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Historic disturbance regimes promote tree diversity only under low browsing regimes in eastern deciduous forest

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Abstract. Eastern deciduous forests are changing in species composition and diversity outside of classical successional trajectories. Three disturbance mechanisms appear central to this phenomenon: fire frequency is reduced, canopy gaps are smaller, and browsers are more abundant. Which factor is most responsible is a matter of great debate and remains unclear, at least partly because few studies have simultaneously investigated more than one process. We conducted a large-scale experiment in mesophytic forests of West Virginia, USA, to test three key hypotheses: (1) the fire hypothesis (fire suppression limits diversity to few shade-tolerant, fire-intolerant species that replace and suppress many fire-tolerant species); (2) the gap hypothesis (small gaps typical of today's forests promote dominance of a few shade-tolerant species); and (3) the browsing hypothesis (overbrowsing by deer limits diversity to a few unpalatable species). We tested these hypotheses using a factorial experiment that manipulated surface fire, large canopy gap formation (gap size ~255 m^2), and browsing by deer, and we followed the fates of >28 000 seedlings and saplings for five years. Understory tree communities in control plots were dominated (up to 90%) by *Fagus grandifolia*, averaging little more than two species, whereas overstories were diverse, with 10–15 species. Fire, large canopy gaps, and browsing all dramatically affected understory composition. However, our findings challenge views that fire and large canopy gaps can maintain or promote diversity, because browsers reduced the benefits of gaps and created depauperate understories following fire. Consequently, two major disturbances that once promoted tree diversity no longer do so because of browsing. Our findings appear to reconcile equivocal views on the role of fire and gaps. If browsers are abundant, these two disturbances either depress diversity or are less effective. Alternatively, with browsers absent, these disturbances promote diversity (three- to fivefold). Our results apply to large portions of eastern North America where deer are overabundant, and we provide compelling experimental evidence that historical disturbance regimes in combination with low browsing regimes typical of pre-European settlement forests could maintain high tree species diversity. However, restoring disturbances without controlling browsing may be counterproductive.

Key words: browsing; canopy gaps; eastern deciduous forest, USA; factorial experiment; fire; forest diversity; Odocoileus virginianus; *regeneration; succession; white-tailed deer.*

INTRODUCTION

Overview

Much of our understanding of forest dynamics comes from extensive study of the eastern deciduous forests of North America (e.g., Runkle 1982, Shugart 1984, Botkin 1993, Pacala et al. 1996, Foster and Aber 2004). Oddly, however, these forests have undergone dramatic changes in species composition throughout the 20th century that appear outside trajectories predicted by classical succession theory (e.g., Shotola et al. 1992, Galbraith and Martin 2005, Nowacki and Abrams 2008, Rogers et al. 2008). Based on long- and short-term studies in both old-growth and secondary forests, canopy diversity is reduced compared to historical records (e.g., Rentch et al. 2003, Rentch and Hicks 2005, Schulte et al. 2007) or may be poised for a serious reduction due to depauperate advance regeneration (e.g., Abrams et al. 1997, 1998, Long et al. 2007). Oaks (*Quercus* spp.) are declining across vast areas, whereas species such as *Fagus grandifolia* and *Acer rubrum* are increasing (Abrams 1998, 2003, Dyer 2006). Introduced pathogens have caused some of this change by removing entire species from the overstory, e.g., *Castanea dentata* (Woods and Shanks 1959), *Tsuga canadensis* (Ellison et al. 2005); more recently even *Fagus grandifolia* is in danger due to the spread of beech bark disease (Gavin and Peart 1993). Also, a few declines can be linked clearly to changes in

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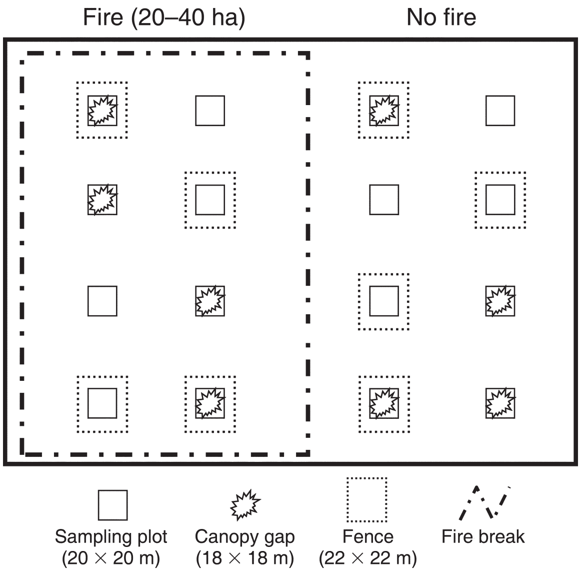

FIG. 1. Schematic diagram of experimental design for one of four replicate stands at the Mead-Westvaco Research Forest, West Virginia, USA.

climatic or edaphic factors such as acid rain, altered hydrology, and climate change (Bailey et al. 2005, Boerner 2006, Dyer 2006). Still, across much of the biome, many shifts in canopy dominance and diversity seem unrelated to changing climate, edaphic conditions, or introduced pathogens. More importantly, these changes differ from expected successional turnover, where much less dramatic shifts in dominance and diversity are expected (see e.g., Runkle 1981).

There is now growing evidence that humans have significantly altered two critical components of the disturbance regime (fire and canopy gaps) as well as abundance of the principal herbivore (white-tailed deer, *Odocoileus virginianus*). Briefly, fire frequency is reduced, altering survival and recruitment of young trees; canopy gaps are smaller, contributing to altered light regimes; and deer are more abundant, resulting in increased browsing rates (Clebsch and Busing 1989, Stromayer and Warren 1997, Abrams et al. 1998, Abrams 2003, Horsley et al. 2003, Côté et al. 2004, Tripler et al. 2005, Long et al. 2007). The full impact of these alterations remains unclear, although they probably have decreased both local and regional species diversity (McKinney and Lockwood 1999), led to the spread of exotic species (Hobbs and Huenneke 1992), and increased mono-dominance (Royo and Carson 2006). Each process—fire, canopy gaps, and browsing—constitutes a competing hypothesis for observed changes in forest dynamics and each has strong advocates. However, the relative impact of these processes and how they interact typically remain unknown because of the difficulty of simultaneously manipulating them. Moreover, results from single-factor experiments or from naturally occurring gradients in these drivers may be misleading if interactions among processes predominate, especially if interactions nullify or reverse the impact of one factor depending on the level of another. Indeed, Royo et al. (2010) found that interactions among fire, browsing, and canopy gaps were pervasive in controlling the abundance and diversity of forest herbs. In contrast to statistical interactions, processes may interact ecologically where statistical effects are additive, but certain combinations of factors (e.g., browser exclusion within large canopy gaps) have particularly high responses in terms of diversity or density.

We conducted a large-scale, factorial experiment (Fig. 1) in which we followed >28 000 individual trees for five years to evaluate how fire, canopy gaps, and deer browsing alone and in concert drive forest dynamics of mesophytic eastern deciduous forests. These forests currently have diverse canopies composed of 10–15 tree species but have understories that are depauperate (<5 woody species, dominated overwhelmingly by *Fagus grandifolia*), and markedly dissimilar to the canopy. The few species currently dominating the understory tend to be fire intolerant, shade tolerant, and browse tolerant, whereas canopy trees come from a variety of fire, shade, and browse tolerance classes. We begin by briefly developing three general hypotheses regarding effects of low-intensity surface fire, large canopy gaps, and deer browsing on forest regeneration. We then describe how interactions among mechanisms might be expected to influence these predictions.

