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POST-FIRE SUCCESSIONAL RESPONSE OF LEPIDOPTERA COMMUNITIES IN THE SIERRA MADRE ORIENTAL MOUNTAIN RANGE

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POST FIRE SUCCESSIONAL RESPONSE OF LEPIDOPTERA IN THE

SIERRA MADRE ORIENTAL MOUNTAIN RANGE

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LIST OF DEFINITIONS AND ABBREVIATIONS

BAMONA: Butterflies and Moths of North America, an online citizen science database of butterfly observations and life history information

CCA: Canonical correspondence analysis, a multivariate ordination technique that determines the relative influence of various independent variables on a species assemblage dataset.

CMNP: Cumbres de Monterrey National Park, a protected area where the study sites are located

Hill numbers: represented by the variable q, each number represents a different diversity measure. Species richness is represented by q=0, Shannon diversity index is represented by q=1 and Simpson diversity index is represented by q=2 **iNEXT:** A statistical analysis procedure in the R statistical program that

interpolates, extrapolates and rarefies Hill numbers given a species dataset.

MMA: Monterrey metropolitan area

SMOr: Sierra Madre Oriental mountain range, the ecosystem containing the pineoak forests where the study sites are located

ABSTRACT

Anthropogenic forest fire accounted for 63% of fire activity in Cumbres de Monterrey National Park between 2000 and 2017. Changing forest fire regimes may have serious implications for forest health, impacting the local economy which depends heavily on ecosystem services in the park. Lepidoptera are important forest pollinators and are potentially useful indicators due to their sensitivity to ecological disturbances, therefore their response to disturbance merits study. The objectives of the current study were 1. to characterize changes in canopy openness, understory cover and flower diversity and 2. to characterize diurnal Lepidoptera communities in terms of species diversity, and proportions of specialist and generalist species in early post-fire succession. Forest structure and butterfly diversity were surveyed in an area recently affected by anthropogenic forest fire and an unburned control site. Four 200m transects were established in each site with two 2 x 2m plots on either end of each transect. Habitat assessments in these plots provided data on understory vegetation and canopy cover. Walkand-count transect surveys and Van Someren-Rydon traps were employed to measure Lepidoptera species richness and abundance. Canopy openness and understory cover were significantly lower in the control site (p<0.001). Rarefied species richness and diversity indices of butterfly communities measured by transect method were not significantly different, but the observed butterfly abundance (p=0.002) and species richness (p=0.005) per sampling day was significantly higher in the burned site throughout the year. Generalist species were significantly more abundant (p=0.037) in the burned site. The differences in forest structure post-fire reflect well-studied successional processes. Changes in butterfly community composition post-fire support the theory that butterflies are early colonizing species and are sensitive to forest disturbances. However, generalist species abundance tends to increase in open habitats while specialist species are more sensitive to disturbances. Specialists A. troglodyta and P. *pilumnus* are suggested as potential indicator species for this ecosystem.

RESUMEN

Incendios forestales antropogénicos comprendieron el 63% de incendios en Parque Nacional Cumbres de Monterrey entre los años 2000 y 2017. Cambios en el régimen de incendios forestales podrían tener impactos importantes en la salud del bosque y la económica local, cual depende sobre los servicios ambientales del parque. Los lepidópteros son polinizadores importantes y podrían ser especies indicadores útiles por su sensibilidad a disturbios ecológicos y por lo tanto, su responsorio a disturbios merece estudio. Los objetivos de este estudio fueron 1. caracterizar cambios en la cobertura del dosel, cobertura del sotobosque y la diversidad de flores y 2. caracterizar comunidades diurnas de lepidópteros en cuanto diversidad y proporciones de especies generalistas y especialistas en la sucesión temprana post-incendio. Estructura forestal y diversidad de mariposas se muestrearon en un área recientemente afectada por un incendio antropogénico, y un área control no quemado. Cuatro transectos de 200m se establecieron en cada sitio con parcelas de 2 x 2m al inicio y el final de cada transecto. Muestreos de hábitat en estas parcelas proporcionaron datos sobre la cobertura del dosel y del sotobosque. Transectos caminar-y-contar y trampas Van Someren-Rydon se emplearon para muestrear la riqueza de especies y abundancia de Lepidópteros. La cobertura del dosel fue más alta, y la cobertura del sotobosque fue más bajo en el sitio control (p<0.001). Las diferencias entre riqueza de especies e índices de diversidad Shannon y Simpson enrarecidos medidos por el método transecto no fueron significativas, pero las diferencias entre la abundancia (p=0.002) y riqueza (p=0.005) de especies observadas por fecha fueron más altas en el lugar quemado. Especies generalistas fueron más abundantes en el sitio quemado (p=0.037). Las diferencias en la estructura del bosque post-incendio reflejan procesos de sucesión de bosque bien conocidos. Cambios en la comunidad de mariposas apoyan la teoría que las mariposas son especies de colonizadores tempranos y son sensibles a disturbios. Sin embargo, especies de generalistas tienden a incrementar en hábitats abiertos mientras vii

especialistas son más sensibles a disturbios. Las especialistas *A. troglodyta* y *P. pilumnus* se sugieren como especies indicadores potenciales para este ecosistema.

1 INTRODUCTION

Disturbances such as fire, extreme weather and disease are a natural component of all forest ecosystems. Forest ecosystems are adapted to natural disturbance regimes which are increasingly being impacted by human activities such as changes in land use, resource extraction, introduced species and climate change (Aguiar et al., 2016; Dale et al., 2001). Because of the economic and cultural importance of forests to human civilization worldwide, understanding the causes and results of these changing disturbance regimes in forests is of utmost importance.

Uncontrolled forest fire creates a particularly interesting disturbance regime given its potential for rapid destruction. Many forest species have evolved to be tolerant of and even reliant on natural fire cycles. Trees with serotinous cones rely on fire to expose the seeds for germination (J. K. Brown, 1975), the soil nutrient cycle is reliant on fire to increase soil nutrient availability (Certini, 2005; DeLuca, Gundale, MacKenzie, & Jones, 2012; Mataix-Solera, Cerdà, Arcenegui, Jordán, & Zavala, 2011) some birds of prey rely on fires to create foraging opportunities (Bonta et al., 2017), and many species benefit from the heterogeneous landscape diversity created by fires (Arellano & Castillo-Guevara, 2014). Ecological relationships with forest fire are specific to the fire regime of the given region and climate, therefore changes to the natural fire regime affect every species within the ecosystem. The effects of anthropogenic changes to natural fire regimes via excessive anthropogenic fire, fire suppression and human-caused climate change have already been observed in forests worldwide (Abatzoglou & Williams, 2016; Balch et al., 2017; Moritz et al., 2012). In the case of northern boreal forests, fires are predicted to become more frequent, more severe and to cover more area as the concentration of atmospheric carbon increases (Flannigan, Stocks, & Wotton, 2000; Stocks et al., 1998; Wotton, Nock, & Flannigan, 2010). Fire suppression and excessive anthropogenic fire relative to the natural fire regime can also have serious negative consequences on forest ecology (Rodríguez-Trejo & Fulé, 2003).

While most species are affected by changes in forest fire regime, many species of insects have been suggested as effective indicator species of forest health. Butterflies are relatively abundant, easy to survey due to their high visibility and they have been demonstrated to respond quickly to environmental change (Forister et al., 2010; Perfecto, Mas, Dietsch, & Vandermeer, 2003; Wood & Gillman, 1998). Because of these characteristics, they are an ideal study subject to monitor the effects of anthropogenic forest fire in this ecosystem. Not all butterfly species are effective indicators of forest health, but a study of the entire butterfly community following a forest fire event may provide useful insights into the characteristics of early forest post-fire succession.

1.1 Literature Review

1.1.1 Butterfly Ecology

There is a large amount of niche diversity within the Lepidoptera which makes them a geographically widespread family adapted to a wide variety of different ecosystems. Most butterflies feed on the nectar of flowering plants (Martínez-Adriano, Díaz-Castelazo, & Aguirre-Jaimes, 2018; Tudor, Dennis, Greatorex-Davies, & Sparks, 2004) while other species feed on fruits (Devries & Walla, 2001) or carrion (Payne & King, 1969). Lepidoptera species exhibit a wide range of behaviours to acquire sodium, minerals, proteins and amino acids as dietary supplements. The males of various families of Lepidoptera also engage in mudpuddling behaviour in order to collect sodium, proteins and minerals to offer as nuptial gifts to female Lepidoptera during mating (J. Beck, Mühlenberg, & Fiedler, 1999; Smedley & Eisner, 1996). Zebra Longwing butterflies (Heliconius charithonia) are known to eat pollen for the nutritional benefit of its amino acid content (O'Brien, Boggs, & Fogel, 2003) which increases fecundity. Many species of moths and butterflies drink the bodily fluids of mammals to acquire salts and minerals (Plotkin & Goddard, 2013). These are just a few examples illustrating the diversity of diet and resource-seeking behaviour within the Lepidoptera.

