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Pervasive interactions between ungulate browsers and disturbance regimes promote temperate forest herbaceous diversity

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Abstract. Disruptions to historic disturbance and herbivory regimes have altered plant assemblages in forests worldwide. An emerging consensus suggests that these disruptions often result in impoverished forest biotas. This is particularly true for eastern U.S. deciduous forests where large gaps and understory fires were once relatively common and browsers were far less abundant. Although much research has focused on how disturbance and browsers affect tree diversity, far less attention has been devoted to forest understories where the vast majority (>75%) of the vascular species reside. Here we test the hypothesis that the reintroduction of disturbances resembling historic disturbance regimes and moderate levels of ungulate browsing enhance plant diversity. We explore whether once-common disturbances and their interaction with the top-down influence of browsers can create conditions favorable for the maintenance of a rich herbaceous layer in a region recognized as a temperate biodiversity hotspot in West Virginia, USA. We tested this hypothesis via a factorial experiment whereby we manipulated canopy gaps (presence/absence) of a size typically found in old-growth stands, low-intensity understory fire (burned/unburned), and deer browsing (fenced/unfenced). We tracked the abundance and diversity of more than 140 herb species for six years.

Interactions among our treatments were pervasive. The combination of canopy gaps and understory fire increased herbaceous layer richness, cover, and diversity well beyond either disturbance alone. Furthermore, we documented evidence that deer at moderate levels of abundance promote herbaceous richness and abundance by preferentially browsing fast-growing pioneer species that thrive following co-occurring disturbances (i.e., fire and gaps). This finding sharply contrasts with the negative impact browsers have when their populations reach levels well beyond those that occurred for centuries. Although speculative, our results suggest that interactions among fire, canopy gaps, and browsing provided a variable set of habitats and conditions across the landscape that was potentially capable of maintaining much of the plant diversity found in temperate forests.

Key words: browsing; canopy gaps; deciduous forest; fire; herbaceous species; Odocoileus virginianus; *understory; West Virginia, USA; white-tailed deer.*

INTRODUCTION

Disturbance and browsing are drivers of vegetation dynamics and diversity patterns in forests worldwide yet rarely are these processes examined simultaneously, even though interactions likely predominate (Sousa 1984, Attiwill 1994, Frelich 2002, Whigham 2004). In the eastern United States, although various forces may influence vegetation dynamics (Pickett and White 1985), overstory disturbance (e.g., canopy gaps), understory fire, and deer browsing are generally recognized among the principal factors determining understory species composition (Roberts 2004; see also Runkle 1982, Oliver and Larson 1996, Gilliam and Roberts 2003). Over the past century, however, the entire region has experienced disruptions to historic disturbance and herbivory regimes including widespread clearcutting and conversion to second-growth forests, fire suppression, and increased ungulate densities (Whitney 1990, Abrams et al. 1995, McCabe and McCabe 1997, Fuller et al. 1998, Yarnell 1998, Guyette et al. 2002). The full impact of these disruptions is unknown but they have been implicated in the spread of exotic species (Hobbs and Huenneke 1992), decreased beta diversity (McKinney and Lockwood 1999), local species losses (Taverna et al. 2005), and increased monodominance (Royo and Carson 2006). We hypothesize that natural disturbances that were once common in the region and co-occurred

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with moderate levels of browsing will promote and maintain high understory diversity and naturally variable patterns of plant species composition. We test this hypothesis via a long-term fully factorial experiment near the geographic center of the North American eastern deciduous forest biome, a region that contains exceptionally high levels of plant diversity and endemism for temperate biomes (Ricketts et al. 1999, Kier et al. 2005).

To date, the vast majority of studies evaluating the influence of disturbance and browsing on plant diversity and composition have relied on natural episodic disturbance events and naturally varying herbivore levels, thereby precluding a rigorous experimental assessment of the independent and interactive roles of both processes (Weisberg and Bugmann 2003, Wisdom et al. 2006). For example, Husheer et al. (2003) found long-term deer browsing altered species composition in forest understories but acknowledged that naturally occurring gaps likely confounded their interpretations. Long-term experimental studies that disentangle disturbance and browsing are required because disturbance and browsing intensity may covary and both may simultaneously influence herbaceous diversity (e.g., Naaf and Wulf 2007).

In addition to the paucity of experimental studies that have evaluated the degree to which disturbance and browsing impact forest communities, the majority of existing work has focused on tree species even though trees typically represent less than one-third of vascular plant species diversity in forest systems (Gentry and Dodson 1990, Ricketts et al. 1999). This focus on overstory tree species can lead to potentially faulty conclusions. For example, in tropical forests Hubbell et al. (1999) concluded that disturbance (i.e., canopy gaps) played a neutral role in the maintenance of tree diversity. They did not consider, however, whether gaps influenced non-arbuscular species groups (e.g., herbs, shrubs, vines), which represented >50% of the flora. When these groups were considered, their conclusions regarding forest-wide biodiversity had to be reevaluated (Schnitzer and Carson 2000, 2001; see also Gilbert and Lechowicz 2004). In temperate and boreal forests, understory plant species represent even more (>75%) of the vascular flora (Gilliam 2007). Consequently, evaluating the impact of disturbance and herbivory on forest plant diversity requires an explicit consideration of species that reside solely in the understory.

Canopy gaps are widely known to strongly influence woody seedling and sapling species recruitment and abundance through their effect on resource (e.g., light) availability and heterogeneity (Runkle 1981, Denslow 1987, Canham 1989, Kneeshaw and Bergeron 1998). In contrast, the impact of canopy gaps on herb dynamics is inconsistent and subtle (Roberts and Gilliam 2003, Whigham 2004, Hart and Chen 2006) and ranges from slightly positive to negligible (e.g., Ehrenfeld 1980, Moore and Vankat 1986). Similarly, gaps apparently only increase the abundance of a small number of understory residents (e.g., Collins and Pickett 1987, Mladenoff 1990). Collins and Pickett (1987) argued that gaps would not enhance light sufficiently for understory herbs perhaps because they are typically trapped beneath an advance regeneration layer of saplings. Meier et al. (1995) have argued that the reason that herbs often show little response to gap formation is the small size of gaps that occur within second-growth forests (e.g., Clebsch and Busing 1989). They further suggested the paucity of large gaps that once characterized old-growth forests might be linked to herbaceous species losses. Ultimately, herbaceous community dynamics are likely determined, not by gap size and frequency alone, but rather by a product of co-occurring forces including fire and herbivory (Collins et al. 1985, Frelich 2002, Roberts 2004).