Hypotheses

Fire hypothesis: fire suppression has allowed fire-intolerant species to become dominant, suppressing fire-tolerant species.—Historically, eastern deciduous forest supported periodic, low-intensity surface fires (Abrams 1992, Lorimer et al. 1994, Sutherland 1997, Van Lear and Brose 2002). Fire tolerance and shade tolerance are loosely inversely correlated (Frelich 2002). Hence, long-term fire suppression has increased overall stand density and dominance of shade-tolerant and fire-intolerant species such as *Acer saccharum* and *Fagus grandifolia*, especially in the understory. Conversely, low-intensity surface fires promote growth and recruitment of fire-tolerant species such as upland oaks because fire reduces the dominance of shade-tolerant species, increases understory light, and prepares favorable seed beds for caching and germination (Abrams 1992, Lorimer et al. 1994, Van Lear and Brose 2002). Specifically, fire will top-kill most advance regeneration, but due to abundant resprouting of fire-tolerant species and enhanced germination from diverse seed pools (owing to diverse canopy composition), we hypothesize that prescribed fire will increase the density and relative abundance of fire-tolerant species across all seedling and sapling size classes at the expense of fire-intolerant species. Because there are more fire-tolerant than intolerant species in this system, overall species diversity in the understory should also increase following prescribed fire. Furthermore, because fire intensity is patchy, surface fires should create a mosaic of fire intensities that support a range of fire tolerances, as opposed to the uniformly unburned landscape that exists now (Chappell and Agee 1996).

Gap hypothesis: canopy gaps in second-growth forests are too small to allow recruitment of all but the most shade-tolerant species.—Rentch and Hicks (2005) reported that presettlement forests in the mesophytic region had a much higher proportion of intermediately shade-tolerant tree species compared with today's forests, which are dominated by a combination of mostly shade-tolerant and shade-intolerant species, depending on stand age. In lieu of large-scale disturbances, gaps are required for most tree species of eastern deciduous forests to gain access to the canopy (Shugart 1984, Pickett and White 1985, Burns and Honkala 1990). Although large-scale disturbances such as those created by wind storms have probably not changed over recent centuries, small-scale disturbances such as canopy gaps have. Gaps in old-growth forests tend to be larger (up to 300 m^2) and hence allow in more light than gaps that occur in second-growth forests (<100 m^2), which now dominate the landscape (Clebsch and Busing 1989). These smaller gaps are often filled by lateral extension from neighbors or by shade-tolerant species present as advance regeneration, but do not allow enough light for less shade-tolerant seedlings to reach larger size classes (Clebsch and Busing 1989). Hence, small-tree gap dynamics allow continued recruitment of shade-tolerant species while impeding recruitment by less shade-tolerant species. In contrast, larger gaps not only let in more light, but also persist longer because lateral extension cannot reach the center of the gap. Hence, we hypothesize that creating larger openings typical of old-growth forests should promote regeneration and recruitment of species from a wider range of shade tolerance classes, contributing to increased density and species diversity in the understory across all size classes of seedlings and saplings.

Deer browsing hypothesis: browsing by high populations of white-tailed deer prevents palatable species from recruiting, leaving only unpalatable or resilient species.—White-tailed deer are overabundant throughout much of eastern North America and are altering patterns of forest regeneration and reducing diversity (McShea et al. 1997, Horsley et al. 2003, Côté et al. 2004). Waller and Alverson (1997) argued that deer are keystone herbivores in eastern deciduous forest because they preferentially browse certain species (Horsley et al. 2003, Côté et al. 2004), making their impact disproportionate to their abundance. Specifically, deer have contributed to failed oak regeneration and the increase in abundance of *Fagus grandifolia* (Waller and Alverson 1997). Furthermore, Long et al. (2007) reported that traditional shade tolerance rankings based on growth and survivorship in the shaded understory held up only in plots protected from deer browsing; for preferred browse species, survival decreased regardless of growth rate when exposed to browsing (see also Krueger et al. 2009). Hence, we hypothesize that excluding deer should increase growth and survivorship of palatable species, increasing density and diversity of forest understories.

Interactions among disturbances and browsing

The three hypotheses just described all have their merits and compelling lines of evidence, but predictions based on them often assume that each process acts alone in shaping forest community dynamics. In reality, these processes act together in forests and interactions among them may be pervasive (e.g., Royo et al. 2010), driving forest dynamics in unique ways. There exists anecdotal but only limited experimental evidence supporting some of the many possible interactions. For example, Tripler et al. (2005) demonstrated that browsing dramatically altered interspecific rankings of sapling survivorship, but only under open canopies. Hence, excluding browsers may increase density or diversity only under larger gaps. Likewise, browsing may eliminate advance regeneration of browse-intolerant species. Hence, larger gaps may increase density and diversity only if deer are excluded. Fire may promote fire-tolerant species such as *Quercus* by increasing understory light levels (Rentch et al. 2003), but not if browsing substantially reduces their survival (Long et al. 2007). Additionally, browsing may differentially reduce sapling growth rates or alter resource allocation, thus reducing their ability to resprout following fire (Frelich 2002). Larger gaps may promote diversity, but only if shade-tolerant species are thinned by fire (Van Lear and Brose 2002, Rentch et al. 2003). Only by experimentally testing the competing hypotheses simultaneously can we rigorously confirm or reject them, identify under what conditions they hold, and assess their relative magnitude in shaping changes in forest composition and dynamics.

Overall, we predict that historically natural disturbances, namely large canopy gaps and low-intensity surface fire, will increase understory density and diversity. However, browsing is predicted to set a first-stage filter on community response to disturbances, constraining any response to the subset of browse-tolerant species. Hence, we hypothesize that gaps and fire will increase density and diversity more (either additively or via an interaction) when browsers are excluded.

METHODS

Study area

We conducted this study in four 20–40 ha stands on the Mead-Westvaco Research Forest in Randolph County, north-central West Virginia, USA. All stands had 10–31% east- or west-facing slopes. In 1999 when our study was initiated, these stands were 64–77 years old and had basal areas of 22–28 m^2/ha, with a closed canopy lacking signs of recent large canopy gaps or fire. Fire return intervals in this system are on the order of 25–30 years or more (Collins and Carson 2003). Typical of mixed mesophytic/northern hardwood transition forests, canopies were species rich, composed of 10–15 species of dominant and codominant trees (Braun 1967, Dyer 2006; for more detailed site description, see Collins and Carson 2003).

Experimental design

We manipulated fire, deer browsing, and canopy gaps using a split-plot, factorial design in a randomized complete block (Fig. 1). We subdivided each of four blocks (i.e., stands) in half. Within each half we established eight 20 × 20 m plots (20 m from block edges, fire breaks, and other plots; 64 experimental units in total). Each half-stand was randomly assigned a fire or a no-fire treatment, and two plots within each half were randomly assigned each of the following four treatment combinations: browsing (no fence) without canopy gap; browsing with canopy gap; canopy gap without browsing (fenced); and neither browsing nor canopy gap. Browsed, unburned plots without a canopy gap are referred to as controls.

Experimental canopy gaps were of a size consistent with those occurring in old-growth stands (Runkle 1982, Clebsch and Busing 1989, Beckage et al. 2000). To create gaps, in spring 1998 we girdled and injected herbicide (Accord by Monsanto, St. Louis, Missouri, USA; Collins and Carson 2003) into all canopy trees that had crowns encroaching on a 9 m radius circle in the center of assigned plots, creating canopy gaps $\geq$255 m^2 in area ("non-expanded" definition of Runkle 1982; "expanded gaps" would be $\geq$380 m^2). By time of data collection (2004), we observed that all targeted trees clearly had been dead for several years.

