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Post-wildfire recovery of an upland oak–pine forest on the Cumberland Plateau, Kentucky, USA

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Abstract

Background: Many forests within the southern Appalachian region, USA, have experienced decades of fire exclusion, contributing to regeneration challenges for species such as oaks (*Quercus* spp. L.) and pines (*Pinus* spp. L.), and threatening the maintenance of oak-dominated forests in the future. While the use of prescribed fire as a forest management tool is increasing within this region, there remains a lack of information on the potential role of wildfire. A wildfire within the Daniel Boone National Forest, Kentucky, USA, provided an opportunity to investigate how wildfire affected forest vegetation response.

Results: We examined the effects of fire severity, quantified using composite burn index (CBI), on basal area, stem density, and sapling recruitment for several key species. We also examined the effects of fire severity on understory species richness and illuminated the consequence of non-native species invasions following fire. Our results demonstrated a negative relationship between fire severity and basal area (stems ≥2 cm diameter at breast height; $P \leq 0.001$), and a positive relationship with the recruitment of oak and pine saplings (both $P \leq 0.001$), oak sapling density ($P = 0.012$), and non-woody understory species richness ($P \leq 0.001$). We also found that increasing fire severity heightened likelihood of invasion by non-native species, specifically princess tree (*Paulownia tomentosa* [Thunb.] Siebold & Zucc. ex. Steud; $P = 0.009$) and Chinese silvergrass (*Miscanthus sinensis* Andersson; $P = 0.028$).

Conclusions: Where it is feasible, public land managers may be able to generate a range of fire severity during future prescribed fires that approximate some characters of wildfire. These fires, when implemented in southern Appalachian upland forests, may help recruit oaks and pines and boost their potential as future canopy dominants. However, the increased occurrence of non-native invasive species invasion following fire conveys the importance of targeted and timely eradication treatments before new populations of non-native species may become established or reproduce, contradicting the ecological benefits of fire.

Keywords: Chinese silvergrass (*Miscanthus sinensis*), fire severity, invasion potential, management, oaks (*Quercus* spp.), pines (*Pinus* spp.), princess tree (*Paulownia tomentosa*), species richness, wildfire

Abbreviations

CBI: Composite Burn Index
DBH: Diameter at Breast Height (1.4 m)
DBNF: Daniel Boone National Forest
NDVI: Normalized Difference Vegetation Index
RRGGA: Red River Gorge Geologic Area
TWI: Topographic Wetness Index
USDA: United States Department of Agriculture

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Background

In the eastern United States, fires ignited from natural and anthropogenic origins have been an important disturbance agent in the development of plant communities within the Appalachian region for millennia (Abrams 1992, Delcourt and Delcourt 1997, Delcourt *et al.* 1998), particularly in oak (*Quercus* spp. L.)-dominated systems (Nowacki and

Abrams 2015). Prior to European settlement, fires were likely low to intermediate on a scale of disturbance severity, with some stand-replacing fires in years of drought, although the exact frequency of fire is unknown (Wade *et al.* 2000). The frequency of historic fires and their fire return intervals were spatially and temporally variable and dependent on several factors, including anthropogenic ignition, surface fuel production, fuel fragmentation, and cultural behavior (Guyette *et al.* 2002, Guyette *et al.* 2006). Following Euro-American settlement (mid 1700s to early 1800s) and widespread logging practices (late 1800s to early 1900s) that occurred in response to a burgeoning timber industry, fire severity, size, and frequency increased throughout the Appalachian region, eventually prompting a policy shift toward widespread fire suppression in the early 1900s (Brose *et al.* 2001). Analysis of fire scar data suggests that most fires in the Appalachian region occurred prior to the 1930s and averaged 6-year fire return intervals before fire suppression was prevalent in these forests (Guyette *et al.* 2010). Today, wildfire suppression is still widely enforced, resulting in the absence of fire from these forests for many decades. In contemporary southern Appalachian forests, overall fire frequency remains lower than historic levels with fire return intervals of 97 to 1196 years, while the area burned is increasing (Lafon *et al.* 2005, Lafon *et al.* 2017). Although wildfires remain infrequent, land managers are increasingly using prescribed fire in an effort to meet multiple management objectives in the Appalachian region (Brose *et al.* 2001).

Unlike prescribed fires, which normally burn with low to moderate severity during pre-determined environmental conditions (Brose *et al.* 2001), wildfires typically create patches of assorted fire severities across the landscape (Hutchinson *et al.* 2008). Wildfires occur periodically in the eastern United States today, but it is predicted that the likelihood of larger and more severe fires may increase in the future in response to a changing climate (Flannigan *et al.* 2000). In the face of this possibility, there is a need to clearly elucidate the effects of wildfire on tree recruitment and overall forest structure within this region. Specifically, land managers need a greater understanding of how tree recruitment of oak and pine (*Pinus* spp. L.) species varies with wildfire severity, as well as a clearer understanding of tree recruitment patterns of competitor species, such as red maple (*Acer rubrum* L.), blackgum (*Nyssa sylvatica* Marshall), and sourwood (*Oxydendrum arboreum* [L.] D.C.) in response to wildfire. Given the contemporary decline in recruitment success of fire-adapted species such as oaks and pines, and the increase in fire-intolerant species throughout the eastern United States (Nowacki and Abrams 2008), information garnered from wildfire studies can also help hone parameters for using prescribed fire to better meet management objectives and develop a greater understanding of vegetative recovery following fires that include higher fire severities than are customary in most prescribed fires.

In addition to the effects of fire on individual tree species, the alteration of forest structure may result in increased light availability and decreased vegetative competition in the understory, leading to greater resource availability at ground level (Reilly *et al.* 2006, Zouhar *et al.* 2008). Thus, fires that burn across a range of fire severity may promote increased species richness (Reilly *et al.* 2006, Hagan *et al.* 2015). For instance, Kuddes-Fisher and Arthur (2002) found increased native herbaceous species richness following a single moderate-severity, late-winter prescribed fire on ridgetops within an oak–pine forest. In another oak–pine-dominated forest within the Appalachian region, total species richness increased following a single wildfire, in which upper slopes and ridges burned with high severity, and also increased in areas twice-burned by wildfire; however, the greatest increases in species richness occurred in areas burned twice (Hagan *et al.* 2015).

