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Threshold Effects of Coastal Urbanization on *Phragmites australis* (Common Reed) Abundance and Foliar Nitrogen in Chesapeake Bay

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ABSTRACT: **The invasion of North American tidal marshes by *Phragmites australis*, or common reed, is a large-scale ecological problem that has been primarily studied at small spatial scales. Previous local-scale studies have provided evidence that the expansion of *Phragmites* is facilitated by disturbance and increased nitrogen (N) associated with agricultural and urban-suburban (developed) land uses along wetland-upland borders. We tested the generality of previous findings across a larger spatial scale and wider range of environmental conditions in Chesapeake Bay, the largest estuarine ecosystem in the USA. We sampled 90 tidal wetlands nested within 30 distinct subestuarine watersheds and examined the relationship between land use and *Phragmites* abundance and foliar N, an indicator of nitrogen availability. We estimated land use adjacent to wetland borders and within subestuary watersheds and explored the importance of spatial proximity by weighting land use by its distance from the wetland border or subestuary shoreline, respectively. Regression tree and changepoint analyses revealed that *Phragmites* abundance sharply increased in almost every wetland where development adjacent to borders exceeded 15%. Where development was <15% but natural land cover at the near the subestuary shoreline was low (<~35%), *Phragmites* was abundant, suggesting that wetlands in highly modified watersheds also were susceptible to invasion, regardless of land use adjacent to wetlands. *Phragmites* foliar N was markedly elevated in watersheds with >14–22% shoreline development, the same level of development that corresponded to high levels of invasion. Our results suggest that development near wetlands is at least partially responsible for patterns of invasion across Chesapeake Bay. Larger-scale phenomena, such as nitrogen pollution at the watershed-subestuary scale, also may be facilitating invasion. Urbanization near coastlines appears to play an important role in the invasion success of *Phragmites* in coastal wetlands of Chesapeake Bay and probably much of eastern North America.**

Introduction

A critical issue in ecology is whether processes identified from small-scale, controlled mechanistic experiments can generate patterns across much larger spatial scales (e.g., Wootton 2001; Steele and Forrester 2005). The rapid invasion of North American tidal marshes by *Phragmites australis* (Cav.) Trin ex Steud (hereafter, *Phragmites*), or common reed, is an excellent example of a large-scale ecological problem that has been studied primarily at small spatial scales. Although *Phragmites* is native to North America, a nonnative genotype is believed to be primarily responsible for its rapid expansion (Saltonstall 2002; Vasquez et al. 2005). This large, clonal grass was historically confined to high marsh fringes with relatively low salinity (Hellings and Gallagher 1992), but now aggressively invades lower elevations once thought to be too physiologically stressful to support dense populations (Amsberry et al. 2000; Burdick and Konisky 2003). *Phragmites* has become a dominant species across a range of wetland habitats, resulting in the displacement of native macrophyte communities (Chambers et al. 1999; Meyerson et al. 2000; Minchinton et al. 2006), degradation of habitat for wildlife (Benoit and Askins 1999; Weinstein and Balletto 1999), and alteration of ecosystem processes (Windham and Ehrenfeld 2003; Windham and Meyerson 2003).

A series of mechanistic studies conducted primarily in small pocket marshes at a local scale in Narragansett Bay, Rhode Island, have provided compelling evidence that the expansion of *Phragmites* is facilitated primarily by disturbance and nitrogen (N) enrichment associated with agricultural and urban-suburban (developed) land uses along wetland-terrestrial borders. In these salt marshes, which spanned a narrow range of salinities

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(25–30‰), the extent of development along wetland-terrestrial borders explained over 90% of the variation in the abundance of *Phragmites* and was attributed to the combined effect of physical disturbance (Minchinton and Bertness 2003) and eutrophication (Bertness et al. 2002) related to shoreline development. Salt marshes with high levels of adjacent developed land were shown to have elevated N availability in comparison to marshes with undeveloped shorelines, presumably due to removal of vegetative buffers between wetland borders and upland source areas (Bertness et al. 2002; Silliman and Bertness 2004). In these same marshes, Minchinton and Bertness (2003) showed that physical disturbance of the vegetation matrix and N enrichment often associated with shoreline development facilitated initial establishment and growth of *Phragmites*. Adjacent development was shown to reduce wetland soil salinity (Silliman and Bertness 2004), which may also support invasion by reducing physiological stress (Burdick et al. 2001). *Phragmites* invades marshes exposed to full-strength sea water via clonal integration (Amsberry et al. 2000), so the ultimate importance of salinity to the invasion success is somewhat equivocal.

Tidal wetlands of other eastern USA estuaries, particularly Chesapeake Bay, have also experienced apparent increases in the abundance of *Phragmites* in recent decades (reviewed by Rice et al. 2000). In contrast to the intensive efforts in Rhode Island, the extent of *Phragmites* invasion of Chesapeake Bay tidal wetlands and its linkages to anthropogenic factors have not been explored in detail. The Chesapeake Bay watershed is rapidly urbanizing and one of the fastest growing coastal regions in North America (Chesapeake Bay Program 2006) and represents an area at increasing risk for coastal wetland degradation. Chesapeake Bay has also experienced significant cultural eutrophication in the past two centuries (Boesch et al. 2001), primarily caused by point and nonpoint source N inputs associated with agricultural and urban (developed) lands (Jordan et al. 1997, 2003). Given the mechanistic relationships between *Phragmites* and development reported elsewhere, the increase in anthropogenic N and shoreline disturbances caused by agricultural and urban-suburban developed lands may be at least partially responsible for the expansion of *Phragmites* in Chesapeake Bay. Because spatial patterns of land use surrounding Chesapeake Bay tidal wetlands vary markedly at local and subwatershed scales (DeLuca et al. 2004; King et al. 2005a), *Phragmites* abundance may also exhibit spatial variability in its distribution that corresponds to proximal land use at one or multiple scales.