Fire has shaped the distribution and diversity of plant communities globally, including large portions of North American temperate forests (Abrams et al. 1995, Delcourt and Delcourt 1998, Guyette et al. 2002, Bond and Keeley 2005). Periodic fires alter understory species composition by intermittently favoring plant species possessing life-history traits that enhance establishment and persistence following fire, including vegetative reproduction and seed bank recruitment (Schiffman and Johnson 1992, Roberts 2004). In contrast, long-term fire suppression efforts have shifted dominance towards fire-sensitive species (Abrams 1992, Brose et al. 2001), facilitated the establishment of dense understory layers (e.g., Vandermast and Van Lear 2002), and potentially degraded propagule availability in the seed bank (see Wienk et al. 2004, Keeley et al. 2005 for examples in other systems). Such changes may limit the ability of herb communities to respond to gap formation (e.g., Kuddes-Fischer and Arthur 2002) and, in conjunction with altered gap regimes, negatively impact herbaceous communities region-wide (Elliott et al. 1999, Hutchinson et al. 2005, Spyreas and Matthews 2006, Peterson and Reich 2008).

In eastern North America, chronic white-tailed deer (*Odocoileus virginianus*) overbrowsing has reduced the abundance, diversity, and fecundity of herb species in many regions (Rooney 2001, Côte et al. 2004), though most research has focused on woody species (reviewed by Russell et al. 2001). Because herbs cannot attain a size refuge, browsers can rapidly shift plant species composition toward a few highly browse-tolerant or unpalatable species (reviewed by Royo and Carson 2006). If so, then disturbance may have little impact on understory communities because numerous palatable herbs may be at very low abundance or locally extirpated. This phenomenon has been called a legacy effect or the ghost of herbivory past (sensu Banta et al. 2005). This may explain why Collins and Pickett (1987) found little impact of gaps on herbs because their study was done in a heavily over-browsed region where the herb layer was dominated by a few unpalatable species

(Horsley et al. 2003). Consequently, the only way to evaluate the historical role of more typical or natural levels of browsers and their interaction with disturbance is to conduct experiments in areas where browsers are not overabundant (see *Methods: Study area*).

Despite the fact that gaps, fire, and herbivory often co-occur, we generally lack the long-term, experimental studies to evaluate how these factors collectively influence plant diversity (Weisberg and Bugmann 2003, Roberts 2004, Whigham 2004, Hart and Chen 2006, Wisdom et al. 2006). Furthermore, because disturbance and herbivory likely interact in complex ways with plant life-history traits, predicting their combined impacts is problematic (Keeley et al. 2003, Royo and Carson 2006). Nevertheless, recent work demonstrating how deer browsing can markedly alter tree seedling competitive hierarchies under canopy openings (Tripler et al. 2005, Long et al. 2007, Eschtruth and Battles 2008) and shift successional outcomes (Horsley et al. 2003) attests to the importance of interactions in structuring vegetation. Here we explore how and to what degree large gaps typical of old-growth forests, fires that were once common in the region, and moderate browsing levels interact to control herbaceous composition in species-rich forests.

Methods

Study area

We studied four stands in central West Virginia, USA, in the heart of the eastern deciduous forest. Two stands were in Monongahela National Forest (39°06′ N, 79°43′ W) and the other two were nearby at the Fernow Experimental Forest (39°01′ N, 79°42′ W). Stands ranged in size from 10 to 40 ha and were 670–810 m elevation. Stands were second-growth forests (60–90 years old) and predominantly upland sites including ridge tops and slopes (0–31%; 14.1% ± 0.9% [mean ± SE]). Stands were dominated by *Quercus rubra* L., *Q. alba* L., and *Q. montana* L. and include *Acer saccharum* Marsh., *A. rubrum* L., *Prunus serotina* Ehrh., *Fagus grandifolia* Ehrh., *Tilia americana* L., and *Betula lenta* L. as associated canopy species. The herbaceous layer is species rich ($\geq$461 species; Coxe et al. 2006), and its response to forest harvesting and nitrogen deposition is well understood (e.g., Gilliam 2002, Gilliam et al. 2006). Mean annual temperature is 9°C, precipitation averages 145 cm/yr, and growing season is ~145 days (Coxe et al. 2006). The region is characterized as having a median canopy disturbance interval of 31 years (Schuler and Fajvan 1999) and a fire return interval conservatively estimated at ~50–75 years (T. Schuler, *personal communication*), although more frequent fires are likely on oak-dominated sites such as ours (Schuler and McClain 2003). The deer population ranges from 4.6 to 7.7 deer/km^2 (M. Ford, *personal communication*). Although these levels are slightly higher than historical estimates (McCabe and McCabe 1997), they are moderate relative to nearby locations in West Virginia and elsewhere across eastern North America (Russell et al. 2001, Campbell et al. 2005; Quality Deer Management Association, *available online*).[7]

Experimental design

We manipulated fire, deer herbivory, and canopy gaps using a split-plot, factorial design. We subdivided each of four stands in half and randomly assigned a fire or a no-fire treatment to each half. Within each half we established eight treatment plots (400 m^2; 20 × 20 m) for a total of 64 treatment plots. Treatment plots were placed at least 20 m from one another, stand edges, and fire breaks. Within each of the fire or no-fire halves, we randomly applied each of the following four treatments to two plots: fence (no deer browsing), canopy gap, fence + canopy gap, and neither a gap nor a fence for a total of eight treatment combinations. Unburned plots without a gap or fence are referred to as controls.

