

The Importance of Disturbance versus Physiography in Defining Vegetation Composition and Predicting Possible Successional Trajectories

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ABSTRACT Regional (climate/soils) and local (aspect) physiography determine plant community composition. However, changes in initial floristic composition after a disturbance may be severe enough to alter the successional trajectory predicted by physiography. We addressed the question of which is more important, disturbance or physiography, in determining vegetation composition and the consequent successional trajectory. We evaluated understory vegetation of forest communities exposed to four disturbance types (control, single burn, diameter-limit cut, and first-removal shelterwood) 2–5 yr postdisturbance. Study sites were located within each disturbance type on northeast and southwest aspects within the Appalachian Plateau and the Ridge and Valley provinces. Vegetation composition was analyzed with nonmetric-multidimensional scaling, two-way nonparametric multivariate ANOVA, and indicator species analysis. The relationship between disturbance and key environmental variables, including canopy opening and soil fertility, was analyzed with generalized linear mixed models. There were 363 species in our study area. Composition differed by province and aspect. Composition also differed by disturbance but with a significant province interaction. Although physiography was more important, some species served as disturbance indicators that differed by disturbance type with two possible outcomes. First, expected successional trajectories (as defined by the regional and local environmental filters) may deviate toward recovery of native species (e.g., *Epigaea repens*) that benefit from low-level disturbance (as defined by fire as a filter). Second, successional trajectories after a relatively severe disturbance (as defined by shelterwood harvest as a filter) may deviate toward systems that are vulnerable to invasion by exotics or dominant native species.

Key words: Appalachian plateau province, diameter-limit cut, fire, ridge and valley province, shelterwood harvest.

INTRODUCTION Plant community composition is broadly defined by regional (climate and soils) and local (slope position, elevation, and slope aspect) physiography (Vankat 1979, Gentry 1988, Prentice et al. 1992). Although the effects of climate are globally shared across similar latitudes, large-scale topographic characteristics, such as mountain ranges and large bodies of water, may influence the availability of

water and further differentiate the composition of plant species. For instance, having a north-to-south oriented mountain range and being relatively near a warm body of water (the Gulf of Mexico) result in unique climatic niches in the temperate deciduous forests of the US Mid-Atlantic compared with the far less-differentiated climatic niches of the temperate deciduous forests of western Eurasia at similar latitudes (Prentice et al. 1992, Mantey and Box 2007). Similarly, the Rocky Mountains affect regional climate in the western USA by modulating

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precipitation and wind, the well-known rain-shadow effect (Antic et al. 2006).

Within regional provinces, there are also microclimatic differences that occur because of local differences in slope position and aspect. These differences, which are often linked to available solar radiation, cause small-scale changes in humidity, soil moisture, soil microbial compositions, and rates of decomposition that may indirectly affect nutrient availability (Sidari et al. 2008, Carletti et al. 2009); all of which affects plant colonization, establishment, and composition (Gilliam et al. 1995, Huebner et al. 1995, van Breemen et al. 1997, Small and McCarthy 2005, Leuschner and Lenzion 2009). For example, Small and McCarthy (2005) found that north-facing slopes had greater nitrogen availability and herbaceous species richness than south-facing slopes had. Even at that scale, there are often distinct species compositions associated with different slope aspects (Huebner et al. 1995).

Regional and local physiography, thus, serves as an environmental filter that help determine the plant community composition (Díaz et al. 1998) and that filter may also have a role at different stages of succession after a disturbance, resulting in predictable plant species pools. However, changes in environmental conditions after a disturbance (i.e., amount of available light, soil moisture, and soil nutrients) are also potential environmental filters that may be severe enough to affect the initial floristic composition, resulting in a change in the successional trajectory predicted by the physiography (Myster and Pickett 1990, McCook 1994). The relative importance of regional and local physiography vs. disturbance-caused environmental filters in defining successional trajectories and ultimate vegetation composition of a site is the focus of this article. Those communities defined less by physiography and more by disturbance may be less predictable and more vulnerable to undesirable changes in composition. This comparison between the effects of disturbance and physiography is especially important for vegetation compositions that are at least partially dependent on disturbance for regeneration.

Common forest-management recommendations for ecosystems dominated by oak (*Quercus* spp.) and similar shade-intermediate tree species, include a sequence of harvesting com-

bined with prescribed fire. Both open up the canopy to increase light reaching the forest floor, and a subsequent burn may also reduce competition from fire-intolerant plants (Hannah 1987; Arthur et al. 1998; Brose et al. 1999a, 1999b, 2013; Hutchinson et al. 2005b; Iverson et al. 2008; Miller et al. 2017). In the absence of disturbance, dominant canopy species with regeneration processes that require disturbance will be depleted and not replaced over the successional trajectory. In terms of fire, some plant communities, such as those of the Sonoran Desert in Arizona, USA, are more responsive to existing physiography (the environmental filters) than they are to historic fire disturbance (Shryock et al. 2015). In contrast, repeated burning applied over 6 yr in an oak-dominated, temperate forest across variable topography has led to a more-homogeneous plant-community composition that was once differentiated by topography (Kim and Arthur 2014). Herbaceous and tree seedling composition have also become more homogeneous in response to fire (burned at least twice within 3 yr) across an integrated moisture index, except that shade-tolerant tree seedlings are more abundant on moist, mesic slopes (Hutchinson et al. 2005a, 2005b). Selectively cut forest stands, which have experienced some kind of harvesting every 4 yr, are more homogeneous and dominated by ruderal species compared with coppice stands with 30 yr of recovery that are dominated by mature forest species. The coppiced stands exhibit differences in microclimate because of topography, but the selectively cut stands do not. Repeated harvesting in those selectively cut stands appears to have altered the microclimate such that previous differences in microclimate are no longer evident (Decocq et al. 2005).

Successional theory holds that the initial floristic vegetation of a site could either contain all potential species found in every stage of succession, although in different proportions (Egler 1954), or it could be represented by species absent from later stages of succession that facilitate the colonization of new species and their own disappearance, also termed *relay floristics* (Clements 1916). In forests, most understory and many overstory species are capable of vegetative reproduction, making persistence after many disturbances likely (Fourrier et al. 2015). However, the more severe a disturbance the more likely relay floristics will

dominate because only a few species can tolerate such harsh conditions (e.g., soil scarification after a harvest or hot burn) and colonization will be by more ruderal species found in the seed bank or dispersed from outside sources (Yoshida et al. 2005). Moreover, if the seed banks of native species have been depleted over time, which can be the result of excessive deer browse of understory species, the species composition may be more dependent on dispersal from adjacent forests (Beauchamp et al. 2013, Hidding et al. 2013). Even if the canopy tree species are producing seed, deer browse of native tree species will prevent regeneration of many species. Thus, for a period of time, we may see those tree species in the seedling stratum but not in the sapling or small-tree stratum. As the seed-producing trees die off, the tree seedlings disappear (Stromayer and Warren 1997, Schumacher and Carson 2013).

A disturbed plant community may also be composed of inhibitory species that, once established, do not give way to new species over successional seres, but instead stall succession and form an alternate stable state dominated by those inhibitory species (Connell and Slatyer 1977, Suding et al. 2004, Didham and Watts 2005, Royo and Carson 2006). Examples of this include the native fern *Dennstaedtia punctilobula* (Michx.) T. Moore and *Rhododendron maximum* L.; both of which have increased in abundance because of the combined effect of increased light from a disturbed forest canopy and deer browse (Hill and Silander 2001, Nilsen et al. 2001). Also, *Microstegium vimineum* (Trin.) A. Camus, an invasive, exotic grass, suppresses tree regeneration, altering tree species composition, often leading to a monotypic understory of itself (Flory and Clay 2010).

We addressed the following question: Is disturbance or physiography more important in determining vegetation composition in managed forests? If disturbance has a more important role than physiography in defining species composition, we postulate one of three possible successional trajectories. First, the disturbance has allowed some disturbance-dependent species to regain dominance in a once disturbance-prone site but other physiographically defined species are also found, and that dominance is only maintained if the disturbance occurs at regular intervals. Second, the disturbance has served as a filter for species characterized as ruderal,

shade-intolerant, or intermediate, which eventually give way to communities dominated by K-selected, shade-tolerant, and intermediate species (i.e., relay floristics). Third, the disturbance has served as a filter for species characterized as ruderal or even invasive, and those species inhibit the establishment of plants normally indicative of the site's physiographic conditions. If a given site, a few years after a disturbance, is made up of species only indicative of the disturbance and not of the physiography, that site is theoretically more prone to colonization by inhibitory species instead of relay floristics. That theory, once tested (which this current study does not do), could be applied globally for early prediction of whether a given plant community is potentially dependent on disturbance or vulnerable to invasion and subsequent alternate stable states. Disturbance-dependent sites often include relatively uncommon or even rare species (Pavlovic 1994) and knowing which sites may show those tendencies enables land managers to prioritize areas for management. Likewise, being able to predict during the early stages of succession the likelihood of an inhibitory, successional trajectory may enable land managers to treat those sites immediately while it is still feasible, such that they amend the initial composition to reflect one dominated by physiographically defined species. Early detection of an inhibitory successional trajectory, thus, may help land managers focus their limited resources as well as use them more efficiently.

