Kirkwood-Cohansey Project

Development of Vegetation Models to Predict the Potential Effect of Groundwater Withdrawals on Forested Wetlands

Cover: Five forest-vegetation types found in the New Jersey Pinelands include (clockwise from top left) pine-oak uplands, pitch pine lowlands, pine-hardwood lowlands, cedar swamps, and hardwood swamps (center). Photographs taken by Robert A. Zampella and Kim J. Laidig.

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The Pinelands Commission

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Abstract

Vegetation models were developed that, when linked to groundwater-hydrology models and landscape-level applications, can be used to predict the potential effect of groundwater-level declines on the distribution of wetland-forest communities, individual wetland species, and wetland-indicator groups. An upland-to-wetland vegetation gradient, comprising 201 forest plots located in five different study basins and classified as either upland pine-oak, pitch pine lowland, pine-hardwood lowland, hardwood swamp, or cedar swamp, paralleled variations in water level. Water levels, woody-species composition, the percentage of wetland- and upland-indicator species, and soil properties varied among the five vegetation types. Because of the functional relationship of hydrology with its correlated soil variables, hydrology represented a good proxy for the complex hydrologic-edaphic gradient associated with the upland-to-wetland vegetation gradient. Two types of vegetation models were developed to predict potential changes in vegetation associated with water-level declines. Logistic regression models predicted the probability of encountering the different vegetation types and 29 community-indicator species in relation to water level. Simple regression models predicted the relative abundance and richness of wetland- and upland-indicator species as a function of water level.

Introduction

Wetland and aquatic habitats cover approximately 25% of the 379,827-ha Pinelands Area. Relatively distinct wetland-forest communities, ranging from lowland pitch pine (*Pinus rigida*) forests on hydric-mineral soils to red maple (*Acer rubrum*) and Atlantic white cedar (*Chamaecyparis thyoides*) swamps on organic soils, are associated with narrow ranges of water levels (Roman et al. 1985, Ehrenfeld and Schneider 1991, Zampella et al. 1992, Zampella 1994, Laidig and Zampella 1999). Unlike riparian-wetland systems, which are periodically flooded by adjacent streams (Mitsch and Gosselink 2000), most Pinelands (Pine Barrens) forested wetlands are influenced primarily by groundwater associated with the Kirkwood-Cohansey aquifer (Rhodehamel 1979a, 1979b, Zapecza 1989).

Although hydrology is a major determinant of wetland-vegetation patterns and physiochemical characteristics of wetlands, including nutrient cycling, organic-matter accumulation, and soil chemistry, morphology, and genesis (Mitsch and Gosselink 2000), empirical evidence relating the effect of altered hydrologic regimes on wetland systems is generally lacking. In an unconfined aquifer with permeable sediments, such as the Kirkwood-Cohansey system, groundwater pumping generally results in a shallow and extensive cone of depression that can directly impact any wetland that it intersects (Winter 1988). McHorney and Neill (2007) demonstrated the direct effect of groundwater withdrawals on a coastal plain pond underlain by glacial-outwash deposits. The potential for such hydrologic impacts in the Pinelands was indicated by a pump test along the Mullica River in Wharton State Forest, where after about six days of pumping, water levels declined in wetlands located on both sides of the river (Lang and Rhodehamel 1963).

This study is a component of the Kirkwood-Cohansey Project, a comprehensive evaluation of the hydrologic and ecological effects of groundwater pumping from the Kirkwood-Cohansey aquifer. The objective of the study was to develop vegetation models that, when linked to groundwater-hydrology models and landscape-level applications, can be used to predict the potential effect of groundwater- level declines on the distribution of wetland-forest communities, individual wetland species, and wetland-indicator groups. The relationship between hydrology and selected soil properties, including percent organic matter, moisture, and bulk density, was also evaluated to determine how well hydrology serves as a proxy for these factors.

Two types of vegetation models, similar to models constructed for riparian-wetland systems (Franz and Bazzaz 1977, Auble et al. 1994, Toner and Keddy 1997, Chapin et al. 2002, Rains et al. 2004), were developed to predict potential changes in vegetation associated with water-level declines. Logistic regression models predict the probability of encountering different wetland-plant communities and wetland-plant species in relation to water level. Simple regression models predict the relative abundance and richness of wetland- and upland-indicator species as a function of water level.

Methods

Study Sites

To ensure that the results of the study have Pinelands-wide applicability, 201 10×10-m forest plots were established in five Pinelands drainage basins that represented a range of ecological and land-use conditions (Figure 1, Table 1). Forested landscapes and acid-water streams with low concentrations of dissolved solids characterized the McDonalds Branch, Skit Branch, and East Branch Bass River basins. Upland agriculture and developed lands were prominent features of the Albertson Brook and Morses Mill Stream basins, which were characterized by streams with circumneutral waters and elevated dissolved-solid concentrations. Available data indicate that groundwater withdrawals were more extensive in the Albertson Brook and Morses Mill Stream basins (Hoffman 2001). Surface and groundwater diversions associated primarily with wetland agriculture in the Skit Branch basin were greater compared to diversions that could potentially affect study plots in the other two forested basins. Three of the basins, including McDonalds Branch, Albertson Brook, and Morses Mill Stream, were the primary focus of intensive hydrologic investigations in related studies conducted as part of the Kirkwood-Cohansey Project.

Based on field reconnaissance and a review of vegetation maps and aerial photographs, the 201 forest plots were selected to represent a range of wetland and transitional-upland-vegetation types, including Atlantic white cedar swamps (Ehrenfeld and Schneider 1991, Laidig and Zampella 1999), red maple swamps (Ehrenfeld and Gulick 1981), mixed pitch pine-red maple wetlands, pitch pine lowlands, and pine-oak (*Quercus* spp.) upland forests (Zampella et al. 1992). The 201 plots comprised 70 plots in the McDonalds Branch basin, 29 in the East Branch Bass River basin, 40 in the Skit Branch basin, 31 in the Albertson Brook basin, and 31 in the Morses Mill Stream basin. The center point of each plot was recorded using a global positioning system.

Water-level Measurements

Water-level observation wells were installed in the center of each forest plot. Wells were constructed from PVC risers fitted to prefabricated 60×1.9 cm screens that were perforated throughout with 0.08-cm slots. Water-level data were collected monthly in 2005 and 2006 using a chalked, graduated steel tape. December water levels were not measured in either year. At plots where hummock-hollow topography was evident, elevation was measured with a transit at 1.0-m intervals along two perpendicular transects that intersected the center of the plot. Raw water levels for the plot were then rescaled to reflect the difference between the elevation at the well base and the average of all the elevation points.

Soil Sampling and Analysis

In October 2005, soil samples for percent organic matter and bulk density (g soil cc^{-1}) determinations were collected from the upper 10 to 12 cm of soil at each plot using a tube sampler. The 10 to 12-cm depth is associated with the highest density of shrub roots along a typical Pinelands soil catena (Laycock 1967). A minimum of three soil cores were collected at random points within 2 to 3 m of each well, aggregated in tins, dried to constant weight, and used to determine bulk density. The soil samples were then pulverized and used to determine percent organic matter based on loss-on-ignition (Storer 1984).

A tube sampler was used to sample soil profiles

Table 1. Basin area, the number of study plots, and land-use characteristics for five study basins. Land-use profiles were developed using land-use/land-cover data based on 2002 aerial photography (New Jersey Department of Environmental Protection 2007). Land-use/land-cover values represent the percentage of basin area associated with each cover type. Land-use/land-cover classification follows Zampella et al. (2001a).

Basin	Basin area (km^2)	Number of study plots	Upland forest	Wetlands	Water	Wetland agriculture	Upland agriculture	Developed land	Barren land
Albertson Brook	52.3	31	42.6	11.0	1.8	0.1	23.0	21.0	0.4
East Branch Bass River	21.4	29	81.2	14.8	1.0	0	<0.1	2.7	0.3
McDonalds Branch	14.3	70	64.7	31.3	2.2	1.4	0	0.1	0.4
Morses Mill Stream	21.6	31	49.6	20.0	1.9	0.6	9.2	18.1	0.6
Skit Branch	28.3	40	69.1	26.3	1.3	2.3	0.7	0.3	0.1

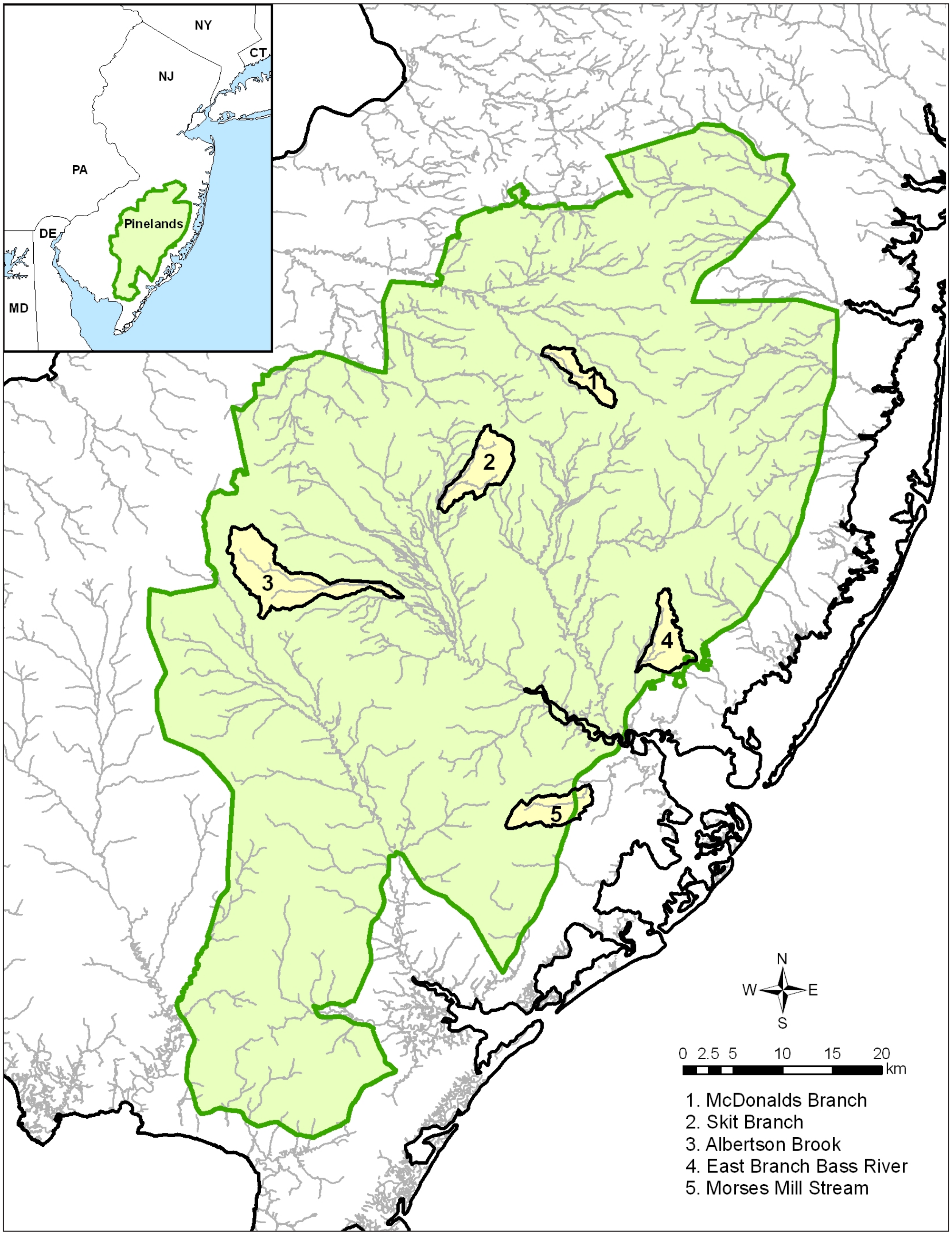

Figure 1. The location of five study basins in the New Jersey Pinelands. Refer to Appendix 1 for aerial photographs of each study basin and the location of forest plots.

at three points in each forest plot between December 2005 and May 2006. Texture was evaluated using a texture-by-feel analysis (Thien 1979). The average proportion of the upper 30 cm of soil characterized as sand and the average thickness of the O- and A-horizons were determined for each mineral-soil plot. Muck depth was measured at a minimum of three points when organic soils were encountered.

Volumetric-soil moisture (cc water cc soil^{-1}) and gravimetric-soil moisture (g water g of dry soil^{-1}), bulk density, and water level were measured monthly from March through October 2005 at a sub-sample of 46 plots. These sampling rounds were in addition to those conducted to collect water-level data for all 201 plots. The sub-sample of 46 plots, which represented a range of vegetation types and hydrologic conditions that occurred in the three primary study basins, included 16 McDonalds Branch plots, 15 Albertson Brook plots, and 15 Morses Mill Stream plots. Volumetric-water content was measured at three points in each plot with a Campbell Scientific hand-held time-domain-reflectometry meter fitted with 12-cm probes. Three 12-cm soil cores, collected from the same three points using a tube sampler, were used to determine gravimetric-soil moisture (Faulkner et al. 1989) and bulk density.

Vegetation Sampling

A point-intercept method was used to sample vegetation along five parallel, 10-m transects established at 2-m intervals within each forest plot. All understory vegetation, including shrubs, herbs, and *Sphagnum* moss, intercepted by a 4-m metal rod, was recorded at 25-cm intervals along each transect for a total of approximately 200 points per plot. At the same 25-cm intervals, a GRS densitometer (Geographic Resource Solutions, Arcata, CA) affixed to the metal rod was used to record canopy-tree species > 4 m in height.

