

# Biogeographic gradients in ecosystem processes of the invasive ecosystem engineer *Phragmites australis*

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**Abstract** Latitudinal gradients in ecosystem patterns arise from complex interactions between biotic and abiotic forces operating at a range of spatial and temporal scales. Widespread invasive species, particularly invasive ecosystem engineers with large effects on their environment, may alter these gradients. We sampled 3–5 stands of the invasive common reed, *Phragmites australis*, in eight coastal wetlands ranging from Massachusetts (42°N) to South Carolina (32°N) to document geographic variation in *P. australis* primary production, associated plant and animal species diversity, and sediment carbon storage and to examine how local-, regional-, and large-scale environmental factors contribute to these patterns. Latitude best explained variation in *P. australis*

density, but contrary to expectations, density increased with increasing latitude across our sites. Latitude also predicted macroinvertebrate species richness, which increased with latitude in a manner similar to *P. australis* density. In addition to latitude, *P. australis* leaf carbon:nitrogen ratios, distance to the open coast, and sediment oxygen levels were most important for explaining variation in *P. australis* production, as well as community (plant or animal species richness) and ecosystem (carbon storage) variables. The percent of developed land was positively associated with *P. australis* density, yet this variable had relatively low predictive power in our study. Our study provides an important biogeographic perspective for documenting and understanding variation in invasive *P. australis* that is fundamental both for managing the invasion and for understanding latitudinal gradients in ecosystem structure and function.

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Phragmites invasion.

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## Introduction

Decreases in species or functional richness and ecosystem-level productivity with increasing latitude are quasi-ubiquitous patterns in biogeography (Turner

1976; Hillebrand 2004; Berke et al. 2014; Mozdzer et al. 2014) resulting from a complex interplay of ecological and evolutionary processes (Rohde 1992; Willig et al. 2003). For example, productivity of salt marsh ecosystems dominated by the native ecosystem engineer *Spartina alterniflora* increases significantly from north to south along the Atlantic Coast of the United States (Kirwan et al. 2009). Biotic interactions such as grazing also generally increase from north to south in marsh ecosystems (Pennings and Silliman 2005; Pennings et al. 2009), consistent with the expectation of greater species diversity and interaction strength at low latitudes (Schemske et al. 2009). Latitudinal gradients in species diversity and ecosystem function are correlated with large-scale environmental forcing factors such as temperature (Kirwan et al. 2009; Guo et al. 2013). However, environmental stress gradients also occur within a given latitude, and these regional- and local-scale processes can create variation in the distribution and ecosystem impacts of engineering species. For example, at higher latitudes along the Atlantic Coast of the U.S., estuarine salinity gradients structure the distribution and composition of marsh plant species due to an interaction between plant tolerance to salinity stress and competitive ability (Crain et al. 2004). In turn, the resulting dominant engineering species dictate how community- and ecosystem-level processes such as species richness and production will be modified at the local scale, and thus ultimately contribute to regional and biogeographic patterns (Wright and Jones 2004).

Many invasive species, particularly plants, act as ecosystem engineers in their invaded range, causing changes in hydrological regimes, nutrient cycling, and primary production (e.g., *Myrica faya*, Vitousek and Walker 1989; *Agropyron cristatum*, Christian and Wilson 1999; *Spartina alterniflora*, Neira et al. 2006; Grosholz et al. 2009). Because of their different evolutionary histories, invasive species may respond differently than natives to environmental gradients in their invaded range (e.g., Cronin et al. 2015), particularly until they have had sufficient time to evolve. Alternatively, invasive species may rapidly evolve in response to environmental gradients in their invaded range (e.g., Gilchrist et al. 2004). Either way, invasive species that are ecosystem engineers could alter established spatial patterns in species diversity and ecosystem function through the introduction of novel traits and species interactions. A biogeographic

approach is thus critical for understanding the multi-scale effects of invasive species on species diversity and ecosystem function.

*Phragmites australis* is a perennial grass that is distributed worldwide and is abundant in wetlands and along the borders of lakes, ponds, and rivers (Saltonstall 2002; Meyerson et al. 2009). Although *P. australis* is native to North America, a non-native lineage (haplotype M) was introduced from Eurasia to the Atlantic Coast in the late 1800s, and beginning in 1960 it spread rapidly south and west (Saltonstall 2002); additional invasive lineages have also been detected, indicating multiple introduction events from Europe (Lambertini et al. 2006, 2012; Meyerson and Cronin 2013). Experimental comparisons of the native and invasive lineages demonstrate that invasive *P. australis* has 30–44 % greater photosynthetic rate and 50 % greater canopy than native *P. australis* (Mozdzer and Zieman 2010). The invasive haplotype also has higher plant nitrogen content and a much greater nitrogen demand (Mozdzer and Zieman 2010), and it is a superior competitor than the native haplotype at high nitrogen concentrations (Mozdzer et al. 2010). As a result, invasive *P. australis* can affect marsh plant species diversity (Silliman and Bertness 2004), as well as a range of ecosystem processes, including decomposition, nitrogen cycling, greenhouse gas emissions, and accretion change (Meyerson 2000; Windham 2001; Rooth et al. 2003; Windham and Ehrenfeld 2003; Mozdzer and Megonigal 2013), greatly altering the coastal ecosystems that it invades. Past efforts have provided detailed documentation of the community and ecosystem effects of *P. australis* in particular regions of its invaded range (e.g., the Chesapeake Bay, New England), yet we have little information regarding variation in ecosystem processes, or the ecological and environmental variables contributing to those processes, across a latitudinal scale (but see Cronin et al. 2015).

