Butterfly richness diversity and abundance in warm, dry mixed conifer 5 years post-fire in Southwest Colorado

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Introduction

Warm dry mixed conifer forests of the Southwestern United States have historically been characterized by open stands of ponderosa pine (*Pinus ponderosa)* which experienced frequent, low-severity fires that maintained forest structure and composition coupled with infrequent crown fires (Stephens et al., 2007). The adaptations of ponderosa pine allowed it to gain dominance; these include high crowns that lower the probability of fatal crown burning, thick bark that protects the vascular cambium, self-pruning of lower branches to avoid low burning fire, and long needles that shed annually. (Fule et al., 2009). Other species commonly found in warm dry mixed conifer forests include Douglas fir (*Pseudotsuga menziesi*), quaking aspen (*Populus tremuloides*) and white fir (*Abies concolor*) (Fule et al., 2009). While wildfire plays an important role in ecosystem health in the Western United States, anthropogenic influences have altered the way fire interacts with and changes these systems (Sugihara et al., 2006). Since Euro-American settlement of the Southwest from 1870-1890, changes in the land's management included over-grazing as well as adamant fire exclusion (Cooper, 1960). Intense overgrazing led to loss of herbaceous understory fuels (Dieterich and Swetnam 1984; Fule et al., 1997) and fire exclusion resulted in higher- density forests and thus higher fuel loads in the 20th century. As a result of higher fuel loads, changes in forest composition, increased temperatures, and drought conditions due to climate change, wildfires are now burning with greater frequency, intensity and severity. This goes against historical fire regimes and threatens biodiversity through higher mortality (Fule et al., 2003; Miller et al., 2008; Marlon et al., 2012; Hurteau et al., 2013).

Insect communities post-fire have been heavily studied (Swengel, 2001). Because insects are the most bio-diverse animal group (Grimaldi and Engel 2005) and have a variety of roles in ecosystems (herbivores, predators, and pollinators), they have been used to understand ecosystem responses to disturbances (Parmesan et al., 1999). Pollinator interaction with environments post-fire is important to understand considering climate change and the current pollinator crisis of reduced diversity and abundance of pollinators largely due to human disturbance (Carbone et al., 2019; Cariveau & Winfree 2015; Goulson et al., 2015). Pollinators generally increase immediately following fire in response to increased diversity and abundance of nectar producing plants (Carbone et al., 2019; Mola & Williams 2018, Van Nuland et al., 2003). However, fire return intervals, spatial scale and species must be considered when evaluating pollinator response to fire. Different pollinators will have different responses to fire due to different mobility levels, feeding and habitat requirements (Kelly et al., 2017; Pausas et al., 2019). Meta-analysis has shown pollinators to increase in diversity immediately post-fire in unburned areas; but repeat burn areas ultimately have a negative impact (Carbone et al., 2019).

Butterflies, of the Order Lepidoptera, are important pollinators and have been used as bio-indicators as they are well understood, sensitive to ecosystem changes, and visual counts are relatively easy to conduct (Kwon et al., 2010). Butterflies are often host-plant specific, thus a diverse butterfly community may signal a diverse understory; (Harding et al., 1995; Kitahara et al., 2008). Butterflies are also sensitive to micro-habitat and micro-climate changes, as different species usually have specific requirements for both the larvae and adult stages (Thomas et al., 1989). Short term changes in butterfly populations have been found to be due to weather, while long-term changes are associated with changes in habitat quality and availability (Thomas, 1984). For short term patterns associated with weather, one study conducted on butterfly populations in Britain found positive correlation between warm temperature and butterfly abundance for 28 of 31 species studied, along with negative correlation for precipitation (Roy et al., 2001). Another study conducted on butterfly populations in the Netherlands from 1990-2008 found the same trends; when comparing populations to weather information from the national meteorological station, positive correlation was found for warm temperatures in seasons besides winter and negative for mild and or rainy winters. General weather conditions were found to have more of an impact than extreme weather events such as heat waves and drought which had more of an impact on specialist species than generalists. (WallisDeVries et al., 2011).