Total cover for each species in each plot was calculated as the number of intercepts divided by the total number of sample points in the plot. Because total canopy cover often exceeded 100% due to multiple layers of tree species, canopy closure was calculated as the opposite of open-canopy areas.

The height of the tallest shrub was recorded every meter along each transect for a total of 50 measurements per plot. Vegetation cover and maximum shrub height were measured during the periods June through September 2004 and May through September 2005. Complete species lists were tallied during each survey and updated in 2006. All tree-stem diameters ≥ 2.5 cm were measured at breast height (1.35 meters) with a diameter tape.

Taxonomic nomenclature for vascular-plant species was based on Gleason and Cronquist (1991). Wetland-indicator status was assigned to each woody-plant species according to the U. S. Fish and Wildlife Service (1988) classification, with "upland" status given to those species that were not assigned a wetland-status category.

Data Analysis

Water levels and soil properties. Monthly water-level data collected over the 2-yr study period were used to calculate a mean value for each of the 201 forest plots. Approximately three percent of the monthly values for individual wells were estimated using simple linear regression and water-level data from nearby wells (Zampella et al. 2001b). To determine how well mean water levels characterized forest-plot hydroperiods, Spearman rank correlation was used to evaluate the relationship between mean water levels and percentile, minimum, maximum, variance, and range statistics and water levels recorded in individual growing-season months (March through October).

To determine if hydrologic conditions during the study period were similar to long-term conditions, monthly mean-discharge data for the McDonalds Branch hydrologic benchmark station (Mast and Turk 1999) and the Mann-Whitney U test were used to compare study-period (2005 through 2006) and long-term (1954 through 2004) stream-discharge values. The data were obtained online from the U. S. Geological Survey (http://waterdata.usgs.gov/nwis/sw). A Mann-Whitney U test was also used to compare monthly growing season (March through October) water levels recorded in well clusters comprising three wells at each of four forest sites located in McDonalds Branch (Zampella et al. 2001b) for the periods 1987-2004 and 2005-2006. The wells were located within and adjacent to four plots included in the present study. The water-level comparison, which was based on the mean monthly value for each well cluster, was limited to the growing season because this period represented the most complete record for wells in the clusters.

Spearman rank correlation was used to evaluate the relationship among depth-to-water table, bulk density, percent organic matter, percent volumetric-soil moisture, percent gravimetric-soil moisture, mineral-soil O- and A-horizon thickness, and percent sand (proportion of the upper 30 cm of mineral soils that was sand).

Ordination and classification of vegetation. Detrended correspondence analysis (DCA, Hill 1979a, Hill and Gauch 1980) and TWINSPAN (Hill 1979b) were used to ordinate and classify woody species and the 201 forest plots based on untransformed species-cover data. Ordination analysis was used to provide an objective means of ordering sites and species based on species-composition patterns and to relate these patterns to environmental variables. Classification analysis was used to group sites with similar species composition and to provide the basis for identifying and comparing vegetation types. Detrended correspondence analysis, rather than non-metric multidimensional scaling (NMS) was used because DCA performs well in gradient analysis with datasets that exhibit a single, strong gradient and because DCA produces species scores, whereas species identities are hidden in NMS. The ordination and classification analyses were performed using PC-ORD 5.10 (McCune and Mefford 1999). Pseudo-species cut levels ranging from 0 to 0.20 (0% to 20%) were used in the TWINSPAN classification.

Only woody species were included in the initial analyses because they are generally more abundant and more frequently encountered than herbaceous species in the forest types studied and form the basic structure of the forest types. These criteria are necessary for the development of Pinelands-wide models. To determine if the inclusion of herbaceous species had a significant effect on the community gradient derived from the woody-species data, a second DCA ordination was completed using both woody- and herbaceous-species cover. The DCA axis-1 and 2 plot scores from this ordination were correlated with those of the woody-species ordination using Spearman rank correlation. Ordination and classification based on woody-species presence-absence data were also completed and compared to the results of the woody-species-cover analyses to determine if the two approaches produced similar outcomes. With the exception of this comparison, all analyses were based on species-cover data. To limit the effect of rare species, single-occurrence species were excluded from the ordination and classification analyses. Seedlings and taxa not identified to species were also excluded from these analyses.

Comparison of vegetation types. Nonparametric multi-response permutation procedures (MRPP, McCune and Mefford 1999) were used to determine if differences in species composition based on species cover existed among the TWINSPAN-derived vegetation types. The MRPP analyses were based on the Sorensen (Bray-Curtis) distance measure. Separate comparisons were completed for woody species and herbaceous species. Indicator-species analysis (Dufrêne and Legendre 1997, McCune and Grace 2002, McCune and Mefford 1999) was used to contrast the woody and herbaceous species associated with each vegetation type and to identify which community-indicator species should be modeled. Indicator-species analysis complements MRPP by describing how well each species separates among vegetation types. Statistical significance of the indicator values was determined by a Monte Carlo method using 1,000 randomizations. A p value of 0.05 was used as the criterion to select community-indicator species.

Variations in the percentage of total cover represented by wetland-indicator groups (Ellison and Bedford 1995, Stromberg et al. 1996), including wetland species (obligate-wetland and facultative-wetland species), facultative species, and upland species (facultative-upland and upland species), among vegetation types were compared graphically. Grouping plant species according to their association with wetlands and uplands provides a means of reducing a large number of species into a manageable number of functional groups (Ellison and Bedford 1995).

Summary water-level, percent organic matter, bulk density, percent sand, muck depth, and O-and A-horizon thickness statistics were calculated for each TWINSPAN-derived vegetation type. Mean water level and volumetric- and gravimetric-soil moisture values for each vegetation type were calculated using data from the sub-sample of 46 plots. Kruskal-Wallis ANOVA was used to compare mean study-period water levels and soil properties among the classified vegetation types. Post-hoc comparisons were conducted using multiple comparisons of mean ranks (Siegel and Castellan 1988).

Vegetation gradients. To determine if the ordination axes produced with DCA represented upland-to-wetland vegetation gradients, Spearman rank correlation was used to evaluate the association between the first two DCA axes based on woody-species-cover data and the percentage of total cover represented by wetland-indicator groups. The association between species composition and stand structure was also evaluated by using Spearman rank correlation to relate the two DCA axes to the percent canopy closure, mean shrub height, tree-stem density, and mean tree-stem diameter of each plot.

Simple linear regression was used to relate the vegetation gradient represented by the DCA axis-1 scores for the 201 forest plots to log-transformed mean study-period water levels. Separate regression analyses were also completed for each of the five study basins. Analysis of covariance (ANCOVA) was used to determine whether the slopes and intercepts of the separate regression lines developed for each of the five study basins differed significantly (Sokal and Rohlf 1995, Zar 1999). For descriptive purposes, separate regressions were also performed for each classified vegetation type.

Model Development

Species and community models. Logistic regression was used to determine the probability of occurrence of each vegetation type and individual species in relation to water level. The logistic regressions were based on presence-absence data and untransformed water-level data. Some vegetation-type and species probabilities followed a Gaussian (bell-shaped) response to water level. In these instances, a polynomial equation was fitted to binary logit data to produce a Gaussian logistic curve (Jongman et al. 1995). Only community-indicator species that occurred with frequencies 10% or greater across all 201 plots were included in the analyses.

Wetland-indicator models. The relative abundance (percentage of total cover) and relative richness of wetland-indicator species (obligate-wetland and facultative-wetland species) and upland-indicator species (facultative-upland and upland species) were related to mean study-period water levels using simple linear regression. Facultative species were not included because they are not associated with either indicator group. Arcsine-transformed relative-abundance values and log-transformed water levels were used in this analysis.

Statistical Significance and Diagnostics

An alpha level of 0.05 was used to assess significance for all statistical tests and, with the exception of the indicator-species analysis, significance levels for related tests were adjusted using the sequential Bonferroni method (Rice 1989). Normal-probability plots and plots of predicted values versus residuals produced by each regression model were inspected to determine if the assumptions of normality and linearity were met. STATISTICA version 7.1 (StatSoft, Inc., Tulsa, OK, USA) was used for all statistical analyses.

Results

Water Levels and Soil Properties

Based on the Mann-Whitney U test, mean monthly discharge at McDonalds Branch for the study period (2005-2006) did not differ significantly from long-term (1954-2004) mean monthly discharge ($p = 0.56$), which indicated that hydrologic conditions during the study period were similar to long-term conditions. Monthly growing-season (March-October) water levels recorded in wells at the four McDonalds Branch forest sites for the periods 2005-2006 and 1987-2004 did not differ significantly (Table 2).

Mean study-period water levels for each forest plot were highly correlated with minimum, maximum, percentile (10^{th}, 25^{th}, median, 75^{th}, and 90^{th} percentile), and mean 2-yr growing-season water levels, with Spearman rank coefficients ranging from 0.92 to 1.00. The relationship between mean water level and both range ($r = 0.60$) and variance ($r = 0.59$) was not as strong. The mean study-period water levels were also correlated with water levels recorded during individual growing-season months, with Spearman rank coefficients ranging from 0.92 to 0.97.

Significant correlations ($p < 0.001$) were found among soil properties and water level (Table 3).

Table 2. Mean monthly growing season (March-October) depth-to-water table recorded in wells at four forest sites located in McDonalds Branch (Zampella et al. 2001b) for the periods 2005-2006 (n = 16 months) and 1987-2004 (n = 132 months). First, second (median), and third quartiles are also given. The wells were located within and adjacent to two pine-hardwood lowland plots, a pitch pine lowland plot, and a pine-oak upland plot included in this study. Long-term (1987-2004) and study-period (2005-2006) means did not differ significantly based on Mann-Whitney U tests.

	Period means (± 1 SD)			1987-2004 Quartiles			2005-2006 Quartiles		
Vegetation type	1987-2004	2005-2006	*p*	1st	median	3rd	1st	median	3rd
Pine-oak upland	110.0 ± 26.8	108.8 ± 23.3	0.87	90.3	107.0	125.7	96.2	104.9	117.0
Pitch pine lowland	82.2 ± 25.5	81.5 ± 21.8	0.97	63.8	78.6	97.2	67.5	79.1	88.3
Pine-hardwood lowland[1]	44.7 ± 27.0	43.1 ± 29.7	0.67	23.4	39.2	58.5	25.8	33.3	50.6
Pine-hardwood lowland	22.0 ± 22.2	20.7 ± 21.1	0.96	6.2	15.3	31.1	9.8	13.5	26.4

[1]n = 131

Bulk density and percent sand decreased and percent organic matter, soil moisture, and O- and A-horizon thickness increased as depth-to-water table decreased. Bulk density and percent organic matter were inversely related. Soil moisture and the thickness of the O- and A-horizons were positively correlated with percent organic matter and negatively correlated with bulk density. Percent sand was positively correlated with bulk density and negatively correlated with percent organic matter and the thickness of the O- and A-horizons.

Species Inventory

Eighty-six vascular species were found in the 201 forest plots, including 14 canopy-tree species, 34 shrub and vine species, and 38 herbaceous species (Table 4). Thirteen canopy-tree species were also found in the understory. In addition to *Sphagnum* species, several non-vascular taxa, including other mosses, liverworts, and lichens, were also found.

Fifty-six taxa were included in the woody-species classification and ordination analyses (Table 4). The 56 taxa included 31 understory species and 14 canopy species. Eleven species were included twice as separate taxa because they were found in both the canopy and understory. The analysis of herbaceous-species cover was based on 26 species (Table 4).

Vegetation Types

Species composition. The first two divisions of the TWINSPAN analysis based on woody-species cover data created four vegetation types that were classified as cedar swamp, mixed pine-hardwood forest, pitch pine lowland, and pine-oak uplands according to the dominant-canopy species. All but three cedar swamps were associated with organic soils. Pitch pine lowlands and pine-oak uplands were associated with mineral soils. Plots in the mixed pine-hardwood type were divided based on the presence of mineral or organic soils, with plots associated with organic soils classified as hardwood swamps and those associated with mineral soils classified as pine-hardwood lowlands.

Table 3. Spearman rank correlations among soil variables and mean depth to water. Variables include mean study-period depth to water, bulk density, % organic matter, % volumetric soil moisture, % gravimetric soil moisture, mineral-soil O- and A-horizon thickness, and percent sand (proportion of the upper 30 cm of mineral soils that was sand). O- and A-horizon and % sand values are for mineral soils found in pine-hardwood lowlands, pitch pine lowlands, and pine-oak uplands. Soil-moisture variables[1] were correlated with water levels and bulk density sampled on the same date at a sub-sample of 46 plots and with mineral-soil O- and A-horizons and % sand sampled at 32 plots[2]. Refer to methods for additional details on the variables. All initial p values were < 0.001 and all associations were significant following the sequential Bonferroni adjustment.

Variable	Mean depth to water	Bulk density	% Organic matter	% Volumetric soil moisture	% Gravimetric soil moisture	O-horizon	A-horizon
Bulk Density (n = 201)	0.73						
% Organic Matter (n = 201)	-0.74	-0.94					
% Volumetric moisture (n = 46) [1]	-0.92	-0.92	0.90				
% Gravimetric moisture (n =46) [1]	-0.92	-0.97	0.95	0.97			
O-horizon (n = 152)	-0.52	-0.70	0.73	0.57[2]	0.71[2]		
A-horizon (n = 152)	-0.51	-0.67	0.71	0.55[2]	0.65[2]	0.59	
% Sand (n = 151)	0.58	0.73	-0.79	-0.78	-0.83	-0.76	-0.75

Table 4. Species inventory for 201 forest plots in the New Jersey Pinelands. Species not included in the analyses are noted with asterisks.

