RESEARCH ARTICLE

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Effects of Forest Management on Running Buffalo Clover (*Trifolium stoloniferum* Muhl. ex A. Eaton) Distribution and Abundance in the Fernow Experimental Forest

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ABSTRACT: Identifying habitat preferences of species of concern is fundamental to the practice of conservation, but disturbances and other environmental processes can substantially affect suitability. *Trifolium stoloniferum*, or running buffalo clover, is a federally endangered plant species that occurs on the Fernow Experimental Forest in West Virginia. Previous work and extensive anecdotal evidence suggests that this species is maintained in part by periodic disturbances to its habitat. In the Fernow Experimental Forest, this disturbance is in the form of intermittent logging activities. We investigated the role of forest harvesting practices and environmental variables in fostering *T. stoloniferum* at the stand level. Censuses have been conducted on *T. stoloniferum* occurrences in the Fernow since 1994, and occurrences are grouped by subcompartment or watershed, which are the basic management units within this experimental forest. Site characteristics and disturbance history were assessed for their impact upon *T. stoloniferum* presence and density. Classification tree analysis identified total number of forest harvest events in a subcompartment since 1948 as the most important predictor of *T. stoloniferum* presence or absence. Regression tree analysis identified aspect as important in determining *T. stoloniferum* abundance, with west-facing compartments supporting larger populations. This study confirms the importance of disturbance in maintaining *T. stoloniferum* populations. However, site characteristics independent of disturbance history are also predictors of *T. stoloniferum* presence and abundance, suggesting that managers attempting to restore or create habitat for *T. stoloniferum* should account for the interaction between disturbance history and site characters in determining suitability of habitat for *T. stoloniferum*.

Index terms: disturbance, endangered plant, non-equilibrium coexistence, timber harvesting

INTRODUCTION

The creation of reserves and habitat protection may often be insufficient for the conservation of species and unique communities (Hobbs and Huenneke 1992). One reason for this failure is a disruption, change, or cessation of the disturbance processes within a reserve that allowed for the persistence of that species, community, or particular landscape structure (Baker 1994; Brawn et al. 2001). Within a local species pool, some species of concern are sensitive to disturbance while others respond favorably to the same disturbance (Kirkpatrick et al. 2005). Restoration or approximation of disturbances that historically maintained select species were determined to be missing and found to be necessary to achieve desired conservation objectives (Kirkpatrick and Gilfedder 1995; Mitchell et al. 2006). Disturbance can alter or maintain the structure and composition of ecological communities by disrupting succession (Glitzenstein et al. 1986), creating and maintaining habitat heterogeneity (McClain and Barry 2010), shifting the dynamics of competitive relationships within communities (Pickett 1980), and facilitating the recruitment of new individuals from outside of, and within, the community (Sousa 1984; van der Maarel 1993; Denslow 1995; Chesson 2000).

Trifolium stoloniferum Muhl. ex A. Eaton, known by the common name running buffalo clover, was assessed in 1983 to be one of the rarest members of the North American flora (Brooks 1983), and may be a species that is dependent upon an appropriate disturbance regime for long-term persistence. It is believed to have been maintained historically by trampling and dispersal associated with large ungulates, particularly bison (*Bison bison athabascae)* (Rhoads 1897). Since 1983, new populations have been discovered in the Missouri Ozarks, the Bluegrass Region of Kentucky and surrounding states, and the Allegheny Mountains of West Virginia (USFWS 2007). The species has persisted and the population appears to be stable or growing at the Fernow Experimental Forest in Tucker County near Parsons, West Virginia (Madarish and Schuler 2002). *Trifolium stoloniferum* is found across its range in seemingly disparate habitats: old cemeteries, lawns of plantation-style homes, rich soils next to roads, lightly grazed pastures, and managed mesic forests (USFWS 2007). However, two commonalities that the majority of these sites have are that they are underlain by calcareous bedrock and they experience periodic disruption of the structure of their habitat (USFWS 2007). The pattern of occurrences of *T. stoloniferum* suggests that the plant is adapted to moderate levels of disturbance (Madarish and Schuler 2002). Mowing, light grazing, moderate logging activity, and prescribed burning can promote asexual and sexual reproduction of *T. stoloniferum* (USFWS 2007).