In this study, we tested whether *Phragmites* abundance and foliar N are linked to the amount of developed lands across an extensive geographic region (Chesapeake Bay) in an effort to scale up from previous small-scale mechanistic studies to a larger ecosystem with more variable environmental conditions. We hypothesized that the distribution and abundance of *Phragmites* would be linked to anthropogenic land use through pathways at both local (e.g., physical disturbance and surface water runoff from local land use will cause elevations in available N and decreases in salinity at the upland-wetland border) and watershed scales (e.g., surface water runoff and point source discharges from watershed-wide land uses including agriculture and development will increase available N at the seaward-wetland border). To test this hypothesis, we related *Phragmites* distribution and abundance data collected from 90 tidal wetlands spanning over 250 km of Chesapeake Bay to digital land cover data summarized at both local and watershed scales. We also explored the potential linkage between land use and increased N availability at the watershed scale using *Phragmites* leaf-tissue N from subestuary shorelines as an indicator of enrichment. We predicted that increasing amounts of urban-suburban development and agricultural lands adjacent to study wetlands or within their proximal watersheds would be related to an increasing frequency of occurrence and abundance of *Phragmites* and increasing foliar N concentrations.

Methods

Study Area and Sampling

This study was conducted in 30 estuarine tributaries, or subestuaries, of Chesapeake Bay (Fig. 1). Subestuaries were selected from an initial population of 60 based on several criteria. Each selected subestuary had a distinct embayment that was well separated from the mainstem or major tributaries (e.g., Potomac River) of Chesapeake Bay in the states of Maryland and Virginia. Selected subestuaries also spanned a north-to-south salinity gradient ranging from oligohaline to upper mesohaline. Nontidal or tidal freshwater systems were not included in this study. Subestuaries were chosen so that land use or land cover among watersheds spanned a gradient from predominately forested to highly agricultural or urban-suburban developed (hereafter, developed). The most heavily developed watersheds were primarily located in the upper and middle bay on the western shore in the Baltimore-Washington D.C. metropolitan area and in a localized area of the lower bay in the Norfolk, Virginia, metropolitan area, although localized shoreline development was widely distributed among most

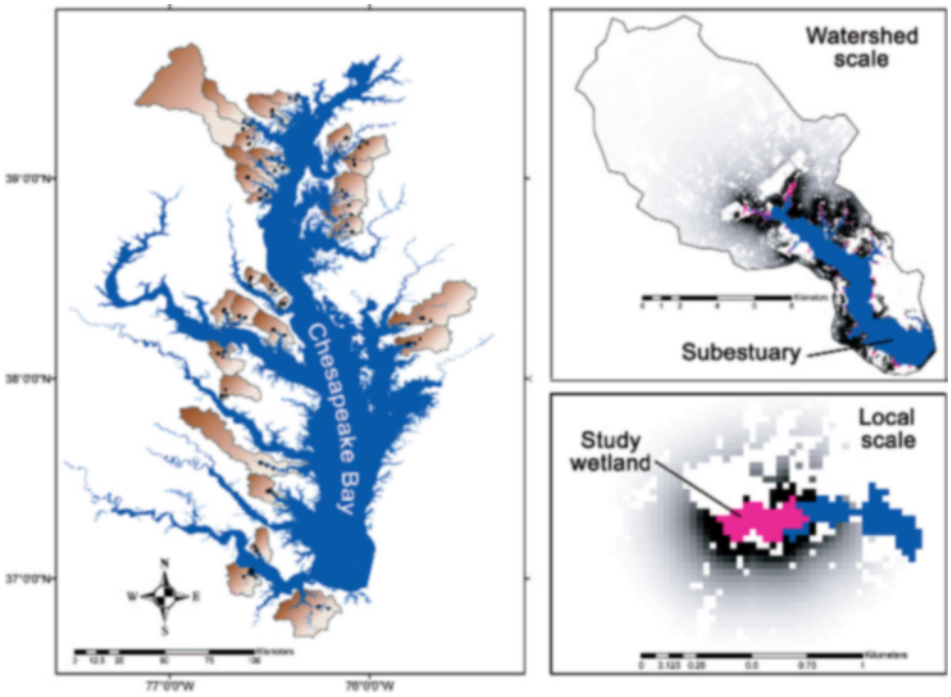

Fig. 1. The larger map is of Chesapeake Bay, USA, illustrating the locations of the 30 subestuaries and their watersheds. Points correspond to the locations of the 90 study wetlands. The Watershed scale illustration is of inverse distance weighted (IDW) developed land in relation to the subestuary (blue)–tidal wetland (magenta) border within a contributing watershed. Weights assigned to each developed land pixel are represented by a gradient from black (near) to light gray (far) and correspond to their inverse distance (m) to the subestuary–tidal wetland border. White corresponds to nondeveloped land covers or developed land that is sufficiently far that it receives minimal weight. In this example, unweighted % developed land in the watershed was 66.5%, whereas the distance-weighted % developed land was 46.8%. The Local scale illustration is of IDW developed land cover within 500 m of an individual tidal wetland. In this example, developed land occupied 34% of the 30-m buffer adjacent to the wetland border, whereas 74% of the area within 500 m of the wetland, weighted by its distance to the border, was developed. This 9.3 ha wetland was heavily invaded by *Phragmites* (abundance index = 7, the maximum value possible).

subestuaries. Agricultural land use was also widely distributed but most intensive in watersheds on the eastern shore of the bay in Maryland. Given these existing spatial patterns of land use, we chose subestuaries that resulted in the greatest spatial distribution of the predominant land use classes across the region to minimize confounding effects of spatial phenomena unrelated to land cover (King et al. 2004b, 2005b). Greater details about watersheds and their subestuaries can be found in King et al. (2004a), DeLuca et al. (2004), and King et al. (2005a).

Phragmites abundance was estimated at three brackish tidal wetlands within each subestuary (Fig. 1). Three wetlands were randomly selected from the larger population of sites, but stratified by wetland size. One wetland from each of three size classes was sampled: < 2 ha, 2–7 ha, and > 7 ha. These numerical criteria were based on the distribution of size classes in subestuaries with the fewest number of tidal wetlands and employed as part of a larger study of these same wetlands on marsh bird communities of Chesapeake Bay (DeLuca et al. 2004), where wetland size was shown to affect bird assemblages. These size criteria ensured that a wide range of wetland sizes were sampled equally throughout the study area. A wide range of wetland sizes also allowed us to evaluate whether size influenced wetland susceptibility to *Phragmites* invasion. Greater description of wetland characteristics and site selection criteria are provided in DeLuca et al. (2004).

