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* Manuscript

LOCAL AND LANDSCAPE FACTORS INFLUENCE MEADOW BUTTERFLY COMMUNITIES IN NORTHEASTERN SIERRA NEVADA

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LOCAL AND LANDSCAPE FACTORS INFLUENCE MEADOW BUTTERFLY COMMUNITIES IN NORTHEASTERN SIERRA NEVADA

Abstract

Local and landscape environmental attributes have been strongly linked to community and population patterns. While landscape context appears to be complementary to local characteristics, the relative importance of local and landscape scales varies according to taxonomic groups. We examined the relative influence of both local and landscape factors on butterfly communities in montane meadows of northeastern California. The strongest patterns in the community were related to three variables. Total butterfly richness and abundance was negatively related to a single landscape variable, the cover of big sagebrush vegetation in the matrix surrounding meadows. The species richness and abundance of meadow specialist butterflies, and the abundance of a single meadow specialist species, *Plebejus podarce*, was positively related to a single local variable, the cover of obligate wetland plants within meadows. The abundance of *Speyeria mormonia* and *Colias eurytheme*, and the abundance of *Coenonympha tullia ssp. ampelos* and *Satyrium behrii* were respectively, positively and negatively related to elevation. Local factors explained more of the variation in butterfly variables than landscape factors, and meadow specialist butterflies were more strongly associated with local factors than generalists or the butterfly community as a whole. The moisture and topographical gradients that are related to meadow butterfly communities in the eastern Sierra Nevada suggest that protecting moist meadow habitats and surrounding matrix habitats across a range of elevations is important for conserving this faunal group.

Keywords: meadow butterflies, fragmented habitat, meadow moisture, food resources, meadow specialist and generalist butterflies, habitat matrix

Introduction

The influence of environmental factors on patterns of species richness and abundance has been explored at two scales: local and landscape. At the local scale, numerous animal population and community patterns have been strongly linked to vegetation structure and patch attributes such as size and shape (e.g., MacArthur and MacArthur 1961, MacArthur and Wilson 1967, Willson 1974, Roth 1976, Vale et al. 1982, Bollinger and Gavin 1989, DeGraaf et al. 1998, Baz and Garcia-Boyero 1995, Luff and Woiwood 1995, Diaz et al. 1998, Morrison et al. 1998, Panzer and Schwartz 1998, Ricklefs and Lovette 1999, Connor et al. 2000, Connor and McCoy 2001, Graham and Blake 2001, Carvell 2002 Kruess and Tscharntke 2002, Steffan-Dewenter and Tscharntke 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, Lynch and Whigham 1984, Kadmon and Pulliam 1993, Diaz et al. 1998, Mazerolle and Villard 1999, Brotons and Herrando 2001, Crooks et al. 2001, Steffan-Dewenter and Tsharntke 2002, Steffan-Dewenter et al. 2002, Tworek 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 was based in part on the success of studies conducted at local scales (MacArthur and MacArthur 1961, Willson 1974, Roth 1976, Vale et al. 1982, DeGraaf et al. 1998, Carvell 2002, Kruess and Tscharntke 2002). However, it was also reinforced by a lack of understanding of potential mechanistic processes operating at regional scales, and by the logistical difficulty of conducting experimental or observational studies at larger scales.

More recently, it has been recognized that the composition of the landscape in which habitat patches are embedded may influence population and community patterns, even if landscape effects are usually secondary or complimentary to local effects (Mazerolle and Villard 1999, Graham and Blake 2001, Brose 2003, Dauber et al. 2003). The landscape matrix has been proposed to represent resources for species that forage into the matrix, risks because predators may be more abundant there, or potential barriers to dispersal (Ricketts 2001, 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 other insects (Collinge 2000, Baum et al. 2004). However, the results of observational studies have not uniformly shown effects of the landscape matrix on species abundance or richness (Lynch and Whigham 1984, Mazerolle and Villard 1999, Diaz et al. 1998, Crooks et al. 2001, Brotons and Herrando 2001, Graham and Blake 2001, Soderstrom et al. 2001, Steffan-Dewenter 2001, Tscharntke et al. 2002, Roni 2002, Tworek 2002, Brose 2003, Dauber et al. 2003, Krauss et al. 2003a, Weibull and Ostman 2003, Krauss et al. 2004). The adequacy of a study of the influence of landscape composition will depend on determining the appropriate scale of the investigation 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).

We examined the effects of local and landscape factors on community and population patterns in the butterfly community of montane meadows in northeastern California. 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 local and landscape effects simultaneously. Butterflies (Lepidoptera: Papilionoidea and Hesperioidea) are an ideal system for examining the contributions of local and landscape processes because they are easy to identify and much is known about the ecology of each species. Using a linear modeling approach, we examined the contribution of environmental variables to observed patterns in the species richness and abundance of butterflies. We asked several related questions: Are local attributes of habitat patches more important in structuring meadow butterfly communities than the composition and configuration of the landscape? Are patterns more evident for habitat specialists? Can these patterns provide information for managing and conserving meadow communities in this region?

Methods

Study sites

We studied the butterfly communities of montane meadows on the eastern slope of the California Sierra Nevada in the Tahoe National Forest (TNF) (Figure 1). 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. Average summer temperatures in this region reach 21.7-28.9° C at middle elevations, and winter temperatures average -10 to 7.2° C (Western Regional Climate Center 2004). Most precipitation falls between October and April as snow with an average depth of 64 cm. Snowmelt occurs from May through July depending on elevation. Summer thundershowers supply a small portion of annual precipitation. In 2003, late-season snowfall delayed snowmelt until mid- to late-May at lower elevations. Precipitation in 2003 was above average in July and August, while temperatures were 3^{o} C 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 (A. Shapiro, pers. comm.). The 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 (Sawyer and Keeler-Wolf 1995). Using a digital map that identified all meadow vegetation units in the region, we randomly selected 18 meadow sites between 1,676 to 2,134 meters a.s.l., and between 2.9 to 51.5 hectares in size to avoid extremes in elevation, and to represent meadow areas falling around the mean (32.2 ha) and median (6.2 ha) area. We excluded meadow sites that were privately owned or occurred more than 1 km from a navigable road or trail.

Butterflies

To estimate species richness and abundance of butterflies, we established five 100 m transects in each meadow (Figure 2). We located one endpoint for each transect using random points generated by GIS and extended these transects along randomly generated compass bearings. We discarded endpoints or bearings that resulted in transects located outside meadows. As most adult butterflies are short-lived and peak flight periods of univoltine species may occur within a span of 4-6 weeks, we 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 m in front of the observer and 3 m to each side. Wind speed, temperature and cloud cover were monitored so that observations were made during conditions that are conducive to butterfly flight.

Butterflies were identified to species using nomenclature in several sources (Opler et al. 1995, Brock and Kaufman 2003, Opler and Warren 2004). When visual identification was not possible, we stopped time and captured individuals for identification. Butterflies that could not be identified in the field were temporarily immobilized, photographed, and released. Immobilization was achieved by cooling butterflies in an ice chest several minutes, and then exposing them to ethyl acetate vapors for 30-60 seconds. Voucher specimens and photographs were verified by regional butterfly specialists and deposited at San Francisco State University. We classified each species as meadow specialists or generalists using information in published sources and provided by experts (A. Shapiro, P. Opler, pers. comm.; Scott 1986, Opler et al. 1995, Opler 1999, Glassberg 2001, Brock and Kaufman 2003).

For each meadow, species richness and abundance were calculated for all butterflies, meadow specialists, and meadow generalists using all transects and visits combined. Since some species not observed during the three visits were potentially present in the meadows, we used the program SPECRICH (Hines 1996) to estimate potential species richness for all butterflies. We also selected the eight most abundant butterfly species to examine the relationship of local and landscape environmental variables with the abundance of individual species. For each of the eight species, abundance was pooled across all transects and visits for each meadow.

Local influences

We estimated nine within-meadow attributes or local variables, including meadow area, elevation, and seven variables focusing on the structure of the vascular plant community within each meadow (Table 1). Because larvae of many butterfly species feed reliably on a restricted group of host plant species (Scott 1986, Scoble 1992), and most adult butterflies feed almost exclusively on floral nectar, butterfly communities should be strongly related to measures of plant resources (Gilbert 1984). Therefore, we measured several variables in an attempt to estimate food resources for larva and adults.