The variety of butterfly feeding behaviours allows them to exist in nearly every terrestrial ecosystem worldwide. Lepidoptera are also an important food source for numerous secondary consumers including birds, bats, terrestrial mammals, amphibians and reptiles. The niche diversity seen in Lepidoptera makes them an important part of nearly all forest food webs as both primary consumers and prey for secondary consumers. In addition to the important role that Lepidoptera play in forest food webs, many species are important pollinators of wild plants (Kato et al., 2008; Kremen et al., 2007; Reddi & Bai, 1984).

The vital role that butterflies play in forest ecosystems is well-documented, and yet butterfly communities in many ecosystems are seriously understudied. This is particularly true in temperate and subtropical climates where seasonal fluctuations in relative abundance of butterfly species, including migratory species, are pronounced (Howard & Davis, 2009; Neck, 1983). It is imperative to study the annual changes in butterfly communities to establish a basis of comparison for future studies of butterfly populations and responses to changes in forest disturbance regimes. This is especially important given the fact that different butterfly species and guilds exhibit highly varied responses to different types of disturbances (Hogsden & Hutchinson, 2004).

1.1.2 Lepidoptera as bioindicators

Lepidoptera are often considered to be ideal bioindicators to use as study subjects in order to save time and resources in forest ecology research (Bonebrake, Ponisio, Boggs, & Ehrlich, 2010). Lepidoptera ecology and systematics have been widely studied, they occupy a diverse range of ecological niches and they have been demonstrated to be sensitive to environmental change (Forister et al., 2010; Perfecto et al., 2003; Wood & Gillman, 1998). Many species of Lepidoptera are highly visible and easily surveyed with baited traps for diurnal species and light traps for nocturnal species and they are relatively easy to handle in a field environment, making them an ideal study group. Although the niche diversity among Lepidoptera makes their ecology an interesting research topic, it also contributes to the fact that various Lepidoptera species have widely varying responses to environmental disturbance. For example, generalist Lepidoptera species have often been shown to be highly adaptable to disturbed habitats while specialist species are often sensitive to disturbance (Cleary & Genner, 2004; Kitahara, Sei, & Fujii, 2000; A. B. Swengel, 2001). Krauss, Steffan-Dewenter, & Tscharntke (2003) demonstrated that rates of turnover and extinction for Lepidoptera species depends on habitat area and that the extinction curve is steeper for specialist species than for generalists. Whitworth, Pillco Huarcaya, Gonzalez Mercado, Braunholtz, & MacLeod (2018) also demonstrated differences in response to disturbance among Lepidoptera species when classified as either carrion feeders or fruit feeders. These examples illustrate the importance of

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determining precisely which species demonstrate the appropriate level of sensitivity to disturbance in order to classify them as appropriate bioindicators within the given system of study (Fleishman & Murphy, 2009; Schulze et al., 2004).

1.1.3 Butterfly response to disturbance

Many studies have focused on butterfly response to various types of disturbance. Special focus has been given to agricultural systems (particularly agroforestry), logging, urban development and forest fire. These disturbances all have similar effects on forest structure: canopy cover is reduced, increased sunlight reaches lower forest strata promoting understory growth and mature forest habitat is fragmented. These characteristics of early forest succession are common among habitats affected by most types of disturbance, and thus any of the disturbances detailed in this section are likely to have similar effects on butterfly communities. Different butterfly responses to different disturbances are more likely to result from variation in the severity of the disturbance, rather than the type of disturbance. While not all types of disturbance provoke the same response in butterfly communities, similar patterns of recolonization emerge in many cases where the severity of the disturbance and the area affected are comparable, regardless of the disturbance type.

In agroecosystems

In modified agroforestry systems, many studies observed no significant difference between butterfly species richness and abundance among systems employing various agroforestry practices (shaded coffee, polycultures, Francesconi, Nair, Levey, Daniels, & Cullen Jr, 2013; pastures, live fences, Tobar L & Ibrahim, 2010), traditional agricultural practices (monocultures) and forest habitats (edge, interior) (Marin, Leon-Cortes, & Stefanescu, 2009; Schulze et al., 2004; Weibull, Bengtsson, & Nohlgren, 2000). A study by Milder et al (2010) of butterfly communities in agricultural systems actually observed higher butterfly diversity and richness in modified habitats than in forest habitats. One compelling explanation for these results is that because butterflies are highly mobile, they are able to take advantage of diverse resources within a mosaic of heterogeneous habitats and the edges between habitat types (Andrieu et al., 2018; Barbaro & van Halder, 2009; van Halder, Barbaro, & Jactel, 2011).

In logged ecosystems

Similar results are observed when quantifying butterfly response to selective logging activities. Forests that had been selectively logged had butterfly communities that were not significantly different from unlogged forests (Lewis, 2001; Summerville & Crist, 2002; Wood & Gillman, 1998). But, in forests that had been recently clear-cut, butterfly communities did have lower species diversity than selectively logged or unlogged forests (Lewis, 2001; Whitworth et al., 2016). These results suggest that butterfly communities are resilient to a low to moderate amount of habitat disturbance, and that diversity will be unaffected until a certain threshold of disturbance intensity.

In urban ecosystems

A very different type of habitat disturbance, urban development, has also been extensively studied in relation to its effect on butterfly assemblages. Arguably, this type of disturbance is very distinct from agroforestry and selective logging because urban ecosystems are often much more isolated from intact forest habitat, both in terms of proximity and habitat connectivity. Nonetheless, this body of research provides many interesting results that shed light on the ecological mechanisms for butterfly response to disturbance. One of the main conclusions drawn from studies of butterfly response to urban development is that butterfly assemblages benefit from a more proliferous and diverse community of larval host and nectar-producing understory plants in urban environments (Brown Jr & Freitas, 2002; Pin Koh & Sodhi, 2004). Other studies show that tree cover is positively correlated with increasing butterfly diversity in urban parks (Ramírez Restrepo & Halffter, 2013; Tam & Bonebrake, 2016).

In early post-fire succession

The response of butterfly communities to fire has been studied in many forest ecosystems worldwide (Table 1). Studies have focused on both uncontrolled wildfire affecting large areas of forest and small areas of prescribed surface fire employed as a forest and agricultural management strategy. Prescribed fires are applied to periodically reduce fuel load and prevent more destructive and costly wildfires in the future. These two types of fire may have very distinct effects on the ecosystem given that they can differ greatly in area and intensity (Baum & Sharber, 2012; Fleishman, 2000; A. B. Swengel, 2001) and therefore the results of studies focusing on wildfire and prescribed fire should be considered independently.

Climate also has a significant effect on fire regime (Moriondo et al., 2006; Moritz et al., 2012) which means that the geographic location of a study site is also important to consider. Temperate climates are characterized by distinct seasons and wide annual variations in temperature and precipitation, while tropical climates are characterized by temperatures consistently above 18 degrees and little annual variation in weather aside from having a marked wet and dry season (Kalvová, Halenka, Bezpalcová, & Nemešová, 2003). Intermediate climate types include Mediterranean which is characterized by wet winters and dry summers (Deitch, Sapundjieff, & Feirer, 2017), and subtropical which is characterized by hot, humid summers and cool to mild winters (H. E. Beck et al., 2018). Differences in climatic conditions are likely to indicate differences in the natural fire regime in a region. These factors are important to consider when interpreting the results of other studies focusing on butterfly response to wildfire (Table 1).

Study	Location	Climate	Fire Type	Result
Baum & Sharber, 2012	Oklahoma , USA	Temperate	Prescribed	Higher monarch abundance in burned area
Campbell, Hanula, & Waldrop, 2007	North Carolina, USA	Temperate	Prescribed	Higher abundance and richness in mechanical & burned treatments
Cleary & Genner, 2004	Indonesia	Tropical	Wildfire, 6000 ha	Lower species richness post-fire

Table 1: Summarized r	esults of studies	of butterfly response	to forest fire
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				Generalists dominate post-fire, specialist abundance increased over time (two years)
Cleary et al., 2004	Indonesia	Tropical	Wildfire, 6000 ha	Richness highest in large, unburned patches Monitored for 3 years
Elia, Lafortezza, Tarasco, Colangelo, & Sanesi, 2012	Italy	Mediterranean	Wildfire, 260 ha	No difference in abundance Monitored for two years
Fleishman, 2000	Nevada, USA	Temperate	Prescribed	No difference Monitored for two years
Gaigher, Pryke, & Samways, 2019	South Africa	Subtropical	Prescribed	No difference between burned and natural forest
Gustafsson et al., 2019	Sweden	Temperate	Wildfire, 13,1000 ha	Lower species richness post-fire, later recovery by certain species
Henderson, Meunier, & Holoubek, 2018	US Midwest	Temperate	Prescribed	Maximum fritillary abundance with 3-5 year burning frequency Monitored for 20 years
Huntzinger (2003)	California, USA	Mediterranean	Prescribed	Higher richness in burned area
Kim & Kwon, 2018	South Korea	Temperate	Wildfire, 1000 ha	Decrease in forest species, increase in open habitat species Monitored for 5 to 9 years
Kwon, Kim, Lee, & Jung, 2013	South Korea	Temperate	Wildfire, 1000 ha	Specialists decreased post-fire Monitored for 5 years
Serrat, Pons, Puig- Girones, & Stefanescu, 2015	Spain	Mediterranean	Wildfire, 13,000 ha	No difference
Ann B Swengel & Swengel, 2007	US Midwest	Temperate	Prescribed	Generalists dominate post-fire Specialists more abundant in refugia
Verdasca et al., 2012	Portugal	Mediterranean	Prescribed	Higher richness and abundance in first 3 years post fire

Of the studies reviewed in Table 1 addressing butterfly response to fire, only three of them did not note differences between post-fire and control butterfly assemblages (Elia et al., 2012; Fleishman, 2000; Serrat et al., 2015). Two studies noted decreases in butterfly species richness post-fire (Cleary & Genner, 2004; Gustafsson et al., 2019), while Baum & Sharber (2012), Campbell et al. (2007),

Gaigher et al. (2019), Henderson et al. (2018), Huntzinger (2003), Kim & Kwon (2018) and Verdasca et al. (2012) all noted increases in butterfly species richness and/or abundance in the early post-fire successional stage.

