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Research article

Pocono mesic till barrens in retreat: topography, fire and forest contagion effects

Keith R. Maurice[1,3], Joan M. Welch[1,*], Christopher P. Brown[1,4] and Roger Earl Latham[2,5]
[1]*Department of Geography, West Chester University, West Chester, Pennsylvania 19383 U.S.A.;* [2]*Department of Biology, Swarthmore College, Swarthmore, Pennsylvania 19081 U.S.A.;* [3]*Normandeau Associates, Spring City, Pennsylvania 19475 U.S.A.;* [4]*Department of Geography, New Mexico State University, Las Cruces, Nm 88003-8001;* [5]*Continental Conservation, Rose Valley, PA 19086 U.S.A., rel@continentalconservation.us;*
[*]*Author for correspondence (e-mail: jwelch@wcupa.edu)*

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Abstract

The Pocono mesic till barrens (PMTB) are a unique assemblage of fire-maintained shrub communities that support numerous rare species. Historically these barrens covered a large area in the vicinity of Long Pond, Pennsylvania, USA. However, due largely to regional fire suppression instituted in the early 1960s, over 70% of the area covered by barrens succeeded to fire-intolerant forest that does not support the rare species. We investigated the influence of forest proximity on barrens succession across three geomorphic types during periods of high fire frequency and fire suppression, testing the hypothesis that forest processes such as seed rain, shading, and detrital enrichment of soils enhances barrens succession through a contagion effect. Evidence of a forest contagion effect should be shown by increased rates of barrens succession with increasing proximity to the nearest forest edge. In order to detect a forest contagion effect, barrens persistence and barrens succession were modeled in proximity zones of 0-50 m, 50-100 m, 100-200 m, and greater than 200 m from the nearest forest edge. We used existing GIS data layers for fire, geomorphology, and vegetation distribution in 1938, 1963, and 1992. The layers were modified and overlain using ArcView software to determine persistence and succession rates for each unique combination of layers in each proximity zone from 1938 to 1963 (pre-fire suppression) and 1963 to 1992 (post-fire suppression). ANCOVA results indicate that proximity to the nearest forest edge significantly affected barrens persistence rates in both time periods, but succession rates were significantly affected in 1938 to 1963 only. Twenty-eight percent of the 1938 barrens succeeded to forest by 1963; 56% of the 1963 barrens became forest by 1992. Results support previous findings that barrens persistence is enhanced by increased fire frequency, and that barrens persist longer where they overlie flat glacial till than on other geomorphology types.

Introduction

The Pocono mesic till barrens (PMTB) of northeastern Pennsylvania, USA, are the remnants of a once extensive assemblage of xeric and mesic shrub savannas. They are a focal point of conservation efforts by the Pennsylvania Chapter of The Nature Conservancy (TNC) due to the presence of numerous rare species of plants and animals (Davis et al. 1991). The barrens are fire-maintained, and large areas burned frequently until regional fire suppression became effective in the early 1960s. Since then over 70% of the barrens visible on 1938 aerial photographs have succeeded to fire-intolerant forest communities that do not support the rare species. Remaining PMTB habitat is fragmented and in danger of

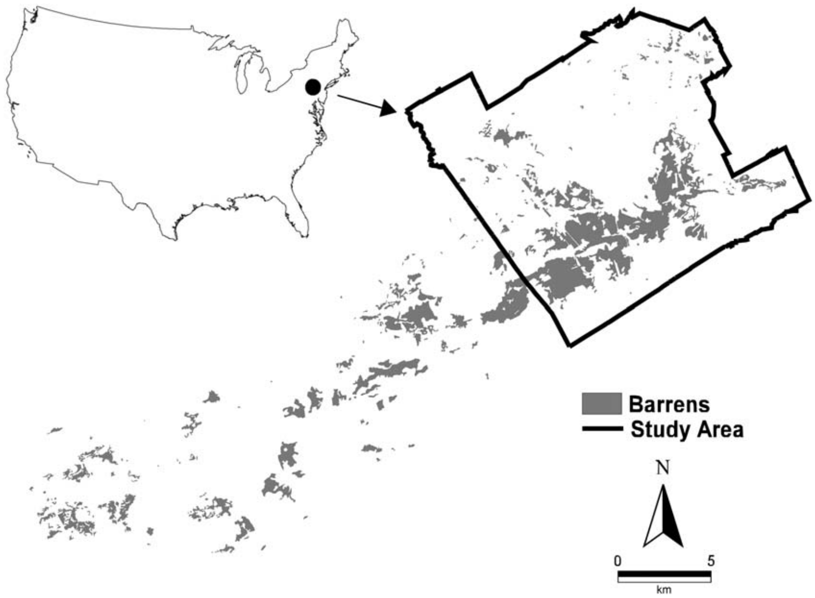

Figure 1. Location of study area in eastern USA

encroachment by forest species (Thompson 1995; Latham et al. 1996).

TNC is currently developing a prescribed burning program to restore and maintain PMTB habitat. Effective deployment of TNC fire management resources requires an understanding of the interaction of fire and successional processes in the PMTB. Recent research conducted in support of this objective confirmed the importance of fire in maintaining the barrens and indicated that fire effects are modified by geomorphology (Thompson 1995; Latham et al. 1997).

The objective of this study is to evaluate patterns of barrens succession in relation to forest proximity and to determine if these patterns are modified by fire and geomorphology. We hypothesized that the transition rate of barrens to forest is greatest near the forest/barrens edge and decreases as the distance from the edge increases. A geographic information system (GIS) and statistical methods provide the tools for spatial analysis of the forest contagion effect on the PMTB. A clearer understanding of the forest contagion effect would allow TNC to more effectively restore and maintain the PMTB.

Study Area and Background Information

Barrens cover approximately 41.5 km^2 along the southern edge of the Pocono Plateau in northeastern Pennsylvania (Figure 1). Mesic barrens overlay glacial till and comprise 21.7 km^2 or 52% of the total barrens on the southern Pocono Plateau. The balance is largely xeric barrens overlying substrates other than glacial till (Latham et al. 1996).

The study area for this project encompasses approximately 18.9 km^2 of barrens located primarily to the south and southeast of Long Pond (Figure 1). These limits are determined by the availability of coincident fire and vegetation data for the years 1938, 1963, and 1992. The barrens occur within a matrix of northern hardwoods and oak forests. The northern hardwoods forest is dominated by red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), American beech (*Fagus grandifolia*), black cherry (*Prunus serotina*), and yellow birch (*Betula alleghaniensis*). White oak (*Quercus alba*), scarlet oak (*Quercus coccinea*), northern red oak (*Quercus rubra*), chestnut oak (*Quercus prinus*) and understory stump sprouts of American chestnut (*Castanea dentata*) predominate in the oak forest (Thompson 1995). Other natural features within the study area include lakes, streams and wetlands. Cultural features consist of residential areas, interstate and state highways, municipal roads, and a raceway.

The PMTB are composed of three distinct barrens vegetation communities dominated by scrub oak (*Quercus ilicifolia*), rhodora (*Rhododendron canadense*), and the ericaceous shrubs sheep-laurel

(*Kalmia angustifolia*) and common lowbush blueberry (*Vaccinium angustifolium*). These communities are found on silt loam soil derived primarily from remnant Illinoian glacial till and to a lesser extent from Wisconsinan glacial till on terrain that is level to gently sloping. The barrens vegetation is fire tolerant but shade intolerant, and in the absence of fire, will eventually be replaced by the surrounding taller, shade-tolerant forest vegetation (Thompson 1995; Latham et al. 1996).

The PMTB became established and have persisted for hundreds, probably thousands of years, as a result of periodic large-scale wildfires attributed largely to anthropogenic causes. Regeneration and expansion of the PMTB is facilitated by fire tolerance, high nitrogen-use efficiency, and possibly allelopathic properties of barrens vegetation combined with the influence of topography and microclimate on these communities. The interaction of these influences provides the barrens species with survival and competitive advantages over trees from the surrounding forest communities (Thompson 1995; Latham et al. 1996; Latham 2003).

In contrast to typical barrens, which are usually associated with droughty, nutrient-poor sandy soils (Anderson et al. 1999), the PMTB are mesic communities growing on deep loamy soils with high water-holding capacity. In fact, there is no significant difference between the PMTB and nearby forest communities in the occurrence of a high water table less than 1 m from the surface or in soil water content in the upper 60 cm through summer droughts (Thompson 1995; Latham et al. 1996; Eberhardt and Latham 2000).