We estimated abundance of *Phragmites* at each of the 90 study wetlands using 100-m diameter study plots. The number of plots used in each wetland varied by wetland size: 1 (< 2 ha), 2 (2–7 ha), and 3 (> 7 ha). Plots were located randomly in the interior of the marsh where plot boundaries did not cross the terrestrial or open water border. Within each plot, four 12-m diameter vegetation sampling circles were established, with the first circle centered in the middle of the plot, and the remaining three circles located 35 m from the center at 0°, 120°, and 240°, respectively. Each vegetation circle was further divided into four equal quadrants. Within each quadrant, *Phragmites* abundance was

estimated using a modified Braun-Blanquet cover scale (hereafter, abundance index) ranging from 0 (absent) to 7 (> 75% cover; Philips 1959; Leps and Hadincova 1992). *Phragmites* abundance index values were averaged among the four quadrants of each circle, and then averaged again among the four circles, resulting in a mean abundance index value for the plot. Intermediate and large wetlands had > 1 plot, so mean abundance index values among plots were averaged at those sites to yield an overall *Phragmites* abundance index value per wetland. We recognize this sampling method may have underestimated abundance of *Phragmites* patches along the upland or seaward borders. Our goal was to characterize the extent of invasion of the majority of the marsh surface (not just the border) and relate this to digital land cover data. Because of the lag time among disturbance, establishment, and expansion of *Phragmites* (Amsberry et al. 2000; Philipp and Field 2005), sampling the interior would yield a more representative estimate of the extent of invasion and its potential linkage to both local (upland-wetland border) and watershed (seaward-wetland border) land use drivers.

Because of the significant spatial extent of the study area and additional goals of the overall estuarine indicator project, not all wetlands could be sampled during the same year. Sampling occurred during the summers (June–August) of 2002 and 2003. Nineteen subestuaries (57 wetlands) were sampled in 2002, whereas 21 subestuaries (63 wetlands) were sampled in 2003. Ten subestuaries were sampled in both years for surface-water salinity, but *Phragmites* distribution and abundance was not sufficiently variable at the scale of our wetland measurements to warrant resampling each wetland for interannual changes in abundance (DeLuca personal observation). The intraannual and interannual sequence in which subestuaries were sampled was determined randomly.

We expected that geographical differences in the distribution of *Phragmites* could be caused by salinity, contagious dispersal, or other factors unrelated to land use, so surface water salinity and geographical coordinates (northing and easting, m) were measured and included as predictors in data analyses (see next section). Geographical location (Universal Trans-Mercator, Zone 18, in meters) of each wetland was recorded using a global positioning system. Surface water salinity was sampled at two locations in the open water at a depth of 10 cm immediately adjacent to the seaward border of each study wetland. Interannual variation in salinity made comparisons difficult among wetlands sampled in different years. We experienced very different levels of freshwater discharge into Chesapeake Bay during 2002 (year 1) and 2003 (year 2). The year 2002 was abnormally dry, particularly during summer (ca. 95 cm annual rainfall, mostly in late winter and fall), whereas 2003 was the wettest year on record for the entire region (ca. 160 cm). We standardized salinity between years using measurements from 30 wetlands in which salinity was sampled in both 2002 and 2003. These 30 wetlands spanned most of the bay's north-to-south salinity gradient and likely captured coarse spatial differences in salinity between years. Salinity observations from the 30 wetlands yielded the following regression equation: 2003 salinity (‰) = 2002 salinity (‰) $\times$ 0.582 $-$ 0.37; $r^2 = 0.75$, $p \leq 0.0001$. Using this equation, we estimated salinity at other wetlands for the year not sampled (2002 or 2003) using the salinity observed during the actual year of sampling (2002 or 2003). Predicted salinity values were averaged with observed measurements for all wetlands to yield a mean salinity value for two consecutive summers, standardizing salinity across all wetlands.

A different sampling design was necessary to estimate *Phragmites* foliar N concentrations because many study wetlands did not host *Phragmites*. Although previous studies have used aboveground N of a phytometer common to all wetlands as an indicator of site-specific N availability (e.g., *Spartina alterniflora*; Bertness et al. 2002; Silliman and Bertness 2004), no such plant was common to all wetlands across the large spatial extent of our study. It was not possible to standardize foliar N or standing stock aboveground N at each individual study wetland in the manner done in these previous studies. Almost all of the subestuaries (29 of 30) had stands of *Phragmites* at other locations along their shoreline (all of which in the general vicinity of the study wetlands), so we compared mean foliar N levels among subestuaries as an indicator of N availability at the watershed scale.

We sampled *Phragmites* leaves from up to 6 shoreline segments in each of 29 subestuaries. Shoreline segments were 100 m in length and selected randomly within each subestuary using methods described in King et al. (2005a). Sampled plants were located on the seaward border of the stand and were in contact with surface water of the subestuary during high tide. We targeted seaward bordering plants rather than interior or upland border plants because seaward plants were more likely to integrate watershed-scale nutrient availability (and this component of the analysis was watershed-scale only). We collected one recently emerged leaf located near the tip of each of 10 distinct shoots (i.e., 10 leaves per sample). In situations where *Phragmites* was not present but in the general vicinity of the segment, we sampled

these adjacent stands instead. Sampled leaves were placed on ice until return to the laboratory.

Leaf composite samples were dried for 48 h at 60°C, ground, and analyzed for total carbon (C) and N using a Perkin-Elmer 2400 CHN Analyzer. Total N was almost perfectly correlated to the C:N ratio ($r^2 = 0.98$), so we only used total N (%) in further analyses. We averaged % total N among composite samples per subestuary to generate a spatially integrated estimate for each subestuary (Weis et al. 2003).

Foliar N samples were collected in 2002 and 2003 following the same sampling schedule described for *Phragmites* abundance. Nine subestuaries, rather than 10, were sampled in both years because one of the 10 subestuaries did not have *Phragmites*. Because interannual variation in precipitation and runoff may have influenced N availability to *Phragmites*, we statistically analyzed foliar N data from each year separately (see Statistical Analyses).

We recognized that % N alone may not fully characterize N availability, as N enrichment can lead to both increased foliar N and greater standing biomass without a difference in tissue concentration (Windham and Meyerson 2003). If an increase in foliar N was found to be related to increasing percentages of probable N source areas (agricultural and developed lands), this would support the hypothesis that land use may be linked to greater N availability to *Phragmites*. We also recognized that the presence of *Phragmites* in a particular location could, in itself, suggest local N enrichment if N is indeed a facilitator in its expansion, so sampling particular stands of *Phragmites* might be a biased indicator of N availability. This bias should be equivalent for all stands among subestuaries, so a positive correlation should again suggest an association between land use and N availability to *Phragmites*. Although leaf tissue % N was not a direct measure of availability, we contend its use as a relative indicator of N availability was sufficiently justified.

