

Butterfly Response and Successional Change Following Ecosystem Restoration

Amy E. M. Waltz
W. Wallace Covington

Abstract—The Lepidoptera (butterflies and moths) can be useful indicators of ecosystem change as a result of a disturbance event. We monitored changes in butterfly abundance in two restoration treatment units paired with adjacent untreated forest at the Mt. Trumbull Resource Conservation Area in northern Arizona. Restoration treatments included thinning trees to density levels comparable to densities at the time of Euro-American settlement, and reintroducing a low to medium intensity fire to the system. One unit was treated in 1996, the second in 1998. Butterfly communities, nectar availability, and herbaceous species richness were compared between treated and adjacent control forests, and between 3-year posttreatment and 1-year posttreatment forests. Butterfly species richness and abundance were two and three times greater, respectively, in restoration treatment units than in adjacent control forests. Nectar plant species richness ranged from two to 10 times greater in restoration treatment units than in adjacent control forests. Comparison of the 3-year posttreatment unit with the 1-year posttreatment unit showed little difference in butterfly species richness and abundance, although no statistical comparisons can be made due to sample size. These restoration treatments offer a unique opportunity to study responses to and recovery from disturbance and restoration at a landscape level.

Introduction

Current studies and methods of ecosystem restoration are often 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 Kaye 1997; Covington and others 1997). As a result, ecosystem restoration often overlooks invertebrates as important components necessary for ecosystem function and process. This emphasis on ecosystem structure is primarily a result of limited available information. Historical records were often inventories of merchantable resources and did not describe how species interacted with each other, or what processes were important to ecosystem functioning (for example, Dutton 1882).

In: Vance, Regina K.; Edminster, Carleton B.; Covington, W. Wallace; Blake, Julie A. comps. 2001. Ponderosa pine ecosystems restoration and conservation: steps toward stewardship; 2000 April 25–27; Flagstaff, AZ. Proceedings RMRS-P-22. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Amy E. M. Waltz is Research Specialist with the Ecological Restoration Institute in the College of Ecosystem Science and Management and a Ph.D. student in the Department of Biological Sciences at Northern Arizona University. W. Wallace Covington is Regent's Professor in the School of Forestry at Northern Arizona University, and is Director of the Ecological Restoration Institute.

Knowledge of ecosystem function and process can be obtained from studying current-day undisturbed ecosystems (Leopold 1949), although few if any “undisturbed” ecosystems exist. In addition, historical function and process can be inferred by studying function and process in experimentally restored ecosystems (Leopold 1949).

In ponderosa pine forests in the Southwest, forest structure can be reconstructed from presettlement remnants and historical records (Covington and Moore 1994; Fulé and others 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 and others 1995; Fredlund and Tieszen 1997). These data show that Southwest forests prior to Euro-American settlement had lower tree densities than current forests (50–150 trees per hectare (tph) in 1870 versus 500–3,000 tph in 1994, Covington and Moore 1994) with grassy openings. Experimental restoration of these forests has been initiated using thinning to reduce current tree densities and reintroducing fire.

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

The Lepidoptera (butterflies and moths) can be excellent indicators of herbaceous community diversity and composition (Gilbert 1984; Erhardt 1985; Kremen 1994; Sparrow and others 1994). Both butterflies and moths can be host-specific as larvae, but become nectar generalists as adults, encompassing a broad range of ecological niches. Changes in butterfly diversity can indicate changes in the abundance and diversity of a wide variety of invertebrates (Scoble 1992). Presence of a butterfly or moth species indicates presence of the larval host plant, as well as sufficient adult food resources. Day-flying butterflies in particular have a well-known taxonomy, and often can be easily identified in the field (Scoble 1992).

In the ponderosa pine ecosystem, the diurnal Lepidopteran (butterflies) can be used to monitor important changes in ecosystem function as a result of disturbance, rehabilitation, or restoration events. Restoration of ponderosa pine forests

involves thinning to create openings, thereby initiating an herbaceous successional pattern (Springer and others, this proceedings). While butterflies have shown decreases in abundance after clear-cut logging events (Hill and others 1995), openings in forests or changes created by roadways and paths often show higher butterfly abundances than nearby forests (Pollard and others 1975). It has also been shown that the butterfly community structure changes in response to successional changes from grasslands to forests in Europe (Erhardt and Thomas 1991). These studies suggest the potential for both an immediate and a long-term response to ponderosa pine restoration. For example, butterfly diversity and abundances could initially decrease in response to logging and ecosystem disturbance, then increase in abundance and diversity with the increasing herbaceous community.

The study presented here was initiated to establish the response of butterflies to ecological restoration treatments and potential mechanisms of that response. If changes in butterfly communities are noted, future studies will examine the role of butterflies as bioindicators of invertebrate pollinator groups.

