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Patch-scale effects of equine disturbance on arthropod assemblages and vegetation structure in subalpine wetlands

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Abstract Assessments of vertebrate disturbance to plant and animal assemblages often contrast grazed versus ungrazed meadows or other larger areas of usage, and this approach can be powerful. Random sampling of such habitats carries the potential, however, for smaller, more intensely affected patches to be missed and for other responses that are only revealed at smaller scales to also escape detection. We instead sampled arthropod assemblages and vegetation structure at the patch scale (400 – 900 m² patches) within subalpine wet meadows of Yosemite National Park (USA), with the goal of determining if there were fine-scale differences in magnitude and directionality of response at three levels of grazing intensity. Effects were both stronger and more nuanced than effects evidenced by previous random sampling of paired grazed and ungrazed meadows: a) greater negative effects on vegetation structure and fauna in heavily used patches, but b) some positive effects on fauna in lightly grazed patches, suggested by trends for mean richness and total and population abundances. Although assessment of disturbance at either patch or landscape scales should be appropriate, depending on the management question at hand, our patch-scale work demonstrated that there can be strong local effects on the ecology of these wetlands that may not be detected by comparing larger-scale habitats.

Keywords: Horse and mule grazing, Pack stock, Subalpine wetland, Terrestrial arthropod assemblages, Vegetation structure, Disturbance

Introduction

Ecological phenomena, and our ability to detect them, change as a function of scale, and such scaling discontinuity is a central problem in ecology and land management (Hansson et al. 1995; Wettstein and Schmid 1999; Hatfield and LeBuhn 2007; Powell et al. 2013). Pattern and process may be investigated at a scale that is larger or smaller than the scale at which the phenomena of interest are most strongly expressed (Holling 1992; Hansson et al. 1995; Dumbrell et al. 2008). The apparent effects of disturbance, particularly of moderate disturbance, on diversity and other faunal assemblage characteristics can be significantly influenced by the spatial scale of sampling, to the extent that directionality of response may be reversed (Hill and Hamer 2004; Dumbrell et al. 2008).

Livestock can produce habitat patchiness at both the landscape scale and at smaller scales (Wiens 1985). Landsberg et al. (2002), in an effort to determine whether conclusions based on larger scales could be scaled down effectively, found positive effects of sheep grazing on plant assemblages at a scale of kilometers but negative effects at a regional scale. Olf and Ritchie (1998) and Deléglise et al. (2011) have similarly demonstrated that grazing produces differing effects on plant assemblage richness and heterogeneity across different scales of examination. In contrast, Wesuls et al. (2013) found little difference in indications of livestock grazing impacts on vegetation at scales of 150 m versus 1500 m.

Many studies focusing on livestock disturbance to plant and animal assemblages contrast grazed versus ungrazed meadows or other larger managed areas (e.g., Reimold et al. 1975; Hatfield and LeBuhn 2007; Holmquist et al. 2010; 2013a; b). Such an approach can be powerful, and in some such studies represents a de facto, replicated, long-term experiment. Random sampling of replicate grazed and ungrazed meadows or pastures, typically 1 - 30 ha in

size, is however accompanied by the potential for smaller, more intensely affected patches to be missed and for other responses that are revealed only at smaller scales to also escape detection. Such random sampling may fail to capture fine-grain differences in grazing effects on diversity and abundance of flora and fauna within grazed areas. Patch-scale, rather than meadow-scale, sampling was the focus of the current study.

Pack stock, primarily mules and horses, are used in many mountainous areas for transportation of people and supplies, and grazing and/or trampling by these large, steel-shoed herbivores are known to alter trails (DeLuca et al. 1998) and wetland vegetation in the sensitive subalpine zone (McClaran 1989; Cole et al. 2004; Holmquist et al. 2010; 2013a; b). Reported effects on wetland arthropod fauna, however, have ranged from minor to nil (Holmquist et al. 2010; 2013a; b), but this comparative lack of response may have been a function of effects that are expressed at a fine scale and might not be detectable by random sampling of meadows. Horses often concentrate grazing in relatively small areas (Loucougaray et al. 2004; Beever and Herrick 2006; Edouard et al. 2009), resulting in patches of short vegetation and disrupted soils (Ödberg and Francis-Smith 1977; Menard et al. 2002). Arthropod response to disturbance can be localized and mediated by such fine-scale habitat heterogeneity (Kruess and Tscharncke 2002a; Hatfield and LeBuhn 2007).

In this study, we sampled 400 – 900 m² patches within complexes of subalpine wet meadows of Yosemite National Park (Sierra Nevada, California, USA), with the goal of determining if there were fine-scale differences in magnitude and directionality of grazing effects at three levels of grazing intensity (Heavy, Light, and Ungrazed). We examined response of all terrestrial arthropod groups as well as vegetation structure in order to assess ecosystem response

across trophic levels and to examine both direct and indirect effects of disturbance (Wettstein and Schmid 1999; Koricheva et al. 2000; Pocock et al. 2012).

