Butterflies, cattle grazing, and environmental heterogeneity in a complex landscape

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Abstract. I investigated the effects of cattle grazing intensity on butterfly species diversity relative to seven other environmental variables in the diverse Cascade-Siskiyou National Monument (CSNM) of southwest Oregon. I sampled twenty-seven transects in 2003 and twenty-nine transects in 2004 in oak savanna and mixed-conifer forests that were subject to different grazing intensities and recorded a total of 89 species across both years. Annual grazing utilization was assessed at each transect using the key-species method, which uses un-grazed palatable reference plants to create a site-specific index of utilization based on the estimated proportion of biomass consumed on grazed plants of the same species. Grazing utilization estimates ranged from low (0-15%) to high (60-75%) on a 5-point scale. Multiple environmental variables were correlated with butterfly community composition and life history characteristics, especially habitat type, plant species richness, the presence or absence of water, and vegetative cover. Cattle grazing utilization did not predict butterfly evenness or total density, and only significantly predicted butterfly species richness in 2003. However, species with grass hostplants (particularly *Cercyonis sthenele*) declined in abundance at higher cattle grazing utilization classes. Management activities related to grazing and butterfly conservation in complex habitats like the CSNM should target specific aspects of butterfly life history, particularly hostplant structure or associated environmental characteristics but those activities cannot be expected to have equivalent effects across species.

Key words: Cascade-Siskiyou National Monument, land management, conservation, life history, species assemblage, ecoregions, *Cercyonis sthenele*

Introduction

Cattle grazing on public lands can create management conflicts, especially in areas of high biodiversity and landscape heterogeneity (Harrison et al., 2003). However, little is known about the interactions between cattle grazing and insect diversity in complex habitat mosaics. The majority of studies examining the influences of livestock grazing and other agricultural practices on insects have been conducted in grassland ecosystems (Swengel & Swengel, 2001; Kruess & Tscharntke, 2002a; Kruess & Tscharntke, 2002b; Saarinen, 2002; González-Megías

et al., 2004; Saarinen & Jantunen, 2005; Dumont et al., 2009) where human-mediated grazers and/or native ungulates have been characteristic modes of disturbance for centuries or millennia. Although the large majority of butterfly species studied to date have shown lowered abundance under high grazing regimes, moderate or high grazing utilization has sometimes been shown to locally increase the abundance of insect species adapted to these habitats (Swengel & Swengel, 1999; Weiss, 1999; Swengel & Swengel, 2001; WallisDeVries & Raemakers, 2001; Pöyry et al., 2004; Saarinen et al., 2005), perhaps by maintaining earlier successional conditions (Dover et al., 2011).

At the landscape level, inverse or more complicated patterns are often reported. Heavy grazing regimes are frequently correlated with lowered insect species richness and niche simplification (Swengel 2001; Kruess & Tscharntke, 2002a; Kruess & Tscharntke, 2002b; Boulton et al., 2005), presumably by disrupting trophic interactions between plants and phytophagus insects. Multiple factors appear to simultaneously influence butterfly diversity and composition, and

the effects of grazing are not uniform across taxa or indices of community composition (Feber *et al.*, 2001; Swengel, 2001; Swengel & Swengel, 2001; WallisDeVries & Raemakers, 2001; Sanford, 2002). Landscape-level variation in management practices may promote diversity (Swengel, 1998; Waltz & Covington, 2004; Pöyry *et al.*, 2005), although landscape-level habitat complexity does not necessarily predict local species composition (Collinge *et al.*, 2003, Krauss *et al.*, 2003).

I studied how variable levels of cattle grazing utilization and other environmental variables were correlated with butterfly diversity and abundance across the ecologically diverse Cascade-Siskiyou National Monument (CSNM), approximately 20 km southeast of Ashland in southwest Oregon, USA. This study was conducted in collaboration with other researchers simultaneously studying the effects of cattle grazing on birds (Alexander *et al.*, 2008), small mammals (Johnston & Anthony, 2008), Greene's mariposa-lily (*Calochortus greenei*) (Frost & Hosten, 2007), and stream habitats and aquatic macroinvertebrates (DellaSala & Barr, 2007). A synthesis of these studies is presented by DellaSala & Barr (2007). This study helps inform grazing prescriptions related to the monument's proclamation (The White House 2000). It also contributes more broadly to the management of ecologically diverse systems where livestock grazing is frequent and butterfly conservation is a concern or rare butterflies have been proposed as indicators of overall environmental health. I asked the following hierarchical questions: 1) Relative to other environmental variables, how important is cattle grazing utilization in affecting local butterfly species richness, evenness, and total density? 2) Do butterflies with similar life history characteristics respond similarly to cattle grazing utilization or other environmental variables? 3) Do individual butterfly species, including those of conservation interest, vary in their responses to cattle grazing utilization and other environmental variables?

Study area

Three ecoregions (the Cascades, Klamath-Siskiyous, and Great Basin) merge in the CSNM (21,427 ha) to create narrow ecotones and complex biodiversity patterns. At least 115 butterfly species are known from the CSNM (Runquist, 1999; 2002; and Runquist unpublished data), representing more than two-thirds of Oregon's known butterfly fauna (Warren, 2005) and one of the most species rich regions in the United States for butterflies. Furthermore, sympatric and synchronic species combinations in the CSNM are often novel and unexpected. Consequently, butterflies are widely cited exemplars of CSNM biodiversity and are federally identified as a research priority for studies on "the impacts of livestock grazing on the objects of biological interest in the monument with specific attention to sustaining the natural ecosystem dynamics" (The White House, 2000).

Grazing by cattle, sheep, and horses on federal lands in the CSNM began in the 1860s, although utilization during the time of this study (an average of 1581 Animal Unit Months between 1995-2004) was approximately 10 times lower than prior to 1960 and only consisted of cattle (USDI Bureau of Land Management, 2005; Hosten *et al.*, 2007a). Free-range grazing began in May at low elevations and gradually moved to higher elevations through summer and ended in October or with the first snowfall.

I studied two broad CSNM habitat types that encompass a range of climatic, structural, and cattle grazing regimes: oak woodlands and mixed-conifer forests. Woodland conditions within the CSNM have increased since European colonization when grasslands were more widespread (Hosten *et al.*, 2007b; Hosten *et al.*, 2007c). Oak woodlands predominate at the lower elevations (730 to 1,250 m) of the southern CSNM and are generally flat, open savannas or shrublands on shallow soils and south-facing hillsides. The climate is Mediterranean with hot, dry summers and mild, wet winters. Summer high temperatures regularly exceed 35°C. Average annual precipitation is about 450 mm. Dominant woody plant species include Garry oak (*Quercus garryana*), California black oak (*Q. kelloggii*), ponderosa pine (*Pinus ponderosa*), western juniper (*Juniperus occidentalis*), and buckbrush (*Ceanothus cuneatus*). Several alien weeds like bulbous bluegrass (*Poa bulbosa*), medusahead (*Taeniatherum caput-medusae*), cheatgrass (*Bromus tectorum*), and yellow star-thistle (*Centaurea solstitialis*) have invaded the understory in many areas, but remnant patches of native bunchgrass habitats remain. Soils are paleosols of thick clay or eroded basalt.