Our goal was to better understand the role of disturbance by quantifying the relationship between forest management activities and environmental characteristics at the Fernow Experimental Forest and the presence and abundance of *T. stoloniferum*. We hoped to identify interactions between disturbance history and environmental characteristics that affect the establishment, growth, or persistence of the species. We also had the more general goal of studying how anthropogenic disturbances can affect conservation activities. In our management situation and with this particular focal species, human activities appear to provide the unexpected benefit of improving habitat for an endangered plant species. We discuss whether this finding is a consequence of the idiosyncratic natural history of this species or a more general response of forest herbs to disturbance.

METHODS

Site description

The study area was entirely within the Fernow Experimental Forest (39.03°N, 79.67°W), a research forest established in the Monongahela National Forest in 1934, approximately 2.5 km south of the town of Parsons, W.Va., in Tucker County. This forest resides within the Allegheny Mountains Section of the Central Appalachian Broadleaf Forest (McNab and Avers 1994). Elevations at the Forest range from 533 to 1112 meters above sea level, and steep slopes predominate, with most of the landscape at 20 to 30 percent (Madarish et al. 2000). All site aspects are represented, but north-, west-, and southeast-facing slopes predominate. Bedrock geology is a combination of sandstone, siltstone, shale, and limestone, with several significant karst formations associated with the limestone. The Greenbrier soil series, which is derived from limestone, is present in the Fernow Experimental Forest, and a majority of the *T. stoloniferum* occurrences in the Allegheny Mountain region are found in association with this soil. Mean temperature is 9 °C, and the mean precipitation of 145 cm is evenly distributed throughout the year. Forest types at the Fernow are mostly mixed mesophytic hardwood forests with northern hardwood forests gaining importance in a few areas at higher elevations and hemlock being important along riparian corridors. Understory vegetation is shaped by the interaction between physiographic characters, disturbance regime, and soils, and varies from moderately to thickly vegetated with forest herbs to dense rhododendron and laurel thickets (*Rhododendron maximum* L. and *Kalmia latifolia* L.) (Gilliam et al. 1995). The study sites included in this study consisted of 39 subcompartments and watersheds located within the Fernow Experimental Forest.

After World War II, the United States Forest Service established a research program in the Fernow oriented towards long-term silviculture of central Appalachian hardwood forests. Single-tree selection, patch cutting, diameter-limit harvesting, small clearcuts, and thinnings have been applied to specific localities referred to as subcompartments on the Fernow since the initiation of the post-World War II research program. Partial harvesting methods are repeated on a schedule of 10, 15, or 20 years. The longevity and continuity of silvicultural experiments allows researchers to assess the long-term effects of each system, and many of the subcompartments included in this study have been continually managed with the same silvicultural system since the late 1940s and early 1950s (Schuler 2004). Watersheds are often exposed to treatments in which the primary research objective does not pertain to silviculture, such as hydrologic responses to clearcutting or nutrient manipulations (Peterjohn et al. 1996), but these management units are also characterized by long-term monitoring of results. Subcompartments and watersheds are the fundamental unit of management within the Fernow: silvicultural prescriptions and other experiments are applied at this level and forest inventories are conducted at this level.

Study design

Trifolium stoloniferum was first detected at the Fernow in 1993, and systematic efforts to annually monitor and count populations have been undertaken since 1994. Newly established or discovered populations were added to census efforts as they were detected. Censuses were total, with efforts being made to find and count all rooted crowns in every known population in the experimental forest. We only consider censuses conducted after 1998 in this analysis; this was the first year that census methods were standardized and followed the population monitoring requirements of the U.S. Fish and Wildlife Service Recovery Plan for *T. stoloniferum* (USFWS 2007).

