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Contrasting effects of urbanization and fire on understory plant communities in the natural and wildland–urban interface

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Abstract

As human populations expand and land-use change intensifies, terrestrial ecosystems experience concurrent disturbances (e.g., urbanization and fire) that may interact and compound their effects on biodiversity. In the urbanizing landscapes of the southern Appalachian region of the United States of America (US), fires in mesic forests have become more frequent in recent years. However, 80 years of forest management practices aimed at fire suppression in this region may have decreased landscape resistance or resilience to high-severity fires. At the same time, housing development is rapidly expanding in the wildland–urban interface, creating opportunities to examine the combined effects of urbanization and fire disturbances on plant communities when fires occur. Here, we investigated how understory plant communities were affected by a fire that varied in severity at sites in Gatlinburg, TN, and in the adjacent Great Smoky Mountains National Park. Our goal was to investigate the individual and combined effects of fire and urbanization on plant community composition in the second growing season after a fire. Overall, we found a significant interaction effect of fire severity and urbanization on total plant abundance and richness, such that increasing fire severity was associated with lower abundance and richness in natural areas but higher abundance and richness in exurban areas. Shannon diversity was significantly affected by fire severity and urbanization, but not interactively. Plant composition was affected by fire severity, urbanization, and their interaction effects. Understory plant communities in exurban locations (low-density residential areas near protected lands) were resilient following the pulse disturbance event (fire), likely because of their consistent exposure to a press disturbance (urbanization). Our study indicates a press disturbance may change the way a subsequent pulse disturbance affects plant communities. Our findings contribute new insights into how disturbances can interact to alter patterns of biodiversity in the southeastern US.

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KEYWORDS
Appalachian region, compounded disturbances, eastern deciduous forest, fire ecology, resilience, resistance, Smoky Mountains

INTRODUCTION

The spatial and temporal heterogeneity of biodiversity on a landscape is often influenced by anthropogenic disturbances that drive the function and succession of ecosystems (Chang & Turner, 2019; Danneyrolles et al., 2019; Turner, 2010), as well as population and community assemblages and ecological processes postdisturbance (Dale et al., 2002; Hillebrand & Kunze, 2020). Humans have promoted heterogeneity intentionally and unintentionally through press and pulse disturbance practices, such as land-use change and human-caused fire (Turner, 2010), often at the same time (i.e., compounded disturbances; Paine et al., 1998).

Pulse disturbances (e.g., storms, droughts, floods, pest outbreaks, and fires) are stochastic events that alter the composition and biomass of ecological communities (Hillebrand & Kunze, 2020; Jentsch & White, 2019). On the other hand, press disturbances persist temporally and are chronic within an ecosystem (Collins et al., 2011). Ecosystems may experience various environmental press events (e.g., eutrophication and nitrogen deposition), including those exacerbated by global change due to human activity (e.g., sea-level rise and mean temperature increase; Collins et al., 2011). Over time, press and pulse events, individually and combined, change community composition and its relationships to ecosystem functioning (Collins et al., 2011; Smith et al., 2009).

Compounded disturbances may produce an increased (i.e., synergistic) change on the landscape compared to the sum of the individual effects of each disturbance, depending on the state of an ecosystem when it was disturbed (Buma, 2015; Paine et al., 1998; Turner, 2010). If a landscape has not recovered from a prior disturbance event or if the prior disturbance is ongoing, the effects of a subsequent disturbance may be stronger (Turner, 2010). With expanding human populations, land-use change, and altered disturbance regimes, there is a growing need to understand how multiple disturbances interact (Buma, 2015; Kleinman et al., 2019; Turner, 2010). Because present disturbances may alter the resilience of forests to future disturbances (Bigler et al., 2005; Paine et al., 1998), understanding the interacting effects of co-occurring disturbances is critically important for predicting landscape-level changes and to successfully meet management goals (Kleinman et al., 2019). The severity of subsequent disturbances may be influenced by complex biotic relationships, which in turn would affect our interpretation of how compounded disturbances transform forests, especially as global pressures from human populations intensify (Tepley et al., 2018).

Fire is an ecological disturbance that is altering plant communities globally and that is expected to become more frequent and intense due to climate change (Jones et al., 2022). Human activities, combined with more frequent droughts, are likely to increase the frequency and intensity of fires across the US (Burkle et al., 2015; Davidson et al., 2012; Pederson et al., 2010). Fire can alter nutrient availability through volatilization and soil water availability through modifying hydrophobicity, among other effects (Certini, 2005), and may ultimately change native plant community composition and structure (Rieske, 2002; Thonicke et al., 2001). For example, in coniferous forests of the western US, species richness may initially increase rapidly postfire and then plateau (Romme et al., 2016), while through time (over 10 years), plant communities in areas of high-fire severity may be characterized by lower richness and diversity compared to those in other burn severities (Strand et al., 2019). Understory species may survive fire disturbances by sprouting from rhizomes or stem bases or reestablish years after fire, and the shifts in abundances of persisting species and colonizing species are gradual (Halpern, 1989). While notable forest fires have occurred frequently in the western US in the last few decades, Radeloff et al. (2018) identified the eastern US as a growing concern, particularly in areas with rapid population growth.

Human population growth increases fire risk in areas denoted as a wildland–urban interface (WUI) (Radeloff et al., 2005). In WUI areas, houses are adjacent to or overlap with wildland vegetation, a setting that complicates fire protection of urban development (Cohen, 2000; Radeloff et al., 2005; Winter & Fried, 2001) and that often facilitates fire ignition by humans (Cardille et al., 2001). Besides fires, native plant communities in the WUI are also threatened by fragmentation and introduction of non-native species (Gonzalez-Abraham et al., 2007; Radeloff et al., 2018). Radeloff et al. (2018) estimated that WUI covered approximately 9.5% of the conterminous US in 2010 and highlighted an area of rapid development centered on Gatlinburg, TN.

Disturbances associated with WUI can lead to changes in native vegetation structure and conditions that lead to a greater likelihood of future fire events (Bowman et al., 2011; Radeloff et al., 2018). The expansion of urbanized areas (such as WUI) has been

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associated with the homogenization of plant communities (Flinn et al., 2018; McKinney, 2006; Walker et al., 2009) and reduced native species richness and species dispersal (Burton & Samuelson, 2008; Freitas et al., 2020). Interactions between fire and urbanization will likely exacerbate fluctuations in plant communities through land-use changes and other anthropogenic pressures (Halofsky et al., 2020). The proximity of protected areas such as the Great Smoky Mountains National Park (GSMNP) to urbanization requires forest fire suppression; thus, studies at the WUI in this region are paramount for understanding the interaction of fire and urbanization disturbances to mitigate effects and restore natural plant communities.

A fire that began in GSMNP in November 2016 and quickly spread to the neighboring town of Gatlinburg, TN (Figure 1), created experimental conditions to investigate the coupling of fire (discrete; pulse disturbance) and urbanization (gradual; press disturbance) along a natural-WUI gradient. Using this rare experiment of varying fire severity in both natural (GSMNP) and exurban (Gatlinburg) locations, we addressed the separate and combined roles of these disturbances on the composition of understory plant communities. We tested three hypotheses: H1, total plant abundance and alpha (α) diversity are negatively affected by the compounded effect of fire and urbanization, while increasing fire severity has a positive effect; H2, the compounded effect of fire severity and urbanization changes plant community composition; and H3, fire homogenizes plant community composition within natural and exurban locations. The results of this study provide new insights into the combined effects of urbanization and fire disturbances on forest understory plant composition.

