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Wildlife Response to Wildfire in a Northern New York Jack Pine Barrens

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Abstract: Natural disturbances are an integral part of forested ecosystem function and successional pathways. In many forested ecosystems, wildfires are critical to shaping composition and structure, which, in turn, has major implications for wildlife usage and behavior. In July 2018, a wildfire burned 225 ha of the Altona Flat Rock pine barrens in northern New York. This event presented the opportunity to study how wildlife respond to the immediate effects of disturbance in this unique habitat but also how that response would change through time as regeneration progressed. Game cameras were deployed from September 2018 to September 2020 at two reference (unburned) and two disturbed (burned) sites within the pine barrens. We analyzed total and seasonal occurrences, to determine how usage differed between disturbed and reference conditions, and with time since disturbance. Additionally, for coyote (*Canis latrans*, Say), white-tailed deer (*Odocoileus virginianus*, Zimmermann), and snowshoe hare (*Lepus americanus*, Erxleben), we evaluated daily activity patterns and overlap to determine how predator–prey relationships differed between conditions, and with time since disturbance. Over 730 days, a total of 1048 wildlife occurrences were captured across 23 wildlife species. Fifty-seven percent of all occurrences were at reference sites with over 100 more occurrences than at disturbed sites; however, differences were most pronounced immediately following the fire and overall occurrences have grown more similar between the sites over time. Specifically, deer and hare were found more often at reference sites immediately following the fire, but shifted to using both conditions equally by the first growing season. Habitat overlap among sympatric prey (deer, hare) can be explained by understory regeneration increasing foraging opportunities and concealment cover in the disturbed condition, while predators (coyotes) tracked prey availability regardless of the habitat condition. This study provides wildlife management guidance on habitat use and response to disturbance for these unique sandstone pavement barrens.

Keywords: disturbance; ecosystem recovery; succession; regeneration; game cameras; predator–prey; diel activity; jack pine

1. Introduction

Natural disturbances are an integral part of forested ecosystem function and successional pathways [1–3]. Disturbance effects on an ecosystem range temporally from days to centuries [4,5], and spatially from small-scale forest gaps (i.e., 10's of meters) to large-scale events such as wildfires (i.e., 100's to 1000's of hectares) [1]. Ecosystem-level disturbance may be biotic (e.g., pests and/or pathogen outbreaks) or abiotic (e.g., windthrow, ice storms, wildfire) with effects ranging from changes in biogeochemical cycling [6], to vegetative structure and assembly [7], to wildlife usage and interactions (i.e., predator–prey relationships) [4,8].

In many forested ecosystems across the globe, wildfires are a natural disturbance critical to shaping regional vegetation [9]. Burning affects not only forest structure, but

may also support seedbank activation and seedling establishment by altering microhabitat conditions including increased pulses of nutrients, shifts in albedo, and greater moisture retention [10–14].

Changes to forest composition and structure may lead to significant changes in wildlife abundance, diversity, and interactions (i.e., predator–prey relationships) [15,16]. Wildfires impact wildlife mainly by altering resource availability, such as refuge and food. Small mammals, such as deer mice (*Peromyscus leucopus*, Rafinesque) and chipmunks (*Tamias striatus*, Linnaeus), have been found to respond positively immediately following severe wildfires possibly due to reductions in coarse woody debris and leaf litter, leading to enhanced access to seed sources [16,17]. Conversely, lagomorphs are largely absent immediately following fires, as understory concealment cover and browse are removed [16,18]. However, as vegetation recovers over time, lagomorphs may find this habitat more appealing [16].

Wildfires can both negatively and positively impact browsing ungulates such as white-tailed deer (*Odocoileus virginianus*, Zimmermann). While in some cases deer utilized recently burned habitat due to increased herbaceous regeneration [19], they have also been found to avoid such habitats during vulnerable life stages (e.g., fawn-rearing), as increased predation risk results in a trade-off in forage quality [20]. Further, following wildfire events, mule deer (*Odocoileus hemionus*, Rafinesque) have been shown to move into adjacent unburned habitat, where hiding cover is greater, which over time also attracts predators [21]. Mustelid predators, such as fisher (*Martes pennanti*, Erxleben), typically avoid early successional forests, but may use recently burned areas for hunting purposes due to increased small mammal prey abundance [22]. However, Paragi et al. [23] in a study on American marten (*Martes americana*, Turton) found that this was true only for juveniles and transients, making recently burned areas population sinks. This finding suggests that the arrangement of burned areas on the landscape may be the critical factor in determining usage [16]. For larger predators, such as coyotes (*Canis latrans*, Say) in eastern North America, wildfires initially reduce concealment cover and prey availability. However, as vegetation and prey recover, predators have been shown to respond by adjusting hunting strategies and consumption rates [24].

The objective of this study was to monitor wildlife response to wildfire following a 2018 wildfire at the Altona Flat Rock pine barrens in northern New York state. In eastern North America, pine barrens are fire-dependent systems, unlike the predominantly mesic hardwood forest in which they are nested. These systems provide a unique habitat for a variety of wildlife species, such as songbirds [25], butterflies [26], and open-habitat species such as grouse [27], yet little to no research has been conducted on how other species utilize these rare disjunct systems, let alone how wildfire disturbance may influence that usage [28].