Using ArcGIS 9.3 (ESRI 2009), we created a map of all known *T. stoloniferum* occurrences and all subcompartments within the Fernow. All occurrences not within the boundaries of a subcompartment or watershed with known disturbance history and measured environmental variables were excluded from analysis. For each year that censuses had been conducted, total *T. stoloniferum* crowns were tallied by subcompartment for every population occurring within its boundaries. *Trifolium stoloniferum* densities by subcompartment were calculated for every annual census by dividing total number of crowns by the area of the subcompartment. We used median crowns/hectare in a subcompartment since standardized censuses were initiated in 1998 until 2008 to account for the range of *T. stoloniferum* population size over time. Median crowns/ha was chosen over mean crowns/ha as a better representation of population size because the median is less sensitive than the mean to extreme variations, particularly with a small sample size (Zar 1999), and to accommodate rapid fluctuations in population size immediately following logging events. In order to draw distinctions and inferences about the relative suitability of a forest management unit as *T. stoloniferum* habitat, we included in this analysis 23 subcompartments for which there were no records of this species having occurred. The criteria for selection of *T. stoloniferum*-absent subcompartments were based on either being contiguous to *T. stoloniferum*-present subcompartments or possessing the Greenbrier soil series. A total of seven watersheds were considered in this analysis, of which one contained *T. stoloniferum* at the time of this study.

Subcompartment disturbance history was determined using forest inventories conducted before and after every harvest that occurred in that subcompartment. The data consisted of total basal area (BA) before harvest, measured in m^2/ha, total BA removed during the harvest, and residual BA for every subcompartment. We constructed four disturbance variables that captured the effects of timber harvest upon stand structure and disturbance state that are relevant to *T. stoloniferum*: (1) time elapsed since last disturbance using 2008 as the baseline, which was the most recent year in which a census was conducted at the time of this study; (2) proportion of basal area removed in the last disturbance; (3) total number of disturbances that have occurred since the initiation of management in that stand; and (4) total basal area removed per hectare from the stand since management began in the stand. The year in which management activities were initiated in a subcompartment or watershed varies, and ranges from 1948 to 1972. We decided to not weight disturbances variables by subcompartment or watershed "age," or the time elapsed since the initiation of management, to better account for possible cumulative effects of long-term, regular disturbance upon the success of *T. stoloniferum.*

Site characteristic variables were also considered for every subcompartment. The northern red oak (*Quercus rubra* L.) site index was used as an indicator of potential productivity of the site. Northern red oak site index is a common and accepted measure of forest productivity within this region (Lamson 1987). The presence of the Greenbrier soil series, a limestone derived soil series and a strong predictor of the presence of *T. stoloniferum*, was included in the analysis. The reason for the inclusion of this variable was to assess why those subcompartments that contain this soil series, an important predictor of habitat suitability for *T. stoloniferum*, did not harbor this species. The aspect of the subcompartment was also considered as a categorical predictor variable, as aspect is a predictor of the growth potential and community composition and structure of a forest stand, particularly in the mountainous region where this study occurred (Fekedulegn et al. 2004).

Statistical analyses

The mixture of categorical and continuous response and predictor variables included in this study and the exploratory nature of this study suggested the use of classification and regression tree analyses (McCune and Grace 2002). These analytical techniques are based on decision tree analyses that continually split the experimental units, in a dichotomously branching pattern, into more homogenous groups (De'ath and Fabricius 2000). The classification or regression tree was initially "overgrown," but subsequently pruned back based upon cross-validation criteria that suggested optimal tree length for balancing predictive capabilities with model specificity.
Trifolium stoloniferum presence or absence and density were examined using classification and regression tree analysis for all subcompartments. The predictor variables for classification and regression trees included: site index, aspect, time since last disturbance (years), presence or absence of the Greenbrier soil series, proportion of basal area removed in the last disturbance, total number of disturbances that have occurred within a unit, and total basal area removed in the last disturbance.

All statistical analyses were conducted in the open-source statistical software package R 2.9.0 (R Development Core Team 2009). The R package used for classification and regression tree analyses was *mvpart* (De'ath 2010).

RESULTS

Classification tree analysis with *T. stoloniferum* presence or absence within a subcompartment as the categorical response variable identified total harvesting disturbances as the most important predictor (Figure 1; Error=0.41, Cross-Validation error= 0.625, Standard error= 0.17). Those subcompartments with five or greater total disturbances since 1948 were much more likely to have *T. stoloniferum* (11 of 13), while the majority of subcompartments disturbed less than five times did not contain *T. stoloniferum* (21 out of 26 had never contained *T. stoloniferum*).