Methods

Overview

We used a 1x3 blocked design that consisted of wetland complexes that included a) patches that were known to have been heavily grazed (Heavy), b) patches that were known to be lightly grazed (Light), and c) patches that were ungrazed (Ungrazed). We located ten complexes of subalpine wet meadow habitat in Yosemite that included portions with a long history of grazing (see Study Area and Sites; Fig. 1) and were known to have both lightly and heavily grazed areas; six complexes also included habitat that had been exposed to less than one stock night/ha/year for the last 20 years (likely no grazing in some of these areas; 26 total sites). We focused on wetland patches dominated by the tall, rhizomatous sedge *Carex utriculata* L. Bailey (Benedict 1983), the balance of habitat being drier (see Benedict 1983 and Stohlgren et al. 1989 for other common plant taxa in these wet meadow assemblages). This forage habitat remains flooded for one or two months after snowmelt, i.e., typically through June and thus well into the subalpine growing season, and during this time provides a wealth of habitat for aquatic fauna (Holmquist et al. 2011). The sedge assemblage also harbors a particularly diverse and abundant terrestrial arthropod fauna, and pack stock have greater effect on the sedges than on drier wetland vegetation (Holmquist et al. 2013b). The sedge habitat is thus both particularly valuable as habitat and among the most likely assemblages to be affected by localized heavy grazing. The strong local dominance by the sedge made its habitat easily distinguishable from other habitats across study locations and among treatments. Arthropod diversity and abundance in Sierra

wetlands decrease sharply at the end of the growing season (Holmquist et al. 2013a; Millar et al. in press), and we therefore sampled sites just prior to meadow senescence in late July of 2012. Both annual and long-term grazing can have effects on flora and fauna, and both influences can be captured by sampling just before senescence (Holmquist et al. 2013a).

Study area and sites

Subalpine wet meadows in the central Sierra Nevada are typically in stream basins surrounded by lodgepole pine (*Pinus contorta* Loudon) forests, at an average elevation of 2,670 m (Holmquist et al. 2011). Stock grazing began about three weeks after snowmelt, and grazing intensities averaged 63 stock nights/ha/year (SE = 44, Yosemite National Park records). Meadow complexes included a range of wetland sizes (1.3 to 25.7 ha; $\bar{x} = 11.5$ ha, SE = 2.9). Elevations were representative of grazed subalpine wet meadows ($\bar{x} = 2,665$ m, SE = 43, range 2,227 – 2,885 m) and differed among meadow complexes ($P < 0.0001$) but did not differ by treatment ($P = 0.29$). We sampled wet meadow complexes at Cold Canyon, Hook Lake, Miller Lake, Matterhorn Canyon, Smedberg Lake, Benson Lake, Emeric Lake, Merced Lake, and two sites in upper Lyell Canyon (Fig. 1). Pack stock tend to use the same areas repeatedly within and among grazing seasons, and patches to be targeted as Heavy, Light, and Ungrazed replicates were selected a priori on the basis of Yosemite National Park observations of stock aggregations within meadows. We verified reported areas of Heavy use by observed concentrations of hoof prints and punches, equine manure, trampling, and cropping marks on vegetation (none of which were response variables to be used in the study) prior to sampling; approximately 15% of grazed sedge habitat showed evidence of such heavy usage. Evidence of stock use in Light areas was verified as being minimal but present by use of the same non-response variable indications of

stock use. Two Heavy, Light, and Ungrazed subsample locations were selected from available habitat of each type within each wetland complex (stratified random selection), and resulting subsample data were averaged for analysis. Centroids of sampled patches were in close proximity within each wet meadow complex ($\bar{x} = 309$ m, SE = 97); Light and Heavy patches were closer ($\bar{x} = 95$ m, SE = 26) than either were to sampled Ungrazed habitat ($\bar{x} = 665$ m, SE = 183), but blocks were separated by up to 32 km.

Fauna methodology

Fifty standard sweep net sweeps (New 1998) at each site were evenly allocated to the two subsampling locations in each patch type of each wetland complex. Samples were collected by the same person. Sweeping was done prior to collecting vegetation data at the sites, so as to minimize disturbance (additional faunal sampling details in Holmquist et al. 2010; 2013a).

We identified samples to family (see also Fahrig and Jonsen 1998; Koricheva et al. 2000) and morphospecies (Oliver and Beattie 1996; Derraik et al. 2002). This investigation was particularly broad in that we analyzed responses across all arthropod families; such an approach enhances detection of responses to habitat characteristics and other emergent patterns that structure the functional ecology of ecosystems (Fahrig and Jonsen 1998; Koricheva et al. 2000; Pocock et al. 2012).