Species	Not included
Woody-canopy species	
Acer rubrum	
Betula populifolia	
Chamaecyparis thyoides	
Ilex opaca	
Magnolia virginiana	
Nyssa sylvatica	
Pinus rigida	
Quercus alba	
Quercus coccinea	
Quercus marilandica	
Quercus prinus	
Quercus stellata	
Quercus velutina	
Sassafras albidum	
Woody-understory species	
Acer rubrum	
Amelanchier canadensis	
Arctostaphylos uva-ursi	*
Aronia arbutifolia	
Betula populifolia	
Chamaecyparis thyoides	
Chamaedaphne calyculata	
Chimaphila maculata	
Clethra alnifolia	
Eubotrys racemosa	
Gaultheria procumbens	
Gaylussacia baccata	
Gaylussacia dumosa	
Gaylussacia frondosa	
Hudsonia ericoides	
Ilex glabra	
Ilex laevigata	
Ilex opaca	
Ilex verticillata	*
Kalmia angustifolia	
Kalmia latifolia	
Leiophyllum buxifolium	
Lyonia ligustrina	
Lyonia mariana	
Magnolia virginiana	
Mitchella repens[1]	
Myrica pensylvanica	
Nyssa sylvatica	
Parthenocissus quinquefolia	
Pinus rigida	
Pyxidanthera barbulata	
Quercus coccinea	*
Quercus ilicifolia	
Quercus marilandica	
Quercus prinus	*
Quercus stellata	
Woody-understory species (continued)	
Quercus velutina	
Rhododendron viscosum	
Rubus hispidus	
Sassafras albidum	
Smilax glauca	
Smilax laurifolia	
Smilax rotundifolia	
Toxicodendron radicans	
Vaccinium corymbosum	
Vaccinium pallidum	
Viburnum nudum	*
Herbaceous species	
Andropogon virginicus var. virgincus	
Aster novi-belgii	*
Bartonia paniculata	
Bartonia virginica	
Calamovilfa brevipilis	
Carex atlantica	
Carex atlantica var. capillacea	*
Carex collinsii	
Carex exilis	
Carex folliculata	
Carex pensylvanica	*
Carex stricta	*
Carex trisperma	
Cypripedium acaule	
Decodon verticillatus	*
Drosera rotundifolia	
Dulichium arundinaceum	
Eleocharis tenuis	*
Habenaria clavellata	*
Leersia oryzoides	*
Melampyrum lineare	
Monotropa uniflora	
Osmunda cinnamomea	
Osmunda regalis	
Panicum dichotomum	
Peltandra virginica	
Pontederia cordata	*
Pteridium aquilinum	
Rhynchospora alba	
Sarracenia purpurea	
Schizachyrium scoparium	*
Thelypteris palustris	*
Thelypteris simulata	
Triadenum virginicum	*
Trientalis borealis	
Woodwardia areolata	
Woodwardia virginica	
Xerophyllum asphodeloides	

[1]An evergreen-herbaceous subshrub

Table 5. Comparison of TWINSPAN classifications based on woody-species-cover data and presence-absence data. Hardwood swamps, which were separated from pine-hardwood lowlands in the species-cover-based classification according to the presence of muck soils, were nearly evenly split between the cedar swamp and hardwood swamp and hardwood swamp and pine-hardwood lowland classes produced by the presence-absence classification. Values represent the percentage of species-cover-based classes associated with the presence-absence-based classes and the total number of plots in each class.

	Presence-absence-based vegetation types				
Cover-based vegetation types	Cedar swamp and hardwood swamp	Hardwood swamp and pine-hardwood lowland	Pitch pine lowland	Pine-oak upland	Total number of plots
Cedar swamp	93.3	6.7	0.0	0.0	30
Hardwood swamp	52.6	47.4	0.0	0.0	19
Pine-hardwood lowland	5.3	89.5	5.3	0.0	57
Pitch pine lowland	0.0	1.6	85.9	12.5	64
Pine-oak upland	0.0	3.2	3.2	93.5	31
Total number of plots	41	64	59	37	201

The vegetation types produced using woody-species cover data were very similar to those obtained using presence-absence data (Table 5).

Results of the MRPP analysis of woody-species cover showed an overall significant difference ($p < 0.001$) in woody-species composition among the five vegetation types. All between-type comparisons were significantly different following the sequential Bonferroni adjustment. Based on the indicator-species analysis, 38 woody species contributed to the contrast among vegetation types (Table 6). The greatest number of community-indicator species was associated with pitch pine lowlands.

The MRPP analysis of herbaceous-species cover also showed an overall significant difference ($p < 0.001$) in species composition among the five vegetation types. No difference was found between pitch pine lowlands and pine-oak uplands or between cedar swamps and hardwood swamps. All other between-type comparisons were significantly different following the sequential Bonferroni adjustment. Based on the indicator-species analysis, 20 herbaceous species contributed to the contrast among vegetation types (Table 7).

The percentage of wetland- and upland-indicator species varied among the five vegetation types. The relative abundance of wetland-indicator species was highest in cedar and hardwood swamps and lowest in pitch pine lowlands and upland pine-oak forests (Figure 2). The opposite trend was observed for upland-indicator species. Cedar swamps and upland pine-oak forests displayed a lower relative abundance of facultative species compared to the other three vegetation types.

Water levels. Seasonal water-level patterns were evident in the mean hydrographs for each vegetation type (Figure 3). Mean (± 1 SD) water levels were highest in April 2005, ranging from an average of 3.7 ± 7.5 cm in hardwood swamps to an average of 86.7 ± 38.1 cm in pine-oak uplands. Mean water levels were lowest in October 2005, ranging from an average of 45.2 ± 14.7 cm in cedar swamps to an average of 180.7 ± 49.9 cm in pine-oak uplands.

Kruskal-Wallis ANOVA revealed significant differences ($p < 0.001$) in mean water levels among the five vegetation types (Table 8). Mean water levels were significantly different among pine-hardwood lowlands, pitch pine lowlands, and pine-oak uplands. Mean water levels did not differ significantly between cedar swamps and hardwood swamps, but water levels for both swamp types

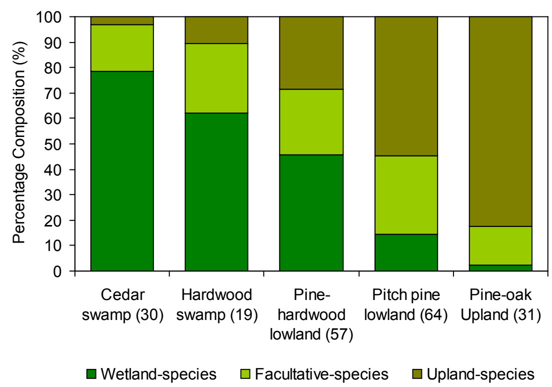

Figure 2. Variation in the average relative abundance (percentage of total cover) of wetland-indicator groups along the upland-to-wetland vegetation gradient comprising five vegetation types. Wetland species include obligate-wetland and facultative-wetland species. Upland species include facultative-upland species and species not assigned a wetland-indicator status. The number of plots for each vegetation type is shown in parentheses.

Table 6. Mean percent cover and frequency of woody-species associated with five vegetation types. Community-indicator species were identified through indicator-species analysis. Canopy and understory tree species are distinguished with a C and a U, respectively. The number of plots for each vegetation type is shown in parentheses.

	Vegetation type									
	Cedar swamp		Hardwood swamp		Pine-hardwood lowland		Pitch pine lowland		Pine-oak upland	
Vegetation type	(30)		(19)		(57)		(64)		(31)	
Community-indicator species	Cover	Freq.	Cover	Freq.	Cover	Freq.	Cover	Freq.	Cover	Freq.
Cedar swamp										
Chamaecyparis thyoides (C)	77.6	100	-	-	0.7	14	< 0.1	2	-	-
Ilex laevigata	0.2	17	-	-	-	-	-	-	-	-
Mitchella repens	0.4	73	0.4	53	0.1	16	< 0.1	2	-	-
Toxicodendron radicans	< 0.1	10	-	-	-	-	-	-	-	-
Hardwood swamp										
Acer rubrum (C)	15.3	77	73.4	100	46.8	91	1.4	14	-	-
Ilex opaca (U)	< 0.1	7	0.2	32	0.1	9	< 0.1	6	< 0.1	10
Ilex opaca (C)	-	-	1.1	11	0.3	4	-	-	< 0.1	3
Kalmia latifolia	2.2	23	8.9	37	0.4	7	0.1	3	0.5	3
Magnolia virginiana (C)	0.4	20	7.7	53	1.0	16	-	-	-	-
Nyssa sylvatica (C)	2.1	23	29.6	89	30.7	70	3.0	20	1.1	6
Rhododendron viscosum	2.0	53	4.2	63	0.9	40	0.1	3	-	-
Rubus hispidus	0.1	30	0.1	32	< 0.1	4	< 0.1	2	-	-
Smilax rotundifolia	< 0.1	17	2.9	89	3.2	70	1.3	23	0.8	13
Pine-hardwood lowland										
Acer rubrum (U)	0.3	40	0.9	37	3.5	49	0.6	22	-	-
Lyonia ligustrina	0.1	10	0.5	42	1.0	30	0.1	6	0.2	10
Vaccinium corymbosum	13.3	90	23.0	95	28.8	100	9.2	72	0.4	13
Pitch pine lowland										
Amelanchier canadensis	-	-	< 0.1	5	< 0.1	9	0.3	45	< 0.1	6
Eubotrys racemosa	4.3	83	7.8	74	4.3	75	16.0	88	3.0	55
Gaultheria procumbens	0.3	7	0.9	21	3.0	60	8.6	100	5.9	90
Gaylussacia dumosa	0.4	27	0.1	11	0.1	16	1.6	39	0.3	10
Gaylussacia frondosa	11.8	83	7.8	53	13.0	86	27.1	92	17.3	84
Kalmia angustifolia	< 0.1	7	1.1	11	0.4	14	16.0	89	4.8	65
Leiophyllum buxifolium	-	-	-	-	-	-	< 0.1	14	-	-
Lyonia mariana	-	-	-	-	0.3	16	5.2	84	2.7	61
Pinus rigida (C)	0.7	13	9.1	53	53.3	96	60.3	100	58.7	100
Pinus rigida (U)	-	-	-	-	0.1	9	2.5	69	0.9	55
Pyxidanthera barbulata	-	-	-	-	-	-	< 0.1	16	< 0.1	3
Smilax glauca	< 0.1	7	< 0.1	16	0.6	44	2.4	80	0.3	42
Pine-oak upland										
Gaylussacia baccata	0.5	13	0.2	11	1.2	30	32.6	98	48.7	100
Hudsonia ericoides	-	-	-	-	-	-	-	-	< 0.1	10
Quercus alba (C)	-	-	-	-	0.3	4	< 0.1	2	4.0	16
Quercus ilicifolia	-	-	-	-	-	-	0.2	11	8.2	71
Quercus marilandica (C)	-	-	-	-	-	-	< 0.1	-	0.9	23
Quercus marilandica (U)	-	-	-	-	-	-	0.0	2	1.1	42
Quercus stellata (C)	-	-	-	-	-	-	-	-	0.5	10
Quercus velutina (C)	-	-	-	-	-	-	0.1	2	1.2	13
Quercus velutina (U)	-	-	-	-	-	-	< 0.1	2	0.4	10
Vaccinium pallidum	-	-	-	-	-	-	0.3	22	18.3	100

Table 7. Mean percent cover and frequency of herbaceous-species community indicators and *Sphagnum* associated with five vegetation types. Community-indicator species were identified through indicator-species analysis. Pine-hardwood lowland had no significant herbaceous-indicator species. The number of plots for each vegetation type is shown in parentheses.

Vegetation type	Vegetation type							
	Cedar swamp (30)		Hardwood swamp (19)		Pitch pine lowland (64)		Pine-oak upland (31)	
Community-indicator species	Cover	Freq.	Cover	Freq.	Cover	Freq.	Cover	Freq.
Cedar swamp								
Bartonia paniculata	< 0.1	20	< 0.1	11	-	-	-	-
Carex atlantica	0.6	20	< 0.1	26	-	-	-	-
Carex collinsii	9.0	67	7.8	47	-	-	-	-
Carex exilis	2.6	13	-	-	-	-	-	-
Carex folliculata	0.2	13	-	-	-	-	-	-
Carex trisperma	2.7	40	1.6	32	-	-	-	-
Drosera rotundifolia	0.1	37	0.1	26	-	-	-	-
Dulichium arundinaceum	< 0.1	7	-	-	-	-	-	-
Osmunda cinnamomea	0.9	63	0.4	53	-	-	-	-
Osmunda regalis	0.5	30	-	-	-	-	-	-
Panicum dichotomum	0.1	13	-	-	-	-	-	-
Peltandra virginica	< 0.1	7	-	-	-	-	-	-
Sarracenia purpurea	0.1	20	-	-	-	-	-	-
Thelypteris simulata	0.2	10	0.1	5	-	-	-	-
Trientalis borealis	0.2	43	0.1	37	0.1	3	-	-
Sphagnum spp.	30.0	100	26.4	95	1.2	36	< 0.1	3
Hardwood swamp								
Bartonia virginica	< 0.1	7	< 0.1	16	-	-	-	-
Woodwardia virginica	0.1	17	1.0	53	-	-	-	-
Pitch pine lowland								
Xerophyllum asphodeloides	-	-	0.2	16	7.2	58	4.8	35
Pine-oak upland								
Melampyrum lineare	-	-	-	-	< 0.1	6	0.1	16
Pteridium aquilinum	< 0.1	3	-	-	2.7	77	3.4	77

differed significantly from the other forest types (i.e., the other forest types had greater depth-to-water-table values). On average, depth-to-water-table values at pine-hardwood lowland and pitch pine lowland sites in the Albertson Brook and Morses Mill Stream basins were greater than those in the other three basins. Mean hardwood-swamp depth-to-water-table values were greatest in the Morses Mill Stream basin (Table 9).