Fenced deer exclosures were erected around the assigned plots ($\geq$1 m outside plot boundaries) in summer 1998 and have been maintained since then. Exclosures consist of 2 m tall wire mesh fences with mesh size of 30 × 15 cm to exclude deer but allow entry of small- to medium-sized animals (e.g., raccoons *Procyon lotor* and Wild Turkey *Meleagris gallopavo*). White-tailed deer density at this site was 11.5–18.0 deer/km^2 (Langdon 2001) and has been at this level for at least 20 years (Storm and Palmer 1995; West Virginia Department of Natural Resources, *unpublished data*).

The half of each stand assigned to the fire treatment was burned between 30 April and 4 May 1999 after 6–10 days without rain, during the sapling layer budbreak but prior to canopy budbreak, and during peak fire season. Fires resembled natural surface fires in being fueled primarily by leaf litter and small woody debris (Abrams 1992; for details, see Collins and Carson 2003). Our next controlled burn is scheduled for 2024, in keeping with the estimated fire return interval of 25 years.

Data collection and analysis

We censused each plot in May through November 2004. We identified and recorded dbh (diameter at breast height, 140 cm) of all woody stems >140 cm tall throughout each 20 × 20 m plot. We identified and counted all stems 20–140 cm tall within a central 10 × 10 m plot. All individuals (28 985 stems) were identified to species (*Betula alleghaniensis* and *B. lenta* were difficult to identify to species when small, so these were grouped under the genus *Betula*). We analyzed the effects of treatments on seedlings (stems 20–140 cm tall) and saplings (stems >140 cm tall with dbh $\leq$5.0 cm). Within each size class, response variables were: relative abundance (p_i) of species achieving $p_i \geq 15\%$ in any size class or treatment combination; total stem density (N); species richness (S); and Shannon diversity ($\exp[H'] = \exp[-\sum p_i \ln(p_i)]$; $\exp[H']$ scales H' to units of number of species; Jost 2005). Because density can affect estimates of diversity (Gotelli and Colwell 2001, Schnitzer and Carson 2001), we calculated the expected species richness (i.e., rarefaction) of each plot for a sample size of 10 individuals per sample. Due to low densities, especially in burned and browsed plots, this analysis excluded 7 seedling plots and 10 sapling plots (of 64 total for each), resulting in an unbalanced design, lower power to detect interactions, and greater chance of Type II error for fire and browsing effects. Although we present results of rarefaction in Table 1, we do not discuss them further due to these problems (note, however, that effects based on rarefaction supported those from species richness for main effects).

We arcsine square-root transformed p_i and square-root transformed N to stabilize their variance prior to statistical analysis. Analysis of p_i excluded plots where $N = 0$ (i.e., plots with no stems of any species in that size class; hence, $n = 62$ for seedlings, $n = 60$ for saplings). Treatments and their two-way and three-way interactions were used as independent variables in split-plot ANOVAs. Analyses were performed using PROC MIXED in SAS 9.1, using fire, gap, and browsing as fixed effects and stand and stand × fire as random effects. Model simplification was performed by removing nonsignificant ($P \geq 0.05$) interactions one by one, starting with the three-way interaction and proceeding from highest to lowest P value among the two-way interactions. Main effects were retained in the model even if they were nonsignificant (Neter et al. 1996). When interactions were significant, multiple comparisons between treatment combination means were performed using least-significant means (LSMEANS). Although we performed many statistical tests, we did not adjust P values because tests were used collectively, not in isolation, to address a priori hypotheses of whole-community response (see Moran 2003).

To test the null hypothesis that tree species composition within a size class did not vary among treatments or treatment combinations, we used nonparametric blocked multi-response permutation procedures, MRBP

TABLE 1. Effects of treatments on density, diversity, and community composition of tree seedlings and saplings at Mead-Westvaco Experimental Forest, north-central West Virginia, USA, five years after treatment.

Treatment, by size class	Total stem density		Species richness		Shannon diversity, $e^{H'}$		Rarefied species richness†		Community composition	
	P	df	*P*	df	*P*	df	*P*	df	*A*	*P*
Fire										
Seedlings	0.3714	1, 3	0.3714	1, 3	0.8000	1, 3	0.9829	1, 3	**0.013**	**0.0040**
Saplings	0.8996	1, 3	0.4731	1, 3	0.3146	1, 3	0.8012	1, 3	**0.015**	**0.0005**
Gap										
Seedlings	**<0.0001** ↑	1, 54	**<0.0001** ↑	1, 53	**0.0007** ↑	1, 53	**0.0247** ↑	1, 47	**0.014**	**0.0013**
Saplings	**<0.0001** ↑	1, 53	**0.0002** ↑	1, 53	**0.0043** ↑	1, 53	0.1175	1, 44	<0.0001	0.4220
Browsing										
Seedlings	**<0.0001** ↓	1, 54	**<0.0001** ↓	1, 53	**<0.0001** ↓	1, 53	**0.0024** ↓	1, 47	**0.017**	**<0.0001**
Saplings	**<0.0001** ↓	1, 53	**<0.0001** ↓	1, 53	**<0.0001** ↓	1, 53	**0.0169** ↓	1, 44	**0.005**	**0.0492**
Gap × fire										
Seedlings	NS		**0.0346**	1, 53	**0.0453**	1, 53	NS		**0.032**	**<0.0001**
Saplings	NS		NS		NS		NS		**0.011**	**0.0344**
Browsing × fire										
Seedlings	NS		NS		NS		NS		**0.035**	**<0.0001**
Saplings	**0.0003**	1, 53	**<0.0001**	1, 53	**0.0300**	1, 53	NS		**0.025**	**0.0006**
Gap × browsing										
Seedlings	NS		NS		NS		NS		**0.036**	**<0.0001**
Saplings	NS		NS		NS		NS		0.004	0.1804

Notes: *P* values in bold are significant ($P < 0.05$). For density, diversity, and richness tests, ↑/↓ indicates the direction of the effect (ANOVA); for effects of significant ($P < 0.05$) interactions, see Fig. 3 (three-way interactions were not significant); nonsignificant interaction terms were removed from the statistical model, and so no statistics are reported. For community composition, *A* is the distance statistic and *P* is the probability of no difference (MRBP).

† Expected species richness based on a sample of 10 individuals from each plot (experimental unit). Seven seedling plots and 10 sapling plots had fewer than 10 individuals and were excluded from rarefaction analysis, possibly biasing results and leading to Type II errors.

(McCune and Grace 2002) with PC-ORD 5.0 (MjM Software Design, Gleneden Beach, Oregon, USA). Effects of single treatments (e.g., browsing) were evaluated by pooling across the other two treatments (e.g., gap and fire treatments). Effects of interactions among treatments (e.g., browsing × fire) were evaluated by pooling across the third treatment (e.g., gaps). For each size class, we relativized abundance values to a common scale (0–1) and deleted rare species (p_i <15% in any size class or treatment combination) in order to equalize the influence of common and rare species (McCune and Grace 2002).

RESULTS

We present results beginning with general comparisons of treatments vs. controls across all analyses of density, diversity, and composition. We then present those pertaining to each factor (browsing, canopy gaps, or fire) independent of the other factors (i.e., statistical main effects). This perspective is analogous to what one might expect for different single-factor experiments when the other factors are unmanipulated but present to varying degrees in the landscape and contribute to variation in the specific factor being investigated. We then present results in response to pairwise combinations of factors (i.e., statistical interaction effects) to show how species and community response to specific factors sometimes depends on the level of other factors occurring at the same time.

General trends

Browsing, fire, canopy gaps, and their interactions caused the formation of contrasting understory communities by dramatically altering relative abundance, density (N), and diversity (S and $\exp[H']$) of woody understory vegetation (Tables 1 and 2, Figs. 2 and 3). The understory in control plots was typically depauperate and sparse (Fig. 2H; *Fagus grandifolia* and *Acer saccharum* dominated). All 10 abundant species responded significantly to at least one of these processes or interactions among them in at least one size class (Table 2). We never found a significant ($P < 0.05$) three-way interaction for any response variable.