Fire may also increase the invasion potential of non-native species into the burned area (Belote *et al.* 2008, Brewer and Bailey 2014), as long as sufficient propagule pressure of the invader is present (Eschtruth and Battles 2009). It has been suggested that areas burned with high fire severity may have the greatest likelihood of invasion by non-native species (Hunter *et al.* 2006, Fornwalt *et al.* 2010), due in part to increased bare mineral soil (Burke and Grime 1996) or greater availability of resources following fire (Hunter *et al.* 2006). Two of the many non-native species in the eastern US capable of invading newly burned areas are princess tree (*Paulownia tomentosa* [Thunb.] Siebold & Zucc. ex. Steud) and Chinese silvergrass (*Miscanthus sinensis* Andersson), which were both imported as ornamental plants from China (Miller *et al.* 2010). Princess tree can quickly invade a range of disturbed sites, as long as adequate light and moisture are available, through excessive propagule pressure of wind-dispersed seeds (as many as 2000 per capsule) and through the formation of a deep taproot (Kuppinger *et al.* 2010). Once established, princess tree rapidly matures to reproductive age within 5 to 7 years (Kuppinger *et al.* 2010). Chinese silvergrass, a plume grass that grows up to three meters in height, can form dense infestations following disturbance and may increase the flammability of a site (Miller *et al.* 2010). Ultimately, the establishment of non-native species such as the aforementioned princess tree and Chinese silvergrass may threaten native plant communities (Hutchinson and Vankat 1997) and have the potential to alter fire frequency and affect fire behavior in the future (Brooks *et al.* 2004, Huebner 2006).

Few studies conducted in the Appalachian region have documented the effects of wildfire severity on forest structure and tree recruitment, or have investigated vegetative recovery after wildfire. A wildfire ignited within the USDA Forest Service Daniel Boone National Forest (DBNF), Kentucky, USA, in 2010 presented an opportunity to study changes in stand structure and tree recruitment across a gradient of variable fire severity. We hypothesized that fire severity would be (H1) negatively related to post-fire stem density and basal area; (H2) positively related to the recruitment of species that depend on high light availability to regenerate (oaks and pines); and (H3) negatively related to the recruitment of competitors with less fire tolerance including red maple, sourwood, and blackgum. The relationships among wildfire severity, non-woody understory species richness, and the probability of non-native species invasion have also not been extensively studied in the Appalachian region. Thus, we further hypothesized (H4) that fire severity would positively impact species richness within our study sites, in part through an increase in the presence of non-native species.

Methods

Fish Trap Fire

The Fish Trap Fire was unintentionally ignited by campers in the Red River Gorge Geological Area (RRGGA) within the Daniel Boone National Forest (DBNF), Kentucky, USA (37°49' N, 83°40' W), during a designated fire ban on 24 October 2010. The Fish Trap Fire was fully contained over two weeks later, on 9 November 2010. The containment perimeter covered 674 ha, 645 ha of which was within USDA Forest Service ownership (E.J. Bunzendahl, DBNF Fire Management Officer, Winchester, Kentucky, USA, personal communication). We used composite burn index (CBI; Key and Benson 2006) to quantify the severity of the Fish Trap Fire, which is a metric used to describe the impacts of a fire on site characteristics including ground fuels and substrates, herbs, shrubs, and trees. CBI values (on a scale of 0 to 3) were calculated using a scoring rubric given in the FIREMON Landscape Assessment publication (Key and Benson 2006) in combination with plot-based measurements described below. The Fish Trap Fire resulted in varied fire severity across the landscape, with the gradient of fire severity represented rather evenly among our study plots, with 35% low to unburned (CBI 0 to 1), 35% moderate (CBI 1 to 2), and 30% high (CBI 2 to 3) severity plots. Some areas of the Fish Trap Fire burned with high-severity stand-replacing fire, consuming vegetation and the litter layer to exposed mineral soil. These severely burned areas, estimated to cover <10% of the area burned, experienced woody vegetation loss nearing 100% in the first year after burning, with minimal recruitment of woody vegetation the following year.

Study area

The region in eastern Kentucky where the RRGGA is located is characterized by highly dissected uplands in the Cliff Section of the Cumberland Plateau (Braun 1950). Elevations in the study area range from 177 m to 479 m (Upadhaya 2015). The ridgetops are covered by Alticrest and Ramsey soil series, both derived from coarse-loamy residuum of sandstone. Alticrest is a well-drained sandy loam that is slightly deeper than Ramsey, a fine sandy loam that is somewhat excessively drained due to the high sand content. Ridgetop soil depths range from 25 cm to 101 cm (NRCS Soil Survey Staff 2017). Steep side slopes and lower slopes are dominated by the Helechawa soil series. The parent material of Helechawa is coarse loamy colluvium derived from sandstone. This loamy sand is somewhat excessively drained and can reach depths of 203 cm (NRCS Soil Survey Staff 2017). Rock outcrops are common in the study area. The underlying geology is composed of Pennsylvanian sandstones and conglomerates and shales of the lower Breathitt formation (McGrain 1983, Hayes 1993). This region receives average annual precipitation of 113 cm and has a mean annual temperature of 12 °C, with mean daily temperatures ranging from 5 °C in January to 30 °C in July (Hill 1976).

The woody vegetation assemblages found on xeric ridgetops and upper side slopes within the DBNF-RRGGA begin with canopy layers with stems >20 cm diameter at breast height (DBH) that are predominantly composed of oaks (chiefly *Quercus coccinea* Münchh and *Q. montana* Willd., but may also include *Q. alba* L. and *Q. velutina* Lam.) and pines (*Pinus rigida* Mill., *P. echinata* Mill., and *P. virginiana* Mill.; Blankenship and Arthur 2006). More specifically, a nearby study site for a long-term prescribed fire study on similar topography had between 67% to 81% of the total basal area (for stems ≥10 cm DBH) composed of oaks, and between 0% to 11% of total basal area of pine in 2003 on fire-excluded sites (Blankenship and Arthur 2006). The woody vegetation in the midstory (stems 2 to 10 cm DBH) was mainly comprised of red maple (*Acer rubrum* L.), eastern white pine (*Pinus strobus* L.), and sourwood (*Oxydendrum arboreum* [L.] D.C.), where the combined species contributed between 80.5% to 90.4% of the midstory stem density in 2003, depending on site (Blankenship and Arthur 2006). Common understory shrub species in this area include mountain-laurel (*Kalmia latifolia* L.) and *Vaccinium* spp. L. (Jones 2005).