Conifer forests dominate higher elevations (1,100 to 1,870 m) and many north-facing slopes at middle elevations in the CSNM. These forests are multi-layered with unlogged stands generally over 180 years old. Summer high temperatures rarely exceed 32°C. Average annual precipitation is approximately 1,000 mm, largely falling as winter snow. The highest elevations (1,600+ m) are characterized by white fir (*Abies concolor*) forests, and middle elevations are mixed conifer forests consisting primarily of Douglas-fir (*Pseudotsuga menziesii*), incense-cedar (*Calocedrus decurrens*), ponderosa pine, sugar pine (*P. lambertiana*), white fir, California black oak, and bigleaf maple

(*Acer macrophyllum*). The shrub and herbaceous layer flora are highly diverse, with snowbrush (*Ceanothus velutinus*), blue elderberry (*Sambucus nigra*), choke cherry (*Prunus virginiana*), serviceberry (*Amelanchier alnifolia*), oceanspray (*Holodiscus discolor*), common snowberry, (*Symphoricarpos albus*), and giant chinquapin (*Chrysolepis chrysophylla*). Alien weeds include timothy (*Phleum pratense*), bull thistle (*Cirsium vulgare*), and Canada thistle (*C. arvense*). Soils are eroded basalts characteristic of the western Cascades.

METHODS

Butterfly sampling

I established 25 butterfly transects in 2003 and conducted 138 total site-visits, averaging 17.6 days (0.55 SE, range of 5–37) between visits (Table 1). In 2004, I added two more transects and conducted 216 total site-visits, averaging 17.8 days (0.07 SE, range of 6–37) between samples. I sampled each transect from April to September following the standard protocols of Pollard & Yates (1993) and Brown & Boyce (1998). This sampling frequency and period effectively captures the entire annual window of butterfly activity, species turnover, and changes in phenology. I identified every butterfly individual observed within 25 perpendicular meters on either side of the baseline transect (a 50-meter wide strip) to species by sight (captured if necessary). I did not include individuals whose specific identity was ambiguous, especially those at far distances. Having studied the butterflies of the CSNM in detail for over 20 years, I have extensive experience with sight-identification of the region's fauna and possess a high degree of accuracy. Taxonomy followed Pelham (2008). Transects were classified by grazing utilization and habitat type: oak woodland (16 in 2003, 17 in 2004) and mixed conifer forest (9 in 2003, 10 in 2004). Mixed conifer transects were largely placed through meadows within the forest matrix because closed-canopy forests had few butterflies and negligible cattle grazing. I could not standardize transect length because of narrow ecotones widespread in the CSNM, and attempted to minimize intra-transect habitat and grazing utilization class variation.

I calculated three measures of butterfly diversity: species richness, evenness, and density. Species richness was standardized across transects using ANALYTIC RAREFACTION 1.3 (Holland, 2003). This method uses the observed distribution of N individuals across species at a site to estimate the number species if only a subset of those individuals had been sampled. Sample size for comparisons was set to equal the number of individuals observed on the transect with the fewest total individuals for each year. Butterfly species richness estimates from rarefaction were log-transformed to satisfy normality. I selected Hill's E5 evenness index to compare the structure of species composition at each transect because this index is less biased by sample size and the addition of rare species (Ludwig & Reynolds, 1988) than other commonly used diversity indices (like the Shannon-Wiener index, H'). I calculated total butterfly density (individuals/ha) at each transect using DISTANCE 4.1,v.2 (Thomas *et al.*, 2003) based on visual estimates of the perpendicular distance of every individual observed off of either side of the transect out to 25 m. I truncated the density data by excluding the farthest 5% of all distance observations at each transect to reduce the influence of potential outliers. This distance sampling method compensates for differences in detectability between sites (Buckland *et al.*, 2001), and has been used successfully in other butterfly studies (Brown & Boyce, 1998; Boughton, 2000). Density estimates were log-transformed.

Environmental variables can influence the composition of butterfly assemblages by potentially constraining the range of life history strategies that can reside in a given habitat (Haddad *et al.*, 2001; Dennis *et al.*, 2004; Haddad *et al.*, 2008). To test this hypothesis, I classified all butterfly species by five life history characteristics: breeding residency, overwintering stage, voltinism (number of generations per year), larval hostplant specialization, and hostplant structure (woody, herbaceous, or graminoid hostplants). I based these classifications on Warren (2005) and personal observations within the CSNM, and assumed that these classifications did not vary across transects. I log-transformed the abundances of each species after adding 1.0 (to avoid irrational numbers for species with zero individuals recorded), and weighted them by their contribution to the overall variance. I conducted multiple mixed ANOVAs in which I nested each species as a random variable within life history characteristics. I only used the abundance data from randomly determined continuous 200 m sections of each transect with 2004 data to standardize sampling effort. I controlled for the false discovery rate to avoid spurious statistical significance due to multiple comparisons when testing for individual species responses using the method of Benjamini & Hochberg (1995). I did not attempt to correct for phylogenetic relatedness between butterfly species in these classifications, which may have the effect of overestimating the importance of some effects because each species cannot be assumed to be an independent replicate of each life history category.

However, the predictive value of evolutionary relatedness between species is often unclear because they may either be more or less likely to utilize related hosts. For example, closely related butterfly species may be expected to be under character displacement pressure to expand host breadth due to inter-specific competition for the same hostplants (e.g. Hesperiinae skippers and *Cercyonis* and *Coenonympha* satyrs all utilize native Poaceae, as well as *Speyeria* and *Boloria* only utilizing *Viola*). Conversely, species may be constrained in their ability to expand host breadth to new hosts due to metabolic limitations to process novel phytochemistry. Furthermore, phylogenetic relatedness is still poorly resolved for many of the species observed in this study and such an effort would be rather speculative.

Habitat structure: Plant species richness and percent cover

I collected plant species richness and percent cover data using point-intercept sampling along randomly located 25-m sub-transects running perpendicular to the primary butterfly transect. Every 50 cm along each sub-transect, I vertically dropped a 2.0 m rod (1 cm in diameter) that had been subdivided into four 0.5 m sections. I recorded intercepts for each species in each section of the rod and estimated species richness and percent cover in four strata up to 2.0 m above the ground. As with the butterfly data, I used rarefaction to calculate plant species richness, with the minimum number of intercepts across transects set as the baseline number of "individuals" for comparison. These estimates were log-transformed to achieve normality. I estimated canopy layer (> 2.0 m above ground) percent cover using the line intercept method along each sub-transect and pooled the data from all sub-transects. I weighted mean percent cover estimates for each vegetation layer by their transect-specific variances. I also recorded the elevation at each transect, and the presence or absence of ephemeral or permanent water sources within 50 m of each transect.

Cattle grazing intensity

In cooperation with the Klamath Bird Observatory (Ashland, OR), I quantified intra-year cattle grazing utilization at each transect in the fall of 2004 using the standard Herbaceous Removal Key Species method (Cooperative Extension Service *et al.*, 1999; Alexander *et al.*, 2003). An ungrazed reference individual of the dominant palatable plant species at each transect was collected, and clipped sections of this reference

plant were weighed to obtain a standardized curve relationship between biomass and plant height. Fifty-meter transects were laid out at each butterfly transect and points were established every meter. The height of each member of the reference key species closest to each of these fifty points was measured, and a continuous metric of utilization for the transect was obtained by averaging the biomass estimates across all plants. These protocols and many of the same data points were used in a simultaneous parallel study on the effects of livestock utilization on bird community composition in the CSNM (Alexander *et al.*, 2008).