METHODS

Study area

This study took place in the GSMNP and the WUI between GSMNP and the exurban area of Gatlinburg, TN, United States. The plant communities in GSMNP are diverse, consisting of about 1600 species of flowering plants, including approximately 100 native tree species and over 100 native shrub species (Jenkins, 2007). The composition of plant communities in the GSMNP is shaped by strong variation in topography, moisture, and other environmental gradients (Kumar et al., 2015; Whittaker, 1956). Gatlinburg is an exurban community located in Sevier County, Tennessee, adjacent to GSMNP, with an estimated U.S. Census resident population of 4144 in 2018 (United States Census Bureau, 2018).

Before fire exclusion practices began in GSMNP in the 1930s, these forests experienced fire frequently, with a return interval of approximately 3–13 years (Harmon, 1982; Reilly et al., 2006), which maintained fire-resistant pine (*Pinus*) and oak (*Quercus*) species. Fire exclusion practices have homogenized forests with mesophytic tree species such as red maple (*Acer rubrum*), black gum (*Nyssa sylvatica*), eastern hemlock (*Tsuga canadensis*), and sourwood (*Oxydendrum arboreum*). These forests also have a well-developed shrub layer that includes mountain laurel (*Kalmia latifolia*) and blueberry (*Vaccinium* spp.) and huckleberry (*Gaylussacia* spp.) species. While communities in the GSMNP and surrounding areas vary greatly, in this study we focused on understory species within oak-dominated and hardwood forests (Table 1, Ecogroup).

Sampling design

We surveyed understory plant communities during the second growing season (2018) after the November 2016 fire at sites in WUI near Gatlinburg (hereafter "exurban") and in GSMNP (hereafter "natural"). Exurban sites are "low-density residential development scattered outside of suburbs and cities, and as commercial strip development along roads outside cities" (Daniels, 1999). We chose sites based on dominant forest vegetation type (available for GSMNP) and elevation to minimize the potential confounding effects of these variables (Table 1); all sites were within 300 m of a road or trail to ensure that they could be accessed safely.

We used stratified random sampling in ESRI ArcMap to select 18 sites, nine in natural locations and nine in exurban locations; within the location type, we randomly selected sites to represent fire severity categories: three no burn, three low/medium burn, and three high burn. We obtained fire severity information from a GIS map provided by the National Park Service (NPS; pixel size 30 × 30 m) and generated by the U.S. Forest Service Remote Sensing Application Center; the map contains delta normalized burn ratio (dNBR) values calculated from Landsat satellite images (spectral bands) directly after the fire in December 2016 as:

$$\text{dNBR} = \text{NBR prefire} - \text{NBR postfire},$$

where NBR is the normalized burn ratio:

$$\text{NBR} = \frac{\text{LandsatBand4} - \text{LandsatBand7}}{\text{LandsatBand4} + \text{LandsatBand7}}.$$

The dNBR scores are used to differentiate between unburned and burned areas, the latter separated into

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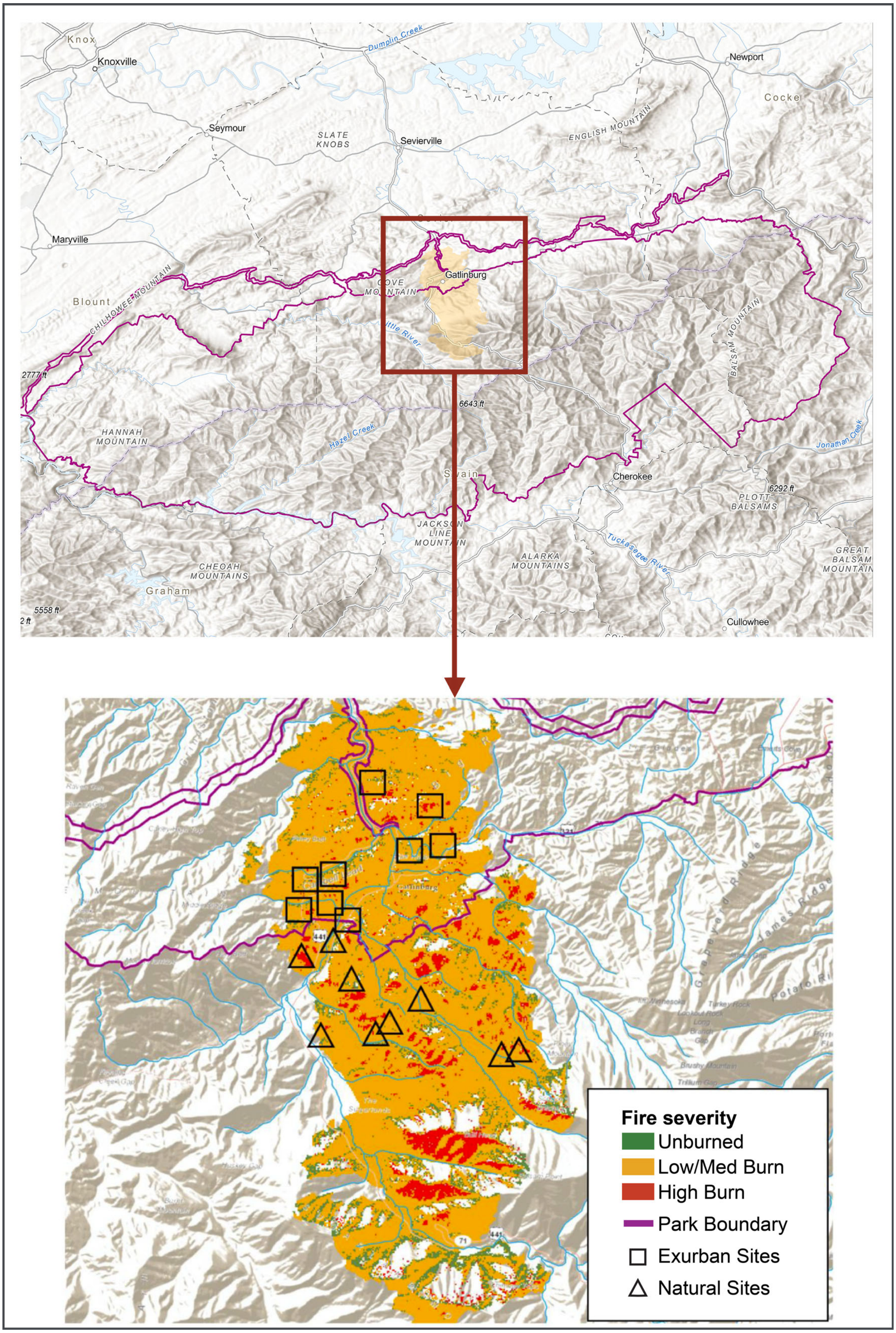

FIGURE 1 Map of 2016 fire (Chimney Tops 2) in the Great Smoky Mountains National Park and Gatlinburg, divided into fire severity categories, and the locations of understory plant community sampling sites (natural and exurban). Map of Gatlinburg, TN greater area and The Smoky Mountains National Park from: ESRI ArcGIS World Topographic Map, ESRI ArcGIS World Hillside, and National Park Service IRMA Portal. Accessed 28 January 2023.