Data collection

Twenty-six plots were installed within the Fish Trap Fire containment boundary in August 2011, near the end of the first growing season post fire (Fig. 1). Plot locations

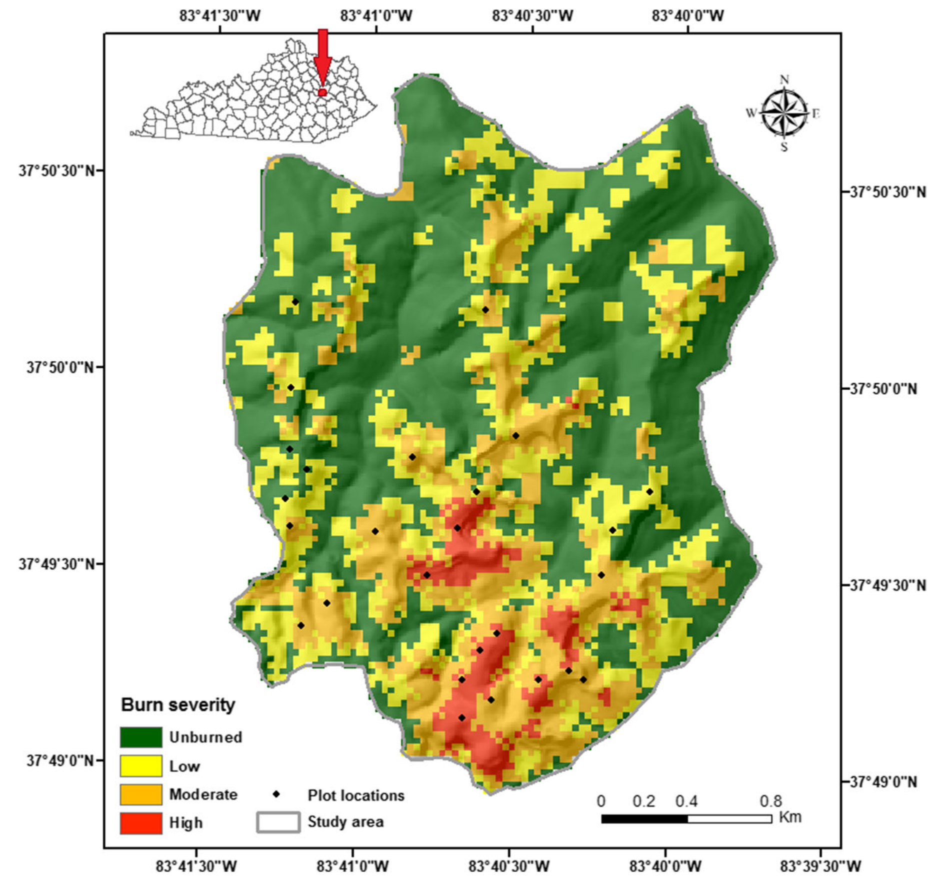

Fig. 1 Map of 26 study plots arrayed across the Fish Trap Fire site, which is characterized by fire severity, in the Daniel Boone National Forest, Kentucky, USA. dNBR, based on NDVI values, was used to create this map in Arc GIS (Upadhaya 2015). Categories correspond to CBI as follows: unburned: 0, low: 0.1 to 1, moderate: 1 to 2, high: 2 to 3.

were selected at random across the entire containment area to capture the ecological effects across fire severities throughout the burned area. Plot centers were permanently marked with rebar and referenced with GPS coordinates. Initial data collection occurred in summer 2011 (year one post fire), with follow up measurements in 2013 and 2016 (year three and year six post fire, respectively). One plot was excluded from analysis of tree sapling density and recruitment due to a 2011 omission in sampling of the sapling layer data. Thus, 25 plots were used for tree data analysis and 26 plots were used for non-woody understory data analysis.

In all years of data collection, we measured all standing trees (stems ≥2 cm DBH) within a 500 m^2 circular plot (0.05 ha). We recorded tree species, measured char height, and assessed tree canopy vigor on a scale of 0 to 3, where 0 denoted a dead canopy, 1 denoted >50% canopy dieback, 2 denoted between 25 and 50% canopy dieback, and 3 denoted <25% canopy dieback. It should be noted that canopy dieback could be attributed to any tree stressor, including damage sustained during burning. We characterized ground cover, noted as bare mineral soil, rock, moss, litter, or vegetation, in 10 cm increments along two 25.2 m transects, oriented north to south and east to west. Within a 25 m^2 circular plot (microplot), co-located at the center of each 500 m^2 plot, tree stems <2 cm DBH were counted, identified to species, and recorded as either small (<50 cm height) or large (≥50 cm height) seedlings. Also within the microplot, understory shrubs, forbs, and grasses were identified to genus or species, and were recorded using an estimate of ground cover (%). Data for the cover of understory shrubs, forbs, and grasses were not collected in 2011; thus, only 2013 and 2016 data for species richness are given in the results.

Lacking on-site pre-burn vegetative data, we used normalized differenced vegetation index (NDVI) values derived from Landsat imagery in October 2010 to gain a value for each plot (Upadhaya 2015). Although NDVI values from October may not be the ideal images to capture all vegetative nuances, in the absence of pre-burn data we chose to compare an image from just before the fire to an image exactly one year after the fire. We compared CBI values in 2011 to pre-burn NDVI values, using linear regression, to test whether pre-burn vegetation was associated with fire severity, as it was post burn ($R^2 = 0.523$, $F_{1,24} = 26.7$, $P \leq 0.001$). We also tested for effects of topographic wetness index (TWI), a measure of topographic effects on the hydrologic processes of a site (Beven and Kirkby 1979), to check for any pre-existing variation in moisture across our study plots. We found no significant effect for TWI ($P = 0.61$) on our study site, indicating that these upland plots were similar in moisture as measured by topographic position. We found no relationship between estimated CBI and pre-burn NDVI ($P = 0.34$) or between TWI and CBI ($P = 0.32$), confirming that variation in CBI values across plots were a reflection of the effects of fire on the landscape rather than pre-fire landscape variability.

