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SUCCESSION DYNAMICS OF PINE BARRENS RIVERSIDE SAVANNAS:

A LANDSCAPE-SURVEY APPROACH

by

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ABSTRACT OF THE THESIS

Succession dynamics of Pine Barrens riverside savannas: a landscape-survey approach

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Pine Barrens riverside savannas are acidic seepage fens found on the flood terraces of streams and rivers of the New Jersey Pine Barrens. Ecologically, they are comprised of six distinct vegetation communities, each listed as globally rare or imperiled. While pollen indicates that some individual savannas may have persisted in an open state for over 8,000 years, floristic studies conducted over the past century suggest a rapid decline in their distribution over that period. Savannas have historically been subject to extensive human exploitation for their iron and turf resources. However, all extant sites have been largely protected from direct anthropogenic alteration for the past 150 years. Succession, then, appears to be the most likely driver of this recent decline in savanna distribution. The goals of this study were to quantify the rate of decline based on a single dataset, identify the dominant succession patterns within the system, and suggest directions for future research. Using a variety of GIS and data visualization techniques, a multifaceted data exploration approach was taken to characterize succession dynamics over a 62-year period across multiple spatial and temporal scales. Dramatic loss of savanna cover was confirmed, with a decrease in total savanna area study-wide of 71.3% between 1940 and 2002. This study-wide decline was generally linear for each of three general classes of savanna (wet, graminoid and shrub). At the site level, these patterns were much more variable; apparently based on the distribution of savanna at the start of the study. Two distinct patterns of succession were

apparent: one of locally persistent graminoid savanna, and one consistent with a shifting mosaic driven by rapid succession and disturbance from both fire and flood. Rapid declines appear to be driven primarily by the shifting mosaic that is not in a steady state. Persistent patches do show signs of slow decline through incursion of Atlantic white cedar. One potential causal factor, the composition of vegetation adjacent to savanna patches did not appear to have any influence on succession dynamics. The focus of future research should be on the influence of changing natural disturbance regimes and the factors that maintain locally persistent savanna patches.

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Introduction

Pine Barrens riverside savannas are acidic seepage fens found on the floodplains of meandering rivers of the New Jersey Pine Barrens, often in abandoned stream channels. They have a complex hydrology fed primarily by groundwater, but are periodically exposed to overbank flooding. The diverse flora of Pine Barrens riverside savannas consists primarily graminoid and forb species, including numerous state ranked rare or endangered species. Many of these are also federal candidate species, and many are ranked globally rare or imperiled (Walz *et al.*, 2006).

Ecologically, Pine Barrens riverside savanna consist of mosaics of six distinct communities corresponding to differences in microtopography (Palmer, 2005) and land use history (Walz *et al.*, 2006). Each of these six is listed as globally vulnerable or imperiled (NatureServe Explorer, 2011). Pine Barrens riverside savanna should be differentiated from pitch pine lowland savanna, both of which are commonly referred to simply as Pine Barrens savanna, but differ in landscape position, hydrology, soils, and flora (Walz *et al.*, 2006).

The ecology of the New Jersey Pine Barrens at large has been studied extensively. It would be nearly impossible to provide a comprehensive list of publications on the subject. A small sample of recent studies is enough to hint at the breadth of research devoted to the region (e.g., Zampella *et al.*, 1999; Gray and Dighton, 2006; Wund *et al.*, 2007; Zampella *et al.*, 2007; Bunnell and Ciraolo, 2010; Clark *et al.*, 2010; Landesman and Dighton, 2010). Savanna, however has gone largely unstudied until very recently; generally treatment of savanna has been limited to inclusion in broader vegetation surveys (Harshberger, 1916; Collins and Anderson, 1994; Breden *et al.*, 2001).

In 2006 Kathleen Strakosch Walz of the New Jersey Department of Environmental Protection and colleagues compiled a series of in-depth studies of Pine Barrens riverside savannas

(Walz, *et al.* 2006). These studies covered a range of topics including geomorphology, hydrology, vegetation and land use history, vegetation community classification, and associated flora and fauna. This represents the first and, to date, most extensive treatment of savanna ecology. Some academic investigations of savannas have also been conducted in recent years. Notably, Palmer (2005) examined the role of micro-topography in organizing vegetation assemblages within savanna sites. Demitroff (2007) studied the periglacial origins of savanna, among other emergent wetland types of the Pine Barrens. To my knowledge, these are the only studies devoted directly to savanna.

Through much of the 18th and early 19th centuries, Pine Barrens river floodplains, and likely many savannas, were subject to extensive anthropogenic disturbance, particularly for extraction of bog iron (Pierce, 1957; Walz *et al.*, 2006) and turf (Walz *et al.*, 2006). Atlantic white cedar, *Chamaecyparis thyoides*--the dominant vegetation across the riparian zone of most Pine Barrens streams--has seen extensive logging repeatedly (Wacker, 1979). By the late 1800s, cranberry production was widely practiced in the Pine Barrens (Applegate *et al.*, 1979). Many early cranberry bogs were located in riverside riparian zones and often converted from savanna (Walz, 2006).

While Pine Barrens floodplains have been heavily disturbed, pollen analysis indicates that at least one Pine Barrens riverside savanna has remained in a relatively undisturbed, open canopy state for millennia (Southgate, 2000). Some landscape-level turnover due to naturally occurring processes is expected in this system (Walz *et al.*, 2006), however botanical studies conducted over the past century indicate that savanna has recently seen an alarming decline in distribution. McCormick (1979) estimates that savanna may have covered thousands of hectares of southern New Jersey at the beginning of the twentieth century; dropping to below 400 ha by 1979. These are limited to small, fragmented patches within highly protected reserves, very few

of which remain undisturbed (Wacker, 1979; Walz *et al.*, 2006). As of 2012, all extant Pine Barrens riverside savannas are found within Wharton State Forest. This 40,000 ha tract of pinelands was designated a state forest in 1955 (NJ Pinelands Commission, 2007) after being purchased from the estate of Joseph Wharton (Pierce, 1957). Wharton began acquiring land in the Pine Barrens with the idea of using its ample reserves of clean water to supply the nearby cities of Philadelphia and Camden. Between 1873 and 1909 he had amassed nearly 400 km² of land, which was left largely to return to "pristine condition". The plan never came to pass, but the land was largely preserved (Yates, 1987). Thus, while there remains a legacy of extensive exploitation, direct alteration of savanna sites has been minimal for nearly 140 years.

The losses estimated by McCormick (1979) then must almost certainly be a result of succession. Early studies of wetland plant succession (e.g. Cowles, 1899; Dachnowski, 1912; Pearsall, 1920; Wilson, 1935) developed the classical *hydrarch* concept of wetland development (Mitsch and Gosselink, 2007). In this view, wetlands represent temporary stages in the gradual transition from open water to terrestrial forest. The most simplistic model describes a linear sequence from submerged aquatic vegetation to emergent vegetation, wet sedge-grass communities, shrub dominated communities, forested swamp, and finally to terrestrial forest (Mitsch and Gosselink, 2007). Despite being quite simplistic, there is evidence that this general trend does appear in natural wetland systems (Golet *et al.*, 1993). Several alternative patterns have also been observed, including expansion of wetland vegetation into terrestrial systems (Heinselman, 1963), significant reversals among major stages of the hydrarch sequence (Schwintzer and Williams, 1974), oscillation between stages (van der Valk, 2005), and the prolonged persistence of wetlands, even in early stages, in a quasi-climax state (Klinger, 1996). In a meta-analysis of 20 published pollen profiles collected from British mires, Walker (1970) found that 46% of conversions corresponded to the expected hydrarch sequence, while 54% indicated various skips and reversals. This variability prompted the author to conclude that "the most

impressive feature of these data is the variety of transitions which have been recorded and which must reflect the flexibility of the succession" and that "it is impossible to select a preferred sequence" (p. 123).

Included in the classic view of succession is that it is an ongoing autogenic process. Vegetation from early successional stages alters the environment such that it promotes the establishment of those species that replace it (Mitsch and Gosselink, 2007). By extension, in order for early successional stages to remain within the system, some allogenic process must act to counter succession. This may occur at the local level as successional processes are balanced directly by countervailing environmental factors. For instance, van der Valk (2005) found that oscillations in water level around a long-term mean in prairie pothole wetlands caused periodic switching between emergent vegetation and communities dominated by terrestrial annuals. In riverine systems, flood dynamics have also shown to contribute to the maintenance of herbaceous wetlands (Johnson, 1994; Bornette and Amoros, 1996; Toner and Keddy, 1997).

Alternatively, disturbance may play a role in the maintenance of a variety of successional stages within the landscape. This phenomenon has been treated extensively (Loucks, 1970, Botkin and Sobel, 1975; Sousa, 1979; Noble and Slatyer, 1980; Halpern, 1989). The process is probably most succinctly described by Bormann and Likens (1979) as a shifting mosaic steady-state condition. Here, small-scale disturbance resets succession at a given location an earlier stage. As such disturbances occur over time throughout the landscape, a mosaic of vegetation patches in varying stages of succession develops. A relatively set proportion of the landscape will be covered by each stage at any point in time, but the spatial distribution of those patches will change constantly.

Radiocarbon dating of peat cores taken from three savanna sites indicates that accumulation of organic matter began between 9,000 and 7,000 years before present (Stanford *et*

al., 2000). Pollen analysis of one of these cores performed by Southgate (2000) revealed the presence of the club moss *Lycopodiella caroliniana*--a species that is locally found only in open savanna--throughout the profile. This indicates that open savanna has been maintained locally over millennia. Hydrology likely plays a key role in this long-term maintenance. Natural fluctuations in the water table around a relatively stable long-term mean has shown to play a role in maintaining herbaceous wetland vegetation (van der Valk, 2005). Another potential contributor to maintenance of savanna is sea level rise. A slowly rising sea level over the past 6,000 years has gradually raised the water table in the floodplains of the Pine Barrens (Stanford, 2000). Lowering of the water table as been shown to initiate succession by altering both hydrology and soil chemistry in studies of calcareous fens in Europe (van der Hoek and Sykora, 2006; van Diggelin *et al.*, 2006; van der Hoek and Heijmans, 2007). Hummock-building vegetation such as that found in savanna may lift the hummock away from the water table over time creating local conditions that promote shrub and tree growth (Johnson, 1997). A rising water table may mitigate this effect.

In a study of Atlantic white cedar swamps in the Pine Barrens, Zampella and Lathrop (1997) describe a shifting mosaic within the floodplains of the region. These areas are subject to natural disturbance in the form of both flood and fire. Large overbank floods occur infrequently (Rhodehamel, 1979) but are known to occur (Thomas, 1964; personal observation). Flooding due to beaver activity may play an even more important role in shaping the floodplain landscape (Zampella and Lathrop, 1997). Impoundments created by beaver dams often maintain elevated water levels for years, killing trees (Reddoch and Reddoch, 2005) and sustaining herbaceous vegetation in their wake by leaving behind moist soils and nutrient rich sediment (Wright *et al.*, 2002). Fire is a common occurrence in the Pine Barrens and integral to the ecology of the region. The effect of fire on swamps of the Pine Barrens is described by Little (1979). Swamps often act as a fire break to fires started in the uplands or pine lowlands. However, during particularly dry

years these fires may spread through the swamp burning not only the above-ground vegetation but portions of the root structure and organic soil as well. The vegetation that fills in this area depends on the amount of peat remaining. If the surface of the remaining peat layer is at or near the water level, recruitment of trees (cedar or hardwoods) may be delayed until sphagnum moss is able to accumulate a sufficient seed bed. If the organic soil depth remains relatively unchanged, new cedar trees will begin to recruit relatively quickly and the new stand may be relatively pure.

In recent history, these key disturbance regimes have been altered by human activity. Dams have been constructed for industry (Pierce, 1957) and agriculture (Procopio, 2006) which may dramatically effect natural flood dynamics (Toner and Keddy, 1997; Nilsson and Berggren, 2000; Tockner and Stanford, 2002). Beaver has only recently been reintroduced after being trapped to extirpation (Applegate *et al.*, 1979), and their populations remain closely managed (NJDEP Division of Fish and Wildlife, 2012). Management of fire has altered its historical frequency and intensity (Little, 1979). Such alterations of natural disturbance regimes have the potential to upset the balance of disturbance and succession and move the system from a steady-state to a transition state.

The purpose of this study was to examine the succession dynamics of Pine Barrens riverside savannas at the landscape level. The focus was on three core objectives. The first was to determine the amount of succession activity and its effect on the overall distribution of savanna: How much change to the total area of savanna has occurred over the course of the study period? how persistent is savanna within the system? and are there differences between savanna types in terms of persistence? The second objective was to describe the nature of succession dynamics within the system: What are the dominant vegetation conversions over relatively short periods of time (20 years)? what are the prevailing longer-term (60 years) succession pathways? and is the general trend consistent with linear hydrarch succession, local persistence, a shifting-mosaic, or

some other pattern? The final objective is to draw new hypotheses from these findings for future research.

Each of these questions was analyzed in multiple ways using a series of overlapping approaches. As such, methods and results are presented according to the general approach employed, rather than the objective the analysis is intended to inform. The discussion will then return the focus to interpreting the results in terms of those core objectives.

Methods

Study sites

The sites included in this study are contained within the Mullica River Basin (NJDEP/NJGS, 2006). Pine Barrens riverside savannas are currently found only in this watershed along the flood terraces of the Mullica, Batsto, Wading, and Oswego Rivers, as well as the Nescochague and Tulpehocken Creeks, and within the boundaries of Wharton State Forest. The sites included in this study are found along all of the above streams with the exception of the Wading River (Figure 1).

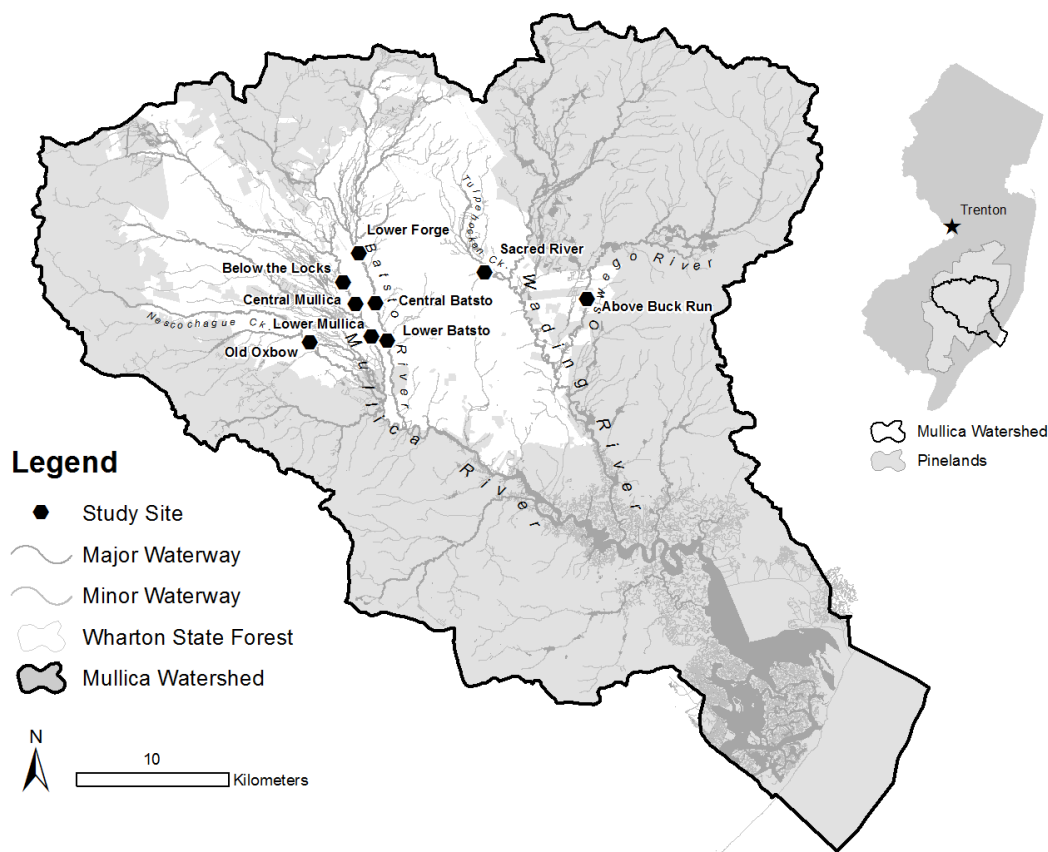


Figure 1 : Site locations. All extant Pine Barrens riverside savannas are found in Wharton State Forest which lies within mostly within the Mullica River. The nine sites included in this study are found on the Batsto, Oswego, and Mullica Rivers as well as the Tulpehocken and Nescochague Creeks. Each site may include multiple patches identified as distinct savannas in other literature. For the purposes of this study, individual patches are grouped into structurally distinct sites based on hydrography.

Study units

For the purposes of this study, three distinct functional units will be discussed: patch, savanna complex, and site. A patch is an distinct area of land cover which differs from surrounding cover in structure and function (Picket and Rogers, 1997). The patch represents a static snapshot of vegetation at a given point in time. A savanna complex consists of the combined area of contiguous savanna cover across all study years (1940, 1961-62, 1978-79, and 2002). A complex, then, represents the extent of the savanna as a system as it changes over time. A site consists of a

group of savanna complexes which are clearly separated from other complexes spatially and hydrographically--either by HUC14 level watershed boundaries or by a confluence of the savanna-associated stream with a stream of third order or higher—along with the surrounding non-savanna vegetation. A site represents a snapshot of structurally linked savanna complexes in a landscape context.

Patch boundaries were delineated from aerial photography as described below, by manually tracing the edges between visually distinct patches of vegetation cover. These were annotated with a code describing the dominant vegetation cover within (Table 2). The resulting data were then digitized and collected into a GIS using ArcInfo version 10. A minimum mapping unit of 100m² was then established. All polygons below the minimum mapping unit were selected and each was merged with the adjacent polygon with the longest shared border using the Eliminate function.

Complex boundaries were delineated by extracting all savanna patches from each study year and merging them into a single layer using the Union function. Each resulting contiguous multi-year savanna area was considered to be a savanna complex (Figure2). Breaks between savanna complexes were used to determine divisions between sites. The complex layer was overlaid with statewide river data (NJDEP/OIRM/BGIA, 1993) and HUC14 level watershed boundary data (NJDEP/NJGS, 2006). In order of delineate site boundaries, savanna complexes were then visually grouped with divisions at the boundaries of HUC14 level watersheds and at confluences involving a savanna-associated stream with a stream of third order or higher. In situations where a division at one of these points could not be made without bisecting a complex, that division was ignored. A large polygon was then digitized around each site such that it overlapped the data for all years. The vegetation data for each study year was then clipped to each site's defining polygon creating the final site boundary. The final sites for each year were then restricted to the

intersection of the collected data for all study years using the Intersect function. This ensured that the total area of each site was consistent among study years. This was done for all years for each site.