Regression tree analysis with median crown/hectare as a continuous response variable identified both total number of disturbances and aspect as important in delineating those subcompartments with higher *T. stoloniferum* density (Figure 2; Error=0.355, CV Error= 1.16, Standard Error= 0.666). Those subcompartments with a western aspect had greater densities of *T. stoloniferum*. Among the subcompartments with a western aspect, those that had not been disturbed in more than 14 years had much lower densities of *T. stoloniferum,* while those that had been disturbed within 14 years had the highest densities of *T. stoloniferum*.

In addition, we have presented plots of median *T. stoloniferum* crowns/hectare against time since last disturbance in years and the total number of disturbances in a subcompartment (Figures 3A and 3B). These plots reinforce the importance of disturbance observed in the regression tree analyses and allow for the identification of threshold behaviors. Plots that have not been disturbed within 20 years appear to have little capacity for supporting *T. stoloniferum (*Figure 3A). One also can note that plots that have been disturbed very recently, within the last 3 - 5 years, also do not support high densities of *T. stoloniferum*. Figure 3B also demonstrates the positive impact that repeated disturbances have upon *T. stoloniferum*. Between four and seven disturbances since management was initiated appears optimal: this is equivalent to a disturbance periodicity of approximately 8 - 14 years. This finding agrees with the threshold of 14 years identified in the regression tree analysis.

DISCUSSION

The results of this study suggest that disturbance history is critical in determining *T. stoloniferum* presence and density, but disturbance history interacts with physiographic factors to influence *T. stoloniferum* success. Among the variables investigated,

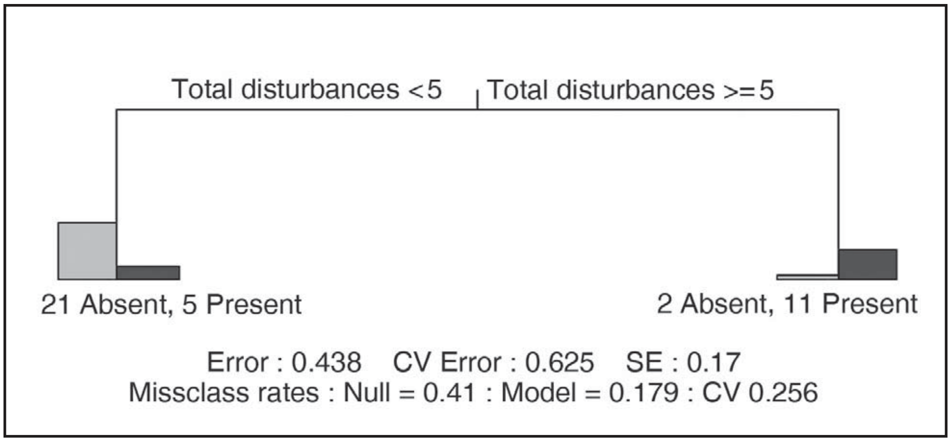

Figure 1. Classification tree analysis of *T. stoloniferum* presence or absence. The bar graphs present the number of subcompartments or watersheds in which *T. stoloniferum* was present or absent. Total disturbances is the total number of disturbances that occurred in a subcompartment since the initiation of management within that unit.

those measuring disturbance history appear to be most important in determining the presence or absence and density of *T. stoloniferum* (Figures 1, 2, and 3). Total disturbances since management was initiated in a stand was the most important variable in the regression tree of *T. stoloniferum* presence or absence (Figure 1). Total disturbances is a cumulative variable, and the presence of *T. stoloniferum* in sites disturbed five or more times during the past 36 - 60 years confirms earlier suggestions that moderate, periodic disturbance promote the establishment and persistence of this species (USFWS 2007). In contrast, we interpret the available evidence to suggest that more intense and less frequent disturbances do not promote *T. stoloniferum*. The majority of subcompartments that have been disturbed less than five times were either undisturbed control sites or were managed in an even-aged silvicultural system, such as patch cuts or small clearcuts, while the majority of subcompartments disturbed five or more times are largely managed in uneven-aged silvicultural systems, such as single tree selection or other forms of partial harvesting.

