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# Local and regional disturbances associated with the invasion of Chesapeake Bay marshes by the common reed *Phragmites australis*

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**Abstract** The invasion of wetlands by *Phragmites australis* is a conservation concern across North America. We used the invasion of Chesapeake Bay wetlands by *P. australis* as a model system to examine the effects of regional and local stressors on plant invasions. We summarized digital maps of the distributions of *P. australis* and of potential stressors (especially human land use and shoreline armoring) at two spatial scales: for 72 subestuaries of the bay and their local watersheds and for thousands of 500 m shoreline segments. We developed statistical models that use the stressor variables to predict *P. australis* prevalence (% of shoreline occupied) in subestuaries

and its presence or absence in 500 m segments of shoreline. The prevalence of agriculture was the strongest and most consistent predictor of *P. australis* presence and abundance in Chesapeake Bay, because *P. australis* can exploit the resulting elevated nutrient levels to enhance its establishment, growth, and seed production. *Phragmites australis* was also positively associated with riprapped shoreline, probably because it creates disturbances that provide colonization opportunities. The *P. australis* invasion was less severe in areas with greater forested land cover and natural shorelines. Surprisingly, invasion was low in highly developed watersheds and highest along shorelines with intermediate levels of residential land use, possibly indicating that highly disturbed systems are

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uninhabitable even to invasive species. Management strategies that reduce nutrient pollution, preserve natural shorelines, and limit nearshore disturbance of soils and vegetation may enhance the resilience of shorelines to invasion.

**Keywords** *Phragmites australis* · Land use · Subestuary · Shoreline armoring · Invasion · Disturbance

## Introduction

Disturbance has long been considered to support the invasion of biological communities by exotic species (Colautti et al. 2006), but disturbance is also a natural part of most environments. In a recent meta-analysis, Moles et al. (2012) reported that disturbance alone is often a poor predictor of community invasibility; but measures of change in the natural disturbance regime, particularly anthropogenic disturbance, provide better predictors. Other factors such as propagule availability and land use surrounding a site also affect invasibility, and these factors may obscure the effects of changes in the disturbance regime (Moles et al. 2012). Pyšek et al. (2010) report that national wealth and human population density (which they considered to be proxies for anthropogenic disturbance, eutrophication, and propagule pressure) were strongly correlated with invasion by alien species.

Understanding and managing the effects of anthropogenic disturbance on invasions requires identifying and integrating proximal factors acting near invaded sites with broader factors acting across the surrounding landscape. Field studies have investigated the effects of disturbances at specific sites, but there has been less attention to comparing the spatial pattern of invasion to the spatial distribution of disturbance across large areas. Broader-scale investigations are needed because the factors driving regional distributions may differ from drivers of distribution within individual ecosystems. Broader-scale analyses have been completed for other ecological responses in estuaries through spatial analysis of digital maps across large regions (Comeleo et al. 1996; Paul et al. 2002; Li et al. 2007; Rodriguez et al. 2007; Patrick et al. 2014, 2016).

Plant invasions of coastal estuarine wetlands provide an ideal system for integrating the effects of disturbance at different scales on invasion success. At

the broad scale of entire watersheds and their receiving waters, human activities on the land release nutrients that drive eutrophication in coastal ecosystems (Nixon 1995; Smith 2006). Nitrogen and phosphorus are introduced from many activities, including crop and livestock agriculture, urban and suburban land use, fossil-fuel combustion, and point sources such as sewage treatment plants (Anderson et al. 2002; Shuster et al. 2005; Conley et al. 2009). Anthropogenic eutrophication is one of the biggest management concerns for aquatic systems (Smith and Schindler 2009) where excess nutrients are often exploited by undesirable or harmful flora and fauna (e.g., algae blooms). Eutrophication is a central problem in Chesapeake Bay (Boesch et al. 2001; Kemp et al. 2005) that has led to federal mandates to reduce nutrient inputs from the land and to multistate efforts to meet that mandate (USEPA 2010).

Disturbances along the shoreline may also contribute to invasion of coastal estuarine systems. Shoreline disturbance includes the removal of vegetation (Silliman and Bertness 2004) and construction of erosion control structures such as riprap, bulkheads, jetties, and groins (Long et al. 2011; Bertness et al. 2002). Removal of vegetation (and its associated nutrient demand) can significantly increase nutrient delivery to the adjacent water (Sweeney and Newbold 2014; Weller and Baker 2014). The construction of shoreline armoring creates disturbed soils that provide openings for invasive plants to establish and proliferate (Strayer et al. 2012). Coastal estuarine wetlands simultaneously integrate the impacts of these multiple stressors operating at different scales.

Coastal marshes in the Chesapeake and throughout North America are being invaded by an aggressive subspecies of common reed (*P. australis* ssp. *australis*). The native strain (*P. australis* ssp. *americanus*) was previously a small part of marsh assemblages, but recently the invasive subspecies has been aggressively extending its distribution in wetlands across North America (Chambers et al. 1999; Saltonstall 2002). In the Chesapeake Bay, the invasive strain was noted in small numbers in several watersheds in the 1970s, but its distribution in the Bay has expanded, reaching 10–30 % of the shoreline in different sections of the upper Bay by 2005 (Chambers et al. 1999, 2008; Meadows and Saltonstall 2007).

The invasion of marshes by *P. australis* ssp. *australis* has a number of ecological and environmental

consequences. Invaded wetlands have experienced declines in native marsh grass biodiversity (Burdick and Konisky 2003; Chambers et al. 1999); epifaunal abundance (Robertson and Weis 2005); and fish, birds, and swimming crustaceans (Osgood et al. 2003; Dibble et al. 2013). The widespread invasion and the negative impacts it has on native species have brought *P. australis* ssp. *australis* to the forefront of wetland studies (Mozdzer et al. 2013; Hazelton et al. 2014), and made it one of the most studied plant systems in North America (Meyerson et al. 2009, 2016).

*P. australis* stands have larger nitrogen pools than other marsh communities (Meyerson et al. 1999, 2000; Windham and Meyerson 2003); and anthropogenic nitrogen can promote the expansion of the invasive *P. australis* strain (King et al. 2007; Chambers et al. 2008; Kettenring et al. 2011). Compared to the native subspecies, the invasive one demands four times more nitrogen to support its biomass than the native subspecies (Mozdzer and Zieman 2010), but the invasive strain can exploit high nitrogen levels to achieve higher growth rates and biomass than the native strain and other species of marsh plants (Mozdzer et al. 2013). Proximity to agriculture (and the associated nitrogen inputs from fertilizer and animal waste) is positively correlated with *P. australis* abundance (Chambers et al. 2008; Mazur et al. 2014). Other anthropogenic disturbance besides nitrogen inputs may also promote the invasive strain, including shoreline alteration, sea level rise, increased anthropogenic carbon, and altered salinity (e.g., Meyerson et al. 2010; Mozdzer and Magonigal 2012; Guo et al. 2013). Few studies have looked at the role of shoreline disturbance in contributing to *P. australis* invasion (Bertness et al. 2002; Silliman and Bertness 2004; Long et al. 2011).