We used game cameras, in a non-invasive wildlife use survey, to continuously monitor both disturbed (burn) and reference (unburned) conditions to determine (1) the extent to which the disturbance changed wildlife usage patterns; (2) how diel activity patterns and predator–prey relationships were affected by the disturbance; and (3) how these relationships change with time since disturbance. We hypothesized that wildfire would have an immediate and pronounced effect on wildlife occurrence and habitat use that would diminish with time since disturbance. Specifically, as the understory regenerates, species will return to the disturbed condition for access to high-quality forage and increased hiding cover [16]. Herbivores (deer, hare) will initially be found less often in the disturbed condition until rhizomatous species (e.g., bracken fern (*Pteridium aquilinum*, Kuhn**)** and bristly sarsaparilla (*Aralia hispida*, Ventenant) are succeeded by the re-established fruiting shrub layer [29]. Likewise, predators will shift habitat use tracking of their prey more tightly immediately following the fire with diminished habitat coupling as succession proceeds.

2. Materials and Methods

2.1. Study Site

The Altona Flat Rock (hereafter referred to as the Flat Rock) is a ~2000 ha sandstone pavement pine barrens (Figure 1a), located in Clinton County, New York. The Flat Rock is characterized by extremely shallow and infertile soils underlain by prostrate, and often exposed, Potsdam Sandstone [30]. Mean annual precipitation at the Flat Rock is ~80 cm with mean monthly air temperatures ranging from −11 °C in January to 20 °C in July. However, summer temperatures in exposed bedrock areas may be as much as 16 °C higher than in surrounding areas, and commonly exceed 38 °C [30].

The Flat Rock pine barrens is considered a globally rare ecosystem and is classified by the New York Natural Heritage Program as a S1G2 site (<5 sites statewide, 6–20 sites globally, ref. [31]). The Flat Rock is dominated by jack pine (*Pinus banksiana*, Lambert), a shade-intolerant boreal species that is near its southern range margin at this location [30]. In wetter areas and scattered pockets, red maple (*Acer rubrum*, Linnaeus), gray birch (*Betula populifolia*, Marshall), northern red oak (*Quercus rubra*, Linnaeus), and eastern white pine (*Pinus strobus*, Linnaeus) are also present. Density of the overstory averages ~2000 trees per hectare resulting in an open forest environment (Figure 2a). The understory is dominated by ericaceous shrubs including lowbush blueberry (*Vaccinium angustifolium*, Aiton) and black huckleberry (*Gaylussacia baccata*, Koch) that form a dense mat over much of the barrens (Figure 2a). Other understory species include sweetfern (*Comptonia peregrine*, Coulter), sheep laurel (*Kalmia angustifolia*, Linnaeus), bracken fern (*Pteridium aquilinum*, Kuhn), rock harlequin (*Corydalis sempervirens*, Linnaeus), bristly sarsaparilla (*Aralia hispida*, Ventenant), reindeer lichen (*Cladonia rangidernia*, Weber), and haircap moss (*Polytrichum commune*, Hedwig).

On 12 July 2018, a wildfire started at the Flat Rock pine barrens. Within six days, the fire was contained, having burned 225 ha of the pine barrens (Figure 1b). Much of the area within the fire perimeter was left devoid of understory vegetation, with standing dead jack pine, contrasting sharply with the live canopy and dense understory present outside of the fire perimeter (Figure 2).

2.2. Study Design and Data Collection

We selected two camera sites within the disturbed condition and two sites in the undisturbed reference condition (Figure 1b). Sites were selected from an established network of 20 m² forest monitoring plots (unpublished data), to minimize non-disturbance-related landscape variability that might affect wildlife usage, while also facilitating monitoring accessibility. All sites were selected to be on level ground, at similar elevations (~243 m), and have similar forest types. Based on pre-disturbance characteristics, all four sites had a jack pine overstory (average of 3800 stems/ha) and a blueberry-dominated understory (on average 50% relative abundance of ground cover). Additionally, the jack pine at all four sites were the same age, having regenerated following a wildfire in 1958, and had the same size class distribution (average diameter at breast height = 7.5 cm).

Further, we selected the two disturbance sites based on their relatively central position within the disturbed area (Figure 1b), and their position in regard to how fire severity differed across the disturbed area (Figure 1c). We categorized fire severity across the disturbed area using a five-point scale adopted from Keeley [32]. We found that severity varied greatly within the fire perimeter at relatively fine spatial scales, dictated by landscape heterogeneity that may have created small-scale wildlife refugia in the wetland areas and small pockets of hardwoods that evaded the fire (green areas within fire perimeter shown in Figure 1b). Sites were selected to capture this variability to the best extent possible, given camera and accessibility limitations. Finally, reference sites were positioned 200 m from the disturbance edge so as not to confound wildlife usage differences with other changes in forest structure or habitat type. Specifically, we did not want the reference sites

to be near an edge of the pine barrens (hardwood forest adjacent), in a different aged, or management history, jack pine forest, or at a significantly different elevation.