Statistical analysis

The effects of fire severity on forest vegetation responses were examined using linear regression. We assessed model assumptions (linearity, homoscedasticity, independence, and normally distributed residuals) using the gvlma (Global Validation of Linear Models Assumption) package (Pena and Slate 2014, R Core Team 2018) and corrected for any violations using square root transformations. We examined the relationship between fire severity (CBI, given as a continuous variable) and total basal area (all stems ≥2 cm DBH), first using a Pearson's correlation test. We found fire severity and basal area to be correlated (Pearson's correlation = −0.77, $t_{1,23} = -5.8$, $P \leq 0.001$), so to avoid any issues with multicollinearity, we refrained from including both variables as co-variates in the same model. Additionally, we used simple linear regression to test the effect of fire severity on total basal area and stem density (stems ≥2 cm DBH) in each sampling year to visualize the response of each at those time points.

We calculated sapling (2 to 10 cm DBH) recruitment from year one to year six post fire for oaks (*Quercus* spp.), pines (*Pinus* spp.), and a few key competitor species on these sites—red maple, sourwood, and blackgum—and tested each species' response to fire severity. The sapling size class was chosen to test based on prevalence of use in prior fire ecology research involving the response of small midstory trees (2 to 10 cm DBH) to prescribed fire (Arthur *et al.* 1998, Blankenship and Arthur 2006), and due to the likelihood that these stems will directly influence future stand composition at this locality. Furthermore, some plots contained zero stems larger than 10 cm DBH.

We used generalized linear mixed-effects models to assess the responses of understory species richness (number of species recorded per unit area; native, non-native, and combined; Poisson distribution) and stem density of princess tree seedlings (Poisson-lognormal distribution) to fire severity across time. We also ran generalized linear mixed-effects models to test the effects of fire severity, basal area, and percent mineral soil on the presence (binomial distribution) of princess tree in years one and three post fire. We included plot as a random effect to account for multiple surveys over time. We also used a generalized linear model to predict the presence of Chinese silvergrass in year six post fire. All data analyses were conducted using R version 3.4.4 (R Core Team 2018) and mixed-effects models were run using the lme4 package in R (Bates *et al.* 2014). Significance for all tests was determined at $\alpha = 0.05$.

Results

Fire severity was negatively related to total basal area (all stems ≥2 cm DBH) after one ($R^2 = 0.49$, $F_{1,\ 24} = 23.44$, $P \leq 0.001$), three ($R^2 = 0.58$, $F_{1,\ 24} = 32.59$, $P \leq 0.001$), and six ($R^2 = 0.59$, $F_{1,\ 23} = 33.65$, $P \leq 0.001$) years post fire (Fig. 2a). Stem density (all stems ≥2 cm DBH) had a negative association with fire severity in years one ($R^2 = 0.22$, $F_{1,\ 24} = 6.94$, $P = 0.015$) and three ($R^2 = 0.28$, $F_{1,\ 24} = 9.09$, $P = 0.006$), but no relationship in year six ($R^2 = 0.01$, $F_{1,\ 24} = 0.26$, $P = 0.616$) post fire (Fig. 2b). However, when we analyzed stem density for only stems >10 cm DBH in year six, there was a negative relationship with fire severity ($R^2 = 0.45$, $F_{1,\ 23} = 19.0$, $P \leq 0.001$).

The reduction in basal area and stem density following the wildfire prompted a recruitment response from several tree species in the understory vegetative layer. From year one to year six post fire, net recruitment (change in stem density between year one and year six) of oak saplings (2 to 10 cm DBH) was positively related to fire severity ($R^2 = 0.43$, $F_{1,\ 23} = 17.45$, $P \leq 0.001$; Fig. 3a), as was the net recruitment of pine saplings ($R^2 = 0.51$, $F_{1,\ 23} = 23.90$, $P \leq 0.001$; Fig. 3b). Conversely, recruitment of red maple ($F_{1,\ 23} = 3.04$, $P = 0.09$), sourwood ($F_{1,\ 23} = 0.07$, $P = 0.80$), and blackgum ($F_{1,\ 23} = 0.16$, $P = 0.69$) saplings was unaffected by fire severity (Fig. 3c).

Although we found greater net recruitment of oak and pine saplings with increasing fire severity, relative stem density (the percentage of the stems that an individual species or species group composes out of all combined stems within a given area) across the gradient of fire severity was mixed for saplings of our primary target species. In year six post fire, relative stem density of oak saplings ($R^2 = 0.25$, $F_{1,\ 23} = 7.53$, $P = 0.012$) was positively related to fire severity (Fig. 4). The relative stem density of pine and red maple was not associated with fire severity ($P = 0.20$ and $P = 0.78$, respectively). A decrease in relative stem density with increasing fire severity was observed for sourwood ($R^2 = 0.36$, $F_{1,\ 23} = 13.11$, $P = 0.001$), while no association was found for another competitor species, blackgum ($P = 0.07$; Fig. 4).

To obtain a clearer picture of the effects of wildfire on understory vegetation response, we examined the effects of fire severity on understory non-woody species richness

