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Fire and non-native grass invasion interact to suppress tree regeneration in temperate deciduous forests

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Summary

1. While many ecosystems depend on fire to maintain biodiversity, non-native plant invasions can enhance fire intensity, suppressing native species and generating a fire–invasion feedback. These dynamics have been observed in arid and semi-arid ecosystems, but fire–invasion interactions in temperate deciduous forests, where prescribed fires are often used as management tools to enhance native diversity, have rarely been investigated.

2. Here we evaluated the effects of a widespread invasive grass on fire behaviour in eastern deciduous forests in the USA and the potential effects of fire and invasions on tree regeneration. We planted native trees into invaded and uninvaded forests, quantified fuel loads, then applied landscape-scale prescribed fires and no-burn controls, and measured fire behaviour and tree seedling and invasive plant performance.

3. Our results show that fires in invaded habitats were significantly more intense, including higher fire temperatures, longer duration and higher flame heights, even though invasions did not alter total fuel loads. The invasion plus fire treatment suppressed native tree seedling survival by 54% compared to invasions without fire, and invasions reduced natural tree recruitment by 66%.

4. We also show that invasive plant biomass did not change from one season to the next in plots where fire was applied, but invader biomass declined significantly in unburned reference plots, suggesting a positive invasive grass–fire feedback.

5. *Synthesis and applications*. These findings demonstrate that fire–invasion interactions can have significant consequences for invaded temperate forest ecosystems by increasing fire intensity and reducing tree establishment while promoting invasive plant persistence. To encourage tree regeneration and slow invasive spread, we recommend that forest managers remove invasions prior to applying prescribed fires or avoid the use of fire in habitats invaded by non-native grasses.

Key-words: eastern deciduous forest, fire behaviour, fire intensity, flame height, forest succession, *Microstegium vimineum*, prescribed fire, stiltgrass

Introduction

Invasions of non-native plants are known to alter disturbance regimes in a wide variety of ecosystems, presenting significant challenges for conservation and restoration (D'Antonio, Dudley & Mack 1999). Invasive plants can affect fire regimes by changing fire intensity and frequency, continuity of fuels and fire return cycles (reviewed by Brooks *et al.* 2004). Changes in fire regimes in invaded areas can in turn decrease the abundance and diversity of native species, expose bare ground, alter soil nutrient availability and promote further invasions, resulting in a positive fire–invasion feedback (Vila *et al.* 2001; Rossiter *et al.* 2003). For example, in the submontane zone of Hawaii invasions of non-native grasses (*Andropogon, Melinis* and *Schizachyrium* spp.) significantly increased the frequency and extent of fires, which promoted more widespread grass invasions and reduced the cover and diversity

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of native shrubs and trees (Hughes, Vitousek & Tunison 1991). Generally, grass invasions produce abundant, highly flammable fuel loads that carry fire quickly and continuously, resulting in the decline of native shrubs and perennial grasses in some systems (reviewed by D'Antonio & Vitousek 1992). Fires can also have a fertilizing effect when nitrogen and other nutrients are released from burned material, further contributing to the spread of non-native grasses and instigating a grass–fire cycle that is difficult to break. Furthermore, increases in fire frequency and severity due to climate change may enhance fire–invasion interactions, accelerate the rate at which landscapes are invaded and cause further damage to native systems (Grigulis *et al.* 2005).

Nearly all cases where non-native plant invasions have promoted more intense fires, generated feedback and caused unnatural damage to native habitats have been in seasonally dry (e.g. Mediterranean) climates and open habitats, including savannas (Rossiter *et al.* 2003; Setterfield *et al.* 2010), shrublands and woodlands (Hughes, Vitousek & Tunison 1991; D'Antonio & Vitousek 1992; Vila *et al.* 2001). To our knowledge, no prior study has evaluated the effects of potential fire-promoting invasions on fire behaviour and tree regeneration in more mesic systems with temperate climates such as deciduous forests. In eastern deciduous forests in the USA, for example, there are extensive invasions of non-native plant species, including grasses, forbs, shrubs and trees, but we have a poor understanding of how these invasions might influence fire regimes or alter the effects of fires on plant communities. There is evidence of historical fires ignited by lightning or by native Americans in eastern deciduous forests, which may have maintained forests dominated by oak and hickory by removing litter, inhibiting fire-intolerant tree species and regulating herbaceous plant diversity and productivity (Dey & Hartman 2005). However, other studies have found weaker evidence for pre-Columbian fires in oak forests (Matlack 2013) and have suggested alternative potential drivers of declining oak–hickory dominance in eastern forests. Regardless of their historical frequency, prescribed fires of low to moderate intensities are commonly used to help promote the dominance of particular tree species and plant communities across much of the eastern USA (Bova & Dickinson 2005; Arthur *et al.* 2012). For example, in 2013, 1585 prescribed fires were used to burn more than 89 000 hectares in eight eastern deciduous forest states (IN, KY, NC, OH, PA, TN, VA, WV; NICC 2013). Clearly, determining how plant invasions might alter the effects of fires on plant communities is essential to developing effective management and habitat restoration strategies.