We quantified biogeographic patterns within and among regions in population, community, and ecosystem structure of the invasive ecosystem engineer *P. australis* and examined how local- and large-scale environmental factors contributed to these patterns. Specifically, we addressed the following questions: (1) How does (a) *P. australis* production, morphology, and reproductive investment, (b) sediment carbon storage, and (c) associated plant and animal species richness vary within and across sites along a latitudinal gradient? (2)

What is the relative explanatory power of local (plant tissue carbon to nitrogen ratio, sediment oxygen availability, soil salinity, leaf litter), regional (distance to open coastal water, percent developed lands, tidal range, water salinity), and latitudinal (sediment temperature, latitude) factors for each of the *P. australis* population, community, and ecosystem responses?

## Methods

We measured *P. australis* production (density and height), the species richness of associated plants and macroinvertebrates, and carbon storage (sediment organic content) across 8 sites on the east coast of the United States, spanning 10° of latitude. We then examined the ability of local, regional, and latitudinal variables to explain these patterns (Table 1). For example, local-scale abiotic conditions such as redox and soil salinity are known to affect (and be affected by) plant production and composition in coastal

marshes (Windham and Lathrop 1999; Windham 2001). In addition, the cover of leaf litter can reduce light availability and decrease the density of *P. australis*, but it also reduces the cover of native plant species that compete with *P. australis* (Minchinton et al. 2006; Holdredge et al. 2011). At a regional scale, *P. australis* invasion success has been linked to shoreline development/urbanization, along with subsequent increases in nutrient availability and decreases in soil salinity (Bertness et al. 2002; Silliman and Bertness 2004; Meyerson et al. 2009; Mozdzer et al. 2010; Mozdzer and Zieman 2010). In addition to affecting salinity, regional variables such as tidal range and distance to open coastal water will also influence the composition and abundance of associated animal and plant species in coastal habitats. Finally, latitudinal variation in temperature is strongly linked to production and sediment microbial activity in coastal wetlands (Kirwan et al. 2009; Mozdzer et al. 2014) and may contribute to large-scale patterns in key *P. australis* ecosystem characteristics.

**Table 1** Predictive variables used in analyses of *P. australis* characteristics (Pa density, height, and flowering) and community and ecosystem processes [sediment organic matter (SOM), animal and plant species richness]

Predictor	Spatial scale of predictor	Pa density	Pa height	Pa flowers	SOM	Animal richness	Plant richness	Mean rank for Pa	Mean rank for all
Latitude	Latitudinal	1	5	2	1	3	7	2.7	3.2
C:N*	Local	3	3	4	5	7	3	3.3	4.2
Redox*	Local	5	7	1	7	1	1	4.3	3.7
Distance to open water	Regional	4	1	8	3	2	6	4.3	4.0
Soil salinity*	Local	7	2	5	4	4	5	4.7	4.5
Leaf litter*	Local	2	4	10	11	6	4	5.3	6.2
Sediment temperature	Latitudinal	8	6	6	2	9	8	6.7	6.5
Percent developed	Regional	9	8	3	9	11	10	6.7	8.3
Tidal range	Regional	6	9	9	8	8	11	8.0	8.5
Water salinity	Regional	10	10	7	6	10	9	9.0	8.7
Phragmites density	Local	NA	NA	NA	10	5	2	NA	5.7
Model R <sup>2</sup>		0.80	0.93	0.91	0.95	0.90	0.92		

*Phragmites australis* density was included as a predictor in the models of SOM and species richness. Variables with a \* can both influence and be influenced by *P. australis*. Predictors were classified by spatial scale: local, regional, or latitudinal. For each response variable, we present the rank order of each predictor. Predictors are ordered from most to least important in explaining *P. australis* responses. We also provide the R<sup>2</sup> for each model, showing the high explanatory power of our models

## Field survey

In September–October 2014, we surveyed *P. australis* communities at 8 sites from South Carolina to Massachusetts (Table A2). At each site, we quantified *P. australis* production (vegetative stem density, vegetative stem height, flowering stem production), associated community and ecosystem variables that exhibit biogeographic gradients in many ecosystems (animal species richness, plant species richness, sediment organic content), as well as a suite of potential explanatory variables previously documented as important for *P. australis* (leaf litter cover, *P. australis* tissue carbon:nitrogen content as a proxy for nutrient availability, sediment temperature, soil and water salinity, sediment oxygen availability (i.e., redox), percent adjacent developed lands, and distance to open coastal water). These variables are explained in greater detail below.