We used the invasion of Chesapeake Bay marshes by *P. australis* as a model system for examining the roles of regional and proximal anthropogenic disturbance in biological invasion. *P. australis* has been acknowledged as a good model organism for advancing understanding of plant invasions (Meyerson et al. 2016). We used available digital spatial data to quantify *P. australis* presence and prevalence and to develop potential predictor variables representing anthropogenic disturbance. At the regional scale, we related *P. australis* prevalence across many embayments (subestuaries) to variables quantifying human activities in the local watershed and along the entire shoreline of each subestuary. At the more proximal

scale, we related *P. australis* presence in 500 m segments of shoreline to variables representing human activities in each segment. We compared and integrated different statistical modeling approaches within and between the two spatial scales. We addressed two basic questions: which anthropogenic factors affect *P. australis* invasion success at the two spatial scales (subestuary and shoreline), and do factors correlated with invasion success differ between the two scales?

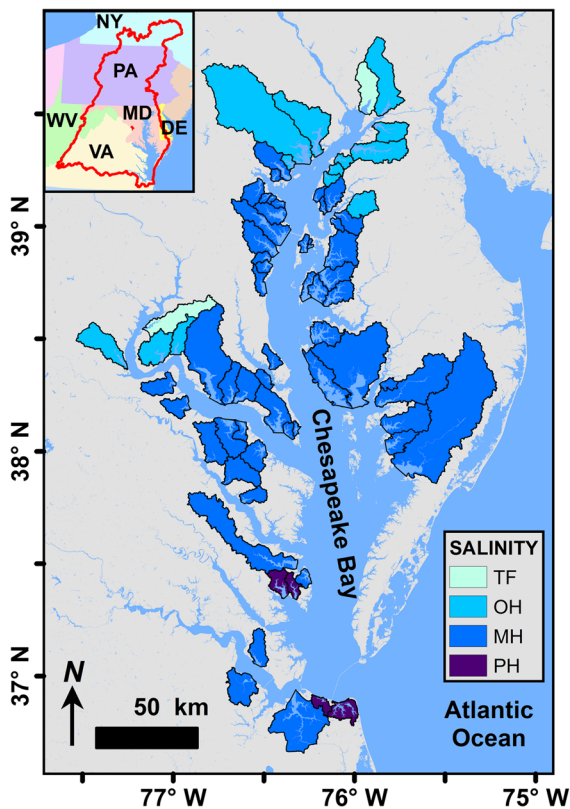
At both the shoreline segment and subestuary scales, we expected that the amounts of agricultural and developed land would be positively correlated with *P. australis* prevalence because of nutrient enrichment from those land uses. We also expected to find that armored shorelines would be positively related to *P. australis* presence because the associated disturbance of soils and native marsh communities provides an opening for invasion. We expected these effects to act synergistically with the nutrient-enriching effects of agricultural and developed lands.

## Methods

### Study area

The Chesapeake Bay (Fig. 1) is the largest estuary in North America, and its 166,000 km<sup>2</sup> watershed includes parts of six states and Washington, DC (Weller and Baker 2014; CBP 2015). Nearly 18 million people live in the watershed (Kemp et al. 2005), many in large metropolitan areas, including Baltimore MD, Washington DC, and Hampton Roads-Norfolk VA. In rural parts of the watershed, forests and other natural lands are interspersed with livestock and row crop agriculture.

The Chesapeake Bay's complex shoreline encloses over 100 tributary embayments (here called subestuaries), each of which has its own local watershed (Li et al. 2007). The local watersheds differ widely in their proportions of forest, agricultural, developed, and other land cover types; and the bay and its subestuaries are commonly divided into four major salinity zones: polyhaline, mesohaline, oligohaline, and tidal fresh (Fig. 1, Li et al. 2007; Patrick et al. 2014). Thus, the subestuaries provide a population of replicate study units well suited for exploring the interacting effects of land use and salinity on estuaries. That replication has been exploited in recent statistical analyses relating watershed



**Fig. 1** The Chesapeake Bay and the local watersheds of 72 subestuaries containing *Phragmites australis* mapped in the shoreline survey (VIMS-CCRM 2009). The local watersheds are shaded by the salinity zone of the subestuary: tidal fresh (TF), oligohaline (OH), mesohaline (MH), and polyhaline (PH). The inset shows the location of the Chesapeake Bay watershed and six states in the mid-Atlantic region of the U.S.

and subestuary characteristics to ecological responses in the subestuaries (King et al. 2004, 2007; Li et al. 2007; Patrick et al. 2014, 2016; Patrick and Weller 2015).

#### *Phragmites australis* and shoreline data

The data on *P. australis* distribution and shoreline characteristics for this study came from a shoreline inventory (VIMS-CCRM 2009) that mapped 17,047 km of shoreline, roughly 80 % of the Chesapeake Bay shore. The shoreline was mapped once, but it took 11 years to cover the study area. Eighty percent of the data were collected between 1998 and 2002, and 20 % between 2003 and 2008. The data set contains three spatial layers. For 99,763 individual segments comprising the surveyed shoreline, a land use layer and bank condition layer reports adjacent land use

(agriculture, forest, marsh, and residential land), bank height (0–5, 5–10, 10–30, and >30 m), and vegetative cover of the bank. All banks >5 m high were steep, so, we simplified the bank height information from five to two categories, low banks (0–5 m) and high banks (>5 m). For a separate set of 74,010 individual segments also comprising the surveyed shoreline, a shoreline armoring layer maps linear armoring structures, such as riprap, bulkhead, groin field, seawall, and breakwater. The third spatial layer maps 47,762 point structures along the shoreline, such as docks, boat ramps, or marinas.

Importantly, the land use and bank condition layer reports the presence or absence of *P. australis* in each mapped segment. That reporting does not distinguish between the native and invasive non-native *P. australis* subspecies; however, in 2003–2004, Meadows and Saltonstall (2007) found the invasive strain in five times more patches than the native strain on the Bay's eastern shore. A 2006 survey of *P. australis* stands on both shores of the Bay found the native strain in only 7 % of the stands (Tulbure et al. 2012). Because most of the *P. australis* stands are the invasive strain, observed spatial relationships of *P. australis* prevalence and abundance with potential controlling factors (below) are strongly dominated by the responses of the invasive strain.

