

LOCAL AND LANDSCAPE INFLUENCES ON MEADOW BUTTERFLY
COMMUNITIES IN NORTHEASTERN SIERRA NEVADA

A thesis submitted to the faculty of
San Francisco State University
In partial fulfillment of
The requirements for
The degree

Master of Sciences
in
Biology: Ecology and Systematics

by

Katrina S. Strathmann

San Francisco, CA

May 2005

Copyright by
Katrina S. Strathmann
2005

CERTIFICATION OF APPROVAL

I certify that I have read *Local and landscape influences on meadow butterfly communities in northeastern Sierra Nevada* by Katrina S. Strathmann, and that in my opinion this work meets the criteria for approving a thesis submitted in partial fulfillment of the requirements of the degree: Master of Sciences in Biology: Ecology and Systematics at San Francisco State University.

Edward F. Connor
Professor of Biology

Gretchen Lebuhn
Professor of Biology

John Hafernik
Professor of Biology

LOCAL AND LANDSCAPE INFLUENCES ON MEADOW BUTTERFLY COMMUNITIES IN NORTHEASTERN SIERRA NEVADA

Katrina S. Strathmann
San Francisco State University
2005

Conservation planning and ecological research aimed at understanding patterns of biological diversity have focused on determining which environmental factors influence populations and communities. While local environmental factors were long considered to be of central importance, an interest in landscape context surged in the 1970s following the development of the theory island biogeography. In this study, I examined the relative influence of both local and landscape factors on butterfly communities in montane meadows of northeastern California. I ask if local attributes of meadows are more important than landscape context in determining butterfly richness and abundance, and I also examine meadow specialist and generalist butterflies, as well as the most abundant individual butterfly species. The strongest patterns were related to three variables. A single landscape variable, the percent of sagebrush vegetation in the matrix surrounding meadows, was strongly and negatively related to total butterfly richness and abundance as well as estimated butterfly richness and the abundance of a meadow generalist butterfly, *Pyrgus communis*. A single local variable, cover of obligate wetland plants within meadows, was strongly and

positively related to species richness and abundance of meadow specialist butterflies, and the abundance of a single meadow specialist species, *Plebejus podarce*. In addition, elevation was positively related to the abundance of two butterfly species, *Speyeria mormonia* and *Colias eurytheme*, and negatively related to the abundance of *Coenonympha tullia* ssp. *ampelos* and *Satyrium behrii*. In general, local factors explained more of the variation for butterfly variables than landscape factors. Further, the moisture and topographical gradients that influence meadow butterfly communities in the eastern Sierra Nevada suggest that protecting both moist meadow habitats and surrounding matrix habitats are important for conserving this faunal group.

I certify that the Abstract is a correct representation of the content of this thesis.

Chair, Thesis Committee

Date

ACKNOWLEDGEMENTS

This project would not have been possible without the support of many people, in particular T. N. Elliott. I am grateful to Dr. E. F. Connor for his open door, fearless encouragement and collegial friendship. I thank Ellen Donald for her good company and thoughtful nature as a volunteer field assistant. The project also benefited from volunteers who assisted with data collection: Lisa Lacabanne, Kathy McGrath, Tom Elliott, Mike Faden, Johanna Rahman, and Courtney Johnson. I am indebted to Drs. Arthur Shapiro and Paul Opler for their assistance with identification of troublesome butterfly species, and for comments on drafts of this thesis and the research proposal. The GIS work was possible with the help of the SFSU GIS lab and colleague Craig Scott. Dave Weixelman provided guidance on identification of *Carex* species. I am also grateful to Carol Boggs, Jessica Hellman, Taylor Ricketts, Virginia Rivers, and the graduate labs of Drs. Connor and Lebuhn for contributing their insight to the research proposal. Thanks to Rich Hatfield and Scott Simono for sharing observations from their 2003 season in Sierra meadows. Drs. Mark Reynolds and Gretchen Lebuhn are credited with suggesting that I consider investigating butterfly communities in the first place. Finally, thanks to my colleagues in the National Park Service and Presidio Trust for their appreciation of the pursuit of higher education, and their patience and support during my pursuit.

TABLE OF CONTENTS

List of Tables	viii
List of Figures	ix
Introduction.....	1
Local influences.....	3
Landscape influences.....	4
Methods.....	9
Butterflies	11
Local influences.....	13
Landscape influences.....	17
Statistical analysis	18
Results	19
Local influences.....	22
Landscape influences.....	24
Discussion	25
Local influences.....	29
Landscape influences.....	37
Moisture and topographical influences	39
Conclusions.....	41
References	44

LIST OF TABLES

Table

1.	Units of inflorescences used to estimate inflorescence density	52
2.	Flowering species observed but not sampled	53
3.	Descriptive statistics of independent variables	54
4.	Butterfly species and number observed during sampling.....	55
5.	Moderately intercorrelated variables	57
6.	Regression models for species richness and abundance of the butterfly community	58
7.	Regression models for abundance of dominant butterfly species.....	59
8.	Model responses to removing intercorrelated variables.....	60

LIST OF FIGURES

Figure

1. Map of study region 61
2. Aerial photograph of a study site, transect locations and matrix area 62
3. The relationship between the species richness and abundance of all butterflies with percentage sagebrush vegetation in the matrix 63
4. The relationship between species richness and abundance of meadow specialist butterflies with cover of obligate wetland plants 65
5. The relationship between abundance of dominant meadow specialist butterfly species with primary explanatory variables 66
6. The relationship between the abundance of dominant meadow generalist butterfly species with primary explanatory variables 68
7. The relationship between the species richness and abundance of all butterflies and meadow specialist butterflies with explanatory variables for high and low elevation meadows 70

Introduction

There is a practical urgency to identify factors responsible for patterns of biological diversity in order to direct conservation priorities and land management actions (e.g., Diamond 1975, Simberloff and Abele 1982, Litwin and Smith 1989, Diaz et al. 1998, Kruess and Tschardtke 2002). Similarly, much of the ecological research aimed at scientific understanding of the distribution and abundance of species has focused on determining which factors influence population or community patterns. Historically, environmental factors that influence patterns of abundance and distribution have been explored at two scales. At the local scale, numerous population and community patterns have been strongly linked to proximal processes such as resource availability (e.g., MacArthur and MacArthur 1961, Willson 1974, Roth 1976, DeGraaf et al. 1998, Carvell 2002). At the landscape scale, the landscape context in which local populations and communities are embedded and regional processes such as immigration and dispersal have been shown to influence the abundance and distribution patterns of individual species and whole communities (e.g., MacArthur and Wilson 1967, Kadmon and Pulliam 1993, Steffan-Dewenter and Tshardtke 2002, Steffan-Dewenter et al. 2002).

Local influences were long considered to be of central importance in explaining patterns in the distribution and abundance of animals and plants. This

perspective is convincing because studies that examine only habitat characteristics at local scales have been relatively successful in explaining community patterns (MacArthur and MacArthur 1961, Willson 1974, Roth 1976, Vale et al. 1982, DeGraaf et al. 1998, Carvell 2002, Kruess and Tschardtke 2002). The primacy of local processes may have been reinforced by an early lack of understanding of potential mechanistic processes operating at regional scales, or by the logistical issues of conducting experimental or observational studies at larger scales. While the foundations for landscape ecology can be found in the 19th century, it was the development of the theory of island biogeography, and its implications for understanding the effects of habitat fragmentation and population dynamics, that challenged the hegemony of local influences in determining population and community patterns (MacArthur and Wilson 1967, Simberloff and Abele 1982, Turner 1989). There is growing understanding that “the consideration of landscape effects in ecological studies is not a mere bandwagon, but represents an important progress toward the prediction of species presence and abundance” (Mazerolle and Villard 1999). At this point, the relative importance of local and landscape factors as an ecological principle is unresolved (Mazerolle and Villard 1999). Meanwhile, the questions that puzzle community ecologists – are local or regional factors most important in structuring species abundance and richness patterns in a particular system? and which factors have primary importance? – continue to be crucial for land

managers in determining which parcels of land to protect in a landscape, or how and which local habitats to manipulate in order to maintain populations and communities.

Local influences

Much of our current thinking about the influence of the local abiotic and biotic environment on animal communities can be attributed to a number of early studies focusing on North American songbird communities. Researchers developed methods to quantify local habitat characteristics and identified strong relationships between bird diversity and local vegetation structure (MacArthur and MacArthur 1961, Willson 1974, Roth 1976, Vale et al. 1982). Later studies showed that local vegetation characteristics influence the patterns of various animal communities including invertebrates (Luff and Woiwood 1995, Panzer and Schwartz 1998, Kruess and Tschardtke 2002, Carvell 2002). Subsequently, a large component of applied research – the development of models for wildlife occurrence or abundance – has evolved from identification of relationships of local habitat characteristics, such as vegetation, with animal species or communities (Morrison et al. 1998).

More recently, the spatial form of a habitat patch, such as size or shape, has been recognized as an influential local factor. A positive effect of habitat patch

size on species richness has been shown in innumerable studies (e.g., Bollinger and Gavin 1989, Diaz et al. 1998, Ricklefs and Lovette 1999, Steffan-Dewenter and Tschamntke 2002). Larger patch size is frequently related to higher species richness, possibly due to increased heterogeneity within a patch, lower extinction rates, or higher colonization rates (MacArthur and Wilson 1967, Connor and McCoy 2001). Few studies have examined the influence of patch size on abundance. While density-area relationships are not uniform among taxonomic groups, many species increase in density as patch area increases, suggesting that populations concentrate in areas of high resource availability (Connor et al. 2000). Most studies examining the effect of habitat patch shape on populations and communities have shown that shape is of little importance in determining species richness but may influence the abundance of individual species (Blouin and Connor 1985, Baz and Garcia-Boyer 1995, Graham and Blake 2001).

Landscape influences

Interest in landscape processes surged in the 1970s, and correlational and experimental studies began to investigate general population and community patterns related to the isolation of habitats and the composition of landscapes surrounding habitats. The theory of island biogeography posits that one major factor in maintaining species number at equilibrium on an island is the distance from other islands (the other factor being the size of an island), resulting in

islands nearer to other islands or to the mainland maintaining higher species richness (MacArthur and Wilson 1967). The theory suggests that the mechanism for this pattern is that greater isolation (and smaller island size) decreases the likelihood of immigration and increases the likelihood of extinction. The theory of island biogeography was later applied to habitat islands, however, the degree of habitat isolation has not been consistently related to population or community patterns. For some taxa, habitat isolation appears to have a strong, negative influence on species abundance, occurrence or richness (Lynch and Whigham 1984, Diaz et al. 1998, Mazerolle and Villard 1999, Brotons and Herrando 2001, Crooks et al. 2001, Tworek 2002), while for others there is no such effect (Lynch and Whigham 1984, Davis and Jones 1986, de Jong 1995, Mazerolle and Villard 1999, Crooks et al. 2001, Tworek 2002). The variation in effects of isolation among species, or lack of effects for some community studies, may be due to the difficulty of identifying a biologically meaningful scale that applies broadly to multiple taxa. This is illustrated by avian community studies where species guilds or habitat specialists showed stronger effects of isolation than the community as a whole (Lynch and Whigham 1984, Brotons and Herrando 2001, Tworek 2002). In a review of studies examining the influence of isolation and patch area on invertebrate communities, Steffan-Dewenter and Tscharrntke (2002) note that large scale investigations were lacking.

More recently, there has been recognition that the composition of the landscape in which habitat patches are embedded may have a strong influence on population and community patterns (Mazerolle and Villard 1999). The landscape matrix is thought to represent resources according to matrix type or heterogeneity, or potential barriers to immigration (Ricketts 2000, Brotons et al. 2003, Dauber et al. 2003, Jules and Shahani 2003). A number of experimental studies that manipulate matrix quality suggest that landscape composition has an effect on species richness or abundance of butterflies (Zschokke et al. 2000) and insects (Collinge 2000, Baum et al. 2004). However, results of observational studies have been mixed in showing effects of the landscape matrix on species abundance or richness (Mazerolle and Villard 1999, Graham and Blake 2001, Soderstrom et al. 2001, Steffan-Dewenter 2001, Tscharrntke et al. 2002, Brose 2003, Dauber et al. 2003, Krauss et al. 2003a, Weibull and Ostman 2003, Krauss et al. 2004). As with the isolation of habitat patches in the landscape, the adequacy of an investigation of the influence of landscape composition will depend largely on determining the appropriate scale for the taxonomic group in question (Turner 1989, Mazerolle and Villard 1999). A few researchers have grappled with this problem by evaluating the effects of the landscape matrix at multiple scales (Graham and Blake 2001, Steffan-Dewenter 2001, Steffan-Dewenter et al. 2002, Dauber et al. 2003).

Until recently, few studies examined the influence of local and landscape factors on populations or communities simultaneously (Lynch and Whigham 1984, Diaz et al. 1998, Crooks et al. 2001, Brotons and Herrando 2001, Graham and Blake 2001, Soderstrom et al 2001, Roni 2002, Tworek 2002, Dauber et al. 2003, Weibull and Ostman 2003). In their review of studies that included both patch-scale and landscape scale variables, Mazerolle and Villard (1999) suggest that landscape context is likely complementary to local characteristics. They note, however, that the problem of determining the appropriate scale at which to examine landscape context may hinder attempts to adequately evaluate the relative importance of local and landscape factors. To illustrate the varying responses of taxa to local and landscape variables, consider a study of plants, ants and bees in German grasslands. Dauber et al (2003) showed that plant species richness was influenced only by local variables, ants species richness was influenced only by landscape variables, and although bee species richness was influenced by both, landscape context explained a smaller portion of the variation than did local variables in regression models. Additionally, when investigations of vertebrate, invertebrate and plant richness were conducted at different spatial scales, these studies echo the conclusion that landscape context is complementary to local habitat characteristics (Graham and Blake 2001, Brose 2003, Dauber et al. 2003). Understanding the relative influence of local and landscape characteristics, and the primary environmental factors, affecting

populations or communities in an ecosystem could provide an effective foundation for developing land conservation or land management strategies (Mazerolle and Villard 1999). For example, Diaz et al. (1998) showed that higher species richness of Spanish plateau breeding bird communities is strongly related to larger forest stand size (local factor), greater forest understory structure (local factor), and decreased isolation of forest stands (landscape factor). Their findings suggest that protecting both local and landscape factors is the most effective means of maintaining bird species richness: protecting large forest stands with diverse understory and high connectivity in the landscape.