We coordinated with land managers at each site to identify and sample 3–5 invasive *P. australis* subsites in order to capture substantial within site variability. When possible, these subsites were discrete; however, the distribution of *P. australis* at some sites necessitated sampling multiple subsites within a single continuous *P. australis* stand. In all cases, replicate subsites were separated by at least 100 m. We are unable to confirm that all subsites are independent of one another, so our inferences of site-level characteristics are limited to the specific subsites sampled. In each *P. australis* subsite, we sampled six 0.25 m<sup>2</sup> quadrats along 3 transects (2 quadrats per transect) running perpendicular from the seaward edge of the subsite into the subsite interior. Within each transect, one quadrat was <5 m from the seaward edge of the subsite and the other quadrat was >5 m from this edge. All sampling locations were separated by at least 5 m. In each quadrat, we recorded GPS coordinates using a Garmin GPS 72H. We also used an Atago 2491 Master-S/Mill $\alpha$  to measure pore-water salinity (ppt) and a Thermo Scientific Orion Star Series A321 Portable pH meter to measure sediment temperature (°C) and sediment redox potential (mV) at a depth of 10 cm in the center of each quadrat.

### *P. australis* responses

In each quadrat, we recorded the number of live and dead vegetative and flowering stems of *P. australis*.

We also collected one leaf from each of 5 randomly selected, live *P. australis* stems and measured their stem height. Each leaf was cut in half (perpendicular to the mid rib) using scissors. The bottom half of each leaf was stored on silica for genetic analysis and the top half of each leaf was wrapped in foil and stored on ice for 2–4 days, and then at –20 °C until processed for tissue carbon (C) and nitrogen (N) content.

### Community and ecosystem responses

We measured the number of co-occurring plant species and the percent cover of leaf litter in each 0.25 m<sup>2</sup> plot. We also identified and counted all visible benthic invertebrate species present in a 0.0625 m<sup>2</sup> quadrat haphazardly placed within the larger plot. We identified a total of 34 co-occurring plant species and 9 benthic macroinvertebrate species. The most abundant co-occurring plant species were *Distichlis spicata*, *Spartina patens*, *Spartina alterniflora*, and *Solidago sempervirens*. *Distichlis spicata*, *Spartina patens*, *Spartina alterniflora*, and *Iva frutescens* were present at over half of the sites. The most abundant benthic macroinvertebrate species were gastropod detritivore *Melampus bidentatus*, gastropod grazer *Littoraria irrorata*, amphipod grazer *Orchestia grillus* and filter-feeding mollusk *Geukensia demissa*. *M. bidentatus* was present at 6 sites; all other benthic macroinvertebrate species were found at less than half of the sites.

We collected one 15 cm depth sediment core in each quadrat and sectioned it into 5 segments (depths: 0–1, 1–3, 3–5, 5–10, and 10–15 cm). Sectioned sediment samples were stored on ice for 2–4 days, and then at –20 °C until processing. We used average sediment organic matter (SOM) across all depths in our analyses.

### Laboratory analyses

#### *P. australis* genetic analysis

Haplotype lineage was determined according to the protocol of Saltonstall (2003) using three leaf tissue samples per subsite (one from the interior and one each from the right and left seaward edges). Briefly, we extracted DNA from dried, ground leaf tissue using an E-Z 96<sup>®</sup> Plant DNA Kit (Omega Bio-Tek), amplified two non-coding chloroplast regions (*trnLb* and *rbcL*)

via polymerase chain reaction (PCR), digested the PCR products using restriction enzymes (*RsaI* for region *trnLb* and *HhaI* for region *rbcL*), and visualized the restriction fragments on 3 % agarose gel (Saltonstall 2003) to determine haplotype lineage.

#### *P. australis* tissue nutrient content

Prior to elemental analysis, we rinsed *P. australis* leaf tissue thoroughly with DI water to remove any non-leaf material from the sample. Leaf tissue was then dried at 60 °C for 48–72 h and homogenized to a fine powder using a Retsch MM400 mixer-mill. Leaf %C and %N were determined on a FlashEA 1112 Elemental Analyzer (Thermo Fisher Scientific) at the Northeastern University Marine Science Center.

#### Sediment carbon storage

Sediment organic content was evaluated according to United Nations Education, Scientific and Cultural Organization protocols (Howard et al. 2014). Core segments were massed after drying at 60 °C for 48–72 h and again after combustion at 450 °C for 6 h. Pre and post ignition masses of each segment were summed by core and SOM was estimated by calculating proportion mass lost on ignition.

#### Additional explanatory variables

##### Developed lands

The percentage of developed land cover for each subsite was based on sampling land cover within 1 km of subsite centers. This approach builds on the local scale influences on stream ecosystems presented in Strayer et al. (2003). For each subsite, land cover data were extracted from the 2011 National Land Cover Database (NLCD) available at <http://www.mrlc.gov> using a circle with a 1 km radius around the subsite center. The area of developed land (NLCD land cover categories 21–24; Homer et al. 2015) within each subsite's circle was determined using ArcGIS. The developed area was then divided by the total circle area to determine the percentage of developed land cover for each subsite. The spatial resolution of the land cover dataset is 30 m by 30 m pixels. Our sites represented a relatively limited range of developed land cover (0–21 %).

##### Distance to open coastal water

The distance to open water represents the flowpath distance, not straight-line distance, from the subsite center to the coastline as defined by the U.S. Geological Survey's National Hydrology Dataset (NHD) available at <http://nhd.usgs.gov/>. The distance was determined using a combination of NHD drainage line distances and flowpaths manually derived from aerial photographs to connect the subsite center to the NHD drainage network. For subsites with no clearly visible flowpath in the aerial photograph, the straight-line distance to the NHD drainage network or the coastline was used. The distance to open coastal water was generally <10 km except for one site (ACE Basin NERR) that had distances ranging from 16 to 60 km across sampled subsites.