In September 2018, two game cameras (Bushnell Trophy Cam HD, Model 119874, Bushnell Inc., Overland Park, KS, USA) were deployed at each of the two reference and two disturbed sites (total number of cameras = 8). At each site, game cameras were erected at ~0.5 m from the base of trees to ensure capture of both small and large wildlife species in the field of view [33]. Images were set to capture every 10 s and ran continuously, ensuring capture of diurnal, crepuscular, and nocturnal wildlife activity. Game cameras were checked twice per season and images were downloaded for analysis over the course of two years (September 2018–September 2020, inclusive). Game cameras were selected as an economical and non-invasive method of capturing a wide array of wildlife species [33].
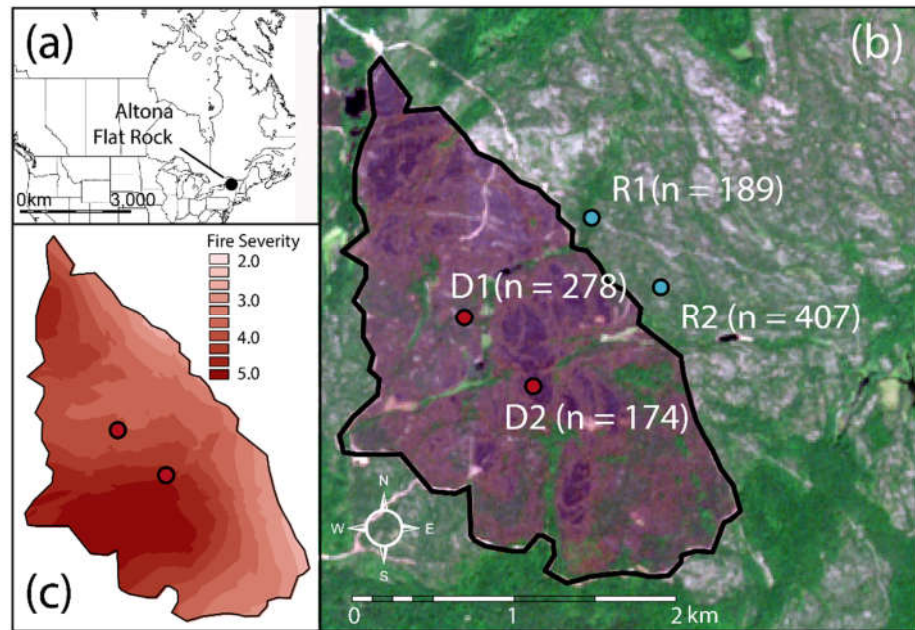

Figure 1. Map of study area showing (**a**) the regional location of the Altona Flat Rock in northern New York; (**b**) satellite image of the Altona Flat Rock centered on the 2018 fire (outlined in black). Camera locations are represented with red points within the disturbed area (sites D1 and D2) and blue points at the reference sites, located 200 m beyond the fire perimeter (sites R1 and R2). Total number of wildlife occurrences over the study duration is given in parentheses for each site; and (**c**) kriged surface [34] of fire severity based on a five-point scale, with 1 being unburned and 5 severely burned [32]. Kriging is interpolated from a network of 40 plots arrayed across the disturbed area.
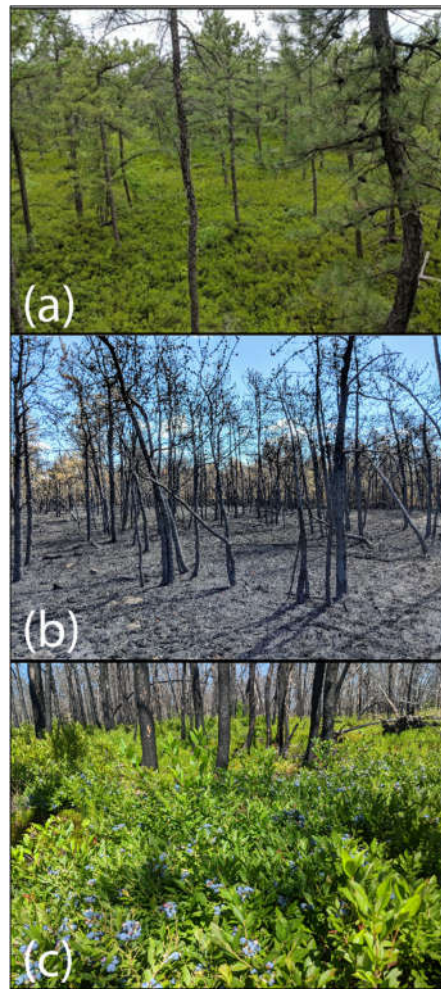
Figure 2. Representative photos of Altona Flat Rock pine barrens (**a**) outside of 2018 wildfire perimeter (reference condition summer 2018), (**b**) inside perimeter of 2018 wildfire (disturbed condition summer 2018), and (**c**) inside perimeter of 2018 wildfire 2 years after the disturbance. Both (**a**) and (**b**) photos were taken in August 2018—within one month following the wildfire. Photo (**c**) was taken in August 2020.

2.3. Data Analysis

To assess wildlife usage in the disturbed versus reference forest, image captures were sorted and analyzed using the camTrapR package in R [35]. To ensure temporal independence between images of the same species on the same camera, we used a minimum delta time of 5 min. [33,35]. While some studies have used times of up to 1 hour to avoid double-counting deer that linger at a camera site [36], other studies have found that shorter time periods are suitable, especially for smaller mammals [33,37]. We processed camera data using delta values ranging from 5 to 60 min. to assess how this affected species counts. We found that deer counts were minimally affected by the shorted delta time (<10% change in occurrences over the entire study timeframe), and that upon inspection of specific photos, many of these potential double-counts were actually due to groups of deer progressing past the camera in single-file. Further, increased deer occurrences at shorter delta times were temporally spread out across the study timeframe and spatially spread out across sites, meaning that at most, we overcounted deer by <2 individuals per season, per forest condition. Finally, we found that longer delta times reduced smaller mammal occurrences (i.e., hare) potentially artificially, as we could not confirm individual identities. Based on this analysis, we determined that the 5-min. interval adequately captured

all wildlife species, while not having a meaningful impact of double-counting larger, lingering animals. All subsequent analysis used these processed data.