To estimate resources available for larval butterflies, we calculated plant richness (PLANTRICH) and cover in each meadow. We randomly located three 0.75 m^2 plots along each butterfly transect for a total of 15 plots per meadow. For each plot, we estimated the abundance of each plant species and assigned a cover class according to the Braun-Blanquet method (Elzinga et al. 2001). To account for seasonal variation in cover, we sampled five plots in each meadow (one along each transect) on each of three visits. We identified plants to species following Hickman (1993), and deposited voucher specimens at San Francisco State University.

To calculate percent cover of vegetation variables within meadows, we used the mid-point of cover class ranges for each plant species in each plot and then calculated the average percent cover for each meadow. For cover of obligate wetland species (WETLAND), we summed cover values in each plot for all species ascribed obligate wetland indicator species status in California by the U.S. Fish and Wildlife Service (NRCS 2004), and then averaged values for plots within each meadow. Cover of obligate wetland plants is a reasonable proxy for biomass and productivity, as positive cover-biomass relationships are common (Bonham 1989). We also consider cover of obligate wetland plants to be a proxy for meadow moisture, since the relationship between water table and abundance of wetland plants has been firmly established (Allen-Diaz 1991) and the prevalence of hydrophilic vegetation is used in wetland delineation (COE 1987). For cover of *Artemisia* species (SAGE-MEADOW), we summed cover values for the two species encountered, *Artemisia cana* (A. Gray) G. Ward and *Artemisia tridentata* Nutt., for each plot before averaging among plots within meadows. For the proportion of native species cover (NATIVE-COVER), we divided the average percent cover of native species in a meadow by the average percent cover of all species.

We estimated nectar resources for butterflies in each meadow based on observations made on two visits between June 15 and August 13, 2003. We estimated the total number of plant families in flower as the average of the values from the two visits (FLORALRICH) and the density of inflorescences by summing the number of inflorescences for both visits (FLORALDENS). Since the number of plant inflorescences is highly correlated with nectar availability (Holl 1995), we recorded the families of plants in flower within a 6 m band along butterfly transects, and estimated the number of inflorescences using a logarithmic scale (1-10, 10-100, 100-1,000, etc.) based on counts of the floral units of each genus or family (Hickman 1993). Based on the characteristics of plants that are preferred nectar species (Scott 1986, Proctor et al. 1996, Glassberg 2001), we did not record minute species in flower such as *Polygonum polygaloides ssp. kelloggii* (E. Greene) J. Hickman.

To estimate vegetation height (PLANTHT), we used a meter stick to measure height of live vegetation at three locations within each vegetation plot. An average height was calculated for each meadow. We estimated meadow elevation (ELEVATION) to the nearest 40 m using digitized topographic maps from the California Spatial Information Library website (CaSIL 2003). We estimated meadow area (AREA) by mapping meadow boundaries in the field onto aerial photographs from the year 2000 (CaSIL 2003), digitizing the mapped boundaries, and calculating area using an Xtools program extension in ArcView (ESRI 2002, Delaune 2001).

Landscape influences

We measured nine landscape scale variables including two measures of isolation and seven characteristics of the habitat matrix surrounding meadows (Table 1). We estimated the average isolation (AVGISOLATION) of each meadow from other meadows by measuring the average distance of each meadow to the three nearest meadows using GIS. We estimated isolation of each meadow from large meadows (ISOLATION) by measuring the distance of each site to the nearest meadow 100 ha in size or larger.

To characterize the composition of the vegetation matrix, first we field checked aerial photographs for vegetation types and management activities and mapped the extent of each. Vegetation types were assigned according to Sawyer and Keeler-Wolf (1995). Areas where logging and burning had occurred were identified by disturbance and debris associated with logging (such as slash and barren staging areas) or burning (burned snags, early post-fire vegetation, and burned soil and vegetation). Because Krauss et al. (2003a) reported that the influence of landscape diversity on butterfly richness in temperate grasslands was only important within 250 m, we examined the habitat matrix within 250 m of each meadow. We calculated area of each vegetation type or management activity within the matrix area using digital maps (Figure 2). We only included matrix variables in our models that accounted for at least 1% of the total area of the surrounding matrix for at least three meadows.

Statistical analysis

To examine the relationships between richness and abundance, and meadow attributes, we 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 $\alpha = 0.05$. We also built and evaluated regression models to examine the relationship between the abundance of individual butterfly species and meadow attributes. We normalized response variables using the log, log + 1, or square root transformation. Since correlations between independent variables were $r < 0.9$, no problems with multicollinearity were encountered (Kleinbaum et al. 1998). To evaluate each model, we examined residuals patterns for heteroscedasticity, checked for outliers, and checked tolerance levels of included variables. In instances with potential outliers, we compared models with and without outliers removed and concluded that the original model was robust if the model structure was unchanged by removal of the potential outliers. We report only models for which the assumptions of normality, linearity and homoscedasticity are met.

Results

Among the 18 meadows, we observed 1,961 individuals of 51 species of butterflies and were able to identify 94.5% of the specimens to the species level (Table 2). 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 meadows. The total number of butterfly species observed in meadow, pooled among visits, ranged from 6 to 20, with an average richness among all sites of 13.3 (± 1.0). The total abundance of butterflies in a meadow, pooled among visits, ranged from 20 to 232 with an average of 108.9 (± 15.1) individuals. The summed abundance of individual species among all meadows ranged from one to 507 individuals. *Plebejus saepiolus* (Boisduval), a meadow specialist, accounted for nearly 25% 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 *Satyrium behrii* [W.H. Edwards]).

Values of local and landscape habitat attributes also varied widely among meadows (Table 1). We identified 228 species and morpho-species of vascular plants, and the average plant species richness in a meadow was 55.7 (± 2.5). Forty-five plant species listed as obligate wetland species by the USFWS constituted the variable WETLAND and on average comprised 33% of the cover in a meadow. The cover of native species ranged from 67% to 100%. Nectar resources were represented by 25 plant families. An average of 10.8 (± 0.6) plant families were in flower displaying 40,873.3 (± 12,659.3) inflorescences/3,000 m^2 per meadow. Five vegetation types composed at least 1% of the total matrix area for at least three meadows (aspen, conifer forest, meadow, sagebrush, and chaparral; see Table 1 for descriptions). Recently logged areas in the matrix averaged 6.2% (± 2.0), and ranged from 0-33.1% of the matrix. We observed burned vegetation in the matrix at only two meadows, so we deleted this variable from the analysis. Plant richness was correlated with the number of flowering plant families, and three variables, WETLAND, ELEVATION, and SAGE-MATRIX, were moderately intercorrelated (r>0.7).

We fitted models for all 15 of the community and individual species variables (Tables 3 and 4). 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 sagebrush vegetation in the matrix (SAGE-MATRIX), explained the largest amount of variation for the three community-wide variables: total species richness, the log of estimated species richness, and total abundance.

For individual species, local attributes were the only variables that explained variation in abundance for three meadow specialists (*P. podarce*, *P. saepiolus*, and *S. mormonia*) and one generalist (*C. eurytheme*; Table 4). Only landscape attributes explained 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 variation.

Local influences

Five of the nine local habitat attributes entered into models for butterfly community variables (Table 3). Cover of obligate wetland plant species within meadows (WETLAND) 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 (NATIVE-COVER) 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 (PLANTHT) greatly improved the fit of the model for estimated total species richness (R^2 change = 24.7%). The number of inflorescences (FLORALDENS) was the only factor accounting for variation in the abundance of meadow generalist butterflies (R^2=39.3%). Finally, the number of flowering plant families (FLORALRICH) slightly improved the fit of the model 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: PLANTRICH, SAGE-MEADOW, ELEVATION and AREA.

Of the eight most abundant butterfly species we examined, local variables accounted for most of the explained variation in the abundance for three of the four meadow specialist species (Table 4, Figure 5). WETLAND was the only variable entering the model for the abundance of *P. podarce* and it explained 66.2% of the variation. 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 (NATIVE-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 4, Figure 6). The abundance of inflorescences (FLORALDEN) explained 66.8% of the variation in abundance for *S. behrii*, and the number of flowering plant families (FLORALRICH) 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 in abundance of *S. behrii* (R^2 change = 17.2%).

Landscape influences

Four landscape variables explained variation in butterfly community structure (Table 3). A single landscape variable, the percent of sagebrush vegetation in the matrix (SAGE-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 abundance (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%). Four landscape variables did not enter into any models for butterfly community variables: ISOLATION, FOREST, MEADOW, and LOGGED.

