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Insect Community Response Following Wildfire in an Eastern North American Pine Barrens

Heather M. Thompson [1,2], Mark R. Lesser [2], Luke Myers [1] and Timothy B. Mihuc [1,2,*]

[1] Lake Champlain Research Institute, SUNY Plattsburgh, Plattsburgh, NY 12901, USA; hthom016@plattsburgh.edu (H.M.T.); myerslw@plattsburgh.edu (L.M.)
[2] Center for Earth and Environmental Science, SUNY Plattsburgh, Plattsburgh, NY 12901, USA; mless004@plattsburgh.edu
* Correspondence: mihuctb@plattsburgh.edu; Tel.: +1-518-564-3039

Abstract: Ecosystem recovery following wildfire is heavily dependent upon fire severity and frequency, as well as factors such as regional topography and connectivity to unburned patches. Insects are an often-overlooked group of organisms impacted by fire and play crucial roles in many ecosystem services. Flying insects are particularly capable of avoiding fire, returning to burned patches following the initial disturbance, making them an important group to study when assessing wildfire impacts. Following a wildfire in July of 2018 at the Altona Flat Rock jack pine barrens in northeastern New York, insects were collected from an unburned reference site and a post-fire site using malaise traps. Samples were collected in the 2018, 2019, and 2020 field seasons. Insect groups were found to have three main responses to the disturbance event: increased abundance post-fire, unchanged abundance post-fire, or reduced abundance post-fire. Several dipteran families and some non-dipteran groups were present in greater abundance in the post-fire study site, such as Diptera Polleniidae, which increased in abundance immediately following the disturbance in 2018. Other fire-adapted taxa exhibited a more delayed positive response in 2019 and 2020. Diversity, particularly among Diptera, increased with time since the disturbance at the post-fire site. Many taxa declined in response to fire disturbance, including Lepidoptera and several Diptera families, most likely due to habitat, moisture, and organic matter requirements. Future studies could prove beneficial in understanding the recovery of this community and informing land management practices.

Keywords: insect community structure; habitat resilience; wildfire; pine barrens

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1. Introduction

It is a well-studied fact that wildfire is capable of dramatically altering landscapes and restructuring ecological communities at a variety of scales [1,2]. The resilience of these communities is heavily dependent upon legacies in the form of resident biota and their adaptations, as well as climate variability, interactions among different disturbances, and the unpredictability of individual disturbance events [3]. Ecosystems respond to fire in a variety of ways. It has been shown that the speed of recovery and the types of plants able to recolonize an area following fire are dependent upon burn severity, as well as the distance between the burned area and refugial patches, which provide a source of propagules [4,5]. The intensity and frequency of fire has been shown to influence how plant communities respond to the disturbance, regenerating with greater diversity in low to moderately burned areas, in line with Connell's intermediate disturbance hypothesis [6]. This coincides with the preservation of refugial patches as well as much of the soil-bacteria community being under low levels of surface charring [7]. Fire-adapted pine barrens have been found to benefit from the charring of the soil layer and organic matter that occurs with regular burn frequency, as it prevents the establishment of a greater canopy of hardwood species, preserving the open barrens habitat [8]. Fire has been found to increase organic carbon in the soil in the form of charcoal and decaying root tissue, which helps promote plant regrowth in the years post-fire [9]. Suppressing the natural fire regime in these systems can lead to accumulation of litter and fuel, oftentimes leading to larger, more intense fires in the long-run [10,11]. Mechanical methods of limiting these fuels without wildfire are utilized in some instances, though studies have shown that this can often remove microhabitat features and heterogeneity that offer crucial niche space that supports a diverse faunal community [12]. Ultimately, the way the vegetative community responds to fire determines what fauna can be supported under the post-fire conditions.

Wildfire disturbance to fauna has been studied extensively, though most effort has been allocated to studying the impacts on vertebrates. Canada lynx (*Lynx canadensis* Kerr) have been found to thrive under the mosaic of habitat types created across fire-controlled landscapes, while snowshoe hare (*Lepus americanus* Erxleben) are negatively impacted by the thinning of pine following fire [13]. Both lynx and hare have been found to utilize mid-successional post-fire stands. Ungulates and small mammals tend to increase in abundance immediately following fire and decrease over time [14]. American beaver (*Castor canadensis* Kuhl) abundance tends to decrease following fire, and studies have shown that they oftentimes do not return to pre-fire densities [15]. The ability of most vertebrates to survive fire and thrive post-fire is dependent upon the mobility of the species, the presence of forage species, and the severity and uniformity of the burn, with reduced severity and uniformity proving more beneficial. Many vertebrates rely on the presence of invertebrates post-fire, as they make up a significant portion of the diets of many birds, reptiles, amphibians, and mammals. However, invertebrates are oftentimes the most vulnerable to these disturbances [16].

Insects are crucial members of forest communities, with key roles in nutrient cycling, pollination, water filtration, and biological control, in addition to serving as forage species for larger fauna. Insects are one of the most abundant and diverse groups on the planet, yet relatively little is known about their responses to wildfire and their ecology in general. Some insects thrive under post-fire conditions, and others are vulnerable to these disturbances [17]. Many insects have been found to avoid fire, flying, leaping, or crawling ahead of the flames or burrowing into the soil to escape the blaze on the surface. Ants have been observed relocating their nests to unburned locations with foliage following fire, to be closer to food. Inversely, some insects are attracted to fire and smoke, such as some dragonfly species that hunt over cooling fires, or a fly species that uses smoke as a marker for mating swarms. The way an insect group responds to fire is determined by their life histories and adaptations, whether fire is common in their environment, and whether there are food sources remaining following the disturbance. Egg and larval insect stages are more vulnerable to fire, given their limited mobility and habitat requirements [18]. Adult insects are able to avoid fire more effectively, as well as recolonize patches after burning. Timing of prescribed fire has been found to significantly influence insect community composition, oftentimes with summer fire promoting greater diversity of predaceous and herbivorous insects [19]. The diversity of ground and litter insects has been found to increase post-fire, due to the increase in evenness caused by the removal of strong competitors [20,21]. Some carabid beetles (Coleoptera: Carabidae) have been found to benefit from fire, increasing in diversity and abundance in post-fire stands of the Mordovia State Nature Reserve in Russia [22]. A majority of insects found at post-fire sites in European Russia have been found to belong to the orders Coleoptera, Diptera, Hymenoptera, and Lepidoptera [18]. Xylophagous, phytophagous, and parasitic insects have been found to represent greater proportions of insect communities following fire, while saprophagous insects make up a smaller percentage of these communities [20]. Predatory and social wasps have been found to utilize post-fire sites effectively, if sufficient resources and habitat conditions are present for nest building and foraging [18]. These groups often utilize dead wood pulp for nest building and utilize floral regrowth and other arthropods for sustenance. Regrowth of forage vegetation facilitated by reduced herbivory immediately post-fire has been found to lead to greater abundance of phytophagous insects in the years following fire [1,23]. The increase in snags and standing dead trees post-fire contributes to high abundance of xylophagous and saproxylic insects as well [16,24]. Some flies and beetles are attracted to smoke following fire because they lay their eggs in the freshly burned wood to ensure competitive advantage over other xylophagous insects [25]. One study found greater diversity of Coleoptera following fire and observed that bark beetles (Coleoptera, Scolytinae) decreased in abundance post-fire and mycetophagids became more abundant due to the scorching of logs and damage to the bark layer [26]. Another study found that the post-fire Coleopteran community associated with coarse woody debris (CWD) shifts from fire-associated subcortical predators and xylophages over time, as standing dead trees are felled by wind and other influences, becoming more accessible to ground dwelling beetles and saprophagous groups [24]. Coleoptera were in greatest abundance two years post-fire in a Mediterranean study, and Lepidoptera showed decreased numbers two years post-fire [2]. Pollinators such as Lepidoptera tend to respond poorly to the loss of vegetation following fire, though have been found to respond more positively to fire if it is of low to moderate severity, and sufficient refugia and resource patches are maintained [27–30]. This is the case for the Karner blue (*Lycaeides melissa samuelis* Nabokov), which recovers significantly if refugial patches of their forage plant wild lupine (*Lupinus perrenis* Linnaeus) remain following fire [31,32].