Geographic Analyses

We used the ARC/INFO 9.1 Geographic Information System (GIS; ESRI, Redlands, California) for geographic analyses. Watershed boundaries around each subestuary were delineated manually from 1:24,000 digital elevation models expressed as a 30-m raster (USGS National Elevation Data Set; www.usgs.gov). Land use data were extracted from the National Land Cover Database (NLCD), a raster data set developed from 30-m Landsat thematic-mapper images taken during 1992 (USEPA 2000). We also considered two more recent land use or land cover data sets derived from satellite images taken in 1999–2000: NLCD 2001 and RESAC (2003); both were experiencing problems along the estuarine-terrestrial border and were being modified by their respective authors at the time of analysis. The NLCD 1992 closely matched our ground-truthed field observations of land cover along the estuarine shoreline (i.e., developed pixels almost always corresponded to real development in the field). We expected abundance of *Phragmites* in 2002–2003 to be more strongly correlated to patterns of land use several years earlier because of the time lag that would be required for establishment and expansion caused by land use (Amsberry et al. 2000; Philipp and Field 2005).

We considered four types of land use or land cover as correlates of *Phragmites*: developed land, which was the sum of NLCD 1992 low-intensity and high-intensity residential and commercial classes; agricultural land, defined as the sum of pasture, hay, cropland, and recreational grasses; cropland, which was examined separately from combined agricultural classes because it is the primary non-point source of nitrate in the Chesapeake Bay watershed (Jordan et al. 1997); and forest-wetland cover, which was the sum of all forest and wetland classes resolved in the NLCD 1992 (i.e., all natural land cover classes combined).

We expected that land use close to shorelines may have a greater unit effect on *Phragmites* abundance and foliar N than land use farther away. To account for land use proximity, we first defined and delineated shorelines in the NLCD 1992 as the border between terrestrial land and herbaceous tidal wetlands or the open water estuary (Fig. 1). We subsequently summarized land use at both whole-watershed (contributing area to the subestuary) and local (area immediately adjacent to the study wetland) scales. At the watershed scale, we estimated percent of the area occupied by certain land uses in three different ways: percentage of the watershed area, excluding the subestuary and tidal wetlands; percentage of a 30-m buffer along the shoreline (i.e., only land use immediately adjacent to the shoreline per results of Bertness et al. [2002] and Silliman and Bertness [2004]); and percentage of the watershed area weighted by its inverse distance (IDW) to the shoreline (Comeleo et al. 1996; Soranno et al. 1996; King et al. 2004a, 2005b).

At the local scale, we constrained our estimates of land use percent cover to a maximum distance of 500 m of the wetland border (Fig. 1). This scale was chosen to avoid spatial overlap in land use percentages among some wetlands and because a previous study found that land use within 500 m of these same wetlands was the strongest correlate of bird communities when compared to other scales (DeLuca et al. 2004). Study-wetland boundaries were delineated as contiguous emergent wetland

pixels resolved in the NLCD 1992 for each of the 90 sites. We summarized local land use adjacent to the study wetlands in each of three ways: percentage contribution of a particular class to the total land area within 500 m of the wetland border, percentage of land immediately adjacent to the wetland border (one-pixel width or 30-m buffer), and percentage area within 500 m of the wetland border, weighted by its IDW to the border. We also estimated the area (ha) of each study wetland, as delineated in the GIS, to evaluate whether wetland size had an influence on *Phragmites* invasion (see next section).

We considered all of these land use metrics as predictors of *Phragmites* variables. The IDW metrics were calculated because they implicitly presume that discharges from more distant land uses may be attenuated by a variety of processes along transport pathways before reaching the wetland or subestuary and should receive less emphasis, but should not be excluded altogether (as is done in buffer analysis). Fixed distance buffers assume that all pixels within a certain distance of a feature of interest have an equivalent effect on a response variable, which is also unlikely (King et al. 2005b). We predicted that the IDW metrics would more effectively describe land cover effects on *Phragmites* than simple whole watershed or fixed distance buffer percentages.

To calculate IDW percent land use, every pixel of each of the four classes was assigned a distance (meters) to the shoreline using simple Euclidean distance. Pixels were weighted by the inverse of their distance to the shoreline (1/distance) and summed for a distance-weighted pixel count for the entire watershed. The process was repeated for all pixels in the watershed. The sum of distance-weighted, land-use pixels was divided by the sum of distance-weighted, total land in the watershed to yield distance-weighted, percentage land use (e.g., IDW percentage developed land is illustrated in Fig. 1).

Statistical Analyses

Preliminary examination of the *Phragmites* abundance and foliar N data revealed relationships to predictor variables that were strongly nonlinear, heteroscedastic, and involved higher order interactions. We used a nonparametric alternative to multiple regression, regression tree (CART) analysis (Breiman et al. 1984; De'Ath and Fabricius 2000; Urban 2002), to predict *Phragmites* distribution, abundance, or foliar N according to land use, salinity, wetland size, and geographical coordinate variables.

CART explains variation of a single response variable using one or more predictor variables. Response variables can either be categorical (classification tree) or numerical (regression tree). CART works by recursively partitioning data into two mutually exclusive groups by selecting a predictor variable that best explains variation in the response variable (i.e., greatest reduction in deviance). The process is repeated until the tree can no longer be grown based on a set of stopping rules and cross validation of the model. The method works particularly well when critical levels of a predictor result in a nonlinear, threshold change in the mean and variance of the response. The objective of the method is to explain as much variation (r^2) in the response variable as possible while minimizing the size of the tree. This is analogous to incorporating explanatory variables into multiple regression.

We built a CART model to explain variance in the *Phragmites* abundance index using the 90 study wetlands as observations. Separate tree models were also developed for the *Phragmites* foliar N data from 2002 (18 subestuaries) and 2003 (20 subestuaries). Models were regression trees because the response variables were continuous. We required that terminal nodes (leaves) and branches have no fewer than 5 and 10 observations, respectively.

We cross validated each tree model to determine the most appropriate size of the tree (i.e., number of explanatory variables included in the model). Cross validation was conducted by randomly partitioning the data (wetlands stratified by subestuary to account for spatial nestedness in abundance analysis, following De'Ath and Fabricius [2000]) into 10 groups of equal or similar size and creating a cross validation regression tree with only nine of the 10 groups. This cross validation tree was subsequently used to predict response variable data from each of the stations remaining in the tenth group. The process was repeated 10 times so that each of the 10 groups of sites was used as the cross validation group once. We retained predictors that resulted in an average overall model r^2 within one standard error (SE) of the minimum model r^2 among all possible trees (1 SE rule; Breiman et al. 1984; De'Ath and Fabricius 2000).