#### Analyses

We summarized data and developed statistical models at two scales of analysis: The coarser-scale analysis related subestuary-wide *P. australis* prevalence to land use in the local watershed and characteristics of the entire shoreline of each subestuary. The finer-scale analysis related *P. australis* presence or absence in individual 500 m segments of shoreline to land use and other characteristics at each 500 m segment. Spatial analyses were performed with ArcGIS 10 geographic information software (ESRI 2011), and statistical analyses were implemented within the R statistical software system (R Core Team 2014).

#### *Phragmites australis* prevalence in subestuaries

From a larger group of previously defined subestuaries (Li et al. 2007; Patrick et al. 2014), we selected the subset of 72 Chesapeake Bay subestuaries that had been

surveyed in the shoreline survey (VIMS-CCRM 2009) and contained *P. australis*. We omitted subestuaries without *P. australis* because we could not determine whether it was absent because of environmental factors or because of a lack of invasive propagules. Including systems lacking propagules would confound analyses relating prevalence to environmental factors. Subestuaries were assigned to salinity zones (tidal fresh, oligohaline, mesohaline, or polyhaline) based on the Chesapeake Bay Program Segmentation salinity segmentation scheme (<http://www.chesapeakebay.net/segmentscheme.htm>, see Patrick et al. 2014).

Land cover proportions in the local watershed of each subestuary were estimated from the circa 2000 National Land Cover Dataset (called NLCD 2001, Homer et al. 2004) by intersecting the polygons defining the local watersheds of the subestuaries with the land cover map within the GIS and then calculating the proportion of each land cover class within each watershed. We aggregated some of the NLCD categories into five broader land cover types: cropland (NLCD code 82, cropland), developed (all developed categories), forest (all types of forest and woody wetland), and wetland (emergent herbaceous wetlands, NLCD code 95).

We summarized the subestuary polygons and their intersection with a digital bathymetry map (NOAA 1998) to calculate the metrics describing subestuaries, including the shoreline perimeter, mouth width, subestuary volume, and the fractal dimension of the shoreline. The fractal dimension is a measure of shoreline complexity calculated as two times the natural logarithm of subestuary perimeter divided by the natural logarithm of subestuary area (Li et al. 2007). Average tidal range was estimated by intersecting the subestuary boundaries with a digital map of coastal vulnerability (Thieler and Hammar-Klose 1999) based on a coastal hazards database (Gornitz and White 1992) updated with more recent data (Thieler and Hammar-Klose 1999). That map included tidal range data interpolated among 657 tide stations by Hubertz et al. (1996).

Shoreline characteristics were summarized for each subestuary and recorded as percentage of total subestuary shoreline length occupied by each shoreline land use and shoreline armoring type (such as bulkhead or riprap); or as number of structures per km of shoreline for point structures like docks, boat-houses, or wharves. *Phragmites australis* prevalence was quantified as the percentage of total subestuary

shoreline length occupied by *P. australis* by adding the lengths of individual segments containing *P. australis* and dividing by the total subestuary shoreline length.

We used univariate linear regression (lm function, R Core Team 2014) to test for hypothesized relationships (see Introduction) between *P. australis* prevalence (% of subestuary shoreline with *P. australis*) and 31 potential predictors from watershed, estuary, and shoreline variables. When considering many univariate regressions, it is necessary to control for experiment wise error across the entire set of regressions. The Dunn–Šidák correction (Ellison and Gotelli 2004) accomplishes this by estimating a more stringent (lower)  $P$  level for statistical significance of an individual regression to preserve the desired overall significance ( $P \leq 0.05$ ) for the set of regressions. With 31 regressions, the corrected  $P$  level for significance of an individual regression is  $P \leq 0.0016$ .

We also applied multiple linear regression to all of the independent variables to identify a multivariate linear model for predicting *P. australis* in a subestuary. All possible multiple regression models with 2–5 predictors were estimated with best subsets analysis (Hosmer et al. 1989) and ranked with the Bayesian information criterion (BIC) using the R Leaps package (Tumley 2009).

As an alternative multivariate model to relate *P. australis* prevalence in subestuaries to watershed, estuary, and shoreline characteristics; we also implemented regression tree analysis with the randomForest package in R (Breiman and Cutler 2014). Regression tree analysis requires fewer assumptions than linear regression analysis and can work well with non-normal variables, non-linear responses, and non-continuous variables (De'Ath and Fabricius 2000). Random forest (RF) analysis is an implementation of tree analysis that works by creating multiple decision trees, each with a different bootstrapped sample of the original data. The final prediction is obtained by aggregating over the ensemble of trees (Biau 2012). We assessed the results of the RF model by examining the rankings of variable importance to model construction and examining partial dependence plots of the most important variables (Cutler et al. 2007). Partial dependence plots visualize the effects of individual predictors on response variables. A partial dependence plot shows the average response of the predicted variable to the predictor, across all other combinations of predictor variables used in the RF analysis (Cutler et al. 2007).

### *Phragmites australis* presence or absence in individual shoreline segments

To quantify *Phragmites* presence in individual shoreline segments, we processed the shoreline data differently from the summary of *Phragmites* prevalence in subestuaries (above). The survey mapped land use, bank condition and *P. australis* presence for 99,763 segments comprising 17,047 km of shoreline (VIMS-CCRM 2009). After eliminating some segments where shoreline features were not recorded or where extensive marshes were not carefully surveyed for *P. australis* presence (Marcia Berman, Virginia Institute of Marine Science, personal communication), there were 13,872 km of shoreline left for further analysis. The lengths of segments reporting *P. australis* presence varied from less than 1 meter to 15.4 km. The variation in size presents a problem for statistical analysis because the factors affecting very small segments may be different from the factors affecting larger segments. Therefore, we resampled the land use and bank condition map to produce a new map divided into shoreline segments of consistent 500 m length. To accomplish this, we merged adjacent segments with identical attributes and then divided the shoreline layer at 500 m intervals. There were 26,590 segments available for analysis after residual segments less than 500 m were eliminated. We also resampled the map layer reporting shoreline armoring to match the 500 m segments created above.

We summarized the shoreline attributes for each 500 m segment. From the resampled land use and bank condition layer, we recorded the presence or absence of *P. australis* in each 500 m segment and the percentages of the segment's 500 m length with three different land uses (agricultural land, residential land, and forest). From the resampled shoreline armoring layer, we recorded the percentages of three different shoreline armoring conditions (natural, riprap, or bulkhead). Minor land uses and armoring types were omitted from the analysis. We also calculated the average bottom slope within 90 m of each 500 m shoreline segment using a slope grid derived from a digital bathymetric model (NOAA 1998).

