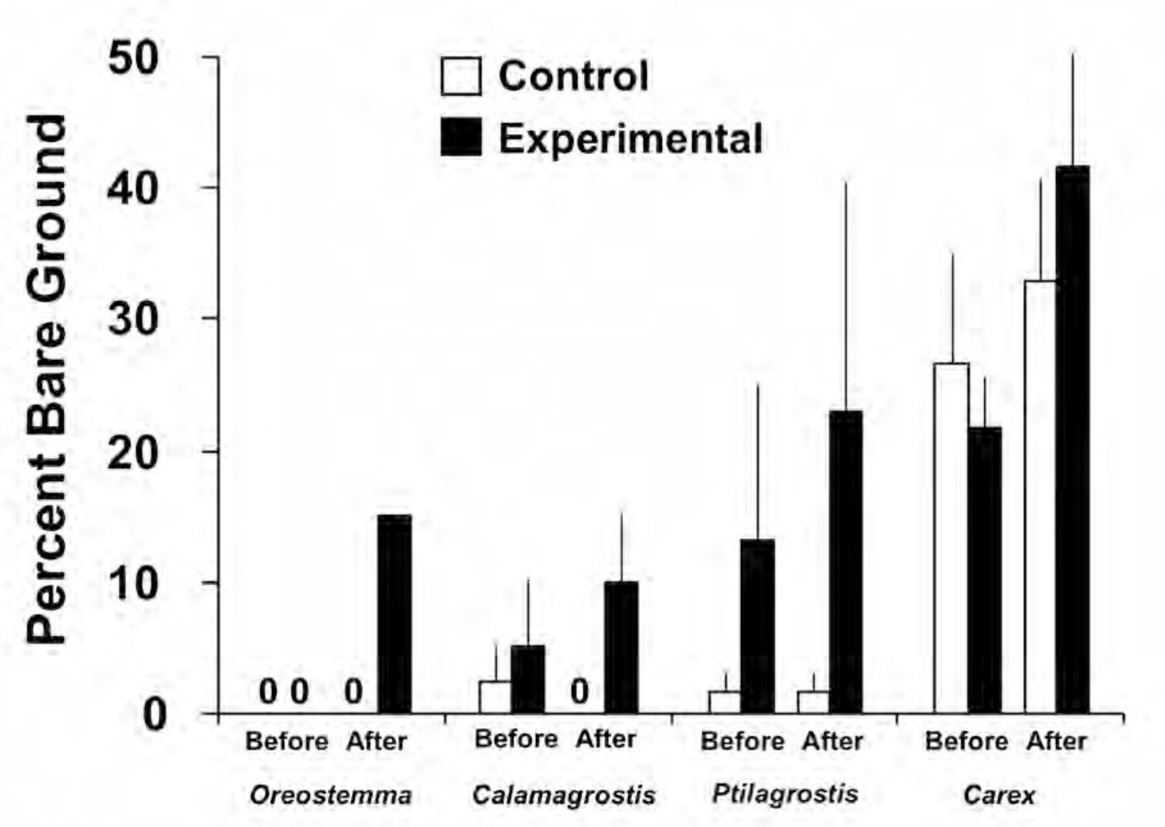


Fig. 15 . Mean (SE) percent bare ground on control and addition plots before and after experiment by vegetation type. *Carex* n= 3; *Calamagrostis* n= 2; *Ptilagrostis* n= 3; *Oreostemma* n= 2.

experiment, *Oreostemma* and *Calamagrostis* had zero bare ground on controls, but there was 15 and 10%, respectively, bare ground on the addition plots (Fig. 15). Results in *Ptilagrostis* were equivocal, because of the disparity at the start of the experiment, but bare ground did increase on the additions and not on the controls. In *Carex*, bare ground was somewhat lower on addition plots before the experiment, but higher on addition plots after the experiment (Fig. 15).

Standing crop was highest in *Calamagrostis* and *Ptilagrostis* at the start of the experiment (Fig. 16). During the experiment, standing crop on controls in *Oreostemma* and *Ptilagrostis* increased more than on the additions, which

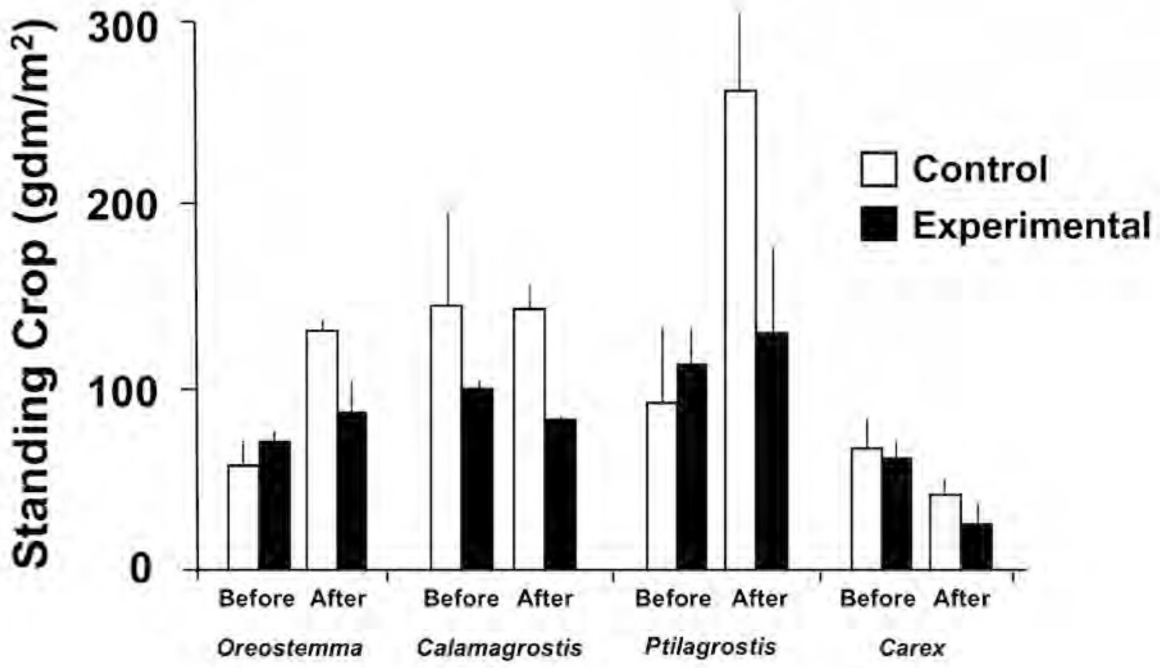


Fig. 16 . Mean (SE) standing crop on control and addition plots before and after experiment by vegetation type. *Carex* n= 3; *Calamagrostis* n= 2; *Ptilagrostis* n= 3; *Oreostemma* n= 2.

showed little increase in standing crop. There was more standing crop on controls than additions in *Calamagrostis* at the start of the experiment, and little change during the experiment (Fig. 16). Standing crop fell on *Carex* plots, particularly on addition plots.

Penetration pressure varied among vegetation types at the start of the experiment, in a descending order of *Carex, Calamagrostis, Oreostemma,* and *Ptilagrostis* (Fig. 17). Penetration pressure on additions increased relative to controls across all vegetation types. At the end of the experiment, penetration pressures on additions were about twice those observed on controls in both

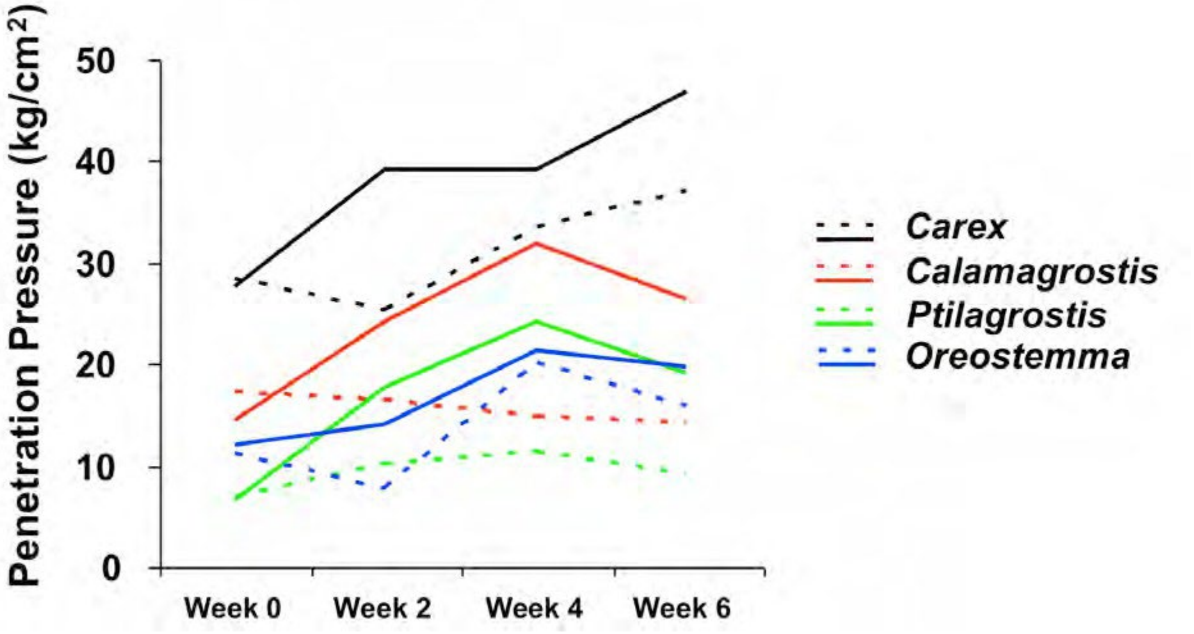


Fig. 17 . Mean penetration pressure on control and addition plots during experiment by vegetation type. Error estimates omitted for clarity. Dashed lines indicate controls; solid lines indicate additions. *Carex* n= 3; *Calamagrostis* n= 2; *Ptilagrostis* n= 3; *Oreostemma* n= 2.

Calamagrostis and *Ptilagrostis*, whereas the least effect was seen in *Oreostemma* (Fig. 17).

Soil moisture decreased during the season on all control and addition plots regardless of vegetation types, and the greatest reduction was seen in *Carex* (Fig. 18). Control-addition differences were not apparent in any vegetation.

There thus were subtle differences in response to the various metrics among vegetation assemblages. However, the overriding trend was that trampling caused degradation of habitat across all plant assemblages and as measured by most metrics.

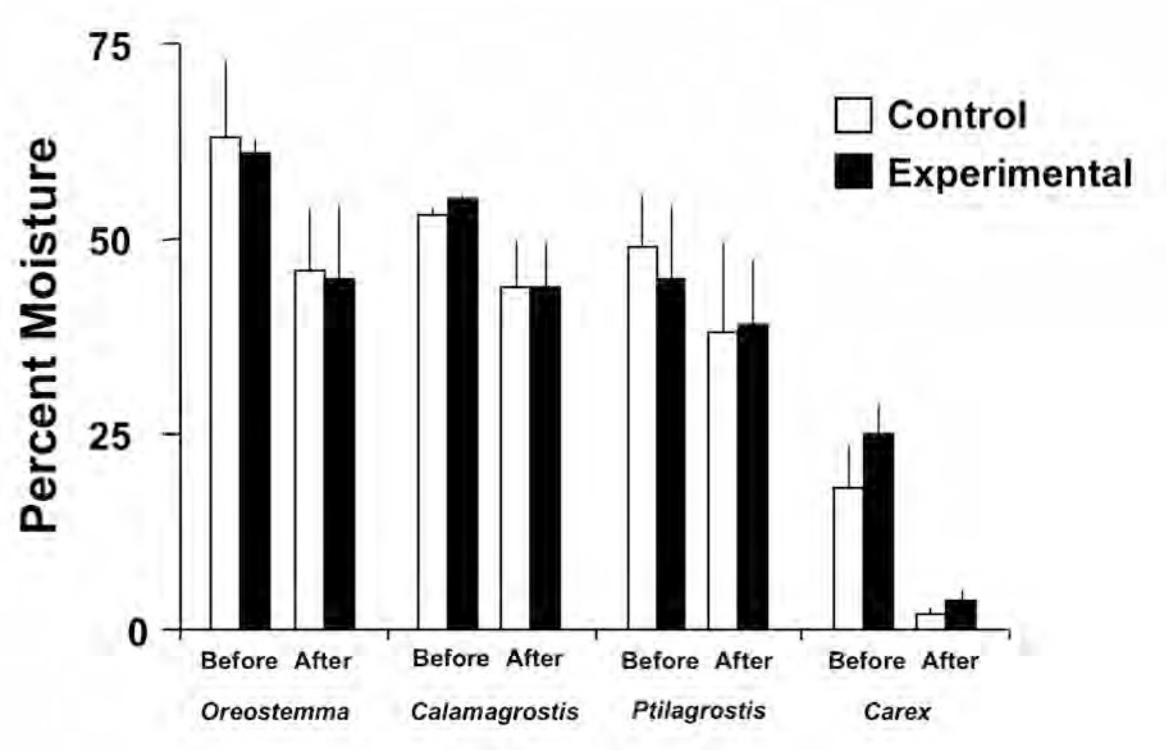


Fig. 18 . Mean soil moisture (SE) on control and addition plots before and after experiment by vegetation type. *Carex* n= 3; *Calamagrostis* n= 2; *Ptilagrostis* n= 3; *Oreostemma* n= 2.

There were minor trends at the level of individual plant taxa in the addition experiment (Table 2). Examining plant taxa across all plant assemblages, there was an overall trend of less cover on a taxon-by-taxon basis on the addition plots than on the control plots at the end of the experiment (one-tailed sign test, $p < 0.0025$). However, addition-addition and control-control comparisons were not significant (one-tailed sign test, $p > 0.25$). There was no change in plant species richness as a result of the experiment (RB-ANOVA with repeated measures TREATMENT p= 0.55; TREATMENTxTIME p= 0.66).

Table 2. Percent cover of plant taxa from addition experiment, by vegetation assemblage. *Oreostemma* n= 2; *Calamagrostis* n= 2; *Ptilagrostis*; n= 3; *Carex* n= 3. Blanks, rather than "zeros," are used to indicate that a given taxon was not present. Continued next page.

	Before				**After**			
	Control		**Addition**		**Control**		**Addition**	
	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)
***Oreostemma* assemblage**								
Antennaria corymbosa	1.0	(1.0)			2.5	(2.5)		
Oreostemma alpigenus					1.5	(0.50)	1.0	(0)
Hypericum anagalloides	0.5	(0.5)	7.0	(2.0)				
Dodecatheon subalpinum					10	(5.0)	10	(5.0)
Ivesia lycopodioides	3.5	(3.5)	2.5	(2.5)				
Penstemon heterodoxus	12	(0)	10	(0)	1.5	(1.5)	2.5	(2.5)
Carex subnigricans	7.0	(1.0)	6.5	(1.5)	10	(5.0)	10	(5.0)
Juncus balticus	3.0	(2.0)	3.0	(2.0)	1.5	(0.50)	1.5	(0.50)
Calamagrostis muiriana	6.0	(2.0)	3.0	(2.0)	5.5	(4.5)	0.5	(0.50)
Danthonia intermedia	1.0	(1.0))						
Muhlenbergii filiformis	0.50	(0.5)	2.5	(2.5)	1.5	(0.50)		
***Calamagrostis* assemblage**								
Antennaria corymbosa	4.5	(0.50)	2.5	(2.5)	3.5	(1.5)	1.0	(0)
Oreostemma alpigenus	1.5	(0.5)	1.0	(1.0)				
Vaccinium caespitosum	19	(6.0)	20	(5.0)	33	(13)	15	(5.0)
Ivesia lycopodioides							0.50	(0.5)
Penstemon heterodoxus					3.0	(2.0)	2.5	(2.5)
Viola adunca					0.50	(0.50)		
Juncus balticus					0.50	(0.5)		
Calamagrostis muiriana	40	(10)	40	(10)	60	(15)	58	(13)
Other	0.50	(0.50)						

Table 2 (cont.). Percent cover of plant taxa from addition experiment.