Canopy gaps.—We created canopy gaps (284 ± 16 m^2) in 32 plots by girdling multiple canopy trees per plot in June 2000. By summer 2001 all girdled trees were either standing dead, had fallen, or had <10% of their original crown alive (R. Collins, *visual estimates*). Our goal was to create relatively large gaps formed by the death of a one to several canopy trees as opposed to small, ephemeral gaps formed by fallen branches or expansive openings formed by catastrophic windthrows. Our canopy gaps, while larger than typical multiple-tree gaps in second-growth forests (median = 152 m^2; Clinton et al. 1993), fall in the range found in old-growth forests (median = 240–290 m^2; Runkle 1982, Barden 1983).

Deer exclusion and surface fires.—We erected and maintained 2 m tall woven wire fences around 32 plots in May and June 2000. The mesh size (30 × 15 cm or 15 × 15 cm) excluded deer but allowed the entry of small- to medium-sized ground-dwelling animals. We conducted four 5–20-ha fires between 27 April and 1 May 2001. We set fires during what had been historically the peak fire season: during the sapling-layer bud break but before canopy-layer bud break. We directly measured fire temperature at 0, 10, 25, 50, and 100 cm from the surface of the ground using Tempil fire-sensitive paints (Tempil, South Plainfield, New Jersey, USA) ranging from 100° to 500°C (100° intervals) on aluminum tree tags. Following the fires, we recorded the highest paint temperature melted and estimated the percentage of each subplot scorched. Our fires simulated historic surface fires fueled primarily by leaf litter and small woody debris (Abrams 1992) and were comparable to similar prescribed surface fires in eastern deciduous forests (Collins and Carson 2003, Hutchinson et al. 2005). Most subplots burned nearly completely (mean = 92%; range 50–100%). Temperatures were the hottest at the surface of the ground (245° ± 15.4°C) and coolest at 1 m from the ground (91.9° ± 1.7°C).

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[7] ⟨http://www.i-maps.com/Qdma⟩

Data collection and analysis

We randomly established five permanent, 1-m^2 sampling quadrats in a 10 × 10 m area centered within each 400-m^2 plot. In summer 2000 we censused the density of understory species (herbs, shrubs, and vines) within the quadrats. In 2001, 2002, and 2006 we also visually estimated percent cover of each species in all quadrats using percent cover templates and recorded all additional species throughout the central 10 × 10 m area. We calculated species richness on a quadrat basis (number of species per square meter), species diversity (Shannon index, H'; Magurran 1988), and total percent cover (except in 2000) for each plot and census period. We also calculated richness and percent cover on four species groups: forbs, graminoids, ferns, and shrubs (non-arborescent woody vegetation including vines).

We quantified the light environment at the herbaceous level by calculating a mean diffuse non-interceptance (DIFN) for each plot using an LAI 2000 canopy analyzer (LI-COR, Lincoln, Nebraska, USA) between June and August 2000 and 2001. Diffuse non-interceptance represents the fraction of the sky visible beneath the canopy and is highly correlated with growing-season light availability (Gendron et al. 1998). We recorded eight evenly spaced light measurements in each plot at 1 m above the ground surface and used a second sensor to record above-canopy measurements in a nearby large clearing.

We used a repeated-measures analysis of variance (rmANOVA) using PROC MIXED (SAS Institute 2005) to analyze treatment effects and interactions. Fire, gap, and fence were fixed effects. Stand, stand × fire, stand × fire × gap, stand × fire × fence, and stand × fire × fence × gap were considered random effects. We modeled the correlation between sample units across time using a spatial power covariance structure. This structure performs well with unequally spaced repeated measures (Moser 2004). The rmANOVA compared overall differences caused by treatment (between-subject effects) and interactions among treatments and time (within-subject effects). Here, we primarily examine the within-subject effects as our interest is in treatment effects over time (von Ende 2001). Dependent variables included richness (number of species per square meter), percent cover, and diversity. We assessed whether the response variable distributions fit the assumptions of normality using residual plots. Percent cover was arcsine square-root transformed and richness was square-root transformed to stabilize the variance. Finally, we also assessed treatment effects on the change in light the year after implementing all treatments,

$$\Delta\mathrm{DIFN} = \frac{\mathrm{DIFN}_{2001} - \mathrm{DIFN}_{2000}}{\mathrm{DIFN}_{2000}}$$

using a mixed-model ANOVA.

Nonparametric blocked multi-response permutation procedures (MRBP; McCune and Grace 2002) were performed with PC-Ord (McCune and Mefford 1999) to test the null hypothesis that plant species composition did not vary among treatments in 2000 (pretreatment) and in 2006 (post-treatment). Each discrete treatment formed the a priori groups for this analysis. We further explored differences using additional MRBP analyses to determine pairwise differences between the control group and each of the manipulative treatments. Finally, we followed the MRBP analyses with indicator species analyses (ISA) in PC-ORD to evaluate the specificity and fidelity of individual species to each of the treatment combinations (Biondini et al. 1988, Dufrene and Legendre 1997). For each year, we relativized abundance values to a common scale (0–1) and deleted rare species (occurring on <5% of plots) leaving 20 and 33 species in 2000 and 2006, respectively, in order to equalize the influence of common and rare species (McCune and Grace 2002).

RESULTS

Species richness and cover

Across all plots and census periods the understory herbaceous community was comprised of 144 species: 95 forbs, 20 graminoids, 17 shrubs, and 12 ferns vs. an overstory of just 23 tree species. Among the herbaceous species, 119 were identified to species and 25 were identified to the level of genus. Less than 1% of the 20 000 individuals sampled were considered unknown morphospecies, and these were generally seedlings or nonflowering juveniles.

Across the entire six-year study period, fire and gaps together increased overall species richness to a greater extent than fire or gaps alone (fire × gap × time interaction; Table 1, Fig. 1A). Significant three-way interactions that included time (e.g., fence × gap × time) were pervasive, demonstrating that impacts on species richness were contingent on the combination of fire, browsing, and gaps. By 2006, both fire and gaps increased richness but these effects were less pronounced inside exclosures (Table 1, Fig. 1B, C). Furthermore, in plots combining fire and canopy gaps, browsing increased overall herbaceous richness (fire + gap + no fence, 5.6 ± 1.1 species/m^2, vs. fire + gap + fence, 2.9 ± 0.7 species/m^2).