Microstegium vimineum (Trin.) A. Camus stiltgrass is an annual grass of Asian origin that is aggressively invading eastern deciduous forests and has the potential to significantly alter the effects of natural and prescribed fires on plant communities, including native tree regeneration. It often first colonizes roadsides and disturbed areas but also invades successional and mature forests (Flory 2010; Warren, Wright & Bradford 2011) across 26 eastern American states (USDA & NRCS 2005). It is a warm-season grass (i.e. C4 photosynthesis mechanism), but can tolerate very low light levels in closed-canopy forests. *Microstegium vimineum* can increase fire temperatures in invaded areas (Emery, Uwimbabazi & Flory 2011), and reductions in litter following fire can promote *M. vimineum* establishment (Glasgow & Matlack 2007). Dense *M. vimineum* invasions can suppress native herbaceous species (Flory & Clay 2010a) and tree regeneration (Flory & Clay 2010b), and result in a dense litter layer that is slow to decompose (Ehrenfeld, Kourtev & Huang 2001).

Here we used a landscape-scale field experiment to evaluate the effects of *M. vimineum* invasions on fire behaviour in eastern US forests and the potential interactive effects of fire and *M. vimineum* invasion on tree regeneration. We predicted that abundant, continuously distributed fine fuels produced by *M. vimineum* invasions would result in more intense fires and inhibition of tree seedlings in invaded areas. To test these predictions, we planted native tree seedlings into invaded and uninvaded deciduous forest stands, applied replicate large-scale prescribed fires and measured fire intensity, tree seedling survival and growth, natural regeneration of trees following fires and the response of *M. vimineum* across multiple years.

Materials and methods

STUDY LOCATION

We conducted the experiment at Big Oaks National Wildlife Refuge (BONWR), a 20 647 ha former military testing facility in south-eastern Indiana, USA. BONWR is one of the largest contiguous natural areas in the mid-western USA and is the most expansive national wildlife refuge in Indiana. BONWR contains extensive (> 800 ha total) invasions of *M. vimineum* in both upland and lowland sites at varying stages of succession from young forests (< 20 years) to mature, closed-canopy forests. Prescribed fires are used to maintain open grassland or savanna areas but also to encourage oak–hickory dominance and regeneration in forested areas. During 2006–2010, BONWR managers applied prescribed fire to an average of 13 management units covering 3360 ha per year (unpublished USFWS data).

Our research sites were composed of predominantly mixed deciduous forest consisting of *Fagus grandifolia* American beech, *Juglans nigra* black walnut, *Quercus* oak spp., *Acer rubrum* red maple, *Liquidambar styraciflua* sweet gum, *Liriodendron tulipifera* tulip-tree and *Platanus occidentalis* sycamore. Understorey communities were dominated by *Lindera benzoin* spicebush, *Viburnum* viburnum spp. and *Smilax* greenbrier spp. (Gleason & Cronquist 1991). All sites had some history of prior anthropogenic disturbance such as prescribed fire or timber harvests.

EXPERIMENTAL DESIGN

To evaluate the effects of *M. vimineum* invasion on fire intensity and the interaction of fire and invasion on tree regeneration, we established a factorial field experiment in 2008 at BONWR in

M. vimineum-invaded and reference (uninvaded) areas that we either exposed to prescribed fires or left unburned. At BONWR, individual prescribed fires are conducted in management units that range in size from 50 to 1000 ha and include mixed grasslands, old fields and intermediate aged (20–60 years) and mature (> 60 years) forests (Table 1). All of our research plots were established in either intermediate or mature mesic forest areas regardless of invasion status or the other habitat types in the management unit.

We established 10 × 15 m plots (Fig. 1) in areas invaded by *M. vimineum* (> 75% cover) and in nearby areas that either were not invaded or had a low density of *M. vimineum* plants (< 10% cover), and had similar characteristics (i.e. slope, aspect, elevation), understorey plant communities and overstorey density. Sometimes the uninvaded reference plot was located within 100 m, but at other times, the plot was located up to 400 m away because nearby areas with similar habitat and environmental conditions were all invaded. At least one invaded and one control plot were burned during each prescribed fire event and therefore pairs of invaded and control plots exposed to fires experienced similar weather and fuel moisture conditions. In total, 26 plots were established in management units scheduled for prescribed fires in spring in either 2009 or 2010. To evaluate the effects of *M. vimineum* invasion on tree regeneration in the absence of fire, we used the same criteria to establish six plots in invaded areas and six plots in reference (uninvaded) areas in units not scheduled for prescribed fires in spring 2009 or 2010. There were no systematic differences in fire histories or other disturbances between management units we exposed to fire or used as controls.

To evaluate the effects of fire, invasion and their interaction on tree regeneration, and to control for the size, number and species of trees in the plots, native tree seedlings were planted in the plots in February 2008 and 2009, 1–2 months prior to prescribed fires each year. We used 1-year-old nursery-grown (Vallonia State Tree Nursery, Vallonia, Indiana) bare-root seedlings of *Quercus alba* white oak, *Quercus velutina* black oak, *Acer rubrum* red maple and *Liriodendron tulipifera* tulip-tree (Gleason & Cronquist 1991). The functionally similar *Quercus macrocarpa* bur oak (Gleason & Cronquist 1991) was used in place of *Q. velutina* in 2009 plantings (due to limited nursery seedling availability), and we combined data from *Q. velutina* and *Q. macrocarpa* for analyses. All of these tree species are native to Indiana and occur at BONWR. Vallonia State Nursery uses only seeds from Indiana genotypes collected from natural populations. Supplemental irrigation and fertility at the nursery resulted in seedlings with well-developed root systems that have high survival rates (Flory & Clay 2010b). Tree seedling size at planting varied from 35 to 50 cm in height among the different species, but seedlings of each species were, on average, of similar size. One individual of each species was planted at six locations in each plot (six individuals per species per plot). Locations within plots were arranged in a 2 × 3 pattern and separated by ~2·5 m (Fig. 1). Trees at each