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TABLE 1 Diveristy indices (Hill numbers) of understory plant communities and environmental characteristics for each site sampled in the Great Smoky Mountains National Park and the wildland-urban interface between the park and Gatlinburg, TN.

Location	Fire severity	Ecogroup	Elevation (m)	Diversity indices			
				Total ^0D	Avg ^0D	Avg ^1D	Avg ^2D
Natural	High burn	Chestnut oak	547.4	8	5.2	4.5	4.09
Natural	High burn	Chestnut oak	547.4	15	8	6.85	5.95
Natural	High burn	Chestnut oak	547.4	9	5.2	4.37	3.79
Natural	Low/medium burn	Chestnut oak	630	28	10.8	5.85	4.04
Natural	Low/medium burn	Montane oak–hickory	576.7	30	16.8	9.45	6.08
Natural	Low/medium burn	Chestnut oak	628.8	24	10.8	7.42	5.83
Natural	No burn	Montane oak–hickory	517.1	34	14.8	8.75	6.58
Natural	No burn	Successional hardwoods	407	25	11.2	7.94	6.3
Natural	No burn	Successional hardwoods	428.7	33	14	5.97	4.14
Exurban	High burn	Unspecified[a]	570.1	21	11	6.2	4.92
Exurban	High burn	Unspecified[a]	392.3	18	6.6	3.45	2.64
Exurban	High burn	Unspecified[a]	585	26	10.6	6.79	5.17
Exurban	Low/medium burn	Unspecified[a]	535	21	10.4	6.98	5.15
Exurban	Low/medium burn	Unspecified[a]	579	18	9.4	3.7	2.3
Exurban	Low/medium burn	Human influence	415.5	16	8.4	6.84	5.84
Exurban	No burn	Unspecified[a]	408.8	18	10.6	7.69	6.21
Exurban	No burn	Unspecified[a]	415.4	22	7.4	3.69	2.61
Exurban	No burn	Montane oak–hickory	524.2	13	7.2	4.75	3.89

Note: Total ^0D is the total number of species recorded across all five sampling occasions at a given site; Avg ^0D is the number of species averaged across the five sampling occasions at a given site; Avg ^1D is the Shannon diversity index averaged across the five sampling occasions at a given site; Avg ^2D is the Simpson diversity index averaged across the five sampling occasions at a given site. Location indicates whether the site was in Great Smoky Mountains National Park (natural) or in the adjacent wildland–urban interface (exurban); fire severity for each site is categorized as no burn, low/medium burn, and high burn; ecogroup refers to dominant forest vegetation type at each site (*Source*: National Park Service, IRMA Portal, Geospatial data for the Vegetation Mapping Inventory Project of Great Smoky Mountains National Park); elevation (in meters) was measured in the field with a GPS unit.

[a] Most exurban ecogroups were classified as unspecified because geospatial data (Vegetation Mapping Invenory Project) was not available for the sampled locations. All exurban sites were generally successional hardwood forests within proximity to commercial or residential buildings.

categories of vegetation fire severity. No-burn sites are within the footprint of the fire but did not experience fire damage directly.

We also used the normalized difference vegetation index (NDVI) derived from MODIS satellite data at 250-m resolution (Didan, 2015) to calculate, for each site, delta normalized difference vegetation index (dNDVI) of the growing season before fire, in 2016, and after fire, in 2017. We downloaded the MODIS NDVI from the United States Geological Survey (USGS) Land Processes Distributed Active Archive Center with the AppEEARS tool (AppEEARS Team, 2020). To calculate dNDVI scores, we subtracted the NDVI average of months June, July, and August 2017 (after the fire) from the NDVI average of months June, July, and August 2016 (before the fire). Resulting dNDVI scores were used in addition to dNBR burn categories to quantify fire damage to forest canopy in the first leaf-on season postfire, relative to canopy greenness in the leaf-on season before the fire. Higher dNDVI scores indicate greater change in forest canopy between the two growing seasons, thus a higher severity of fire. The purpose of using dNDVI scores was to more accurately estimate fire severity through differences in canopy cover during the leaf-on season, in contrast to NPS map of dNBR scores that estimated fire severity during the leaf-off season.

Data collection

Field data collection took place from May to September 2018. Sampling dates were set to capture seasonal differences in plant community composition (spring, summer, and fall). Annual leaf-out and first bloom data from the National Phenology Network were assessed to determine the start of the sampling season, and monthly samples were taken thereafter.

Each randomly selected site in ESRI ArcMap represented a 90 × 90 m area of a single burn severity category. In the field, from the center point of the

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90 × 90 m site located with a GPS unit, we randomly selected two 1 × 1 m permanent plots that we marked with metal pins and flags. We used a 1 × 1 m quadrat to survey and identify each individual plant in the understory to at least genus level (plant taxa richness) and to count the number of individuals for each taxon (stem count). Our plot size selection was based on the National Ecological Observatory Network protocol (NEON; Elmendorf, 2020). We surveyed the 36 plots five times in 2018 (spring: 20 April–4 May; summer: 4–6 June, 16–18 July, and 13–15 August; and fall: 14–16 September). We generated taxon lists and count of individuals per taxa by aggregating plot-level records by month. We used field guides and dichotomous keys (Chester et al., 2015; Horn & Cathcart, 2005; Petrides, 1986) to identify to genus or species all herbaceous and woody plants (vines, shrubs, and tree seedlings) within the quadrat. Unidentified plants were photographed, and specimens were collected from outside of the plots to reduce disturbance within the established long-term plots. Samples and photographs were keyed and verified with herbarium specimens at the University of Tennessee, Knoxville Herbarium (TENN Herbarium). Plants were identified to the species or genus level whenever possible. Individuals that could not be identified to at least genus level due to immature characteristics or herbivore damage were assigned observational taxonomic unit numbers (OTUs).

Data analysis

We calculated site-level α diversity for each sampling month by combining data from the two 1 × 1 m plots in a given sampling month and calculated three different diversity indices corresponding to Hill numbers of orders 0 (${}^{0}D$; taxa richness), 1 (${}^{1}D$; Shannon diversity; Shannon, 1948), and 2 (${}^{2}D$; Simpson diversity; Simpson, 1949), which represents diversity of all taxa, common taxa, and the most dominant taxa, respectively (Chao et al., 2014). Quantifying diversity using Hill numbers is advantageous because each Hill number represents “the effective number of taxa” in a community, defined as the count of equally abundant taxa, which gives the same diversity metric value as the focal assemblage (Chao et al., 2014; Jost, 2006). The Hill numbers also provide diversity metrics that vary in their sensitivity to relative taxa abundances. ${}^{0}D$, commonly known as species richness, counts the number of unique taxa regardless of their abundances, whereas ${}^{1}D$, the Shannon diversity, weighs taxa proportional to their relative abundance, and ${}^{2}D$, the Simpson diversity, weighs abundant taxa more heavily than in ${}^{1}D$ (Chao et al., 2014). We report ${}^{1}D$ (Shannon diversity) as:

$${}^{1}D = -\sum_{i=1}^{S} p_i \ln p_i,$$

where p_i is the proportion of the ith species (Shannon, 1948). We analyze and report results for ${}^{0}D$ (richness) and ${}^{1}D$ (Shannon diversity) in the text. Analyses of ${}^{2}D$ (Simpson diversity) yielded similar results to those of ${}^{1}D$; we therefore did not further analyze these results. We used the hillR R package (Li, 2018) to calculate Hill numbers.

