AN ABSTRACT OF THE THESIS OF

Breanna F. Powers for the degree of Master of Science in Wildlife Science
presented on May 13, 2014.
Title: Butterfly and Flower Community Composition among Prairie-oak Ecosystem Habitats in the Willamette Valley, Oregon

Abstract approved:

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W. Daniel Edge

Prairie-oak ecosystems in the Willamette Valley, Oregon have experienced habitat loss and degradation; most of these ecosystems are fragmented into smaller patches. Prairie-oak butterfly species, in the Willamette Valley, have decreased dramatically due to loss or degradation of habitat. More research is needed on sustaining the populations of butterflies in prairie-oak ecosystems. The purpose of my study was to examine the role prairie-oak habitats have in structuring butterfly communities in the Willamette Valley. My objectives were to: (1) assess how butterfly community structure and species composition (density, abundance, and species richness) varies along an oak canopy cover gradient in order to understand the role of habitat type in structuring butterfly communities in prairie-oak ecosystems; (2) characterize community composition of nectar resources and environmental variables known to be important for butterfly species. I also investigated temporal and structural relationships between butterfly and flower communities. I found that butterfly abundance and density were greater ($p \leq 0.02$) in prairies than in oak savannas or oak woodlands; however, species richness did not differ among habitats ($p = 0.54$).

Ordination of prairie-oak habitats in butterfly species space with a joint plot overlay of environmental variables revealed several strong correlations; butterfly community structure was negatively correlated with litter and oak canopy cover and positively correlated to vegetation cover. The prairie, oak savanna, and oak woodland habitat types differed in nectar species community structure, though this difference was small. Non-native species were some of the most abundant flowers species found in all stands. Butterfly communities were positively related to flower communities. I detected significant seasonal patterns among the habitat types in butterfly and flower communities. Prairies appear to be the most important habitat for native butterfly populations compared to oak savanna and oak woodlands. Flowers were most prevalent in prairies and prairies had the highest percentage of native flower species; the prevalence of non-native flower species was greatest in oak woodlands. My study may represent a short-term community transition as a result of management or it may represent a more permanent community. Further study is needed to understand the effects of different management strategies for habitat restoration and the presence of non-native flower species on butterflies in prairie-oak ecosystems in the Willamette Valley.

Butterfly and Flower Community Composition among Prairie-oak Ecosystem Habitats in the Willamette Valley, Oregon

by
Breanna F. Powers

A THESIS

Submitted to

Oregon State University

In partial fulfillment of
the requirements for the
degree of

Master of Science

Presented May 13, 2014
Commencement June 2014

Master of Science thesis of Breanna F. Powers presented on May 13, 2014.

APPROVED:

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Major Professor, representing Wildlife Science

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Head of the Department of Fisheries and Wildlife Science

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Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Breanna F. Powers, Author

ACKNOWLEDGEMENTS

I am extremely thankful for this opportunity to complete my graduate degree and conduct research, and deeply grateful to those who made it possible. Appreciation and thanks to Dan Edge for taking me on as his graduate student, for supporting me, and for guiding me through this journey, and to my committee members Sandra DeBano and Dave Hibbs for their expertise and input. My gratitude goes out to the federal agency and landowners who provided me with study sites--to Molly Monroe and Jock Beall at Finley National Wildlife Refuge, Jim and Ed Merzenich at Oak Basin Tree Farm, and Lynda Boyer at Jefferson Farm. Thanks to Paul Hammond for his butterfly expertise, and Bruce McCune for his community analysis expertise.

Furthermore, I am deeply thankful for my undergraduate advisor, Cynthia Dott, for her mentorship, knowledge, and friendship. Thanks to Steve Hanser, Matthew Johnson, Adam Rich, and to those who directly and indirectly helped me get here over the years.

I would like to thank my family and friends who always encouraged me to follow my passions; to my mother Cynthia, my brothers, and to Benjamin Cranston for his continual love and support.

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GENERAL INTRODUCTION

"In the timbered portions of the county, there was absolutely no brush. The trees were very massive and the ground underneath covered with prairie grass. The massive trees, the prairie flowers and grass all combined to make this a truly beautiful and inviting country."
~ Thomas Dockery

Prairie-oak ecosystems (i.e. prairies, oak savannas and oak woodlands) in the Willamette Valley have experienced habitat loss and degradation; most of these ecosystems are fragmented into smaller patches (Vesely and Rosenberg 2010). The Willamette Valley historically consisted of more than 400,000 ha of Oregon White Oak (*Quercus garryana*) savanna, hereafter referred to as oak savanna, and upland prairie when the Kalapuya Native Americans lived in the area (Hulse 1998, Murphy 2008, Thomas and Spicer 1987). Prairies and oak savannas were maintained by the local Native Americans through a combination of burning and other management practices (Brudvig and Asbjornsen 2005). Today, prairie-oak ecosystems are one of the most threatened and rapidly declining ecosystems in the Willamette Valley (Noss et al. 1995, U.S. Fish and Wildlife Service [USFWS] 2011). Primary reasons for the loss of these ecosystems include tree invasion, mainly conifers, fire suppression, and the presence of invasive species; other major contributors are land conversion and human population increases (Dunwiddle and Bakker 2011, Legacy Oaks Task Force and Prairie Task Force 2008). In the Willamette Valley, a large portion of original oak savanna have transitioned to conifer forest and less than one percent of the original oak savanna ecosystem remain (Hulse et al. 2002, Murphy 2008).

In the Willamette Valley prairie-oak systems all have undergone dramatic loss (Vesely and Rosenburg 2010). Restoration projects are increasingly important for preserving these remnant ecosystems and conserving the associated biodiversity (Barrioz 2010, Groom et al. 2006, Schultz et al. 2011). The decline of prairie-oak habitats has resulted in a decrease in biodiversity and some species have become rare (USFWS 2006, Barrioz 2010). Many prairie-oak-dependent species are on state and federal government lists as sensitive, threatened, or endangered species (Dunwiddie and Bakker 2011, Legacy Oaks Task Force and Prairie Task Force 2008) and restoring prairie-oak habitat is a high-priority conservation strategy (Brock and Brock 2004, Dunwiddle and Bakker 2011, Oregon Department of Fish and Wildlife [ODFW] 2006). In the Willamette Valley, the majority of oak savanna remnants persist on private lands. Several private organizations (e.g., The Nature Conservancy), federal and state agencies and private land owners have started prairie and oak ecosystem restoration projects (Dunwiddie and Bakker 2011, Legacy Oaks Task Force and Prairie Task Force 2008).

Prairie-oak ecosystem restoration efforts are initiated and maintained by prescribed burns, mowing, herbicides, or removal of invasive and encroaching species. Prairies and oak savannas are a fire-dependent ecosystem; fire frequency is known to influence the structure and composition of the plant community (Arthur et al. 1999). Fire as a management tool is most effective for conservation and restoration efforts (Mcpherson 1997) to reduce invasive species when a follow-up fire is used several years later or is combined with another management strategy. Otherwise, fire stimulates the growth of several invasive species (e.g., Scotch broom [*Cytisus scoparius*]) (Agee 1996 Schultz et al. 2011).

As a result of decreases in natural fire frequencies, more shade-tolerant and less fire-tolerant species, such as the Douglas-fir (*Pseudotsuga menziesii*) have encroached on oak savannas causing a transition to later successional stages (Barnes et al. 1998, Barrioz 2010, Swengel and Swengel 2001). Fires allow for oak regeneration. Burning increases the mortality of the fire-intolerant overstory species, which results in a decrease of tree canopy cover, thus allowing for more light to reach the ground, which in turn increases herbaceous ground cover (Apfelbaum and Haney 1987, Vogl 1964).

Although certain aspects of the Willamette Valley prairie-oak habitats have been well studied (Dunwiddie and Bakker 2011), little work has focused on invertebrates, such as butterflies (Schultz et al. 2011, Vesely and Rosenburg 2010). Butterflies associated with prairie-oak habitats, in the Willamette Valley, have decreased dramatically due to loss or degradation of habitat (Schultz et al. 2011). Butterflies are good indicators of environmental changes and are sensitive to changes in habitat quality

(Williams 2010). Furthermore, butterflies provide important ecosystem functions such as pollination and serve as an important prey base for other species (Yarrish 2011).

The purpose of my study was to examine butterfly species richness and abundance across a representation of different habitat types: prairie, oak savanna, and oak woodlands in the Willamette Valley, Oregon. My objectives were to: (1) assess how butterfly community structure and species composition (density, abundance, and species richness) varies along the oak canopy cover gradient in order to understand the role of prairie, oak savanna, and oak woodland habitats in structuring butterfly communities in prairie-oak ecosystems; and (2) characterize community composition of nectar resources and environmental variables known to be important for individual butterfly species; and (3) to determine if butterfly and flower community structures display seasonal patterns. My thesis contains three main chapters. In Chapter Two, I examined butterfly community structure and species composition across prairie, oak savanna, and oak woodland habitat types (based upon an overstory oak canopy-cover gradient). I also examined the community structure of butterflies in relation to landscape and vegetation structural elements. In Chapter Three, I describe the flower community structure and species composition among prairies, oak savanna, and oak woodlands. I also investigate the relationships among environmental and vegetation structural elements and nectar community structure. In Chapter Four, I assess the relationship between butterfly community structure and nectar plant community structure. I describe how butterfly and flower abundance and species richness changed seasonally among prairies, oak savannas, and oak woodlands.

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Chapter Two

Butterfly community composition varies among prairie-oak ecosystem habitats in Willamette Valley, Oregon

"Beautiful and graceful, varied and enchanting, small but approachable, butterflies lead you to the sunny side of life. And everyone deserves a little sunshine."

~Jeffrey Glassberg

ABSTRACT

Prairie and oak savanna and woodland ecosystems consist of Oregon white oak (*Quercus garryana*) along an overstory canopy cover gradient. There has been considerable loss of these ecosystems in the Willamette Valley. Butterfly species in the Willamette Valley have decreased dramatically due to loss or degradation of habitat. Although certain aspects of the Willamette Valley prairie-oak habitats have been well studied, little work has focused on invertebrate communities, such as butterflies. The objective of my study was to determine if butterfly community structure (i.e., richness, density, species composition, and abundance) varies across an oak canopy cover gradient and how butterfly community structure correlate with environmental variables associated with this gradient. I predicted that the abundance and density of all butterflies and species richness and diversity of the butterfly community would be negatively correlated with an oak canopy cover gradient. An alternative prediction is oak

savanna habitat will have a higher butterfly species richness and abundance compared to prairies and oak woodlands. I found that butterfly abundance and density were greater ($p \leq 0.02$) in prairies than in oak savannas or oak woodlands; however, species richness was not different ($p = 0.54$). Canopy cover appeared to have a strong influence on butterfly community structure. Prairie ecosystems appear to be more important habitat for native butterfly populations, compared to oak savannas and oak woodlands.

INTRODUCTION

Butterfly populations are experiencing a decline worldwide mainly attributed to habitat loss and degradation (Maes and Dyck 2001, Van Swaay et al. 2006). Habitat loss is one of the major factors of mass species decline and extinction (Groom et al. 2006, Schultz et al. 2011). Prairie-oak ecosystems are themselves of concern because of the dramatic loss of this ecosystem in the region (DeMars et al. 2010, Murphy 2008). Oregon white oak (*Quercus garryana*) is an important element in the prairie-oak habitats providing food resources, cover, nesting, and other habitat characteristics for multiple species (Brawn 2006, DeMars et al. 2010, Miller and Hammond 2007). Furthermore, conservation efforts for butterfly habitat also serves as a means to protect other species dependent upon the same habitat types (Yarrish 2011). Prairie-oak habitats, especially oak woodlands (Vesely and Roenburg 2010) support various wildlife including camas pocket gopher (*Thomomys bulbivorus*), white-breasted nuthatch (*Sitta carolinensis*), and acorn woodpecker (*Melanerpes formicivorus*) (USFWS 2011).

Prairie-oak ecosystems are noted for containing an open overstory of scattered oak trees and a diverse herbaceous ground layer (Abrams 1992). Prairies are a grassland ecosystem with a herbaceous community (Swengel and Swengel 2001, Vogel et al. 2007), and oak savannas share similar plant species composition, dominated by bunchgrasses and forbs; however, oak savanna has a higher density of oak trees. Oak woodland have a higher density of oak trees per ha than oak savannas and prairies (Vesely and Rosenburg 20010). The understory vegetation community in oak woodlands are also different than oak savannas or prairies. Oak woodlands, in the Willamette Valley, are noted for being associated with one of five different vegetation types that are based open understory vegetation community, slope, exposed or sheltered ridges, and soil moisture (Kagan et al. 2004, Murphy 2008, Thelineus 1968, Vesely and Rosenburg 2010). Disturbance by fire, has been greatly reduced in the Willamette Valley resulting in higher tree densities and increased encroachment of conifers, the majority being Douglas fir (*Pseudotsuga menziesii*).

The loss of prairie-oak ecosystems in the Willamette Valley, caused some private land owners and federal land managers to be interested in the restoration or maintenance of upland prairie, oak savanna, or oak woodland habitats. Once restoration occurs or if the land is remnant oak savanna or prairie, then maintenance (herbicide treatment or burning) is required to keep the upland prairie, oak savanna, or oak woodland intact. Restoration includes prescribed burning, removal of encroaching trees, seeding native species, herbicide treatments, or mowing (Boyer 2008). Controlled burns produce early successional environments in oak communities (Reed 1997) and over the growing season, after the burn, the plant community continually changes. This, in turn, affects which species and the rate those species (re)colonize a site (Andersen and Muller 2000, Reed 1997).

In the Willamette Valley, prairie-oak butterfly species are rapidly declining and some, such as the Fender's blue butterfly (*Icaricia icarioides fenderi*) and Taylor's checkerspot (*Euphydryas editha taylori*), are on the US Endangered Species list (Miller and Hammond 2007, U.S. Fish and Wildlife Service [USFWS] 2006). Historically, 24 species of butterfly were once present in upland prairies in the Willamette Valley; now seven species are extinct and six species only exists in small isolated populations (Wilson 1998). This is mainly attributed to loss and degradation of prairie-oak ecosystems upon which some butterfly populations rely (Miller and Hammond 2007, Schultz et al. 2011).

Butterflies are crucial components of a properly functioning ecosystem. They provide ecosystem services such as pollination, prey species (energy transfer), and decomposition (Andersen and Sparling 1997, Ramírez 2004, Waltz and Covington 2004). Adult butterflies have been proposed as indicators of environmental change (Yarrish 2011), and may also be predictors of species richness for other taxa (Fleishman et al. 2000). Butterflies can also be used as an indicator of restoration success because they respond quickly to changes in their environment and because adults and larvae have different resource requirements (Erhardt 1985, Erhardt and Thomas 1991, Waltz and Covington 2004). Landscape management practices such as burning can positively affect butterfly abundance and species richness (Vogel et al. 2007).

Different species of butterflies prefer different types of environments. This is based upon the specific nectar and host plant requirements of each species. Some species are specialist and other species are generalist. For example, the common wood-nymph (*Cercyonis pegala*) and common ringlet (*Coenonympha tullia*) are generalist when it comes to nectar and host plants are grasses. I would expect to find these two species in high density in the prairie and oak savanna habitats, where nectar and grass species are in greater abundance. Prairie-oak butterfly species communities in the three habitat types may be different due to each species' habitat requirements, mainly nectar and host plant presence. Non-native grasses, forbs, and other plants may affect community composition because of the specific host and nectar plant needs of local butterfly species (Appendix A). Community composition is also influenced by spatial scale (Loreau 2000).

