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# Impacts of repeated wildfire on long-unburned plant communities of the southern Appalachian Mountains

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**Abstract.** The infrequent occurrence of large wildfires in the southern Appalachian Mountains over the last several decades has offered few opportunities to study their impacts. From 2000 to 2008, five wildfires burned a large portion of the area in and surrounding the Linville Gorge Wilderness in North Carolina. Areas were burned either once or twice. The response of acid cove and thermic oak plant communities (structure, cover, richness, diversity) was measured in 78 vegetation monitoring plots, established in 1992 and remeasured in 2010–11. Fire altered forest structure in both communities, resulting in the mortality of larger trees and increases in the abundance of smaller (<5 cm diameter at breast height (DBH)) stems. Burning twice decreased stem counts for mountain laurel (*Kalmia latifolia*) in both communities, whereas oaks (*Quercus* spp.) responded positively to burning twice in the thermic oak community. Table Mountain pine stem counts increased in acid cove and thermic oak communities burned once. Fire appears to promote princesstree (*Paulownia tomentosa*) invasion. Herbaceous species cover responded positively to fire (once or twice; both communities), with concurrent increases in woody species richness and diversity. Tree species composition in acid cove plots was not affected by burning, although some slight changes occurred in thermic oak plots burned twice.

**Additional keywords:** climate change, ecosystems, fire frequency, fire management.

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## Introduction

The area of land burned annually by wildfire in the Appalachian region has increased steadily over the last three decades with the rate of increase nearly doubling in recent years (Lafon *et al.* 2005). Fire activity projections under climate change scenarios strongly suggest the area of recently burned land in the southern Appalachian Mountains is likely to continue increasing (Bachelet *et al.* 2001). As a result, there is a growing need for managers to understand how repeated fire affects management goals. Information on re-burns in the southern Appalachian Mountains is limited (Arthur *et al.* 1998) and managers in the region can only use inference from past studies of re-burns in the western US for insights into effects of previous fires on re-burn severity (Romme 1982; Thompson *et al.* 2007). With little information available from within the region, managers of forests in the southern Appalachian Mountains have a need to understand the effects of repeated fire on woody regeneration, understorey diversity and invasion of exotic species in both managed forests and wilderness areas.

Fire historically increased landscape heterogeneity in the southern Appalachian Mountains by maintaining a variety of community types (Delcourt and Delcourt 1997). It is believed that anthropogenic fires, coupled with lightning ignitions, perpetuated oak (*Quercus* spp.) and chestnut (*Castanea dentata*) on upper slopes and fire-adapted species such as Table Mountain pine (*Pinus pungens*) and pitch pine (*Pinus rigida*) on drier ridges. Mesophytic species were largely relegated to lower slopes and drainages, where fires were less frequent. Active prescribed fire programs began in the region as late as the 1980s and have gradually increased in importance (Waldrop *et al.* 2008), but a long period of fire exclusion has left many forest communities in a degraded state due to encroachment of fire-sensitive species such as mountain laurel and thin-barked hardwoods (Williams 1998; Nowacki and Abrams 2008). Mountain laurel is especially problematic owing to its propensity to behave as a 'ladder fuel', enabling ground-level flames to ascend to the canopy and creating the potential for fires of much greater intensity and severity.

Although some research has been done on the effects of fire in the southern Appalachian Mountains, the information available to managers has been largely derived from the results of single small-scale prescribed fires intended to restore decadent Table Mountain pine stands, promote oak regeneration and increase understorey diversity and productivity. These studies have documented effects on vegetation structure, woody regeneration of pine and oak species, and diversity in the understorey (Elliott *et al.* 1999; Turrill-Welch and Waldrop 2001; Kuddes-Fisher and Arthur 2002). Additionally, studies on Table Mountain pine have elucidated microsite conditions and levels of fire severity necessary for seedling establishment (Waldrop and Brose 1999; Welch *et al.* 2000; Welch and Waldrop 2001; Mohr *et al.* 2002). In oak-dominated forests, fire is thought to promote regeneration by reducing the density of undesirable hardwood saplings and mid-storey shrubs and increasing light levels (Van Lear and Watt 1993). However, studies on the application of single prescribed fires in oak forests found little effect on oak regeneration and species composition in the understorey owing to vigorous sprouting of other hardwood species and shrubs (Kuddes-Fisher and Arthur 2002; Brose *et al.* 2013). This suggests that repeated burning or fires of higher intensity may be necessary.

A rare study of large wildfires in the southern Appalachian Mountains was done in Linville Gorge after a wildfire in 2000. Fire increased herbaceous species richness at intermediate scales ($\geq 100$ $m^2$), but increases in tree species richness were limited to small scales ($<10$ $m^2$) owing to lack of immigration (Reilly *et al.* 2006*a*). Severity was correlated with the same environmental gradients structuring spatial patterns of community composition across the landscape and ultimately maintained species turnover and β-diversity (Reilly *et al.* 2006*b*). A spatial analysis of remotely sensed images found that patterns of fire severity were strongly constrained by forest type and topography (Wimberly and Reilly 2007; Reilly *et al.* 2014). These results underscore the notion that fire promotes landscape-level community heterogeneity, but also suggest that woody regeneration in areas of high tree mortality could be inhibited by strong dispersal limitation in some species. Interactions between fire and plant invasions create the potential for novel successional trajectories (Brooks *et al.* 2004), although this is an area that has received little research attention. There is some evidence that princesstree (*Paulownia tomentosa*) invades after fire is reintroduced in the southern Appalachian forests (Kuppinger *et al.* 2010).