To test H1, that total plant abundance and taxa diversity are negatively affected by the compounded effect of fire and urbanization, while increasing fire severity will have a positive effect, we fitted linear mixed models (LMMs) and generalized linear mixed models (GLMMs) that modeled site-level total plant abundance (individual stem counts summed per sampling event), taxa richness (${}^{0}D$), and Shannon diversity (${}^{1}D$) as a function of three fixed effect variables: dNDVI (quantitative measure of fire severity), location type (natural, exurban), sampling month, and their two-way interactions. Site was included as a random intercept to account for the repeated sampling of sites across seasons. Total plant abundance (TAb) and taxa richness (${}^{0}D$) are integer (count) values; therefore, we compared small-sample Akaike information criterion (AIC) scores of the full GLMMs (with three fixed predictors and their two-way interactions) fitted with Poisson, negative binomial with linear parameterization, and negative binomial with quadratic parameterization distributions to identify the most appropriate error distribution. We found that TAb was best modeled with a quadratic negative binomial distribution, whereas ${}^{0}D$ was best modeled with a Poisson distribution. For Shannon diversity (${}^{1}D$), a continuous variable, we used a Gaussian distribution and LMMs. For all response variables, we used all-subsets AIC model selection (Burnham & Anderson, 2002) implemented in the function “dredge()” in the MuMIn R package (Barton, 2009) to select the top AIC-ranked fixed effects structure for statistical inference. We used marginal effects plots implemented in the function “ggpredict()” in the ggeffects R package (Lüdecke, 2018) to graphically visualize the effect of each predicted variable on the response variable. All models were fitted using the glmmTMB package in R (R Core Team, 2022).

To examine H2 and H3 regarding plant compositional differences by fire severity and location, we aggregated data across sampling dates for each location (natural and exurban) and fire severity combination (high burn, low/medium burn, and no burn). We organized our data in site-by-taxa matrices of taxa presence–absence data (converted to Sørensen distances) and abundance data (converted to Bray–Curtis distances) for each site;

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distance matrices were generated using the "vegdist()" function of the vegan R package (Oksanen et al., 2016). Both Bray–Curtis and Sørensen distances were used to validate the results of the plant abundance data. To test H2, plant taxa composition is changed by the compounded effect of urbanization and fire, we used the "adonis 2()" function of the vegan R package (Oksanen et al., 2016) to run a nonparametric permutational analysis of variance (PERMANOVA; Anderson, 2006; McArdle & Anderson, 2001) on the Bray–Curtis and Sørensen distance matrices to investigate the relative effect of each variable (fire severity and location) and their interaction. For visual interpretation of plant community composition among sites, we constructed a two-dimensional nonmetric multidimensional scaling (NMDS) ordination on the taxa plant abundance and presence–absence matrices using the "metaMDS" function in the R package vegan (Oksanen et al., 2016). NMDS ordination was performed on both taxa abundance and presence–absence matrices to investigate whether shifts in plant community composition were driven by taxa replacements in addition to changes in taxa abundance, and not merely the latter.

To test whether fire homogenizes plant communities in natural and exurban locations (H3), we used the "betadisper()" function in the R package vegan (Oksanen et al., 2016) that compares the multivariate (i.e., plant community-based) dispersion of sites within each fire severity-by-location category. We also calculated beta diversity (β) using Whittaker's multiplicative method (Whittaker, 1960) that divides γ, the number of taxa present across all sites within each fire severity and location combination, by α, the site-level diversity of Hill order 0 (Total ^0D in Table 1), averaged across sites within each fire severity by location combination. According to our hypothesis, we expect β to decrease with fire severity in both natural and exurban locations.

RESULTS

We identified a total of 222 plant taxa in the understory at 18 sites in natural and exurban locations. Overall, the understory consisted of 89% perennial and 11% annual taxa, separated into forbs (61%), graminoids (6%), shrubs (9%), subshrubs (4%), tree saplings (12%), and vines (8%). The most abundant herbaceous taxa among all sites were *Chamerion angustifolium* (fireweed), *Hepatica* spp., *Lysimachia quadrifolia* (whorled loosestrife), *Urtica dioica* (stinging nettle), and *Packera aurea* (golden ragwort). The most abundant tree saplings were of *Acer* (maple) and *Quercus* (oak) species; see Table 2 for species with the highest maximum abundance by location and fire severity.

TABLE 2 Common understory plant taxa observed across natural and exurban locations by fire severity.

Location	Fire severity	Taxa	Abundance (stem count)
Natural	No burn	*Hepatica* spp.	100
		Packera aurea	53
		Viola spp.	32
		Panicum spp.	23
		Acer spp.	21
		Galium aparine	21
	Low/medium burn	*Lysimachia quadrifolia*	65
		Potentilla canadensis	41
		Oxydendrum arboreum	40
		Packera aurea	40
		Fagus grandifolia	23
		Euonymus americanus	16
	High burn	*Smilax* spp.	8
		Chamerion angustifolium	7
		Panicum spp.	7
		Carex spp.	5
		Kalmia latifolia	5
Exurban	No burn	*Urtica dioica*	57
		Glechoma hederacea	33
		Ailanthus altissima	29
		Amphicarpaea bracteata	21
		Galium aparine	21
		Acer spp.	18
	Low/medium burn	*Lysimachia quadrifolia*	77
		Rubus spp.	37
		Panicum spp.	30
	High burn	*Chamerion angustifolium*	113
		Lactuca spp.	46
		Packera aurea	43
		Panicum spp.	36

Note: Common taxa are those with the highest maximum abundance (stem count), representing 50% of all taxa observed per location and fire severity across all sampling months.

For natural sites, taxa richness averaged across sampling occasions was highest at no-burn sites (mean of Avg ^0D across no-burn sites $= 13.3$; Table 1), followed by low/medium-burn sites (mean of Avg $^0D = 12.8$), while

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high-burn sites had the lowest richness (mean of Avg $^{0}D = 6.1$). Similarly, Shannon diversity (^{1}D) at natural sites was lowest at high-burn sites (mean of Avg $^{1}D = 5.24$) and highest at low/medium-burn sites (mean of Avg $^{1}D = 7.57$), closely followed by no-burn sites (mean of Avg $^{1}D = 7.55$; Table 1). Within exurban sites, average richness (mean of Avg ^{0}D) was comparable among fire severity categories: 9.4 for both high-burn and low/medium-burn sites and 8.4 for no-burn sites. Average Shannon diversity (mean of Avg ^{1}D) was also comparable among fire severity categories at exurban sites: 5.37 at no-burn sites, 5.84 for low/medium-burn sites, and 5.48 at high-burn sites.