MATERIALS AND METHODS

Study Area

This study took place in the Appalachian Plateau (AP; with sites in West Virginia and Ohio of the eastern USA) and Ridge and Valley (RV; with sites in West Virginia and two sites just across the border in Virginia) physiographic regions or provinces (Figure 1). The AP province receives 101 (eastern Ohio)–127 (western West Virginia) cm or more precipitation annually and recharges ground water at rate of 54.4 cm annually. Because of a rain shadow effect, the RV province receives 76–83 cm of precipitation and recharges ground water at a rate of 23.9 cm annually (Abrams and McCay 1996, Kozar and Mathes 2001, ODNR 2011). These provinces share a wide range of elevations, with the west to east elevation gradient generally increasing in the AP from 187 m in Marietta, Ohio, along the Ohio River, to 1,200 m on the Allegheny Front at Dolly

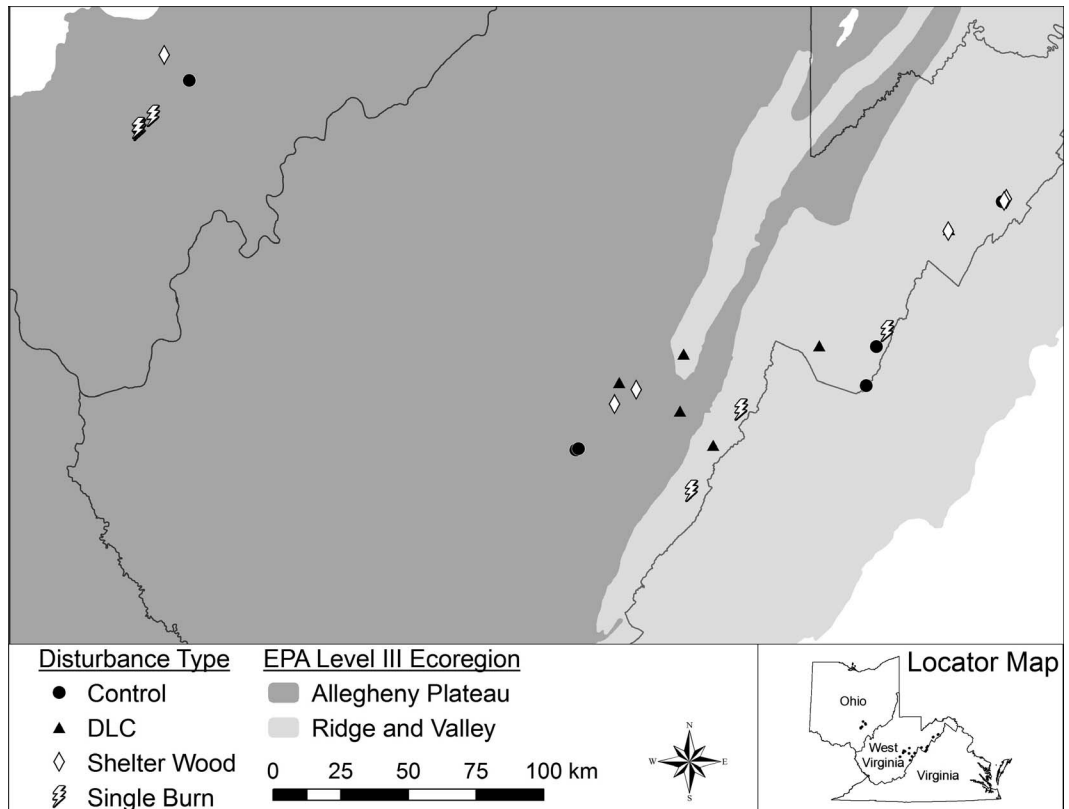


Figure 1. Site locations. Only northeast (NE)-facing slopes of the paired NE and southwest (SW) aspects are shown because of proximity. Some points are moved slightly for better visibility because their proximity to each other does not allow them to be separated at this scale. Actual coordinates for each site are available in Supplemental Table 1. Physiographic provinces are drawn from a US Geological Survey (USGS) map (Kozar and Mathes 2001).

Sods, West Virginia, then dropping off in the rain shadow of the RV to 285 m at Petersburg, West Virginia. The average daily temperatures are 20.6°C and 21.4°C for the AP and RV, respectively (Clarkson 1964, Pyle et al. 1982, Estep 1992, Abrams and McCay 1996). Sites were located on federal, state, and private lands. Sites located on private land were owned by industrial wood products companies as well as single families (Supplemental Table 1). The drier and warmer climate of the RV province has been associated with *Quercus* spp. L., *Carya* spp. Nutt., and *Pinus* spp. L., with *Acer rubrum* L. increasing since the loss of *Castanea dentata* (Marshall) Borkh. to chestnut blight. The more mesic AP province has been associated with *Fagus grandifolia* Ehrh., *Acer saccharum* Marshall, *Betula* spp. L., and *Tsuga canadensis* (L.) Carrière with increases in *Prunus serotina* Ehrh., *Acer rubrum*, and *Betula* spp. since the loss of *C.*

dentata (Clarkson 1964, Abrams and McCay 1996). Kaeser et al. (2008) found a *Gaylussacia baccata* (Wangenh.) K. Koch-dominated understory to be more common in the RV province than in the AP province in Pennsylvania. Thus, evident regional compositional differences make this an ideal location to evaluate the relative importance of disturbance as an environmental filter on vegetation composition. Taxonomic information followed International Plants Names Index (IPNI 2012) and the Integrated Taxonomic Information System (ITIS 2016).

Experimental Design

We focused on four forest disturbance types typical to the eastern deciduous forests of the USA. Our intent was to evaluate disturbance types that represent forest management regimes common to each region. Thus, our selection was from existing, disturbed sites with documented

histories. These disturbance types included (a) the control treatment with no management of forests at least 70 yr old; (b) single prescribed burns of forests at least 70 yr old, where a single burn took place within 5 yr of the vegetation sampling of this study; (c) a 2–4-yr-old, diameter-limit cut (DLC) in which about 50–75% of the total basal area of merchantable trees 40.6–45.7 cm (16–18 inches) in diameter or greater (i.e., removing the largest trees) was harvested (largest remnants trees were ≥ 70 yr old); and (d) a 3–4-yr-old, first-removal shelterwood (SHW) in which 50–75% of the overstory basal area from trees of mixed-sized classes was removed (largest residual trees were ≥ 70 yr old). Trees aged from three cores taken from the largest trees at each site confirmed the site-age estimates. The heavily cut SHWs and DLCs were a more-typical practice of the land managers in the RV province. The DLC harvests are commonly carried out on private, nonindustrial lands in the eastern USA because they usually result in a profit for both buyer and seller, with harvests every 15–20 yr but may lead to a loss of valuable species over time (Nyland 1992; Kenefic et al. 2005). Regeneration prescriptions involving SHW harvests have been used by the US Forest Service and some large industrial forestry companies but are less common on private lands because it usually takes at least 5–10 yr before adequate regeneration is achieved, and a more-complete overstory harvest can be conducted to yield additional revenue (Brose et al. 1999a, 1999b). Each site was likely harvested once before the applied disturbances here as part of the extensive land clearings (clear cuts and fires) that took place in the early 1900s in this region for railways, with most fires being started by locomotives in West Virginia (Brooks 1910) and to supply the charcoal iron industry in Ohio (Stout 1933). Single burns are commonly used by public and private land managers to temporarily reduce competing vegetation, as mentioned earlier; repeat burns may be more effective but are relatively uncommon in the AP because of fewer adequate weather windows to burn. Indeed, we could not find enough repeat burn sites in the AP region to allow for a comparison.

Three replicates of each disturbance type were located on both northeast (NE)- and southwest (SW)-facing slopes in both the AP and RV provinces, representing a total of 48 sites (3 replicates \times 2 slope aspects \times 2 provinces \times 4

disturbance types = 48). Replicate sites were randomly selected from available sites within each category that met all the criteria. Slope inclination averaged 34.9% for the AP and 37.7% for the RV. Elevations averaged 623 m for the AP and 805 m for the RV. All data were collected once between June and August 2010.

Site Environmental Conditions—Soil and Light

At each site, a 100-m transect that ran along the elevational contour in the middle of the stand was set up, with four circular 1-m² plots nested within 10 circular 10-m² plots located every 10 m along the transect. Every other 10-m² plot was fenced to keep out deer. Fencing primarily ensured we had data for another portion of the study involving planting particular species, including *Q. rubra* L. Vegetation in fenced and unfenced plants did not differ for the duration of this study. A soil sample was taken at each cardinal direction outside each 10-m² plot and always outside each fence. Soil was collected from the top 10 cm (a depth sample that may contain just the A horizon or multiple horizons, e.g., A, E, and B horizons, depending on how deep each horizon was) in the odd-numbered plots, and from the first 10 cm of the B horizon (horizons above B were removed from the sample) in the even-numbered plots. The depth samples are located in the upper root zone of most understory plants but can be relatively variable because of differences in processes, such as litter decomposition rates. The B-horizon samples provide a relatively more-stable assessment of the available soil nutrients, although many of the understory plant roots may not be directly within this horizon. Samples were combined for all odd-numbered and all even-numbered plots, resulting in two mixed soil samples, a depth sample, and a B-horizon sample, per site. Soils were sent for a full forest-soil analysis to the University of Maine Analytical Laboratory and Maine Soil Testing Service (Orono, Maine). Their forest-soil protocols were followed and included analyses for soil pH (measured in distilled water), percentage of soil organic material (determined by loss on ignition at 550°C), percentage of total N and C (using combustion and a Leco Tru-Mac CN [LECO Corporation, St. Joseph, Michigan]), concentrations (mg/kg) of Ca, K, Mg, P, Al, Mn, and Zn in a Mehlich 3 or modified Morgan extract using the inductively coupled plasma atomic

emission spectroscopy method, (McIntosh 1969, Mehlich 1984), and cation-exchange capacity (CEC, which is the sum of milliequivalent levels of Ca, K, Mg, Na, and acidity, the latter two are not presented in this article) measured in meq/100 g. The Ca, K, Mg, and P are well-established important plant macronutrients, and Al is a known plant toxin (Delhaize and Ryan 1995). The Mn and Zn are important plant micronutrients that have been attributed to more-acidic soils and can be toxic to plants in high concentrations (El-Jaoual and Cox 1998, Long et al. 2003).