To determine overall habitat usage, we calculated the number of individual occurrences per day for all observed wildlife species in both the disturbed and reference sites over the full course of the study (fall 2018 to summer 2020 inclusive = 730 days). Occurrences from all four cameras in each of the forest conditions (2 cameras per site, 2 sites per condition) were pooled for this and all subsequent analyses. Further, we calculated occurrences per day by season over the study period for white-tailed deer, snowshoe hare (*Lepus americanus*, Erxleben), and predators (combined totals of coyote, bobcat (*Lynx rufus*, Schreber), fisher, and red fox (*Vulpes vulpes*, Linnaeus)). We used a chi-square test to determine if occurrences differed between the forest conditions based on the assumption that if no habitat selection was occurring, expected proportions would be equal in the two conditions. Finally, to explore the major predator–prey relationships, we used the activity kernel density estimation tool in camTrapR [35] to examine diel activity patterns in deer, hare, and coyote. We analyzed diel activity patterns for these three species and calculated the percent overlap between deer and coyote, and hare and coyote seasonally in both the disturbed and reference forests.

3. Results

Over the entire course of the study (21 September 2018–20 September 2020 = 730 days), we cataloged a total of 1048 unique wildlife occurrences (Tables 1 and A1, Figures 3 and A1). Overall, there were over 100 more occurrences in the reference condition (57% of all occurrences) compared to the disturbed condition; overall species richness was equal; and similarity was relatively high between conditions (Table 1). Of the 23 species catalogued across the two forest conditions over the course of the study, 19 occurred in both conditions, with 8 species occurring in only one of the conditions, being predominantly avifauna (raptors and songbirds, Figure 3, Table A1). The one exception to this was the gray squirrel (*Sciurus carolinensis*, Gmelin) which was only catalogued in the reference condition. All of the species that occurred in only one forest condition were rare ($n \leq 2$) over the study duration (Figure 2, Table A1). Even though richness was equal, diversity was higher in the disturbed condition due to the greater evenness of the most common species (i.e., deer, hare, and coyote), with deer comprising almost 50% of total occurrences in the reference condition, but only 36% in the disturbed condition (Figure 3, Table A1).

Table 1. Summary of total wildlife observations (*n*) over the entire study period. Between site averages, and standard deviations in parentheses, are given for occurrences, richness, and diversity for the disturbed and reference conditions. Average similarity between the disturbed and reference conditions are also reported.

Condition	*n*	Occurrences	Richness	Diversity [1]	Similarity [2]
Disturbed (burned)	452	226 (±73.54)	14 (±1.41)	5.56 (±0.48)	0.66 (±0.14)
Reference (unburned)	596	298 (±154.15)	14 (±5.66)	4.41 (±1.21)	/

[1] Diversity is calculated as the transformed Shannon–Weiner Diversity Index ($e^{H'}$). [2] Similarity is calculated as 1—the Bray–Curtis Dissimilarity Index.
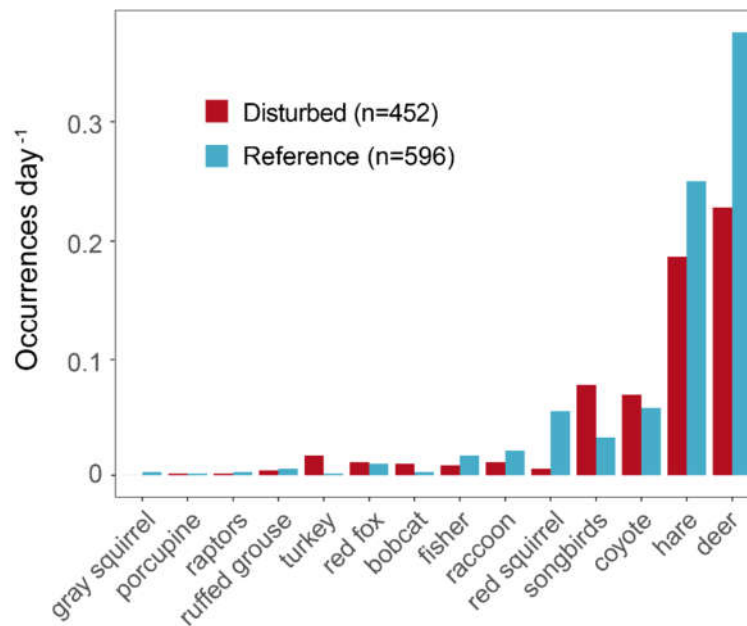
Figure 3. Species-specific wildlife occurrences per day in both disturbed and reference conditions from fall 2018 to summer 2020. The raptors category includes Cooper's (*Accipiter cooperii*, Bonaparte), red-tailed (*Buteo jamaicensis*, Gmelin), and sharp-shinned hawks (*Accipiter striatus*, Vieillet). The songbird category includes hermit thrush (*Catharus guttatus*, Pallus), northern flicker (*Colaptes auratus*, Linnaeus), dark-eyed junco (*Junco hyemalis*, Linnaeus), cedar waxwing (*Bombycilla cedrorum*, Vieillet), eastern phoebe (Say*ornis phoebe*, Latham), American robin (*Turdus migratorius*, Linnaeus), blue jay (*Cyanocitta cristata*, Linnaeus), and American crow (*Corvus brachyrhynchos*, Brehm). Refer to Table A1 for species-specific abundance in these categories.

When considered in terms of time since disturbance, total wildlife occurrences were much higher in the reference condition immediately following the wildfire in fall and winter of 2018–2019 (Figure 4a). However, by spring 2019, occurrences became similar between the two conditions (Figure 4a). Notable discrepancies to similarity between conditions were in winter and spring 2020, when the reference and disturbed conditions each had significantly higher occurrence rates, respectively, than the other condition (Figure 4a).