While regional scale weather patterns certainly affect butterflies, micro-climates are extremely important as well. Due to many species of butterfly having certain thermal requirements for egg laying, micro-climate is an extremely important factor to consider when evaluating butterfly abundance and distribution. One study conducted in the calcareous grasslands of the Diemel valley in Germany, focused on butterfly larvae production of one species found this to be a balance between micro-climate and food availability – with warm micro-climate conditions generally favored. However, if weather was too hot, food availability may have decreased due to drought conditions leading to unfavorable conditions (Kramer et al., 2012). Another study focusing on micro-climate effect on butterfly communities was conducted in a neotropical dry forest of Ecuador. Transects for butterfly survey and micro-climate evaluation were created on a ridgetop with deciduous forest as well as a valley transect through evergreen forest, which differed by 150m in elevation. Ultimately, they found all vegetation (canopy cover, vegetation density, and tree diameter) and climatic variables to be significantly correlated with butterfly community dynamics, with the most significant of these being relative humidity and temperature. Species richness and abundance was found to be highest during the wet season in both habitats, presumably due to precipitation as a limiting factor in this system (Checa et al., 2014).

Despite the capability of fire to greatly alter micro-climate conditions through vegetation and canopy loss, there is a lack of studies which directly assess micro-climate conditions in fire affected areas in conjunction with butterfly dynamics. One study that does touch on this, conducted in the southeastern Amazon Forest on fruit-feeding butterflies, evaluated community dynamics in an unburned plot, and two burned plots with fire intervals of 1 and 3 years; temperature measurements were taken at transect level as well. While the low number of plots suggests pseudo replication, the authors acknowledge this stating there were no other suitable areas available; and that the high number of trappings (over 13,000) mitigate this. There were no great differences between the plots for species richness and abundance; however, the burned plot with a 3-year burn interval did have slightly higher abundance. Unburned plots showed forest specialist species present not found in the other plots, showing the sensitivity of these species to certain vegetation requirements. Ultimately, the researchers were able to conclude that micro-climatic conditions could be associated with butterfly community and composition up to 4 years post fire, with canopy openness and associated temperatures as a key factor (Andrade et al., 2017).

Meta-analysis has shown that butterflies have the strongest response to wildfire in coniferous forest systems – with significant increase in richness, but lowered abundance (Mason et al., 2021). This is thought to be due to fires creating an environment which allows for more generalist butterfly species, whilst simultaneously eliminating individuals; it is also important to note, that studies for butterfly response in coniferous systems is lacking overall, which could influence meta-analysis findings (Kwon et al., 2013; Mason et al., 2021). Studies have often focused on grassland systems (e.g. Swengel & Swengel 2013). Oligolectic or habitat specific butterfly species usually decrease post-fire (Swengel & Swengel, 2013; Cleary et al., 2004). Loss of leaf tissue (which butterfly larvae require) and loss of habitat are thought to be causes of decreased abundance post-fire (Carbone et al., 2018). Fire-severity also plays a role with high severity significantly decreasing abundance and low severity having a positive effect due to survival of understory. Over time, it has been found that butterfly response to fire may be positive due to increased plant diversity after succession (Mason et al., 2021). Time post-fire, ecosystem, and spatial scale are all important things to consider when evaluating butterfly response to fire.

Meta-analysis has found generally that butterfly species richness will increase immediately post-fire with some longer-term studies showing similar trends (Mason et al., 2021). In South Korea, after a fire burnt a pine forest in 2007 (which had already burnt in 2000), much of the forest was transformed into a grassland. Two burned and unburned sites were surveyed, and in the first year immediately following the fire, forest specialist species decreased, grassland generalists increased (along with the vegetation change) and by the second year, specialist grassland species had moved in. Overall, species abundance was found to be higher in the burned sites, while diversity was lower. This was largely due to the dominance of one species in the burned grasslands, and the presence of specialist forest species in the unburned habitat (Kim & Kwon, 2018). The lower diversity in the burned site could perhaps support the idea that areas with repeat burns do not benefit butterflies as opposed to areas with longer fire return intervals (Mason et al., 2021). Furthermore, the study supported the idea that generalists tend to increase post-disturbance, and specialists decrease. It is also important to note the presence of a rare and endangered grassland species in the burned sites, indicating the possible value of fire for some species of butterfly (Kim & Kwon, 2018).

Another study conducted in Borneo illustrates the need for understanding spatial scale. Butterfly surveys were conducted in forests affected by large scale logging and ENSO induced burning, with plots located in either continuous forest (unaffected), adjacent forest (unburned but directly adjacent to burned) and burned forest. Fire occurred partially in 1982 to 1983 and fully from 1997 to 1998, with surveys conducted in 1998 for continuous forest and 2000 for affected plots. Species richness was found to be lower in directly burned and adjacent forests compared to unburned; these effects were found to be greatest on a larger landscape scale compared to small plot samples. Large scale richness was found to be 33-54% lower in affected forest lower than continuous forest, while small scale richness was 17-39% lower, although larger scale lacks the statistical power of small scale. In this ecosystem, forest is an important habitat for butterflies, and the time scale at which the study was conducted will also have influenced the findings – 2 years post disturbance. Furthermore, the area was affected by drought, leading to synergistic interactions between disturbances. This study clearly shows the need for spatial scales as well as understanding of ecosystem – this study had lowered richness, presumably due to the large-scale disturbances as well as loss of habitat (Cleary, 2003).