Dataset robustness and variable selection

Although each transect was sampled multiple times each year, time series analyses are not suitable to test the effects of various environmental effects on the whole of butterfly species richness, evenness, and density because there is a large turnover in species composition and abundance between weeks. Instead, I was interested in the relative effects of these environmental variables on the entire butterfly fauna using weighted least squares linear models. I excluded transect length whenever it was a non-significant main effect, and explored interactions between significant main effects. I placed these interactions into a final model with their main effects to weigh their relative importance. Sampling effort was greater in 2004, so data collected over the two years were analyzed separately. I also partitioned the dataset by habitat type in some analyses to test for differences in effects between oak woodland and mixed conifer forest. All analyses were conducted in JMP 9.0.2 (SAS Institute Inc., Cary, NC, USA). Statistical significance was set at $\alpha = 0.05$, except when controlling for false discovery rate. I selected the following independent variables: transect length, grazing utilization class, elevation (as a continuous surrogate for habitat type), the presence/absence of water, herbaceous layer (0- to 0.5-m) species richness, herbaceous layer weighted percent cover, shrub layer (0.5- to 2.0-m) species richness, shrub layer weighted percent cover, and canopy layer (>2.0 m) weighted percent cover (Table 1). I bracketed mean utilization estimates into ranked intervals of 15% due to high individual variances and grouped transects into the following utilization classes: 0%-14.9% = "1", 15%-29.9% = "2", 30%-44.9% = "3", 45%-59.9% = "4", and 60%-74.9% = "5". No transect had a mean utilization score of more than 75%. These classifications are largely consistent with a coarser landscape-level map of CSNM grazing utilization estimated by Hosten *et al.* (2007a), and additional subjective observations (e.g. "no grazing

Table 1. Butterfly transects by habitat type, grazing utilization ("1" = 0 to 14.9%, ... "5" = 60 – 75%), elevation, the presence/absence of water resources, transect length, and variance-weighted mean vegetation percent cover and log plant species richness in three strata in the Cascade-Siskiyou National Monument, 2004.

Transect	# Sampling Visits 2003	2004	Habitat	Grazing utilization class	Elevation (m)	Water	Transect length (m)	Weighted mean percent cover by layer Herb	Shrub	Canopy	Log plant richness by layer Herb	Shrub
AF6	5	8	oak	1	1012	No	200	0.12	0.549	0.074	3.807	1.609
BO1	6	8	oak	1	1097	No	500	0.16	0.108	0.102	3.704	1.808
BO2	6	8	oak	1	975	Yes	400	0.22	0.073	0.116	4.237	2.715
OG3	6	8	oak	1	1250	No	250	0.14	0.045	0.099	3.578	1.686
LH1	7	8	conifer	1	1435	No	250	0.08	0.301	0.037	3.98	2.728
LH3	7	8	conifer	1	1463	Yes	450	0.16	0.049	0.044	4.422	2.955
OGH	6	8	conifer	1	1265	Yes	300	0.03	0.116	0.100	4.104	2.728
PR	0	8	conifer	1	1515	No	200	0.12	0.073	0.059	4.132	2.58
AF4	5	8	oak	2	1006	No	200	0.2	0.072	0.147	3.875	1.792
AF5	5	8	oak	2	1006	No	200	0.15	0.143	0.089	3.544	1.74
JC5	5	8	oak	2	967	No	500	0.13	0.167	0.087	4.231	1.589
OG1	6	8	oak	2	1231	No	400	0.32	0.058	0.058	4.029	1.74
OG2	6	8	oak	2	1158	No	500	0.12	0.137	0.067	3.745	1.841
OG4	6	8	oak	2	1052	Yes	500	0.25	0.169	0.181	4.233	2.14
BECR	5	8	conifer	2	1542	Yes	400	0.09	0.05	0.054	4.104	2.407
AF3	6	8	oak	3	1030	No	300	0.42	0.18	0.104	3.437	1.386
JC3	5	8	oak	3	954	Yes	200	0.11	0.131	0.263	3.421	1.504
JC4	5	8	oak	3	938	Yes	400	0.07	0.079	0.104	4.394	2.701
SKCR2	0	8	oak	3	1109	Yes	300	0.16	0.162	0.049	4.038	2.493
SKC1	5	8	conifer	3	1402	Yes	500	0.14	0.052	0.138	4.279	2.625
WIGL	5	8	conifer	3	1570	Yes	400	0.16	0.117	0.056	4.205	2.542
SKCR1	6	8	oak	4	1036	Yes	500	0.16	0.07	0.039	4.265	1.887
KCR	5	8	conifer	4	1189	Yes	200	0.1	0.052	0.083	4.371	2.688
MAR	6	8	conifer	4	1579	Yes	300	0.12	0.103	0.074	3.93	2.389
AF1	6	8	oak	5	1006	No	350	0.25	0.145	0.090	3.638	1.335
AF2	6	8	oak	5	1006	No	300	0.22	0.189	0.165	3.561	1.526
SKC2	5	8	conifer	5	1449	Yes	450	0.09	0.028	0.113	4.264	2.389

observed", "heavily grazed since last visit", etc.). The binning process used to classify transects by their mean grazing utilization estimates is conservative in that it reduces potentially real and biologically significant differences between transects by incorporating the variance around their estimates.

RESULTS

Variable transect lengths led to unequal sampling effort and increasing variance around butterfly and plant species richness estimates on longer transects. Plant species richness of the herbaceous layer was the

only environmental effect biased by transect length ($F1,26 = 6.05$, $P = 0.021$). However, this layer positively covaried with the richness of the shrub layer and with elevation (neither of which were biased by transect length), so significant correlations with species richness in the herbaceous layer are not necessarily invalid. Cattle grazing utilization class was not biased by any environmental variable for either pairwise correlation coefficients or in a nominal logistic model (all $P > 0.05$).

Butterfly diversity and cattle grazing

I recorded 5,423 individual butterflies in 77 species in 2003 and 8,846 individual butterflies constituting 84 species in 2004 (Table 2). I observed a total of 89 species over both years. Species composition was dominated by a few species, and the five most commonly observed species in each year collectively constituted 51.6% and 54.1% of all individuals observed, respectively. Consequently, the majority of the species were rare and/or local.

In the full ANOVA model of all environmental variables listed above, more butterfly species were recorded on transects with moderate grazing (Class 3, 30-45% mean utilization) than those with no or very low grazing (Class 1, 0-15% mean utilization) in 2003, but this trend was not significant in 2004 (Fig. 1, Table 3). Butterfly species richness also increased with elevation (Fig. 3) and herbaceous layer species richness in both years (Fig. 4), and with shrub layer species richness in 2003 (Fig. 5). Butterfly evenness

was higher at transects near water in 2004. Total butterfly density was not related to any environmental variable in either year. No effects interacted significantly with grazing utilization class for butterfly species richness, evenness, or total density.

Cattle grazing utilization and butterfly life history characteristics

Since butterflies with similar life history characters may respond in similar manners to environmental variation, I began testing Question #2, by testing the relative predictive value of all eight main effect environmental variables plus transect length and species identity in a full ANOVA model using the log abundance of all 2004 butterfly records. The abundance of each butterfly species was weighted by the inverse of its contribution to overall variance. Only grazing utilization ($F_{4,2171} = 2.49$, $P = 0.041$), water ($F_{1,2171} = 7.90$, $P = 0.005$), and herbaceous layer plant species richness ($F_{1,2171} = 4.36$, $P = 0.037$) significantly predicted butterfly abundance. As in the diversity data, the effect size of cattle utilization (based on the F statistics above) was lower than the effects of water or herbaceous plant richness. I then isolated these three main environmental effects and tested for their interactions with each of the life history categories in reduced ANOVAs described below.