Research Questions

To address the usefulness of butterflies as indicators of restoration treatments, this paper specifically addresses the questions:

1. Does the butterfly community differ between ponderosa pine restoration treatment units and untreated forest?
2. What are potential mechanisms of these differences: (a) Are nectar resources distributed differently? (b) Are host plants distributed differently? (c) Does butterfly habitat preference explain butterfly distribution?
3. Finally, do butterflies show a successional response to restoration treatments?

Methods

Study Site

The study site used for this research is a ponderosa pine (*Pinus ponderosa*) and Gambel oak (*Quercus gambelii*) forest located between Mt. Logan and Mt. Trumbull, about 35 km north of the Grand Canyon on the Arizona Strip. This land is currently managed by the Bureau of Land Management, and falls within the newly 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 is about 100 km east, on the Kaibab Plateau. The elevation of the sky island ranges from 1,675 m to 2,620 m. The area receives an average of 40–45 cm of rainfall annually, and contains some of the biota of the Great Basin (Utah Flora 1986), in addition to the flora of northern Arizona (Kearney and Peebles 1951). The forest is predominately ponderosa pine, although Gambel oak composes 15 percent of the overstory. Other tree species in the area include aspen (*Populus tremuloides*), pinyon (*Pinus edulis*), juniper

(*Juniperus osteospermus*), and New Mexican locust (*Robinia neomexicanus*). Although New Mexican locust is classified as a shrub, it grows to tree stature at this site, and is sampled as a tree. The understory component is dominated by sagebrush (*Artemisia tridentata*), and shows evidence of invasion by nonnative species, such as cheatgrass (*Bromus tectorum*) and wheatgrasses (*Agropyron* spp.). Although 150 herbaceous species have been documented at Mt. Trumbull since the late 1990s (J.D. Springer, personal communication), the forest floor cover prior to restoration treatments was 70 percent litter and duff, with only 15 percent of the cover represented by understory species.

Approximately 1,450 ha of the 5,000-ha forest is targeted for restoration treatment (Covington and others 1995), and as of 1999, approximately 200 ha had been thinned and burned. This restoration project is jointly sponsored by the BLM, the Arizona Game and Fish Department, and Northern Arizona University Ecological Restoration Institute. The ponderosa pine ecosystem restoration project takes an adaptive management approach, so that results from initial treatments can be incorporated into later treatments. The actual treatments in place are therefore continuing to evolve. At this site, analysis of fire scars provided a fire exclusion date (in other words, the date of the last widespread fire) of 1870. All treatment sites incorporate thinning trees to densities resembling those at the time of fire exclusion. Trees established at the time of fire exclusion are retained, as well as younger “replacement” trees for presettlement era trees that have died since fire exclusion. Fire is used preliminary to help reduce slash, and then will be returned to the landscape every 4–7 years, depending on weather conditions. For complete details of the treatment, please see the 1996 Annual Report to BLM. Treatment of all 1,450 ha is to be completed by 2002.

Butterfly Sampling

Butterfly monitoring data presented in this paper were taken from two units treated in 1996 (Lava Unit) and in 1998 (Trick Tank Unit). Butterfly monitoring transects (Pollard 1977) were established in the two treatment units, and were paired with monitoring transects in untreated forests (control) adjacent to each unit. Transects were placed 50 m from unit boundaries to minimize edge effects and were at least 50 m apart. Although length of transects varied with total treatment unit size to maintain buffer from edges, lengths of the paired treatment-control transects were the same. Transects in the Lava unit totaled 450 m in each the treatment and the control; transects in the Trick Tank unit totaled 600 m in each the treatment and the control for a total of 2,100 m per survey.

Transects were monitored every week, between May and September of 1999. Diurnal butterflies are very sensitive to cool and windy conditions, often limiting their flights on cloudy, cool days, thereby reducing chance of observation. Therefore, sampling was done between 1,000 and 1,600 hours, on days warmer than 17 °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, along with location along transect, and lateral distance from

Table 1—Butterfly species found at Mt. Trumbull Resource Conservation Area, Summer 1999. * denote most common species.