To explore questions about the effects of local and landscape factors on community and population patterns, I selected the butterfly community of montane meadows in northeastern California. These meadows have been subjected to historic habitat degradation and are currently under pressure for development. Butterflies (Lepidoptera: Papilionoidea and Hesperioidea) are an ideal system for examining the contributions of local and landscape processes for a variety of reasons. Patterns of species richness of butterfly assemblages are well-studied, due to ease of identification and because of the charismatic qualities of these superfamilies of Lepidoptera. A relatively large body of knowledge has been accumulated for individual species such as host plants, flight periods, geographic ranges, and overwintering life stage. Meadows provide

adult food resources to generalist butterflies during summer months, as well as larval and adult food resources for butterflies specializing in meadow habitats. In addition, montane meadows are naturally fragmented habitats, and are embedded in landscape matrices of different vegetation and land-use types, so that they provide an opportunity to explore several local and landscape attributes at once. To my knowledge, no studies in this region have investigated the importance of local and landscape attributes simultaneously on the richness and abundance of butterfly assemblages. Using a linear modeling approach, I ask what environmental variables account for observed patterns in the species richness and abundance of butterflies. Are local attributes of habitat patches more important in structuring communities than the composition and configuration of the landscape? Are patterns more evident for habitat specialists? And can these patterns provide information for managing and conserving meadow communities in the region?

Methods

I studied the butterfly communities of montane meadows located on the eastern slope of the California Sierra Nevada in the Tahoe National Forest (TNF). The approximate northern and southern extents of the study region are, respectively, the towns of Sierraville and Truckee, California (Figure 1). Fifty-year averages

for climate in the region show summer temperatures reaching 71-84° F at middle elevations, and winter temperatures average 14-45° F (Western Regional Climate Center 2004). Most precipitation falls between October and April as snow, with a 50-year average depth of 64 cm per year, and snowmelt occurs from May through July depending on elevation. Occasional summer thundershowers supply a portion of annual precipitation. In 2003, late-season snowfall delayed snowmelt until mid- to late-May at lower elevations. Precipitation in 2003 was above the 50-year average in July and August, while temperatures were nearly five degrees above the average in June and July. The butterfly flight season typically begins in early May, but some species are observed to fly at lower elevations in the study region as early as April (Art Shapiro, personal communication). Dominant plant communities are lodgepole pine, Jeffrey pine, ponderosa pine, montane meadow, Nebraska sedge, big sagebrush, bitterbrush, tobacco brush, aspen and greenleaf manzanita vegetation series, as described by Sawyer and Keeler-Wolf (1995).

I obtained a digital map from the TNF that identified all meadow vegetation units in December 2002 (A. Doerr, M. Triggs, and T. York, 1998 meadow vegetation units map, Tahoe National Forest). The elevation range for all meadows in the study region is 1,494 to 2,713 meters a.s.l., and the range in area is 0.002 to 1,085 hectares. To avoid extremes in elevation, and to represent meadow areas

falling around the mean (32.2 ha) and median (6.2 ha) area, I randomly selected 18 meadow sites between 1,676 to 2,134 meters a.s.l., and between 4 to 60 hectares in size. I excluded meadow sites that were privately owned or occurred more than 1 km from a navigable road or trail. After selection, I verified the areas of each meadow by field checking, which resulted in an actual range of area between 2.9 and 51.5 hectares for the study meadows.

Butterflies

To estimate the species richness and density of butterflies, I established five 100-meter transects in each meadow (Figure 2). I located one endpoint for each transect using computer-generated random points (Arcview GIS v3.3, Environmental Systems Research Institute; AlaskaPak extension feature v4.1, National Park Service) and randomly generated compass bearings along which to extend the transects. I discarded endpoints or bearings that resulted in transects located outside meadow sites and randomly selected new points or bearings. I marked both transect endpoints with stakes and blue pinflags for easy relocation on repeated visits. Most adult butterflies are short-lived and peak flight periods of univoltine species may occur within a span of 4-6 weeks. Therefore, I visited each meadow three times at 3-4 week intervals, between May 27 and August 14, 2003. At each visit, observers walked each transect during a 10-minute period and recorded species and number of all butterflies observed 5

meters in front of the observer and 3 meters to each side. Weather conditions were monitored so that observations were made during conditions that are conducive to butterfly flight.

Butterflies were identified to species, genus and family following nomenclature in *Butterflies of North America* (Brock and Kaufman 2003), the USGS Butterflies of North America website (Opler et al 1995) and Opler and Warren (2004). When visual identification was not possible, I stopped time and captured individuals for identification. For individuals that could not be readily identified in the field, specimens were temporarily immobilized, digitally photographed, and released. Immobilization was achieved by placing specimens in small jars, cooling them in an ice chest for several minutes, then exposing butterflies to ethyl acetate vapors for 30-60 seconds. I also collected voucher specimens. Identifications of voucher specimens and digital photographs were verified by regional butterfly specialists. Vouchers are stored at San Francisco State University.

I classified each species according to habitat specialization (meadow specialists or meadow generalists) using species information described in published sources and reported by regional experts (Art Shapiro, personal communication; Paul Opler, personal communication; Scott 1986, Opler et al 1995, Opler 1999,

Glassberg 2001, Brock and Kaufman 2003). A small number of meadow generalist butterflies are specialists in other habitats, but not meadow habitats.

For each meadow, species richness and abundance were calculated using all transects and visits combined. Species richness and abundance were calculated for all butterflies, meadow specialists, and meadow generalists. As all species present in meadows were potentially not observed during the three visits, I used the program SPECRICH (Hines 1996), which relies on observed abundance data to estimate potential species richness for all butterflies. I also selected the eight most abundant butterfly species to examine the influence of local and landscape environmental variables on the abundance of individual species. For each of the eight species, abundance was pooled across all transects and visits for each meadow.

Local influences

I measured nine local variables in each meadow (Table 3). Nectar resources were measured because most adult butterflies feed almost exclusively on flower nectar. Number of plant inflorescences is highly correlated with actual nectar availability in other systems (Holl 1995), so I considered number of inflorescences to be a reasonable proxy for nectar resources. To estimate nectar resources for butterflies in each meadow, at each visit I recorded the family of

plants in flower within a 6 meter band along butterfly transects and estimated the number of inflorescences using a logarithmic scale as follows: 1-10, 10-100, 100-1,000, etc. Number of inflorescences was estimated based on floral units of each genus or family, according to Table 1. I estimated the total number of flowering plant families observed and the density of inflorescences in each meadow from all samples taken on two visits between June 15 and August 13, 2003. Mid-points of each range were calculated, and density was calculated for each meadow by summing the number of inflorescences for all families at both visits. Based on the characteristics of plants that are preferred nectar species (Scott 1986, Proctor et al. 1996, Glassberg 2001), I did not record minute species in flower such as *Polygonum polygaloides ssp. kelloggii* (E. Greene) J. Hickman. Of flowering plant species observed but not included in estimates (Table 2), two butterfly species (*Polites sonora* [Scudder] and *Pontia protodice* [Boisduval & Leconte]) were observed visiting *Epilobium brachycarpum* C. Presl, and one butterfly species (*P. protodice*) was noted visiting a *Gayophytum sp.* late in the season when many other plant species had completed flowering. A small number of flowering plant species were included in inflorescence estimates that were later determined to be unimportant as nectar resources (Table 1; Arthur Shapiro, personal communication).

As larvae, many butterfly species feed reliably on a restricted group of host plant species (Scott 1986, Scoble 1992), suggesting that butterfly communities should be strongly related to measures of plant resources (Gilbert 1984). To estimate plant richness and cover in each meadow, I randomly located three 0.75 m² plots along each butterfly transect, for a total of 15 plots in each meadow. I identified all plant species in each plot, and assigned a cover class according to the Braun-Blanquet method (Elzinga et al 2001): (1) 0-5%; (2) 5.1-25%, (3) 25.1-50%, (4) 50.1-75%, and (5) 75.1-100%. To account for seasonal variation in cover, I sampled five plots in each meadow (one along each transect) on each visit. I identified plants to species according to classifications in *The Jepson Manual* (Hickman 1993), and I deposited voucher specimens at San Francisco State University. Although I did not include the parameters in my analysis, I also estimated cover of bare soil, and of water standing or flowing on the soil surface, in vegetation plots.

For calculations of percent cover within meadows, I used the mid-point of cover class ranges for each plant species in each vegetation plot and then calculated the average percent cover for each meadow. For cover of obligate wetland species, I summed cover values for all species ascribed obligate wetland indicator species status in California by the U.S. Fish and Wildlife Service (NRCS 2004) in each plot prior to averaging plot values for each meadow. Aerial cover

of obligate wetland plants is a reasonable proxy for biomass and productivity, as positive cover-biomass relationships are common (Bonham 1989). I also consider wetland plant cover a proxy for meadow moisture, as “prevalence” of hydrophilic vegetation is one of three parameters used in wetland delineation in the U.S. Corps of Engineers *Wetland Delineation Manual* (COE 1987). For cover of *Artemisia* spp., I summed cover values for the two species I encountered, *Artemisia cana* ssp. *bolanderi* (A. Gray) G. Ward and *Artemisia tridentata* Nutt., for each plot before averaging the values for each meadow. For the proportion of native species cover, I divided the average percent cover of native species in a meadow by the average percent cover of all species.

To estimate vegetation height, I placed a meter stick on the soil surface at three systematic locations within each vegetation plot and recorded height of live vegetation within 1 cm of the meter stick. An average height was calculated for each meadow.

I estimated elevation of each meadow to the nearest 40-meters using digitized topographic maps from the California Spatial Information Library website (CaSIL 2003). I estimated meadow sizes by mapping meadow boundaries in the field onto printed versions of digital aerial photographs from the year 2000 (CaSIL 2003), digitizing the mapped boundaries, and calculating area using the Xtools

program extension in Arcview (Arcview GIS v3.3, Environmental Systems Research Institute; Xtools v6/1/2001, Mike Delaune, Oregon Department of Forestry).

Landscape influences

I measured nine landscape scale variables (Table 3). I estimated the average isolation distance of each meadow from other meadows by digitally measuring the distance of each site to the nearest three meadows using GIS (Arcview GIS v3.3, Environmental Systems Research Institute) and averaging these values. I estimated isolation of each meadow from large meadow sites by digitally measuring the distance of each site to the nearest meadow 100 hectares in size or larger.

To characterize the composition of the vegetation matrix, I first field checked aerial photographs for vegetation types and management activities (logging and burning). Vegetation types were assigned according to Sawyer and Keeler-Wolf (1995). Areas where the two management activities had occurred were identified by disturbance and debris associated with recent logging (such as slash and barren staging areas) or recent burning (burned snags, early post-fire vegetation, and burned soil and vegetation). Krauss et al. (2003) studied the influence of landscape diversity on butterfly richness in temperate grasslands at varying

scales from 250 m up to 3 km, and landscape diversity had a significant effect only at the smallest scale. Therefore, I determined that the 250 m scale was likely a biologically meaningful scale for most butterfly species, particularly for more sedentary meadow specialists. I calculated area of each vegetation type or management activity within a 250 m band around each meadow using digital maps (Figure 2; Arcview GIS v3.3, Environmental Systems Research Institute; Xtools v6/1/2001, Mike Delaune, Oregon Department of Forestry). I included only matrix variables in the analysis that accounted for at least 1% of the total area of the surrounding matrix in at least three meadow sites.

Statistical analysis

I evaluated the distribution of response variables, and normalized them if necessary using log, log + 1, or square root transformations to meet the assumptions of ordinary least-squares regression. I evaluated meadow attributes for intercorrelation prior to analysis. However, I judged that multi-collinearity was not a problem since I used a forward procedure for model-building, and because no two intercorrelated variables had significant partial t values in one model and thus did not enter any one model together. Further, Kleinbaum et al (1998) suggest that collinearity is not a concern when $r^2 < 0.9$.

To determine relationships between richness and abundance variables, and estimated richness of the total butterfly community, and meadow attributes, I built and evaluated multiple regression models for each dependent variable using a forward procedure with the entry criteria for variables set to a significance value of $\alpha = 0.05$. This approach allowed the local or landscape attributes with the highest partial *t*-statistics to enter the model first. Using this method, I also built and evaluated regression models to examine the relationship between the abundance of individual butterfly species and meadow attributes. To evaluate models, I visually examined residuals patterns for heteroscedasticity, checked for outliers, and checked tolerance levels of excluded variables. In those cases where outliers were a problem, I built and evaluated a model with potential outliers removed and compared these to the original. I determined that the original model was robust if the variables entering the model with the outlier removed were not altered from the original model.

