RIVER RESEARCH AND APPLICATIONS

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BIOGEOMORPHIC CHARACTERIZATION OF FLOODPLAIN FOREST CHANGE IN RESPONSE TO REDUCED FLOWS ALONG THE APALACHICOLA RIVER, FLORIDA

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ABSTRACT

The Apalachicola–Chattahoochee–Flint (ACF) River basin is an important ecological and economic component of a three-state region (Florida, Alabama and Georgia) in the southeastern U.S. Along the Apalachicola River in northwest Florida, the duration of floodplain inundation has decreased as a result of declining river levels. Spring and summer flows have diminished in volume because of water use, storage and evaporation in reservoirs, and other anthropogenic and climatic changes in the basin upstream. Channel erosion from dam construction and navigation improvements also caused river levels to decline in an earlier period. In this paper, we document trends in floodplain forest tree species composition for the interval spanning these influences. Historic tree inventories from the 1970s were compared to present-day forests through non-metric multidimensional scaling, indicator species analysis (ISA) and outlier detection. Forests are compositionally drier today than in the 1970s. Overstory to understory compositional differences within habitats (levees, high/low bottomland forest and backswamps) are as large as the species contrasts between habitats. Present-day forests are also compositionally noisier with fewer indicator species. The largest individual declines in species density and dominance were in backswamps, particularly for *Fraxinus caroliniana Nyssa ogeche* and *Nyssa aquatica*. We discuss how contrasts in the compositional change signal for levee and backswamp landform habitats reflect a complex biogeomorphic response to fluctuating river flows for alluvial rivers in humid climates. Copyright © 2009 John Wiley & Sons, Ltd.

KEY WORDS: Apalachicola River; Atlanta; floodplain forest; biogeomorphology; *Nyssa*; honey

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INTRODUCTION

It is well-recognized that dams modify floodplain forests by their propensity to alter flood regime (Magilligan and Nislow, 2005; Graf, 2006). Downstream channels may incise because sediment trapped behind impoundments leads to flows with reduced load and more capacity to scour (Williams and Wolman, 1984). River stages may then drop for a given level of discharge, disconnecting floodplains from the main channel. Consequently, flooding becomes less frequent and more fragmented (Ward and Stanford, 1995; Steiger *et al*., 2005). Because flood regime acts as a forest disturbance agent and a control of soil moisture gradients, engineered rivers may undergo shifts in floodplain tree species composition (Malanson, 1993; Parker and Bendix, 1996; Bendix and Hupp, 2000).

However, dam impacts are influenced by geographic context (Brandt, 2000; Poff and Hart, 2002; Katz *et al*., 2005; Simon and Rinaldi, 2006). Low storage capacity dams influence downstream hydrographs differently than high storage capacity dams (Beauchamp and Stromberg, 2008). Channelization can lead to complex patterns of sediment mobilization (Shankman and Smith, 2004; Davis, 2007). Climatic fluctuations may mitigate or enhance the impacts of lower stages or reduced flow (Enfield *et al*., 2001; Whited *et al*., 2007). Water diversion for agriculture and population growth can become intertwined with how dams have modified channel processes and forms (Thoms *et al*., 2005).

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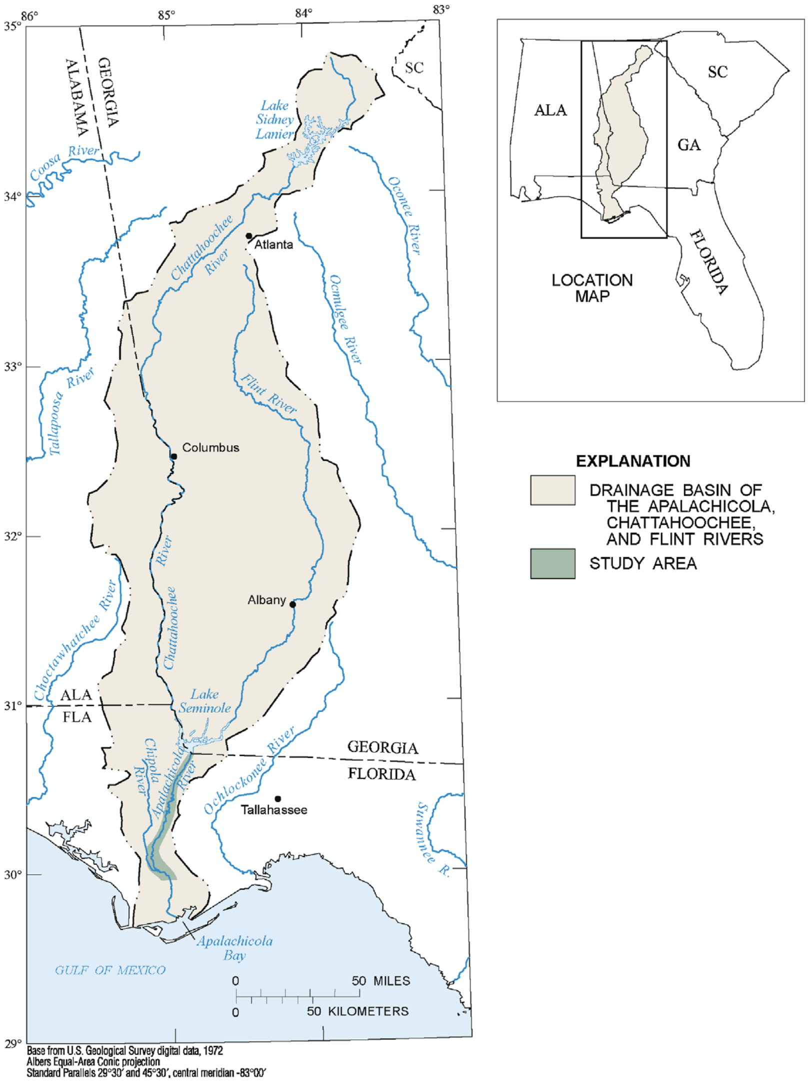
Similarly, vegetation responses to altered flows are dependent upon geographic context (Ligon *et al.*, 1995; Poff and Hart, 2002; Petts and Gurnell, 2005). Successional change reflects geographic differences in hydrological connectivity (Junk *et al.*, 1989; Kondolf *et al.*, 2006). Floodplain forest composition is a function of the flood tolerance of individual tree species and how they respond to canopy gap light and shade (Battaglia *et al.*, 2004; Battaglia and Sharitz, 2006). Local topography and elevation shape the environmental gradients and flood disturbance exposures controlling the distribution of vegetation among fluvial landforms (Parker and Bendix, 1996). In sum, floodplain forest dynamics on dammed rivers reflect the local outcomes of channel modification, basin-wide controls on water levels, canopy gap dynamics and individual species responses to changing flood regimes. This tension, between the generalized models of river modification and the particulars of how it plays out, highlights the value of regional and local interpretation of vegetation change along human-altered rivers (Phillips, 2003; Gregory, 2006; Chin *et al.*, 2008).

This study documents three decades of floodplain forest change along the Apalachicola River, a large alluvial river in the north Florida panhandle (Figure 1). The duration of floodplain innundation on the Apalachicola has decreased substantially as a result of declining river levels over the last 50 years. Spring and summer flows have



Base from U.S. Geological Survey digital data, 1972
Albers Equal-Area Conic projection
Standard Parallels 29°30′ and 45°30′, central meridian -83°00′

Figure 1. The Apalachicola, Flint and Chattahoochee River basin. Map courtesy of U.S. Geological Survey. This figure is available in colour online at www.interscience.wiley.com/journal/rra

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decreased since 1975 because of water use, storage and evaporation in reservoirs, and other anthropogenic and climatic changes in the basin upstream. Channel incision from dam construction and navigation improvements also caused river levels to decline in an earlier period from 1954–1980 (Gibson *et al*., 2005; Light *et al*., 2006). As a result, the quality and quantity of floodplain habitats for fish, mussels and other aquatic organisms have declined (Light *et al*., 1998). A recent U.S. Geological Survey (USGS) (Darst and Light, 2008) found present-day floodplain forests compositionally drier than forests sampled in the 1970s. In this paper, we employ the USGS repeat sampling dataset assembled by Darst and Light to (1) develop visualizations of the trajectories of forest compositional change through time and (2) to rank species according to their contribution to these trends. These results are then used to synthesize more detail about the contingencies in the processes driving the patterns of floodplain forest change.