For the individual species we examined, only one landscape variable entered into any models of abundance for meadow specialist species (Table 4). In contrast, three landscape variables entered models for meadow generalist butterfly species. A large proportion of the variation in abundance of the meadow generalist butterfly, *P. communis*, was explained by one landscape variable, the proportion of sagebrush vegetation in the matrix (SAGE-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 (LOGGED) improved the fit of the model for *J. coenia* (R^2 change = 16.8%), and the average isolation of meadows (AVGISOLATION) improved the fit of the model for *S. behrii* (R^2 change = 5.2%).

Discussion

Our results suggest that both the local and regional environment is important in structuring California's montane meadow butterfly communities. Landscape variables were strongly associated with 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. For the individual species we examined, the abundance of meadow specialists was almost exclusively related to local variables, and the abundance of meadow generalists was related to both local and landscape variables. Furthermore, 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 we found that landscape variables were most important in explaining variation in the total butterfly community, other studies of butterflies have shown that landscape variables account for a small part of the variability in species richness or abundance (Baz and Garcia-Boyero 1995, Steffan-Dewenter and Tscharntke 2000, Collinge et al. 2003, Krauss et al. 2003a, Krauss et al. 2003b). Communities of many other taxa (e.g., plants, bats, bees and birds) also are more strongly linked to local factors even though landscape context accounts for some 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). However, one study of species richness of grassland ants found that only landscape factors were important (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 Tscharntke 2000, Collinge et al. 2003, Krauss et al. 2003a, Krauss et al. 2003b). However, those studies that have found as we did that local factors contribute more to explaining variation in the abundance or richness of common and uncommon (Collinge et al. 2003), generalist or specialist (Krauss et al. 2003a, Krauss et al. 2003b), and migratory and resident (Steffan-Dewenter and Tscharntke 2000) butterfly species than do landscape factors.

In contrast, avian studies that have examined the relative influence of local and landscape factors on subsets of the community show more varied results (Lynch and Whigham 1984, Diaz et al. 1998, Brotons and Herrando 2001, Graham and Blake 2001, Tworek 2002, Brotons et al. 2003). For example, local factors were more important in explaining species richness and abundance of forest specialists, but both local and landscape factors were equally important for forest generalists (Graham and Blake 2001). Conversely, Lynch and Whigham (1984) and Brotons and Herrando (2001) found that both local habitat and landscape attributes influenced the richness of avian forest specialists, but only local factors influenced forest generalists.

Local influences

The abundance and species richness of meadow specialist butterflies were strongly and positively related to the abundance of wetland plant species. We assume that wetland plant cover reflects both meadow moisture and plant productivity. Not surprisingly, wetland plant cover was positively correlated with the amount of water on the soil surface

($r = 0.55$, $p = 0.02$), total plant cover ($r = 0.86$, $p < 0.001$) and vegetation height ($r = 0.56$, $p = 0.02$). Wetter meadows appear to provide more larval food resources for meadow specialist butterflies, since wetland-plant cover was positively correlated with the abundance of the larval food plants of meadow specialist butterflies ($r = 0.51$, $p = 0.03$). For example, cover of wetland plants was strongly correlated with the abundance of *P. podarce* which feeds on a 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 Tscharntke 1997, Clausen et al. 2001, Matter and Roland 2002). The larval host plants of the other meadow specialist species are also more abundant in wetter meadows. 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 desert mountain ranges where wet meadows, springs, and riparian canyons provide important resources for animals, the distance of sites to water predicted the presence of one-fifth of butterfly species studied (Fleishman et al. 2001). Greater primary productivity has also been related to higher species richness of neotropical migratory birds and of butterflies (Bailey et al. 2003). In agricultural habitats, the presence of streams was positively related to the richness and abundance of butterflies (Clausen et al. 2001). Positive correlations between habitat moisture and species richness or abundance has also been reported for other taxa (Tworek 2002, Luff and Woiwood 1991).

The density of inflorescences was strongly and positively related to the abundance of all meadow generalist butterflies combined. One 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 was also correlated with the abundance of a meadow generalist, *J. coenia*, and the abundance of meadow specialists. *J. coenia* is uncommon in most years in the eastern Sierra Nevada (J. Hafernik, A. Shapiro, pers. comm.), so they may be selecting 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 Tscharntke 1997, Clausen et al. 2001, Matter and Roland 2002). In a study of *Parnassius smintheus* Doubleday in montane meadows, Matter and Roland (2002) showed that the abundance of males was lower in meadows with experimentally reduced nectar resources due to lower immigration. We found that meadow specialists appear to be strongly related to the availability of larval food resources within meadows, while 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 for the study meadows. Vessby et al. (2002) and Soderstrom et al. (2001) suggest that a positive correlation between butterfly species richness or abundance and vegetation height to represent responses to increased plant productivity or lower grazing intensity. Similarly, Kruess and Tscharntke (2002) found that for insect herbivores, vegetation height was the main predictor of species richness and abundance in grasslands. We found that vegetation height was negatively associated with the log of estimated butterfly species richness. However, this association is difficult to explain biologically and may be an artifact of the richness estimator (SPECRICH), which is 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 more species represented by single specimens. Therefore, SPECRICH may inflate estimates of species richness in drier meadows with shorter vegetation and lower butterfly abundance.

The proportion of native plant cover in meadows (NATIVE-COVER) was inversely correlated with the abundance of the meadow specialist, *C. tullia*, and with total butterfly richness and meadow specialist richness. This result appears counter-intuitive, given that two meadow sites with the most visible disturbance and highest cover of the invasive grass, *Bromus tectorum* L., also had the lowest proportion of native plant cover. However, several meadows with a high proportion of native cover are also the driest meadows 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 origin of the flora.

Elevation did not explain variation in 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*, 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 at lower elevations (A. Shapiro, pers. comm.). 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, ibid. 2001a, ibid. 2001b). When examining butterfly richness or abundance over a range of elevations, some researchers found a peak at middle elevations (Fleishman et al. 1998, 2001a), and reduced fecundity at higher elevations (Boggs and Murphy 1997). These varied responses to elevation underscore the importance of the life history traits of individual species that influence species distributions differentially.

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 and density-area relationships for butterflies (e.g., Boggs and Murphy 1997, Panzer and Schwartz 1998, Steffan-Dewenter and Tscharntke 2000, Krauss et al. 2003a, except Vessby et al. 2002). In this case, the lack of a species-area relationship is likely due to sampling design. We used a fixed level of sampling effort in each meadow rather than scaling effort to meadow area. We found the lack of a relationship between butterfly variables and plant species richness surprising given the strong dependence of the butterfly community on a broad range of larval food plant species. However, 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 Tscharntke 2000, Panzer and Schwartz 1998, Thomas and Mallorie 1985). For other taxa, the relationship between plant richness and the animal community is also inconsistent. Dauber et al. (2003) found that plant species richness was not correlated with the richness of either ants or birds, but Kruess and Tscharntke (2002) found that plant species richness accounted for variation in grassland insect communities. We found that the number of plant species was much less important in determining butterfly richness or abundance than variables more directly representing plant resources 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).

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. The sagebrush vegetation type is a less productive, more xeric vegetation than other types we surveyed, and the dominant species (*A. tridentata* and *A. cana*) are not known to be 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 was negatively associated with 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 were related to the richness or abundance of butterflies, but these relationships are weak compared to 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 or the biology of the organisms (Turner 1989, Mazerolle and Villard 1999, Krauss et al. 2003a, Dauber et al. 2003). We examined the landscape matrix at a scale that is comparable to that of other butterfly and invertebrate studies which reported an influence of landscape composition (Steffan-Dewenter et al. 2002, Krauss et al. 2003a, Dauber et al. 2003).

We found that isolation of meadow sites accounted for little or no variation in the species richness or abundance of butterflies. Our 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 Tscharntke 2000, Krauss et al. 2003a, Krauss et al. 2003b), but contrast with studies by Boggs and Murphy (1997) and Sawchik et al. (2003) that reported that the species richness or abundance of butterflies is negatively associated with isolation.

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. At higher elevations, the cover of wetland plants within meadows is greater and meadows are more lush, while the proportion of sagebrush vegetation in the landscape is lower. Shifts in montane plant communities occur between 1500 to 2700 m; 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 a gradient in elevation rather than in moisture.

To tease apart elevational and moisture gradients, we examined plots of butterfly abundance and species richness with the moisture variables, after dividing the meadows into the nine highest and nine lowest elevation meadows (Figure 7). The associations 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 wetland plants are still apparent within each restricted elevation range. In addition, even after we removed the primary significant predictor variables from nine models for richness and abundance of community-wide, meadow specialist, and individual butterfly variables, elevation only entered two models (Chatterjee and Price 1977, Table 5). We interpret these results to suggest that the butterfly community is correlated with elevation via the effects of elevation on patch-scale and landscape-scale moisture gradients. In addition, 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

We 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 abundance 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*). Besides strong associations with moisture and topography, we found a number of other less pronounced relationships between the butterfly community and environmental variables.