Soil properties. Based on Kruskal-Wallis ANOVA tests, soil properties varied among the five vegetation types (Table 10). With the exception of the comparison between pine-oak uplands and pitch pine lowlands and between cedar and hardwood swamps, significant differences in percent organic matter and bulk density existed among the vegetation types. The thickness of the O- and A-horizons and the proportion of the upper 30 cm of soil characterized as sand differed significantly among the three vegetation types associated with mineral soils.

Vegetation Gradients

Community and species patterns. The same woody-species data included in the TWINSPAN analysis were used in the ordination analysis (Table 4). The first DCA axis of the plot ordination represented a community gradient that contrasted pine-oak upland plots and cedar swamp plots. Pitch pine lowland, hardwood swamp, and pine-hardwood lowland plots occupied transitional positions along the gradient (Figure 4). The second DCA axis contrasted cedar swamp plots with hardwood swamp and pine-hardwood lowland plots (Figure 4). The proportion of variance (R^2) represented by the first and second axis was 0.48 and 0.14, respectively.

The first DCA axis of the woody-species

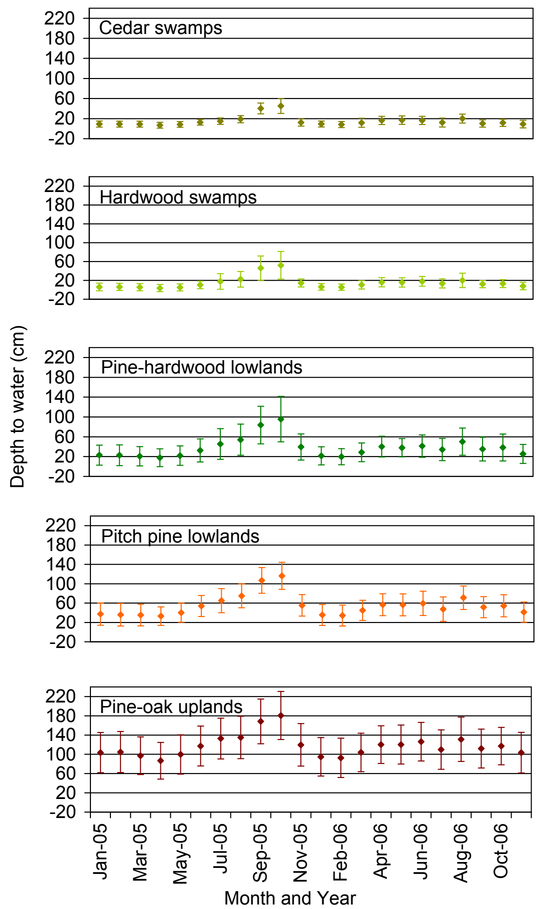

Figure 3. Monthly depth-to-water-table values (mean ± 1 SD) associated with cedar swamps (n = 30), hardwood swamps (n = 19), pine-hardwood lowlands (n = 57), pitch pine lowlands (n = 64), and pine-oak uplands (n = 31) for the period 2005-2006. Water levels were not measured in December of either year.

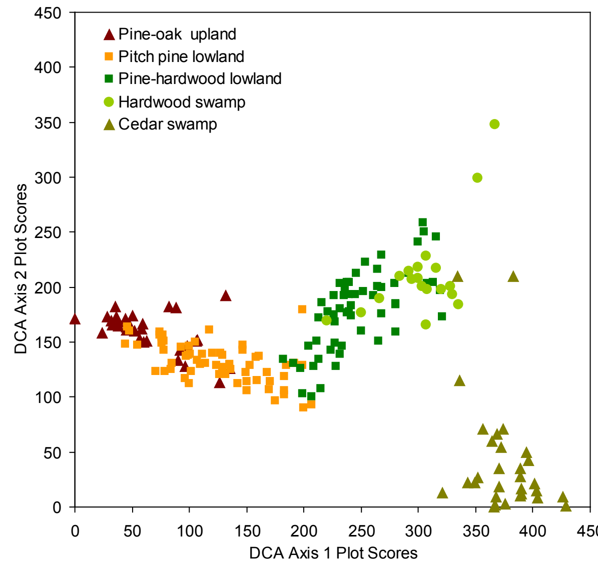

Figure 4. Site diagram based on a DCA ordination of cover data for 56 woody species at 201 forest-vegetation plots. Each plot was classified as representing one of five vegetation types, including pine-oak upland, pitch pine lowland, pine-hardwood lowland, hardwood swamp, and cedar swamp. Plots initially classified as a single type by TWINSPAN were divided based on the presence of mineral or organic soils, with plots associated with organic soils classified as hardwood swamps and those associated with mineral soils classified as pine-hardwood lowlands.

ordination was positively correlated with the relative abundance of wetland species (r = 0.91, $p < 0.001$) and negatively correlated with the relative abundance of upland species (r = -0.93, $p < 0.001$), which indicated that it represented an upland-to-wetland vegetation gradient. This conclusion is supported by the species ordination which also contrasted species classified as wetland species with those classified as upland species (Figure 5) and by the variation in the relative abundance of the three wetland-indicator groups among the five vegetation types (Figure 2). The second DCA axis was weakly correlated with the relative abundance of facultative species (r = 0.16, $p = 0.02$). The lack of a relationship between wetland- or upland-species groups and the contrasting positions of cedar and hardwood swamp plots indicated that the second axis was not associated with a wetland-species or an upland-to-wetland community gradient.

The first DCA axis of the plot ordination based on woody-species cover was strongly correlated

Table 8. Summary depth-to-water-table statistics for five vegetation types, including mean ± 1 SD, median, and percentile-boundary values. Mean water-level values followed by a different letter differ significantly ($p < 0.01$) based on the Kruskal-Wallis ANOVA. The number of plots for each vegetation type is shown in parentheses.

Water-level statistic	Cedar swamp (30)	Hardwood swamp (19)	Pine-hardwood lowland (57)	Pitch pine lowland (64)	Pine-oak upland (31)
Mean ± 1 SD	14.9 ± 5.9 [a]	14.9 ± 8.6 [a]	37.7 ± 21.7 [b]	54.9 ± 20.7 [c]	117.2 ± 39.6 [d]
Median	14.5	12.5	34.6	56.8	110.3
25th and 75th percentile boundary	11.2-19.0	10.3-17.9	22.7-47.7	38.9-68.5	89.2-133.2
10th and 90th percentile boundary	8.3-21.5	3.3-33.6	12.7-66.3	31.3-82.1	75.7-176.9

Table 9. Mean (± 1 SD) and median depth-to-water-table values for vegetation-types by study basin.

	n	Mean ± SD	Median
Cedar swamp			
Albertson Brook	6	12.8 ± 5.8	13.3
Bass River	6	15.6 ± 6.9	12.7
McDonalds Branch	9	16.7 ± 7.3	18.3
Morses Mill Stream	5	15.0 ± 3.3	15.3
Skit Branch	4	13.2 ± 4.1	13.6
All cedar swamps	30	14.9 ± 5.9	14.5
Hardwood swamp			
Albertson Brook	5	14.3 ± 4.3	14.8
Bass River	5	10.4 ± 4.1	11.5
McDonalds Branch	6	14.2 ± 10.7	10.7
Morses Mill Stream	3	24.9 ± 10.4	23.0
All hardwood swamps	19	14.9 ± 8.6	12.5
Pine-hardwood lowland			
Albertson Brook	8	48.0 ± 15.0	46.2
Bass River	4	18.9 ± 12.6	15.4
McDonalds Branch	25	25.8 ± 12.8	23.7
Morses Mill Stream	15	58.0 ± 23.4	51.1
Skit Branch	5	35.2 ± 13.4	33.9
All pine-hardwood lowlands	57	37.7 ± 21.7	34.6
Pitch pine lowland			
Albertson Brook	8	72.9 ± 10.5	72.9
Bass River	9	52.0 ± 12.4	58.1
McDonalds Branch	21	54.1 ± 17.4	54.3
Morses Mill Stream	3	84.5 ± 17.7	74.5
Skit Branch	23	46.5 ± 22.7	39.7
All pitch pine lowlands	64	54.9 ± 20.7	56.8
Pine-oak upland			
Albertson Brook	4	91.7 ± 17.1	95.8
Bass River	5	123.1 ± 57.9	96.1
McDonalds Branch	9	112.8 ± 40.0	113.1
Morses Mill Stream	5	134.9 ± 35.6	127.6
Skit Branch	8	120.0 ± 38.4	110.0
All pine-oak uplands	31	117.2 ± 39.6	110.3

(r = 0.998, $p < 0.001$) with the first DCA axis of the ordination based on woody- and herbaceous-species cover, which demonstrated that the woody-species ordination adequately characterized the upland-to-wetland vegetation gradient represented by the 201 forest plots. The second axes of the two ordinations were also correlated (r = 0.98, $p < 0.001$). The first (r = 0.94, $p < 0.001$) and second (r = 0.54, $p < 0.001$) axes of the ordinations based on woody-species cover and presence-absence data were also correlated. The strong correlation between the two primary DCA axes indicated that both provide a similar measure of the upland-to-wetland community gradient.

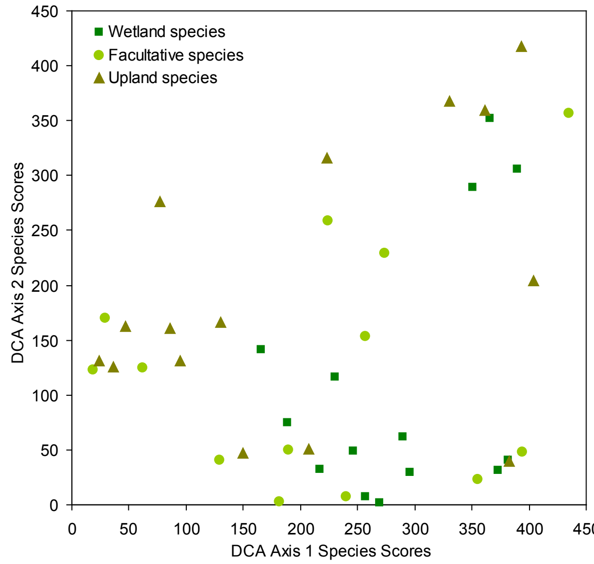

Figure 5. Species diagram based on a DCA ordination of cover data for 56 woody species at 201 forest-vegetation plots. Species were classified according to wetland-indicator status. Wetland species include obligate-wetland and facultative-wetland species. Upland species include facultative-upland species and species not assigned a wetland-indicator status.

Stand structure. Canopy closure (r = 0.75, $p < 0.001$) and mean maximum-shrub height (r = 0.83, $p < 0.001$) increased along the upland-to-wetland gradient represented by the first DCA axis. Mean stem diameter was weakly correlated with this primary axis (r = 0.35, $p < 0.001$). Both canopy closure (r = 0.43, $p < 0.001$) and mean stem diameter (r = 0.24, $p < 0.001$) were weakly correlated with the second DCA axis.

Vegetation-gradient and water-level relationships. The R-square (R^2) value produced by the linear regression analysis based on the 201 forest plots indicated that water level explained 56% of the variation in the upland-to-wetland community gradient represented by the DCA axis-1 scores (Table 11). The percentage of variation in vegetation explained by water level in each of the five basins ranged from 57% in Skit Branch to 76% in Albertson Brook, with an identical value of 66% for each of the other three basins (Table 11). The ANCOVA revealed that the slopes of the five regression lines were similar ($p = 0.83$) although the intercepts differed ($p < 0.001$) (Figure 6). The similarity in slopes indicated that the relative variation in species composition within individual drainage basins was similar for all five drainage basins. The difference

Table 10. Soil properties associated with five vegetation types. Variables include bulk density (g soil cc^{-1}), % organic matter (loss-on-ignition), % volumetric soil moisture (cc water cc $soil^{-1}$), % gravimetric soil moisture (g water grams of dry $soil^{-1}$), mineral-soil O- and A-horizon thickness, and percent sand (proportion of the upper 30 cm of mineral soils that was sand). All values are means ± 1 SD. Mineral soils were associated with pine-oak uplands, pitch pine lowlands, and pine-hardwood lowlands. With the exception of three cedar plots with mineral soils, muck soils were associated with hardwood and cedar swamps. Refer to methods for additional details on the variables. Mean bulk density, % organic matter, O- and A-horizon thickness, and % sand values followed by a different letter differed significantly (p < 0.01) based on Kruskal-Wallis ANOVA.

