# Butterfly Response to Ponderosa Pine Restoration and the Efficacy of Butterflies as Indicators of Pollinators

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# Abstract

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Few ecosystem restoration studies monitor arthropods as important components of ecosystem recovery. We tested the hypothesis that ponderosa pine restoration treatments would increase adult butterfly species richness and abundance by monitoring changes in butterfly abundance following restoration. To examine potential mechanisms of adult butterfly distribution, the host plant availability, nectar plant availability and insolation (light intensity) were sampled in restoration treatment units and control forests. Three patterns emerged: 1. Butterfly species richness and abundance were 2 and 3 times greater, respectively, in restoration treatment units than in paired control forests one year following treatment, and 1.5 and 3.5 times greater two years following treatment. 2. Host plant and nectar plant species richness showed little difference between treated and control forests even 2 years following treatment. 3. Insolation (light intensity) was significantly greater in treated forests following restoration.

To more specifically examine butterfly response to restoration treatments, larval distributions were assessed to predict the responses of butterflies to land management changes. *Epargyreus clarus* Cramer larvae were found in highest abundances on juvenile host plants (New Mexico locust), and were significantly higher on host plants located in sunny patches. Resprout vegetation was not utilized as extensively by larvae as nearby, non-resprout vegetation. From these data, we predicted an increase in *E. clarus* larvae

following ecological restoration treatments. Our study supported this prediction; further sampling revealed larval densities were 4 times higher in treated than in control forests.

We also examined the effectiveness of butterflies as indicators of the pollinator community, and the contribution of restoration treatments to indicator development. We suggested regional indicator development and testing could be more effectively accomplished using a landscape-scale restoration experiments and present a format for developing indicator species. We presented existing evidence supporting the use of indicators in restoration studies and a case study, using ponderosa pine restoration to test the effectiveness of adult, day-flying Lepidoptera as indicators of pollinator groups. Adult butterfly abundances were found to have a significant, positive relationship with pollinator group abundances in restoration treatments.

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# Table of Contents

# List of Tables

CHAPTER 2

CHAPTER 4

# List of Figures

CHAPTER 2

CHAPTER 3

CHAPTER 4

# Preface

This dissertation was written in journal format. Chapters 2 – 4 will be individually submitted to different journals as follows: Chapter 2, Ecological Applications; Chapter 3, Ecological Entomology; and Chapter 4, Forest Ecology and Management. Because of this format, there was some redundancy in the methods within each chapter, and between the general abstract and general introduction and the manuscript chapters. In addition, each chapter was formatted for its respective journal and used different reference citation formats. These journal manuscripts will be co-authored with W. Wallace Covington as the second author.

# Chapter 1: Introduction

Ecosystem restoration often overlooks invertebrates as important components necessary for ecosystem function and process. Most current studies and methods of ecosystem restoration remain focused on structural components, such as overstory or understory plant composition, and not on functional processes, such as nitrogen cycling, plant pollination, and/or trophic level interactions (but see Covington *et al.* 1997; Kaye & Hart 1998). This focus on ecosystem structure is primarily a result of available reference information; often obtained from historical records. These historical records do not describe how species interacted with each other, or what processes were important to ecosystem functioning (e.g., Dutton 1882). Knowledge of ecosystem function and process can be obtained from studying current-day undisturbed ecosystems (Leopold 1937). In addition, historical function and process can be inferred by studying function and process in experimentally restored ecosystems (Covington *et al.* 1994; Michener 1997).

In ponderosa pine forests in the Southwest, forest structure can be reconstructed from presettlement remnants and historical records (Covington & Moore 1994; Covington *et al.* 1997; Fulé & Covington 1997). This information is limited to overstory species, with some information on herbaceous components also available from early land surveys (Dutton 1882) and phytolith studies (Rovner 1971; Bozarth 1993; Fisher *et al.* 1995; Fredlund & Tieszen 1997). From these data, pre Euro-American Southwest forest structure is known to have lower tree densities than current forests (50-150 tph in 1870 vs. 500-3000 tph in 1994, Covington and Moore 1994), with grassy openings.

Restoration of these forests is being attempted by protecting trees of presettlement age, using thinning to reduce postsettlement tree densities and reintroducing fire.

Restoration treatments in ponderosa pine are hypothesized to impact all components of the ecosystem, including arthropods. The change from a closed canopy forest with little or no herbaceous community to an open canopy forest with a dominant herbaceous community results in plant diversity and plant production increases (Covington et al. 1997). This in turn can result in increases in herbivore arthropod abundance and diversity (Erhardt & Thomas 1991). In addition, treated forests show increases in soil moisture and soil temperature when compared to control forests (Covington et al. 1997); both factors directly influence the success rate of arthropod pupation (Erhardt and Thomas 1991, Scoble 1992).

Reconstructing entire invertebrate communities is difficult, due mostly to the lack of knowledge about reference conditions of arthropod species richness and abundance. Pest species (outbreak species) and some showy arthropods, such as butterflies, do appear in historic natural history notes (Dutton 1882), however, full-scale arthropod censuses are difficult to find prior to and at the time of Euro-American settlement. My research will examine the role a key arthropod taxon group, the Lepidoptera, play in ecosystem structure and function, with specific applications to monitoring effects of ecosystem restoration.

The Lepidoptera can be excellent indicators of herbaceous community diversity and composition (Gilbert 1984; Kremen 1994; Beccaloni & Gaston 1995; Steffan-Dewenter & Tscharntke 1997; Kerr *et al.* 2000; Fleishman 2000). Both butterflies and moths can be host-specific as larvae, but become nectar generalists as adults, representing several invertebrate guilds within one generation. Presence of a butterfly or moth species indicates presence of the larval host plant, as well as sufficient adult food source. Day-flying butterflies in particular have a well-known taxonomy, and often can be easily identified in the field (Scoble 1992).

The specific objective addressed in this study was to determine how the abundance and diversity of the diurnal Lepidopteran (day flying butterflies) assemblage responded to ponderosa pine restoration treatments. Because significant changes in butterfly community structure were determined, we also examined three mechanistic objectives as follows: 1. we determined if the Lepidopteran community responded to light intensity differences (i.e., insolation) between control and restored ponderosa pine forests. 2. we determined if nectar resources varied greatly between control and restored forests. 3. we determined if host plant distributions varied between control and restored forests (Chapter 2).

To further understand the mechanisms behind adult butterfly distribution we examined how a specific species (i.e., the Silver-spotted skipper [*Epargyreus clarus*]) responded to the changes in the woody overstory and herbaceous vegetation following restoration treatments as mediated through its host plant, New Mexico locust (*Robinia neomexicana*) (Chapter 3). Finally, we examined the suitability of butterflies as potential indicators of pollinators in ponderosa pine forest restoration treatments (Chapter 4). Bees, wasps and bee-flies are much more difficult to census than butterflies, but contribute significantly more to pollination events than butterflies do (Jennersten 1984).

We hypothesized that the butterfly community would show significant increases in species richness and diversity to ponderosa pine restoration. Mechanisms contributing to adult butterfly distribution include the light intensity differences found between closed canopy forests and open canopy forests (Covington et al. 1997). Increased herbaceous production in restored, open canopy forests would have increased nectar resources for adult butterflies. In addition, although overall community diversity and abundance will increase, some species, such as the non-nectar feeding species (Waltz, pers. obs.), will decline with ponderosa pine restoration. Still other species may show no effect after forest restoration. Finally, we hypothesize that the butterfly abundance would indicate pollinator community abundance.

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# Chapter 2: Ecosystem Restoration Treatments Increase Butterfly Richness and Abundance: Mechanisms of Response

## ABSTRACT

Few ecosystem restoration studies monitor arthropods as important components of ecosystem recovery. We tested the hypothesis that ponderosa pine restoration treatments would increase adult butterfly species richness and abundance as a direct result of increased understory diversity and abundance. To examine potential mechanisms of adult butterfly distribution, the host plant availability, nectar plant availability and insolation (light intensity) were sampled in restoration treatment units and control forests. Four experimental blocks each containing a randomly assigned control unit and a restoration treatment unit were sampled for adult butterfly assemblages 2 years prior to and 2 years following restoration treatments. These treatments are the first replicated ponderosa pine restoration treatments at a landscape scale and offer a unique opportunity to study responses to and recovery from disturbance and restoration. Three patterns emerged: 1. Butterfly species richness and abundance were 2 and 3 times greater, respectively, in restoration treatment units than in paired control forests one year following treatment, and 1.5 and 3.5 times greater two years following treatment. 2. Host plant and nectar plant species richness showed little difference between treated and control forests even 2 years following treatment. 3. Insolation (light intensity) was significantly greater in treated forests following restoration.

**Keywords:** biodiversity, butterfly, ecological restoration, host plant, insolation, light intensity, nectar resource, Lepidoptera, ponderosa pine.

# INTRODUCTION

The goal of ecological restoration is to return ecosystems to their pre-disturbed state with respect to ecosystem structure, function and composition (Hobbs & Norton 1996). However, most monitoring of terrestrial ecosystem restoration projects in the past has not reflected these goals but has instead primarily focused on structural ecosystem components, such as overstory or understory plant composition, rather than on ecosystem functions and processes, such as nitrogen cycling, plant pollination, and/or trophic level interactions (Aronson et al. 1993, Hobbs and Norton 1996, but see Kaye 1997, Covington et al. 1997).

To accurately address questions of restoration success, monitoring must include measures of process, function and ecosystem integrity (Aronson et al. 1993), notably difficult attributes to understand, let alone measure (Hobbs and Norton 1996). To address this, researchers have increasingly used invertebrate monitoring to establish linkages between species composition and ecosystem functions (Majer 1997, Andersen & Sparling 1997, Davies et al. 1999). Invertebrates show quick responses to ecosystem change and disturbance, and contribute to system sustainability through processes such as decomposition, energy transfer, and pollination (Recher 1993, Andersen and Sparling 1997). This study was the first invertebrate monitoring study in ponderosa pine forest restoration treatments in the U.S. Southwest.

Open, park-like stands of ponderosa pine were converted to dense pole stands with little understory plant richness or abundance in the last 100-150 years by the introduction of livestock grazing and the disruption of fires (Covington et al. 1997). Experimental restoration of these forests has been initiated by using thinning to reduce current tree densities and returning fire to the landscape. This change from a closed canopy forest with little or no herbaceous plant community to an open canopy forest with a dominant herbaceous community increased plant diversity and plant production (Covington et al. 1997, Springer et al. 2000). This in turn has ramifications for changes in the abundance and diversity of herbivore arthropods (Siemann et al. 1997, Erhardt and Thomas 1991). Treated forests also showed increases in soil moisture and soil temperature when compared to control forests due to decreased above-ground biomass (trees) (Covington et al. 1997). Both factors are positively correlated with the success rate of arthropod pupation (Erhardt and Thomas 1991, Scoble 1992). Finally, fire intensity, patchiness, and seasonality have been shown to determine arthropod community structure (Whelan 1995, Reed 1997, Andersen & Muller 2000, Wikars & Schimmel 2001).

The above studies suggested thinning and burning projects could alter arthropod community structure. Therefore, we examined the response of the butterfly assemblage to ecosystem restoration treatments. Because of the broad life history traits found in butterflies, this taxon has been suggested as potential indicators of herbaceous communities (Scoble 1992), other herbivorous arthropods (Brown Jr. 1991, Scoble 1992, Beccaloni and Gaston1995) and even other taxonomic groups ( Wilcox et al. 1986, Carroll & Pearson 1998,). Many butterfly larvae are host-specific, with host plants including grasses, forbs, shrubs and trees. As adults, butterflies are nectar generalists, representing a broad range of ecological niches within an ecosystem. Butterfly species also have well-known natural histories, and are easily identified in the field. Changes in butterfly diversity can correlate with changes in the abundance and diversity of a wide variety of invertebrates (Scoble 1992).

Butterfly response to habitat disturbances such as logging has been mixed. While butterflies have shown decreases in abundances after clear-cut logging events (Hill et al. 1995), other studies showed that openings in forests, including changes created by roadways and paths, often had higher butterfly abundances than nearby forests (Pollard et al. 1975). This butterfly abundance increase in forest gaps was most likely due to increased host plant diversity and light availability (Sparks et al. 1996). Butterfly community structure may reflect these plant community changes. For example, successional changes in abandoned agricultural grasslands in Europe were mirrored by butterfly community structure changes (Erhardt 1985, Erhardt and Thomas 1991). In addition, flowering plant species richness was shown to correlate with butterfly abundance (Kremen 1994, Holl 1995).

These responses suggested two general hypotheses of adult butterfly response to ponderosa pine forest restoration treatments. We tested the hypotheses that: 1. butterfly richness and abundance would initially decrease in response to logging and ground disturbance, and then increase with the increasing herbaceous community (Hill et al. 1995, Spitzer et al. 1997); and 2. that generalist butterflies would dominate the initial butterfly assemblage, with turnover to specialist butterflies in subsequent years (Steffan-Dewenter & Tscharntke 1997). We then examined potential mechanisms that might explain adult butterfly distributions in treated and control forests. We asked: 1. Do host plant distributions differ between restoration treatment units and control units? 2. Do nectar resources differ between restoration treatment units and control units? and 3. Does insolation (light intensity) change following restoration treatments?

## METHODS

### Study Site

The study site used for this research was a ponderosa pine (*Pinus ponderosa*) and Gambel oak (*Querqus gambelii*) forest located between Mt. Logan and Mt. Trumbull, about 35 kilometers north of the Grand Canyon on the Arizona Strip. This land is managed by the Bureau of Land Management, and falls within the recently designated Grand Canyon – Parashant National Monument. Mt. Logan, Mt. Trumbull and the surrounding highlands form a sky island of ponderosa pine, with desert grassland to the north and the Grand Canyon to the south. The nearest ponderosa pine forest was about 100 km east, on the Kaibab Plateau. The elevation of the sky island ranged from 1675 m to 2620 m. The area received an average of 40 - 45 cm of rainfall per year, and contained some of the biota of the Great Basin (Welsh 1987), in addition to the flora of northern Arizona (Kearney and Peebles 1951). The forest was predominately ponderosa pine, although Gambel oak composed 15% of the overstory (Waltz & Fulé 1998). Other tree species in the area included New Mexico locust (*Robinia neomexicana*), aspen (*Populus tremuloides*), pinyon (*Pinus edulis*) and juniper (*Juniperus osteospermus*). The herbaceous component was dominated by sagebrush (*Artemesia tridentata*), and showed evidence of invasion by non-native species, such as cheat grass (*Bromus tectorum*), and some wheatgrasses (*Agropyron spp.*). Although over 300 herbaceous species were documented at the Mt. Trumbull site in the last 5 years (J.D. Springer, pers. comm.), the forest floor cover prior to restoration treatments was 70% litter and duff, with only 15% of the cover represented by live plants.

Approximately 1,450 hectares of the 5,000-hectare forest was targeted for ponderosa pine restoration treatment in 1995, and as of 2001, approximately 250 ha were thinned and burned. Within this area, four experimental blocks were established in 1997 (Figure 2.1). Each block was divided into two units, with each unit randomly assigned as control or restoration treatment. The treatment units were treated fall/winter of 1999-2000. Each block had 20 vegetation monitoring plots placed on a 60-meter grid. Plot grids were established at least 50 meters from treatment unit boundaries.

The five experimental blocks varied in soil type, forest density, forest composition and herbaceous cover (Figure 2.1). **Block 1:** Located on shallow lava/cinder soils, this block had low tree density, consisting almost entirely of ponderosa pine, with many living presettlement (old-growth) trees. There was a large shrub component in this block, primarily serviceberry and wax currant. **Block 2:** This block had a strong Gambel oak component with an abundant herbaceous understory, including sagebrush openings, on basalt soils. **Block 3:** At the highest elevation, block 3 was dominated by large, presettlement ponderosa pine, but also had Gambel oak and New Mexico locust throughout the unit. This unit was one of the largest (~40 ha) and was predominately on cinder soils. **Block 4:** Block 4 was representative of the densest stands of ponderosa pine forest at the Mt. Trumbull site. The overstory consisted of dense ponderosa poles, some oak clumps, and some pinyon and juniper at its western end. This block was on basalt soils and had few living presettlement ponderosa pines.

This complete randomized block design was one of the first in landscape-level terrestrial restoration treatments, and allowed a larger inference for results. The paired treatment and control units accounted for annual fluctuations due to weather. This was important because the four sampling years represented seasons following severe drought (1997 and 2000), and record snowfall years (1998 and 2001). Butterfly populations showed drastic differences in total species richness and abundance throughout these years, but overall trends between treatment and control units were consistent. Throughout the analyses, an n of 4 is used to determine differences between restoration treatments and control forest stands.

**Butterfly Sampling**

Butterfly monitoring data presented were collected from control and treatment units within each block in 1997, 1998, 2000 and 2001. Sampling years 1997 and 1998 were prior to treatment, sampling years 2000 and 2001 followed restoration treatment. Butterfly monitoring transects (Pollard 1977) totaling 900 meters per unit were established in control and treatment units of every block except block 2, where only 600 transect meters were established in each treatment unit due to block shape and size. Transects followed the monitoring plot grid of 20 plots placed 60-meters apart (Figure 2.2). Plot grids were centered in units, and butterfly transects were placed 50 m from unit boundaries to minimize edge effects.

Transects were monitored every 2 weeks, between May and August, for a total of 6 surveys per year. Diurnal butterflies are very sensitive to cool and windy conditions and often limit their flights on cloudy, cool days, thereby reducing chance of observation. Therefore, sampling occurred between 1000 and 1600 hours, on days warmer than 17 degrees C, with winds less than 15 kph, and mostly sunny skies (Pollard 1977). A total of 5 minutes per 100 m was spent looking for butterflies. Butterfly species encountered on each transect were recorded, along with location along transect, and lateral distance from transect (perpendicular to transect). In addition for each observation, we recorded behavior (i.e., nectaring, basking, flying), and if a specimen was collected. If the butterfly could not be identified in flight, attempts were made to capture and collect the insect. The timed portion of the survey corresponded only to the search time and did not include time spent in pursuit of a butterfly.

Species richness and abundance data were totaled from the 6 surveys taken each year and summarized for each block and treatment. Summaries of species richness were used to get the total number of species observed over the summer. Abundances were also summed because many of the species observed had a 2- or 3-week life span. Although there were some exceptions, abundance surveys every 2 weeks were assumed to count different individuals. Changes in butterfly richness and abundance were analyzed for a significant treatment * year interaction with a repeated measures ANOVA ($n = 4$ blocks) using repeated contrasts to test for differences between treatment units among years (Hopkins 2000). To determine which butterfly families contributed to overall patterns, family abundances were also analyzed for changes due to treatment with repeated measures analysis followed by repeated contrasts. Because of the low sample sizes ($n = 4$ blocks), probabilities of a type a error less than 0.10 were used to denote significant differences.