Fire and gap formation together increased total herbaceous cover significantly more than either disturbance alone (fire × gap interaction; Table 1, Fig. 1D). Briefly, burning alone increased cover nearly fivefold and gaps alone doubled cover, whereas burning and gaps together increased cover nearly 10-fold (no fire + no gap, 6.1% ± 1.2%, vs. fire + gap, 63.1% ± 6.3%; Fig. 1D). Browsing alone did not cause a significant change in overall plant cover during the study.

Species diversity and composition

Species diversity (H') increased significantly after fire (no fire, 1.06 ± 0.11, vs. fire, 1.31 ± 0.09; Table 1). Gaps and fencing had no significant effect on species diversity. Species composition among treatment units was not

TABLE 1. Results of repeated-measures, mixed-model ANOVA used to test response of species richness (no. species/m^2), percent cover, and diversity (H') in a factorial experiment with two canopy disturbance conditions (gap and no gap), two understory fire conditions (burned and unburned), and two deer density levels (exclosure and control) in a temperate deciduous forest in central West Virginia, USA.

	Richness		Cover		Shannon index (H')	
Source	*F*	df	*F*	df	*F*	df
Between subjects (variation among treatments averaged across all years)						
Fire	3.36	1, 3	6.30	1, 3	0.20	1, 3
Fence	1.23	1, 6	0.19	1, 6	0.91	1, 6
Gap	0.10	1, 6	13.09*	1, 6	0.77	1, 6
Fence × gap	0.48	1, 6	0.69	1, 6	1.91	1, 6
Fire × fence	1.40	1, 6	1.13	1, 6	0.11	1, 6
Fire × gap	1.92	1, 6	5.65	1, 6	1.86	1, 6
Fire × fence × gap	0.04	1, 6	1.78	1, 6	0.29	1, 6
Within subjects (variation among treatments differs across time)						
Time	18.26****	3, 199	86.93****	3, 143	11.18****	3, 196
Fire × time	15.87****	3, 199	40.35****	3, 143	5.87***	3, 196
Fence × time	0.20	3, 199	0.36	3, 143	0.05	3, 196
Gap × time	2.91*	3, 199	16.09****	3, 143	0.35	3, 196
Fence × gap × time	2.90*	3, 199	0.10	3, 143	1.65	3, 196
Fire × fence × time	2.63*	3, 199	0.24	3, 143	0.41	3, 196
Fire × gap × time	6.07***	3, 199	6.32**	3, 143	1.99	3, 196
Fire × fence × gap × time	1.86	3, 199	0.73	3, 143	2.56	3, 196

Note: For species richness we considered $P = 0.051$ significant for fire × fence × time.
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P \leq 0.0001$.

significantly different among treatments prior to implementing any treatment in 2000 (MRBP, $P = 0.39$). By 2006, however, species composition among treatments was significantly different (MRBP, $P = 0.004$). The combination of fire and canopy gaps created two divergent community assemblages that were entirely dependent upon whether areas were browsed (MRBP, $P = 0.01$) or protected from browsing (MRBP, $P = 0.03$).

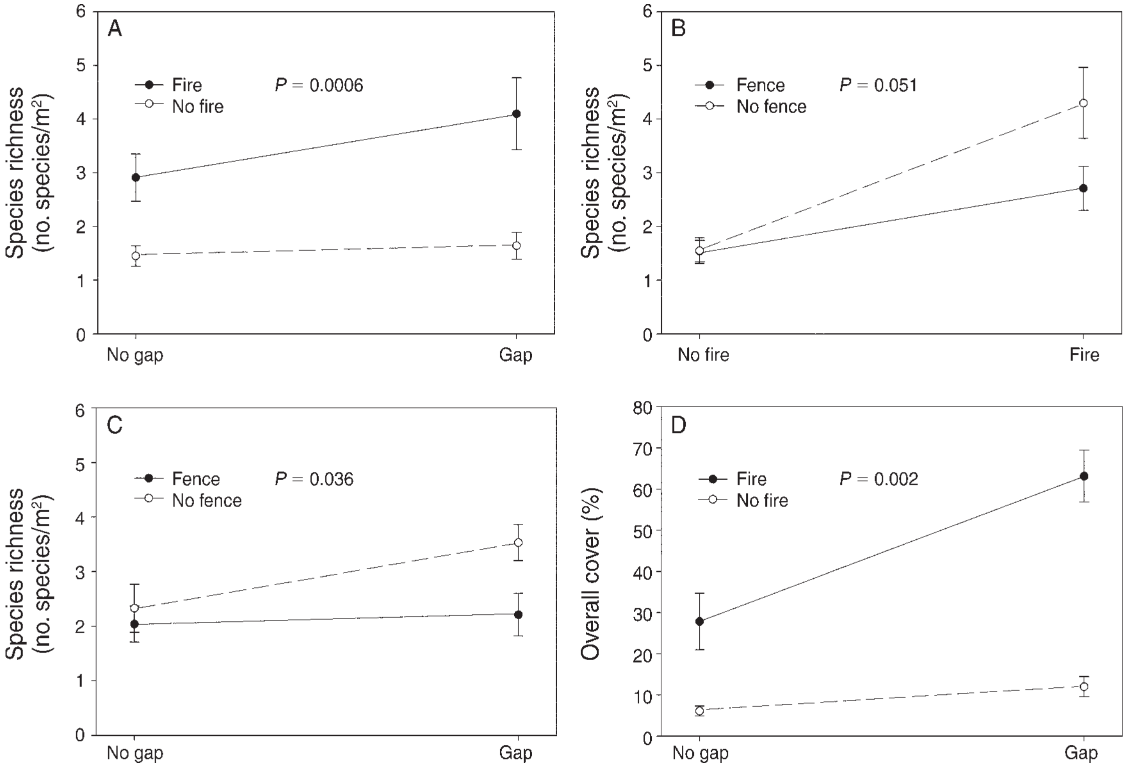

FIG. 1. Effects of significant two-way interactions between fire, canopy gap, and browsing (see Table 1) on (A–C) overall species richness and (D) percent cover in 2006. Means (±SE) for each depicted two-factor combination are averaged across the third factor.