The GLMMs and LMMs found partial support for our H1: exurban sites had lower Shannon diversity (^{1}D) but not total plant abundance and richness (^{0}D) than natural sites. Fire severity decreased plant abundance and taxa richness only in natural sites; in exurban sites, increased fire severity was associated with increased total plant abundance (TAb) and richness (^{0}D), such that at sites with high-fire severity, total abundance and taxa richness were higher in exurban areas than in natural areas (Table 3; Figure 2a,b). This finding is a result of the location-by-fire severity interaction being retained in our best AIC models for total abundance and taxa richness (Table 4) and is contrary to our initial expectation because it shows that urbanization reverses (rather than compounds) the effect of fire on total abundance and richness. By contrast, Shannon diversity (^{1}D) decreased with fire severity in both exurban and natural sites; here, the lack of an interaction effect indicates that urbanization neither compounds nor reverses the effect of fire on Shannon diversity (Figure 2c and Table 4). Species richness and total abundance of species were consistently higher in natural sites with no-burn and low/medium-burn severity than in all exurban sites, regardless of fire severity (Figure 2c).

TABLE 3 Alpha (α), gamma (γ), and beta (β) diversity of understory plant communities across sites in different location-by-fire severity combinations.

		Diversity indices		
Location	Fire severity	α	γ	β
Natural	High burn	10.67	21	1.97
	Low/medium burn	27.33	57	2.09
	No burn	30.67	62	2.02
Exurban	High burn	21.67	50	2.31
	Low/medium burn	18.33	41	2.24
	No burn	17.67	48	2.72

Note: α, species richness (total ^{0}D in Table 1) averaged across the three sites in a given location-by-fire severity combination; γ, the total number of species pooled across the three sites in a given location-by-fire severity combination; β, the ratio between γ and α (i.e., $\beta = \gamma/\alpha$; Whittaker's multiplicative β, Whittaker, 1960).

Our results support H2, that the compounded effect of fire and urbanization changes plant taxa composition. PERMANOVA analyses on both taxa abundance (Figure 3) and presence–absence (Appendix S1: Figure S1) data indicated that fire severity and location (exurban and natural) drive plant composition (Table 5; Figure 3). The main effect of fire severity ($R^2 = 22.3\%$ and 24.4%; $p = 0.001$ and 0.003 for PERMANOVA on Bray–Curtis and Sørensen distances, respectively) was more important than that of location ($R^2 = 7.0\%$ and 7.5%; $p = 0.058$ and 0.062; Table 5). We also found that the location-by-fire severity interaction effect was important ($R^2 = 16.3\%$ and 13.6%; $p = 0.003$ and 0.042). The NMDS plots show natural sites clustered by fire severity category, whereas for exurban sites this clustering was less distinct (Figure 3; Appendix S1: Figure S1), which corroborates our finding of an important location by fire severity interaction effect in our above PERMANOVA analysis. These differences in clustering indicate that fire has a stronger effect on understory plant composition in natural locations than in exurban locations.

At natural sites, abundance was high for herbaceous ground-spreading and/or basal taxa (e.g., *Hepatica* spp., *Galium aparine*, *P. aurea*, *Potentilla canadensis*, and *Viola* spp.) in both the no-burn and low/medium-burn areas, whereas high-burn areas often have hardier, evergreen taxa (e.g., *Smilax* spp. and *K. latifolia*). By contrast, at exurban no-burn and low/medium-burn sites, abundance was high for non-native and weedy species (e.g., *Ailanthus altissima* and *Glechoma hederacea*) as well as fast-growing, pioneer species (e.g., *Robinia pseudoacacia*) and herbaceous flowering perennials (e.g., *L. quadrifolia* and *U. dioica*). Similar to natural high-burn sites, exurban high-burn sites often contained hardy evergreen taxa (e.g., *Pinus* spp., *Smilax* spp., and *Vaccinium pallidum*) in addition to herbaceous flowering species with extensive root systems (e.g., *C. angustifolium* and *Conyza canadensis*). See Appendix S1: Table S1 for a list of representative taxa shown in Figure 3.

Our last hypothesis that fire homogenizes plant taxa composition within natural and exurban locations (H3) received weak support. Multivariate dispersion analysis based on taxa abundance (Bray–Curtis distances) and presence–absence (Sørensen distances) found that among natural sites, high-burn sites had lower beta dispersion (i.e., more similar plant taxa composition; mean Euclidean distance between each site and the median of the group of sites = 0.28 and 0.31 based on taxa abundance and taxa presence–absence, respectively) than low/medium burn (0.41 and 0.36) and no-burn sites (0.45 and 0.34). At exurban sites, fire had a similar homogenizing effect when analyzing plant composition

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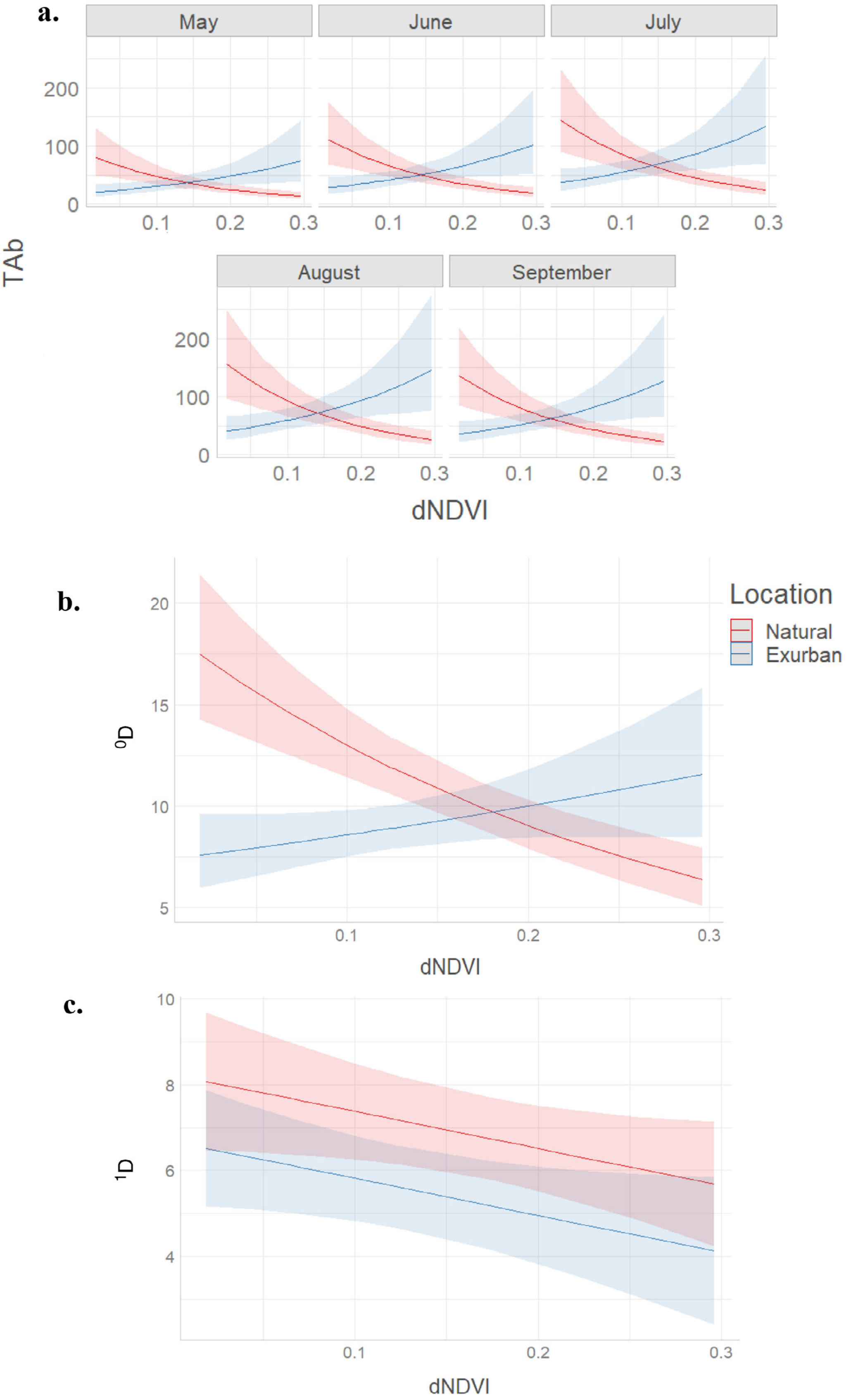