Results

Among the 18 meadows sampled, I observed 1,961 individuals of 51 species of butterflies and was able to identify 94.5% of the specimens to the species level (Table 4). Meadow specialists accounted for a large portion of the butterflies observed. Nine species of meadow specialists comprised 42.8% of all

butterflies, but only 15.7% of species. Species richness and abundance of butterflies varied greatly among meadow sites. The total number of butterfly species observed at a meadow, pooled across three visits, ranged from 6 to 20, with an average richness among all sites of 13.3 (\pm 1.0). The abundance of butterflies in a meadow, again pooled across all visits, ranged from 20 to 232 individuals with an average of 108.9 (\pm 15.1) individuals. The abundance of individual species ranged from one to 507 individuals summed across all sites, and a single species, *Plebejus saepiolus* (Boisduval), accounted for nearly one-quarter of all individuals observed. The eight most abundant species included four meadow specialists (*Coenonympha tullia* ssp. *ampelos* [W.H. Edwards], *Plebejus podarce* [Felder & Felder] Opler & Warren, *P. saepiolus*, and *Speyeria mormonia* [Boisduval]) and four meadow generalists (*Colias eurytheme* Boisduval, *Junonia coenia* [Hubner], *Pyrgus communis* [Grote], and *Satyrrium behrii* [W.H. Edwards]).

Values of local and landscape habitat attributes also varied widely among sites (Table 3). I identified 228 species and morpho-species of vascular plants at all sites, and the average plant species richness in a meadow was 55.7. Forty-five of the plant species listed as obligate wetland species by the USFWS constituted the variable “cover of obligate wetland plants,” which averaged 33% cover across all meadows. The percentage of native species cover ranged from 67% to

100%. Nectar resources were represented by 25 plant families throughout all sites, with an average of 10.8 (± 0.6) plant families flowering and inflorescence density of 40,873.3 ($\pm 12,659.3$) per meadow. Five matrix vegetation types composed at least 1% of the total matrix area for a meadow and occurred in the matrix in at least three meadow sites (aspen, conifer forest, meadow, sagebrush, and chaparral; see Table 3 for descriptions). Recently logged areas in the matrix averaged 6.2% (± 2.0) across all sites, and ranged from 0-33.1% of the matrix. Burned vegetation in the matrix was observed at only two meadow sites and therefore this variable was not included in the analysis. Five of the 17 explanatory variables were moderately intercorrelated ($0.7 > r > 0.8$) with at least one other explanatory variable (Table 5). Plant richness was correlated with the number of flowering plant families, and three variables (obligate wetland plant cover, elevation, and percent of sagebrush vegetation in the matrix) were all intercorrelated.

I fitted models for all 15 of the butterfly community and individual species variables (Tables 6 and 7). Local attributes were the only variables explaining variation for three butterfly community response variables: richness and abundance of meadow specialists, and abundance of meadow generalists. A single landscape attribute, the proportion of big sagebrush series vegetation in the matrix, explained the largest amount of variation for the three community-

wide butterfly variables: total species richness, the natural log of estimated species richness, and total abundance.

For individual species, local attributes were the only variables explaining the variation in abundance for three meadow specialists (*P. podarce*, *P. saepiolus*, and *S. mormonia*) and one generalist (*C. eurytheme*; Table 7). Landscape attributes explained all of the variation in abundance for one generalist (*P. communis*). The abundance of one specialist butterfly (*C. tullia*) and of two generalist species (*J. coenia* and *S. behrii*) was explained by a combination of both local and landscape attributes, although landscape attributes explained less of the variation.

Local influences

Five of the nine local habitat attributes entered into models for butterfly community variables (Table 6). Cover of obligate wetland plant species within meadows explained a large portion of the variation for richness and abundance of butterflies that are meadow specialists (r^2 change of 38.3% and 49.0%, respectively; Figure 4). The proportion of native plant species cover within meadows improved the fit of the models of total species richness (r^2 change=17.5%) and of species richness of meadow specialist butterflies (r^2 change=17.8%). Average plant height greatly improved the fit of the model for

estimated total species richness (r^2 change=24.7%). The number of inflorescences was the only factor explaining 39.3% of the variation in number of meadow generalist butterflies. Finally, the number of flowering plant families observed in meadows improved the fit of the model slightly for the abundance of meadow specialist butterflies (r^2 change=12.2%). Four local variables did not explain any of the variation in butterfly community variables: plant species richness, cover of *Artemisia* spp. in meadows, meadow elevation and meadow area.

Of the dominant butterfly species I examined, local variables explained nearly all of the variation in abundance of three of the four meadow specialist species (Table 7, Figure 5). Cover of obligate wetland plants was the only variable explaining 66.2% of the variation in *P. podarce*. Similarly, average plant height explained 50.5% of the variation in *P. saepiolus*. Variation in *S. mormonia* abundance was attributed to elevation (40.1%). Finally, variation in the abundance of *C. tullia* was explained by the proportion of native species cover (40.5%) and elevation (21.5%).

Local variables also explained much of the variation in abundance for three of the four meadow generalist species (Table 7, Figure 6). The density of inflorescences explained 66.8% of the variation in abundance for *S. behrii*, and

the number of flowering plant families explained 30.7% of the variation in *J. coenia*. Elevation explained all of the variation in abundance of *C. eurytheme* (29.8%) and a portion of the variation abundance of in *S. behrii* (r^2 change=17.2%).

Landscape influences

Four landscape variables explained variation in butterfly community variables (Table 6). A single landscape variable, the percent of sagebrush vegetation in the matrix, explained a moderate portion of the variation in species richness of all butterflies (25.2%), the log of estimated total butterfly species richness (28.5%), and total butterfly density (27.6%; Figure 3). The percent of aspen in the matrix explained a portion of the variation in total species richness (25.0%). Similarly, the average isolation distance of meadows explained a small portion of the variation in total species richness (12.6%). Another landscape matrix variable, the percent of chaparral vegetation in the surrounding matrix, explained 23.7% of the variation in the species richness of meadow generalist butterflies. However, I determined the model fit to be poor based on the pattern of the residuals. Four landscape variables did not enter into any models for butterfly community variables: the distance from large (>100 ha) meadows, the proportion of forest and meadow vegetation in the matrix, and the proportion of logged area in the matrix.

For the eight individual species I examined, only one landscape variable entered into any models of abundance for meadow specialist species (Table 7). The percentage of chaparral vegetation in the matrix, explained an additional 11.9% of the variation in *C. tullia*, but again the residuals pattern for this variable was poor. In contrast, three landscape variables entered models for meadow generalist butterfly species. The abundance of a meadow generalist butterfly, *P. communis*, was explained entirely by one landscape variable, the proportion of sagebrush vegetation in the matrix (59.3%; Figure 6). The two additional landscape variables entered models but explained little of the variation in abundance of species: the percent of logged vegetation in the matrix improved the fit of the model for *J. coenia* (r^2 change=16.8%), and the average isolation of meadows improved the fit of the model for *S. behrii* (r^2 change=5.2%).

Discussion

My results illustrate the overall importance of both the local and regional environment in structuring California's montane meadow butterfly communities. Landscape variables strongly influenced the abundance and richness of the total butterfly community. However, when the community was partitioned into meadow specialists and generalists, local environmental variables had the

strongest influence on variation in species richness and abundance for each of these two groups. For the eight individual species I examined, the abundance of the meadow specialists was almost exclusively related to local scale variables, and the abundance of meadow generalists were related to both local and landscape variables. For both the butterfly community and the individual butterfly species, the variance explained by local factors was generally greater than the variance explained by landscape factors.

While I found that landscape variables were most important in explaining variation in the total butterfly community, other studies of butterflies in temperate systems have shown that landscape variables account for a small percentage of the variability in species richness or abundance relative to local habitat characteristics (Baz and Garcia-Boyero 1995, Steffan-Dewenter and Tscharrntke 2000, Collinge et al 2003, Krauss et al. 2003a, Krauss et al. 2003b). Many taxa, such as plant, bat, bee and bird communities, also responded most strongly to local factors even while landscape context explained some of the variation in species richness or abundance (de Jong 1995, Diaz et al. 1998, Mazerolle and Villard 1999, Brotons and Herrando 2001, Tworek 2002, Dauber et al. 2003). In contrast, species richness of ants in German grasslands responded only to landscape factors, illustrating the differing responses of taxa to local or landscape scale factors (Dauber et al. 2003).

Few studies have examined the relative influence of local and landscape variables on subsets of the butterfly community, such as specialists and generalists (Steffan-Dewenter and Tscharrntke 2000, Collinge et al. 2003, Krauss et al. 2003a, Krauss et al. 2003b). Similar to the results of this study, Collinge et al (2003) found that the abundance of common and uncommon butterfly species in Colorado grasslands was related only to local environmental variables.

Likewise, in a study of German grasslands, the richness and abundance of specialists were only related to grassland patch size and unrelated to isolation or landscape diversity (Krauss et al. 2003a, Krauss et al. 2003b). When butterflies were grouped according to food plant specialization or migratory status, species richness of these subsets of a grassland butterfly community were again entirely associated with local habitat size and habitat quality, and unrelated to habitat isolation (Steffan-Dewenter and Tscharrntke 2000).

Several avian studies have examined the relative influence of local and landscape environment on subsets of the community, such as species with similar life-history traits or habitat specialization (Lynch and Whigham 1984, Diaz et al. 1998, Brotons and Herrando 2001, Graham and Blake 2001, Tworek 2002, Brotons et al. 2003). Results of these studies are varied. For example, local factors are more important in explaining species richness or abundance of avian

forest specialists in Mexican tropical forests, but both local and landscape factors appear to be equally important for forest generalists (Graham and Blake 2001). Conversely, in Maryland and Mediterranean basin forests, both local habitat and landscape configuration attributes influenced the richness of avian forest specialists but only local factors influenced forest generalists (Lynch and Whigham 1984, Brotons and Herrando 2001). Clearly, for butterflies or birds, the life history traits of the species or community will determine which environmental factors are influential and at which scale.

I identified three strong environmental patterns in the butterfly community. First, a landscape scale variable, the amount of sagebrush vegetation in the matrix, was negatively associated with species richness, estimated richness and density of the total butterfly community, and the abundance of the meadow generalist, *P. communis*. Second, a local scale variable that represents meadow moisture and productivity, the cover of wetland plants within meadows, was positively related to richness and abundance of meadow specialist butterflies and a dominant meadow specialist species, *P. podarce*. Third, elevation was related to the abundance of two specialists (*C. tullia* and *S. mormonia*) and two generalist species, (*C. eurytheme* and *S. behrii*). In addition to the strong associations of moisture and topography, I found a number of other less pronounced patterns between the butterfly community and environmental variables.

Local influences

The abundance of obligate wetland plant species had a strong, positive influence on the abundance and species richness of meadow specialist butterflies. As assumed, wetland plant cover represents both meadow moisture and plant productivity. Not surprisingly, wetland plant cover was positively correlated with the amount of water observed on the soil surface ($r=0.55$, $p=0.02$), total plant cover ($r=0.86$, $p<0.001$) and vegetation height ($r=0.56$, $p=0.02$) within meadows. Wetter meadows provide more larval food resources for meadow specialist butterflies, as evidenced by the fact that wetland plant cover was also positively correlated with the abundance of all potential larval food plants of meadow specialist butterflies ($r=0.51$, $p=0.03$). For example, cover of wetland plants has a strong, positive influence on the abundance of a meadow specialist, *P. podarce*, which feeds as larvae on an obligate wetland plant species *Dodecatheon alpinum* (A. Gray) E. Greene. Such relationships between larval host plant cover and butterfly abundance are well established (Thomas and Mallorie 1985, Scoble 1992, Steffan-Dewenter and Tschardtke 1997, Clausen et al 2001, Matter and Roland 2002). For the eight other meadow specialists species, their larval host plants are not obligate wetland species but are herbaceous plants such as graminoids commonly found in meadow habitats. These herbaceous species are also more abundant in wetter conditions. While

hydrology is a defining characteristic of meadows, the abundance of wetland plants did not influence the butterfly community as a whole, or meadow generalist species individually. These results reflect the importance of larval food resources within Sierra Nevada meadows for meadow specialist butterflies.

Moisture availability or primary productivity has been shown to influence other butterfly and animal communities (Luff and Woiwood 1991, Clausen et al. 2001, Fleishman et al. 2001, Tworek 2002, Bailey et al. 2003). In the Great Basin's desert mountain ranges where wet meadows, springs, and riparian canyons provide important resources for animals, the distance of sites to running or standing water predicted the presence of one-fifth of butterfly species studied (Fleishman et al 2001). Greater primary productivity in the Great Basin was also related to higher species richness of neotropical migrant birds and of butterflies (Bailey et al 2003). Similarly, in Danish agricultural habitats the presence of streams was positively related to the richness and abundance of butterflies (Clausen et al 2001). This positive relationship between greater habitat moisture and higher species richness or abundance has been identified for other taxa, such as ground-nesting birds in Polish agricultural habitats (Tworek 2002) and British ground beetles (Luff and Woiwood 1991).

Elevation was not significantly related to any butterfly community variables. However, elevation alone predicted the abundance of two individual species, *S. mormonia*, a meadow specialist, and *C. eurytheme*, a meadow generalist. For both species, abundance increased at higher elevations. Additionally, abundance of another meadow specialist, *C. tullia*, and a generalist species, *S. behrii*, each decreased at higher elevations, although these relationships are less pronounced. In the case of *S. behrii*, its range is restricted by its host plant *Purshia tridentata*, which occurs in association with *A. tridentata*, *Pinus ponderosa* Laws and *Pinus jeffreyi* Grev. & Balf at lower elevations (Art Shapiro, personal communication). Many authors have shown strong associations between elevation and the presence, species richness or total abundance of butterflies (Boggs and Murphy 1997, Fleishman et al 1998, Fleishman et al 2001a, Fleishman et al. 2001b). When examining butterfly richness or abundance over the altitudinal range of a mountain system, some researchers found a unimodal distribution peaking at middle elevations (Fleishman et al. 1998, Fleishman et al. 2001a), and reduced fecundity at higher elevations is suggested (Boggs and Murphy 1997). It is difficult to identify the elevation of peak abundance for the four species I examined because the study region included only meadows at middle elevations. Nonetheless, the positive and negative correlations with elevation suggest generally higher elevation ranges for *S. mormonia* and *C. eurytheme*, and lower ranges for *C. tullia* and *S. behrii*.