TABLE 2. Results of repeated-measures mixed-model ANOVA used to test response of species richness (no./m^2) and cover (%) of four different species groups in a factorial experiment with two canopy disturbance conditions (gap and no gap), two understory fire conditions (burned and unburned), and two deer density levels (exclosure and control) in a temperate deciduous forest.

	Forbs				Shrubs			
	Richness		Cover		Richness		Cover	
Source	*F*	df	*F*	df	*F*	df	*F*	df
Between subjects (variation among treatments averaged across all years)								
Fire	3.30	1, 3	2.83	1, 3	0.01	1, 3	3.26	1, 3
Fence	0.99	1, 6	0.34	1, 6	0.42	1, 6	3.63	1, 6
Gap	0.02	1, 6	2.31	1, 6	0.01	1, 6	5.03	1, 6
Fence × gap	0.52	1, 6	0.76	1, 6	0.01	1, 6	0.20	1, 6
Fire × fence	0.99	1, 6	0.72	1, 6	0.15	1, 6	0.76	1, 6
Fire × gap	2.77	1, 6	3.02	1, 6	0.19	1, 6	0.77	1, 6
Fire × fence × gap	0.35	1, 6	0.90	1, 6	0.11	1, 6	0.24	1, 6
Within subjects (variation among treatments differs across time)								
Time	12.76****	3, 199	27.97****	2, 143	7.78****	3, 199	58.75****	2, 143
Fire × time	3.71*	3, 199	18.05****	2, 143	11.27****	3, 199	25.03****	2, 143
Fence × time	1.37	3, 199	0.95	2, 143	1.39	3, 199	7.07**	2, 143
Gap × time	2.60	3, 199	7.69***	2, 143	4.96**	3, 199	14.58****	2, 143
Fence × gap × time	4.73**	3, 199	0.20	2, 143	1.92	3, 199	0.32	2, 143
Fire × fence × time	0.33	3, 199	0.96	2, 143	2.79*	3, 199	1.62	2, 143
Fire × gap × time	5.46**	3, 199	6.79**	2, 143	0.29	3, 199	3.59*	2, 143
Fire × fence × gap × time	0.07	3, 199	0.19	2, 143	1.33	3, 199	0.31	2, 143

Note: Species richness was measured in 2000, 2001, 2002, and 2006; percent cover was measured in 2001, 2002, and 2006.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P \leq 0.0001$.

Species groups: forbs, shrubs, and ferns

Across the six-year study period, fire more than doubled forb richness and richness increased further when combined with a canopy gap (Table 2, Fig. 2A). Canopy gaps increased forb richness but only in the presence of browsers (Table 2, Fig. 2B) and this effect was more pronounced in burned areas (Fig. 3A). Fire increased forb cover by an order of magnitude when compared to areas without fire, and this effect nearly doubled when combined with a gap (Table 2, Fig. 2C). Excluding deer, alone or in combination with other treatments, did not affect forb cover in the rmANOVA (Table 2); however, forb cover in areas combining burning and gaps was greatest in the presence of browsers (Fig. 3B).

Shrubs were sparse (<1% cover) at the outset of the study. Across the six-year study period, both gaps and fire alone significantly increased shrub richness (Table 2). Fire more than doubled shrub richness but only in the absence of browsers (Table 2, Fig. 2D). Gaps alone modestly increased shrub richness and augmented richness additively with other treatments (i.e., no significant interactions; Table 2). Fire, canopy gaps, and deer exclusion alone all significantly increased shrub cover; however, burning and canopy gaps combined increased shrub cover by an order of magnitude (Table 2, Fig. 2E). By 2006, shrubs dominated the understory in areas combining fire and gaps, particularly when protected from deer browsing (Fig. 3D).

Both burning and gap creation alone caused moderate increases in fern richness (Table 2), whereas burning and gaps combined increased fern richness nearly fourfold (fire × gap × time interaction, $P = 0.075$). Browsing alone had no direct impact on fern richness in the rmANOVA (Table 2). Nevertheless, fern richness following fire and gaps nearly tripled outside exclosures (Fig. 3E). Analyses on fern cover contained recurrent three-way treatment interactions that included time, demonstrating that fern abundance was entirely dependent upon the particular combination of fire, canopy gaps, and browsing. Specifically, browsing increased fern cover but only in the presence of fire or gaps (Table 2, Fig. 2F, G). Fire and canopy gaps collectively increased fern cover more than either effect in isolation (Table 2, Fig. 2H); however, only when exposed to browsing did fern cover increase by an order of magnitude (Fig. 3F). We did not analyze graminoids because they were patchily distributed and had low species richness and cover (<0.26 per m^2 and <1%, respectively).

Indicator species analyses (ISA) revealed that of the 33 common species found in 2006, eight species were consistently more abundant in plots combining fire and gaps (ISA, P values < 0.05). These were *Ageratina altissima* L., *Amphicarpaea bracteata* L., *Dennstaedtia punctilobula* (Michx.) T. Moore, *Galium triflorum* Michx., *Phytolacca americana* L., *Potentilla canadensis* L., *Rubus* spp., and *Thelypteris noveboracensis* (L.) Nieuwl. In plots combining fire and gaps, *Rubus* spp. and *Phytolacca americana* were most abundant in the absence of browsing and the other six species were most abundant in areas open to browsing (Appendix A). Another eight species were marginally more abundant (<0.1 and >0.05) in plots combining fire and gaps.

TABLE 2. Extended.