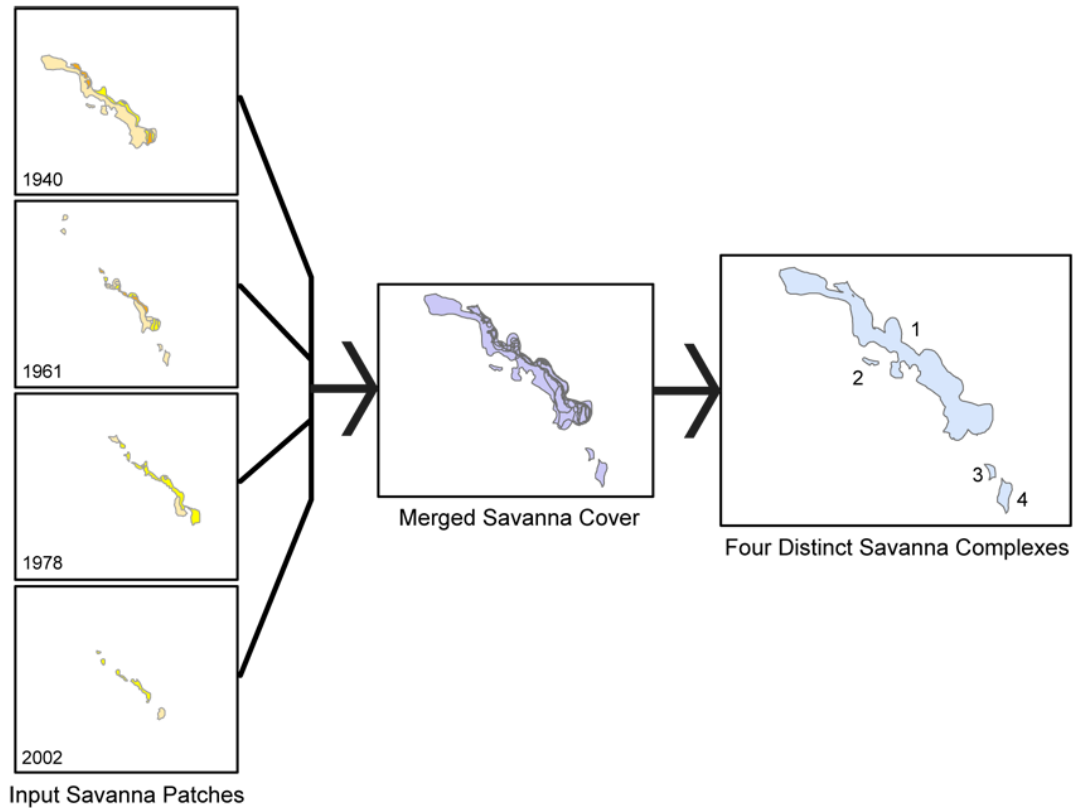


Figure 2: Summary of savanna complex delineation process. In order to capture the extent of the savanna as it changes through time, all savanna patches were extracted from the vegetation cover data from each year and merged. The final boundaries represent the full extent of each savanna as a unit which changes throughout the study period.

Vegetation delineation and identification

Vegetation patches were delineated and identified by visual interpretation of a series of aerial photographs from 1940, 1961-62, 1978-79, and 2002. A summary of the specifications of imagery used is provided in Table 1.

	Format	Scale	Time of Year	Source
1940	9"x9" transparent slide Black and white air photo	1:20,000	Leaf-off (February)	NJDEP Bureau of Tidelands Management
1961 (1962)	9"x9" transparent slide Black and white air photo	1:18,000	Leaf-off (November)	NJDEP Bureau of Tidelands Management
1978 (1979)	9"x9" transparent slide CIR air photo	1:12,000	Leaf-off (November, 78) (March, 79*)	NJDEP NJ Geological Survey
2002	Web Map Service CIR digital orthophoto	1:2,400	Leaf-off (Spring)	NJ Office of Information Technology (NJOIT) Office of Geographic Information Systems (OGIS)

*Limited use of March imagery to minimize flooding influence.

Table 1: Specifications of imagery used to delineate and identify vegetation patches.

Vegetation was classified under a simple system consisting of ten classes (Table 2). In cases of transitional cover--i.e. areas with a mixture of two or more classes--a visual estimate of percent cover of each type was made, and the patch was included in the class corresponding to the dominant cover. When a conflict between interpretation on two overlapping sheets was found, the sheet where the patch in question was situated more toward the center of the photograph was given precedence. Aerial photographs are prone to darkening and spatial distortion toward the edges of the scene, making those areas less clear and interpretation potentially less accurate.

Because of the difficulty of distinguishing precise species composition from historical aerial photographs, the six savanna communities were grouped into three general categories for this study based on broadly defined vegetation classes. **Wet savanna** is generally found in

seepage channels and wet depressions. The vegetation in these savannas is sparsely distributed, with substrate visible over much of the surface. This category consists of a single community:

Eriocaulon aquaticum - *Juncus pelocarpus* - *Drosera intermedia* Herbaceous Vegetation.

Graminoid savanna is characterized by predominantly graminoid vegetation cover with dwarf-

from *Chamaecyparis thyoides* sporadically interspersed. Included in this category are three

distinct communities: *Cladium mariscoides* - *Panicum longifolium* Herbaceous Vegetation,

Muhlenbergia torreyana - *Lobeila canbyi* - *Rhynchospora alba* Herbaceous Vegetation, and

Rhynchospora (alba, cephalantha) - *Muhlenbergia uniflora* - *Lophiola aurea* Herbaceous

Vegetation. **Shrub savanna** is characterized by a mix of graminoid and shrub cover with dwarf-

form trees interspersed. This category includes two communities: *Chamaecyparis thyoides* -

Gaylussacia dumosa - *Andropogon glomeratus* var. *glomeratus* Woodland and *Chamaecyparis*

thyoides - *Nartheceum americanum* - *Sarracenia purpurea* - *Drosera filiformis* - *Sphagnum*

pulchrum Woodland.

Class	Code
Upland	0
Cedar Swamp	1
Pine-hardwood Swamp	2
Shrub Swamp	3
Wet Savanna	4
Graminoid Savanna	5
Shrub savanna	6
Burned Land	7
Water	8
Undetermined	9

Table 2: Custom land cover classification system. This study uses a simple classification scheme consisting of 10 broad land cover classes that can be identified with relative ease from historical aerial photographs.

The baseline dataset for this study was the 2002 imagery. This imagery consisted of color-infrared orthophotography provided as a Web Mapping Service (WMS) by the NJ Office of

Information Technology (NJOIT) and Office of Geographic Information Systems (OGIS) (NJOIT/OGIS, 2002). Orthophotography is georeferenced to a high degree of positional accuracy-- \pm 4.0 ft. (1.22 m) at a 95% confidence level. As the most recently collected data, it was also possible to field validate the interpretation. Vegetation patches were delineated from the 2002 imagery by way of heads-up digitizing at an on-screen scale of 1:5000 using ArcGIS's ArcMap module and stored as feature classes in a file geodatabase. Each resulting polygon was annotated with the dominant vegetation cover of the associated patch. The perimeter and area of each polygon was calculated automatically by the software.

1961 and 1978 patch boundaries were traced directly from 9"x9" slides onto transparent Mylar sheets under a 1.75x magnifying lens. The resulting vegetation maps were then scanned at a resolution of 600 dots per inch (dpi) and georeferenced to the 2002 orthophotography. Boundaries were then digitized at an on-screen scale of 1:5000, annotated, and added to the geodatabase. Vegetation cover within patches was interpreted by both stereoscopic viewing of the slides themselves and on-screen interpretation of high resolution (600 dpi) scans of slides. Both methods have advantages. Stereoscopic viewing simulates a three-dimensional view by isolating a different angle of the scene in each eye. On-screen interpretation enables enhancement of the clarity of specific features as needed by adjusting sharpness, lightness, and contrast of the image with Adobe Photoshop and features within ArcInfo.

1940 vegetation boundaries were hand-traced and annotated according to the same method by Kathleen Strakosch Walz (Ecologist, NJ Natural Heritage Program NJDEP, Division of Parks and Forestry, Office of Natural Lands Management). These vegetation maps were also scanned at 600 dpi and georeferenced to the 2002 orthophotography. Boundaries were digitized at an on-screen scale of 1:5000, annotated, and added to the geodatabase. The original classification scheme used for interpretation of this dataset included multiple upland classes as well as

transitional or successional classes. These were simplified to match the classification scheme of the rest of the study (see Table 3).

Original Class	Code	Study Class	Code
upland forest: oak-pine, pine-oak-heath	Upf	Upland	0
upland woodland: oak	Upw	Upland	0
upland woodland: Carex; sparse	Usw	Upland	0
upland scrub	scr	Upland	0
cedar swamp	1	Cedar Swamp	1
cedar swamp; successional	1s	Cedar Swamp	1
pine-hardwood swamp	2	Pine-hardwood Swamp	2
pine-hardwood swamp; successional	2s	Pine-hardwood Swamp	2
shrub swamp	3	Shrub Swamp	3
wet savanna	4	Wet Savanna	4
graminoid savanna	5	Graminoid Savanna	5
shrub savanna	6	Shrub savanna	6
cedar swamp; burned	1b	Burned Land	7
pine-hardwood swamp; burned	2b	Burned Land	7
shrub swamp; burned	3b	Burned Land	7
water	h2o	Water	8
Unlabeled	--	Undetermined	9

Table 3: Reclassification of land cover interpretation performed by K. Walz. Aerial photograph interpretation performed by Kathleen Strakosch Walz of the NJDEP was included in this study. This dataset was simplified to match the classification scheme designed for this study.

Once digitizing was completed, all feature classes were projected from World Geodetic System of 1984 (WGS 1984) to Universal Transverse Mercator zone 18 north (UTM18N) using transformation NAD83 to WGS84 1. This transformation from geographic coordinates based on angular units to projected coordinates based on linear units allows for easier and more precise calculation of patch size.

Validation of vegetation identification

2002 imagery was field validated summer 2010. Between three and five patches of each cover class was selected based on accessibility from local sand roads. A significant span of time had

elapsed between the collection of the imagery in 2002 and field validation. To account for this, 2007 imagery was consulted to look for detectable changes in cover at sample sites. None of the sample sites had shown a detectable change in cover type. A point within each sample patch was entered into a GPS unit. Each point was then visited and the vegetation cover was determined. These updated designations were then compared against the corresponding visual signature in the 2002 imagery. The annotation was then corrected where designations associated with given visual signatures had been updated.

The 1940 imagery was interpreted by Kathleen Strakosch Walz. In order to ensure agreement between this interpretation and that of the rest of the study, several randomly selected patches were interpreted according to the methods described above for the 1961 and 1978 imagery. In all but one patch, the interpretations agreed. In addition, partial coverage of the study sites were interpreted by Ms. Walz for 1961 and 1978. This interpretation was compared with that of the interpretation preformed for this study. Again, in almost all cases the results agreed.

All of the interpretation was validated against a wide variety of additional imagery. This included extensive imagery sets of online imagery served by NETR Online (2012), New Jersey Geographic Information Network (2012), Google Earth, and Bing Maps (Microsoft Corporation, 2012), as well as prints owned by the Grant F. Walton Center for Remote Sensing and Spatial Analysis (CRSSA) at Rutgers University. While not as objective as other means of validation, including a variety of different image collection conditions (time of year, lighting, sensor technology, etc.), as well as important contextual clues from imagery collected in the period between study years, provides a more complete view of the study area and changes as they have occurred. This imagery was consulted specifically to correct for anomalies such as difficult-to-interpret patches, counterintuitive land cover conversions, and inexplicable disagreements between independent interpretations.

In order to provide some quantitative measure of the uncertainty associated with image interpretation, a direct comparison was made between the 1978 layer developed for this study with a high resolution statewide land use-land cover dataset from 1986 developed by the New Jersey Department of Environmental Protection (NJDEP/OIRM/BGIA, 1986). The two datasets used different classification schemes. In order to make the best comparison, these were combined into a single validation scheme based on the best match for each vegetation class. The specific class-by-class matches are given in Table 4. To make this comparison, the NJDEP data layer was clipped to the extent of each study site, with the exception of the Sacred River site which was completed later. The two datasets used different classification schemes. In order to make the best comparison, these were combined into a single validation scheme based on the best match for each vegetation class. The specific class-by-class matches are given in Table 4. Both the study dataset and the NJDEP dataset were then converted from vector-based feature classes to raster-based format (3mx3m cell size) The value of each cell was set equal to the numeric code associated with its vegetation cover class. These raster layers were then reclassified to remove the water class. The purpose here was to avoid disagreement between the two interpretations due to changes in surface water level, which is naturally highly variable.

1986 NJDEP DATA CLASS	VALIDATION CLASS	1978 STUDY DATA CLASS
CONIFEROUS FOREST CONIFEROUS FOREST (>50% CROWN CLOSURE) CONIFEROUS FOREST (10-50% CROWN CLOSURE) MIXED DECIDUOUS/CONIFEROUS BRUSH/SHRUBLAND MIXED FOREST (>50% CONIFEROUS WITH >50% CROWN CLOSURE) MIXED FOREST (>50% DECIDUOUS WITH >50% CROWN CLOSURE) OLD FIELD (< 25% BRUSH COVERED)	Upland	UPLAND
ATLANTIC WHITE CEDAR SWAMP	Cedar Swamp	CEDAR SWAMP
CONIFEROUS WOODED WETLANDS DECIDUOUS WOODED WETLANDS MIXED FORESTED WETLANDS (CONIFEROUS DOM.) MIXED FORESTED WETLANDS (DECIDUOUS DOM.) DECIDUOUS SCRUB/SHRUB WETLANDS	Non-Cedar Swamp Wooded Wetland	PINE-HARDWOOD SWAMP
CONIFEROUS SCRUB/SHRUB WETLANDS MIXED SCRUB/SHRUB WETLANDS (CONIFEROUS DOM.) MIXED SCRUB/SHRUB WETLANDS (DECIDUOUS DOM.)	Shrub Wetland	SHRUB SWAMP SHRUB SAVANNA
HERBACEOUS WETLANDS	Herbaceous wetland	WET SAVANNA GRAMINOID SAVANNA
ARTIFICIAL LAKES STREAMS AND CANALS	Water	WATER
OTHER	Other	BURNED UNDETERMINED

Table 4: Classification scheme for validation of imagery interpretation. This classification scheme was designed for the closest match of classification schemes of this study and that of 1986 NJDEP land cover classification data in order to validate accuracy of aerial photo interpretation.

A simple raster subtraction was applied in which the numeric code corresponding to the land cover class of each cell in the 1978 dataset is subtracted from that of the spatially corresponding cell in the 1986 dataset, resulting in a new raster layer with cell values equal to the results of this subtraction. Those cells with a value of zero indicate agreement between the interpretation of the two datasets, while those cells with nonzero values indicate disagreement. The total and proportional area of agreement was then calculated for each site and the mean percent agreement across sites was calculated.

Full results are presented in Table 5. The mean agreement between the interpretation used in this study and that of the 1986 NJDEP data was approximately 66.9% ($SD = 8.7\%$). Differences in the image interpretation process and in the imagery itself may explain much of the residual disagreement between the two datasets. First, and probably most significant, is the difference in

classification schemes. The NJDEP data is designed to incorporate the broader spectrum of land cover than that of this study. Some classes simply do not match neatly between the two systems. Also, the minimum mapping unit of the NJDEP data is approximately one hundred times that of the study data. Thus some areas may disagree simply because the patch was omitted from the NJDEP data as too small. Additionally, the two sets of imagery are eight years removed from one another and conditions on the ground are likely to have changed considerably in the interim. Bearing these factors in mind, and accepting that this is the best available dataset for comparison, this level of agreement was deemed acceptable.

	abrun	centbat	centmul	locks	lowbat	lowfrg	lowmul	ooxb
<i>Agreed Area (cells)</i>	49,471	26,152	10,376	10,503	46,928	22,912	23,220	35,272
Total Area (cells)	63,455	44,531	14,299	14,597	66,107	41,343	41,125	49,468
% Agreement	77.96	58.73	72.56	71.95	70.99	55.42	56.46	71.30

Table 5: Results of comparison between 1978 aerial photograph interpretation and 1986 land cover dataset developed by NJDEP. In order to develop some quantitative validation of aerial photo interpretation, the 1978 land cover dataset developed for this study was compared against a land cover dataset developed by NJDEP for the year 1986. The level of agreement varied among sites, with a mean value of 66.9% ($SD= 8.7\%$). Given differences between the two datasets in terms interpretation process and the span of time between the two datasets, this level of agreement was deemed acceptable.

Assessment of spatial precision

In order to determine the spatial precision of the data, variation among the recorded position of detectable landmarks among study years was measured. Sand road intersections were used as reference points, being both relatively static and widespread. Each intersection was converted to a point. From this full set of points, those that represented intersections that were recorded in all four study years were selected, producing a total of six reference intersections*. The points corresponding to each of these six intersections in each year were then merged into a single

* This number is low because narrow sand roads are often obscured by foliage. As these intersections are the most dependable reference points for georectifying datasets, those intersections that were obscured were omitted from the data to avoid distortions caused by spurious reference points.

dataset. For each intersection the mean distance between points was determined, and a grand mean calculated.

The grand mean was 14.9m. Thus, for any given point in the data, it can be expected that on average it will be 14.9m from the corresponding point in any other year. To put it more clearly in the context of this study, this can be viewed as a 14.9m zone of uncertainty at the boundary of each vegetation patch.

Net distribution change analysis

To determine the amount of change in savanna area at the site level, a simple summary table was generated to calculate the total area of each land cover class in a given study year for each site.

The change in coverage area of each land cover class from one study year to the next was calculated both in terms of difference in total area ($A_0 - A_1$) and as percent change $((1 - (A_1/A_0)) * 100)$. These calculations were made both at the site level and across all sites. In addition, changes to the number and mean area of savanna patches were calculated.