Residency: Permanent breeding residents were more than five times as abundant as species that irregularly immigrate into the CSNM ($F_{1,2171} = 9.79$, $P = 0.002$). No main effects were significant in the
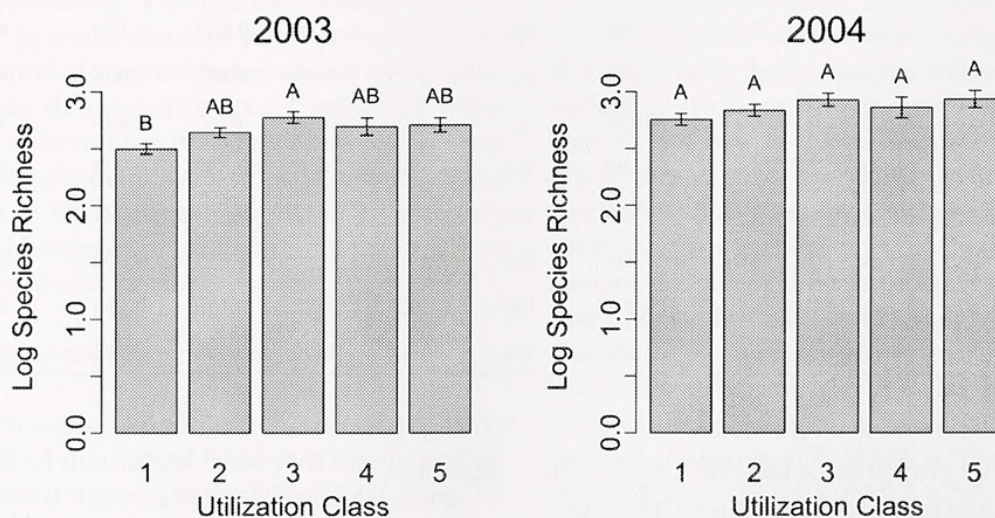

Figure 1. The effect of cattle grazing utilization class on mean log butterfly species richness (+/- SE) in the Cascade-Siskiyou National Monument in 2003 and 2004. Grazing utilization is lowest for class 1 and highest for class 5. Letters indicate statistically significant groups in species richness between utilization classes within each year following post-hoc Tukey tests.
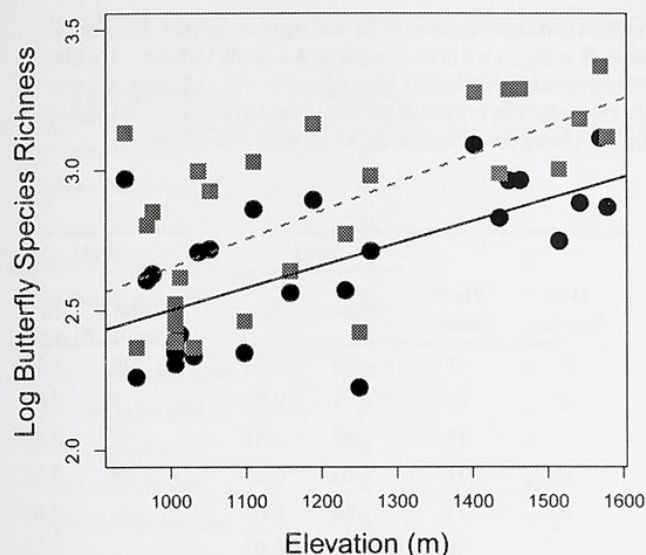
Figure 2. The relationship of butterfly species richness with elevation. Black circles and the associated solid line of fit are the 2003 data. Grey squares and the associated dashed line of fit are the 2004 data.

Figure 4. The relationship of butterfly species richness with plant species richness in the shrub layer (0.5-2.0 m from the ground). Black circles and the associated solid line of fit are the 2003 data. Grey squares and the associated dashed line of fit are the 2004 data.
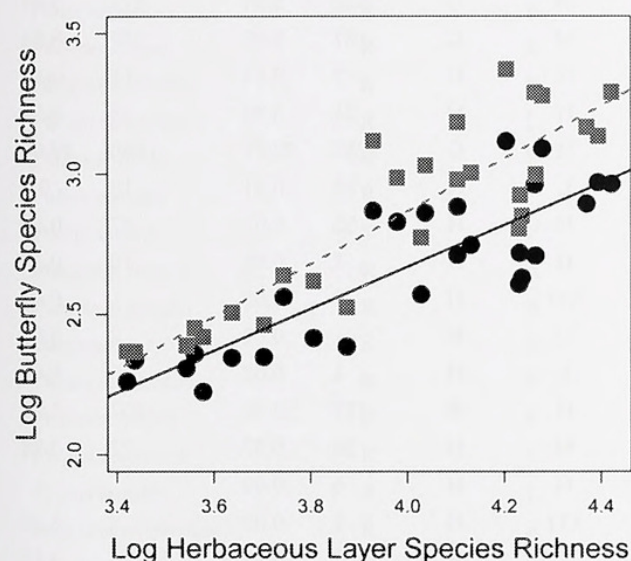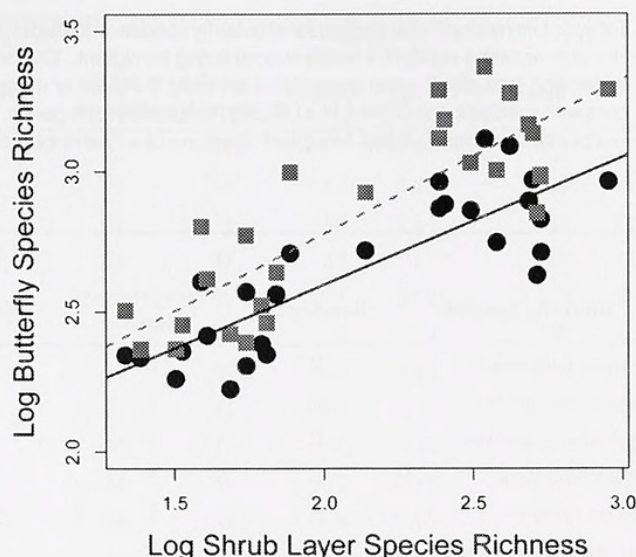

Figure 3. The relationship of butterfly species richness with plant species richness in the herbaceous layer (0-0.5 m from the ground). Black circles and the associated solid line of fit are the 2003 data. Grey squares and the associated dashed line of fit are the 2004 data.

reduced ANOVA model, nor were there any significant interactions between main effects.

Overwintering stage: Species that hibernate as larvae were about five times more abundant than those that overwinter in all other stages ($F_{3,2159}$ = 104.75, P < 0.001). Abundance remained positively related to herbaceous layer plant species richness

in the reduced ANOVA model ($F_{1,2159}$ = 10.78, P = 0.001), but overwintering stage did not interact with any effect.

Voltinism: Butterfly species with one or two broods per year were both about five times more abundant than species with at least three annual broods ($F_{2,2165}$ = 8.40, P < 0.001). Only herbaceous layer richness predicted abundance (positively, $F_{1,2165}$ = 5.29, P = 0.022), and no interactions were found.