Differences in overall wildlife occurrences between the two conditions were primarily driven by deer and hare dynamics (Figure 4b,c). Deer occurrences were initially much lower in the disturbed condition following the wildfire; however, occurrence rates became similar by winter 2019 and generally remained so until winter 2020, when deer were much more abundant in the reference condition (Figure 4b). The other notable difference in deer occurrence rate was during summer 2020—the only season, over the course of the study, where deer occurred more frequently in the disturbed condition (Figure 4b).

Hare occurrences were at their lowest level, across both forest conditions, in fall 2018 immediately following the disturbance. However, by winter 2019, hare occurrences in the reference condition were at their highest, and the difference between the conditions was at its greatest (Figure 4c). Following winter 2019, occurrence rates became similar with the one exception of spring 2020, when occurrences were significantly higher in the disturbed condition (Figure 4c).
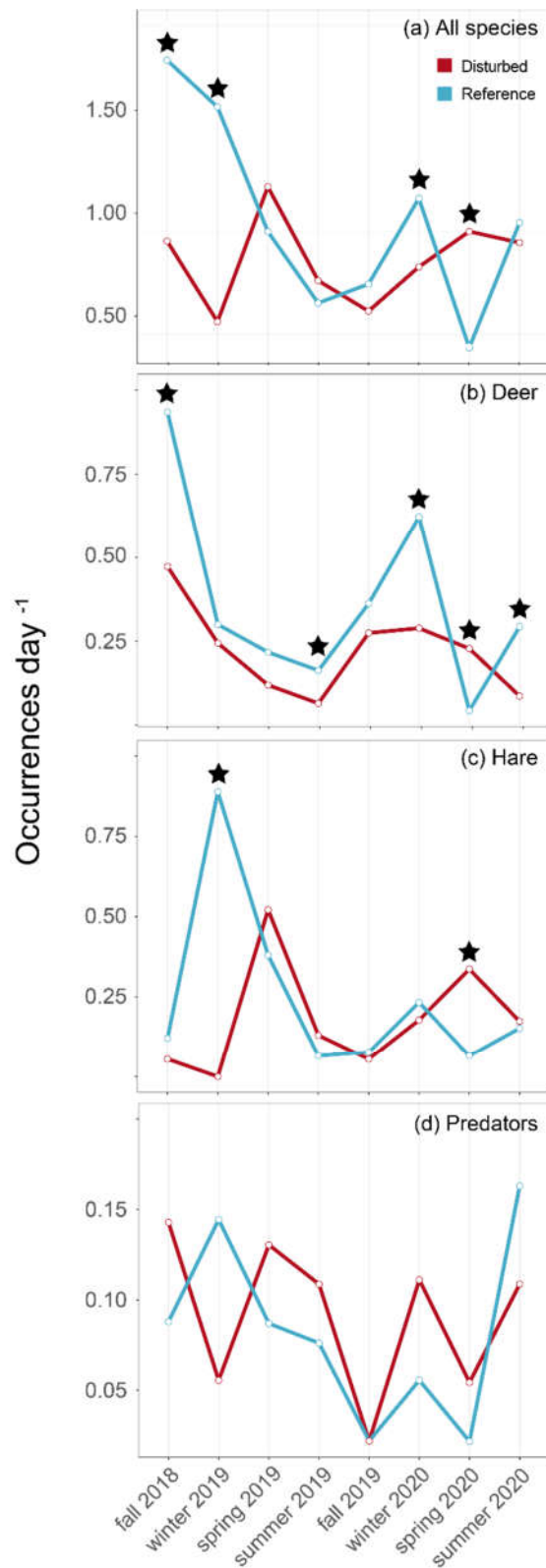
Figure 4. Occurrences per day for (**a**) all species, (**b**) deer, (**c**) hare, and (**d**) all predators combined (coyote, bobcat, fisher and red fox) from fall 2018 to summer 2020 for the reference and disturbed forest conditions. Stars indicate a significant difference ($p \le 0.05$) between forest conditions based on chi-square tests. Note scale differences on y-axes.

Predator occurrences showed no significant differences, based on the chi-square test results, between the conditions at any point over the course of the study. However, predators were generally higher in the disturbed condition (Figure 4d). Interestingly, this is the case even when prey species (deer and hare) are more abundant in the reference condition (e.g., winter 2020) or similar between the two conditions (e.g., spring and summer 2019). Two notable exceptions to this are in winter 2019 and summer 2020, when predators occurred more often in the reference condition. Fall 2019 is also notable in that there were very low numbers of predators recorded in either of the forest conditions (Figure 4d).