In the center of each 10-m² plot, the percentage of the canopy opening was determined using a fish-eyed lens hemispherical photograph. Photographs were taken under variable conditions, primarily full or partial sun. Glare was avoided by waiting for cloud or sun movement. Photographs were analyzed with HemiView 2.1 (Delta-T Devices Ltd 1999, Cambridge, UK). The percentage of the visible sky was measured from each photograph and averaged for each site.

Understory Vegetation

In each 1-m² plot, the percentage of cover for all herbaceous species, vines, and shrubs was estimated to the nearest 0.5%, and both the cover and density were measured for all the tree seedlings. Cover of herbs was only included for those herbs that were rooted in the plot, but shrub and vine cover was included without the requirement of being rooted inside the plot. Tree seedlings were defined as any tree species less than 1-m tall. Average cover for the herbs, vines, and shrubs was determined per site and used as the importance value. Average cover and average density were determined for each tree seedling species. These were then averaged for each species and used as the importance value. Importance values for all species were relativized within the following two categories: (a) herbs, vines, and shrubs (henceforth referred to as *herbs*); and (b) tree seedlings.

Data Analyses

Soil C:N, Ca:Al, and the percentage of organic C were calculated as measures of soil fertility (Cronan and Grigal 1995, Knops and Tilman 2000). The Al may inhibit Ca uptake, and ratios (Ca:Al) as high as 1 and as low as 0.2 indicate a 50% chance and a 100% chance, respectively, of Al stress and nutrient imbalances causing low soil fertility (Cronan and Grigal 1995). This

information along with concentrations of K, Mg, P, Mn, and Zn were used as indicators of soil fertility (or lack thereof). Herb and tree seedling species richness and the Shannon-Wiener diversity index were calculated for each site. Total herb cover was also determined by summing actual cover values. Diversity calculations were performed with the log-transformed data that was also used in the nonmetric multidimensional scaling (NMS) analyses described below. Each soil variable, visible sky, herb cover, herb and tree seedling richness, herb and tree seedling diversity variables was included as response variables in a generalized linear mixed model, with *site* as the random effect and *province*, *aspect*, *disturbance type*, and their interaction as fixed effects (Proc GLIMMIX; SAS 9.4 2013, Cary, North Carolina). Visible sky, Ca:Al, percentage of soil organic material, soil P concentration from a 6-cm depth, and concentrations of soil K, Mg, Mn, and Zn at the 10-cm depth, and from the B horizon, herb cover, herb richness, and tree seedling richness were best fit using a lognormal distribution and identity link function. The C:N, CEC, soil P concentration from the B horizon, and herb and tree seedling diversity were best fit with a normal distribution and identity link function. Distributions were also confirmed using a univariate analysis for each response variable (Proc Univariate; SAS 9.4).

The understory vegetation data matrices were evaluated as log-transformed values because the data were positively skewed to the right. The log transformation served to compress high values and spread the more common but variable low values as orders of magnitude. The following transformation equation was used: $\log(x + 0.001) - \text{Integer value of } \log(\text{Minimum nonzero value in data set})$ or $\log(x + 0.001) - (-3)$ for the herbs and $\log(x + 0.01) - (-2)$ for the tree seedlings. This allows values that were originally zero to remain zero. The NMS with a Sørenson distance measure (PCOrd version 5, MjM software 2006, Gleneden Beach, Oregon) was used for (a) herbs, and (b) tree seedlings, separately. Soil variables that were significant at the $p \leq 0.15$ level in the mixed models were included in the NMS analysis as a constrained ordination using multiple regression (Heiser and Meulman 1983; PCOrd version 5). Only the percentage of organic matter from the B horizon and the soil nutrients (log-normal transformation) from the

soil-depth samples were used because including both for one soil measure would result in multicollinearity because of significant correlations between those variables and because the percentage of organic matter from the B horizon had a lower p value than the p value from the depth-soil sample. Likewise, the soil nutrients meeting the significant p value cutoff were associated with the depth sample and not the B-horizon sample.

Statistically significant differences among the species compositions associated with the two regions, the two aspects, and the four disturbance types were determined using a two-way permutation-based nonparametric multivariate analysis of variance (PERMANOVA; PCOrd version 5). The PERMANOVA provides similar information as the analysis of similarities and Mantel tests but is less sensitive to within-group, heterogeneous dispersion. (All three tests assume homogeneity of within-group variance.) Indicator species analysis (Dufrene and Legendre 1997; PCOrd version 5) was used to determine the species that best defined each region, aspect, and disturbance type. That analysis calculates the proportional abundance of each species in a single group compared with its abundance in all groups being examined and the proportional frequency of each species in a single group relative to its frequency in all groups. The proportional abundance and frequency are then multiplied to obtain a relative importance value. Statistical significance of each importance value was determined with a Monte Carlo method, comparing their values against what would be expected by chance over 1,000 random iterations (McCune and Grace 2002).

RESULTS

Environmental Variables—Soil and Light

Forest canopies of sites in the RV province were significantly more open (20% visible sky on average) than those in the AP province (8.5% visible sky on average). The SHW sites (28%) had significantly more open canopies than the control sites had (4.6%; Tables 1–2). There was a general trend for AP sites to exhibit greater soil fertility than the RV sites with higher values of Ca:Al, K, Mg, percentage of organic matter, and CEC, and lower values of C:N (Tables 1–2), but only the percentage of organic matter and the C:N ratio were statistically significant.

Environmental Variables—Understory Vegetation

There were 313 herb species and 50 tree seedling species within our study plots. Although sites in the AP province averaged 42.0 species compared with the RV average of 25.6, that difference and the differences in diversity were only significant at the $p \leq 0.1$ level. The harvested (DLC and SHW) disturbance sites had the highest cover values, and although the SHW had the greatest cover at 21.8% and the control had the lowest at 7.2%, that difference was not significant (Tables 1–2).

Disturbance vs. Environmental Effects

The most stable NMS ordination for herbs was a three-dimensional solution and had a final stress value of 13.2 and a final instability value of 0.0 after 124 iterations. Each dimension up to six was evaluated with a maximum of 500 iterations. Axis one explained 43.4% of the variation, axis two 22.9%, and axis three 14.5%. Sites separated well based on species composition by province and less so by aspect. Although no pattern of separation was evident using the four disturbance types, there was a weak grouping of the control sites with the single burn sites and the DLC sites with the SHW sites. The percentage of canopy opening (light) and C:N were most closely and positively correlated ($r^2 > 0.45$) with the RV province and the SW aspect. The Mg, CEC, and percentage of organic matter were most closely and positively correlated ($r^2 > 0.25$) with the AP province and the NE aspect. It was much more difficult to discern any pattern of soil or light environmental variables with the disturbance types, although the SHW sites were positively correlated with canopy opening (Figures 2a, 2b, and 2c). Likewise, the NMS ordination for the tree seedlings was also a three-dimensional solution with a stress value of 15.0, and a final instability value of 0.0 after 138 iterations. Six dimensions were also tested using a maximum of 500 iterations. Axis one explained 52.1% of the variation, axis two 22.3%, and axis three 15.3%. Sites also distinctly separated by province based on tree-seedling species composition, less so by aspect, and least by disturbance type. The grouping of the control sites with the single-burn sites for tree seedlings was less evident than the grouping with the herbs. The percentage of canopy opening and C:N were most closely and positively correlated with the

Table 1. Generalized linear mixed model F values (Proc GLIMMIX, SAS version 9.4) using *site* as the random effect and *province*, *aspect*, *disturbance type*, and their interaction as fixed effects. Numbers in parentheses are the p values. Values in bold are significant at $p \leq 0.05$; values in italics are significant at $p \leq 0.15$ and were also included in the nonmetric multidimensional scaling analyses because of an apparent trend. B = B horizon soil sample; CEC = cation-exchange capacity; D = sample from soil depth.