I studied the distribution of butterflies (abundance and species richness) along an environmental gradient of oak canopy cover from native prairies to oak woodlands in the mid-Willamette Valley, Oregon. My objectives were to determine how: (1) butterfly community structure (relative density, abundance, and species richness) and species composition varies along an oak canopy cover gradient; and (2) butterfly community structure relates to environmental elements and sub-canopy vegetation known to be important for butterflies (Schultz et al. 2011). The role of prairie, oak savanna, and oak woodland habitats in structuring butterfly communities in prairie-oak ecosystems is unclear. Some studies suggest that butterfly nectar source abundance, density, and species richness are affected by overstory canopy coverage; an open canopy provides more light and area for the establishment of herbaceous plants (i.e., nectar and host plant resources) and other studies have shown light availability is linked to both increased host plant diversity and butterfly abundance (Grundel et al. 1998, Waltz and Covington 2004). In contrast, other studies suggest that oak savanna would have higher butterfly richness and abundance than prairie or woodland because of the heterogeneous mosaic of plant communities, varied micro-habitats, and greater structural elements associated with this intermediate habitat (Lane and Andow 2003, Reeder et al. 2005, Yarrish 2011). Structural elements that may display greater heterogeneity in the oak savanna include litter and ground vegetation height. These elements create different habitat types and varied microclimates (Grudnel et al. 1998), and heterogeneity at multiple scales is important for persistent and stable butterfly populations (Oliver et al. 2010, Yarrish 2011).

METHODS

Study area and season

My study was conducted in the mid-Willamette Valley, Oregon. I selected sites in three habitat types that represent the oak canopy-cover gradient in the prairie-oak ecosystem: prairie, oak savanna, and oak woodland. These habitat types were defined based upon percentage of oak canopy cover: prairie (< 10% tree canopy cover and predominately prairie ground cover); oak savanna (10-30% canopy cover); and oak woodland (> 31% canopy cover) (Au et al. 2008, Bray 1960, Vesely and Rosenberg 2010). Study sites were located at three different locations (Figure 2.1). My criteria for selecting survey locations included that they were located within 65 km of Corvallis in the Willamette Valley, and that each encompassed at least one prairie, oak savanna, and oak woodland site representing my canopy cover gradient.

I sampled 12 study sites at three different locations. The three different survey locations were Finley National Wildlife Refuge (FNWR), Jefferson Farm and Oak Basin Tree Farm (Appendix B). At each location I had four different study sites representing prairie-oak habitats: prairie, oak savanna, and oak woodland. Sites varied with respect to whether they were remnant or restored habitats and the methods used for maintenance and restoration.

The climate of the Willamette Valley, Oregon is relatively mild throughout the year with cool, wet winters and warm, dry summers. The majority of the rainfall occurs in the winter typically from December to February (Taylor et al. 2000). Average annual temperatures for Corvallis range from 5.4 to 17.1°C. Average annual precipitation is 104 cm (Western Regional Climate Center 2012).

Common native forbs associated with prairies and oak savanna are field cluster lily (*Dichelostemma capitatum*), large camas (*Camassia leichtlinii* spp)**,** Nelson's checkermallow (*Sidalcea nelsoniana*), common yarrow (*Achillea millefolium*), purple clarkia (*Clarkia purpurea*), blueheaded gilia (*Gilia capital*), and willowherb (*Epilobium densilorum*). Woody vegetation associated with oak woodlands are sword fern (*Polystichum munitum*), western serviceberry (*Amelanchier alnifolia*), snowberry (*Symphoricarpos albus*), poison oak (*Toxicodendron diversilobum*); and forbs include shooting star (*Dodecatheon hendersonii*), Oregon fawn lily (*Erythronium oregonum*), peavines (*Lathyrus* spp.), and woody strawberry (*Fragaria vesca*) (Vesely and Rosenburg 2011).

Butterfly species abundance and diversity

I conducted butterfly surveys every two weeks at each study site from July to September 2012, for a total of six butterfly surveys per site. Butterflies were identified to species level by using field guides (Neill 2001) and local expert knowledge either in the field or from photographs taken during a field observations. Butterfly life cycles including the number of broods per season and timing of flight vary among species (Miller and Hammond 2007). The number of broods per season range from one to several and the timing of flights occur from early spring (March) to late summer (September) (York 2003). Due to the unusual cold and wet spring and summer in the Willamette Valley in 2012 and site accessibility, I began sampling using point-counts in July. I recorded butterfly observations on days warmer than 17 °C and with wind speeds less than 15 kph between 0930 h and 1600 h (Miller and Hammond 2007, Waltz and Covington 2004). Many diurnal butterflies are highly sensitive to weather conditions such as cool temperatures and wind and may limit flight activities in these conditions, decreasing the chance of an observation (Waltz and Covington 2004).

Point counts were conducted along transects within each study site (Figure 2.2). I randomly chose one starting point and direction (left or right) and ran the first transect parallel to the border of the site and at least 25 m from the border to reduce edge effects (Dover and Settele 2009). All transect had multiple segments and a total length of transects of 500 m. Segments of transects were separated from each other >25 m. For each transect the plot locations and start and end coordinates (Universal Transverse Mercator) were marked by a Global Position System unit (Garmin, Model: e Trex Venture HC).

I used a line-transect and circular plots (Buckland et al. 2001, 2004) to quantify the number of butterflies (total abundance) and species richness. Every 25 m along the butterfly transect I established a 5-m radius circular plot. I sampled 20 plots along the transect line for each site; a total of 80 plots per habitat type. I surveyed study sites in different order to avoid the temporal effects of time and day. I assumed a survey conducted every two weeks (Waltz and Covington 2004) captured at least one adult phase lifecycle for all species known in the prairie-oak habitats (Miller and Hammond 2007). I spent 1 minute counting and capturing butterflies within each plot (Kadlee et al. 2012). For each butterfly observed, I recorded the species. For species that were not identified in the field, individuals were netted and taken for identification with help by Dr. Paul Hammond (Oregon State University).

Environmental variables

I measured environmental variables known to be important to butterflies once at each sample site: maximum understory vegetation height, ground percent cover, litter, bare ground cover, and elevation (Calvert and Brower 1986, Dennis 2004a, 2004b, Williams 2010). All vegetation, except flowers, were sampled once, at a time of the season (late July/early August) to capture the most plant species present (Grundel et al.

1998). I conducted vegetation surveys by establishing a 2-m^2 square plot at the center point of each butterfly plot. The maximum vegetation height of understory vegetation was measured in centimeters. I measured tree canopy cover using a moosehorn instrument. It has a square grid with 36 intersecting points used to estimate canopy cover by using an angled mirror to reflect the number of intersections by canopy cover (Fiala et al. 2006). Ground vegetation cover was estimated using the Braun-Blanquet scales (Bullock 2006).

Statistical analysis and modeling

Butterfly community characteristics

I calculated the density (number of individuals/ha), abundance (average number of individuals), richness averaged for each site. I performed a parametric analysis of variance (ANOVA) to determine differences in butterfly abundance, density, diversity, and richness among the habitat types. I correlated butterfly density, abundance, and richness with and canopy cover.

I used PC-ORD v.6 (McCune and Mefford 2009) for all ordination analyses to reveal patterns in species composition among communities (McCune and Grace 2002). To test the null hypothesis that butterfly community structure does not differ among habitat types, I used a multi-response permutation procedure (MRPP; Mielke and Berry 2001) with a Sørensen distance measure. MRPP is a nonparametric procedure that tests for differences between two or more pre-existing groups by providing a p-value and an effect size (A) that “describes within-group homogeneity compared to the random expectation" (McCune and Grace 2002: 190). I also used an indicator species analysis (ISA, Dufrene and Legendre 1997) to describe butterfly species relationships to stand types (McCune and Grace 2002). ISA calculates the concentration of abundance of a species within a particular group based on environmental conditions. This method reveals an indicator species for a habitat type if that species is present or exclusive to that habitat type.

I used a nonmetric multidimensional scaling ordination (NMS; Kruskal 1964) using the Sørensen distance measure and Kruskals' secondary approach for tie-handling to ordinate stands in species space. I used a butterfly species matrix (12 sites x 17 species) using counts of individual butterflies averaged from each stand over the six survey periods. The NMS ordination method is an appropriate tool for this data set because it avoids the assumption of linear relationships among variables and is suitable for non-normal data (McCune and Grace 2002).

Data adjustments and transformations are a common and effective tool to use on community data. Relativizations can change the relative weighting of rare and abundant species in raw data or can put variables that were measured in different units on equal scaling (McCune and Grace 2002). I performed a monotonic transformation on my butterfly species matrix in the program PC-ORD. I log transformed (log(x + 1)) the butterfly species matrix to compress the highly abundant species values and give more emphasis to minor species, and therefore reducing skewness. I conducted an outlier analysis for the butterfly matrix by calculating sample units (rows) with an average Sørensen distance from other samples units of more than 2 standard deviations from the grand mean of distances among sample units. One site O2 (SD = 2.18) was considered an outlier in the data, but I retained this site because it was part of the statistical populations of oak woodland. I used an alpha value of 0.05 for all analyses.

Butterfly community structure relating to environmental variables

I related butterfly communities to vegetation variables using PC-ORD v.6 for ordination analyses. I created an environmental matrix (12 sites x 6 variables) that contained the following variables: oak canopy cover (%), vegetation ground cover (%), litter (%), bare ground (%), elevation (m), and the categorical variable habitat type (prairie, oak savanna, and oak woodland). In the NMS ordination, a joint plot overlay of habitat type and environmental variables was placed on the butterfly community ordination graph to assess the correlations of butterfly community composition with environmental variables. The NMS ordination analysis produces Pearson's correlations (*r*) of environmental variables with ordination axes of butterfly species space for butterfly communities in habitat types.

RESULTS

Butterfly density, abundance, and richness

I observed a season total of 925 individual butterflies of 17 different species across the three study locations (Appendix B). Butterfly density differed significantly among the three habitat types (ANOVA, $F_{(2,9)} = 5.8$, $p = 0.02$) (Table 2.2). Butterfly density and canopy cover were negatively correlated (n = 12, $r = -0.74$, $p = 0.005$) (Figure

2.3). Butterfly abundance (average abundance per site) also differed among the three habitat types (ANOVA, $F_{(2,9)} = 5.8$, $p = 0.02$) (Table 2.2); the average abundance for all species was highest in prairie stands, intermediate in oak savanna, and lowest in oak woodlands. Butterfly species richness did not differ (ANOVA, $F_{(2,9)} = 0.1$, $p = 0.54$) among the three habitat types. Among all three habitat types 64% of all butterflies observed were common wood-nymphs, about 25% were common ringlets, and 3% were the Chalcedon checkerspot, although only found at one prairie site. And 92% of all individuals detected were of these three species. Red admiral (*Vanessa atalanta),* American lady (*V. virginiensis),* green-veined white (*Pieris napi),* cabbage white (*P. rapae)* were only observed once during the season.

Butterfly community structure among environmental variables and habitat types

Habitat types differed in butterfly community structure (MRPP; $p = 0.036$), although differences were fairly small (A = 0.076). The oak savanna habitat had the tightest structure (average within-group distance = 0.25) while prairie and oak woodland had similar average within-group distances (0.42 and 0.44, respectively). ISA revealed no indicator species for any habitat type.

A NMS ordination resulted in a stable three-dimensional solution that was stronger than predicted by chance ($p = 0.01$) and explained a total of 92% of variance in the data; axis 1 explained 25%, axis 2 explained 41%, and axis 3 explained 26%. A joint plot overlay of environmental variables on the ordination of sites in butterfly species space revealed associations with several environmental variables (Figure 2.4). Canopy cover, bare ground and, litter were positively correlated with axis 1 (*r* = 0.868, *r* = 0.577, *r* = 0.429, respectively); vegetation height was positively correlated with axis 3 (*r* = 0.709) and elevation was negatively correlated with axis 1 (*r* = -0.556) (Table 2.3). The common ringlet was negatively correlated with axis 1; margined white (*Pieris marginalis*) was positively correlated with axis1. The common wood-nymph was negatively correlated with axis 3; western tiger swallowtail (*Papilio rutulus*) was positively correlated with axis 3. Mylitta crescent (*Phyciodes mylitta*), woodland skipper (*Ochlodes sylvanoides*), and propertius duskywing (*Erynnis propertius*) were negatively correlated with axis 2 (Table 2.4).

DISCUSSION

Butterfly community composition

My study showed that butterfly density and community composition differed along a successional gradient in a threatened prairie-oak ecosystem in in the Willamette Valley of Oregon. I expected that oak savanna would have the highest abundance of butterflies because of the varied mosaic of plant communities (Lane and Andow 2003, Reeder et al. 2005). However, I found that prairie stands had the highest abundance and density of butterflies. Butterfly abundance and density is highly correlated with nectar resource availability (Kubo et al. 2009, York 2003) and my prairie stands had the highest abundance and diversity of nectar resources (Chapter 4). The most abundant species of butterfly that were detected at all 12 sites were the common ringlet and the common wood-nymph. York (2003) also found that these two species were the most common and abundant in Willamette Valley prairie sites. These two ubiquitous butterfly species seem to be able to persist without native grasses (York 2003). The third most abundant species was the Chalcedon checkerspot, though only detected at one of the 12 sites. This species is known for occurring in high prairies, and the one location at which this species was observed had the highest elevation prairie site (600 m).

Differences in prairie, oak savanna, and oak woodlands appear to be related to several environmental variables, including oak canopy cover, and the presence of understory vegetation. The spatial heterogeneity created by diverse oak canopy cover is known to affect Lepidoptera habitat quality, and consequently butterfly population biology (Lane and Andow 2003, Weiss et al. 1988). Lane and Andow (2003) found that oak savanna sub-habitat variation was important for the Karner Blue Butterfly (*Lycaeides Melissa samuelis*). Furthermore, Weiss et al. (1988) documented microclimates created by topography and the amount of sunlight exposure are important for creating suitable habitat of for Edith's checkerspot (*Euphydryas editha).* Again, this suggests that oak savanna should have the highest density and richness of butterflies.

Butterfly abundance and species richness are related to different plant community characteristics (Murdoch et al. 1972, Southwood et al. 1979, Viejo 1985). Vegetation community structures strongly influences species' distributions (Ehrlich and Raven 1964, Hill 1992, Schultz and Dlugosch 1999), and butterfly abundance and species richness may be influenced by adult nectar resources and host plant species richness and abundance (York 2003). I expected that oak savanna would have the highest butterfly species richness because of varied micro-habitats and herbaceous plant diversity providing nectar and host plant resources for a larger variety of butterflies (Murphy 1983). The micro-habitats created by oak savanna also supply potential protection from predators or environmental conditions, more sites for roosting and hibernation, and mating sites (Dennis 2004b). My study supports the view that vegetation structure is important for creating habitat for various butterfly species (Kubo et al. 2009, Lane and Andow 2003). Common ringlet abundance generally increased with a decreasing canopy cover and increasing percent ground cover, which is consistent with Opler et al. (2012) description of common ringlet habitat as grassy, open areas and meadows. Woodland skipper abundance increased with elevation and canopy cover, and this species is reported to occur in grassy areas in chaparral, sagebrush, and woodlands (Opler et al. 2012).