Despite the fact that prescribed surface fire and uncontrolled wildfire differ greatly in affected area and fire intensity, the studies presented in Table 1 illustrate mixed results in studies of each fire type. However, the wildfires studied in Sweden (Gustafsson et al., 2019) and Indonesia (Cleary & Genner, 2004) both negatively affected butterfly species richness in the disturbed area in the study period following the fire, while no studies of prescribed surface fire showed this trend.

Many potential explanations are presented for the reported higher levels of butterfly species abundance and diversity in disturbed forest habitats. As was the case in agroecosystems, butterfly assemblages seem to benefit from habitat heterogeneity which is increased following a fire event by creating habitat edges and patches in an otherwise homogeneous habitat. One of the mechanisms for this increase in butterfly species and abundance in disturbed habitats is the opening of the forest canopy which allows an increase in light intensity (Elia et al., 2012; Waltz & Wallace Covington, 2004) and promotes understory growth (Campbell et al., 2007) which results in increased larval host plants (Baum & Sharber, 2012; Pin Koh & Sodhi, 2004; van Halder et al., 2011) as well as nectar resources for butterflies (Andrieu et al., 2018; Brown Jr & Freitas, 2002; van Halder et al., 2011; Waltz & Wallace Covington, 2004).

Butterfly community response to fire is very similar to butterfly response to agricultural activities. The studies reviewed here, together with the ecological relationships studied in urban ecosystems between butterflies, larval host plants and nectar producing plants establish some important concepts for predicting butterfly response to disturbance. Disturbances that decrease forest canopy cover to allow increased understory growth and that create habitat heterogeneity are likely to be followed by an increase in overall butterfly species richness and abundance.

1.1.4 Generalists vs Specialists

Many studies of butterfly response to various types of disturbance classify butterfly species by niche. Some common criteria for classifying generalist and specialist butterfly species are presented in Table 2. Using these classification criteria, generalist species are often more widespread and found in disturbed habitats in higher abundance than specialists (Balam-Ballote & Leon-Cortes, 2010; Kitahara & Fujii, 1994; Kitahara et al., 2000; Soga & Koike, 2013). These results illustrate differential response to disturbance among butterfly species that occupy distinct niches. This also supports the idea that not all butterfly species are appropriate indicators of forest health, rather indicator species should be identified based on their life history traits rather than using the community as a whole (Fleishman & Murphy, 2009).

Criterion	Generalist	Specialist
Geographic range (Balam-Ballote & Leon-Cortes, 2010)	Wide	Narrow
Generation time ("voltinism"; Kitahara & Fujii, 1994; Soga & Koike, 2013)	Oligovoltine: >2 generations per year	uni or bi-voltine (one or two generations per year)
Number of larval host plants (Kitahara & Fujii, 1994)	>10 plant species or plants of 2+ families	≤10 species belonging to one family

Table 2: Common criteria used to classify generalist and specialist butterfly species

In open habitats such as burned areas, generalist species are often dominant in early stages of succession (Cleary & Genner, 2004; Krauss, Steffan-Dewenter, & Tscharntke, 2003a) because they are highly mobile and able to take advantage of a wide range of resources (Dapporto & Dennis, 2013) which allows them to thrive in disturbed habitats. The dominance of generalist species in early succession may contribute to increases in butterfly abundance. Conversely, specialist populations have been shown to decline in early post-fire succession (Ann B Swengel & Swengel, 2007). Specialists are adapted to specific habitats and they need large, unfragmented areas of intact habitat to maintain healthy population sizes (Brückmann, Krauss, & Steffan-Dewenter, 2010; Krauss et al., 2003b, 2003a;

Soga & Koike, 2013; Verdasca et al., 2012). Specialists have been shown to dominate assemblages in large areas of intact habitat because they are better adapted than generalists to using the more limited resources (Dapporto & Dennis, 2013). For these reasons, generalists tend to dominate disturbed habitats in early stages of succession, while specialist species tend to recover in the middle and later stages of succession (Cleary & Genner, 2004). However, specialists require nearby areas of intact habitat to use as refugia during the early stages of succession which allow them access to habitats undergoing mid to late succession once they become suitable for the specialists (Cleary & Genner, 2004; Ann B Swengel & Swengel, 2007).

1.1.5 Cumbres de Monterrey National Park

Cumbres de Monterrey National Park (CMNP) is located in the Mexican state of Nuevo León. Five of eight municipalities that make up CMNP (Santa Catarina, Garcia, Monterrey, San Pedro Garza Garcia and Santiago) belong to the Monterrey Metropolitan Area (MMA) which has a population of nearly 4.7 million (SEDATU, CONAPO, & INEGI, 2015). CMNP is one of the largest national protected areas in Mexico and it contributes extensive economic value for the MMA as well as for the three municipalities outside of the MMA that make up the park: Allende, Montemorelos and Rayones (Comisión Nacional de Áreas Naturales Protegidas, 2006).

CMNP encompasses a large portion of the Sierra Madre Oriental (SMOr) mountain range. The SMOr extends from the Rio Grande along the border between Texas and Coahuila and continues through the Mexican states of Nuevo Leon, Tamaulipas, San Luis Potosi, Queretaro, Hidalgo before coming to an end in the state of Puebla where the SMOr meets with the trans Mexican Volcanic Belt. Within the boundary of CMNP, the elevation of the SMOr ranges between 600 to 3400 masl and the primary form of vegetation is pine-oak forest (Comisión Nacional de Áreas Naturales Protegidas, 2006).

Forests like that of CMNP provide economically valuable ecosystem services such as water filtration and storage, air filtration, climate regulation, oxygen production, pollination, recreation, cultural value as well as countless natural resources including lumber and edible products (Grêt-Regamey, Brunner, & Kienast, 2012). For example, the monetary value of recreational services provided in Chipinque Ecological Park, which makes up just 1625 ha of CMNP's total area of 177,395 ha (González Ocampo, Cortés Calva, Íñiguez Dávalos, & Ortega Rubio, 2014), is estimated between 13 and 20 million MXN annually (Gándara, 2006). Hydrological services provided by CMNP also are of utmost importance given that the state of Nuevo Leon is considered a region of water stress where the water demand exceeds the availability and capacity to process and transport the water throughout the state (Saldivar, Olivera, & Isidro-Casas, 2013). Health benefits provided by CMNP extend beyond the availability and accessibility of potable water. Sánchez-González, Adame Rivera, & Rodríguez-Rodríguez (2018) demonstrated a significant correlation between perceived physical health in people over the age of 60 and proximity and frequency of visits to the CMNP. The park also contains various economically important plant species that provide resources such as lumber (pines, oaks, Arizona cypress, Alligator juniper), food (apple, peach and quince trees) and medicinal uses (Equisetum laevigatum, Tagetes lucida; Comisión Nacional de Áreas Naturales Protegidas, 2006). These are just a few examples of the ecosystem services provided by the park which emphasize its importance to local quality of life.

The diverse biogeography of Mexico contributes to its high biodiversity and number of endemic species (J Rzedowski, 1975; Jerzy Rzedowski, 2006). Much of the economic and social value of the CMNP is derived from the biodiversity of the SMOr. CMNP is home to high plant diversity (Estrada-Castillón, Villarreal-Quintanilla, Salinas-Rodriguez, Magdalena María Rodriguez-Gonzales, Jimenez-Perez, & Garcia-Aranda, 2013), high numbers of endemic vascular plants (Salinas-Rodríguez, Sajama, Gutiérrez-Ortega, Ortega-Baes, & Estrada-Castillón, 2018) and endemic butterfly species (Luis-Martinez, Llorente-Bousquets, Vargas-Fernández, & Warren, 2003), making this region an important biodiversity hotspot (Salinas-Rodríguez et al., 2018). The SMOr forms a vital part of the Madrean Pine-Oak Woodlands ecoregion; it connects various habitats and provides a migration corridor for important species like the Monarch butterfly (*Danaus plexippus*; Howard & Davis, 2009) and the jaguar (*Panthera onca*; Carrera-Treviño, Cavazos, Briones-Salas, & Lira-Torres, 2016). The economic and social value of the ecosystem services of CMNP together with high levels of biodiversity and endemism found in CMNP make it a vital region for ecological study in order to identify threats to ecosystem health and to develop and improve conservation strategies.