Most plant and faunal fire studies are conducted in specific regions or habitats, typically those that burn regularly or severely, or are socially or economically significant, with the majority of studies in North America occurring in the western United States and northeastern Canada. Some research has been focused on pitch pine (*Pinus rigida* Miller), as well as jack pine (*Pinus banksiana* Lambert), barrens, though most of these efforts have been focused in Wisconsin and Albany, NY [33,34], with the exception of a wildlife study at the Altona Flat Rock pine barrens by Cave et al. [35]. A significant amount of the existing literature analyzes the relationship between pest insect outbreaks and wildfire severity and frequency, though relatively few studies assess the impacts fire has on the flying insect community [36–39]. Insect response studies tend to focus on particular taxonomic groups [24,31,32,40] or functional groupings [20,27–29,41–43] of insects, so each study provides a glimpse at how one portion of the insect community responds to fire.

This specialization of research has allowed us to note gaps that remain in our understanding of insect community responses to wildfire. Sampling of entire insect communities is difficult due to the variety of sampling methods necessary to sample all insect functional groups and life stages. Most existing research on post-fire insect responses is focused on beetles [22,24,44], aquatic insects [41,42], pollinators [27–29,31,32,40], herbivores [45], and soil insects [46], so collection techniques and sampling methodologies are selected according to the group being studied. In studying terrestrial insects, pitfall traps are the most commonly used sampling method [2,20,46]. Pitfall traps are ideal for collecting insects that cannot fly well, if at all; sweep-netting, light traps, and malaise traps are better suited for collecting flying insects. A few studies have included multiple sampling methods, such as combining sweep netting and vacuum samplers [43]; combining sweep-netting, pitfall traps, and light traps [47]; and using Berlese funnels, pitfall traps, and sweep nets [21]. However, large knowledge gaps remain in the ecology of many groups of insects and how wildfire in different ecosystems impacts much of the insect community. Insect diversity and abundance has been declining globally due to multiple factors such as land use change, range shifts, and invasions of non-native insects, as well as changes in precipitation and temperature, which can influence the frequency and severity of wildfire and alter insect life cycles [48]. During the current biodiversity crisis, insects are seeing some of the most significant losses [49], so it is imperative that we attempt to monitor their diversity and abundance, especially in unique or globally rare habitats.

The primary aim of this study was to assess the responses of flying insects to wildfire disturbance in a pine barrens ecosystem. Our study focus was on dipteran families, with a secondary focus on other insect Orders, as Diptera are oftentimes some of the first to recolonize sites post-fire [50]. Based on an extensive review of the literature, we expect to see an initial reduction in abundance and diversity of pollinating groups [20,28], and a higher relative abundance of phytophagous, parasitic, and saproxylic insects immediately post-fire [20,24]. In subsequent years, we expect to see the return of even more phytophagous and herbivorous insects, pollinating groups [27,29], and the predatory groups that rely on them [20]. Further, this study seeks to contribute substantially to knowledge of the insect community composition in a jack pine barrens.

2. Materials and Methods

2.1. Study Site

The Flat Rock Pine Barrens located in Altona, New York (Figure 1a, henceforth referred to as the Flat Rock), is a globally rare sandstone pavement pine barrens that was formed more than 12,000 years ago by flooding glacial lakes [51]. It has a New York Natural Heritage Program S1, G2 designation, with >5 similar sites in New York State, and only 6 to 20 similar sites globally [52]. The Flat Rock is characterized by a thin, infertile soil layer on sandstone pavement, with a unique fire-adapted vegetative community dominated by relatively even-aged jack pine in the canopy with a lowbush blueberry (*Vaccinium angustifolium* Aiton) and black huckleberry (*Gaylussacia baccata* Koch) understory. Reindeer lichen (*Cladonia rangiferina* Weber), haircap moss (*Polytrichum commune* Hedwig), bracken fern (*Pteridium aquilinum* Kuhn), and *Sphagnum* sp. offer groundcover on areas that are not just exposed rock [39]. The site supports relatively low diversity for the region, at least within the plant community. The mammalian fauna is comprised of common representatives from the region, such as eastern coyote (*Canis latrans* Say), white-tailed deer (*Odocoileus virginianus* Zimmermann), snowshoe hare, and American beaver [35].