Fire mapping indicates that large areas of the PMTB regularly burned over until organized fire suppression became effective in the early 1960s (Thompson 1995). Fire return intervals vary widely from place to place before fire suppression, but the average is approximately 9 years. The periodic wildfires facilitated the maintenance of the barrens by inhibiting invasion by faster growing fire-intolerant species of trees that would shade out the barrens plants. Commercial blueberry pickers ignited most of the fires during the late 1800s and early 1900s to stimulate the production of blueberries. Subsequent fire suppression efforts have resulted in a much smaller area of the barrens being burned each year, rapid invasion by fire-intolerant trees, and loss of close to 75% of barrens habitat (Thompson 1995; Latham et al. 1996).

Originally the distribution of barrens habitat in the PMTB region was thought to be closely linked to the remnant Illinoian glacial till which covers a large portion of the land surface in the area. However, it was later discovered that, although barrens habitat is predominantly found on soils derived from Illinoian till, it also occurs on soils derived from Wisconsinan till (Thompson 1995).

Fire is of crucial importance in the distributions of many kinds of barrens habitat (Anderson et al. 1999). Surficial geology and slope are also found to influence the relationship between barrens persistence and fire frequency, but to a far lesser degree. Evidence from Thompson (1995) and Latham et al. (1996, 1997) includes the following.

I) All dominant barrens plants possess adaptations to survive recurring fire.

II) Fire-intolerant plant species predominate downwind of wetlands, which act as firebreaks for PMTB fires.

III) Areas that have not burned for a long period of time (over 60 years) are far more likely to have succeeded to forest or woodland than areas that have burned more recently.

IV) Recent fires have maintained areas as barrens.

V) Barrens habitat has persisted best on flat areas of Illinoian till (Thompson 1995; Latham et al. 1996, 1997).

A review of PMTB vegetation mapping for 1938, 1963, and 1992 (Figure 2) clearly shows a pattern of large areas of barrens succeeding to forest over time. Barrens succession appears to have been most rapid close to the forest edge, suggesting that barrens-to-forest transitions may be accelerated by forest contagion. Forest contagion results when biotic and abiotic processes active within a forest are projected beyond the forest edge and influence processes in adjacent nonforest habitats like the PMTB. At the boundary between forest and nonforest habitat, such phenomena are known as edge effects and encompass a wide variety of processes including seed rain, shading, and detrital enrichment of soils (Forman and Godron 1986; Urban et al. 1987).

The PMTB consists of numerous fragments of barrens habitat within a forest matrix, along with larger barrens patches in which fragments of forest habitat are embedded (Forman and Godron 1986). The boundaries between barrens and forest are long and highly convoluted (Figure 2(c)). By nature of the extent and spatial arrangement of the barrens-forest boundaries, large areas of the PMTB are in close

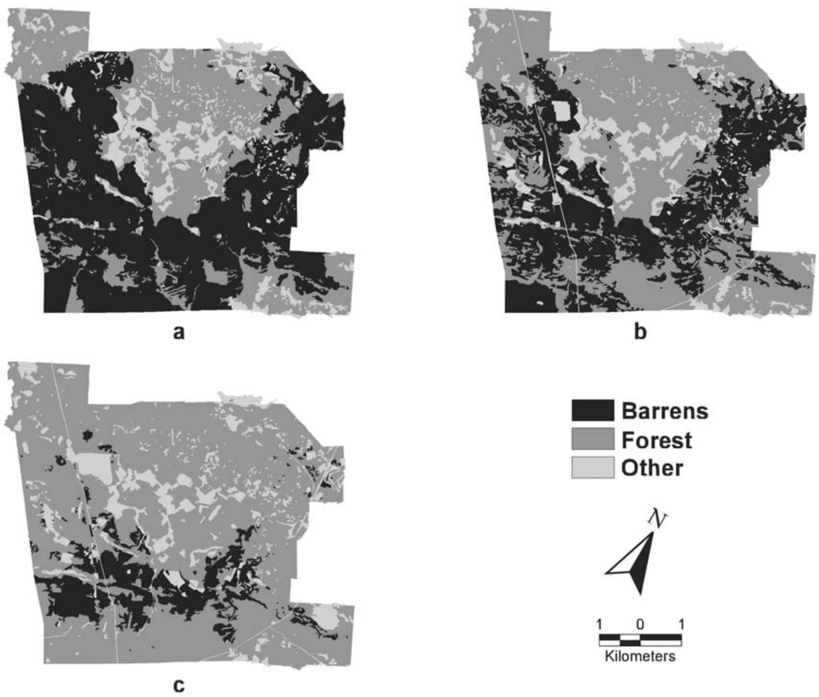

Figure 2. Distribution of barrens and forest communities in 1938 (a), 1963 (b), and 1992 (c)

proximity to forest and potentially influenced by edge effects.

Historically, PMTB succession was held in check by frequent fires and low levels of nitrogen in the soil. Barrens are favored because barrens vegetation is fire-tolerant and highly flammable, unlike forest vegetation, and uses nitrogen more efficiently while curtailing N mineralization in its organic residues to readily available forms (Van Vuuren et al. 1992). In modern times of active fire suppression, successional processes now favor transitions from barrens to forest and likely include a combination of forest edge effects, perhaps interacting in a synergistic manner (Thompson 1995; Latham et al. 1996).

Red maple, a species intolerant of crown fires, which includes all PMTB fires, has been the most successful PMTB invader to date (Latham et al. 1996). Red maple is abundant in the northern hardwoods forest surrounding portions of the PMTB (Thompson 1995) and possesses a suite of traits that may contribute to its unique ability among full-stature tree species of northern hardwood forests to colonize barrens habitat. These traits include an ability to grow well in a wide variety of habitats, shade tolerance, early sexual maturation, and prolific seed production. Red maple is also unique among upland hardwoods in the northeastern United States in that seeds are produced, disseminated, and germinate in the spring and early summer (Abrams 1998).

Forest colonization of the PMTB by red maple and other species likely occurs in a manner similar to forest colonization of other habitats. In the eastern United States, early patterns of forest colonization have been studied in a beaver meadow (Breden 1984), a clear-cut area (Hughes and Fahey 1988), reclaimed strip mines (Hardt and Forman 1989), and utility right-of-way corridors (McDonnell and Koch 1990; Hill et al. 1995). Forest succession in old-field habitats in the region has undergone extensive long-term study (Gill and Marks 1991; Myster and Pickett 1992; Myster 1993). In all of these studies, colonization, as reflected by seed dispersal and seedling establishment, displays edge-related patterns.

Seed dispersal patterns, also known as seed shadows or seed rain, result from the interaction of numerous factors. Tree seeds dispersed into openings within or adjacent to a forest typically decrease in density with increasing distance from the forest edge, with overall dispersal patterns depending on the distance between adjacent forest edges (Breden 1984; Hughes and Fahey 1988; McDonnell and Koch 1990; Myster 1993). Seeds dispersed from sugar maple

(*Acer saccharum*), American beech (*Fagus grandifolia*), and yellow birch (*Betula allegheniensis*) each display an exponential decline in density with distance from the forest edge (Hughes and Fahey 1988), yet dispersal distance varies by species.

Red maples effectively disperse seeds over substantial distances even under relatively light wind conditions. Models of seed dispersal from two-thirds of mature red maple height (26 m), and at wind velocities of 2, 10, and 20 m s^{-1}, predicted dispersal distances of 66 m, 330 m, and 660 m, respectively (Guries and Nordheim 1984). Dispersal distances documented for red maple provide some support for these models. Breden (1984) found seeds from red maples dispersed throughout a 200-m by 125-m beaver meadow study area. Red maple is common in the forest surrounding the PMTB and most barrens remnants are at most only a few hundred meters in diameter. Therefore, most if not all of the PMTB are within the potential dispersal range of red maple, and those areas in close proximity to the forest edge will likely receive the heaviest seed input.

The broader category of 'woody stems' (primarily seedlings but also including some saplings and small trees), reflecting a longer period of forest colonization, also shows an exponential decline in density with distance into old fields from the nearest forest edge. However, this relationship declines over time as the fields became more structurally complex (Myster and Pickett 1992; Myster 1993). Hardt and Forman (1989) also found that woody plants (seedlings through trees, a category reflecting approximately 10 years of forest colonization) display a logarithmic decline in numbers with distance from the nearest forest edge.