We note that our treatment of the data and our statistical techniques differ from the USGS study. As an additional caveat, our goal is not to resolve the relative importance or causal order of anthropogenic and natural agents influencing the river and its floodplain, although we summarize several intensive field-based studies that do. Instead, we use forest compositional and structural change as a composite ecological indicator. Vegetation change in this sense is a lens to verify observations of the changes to channel morphology and water levels in the Apalachicola River. We also recognize that the choice of a baseline for characterizing ecological or hydrological patterns through time influences the trends detected (Kelly and Gore, 2008).

BACKGROUND

The Apalachicola River of the north Florida panhandle is the state's largest river by discharge and the fourth largest river in the southeastern U.S. (Iseri and Langbein, 1974). The floodplain forest of the Apalachicola is Florida's largest, and has long been recognized for its tree species richness (Harper, 1911; Kurz, 1938; Clewell, 1977). On high, infrequently flooded floodplain landforms, *Liquidambar styraciflua*, *Celtis laevigata* and *Carpinus caroliniana* are dominant tree species. Low bottomland forest increases in the importance of *Carya aquatica*, *Quercus lyrata*, *Quercus laurifolia* and *Fraxinus pennsylvanica*. At the lowest elevations are the frequently inundated backswamps and their cover of *Nyssa aquatica*, *Nyssa ogeche*, *Taxodium distichum* and *Fraxinus caroliniana*. Of the 70 tree species that occur along the river, several have direct economic importance today. Dense stands of *Nyssa aquatica* and *N. ogeche* support the production of tupelo honey. Bottomland hardwoods and cypress are still commercially logged on the floodplain, although the intensity of this present-day timbering is far less than what was practiced a century ago. The river and its floodplain are also coupled to estuarine trophic webs that support a commercial seafood industry and nursery grounds for Gulf of Mexico fisheries (Elder and Cairns, 1982; Wilber, 1992; Livingston *et al*., 1997).

The Apalachicola River begins at the confluence of the Chattahoochee and Flint Rivers (Figure 2). Ninety percent of this three-river basin is drained by the Chattahoochee and the Flint in Georgia and Alabama, with the remainder originating in Florida from the Apalachicola and its largest tributary, the Chipola River (Leitman *et al*., 1983). Upstream streamflow is the principal component in the Apalachicola's water budget, with precipitation, groundwater discharge, and other inputs contributing little to the magnitude or variability of flow (Mattraw and Elder, 1984). Atlanta's population at the headwaters of the ACF basin has increased from one million in 1959 to over five million in 2007. Because of population growth and agriculture in Georgia, water is diverted from the Apalachicola via withdrawals along the Chattahoochee and the Flint Rivers. In conjunction with drier climate (Barber and Stamey, 2000; Groisman and Knight, 2008; Knapp *et al*., 2008), these human demands have lowered flows into the Apalachicola and fomented debate among Florida, Alabama and Georgia over water allocation in the ACF basin (Feldman, 2008).

Low flows on the Apalachicola are superimposed upon the historic effects of channel incision initiated by the Jim Woodruff Dam during the period 1954–1980. The Jim Woodruff was built for flood regulation and recreation at the head of the Apalachicola River on the Florida–Georgia border. Construction of the dam began in the late 1940s and the reservoir (Lake Seminole) was filled by the late 1950s. Elder *et al*. (1988) and Leitman *et al*. (1983) compared multidecadal periods before and after construction of the dam and found a decline in the stage-duration curve, which represents the percentage of time that a given river stage is equaled or exceeded. Simons *et al*. (1985) also

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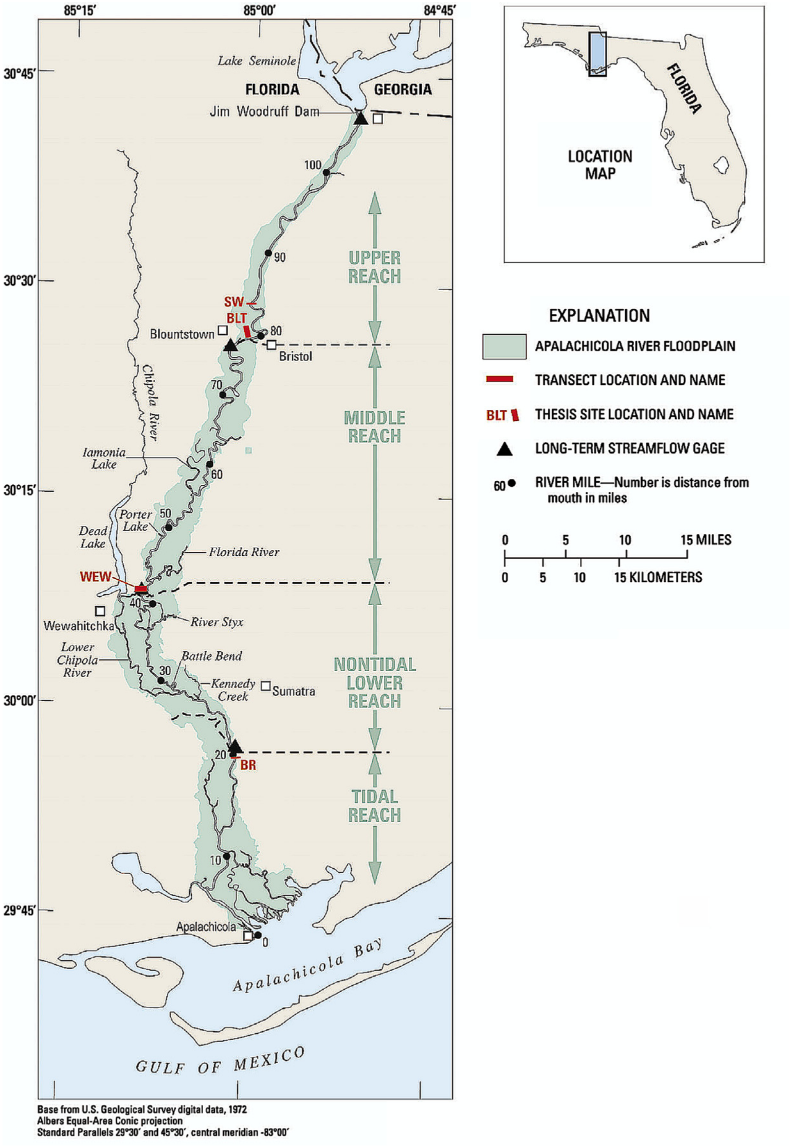

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Figure 2. The Apalachicola River floodplain and sampling sites for this study. Map courtesy of U.S. Geological Survey. Historic Blountstown and Wewahitchka data collected by Leitman (1978). Historic data for Sweetwater and Brickyard collected by Leitman *et al*. (1983). This figure is available in colour online at www.interscience.wiley.com/journal/rra

documented incision of the main river channel over the two decades following dam closure. Stage-discharge relationships detailed by Light *et al*. (2006) indicated lower river stages for the same discharges in the post-dam (1995–2004) versus the pre-dam (1929–1954) period. Smith (2007) employed indicators of hydrologic alteration (IHA) to compare 28-year intervals before and after the dam construction (1929–1956 and 1977–2004) and found statistically significant mean declines in annual average stage, with the greatest decline developing in the spring and summer months. Mean minimum annual stages, rise rates and fall rates decreased significantly, while hydrograph reversals have increased. Gibson *et al*. (2005) found similar trends in their IHA analysis of hydrographic data for another monitoring station on the Apalachicola.