	Before				**After**			
	Control		**Addition**		**Control**		**Addition**	
	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)
***Ptilagrostis* assemblage**								
Antennaria corymbosa	1.7	(1.7)	5.0	(5.0)	3.3	(1.7)	2.0	(1.5)
Oreostemma alpigenus					0.67	(0.67)		
Vaccinium caespitosum	0.67	(0.33)			1.7	(1.7)		
Polygonum bistortoides	2.7	(1.3)	2.3	(1.5)	14	(6.3)	7.0	(6.5)
Dodecatheon subalpinum	0.33	(0.33)			0.67	(0.67)		
Ivesia lycopodioides	0.33	(0.33)						
Juncus balticus	0.67	(0.33)	0.67	(0.33)			0.33	(0.33)
Danthonia intermedia					1.7	(1.7)		
Ptilagrostis kingii	45	(10)	43	(12)	63	(8.8)	28	(7.3)
Other			0.33	(0.33)			0.67	(0.33)
***Carex* assemblage**								
Antennaria corymbosa			0.67	(0.67)			0.67	(0.67)
Hypericum anagalloides	0.67	(0.67)	1.0	(1.0)				
Penstemon heterodoxus					0.67	(0.67)		
Carex filifolia	29	(4.6)	30	(2.9)	65	(5.0)	58	(10)
Muhlenbergia filiformis	0.67	(0.67)	1.0	(1.0)				
Other			0.33	(0.33)			0.67	(0.33)

We collected 783 arthropods from 40 families during the addition experiment; Diptera had the greatest abundance as well as the highest species and family richness (Table 3). There were broad trampling impacts across most taxa (Table 3). Total number of individuals decreased on both control and addition plots (Fig. 19; TIME p= 0.00040), but the decrease was much more dramatic on addition plots (TREATMENTxTIME p= 0.0054). Species richness decreased on both controls and additions (Fig. 20; TIME p= 0.00062) and was initially higher on additions than controls, but this relationship reversed by the end of the experiment (Fig. 20; TREATMENTxTIME p= 0.0072). Family richness showed the same trends (Fig. 21; TIME p= 0.0016; TREATMENTxTIME p= 0.038).

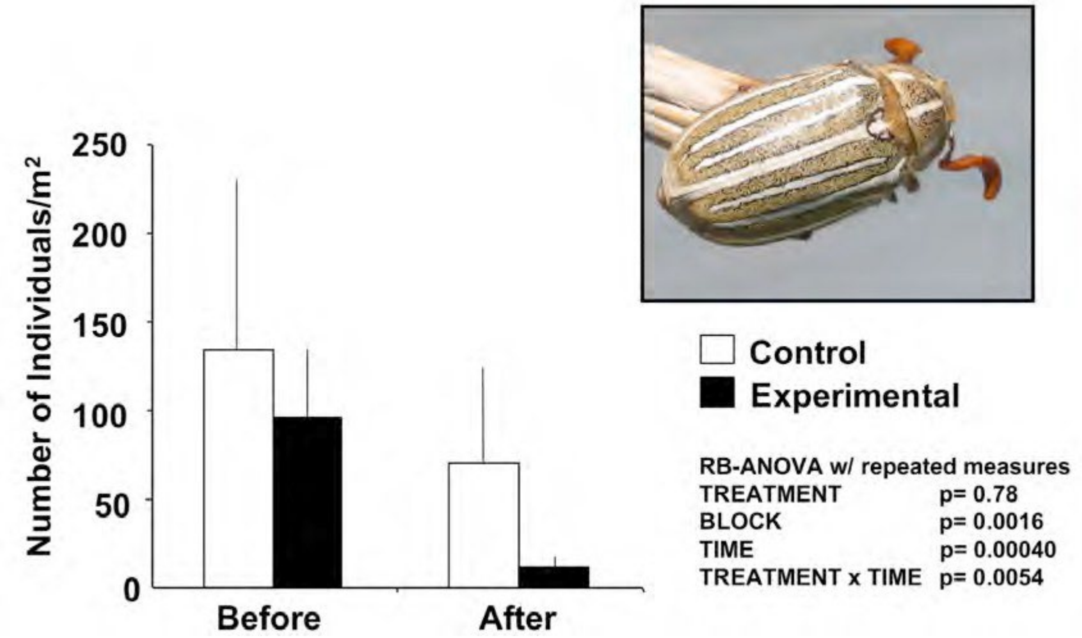


Fig. 19. Mean (SE) total faunal abundance on control and addition plots before and after experiment. BLOCK represents plot effects. n= 10.

Table 3. Densities per m^2 of fauna from trampling addition experiment. Blanks, rather than "zeros," are used to indicate that a given taxon was not present. n= 10. Continued next page.

	Before				**After**			
	Control		**Addition**		**Control**		**Addition**	
	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)
Orthoptera	0.40	(0.40)			0.40	(0.40)		
Acrididae	0.40	(0.40)			0.40	(0.40)		
Hemiptera	4.8	(3.9)	6.4	(4.5)	2.4	(1.6)	0.40	(0.40)
Lygaeidae	0.80	(0.53)	4.4	(2.8)	1.2	(1.2)	0.40	(0.40)
nymphs	4.0	(4.0)	2.0	(1.08)	1.2	(1.2)		
Homoptera	2.0	(1.2)	6.0	(2.4)	3.6	(1.6)		
Cicadellidae	1.6	(0.88)	3.2	(1.2)	2.8	(1.3)		
Delphacidae	0.40	(0.40)	2.8	(1.7)	0.40	(0.40)		
Aphididae					0.40	(0.40)		
Coleoptera	2.4	(1.4)	5.6	(2.1)	1.2	(0.85)	4.0	(3.6)
Carabidae	0.40	(0.40)	0.40	(0.40)			0.40	(0.40)
Staphylinidae			0.40	(0.40)				
Scarabaeidae	1.2	(0.61)	1.2	(0.61)	0.80	(0.80)	2.8	(2.8)
Cantharidae							0.40	(0.40)
Coccinellidae	0.40	(0.40)						
Mordellidae							0.40	(0.40)
Anthicidae	0.40	(0.40)	1.2	(0.61)				
Chrysomelidae			0.40	(0.40)	0.40	(0.40)		
Curculionidae			0.80	(0.80)				
Other			1.2	(0.85)				

Table 3 (cont.). Densities per m^2 of fauna from trampling addition experiment. Continued next page.

	Before				After			
	Control		Addition		Control		Addition	
	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)
Hymenoptera	5.2	(2.7)	17.4	(6.6)	4.0	(1.7)	1.6	(1.4)
Braconidae			0.40	(0.40)	0.40	(0.40)	0.40	(0.40)
Pteromalidae	0.40	(0.40)						
Formicidae	4.8	(2.7)	16	(6.6)	3.6	(1.7)	1.2	(0.61)
Other wasp			0.40	(0.40)				
Lepidoptera			0.80	(.53)	0.40	(0.40)		
Other			0.80	(.53)	0.40	(0.40)		
Diptera	111	(100)	52	(42)	55	(52)	7.6	(4.7)
Culicidae	0.80	(0.80)	2.4	(1.6)				
Sciaridae	3.6	(1.9)	0.40	(0.40)	0.40	(0.40)		
Empididae	0.40	(0.40)						
Lonchopteridae	4.0	(4.0)	1.6	(1.6)	0.80	(0.80)	0.40	(0.40)
Phoridae			0.40	(0.40)	0.40	(0.40)		
Anthomyiidae	2.0	(1.1)	0.40	(0.40)			0.80	(0.80)
Muscidae	0.80	(0.80)	1.2	(0.61)	0.80	(0.80)	0.40	(0.40)
Sepsidae							0.40	(0.40)
Chloropidae	0.80	(0.80)	1.6	(1.2)	0.40	(0.40)	0.40	(0.40)
Sphaeroceridae	95	(92)	42	(41)	42	(41)	3.2	(2.8)
Drosophilidae	2.4	(2.4)	0.40	(0.40)	9.2	(9.2)	2.0	(1.6)
Ephydridae					0.40	(0.40)		
Other	0.8	(0.53)	1.2	(0.61)	0.40	(0.40)		

Table 3 (cont.). Densities per m^2 of fauna from trampling addition experiment.

	Before				After			
	Control		**Addition**		**Control**		**Addition**	
	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)
Araneae	5.2	(2.1)	2.8	(1.13)	1.6	(0.88)	0.40	(0.40)
Tetragnathidae	1.2	(1.2)						
Linyphiidae	2.4	(1.6)	2.0	(1.1)				
Lycosidae			0.40	(0.40)				
Thomisidae					1.6	(0.88)		
Salticidae	1.2	(0.61)						
Other	0.40	(0.40)	0.40	(0.40)			0.40	(0.40)
Acari	3.6	(2.3)	2.8	(1.6)	2.4	(1.7)		

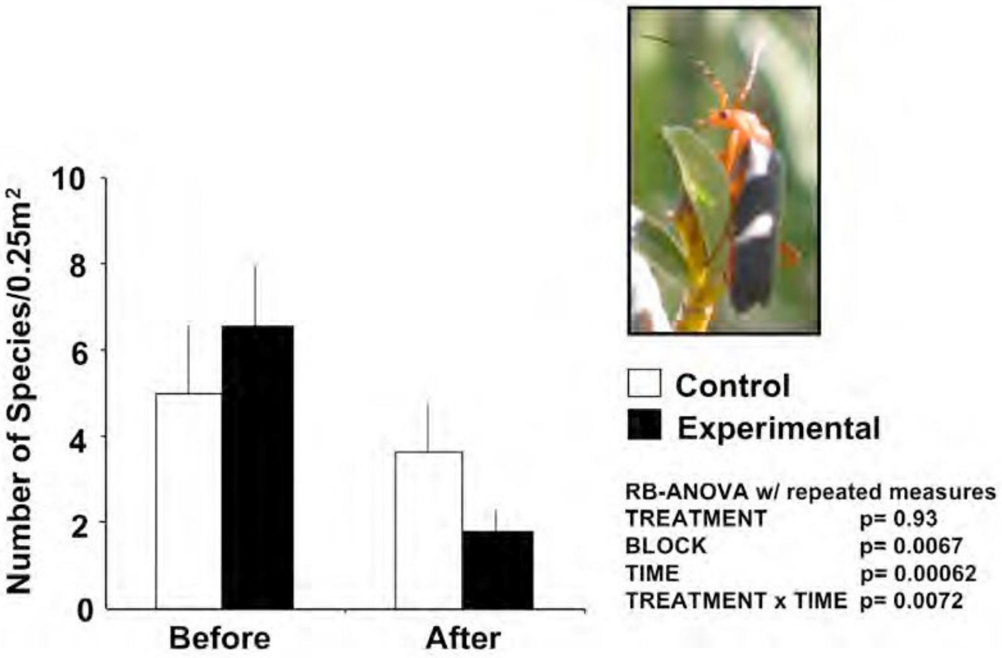


Fig. 20 . Mean (SE) faunal species richness on control and addition plots before and after experiment. BLOCK represents plot effects. n= 10.

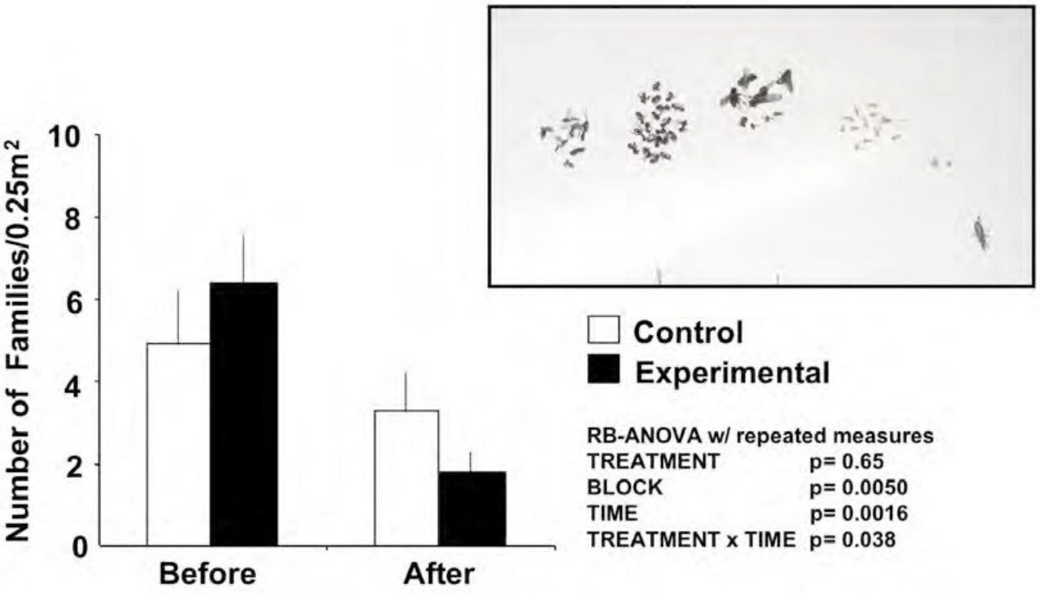


Fig. 21 . Mean (SE) faunal family richness on control and addition plots before and after experiment. BLOCK represents plot effects. n= 10. Inset shows initial sorting of fauna in lab.

The two most common taxa, Sphaeroceridae (Diptera) and Formicidae (ants, Hymenoptera), both lost abundance on the experimental plots. Sphaerocerids decreased on both controls and additions (Fig. 22; TIME p= 0.0098). Although there were very few of these flies on the addition plots after the experiment, there was not a significant TREATMENTxTIME interaction (p= 0.52). There were three times as many ants on addition plots as on controls before the experiment, but there were only one-third as many ants on additions as on controls after the experiment (Fig. 23). However, there was not a clear experimental effect (TREATMENTxTIME p= 0.041).