FIGURE 2 Marginal effects plots of the relationship between predictors and the response variables (a) total plant abundance (TAb), (b) taxa richness (^0D), and (c) Shannon diversity (^1D) in the top AIC models. dNDVI is the delta normalized difference vegetation index.

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TABLE 4 Coefficients and associated *p* values of the top AIC generalized linear mixed models for total plant abundance (TAb) and species richness (^{0}D) and the top linear mixed model for Shannon diversity (^{1}D).

	Model response: TAb			Model response: ^{0}D			Model response: ^{1}D		
Predictors	***b***	**SE (*b*)**	***p***	***b***	**SE (*b*)**	***p***	***b***	**SE (*b*)**	***p***
dNDVI	4.58	1.80	0.011	1.53	0.91	0.09	−8.63	4.35	0.048
Location	1.55	0.36	<0.001	0.93	0.18	<0.001	1.56	0.71	0.029
dNDVI:location	−10.98	2.22	<0.001	−5.16	1.12	<0.001			
Month									
June	0.31	0.13	0.018						
July	0.58	0.13	<0.001						
August	0.65	0.13	<0.001						
September	0.52	0.13	<0.001						

Note: Coefficient estimates (*b*), standard errors of coefficients [SE (*b*)], and associated *p* values (*p*) are shown for the predictor variables delta normalized difference vegetation index (dNDVI; a continuous metric of fire severity), location (1 for natural sites, 0 for exurban sites), month (a dummy variable for month of sampling, 1 if sampling was conducted in the listed month, 0 if not), and dNDVI:location (the interaction term between burn severity and location).

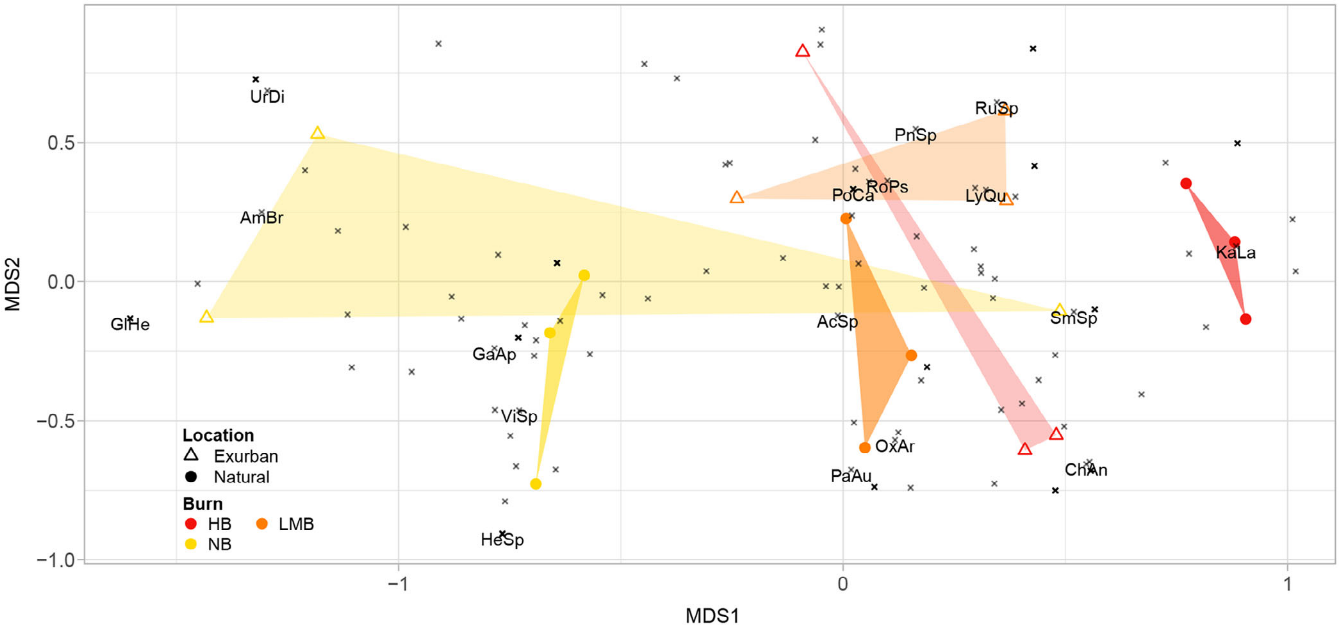

FIGURE 3 Nonmetric multidimensional scaling (MDS) ordination plots of understory plant communities using abundance-based Bray–Curtis distances. Communities are represented by color symbols and grouped by fire severity (HB, high burn; LMB, low/medium burn; NB, no burn) and location (exurban and natural). Taxa are represented by crosses; the four taxa with the highest abundance in each location by fire severity category are highlighted with four-letter codes. See Appendix S1: Table S1 for taxa abbreviations.

TABLE 5 Effects of fire and urbanization on understory plant community composition.

	Bray–Curtis distances				Sørensen distances			
Fixed effects	**SS**	***R*²**	***F***	***p***	**SS**	***R*²**	***F***	***p***
Location (exurban and natural)	0.466	0.070	1.540	0.058	0.397	0.075	1.659	0.062
Fire severity	1.489	0.223	2.458	0.001**	1.285	0.244	2.684	0.003**
Location:fire severity	1.089	0.163	1.799	0.003**	0.720	0.136	1.503	0.042*

Note: Differences in plant community composition were measured by location (natural and exurban), fire severity (high burn, low/medium burn, no burn), and their interaction. Sum of squares (SS), R^2 value, *F* value, and associated *p* values (*p*) for permutational analysis of variance (PERMANOVA) analyses based on Bray–Curtis and Sørensen distances are reported.

*$p < 0.05$.