Ferns			
Richness		Cover	
F	df	*F*	df
2.00	1, 3	1.20	1, 3
0.32	1, 6	0.81	1, 6
0.19	1, 6	0.69	1, 6
0.00	1, 6	0.44	1, 6
0.42	1, 6	1.77	1, 6
2.07	1, 6	0.75	1, 6
1.24	1, 6	0.10	1, 6
8.78****	3, 199	20.29****	2, 143
5.46**	3, 199	7.01**	2, 143
1.94	3, 199	4.28*	2, 143
2.88*	3, 199	2.04	2, 143
2.23	3, 199	3.91*	2, 143
1.58	3, 199	5.73**	2, 143
2.34	3, 199	3.91*	2, 143
1.22	3, 199	1.48	2, 143

Light environment

Both canopy gaps ($F_{1,6} = 9.69$, $P = 0.021$) and fire ($F_{1,3} = 16.38$, $P = 0.027$) increased canopy openness into the forest understory by ~260% (Appendix B). Their impact on light availability was additive (i.e., no significant interactions). Excluding browsers had no impact on light availability.

DISCUSSION

Pervasive interactions occurred among all treatments

Surface fires and canopy gaps typical of old-growth forests were frequent events that occurred across much of the mixed-oak forests of the central Appalachians for thousands of years (Delcourt and Delcourt 1998, Brose et al. 2001). Large-scale logging converted these old-growth forests to younger, second-growth stands characterized by smaller and more ephemeral gaps (Clebsch and Busing 1989). Pervasive fire suppression policies dramatically reduced the prevalence of fires across the region (Guyette et al. 2002). To our knowledge, this is the first study to demonstrate experimentally that interactions between understory fire and large canopy gaps strongly influence herbaceous-layer dynamics and jointly play a strong role in enhancing species richness and abundance. We repeatedly found that interactions between fire and canopy gaps increased herb layer richness and abundance beyond either disturbance alone. Indeed, indicator species analyses revealed that between 8 and 16 species were more abundant in plots that were burned and had canopy gaps.

The interaction between disturbances and their interaction with browsing and plant life-history traits created communities with contrasting plant composition

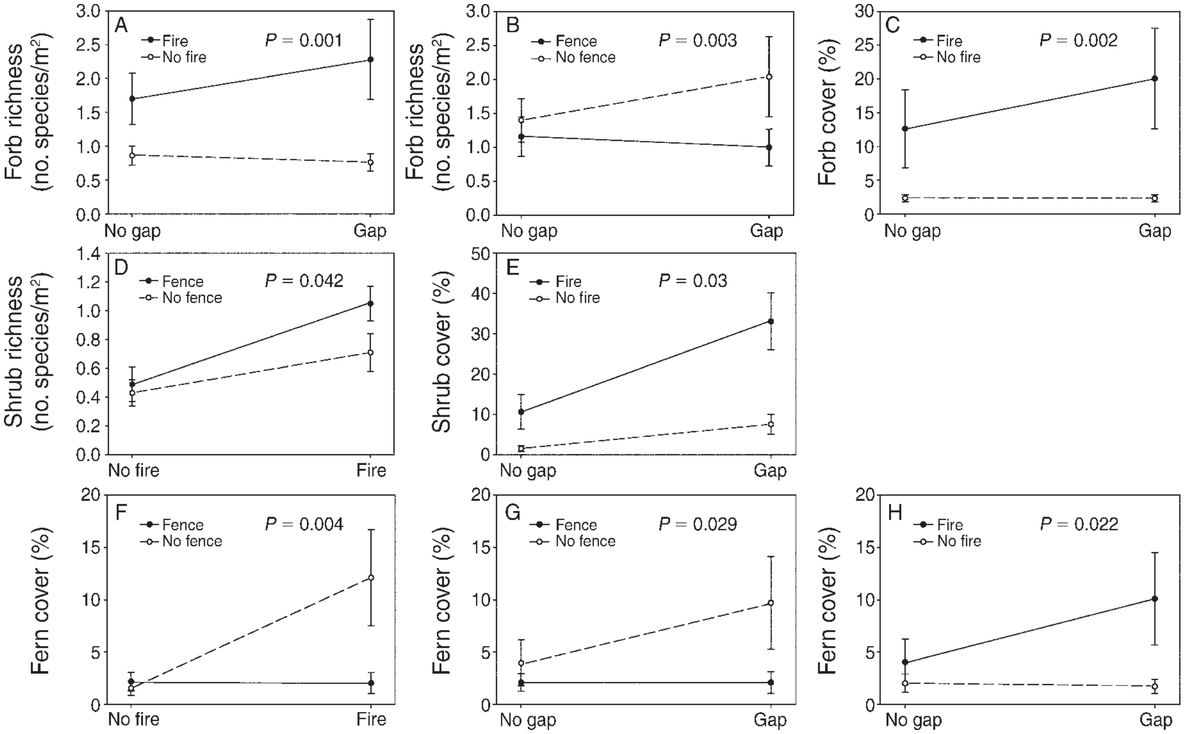

FIG. 2. Effects of significant two-way interactions between fire, canopy gap, and browsing (see Table 2) on (A–C) forb species richness and cover, (D–E) shrub richness and cover, and (F–H) fern cover in 2006. Means (±SE) for each depicted two-factor combination are averaged across the third factor (see Fig. 3 for each specific treatment mean).