Prairie-oak butterfly community structure appears to be related to sub-canopy vegetation and environmental structural components including topographic elements (Reeder et al. 2005). The strongest environmental variable related to butterfly community structure was canopy cover (Reeder et al. 2005, Schultz et al. 2011). Canopy cover appeared to have a strong influence on butterfly communities; however, there were strong inter-correlations among environmental variables, which may have confounded my results (Appendix C). Butterfly abundance and density were highest in habitats with canopy cover < 20%, and thus prairie habitat may provide butterflies with more time in direct sunlight and higher temperatures (Weiss et al. 1988). Overstory canopy cover creates varied micro-habitats that play an important role in adult butterfly abundance, feeding, oviposition, and mating (Lane and Andow 2003, Murphy 1983). Structural elements of habitats created by vegetation such as litter, shrubs, and tall grasses are important for butterflies to escape predators, thermoregulate, find mates, and overwinter (Dennis 2004b, Dennis et al. 2006, Reeder et al. 2005, Yarrish 2011). Contrary to my expectations, I found that butterfly density was negatively correlated with canopy cover. Decreasing canopy cover is also known to be directly correlated with butterfly host plant and nectar source abundance (Lane and Andow 2003), which are also related to butterfly population biology (Lane and Andow 2003).

The results of the NMS suggest that prairie-oak butterfly communities have habitat-specific characteristics. Prairie and oak savanna butterfly communities were more similar than oak woodland communities. More vegetation cover and lower canopy cover was associated with prairie and oak savanna habitats. A potential factor affecting my NMS ordination results were site outliers. My NMS ordination (Figure 2.4) displayed two sites (O2 and F2) as being very different in butterfly species space than other sites. The site O2 was an oak woodland stand at Jefferson Farm that had a high abundance of an infrequently observed species (e.g., margined white). Stand F2, a prairie site also at Jefferson Farm had high abundance of two uncommon species, sonoran skipper (*Polites sonora*) and pale swallowtail (*Papilio eurymedon*). Additionally, the ISA revealed no indicator species of butterflies for the different habitat types. This result may be attributed to several species occurring in all stand types and many species being observed only once or twice. Oak woodland and prairie habitats had individual species that were inconsistently present among these two habitat types, such as the Chalcedona checkerspot.

Host plant availability and nectar resources are factors that define butterfly species' distributions (Feber et al. 1996, Schultz and Dlugoshch 1999, York 2003). However, several studies suggest that butterfly species' distributions are more closely associated with nectar resource abundance than host plant availability (Grossmueller and Lederhouse 1987, Loertscher et al. 1995, cited in Kubo et al. 2009). Furthermore, different species of butterfly may be more sensitive in responding to nectar or host plant availability (York 2003). Fender's blue butterfly, for example, uses only Kincaid's lupine (*Lupinus sulphureus*) as host plants and has been documented using more native nectar resources than non-native (Schultz and Dlugoshch 1999). York (2003) found that prairie-obligate butterfly functional groups (e.g. mallow-feeder, pea-feeder, composite-feeder, grass-feeder) responded differently to the presence of host plants and nectar resources. Mallow-feeders, such as the checkered skipper (*Pyrgus communis*), increased as mallow species (*Malvacease*) presence increased and native nectar sources became more abundance.

Another factor that may explain why butterfly communities did not differ as strongly among habitats as I expected is that many of the sites in this study were exposed to different land management practices. Different management approaches have a large effect on prairie-oak ecosystems, especially on the plant communities (Abella et al. 2004, Apfelbaum and Haney 1987). Fire is an effective management tool for restoring prairie and oak savannas if used appropriately (Agee 1996). Fire duration, pattern, intensity, and burn regime may impact different plant and butterfly species in varied ways (Senzota 1985). Little is known about the effects of different fire treatments on butterflies (Schultz et al. 2011). The study areas in my study had implemented several restoration approaches on the prairie, oak savanna, and oak woodland sites, and each of these sites were managed by private landowners and government agencies with different policies and management strategies. These discrepancies may be a contributing factor in my results.

Implications and Future Management

Prairie-oak obligate butterfly species are at risk in the Willamette Valley due to several threats --mainly habitat loss, degradation, invasive species, and habitat fragmentation (Schultz et al. 2011). Invasive plants are a threat to prairie-oak systems; these invasive plants may out-compete native species or alter the functional structure and microclimates of this ecosystem. Little is known about nutritional differences among non-native plants and invasive nectar resources or if eradication is even desired because some butterfly species have been known to rely on invasive species as host plants (i.e., Taylor's checkerspot and English plantain [*Plantago lanceolata*], Schultz et al. 2011). I observed the Chalcedona checkerspot using ox-eyed daisy (*Leucanthemum vulgare*) frequently at the Oak Basin prairie sites.

Butterfly community structure may be a function of the availability of nectar sources (Schultz and Dlugosch 1999), or a combination of different management practices or sub-canopy vegetation structure (Dennis 2004b, Holl 1995, Spitzer et al.

1997 cited in Kubo et al. 2009, Weiss et al. 1988), patch size and fragmentation (Williams 2011), and the availability of host plants (Feber et al. 1996 cited in York 2003, Rausher 1981, Schultz and Dlugosch 1999), and habitat quality (Dover and Settele 2009, York 2002). Future research and conservation efforts need to consider all these variables associated with butterflies and synthesize a more complete understanding of prairie-oak butterflies in the Willamette Valley. Conservation of native butterfly species requires attention to preserving native habitat and understanding how other factors, such as climate change and invasive species, will affect butterfly populations. It is uncertain the extent of the effects of invasive flower species have on native butterflies (Schultz et al. 2011), but invasive plants have been known be attributed to population decline (Keeler et al. 2006).

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Table 2.1. Butterfly community metrics averaged per site for prairie, oak savanna and oak woodland habitats in the Willamette Valley, Oregon, summer 2012.

	Prairie	Oak savanna	Oak Woodland	F-statistic	P-value
Butterfly[a]					
Average Abundance	20 ± 4.3	13.5 ± 2.5	5.6 ± 1.1	5.8	0.02
Species richness	5.8 ± 0.8	4.8 ± 1.3	4.2 ± 0.6	0.65	0.54
Density (# butterfly/ha)	126 ± 27	88 ± 15	36 ± 7.3	5.8	0.02

[a]Data reported is averaged for each site and each habitat type. Species richness is total species richness for the season for each habitat type.

Table 2.2. Total abundance (No. of individuals of the species/site) and relative density (No. of individual of the species/ No. of individuals of all species X 100) of native butterfly species detected in prairies, oak savanna, and oak woodland habitats, Willamette Valley, Oregon, summer 2012 for the season.

Stand	Butterfly Species	Common Name	Abundance (#/site)	Relative Density
Prairie	*Papilio rutulus*	Western tiger swallowtail	4	0.85
	Coenonympha tullia	Common ringlet	113	23.9
	Ochlodes sylvanoides	Woodland skipper	7	1.48
	Euphydryas chalcedona	Chalcedon checkerspot	26	5.51
	Cercyonis pegala	Common wood-nymph	310	65.7
	Vanessa atalanta	Red admiral	1	0.21
	Vanessa virginiensis	American lady	1	0.21
	Phyciodes mylitta	Mylitta crescent	7	1.48
	Vanessa cardui	Painted lady	1	0.21
	Polites sonora	Sonoran skipper	2	0.42
Oak savanna	*Coenonympha tullia*	Common ringlet	95	28.9
	Cercyonis pegala	Common wood-nymph	219	66.8
	Limenitis lorquini	Lorquin's admiral	1	0.30

	Phyciodes mylitta	Mylitta crescent	4	1.22
	Papilio rutulus	Western tiger swallowtail	1	0.30
	Vanessa cardui	Painted lady	1	0.30
	Pieris rapae	Cabbage white	1	0.30
	Pieris napi	Green-veined white	1	0.30
	Phyciodes pulchella	Field crescent	1	0.30
	Ochlodes sylvanoides	Woodland skipper	4	1.22
Oak woodland	*Papilio rutulus*	Western tiger swallowtail	7	5.56
	Pieris marginalis	Margined white	2	1.59
	Cercyonis pegala	Common wood-nymph	73	57.9
	Coenonympha tullia	Common ringlet	22	17.5
	Erynnis propertius	Propertius duskywing	1	0.79
	Limenitis lorquini	Lorquin's admiral	1	0.79
	Phyciodes mylitta	Mylitta cresent	11	8.73
	Ochlodes sylvanoides	Woodland skipper	8	6.35
	Papilio eurymedon	Pale swallowtail	1	0.79

Table 2.3. Pearson's correlations (*r*) of environmental variables with ordination axes of butterfly species space for butterfly communities in prairies, oak savanna, and oak woodland habitats in the Willamette Valley, Oregon, summer 2012.

Environmental Variable	Axis 1	Axis 2	Axis 3
Elevation	-0.556	-0.396	-0.345
Bare ground	0.577	0.427	0.248
Litter	0.429	-0.091	0.402
Vegetation ground cover	-0.596	-0.154	-0.406
Vegetation height	0.050	-0.197	0.709
Canopy cover	0.868	0.055	0.226

Table 2.4. Pearson's correlations of butterfly species with ordination axes in prairie, oak savanna and oak woodland habitats in the Willamette Valley, Oregon, summer 2012.

Species	**Axis 1** *r*	**Axis 2** *r*	**Axis 3** *r*
Common wood-nymph (*Cercyonis pegala)*	-0.195	0.245	-0.887
Mylitta crescent (*Phyciodes mylitta)*	-0.464	-0.601	-0.400
Common ringlet (*Coenonympha tullia)*	-0.893	-0.085	-0.169
Western tiger swallowtail (*Papilio rutulus)*	0.339	0.299	0.620
Sonoran skipper (*Polites sonora*)	-0.249	-0.129	0.770
Woodland skipper (*Ochlodes sylvanoides)*	-0.293	-0.878	0.219
Pale swallowtail (*Papilio eurymedon)*	-0.073	0.107	0.618
Chalcedon checkerspot (*Euphydryas chalcedona*)	-0.510	-0.158	-0.112
Red admiral (*Vanessa atalanta*)	0.313	0.130	-0.279
American lady (*Vanessa virginiensis*)	-0.402	-0.221	0.002
Field crescent (*Phyciodes pulchella*)	-0.186	0.246	-0.020
Lorquin's admiral (*Limenitis lorquini*)	0.071	-0.620	0.175
Cabbage white (*Pieris rapae*)	-0.164	-0.218	-0.298
Painted lady (*Vanessa cardui*)	-0.420	0.325	-0.220
Green-veined white (*Pieris napi*)	-0.164	-0.218	-0.298
Margined white (*Pieris marginalis*)	0.754	0.478	0.330
Propertius duskywing (*Erynnis propertius*)	0.020	-0.618	-0.148

Figure 2.1. Map of prairie-oak woodland study sites in Willamette Valley, Oregon 2012; shaded areas indicated sampling locations. Jefferson Farm is located the furthest north, Finley National Wildlife Refuge is located the furthest west, and Oak Basin Farm is located the furthest east on this map.

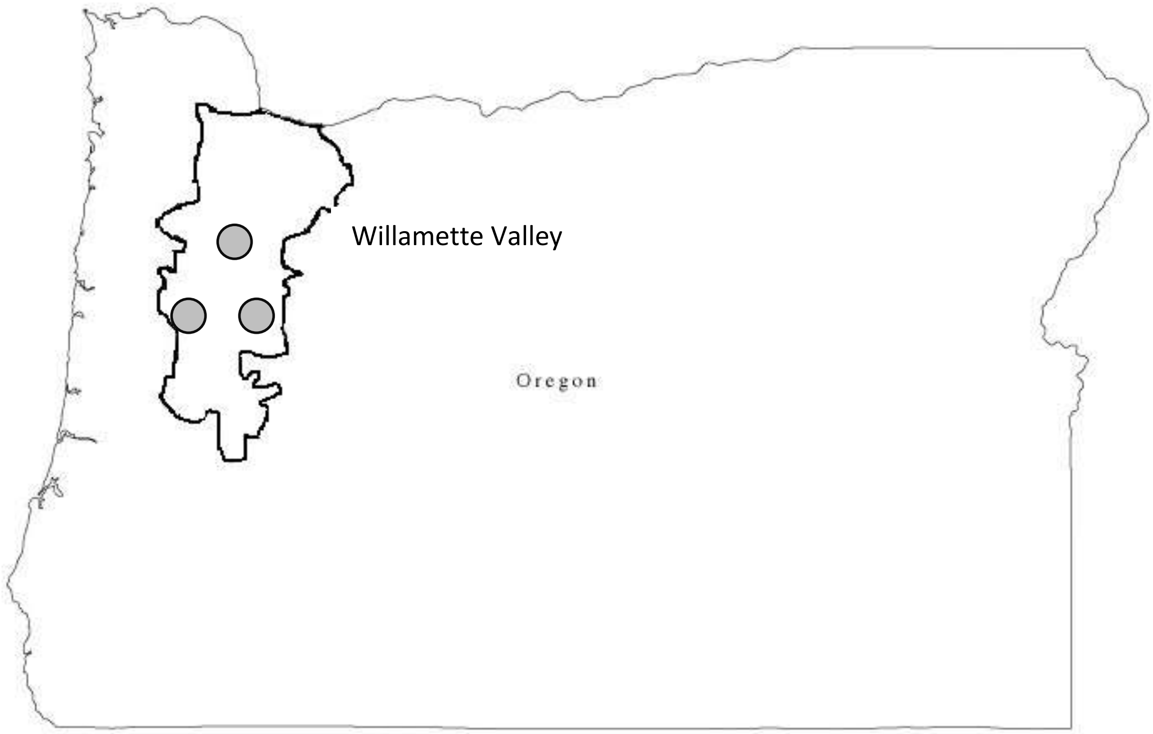


Figure 2.2. Layout of transects and sample plots for butterfly, flower, and environmental sampling of sites of different habitat types at each location in the Willamette Valley, Oregon.

