RESEARCH ARTICLE

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Influence of Historic Upland Silviculture on the Composition of Ravine Forests along the Apalachicola River, Florida, USA

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ABSTRACT: The ravines along the Apalachicola River are recognized for their species-rich mixed hardwood forests. Although steep slopes may have limited logging, much of the surrounding sandhill and scrub uplands were extensively modified for silviculture in the late 1950's. We examined how contrasts in the intensity of historic upland silviculture have influenced present-day woody species composition in ravine slope forests. To maximize ravine differences due to upland silvicultural intensities while concurrently minimizing the potentially confounding influences of aspect and slope angle, ravine sampling areas were delineated using a combination of historical air photos, field reconnaissance, and a digital elevation model. Ordination (principal coordinates analysis) and permutation-based tests of group differences (multiple response permutation procedures) confirmed that where uplands were selectively-cut longleaf pinelands, tree composition on neighboring ravine slopes was dominated by three species: *Quercus hemisphaerica* Bartr., *Pinus glabra* Walt., and *Quercus alba* L. By contrast, where the uplands had undergone intensive mechanical site preparation for slash pine cultivation, only one species, *Quercus hemisphaerica*, was dominant. Intensive upland silviculture was also correlated with a decreased importance of *Fagus grandifolia*, a species identified as a major constituent of presettlement ravine forests. We discuss how fire suppression, geomorphic disturbance, and logging along upper ravine slopes may explain these compositional differences.

Index terms: Apalachicola, disturbance, fire suppression, land use legacies, *Quercus hemisphaerica*, ravines

INTRODUCTION

The species-rich mixed hardwood forests in the Apalachicola River ravines of the Florida panhandle have been studied for well over a century (Chapman 1885, Harper 1914, Kurz 1938, Kwit et al. 1998). Much of this work has focused on the endemic and disjunct plant populations of the ravines, which include two globally endangered conifers, the Florida yew (*Taxus floridana* Nutt.) and *Torreya taxifolia* Arnott (Schwartz et al. 1995). These plant species, and others typical of cool climates, were stranded within the mild microclimates in the river valley and tributary ravines following the last pulse of Pleistocene glaciation (James 1961).

The protected, relict quality of ravine vegetation reflects, in part, a unique ecosystem that has evolved independently of the surrounding uplands. However, current ideas in disturbance theory and landscape ecology suggest a potential interaction between the ravines and their uplands (Swanson et al. 1988, Parker and Bendix 1996, Reiners and Driese 2001). Disturbance effects may propagate along gravitational gradients, linking vegetation changes at lower elevations to upland land use (Nakamura et al. 2000). Past land use practices may continue to influence compositional patterns and disturbance through ecological legacies (Foster et al. 2003). During the late 1950's, slash pine (*Pinus elliottii* Engelm.) silviculture expanded across much of the uplands surrounding the ravines. Intensive site preparation practices accompanying slash pine silviculture have been often suggested as a direct and indirect influence upon present-day ravine slope forest composition (Schwartz 1990, Platt and Schwartz 1990, Kwit et al. 1998), but this hypothesis has not been examined in detail. We describe the variability in ravine woody tree and shrub species composition as it relates to upland land use history. Clarifying the changes that may have been initiated by past land use provides a foundation for directing future research needs, setting conservation priorities, and focusing ecological restoration efforts (Black et al. 1998, Kettle et al. 2000).

BACKGROUND

The Apalachicola River begins at the borders of Alabama, Florida, and Georgia at the confluence of the Flint and Chattahoochee Rivers. Along a 15-km stretch of the eastern shore of the Apalachicola in Liberty County, Florida, fluvially-eroded ravines, or 'steepheads', form a network of steep-walled tributary valleys. These landforms are the result of spring seepage in the floor of the ravines, which undercuts overlying sands and causes tributary streams to migrate inland by erosion (Rupert 1991). This unique topography provides a refuge within the surrounding xeric uplands for plant species common to moister soils and cooler temperatures. Because of increasing development pressures in the Florida panhandle, ravine communities are classified as imperiled by the Florida Natural Areas Inventory (FNAI 1990).

Quercus hemisphaerica, *Carya* spp., *Fagus grandifolia* Ehrh., *Magnolia grandiflora* L., *Quercus alba*, and *Pinus glabra* are the dominant overstory species in the present-day ravine forests. Important understory tree species include *Osmanthus americanus* (L.) Benth. & Hook., *Kalmia latifolia* L., *Vaccinium arboreum* Marsh., *Ilex opaca* Ait., *Ostrya virginiana* (Mill.) K. Koch, *Oxydendron arboreum* (L.) DC., *Illicium floridanum* Ellis., and *Ilex coriacea* (Pursh) Chapm. (Kwit et al. 1998). Slope position is an important control on the distribution on these woody species (Kwit et al. 1998). Lower slopes are typically dominated by more mesic species, such as *Ilex coriacea* and *Illicium floridanum*. The more xeric-adapted species *Quercus hemisphaerica* and *V. arboreum* increase in abundance at upslope positions. Midslopes may be characterized by a higher cover of *Quercus alba*, *F. grandifolia*, and *Osmanthus americanus*. Aspect has an overall weaker effect on species distributions (Kwit et al. 1998).