A plot-level composite burn index (CBI), employed in areas burned once (1×) and twice (2×), indicated that landform characteristics such as slope, aspect and elevation influenced fire severity more so than fire history (Reilly *et al.* 2014). Past studies on areas subject to re-burn in the western US may provide additional insight on the effects in Linville Gorge. These studies agree that fire severity depends on the potential of young regeneration and other understorey vegetation to carry fire (Romme 1982; Thompson *et al.* 2007). The abundant pine regeneration and vigorous sprouting of hardwood trees and ericaceous shrubs typical after fire in the southern Appalachians suggest that fuels are likely capable of carrying severe fires, even when the return interval is short. Re-burn severity in recently regenerated conifer stands in Oregon was higher than that of the initial burn (Thompson *et al.* 2007). If this is the outcome of Appalachian wildfires and young Table Mountain pine stems are destroyed without having produced sufficient cones, subsequent regeneration will depend on the recruitment of seeds from adjacent areas. Likewise, if oak trees are killed by higher-severity fire in the re-burned areas, regeneration will depend on resprouts, as well as the immigration of acorns. These outcomes could ultimately affect landscape diversity and productivity. However, higher-severity re-burns may be more successful than initial burns at eliminating understorey shrubs (e.g. mountain laurel) and saplings and reducing litter and duff depth. These effects would further promote the establishment of Table Mountain pine and desired hardwoods as well as diversity in the understorey, assuming that there is sufficient seed stock and mature trees survive.

The present project was conducted to determine how fire effects on vegetation differ among areas with different recent burn histories. We used study plots established by Newell and Peet (1998) to assess the effects of burn history (burned once vs burned twice vs unburned) on plant communities (in terms of cover, richness and diversity) and to assess differences in tree species composition in these same areas.

## Methods

### *Study site*

Linville Gorge is in the Pisgah National Forest south of Boone, NC, and contains a 4390-ha federally designated wilderness area. Elevations range from 320 m at the bottom of the gorge to 1250 m on the upper slopes of the ridges. Topography is complex and the presence of steep environmental gradients has resulted in an extremely diverse landscape, much of which has never been logged (Newell and Peet 1998). Upper slopes and ridges are dominated by thermic pine and oak communities with a thick layer of ericaceous shrubs. Thermic pine forests are composed predominantly of Table Mountain pine, pitch pine and Virginia pine (*Pinus virginiana*). Thermic oak forests are dominated by chestnut oak (*Quercus prinus*), scarlet oak (*Quercus coccinea*) and white oak (*Quercus alba*), often with a substantial pine component. Mountain laurel, a major component of live fuel, is abundant in both. Lower slopes and coves are dominated by chestnut oak, eastern white pine (*Pinus strobus*) and eastern hemlock (*Tsuga canadensis*) with a thick layer of rhododendron (*Rhododendron* spp.) and mountain laurel in the understorey and midstorey.

Prior to 2000, the last widespread surface fires in the area occurred in the early 1950s. In 2000, a wildfire burned ~4000 ha in and surrounding Linville Gorge. Fire severity was heterogeneous across the landscape with high-severity crown fires occurring on steep slopes and upper ridges and low-severity surface fires occurring on mid-slopes and coves (Wimberly and Reilly 2007). In spring 2007, two separate fires burned a large portion of the landscape previously burned in 2000 as well as much of the remaining unburned area surrounding Linville Gorge. Another large wildfire occurred in 2008 and burned much of the area immediately adjacent to the area that burned in 2000 and 2007.

## Sampling and data analysis

During the growing seasons of 2010 and 2011, we remeasured a set of plots established in 1992 to document the variation in

**Table 1. Number of plots in each burn history category for acid cove and thermic oak communities in Linville Gorge Wilderness Area, North Carolina, USA**

| Fire history | Acid cove | Thermic oak |
|---|---|---|
| Unburned | 13 | 12 |
| Burned once | 9 | 14 |
| Burned twice | 9 | 21 |
| Total | 31 | 47 |

composition and structure of vegetation in Linville Gorge (Newell and Peet 1998). As the highly diverse topography of Linville Gorge provided an almost infinite number of site and cover types, we chose to focus our analyses of plant response on the subset of plots in two community types near the extremes of the moisture gradient: mesic acid coves and xeric thermic oak sites (Newell and Peet 1998) (Table 1). Each plot consisted of four to five 10 ×10-m sampling 'modules'. Plots were characterised as burned twice (2000 and 2007), burned once (2000, 2007 or 2008) and unburned, and sampled following the North Carolina Vegetation Survey (NCVS) protocols (Peet *et al.* 1998). Woody stems with a measurable diameter at breast height (DBH; 1.4 m) were identified to species and tallied. As pre-fire woody stem counts of stems <1.4 m were unavailable, post-fire stem counts for this stratum were not collected. All species (woody and herbaceous) from canopy to ground level were identified and assigned cover estimates (0.1–100%) in each 10 × 10-m sampling module.

Data from the four to five modules were averaged for analysis. In each community type, these data were used to calculate mean stem counts, cover, species richness and Shannon diversity ($H'$) for all species combined, and for each growth form type (graminoids, herbs, shrubs, trees and vines). One-way analysis of variance (ANOVA) was used to assess effects of burn history (unburned, burned once, burned twice) on the changes in these measures of plant community structure (numerator degrees of freedom (ndf)/denominator degrees of freedom (ddf) = 2/29 and 2/45 for acid cove and thermic oak plots respectively). Additional one-way ANOVA analyses were conducted to compare changes in mean stem counts for species of interest (mountain laurel, oaks, Table Mountain pine and princesstree (*Paulownia tomentosa*)). When these tests indicated significant effects at $\alpha = 0.05$, Dunnett's test was used to for post-hoc comparisons of change relative to unburned (control) plots. These analyses were conducted in *SAS Version 9.3* (SAS Institute 2008). Additionally, non-metric multidimensional scaling (NMS) (Bray–Curtis dissimilarity distance measure), in conjunction with a multi-response permutation procedure (MRPP) was used in *PC-ORD Version 6.15* (McCune and Mefford 2011) to ordinate plots and to assess changes in patterns of tree species composition in each burn history category for each community type (McCune and Grace 2002). These analyses were based on relative cover values and calculated by dividing the cover of each species by the total cover of all species within that functional group in the plot. For the NMS analyses, $P$ values (Pearson's coefficients) of pairwise comparisons of the effects of burn history were corrected for multiple comparisons using the Bonferroni correction. Kendall's tau ($\tau$) coefficient was used to assess the rank relationships between the ordination scores and burn history. We elected to focus solely on trees (all strata combined) for the multivariate analyses because, as long-lived-perennials, they are probably the most reliable indicator of forest compositional change over longer time scales.