Variable	Cedar swamp	n	Hardwood swamp	n	Pine-hardwood lowland	n	Pitch Pine lowland	n	Pine-oak upland	n
Bulk density	0.3 ± 0.1[a]	30	0.3 ± 0.1[a]	19	0.5 ± 0.2[b]	57	0.7 ± 0.1[c]	64	0.9 ± 0.1[c]	31
% Organic matter	84.9 ± 7.7[a]	30	82.5 ± 11.7[a]	19	24.2 ± 21.1[b]	57	9.0 ± 4.0[c]	64	5.9 ± 3.0[c]	31
% Volumetric moisture	90.2 ± 9.3	9	77.3 ± 4.2	5	26.7 ± 14.1	15	12.6 ± 5.7	10	9.1 ± 1.6	7
% Gravimetric moisture	671.6 ± 170.1	9	521.2 ± 137.4	5	55.6 ± 34.5	15	23.1 ± 9.1	10	12.7 ± 3.1	7
O-horizon thickness (cm)	-	-	-	-	6.9 ± 1.7[a]	57	5.2 ± 1.1[b]	64	4.0 ± 1.0[c]	31
A-horizon thickness (cm)	-	-	-	-	12.4 ± 6.3[a]	57	5.4 ± 4.2[b]	64	3.1 ± 2.3[c]	31
% Sand	-	-	-	-	25.6 ± 26.1[a]	56	62.0 ± 22.8[b]	64	76.1 ± 20.3[c]	31
Muck depth (cm)	95.6 ± 40.7	27	74.6 ± 40.9	19	-	-	-	-	-	-

in intercepts indicated that species composition associated with a particular water level varied across the basins. For example, plots in the Morses Mill Stream basin generally displayed greater depth-to-water-table values compared to plots with similar species composition in the other basins. Skit Branch plots displayed the opposite trend. The average slope and intercept of the regression lines produced for each of the basins was similar to the overall regression based on all 201 forest plots (Table 11). As indicated by the regression lines and descriptive R^2 statistics (Figure 7), the relationship between vegetation and water level was much less apparent when hardwood swamps, pine-hardwood lowlands, and pine-oak uplands were analyzed separately and was lacking within cedar swamps and pitch pine lowlands.

Table 11. Regression equations relating DCA axis-1 scores (y) to the $\log_{10}$ of depth-to-water table (x) for individual study basins and all 201 forest plots. All relationships were significant at $p < 0.001$. The estimated regression equation was based on an average of the slopes and intercepts for the five study-basin equations. The regression lines are shown in Figure 6.

Basin	n	Regression equation	R^2
Albertson Brook	31	$y = -254.61x + 628.26$	0.76
Bass River	29	$y = -220.37x + 519.9$	0.66
McDonalds Branch	70	$y = -243.03x + 572.17$	0.66
Morses Mill Stream	31	$y = -218.19x + 621.12$	0.66
Skit Branch	40	$y = -217.75x + 495.79$	0.57
All five basins	201	$y = -222.79x + 550.81$	0.56
Mean slope and intercept	-	$y = -230.79x + 567.45$	-

Wetland-indicator Models

Water level explained 64% and 61% of the variation in the relative abundance of wetland-indicator species (obligate-wetland plus facultative-wetland species) and upland-indicator species (facultative-upland plus upland species), respectively (Figure 8). The predictive models produced species-distribution curves which indicated that depth-to-water-table values greater than about 35 cm represented the point at which the relative abundance of upland species exceeds that of wetland species (Figure 9). Similar results were obtained when the percentage of species richness represented by wetland-indicator and upland-indicator species were analyzed (Figures 8 and 9),

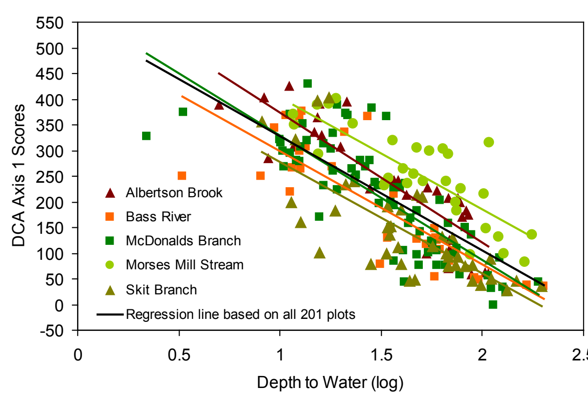

Figure 6. Scatterplot and regression lines relating depth-to-water table ($\log_{10}$ cm) to the upland-to-wetland community gradient represented by DCA axis-1 scores for plots in each of five drainage basins and all 201 forest plots. Refer to Table 11 for regression equations and associated R^2 values.

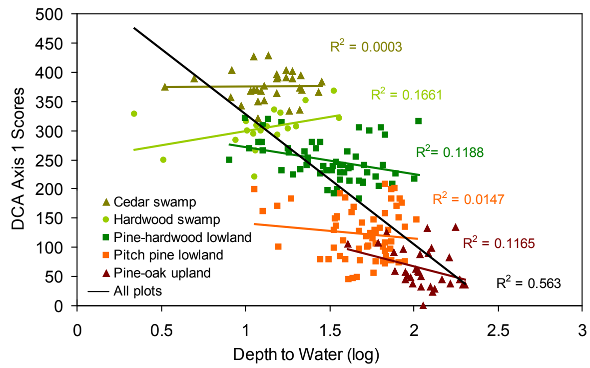

Figure 7. Regression lines and descriptive R^2 statistics for within-vegetation-type relationships between vegetation, represented by DCA axis-1 scores based on 201 forest plots, and depth-to-water table ($\log_{10}$ cm).

although water level explained less of the variation in wetland-species richness (59%) and upland-species richness (51%).

Species and Community Models

Five canopy species, 18 woody understory species, five herbaceous understory species, and *Sphagnum* were included in logistic-model development. The analyses indicated that the different species and vegetation types were associated with varying hydrologic regimes and displayed different optimum water levels (Table 12, Figure 10). The probability curves for cedar swamps and hardwood swamps in relation to water level had similar shapes. The probability of encountering either swamp type decreased monotonically as depth-to-water table increased. Both swamp types were most likely to be found where the water table was closest to the surface. The opposite trend was found for pine-oak uplands. The probability of encountering pine-oak uplands increased as depth-to-water table increased, with a 99% probability of

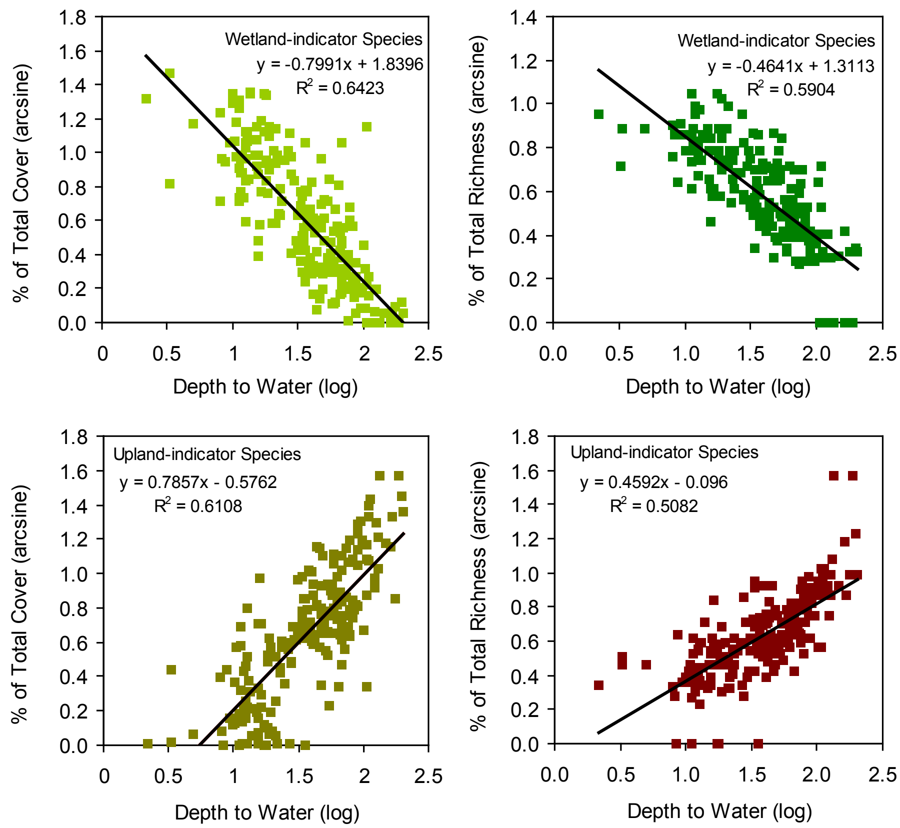

Figure 8. Relationship between depth-to-water table ($\log_{10}$ cm) and the relative abundance (percentage of total cover) and relative species richness (percentage of total species richness) of wetland-indicator species and upland-indicator species. Using these models, predictions for the relative abundance of wetland species and relative species richness of wetland and upland species are limited to depth-to-water-table values ranging from 2 to 201 cm. For relative abundance of upland species, the range for predictions is 8 to 201 cm, with relative abundance assumed to be 0 for depth-to-water-table values between 2 and 8.

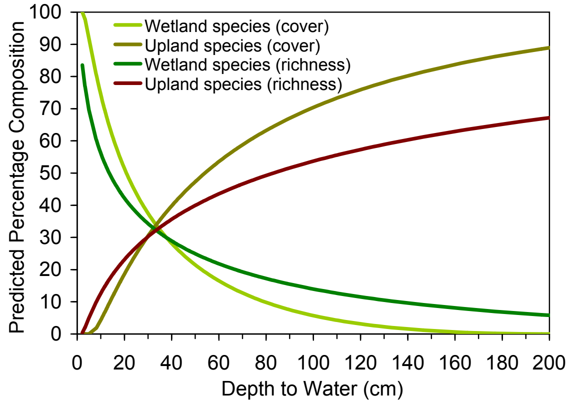

Figure 9. Predicted relative abundance (percentage of total cover) and relative species richness (percentage of total species richness) of wetland species and uplance species groups in relation to depth-to-water table (cm). Refer to Figure 8 for predictive equations. Using these models, predictions for the relative abundance of wetland species and relative species richness of wetland and upland species are limited to depth-to-water-table values ranging from 2 to 201 cm. For relative abundance of upland species, the range for predictions is 8 to 201 cm, with relative abundance assumed to be 0 for depth-to-water-table values between 2 and 8.

occurrence at water levels greater than 140 cm.

Pine-hardwood lowlands and pitch pine lowlands displayed a Gaussian response to variations in water level. Although both vegetation types occurred over a similar range of water levels, the depth-to-water-table value associated with the maximum probability of encountering pine-hardwood lowlands was approximately 40 cm compared to about 65 cm for pitch pine lowlands, with a higher probability of encountering pitch pine lowlands at water levels greater than about 35 cm. The depth-to-water-table values at which the probability of encountering pine-oak uplands was greater than that for pine-hardwood lowlands and pitch pine lowlands were approximately 80 cm and 90 cm, respectively.

Significant relationships between water level and probability of occurrence were found for *Sphagnum* and 28 community-indicator species (Table 12). Species with similar distributions appear as groups associated with different overlapping communities (Figure 10). The occurrence of four cedar swamp indicator species and *Sphagnum* followed a pattern very similar to that of cedar swamp communities (Figure 11). Although hardwood swamp indicators did not track the occurrence of hardwood swamps as closely, the probability of encountering any of the three associated indicators also decreased as depth-to-water table increased. Although the pine-hardwood lowlands displayed a Gaussian response in relation to water level, the six associated indicators decreased monotonically as depth-to-water table increased. Similar to the pattern found for the pitch pine lowland vegetation type, five of the ten associated community-indicator species displayed a Gaussian response to variations in water level. The distribution of three pine-oak upland-indicator species paralleled that of the pine-oak upland vegetation type, increasing as depth-to-water table increased.

Management Applications

The logistic regression and wetland-indicator models developed in this study can be linked directly to groundwater hydrology models and landscape-level applications, developed through other components of the Kirkwood-Cohansey Project, to simulate potential changes in the distribution of wetland species, communities, and wetland-indicator groups resulting from groundwater withdrawals.

Species and Community Models

The logistic regression models describing the probability of encountering one of the five vegetation types can be applied in two ways. The

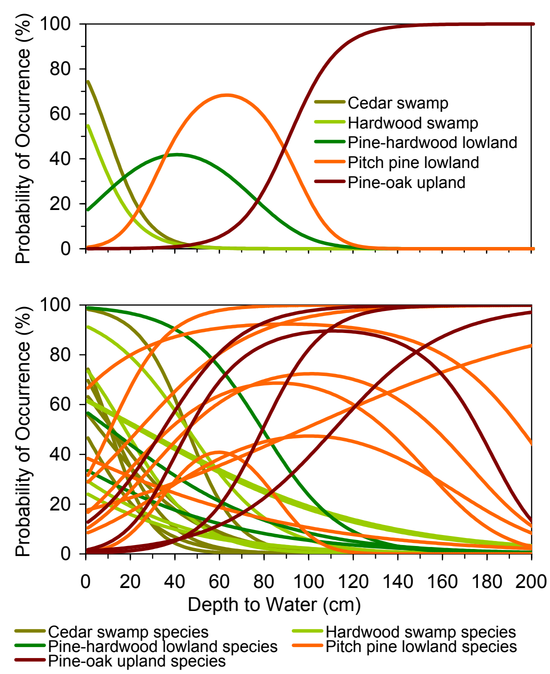

Figure 10. Logistic regression curves describing the probability of occurrence of five vegetation types and associated indicator species in relation to depth-to-water table (cm).

Table 12. Simple (SLR) and Gaussian (GLR) logistic regression models for predicting the probability of occurrence (y) of five vegetation types, 28 associated woody and herbaceous community-indicator species, and *Sphagnum* species in relation to depth-to-water table (x, cm). Species are ordered alphabetically within vegetation types. Models were constructed only for those community-indicator species present at ≥10% of the plots. Canopy and understory tree species are distinguished with a C or a U. In each of the model equations, *e* is equal to the base of natural logarithm (approximately 2.71828). Refer to methods for additional details on model selection criteria.