Public lands survey descriptions of ravine slope forests from the early 1800's note a paucity of oaks and hickories when compared to the present-day vegetation. *Magnolia grandiflora* and *F. grandifolia* were more important (Delcourt and Delcourt 1977). Timbering within the ravines is one of several hypotheses to explain this change. Even though the present-day ravine forests may have been selectively cut in the 1930's, it is generally acknowledged that their steep slopes have limited the extent of intensive timbering (Schwartz 1990). A complementary hypothesis is that upland land use changes may have cascaded downslope into the ravines, a scenario strengthened by the recognition that sediments, plant propagules, and disturbance can propagate across some landscapes, often asynchronously to the initiating event (Swanson et al. 1988, Parker and Bendix 1996).

Following the widespread decline of longleaf pine (*Pinus palustris* Mill.) in the southeastern U.S. (Means 1996, Smith et al. 2000), slash pine silviculture grew in economic importance and areal extent. These early slash pine silvicultural methods were often associated with fire suppression and intensive mechanical site preparation (Abrahamson and Hartnett 1990). Fire suppression could be expected to augment the cover of fire-intolerant species in the uplands, some of which may be able to germinate in the protected ravines (Kwit et. al. 1998). Moreover, in sandy unconsolidated substrates of the humid subtropical Gulf Coastal Plain, increased erosion, downslope sediment transport, and vegetation change are well-documented responses to agricultural alteration of upland ground cover (Magilligan and Stamp 1997, Edwards, 2001). Platt and Schwartz (1990) speculate along these lines that logging-enhanced erosion initiated in the Apalachicola uplands is one explanation for the difference between present-day ravine vegetation and descriptions recorded in the 1800's.

METHODS

Study Area

Our study area was purchased in 1982 by The Nature Conservancy and is known as the Apalachicola Bluffs and Ravines Preserve (ABRP) (Figure 1). Current land management in the ABRP has focused on restoring the uplands from rows of planted slash pine to longleaf pine forest. Restoration efforts have included prescribed fire, physical removal of old plow lines and successional hardwoods, and groundcover restoration.

Logging of longleaf was persistent in the uplands throughout the first half of this century. Aerial photographs from 1940 indicated that the uplands surrounding ABRP were open and sandy with well-spaced longleaf pine. However, by 1957, most of the longleaf pine had been timbered.

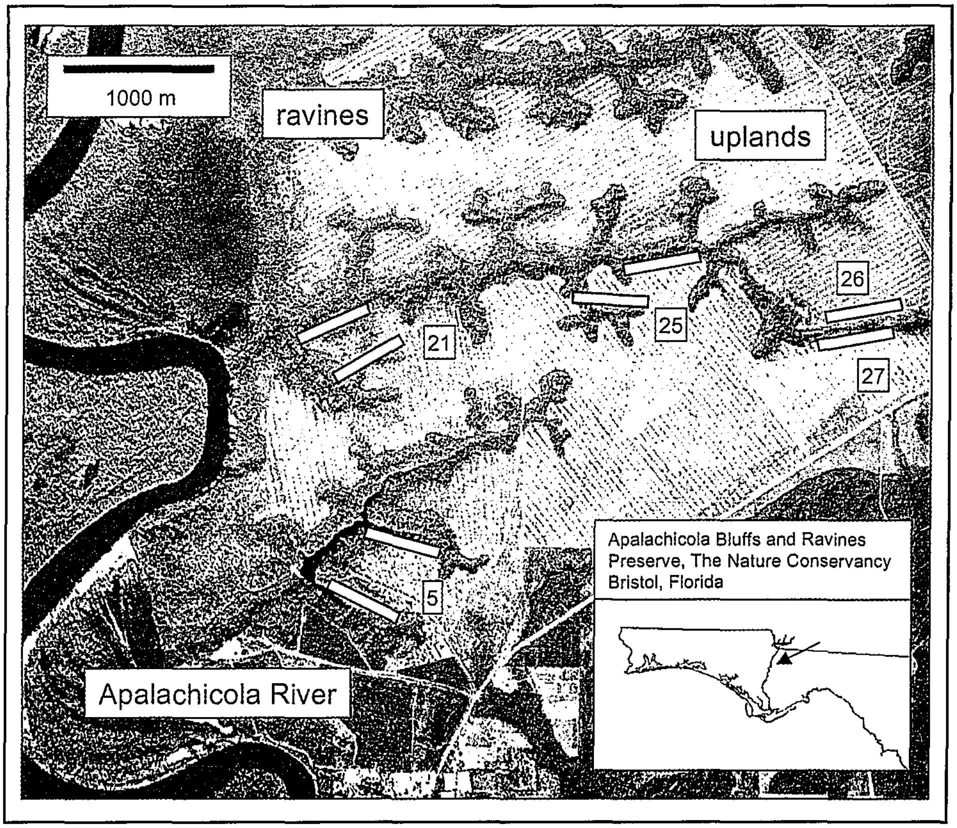


Figure 1. Our study area along the Apalachicola River. Windrowed uplands correspond to ABRP land management units 25, 26, and 27. Native uplands correspond to ABRP units 5 and 21. Rectangles in land management units indicate areas in which transects were randomly located. Lowermost ravine system is Kelly Branch. Little Sweetwater Creek is above it. The northernmost ravine is Beaverdam Creek.