Vegetation and Physical Data

We used a randomly-oriented point-intercept transect (20 points, 0.25 m interval) to estimate plant species richness, percent green, standing brown (senescent), and litter cover, as

well as percent bare ground at the same subsample locations that were used for sweep samples. We recorded plant species richness as the number of taxa directly crossed by the transect line, not just at the 20 intercepts that were used for cover estimates. This variable was thus a coarse relative measure only, and plant richness was underestimated, even for this low diversity habitat. We measured soil strength, canopy height, litter depth, stem density, and habitat complexity at two randomly-selected locations along each transect, and data were composited for each site. Soil strength was recorded with a Ben Meadows pocket penetrometer, stem density with a 0.125 x 0.125 m quadrat, and complexity using the pole-touch method (Bestelmeyer and Wiens 2001).

Analysis

Univariate analyses were via 1x3 general linear mixed models that included both a fixed effect (Treatment) and a random effect (Block; df 2,9,14; SYSTAT 12) followed by Tukey's tests. Faunal response variables included abundance, richness, dominance (percent of total sample abundance represented by the most abundant taxon of each sample), percentages of predators and herbivores, and expected number of species ($E(S_{18})$; i.e., richness expected in a sample of eighteen individuals, the lowest observed sample abundance, Hurlbert 1971; Magurran 2004). Vegetation variables were as listed above. We calculated $E(S_{18})$ using Diversity 1.4. Heteroscedasticity was observed for some response variables (Cochran's and $F_{\max}$ tests; Kirk 2013) but was corrected by square-root transformation ($((y)^{0.5} + (y+1)^{0.5})$) of proportional variables and log transformation ($\log(y+1)$) of other variables (Kirk 2013). Total Ungrazed richness expected for ten meadow complexes was estimated via extrapolation (Colwell et al. 2012) using Estimate S 9.1.0 (Colwell 2013). Power for ANOVAs was estimated a priori using G*Power (Mayr et al. 2007). We determined the alpha level necessary in order to have equivalent beta

error (Mapstone 1995; Erdfelder et al. 1996; Dayton 1998; Downes et al. 2002): $\alpha = \beta = 0.16$, and the associated power ($1 - \beta$) was 0.84. Both $\alpha = 0.05$ and $\alpha = 0.16$ are presented as significance thresholds to offer additional perspective for our results, the goal being to avoid Type II error because of the potential anthropogenic effects being investigated (see Holmquist et al. 2010 for additional discussion). We also assessed some trends across variables with two-tailed sign tests and compared rank-abundance distributions with Kolmogorov-Smirnov tests (Magurran 2004).

Multivariate analyses of faunal response included comparisons as a function of Treatment using multi-response permutation procedures (MRPP) in PC-ORD 6 (Peck 2010) and accompanying analyses of dispersion using PERMDISP2 software developed by MJ Anderson (see also Anderson 2001; Ratkowsky 2008). Response and explanatory matrices contained all sites, and the response matrix included morphospecies that were collected in three or more samples (McCune and Grace 2002; Peck 2010; but see Poos and Jackson 2012). We relativized the response matrix by morphospecies totals. The final response matrix had a coefficient of variation of 39%, and 74% of the cells contained zeros. The explanatory matrix contained a coding variable for Treatment. The Sørensen distance measure was used for all analyses, and the distance matrix was rank-transformed prior to the MRPP analyses. The permutational dispersion analysis was based on 9,999 permutations, deviations from centroids, and p-values from ANOVA tables.

Results

A number of vegetation parameters indicated poorer habitat quality in the Heavy patches, whereas Light and Ungrazed patches did not differ (Table 1). Heavy patches had significantly

higher proportions of bare ground (up to 40x greater) and lower green cover, canopy height, complexity, and litter depth relative to the other two treatments. There were also significant block effects for all variables (Table 1).

We identified 7,880 arthropods that represented 78 families (Online Resource 1) and 172 morphospecies, 90 of which were collected in at least three samples. Hemiptera and Diptera dominated the overall assemblage. Abundant taxa included cicadellid leafhoppers ($\bar{x} = 200/50$ sweeps, $SE = 116$), aphids ($\bar{x} = 5.8$, $SE = 1.8$), muscid ($\bar{x} = 20$, $SE = 4.3$), lonchopterid ($\bar{x} = 16$, $SE = 16$), anthomyiid ($\bar{x} = 4.5$, $SE = 1.5$), dolichopodid ($\bar{x} = 4.5$, $SE = 1.5$), and sciarid ($\bar{x} = 4.4$, $SE = 1.2$) flies, chironomid midges ($\bar{x} = 5.7$, $SE = 2.4$), limnephilid caddisflies ($\bar{x} = 6.3$, $SE = 5.3$), and pteromalid wasps ($\bar{x} = 2.6$, $SE = 1.5$; Online Resource 1). Richness of families and morphospecies was highest for Diptera (30 and 68, respectively), Hymenoptera (12, 36), and Hemiptera (11, 30) at the order level. At the family level, we found the highest morphospecies richness among cicadellids (14) and ichneumonid wasps (12).