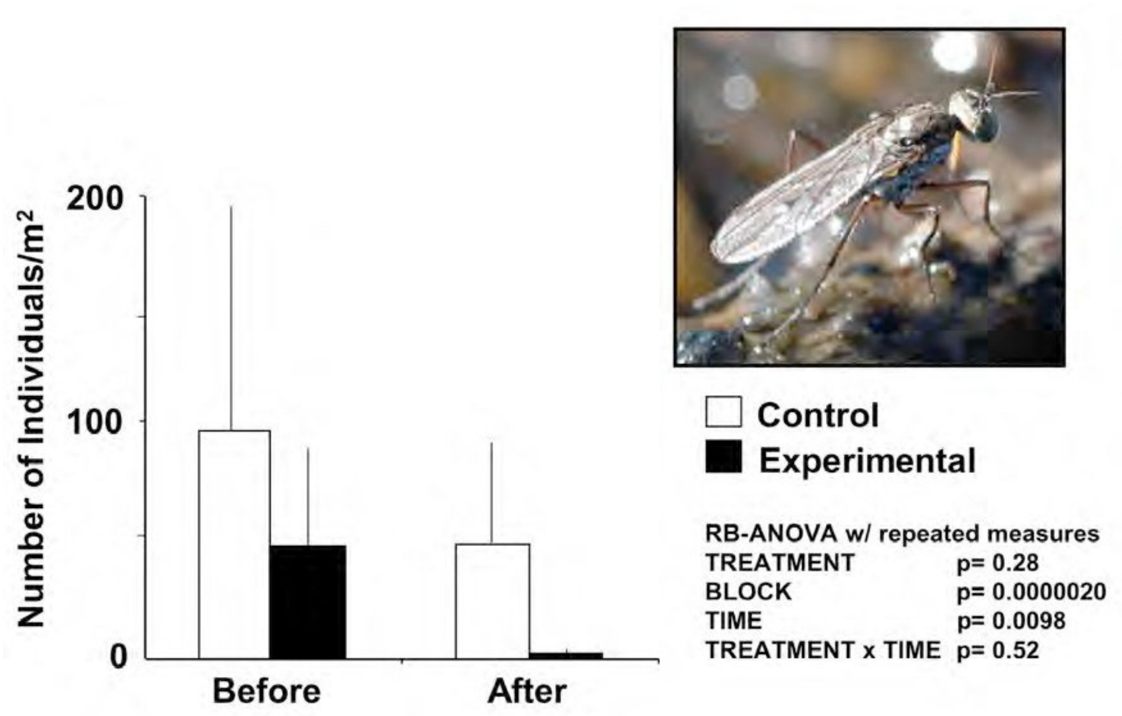


Fig. 22 . Mean (SE) sphaerocerid abundance on control and addition plots before and after experiment. BLOCK represents plot effects. n= 10. Inset photo JK Lindsey.

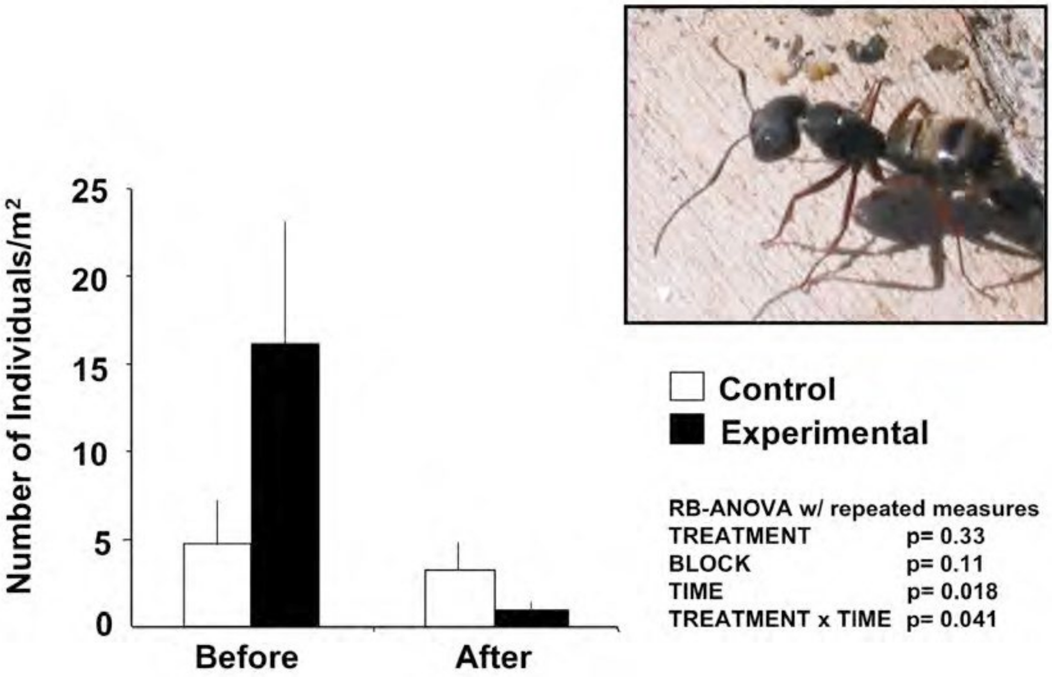


Fig. 23. Mean (SE) ant abundance on control and addition plots before and after experiment. BLOCK represents plot effects. n= 10.

Significantly more taxa on addition plots decreased in abundance relative to controls at the end of the experiment (one-tailed sign test; p< 0.025). Taxa on both control and experimental plots showed decreases by the end of the experiment; decreases on addition plots were significant (one-tailed sign test; p< 0.005), whereas those on control plots were not (one-tailed sign test; p< 0.10).

In summary, trampling addition caused negative effects across almost all measured variables; there were no positive trends (Fig. 24). Both vegetation and higher trophic levels were negatively affected in a variety of ways (one-tailed sign test; p< 0.0025).

• Canopy height	↓
• Percent green cover	↓
• Percent bare ground	↑
• Standing crop	↓
• Litter depth	↓
• Soil compaction	↑
• Soil moisture	↔
• Percent cover trends across all plant taxa	↓
• Plant species richness	↔
• Total number of invertebrates	↓
• Invertebrate family richness	↓
• Invertebrate species richness	↓
• Ant density	↓
• Density trends across all invertebrate taxa	↓

Fig. 24 . Summary of changes on trampling addition plots. Upward facing arrows indicate an increase for a given metric, whereas downward facing arrows indicate decreases. The double-headed horizontal arrow indicates no change. Red arrows represent strong negative effects, and the orange arrow represents a weak negative effect.

Exclosure experiment

The exclosures were effective at modifying visitor behavior. Visitors respected the exclosure plots, and we found no evidence of vandalism or intentional intrusion, either via footprints or direct observation. When we occasionally found breakage, it was apparent that visitors had attempted to repair or support broken dowels, etc.

The exclosures produced only minimal effects on habitat. Canopy height increased during the growing season in the exclosures, while height on the controls decreased to half that of the exclosures (Fig. 25). However, these

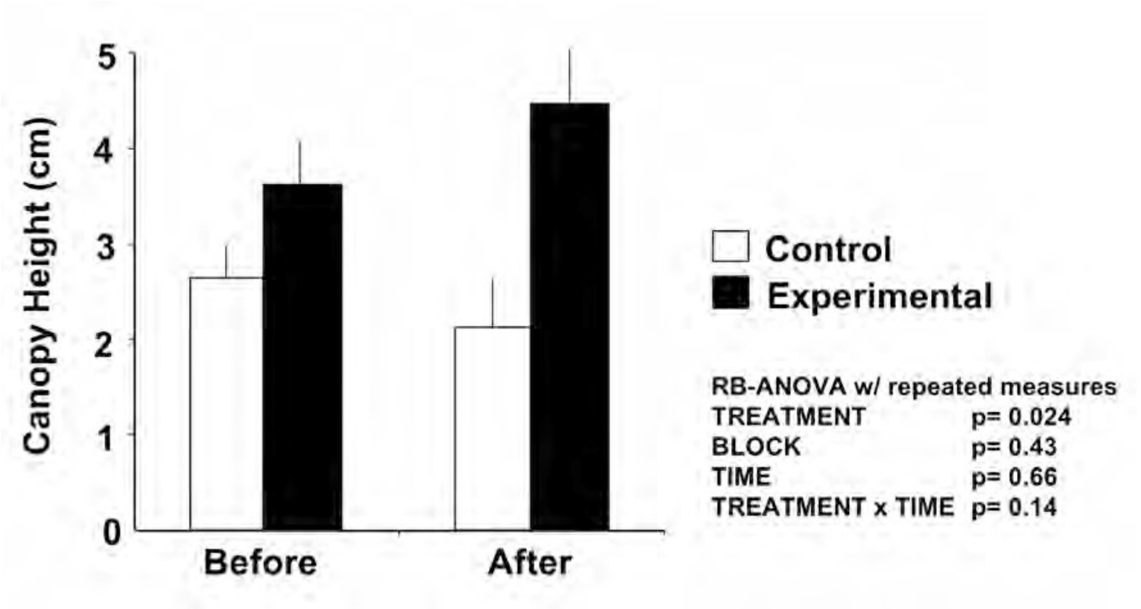


Fig. 25. Mean (SE) canopy height on control and exclosure plots before and after the 2006 experiment. BLOCK represents plot effects. n= 10.

differences were not significant (TREATMENTxTIME p = 0.14). Similarly, percent green cover decreased on the control plots versus the exclosures, but this trend was not significant either (Fig. 26; TREATMENTxTIME p = 0.14). Percent bare ground increased during the experiment (Fig. 27; TIME p= 0.0030), but there was little experimental effect (TREATMENTxTIME p = 0.31). The experiment also had little effect on standing crop (Fig. 28; TREATMENTxTIME p = 0.91) or penetration pressure (Fig. 29; TREATMENTxTIME p = 0.95). Soil moisture decreased precipitously on both controls and exclosures during the summer (Fig. 30; TIME p< 0.0001), but there was no experimental effect (TREATMENTxTIME p = 0.65). Trends on exclosure controls were similar to

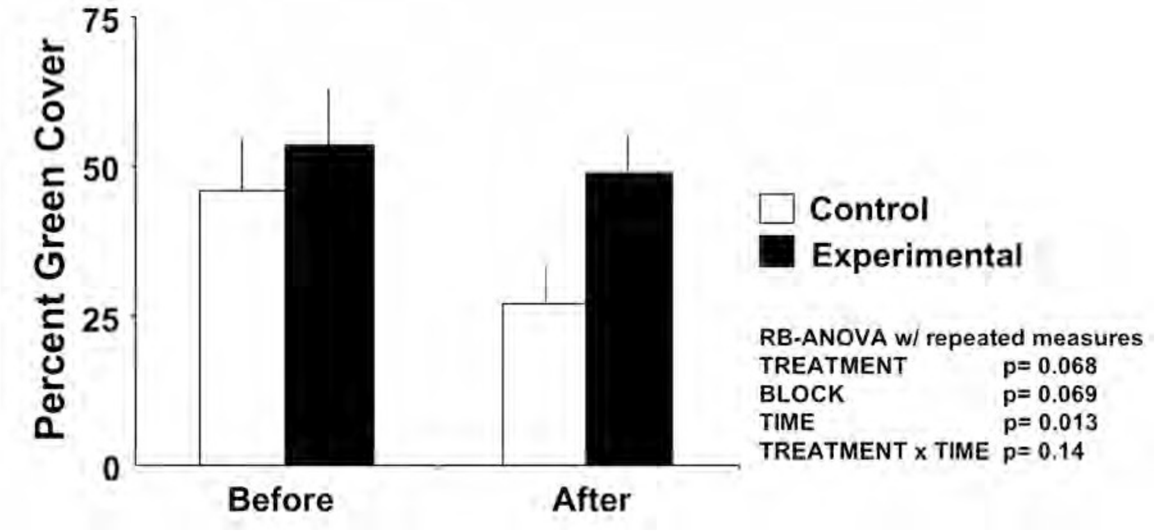


Fig. 26. Mean (SE) percent green cover on control and exclosure plots before and after the 2006 experiment. BLOCK represents plot effects. n= 10.

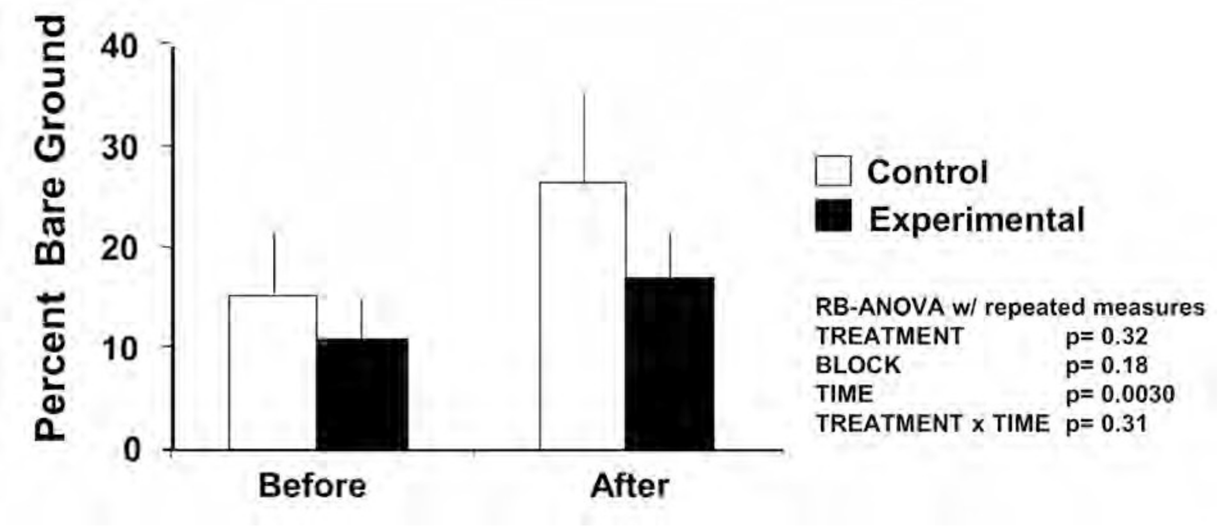


Fig. 27. Mean (SE) percent bare ground on control and exclosure plots before and after the 2006 experiment. BLOCK represents plot effects. n= 10.

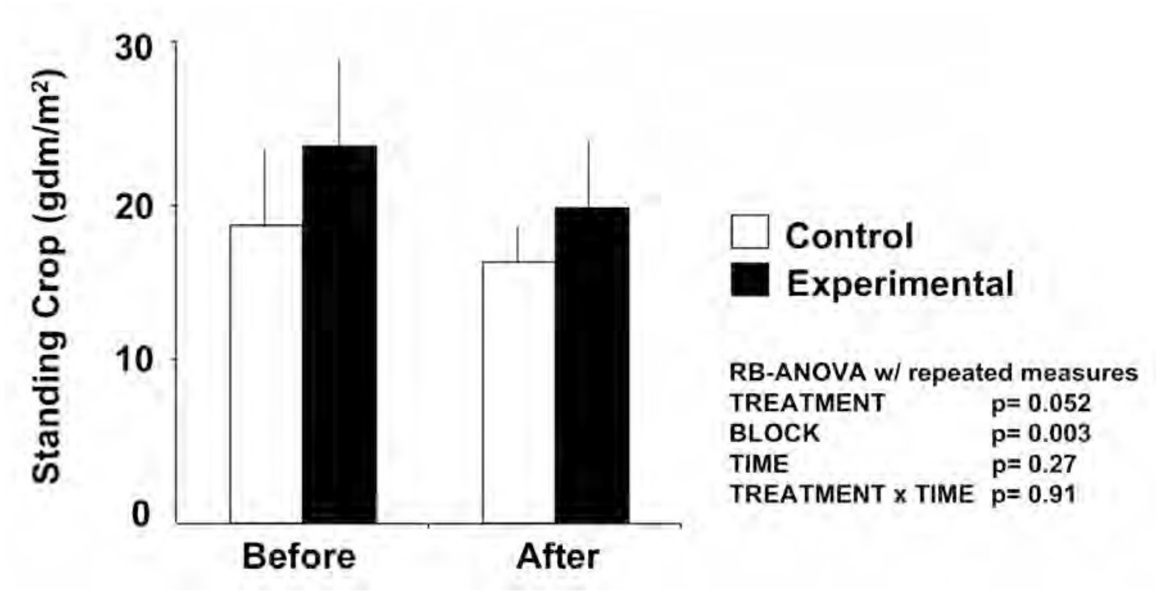


Fig. 28. Mean (SE) standing crop on control and exclosure plots before and after the 2006 experiment. BLOCK represents plot effects. n= 10.