Hesperiidae	Lycaenidae	Nymphalidae	Papilionidae	Pieridae
<i>Epargyreus clarus*</i>	<i>Callophrys gryneus</i>	<i>Chlosyne californica</i>	<i>Papilio multicaudata</i>	<i>Anthocharis sara</i>
<i>Erynnis telemachus*</i>	<i>Strymon melinus</i>	<i>Danaus gilippus</i>		<i>Colias eurytheme*</i>
<i>Heliopetes ericetorum</i>	<i>Hypaurotis crysalis</i>	<i>Danaus gilippus</i>		<i>Nathalis iole</i>
<i>Pyrgus communis</i>	<i>Glaucopsyche lygdamus*</i>	<i>Euphydryas chalcedona</i>		<i>Pieris protodice*</i>
<i>Thorybes pylades</i>	<i>Hemiargus isola</i>	<i>Euptoieta claudia</i>		
	<i>Leptotes marina</i>	<i>Limenitis bredowii</i>		
	<i>Plebejus acmon</i>	<i>Limenitis weidemeyerii</i>		
	<i>Plebejus icarioides</i>	<i>Nymphalis antiopa</i>		
		<i>Nymphalis californica</i>		
		<i>Phycoides campestris</i>		
		<i>Polygonia gracilis</i>		
		<i>Precis coenia</i>		
		<i>Vanessa cardui</i>		
		<i>Vanessa atalanta</i>		
		<i>Vanessa carye</i>		

transect (perpendicular to transect). In addition for each observation, we recorded behavior (in other words, nectaring, basking, flying), and if 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 observations and did not include time spent in pursuit of a butterfly.

Nectar Resources and Host Plant Distribution and Habitat Preferences

To quantify nectar resources and host plant distribution, vegetation along the butterfly monitoring transects were monitored in 1-m² plots every 20 m along the established transect. A total of 30 plots were sampled in both the Trick Tank treatment and the nearby control, and 23 plots were sampled in both the Lava treatment and its adjacent control. Plots were monitored three times during the summer: May, June and August. At each plot, flowering and nonflowering plants were tallied by species. In addition, total number of flowers per 1-m² plots was tallied. These data were summarized by unit and treatment to determine differences in flowering plant species richness and host plant abundance.

Habitat preferences for each butterfly were determined from the literature, predominately Scott (1984). All butterfly observations from both units and the entire season were then grouped into habitat preference classes. Total tallies are presented here. No statistical analysis was done because data were lumped, resulting in no replication.

Successional Response to Restoration

To address whether butterflies show a successional response to restoration, we compared the butterfly communities from Lava and Trick Tank units, using the same monitoring data from above. The Lava unit was treated in 1996, and is referred to as a 3-year posttreatment unit. The Trick Tank unit, treated in 1998, is referred to as a 1-year posttreatment unit. Butterfly species richness, abundance, and composition were compared.

Results

Thirty-three butterfly species were collected at the Mt. Trumbull site in 1999 (table 1). The most common of these included the silver-spotted skipper (*Epargyreus clarus*, EPCL), the Gambel oak dusky-wing (*Erynnis telemachus*, ERTE), the silvery blue (*Glaucopsyche lygdamus*, GLLY), the orange sulfur (*Colias eurytheme*, COEU), and the checkered white (*Pieris protodice*, PIPR). The butterflies used a range of hostplants, including legumes, mustards, various shrubs, shrub-trees (New Mexican locust) and trees (oak).

Butterfly Community Response to Restoration Treatments

We found up to three times as many butterfly species in restoration treatments as in the adjacent, untreated control forests (fig. 1, Repeated Measures ANOVA, $F = 12.9$, $p < 0.10$). Table 2 lists species found in the Lava and Trick

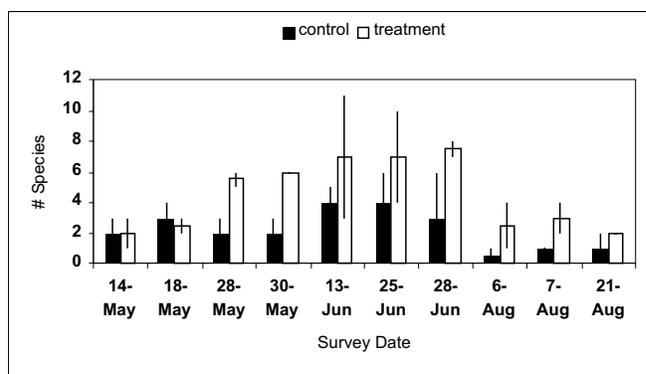


Figure 1—Butterfly species richness encountered in restoration treatment and adjacent control units. Up to three times as many species were observed in restoration treatments than in adjacent controls. Repeated measures ANOVA, $F = 12.0$, $p < 0.10$.

Table 2—Butterfly species and total observations found in restoration treatments and adjacent controls of Lava and Trick Tank units. Tally is total observations from 10 surveys, each survey covered 2,100 m (1,050 in control, 1,050 in treatment).