Overall, daily activity patterns for deer and hare did not differ greatly between seasons and forest condition (Figure 5). Deer were generally more active during daylight hours (between 6:00 and 18:00). In several cases, deer activity was bimodal, with activity being greatest in early morning (~6:00) and early evening (~18:00) (e.g., fall 2018 reference condition), while in other cases, activity remained relatively high throughout the day (e.g., fall 2018 disturbed condition) (Figure 5). In contrast, hare were more active during nighttime hours (18:00–6:00) and activity patterns remained distinctly constant across seasons and forest condition for the duration of the study (Figure 5). Following the wildfire, coyote activity initially tracked hare activity patterns in the reference condition, where hare were much more prevalent (Figure 4). However, as hare occurrences increased in the disturbed condition (spring 2019 onward, Figure 4), coyote activity followed suit, with overlap first increasing and then becoming similar to the reference condition by fall 2019 (Figure 6). Throughout the study, coyote tracked deer to a greater degree in the reference condition compared to the disturbed condition, with the one notable exception being in spring 2020, when both deer and hare occurrences in the disturbed condition were high, and reflected coyote behavior (Figures 4–6). Interestingly, coyote overlap with deer in the reference condition is notably higher than any of the other overlap combinations in three seasons (fall 2019, and winter and summer 2020, Figure 6).
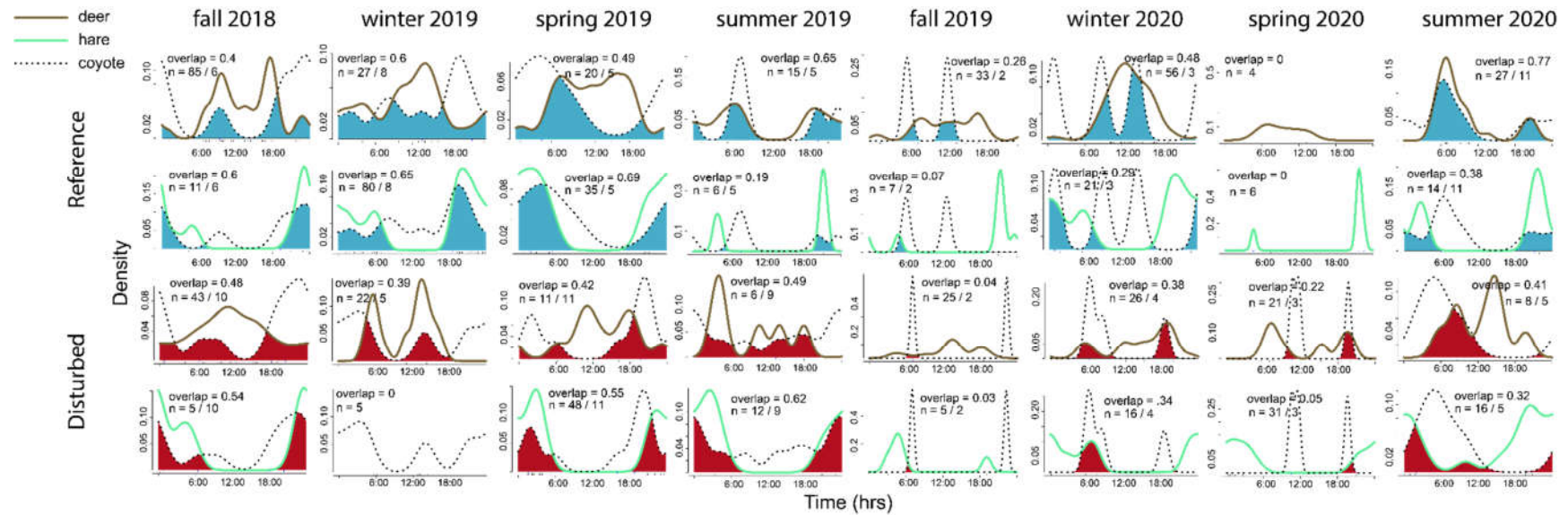
Figure 5. Seasonal daily activity plots for deer (solid brown line), hare (solid green line), and coyote (dashed black line) in the reference and disturbed forest conditions from fall 2018 to summer 2020. Activity overlap between deer and coyote or hare and coyote is shown by the shaded areas in each plot and as a percentage value. The number of individuals (*n*) is given in each plot with the first value being either deer or hare and the second coyote. Note differences in scale on y-axes.
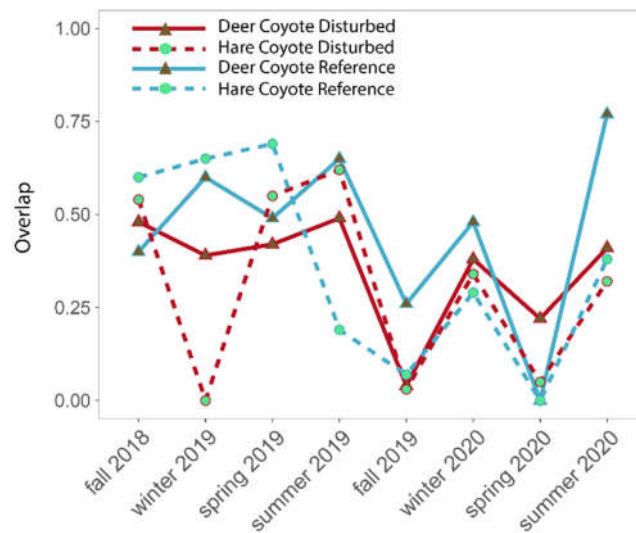
Figure 6. Summary of activity between deer and coyote and hare and coyote seasonally from fall 2018 to summer 2020 for the reference and disturbed forest conditions. Values correspond to overlap percentages in Figure 5.

4. Discussion

4.1. Herbivore Habitat Use

Herbivore habitat use varied by species and over time at the Flat Rock barrens, largely associated with understory structure. We found that both deer and hare strongly favored the reference condition in the immediate wildfire aftermath. Numerous studies have documented hare avoidance of recently burned habitat [18,38–40]. In our study, this avoidance of the disturbed condition was most evident during the first winter following the wildfire, when occurrences were almost exclusively in the reference condition; this likely reflected their reliance on understory shrubs for food, predator concealment, and thermal benefits [16]. However, following that first winter, hare began using the disturbed and reference condition habitat equally over the course of 2019, and were found in the disturbed condition more often in the spring of 2020—the beginning of the second growing season following the wildfire.