Browsing creates depauperate understory communities

Averaged across experimental treatments of large canopy gaps and fire, the exclusion of browsers significantly increased density, richness, and diversity of seedlings and saplings, thereby creating dense and diverse understory communities (significant browsing main effects; Table 1). Browsing created seedling and sapling communities that contrasted sharply with those in unbrowsed plots (MRBP, $P < 0.0001$ for seedlings and $P = 0.0492$ for saplings; Fig. 2 left side vs. right side). Browsing decreased the relative abundance of *Acer*

TABLE 2. Effects of treatments on relative abundances of tree seedlings and saplings at Mead-Westvaco Experimental forest five years after treatment.

Species (shade/fire tolerance)†, and size class	Fire		Gap		Browsing		Gap × Fire		Browsing × Fire		Gap × Browsing
	P	df	*P*	df	*P*	df	*P*	df	*P*	df	*P*
Acer pensylvanicum (high/germination, sprouting)											
Seedlings	0.5170	1, 3	0.4662	1, 52	0.8433	1, 52	NS		NS		NS
Saplings	0.3210	1, 3	**0.0189** ↑	1, 49	0.4295	1, 49	NS		**0.0284**	1, 49	NS
Acer rubrum (med/nt)											
Seedlings	0.8912	1, 3	**0.0001** ↑	1, 50	<**0.0001** ↓	1, 50	**0.0003**	1, 50	**0.0117**	1, 50	NS
Saplings	0.2793	1, 3	0.0851	1, 50	**0.0426** ↓	1, 50	NS		NS		NS
Acer saccharum (high/nt)											
Seedlings	0.2690	1, 3	0.5938	1, 52	**0.0400** ↓	1, 52	NS		NS		NS
Saplings	0.8912	1, 3	0.4883	1, 50	**0.0171** ↑	1, 50	NS		NS		NS
Betula spp. (med/germination)											
Seedlings	0.1774	1, 3	<**0.0001** ↑	1, 52	**0.0047** ↑	1, 52	NS		NS		NS
Saplings	0.8855	1, 3	0.8640	1, 50	0.8569	1, 50	NS		NS		NS
Fagus grandifolia (high/nt)											
Seedlings	0.4230	1, 3	**0.0007** ↓	1, 52	**0.0431** ↑	1, 52	NS		NS		NS
Saplings	**0.0484** ↓	1, 3	0.0748	1, 50	0.6507	1, 50	NS		NS		NS
Prunus pensylvanica (nt/germination)											
Seedlings	0.0727	1, 3	0.2278	1, 52	0.7352	1, 52	NS		NS		NS
Saplings	0.3518	1, 3	0.2471	1, 49	0.0004 ↓	1, 49	NS		**0.0016**	1, 49	NS
Prunus serotina (nt/sprouting)											
Seedlings	0.4875	1, 3	0.5041	1, 52	**0.0047** ↓	1, 52	NS		NS		NS
Saplings	0.2457	1, 3	0.4440	1, 50	0.1682	1, 50	NS		NS		NS
Quercus rubra (med/sprouting)											
Seedlings	0.1629	1, 3	0.7234	1, 52	<**0.0001** ↓	1, 52	NS		NS		NS
Saplings	0.0767	1, 3	0.3137	1, 50	0.8347	1, 50	NS		NS		NS
Robinia pseudoacacia (nt/sprouting)											
Seedlings	0.9492	1, 3	0.6723	1, 51	**0.0398** ↑	1, 51	**0.0301**	1,51	NS		NS
Saplings	0.2203	1, 3	0.2630	1, 50	0.7289	1, 50	NS		NS		NS
Tilia americana (med/nt)											
Seedlings	0.3183	1, 3	0.0956	1, 52	0.1441	1, 52	NS		NS		NS
Saplings	0.3899	1, 3	0.7326	1, 50	**0.0031** ↓	1, 50	NS		NS		NS

Notes: *P* values in bold are significant ($P < 0.05$), and ↑/↓ indicates the direction of the effect. Effects of significant ($P < 0.05$) two-way interactions are depicted in Fig. 4 (see also Fig. 2; no three-way interaction was significant). Nonsignificant interaction terms were removed from the statistical model so no statistics are reported.

† Shade and fire tolerance ratings are from Fire Effects Information System (http://www.fs.fed.us/database/feis/): high, shade tolerant; med, intermediately shade tolerant; germination, fire tolerant due to new germination; sprouting, fire tolerant due to resprouting; nt, not tolerant to shade or fire.

rubrum, *Acer saccharum*, *Prunus serotina*, and *Quercus rubra* seedlings, and *Tilia americana* and *Prunus pensylvanica* saplings, whereas browsing increased the relative abundance of *Betula*, *Fagus*, and *Robinia pseudoacacia* seedlings and *Acer saccharum* saplings (Table 2, Fig. 2 left side vs. right side; *Robinia* seedlings were only observed in browsed plots). Note that because browsing also decreased total density, positive browsing effects on a species' relative abundance did not coincide with a positive effect on absolute abundance except for the most abundant species in browsed plots.

Large canopy gaps created dense and diverse understories

As with excluding browsers, the creation of large canopy gaps caused the formation of a significantly more diverse and dense understory (Table 1) and created seedling communities that contrasted between plots beneath a gap vs. ones under an intact canopy (MRBP, $P = 0.0013$; Fig. 2), although gap creation did not alter composition of sapling communities (MRBP, $P = 0.4420$). Gaps increased the relative abundance of *Acer rubrum* seedlings (but only in unburned plots; Table 2, Fig. 4), *Acer pensylvanicum* saplings, and *Betula* seedlings, but reduced the relative abundance of *Fagus* seedlings (Table 2); these effects contributed to substantially reduced dominance of *Fagus* within gaps (also compare gap vs. non-gap graphs in Fig. 2).

Fire creates contrasting communities but has no effect on understory diversity or density by itself

Fire dramatically altered seedling ($P = 0.0004$) and sapling ($P = 0.0005$) communities compared to unburned plots (MRBP on fire main effect). However, the effect of fire on density, richness, or diversity of seedlings