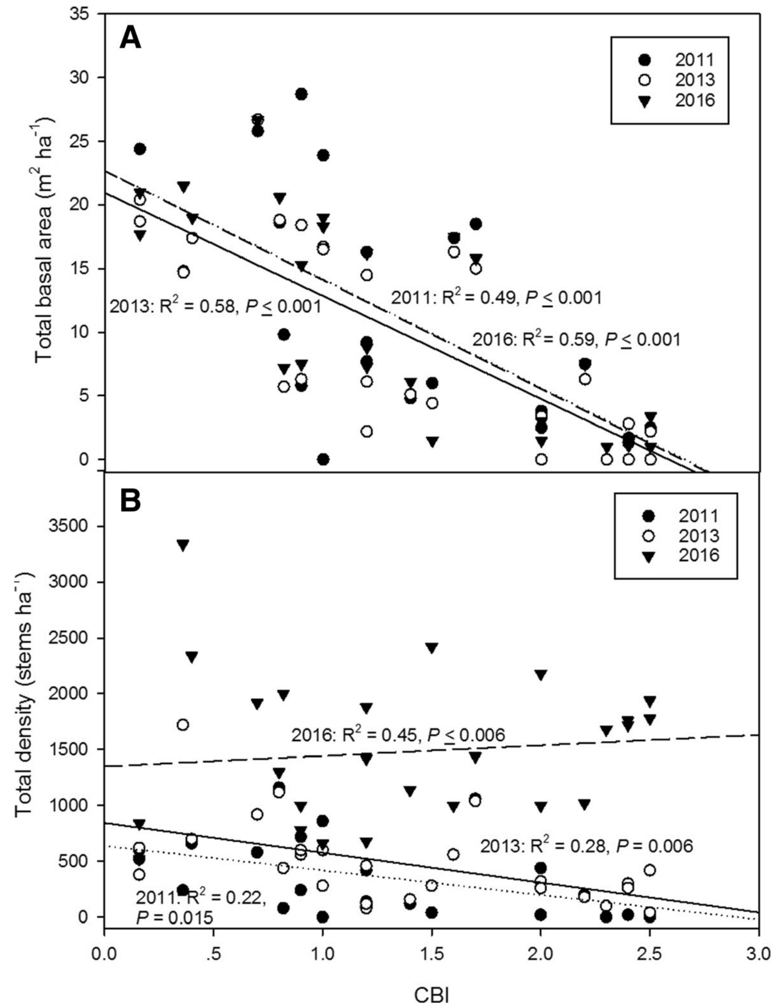

Fig. 2 Relationship between CBI, as a proxy for fire severity, and (**a**) total basal area (all stems ≥2 cm DBH, m^2 ha^{-1}), and (**b**) stem density (all stems ≥2 cm DBH, stems ha^{-1}) in years one (2011), three (2013), and six (2016), following a 2010 wildfire on the Cumberland Plateau, Kentucky, USA.

across time (years three and six post fire). Species richness increased between years three and six ($z = 10.39$, $P \leq 0.001$) and was positively associated with increased fire severity ($z = 2.17$, $P = 0.03$). Additionally, fire severity positively affected species richness of both native ($z = 2.33$, $P = 0.02$) and non-native ($z = 2.19$, $P = 0.028$) species in year six (Fig. 5). For a predominant non-native species present on our study sites following fire, fire severity was positively related to the presence of princess tree ($z = 2.61$, $P = 0.009$). Conversely, year had a negative relationship to princess tree presence ($z = -3.19$, $P = 0.001$). The presence of princess tree could also be predicted by basal area, where princess tree was significantly negatively related to total basal area ($z = -3.7$, $P \leq 0.001$; data not shown). Percent mineral soil was not found to be a predictor of princess tree presence ($P = 0.23$). Additionally, princess tree seedling (stems <2 cm DBH) stem density was positively influenced by fire severity ($z = 3.23$, $P = 0.001$), but was not affected by sampling year ($P = 0.22$) in the model that included CBI (Fig. 6).

We found fire severity to also be positively related to the presence of Chinese silvergrass in year six ($z = 2.19$, $P = 0.028$). Chinese silvergrass presence was recorded on five plots (19% of plots surveyed); four of these plots had high CBI values. Chinese silvergrass had a mean percent ground cover of 2% where it was present. Neither basal area ($P = 0.073$) nor percent mineral soil were predictors of Chinese silvergrass presence ($P = 0.35$).

Discussion

Fire severity impacted the recruitment of oaks and pines, and also affected the response of several species in the understory in the years following the Fish Trap Fire. In support of our first two hypotheses, we found (H1) that fire severity was negatively related to post-fire stem