Hostplant specialization: Butterfly abundance generally declined with increasing hostplant specificity ($F_{3,2159}$ = 32.52, P < 0.001), although species utilizing multiple plant families as hosts were least abundant (represented by only six species). Grazing utilization class and the presence of water were not important effects, but abundance increased with herbaceous layer richness ($F_{1,2159}$ = 8.12, P = 0.004). However, butterflies using one hostplant genus were less abundant in the presence of water and species with one host family were more abundant around water ($F_{3,2159}$ = 2.99, P = 0.031). Partitioning the dataset by habitat type, this interaction was non-significant in both habitats, and herbaceous layer plant species richness only positively predicted abundance in oak woodlands ($F_{1,1320}$ = 11.13, P < 0.0001). Hostplant specialization was not related to cattle grazing utilization.

Hostplant structure: Butterflies utilizing graminoid hostplants were 2.7 to 3.4 times more abundant than those with woody or herbaceous structured hosts ($F_{2,2165}$ = 179.46, P < 0.001). This difference was

Table 2. Life history characteristics for all butterfly species recorded in 2003 and 2004 and abundance totals for each species by year. Residency: R = overwintering resident, I = non-overwintering immigrant. Overwinter stage: E = egg, L = Larva, P = pupa, A = adult. Voltinism: 1 = one generation annually, 2 = two generations annually, 3 = three or more generations annually. Hostplant Specialization: VH = Utilizing only one hostplant species in the CSNM, H = Utilizing hostplants in one genus, M = Utilizing hostplants in multiple genera in the same family, L = Utilizing hostplants in multiple families. Hostplant Structure: G = Graminoid hostplants, H = Herbaceous hostplants, W = Woody hostplants.

Butterfly Species	Residency	Overwintering-Stage	Voltinism	Host Special.	Host Struct.	2003 Total	2003 %	2004 Total	2004 %
Adelpha californica	R	L	2	H	W	20	0.37	99	1.12
Amblyscirtes vialis	R	L	1	H	G	3	0.06	2	0.02
Anthocharis lanceolata	R	P	1	H	H	20	0.37	31	0.35
Anthocharis sara	R	P	1	H	H	19	0.35	33	0.37
Boloria epithore	R	L	1	H	H	34	0.63	46	0.52
Callophrys augustinus	R	P	1	L	W	1	0.02	11	0.12
Callophrys eryphon	R	P	1	H	W	13	0.24	48	0.54
Callophrys gryneus	R	P	1	M	W	70	1.29	120	1.36
Callophrys mossii	R	P	1	H	H			1	0.01
Carterocephalus palaemon	R	L	1	M	G			3	0.03
Celastrina echo	R	P	2	L	W	4	0.07	34	0.38
Cercyonis oetus	R	L	1	M	G	42	0.77	42	0.47
Cercyonis pegala	R	L	1	M	G	322	5.94	572	6.47
Cercyonis sthenele	R	L	1	M	G	167	3.08	587	6.64
Chlosyne hoffmanni	R	L	1	H	H	7	0.13	11	0.12
Chlosyne palla palla	R	L	1	H	H	21	0.39	48	0.54
Coenonympha tullia	R	L	2	M	G	1235	22.77	1686	19.06
Colias eurytheme	I	L	2	L	H	33	0.61	18	0.2
Colias occidentalis	R	L	1	H	H	55	1.01	47	0.53
Danaus plexippus	I	A	3	H	H	1	0.02	16	0.18
Epargyreus clarus	R	P	1	VH	H	1	0.02	1	0.01
Erynnis icelus	R	L	1	M	W	1	0.02	2	0.02
Erynnis persius	R	L	2	L	H	1	0.02	3	0.03
Erynnis propertius	R	L	1	H	W	177	3.26	267	3.02
Euchloe ausonides	R	P	1	M	H	20	0.37	21	0.24
Euphilotes enoptes	R	P	1	H	H	5	0.09		
Euphilotes glaucon	R	P	1	VH	H	1	0.02	2	0.02
Euphydryas chalcedona	R	L	1	H	W	443	8.17	458	5.18
Euphydryas editha	R	L	1	H	H	3	0.06	5	0.06
Euphyes vestris	R	L	1	M	G	7	0.13		
Everes amyntula	R	L	1	L	H	7	0.13	27	0.31
Glaucopsyche lygdamus	R	P	1	M	H			3	0.03
Habrodais grunus	R	E	1	VH	W			1	0.01
Hesperia colorado	R	L	1	M	G	74	1.36	92	1.04
Hesperia columbia	R	L	2	M	G	6	0.11		
Hesperia juba	R	L	2	M	G	6	0.11	17	0.19
Hesperia lindseyi	R	L	1	M	G	405	7.47	1003	11.34
Junonia coenia	I	A	2	L	H	51	0.94	4	0.05
Limenitis lorquini	R	L	1	L	W	95	1.75	150	1.7
Lycaeides anna	R	L	1	M	H	63	1.16	66	0.75
Lycaena arota	R	E	1	H	W			21	0.24
Lycaena gorgon	R	E	1	VH	H	3	0.06	6	0.07