1.1.6 Fire Regime in CMNP

One of the most prominent threats to the CMNP ecosystems is forest fire (Comisión Nacional de Áreas Naturales Protegidas, 2006). The natural fire regime in the forests of the SMOr is characterized by relatively frequent surface fires occurring every 8.6 to 9.6 years with less frequent, more severe fires occurring every 11.9 to 18.6 years (Yocom et al., 2010). Native flora and fauna are well adapted to this natural fire regime (Rodríguez-Trejo & Fulé, 2003). But since 1929, the natural fire regime has been altered both by fire suppression as a forest management strategy (Yocom et al., 2010) as well as excessive anthropogenic forest fires due to increasing levels of tourism and urbanization (Comisión Nacional de Áreas Naturales Protegidas, 2006). In the state of Nuevo Leon, 63% of the forest fires recorded by the Mexican National Forestry Commission between 2000 and 2017 were started by campfires, smokers, agricultural burning and burning of solid wastes (CONAFOR, unpublished data).

These data do not account for changes in the natural fire regime that occur due to anthropogenic climate change which are predicted to be significant in North American forests (Flannigan et al., 2000; Stocks et al., 1998; Wotton et al., 2010). It's possible that changes in a natural fire regime due to anthropogenic climate 13

change may have a more serious effect on the species in a forest than the direct effects of climate change on forest species (Dale et al., 2001).

Many factors have already affected the natural fire regime in the SMOr in recent decades and these effects will likely continue to change the fire regime in ways that are still not clearly understood. Understanding the ecological results of a changing fire regime in the SMOr is of utmost importance in order to conserve this vital ecosystem.

1.2 Justification

Butterflies are an important component of forest ecosystems due to their important role in the food web and as forest pollinators. They have also been suggested as useful indicator species to measure forest health. They make an ideal study taxon due to their high visibility and the existence of easy, inexpensive and effective survey methods. Butterfly community ecology has never been studied in CMNP, nor has butterfly response to uncontrolled wildfire been studied anywhere in Mexico. Even studies of butterfly response to forest fire in other regions with subtropical climates are scarce.

Continuously evaluating the health of the ecosystems in CMNP and threats to ecosystem health is critical in order to improve conservation strategies and protect economically valuable ecosystem services within the park. Given the increasing threat of forest fires in CMNP due to fire suppression, increasing tourism and the potential (so far unmeasured) effects of climate change, it is vital to understand the effect of forest fire on this forest.

Given that butterfly assemblages in CMNP have not been studied in detail so far, the resulting species lists, niche classifications and suggestions for effective indicator species will provide a useful to guide future monitoring and research in this region.

1.3 Objectives

General Objectives

- 1. Characterize environmental variables in early post-fire succession
- 2. Characterize the response of butterfly assemblages in CMNP to an uncontrolled, moderate intensity, anthropogenic wildfire in comparison with a recently unburned site

Specific Objectives

- 1. Identify changes in forest structure post-fire
- 2. Compare flower assemblages in burned and control sites in terms of diversity
- 3. Compare post-fire response of different butterfly species based on ecological niche
- 4. Suggest possible indicator species to use in future studies of forest health in CMNP

1.4 Hypotheses

- 1. Butterfly and flower abundance and species richness will be higher in the burned area due to less canopy cover post-fire.
- 2. Generalist species are more abundant in the burned area than in the control area.

2 METHODS

2.1 Study Site

The study sites are located in Cumbres de Monterrey National Park in the municipality of Santiago, Nuevo León in northeast Mexico (Figure 1). According to the National Forestry Commission's registry of all fires between 2000 and 2017, a 580 ha area of pine-oak forest near the hamlet Ciénega de González (25°22'22.8" N, 100°14'46.0" W) was affected by a moderate-intensity forest fire ignited by burning waste. The fire burned from March 23, 2016 to April 2, 2016 (CONAFOR, unpublished data). At the site, lack of canopy cover, charred fallen trucks and fire scars on standing trees all provide visual evidence of the recent fire (Figure 3a).

A control area unaffected by fire in recent history near the hamlets of Laguna de Sánchez and Las Guacamayas (25°21'28.2" N, 100°18'45.3" W) was selected as the control site (Figure 1). According to the National Forestry Commission, the unburned site had not been affected by fire between 2000 and 2017 and there was no visual evidence of fire. However, detailed records on fire history in Santiago prior to 2000 are not available, therefore the true fire history in the control site (and indeed, in the entire forest) prior to 2000 cannot be known without dendrochronological analysis. The region of study was widely impacted by widespread, intense forest fires in 1998 (Comisión Nacional de Áreas Naturales Protegidas, 2006), so it is possible that the study sites were affected by other unregistered fires in recent decades.



Figure 1: Location of survey sites near the hamlets of Cienega de Gonzalez and Las Guacamayas in the municipality of Santiago, Nuevo Leon, Mexico. Survey sites are inside Cumbres de Monterrey National Park between 1500 and 1800masl.

Topography & Soils

The study sites fall within a 1500-1800 masl elevation range and are all located on East-facing slopes to control for differences in microclimate based on slope aspect. The soil at all sites is characterized as leptosol which includes shallow soil covering hard rock or calcareous material, or very stony soil (Instituto Nacional de Estadística y Geografía, 2009).

Climate

CMNP belongs to the Nearctic bioregion and has a subtropical climate. The climate at the study site locations is classified by the Instituto Nacional de Estadística y

Geografía (2009) as temperate sub-humid with summer rains and medium humidity. The annual average temperature range is 10 to 24 degrees Celsius and the annual precipitation range is 500 to 1100mm with marked rainy and dry seasons (Instituto Nacional de Estadística y Geografía, 2009).

Vegetation

The study sites are located in the Sierra Madre Oriental physiographic province. The primary vegetation type is pine-oak forest; the region includes high biodiversity (Estrada-Castillón et al., 2013) and endemism (Salinas-Rodríguez et al., 2018) of vascular plants.

2.2 Study Design

Four 200m-long transects each with $2m \times 2m$ plots at the beginning and end of each transect were established the burned area and control site for a total of eight plots per site, 16 plots in total. Sites were established within rural communities, therefore structures and private property limits as well as restricted access due to steep and uneven terrain limited the spacing of transects (Figure 1).

2.3 Survey Methods

Environment

Prior to starting each walk and count survey, the temperature, wind speed and relative humidity were measured using the pocket case thermometer (stock #89136), Dwyer handheld wind meter (stock #89001) and sling psychrometer (stock #89288) from Forestry Suppliers in Jackson, MS, USA. Cloud cover was also estimated and scored on a three-point scale immediately before surveys. The percentage of understory cover was estimated in each subplot. Canopy openness was measured from the center of each plot with a canopy scope as per N. Brown, Jennings, Wheeler, & Nabe-Nielsen (2000; Figure 2a).

Flower Surveys

Flowers within 0.5m perpendicular to the transect were counted and identified. Specimens of flowers unidentifiable in the field were collected and brought back to the collection at the Faculty of Forest Sciences of the Universidad Autónoma de Nuevo León in Linares, Nuevo León for identification.

Lepidoptera Surveys

Lepidoptera communities were surveyed on ten occasions between February 2018 and January 2019. Surveys were conducted under appropriate weather conditions with the temperature above 17° and minimal wind, precipitation and cloud cover (Pollard & Yates, 1993).

A walk-and-count transect method (Pollard & Yates, 1993) was used to survey Lepidoptera communities along each transect. Individuals up to 3m ahead of the observer and 2m to either side of the transect were counted. Adult Lepidoptera were also surveyed in each site using rotten banana-baited Van Someren-Rydon traps (Platt, 1969; Figure 2b).Two traps were placed in each the control and the burned site in a randomly selected 2m × 2m plot and were left open for four-hour sessions between 9:30 and 16:30. At the end of each session individuals were identified, counted and released. When species could not be identified in the field, individuals were caught in entomological nets for later identification. Unidentified or unique individuals were collected and added to the entomological collection at the Faculty of Forest Sciences of the Universidad Autónoma de Nuevo León in Linares, Nuevo León. Adult Lepidoptera were identified using the guide Butterflies of Northeastern Mexico (Garwood & Lehman, 2005).



Figure 2a: A canopy scope being used to measure the forest canopy openness. Each dot corresponding to open sky in the largest canopy opening corresponds to 4% canopy openness. Here, five dots correspond to uninterrupted sky which represents 20% canopy openness.