There was a trend of highest mean faunal abundance and richness in the Light patches, but diversity was highest in Ungrazed habitat, as indicated by differing dominance and $E(S)$ (which adjusts richness as a function of abundance; Table 2). Total richness across all sites was highest on the Light (132) relative to the Heavy (107), and Ungrazed (84, extrapolated to 110.7) patches. There was an overall trend across assemblage metrics of lowest diversity on the Heavy patches (two-tailed sign test, $P = 0.016$). Patterns were also apparent in the rank-abundance relationships, and these distributions differed among the treatments: Light vs. Ungrazed ($P < 0.0001$), Light vs. Heavy ($P = 0.055$), Heavy vs. Ungrazed ($P = 0.096$; Kolmogorov-Smirnov test; note that the Ungrazed relationship would have been somewhat different if based upon ten sites). Although MRPP did not indicate compositional differences across treatments ($P = 0.29$),

there was greater multivariate dispersion for the two grazing treatments (overall $P = 0.041$; $L > U$, $P = 0.0095$; $H > U$, $P = 0.036$; L vs. H , $P = 0.89$).

Patterns across individual taxa indicated an overall positive response to Light grazing (Online Resource 1). There was a strong trend of highest means for individual family abundances in the Light patches relative to both Ungrazed and Heavy (two-tailed sign tests, both $P < 0.0001$), whereas Ungrazed and Heavy did not differ ($P = 0.99$). The trend across morphospecies was similar ($L > U$, $P < 0.0001$; $L > H$, $P < 0.0001$; U vs. H , $P = 0.49$). Further, there were 39 taxa that occurred only in Light patches, versus sixteen uniquely-occurring taxa in Heavy and seventeen in Ungrazed patches (the latter would be an underestimate as a function of sample size).

Discussion

Pack stock grazing produced effects on fauna and vegetation that differed across the investigated grazing intensities and also from effects indicated by larger-scale studies using random sampling in paired grazed and ungrazed meadows (Holmquist et al. 2013a; b; Table 3). The current patch-scale study revealed effects that were at once stronger and more nuanced: a) greater negative effects on vegetation and fauna in heavily used patches, but b) some positive effects on fauna in lightly grazed patches. There were strong negative effects on canopy height, green cover, and bare ground at the patch-scale, whereas significant differences for these variables were either absent or weaker when assessed via random sampling of grazed versus ungrazed meadows (Holmquist et al. 2013b; Table 3). Similarly, previous work has not detected differences for individual faunal assemblage metrics as a function of pack stock grazing, but we found a number of significant trends for faunal assemblage metrics across the three grazing

treatments at the patch scale, in particular lower diversity in the heavily used patches (Table 3).

Although there were positive stock effects apparent for a small number of taxa in one previous

grazed-ungrazed study focused on early-season conditions (Holmquist et al. 2010), our patch-

scale sampling also revealed broader positive effects of light grazing on assemblage-level

responses suggested by trends for mean richness, and total and population abundances.

Important epigeal taxa such as cicadellid leafhoppers (Schuch et al. 2012) were among the taxa

with a strong positive response to light grazing. A trend of highest abundance and richness in

lightly grazed areas was not necessarily expected. Kruess and Tschardtke (2002a; b) found

abundance and richness to decrease in response to an increasing gradient of cattle grazing

treatments (ungrazed, low intensity, high intensity); differing responses could be a result of

differences in foraging behavior between cattle and equines (Menard et al. 2002; Loucougaray et

al. 2004).

Why were negative effects in heavily used patches so much greater than those detected

by random sampling of paired grazed and ungrazed wetlands (Holmquist et al. 2013a; b)?

Equines do not graze habitat uniformly (Loucougaray et al. 2004; Beever and Herrick 2006;

Edouard et al. 2009) but instead tend to use the same patches repeatedly, creating areas of

reduced canopy height ("grazing lawns") and highly-disturbed substrate (Ödberg and Francis-

Smith 1977; Menard et al. 2002), and the effects on the heavily used patches are probably the

ultimate result of such "patchy" grazing disturbance. A positive feedback mechanism (Rykiel

1985; Turner et al. 1993) was thus likely present and would tend to concentrate impact. Canopy

height, along with other structural elements, was reduced on the heavily used patches (see also

Nolte et al. 2014); canopy height in particular is an important driver of arthropod assemblage

structure (Morris 2000; Kruess and Tschardtke 2002 a; b; Holmquist et al. 2011; 2013b), and

indirect negative effects on arthropods may have been a result. Heavily grazed habitat can be estimated as representing 20.3% (SE = 2.1, personal observation) of grazed meadow area in Yosemite. Random sampling of entire meadows would tend to miss these heavily affected areas, and the divergent patterns seen at the two scales of investigation were likely the result. The lightly grazed patches were apparently below a threshold for significant negative effects on vegetation, although responses were in general nominally intermediate between Heavy and Ungrazed. An additional factor is that the current study was located in a different Park, 160 km to the north of the earlier work (Holmquist et al. 2013b), and was conducted during a different year. These differences could also have contributed to the divergent results observed across studies, although both investigations were conducted at similar elevations and in similar subalpine habitat.