Table 1. Invasion status (invaded or uninvaded reference), habitat descriptions, area of management units (ha) and approximate total area of each unit burned (ha) for the 24 plots exposed to prescribed fires

Plot	Unit	Invasion status	Habitat	Unit area (ha)	Unit area burned (ha)	Burn date	Wind speed (mph)	RH (%)	Air temperature (°C)
1	1	Invaded	Mid-successional forest	649	649	1 April 2010	2·2 ± 0·3	32·2 ± 0·2	28·9 ± 0·2
2	1a	Invaded	Forest opening	649	649	18 March 2009	3·4 ± 0·2	28·8 ± 0·1	25·3 ± 0·1
3	3	Invaded	Mature forest	879	379	1 April 2010	2·5 ± 0·3	36·8 ± 0·3	26·3 ± 0·2
4	3	Invaded	Mid-successional forest	879	379	1 April 2010	2·0 ± 0·2	37·1 ± 0·3	25·8 ± 0·2
6	32	Invaded	Mid-successional forest	708	63	23 March 2009	4·8 ± 0·3	32·7 ± 0·3	18·1 ± 0·1
7	5	Invaded	Bottomland edge	430	430	23 March 2009	4·0 ± 0·3	33·7 ± 0·2	18·1 ± 0·1
8	1	Reference	Mid-successional forest	649	649	1 April 2010	2·2 ± 0·3	32·2 ± 0·2	28·9 ± 0·2
9	1a	Reference	Mid-successional forest	649	649	18 March 2009	3·4 ± 0·2	28·8 ± 0·1	25·3 ± 0·1
10	3	Reference	Mature forest	879	379	1 April 2010	2·5 ± 0·3	36·8 ± 0·3	26·3 ± 0·2
11	3	Reference	Forest opening	879	379	1 April 2010	2·0 ± 0·2	37·1 ± 0·3	25·8 ± 0·2
13	32	Reference	Mid-successional forest	708	63	23 March 2009	4·8 ± 0·3	32·7 ± 0·3	18·1 ± 0·1
14	5	Reference	Bottomland edge	430	430	23 March 2009	4·0 ± 0·3	33·7 ± 0·2	18·1 ± 0·1
15	32a	Reference	Mature forest	708	20	12 April 2010	1·9 ± 0·3	34·0 ± 0·6	24·9 ± 0·2
16	32a	Reference	Mature forest	708	20	12 April 2010	1·9 ± 0·3	34·0 ± 0·6	25·0 ± 0·2
17	32a	Invaded	Forest edge	708	20	12 April 2010	1·7 ± 0·3	33·1 ± 0·6	24·9 ± 0·2
18	32a	Invaded	Forest edge	708	20	12 April 2010	1·7 ± 0·3	33·1 ± 0·6	25·0 ± 0·2
19	30	Reference	Young dense forest	544	52	11 April 2010	1·1 ± 0·2	20·7 ± 0·2	25·6 ± 0·2
20	30	Invaded	Young dense forest	544	52	11 April 2010	1·1 ± 0·2	20·7 ± 0·2	25·6 ± 0·2
21	30	Invaded	Mid-successional forest	544	52	11 April 2010	1·9 ± 0·3	21·5 ± 0·2	24·7 ± 0·2
22	30	Reference	Mid-successional forest	544	52	11 April 2010	1·9 ± 0·3	21·5 ± 0·2	24·7 ± 0·2
23	2	Reference	Mid-successional forest	252	252	31 March 2010	3·6 ± 0·3	29·7 ± 0·2	25·9 ± 0·2
24	2	Invaded	Mid-successional forest	252	252	31 March 2010	3·6 ± 0·3	29·7 ± 0·2	25·9 ± 0·2
25	2	Invaded	Forest edge	252	252	31 March 2010	3·5 ± 0·3	29·6 ± 0·2	26·4 ± 0·1
26	2	Reference	Forest edge	252	252	31 March 2010	3·5 ± 0·3	29·6 ± 0·2	26·4 ± 0·1

Dates of prescribed fires and average (± SE) wind speed (mph), relative humidity (percentage RH) and air temperature (°C) during fires are also shown. Weather data were recorded every minute with a tripod mounted Kestrel 4000 pocket weather tracker (Nielson-Kellerman, Boothwyn, PA). Data shown are the means and standard errors (SE) for the 15 min prior to and following the time at which fire first reached each invaded and uninvaded pair of plots (31 measurements). Plots 5 and 12 were not burned and were not included in the analysis.