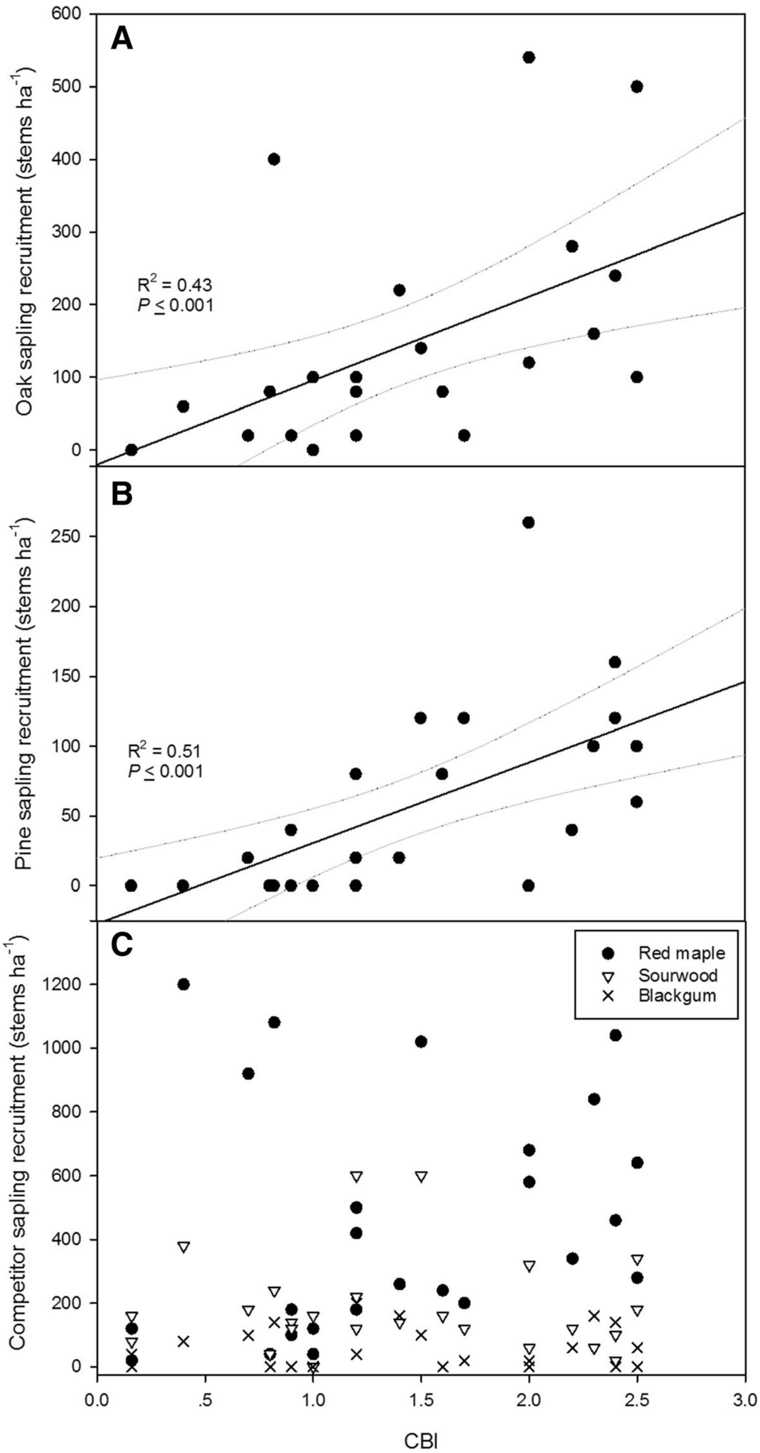

Fig. 3 Relationship between CBI, as a proxy for fire severity, and sapling recruitment (stems 2 to 10 cm DBH) from year one to year six (2011 to 2016) for (**a**) oaks (all species in the genus *Quercus* L.), (**b**) pines (all species in the genus *Pinus* L.), and (**c**) red maple, sourwood, and blackgum after a 2010 wildfire on the Cumberland Plateau, Kentucky, USA. Regression equations, *P*-values, and R^2 values are only shown if the regression analysis was significant ($\alpha = 0.05$).

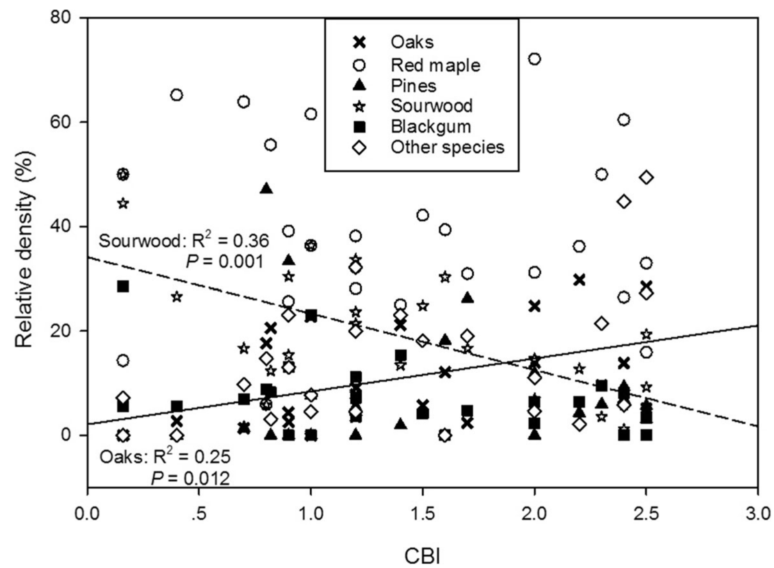

Fig. 4 Relative density (%) of sapling layer stems (2 to 10 cm DBH) for red maple, oaks (all species in the genus *Quercus* L.), pines (all species in the genus *Pinus* L.), sourwood, blackgum, and other species (*Juglans nigra* L., *Liriodendron tulipifera* L., *Populus grandidentata* Michx., *Rhus copallina* L., *Robinia pseudoacacia* L., and *Sassafras albidum* [Nutt.] Nees.) across a gradient of fire severity in year six post wildfire on the Cumberland Plateau, Kentucky, USA.

density and basal area, and (H2) that fire severity was positively related to the recruitment of tree species dependent on high-light environments (oaks and pines).

In the southern Appalachians, Hagan *et al.* (2015) found that wildfires that included moderate to high fire severity resulted in the mortality of large overstory trees, leading to increased sapling stem density, and that twice-burned plots experienced the greatest increases in oak stem density. The authors attributed the increase in sapling density to the mortality of large overstory trees, vigorous resprouting, and the establishment of new individuals (Hagan *et al.* 2015). Similarly, following a wildfire in a table mountain–pitch pine forest in the southern Appalachians, areas that burned with high fire severity experienced nearly complete stand mortality (Groeschl *et al.* 1992). The response to wildfire included greatly reduced basal area and density of residual trees (averaging 98% overstory mortality) compared to areas burned with low severity, while complete shrub layer mortality was observed regardless of severity (Groeschl *et al.* 1992). This altered stand structure in areas of higher fire severity contributed to greater pine seedling germination than in the less altered areas of low fire severity (Groeschl *et al.* 1992). On our study site, the newly opened stand structure (based on field observations from US Forest Service personnel and NDVI values; refer to Methods: Fish Trap Fire) in areas that experienced greater fire severities allowed oak and pine seedlings to grow into the sapling (2 to 10 cm DBH) size class within a time spanning less than six years post fire. Increasing fire severity enhanced the net recruitment of oaks and pines and positively shifted the relative density of oak saplings compared to other species.

In contrast to greater oak and pine recruitment with increasing fire severity, red maple, sourwood, and blackgum sapling recruitment was not directly affected by fire severity, contradicting our hypothesis (H3) that increasing fire severity would lead to decreased recruitment of these species. Red maple is a good competitor to oak and other fire-adapted species in this region (Fei *et al.* 2011), with the ability to sprout prolifically, take advantage of canopy disturbance, reach sexual maturity quickly, and produce a tremendous number of propagules each year (Burns and Honkala 1990, Blankenship and Arthur 2006). When fire was prevalent across the landscape historically, recurring fire likely kept red maple and other mesophytic species at low densities in oak–pine forests, except at protected sites, by eliminating or reducing the density of seedlings before they were fully established (Lafon *et al.* 2017). In the current state of prolonged fire suppression across much of the landscape, many formerly open-structured forests have transitioned to closed forests composed of mesic species through a process known as mesophication (Nowacki and Abrams 2008).