None of these studies was designed to evaluate the potential influence of adjacent forest communities on barrens succession rates. The study detailed in this paper expands upon previous research in the PMTB and is the first to examine the potential influence of forest contagion on barrens succession in relation to geomorphology and fire frequency. The primary objective of the research is to test the hypotheses that forest contagion negatively influences barrens persistence and that persistence decreases with increasing proximity to forest edge. A second objective is to evaluate how forest contagion-related patterns of succession in barrens are modified by geomorphology and fire frequency.

Methods

Data

Surficial geology, slope, vegetation, and fire history GIS data layers created for previous studies (Thompson 1995; Latham et al. 1996, 1997) provided baseline data for this study. The surficial geology data layer (Berg et al. 1977; Sevon 1975a, 1975b; Crowl and Sevon 1980) describes the glacial till, bedrock, and other surficial geology underlying the study area. A previously created slope layer generated from U. S. Geologic Survey (USGS) digital quadrangle maps (Gless 1997) provided raw slope data that were aggregated within ArcView. USGS quadrangle maps also provide base map features including roads, water bodies, streams, and political and other boundaries.

Aerial photography interpretation and ground-truthing were used in earlier studies to create vegetation community data layers for 1938, 1963, and 1992 (Thompson 1995; Latham et al. 1996). The earliest aerial photographs available for the site are from October 1938 and May 1939. Comparing these with photographs taken in April 1963 and May-June 1992 enabled quantification of vegetation changes during 25 years with no fire suppression (1938-63) and 29 years with vigorous fire suppression (1963-92). The 1992 vegetation data layer is based on ground-truthed infrared photographs while the 1938 and 1963 data layers are based on larger scale panchromatic photographs. These latter photographs could not be ground-truthed, however, the knowledge Thompson (1995) gained in field checking photo-interpretations for 1992 maximized photointerpretation consistency among all three time periods.

Numerous sources contributed to creation of the fire data layers including aerial photography, state records and fire maps, and local newspaper accounts of fires. This data layer likely underestimates the true 1932 to 1992 fire occurrence due to incomplete data coverage and inherent inaccuracies of the data sources (Thompson 1995). Only a small number of fires could be mapped from the limited aerial photograph coverage, as in some instances, fire boundaries are no longer visible after the first post-fire growing season (Thompson 1995).

Pennsylvania Bureau of Forestry fire mapping was available for 1932 to 1992 but varied in detail. Researchers mapped the aerial extent of 1932 to 1967 fires, but thereafter, single points on a map indicate

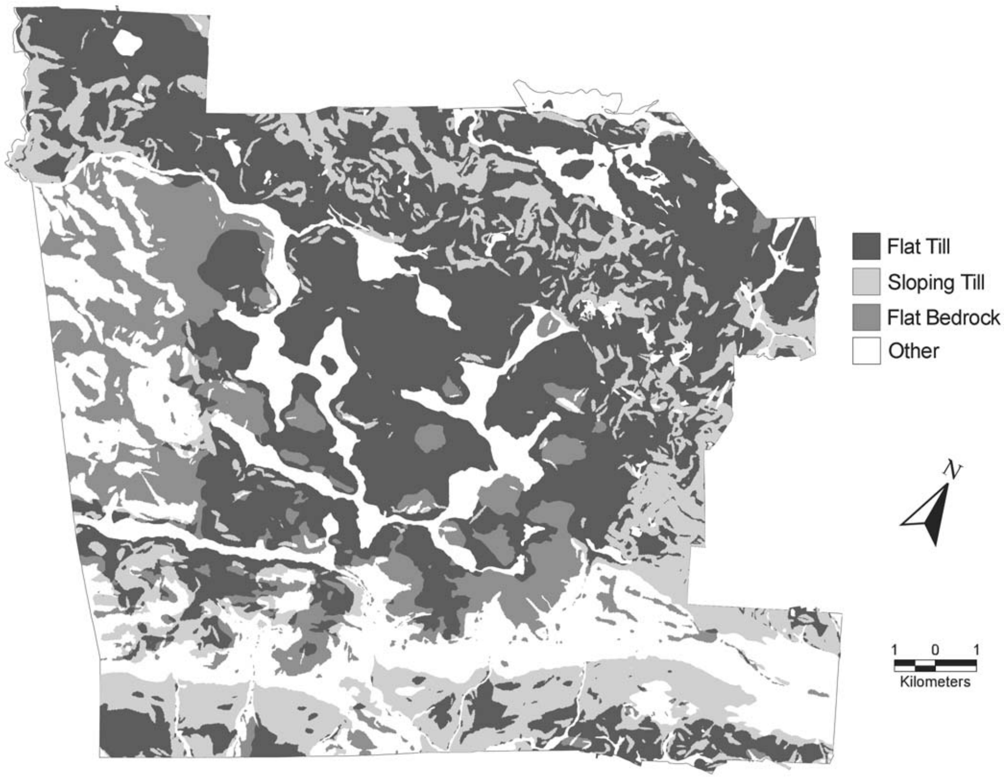

Figure 3. Geomorphology of the Pocono mesic till barrens

fire locations. To compensate for this lack of data, burn areas for 1968 to 1992 fires are mapped from aerial photography when possible, or approximated as circular polygons using state fire records and a GIS. The loss of accuracy using this technique is minimal as from 1968 to 1992 fires accounted for only 1 percent of the area burned from 1932 to 1992 (Thompson 1995).

GIS Analyses

GIS analyses were performed using ArcView 3.1 software (Environmental Systems Research Institute, 1998) and computer workstations at the West Chester University Center for GIS and Spatial Analysis and at Swarthmore College. We provide details of modifications of the original vegetation, surficial geology, fire and data layers in the following sections. The modified data layers were then overlain to determine rates of transition for the vegetation communities.

Barrens and Forest Data Layers

We queried vegetation data layers to create separate barrens and forest data layers for 1938, 1963 and 1992 (Figure 2). The barrens and forest data layers were then intersected to evaluate barrens persistence (barrens-to-barrens transitions) and barrens succession (barrens-to-forest transitions) in 1938 to 1963 and in 1963 to 1992. Forest-to-barrens transitions were examined only for the years 1938 to 1963, as the1963 to 1992 forest-to-barrens transitions are too small to provide meaningful information.

Geomorphology

Creation of the geomorphology (surficial geology-slope) data layer (Figure 3) required several steps. First, we extracted bedrock and glacial till soil layers from the surficial geology data layer using queries. These layers were then combined with layers representing relatively flat terrain (slopes $\leq$ 6%) and sloping terrain (slopes $>$ 6%) to create a geomorphology data layer consisting of flat till (till slopes $\leq$ 6%), sloping till (till slopes $>$ 6%), and flat bedrock

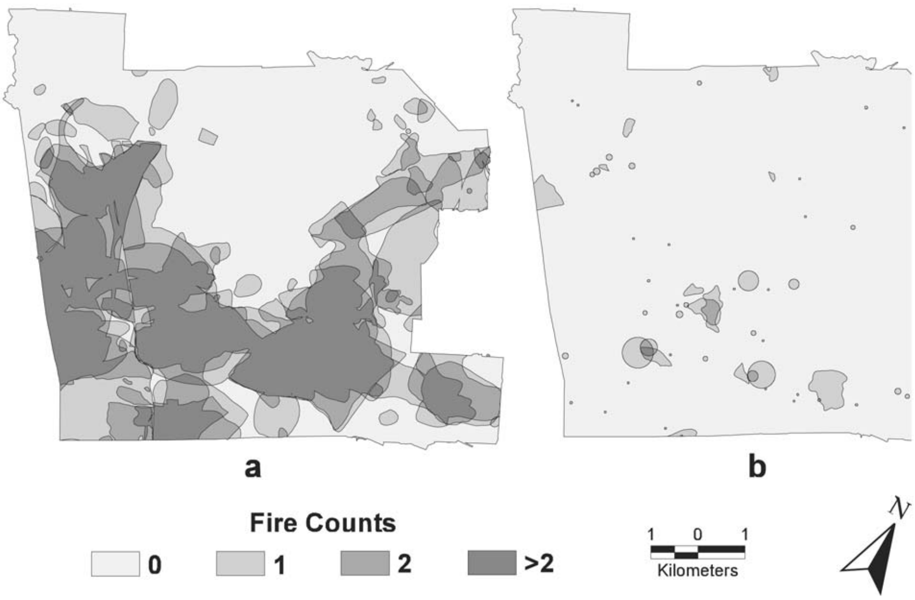

Figure 4. Fire frequency at the Pocono mesic till barrens 1932 to 1963 (a), and 1964 to 1992 (b)

(bedrock slopes $\leq$ 6%). As noted above, the slope data that were included in this surficial geology analysis were derived from a previously generated slope map (Gless 1997); accordingly, GRID analysis of raster-based digital elevation models was not necessary. The 6% cutoff reasonably divides flat from sloping terrain. Sloping bedrock is not included in the analyses since barrens in general do not persist well on slopes $\geq$ 3 percent regardless of fire frequency (Latham et al. 1997). However, sloping till is included in the study because this geomorphology type does support several heath barrens of exceptional quality.