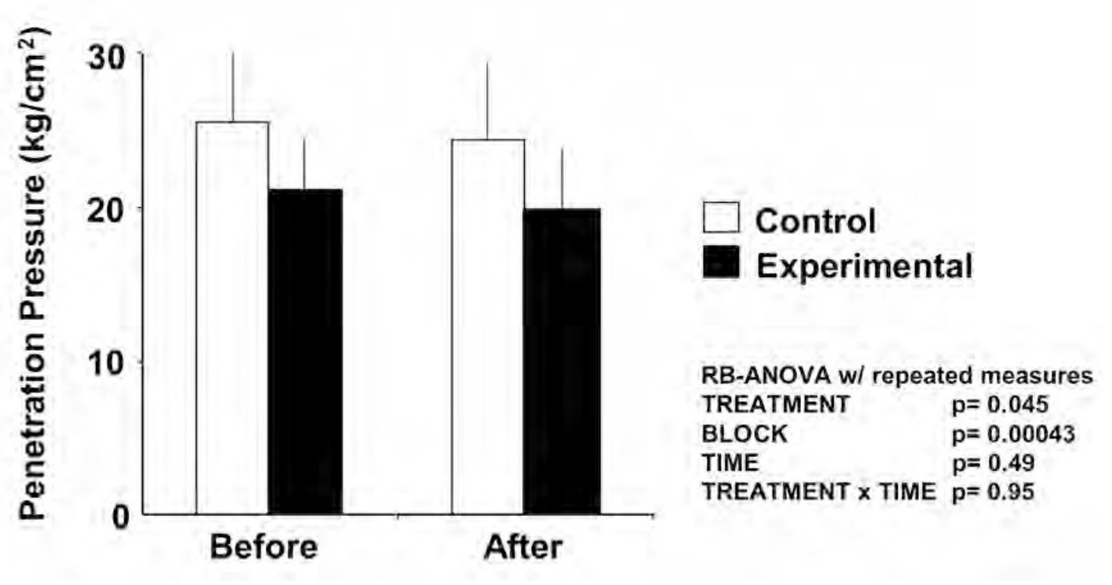


Fig. 29. Mean (SE) penetration pressure on control and exclosure plots before and after the 2006 experiment. BLOCK represents plot effects. n= 10.

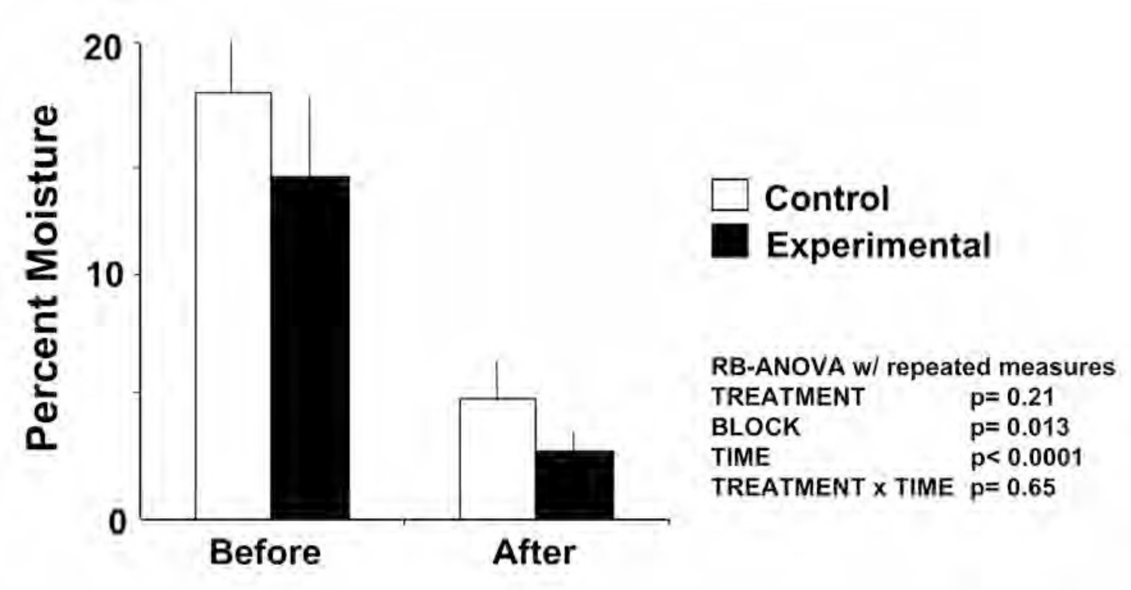


Fig. 30. Mean (SE) percent soil moisture on control and exclosure plots before and after the 2006 experiment. BLOCK represents plot effects. n= 10.

those observed on control plots, albeit with more variance as a result of the smaller sample size.

All three of the most common plant taxa *Carex filifolia, Carex rossii*, and *Juncus balticus* increased percent cover during the course of the experiment (Table 4; TIME p= 0.0067, 0.022, and p< 0.000001, respectively). However, only *Carex rossii* showed a significant increase in cover in response to the elimination of trampling (TREATMENTxTIME p= 0.038 versus p= 0.19 and 0.17, respectively, for *Carex filifolia* and *Juncus balticus*). There were no differences in plant species richness as a function of experimental treatments (RB-ANOVA with repeated measures; TREATMENT p= 0.92; TREATMENTxTIME p= 0.51).

Table 4. Percent cover of plant taxa from the 2006 exclosure experiment. Blanks, rather than "zeros," are used to indicate that a given taxon was not present. n=10.

	Before				**After**			
	Control		**Exclosure**		**Control**		**Exclosure**	
	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)
Pinus contorta			0.10	(0.10)			0.10	(0.10)
Antennaria corymbosa	0.30	(0.21)	0.30	(0.21)	0.10	(0.10)	0.70	(0.52)
Oreostemma alpigenus							0.50	(0.50)
Vaccinium caespitosum	0.30	(0.15)	0.20	(0.13)				
Penstemon heterodoxus					1.0	(0.79)	1.2	(1.0)
Carex filifolia	9.8	(2.7)	6.8	(2.1)	16	(5.0)	22	(7.6)
Carex rossii	3.2	(1.7)	3.9	(1.9)	3.7	(1.9)	11.4	(4.9)
Juncus balticus	1.0	(0.79)	1.3	(0.79)	4.3	(3.0)	5.8	(3.3)
Other	1.0	(0.49)	1.2	(0.53)	0.40	(0.16)	0.70	(0.5)

Although as a rule recovery during this first season was minimal on the exclosure plots, replicates in the most heavily used areas were something of an exception. On the two replicates placed in high traffic areas near the Soda Springs trailhead, the manipulation resulted in striking differences that were apparent upon casual inspection (Fig. 31). On these plots, control canopy height fell from a mean of 3.0 to 0.5cm during the season, whereas height increased from 2.5 to 4.5cm in the exclosures. Similarly, standing crop decreased from 26 to 17gdm/m^2 on the controls but increased from 6 to 33gdm/m^2 inside the exclosure plots.

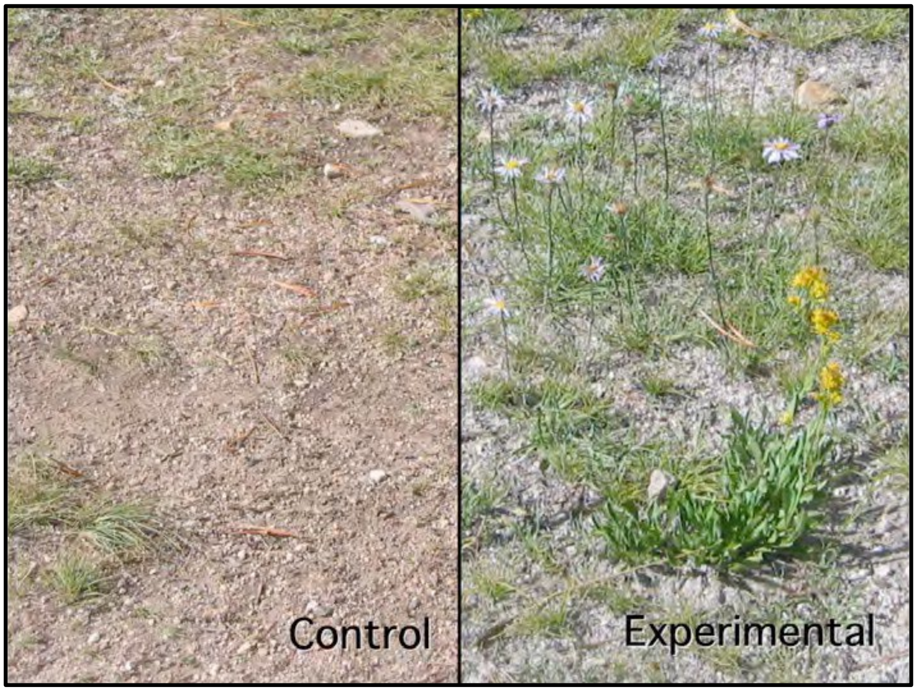


Fig. 31 . Pronounced control-exclosure differences at a heavily-used replicate near the Soda Springs trailhead. Note bare ground on the control versus *Oreostemma (Aster)* in flower on the exclosure plot.

In contrast to the plots used for the addition experiment, the heavily-used exclosure experiment plots had low faunal abundance and diversity (Table 5). We collected 124 arthropods from five families during the exclosure experiment. There were no clear trends. For instance, although both total abundance (Fig. 32) and species richness (Fig. 33) decreased on controls and increased on exclosure plots, these trends were not significant (TREATMENTxTIME p= 0.53 and 0.52, respectively).

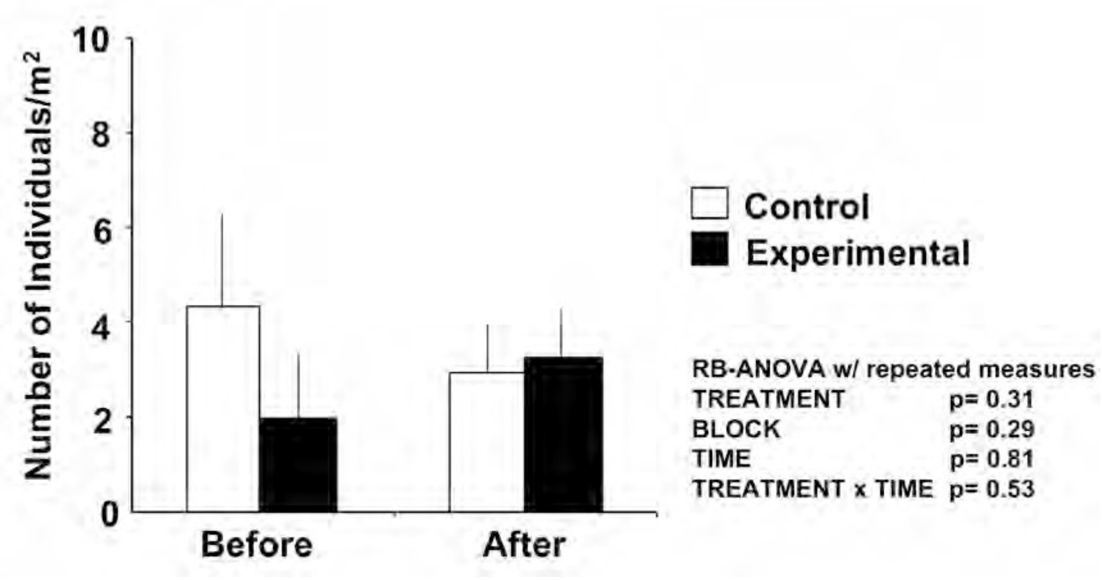


Fig. 32. Mean (SE) total faunal abundance on control and exclosure plots before and after the 2006 experiment. BLOCK represents plot effects. n= 10.

Table 5. Densities per m^2 of fauna from the 2006 trampling exclosure experiment. Blanks, rather than “zeros,” are used to indicate that a given taxon was not present. n= 10.

	Before				**After**			
	Control		**Exclosure**		**Control**		**Exclosure**	
	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)
Hemiptera							0.80	(0.53)
Lygaeidae							0.80	(0.53)
Homoptera	0.8	(0.53)	1.6	(1.2)	1.2	(1.2)		
Cicadellidae	0.8	(0.53)	1.2	(1.2)	1.2	(1.2)		
Delphacidae			0.40	(0.40)				
Diptera			0.40	(0.40)				
unidentified			0.40	(0.40)				
Hymenoptera	3.6	(2.0)			1.6	(0.88)	2.4	(1.2)
Formicidae	3.6	(2.0)			1.6	(0.88)	2.4	(1.2)

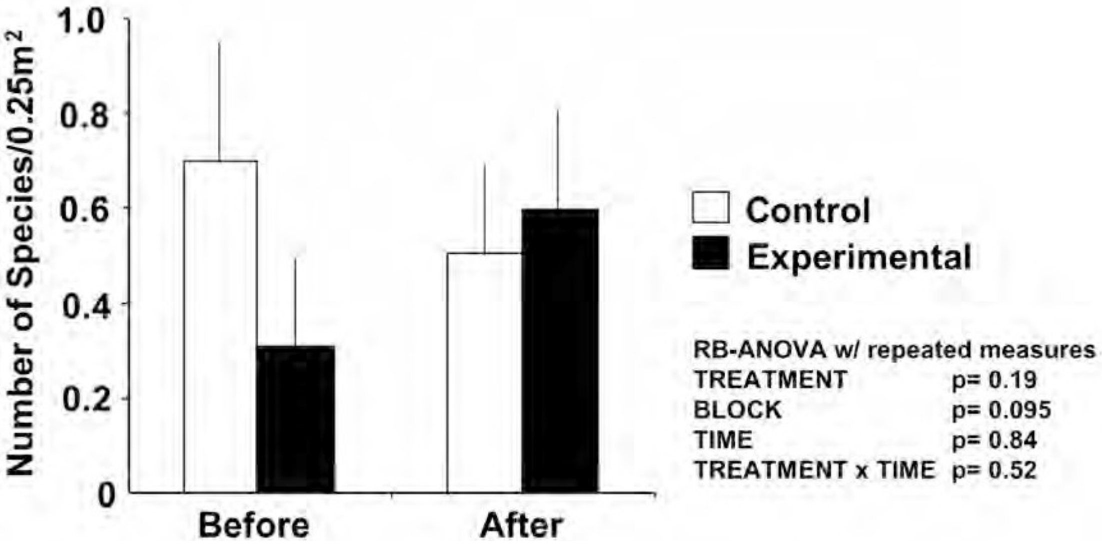
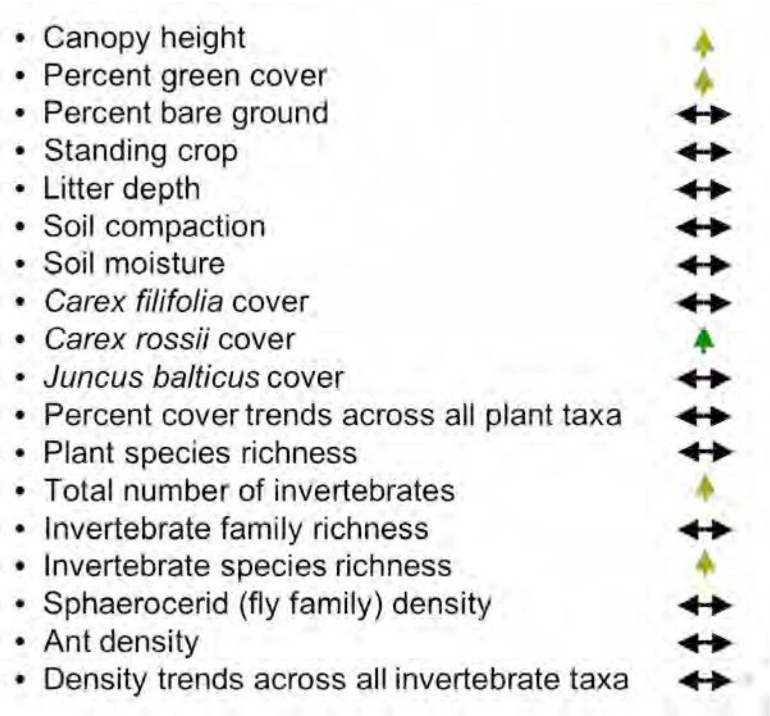


Fig. 33 . Mean (SE) faunal species richness on control and exclosure plots before and after experiment. BLOCK represents plot effects. n= 10.