Identifying the local and landscape factors that influence communities has been suggested as an effective basis to plan management activities to enhance local habitats, or to develop land conservation strategies that incorporate landscape context and configuration (Mazerolle and Villard 1999). Our 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 as reported for other montane butterfly communities

(Fleishman et al. 1998, ibid. 2001a, ibid. 2001b, Simonson et al. 2001). In particular, we show that the total butterfly community is influenced primarily by landscape context, while meadow generalists are related to both landscape context and local adult food resources. Meadow specialist butterflies are most strongly associated with local meadow characteristics that represent larval and adult food resources.

Since 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 over a wide elevational range. Further, changes to moisture regimes that reduce the abundance of 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 would 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.

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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., Horner-Devine, M.C., Luck, G., Moore ,L.A., Carney, K.M., Anderson, S., Betrus, C., and Fleishman, E. 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., Haynes, K.J., Dillemuth, F.P., and Cronin, J.T. The matrix enhances the effectiveness of corridors and stepping stones. 2004. Ecology 85:2671-2676.

Baz, A. and Garcia-Boyero, A. 1995. The effects of forest fragmentation on butterfly communities in central Spain. Journal of Biogeography 22:129-140.

Berlow, E.L., D'Antonio, C.M., and Reynolds, S.A. 2002. Shrub expansion in montane meadows: The interaction of local-scale disturbance and site aridity. Ecological Applications 12: 1103-1118.

Boggs, C.L. and Murphy, D.D. 1997. Community composition in mountain ecosystems: climatic determinants of montane butterfly distributions. Global Ecology and Biogeography Letters 6:39-48.

Bollinger, E.K. and Gavin, T.A. 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 Kaufman, K. 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 Herrando. S. 2001. Factors affecting bird communities in fragments of secondary pine forests in the north-western Mediterranean basin. Acta Oecologica 22:21-31.

Brotons, L., Monkkonen, M., and Martin, J.K. 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., Chambers, J.C., and Tausch, R.J. 2000. Soil-plant relations along a soil-water gradient in Great Basin riparian meadows. Wetlands 20: 251-266.

Chatterjee, S. and Price, B. 1977. Regression Analysis by Example. J. Wiley and Sons, New York, New York, USA.

Clausen, H.D., Holbeck, H.B., and Reddersen, J. 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., Prudic, K.L., and Oliver, J.C. 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/regs/tlpge02e.htm 2/27/04).

Connor, E.F., Courtney, A.C., and Yoder, J.M. 2000. Individuals-area relationships: The relationship between animal population density and area. Ecology 81:734-748.

Connor, E.F. and McCoy, E.D. 2001. Species-area relationships. In Levin, SA (ed.) Encyclopedia of Biodiversity, Vol. 5. Academic Press.

Crooks, K.R., Suarez, A.V., Bolger, D.T. , and Soulé, M.E. 2001. Extinction and colonization of birds on habitat islands. Conservation Biology 15:159-172.

Dauber, J., Hirsch, M., Simmering, D., Waldhardt, R., Otte, A., and Wolters, V. 2003. Landscape structure as an indicator of biodiversity: matrix effects on species richness. Agriculture, Ecosystems and Environment 98:321-329.

de Jong, J. 1995. Habitat use and species richness of bats in a patchy landscape. Acta Theriologica 40:237-248.

DeGraaf, R.M., Hestbeck, J.B., and Yamasaki, M. 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.

Delaune, M. 2001. Xtools v6/1/2001. Oregon Department of Forestry. http://www.odf.state.or.us/divisions/management/State_forests/XTools.asp.

Diaz, M., Carbonell, R., Santos, T., and Telleria, J.L. 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., Salzer, D.W., Willoughby, J.W., and Gibbs, J.P. 2001. Monitoring Plant and Animal Populations Malden, MA: Blackwell Science, Inc.

Environmental Systems Research Institute (ESRI). 2002. ArcView v3.3. Redlands, CA.

Fleishman, E., Austin, G.T., and Weiss, A.D. 1998. An empirical test of Rapaport's rule: elevational gradients in montane butterfly communities. Ecology 79:2482-2493.

Fleishman, E., MacNally, R., Fay, J.P., and Murphy, D.D. 2001a. Modeling and predicting species occurrence using broad-scale environmental variables: an example with butterflies of the Great Basin. Conservation Biology 15:1674-1685.

Fleishman, E., Austin, G.T., and Murphy, D.D. 2001b. Biogeography of Great Basin butterflies: revisiting patterns, paradigms and climate change scenarios. Biological Journal of the Linnean Society 74:501-515.

Gilbert, L.E. 1984. The biology of butterfly communities, in: R.E. Vane-Wright and P.R. Ackery (eds.), The Biology of Butterflies. 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 Blake, J.G. 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 Shahani, P. 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 Pulliam, H.R. 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., Kupper, L.L., Muller, K.E., and Nizam, A. 1998. Applied Regression Analysis and Other Multivariable Methods Pacific Grove, CA: Duxbury Press.

Krauss, J. A., Klein, M., Steffan-Dewenter, I., and Tscharntke, T. 2004. Effects of habitat area, isolation, and landscape diversity on plant species richness of calcareous grasslands. Biodiversity and Conservation 13:1427-1439.

Krauss, J., Steffan-Dewenter, I., and Tscharntke, T. 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., Steffan-Dewenter, I., and Tscharntke, T. 2003b. Local species immigration, extinction, and turnover of butterflies in relation to habitat area and habitat isolation. Oecologia 442:591-602.

Kruess, A. and Tscharntke, T. 2002. Contrasting responses of plant and insect diversity to variation in grazing intensity. Biological Conservation 106: 293-302.

Luff, M.L. and Woiwood, I.P. 1995. Insects as indicators of land-use change: A European perspective, focusing on moths and ground beetles, in: Harrington, R. and N. E. Stork eds.), Insects in a Changing Environment, 17th Symposium of the Royal Entomological Society. London: Academic Press.

Lynch, J.F. and Whigham, D.F. 1984. Effects of forest fragmentation on breeding bird communities in Maryland, USA. Biological Conservation 28:287-324.

MacArthur, R.H. and MacArthur, J.W. 1961. On bird species diversity. Ecology 42: 594-598.

MacArthur, R.H. and Wilson, E.O. 1967. The Theory of Island Biogeography Princeton, NJ: Princeton University Press.

Matter, S.F. and Roland, J. 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 Villard, M. 1999. Patch characteristics and landscape context as predictors of species presence and abundance: A review. Ecoscience 6: 117-124.

Morrison, M.L., Margot, B.G., and Mannan, R.W. 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. and Warren, A.D. 2004. Scientific names list for butterfly species of North America north of Mexico. Contributions of the C.P. Gillette Museum of Arthropod Diversity, Colorado State University.

Opler, P.A., Pavulaan, H., and Stanford, R.E. (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 Schwartz, M.W. 1998. Effectiveness of a vegetation-based approach to insect conservation. Conservation Biology 12: 693-702.

Proctor, M., Yeo, P. and Lack, A. 1996. The Natural History of Pollination. Portland, OR: Timber Press.

Ricklefs, R.E. and Lovette, I.J. 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., Dufrene, M., and Lebrun, P. 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 Keeler-Wolf, T. 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.

Sharp, M.A., Parks, D.R., Ehrlich, P.R. 1974. Plant resources and butterfly habitat selection. Ecology 55: 870-875.

Simonson, S.E., Opler, P.A., Stohlgren, T.J., and Chong, G.W. 2001. Rapid assessment of butterfly diversity in a montane landscape. Biodiversity and Conservation 10:1369-1386.

Soderstrom, B., Svensson, B., Vessby, K., and Glimskar, A. 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., Munzenberg, U., Burger, C., Thies, C., and Tscharntke, T. 2002. Scale-dependent effects of landscape context on three pollinator guilds. Ecology 83:1421-1432.

Steffan-Dewenter, I. and Tscharntke, T. 1997. Early succession of butterfly and plant communities on set-aside fields. Oecologia 109:294-302.

Steffan-Dewenter, I. and Tscharntke, T. 2000. Butterfly community structure in fragmented habitats. Ecology Letters 3: 449-456.

Steffan-Dewenter, I. and Tscharntke, T. 2002. Insect communities and biotic interactions on fragmented calcareous grasslands – a mini review. Biological Conservation 104:275-284.