Figure 2b: An open banana-baited Van Someren Rydon trap.

2.4 Statistical Analysis

All analyses were run using R version 3.5.2 (R Core Team, 2018).

2.4.1 Environmental Variables

Canonical Correspondence Analysis

Canonical correspondence analysis (CCA) is an ordination technique that determines the influence of measured environmental variables on a species composition data set. The influence of an environmental variable is determined based on the dispersion of average of values of a given environmental variable for each species: the variable that has the widest dispersion (range; scaled for order of magnitude) is the variable that best explains the species data. Using CCA, a theoretical value that explains the species data (ie, gives the widest dispersion of the average environmental variable for each species) even better than the "best" known environmental variable is calculated and this dispersion is used to create the first CCA axis. Subsequent axes are calculated the same way, with the condition that they be independent from the first axis (Jongman, Ter Braak, & Van Tongeren, 1995).

Weather variables and butterfly species abundance were used in canonical correspondence analysis in each site. Singleton and doubleton butterfly species were not included in the analysis. Weather data from early sampling days (February to May of 2018) was incomplete and therefore only data from June 2018 to January of 2019 was analyzed. Calculations and graphics were made using the *vegan* package in R (Oksanen et al., 2019).

2.4.2 Butterflies and Flowers

Butterfly numbers across all ten field trips were pooled in each site and flower numbers were pooled by genus to minimize the statistical effects of identification uncertainty at the species level. Analyses were conducted for both butterfly sampling methods (trapping and transects) as well as for the flower communities surveyed on transect. Rarefied species richness curves were calculated and graphed using the *iNEXT* (Hsieh, Ma, & Chao, 2019) and *ggplot2* (Wickham & Chang, 2019) packages in R (R Core Team, 2018). Species richness curves

illustrate the number of species observed as a function of total number of individuals recorded (n) and using rarefaction these curves can be extrapolated to predict the shape of the species accumulation curve as the number of species observed increases.

Diversity Indices

Simpson and Shannon indices were calculated and graphed using the *iNEXT* (Hsieh et al., 2019) and *ggplot2* (Wickham & Chang, 2019) packages in R (R Core Team, 2018). *iNEXT* was used to create rarefaction curves of both diversity indices as a function of the number of individuals recorded to show both interpolated and extrapolated diversity index calculations as a function of sample size (Hsieh, Ma & Chao, 2016). Curves were created for both butterfly sampling methods (trapping and transects) as well as for the flower communities surveyed on transect.

Rank-Abundance curves

Rank-abundance curves illustrate the relative abundance of each species surveyed as a function of the species rank, with the most abundant species having a rank of 1 and the least abundant species having the rank of n. Log transformed rank-abundance curves were created for both butterfly sampling methods (trapping and transects) as well as for the flower communities surveyed on transect.

Niche Classification

Butterflies were classified as either generalist or specialist species based on criteria modified from the criteria used by Kitahara & Fujii (1994). Kitahata & Fujii defined generalist species as "species the larvae of which feed on more than 10 plant species belonging to one taxonomic family, or on a variety of host plants belonging to two or more taxonomic families" and having more than two generations per year ("oligovoltine"), and they defined specialists as "species whose larvae had been reported to feed on 10 or less plant species belonging to one taxonomic family" and having one or two generations per year (uni- or 23
bivoltine). While Kitahara and Fujii had detailed life history information readily available for the butterfly species in their study area, information on each butterfly species found in CMNP is not as available. Therefore, species were classified as generalists or specialists only based on larval diet using information from the Butterflies and Moths of North America citizen science project (BAMONA; Lotts & Naberhaus, 2019) since information on generation time was only available for a small fraction of the species observed. Additionally, the larval diet criteria were modified slightly to include species whose larvae feed on plants belonging only to one genus as specialists, even if their diet includes more than 10 plants from that genus which would classify them as generalists under Kitahara and Fujii's classification system. The complete table of species, life history traits and niche classification is included in Appendix 1.

3 RESULTS

3.1 Environment

Significant differences in forest structure between the burned and control site were observed (Figure 3). The forest canopy was significantly more open in the burned site (p<0.001), and the forest understory coverage was significantly higher in the burned site (p<0.001).



Figure 3a: A survey site in the burned area shows an open canopy, understory growth and a burned stump of a tree that was damaged during the fire.

Figure 3b: A survey site in the control area shows a full forest canopy and relatively bare forest floor.

Flowers

Flower communities in the burned and control sites were significantly different in the calculation and rarefaction of all three Hill numbers. Species richness (q=0),

Simpson diversity index (q=1) and Shannon diversity index (q=2) were all significantly higher in the burned area (Figure 4). The rank-abundance curve of flower communities in each site also shows that a higher number of unique flower genera were observed in the burned site, and that the relative abundance of each species was noticeably higher for nearly every species in the burned site (Figure 5).



Figure 4: Results of the iNEXT analysis of flower genera recorded on transect surveys. Rarefied Hill numbers (species richness, q=0; Shannon diversity index, q=1; Simpson diversity index, q=2) are represented as a function of the number of individuals observed. Translucent shading represents standard error.



Figure 5: Log-transformed rank-abundance curve of flower genera observed on transect surveys in each site.

Canonical Correspondence Analysis

CCA was performed independently for each site as well as using combined data with the site included as a variable (Figure 6). There were no variables that had significant effects on the species composition in the burned site. In the control site, temperature and wind had slightly significant (temperature: p=0.045; wind: p=0.05) impacts on species composition.

When the species composition data from both sites was combined and the site included as a variable, site was the most significant variable in determining the species composition (p=0.005), followed by wind (p=0.01). Most species clustered around the origin of the plot, indicating that they were only slightly affected by any of the variables, if at all. The two species most visibly associated with the control site ("siteLS") were *Pterourus pilumnus* and *Anaea troglodyta aidea* (Figure 6). Butterflies of the family Lycaenidae as well as *Abaeis nicippe* were the taxa whose abundance most negatively correlated with all of the variables analyzed.



Figure 6: Canonical correspondence analysis ordination diagram produced by combined species abundance data from all sites with vectors representing weather variables and the burned and control sites represented as points. The control site is represented by "siteLS" and the burned site is represented by "siteCG". Species abbreviations are included in Appendix 1. Some species that were unidentifiable in the field are represented only by the abbreviated family or genus. "Lyca" = Lycaenidae, "Hesp" = Hesperiidae, "Eryn" = *Erynnis* sp., "Urba" = *Urbanus* sp. Site (p=0.005) and wind (p=0.01) were the only variables with significant influence over the species composition data.

3.2 Butterflies

Transect Method

Rarefied *iNEXT* analysis was run separately on butterfly data collected by transect and trap surveys. The butterfly communities recorded on transect surveys show no significant differences between species richness (q=0), Simpson diversity (q=1) or Shannon diversity (q=2) in the burned and control sites (Figure 7).

In the burned site on transect, 49 species were observed while 26 were observed in the control site. The estimated species richness (q=0) asymptotes for the burned and control sites are 59 and 36 respectively, but relatively wide margin of error indicates that further sampling effort could generate a more accurate estimate of the true species richness in each site. The rank-abundance curve of transect data also shows noticeably higher species richness and overall abundance in the burned site (Figure 8).



Figure 7: Results of the iNEXT analysis of butterfly species recorded on transect surveys. Rarefied Hill numbers (species richness, q=0; Shannon diversity index, q=1; Simpson diversity index, q=2) are represented as a function of the number of individuals observed. Translucent shading represents standard error.



Figure 8: Log-transformed rank-abundance curve of butterfly species observed on transect surveys in each site.

Trap Method

The differences between all three rarefied Hill numbers (q=0, q=1, q=2) were significant between butterfly communities surveyed with the trap method in the burned and control sites. The true maximum species richness in each community, represented by the asymptote of the species richness graph (Figure 9, q=0) appears to have been surveyed almost completely with the trap surveys, with 11 species attracted to fruit bait in the burned site and five in the control site. *A. troglodyta* was the most frequently trapped species in both sites, making up 63% of butterflies trapped in the burned site and 80% of butterflies trapped in the control site. There was a lower number of species surveyed in the control site both by transect (Figure 7) and trap (Figure 9) methods. Although there were more unique species caught in traps in the burned area, overall abundance of all butterfly species was comparable in each site (Figure 10).



Figure 9: Results of the iNEXT analysis of butterfly species recorded on trap surveys. Rarefied Hill numbers (species richness, q=0; Shannon diversity index, q=1; Simpson diversity index, q=2) are represented as a function of the number of individuals observed. Translucent shading represents standard error.



Figure 10: Log-transformed rank-abundance curve of butterfly species observed on trap surveys in each site.