## Results and discussion

### Diameter distributions and woody species abundance

The forest communities in the Linville Gorge region have many similarities with those in surrounding southern Appalachian landscape. Several decades of fire exclusion and suppression resulted in the succession of fire-dependent species assemblages into dense mesophytic forests with novel structural, functional and compositional characteristics (Newell and Peet 1998). This was clearly evident in the pre-fire data. In 1992, mean DBH for woody species in the acid cove and thermic oak communities was 7.4 ± 1.3 and 5.6 ± 1.5 cm (mean ± s.e.) respectively. Acid cove plots averaged 4501 ± 875 stems ha$^{-1}$ and thermic oak plots averaged 10 049 ± 1701. Diameter distributions were unimodal and heavily skewed to the right, with both communities having modes in the 2.5–5-cm DBH class. Forest structure in unburned plots changed slightly during the study period, with mean DBH dropping to 5.0 ± 1.5 and 3.9 ± 1.4 cm and stems ha$^{-1}$ increasing to 7500 ± 1009 and 14 246 ± 2871 for acid cove and thermic oak plots respectively. These changes corresponded with increases in trees in the smaller-diameter (<5 cm) classes and decreases in the larger-diameter classes. This reflects substantial overstorey mortality due to drought, beetle and hemlock woolly adelgid during the study period, along with the regeneration of young trees and vigorous resprouting of hardwood trees and ericaceous vegetation such as mountain laurel.

Changes in structure were magnified in plots burned once, where a typical 'reverse-J'-shaped distribution appeared to be developing in both communities (Fig. 1). Mean DBH in acid cove and thermic oak plots burned once was 1.8 ± 0.6 and 2.2 ± 1.0 cm, and there were 17 888 ± 2497 and 21 664 ± 3020 trees ha$^{-1}$ respectively. Plots burned twice had a slightly larger mean DBH (3.0 ± 1.1 and 2.7 ± 1.0 cm) and substantially fewer stems ha$^{-1}$ (6525 ± 1277 and 7147 ± 1480) than plots burned once, although it is likely that many young trees and shrubs in these plots were not recorded because they had yet to reach measurable height after the second burn (2007 or 2008). Similar studies that focussed on the seedling layer reported large post-fire increases in the establishment of seedling-size (height < 1.4 m) woody plants. This has been attributed to seedbed modification (Mohr *et al.* 2002), resprouting following top-kill (Thompson and Spies 2010) and increased resource availability (Markwith and Parker 2003). Substantial decreases in stems >2.5 cm DBH in the thermic oak community, relative to unburned plots, can likely be attributed to the extreme severity of fires on these upper slopes and ridges (Reilly *et al.* 2014) Indeed, partial to complete canopy consumption occurred in many of these areas after the first fire (Wimberly and Reilly 2007), with additional mortality likely occurring afterwards – owing to delayed mortality and in some cases consumption by the second fire. This, in turn, may have facilitated the recruitment of trees and shrubs into the smaller-diameter classes.

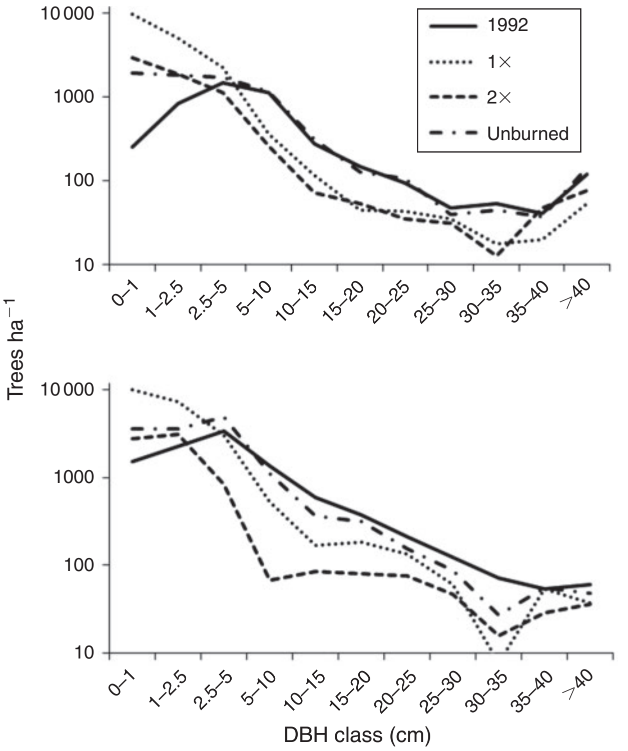

**Fig. 1.** Diameter distributions for woody species (trees and shrubs) >1.4 m in height in acid cove communities (top) and thermic oak communities (bottom) in Linville Gorge Wilderness Area, North Carolina, USA.

Burn history affected the abundance (stem counts) of several key species. In 1992, before the fires, there were 1008 stems $ha^{-1}$ of mountain laurel in the acid cove community and 2789 stems $ha^{-1}$ in the thermic oak community. In the absence of fire, mountain laurel increased in both communities (mean ± s.e. = 69 ± 46.1 and 3775 ± 1145 stems $ha^{-1}$ respectively). The effect of fire was significant in both the acid cove community ($F = 3.51$, $P = 0.04$) and the thermic oak community ($F = 10.47$, $P < 0.01$). Whereas the density change in acid cove plots burned once was not statistically different from the unburned plots, there was a significant decrease in mountain laurel (1959 ± 854.7 stems $ha^{-1}$) in plots burned twice (Fig. 2). Thermic oak plots burned once saw a significant increase in mountain laurel stems $ha^{-1}$, but not to the extent that they likely would have increased had they not burned. There was a significant decrease (nearly 3000) in mountain laurel stem counts in thermic oak plots that burned twice. Although there is a paucity of available information on the effects of repeated wildfire in the region, similar patterns have been observed in other southern Appalachian plant communities managed with prescribed fire. The vigorous resprouting that occurs after a single prescribed fire does not negatively affect the density of most woody plant species (Arthur *et al.* 1998). A second fire, perhaps more intense and severe than the first owing to the increase in sprouts and fine-fuel loading (Reilly *et al.* 2014), may be needed if an objective is to reduce mountain laurel density. However, one important difference between wildfires and prescribed fires in the southern Appalachians is that the latter typically occur during the growing season, whereas the former are almost