These varied responses to elevation underscore the importance of the unique life history of individual species, such as overwintering, hostplant, and oviposition requirements, that influence species distributions differentially.

The density of inflorescences, a measure of nectar resources for adult butterflies, had a strong, positive influence on the abundance of all meadow generalist butterflies combined and one individual meadow generalist species, *S. behrii*. *S. behrii* was observed in large numbers late in the season, nectaring on the flat-topped inflorescences of *Perideridia* spp. The number of plant families in flower also represents nectar resources, and was strongly related to the abundance of a meadow generalist, *J. coenia*, and weakly related to the abundance of meadow specialists. In the case of *J. coenia*, since the species is uncommon in the eastern Sierra Nevada (John Hafernik, personal communication; Art Shapiro, personal communication), individuals may select meadows with greater nectar resources as they migrate from western slopes. The abundance of nectar resources in a habitat has been shown to strongly influence the distribution and abundance of butterfly species (Sharp et al 1974, Holl 1995, Steffan-Dewenter and Tschamntke 1997, Clausen et al 2001, Matter and Roland 2002). In a study of *Parnassius smintheus* Doubleday in Rocky Mountain meadows, Matter and Roland (2002) showed that abundance of males was lower in meadows with experimentally reduced abundance of nectar resources due to reduced

immigration into the resource-poor sites. In this study, in contrast to meadow specialists which appear to be strongly influenced by the availability of larval food resources within meadows, meadow generalist butterflies may select meadows based on available nectar.

Vegetation height within meadows was strongly associated with the abundance of the dominant butterfly species observed at all sites, *P. saepiolus*. Plant height may represent both meadow moisture and plant productivity, since as mentioned above plant height is positively correlated with wetland plant cover. *P. saepiolus*, a meadow specialist, feeds as larvae and adults on *Trifolium longipes* Nutt., a tall clover classified by the USFWS as a facultative wetland species. Where *T. longipes* occurs, vegetation height averages 23 cm, which is above the average height of vegetation within the study meadows. Vessby et al (2002) and Soderstrom et al (2001) suggest that a positive relationship of butterfly species richness or abundance with vegetation height to represent responses to increased plant productivity or lower grazing intensity. Similarly, Kruess and Tscharrntke (2002) found that for insect herbivores, vegetation height was the main predictor of species richness and abundance in German grasslands.

In this study, vegetation height was also negatively associated with the natural log of estimated butterfly richness. However, this association is difficult to explain

biologically and may be an artifact of the richness estimator (SPECRICH). Calculations for this estimator are based on the abundance distribution of species observed in meadows, as well as observed richness. Drier meadows with shorter vegetation height had fewer butterflies but also more species represented by single specimens. Therefore, SPECRICH may inflate estimates of species richness in drier meadows with shorter vegetation and overall lower butterfly abundance.

A greater proportion of native plant cover in meadows was strongly related to lower numbers of a meadow specialist, *C. tullia*, and slightly related to lower total butterfly richness and to lower meadow specialist richness. This result is initially counter-intuitive, given that two meadow sites with the most visible disturbance and highest cover of *Bromus tectorum* L., an invasive grass associated with disturbance, also had the lowest proportion of native plant cover. However, several meadows with a higher proportion of native cover are also the driest meadows sites with the lowest cover of wetland plants. As a result, the proportion of native plant cover could be high, even while total vegetation cover was low. For meadow specialist butterflies in particular, this result implies that availability of plant resources is more important than the relative quality (proportion of native or non-native species).

Two local variables were unrelated to any of the butterfly variables: meadow area and plant richness. In other temperate systems, many researchers have found positive species-area relationships for butterflies (e.g., Boggs and Murphy 1997, Panzer and Schwartz 1998, Steffan-Dewenter and Tschardtke 2000, Krauss et al 2003a). Several mechanisms have been offered to explain nearly ubiquitous species-area relationships in organisms, such as the habitat heterogeneity, area *per se*, and sampling hypotheses (Connor and McCoy 2001; Ricklefs and Lovette 1999). In this case, the notable lack of a relationship does not represent habitat homogeneity, but is likely due to sampling design. I allotted a fixed level of sampling effort to each meadow: five transects of equal size, regardless of meadow size. If the number of species detected is correlated with the proportion of area sampled, it is not surprising that I found no relationship in our study. In recent years studies have also begun to examine density-area relationships, for individual species as well as taxonomic communities. Positive density-area relationships have been identified for some insects (Connor et al. 2000), however, in German grasslands both positive (Krauss et al 2003a), and negative (Steffan-Dewenter and Tschardtke 2000) density-area relationships have been observed for butterflies. Like Vessby et al. (2002), I found no density-area relationship for butterflies.

Plant richness was also unrelated to any butterfly variable, a surprising result given the strong dependence of the butterfly community on a broad range of larval food plant species. The universality of the relationship between plant richness and butterfly richness or abundance is unclear. Several other researchers did not find significant relationships between plant species richness and butterfly community variables (Kitahara 2004, Vessby et al 2002, Soderstrom et al 2000, Sharp et al 1974), while others found positive associations (Simonson et al 2001, Steffan-Dewenter and Tscharrntke 2000, Panzer and Schwartz 1998, Thomas and Mallorie 1985). For other taxa, the relationship of plant richness to the animal community is also inconsistent. In a study of ants and birds, plant species richness was not correlated with the richness of either taxa (Dauber et al. 2003), but Kruess and Tscharrntke (2002) found that plant species richness explained variation in grassland insect communities. In my study, the number of plant species is less important in determining butterfly richness or abundance than other variables more directly representing plant resources available for butterflies. Indicators of plant resources, such as larval host plant abundance and nectar plant richness, have been shown to have a strong influence on the butterfly community (e.g., Sharp et al. 1974, Holl 1995). Another means for evaluating the influence of plant resources is plant composition, as distilled through multivariate analyses or community similarity indices. Analysis of plant composition captures differences in the species present and their relative

abundance, contrasted with species richness where the same number of species may occur in different sites although the identity of the species in the sites is quite different. In spite of the potential usefulness of plant composition in representing plant resources, I encountered few butterfly studies that used this analysis (Vaisanen 1992, Sawchik et al. 2003).

Landscape influences

The amount of sagebrush vegetation in the matrix was the most influential landscape-scale variable for the three community-wide butterfly variables, and for the abundance of the generalist, *P. communis*. In spite of the open structure of sagebrush vegetation that increases insolation necessary for flight and does not structurally inhibit movement, sagebrush vegetation in the matrix likely represents regionally drier sites and reduced food resources for butterflies in the landscape. The sagebrush vegetation type is less productive, more xeric vegetation than other types I surveyed, and the dominant species (*A. tridentata* and *A. cana*) are not a known food resource for adults or larvae. Sagebrush vegetation in the matrix may also represent drier meadow sites with fewer within-meadow food resources. For example, *P. communis* is strongly associated with a larval host plant, *Sidalcea oregana* (Torrey & A. Gray) A. Gray ($r^2=0.60$, $p=0.01$), which is less abundant in meadows with a large percentage of sagebrush vegetation in the matrix. That sagebrush vegetation had a negative

influence on community-wide variables and a meadow generalist, and not meadow specialists, underscores the relative importance of landscape context for generalists compared to specialists. Three other matrix variables influenced the richness or abundance of butterflies, but these relationships are weak compared to the repeated pattern of the negative influence of sagebrush vegetation in the matrix.

Researchers have argued that detection of significant relationships between landscape composition variables and plant and animal communities, or lack thereof, may be due to the scale of measurements and the biology of the organisms (Turner 1989, Mazerolle and Villard 1999, Krauss et al. 2003a, Dauber et al. 2003). In this study, the scale at which I measured the landscape matrix is comparable to that of other butterfly and invertebrate studies which detected an influence of landscape composition (Steffan-Dewenter et al. 2002, Krauss et al. 2003a, Dauber et al. 2003). In temperate calcareous grasslands, when the influence of landscape diversity was examined on scales of 250 m up to 3 km, only the smallest scale had a significant effect on butterfly richness, but not density (Krauss et al 2003a). Similarly, the species richness of ants and bees in German grasslands were strongly influenced by landscape matrix variables at both 50 m and 200 m scales (Dauber et al 2003).

I found that isolation of meadow sites accounted for little or no variation in the species richness or abundance of butterflies. My results parallel those reported in other studies which showed no effect of isolation on butterfly richness or abundance (Baz and Garcia-Boyero 1995, Steffan-Dewenter and Tschardtke 2000, Krauss et al 2003a, Krauss et al. 2003b). In contrast, a smaller number of studies reported that isolation is negatively associated with species richness or abundance of butterflies (Boggs and Murphy 1997, Sawchik et al. 2003). The effect of meadow isolation on butterflies is small compared to other environmental variables I considered. This is probably not due to a problem of scale appropriate to individual species or the community, except for the most vagile species. Vagility varies greatly among species, so it may be expected that isolation was relatively unimportant for community-wide variables in this study. Yet isolation was also unimportant for specialist or generalist community groups and for the eight species I examined, which range from sedentary to highly dispersive.

Moisture and topographical influences

The abundance of obligate wetland plants within meadows and the amount of sagebrush vegetation in the matrix surrounding meadows represent local and regional moisture gradients, respectively. Sagebrush is more abundant in montane areas of low water table (Castelli et al 2000, Berlow 2002) and,

conversely, obligate wetland plant species in meadows are associated with areas of higher water table (Allen-Diaz 1991, Castelli et al 2000). These two variables representing sagebrush and wetland plants, and meadow elevation, are moderately intercorrelated (Table 5). At higher elevations, the cover of wetland plants within meadows is greater and meadows are visibly more productive, while the proportion of sagebrush vegetation in the landscape is lower. Shifts in montane plant communities are visible in the 1500 to 2700 m elevation range: at lower elevations, big sagebrush, bitterbrush, ponderosa pine and Jeffrey pine associations dominate in the landscape surrounding meadows; at higher elevations, these cede to lodgepole pine and tobacco brush associations. Therefore, it is possible that the patterns observed in the butterfly community are due in part to an elevation gradient rather than a moisture gradient.

To tease apart altitudinal and moisture gradients, I visually examined scatterplots of butterfly abundance and species richness with the two explanatory variables related to moisture, after dividing the meadow sites into the nine highest and nine lowest elevation meadows (Figure 7). The association of total butterfly abundance and species richness with percent cover of sagebrush in the matrix, and of meadow specialist abundance and species richness with cover of obligate wetland plants, are generally still present within each restricted elevation range, although the strengths of these relationships are weaker due to smaller sample

size. In addition, I removed each of the primary significant predictor variables of wetland plant cover, sagebrush vegetation in the matrix and elevation from nine models for richness and abundance of community-wide, meadow specialist, and individual butterfly variables, similar to the process suggested by Chatterjee and Price (1977). When sagebrush in the matrix or wetland plants within meadows was removed from models where they had entered initially, elevation entered two models (Table 8). However, in other cases, either no variable entered the model after the original explanatory variable was removed (three cases), wetland plant cover entered the model (two cases), or another local variable, average plant height in meadows, entered the model (two cases). I interpret these results to suggest that the butterfly community is influenced by elevation as it affects patch-scale and landscape-scale moisture gradients. However, the effect of elevation acting via moisture gradients seems to be an added effect above and beyond the stronger more proximal effects of local and landscape scale moisture availability.

Conclusions

Identifying the local and landscape factors influencing communities has been suggested by other authors as an effective way to identify management activities to enhance local habitats, or to develop land conservation strategies that account for landscape context and configuration (Mazerolle and Villard 1999). My results suggest that montane butterflies in the eastern Sierra Nevada are greatly

influenced by moisture and topographic gradients, operating at both local and landscape scales. This pattern has been noted by other authors for montane butterfly communities (Fleishman et al 1998, Fleishman et al 2000, Fleishman et al 2001, Simonson et al 2001). In particular, my study shows that the total butterfly community is influenced by primarily by landscape context, while meadow generalists respond to both landscape context and local adult food resources. Not surprisingly, meadow specialist butterflies are most strongly influenced by local meadow characteristics that represent larval and adult food resources.

As the total butterfly community and meadow generalists appear to be particularly sensitive to landscape composition and elevation, conservation and land-use planning in the region should seek to preserve both meadow and matrix habitats throughout elevational ranges. Further, changes to meadow moisture regimes that reduce the abundance of obligate wetland plants could be expected to have a large effect on the species richness and abundance of meadow specialist butterflies. In meadows where stream hydrology has been degraded, and wetland plants have been reduced due to lowered water tables, restoration of hydrologic processes could be expected to have a positive effect on meadow specialists. With a relatively small number of easy to identify butterfly species (nine in this study) compared to wetland plant species (45 in this study, many of

them graminoids), meadow specialist butterflies may be an efficient indicator of the effect of management actions on meadow plants, insects and hydrology.

Such large-scale manipulations also present an opportunity to empirically test the effect of local-scale meadow moisture on richness and abundance of meadow specialists.