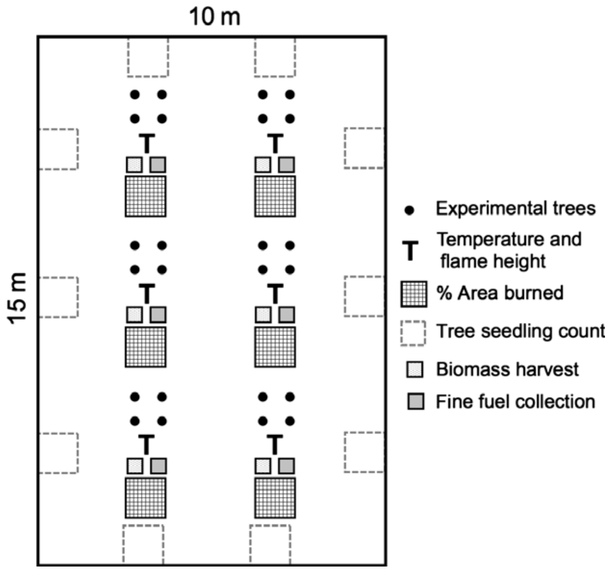

Fig. 1. Diagram of plots showing the location of experimentally planted trees, passive flame height sensors and data loggers for fire temperature, and quadrats for percentage area burned, tree seedling count for natural regeneration, destructive biomass harvest and collection of fine fuels immediately prior to fires. One individual of each of four tree species was planted at the six tree planting locations. Quadrat size and spacing of locations and quadrats are not to scale. See Materials and methods for additional details.

location were separated by 0·75 m. In total, the experiment included 216 trees per species and 864 total trees. Additionally, natural recruitment of trees from seed was quantified in these same plots (see Data collection below, Fig. 1).

Prescribed fires were conducted in late March and early April 2009 and 2010 (Table 1) by first igniting backing and flanking fires with drip torches and then lighting a single strip head fire. Prescribed fire was applied to three and nine pairs of reference and invaded plots in 2009 and 2010, respectively (24 plots total). Data on relative humidity, wind speed and air temperature during fires were recorded with a Kestrel 4000 pocket weather tracker (Nielson-Kellerman, Boothwyn, PA, USA) (Table 1).

DATA COLLECTION

To characterize the fuels in each plot, immediately prior (<1 h) to each prescribed fire, we collected all fine fuels (i.e. < 2 cm diameter) from 25 × 25 cm quadrats at six locations in each plot (Fig. 1). Samples were sorted by green and senesced material and weighed before and after drying to constant mass in a 60 °C oven to determine fuel moisture.

To quantify fire behaviour, we measured thermocouple fire temperature, flame height and fire extent immediately adjacent (~1 m) to the six locations where we planted experimental tree seedlings (Fig. 1). Fire temperatures were measured using type K thermocouples sheathed in fire resistant cloth with twisted bare wires exposed at the end that were connected to data loggers (HOBO U12-014, Onset Computer Corporation, Bourne, MA, USA) housed within waterproof cases (Pelican 1010, Pelican Products, Torrance, CA, USA) and buried 5 cm below the soil surface. Thermocouples were fixed 10 cm above the soil surface by attaching them with binder clips to the rebar of the passive flame height sensors described below. Fire temperatures were recorded every second. Flame heights were quantified with passive flame height sensors consisting of twisted cotton string that had been soaked with flame retardant (Phos-Chek LC-95, ICL Performance Products LC, Ontario, CA, USA) and dried, allowing the string to be charred but not consumed (Ryan 1981). Strings were then tied to each side of a 2·4-m-tall by 0·6-m-wide rebar ‘T’ that was pushed into the soil so that the strings hung vertically. Flame heights were measured from the soil surface to the highest burned point on the strings. This method has been shown to provide a repeatable measure of relative flame heights that is unaffected by radiant or convective heat, or by human bias (Kolaks *et al.* 2004). There were 12 passive flame height sensors per plot (two at each of six locations in each plot). Immediately after each fire, we quantified the percentage area burned at six locations in each plot using a 1 × 1 m quadrat divided into 100 10 × 10 cm squares (Fig. 1).

To quantify the natural recruitment of trees in plots not exposed to fire and with fire applied and in reference and invaded plots, we counted all naturally regenerating tree seedlings in ten 1 × 1 m quadrats evenly spaced along the perimeter of each plot in autumn 2010 (Fig. 1). All seedlings were identified to genus and to species when possible. We were interested specifically in the number of tree seedlings that were recruited into the plots following the prescribed fire treatment so we only counted newly emergent seedlings (< 15 cm tall).

In February 2011, the survival, root crown diameter and height of the experimentally planted tree seedlings were quantified. To measure the response of *M. vimineum* to the 2010 prescribed fires, we harvested six 25 × 25 cm quadrats of vegetation near the tree planting and fire behaviour monitoring locations in each plot (Fig. 1) in early September 2009 (prior to spring fires) and September 2010 (following fires). Biomass and fuel harvest locations did not overlap. *Microstegium vimineum* was sorted from the samples, dried to a constant mass in a 60 °C oven and weighed.

DATA ANALYSIS

We tested for differences in average pre-fire fuel characteristics (total mass of fine fuels, proportion living (i.e. green) plant material and fuel moisture) among the control and invaded plots in the burned treatment using general linear mixed models (Proc MIXED, SAS Institute Inc. 2010). Invasion status, year and their interaction were included as fixed effects and management unit as a random blocking effect. We determined the average maximum thermocouple temperature reached in each plot and calculated the average number of seconds fires were above 300 °C because the amount of time tree stems are exposed to flame heating is a significant determinant of tree survival during fires (Bova & Dickinson 2005), and 300 °C has been reported as the average peak fire temperature in uninvaded eastern oak forests at 10 cm above-ground level (Cole, Klick & Pavlovic 1992). The same model as above was then used to determine whether *M. vimineum* invasion increased maximum thermocouple fire temperature, number of seconds fire temperatures were > 300 °C, flame height or percentage area burned compared to control plots. Maximum fire temperatures were natural log transformed to improve normality. The Bonferroni correction was used to adjust the alpha for the multiple tests of fire intensity (α = 0·0125). Multiple data points from within each plot (e.g. fire temperatures) were averaged such that plot was the level of replication.