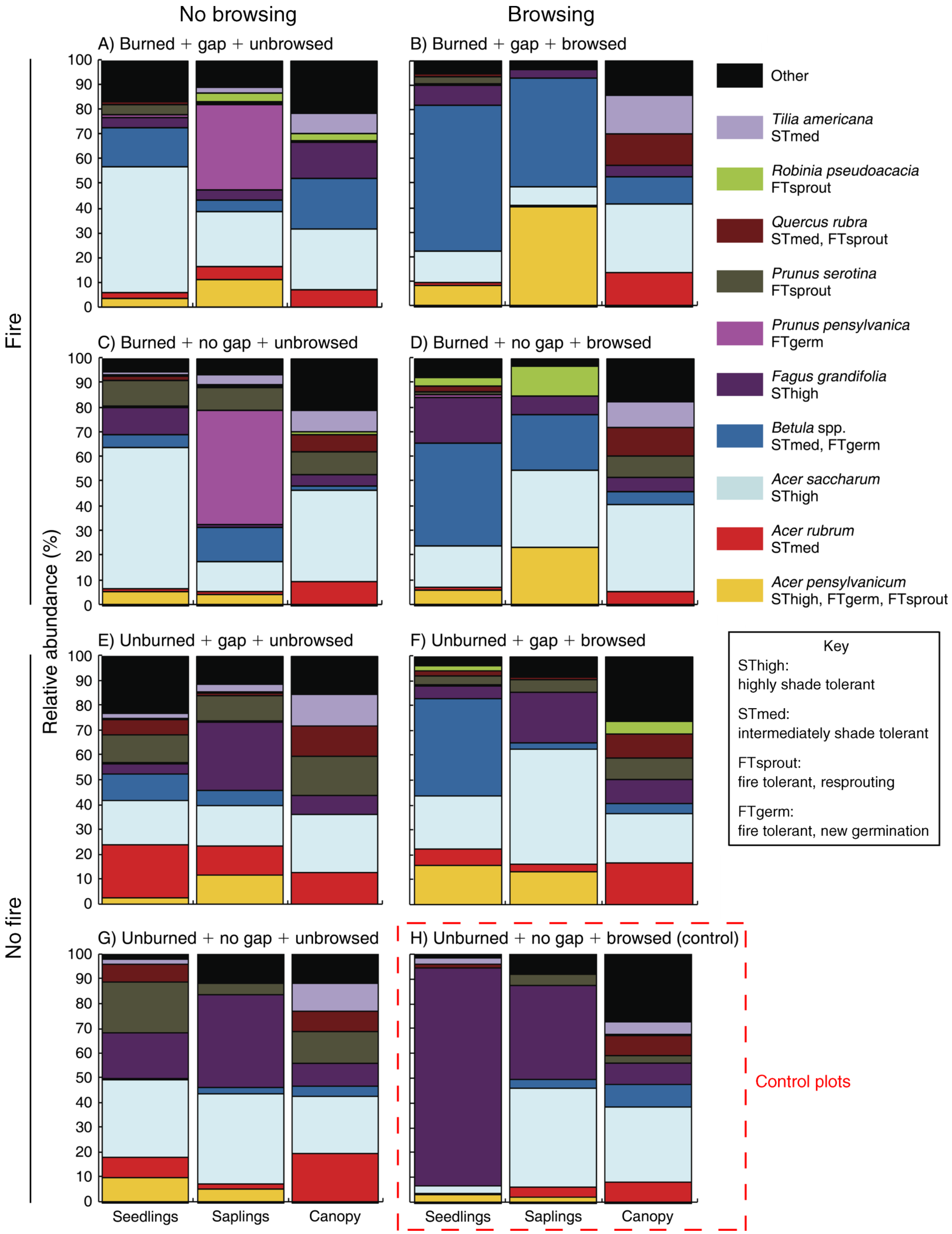

FIG. 2. Relative abundance of the 10 most common tree species in different treatment combinations and size classes (A–H). Graphs in the left column show data from plots protected from deer browsing whereas those in the right column show data from plots exposed to browsing; the top four graphs show data from burned plots, and the bottom four unburned plots; canopy gap treatment alternates from top to bottom in both columns: gap, no gap, gap, no gap. Control plots are shown in panel (H). Shade and fire tolerance ratings are from the U.S. Forest Service's *Fire Effects Information System* (http://www.fs.fed.us/database/feis/).

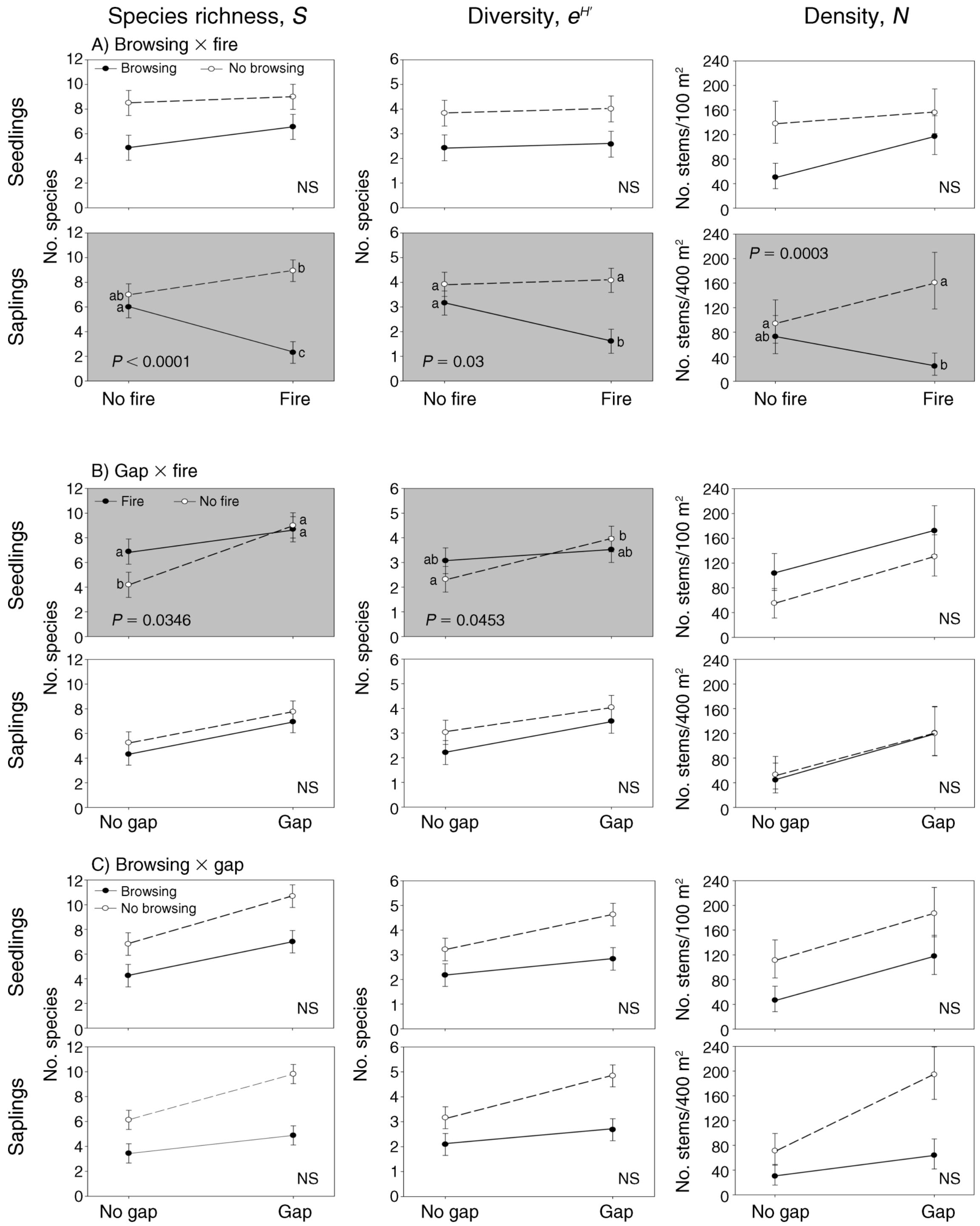

FIG. 3. Interactions between fire, canopy gap, and browsing treatments on species richness (S), diversity ($e^{H'}$), and density (N) of seedlings and saplings. Significant interactions are highlighted with gray backgrounds. Error bars represent SE. For significant interactions, effects of treatment combinations with the same lowercase letters are not significantly different ($P > 0.05$).

and saplings depended entirely on its interaction with gap formation and browsing (i.e., the main effect of fire on these metrics was never significant, but fire × browsing and fire × gap interactions were common; Table 1, Fig. 3).