In summary, examined metrics demonstrated either non-response to the exclosure experiment or weak positive responses (Fig. 34). There was not an overall positive trend (one-tailed sign test; $p > 0.25$). There were, however, no negative responses.

Continued recovery time on the exclosure plots during the 2007 growing season did not result in major changes in habitat quality. Canopy height on the control and exclosure plots in early 2007 was similar to that observed in early 2006, and though there was a divergence between treatments during the second year, this difference was not significant (Fig. 35; TREATMENTxTIME $p = 0.11$). There was even less of an effect for percent green cover (Fig. 36). More bare ground was observed on both treatments in 2007 than in 2006, and there was no indication of decreasing percentage of bare ground in the 2007



• Canopy height	↑
• Percent green cover	↑
• Percent bare ground	↔
• Standing crop	↔
• Litter depth	↔
• Soil compaction	↔
• Soil moisture	↔
• *Carex filifolia* cover	↔
• *Carex rossii* cover	↑
• *Juncus balticus* cover	↔
• Percent cover trends across all plant taxa	↔
• Plant species richness	↔
• Total number of invertebrates	↑
• Invertebrate family richness	↔
• Invertebrate species richness	↑
• Sphaerocerid (fly family) density	↔
• Ant density	↔
• Density trends across all invertebrate taxa	↔

Fig. 34 . Summary of 2006 changes on trampling exclosure plots. Upward facing arrows indicate an increase for a given metric, there were no decreases. The double-headed horizontal arrows indicate no change. The dark green arrow represents a strong positive effect, and the light green arrows represent weak positive effects.

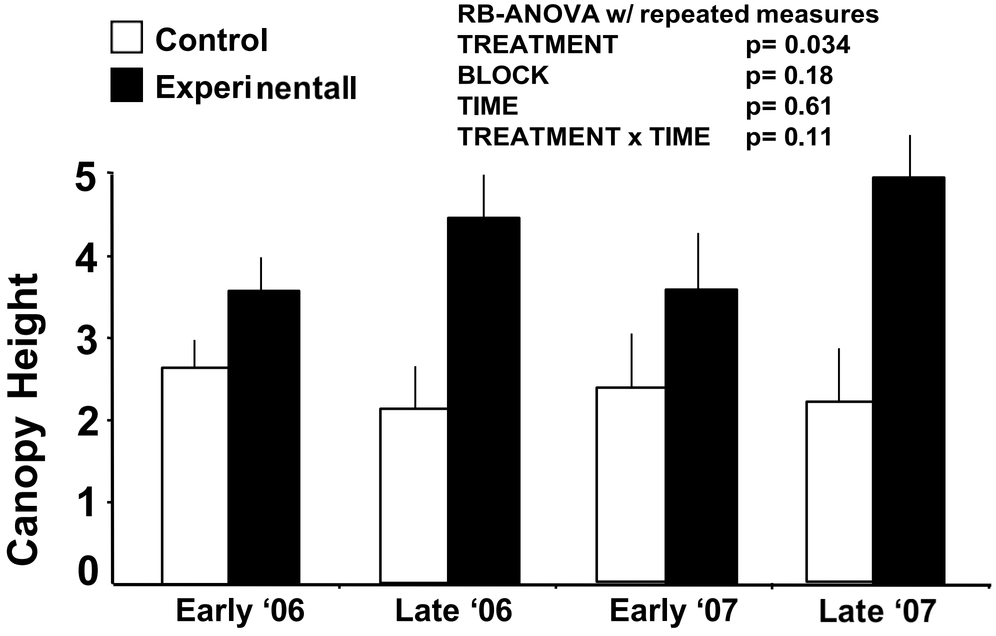


Fig. 35. Mean (SE) canopy height on control and exclosure plots 2006-7. BLOCK represents plot effects.

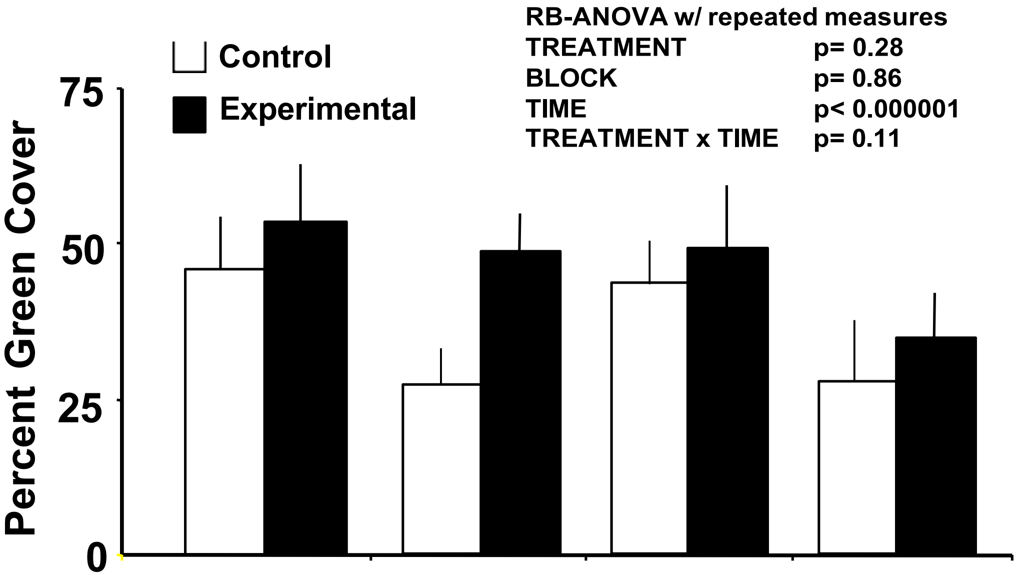


Fig. 36. Mean (SE) percent green cover on control and exclosure plots 2006-7. BLOCK represents plot effects.

exclosures (Fig. 37). Neither did a second year of exclosure result in significant improvements for soil compaction, as indicated by penetration pressure (Fig. 38).

Differences between treatments were apparent however in late season, after vegetation had become senescent, and these differences were visually striking on many plots (Fig. 39). Exclosures had a taller canopy height than the controls (4.3 vs. 1.8 cm, respectively; one-tailed paired t-test, p= 0.00037). Though there was virtually no green vegetation on either set of plots this late in the season (exclosures: 0.17%; controls: 0.0%,), there was almost three times as much standing brown vegetation on the exclosures than on the controls

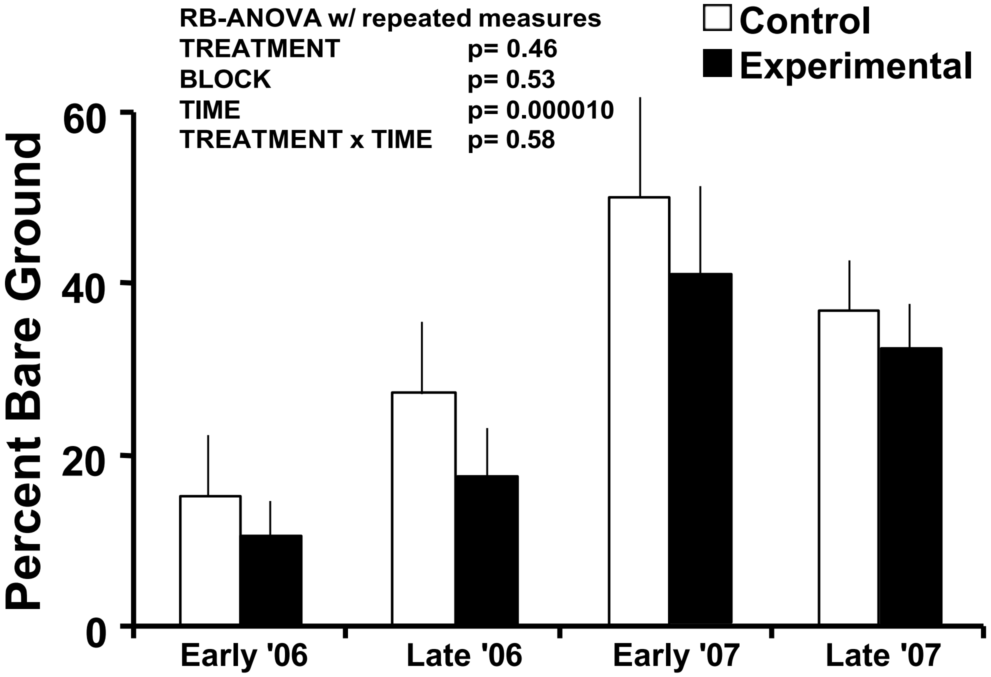


Fig. 37. Mean (SE) percent bare ground on control and exclosure plots 2006-7. BLOCK represents plot effects.

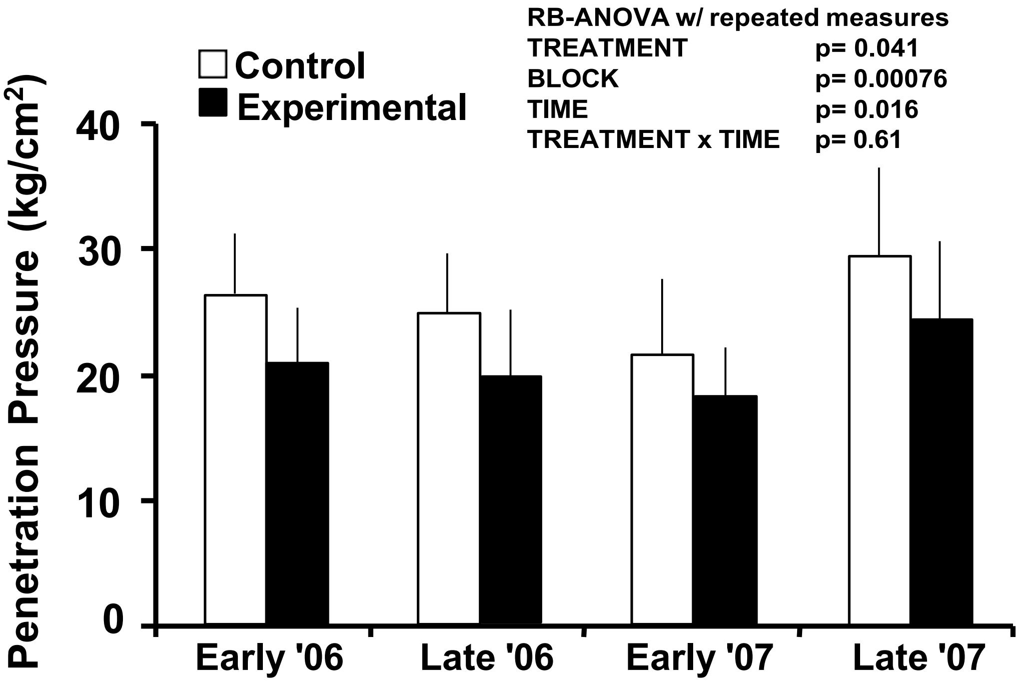


Fig. 38. Mean (SE) penetration pressure on control and exclosure plots 2006-7. BLOCK represents plot effects.

Fig. 39 . Exclosure plot in late season (October 2007) showing striking contrast with absence of standing vegetation in surrounding habitat. Color is enhanced for contrast.

(73% vs. 27%, respectively; one-tailed paired t-test, $p= 0.0055$). Conversely, there was only 19% bare ground on the exclosures versus 66% on the controls (one-tailed paired t-test, $p= 0.0096$). There was no accumulated litter on either set of plots, and penetration pressure did not differ on the plots (exclosures: 29kg/cm^2; controls: 32kg/cm^2; one-tailed paired t-test, $p= 0.14$).

Comparison of heavily and moderately used portions of the Meadows

Meadow condition was poorer in heavily used areas. Further, meadow condition often improved during the course of the season on moderately used sites, particularly as measured by vegetation parameters. However, condition in heavily used areas either deteriorated, or at best showed little change, throughout the growing season. Canopy height was three times as high on moderately used plots as on heavily used plots (Fig. 40; TREATMENT p= 0.0027). Canopy height doubled on the moderately used plots but did not change on the heavily used plots (Fig. 40; TREATMENTxTIME p= 0.040). Percent green cover on moderately used plots was twice that of the heavily used plots

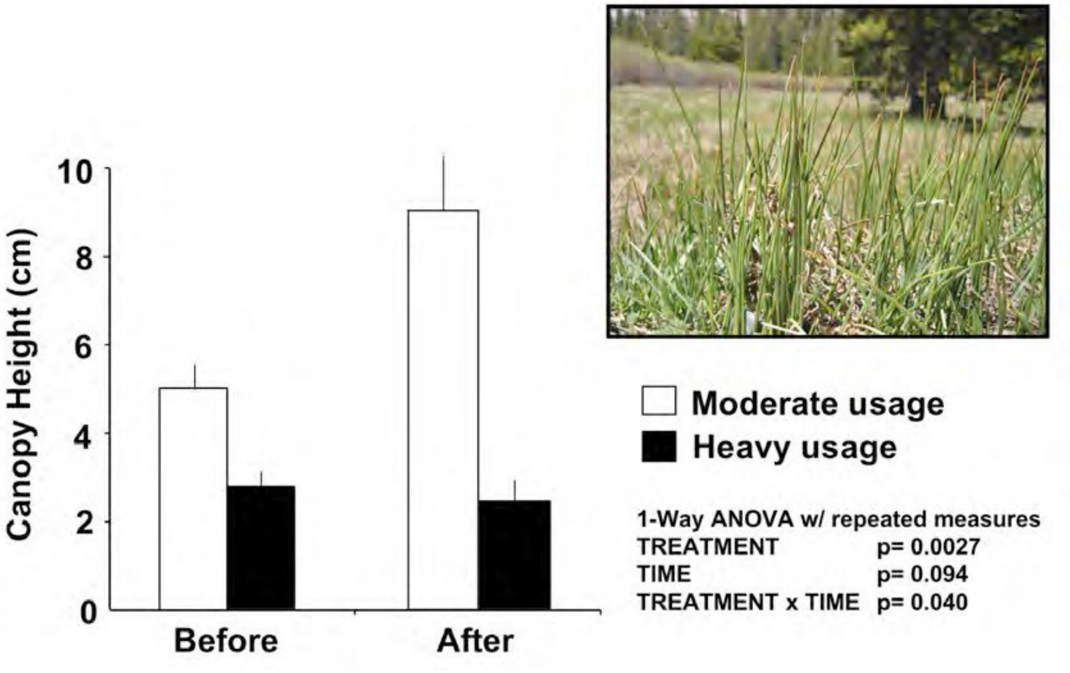


Fig. 40. Mean (SE) canopy height in moderately and heavily used portions of the Meadows before and after experiment. n= 10.