Linear regression models (Proc REG, SAS Institute Inc. 2010) were used to evaluate the relationship between peak *M. vimineum* biomass in autumn and maximum fire temperature, and the number of seconds fires were over 300 °C during spring fires the following year. We restricted our analysis to data from the second year of the experiment (autumn 2009 biomass and spring 2010 fire intensity measurements) due to the relatively low number of fires conducted in the first year of the experiment. We used the same models to examine the influence of total fuel biomass on fire intensity measures. Locations within plots were treated as the unit of replication for these analyses due to the fine-scale nature of fuel loads in this habitat.

We used general linear mixed models (Proc MIXED, SAS Institute Inc. 2010) to test for the individual and interactive effects of fire and invasion on the proportion of experimental trees that were alive at the end of the experiment. Fire exposure, invasion status, tree species and their interactions were included as fixed effects, and to account for the occurrence of multiple tree species within each plot, plot nested within unit was included as a random effect in the model. We used Tukey–Kramer post hoc tests to evaluate differences among treatment combinations. Our design is unbalanced with more plots exposed to fire than not so we used type III sums of squares in our models. Type III sums of squares are preferred in testing effects in unbalanced cases because they test a function of the underlying parameters that is independent of the number of observations per treatment combination (Littell, Stroup & Freund 2002). We present least squares (LS) means and SEs, which generate corrected means and standard errors. The effects of fire and *M. vimineum* invasion on the height and diameter of planted trees were evaluated using MANOVA (Proc GLM, SAS Institute Inc. 2010) with fire, invasion, species and their interactions as fixed effects.

We calculated the average number of naturally recruiting seedlings per species in 1 m^2 for each plot (from the 10 quadrats sampled per plot) and log transformed the data to improve normality. A general linear mixed model (Proc GLM, SAS Institute Inc. 2010) with the fixed effects of fire, invasion, species and their interactions was applied to the average number of naturally regenerating tree seedlings per plot. Plot was included as a random effect to account for the multiple species found within each plot and to avoid pseudoreplication. It has been suggested that generalized linear mixed models may better fit this type of data (O'Hara & Kotze 2010), but there was insufficient data across individual tree species to parameterize such models, thus we interpret these results with caution.

To determine whether fires promoted *M. vimineum*, we tested for differences in *M. vimineum* biomass in 2009 and 2010 in 'reference' and 'invaded' plots with and without spring 2010 prescribed fire using paired *t*-tests (Proc TTEST, SAS Institute Inc. 2010). The alpha level was adjusted for the multiple comparisons using the Bonferroni correction ($\alpha = 0{\cdot}0125$).

Results

FUELS AND FIRE INTENSITY

There were no differences in total biomass of pre-fire fine fuel loads, proportion of fuels consisting of living (i.e. green) plant material or fuel moisture between reference (uninvaded) and *M. vimineum*-invaded plots across the 2009 and 2010 prescribed fires (all $P > 0{\cdot}05$). However, fires in invaded plots were significantly more intense (Fig. 2). Maximum fire temperatures were 80% greater (Fig. 3a, $F_{1,14} = 12{\cdot}34$, $P = 0{\cdot}003$) and fires burned at temperatures over 300 °C for 175% longer (Fig. 3b, $F_{1,14} = 13{\cdot}52$, $P = 0{\cdot}002$) in invaded than control plots. In addition, flame heights were 160% higher in invaded than control plots (Fig. 3c, $F_{1,14} = 12{\cdot}57$, $P = 0{\cdot}003$), but invasion did not significantly increase the percentage area of plots burned (Fig. 3d, $F_{1,20} = 3{\cdot}28$, $P = 0{\cdot}09$). There were no effects of year or year by invasion interactions on any of the fire intensity measures (all $P > 0{\cdot}05$), so we present the combined data from both years.

There were significant positive relationships between *M. vimineum* biomass and maximum fire temperatures ($F_{1,98} = 7{\cdot}70$, $P = 0{\cdot}007$, $R^2 = 0{\cdot}07$) and between *M. vimineum* biomass and the number of seconds over 300 °C ($F_{1,98} = 10{\cdot}68$, $P = 0{\cdot}002$, $R^2 = 0{\cdot}10$). Similarly, total dry mass of fine fuels was positively related to both maximum