Although a number of faunal metrics responded negatively to both light and heavy grazing, why were there some positive effects of light grazing? A number of factors may be influential at the patch scale. Relatively minor disturbance, such as on Light patches, may injure plants and cause a shift in allocation of plant resources from defenses to below-ground reserves, resulting in increased susceptibility to invertebrate herbivory (Schowalter 1985; but see Boschi and Baur 2007), although the primary defense for many sedges is likely to be silica rather than secondary metabolites (Carnelli et al. 2001). Grazing interacts with nitrogen cycling and soil biota via complex pathways (Ruan et al. 2012; Francini et al. 2014); grazing can increase microbial activity and nitrogen availability (Wardle et al. 2004) which can in turn lead to increases in abundances of herbivorous insects (Bonkowski et al. 2001). Herbivores preferentially colonize lightly disturbed vegetation (Schowalter 1985) and in turn predators and parasites respond to increased prey abundance or release of volatile organic compounds by plants

(Kessler and Baldwin 2001; Howe and Jander 2008), thus potentially increasing patch-scale richness and abundance. Moderate disturbance may increase temperatures within the canopy and at the soil surface of patches, possibly benefiting taxa that are thermophilous at one or more life stages (Bock et al. 2006; Lenoir and Lennartsson 2010). Stem density of this sedge has been shown to increase in response to light to moderate grazing (Allen and Marlow 1994), and fauna may have responded positively to the non-significantly greater stem density that we observed on our Light patches. Livestock dung may benefit arthropods directly via food provision for multiple life stages (Gibson et al. 1992; Morris 2000; Keiper et al. 2002) and indirectly via localized enhancement of vegetation productivity (Wiens 1985) which may in turn positively influence fauna (Bell et al. 2001). Lightly grazed patches may also serve as refugia for fauna displaced from neighboring heavily used patches, particularly for slow-moving animals (Ausden et al. 2005; see also Humbert et al. 2012, Buri et al. 2013), thus potentially enhancing local diversity and abundance. As grazing disturbance becomes more intense and negative effects on vegetation increase, as in our Heavy patches, a threshold may be surpassed such that overall habitat losses become more important than the potential positive influences of grazing in structuring arthropod assemblages. Fahrig and Jonsen (1998) similarly observed highest arthropod species richness with intermediate disturbance frequency (see also Gibson et al. 1992; Bell et al. 2001).

At the meadow scale, light grazing disturbance can result in positive responses from arthropods relative to heavy grazing or lack of grazing (Samways and Kreuzinger 2001, but see van Klink et al. 2013), in some cases because of grazing-induced increases in habitat heterogeneity (Wettstein and Schmid 1999; Carvell 2002; Zahn et al. 2007). The increase in overall structural heterogeneity created by grazing disturbance (Loucougaray et al. 2004; Nolte

et al. 2014) may benefit arthropods via creation of a mosaic of varying canopy height, litter depth, percentage of bare ground (Zahn et al. 2007), and varying abundances of flowering plants (Wettstein and Schmid 1999; Carvell 2002). Such a positive influence on arthropod richness (Wettstein and Schmid 1999; Morris 2000) may partially offset localized losses of habitat due to intense, patchy grazing. Arthropods do nevertheless respond to small-scale landscape elements as well (Hatfield and LeBuhn 2007; Batáry et al. 2008; Barton et al. 2011; previous paragraph), and response at a given scale is likely to vary by taxon (Murakami et al. 2008; Dumbrell et al. 2008; Banks-Leite et al. 2013).

Such potential mitigation of impact at both patch and meadow scales, while encouraging, does not suggest that these wetlands benefit from equine grazing. Herbivores larger than mule deer (*Odocoileus hemionus* Rafinesque) were historically absent from these mountain wetlands (see Loomis et al. 1991; Loft et al. 1991; Dull 1999). Foraging effects of deer and equines are different (Austin et al. 1994; Beever 2003), and deer are still abundant in the subalpine Sierra Nevada (Loomis et al. 1991; Loft et al. 1991). These wilderness wetlands thus differ greatly from environments in which large native herbivores have been largely replaced by livestock (Samways and Kreuzinger 2001; Levin et al. 2002) or that have a long history of intensive multi-purpose management and for which grazing can be a useful tool in retaining biodiversity (Wettstein and Schmid 1999; Boschi and Baur 2007; Lenoir and Lennartsson 2010).