Seasonality

Clear differences were measured in the number of butterflies and number of species observed in the burned and control sites. Unpaired t-tests indicate that these results are significant (p < 0.01). The number of butterflies (Figure 11) and species (Figure 12) peak in late July in the control site, while the number of butterflies observed peaked between August and November in the burned site, and the number of species peaked in August. Surveys conducted in January and February showed the least difference between communities in the control and burned site, with very low numbers of butterflies and unique species observed in both sites on these dates.



Figure 11: Mean number of butterflies observed on transect surveys in each site over time. Overall differences in number of butterflies observed was significant between the burned and control sites (p=0.001911). Error bars represent standard error.



Figure 12: Mean number of butterfly species observed on transect surveys in each site over time. Overall differences in number of species observed was significant between the burned and control sites (p=0.005). Error bars represent standard error.

Niche Classification

Specialist species were slightly more abundant in the control site than generalists according to the rank-abundance curve (Figure 13), but this difference was not significant. There was virtually no difference between specialist and generalist abundance in the burned area according to the rank abundance curve (Figure 14), and this is confirmed by the t-test. However, there were more species of generalists (24) observed in the burned site than specialists (13; Figure 14), while the number of generalist and specialist species recorded in the control site was comparable (10 and 9 respectively; Figure 13). There was no significant difference between the abundance of specialist species between the control and burned areas, but the abundance of generalist butterflies was significantly higher in the burned area than in the control area (p=0.037).



Species by Rank

Figure 13: Log-transformed rank-abundance curve of butterfly species observed on transect surveys in the control site classified by niche. Seven species observed in the control site were not classified due to lack of information or inability to identify the species and are not included in this figure.



Species by Rank

Figure 14: Log-transformed rank-abundance curve of butterfly species observed on transect surveys in the burned site classified by niche. Twelve species observed in the control site were not

classified due to lack of information or inability to identify the species and are not included in this figure.

Because the overall abundance of butterflies in the control site was significantly higher than butterfly abundance in the control site, it is expected that the abundance of butterflies in each of the recorded families will also be higher in the control site, as is illustrated in Figure 15. Nymphalids were the most abundant butterflies in both sites while Lycaenids were the least abundant. The abundance of Pieridae butterflies was the most similar between the two sites, while the number of Lycaenids and Papilionids in the burned site was nearly triple the abundance of each family in the control site.



Figure 15: Abundance of individual butterflies recorded on transect surveys classified by family.

4 DISCUSSION

4.1 Environment

Differences in forest structure between the control site and burned site were clear over the course of this study. Trees with fire scars both standing and fallen provided evidence of the recent fire in the burned site (Figure 2). This moderate-intensity fire cleared the forest understory and opened the forest canopy, allowing more sunlight to reach the forest floor and promote understory growth. This is a very important and well-studied mechanism for early forest succession following many types of disturbance, including forest fire (Finegan, 1984; Fulé & Laughlin, 2007; Horn, 1975). Because this was a moderate-intensity fire, the forest understory was cleared which promotes understory growth post-fire, but the fire wasn't so intense as to completely clear vegetation. While some trees were seriously damaged and felled by the fire, many were left scarred but still standing and otherwise healthy. In the case of more severe forest fires the successional process can be much longer because the soil requires more time to recover and vegetation is more seriously damaged and therefore slower to regenerate (Mataix-Solera et al., 2011).

Many environmental factors have been associated with a post-fire increase in butterfly species richness and abundance, including canopy cover, understory vegetation and flower diversity. Both Elia et al. (2012) and Huntzinger (2003) showed that decreases in canopy cover following fire contributed to changes in butterfly community composition. Less canopy cover leads to increased understory growth, and understory vegetation cover and diversity have also been positively correlated with butterfly diversity (Campbell et al., 2007; Schulze et al., 2004).

CCA shows that the site was a significant factor influencing butterfly species composition but weather variables were not (Figure 6). The difference in species composition described by the results of the CCA reflects the trends in butterfly species richness and abundance between the burned and control sites. This is an

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expected result given that surveys were conducted under ideal weather conditions for butterfly activity, and therefore no negative impacts of weather should have been recorded. When the butterfly data from each site was combined in one CCA with the site being considered as an additional variable, the wind speed did have a significant effect on butterfly communities which is a result of decreased butterfly activity and increased difficulty to observe butterflies in windier conditions (Pollard & Yates, 1993). However, this effect was consistent across all survey sites and therefore has no impact on the results of this study.

The proliferation of the flower community in the burned site was very evident due to the opening of the forest understory and canopy, allowing more light to reach the forest floor and promoting flower growth. The significantly higher flower abundance and species diversity in the burned site (Figure 4) provides more habitat and food resources for both larvae and adult butterflies. Similarly, Andrieu et al. (2018), Brown Jr & Freitas (2002), Henderson et al. (2018), Serrat et al. (2015) and Steffan-Dewenter & Tscharntke (1997) all noted positive correlations between flower and butterfly diversity following various types of disturbance due to the importance of flowering plants as larval food and nectar sources. Changes in these factors are all interrelated results of forest disturbances. When forest vegetation is disturbed, the canopy cover is decreased which allows more sunlight to enter to the lower forest strata which promotes vegetation growth. Herbaceous understory plants are vital for butterfly communities because they act as both larval hosts and nectar-producers for adult butterflies. This result of early forest succession has been consistently associated with butterfly diversity.

The forest structure and flower communities were significantly different between the control and burned sites indicating that the recent fire did have a noticeable impact on the ecosystem. However, the fire history of the control site is only known since 2000 when CONAFOR began keeping detailed fire records in the state of Nuevo León. Due to adverse climatic conditions in the year 1998, severe forest fires were widespread throughout the entire country, including CMNP (Comisión Nacional de Áreas Naturales Protegidas, 2006). It is possible that the control area was also impacted by forest fire in 1998 or at any point prior to the beginning of detailed record keeping in 2000. The most recent fire history prior to 2000 is not known in the control site, and although the ecosystem was measurably in later stages of succession at the time of surveying, previous fire history may have impacted the ecosystem in unmeasured ways.

While the fire and climatic history could be better understood by conducting dendrochronological analysis of trees in the control site, a true control ecosystem to compare with the burned site would be the same site prior to the fire (as in Cleary & Genner, 2004). Given that controlled burns are not conducted in CMNP, monitoring the same site before and after a forest fire would be difficult to plan, but this would be a truly ideal system for studying early post-fire succession. Additionally, to fully understand the process of ecological succession in this site, long-term monitoring over many years would be useful to track the recovery of the flower and butterfly communities.

4.2 Butterflies

While butterfly species richness and diversity measured on transect surveys was higher in the burned area, these differences did not appear to be significant in the rarefied iNEXT analysis (Figure 7). The differences in these results likely stem from the fact that the number of individuals sampled in the burned site on transects was significantly higher than the number sampled in the control site (Figure 11). The diversity and species richness were extrapolated for higher numbers of individuals observed using the iNEXT rarefaction and these extrapolated values of the control site were compared with observed species richness and diversity in the burned area. Although observed abundance and richness varied significantly between the two sites, rarefaction does not represent the observed results but rather the hypothetical difference in the Hill numbers if an equal number of individuals were recorded in each site. Natuhara, Imai, & Takahashi (1999) observed a similar

discrepancy between the diversity index and observed species richness in their study of butterfly communities in disturbed habitats in Japan. Even though species richness was notably higher in disturbed habitats, the diversity index did not reflect this difference because of the difference in number of individuals observed.

The observed differences in species richness and abundance on the transect survey are clearly illustrated by the rank abundance curve (Figure 7) as well as the seasonal variation of number of species (Figure 12) and number of individuals recorded (Figure 11). Significantly higher numbers of species and individuals in the burned site mirror the increased flower diversity in the burned site which provides butterflies with additional food resources and therefore attracts them to the newly disturbed habitat. Following various types of disturbance including agricultural activity, fire, logging and urban development, many studies have also recorded higher butterfly species richness and abundance in disturbed sites than undisturbed sites (Andrieu et al., 2018; Balmer & Erhardt, 2000; Baum & Sharber, 2012; Blair & Launer, 1997; Campbell et al., 2007; Huntzinger, 2003; Milder et al., 2010; Natuhara et al., 1999; Schulze et al., 2004; Spitzer, Jaros, Havelka, & Leps, 1997; van Halder et al., 2011; Van Lien & Yuan, 2003; Verdasca et al., 2012; Wood & Gillman, 1998).

The higher observed species richness and abundance in the burned site is consistent with the results of many other studies specifically of post-fire butterfly community composition. In many studies following both wildfire and prescribed fire, butterfly communities have had increased overall species richness (Campbell et al., 2007; Verdasca et al., 2012) and abundance (Baum & Sharber, 2012; Henderson et al., 2018; Verdasca et al., 2012) following fire. It's important to note that these examples study small areas of low intensity, controlled fire used as a land management strategy rather than uncontrolled wildfire. These prescribed fires could be considered comparable to the fire in this study because it was a moderate intensity fire that did not entirely clear vegetation.