Response Variable	Province	Aspect	Disturbance Type	Interaction
Herb cover (%)	3.6 (0.2)	0.05 (0.9)	4.4 (0.2)	0.9 (0.6)
Herb richness	7.7 (0.1)	2.3 (0.3)	0.5 (0.7)	2.1 (0.4)
Herb diversity	6.1 (0.1)	2.3 (0.3)	0.7 (0.6)	0.9 (0.6)
Tree seedling richness	29.3 (0.03)	0.3 (0.6)	0.8 (0.6)	1.5 (0.5)
Tree seedling diversity	16.2 (0.06)	0.4 (0.6)	0.1 (0.9)	0.6 (0.7)
Visible sky (%)	27.8 (0.03)	0.0 (1.0)	21.6 (0.05)	0.3 (0.9)
B-pH	0.08 (0.8)	2.7 (0.2)	2.0 (0.4)	2.0 (0.4)
D-pH	0.3 (0.7)	6.7 (0.1)	3.9 (0.2)	1.7 (0.4)
B-% organic matter	21.0 (0.05)	0.01 (0.9)	1.5 (0.4)	3.3 (0.3)
D-% organic matter	10.2 (0.09)	0.03 (0.9)	2.1 (0.3)	1.2 (0.6)
B-CEC	17.0 (0.05)	0.09 (0.8)	1.0 (0.5)	4.2 (0.2)
D-CEC	17.6 (0.05)	0.1 (0.8)	3.6 (0.2)	2.8 (0.3)
B-C:N	13.4 (0.07)	9.5 (0.09)	0.7 (0.6)	1.2 (0.5)
D-C:N	20.3 (0.05)	22.6 (0.04)	1.5 (0.4)	2.3 (0.3)
B-Ca:Al	0.5 (0.6)	6.3 (0.1)	0.4 (0.8)	1.9 (0.4)
D-Ca:Al	0.3 (0.7)	10.0 (0.09)	0.6 (0.7)	1.9 (0.4)
B-K	7.5 (0.1)	0.06 (0.8)	7.3 (0.1)	2.7 (0.3)
D-K	6.0 (0.1)	0.08 (0.8)	5.0 (0.2)	1.6 (0.5)
B-Mg	8.2 (0.1)	1.1 (0.4)	1.1 (0.5)	0.6 (0.8)
D-Mg	10.5 (0.08)	4.4 (0.2)	0.3 (0.8)	0.8 (0.7)
B-Mn	0.7 (0.6)	14.3 (0.06)	0.2 (0.9)	0.9 (0.6)
D-Mn	0.0 (1.0)	22.1 (0.04)	1.2 (0.5)	1.1 (0.6)
B-P	0.1 (0.8)	3.9 (0.2)	1.4 (0.5)	2.0 (0.4)
D-P	2.1 (0.3)	0.3 (0.6)	1.2 (0.5)	1.4 (0.5)
B-Fe	0.7 (0.5)	5.8 (0.1)	1.4 (0.4)	1.2 (0.5)
D-Fe	0.01 (0.9)	9.5 (0.09)	0.8 (0.6)	1.1 (0.6)
B-Zn	2.0 (0.3)	0.4 (0.6)	1.4 (0.4)	1.2 (0.5)
D-Zn	4.4 (0.2)	1.1 (0.4)	3.1 (0.3)	1.2 (0.6)

RV province and SW aspects ($r^2 > 0.20$). The percentage of organic matter, K, Mg, and Mn were most closely and positively correlated ($r^2 > 0.20$) with the AP province and NE aspects (Figures 3a, 3b, and 3c).

A two-way factorial PERMANOVA showed that the groupings of herb species as categorized within disturbance ($F = 2.13$; $p = 0.00020$) as the fixed factor and province ($F = 7.52$; $p = 0.00020$) were significantly different from each other, but their interaction was also significant ($F = 1.49$; $p = 0.020$). The province variable explained 18.9% of the variation under the scenario with disturbance as the fixed factor. After removing the effects of province, control sites differed significantly in composition from SHW and single-burn sites, but not DLC sites, whereas DLC sites differed significantly from SHW and single-burn sites, and SHW sites differed significantly from single-burn sites. Without removing the effects of province, only control and single-burn sites differed significantly from SHWs (Table 3).

Using province as the fixed factor, disturbance explained 4.7% of the variation, and all other pair-wise comparisons showed the same significant comparisons as the analysis with disturbance as the fixed factor.

Similarly, tree seedling species show groupings by province and disturbance using two-way PERMANOVA. The categories within province ($F = 10.44$; $p = 0.00020$) and disturbance type ($F = 1.97$; $p = 0.0060$) were both significantly different with a significant interaction ($F = 1.95$; $p = 0.0054$). With disturbance as the fixed factor, province explained 23.4% of the variation. Single-burn sites were significantly different from control and DLC sites, and SHW sites were significantly different from DLC sites after partitioning province out. Control sites were no longer significantly different from single-burn sites when province was not partitioned out (Table 4). In addition, if province was the fixed factor, disturbance type explained 0.1% of the variation and all pair-wise comparisons showed

Table 2. Means of species (cover, richness, and diversity), light, and soil variables. Numbers in parentheses are the standard errors. Numbers in bold are significantly different at $p \leq 0.05$, and means with different letters are significantly different within each category. Values in italics are statistically different at the $p \leq 0.15$ level and were also included in the nonmetric multidimensional scaling analyses because of an apparent trend. B = B horizon; C = control; CEC = cation-exchange capacity; D = sample from soil depth; DLC = diameter-limit cut; SB = single burn; SHW = shelterwood.

Response Variable	Province			Aspect			Disturbance Type			
	AP	RV	NE	SW	C	DLC	SHW	SB	SB	
Herb cover (%)	14.6 (2.8)	10.3 (1.7)	12.1 (2.0)	12.8 (2.7)	7.2 (2.8)	12.5 (4.5)	21.8 (4.5)	8.4 (1.7)		
Herb richness	<i>42.6 (4.1)</i>	<i>25.6 (2.0)</i>	36.3 (3.5)	31.3 (6.4)	28.3 (3.4)	37.1 (6.7)	34.3 (5.7)	35.7 (4.3)		
Herb diversity	<i>2.5 (0.2)</i>	<i>1.7 (0.1)</i>	2.2 (0.2)	1.9 (0.2)	2.1 (0.2)	2.0 (0.3)	1.8 (0.3)	2.3 (0.2)		
Tree seedling richness	16.4a (0.8)	11.3b (0.6)	13.4 (0.8)	14.3 (1.0)	13.6 (1.3)	13.9 (1.3)	13.2 (1.4)	14.7 (1.0)		
Tree seedling diversity	<i>2.5 (0.06)</i>	<i>2.1 (0.08)</i>	2.3 (0.09)	2.3 (0.08)	2.4 (0.09)	2.3 (0.1)	2.3 (0.1)	2.3 (0.1)		
Visible sky ($\times 100$; %)	0.08a (0.02)	0.2b (0.03)	0.1 (0.03)	0.1 (0.03)	0.07a (0.01)	0.1ab (0.03)	0.3b (0.05)	0.10ab (0.02)		
B-pH	4.6 (0.06)	4.6 (0.03)	4.7 (0.05)	4.5 (0.04)	4.6 (0.08)	4.6 (0.03)	4.5 (0.06)	4.7 (0.04)		
D-pH	4.3 (0.08)	4.4 (0.05)	<i>4.4 (0.08)</i>	<i>4.3 (0.05)</i>	4.3 (0.07)	4.4 (0.08)	4.2 (0.1)	4.6 (0.06)		
B-% organic matter	5.8a (0.4)	3.7b (0.3)	4.7 (0.4)	4.8 (0.4)	4.8 (0.5)	5.1 (0.5)	5.0 (0.9)	4.0 (0.2)		
D-% organic matter	<i>8.3 (0.5)</i>	<i>6.0 (0.5)</i>	7.1 (0.6)	7.2 (0.6)	7.8 (0.9)	7.9 (0.7)	7.4 (1.0)	5.5 (0.2)		
B-CEC	7.1 (0.6)	4.4 (0.4)	5.8 (0.6)	5.7 (0.6)	5.8 (0.5)	6.0 (0.7)	6.1 (1.3)	5.1 (0.5)		
D-CEC	<i>8.2 (0.5)</i>	<i>5.4 (0.4)</i>	6.9 (0.6)	6.7 (0.5)	7.2 (0.6)	7.7 (0.8)	6.7 (1.1)	5.7 (0.4)		
B-C:N	<i>13.6 (0.5)</i>	<i>17.3 (0.8)</i>	14.1 (0.7)	16.8 (0.7)	16.0 (1.3)	15.2 (1.1)	16.2 (1.1)	14.5 (0.9)		
D-C:N	14.9 (0.5)	19.0 (0.4)	15.4 (0.6)	18.5 (0.7)	17.5 (0.6)	16.5 (0.8)	17.7 (0.4)	16.1 (1.1)		
B-Car:Al	0.9 (0.4)	0.3 (0.05)	1.0 (0.4)	<i>0.2 (0.04)</i>	0.9 (0.7)	0.4 (0.2)	0.4 (0.1)	0.7 (0.3)		
D-Car:Al	2.4 (0.8)	1.0 (0.3)	<i>2.9 (0.8)</i>	<i>0.5 (0.1)</i>	1.2 (0.8)	1.3 (0.8)	2.4 (1.0)	2.1 (0.9)		
B-K	<i>69.4 (4.5)</i>	<i>54.9 (5.3)</i>	61.2 (5.3)	63.1 (5.0)	66.0 (7.2)	72.0 (9.8)	47.7 (5.8)	63.0 (3.2)		
D-K	<i>94.4 (7.3)</i>	<i>75.5 (7.1)</i>	88.8 (8.5)	81.1 (6.1)	<i>66.0 (10.6)</i>	<i>72.0 (13.1)</i>	<i>47.7 (8.5)</i>	<i>75.8 (4.6)</i>		
B-Mg	<i>41.0 (9.0)</i>	<i>19.2 (5.7)</i>	38.3 (9.9)	21.8 (4.6)	36.9 (15.8)	36.5 (12.6)	16.5 (5.0)	30.4 (7.8)		
D-Mg	<i>59.2 (10.8)</i>	25.5 (4.3)	55.8 (11.1)	28.9 (4.4)	41.3 (11.8)	51.3 (15.9)	32.6 (10.4)	44.2 (12.2)		
B-Mn	24.4 (4.1)	19.3 (3.0)	<i>29.2 (4.1)</i>	<i>14.5 (2.3)</i>	23.4 (4.8)	25.1 (6.0)	22.0 (6.6)	17.0 (2.4)		
D-Mn	<i>52.9 (7.7)</i>	49.5 (7.4)	67.0 (6.5)	35.4 (7.2)	61.2 (14.6)	53.4 (9.6)	53.9 (10.0)	36.2 (6.9)		
B-P	1.0 (0.07)	1.0 (0.1)	0.9 (0.08)	1.1 (0.09)	1.2 (0.1)	0.9 (0.1)	0.8 (0.1)	0.9 (0.1)		
D-P	1.4 (0.1)	2.1 (0.4)	1.5 (0.1)	1.9 (0.4)	2.1 (0.4)	2.1 (0.8)	1.5 (0.2)	1.3 (0.08)		
B-Pe	9.8 (2.3)	5.6 (1.2)	6.6 (2.1)	8.8 (1.6)	7.4 (3.2)	8.5 (1.9)	10.6 (3.7)	4.4 (0.8)		
D-Pe	10.9 (2.9)	8.0 (1.7)	6.7 (2.5)	<i>12.3 (2.9)</i>	7.4 (1.9)	10.3 (2.4)	13.7 (5.5)	6.5 (2.1)		
B-Zn	1.6 (0.1)	1.4 (0.2)	1.4 (0.2)	1.5 (0.1)	1.4 (0.1)	1.6 (0.3)	1.7 (0.3)	1.1 (0.1)		
D-Zn	2.5 (0.2)	1.9 (0.2)	2.0 (0.2)	2.3 (0.3)	2.7 (0.2)	2.0 (0.2)	2.4 (0.4)	1.5 (0.2)		