Conversion analysis

Looking at the changes in area of each land cover class at the site level, it is possible to determine if there is an increase in Class A and a decrease in Class B, not whether this is a result of Class A replacing Class B. This provides general insight into the rate and direction of vegetation change within the landscape, but not the amount of succession activity or the conversions involved. In order to analyze specific conversions between land cover classes, a spatially explicit change detection model was developed using the ModelBuilder module in ArcInfo.

The model was designed to take advantage of simple raster algebra, which provides more flexibility and faster processing speeds than similar vector-based techniques. Each dataset is first converted from vector to raster format with a cell size of 3x3m. Each resulting raster is then broken out into a series of binary rasters for each class, in which each cell falling within a patch of the given class is given a value of 1, and all other cells a value of 0. Each binary raster for a given year is then multiplied by the binary raster for each class in the subsequent study year's data (in order to simplify interpretation and reduce processing time, non-savanna to non-savanna conversions were excluded). This results in forty-eight individual change classes and three persistent classes, each with their own binary raster. Each change class is then given a unique value by replacing 1 values in its with a numeric code. Finally these binary rasters are combined into a single layer to produce a map of all specific vegetation conversions between the two study years in question.

In many cases this process leaves artifacts in the form of small, often linear, clusters of cells at the edges of larger conversion areas. To eliminate these artifacts, clusters of less than ten cells (90m²) were selected and removed using the Region Group and Nibble functions. The Region Group function aggregates contiguous groups of cells of the same value (in this case change class) into clusters or regions, each with a unique identifier. Specific regions may then be selected for elimination (in this case regions of less than ten cells in area) and the raster reclassified, the values of these cells are then replaced with a null value. The Nibble function then replaces those null values with the value of the nearest non-null cell.

Finally, the total area of each change class was calculated for each site at each time step. These results were then summarized to determine dominant change classes by calculating the percent of total change area accounted for by each change class, both at the site level and study-wide.

To determine the amount of short-term conversion activity, the area associated with a given savanna class that was lost by conversions to another class (loss), was gained by conversion from another class (gain), or remained in place (persistence) was calculated. Persistence, gain and loss were calculated both as total area change (in square meters) and as percent change across each time step.. Loss, gain, and persistence were then calculated for each individual conversion to provide a more specific view of conversion trends. These results are summarized in Figures 13 and 14.

Succession pathway analysis

To analyze succession pathways, 500 sample points were randomly selected from the combined savanna complex boundaries for all sites. The vegetation cover found at each point was determined for each study year and compiled into a single point dataset by intersecting the sample point layer with the vegetation polygon layer for each study year. The attribute table was then exported and summarized.

To determine dominant succession patterns associated with each savanna class, the ten most frequently occurring vegetation sequences were isolated for each (Tables 9 and 10). These were then plotted, vegetation class against time (Figure 15). The thickness of the line indicates the number of points that underwent a given conversion--or remained the same class-- from one study year to the next. Sequences of conversions were interpreted as dominant pathways if they were found in a conspicuously high number of sample points or appeared to indicate a repeating pattern.

To get a sense of the long-term persistence of each savanna class, a simple tally system was used. The number of sample points matching a given vegetation class in no more than one

consecutive study year were tallied, then those persisting for two consecutive study years, then three, then four (Figure 16 and Table 11). It is important to clarify that these data are not presented in terms of cumulative change over time, which is addressed elsewhere in this study, but rather the total number of sample points found to persist for a given duration regardless of where the period of that duration begins and ends. This avoids the effect of loss of savanna in one location being masked by gain at another location, or vice versa.

Adjacent vegetation analysis

In order to determine the composition of vegetation adjacent to a given savanna class, all patches of a target savanna class were selected, and 1-meter buffer was created around each. The site-wide vegetation dataset was clipped to this buffered area. Percent cover of each vegetation class within each buffer was then calculated. Edge patches with significant buffer area that lay outside of the original study area were removed to avoid artificially altering values by omitting unknown cover.

To calculate the change in patch area across each time step, vegetation data from the end of the time step (end-year) was laid over the savanna patch vegetation from the start of the time step (start-year). Patches of the target class in the end-year data that significantly overlapped patches of the same class in the start-year were then extracted. Patches were considered to overlap only if at least 50% of the smaller patch lay within the boundary of the larger patch. In cases where a single patch in the start-year was fragmented into multiple patches in the end-year, the area of all fragments was included. Conversely, in those cases where multiple patches in the start-year dissolved into a single patch in the end-year, all patches were combined and treated as a single patch. Finally, percent change in the patch area across the time step was then calculated.

Due to limitations of the data--which do not fit the underlying assumptions of traditional statistical analysis--correlations were assessed using parallel coordinate plots. This method allows for the visualization of multivariate data of n variables by expanding the n -dimensional hypervolume concept; laying each axis of the hypervolume in parallel series. A line representing each study unit (a savanna patch in this case) is produced from a series of segments drawn between that unit's value for each variable. Correlations may then be detected by highlighting those lines that have a range of values in a variable of interest (e.g., percent change in patch area) and looking for consistent clustering of values in some other variable or variables (e.g., the percent of adjacent area covered by a given vegetation class).

Results:

Net distribution change analysis

Study-wide, savanna saw a steady decline of total area from ~110.9 ha to ~31.8 ha--a 71.32% loss--over the study period. Wet savanna saw the most rapid decline (89.32% loss), and graminoid savanna the slowest (59.98% loss), with shrub savanna in the middle (73.28% loss), see Table 6. In each case the trend is a generally linear decline, with the exception of a small introduction of wet savanna between 1978 and 2002 (Figure 3).

Class	1940	1961	1978	2002	1940-2002 Change (m ²)	1940-2002 Change (%Δ)
Wet Savanna	230,339	82,280	5,671	24,369	-205,970	-89.42
Graminoid Savanna	427,118	285,032	282,118	173,086	-254,032	-59.48
Shrub savanna	451,746	371,634	201,238	120,709	-331,036	-73.28
TOTAL	1,109,203	738,946	489,028	318,164	-791,039	-71.32

Table 6: Study-wide change in savanna area by class. There was an overall decline in total savanna area of over 71% between 1940 and 2002. Wet savanna saw the most dramatic decline of nearly 90%, followed by shrub and graminoid savanna.

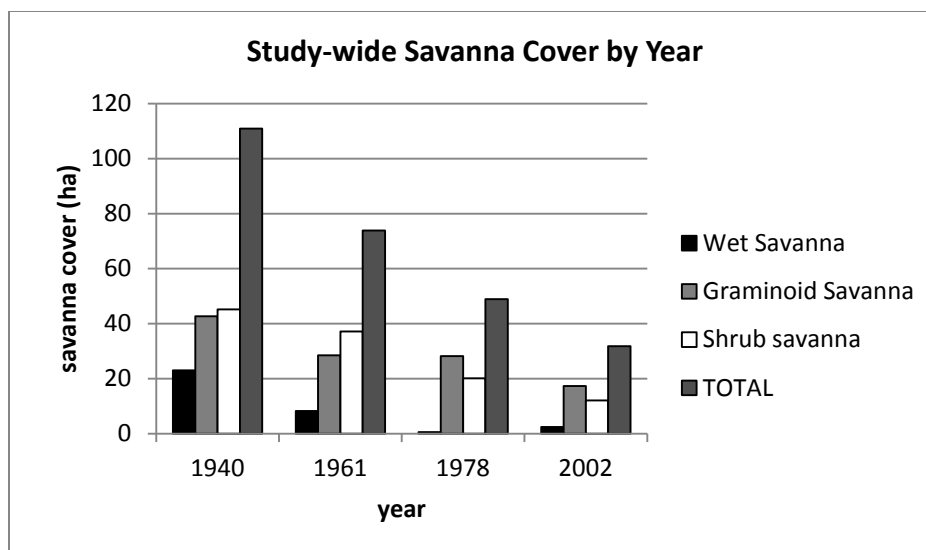


Figure 3: Study-wide savanna cover by year. Study-wide, declines in savanna area followed a generally linear pattern both for total savanna and for each individual savanna class (one exception being a slight increase in wet savanna between 1978 and 2002).

Figure 4 shows some significant observable differences among sites in terms of patterns of change. These differences appear to be largely reflective of the initial distribution of each savanna class across the study area rather than differences in patterns of how those distributions change. The general pattern of change is fairly consistent: a linear decline of the predominant vegetation class coupled with an increase of drier savanna classes as wetter classes decline; these drier classes then declining in turn.

Differences in distribution appear to be largely based on the stream association rather than downstream gradient. Most strikingly, the vast majority of wet savanna is found in sites along the Mullica River (Below the Locks, Central Mullica, and Lower Mullica). In fact, the general study-wide patterns concerning wet savanna are driven predominantly by the Lower Mullica Site which contained %74 percent of all wet savanna study-wide in 1940. Graminoid savanna was generally prominent throughout the study period in sites along both the Mullica and Batsto (Lower Forge,

Central Batsto, and Lower Batsto) but less so on the Nescochague (Old Oxbow), Oswego (Above Buck Run), or Tulpehocken (Sacred River). Shrub savanna was moderately common at all sites.

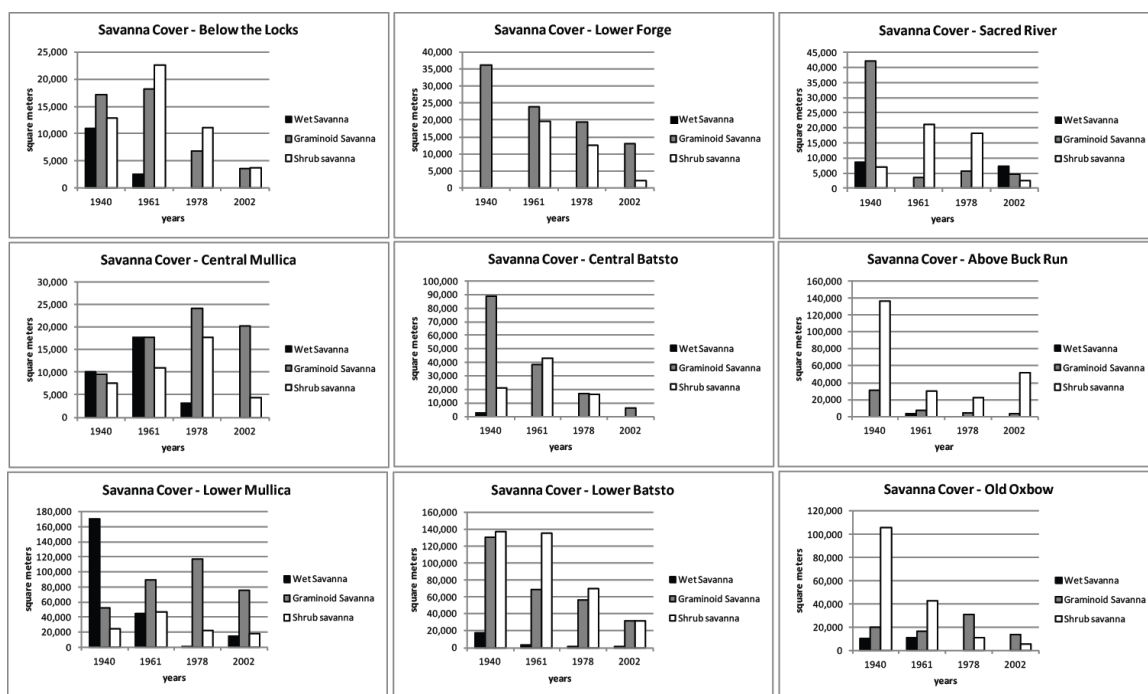


Figure 4: Site-level savanna cover by year. When broken down to the site level, the simple pattern of linear decline seen at the study-wide level becomes much more complex. Here, the most common pattern shows early succession communities declining along with an increase and subsequent decline later succession communities. Differences among sites appear to be driven for the most part by the distribution of savanna at the site at the beginning of the study period rather than differing extrinsic conditions.

Determining changes at the patch level was difficult due to the high level of variability in the size of individual patches (Figure 5). When comparing changes in patch size with changes in patch count (Figure 6) it is possible to begin to form some inference into the patch level dynamics. In the cases of graminoid and shrub savanna we see the two trends inverted; mean patch size declining through 1978 with a small increase in 2002, while the patch count increases through 1978, and dropping off at 2002. This would appear to indicate an increase in the number of small patches. There are three possible explanations for this: fragmentation of larger patches, addition

of small patches via savanna-to-savanna conversion, or introduction of small patches of new savanna converted from non-savanna vegetation.

In the case of wet savanna, on the other hand, the trend is the same for both patch size and number of patches as well as total area: a decline through 1978 with a small but significant increase at 2002. This would appear to indicate a general shrinkage of patches with smaller patches being lost faster than they are replaced by fragmentation. Again, it is important to note that the high degree of variability in patch size makes any conclusion drawn from results an educated guess at best.

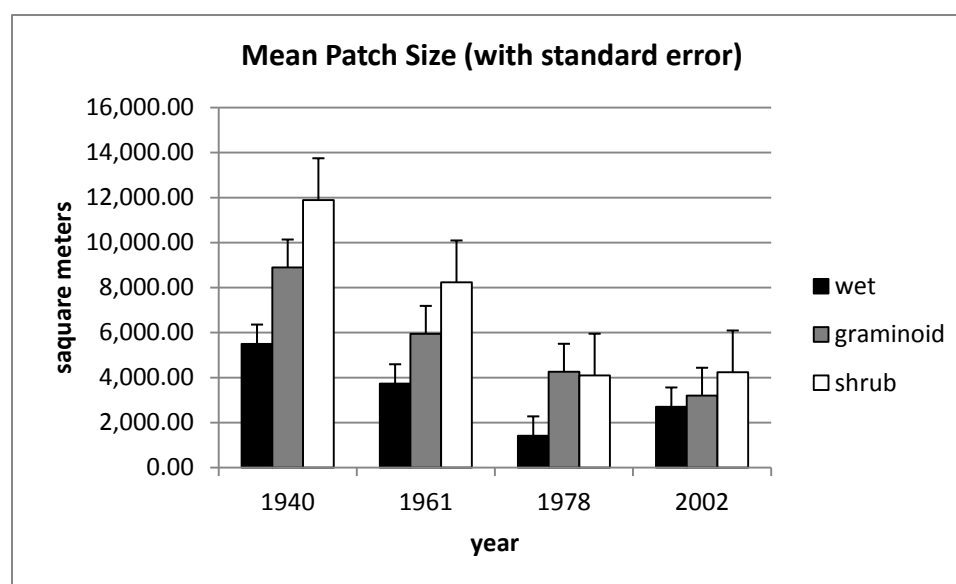


Figure 5: Study-wide mean patch size by year. The general trend in mean patch size is remarkably similar to the general trend in overall savanna distribution. However, the high variability in patch size makes drawing any definitive conclusions about how changes in mean patch size drive changes in distribution difficult.

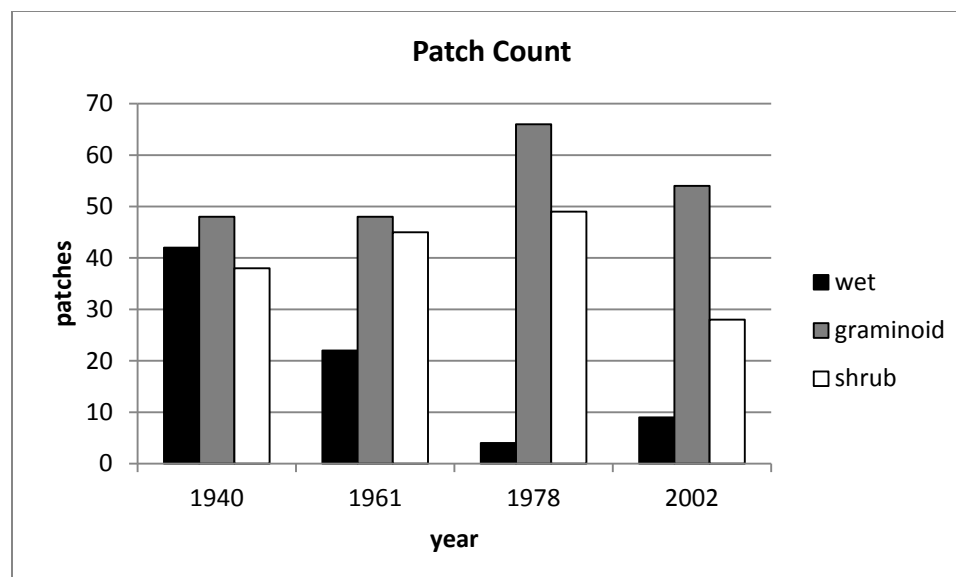


Figure 6: Study-wide patch count by year. Patch count presents two diverging patterns. The number of wet savanna patches follows a strikingly similar pattern to the mean patch size and total area of that class. This suggests a general shrinkage of patches. Graminoid and shrub savanna, on the other hand show an initial linear increase in the number of patches as opposed to a linear decline in total area and patch size. Possible explanations for this include fragmentation, addition of small patches via savanna-to-savanna conversion, or introduction of small patches of new savanna.

Looking at the vegetation sequence maps in Figures 7 through 12, there are a few consistent patterns of note. In the case of shrub savanna, rates of conversion vary somewhat, but long-term persistence is rare. The conversion process appears to occur by incursion of trees into the area causing fragmentation or partial fragmentation to the patch--an effect only detectable in large patches. The apparent variability in conversion of shrub savanna to forested swamp appears to be a reflection of differences in the time since conversion from graminoid to shrub savanna. This effect is well illustrated in the Lower Batsto site (Figure 7). In the 1940 image the lower half of this site contains a number of graminoid savanna patches embedded within or adjacent to patches of shrub savanna. As time progresses, these areas are among the last to convert to cedar swamp. Those patches that convert from graminoid savanna after 1961 remain shrub savanna even into 2002. There does also appear to be a difference in rates of conversion among sites, as is seen

when comparing the Lower Batsto site with the Lower Mullica site (Figure 12), where the conversion from wet savanna through shrub to cedar swamp appears to be much more rapid.

Aside from conversion from wet and graminoid savanna, patches of shrub Savanna have in some cases been introduced to areas that were previously occupied by forested swamp. The two most notable cases of this are in the Lower Forge (Figure 8) and Above Buck Run (Figure 9) sites. In both cases large patches of graminoid savanna are introduced, Lower Forge in 1961 and Above Buck Run in 2002. In both cases, evidence of fire in surrounding upland area is present. This would indicate a strong possibility of shrub savanna acting as an early post-fire successional stage.