References

- Allen-Diaz, B.H. 1991. Water table and plant species relationships in Sierra Nevada meadows. *American Midland Naturalist* 126:30-43.
- Bailey, S. A., M.C. Horner-Devine, G. Luck, L.A. Moore, K.M. Carney, S. Anderson, C. Betrus, and E. Fleishman. 2004. Primary productivity and species richness: relationships among functional guilds, residency groups and vagility classes at multiple spatial scales. *Ecography* 27: 207-217.
- Baum, K.A., K.J. Haynes, F.P. Dilleuth, and J.T. Cronin. The matrix enhances the effectiveness of corridors and stepping stones. 2004. *Ecology* 85:2671-2676.
- Baz, A. and A. Garcia-Boyero. 1995. The effects of forest fragmentation on butterfly communities in central Spain. *Journal of Biogeography* 22:129-140.
- Berlow, E.L., C.M. D'Antonio, and S.A. Reynolds. 2002. Shrub expansion in montane meadows: The interaction of local-scale disturbance and site aridity. *Ecological Applications* 12: 1103-1118.
- Blouin, M.S. and E.F. Connor. 1985. Is there a best shape for nature preserves? *Biological Conservation* 32:277-288.
- Boggs, C.L. and D.D. Murphy. 1997. Community composition in mountain ecosystems: climatic determinants of montane butterfly distributions. *Global Ecology and Biogeography Letters* 6:39-48.
- Bollinger, E.K. and T.A. Gavin. 1989. Eastern Bobolink populations: Ecology and conservation in an agricultural landscape. In *Ecology and Conservation of Neotropical Migrant Birds*, J.M. Hagan, III and D.W. Johnston, eds. Washington: Smithsonian Institution Press. p.497-506.
- Bonham, C.D. 1989. *Measurements for Terrestrial Vegetation* New York: John Wiley & Sons.
- Brock, J.P. and K. Kaufman. 2003. *Butterflies of North America*. New York, Houghton Mifflin Com.
- Brose, U. 2003. Island biogeography of temporary wetland carabid beetle communities. *Journal of Biogeography*. 30:879-888.

- Brotons, L. and S. Herrando. 2001. Factors affecting bird communities in fragments of secondary pine forests in the north-western Mediterranean basin. *Acta Oecologica* 22:21-31.
- Brotons, L., M. Monkkonen, and J.K. Martin. 2003. Are fragments islands? Landscape context and density-area relationships in boreal forest birds. *The American Naturalist* 162: 343-357.
- Carvell, C. 2002. Habitat use and conservation of bumblebees (*Bombus spp.*) under different grassland management regimes. *Biological Conservation* 103: 33-49.
- California Spatial Information Library (CaSIL), State of California. 2003. The California spatial information library. (<http://casil.ucdavis.edu/casil/usgs.gov/doqq/11/11/03>)
- Castelli, R.M., J.C. Chambers, and R.J. Tausch. 2000. Soil-plant relations along a soil-water gradient in Great Basin riparian meadows. *Wetlands* 20: 251-266.
- Chatterjee, S. and B. Price. 1977. *Regression Analysis by Example*. J. Wiley and Sons, New York, New York, USA.
- Clausen, H.D., H.B. Holbeck, and J. Reddersen. 2001. Factors influencing abundance of butterflies and burnet moths in the uncultivated habitats of an organic farm in Denmark. *Biological Conservation* 98: 167-178.
- Collinge, S.K. 2000. Effects of grassland fragmentation on insect species loss, colonization and movement patterns. *Ecology* 81:2211-2226.
- Collinge, S.K., K.L. Prudic, and J.C. Oliver. 2003. Effects of local habitat characteristics and landscape context on grassland butterfly diversity. *Conservation Biology* 17:178-187.
- Corps of Engineers, Environmental Laboratory. 1987. Corps of Engineers wetlands delineation manual. Technical Report Y-87-1 U.S. Army Engineer Waterways Experiment Station, Vicksburg, MS. (The Wetlands Regulation Center website <http://www.wetlands.com/regstlpge02e.htm> 2/27/04).
- Connor, E.F., A.C. Courtney and J.M. Yoder. 2000. Individuals-area relationships: The relationship between animal population density and area. *Ecology* 81:734-748.

- Connor, E.F. and E.D. McCoy. 2001. Species-area relationships. In *Encyclopedia of Biodiversity*, Vol. 5. Academic Press.
- Crooks, K.R., A.V. Suarez, D.T. Bolger, and M.E. Soulé. 2001. Extinction and colonization of birds on habitat islands. *Conservation Biology* 15:159-172.
- Dauber, J., M. Hirsch, D. Simmering, R. Waldhardt, A. Otte, and V. Wolters. 2003. Landscape structure as an indicator of biodiversity: matrix effects on species richness. *Agriculture, Ecosystems and Environment* 98:321-329.
- Davis, B.N.K. and P.E. Jones. 1986. Insects on isolated colonies of common rock rose *Helianthemum chamaecistus*. *Ecological Entomology* 11:267-281.
- de Jong, J. 1995. Habitat use and species richness of bats in a patchy landscape. *Acta Theriologica* 40:237-248.
- DeGraaf, R.M., J.B. Hestbeck, and M. Yamasaki. 1998. Associations between breeding bird abundance and stand structure in the White Mountains, New Hampshire and Maine, USA. *Forest Ecology and Management* 103:217-233.
- Diamond, J.M. 1975. The island dilemma: Lessons of modern biogeographic studies for the design of natural reserves. *Biological Conservation* 7:129-146.
- Diaz, M., R. Carbonell, T. Santos, and J.L. Telleria. 1998. Breeding bird communities in pine plantations of the Spanish plateaux: biogeography, landscape and vegetation effects. *Journal of Applied Ecology* 35:562-574.
- Elzinga, C.L., D.W. Salzer, J.W. Willoughby, and J.P. Gibbs. 2001. *Monitoring Plant and Animal Populations* Malden, MA: Blackwell Science, Inc.
- Fleishman, E., G.T. Austin, and D.D. Murphy. 2001. Biogeography of Great Basin butterflies: revisiting patterns, paradigms and climate change scenarios. *Biological Journal of the Linnean Society* 74:501-515.
- Fleishman, E., G.T. Austin, and A.D. Weiss. 1998. An empirical test of Rapaport's rule: elevational gradients in montane butterfly communities. *Ecology* 79:2482-2493.
- Fleishman, E., R. MacNally, J.P. Fay, and D.D. Murphy. 2001. Modeling and predicting species occurrence using broad-scale environmental variables:

- an example with butterflies of the Great Basin. *Conservation Biology* 15:1674-1685.
- Gilbert, L.E. 1984. The biology of butterfly communities. In *The Biology of Butterflies*, R.E. Vane-Wright and P.R. Ackery, eds. London: Academic Press, Inc. p.51-54.
- Glassberg, J. 2001. *Butterflies through Binoculars: The West* New York, NY: Oxford University Press.
- Graham, C.H. and J.G. Blake. 2001. Influence of patch- and landscape-level factors on bird assemblages in a fragmented tropical landscape. *Ecological Applications* 11:1709-1721.
- Hickman, J.C. 1993. *The Jepson Manual: Higher Plants of California* Berkeley, CA: University of California Press.
- Hines, J.E. 1996. SPECRICH Software to compute species abundance from empirical species abundance distribution data. USGS-PWRC. (<http://www.mbr-pwrc.usgs.gov/software.html#specrich> 2/14/04).
- Holl, K.D. 1995. Nectar resources and their influence on butterfly communities on reclaimed coal surface mines. *Restoration Ecology* 3: 76-85.
- Jules, E.S. and P. Shahani. 2003. A broader ecological context to habitat fragmentation: Why matrix habitat is more important than we thought. *Journal of Vegetation Science* 14:459-464.
- Kadmon, R. and H.R. Pulliam. 1993. Island biogeography: Effect of geographical isolation on species composition. *Ecology* 74:977-981.
- Kitahara, M. 2004. Butterfly community composition and conservation in and around a primary woodland of Mount Fuji, central Japan. *Biodiversity and Conservation* 13: 917-942.
- Kleinbaum, D.G., L.L. Kupper, K.E. Muller, and A. Nizam. 1998. *Applied Regression Analysis and Other Multivariable Methods* Pacific Grove, CA: Duxbury Press.
- Krauss, J. A.-M. Klein, I. Steffan-Dewenter, and T. Tscharntke. 2004. Effects of habitat area, isolation, and landscape diversity on plant species richness of calcareous grasslands. *Biodiversity and Conservation* 13:1427-1439.

- Krauss, J., I. Steffan-Dewenter, and T. Tscharntke. 2003a. How does landscape context contribute to effects of habitat fragmentation on diversity and population density of butterflies? *Journal of Biogeography* 30: 889-900.
- Krauss, J., I. Steffan-Dewenter, and T. Tscharntke. 2003b. Local species immigration, extinction, and turnover of butterflies in relation to habitat area and habitat isolation. *Oecologia* 442:591-602.
- Kruess, A. and T. Tscharntke. 2002. Contrasting responses of plant and insect diversity to variation in grazing intensity. *Biological Conservation* 106: 293-302.
- Litwin, T.S. and C.R. Smith. 1989. Factors influencing the decline of Neotropical migrants in a northeastern forest fragment: Isolation, fragmentation or mosaic effects? In *Ecology and Conservation of Neotropical Migrant Birds*, J.M. Hagan, III and D.W. Johnston, eds. Washington: Smithsonian Institution Press. p. 483-496.
- Luff, M.L. and I.P. Woiwood. 1995. *Insects as indicators of land-use change: A European perspective, focusing on moths and ground beetles*. In *Insects in a Changing Environment, 17th Symposium of the Royal Entomological Society*. London: Academic Press.
- Lynch, J.F. and D.F. Whigham. 1984. Effects of forest fragmentation on breeding bird communities in Maryland, USA. *Biological Conservation* 28:287-324.
- MacArthur, R.H. and J.W. MacArthur. 1961. On bird species diversity. *Ecology* 42: 594-598.
- MacArthur, R.H. and E.O. Wilson. 1967. *The Theory of Island Biogeography* Princeton, NJ: Princeton University Press.
- Matter, S.F. and J. Roland. 2002. An experimental examination of the effects of habitat quality on the dispersal and local abundance of the butterfly *Parnassius smintheus*. *Ecological Entomology* 27:308:316.
- Mazerolle, M.J. and M. Villard. 1999. Patch characteristics and landscape context as predictors of species presence and abundance: A review. *Ecoscience* 6: 117-124.
- Morrison, M.L., B.G. Margot and R.W. Mannan. 1998. *Wildlife-habitat relationships: Concepts and applications* Madison, WI: University of Wisconsin Press.

- Natural Resources Conservation Service, USDA. 2004. The PLANTS Database, Version 3.5 (<http://plants.usda.gov>). National Plant Data Center, Baton Rouge, LA 70874-4490 USA.
- Opler, P. 1999. *A Field Guide to Western Butterflies* Boston, MA: Houghton Mifflin Co.
- Opler, P.A., H. Pavulaan, and R.E. Stanford (coordinators). 1995. Butterflies of North America. Jamestown, ND: Northern Prairie Wildlife Research Center Home Page.
<http://www.npwrc.usgs.gov/resource/distr/lepid/bflyusa/bflyusa.htm> (Version 12DEC2003).
- Panzer, R. and M.W. Schwartz. 1998. Effectiveness of a vegetation-based approach to insect conservation. *Conservation Biology* 12: 693-702.
- Proctor, M., P. Yeo and A. Lack. 1996. *The Natural History of Pollination*. Portland, OR: Timber Press.
- Ricklefs, R.E. and I.J. Lovette. 1999. The role of island area per se and habitat diversity in species-area relationships of four Lesser Antillean faunal groups. *Journal of Animal Ecology* 68:1142-1160.
- Ricketts, T.H. 2001. The matrix matters: Effective isolation in fragmented landscapes. *The American Naturalist* 158:87-99.
- Roni, P. 2002. Habitat use by fishes and Pacific giant salamanders in small western Oregon and Washington streams. 2002. *Transactions of the American Fisheries Society* 131:743-761.
- Roth, R.R. 1976. Spatial heterogeneity and bird species diversity. *Ecology* 57:773-782.
- Sawchik, J., M. Dufrene, and P. Lebrun. 2003. Estimation of habitat quality based on plant community and effects of isolation in a network of butterfly habitat patches. *Acta Oecologica* 24:25-33.
- Sawyer, J.O. and T. Keeler-Wolf. 1995. *A Manual of California Vegetation* Sacramento, CA: California Native Plant Society.
- Scoble, M.J. 1992. *The Lepidoptera: Form, Function and Diversity* Oxford: Oxford University Press.

- Scott, J.A. 1986. *The Butterflies of North America* Stanford, CA: Stanford University Press.
- Shapiro, A.M. 1996. Status of butterflies. In *Sierra Nevada Ecosystem Project: Final report to Congress, Vol. II, Assessments and scientific basis for management options*. Davis: University of California, Centers for Water and Wildland Resources p. 743-757.
- Sharp, M.A., D.R. Parks, P.R. Ehrlich. 1974. Plant resources and butterfly habitat selection. *Ecology* 55: 870-875.
- Simberloff, D. and L.G. Abele. 1982. Refuge design and island biogeographic theory: Effects of fragmentation. *The American Naturalist* 120:41-50.
- Simonson, S.E., P.A. Opler, T.J. Stohlgren, and G.W. Chong. 2001. Rapid assessment of butterfly diversity in a montane landscape. *Biodiversity and Conservation* 10:1369-1386.
- Soderstrom, B., B. Svensson, K. Vessby, and A. Glimskar. 2001. Plants, insects, and birds in semi-natural pastures in relation to local and landscape factors. *Biodiversity and Conservation* 10: 1839-1863.
- Steffan-Dewenter, I. 2001. Importance of habitat area and landscape context for species richness of bees and wasps in fragmented orchard meadows. *Conservation Biology* 17:1036-1044.
- Steffan-Dewenter, I., U. Munzenberg, C. Burger, C. Thies and T. Tschardtke. 2002. Scale-dependent effects of landscape context on three pollinator guilds. *Ecology* 83:1421-1432.
- Steffan-Dewenter, I. and T. Tschardtke. 1997. Early succession of butterfly and plant communities on set-aside fields. *Oecologia* 109:294-302.
- Steffan-Dewenter, I. and T. Tschardtke. 2000. Butterfly community structure in fragmented habitats. *Ecology Letters* 3: 449-456.
- Steffan-Dewenter, I. and T. Tschardtke. 2002. Insect communities and biotic interactions on fragmented calcareous grasslands – a mini review. *Biological Conservation* 104:275-284.
- Summerville, K.S. and T.O. Crist. 2001. Effects of experimental habitat fragmentation on patch use by butterflies and skippers (Lepidoptera). *Ecology* 85:1360-1370.