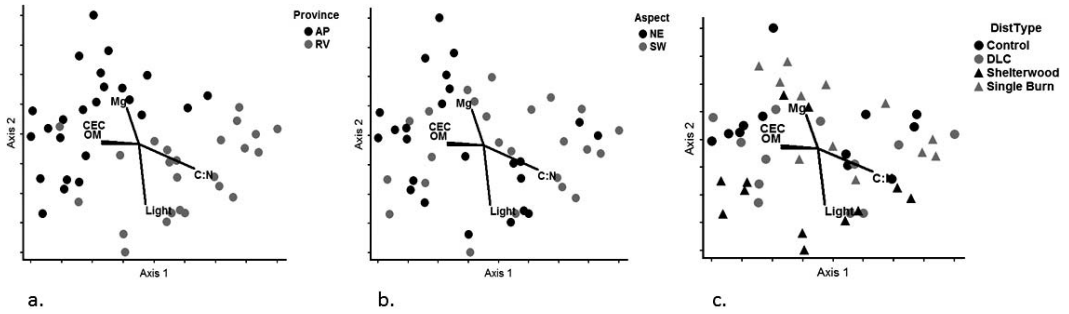


Figure 2. Nonmetric multidimensional scaling ordination results for herbs showing (a) province, (b) aspect, and (c) disturbance type. The final stress value was 13.18 and the final instability value was 0.00 after 124 iterations for a three dimensional solution (showing only axes 1 and 2). Environmental variables with correlation of 0.2 or greater are shown.

the same significant comparisons as when disturbance was the fixed factor.

Comparing herb species as categorized within disturbance and aspect using a two-way factorial PERMANOVA showed significant differences among the four disturbance types ($F = 1.80$; $p = 0.0034$) and between the two aspects ($F = 2.33$; $p = 0.0054$) with no significant interaction ($F = 0.57$; $p = 0.99$). Using disturbance as the fixed factor, aspect explained 7.3% of the variation. Pairwise comparisons with aspect partitioned out showed that control and single-burn sites differed significantly from the SHW sites, but there were no other significant differences. Retaining aspect in these pairwise comparisons did not change the results (Table 3). If aspect was the fixed factor, disturbance explained 10.0% of the variation, and the same patterns occurred with the pair-wise comparisons found with disturbance as the fixed factor. Tree-seedling species compositions did not differ

significantly in a two-way factorial PERMANOVA comparing categories within aspect ($F = 1.64$; $p = 0.10$) and disturbance ($F = 1.50$; $p = 0.063$), both with aspect and disturbance as fixed factors (Table 4).

A two-way factorial PERMANOVA comparing herb species as categorized within province (fixed factor) and aspect showed that although the groups within aspect ($F = 2.59$; $p = 0.0010$) and province ($F = 7.061$; $p = 0.00020$) were each significantly different, there was no significant interaction ($F = 1.15$; $p = 0.29$) between aspect and province. With province as the fixed factor, aspect explained 5.6% of the variation. With aspect as the fixed factor, province explained 19.6% of the variation. Tree seedlings, when categorized within province and aspect using a two-way factorial PERMANOVA with aspect as the fixed factor, also showed significant differences for province ($F = 9.43$; $p = 0.00020$) and marginally significant differences for aspect ($F =$

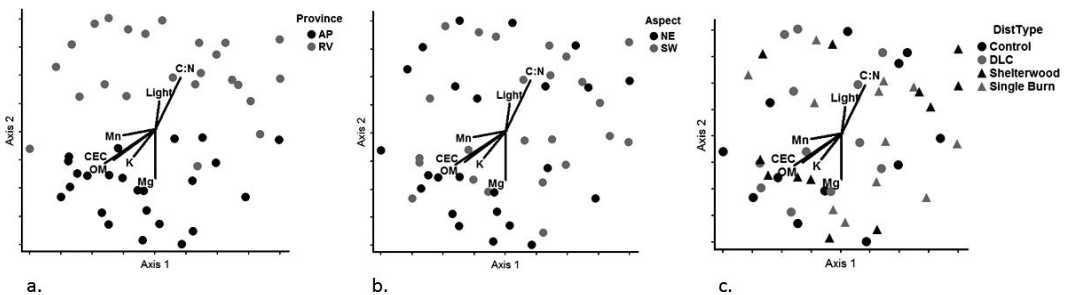


Figure 3. Nonmetric multidimensional scaling ordination results for tree seedlings showing (a) province, (b) aspect, and (c) disturbance type. The final stress value was 15.02, and the final instability value was 0.00 after 138 iterations for a three-dimensional solution (showing only axes 1 and 2). Environmental variables with correlation of 0.2 or greater are shown.

Table 3. Disturbance type variable pair-wise comparisons of the two-way PERMANOVA using disturbance and province or disturbance and aspect as variables for herb species. Comparisons beginning with an * are significantly different ($p \leq 0.05$).

Fixed Factor	Second Variable and Interaction		Comparison	t value	p value	
	Removed					
<i>Disturbance and Province</i>						
Disturbance	Yes		Control vs. DLC	1.14	0.17	
			*Control vs. Shelterwood	1.70	0.0030	
			*Control vs. Single Burn	1.32	0.046	
			*DLC vs. Shelterwood	1.38	0.031	
			*DLC vs. Single Burn	1.34	0.043	
	Disturbance	No		*Shelterwood vs. Single Burn	1.82	0.0012
				Control vs. DLC	1.068	0.28
				*Control vs. Shelterwood	1.56	0.0068
				Control vs. Single Burn	1.23	0.094
				DLC vs. Shelterwood	1.26	0.085
	DLC vs. Single Burn	1.23	0.088			
	*Shelterwood vs. Single Burn	1.65	0.0034			
<i>Disturbance and Aspect</i>						
Disturbance	Yes		Control vs. DLC	1.07	0.29	
			*Control vs. Shelterwood	1.55	0.0046	
			Control vs. Single Burn	1.24	0.090	
			DLC vs. Shelterwood	1.25	0.099	
			DLC vs. Single Burn	1.24	0.084	
	Disturbance	No		*Shelterwood vs. Single Burn	1.64	0.0038
				Control vs. DLC	1.07	0.29
				*Control vs. Shelterwood	1.56	0.0070
				Control vs. Single Burn	1.23	0.10
				DLC vs. Shelterwood	1.26	0.079
	DLC vs. Single Burn	1.23	0.086			
	*Shelterwood vs. Single Burn	1.65	0.0032			

1.95; $p = 0.052$). Province explained 27.0% of the variation with aspect as the fixed factor. With province as the fixed factor, aspect explained 4.5% of the variation, and both province ($F = 9.43$; $p = 0.0002$) and aspect ($F = 1.95$; $p = 0.048$) differed significantly. Because results are similar to those presented in Tables 3–4, we did not provide separate tables.

Indicator Species

There were a total of 42 significant ($p \leq 0.05$) indicator herb species in the AP province. The top five most-important (highest importance value) species were *Smilax rotundifolia* L., *Rubus* L. spp., *Carex laxiflora* Lam., *Eurybia divaricata* (L.) G.L. Nesom, and *Solidago caesia* L. (Table 5). There were 11 significant ($p \leq 0.05$) indicator tree-seedling species in the AP province, and the top five most-important species were *Acer saccharum*, *Prunus serotina*, *Fagus grandifolia*, *Liriodendron tulipifera* L., and *Fraxinus americana* L. (Table 6). In the RV region, there were 11 significant indicator herb species and five significant tree-seedling species.

The top five most-important herb species in the RV province were *Vaccinium pallidum* Aiton, *Carex pensylvanica* Lam., *Erechtites hieracifolius* Raf. ex DC., *Kalmia latifolia* L., and *Gaylussacia baccata* (Table 5). The four significant ($p < 0.05$) indicator tree-seedling species in the RV province were *Acer rubrum*, *Pinus strobus* L., *Nyssa sylvatica* Marshall, and *Pinus* spp. (Table 6).