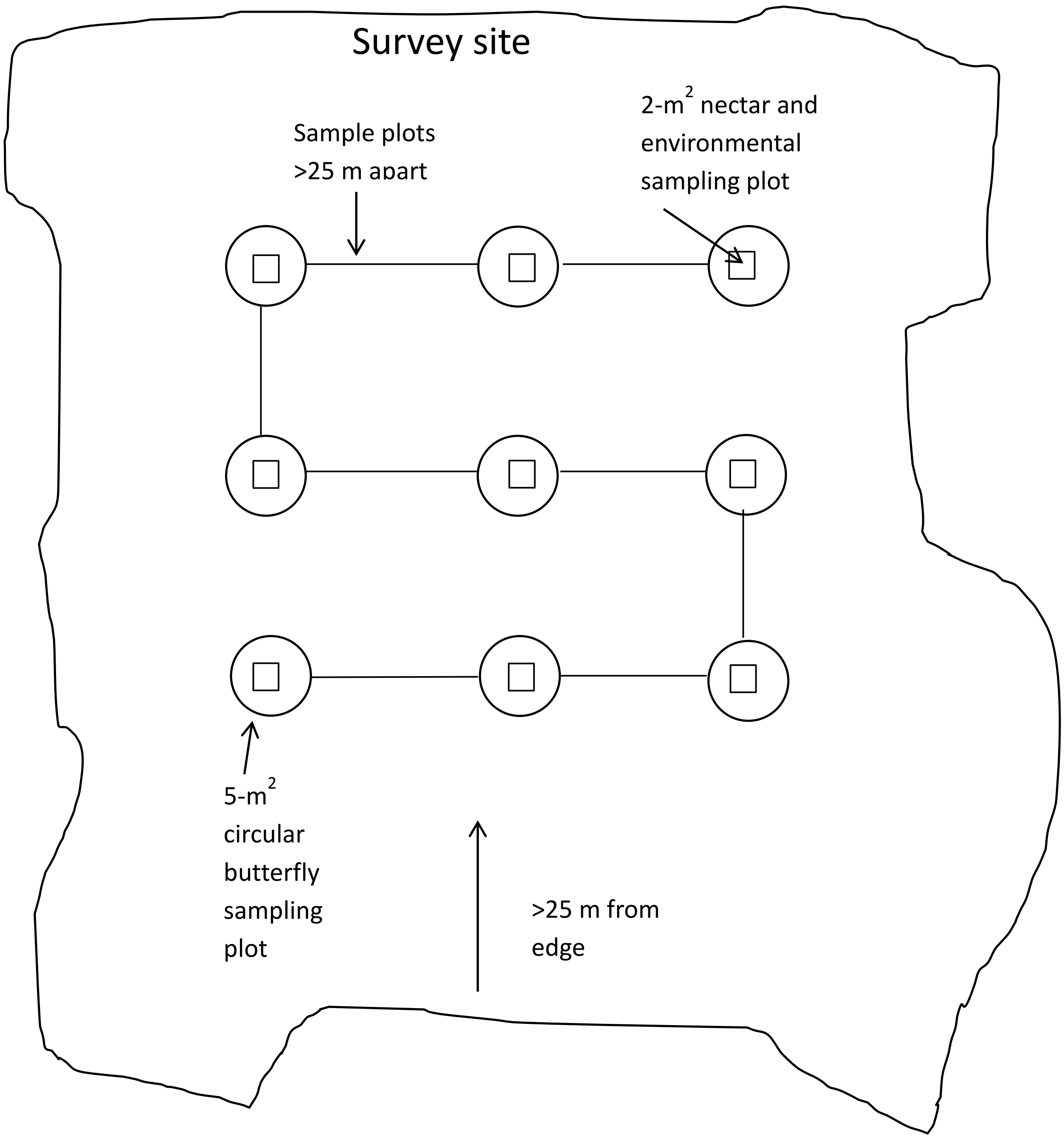


Figure 2.3. Relationship between average butterfly density and percent canopy cover for prairie, oak savanna and oak woodland habitats in the Willamette Valley, Oregon, July-September 2012.

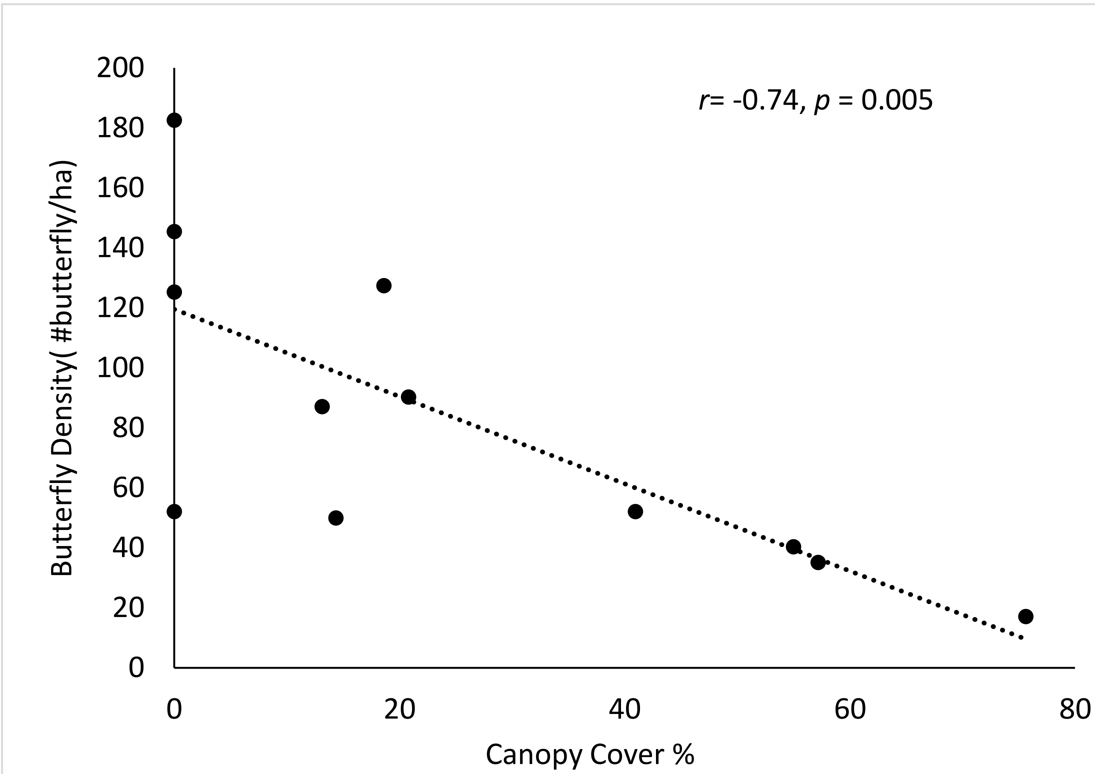
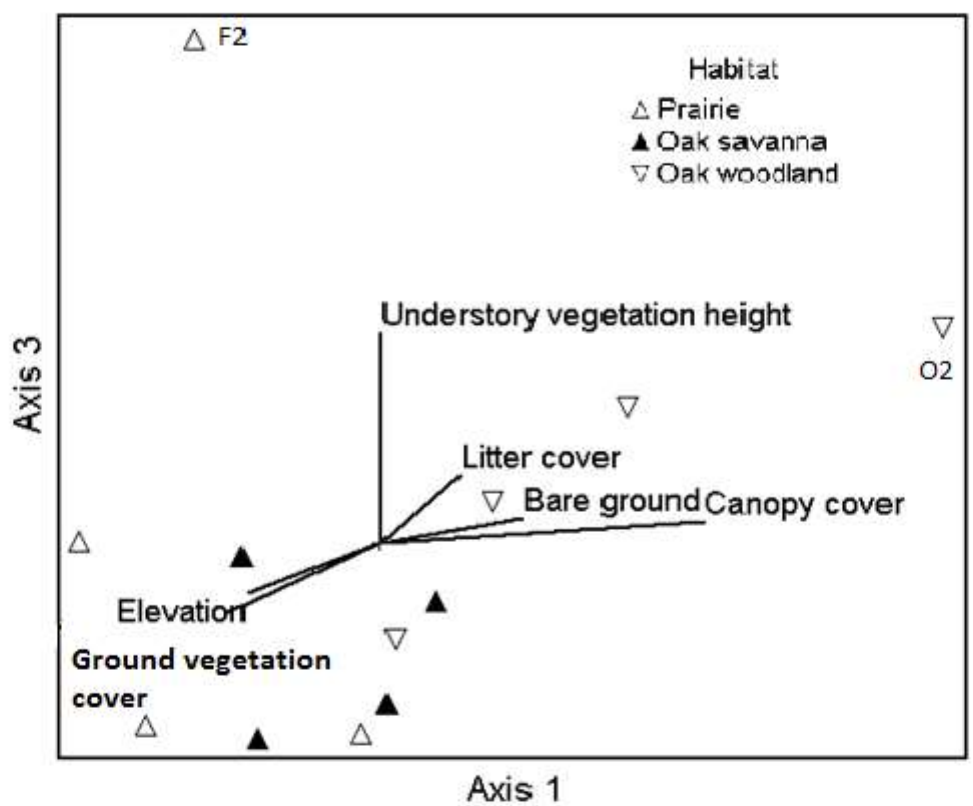


Figure 2.4. Ordination of prairie-oak woodland sites in butterfly species space with a joint plot overlay of environmental variables within site types in the Willamette Valley, Oregon, summer 2012. Symbols represent sites (averages of all plots for a site). The distances between sites represent the dissimilarities in butterfly community composition. The joint plot overlay shows the strength of correlations of environmental variables (vector lines); the longer the vector line the stronger the correlation. A three dimensional solution was recommended which explained 93% of the data. Outlier sites are named in the figure (F2 and O2).



Chapter Three

Flower community composition among prairie-oak woodland habitats in Willamette Valley, Oregon

"I hold no preference among flowers, so long as they are wild, free, spontaneous. Love flowers best in openness and freedom"

~Edward Abbey

ABSTRACT

Butterflies are dependent upon the resources provided by prairie-oak woodland ecosystems. Habitat structure and quality that results from prairie-oak woodland mosaics contain nectar resources for adults and food sources for butterfly larvae. The purpose of my study was to characterize community composition of nectar resources known to be important for individual butterfly species. My objectives were to determine how flower community structure (density, abundance, species richness and species composition) varies along an oak canopy cover gradient in order to understand the role of prairie, oak savanna, and oak woodland habitats in structuring flower communities in prairie-oak woodland ecosystems. In general, prairie habitat had the highest flower density, abundance, and species richness compared to oak savannas and oak woodland habitats; although these differences were not significantly different. The habitats differed in nectar species community structure, though this difference was relatively

small. Non-native species were some of the most abundant flower species found in all sites. Further study is needed to understand the effects of different management strategies for habitat restoration and maintenance in native prairie- oak woodland habitats. The prevalence of non-native species in my study may represent a short-term community transition as a result of management or it may represent a more permanent community. Prairie and oak savanna habitats appear to be more important than oak woodland habitat for butterflies in the Willamette Valley.

INTRODUCTION

Vegetation communities are the result of numerous factors and environmental conditions (Matthews et al. 2009). Tree canopy cover, correlated with light gradients, influences the composition and variability of understory plant species in oak savannas and oak woodlands (Peterson et al. 2007). This direct relationship between light intensity (Bray 1958) and understory vegetation composition is associated with soil moisture and temperature, and nutrient content. The structure of the overstory canopy cover creates different microsites and microclimates (Bray 1958). Plant responses to canopy cover are influenced by light availability, and also competition, soil evaporation, nutrients, soil water, soil evaporation, and root distribution (Scholes and Archer 1997). Numerous interactions among woody plants, forbs, and grasses, hereafter referred to as functional groups, occur as a function of these environmental characteristics influenced by overstory and understory canopy coverage.

Savanna community types consist of a mosaic of microsites that are distributed across the landscape at different spatial scales. These mosaics can be open, shaded, partially shaded, moist or dry (Leach and Givnish 1999, Peterson et al. 2007) creating a broad array of niches, and diverse plant communities. The variation in microsites and community structure, especially the openness, is created and maintained through frequent disturbances such as drought, fire, or grazing (Leach and Givnish 1999).

The relationship between disturbance regimes and frequencies and biodiversity are associated with several hypothesis that predict these relationships (Kershaw and Mallik 2013). The intermediate disturbance hypothesis predicts that biodiversity will be highest when disturbance regimes and frequencies are intermediate, in contrast to disturbances that are rare or frequent (Kershaw and Mallik 2013). Prairies and oak savannas ecosystems and the species associated with these environments are dependent upon natural or managed disturbance for continued persistence (Duren et al. 2012).

Butterflies are dependent upon the resources provided by these prairie-oak woodland ecosystems. Habitat structure and quality that results from oak savanna mosaics contain nectar resource for adults and food sources for butterfly larvae (Yarrish 2011). Structural elements in these communities created by vegetation and litter allow butterflies to escape predators, thermoregulate, find a mate, and overwinter (Dennis et al. 2006, Reeder et al. 2005, Yarrish 2011). The purpose of this study was to characterize understory vegetation composition across a canopy cover gradient in the Willamette

Valley, Oregon. My emphasis and specific data collection was on nectar community composition due to its importance to adult butterflies as a food source.

My objectives were to determine how flower community structure and species composition varied among different habitat types: prairie, oak savanna, and oak woodlands and how community composition correlated with environmental variables. Another objective was to determine the presence of non-native flowering plant species among the different habitat types. I expected that as tree canopy cover decreased flower richness, abundance, and density would increase. Open areas, like prairies, offer more space and direct light (Peterson et al. 2007). My alternative prediction was that nectar species richness would be greater in oak savannas than prairies and oak woodlands because of the heterogeneous characteristics of oak savanna create different niches and microclimates.

METHODS

Study area and season

My study was conducted in the mid-Willamette Valley, Oregon. I selected sites in three habitat types that represent the oak canopy-cover gradient in the prairie-oak ecosystem: prairie, oak savanna, and oak woodland. These habitat types were defined based upon percentage of oak canopy cover: prairie (< 10% tree canopy cover and predominately prairie ground cover); oak savanna (10-30% canopy cover); and oak woodland (> 31% canopy cover) (Au et al. 2008, Bray 1960, Vesely and Rosenberg 2010). Study sites were located at three different locations (Figure 2.1). My criteria for selecting survey locations included that they were located within 65 km of Corvallis, that each encompassed at least one prairie, oak savanna, and oak woodland site that represented my canopy cover gradient.

I sampled 12 study sites at three different locations. The three different survey locations were Finley National Wildlife Refuge (FNWR), Jefferson Farm and Oak Basin Tree Farm (Appendix B). At each location I had four different study sites representing prairie-oak habitats: prairie, oak savanna, and oak woodland. Sites varied with respect to whether they were remnant or restored habitats and the methods used for maintenance and restoration.

The climate of the Willamette Valley, Oregon is relatively mild throughout the year with cool, wet winters and warm, dry summers. The majority of the rainfall occurs in the winter typically from December to February (Taylor et al. 2000). Average annual temperatures for Corvallis range from 5.4 to 17.1°C. Average annual precipitation is 104 cm (Western Regional Climate Center 2012).

Common native forbs associated with prairies and oak savanna are field cluster lily (*Dichelostemma capitatum*), large camas (*Camassia leichtlinii* spp)**,** Nelson's checkermallow (*Sidalcea nelsoniana*), common yarrow (*Achillea millefolium*), purple clarkia (*Clarkia purpurea*), blueheaded gilia (*Gilia capital*), and willowherb (*Epilobium densilorum*). Woody vegetation associated with oak woodlands are sword fern (*Polystichum munitum*), western serviceberry (*Amelanchier alnifolia*), snowberry (*Symphoricarpos albus*), poison oak (*Toxicodendron diversilobum*); and forbs occurring include shooting star (*Dodecatheon hendersonii*), Oregon fawn lily (*Erythronium* *oregonum*), peavines (*Lathyrus* spp.), and woody strawberry (*Fragaria vesca*) (Vesely and Rosenburg 2011).