##### Tidal range

The tidal amplitude for each subsite was based on NOAA tide predictions ([http://tidesandcurrents.noaa.gov/tide\\_predictions](http://tidesandcurrents.noaa.gov/tide_predictions)) for the site closest to our sampled *P. australis* subsites. For each subsite, we extracted the predicted height of all daily high and low tides in 2015 and calculated an average height of low and high tide. The tidal range for each subsite was then calculated as the difference between the average high and low tide.

##### Water salinity

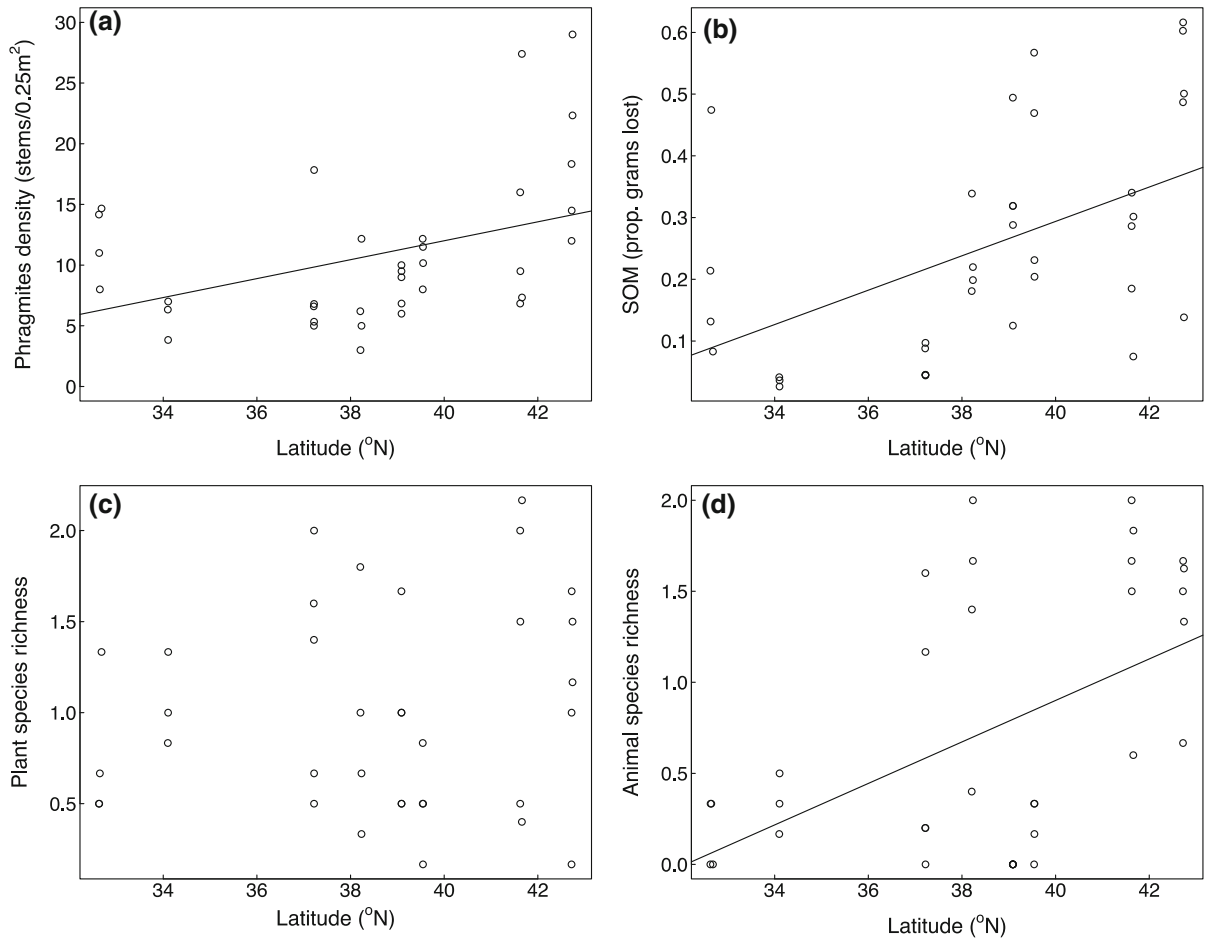
Water salinity for each subsite was obtained from data collected by the National Estuarine Research Reserve System's (NERRS) long-term water quality monitoring sites (<http://cdmo.baruch.sc.edu/>) in 2014 and Plum Island Ecosystems Long Term Ecological Research (PIE-LTER) station's estuary salinity transects (<https://portal.lternet.edu/nis/home.jsp>) in 2010. The water salinity for each subsite was calculated as the yearly average water salinity from the nearest NERRS or PIE-LTER station.