Vegetation type Indicator species	Model	Model Equation	p
Cedar swamp	SLR	$y = [e(1.178 - 0.113x)] / [1 + e(1.178 - 0.113x)]$	<0.001
Carex collinsii	SLR	$y = [e(1.167 - 0.107x)] / [1 + e(1.167 - 0.107x)]$	<0.001
Chamaecyparis thyoides (C)	SLR	$y = [e(0.908 - 0.076x)] / [1 + e(0.908 - 0.076x)]$	<0.001
Mitchella repens	SLR	$y = [e(0.280 - 0.045x)] / [1 + e(0.280 - 0.045x)]$	<0.001
Osmunda cinnamomea	SLR	$y = [e(0.588 - 0.049x)] / [1 + e(0.588 - 0.049x)]$	<0.001
Sphagnum	SLR	$y = [e(4.126 - 0.090x)] / [1 + e(4.126 - 0.090x)]$	<0.001
Trientalis borealis	SLR	$y = [e(-0.073 - 0.064x)] / [1 + e(-0.073 - 0.064x)]$	<0.001
Hardwood swamp	SLR	$y = [e(0.289 - 0.101x)] / [1 + e(0.289 - 0.101x)]$	<0.001
Acer rubrum (C)	SLR	$y = [e(2.386 - 0.052x)] / [1 + e(2.386 - 0.052x)]$	<0.001
Kalmia latifolia	SLR	$y = [e(-1.125 - 0.027x)] / [1 + e(-1.125 - 0.027x)]$	0.002
Magnolia virginiana (C)	SLR	$y = [e(-0.855 - 0.029x)] / [1 + e(-0.855 - 0.029x)]$	<0.001
Nyssa sylvatica (C)	SLR	$y = [e(0.472 - 0.020x)] / [1 + e(0.472 - 0.020x)]$	<0.001
Rhododendron viscosum	SLR	$y = [e(1.076 - 0.061x)] / [1 + e(1.076 - 0.061x)]$	<0.001
Smilax rotundifolia	SLR	$y = [e(0.493 - 0.019x)] / [1 + e(0.493 - 0.019x)]$	<0.001
Pine-hardwood lowland	GLR	$y = [0.716e{-0.5(x - 41.164)^2 / 25.605^2}] / [1 + 0.716e(-0.5(x - 41.164)^2 / 25.605^2)]$	<0.001
Acer rubrum (U)	SLR	$y = [e(0.293 - 0.027x)] / [1 + e(0.293 - 0.027x)]$	<0.001
Lyonia ligustrina	SLR	$y = [e(-0.665 - 0.022x)] / [1 + e(-0.665 - 0.022x)]$	<0.001
Vaccinium corymbosum	SLR	$y = [e(4.502 - 0.057x)] / [1 + e(4.502 - 0.057x)]$	<0.001
Pitch pine lowland	GLR	$y = [2.155e{-0.5(x - 63.307)^2 / 18.380^2}] / [1 + 2.155e(-0.5(x - 63.307)^2 / 18.380^2)]$	<0.001
Amelanchier canadensis	GLR	$y = [0.691e{-0.5(x - 59.792)^2 / 19.612^2}] / [1 + 0.691e(-0.5(x - 59.792)^2 / 19.612^2)]$	<0.001
Gaultheria procumbens	SLR	$y = [e(-0.939 + 0.039x)] / [1 + e(-0.939 + 0.039x)]$	<0.001
Gaylussacia dumosa	SLR	$y = [e(-0.458 - 0.017x)] / [1 + e(-0.458 - 0.017x)]$	<0.001
Gaylussacia frondosa	GLR	$y = [12.037e{-0.50(x - 90.333)^2 / 47.140^2}] / [1 + 12.037e(-0.50(x - 90.333)^2 / 47.140^2)]$	0.004
Kalmia angustifolia	GLR	$y = [2.621e{-0.5(x - 101.145)^2 / 40.161^2}] / [1 + 2.621e(-0.5(x - 101.145)^2 / 40.161^2)]$	<0.001
Lyonia mariana	GLR	$y = [3.952e{-0.5(x - 85.637)^2 / 26.171^2}] / [1 + 3.952e(-0.5(x - 85.637)^2 / 26.171^2)]$	<0.001
Pinus rigida (C)	SLR	$y = [e(-0.851 + 0.078x)] / [1 + e(-0.851 + 0.078x)]$	<0.001
Pinus rigida (U)	SLR	$y = [e(-1.552 + 0.016x)] / [1 + e(-1.552 + 0.016x)]$	<0.001
Smilax glauca	GLR	$y = [2.194e{-0.5(x - 86.121)^2 / 38.925^2}] / [1 + 2.194e(-0.5(x - 86.121)^2 / 38.925^2)]$	<0.001
Xerosphyllum asphodeloides	GLR	$y = [0.903e{-0.5(x - 100.283)^2 / 46.625^2}] / [1 + 0.903e(-0.5(x - 100.283)^2 / 46.625^2)]$	0.002
Pine-oak upland	SLR	$y = [e(-8.350 + 0.091x)] / [1 + e(-8.350 + 0.091x)]$	<0.001
Gaylussacia baccata	SLR	$y = [e(-1.976 + 0.057x)] / [1 + e(-1.976 + 0.057x)]$	<0.001
Pteridium aquilinum	GLR	$y = [8.596e{-0.5(x - 111.206)^2 / 31.311^2}] / [1 + 8.596e(-0.5(x - 111.206)^2 / 31.311^2)]$	<0.001
Quercus ilicifolia	SLR	$y = [e(-4.403 + 0.040x)] / [1 + e(-4.403 + 0.040x)]$	<0.001
Vaccinium pallidum	SLR	$y = [e(-5.847 + 0.074x)] / [1 + e(-5.847 + 0.074x)]$	<0.001

first approach, which evaluates each vegetation type separately, involves several steps: 1) rescale the raw probabilities from 0 to 100 and classify the rescaled values as high (67-100), medium (33-67), and low (<33) probability of occurrence; 2) determine the relative probability of encountering each vegetation type in relation to water levels assigned to individual cells in a raster-based water-table map; 3) calculate the area associated with each rescaled probability class under baseline water-level conditions; and 4) determine the change in the area of high, medium, and low probability due to simulated water-level declines associated with different groundwater-pumping scenarios. The same method can be used to model the distribution of selected plant species in relation to baseline water levels and water declines.

The second approach analyzes all five vegetation types simultaneously and follows a method similar to that of Rains et al. (2004), where in the case of vegetation types with overlapping

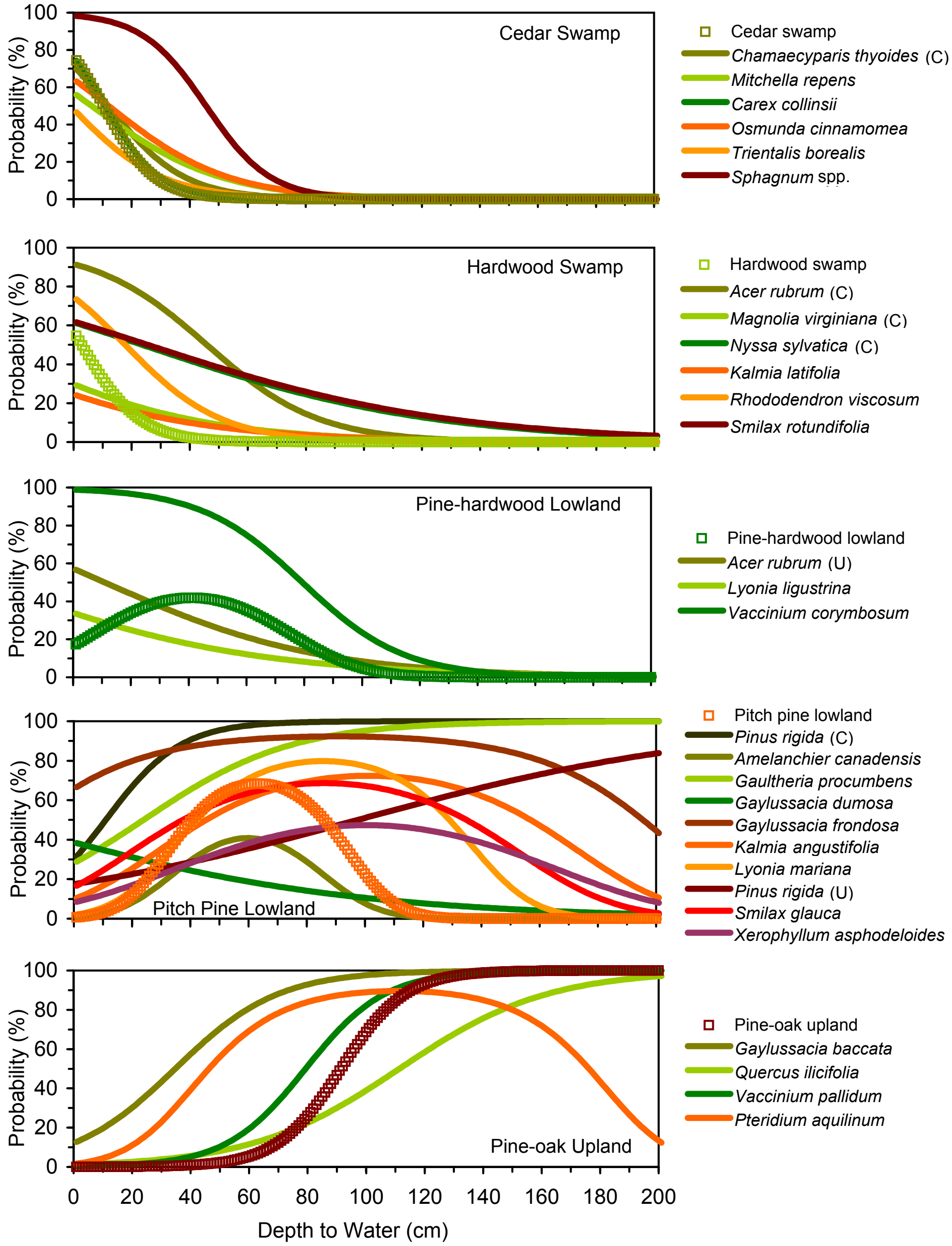

Figure 11. Logistic regression curves describing the probability of occurrence of indicator species and *Sphagnum* spp. in relation to depth-to-water table for each of five vegetation types. The individual vegetation types are represented by squares.

distributions the one with the highest probability of occurrence is assigned to cells with a particular water level. Based on the logistic regression curves presented in Figure 10, individual vegetation types would be assigned to cells characterized by the following depth-to-water-table ranges: cedar swamp (2 to 17 cm), pine-hardwood lowland (18 to 35), pitch pine lowland (36 to 89), and pine-oak upland (≥ 90). Hardwood swamps and cedar swamps would not be included in the same model because cedar swamps always have a higher probability of occurrence. A second analysis would have to be completed using hardwood swamps instead of cedar swamps. This approach, which is more straightforward than the first one, produces a full-coverage map that can be used to determine the area covered by each vegetation type under baseline conditions and conditions resulting from different groundwater-pumping scenarios.

Wetland-indicator Models

By linking the results of the groundwater-hydrology models to the wetland-indicator models, landscape-level applications can predict the probable distribution of wetland- and upland-species cover under baseline conditions across the three modeled study basins. The effect of groundwater-pumping scenarios on the wetland-indicator or functional groups can then be evaluated by comparing the percentage of basin area with varying percentages of wetland- and upland-indicator-species cover or relative-species richness under baseline conditions and conditions resulting from the different scenarios. The models can also be used to compare the change in the area where either wetland- or upland-indicator species dominate based on species cover or species richness.

Discussion

The objective of the study was to develop wetland-vegetation models that can be linked to groundwater-hydrology models and landscape-level applications to predict potential changes in vegetation associated with water-table declines. Such changes may be viewed as altering the capacity of the landscape to sustain some species or communities. For example, cedar swamps are associated with a specific range of water levels and a reduction in the area falling within this range may represent a decrease in the area capable of supporting cedar swamps and associated species.

The community gradient revealed through ordination clearly represented an upland-to-wetland gradient as indicated by its relationship to water level and the distribution of wetland- and upland-indicator groups. The equally strong relationship between the two functional groups, which can serve as surrogates for the community gradient, and water level further supported this conclusion. The probability distributions of the 29 taxa followed a pattern similar to one described by Whittaker (1975) for species where competition does not result in sharp boundaries between populations. Although the distribution of vegetation types and species represented a continuum, the vegetation types were characterized by relatively distinct woody-species composition, hydroperiod, and soil characteristics. The major exception was the comparison of cedar swamps and hardwood swamps, which although displaying differences in species composition, had similar hydroperiods and soils characteristics.

Each of the five vegetation types and associated species occurred within a defined range of water levels. Overlapping ranges in the measured water levels, the amount of variation in species composition explained by water level, and the relationship between the upland-to-wetland vegetation gradient and several soil variables indicated that factors other than hydrology also influence the distribution of the different vegetation types and species.