Interactions between processes create contrasting patterns of density, diversity, and community composition

Fire exacerbates negative effects of browsing.—Although browsing as a main effect (averaged across other

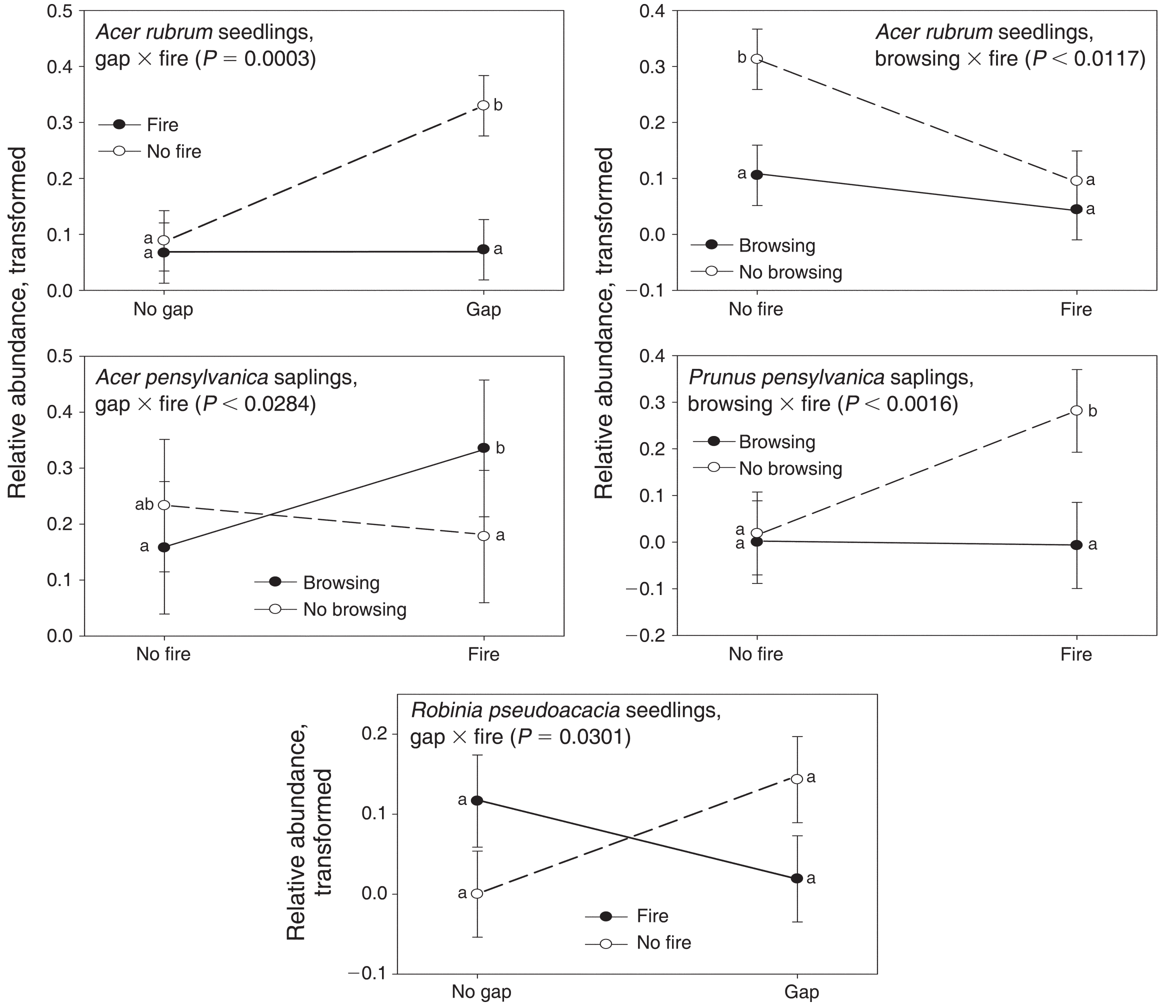

FIG. 4. Significant interactions between fire, canopy gaps, and browsing treatments on relative abundance (transformed arcsine[(relative abundance)$^{1/2}$]). Error bars represent ±SE. Within each interaction diagram, means with the same lowercase letters are not significantly different ($P > 0.05$).

treatments) strongly depressed seedling and sapling density, richness, and diversity, this negative effect of browsing for saplings was only present in burned plots (browsing × fire interaction). Put another way, fire caused significant reductions in density, richness, and diversity of saplings when browsers were present (Table 1, Fig. 3A). When there is protection from browsing, fire may increase richness and density of saplings, but this effect was not significant (Table 1, Fig. 3A). Species composition for both seedlings and saplings contrasted sharply between burned plots that were browsed vs. burned plots that were unbrowsed (Tables 1 and 2, Fig. 2A vs. 2B and 2C vs. 2D). Fire increased the relative abundance of *Acer rubrum* seedlings and *Prunus pensylvanica* saplings only when browsers were excluded, whereas fire increased the relative abundance of *Acer pensylvanicum* saplings only in the presence of browsers (significant browsing × fire interactions; Table 2, Fig. 4). *Prunus pensylvanica* dominated in burned plots protected from browsers, whereas *Betula* and *Acer pensylvanicum* dominated in burned plots with browsers present (Fig. 2, although the interaction was not significant for *Betula*; Table 2, Fig. 4).

Fire and large gaps are largely compensatory disturbances.—Considering the specific combination of gap and fire treatments, gaps and fire separately each increased richness and diversity of seedlings by roughly the same amount, but their combination was not additive (gap × fire interaction, Table 2, Fig. 3B). In other words, with respect to richness and diversity of seedlings, these two different disturbances were somewhat compensatory (Fig. 3B). There was no fire × gap interaction for sapling density, diversity, or richness. However, fire created seedling and sapling communities that differed from those created by gaps without fire (Table 1, Fig. 2A vs. 2E). Fire decreased the relative abundance of *Acer rubrum* in plots with a gap (Table 2, Fig. 4).

Gaps in combination with exclusion of browsers created the densest, most diverse understory communities.—Although the browsing × gap interaction was not significant for any community metric, when added together, large canopy gaps and exclusion of browsers created communities with the highest density and diversity of seedlings and saplings (Table 1, Fig. 3C). As hypothesized, exclusion of browsers caused a somewhat greater increase in density and diversity under gaps than under closed canopies (Fig. 3C).

Discussion

Historic disturbance regimes may maintain diversity only under historic browsing regimes

Although large canopy gaps and understory fire are widely recognized as drivers of forest dynamics, our results demonstrate that restoring these disturbances to eastern deciduous forest may not restore understory density and diversity unless excessive browsing is controlled. This finding is critical because deer are overabundant in vast areas of eastern deciduous forest. Consequently, historical disturbance regimes that once enhanced diversity will now no longer do so where deer are overabundant. More specifically: (1) under ambient deer density (11.5–18.0 deer/km^2), fire reduced density and diversity in the understory, but fire may increase density and diversity if browsers are excluded (Fig. 3A); (2) creation of large canopy gaps characteristic of old-growth forests promoted growth of a wider range of shade tolerance classes (Table 2), including shade-intolerant species, even more so with the additive effects of browser exclusion (Fig. 3C); (3) browsing altered the template of species upon which both disturbances could act (Fig. 2) and exclusion of browsers enhanced density and diversity in the understory more than either disturbance alone (compare browsing effect sizes to those of gaps and fire in Fig. 3); and (4) most importantly, diversity and composition of the key regeneration layer of these forests can be restored and maintained by mimicking historic gap regimes in combination with eliminating browsing—or more appropriately, reducing browser density closer to historic levels (Fig. 2). These points are elaborated and supported in the next sections. Overall, these results provide compelling evidence that browsing by deer constitutes a critical first-stage filter that constrains community response to disturbance by fire and large canopy gaps.

Fire exacerbates negative effects of browsing on tree regeneration.—Many have argued that fire promotes diversity by reducing understory shading and dominance by shade-tolerant species, thereby promoting growth of fire-tolerant species, especially oaks (e.g., Abrams 1992, Lorimer et al. 1994, Sutherland 1997, Brose et al. 2001, Van Lear and Brose 2002). Although fire did alter community composition (Table 1), contrary to our fire hypothesis, over the relatively short course of our study (five years) and with a single fire, we saw no positive effects of fire on density or diversity of understory regeneration (Table 1). Indeed, our results suggest that when browsers are abundant, burning may be detrimental because with browsers present, fire tended to reduce density and diversity of saplings (Fig. 3A). Under browsing pressure, burning essentially substituted one low-diversity community with two dominant species without fire (*Fagus* and *Acer saccharum*) for another with three dominant species with fire—two of which can become canopy trees (*Betula* and *Acer saccharum*) and the other of which cannot (*Acer pensylvanicum*, cf. Fig. 2D, H). These findings may well apply broadly because of deer overabundance over vast areas of the eastern United States and they suggest that the use of fire alone to promote diversity may be counterproductive unless deer are brought under control.