Control		Treatment	
Species	Tally	Species	Tally
<i>Erynnis telemachus</i>	22	<i>Epargyreus clarus</i>	70
<i>Epargyreus clarus</i>	16	<i>Erynnis telemachus</i>	59
<i>Glaucopsyche lygdamus</i>	12	<i>Glaucopsyche lygdamus</i>	46
<i>Limenitis bredowii</i>	10	<i>Colias eurytheme</i>	42
<i>Colias eurytheme</i>	8	<i>Pieris</i> sp.	35
<i>Plebejus icarioides</i>	3	<i>Plebejus icarioides</i>	9
<i>Phycoides campestris</i>	2	<i>Vanessa cardui</i>	9
<i>Plebejus acmon</i>	2	<i>Leptotes marina</i>	6
<i>Papilio multicaudata</i>	1	<i>Plebejus acmon</i>	6
<i>Euphydryas chalcedona</i>	1	<i>Phycoides campestris</i>	5
<i>Limenitis weidemeyerii</i>	1	<i>Strymon melinus</i>	4
<i>Pieris</i> sp.	1	<i>Limenitis bredowii</i>	4
		<i>Papilio multicaudata</i>	2
		<i>Polygonia gracilis</i>	2
		<i>Pyrgus communis</i>	2
		<i>Heliopetes ericetorum</i>	1
		<i>Vanessa carye</i>	1
		<i>Thorybes pylades</i>	1
		<i>Euptoieta claudia</i>	1

Tank treatment and control units. Common species were observed in both control and restoration treatment units but were seen more often in restoration treatments. Rare species (such as *Heliopetes ericetorum*) were observed in restoration treatments, when seen.

Butterfly abundance was also significantly greater in restoration treatment areas as in adjacent control forests (Repeated Measures ANOVA, $F = 7.98$, $p = 0.106$). Four to eight times as many butterflies were observed in treatment units as in adjacent controls on any given survey date. As shown in table 2, silver-spotted skipper (*Epargyreus clarus*) was the most common species observed, and was observed five times as frequently in the treatment unit as in the control units. *Pieris* species (whites) were highly abundant in the area, but were observed only once in the control units. Only one butterfly showed higher abundances in the control units than in the treatment units. The Arizona sister (*Limenitis bredowii*) was rare in 1999 but was observed 10 times in control units and only four times in treatment units. This pattern for the Arizona sister is consistent with 1998 data (Waltz and Covington 1999).

Nectar Resource Richness and Abundance

We examined potential mechanisms for increased butterfly species richness and abundance in treated forests. From the 1-m² plots surveyed along butterfly transects, we compared the species richness, species abundance, and flower abundance of the plants that were flowering at the time of survey. Number of flowering species (species richness) was significantly greater in treatment vegetation plots than in

control vegetation plots (fig. 2, Kruskal-Wallis test (effects = survey and trt), treatment $Z = 5.45$, $p < 0.05$). In addition, flowering plant abundance (or number of plants) was also significantly greater (fig. 3, Kruskal-Wallis, treatment $Z = 5.50$, $p < 0.05$). Not surprisingly, abundance of flowers per 1-m² plot was also significantly greater in treated units, with up to 200 times as many flowers in 1-m² plots (Kruskal-Wallis, $Z = 5.77$, $p < 0.05$). These results showed that both a higher diversity of plants and a higher total number of plants were flowering in restoration treatment units.

Host Plant Distributions and Habitat Preferences

We examined host plant distributions for the five most common butterfly species (table 1, * species denote most common). Table 3 lists these butterflies, their associated

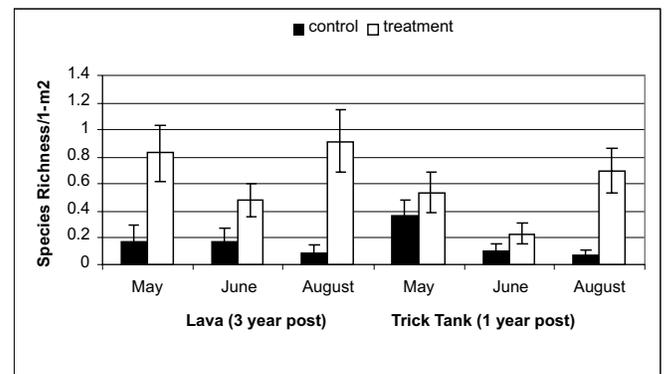


Figure 2—Nectaring plant species richness per 1-m² plot was significantly higher in restoration treatment units than in adjacent controls. Kruskal-Wallis for effects survey and treatment. Treatment $Z = 5.45$, $p < 0.05$.