| Butterfly Species	Residency	Overwintering. Stage	Voltinism	Host Special.	Host Struct.	2003		2004	
						Total	%	Total	%
Lycaena helloides	R	E	2	L	H	7	0.13	3	0.03
Lycaena heteronea	R	E	1	H	H	12	0.22	13	0.15
Lycaena nivalis	R	E	1	H	H	138	2.54	88	0.99
Lycaena xanthoides	R	E	1	H	H	38	0.7	39	0.44
Neophasia menapia	R	E	1	M	W	1	0.02	3	0.03
Nymphalis antiopa	R	A	1	H	W	2	0.04	30	0.34
Nymphalis californica	R	A	2	H	W	66	1.22	127	1.44
Ochlodes sylvanoides	R	L	1	L	G	238	4.39	258	2.92
Oeneis nevadensis	R	L	1	M	G	1	0.02	53	0.6
Papilio eurymedon	R	P	1	M	W	7	0.13	59	0.67
Papilio multicaudatus	R	P	2	M	W	8	0.15	49	0.55
Papilio rutulus	R	P	1	L	W	29	0.53	53	0.6
Papilio zelicaon	R	P	2	M	H	4	0.07	14	0.16
Parnassius clodius	R	L	1	VH	H	22	0.41	44	0.5
Phyciodes mylitta	R	L	2	H	H	44	0.81	83	0.94
Phyciodes orseis	R	L	1	H	H	54	1	37	0.42
Phyciodes pulchella	R	L	2	H	H	5	0.09	17	0.19
Pieris marginalis	R	P	1	M	H	5	0.09	4	0.05
Pieris rapae	R	P	3	L	H	1	0.02	3	0.03
Plebejus acmon	R	L	2	L	H	141	2.6	141	1.59
Plebejus icarioides	R	L	1	H	H	3	0.06	24	0.27
Plebejus saepiolus	R	L	1	H	H	270	4.98	491	5.55
Polites mardon	R	P	1	M	G	25	0.46	16	0.18
Polites sabuleti	R	P	1	L	G	1	0.02	2	0.02
Polites sonora	R	P	1	L	G	13	0.24	14	0.16
Polygonia faunus	R	A	1	H	W			6	0.07
Polygonia gracilis	R	A	1	H	W			13	0.15
Polygonia satyrus	R	A	1	H	W			1	0.01
Pontia occidentalis	R	P	2	M	H			2	0.02
Pontia sisymbrii	R	P	1	M	H	3	0.06	2	0.02
Pyrgus communis	R	L	2	L	H	48	0.89	63	0.71
Pyrgus ruralis	R	L	2	M	H	6	0.11	7	0.08
Satyrium californica	R	E	1	H	W	6	0.11	1	0.01
Satyrium saepium	R	E	1	H	W	51	0.94	97	1.1
Satyrium sylvinum	R	E	1	H	W	9	0.17	11	0.12
Satyrium tetra	R	E	1	H	W			1	0.01
Speyeria callippe	R	L	1	H	H	392	7.23	934	10.56
Speyeria coronis	R	L	1	H	H			15	0.17
Speyeria cybele	R	L	1	H	H	3	0.06	5	0.06
Speyeria hesperis	R	L	1	H	H	7	0.13	4	0.05
Speyeria hydaspe	R	L	1	H	H	80	1.48	114	1.29
Speyeria zerene	R	L	1	H	H	134	2.47	257	2.91
Strymon melinus	R	P	3	L	H	1	0.02		
Thorybes pylades	R	L	1	H	H			16	0.18
Vanessa atalanta	R	A	2	H	H	3	0.06		
Vanessa cardui	I	A	3	L	H	8	0.15	10	0.11
Vanessa virginiensis	I	A	2	L	H	1	0.02	1	0.01
Undetermined						100	1.84	17	0.19
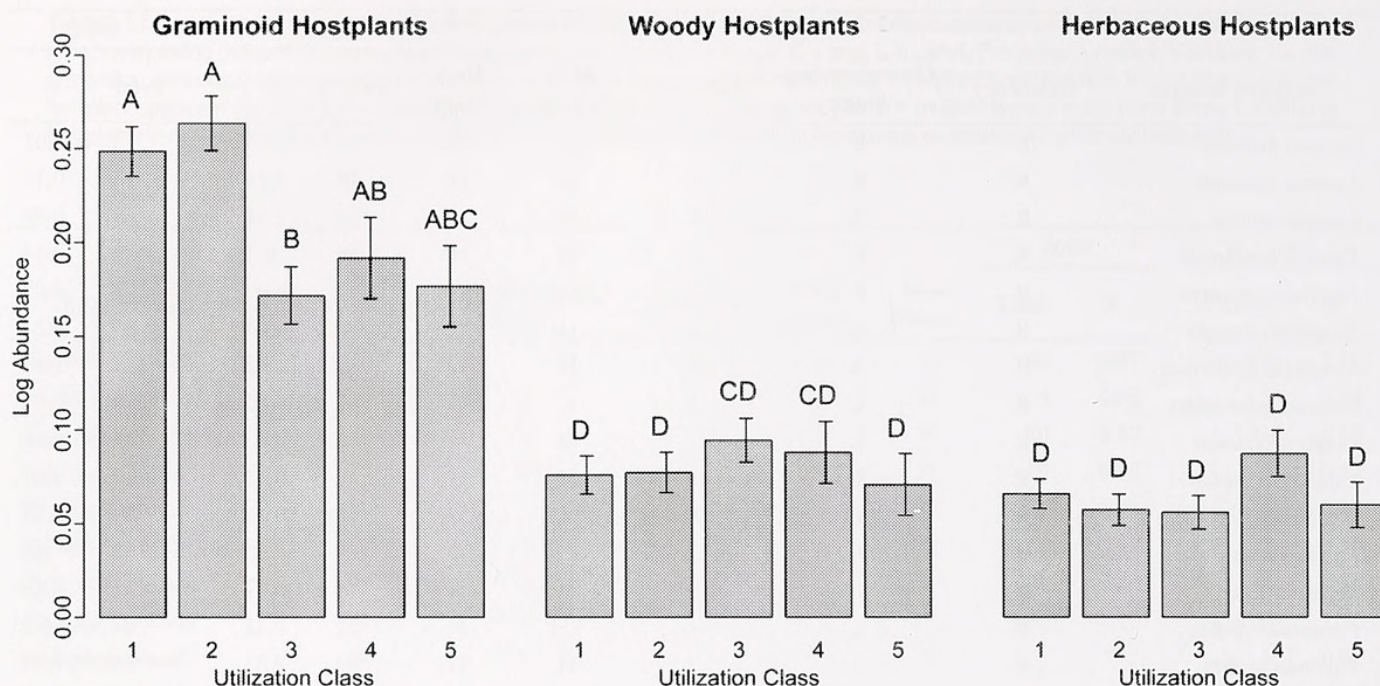
Figure 5. The interaction between cattle grazing utilization class and log butterfly abundance (+/- SE) categorized by butterfly hostplant structure (Graminoid, woody, and herbaceous) in the Cascade-Siskiyou National Monument in 2004. Grazing utilization is lowest for class 1 and highest for class 5. Letters indicate statistically significant differences in mean log abundances across hostplant structures and utilization class following post-hoc Tukey tests.

partially driven by the hyper-abundant grass-feeding *Coenonympha tullia* (Müller, 1764), which represented about one-fifth of all records in both 2003 and 2004. Graminoid-feeding species were less abundant at sites with water sources present while woody- and herbaceous hostplant feeding species were both more abundant near water resources ($F_{2,2165}$ = 4.40, P = 0.012). This interaction was not significant when the dataset was partitioned by habitat type, as well as the main effect of water at mixed conifer forests. Most notably however, graminoid-feeders were 30-33% less abundant at higher grazing utilization classes while the abundances of herbaceous- and woody-feeders were relatively unchanged across utilization levels (Fig. 5; $F_{8,2165}$ = 2.06, P = 0.036).

Individual species responses to cattle grazing

Testing question #3 on the influences of environmental variation and cattle grazing utilization on individual species responses, I found that abundance was significantly related to at least one environmental effect for 34 of the 84 species recorded in 2004 (Table 4). The most widespread effect on individual species abundances was elevation (19 species), highlighting the importance of habitat type in CSNM butterfly diversity patterns. Four species