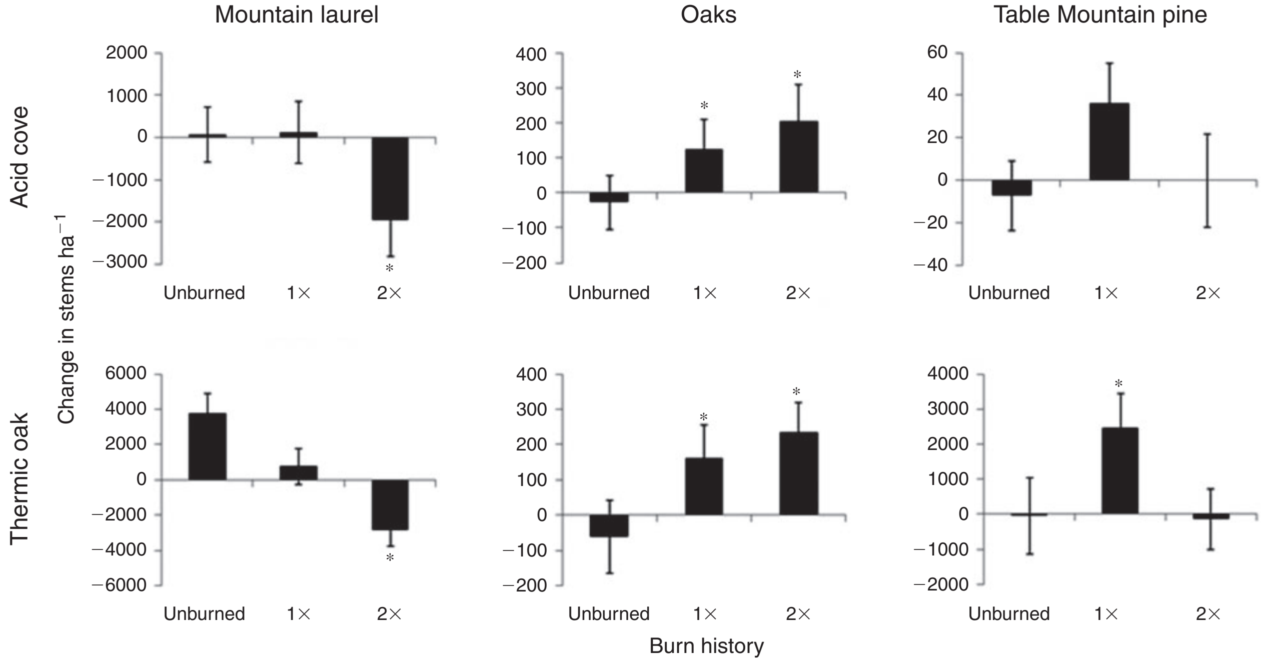

**Fig. 2.** Change in stems $ha^{-1}$ >1.4 m from 1992 to 2010–11 for mountain laurel, oaks and Table Mountain pine in unburned plots and plots burned once or twice in acid cove (top) and thermic oak communities (bottom) in Linville Gorge Wilderness Area, North Carolina, USA. Means and standard errors; asterisks indicate a magnitude of change that was statistically different from unburned plots at alpha = 0.05 using Dunnett's post-hoc test.

exclusively restricted to the dormant season. Basic research on the effects of burn season on fire behaviour and vegetative response is largely absent for the southern Appalachian region. This is clearly an area where further research is needed.

Fire plays an important role in southern Appalachian forests by killing thin-barked hardwoods such as red maple and American beech (*Fagus grandifolia*) and encouraging the establishment and resprouting of pyrogenic species such as oaks (Abrams 1992; Brose and Van Lear 1998). Oak regeneration is hindered, and fire-sensitive woody species become increasingly abundant, when fire is suppressed for long periods of time (Brose and Van Lear 1998). As mature oaks in the overstorey decline and eventually die, an opportunity is created for non-oak species to ascend into the overstorey. Appalachian forests that are undergoing this 'mesophication' process typically have a fairly minor oak component (Nowacki and Abrams 2008). In 1992, there were 158 oak stems $ha^{-1}$ in the acid cove community and 248 stems $ha^{-1}$ in the thermic oak community. Although clear trends were observed in both communities, the effect of fire was significant only in the thermic oak community ($F = 4.01$, $P = 0.025$). For unburned plots in both communities, there were slight decreases in oak stem counts (all species combined) during the study period (Fig. 2), likely due to the absence of fire. There was an increase of $123 \pm 87.1$ stems $ha^{-1}$ in acid cove plots burned once, and $206 \pm 102.1$ stems $ha^{-1}$ in plots burned twice, but again these changes were not statistically significant. Thermic oak plots responded similarly to acid cove plots, with increases of $164 \pm 92.8$ and $235 \pm 83.0$ stems $ha^{-1}$ for plots burned once and twice respectively, with the magnitude of change for plots burned twice being significantly different from that of unburned plots. Kuddes-Fisher and Arthur (2002) suggested that multiple fires are needed in order to encourage the establishment of sapling-sized oaks, which our findings corroborate. There was no evidence to suggest that substantial numbers of small trees were killed by the second fire, as suggested by Alexander *et al.* (2008) – despite the fact that plots burned twice had less than 7 years of recovery between fires.