In 1958, the uplands were converted to slash pine monoculture. Aerial photographs from 1959 show several different slash pine silvicultural practices in the uplands, including the emplacement of the elevated plow-line berms that are still visible in the present-day landscape. These plow lines, or windrows, were bulldozed piles of woody debris and groundcover placed in rows during the preparation process for planting pine. Windrows have been found to increase overland erosion, especially where upslope contributing areas are large (Prosser and Abernethy 1999). In the majority of the ABRP, woody debris was either pushed into the ravines or bulldozed into windrows just upslope from the ravine edge (Schwartz 1990).

A few areas in the Apalachicola Bluffs and Ravines Preserve were not windrowed or converted to slash pine silviculture. These tracts of longleaf pine, although selectively cut in the past and left to regenerate, are the only remaining areas of native uplands in the preserve. They are characterized by an overstory of longleaf pine, midstory hardwoods such as turkey oak (*Quercus laevis* Walt.), and a groundcover dominated by wiregrass (*Aristida stricta* Michx.). We defined two ravine types based upon their differences in past upland land use. 'Windrowed' ravines were those ravine slope forests where upland windrows and slash pine plantings extended to the edge of the ravines, utilizing the most land possible for silviculture. 'Native' ravines were those ravine slope forests where non-mechanized selective cutting of longleaf pine, rather than windrowed slash pine, characterized historic upland land use. Field reconnaissance, aerial photos, and consultation with ABRP staff facilitated the selection of the specific land management units to sample.

Variability in slope angles and aspects were expected to confound comparisons of species composition among these two ravine types. To address this limitation, a U.S. Geological Survey (1:24,000) digital elevation model with 30-m resolution was used to select a subset of ravine slopes having a uniformity in these descriptors, which were then subsequently field verified. North was constrained to those slopes between 0° ± 20° and south was similarly restricted to 180° ± 20°. Slope angles were initially confined to those between 20-30°. In the areas within land management units delimited by these topographic parameters, three transects were randomly established. Each transect was aligned perpendicular to the true (steepest) dip of the ravine slope. A total of 24 transects were sampled, 12 each in native and windrowed ravines (Figure 1). The transect starting point was positioned to correspond to the topographic break at the bottom of each ravine slope. In some cases the exact upper slope terminus point was difficult to perceive because the boundary between the ravines and the uplands was indistinct. End points for these transects were arbitrarily located. Transects ranged from 30-40 m in length.

Three 100 m^2 circular plots, each with a radius of 5.64 m, were systematically distributed along the centerline of each transect. These quadrats corresponded to lower, middle, and upper ravine slope positions. Within each quadrat, diameter at breast height (dbh) was recorded for every stem 2.0 cm dbh and greater. If stems less than 2.0 cm dbh were present, they were counted and recorded as recruits, with an estimated 1.0 cm dbh. All woody seedlings and saplings were tallied irrespective of height. Raw dbh data for each species was converted to basal area (cm^2/m^2), density (stems/m^2) and importance. Importance was defined as the average of relative percent dominance (basal area in cm^2/m^2) and relative percent density. All sampling occurred along Kelley Branch and Little Sweetwater creeks, just north of Bristol, Florida, in May through August 2002.

Data analysis

To test for compositional differences between ravine slopes based upon their upland land use type, we employed multi-response permutation procedures (MRPP). MRPP non-parametrically measures the extent to which two or more multivariate data sets differ based on comparisons of the observed and permutated average within-group distance among samples (Biondini et al. 1991, McCune and Grace 2002). MRPP employs an effect size statistic (A) to gauge whether statistical significance reflected in p values is robust or an artifact of within-group variability no different from random expectation. This statistic typically ranges from 0-1. Values converging upon zero indicate that the heterogeneity within groups equals expectation by chance. Values approaching one indicate that all items within groups are identical and the heterogeneity within groups is greater than random expectation. Statistical significance in conjunction with high A values is indicative of stronger group differences. In community ecology, an A value of 0.3 is fairly high. All MRPP significance tests were conducted at the 0.05 significance level using PC-Ord Version 4.04 (McCune and Mefford 1999). Euclidean distances were employed as the distance metric (Zimmerman et al. 1985).

Principle coordinates analysis (PCO) was used to visualize compositional trends tested with MRPP (MVSP software, Kovatch Computing Service 1999). PCO is similar to principal components analysis in that it maximizes the variance in the data set along the first axis. However, PCO is a distance-based ordination method and is better suited to process the large number of zero values that typify ecological data sets (Legendre and Legendre 1998). Deletion of infrequently encountered species is generally not necessary. Bray-Curtis was employed as the distance metric.

RESULTS

A total of 49 woody tree and shrub species were identified from a total of 4131 stems. Species richness was slightly greater in native ravines (44 vs. 38 spp.). Total woody species basal area was greatest on native slopes (40.8 vs. 28.9 cm^2/m^2). Total stem density was slightly higher in windrowed ravines (0.6 vs. 0.5 stems/m^2). Native slopes (30.7 ± 7.5°) had a higher mean slope angle than windrowed slopes (24.2 ± 3.7°). Torreya taxifolia did not occur along any of our transects. Only three individuals of *Taxus floridana* were encountered, all on the ravine slopes of native uplands.