There were a total of 11 significant ($p \leq 0.05$) indicator herb species associated with NE-facing slopes, and the five most-important species were *Arisaema triphyllum* (L.) Schott, *Viola pubescens* Aiton, *Dryopteris intermedia* (Muhl. ex Willd.) A. Gray, *Conopholis americana* (L.) Wallr., and *Actaea racemosa* L. (Table 5). No tree-seedling species were indicators of NE-facing slopes (Table 6). There were seven significant ($p \leq 0.05$) indicator herb species associated with SW-facing slopes, and the five most-important species were *Vaccinium pallidum*, *Potentilla simplex Michx./canadensis* L., *Danthonia spicata* (L.) P. Beauv. ex Roem. & Schult., *Gaylussacia baccata*, and *Carex will-*

Table 4. Disturbance type variable pair-wise comparisons of the two-way PERMANOVA using disturbance and province or disturbance and aspect as variables for tree-seedling species. Comparisons beginning with an * are significantly different ($p \leq 0.05$).

Fixed Factor	Second Variable and Interaction		Comparison	t-value	p-value	
	Removed					
<i>Disturbance and Province</i>						
Disturbance	Yes		Control vs. DLC	1.29	0.098	
			Control vs. Shelterwood	1.082	0.31	
			*Control vs. Single Burn	1.46	0.045	
			*DLC vs. Shelterwood	1.58	0.015	
			*DLC vs. Single Burn	1.72	0.0072	
	No		Shelterwood vs. Single Burn	1.20	0.18	
			Control vs. DLC	1.18	0.18	
			Control vs. Shelterwood	0.99	0.45	
			Control vs. Single Burn	1.26	0.13	
			*DLC vs. Shelterwood	1.43	0.044	
<i>Disturbance and Aspect</i>	Yes		*DLC vs. Single Burn	1.48	0.037	
			Shelterwood vs. Single Burn	1.02	0.39	
		No		Control vs. DLC	1.18	0.18
				Control vs. Shelterwood	0.98	0.47
				Control vs. Single Burn	1.24	0.16
			*DLC vs. Shelterwood	1.42	0.044	
			*DLC vs. Single Burn	1.45	0.045	
	Disturbance	No		*Shelterwood vs. Single Burn	0.99	0.45
				Control vs. DLC	1.18	0.18
				Control vs. Shelterwood	0.98	0.46
			Control vs. Single Burn	1.26	0.13	
			*DLC vs. Shelterwood	1.43	0.041	
	*DLC vs. Single Burn	1.48	0.040			
	Shelterwood vs. Single Burn	1.02	0.39			

denowii Schkuhr ex Willd. (Table 5). Two tree-seedling species significantly ($p \leq 0.05$) defined the SW-facing slopes, including *Quercus montana* Willd. and *Quercus coccinea* Münch (Table 6).

No significant indicator herb species were associated with the control or DLC sites (Table 5). In contrast, nine significant ($p \leq 0.05$) indicator herb species were associated with the SHW sites, with *Anaphalis margaritacea* (L.) Benth., *Erechtites hieraciifolius*, *Phytolacca americana* L., *Carex communis* L.H. Bailey, and *Dichanthelium acuminatum* (Sw.) Gould & C.A. Clark, representing the top five. *Erechtites hieraciifolius* was also significantly associated with the RV province, and *Rubus* spp. was significantly associated with the AP province. Five herb species were significantly ($p \leq 0.05$) associated with single-burn sites, and these were *Vaccinium stamineum* L., *Carex digitalis* Willd., *Epigaea repens* L., *Goodyera pubescens* (Willd.) R. Br., and *Conopholis americana*. Only *C. americana* was also significantly associated with another category (SW-facing slopes; Table

5). *Quercus rubra* was the only significant ($p \leq 0.05$) indicator tree-seedling species for the control sites. No tree seedlings served as indicator species for DLC, but *Betula* spp. was marginally significant ($p = 0.055$). *Aralia spinosa* L. and *Prunus pensylvanica* L.f. were significant ($p \leq 0.05$) indicators of the SHW sites. *Carya glabra* (Mill.) Sweet and *Carya* spp. were indicators of single-burn sites. None of the tree species significantly associated with the SHW or single-burn sites were also indicators of province or aspect (Table 6).

DISCUSSION

Relative Importance of Physiography and Disturbance

Physiography was more important than disturbance in defining vegetation composition in our study. Both herbs and tree seedling compositions, according to the NMS analyses and the PERMANOVAs, were defined best by regional (province) and local (aspect) physiography with most of the variation being explained by the province variable. Our results support the many

studies showing plant species compositional differences in these provinces (Clarkson 1964, Abrams and McCay 1996, Kaeser et al. 2008). Disturbance type was also important in our study, but it showed significant interaction with the province variable. Thus, our findings support the possibility that nonanthropogenic regional differences, as defined by climate and soil parent material, are the primary drivers of vegetation composition in our study area. Similarly, managed and unmanaged forest stands in Belgium, within both a site with acidic soil and another site with a neutral soil pH, showed compositional differences mainly associated with each site's soil pH (Verstraeten et al. 2013). Whether climate or soils are the most important variables defining the provinces and, thus, the vegetation, cannot be determined from our study. Although the AP province tended to have more fertile soils than the RV province, these differences were relatively weak, in part, because the soil pH and fertility within the AP are so variable, namely with Ohio soils being much higher in Ca than West Virginia soils (Huebner et al. 2014). Given that few soil-fertility variables were significant in our study, variables associated with water availability are likely the key drivers of understory species composition among our sites.

Because not all variation was accounted for in our analyses, it is possible a regional anthropogenic variable could be interacting with our disturbance and physiographic variables and affecting resource availability and subsequent plant species' responses. We did not include the potential effects of anthropogenic regional effects, such as climate change and acid rain; nonetheless, they could have a role. For instance, managed (agriculture and harvesting) and unmanaged, protected beech forests in Poland follow the same trends of fewer tree species in the shrub layer, canopy openings (because of harvesting in the managed forests and tree mortality in the unmanaged forests), acidification of the top soil layer, and an increase in generalist ruderal species and decrease in forest specialists (Durak 2010). The Durak (2010) research outcome may indicate that large-scale anthropogenic forces (climate change and acid rain) have effects.

Local physiography (aspect) had a weaker, but significant, role in defining the understory vegetation composition in our study area. Our findings support the importance of local micro-

climates in defining vegetation (Huebner et al. 1995, Abrams and McCay 1996, Small and McCarthy 2005, Kaeser et al. 2008, Leuschner and Lenzen 2009). In addition, although several studies within the AP and RV provinces support our findings, the aspect effects are usually associated with a particular province type. For instance, in the RV province of West Virginia, *Q. rubra* is more abundant on north-facing slopes, whereas *Q. montana* is more abundant on south-facing slopes. Likewise, in the AP province, north-facing slopes or bottomlands contain more *Acer saccharum*, and the south-facing slopes contain more *Betula* spp. (Abrams and McCay 1996). In the AP, Desta et al. (2004) found *Liriodendron tulipifera* and *Prunus serotina* more prevalent on northern aspects and *Q. alba* L. and *Q. montana* more prevalent on southern aspects. Nonetheless, our results showed no significant interaction between province and aspect.

Unlike our findings, some studies show that severe disturbances affect vegetation composition more than existing local physiography and microclimates do. Repeat burns and frequent harvests often lead to homogeneous plant-species compositions dominated by ruderal species (Hutchinson et al. 2005a, 2005b; Kim and Arthur 2014). Indeed such severe disturbances may lead to homogeneous species compositions because of a homogenized microclimate. The disturbance types in our study (single burns, DLCs that were cut every 15–20 yr, or SHW harvests with 50–75% of the tree volume left behind) would not be classified as severe compared with repeat burns or harvests every 5 yr. Because our results showed microclimate still had a role in defining understory species composition, the disturbances evaluated in our study were not severe enough to remove the effects of local physiography, although they were strong enough not to show a significant interaction with local physiography. In contrast, the effects of disturbance in our study could not be separated from the regional physiographic effects.

However, a lack of disturbance has also been shown to have a homogenizing effect on species composition. For instance, fire suppression in the Ozark Highlands has led to a more homogeneous landscape of oak and mixed-species forests, replacing forests that were once divided among the wet river bluffs and glades for fire-

Table 5. Indicator species by province, aspect, and disturbance for herb species. Species are ranked within each variable category by importance value (highest to lowest). Only significant ($p \leq 0.05$) indicator species are included in this list. Only the top 20 species of the 42 indicators for the Appalachian Plateau (AP) province are listed, plus an additional three species that were shared with other categories. All indicator species of the other categories are included. Species that occur in more than one category are in bold. Nomenclature follows the Integrated Taxonomic Information System (ITIS). C = control; DLC = diameter limit cut; NE = northeast; RV = Ridge and Valley; SB = single burn; SHW = shelterwood; SW = southwest.