Thomas, C.D., Mallorie, H.C. 1985. Rarity, species richness and conservation: Butterflies of the Atlas mountains in Morocco. Biological Conservation 33:95-117.

Tscharntke, T., Steffan-Dewenter, I., Krauss, A., and Thies, C. 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., Parker, A.J., Parker, K.C. 1982. Bird communities and vegetation structure in the United States. Annals of the Association of American Geography 72:120-130.

Vessby, K., Soderstrom, B., Glimskar, A., and Svensson, B. 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/cgibin/cliMAIN.pl?ca7641. 1/30/2004

Weibull, A.C. and Ostman, O. 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., Dolt, C. , Rusterholz, H.P., Oggier, P., Braschler, B., Thommen, G.H., Ludin, E., Erhardt, A., and Baur, B. 2000. Short-term responses of plants and invertebrates to experimental small-scale grassland fragmentation. Oecologia 125:559-572.

Table 1. 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.

Table 2. 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).

Table 3. 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 1 for definitions of explanatory variables.

Table 4. 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 1 for definitions of explanatory variables.

Table 5. 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.

Figure 1. Map of study region. Small, black polygons represent meadow sites in their approximate location in the Tahoe National Forest in California, USA.

Figure 2. Aerial photograph of example study site, transect locations and matrix area. Aerial photograph shows 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.

Figure 3. The relationship between the species richness and abundance of all butterflies with percent sagebrush vegetation in the matrix. The relationship between (a) species richness, (b) total abundance and (c) estimated species richness of all butterflies and the primary explanatory variable in each of the models: percent of sagebrush vegetation in the surrounding matrix. Species richness and total abundance are the number of species and the sum of all individuals, respectively, pooled across all transects and visits for each meadow. Estimated species richness was calculated using the program SPECRICH (Hines 1996), and was log-transformed to improve distribution.

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.

Figure 5. The relationship between abundance of dominant meadow specialist butterfly species with primary explanatory variables. The relationship between abundance of the four dominant meadow specialist species and the primary explanatory variable in each of the regression models: (a) *Coenonympha tullia* ssp. ampelos, (b) *Plebejus podarce*, (c) *Plebejus saepiolus*, and (d) *Speyeria mormoni*a. Abundance values were transformed using log (abundance +1) to improve distributions.

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) *Satyrium behrii*. Abundances were transformed using log (abundance + 1) to improve distributions.

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.

Table 1.

Variable	Description	Mean ± se	Range	Units
Local				
PLANTRICH	Number of vascular plants species	55.7 ± 2.5	40 – 79	number of species
PLANTHT	Average plant height	20.6 ± 1.7	9.7 – 37.3	cm
WETLAND	Cover of obligate wetland plant species	33.0 ± 5.2	4.0 – 75.5	percent aerial cover
NATIVE-COVER	Proportion native species cover of total plant cover	0.904 ± 0.020	0.666 – 0.993	proportion
SAGE-MEADOW	Cover of *Artemisia* spp.	4.5 ± 1.4	0 – 19.4	percent aerial cover
FLORALRICH	Number of plant families in flower	10.8 ± 0.6	7 – 15	number of families
FLORALDENS	Density of inflorescences	40,873.3 ± 12,659.3	735 – 239,400	inflorescences per 3,000 m2
ELEVATION	Elevation	2,051.2 ± 33.5	1,852 – 2,286	m
AREA	Area	14.4 ± 2.9	2.9 – 51.5	ha
Landscape				
AVGISOLATION	Average distance to 3 nearest meadow habitats	1,287.7 ± 150.0	337 – 2,660	m
ISOLATION	Distance to nearest meadow >100 ha in size	2,419.6 ± 448.2	303 – 7,198	m
ASPEN	Aspen vegetation*	0.74 ± 0.41	0 – 5.2	percent of matrix area
FOREST	Jeffrey pine, Lodgepole pine, Ponderosa pine vegetation*	67.4 ± 6.1	23.2 – 97.0	percent of matrix area
MEADOW	Montane meadow, Nebraska sedge vegetation*	1.5 ± 0.7	0 – 12.9	percent of matrix area
SAGE-MATRIX	Big sagebrush, Bitterbrush vegetation*	20.2 ± 5.5	0 – 66.4	percent of matrix area
CHAPPARAL	Tobacco brush, Greenleaf manzanita vegetation*	8.1 ± 5.2	0 – 69.7	percent of matrix area
LOGGED	Recently logged area determined by visual survey	6.2 ± 2.0	0 – 30.1	percent of matrix area
BURNED	Recently burned area determined by visual survey	9.5 ± 6.6	0 – 100	percent of matrix area

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

Table 2.

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

Species	Family	Total individuals recorded	No. sites where observed	Meadow specialization	Larval host plant specialization
Pontia sisymbrii (Boisduval)	Pieridae	2	1	generalist	oligophagous
Strymon melinus (Hubner)	Lycaenidae	2	1	generalist	polyphagous
Cercyonis pegala (Fabricius)	Nymphalidae	1	1	specialist	oligophagous
Lycaena editha (Mead)	Lycaenidae	1	1	generalist	oligophagous
Lycaena gorgon (Boisduval)	Lycaenidae	1	1	generalist	monophagous
Polygonia gracilis (Grote & Robinson)	Nymphalidae	1	1	generalist	monophagous
Thorybes mexicana ssp. nevada (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 3.

Response variable	Constant	Local attribute(s)	Landscape attribute(s)	r^2 Change (%)	F	df	p	Model r^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
Habitat specialization								
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(FLORALRICH)*		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(FLORALDENS)**		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 4.

Response variable	Constant	Local attribute(s)	Landscape attribute(s)	r^2 Change (%)	*F*	*df*	*p*	Model r^2 (%)
<u>*Meadow specialists*</u>								
Coenonympha tullia	6.46	-2.998(NATIVE-COVER)**		40.5	13.25	3,14	<.001	74.0
		-0.002(ELEVATION)**		21.5				
			-0.008(CHAPARRAL)*	11.9				
Plebejus podarce	-0.29	0.023(WETLAND)***		66.2	31.33	1,16	<.001	66.2
Plebejus saepiolus	0.05	0.056(PLANTHT)***		50.5	16.35	1,16	0.001	50.5
Speyeria mormonia	-4.72	0.025(ELEVATION)*		40.1	10.72	1,16	0.005	40.1
<u>*Meadow generalists*</u>								
Colias eurytheme	-2.19	0.001(ELEVATION)*		29.8	6.80	1,16	0.019	29.8
Junonia coenia	-0.80	0.116(FLORALRICH)**		30.7	6.80	2,15	0.008	47.5
			+0.022(LOGGED)*	16.8				
Pyrgus communis‡	1.25		-0.021(SAGE-MATRIX)***	59.3	21.84	1,15	<.001	59.3
Satyrium behrii	2.21	7.6×10^{-6}(FLORALDENS)***		66.8	38.31	3,14	<.001	89.1
		–0.001(ELEVATION)*		17.2				
			+0.0002(AVGISOLATION)*	5.2				

‡ 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 5.

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 *Agriades podarce*)	+WETLAND	+ELEVATION
Log(Abundance of *Colias eurytheme*)	+ELEVATION	no model
Log (Abundance of *Pygus communis*)	-SAGE-MATRIX	+PLANTHT
Log(Abundance of *Speyeria mormonia*)	+ELEVATION	+WETLAND

Figure 1.