## Host Plant and Nectar Resource Distribution

To examine the first mechanistic question, how host plant availability differed between control and restoration treatment units, the herbaceous community was quantified through experimental sampling plots established in each block by Ecological Restoration Institute staff (Figure 2.2, monitoring plots). In 1997 and 1998, pre-treatment data were collected from 40 plots per block, 20 each in control and treatment units. Post-treatment herbaceous data were collected from all plots in both 2000 and 2001 to establish the early successional herbaceous patterns following treatment. Herbaceous monitoring consisted of the point-intercept method along one 50-meter transect per plot. Every 30 cm along this transect, all species encountered at the point were recorded. These methods provided plant species composition and frequency data.

Host plant availability was assessed by analyzing plant families known to contain important hosts to the 10 most common butterflies. Six of the 10 most abundant butterflies were family specific as larvae, meaning larvae can successfully develop on multiple species within one family (Scott 1984). Three of the 10 were species specific as larvae, developing on only one species. Only one top-10 butterfly larva was a generalist, and could have developed on a variety of species from several plant families. We examined legumes (Fabaceae), mustards (Brassicaceae), asters (Asteraceae), the foxgloves (Scrophulariacea) and grasses (Poaceae) for changes in abundance between untreated and restoration treatment units. Because 3 of the most common butterflies hosted on tree species (New Mexico locust and Gamble oak), changes in tree species abundances were summarized from Waltz et al. (2001). The abundances of the plant families were analyzed for differences between control and treatment forests within each year, 1998, 2000 and 2001, with a MANOVA.

To address the second mechanistic question, how nectar resource availability differed between restoration treatment and control units, we used 1-m$^2$ plots to examine flowering species richness 3 times during the year. In May, June and July following treatment in 2000 and 2001, 1-m$^2$ plots were established every 20-meters along the butterfly monitoring transect following the vegetation monitoring plot grid (Figure 2.2, nectar resource plots). A total of 45 plots was sampled in each treatment and control unit in blocks 1, 3 and 4, and 30 plots were sampled per treatment unit in block 2. At each plot, plants with blooming flowers were tallied by species. The flowering plant species richness and abundance were summed across all three surveys, as patterns were consistent through the year, although flowering species composition changed. These data were summarized by block and treatment and then analyzed with a Kruskall-Wallace non-parametric test to determine differences in flowering plant species richness ($n = 4$ blocks).

We sampled insolation in log (lumens) per m$^2$ (a measure of light intensity) to address the third mechanistic question. Insolation was measured and recorded with an integrated Hobo datalogger (Spectrum Technologies, Plainsfield, Illinois, U.S.A.). Sensors were calibrated by the manufacturer prior to purchase. These dataloggers measured light wavelengths between 400 and 1100 nanometers. We modified the dataloggers by removing a sticker on the front cover, which obstructed the sensor at lower sun angles. In the field, the sensors were placed in a clear plexiglass case for protection from moisture.

A total of 10 dataloggers was used to determine insolation differences between treatment units within blocks. Insolation data were collected once per season in 1998 and 2000. Five stations were set up on randomly selected vegetation monitoring plots in the treatment and control of each block (Figure 2.2, light intensity dataloggers). Sensors were placed 1-m from the ground. Data were collected in 4-minute intervals from one 24-hour period, during clear weather. Insolation values were averaged for three time periods during daylight hours to examine differences between restoration treatment and control units. The midday hours, 11am to 3:59pm, coincided with the butterfly-sampling period. The morning hours, 8am to 10:59am, were examined because insolation and air temperature determine the time to flight temperature for butterflies (Johnson 1969). Finally, hours between 4pm and 5:59pm were tested for differences between control and treatment. Light intensity differences at this time of day may influence length of foraging and mate search. A block – treatment unit average (e.g., Block 3 – control) was calculated from the 5 insolation dataloggers for each survey. Blocks were used as replications with n = 4. Differences between restoration treatment and control units were assessed with a two-way ANOVA with treatment unit and time class as factors.

## RESULTS

### Butterfly Community Response to Restoration Treatments

Thirty-seven butterfly species were collected at the Mt. Trumbull site between the years 1997 and 2001 (Table 2.1). Although year-to-year variation was great, the most common of these included the silver-spotted skipper (*Epargyreus clarus* Cramer, EPCL), the Gambel oak dusky-wing (*Erynnis telemachus* Burns, ERTE), the silvery blue (*Glaucopsyche lygdamus* Doubleday, GLLY), the orange sulfur (*Colias eurytheme*

Boisduval, COEU) and the checkered white (*Pieris protodice* Boisduval and LeConte, PIPR). Host plants used by the larvae of these butterflies ranged from legumes, mustards, various shrubs, shrub/trees (New Mexico locust) and trees (oak).

Although no significant butterfly assemblage differences were found prior to restoration treatment (1997 and 1998), we found up to 2 times as many butterfly species in restoration treatments as in the control units 1-year following treatment, and 1 ½ times as many species 2-years following treatment (Figure 2.3a, Repeated Measures ANOVA, year * treatment effect $F = 4.42$, $p < 0.10$). Five times as many butterflies were observed in treatment units as in paired control units in post-treatment year 1, and 3 ½ times as many butterflies were observed in post-treatment year 2 (Figure 2.3b, Repeated Measures ANOVA year * treatment effect $F = 7.28$, $p < 0.10$). These restoration treatments create an initial disturbance, but it is not apparent that this adversely affects butterfly species richness or abundance.

**Butterfly Family Responses:** Repeated measures analysis of family abundances showed the increases in the abundances of Lycaenidae and Pieridae in treatment units were significant in years 2000 and 2001 (Figure 2.4a, Lycaenidae Repeated Measures ANOVA year * treatment $F = 2.9$, $P < 0.10$ followed by repeated contrasts; Figure 2.4b, Pieridae Repeated Measures ANOVA year * treatment $F = 5.6$, $p < 0.10$ followed by repeated contrasts). These results suggest the community patterns observed above were driven entirely by the Lycaenids and Pierids.

Both the Nymphalidae and the Hesperiidae family abundances were dominated by one species each in at least one sampling year. Because of this, data were analyzed both with and without *Epargyreus clarus* (EPCL) from the Hesperiidae (Figure 2.4c), and with and without *Vanessa cardui* (VACA) from the Nymphalidae (Figure 2.4d). However, both analyses in each family group showed no significant year * treatment effects in the Nymphalidae or Hesperiidae (Figure 2.4c, Hesperiidae Repeated Measures ANOVA year * treatment F = 1.5, p > 0.1; Figure 2.4d, Nymphalidae Repeated Measures ANOVA year * treatment F = 2.0, p > 0.1). The figures 2.4c and 2.4d suggest that both species showed highest abundances in treated forests in their respective "boom" years, but this was not supported statistically.

**Species Composition:** While common species were observed in both control and restoration treatment units, less common species (such as *Copaeodes aurantiaca*) when seen were in restoration treatments (Table 2.2). The restoration treatment supported a more diverse butterfly community than the control forests.

As shown in Table 2.2, *Vanessa cardui* was the most common individual species observed, and was observed 3 times as frequently in treatment units as in control units. This species was rarely seen prior to 2001, but extremely high migration rates made this the most common species observed. Total Lycaenids ranked first in the treatment units, but were the 6th most observed taxon in control units. Lycaenidae species were often difficult to identify during transect observations. As a result, a total for the family was recorded, with the identified species and their corresponding tallies sub-listed immediately following in Table 2.2. *Pieris* species (whites) were highly abundant in the area, but observed 3 times as frequently in treated areas following treatment. In 1998, *Limenitis bredowii* was found in higher abundances in control forests (Waltz and Covington 1999). This pattern did not remain consistent in 2000 and 2001, partly due to extremely low numbers of this butterfly, which made distribution patterns difficult to determine in the experimental block design.

**Mechanisms of Adult Butterfly Distribution**

We next examined potential mechanisms for increased butterfly species richness and abundance in treated forests by asking three questions. 1. Did host plant availability differ between restored and treated plots? Pre-treatment data from the monitoring plots showed that blocks had similar abundances within the 5 plant families most commonly utilized by butterfly larvae (Table 2.3, MANOVA treatment $F = 5.9$, $p > 0.1$). One and two years following treatment, total family abundances continued to show no differences between treatments (Table 2.3, 2000 MANOVA treatment $F = 12.3$, 2001 MANOVA treatment $F = 2.4$; all p's $> 0.1$). The only plant family with trends towards differences between restoration treatments and control forest was the Chenopodiaceae (not shown in Table 2.3). This family contained several native and non-native annuals, such as lambsquarters (*Chenopodium album*), which was ubiquitous in the seed bank (Springer 1999). This species was not utilized by any of the common butterflies found in the study area.

Tree species composition was highly variable among the 5 blocks, and showed no significant differences between control and treatment units prior to restoration. Following restoration, *Quercus gambelii* (QUGA) appeared to be reduced in restoration treatments (Table 2.3). However, neither *Q. gambelii* nor *Robinia neomexicana* (RONE) showed significant differences, although this was likely due to the high variability found between experimental blocks (Waltz et al. 2001).

The second mechanistic question addressed was 2. Did nectar resource availability differ between restored and control units? When flowering plants were specifically examined in experimental blocks, flowering species richness and abundance showed no differences 1 or 2 years following treatment (Figure 2.5a, species richness Repeated Measures, treatment * year $F = 1.424$, $p > 0.1$, Figure 2.5b, species abundance Repeated Measures, treatment * year $F = 0.414$, $p > 0.1$). Although mean flowering plant richness and abundances were higher in the treated areas, there was high variance in both the treatment and control units, and much variation between treatment years. This reflected the patchiness of understory growth in the control and understory recovery in the treated areas. Two years following treatment showed similar patterns, with overall higher flowering species richness than in 2000, likely due to changes in yearly precipitation.

These results support other studies showing that the responses of vegetation to restoration in arid ecosystems are typically slow (Aronson et al. 1993). Interestingly, even though the host plant and nectar resource data did not show increases following restoration treatments, the first and second post-treatment year butterfly species richness increased dramatically following restoration treatment. Regardless of host plant and nectar resource availability, butterflies were observed in higher abundances in treatment units as quickly as one year following restoration treatments.

The final mechanistic question asked 3. How did insolation differ between restoration treatment units and control units? Insolation showed no differences prior to restoration treatments, but was significantly higher in restoration treatment units than control units with no significant treatment * time class interaction (Figure 2.6, 2-way

ANOVA treatment $F = 26.7, p < 0.10$). Directly related to canopy cover, this measurement reflects the increased solar radiation due to canopy removal.

## DISCUSSION

While ecosystem restoration monitoring often overlooks invertebrates as important contributors to ecosystem function and process, we suggest invertebrate monitoring provides broader analyses of ecosystem response to restoration treatments. Butterflies have been shown as important herbivores and prey species in ecosystem trophic interactions (Scoble 1992). For example, lepidopteran larvae comprised 73% of the Blue tit nestling diet (Cowie and Hinsley 1988). Adult butterflies contribute directly to pollination; however, the Hymenoptera, Diptera and Coleoptera surpass their effectiveness in pollination events.

These results showed that butterflies responded quickly to ecological changes, and would be useful in ecosystem monitoring schemes. We showed that the butterfly community had up to 2 times higher species richness and 3 - 5 times higher abundance in restoration treatments when compared with paired control forests. We also found that low abundance species were censused more often in restoration treatment units than in control units. The fast response of the butterfly assemblage to these thinning and burning treatments (within one season after treatment) suggest multiple mechanisms operating at different scales were affecting adult butterfly distribution.

**Hypotheses tests:** These results showed an immediate increase in butterfly richness and abundance one year following restoration treatments and therefore **do not support** the first hypothesis that butterfly species richness and abundance would initially decline due to logging and burning treatments. The majority of the butterfly species responded positively to the restoration treatment. This differs from other studies showing negative lepidopteran response to logging and fragmentation (Hill et al. 1995, Spitzer et al. 1997). However, in these ponderosa pine restoration treatments, the intent of logging was not to extract resources but instead to thin current stands to resemble the forests prior to Euro-American settlement. The butterfly assemblage is native, and in all likelihood evolved in more open forests. In this context, it is not surprising that butterfly species richness and abundance increase following thinning and burning treatments. Similarly, other systems have shown lower butterfly richness with higher overstory canopy and denser stands, associated with decreasing understory species richness (Sparks et al. 1996). The habitat disruption and change in ponderosa pine forests that potentially adversely affected these butterfly species happened 80 – 120 years ago, when grazing eliminated the understory, fires were halted, and ponderosa pine trees irrupted. Ponderosa pine forests today show much lower herbaceous diversity and abundance than historical and undisturbed forests. The thinning represented in this study resulted in increased biodiversity and production in understory primary producers, with corresponding increases in common herbivores.

Examination of butterfly assemblage results (Table 2.2) **does not support** the second hypothesis that generalists will dominate the early successional butterfly assemblage. In fact, no new generalist species were observed following restoration treatments. Generalist species *Vanessa cardui*, *Colias eurytheme* and *Pieris* sp. were the three of the four most abundant species in control forests. However, in the treated units, these species were out-numbered by lycaenid species, which have much higher host plant fidelity. For example, *Plebejus icariodes* and *Glaucopsyche lygdamus* were two of the most common butterflies in treatment units and at this site their larvae were most likely feeding on *Lupinus argenteus*.

**Potential Mechanisms**

Host plant availability, nectar resources and abiotic variables all have the ability to affect adult butterfly distribution. In this study, the plant community showed no significant differences between restoration treatments and controls two years following treatment. We know that sustainable butterfly habitat must include sufficient larval and adult food resources (Pollard 1991), but our sampling and analyses did not find significant changes in potential host plant abundances. However, 12 of the 27 butterfly species found in treatment units were local species, with limited adult dispersal (Scott 1984), suggesting host plants were found locally.

We further suggest butterflies may indicate patchy changes in plant abundances, which are notably difficult to measure with standardized sampling. Evidence for this includes a study by Erhardt and Thomas (1991), which documented butterfly responses to plant successional changes. They showed butterfly community changes, probably due to plant stress, even before plant community changes could be detected. Steffan-Dewenter and Tscharntke (1997) also observed butterfly community composition changes tracked four years of agricultural field succession in Germany. However, these studies did not link the changes in butterfly abundances directly to plant stress or fitness changes. But with appropriate mechanistic studies, butterfly communities may be very useful indicators of vegetative state following a disturbance or a restoration treatment.

Nectar resources are important in determining adult butterfly oviposition selections; studies show host plants are utilized only when sufficient adult resources (nectar) are also available (Murphy 1983, Grossmueller and Lederhouse 1987). While nectar resource is undeniably an important component for adult butterfly distributions, our early post-treatment data suggest it is not the main contributing factor in our study. Butterflies were very fast to respond to habitat changes, and showed increases in the restoration treatment units one year following treatment; however, the nectar resources did not differ significantly between restoration treatment units and control units even two years post-treatment.

The only mechanism of adult butterfly distribution we measured that showed significant differences between restoration treatment units and control units was insolation, which increased significantly in treatments as soon as the canopy was thinned. Solar radiation has been shown to determine butterfly minimum and maximum flight conditions (Douwes 1976), as well as flight duration (Shreve 1984). Time to flight in the morning, and duration of flight during the day can have implications for butterfly dispersal, life span and reproductive success (Tsuji 1986). Our data showed that although host plant and flowering plant resources did not differ between control and restoration treatment units, more butterflies were found in areas with the highest light intensity.

### Implications

The response of butterfly communities suggests other arthropod herbivores may respond to restoration treatments in similar ways. Arthropods utilizing light intensity may show increased activity in restoration treatments. Bees and other nectar or pollen feeding arthropods may show increases in diversity and abundances as a response to increased nectar resources, and therefore may parallel the responses of the butterfly community. The importance of pollinators to ecosystem functioning has recently become the focus of conservation groups and researchers due to the decreasing abundance of native bees (Buchmann and Nabhan 1996, Kevan 1999). Although butterflies are not as efficient at pollination as the Hymenoptera (bees and wasps) or Diptera (flies) (Scoble 1992), they are easier to monitor and identify. Using these restoration experiments, the efficacy of butterflies as indicators of other pollinators can be easily tested, by increased sampling of other taxonomic groups, correlations, and finally testing in other areas undergoing restoration treatments.

### Problems/ Confounding factors

This study discussed species compositional differences in general, however, no statistical tests were designed or conducted on individual species responses. A valid concern remains that not all species will respond positively to restoration treatments. While it appears ponderosa pine restoration has entirely positive effects on butterfly communities, burning can also have negative affects on butterflies by damaging larval or pupal stages (Pickering 1997). Several studies support the concept that burning at the natural intensity and at the natural season in a system that has evolved with fire will not be harmful to the native organisms (Collett 1998, Panzer & Schwartz 2000). An acknowledged concern with ponderosa pine forest restoration projects is that current fuel loadings do not resemble historic or reference site fuel loadings, and therefore the burning cannot take place in the "natural season". Instead of fires in the mid-summer drought that periodically burned through ponderosa pine forests prior to Euro-American settlement, initial burns following restoration thinning are usually started under cooler prescriptions. For example, these fires either follow fall rains, when air temperatures are low, or take place in the spring, after the snow melts. At these times, insects are in dormant life stages and are more susceptible to mortality by burning.

Comparisons with reference old-growth stands is also necessary to understand the reference butterfly community composition and accurately address restoration goals. At Mt. Trumbull, Lycaenids ("blue" butterflies) are readily found in treated habitats, probably due to the abundances of their early successional host plants (legumes) and available nectar. However, butterfly larvae utilizing grasses as hosts (e.g. *Cercyonis* sp.) are uncommon at the Mt. Trumbull site. These species were very common at nearby "reference" sites that still maintained frequent fire regimes and subsequently a grass-dominated understory (Waltz, unpublished data). The return of *Cercyonis* sp. to the Trumbull restoration treatments may indicate a shift from early successional legumes and other forbs to a grass dominated understory.

### Future Studies

To successfully examine butterfly population responses to restoration treatments, reproductive success and host plant usage should also be documented. Our current design monitors only adult butterfly populations. While some studies have shown positive correlations between adult butterfly densities and larval densities (Steffan-Dewenter and Tscharntke 1997), knowledge of larval fitness would be imperative to determine habitat quality. Of all 37 species recorded in the Mt. Trumbull experimental blocks, 20 were classified as locally distributed, and not found far from their host plants as adults. The other 19 were classified as migratory, although their migratory distances range from one kilometer (*Leptotes marina*) to thousands of kilometers (*Danaus plexippus*). While migratory adults are moving to sites with suitable host plants, they can easily be surveyed in areas that are not suitable for maintaining their larval population.