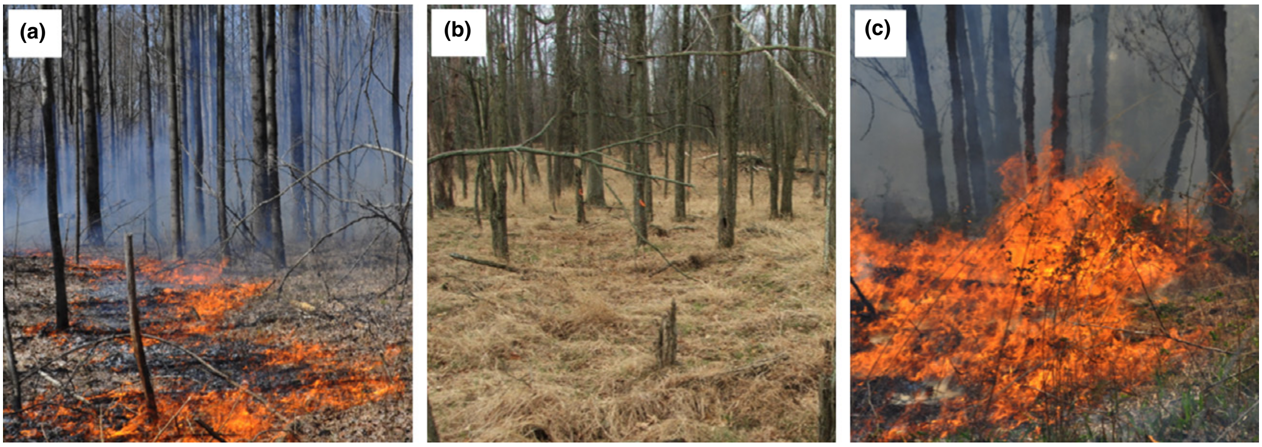

Fig. 2. Prescribed fire in uninvaded deciduous forest area (a), continuous bed of fine fuels created by senesced *M. vimineum* (b) and prescribed fire in *M. vimineum*-invaded area (c) at Big Oaks National Wildlife Refuge, Indiana.

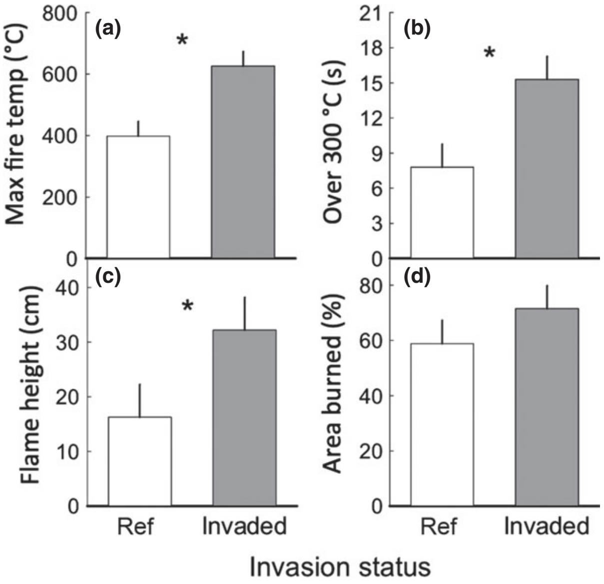

Fig. 3. Least squares means (± SE) of maximum fire temperatures (a), number of seconds fires were above 300 °C (b), maximum flame heights (c) and percentage area burned (d) in uninvaded reference (Ref) and *M. vimineum*-invaded plots. Data are averaged across 2009 and 2010 prescribed fires. Asterisks indicate significant differences at Bonferroni-corrected $P < 0{\cdot}0125$.

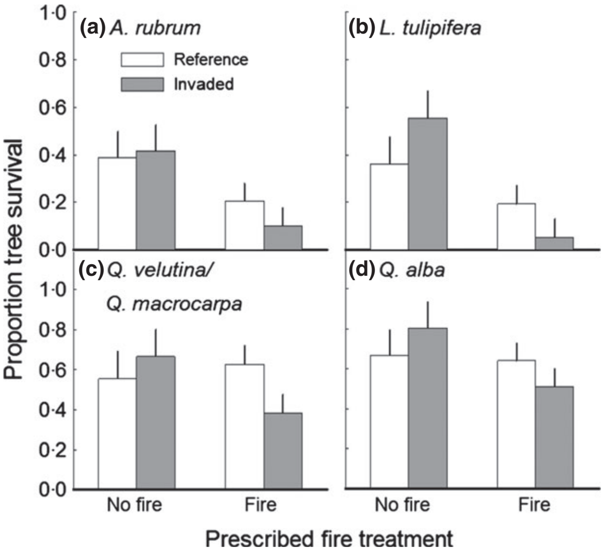

Fig. 4. Proportion of experimental trees alive at the end of the experiment (least squares means ± SE) for *Acer rubrum* (a), *Liriodendron tulipifera* (b), *Quercus velutina* and *Quercus macrocarpa* (c) and *Quercus alba* (d), in uninvaded reference and *M. vimineum*-invaded plots that were or were not exposed to prescribed fire. Tree species varied in their response to fire (fire × species $F_{3,93} = 3{\cdot}31$, $P = 0{\cdot}024$), but there was no difference in the response of tree species to the fire and invasion treatments (fire × invasion × species $F_{3,93} = 0{\cdot}67$, $P = 0{\cdot}57$). Tree survival was evaluated in February 2011, and data shown include trees exposed to fire in either 2009 or 2010.

fire temperature ($F_{1,98} = 7{\cdot}40$, $P = 0{\cdot}008$, $R^2 = 0{\cdot}07$) and duration of 300 °C fires ($F_{1,98} = 5{\cdot}78$, $P = 0{\cdot}02$, $R^2 = 0{\cdot}06$).