##### Statistical analyses

*Phragmites australis* production, SOM, and animal species richness exhibited significant linear relationships with latitude (Fig. 1), but strong collinearity between latitude and other predictors (Table A1,

Fig. A1) limited our ability to interpret the factors contributing to these patterns. Thus, we used Random Forests (RF; Breiman 2001) to investigate the relationship between *Phragmites* population, community, and ecosystem properties and a suite of biotic and abiotic environmental variables (Table 1). RF is a powerful data mining technique commonly used in the ecological field of species distribution modeling that can detect and model complex relationships between variables (Prasad et al. 2006; Cutler et al. 2007; Fenberg et al. 2015). RF is an extension of classification and regression trees (CART; Breiman et al. 1984) designed to produce accurate predictions without overfitting the data. RF models are constructed by fitting a single classification or regression tree to each of many random (bootstrap) samples drawn from the

data. Each tree is grown by recursively partitioning the response variable using a random subset of the explanatory variables. By finding the optimal split (i.e., the one that maximizes node purity) among a small set of randomly selected explanatory variables, RF reduces the correlation between the trees and thus keeps bias low. Unlike CART, which uses pruning to reduce overfitting, the trees in RF are grown to their maximum size and aggregated into an ensemble or forest. Aggregation also reduces variance and thus promotes the predictive ability of RF (Prasad et al. 2006). We chose to use RF because it provides critical benefits over classical approaches such as General Linear Models in the face of strong nonlinearities and multicollinearity: (1) RF can detect nonlinear relationships between explanatory and response variables



**Fig. 1** Relationships between latitude and **a** *Phragmites* live stem density ( $R^2 = 0.16$ ,  $P = 0.02$ ), **b** sediment organic content (SOM:  $R^2 = 0.25$ ,  $P = 0.002$ ), **c** associated plant species

richness (not significant:  $R^2 = 0.02$ ,  $P = 0.43$ ), and **d** associated animal species richness ( $R^2 = 0.25$ ,  $P = 0.002$ )

without overfitting; (2) RF does not suffer from multicollinearity issues such as variance inflation (Dormann et al. 2013); (3) RF uses a Monte Carlo resampling approach to maximize generality (i.e., out-of-sample predictive ability).

To gain ecological insights into the fitted RF models, we determined variable importance by computing the total decrease in node purity associated with each explanatory variable used to split the response variable, and then averaging this value across all trees in the forest. Because all of our response variables were numerical, node purity was assessed by computing the Residual Sum of Squares (RSS). Hence, explanatory variables that decreased RSS the most were deemed to have greater importance. We also examined the ability of the models to explain variation in our response variables by calculating the (pseudo)  $R^2$  of each ensemble model. To visualize the relationships between each explanatory variable and the response, we used partial dependency plots that show the average trend in the response variable as a function of the focal explanatory variable, while keeping all other explanatory variables in the model constant. Since most of our explanatory variables were measured at the subsite-scale, we performed all analyses on subsite averages. Analyses were conducted in R version 3.2.2 using the randomForest package (R Development Core Team 2015). For each RF model, we grew 500 trees and for each split, we selected 3 explanatory variables at random. See the Appendix of ESM for the code used in our RF analyses.