(Fig. 41; TREATMENT p= 0.00030), and green cover increased on the moderately used plots during the growing season while decreasing in the heavily used portions of the meadow (Fig. 41; TREATMENTxTIME p= 0.0085). Although neither treatment or interaction terms were significant for mean bare cover (Fig. 42; TREATMENT p= 0.19; TREATMENTxTIME p= 0.060), there was a significant increase across plots with time (Fig. 42; TIME p= 0.021). As there was no change on the moderately used plots, this temporal increase can be attributed to the increase in bare ground on the heavily used plots. Standing crop was about six times greater on the moderately used plots as on the heavily

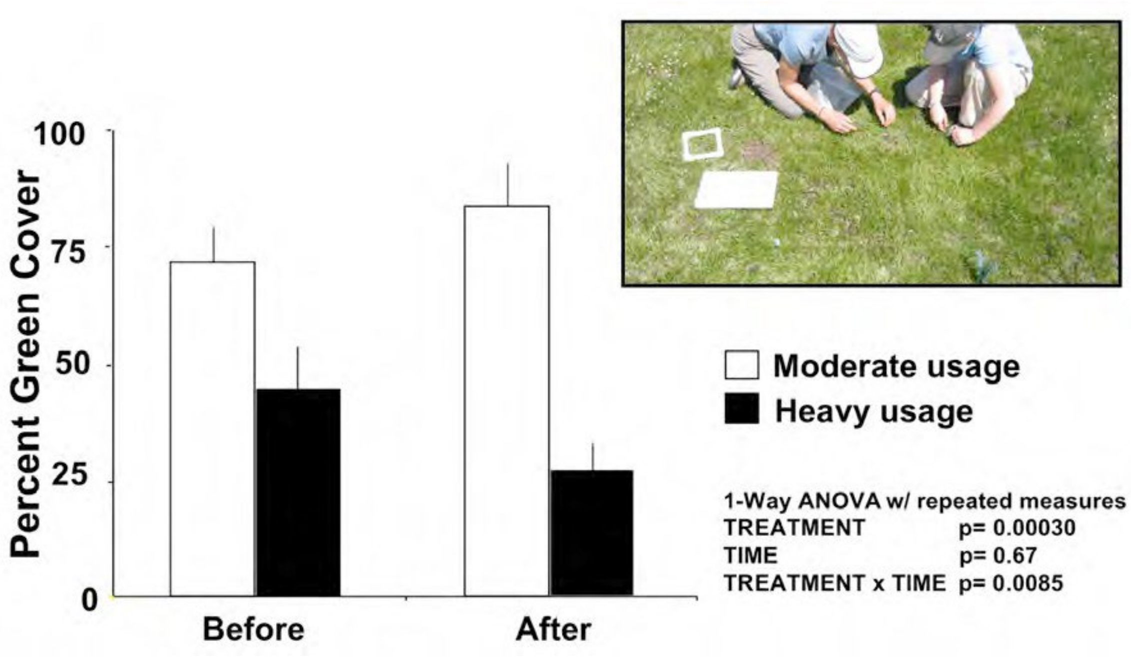


Fig. 41. Mean (SE) percent green cover in moderately and heavily used portions of the Meadows before and after experiment. n= 10.

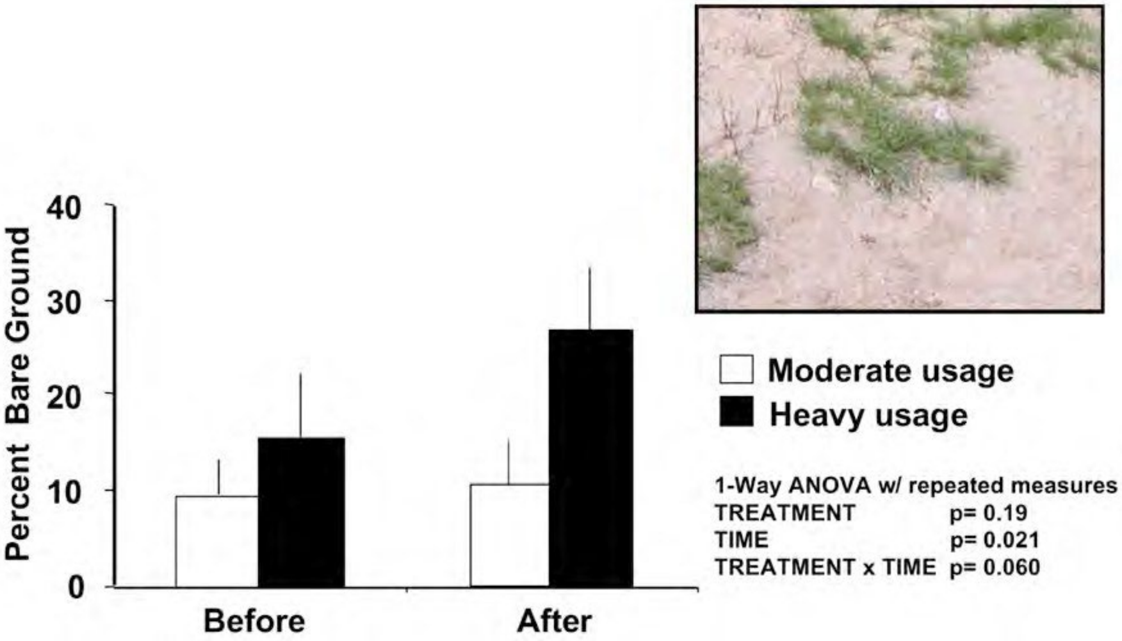
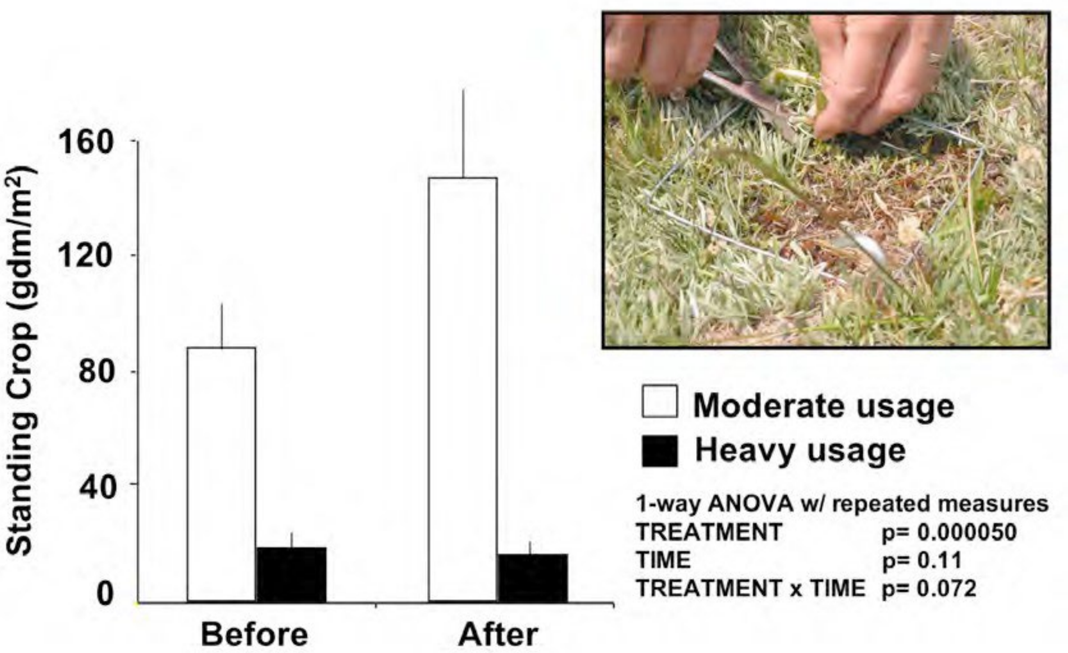


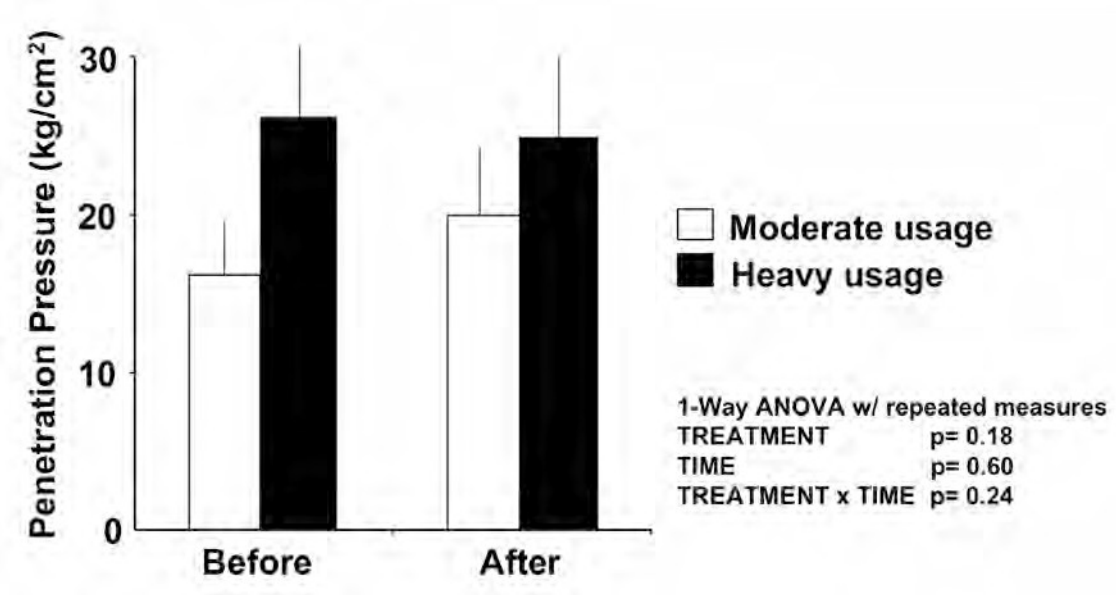
Fig. 42. Mean (SE) percent bare ground in moderately and heavily used portions of the Meadows before and after experiment. n= 10.

used plots (Fig. 43; TREATMENT p= 0.000050), but the observed increase during the season relative to the heavily used plots was not significant (Fig. 43; TREATMENTxTIME p= 0.072). Although penetration pressure was greater on the heavily used plots, there was an increase in pressure on the moderately used plots, though neither of these trends was significant (Fig. 44; TREATMENT p= 0.18; TREATMENTxTIME p= 0.24). Soil moisture was at least twice as high on the moderately used plots as on the heavily used plots (Fig. 45; TREATMENT p= 0.0018) and decreased markedly on all plots through the season (Fig. 45; TIME p= 0.000010; TREATMENTxTIME p= 0.97).



1-way ANOVA w/ repeated measures
TREATMENT p= 0.000050
TIME p= 0.11
TREATMENT x TIME p= 0.072

Fig. 43. Mean (SE) standing crop in moderately and heavily used portions of the Meadows before and after experiment. n= 10.



1-Way ANOVA w/ repeated measures
TREATMENT p= 0.18
TIME p= 0.60
TREATMENT x TIME p= 0.24

Fig. 44. Mean (SE) penetration pressure in moderately and heavily used portions of the Meadows before and after experiment. n= 10.

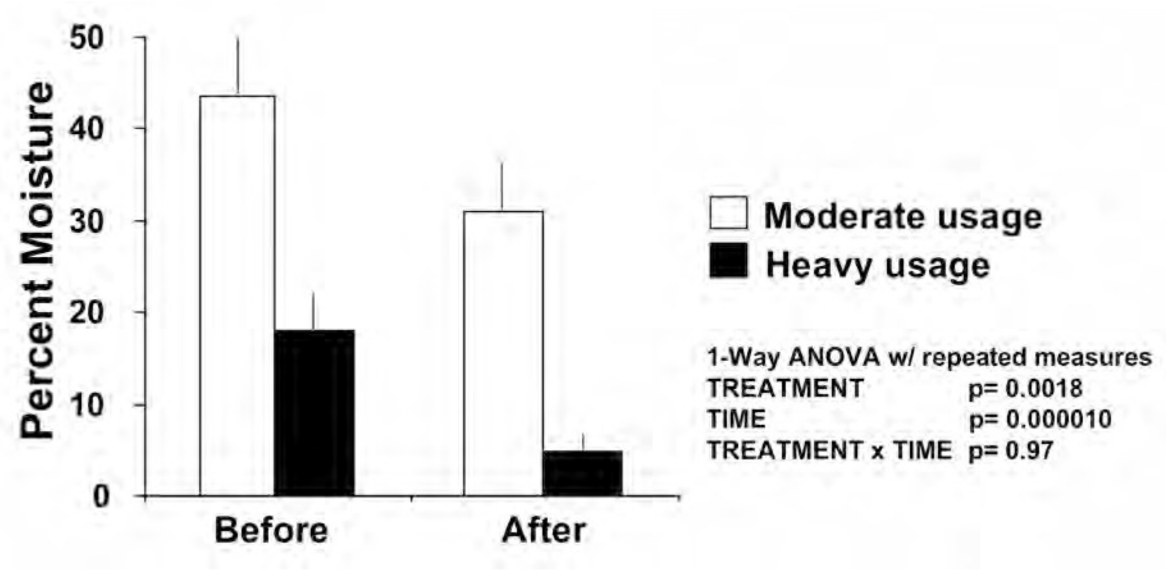


Fig. 45. Mean (SE) soil moisture in moderately and heavily used portions of the Meadows before and after experiment. n= 10.

Fauna assemblages were generally much more abundant and diverse where usage was less. There were over *30 times* more fauna on moderately used plots than on heavily used plots (Fig. 46; TREATMENT p= 0.017). Although numbers dropped on the moderately used plots, there were still 20 times more animals than on the heavily used plots at the end of the season (Fig. 46). Species richness and family richness showed similar patterns and were many times greater on moderately used plots (Figs. 47, 48; TREATMENT p= 0.0075 and p= 0.0067, respectively). There was an average of only 0.5 species/0.25m^2 on the heavily used plots. Ants demonstrated similar relationships in space and time, though not as strongly, and the spatial differences were non-significant (Fig. 49; TREATMENT p= 0.41).