TREE SEEDLING SURVIVAL AND REGENERATION

The number of tree seedlings alive at the end of the experiment was significantly reduced by fire ($F_{1,93} = 4{\cdot}55$, $P = 0{\cdot}036$) and the fire × invasion interaction ($F_{1,93} = 4{\cdot}51$, $P = 0{\cdot}036$). Post hoc Tukey tests showed no differences in tree survival among plots with or without *M. vimineum* that were not exposed to fire (main effect of invasion $F_{3,93} = 0{\cdot}34$, $P = 0{\cdot}56$), but the interaction between fire and invasion reduced tree survival by 54% compared to invaded plots not exposed to fires. There were significant overall differences in survival among tree species across treatments ($F_{3,93} = 32{\cdot}72$, $P < 0{\cdot}0001$) and an interaction between fire treatment and tree species ($F_{3,93} = 3{\cdot}31$, $P = 0{\cdot}024$, Fig. 4), but there was no significant three-way interaction (fire × invasion × species $F_{3,93} = 0{\cdot}67$, $P = 0{\cdot}57$). *Acer rubrum* and *L. tulipifera* together had 61% lower overall survival regardless of treatment, and 75% fewer individuals of those species survived the fire treatment compared to the *Quercus* (oak) species (Fig. 4).

The MANOVA used to evaluate final planted tree height and root crown diameter of surviving trees indicated significant effects of fire on tree size. Follow-up ANOVAS that individually tested for the effects of tree height and diameter revealed that the multivariate effect in the MANOVA was driven by a significant reduction in tree diameter in plots exposed to fire ($F_{1,90} = 35{\cdot}35$, $P < 0{\cdot}0001$). There were no effects of invasion, invasion × species, fire × invasion, fire × species or the three-way interaction on tree size (all $P > 0{\cdot}05$ in the MANOVA).

Microstegium vimineum invasion reduced the average number of tree seedlings that naturally colonized the plots by 66% relative to uninvaded plots ($F_{1,306} = 8{\cdot}95$, $P = 0{\cdot}003$), driven primarily by significant differences in *Acer* spp. and *L. tulipifera* recruitment (Fig. 5, species × invasion: $F_{6,306} = 2{\cdot}56$, $P = 0{\cdot}02$). There were no effects of fire or the fire × invasion interaction ($P \gg 0{\cdot}05$) on natural tree regeneration after fires were applied.

MICROSTEGIUM VIMINEUM BIOMASS

There was a 57% reduction in mean *M. vimineum* biomass from 2009 to 2010 in invaded unburned plots ($t = 5{\cdot}88$, $P = 0{\cdot}002$). By contrast, there was no change in *M. vimineum* biomass between years in invaded plots where prescribed fires were conducted in spring 2010 (Fig. 6).

Discussion

Our results demonstrate that invasions of a non-native grass into temperate deciduous forests significantly increased fire intensity (measured as maximum temperature, burn time and flame height) and that the interaction

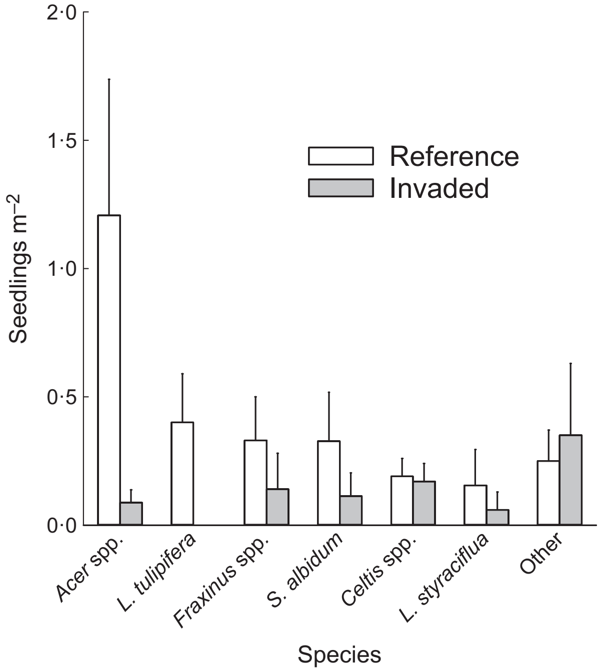

Fig. 5. Average (± SE) number of naturally regenerating tree seedlings in uninvaded reference and *M. vimineum*-invaded plots that were or were not exposed to prescribed fire for *Acer* spp., *Liriodendron tulipifera*, *Fraxinus* spp., *Sassafras albidum*, *Celtis* hackberry spp., *Liquidambar styraciflua* and other less common species (e.g. *Quercus* spp., *Prunus serotina* black cherry and *Cercis canadensis* redbud). Data shown are for sites burned in spring 2010 and evaluated in autumn 2010 only.

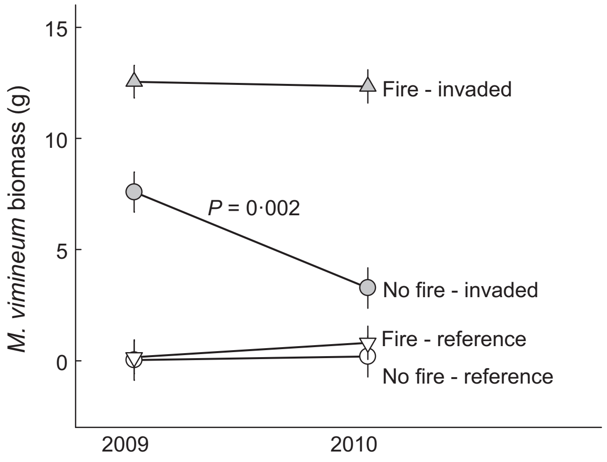

Fig. 6. Least squares means (± SE) of *M. vimineum* biomass in 2009 and 2010 for uninvaded reference and *M. vimineum*-invaded plots exposed to fire or not in spring 2010. Lines without *P* values are not significantly different.

between invasions and fire inhibited native tree seedling establishment. Additionally, we found evidence that fire facilitates *M. vimineum*, indicating the possibility of a fire–invasion feedback cycle. Inhibition of tree regeneration via seedling mortality in eastern deciduous forests by fire–invasion interactions provides some of the first evidence that non-native plant invasions can significantly alter the effects of fires in temperate ecosystems.