## Results

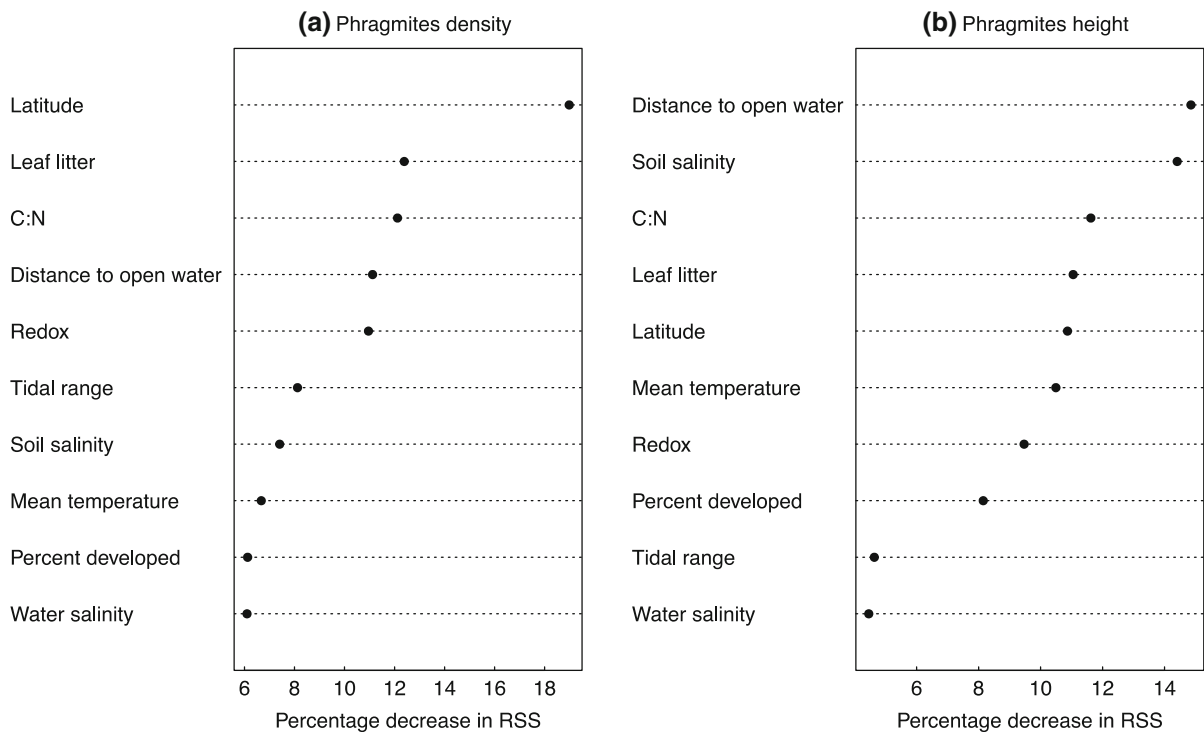
### *P. australis* responses

Identification of *Phragmites* population type via genetic analysis confirmed that all subsites consisted of an invasive haplotype. The density of live and dead *P. australis* stems was most strongly related to latitude (Fig. 2a). Specifically, *P. australis* density increased slightly with latitude from 38 to 41°N and exponentially from 41 to 43°N (due to high densities at our MA site; Fig. 3d). Percent cover of leaf litter, leaf C:N, distance to open water, and sediment oxygen (redox) had similar and moderate importance for *P. australis* density (Fig. 2a). *P. australis* density underwent a dramatic decrease as leaf litter cover increased from

10 to 20 %, followed by a much more gradual decrease (Fig. 3j). *P. australis* density was also strongly negatively correlated with leaf C:N between 10 and 20 and then remained consistently low at higher C:N values (Fig. 3h). Conversely, *P. australis* density increased rapidly with distances from the open coast ranging between 0 and 10 km before stabilizing (Fig. 3b). Finally, *P. australis* density remained relatively unchanged for redox <150 mV, but then rose dramatically when redox potential increased from 150 to 200 mV (Fig. 3e). Soil salinity, tidal range, mean sediment temperature, water salinity, and percent developed land were the least important variables for explaining *P. australis* density (Fig. 2a).

*Phragmites australis* stem height was most strongly associated with distance to open water and soil salinity (Fig. 2b). *P. australis* height was nonlinearly related to distance to open water, decreasing rapidly in the first few km from the open coast and then increasing for distances between 5 and 30 km before stabilizing (Fig. 4b). *P. australis* height decreased gradually for soil salinities between 5 and 20 ppt, increased slightly from 20 to 23 ppt, and then showed a sharp decrease between 23 and 25 ppt (Fig. 4f). Leaf C:N, leaf litter percent cover, latitude, mean sediment temperature, redox, and percent developed land had moderate importance for *Phragmites* height (Fig. 2b). Stem height was nonlinearly related to leaf C:N, with a peak in height between values of 20–28 (Fig. 4h). Stem height was consistently high up to 50 % leaf litter cover and then declined dramatically (Fig. 4j). Stem height also decreased with latitude, most dramatically at 34°N and again at 41°N (Fig. 4d). Stem height was similar for sediment temperatures between 14 and 19 °C, decreased between 19 and 22 °C, and then increased again (Fig. 4a). *P. australis* height remained unchanged for redox between –300 and –100 mV, but then decreased gradually for redox values between –100 and 100 (Fig. 4e). Finally, stem height generally increased with 1–10 % developed land and then stabilized (Fig. 4c). The remaining variables (tidal range, water salinity) had little explanatory power for stem height (Fig. 2b).

The number of *Phragmites* flowering stems was most strongly related to redox (Fig. A2), exhibiting a strong increase with redox potentials between –200 and 200 (Fig. A3e). Flowering also declined with both latitude (Fig. A3d) and percent developed land over the range included in this study (Fig. A3c), but it was



**Fig. 2** Importance of each explanatory variable for explaining *Phragmites* **a** density and **b** height in the Random Forest model. Variable importance is measured in terms of node impurity and computed as the decrease in the residual sum of squares (RSS)

that results from splitting the response variable based on each explanatory variable. Explanatory variables are sorted from high (large decrease in RSS) to low (small decrease in RSS) importance

only weakly related to the rest of the explanatory variables (Fig. A2).