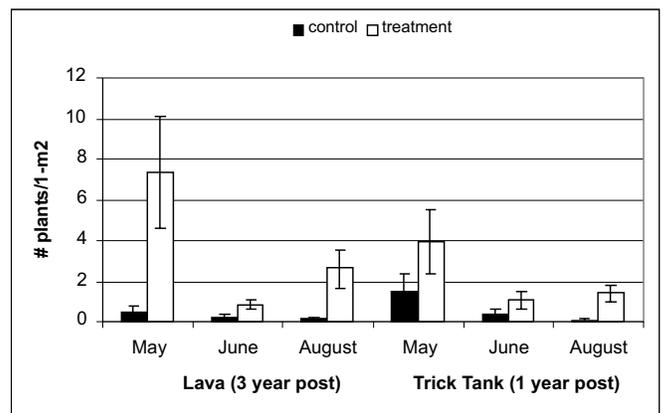


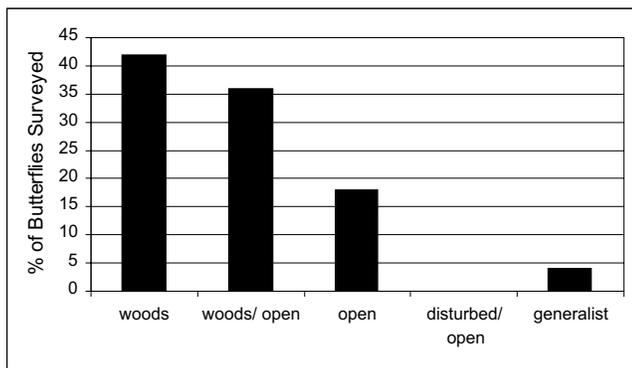
Figure 3—Nectaring plant abundance (number of plants observed) per 1-m² plot was significantly higher in restoration treatment units than in adjacent controls. Kruskal-Wallis for effects survey and treatment. Treatment $Z = 5.50$, $p < 0.05$.

Table 3—Distribution of host plants for the five most common butterfly species. Distributions showed no significant differences between restoration treatments and adjacent control units. Sampling design does not incorporate the tree species well. Butterfly species codes refer to first two letters of genus and first two letters of species.

Butterfly	Host plant	Plants / 1-m ²	
		Control	Treatment
EPCL	<i>Robinia neomexicana</i>	0.02	0.02
ERTE	<i>Quercus gambelii</i>	0.21	0.21
GLLY	Fabaceae	1.26	2.47
<i>Pieris</i> sp.	Brassicaceae	0	0.17
COEU	Fabaceae	1.26	2.47

host plants and the host plant abundance per 1-m² plot. Two of the species, the silver-spotted skipper (EPCL) and the Gambel oak dusky-wing (ERTE), host on tree species. Only tree seedlings are measured on 1-m² plots. However, we included the tally of tree seedlings per 1-m² plot in this table, which shows no differences in tree abundances between treatment and control. In fact, host plant species were distributed equally between control and treatment units.

a. control



b. treatment

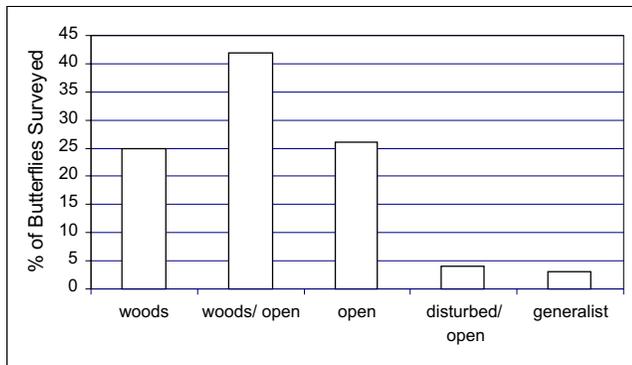


Figure 4—Habitat preferences of observed butterflies in (a) control and (b) restoration treatment units. Graphs represent proportion of observed butterflies only, lumped from 10 surveys from both sites. No statistical analysis performed.

Alternative methods are planned to adequately assess host plant distributions in treatment and control units.

Data on habitat preference and host plant preference are reported only as observed trends, and will be used to generate hypotheses to be tested in future field seasons. The highest proportion of the butterflies observed in control units were species preferring wooded habitat (fig. 4a). The highest proportion of the butterflies observed in treatment units were species preferring woods/open habitat (fig. 4b). Host plant preferences also displayed interesting trends. Butterfly species that hosted on tree species made up the highest proportion of the butterflies observed in the control areas. Alternatively, butterfly species hosting on legumes and forbs made up the highest proportion of the butterflies observed in the treatment areas. Basically, the butterfly species observed in control areas were species that preferred wooded habitat, and most often were species that hosted on tree species. Butterflies observed in treated areas were species that preferred more open habitat, and most often were species that hosted on legumes or forbs. Because of lack of sample size, the variables habitat preference and host plant type were not statistically tested. These results represent proportional trends only.