We used univariate logistic regression to test our hypotheses (see “Introduction” section) about the effects of land use and shoreline armoring in shoreline segments on *P. australis* presence in those segments. We implemented logistic regression with the R glm function (R Core Team 2014), and we related

*P. australis* presence or absence to seven candidate predictor variables: three land uses (% forest, % agricultural land, and % residential land), three shoreline armoring conditions (% unarmored, % bulkhead and % riprap), and average slope at the shoreline. The number of shoreline segments was quite large (26,590), so it was possible to omit some of the segments from model fitting and use the reserved data for model validation. We randomly selected half of the 500 m aggregated shoreline segments for fitting the logistic models. As above, we used the Dunn–Šidák correction (Ellison and Gotelli 2004) to control for experiment wise error across the set of univariate predictors when testing whether models were statistically significant. With seven logistic regressions, setting the corrected  $P$  level for significance of an individual regression to  $P \leq 0.0073$  yields an experiment wise significance level of  $P < 0.05$ . The optimal classification threshold for each significant logistic model was calculated using receiver operator characteristic (ROC) analysis, which evaluates the percentages of correctly predicted presences and absences across a range of probability thresholds to identify the threshold that maximizes correct predictions (Hosmer and Lemeshow 2000).

We evaluated model performance with Cohen's kappa ( $\kappa$ ). Values of  $\kappa$  can range from  $-1$  to  $1$ . Positive values indicate that the classification is more successful than would be expected from chance alone, whereas negative values indicate worse results than expected from chance alone. A value of  $+1$  indicates perfect agreement between the modeled and measured classifications (Cohen 1960; Manel et al. 2001). We selected a best model from the seven univariate logistic models based on the statistical significance levels ( $P$ ), the  $\kappa$  values, and AIC scores (Burnham and Anderson 2002). Then, we applied that model to the other half of the data that had been reserved for validation and assessed model performance for the validation data with  $\kappa$ .

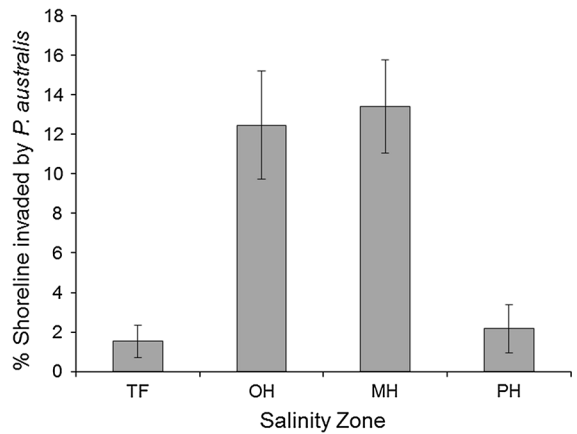
We implemented multiple logistic regression (R glm function; R Core Team 2014) to assess whether some of the seven predictor variables could be combined in a multivariate model to improve success in predicting *P. australis* presence or absence. We programmed a simple permutation procedure to generate potential models and then performed model comparison (see “Methods” section above) to identify which combination of land use and shoreline structure variables constituted the best model. As above, that model was further tested by applying it to the validation data and calculating  $\kappa$ .



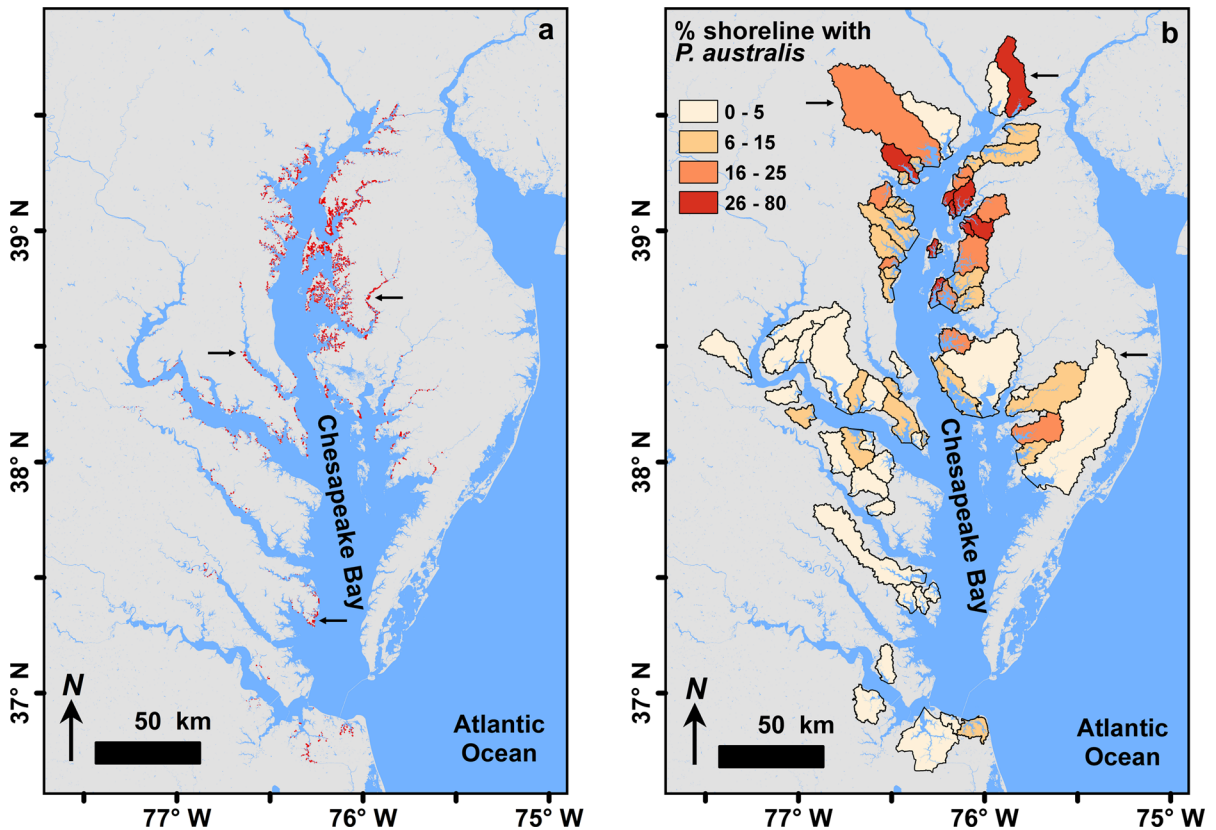
**Results**

*Phragmites australis* distribution within Chesapeake Bay

Of the 13,872 km of shoreline analyzed, 6.6 % was occupied by *P. australis* (Fig. 1). *Phragmites australis* prevalence in the Chesapeake Bay decreased from the north to south. Subestuaries with the greatest percentage of shoreline occupied by *P. australis* were in the northeastern portion of the bay (Fig. 2). *Phragmites australis* was more prevalent in subestuaries within the oligohaline and mesohaline salinity zones than in the tidal fresh and polyhaline subestuaries (Fig. 3).