Interestingly, the rank abundance curve of the trap data (Figure 10) does not show such clear differences between sites. Clearly, more unique species were trapped in the burned site, but overall abundances in trapped butterflies appear similar between the sites. Conversely, according to the iNEXT analysis, species richness and diversity were significantly higher in the burned site when taking into account the assemblages measured with the fruit-baited traps (Figure 9). This is the inverse result of the analyses of transect data: because similar numbers of individuals were observed in the trap surveys, the difference in diversity was detected in the rarefaction analysis. Jakubikova & Kadlec (2015) also employed walk-and-count transects together with trap surveys in their study of butterflies in central Europe. They noted that although more butterflies were caught in traps than were observed on transects, more unique species were recorded on transect surveys. In contrast, more unique species and individuals were recorded on transects than in traps in this study, but this may be due to the fact that Jakubikova & Kaldec used two types of bait, one with a banana base and one with a cheese base, while in this study only a banana bait was used. Using multiple bait types has the potential to attract more unique butterfly species with a wider range of diets.

The differing results of the trap and transect data illustrate the importance of using multiple methods to measure a community with high niche diversity (Jakubikova & Kadlec, 2015; Wood & Gillman, 1998). Fruit-baited traps are designed to only sample a subset of the butterfly community: fruit feeders. The advantage of trap surveys is that there is a relatively low level of bias because the active involvement of the researcher is not required. All fruit-feeding butterflies are equally likely to be surveyed. While transect surveys in theory allow a wider range of Lepidoptera species to be recorded than just fruit feeders, the results can be biased towards large, low-flying, highly visible species and are subject to the bias of the observer. Low-flying and less visible species are less likely to be recorded than easily visible species. Because of these differences, the trap and transect surveys essentially measure unique subsets of the butterfly community which is why different results

were produced from each dataset. Each survey type has pros and cons, and the combination of the two techniques allows for a more complete sample to be measured than either technique alone.

The species richness curves of both the flower and butterfly assemblages observed on transect (Figures 4 & 7, q=0) do not show plateaus within the first 500 individuals observed, which may be due to the fact that both butterfly and flower assemblages changed in species composition steadily throughout the year. The subtropical climate of the region creates marked seasons which means that climatic conditions vary over the year and therefore a variety of environmental conditions allow for yearly fluctuations in community composition (Howard & Davis, 2009). Many species of both butterfly and flower appeared for the first time in the last half of the year due to their preference for certain seasonal conditions. Additionally, at least two butterfly species observed late in the year (November), D. plexippus and L. carinenta are known to be migratory species which contributed to higher species richness in the fall sampling days (Howard & Davis, 2009; Kawahara, 2006). The fact that new species were consistently observed throughout the year means that the species richness curve did not plateau within the year, but it's likely that upon surveying for a second year during each of the four seasons for a second time, the species richness curve would have a clear plateau.

4.2.1 Niche Classification

The most compelling result of the classification of butterflies observed in this study by niche is the significantly higher abundance of generalist species in the burned area than in the control area. Various studies have found that specialist species are strongly associated with large areas of closed, undisturbed habitat (Brückmann et al., 2010; Cleary & Genner, 2004; Spitzer et al., 1997; Ann B Swengel & Swengel, 2007; Van Lien & Yuan, 2003; Verdasca et al., 2012; Warren et al., 2001), while generalists increase with disturbance, habitat openness and heterogeneity (Balam-Ballote & Leon-Cortes, 2010; Hogsden & Hutchinson, 2004; Krauss et al., 2003a; Natuhara et al., 1999) and are better able to take advantage of resources in heterogeneous habitats due to their high mobility (Dapporto & Dennis, 2013). The higher abundance of generalists in the burned area in this study is mirrored by these numerous studies.

Many studies have also emphasized the importance of areas of nearby undisturbed habitat ("refugia") where butterflies can survive and be protected while the disturbance is taking place. This is especially important for specialist species that rely on environmental conditions of a specific habitat type and cannot easily relocate to avoid a disturbance (Cleary & Genner, 2004; Henderson et al., 2018; Ann B Swengel & Swengel, 2007). For this reason, it could be interesting to measure butterfly diversity in the interior of undisturbed habitats directly adjacent to the disturbed area as well as habitat edges to test the extent to which refugia house specialist species in this region.

While the results of this study are consistent with the literature in that generalist species are better able to take advantage of resources in disturbed habitats than are specialists (Dapporto & Dennis, 2013), it is worth noting that many of these studies classified "specialists" and "generalists" based on inconsistent criteria based on the information that was available. Because limited information was available on the species in the study region, niche classification was solely based on larval host plant range, but even this classification likely isn't fully accurate due to the lack of ecological information on Mexican butterfly species. There is a lack of information available on larval host plants from this region; it is likely that this classification of niche was based on highly underestimated larval host plant ranges due to incomplete species level information being available. Furthermore, insufficient information on voltinism was available for this to be used as a classification criterion, despite its importance in determining species niche (Kitahara & Fujii, 1994; Kitahara et al., 2000). Surveying the study site for larvae in future studies would provide more species-specific ecological information for use in future niche classifications. Expanding citizen science databases like

butterfliesandmoths.org and inaturalist.org to include more detailed information on seasonality and interactions with plants may also potentially be useful in applying more precise and detailed niche classification criteria in future studies.

4.2.2 Indicators

Butterflies are often considered effective biological indicators due to their complex variety of ecological interactions and sensitivity to environmental change (Forister et al., 2010; Warren et al., 2001; Wood & Gillman, 1998). But the results of this study indicate that within the assemblages surveyed, different species respond very differently to disturbance (Hogsden & Hutchinson, 2004), and therefore the butterfly community as a whole should not be taken as a bioindicator (Fleishman & Murphy, 2009; Schulze et al., 2004; Tremlett, 2014). Rather, only certain species that are abundant and visible enough to be well surveyed and that are also sensitive enough to indicate changes in forest health should be considered appropriate indicator species.

Brown Jr & Freitas (2002) suggested that Nymphalid butterflies are the best indicator species due to their abundance, sensitivity and the fact that they are often more easily identified than small and cryptic species in other families. Nymphalid butterflies were the most surveyed family in this study (Figure 15), supporting the suggestion of Nymphalidae as an ideal focus taxon for studying forest disturbance. Nymphalids are the easiest to survey due to their generally large size and colourful patterns, but just because they are abundant and easy to survey doesn't necessarily mean that they are the best indicators of forest health. In fact, within the Nymphalidae family there is a wide range of niche diversity and varying responses of different species to disturbance (Hogsden & Hutchinson, 2004). Thus, a more effective strategy would be to choose only certain species of Nymphalids which exhibit the appropriate response to disturbance as indicators.

Ecologically, butterflies in the family Pieridae are often associated with open and disturbed habitats (Lotts & Naberhaus, 2019), so high abundances of Pieridae

butterflies could be a more useful indicator of habitat disturbance. However, in this study the cumulative abundance of Pieridae butterflies observed between the control and burned sites varied the least of all the families recorded (Figure 15). Similarly, no Pieridae species showed a strong correlation with either control or burned sites in the CCA (Figure 6). While in theory Pieridae could be good indicator species, there are no results presented here to support that theory in this ecosystem.

In the CCA, A. troglodyta and P. pilumnus were the only two species that showed a strong correlation with the control site. Neither of these species was ever observed on transect surveys in the burned site. A. troglodyta was observed in both sites on nearly every session in the trap surveys and was the most abundantly trapped species in both sites. Similarly, the abundance of A. troglodyta in trapping surveys was 30% higher in the control site than in the burned site. A. troglodyta is the easiest species to survey with fruit-baited traps in this region because it's highly abundant and very easy to identify. P. pilumnus is not attracted to the fruit bait used in the traps, but it is large, low-flying and its distinctive colour pattern of bright vellow with thin contrasting black stripes make it unmistakably easy to identify on the wing. Both A. troglodyta and P. pilumnus are classified as specialist species based on the modified larval-host plant criteria (Appendix 1) and therefore, according to the conclusions drawn by multiple other studies (Brückmann et al., 2010; Spitzer et al., 1997; Van Lien & Yuan, 2003; Verdasca et al., 2012; Warren et al., 2001), their abundance should coincide with low levels of forest disturbance as they did in this study. Determining ideal indicator species in this system with more certainty will require further study, but A. troglodyta and P. pilumnus are promising candidates.

5 CONCLUSIONS

The results of this study support the hypotheses proposed. Butterfly species richness and abundance, as well as generalist abundance were all higher in the burned area. Forest structure was significantly impacted by the disturbance, lowering the amount of canopy cover and allowing increases in understory vegetation. Flower diversity was also significantly higher in the disturbed site. *A. troglodyta* and *P. pilumnus* are suggested as potential indicator species for this ecosystem, being specialists associated with the undisturbed site.