**$p < 0.01$.

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based on taxa abundance (beta dispersion in high-burn sites = 0.43, low/medium burn = 0.46, no burn = 0.54) and composition based on taxa presence–absence (high-burn sites = 0.42, low/medium burn = 0.39, no burn = 0.52). However, despite the beta dispersion values being in the hypothesized direction, only the difference between exurban high-burn and no-burn sites based on taxa presence–absence was statistically significant (permutation $p = 0.021$). Our results on Whittaker's multiplicative β were consistent with those of the multivariate dispersion analysis: β was lower in high-burn sites (in natural sites: $\beta = 1.97$; in exurban sites: $\beta = 2.31$) than no-burn sites ($\beta = 2.02$ and 2.72 in natural and exurban sites, respectively).

DISCUSSION

In this study, we analyzed differences in understory plant communities in the second growing season after a mixed-severity fire affected both natural and exurban areas in the southern Appalachian region. Our results show that the variation in plant taxa abundance and richness across different fire severities depends on location type (natural or exurban). Among natural sites, taxa abundance and richness are lower in sites with higher fire severity, while the opposite is true for exurban sites, where taxa abundance and richness increased with increasing fire severity. It is notable that the interaction effect (location-by-fire severity) was absent from the model predicting Shannon diversity. This could indicate that changes in rare taxa with low abundance and changes in taxa abundance distribution determined the effect of fire by location in our study. Specifically, the increase in taxa richness with increasing fire severity in exurban sites was likely driven by an increase in the number of taxa with low abundance along with a decrease in community evenness (i.e., an increase in the relative abundance of the most common taxa).

Disturbance processes, especially fire, have been known to drive diversity in ecosystems (Connell, 1978; Huston, 1979, 2014; Pausas & Riberio, 2017). A study in the western US by Lentile et al. (2007) noted that plant cover was dominated by forbs after a high-severity fire and that landscape-level plant species richness declined with fire severity. This is consistent with our findings for natural sites where taxa richness declined from no burn to high-burn sites at the landscape scale (richness of taxa pooled across all sites and sampling occasions; γ in Table 3) as well as the site scale (Figure 2; α in Table 3; Table 4). Similarly, our findings agree with three studies within a review by Miller and Safford (2020), which found that plant richness peaked at low to intermediate levels of fire severity (DeSiervo et al., 2015; Morgan et al., 2015; Richter et al., 2019).

The heterogeneity established by mixed-severity fires can create conditions suitable for multiple species, thus potentially increasing landscape richness over the long term (Strand et al., 2019). In the short term, two years after the fire, greater taxa richness at high-fire severity sites compared to lower fire severity sites among our exurban locations could indicate that opportunistic and fire-adapted, early successional species are recolonizing from a historic seedbank or immigrating from a local species pool (Pearse et al., 2018). Additionally, in exurban landscapes where anthropogenic pressures are strong, biodiversity is often driven by human values, preferences, and activities (Aronson et al., 2016). Species in these areas often must pass through several filters (e.g., land-use history, microclimate, and species interactions) to establish populations and persist (Aronson et al., 2016). The frequency of disturbance in the exurban area of Gatlinburg is inherently greater than in the GSMNP; therefore, species that persist within the exurban matrix are exposed more often to disturbances. Lastly, greater taxa richness at high-fire severity locations at our exurban sites could be explained by the moderate levels of human disturbance promoting coexistence among disturbance-adapted species (McKinney, 2008).

Persistent land alteration and management can often homogenize environmental conditions and communities; thus, rare species, adapted to environmental conditions before management, become sparse or functionally eliminated after new disturbance events (MacDougall et al., 2013). Here, we found that fire and urbanization, both individually and interactively, affected plant community composition among our sampling sites, with the individual effect of fire severity being the most important driver. In addition, trends in our results (multivariate dispersion analysis and Whittaker's multiplicative β) indicate that fire weakly homogenized plant communities in both natural and exurban areas. This suggests that fire is an environmental filter that selects a small subset of plant taxa that are able to colonize new gaps created by fire.

A study by Reilly et al. (2006) proposed that life history characteristics of dominant trees and shrubs, and community resilience from fire-adapted taxa, such as pine, could explain the minimal effect of fire on β diversity and species turnover. However, fire suppression in the GSMNP has generally reduced the distribution of fire-adapted plant communities (such as pine and spruce-fir stands) to dry south- or west-facing slopes (among mesophytic hardwood species) or more extensive stands at higher elevations (Lafon et al., 2017). The prevalence of pine–oak dominated forests in the southern Appalachians that are associated with drier mid-elevation slopes and ridges can be

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attributed to past frequent fires (Harmon, 1982; Reilly et al., 2006; Whittaker, 1956).

Exurban conditions alter plant responses to other disturbances

Due to population growth and expansion, urbanized areas are more likely to experience more frequent disturbance events compared to natural landscapes (Beal-Neves et al., 2020). Exurban areas are often more frequently disturbed than natural areas because of increased habitat loss and human interaction with the environment bolstered by fragmentation (Hansen et al., 2005). In our study, exurban areas experienced greater taxa abundance and richness at sites with higher fire severities, while the converse was true in natural areas (Figure 2). The increase in plant abundance at sites with higher fire severities compared to sites with lower fire severities in exurban areas could be attributed to species with short time to reproductive age and press disturbance (i.e., urbanization) limiting competition with species more sensitive to disturbance (Kondoh, 2001; O'Connor et al., 2017). Our finding that plant community composition was more similar across the fire severity gradient in exurban sites than in natural sites represents further evidence for community persistence, and tolerance to disturbance, in exurban areas.

Taxa that were commonly observed at natural sites were: *Smilax* spp. in high-burn areas, *P. canadensis* in low/medium-burn areas, and *Hepatica* spp. in no-burn areas. Several species were found only in exurban areas: *Cardiospermum grandiflorum*, *Caulophyllum thalictroides*, *Fragaria vesca*, *Hedera helix*, *Lactuca canadensis*, *Rosa multiflora*, *Stellaria media*, *Trifolium campestre*, and *Urochloa platyphylla*. Of these species, *C. grandiflorum*, *H. helix*, *R. multiflora*, *S. media*, and *T. campestre* are considered non-native or invasive (USDA, 2023). Urban environments create pressures that often select for habitat generalists and traits that confer increased tolerance of urban environments (Borden & Flory, 2021). These selective pressures in urban areas inevitably act favorably on the many non-native species introduced to new regions and promote invader establishment (Borden & Flory, 2021). It has also been suggested that non-native and invasive species in urban areas may be more adaptable to changing conditions (i.e., climate change and related anthropogenic disturbances) compared to native species (Borden & Flory, 2021). For example, *H. helix* can form dense mats that reduce growth rates of native species, survive freezing temperatures, and regenerate well after fire.