In addition, time since last disturbance appears to be very important in promoting *T. stoloniferum*. Those subcompartments that have not been disturbed in the last 20 years appear to have limited to no possibility of supporting *T. stoloniferum* (Figure 3A), and it appears that the ability of a subcompartment to support high abundances decreases after 14 years (Figure 2). Disturbance history interacts with site characteristics, such as aspect, to influence the favorableness of a site for *T. stoloniferum*. Based upon observations in the field, aspect, slope, site fertility, and soil disturbance all interact to promote *T. stoloniferum* when logging has created small canopy gaps in the forest that allow for *T. stoloniferum* and other understory herbs to gather light. Favorable aspects and rich growing conditions are conducive to the growth of *T. stoloniferum,* but disturbance both promotes the dispersal of *T. stoloniferum* to favorable sites and creates microsite conditions suitable for its establishment and growth. In short, without disturbances in forested sites, such as those that occur in the practice of uneven-aged silviculture using single-tree selection and other forms of partial harvesting, it appears that *T. stoloniferum* will not persist or thrive and will most likely not establish.

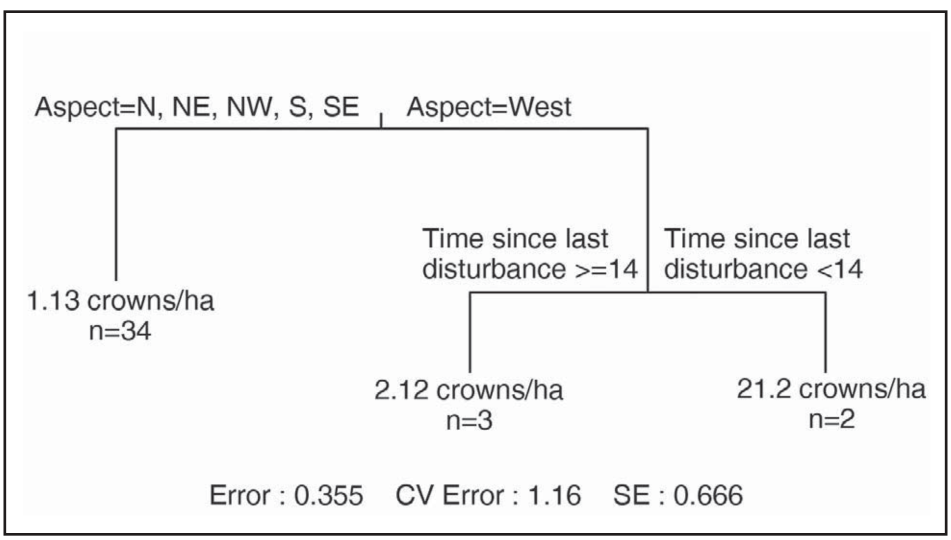

Figure 2. Regression tree analysis with median *T. stoloniferum* density as response variable.

Our findings are in agreement with other studies that examined the response of forest herbs to disturbance. Scheller and Mladenoff (2002), in a study conducted in northern Wisconsin and the upper peninsula of Michigan, found that plant diversity was higher in forests managed in uneven-aged silvicultural systems with frequent stand entries as compared to old-growth and even-aged forests. The differences in diversity were largely the result of higher light levels found in the uneven-aged forest. The phenomenon of increased vigor among understory plants after disturbance to forest canopies, particularly among herbs flowering after tree leaves have developed, is widely recorded (Pitelka et al. 1980; Moore and Vankat 1986; Whigham 2004). However, the response of forest herbs to disturbance is not uniform, and it is likely that a subset, but not all, of the community of forest herbs respond similarly to the disturbance intervals favored by *T. stoloniferum* at the Fernow. Reader and Bricker (1992) conducted a study to follow the response of five forest herbs to forest cuttings of varying size (0.015, 0.053, and 0.196 ha) and intensity (33% and 66% of basal area