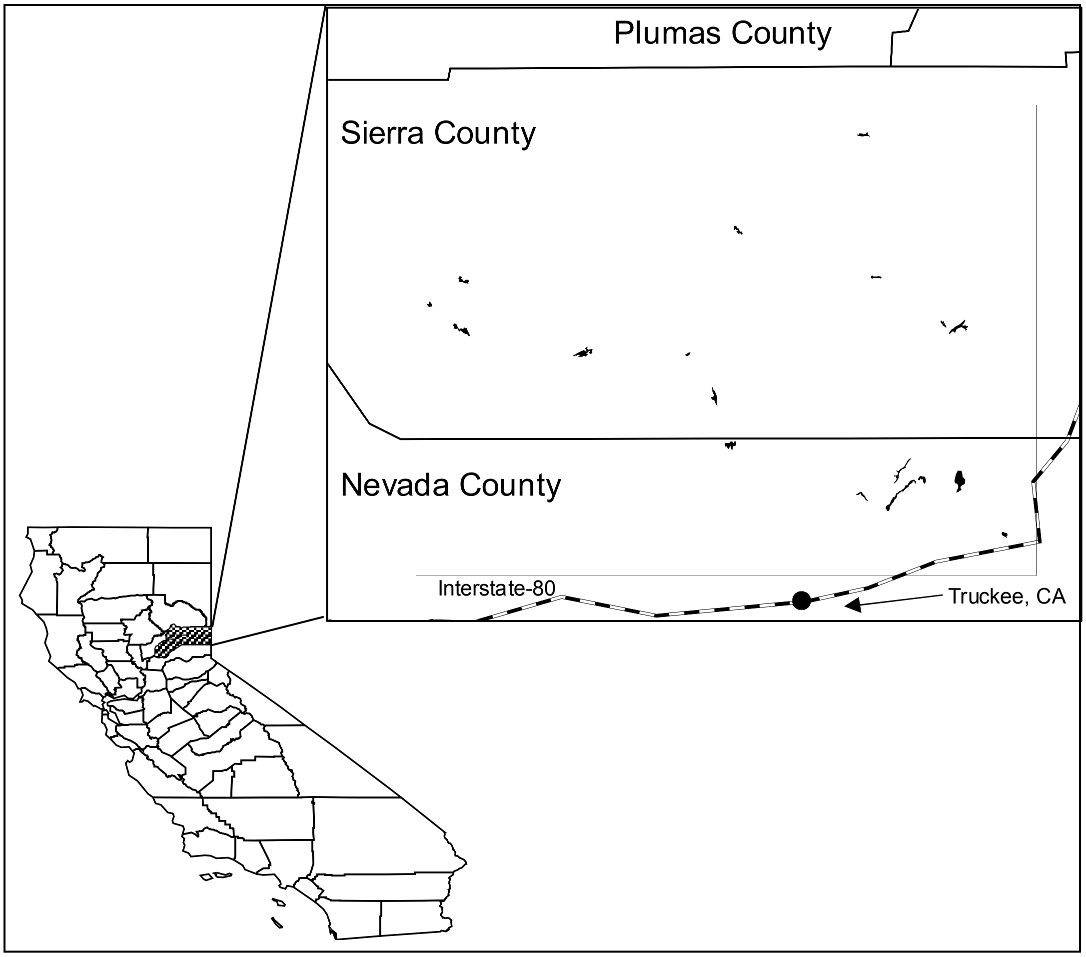
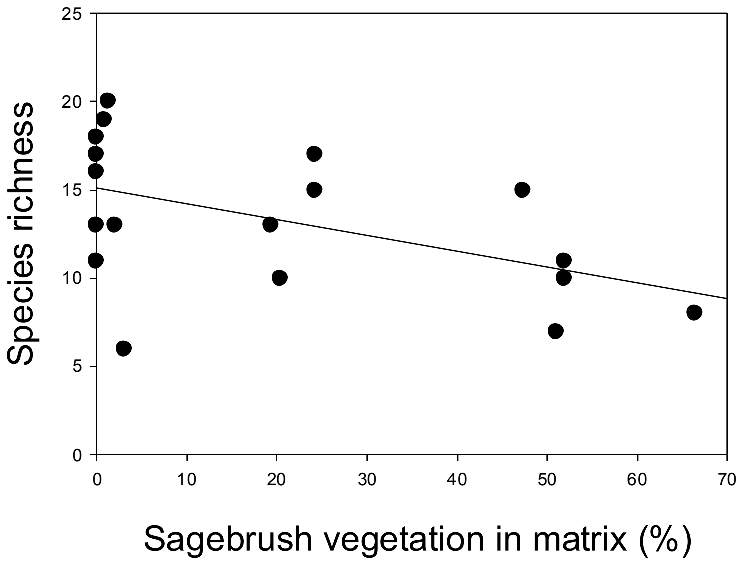

Plumas County
Sierra County
Nevada County
Interstate-80
Truckee, CA

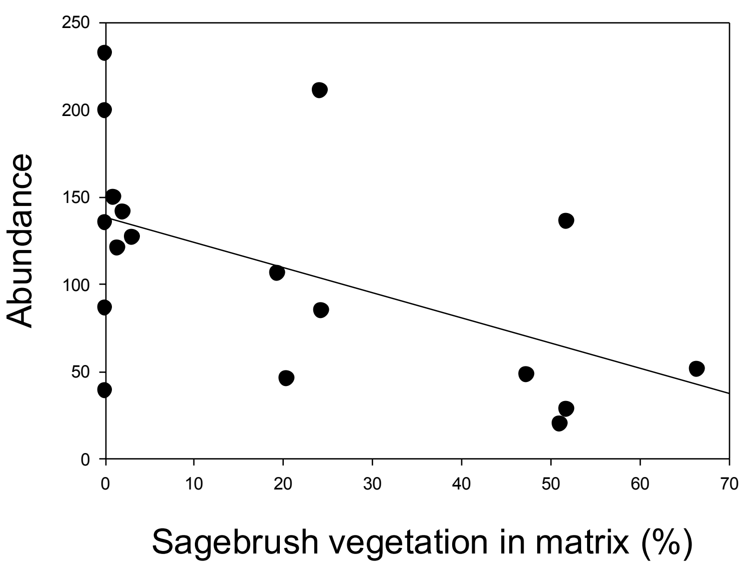
Figure 2.

Figure 3.

A. Total butterfly richness



B. Total butterfly abundance



C. Estimated species richness

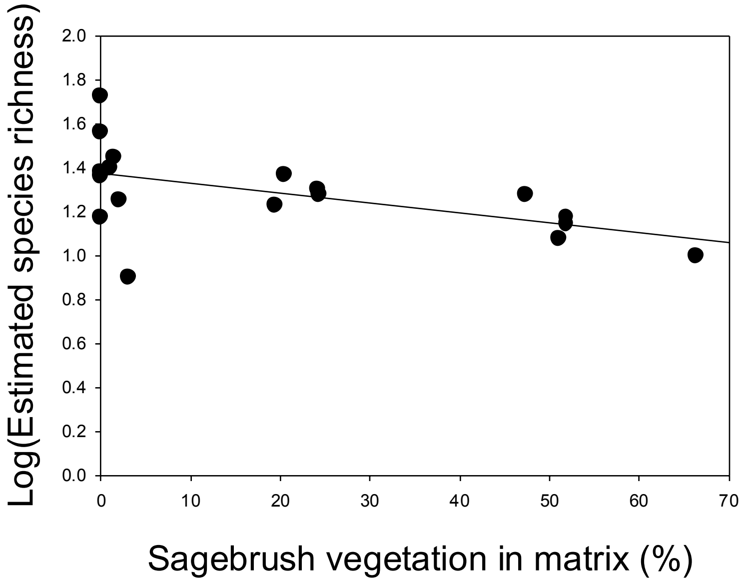
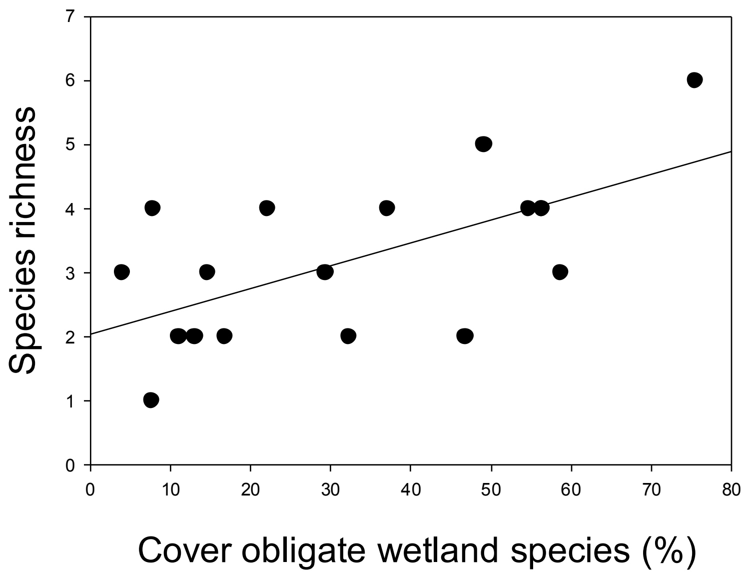


Figure 4.