Channel incision from the dam extended into the middle reaches of the river with the magnitude of the stage decline becoming steadily smaller with increasing distance downstream (Figure 3). However, in terms of ecological

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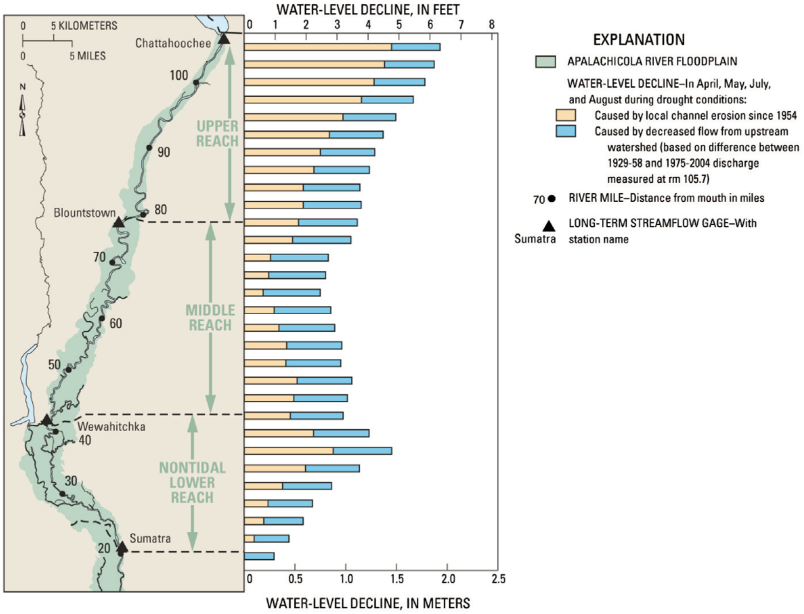

Figure 3. Long-term water level decline corresponding to map locations in April, May, July and August during drought conditions. Drought conditions are defined as the lowest 10% of flows. Declines in non-tidal lower reach of river attributed to channel dredging and straightening. See Darst and Light (2008) for details. Map courtesy of U.S. Geological Survey. This figure is available in colour online at www.interscience.wiley.com/journal/rra

consequences, this downstream attenuation may be partially offset by the progressively flatter floodplain topography. Water-level decline in the lower non-tidal reaches of the river is also attributed to direct channel modification. Between 1956 and the early 2000s, the U.S. Corps of Engineers maintained a navigation channel in the river. Dredge spoil was deposited on the floodplain, leading to areas of localized forest loss. To straighten the river, the Corps of Engineers disconnected several meanders from the main channel (Light *et al*., 1998). River straightening steepens channels, thereby increasing flow velocities and the capacity to scour and entrench (Schumm *et al*., 1984). Climate fluctuations accompanied these channel modifications and upstream water diversion. A severe 3-year drought characterized the period from 1954–1956. The two decades (1958–1979) following dam construction had higher average annual flows than the equivalent period (1929–1957) preceding it (Leitman *et al*., 1983; Elder *et al*., 1988). Drought conditions arrived again in the 1980s and have become particularly acute over the last several years (Barber and Stamey, 2000; Verdi *et al*., 2006).

The source of water level declines in the Apalachicola is a synergism of ongoing upstream withdrawals, historic river engineering and drought. Upstream withdrawals exacerbate drying of the floodplain because the Jim Woodruff dam and other dams in the ACF basin are low storage capacity dams. Whereas dams with high storage capacity can smooth out hydrograph extremes, dams with low storage capacity retain a wider range of flow variability. Low flows cannot be counteracted downstream with supplemental water release. Conversely, high water events are not completely absorbed by upstream impoundments. As a result, peak flooding in late winter and early spring persists on the Apalachicola today. However, the effects of stage decline have become pronounced during low and medium flows ($<850\,\mathrm{m^3\,s^{-1}}$), which constitute about 80% of the flow conditions on the Apalachicola (Darst and Light, 2008). Consequently, the hydrological connectivity between the main channel and floodplain habitats along the Apalachicola River has decreased (Light *et al*., 1995, 1998).

Fragmentation of hydrological connectivity can impact large areas of floodplain forest (Tockner and Stanford, 2002; Pringle, 2003; Thoms *et al*., 2005). Using repeat sampling plots, the USGS found that the present-day forest composition along the Apalachicola reflects drying conditions when compared to data collected in the 1970s. Subcanopy trees, individuals that will comprise the future canopy, were the driest size class in present-day forests (Darst and Light, 2008). We contribute to this characterization of Apalachicola River floodplain forests by

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statistically ranking individual species changes spanning the same three-decade interval assessed by the USGS. We describe how forest floodplain dynamics along the Apalachicola River differ across fluvial landforms spanning levees to backswamps. Ordination was employed to visualize the broad trajectories of change in tree species composition by size class and landform habitat over the interval 1970–2004. Indicator species analysis (ISA) was used to statistically delineate tree species that characterized the 1970 (historic) and the 2004 (present day) time periods. Lastly, outlier analysis identified species with high net increases or decreases over time. Our results are discussed in light of how lower water levels in the channel differentially impact levee and backswamp habitats, and what this implies for the geographic consistency of a floodplain forest change signal under a scenario of ongoing flow reductions.

METHODOLOGY

Leitman *et al*. (1983) and Leitman (1978) delineated four forest habitats corresponding to fluvial landforms along the Apalachicola River (levees, high bottomland, low bottomland and backswamps) and delineated their tree species composition. Repeat sampling of these landform habitats at four historic survey sites (SW, BLT, WEW and BR) was undertaken with the USGS during 2004–2006 (Table I). Because some tree species are not abundant in the upper reaches of the river directly below the dam, the four sites selected for analysis in this paper represented the greatest overlap of tree species ranges. These sites are also where the floodplain is at its largest areal extent, and where historic sampling by the USGS was most intensive. As the river directly below the dam underwent the greatest incision, selecting sites well below the dam balanced out the relative influence of channel incision with flow reductions due to natural and anthropogenic sources. Estimated innundation frequencies for habitats and sites are presented in Darst and Light (2008).

A total of 37 woody tree species, comprising 2822 individual stems, defined the final analysis dataset (Table II). To elucidate structural changes associated with gap dynamics, trees were classified into three stem size (dbh, diameter at breast height) classes: 7.5–10, 10–25 and >25 cm. Dendrochronological analysis (Smith, 2007) of 140 cores (two cores per tree) among four tree species (*Taxodium distichum*, *Celtis laevigata*, *Quercus lyrata* and

Table I. Sampling locations and intensities selected for this study

Site	Historic (1976–1977, 1979)	Present (2004–2006)
SW	7 plots 3542 m^2 299 trees 3A, 1B, 1C, 2D habitats	8 plots 4247 m^2 281 trees 5A, 1B, 1C, 1D habitats
BLT	5 plots 12 051 m^2 581 trees 1A, 3B, 1C habitats	5 plots 11 331 m^2 544 trees 1A, 3B, 1C habitats
WEW	5 plots 7600 m^2 375 trees 3B, 2C habitats	6 plots 4722 m^2 255 trees 3B, 2C, 1D habitats
BR	4 plots 2024 m^2 174 trees 2B, 2D habitats	8 plots 4247 m^2 313 trees 2B, 1C, 5D habitats
All sites	1429 trees 25 217 m^2 4A, 9B, 4C, 4D habitats	1393 trees 24 547 m^2 6A, 9B, 5C, 7D habitats

The number of plots, total area sampled, the number of trees and a count of plot habitat types are given. Sites: Sweetwater—SW, Blountstown—BLT, Wewahitchka—WEW and Brickyard—BY. Habitats: A—levee, B—high bottomland, C—low bottomland, D—backswamp. See Darst and Light (2008) for full description of sampling methods.