In the U.S. Midwest, the endangered tall grass prairie ecosystem is one in which fire is a part of the ecosystem, like it is for the warm-dry mixed conifer forest of the Southwest. In one long term study, butterfly surveys were conducted (which focused on one endangered species) in these prairie systems from 1997 to 2016 and compared to 1) frequency of (controlled) burning, 2) number of years since last fire and 4) distance to nearest unburned suitable habitat (Henderson et al., 2018). Short term scale studies in the same system (1-3 years post-fire) generally showed decrease in butterfly presence immediately with recovery occurring shortly thereafter (Powell et al., 2007; Vogel et al., 2010). In this longer-term study, similar trends were found as with many other systems, in which populations declined immediately post-fire, however numbers recovered

2-4 years post-fire, thought largely to be due to proximity to unburned refugia habitat. Overall, they determined availability of habitat quality to be the determining factor for the presence of the endangered butterfly they were evaluating (Henderson et al., 2018).

There are many studies evaluating butterfly species richness and diversity in varying ecosystems and time scales; however, studies in coniferous forest systems with longer time intervals post-fire are lacking (particularly in the Southwest), as well as in conjunction with micro-climate conditions. Thus, our research objectives were to: 1) to quantify butterfly species richness, diversity and abundance; 2) butterfly community dynamics and indicator species analysis; and, 3) determine micro-climate (ambient surface air temperature) patterns and how they correlate with butterfly richness, diversity and abundance five years post-fire in the 416 Fire burn area (no burn, low severity, moderate severity, and high severity) in warm, dry mixed conifer in southwestern Colorado. We hypothesized butterfly species richness and abundance to be greatest in high burn severity areas due to early post-fire plant succession that allows micro-habitat for annuals, ruderals (native generalists), and non-natives and the higher presence of flowering plants as well as warmer micro-climates provided by vegetation. For community dynamics, we hypothesized moderate and high burn severities would be populated with more generalist species and no burn to low severity would have a higher proportion of specialist species present. Previous studies have indicated that post-fire, generalists tend to increase as specialists lose habitat (e.g., forest butterfly species) (Kwon et al., 2013; Mason et al., 2021). Lastly, we hypothesized that warmer micro-climates would have a higher abundance of butterflies as warmer temperatures tend to be preferred; however, there is a balance, as too hot of temperatures may lower the availability of resources in extreme conditions. Studies have found that general weather conditions have a bigger impact on overall butterfly abundance than extreme weather events showing the importance of micro-climate conditions; however, extreme weather can negatively affect specialist species.

Methods

Study Area:

The study site is located approximately 21 km north of Durango, Colorado in the southern portion of the San Juan National Forest adjacent to Hermosa Creek within the Hermosa Special Management Area and Hermosa Wilderness (BAER 2019). The study area ranges in elevation from 2277 m to 2470 m on steep slopes that range from 30 to 45 degrees. Average daily temperatures range from a maximum of 26.7°C in July to a minimum of -12.2°C in January. Average annual precipitation is 58.4 cm, with the greatest amounts occurring in July and August due to summer thunderstorm activity. Precipitation from November to March is dominated by snowfall (Western Regional Climate Center, Tacoma, 1971–2000, www.wrcc.dri.edu). Forest types in the study area vary from ponderosa pine (*Pinus ponderosa*) and pine oak forest to warm-dry and cool-moist mixed conifer. Aspen is present in the study area and continuous stands of aspen exists adjacent to plots, however, aspen is only a minor component of overstory trees in plots. The study area has never been logged and has a high proportion of large diameter trees for all species present with many stands having old growth characteristics (Mehl 1992). *Pinus ponderosa, Pseudotsuga menzesii* (Douglas-fir), *Abies concolor* (white fir), *Abies lasiocarpa, Pinus flexilis, Picea pungens, Populus tremuloides* are the common tree species. Common sprouting shrubs including *Quercus gambelii* (Gambel oak), *Symphoricarpos oreophilus* (snowberry), *Prunus virginiana* (chokecherry), and *Amalanchier alnifolia* (Utah serviceberry).