Fire Data layers

We modified the original fire layer to create the data layers representing total fire counts per individual polygon for the unsuppressed 1932 to 1963 fire regime (Figure 4a), and the suppressed 1964 to 1992 fire regime (Figure 4b). Fire counts of 3 or more are aggregated into a '$>$ 2' category to allow comparisons of the 1932 to 1963 and 1964 to 1992 periods, which experienced maximum fire counts per polygon of 8 and 3 fires, respectively.

Forest Buffer Data layers

Concentric buffers of the 1938 and 1963 forest layers were created to enable testing for effects of forest contagion. The 1938 forest data layer was buffered into the 1938 barrens data layer, and the 1963 forest data layer was buffered into the 1963 barrens data layer (Figure 5). Buffer widths were 0-50 m, 50-100 m, 100-200 m and greater than 200 m. These widths were designed to test the hypothesis that forest contagion effects, if present, would likely be stronger and more detectable near the forest edge and decrease with distance.

Transition Rates

Through the use of GIS overlay procedures, we determined rates of barrens persistence and barrens succession from 1938 to 1963 and 1963 to 1992, and barrens origination from 1938 to 1963. The barrens transition rates are calculated by dividing the transition area by the original barrens area for each unique combination of vegetation, geomorphology, fire count, and proximity to forest edge. Barrens origination (creation) rates are calculated in the same manner except the original forest area is used as the divisor. The basic unit for statistical analysis is the area generated by each unique combination of geomorphlogy type, fire count category, and buffer width category the total of which is 48 (numbers of categories for each variable are: geomorphology, 3; fire count, 4; buffer widths, 4). Thus, irrespective of how many fragments or polygons comprise the area of

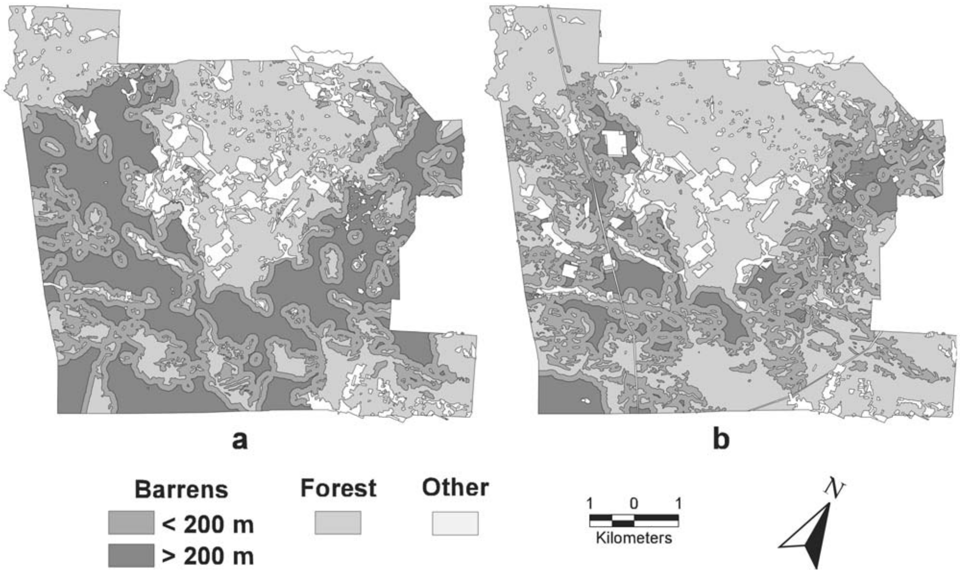

Figure 5. Buffers around forest areas 1938 (a), and 1963 (b)

each unique combination, the number of observations for the analysis of data from 1938-63 is 48, and the potential total number of observations for the analysis of data from 1963-1992 is also 48. Because the area of some combinations for the data for 1963-1992 do not add up to at least 5 hectares, the number of observations for some of the analyses for 1963-1992 have observation numbers less than 48.

Compensation for Potential Mapping Error

Any mapping error is likely to be compounded when multiple GIS data layers are overlain. On maps of vegetation change involving the overlay of a time series of vegetation maps, small polygons are less likely than large polygons to reflect transitions accurately. Adding fire history, geomorphology and forest proximity layers further increases the risk of error. To reduce the effect of mapping error on the results, we dropped any transition category from the analyses in which the constituent polygons sum to less than 5 ha.

Another issue related to different size polygons that can impact the validity of mapping and related statistical analysis is that of the modifiable area unit problem (MAUP), which arises when areal units of different sizes yield data used in subsequent statistical analysis. The mean and variance of data collected from different sized collection units will vary, due to both a scale and a zonation effect (Arnheim 1995). Although this problem is reasonably well documented in social science research, especially in cases where collection units are arbitrarily determined, redress of difficulties this problem may cause is limited, due to the limited number of practical solutions that have been developed. Although the polygons generated in our analysis arose from the natural co-occurrence of various landscape factors, not an arbitrary delineation by human agency, some variation of the MAUP may be present in our data.

Statistical Evaluation

Analysis of covariance (ANCOVA) was used to evaluate the relationships between transition rates and geomorphology, fire count and proximity to forest edge from 1938 to 1963 and 1963 to 1992. Geomorphology was the main effect and fire count and proximity to forest edge were covariates. The experiment-wise error rate was adjusted using the Dunn-Sidak method ($\alpha' = 1-(1-\alpha)^{1/k}$) to ensure that the overall probability of making a Type I error (false positive) is less than 0.05 (Sokal and Rohlf 1995).

Multiple comparisons of mean persistence rates and mean succession rates in 1938 to 1963 and in 1963 to 1992 on flat till, sloping till, and flat bedrock were made with the Tukey honestly significant difference (HSD) test. The significance level (P) is set at 0.05, representing the probability of encountering one Type I error during the course of comparing all pairs of means (Zar 1984). Statistical analyses are performed with Statistica 4.1 (STATSOFT Inc. 1994).

Limitations of the Statistical Analysis

The analysis of covariance results must be interpreted with caution. It is unknown how robust the tests were to three violations of underlying assumptions. First, ANCOVA does not take into account positive spatial autocorrelation in the vegetation, geomorphology, and fire count data layers used to calculate transition rates. Positive autocorrelation produces lower within-group variance that is more likely to yield significant results at $P < 0.05$ and increase the risk of making a Type I error (Underwood 1997). Secondly, the relationship between the independent variable (proximity) and the dependent variables (rates of persistence and succession) are not linear within the 0 to 50 m buffer zone, and ANCOVA is insensitive to curvilinear relationships. Also, barrens persistence rates in 1963 to 1992 are not normally distributed.

Results

Barrens Persistence

Areas of barrens persistence and rates of barrens persistence in 1938 to 1963 ranged from 5.7 to 611 ha and 0.18 to 0.86, respectively (Table 1). In 1963 to 1992, these values were 0 to 330 ha and 0.13 to 1.00 (Table 2). Mean persistence rates in 1938 to 1963 were greatest on flat till (0.68), intermediate on flat bedrock (0.59), and lowest on sloping till (0.53) (Table 1). In 1963 to 1992, mean persistence rates followed the same trend for flat till (0.61), flat bedrock (0.54), and sloping till (0.40), but were lower in all cases (Table 2). Mean rates of barrens persistence in 1938 to 1963 differed significantly with geomorphology ($F = 7.2$, $P = 0.002$, N=48). Multiple comparisons of mean persistence rates show significant differences between flat till and sloping till for 1938 to 1963 ($t = 5.3$, $P = 0.002$, N=48). Comparisons in 1963 to 1992 show no significant differences among geomorphology types.