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Table II. Species occurring in sample plots on at least one of the four sampling sites and grouped by floodplain species code (FSC)

Scientific name	Code	Common name	Shade tolerance
FSC = 1 (obligate wetland species)			
Cephalanthus occidentalis L.	cepocc	buttonbush	3
Fraxinus caroliniana Mill.	fracar	pop ash	2
Nyssa aquatica L.	nysaqu	water tupelo	3
Nyssa ogeche Bartr. ex Marsh.	nysoge	white tupelo	3
Planera aquatica Walt. ex. Gmel.	plaaqu	water elm	2
Populus heterophylla L.	pophet	swamp cottonwood	3
Salix nigra Marsh.	salnig	black willow	3
Taxodium distichum (L.) Rich.	taxdis	bald cypress	2
FSC = 2 (facultative wetland species)			
Acer rubrum L.	acerub	red maple	1
Betula nigra L.	betnig	river birch	3
Carya aquatica (Michx. f.) Nutt.	caraqu	water hickory	2
Cornus foemina Mill.	corfoe	stiff dogwood	1
Crataegus viridis L.	cravir	green hawthorn	2
Forestiera acuminata (Michx.) Poir. in Lam.	foracu	swamp privet	2
Fraxinus pennsylvanica Marsh.	frapen	green ash	2
Gleditsia aquatic Marsh.	gleaqu	water locust	2
Quercus laurifolia Michx.	quelau	swamp laurel oak	1
Quercus lyrata Walt.	quelyr	overcup oak	2
Ulmus americana L.	ulmame	American elm	2
FSC = 3 (facultative upland species)			
Acer negundo L.	aceneg	box elder	2
Carpinus caroliniana Walt.	carcar	American hornbeam	1
Celtis laevigata Willd.	cellae	hackberry	1
Cyrilla racemiflora L.	cyrrac	titi	3
Diospyros virginiana L.	diovir	persimmon	1
Halesia diptera Ellis.	haldip	silverbell	1
Ilex decidua Walt.	iledec	possum haw	2
Ilex opaca Ait.	ileopa	American holly	1
Liquidambar styraciflua L.	liqsty	sweetgum	3
Morus rubra L.	morrub	red mulberry	3
Nyssa biflora Walt.	nysbif	black tupelo	1
Platanus occidentalis L.	plaocc	sycamore	2
Quercus nigra L.	quenig	water oak	2
Sapium sebiferum (L.) Roxb.	sapseb	popcorn tree	1
FSC = 4 (Upland species)			
Juglans nigra L.	jugnig	black walnut	3
Melia azedarach L.	melaze	chinaberry	3
Quercus hemispherica Batr. ex. Willd.	quehem	laurel oak	1
Ulmus alata Michx.	ulmala	winged elm	1

Shade tolerance ranges from shade tolerant (1), intermediate shade tolerance (2) and shade intolerant (3) based on Burns and Honkala (1990).

Quercus laurifolia) indicated that trees in the intermediate (10–25 cm) size class had establishment dates roughly corresponding to the period during dam construction and immediately after (median age = 48 years). The largest diameter size class would be more likely to have established before the dam (median age = 80 years), and the smallest size class more likely to have established during or after the 1970s (median age = 27 years). Given variability in growth due to species life history traits and local conditions, these size-date associations provide only approximate establishment windows and are best used to infer gap dynamics.

Habitat and species observations were decomposed into size classes to enhance the gap dynamics signal. For example, instead of four habitat observations in our ordination analyses, we had 12 (4 habitats × 3 size classes). In

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outlier and indicator analyses, species were also broken down into three size classes. So instead of one species (for example, *Fraxinus caroliniana*) there were three, one for each size interval (fracar1, fracar2, fracar3). Thus there were 111 species observations (37 × 3) when accounting for dbh size class. These groupings are herein referred to as habitat × size and species × size. Plant nomenclature follows Godfrey (1988).

Each species was matched to a floodplain species category (FSC) according to methods described in Darst and Light (2008). The FSC varies from 1 to 4, based on information synthesized from the National Wetlands Inventory, tree species dominance patterns in other north Florida floodplains, and the original 1970s vegetation surveys along the Apalachicola. A FSC value of 1 corresponds to an obligate wetland species that occurs nearly always in wetlands; a FSC of 2 corresponds to a facultative wetland species which usually occurs in wetlands; a 3 is assigned to a species equally likely to occur in wetlands; and a 4 represents a facultative upland species that usually does not occur in wetlands. A FSC of 4 approximates conditions on Apalachicola River levees, high bottomland converges on a FSC of 3, low bottomland has a FSC of 2 and backswamps correspond to a FSC of 1.

Non-metric multidimensional scaling (NMS; McCune *et al.*, 2002) was used to visualize compositional change between sampling times and among different habitat × sizes. NMS was applied to two forest descriptors, species dominance ($m^2\,ha^{-1}$) and species density (stems m^{-2}). NMS summarizes the similarity among observations (rows) as a function of the species (columns) that comprise them. Distance metrics are calculated for each observation's similarity with all other observations. Observations are then iteratively positioned into a multidimensional ‘‘species’’ space, a scatterplot, based on these similarity distances. Observations closer to each other in the scatterplot are more similar in composition, distant observations less so. To gauge the utility of a NMS solution, one compares the reduction in stress, a measure of fit between similarity distances and graphical distances, as dimensionality increases. Increasing dimensionality implies moving from a one-dimensional to two- and three-dimensional representation. Higher dimensionality has less stress, but interpretability decreases as more axes are used. Multiple NMS runs were performed in PC-Ord Version 5 (McCune and Mefford, 1999). A range of dimensionalities was employed to optimize selection of a low dimensional representation with the greatest stress reduction while minimizing the likelihood of local optima. Monte Carlo permutations of the data indicated the degree any corresponding decrease in stress is greater than expected by chance. Sorenson's (Bray–Curtis) distance was selected for the distance metric. Observations were relativized to 1 prior to ordination. Varimax rotation was performed on the final NMS solution.

ISA (McCune *et al.*, 2002; Bakker, 2008) identified tree species × size that had statistically higher frequencies and abundances across all plots of each habitat type within each time period. ISA ranked the dominance and density of species based on a relativized indicator value. Indicator values are the product of relative abundance and relative frequency expressed as a percentage. Statistical significance is based on the proportion of times that the maximum indicator value for a species from a randomized data set equals or exceeds the indicator value from the actual data set. The level of significance was set to values of $p < 0.10$. Twenty-four indicator tests were performed for density and for dominance, one test for each of the three species × size classes among the four habitats in the historic and present time periods (3 × 4 × 2).

Net increases and decreases in species dominance and density were identified and ranked through outlier analysis (McCune *et al.*, 2002). First, net changes in species × size for dominance and for density were each converted to a matrix of similarity distances. Outliers were identified in the dominance matrix and the density matrix by calculating an average distance for individual species, and then comparing this value to a frequency distribution of average distances. Average distances falling beyond one standard deviation were designated as outliers. Four species × size outlier tests, one for each habitat, were conducted for density and for dominance. Species × sizes were then ranked according to how many of the four criteria (density indicator, density outlier, dominance indicator and dominance outlier) were met. In this manner, we were able to rank species according to their relative fidelity within plots of each time period, as well as the magnitude of their net change between time periods. Only species meeting two or more of the four criteria were considered in the final summary of compositional change.

Multivariate permutation-based tests of group differences (MRPP) were used to ascertain whether the historic and present plot compositions for the final ranked species from each habitat were significantly different (McCune *et al.*, 2002; Cade and Richards, 2005). In MRPP, an average similarity distance among all observations is compared to the average distance obtained when all permutations of group membership are considered. Significance is calculated from the proportion of permutation-derived distances that fall below the observed

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average within group distance. For these tests, species importance, the average of relative percent dominance and relative percent frequency, was employed. Sorenson's distances were used as the distance metric. Outlier analysis, ISA and MRPP were conducted in PC-Ord Version 5 (McCune and Mefford, 1999).

RESULTS

Non-metric multidimensional scaling

Based on Monte Carlo randomizations ($n = 999$) and multiple runs of NMS ($n = 50$), a two-dimensional solution optimized stress reduction for species density ($p = 0.004$) and for species dominance ($p = 0.004$). Habitat types were well defined in the scatterplots, with a propensity for upland (A and B) and lowland (C and D) landform habitats to cluster (Figures 4 and 5). Historic composition was more distinct, as indicated by the greater dispersion of historic vectors. Present-day forest habitats are compositionally more similar, as indicated by the shift in vectors toward each other. C and D habitat vectors shifted over time toward A and B positions, drier and higher floodplain forest. Conversely, A and B vectors shifted toward bottomland C and D compositions over time.