In 2008, portions of the study area were burned in a broadcast prescribed fire using aerial ignitions. Ten years later in 2018, the study area was burned by an unplanned, artificial ignition that burned a total of 54,130 acres (416 Fire). The 416 Fire burned during an extreme drought year resulting in mixed soil burn severities from overall moderate fire behavior driven primarily by available fuels and topography. Suppression efforts focused on the wildland urban interface and no slurry drops or direct attack measures were taken in the study area (Communication with Incident Section Chief).

Experimental Design:

Random points were generated using ArcGIS with a minimum spacing distance of 100 meters and within a mile buffer of existing trails to ensure accessibility to sites given the steep slopes of the drainage. We then stratified these points across burn severities as determined by Rapid Assessment of Vegetation Condition After Wildfire (RAVG) data. Burn severities across the entire 54,130 acres fire in percent include: low (44%), moderate (20%), high (19%) and unburned (17%). Once random points were established in GIS, a random number generator was used to select 9 points for each burn severity, not including unburned, to be established as "full" plots that include forest overstory, shrub, tree regeneration, herbaceous understory, and fuel measurements.

Field Methods:

Butterfly species richness, diversity, abundance, frequency

We conducted butterfly surveys from mid-June to mid-July for approximately 4 weeks of surveying in the summer of 2023. Surveys were completed on sunny days with temperatures 17° C or above, with low wind, no precipitation, minimal clouds and in between the hours of 10:00 to 16:00 to account for daily activity variability among species (Frahtia et al., 2022; Schlegl, 2022). As much care as possible was taken to ensure individuals were not counted twice through careful watch of butterflies after capture; only butterflies in front of us whilst moving along the transect were counted. We established transects from point centers with 25 m above and 25 m below a permanent rebar along the greatest environmental gradient. Transects created a belt transect with 5m extended to each side for a 500m^2 survey area for each plot of each severity type (unburned, low, moderate, and high) and were walked for 20 minutes. We surveyed each burn severity in a randomized order in addition to sampling time so that it was not conducted in a systematic way and accounted for variability. We surveyed 9 plots for each severity type twice during the summer. We used a sweep net to capture to identify species and live release for all unknown species; photography was also used to record species that we could not identify in the field.

Microclimate

We used iButtons to record temperatures throughout the sampling periods to determine microclimates in the plots. I-buttons were placed approximately 12 inches above the ground on PVC with a shield to lower inflated ambient air temperatures (Cerrato et al., 2019; Xing et al., 2016). Dixie cups were used as shields and we placed the I-buttons at the lower edge of the cup to avoid inflated temperatures. Each plot had 2 iButtons at 5m and 45m along the transect which recorded temperatures every 30 minutes. I-buttons recorded microclimate over a 6-week period to quantify daily and seasonal microclimate variation.

Statistical Analysis

We used SPSS version 27 software for all analyses. We used non-parametric Kruskal Wallis tests to quantify differences among burn severities (low, moderate, and high) followed by a post-hoc Bonferroni test. We used non-metric multidimensional scaling (NMS) analyses utilizing PC-ORD software for community statistics (Clark, 1993; McCune and Mefford, 2006)The NMS ordination was ran utilizing a Bray-Curtis distance measure (Faith et al., 1987), random starting configurations, 50 runs using real data and a stability value of .00001. Only species present in at least 5% of the plots were analyzed (McCune and Grace, 2002). Lastly, we used indicator-species analysis which utilizes species richness and abundance values to determine any species that could be identified as indicators amongst the burn severities. We compared the maximum indicator value (0-100) and random trials for the presence of a given species and the corresponding p-value for indicators (McCune and Grace, 2002). Species with a p-value less than or equal to .05 and an indicator value greater than 25 were considered an indicator species (Dufrene and Legendre, 1997).

Results

Vegetation

We found no significant differences among burn severities for total shrub cover (%), although unburned had the highest average shrub cover and low severity the least **(Table 1)**. Significance was found for both live (p =.001) and dead tree density/ha (p=.007). Unburned had the highest live tree density (114.6 trees/ha) and high burn severity the least (7 trees/ha). High severity had the greatest dead tree density (116 trees/ha) and moderate the least (23 trees/ha) **(Figure 1)**.

Microclimate

We found marginal significance for differences in daytime ambient air temperatures among burn severities (p=.088) and significanct differences (p=.001) for nighttime ambient air temperatures. Pairwise comparisons showed marginal significance between unburned and high severity for daytime (p=.097) and significance between unburned and low severities (p=.002) and unburned and high severities (p=.004). Unburned had the coolest average daytime temperature (22.6 ℃) and warmest average nighttime temperature (13.2 ℃). High severity had the highest average daytime temperature (24.8℃) and the largest fluctuation from average daytime temperature (14.4 ℃) **(Table 2)**.