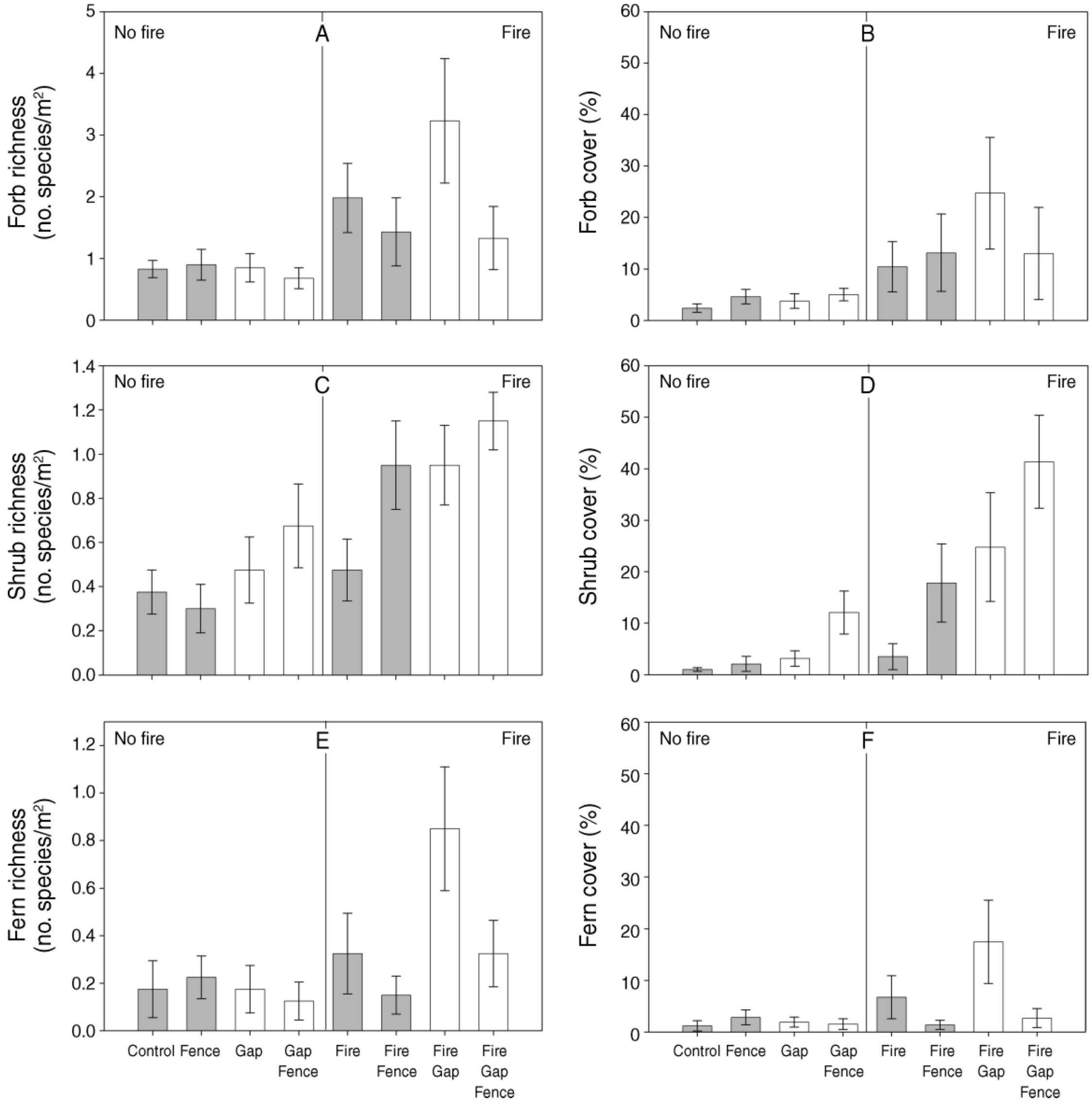

FIG. 3. Species richness and percent cover in 2006 for each of the eight treatment combinations in each of the species groups: (A, B) forb richness and cover, (C, D) shrub richness and cover, and (E, F) fern richness and cover. Gray bars denote plots without overstory gaps; white bars denote plots with gaps. The species richness axis varies in magnitude, whereas percent cover is standardized. Bars represent mean ± SE.

and richness (Mallik 2003, Roberts 2004). For example, fire and gaps together promoted rapid dominance of species possessing post-fire recruitment and persistence mechanisms. Six of the eight species that thrived following the combination of fire and gaps were not found within these areas prior to burning (Appendix A). These six species are fast-growing, shade-intolerant species (Hughes and Fahey 1991) that are known to increase in abundance after fire through copious recruitment from the seed bank (*Ageratina altissima*, *Phytolacca americana*, *Rubus* spp.), aggressive expansion from fire-tolerant underground rhizomes (*Amphicarpaea bracteata*, *Dennstaedtia punctilobula*), or both (*Galium triflorum*; Hutchinson et al. 2005; Fire Effects Information System, *available online*).[8] Additionally, both gaps and fire independently increased light availability over the herbaceous layer (~1 m) and several species (e.g., *Potentilla canadensis* and *Thelypteris noveboracensis*) likely increased in abundance for this reason. Alternatively, fire may increase nutrient availability (e.g., nitrogen; Christensen 1987, Boerner et al. 2000), and the ensuing nutrient pulse is known to alter herbaceous composition and abundance (reviewed by Gilliam 2006). Nevertheless, manipulative studies at the Fernow have shown the herbaceous response to experimental nitrogen

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[8] ⟨http://www.fs.fed.us/database/feis/⟩

additions is "negligible" in these already N-saturated forests (Gilliam et al. 1994, 2006). Therefore, although fire-mediated nutrient enrichment may influence herbaceous dynamics at non-saturated sites, we believe increased light availability following understory fire is the most parsimonious explanation for the observed response.

Deer browsing creates contrasting communities following disturbance

Browsing in understories where both fire and gaps occurred together created a very different community from the one formed when browsers were excluded (contrasting patterns of richness and abundance; Fig. 3). Specifically, the exclusion of browsers created depauperate communities dominated by rapidly growing woody species, particularly *Rubus* spp. and *Prunus pensylvanica* seedlings (Fig. 3D; W. P. Carson and M. B. Adams, *personal observations*). In contrast, deer browsing reduced the abundance of these palatable species (Horsley et al. 2003), thereby indirectly causing greater richness and a more even mixture of forbs, shrubs, and ferns (Fig. 3). This was unexpected and it occurred because of the complex interactions among gaps, fire, and browsing. These findings demonstrate that an important vertebrate browser can significantly enhance diversity when disturbances that were designed to mimic historical disturbance regimes were reintroduced. Although interactions of herbivory and disturbance are widely known to benefit herbaceous diversity in grasslands and rangelands (e.g., Belsky 1992, Knapp et al. 1999), such indirect effects in forest communities remain largely unexplored (Wisdom et al. 2006, but see Naaf and Wulf 2007).