Species	Province		Aspect		Disturbance			
	AP	RV	NE	SW	C	DLC	SHW	SB
<i>Actaea racemosa</i> L.	39	—	5	—	—	—	—	—
<i>Anaphalis margaritacea</i> (L.) Benth.	—	—	—	—	—	—	1	—
<i>Anemone quinquefolia</i> L.	16	—	—	—	—	—	—	—
<i>Arisaema triphyllum</i> (L.) Schott	—	—	1	—	—	—	—	—
<i>Carex communis</i> L.H. Bailey	—	—	—	—	—	—	4	—
<i>Carex digitalis</i> Willd.	—	—	—	—	—	—	—	2
<i>Carex laxiflora</i> Lam.	3	—	—	—	—	—	—	—
<i>Carex pennsylvanica</i> Lam.	—	2	—	—	—	—	—	—
<i>Carex willdenowii</i> Schkuhr ex Willd.	—	—	—	5	—	—	—	—
<i>Chimaphila maculata</i> (L.) Pursh	—	9	—	—	—	—	—	—
<i>Circaea lutetiana</i> L.	—	—	7	—	—	—	—	—
<i>Conopholis americana</i> (L.) Wallr.	—	—	4	—	—	—	—	5
<i>Danthonia spicata</i> (L.) P. Beauv. ex Roem and Schult	—	6	—	3	—	—	—	—
<i>Demstaedtia punctilobula</i> (Michx.) T. Moore	—	—	—	—	—	—	8	—
<i>Dichantherium acuminatum</i> (Sw.) Gould and C.A. Clark	—	—	—	—	—	—	5	—
<i>Dichantherium depauperatum</i> (Muhl.) Gould	—	10	—	—	—	—	—	—
<i>Dichantherium dichotomum</i> (L.) Gould	—	—	—	6	—	—	—	—
<i>Dryopteris intermedia</i> (Muhl. ex Willd.) A. Gray	25	—	3	—	—	—	—	—
<i>Dryopteris marginalis</i> (L.) A. Gray	—	—	9	—	—	—	—	—
<i>Epigaea repens</i> L.	—	—	—	—	—	—	—	3
<i>Erechtites hieracifolius</i> (L.) Raf. ex DC.	—	3	—	—	—	—	2	—
<i>Eurybia divaricata</i> (L.) G.L. Nesom	4	—	—	—	—	—	—	—
<i>Galium triflorum</i> Michx.	15	—	—	—	—	—	—	—
<i>Geranium maculatum</i> L.	—	—	11	—	—	—	—	—
<i>Gaultheria procumbens</i> L.	—	7	—	—	—	—	—	—
<i>Gaylussacia baccata</i> (Wangenh.) K. Koch	—	5	—	4	—	—	—	—
<i>Goodyera pubescens</i> (Willd.) R. Br.	—	—	—	—	—	—	—	4
<i>Houstonia longifolia</i> Gaertn.	—	11	—	—	—	—	—	—
<i>Juncus tenuis</i> Willd.	—	—	—	—	—	—	9	—
<i>Kalmia latifolia</i> L.	—	4	—	—	—	—	—	—
<i>Lindera benzoin</i> (L.) Blume	36	—	10	—	—	—	—	—
<i>Maianthemum racemosum</i> ssp. <i>racemosum</i> (L.) Link	23	—	—	—	—	—	—	—
<i>Medeola virginiana</i> L.	22	—	—	—	—	—	—	—
<i>Osmorhiza claytonia</i> (Michx.) C.B. Clarke	27	—	8	—	—	—	—	—
<i>Parthenocissus quinquefolia</i> (L.) Planch.	14	—	—	—	—	—	—	—
<i>Phytolacca americana</i> L.	—	—	—	—	—	—	3	—
<i>Polygonatum biflorum</i> (Walter) Elliott	19	—	—	—	—	—	—	—
<i>Polystichum acrostichoides</i> (Michx.) Schott	7	—	—	—	—	—	—	—
<i>Potentilla canadensis/simplex</i> L./Michx.	—	—	—	2	—	—	—	—
<i>Prenanthes</i> spp. L.	8	—	—	—	—	—	—	—
<i>Rubus</i> spp. L.	2	—	—	—	—	—	6	—
<i>Sanicula</i> spp. L.	17	—	—	—	—	—	—	—
<i>Smilax rotundifolia</i> L.	1	—	—	—	—	—	—	—
<i>Smilax tamnoides</i> L.	20	—	—	—	—	—	—	—
<i>Solidago caesia</i> L.	5	—	—	—	—	—	—	—
<i>Stellaria pubera</i> Michx.	6	—	—	—	—	—	—	—
<i>Thelypteris noveboracensis</i> (L.) Nieuwl.	10	—	—	—	—	—	—	—
<i>Toxicodendron radicans</i> (L.) Kuntze	21	—	—	—	—	—	—	—
<i>Trillium undulatum</i> Willd.	18	—	6	—	—	—	—	—
<i>Uvularia sessilifolia</i> L.	—	—	—	7	—	—	—	—
<i>Vaccinium pallidum</i> Aiton	—	1	—	1	—	—	—	—
<i>Vaccinium stamineum</i> L.	—	8	—	—	—	—	—	1
<i>Verbascum thapsus</i> L.	—	—	—	—	—	—	7	—
<i>Viburnum acerifolium</i> L.	12	—	—	—	—	—	—	—

Table 5. Continued

Species	Province		Aspect		Disturbance			
	AP	RV	NE	SW	C	DLC	SHW	SB
<i>Viola blanda</i> Willd.	24	—	—	—	—	—	—	—
<i>Viola hastata</i> Michx.	13	—	—	—	—	—	—	—
<i>Viola pubescens</i> Aiton	—	—	2	—	—	—	—	—
<i>Viola rotundifolia</i> Michx.	11	—	—	—	—	—	—	—
<i>Viola</i> spp. L.	9	—	—	—	—	—	—	—

sensitive species, white oak dominated forests with occasional fires, and the oak savannahs with frequent burns (Hanberry et al. 2012). Even if we evaluate only the tree seedlings, our study area still revealed significant species preferences at the local and regional scales based on physiography and no evidence of homogenization because of lack of fire.

Potential Successional Trajectories

The fact that plant species defined by regional physiographic features appear to predominate in our sites and that many of these species are late successional suggests our disturbed sites have several late-successional species in their initial

floristic vegetation, only in relatively lower numbers, as Egler (1954) would predict. Nonetheless, our disturbed sites also have several early successional plants as indicator species, which supports relay floristics. Thus, both the Egler (1954) succession and relay floristics appear to define, at least in part, the early stages of succession of our disturbed sites. Some of these disturbed sites also have indicator species not defined by regional or local physiography, including exotic, early successional, and fire-adapted native plants. Having such species as indicators supports a disturbance effect, although weak compared with the effect of physiography, and the potential for changes in

Table 6. Indicator species by province, aspect, and disturbance for tree seedlings. Species are ranked within each variable category by importance value (highest to lowest). Only significant ($p \leq 0.05$) indicator species are included in this list. Nomenclature follows the Integrated Taxonomic Information System (ITIS). AP = Appalachian Plateau; C = control; DLC = diameter limit cut; NE = northeast; RV = Ridge and Valley; SB = single burn; SHW = shelterwood; SW = southwest.

Species	Province		Aspect		Disturbance			
	AP	RV	NE	SW	C	DLC	SHW	SB
<i>Acer rubrum</i> L.	—	1	—	—	—	—	—	—
<i>Acer saccharum</i> Marshall	1	—	—	—	—	—	—	—
<i>Aralia spinosa</i> L.	—	—	—	—	—	—	1	—
<i>Carya cordiformis</i> (Wangenh.) K. Koch	8	—	—	—	—	—	—	—
<i>Carya glabra</i> (Mill.) Sweet	—	—	—	—	—	—	—	1
<i>Carya</i> sp. Nutt.	—	—	—	—	—	—	—	2
<i>Fagus grandifolia</i> Ehrh.	3	—	—	—	—	—	—	—
<i>Fraxinus americana</i> L.	5	—	—	—	—	—	—	—
<i>Fraxinus pennsylvanica</i> Marshall	6	—	—	—	—	—	—	—
<i>Liriodendron tulipifera</i> L.	4	—	—	—	—	—	—	—
<i>Magnolia fraseri</i> Walter	10	—	—	—	—	—	—	—
<i>Magnolia</i> sp. L.	11	—	—	—	—	—	—	—
<i>Nyssa sylvatica</i> Marshall	—	3	—	—	—	—	—	—
<i>Ostrya virginiana</i> (Mill.) K. Koch	9	—	—	—	—	—	—	—
<i>Pinus</i> spp. L.	—	5	—	—	—	—	—	—
<i>Pinus strobus</i> L.	—	2	—	—	—	—	—	—
<i>Prunus pensylvanica</i> L. f.	—	—	—	—	—	—	2	—
<i>Prunus serotina</i> Ehrh.	2	—	—	—	—	—	—	—
<i>Quercus coccinea</i> Münchh.	—	—	—	2	—	—	—	—
<i>Quercus montana</i> Willd.	—	—	—	1	—	—	—	—
<i>Quercus rubra</i> L.	—	—	—	—	1	—	—	—
<i>Quercus velutina</i> Lam.	—	4	—	—	—	—	—	—

future vegetation composition that would not be predicted by physiography. We describe these indicator species patterns below.

Aside from *Quercus rubra* in the control sites and *Betula* spp. (only marginally significant) in the control and DLC sites, respectively, the most significant indicator species of the four disturbance categories were associated with the SHW and single-burn sites. Consequently, the impact of disturbance on species composition in our study area on species composition appears to be governed by disturbance severity and the associated relative increase in light (SHW sites having the most open canopy) as well as the nature of the disturbance type (burn vs. harvest).