While many graminoid savanna patches are short-lived, others are quite stable, persisting throughout the study period. Notice in the Lower Batsto site (Figure 7) the large linear patch of graminoid savanna in the western-central area of the site--known as Long Savanna--and the smaller patch near the upstream end--known as Savanna Verde--are highly stable, persisting with little change throughout the study period while other sizeable patches are converted to shrub savanna or cedar swamp early on. While Long Savanna is one of the largest savanna areas in the study at $\sim 45,000 \text{ m}^2$ at its peak in 1961, patch size appears not to be a major factor in maintaining these stable patches. This is well illustrated at the Above Buck Run site (Figure 9). This is a highly active site in terms of savanna-related conversions, with large patches of both graminoid and shrub savanna lost, yet one small patch ($\sim 2000 \text{ m}^2$ in 1940) persists with little change throughout the study period. A similar pattern occurs at almost every site to varying degrees. It is important to note that even the most persistent savannas appear to be undergoing a slow process of shrinking and fragmentation by conversion directly to cedar swamp (see Figure 8).

Wet savanna appears to be short-lived as a rule. Wet savanna may be maintained within the landscape by introduction of new patches where flooding occurs. A good example of this are seen in the Sacred River site (Figure 10), where we see several patches of wet savanna lost by 1961

but a sizable new patch introduced in 2002 in an area appearing as open water in both 1961 and 1978. A similar pattern is seen at the Central Mullica site (Figure 11).

The dramatic study-wide loss of wet savanna is dominated by the Lower Mullica site (Figure 12). In this case, almost the entire downstream half of the site is composed of wet savanna in 1940. By 1961 the vast majority of this had converted to shrub or graminoid savanna. By 2002 essentially the entire area has converted to cedar swamp. During this time the upstream half of the site underwent a much slower conversion wherein wet savanna intermixed with patches of graminoid savanna converts to highly stable graminoid savanna, most of which persists throughout the study period. Consulting an expanded collection of imagery shows evidence of dramatic flooding in 1931 and again in 1940--observed in a different set of imagery (NETR Online, 2012). In this imagery, there appears to be a dam or some other obstruction creating a sizeable impoundment covering the downstream half of the site. This area may have been covered by water for a period of many years, while the upstream half of the site appears to be almost entirely above the water level.

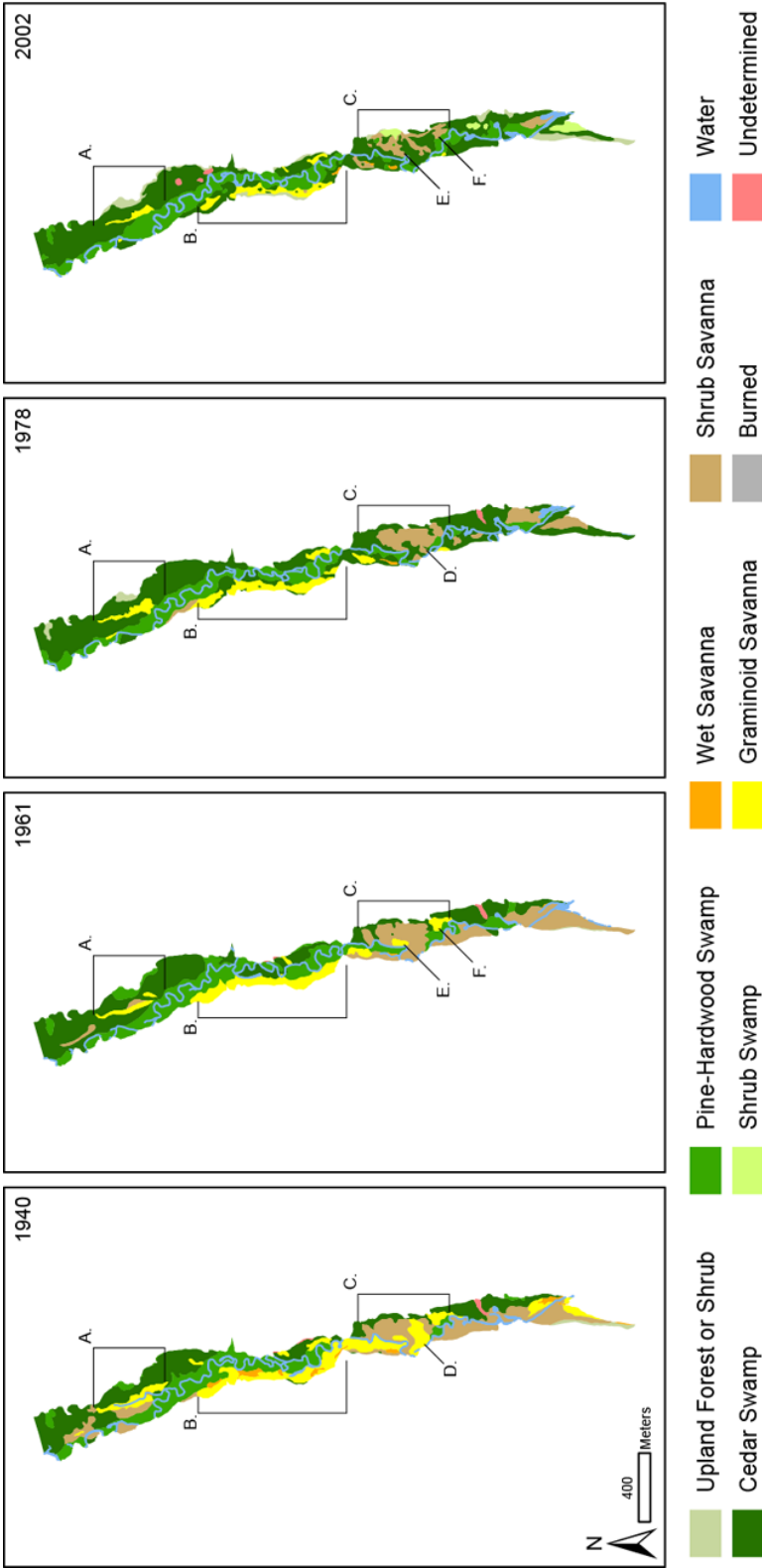
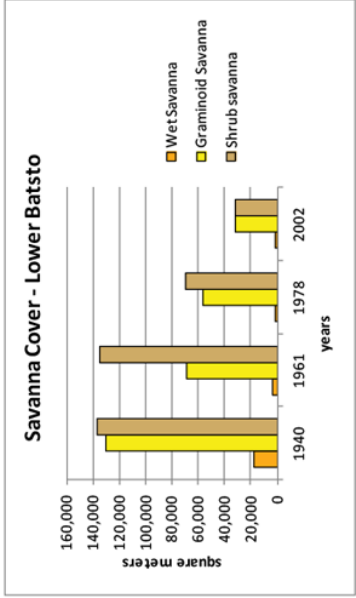


Figure 7: Vegetation sequence of the Lower Batsto site
A and B: Savanna Verde (A) and Long Savanna (B) are highly stable savannas, showing much greater persistence than other savanna within the site. Such highly stable savannas are distributed throughout the study area, and vary greatly in size (see Figure 9). In all cases they are dominated by graminoid savanna.
C: This group of patches illustrates a conversion pattern common in large areas of shrub savanna. It appears that time since conversion from graminoid savanna drives variations in the apparent. Notice that the patches at D, E, and F persist remain in a shrub state for between 40 and 60 years.



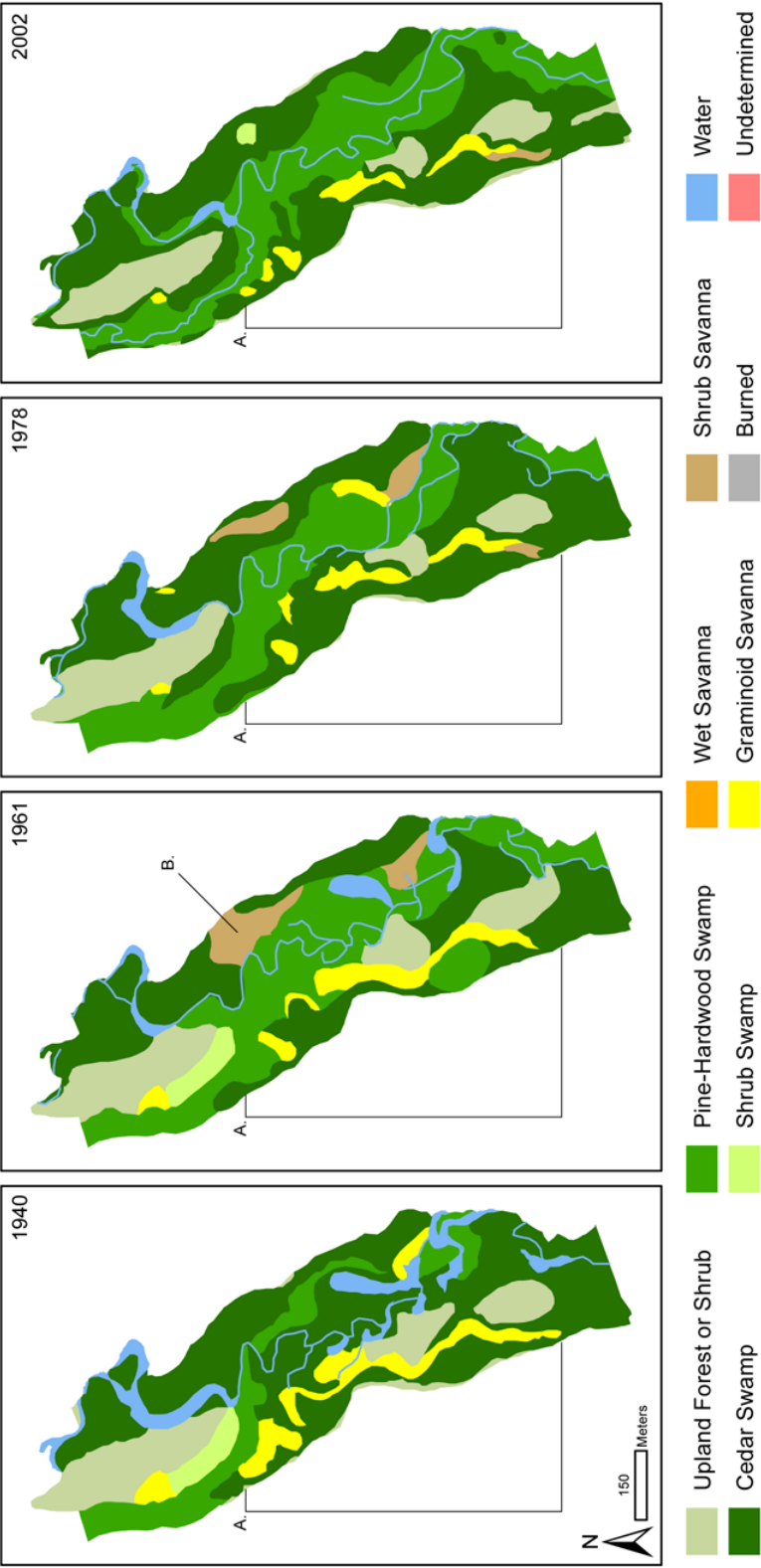
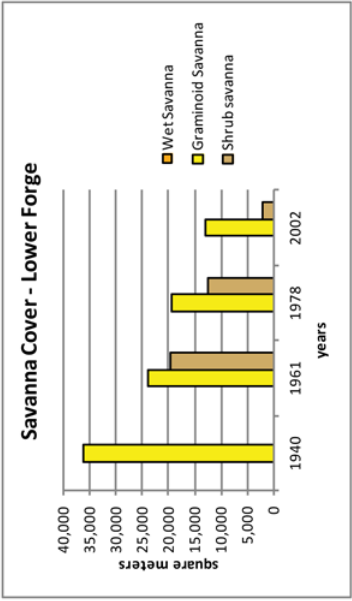


Figure 8: Vegetation sequence of the Lower Forge site

A: Stable graminoid savanna, while considerably more persistent throughout the study period, is still subject to considerable loss through the incursion of tress around the margins. This causes shrinkage and fragmentation of long narrow patches.

B: This sizable introduction of shrub savanna is associated with evidence of fire in the uplands east of the site.



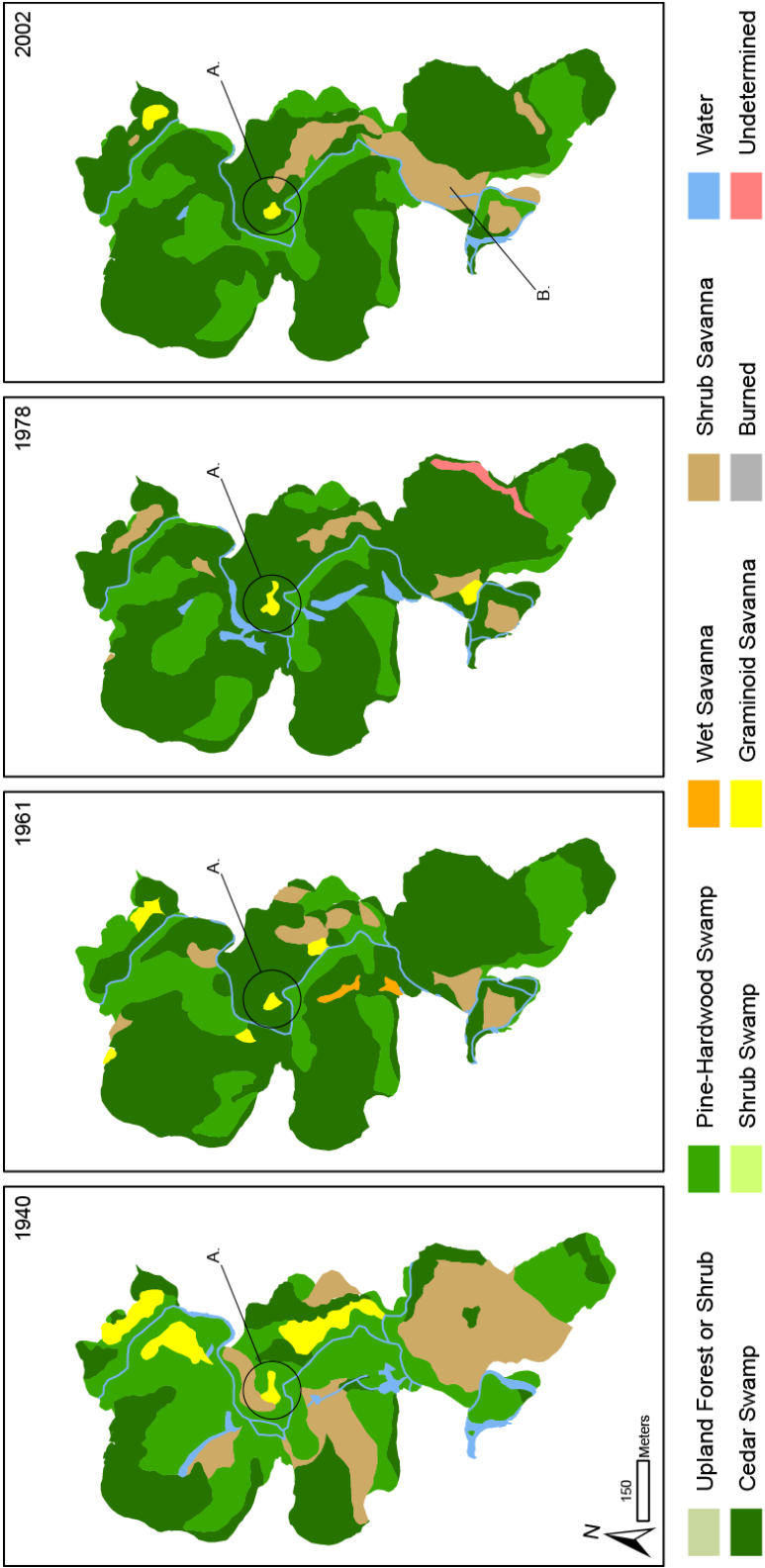
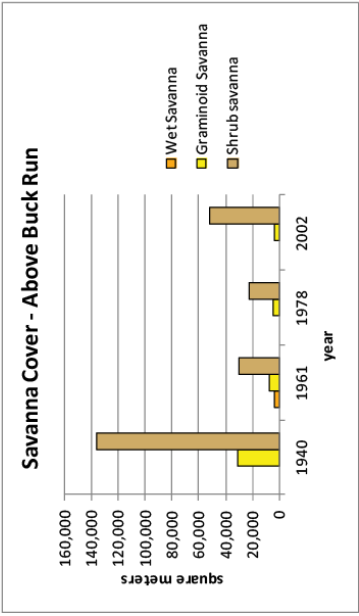


Figure 9: Vegetation sequence of the Above Buck Run site

A: While many highly stable savannas are quite large, size does not appear to play a major role in their persistence. Compared with Long Savanna (Figure 7) which reached a peak patch size of ~45,000 m² this patch--a modest 2000 m²--shows the same degree of persistence while surrounded by rapid and dramatic succession activity.

B: This sizable introduction of shrub savanna is associated with strong evidence of fire in the surrounding upland vegetation. A similar introduction occurred at the Lower Forge site (Figure 8) between 1940 and 1961, also associated with evidence of fire.