The research presented here provides insight into how a butterfly assemblage responded to habitat change, and some of the mechanisms behind that response. Not only do butterfly communities contribute to ecosystem functioning through herbivory, pollination and energy transfer, they also have the potential to be bioindicators of biodiversity in other arthropod guilds.

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Table 2.1: Butterfly species observed at Mt. Trumbull Resource Conservation Area, 1997- 2001.

| SpeciesCode | Family | Genus species | Host Plant Family | Total Observations |
|---|---|---|---|---|
| COAU | Hesperiidae | *Copaeodes aurantiaca* | Poaceae | 2 |
| EPCL | Hesperiidae | *Epargyreus clarus* | Fabaceae | 219 |
| ERTE | Hesperiidae | *Erynnis telemachus* | Fagaceae | 41 |
| ERFU | Hesperiidae | *Erynnis zarucco* | Fabaceae | 7 |
| HEER | Hesperiidae | *Heliopetes ericetorum* | Malvaceae | 7 |
| PYCO | Hesperiidae | *Pyrgus communis* | Malvaceae | 9 |
| THPY | Hesperiidae | *Thorybes pylades* | Fabaceae | 50 |
| CEAR | Lycaenidae | *Celastrina argiolus* | Rhamnaceae, Rosaceae | 1 |
| GLLY | Lycaenidae | *Glaucopsyche lygdamus* | Fabaceae | 50 |
| HEIS | Lycaenidae | *Hemiargus isola* | Fabaceae | 10 |
| LEMA | Lycaenidae | *Leptotes marina* | Fabaceae | 22 |
| PLIC | Lycaenidae | *Plebejus icarioides* | Fabaceae | 102 |
| PLAC | Lycaenidae | *Plebejus acmon* | Polygonaceae | 54 |
| STME | Lycaenidae | *Strymon melinus* | Fabaceae, Malvaceae | 38 |
| CERCSP | Nymphalidae | *Cercyonis sp.* | Poaceae | 3 |
| CYPE | Nymphalidae | *Cyllopsis pertepida* | Poaceae | 1 |
| DAGI | Nymphalidae | *Danaus gilippus* | Asclepiaceae | 8 |
| DAPL | Nymphalidae | *Danaus plexippus* | Asclepiaceae | 5 |
| EUCH | Nymphalidae | *Euphydryas chalcedona* | Scrophulariacea | 5 |
| EUCL | Nymphalidae | *Euptoieta Claudia* | Violaceae, others | 10 |
| LIBR | Nymphalidae | *Limenitis bredowii* | Fagaceae | 49 |
| LIWE | Nymphalidae | *Limenitis weidemeyerii* | Rosaceae, Salicaceae | 58 |
| NYCA | Nymphalidae | *Nymphalis californica* | Rhamnaceae | 9 |
| NYAN | Nymphalidae | *Nymphalis antiopa* | Salicacea, Rosaceae | 11 |
| PHCA | Nymphalidae | *Phycoides campestris* | Asteraceae | 46 |
| POMI | Nymphalidae | *Poladryas minuta* | Schrophulariaceae | 1 |
| POGR | Nymphalidae | *Polygonia gracilis* | Grossulariaceae | 10 |
| PRCO | Nymphalidae | *Precis coenia* | Scrophulariaceae | 4 |
| VACARD | Nymphalidae | *Vanessa cardui* | Asteraceae | 251 |
| VACARY | Nymphalidae | *Vanessa carye* | Malvaceae | 2 |
| PAMU | Papilionidae | *Papilio multicaudata* | Rosaceae, others | 23 |
| ANSA | Pieridae | *Anthocharis sara* | Brassicaceae | 6 |
| COEU | Pieridae | *Colias eurytheme* | Fabaceae | 189 |
| NAIO | Pieridae | *Nathalis iole* | Asteraceae | 26 |
| PIPR | Pieridae | *Pieris protodice* | Brassicaceae | 2 |
| PISI | Pieridae | *Pieris sisymbrii* | Brassicaceae | 3 |
| ZECE | Pieridae | *Zerene cesonia* | Fabaceae | 2 |

Table 2.2. Butterfly species and total observations from most abundant to rarest found in restoration treatment units and control units. Tally is total observations from 6 surveys, across four experimental blocks from post-treatment years 2000 - 2001

| **Control** | | **Treatment** | |
|---|---|---|---|
| **Species** | **Tally** | **Species** | **Tally** |
| *Vanessa cardui* | 59 | *Lycaenidae** | 298 (116) |
| *Colias eurytheme* | 35 | *Plebejus icariodes* | 83 |
| *Epargyreus clarus* | 28 | *Glaucopsyche lygdamus* | 41 |
| *Pieris sp.* | 24 | *Strymon melinus* | 20 |
| *Limenitis weidemeyerii* | 18 | *Leptotes marina* | 17 |
| *Lycaenidae** | 17 (9) | *Plebejus acmon* | 15 |
| *Leptotes marina* | 3 | *Hemiargus isola* | 6 |
| *Strymon melinus* | 3 | *Vanessa cardui* | 162 |
| *Plebejus icarioides* | 1 | *Pieris sp.* | 100 |
| *Glaucopsyche lydgamus* | 1 | *Colias eurytheme* | 89 |
| *Limenitis bredowii* | 8 | *Epargyreus clarus* | 79 |
| *Papilio multicaudata* | 7 | *Nathalis iole* | 20 |
| *Erynnis telemachus* | 6 | *Erynnis telemachus* | 17 |
| *Polygonia gracilis* | 4 | *Limenitis weidemeyerii* | 14 |
| *Euptoieta Claudia* | 3 | *Phycoides campestris* | 13 |
| *Euphydryas chalcedona* | 3 | *Limenitis bredowii* | 10 |
| *Nathalis iole* | 3 | *Erynnis zarucco* | 5 |
| *Heliopetes ericetorum* | 2 | *Danaus plexippus* | 5 |
| *Nymphalis antiopa* | 2 | *Papilio multicaudata* | 4 |
| *Phycoides campestris* | 2 | *Euptoieta Claudia* | 4 |
| *Cyllopsis pertepida* | 1 | *Heliopetes ericetorum* | 4 |
| *Polydryas minuta* | 1 | *Nymphalis antiopa* | 3 |
| *Zerene cesonia* | 1 | *Pyrgus communis* | 2 |
| *Nymphalis californica* | 1 | *Copaeodes aurantiaca* | 2 |
| | | *Thorybes pylades* | 2 |
| | | *Precis coenia* | 2 |
| | | *Zerene cesonia* | 1 |
| | | *Polygonia gracilis* | 1 |

*Large numbers of Lyaceanidae (blues) were difficult to identify to species. Lycaenidae number is total (unidentified in parenthesis), with individual species contributions listed below. Often, when 6 or more blues were observed, species were determined for 2 – 5, and the others were lumped as Lycaenidae.

Table 2.3. Understory (herbaceous) average abundance/ transect (standard error) by treatment (5 families most commonly used as butterfly host plants) from pre-treatment year 1998 and post-treatment years 2000 and 2001. Pre-treatment (1998) MANOVA $F = 5.9$, $p > 0.10$; Post-treatment 1 (2001) MANOVA $F = 12.3$, $p > 0.10$; Post-treatment 2 (2001) MANOVA $F = 2.4$, $p > 0.10$. Trees per hectare from Waltz et al. 2001; QUGA = *Quercus gambelii*, Gambel's oak; RONE = *Robinia neomexicana*, New Mexico locust. Tree composition was highly variable among the 4 experimental blocks and susceptible to low sample size effects. *Q. gambelii* and *R. neomexicana* showed no significant differences between treatment and control units following restoration.

| | | Herbaceous Families | | | | | Tree species | |
|---|---|---|---|---|---|---|---|---|
| **Year** | **Trt** | **Fabaceae** | **Brassicacea** | **Poaceae** | **Scrophulariacea** | **Asteraceae** | **QUGA** | **RONE** |
| 1998 | Con | 0.64 (0.475) | 0 | 3.34 (1.025) | 0.26 (0.107) | 0.15 (0.054) | 283.9 (137.40) | 45.5 (15.95) |
| | Trt | 3.13 (2.601) | 0.03 (0.014) | 8.94 (7.575) | 0.98 (0.316) | 0.39 (0.288) | 268.0 (108.91) | 286.6 (219.7) |
| 2000 | Con | 0.83 (0.759) | 0.03 (0.025) | 2.5 (1.392) | 0.24 (0.052) | 0.13 (0.052) | 253.5 (121.10) | 38.5 (15.04) |
| | Trt | 3.36 (2.991) | 0.01 (0.013) | 7.11 (6.006) | 0.74 (0.357) | 0.19 (0.171) | 94.5 (67.27) | 61.0 (54.22) |
| 2001 | Con | 1.03 (0.944) | 0.04 (0.038) | 1.99 (1.199) | 1.08 (0.536) | 0.04 (0.038) | n/a | n/a |
| | Trt | 2.76 (2.487) | 0.04 (0.038) | 9.43 (7.560) | 2.44 (0.842) | 0.20 (0.079) | n/a | n/a |

## FIGURE CAPTIONS

Figure 2.1. Map of Mt. Trumbull Resource Conservation Area within the Grand Canyon –Parashant National Monument. Experimental blocks (EB's) were systematically placed throughout the unit to represent the forest types characteristic of the Mt. Trumbull RCA. Treatment and control units were randomly assigned in all blocks. Experiment block 3 (EB3) lost the control unit to wildfire in spring of 2000; EB3 Control – 2000 was established May 2000. Block 5 was dropped from the experiment in 1999 because the thinning treatments fell behind and it could not be treated in the same time-frame as the other blocks.

Figure 2.2. Map of Experimental Block 1, detailing monitoring sampling grid, butterfly transects, nectar resource plots and light intensity measurement plots. Monitoring plots consisted of 20 plots per treatment unit and were placed on a 60 meter grid, centered in the treatment units. Butterfly transects ran along plot grids, a total of 900 meters per treatment unit. Nectar resource plots were 2 m X 0.5 m sampling rectangles located every 20 meters along the butterfly transects, for a total of 45 plots per treatment unit. Light intensity dataloggers were placed at random plots in each experimental block, all other sampling designs were identical in each experimental block.

Figure 2.3a. Butterfly species richness showed no differences between treatment and control units prior to treatment (1998 and 1999), but showed higher richness in treatment units following thinning and burning (repeated measures ANOVA, year * trt $F = 4.42$, $p < 0.1$). Figure 2.2b. Butterfly species abundance was highly variable, but showed no significant differences prior to treatment, and significantly greater abundances in the treatment following thinning and burning (repeated measures ANOVA, year * trt F = 7.28, $p < 0.1$ ).

Figure 2.4. Family responses to restoration treatment. a. Lycaenidae showed significant increases in treatment units following restoration. b. Pieridae showed significant increases in restoration units in 2001, two years following treatments. c. Hesperiidae showed no changes to restoration treatments. Family abundances with and without the dominant species, *Epargyreus clarus* are shown. d. Nymphalidae also showed no changes to restoration treatments. Family abundances with and without the dominant species in 2001, *Vanessa carye* are shown.

Figure 2.5a. Flowering plant species richness per 1-$m^2$ plot showed no difference 1-year and 2-year post treatment (Repeated Measures ANOVA, treatment * year F = 1.424, $p > 0.1$). Figure 2.5b. Flowering plant abundance showed no difference 1-year and 2-year post treatment (Repeated Measures ANOVA, treatment * year F = 0.414, $p > 0.1$)..

Figure 2.6. Insolation, log (lumens)/ $m^2$ was significantly higher in treated units following restoration treatment. Two-way ANOVA treatment F = 26.7, $p < 0.10$. Morning = 8am – 10:59am; Midday = 11am – 3:59pm; Afternoon = 4pm – 5:59pm.

Figure 2.1.

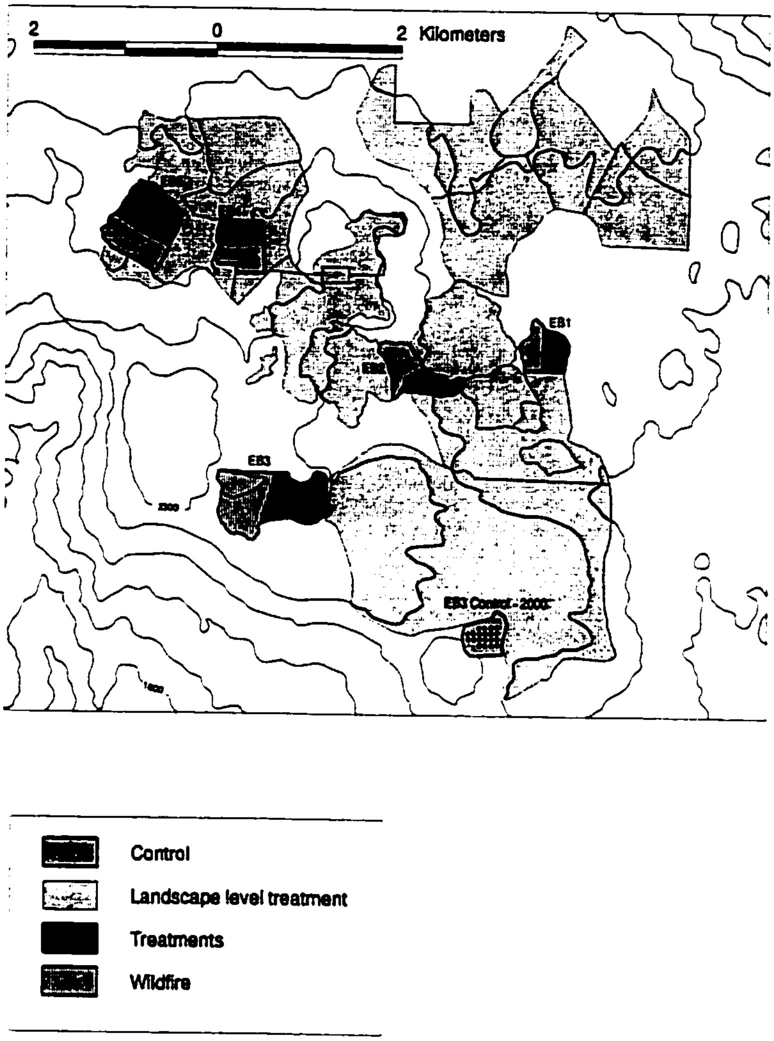
2 0 2 Kilometers
EB1
EB2
EB3
EB3 Control - 2000
Control
Landscape level treatment
Treatments
Wildfire