Other studies have found that hare will return to burned areas 1–6 years following disturbance in scrub oak (*Quercus ilicifolia*, Wangenheim) and pitch pine (*Pinus rigida*, Miller) barrens [18], and in two summers post-fire in a boreal upland forest site [41]. In all cases, it has been found that avoidance is largely based on the lack of understory vegetation as concealment against predators [18,40,42]. Sievert and Keith [42] reported that 87% of hare mortality is attributed to predation, such that much of their habitat selection must weigh the risk of foraging and predation pressure. Wolfe et al. [38] noted that hare select habitat with a shrub layer taller than 1 m [38]. At the Flat Rock, the ericaceous understory rarely, if ever, reaches that height, but does provide a dense continuous 'mat' of cover that had almost completely regrown to reference-like conditions by spring 2020. This relatively quick recovery of the understory, along with microhabitat heterogeneity resulting from varied fire severity across the disturbed area, may have hastened the hare's return to the disturbed condition even sooner than other studies have found [16]. Further, Litvaitis et al. [39] found that understory diversity is not as critical compared to structural complexity, making the Flat Rock understory an ideal hare habitat, even at this early successional stage.

Similar to the hare, and other studies [43,44], we found that deer were far more prevalent in the reference condition than the disturbed condition immediately following the wildfire. However, deer, again similar to the hare, returned quickly to using the disturbed condition habitat in relatively equal proportions to the reference condition by spring 2019. Deer are commonly associated with early successional habitat [45] and their use of mid-

successional stages is expected to increase until light limitations due to canopy closure reduces understory browse [46]. Further, deer may be responding to increased plant quality, palatability and fruit production, coupled with lower chemical defense production, following a fire [19,20,47]. Lowbush blueberry, the dominant understory species at the site, may respond to burning with increased fruiting, but this response has been shown to be highly variable due to differences in fire severity and ash nutrient loads [48].

While deer occurrences generally became more similar between the disturbed and reference conditions from spring 2019 onwards, there were notable differences from the hare behavior in that deer occurrences remained slightly higher in the reference condition throughout the study. Lyon and Jensen [49] noted a tradeoff between available browse and hiding cover, and Cherry et al. [20] showed that maternal deer shift their habitat use patterns, favoring hiding cover to conceal calves at the expense of higher quality browse. In an open-canopy forest, such as the Flat Rock, lack of concealment cover may always be an issue, but becomes heightened following the disturbance until the understory at least partially obstructs sightlines. While this may be especially important during parturition in late May–early June, it does not explain the higher use of the reference condition during other seasons. It may, however, indicate that concealment in the reference condition was no longer a significant issue by spring 2020, the one season during the study when deer occurred more frequently in the disturbed condition than the reference. There is also evidence that reduction in browse height may benefit herbivores by increasing sightlines and enhancing their ability to respond to predators—but this depends upon the type of predator (e.g., sit and wait/ambush vs. cursorial). Both deer and hare antipredator tactics versus cursorial predators (coyote, foxes) involve hiding and crypsis [50], making understory reduction detrimental for these species.

4.2. Predator–Prey Relationships

Studies of coyote response to wildfire are few; however, Oehler and Litvaitis [51] suggest canids would generally respond positively to wildfire disturbance, as they do to habitat fragmentation. In our study, coyotes occurred more often in the disturbed condition immediately following the wildfire, perhaps due to increased sightlines and openness [16] or increases in alternative prey such as rodents. However, after the initially high use of the disturbed condition following the wildfire, coyotes shifted to using the reference condition in the winter of 2019, most likely due to the paucity of prey in the disturbed condition regardless of any benefits the lack of understory might convey [52]. Shifts back to use of the disturbed condition in spring 2019 and winter/spring 2020 could be explained by efforts to be less constrained by snow, although by 2020, the understory was almost completely regrown and it appears likely that habitat use is overall more tightly linked to prey availability rather than habitat characteristics, similar to what Ballard et al. [11] found to be the case with wolves. Overall, coyotes had higher activity overlap in the reference condition throughout the study. However, they notably tracked deer in the disturbed condition during the spring of 2020, and had considerably higher, or equal overlap with both hare and deer in the disturbed condition at other time periods as well. This may be due to their ability to shift foraging strategy from being visually based (their dominant sense) during the day to auditory and/or olfactory sense-based at night [53]. This shift might afford these predators greater access to more spatially complex hunting habitat [53] in the open disturbed condition where longer sightlines may favor daytime hunting, while the reference condition would be favored for nocturnal hunting. Again however, the almost complete regrowth of the Flat Rock understory by the second growing season confounds this explanation and strengthens our position that coyotes are responding almost entirely to prey availability in their habitat selection and not any inherent habitat qualities themselves.

Diel activity for herbivores did not vary dramatically across year or season. Hare activity was largely nocturnal (18:00–6:00) and activity patterns persisted over time since disturbance, season, and across forest condition, which supports the findings of other studies in Montana [54]. Feierbend and Kielland [55] noted that Alaskan snowshoe hares

were most active between 18:00 and 8:00 and their nocturnal movements were 4–7 times greater than at mid-day. However, these researchers also noted that hare activity is more variable in heterogeneous landscapes, a result we did not find at the Flat Rock. Further, other studies have shown that hare activity was restricted to night during the more stressful winter season, but was more crepuscular during other seasons [56], also a result that our data do not support.