**Fig. 3** *Phragmites australis* prevalence within in the surveyed subestuaries (Fig. 2b) summarized by salinity zone (Fig. 1)



**Fig. 2** *Phragmites australis* distribution in the Chesapeake Bay as mapped by the shoreline survey (VIMS-CCRM 2009). **a** Individual shoreline segments containing *P. australis*, **b** local watersheds of 72 Chesapeake Bay subestuaries (Fig. 1) shaded by the percent of shoreline occupied by *P. australis*. Some of the shoreline occupied by *P. australis* (e.g., arrows in **a**) is not

within one of the 72 study subestuaries in **b**. Some subestuaries are small but have relatively large local watersheds (arrows in **b**). The shading of local watersheds in **b** represents the prevalence of *P. australis* along the shoreline of the corresponding subestuary near the bay, not throughout the local watershed

**Table 1** Univariate regressions of the *P. australis* prevalence in subestuaries versus 16 shoreline variables from the shoreline survey (VIMS-CCRM 2009) and versus 15 other variables describing the subestuary-watershed system

Predictor	Intercept	Slope	R <sup>2</sup>	P
Shoreline characteristics				
% Agriculture	7.01	0.60	0.20	< 0.001
% Beach	15.91	-0.49	0.04	0.08
% High banks	15.47	-0.18	0.04	0.09
Boat ramp density	9.39	8.63	0.03	0.13
% Forested shoreline	16.87	-0.15	0.03	0.15
Length of surveyed shoreline	15.10	-0.03	0.03	0.16
% Vegetated shore	17.87	-0.13	0.03	0.17
% Riprap	9.34	0.33	0.02	0.22
% Developed shoreline	16.12	-0.11	0.02	0.24
% Bulkhead shoreline	13.68	-0.15	0.01	0.40
Average slope at shore	15.69	-1.19	0.01	0.41
% Other shoreline hardening	13.44	-0.44	0.01	0.51
% Low banks	9.03	0.05	0.00	0.58
Dock and boathouse density	13.00	-0.14	0.00	0.71
Marina and wharf density	12.79	-3.62	0.00	0.72
% Residential shoreline	13.01	-0.02	0.00	0.81
Subestuary or watershed characteristics				
% Cropland	3.90	47.99	0.20	< 0.001
% Forest	26.72	-35.36	0.19	< 0.001
Tidal range	28.28	-35.13	0.10	0.01
Watershed perimeter	17.28	-0.05	0.06	0.04
% Grassland	8.23	57.62	0.05	0.05
Fractal dimension	95.41	-59.34	0.04	0.09
Watershed area (km <sup>2</sup> )	14.04	-0.01	0.03	0.17
Subestuary shoreline perimeter (km)	14.09	-0.01	0.02	0.19
Watershed/subestuary area ratio	14.38	-0.17	0.02	0.23
Subestuary basin volume (km <sup>3</sup> )	13.79	-39.51	0.02	0.24
Subestuary area (km <sup>2</sup> )	13.83	-0.09	0.02	0.29
% Wetland	11.07	37.43	0.01	0.37
Subestuary mouth width	14.03	-0.70	0.01	0.43
% Developed land	13.43	-6.54	0.01	0.48
Salinity (ppt)	14.11	-0.18	0.00	0.60

Variables are sorted by decreasing R<sup>2</sup> within groups. The three relationships with P < 0.001 are significant below the Dunn-Šidák threshold (P < 0.0016) that controls experiment wise error to P < 0.05

### Predicting *Phragmites australis* prevalence in subestuaries

Three of the 31 variables representing shoreline, estuary, or watershed characteristics had statistically significant univariate linear relationships with *P. australis* prevalence in subestuaries after applying the Dunn-Šidák correction (P < 0.0016) to control experiment wise error at P < 0.05 (Table 1). The percentage of agricultural land use on the shoreline and the percentage of agricultural cover in the local

watershed had the strongest positive relationships with *P. australis* prevalence (both R<sup>2</sup> = 0.20, P < 0.001), while the percent of forested cover within the local watershed was negatively related to *P. australis* prevalence (P < 0.001, R<sup>2</sup> = 0.19).

Among multiple regression models with five or fewer independent variables, there were four models that were equivalently good at predicting *P. australis* prevalence in subestuaries (Table 2). All four explained more of the variability in prevalence among subestuaries (R<sup>2</sup> > 0.5, P < 0.0001, Table 2) than did the best

**Table 2** Variables included and  $R^2$  values of the four best multiple linear regression models for predicting *Phragmites australis* prevalence in subestuaries from combinations of the predictors in Table 1

Predictor	Model number			
	1	2	3	4
% Cropland in the watershed	X	X	X	X
% Wetland in the watershed			X	X
Tidal range	X	X	X	X
Boat ramp density	X	X	X	X
% High banks	X			X
Average slope at the shoreline		X	X	
$R^2$	0.51	0.51	0.54	0.55

All four models are statistically significant at  $P < 0.001$

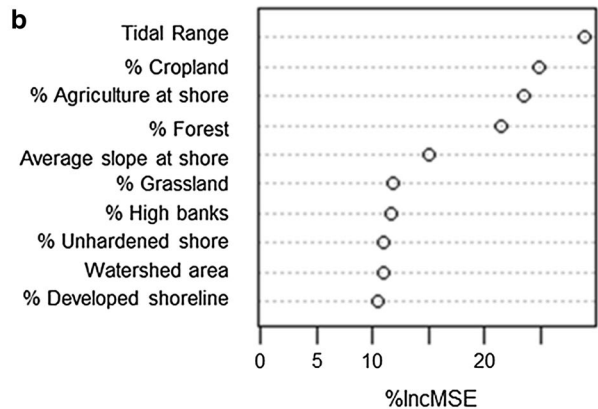
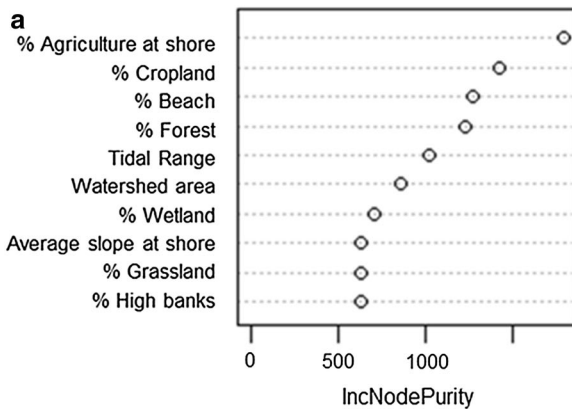
univariate models ( $R^2 = 0.20$ , Table 1). Across the four multiple regression models, *P. australis* prevalence was positively related to three variables (cropland and wetland land cover in the watershed and boat ramp density) and negatively related to three others (proportion of shore with high banks, the average slope at shore, and average tidal range).