Fire had no effect on altering density or diversity of seedlings and saplings independent of gaps and deer browsing because communities responded differently to fire depending on whether they were browsed or unbrowsed or whether they had gaps (Table 1). The main effect of fire averages over the other factors and was therefore small (Fig. 3A, B). In an observational study in mixed oak–pine forest, Patel and Rapport (2000) reported significant negative effects of increasing deer abundance on seedling density and plant species richness, but no average effect of prescribed fire. They hypothesized that fire may enhance regeneration but only under low browser density; however, their study design did not allow interactions to be tested. Our controlled experiment provides evidence supporting their hypothesis in that we found no effect of fire on density and diversity when averaged over different browsing treatments (i.e., no fire main effect), but significant browsing × fire interactions where the combination of browsing and fire tended to depress density and diversity (Fig. 3A). Our fire treatment killed or burned aboveground biomass of most seedlings and saplings (Collins and Carson 2003). After fire, new seedlings or resprouting saplings of most species could only recruit when protected from browsing. Five years later, browsed plots still had lower density and diversity of large saplings, but density and diversity in burned, unbrowsed plots recovered to the levels in unburned plots (Fig. 3A).

Rentch et al. (2003) argued that higher light levels following a surface fire formerly allowed oaks to survive longer in the understory, thus allowing them to fill gaps. However, prolonged browsing can reduce growth rates of understory trees and reduce their survival regardless of light levels or growth rate (Long et al. 2007, Krueger et al. 2009). Our findings suggest that tree species such as oaks that are intermediate in shade tolerance may have persisted in the understory because of low browsing pressure alone (or when it occurred in combination with higher light levels created by fire or large canopy gaps). However, because of widespread overabundance of browsers, gaps and fire may no longer promote less shade-tolerant tree species (except *Betula*).

Fire—with or without browsing—created understory communities dramatically different from the current canopy (Fig. 2A–D). As predicted, fire reduced the abundance of a highly shade-tolerant species, *Fagus*, but the resulting community depended on browsing. With browsing, a highly shade-tolerant, browse-tolerant subcanopy tree, *Acer pensylvanicum*, became dominant, forming dense layers that could suppress the recruitment of other species and potentially form either a highly recalcitrant understory layer (sensu Royo and Carson 2006) consisting of a much lower-statured canopy or a very different successional trajectory (Frelich 2002). In sharp contrast, the exclusion of browsers caused the dominance of a short-lived (25–35 years; Marks 1974) pioneer tree, *Prunus pensylvanica*, in the sapling layer along with shade-tolerant *Acer saccharum* in the seedling layer, which also dominates control plots (Fig. 2A–D). Thus fire did not promote diversity of understory regeneration as predicted because under either browsing scenario, reduction in dominance by a few shade-tolerant species was matched by increased dominance of a few (not many) fire-tolerant species.

Promotion of oak regeneration is one of the primary reasons given for prescribed fire (Brose et al. 2001, Van Lear and Brose 2002). Indeed, Rentch et al. (2003) argued that the only surface disturbance capable of favoring oaks and disfavoring *Acer saccharum* and *Fagus* is surface fire. However, fire had no effect in promoting oaks or a diverse array of other species in our study, even when protected from deer browsing (in fact, only browsing significantly affected *Quercus rubra*; Table 2, Fig. 2 left vs. right side). Although fire was not effective at increasing oaks or tree diversity in our study, it may be more effective in more oak-dominated forests or with more burns (the next is scheduled for 2024, 25 years after the first) because oaks are expected to be better able to resprout following fire than other species such as beech and maples (Lorimer 1992), as long as deer browsing is controlled. However, even in oak–hickory forests of Ohio, USA, repeated burns did not increase oak regeneration (Hutchinson et al. 2005). Overall, there exists only weak evidence that multiple burns promote oak regeneration; oaks did not produce vigorous sprouts in our study under any treatment combination (Collins and Carson 2003). Masting events may provide periodic pulses of oak regeneration that may promote oak persistence over the long term; although oaks did not mast during our study, for masting to be effective, seedlings would have to resprout following fire, which the oaks we measured did not do well (Collins and Carson 2003), and would have to avoid being browsed (note: *Fagus* and *Acer* spp. also did not mast during our study).

Van Lear and Brose (2002) suggested that several burns over many years, in combination with overstory release, might be necessary to substantially alter composition of forest regeneration; however, they did not recommend this strategy in areas with high deer densities because it would create "magnets for deer." Such an increase in browsing pressure in response to fire has been referred to as "pyric herbivory" (Fuhlendorf et al. 2009). In contrast to the original usage, where fire-dependent grazing was essential to restore prairie plant communities, in our system, browsing in combination with or in response to fire resulted in a "double whammy" for understory tree regeneration. However, in another study where ambient deer density was lower ($\sim$4–7 deer/km^2), moderate levels of browsing following gap formation and fire enhanced understory herbaceous diversity (Royo et al. 2010). It seems that the nature of the fire × herbivore interaction and its effect on native plant communities depends in large part not only on how herbivores respond to fire (Fuhlendorf et al. 2009) but also on how high their densities are relative to that within the evolutionary history of the community.

Gaps caused dramatic increases in density and diversity, but only in the absence of browsers.—There is compelling evidence that large gaps promote diversity by allowing for the coexistence of tree species that are intermediate in shade tolerance or are intolerant of shade (Runkle 1981, Shuggart 1984, Clebsch and Busing 1989, Burns and Honkala 1990, Rentch et al. 2003), whereas small gaps are mainly filled by lateral extension or recruitment of shade-tolerant advance regeneration or sprouts (Canham et al. 1994, Dietze and Clark 2008). However, in one of the few experimental tests of the effect of gap creation on forest diversity, Beckage et al. (2000) reported that "intermediate-sized" gaps ($\sim$300-m^2 expanded gaps, slightly smaller than ours) did not promote diversity of tree regeneration compared to undisturbed forest. Similarly, Shure et al. (2006) reported little effect of gaps or gap size on tree diversity in clearcuts ranging from 160 to 20 000 m^2 (non-expanded gaps). In contrast, our experimental gaps increased richness and diversity somewhat ($<$50% increase; Fig. 3C) when browsers were present. But, when browsers were excluded, the creation of a large gap typical of old-growth forests more than doubled the richness and diversity of seedlings and saplings (Fig. 3C; browsing + no gap vs. no browsing + gap), creating a reservoir of less shade-tolerant species in the community (Fig. 2E). Indeed, the additive effects of large gaps and exclusion of browsers promoted growth of species found in the canopy but that were uncommon or absent in seedling or sapling layers of any other treatment combination (e.g., compare Fig. 2E to 2F–H; note also the large proportion of seedlings in the "other" category, representing uncommon species, in Fig. 2E but not in Fig. 2F–H, a proportion similar to that in the canopy). Our findings demonstrate that larger gaps typical of old-growth forests can promote tree species diversity of the regeneration layer, but only when browsers are not overabundant.