Most research on the impact of deer browsing on plant communities has found, almost without exception, that deer depress species richness of understory herbaceous species (e.g., Rooney 2001, Russell et al. 2001). These studies, however, were typically not designed to evaluate the interaction among browsers and disturbances and often occurred in areas where deer populations have been chronically high for decades (e.g., Banta et al. 2005, Webster et al. 2005). Although we did not measure deer densities in the vicinity of our plots, estimates of deer populations in the area range from 4.6 to 7.7 deer/km^2 (M. Ford, *personal communication*), which is typically much less than in other areas of West Virginia (Campbell et al. 2005) and in large portions of the eastern United States (Quality Deer Management Association, see footnote 7). Our results lend even greater weight to those concerned with overabundant deer populations (e.g., Rooney 2001, Russell et al. 2001, Latham et al. 2005) because we found that when deer where closer to historical levels (McCabe and McCabe 1997) they enhanced diversity rather than depressed it. Our results extend theoretical and experimental studies conducted in grasslands and old fields to forests; these studies all indicate that moderate or intermediate browsing intensities cause the greatest herbaceous diversity following disturbance (e.g., Grime 1973, Bowers 1993, Vujnovic et al. 2002). In contrast, understories lacking browsing may become dominated by palatable, fast-growing plants (Larson and Paine 2006), whereas chronic overbrowsing promotes dominance of unpalatable plants (reviewed by Royo and Carson 2006).

In the most comprehensive study to date in eastern forests, Horsley et al. (2003) found that deer begin causing declines in diversity when they reach levels of $\sim$8 deer/km^2 in forests without any particular history of fire (see also Tremblay et al. [2006] for a similar threshold in boreal forests). We found no negative impacts of browsing on diversity at these levels in any treatment. We suggest these contrasting findings may arise from our focus on the interaction of browsing with gaps and fire that attempted to simulate natural disturbance regimes in our region. The impact of browsers, however, also depends on forage availability (deCalesta and Stout 1997, Schmitz and Sinclair 1997). For example, Horsley et al. (2003) studied depauperate forests in which nearly a century of overbrowsing had created understories dominated by unpalatable species (e.g., *D. punctilobula*, *F. grandifolia*). This situation is common in many eastern forests (i.e., "legacy effects" sensu Banta et al. 2005; de la Cretaz and Kelty 1999, Webster et al. 2005). In contrast, in forests in which deer populations remain at low to moderate levels and canopies are dominated by mast producing species such as oaks, forage quality and availability will likely be much higher. Consequently, we suggest that whether deer promote species richness (our study site) or depress it will depend upon three primary factors: deer abundance, food supply, and disturbance. Moderate browsing may only promote diversity in forage-rich, high-light patches that occur following disturbance, whereas moderate deer browsing may suppress diversity in depauperate areas, particularly in the absence of natural disturbances.

The role of fire and gaps in the maintenance of understory diversity

Alterations to historical fire regimes have altered vegetation dynamics and composition globally (Thonicke et al. 2001, Bond and Keeley 2005). There is a broad, emerging consensus that restoring fire regimes is critical to perpetuating tree species diversity in fire-dependent communities (Abrams 1992, Whelan 1995, Brose et al. 2001). Our findings help to extend this consensus to herbaceous species. Restoring fire regimes may be particularly beneficial to seed banking herbaceous species. Seed dormancy provides a buffering mechanism or storage effect that promotes recruitment and enhances diversity when favorable conditions arise (Warner and Chesson 1985). For most species, seed longevity is far less than 100 years (Nakagoshi 1985, Thompson et al. 1997) and even the most long-lived seeds steadily decline in viability after the first few decades (Peterson and Carson 1996). In fact, Suding et al. (2004) hypothesized this degradation in propagule availability may limit vegetation response and recovery following the restoration of disturbance regimes. Thus, a century of institutionalized fire suppression across North America (Pyne 1997) may have weakened the advantages of a storage effect by decreasing seed replenishment, eroding the seed bank, and possibly causing the extirpation of some species from the community (see Keeley et al. [2005] for example in chapparal communities). We demonstrate that the reintroduction of fire and gaps provides significant and timely biodiversity benefits in relatively mesic, mixed-oak forests by providing a recruitment and reproductive opportunity for some herbaceous species. Furthermore, our results may underestimate the value of restoring fire to herbaceous diversity in more xeric forests systems that historically experienced more frequent fire intervals (e.g., Christensen 1987).

Our results were consistent with previous conclusions that gap creation alone does not enhance herbaceous richness or abundance (e.g., Ehrenfeld 1980, Moore and Vankat 1986, Collins and Pickett 1987, 1988), even when the gaps examined were large ones more typical of old-growth forests (cf. Meier et al. 1995). We hesitate to draw broad conclusions here because our method of gap formation (girdling) created openings of standing dead trees that gradually fell down and decayed whereas wind events often uproot trees, creating large pits and mounds that are known to enhance herbaceous diversity (e.g., Bratton 1976, Beatty 1984). If these pits and mounds are the key, then this suggests the soil disturbance associated with gaps is more important than enhanced light availability for herb species. Nonetheless, our findings suggest that gaps alone without fire will not be sufficient to promote understory diversity.

Conclusion

Recent reviews lament the dearth of experimental work that disentangles the relative impact of important processes that likely control herbaceous diversity; indeed the current state of knowledge is considered "anecdotal and uncertain" (Roberts 2004, Wisdom et al. 2006). Our study demonstrates clearly that synergies between understory fire and canopy gaps promote substantially more diverse understory plant assemblages. Furthermore, vertebrate browsers at moderate levels of abundance can enhance species richness following co-occurring disturbances by reducing the dominance of several highly palatable, rapidly growing, shade-intolerant species. Historically, all of these processes (large canopy gaps, understory fire, and browsing) almost certainly occurred in a mosaic across the landscape. We suggest that this heterogeneity would have contributed substantially to an array of habitats and conditions and thus helped promote diversity in understory communities that represent >75% of the vascular species richness in many temperate forests.

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APPENDIX A

Mean frequencies of 74 species censused among all treatments at the onset (2000) and the end (2006) of the experiment (*Ecological Archives* E091-009-A1).

APPENDIX B

Diffuse non-interceptance values (DIFN) for each of the eight treatment combinations the year after implementing all treatments (*Ecological Archives* E091-009-A2).