Butterfly Community Successional Response to Restoration

Figure 5 displays the butterfly species richness data across surveys between the Lava unit (3-years posttreatment) and the Trick Tank unit (1-year posttreatment). Because we observed only one unit for each successional stage, these data are presented as trends. Although some trend exists toward higher numbers of species in the 3-year posttreatment unit, we cannot assess those differences with only one sampling unit per successional stage. Plant communities shift from an annual forb community in 1-year post-treatment units to more perennial forbs and grasses in the 3-year posttreatment unit (Springer, personal communication). We did see increases in diversity of flowering species

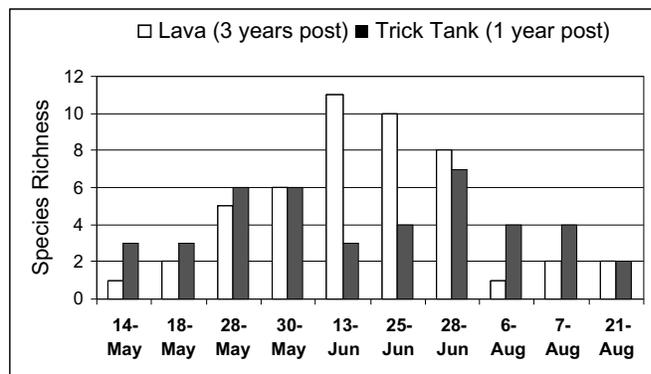


Figure 5—Butterfly species richness in Lava (treated 1996) and Trick Tank (treated 1998) units. Although there are trends toward higher species numbers in the Lava unit (treated in 1996), statistical analysis is not possible with only one sampling unit per successional state.

in the 3-year posttreatment unit compared with the 1-year posttreatment unit. Future studies will be designed to increase sample size and address the successional response of butterflies to ecological restoration.

Discussion

We have shown that the butterfly community had higher species richness and abundance in restoration treatments when compared with adjacent control forests. We also suggest that species with low abundance are more often found in treated units than in control units. Ponderosa pine restoration treatments alter habitat by opening up tree canopies and increasing herbaceous production. The fast responses of butterflies to these changes (within one season after treatment) suggest that arthropods may be one of the first responders to ecological changes. Erhardt and Thomas (1991) also documented butterfly responses to plant successional changes, showing butterfly community changes even before plant community changes could be detected. While some studies show that butterflies decrease after logging events (Hill and others 1995), the logging monitored in those cases was clear-cutting, with little regard for understory establishment. Our results agree with several studies that show gaps created in forest canopies increase butterfly abundances, whether through increased host plant diversity, or changes in microhabitats (abiotic variables) (Pollard 1977; Pollard and others 1975; Holl 1996).

The mechanistic hypotheses we examined to explain butterfly distributions suggest nectar resource availability may contribute greatly to adult butterfly distribution patterns. Our preliminary results showed large differences in available nectar resources in Lava and Trick Tank treatment units, when compared with adjacent control forests. Increased nectar resources can be associated with disturbed areas; many early successional plants are flowering forbs (Springer 1998). Studies have shown that nectar resources are important to adult oviposition selections. Host plants are utilized only when sufficient adult resources (nectar) are also available (Grossmueller and Lederhouse 1987; Murphy 1983). Successful butterfly habitat must therefore include sufficient larval and adult food resources.

Our restoration treatments have much higher plant diversity than control forests (Springer and others, this proceedings), implicating a higher diversity of butterfly host plants in these areas. Our results showed no differences in the host plant distributions of five common butterflies between treatment and control forests. However, the sampling method used here was not designed for tree species, which act as host plants for two of the most common butterflies. In addition, the variability of plant abundance measured in these units was also very high, suggesting plant distributions should be measured on a greater than 1-m² scale. Both reasons suggest our current sampling method is not adequate to address questions of host plant distributions.

Habitat preference may also contribute to butterfly community composition shifts. A habitat change from closed-canopy, low plant diversity forests to open canopy grasslands may also see a corresponding shift in butterfly community composition. Our preliminary observations suggest that butterflies found in treated forests were more likely to be

species preferring open habitat, requiring legume and forb host plants. Conversely, butterflies observed in control forests were more likely to be species preferring wooded habitat, and hosting on tree species. Although we could not test these patterns statistically, other papers have shown the importance of habitat selection in community composition (Ehrlich and Raven 1964; Ehrlich 1993; Erhardt and Thomas 1991).