Figure 2.2

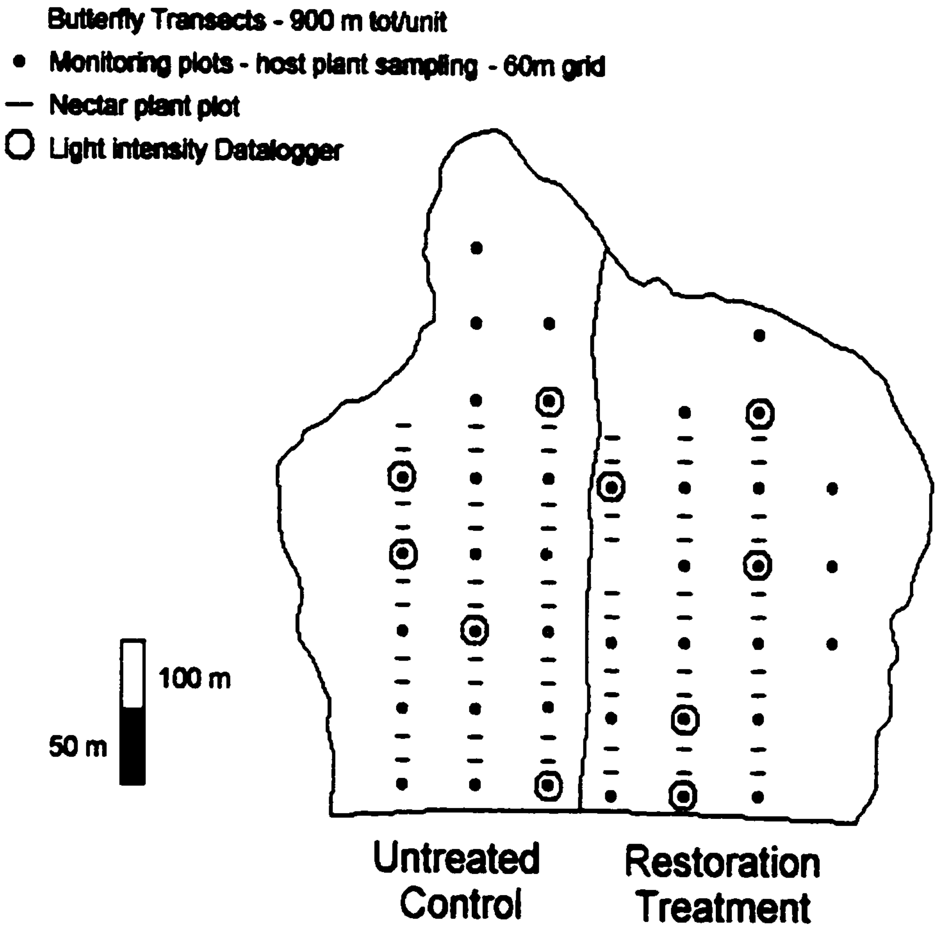

Figure 2

Figure 2.3a

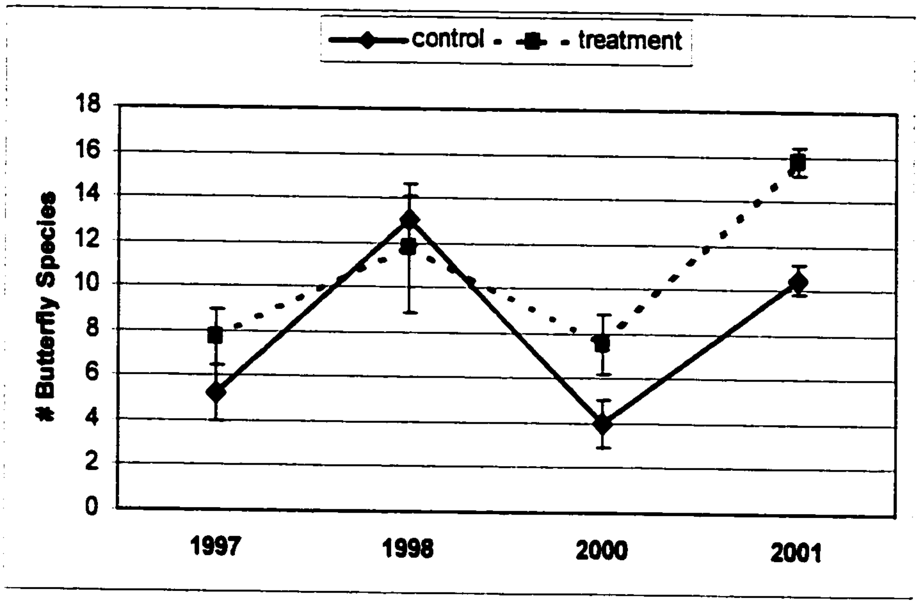

Figure 2.3b

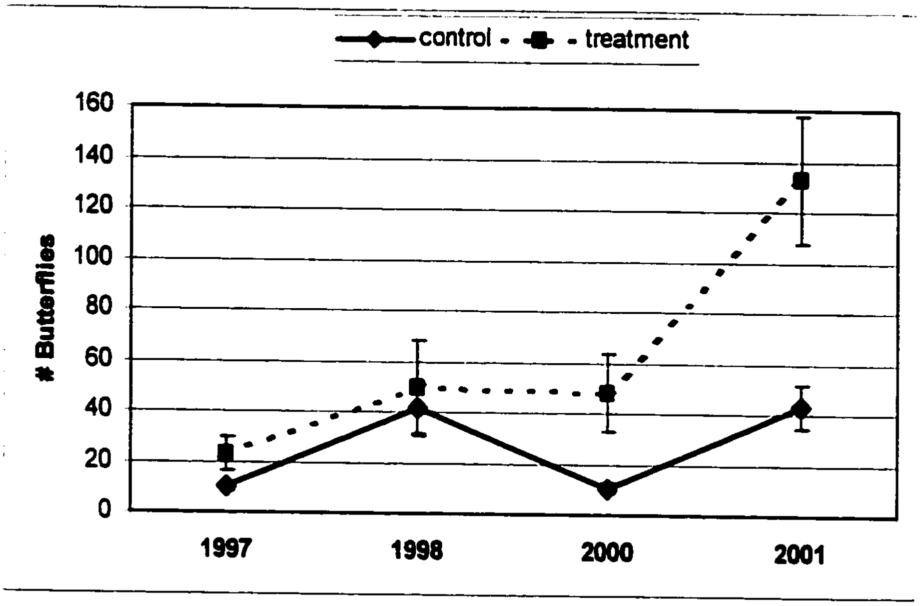

Figure 2.4A -D

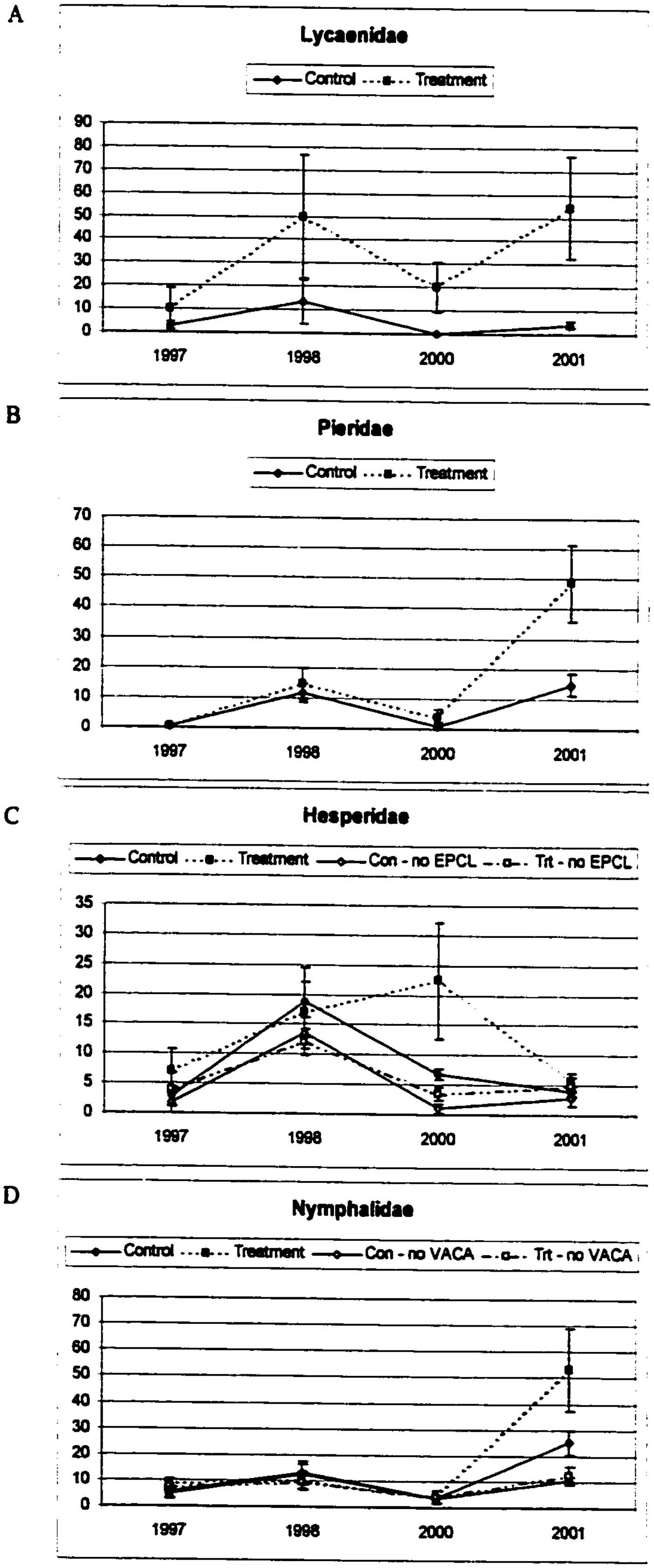
A
Lycaenidae
Control
Treatment
90
80
70
60
50
40
30
20
10
0
1997
1998
2000
2001
B
Pieridae
Control
Treatment
70
60
50
40
30
20
10
0
1997
1998
2000
2001
C
Hesperidae
Control
Treatment
Con - no EPCL
Trt - no EPCL
35
30
25
20
15
10
5
0
1997
1998
2000
2001
D
Nymphalidae
Control
Treatment
Con - no VACA
Trt - no VACA
80
70
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Figure 2.5A.

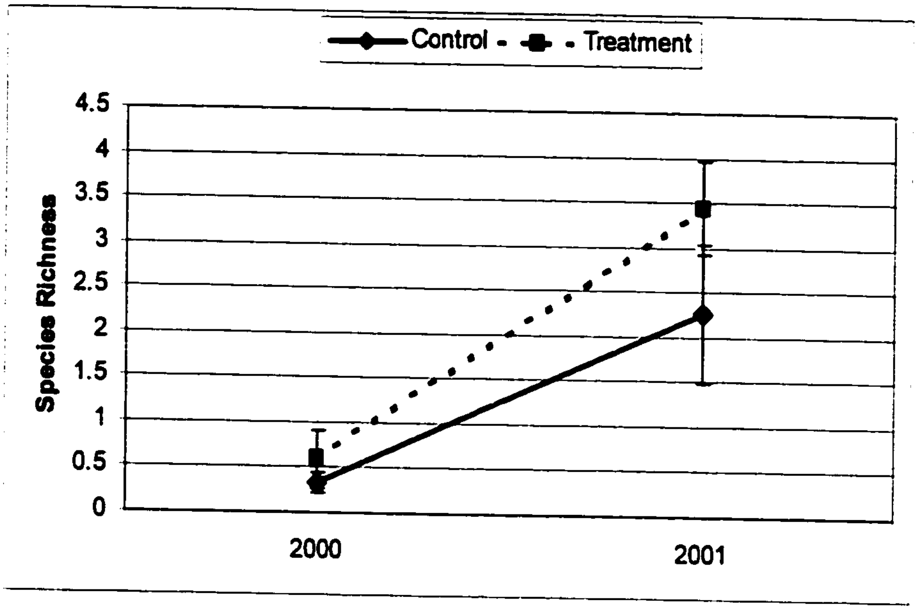


Figure 2.5B.

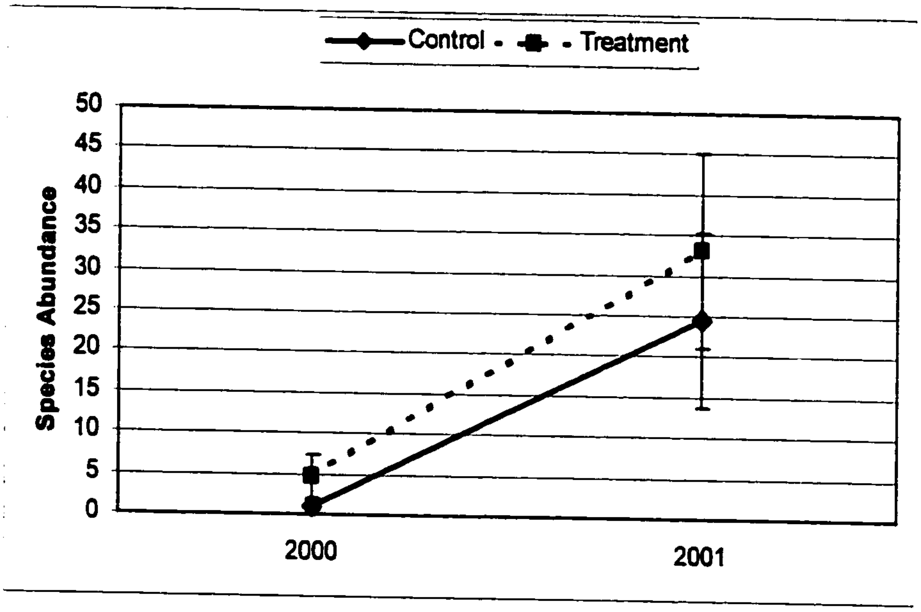
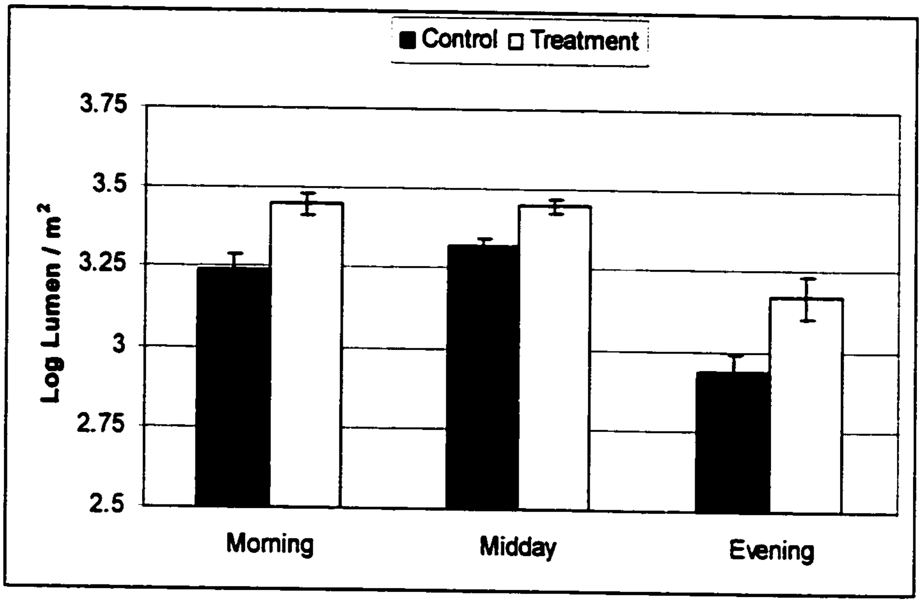


Figure 2.6.


■ Control □ Treatment
Log Lumen / m²
3.75
3.5
3.25
3
2.75
2.5
Morning
Midday
Evening

# Chapter 3: Response of *Epargyreus clarus* Cramer to Ecological Restoration Treatments: Testing Predictions of Larval Habitat Preference

## Abstract

Larval distributions were assessed to predict the responses of invertebrates to land management changes. Public land managers are increasingly incorporating terrestrial restoration treatments to improve the sustainability of landscapes. However, a valid critique of these techniques is that not enough experimental data exists to understand individual species responses to these restoration treatment methods. In particular, invertebrate habitat use is the most difficult to determine because adult distributions, while often the most easily censused, may not be indicative of larval habitat needs. We examined larval distribution of a butterfly, *Epargyreus clarus* Cramer, in ponderosa pine forests and on its host plant, New Mexico locust (*Robinia neomexicana* Gray), to develop response predictions to ponderosa pine restoration treatments. *E. clarus* larvae were found in highest abundances on juvenile host plants and were significantly higher on host plants located in sunny patches. Resprout vegetation was not used as extensively by larvae as nearby, non-resprout vegetation.

From these data, we predicted an increase in *E. clarus* larvae following overstory thinning and prescribed fire, part of an on-going restoration treatment in Southwest ponderosa pine forests. Because Lepidoptera adult densities are known to correlate with larval densities, we predicted increases in adult *E. clarus* in restoration treatments as well. Following restoration treatments, larval densities were 4 times higher in restored than in control forests. However, no significant differences were observed in adult *E. clarus*. Adult and larval abundances did not show significant correlations. We concluded that larval populations respond positively to restoration treatments mediated through host plant characteristics. Conversely, *E. clarus* adults do not distinguish between treatment units and control units but can remain opportunistic because of their more general food requirements.

Keywords: *Epargyreus clarus*, habitat restoration, New Mexico locust, ponderosa pine, *Robinia neomexicana*, silver-spotted skipper

## Introduction

Predicting faunal responses to land management changes is difficult even when habitat use and requirements are well understood. However, the existing knowledge of invertebrate habitat use is limited at best, even though invertebrates have been cited as contributing up to 93% of the faunal biomass in some terrestrial ecosystems (Wilson 1987). Without the successful adaptation of the invertebrate community to ecosystem disturbance and structural changes associated with land management options, processes as critical as decomposition and pollination can come to a standstill (Didham et al. 1996, Longcore et al. 2000).

In particular, invertebrate responses to ecosystem restoration are seldom studied, although it is the invertebrates that are the main contributors to the success of a restoration treatment (Parmenter et al. 1991, Majer 1989, 1997, Reay & Norton 1999). Restoration of ecosystems is an emerging land management option on our public lands readily acknowledged as an extension of conservation work (Young 2000, Clout 2001). The restoration of disturbed or fragmented land provides a valuable contribution to increasing sustainability, maintaining biodiversity, buffering existing wilderness areas and reducing the effects of fragmentation (Dobson et al. 1997, Jordan III et al. 1987, Young 2000, Clout 2001). But a valid concern and criticism of ecosystem-level restoration projects is the lack of knowledge about faunal species responses to large-scale restoration efforts (Majer 1989, Holl 1996, Parmenter et al. 1991, Block 2001).

For example, restoration of ponderosa pine systems in the U.S. Southwest is supported politically because the degraded, dense stands of ponderosa pine are highly susceptible to dangerous and costly high intensity fires. These stands are restored to forest structure at the time of disturbance (Euro-American settlement) by thinning the overstory, and reintroducing fire to the system. As a result, ponderosa pine forest restoration treatments are currently proposed over much of the Southwest, even though researchers state that little is known about faunal responses to burning and thinning treatments associated with ponderosa pine restoration (Block et al. 2001, Germaine 2001).

By examining current habitat requirements of invertebrates we can hypothesize the responses to restoration treatments and other land management changes. The Lepidoptera are a well-studied invertebrate order, but little work has been done to show their responses to ecosystem level restoration (Holl 1996, Majer 1997). Several factors known to influence the distribution of the Lepidoptera include larval host plant distribution, nectar and pollen resources, and abiotic characteristics (Gilbert & Singer 1973, Grossmueller & Lederhouse 1987, Weiss et al. 1988, Scoble 1992, Holl 1995, Waltz in prep). Restoration of ponderosa pine forests has been shown to increase the understory herbaceous diversity and production (Covington et al. 1997). In addition, restoration treatments can initially increase exotic plant densities (Springer et al. 2001).

Environmental changes on this order will shift the invertebrate community according to their specific habitat needs (Majer 1989).

Current studies of the Lepidoptera typically sample only adults, as larval populations are difficult to locate and sample. Surveying adult butterflies may indicate the presence of the species, but not the specific habitat utilized by all developmental stages (Gilbert and Singer 1973 but see Steffan-Dewenter & Tscharntke 1997). In fact, adult food resources can be discreet patches isolated from larval host plant patches (Gilbert and Singer 1973, Grossmueller and Lederhouse 1987, Brommer & Fred 1999). We examined the distribution of butterfly larvae and adults in unrestored forests to make testable predictions about the response of this butterfly to restoration treatments.

The response of *Epargyreus clarus* Cramer to ecosystem restoration treatments was predicted and then tested. We assessed larval distributions in stands of ponderosa pine prior to restoration treatments. We examined how larvae were distributed on its preferred host plant, New Mexico locust (*Robinia neomexicana* Gray) by asking 1. Do sun and shade affect larval densities? 2. Do mature and juvenile foliage affect larval densities, and finally, 3. Are larvae distributed differently on non-resprout than on resprout following fire? **From these results, we predicted higher larval and adult abundances in restored units.** We then assessed larval distributions and accompanying host plant characteristics in restoration treatment units and adjacent paired control units to test our prediction. In addition, we sampled adult butterflies to see if adult distributions could be predicted from larval distribution patterns.

## Methods

**Study site:** This study was conducted in a ponderosa pine (*Pinus ponderosa* Lawson & Lawson) and Gambel oak (*Querqus gambelii* Nutt.) forest located between Mt. Logan and Mt. Trumbull, about 35 kilometers north of the Grand Canyon on the Arizona Strip. Mt. Logan, Mt. Trumbull and the surrounding highlands form a sky island of ponderosa pine, with desert grassland to the north and the Grand Canyon to the south. The elevation of the sky island ranges from 1675 m to 2620 m and the area receives an average of 40 - 45 cm of rainfall.

The forest was predominately ponderosa pine, although Gambel oak represented 15% of the overstory. New Mexico locust (*Robinia neomexicana* Gray) comprised about 3% of the total trees, but could represent as much as 10% in some areas. Other tree species in the area included aspen (*Populus tremuloides* Michx.), pinyon (*Pinus edulis* Englem.) and juniper (*Juniperus osteosperma* Little). The herbaceous component was dominated by sagebrush (*Artemesia tridentata* Nutt.), and showed evidence of invasion by non-native species, such as cheat grass (*Bromus tectorum* Linneas), and some of the wheatgrasses (*Agropyron spp.*).