Flower sampling

I randomly chose one starting point and direction (left or right) and ran the first transect parallel to the border of the site and at least 25 m from the border to reduce edge effects (Dover and Settele 2009). All transects had multiple segments and the total length of each transect was 500m. Segments of transects were separated from each other at least >25 m. For each transect the plot locations and start and end coordinates (Universal Transverse Mercator) were marked by a Global Position System unit (Garmin, Model: e Trex Venture HC). I used a line-transect and 2-m^2 plots (Buckland et al. 2001, 2004) to quantify the number of butterflies (total abundance) and species richness. Every 25 m along the transect I established a 2-m^2 plot. I sampled 20 plots, at each site, for a total of 80 plots per habitat type (Figure 2.2). I surveyed sites in different order to avoid the temporal effects of time and day.

I conducted flower surveys every two weeks at each site from July to September 2012, for a total of six surveys per site. Along the line transect (500 m) I established vegetation plots within the circular plots. I conducted vegetation surveys by establishing a 2-m^2 square plot at the center point of each plot (Kent and Coker 1992). I counted flowers by the number of flowering stems in each plot. Due to the unusual cold and wet spring and summer in the Willamette Valley in 2012 and site accessibility, I began sampling in July.

Environmental variables

I measured environmental variables known to be important to butterflies once at each sample site. Variables sampled included vegetation height and percent cover of vegetation by plant type, litter and bare ground cover, and elevation (Calvert and Brower 1986, Dennis 2004a, 2004b, Williams 2010). All vegetation, except flowers, were sampled once, at a time of the season (late July/early August) to capture the most plant species present (Grundel et al. 1998). I conducted environmental element surveys in the 2-m^2 square plot at the center point of each butterfly plot. The maximum vegetation height of understory vegetation was measured in centimeters. I measured tree canopy cover using a moosehorn instrument, which has a square grid with 36 intersecting points used to estimate canopy cover by using an angled mirror to reflect the number of intersections by canopy cover (Fiala et al. 2006). Ground vegetation cover was estimated using the Braun-Blanquet scale (Bullock 2006).

Statistical analysis and modeling

Flower community structure

Flower data was averaged by site for each habitat type across all surveying periods. I calculated the average flower species density (number of flowers of each species per ha), abundance (average number of individuals), species richness. I performed a Kruskal-Wallis one-way analysis of variance (ANOVA) to determine differences in flower abundance, diversity, and species richness among the stand types. Means were reported ± 1 SE.

I used program PC-ORD v.6 (McCune and Mefford 2009) for ordination data analyses. I used a multi-response permutation procedure (MRPP, Mielke and Berry 2001) using the Sørensen distance measure to test the null hypothesis that flower community structure did not differ among habitat types (McCune and Grace 2002). I used an indicator species analysis (ISA; Dufrene and Legendre 1997) to describe flower species relationships to the habitat types (McCune and Grace 2002). This method reveals an indicator species for a habitat type if that species is always present or exclusive to that habitat. A p-value and an indicator value (IV) were estimated using the Monte Carlo randomization technique (McCune and Grace 2002) with 4999 randomizations.

I used a nonmetric multidimensional scaling ordination (NMS, Kruskal 1964) using the Sørensen distance measure and Kruskal's secondary approach for tie-handling to ordinate stands in species space. NMS ordination is an appropriate tool for this data set because it avoids the assumption of linear relationships among variables and is good for data that is not normally distributed (McCune and Grace 2002).

Flower community structure and environmental characteristics

Flower data was averaged for each site for all survey periods into a single matrix. I related flower communities to vegetation characteristics using PC-ORD v.6 for ordination analyses. I created an environmental matrix (12 sites x 6 variables) with the following variables: oak canopy cover (%), vegetation ground cover (%), litter (%), bare ground (%), elevation (m), and the categorical variable habitat type (prairie, oak savanna, and oak woodland). Using NMS ordination, I constructed a joint plot overlay of habitat type and environmental variables on the ordination graph to determine correlations of flower community composition with environmental variables. The NMS ordination analysis estimated Pearson's correlations (*r*) of environmental variables with ordination axes of flower species space for flower communities in prairie oak savanna, oak woodland habitats. I used an alpha value of 0.05 for all analyses.

RESULTS

Flower density, abundance and diversity

I recorded 11,932 flowering stems of 47 different species across the three study locations. In general, prairie habitat had higher flower density, abundance, and species richness than oak savannas and oak woodland habitats. However, differences were not statistically significant for any of the three variables (Table 3.1) The most abundant flowers were oxeye daisy (*Leucanthemum vulgare*), yellow glandweed (*Parentucellia viscosa*), Scouler's woollyweed (*Hieracium scouleri*), tall annual willowherb (*Epilobium brachycarpium*), dense-flowered willowherb (*Epilobium densiflorum*), Muhlenberg's centaury (*Centaurium muehlenbergii*), Queen Anne's Lace (*Daucus carota*), farewell-to-spring (Clarkia amoena), redstem storksbill (*Erodium cicutarium*), and common St. Johnswort (*Hypericum perforatum*) (Table 3.2).

Flower community structure and environmental characteristics

The habitat types differed in nectar species community structure (MRPP, p = 0.05), though this difference was small (A = 0.05). Oak savanna habitat had the tightest structure (average within group distance = 0.59) compared to the within group distances for prairie and oak woodland habitats (0.60 and 0.73, respectively). A NMS ordination resulted in a stable three-dimensional solution that was stronger than predicted by chance (p = 0.02) and explained 88% of variance in the data; axis 1 represented 47%, axis 2 represented 15%, and axis 3 represented 26% of the variance. A joint plot overlay of environmental variables in species space resulted in correlations with several environmental variables (Figure 3.1, Table 3.4). Many flower species had strong relationships with the axes (Table 3.5). Four plant species were identified as indicator species in the prairie habitat (Table 3.3); none were identified for the oak savanna and oak woodland habitats. Of the four indicator species in prairie habitat, two species were non-native species, redstem storksbill and hairy cat's-ear (*Hypochaeris radicata*).

DISCUSSION

My study revealed that flower species richness and abundance was highest in prairie habitat, followed by oak savanna, then oak woodland habitats; however, these results were not significantly different. My results were not consistent with my original predictions that species richness would be highest in oak savanna habitat because of more niche diversity and microhabitats due to the spatial heterogeneity in this habitat.

A possible reason for this outcome is that there tends to be a higher abundance and species richness of flowers found in open areas (Peterson et al. 2007). Open areas, like prairies, offer more space and availability of direct light.

Flower density and abundance conformed to my predictions and were greatest in prairie habitat, followed by oak savanna, and then oak woodland habitats. I predicted that flower species abundance would be negatively correlated with percent overstory canopy cover. Overstory canopy cover reduces understory vegetation because of shading (Leach and Givnish 1999 from Peterson et al. 2007, Scholes and Archer 1997).

Non-native species were some of the most abundant flowers species found in all sites. On average, about 30% of the species observed in prairies were non-native species; non-natives made up about 40 and 50% of oak savanna and oak woodlands, respectively. The oxeye daisy, a non-native, was the most abundant species overall, and occurred at all stands expect for an oak woodland site at Jefferson Farm, and was especially abundant early in the season at FNWR. The second most abundant species, yellow glandweed (*Parentucellia viscosa*) is also non-native. Other highly abundant non-native species were Queen Ann's lace (*Daucus carota*), redstem storksbill, St. Johnswort (*Hypericum perforatum*), Scotch broom (*Cytisus scoparius*) and Himalayan blackberry (*Rubus armeniacus*). Many non-native species were found in disturbed areas.

Native flower species were abundant at all the sites (Turner and Gustafson 2006). Highly abundant native species included Scouler's woollyweed (*Hieracium scouleri*), tall annual willowherb (*Epilobium brachycarpium*), dense-flowered willowherb (*Epilobium densiflorum*), Muhlenberg's centaury (*Centaurium muehlenbergii*), and farewell-to-spring (*Clarkia amoena*). Native species were more prevalent at prairie sites than at oak savanna and oak woodland sites (Table 3.1).

Habitat modifications and different management strategies for maintenance or restoration of prairie and oak habitats may have resulted a high abundance of non-native flower species. My study was limited by the non-random selection of treatments. Landowners and federal agencies who managed these sites used a combination of burning, mowing, thinning, and herbicide (Appendix B) to maintain or to restore prairies, oak savannas, and oak woodlands. Natural disturbances such as burning that maintained these types of habitats were important for native species (Abrams 1992, Davis et al. 2001, Senzota 1985); many flower species require disturbance for reproduction or regeneration (Peterson and Reich 2008). However, an anthropogenic disturbance that does not mimic the natural disturbance regime may induce an environment that facilitates population increase in certain species, allows them to persist when they otherwise would not, or reduce native species abundance by competition mechanisms (Bowles and Whelan 1994).

My analyses identified four indicator species in prairie habitat, two native (common yarrow and small-flowered godetia) and two non-native species (hairycat's ear and redstem storksbill), but no indicator species in oak savanna and oak woodland habitats. The presence of two non-native indicator species in prairie habitat reveals the degree to which non-native flower species dominate these environments. These species are associated with habitat disturbance. More research is needed to understand the long-term impacts of non-natives on native plant communities and if the presence of these non-natives species may cause a loss in flora diversity over time (Didham et al. 2005).

Flower community structure differed among the three habitat types and were correlated with several environmental factors: litter, vegetation ground cover, and overstory canopy cover. Community composition of understory species is known to be correlated with overstory canopy cover and light availability (Knoop and Walker 1985, Peterson et al. 2007). I found that litter cover was negatively correlated with an ordination axis and correlated with canopy cover (Appendix C) and is related to flower community structure. Litter is known to affect recruitment of plants from seeds by making the environment less conducive for germination or seedling survival (Jenson 2001 and Meyer 2001). Litter may chemically change soil, prevent the movement of seeds, create differences in microclimate, and decrease the availability of light (Jensen and Meyer 2001). Light availability also effects the establishment of flowers (Jensen and Meyer 2001). Peterson et al. (2007) observed that forb species were correlated with light availability as a result of tree canopy cover, and were more abundant when percent canopy cover was less than 30% in oak savanna and oak woodlands.

Further study is needed to understand the effects of different management strategies for habitat restoration and maintenance in native prairie and oak savanna habitats (Swengel and Swengel 2001). The prevalence of non-native species in my study may represent a short-term community transition as a result of management or it may represent a more permanent community (Caplat et al. 2013). Fire is an important component of maintaining or restoring prairie and oak savannas (Peterson et al. 2007);

however, fire may not be completely effective or be an impractical option due to seasonal restrictions on fire use. Landowners are sometimes reluctant to use prescribed burning and instead use other treatments such as mechanical thinning, mowing, seeding or herbicides. Therefore, future studies should include a component of different treatment types and their effects on the vegetation community structure.

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Table 3.1. Average (+ 1 SD) abundance (number of flowering stems/site), total species richness (number of species/site) density (number of flowering stems/2 m^2) for the season of flower resources among prairie, oak savanna and oak woodland habitats in the Willamette Valley, Oregon, summer 2012.

	Prairie	Oak savanna	Oak woodland	F-statistic	P-value
Flower[a]					
Average Abundance	290 ± 115	153 ± 32	54 ± 24	2.8	0.11
Species Richness	20 ± 4.34	17.3 ± 3.82	11.8 ± 3.06	1.23	0.33
Density (No. flowering stems/2 m^2)	14.5± 5.8	7.6± 1.6	2.7 ± 1.2	2.8	0.11

[a]Data reported is averaged for each site and each habitat type. Species richness is total species richness for the season for each site for each habitat type.

Table 3.2. Flower species total and relative abundance, and native or non-native status among prairies, oak savanna, and oak woodland habitats in the Willamette Valley, Oregon, summer 2012.

		Prairie		
Species	**Common Name**	**Abundance**	**Relative abundance**	**Native**
Achillea millefolium	common yarrow	181	0.0259	Yes
Agoseris *grandiflora*	bigflower agoseris	38	0.0054	Yes
Anthemis cotula	stinking chamomile	8	0.0014	No
Arnica chamissonis	chamisso arnica	1	0.0001	Yes
Aster subspicatus	Douglas's aster	35	0.0050	Yes
Brodiaea elegans	harvest brodiaea	89	0.0127	Yes
Centaurea cyanus	bachelor's button	3	0.0004	No
Centaurium muehlenbergii	Muhlenberg's centaury	185	0.0265	Yes
Clarkia amoena	farewell-to-spring	59	0.0085	Yes
Clarkia purpurea	small-flowered godetia	23	0.0033	Yes
Claytonia sibrica	candy flower	64	0.0092	No
Crocidium multicaule	common spring-gold	30	0.0043	Yes
Daucus carota	Queen Anne's lace	565	0.0809	No
Dianthus armeria	deptford pink	7	0.0010	No
Dichelostemma multiflorum	roundtooth snakelily	1	0.0001	Yes
Phlox gracilis	slender phlox	157	0.0225	Yes
Epilobium brachycarpium	tall annual willowherb	792	0.1134	Yes
Epilobium densiflorum	dense-flowered willowherb	811	0.1162	Yes
Erodium cicutarium	redstem storksbill	377	0.0540	No
Geranium dissectum	cutleaf geranium	1	0.0001	No

Geranium richardsonii	Richardson's geranium	145	0.0208	Yes
Gilia capitata	blue-headed gilia	25	0.0036	Yes
Grindelia integrifolia	Puget Sound gumweed	96	0.0137	Yes
Hieracium scouleri	Scouler's woollyweed	380	0.0544	Yes
Hypericum concinnum	goldwire	1	0.0001	Yes
Hypericum perforatum	common St. Johnswort	22	0.0032	No
Hypochaeris radicata	hairy cat's ear	94	0.0135	No
Leucanthemum vulgare	oxeye daisy	1694	0.2426	No
Ligusticum apiifolium	celeryleaf licorice-root	24	0.0034	Yes
Mentha arvensis	wild mint	49	0.0070	Yes
Mentha spp.	mint	50	0.0072	-
Navarretia intertexta	needle-leaved navarretia	43	0.0062	Yes
Parentucellia viscosa	yellow glandweed	612	0.0877	No
Perideridia oregano	Oregon yampah	37	0.0053	Yes
Prunella vulgaris var. lanceolata	lance selfheal	174	0.0249	Yes
Trifolium spp.	-	101	0.0145	-
Trifolium willdenovii	tomcat clover	4	0.0006	Yes
Vicia villosa	winter vetch	4	0.0006	No
	Oak savanna			
Arnica chamissonis	chamisso arnica	12	0.0031	Yes
Agoseris grandiflora	bigflower agoseris	21	0.0054	Yes
Aster subspicatus	Douglas's aster	2	0.0005	Yes
Brodiaea elegans	harvest brodiaea	46	0.0119	Yes
Centaurea cyanus	bachelor's button	15	0.0039	No
Centaurium muehlenbergii	Muhlenberg's centaury	361	0.0930	Yes
Centaurium erythraea	European centaury	10	0.0026	No