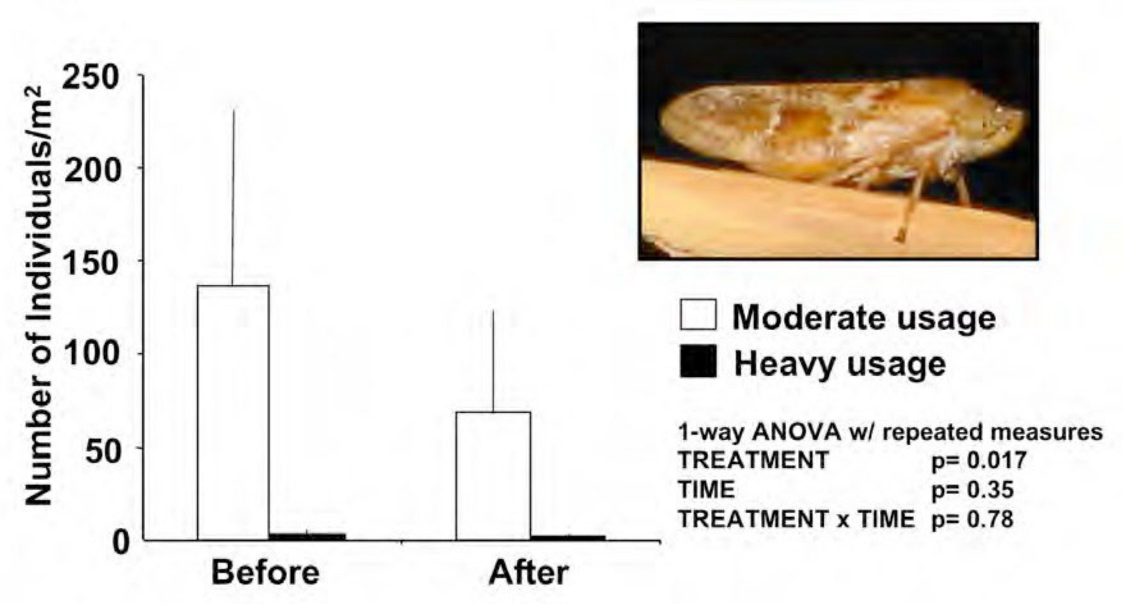


Fig. 46. Mean (SE) arthropod abundance in moderately and heavily used portions of the Meadows before and after experiment. n= 10.

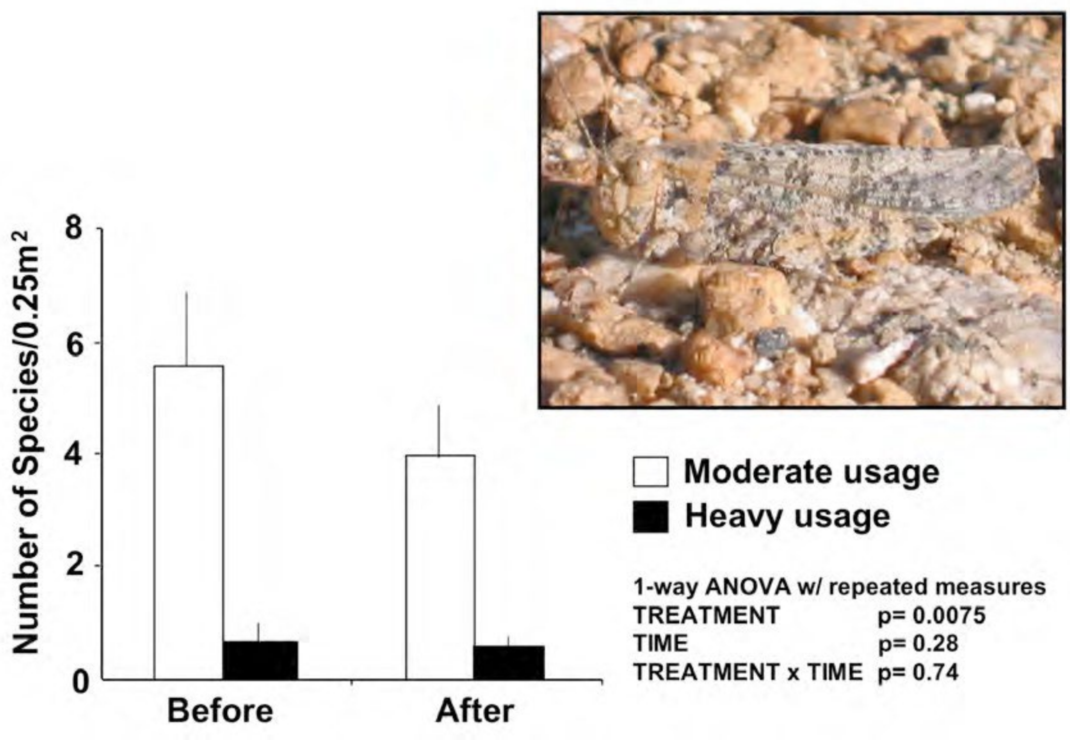
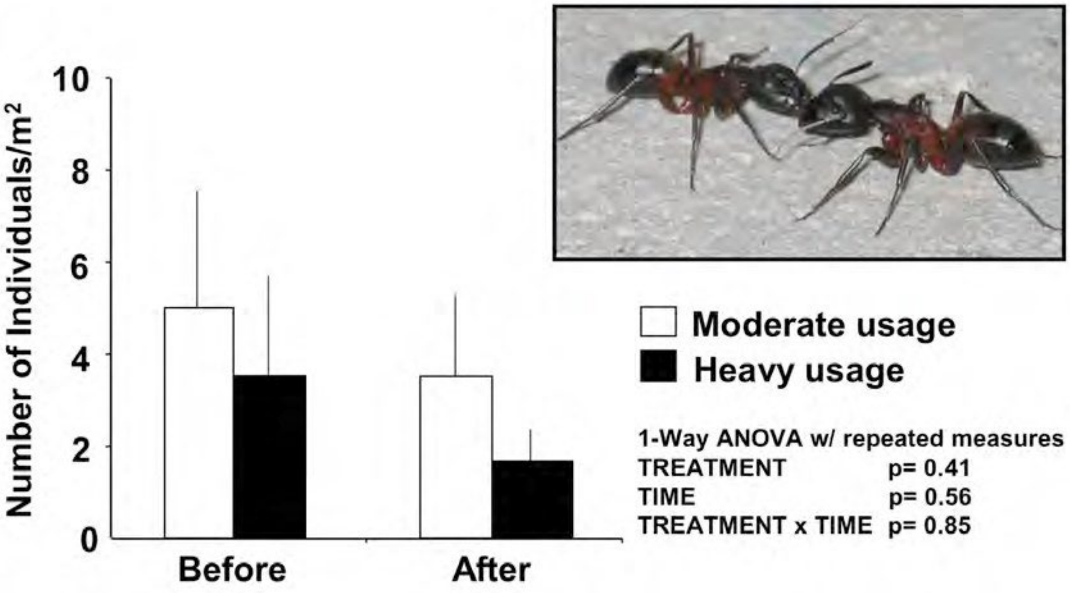


Fig. 47. Mean (SE) arthropod species richness in moderately and heavily used portions of the Meadows before and after experiment. n= 10.

1-Way ANOVA w/ repeated measures
TREATMENT p= 0.0067
TIME p= 0.16
TREATMENT x TIME p= 0.51

Fig. 48. Mean (SE) arthropod family richness in moderately and heavily used portions of the Meadows before and after experiment. n= 10.



1-Way ANOVA w/ repeated measures
TREATMENT p= 0.41
TIME p= 0.56
TREATMENT x TIME p= 0.85

Fig. 49. Mean (SE) ant density in moderately and heavily used portions of the Meadows before and after experiment. n= 10.

The fauna on the heavily used plots was strikingly depauperate (Table 6). The only arthropods present were a small number of leafhoppers and ants. In contrast, more than 30 families were represented in the moderately used meadow. There were no grasshoppers, true bugs, beetles, wasps, butterflies, moths, flies, spiders, or mites present where foot traffic was heavy.

All measured metrics indicated poorer ecological condition on the heavily used plots relative to the moderately used areas (Fig. 50; one-tailed sign test, $p < 0.0005$). Further, no metrics showed a positive change during the growing season on the heavily used plots (Fig. 50; one-tailed sign test, $p < 0.0005$), whereas there was no overall pattern on the moderately used plots (Fig. 50; one-tailed sign test, $p > 0.25$).

Visitation patterns

Daily visitation patterns approximated a normal distribution (two-tailed sign test; $p < 0.05$) with the apex of usage at mid-day (Fig. 51). Daily use dropped off dramatically at 1800 hours. Highest usage was in the meadow habitat near the Soda Springs trailhead (Fig. 52).

Table 6. Densities per m^2 of fauna in areas of the Meadows that receive moderate versus heavy usage. "Moderate" plots were controls from the addition experiment, whereas "Heavy" plots were controls from the exclosure experiment. Blanks, rather than "zeros," are used to indicate that a given taxon was not present. n= 10. Continued next page.

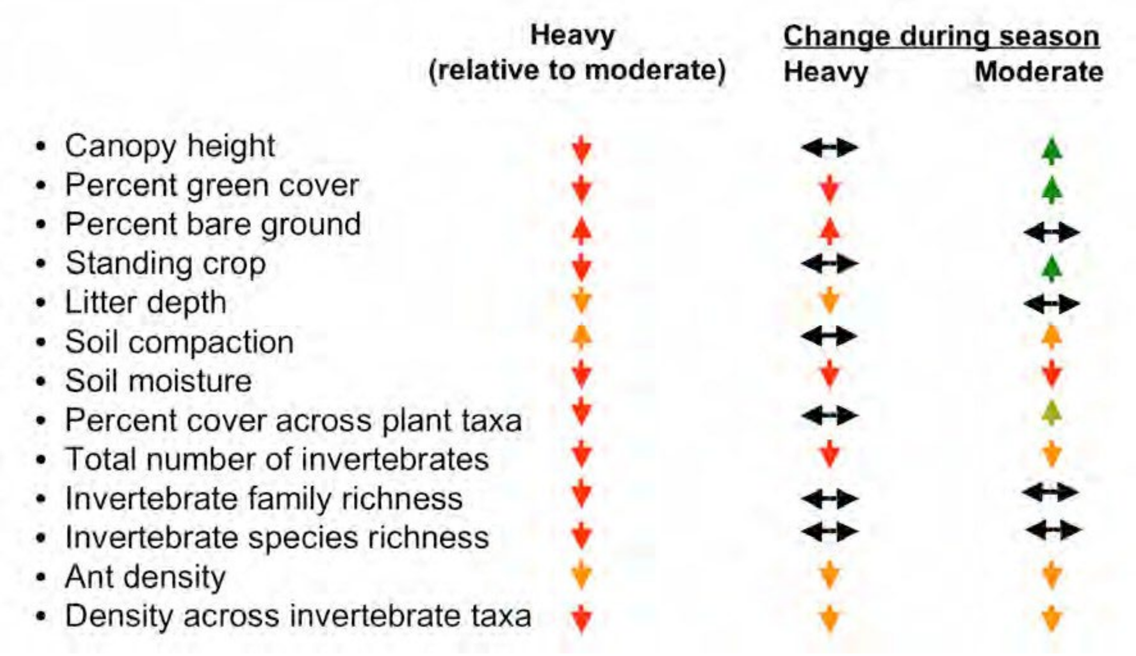
	Before				**After**			
	Moderate		**Heavy**		**Moderate**		**Heavy**	
	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)
Orthoptera	0.40	(0.40)			0.40	(0.40)		
Acrididae	0.40	(0.40)			0.40	(0.40)		
Hemiptera	4.8	(3.9)			2.4	(1.6)		
Lygaeidae	0.80	(0.53)			1.2	(1.2)		
nymphs	4.0	(4.0)			1.2	(1.2)		
Homoptera	2.0	(1.2)	0.8	(0.53)	3.6	(1.6)	1.2	(1.2)
Cicadellidae	1.6	(0.88)	0.8	(0.53)	2.8	(1.3)	1.2	(1.2)
Delphacidae	0.40	(0.40)			0.40	(0.40)		
Aphididae					0.40	(0.40)		
Coleoptera	2.4	(1.4)			1.2	(0.85)		
Carabidae	0.40	(0.40)						
Scarabaeidae	1.2	(0.61)			0.80	(0.80)		
Coccinellidae	0.40	(0.40)						
Anthicidae	0.40	(0.40)						
Chrysomelidae					0.40	(0.40)		

Table 6 (cont.). Densities per m^2 of fauna in areas of the Meadows that receive moderate versus heavy usage. Continued next page.

	Before				**After**			
	Moderate		**Heavy**		**Moderate**		**Heavy**	
	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)
Hymenoptera	5.2	(2.7)	3.6	(2.0)	4.0	(1.7)	1.6	(0.88)
Braconidae					0.40	(0.40)		
Pteromalidae	0.40	(0.40)						
Formicidae	4.8	(2.7)	3.6	(2.0)	3.6	(1.7)	1.6	(0.88)
Lepidoptera					0.40	(0.40)		
Other					0.40	(0.40)		
Diptera	111	(100)			55	(52)		
Culicidae	0.80	(0.80)						
Sciaridae	3.6	(1.9)			0.40	(0.40)		
Empididae	0.40	(0.40)						
Lonchopteridae	4.0	(4.0)			0.80	(0.80)		
Phoridae					0.40	(0.40)		
Anthomyiidae	2.0	(1.1)						
Muscidae	0.80	(0.80)			0.80	(0.80)		
Sepsidae								
Chloropidae	0.80	(0.80)			0.40	(0.40)		
Sphaeroceridae	95	(92)			42	(41)		
Drosophilidae	2.4	(2.4)			9.2	(9.2)		
Ephydridae					0.40	(0.40)		
Other	0.8	(0.53)			0.40	(0.40)		

Table 6 (cont.). Densities per m^2 of fauna in areas of the Meadows that receive moderate versus heavy usage.

	Before				**After**			
	Moderate		**Heavy**		**Moderate**		**Heavy**	
	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)
Araneae	5.2	(2.1)			1.6	(0.88)		
Tetragnathidae	1.2	(1.2)						
Linyphiidae	2.4	(1.6)						
Thomisidae					1.6	(0.88)		
Salticidae	1.2	(0.61)						
Other	0.40	(0.40)						
Acari	3.6	(2.3)			2.4	(1.7)		



	Heavy (relative to moderate)	Change during season Heavy	Change during season Moderate
Canopy height	↓	↔	↑
Percent green cover	↓	↓	↑
Percent bare ground	↑	↑	↔
Standing crop	↓	↔	↑
Litter depth	↓	↓	↔
Soil compaction	↑	↔	↑
Soil moisture	↓	↓	↓
Percent cover across plant taxa	↓	↔	↑
Total number of invertebrates	↓	↓	↓
Invertebrate family richness	↓	↔	↔
Invertebrate species richness	↓	↔	↔
Ant density	↓	↓	↓
Density across invertebrate taxa	↓	↓	↓

Fig. 50 . Summary of differences between moderately and heavily used portions of the Meadows as well as changes over the course of the growing season. Upward and downward facing arrows indicate an increase or decrease, respectively, for a given metric. Dark green arrows represent strong positive changes, the light green arrow represents a weak positive change, orange arrows indicated weak negative effects or relative differences, and red arrows indicate strong negative changes or relative differences. The double-headed horizontal arrows indicate no change.