varied significantly with cattle grazing utilization class. Specifically, *Anthocharis lanceolata* Lucas, 1852 ($F_{4,15}$ = 4.22, P = 0.017) and *Euchloe ausonides* (Lucas, 1852) ($F_{4,15}$ = 3.23, P = 0.042) were more common at transects with Class 5 mean utilization than Class 4. *Phyciodes pulchella* (Boisduval, 1852) was more abundant at moderate utilization classes ($F_{4,15}$ = 3.54, P = 0.032). However, these species collectively accounted for less than 1% of all individuals observed in 2004. *A. lanceolata* and *E. ausonides* were also more abundant in mixed conifer forest than oak woodland (both P < 0.01), and only one mixed conifer transect was classified into utilization Class 5. Utilization class is a non-significant effect for these when this transect is excluded. Thus, the significant response of these three species cannot be separated from a site-specific factor unrelated to utilization class. The most notable species response was found with the graminoid-feeding *Cercyonis sthenele* (Boisduval, 1852), which was 70% less abundant at higher grazing utilization transects (Classes 3-5) than low grazing utilization transects (Classes 1 and 2) ($F_{4,15}$ = 5.32, P = 0.007) (Fig. 6), although abundance of this species was statistically significantly higher only at utilization Class 1 transects than at utilization Class 3 transects according to a post-hoc Tukey test. A very similar but slightly non-significant trend was
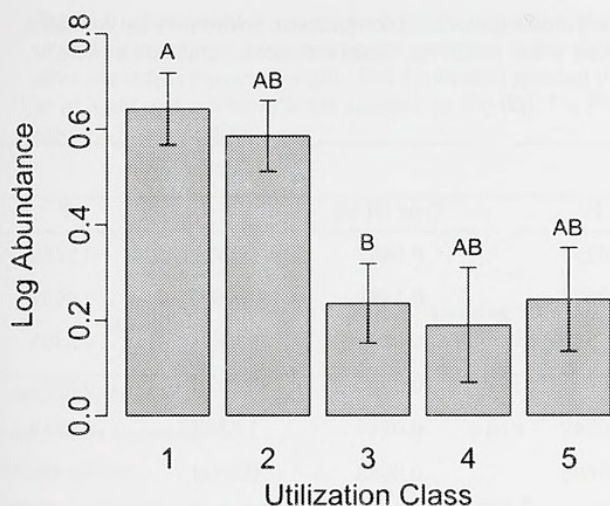
Figure 6. The effect of cattle grazing utilization class on the log abundance of the Great Basin Wood Nymph, *Cercyonis sthenele*, (+/- SE) in the Cascade-Siskiyou National Monument in 2004. Grazing utilization is lowest for class 1 and highest for class 5. Letters indicate statistically significant groups in species richness between utilization class following post-hoc Tukey tests.

also suggested in *Cercyonis pegala* (Fabricius, 1775) ($F_{4,15}$ = 2.37, P = 0.099). Cattle grazing utilization did not significantly predict the abundance of other grass-feeding butterfly species in this way (all P > 0.10).

Since many of the species that I observed were relatively rare in terms of their percentage contribution to the yearly abundance totals (Table 2), it is possible that some statistically significant results are actually artifacts of sampling bias for some or many of these species. When I limited the above analyses to the seven most abundant species (those composing at least 5% of the total observed 2004 individuals; 443+ individuals), four species were related to at least one of the eight environmental variables with α = 0.05. Transect length was unimportant for all these species. However, after correcting for the false discovery rate of incorrectly rejecting true nulls due to multiple statistical comparisons (Benjamini & Hochberg, 1995) (n=7, α = 0.0071,) only two species, *Cercyonis sthenele* and *Hesperia lindseyi* (Holland, 1930), were still significantly related to environmental variables, and *C. sthenele* still significantly declined with increasing grazing utilization class. Although it may be considered a habitat specialist and feeds exclusively on native perennial grasses like Roemer's fescue (*Festuca roemerii*), *C. sthenele* is widespread throughout the western United States and southwestern Canada and is not a species of conservation concern.

Species of special conservation concern

I recorded two species during transect sampling that are listed as being of special conservation concern by the Oregon Biodiversity Information Center (ORBIC 2010): *Polites mardon klamathensis* Mattoon, Emmel, & Emmel, 1998 (ORBIC List 1 and a federal candidate under the U.S. Endangered Species Act) and *Speyeria coronis coronis* (Behr, 1864) (ORBIC List 2). Both of these species were relatively rare on transects, and reasonable statistical estimates on effects of the environmental variables or grazing utilization are not possible. However, subjective evidence based on personal observations and unpublished data suggests that *P. mardon klamathensis* prefers short-statured native meadows dominated by Roemer's fescue and California oatgrass (*Danthonia californica*) and avoids meadows invaded by tall alien grasses like timothy. Light seasonal grazing by cattle may help to maintain the short-statured meadows preferred by *P. mardon klamathensis* since experimental cattle exclusion plots established by the Bureau of Land Management seem to show a long-term transition to tall, timothy-dominated meadows and reductions in *P. mardon klamathensis* abundance. A third rare species, *Callophrys johnsoni* (Skinner, 1904) (ORBIC List 1), is also known from the CSNM. I observed one individual in the vicinity of one transect at the Oregon Gulch headwaters in 2004 (representing only the third known record for the CSNM), but not during a sampling period, and thus was not included in any analyses for this study.

DISCUSSION

Multiple environmental factors, especially plant species richness, contribute to local CSNM butterfly diversity. It is perhaps not surprising that plant species richness consistently provided the strongest predictive value for local butterfly species richness and composition given that butterflies are phytophagous insects. Sites with higher plant species richness and diversity should also be expected to have higher butterfly diversity (Siemann *et al.*, 1998). Similar to Dover *et al.* (2011), cattle grazing utilization class appears to play a secondary role relative to this broader influence and may modulate local butterfly diversity by impacting ecosystem dynamics and plant-insect interactions. For example, cattle are more likely to graze near water sources (Hosten *et al.*, 2007a), and even if these locations do not possess the suitable hostplants, cattle can still affect resource availability by consuming nectar sources and/or alter local hydrology and water availability through trampling

Table 3. Butterfly species richness, evenness (Hill's E5), and total density (individuals ha-1) compared to environmental variables in the Cascade-Siskiyou National Monument in 2003 and 2004 in mixed linear ANOVAs. **Bold** indicates significant effects.

Species Richness			2003		2004		
Source	DF	Type III SS	F	P	Type III SS	F	P
Utilization Class	4	**0.1605**	**4.0876**	**0.0257**	0.0852	1.4374	0.2732
Elevation	1	**0.0663**	**6.7596**	**0.0232**	**0.1791**	**12.0937**	**0.0037**
Water	1	0.0007	0.0756	0.7880	0.0144	0.9739	0.3405
Herb Cover/Var	1	0.0019	0.1976	0.6646	0.0036	0.2419	0.6305
Shrub Cover/Var	1	0.0348	3.5442	0.0842	0.0243	1.6388	0.2213
Canopy Cover/Var	1	0.0007	0.0743	0.7898	0.0083	0.5602	0.4666
Log Herb Richness	1	**0.0489**	**4.9796**	**0.0455**	**0.1771**	**11.9587**	**0.0038**
Log Shrub Richness	1	**0.0487**	**4.9592**	**0.0459**	0.0059	0.3960	0.5393
Length	1	0.0160	1.6259	0.2264	0.0012	0.0801	0.7814

Evenness (E5)			2003		2004		
Source	DF	Type III SS	F	P	Type III SS	F	P
Utilization Class	4	0.0621	0.6100	0.6633	0.0404	0.8752	0.5032
Elevation	1	0.0195	0.7654	0.3988	0.0049	0.4224	0.5263
Water	1	0.0031	0.1217	0.7333	**0.0637**	**5.5202**	**0.0340**
Herb Cover/Var	1	0.0153	0.6022	0.4528	0.0035	0.3075	0.5880
Shrub Cover/Var	1	0.0033	0.1283	0.7264	0.0003	0.0240	0.8792
Canopy Cover/Var	1	0.0076	0.2983	0.5949	0.0289	2.5034	0.1359
Log Herb Richness	1	0.0006	0.0244	0.8784	0.0017	0.1457	0.7084
Log Shrub Richness	1	0.0031	0.1215	0.7334	0.0269	2.3336	0.1489
Length	1	0.0074	0.2914	0.5992	0.0239	2.0722	0.1720

Total Density			2003		2004		
Source	DF	Type III SS	F	P	Type III SS	F	P
Utilization Class	4	0.6098	1.2350	0.3475	1.2377	0.7942	0.5483
Elevation	1	0.0082	0.0666	0.8007	0.0127	0.0325	0.8596
Water	1	0.0077	0.0622	0.8072	0.5390	1.3835	0.2591
Herb Cover/Var	1	0.2461	1.9934	0.1834	0.0857	0.2200	0.6463
Shrub Cover/Var	1	0.0042	0.0342	0.8563	0.2543	0.6527	0.4327
Canopy Cover/Var	1	0.1441	1.1669	0.3013	0.0114	0.0291	0.8669
Log Herb Richness	1	0.2174	1.7609	0.2092	0.1793	0.4603	0.5085
Log Shrub Richness	1	0.0554	0.4491	0.5154	0.1738	0.4461	0.5151
Length	1	0.0403	0.3268	0.5781	0.0572	0.1467	0.7074

Table 4. Significant P values (< 0.05) for the 2004 abundance of butterfly species related to transect length, cattle grazing utilization, and seven environmental variables in the CSNM. Values for utilization and environmental variables are calculated after excluding transect length. **Bold** indicates species that comprise at least 5% of the total 2004 observations and are related to at least one environmental variable (α = 0.05). * = P values that are still significant after controlling for the false discovery rate (n=7, α = 0.0071).