The restoration of Table Mountain pine, which was once common on drier ridge tops and upper slopes in the southern Appalachians, has been of keen interest to scientists and land managers in the southern Appalachians in recent years (Mohr *et al.* 2002; Waldrop *et al.* 2002). As a fire-dependent tree with serotinous cones, Table Mountain pine performs poorly in areas where fire has been suppressed (Waldrop *et al.* 2002). In 1992, there were <10 Table Mountain pine stems $ha^{-1}$ in the acid cove community – concentrated in one plot – and 197 stems $ha^{-1}$ in the thermic oak community. For the acid cove community, there was a small (insignificant) increase in plots burned once ($36 \pm 18.6$ stems $ha^{-1}$), whereas no change occurred in plots burned twice (Fig. 2). Table Mountain pine would generally not be found in acid cove communities – indeed, it was only found in three plots post-fire and it is unlikely to persist there. As would be expected, post-fire increases in Table Mountain pine regeneration were much more substantial in the thermic oak community ($F = 3.31$, $P = 0.04$), where we observed $2643 \pm 980.0$ additional stems $ha^{-1}$ in plots burned once. These increases are comparable with those that Waldrop *et al.* (2002) observed in a over-mature north Georgia Table Mountain pine community subjected to moderate- to high-intensity prescribed fire. Plots that burned twice had no significant change in stems counts relative to that of unburned plots, suggesting substantial fire-related mortality of young trees, most of which had yet to reach reproductive maturity. It is also possible that seedling Table Mountain pines were present, but were not accounted for because they were below the 1.4-m measurement height.

Invasive alien plants often thrive on disturbed sites such as those impacted by fire (Brooks *et al.* 2004). Such invasions can be problematic because they can impede the establishment and performance of desirable native species (Hutchinson and Vankat 1997) and alter vital ecological processes – including fire behaviour (Brooks *et al.* 2004). Princesstree, a deciduous hardwood native to China, was not present in the study area in 1992, but in 2010–11, it was observed in both communities. In the acid cove community, we observed it in 9% of plots burned once and 14% of plots burned twice. Likewise, in the thermic oak community, we observed it in 14% of plots burned once and 45% of plots burned twice. In plots where it was present, there were generally only a few stems and coverage values averaged less than 1%. However, one plot in the acid cove community had 1600 stems $ha^{-1}$, with 5.5% coverage, and a plot in the thermic oak community had 900, with 3.5% coverage. As a light-demanding ruderal tree that produces tens of thousands of tiny positively photoblastic wind-dispersed seeds per year, it would be expected to perform well after a disturbance such as a crown fire (Todorovic *et al.* 2010). Patterns of princesstree invasion suggest that burning – especially more than once – may cause it to break out of a 'lag phase' and enter a phase of exponential growth and spread (Hobbs and Humphries 1995). However, a model developed by Kuppinger *et al.* (2010) suggests that the ruderal nature of princesstree will prevent it from persisting beyond the early stages of succession, except perhaps in highly exposed xeric sites. As this model has yet to be validated with data from long-term studies, it is imperative that burned sites continue to be monitored.

## Species cover, richness and diversity

The effects of wildfire on vegetative cover were similar in acid cove and thermic oak communities. Prior to the fires, total cover (all strata combined) was 269.4% in the acid cove community and 342.3% in the thermic oak community. Substantial reductions in total cover (>100%) were observed in unburned plots for both communities (Fig. 3). This can be attributed to the above-mentioned impacts of hemlock woolly adelgid (*Adelges tsugae*) on eastern and Carolina hemlocks, as well as drought and pine beetle (*Dendroctonus frontalis*)-related mortality during the study period. The response of cover to fire was significant in areas subjected to two burns, as we observed small but significant increases in graminoid (acid cove $= F = 5.29$, $P < 0.01$; thermic oak $= F = 7.43$, $P < 0.01$) and herb cover (acid cove $= F = 5.95$, $P < 0.01$; thermic oak $= F = 4.31$, $P = 0.02$) in these plots. This is not surprising considering that these species groups largely comprised ruderals and ephemerals, which would be expected to respond quickly – if only temporarily – to such a disturbance. These findings suggest that single or once-repeated burns, regardless of severity, may not significantly alter the composition of acid cove and thermic oak plant

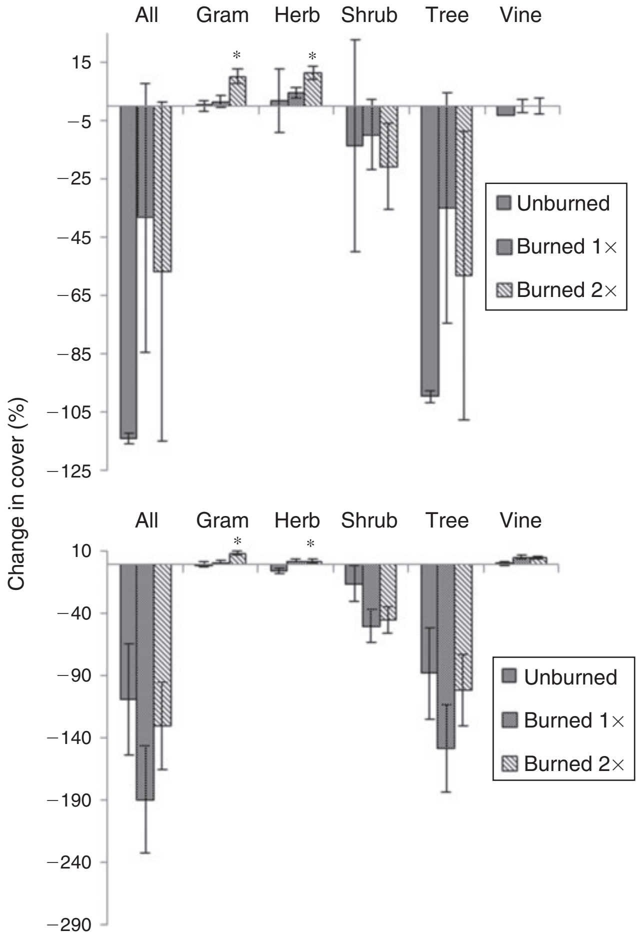

**Fig. 3.** Change in cover from 1992 to 2010–11 for all species combined and for different growth forms – in unburned plots and plots burned once or twice in acid cove (top) and thermic oak communities (bottom) in Linville Gorge Wilderness Area, North Carolina, USA. Means and standard errors; asterisks indicate a magnitude of change that was statistically different from unburned plots at alpha = 0.05 using Dunnett's post-hoc test.