In the Pinelands, as elsewhere in North America, wetland-community gradients are associated with complex environmental gradients that include edaphic factors as well as hydrology (Robertson et al. 1984, Frye and Quinn 1979, Marks and Harcombe 1981, Huenneke 1982, Paratley and Fahey 1986, Zampella et al. 1992, Bledsoe and Shear 2000, De Steven and Toner 2004, among others). In the present study, water level was correlated with several soil properties, which varied among vegetation types. The vegetation along the upland-to-wetland gradient probably responds to a complex environmental gradient comprising the combined effect of hydrology, soil-organic matter, moisture, and texture. However, as suggested by Zampella et al. (1992), water level can be considered the primary factor underlying the observed vegetation gradient since the accumulation of organic matter is related to water level, soil moisture is related to both soil organic matter and water level, and bulk density is inversely related to organic-matter content. The effect of a decrease in the proportion of surface soil composed of sand among vegetation types distributed along the upland-to-wetland gradient is probably overshadowed by the increase in organic matter and decrease in depth to water. Because of the functional relationship of hydrology with its correlated soil variables, hydrology represented a good proxy for the complex hydrologic-edaphic gradient associated with the upland-to-wetland vegetation gradient. This is especially true along portions of the community gradient characterized by mineral soils derived from similar parent material (Roman et al. 1985, Zampella et al. 1992), where subtle changes in O- and A-horizon organic matter are associated with variations in water levels (Zampella et al. 1992, Zampella 1994). Our conclusion contrasts with that of Yu and Ehrenfeld (2009) who, based on an analysis of our data from only six of our 201 forest plots, concluded that soil genesis is the main factor affecting similarities in plant-community composition.

Factors other than hydrology and soil properties may have a greater influence on within-type variation in species composition compared to differences between vegetation types. Fire and timber harvesting, two factors not directly evaluated in this study, can have a significant effect on the structure and composition of Pinelands forests. In cedar swamps, such disturbances may be followed by recruitment of hardwood rather than cedar-dominated species assemblages (Little 1950, 1979, Whittaker 1979). As with the present study, Laidig and Zampella (1999) found that species composition in cedar swamps was not related to variations in water level. In that study, differences in understory-species composition among cedar swamps were associated with the presence of red maple, which is a dominant canopy species in hardwood swamps.

Canopy gaps created by disturbance may benefit some species such as lowbush blueberry (*Vaccinium pallidum*) and black huckleberry (*Gaylussacia baccata*) (Reiners 1965, Matlack et al. 1993a), although severe upland fires may favor the former species over the latter one (Buell and Cantlon 1953, Matlack et al. 1993b). In the case of pitch pine lowlands, wildfire may encourage the growth of more xeric vegetation (Zampella et al. 1992). In the present study, the depth to water did not vary along that portion of the upland-to-wetland gradient represented by pitch pine lowlands. However, the abundance of black huckleberry, a facultative-upland species, and sheep laurel (*Kalmia angustifolia*), a facultative species, decreased and canopy closure and tree-stem diameter, attributes that may reflect the time and intensity of past disturbances, increased along the pitch pine lowland portion of the gradient.

Other modeling studies have related vegetation to the timing and frequency of flooding and water depth, either separately or in different combinations (Franz and Bazzaz 1977, Auble et al. 1994, Stromberg et al. 1996, Toner and Keddy 1997, Chapin et al., 2002, Rains et al. 2004). In this study, mean water level was a good proxy for a range of water depth variables, including ordinal statistics, such as the median, and seasonal variations in water level. Ordinal statistics provided an indirect measure of the frequency of measured water depths by describing levels that were greater or less than those recorded on a given proportion of sampling dates and the mean study-period water level was highly correlated with levels recorded in individual growing-season months.

Sixty-nine percent of the study plots were located within the McDonalds Branch, Bass River, and Skit Branch basins, the three watersheds characterized by forested landscapes. The remaining thirty-one percent of the sites were located within the Albertson Brook and Morses Mill Stream basins, which were characterized by a higher percentage of upland agriculture and developed lands. A relatively deep 1.2-km-long ditch located on the southeastern side of the Morses Mill Stream may have affected water levels in several nearby forest plots. The possible effect of existing groundwater withdrawals on wetlands in each of the five basins is unknown. Differences in the relationship between vegetation and hydrology among the three forested basins may be attributed primarily to natural variation and the possible effect of different fire or timber-harvesting histories. Although upland agriculture and urban land can influence the species composition of Pinelands wetlands (Ehrenfeld 1983, Ehrenfeld and Schneider 1991, 1993, Laidig and Zampella 1999), it is difficult to separate the effect of natural variation and different fire or timber-harvesting histories from the potential effect of land-use disturbance on wetlands in the Albertson Brook and Morses Mill Stream basins, which were generally drier than those in the other three basins. Including a range of wetlands geographically distributed over the Pinelands helps to ensure that the vegetation models have regional application.

In their models, both Franz and Bazzaz (1977) and Auble et al. (1994) assumed that a change in hydrology would result in a shift to a new equilibrium or quasi-equilibrium vegetation. Equilibrium is a Clementsian concept in which stable-climax communities, comprised of species in competitive equilibrium, represent the endpoint of succession over long disturbance-free periods (Pickett 1980, Glenn-Lewin et al.

1992). The concept of equilibrium is controversial because disturbances that interrupt succession are common and long disturbance-free periods are not considered the norm (Pickett and White 1985). Non-equilibrium is an alternative concept explaining coexistence of species (Pickett 1980). In this viewpoint, frequent disturbance disrupts the competitive advantage of dominant species and prevents the extinction of inferior competitors, thus allowing the persistence of species that display a range of competitive ability.

It is doubtful that equilibrium and climax endpoints exist in the Pinelands where the landscape is recovering from an intense fire and timber-harvesting history (Little 1979, Forman and Boerner 1981, Zampella and Lathrop 1997). Over the past century several authors have described Pinelands vegetation gradients associated with variations in hydrology or soil moisture and disturbance (Harshberger 1916, Little and Moore 1953, McCormick 1955, 1979, Olsson 1979, Whittaker 1979, Roman et al. 1985, Zampella et al. 1992). Although the names assigned to the various forest types differ, their qualitative composition and landscape position correspond to a few basic and generally recognized communities, including those dominated by Atlantic white cedar or swamp hardwoods and different pitch pine dominated forests distributed along a wetland to upland gradient. Disturbance and competition may affect the abundance and quantitative stability of wetland species, but there appears to be a fairly consistent relationship between the presence of common species and the upland to wetland hydrosequence. The similarity between the ordinations based on species presence and abundance in the present study supports this observation. Qualitative persistence rather than quantitative equilibrium (Veblen 1992) is a concept that may best characterize Pinelands wetlands.

The use of functional-species groups to describe the wetland status of a site provides an alternative to grouping species in community types. The strong relationship of wetland- and upland-indicator composition and the community gradient strengthens the assumption that species and vegetation types respond to variations in water level across a range of disturbances.

The results of this study demonstrate that the distribution of wetland vegetation types and species is associated with specific water levels, lending support to the assumption that water-level declines in wetlands could result in a shift towards more mesic or xeric vegetation. The models provide a relatively simple means of determining the capacity of an area to sustain different types of wetland communities and evaluating the potential change in wetlands under different water-decline scenarios. Because mature trees and shrubs may tolerate altered hydrology, in the absence of secondary disturbances, such as wildfire and timber harvesting that reset succession, transitions may take decades or centuries to occur. Protecting the continuity of the forest as a dynamic system involving reproduction and mortality requires a long-term perspective (Franz and Bazzaz 1977).

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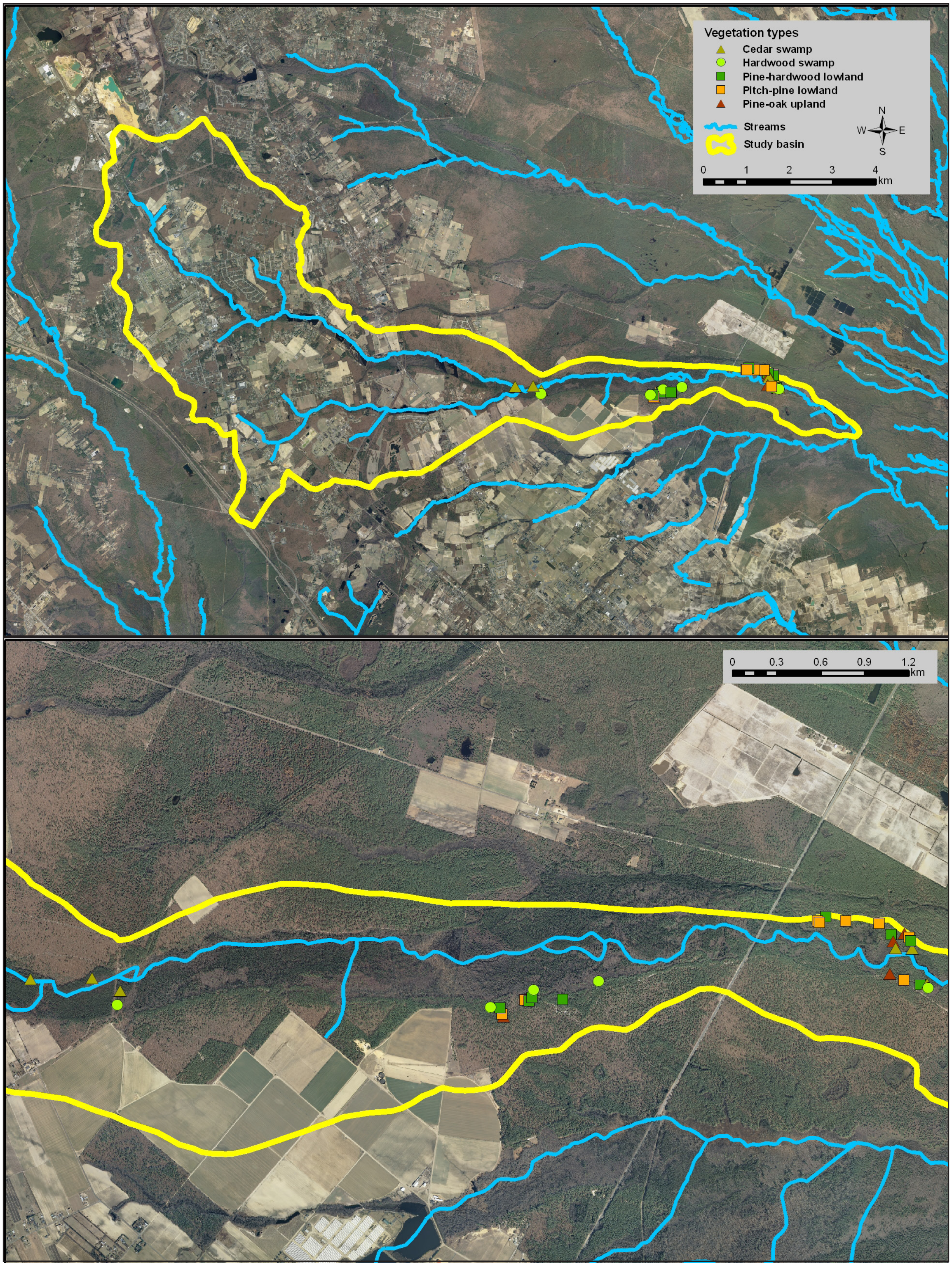
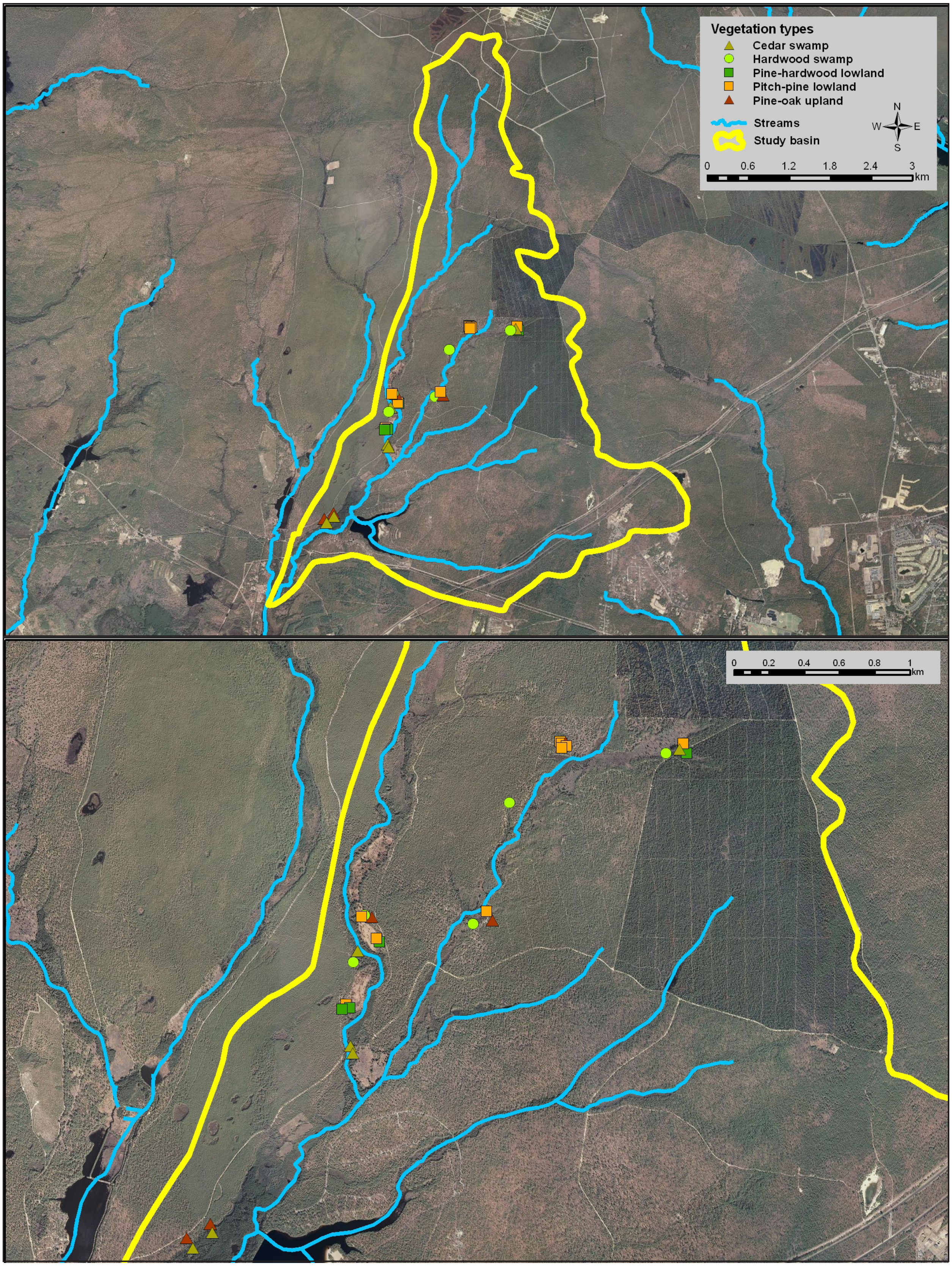
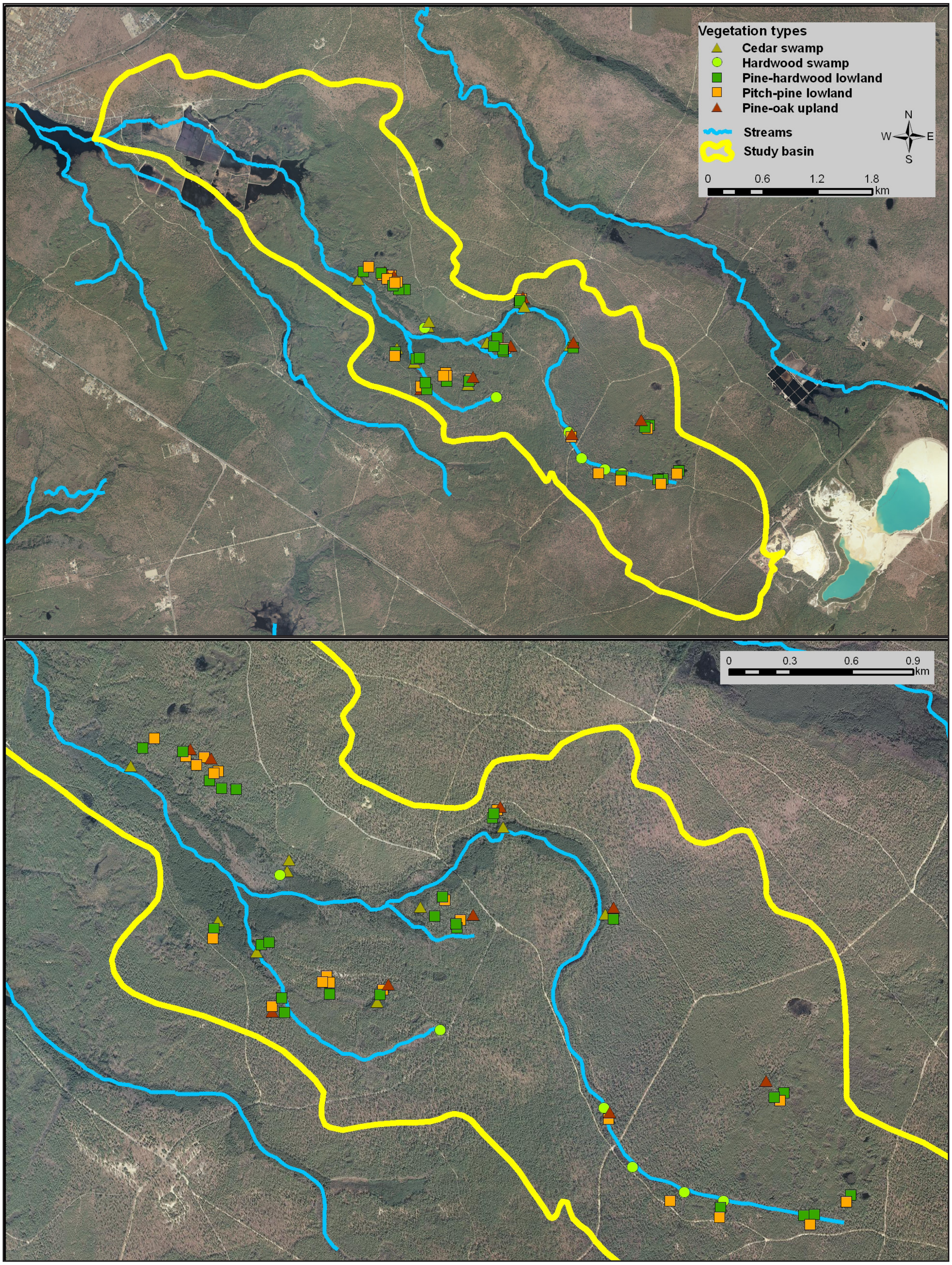
Appendix 1. Aerial photographs (2007) of each of five Pinelands Area study basins and the location of individual forested-wetland study plots. Refer to Figure 1 for regional location.