Evaluation of disturbance at either patch or landscape scales should be appropriate, depending on the management question at hand (see also Leung et al. 2011). Although we detected the strongest negative and positive effects of this disturbance at the patch scale (Table 3), such small-scale, stratified sampling may not detect larger scale processes (Syms and Jones 1999; see also Bell et al. 2001), and directionality of responses may differ at larger scales

(Landsberg et al. 2002; Hill and Hamer 2004; Dumbrell et al. 2008). Evaluations of assemblage and population metrics at plot, patch, and landscape scales provide multiple perspectives on phenomena, and assessments by managers and scientists at all scales are ideal (Dumbrell et al. 2008; Banks-Leite et al. 2013). Random sampling of paired grazed and ungrazed wetlands, with inference at the level of the landscape, effectively captures overall ecosystem effects and may be of greatest interest to managers. The more muted responses of arthropods and vegetation structure at this scale (Holmquist et al. 2010; 2013a; b; Table 3) may be a function of the positive effects of increased habitat heterogeneity within individual meadows. The core conclusion of our current study is that this allochthonous disturbance can nonetheless have strong local effects on the ecology of these wetlands that may not be detected at the scale of paired grazed and ungrazed wetlands. Although heavily affected patches make up a minority of total habitat in any given meadow, in aggregate such patches may represent significant losses of habitat and fauna at the landscape scale. In addition, patches of heavily used habitat can functionally fragment habitat (Wettstein and Schmid 1999; Collinge and Palmer 2002; Ewers and Didham 2006) by creating gaps, increasing boundary contrast, and decreasing permeability (Wiens 1985; Stamps et al. 1987; Holmquist 1998). It is largely for these ecological reasons that smaller areas, as well as entire wetlands, are the focus of restoration efforts (e.g., Newsome et al. 2004; Barton et al. 2011). Further, in lands that are also managed for recreation, small areas of highly visible impacts can be disturbing to visitors (see also Watson et al. 1994; Cole 2004; Manning et al. 2004), and thus small-scale effects warrant attention from a sociological perspective as well. Land managers often close individual wetlands to stock use, and some of these areas have been closed for decades. This strategy results in concentration, versus dispersal (Cole 1989; Monz et al. 2010; Juutinen et al. 2011), of grazing effects at the landscape scale. Our work indicates that

the greatest effects of stock were also functionally concentrated at the patch scale within wetlands that are open to grazing. This concentration of effect may or may not be desirable and is worthy of further management consideration.

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Ethical Standards This study complies with the laws of the USA. We obtained a Scientific Research and Collecting permit from the US National Park Service for work in Yosemite National Park. No protected species were sampled.

Conflict of Interest The authors declare that they have no conflict of interest.

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Figure Legend

Fig. 1 Yosemite National Park in the Sierra Nevada of California. Black circles represent meadow complexes, and stars represent landmarks

Table 1 Means (untransformed; standard errors) for vegetation and physical parameters by treatment and results of ANOVAs and accompanying Tukey's tests on log or square-root transformed data. *U*, *L*, and *H* refer to Ungrazed, Light, and Heavy, respectively

	Treatment Means (SE)			Test Results		
	Ungrazed	Light	Heavy	Treatment	Block	Tukey's
Bare ground (%)	1.67 (1.7)	1.00 (0.76)	40.8 (6.5)	<0.0001**	0.00058**	<i>H>U, H>L</i>
Green cover (%)	85.4 (3.5)	85.0 (2.8)	39.0 (6.1)	<0.0001**	0.011**	<i>U>H, L>H</i>
Litter cover (%)	8.33 (1.9)	7.50 (2.3)	11.8 (3.9)	0.48	0.00053**	
Brown cover (%)	4.58 (3.2)	6.50 (1.3)	8.50 (3.0)	0.45	0.052*	
Canopy height (cm)	39.6 (4.2)	32.3 (4.9)	10.3 (1.8)	<0.0001**	<0.0001**	<i>U>H, L>H</i>
Complexity (touches)	8.79 (1.0)	8.65 (0.98)	3.40 (0.85)	<0.0001**	0.014**	<i>U>H, L>H</i>
Stem density/m ²	621 (119)	888 (190)	710 (141)	0.51	0.046**	
Litter depth (cm)	4.21 (1.7)	2.55 (0.62)	0.75 (0.17)	0.015**	<0.0001**	<i>U>H, L>H</i>
Plant species richness	2.7 (0.56)	2.6 (0.72)	1.7 (0.42)	0.71	0.040**	
Soil strength (kg/cm ²)	0.950 (0.22)	1.05 (0.15)	1.13 (0.12)	0.68	<0.0001**	