Prior research conducted within the Cumberland Plateau region has shown that repeated prescribed fire can initially reduce shade-tolerant, mesic competitors (Blankenship and Arthur 2006). On plots falling within the lower fire severity areas within the Fish Trap Fire site, the relative stem densities of individual species were comparable to the results from a study conducted on a

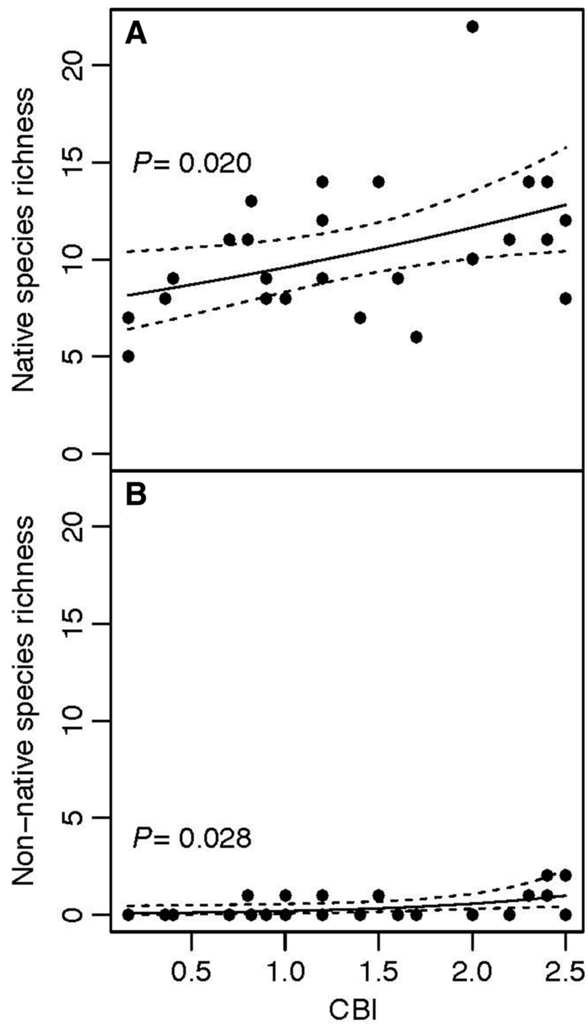

Fig. 5 Relationship between fire severity (CBI) and species richness in 2016 (year six post fire) for (**a**) native species, and (**b**) non-native species following a 2010 wildfire on the Cumberland Plateau, Kentucky, USA.

similar site that implemented repeated, low-severity prescribed fires. In the prescribed fire study, red maple dominated the sapling layer, and oaks were only present in low numbers (Poynter 2017). Although we found that red maple sapling stem density and relative stem density were unaffected by fire severity nearly six years following a single wildfire, a study of prescribed fire on similar sites found that repeated prescribed fire resulted in significantly increased red maple sapling stem density (Poynter 2017). However, the relative stem density of red maple was reduced from 49% to 38% after a fire-free period (Poynter 2017). While we did not observe an overall reduction of shade-tolerant competitor species (red maple, blackgum) in the sapling layer, our results suggest that a single fire that includes high fire severity in some areas may have more lasting effects on the density of these competitor species in the understory than multiple low-severity fires. However, since our results are limited to addressing vegetative recovery following a single fire, further research is needed to determine if the fire-adapted species (oak and pine) will continue to persist and compete with competitor species in the future. It is likely that periodic prescribed burning or other targeted management efforts may be warranted in coming years, given that even at higher fire severity, oak and pine compose less than 25% of relative stem density (for stems 2 to 10 cm DBH) on the study site.

In a similar upland forest near our study site, a single moderate-severity prescribed fire increased the seedling density of yellow-poplar (*Liriodendron tulipifera* L.) and decreased seedling density of sourwood (Kuddes-Fischer and Arthur 2002), two shade-intolerant competitors of oaks and pines. Other research has noted that small diameter yellow-poplar stems are readily top-killed then resprout following a fire, but can be killed by repeated fires (Barnes and Van Lear 1998). In this study, we found that areas of higher fire severity had considerably lower relative stem density of sourwood saplings, giving further evidence that small-diameter sourwood stems are fire sensitive. Offering some support for this idea, a related study found frequent low-severity prescribed fire greatly reduced stem density of sourwood saplings in the short term; however, stem density of sourwood rebounded after a fire-free period (Poynter 2017). Populations of yellow-poplar were low across all of our sites, due to the acidic soil on the sandstone capped ridges within the study area. The reduction (sourwood) or absence (yellow-poplar) of these light-loving, fast-growing competitors may have generated an advantage that contributed to the increase in oak and pine recruitment that we observed amidst the presence of other competitors.

Prior research suggested that increased understory species richness may follow in the wake of fires that include some areas of higher fire severity (Arthur *et al.* 1998, Kuddes-Fischer and Arthur 2002, Hagan *et al.* 2015, Knapp *et al.* 2015). After several repetitions of prescribed fire in Virginia's Piedmont region, herbaceous species groundcover gained dominance following intense spring and summer fires (Keyser *et al.* 2004). A study following wildfire in the Linville Gorge of North Carolina, USA, found a significant and positive relationship between fire severity and species richness, and suggested that the immigration of wind-dispersed seeds were a key driver of increased species richness in areas of high fire severity (Reilly *et al.* 2006). Similarly, in areas burned with higher fire severities, we observed increases in princess tree, *M. sinensis*, and *Solidago* spp. L, which commonly utilize wind as a seed dispersal method. Other species including *Smilax* spp. L., *Rubus* spp. L., *Vaccinium* spp., and *Helianthus* spp.L. were bird or animal