**Land management changes and ecological restoration treatment:** The Bureau of Land Management manages the Mt. Trumbull area. In collaboration with Northern Arizona University's Ecological Restoration Institute and the Arizona Game and Fish Department, the BLM targeted approximately 1,450 hectares of the 5,000-hectare forest for ponderosa pine restoration treatment in 1995. The initial ponderosa pine restoration treatment significantly reduced tree density and canopy cover and reintroduced a low intensity surface fire. These treatments were shown to increase herbaceous production

(Covington et al. 1997) and herbaceous diversity (Waltz and Fulé 1998). The restoration treatments were based on Covington et al.'s (1997) restoration methods at the Gus Pearson Natural Area, near Flagstaff, AZ. Trees were thinned to densities resembling those at the time of fire exclusion, which was approximately 1870 at this site. Fire was used preliminary to help reduce slash, but is planned to be returned to the landscape every 4-7 years, dependent on weather conditions.

**Study Species:** *Epargyreus clarus* Cramer (the silver-spotted skipper) is a widespread butterfly, commonly found from southern Canada to Central America (Scott 1986). In the U.S. Southwest, the larvae host on a common shrub/tree, New Mexico locust (*Robinia neomexicana* Gray), and are readily identified. Adults were often found sipping nectar on the host plant, or patrolling for mates around host plant clumps. Eggs are laid on the upper side of host leaves (Scott 1986). Larvae are green, with a brownish-black head marked by distinct, symmetrical orange eyespots (Ferris and Brown 1981). Early instar larvae create a distinctive leaf cut/fold, and late instars tie leaves together and are easily monitored on the host plant (Scott 1986 and personal observation).

New Mexico locust occurred in shrub to tree-like stature in open areas of current stands of ponderosa pine forests. It flowered from late May through June, and adult *E. clarus* were observed sipping nectar from these flowers. With the reintroduction of fire following ponderosa pine thinning, this locust resprouted readily, and may maintain a more shrub-like architecture with frequent fire. Fire adaptions of this host plant include seed dormancy and resprouting, but above-ground living stems do not have much resistance to fire (Gottfried 1980, Boring & Swank 1984).

**Larval censusing**: To predict responses to restoration, *E. clarus* larvae, leaf cuts ($1^{st}$ and $2^{nd}$ instars) and leaf ties ($3^{rd}$ and $4^{th}$ instars) were sampled in 1999 and 2000 prior to any treatment on a set of paired 60 host plants found in sun or shade (30 each). In 1999, 30 juvenile locust plants paired with 30 mature locust plants were surveyed for *E. clarus* larvae. Mature locust growth was determined by the presence of flowers. Sampling of juvenile and mature growth was completed after larvae had pupated, therefore, only evidence of the larvae in the form of distinctive leaf ties ($3^{rd}$ and $4^{th}$ instars) were sampled on the trees. Although one larva can create more than one leaf-tie, the number of ties is equivalent to larval use and duration of stay, and was comparable to address these questions. We sampled from at least 6 different New Mexico locust clumps to avoid site-specific patterns. Larvae, leaf cut and leaf tie densities were counted on a per shoot basis, standardized to abundance per 20 shoots, and analyzed with a paired-t test at an alpha level of 0.05 to denote significance.

In addition, in 2000, larval distributions on locust resprouts were assessed in an unplanned wildfire site. Larval densities were observed on 30 resprout plants paired with 30 non-resprout plants. Resprout and non-resprout locust pairs were within 10 meters. The pairing was done to limit adult dispersal differences, however, it also limited resprout examination to plants on the edge of high intensity burn patches. Larval densities were analyzed with a paired t-test for differences with an alpha $< 0.05$ to denote significance.

Predictions were determined based on significant distribution patterns observed from these data. These predictions were tested in 2001 by surveying existing experimental blocks of paired restoration treatment and control units. The experimental blocks were established in 1997 with randomly assigned treatment and control units, and were thinned and burned in 1999. Both *E. clarus* larval and adult responses to restoration were assessed. New Mexico locust host plants were chosen along a systematic 900m transect within each treatment and control unit of each block. Every 20 meters along this transect, the nearest New Mexico locust was surveyed, for a maximum total of 45 plants per treatment unit per block. Points with no locust were skipped. Twenty shoots from each host plant were sampled for *E. clarus* larvae, empty leaf folds (1st – 2nd instars) and empty leaf ties (3rd - 4th instars). Numbers of larvae, leaf cuts and leaf ties were averaged for each treatment unit and block to avoid pseudoreplication, and then analyzed across blocks with Wilcoxin-signed rank test. These data were not normally distributed and better fit the assumptions of a non-parametric test. An alpha of 0.10 was used to determine significant differences, as sample sizes for this comparison were small ($n = 4$ blocks).

At each *E. clarus* larval survey point, we also assessed host plant canopy cover class. Each New Mexico locust was classified to one of 5 canopy cover classes: 1. < 10% cover, open; 2. 10 - 35% cover; 3. 35% - 65% cover; 4. 65% - 90% cover; and 5. >90% cover, full cover. Average cover per treatment unit was analyzed with a paired t-test using an alpha of 0.10 to denote significance.

**Adult butterfly censusing:** Adult *E. clarus* were sampled along the same, systematic 900 meter transect in the experimental blocks as the 2001 larval survey method. Adults were surveyed using a modified transect method (Pollard 1977) from May to August in 2000 and 2001 following restoration treatments. For these data, total adult butterfly abundance in control and treated units was assessed, regardless of host plant distributions. Data were analyzed across the two years with repeated measures ANOVA. Adult butterfly abundance in 2001 was correlated with larval densities from the same sampling block to address if adult distributions were indicative of larval distributions.

## Results

*E. clarus* larvae were highly abundant in 1999 and 2000, when pre-treatment habitat preference data were collected. In 2000, the species experienced a boom, with the highest adult abundances observed in a 4–year period. This year was a severe drought year, with notable declines in several other species in the butterfly assemblage at this site. These combined factors made *E. clarus* the most abundant butterfly observed in 2000. In 2001, *E. clarus* suffered a "bust" in population numbers, with the lowest adult abundances observed since 1998. The predictions developed in the "boom" years were tested in the "bust" year, and although the larval development seemed much later in the year than in previous years, the overall larval abundances per 20 shoots surprisingly remained similar.

**Larval Distributions:** In 1999, New Mexico locust host plants in the sun had 160 % significantly higher *E. clarus* larvae than on nearby host plants that were shaded (Figure 3.1, paired $t = 4.65$, $p < 0.05$). The dominant overstory species shading the New Mexico locust was ponderosa pine (*Pinus ponderosa*). Evidence of *E. clarus* in the form of empty leaf-ties, and leaf folds, was also found in higher abundances on host plants in full sun.

Juvenile, non-flowering host plants supported significantly higher numbers of *E. clarus* leaf ties than mature host plants did (Figure 3.2, leaf-tie abundance, paired t =

23.8, $p < 0.05$). Although *E. clarus* adults were often observed sipping nectar on mature New Mexico locust plants, these mature plants supported only 1/3 the number of leaf ties found on juvenile plants.

Finally, *E. clarus* larvae were more than twice as abundant on non-resprout foliage than on nearby resprout foliage (Figure 3.3, paired $t = 2.62$, $p < 0.05$). Resprouted shoots from New Mexico locust had larger leaves than non-resprout tissue, and may make resprouted shoots more difficult to tie together.

**Predicted response to restoration:** From these results, we predicted the response of *E. clarus* to restoration treatments. We predicted that *E. clarus* would show higher abundances in restoration treatments than in controls because of two expected changes in host plant characteristics: 1. a higher probability of the host plant occurring under open canopy due to overstory thinning; and 2. a higher probability of juvenile New Mexico locust foliage due to returning fire to the system. We also predicted initial declines of *E. clarus* in restored areas experiencing high intensity burns resulting in New Mexico locust death and resprout, although this prediction was not tested.

**Tests of Predictions:** In 2001, larval densities in the paired treatment and control blocks were significantly greater in treated units following restoration (Figure 3.4, Wilcoxin Signed Rank test $Z = -1.826$ for larvae, leaf cuts and leaf ties, $p < 0.10$). Almost 4 times as many larvae were censused on host plants in treated units than in control units. Utilizing the paired blocks required a small sample size, and the proportion of the host plant was not the same in each block. Even with these considerations, patterns across the paired blocks were consistent.

New Mexico locust plants sampled in treated units were found to be under significantly less canopy (Figure 3.4, paired $t = 2.89$, $p < 0.10$) than locust plants sampled in control units. This is not unexpected, as thinning in restoration treatments can remove up to 80% of the ponderosa pine canopy (Waltz et al. 2001).

If adult *E. clarus* distributions were correlated with larval distribution patterns, then we would predict higher abundances in restored units than in control. However, data from 2000 and 2001 in the paired experimental blocks showed adult *E. clarus* were not found in higher densities in restoration treatments, as predicted from patterns of larval host plant usage (Figure 3.5, repeated measures ANOVA treatment * year $F = 1.76$, $p > 0.10$). There was no significant correlation between adult abundances and larval abundances in 2001 (Figure 3.6, $F = 2.83$, Adjusted $R^2 = 0.205$). These results suggest that adult butterflies are not distributed in similar patterns as their larvae, and probably have different habitat requirements.

## Discussion

Assessing habitat requirements of *Epargyreus clarus* larvae enabled us to predict larval responses to an ecosystem restoration project. Larvae were found in highest abundances on their host plant, New Mexico locust, when 1. the host plant was found under open canopy; 2. the host plant was juvenile, and 3. the host plant was non-resprout growth. Knowing that the ponderosa pine forest restoration thinning reduces canopy cover and that returning frequent fire to the system maintains a more shrub-like, juvenile host plant (Gottfried 1980, Boring and Swank 1984), we predicted higher larval abundances in treated areas. These predictions were shown to be accurate, with up to 4 times as many larvae found on host plants in restoration treatment units. We did not have high-intensity fire patches to test how large stands of New Mexico locust resprout would affect larval distributions. Large areas of resprout are unlikely in these treatments, as reduced aerial fuels limit intense fire, or "hotspots", to localized patches.

Higher larval abundances in restoration treatment units could be the result of either higher oviposition rates in these areas or the result of increased larval survivorship in these treatment units. This study did not measure oviposition or larval survivorship directly. Adult distributions suggest no extra time was spent in treatment units versus control units, and we recommend future studies to look directly at larval survivorship patterns in treated and control units.

The differences in habitat requirements for adult and larval stages increase the difficulty of assessing invertebrate habitat requirements. Adult *E. clarus* did not show significant differences between restored and control units at the site. Not surprisingly, correlations of adult butterfly abundance with larval abundance were not significant. Often adult Lepidoptera are used as the primary assessment tools for Lepidoptera populations (Pollard 1977, Kremen 1992). Adults are easier to locate and identify than larval populations, and can be monitored with relatively little training. Unlike many Lepidopteran larvae, *E. clarus* larvae are easy to locate and monitor, and so make useful study organisms for habitat requirement questions. Our study suggests that adult butterfly monitoring schemes may not be appropriate for habitat assessment or habitat use studies.

**Implications for restoration:** Ponderosa pine restoration treatments are currently proposed over much of the U.S. Southwest. The larval host plant, New Mexico locust, resprouts readily after fire, and can maintain a more shrub-like architecture with frequent fire. While restoration treatments would create more open canopy for the host plant, treatments that include prescribed fire may initially result in New Mexico locust mortality and increased resprouting. However, the patchiness nature of subsequent fires will likely support a mosaic of New Mexico locust age classes, Which may benefit not only *E. clarus*, but a broad range of herbivores.

Response of *E. clarus* larvae to ponderosa pine restoration may be due to the changes in microclimate associated with overstory removal, including increased insolation (Meyer 2000, Waltz, unpublished data). Alternatively, the larvae may be responding to physical and chemical properties of the host plant in response to thinning and burning. Other studies show increases in chemicals in resprouted vegetation (Martinsen et al. 1998), and insect community differences between juvenile and mature leaves (Waltz & Whitham 1997).

Restoration goals cannot incorporate every possible faunal response (Aronson et al. 1993, Hobbs & Norton 1996, Ehrenfeld 2000). However, monitoring diverse taxa in restoration treatments broadens the scope of environmental variables that we can perceive (Kremen et al. 1993, Block et al. 2001). Invertebrate populations, in particular, represent a broad range of ecological niches. In many cases, invertebrates are easy to census in high enough numbers to provide good statistical comparisons (Kremen et al. 1993). We suggest wildlife life-history traits and habitat-use data can help develop predictions for wildlife response to restoration treatments, and provide testable hypotheses when these restoration treatments are implemented (Jordan III et al. 1987, Bradshaw 1987, Michener 1997).

**Implications for land managers:** The strength of this study was that our developed predictions were tested in a paired design with replication. The research design and these treatment units provided a unique opportunity to develop and test predictions of an individual species response to a land management option. Unfortunately, land management decisions are usually made using predictions based on current habitat use, but with no experimental tests of the predictions (Block et al. 2001). This study showed adult *E. clarus* distributions could not be predicted by larval distributions as previously expected. We conclude that testing of predicted responses are imperative to properly assess management changes.

The use of indicator species has been widely touted to be an economically feasible way for land managers to monitor elements of managed ecosystems otherwise too costly or difficult to monitor (Brown 1991, Kremen 1992, Williams 1997). Recent work has advocated invertebrates as valuable monitoring tools (Kremen 1992), and indicators of restoration success (Andersen 1993, Andersen & Sparling 1997, Davies et al. 1999, Williams 1997). Butterflies have been suggested as excellent indicator species (Kremen 1992), with studies showing butterflies may indicate plant species richness(Scoble 1992), other taxa (Pearson & Cassola 1992, Beccaloni & Gaston 1995) and restoration success (Waltz, in prep).

We suggest that the *E. clarus* response can potentially indicate other New Mexico locust herbivore behavior, which may show positive responses to restoration treatments mediated through their food-plant response. Other herbivores observed on this plant include Lepidopteran leaf rollers, free feeding sawfly larvae, and an abundance of aphids and leaf hoppers. As always, careful definitions of what indicator species are indicating are necessary. Sampling of other herbivores, followed by correlations with *E. clarus* distributions, may determine the effectiveness of this skipper as an indicator of other New Mexico locust herbivores. It was also evident from this study that monitoring one developmental stage of an invertebrate does not necessarily provide information on the habitat requirements of all developmental stages.

Designing replicated experiments to test faunal responses to proposed treatments is expensive, and may not meet the intended goals of land managers. Large mammal censusing requires multiple years to develop patterns. In many cases, this time frame is not compatible with other goals of the land management practices (e.g., fire protection). However, we believe that examining invertebrates adds this valuable experimental component to land management treatments, without great expense or long time horizons.

## Acknowledgements

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## Figure Legends

Figure 3.1. *Epargyreus clarus* larvae were 160% greater on shoots located in sunshine than on shoots in shade (paired t-test = 4.65, $p < 0.05$).

Figure 3.2. *E. clarus* leaf ties were 3 times as abundant on juvenile, non-flowering host plants than on mature host plants (paired t-test = 23.8, $p < 0.05$).

Figure 3.3. *E. clarus* larvae were more than twice as abundant on non-resprout foliage than on nearby resprout foliage (paired t-test = 2.62, $p < 0.05$).

Figure 3.4. Larval, leaf cut and leaf tie counts on New Mexico locust host plant in paired restoration treatments and control units. These results analyzed with Wilcoxin-signed ranks test to account for non-normal distribution patterns across the four blocks ($Z = -1.826$ for larvae, leaf cuts and leaf ties, $p < 0.10$). Canopy cover class averages of the host plant showed significantly less canopy in restoration treatment units than in control units (Paired t-test = 2.89, $p < 0.1$). Canopy cover classes: 1. < 10% cover, open; 2. 10 - 35% cover; 3. 35% - 65% cover; 4. 65% - 90% cover; and 5. >90% cover, full cover.

Figure 3.5. Adult *Epargyreus clarus* distribution two years following restoration treatment (2000 and 2001) showed no significant differences in distributions between restoration treatment and control units (repeated measures ANOVA treatment * year $F = 1.76$, $p > 0.10$).

Figure 3.6. There was no significant correlation between adult abundances and larval abundances in 2001 (Regression $F = 2.83$, Adjusted $R^2 = 0.205$, $p > 0.10$).