* *P* < 0.16 (see Methods section), ** *P* < 0.05

Table 2 Means (untransformed; standard errors) for faunal assemblage metrics by treatment and results of ANOVAs and accompanying Tukey's tests on log or square-root transformed data. *U*, *L*, and *H* refer to Ungrazed, Light, and Heavy, respectively

	Treatment Means (SE)			Test Results		
	Ungrazed	Light	Heavy	Treatment	Block	Tukey's
Total individuals	104 (26)	547 (298)	178 (48)	0.078*	0.18	<i>L>U</i>
Family richness	18.5 (1.5)	21.2 (3.2)	16.2 (2.1)	0.17	0.020**	
Morphospecies richness	25.8 (2.9)	31.5 (4.5)	24.0 (3.2)	0.11*	0.028**	<i>L>H</i>
Expected number of morphospecies	9.94 (0.56)	7.19 (0.91)	6.87 (0.71)	0.098*	0.0034**	<i>U>H</i>
% Family dominance	34.2 (6.0)	53.6 (8.1)	57.9 (5.4)	0.060*	0.11*	<i>H>U</i>
% Species dominance	22.7 (2.3)	46.4 (8.8)	48.8 (7.2)	0.054*	0.10*	<i>H>U, L>U</i>
% Predators	9.94 (2.5)	16.6 (6.1)	9.85 (2.0)	0.63	0.020**	
% Herbivores	48.6 (5.7)	39.7 (9.6)	46.7 (11)	0.56	0.089*	

All non-percentage measures were based on 50-sweep samples

* $P < 0.16$ (see Methods section), ** $P < 0.05$

Table 3 Summary and comparison of results from patch-scale (Ungrazed, Light, Heavy patches; this study) and meadow-scale (Grazed versus Ungrazed meadows; Holmquist et al. 2013b) investigations of pack stock effects on vegetation and arthropods in *Carex utriculata*-dominated habitat in subalpine wet meadows.

Responses	Patch-scale	Meadow-scale
Vegetation structure	Less green cover, canopy height, complexity, and litter depth, and more bare ground, in Heavy than in Light and Ungrazed	Less litter depth, litter cover, and higher soil strength in Grazed relative to Ungrazed
Individual faunal assemblage metrics	Higher abundance and richness in Light, higher diversity and lower abundance and dominance in Ungrazed, higher dominance and lower richness and diversity in Heavy	No differences
Trends across faunal assemblage metrics	Lower diversity in Heavy patches	None
Faunal rank-abundance distribution	Light and Ungrazed distributions differed	No difference
Trends across faunal taxa	Higher abundances of individual families and morphospecies in Light than in Ungrazed or Heavy	No overall trend; differences for some individual taxa, but inconsistent directionality
Multivariate dispersion	Greater variability in both Light and Heavy relative to Ungrazed	No difference

Fig.1

Online Resource 1 Mean abundances (per 50 sweeps, SE) for orders and families by treatment. Zeros omitted for clarity

	Ungrazed	Light	Heavy
Odonata	0.167 (0.17)	0.200 (0.20)	0.100 (0.10)
Lestidae	0.167 (0.17)	0.200 (0.20)	0.100 (0.10)
Orthoptera		0.300 (0.30)	0.300 (0.21)
Acrididae		0.300 (0.30)	0.300 (0.21)
Hemiptera	50.8 (18)	406 (302)	111 (40)
Anthocoridae	0.333 (0.21)		
Aphididae	2.83 (1.9)	6.90 (3.3)	6.70 (3.1)
Cicadellidae	40.7 (16)	393 (299)	102 (39)
Delphacidae	1.83 (0.75)	2.40 (0.93)	1.60 (0.62)
Lygaeidae	0.167 (0.17)	0.100 (0.10)	0.100 (0.10)
Miridae	2.83 (2.8)	0.900 (0.48)	0.200 (0.13)
Nabidae	0.167 (0.17)	0.400 (0.31)	0.100 (0.10)
Pentatomidae	0.167 (0.17)		
Psyllidae	1.83 (1.8)	0.100 (0.10)	
Saldidae			0.400 (0.22)
Scutelleridae		2.00 (1.8)	0.100 (0.10)
Thysanoptera	0.167 (0.17)	0.400 (0.16)	0.200 (0.20)
Thripidae	0.167 (0.17)	0.400 (0.16)	0.200 (0.20)
Coleoptera	1.50 (0.56)	1.50 (0.62)	0.400 (0.16)
Anthicidae	0.167 (0.17)		0.100 (0.10)
Brentidae		0.100 (0.10)	
Cantharidae		0.200 (0.13)	
Chrysomelidae		0.100 (0.10)	0.100 (0.10)
Coccinellidae	0.833 (0.40)	0.700 (0.30)	0.200 (0.13)
Hydrophilidae		0.100 (0.10)	
Mordellidae		0.200 (0.20)	
Scarabaeidae	0.167 (0.17)		
Staphylinidae	0.333 (0.33)	0.100 (0.10)	
Neuroptera		0.100 (0.10)	
Chrysopidae		0.100 (0.10)	
Hymenoptera	2.17 (1.1)	11.0 (3.9)	3.30 (1.3)
Andrenidae		0.100 (0.10)	
Apidae			0.100 (0.10)
Braconidae	1.00 (0.82)	1.40 (0.83)	1.50 (0.98)
Diapriidae		0.200 (0.13)	
Dryinidae		0.100 (0.10)	
Eulophidae		0.200 (0.13)	
Formicidae		0.300 (0.21)	
Halictidae		0.100 (0.10)	0.100 (0.10)
Ichneumonidae	0.833 (0.31)	2.40 (0.91)	0.800 (0.42)
Pteromalidae	0.333 (0.33)	6.10 (3.8)	0.500 (0.27)
Sphecidae			0.100 (0.10)