Coyote activity was primarily nocturnal from fall 2018 through spring 2019 and had the highest overlap with hare in the reference condition, but behavior became more crepuscular and had higher overlap with deer in subsequent seasons. Interestingly, however, is that in summer 2020, when hare abundance was low in both forest conditions, we observed coyote occurrences shift to favor the reference condition where deer were more commonly observed and potentially timed with parturition. Similar to our findings, Hidgon et al. [57] noted that adult deer, regardless of gender, were crepuscular whereas family groups with fawns were more diurnally active during parturition and the sensitive summer lactation period [57]. Crawford et al. [58] noted that predator presence during parturition often shifted deer towards diurnal activity to avoid nocturnal coyote. As deer fawns age, we can expect there to be a shift in activity that develops as they become more aware of their surroundings and large enough to escape predators [58,59]. While this might explain coyote behavior in late spring and summer, our data are not robust enough (i.e., not enough occurrences at finer timescales) to assess this properly.

5. Conclusions

We found that wildlife species' habitat use was strongly impacted by the wildfire; however, this effect did not last as long as has been reported in other studies [16]. Our results indicate that species returned to the disturbed condition as early as the first growing season following the wildfire. This result points to the uniqueness of the Flat Rock pine barrens ecosystem, where later successional stages of mature jack pine form a relatively open canopy over a dense understory of ericaceous shrubs. As such, the later successional forest architecture does not differ structurally from the early successional stages immediately following the wildfire, where standing dead trees still formed a quasi-canopy and the shrub layer almost completely regrew in the first two growing seasons. Similar to the findings of Monamy and Fox [60], this appears to have led to species, who in other systems would otherwise not repopulate disturbed areas for up to 10 years (during the initiation stage), instead returning much sooner temporally but at a similar time in terms of successional/ecological stage.

While our study demonstrates this result for common mammals in the region (i.e., deer, hare, and coyotes), our game-camera approach does not allow us to draw strong conclusions for other mammal and bird species—many of whom may be more strongly affected by structural changes in living versus dead standing trees as nesting habitat and forage availability than the larger mammals we observed. For instance, granivores have been found to respond positively immediately following wildfire due to increased seed supply, while other groups such as folivores and omnivores do not appear until much later in the successional pathway [16,61].

An important component of this, and other studies, on wildlife response to disturbance is that changes in successional stage and forest structure, and subsequent wildlife usage, continue to unfold over the course of multiple decades [28]. Further complicating predictions is that climate change, coupled with changes to historic disturbance regimes, may lead to phenological mismatches in species' life-history traits, resulting in novel plant and animal communities, successional pathways, and ecosystem functioning [62]. The Flat Rock, located at the southern extent of jack pine's range, may be particularly susceptible to changes in climate and disturbance regime [63,64], making continued long-term study of this, and other ecosystems, paramount for wildlife and forest management. We plan on continuing monitoring wildlife usage over the ensuing decades as forest structure

continues to change. Further, we plan on expanding our camera array to more fully capture the landscape heterogeneity of the pine barrens and surrounding areas. Camera locations based on specific habitat conditions, replicated across the study area, are necessary to fully understand wildlife usage.

Appendix A

Table A1. Species raw count occurrences for the reference and disturbed conditions.

Species	Scientific Name	Reference	Disturbed
American crow	*Corvus brachyrhynchos*, Brehm	1	5
American robin	*Turdus migratorius*, Linnaeus	11	43
Blue jay	*Cyanocitta cristata*, Linnaeus	1	0
Bobcat	*Lynx rufus*, Schreber	2	7
Cedar waxwing	*Bombycilla cedrorum*, Vieillet	0	1
Cooper's hawk	*Accipiter cooperii*, Bonaparte	1	0
Eastern coyote	*Canis latrans*, Say	41	49
Eastern phoebe	*Sayornis phoebe*, Latham	0	1
Eastern turkey	*Meleagris gallopavo*, Linnaeus	1	12
Fisher	*Pekania pennanti*, Erxleben	12	6
Gray squirrel	*Sciurus carolinensis*, Gmelin	2	0
Hermit thrush	*Catharus guttatus*, Pallas	5	1
Dark-eyed junco	*Junco hyemalis*, Linnaeus	0	1
Northern flicker	*Colaptes auratus*, Linnaeus	1	3
Porcupine	*Erethizon dorsatum*, Linnaeus	1	1
Raccoon	*Procyon lotor*, Linnaeus	15	8
Red fox	*Vulpes vulpes*, Linnaeus	7	8
Red squirrel	*Sciurus vulgaris*, Linnaeus	39	4
Red-tailed hawk	*Buteo jamaicensis*, Gmelin	0	1
Ruffed grouse	*Bonasa umbellus*, Linnaeus	4	3
Sharp-shinned hawk	*Accipiter striatus*, Vieillot	1	0
Snowshoe hare	*Lepus americanus*, Erxleben	180	134
White-tailed deer	*Odocoileus virginianus*, Zimmermann	271	164

Appendix B
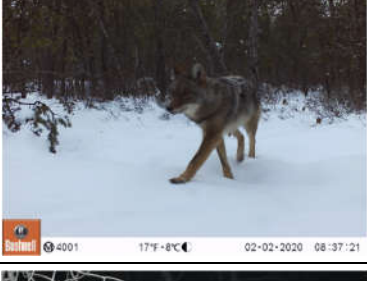
Species	Reference	Disturbed
White-tailed deer *Odocoileus virginianus*, Zimmermann		
Coyote *Canis latrans*, Say		
Snowshoe hare *Lepus americanus*, Erxleben		

Red fox *Vulpes vulpes*, Linnaeus		
Bobcat *Lynx rufus*, Schreber		
Fisher *Pekania pennanti*, Erxleben		
Raccoon *Procyon lotor*, Linnaeus		
Turkey *Meleagris gallopavo*, Linnaeus		

Figure A1. Representative game camera photos from the reference and disturbed conditions.

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