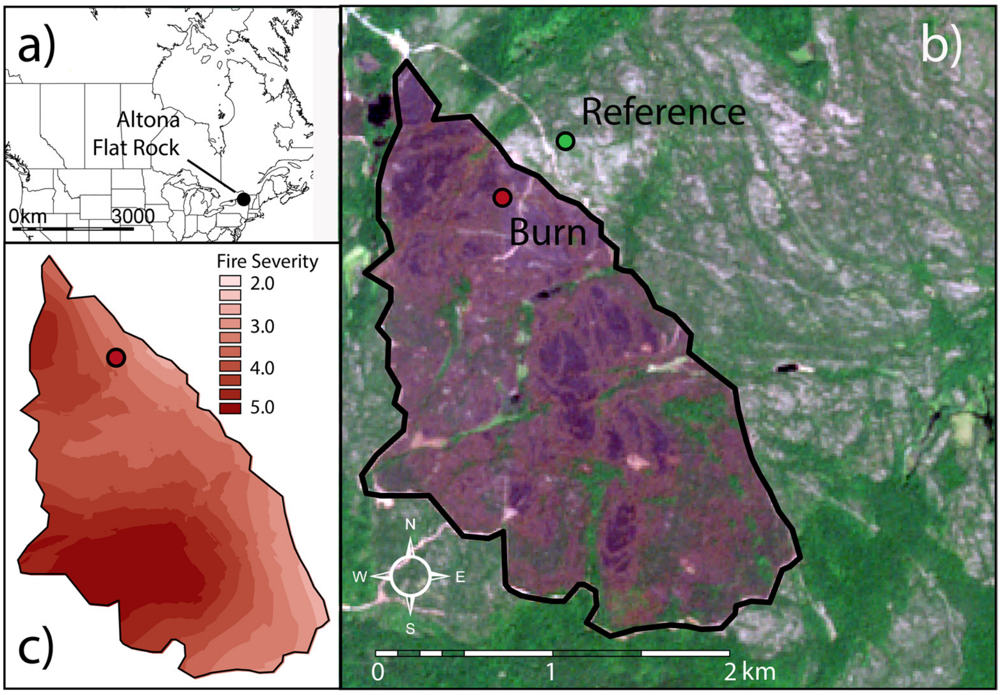

Figure 1. Study site map illustrating (**a**) geographic region, (**b**) map of 2018 wildfire extent with reference and burn sites indicated, and (**c**) fire severity gradient with burn site indicated.

Commonly observed arthropods along trails at the Flat Rock include the tricolored bumblebee (*Bombus ternarius* Say), greater bee fly (*Bombylius major* Linnaeus), six-spotted tiger beetle (*Cicindela sexgutatta* Fabricius), band-winged grasshoppers (Orthoptera: Oedipodinae), flesh flies (Diptera: Sarcophagidae), wolf spiders (family Lycosidae), and a wide variety of moth and butterfly species (Lepidoptera). Other common taxa that were found in the samples collected off-trail were long-legged flies (Diptera: Dolichopodidae), leafhoppers (Hemiptera: Cicadellidae), root maggot flies (Diptera: Anthomyiidae), parasitic wasps

(Hymenoptera) and flies (Diptera: Tachinidae), and a variety of beetles (Coleoptera). In a two-year survey conducted at the nearby Gadway Pine Barrens, just over 400 species from 15 families of Lepidoptera were identified; that this was just one Order of insects illustrates the vast diversity of the insect communities of sandstone pavement pine barrens [53]. Several species of conservation concern have been documented from the Altona Flat Rock and represent the only known locations for these species in the state. These include: the northern barrens tiger beetle (*Cicindela patruela* Dejean, Coleoptera: Carabidae) S1, G3 Conservation Status, documented at the Flat Rock and other scattered pine barrens in the northeast; the zale moth (*Zale largera* Forbes, Lepidoptera: Erebidae) S1, G1 Conservation Status, only known records for the state from the Flat Rock; and the jack pine looper (*Macaria marmorata* Ferguson, Lepidoptera: Geometridae) S1, G1 Conservation Status, only known records for the state from the Flat Rock and Gadway Pine Barrens, also in Clinton County, NY [53,54]. Both species of rare Lepidoptera are known to benefit from jack pine forest regeneration following fires. Attempts were made to introduce jack pine to Albany Pine Bush to support zale moth establishment, but the jack pine were defoliated by pine sawflies (Hymenoptera: Diprionidae). This further implies that jack pine is restricted in New York to formations, as we see at the Flat Rock, due to the lack of a sufficient soil layer necessary for pine sawfly development [53].

During the summer of 2018 a wildfire occurred at the Flat Rock, beginning on 12 July 2018 and lasting for six days. This wildfire burned 225 ha of jack pine barrens and presented a unique opportunity to study wildfire in a northeastern fire-adapted ecosystem. Topographic heterogeneity and past management practices have created a mosaic of forest structure and composition within the Flat Rock post-fire landscape. Some areas of the pine barrens had regenerated following wildfire in 1958, and some of these areas were mechanically thinned to reduce wildfire risk in 1999, creating a much-lower-density forest than surrounding areas and reducing available fuel. Further, low-lying depressions and beaver activity have led to the encroachment of hardwood species, which has created patches of northern hardwood dominated wetlands that fragment the otherwise jack-pine-dominated system (see green areas in Figure 1b). The unique structure, history of the forest, and its global rarity, as well as the heterogeneity of the habitat following the fire in 2018, make the Flat Rock an ideal location to study insect community responses to fire.

2.2. Sample Collection

Samples were collected using malaise traps installed at two plots, one within the fire perimeter and one outside in the undisturbed reference forest (Figure 1). Plot locations were based on accessibility and sampling limitations. Additionally, we selected the burned site based on its position within the fire severity gradient (Figure 1c) and its distance from unburned wetland areas within the fire perimeter (green banding throughout the burned area in Figure 1b). We sought to avoid these wetland areas to ensure the samples would be representative of the pine barrens community and not the aquatic communities associated with wetland habitat. The reference site was then selected to minimize and control for landscape heterogeneity and forest structure between the two plots. Jack pine stand age was the same at both plots, having regenerated following the wildfire in 1958, and structure was similar, with both sites having been mechanically thinned in 1999. Both sites offered relatively open habitat with comparable amounts of exposed rock (Figure 2). One malaise trap was placed at each site to passively capture flying insects from the immediate vicinity of the trap, each with a funnel-opening diameter of (22 mm). The size of the funnel opening slightly limited our collection, excluding any particularly large-bodied lepidopterans, coleopterans, and hymenopterans. This method is a passive capture method used primarily for sampling adult flying insects. Multiple malaise traps were not employed due to the passive nature of the sampling gear. Samples were collected biweekly for two consecutive summers, beginning immediately following the wildfire in July of 2018 through late September of 2018, and during June to August in the summer of 2019. Samples were collected triweekly from early July to mid-August in 2020.

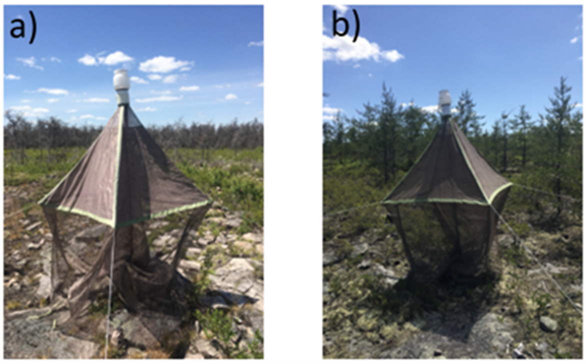

Figure 2. Malaise traps at the burned site (**a**) and reference site (**b**) in the summer of 2020.

We sampled pre-fire stand density, ground cover, and collected soil samples in June 2019 at each of the sites from a 20 m^2 plot centered on the Malaise trap. Subsamples of 5 mL were taken from collected soil and placed in a drying oven at 60 °C for 48 h to determine moisture content. Samples were then ashed in a 500 °C muffle furnace to determine organic content. We used a spherical densiometer to calculate canopy closure at each site and assessed fire severity on a five-point scale ranging from 1 being unburned to 5 being no live material remaining on completely burned trees/crowns.