Quercus hemisphaerica was the most important species in both upland land use types. The largest importance value for this species (36.3%) was observed in the ravines downslope of windrowed uplands (Figure 2). Windrowed ravines had a greater importance value for *Ilex coriacea* (9.9%) and an overall greater occurrence of xeric sandhills species among those with importance values > 1.0 [*Pinus palustris*, *Cornus florida* L., *V. arboreum* and *Quercus laevis*]. Ravines adjoining native uplands had a higher importance of *Pinus glabra*, *Quercus alba*, *F. grandiflora* and the woody shrubs *Symplocos tinctoria* (L.) L'Her. and *K. latifolia*.

Species relative percent dominance on native sites was highest for *Pinus glabra* (22.1%), followed by *Quercus hemisphaerica*, *Quercus alba*, *F. grandifolia*, and *M. grandiflora*. On windrowed sites, *Quercus hemisphaerica* had the largest percentage relative dominance, followed by *Pinus palustris*, *M. grandifolia*, *Carya tomentosa* (Poir. in Lam.) Nutt., and *Pinus glabra*. The relative percent density of the shrubs *S. tinctoria*, *Illicium floridanum*, *K. latifolia*, and *Hamamelis virginiana* L. exceeded *Quercus hemisphaerica* on native sites. By contrast, *Quercus hemisphaerica* surpassed all other species in its relative contribution to stem density on windrowed sites. Lower relative densities were observed for *Ilex coriacea*, *Illicium floridanum*, *V. arboreum*, and *Ilex glabra* (L.) Gray.

Compositional differences were also observed among slope positions (Figure 3). For upper and middle slopes, importance values for *Quercus hemisphaerica* were much higher on windrowed slopes, ranging as high as 50-57%. Windrowed transects also had greater positional importance values for *Ilex coriacea* (lower slopes), *Pinus*