We also recognized that although CART will choose the single best predictor at any given level of a tree, other predictors may explain similar amounts of variance in the response. This was a particular concern in our use of multiple measures of land use as predictors, which were necessarily correlated (King et al. 2005b). For every split in the tree, we also reported up to the top three alternative predictor variables that were deemed statistically significant (χ^2, 1 df). CART analyses were conducted using the RPART library (Therneau and Atkinson unpublished data) in S-Plus 6.1 (Insightful Corp., Seattle, Washington).

We further validated the predictors that explained the most variance in *Phragmites* regression tree

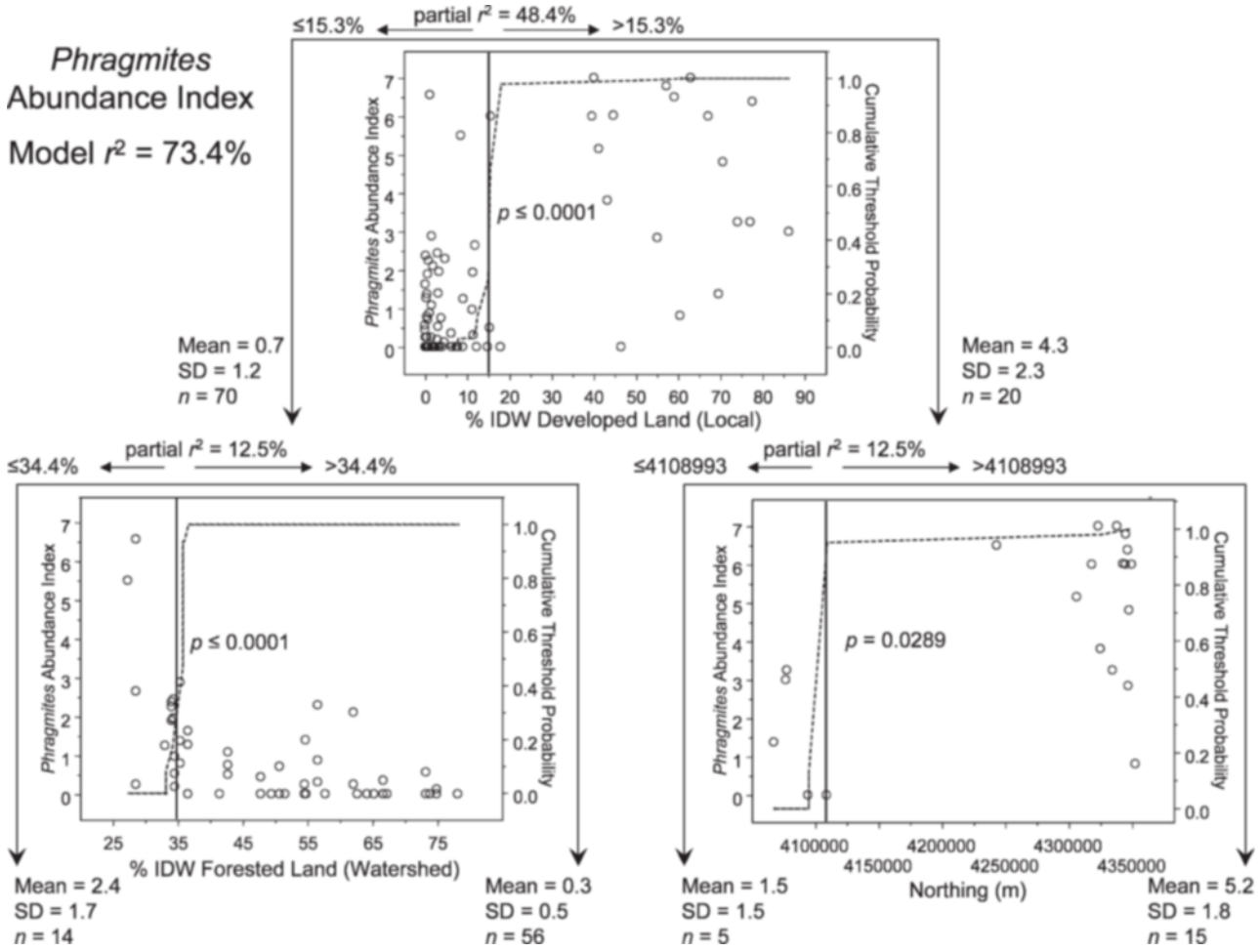

Fig. 2. Results from regression tree and changepoint analysis of *Phragmites* abundance (n = 90 wetlands). Variance in *Phragmites* abundance was best explained by IDW % developed land adjacent to the wetland border, IDW % forest-wetland (for-wet) cover in the watershed, and geographical location along the north-to-south axis of Chesapeake Bay (northing, m). Scatterplots illustrate the response of *Phragmites* abundance to each predictor in the tree. The solid vertical line within each plot identifies the value of each predictor that best explained variance in *Phragmites*. Threshold values of predictors are shown to the left and right of each split in the tree. Variance explained (r^2) is shown above each split. Means, standard deviations (SD), and number of wetlands are reported for each split. Within each scatterplot, dotted lines represent the cumulative probability (y-axis, right side) of a threshold response in *Phragmites* abundance with increasing values of each predictor, as estimated using changepoint analysis. p values correspond to the likelihood that there was no changepoint in the data.

models using nonparametric changepoint analysis (King and Richardson 2003; Qian et al. 2003). Changepoint analysis estimates the numerical value of predictor, x, resulting in a threshold in the response variable, y. Because changepoint analysis uses the same test statistic as tree regression to identify nonlinear breaks or splits in a response variable (deviance reduction), the two methods are similar. Unlike tree regression, the changepoint method employs a bootstrapping (resampling) technique to estimate a percentile confidence interval around the observed threshold. We conducted changepoint analysis for each variable included in the final tree models. We overlaid the cumulative distribution of the percentile confidence limits on each predictor in the tree models as a measure of the cumulative probability of a threshold (DeLuca et al. 2004; King et al. 2005b; Fig. 2). We also estimated the probability that the observed variance explained by the changepoint was not different from zero (deviance reduction = 0), a test that further validated the inclusion of variables in tree models.