Cirsium arvense	Canada thistle	6	0.0015	No
Cirsium brevistylum	clustered thistle	7	0.0018	Yes
Clarkia amoena	farewell-to-spring	123	0.0317	Yes
Claytonia sibrica	Candy flower	8	0.0021	No
Collinsia grandiflora	giant blue-eyed Mary	7	0.0018	Yes
Crepis capillaris	smooth hawksbeard	2	0.0005	No
Crocidium multicaule	common spring-gold	1	0.0003	Yes
Daucus carota	Queen Anne's lace	94	0.0242	No
Dianthus armeria	deptford pink	3	0.0008	No
Epilobium brachycarpium	autumn willowherb	34	0.0088	Yes
Epilobium densiflorum	dense-flowered willowherb	9	0.0023	Yes
Erodium cicutarium	redstem storksbill	5	0.0013	No
Geranium dissectum	cutleaf geranium	4	0.0010	No
Geranium richardsonii	Richardson's geranium	24	0.0062	Yes
Gilia capitata	blue-headed gilia	5	0.0013	Yes
Hieracium scouleri	Scouler's woollyweed	572	0.1474	Yes
Hypericum perforatum	common St. Johnswort	68	0.0175	No
Hypochaeris radicata	hairy cat’s ear	186	0.0479	No
Leucanthemum vulgare	Oxeye daisy	1010	0.2602	No
Mentha spp.	mint species	135	0.0348	-
Mimulus guttatus	seep monkeyflower	1	0.0003	Yes
Parentucellia viscosa	yellow glandweed	982	0.2530	No
Perideridia oregano	Oregon yampah	21	0.0054	Yes
Potentilla gracilis	slender cinquefoil	2	0.0005	Yes
Prunella vulgaris var. lanceolata	lance selfheal	47	0.0121	Yes

Ranunculus orthorhynchus	straightbeak buttercup	3	0.0008	Yes
Rubus fruticosus	blackberry	49	0.0126	No
Vicia villosa	winter vetch	6	0.0015	No
		Oak woodland		
Aster radulinus	roughleaf aster	11	0.0084	Yes
Brodiaea elegans	harvest brodiaea	2	0.0015	Yes
Centaurium muehlenbergii	Muhlenberg's centaury	162	0.1232	Yes
Cirsium arvense	canada thistle	2	0.0015	No
Cirsium brevistylum	clustered thistle	2	0.0015	Yes
Clarkia amoena	farewell-to-spring	4	0.0030	Yes
Claytonia sibrica	candy flower	177	0.1346	No
Crepis capillaris	smooth hawksbeard	22	0.0167	No
Daucus carota	Queen Anne's lace	18	0.0137	No
Dianthus armeria	deptford pink	3	0.0023	No
Digitalis purpurea	purple foxglove	19	0.0144	No
Phlox gracilis	slender phlox	14	0.0106	Yes
Geranium richardsonii	Richardson's geranium	35	0.0266	Yes
Gilia capitata	blue-headed gilia	2	0.0015	Yes
Hieracium scouleri	Scouler's hawkweed	12	0.0091	Yes
Hypericum concinnum	goldwire	1	0.0008	Yes
Hypericum perforatum	common St. Johnswort	133	0.1011	No
Hypochaeris radicata	hairy cat's ear	5	0.0038	No
Lathyrus pauciflorus	steppe sweetpea	32	0.0243	Yes

Leucanthemum vulgare	oxeye daisy	539	0.4099	No
Mentha spp.	mint species	3	0.0023	-
Myosotis scorpioides	true forget-me-not	40	0.0304	No
Parentucellia viscosa	yellow glandweed	15	0.0114	No
Prunella vulgaris var. lanceolata	self-heal	41	0.0312	Yes
Rubus fruticosus	blackberry	16	0.0122	No
Trifolium repens	white clover	5	0.0038	No

Table 3.3. Nectar plant indicator species for prairie habitat in the Willamette Valley, Oregon, summer, 2012.

Species	Native	Habitat	Indicator value	p-value
Common yarrow	Yes	Prairie	75	0.054
Hairy cat’s-ear	No	Prairie	67	0.032
Small-flowered godetia	Yes	Prairie	75	0.054
Redstem storksbill	No	Prairie	67	0.05

Table 3.4. Pearson's correlation (*r*) of environmental variables with ordination axes of flower species space for flower communities in prairie, oak savanna, and oak woodland habitats in the Willamette Valley, Oregon, summer 2012.

Environmental Variable	Axis 1	Axis 2	Axis 3
Elevation	-0.106	0.645	-0.325
Bare ground	0.314	0.026	-0.193
Litter	0.585	0.504	-0.552
Vegetation ground cover	-0.561	-0.364	0.476
Vegetation height	-0.116	-0.130	0.039
Canopy cover	0.831	0.112	-0.33

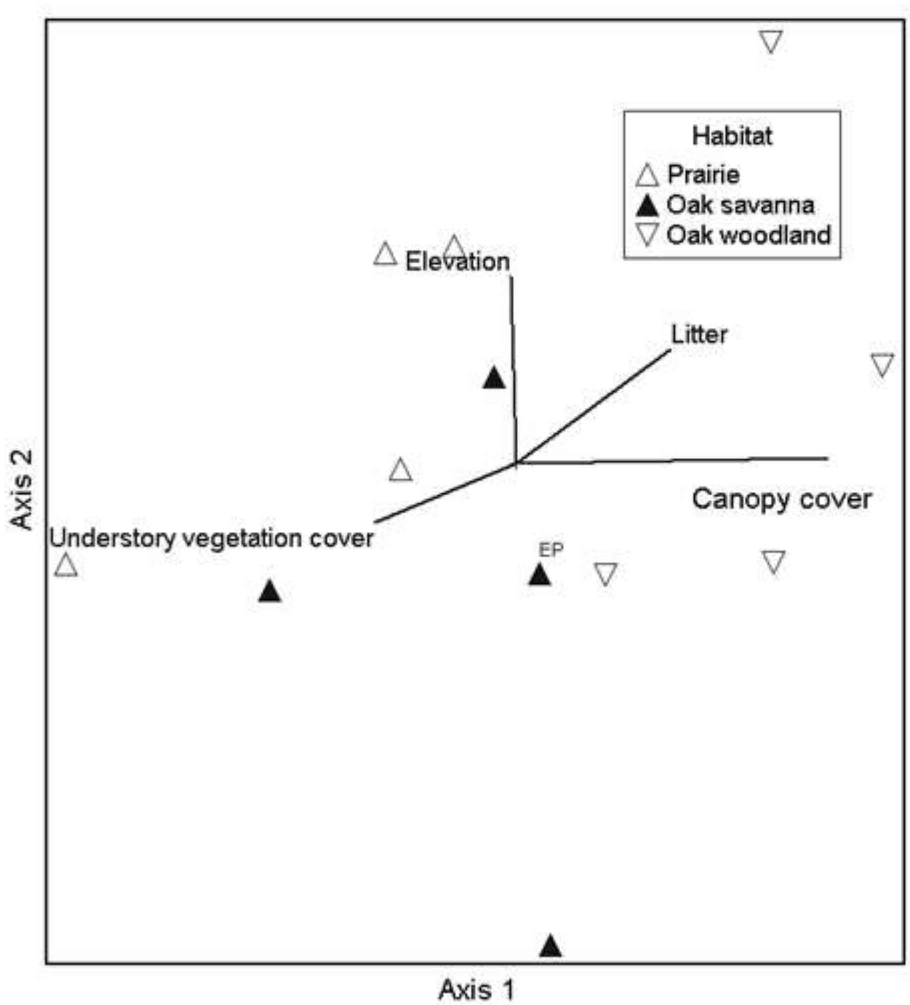
Table 3.5. Pearson's correlations with ordination axes for flower species in prairie, oak savanna and oak woodland habitat in the Willamette Valley, Oregon, summer 2012.

	Axis 1	**Axis 2**	**Axis 3**
Species	*r*	*r*	*r*
Achillea millefolium	0.445	0.252	-0.302
Agoseris grandiflora	-0.341	-0.174	0.211
Anthemis cotula	-0.621	-0.138	0.055
Arnica chamissonis	-0.376	-0.174	0.356
Aster subspicatus	-0.670	0.024	-0.071
Brodiaea elegans	-0.609	-0.327	-0.169
Centaurea cyanus	-0.316	0.047	-0.014
Centaurium muehlenbergii	-0.486	-0.484	0.496
Centaurium erythraea	-0.713	-0.231	0.198
Cirsium arvense	-0.020	-0.274	0.211
Cirsium brevistylum	0.259	-0.274	0.385
Clarkia amoena	-0.695	-0.277	0.295
Clarkia purpurea	-0.677	-0.006	-0.069
Claytonia sibrica	0.400	0.855	-0.493
Collinsia grandiflora	0.346	-0.018	0.135
Collomia grandiflora	0.341	-0.174	0.211

Crepis capillaris	0.286	0.393	0.299
Crocidium multicaule	-0.688	-0.173	0.098
Daucus carota	-0.600	-0.240	0.619
Dianthus armeria	0.024	0.750	-0.211
Dichelostemma multiflorum	-0.085	0.299	-0.286
Digitalis purpurea	0.352	0.579	0.252
Elegant gracilis	-0.142	0.346	-0.384
Epilobium brachycarpium	-0.603	-0.106	0.082
Epilobium densiflorum	-0.593	-0.185	0.134
Erodium cicutarium	-0.586	0.316	-0.331
Geranium dissectum	-0.282	0.057	-0.018
Gilia capitata	-0.624	-0.035	0.232
Hieracium scouleri	-0.813	0.003	-0.113
Hypochaeris radicata	-0.726	-0.200	0.289
Hypericum concinnum	-0.027	-0.120	0.231
Hypericum perforatum	0.152	-0.371	-0.122
Leucanthemum vulgare	-0.339	0.231	0.613
Ligusticum apiifolium	-0.159	-0.008	0.443
Mentha	0.080	0.181	0.147
Mimulus guttatus	0.047	-0.660	0.006
Myosotis scorpioides	0.352	0.579	0.252

Navarretia intertexta	-0.621	-0.138	0.055
Parentucellia viscosa	-0.620	-0.724	0.462
Perideridia oregano	-0.685	-0.153	0.163
Potentilla gracilis	- 0.341	-0.174	0.211
Prunella vulgaris var. lanceolata	-0.177	0.105	0.781
Ranunculus orthorhynchus	- 0.341	-0.005	-0.151
Rubus fruticosus	0.123	-0.799	0.306
Trifolium willdenovii	-0.180	0.290	-0.270
Tripholium spp	-0.621	-0.138	0.055
Vicia villosa	-0.621	-0.138	0.055

Figure 3.1. Ordination of stands in flower species space with a joint plot overlay of environmental variables. Symbols represent sites (averages of all plots for a site). The distances between sites represent the dissimilarities in flower community composition. The joint plot overlay shows the strength of correlations of environmental variables (vector lines); the longer the vector line the stronger the correlation.



Chapter Four

Seasonal patterns and relationship between butterfly and flower community composition among prairie-oak ecosystem habitats

"Look deep into nature, and then you will
understand everything better"

~Albert Einstein

ABSTRACT

I investigated temporal relationships between butterfly and flower community structure among prairie, oak savanna, and oak woodland habitats in the Willamette Valley, Oregon. I documented seasonal patterns of butterfly and flower species abundance from July to September, 2012. My objective was to determine if butterfly and flower communities were related and if seasonal butterfly patterns were correlated with seasonal changes in flower communities. Butterfly communities were positively correlated (r = 0.51, p = 0.01) with flower communities. I detected seasonal patterns in flower species across all habitat types; the highest abundance and species richness occurred during early July and declined over the summer in all three habitats. However, flower abundance and species richness increased again in prairies from late August to early September. Butterfly temporal patterns varied by species. My results suggest that butterfly communities are related to nectar communities and revealed that sites that are similar environmentally have similar compositions of butterflies and flowers.

INTRODUCTION

There is a close association between butterflies and flowers. Nectar plants and bloom abundances are known to directly affect adult butterfly distributions and abundance; the majority of butterfly species rely on specific nectar resources (Kubo et al. 2009, Ramírez 2004, Waltz and Covington 2004). Nectar resources are also important for butterfly oviposition because reproduction occurs only when nectar resources are sufficient (Murphy 1983, Waltz and Covington 2004). Furthermore, butterflies often use areas where host plants are in close proximity to nectar sources (Murphy 1983, York 2003).

Although certain aspects of the Willamette Valley prairie-oak ecosystems have been well studied (Dunwiddie and Bakker 2011), little work has focused on invertebrate community assemblages in these systems, such as butterflies (Schultz et al. 2011, Vesely and Rosenburg 2010). Prairie-oak butterfly species, in the Willamette Valley, have decreased dramatically due to loss or degradation of habitat (Schultz et al. 2011). Butterflies are good indicators of environmental changes and are sensitive to changes in habitat quality (Williams 1998). Furthermore, butterflies provide important ecosystem functions such as pollination and serve as an important prey base for other species (Yarrish 2011).

I investigated temporal relationships between butterfly community structure and nectar species richness and abundance along an environmental gradient of prairie, oak savanna, and oak woodland habitats in the Willamette Valley. Several studies propose that butterfly community composition is more influenced by nectar species presence than host plant presence (Loertscher et al. 1995) and therefore my study focused on the relationship between butterflies and flowers, rather than butterflies and host plants (Kubo et al. 2009). Adult butterflies rely on nectar as their main food resource for nutrients (e.g., amino acids) and water (Schultz and Dlugosch 1999, Waltz and Covington 2004), and some species are nectar generalist while others rely upon specific nectar sources. For example, populations of the Gillett's checkerspot (*Euphydryas gillettii*) butterflies in Willamette Valley prairies were found to increase as nectar diversity increased (Schultz and Dlugosch 1999, Williams 1988). Butterflies live longer and lay more eggs as nectar availability increases (Boggs and Ross 1993, Schultz and Dlugosch 1999). For example, the imperial common blue butterfly (*Jalmenus evagoras*) was found to lay more eggs when nectar availability increased in managed oak savannas in the mid-west (Yarrish 2011).

This study will provide information to better understand the sustainability of butterfly species that rely on prairie-oak ecosystems. My objective was to determine if butterfly and flower community structures are related and if seasonal butterfly patterns are correlated with seasonal changes in flower communities. I predicted that butterfly community structure would be correlated with flower community structure (Holl 1995). Secondly, I predicted a seasonal pattern would emerge among the different habitat types for butterflies and flowers. I also expected that butterfly species richness and abundance would be positively associated with nectar resources; sites with greater abundance and species richness of nectar sources should have higher butterfly abundance (Grossmueller and Lederhouse 1987).

METHODS

Study area and season

My study was conducted in the mid-Willamette Valley, Oregon. I selected sites in three habitat types that represent the oak canopy-cover gradient in the prairie-oak ecosystem: prairie, oak savanna, and oak woodland. These habitat types were defined based upon percentage of oak canopy cover: prairie (< 10% tree canopy cover and predominately prairie ground cover); oak savanna (10-30% canopy cover); and oak woodland (> 30% canopy cover) (Au et al. 2008, Bray 1960, Vesely and Rosenberg 2010). Study sites were located at three different locations (Figure 2.1). My criteria for selecting survey locations included that they were located within 65 km of Corvallis in the Willamette Valley, that each encompassed at least one prairie, oak savanna, and oak woodland site that represented my canopy cover gradient.

I sampled 12 study sites at three different locations. The three different survey locations were Finley National Wildlife Refuge (FNWR), Jefferson Farm and Oak Basin Tree Farm (Appendix B). At each location I had four different study sites representing prairie-oak ecosystems. Sites varied with respect to whether they were remnant or restored habitats and the methods used for maintenance and restoration.

The climate of the Willamette Valley, Oregon is relatively mild throughout the year with cool, wet winters and warm, dry summers. The majority of the rainfall occurs in the winter typically from December to February (Taylor et al. 2000). Average annual temperatures for Corvallis range from 5.4 to 17.1°C. Average annual precipitation is 104 cm (Western Regional Climate Center 2012).