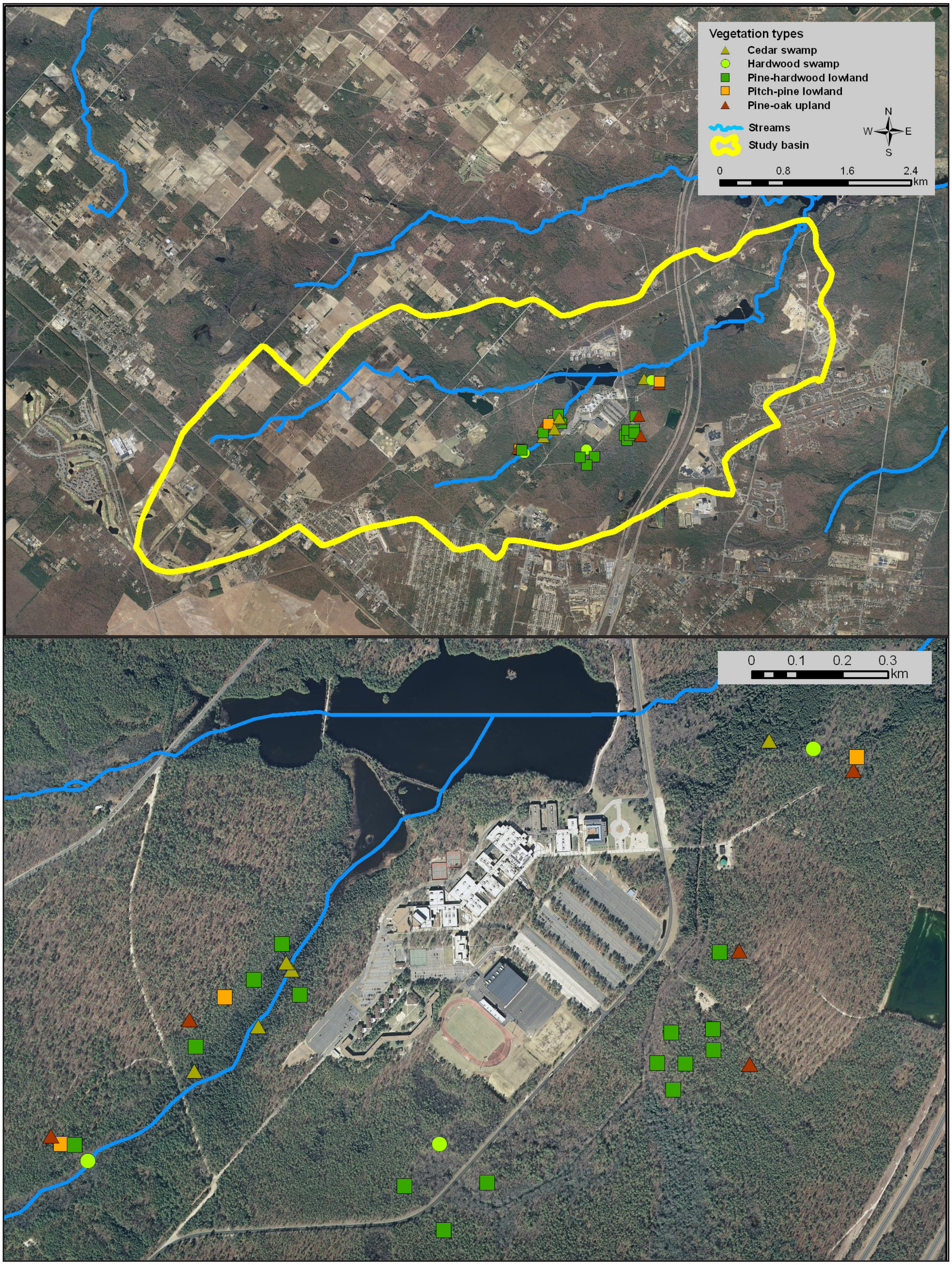
Appendix 1.1. Albertson Brook study basin and the location of 31 individual forested-wetland study plots. Refer to Figure 1 for regional location.



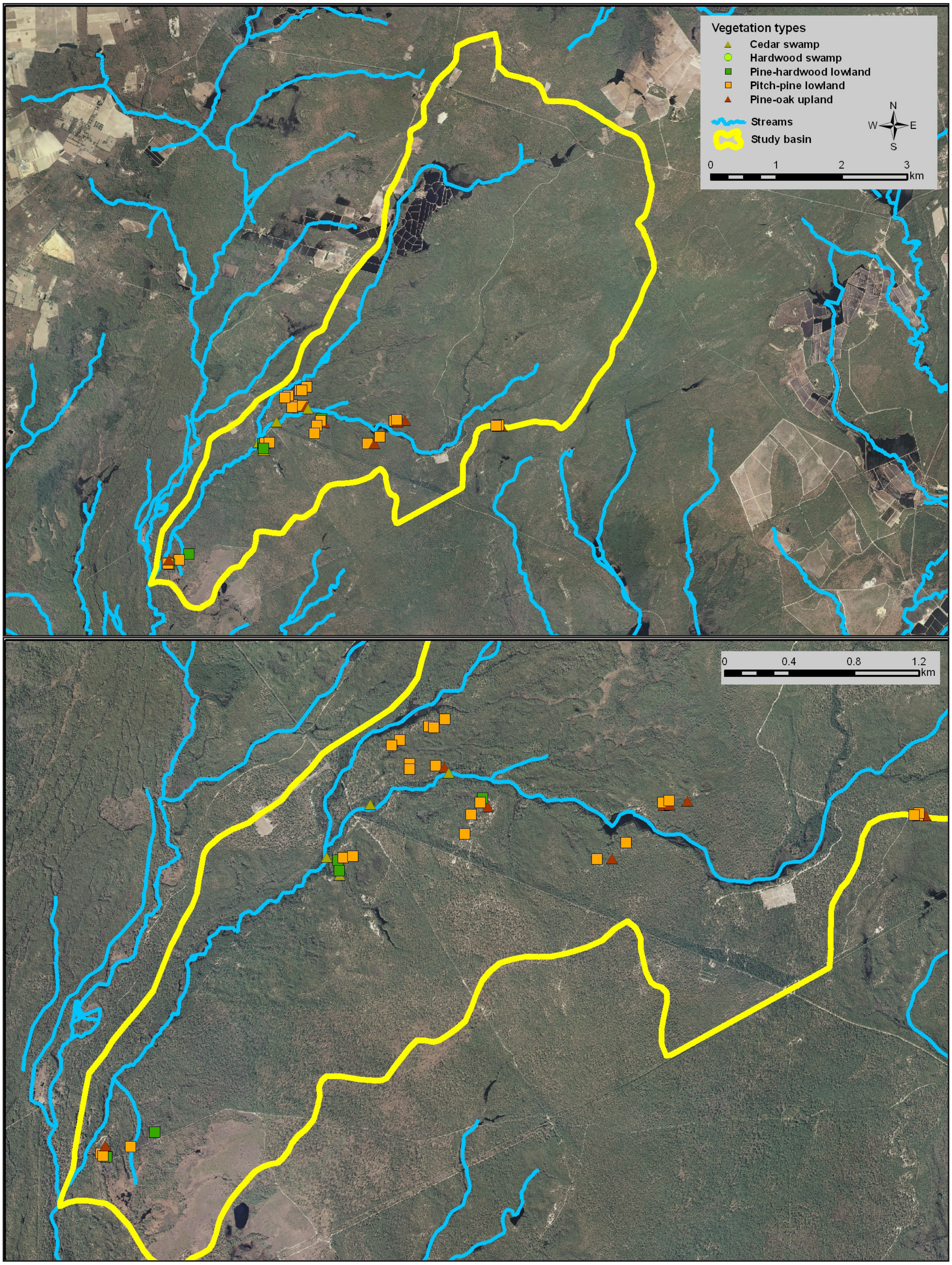
Appendix 1.2. East Branch Bass River study basin and the location of 29 individual forested-wetland study plots. Refer to Figure 1 for regional location.



Appendix 1.3. McDonalds Branch study basin and the location of 70 individual forested-wetland study plots. Refer to Figure 1 for regional location.



Appendix 1.4. Morses Mill Stream study basin and the location of 31 individual forested-wetland study plots. Refer to Figure 1 for regional location.



Appendix 1.5. Skit Branch study basin and the location of 40 individual forested-wetland study plots. Refer to Figure 1 for regional location.