2.3. Identification

All individuals in malaise trap samples for 2018, 2019, and 2020 were enumerated and identified to Order [55]. The true flies (Diptera) were identified to family due to their high abundance and diversity. Samples were identified using standard taxonomic keys and sorted using a dissection microscope. After separating Diptera into morphotypes, physical resources [56,57] were consulted to compare each morphotype to the images, descriptions, and keys to provide proper family determinations. Small Diptera such as Chironomidae and Mycetophilidae were not enumerated due to their small size, their fragility, and the difficult techniques necessary for identification, though they were present at both sites. Some arachnids were collected, and though this study is focused on insects, they were included in the site counts due to their significant role as predators.

After identifying each taxon, resources were gathered outlining habitat preferences, life history strategies, and feeding behaviors for the groups that were identified. Habitat preference was determined by known moisture requirements, as well as vegetative structure preferences for each taxon, which were gathered from a variety of physical and online resources. Feeding behaviors were specified for adult and larval forms to account for the commonality of insects to partition resources between different life stages. The diversity of Hemiptera, Neuroptera, Coleoptera, and Orthoptera was relatively low, so feeding habits for these Orders were determined based on the groups found in the samples. Diptera showed impressive diversity, even sometimes within families, so functional traits were assigned according to those common at the family level. Though functional groupings are broad, and assumptions were likely made for each taxon, as species were not known and there are typically exceptions, they can still provide a glimpse at community structure and what roles are assumed by the flying insects at the Flat Rock.

2.4. Data Analysis

Transformed Shannon–Wiener family level diversity was calculated using family or order level data for all years for the burn and reference site. Sørensen's similarity coefficient was also calculated to compare burn vs. reference site community composition. To assess how the heterogeneity introduced by the wildfire impacted diversity across the landscape, burn and reference taxa counts were combined for all sampling weeks and diversity was calculated and averaged for each year. A community ordination method, Nonmetric Multidimensional Scaling (NMDS), was used to identify patterns between burn and reference samples in community composition. NMDS analysis used Sørensen's similarity as the distance parameter and removed any taxa less than 1% total abundance across all samples prior to analysis. Relative (percent) abundance of taxa was assessed to determine if a taxon was negatively, neutrally, or positively impacted by the fire, and NMDS results were sorted and arranged according to each taxon's response.

3. Results

3.1. General Patterns in Insect Abundance and Diversity

Our results suggest that patterns in insect communities differed between the reference and burned study sites. The reference site had significantly greater abundance of insects over the course of the study period, though during the 2018 sampling season abundance was marginally greater at the burn site (Table 1, Figure 3). Initial abundance was similarly low between sites immediately following the fire in 2018, while the reference site contained much higher total insect abundance in subsequent years.

Table 1. Summary table for site characteristics, richness, and mean similarity between burn and reference sites for all years. All site characteristic data were collected during the spring of 2019.

Site Data	Reference	Burn
Fire severity	1	3
Soil organic matter	32%	18.534%
Soil moisture	27.258%	11.77%
Canopy cover	0.16	0
Number of samples	2018: 4 (biweekly) 2019: 4 (biweekly) 2020: 3 (triweekly)	2018: 4 (biweekly) 2019: 4 (biweekly) 2020: 3 (triweekly)
Total abundance	13,860	5879
Richness	Mean: 23.64 ± 5.464 Maximum: 29 (August–September 2020)	Mean: 22.64 ± 3.931 Maximum: 29 (June–July 2019)
Mean Sørensen's (all years)	0.599 ± 0.049	—

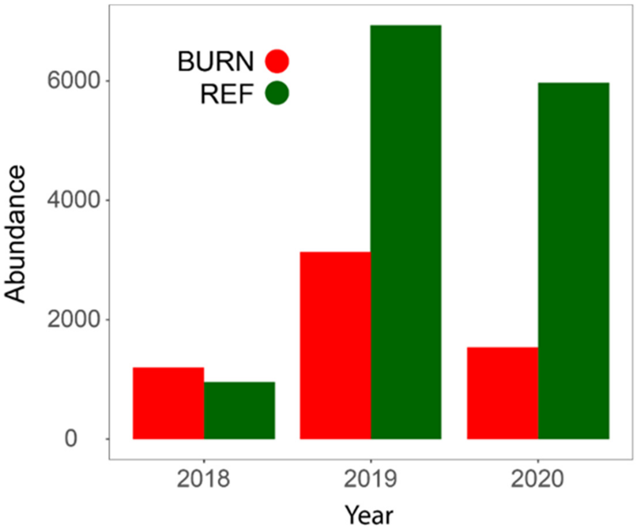

Figure 3. Total number of insects at both study sites for each study year.

There were no major patterns in taxa richness as both sites maintained similar richness on average. Each site reached a maximum richness of 29 taxa, though the burn site reached this maximum in the 2019 early sample season, and the reference site reached this richness later in the season in 2020 (Table 1). This shows clear evidence of the successful recolonization of many taxa, just one year post-fire. In general, Shannon–Wiener diversity for family/order level taxa was marginally higher at the reference site in 2018 due to the initial reduction in taxa post-fire, though diversity was greatest at the burned site during the following two years (Figure 4). The low diversity of insect families/orders at the reference site can be attributed to the over-dominance of some taxa in some of the samples, and the fact that many other taxa were relatively rare (17 taxa made up <1% of the community). The combined diversity was greater than at both sites individually, which indicates that the fire disturbance increased overall diversity in this stand of jack pine (Figure 4). In 2019 and 2020, the combined site diversity was similar to the burned site, while diversity at the reference site was lower (however, ANOVA found the differences to be insignificant, results not shown).

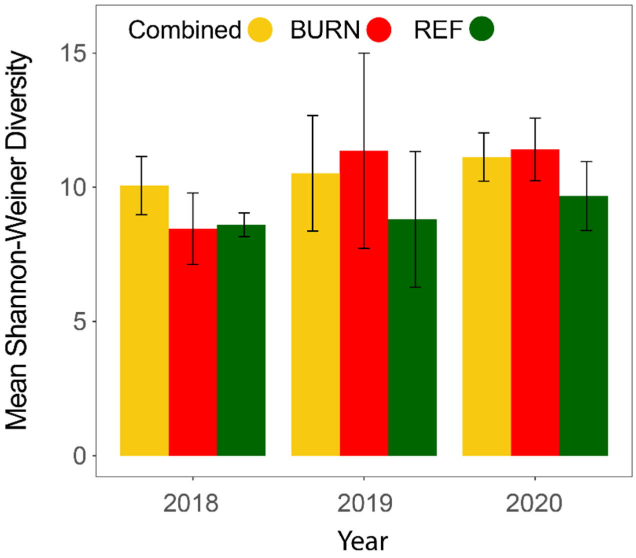

Figure 4. Mean Shannon–Wiener index values (transformed) for the reference site, burn site, and both sites, combined for each year.