Butterfly abundance, diversity, richness and community composition

We found no significant differences among burn severities for butterfly diversity and abundance; however, there was marginal significance (p=.088) for richness. Low severity had the highest average species richness per plot (11.8), and though not significant, the highest diversity and abundance as well **(Table 3).** Significant differences were found among burn severities for community composition with unburned and moderate burn severities showing higher variability and low and high severities more homogeneity in community structure **(Figure 2).** Indicator species were detected only for unburned and low severities with some differences in indicators for the early, late, and overall sampling periods. Unburned had a total of four indicator species while low had five; however, no indicators were found for the low severity early sampling period. Indicator species for unburned included *Phyciodes cocyta*, *Glaucopsyche piasus*, *Echinargus isola* and *Erynnis persius*. Indicator species for low severity included *Colias eurytheme, Polygonia gracillis, Speyeria atlantis, Pontia occidentalis,* and *Colias alexandra* **(Table 4).** Thirty-six species were encountered across all severities with two unique in unburned, five in low, and two in high severity.

Discussion

Butterfly richness, abundance, and diversity

Our study showed no significant differences in butterfly abundance, richness, and diversity five years post-fire among burn severities for butterflies **(Table 3).** This supports other studies that showed butterflies can re-colonize relatively quickly after a fire with the biggest fluctuations in populations occurring immediately post-fire. A study in South Korea that surveyed butterflies 1-5 years post-fire showed no significant differences in species richness and a slight decrease in diversity with increases in generalists observed only in the first-year post-fire (Kwon et al., 2013). Another study conducted two years post-fire in a Mediterranean landscape consisting of pine forests and shrublands showed insignificant differences in abundance, richness, and diversity compared with unburned sites despite the severity of the wildfire leading researchers to conclude that butterflies were able to successfully re-colonize the area relatively quickly (Serrat et al., 2015). Although not significant, this study did find higher abundance in burned sites but lower overall diversity, which is congruent with many other studies that show similar trends for butterflies and other pollinators post-fire. The lack of significant differences and comparable diversity levels among severities in our study align with other studies with longer interval times post-fire and may illustrate forest and ecosystem recovery.

There was no significant difference for butterfly abundance or diversity with marginal significance (p=.088) for richness. Low severity had the highest richness, abundance and diversity; however, our small sample size may have impacted the ability to detect significant differences among burn severities **(Table 3).** Relatively frequent, low-severity fires are the historical fire regime for warm-dry mixed conifer forests in the Southwest. Studies in various ecosystems support the idea that fire disturbance on some level is beneficial for butterflies – for instance, one study in Oregon documented that although prescribed fire initially killed larvae of an endangered butterfly species, the fecundity of the species was increased compared to unburned sites in the years following prescribed burns (Warchola et al., 2017). Another study that looked at burning practices on grasslands found that although butterfly diversity in sites one-two years post-burn were comparable to unburned, unburned sites that had experienced five years or more without fire had lower diversity than sites with regular fire intervals (Gaigher et al., 2018). When considering fire effects on butterflies and other species in ecosystems adapted to disturbance, one must consider the balance between short- and long-term ecological costs and benefits. Allowing for some level of disturbance promotes a heterogenous habitat with various species and preferences, although some specific species may not benefit as much as others in response to disturbance (Ponsio et al., 2016). The general patterns in our study where areas with low severity fire had higher richness, abundance and diversity, although not significant, is in alignment with other literature demonstrating long-term benefits of low to intermediate burn severities for butterflies (Gaigher et al., 2019; Huntzinger, 2003; Vogel et al., 2010; Warchola et al., 2012).

Community composition

We quantified significant differences in butterfly communities among burn severities five years post-fire. High severity areas had the most homogenous composition while unburned and moderate burn areas had the most heterogeneity **(Figure 2).** Variation in unburned areas may be from specific forest patches supporting less mobile butterfly species thus creating a more varied species composition. Other studies have shown a persistent change in butterfly community composition post-fire. One study in South Korea determined burn history to be a main factor driving differences in butterfly assemblages five years plus post-fire (Kim & Kwon, 2018). Another study found butterfly assemblages to be significantly different two years post-fire in the tropical forests of Indonesia due to an altered forest structure between burned and unburned areas

(Cleary, 2003). However, another study found no significant differences two years after a severe wildfire in a Mediterranean pine/oak forest, which may be do the rapid regeneration of shrubs post-fire (Serrat et al., 2015). Although there are some discrepancies in various studies with differing ecosystems and disturbance histories, our study illustrates the ability of fire to transform habitats and create heterogenous stands with varied and complex canopy structure that results in diverse butterfly community assemblages.