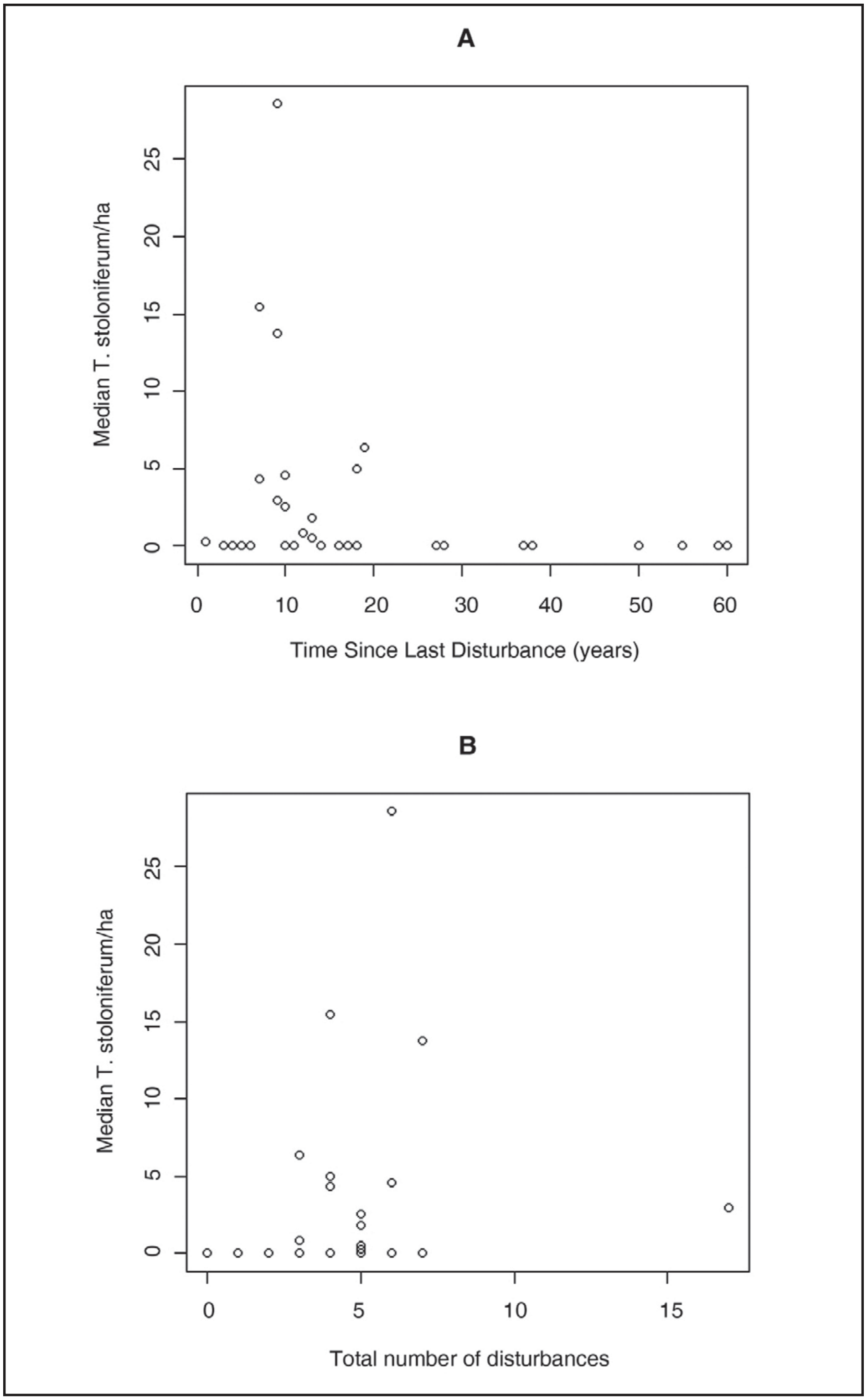

Figure 3. A) Median *T. stoloniferum* per hectare plotted against time since last forestry-related disturbance in years. B) Median *T. stoloniferum* per hectare plotted against total number of forestry-related disturbances since management was initiated in a stand.

removed). The five herbs all demonstrated unique responses, with different species responding more favorably to different size and intensity combinations. In large openings that had been cut intensively, woody stem competition precluded a vigorous herb response. We, too, found no instances of *T. stoloniferum* persisting at the Fernow Experimental Forest in subcompartments with larger forest openings that received direct sunlight throughout the day.