	Ungrazed	Light	Heavy
Hymenoptera, cont.			
Tenthredinidae		0.100 (0.10)	0.200 (0.13)
Trichoptera	3.33 (1.9)	14.2 (14)	0.200 (0.20)
Limnephilidae	3.33 (1.9)	14.2 (14)	0.200 (0.20)
Lepidoptera	2.17 (0.91)	2.50 (1.5)	0.600 (0.27)
Lycaenidae	0.167 (0.17)		
Noctuidae	2.00 (0.93)	2.40 (1.5)	0.600 (0.27)
Pyrilidae		0.100 (0.10)	
Diptera	39.8 (13)	105 (50)	59.0 (14)
Agromyzidae	1.17 (0.60)	0.700 (0.33)	1.30 (0.50)
Anthomyiidae	1.00 (0.63)	3.80 (1.7)	7.40 (3.4)
Calliphoridae			
Ceratopogonidae	0.167 (0.17)	0.400 (0.31)	
Chamaemyiidae		0.100 (0.10)	0.300 (0.15)
Chironomidae	8.17 (5.8)	8.40 (5.2)	1.60 (1.3)
Chloropidae	3.00 (1.6)	5.50 (2.1)	8.50 (6.1)
Culicidae	0.333 (0.33)	0.200 (0.20)	0.100 (0.10)
Dolichopodidae	0.667 (0.33)	5.20 (2.6)	6.10 (2.9)
Drosophilidae	0.333 (0.21)	0.800 (0.80)	
Empididae	0.333 (0.21)	0.500 (0.27)	0.100 (0.10)
Ephydriidae	1.50 (0.81)	1.60 (0.56)	2.50 (0.97)
Heleomyzidae	1.33 (1.3)	0.100 (0.10)	0.100 (0.10)
Lonchopteridae	0.333 (0.21)	40.9 (41)	0.500 (0.40)
Micropezidae	3.33 (2.1)	1.50 (0.65)	0.200 (0.13)
Muscidae	11.2 (3.7)	21.2 (8.7)	24.2 (6.8)
Mycetophilidae		0.100 (0.10)	
Phoridae	1.00 (0.52)	1.60 (1.1)	0.500 (0.27)
Pipunculidae	0.167 (0.17)	0.400 (0.22)	0.300 (0.21)
Psilidae	0.167 (0.17)	0.600 (0.60)	0.200 (0.13)
Rhagionidae	0.167 (0.17)	0.5500 (0.40)	0.400 (0.22)
Sarcophagidae		0.300 (0.15)	0.200 (0.13)
Sciaridae	4.00 (1.9)	6.40 (2.9)	2.60 (0.76)
Sciomyzidae		0.100 (0.10)	0.100 (0.10)
Sepsidae		0.800 (0.51)	0.300 (0.21)
Sphaeroceridae	0.333 (0.21)	1.80 (1.4)	1.00 (0.60)
Syrphidae		0.100 (0.10)	
Tachinidae	0.167 (0.17)	0.700 (0.26)	0.300 (0.15)
Tephritidae	0.333 (0.21)	0.100 (0.10)	0.200 (0.13)
Tipulidae	0.667 (0.67)		

	Ungrazed	Light	Heavy
Araneae	3.67 (0.95)	6.10 (2.1)	2.90 (0.73)
Araneidae	1.83 (0.65)	1.60 (0.70)	1.10 (0.31)
Linyphiidae		0.300 (0.15)	0.200 (0.13)
Lycosidae	0.167 (0.17)		0.100 (0.10)
Tetragnathidae	1.00 (0.52)	2.20 (0.85)	0.300 (0.15)
Theridiidae		0.300 (0.15)	
Thomisidae	0.500 (0.22)	1.40 (0.79)	1.20 (0.61)
Unknown spider	0.167 (0.17)	0.300 (0.30)	
Acari		0.700 (0.70)	
Unknown mite		0.700 (0.70)	