Microclimate and implications for butterflies

Significant differences were found for microclimates among burn severities with high severity having the warmest ambient average daytime temperature and the lowest nighttime temperature, while unburned had the coolest daytime and warmest nighttime temperatures **(Table 2).** These differences are presumably due to canopy and vegetation cover with high severity having the lowest live tree cover while unburned had the highest illustrating that five years post-fire, microclimate is still significantly altered via canopy loss and vegetation structural changes **(Figure 1)**. Some canopy loss which creates gaps that allow for understory growth is positive; however, too much can be detrimental if it causes microclimate temperatures to be too extreme and reduces conifer regeneration, converting forest to shrubland (Crockett & Hurteau, 2022). Areas of high-severity burn may experience more microclimatic extremes, with excessive soil frost in the winter (Goulet 1995) or excessive heat in the summer, which may cause conifer seedling mortality (Loupushinsky & Max, 1990). Although an understory of flowering shrubs may be beneficial to butterflies, complete loss of tree canopy cover may be damaging to their larval stage in which canopy and/or thick shrubs moderate microclimate. In our study, high severity burn areas had the largest fluctuations in microclimate, which was expected **(Table 2)**, but lacked significant corresponding findings in butterfly richness, diversity and abundance suggesting that these fluctuations were not extreme enough to cause detrimental effects. Furthermore, there are numerous studies that support the idea that heterogenous forest structure with canopy gaps and warmer microclimates are beneficial to butterflies. Researchers quantified live understory vegetation and tree canopy cover as strong indicators of butterfly presence due to solar insolation increasing with decreasing tree canopy cover, which could affect butterflies through altering nectar source availability, or physiologically when butterflies are in the larval or adult stage (Pavlik et al., 2017). Another study conducted in Yosemite and Southern Oregon illustrated 80% of butterfly richness variability was associated with gaps in the tree canopy (Huntzinger 2003). We found the highest abundance of butterflies in the relatively moderated microclimate of low severity where daytime temperatures were not too hot, although nighttime temperatures were the coolest. The change in day to night temperature was presumably not large enough to cause detrimental effects to either the butterfly's nectar source or their physiological requirements.

Indicator species

Indicator species were only detected for unburned and low severities; potentially suggesting sensitivity of species in these habitats and their need for a specific, established habitat structure of high tree density, although, it is interesting to note that moderate severity had slightly higher live tree cover compared to low **(Figure 1, Table 4).** Generally, more forested habitats house more sensitive and specialized species of butterflies. However, in our study, low and moderate severities may be considered more homogenous habitats as vegetation was relatively similar with the most extreme vegetation differences observed between unburned and high. Low severity burn areas had two indicators *Colias eurytheme* and *Polygonia gracillis. Colias eurytheme* is considered a habitat generalist and is widespread throughout North America in a variety of habitats; it feeds on plants in the Fabaceae in the larval stage and a variety of nectar sources in the adult stage. *Colias eurytheme* typically produce 3-4 broods a season with a life cycle which usually lasts a few weeks; though they do have the ability to hibernate. *Polygonia gracillis* is also a generalist that is found in a variety of habitats though they are less widespread than *C. eurytheme* with differing life history traits. They emerge in the spring to mate, take flight during the summer, and overwinter as adults. *Polygonia gracillis* does not make extended migrations, but rather small 'elevational migrations' for wintering grounds and generally travels to higher elevations in the summer (Glassberg, 2001). It is possible that the microclimate conditions in low severity provided either the correct temperatures which ensured winter survival; or perhaps provided the appropriate nectar sources and were the 'summer grounds' of the species in our area. Mobility and migration patterns are important to understand when examining butterfly species as species which have low movement tend to be more sensitive to disturbance (Pavlik et al., 2017).