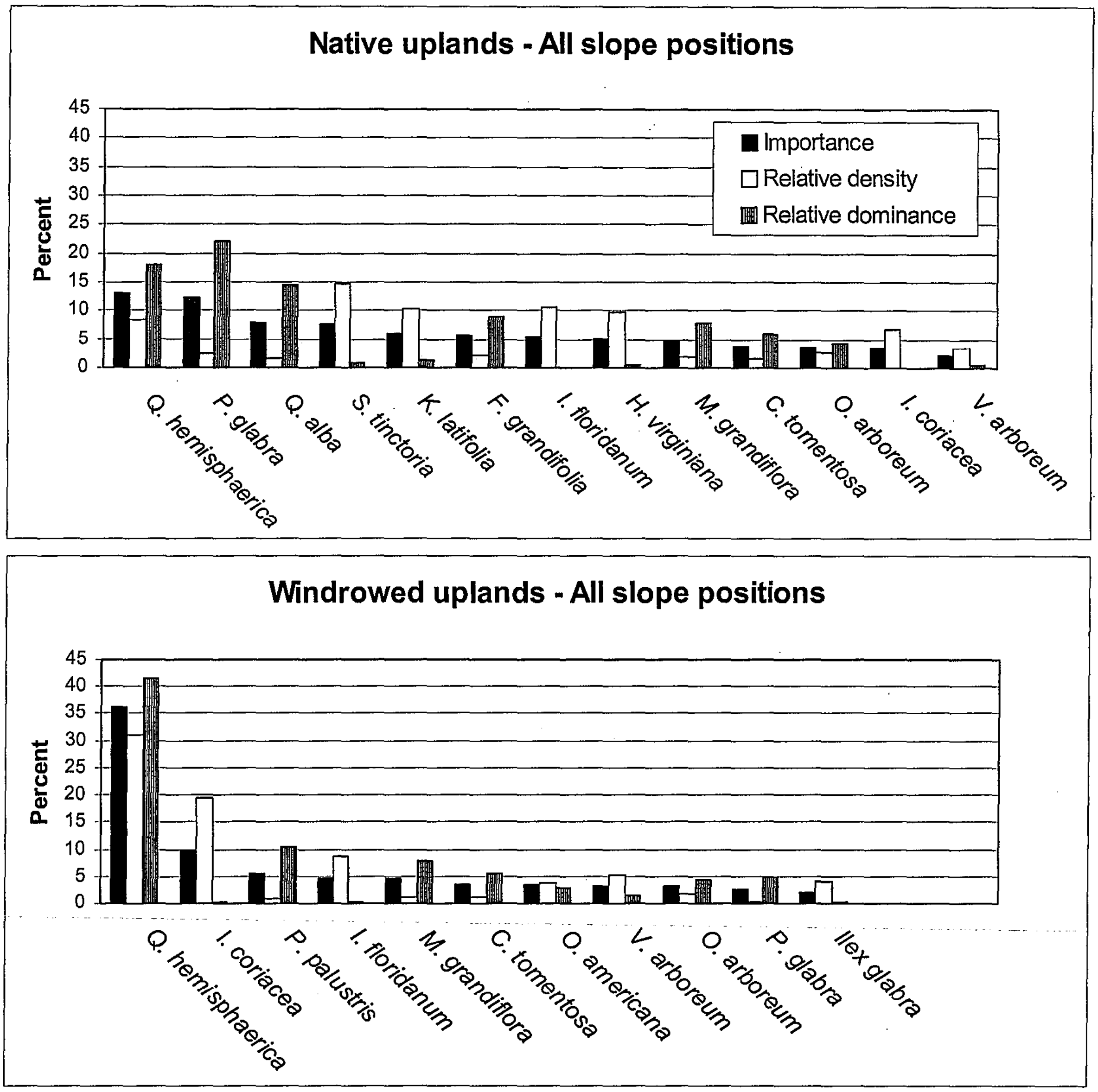
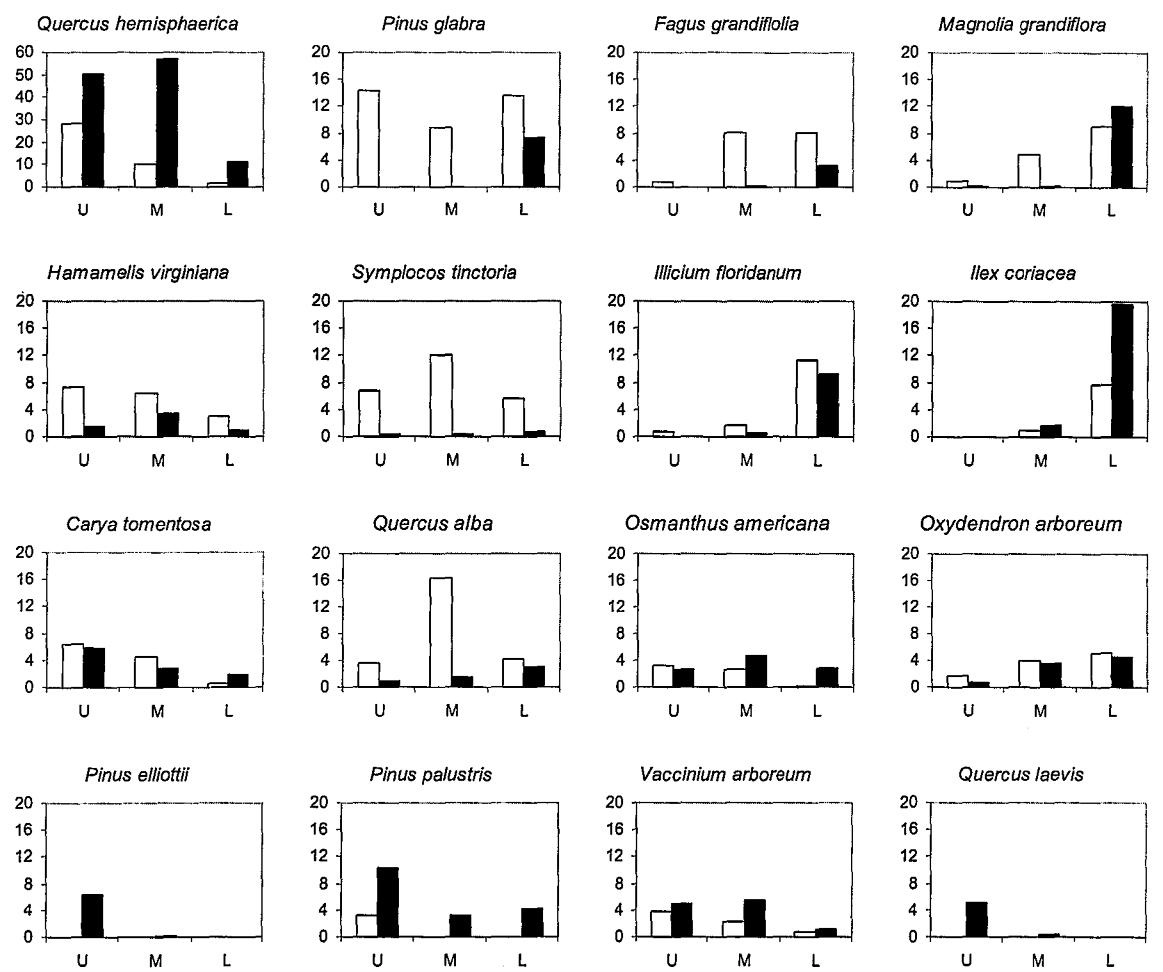


Figure 2. Importance values for tree and woody shrub species by upland land-use category. Only species with importance values > 1.0 are shown. Taxonomic nomenclature follows Clewell (1985).

palustris (upper slopes), and *Pinus elliottii* (upper slopes). On native ravine slopes, high importance values were observed for *Pinus glabra* (all slope positions), *S. tinctoria* (upper slopes), and *Quercus alba* (middle slopes). Overall, importance values for the species accompanying *Quercus hemisphaerica* on windrowed transects were skewed toward relatively lower values (Figure 3). By contrast, on middle and upper slopes of native sites where *Quercus hemisphaerica* was abundant, its importance did not greatly exceed other species.

MRPP tests indicated significant differences in species importance between land use categories (A = 0.22, p < 0.01; Table 1). This result was not a consequence of within land use group variability, as the differences in species importance among the individual land management units for each upland land use type were non-significant [native units (A = 0.04, p = 0.22) windrowed units (A = 0.04, p = 0.28)]. Comparisons of land use types by slope position indicated that middle slopes (A = 0.28, p < 0.01) had significantly different species importances. Upper and lower slopes were significantly different, but lower *A* values suggested that these differences were not as robust. Differences in species importance between north and south aspects and for aspects by slope position were similarly weak. Thus, the strongest differences in species importance, as indicated by statistical significance and high *A* values, can be attributed to land use, particularly on middle slopes. MRPP comparisons of relative percent dominance and relative percent density corroborated that land use accounted for greater compositional differences than aspect. Upper and middle slope species dominance and densities were significantly different with relatively high *A* values.