The positive response of *T. stoloniferum* to relatively frequent, moderate disturbance is consistent with the non-equilibrium model of plant coexistence put forth by Pickett (1980). Competitive exclusion by shade-tolerant woody species is characteristic of communities in which succession is allowed to proceed uninterrupted for biologically relevant time periods. But periodic disturbances prevent this exclusion, and communities that are disturbed periodically will have greater richness and diversity (Collins et al. 1995). This hypothesis is also consistent with the intermediate disturbance hypothesis developed by Connell (1978), which was extended to marine systems by Sousa (1979) and extended to terrestrial systems by Huston (1979). The general response of relatively stable communities to episodic or periodic disturbance is an increase in diversity, as resources that would be dominated by more competitive members of the community are liberated. Disturbance in the form of forestry-related harvesting activities at the Fernow Experimental Forest appear to prevent competitive exclusion and allow for the establishment and persistence of *T. stoloniferum*.

CONCLUSIONS

With this study, we identified a range of disturbance return intervals that were most conducive to the maintenance of *T. stoloniferum* at the stand level. We also demonstrated that disturbance interacted with physiography to impact plant success. Over the 60+ years of management history at the Fernow Experimental Forest, the sites that have been disturbed five or more times are much more likely to support *T. stoloniferum*; in addition, the sites that have been disturbed more recently than 14 years are more likely to support greater abundances of *T. stoloniferum*. Stands with western-facing aspects also were more likely to support more abundant populations of *T. stoloniferum*. The results of this study agree with general models of species richness and diversity in forests, such as the non-equilibrium coexistence model (Pickett 1980), in which diversity is maintained by preventing competitive exclusion by shade-tolerant tree species by means of disturbance.

Managers of natural areas are increasingly interested in using surrogates to emulate natural disturbance (Arkle and Pilliod 2010). Here we have provided a compelling example of forest management related disturbances leading to the enhancement of habitat for an endangered plant species. The use of human-initiated disturbances as ecological surrogates is not without social and political controversy or cost (Shindler et al. 2002); in addition, there are potential ecological drawbacks to the use of surrogates, such as facilitating the spread of invasive species (Oswalt et al. 2007). Our finding that aspect interacts with disturbance to promote *T. stoloniferum* suggests that the effectiveness of surrogate disturbances as management tools varies across time and space, and that managers should work to identify where and when the desired conservation objectives of disturbance are maximized.

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Appendix- R Code for Statistical Analyses

Regression tree analysis with medRBC/acre as the response variable.

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RBCmed.regress.tree=mvpart(medRBC.ac~SI+minelev+maxelev+Aspect+Greenbrier+TSLD+Propremlast+Disttot+TotalBArem,data=RBCcat)
RBCmed.regress.tree=mvpart(medRBC.ac~SI+minelev+maxelev+Aspect+Greenbrier+TSLD+Propremlast+Disttot+TotalBArem,data=RBCcat, size=3))
plotcp(RBCmed.regress.tree)
plot(RBC.med.regress.tree)
text(RBCmed.regress.tree)
```

Classification tree analysis with RBC presence or absence as presence variable

```
RBCpa.tree=mvpart(RBCpa~SI+minelev+maxelev+Aspect+Greenbrier+TSLD+Propremlast+Disttot+TotalBArem, data=RBCcat)
RBCpa.tree=mvpart(RBCpa~SI+minelev+maxelev+Aspect+Greenbrier+TSLD+Propremlast+Disttot+TotalBArem, data=RBCcat, xval=10, xvmult=50, prn=TRUE, all.leaves=TRUE, legend=TRUE, bord=TRUE)
plotcp(RBCpa.tree)
```

Plots

```
attach(rbc)
plot(Disttot, medRBC.ha, xlab="Total number of disturbances", ylab="Median T. stoloniferum/ha", main="B")
plot(TSLD.years., medRBC.ha, xlab="Time since last disturbance", ylab=" Median T. stoloniferum/ha", main="Response of T. stoloniferum to time since last disturbance")
```