Unburned areas had two indicator species for the overall season: *Phyciodes cocyta* and *Glaucopsyche piasus*. *Phyciodes cocyta* is a non-migratory species that hibernates with Colorado being the southern reach of its range, and it can be found generally in moist habitats feeding on asters as a caterpillar and a slightly wider variety of nectar plants as an adult (Glassberg, 2001). Though we did not take detailed species vegetation data, many asters were observed in the unburned plots. *Glaucopsyche piasus* is another non-migratory, generally local butterfly that requires larval host plants in the Fabaceae family but can source nectar from a variety of plants as an adult. *Glaucopsyche piasus* is common in ponderosa pine forest with flight occurring from late spring to mid-summer. Larvae overwinter, and the unburned habitat in our study may provide the correct microclimate conditions that do not have extreme fluctuations allowing for larval survival (Glassberg, 2001). Unburned areas also had different indicator species by growing season (early vs late) *Phyciodes cocytas* was an indicator for late season and *Echinargus isola* and *Erynnis persius* for the early sampling period. *Erynnis isola* is a migratory species which hibernates in the south and travels north in the summer; *E. persius* is non-migratory, and usually found in more open habitats (Glassberg, 2001). Low severity had an additional three indicator species during the late sampling period: *Speyeria atlantis, Pontia occidentalis,* and *Colias alexandra*. All three species are non-migratory with maximum travel being relatively short. Nearly all indicators (except for *E. isola*) can be considered relatively restricted in their movements; thus, they may be more sensitive to disturbance, with unburned and low severity maintaining habitat requirements for their larval and adult stages.

The five most common species which were found among all burn severities included *Pontia occidentalis, Spreyeria mormonia, Pieris rapae, Pieris oleracea*, and *Phyciodes pulchella*. *Pontia occidentalis* alone accounted for 17.5% of butterflies observed in high severity burn areas and was also an indicator species for the late season in low severity. This demonstrates *P. occidentalis* as able to move through different habitats, in various times throughout the growing season. Overall, these five butterflies accounted for 47% of butterflies observed in high severity, 48.2% in moderate, 43.6% in low, and 26.3% in unburned **(Table 5).** The significantly lower proportion of these species in unburned is potentially congruent with butterfly community composition and supports the idea that generalists tend to inhabit disturbed habitats. However, of these species, *P. oleraceae* is the only species which migrates; and while *S. mormonia* does not migrate, it may travel far distances. This diversity of butterflies with varied mobility may signal a recovered ecosystem which can support species limited with their movement; and the presence of butterflies with higher mobility may signal a disturbed habitat.

Limitations of study and conclusion

It is important to note that our study conducted butterfly surveys for approximately 4 weeks throughout the growing season (late June – late July), and therefore we only have a snapshot of butterfly richness, diversity, and abundance that may be present throughout the 416 Fire during a wide study period extending into early summer and late fall . Butterflies have short life cycles, with many species only living a couple of weeks producing only a single brood. Thus, we most likely did not capture the full variability of butterfly species possible throughout the entire growing season, nor the full picture of how differing severities and microclimates may support diverse species throughout the duration of the season. However, we still collected data, which can support two main conclusions – 1) that the 416 Fire is likely on its way or is recovered. Our overall insignificant findings for butterfly diversity, richness, and abundance support this, along with insignificance for shrub cover, and shrub/forb biomass among burn severities five years post-fire. However, it is important to note some effects are still seen five years post-fire including significant differences in microclimate and live/tree dead density. 2) changes after the 416 Fire are not necessarily negative as we quantified that different burn severities support diverse and unique butterfly assemblages. Our study findings suggest that managers should aim to maintain intermediate levels of disturbance to create heterogenous habitats, which have complex vegetation structure that can maintain microclimatic and general habitat conditions for numerous butterfly species in both the larval and adult stages resulting in increased ecosystem health.

Table 1. Mean (± SEM) total shrub cover (%) in the 416 Fire by burn severity five years post-fire, Durango, Colorado. There was no significant difference among burn severities using a Kruskal-Wallis test ($p \leq 0.05$). N=10/burn severity.

	Unburned	**Low**	**Moderate**	**High**
Total Shrub Cover	52.8% (7.3)	28.3% (11.1)	33.5% (6.4)	35.4% (6.5)

Table 2. Mean (± SEM) daytime and nighttime temperatures between 6/20/23 and 7/22/23 in the 416 Fire, Durango, Colorado, five years post-fire by burn severity using a Kruskal-Wallis test followed by post-hoc Bonferroni tests. Significant differences in microclimate are denoted by different letters among burn severities. There was a significant difference for mean nighttime temperatures ($p=0.001$) and marginal for daytime temperatures ($p=0.08$) between unburned and high severity burn areas. N=7/burn severity.

Temperature	**Unburned**	**Low**	**Moderate**	**High**
Day	22.6 (.5)	23.1 (.5)	23 (.4)	24.9 (.7)
Night	13.2 (.3)	10.3 (.5)	11.43 (.4)	10.4 (.2)

Table 3. Mean (± SEM) butterfly abundance, richness and Shannon's Diversity in the 416 Fire, Durango, Colorado, by burn severity five years post-fire. We found no significant differences among burn severities using a Kruskal-Wallis test. N=9/burn severity. Low severity had the highest abundance, richness and diversity.