PCO results corroborated the compositional differences observed with MRPP. Ordination of species importance data for all 24-ravine slope transects indicated a clear separation of upland land use types along the first axis (Figure 4). The species importance values having significant correlations (Spearman's non-parametric rank order coefficient, r_s) with the first axis include *Ilex coriacea* (r_s = -0.75, > 0.01), *Pinus glabra* (r_s = 0.75, p < 0.01), *Quercus alba* (r_s = 0.60, p < 0.01), and *Quercus hemisphaerica* (r_s = -0.64, p < 0.01). Axis 2 had an eigenvalue < 1 and is not reported.



'igure 3. Tree and woody shrub species by upland land use and slope position. Unshaded bars represent ravine slopes adjacent to selectively-cut longleaf pine plands. Shaded bares represent ravine slopes adjacent to mechanically windrowed slash pine uplands.

DISCUSSION

The results of earlier studies conducted in these ravines confirmed that our sampling adequately characterized ravine slope vegetation. Kwit et al.'s (1998) list of the six most important ravine slope tree species in the ABRP were replicated in our investigation in the very same rank order (*Quercus hemisphaerica*, *Carya* spp., *F. grandifolia*, *M. grandiflora*, *Quercus alba*, and *Pinus glabra*). They sampled the same two ravines as our study, but included an adjacent ravine system to the north (Beaverdam Creek) and a wider range of aspects and slope angles. Schwartz (1990) sampled this same northern ravine along with one of the two examined in our study (Little Sweetwater Creek). His values for species relative density and relative dominance were also similar to ours. Kwit et al. (1998) noted that aspect only weakly influenced ravine tree distribution, a result we additionally confirmed.

Strong differences in ravine slope forest composition and structure were observed among our two upland land use history categories. *Quercus hemisphaerica* was the most abundant species in both land use types, but its importance was much higher in the ravines of windrowed uplands. Total stem density for *Quercus hemisphaerica*

Table 1. MRPP comparisons of species composition by land use category (native vs windrow), aspect (north vs. south), and slope position (lower, middle, upper). MRPP tests for land use and aspect compared two groups of twelve transects. MRPP tests for slope position by land use and aspect compared two groups of twelve quadrats.

	Importance		Relative Dominance		Relative Density	
Groups	*A*	*p*	*A*	*p*	*A*	*p*
Land use (native vs. windrow)	0.22	< 0.01	0.09	0.01	0.18	< 0.01
Upper slopes	0.11	< 0.01	0.03	0.13	0.24	< 0.01
Mid slopes	0.28	< 0.01	0.22	< 0.01	0.19	< 0.01
Lower slopes	0.07	0.01	0.03	0.13	0.07	< 0.01
Aspect (north vs. south)	0.06	0.04	0.02	0.20	0.04	0.05
Upper slopes	0.03	0.13	0.04	0.09	0.01	0.28
Mid slopes	0.03	0.14	-0.01	0.76	0.06	0.03
Lower slopes	0.05	0.02	0.04	0.09	0.04	0.04