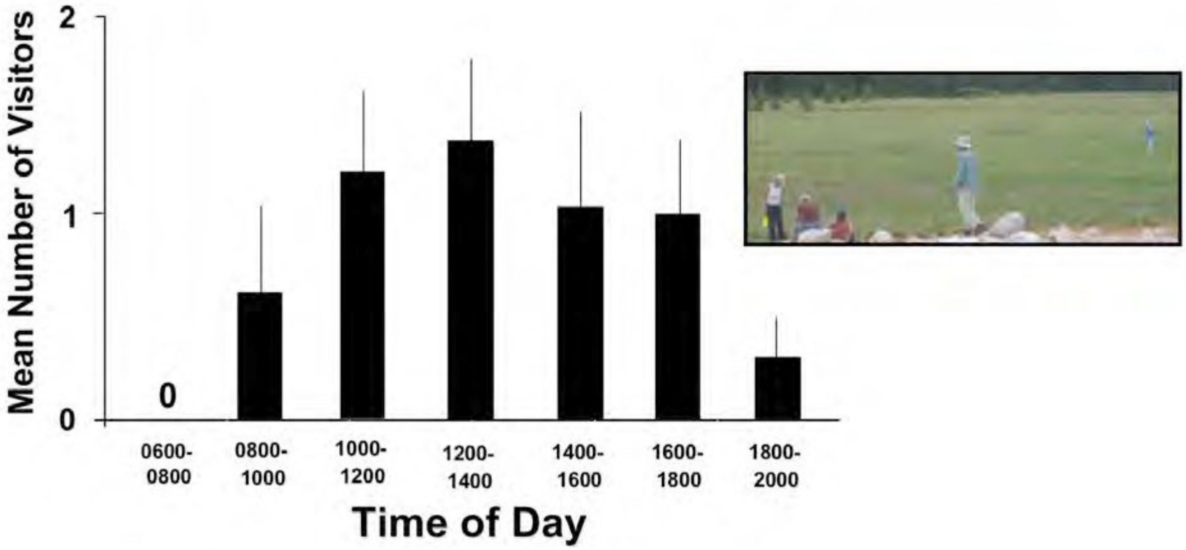


Fig. 51. Temporal distribution of visitation patterns in Tuolumne Meadows. n= 87.

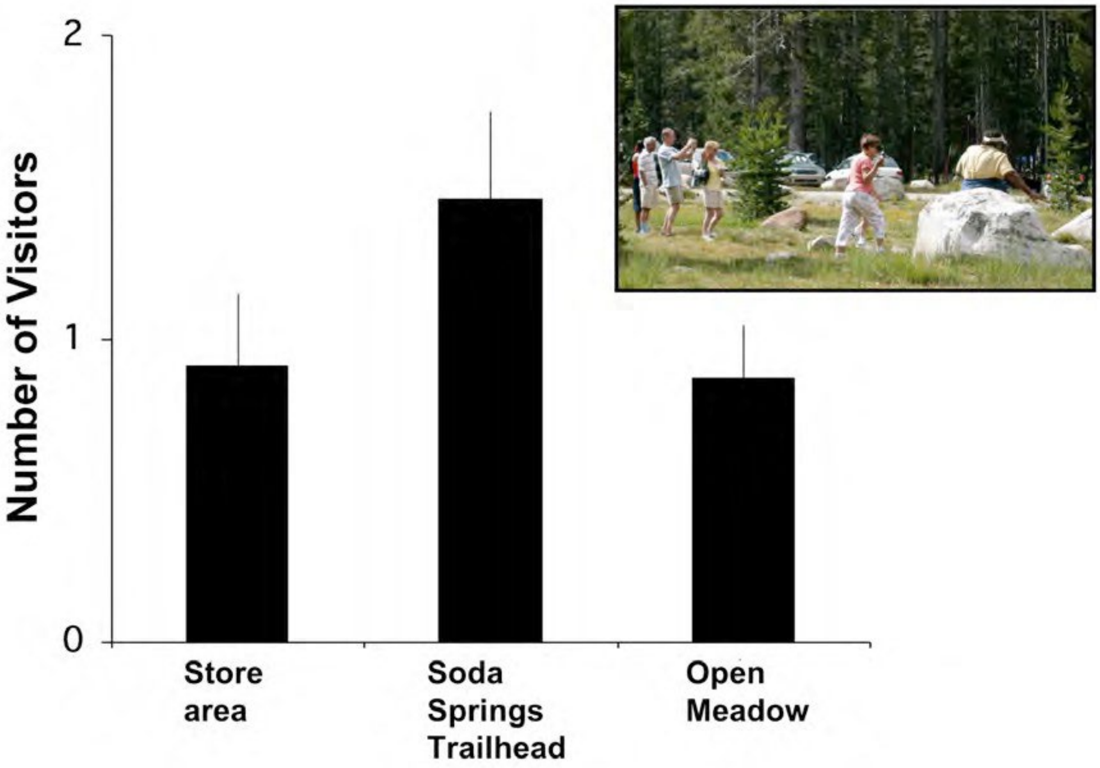


Fig. 52. Visitation in three heavily used portions of the Meadows. n= 87 for the "Store" and "Trailhead" areas and n= 79 for the "Open Meadow."

Discussion

Addition experiment

At the outset of the study, we thought that the long history of heavy usage in Tuolumne Meadows might have left highly resistant assemblages and that addition plots could be slow to respond to experimental trampling pressure. However, impact was immediate and severe. The Meadows are clearly still very sensitive to additional impact, and the threshold for impact appears to be remarkably low, as plots showed negative effects of trampling after only one or two weeks of added trampling pressure. Further, these results should be viewed as conservative as vegetation, soil moisture, and fauna on the small addition plots may have had various forms of subsidy from unaffected neighboring habitat. This initial first year of study sought to determine general susceptibility to trampling by establishing a coarse threshold for impact. The actual threshold for damage is clearly much lower than the levels of disturbance applied in this first year, and further work is strongly recommended in order to identify minimum levels of trampling that are likely to cause impact.

Various forms of habitat degradation in response to trampling were apparent across almost all measures. One interesting exception was soil moisture which decreased equally on both control and addition plots. Decreases in soil moisture through the growing season have been previously noted in

Sierra subalpine meadows across plant assemblages (e.g., Klikoff 1965). Although our Tuolumne plots generally had higher moisture levels than Klikoff's Gaylor Lakes plots, our *Carex* plots had somewhat lower moisture levels than his *Carex* samples. The lack of trampling control-experimental differences in soil moisture has also previously been noted (Harvey et al. 1972). Possible explanations include: 1) the soil compaction sealed water into the interstices of the soil and thus offset moisture losses (A and L Flint, pers. comm.), 2) there was seeping into the addition plots from surrounding unmanipulated soil, and/or 3) transpiration was reduced on the experimental plots as a result of reduced plant cover and standing crop.

Comparisons across vegetation assemblages indicated remarkable consistency of trampling effect. Moore et al. (2000) also found more similarities than differences among *Calamagrostis*, *Carex*, and *Deschampsia cespitosa* assemblages in response to a stock grazing experiment, although increases in bare ground and decreases in plant cover appeared earlier for *Carex* than for *Calamagrostis*. As with our trampling work, Moore et al. did not observe changes in plant species richness in response to the experiment. There were subtle differences in responses to human trampling as a function of vegetation type, and there are some indications that *Ptilagrostis* may be slightly more vulnerable than other assemblages. We initially thought that the generally wetter *Oreostemma* assemblage might demonstrate the most impact, because 1) visual impact was the most apparent in this habitat (Fig. 9), 2) previous work indicates that herbaceous flora is less resistant to trampling (Wagner 1964, Harvey et al. 1972) than grasses and in particular sedges (Harvey et al. 1972), and 3) trampling disturbance can be greater in softer substrate conditions (Eckrich and Holmquist 2000). However, there is no evidence to suggest that *Ptilagrostis* is overly sensitive and that the other assemblages are relatively resistant to trampling. We cannot recommend special treatment for some assemblages and less for others. Instead, there is substantial evidence that all common vegetation types are very sensitive to trampling.

Higher trophic levels were also affected by the experimental trampling. Although this impact is not visible upon casual observation, the propagation of trampling disturbance through the food web is of concern. Affected fauna included 1^{o} through 4^{o} consumers, including a number of taxa that are in turn important prey for vertebrate taxa. Some of the affected groups, such as ants, are particularly important as processors of organic material and as bioturbators (Holmquist 2004; Holmquist and Schmidt-Gengenbach 2006). Ants may serve as keystone taxa in a number of systems (Andersen and Majer 2004). The observed impacts on fauna were likely a function of habitat modification and destruction, and given that the trampling lanes were only 0.5m wide, the significant effects on fauna were striking. It is likely that many of the animals collected after the experiment on the addition plots were transients subsidized by the surrounding habitat. Even moderately larger plots would likely have had even more pronounced effects on invertebrates.

This experiment used a *known* level of disturbance to examine effects on the entire meadow assemblage. In the accompanying exclosure experiment, we assessed recovery from *unknown* levels of disturbance. The following years represent a remarkable opportunity to track recovery following the known levels of impact applied in 2006. Indeed, tracking of recovery on experimentally disturbed plots is standard practice in trampling projects, e.g., (Harvey et al. 1972, Cole and Bayfield 1993, Eckrich and Holmquist 2000). The plots used in our 2006 trampling additions will recover, at some unknown rate, regardless of whether or not follow-up assessment is done. This information will be lost if an assessment is not conducted through the next growing seasons. We advocate follow-up work in 2009 and 2010, in order to gain a precise understanding of how much time is required for recovery from moderate trampling pressure.

Exclosure experiment

We initially thought that it would be difficult to exclude visitors from heavily-used areas, but our low profile exclosures were very effective. The support from visitors is encouraging, and this success suggests that minimal, unobtrusive techniques can be used to virtually eliminate pressure on habitat targeted for restoration.

The addition experiment indicated that the subalpine habitat in Tuolumne Meadows is still exquisitely sensitive to trampling impact, and the exclosure experiment indicated that, once severely damaged, habitat is slow to recover. Although there were indications that some minimal recovery was beginning (Fig. 34), there was no significant recovery demonstrated by any of the examined vegetation, physical, or faunal metrics in the first two years of study. Although the $2m^2$ exclosure plots were not as small as the trampling addition plots, larger exclosures would likely have had somewhat more recovery, because the ambient trampling surrounding the additions probably lessened the habitat quality present within the exclosures. Further, the exclosures represented relatively small “islands” for fauna (the inverse of the landscape context for the addition plots), and larger exclosures might be expected to recruit more fauna.

Although little recovery was noted on the exclosure plots during the growing season, differences in late fall, after vegetation had become senescent, were significant and visually apparent in the field (e.g., Fig. 39). It appears that the meadow vegetation was less resistant to trampling after senescence and that heavy trampling in the fall broke down standing plant structure and opened bare space. Trampling apparently reduced senescent vegetation to litter. Although litter accumulations might therefore be expected on the control plots, there was no apparent litter accumulation on either controls or exclosures. If standing brown vegetation was removed by trampling on the control plots and litter accumulations were not observed, then the litter must either be finely divided and completely incorporated into the substrate or exported from the plots by wind. The substrate on the two sets of plots did not differ visually, suggesting wind export. Litter export by increasing fall winds might be further exacerbated by the reduction in canopy height and a commensurate decrease in boundary layer thickness (e.g., Geiger 1959, Vogel 1994). If litter is consistently exported from trampling areas, this nutrient loss may represent a positive feedback and lead to further habitat degradation.

There was no indication of artifacts resulting from the experimental exclosures. A single warbler was observed perching on an exclosure dowel on the first day of the experiment, but we did not observe bird usage of the exclosure structures after that first day, nor did we note any other sources of artifacts.

We maintained the exclosures through fall in both 2006 and 2007 in order to extend the period of trampling reduction well past the end of the growing season. We advocate longer exclosure experiments to determine whether or not recovery can be expected within a reasonable period of time. It is likely that recovery is not a linear process, and three or more years may be required before significant recovery processes are observed.

Comparison of heavily and moderately used portions of the Meadows

Some of the heavily used sites are more upland in character than the moderately used sites (see also Cooper et al. 2006), and this context could explain some of the observed differences. However, meadow habitat subject to the greatest amount of foot traffic demonstrated strikingly poorer ecological condition relative to the less trammeled portions of the Meadows. In particular, a massive loss of trophic diversity was apparent in the heavily trampled areas, as only a remnant of the typical subalpine meadow fauna (Table 6; see also Holmquist and Schmidt-Gengenbach 2006) was present on these heavily used sites (Table 6). Much of the food web was non-existent: gone were the miners, borers, frugivores, pollen feeders, nectar feeders, root feeders, scatophages, obligate predators of all levels, and parasites. Pollinators were absent. Arthropod biodiversity losses of this nature are likely to in turn affect plant assemblage structure and fitness (e.g., Johnson et al. 2006). Trampling pressure probably explains much, though doubtless not all, of the observed differences in ecological condition, and this contention is supported by causal relationships revealed by the addition experiment.

The deterioration of habitat quality in heavily used areas within the growing season is also of concern. While most vegetation parameters showed increases through the growing season on the moderately used plots, these same measures generally decreased during the season on the heavily used plots. Assessment of meadow condition at only the start of the growing season would have overestimated habitat quality in heavily trampled areas.

Invertebrate assemblages in subalpine meadows become more depauperate at the end of the growing season (Holmquist and Schmidt-Gengenbach 2004, 2006), and these decreases in diversity and abundance were seen on both heavily and moderately trampled areas of the Meadows. Decreases were more pronounced for some metrics in heavily trampled areas than in moderately trampled areas, whereas differences were not apparent for others. In the latter cases, the values were generally very low in the heavily trampled areas. These very low numbers suggest that the few ants and leafhoppers present may have been transients rather than residents in this poor quality habitat.

It should be remembered that the heavily trampled areas were not compared with “pristine” meadow habitat. Rather, the comparison group was meadow habitat that currently receives moderate trampling. The clear differences in the plant and animal assemblages between the two areas of the Meadow further suggest the presence of thresholds for trampling damage and underscores the need for experimentation designed to determine the levels of these thresholds for damage resulting from trampling pressure.

Visitation patterns

The heaviest used portions of the Meadows were near the store and Soda Springs trailhead. We were surprised to find that the store area had less usage than the off-trail area near the parking for Soda Springs Trailhead. It is likely that visitors are simply more visible from the road near the store. These results emphasize the need for quantitative assessment of visitor use patterns versus over-reliance on the casual observations that we all make as we work in the Park.

The area near the Soda Springs trailhead has several prominent social trails that have received some attention (J Bacon, pers. comm.). It should be noted that in addition to this social trail usage there is also a great deal of diffuse trampling away from both the Park maintained Soda Springs trail and the social trail network. This area appears to receive the greatest use of any meadow habitat in Tuolumne Meadows, and it is unfortunate that visitors encounter such degraded habitat at what will in many cases be their only stop in the Meadows. Interventions to appropriately channel visitors and protect habitat may be advisable for this area.

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