The random forest model explained 39 percent of the variation in *P. australis* prevalence among subestuaries ( $P < 0.0001$ ). The six most important variables in the model were the percentage of cropland in the watershed, the percentage of agriculture land use at the shoreline, tidal range, the percentage of forest in the watershed, the slope at shoreline, and the percentage of

shoreline with beach (see variable importance plot, Fig. 4). *Phragmites australis* prevalence increased sharply at watershed cropland levels above 25 %, and increased gradually with the percentage of shoreline with agricultural land use (see partial dependence plots, Fig. 5). *Phragmites australis* prevalence decreased gradually with increasing forest cover in the watershed, but had sharp negative threshold responses to increasing tidal range, slope at the shoreline, and the percentage of shoreline with beach (Fig. 5).

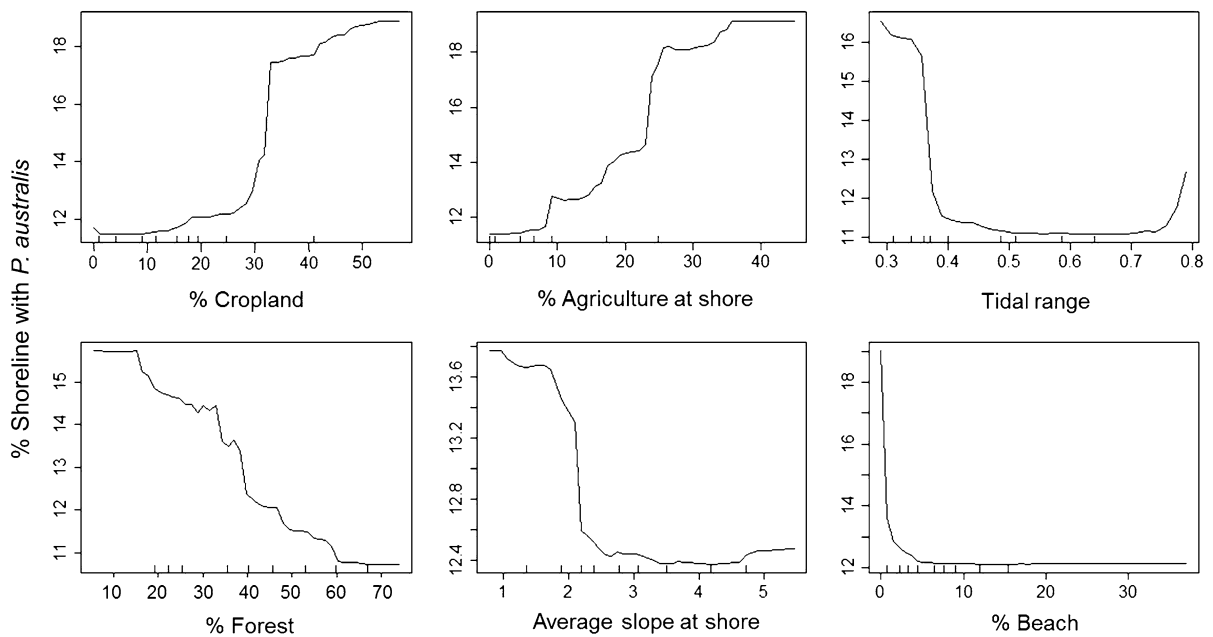
Predicting *Phragmites australis* presence or absence in shoreline segments

After applying the Dunn-Šidák correction to control experiment wise significance to  $P < 0.05$ , five of the seven characteristics of shoreline segments yielded significant univariate logistic models for predicting *P. australis* presence or absence in 500 m shoreline segments. The probability of *P. australis* presence was positively related to the percentage of shoreline with agricultural land use, the percentage with residential land use, and the percentage with riprap; and negatively related to the percentages of forested and unarmored shoreline (Table 3). The models with the percentage of riprap and the percentage of agricultural shoreline had similar success classifying the training data ( $\kappa = 0.16$  Table 3), but the AIC score of the model based on the percentage of agricultural shoreline was far lower ( $\Delta AIC = 139$ ), so we selected it as the best univariate model of the set (Table 3).



**Fig. 4** Variable importance plot of the top ten predictor variables from the random forest analysis relating *Phragmites australis* prevalence in subestuaries to predictor variables at the shoreline and throughout the watershed (Table 1). The

independent variables are ranked from top to bottom in order of importance, as measured by a the average increase in node purity (IncNodePurity) and by b the mean squared error (%IncMSE)



**Fig. 5** Partial dependence plots from the random forest analysis relating *Phragmites australis* prevalence in subestuaries to 31 possible predictor variables. Only the six most important variables are shown

**Table 3** Univariate logistic regression models relating the probability of *Phragmites australis* presence in shoreline segments to seven characteristics of those shoreline segments

Predictor	Intercept	Slope	AIC	<i>P</i>	$\kappa$
% Agriculture	-1.64	1.53	11,577	<0.001	0.18
% Forest	-1.28	-0.70	11,715	<0.001	0.07
% Residential shoreline	-1.64	0.50	11,784	<0.001	0.10
% Riprap	-1.61	1.17	11,739	<0.001	0.16
% Bulkhead	-1.51	0.25	11,846	0.42	
% Unhardened shore	-1.09	-0.55	11,779	<0.001	0.12
Average slope at shore	-1.56	0.02	11,842	0.01	

$\kappa$  values, which quantify success in classifying the training data, were calculated for significant models. The five relationships with  $P < 0.001$  are significant below the Dunn-Šidák threshold ( $P < 0.0016$ ) that controls experiment wise error to  $P < 0.05$

The best multiple logistic regression model for predicting *P. australis* presence or absence in shoreline segments contained the percentages of shoreline with forest and bulkhead as negative predictors and the percentages of shoreline with agricultural land, residential land, and riprap as positive predictors (Table 3). When compared to the best univariate model based on shoreline agriculture only, the multiple logistic model had a slightly lower classification success ( $\kappa = 0.17$  vs. 0.18) but a lower AIC ( $\Delta$ AIC score = 180), so the metrics fail to conclusively rate

one model as better than the other in the training data. However, model performance diverged when the models were used to predict *P. australis* presence in the validation data. While classification success on the validation data was lower than success on the training data for both models, the drop was far smaller ( $\Delta\kappa = 0.02$ ) for the multivariate model than for the univariate agriculture model ( $\Delta\kappa = 0.07$ ). Both models were better at predicting *P. australis* absence ( $\geq 83$  % success) than at predicting presence ( $\leq 35$  % success, Table 4).