3.2. *Patterns in Insect Community Composition*

Sørensen's similarity comparisons between sites, and within site samples (Figure 5), shows higher community similarity among reference site samples than among burn site samples in 2018 and 2019. In 2020, there was greater similarity across burn site samples than across reference site samples, indicating that the burn site community became more similar in composition from 2018–2020. Community similarity between burn and reference sites was lower than either within the site sample comparison throughout the study period, indicating that the burn site diverged from the reference site quickly following wildfire and remained dissimilar, two years post-fire. The lower community similarity, when comparing between burn and reference sites, is a result of changes in abundance in several taxa, including many dipteran families in the burn site following the fire (see NMDS results, Figures 6–10).

Community ordination patterns reflect a change in community composition between burn and reference locations, with distinct grouping of reference samples versus burn samples across all study years (Figure 6). Several taxa showed initial increases in the burn site, including cluster flies (Diptera: Polleniidae). Very few groups show a clear preference for pre-fire conditions, and those that do have requirements that could not be fully met under post-fire conditions (Phoridae and Dolichopodidae: moisture/vegetation; Bombyliidae and Pipunculidae: vegetation/host presence). Burn site orientation progresses closer to the origin point over time, with the 2020 sample points relatively close to the origin, suggesting that the burn site characteristics are slowly shifting away from the post-fire conditions. Decreased distance between burn site ordination points in 2020 suggests that the community is also becoming more similar, as opposed to the greater distance between the 2020 reference points.

Patterns across non-dipteran insect orders also showed some responses to the fire disturbance event. Coleoptera, Hemiptera, and Orthoptera tended to make up a greater percentage of the insect community at the burn site, while Hymenoptera and Lepidoptera had a greater percent of abundance at the reference site (Figure 7). These patterns are particularly evident in 2019.

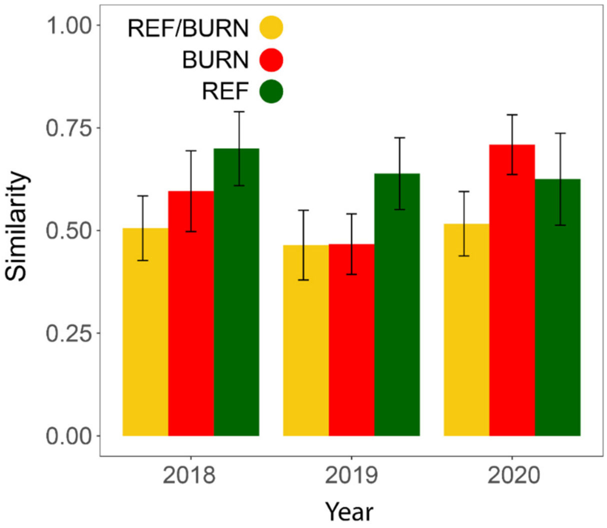

Figure 5. Average Sørensen's similarity coefficient within reference and burn sites and between burn and reference sites, for all years.

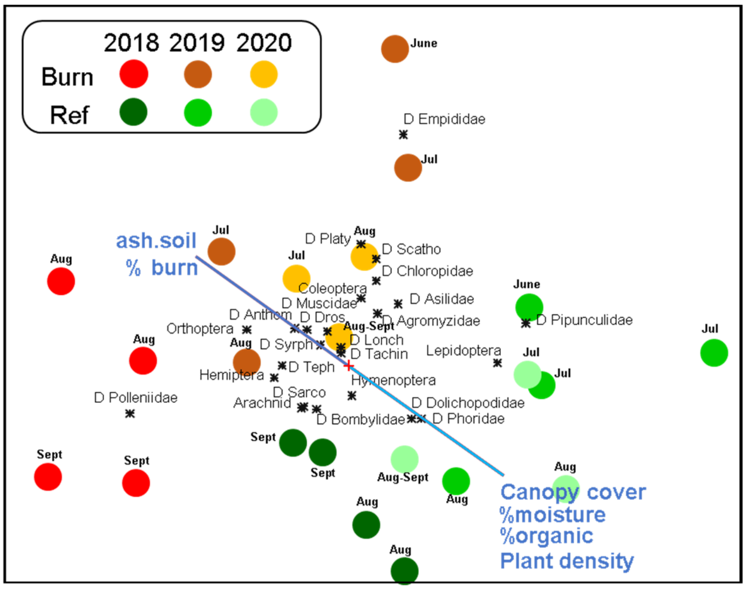

Figure 6. NMDS results for Altona fire versus reference study sites. * indicates insect taxon, circles indicate burn and reference study sites and year. Environmental variables associated with burn and reference sites are shown in blue. NMDS ordination stress was <0.10, using Sørensen's similarity to determine ordination distance. All Diptera families are labeled as D, followed by family name or abbreviation.

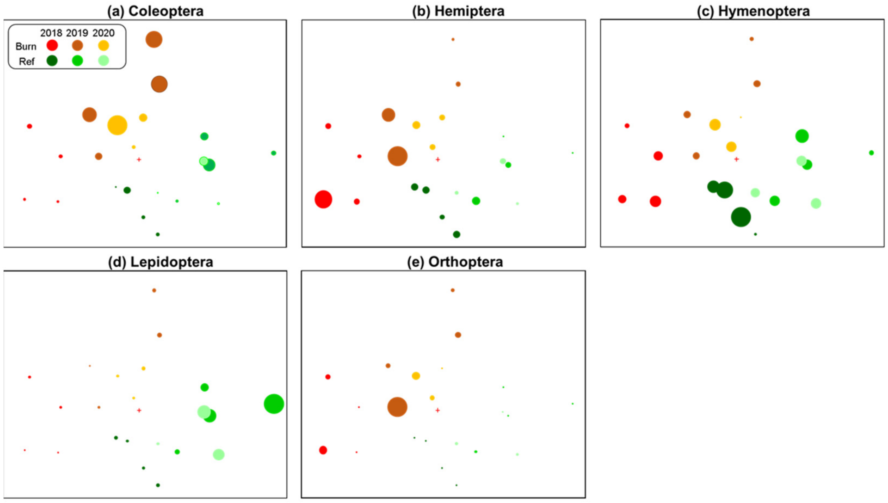

Figure 7. NMDS ordination results for non-dipteran insect Orders in burn and reference study sites. Panels (**a**–**e**) show results for each Insect order; (**a**) Coleoptera (**b**) Hemiptera, (**c**) Hymenoptera, (**d**) Lepidoptera and (**e**) Orthoptera. Symbol size is scaled by percent abundance within each sample.