There were clear differences in the butterfly assemblage measured in the burned and unburned sites in CMNP, but not all species are affected equally. Although species diversity increases in early post-fire succession due to increases in understory growth and therefore higher density and diversity of larval host and nectar producing plants, the increase in diversity is largely caused by increases in generalist populations, while specialists do not benefit from habitat disturbance. Further, the recolonization of the disturbed area, especially by specialist species, likely depends on the area and quality of undisturbed habitat surrounding the disturbed area. It may be interesting to study butterfly diversity in the habitat immediately surrounding a disturbed area to test this hypothesis.

This forest ecosystem is adapted to a natural forest regime of somewhat frequent surface fires (Yocom et al., 2010), but with increases in anthropogenic forest fires reported over the last two decades, the habitat housing vulnerable specialist species could be under threat. Conservation strategies for CMNP should take into account the importance of protecting forest habitat from further destruction and fragmentation due to anthropogenic forest fires.

6 BIBLIOGRAPHY

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7 APPENDIX

Species	Larval Hosts	Niche	Abbreviation
<i>Abaeis nicippe</i> (Cramer, 1779)	 Fabaceae Chamaecrista sp (fasciculata, nictitens) Senna sp (bebecarpa, ligustrina, marilandica, mexicana, obtusifolia Cassia sp 	G	AbaeNici
Adelpha basiloides (HW Bates, 1865)	Rubiaceae Alibertia sp Faramea sp Ixora sp 	G	
Adelpha eulalia (Doubleday, 1848)	Fagaceae • Quercus sp	S	
Agraulis vanillae (Linnaeus, 1758)	Passifloraceae Passiflora incarnata Passiflora foetida	S	AgraVani
<i>Aguna asander</i> (Hewitzon, 1867)	Fabaceae	G	
Anaea troglodyta aidea (Fabricius, 1775)	Euphorbiaceae • Croton sp	S	AnaeTrog
Anthanassa texana texana (W.H. Edwards, 1863)	Acanthaceae Dicliptera brachiata Jacobinia carnea Justicia sp Siphonoglossa sp Ruellia sp 	S	AnthTexa
Asterocampa celtis (Boisduval & Leconte, 1835)	Cannabaceae • Celtis sp	S	
Asterocampa clyton (Boisduval & Leconte, 1835)	Cannabaceae • Celtis sp	S	
Astraptes fulgerator (Walch, 1775)	Rhamnaceae • Karwinskia humboldtiana Lamiaceae • Vitex sp	G	
Autochton cincta (Plotz, 1882)	No Information	-	AuCi
Battus philenor (Linnaeus, 1771)	Aristolochiaceae • Aristolochia sp	S	
<i>Biblis hyperia</i> (Fabricius, 1807)	Euphorbiaceae	S	
Calephelis nemesis (WH Edwards, 1871)	Asteraceae • Baccharis glutinosa Ranunculaceae • Clematis sp	G	

Appendix 1: Niche classification, information from citizen science site Butterflies and Moths

Celanorrhinus	No information	-	
fritzgaertneri (Bailey,			
1880)			
Celastrina argiolus	Cornaceae	G	
(Cramer, 1870)	Cornus fiorida		
	Rhamhaceae		
	Ceanotrus americanus		
	Spiraga salicifolia		
	Collinsia sp		
Cercyonis pegala	Poaceae	G	
(Fabricius, 1775)	Tridens flavus	-	
Chlosvne janais (Drurv.	Acanthaceae	G	
1782)	Anisacanthus wrightii	-	
Chlosvne lacinia	Asteraceae	G	
(Gever, 1837)	Helianthus sp	-	
()	 Ambrosia trifida 		
	 Verbesina sp 		
	Xanthium sp		
Chlosyne theona	Scrophulariaceae	S	ChloTheo
(Ménétriés, 1855)	 Leucophyllum sp (texanum, 		
	frutescens)		
Cyllopsis gemma	Poaceae	S	
(Hubner, 1808)	 Cynodon dactylon 		
Cyllopsis pertepida	Poaceae	G	
(Dyar, 1912)			
Danaus gilippus	Apocynaceae: Asclepiadoidae	S	DanaGili
(Cramer, 1775)			
Danaus plexippus	Apocynaceae: Asclepiadoidae	S	
<i>plexippus</i> (Linnaeus,	 Asclepias sp, observed 		
1758)	Calotropis sp		
	Cynanchum sp		
	Sarcostemma sp		
Echinargus Isola	Fabaceae	G	Echilsol
(Reakirt, 1866)	Melilotus officinalis		
	Astragalus sp		
	Prosopis sp Deleo op		
	 Dalea sp Albizia sp 		
	 Albizia sp Indigofera sp 		
Epargyreus clarus	Fabaceae	G	EparSocu
(Cramer 1775)	Robinia pseudacacia	0	
	Gleditsia triacanthos		
	Amorpha sp		
	Glycyrrhiza sp		
Epargyreus zestos	Fabaceae	S	
(Gever, 1832)	Galactia sp	•	
Epiphile adrasta	Sapindaceae	G	
(Hewitson, 1861)	• vines	-	
Erynnis funeralis	Fabaceae	G	Eryn
(darker)	Robinia neomexicana		
	Medicago hispida		

(Scudder & Burgess, 1870)	 Lotus scoparius Olneya tesota 		
Erynnis tristis	Vicia sp Fagaceae	S	Eryn
(Boisduval, 1852)	Quercus sp		
Euptoieta claudia	Passifloraceae	G	
(Cramer, 1776)	 Passiflora incarnata 		
	Berberidaceae		
	 Podophyllum peltata 		
	Violaceae		
	 Viola sp 		
	Portulacaceae		
	Portulaca sp		
	Crassulaceae		
	Sedum sp		
	Menispermaceae		
	Menispermum sp		
Eurema mexicana	Fabaceae	G	EureMexi
(Boisduval, 1836)	 Robinia neomexicana 		
	 Acacia angustissima 		
	 Cassia sp 		
	 Diphysa robinoides. 		
Heliconius charithonia	Passifloraceae	S	HeliChar
(Linnaeus, 1767)	 Passiflora sp (suberosa, lutea, 		
	affinis)		
Heraclides anchisiades	Rutaceae	G	
<i>idaeus</i> (Esper, 1788)	Citrus sp		
	Casimiroa sp		
	Zanthoxylum sp		
Heraclides thoas	Rutaceae	G	HeraThoa
(Rothschild & Jordan	 Zanthoxylum americanum 		
1906)	Ptelea trifoliata		
	Piperaceae		
	six species		
Libytheana carinenta	Cannabaceae	S	
(Cramer, 1777)	Celtis sp		
Megisto rubricata (WH	Poaceae	S	MegiRubr
Edwards, 1871)	 Cynodon dactylon 		
	Stenotaphrum secundatum		
Mestra dorcas	Euphorbiaceae	S	MestDorc
amymone (Fabricius,	 Tragia neptifolia 		
1775)			
Myscelia ethusa	Euphorbiaceae	S	
(Doyère, 1840)	Dalechampia sp		
Nathalis iole iole	Asteraceae	G	Nathiole
(Boisduval, 1836)	 Bidens sp (inc Bidens bipinnata) 		
	 Dyssodia sp, observed 		
	Helenium sp		
	Thelesperma sp		
	Tagetes sp		
	Aster sp		
	Chrysothamunus sp		
	Ericameria sp		
	 Lorandersonia sp 		
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	Carvophyllaceae		
	Stellaria media		
Noctuana lactifera	No information	-	
(Butler & Druce 1872)			
Phoebis agarithe	Fahaceae	G	PhoeAgar
agarithe (Boisduval		U	Послуа
1836)			
Phyciodes mylitta (WH	Asteração	G	
Edwards 1861)		0	
Edwards, 1001)	 Cilisium sp Silubum morionum 		
Ptorourus polomodos		<u> </u>	DtorDolo
Plerourus palamedes	Lauraceae	G	PleiPala
leonus (Rouschild &	Persea borbonia		
Diudii, 1906)		0	DtorDilu
Pterourus pliuminus		5	PterPliu
(Bolsduval, 1836)	• Litsea sp	0	
Pyrgus communis		G	
(Grote, 1872)	Spnaeraicea sp		
	• Maiva sp		
	Althaea sp		
	• Sida sp		
	Abutilon sp		
	Callirhoe sp		
Strymon melinus	Fabaceae	G	
(Hubner, 1818)	 Phaseolus sp 		
	 Trifolium sp 		
	Malvaceae		
	 Malva sp 		
	 Gossypium sp 		
Thorybes drusius (WH	Fabaceae	G	
Edwards, 1884)	 Cologania angustifolia 		
Thorybes pylades	Fabaceae	G	
(Scudder, 1870)	 Desmodium sp 		
	Lespedeza sp		
	Trifolium sp		
	 Hosackia sp 		
Urbanus dorantes	Fabaceae	G	Urba
(Stoll, 1790)	Phaseolus sp		
	Desmodium ['] sp		
	Clitoria sp		
Zerene cesonia (Stoll.	Fabaceae	G	ZereCeso
1790)	Medicago sativa	-	
,	Dalea sp		
	Trifolium sp		