**Table 4** Classification success for two models predicting *Phragmites australis* presence in shoreline segments: the best univariate logistic model (based on shoreline agriculture only) and the multivariate logistic model (based on five variables, the

percentages of the shoreline with agriculture, forest, or residential land and the percentages of the shoreline with bulkhead and riprap)

Data	$\kappa$	Total proportion correct	Proportion of predicted presence that is correct	Proportion of predicted absence that is correct
Univariate model				
Training	0.18	0.77	0.35	0.84
Validation	0.11	0.75	0.28	0.83
Multiple logistic model				
Training	0.17	0.74	0.31	0.85
Validation	0.15	0.68	0.28	0.85

Half of the data were used to fit the models (training data), and the other half was reserved as validation data to provide independent model testing

## Discussion

We took an integrative, spatial modeling approach to analyzing the regional and local factors affecting an ongoing invasion. Our study of the *Phragmites australis* invasion of Chesapeake Bay exploits the value of *P. australis* as a model organism for advancing more general understanding of plant invasions (Meyerson et al. 2016). Our analysis is unprecedented in the spatial extent of the analysis, the breadth and types of predictors considered, and the simultaneous investigation of drivers that affect entire watershed-subestuary systems as well drivers that affect individual shoreline segments. The analysis revealed strong anthropogenic impacts on the *P. australis* invasion of estuarine wetlands and distinguished factors affecting invasion at both scales from specific factors affecting only one.

Agriculture and shoreline armoring were significant predictors of *P. australis* occurrence in subestuaries and in individual shoreline segments (Table 5). Conversely, variables associated with reduced anthropogenic impact, specifically forested and unmodified shoreline, were negatively correlated with *P. australis* occurrence in the Chesapeake Bay (Table 5). Some variables were significant predictors only at the shoreline segment scale, including: % residential shoreline, % bulkhead, and % unarmored shoreline (Table 5). These local-scales associations likely reflect more direct mechanistic connections of shoreline activities to *P. australis* invasion (see below).

Agriculture was the strongest and most consistent correlate of *P. australis* prevalence, and the

percentage of cropland in the watershed was a significant positive predictor of *P. australis* prevalence in a subestuary in every test where it was used (Table 5). *Phragmites australis* commonly grows at the edges of agricultural fields throughout the world (Haslam 2010). Agricultural activities increase nitrogen levels in receiving waters (Jordan et al. 1997a, b; Liu et al. 2000; Savage et al. 2010). Total nitrogen concentrations were measured in 20 of our 72 subestuaries (Fig. 1) that had low percentages of developed land in their local watersheds, and estuarine nitrogen concentration increased strongly with the percentage of cropland in the local watershed ( $R^2 = 0.63$ ,  $P < 0.001$ , Thomas E. Jordan et al. unpublished data).

Elevated nitrogen levels promote *P. australis* in several ways. Elevated nitrogen increases *P. australis* sexual reproduction and expansion in Chesapeake Bay (Kettenring et al. 2011); increases *P. australis* density, height, and above-ground shoot biomass (Bastlova et al. 2004; Engloner 2009); and allows seedlings to rapidly escape from a vulnerable life stage (Saltonstall and Stevenson 2007; Kettenring et al. 2015; Hazelton et al. 2014). *P. australis* stands have larger nitrogen pools than other marsh communities (Meyerson et al. 1999, 2000; Windham and Meyerson 2003). Foliar nitrogen was higher in *P. australis* from Chesapeake Bay subestuaries with more agriculture, even if total human land use was relatively low, suggesting that even a relatively small amount of agriculture may raise nitrogen levels enough to benefit *P. australis* (King et al. 2007). Watersheds dominated by forests export less nitrogen than watersheds with agriculture

**Table 5** Summary of 14 statistically significant predictors of *Phragmites australis* across five statistical models predicting *P. australis* prevalence in subestuaries or *P. australis* presence in 500 m shoreline segments

Predictor	Prevalence in subestuaries			Presence in shoreline segments	
	Univariate regression	Multiple regression	Random forest	Univariate logistic	Multiple logistic
Shoreline characteristics					
% Agriculture	+		+	+	+
% Forest				-	-
% Residential				+	+
% Riprap		+		+	+
% Bulkhead					-
% Unhardened				-	
Boat ramp density		+		NA	NA
Average slope		-	-		
% High banks		-		NA	NA
% Beach			-	NA	NA
Watershed or estuary characteristics					
% Cropland	+	+	+	NA	NA
% Forest	-		-	NA	NA
% Wetland		+		NA	NA
Tidal range		-	-	NA	NA

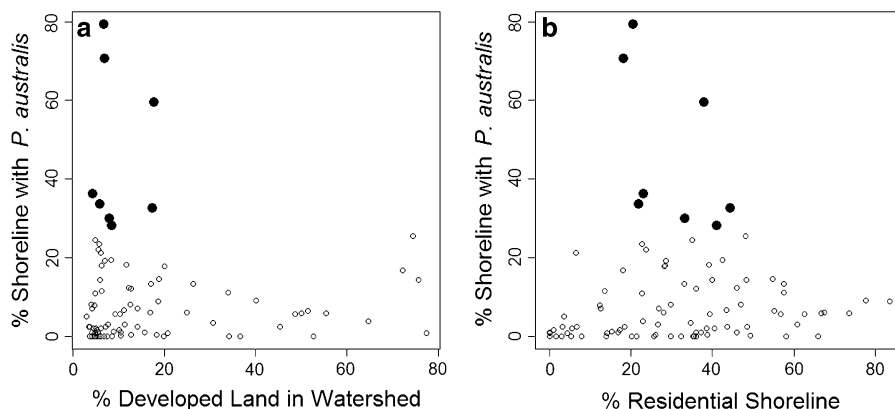
NA indicates that a variable was not included in a particular analysis, while “+” or “-” mark variables that had significant positive or negative relationships with *P. australis*

(Dillon and Kirchner 1975; Jordan et al. 1997a, b; Liu et al. 2000), and this is consistent with negative relationship of watershed forest with *P. australis* prevalence (Table 5).