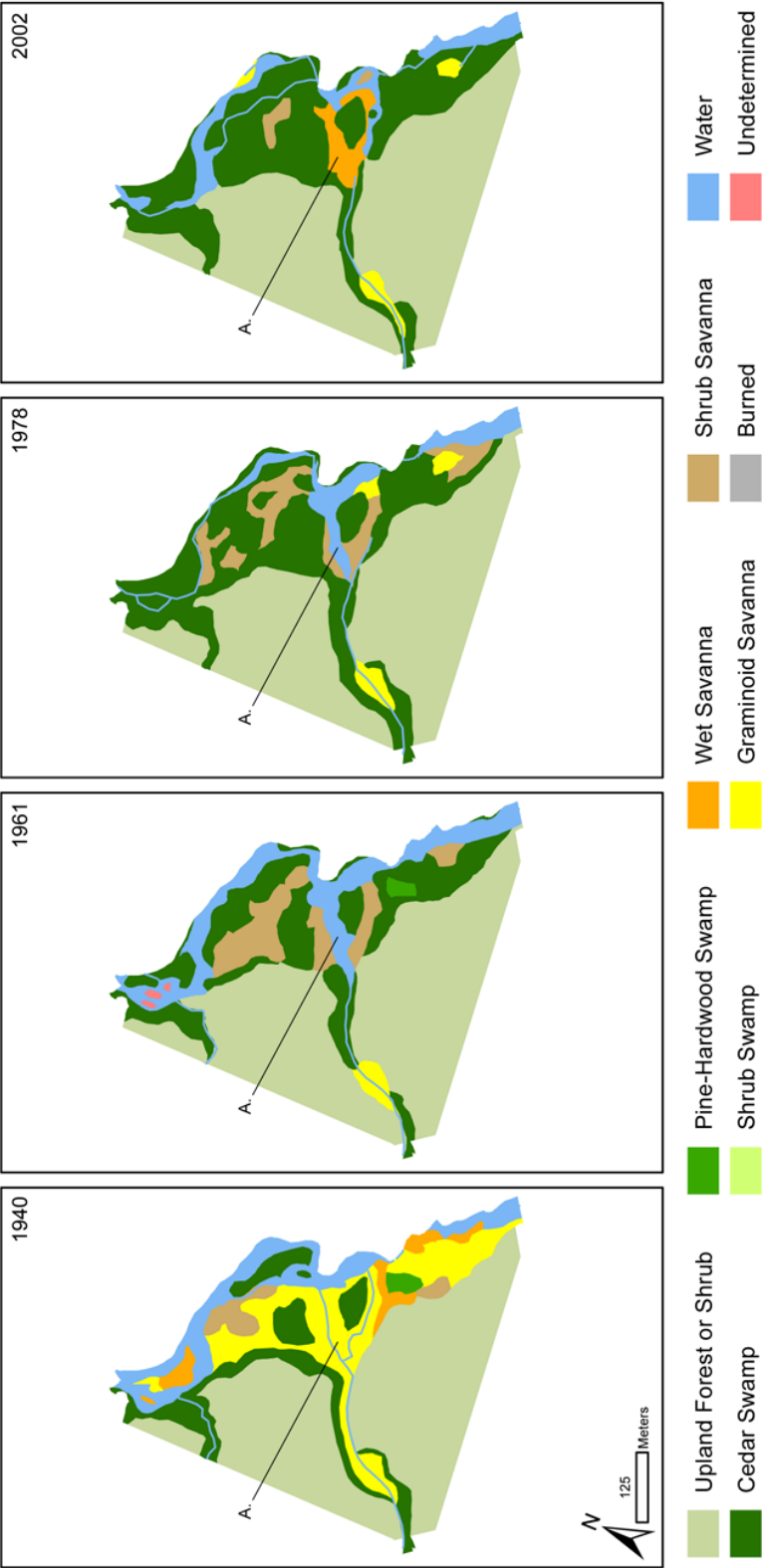
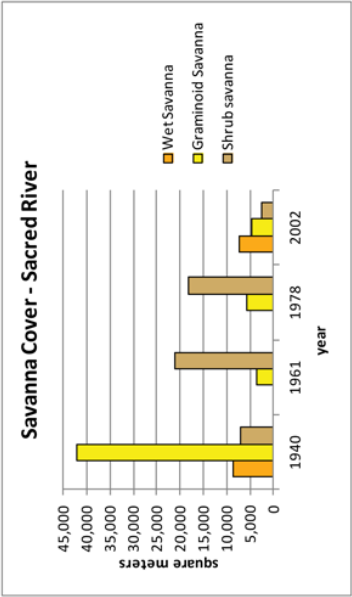


Figure 10: Vegetation sequence of the Sacred River site

A: While the overwhelming trend in this site is rapid loss of savanna, a large introduction of wet savanna occurs at this periodically flooded confluence.



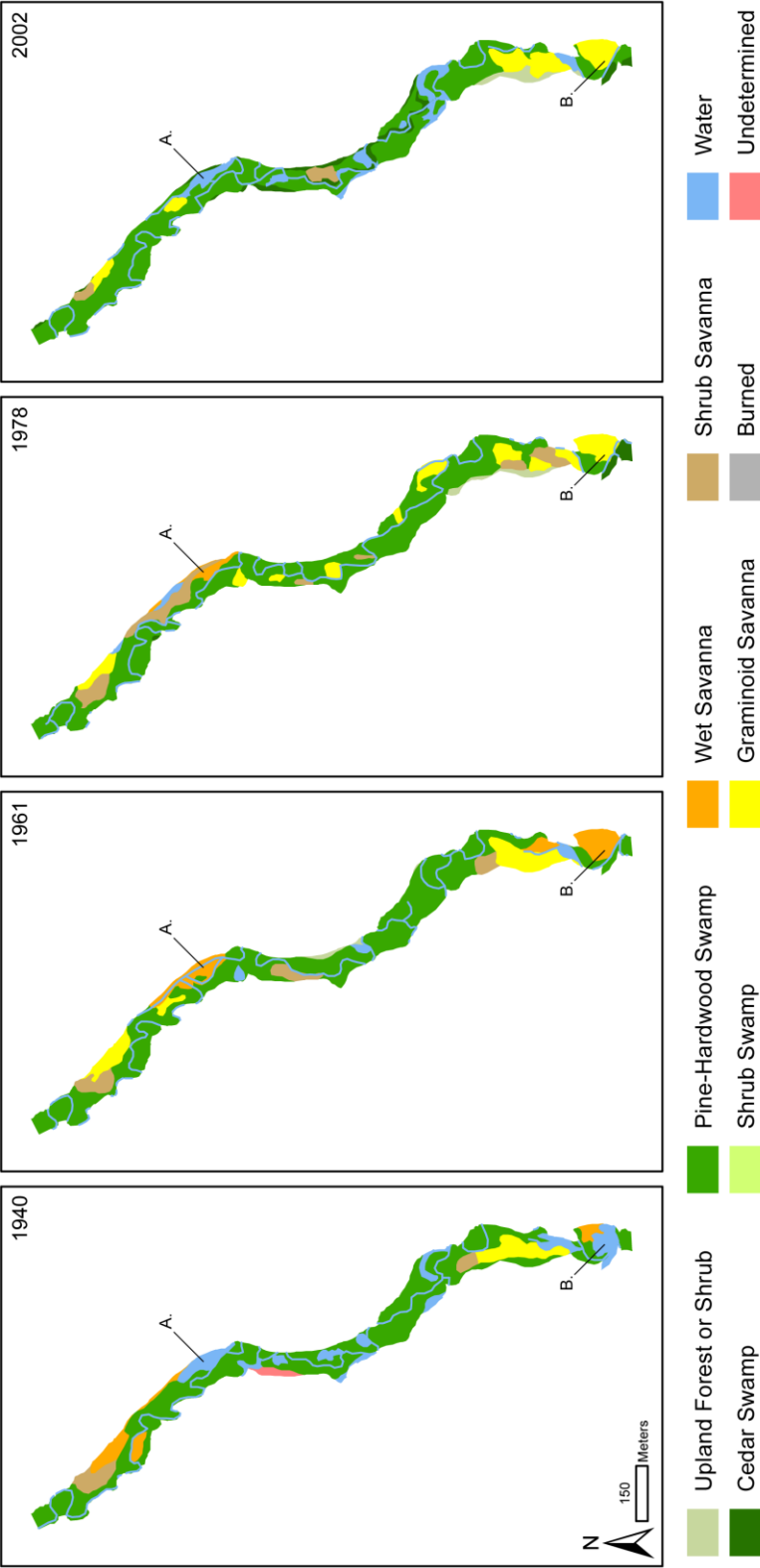
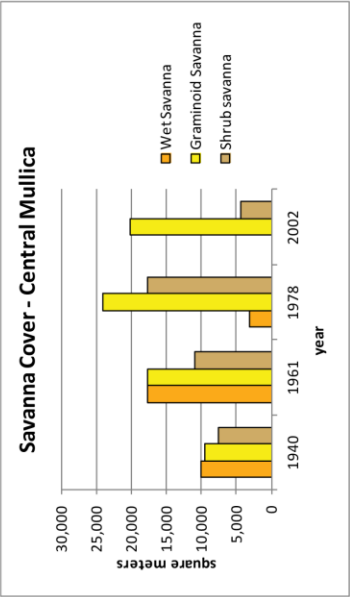


Figure 11: Vegetation sequence of the Central Mullica site

A: This small, periodically flooded location appears to maintain one of the most persistent patches of wet savanna in the study.

B: This flood event is followed by introduction of wet savanna which converts to what appears to be a patch of highly persistent graminoid savanna. This may indicate that the stability such communities is not harmed by common disturbance, but will return as the dominant persistent vegetation in time.



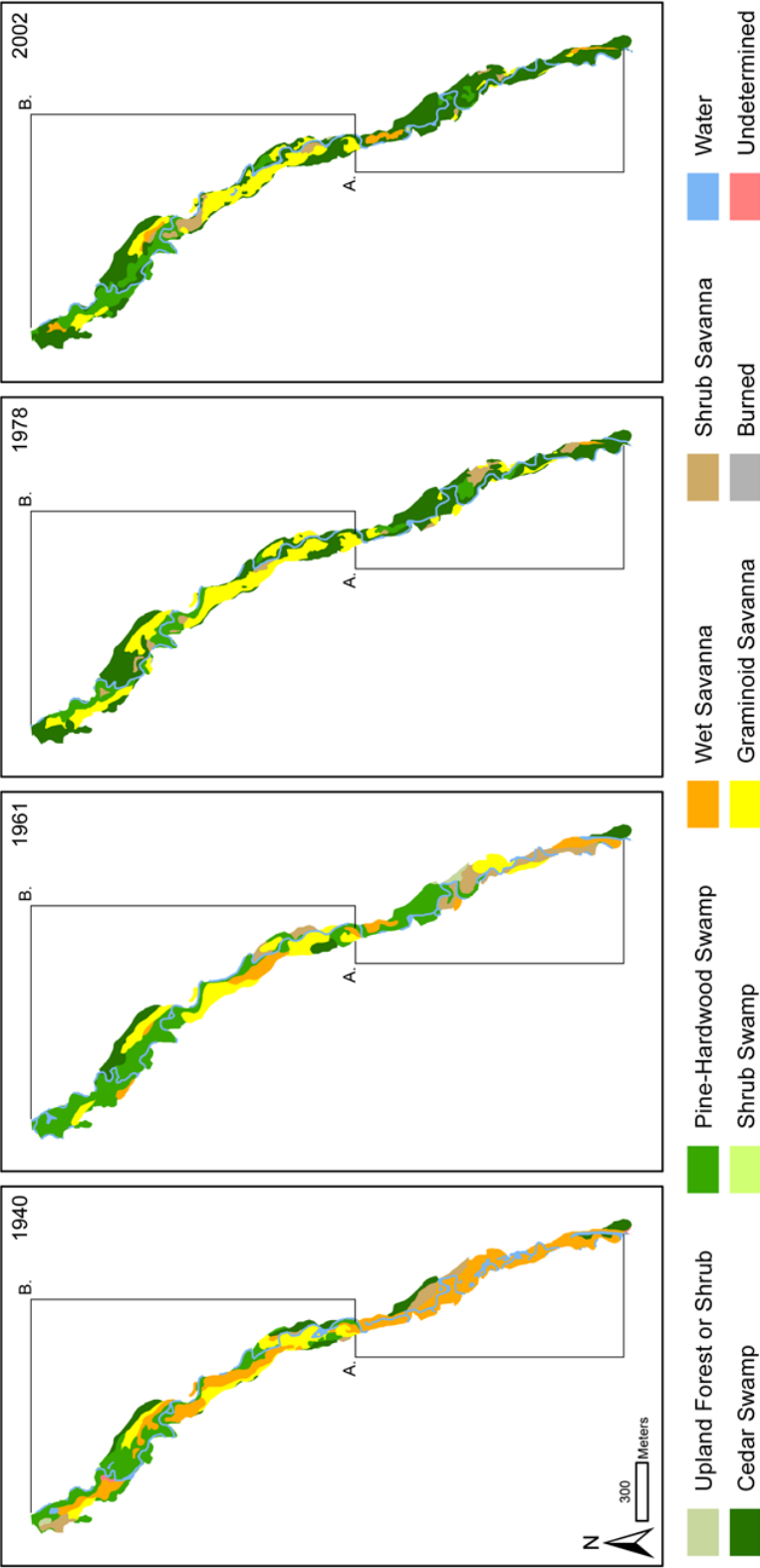
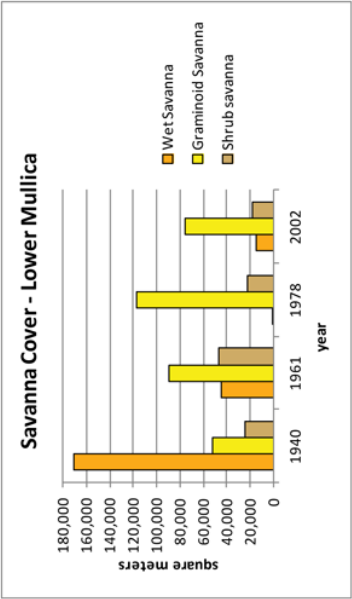


Figure 12: Vegetation sequence of the Lower Mullica site

This site dominates the succession dynamics of wet savanna observed in this study. Examination of an expanded set of aerial photographs indicates that the site was impacted by a dramatic flood event in 1931.

A: During the 1931 flood, this portion of the site was almost entirely covered by open water. Observe that the dominant cover of this area in 1940 was wet savanna, and that it underwent rapid succession such that by 2002 very little savanna remained.

B: By contrast, the upper portion of the site saw much less widespread flooding. In 1940, this site is dominated by a mix of wet and graminoid savanna, developing into highly stable



Conversion analysis

Table 7 summarizes the overall change dynamics for each savanna class in terms of gain, loss, and persistence. This reiterates a number of those patterns found above; in particular: There is a general pattern of net loss of each class from study year to study year (the single exception is an increase in wet savanna in the 1978-2002 period*), graminoid savanna consistently shows higher short-term persistence than either shrub or wet savanna, and introduction of new patches of each savanna class does occur. In addition, it shows a much more variable and dynamic process underlying the relatively linear downward trends seen in Figure 3. Rather than a simple progressive loss of each class, large areas of loss are offset by often considerable gains in other locations. The amount of loss and gain tends to be quite variable.

		1940-1961				1961-1978				1978-2002			
		persistent	gain	loss	net	persistent	gain	loss	net	persistent	gain	loss	net
Wet Savanna	m ²	38,943	43,317	191,385	-148,068	3,294	2,367	78,966	-76,599	1,530	22,878	4,131	18,747
	%	16.91	18.81	83.09	-64.29	4.00	2.88	96.00	-93.12	27.03	404.13	72.97	331.16
Graminoid Savanna	m ²	169,614	115,317	257,184	-141,867	147,897	133,677	137,034	-3,357	139,599	33,651	141,975	-108,324
	%	39.74	27.02	60.26	-33.24	51.91	46.92	48.09	-1.18	49.58	11.95	50.42	-38.47
Shrub Savanna	m ²	143,937	228,159	307,665	-79,506	95,706	105,732	276,390	-170,658	42,390	78,264	159,048	-80,784
	%	31.87	50.52	68.13	-17.61	25.72	28.42	74.28	-45.86	21.04	38.85	78.96	-40.10

Table 7: Study-wide gain, loss and persistence of savanna by class. As seen above (table 6), net changes in savanna area study-wide were dominated by losses across each time step. Looking at actual losses and gains reveals a highly active system with large losses offset by significant introductions of each class at other locations. Local short-term persistence tends to be low to moderate with graminoid savanna consistently showing the greatest persistence.

This variability is even greater when viewed at the site level. Table 8 shows the same gain-loss dynamics broken down by site. The losses and gains in each class vary greatly among sites. Some sites, in fact, see considerable net gains, while others see losses. Losses without some compensating gain are rare, occurring in only five cases; each case leading to the complete

* This is largely the effect of a small starting size, of only 5,661 m²--distributed across the study area encompassing 3.6×10^6 m². The majority of this initial pool is actually lost with only 1,530 m² persisting. The increase in area is mostly from the introduction of new patches in two sites: Sacred River (figure 10) and Lower Mullica (figure 12). Despite this late increase, the total area of wet savanna is ~60,000 m² less than in 1961, and ~210,000 m² less than in 1940.

removal of that class from the site. Gains without accompanying losses are even more rare, occurring only in three cases. In each case these gains represented introduction of the class to the site where none existed at the start of the time-step.

One additional pattern worth noting involves the changing distribution of wet savanna. As time proceeds, wet savanna is completely removed from an increasing number of sites. By 2002 wet savanna was present at only three of the nine sites. Despite net gains at these sites, the remaining area at each site is well within the range of area lost at that site in previous years (Lower Mullica: 15,354 m² remain, greatest 20 year net loss was 126,261 m²; Lower Batsto: 1,791 m² remain, greatest 20 year net loss was 14,022 m²; Sacred River 7,119 m² remain, greatest 20 year net loss was 8,577 m²).