Species	Transect length	Grazing utilization class	Elevation	Water	Weighted mean percent cover by layer			Log plant species richness by layer	
					Herb	Shrub	Canopy	Herb	Shrub
Adelpha californica				0.020					
Anthocharis lanceolata		0.017	0.008						
Boloria epithore			0.005						
Cercyonis sthenele		**0.007 ***	**<0.001 ***						
Chlosyne palla			0.012						
Coenonympha tullia				0.048					
Colias occidentalis			0.027						
Erynnis persius				0.016					
Erynnis propertius			0.006						
Euchloe ausonides		0.042	0.005						
Euphilotes glaucon					0.012				
Euphydryas chalcedona			**0.021**	0.041					
Euphydryas editha	0.010								
Hesperia lindseyi			**0.005 ***						
Limenitis lorquini				0.013					
Lycaena nivalis			0.003						
Papilio multicaudatus			0.002						
Papilio zelicaon				0.030					
Parnassius clodius			0.046						
Phyciodes pulchella		0.032							
Pieris rapae									0.018
Plebejus icarioides			0.007						
Polites mardon			0.024						
Polygonia gracilis			0.008						
Pontia occidentalis								0.030	
Pontia sisymbrii	0.031			0.027					
Pyrgus communis			0.001						
Satyrium saepium						0.050			
Satyrium sylvinum			0.010				0.039		
Satyrium tetra	0.028								
Speyeria coronis	0.029								
Speyeria hydaspe			<0.001						
Speyeria zerene			0.005						
Vanessa cardui							0.039		
No. species	4	4	19	7	1	1	2	1	1

and manure deposition.

The historical grazing and ecological context of the CSNM has important implications for the interpretation of these results (Borman, 2005; Hosten *et al.*, 2007a; Hosten *et al.*, 2007b; Hosten *et al.*, 2007c). For instance, grassland conditions across the CSNM have generally declined since the concurrent decrease of very heavy livestock grazing and advent of strict fire suppression in the 1950s, which has resulted in corresponding increases in Douglas-fir, Ponderosa pine, western juniper, and other woody vegetation. At the same time that native perennial bunchgrasses have increased in some areas under reduced grazing pressure, other locations have seen increases of non-native bulbous bluegrass (Hosten *et al.*, 2007c). While not an aspect addressed in this study, approximately 85% of CSNM forests have also experienced some history of selective timber harvesting (USDI Bureau of Land Management 2002). It is possible therefore that butterflies respond to site-specific factors related to utilization or management history rather than directly to intra-year utilization intensity, such as the long-term conversion of native bunchgrass meadows to non-native annual grasslands by some grazing regimes (Masters & Sheley, 2001; Hosten *et al.*, 2007c). Indeed, the significant difference in butterfly species richness observed in 2003 between Class 1 and Class 3 utilization transects may be largely attributable to the high prevalence of invasive plants like medusahead and bulbous bluegrass, that are unpalatable to both butterflies and cattle, at several oak woodland Class 1 transects. Habitat disturbance effects like cattle grazing can also operate over different spatial and/or temporal scales (Hamer & Hill, 2000), and many butterfly species may be able to disperse over long enough distances to not be significantly sensitive to local variation in intra-year grazing utilization level, particularly if suitable patches are connected (Debinski *et al.*, 2001; Pöyry *et al.*, 2009).

Unrelated species with similar life history characteristics may be predicted to respond in similar manners to these environmental factors. As observed in many European grasslands that have undergone long-term grazing, it is possible that the current CSNM butterfly fauna has been modified such that those species that are tolerant of grazing are in greater abundance now than prior to the influences of cattle grazing. This is particularly relevant given that a primary effect of cattle grazing utilization on butterfly diversity may be to decrease the abundance of species utilizing native graminoid hostplants like *Cercyonis sthenele* at high grazing utilization levels. However, this decrease did not result in a corresponding detectable increase in the abundance of woodland associates.

Comparisons between butterflies and other fauna

Many of the butterfly transects overlapped with the sampling locations used by Alexander *et al.* (2008) and Johnston & Anthony (2008) in their concurrent grazing effect studies on birds and small mammals, so some trends found across taxa can be compared, at least in terms of the effects of cattle grazing utilization. Alexander *et al.* detected significantly fewer birds within several life history suites at high grazing utilization routes than at low utilization routes, and that these effects were more pronounced in oak woodlands. In contrast, Johnston & Anthony (2008) found lower mean diversity and evenness of small mammals in high utilization versus low utilization sites in mixed conifer forest, but no such effects in oak woodlands. Given the decline in grass-feeding butterflies with increased grazing and that most grass-feeding butterfly species were more abundant in oak woodlands, the effects of cattle grazing utilization on butterflies appear to be more similar to birds than to small mammals. Both of these studies found significant and sometimes inconsistent differences between upland and riparian areas in terms of species richness, diversity, and responses by species and/or feeding guilds. Unlike this butterfly study though, Alexander *et al.* (2008) did not collect detailed vegetation data at each of their survey points, and classified grazing as either low (0-40%) or high utilization (>40%). Johnston & Anthony (2008) did estimate forest structure and percent cover, but similarly did not survey plant species richness at each trapping point, and also categorized cattle grazing utilization into subjective "light" or "high" categories. Therefore, this butterfly study incorporates more environmental data into its analyses than either of these bird or small mammal studies.

Management implications

The Presidential Proclamation (2000) establishing the CSNM suggests that high butterfly diversity is a desirable attribute of the CSNM. Management practices that promote local plant species richness should be expected to broadly promote butterfly species richness. However, there is no evidence of a uniform response of individual butterfly species to grazing or other environmental influences given that multiple environmental factors helped explain the trends in the spatial variation in butterfly species composition and abundance. The complex ecological landscape of the CSNM likely amplifies all of these factors, and some underlying patterns may not have been detected. Additional years of

research would likely be necessary to tease out the relative importance of these effects, and help account for long-term population fluctuations (Thomas *et al,*. 2002; Hellmann *et al.*, 2003). Therefore, a diversity of integrative management tools may be necessary since species-specific management frequently creates conflicts in which other species may be adversely affected (Schultz & Crone, 1998; Kwilosz & Knutson, 1999; Panzer, 2002; Huntzinger, 2003; Panzer, 2003).

ACKNOWLEDGEMENTS

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