- Thomas, C.D., H.C. Mallorie. 1985. Rarity, species richness and conservation: Butterflies of the Atlas mountains in Morocco. *Biological Conservation* 33:95-117.
- Tscharntke, T., I. Steffan-Dewenter, A. Krauss, and C. Thies. 2002. Contribution of small habitat fragments to conservation of insect communities of grassland-cropland landscapes. *Ecological Applications* 12: 354-363.
- Turner, M.G. 1989. Landscape ecology: The effect of pattern on process. *Annual Review of Ecology and Systematics* 20:171-197
- Tworek, S. 2002. Different bird strategies and their responses to habitat changes in an agricultural landscape. *Ecological Research* 17:339-359.
- Vaisanen, R. 1992. Distribution and abundance of diurnal Lepidoptera on a raised bog in southern Finland. *Annales Zoologici Fennici* 29:75-92.
- Vale, T.R., A.J. Parker, K.C. Parker. 1982. Bird communities and vegetation structure in the United States. *Annals of the Association of American Geography* 72:120-130.
- Vessby, K., B. Soderstrom, A. Glimskar, and B. Svensson. 2002. Species-richness correlations of six different taxa in Swedish seminatural grasslands. *Conservation Biology* 16:430-439.
- Western Regional Climate Center. 2004. Climate data for Sagehen Creek, California, station no. 047641. <http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?ca7641>. 1/30/2004
- Weibull, A.-C. and O. Ostman. 2003. Species composition in agroecosystems: The effect of landscape, habitat and farm management. *Basic and Applied Ecology* 4:349-361.
- Willson, M.F. 1974. Avian community organization and habitat structure. *Ecology* 55: 1017-1029.
- Zschokke, S., C. Dolt, H.-P. Rusterholz, P. Oggier, B. Braschler, G.H. Thommen, E. Ludin, A. Erhardt, and B. Baur. 2000. Short-term responses of plants and invertebrates to experimental small-scale grassland fragmentation. *Oecologia* 125:559-572.

Table 1. Units of inflorescences used to estimate inflorescence density.

Listed are the counting units used in estimating number of plant inflorescences along transects, according to plant family and genera. Units are according to Hickman (1993). Those genera marked with an asterisk reportedly may be unimportant as a nectaring resource (Arthur Shapiro, personal communication), however, some butterflies exhibited nectaring behavior (perching, extended proboscis) on these plants.

Family	Genera	Counting unit
Apiaceae	<i>Conium, Osmorhiza*</i> , <i>Perideridia</i>	umbel
Asteraceae	<i>Achillea</i>	cyme
Asteraceae	<i>Aster, Arnica, Cirsium, Madia, Taraxacum</i>	head
Boraginaceae	<i>Mertensia</i>	panicle
Brassicaceae	<i>Arabis, Thelypodium</i>	raceme
Campanulaceae	<i>Downingia</i>	flower
Caryophyllaceae	<i>Cerastium, Silene, Stellaria</i>	cyme
Convolvulaceae	<i>Convolvulus</i>	flower
Fabaceae	<i>Lupinus, Trifolium, Vicia</i>	raceme
Gentianaceae	<i>Gentiana, Gentianopsis</i>	flower
Hydrophyllaceae	<i>Phacelia</i>	cyme
Hypericaceae	<i>Hypericum*</i>	cyme
Lamiaceae	<i>Agastache, Prunella, Stachys</i>	spike
Liliaceae	<i>Allium, Tritoleia,</i>	umbel
Liliaceae	<i>Camassia</i>	raceme
Liliaceae	<i>Calochortus</i>	flower
Liliaceae	<i>Veratrum*</i>	panicle
Malvaceae	<i>Sidalcea</i>	raceme
Onagraceae	<i>Camissonia</i>	flower
Orchidaceae	<i>Spiranthes*</i>	spike
Orobanchaceae	<i>Orobanche</i>	spike
Papaveraceae	<i>Argemone</i>	flower
Polemoniaceae	<i>Collomia, Polemonium</i>	head
Polygonaceae	<i>Eriogonum</i>	head
Polygonaceae	<i>Polygonum</i>	head
Portulacaceae	<i>Calyptridium</i>	head
Primulaceae	<i>Dodecatheon</i>	umbel
Ranunculaceae	<i>Caltha*</i> , <i>Ranunculus*</i>	flower
Ranunculaceae	<i>Delphinium*</i>	raceme
Rosaceae	<i>Amelanchier</i>	cluster
Rosaceae	<i>Geum, Horkelia, Ivesia, Potentilla, Purshia, Rosa</i>	flower
Scrophulariaceae	<i>Castilleja, Orthocarpus, Pedicularis, Penstemon</i>	spike
Scrophulariaceae	<i>Mimulus, Veronica</i>	flower

Table 2. Flowering plant species observed but not sampled.

Plant species observed in flower along transects but not recorded in counts of inflorescence abundance or number of flowering plant families, based on reported characteristics of preferred nectaring species (Scott 1986, Glassberg 2001, Proctor et al. 1996).

Species	Family
<i>Cryptantha</i> spp.	Boraginaceae
<i>Epilobium</i> spp.	Onagraceae
<i>Gayophytum</i> spp.	Onagraceae
<i>Gilia leptalea</i>	Polemoniaceae
<i>Linanthus</i> spp.	Polemoniaceae
<i>Lotus purshianus</i>	Fabaceae
<i>Plagiobothrys</i> spp.	Boraginaceae
<i>Polygonum douglasii</i>	Polygonaceae
<i>Polygonum polygaloides</i> ssp. <i>kelloggii</i>	Polygonaceae

Table 3. Descriptive statistics of independent variables.

Descriptive statistics of local and landscape habitat attributes for all study sites ($n=18$). Mean is presented with one standard error. Range is the minimum and maximum values observed among meadows.

Variable	Description	Mean \pm se	Range	Units
<i>Local</i>				
PLANTRICH	Number of vascular plants species	55.7 \pm 2.5	40 – 79	number of species
PLANTHT	Average plant height	20.6 \pm 1.7	9.7 – 37.3	cm
WETLAND	Cover of obligate wetland plant species	33.0 \pm 5.2	4.0 – 75.5	percent aerial cover
NATIVE-COVER	Proportion native species cover of total plant cover	0.904 \pm 0.020	0.666 – 0.993	proportion
SAGE-MEADOW	Cover of <i>Artemisia</i> spp.	4.5 \pm 1.4	0 – 19.4	percent aerial cover
FLORALRICH	Number of plant families in flower	10.8 \pm 0.6	7 – 15	number of families
FLORALDENS	Density of inflorescences	40,873.3 \pm 12,659.3	735 – 239,400	inflorescences per 3,000 m ²
ELEVATION	Elevation	2,051.2 \pm 33.5	1,852 – 2,286	m
AREA	Area	14.4 \pm 2.9	2.9 – 51.5	ha
<i>Landscape</i>				
AVGISOLATION	Average distance to 3 nearest meadow habitats	1,287.7 \pm 150.0	337 – 2,660	m
ISOLATION	Distance to nearest meadow >100 ha in size	2,419.6 \pm 448.2	303 – 7,198	m
ASPEN	Aspen vegetation*	0.74 \pm 0.41	0 – 5.2	percent of matrix area
FOREST	Jeffrey pine, Lodgepole pine, Ponderosa pine vegetation*	67.4 \pm 6.1	23.2 – 97.0	percent of matrix area
MEADOW	Montane meadow, Nebraska sedge vegetation*	1.5 \pm 0.7	0 – 12.9	percent of matrix area
SAGE-MATRIX	Big sagebrush, Bitterbrush vegetation*	20.2 \pm 5.5	0 – 66.4	percent of matrix area
CHAPPARAL	Tobacco brush, Greenleaf manzanita vegetation*	8.1 \pm 5.2	0 – 69.7	percent of matrix area
LOGGED	Recently logged area determined by visual survey	6.2 \pm 2.0	0 – 30.1	percent of matrix area
BURNED	Recently burned area determined by visual survey	9.5 \pm 6.6	0 – 100	percent of matrix area

*Vegetation series are described in Sawyer and Keeler-Wolf (1995).

Table 4. Butterfly species and number observed during sampling.

Species and number of individuals observed along transects in three visits from May 27 to August 14, 2003. Each species was categorized according to habitat specialization and larval host plant specialization prior to conducting statistical analysis. The nine meadow specialists observed are indicated by shaded rows. Nomenclature follows Brock and Kaufman (2003), Opler et al (1995), and Opler and Warren (2004).

Species	Family	Total individuals recorded	No. sites where observed	Meadow specialization	Larval host plant specialization
<i>Plebejus saepiolus</i> (Boisduval)	Lycaenidae	507	17	specialist	monophagous
<i>Pyrgus communis</i> (Grote)	Hesperiidae	218	12	generalist	oligophagous
<i>Colias eurytheme</i> Boisduval	Pieridae	161	18	generalist	oligophagous
<i>Satyrium behrii</i> (W.H. Edwards)	Lycaenidae	133	6	generalist	monophagous
<i>Plebejus podarce</i> (Felder & Felder) Opler & Warren	Lycaenidae	132	8	specialist	monophagous
<i>Junonia coenia</i> Hubner	Nymphalidae	106	14	generalist	polyphagous
<i>Speyeria mormonia</i> (Boisduval)	Nymphalidae	93	7	specialist	monophagous
<i>Coenonympha tullia</i> ssp. <i>ampelos</i> (W.H. Edwards)	Nymphalidae	91	11	specialist	oligophagous
<i>Satyrium saepium</i> (Boisduval)	Lycaenidae	41	9	generalist	monophagous
<i>Polites sonora</i> (Scudder)	Hesperiidae	40	9	specialist	oligophagous
<i>Speyeria zerene</i> (Boisduval)	Nymphalidae	29	6	generalist	monophagous
<i>Plebejus acmon</i> (Westwood & Hewitson)	Lycaenidae	28	5	generalist	polyphagous
<i>Ochlodes sylvanoides</i> (Boisduval)	Hesperiidae	26	3	generalist	oligophagous
<i>Satyrium californica</i> (W.H. Edwards)	Lycaenidae	26	4	generalist	polyphagous
<i>Phyciodes pulchella</i> (Behr) Opler & Warren	Nymphalidae	21	10	generalist	monophagous
<i>Nymphalis californica</i> (Boisduval)	Nymphalidae	16	5	generalist	monophagous
<i>Speyeria cybele</i> (Fabricius)	Nymphalidae	16	3	specialist	monophagous
<i>Speyeria callippe</i> (Boisduval)	Nymphalidae	15	3	generalist	monophagous
<i>Vanessa virginiensis</i> (Drury)	Nymphalidae	15	9	generalist	oligophagous
<i>Papilio eurymedon</i> Lucas	Papilionidae	10	6	generalist	oligophagous
<i>Plebejus icarioides</i> (Boisduval)	Lycaenidae	10	5	generalist	oligophagous
<i>Celastrina ladon</i> (Cramer)	Lycaenidae	9	5	generalist	polyphagous
<i>Limenitis lorquini</i> (Boisduval)	Nymphalidae	8	3	generalist	monophagous
<i>Phyciodes mylitta</i> (W.H. Edwards)	Nymphalidae	8	5	generalist	monophagous
<i>Hesperia juba</i> (Scudder)	Hesperiidae	7	5	generalist	oligophagous
<i>Speyeria coronis</i> (Behr)	Nymphalidae	7	3	generalist	monophagous
<i>Euchloe hyantis</i> (W.H. Edwards)	Pieridae	6	1	generalist	oligophagous
<i>Speyeria hesperis</i> (W.H. Edwards)	Nymphalidae	6	3	generalist	monophagous
<i>Vanessa annabella</i> (Field)	Nymphalidae	6	5	generalist	polyphagous
<i>Lycaeides idas</i> (Linnaeus)	Lycaenidae	5	2	generalist	monophagous
<i>Papilio rutulus</i> Lucas	Papilionidae	5	4	generalist	oligophagous
<i>Pontia protodice</i> (Boisduval & Leconte)	Pieridae	5	4	generalist	oligophagous
<i>Anthocharis stella</i> Lucas	Pieridae	4	4	generalist	oligophagous