Varimax rotation aligned the greatest compositional variance along the first axis in each NMS scatterplot. As a null hypothesis, it was expected that the first axis would be dominated by the prominent dry (levee—A) to wet (backswamp—D) compositional gradient that typifies floodplain landform habitats subject to predictable flood

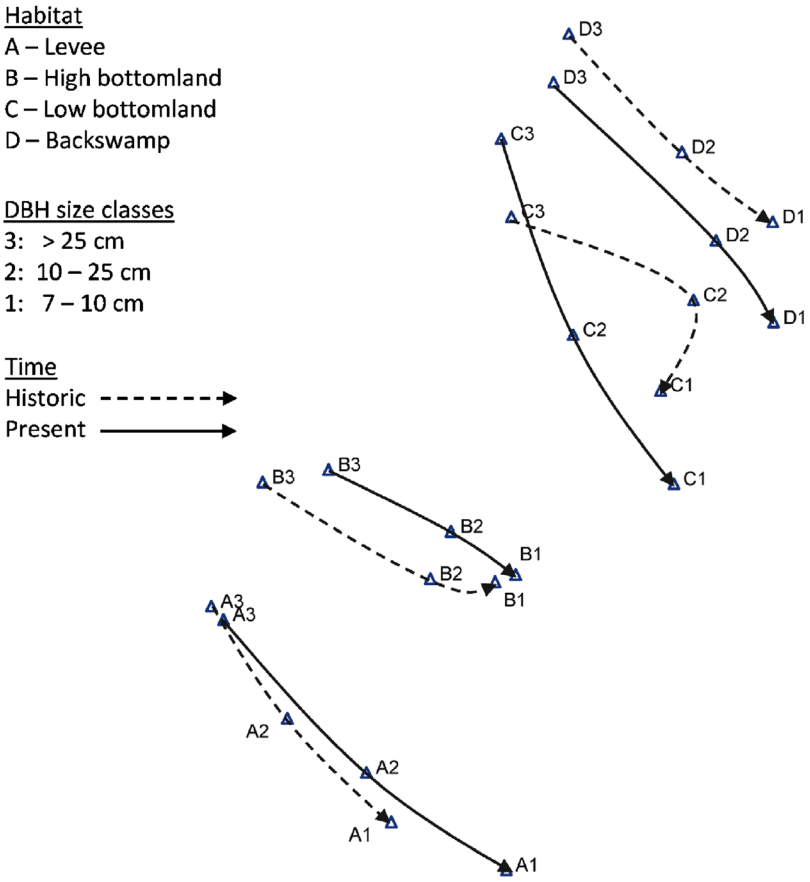

Figure 4. NMS plot for species density. Axes are scaled relative to Sorenson's distance, which expresses percent dissimilarity. Horizontal distance along on x-axis between A3—historic and D1—present data points represents 100% dissimilarity. Vertical distance along y-axis between A1—present and D3—historic data points represents 100% dissimilarity. This figure is available in colour online at www.interscience.wiley.com/journal/rra

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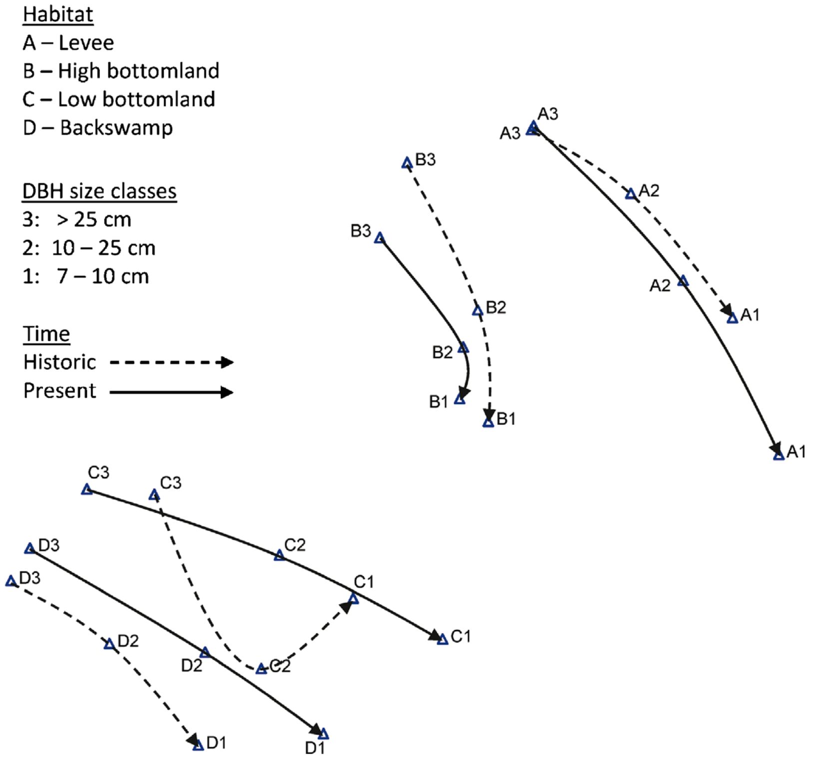

Figure 5. NMS plot for species dominance. Axes are scaled relative to Sorenson's distance, which expresses percent dissimilarity. Horizontal distance along on *x*-axis between D3—historic and A1—present data points represents 100% dissimilarity. Vertical distance along *y*-axis between D1—historic and A3—present data points represents 100% dissimilarity. Reversal of order of sites from right to left is a common artefact of NMS solutions. This figure is available in colour online at www.interscience.wiley.com/journal/rra

disturbance (see Turner *et al.*, 2004). However, the wet-dry gradient was distributed across the first (*x*) and the second (*y*) axis, indicating that flood exposure is not the major source of compositional turnover across the floodplain. Based on relative length of density and dominance vectors in Figures 4 and 5, compositional differences across the size classes of each habitat were as great as or greater than differences between habitats. In other words, for both present and historical observations, the dissimilarity in composition from overstory (size class 3) to understory (size class 1) is as large as what separates habitats in terms of their relative wetness or dryness. Furthermore, the lengths of the vectors in the present-day observation are slightly longer, suggesting more compositional dissimilarity between overstory and understory trees today than in the past.

Outlier analysis

The backswamp (D) had a prominent decline in species density (556 stems ha^{-1}; Table III). All backswamp outliers were declines, notably *N. aquatica* and *Taxodium distichum*. The other three habitats had a mix of increasing and decreasing outliers. *Liquidambar styraciflua* was a strong outlier on the levee (A) and high bottomland (B). Density decreased for the two smallest size classes of this shade-intolerant tree. For low bottomland (C), gains were recorded for large individuals of *Nyssa* spp. and *T. distichum*. Declines in *Fraxinus pennsylvatica* were a prominent outlier.

Dominance outliers were more numerous, but species contrasts within habitats were muted (Table IV). Losses exceeded gains only in the backswamp, where declines were concentrated among all size classes of the genus *Nyssa*. Large individuals of *T. distichum* had the only notable increase. Low bottomland habitats also gained basal area within the larger size classes of *T. distichum* as well as *N. aquatica*. Smaller stems of *L. styracuflua* decreased in basal area on the levee and high bottomland, while larger, unshaded individuals increased.