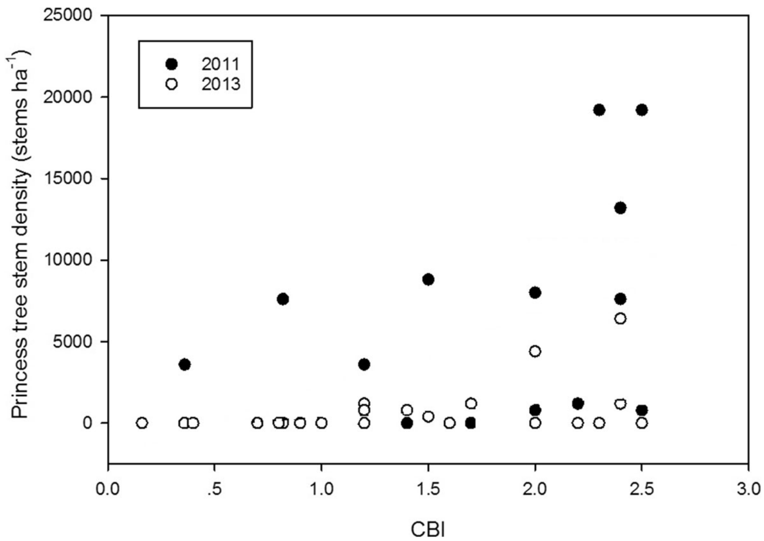

Fig. 6 Density of princess tree <2 cm DBH (stems ha^{-1}) across a gradient of fire severity in years one and three (2011 and 2013) after a 2010 wildfire on the Cumberland Plateau, Kentucky, USA.

dispersed. Conversely, increasing fire severity appeared to have a minor negative effect on *Kalmia latifolia* L. and *Pteridium aquilinium* (L.) Kuhn populations where they were present on our study sites.

Unfortunately, disturbances such as fire may increase the likelihood of invasion by non-native species. Disturbance-mediated reductions in basal area (Von Holle and Simberloff 2005, Belote *et al.* 2008), including high-severity fires, may increase the invasion potential of sites for non-native species (Hunter *et al.* 2006, Fornwalt *et al.* 2010). For instance, Belote *et al.* (2008) found higher species richness of both native and non-native species in areas of reduced basal area. Similarly, we found fire severity (inversely related to basal area) to significantly affect species richness for both native and non-native species. We predicted here that areas with lower residual basal area following fire could experience an increased likelihood of invasion by the non-native princess tree. The absence of princess tree stems on our study plots in 2016 indicated that effective removal was achievable through repeated (four consecutive years) direct management efforts closely following canopy disturbance. Removal treatments (hand pulling, wrenching from the soil, or stem clipping) implemented by the USDA Forest Service targeted princess tree seedlings following the wildfire. In year one, princess tree stem density was 3662 (±1144 SD) stems ha^{-1}, but by year thre princess tree stem density had been reduced to 631 (±293 SD) stems ha^{-1} after three treatments. A final treatment in year four eliminated the remaining stems, at least within the area of our study site.

In support of our hypothesis (H4), the plots that burned with higher fire severity supported understory plant communities with greater species richness of both native and non-native species than areas of lower fire severity. While the areas burned with the highest severity had the lowest residual basal area of standing trees, field-based observations indicated that these areas also had a reduction in all vegetative layers. During the first 1 to 2 years following the Fish Trap Fire, these areas where fire severity was highest also had exposed mineral soil and had increased moisture availability, as evidenced through the emergence of wetland plants, large bryophyte mats, and seeps on these predominantly xeric uplands. All of these factors combined likely contributed to the increased species richness that we documented at the Fish Trap Fire site. Because the increase in species richness became more pronounced over time since the wildfire, further research may be needed to determine the duration of the effects of fire severity on species richness, especially concerning the increased potential for non-native species invasions in areas of high fire severity.

Conclusions

With one of the primary goals of forest management in the southern Appalachians being the restoration of fire-adapted ecosystems to recruit fire-adapted species and limit mesic competitor species, it is important to determine the best combination of treatments to reach this objective. Currently, low- to moderate-severity prescribed fires are often failing to promote growth of desired species, or restrict growth of fire-sensitive, mesic species (Ryan *et al.* 2013). However, the combination of a shelterwood harvest followed by prescribed fire has shown promise (Brose *et al.* 1999). During spring or summer burns in areas 3 to 5 years post harvest, moderate- to high-severity patches showed greater oak regeneration (Brose et al. 1999). Our data show that a single wildfire (an infrequent event in this area) that included areas of moderate to high fire severity promoted the recruitment of oak and pine saplings within six years post fire. However, because the response of a resilient competitor species, red maple, was not notably suppressed by wildfire, it is probable that additional fire or other management methods may be needed in the future for these oak–pine dominated systems to persist in the face of vegetative competition. Implementing periodic, controlled fire, or using practices like mechanical thinning or herbicide applications to control competitor species, may be necessary to ensure a viable advantage for oaks and pines over the long term.

The results of this study also suggest that there are other ecological benefits to areas burned with higher fire severity, such as increased species richness over time. However, as we have elucidated here, increasing fire severity in this region of the southern Appalachians has the potential to increase princess tree in conditions wherein propagule pressure is adequate. We also found that, at least for princess tree, concentrated and timely suppression efforts can be successful in controlling newly invaded non-native species following disturbance. Armed with this knowledge, land managers may begin to enact prevention measures to minimize the risk of severe fire and non-native species introductions within ecologically sensitive areas, or more quickly pinpoint areas to monitor or target for eradication of non-native species following fire. It would be prudent to allocate resources to these areas to manage non-native, invasive species before they become established and reach reproductive age, in support of maintaining native species richness and supporting dynamic plant communities across the burned landscape.

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Availability of data and materials
The datasets generated or analyzed during this study are not publically available due to privacy concerns for study plot locations in close proximity to a popular public recreation area but are available from the corresponding author on reasonable request.

Authors' contributions
DB was the primary writer of this manuscript and collected all field data with ZP in 2016. MA, CC, and DT designed and implemented the study following the Fish Trap wildfire in 2010, and were involved in data collection during the initial study years. CC provided soils information and DT provided botanical species identification for understory species in 2016 field data. S. Upadhaya conducted separate research using these sites to categorize fire severity (dNBR); SU burn severity values were used for comparison to CBI within this study.
SU also created Fig. 1. WL conducted the statistical analyses and wrote the statistical analysis section of the manuscript.
BB was the lead editor of the manuscript and provided figures. All authors contributed to revisions and approved the final draft.

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Competing interests
The authors declare that they have no competing interests.

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