Results

Phragmites Abundance

Phragmites was present in 52 of the 90 study wetlands (57.8%). Variance in *Phragmites* abundance

among wetlands was best explained by local-scale development, forest-wetland cover near the subestuary shoreline, and geographical location along the north-to-south axis of Chesapeake Bay (regression tree model $r^2 = 73.4\%$; Fig. 2). The most influential factor in the regression tree was local IDW % developed land (partial $r^2 = 48.4\%$; Fig. 2; also see Fig. 1). Where local IDW developed land was > 15.3%, *Phragmites* abundance increased dramatically and was relatively high at all but a few wetlands. The range of developed land within the percentile confidence limits was small, with the lower 5% limit corresponding to 10% developed land, with 95% certainty that the threshold was no higher than 20% (Fig. 2). Percent developed land within 500 m of the wetland border was the best alternative predictor to local IDW % developed land ($r^2 = 46.4\%$), followed by % IDW forest-wetland cover at the watershed scale ($r^2 = 36.4\%$), and % IDW developed land at the watershed scale ($r^2 = 35.7\%$).

Where local development was ≤ 15.3%, wetlands located in subestuaries with ≤ 34.4% IDW forest-wetland cover at the watershed scale also tended to have a higher abundance of *Phragmites* (partial $r^2 = 12.5\%$; Fig. 2, left branch). This threshold was most probable between 34% and 40% IDW forest-wetland. Wetlands with relatively low local development and moderate amounts of natural land cover near the shoreline in their proximal watershed also had the lowest cover of *Phragmites*. The only significant alternative predictor was % forest-wetland in the watershed ($r^2 = 10.4\%$).

Wetlands with relatively high adjacent development and located in the middle and northern regions of Chesapeake Bay had more *Phragmites* than similar wetlands in the southern part of the bay (northing, partial $r^2 = 12.5\%$; Fig. 2, right branch). Wetlands in the southern bay with locally high development had low-to-moderate abundance of *Phragmites*, whereas middle and upper bay sites subject to the same levels of local development had more. Salinity ($r^2 = 7.7\%$) was the best alternative predictor to northing, although none of the alternate predictors at this node of the tree were significant.

Phragmites Foliar Nitrogen

N concentrations in *Phragmites* leaves were related to watershed land use during both years (Fig. 3). In 2002, N increased markedly from an average of 2.3% to 2.9% once IDW developed land exceeded 14.3% ($r^2 = 65.3\%$). The 95% confidence limits for the threshold ranged from 7% to 30% IDW developed land, with high certainty (> 80%) that the threshold was at or below the observed regression tree split of 14.3%. Percent N was consistently elevated among subestuaries with relatively high levels of development near the shoreline, including the Elizabeth River, a southern-bay subestuary with the highest average salinity. During this dry year, % N in subestuaries with predominantly agricultural watersheds (Fig. 3; IDW % agriculture proportional to increasing size of symbols) were not consistently elevated over forested systems, and were always much lower than developed watersheds. The only alternative predictor in the regression tree that was significant was % developed land (unweighted by distance) in the watershed ($r^2 = 41.2\%$).

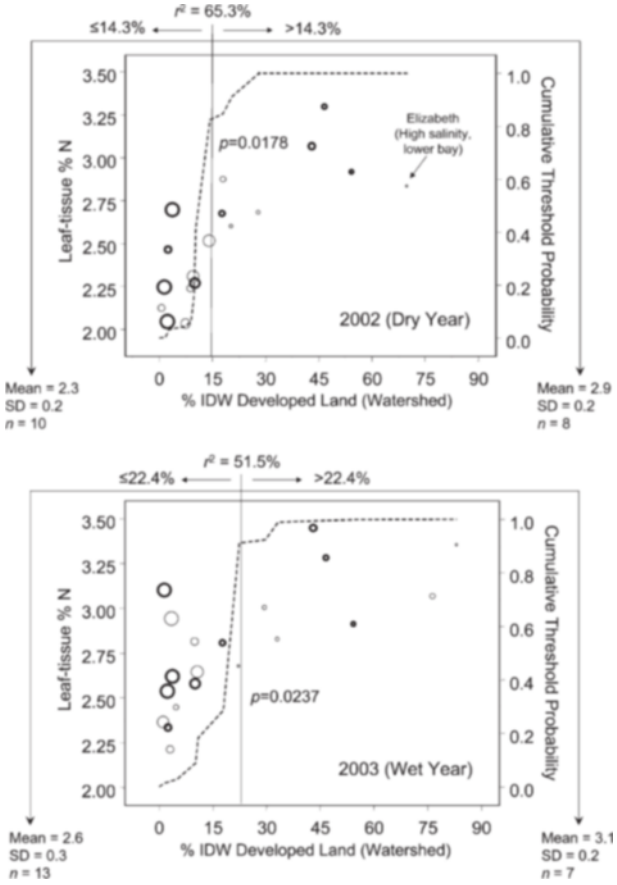

Fig. 3. Results from regression tree and changepoint analysis of *Phragmites* foliar nitrogen (N, %) composite samples collected from 29 subestuaries during 2002 (n = 18) and 2003 (n = 20). Bold symbols correspond to subestuaries sampled in both years. Symbol size is proportional to IDW % agriculture in the watershed. See Fig. 2 for other details.

In 2003, a wet year, IDW % developed land in the watershed was again the best predictor of foliar N ($r^2 = 51.5\%$; Fig. 3). Above 22.4% IDW developed land, foliar N averaged 3.1% compared to 2.6% in less developed watersheds. Subestuaries sampled in both years (bold symbols in Fig. 4) showed similar patterns to other subestuaries sampled in the same year, demonstrating these trends were not limited just to those nine systems. Unlike 2002, several