#### Community and ecosystem responses

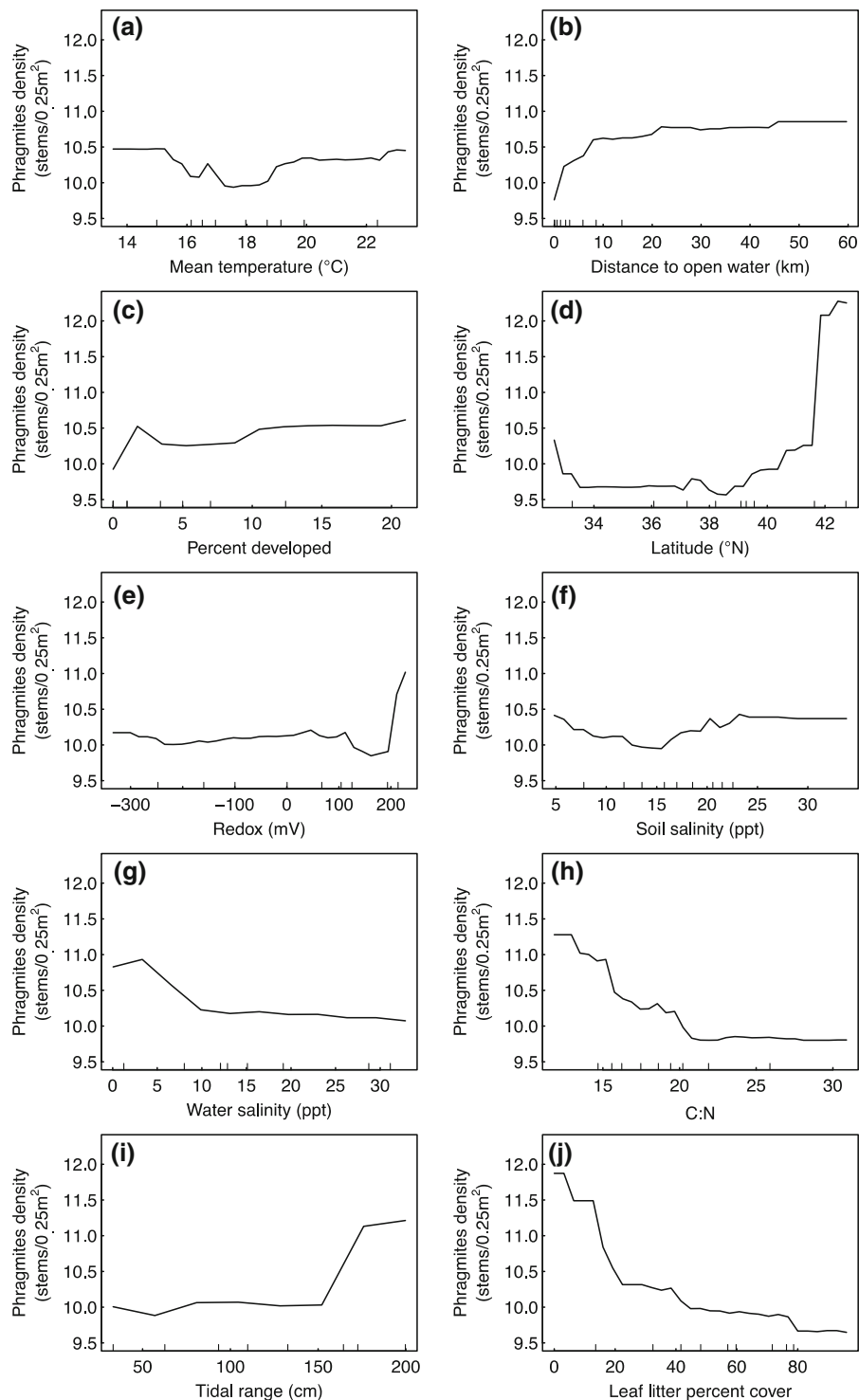
SOM was most strongly related to latitude, mean sediment temperature, and distance to open water (Fig. 5). SOM increased nonlinearly with latitude, remaining relatively low for latitudes between 32 and 38°N and then increasing dramatically between 38 and 43°N (Fig. 6e). SOM decreased with sediment temperature (Fig. 6b). SOM increased dramatically between 0 and 10 km from open water and then stabilized (Fig. 6c). The remaining predictors were only weakly related to SOM (Fig. 5).

Benthic macroinvertebrate species richness was most strongly associated with redox (Fig. 7a), increasing rapidly with redox between 0 and 150 mV (Fig. 8f). Conversely, animal richness decreased dramatically between 2 and 10 km from coastal water (Fig. 8c). In contrast to most diversity gradients,

animal richness increased between 40 and 42°N compared to lower latitudes (Fig. 8e). Animal richness was only weakly related to the rest of the explanatory variables (Fig. 7a).