Common native forbs associated with prairies and oak savanna are field cluster lily (*Dichelostemma capitatum*), large camas (*Camassia leichtlinii* spp.)**,** Nelson's checkermallow (*Sidalcea nelsoniana*), common yarrow (*Achillea millefolium*), purple clarkia (*Clarkia purpurea*), blueheaded gilia (*Gilia capital*), and willowherb (*Epilobium densilorum*). Woody vegetation associated with oak woodlands include sword fern (*Polystichum munitum*), western serviceberry (*Amelanchier alnifolia*), snowberry (*Symphoricarpos albus*), poison oak (*Toxicodendron diversilobum*); and forbs include shooting star (*Dodecatheon hendersonii*), Oregon fawn lily (*Erythronium oregonum*), peavines (*Lathyrus spp.),* and woody strawberry (*Fragaria vesca*) (Vesely and Rosenburg 2011).

Butterfly and flower surveys

I conducted butterfly and flower surveys every two weeks at each site from July to September 2012, for a total of six surveys per site. Butterflies were identified to species level by using field guides (Neill 2001) and local expert knowledge either in the field or from photographs taken during a field observations. Butterfly life cycles including the number of broods per season and timing of flight vary among species (Miller and Hammond 2007). The number of broods per season range from one to several and the timing of flights occur from early spring (March) to late summer (September) (York 2003). Due to the unusual cold and wet spring and summer in the Willamette Valley in 2012 and site accessibility, I began sampling using point-counts in July. I recorded butterfly observations on days warmer than 17 °C and with wind speeds less than 15 kph between 0930 h and 1600 h (Miller and Hammond 2007, Waltz and Covington 2004). Many diurnal butterflies are highly sensitive to weather conditions such as cool temperatures and wind and may limit flight activities in these conditions, decreasing the chance of an observation (Waltz and Covington 2004).

Point counts were conducted along transects within each site (Figure 2.2). I randomly chose one starting point and direction (left or right) and ran the first transect parallel to the border of the site and at least 25 m from the border to reduce edge effects (Dover and Settele 2009). All transect had multiple segments and the total length of transect was 500 m. Segments of transects were separated from each other by $\geq$25 m. For each transect the plot locations and start and end coordinates (Universal Transverse Mercator) were marked by a Global Position System unit (Garmin, Model: e Trex Venture HC).

I used a line-transect and circular plots (Buckland et al. 2001, 2004) to quantify the number of butterflies (total abundance) and species richness. Every 25 m along the butterfly transect I established a 5-m radius circular plot. I sampled 20 plots, at each site, for a total of 80 plots per habitat type (Figure 2.2). I surveyed sites in different order to avoid the temporal effects of time and day. I assumed a survey conducted every two weeks (Waltz and Covington 2004) captured at least one adult phase lifecycle for all species known in the prairie-oak habitats (Miller and Hammond 2007). I spent 1 minute counting and capturing butterflies at each plot (Kadle et al. 2012). For each butterfly observed, I recorded the species. For species that were not identified in the field, individuals were netted and taken for identification with help from Dr. Paul Hammond (Oregon State University).

Along the line transect I established vegetation plots within the circular plots. I conducted vegetation surveys by establishing a 2-m^2 square plot at the center point of each plot (Kent and Coker 1992). I counted flowers by the number of flowering stems in each plot.

Butterfly and flower relationships and seasonal fluctuations

Seasonal data for butterflies and flowers were condensed into a single matrix for the Mantel test by taking the average for each habitat type. I used a Mantel test to determine the linear correlation between distances matrices of butterflies and flowers (McCune and Grace 2002), to test the null hypothesis of no relationship between the Sørensen distance values of my butterfly matrix and the Sørensen distance values of my flower matrix. I tested the significance of these correlations by using Mantel's asymptotic approximation of the distribution and reported the standardized Mantel's statistics (r) (Mantel 1967).

Data values used for the seasonal fluctuation patterns were the mean value for each 2-week survey period. To determine if there were seasonal differences in butterfly and flowers community response among the habitat types I used a repeated measures two-factor ANOVA. I reported and analyzed seasonal fluctuations of adult butterfly abundance and species richness and flower abundance and species richness using the mean value and standard deviation for each survey period for each habitat type across the sampling period (July to September). An alpha value of 0.05 was used for all analyses and standard deviations were reported.

RESULTS

I observed a total 925 individual butterflies of 17 different species across the three locations for the season. Prairie sites had the highest average butterfly density and abundance, while oak woodlands had the lowest butterfly density and abundance (Table 2.1). I recorded 11,932 flowering stems of 47 different species for the entire season among all sites. There was no difference ($p > 0.33$) in flower density, abundance, and species richness among the three habitat types. My butterfly species matrix was positively related to the flower species matrix for the surveyed sites ($r = 0.51$, Mantel statistic, $p = 0.011$; Figure 4.1).

Butterfly community composition fluctuated over time in each habitat type (Figure 4.2a, b). Butterfly abundance differed significantly among survey periods (ANOVA, $F_{(5,54)} = 3.67$, $p = 0.006$) and among different habitat types ($F_{(2,54)} = 7.32$, $p = 0.001$). There was no interaction effect between survey period and habitat type (ANOVA, $F_{(10,54)} = 1.6$, $p = 0.13$). Butterfly species richness did not differ among the three habitat types or survey periods. In general butterflies increased in abundance through mid or late July or early August and then declined throughout most of the rest of the summer (Figure 4.2a). Butterflies were most abundant in prairie habitat during the late July/early August period, and abundance in oak woodlands was always lower than the other habitats throughout the summer. Butterfly abundance increased again in early September in prairie and oak savanna habitats, but not in the oak woodlands.

Patterns in butterfly species richness (Figure 4.2b) varied over the season and did not have consistent responses across habitat types. The average species richness for each habitat type was relatively low and seasonal changes sometimes varied by one species. Species richness was lower in oak woodlands than the other habitats except for the late August sampling period. Species richness in the oak savanna habitat was similar to or greater than in the prairie habitat the first half of the summer, but lower than the prairie habitat later in the summer.

Individual butterfly species displayed seasonal patterns in abundance across stand types. The most common butterfly species that occurred from early July to late September were the common wood-nymph (*Cercyonis pegala*) and the common ringlet (*Coenonympha tullia*); these species were the most common in all stands. I observed a large spike in abundance of the common wood-nymph in late July/early August, while all other species declined during this period. Six species, western tiger swallowtail (*Papilio rutulus*), common ringlet, woodland skipper (*Ochlodes sylvanoides*), Chalcendon checkerspot (*Euphydryas chalcendona*), common wood-nymph, and mylitta crescent (*Phyciodes mylitta*) accounted for 90% of all butterflies observed throughout the summer (Table 2.2).

Flower abundance and species richness also changed seasonally across all stand types (Figure 4.3a, b). Flower abundance differed among survey periods (ANOVA, $F_{(5,54)}$ = 11.4, p < 0.005) and habitat types (ANOVA, $F_{(2,54)}$ = 8.0, p = 0.001). There was no interaction effect between survey period and habitat type (ANOVA, $F_{(10,54)} = 1.07$, $p = 0.40$). Flower species richness also differed among survey periods (ANOVA, $F_{(5,54)} = 16.9$, $p < 0.005$) and habitat types (ANOVA, $F_{(2,54)} = 4.5$, $p = 0.02$). There was no interaction effect between survey period and habitat type for flower species richness (ANOVA, $F_{(10,54)} = 0.46$, $p = 0.90$). Flowers were most abundant in early July in all habitats and declined throughout the summer except in prairie habitat, where flower abundance increased again slightly in early September. In general, flower species richness was highest early in the summer and then declined throughout the summer in all habitats with the exception of prairie habitat that peaked in mid-July and increased again slightly in early September. Oak savanna and oak woodlands had similar trends in species richness; species richness was the highest at the beginning of the season and steadily declined over the summer.

Abundance of individual flower species changed seasonally across all habitat types, and each species had different periods of peak abundance. In general, the total number of flowers decreased from a high in early July through late August and increased again in September. The most common species, representing >80% of all flowers observed, were tall annual willowherb (*Epilobium brachycarpium*), which was observed each survey period, and the Muhlenberg's centaury (*Centaurium muehlenbergii*), Farewell to spring (*Clarkia amoena*), candy flower (*Claytonia sibrica*), Queen Anne's lace (*Daucus carota*), denseflower willowherb (*Epilobium densiflorum*), St. Johnswort (*Hypericum perforatum*), oxeye daisy (*Leucanthemum vulgare*), yellow glandweed (*Parentucellia viscosa*), and lance selfheal (*Prunella vulgaris var. lanceolata*).

DISCUSSION

I documented an association between butterfly and flower community composition across all sites within my prairie, oak savanna, oak woodland gradient. I also found seasonal patterns for species richness and abundance for flowers and butterflies across all habitats.

I predicted that a correlation between butterfly and flower community structures would emerge among the habitat types because the distribution of adult butterflies is known to be correlated with the availability of nectar sources (Grossmueller and Lederhouse 1987). My results supported this prediction and revealed that habitat types that are similar environmentally have similar compositions of butterflies and flowers. The spatial pattern of nectar sources are known to affect the distribution of adult butterflies (Grossmueller and Lederhouse 1987, Grundel and Pavlovic 2007, Kubo et al. 2009), and are associated with differences in vegetation structure (Blair and Launer 1997, Ehrlich et al. 1972, Hill et al. 1995, Kubo et al. 2009 Weiss et al. 1987, Wood and Gillman 1998).

I predicted a seasonal pattern would emerge between nectar community structure and butterflies community structure. My results showed that flowers and butterflies exhibited significant changes in seasonal patterns among prairies, oak savanna, and oak woodlands. Butterfly populations fluctuate due to density dependent factors (Pollard 1991), or differences in life history traits and historic factors (Gutiérre 1997). Flower phenology can evolve and adapt over time to seasonal variation, latitude, and pollinator presence (Devaux and Lande 2010). The phenology of flowers may also be influenced by changes in pollinator visitation patterns as well as species abundance and presence (Devaux and Lande 2010, Essenberg 2013). Reproductive success of flowers is affected by declines or increases in butterfly or other pollinator visitation rates (Mitchell et al. 2009, Stead 1992).

On average, prairie habitat had the highest abundance and species richness of flowering plants and butterflies throughout most the summer. Oak savanna habitat was intermediate in abundance and species richness of flowers and butterflies and, in general, oak woodlands had the lowest abundance of butterflies and flowers throughout the season. The highest flower abundance occurred in early July and declined until late August in all habitats. From late August and early September flower abundance increased in prairie habitat mainly due to the large influx of tall fireweed in the prairie at one of my study sites (Jefferson Farm). I also observed an increase in butterfly abundance from late August to early September, mainly due to the increase in the common ringlet across sites. In oak savanna habitat butterfly abundance increased during early September due to an increase in the common ringlet and the common wood-nymph, which were most abundant at FNWR. In contrast, flower abundance did not increase again in oak savanna and oak woodland habitats late in the summer.

There are limitations to this study that may be attributed to the abnormal summer weather, presence and absence of invasive species in the communities, field sampling issues, or differences in management regimes across the stands (Vogel et al. 2007). The summer of 2012 was wetter and colder in the Willamette Valley, Oregon compared to the average climate for the area (Western Regional Climate Center 2012).

This change in weather likely influenced the flight seasons of the local butterfly populations. For example, the Chalcedona checkerspot was most abundant during early July and declined after mid-July; this species flight season is known to start in April and end in June, or at the latest in July at higher elevations in Oregon (Opler and Wright 1999). The mylitta crescent displayed low abundance for most of the season and peaked in mid-September, although this species flight season typically ends in August (Paul Hammond, personal communications, 2010). However, most nectar species were observed during their known flowering times for the area (Turner and Gustafson 2006). The abundance and distribution of invasive plant species was not consistent across all sites. Because of a lack of research and information about the effects of invasive flowering species, it is difficult to know the extent of their effect on the local butterfly populations (Schultz et al. 2011). Butterfly sampling methods in this research project may have underestimated butterfly abundance and species richness (Miller and Hammond 2007).

Pollinator and flower relationships in these ecosystems are complex and should be further investigated. My results showed that butterfly communities are associated with the nectar communities (Bergman et al. 2008, Kubo et al. 2009, Feber et al. 1996), but the two are not closely linked across habitat types and throughout the summer. Other environmental factors besides nectar resources also play an important part in shaping butterfly and flower assemblages such as sub-canopy structural elements (Lane and Andow 2003) and habitat quality and isolation (Williams 2010).

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Figure 4.1. Scatterplot of the linear relationship between butterfly and nectar species matrices (Sorensen distances) in prairie, oak savanna, and oak woodland habitats in the Willamette Valley, Oregon, summer 2012. The similarities in butterfly community structure are positively related to the similarities in nectar species community structure.

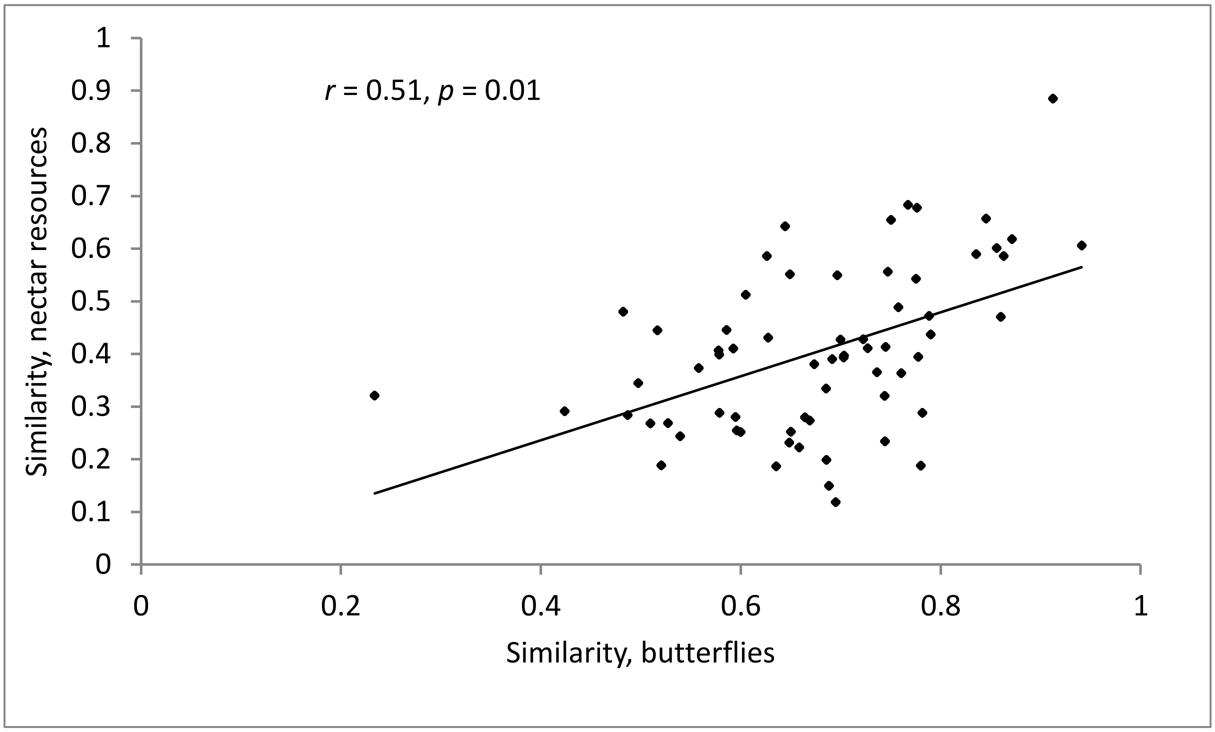


Figure 4.2. Seasonal fluctuations in mean (+ 1 SE) butterfly abundance (a) and mean (+ 1 SE) species richness (b) by survey period for prairie, oak savanna and oak woodland stands in the Willamette Valley, Oregon, summer 2012.