A. Meadow specialist species richness



B. Meadow specialist abundance

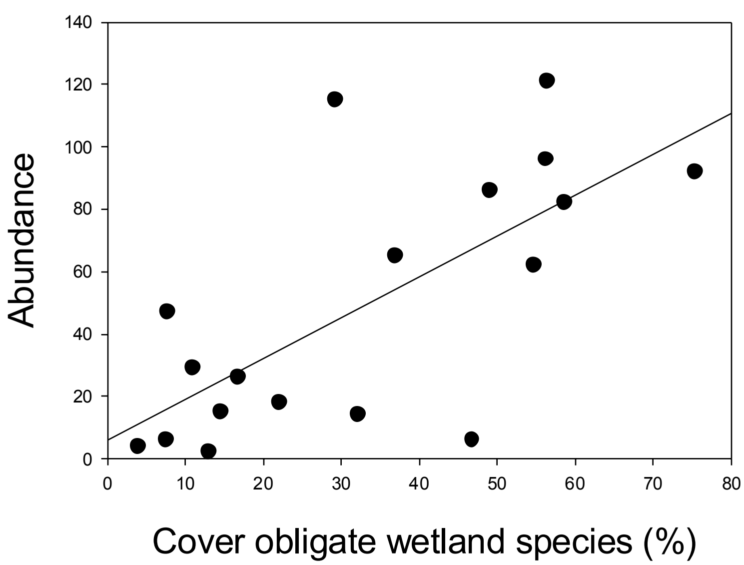
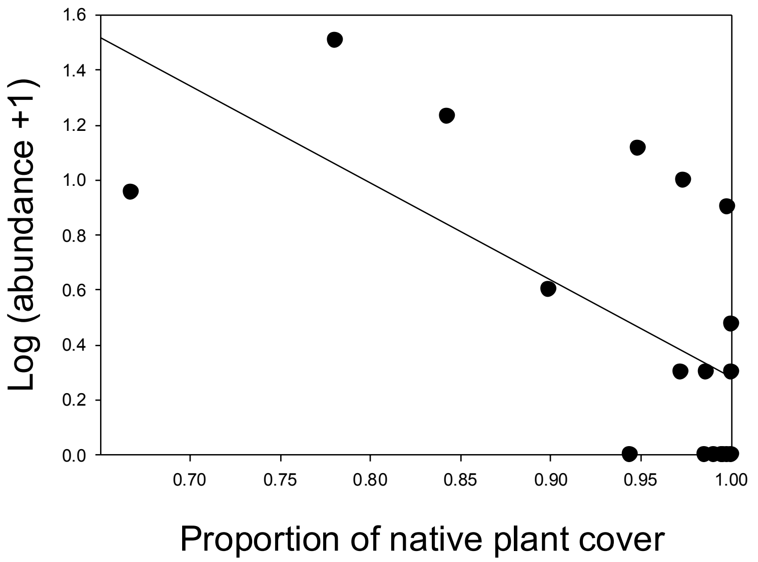
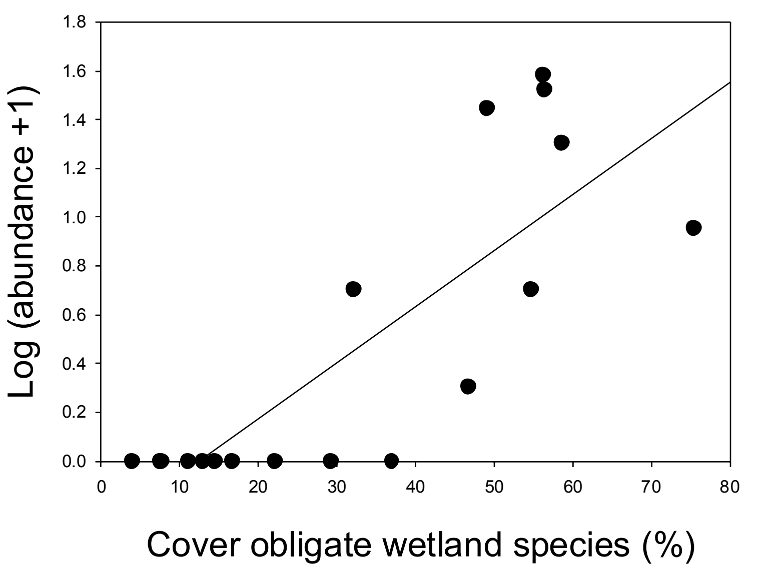


Figure 5.

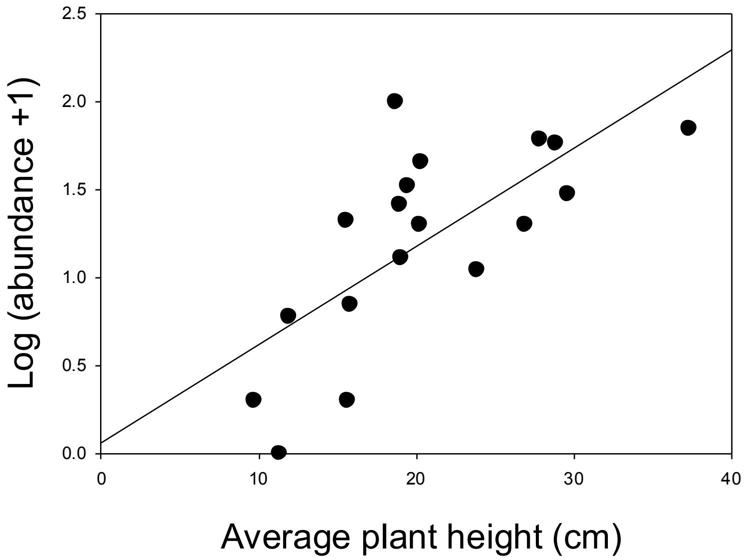
A. *Coenonympha tullia*



B. *Plebejus podarce*



C. *Plebejus saepiolus*



D. *Speyeria mormonia*

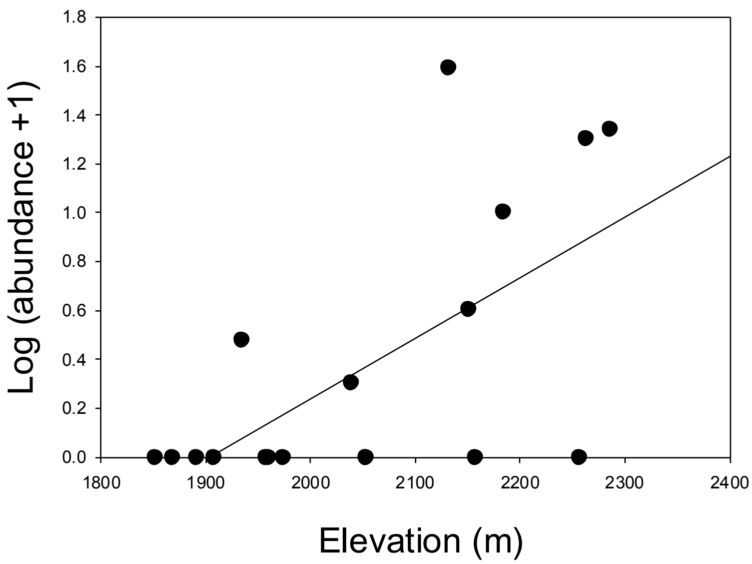
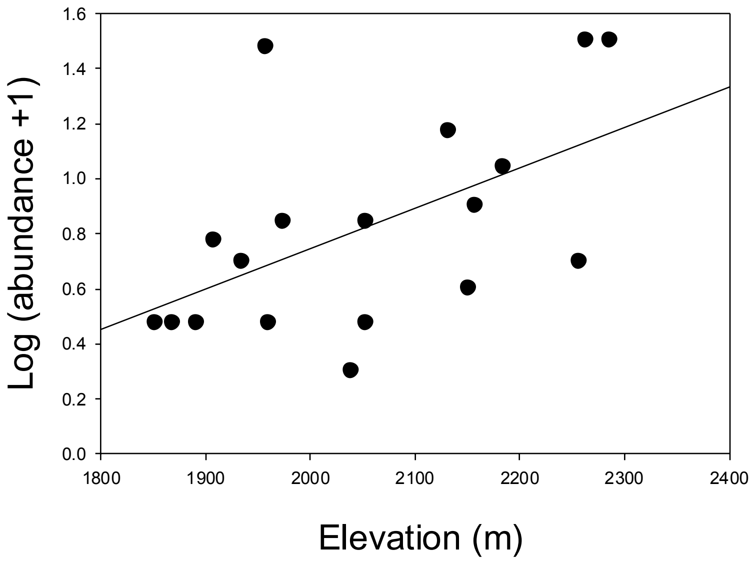
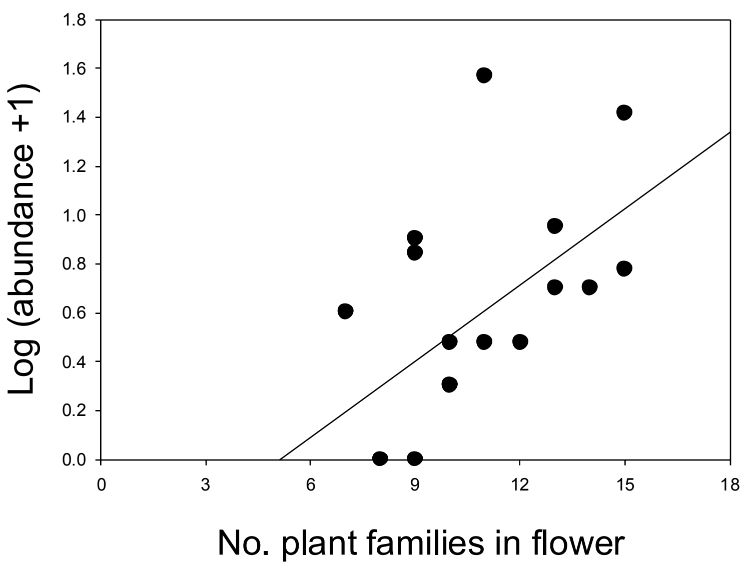