Studies of the successional response of butterflies to restoration may give insight to how fine of a scale butterflies can respond to. The successional change in plant communities following thinning and burning can be dramatic. In the Lava unit, plant species richness increased from less than 5 species in 1995 to 7, 16, and 20 species in posttreatment years 1, 2, and 3 respectively. However, it may take longer for these plant species to establish viable, reproducing populations. Steffan-Dewenter and Tschardt (1997) observed successional responses of butterfly communities in set-aside fields in Germany. Although species richness of the butterfly communities did not change through 4 years of agricultural field succession, the butterfly community composition did show differences. If butterfly communities can show responses at these yearly scales, they may be very useful indicators of successional stage following a disturbance or a restoration treatment.

Problems/Confounding Factors

These results are from a small sample size (two units with paired controls) and should be treated as preliminary, but at the same time suggest more rigorous studies are validated. Currently, a paired block design is set up to monitor butterfly response to restoration treatments and mechanisms of these responses. This increased sample size should help reduce this problem in 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. However, studies have shown positive correlations between adult butterfly densities and larval densities, suggesting monitoring of adult butterflies may provide a close indication of larval densities (Steffan-Dewenter and Tschardt 1997). Of the 20 species recorded in the Lava and Trick Tank units and associated controls, 12 were classified as locally distributed, not ranging far from their host plants as adults (Scott 1984).

Implications

The response of butterfly communities suggests other arthropod herbivores may respond to restoration treatments in similar ways. Arthropods constitute the largest biomass of any taxon and occupy a large range of functional niches (Kremen and others 1993). Bees and other nectar or pollen feeding arthropods may show increases in diversity and abundance as a response to increased nectar resources, and therefore may parallel the responses of the butterfly community. The importance of pollinators to ecosystem function has recently become the focus of many questions, 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. In addition, arthropods decompose organic material, release nutrients back into the ecosystem, and provide the largest food source in almost every ecosystem (Wilson 1987).

Using these restoration experiments, the efficacy of butterflies as biodiversity indicators of these other arthropods can easily be tested, by increased sampling of other taxonomic groups, correlations, and finally testing in other areas undergoing restoration treatments.

The research presented here provides insight into how the butterfly community responds to habitat change, and some of the mechanisms behind that response. Not only do butterfly communities contribute to ecosystem functioning through herbivory, providing food source and pollination events, they also have the potential to be bioindicators of biodiversity in other arthropod guilds.

Acknowledgments

We thank Holly Petrillo, Peter Fulé, Gina Vance, and the Ecological Restoration Institute for field and analysis support. We also thank an anonymous reviewer for comments. The Arizona Strip District, Bureau of Land Management, especially Greg Taylor, Ken Moore, and Roger Taylor made this study possible. Funding was provided by Bureau of Land Management, Department of the Interior.