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Table III. Stem density outliers. Species × size class ranked by magnitude of absolute change in stem density (stems ha^{-1}) between historic and present-day sampling

Levee		High bottomland		Low bottomland		Backswamp	
Spp × size	Δ stems ha^{-1}	Spp × size	Δ stems ha^{-1}	Spp × size	Δ stems ha^{-1}	Spp × size	Δ stems ha^{-1}
liqsty2	−72	liqsty2	−13	fracar2	−54	taxdis2	−121
iledec2	−19	ulmame2	−11	betnig2	−14	nysaqu2	−118
liqsty1	−16	quelyr2	−10	nysaqu2	−13	fracar1	−64
frapen2	−13	iledec2	−8	fracar1	−13	nysbif3	−64
ileopa1	11	caraqu2	−7	nysoge1	17	nysoge2	−62
ulmala2	14	corfoe1	3	plaaqu1	20	nysaqu3	−60
cellae2	20	nysoge3	5	taxdis2	20	taxdis1	−37
carcar2	24	nysoge2	5	taxdis3	23	plaaqu1	−30
				nysoge2	41		
				nysaqu3	46		
Gain	+69		+13		+167		0
Loss	−120		−49		−94		−556
Net	−51		−36		+73		−556

Size classes (dbh): Class 1 = 7.5–10 cm, Class 2 = 10–25 cm, Class 3 >25 cm. Similarity in magnitude of change calculated as Euclidean distances.

Indicator species analysis

Of the seventeen indicator species identified, all but two originated from the historic data set. This suggests that species frequencies and abundances within present-day habitats are less consistently structured than in the 1970s (Tables V and VI). Indicator species for stem density on levees were intermediate (size class = 2) stem diameters of

Table IV. Species dominance outliers. Species × size class ranked by magnitude of absolute change in basal area ($m^2 ha^{-1}$) between historic and present-day sampling for all sites

Levee		High bottomland		Low bottomland		Backswamp	
Spp × size	Δ ($m^2 ha^{-1}$)	Spp × size	Δ ($m^2 ha^{-1}$)	Spp × size	Δ ($m^2 ha^{-1}$)	Spp × size	Δ ($m^2 ha^{-1}$)
liqsty2	−1.7	liqsty2	−0.3	quelyr3	−1.7	nysbif3	−6.3
frapen3	−0.5	quenig3	−0.3	pophet3	−0.9	taxdis2	−2.9
frapen2	−0.3	ulmame2	−0.3	fracar2	−0.9	nysaqu2	−2.6
ulmame2	−0.2	quelyr2	−0.3	fracar3	−0.8	nysaqu3	−1.8
iledec2	−0.2	caraqu2	−0.2	nysoge3	−0.6	nysoge2	−1.5
cellae3	−0.2	plaocc3	0.2	betnig2	−0.2	nysoge3	−0.6
aceneg2	0.2	plaaqu2	0.3	gleaqu2	0.2	nysbif2	−0.5
aceneg3	0.2	cellae2	0.3	gleaqu3	0.3	fracar1	−0.4
caraqu3	0.2	quelau2	0.3	taxdis2	0.4	plaaqu3	−0.3
ulmala2	0.4	acerub3	0.3	ulmame3	0.4	taxdis1	−0.2
cellae2	0.4	ulmame3	0.4	ulmame2	0.4	plaaqu2	−0.2
plaocc3	0.4	quelyr3	0.4	nysoge2	0.5	plaaqu1	−0.2
nysbif3	0.4	nysaqu3	0.6	caraqu3	0.6	fracar3	0.4
carcar3	0.4	frapen3	0.6	acerub3	0.7	quelau3	0.8
carcar2	0.7	nysoge3	0.7	nysaqu3	5.7	acerub3	0.9
liqsty3	2.7	taxdis3	0.8	taxdis3	6.3	taxdis3	6.7
		liqsty3	1.4				
		quelau3	1.6				
Gain	+6.0		+7.9		+15.5		+8.8
Loss	−3.1		−1.4		−5.1		−17.5
Net	+2.9		+6.5		+7.4		−8.7

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Table V. Density indicator species × size for historic (H) and for present (P) forests

Habitat	Spp × size	Time period	Trend (+/−)	IV	*p*
Levee	liqsty2	H	−	78%	0.05
	frapen2	H	−	64%	0.10
High bottomland	ulmame2	H	−	63%	0.06
	quelyr2	H	−	58%	0.10
	corfoe1	P	+	44%	0.08
Low bottomland	fracar3	H	−	100%	0.01
	fracar1	H	−	76%	0.07
Backswamp	nysaqu1	H	−	75%	0.03

Analyses performed on plot level data. IV designates indicator value. Net change over time indicated as + or −.

historic *Liquidambar styraciflua* and *Fraxinus pennsylvanica*. In high bottomland, intermediate-sized stems of *Ulmus americana* and *Quercus lyrata* qualified as indicators. *Cornus foemina,* a relatively uncommon shade tolerant understory tree in high bottomland forest, was one of the two species meeting indicator criteria from the present-day data. A range of stem diameters for *Fraxinus caroliniana* characterized historic low bottomland. Young, small-diameter *Nyssa aquatica* were the only indicator species in the backswamp. Stem densities decreased for both of these obligate wetland species.

Indicator species for dominance were similar to density, especially in the low bottomland and backswamp (Table VI). High bottomland picked up declines in basal area for intermediate-sized stems of *Carya aquatica*. A common understory tree, *Celtis laevigata,* was the second of the two species in the present-day data with the plot fidelity and abundance to meet indicator criteria.

Ranking of species change

For levees, two species met all four criteria (Table VII), *Liquidambar styraciflua* and *Fraxinus pennsylvatica*. Intermediate-size stems for these to species exhibited consistent declines across indicator and outlier measures. Four species × size met only two outlier criteria: declines in *Ilex decidua* accompanied gains in *Carpinus caroliniana*, *Celtis laevigata* and *Ulmus alata*.

In the high bottomland, reductions in *Quercus lyrata* and *Ulmus americana* were expressed in all four criteria. Less consistent declines were observed for *Carya aquatica* and *Liquidambar styraciflua*. Two shade-tolerant trees, *Celtis laevigata* and *Cornus foemina*, and larger stems of *Nyssa ogeche* met two ranking criteria for their increases in density and dominance.

No species met all four criteria in the low bottomland and backswamp (Table VIII). Outliers were more prevalent than indicators, and declines led increases. In low bottomland, *Fraxinus caroliniana* met three of the four ranking

Table VI. Dominance indicator species × size for historic (H) and present (P) forests

Habitat	Spp × size	Time period	Trend (+/−)	IV	*p*
Levee	liqsty2	H	−	78%	0.06
	frapen2	H	−	69%	0.07
High bottomland	ulmame2	H	−	64%	0.04
	caraqu2	H	−	58%	0.10
	quelyr2	H	−	60%	0.08
	cellae2	P	+	59%	0.10
Low bottomland	fracar3	H	−	100%	0.01
	fracar1	H	−	78%	0.06
Backswamp	nysaqu1	H	−	75%	0.03

Analyses performed on plot level data. IV designates indicator value. Net change over time indicated as + or −.

Table VII. Ranked species meeting at least two of the four criteria indicative of significant compositional change on levee and in high bottomland habitats

Habitat and FSC equivalent	FSC	Density		Dominance		Size class
		Indicator	Outlier	Indicator	Outlier	
Levee (FSC = 4)						
Liquidambar styraciflua[a]	3	−	−	−	−	2
Fraxinus pennsylvanica[a]	2	−	−	−	−	2
Ilex decidua[a]	3		−		−	2
Carpinus caroliniana[b]	3		+		+	2
Celtis laevigata[b]	3		+		+	2
Ulmus alata[c]	4		+		+	2
High bottomland (FSC = 3)						
Quercus lyrata[a]	2	−	−	−	−	2
Ulmus americana[a]	2	−	−	−	−	2
Carya aquatica[a]	2		−	−	−	2
Liquidambar styraciflua[d]	3		−		−	2
Celtis laevigata[b]	3			+	+	2
Cornus foemina[b]	3	+	+			1
Nyssa ogeche[e]	1		+		+	3

Net change in density and dominance indicated as + or −.

[a] Declining due to drier conditions.

[b] Increasing due to shade tolerance.

[c] Increasing due to drier conditions.

[d] Declines due to shade intolerance.

[e] Increases due to large size of tree and resistance to drier conditions.

criteria. Decline for *Fraxinus* occurred across all three stem sizes. Large stems of *Nyssa aquatica*, *Nyssa ogeche* and *Taxodium distichum* ranked as outliers in low bottomland due to relatively large increases in density and dominance over time. The backswamp was characterized by a strong and consistent decline in *Nyssa*.