Traditionally, prescribed fires have been used to manage invasive plants and promote the abundance of native plant species or alter community composition in a wide variety of ecosystems. In eastern deciduous forests, it has long been recommended to apply prescribed fires to maintain open woodland habitats, suppress woody understorey development and encourage *Quercus* oak spp. rather than *F. grandifolia* beech or *Acer* maple spp. regeneration (Arthur *et al.* 2012). The use of fire to promote the relative dominance of *Quercus* over *F. grandifolia* or *Acer* spp. relies on fire temperatures that are high enough to reduce survival of the less desirable tree species but allow *Quercus* seedlings to survive or regrow from roots (Bova & Dickinson 2005; Hutchinson *et al.* 2012). Our results demonstrate that fire had no effect on *Quercus* survival in uninvaded areas, but in *M. vimineum*-invaded areas, fire temperatures and duration were increased to the point where the survival of all tree species, including *Quercus*, was significantly reduced. Thus, these results suggest that fire–invasion interactions may generally inhibit tree seedling establishment in invaded areas. Clearly, seedling survival is important for tree regeneration, but longer-term demographic studies are needed to determine whether suppression of tree regeneration by invasions (Johnson *et al.* 2015), and fire–invasion interactions, will ultimately lead to changes in forest canopy structure (Harcombe 1987).

The lack of differences in fine fuel biomass between invaded and uninvaded sites was unexpected. Invasive grasses such as *Imperata cylindrica* (L.) P. Beauv., a C4 perennial grass invading forests in south-eastern USA, have been associated with both higher fuel loads (Platt & Gottschalk 2001) and greater fire intensity (Lippincott 2000), and we expected to find a similar pattern with *M. vimineum* invasions. While we found pronounced differences in fire behaviour in invaded plots, including greatly increased fire temperatures, there was no difference in fine fuel biomass between invaded and uninvaded plots, possibly due to the relatively small number of sites we sampled for fuel loads compared to the large amount of variation in habitats where *M. vimineum* is found (Flory 2010; Warren, Wright & Bradford 2011). Alternatively, greater fire intensities may be driven by differences in fuel bed characteristics other than fuel biomass, such as fuel structure or properties. Although *M. vimineum* leaves decompose rapidly, the stems are very persistent (Ehrenfeld, Kourtev & Huang 2001), which may generate a fuel bed structure with generous air flow and greater fuel consumption, leading to enhanced fire intensity compared to areas dominated by native herbaceous species. Differences in fire intensity could also be due to other characteristics of *M. vimineum,* such as flammability. However, in a cone calorimeter study that included more than three dozen native and non-native plant species found in north-east USA, *M. vimineum* had one of the lowest heat of combustion values, a measure of the heat produced when burned, and the lowest overall time of sustained ignition (Dibble, White & Lebow 2007). Further research on differences in fuel loads, fuel bed structural characteristics and fuel flammability (Hiers *et al.* 2009) may help explain differences in fire intensity between areas dominated by native and invasive plant species.

Despite lack of differences in fuel biomass between invaded and uninvaded sites, we found much greater fire intensity in invaded areas and evidence that fires helped maintain invasions. *Microstegium vimineum* biomass declined by more than 50% between 2009 and 2010 in invaded areas not exposed to spring 2010 fires, but there was equivalent biomass in 2009 and 2010 when fire was applied, indicating that fire helped sustain *M. vimineum* productivity. This dynamic occurred despite the fact that during the 2010 growing season south-eastern Indiana experienced a significant drought, with precipitation about 75% below normal (NCDC 2013). Fire may cause an even greater positive effect on *M. vimineum* abundance during years with average or above average rainfall, as *M. vimineum* can be limited by moisture availability (Droste, Flory & Clay 2010). Positive effects of fire on invasions could result from increased germination or seedling establishment after litter is removed by fire (Glasgow & Matlack 2007) or through reduced competition with native species that are susceptible to high intensity fires in invaded areas.

Given the widespread distribution of *M. vimineum* across more than half of the lower 48 states (USDA & NRCS 2005) and the rapid infilling of uninvaded habitats, changes in fire behaviour in invaded areas may have important implications for forest biodiversity and management. Furthermore, climate change is projected to increase fire activity across parts of the *M. vimineum* range in the USA (Flannigan, Stocks & Wotton 2000), potentially exacerbating fire–invasion interactions. If logistically and economically feasible, prescribed fires should not be applied in forest stands until invasions have been removed using one of the recommended methods such as application of a grass-specific herbicide (Flory 2010). In general, management to promote native tree regeneration, alter tree species composition or control invasions using prescribed fire should consider how the use of fire might affect invasion dynamics and forest succession processes. Future research should focus on understanding how fires influence colonization of new habitats and the rate of invasive spread, effects of invasions on fuel bed characteristics, longer-term changes in forest canopy structure in invaded areas and how fire–invasion interactions affect other community traits and ecosystem functions.

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Data accessibility

Data used in the paper may be accessed at Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.fj7kd (Flory *et al.* 2015).

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