Among dipteran families there were three main response trends: taxa that increased in abundance in the burn site (fire-adapted) (Figure 8), taxa that remained neutral in abundance in both sites (Figure 9), and taxa that were abundant primarily in the reference site (fire-vulnerable) (Figure 10). Taxa that increased in the burn site (Figure 8) included Asilidae, Drosophilidae, and Tachinidae; all of these increased at the burn site over the three-year sampling period, with Asilidae and Drosophilidae remaining present in very low abundances at both sites during the first two years before spiking at the burn site during the 2020 sampling period. Polleniidae were present in high abundance in the burn site in 2018, though were nearly absent in the following years (Figure 8). Tachinidae also spiked at the burn site in 2020 and were present in numbers comparable to the reference site prior to 2020. Anthomyiidae showed a clear seasonality, as well as site preference. Anthomyiidae were present in low numbers during the earliest and latest sampling periods at the burn site (early July and mid-late September) and made up the greatest proportion of the community during July-August sampling at the burn site for all years. Anthomyiidae made up the greatest percentage of the community at the reference site only during the latest sampling dates in 2018 (Figure 8). Agromyzidae and Chloropidae had comparable abundances at the reference and burn sites during most of the sampling period as well, though their numbers saw increases at the burn site during the 2019 and 2020 sampling periods. Muscidae were present in relatively low numbers at both sites, though increased in 2019 at the burn site.

Diptera families Lonchaeidae, Sarcophagidae, Scathophagidae, and Syrphidae were present at the burn site in abundances similar with those at the reference site, indicating that these groups were likely not only perturbed by the disturbance but also did not necessarily benefit from it (Figure 9).

Dipteran groups impacted most negatively by the fire are illustrated in Figure 10. Bombyliidae were present at the burn site in abundances comparable to the reference site in 2018, though composed a greater proportion of the reference site community in the following years. Dolichopodidae, Phoridae, and Pipunculidae all showed clear preferences for the reference site, with Dolichopodidae showing the greatest abundance in 2018, Phoridae spiking for one sampling period in 2020, and Pipunculidae showing clear seasonality by spiking in July samples of 2019 and 2020. None of these taxa showed any recovery in the burn site from 2018–2020.

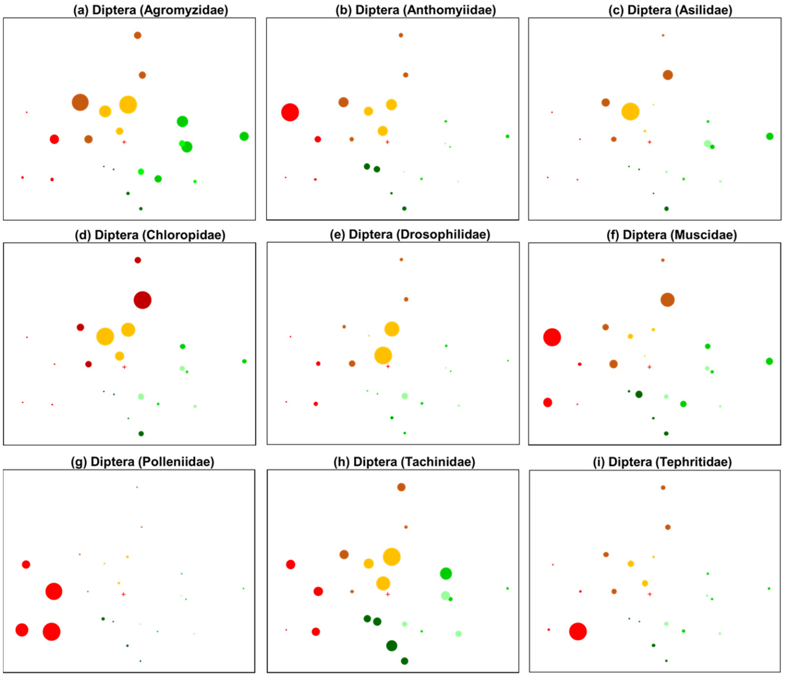

Figure 8. NMDS ordination results for fire-adapted Diptera in burn and reference study sites. Panels (**a**–**i**) show results for Diptera Families; (**a**) Agromyzidae, (**b**) Anthomyiidae, (**c**) Asilidae, (**d**) Chloropidae (**e**) Drosophilidae (**f**) Muscidae (**g**) Polleniidae, (**h**) Tachinidae (**i**) Tephritidae. Symbol size is scaled by percent abundance within each sample.

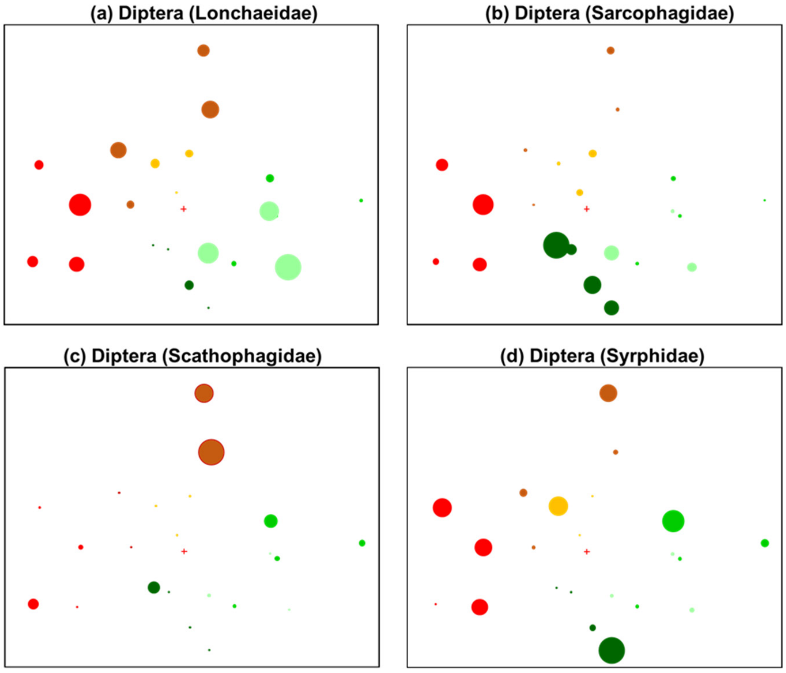

Figure 9. NMDS ordination results for neutral-response Diptera in burn and reference study sites. Panels (**a**–**d**) show results for Diptera Families; (**a**) Lonchaeidae, (**b**) Sarcophagidae, (**c**) Scathophagidae, (**d**) Syrphidae. Symbol size is scaled by percent abundance within each sample.