Rates of barrens persistence also differed significantly with fire count in 1938 to 1963 ($t = 6.7$, $P = 0.0$, N=48) and in 1963 to 1992 ($t = 8.7$, $P = 0.0$, N=26). Persistence on glacial till soils was strongly affected by fire count (Figure 6). Persistence rates increased with fire count, but were similar within slope types at counts of 2 or greater. Fire count had little or no relationship to barrens persistence on flat bedrock. Overall variation in persistence rates among fire count categories was greatest on sloping till and least on flat bedrock.

Barrens persistence rates generally increased with distance from the forest edge in 1938 to 1963 (Table 1; $t = 2.8$, $P = 0.008$, N=48) and in 1963 to 1992 (Table 2; $t = 3.6$, $P = 0.002$, N=26). Effects of proximity to forest edge on barrens persistence were most evident in the 0-50-m buffer. In both time periods, there was a slight to steep increase in persistence rates from the 0-50-m to the 50-100-m buffer for all fire counts on all types of geomorphology (Figure 6). In both periods the proximity effect was greatest at fire counts of 0 and 1, and in particular on flat bedrock at a fire count of 1. At fire counts of 2 and greater in 1938 to 1963, the proximity effect was similar, although smaller in magnitude.

At distances from the forest edge exceeding 50 m, barrens proximity effects on persistence rates varied by geomorphology and fire count. On flat till, proximity to forest edge beyond 100 m had little or no relationship to barrens persistence. On sloping till, effects of proximity to forest edge on barrens persistence were variable. Only one clear trend emerged: barrens persistence at a fire count of 1 showed a sharp increase with distance from forest edge.

On flat bedrock, barrens persistence in 1938 to 1963 at fire counts of 0 and 1 increased sharply out to 200 m from the forest edge and then decreased at greater distances. Persistence at fire counts of 2 and greater displayed a steady gradual increase with distance from the forest edge. Barrens persistence in 1963 to 1992 at fire counts of 0 and 1 increased gradually with distance.

Barrens Succession

Area values for succession of barrens to forest, and barrens succession rates in 1938 to 1963 ranged from 5.2 to 147 ha and 0.05 to 0.79, respectively (Table 1). In 1963 to 1992, these values were 0 to 447 ha and 0 to 0.84 (Table 2). Barrens transitions to uses such as agricultural, residential and commercial development amounted to 498 ha in 1938 to 1963 and 523 ha in 1963 to 1992, representing transition rates of 0.07 and 0.10, respectively. Mean succession rates in 1938 to 1963 were greatest on sloping till (0.45), intermediate on flat bedrock (0.32), and lowest on flat till (0.27) (Table 1). In 1963 to 1992, mean succession rates

Table 1. Procono Mesic Till Barrens Area Values and Transition Rates By Geomorphology, Fire Frequency, and Proximity To Forest Edge 1938 to 1963.*

Terrain	Fire Frequency	Proximity	1938 Barrens (ha)	Barrens Persistence Rate (ha)	Barrens Persistence Rate	Barrens Succession (ha)	Barrens Succession Rate
flat bedrock	0	0-50	15.16	5.96	0.39	8.78	0.58
flat bedrock	1	0-50	19.46	5.70	0.29	11.07	0.57
flat bedrock	2	0-50	36.39	16.95	0.47	18.10	0.50
flat bedrock	> 2	0-50	98.13	48.36	0.49	42.12	0.43
flat bedrock	0	50-100	16.65	9.49	0.57	5.89	0.35
flat bedrock	1	50-100	20.51	12.40	0.60	5.23	0.26
flat bedrock	2	50-100	26.95	16.06	0.60	9.40	0.35
flat bedrock	> 2	50-100	97.30	58.29	0.60	31.00	0.32
flat bedrock	0	100-200	38.15	27.44	0.72	6.16	0.16
flat bedrock	1	100-200	48.18	33.85	0.70	10.16	0.21
flat bedrock	2	100-200	64.73	43.12	0.67	14.57	0.23
flat bedrock	> 2	100-200	185.29	122.63	0.66	45.32	0.24
flat bedrock	0	> 200	92.63	63.08	0.68	20.45	0.22
flat bedrock	1	> 200	254.04	149.33	0.59	92.63	0.36
flat bedrock	2	> 200	235.30	165.40	0.70	50.28	0.21
flat bedrock	> 2	> 200	710.97	537.26	0.76	147.06	0.21
mean					0.59		0.32
flat till	0	0-50	138.10	56.39	0.41	74.44	0.54
flat till	1	0-50	107.00	57.91	0.54	47.60	0.44
flat till	2	0-50	80.78	59.75	0.74	17.30	0.21
flat till	> 2	0-50	101.05	78.50	0.78	20.85	0.21
flat fill	0	50-100	94.48	47.70	0.50	42.48	0.45
flat till	1	50-100	104.45	69.25	0.66	33.34	0.32
flat till	2	50-100	82.78	69.60	0.84	10.61	0.13
flat till	> 2	50-100	127.16	108.89	0.86	16.01	0.13
flat till	0	100-200	123.54	53.79	0.44	63.61	0.51
flat till	1	100-200	185.60	109.45	0.59	71.94	0.39
flat till	2	100-200	174.59	148.86	0.85	18.99	0.11
flat till	> 2 100-200	242.77	206.23	0.85	26.58	0.11	
flat till	0	> 200	222.48	114.41	0.51	94.68	0.43
flat till	1	> 200	439.55	313.69	0.71	105.37	0.24
flat fill	2	> 200	370.03	308.69	0.83	38.84	0.10
flat till	> 2	> 200	731.77	611.31	0.84	37.21	0.05
mean					0.68		0.27
sloping till	0	0-50	55.23	9.87	0.18	43.71	0.79
sloping till	1	0-50	99.56	32.75	0.33	65.53	0.66
sloping till	2	0-50	47.56	31.90	0.67	15.23	0.32
sloping till	> 2	0-50	74.76	51.75	0.69	22.95	0.31
sloping till	0	50-100	45.40	12.46	0.27	32.03	0.71
sloping till	1	50-100	85.11	35.13	0.41	49.71	0.58
sloping till	2	50-100	53.20	39.07	0.73	13.84	0.26
sloping till	> 2	50-100	71.01	53.09	0.75	17.79	0.25
sloping till	0	100-200	70.19	25.88	0.37	42.62	0.61
sloping till	1	100-200	134.93	69.50	0.52	64.77	0.48
sloping till	2	100-200	96.62	70.35	0.73	25.39	0.26
sloping till	> 2	100-200	120.21	87.20	0.73	31.44	0.26
sloping till	0	> 200	81.69	22.63	0.28	55.70	0.68
sloping till	1	> 200	292.26	154.82	0.53	131.08	0.45
sloping till	2	> 200	212.67	136.49	0.64	71.09	0.33
sloping till	> 2	> 200	215.44	152.96	0.71	51.15	0.24
mean					0.53		0.45

*Barrens transitions to cultural features are the reason persistence and succession rates do not sum to 1.0

Table 2. Pocono Mesic Till Barrens Area Values and Transition Rates By Geometry, Fire Frequency, and Proximity To Forest Edge 1963 to 1992.*