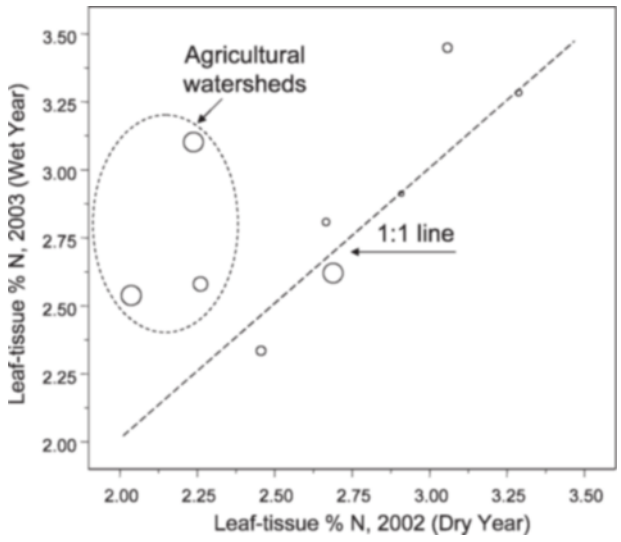

Fig. 4. Relationship between *Phragmites* foliar nitrogen (N, %) composite samples collected from the same locations in 9 subestuaries in 2002 (a dry year) and 2003 (a record wet year). Symbol size corresponds to IDW % agriculture in the watershed.

watersheds below the developed land threshold but with relatively high IDW % agriculture trended upward in % N in comparison to watersheds with the most remaining forest-wetland cover near the shoreline (Fig. 4; increasing size of symbols proportional to IDW % agriculture) and when compared to the previous, much dryer year. Despite this apparent interannual effect of agriculture on % N, cross validation (1 SE rule) excluded % agriculture from the tree model as a second predictor, likely due to a small sample size below the developed-land threshold. The best alternative predictor to IDW % developed land as the primary predictor was IDW % forest-wetland in the watershed ($r^2 = 50.5\%$). It was a strong alternative variable because of the trend of increasing % N in both developed and agricultural systems in 2003, both of which were negatively correlated with % forest-wetland.

Discussion

Phragmites abundance exhibited a nonlinear response to development that was consistent with an ecological threshold (Muradian 2001; King and Richardson 2003; Huggett 2005), beyond which most wetlands were predictably invaded by *Phragmites*. Changepoint analysis revealed that *Phragmites* may proliferate in wetlands with as little as 10% local developed land, whereas there was a high probability of a nonlinear change in *Phragmites* abundance beyond 20%. This finding is consistent with results reported by Bertness et al. (2002) and Silliman and Bertness (2004), who concluded that human development of adjacent uplands was the critical factor driving the successful expansion of *Phragmites* in Narragansett Bay salt marshes. Their results also suggested a similar threshold level of local development: salt marshes with < 15–25% of the border developed consistently had low percentages of their borders dominated by *Phragmites*, whereas wetlands above this threshold were heavily invaded. Many of the mechanisms driving *Phragmites* invasion at a much smaller spatial extent in Narragansett Bay may also be operating at a much larger scale across Chesapeake Bay. It is intuitive that *Phragmites* is likely to completely invade wetlands once they have been disturbed and sufficiently enriched by bordering development, rather than only invading wetlands in proportion to bordering development (e.g., 50% bordering development resulting in 50% *Phragmites* cover). Our findings suggest that relatively low cover of adjacent development may be all that is required to create an ideal environment for establishment and domination of Chesapeake Bay tidal wetlands by *Phragmites*.

One distinction between our results and those of Bertness et al. (2002) and Silliman and Bertness (2004) was that we considered agricultural land uses separately from urban-suburban development in our analysis. We expected both developed and agricultural lands would be related to *Phragmites* abundance, but separating these two land use classes would allow us to distinguish whether *Phragmites* responded differently to each land use. Agricultural cover, both in terms of cropland or all agricultural classes combined, was not as clearly linked to *Phragmites* abundance as developed land, at least at a local scale. Several wetlands with relatively high cover of adjacent agriculture had little *Phragmites*, whereas virtually all wetlands with similar cover of adjacent development hosted abundant stands of *Phragmites*. This may have reflected variability in the status or type of local-scale agriculture among wetlands (active row crop versus fallow fields, which would not be distinguished accurately in the NLCD data set), or that urban land use is simply a more predictable stressor. Broader-scale agriculture may still have been an important driver of *Phragmites* invasion in several of the wetlands we sampled. Where local-scale development was low (< 15%) but watershed-scale forest-wetland cover near shorelines was also relatively low (< 35%, agricultural and developed land cover were high), wetlands tended to have high abundance of *Phragmites*. Several wetlands located in highly agricultural watersheds on the eastern shore of Maryland were heavily invaded by *Phragmites* (although these wetlands did not consistently have cultivated wetland borders). This result implies that even in wetlands where local-scale development is relatively low, *Phragmites* invasion is still probable if

subestuaries are located in highly agricultural or developed watersheds, particularly if these land uses occur near the subestuary shoreline. The watershed-scale results linking increasing urbanization near shorelines to elevated foliar N in *Phragmites* provides further support that watershed-scale nutrient pollution may also facilitate invasion beyond the effects of local development alone. The distribution of both local and watershed land use is likely an important consideration in predicting areas susceptible to the invasion of *Phragmites*.

Latitude or other geographical covariates also may have played a secondary or tertiary role in regulating the degree of invasion by *Phragmites* in these tidal wetlands. We observed a relationship between latitude (northing) and *Phragmites* abundance in wetlands with > 15% IDW local development. Wetlands in the southern third of the bay with relatively high amounts of development near their borders tended to have lower amounts of *Phragmites* cover than their northern counterparts, although all three of the wetlands sampled in the highly urbanized Elizabeth River were moderately invaded by *Phragmites*, despite being the farthest south and having the highest salinities of the study wetlands. Most of the remaining wetlands we sampled in the southern bay were not yet invaded by *Phragmites*. This may reflect several factors, some of which have been previously proposed (Saltonstall 2002; Silliman and Bertness 2004). At a regional scale, the lower bay is less developed than the middle and upper bay and hosts a large proportion of the remaining forest cover in the region. This spatial pattern further supports a linkage between development and *Phragmites* because low regional development may be limiting *Phragmites* invasion by reducing physical disturbance and nutrient inputs to wetlands (which also would reduce the probability of spreading propagules to neighboring wetlands via contagious dispersal). Others have reported a trend of decreasing prevalence of *Phragmites* moving southward along the Atlantic coast. Saltonstall (2002) suggested that the northeastern USA was the initial invasion point for the aggressive, nonnative genotype that is believed to be responsible for most of the invasions in Atlantic tidal wetlands. Because *Phragmites* expansion rate is reported to be about 1–2 m yr^{-1} (Amsberry et al. 2000; Philipp and Field 2005), it would require up to several decades for *Phragmites* to completely invade a marsh of moderate size. *Phragmites* may be spreading from north-to-south and simply has not had sufficient time to invade wetlands in the southern bay as completely as it has in the north. Higher salinities in the southern bay may also be limiting dispersal and germination of propagules (Bart and Hartman 2003), although this seems less likely given that others have demonstrated the ability of *Phragmites*, especially the nonnative genotype M, to become established and invade salt marshes exposed to full strength seawater (Amsberry et al. 2000; Minchinton and Bertness 2003; Vasquez et al. 2005). We believe that both the first and second explanations are two of the most likely causes for the regional pattern observed in our study, although these and other potential explanations deserve closer scrutiny.