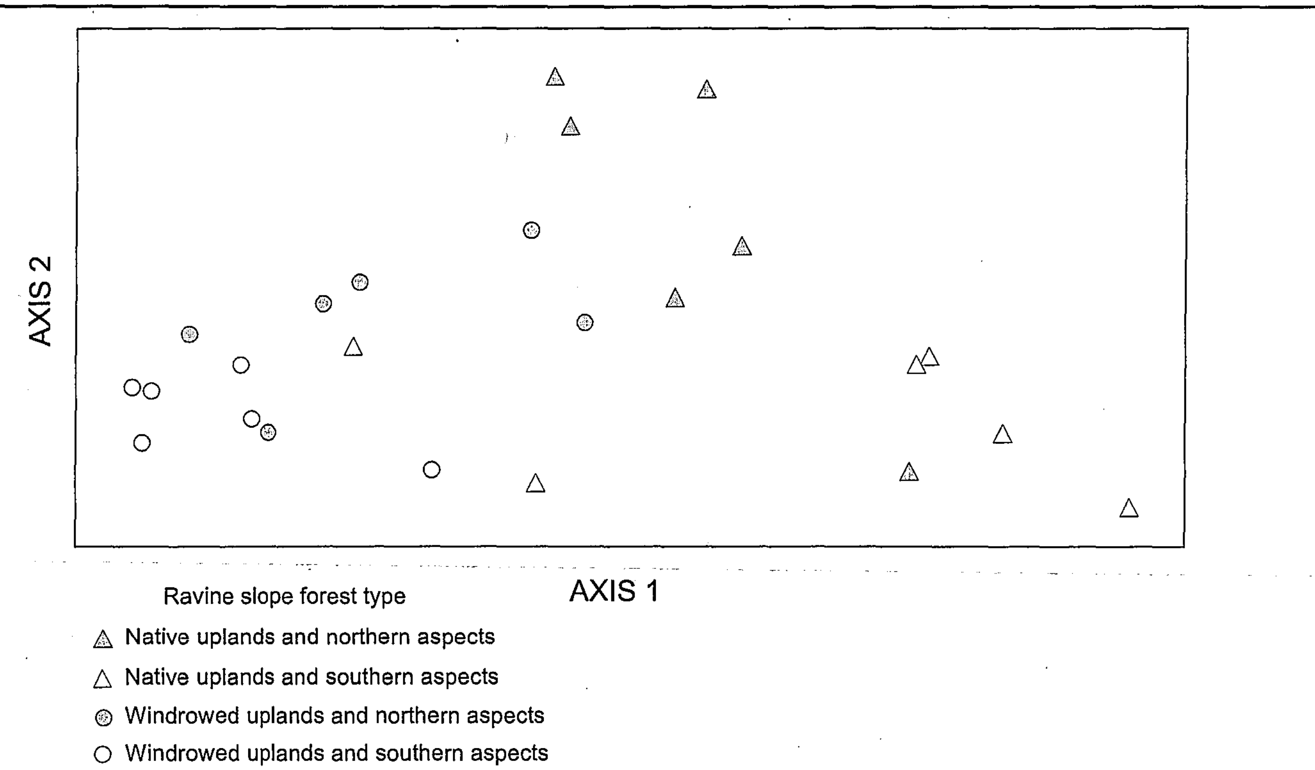


Figure 4. Principal coordinates scatterplot of transect-level data (n = 24). Axis 1 extracted 33% of the underlying variance in the data set.

was four times greater in ravines adjacent to windrowed uplands (0.17 stems/m^2 vs. 0.043 stems/m^2). These ravine slopes also had a greater frequency of sandhills species, particularly on upper and middle slopes. By contrast, *Pinus glabra*, a conifer more typical of rich woods and hammocks, was more important in native ravines. Accompanying *Pinus glabra* were higher basal areas of *Quercus alba* and *F. grandifolia*, particularly at mid and lower slope positions. The relative abundance of *F. grandiflora* has been proposed to decrease during periods of frequent canopy disturbance and to increase when the rate of canopy disturbance is low (Batista et al. 1998).

The high stem density and overall greater importance of *Quercus hemisphaerica* in windrowed ravines is likely due to land use history. *Quercus hemisphaerica* is fire intolerant and frequently weedy in north Florida. In addition to open woods, it occurs in disturbed areas, cut-over forests and old fields (Hall 1999). One possible scenario is that the silvicultural modification of these uplands facilitated the downslope expansion of *Quercus hemisphaerica* into the adjacent ravines. *Quercus hemisphaerica* commonly occurs in sandy xeric uplands as an early successional species following fire, or may re-invade a site after fire exclusion. It is a generalist species that responds to increased inputs of moisture, often becoming abundant in mesic habitats (Veno 1976, Vaitkus and McLeod 1995). These conditions were likely made available by the suppression of fire in the managed uplands and by the proximity of mesic ravine edge habitats.