Burn Severity	**Abundance**	**Richness**	**Shannon's Diversity Index**
Unburned	8.9 ± 0.8	7.8 ± .66	1.9 ± .08
Low	13.6 ± 2.7	11.8 ± .84	2.2 ± .15
Moderate	9.4 ± 1.9	7.7 ± 1.3	1.8 ± .11
High	10.1 ± 1.2	8.3 ± .57	1.9 ± .08

Table 4. Indicator species associated with different burn severities in the 416 Fire, Durango, Colorado, across the entire growing season. Species with $P \leq 0.05$ and indicator values (relative abundance × relative frequency) > 25 were accepted as indicator species for a particular burn severity using Pc-Ord.

	Species	**Indicator Value**	**p-value**
Unburned (Early)	Reakirt's Blue (*Echinargus isola)*	37+/- 7.03	.0332
	Persius Duskywing (*Erynnis persius*)	33.3+/-6.82	0474

Unburned (Late)	Northern Crescent (*Phyciodes cocyta*)	33.3 +/- 6.91	0446
Unburned (Overall)	Northern Crescent (*Phyciodes cocyta*)	44.4 +/- 7.72	.0106
Low (Late)	Atlantis Fritillary (*Speyeria atlantis*) Western White (*Pontia occidentalis*) Queen Alexandra's Sulphur (*Colias alexandra*)	47.3+/- 7.07 49.4+/- 8.07 38.3+/- 7.02	.0030 .0086 .0302
Low (Overall)	Orange Sulphur (*Colias eurytheme*) Hoary Comma (*Polygonia gracillis*)	44.4 +/- 6.20 43.7 +/- 6.43	.0050 .0154

Table 5. The three most common butterfly species found in the 416 Fire, Durango, Colorado, and their percentage relative to total abundance across the severities**.**

Species	**Unburned**	**Low**	**Moderate**	**High**
Western White (*Pontia occidentalis*)	7.9%	12.8%	10.2%	17.5%
Mormon Fritillary (*Speyeria mormonia*)	7%	12%	10.2%	6%
Cabbage White (*Pieris rapae*)	3.5%	6.4%	13.1%	12.1%
Mustard White (*Pieris oleracea*)	5.3%	4.4%	8.7%	7.4%
Field Crescent (*Phyciodes pulchella*)	2.6%	8%	6%	4%

Figure 1. Mean (± SEM) live and dead tree density/ha in the 416 Fire, Durango, Colorado, by burn severity five years post-fire. We found significant differences among burn severities for live ($p<0.001$) and dead tree density/ha ($p=0.007$) using a Kruskal-Wallis test followed by post-hoc Bonferroni tests. Significant differences among severities for live/dead trees are denoted by different letters. N=10/burn severity.

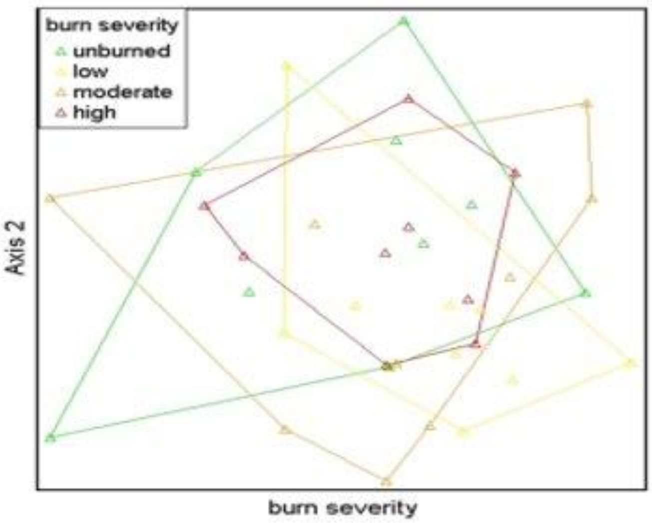

Figure 2. Non-metric multi-dimensional scaling ordination of butterfly communities five years post-fire in the 416 Fire, Durango, Colorado. Each color represents a burn severity type with each triangle representing an individual plot. The closer the two plots are together; the more similar butterfly species composition and corresponding abundance are for the two plots. N=10/burn severity. There were significant differences in butterfly communities by burn severities ($p=.043$) using PERMANOVA in Pc-Ord.

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