			1940-1961				1961-1978				1978-2002			
			persistent	gain	loss	net	persistent	gain	loss	net	persistent	gain	loss	net
Wet Savanna	ABRUN	m ²	0	3,258	0	3,258	0	0	3,258	-3,258	0	0	0	0
		%	--	--	--	--	0.00	0.00	100.00	-100.00	--	--	--	--
	OOXB	m ²	1,008	10,224	9,549	675	0	0	11,232	-11,232	0	0	0	0
		%	9.55	96.85	90.45	6.39	0.00	0.00	100.00	-100.00	--	--	--	--
	LOWMUL	m ²	32,229	12,294	138,555	-126,261	135	1,350	44,388	-43,038	1,062	14,292	423	13,869
		%	18.87	7.20	81.13	-73.93	0.30	3.03	99.70	-96.66	71.52	962.42	28.48	933.94
	CENTMUL	m ²	2,835	14,814	7,209	7,605	2,637	450	15,012	-14,562	0	0	3,087	-3,087
		%	28.23	147.49	71.77	75.72	14.94	2.55	85.06	-82.51	0.00	0.00	100.00	-100.00
	LOCKS	m ²	495	1,953	10,476	-8,523	0	0	2,448	-2,448	0	0	0	0
		%	4.51	17.80	95.49	-77.69	0.00	0.00	100.00	-100.00	--	--	--	--
Graminoid Savanna	LOWBAT	m ²	2,340	828	14,850	-14,022	486	603	2,682	-2,079	441	1,350	648	702
		%	13.61	4.82	86.39	-81.57	15.34	19.03	84.66	-65.63	40.50	123.97	59.50	64.46
	CENTBAT	m ²	0	0	2,331	-2,331	0	0	0	0	0	0	0	0
		%	0.00	0.00	100.00	-100.00	--	--	--	--	--	--	--	--
	LOWFRG	m ²	0	0	0	0	0	0	0	0	0	0	0	0
		%	--	--	--	--	--	--	--	--	--	--	--	--
	SACR	m ²	0	0	8,577	-8,577	0	0	0	0	0	7,119	0	7,119
		%	0.00	0.00	100.00	-100.00	--	--	--	--	--	--	--	--
	ABRUN	m ²	4,653	2,835	26,109	-23,274	990	3,087	6,498	-3,411	981	2,781	3,096	-315
		%	15.13	9.22	84.87	-75.66	13.22	41.23	86.78	-45.55	24.06	68.21	75.94	-7.73
Shrub Savanna	OOXB	m ²	7,191	9,234	12,762	-3,528	11,907	19,233	4,518	14,715	12,555	1,314	18,585	-17,271
		%	36.04	46.28	63.96	-17.68	72.49	117.10	27.51	89.59	40.32	4.22	59.68	-55.46
	LOWMUL	m ²	38,268	51,588	13,347	38,241	60,624	56,520	29,232	27,288	65,781	9,981	51,363	-41,382
		%	74.14	99.95	25.86	74.09	67.47	62.90	32.53	30.37	56.15	8.52	43.85	-35.33
	CENTMUL	m ²	6,516	11,268	3,150	8,118	6,957	17,190	10,827	6,363	11,844	8,325	12,303	-3,978
		%	67.41	116.57	32.59	83.99	39.12	96.66	60.88	35.78	49.05	34.48	50.95	-16.47
	LOCKS	m ²	7,623	10,692	9,558	1,134	3,060	3,681	15,255	-11,574	1,935	1,674	4,806	-3,132
		%	44.37	62.23	55.63	6.60	16.71	20.10	83.29	-63.19	28.70	24.83	71.30	-46.46
	LOWBAT	m ²	54,072	15,156	76,590	-61,434	42,786	14,067	26,442	-12,375	27,972	3,663	28,881	-25,218
		%	41.38	11.60	58.62	-47.02	61.80	20.32	38.20	-17.88	49.20	6.44	50.80	-44.36
Shrub Savanna	CENTBAT	m ²	30,195	8,280	58,689	-50,409	7,722	9,441	30,753	-21,312	6,021	513	11,142	-10,629
		%	33.97	9.32	66.03	-56.71	20.07	24.54	79.93	-55.39	35.08	2.99	64.92	-61.93
	LOWFRG	m ²	18,216	5,787	18,072	-12,285	11,475	7,821	12,528	-4,707	9,450	3,699	9,846	-6,147
		%	50.20	15.95	49.80	-33.85	47.81	32.58	52.19	-19.61	48.97	19.17	51.03	-31.86
	SACR	m ²	2,952	432	38,988	-38,556	2,790	2,835	639	2,196	3,294	1,377	2,277	-900
		%	7.04	1.03	92.96	-91.93	81.36	82.68	18.64	64.04	59.13	24.72	40.87	-16.16
	ABRUN	m ²	4,752	24,957	131,499	-106,542	13,149	9,774	16,560	-6,786	14,328	37,881	8,595	29,286
		%	3.49	18.32	96.51	-78.20	44.26	32.90	55.74	-22.84	62.50	165.25	37.50	127.76
	OOXB	m ²	26,739	16,380	79,164	-62,784	8,082	2,646	35,037	-32,391	0	5,400	10,728	-5,328
		%	25.25	15.47	74.75	-59.28	18.74	6.14	81.26	-75.12	0.00	50.34	100.00	-49.66
Shrub Savanna	LOWMUL	m ²	981	45,765	23,166	22,599	2,817	18,945	43,929	-24,984	2,124	16,209	19,638	-3,429
		%	4.06	189.53	95.94	93.59	6.03	40.53	93.97	-53.45	9.76	74.48	90.24	-15.76
	CENTMUL	m ²	4,257	6,624	3,375	3,249	3,591	14,157	7,290	6,867	693	3,699	17,055	-13,356
		%	55.78	86.79	44.22	42.57	33.00	130.11	67.00	63.11	3.90	20.84	96.10	-75.25
	LOCKS	m ²	10,161	12,510	2,673	9,837	234	10,872	22,437	-11,565	1,251	2,520	9,855	-7,335
		%	79.17	97.48	20.83	76.65	1.03	47.96	98.97	-51.01	11.26	22.69	88.74	-66.05
	LOWBAT	m ²	87,831	46,737	49,176	-2,439	47,583	22,401	86,985	-64,584	21,240	10,674	48,744	-38,070
		%	64.11	34.11	35.89	-1.78	35.36	16.65	64.64	-47.99	30.35	15.25	69.65	-54.40
	CENTBAT	m ²	7,434	35,595	13,509	22,086	1,836	14,544	41,193	-26,649	0	0	16,380	-16,380
		%	35.50	169.96	64.50	105.46	4.27	33.80	95.73	-61.93	0.00	0.00	100.00	-100.00
Shrub Savanna	LOWFRG	m ²	0	19,656	0	19,656	9,693	2,844	9,963	-7,119	1,170	1,017	11,367	-10,350
		%	--	--	--	--	49.31	14.47	50.69	-36.22	9.33	8.11	90.67	-82.56
Shrub Savanna	SACR	m ²	1,521	19,656	5,499	14,157	9,126	8,730	12,006	-3,276	1,719	819	16,173	-15,354
		%	21.67	280.00	78.33	201.67	43.19	41.31	56.81	-15.50	9.61	4.58	90.39	-85.81

Table 8: Site-level gain, loss and persistence of savanna by class. At the site level, patterns of gain and loss are far more variable than at the study-wide level. Also of note is the complete removal of wet savanna from an increasing number of sites over time.

Figure 13 breaks the study-wide loss-gain dynamics down into specific conversions. The gray block in each graph represents the amount of that class' total study-wide area that persisted throughout a given time step. The area above represents the amount of new area of that class

introduced, broken into the vegetation classes from which they converted, while the area below represents the amount of area that was lost, broken into the vegetation classes to which they converted. This visualization reveals some key patterns about the origin and fate of each class.

Savanna-to-savanna conversions tend to follow expected pattern of linear succession toward drier, woodier vegetation predicted by the hydrarch model--wet savanna → graminoid savanna → shrub savanna→ forested swamp --with little reversal toward wetter herbaceous communities. However this slow savanna-to-savanna conversion is not the dominant pattern indicated. Direct conversion from savanna to forested swamp makes up a large proportion of losses for each class. This indicates that succession may proceed quite rapidly, with transition states being either short-lived or skipped altogether. In addition, forested swamp to savanna conversions are relatively common for each class indicating some level of shifting mosaic dynamics, but with losses far exceeding introduction of new savanna.

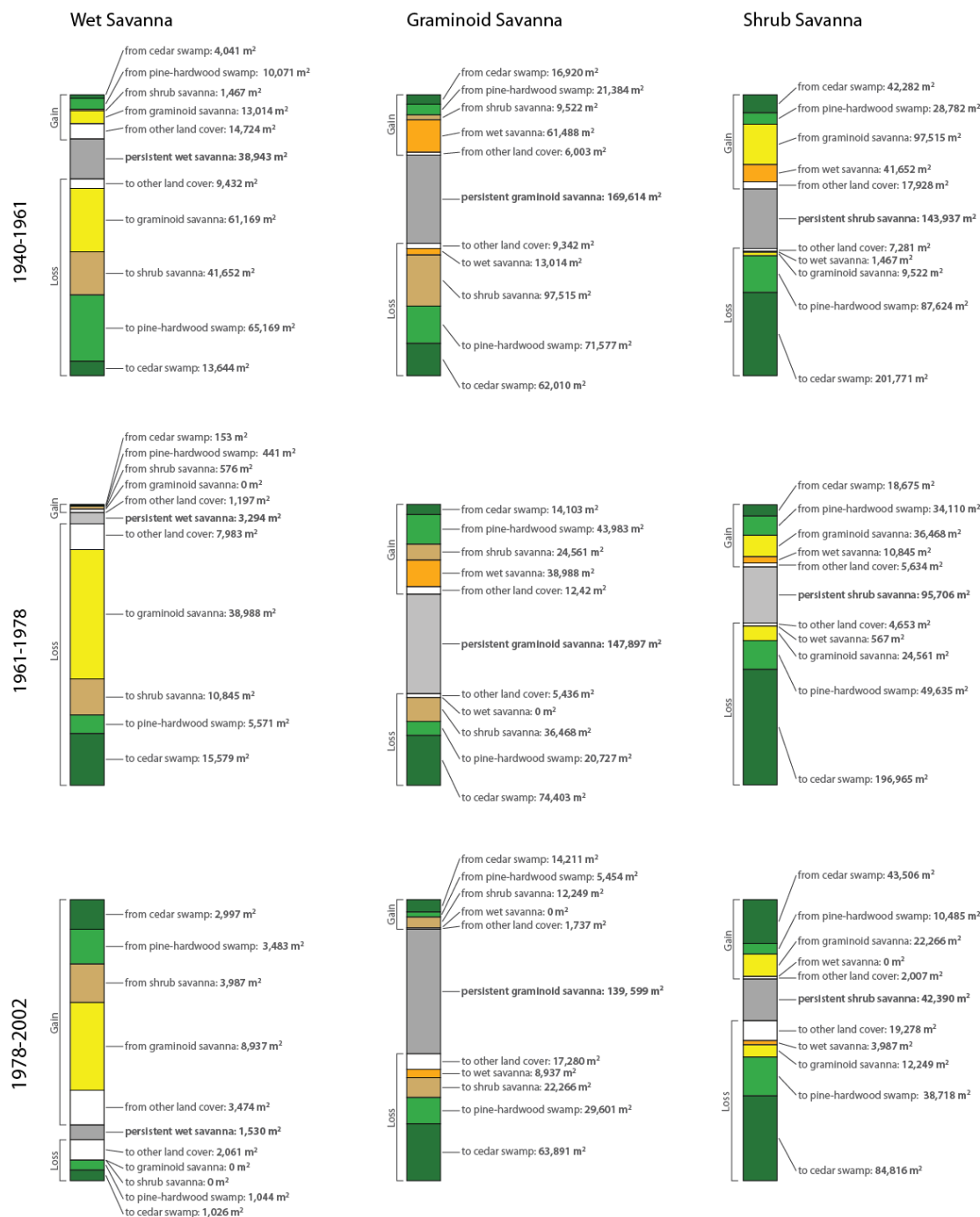


Figure 13: Short-term class-by-class conversions study-wide. This figure shows the specific conversions to and from each savanna class across each time step study-wide. The gray block in each graph indicates the proportion of that class that remains locally persistent across the given time step. The colored blocks above indicate specific conversions to the given savanna class (gain) while those below indicate conversions of the given savanna class to other vegetation cover (loss). The specific class converted from or to is labeled in each case. The blocks labeled "other land cover" consists of upland, shrub swamp, burned land, water, and undetermined classes. These were grouped because each accounts for only a small proportion of total conversion.

Breaking these results down to the site level (Figure 14) reveals a more complex and variable picture. The colored bars indicate conversions by proportion as in Figure 13. Again, the gray box in each represents the relative amount of persistent savanna of the target class. The colored bars above represent specific conversions to the target class, while those below represent conversions away. Below each group of colored graphs is a black and white graph showing the relative amount of conversion activity among sites involving the target class. Again, the gray block represents persistence, while the black blocks above and below represent introduction of gain and loss of savanna area respectively. The scale has been removed to streamline the display, however it is consistent among graphs with a range of $-20,000 \text{ m}^2$ to $15,000 \text{ m}^2$. The site area graph indicates the relative difference in size of each sites and has a range of 0 m^2 to $80,000 \text{ m}^2$.

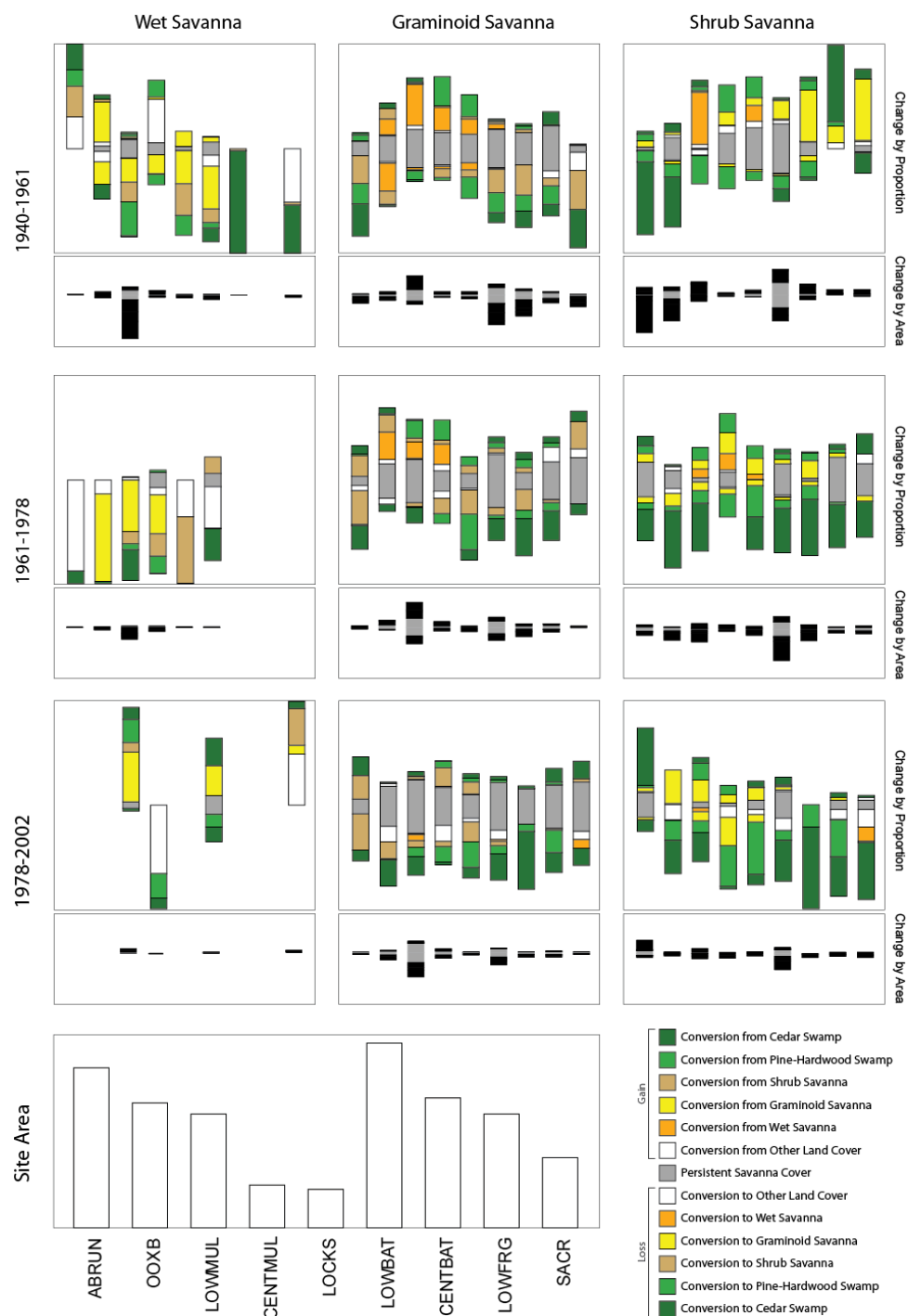


Figure 14: Short-term class-by-class conversions by site. This figure shows the specific conversions to and from each savanna class across each time step by site. As in Figure 13, local persistence is represented by the gray blocks, gains by the colored blocks above, and losses by the colored blocks below. The specific conversions represented by each color is shown in the key. The absolute amount of persistent, gained, and lost area of each class is presented in the black and white graphs below each colored graph. The order of sites from left to right are Above Buck Run, Old Oxbow, Lower Mullica, Central Mullica, Below the Locks, Lower Batsto, Central Batsto, Lower Forge, and Sacred River. The relative total area of each site is given at the graph at the bottom of the figure.

The dynamics of wet savanna in particular are highly variable among sites. However, some patterns do stand out. The most obvious is that progressively fewer sites support wet savanna. From 1940 to 1961 wet savanna was eliminated from two sites (and introduced to one site), from 1961 to 1978 wet savanna was eliminated from three sites, and from 1978-2002 wet savanna was eliminated from one site (and introduced to one site); where six sites supported wet savanna at the start of the study period, only three did so at the end.

While the general trend in wet savanna is this dramatic loss, small gains--and even introduction to sites where it has previously been eliminated--do occur. Also, there appears to be no consistent pattern as to what classes convert to wet savanna. In most cases, the dominant conversions from wet savanna are toward graminoid and shrub savanna. These patterns would be in keeping with an early succession community. Those sites that do not show large conversions to drier savanna vegetation show (with a single exception) significant conversions to the "other land cover" class. In these cases this may be taken to mean water, as it is by far the dominant component of that class in terms of conversions to and from wet savanna.

It is important to note again that the study-wide patterns of wet savanna conversions are dominated by the Lower Mullica site. This site is exceptional in that it saw major flooding prior to the period covered in this study. While this is the exception in terms of scale, it does lend credence to the hypothesis that wet savanna is the first stage in succession initiated by flood disturbance.

Graminoid savanna is somewhat more consistent among sites. Some sites see significant gains, particularly early on, while others do not. Large gains are generally associated with conversion from wet savanna. These eventually decline as wet savanna is lost from those sites and not replaced. Interestingly, conversions to graminoid savanna from shrub savanna and

forested swamp classes appear to be greater in those sites where conversion from wet savanna also occurs. Conversions from graminoid to shrub savanna and forested swamp classes occur in varying proportions among sites and from time step to time step. With the exception of the Old Oxbow Site from 1940-1961, conversions from graminoid to wet savanna are minimal, indicating that such reversals are rare at the site level as well as study-wide.

Shrub savanna is highly variable among sites, with some showing large net gains and some showing large net losses. Gains are dominated by conversion from both wet and graminoid savanna, while losses are dominated by conversion to forested swamp along with some minor reversals to graminoid savanna. There are two exceptions to this general pattern of. The Lower Forge site sees a sizable conversion from cedar swamp to shrub savanna between 1940 and 1961, as does the Above Buck Run site between 1978 and 2002. As noted previously, both of these sites show evidence of fire in the adjacent upland area during the time step in question.

From the standpoint of persistence graminoid savanna is also fairly consistent at the site level, as it is study-wide. Among the three savanna classes, graminoid is by far the most consistent by proportion both among sites and from time step to time step. Wet savanna shows little persistence, in many cases carrying no persistent area from one study year to the next. Shrub savanna shows generally greater persistence than wet savanna, but is highly variable both among sites and time steps.