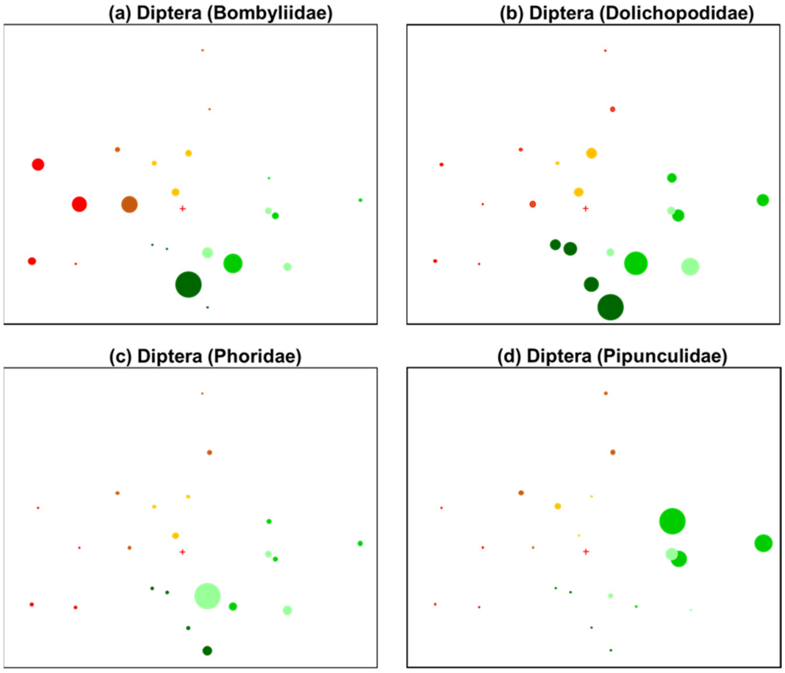

Figure 10. NMDS ordination results for negatively impacted Diptera in burn study sites. Panels (**a**–**d**) show results for Diptera Families; (**a**) Bombyliidae, (**b**) Dolichopodidae, (**c**) Phoridae, (**d**) Pipunculidae. Symbol size is scaled by percent abundance within each sample.

4. Discussion

Briefly, our results suggest that pine barrens insect communities are impacted by wildfire in a variety of ways, and groups present in fire-prone habitats are often adapted to the "natural" disturbance regime. Given the global rarity of pine barrens, and their potential to support locally rare species, it is crucial to develop a baseline of the insect diversity at the Flat Rock. The diversity results suggest that fire-vulnerable taxa are moving back into the burn over time while fire-adapted taxa remain, though these groups are likely declining as conditions become less favorable as time increases post-fire. Though the differences in diversity were found to be insignificant, our results still illustrate an increase in diversity across the pine barrens landscape post-fire, and the subsequent reconfiguration of insect community dynamics as succession takes place. Many Diptera clearly benefitted from the wildfire, as did a variety of other non-dipteran groups, indicating that insect communities in this unique ecosystem benefit when disturbed and restructured by fire. Insects provide necessary services in forests, and the recovery of the insect community we observed post-fire implies that some insect groups may benefit from natural wildfire disturbance.

4.1. Fire-Adapted Responses

The post-fire insect community of the Flat Rock appears to be recovering, though some insects are returning more readily than others. Each site has distinct dominant dipteran taxa (Burn: Anthomyiidae, Polleniidae; Reference: Dolichopodidae), and many of the groups found to inhabit the Flat Rock were determined to be fire-adapted. A summary of the post-fire response and ecological traits of the taxa in this study can be found in Table 2. Cluster flies (Polleniidae) were prevalent in the 2018 late season but almost completely absent in the 2019 and 2020 samples, indicating that they may have been attracted by the post-fire conditions. Cluster flies parasitize earthworms [58] and likely benefitted in 2018 from the removal of vegetation and groundcover post-fire, as it would aid them in finding hosts. By 2019, understory vegetation (i.e., blueberry and huckleberry) had largely returned to pre-fire conditions, possibly making the site less suitable for this group. Understory regrowth also likely contributed to the increase in other groups such as Tachinidae, Drosophilidae, and

Asilidae in the 2020 burn samples. Tachinidae and Asilidae are reliant upon the presence of lower trophic levels, which are directly reliant upon the availability of forage plant and/or insect species [57,59]. Parasitic groups that recovered quickly at the burn site were typically generalists in regards to host species (excluding Polleniidae). Groups that thrived at the reference site tended to have moisture preferences and vegetation requirements that were not met at the burn site, and those that thrived at the burn site typically prefer very open habitat and can tolerate or compensate for low moisture conditions (Table 2).

Table 2. Insect taxa ecological traits and response trends from this study, with "+" indicating a positive response, "~" indicating a neutral response, and "−" indicating a negative response.

Common Name	Taxon	Post-Fire Response	Ecological Traits (Environmental Niche Dimensions, Life History Traits, Habitat/Food Preferences)
Leafmining flies	Diptera (Agromyzidae)	+	Phytophagous; oviparous; requirements: vegetation (host plant specific)
Root-maggot flies	Diptera (Anthomyiidae)	+	Pollinator, phytophagous, some parasitic; oviparous; requirements: moist vegetated/wooded habitat and sometimes open habitat [60]
Robber/Assassin flies	Diptera (Asilidae)	+	Predatory; oviparous; requirements: prey species, dry open habitat; Perching behaviour require vegetation or elevated substrates, decaying matter (larval prey species) [57]
Frit/Grass flies	Diptera (Chloropidae)	+	Varied feeding based on species, grass feeding, stem mining, saprophagous, scavenger, or parasitic; oviparous; requirments: low-lying vegetation, open habitat [61]
Vinegar/fruit flies	Diptera (Drosophilidae)	+	Saprophageous, fungivore, pollinator; oviparous; requirements: adult and larval food source (typically decaying fruit) [57]
Dance flies	Diptera (Empididae)	+	Predatory, pollinator, saprophagous; oviparous; requirements: prey species, decaying matter, moisture [62]
House flies	Diptera (Muscidae)	+	Saprophagous; oviparous; requirements: adult and larval food source [57]
Cluster flies	Diptera (Polleniidae)	+	Pollinator, parasitic (earthworms, some sp. parasitize caterpillars and bees); oviparous; prefer warm, open habitat [58]
Beetles	Coleoptera	+	Pollinator, xylophageous, predatory, etc.; oviparous; varied requirements [55]
True Bugs	Hemiptera	+	Phytophageous; oviparous; requirements: vegetation [55]
Grasshoppers and Katydids	Orthoptera	+	Phytophagous; oviparous; requirements: vegetation, open habitat [55]
Lance flies	Diptera (Lonchaeidae)	~	Oviparous; feed on decaying plant material [57]
Flesh flies	Diptera (Sarcophagidae)	~	Parasitic; viviparous [57]
Flower/Hover flies	Diptera (Syrphidae)	~	Pollinator, predatory, saprophagous; oviparous; requirements: flowering vegetation, larval food source; open habitat [57]
Parasitic flies	Diptera (Tachinidae)	~	koinobiont parasitoid (caterpillars common); pollinator, saprophagous; oviparous; requirements: adult and larval food source, open habitat for mating [59]
Bee flies	Diptera (Bombyliidae)	−	Pollinator and parasitic (bees); oviparous; requirements: host species and flowering vegetation [57]
Long-legged flies	Diptera (Dolichopodidae)	−	Predatory; oviparous; requirements: prey species, vegetation, moisture [57,63]
Scuttle flies	Diptera (Phoridae)	−	Saprophagous, fungivorous; oviparous; requirements: moisture, organic matter [57]
Big-eye flies	Diptera (Pipunculidae)	−	Parasitic (Hemiptera); oviparous; requirements: host species [57]
Wasps, bees, ants, sawflies	Hymenoptera	−	Pollinator (bees and wasps), parasitic (wasps), predatory (wasps), generalists (wasps and ants); oviparous; requirements: nesting habitat, adult and larval food sources [55]
Moths and butterflies	Lepidoptera	−	Pollinator, phytophagous; oviparpous; requirements: adult and larval food sources, relatively open habitat [55]