Figure 3.1

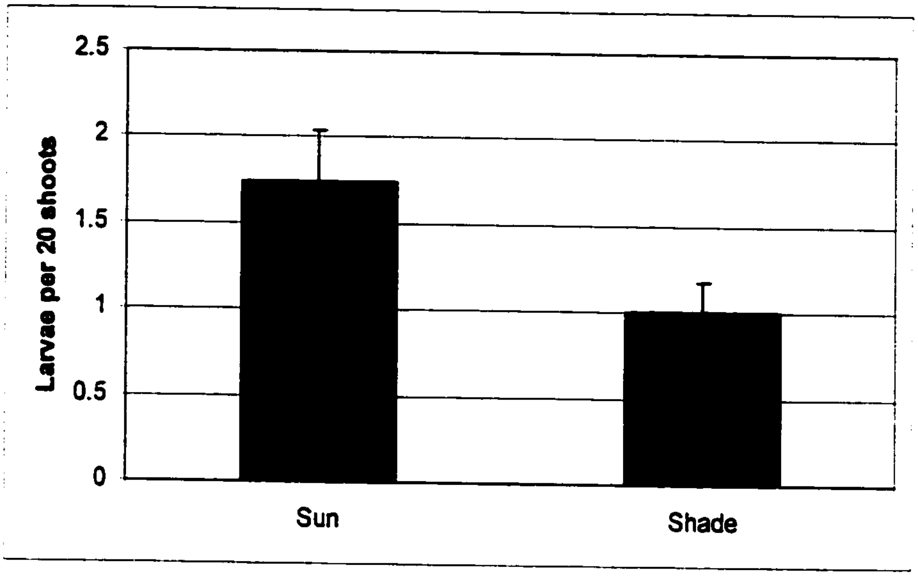


Figure 3.2

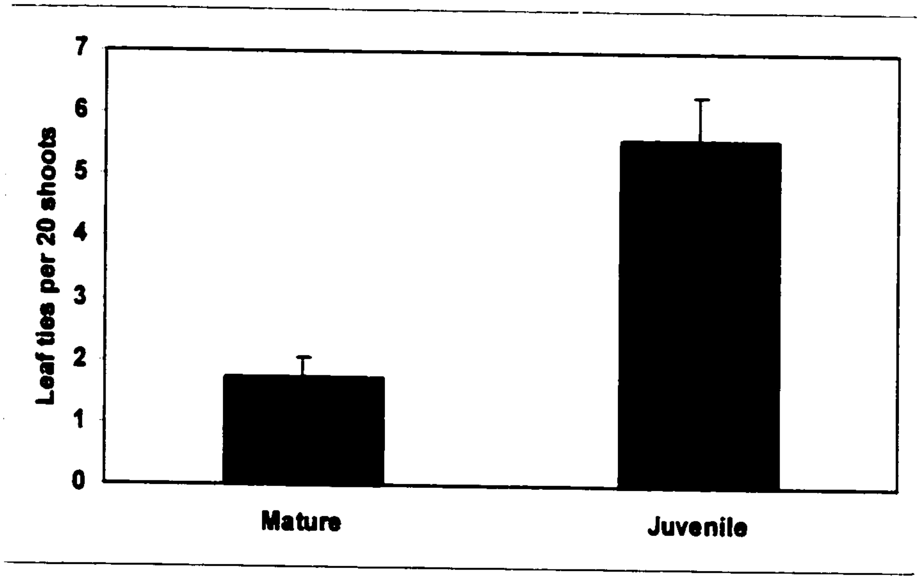


Figure 3.3

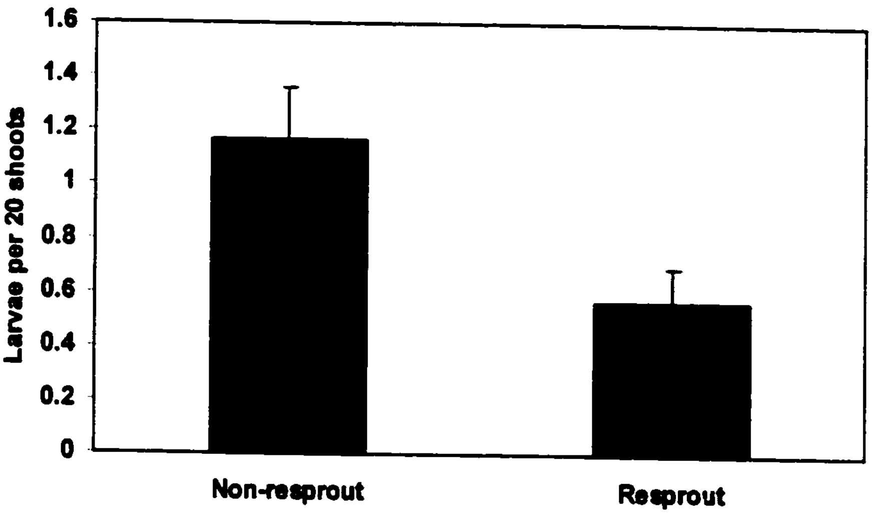


Figure 3.4

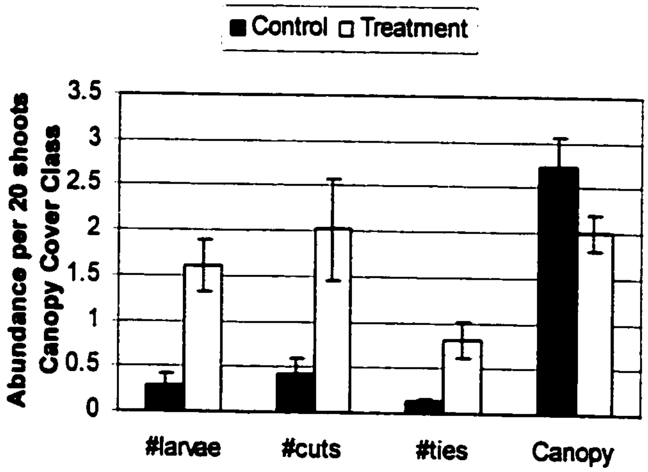


Figure 3.5

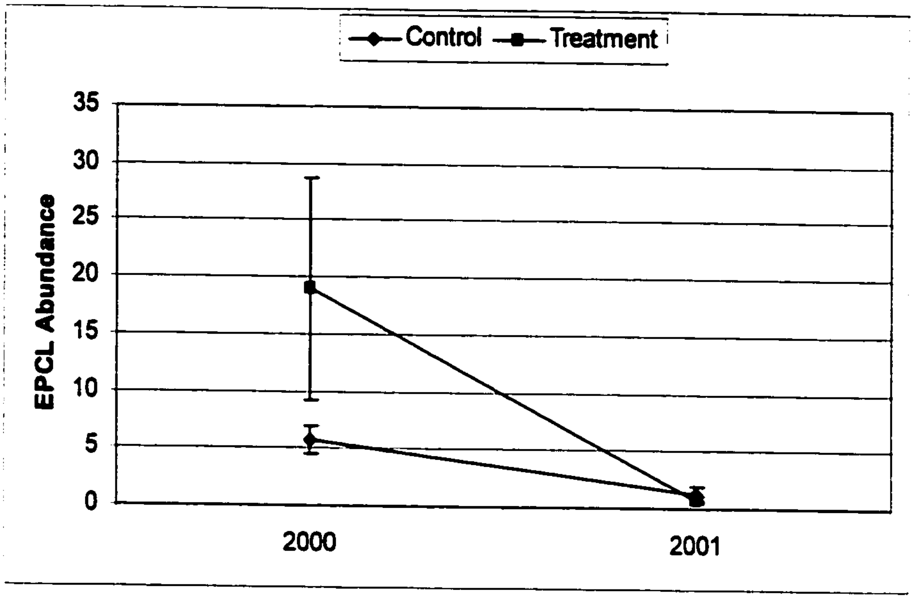
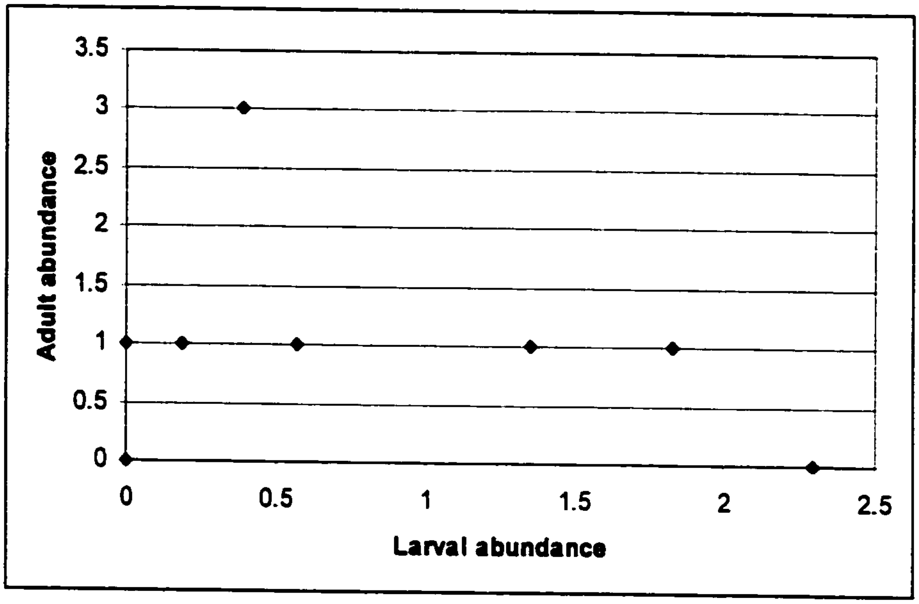


Figure 3.6



# Chapter 4: Using Forest Restoration Treatments to Develop and Test Effective Indicator Species

## Abstract

We present existing evidence supporting the use of indicators in restoration studies and outline a methodology for the development of indicator species in restoration treatments. In temperate zone forests, current-day forest management reflects an increased focus on biodiversity conservation, and uses restoration treatments to restore natural composition, structure, and processes lost to intensive management. Land and resource managers perceive the use of indicators as an economical and time sensitive means to track changes in biodiversity, target conservation priorities, or monitor ecosystem health. Much has been published debating indicator use as a conservation tool, and many valid concerns about the effectiveness of indicator species exist. This paper reviews the acknowledged benefits and problems of indicators in general. Although there is little support for effective indicator species on a global level, regional indicator species of specified attributes have been shown to be successful. We suggest regional indicator development and testing can be more effectively accomplished utilizing landscape restoration experiments. Terrestrial restoration monitoring, which is often accomplished under tight budgets, would also benefit from effective indicator species, but few studies examine the use of indicator species as a monitoring tool in landscape-level restoration projects.

We present a case study, using ponderosa pine restoration in the U.S. Southwest to test the effectiveness of adult, day-flying Lepidoptera as indicators of pollinator groups. Pollinator return to restored ponderosa pine forests would signify one functional recovery of the system. Adult butterfly abundances were found to have a significant, positive relationship with pollinator group abundances in restoration treatments. We discuss how to test this relationship in alternative forest restoration treatments to broaden the application of this particular indicator.

## 1. Introduction

Management of today's temperate forests requires effective monitoring and assessment to adequately address current biodiversity and restoration goals. For land and resource managers, many potential advantages derive from using indicator species or assemblages to accomplish this monitoring. Studies show indicators can help determine conservation goals and disturbance intensity by indicating changes in habitat quality, biodiversity, ecosystem function and process (Landres *et al.*, 1988; Noss, 1990; Erhardt & Thomas, 1991; Kremen, 1992; Launer & Murphy, 1994; Beccaloni & Gaston, 1995; Majer, 1997; Flather *et al.*, 1997; Miller *et al.*, 1998; McGeoch & Chown, 1998). Most importantly, the use of indicator species allows these attributes to be examined in relatively small time frames and at reduced costs to land managers (Fleishman, 2000).

Indicator assessment can provide managers the initial data to focus limited resources or prioritize areas for conservation or restoration. Land managers and conservation planners are often faced with limited resources and short assessment times (Noss, 1999; Lindenmayer, 1999; Simberloff, 1999). Often, full-scale inventories of managed lands or lands proposed for management are impractical. Restoration projects are similarly constrained: while money is available to initiate restoration, it is difficult to find funding to continue monitoring the effects of the restoration treatment. Many restoration projects take years or even decades to see the establishment of pre-disturbance communities (Majer, 1989; McIver *et al.*, 1992). Few funding cycles provide this level of support. Proper use of indicator assemblages can provide information on many attributes of ecosystems but still fit land managers' budgets.

For the purpose of this paper, we define indicators as species or assemblages of species that are indicative of the diversity of other taxa, ecosystem attributes or ecosystem functions in the same habitat (McGeoch, 1998). Often, indicator species show responses to environmental change, and can represent the responses of other species or taxa to the same environmental change (Noss, 1990; McGeoch & Chown, 1998). Noss (1990) states an effective indicator should: 1. be sensitive to environmental change but robust enough to be continuously measured over different stress levels; 2. have a broad geographic range; 3. be cost effective to monitor; 4. be able to differentiate between natural and anthropomorphic induced stress; and 5. be independent of sample size.

The purpose of this paper is to create a structured approach for developing indicator species for specialized goals using specified land management experiments. We discuss the current status of indicator species efficacy and the potential role of indicator species in monitoring long-term experimental projects. Finally, we present a preliminary case study of indicator species development in ponderosa pine restoration.

## 2. State of indicator species effectiveness

Indicator species efficacy has been reviewed extensively (Landres *et al.*, 1988; Noss, 1990; Kremen, 1992; Prendergast *et al.*, 1993; Williams & Gaston, 1994; Launer & Murphy, 1994; Keddy & Drummond, 1996; Prendergast, 1997; Flather *et al.*, 1997; Miller *et al.*, 1998; Lawton *et al.*, 1998; Simberloff, 1998), and we do not intend to accomplish another review. Instead, we will summarize where indicators have been successful, and some of the major criticisms of indicator species studies.

Indicator assemblages have been beneficial for monitoring disturbance levels on local scales in natural areas or defining conservation boundaries. For example, Hill *et al.* (1995) showed butterflies responded to logging in Southeast Asia, having lower species richness, evenness and diversity in logged compared with unlogged stands and thus potentially indicating levels of logging disturbance. Selectively logged boreal forests in Sweden also showed lower invertebrate diversity than unlogged forests (Pettersson, 1996). These patterns are useful on a local scale, but are not supported globally; other studies show invertebrates increase in diversity with forest disturbance. Wood and Gillman (1998) found higher butterfly species richness in disturbed forests (selectively logged) than in undisturbed forests in Trinidad. Spitzer *et al.* (1997) found higher butterfly diversity in small forest gaps created by illegal logging in Vietnam.

On larger scales, Kremen (1992) found butterflies were appropriate indicators of topographic and environmental gradients but were not indicative of smaller scale patterns, such as plant species richness. Her results suggested butterflies may also respond to temporal variation in environmental gradients, and may reflect shifts due to climatic change. Species showing fast responses to fragmentation can provide early warning signals to land managers of detrimental ecological consequences (Kremen *et al.*, 1993).

One of the most advocated uses of indicator assemblages is to use easily monitored taxa to indicate composition and/or diversity of other taxa (biodiversity indicators, Noss, 1990; Pearson & Cassola, 1992). Biodiversity indicators have been shown to indicate similar taxa or unrelated taxa. For example, the butterfly subfamily Ithomiinae (Nymphlidae) was shown to correlate highly with total butterfly species richness in Neotropical forests (Beccaloni & Gaston, 1995). In another study, Osborn *et al.* (1999) found significant correlations between ground ants and canopy ants in different forest types in Venezuela. However, the same study found mixed indicator success when unrelated taxa were examined. Positive correlations existed between vegetation diversity indices and butterfly richness and diversity indices. But no significant relationship was found between ants and butterflies and the authors concluded that using a single taxon for biodiversity assessments was inaccurate (Osborn *et al.*, 1999).

Other biodiversity indicator studies have been sharply criticized. Pearson and Cassola (1992) found tiger beetles could act as indicators for butterflies using data from multiple continents. In this example, both taxa were relatively easy to monitor and both were potential indicator species. Problems with spatial dependencies (e.g., adjacent sampling blocks were autocorrelated) led to several critical reviews of this paper (Carroll & Pearson, 1998). However, when Carroll and Pearson re-examined the data using geostatistical methods that incorporate spatial dependencies, they still found significant correlations between tiger beetles and butterflies (Carroll & Pearson, 1998).

In contrast, many studies specifically examining diversity indicators showed no correlations between targeted groups. For example, Prendergast (1997) found poor correlations between butterflies, birds and Odonates (dragonflies and damselflies) at small spatial scales. Flather *et al.* (1997) found little spatial concordance between the species rich "hotspot" areas of one potential indicator taxon when compared to the species rich areas for other potential indicator taxa. Although these taxa are thought to predict patterns of less common, "hard-to-survey" taxa, they were not effective at predicting biodiversity hotspots for other common taxa. Van Jaarsveld *et al.* (1998) also found little overlap of "hotspots" among eight taxa groups, five of which were invertebrates. In addition, the same study showed that using higher taxa to indicate species-level diversity was unsuccessful at conservation-level scales (van Jaarsveld *et al.*, 1998).

The uses of indicator species of ecosystem function were not common in conservation literature, although indicators of ecosystem function have been explored in restoration experiments (Majer, 1997). Monitoring ecosystem processes, such as decomposition, pollination and soil processes can be time consuming and expensive for land managers (Simberloff, 1999). Indicator species with close linkages to ecosystem processes would provide a particularly good assessment tool (Noss, 1999; Lindenmayer, 1999).

The above studies demonstrate that the presence and abundance of certain taxa can indicate disturbance or multiple taxa diversity, but that the responses were specific to the site and the disturbance. The opposite trends observed in the above studies may be due to differences in the measured disturbance, the study sites or the specific land-use history, suggesting that global indication patterns are difficult to establish. In contrast, indicator response in a specified restoration context can be clearly defined by pilot studies specific to each restoration project, and would significantly contribute to long-term monitoring of the indicated attribute in that system (Williams, 2000). This specified use of indicator species limits the immediate global potential of indicators, but we think small-scale tests could generate testable hypotheses in a scientifically defensible manner, with possible implications for global uses of indicator species (Noss, 1999).

There remain many valid critiques of indicator species effectiveness, briefly summarized into three areas. First, there exists a lack of clear selection criteria for indicator species, and a lack of clear definition of the indicated attributes. Often indicators are selected based on popularity or familiarity (e.g., butterflies), with no other selection criteria (Landres *et al.*, 1988; Prendergast, 1997). In addition, whether or not an indicator species is responsible for indicating ecosystem health, biodiversity, or disturbance is seldom defined (Landres *et al.*, 1988; Williams & Gaston, 1994; McGeoch, 1998; Simberloff, 1998). Secondly, studies of indicator species often lack clear hypotheses, goals or "sub-end points" (Noss, 1990), which are necessary to validate the use of indicator species or groups. Studies of indicator species that include hypothesized mechanisms of indication would help establish ecosystem linkages and facilitate a clearer understanding of specific ecosystems with potential implications at the global level (Noss, 1990). And finally, a third major critique is that field tests of the correlation strength or the predictive power of the indicator organisms do not exist (Landres *et al.*, 1988; Noss, 1990). Correlated patterns established at one site require experimentation at additional sites with varying disturbance or treatment levels to test the limits of indicator species effectiveness. In a few studies, it was assumed that the response of a species indicates the response of all species within the same guild, without any correlative data (Landres *et al.*, 1988). This assumption does not take into account species individuality in habitat usages, breeding requirements, diet, responses to disturbance, nor potential within-guild competition (Landres *et al.*, 1988; Lawton *et al.*, 1998).

We agree that using indicator species or assemblages without properly defined goals is futile. In addition, current empirical support for indicators of global diversity is scant. We suggest, however, that the development and usefulness of indicators as a valuable monitoring tool is in smaller, more clearly defined landscapes with careful experimental design using replicated experiments (Figure 1). We feel an appropriate area for the development, testing and eventual use of indicators is in terrestrial restoration projects. Specifically, if indicators species: 1. have properly defined indicators and indicated attributes; 2. are developed using clearly established hypotheses, goals and sub-end points; 3. are properly tested; and 4. are re-assessed through time for continued effectiveness, then a clear, useful parameter can be developed to aid resource managers (Figure 1). As restoration projects move from early successional systems to later-successional stages, the appropriateness of indicator species may change.

## 3. Restoration on Public Lands

The most important step in developing an effective indicator is to use a statistically defensible experimental design. Carefully designed restoration treatments on public lands can contribute to indicator development and testing, which in turn would benefit the restoration treatment monitoring. The restoration of degraded landscapes has gained more attention as numerous wildlands are lost to development (Jordan *et al.*, 1987; Bradshaw, 1993; Hobbs & Norton, 1996). The percentage of ecosystem-level studies concerning restoration rose tenfold from 0.5% in 1990 to 5% of ecosystem studies in 2000. This increased attention is due, in part, to an increasing use of restoration practices by land managers. Habitats ranging in size from prairie remnants on roadside margins (Feber *et al.*, 1994) to the 100,000 ha Kissimmee River restoration (Dahm *et al.*, 1995) have been incorporated in restoration plans.