Terrain	Fire Frequency	Proximity	1963 Barrens (ha)	Barrens Persistence (ha)	Barrens Persistence Rate	Barrens Succession (ha)	Barrens Succession Rate
flat bedrock	0	0-50	453.95	147.24	0.32	285.23	0.63
flat bedrock	1	0-50	14.64	5.82	0.40	8.56	0.58
flat bedrock	2	0-50	0.76	0.70	0.92	0.06	0.08
flat bedrock	> 2	0-50	0.22	0.08	0.35	0.10	0.43
flat bedrock	0	50-100	313.92	143.15	0.46	145.11	0.46
flat bedrock	1	50-100	8.69	5.59	0.64	2.95	0.34
flat bedrock	2	50-100	0.89	0.87	0.99	0.01	0.01
flat bedrock	> 2	50-100	0.41	0.27	0.64	0.00	0.00
flat bedrock	0	100-200	334.88	170.31	0.51	124.62	0.37
flat bedrock	1	100-200	13.37	9.08	0.68	4.05	0.30
flat bedrock	2	100-200	2.45	2.45	1.00	0.00	0.00
flat bedrock	> 2	100-200	0.38	0.38	1.00	0.00	0.00
flat bedrock	0	> 200	201.13	110.24	0.55	70.06	0.35
flat bedrock	1	> 200	9.53	7.76	0.81	0.21	0.02
flat bedrock	2	> 200	1.79	1.75	0.98	0.00	0.00
flat bedrock	> 2	> 200	0.46	0.46	1.00	0.00	0.00
mean**					0.54		0.48
flat till	0	0-50	552.63	149.82	0.27	359.03	0.65
flat till	1	0-50	10.28	5.81	0.57	3.67	0.36
flat till	2	0-50	0.98	0.98	1.00	0.00	0.00
flat till	> 2	0-50	0.00	0.00	0.00	0.00	0.00
flat till	0	50-100	475.79	175.63	0.37	253.59	0.53
flat till	1	50-100	16.22	10.92	0.67	3.79	0.23
flat till	2	50-100	4.68	4.68	1.00	0.00	0.00
flat till	> 2	50-100	0.11	0.02	0.21	0.10	0.95
flat till	0	100-200	699.49	274.22	0.39	343.65	0.49
flat till	1	100-200	35.51	25.59	0.72	6.47	0.18
flat till	2	100-200	19.04	18.95	1.00	0.09	0.005
flat till	> 2	100-200	1.42	1.42	1.00	0.00	0.00
flat till	0	> 200	875.31	330.45	0.38	446.90	0.51
flat till	1	> 200	38.57	30.47	0.79	4.92	0.13
flat till	2	> 200	10.49	10.28	0.98	0.20	0.02
flat till	> 2	> 200	1.08	1.08	1.00	0.00	0.00
mean**					0.61		0.47
sloping till	0	0-50	343.34	52.33	0.15	278.39	0.81
sloping till	1	0-50	24.61	9.02	0.37	14.61	0.59
sloping till	2	0-50	0.64	0.27	0.42	0.37	0.58
sloping till	> 2	0-50	0.25	0.00	0.00	0.07	0.28
sloping till	0	50-100	247.37	53.37	0.22	185.11	0.75
sloping till	1	50-100	18.60	10.10	0.54	7.92	0.43
sloping till	2	50-100	0.88	0.61	0.70	0.21	0.24
sloping till	> 2	50-100	1.10	0.76	0.69	0.00	0.00
sloping till	0	100-200	237.83	55.37	0.23	173.47	0.73
sloping till	1	100-200	20.09	13.87	0.69	6.14	0.31
sloping till	2	100-200	0.18	0.16	0.88	0.00	0.00
sloping till	> 2	100-200	2.74	2.72	0.99	0.00	0.00
sloping till	0	> 200	303.01	39.91	0.13	254.80	0.84
sloping till	1	> 200	8.28	7.23	0.87	1.05	0.13
sloping till	2	> 200	0.10	0.10	1.00	0.00	0.00
sloping till	> 2	> 200	0.80	0.80	1.00	0.00	0.00
mean**					0.4		0.64

*Barrens transitions to cultural features are the reason persistence and succession rates do not sum to 1.0 **Includes values of rates where the area of transition is greater than 5 ha

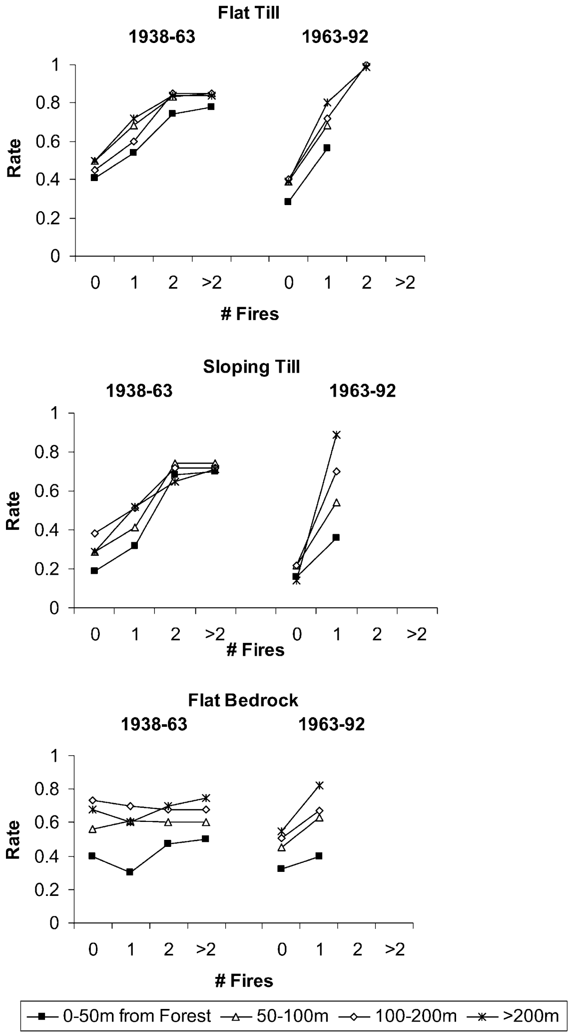

Figure 6. Barrens persistence rates for flat till, sloping till, and flat bedrock versus number of fires and proximity to forest edge

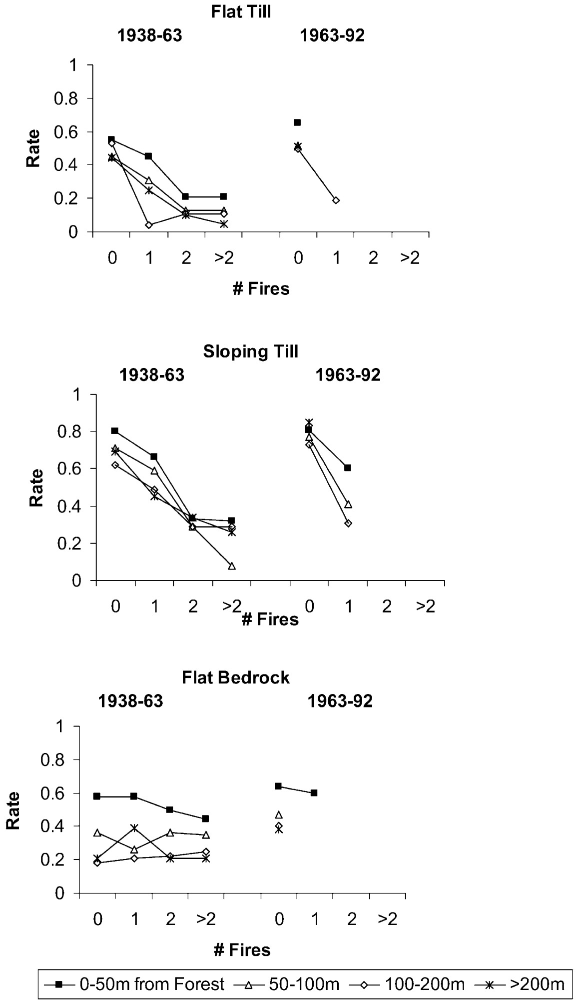

Figure 7. Barrens succession rates for flat till, sloping till, and flat bedrock versus number of fires and proximity to forest edge

followed the same trend for sloping till (0.64), flat bedrock (0.48), and flat till (0.47), but were higher in all cases (Table 2). Mean barrens succession rates in 1938 to 1963 differed significantly with geomorphology ($F = 10$, $P = 0.0$, N=48). Multiple comparisons of mean barrens succession rates show significant differences between flat till and sloping till ($t = 6.2$, $P = 0.000$, N=48), and sloping till and flat bedrock ($t = 4.4$, $P = 0.010$, N=48) in 1938 to 1963. Comparisons for 1963 to 1992 show no significant differences.

Barrens succession rates were roughly mirror opposites of barrens persistence rates (Figure 7). Barrens succession rates differed significantly with fire count in 1938 to 1963 ($t = -6.5$, $P = 0.0$, N=48) and in 1963 to 1992 ($t = -3.6$, $P = 0.003$, N=17). On glacial till soils, barrens succession rates displayed a negative relationship to fire count and were similar within slope type at counts of 2 fires or greater. Succession rates on flat bedrock showed little or no relationship to fire count. Overall variation in succession rates by fire count was greatest on sloping till, slightly less on flat till, and least on flat bedrock.