MRPP indicated that the compositional change over time for these ranked species was strongest in the levee and high bottomland (Table IX). The compositional change signal declined in strength and significance in the low bottomlands and backswamp.

DISCUSSION

NMS vector lengths and their shifts in position between 1970 and 2004 suggest historically persistent floodplain forest drying. The wet-dry gradient of environmental conditions and flood exposure among landform habitats was not the primary source of compositional variability in either the historic or present-day forest, as might be expected if flooding was a dominant control of forest composition. Instead, compositional dissimilarity across size classes (the length of the NMS vectors) within present and historic habitats was as great as the distances between habitats. The magnitude of size class dissimilarity relative to the compositional sorting among habitats suggests that drying, and the gap dynamics factors that come into play once the forest is divorced from immediate extrinsic flood-related drivers, are heightened controls of the historic and present-day forest.

Drying can also account for how the compositional gradient of floodplain habitats has contracted and become more similar through time. Increasing similarity of habitats reflects in part how larger, mature canopy dominants withstand drying. With water-level declines, older *Nyssa* and *T. distichum* that established widely under historically wetter conditions may have gained in importance because their size now confers more resistance to dessication. The persistence of these larger, well-established canopy dominants, when paired with changing recruitment trends associated with lower flows and drier conditions, would also account for why compositional dissimilarity across habitat size classes is as large as the wet-dry compositional gradient. Although drying increases habitat similarity

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Table VIII. Ranked species meeting at least two of the four criteria indicative of significant compositional change for the low bottomland and backswamp

Habitat and FSC equivalent	FSC	Density		Dominance		Size class
		Indicator	Outlier	Indicator	Outlier	
Low bottomland (FSC = 2)						
Fraxinus caroliniana[a]	1	−	−	−		1
Fraxinus caroliniana[a]	1	−		−	−	3
Betula nigra[a]	2		−		−	2
Fraxinus caroliniana[a]	1		−		−	2
Nyssa aquatica[e]	1		+		+	3
Nyssa ogeche[b]	1		+		+	2
Taxodium distichum[b]	1		+		+	2
Taxodium distichum[b]	1		+		+	3
Backswamp (FSC = 1)						
Fraxinus caroliniana[a]	1		−		−	1
Nyssa aquatica[a]	1	−		−		1
Nyssa aquatica[a]	1		−		−	2
Nyssa aquatica[a]	1		−		−	3
Nyssa biflora[a]	1		−		−	3
Nyssa ogeche[a]	1		−		−	2
Planera aquatica[a]	1		−		−	1
Taxodium distichum[a]	1		−		−	1
Taxodium distichum[a]	1		−		−	2

Net change in density and dominance indicated as + or −.

[a] Declining due to drier conditions (FSC < FI).

[b] Increases due to large size of tree and resistance to drier conditions.

by favoring the persistence of larger trees, drying also decreases the similarity between overstory and subcanopy by altering recruitment trends.

The ranked species (Table VIII) for the low bottomland and backswamp are also indicative of drier conditions in the floodplain. Lower elevation habitats experienced widespread declines in the importance of *Fraxinus caroliniana* (pop ash), a moderately shade tolerant subcanopy tree. Pop ash is an obligate wetland species (FSC = 1) and could be expected to decline under drier conditions. Trends in the obligate wetland species *Nyssa aquatica, Nyssa ogeche* and *Taxodium distichum* also support a scenario of drying. Small stem diameters of these species decreased in bottomland and backswamp over time, indicating that flood-dependent regeneration has diminished.

Table IX. MRPP comparisons of significant changes in ranked species over time

Habitat	Number of species	Number of species × size	Historic plots	Present plots	T	A	p
Levee	6	6	4	6	−2.55	0.16	0.02
High bottomland	7	7	9	9	−2.38	0.06	0.02
Low bottomland	5	8	4	5	−0.69	0.05	0.23
Backswamp	6	9	4	7	0.78	−0.04	0.77

Numbers of species and species × sizes taken from Tables VII and VIII. The test statistic T describes the separation between groups. The more negative T, the stronger the separation. The p value associated with T evaluates how likely that the observed separation is due to chance. A chance-corrected within-group agreement statistic, A, evaluates how strong the separation of groups is independent of sample size. Values for A are commonly below 0.1 for ecological data. Larger A values are needed when sample sizes are small. When all items are identical between groups $A = 1$. When heterogeneity within groups equals expectation by chance, A approaches zero. $A < 0$ when there is less agreement between groups than expected by chance (McCune *et al.*, 2002).

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Large *Nyssa* spp. and *T. distichum* stems increased in importance in low bottomland because these well-established individuals may have more resistance to short-term drying.

Drying was also evident for the ranked species in levee and high bottomland habitats. Declines were observed for the facultative wetlands trees *Quercus lyrata* and *Fraxinus pennsylvatica* (FSC = 2). Declines for another facultative wetland species, *Ulmus americana,* may also be associated with drying. However, this tree is susceptible to Dutch elm disease. *Ulmus alata* is a facultative uplands tree (FSC = 4) and does not typically occur in wetlands. Drier conditions may be responsible for its increased importance over time, although its overall abundance still remains low. Floodplain drying, in tandem with gap dynamics, can account for the sharp declines in sweetgum, *Liquidambar styraciflua*, at higher elevations. Sweetgum is classified as shade intolerant, and equally likely to occur in wetlands or non-wetlands (FSC = 3). On the levee, declines may be more directly related to drying. Loss of sweetgum in the high bottomland may be more directly due to its shade intolerance. Observed increases in sweetgum for larger stem sizes more exposed to full sun support this interpretation. Conversely, increases in *Carpinus caroliniana*, *Celtis laevigata* and *Cornus foemina* recorded at higher elevations may be due to their shade tolerance.

We emphasize that gap dynamics does not supercede drying-related forest change, but is intertwined with it. Gap dynamics is driven in part by flood regime: drying modifies flood-related tree mortality, changes canopy light availability, and alters dispersal and recruitment. Gap dynamics can also be a reflection of past land use (Turner *et al*., 2004). The source of the gap dynamics signal in the forests in this study is likely a complex mosaic of logging, hurricanes, as well as flood disturbance (Smith, 2007). Widespread logging of cypress and hardwoods in the region occurred between the 1880s and the early 1920s (Mattoon, 1915; Devall, 1998). Historic removal of cypress in the backswamps may have initiated tupelo regeneration that brought about the dense stands of shade-intolerant *Nyssa* spp. that characterize these habitats today (Penfound, 1952). Historic logging also included *Nyssa*, which was used to produce wood veneer prior to the introduction of plastics (Kendrick and Walsh, 2007). Thus our observed decline in *Nyssa* may reflect the coincidental timing of historic logging, canopy closure and more recent drying.

Declines in *Nyssa* have economic consequences. The floodplain of the Apalachicola River is one of the few areas in U.S. where large, dense stands of *Nyssa ogeche* support commercial production of tupelo honey (Eyde, 1963). Honey producers prefer the blooms of *Nyssa ogeche* for a better grade of tupelo honey, although the pollen of *Nyssa aquatica* is used to feed and strengthen the bees prior to the spring nectar flow in *N. ogeche*. Informal interviews with beekeepers indicate that tupelo honey production per hive has declined over the past several decades. More bees are needed to make the same volume of honey. This suggests that pollen and nectar resources from *Nyssa* may have lessened in quality or quantity due to stand age and drier conditions. Although other issues affecting honey production, notably invasive hive pests, likely contribute to this decline in honey yield, our results indicate that backswamps are composed of an aging cohort of *Nyssa* spp. and conditions may be too dry and too shady for robust tupelo recruitment. *Nyssa ogeche* does not possess dessication avoidance mechanisms found in *Nyssa aquatica* (Boyer and Graves, 2008) and may be more susceptible to drying-related declines. However, the long term responses of these two taxa may also reflect their contrasts in shade tolerance, which have not been as well documented. *Nyssa aquatica* will survive as a forest codominant, but does poorly when overtopped. New growth in *Nyssa ogeche,* a species which does better in more permanently flooded sites, occurs from stem sprouts on existing trunks. *N. ogeche* also has a more limited distribution, and its hollowed, multi-branching trunks provide habitat for other species (Whitney *et al*., 2004).