Common plants in exurban areas were: *C. angustifolium* in high-burn locations, *Panicum* spp. in low/medium-burn locations, and *U. dioica* in no-burn locations. These species are considered hardy flowering perennials (USDA, 2023). *Chamerion angustifolium* colonizes disturbed ground and has rhizomes that persist postdisturbance; *Panicum* spp. reproduces vegetatively by rhizomes and seeds, and colonizes wooded and naturalized areas; and *U. dioica* has abundant seeds and can also spread by rhizomes, and often colonizes disturbed sites (USDA, 2023). A study by Latzel et al. (2008) suggests that a species with multiple regenerative strategies is more likely to colonize a variety of habitats and withstand persistent disturbance. The three species common in exurban areas have reproductive strategies (i.e., rhizomatic networks, high seed production, and high dispersal rates) and fast growth rates that are conducive to colonization after disturbance events (Carey, 1995; Pavek, 1992). While it is apparent in our study that high-severity fire homogenized plant communities in comparison to no-burn sites within exurban locations, more research is needed to fully understand community responses to these combined pulse and press disturbances.

Interactions of successive disturbances

Studies have shown that prior disturbance events can strongly influence the response of plant communities to successive disturbances and that low-severity press disturbances may be beneficial to increase resilience to more severe disturbances (Davies et al., 2009; Kulakowski & Veblen, 2002, 2007). However, the effects of successive disturbances on the community depend heavily on the impact of the preceding disturbance (Shinoda & Akasaka, 2020). The negative impact of a subsequent disturbance can be amplified by the negative effect of a prior disturbance (Paine et al., 1998), and increases in fuel from prior disturbances can increase fire severity (Kulakowski & Veblen, 2007). Pulse disturbance characteristics reflect ecosystem resistance and define the level of resilience of that ecosystem (Jentsch & White, 2019). In our study, the effect of fire on plant abundance and richness differed between natural and exurban areas. The significant increase in plant abundance, richness, and change in community composition as fire severity increased in exurban locations indicates a positive effect of press disturbance (urbanization) after a subsequent pulse disturbance event (fire).

Fire suppression creates homogenized, fire-intolerant plant communities

Fire-adapted species may propagate to mesic landscapes; however, community resilience is weak in the absence of

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recurrent fire, with fire-intolerant and shade-tolerant species promoting mesophication, thus leading to fire-intolerant mesophytic hardwood communities (e.g., *Fagus grandifolia*, *Liriodendron tulipifera*, and *Acer* spp.; Nowacki & Abrams, 2008). Mesophication is often initiated by intentional fire suppression or exclusion, whereby opportunistic species gradually create environmental conditions favorable for their own persistence and exclude fire-adapted species (Alexander et al., 2021). In the absence of fire, the continuous process of forest mesophication in GSMNP may suggest that the landscape has become homogenized over time (Nowacki & Abrams, 2008), despite high biodiversity overall.

In our study, plant composition was statistically different when considering fire severity and location type, as well as the interaction of the two disturbances (i.e., fire had a stronger effect on plant community composition in natural sites compared to exurban sites). This may indicate that the continuous process of mesophication (and possibly homogenization) that GSMNP has been experiencing for decades has hindered community resilience and resistance to high-severity fire. In exurban areas, higher abundance and richness across increasing fire severity could be occurring because of environmental filtering, effectively selecting for disturbance-resilient and resistant species, thus changing the community composition of the area (Pearse et al., 2018). The rate of expansion of the WUI is faster than any other land cover category (water, developed, barren, forested upland, shrubland, nonnatural woody, herbaceous upland, natural/semi-natural vegetation, herbaceous planted/cultivated, and wetlands) included in the National Land Cover Database (NLCD) (Homer et al., 2015; Radeloff et al., 2018). This expansion implies an increased risk of fire (Radeloff et al., 2018), which poses risks for humans, in addition to native plant diversity.

Limitations

Our study has two main limitations. First, prefire plant community data (abundance, richness, and diversity metrics) were not available for the postfire plots that we sampled. Because this study focused on understory plant communities, these metrics could not be estimated from remotely sensed (e.g., satellite) data collected before the fire. Our site selection followed a stratified random approach to capture three fire severities, so we could not use previously surveyed vegetation plots in GSMNP (Great Smoky Mountains National Park); additionally, no vegetation plots were established in the exurban landscape before the fire.

Second, our sample size was small: two replicate plots of two 1 × 1 m at each site location, within three fire severities across two locations, for a total of 36 plots. This was in part due to the heterogenous nature of the Chimney Tops 2 fire, which limited the availability of site locations with a 90 × 90 m homogenous burn area. This condition was necessary to meet one of the goals of this study, that of sampling from an area with homogeneous fire severity. Lack of access to many of the burned areas further complicated the fire heterogeneity issue.

Management applications and future directions

Wildfire suppression leads to ecologically significant wildfires that prove difficult to control. Management goals often attempt to achieve fire exclusion, though eliminating wildfire completely is not feasible. Within the WUI, homeowner engagement in fire-wise practices, planting native fire- and disturbance-adapted vegetation, and eliminating non-native vegetation near homes are crucial in preventing structural damage from a wildfire (Calkin et al., 2014).

Although the GSMNP and surrounding WUI have experienced mesophication for decades, management efforts should continue to aim to restore fire-dependent plant communities (e.g., pine–oak) that were common prior to extensive fire suppression efforts. This would entail creating conditions that are most conducive to implementing low-severity fires (e.g., canopy removal to increase light to understory, reduce relative humidity, and dry out fuels) in areas with low risk to the WUI (Alexander et al., 2021). Recurrent fire in these areas would ultimately restore some of the vegetation that was present prior to fire suppression efforts and further reduce large severity fire risk to the WUI.

CONCLUSIONS

Compounded disturbance ecology is a relatively understudied field that to date has focused on fire, wind, and salvage logging (Kleinman et al., 2019), with few investigations of urbanization, even though WUI areas are expanding with human population growth. Our study addresses this gap by examining the effects of a pulse fire event in conjunction with the press disturbance of urbanization on herbaceous and woody understory plant communities in the southern Appalachian region. We found a compounded effect of urbanization and fire on plant abundance and richness (^0D): increasing fire severity in natural areas decreased plant abundance and taxa richness, but it had the *opposite* effect on abundance and richness in exurban areas. Additionally, plant community composition was driven by urbanization, fire severity,

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and their interaction, with fire severity being the most important driver and particularly more so in natural locations than exurban locations. In other words, the effect of fire on plant abundance and richness, as well as community composition, depended on location. Fire was also associated with signals of plant community homogenization in both natural and exurban locations, but only one of these effects was statistically significant. Species at exurban sites may be subjected to environmental filtering from the natural pool of species and therefore may be inherently more disturbance-adapted and resilient following a subsequent pulse disturbance event (i.e., fire). The differences in plant community response due to varying degrees of disturbance will require nuanced management strategies going forward.

Future work on compounded disturbances is needed to better understand their direct effects on plant communities and possible indirect effects on consumers and ecosystem processes. In the context of prevalence and abundance of non-native species within the WUI, questions remain about their impact on fire ignitions. Finally, these questions are relevant beyond plant species to understand dynamics of species interactions and their role in regeneration and recovery of communities after mixed-severity wildfires. Ultimately, compounded pulse and press disturbances have the potential to make wholesale changes to forest ecosystems.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Hubert, 2023) are available from the Environmental Data Initiative (EDI): https://doi.org/10.6073/pasta/7b2c7d8c5b50f59e5328652e45622879.

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