Rates of barrens succession displayed a negative relationship to distance from forest edge in 1938 to 1963 (Table 1) and in 1963 to 1992 (Table 2) and differed significantly with proximity to forest edge in 1938 to 1963 ($t = -3.19$, $P = 0.003$, N=48). Succession rates decreased between the 0-50-m and 50-100-m buffers for all fire counts on all types of geomorphology during both periods (Figure 7). This

Table 3. Forest to Pocono Mesic Till Barrens Area Values and Creation Rates by Geomorphology and Fire Frequency 1938 to 1963.

Terrain	Fire Frequency	Forest 1938 (ha)	Barrens Creation (ha)	Barrens Creation Rate
flat bedrock	0	97.44	1.91	0.02
flat bedrock	1	31.48	1.33	0.04
flat bedrock	2	42.03	21.21	0.29
flat bedrock	> 2	73.01	23.53	0.32
flat till	0	2817.35	67.34	0.02
flat till	1	292.44	83.14	0.28
flat till	2	129.86	68.86	0.53
flat till	> 2	92.69	49.97	0.54
sloping till	0	1028.08	35.66	0.03
sloping till	1	213.69	66.66	0.31
sloping till	2	98.31	39.99	0.41
sloping till	> 2	110.81	36.97	0.33

effect was pronounced on sloping till and flat bedrock extending out to the 100 to 200-m buffer at fire counts of 0 and 1 in 1938 to 1963 (Table 1).

At greater than 100 m from the forest edge and at fire counts of 0 and 1, succession rates generally displayed a decreasing trend with a few increasing at distances greater than 200 m. At fire counts of 2 or greater, succession rates declined gradually on flat till and flat bedrock, and changed very little on sloping till.

Barrens Origination

Areas of barrens origination in 1938 to 1963 ranged in size from 1.3 to 83 ha and origination rates ranged from 0.02 to 0.54 (Table 3). Approximately 9.7% (488 ha) of forest in the study area in 1938 changed to barrens. Rates of barrens origination increased directly with fire count, leveling off or decreasing slightly beyond 2 fires (Figure 8). Data are insufficient for analysis of 1963 to 1992 barrens origination because polygons do not meet the 5-ha minimum size threshold to control for possible mapping inaccuracy.

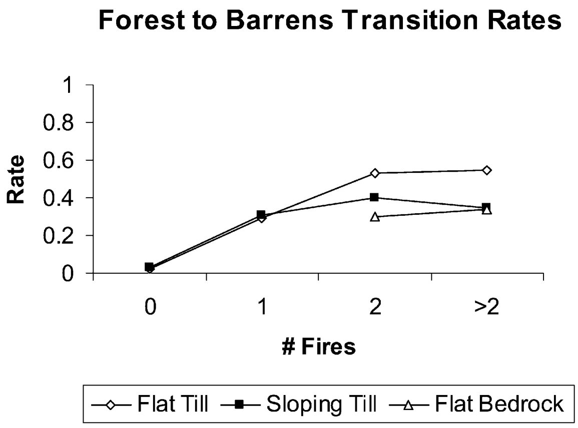

Figure 8. Forest to barrens transition rates versus number of fires for flat till, sloping till, and flat bedrock, 1938 to 1963. Data points are omitted for transition areas < 5 ha.

Discussion

Fire and Geomorphology

Thompson (1995); Latham et al. (1997), and this study identify interactions between fire and geomorphology as the primary mechanisms regulating Pocono mesic till barrens persistence. In all three studies, persistence rates follow the general trend of flat till > flat bedrock > sloping till > sloping bedrock at equivalent fire counts. Rates of barrens persistence on glacial till are positively influenced by fire count, and persistence rates are highest on flat till exposed to repeated fires (Latham et al. 1997, Thompson 1995).

Effective deployment of limited fire management resources by future PMTB fire managers requires a knowledge of the minimum fire frequency needed to achieve high barrens persistence within a given geomorphology type. Thompson (1995) observed that the extent and vigor of barrens habitat for 1938 to 1963 indicated that fire frequency during this era is probably similar to the natural PMTB fire rotation. Therefore, barrens transitions during this period would closely reflect the influence of a natural fire regime.

We find that rates of barrens persistence for 1938 to 1963 on flat and sloping till reach a threshold at 2 fires. For the same period, Latham et al. (1997) found that persistence rates on flat till approach a maximum at 2 fires, and increase only slightly at counts of 3 and 4 fires. On sloping till, persistence rates peak at 3 fires. Both Latham et al. (1997) and this study determined that fire has little or no effect on persistence rates in barrens overlying bedrock rather than glacial till, where rates are generally low regardless of fire frequency.

Barrens persistence through a particular interval may not be as closely related to the number of fires during the interval as it is to the time elapsed since the most recent fire. Thompson (1995) found that persistence of barrens on both till and bedrock is inversely related to time since the last fire. Persistence rates on till soils burned in 1978 or later are approximately 50% higher than in areas that last burned between 1932 and 1977. Persistence rates on bedrock in areas burned in 1978 or later are approximately 15% to 25% higher than rates from areas that last burned between 1932 and 1977. Persistence rates are generally very low for barrens on till or bedrock that last burned prior to 1932. Future research will need to address these issues as the overall effect of fire on PMTB persistence is likely to depend on specific aspects of the fire regime, including fire frequency, severity, intensity, and time since the last fire.

PMTB fire managers must also understand how geomorphology modifies the barrens fire regime. Rates of barrens persistence are higher on flat than on sloping terrain, and higher on till than bedrock. The difference in persistence rates between till and bedrock within the same slope category is unrelated to fire frequency, but may be related to characteristics of the substrate. Differences in barrens persistence according to slope may be related to the invasiveness of adjacent forest types. Sloping terrain tends to be adjacent to rapidly spreading oak forest while flat terrain is adjacent to northern hardwood and mixed woodland forests that, with the exception of red maple, invade barrens slowly or not at all (Thompson 1995).

Lower rates of barrens persistence on sloping terrain may also be explained by the presence of streams and ravines which can act as firebreaks (Thompson 1995). Similar findings are reported by Loehle et al. (1996) for forest colonization of fire-maintained prairie habitat. Forest colonization in the absence of fire suppression was minimal in an area that is largely flat with few roads or streams to act as firebreaks. Forest colonization during the same period on two nearby tracts dissected by more streams and with more roads was 42% and 76% (Loehle et al. 1996).

Forest Contagion

Forest contagion negatively affects barrens persistence within 50 m of the forest edge in all cases, with persistence reduced further on sloping till and flat bedrock out to a distance of 200 m in some instances. Seed rain from adjacent forest is likely the most influential contagion effect driving barrens-to-forest succession near the forest edge. Previously cited research (Breden 1984; Hughes and Fahey 1988; McDonnell and Koch 1990; Myster 1993) indicates that most tree seeds dispersed into the PMTB are likely to fall within a few meters of the forest edge. Indications that contagion effects may extend out to 200 m in some cases on sloping till and flat bedrock may be the result of noisy data. An alternative explanation is that these patterns represent large numbers of seeds dispersed long distances by a combination of wind, birds and other animals.

Long-term PMTB successional trends illustrate the cumulative effects of forest contagion. Barrens succession has accelerated with time through a likely synergism between forest contagion and barrens fragmentation, which has placed forest edge in closer proximity to more of the barrens. Rates of barrens succession from 1938 to 1963 showed a distinct and statistically significant pattern of decline with distance from the forest edge. Succession rates from 1963 to 1992 were not as strongly patterned as in the previous period, and the pattern is not statistically significant, but succession rates were 55% to 135% greater than those of the earlier period.

A possible explanation is that in 1938, much of the barrens was located in large core areas away from surrounding forest (Figure 5a). In contrast, by 1963 the barrens were more highly intermixed and in closer proximity to forest (Figure 5b), creating a large extent of highly convoluted barrens-forest boundary. The closer proximity of barrens to forest and the large extent of common boundary subjected much more barrens habitat to forest edge effects, likely increasing the rate of barrens succession.