One peculiar site in this study is Sacred River. This site shows a particularly high degree of variability in all aspects of these conversion dynamics. It is difficult, given the data available, to determine the cause of this variability. However, one possible explanation is that the concentration of savanna at this site is at the confluence of Tulpehocken Creek and one of its minor tributaries, potentially leading to more variable hydrology. While confluences are present in other sites as well the distribution of savanna in this case appears to be more closely associated

with the confluence itself than in other sites. Also, the channel of the tributary at the confluence is not well defined, making it more likely to flood.

Succession pathway analysis

500 randomly selected points produced 156 individual sequences. Of these 500 points, wet savanna occurred in 100 (20.0%), graminoid savanna occurred in 233 (46.6%), and shrub savanna occurred in 303 (60.6%).

Slow transition through hydrarch stages (i.e., wet savanna → graminoid savanna → shrub savanna → forested swamp) was surprisingly very rare, occurring in only 2 of the 500 sample points (0.4%). Other slow transitions were also relatively rare. Wet savanna → graminoid savanna occurred in 28 samples (5.6%) and graminoid savanna → shrub savanna occurred in 48 samples (9.6%). The transition from wet savanna to shrub savanna occurred in 23 samples (4.6%).

The most common sequence overall was by far an early conversion from shrub savanna to persistent cedar swamp between 1940 and 1961: 71 of 500 samples (14.2%). A distant second in terms of common sequences was the persistence of graminoid savanna throughout the study period: 24 of 500 samples (4.8%). This was followed closely by the early conversion of graminoid savanna to persistent cedar swamp: 21 samples (4.2%). The top ten most common sequences are summarized in Table 9.

Sequence	Occurrence
shrub savanna → cedar swamp → cedar swamp → cedar swamp	71
graminoid savanna → graminoid savanna → graminoid savanna → graminoid savanna	24
graminoid savanna → cedar swamp → cedar swamp → cedar swamp	21
shrub savanna → pine-hardwood swamp → pine-hardwood swamp → pine-hardwood swamp	18
shrub savanna → shrub savanna → cedar swamp → cedar swamp	17
graminoid savanna → shrub savanna → cedar swamp → cedar swamp	16
graminoid savanna → graminoid savanna → graminoid savanna → cedar swamp	13
shrub savanna → shrub savanna → shrub savanna → cedar swamp	13
graminoid savanna → pine-hardwood swamp → cedar swamp → cedar swamp	10
shrub savanna → pine-hardwood swamp → cedar swamp → cedar swamp	10

Table 9: Ten most commonly occurring 62-year succession sequences observed.

When the system is generalized to combine cedar swamp and pine-hardwood swamp into a single category, the results show an even stronger trend toward wooded swamp. 113 samples showed an early conversion to some form of forested swamp (22.6%). This was followed by early conversion from graminoid savanna to persistent forested swamp with 40 samples (8.0%), followed by a later conversion of shrub savanna to persistent wooded swamp (1961-1978) with 29 samples (5.8%) and persistent graminoid savanna again with 24 samples (4.8%). The top ten generalized sequences are summarized in Table 10.

Sequence	Occurrence
shrub savanna → wooded swamp → wooded swamp → wooded swamp	113
graminoid savanna → wooded swamp → wooded swamp → wooded swamp	40
shrub savanna → shrub savanna → wooded swamp → wooded swamp	29
graminoid savanna → graminoid savanna → graminoid savanna → graminoid savanna	24
wet savanna → wooded swamp → wooded swamp → wooded swamp	19
graminoid savanna → shrub savanna → wooded swamp → wooded swamp	17
shrub savanna → shrub savanna → shrub savanna → wooded swamp	16
graminoid savanna → graminoid savanna → graminoid savanna → wooded swamp	14
wooded swamp → shrub savanna → wooded swamp → wooded swamp	12
graminoid savanna → graminoid savanna → wooded swamp → wooded swamp	12

Table 10: Ten most commonly occurring 62-year succession sequences observed, generalized to combine wooded swamp into a single class.

Introduction of new savanna was common, with 78 sample points (15.6%) seeing the first appearance of savanna after 1940 and an additional 40 instances of reintroduction of savanna after loss. However these appear to be generally short-lived. 41 of those 78 points saw savanna only for a single study year, while another 12 points saw the first appearance of savanna in 2002, making their persistence impossible to measure.

Focusing individually on the fates of each savanna class reveals some patterns. Figure 15 traces the ten most frequently occurring vegetation change sequences associated with each savanna class. In the case of wet savanna three main patterns stand out: wet savanna to cedar swamp, in most cases through an intermediary phase of graminoid savanna, shrub savanna, or pine-hardwood swamp; wet savanna to pine-hardwood swamp, with no intermediate phase; and wet savanna to graminoid savanna which persists with some points periodically converting to cedar swamp.

This last pattern is carried through when tracing the fate of graminoid savanna. Here we see a persistent line of graminoid savanna with some sample points periodically converting to

cedar swamp. Most often in these cases there is no intermediate phase. Some notable exceptions are found in the 1940-1978 period where significant transitions through shrub savanna and pine-hardwood swamp are noted in 1961.

Shrub savanna succession is strongly dominated by conversion to cedar swamp. This trend follows a pattern similar to that of graminoid savanna, in which some portion of the sample is converted to cedar swamp at each time step while the remainder persists as savanna. However, the rate of conversion appears to be much greater in this case, causing a much more rapid loss of shrub savanna than of graminoid savanna. There is a similar--though far less dramatic--trend of conversion of to pine-hardwood swamp. Also worth mentioning here is that the conversion of graminoid to shrub savanna between 1940 and 1961 left no persistent shrub savanna by 1978.

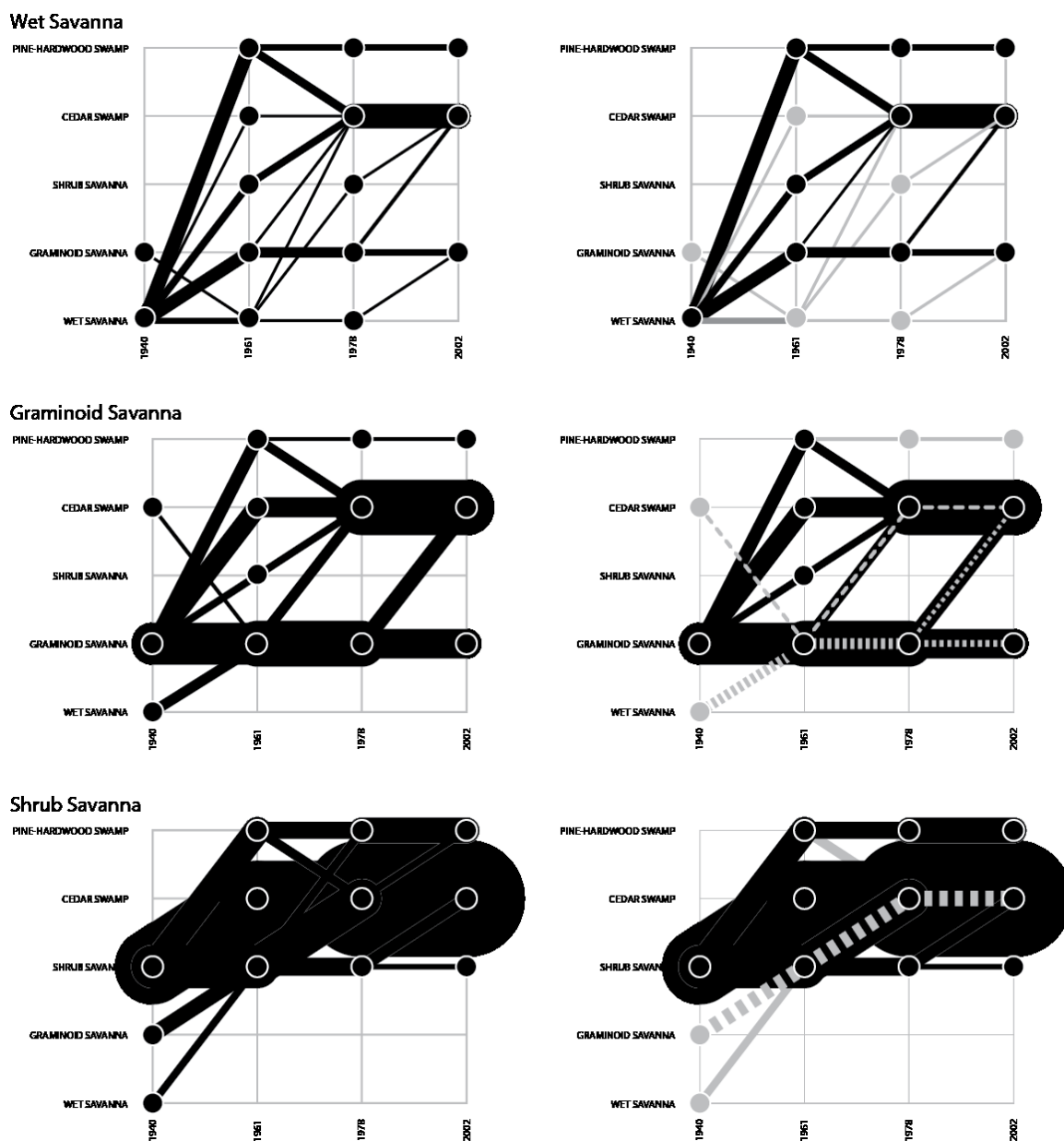


Figure 15: Dominant 62-year succession patterns. These plots represent the ten most frequently occurring succession sequences affecting each savanna class. The thickness of the line reflects the number of sample points, out of 500, that underwent a given conversion between two study years. The plots on the left show all of the included sequences, while those on the right are modified to highlight the dominant patterns.

Not surprisingly, long-term persistence of savanna is uncommon. The majority of savanna cover over this study period is short-lived. Each class sees the greatest area by far persisting for less than 20 consecutive years. Of the full 500 sample points taken, a total of 62 of

which (12.40%) persisted throughout the study period as savanna in some form. Of these 62 points, 32 points saw some savanna-to-savanna conversion. Savanna-to-savanna conversions tend to occur in a linear fashion toward later succession vegetation. Thus it would be questionable to assume ongoing persistence at those points. The remaining 30 points persisted throughout the study as a single class.

In terms of the long-term persistence of individual savanna classes, it is most informative to compare the number of points that remained associated with each class to the number of points where that class appeared in at least one study year. Of 100 sample points where wet savanna was found none persisted for as long as 40 consecutive years. Shrub savanna was found at 303 sample points with 6 points (1.98%) persisting throughout the study period. Graminoid savanna showed significantly greater persistence. It was found at 233 sample points with 24 points (10.30%) persisting throughout the study period.

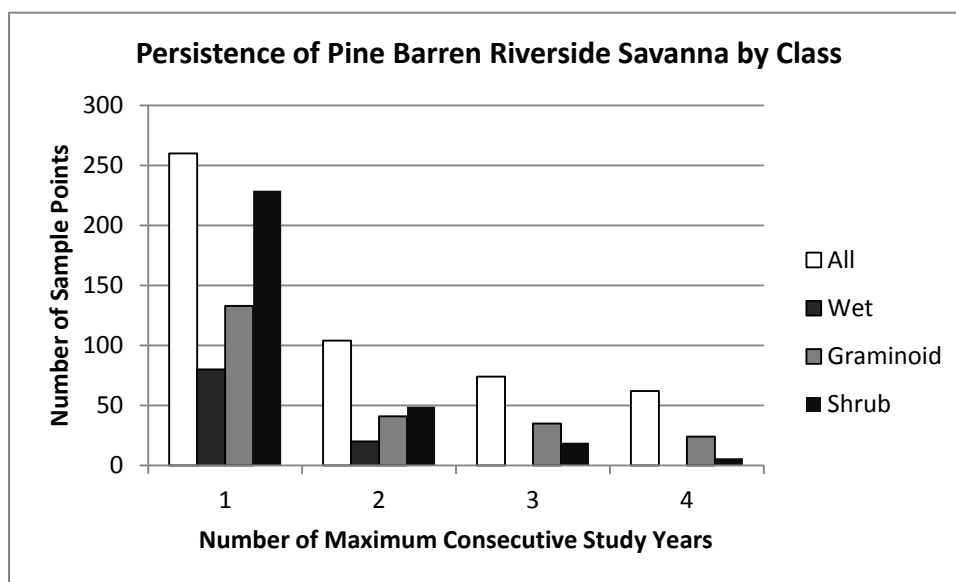


Figure 16: Persistence of Pine Barrens riverside savanna by class. The x-axis represents not a time series, but the number of consecutive years in which a class was observed at a given sample point.

ALL SAVANNA		
consecutive study years	sample points	percent
1	260	52.00
2	104	20.80
3	74	14.80
4	62	12.40
<i>total</i>	<i>500</i>	<i>100</i>

WET SAVANNA		
consecutive study years	sample points	percent
1	80	80.00
2	20	20.00
3	0	0.00
4	0	0.00
<i>total</i>	<i>100</i>	<i>100</i>

GRAMINOID SAVANNA		
consecutive study years	sample points	percent
1	133	57.08
2	41	17.60
3	35	15.02
4	24	10.30
<i>total</i>	<i>233</i>	<i>100</i>

SHRUB SAVANNA		
consecutive study years	sample points	percent
1	229	75.58
2	49	16.17
3	19	6.27
4	6	1.98
<i>total</i>	<i>303</i>	<i>100</i>

Table 11: Persistence of Pine Barrens riverside savanna by class.

Adjacent vegetation analysis

Figure 17 shows parallel coordinate plots for graminoid and shrub savanna. The first axis indicates the percent change in area of each patch across a given time-step. The other ten axes

show the percent cover of the 1m buffer around each patch that is occupied by the class indicated. The lines are colored to indicate the direction and intensity of change: green lines indicate an increase in patch size, gray lines indicate a reduction in patch size, and red lines indicate a complete loss of the patch. The intensity of color of a given line segment relates to the number of individual lines that share a set of values at two adjacent axes. If correlations between change in patch area and the presence of any given vegetation class were present, one would expect to see lines of the same color clustering around a value range at that class' axis.

In the case of wet savanna, it is difficult to determine any pattern. Meaningful sample patches are few and strongly dominated by complete loss. Even so there is no clustering at any of the adjacent vegetation class axes. There is also little in the way of clustering apparent in either the case of graminoid or shrub savanna. While there is strong clustering around the 0% cover mark for several of the adjacent vegetation classes such as shrub swamp and burned land, this is attributable to the general scarcity of these classes across the study sites rather than correlation with any degree of change in the size of the target patch. There is some potentially meaningful clustering in the case of shrub savanna in the 1961-1978 and 1978-2002 time steps. Shrub savanna patches undergoing complete loss across those time steps show approximately 50% or more of the adjacent vegetation consisting of cedar swamp.

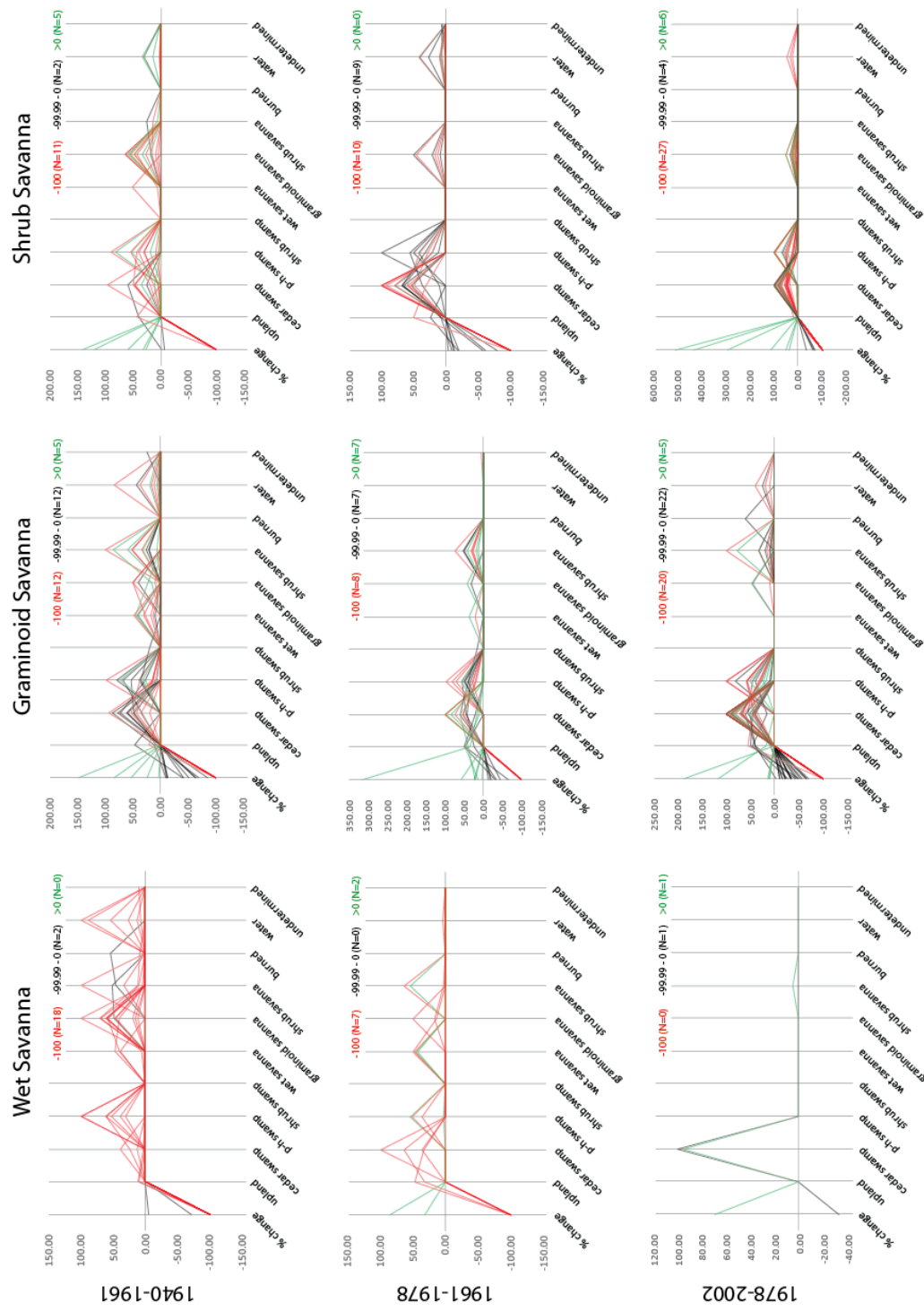


Figure 17: Relating change in patch size to adjacent vegetation composition. These parallel coordinate plots trace possible correlations between changes in size of patches of each savanna class and the composition of vegetation within a 1m buffer zone around the patch represented as the percent cover of each vegetation class. Each line represents a single patch. Red lines indicate a patch that was lost completely, black lines represent patches that were reduced in size but not lost completely, and green lines represent patches that increased in size.