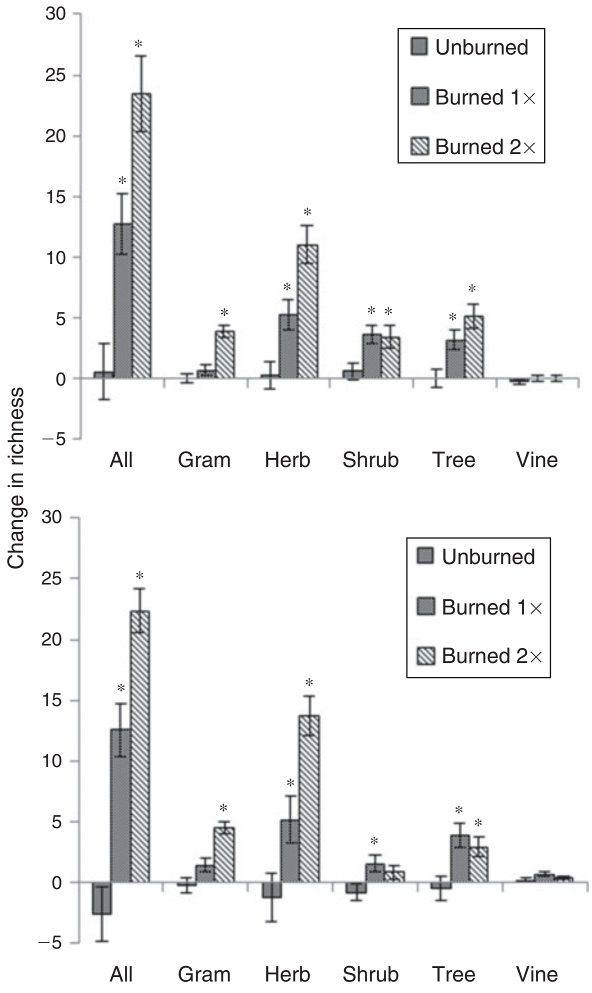

**Fig. 4.** Change in species richness from 1992 to 2010–11 for all species combined and for different growth forms – in unburned plots and plots burned once or twice in acid cove (top) and thermic oak communities (bottom) in Linville Gorge Wilderness Area, North Carolina, USA. Means and standard errors; asterisks indicate a magnitude of change that was statistically different from unburned plots at alpha = 0.05 using Dunnett's post-hoc test.

communities in the long term, despite substantial changes in forest structure. These findings corroborate observations from other studies (Arthur *et al.* 1998; Elliott *et al.* 1999).

Burning also influenced species richness. Prior to the fires, there were 19.0 species 100 $m^{-2}$ in the acid cove community and 29.5 in the thermic oak community. In the acid cove community, species richness remained fairly constant in unburned plots during the study period (Fig. 4). However, significant increases in total richness were observed in plots burned once and twice (12.7 ± 2.5 and 23.4 ± 3.2 respectively; $F = 17.97$; $P < 0.01$), largely owing to substantial increases in graminoid ($F = 17.97$; $P < 0.01$), herb ($F = 15.39$; $P < 0.01$), shrub ($F = 5.35$; $P = 0.01$) and tree richness ($F = 9.84$; $P < 0.01$). Post-hoc analyses indicated that no significant change for graminoids occurred in plots burned once. Similar patterns were observed in the thermic oak community (Fig. 4). In this community, total species richness increased by 12.6 ± 2.2 in plots burned once and 22.3 ± 1.8 in plots burned twice ($F = 21.4$; $P < 0.01$). These increases corresponded with increases in the richness of graminoids ($F = 18.3$; $P < 0.01$), herbs ($F = 18.0$; $P < 0.01$), shrubs ($F = 3.49$; $P = 0.039$) and trees ($F = 5.63$; $P < 0.01$) – which were again generally more pronounced in plots burned twice. Post-hoc analyses indicate no effect for graminoids in plots burned once or for shrubs in plots burned twice. Reilly *et al.* (2006*a*) reported similar increases in tree and non-tree species richness in southern Appalachian plant communities after a single fire. As most late-successional woody species in the southern Appalachians are strongly dispersal-limited (Clark *et al.* 1998), and seed dormancy in litter and soil is likely low (Reilly *et al.* 2006*a*), increases in tree and shrub richness can be attributed to recruitment from nearby surviving woody plants and low rates of fire-driven local extinction. Many herbaceous species have strongly expressed ruderal characteristics, with long-lived seeds that readily disperse over long distances (Reilly *et al.* 2006*b*; Keyser *et al.* 2012). Large increases in graminoid