Restoration projects continue to be implemented across the US. For example, a 2000 congressional appropriation provided more than $8 million to restore ponderosa pine forests in the southwest as a fire prevention tool (Appropriations Bill, 2000). This increased use of restoration practices by land managers creates expanding opportunities for research in manipulated systems (Jordan *et al.*, 1987; Hobbs & Norton, 1996). More importantly, we need improved monitoring to provide effective feedback for the land managers using ecological restoration treatments (Berger, 1991; Lindenmayer, 1999). Restoration techniques are still in progress, and additional variables can contribute to future treatment modifications.

The implementation and monitoring of terrestrial ecosystem restoration projects currently remain focused on structural components, such as overstory or understory plant composition (Majer, 1989; Andersen, 1993; Williams, 1997); disturbance regimes, such as returning fire (Parsons *et al.*, 1996); or vertebrate management (Landres *et al.*, 1988). Although monitoring functional processes is prevalent in wetland and riparian restoration, few terrestrial ecosystem restoration projects focus on functional processes, such as nitrogen cycling, plant pollination, or the restoration of trophic level interactions (Aronson *et al.*, 1993; Bradshaw, 1993, but see Covington *et al.*, 1997; Kaye & Hart, 1998). However, to accurately address questions of restoration success or stage, restoration monitoring must include measures of process, function and ecosystem integrity (Aronson *et al.*, 1993), notably difficult attributes to understand, let alone measure (Hobbs & Norton, 1996). However, the use of indicators can broaden the scope of perceived variables to ecosystem processes as varied as plant production, nutrient cycling and plant pollination, while addressing time and financial constraints of land managers (Noss, 1999; Fleishman, 2000).

The use of indicator taxa in restoration projects can be successfully tested if experimental design considerations, such as untreated-controls and pre-treatment sampling, are incorporated into the restoration plan (Simberloff, 1999; Block *et al.*, 2001). Finally, restoration projects have established end point or goals to approach remnant or model reference conditions in structure and function (Aronson *et al.*, 1993; Hobbs & Norton, 1996; Moore *et al.*, 1999). Although the use of indicators is relatively recent in restoration projects, there are specific examples (mostly from Australia) where indicators have played an effective role in a restoration context.

## 4. Structural Approach to Developing Indicator Species

We suggest successful indicator species development can occur by meeting four criteria: 1. indicator species and indicated attributes or taxa are clearly defined; 2. hypotheses and goals are established; 3. indicator species are properly tested; and 4. indicator effectiveness is continually tested through time (Figure 1). Although global patterns of indicator species effectiveness may not exist, clearly identified indicator relationships can improve monitoring and land management decisions in specified ecosystems. Table 1 lists studies examining indicator effectiveness in restoration experiments. We examined these studies to evaluate how well these studies met the above criteria.

The selection and definition of indicator species and indicated attributes (Figure 1, Step 1) should be based on how well the indicator meets indicator criteria (Noss, 1990) and how directly the indicator and monitored attribute contribute to the study goals. All but one study in Table 1 defined the potential indicator species, and the indicated variable. However, ill-defined indicators and attributes can cause problems in subsequent steps if, for example, the indicator species show no changes to across ecosystem types or the definitions of predicted attributes are too general. In this case, attempting to indicate ecosystem health or ecosystem recovery may create difficulties in hypotheses generation (Step 2), due to different interpretations of ecosystem health (Landres *et al.*, 1988). Establishing testable hypotheses about the relationships between indicator and indicated attributes then becomes less feasible.

Developing hypotheses about the relationship between indicator species and indicated attributes is one of the most important steps in the development of indicator species (Figure 1, Step 2). These hypotheses allow indicator studies to address potential ecosystem linkages, and the mechanisms influencing indicator species distributions. It is these hypotheses that will contribute most to indicator species usages at global scales. For example, Davies *et al.* (1999) tested the hypothesis that selecting different logging slash treatments would alter the successional pathway of termites, which in turn would have significant impacts on soil processes. This study found significant changes in termite community structure and soil processes in different slash treatments, supporting the hypothesis (Davies *et al.*, 1999). Future studies can examine this hypothesis in different ecosystems, or with different decomposer assemblages.

Testing the correlative relationship (Figure 1, Step 3) establishes the ultimate effectiveness of indicator species. Although this establishes the validity of the indicator species, only 4 of the 19 studies (Table 1) that resulted in significant correlative relationships between indicator species and indicated attributes tested this relationship further. In Australia, Andersen and Sparling (1997) showed positive relationships between ant species richness and soil microbial biomass at disturbed and restored sites. Interestingly, when this relationship was tested outside restoration projects across habitat types, it broke down (Andersen & Sparling, 1997). The relationship was significant only in sites undergoing restoration. Thus, testing of indicator effectiveness showed the local, specific indicator success in restoration could not be expanded to a more general use, which clearly defined the limits of ants as indicators of soil microbial biomass in this system.

We include a fourth step for indicator species development (Figure 1, Step 4) which is the reassessment of indicator effectiveness through time. Particularly in restoration sites, which have in common continuing successional change following initial restoration treatments, indicator relationships may vary through time. Clearly there is potential for effective indicator species use in restoration treatments. Although indicator studies most often lack the testing of the indicators, these existing relationships can now be incorporated into further testing. Many of these studies would produce measurable indices of plant productivity, decomposition, etc. Below we present our efforts to develop an indicator species in ponderosa pine restoration.

## 5. A Case Study: Butterflies as indicators of pollinators

Ponderosa pine restoration seeks to restore ponderosa pine ecosystems to emulate structure, composition and processes found prior to Euro-American settlement, with frequent fire maintaining low tree densities and a diverse understory. Restoration treatments incorporate thinning the current dense stands, re-introducing fire, and applying different combinations of seeding and natural re-vegetation to restore the understory. Additional benefits include the reduction of crown-burning wildfires, which has generated much public and political support of these restoration projects.

### *5.1 Defining indicator taxa and indicated attributes*

Using Figure 1 as a guideline, we first identified adult butterflies as potential indicator species of bees, wasps and bee-flies ("pollinator group"). Implications of a more diverse understory following ponderosa pine restoration include changes of the processes needed to sustain the new structure, specifically pollination. Pollinators are currently in decline globally due to habitat loss and fragmentation (Buchmann & Nabhan, 1996). Therefore, the successful re-establishment of understory plants may be dependent on missing associated pollinators. We suggest understory monitoring in forest restoration should include a measure of the pollinators needed to service the new herbaceous structure. However, measuring pollinator communities can be time consuming and expensive. Further, little is known about current life history traits (Kerr *et al.*, 2000). In contrast, the day-flying Lepidoptera (butterflies) are a well studied taxon currently surveyed once a year across the U.S. by volunteers (North American Butterfly Association annual butterfly count). Butterflies meet many of the proposed indicator attributes (Noss 1990); they show fast responses to environmental change, have broad distributions, varied life histories and can be easily monitored.

### *5.2 Indicator Assessment Goals and Hypotheses*

We determined the goal of this particular indicator development in ponderosa restoration was to assess the status of the pollinator community to a restored understory, which would correspond to one measure of functional recovery of the ecosystem. Adult butterflies feed on nectar and in some cases pollen, but often do not contribute significantly to pollination events (Jennersten, 1984; Yeboah Gyan & Woodell, 1987). Because of the similar general diet requirements, it is logical to hypothesize that adult butterfly abundance may be correlated with pollinator abundance. However, these assumptions are tenuous without empirical data, as mentioned by Lawton *et al.*(1998). We tested this hypothesis in ponderosa pine restoration treatments and present preliminary data here. Complete methods are detailed in Appendix 1.

### *5.3 Developing the prediction*

To develop the predictive relationship between butterflies and pollinators, we used restoration projects at two sites in northwestern Arizona, Mt. Trumbull and Ft. Valley. Butterfly monitoring data presented here were collected from line-transects (Pollard, 1977) located in 5 untreated forested units (control), 5 restoration treatment units and a natural meadow in 2000 and 2001. Pollinators were assessed using two methods to determine if a predictive relationship between butterflies and pollinators existed. In 2000, we swept flowering plants in 4 untreated units and 4 restoration treatment units with aerial nets, and in 2001 we used water traps in 5 additional study areas to collect potential pollinators. Pollinator samples from aerial sweep netting (2000) and water traps (2001) were summarized by order and morphospecies. Bees and wasps (Hymenoptera) were combined with bee-flies (Diptera) to create a potential pollinator group (detailed methods in Appendix 1).

Butterfly abundance at Mt. Trumbull and Ft. Valley ranged from 4 to 70 butterflies per transect in 2000 and from 5 to 64 butterflies per transect in 2001. The collected pollinator group consisting of bees, wasps and bee-flies ranged from 0 to 25 in

2000, and 1 to 22 in 2001. The regression of adult butterfly abundances with pollinator abundances was significant ($F = 9.56$, $p < 0.05$, adjusted $r^2 = 0.46$), following a natural log transformation of both variables to reduce the "funnel" effect of the residuals (Glantz & Slinker 1990). The resulting regression formula was: pollinator group abundance = $0.184 * (\text{adult butterfly abundance})^{1.425}$ (Figure 2).

### *5.4 Testing the prediction*

Testing the predictive relationship of day-flying butterflies and pollinator is planned in 2002. This testing will be continued in sites of differing restoration stage (i.e., time since thining and burning) as well as in natural meadows and ponderosa pine ecotones. These tests will establish to range of butterfly indicator effectiveness of pollinator communities. As restoration treatment units continue to change through successional time, we hypothesize the correlative relationship between butterflies and pollinator taxa will also change. Re-assessment through time then also becomes imperative, to assess the validity of the indicator relationship (Figure 1, Step 4).

### *5.5 Implications*

These data suggest butterfly indicator species have a potential use in ecosystem monitoring of ponderosa pine restoration treatments. Butterflies, which are relatively easy to monitor, showed a significant positive relationship with pollinator group abundances in ponderosa pine restoration sites. The restoration of ponderosa pine has been shown to increase understory diversity and production (Covington *et al.*, 1997). We have also shown increases in nectar resources associated with early successional responses to ponderosa pine restoration (Waltz & Covington, 1999). As pollinator groups and butterflies share these resources, it is reasonable to suggest fluctuations in one group may be reflected by fluctuations in the second group. However, this experiment does not examine the mechanisms of butterfly and pollinator distributions and cannot specifically address that assumption.

The acid test of indicator species relationships is to use predictive relationships at different sites. Further tests in different habitats (meadow, high elevation forests, low elevation forests) may show the limits of using butterflies as indicators of pollinators. For example, some forest butterflies feed from tree sap, and correlations with pollinator taxa may decrease in these more closed canopy forests. In addition to further testing, a more specific definition of pollinator communities is needed to strengthen the power of the indicator species. As ponderosa pine restoration treatments continue to be implemented across the U.S. Southwest, results from these pollinator studies could help determine seeding strategies and fire return intervals. Finally, re-assessment of the indicator value of butterflies will be necessary as ponderosa pine restoration treatments develop a more grass-dominated understory.

## 6. Conclusions

Consistent with other studies (Pearson & Cassola, 1992; Beccaloni & Gaston, 1995; Osborn *et al.*, 1999), our examination of existing indicator species studies has established that correlated patterns between easy-to-assess organisms and harder-to-assess attributes are possible . At the same time, the opposing responses of many of the studies we reviewed suggest that global patterns of indication may be impossible to attain (Prendergast, 1997; Flather *et al.*, 1997; van Jaarsveld *et al.*, 1998). We cannot overlook the potential benefits of indicator species and more importantly, the need for indicator species in systems undergoing experimental management or habitat alteration. We therefore suggest that on a localized level, the development and use of indicator species or assemblages can make valuable contributions to ecology, restoration and land management. In particular, indicator species are needed with close linkages to ecosystem processes, such as decomposition, nutrient cycling, pollination and seed dispersal (Majer, 1997).

In well-planned landscape experiments, such as some terrestrial restoration projects, we can address several of the concerns of indicator development while benefiting the field of restoration monitoring. Specifically, indicator development research must first have clear definitions of indicators and indicated variables. Secondly, clearly conceived hypotheses and goals will contribute to the understanding of ecological processes as well as provide mechanistic linkages between indicator species and the indicated attribute. Thirdly and most importantly, testing of proposed indicator relationships can help establish the hypothesized inferences and scope of indicator relationships.

Restoration monitoring will also benefit through increased monitoring and from effective indicator establishment. Because of limited funding for long-term monitoring (Simberloff, 1999), the use of effective indicators as low-cost linkages to ecosystem function or restoration trajectories can broaden the ecosystem variables perceived by land and resource managers (Kremen, 1992; Noss, 1999). In particular, these indicators are necessary to contribute to on-going restoration projects incorporating adaptive management goals.

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Table 4.1. Studies of indicator species effectiveness in restoration experiments. Three major criteria of developing indicator species are itemized in the top row. 1. Defined indicator and indicated attribute, 2. defined hypothesis, and 3. sufficient testing of established relationships. Testing is not applicable when no significant relationships were found between indicator and indicated attribute. Potential effectiveness refers to studies that did not directly address the question of indication, but whose data suggests correlative relationships occur. Some papers are listed twice, as they have multiple indicated attributes.

| ***From Figure 1:*** | | ***1a. Defined Indicator*** | ***1b. Defined Attribute*** | ***2. Defined Hypothesis*** | | ***3. Testing*** | |
|---|---|---|---|---|---|---|---|
| **Study Site** | **Restoration of** | **Study taxa** | **Indicated Attribute** | **Stated Hypothesis** | **Effective?** | **Predictive Testing** | **Author** |
| Australia | Mining | Ants | Fire regime | Yes | Yes | No | Andersen 1993 |
| Australia | Mining | Ants | Microbial biomass | Yes | Yes | Yes, Hypo rej. | Andersen and Sparling 1997 |
| Cameroon | Logging | Termites | Not well defined | No | Potential | No | Davies et al. 1999 |
| Alabama, U.S. | Mining | Arthropods | Plant species diversity | Yes | No | Not Applicable | Hawkins 1982 |
| Alabama, U.S. | Mining | Phytophagous Insects | Dominant plant density | Yes | Yes | No | Hawkins 1982 |
| Virginia, U.S. | Mining | Butterflies | Plant species richness | Yes | No | Not Applicable | Holl 1996 |
| Virginia, U.S. | Mining | Moths | Plant species richness | Yes | Yes | No | Holl 1996 |
| Australia | Mining | Invertebrates | Nutrient turnover | No | Yes | No | Hutson 1989 |
| Australia | Road cuts | Collembola | Decomposition | No | Potential | No | Jansen 1997 |
| Australia | Mining | Ants | Seed removal | | Yes | No | Majer 1985 |

| ***From Figure 1:*** | | ***1a. Defined Indicator*** | ***1b. Defined Attribute*** | ***2. Defined Hypothesis*** | | ***3. Testing*** | |
|---|---|---|---|---|---|---|---|
| **Study Site** | **Restoration of** | **Study taxa** | **Indicated Attribute** | **Stated Hypothesis** | **Effective?** | **Predictive Testing** | **Author** |
| Australia | Mining | Ants | Ecosystem recovery | | Yes | No | Majer & Nichols 1998 |
| West Africa | Over-grazing | Termites | Plant cover, plant richness | Yes | Yes | Yes | Mando et al. 1999 |
| West Africa | Over-grazing | Termites | Rainfall use efficiency | Yes | Yes | Yes | Mando et al. 1999 |
| Arizona, U.S. | Grazing/ Agriculture | Butterflies | Riparian restoration/ habitat condition | Yes | Yes | No | Nelson and Andersen 1994 |
| Netherlands | Agriculture | Ellenberg's I.V. Nutrient richness/ acidity/ soil moisture | Butterflies | Yes | Yes | Yes | Oostermeijer and Swaay 1998 |
| Wyoming, U.S. | Mining | Beetles | Mine reclamation/ Vegetation | Yes | No | Not Applicable | Parmenter and MacMahon 1987 |
| Wyoming, U.S. | Mining | Herbivorous Beetles | Vegetation | Yes | Yes | No | Parmenter and MacMahon 1985 |
| Wyoming, U.S. | Mining | Grasshoppers | Plant species richness & diversity | Yes | Yes | No | Parmenter et al. 1991 |
| New Zealand | Logging | Invertebrates | Reforestation | Yes | Yes | No | Reay and Norton 1999 |
| Australia | Mining | Invertebrates | Plant productivity | Yes | Yes | No | Urbanek 1989 |

| ***From Figure 1:*** | | ***1a. Defined Indicator*** | ***1b. Defined Attribute*** | ***2. Defined Hypothesis*** | | ***3. Testing*** | |
|---|---|---|---|---|---|---|---|
| **Study Site** | **Restoration of** | **Study taxa** | **Indicated Attribute** | **Stated Hypothesis** | **Effective?** | **Predictive Testing** | **Author** |
| South Africa | Mining | Multiple | Restoration and succession | Yes | Yes | No | van Aarde 1996 |
| Australia | Mining | Collembola | Decomposition | Yes | Yes | No | Ward et al. 1991 |
| Australia | Mining, Multiple | Invertebrates | Plant species composition | Yes | Yes | No | Whelen 1989 |
| California, U.S. | Riparian | Arthropods | Least Bell's vireo | Yes | Mixed | No | Williams, K.S. 2000 |
| California, U.S. | Wetland/ Marsh | Arthropods | Restoration, Decomposition | Yes | Yes | No | Williams, K.S. 1997 |

## Figure Legends

Figure 4.1. Flow chart of effective indicator species development. General patterns listed in **bold**; specific application of butterflies as indicators of pollinators in ponderosa pine forest listed in *italics*. Scientifically defensible indicator development starts with replicated, experimental design. We suggest this can be achieved in terrestrial restoration projects. Effective indicator development should meet 3 basic criteria, with further re-assessment through time as needed (point 4). Criteria 1. Clearly defined indicators and indicated attributes. Criteria 2. Hypothesized relationships and goals of indicator species. Criteria 3. Testing of established correlative relationship in additional sites and stress levels. Finally, indicators in restoration sites should be re-assessed for effectiveness through time.

Figure 4.2. Regression of pollinator group and butterflies. Each point is average number of pollinators and average number butterflies per transect, natural log transformed. A significant linear regression ($F = 9.56$, $p = 0.01$, $r^2 = 0.46$) establishes the correlative relationship: pollinator group abundance = $0.184*(\text{butterfly abundance})^{1.425}$.