Figure 6.

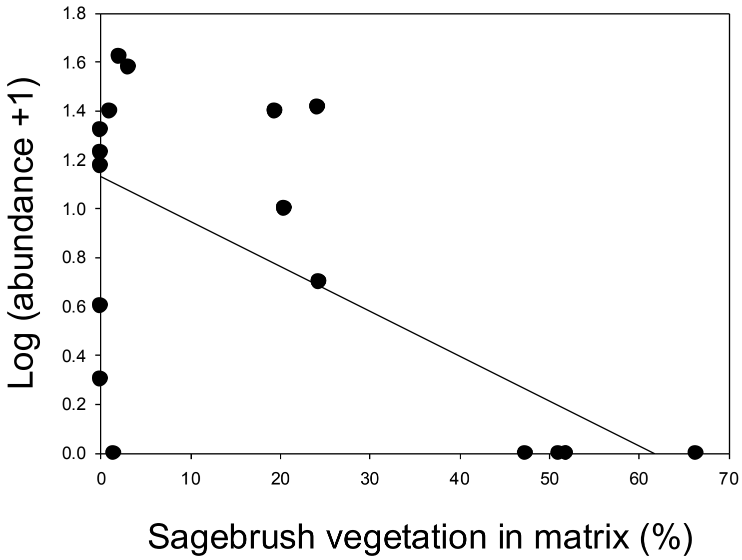
A. *Colias eurytheme*



B. *Junonia coenia*



C. *Pyrgus communis*



D. *Satyrium behrii*

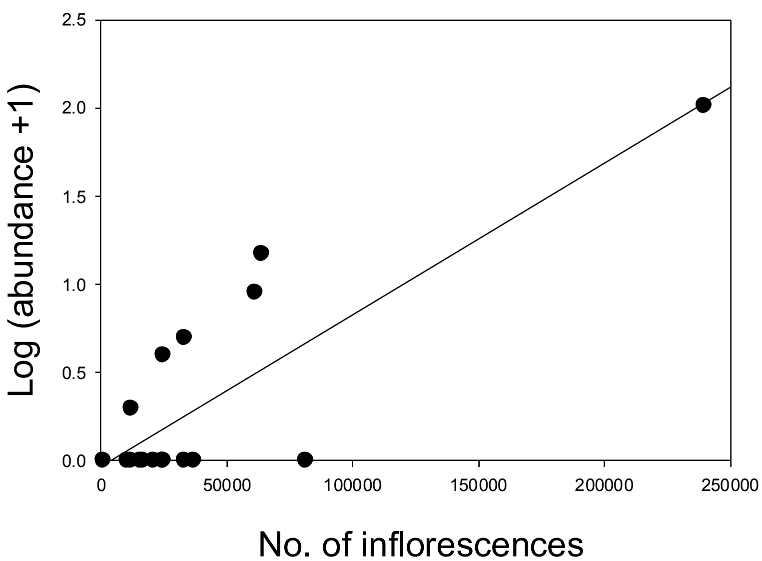
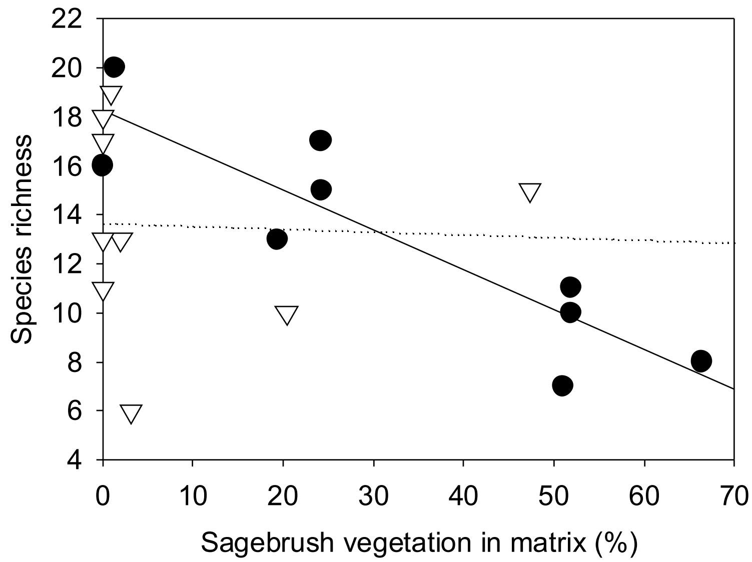
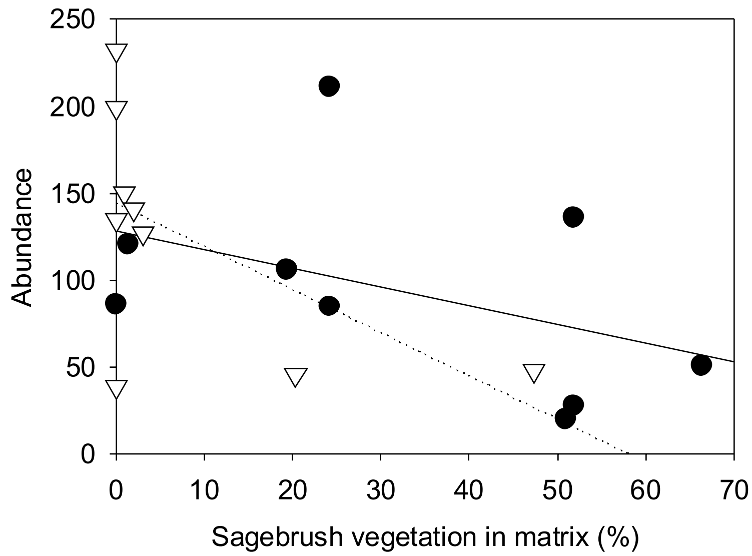


Figure 7.

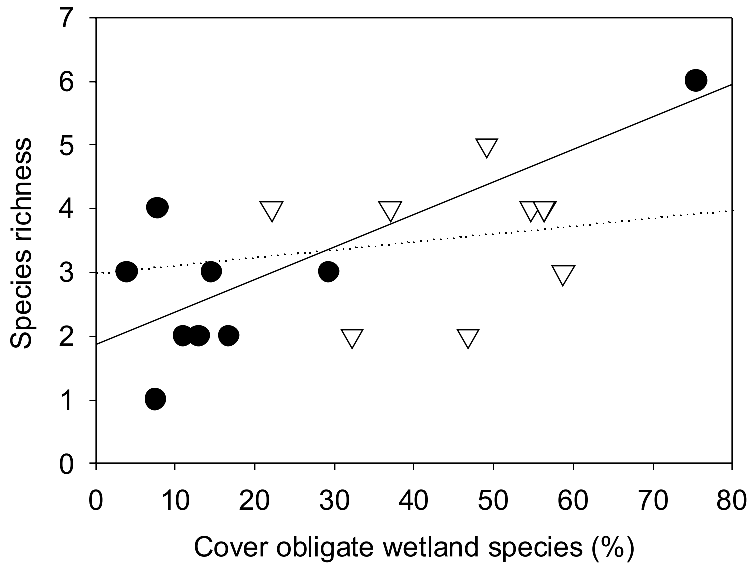
A. Total butterfly species richness



B. Total butterfly abundance



C. Meadow specialist species richness



D. Meadow specialist abundance