Agriculture on the shoreline increased the probability of *P. australis* invasion in individual shoreline segments (Tables 3, 5). Previous studies also reported a correlation between *P. australis* invasion and agriculture at the shoreline (King et al. 2007; Chambers et al. 2008). Shoreline agriculture can deliver nitrogen directly to adjacent waters. However, natural riparian zones not only release less nitrogen directly to adjacent waters, they can absorb nitrogen moving downhill and reduce nitrogen inputs to the water from disturbed uphill systems (Sweeney and Newbold 2014; Weller and Baker 2014). Natural riparian vegetation may also be more difficult to invade than other shoreline land uses with reduced vegetative cover and disturbed soils (Bertness et al. 2002; DeSimone et al. 2010; Finnegan et al. 2012).

Surprisingly, *P. australis* prevalence in subestuaries was not significantly related to developed land in the watershed or to shoreline development (Tables 1, 2;

Fig. 4). We expected these factors to increase *P. australis* prevalence because developed lands can release nitrogen and can contain disturbed sites that are open for invasion (see “Introduction” section). An earlier study did report a positive association between watershed development and *P. australis* abundance (King et al. 2007); however, that study only considered existing wetlands, while this study accounted for the entire shoreline, including segments lacking wetlands. Other studies have reported that residential development in any part of a subestuary is associated with higher foliar nitrogen concentrations and abundance of *P. australis* for the entire subestuary (King et al. 2007; McCormick et al. 2010a). Our study did find a significant relationship between *P. australis* presence in 500 m shoreline segments and adjacent shoreline development (Table 3). Among subestuaries, there was a tendency for higher *P. australis* prevalence to occur in subestuaries with intermediate levels of residential shoreline but low levels of developed land in their local watersheds (Fig. 6). Subestuaries with highly developed watersheds and mostly armored shoreline may be so impacted that little tidal wetland remains.



**Fig. 6** Relationships of *Phragmites australis* prevalence in subestuaries to two measures of residential development. **a** The percentage of developed land in the local watershed, **b** the percentage of subestuary shoreline with residential

development. Subestuaries with higher *P. australis* prevalence (>26 % of shoreline occupied, highlighted as filled symbols) occur at low levels of watershed development (<20 % **a**) and intermediate levels residential shoreline (19–41 % **b**)

The presence of riprap was also positively correlated with *P. australis* prevalence in subestuaries and with its presence in individual shoreline segments. These positive associations likely arise because the construction of riprap creates disturbed sites for colonization, and wave action can continue to disturb vegetation and substrate at the end of the protected shoreline. *Phragmites australis* stands often grow at the edges of structures such as riprap and bulkhead (Melissa McCormick, unpublished data), and disturbances as small as 30 cm in diameter can promote *P. australis* invasion (Kettenring et al. 2015).

Tidal range and average slope at the shoreline were negatively related to *P. australis* prevalence in subestuaries (Table 5), but these relationships were driven by three subestuaries (Chester River, Swan Creek, and Tavern Creek) that are very heavily invaded (60–80 % of shoreline occupied) and also have low values of tidal range and average slope at the shoreline. It is possible that high tidal amplitude could push propagules above the flood zone during lunar and storm tides, contributing to establishment. However, we refrain from interpreting these relationships because further study is needed to determine if they are robust or are artifacts of this particular data set.

Our study has identified several important correlates of *P. australis* occurrence in estuarine wetlands. By considering a large population of subestuary-watershed systems, testing for both regional and local associations, and applying different statistical models; we demonstrated the correlates of *P. australis* invasion

more clearly than previous studies (King et al. 2007; Chambers et al. 2008). Our analyses complement site-specific field studies and support the importance of factors identified in those studies (reviewed in Hazelton et al. 2014). Thus, our study enhances understanding of how nitrogen and disturbance drive the *P. australis* invasion of Chesapeake Bay and is also relevant to understanding the broader importance of those factors in plant invasions in general. Despite these contributions, the predictive power of our models was somewhat low. We explained at most 55 % of the variation in *P. australis* prevalence among subestuaries (Tables 1, 2), and the best models for *P. australis* presence in 500 m shoreline segments were far better at predicting absence than at predicting presence (Table 4). Our models for the 500 m shoreline segments may have been limited by quantifying *P. australis* as a binary response (present or absent in each segment), but we were reluctant to interpret the *P. australis* response more finely because the data were collected over a ten-year interval. More importantly, poor predictive ability reflects a key gap in the information available for our models. Plant invasions typically depend on three factors: nutrient amendment, altered disturbance regime, and propagule pressure (Colautti et al. 2006). The independent variables that we considered capture the first two factors well, but supply no information on propagule availability or on spatial variation in availability across the Chesapeake Bay. We do know that *P. australis* seeds increased as the invasion in Chesapeake Bay progressed because

greater genetic diversity promotes seed production in *P. australis* (McCormick et al. 2010b). Further genetic studies may provide the missing information on the spatial distribution of propagules that is needed to build more powerful predictive models.

## Conclusion

Our results add to the growing body of evidence that *P. australis* ssp. *australis* growth and proliferation are aided and accelerated by system-wide anthropogenic disturbances and by localized disturbances directly on the shoreline. Our findings strengthen the established relationship between *P. australis* and agriculture by demonstrating that agriculture is a robust positive predictor at regional and local scales. Riprapped shorelines are also associated with *P. australis* invasion, likely because of the disturbances associated with installation and erosion at the edges. We suggest that systems with low watershed development, some agricultural land, and intermediate levels of development and disturbance at the shoreline are most at risk of invasion because there is enough anthropogenic eutrophication and disturbance to help *P. australis* ssp. *australis* invade, but not so much shoreline alteration that available habitat is lacking. *Phragmites australis* ssp. *australis* is well established in North America, but large swathes of habitat are still uninvaded. For example, the polyhaline and tidal fresh parts of Chesapeake Bay have low levels of invasion, and there are some systems within the middle salinity zones that are relatively free of *P. australis*. While eradication in heavily invaded areas is probably not possible (see review in Hazelton et al. 2014), management efforts focused on preventing the continued spread of this invasive plant into areas with low levels of invasion might be successful. Management strategies that reduce nutrient pollution, preserve natural shorelines, and limit nearshore disturbance of soils and vegetation may enhance the efforts to increase the resilience of shorelines to new invasion. These efforts are not likely to succeed unless they consider both regional and local factors and can address disturbance, nitrogen, and propagules together (Hazelton et al. 2014; Kettenring et al. 2011; 2015; McCormick et al. 2016).

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