Unfortunately, but not surprisingly, neither single burns nor SHW harvests appear to be promoting regeneration of the initial species composition, including the dominant oak overstory species. A large part of this could be due to several years of deer herbivory, recovery from which is not possible after only one growing season of fencing (which was not the intent of the fencing in our study). Moreover, these first-removal SHWs were not followed by or preceded by a prescribed burn (Arthur et al. 2012, Dey 2014). Competing vegetation, including *Rubus* spp., may be dominating before the oaks can become established (Brose et al. 1999a 1999b). Single burns often do not provide the longer-term removal of competition needed by oaks (Brose et al. 2013). However, *Q. rubra* was found in every control site and, although comparatively abundant when it was present, it was not found as commonly in the DLC, single-burn, and SHW sites and most of the sites without *Q. rubra* present were in the RV province. Evidence of deer browse was significantly higher in the RV province than the AP (Huebner, unpubl. data). Deer show a preference for oaks and recently harvested or burned areas (Masters et al. 1993, Miller et al. 2009). Moreover, tree overstory data from most (but not all) the DLC sites reveals a likely decline in more-merchantable tree species and oak seed sources, such as *Q. rubra*, and an increase in less-merchantable tree species, such as *Betula* spp., because of consistent removal of only the merchantable trees over time (Huebner, unpubl. data). A reduction in seed-bearing *Q. rubra* trees will result in fewer *Q. rubra* seedlings. This consequence of high-grading is a well-documented outcome associated with DLCs (Nyland 1992,

Angers et al. 2005). Thus, in terms of tree species, none of our disturbed sites, regardless of the type, appear to be following a successional trajectory toward stand replacement based on indicator species. Many other studies have come to similar conclusions (Arthur et al. 2012, Brose et al. 2013, Dey 2014).

Carex digitalis, *Epigaea repens*, *Goodyera pubescens*, and *Carya* spp. (all late-successional species) were significant indicator species only for the single-burn sites, although *C. digitalis* and *Carya* spp. were commonly found in the other disturbance types. However, *E. repens* and *G. pubescens* occurred only in burn sites (although we know them to occur in other site types outside our study). *Epigaea repens*, an evergreen decumbent, diminutive shrub (Gleason and Cronquist 1993) is often associated with burned sites (Reed 1985) and fire-dependent communities, including red pine, white pine (Glass et al. 2009), table mountain pine, pitch pine (McIntosh 1959), and pine-oak woodlands (Habeck 1959, Murphy and Nowacki 1997), and is found in shade (Beckman 1994), partial shade, and full sun (Reed 1985) in dry or moist soils (Beckman 1994). Tolerant to frequent (every 2 yr) fire (Clay and Ellstrand 1981, Binninger 2016), this species may respond to fire with a small increase in growth (Randles et al. 2002). However, it has also responded negatively to fire with reduced shoot growth (Ducey et al. 1996) and flowering (Beckman 1994). This species has responded more positively to a harvest mimicking savannah conditions than to a clearcut, suggesting the increased light stimulates growth, but some shading is preferred (Lezberg et al. 2006). Likewise, *E. repens* grows well under *Gaylussacia baccata*, which forms shallow roots (Harper 1995), but poorly under *Vaccinium pallidum*, which forms a deep tap root and can grow in shadier conditions than *G. baccata* (Beckman 1994). Thus, the response of *E. repens* to fire or any disturbance is more likely a response to competing vegetation and subsequent availability of resources, which would include soil nutrients as well as light. Our harvested sites may have produced too much light and subsequent competition from other species, which made colonization or survival of *E. repens* unlikely. Similarly, *Goodyera pubescens*, an orchid, has been most closely associated with upland hardwood forests (Habeck 1959), oak savannas (Brock and Brock 2004) in dry to

moist soils (Campbell et al. 1995), and an intermediate level of winter light (Diez et al. 2014). It may respond positively to low-severity burns (Binninger 2016) but also persist long after a fire (De Grandpré et al. 1993), suggesting that, as with *E. repens*, *G. pubescens* is responding more to resources and competition than to the actual disturbance type. Nonetheless, although these species may not require fire, our results show that they are more likely to persist in our study area with nonsevere, infrequent burns.

Conopholis americana, a holoparasite, was a significant indicator of both NE-facing slopes and single burns, which is supported in the literature (Olivero and Hix 1998). Although fire does not appear to harm *C. americana* (Hutchinson 2006), it is also not required for successful establishment and growth of this species. *Conopholis americana*, like *E. repens* and *G. pubescens*, is likely responding to a reduction in understory species competition. In contrast, *Vaccinium stamineum* benefits directly from fire (Elliott et al. 1999), but, as shown in our study, also has a strong preference for the drier sites of the RV province (Stephenson and Mills 1999). Thus, our research does not support the existence of any fire-dependent plant communities but does support the likely persistence of some species that respond well to changes in dominance of competing species because of low-impact burns.

Several ruderal or pioneer species were significant indicators of only the SHW sites, including *Anaphalis margaritacea*, *Dichanthelium acuminatum*, *Juncus tenuis* Willd., *Phytolacca americana*, *Verbascum thapsus* L., *Aralia spinosa*, and *Prunus pensylvanica* (Gleason and Cronquist 1993). Of those, *V. thapsus*, the sole exotic, was found only in SHWs. The other species were also found, although not as significant indicator species, in a few DLC sites. None showed a preference for province or aspect, supporting relay floristics as a successional trajectory. *Carex communis* was also a significant indicator of only SHWs, although it is not a typical early successional species. Nonetheless, it is associated with forest disturbances, including medium to large gaps (Leckie et al. 2000, Holmes and Webster 2011), and grows rapidly compared with many sedges (Vellend et al. 2000). These species are all commonly found in persistent seed banks of eastern deciduous forests (Hyatt and Casper

2000, Hopfensperger 2007), are relatively shade intolerant, and may facilitate the colonization of more shade-tolerant species over time, (i.e., relay floristics). *Erechtites hieraciifolius* and *Rubus* spp., which were found as significant indicators in SHWs as well as the RV and AP provinces, are also early successional species (Gleason and Cronquist 1993) and are persistent in many forest seed banks (Baskin and Baskin 1996, Leckie et al. 2000). *Rubus* spp. is a frequent forest-gap colonizer and can germinate in low-light conditions (Hyatt and Casper 2000, Leckie et al. 2000). Being both an indicator of early successional communities and regional physiography supports the possibility that some early successional community compositions could also be differentiated across physiographic gradients. We postulate that plant communities sharing many early successional species across physiographic gradients, e.g., are homogenized, may be less resilient to perturbations and more vulnerable to invasion by dominating native and nonnative plants. The fact that the most disturbed sites in our area still have a few early successional species, albeit no mid- to late-successional species, serving as indicators of a particular province is, potentially, a sign of some remnant resilience (Halpern 1988, Cramer et al. 2007, Scott et al. 2010, Swanson et al. 2011).

Unfortunately, *Dennstaedtia punctilobula*, a native invasive species, was also a significant indicator species of the SHW sites. The nine SHW sites with *D. punctilobula* are vulnerable to inhibitory succession resulting in an alternate state dominated by *D. punctilobula* in the understory (Hill and Silander 2001). Likewise, the four SHW sites with *V. thapsus*, an invasive exotic, are also vulnerable to inhibitory succession or, possibly, an invasional meltdown (Simberloff and VonHolle 1999) because that species facilitates the invasion of other exotics. An alternate state dominated by *D. punctilobula*, *V. thapsus*, or additional exotic invaders that colonize the site later is more likely if the transient and persistent seed and sprout banks become increasingly depleted because of excessive deer browse (Beauchamp et al. 2013, Hidding et al. 2013). We hypothesize that sites without any indicator species associated with regional or local environmental gradients, but instead, with generic (and potentially inhibitory) disturbance indicator species shared across environmental gradients and regions are the

most vulnerable to alternative stable states. Our study provides a method of predicting potentially vulnerable sites using vegetation composition data collected from recovering disturbed sites during a single growing season, but was not designed to test that hypothesis. This method may be thought of as a tool for early detection of forests lacking in resilience. To test that hypothesis would require an evaluation, over time, of the successional vegetation composition of sites predicted to be vulnerable to a deviation from a successional trajectory, leading to a species composition composed of a diverse set of native climax species (e.g., disturbed sites characterized only by disturbance indicator species) vs. sites that are unlikely to deviate from such a successional trajectory (e.g., disturbed sites characterized by environmental indicator species).

CONCLUSIONS The vegetation of the sites in West Virginia, Ohio, and Virginia under four different forest disturbance types were best defined by their respective physiographic provinces and not their disturbance type. All but 3 of the 12 most-disturbed sites had indicator species defined by the disturbance type as well as the physiographic region, suggesting these sites were experiencing relay floristics at the time of data collection. Three of the most severely disturbed sites were defined by indicator species unique to the SHW disturbance type but not by species that were indicators of the physiographic provinces or slope aspect, suggesting these sites may be more susceptible to inhibitory succession and alternate stable states. Likewise, our results showed two species that were most likely to be associated with a low-impact burns. Thus, although physiography was more important than disturbance, some species served as disturbance indicators, differing by disturbance type. When disturbance-indicator species replace regional-indicator species, successional trajectories may deviate toward recovery of native species that benefit from low-level disturbance (e.g., *E. repens*) or toward systems vulnerable to invasion by exotics (e.g., *V. thapsus*) or interfering native species (e.g., *D. punctilobula*). We argue that floristic data of forest understory species compositions in recently disturbed areas may be used as an early detection tool to predict likely successional trajectories and, consequently, sites that are most vulnerable to alternative stable states or most likely to harbor uncommon

plant species dependent on particular disturbance types.

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