Discussion

Change in savanna distribution

While previous studies have pointed toward dramatic loss of savanna vegetation across the Mullica Basin, these have been gleaned from estimates of distribution taken from various sources, each using its own methods and definitions. This study, based on a single consistent survey protocol over a period of sixty-two years, supports the hypothesis that Pine Barrens riverside savanna communities continue to undergo rapid, dramatic decline in area across their range. Study-wide, over 70% of savanna present in 1940 was lost by 2002. Individually each class saw dramatic declines as well, with wet savanna seeing the greatest loss at 89.4 % and graminoid the least at 59.5%.

Over time, savanna study-wide underwent a more or less linear decline from study year to study year, both in terms of each individual savanna class and in aggregate. Changing scales shows a much more variable picture. At the site level--while still seeing a general trend of loss over time--changes in the distribution of individual classes vary greatly among sites. This variation appears to be controlled largely by the pool of each class present at the start of the study.

Of particular note is the dominance of the Lower Mullica site in the study-wide decline of wet savanna. In 1940, while graminoid and shrub savanna were more or less evenly distributed across the study area, this site accounted for approximately 74% of wet savanna study-wide--approximately 17 ha. By 1978, less than 0.5 ha remained (a small reintroduction brought the total wet savanna cover of the site to just under 2 ha). Evidence of major flooding prior to the start of the study period--possibly persisting for several years--may indicate that the total area of wet savanna at this site may have been abnormally high in 1940 as a result of unusual hydrological conditions. This localized event appears to have dramatically affected the apparent study-wide distribution of wet savanna.

This overall pattern of linear decline is a simplification. In fact each class sees greater losses offset by gains in cover area throughout the study. Much of these gains are a result of savanna-to-savanna conversions, but significant introduction of new savanna--by conversion mostly from wooded swamp--account for as much if not more of these gains.

The causes of much of this gain are not accounted for. However, some large introductions can be related to significant disturbance events. In addition to the above-mentioned flooding at the Lower Mullica site which preceded the presence of a very large but short-lived distribution of wet savanna; smaller introductions appear also to coincide with more localized floods. Large introductions of shrub savanna associated with evidence of fire were observed at the Lower Forge and Above Buck Run sites. This appears to point toward, rather than a slow linear loss of previously stable widespread savanna communities, a disturbance driven shifting mosaic where overall decline is driven by alteration of natural disturbance regimes.

Persistence within the system

General persistence of savanna within the system is evidently quite low. The great majority of savanna patches appeared in a given state for less than 20 consecutive years. While losses of savanna cover are dramatic, they are offset to some degree by introductions, apparently due to flood and fire disturbance. This would indicate that the system as a whole is consistent with a shifting mosaic in a nonsteady-state condition.

At the local level, however, some savanna appears to display a high level of persistence. Graminoid savanna in particular shows evidence of persistence both in the short term (20 years) and the long term (60 years). On average, 47% of the total area of graminoid savanna persists in place across a given 20-year time step. By comparison, 26% on average of shrub savanna persists

across the same time step. Short-term persistence wet savanna is highly variable over time, largely due to the influence of early rapid conversion at the Lower Mullica site. In terms of long-term persistence 10.30% of sample points where graminoid savanna was detected persisted throughout the study period. By comparison, points where shrub and wet savanna were detected saw 60-year persistence of 1.98% and 0% respectively.

Visual interpretation of the vegetation sequence maps in Figures 7 through 12 indicates that persistence in graminoid savanna occurs at the patch level. Some patches prove to be highly stable while others are quite short-lived. Further, size would appear to have little bearing on the persistence of a given patch, as both very large patches ($\sim 45,000 \text{ m}^2$) and quite small patches ($2,000 \text{ m}^2$) remain largely unchanged throughout the study period. It is likely that conditions at those locations are more suitable to the maintenance of savanna--particularly in the graminoid form.

This points to the possibility of savanna existing within the landscape as both a locally stable, persistent system, and as a series of intermediate successional stages in a shifting mosaic. Determining the distinction between these two dynamics could be of great importance for management, as drawing a balance between restoring natural disturbance regimes and maintaining conditions that allow those stable savannas to persist, could be key to preserving the full diversity of savanna to exist.

Short-term conversions

Short-term conversion patterns at the study-wide level tend to move from wetter, herbaceous communities to drier, woodier communities as predicted by the hydrarch model of succession. This pattern is rarely reversed; however, wooded swamp to savanna conversions are common.

Intermediate savanna-to-savanna conversions are not the dominant pattern. A large proportion of herbaceous savanna (including both wet and graminoid) lost is replaced by wooded swamp by the end of a given 20-year time step, indicating that shrub savanna is either short-lived as a successional transition or is frequently skipped altogether.

In terms of short-term conversions, scale is again an important consideration. The study-wide conversion patterns in wet savanna are strongly dominated by activity at the Lower Mullica site. While wet savanna activity at other sites is characterized mainly by conversion to graminoid savanna, shrub savanna, or water, this pattern is minimized at the study scale by rapid conversion to forested swamp at Lower Mullica. This is particularly important, as this site appears to be uniquely affected by major flooding prior to the study period.

Graminoid savanna conversions are characterized by losses through conversion variably to shrub savanna and wooded swamp, and gains associated largely with wet savanna. At the sites where significant wet savanna occurs, not only do large wet-to-graminoid savanna conversions occur, but conversions from wooded swamp and shrub savanna also tend to be somewhat higher at these sites as well. As wet savanna declines, so do gains in graminoid savanna from both wet savanna and woody communities.

Shrub savanna, at the site level is dominated mainly by losses through conversion to wooded swamp. Significant gains occur both through savanna-to-savanna conversions and through large introductions by conversion from wooded swamp at the Lower Forge (1940-1961) and Above Buck Run (1978-2002) sites. Both of these sites show evidence of fire during these periods indicating fire disturbance as a driver in maintaining the shifting mosaic.

Long-term succession patterns

The most common long-term succession patterns involve direct conversion of savanna to wooded swamp. Early conversion from shrub savanna to wooded swamp is the dominant pattern. Direct conversions of wet and graminoid savanna to wooded swamp are both common as well. Savanna-to-savanna conversions, on the other hand, were rarely observed.

When considering patterns associated with the fate of individual classes, wet savanna appears to succeed to cedar swamp through a transitional stage of shrub savanna or pine-hardwood swamp or to graminoid savanna. Graminoid savanna shows a persistent thread with some portion periodically converting to directly to cedar swamp (early on there are some transitions through pine-hardwood swamp and shrub savanna intermediates). Conversions from wet to graminoid savanna appear to follow this trend of persistence with periodic conversion of some portion to cedar swamp. Shrub savanna shows a similar pattern, with a single pool of shrub savanna periodically shedding large portions by conversion to cedar swamp. Shrub savanna again shows considerably less persistence than graminoid savanna. Observed conversions to shrub savanna appear to be short-lived rather than persistent--as with wet to graminoid savanna conversions. While the general pattern of shrub savanna conversions appears to be strong, it is quite clear from the analysis of short-term conversions that introduction of shrub savanna is not uncommon. It is curious that they should appear so in this analysis. Including additional sample points may account for this disparity.

General succession trends

Based solely on the 60-year succession pathway analysis, it is difficult to draw meaningful conclusions about general trends in the succession dynamics of savannas. The sheer

number of unique sequences indicates a fairly unpredictable system. The sequence predicted by the classical hydrarch succession model is observed rarely. This disagrees with the short-term conversion analysis. Some of this unpredictability is almost certainly a by-product of the level of spatial precision of the data. It is also likely that, given the temporal scale of this study, short-lived transitional stages may be omitted. Additional data, taken at a shorter time-step may be required to get a more accurate picture of long-term succession dynamics. However, combining these results with the short-term conversion analysis and interpretation of vegetation sequence maps provides a more complete view. The combination of these three approaches leads to the proposed hypothetical succession model presented in Figure 18.

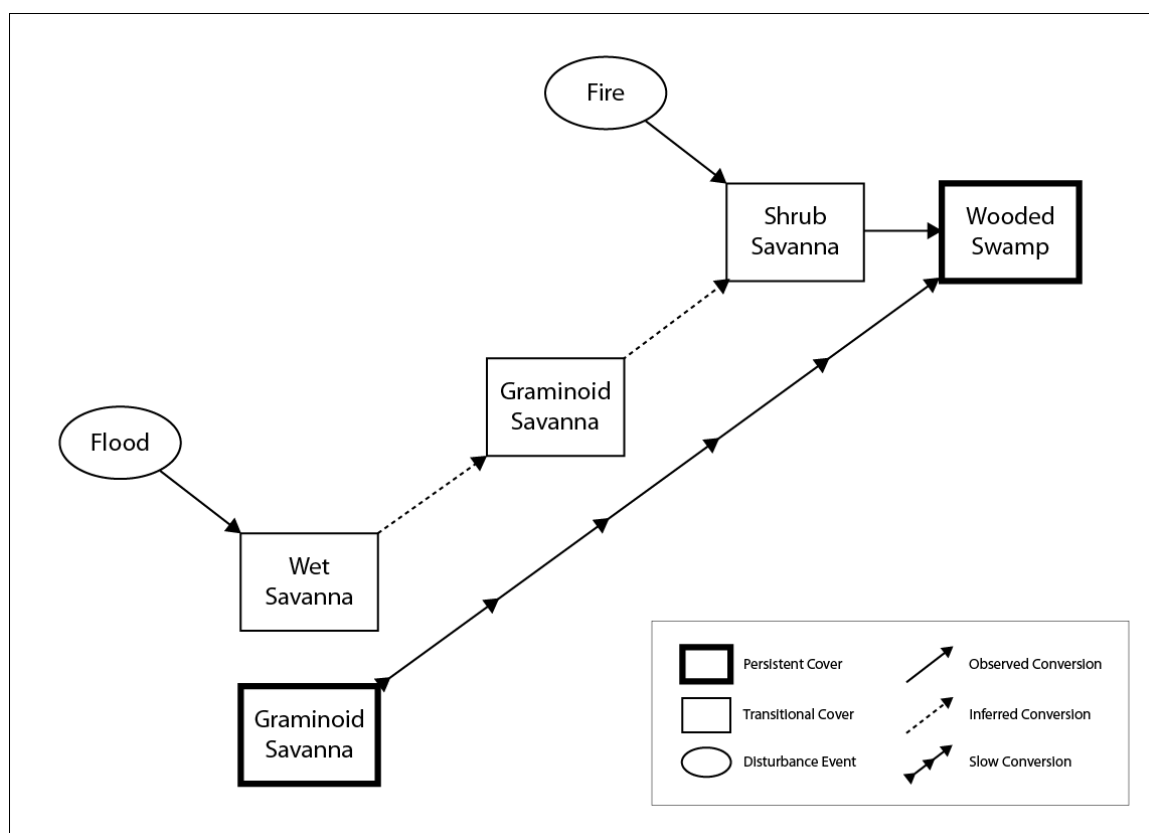


Figure 18: Proposed two-pathway succession model. Local persistence and a shifting mosaic are both indicated within this system. The rapid decline in savanna distribution appears to be associated with an imbalance between disturbance and succession in the latter pathway creating a shifting mosaic that is not in a steady state. Locally persistent graminoid savanna has declined more slowly. Better understanding both of these processes will be important to effective conservation of these communities.

The key feature of this model is that it presents two distinct pathways describing the role of savanna within the system, a local persistence pathway and a shifting mosaic pathway. The former is characterized by patches of graminoid savanna persisting over long periods of time--i.e., the full study period and likely beyond--with slow incursion of trees over time. In the latter, each savanna class acts as an intermediate stage in post-disturbance succession toward persistent wooded swamp cover. Disturbance in this system occurs in the form of both flood and fire. The presence of both of these two pathways accounts for both the long-term persistence found by Southgate (2000) and reports and the shifting mosaic described by Zampella and Lathrop (1997).

The steady conversion sequence proposed by the hydrarch model was not detected as a strong pattern in the long-term succession analysis. This is most likely the result of the coarse temporal scale of the study. It is likely that these conversions occur too rapidly to be traced from beginning to end, given a 20-year time step. However, the individual conversions involved are strongly supported by the short-term conversion analysis and interpretation of vegetation sequence maps.

Adjacent vegetation

There appears to be little or no correlation between loss of savanna area and adjacent vegetation. There is potentially a weak relationship between shrub savanna and cedar swamp, wherein complete loss of shrub savanna patches correlate with relatively high proportions (>50% cover) of cedar swamp in the adjacent vegetation. However, this could likely be explained by the general prominence of cedar swamp in the system and the high frequency of completely lost shrub savanna patches.

Further research

The findings of this study provide a number of hypotheses and questions for further study. The First is the proposed succession model presented above. While the general two-pathway conclusion is strongly supported by the current data, there remain patterns that are drawn from inference based on short-term conversion analysis rather than directly observed over the long term. The supposition behind this inference is that these intermediate stages in the succession sequence are too short-lived to be detected given at 20 year time-step. Additional data taken from imagery collected in the intervening periods should shed light on the accuracy of these inferences.

The next question would be to determine the cause of the general decline in savanna distribution. It appears most likely that this is due to some change in the dynamics of the more active succession pathway. A likely hypothesis would be that some change to the natural flood and fire regimes of the study area has limited the introduction of new savanna. This is a reasonable hypothesis as both have been dramatically altered by human activity. Every site in this study has been subject to significant modification of its hydrology due to the presence of dams either for industry or agriculture. In addition, the absence of natural dams due to the extirpation of beaver and clearing of debris for the purpose of navigation may eliminate localized flooding events. Since the 1940s, fire management in the Pine Barrens has largely involved prescribed burns in order to remove fuel, thus reducing the frequency and intensity of wildfires (Little, 1979). This would effectively limit the likelihood of intense damaging swamp fires.

Another important question is what differentiates persistent and transitional patches from one another. One viable hypothesis is that certain characteristics of the configuration of vegetation itself within the landscape controls the persistence of savanna at the patch level. However, based on preliminary analysis performed in conjunction with this study, there is little evidence to support this hypothesis. Initial patch size, nearest neighbor distance, and the

composition of adjacent vegetation showed little relation to changes in patch size. These patches are highly localized, vary greatly in size and surrounding vegetation, and yet are exposed to much the same environmental conditions such as climate, disturbance, position within the larger landscape, etc. A more likely hypothesis is that these differences in persistence are related to local hydrology and geomorphology; specifically, that patches found in abandoned stream channels where groundwater seeps directly into a relatively deep bed of organic soil produce conditions that are more consistent and suitable for the maintenance of open canopy herbaceous vegetation than for trees. The history of anthropogenic disturbance across the riparian zone may also play a role; either by initiating succession at sites that were once stable or by introducing transient savanna communities.

An important consideration for future research is the effect of scale. This study focused primarily on two scales, and found that general patterns of succession dynamics clearly differed between the two. Given these results, it is especially important to ensure that the scales at which future studies are conducted are appropriate to the questions being asked. It is also important to recognize that viewing the succession dynamics of this system at any one scale alone presents an incomplete picture. Ideally, future studies should strive to contribute to a base of knowledge that incorporates multiple scales.

Conclusions

This study was a survey of the succession dynamics of Pine Barrens riverside savanna—a unique and little-studied group of endangered ecological communities. These dynamics were studied from aerial photographs spanning a period of sixty-two years enabling the full transition from herbaceous emergent vegetation to forested swamp to be captured.

The changing distribution of savanna is marked by dramatic losses of area. Study-wide, savanna area declined by 71.3% between 1940 and 2002. Over time these losses appear to occur in a generally consistent linear fashion study wide. The total losses represent only the net change in a highly successional dynamic system, in which even greater losses are offset by modest gains. When viewed at a smaller scale, these patterns are highly variable among sites, reflecting differences in local conditions, vegetation pools, and disturbance events. Local persistence is quite low in general, both in the short and long term. While the dominant trends indicate a highly active system, some patches of graminoid savanna were found to persist throughout the study period. These persistent savannas accounted for 10.3% of all sample points where that class was found to occur at any time.

Succession appears to occur along two distinct pathways. One pathway is characterized by persistent patches of graminoid savanna, which appear to lose area slowly by intrusion of scattered trees. The second pathway is indicative of a highly active shifting mosaic, wherein succession occurs in a fashion consistent with the classical hydrarch succession model and new savanna is introduced by natural disturbance in the form of flood and fire. This succession model remains hypothetical, as hydrarch sequences are inferred from short-term conversion data and not observed directly in long-term tracking. This is likely a result of the coarse temporal scale of the data. Expanding the study to include data from intermediate years may help to clarify this disparity.

The results of this study open up several questions. Key among these are: what has caused such a rapid decline in the absence of direct anthropogenic alteration? and what is the difference between those patches that do persist over long periods and those that do not? In terms of the former question, alterations to natural flood and fire regimes are a likely driver of these recent declines. Damming of rivers, extirpation of beaver from the region, and fire management

strategies have all likely impacted the frequency and intensity of those disturbances that may introduce new savanna patches to the system. In terms of the latter question, the most likely hypothesis seems to be that persistent and transient savanna patches differ in local geomorphology and hydrology, with the more stable patches likely being those that are associated with well-developed former stream channels. Historical anthropogenic disturbance may also play a role in differentiating persistent and transient patches.

An important consideration for any future research is scale. This study focused on two distinct scales and found that general succession patterns differed between the two. This indicates that it is particularly important that future studies be conducted at scales that are appropriate to the questions being asked. Overall the goal should be to develop a base of knowledge that incorporates analysis of succession dynamics across multiple scales.

Managing for the conservation of these rare and imperiled communities requires careful consideration of the succession dynamics that drive the observed declines in their distribution. This includes understanding the roles of two distinct succession pathways; how each contributes to the overall persistence of savanna within the landscape, how each can best be managed to maximize this persistence, and how to match persistent and transitional savanna patches with the most appropriate management strategies. Given the dramatic decline in their distribution over the past several decades, I strongly recommend continued research into the succession dynamics of Pine Barrens riverside savannas with the specific goal of developing actionable management strategies within the next five years.

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