Our study found many parasitic wasps and flies at the Flat Rock, many of which are known to specialize on specific host groups such as leafhoppers (Hemiptera: Cicadellidae) or bees (Hymenoptera: Apoidea). Parasitic insects made up a significant portion of the community at the burn site. Phytophagous Hemiptera returned to the fire site readily, as did members of the order Orthoptera. Orthoptera had greater diversity [Reference: S = 1; Burn: S = 2] and abundance at the burn site in 2019. This high abundance of parasitic and phytophagous insects post-fire supports the post-fire insect community findings of Ferrenberg et al. [20]. Additionally, the influx of Diptera immediately post-fire, and the return of high abundances of cicadellids post-fire, has been observed in other studies [50]. An increase in xylophagous and saproxylic representatives was observed at the burn site in 2019, and even more so in 2020 (Cerambycidae: Buprestidae). This shift in the Coleopteran community is contributed to the presence of standing dead trees and is consistent with the results obtained by Boulanger and Sirois, in their study on Coleoptera of a northern Canadian boreal forest [24]. Most trees killed during the fire are still standing, thus making it an ideal habitat for these groups. There was a greater abundance of carabid beetles at the burn site as well, agreeing with the findings of Ruchin et al. [22]. Future studies could be conducted on the coleopteran community specifically, given their diversity and the initial divergence in composition at the reference and burn sites.

4.2. Fire-Vulnerable Responses

The dominant dipteran taxa at the reference site (Dolichopodidae) did not recover to pre-fire abundances at the burn site, likely due to the group's organic matter and moisture requirements (Table 2). Dolichopodidae have been found to be one of the most abundant Diptera in humid locations, so the xeric pine barrens is likely not ideal habitat [63]. Dipteran and non-dipteran pollinators were more prevalent in 2019 and 2020 samples from both sites, likely due in part to the earlier sampling period and the regeneration of vegetation post-fire. There was a high abundance of Lepidoptera at the reference site in 2019 and 2020, and greater richness among bee flies (Diptera Bombyliidae) and bees (Hymenoptera, Apoidea) was observed in 2020. No bees were found in the 2018 samples, potentially due to the late sampling period and disturbance of the soil layer where many solitary species nest. There was a low diversity of bees at the burn site in 2019 and 2020, and generally low abundance at both sites during both years. Flower longhorn beetles (Lepturinae) were present at the reference site during 2019 and 2020 and were only found at the burn site in 2020, indicating a return of flowering vegetation two years post-fire. These results are consistent with a variety of studies on pollinators post-fire [27,28]. Lepidoptera did not return to the burn site readily, likely due to the lack of forage plant availability for adults and larvae post-fire. Increased Lepidoptera abundance at the reference site during July of 2019 and 2020 coincided with dispar moth (*Lymantria dispar* Linnaeus) emergence and regional population outbreaks over the past few years. The lack of dispar moths at the burn site even two years post-fire indicates a lack of resources, potentially limiting this invasive species in post-fire jack/pitch pine stands. This offers an additional avenue for potential study, focused on assessing how vulnerable native lepidopteran species respond to fire as well.

Egg parasites (Hymenoptera: *Mymaridae* spp.), as well as parasitoids (Diptera: Pipunculidae, Tachinidae; Hymenoptera: Ichneumonidae, Braconidae, etc.), were found at both sites in 2019 and 2020, though they were more diverse and abundant at the reference site. This likely contributed to the fact that host species for these groups are commonly tied to specific host plants, which may not have regenerated as readily post-fire. Actively parasitized adult leafhoppers were found in some of the 2020 samples (Hemiptera: *Delphacidae* spp.). Some potential parasites of dispar moths were found, indicating the presence of possible biological control mechanisms for this invading species.

Future studies could investigate insect recovery rates across a variety of burn severities and locations in pine barrens habitat to assess the role of heterogeneity in the post-fire recovery process. Additionally, efforts could be made to explore other sampling methods and techniques to assess the insect community in its entirety. Changes to natural disturbance regimes can lead to a misalignment between the adaptations developed by the biota present and the environmental conditions observed, which can lead to significant structural changes in the habitat of concern [3]. Fire suppression can contribute directly to these structural shifts, as succession is unchecked, and organic matter is able to accumulate in the soil [8]. Accumulation of organic matter and an increase in soil depth could allow opportunities for insects such as pine sawflies that require a substantial soil layer to colonize the Flat Rock Pine Barrens. This result would be detrimental to the community of the Flat Rock, given the sawflies' tendency to defoliate jack pine [53]. Additionally, climate change has the potential to increase the frequency and severity of wildfires such as the one in 2018, especially in forests that have undergone fire suppression, so regular monitoring of the conditions at the Flat Rock could prove beneficial for ongoing and future studies on pine barrens habitats. As climate change becomes more severe, it is crucial to assess the resilience of pine barrens habitats such as the Flat Rock, given that they often support rare species and tend to maintain above-average temperatures and below-average moisture levels for their regions.

5. Conclusions

Given how little is known about insect responses to disturbance in general, and how crucial insects are to the ecosystems in which they reside, it is important to study how they are impacted by environmental change, be it from a "natural" or anthropogenic source. This study illustrated the resilience of fire-adapted habitats and the insect biota within them, with some insect groups benefitting from post-fire conditions such as Diptera Polleniidae, while others were negatively impacted (including Lepidoptera and several Diptera families), most likely due to post-fire changes in habitat, moisture, and organic matter requirements. Our study illustrates the important role of wildfire to maintain insect biodiversity in globally rare pine barrens ecosystems. Post-fire insect responses suggest that some taxa may be adapted to fire disturbance to maintain populations in the pine barrens, similar to the fire-adapted jack pine trees that inhabit these systems. Additionally, with the continued introduction of invasive species, it is important to assess our native communities to determine their vulnerability to wildfire disturbance. Moving forward, wildfire studies on insect communities will become increasingly pertinent, especially under changing climatic conditions. Long histories of fire suppression have occurred in systems where fire is a natural disturbance, including the Altona pine barrens. As efforts are made to inform fire management practices in these systems, studies assessing impacts of wildfire on insect communities will provide valuable information.

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