A similar pattern of accelerated forest colonization is reported by Loehle et al. (1996) for the spread of riparian forest into prairie. They found that forest spread is slow and steady at first, but then accelerates when the forest edge exceeds a critical density as measured by its fractal dimension. They concluded that the finger-like boundary form of invading forest produces a self-reinforcing, accelerating feedback between the creation of new forest edge and rate of forest colonization (Loehle et al. 1996). Our results are consistent with this previous work, reinforcing the concept that 'edge and shape matter' in examining the dynamics of forest contagion.

Management Implications

Preparation of a fire management plan for the PMTB requires consideration of a number of issues including the timing, frequency, intensity, and severity of prescribed burns, and where to focus limited fire management resources. Current information indicates that barrens on flat till would be the most amenable to prescribed burn management (Thompson 1995). Equally high persistence rates may be achievable on sloping till but would require a greater input of fire management resources given the lower rates of barrens persistence on this geomorphology type.

Recommendations for prescribed burning rates for achieving high levels of barrens persistence on a particular geomorphology type can be made using findings from the 1932 to 1963 period. This study and Latham et al. (1997) suggested that on flat till, approximately two fires were sufficient over the 31-year period to achieve rates of barrens persistence in the range of 0.74 to 0.85 (although, as noted earlier, our data may underestimate the actual number of fires that occurred at some points in the landscape). Only marginally higher persistence is gained at higher fire counts (Latham et al. 1997). On sloping till, fire frequencies of at least 3 were needed to achieve similar rates of persistence (Latham et al. 1997). However, Thompson (1995) calculated that the average fire return intervals before the era of fire suppression for scrub oak, heath, and rhodora barrens were 9, 18, and 26 years, respectively. Additional research will be needed to determine optimum intervals between fires for each barrens type, as well as the intensity and severity of prescribed burns needed to achieve long-term persistence.

Maintaining barrens habitat on sites underlain by bedrock and not glacial till would present considerable challenges to PMTB managers. Both this study and Latham et al. (1997) indicate that repeated burning has a minimal effect on barrens persistence on bedrock. More labor-intensive methods involving the cutting and removal of invading trees or use of herbicides to kill trees may be necessary.

Boundary form (configuration) can greatly modify the pattern and rate of forest colonization near the forest edge (Breden 1984; Hardt and Forman 1989). Breden (1984) found that fruiting red maples along the edges of concavities in the forest boundary (convexities in the beaver meadow) are in closer proximity to each other and had seed shadows with greater overlap than along straight edges. Closer proximity of fruiting trees results in a given concentration of red maple seed dispersing farther into the beaver meadow from concave edges than from fruiting trees along straight edges. This phenomenon may have considerable impact on patterns of forest colonization of the PMTB, as barrens-forest boundaries, although generally quite distinct, are very irregular with numerous concave and convex undulations.

Hardt and Forman (1989) reported a similar 'cove concentration effect' in the form of enhanced rates of woody plant colonization opposite concave undulations in the forest boundary. Colonization rates are reduced adjacent to convex boundaries, and rates are intermediate adjacent to straight boundaries. In their study, colonizing woody plants opposite concave and straight boundaries were 2.5 and 1.7 times the number opposite convex boundaries, respectively. The differential rates of woody plant colonization linked to boundary form produced a 'concave-convex reversal' in which the extent of abundant woody plant colonization opposite concave boundaries (40 m) minus the length of the concavity (average 20 m) was twice that of convex boundaries (10 m) in only 10 years. This phenomenon suggests a pattern of colonization in which the forest boundary moves forward through an alternating spatial reversal of concavities and convexities over time (Hardt and Forman 1989).

Based on the findings of Thompson (1995), Latham et al. (1997), this study, and previously cited literature, management should focus on large core areas of barrens habitat with broadly rounded corners and barrens-forest boundaries that are relatively straight and smooth. Large core areas, as opposed to small and scattered areas, would place a greater proportion of barrens at distances greater than 50 m from nearby forest, thus minimizing the adverse effects of edges on barrens persistence. Large core areas would also serve to reduce other impacts associated with ecosystem fragmentation (Saunders 1991). A boundary form with few coves and with broadly rounded corners would minimize forest colonization that results from expanded edge area (Loehle et al. 1996) and the cove concentration effect (Hardt and Forman 1989; Breden 1984). Hand or mechanical trimming may be required to achieve the desired edge configuration for managed areas and could be accomplished concurrently with the construction of firebreaks.

Control of Nascent Foci

Succession in the PMTB is the product of encroachment at the leading edge of the larger body of surrounding forest and the expansion and consolidation of numerous scattered forest patches within the barrens matrix. It seems likely that much of the observed PMTB succession since 1963 followed this pattern. Forest patches of various shapes and sizes are present within the PMTB matrix in the 1938 vegetation data layer (Figure 2a) and are particularly well represented in the 1963 vegetation data layer (Figure 2b). Many patches were located on sloping terrain and in close proximity to each other, which should have facilitated rapid colonization of the barrens separating them. Most patches had irregular boundaries that would have accelerated edge expansion via the cove concentration effect (Hardt and Forman 1989; Breden 1984). Patch consolidation occurred during 1938 to 1963 despite numerous fires and was particularly evident during 1963 to 1992, resulting in the formation of large blocks of contiguous forest.

Control of small forest patches may be of considerable importance for maintaining high levels of barrens persistence within PMTB management areas. Models of invasive plant spread indicate that control of small populations of invaders (nascent foci) disjunct from the main focus of invasion is crucial to controlling an overall invasion. A group of nascent foci can spread more rapidly than a single large focus of equal area (Moody and Mack 1988). Disjunct patches of forest within PMTB management areas could act as nascent foci and hasten forest succession. The patch-related succession documented by the PMTB GIS vegetation data layers appears to be a real-world example of this process.

Conclusions

The Pocono mesic till barrens are rare, fire-maintained, mesic shrub communities consisting of scrub oak, heath, and rhodora barrens. Barrens vegetation is characterized by its fire tolerance and high nitrogen-use efficiency. In the past, these adaptations enabled barrens vegetation to persist over long time periods despite invasion pressure from the surrounding forest. However, as a result of regional fire suppression efforts beginning in the early 1960s, the area of the barrens has shrunk by 73% and become highly fragmented.

The Nature Conservancy has designated the PMTB as one of its highest priority areas for biodiversity conservation in Pennsylvania because it provides habitat for a variety of state, regionally, and globally rare plants and animals. TNC has devoted substantial resources toward the goal of restoring and managing the barrens habitats. A number of scientific studies (Thompson 1995; Latham et al. 1996; Latham et al. 1997; Latham 2003; Wibiralske et al. 2004) have already been undertaken to understand and define the limits of the mechanisms regulating barrens persistence. Findings to date indicate that fire modified by geomorphology is the primary mechanism driving barrens persistence. These and future findings are vital for TNC in devising and updating the management plan for the barrens.

Our findings indicate that the forest contagion effect negatively affected barrens persistence on all geomorphology types at less than 50 m from the forest edge. The results also support previous findings by Thompson (1995) and Latham et al. (1997) that fire modified by geomorphology is the primary mechanism regulating barrens persistence in the PMTB. A phenomenon of particular interest is the substantial increase in rates of barrens succession in 1963 to 1992 in comparison to 1932 to 1963. This pattern suggests that forest colonization is enhanced by a highly convoluted barrens-forest boundary form, accelerated forest edge expansion, barrens fragmentation, and rapid expansion of small patches of nascent forest within the barrens matrix. These latter findings may be of particular importance to future efforts to preserve the barrens ecosystems; as noted previously, 'shape and edge matter,' and these findings can guide future preservation and restoration activities.

TNC has to overcome many obstacles to restore and manage the barrens. Important challenges that remain are to develop a better understanding of barrens succession, mitigate the effects of barrens fragmentation, address anthropogenic perturbations such as nitrogen enrichment of ecosystems, and sustain populations of rare species. Future research efforts should be directed at resolving these issues, as well as examining the specifics of fire dynamics (optimal fire intervals, intensity, and severity) that lead to longer term barrens persistence. Despite the challenges noted above, there is reason for considerable optimism. TNC has an impressive record of accomplishment in conserving our natural heritage. Given adequate resources and partnerships, TNC should be successful in preserving the rare species and habitats that make up the Pocono mesic till barrens.

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