N enrichment may provide one important, mechanistic explanation for the local and watershed-scale linkages between *Phragmites* expansion and land use in the subestuaries we studied. N enrichment is an important driver of invasion because it reduces belowground competition for nutrients and increases the importance of aboveground competition for light, a shift that dramatically favors towering *Phragmites* shoots over much shorter native species (Minchinton and Bertness 2003). Although we acknowledge the association in our study is correlative, the fact that N enrichment has been shown to be critically important in the expansion of *Phragmites* in northeastern USA salt marshes and elsewhere (e.g., Rickey and Anderson 2004) based on mechanistic, experimental research provides strong evidence that the positive correlations observed in this study were not spurious. Nitrogen concentrations in *Phragmites* leaf samples were higher in subestuaries with > 14–22% IDW development in their watersheds, approximately the same threshold level of local development that corresponded to high abundance of *Phragmites*. This result was consistent between two consecutive years of sampling despite wildly different interannual precipitation, freshwater and nutrient runoff, and salinities. This pattern also was consistent across the north-to-south salinity gradient of the bay. The highest foliar N was detected in both northern, low salinity watersheds in the Baltimore-Washington, D.C. metropolitan areas as well as the Elizabeth River (Norfolk metropolitan area), a highly urban watershed in the southern bay with the highest salinity of all watersheds studied. Given that the spatial extent of this observed phenomenon spanned the entire length of the bay, it is highly likely that elevated N in *Phragmites* was related to developed land uses in these watersheds rather than some other spatial covariate (e.g., salinity or N discharges from the Susquehanna River in the upper bay).

We hypothesized that land use would be linked to increased N availability to *Phragmites*, but did not anticipate that foliar N would be much more clearly related to developed than agricultural land. Freshwater streams in agricultural watersheds in the Coastal Plain of Chesapeake Bay maintain higher

nitrate-N concentrations than those of developed watersheds (Jordan et al. 1997; King et al. 2005b) and agricultural watersheds discharge more N from surface-water runoff into Chesapeake Bay subestuaries than watersheds in other types of land use (Jordan et al. 2003; Weller et al. 2003). Urban areas contribute large quantities of nutrients via point-source discharges from wastewater treatment plants, so much of the nutrient pollution associated with urban land avoids stream networks altogether and is discharged directly into estuarine ecosystems (Castro et al. 2003). Point source discharges represent a constant level of input to systems and are relatively invariant to hydrologic flux (although can be diluted by high freshwater flux into the estuary). Agricultural sources of nutrients are chiefly non-point, so loadings exhibit dynamic variability in concert with watershed hydrological flux. In this study, we observed no apparent interannual difference in *Phragmites* foliar N among highly developed subestuaries, but did observe such a difference in a few agricultural watersheds. *Phragmites* foliar N may have been responding to increased N availability during a period of very high hydrological flux from these systems, but this pattern was not consistent across all subestuaries (Figs. 3 and 4). We believe these patterns indicate that direct discharges or other nutrient sources associated with watershed development, particularly near shorelines, appear to increase N availability to *Phragmites* in Chesapeake Bay subestuaries, whereas N availability in agricultural systems may be much more dependent upon the magnitude of annual freshwater runoff. The observed lower foliar N in agricultural watersheds, particularly in 2002, may be one explanation why *Phragmites* invasion is less prevalent in these systems.

We acknowledge that our study was correlative and did not establish a causal linkage among land use, foliar N, and *Phragmites* abundance, but our findings do support the mechanistic explanations for similar invasions elsewhere and expand their potential applicability to a different estuarine ecosystem across a much large spatial extent. Our findings provide regional-scale documentation of patterns not previously reported in the literature and have significant conservation implications for Chesapeake Bay and other tidal wetlands throughout North America. These findings may also offer insight into causes of other plant species invasions of tidal wetlands in other parts of the world.

One obvious application of our findings is the prediction of *Phragmites* abundance and foliar N in wetlands and subestuaries not sampled in this study using readily available digital land cover and other spatial data sets. The models reported herein may serve as a starting point for identifying wetlands that are likely of high conservation value or targeting locations for planning more detailed experiments. Our study points toward a host of new questions that can only be addressed experimentally. One critical question raised by this study relates to the degree to which N availability and watershed versus local sources of N influence *Phragmites* expansion in individual wetlands of Chesapeake Bay. Another key issue is the relationship among N availability, salinity, and genotypic differences in *Phragmites*. Based on recent studies by Vasquez et al. (2005) and Bertness and his colleagues (Bertness et al. 2002; Minchinton and Bertness 2003; Silliman and Bertness 2004), it seems likely that haplotype M would spread more rapidly than native genotypes in subestuaries once critical thresholds of N availability are exceeded. Native genotypes also do not do as well at higher salinities (Vasqauez et al. 2005) and their expansion might be limited to lower salinity estuarine systems.

These results also suggest compelling evidence for critical, nonlinear thresholds related to the amount of local development near the wetland border and throughout the entire watershed. The relationships reported here add to the increasing body of literature documenting surprisingly strong linkages between watershed or local scale development and ecological indicators in streams and subestuaries of the Chesapeake Bay region (e.g., Comeleo et al. 1996; Hale et al. 2004; Bilkovic et al. 2005; King et al. 2004a, 2005a), with a few studies demonstrating land use thresholds within a very similar range to those reported in this study (DeLuca et al. 2004; King et al. 2005b; Bilkovic et al. 2006). These studies present a case for the importance of better understanding the effects of land use, particularly shoreline development, on estuarine ecosystems. Environmental and ecological conditions in estuaries appear to be strongly tied to spatial patterns of land use in their proximal watersheds, and relatively little development and associated increased N availability may be all that is required to cause a regime shift at an ecosystem scale (Carpenter 2005). It is already clear that *Phragmites* invasion of tidal wetlands may be one indicator of irreversible change to our coastal ecosystems.

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