References

- Beccaloni, G.W. and K.J. Gaston. 1995. Predicting the species richness of neotropical forest butterflies: Ithomiinae (Lepidoptera: Nymphalidae) as indicators. *Biological Conservation* 71:77–86.
- Bozarth, S. 1993. Biosilicate assemblages of boreal forests and aspen parklands. *Current Research in Phytolith Analysis: Applications in Archaeology and Paleoecology*. MASCA Research Papers in Science and Archaeology. D.M. Pearsall and D.R. Piperno, editors. Philadelphia: The University Museum of Archaeology and Anthropology.
- Buchmann, S. and G. Nabhan. 1996. *The forgotten pollinators*. Washington, DC: Island Press/Shearwater Books.
- Covington, W.W., P.Z. Fulé, M.M. Moore, S.C. Hart, T.E. Kolb, J.N. Mast, S.S. Sackett, M.R. Wagner. 1997. Restoring ecosystem health in ponderosa pine forests of the Southwest. *Journal of Forestry* 95(4):23–29.
- Covington, W.W. and M.M. Moore. 1994. Southwestern ponderosa forest structure: changes since Euro-American settlement. *Journal of Forestry* 92(1):39–47.
- Dutton, C. 1882. Tertiary history of the Grand Canyon. Report to Department of the Interior, United States Geological Survey.
- Ecological Restoration Program, Northern Arizona University. 1996. *Ecosystem Restoration Project: Annual Report for the year October 1, 1995 to September 30, 1996*. Prepared for the Bureau of Land Management, Arizona Strip District, St. George, UT.
- Ehrlich, P.R. 1993. Birds, butterflies, and forest patches. *American Birds* 47(5):1044–1046.
- Ehrlich, P.R. and P.H. Raven. 1964. Butterflies and plants: a study in coevolution. *Evolution* 18: 586–608.
- Erhardt, A. 1985. Diurnal Lepidoptera: sensitive indicators of cultivated and abandoned grassland. *Journal of Applied Ecology* 22:849–861.
- Erhardt, A. and J.A. Thomas. 1991. Lepidoptera as indicators of change in the semi-natural grasslands of lowland and upland Europe. pages 213–236 in *The Conservation of Insects and Their Habitats*. Edited by N.M. Collins and J.A. Thomas. Academic Press, New York.
- Fisher, R.F., C.N. Bourn, W.F. Fisher. 1995. Opal phytoliths as an indicator of the floristics of prehistoric grasslands. *Geoderma* 68:243–255.
- Fulé, P.Z. and W.W. Covington. 1997. Fire regimes and forest structure in the Sierra Madre Occidental, Durango, Mexico. *Acta Botanica Mexicana* 41:43–79.
- Fredlund, G.G. and L.L. Tieszen. 1997. Phytolith and carbon isotope evidence for the late quaternary vegetation and climate change in the southern Black Hills, South Dakota. *Quaternary Research* 47:206–217.
- Gilbert, L.E. 1984. The biology of butterfly communities. Pages 41–61 in R.I. Vane-Wright and P.R. Ackery, editors. *The Biology of Butterflies*. New York: Academic Press.
- Grossmueller, D.W. and R.C. Lederhouse. 1987. The role of nectar source distribution in habitat use and oviposition by the tiger swallowtail butterfly. *Journal of the Lepidopterists' Society* 41(3):159–165.
- Hill, J.K., K.C. Hamer, L.A. Lace, W.M.T. Banham. 1995. Effects of selective logging on tropical forest butterflies on Buru, Indonesia. *Journal of Applied Ecology* 32:754–760.
- Holl, K.D. 1996. The effect of coal surface mine reclamation on diurnal Lepidopteran conservation. *Journal of Applied Ecology* 33(2):225–236.
- Kaye, J. 1997. Effects of succession and ecological restoration on the biogeochemistry of a ponderosa pine-bunchgrass ecosystem. Master's Thesis. Northern Arizona University.
- Kearney, T.H. and R.H. Peebles. 1951. *Arizona flora*. Berkeley, CA: University of California Press.
- Kevan, P.G. 1999. Pollinators as bioindicators of the state of the environment: species, activity and diversity. *Agriculture, Ecosystems and Environment* 74:373–393.
- Kremen, Claire. 1994. Biological inventory using target taxa: a case study of the butterflies of Madagascar. *Ecological Applications* 4(3):407–422.
- Kremen, C., R.K. Colwell, T.L. Erwin, D.D. Murphy, R.F. Noss, M.A. Sanjayan. 1993. Terrestrial arthropod assemblages: their use in conservation planning. *Conservation Biology* 7(4):796–808.
- Leopold, A. 1949. *A Sand County almanac*. New York: Oxford University Press.
- McGeoch, M.A. 1998. The selection, testing and application of terrestrial insects as bioindicators. *Biological Review* 73:181–201.
- Murphy, D. 1983. Nectar sources as constraints on the distribution of egg masses by the checkerspot butterfly, *Euphydryas chalcedona* (Lepidoptera: Nymphalidae). *Environmental Entomology* 12(2):463–466.
- Pollard, E. 1977. A method for assessing changes in the abundance of butterflies. *Biological Conservation* 12:115–134.
- Pollard, E., D.O. Elias, M.J. Skelton, J.A. Thomas. 1975. A method of assessing the abundance of butterflies in Monks Wood National Nature Reserve. *Entomologist's Gazette* 26:79–88.
- Rovner, I. 1971. Potential of opal phytoliths for use in paleoecological reconstruction. *Quaternary Research* 1:343–359.
- Scoble, Malcolm J. 1992. *The Lepidoptera*. Oxford University Press. Oxford, UK.
- Scott, J.A. 1984. *Butterflies of North America*. Stanford, CA: Stanford University Press.
- Sparrow, H.R., T.D. Sisk, P.R. Ehrlich, D.D. Murphy. 1994. Techniques and guidelines for monitoring neotropical butterflies. *Conservation Biology* 7:800–809.
- Springer, J.D. 1999. Soil seed bank in Southwestern ponderosa pine: implications for ecological restoration. Master's Thesis. Northern Arizona University.
- Steffan-Dewenter, I. and T. Tscharntke. 1997. Early succession of butterfly and plant communities on set-aside fields. *Oecologia* 109:294–302.
- Waltz, A.E.M. and W.W. Covington. 1999. Butterfly richness and abundance increase in restored ponderosa pine ecosystem (Arizona). *Ecological Restoration* 17(4):244–246.
- Welsh, S.L. 1987. *A Utah flora*. Provo UT: Brigham Young University Press.
- Wilson, Edward O. 1987. The little things that run the world: the importance and conservation of invertebrates. *Conservation Biology* 1(4):344–346.