Species	Family	Total individuals recorded	No. sites where observed	Meadow specialization	Larval host plant specialization
<i>Euphydryas chalcedona</i> (Doubleday)	Nymphalidae	4	2	generalist	oligophagous
<i>Glaucopsyche lygdamus</i> (Doubleday)	Lycaenidae	4	1	generalist	oligophagous
<i>Lycaena nivalis</i> (Boisduval)	Lycaenidae	4	2	generalist	monophagous
<i>Euchloe ausonides</i> (Lucas)	Pieridae	3	1	specialist	oligophagous
<i>Euphyes vestris</i> (Boisduval)	Hesperiidae	3	2	generalist	monophagous
<i>Hesperia comma</i> (Linnaeus)	Hesperiidae	3	1	generalist	oligophagous
<i>Pieris rapae</i> (Linnaeus)	Pieridae	3	3	generalist	oligophagous
<i>Polites sabuleti</i> (Boisduval)	Hesperiidae	3	1	specialist	oligophagous
<i>Pontia occidentalis</i> (Reakirt)	Pieridae	3	3	generalist	oligophagous
<i>Callophrys augustinus</i> (W. Kirby)	Lycaenidae	2	1	generalist	polyphagous
<i>Pontia beckerii</i> (W.H. Edwards)	Pieridae	2	1	generalist	oligophagous
<i>Pontia sisymbrii</i> (Boisduval)	Pieridae	2	1	generalist	oligophagous
<i>Strymon melinus</i> (Hubner)	Lycaenidae	2	1	generalist	polyphagous
<i>Cercyonis pegala</i> (Fabricius)	Nymphalidae	1	1	specialist	oligophagous
<i>Lycaena editha</i> (Mead)	Lycaenidae	1	1	generalist	oligophagous
<i>Lycaena gorgon</i> (Boisduval)	Lycaenidae	1	1	generalist	monophagous
<i>Polygonia gracilis</i> (Grote & Robinson)	Nymphalidae	1	1	generalist	monophagous
<i>Thorybes mexicana ssp. nevada</i> (Herrich-Schaffer)	Hesperiidae	1	1	generalist	monophagous
Unknown Fritillary*	Nymphalidae	43	12		
Unknown Skipper*	Hesperiidae	22	10		
Unknown Crescent*	Nymphalidae	21	6		
Unknown Blue*	Lycaenidae	14	5		
Unknown Hairstreak*	Lycaenidae	3	2		
Unknown Copper*	Lycaenidae	2	1		
Unknown*	Unknown	2	2		
Unknown Duskywing*	Hesperiidae	1	1		

*Individuals not identified to species (5.5% of total) were included only in the analysis of total density of individuals. Only individuals identified to species were included in totals of species richness and of density categories for habitat specialization.

Table 5. Moderately intercorrelated variables.

Pearson's correlation coefficients for five moderately intercorrelated ($r > 0.7$) independent variables. Asterisks indicate $p < 0.001$. See Table 3 for definitions of variable codes.

Variable	PLANTRICH	WETLAND	ELEVATION
FLORALRICH	.71*		
ELEVATION		.77*	
SAGE-MATRIX		.77*	.73*

Table 6. Regression models for species richness and abundance of the butterfly community.

Final regression models for species richness and abundance of the butterfly community. Abundance is the sum of butterflies observed in meadows for all transects and visits combined. The standardized regression coefficients indicate the strength and direction of the relationship for each independent variable. The *F* statistic, *p* value, and the degrees of freedom (*df*) for the final model ANOVA are shown. The order in which local and landscape attributes are listed indicate the order in which they entered the model. See Table 3 for definitions of explanatory variables.

Response variable	Constant	Local attribute(s)	Landscape attribute(s)	<i>r</i> ² Change (%)	<i>F</i>	<i>df</i>	<i>p</i>	Model <i>r</i> ² (%)
Total richness	56.89		-0.114(SAGE-MATRIX)***	25.2	13.17	4,13	<.001	80.2
		-45.127(NATIVE-COVER)***		17.5				
			-1.907(ASPEN)***	25.0				
			0.003(AVGISOLATION)**	12.6				
Log(Total estimated richness) [‡]	1.80		-0.008(SAGE-MATRIX)***	28.5	8.55	2,15	0.003	53.3
		-0.018 (PLANTHT)*		24.7				
Total abundance	138.13		-1.443(SAGE-MATRIX)*	27.6	6.10	1,16	0.025	27.6
<i>Habitat specialization</i>								
Meadow specialists richness	7.50	0.036(WETLAND)**		38.3	9.58	2,15	0.002	56.1
		-5.802(NATIVE-COVER)*		17.8				
Meadow specialists abundance	-53.01	1.073(WETLAND)**		49.0	11.83	2,15	0.001	61.2
		6.236(FLOALRICH)*		12.2				
Meadow generalists richness	9.44		0.076(CHAPARRAL)*	23.7	4.97	1,16	0.041	23.7
Meadow generalists abundance	37.62	0.004(FLOALDENS)**		39.3	10.36	1,16	0.005	39.3

[‡] Log(Total estimated richness) is the natural log of butterfly species richness estimated using SPECRICH program for estimating true richness based on rare species in a sample.

Asterisks indicate the significance level for variables entering the models: **p*<0.05, ***p*<0.01, ****p*<0.001.

Table 7. Regression models for abundance of eight dominant butterfly species.

Final regression models for the abundance of each of the eight most abundant butterfly species in all meadows. Abundance is the sum of individuals observed in a meadow for all transects and visits combined. Abundances were log-transformed to improve distributions prior to analysis. The standardized regression coefficients indicate the strength and direction of the relationship. The *F* statistic, *p* value, and the degrees of freedom (*df*) for the final model ANOVA are shown. The order in which local and landscape attributes are listed indicate the order in which they entered the model. See Table 3 for definitions of explanatory variables.

Response variable	Constant	Local attribute(s)	Landscape attribute(s)	<i>r</i> ² Change (%)	<i>F</i>	<i>df</i>	<i>p</i>	Model <i>r</i> ² (%)
<u>Meadow specialists</u>								
<i>Coenonympha tullia</i>	6.46	-2.998(NATIVE-COVER)** -0.002(ELEVATION)**	-0.008(CHAPARRAL)*	40.5 21.5 11.9	13.25	3,14	<.001	74.0
<i>Plebejus podarce</i>	-0.29	0.023(WETLAND)***		66.2	31.33	1,16	<.001	66.2
<i>Plebejus saepiolus</i>	0.05	0.056(PLANTHT)***		50.5	16.35	1,16	0.001	50.5
<i>Speyeria mormonia</i>	-4.72	0.025(ELEVATION)*		40.1	10.72	1,16	0.005	40.1
<u>Meadow generalists</u>								
<i>Colias eurytheme</i>	-2.19	0.001(ELEVATION)*		29.8	6.80	1,16	0.019	29.8
<i>Junonia coenia</i>	-0.80	0.116(FLORALRICH)**	+0.022(LOGGED)*	30.7 16.8	6.80	2,15	0.008	47.5
<i>Pyrgus communis</i> [‡]	1.25		-0.021(SAGE-MATRIX)***	59.3	21.84	1,15	<.001	59.3
<i>Satyrrium behrii</i>	2.21	7.6x10 ⁻⁶ (FLORALDENS)*** -0.001(ELEVATION)*	+0.0002(AVGISOLATION)*	66.8 17.2 5.2	38.31	3,14	<.001	89.1

[‡] The best model fit for log(*Pyrgus communis*) was obtained by removing one outlier, which resulted in the same initial explanatory variable, SAGE-MATRIX, entering the model and removed one explanatory variable, MEADOW, that had been present when the outlier was included in model-building.

Asterisks indicate the significance level for variables entering the models: **p*<0.05, ***p*<0.01, ****p*<0.001.

Table 8. Model responses to removing intercorrelated variables.

For each dependent variable where obligate wetland plant species cover, the percent of sagebrush vegetation in the matrix, or elevation entered models first, those primary variables were removed and new models were built. New primary variables entering models when the original explanatory variables removed are shown in the column at right. Positive (+) and negative (-) signs preceding the variables indicate the direction of the relationship.

Dependent variable	Primary explanatory variable in original model	New primary variable when original variable is removed
Total species richness	-SAGE-MATRIX	no model
Log (Estimated species richness)	-SAGE-MATRIX	+ELEVATION
Total abundance	-SAGE-MATRIX	+WETLAND
Meadow specialists richness	+WETLAND	no model
Meadow specialists abundance	+WETLAND	+PLANTHT
Log (Abundance of <i>Agriades podarce</i>)	+WETLAND	+ELEVATION
Log (Abundance of <i>Colias eurytheme</i>)	+ELEVATION	no model
Log (Abundance of <i>Pygus communis</i>)	-SAGE-MATRIX	+PLANTHT
Log (Abundance of <i>Speyeria mormonia</i>)	+ELEVATION	+WETLAND

Figure 1. Map of study region.

Small, black polygons represent meadow sites in their approximate location in the Tahoe National Forest.

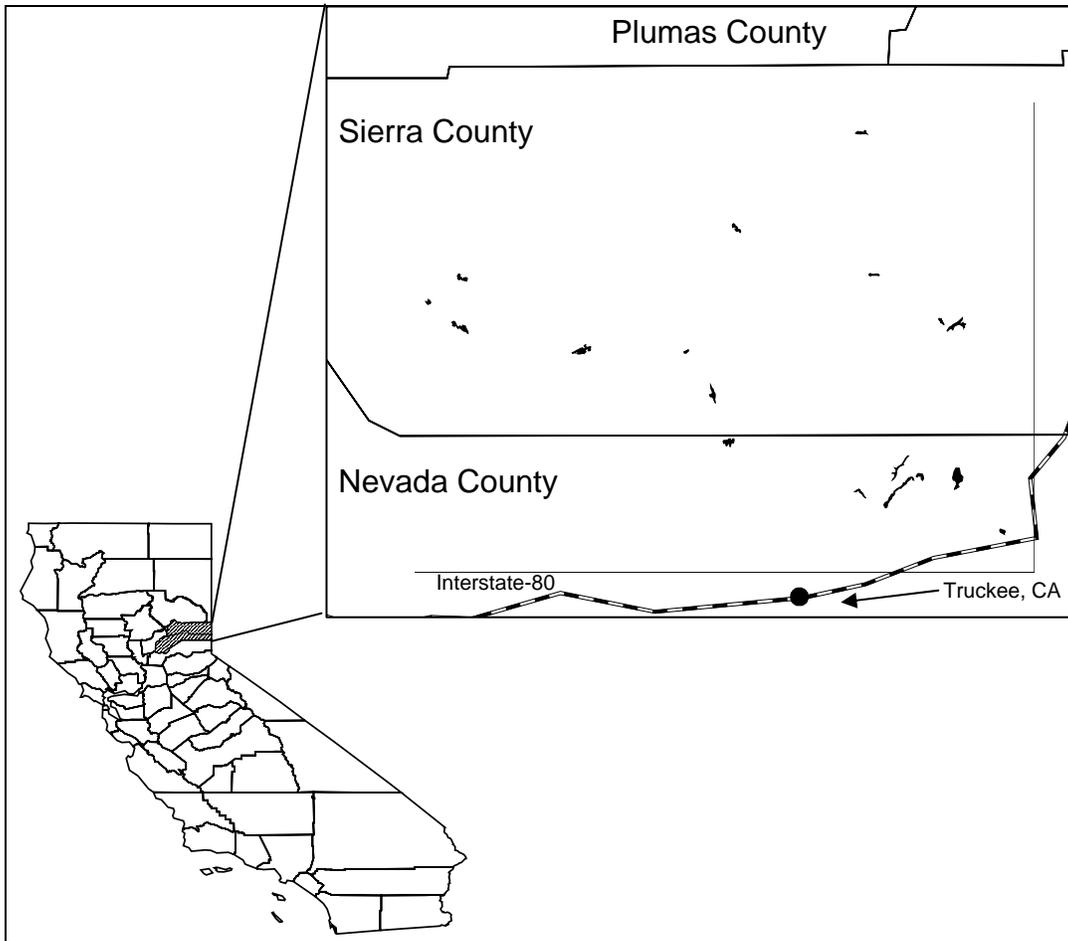


Figure 2. Aerial photograph of example study site, transect locations and matrix area. Aerial photograph showing a single meadow study site. The interior white line corresponds to the meadow extent mapped visually during field visits. Black and white bars correspond to 100 m transects used for sampling butterflies. The outer white line corresponds to the 250 m band surrounding the meadow site where matrix vegetation types were determined.