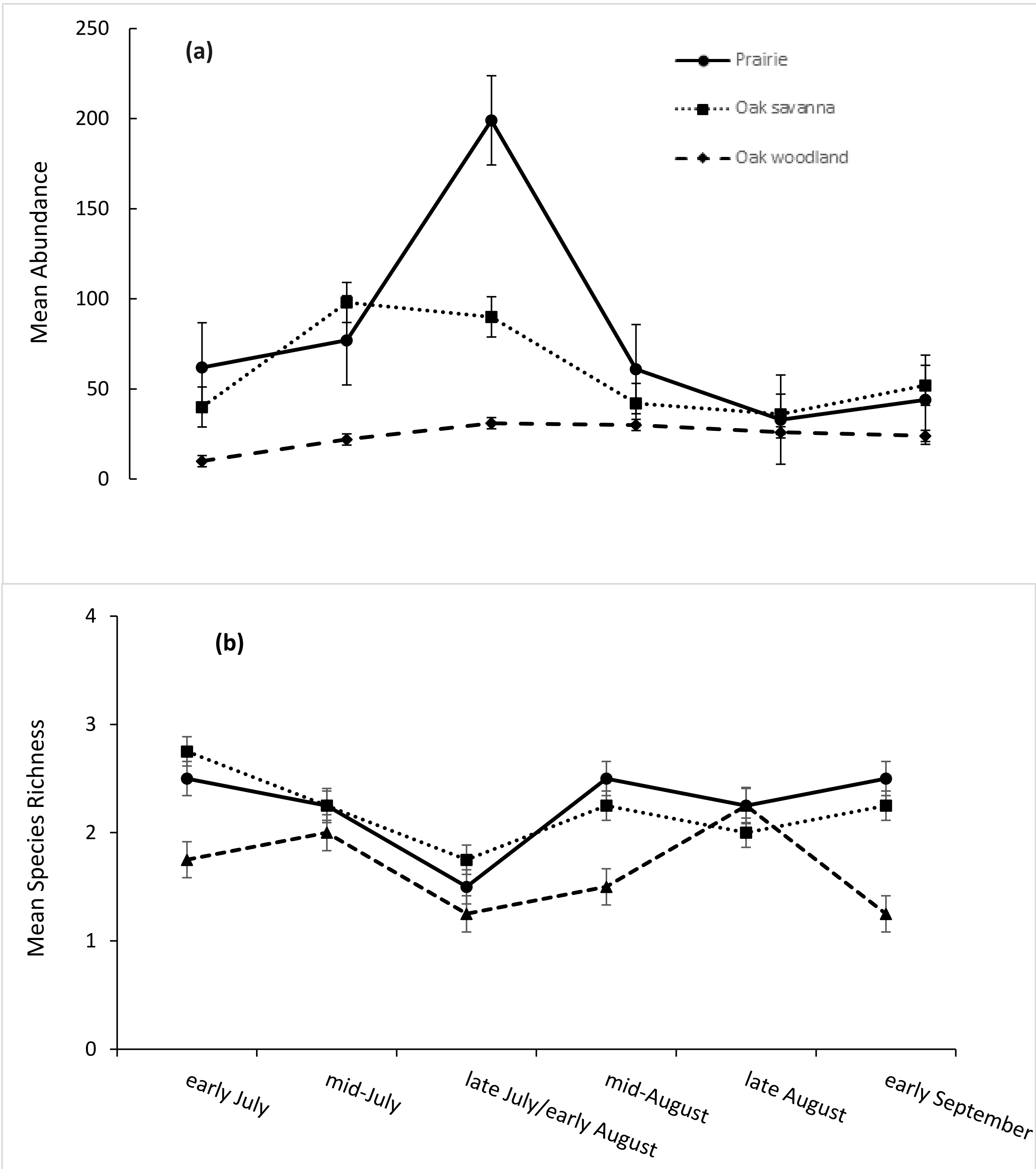
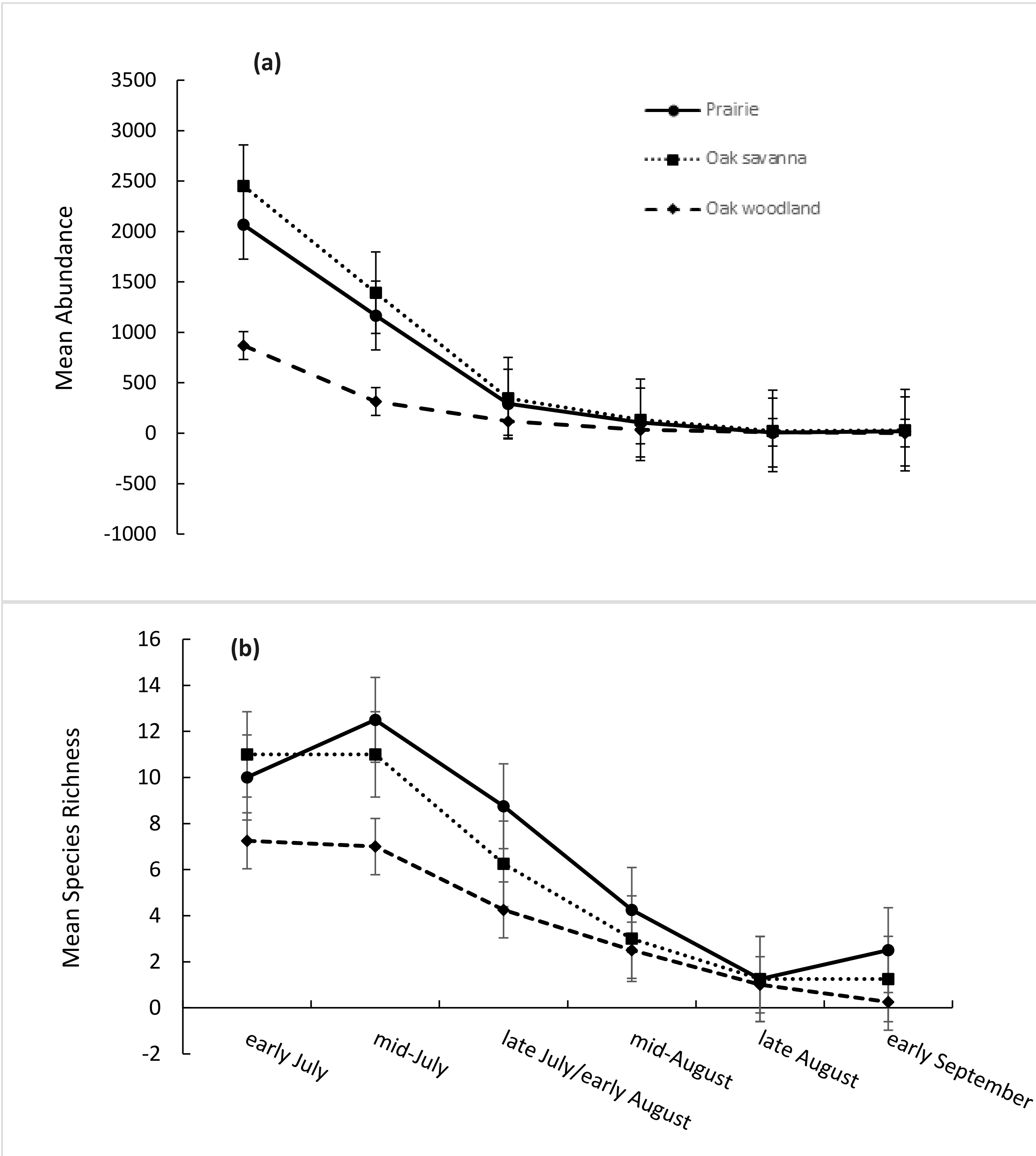


Figure 4.3. Seasonal fluctuations in mean (+ 1 SE) flower abundance (a) and mean (+ 1 SE) species richness (b) by survey period for prairie, oak savanna and oak woodland habitats in the Willamette Valley, Oregon, summer 2012.



Appendix A. List of common butterfly species in western Oregon, primary food plants, flight season (Hammond, P., personal communications, Opler et al. (2012)).

Species	**Nectar Plant**	**Host Plant**	**Flight Season**
Propertius dusky wing *(Erynnis propertius)*	Generalist	Oak and chinquapin	May
Woodland skipper (*Ochlodes sylvanoides*)	Generalist	Grasses including: Bermuda grass, canary grass (*Phalaris*), wildry (*Elymus*), and wheatgrass (*Agropyron*)	August-Sept
Western tiger swallowtail (*Papilio rutulus*)	Flower nectar including: thistles, abelia, California buckeye, zinnia, and yerba santa	Hardwoods including: cottonwoods, apsen (Populus), willows (Salix), wild cherry (Prunus), and ash (Fraxinus)	June-July
Cabbage white (*Pieris rapae*)	Flower nectar including: mustards, dandelion, red clover, asters, and mints	Plants in mustard family (*Brassicaceae*) and caper family (*Capparidaceae*) and crucifers	April-October
Pale swallowtail (*Papilio eurymedon*)	Generalist, California buckeye, yerba santa, and walflower	Trees and shurbs in the Rosacease, Rhamnaceae and Betulaceae families	April-July
Chalcedon checkerspot (*Euphydryas chalcedona)*	Generalist	Besseya, penstemon, Indian paintbrush (*Scrophularaceae*),	April-June

		snowberry and honeysuckle, Rosaceae, Boraginaceae families	
Red admiral (*Vanessa atalanta*)	Sap flows on trees, fermenting fruit, bird droppings, flowers: red clover, aster, milkweed	Nettle family	March-October
American lady (*Vanessa virginiensis*)	Dogbane, aster, goldenrod, marigold, selfheal, common milkweed, and vetch	Sunflower family everlasting (*Gnaphalium obtusifolium*), pearly everlasting (*Anaphalis margaritacea*), plantain-leaved pussy toes (*Antennaria plantaginifolia*), wormwood (*Artemisia*), ironweed (*Vernonia*), and burdock (*Arctium*)	May-November
Field crescent (*Phyciodes pulchella*)	Generalist	Various asters	May-September
Margined white (*Pieris marginalis*)	Generalist, mustard family	Brassicaceae family	February-September

Green-veined white (*Pieris napi*)	Generalist	Crucifers	April-August
Mylitta crescent (*Phyciodes mylitta*)	Generalist	Thistles including: Native thisles (Cirsium), milk thistle (*Silybum marianum*), and European thistles (Carduus)	May-August
Sonora skipper (*Polites sonora*)	Generalist, white-flowered thistles	Undetermined grasses	June-August
Painted lady (*Vanessa cardui*)	Flower Nectar, especailly from thistles, aster, cosmos, blazing star, ironweed, and joe-pye weed; other families visted include: clover, buttonbush, privet, and milkweeds	Herbs; more than 100 host plants including: thistles (Asteraceae), legumes (Fabaceae), hollyhock and mallow (malvacease)	May-September
Lorquin's admiral (*Limenitis lorquini*)	Flower Nectar including: California buckeye, yerba santa, and privet; bird dropping	Wild cherry, willows, poplar and cottonwood, and orhcard trees	June-July
Common ringlet (*Coenonympha tullia*)	Generalist	Grasses and rushes	May-August
Common wood-nymph (*Cercyonis pegala*)	Generalist	Grasses including purpletop (*Tridens flavus*)	July-August

Appendix B. Description of the 12 study sites and locations in the Willamette Valley, Oregon

Habitat type	Location	Site Name	Elevation (m)	Site size (ha)	Treatment type
Prairie	FNWR[1]	Belfountain Prairie (BP)	134	4.6	Burn
Prairie	JF[2]	F2	109	11.8	Herbicide, seeded, burn
Prairie	OB[3]	365	591	>4	Mow, burn, herbicide
Prairie	OB	366	621	4.9	Mow, burn, herbicide
Oak savanna	FNWR	Bald Top (BT)	127	10	Burn
Oak savanna	JF	FB	157	10.2	Burn, seeded, herbicide
Oak savanna	OB	OS (286)	283	10.1	Mow, herbicide
Oak savanna	FNWR	Elk Pasture (EP)	116	>9	Mow
Oak woodland	FNWR	North Bald Top (NBT)	102	12	Burn
Oak woodland	JF	O2	106	5.3	Thinned and seeded
Oak woodland	OB	OW (284+282)	343	8.1	Thinned
Oak woodland	JF	FO	173	4.2	Thinned

Location descriptions.

[1] Finley National Wildlife Refuge (FNWR) is 2,155 ha and is located 15 km south of Corvallis along the foothills of the Coastal Mountain Range (44°25'N, 123°9'W). FNWR is comprised of several habitats including upland prairie, oak woodland, grasslands, upland forest, riparian, wetlands, farm fields, and oak savanna (USFW 2011). The topography is rolling hills and elevations range from 85-165 m—with a mean elevation of 125 m (Murphy 2008).

[2] Jefferson Farm (JF) is a private rural property located in western Marion County, Oregon, 43 km north of Corvallis. Jefferson Farm began restoration projects in 2003 to restore or enhance native habitats using burning, seeding, mowing, and herbicide applications. Jefferson Farm is comprised of about 157 ha of which 55 ha are dedicated to restoration of upland prairie, oak savanna, and oak woodland. Elevations range from 60 -168 m among rolling hills.

[3] Oak Basin Tree Farm (OB) is also privately owned and is located in the Coburg Hills, ~ 16 km south of Brownsville, Oregon. Elevation ranges from 168 to 658 m. Restoration projects were initiated in 2005 to restore native upland prairie and oak savanna by thinning, burning, herbicide applications, and replanting (Merzenich 2010). The property contains stands of Douglas fir, upland prairie, oak savanna, oak woodland, mixed hardwoods, moist and dry meadows, and Ponderosa pine (*Pinus ponderosa*). The south and west aspects of the property support oak and oak savanna. There are ~ 67 ha of oak woodland, 27 ha of upland prairie, and 13 ha oak savanna (Merzenich 2010).

Appendix C. Correlation matrix of environmental structural variables for prairie, oak savanna and oak woodland stands in the Willamette Valley, Oregon, summer 2012.

	Canopy cover (%)	Maximum vegetation height (cm)	Ground vegetation cover (%)	Litter (%)	Bare ground (%)
Canopy cover (%)	1				
Maximum vegetation height (cm)	0.186	1			
Ground vegetation cover (%)	-0.655	-0.061	1		
Litter (%)	0.662	0.312	-0.865	1	
Bare ground (%)	0.378	-0.298	-0.754	0.324	1

Note: N=12, correlations greater than 0.58 are statistically significant (p<0.05).