CONCLUSION

Although historic land use has often been

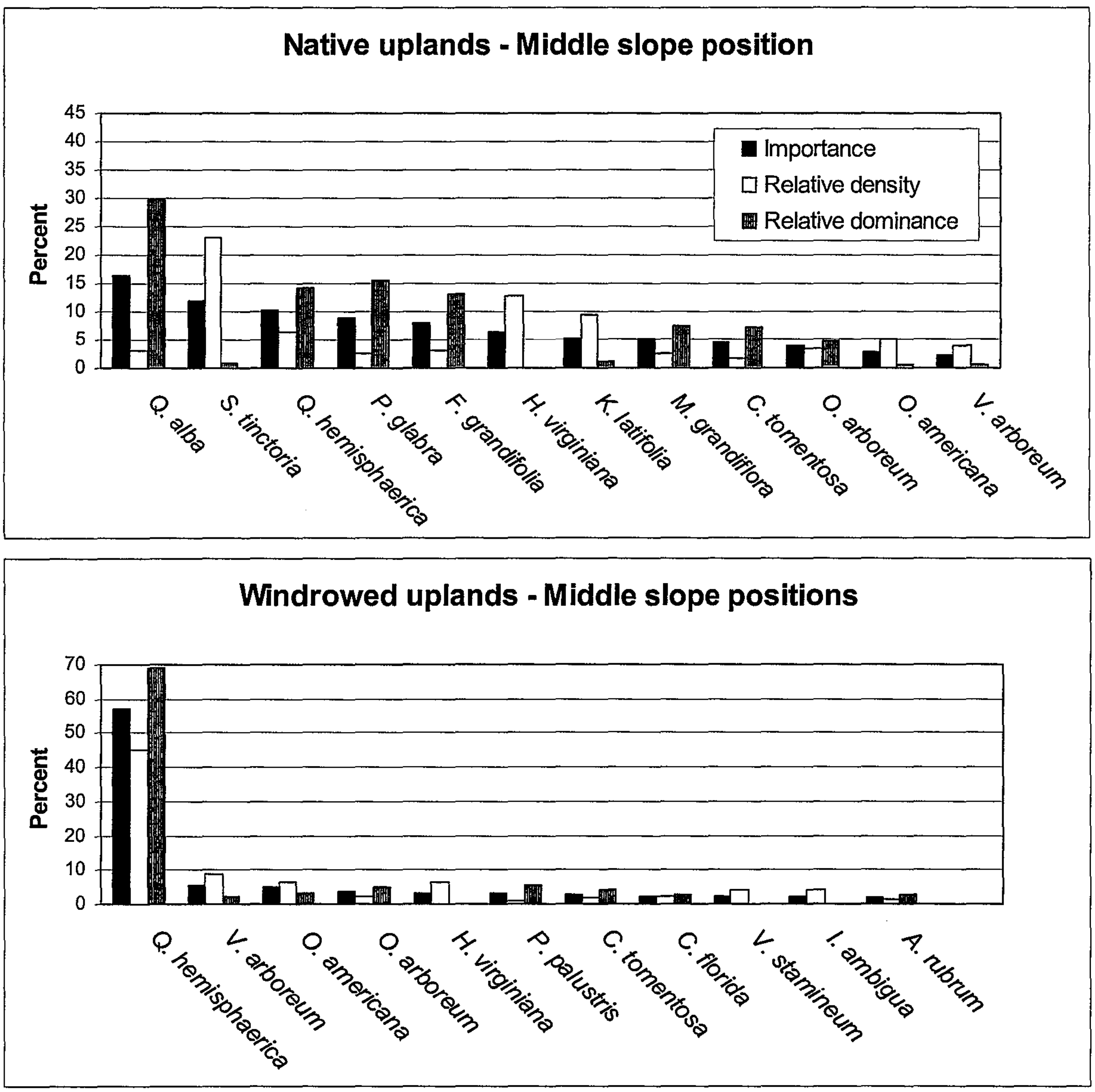


Figure 5. Ravine mid-slope woody species importance values by upland land use type. Only species with importance values > 2.0 are shown.

suggested as an important influence on Apalachicola ravine forests, our paper documents this relationship. We observed strong differences in ravine vegetation among contrasting upland lands use types, particularly at mid-slope positions. We viewed the composition of mid-slope ravine forests in windrowed uplands as representative of the broad vegetation changes initiated by slash pine silviculture (Figure 5). Overstory tree composition shifted from three tree species (*Quercus hemisphaerica*, *Pinus glabra* and *Quercus alba*) to one (*Quercus hemisphaerica*). *Fagus grandifolia*, a dominant species recorded in the Public Land Survey of the presettlement ravines in the 1820's (Delcourt and Delcourt 1977), was abundant where the uplands had not been windrowed. This lends more support to the idea that upland silvicultural practices have allowed oaks, particularly *Quercus hemisphaerica*, to dominate in the ravines.

Fire suppression accompanying slash pine cultivation appears to have initiated this shift by creating more opportunities for the encroachment of the fire-intolerant, generalist species such as *Quercus hemisphaerica* (Quarterman and Keever 1962). However, it is likely that fires were suppressed not only in the windrowed uplands, but also in the uplands with longleaf pine (see Outcalt 2000), as these land management units were embedded within the fire-suppressed silvicultured uplands. In this case, a greater abundance of *Quercus hemisphaerica* should have been observed in native ravines. In other words, if fire suppression was the only factor initiating vegetation change, there should have been fewer compositional differences between ravine types. Two hypotheses may explain why ravine slopes were not more similar.

Geomorphic disturbance (Swanson et al. 1988, Parker and Bendix 1996) may have been an additional component in the sequence of events leading to vegetation change in windrowed ravines. Platt and Schwartz (1990) suggested that removal of native vegetation in the uplands may have accelerated rates of groundwater seepage into the steepheads, thereby increasing the frequency of slumping and disturbance. Lower slope angles were observed in ravines adjacent to windrowed uplands, suggesting that slumping processes may be more active at these locations. Moreover, increased retreat of ravine slopes into upland habitats and the gravity-induced transport of soil and seed beds downslope may in part explain the increased importance of sandhills species in windrowed ravines. This scenario would have also increased gap establishment opportunities in the ravines for the generalist *Quercus hemisphaerica*. Alternatively, selective logging on the upper slopes of the windrowed ravines could have also led to more xeric conditions and the increased abundance of *Quercus hemisphaerica*. *Quercus hemisphaerica*, as a natural component of the transition zone between the ravines and the uplands (Schwartz 1990), may have expanded its range downslope with the removal of ravine slope hardwoods. Tree ring chronologies, soil profile descriptions, and quantification of geomorphic processes on ravine slopes are needed to examine these mutually compatible hypotheses in more detail.

A larger geographical study is needed to ascertain the generality of our findings to other ravine systems in the Florida panhandle (see Phillips 2001, Swetnam et al. 1999). For example, the extensive ravine system in Torreya State Park, just north of our study area, differs in both physiography and upland land use history (Platt and Schwartz 1990). However, our present study underscores how the legacies of land use activities may continue to influence species abundances and management strategies long after their occurrence (Foster et al. 2003, Suding et al. 2003). We are uncertain how upland restoration of native longleaf pine groundcover in the ABRP may influence ravine slope forest composition and structure. Reinstatement of fire frequencies that existed before intensive silviculture may not necessarily revert slope ravines back to their previous state (Vale 1982, Wallin et al. 1994). Other factors, including climate variability and forest pathogens (see Schwartz et al. 1995), may have also influenced the changes in ravine vegetation initiated by fire suppression, geomorphic disturbance, and selective logging. Our study is one component of the information needed to address this management issue.

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