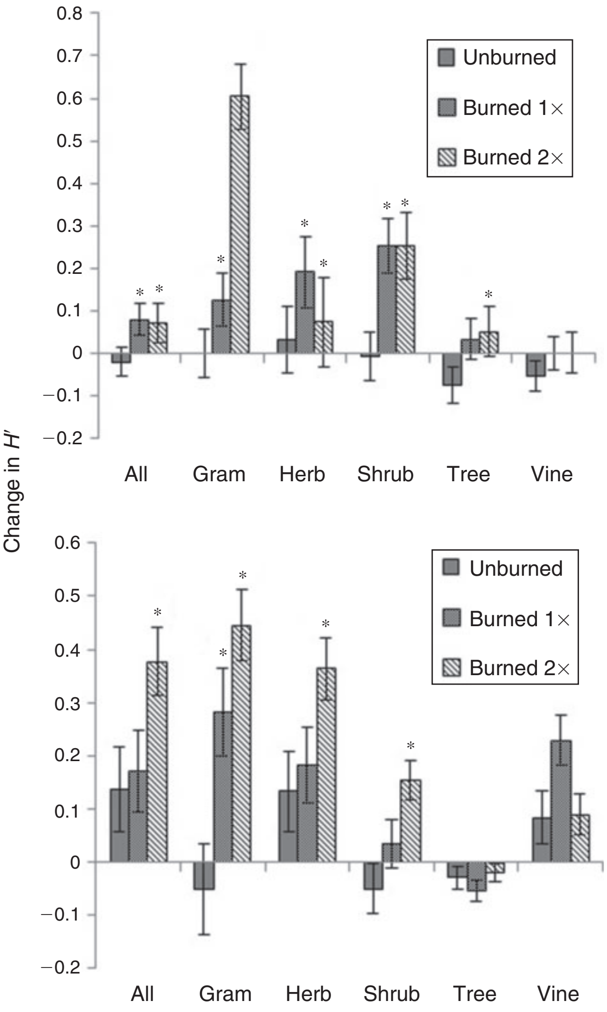

**Fig. 5.** Change in Shannon diversity ($H'$) from 1992 to 2010–11 for all species combined and for different growth forms – in unburned plots and plots burned once or twice in acid cove (top) and thermic oak communities (bottom) in Linville Gorge Wilderness Area, North Carolina, USA. Means and standard errors; asterisks indicate a magnitude of change that was statistically different from unburned plots at alpha = 0.05 using Dunnett's post-hoc test.

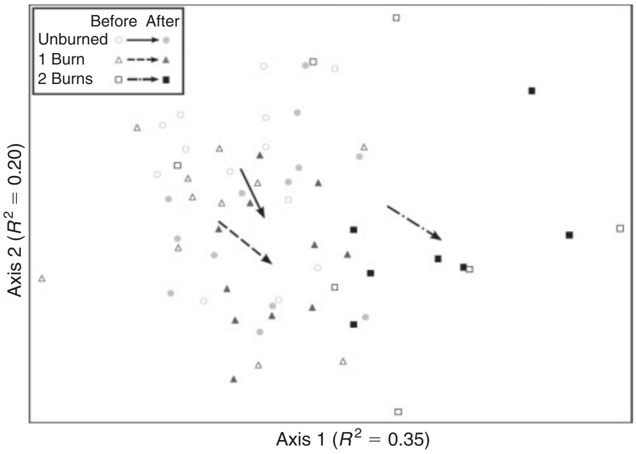

**Fig. 6.** Non-metric multidimensional scaling ordination of trees in the acid cove dataset using a Bray–Curtis dissimilarity distance measure. Analysis was based on species composition, using the relative covers of trees in each plot. Open circles are unburned plots during the first measurement period. Closed circles are unburned plots during the second measurement period. Open triangles represent plots measured before one burn, whereas closed triangles are plots measured after one burn. Open squares are plots measured before two burns whereas closed squares are the same plots after two burns. Arrows represent change in centroids of each treatment group between measurements. Final stress for the three-dimensional solution was 16.8 over 174 iterations. Axis 3 was not included, having the lowest explanatory power ($R^2 = 0.19$).

and herb richness, particularly in acid cove and thermic oak plots burned twice, may therefore be attributable to long-distance dispersal and low rates of extinction, coupled with favourable conditions for local post-fire establishment.

In the acid cove community, plots burned once and twice had significant increases in total Shannon diversity ($H'$) relative to unburned plots ($F = 9.68$; $P < 0.01$), due to increases in the diversity of graminoids ($F = 29.02$; $P < 0.01$), herbs ($F = 3.47$; $P = 0.044$), shrubs ($F = 8.91$; $P < 0.01$) and trees ($F = 6.10$; $P < 0.01$) (Fig. 5). Graminoid diversity increased approximately five-fold in plots burned twice and herb diversity increased more than four-fold in plots burned once. Herb and shrub diversity increased in plots burned once and twice and tree diversity increased in plots burned twice. A similar pattern of increased total diversity was observed in the thermic oak community ($F = 3.49$; $P = 0.039$), where significant effects (increases) were observed for graminoids ($F = 13.14$; $P < 0.01$), herbs ($F = 10.26$; $P < 0.01$) and shrubs ($F = 6.93$; $P < 0.01$). Post-hoc analyses indicated that the effects were more pronounced in plots burned twice, as significant change relative to unburned plots was only observed for graminoids in plots burned once. Reilly *et al.* (2006*b*) observed similar increases in total diversity in southern Appalachian communities post-fire, which they attributed to rapid increases in herbaceous species richness, coupled with decreased dominance of woody species. These differences were generally magnified in plots burned twice owing to overstorey mortality and the fact that woody species, owing to their slow growth and dispersal limitation, had less time to recover before the plots were remeasured.

## Multivariate analyses

Although there was some evidence to suggest that fire history influenced the composition of the two plant communities, results of multivariate analyses of the tree community were less compelling. Non-metric multidimensional scaling outputs of plots burned once or twice, relative to unburned plots, do not strongly indicate that fires had substantial effects on tree community composition. These communities were highly heterogeneous before burning, and they remained so after being burned once or twice. Some separation, however, occurred along ordination axes owing to differences in the relative covers of a handful of common species. For the acid cove community, the greatest separation occurred along axis 1 ($R^2 = 0.35$) (Fig. 6). Kendall ($\tau$) coefficients and $R^2$ values, calculated for species in acid cove plots, identify red maple as the species most