Figure 4.1

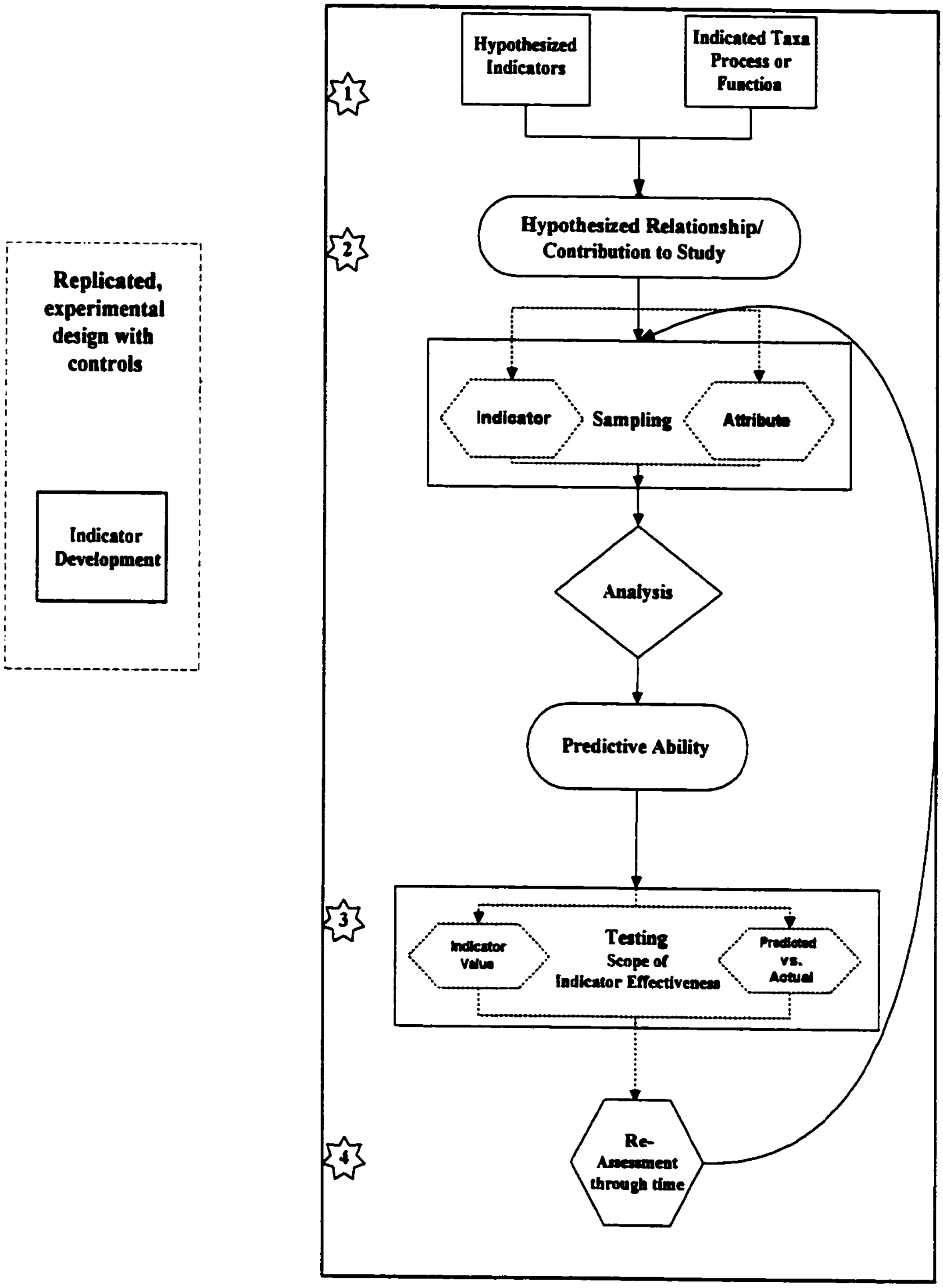
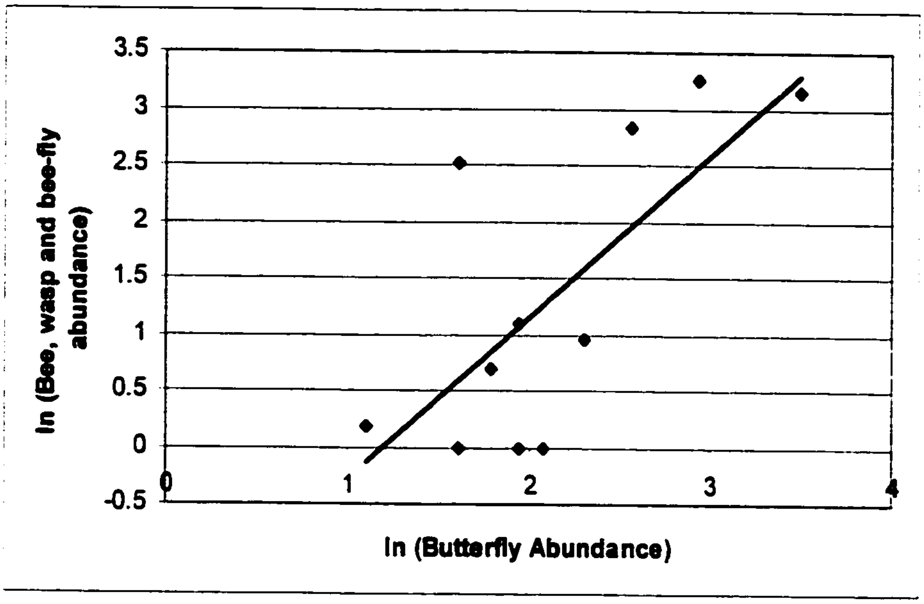

Replicated, experimental design with controls
Indicator Development
1
Hypothesized Indicators
Indicated Taxa Process or Function
2
Hypothesized Relationship/ Contribution to Study
Indicator
Sampling
Attribute
Analysis
Predictive Ability
3
Indicator Value
Testing
Scope of
Indicator Effectiveness
Predicted vs. Actual
4
Re-Assessment through time

Figure 4.2


3.5
3
2.5
2
1.5
1
0.5
0
-0.5
0
1
2
3
4
ln (Bee, wasp and bee-fly abundance)
ln (Butterfly Abundance)

## Appendix 1 - METHODS

### Study Site

Two study sites were used for this research. To develop the predictive relationship between butterflies and pollinators, we used a 5–year old restoration project located in northwestern Arizona. This study site was a ponderosa pine (*Pinus ponderosa*) and Gambel oak (*Querqus gambelii*) forest located between Mt. Logan and Mt. Trumbull, about 35 kilometers north of the Grand Canyon on the Arizona Strip. This land is managed by the Bureau of Land Management, and fell within the recently designated Grand Canyon – Parashant National Monument. Mt. Logan, Mt. Trumbull and the surrounding highlands form a sky island of ponderosa pine, with desert grassland to the north and the Grand Canyon to the south. The nearest ponderosa pine forest was about 100 km east on the Kaibab Plateau. The forest was predominately ponderosa pine, although Gambel oak composed 15% of the overstory (Waltz & Fulé, 1998). Other tree species in the area included New Mexico locust (*Robinia neomexicana*), aspen (*Populus tremuloides*), pinyon (*Pinus edulis*) and juniper (*Juniperus osteospermus*). The herbaceous component was dominated by sagebrush (*Artemesia tridentata*), and showed evidence of invasion by non-native species, such as cheat grass (*Bromus tectorum*), and some wheatgrasses (*Agropyron spp.*). Although over 300 herbaceous species were documented at the Mt. Trumbull site in the last 3 years (J.D. Springer, pers. comm.), the forest floor cover prior to restoration treatments was 70% litter and duff, with only 15% of the cover represented by herbaceous material.

Approximately 1,450 hectares of the 5,000-hectare forest was targeted for ponderosa pine restoration treatment in 1995. This treatment used a combination of commercial and non-commercial logging to thin the forests to tree densities similar to those found at the time of Euro-American settlement. Frequent fire had been eliminated with the onset of grazing and logging practices following Euro-American settlement. A low intensity fire was re-introduced to the site following logging. As of 2001, approximately 250 ha were thinned and burned.

The predictions developed at the first study site were tested at a 2–year old restoration site in northern Arizona, 15 miles north of Flagstaff, AZ. This second site, Ft. Valley, was located in the Coconino National Forest, and fell within the largest contiguous stand of ponderosa pine in North America. The thinning and burning restoration treatments at this site were part of a 100,000-acre urban-wildland fire prevention proposal. Logging and burning treatments similar to the Mt. Trumbull prescriptions were implemented in 1999. The predictions were tested here in a 20-acre untreated control and 20 acre restoration treatment. In contrast to the Mt. Trumbull site, the overstory at this site was 99% ponderosa pine. The understory had a higher native plant composition, and was dominated by native grasses and forbs, with few shrubs. The dominant exotic at Ft. Valley was Dalmation toadflax.

### Butterfly Sampling

Butterfly monitoring data presented here were collected from transects located in untreated forested units (control), restoration treatment units and a natural meadow in 2000 and 2001. Butterfly monitoring transects (Pollard 1977) totaling 300 meters were established in 5 control and 5 treatment units and 1 natural meadow. Transects were taped in and marked by orange pin-flags every 20 meters. Butterfly transects were placed 50 m from habitat boundaries to minimize edge effects.

Transects were monitored for butterflies in June and July in 2000 and 2001, at the same approximate time as the pollinator surveys, below. Diurnal butterflies are very sensitive to cool and windy conditions and often limit their flights on cloudy, cool days, thereby reducing chance of observation. Therefore, sampling was done between 1000 and 1600 hours, on days warmer than 17 degrees C, with winds less than 10 mph, and mostly sunny skies (Pollard 1977). A total of 5 minutes per 100 m was spent looking for butterflies. Butterfly species encountered on each transect were recorded. In addition, for each observation, we recorded behavior (i.e., nectaring, basking, flying), and if collected. The timed portion of the survey corresponded only to the search time and did not include time spent in pursuit of a butterfly.

### Pollinator Sampling

Pollinators were assessed using two methods at Mt. Trumbull to determine if a predictive relationship between butterflies and bees existed. In 2000, we swept flowering plants in 4 untreated units and 4 restoration treatment units with aerial nets to collect potential pollinators. Thirty flowering plants were selected from a 300 X 120 meter area within each treatment or control unit. Each plant was swept with a standard aerial net and all netted specimens were killed and collected. In the lab, species were tallied by order. Flowering plants were in very low abundance in the untreated-control units and some of the treated units. We found only 1 to 7 flowering plants per 300 X 120 m grid in the control units. Although the disproportional distribution of flowering plants suggests some standardized pollinator count is needed, we felt the difference in flowering plants was one of the characteristics of the control and restoration treatment units, and that the

3600 $m^2$ grid accounted appropriately for pollinator abundance in those habitats. Because of this, no standardization was done.

A different sampling method was used to collect Hymenoptera in 2001. Water traps were placed 60 meters apart along the 300 meter transects in untreated forests, treated forests and natural meadow, for a total of 5 traps per transect. Water traps were constructed with a yellow plastic bowl mounted 18 inches from the ground, which was the approximate height of understory vegetation. The color yellow has been shown to be an attractant for bees and wasps (Ausden, 1999). Bowls were filled with water and a drop of dishwashing detergent to break the surface tension. A mesh cover (1 cm grid) was place over the bowl to limit foraging by birds and small mammals. Once in June and once in July, these bowls were set out for 72 hour periods in untreated control units, restoration treatment units and a natural meadow. Specimens were collected and preserved in 70% ETOH, and later tallied by order in the lab.

**Analysis**

Adult butterfly abundance was summarized across both surveys for each treatment unit. The two surveys per year were summed, because the majority of these butterflies live two weeks or less. Thus, sampling in June and in July picked up different individuals. Pollinator samples from aerial sweep netting (2000) and water traps (2001) were summarized by order and morphospecies. Bees and wasps (Hymenoptera) were combined with bee-flies (Diptera) to create a potential pollinator group. Aerial net data was summed across both surveys. Trap data was averaged to provide the hymenoptera count per transect, and then summed across both survey dates. Overall, pollinator group abundances were similar between years with both sampling techniques, and so data from both years were combined to examine predictive relationships between butterflies and pollinators.

Adult butterfly counts and pollinator counts were analyzed with linear regression to examine the predictive value of butterflies. Residuals were examined for goodness of fit, and an alpha level less than 0.05 determined significant relationships. Two outliers were excluded from the analyses, and data were natural log transformed to improve residual fit.

### Testing of indicator effectiveness

The significant relationship determined by the Mt. Trumbull sampling was tested in 2001 at the Ft. Valley restoration site. At the Ft. Valley site, one control and restoration treatment unit was sampled. Butterflies were sampled in June along 300 meter transects in each control and restoration treatment unit. Adult butterfly sampling techniques were identical to butterfly sampling above, as modified from Pollard (1977). Butterfly counts were summarized per treatment unit, and then used in the linear equation developed from Mt. Trumbull data to predict Hymenoptera abundances. Pollinators were collected once at Ft. Valley in July utilizing water traps. Predicted abundances and observed abundances were compared with a Chi$^2$ test

## Chapter 5: Conclusions

These papers on the butterfly response to ecological restoration treatments have shown the butterfly assemblage changed as a direct result of the ponderosa pine restoration treatment (Chapter 2). Contributing factors to these changes in the early successional years following restoration probably include changes in light intensity with the removal of the canopy. Although nectar resources did not show significant changes in this replicated design, previous studies (Waltz & Covington 1999) have shown nectar resources do increase with restoration treatments. Chapter 3 showed that some butterfly species may also respond to changes in the characteristics of their hostplants. The fast response of the butterfly assemblage to human-induced ecological change combined with their broad ecological requirements and ease of monitoring make these taxa ideal as indicators. Chapter 4 examined the relationship between butterflies and pollinators, and tests the indicator effectiveness of this predictive relationship.

These studies supported our general hypothesis that invertebrate monitoring provided broader analyses of ecosystem response to restoration treatments. These results showed that butterflies responded quickly to ecological changes, and would be useful in ecosystem monitoring schemes. We showed that the butterfly community had up to 2 times higher species richness and 3 - 5 times higher abundance in restoration treatments when compared with paired control forests (Chapter 2). We also found that low abundance species were censused more often in restoration treated units than in control units. The fast response of the butterfly assemblage to these thinning and burning treatments (within one season after treatment) suggests multiple mechanisms operating at different scales were affecting adult butterfly distribution.

Host plant availability, nectar resources and abiotic variables all have the ability to affect adult butterfly distribution. In this study, the plant community showed no significant differences between restoration treatments and controls two years following treatment. We know that sustainable butterfly habitat must include sufficient larval and adult food resources (Pollard & Yates 1993), but our sampling and analyses did not find significant changes in potential host plant abundances.

We suggest butterflies may indicate patchy changes in plant abundances that are notably difficult to measure with standardized sampling. If butterfly communities can show responses at these yearly scales, with or without measurable herbaceous changes, they may be very useful indicators of vegetative state following a disturbance or a restoration treatment (Chapter 2).

Arthropod host plants could show both negative and positive responses to host plant changes. For example, the larval host plant, New Mexico locust, resprouts readily after fire, and can maintain a more shrub-like architecture with frequent fire. While restoration treatments would create more open canopy for the host plant, treatments that include prescribed fire may initially result in New Mexico locust mortality and increased resprouting. However, the patchiness subsequent fires will likely support a mosaic of New Mexico locust age classes (Chapter 3).

Assessing habitat requirements of *Epargyreus clarus* larvae on New Mexico locust enabled us to predict larval responses to an ecosystem restoration project. Larvae were found in highest abundances on their host plant, New Mexico locust, when 1. the host plant was found under open canopy; 2. the host plant was juvenile, and 3. the host plant was non-resprout growth. Knowing that the ponderosa pine forest restoration thinning reduces canopy cover and that returning frequent fire to the system maintains a more shrub-like, juvenile host plant (Gottfried 1980; Boring & Swank 1984), we predicted higher larval abundances in treated areas. These predictions were shown to be accurate, with up to 4 times as many larvae found on host plants in restoration treatment units (Chapter 3).

Restoration goals cannot incorporate every possible faunal response (Aronson *et al.* 1993; Hobbs & Norton 1996; Ehrenfeld 2000). However, monitoring diverse taxa in restoration treatments broadens the scope of environmental variables that we can track (Kremen *et al.* 1993). Invertebrate populations, in particular, represent a broad range of ecological niches. In many cases, invertebrates are easy to census in high enough numbers to provide good statistical comparisons (Kremen *et al.* 1993). We suggest wildlife life-history traits and habitat-use data can help develop predictions for wildlife response to restoration treatments, and provide testable hypotheses when these restoration treatments are implemented (Bradshaw 1987; Jordan III *et al.* 1987; Michener 1997).

The response of butterfly communities suggests other arthropod herbivores may respond to restoration treatments in similar ways. Other herbivores feeding on New Mexico locust may also respond positively to the changes in host plant characteristics following restoration. Arthropods dependent upon light intensity may show increased activity in restoration treatments. Bees and other nectar or pollen feeding arthropods may show increases in diversity and abundances as a response to increased nectar resources, and therefore may parallel the responses of the butterfly community.

The importance of pollinators to ecosystem functioning has recently become the focus of conservation groups and researchers due to the decreasing abundance of native bees (Buchmann and Nabhan 1996). Although butterflies are not as efficient at pollination as the Hymenoptera (bees and wasps) or Diptera (flies) (Scoble 1992), they are easier to monitor and identify. Using these restoration experiments, the efficacy of butterflies as indicators of other pollinators was tested (Chapter 4).

In well-planned terrestrial restoration projects, we addressed several of the concerns of indicator development. Specifically, we were able to clearly define indicators and indicated variables. Secondly, we conceived hypotheses and goals that would contribute to the understanding of ecological processes as well as provide mechanistic linkages between indicator species and the indicated attribute. Thirdly and most importantly, we initiated testing of this proposed indicator relationships to help establish the hypothesized inferences and scope of indicator relationships (Chapter 4).

The strength of this study was that our research hypotheses and questions were tested in a paired design with replication. The research design and these treatment units provided a unique opportunity to monitor taxa responses to restoration treatments, develop and test predictions of an individual species response to this land management activity, and finally, to test ecological theory and indicator species effectiveness. Incorporation of experimental design into land management decision processes is imperative to inform management decisions, and can also contribute to ecological theory and understanding (Bradshaw 1987; Bradshaw 1993; Higgs 1994).

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