Ranked species from the lowest-elevation habitats were expected to have the strongest signal of compositional change. Yet the converse was true. MRPP test statistics weakened in the low bottomland and the backswamp. We attribute this to how fluvial landforms differ in their biogeomorphic responses to reduced channel flow. The availability of flood water in backswamp forests is dependent upon abiotic and biotic microtopography and other local geomorphic controls (Swanson *et al*., 1988; Huenneke and Sharitz, 1990; Titus, 1990; Tockner *et al*., 2000). With lower flows, flooding across the backswamp may be more sensitive to the local geometry of elevational contours to direct the movement and drainage of pooled surfaces, rainfall, tributary water, overland runoff, upland seepage and subsurface water. These structurally complex lateral components of floodplain hydrology would foster more spatial and temporal heterogeneity in the patterns of innundation relative to actual river levels and distance to the main channel (Thorpe *et al*., 2006; Dufour and Piégay, 2008). Our analyses identified a greater variability in

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species abundances among sample plots in the lowermost fluvial landforms: low bottomland and backswamps had more outliers and relatively few indicator species. Even though there were strong individual species changes in the backswamp over time, MRPP yielded weaker statistical significance because these changes were localized. They developed in some but not all sample plots because of local controls of flood exposure and water availability.

At higher elevations, thresholds of exposure to flooding would be more uniform, particularly along the contours of the levee. Compositional controls would be more consistent among sites and plots. This was corroborated in the greater number of indicator species in the high bottomland and levee, as well as stronger and more statistically significant MRPP test statistics. Vegetation change was uniform at higher elevations because flood exposure and water availability is more directly coupled to water levels in the main channel. This convergence of compositional trends in the levee and their divergence among sites in backswamps are similar to the antagonistic effects described by Amoros and Bornette (2002). Additional findings corroborate this complex biogeomorphic response to floodplain drying. Leitman *et al*. (1983) observed instantaneous water levels that varied considerably across the Apalachicola floodplain at medium flood stages, but were nearly uniform at high flood stages. Hummocks only a few meters in diameter modulated the effects of flooding for the trees established on them in the backswamp. Smith's (2007) assessment of compositional changes in the backswamp for one of the field sites in this study (Blountstown) indicated wetter instead of drier conditions. Local ponding after high water events was a more immediate control of water levels than the main river channel. The patterns of recruitment among smaller stem sizes also support more variable conditions in the backswamp. Sampling in 2004 included stems 2–7.5 cm in diameter, a size class not included in the historic forest surveys. *T. distichum* was the dominant recruit (344 stems ha^{-1}). However, 93% of these individuals were confined to a single site (SW—Sweetwater), where upland drainage and landscape configuration create locally wet conditions divorced from channel water levels. Censusing of these smaller stem sizes would enhance understanding of backswamp vegetation dynamics.

SUMMARY

Our results support Darst and Light's (2008) description of floodplain forest change along the Apalachicola. Forests are compositionally drier in 2004 than in the 1970s. Drying was evident in the 1970s and appears to have grown more pronounced since that time. The strongest species declines were in the backswamps for the obligate wetland tree species *Nyssa aquatica*, *Nyssa ogeche* and *Fraxinus caroliniana* (Figure 6). Reductions in stem density in the backswamp were pronounced. The persistence of high water events (due to low capacity impoundments) may make it difficult for upland species to establish in the low-elevation backswamps even though drier conditions develop in the interims between floods. Drying has lessened compositional contrasts along the dry-to-wet gradient that typifies floodplain vegetation. Compositional differences between overstory dominants and understory trees have widened. Perhaps of greater ecological importance, the fidelity of tree species to floodplain habitats has decreased over time. As indicated by the absence of indicator species, today's floodplain forest is compositionally noisier and less consistently structured.

This study illustrates that floodplain drying in humid climates is more than just an increase in tree species adapted to drier conditions or a decrease in species requiring frequent innundation. Forest compositional change due to declining river flows is also a function of canopy gap dynamics and how different geomorphic thresholds to flood exposure and moisture availability influence vegetation succession across the lateral and longitudinal dimensions of a floodplain (Ward, 1989; Thorp *et al*., 2006). Approaches the capture and compare the variance of observations are better suited than methods that homogenize forest change by ignoring geographic context. For the non-tidal floodplain forests of the Apalachicola River, we observed a geographic divergence of compositional patterns in the backswamp and a convergence in higher elevation habitats. This pattern may be considered a spatial and temporal biogeomorphic response to declining river flows in humid climates. The bi-directionality of biogeomorphic processes (Corenblit *et al*., 2007) may also play a role in reinforcing this dynamic and merit further investigation.

Because channel incision was a short-term response to the dam and diminished in the 1980s, basin-wide variables that determine flow volumes may now be the driving influence on floodplain forest dynamics. If flows continue to decline, the divergence of successional pathways in the backswamp may eventually give way to greater

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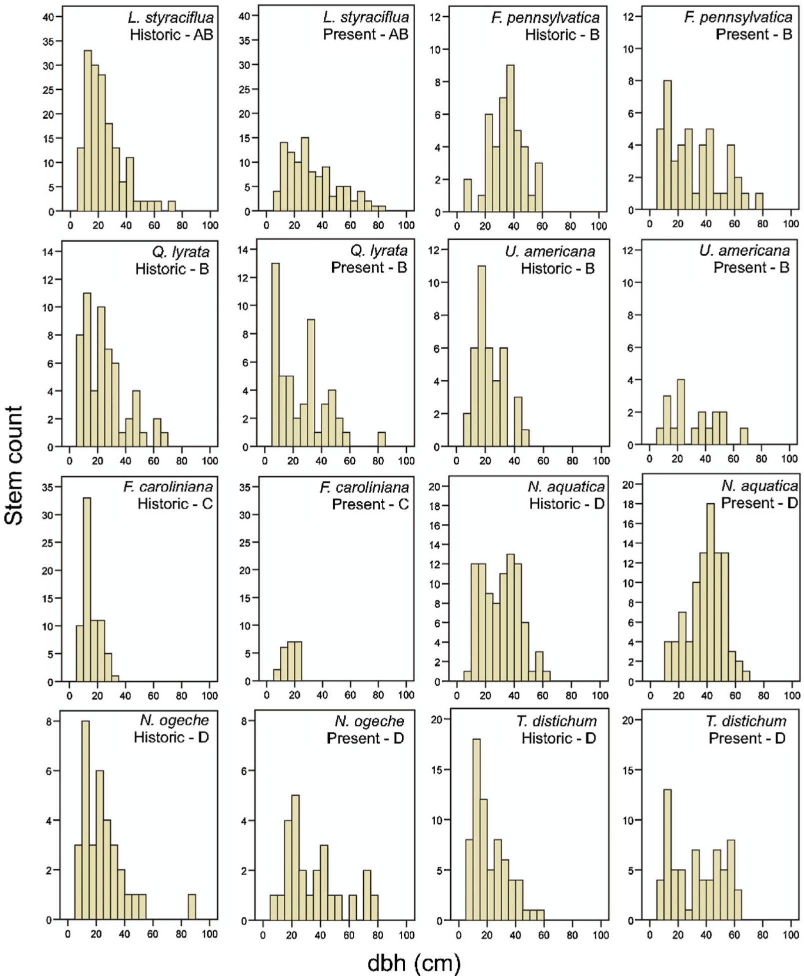

Figure 6. Histograms for final ranked species for levee (A), high bottomland (B), low bottomland (C) and backswamp (D). This figure is available in colour online at www.interscience.wiley.com/journal/rra

compositional similarity as drying progresses. Because the directions in which forest dynamics play out reflect ongoing climatic fluctuations as well as indeterminancies in the human institutions operating with the river's drainage basin, there remains a strong element of unpredictability for future vegetation states (Gibson *et al*., 2005; Williams and Jackson, 2007) along the Apalachicola River.

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