C. Estimated species richness

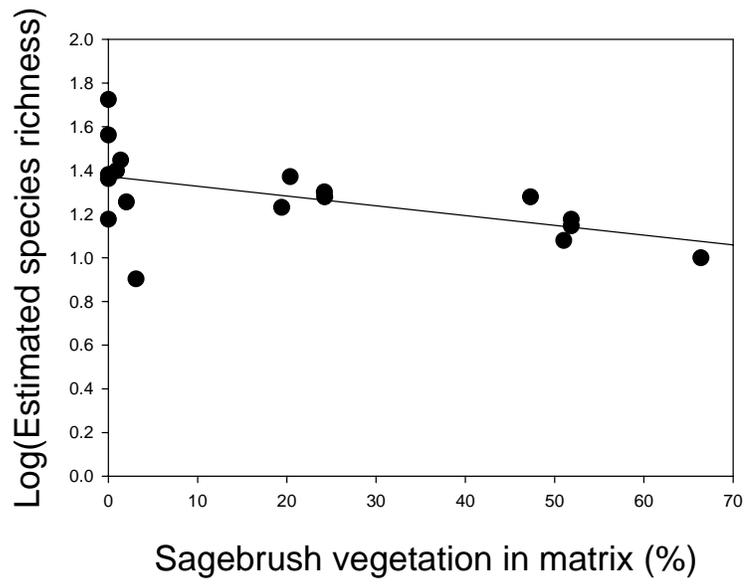
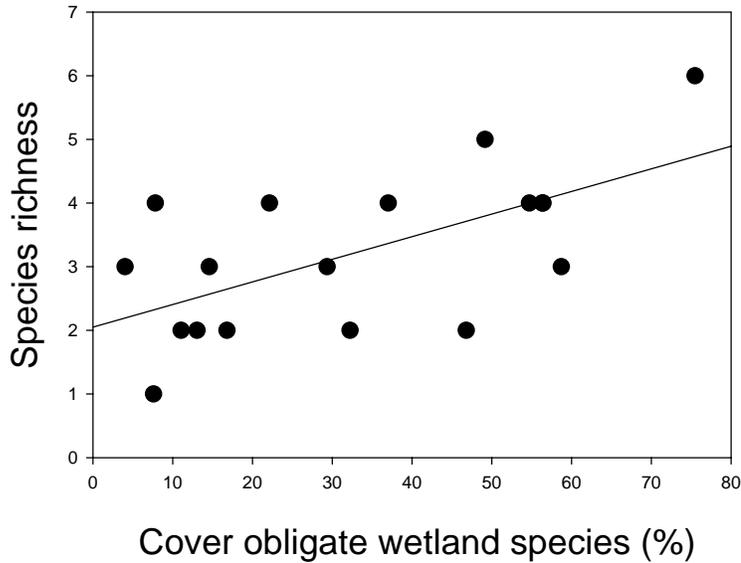


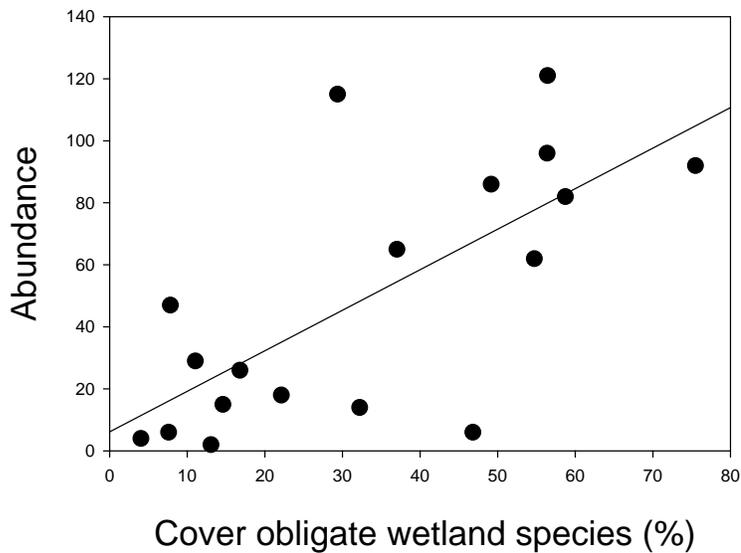
Figure 4. The relationship between species richness and abundance of meadow specialist butterflies with cover of obligate wetland plants.

The relationship between meadow specialists (a) species richness and (b) abundance and relative percent cover of obligate wetland plant species within meadows. Species richness and abundance are pooled for all transects and visits in each meadow for the nine meadow specialists observed in the region.

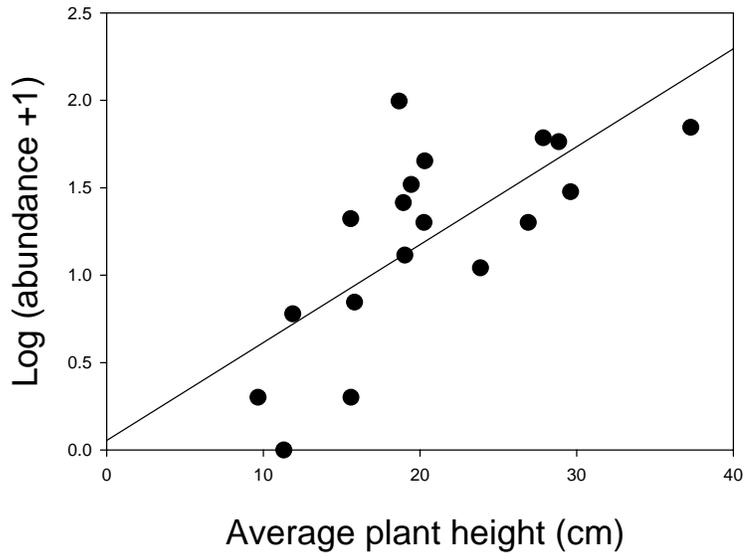
A. Meadow specialist species richness



B. Meadow specialist abundance



C. *Plebejus saepiolus*



D. *Speyeria mormonia*

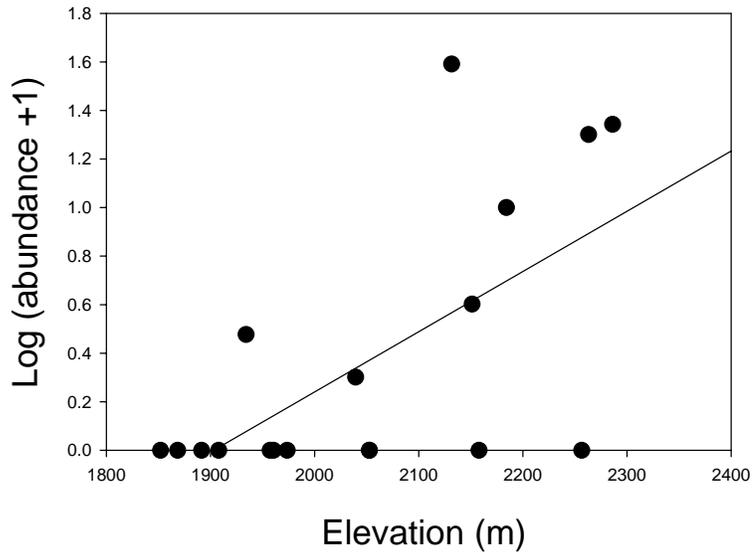
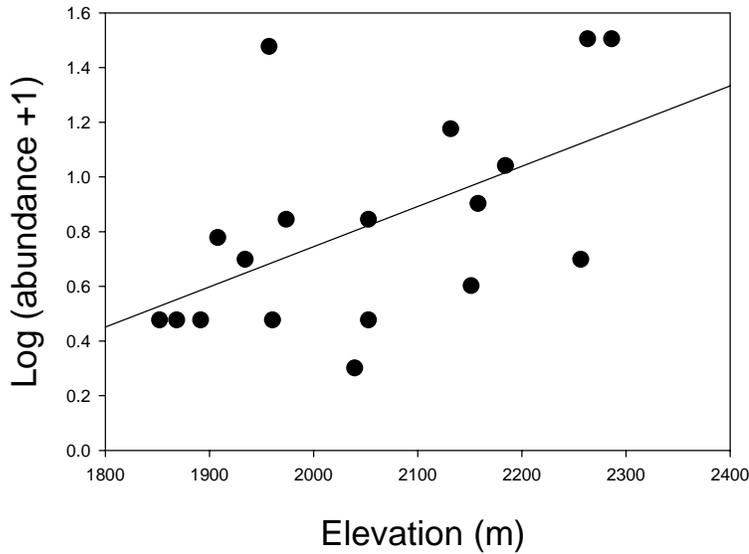


Figure 6. The relationship between the abundance of dominant meadow generalist butterfly species with primary explanatory variables.

The relationship between abundance of the four dominant meadow generalist species and the first explanatory variable entering the regression models: (a) *Colias eurytheme*, (b) *Junonia coenia*, (c) *Pyrgus communis*, and (d) *Satyrrium behrii*. Abundances were transformed using log (abundance + 1) to improve distributions.

A. *Colias eurytheme*



B. *Junonia coenia*

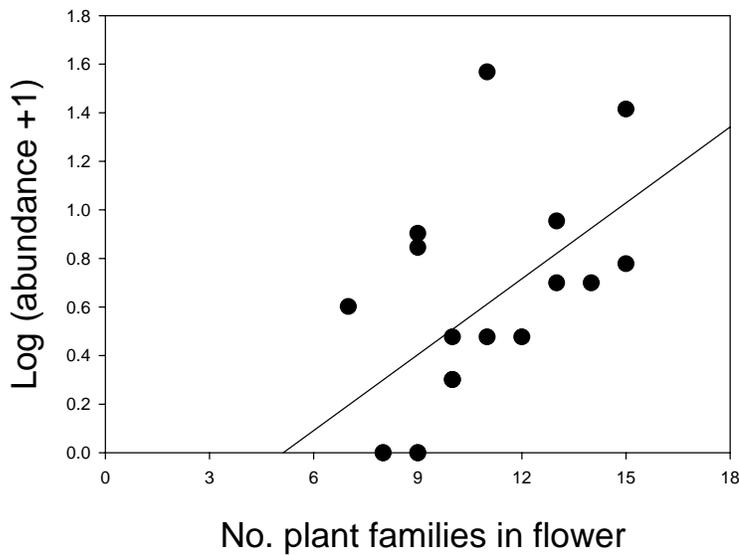
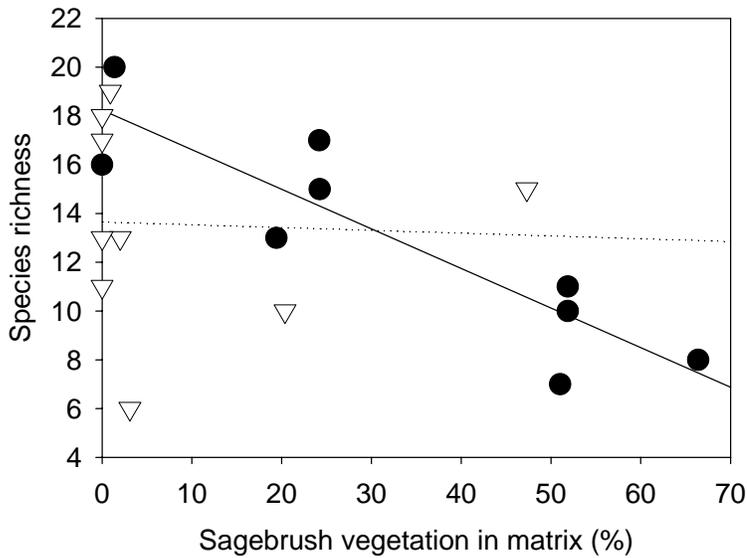


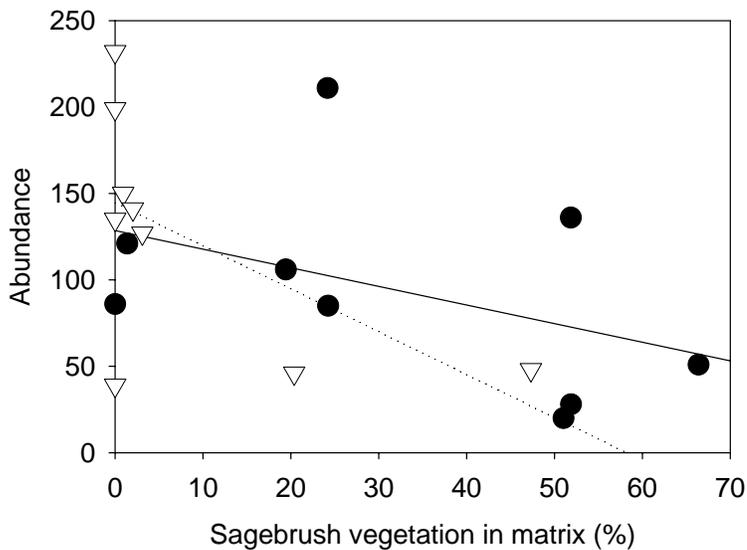
Figure 7. The relationship between the species richness and abundance of all butterflies and meadow specialist butterflies with predictor variables for high and low elevation meadows.

The relationship of (a) total butterfly species richness and percent sagebrush vegetation in the matrix, (b) total butterfly abundance and percent sagebrush vegetation in the matrix, (c) meadow specialist species richness and obligate wetland plant cover within meadows, and (d) meadow specialist abundance and cover of obligate wetland species at high and low elevations meadow sites. Circles (●) and solid slope lines (—) correspond to low elevation meadows, and triangles (▽) and dashed lines (-----) correspond to high elevation meadows.

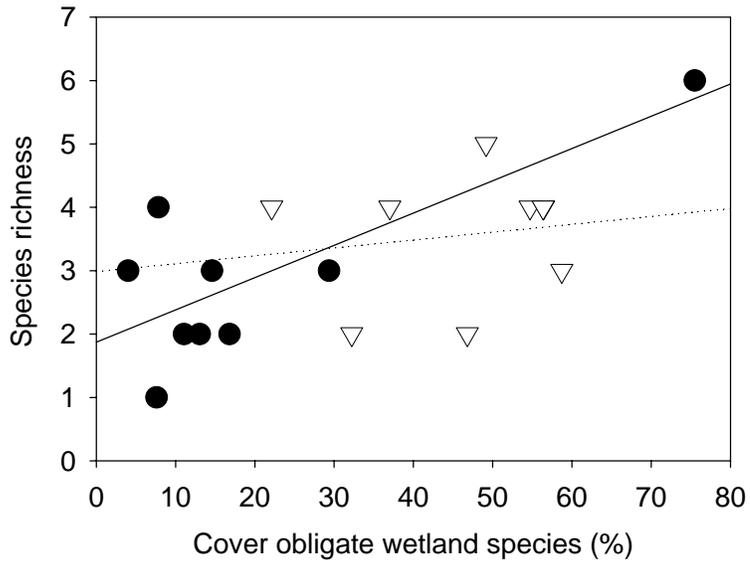
A. Total butterfly species richness



B. Total butterfly abundance



C. Meadow specialist species richness



D. Meadow specialist abundance