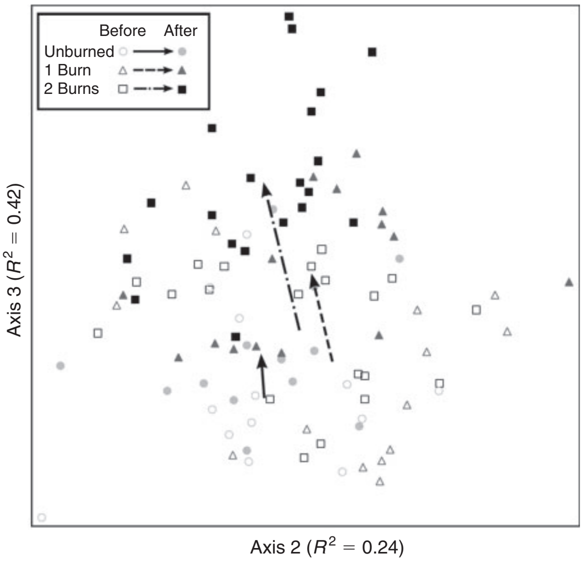

**Fig. 7.** Non-metric multidimensional scaling ordination of trees in the thermic oak dataset using a Bray–Curtis dissimilarity distance measure. Analysis was based on species composition, using the relative covers of trees in each plot. Open circles are unburned plots during the first measurement period. Closed circles are unburned plots during the second measurement period. Open triangles represent plots measured before one burn, whereas closed triangles are plots measured after one burn. Open squares are plots measured before two burns whereas closed squares are the same plots after two burns. Arrows represent change in centroids of each treatment group between measurements. Final stress for the three-dimensional solution was 16.5 over 84 iterations. Axis 1 was not included, having the lowest explanatory power ($R^2 = 0.09$).

**Table 2. Results of the multi-response permutation procedure (MRPP) for the acid cove and thermic oak community datasets**

Similarity was determined using a Bray–Curtis dissimilarity measure. The *P* values of pairwise comparisons of treatments (U = unburned, 1 = 1 burn, 2 = 2 burns) were corrected for multiple comparisons using the Bonferroni correction. Irrelevant pairwise comparisons were excluded. The within-group agreement value, A, represents the similarity of sample units within each group. $A = 1$ when all items are identical within groups; $A = 0$ when heterogeneity within groups is equal to that which would be expected by chance; $A < 0$ when there is more heterogeneity within groups than expected by chance

| Burn history | | Community | | | |
|---|---|---|---|---|---|
| | | Acid cove | | Thermic oak | |
| | | *A* | *P* | *A* | *P* |
| U Before | U After | −0.002 | 7.961 | −0.017 | 14.884 |
| 1 Before | 1 After | 0.021 | 0.864 | 0.029 | 0.154 |
| 2 Before | 2 After | −0.001 | 6.879 | 0.062 | <0.01*** |
| U Before | 1 Before | −0.001 | 7.072 | 0 | 6.112 |
| U Before | 2 Before | 0.03 | 0.345 | 0.028 | 0.044 |
| 1 Before | 2 Before | 0.024 | 1.043 | 0.012 | 1.253 |
| U After | 1 After | 0.011 | 2.68 | 0.04 | 0.016 |
| U After | 2 After | 0.068 | 0.002 | 0.092 | <0.01*** |
| 1 After | 2 After | 0.055 | 0.016 | 0.021 | 0.119 |
| Overall | | 0.047 | <0.01*** | 0.058 | <0.01*** |

negatively correlated with axis 1 ($\tau = -0.698$; $R^2 = 0.548$; see Table S1 in the Supplementary Material, available online only). This indicates it decreased in relative cover between the first and second measurement period – particularly in plots that burned. This observation corroborates the findings of Abrams (1992), who described red maple as one of the most fire-sensitive tree species in eastern North America, and Lorimer (1984), who concluded that dominance by red maple would be negatively correlated with disturbance frequency. American holly (*Ilex opaca*) and sweetgum (*Liquidambar styraciflua*) had the strongest positive correlations ($\tau = 0.364$ and 0.394 respectively). However, low $R^2$ values for all species other than red maple (generally <0.3) indicate that the relationships were not strong. For the thermic oak community, the greatest separation occurred along axis 3 ($R^2 = 0.42$) (Fig. 7). Red maple ($\tau = -0.39$) and sourwood (*Oxydendrum arboreum*) ($\tau = -0.411$) were the species most negatively correlated with axis 3, indicating decreases in their relative cover (Table S2). Princesstree ($\tau = 0.344$) was the most positively correlated. Again, however, these relationships were not strong ($R^2 < 0.4$). The MRPP procedure provided further evidence that burn history had no significant effect on tree composition in the acid cove tree community, and that only slight effects occurred in the thermic oak plots burned twice (Table 2). Overall, the results of these multivariate analyses indicate that one or two high-severity fires may not result in substantial long-term alterations to Appalachian forest communities. Top-killed trees generally resprouted, resulting in post-fire community assemblies that were similar to what was present before the first fire.

## Conclusions

Fire is known to alter plant species composition and increase community heterogeneity in forest ecosystems. However, knowledge about the landscape-effects of fire – particularly high-intensity wildfire – is lacking for the much of the Appalachian region of eastern North America. Five wildfires that burned in and around Linville Gorge of North Carolina between 2000 and 2008, some of which burned the same area twice, offered a rare glimpse into the effects of fire on long-unburned plant communities in the southern Appalachian Mountains. Smaller stems (<5 cm DBH) increased in abundance in response to fire, likely owing to the mortality of larger overstorey trees, vigorous resprouting and the establishment of young trees. Mountain laurel stem counts decreased in acid cove and thermic oak plots burned twice, oak stems increased in thermic oak plots burned twice and Table Mountain pine stems increased in thermic oak plots burned once. For most growth forms, the effects of one burn vs two burns were more pronounced in the thermic oak communities than in acid cove communities. Ruderal graminoid and forb cover responded positively to fires in both communities. Only modest changes in tree community composition were observed, even after two fires. Taken as a whole, these findings suggest that the vegetative composition and structure of burned areas will eventually return to a pre-fire state, unless the current short fire-return interval is maintained. However, monitoring and control efforts will likely be necessary in order to ensure that princesstree invasion does not result in an undesirable successional trajectory. Future studies should address the effects of season of burn and time since fire on plant community characteristics. Additionally, the effects of repeated wildfire fire on other ecosystem components (e.g. pathogens, fauna, soil, water, air) should be addressed.

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