In contrast to the pervasive negative effects of deer browsing reported in the literature (Côté et al. 2004), the reported effects of canopy gaps are more variable and seem to depend not only on gap size but also on whether a dense understory layer of advance regeneration or shrubs creates a barrier to recruitment by other species (Runkle 1981, Beckage et al. 2000, Webb and Scanga 2001, Webster and Lorimer 2005, Royo and Carson 2006). This variation also might be due to interactions with other, unmanipulated factors such as deer density, which varies across the region (Quality Deer Management Association 2009). Our highly replicated study (32 experimental gaps) provides evidence reconciling the conflicting studies on the effectiveness of large gaps in promoting diversity: effectiveness of gaps depends on whether browsing has eliminated advance regeneration that can respond to gap creation. Indeed, deer will seek out gaps for foraging due to increased browse availability, similar in concept to pyric herbivory, but when deer are overabundant, any increased regeneration may nevertheless fail to recruit past the browsing filter. Consequently, an important and region-wide disturbance regime (gap formation) that once promoted diversity across the landscape fails to do so or is far less effective under elevated browsing pressure.

Pervasive impacts of deer have wide-ranging, regional implications

Because browsing can reduce or even reverse the effects of the other hypothesized drivers of forest change, we conclude that browsing by elevated deer populations is the primary factor driving forest change in this study. Browsing is "primary" in the sense that it is a first-level filter constraining the species pool upon which disturbances can act (Hobbs and Norton 2004), either because browsers eliminate advance regeneration or because they prevent species that would otherwise respond to disturbance from recruiting. It is also "primary" in the sense of "most important": interactions of browsing with fire and canopy gaps were secondary to the main browsing effect because in almost every case of a significant fire × browsing and gap × browsing interaction there was also a significant browsing main effect (Tables 1 and 2).

Tripler et al. (2005) and Horsley et al. (2003) both reported relatively little impact of deer browsing on sapling growth and survival under closed-canopy conditions, but dramatic effects under open-canopy (large clearcut) conditions. In contrast, we demonstrated dramatic effects of deer browsing on richness, diversity, density, and relative abundance under both closed canopy and in gaps, even though our gaps were much smaller than the clearcut conditions they investigated. Similarly, in a study investigating the effects of deer, fire, and thinning in mixed oak forests in southeastern Ohio, Apsley and McCarthy (2004) reported only small effects of deer on understory vegetation composition and sapling height two years after treatment. However, deer density in their area (5.4–6.3 deer/km^2) was one-half to one-third that in our area, and their analysis did not investigate interactions among deer browsing and thinning or fire. Horsley et al. (2003) reported a threshold of significant negative effects of deer browsing on forest vegetation at densities of >8 deer/km^2. Current deer densities are far above this threshold in vast areas across the United States; according to this recommendation, browsing pressure is likely to play a major role in the approximately 50% of eastern deciduous forest where deer density is at or above that in our study (Quality Deer Management Association 2009). Browsers are also overabundant in many other ecosystems worldwide (Royo and Carson 2006). If, as we suspect, correlations between browse and shade tolerance are widespread, these ecosystems may also see an unraveling of the connection between historic disturbance regimes and diversity.

At the time these stands were established in the early 20th century, white-tailed deer were almost extinct throughout eastern North America (Redding 1995, McCabe and McCabe 1997). Hence, these conditions of low browsing pressure provided the opportunity for many browse-intolerant species to establish and recruit into the canopy. Although deer density at the time of stand establishment was abnormally low, the current density is four to five times higher than pre-Columbian estimates (3.5 deer/km^2; McCabe and McCabe 1997). We found that even species thought to be highly tolerant of browsers were not (e.g., *Prunus serotina*, Horsley et al. 2003). Thus, even highly browse-tolerant species were reduced in abundance and this probably contributed to the low density and depauperate understories that characterized our control plots and are often seen elsewhere (e.g., Banta et al. 2005, Royo and Carson 2006).

We furthermore demonstrate that the current dominance of *Acer saccharum* and *Fagus* in the understory of control plots cannot be attributed solely to succession driven by shade tolerance, because species such as *Tilia americana*, *Prunus serotina*, and *Quercus rubra*, which are not shade tolerant, increased when browsing was eliminated but did not respond to the gap treatment (Table 2; compare also Fig. 2F–H). Indeed, excluding deer increased understory density (Table 1, Fig. 4), which should actually increase understory shade. Hence, the current dominance of *Fagus* and *Acer saccharum* and lack of "shade"-intolerant or intermediate species in the understory of these forests may be a function of both browse and shade tolerance (see Krueger et al. 2009).

If forest managers are interested in reversing the downward trend in diversity of regenerating mixed mesophytic forests—including promoting important commercial species such as *Quercus* and *Prunus serotina*—reduction of browsing pressure by deer is clearly in order. Because the density and diversity of forest regeneration were co-limited by browsing and low light, perpetuating diverse forests most similar to the existing canopy probably will require larger canopy openings in combination with reduction of browsing by deer in areas of high deer density (compare seedling vs. canopy layers in Fig. 2E). Deer browsing can be reduced by fencing to exclude browsing following timber harvest, as is currently common practice in Pennsylvania, USA, or by reducing regional deer density through effective population management. Short of fencing large areas of forest, these lines of evidence suggest that a regional reduction in deer density is a reasonable management goal if maintenance of forest diversity is a priority. Overall, however, our findings suggest that unless deer numbers are brought down, vast regions of forested land where deer are overabundant will have forest canopies where a small number of species dominate that are both highly shade tolerant and highly browse tolerant.

Fate of forest diversity under high browsing pressure and beech bark disease

Because *Fagus grandifolia* was one of just two species that dominated control plots, our findings have pressing conservation implications under threat of the continued spread of beech bark disease throughout large portions of the eastern deciduous forest (Gavin and Peart 1993, Houston 1994, Hane 2003, Runkle 2007). By killing mature trees, thereby stimulating formation of root sprouts, beech bark disease, in combination with overbrowsing, may create novel mono-dominant communities composed of dense glades of *Fagus* root sprouts. These glades may severely depress recruitment by other tree species because *Fagus* is highly browse tolerant, casts very deep shade, and is highly shade tolerant (Canham et al. 1994). However, our study shows that relatively shade-intolerant species such as *Prunus serotina* and *Quercus rubra* can and do increase in relative abundance when browsing is controlled, even under deep shade (although longer-term survival and recruitment would probably require increased light). Hence, understanding the dynamics triggered by beech bark disease, including how they interact with browsing and other disturbance regimes, deserves much more attention.

Conclusion

Our two most important conclusions are: (1) two region-wide disturbances (surface fire and large canopy gaps) widely thought to promote forest diversity will not do so if browsers are overabundant; (2) the interaction of these ameliorated disturbance regimes (i.e., fire suppression and small canopy gaps) in combination with overbrowsing is causing the formation of a depauperate understory that sets the stage for ever-increasing risk of collapse of forest diversity (compare seedling layer to canopy in Fig. 2H).

Texts dedicated to descriptions of forest dynamics devote chapters to effects of disturbances such as canopy gaps, wind, and fire, yet tend to treat browsing by mammalian herbivores as of secondary importance, a temporary anomaly, or special case that deserves only a few pages (e.g., West et al. 1981, Oliver and Larson 1996). Frelich (2002) concluded that browsers mainly shape the response of the minor vegetation, whereas the major vegetation is determined mainly by fire and wind disturbances. By manipulating deer browsing, canopy gap formation, and fire together in a factorial experiment, we demonstrated the dramatic power of browsing to suppress diversity and density of trees, as well as how browsing created a first-level filter that constrained response of the major vegetation to disturbance. Hence, browsing by deer is by far the most important process regulating forest dynamics in our system. Far from being an anomaly, deer density has been high for decades across much of the continent. In these areas, browsing is likely to be just as important, as well as in forest ecosystems worldwide facing similar browsing pressures (Royo and Carson 2006).

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Supplemental Material

Data Availability

Data associated with this paper have been deposited in Dryad: http://dx.doi.org/10.5061/dryad.sq633