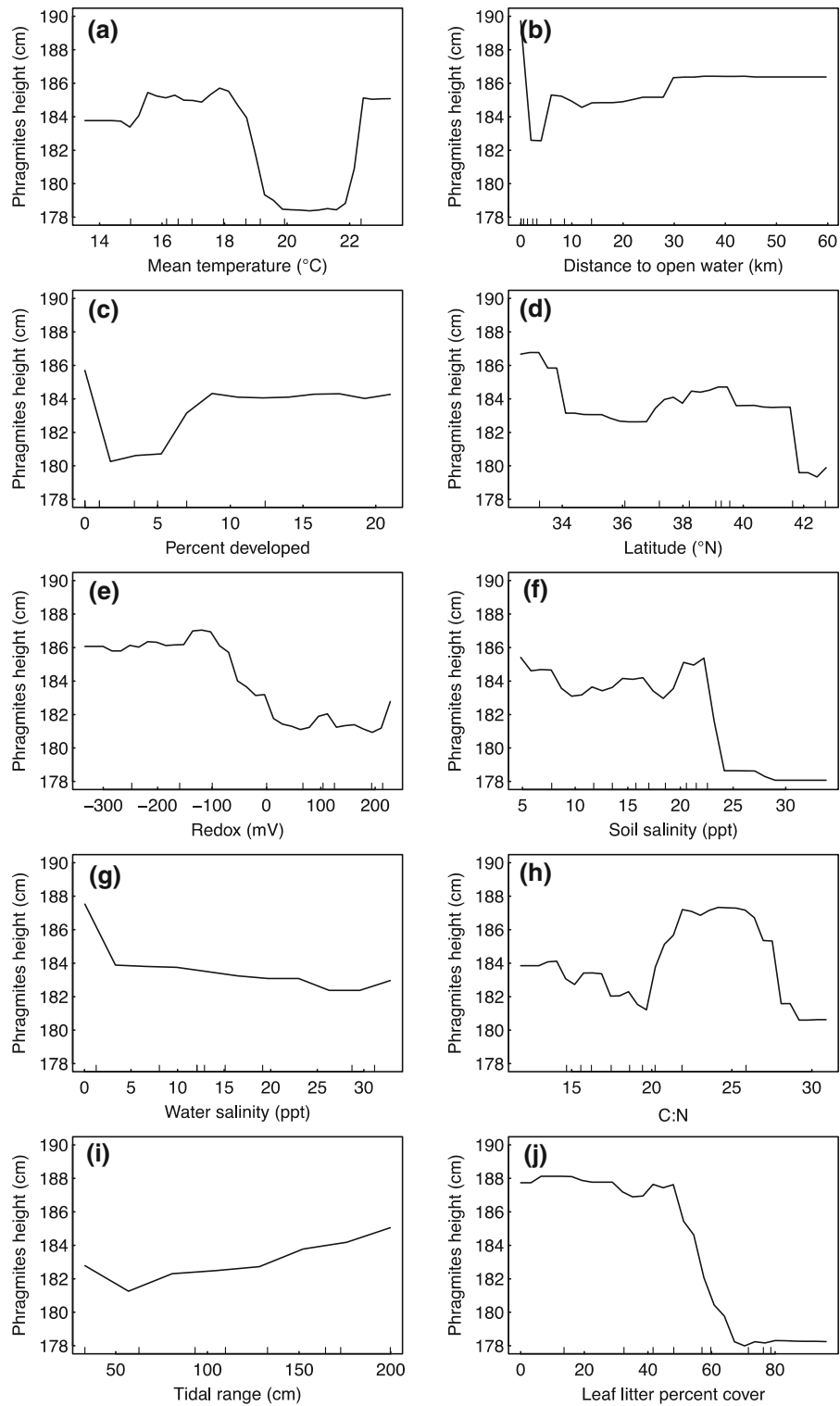
The species richness of associated plants was most strongly related to redox and *P. australis* stem density (Fig. 7b). Plant richness increased from −300 to −200 mV and then increased dramatically above 200 mV (Fig. 9f). In contrast, plant richness generally declined with *P. australis* stem density (Fig. 9a). *P. australis* leaf C:N, percent cover of leaf litter, soil salinity, and distance to open water were also important predictors of plant species richness (Fig. 7b). Plant richness increased rapidly with *P. australis* leaf C:N between 25 and 30 (Fig. 9i). Plant species richness was lower when leaf litter cover was >30 % (Fig. 9k). As with animal richness, plant richness decreased between 0 and 10 km from coastal water (Fig. 9c) and increased linearly with soil salinity between 10 and 30 ppm (Fig. 9g). The remaining predictors had low predictive power for plant richness.



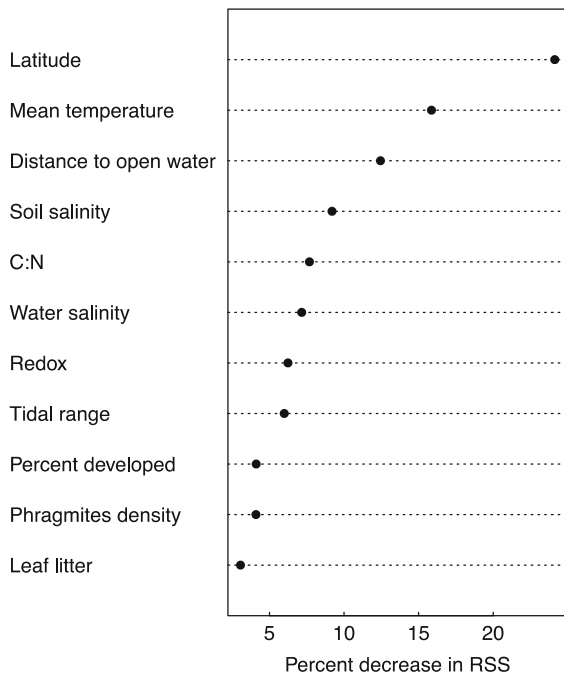


**Fig. 3** Partial dependency plots showing the marginal effect of each explanatory variable on *Phragmites* density in the Random Forest model. The partial dependency plots show the average trend in the response variable as a function of the focal

explanatory variable, while keeping all other explanatory variables fixed; thus, the values of the y-axis do not represent the raw data. Ticks on the x-axis indicate the raw data



**Fig. 4** Partial dependency plots showing the marginal effect of each explanatory variable on *Phragmites* height in the Random Forest model. The partial dependency plots show the average trend in the response variable as a function of the focal explanatory variable, while keeping all other explanatory variables fixed; thus, the values of the y-axis do not represent the raw data. Ticks on the x-axis indicate the raw data



**Fig. 5** Importance of each explanatory variable for explaining sediment organic matter (SOM) in the Random Forest model

## Discussion

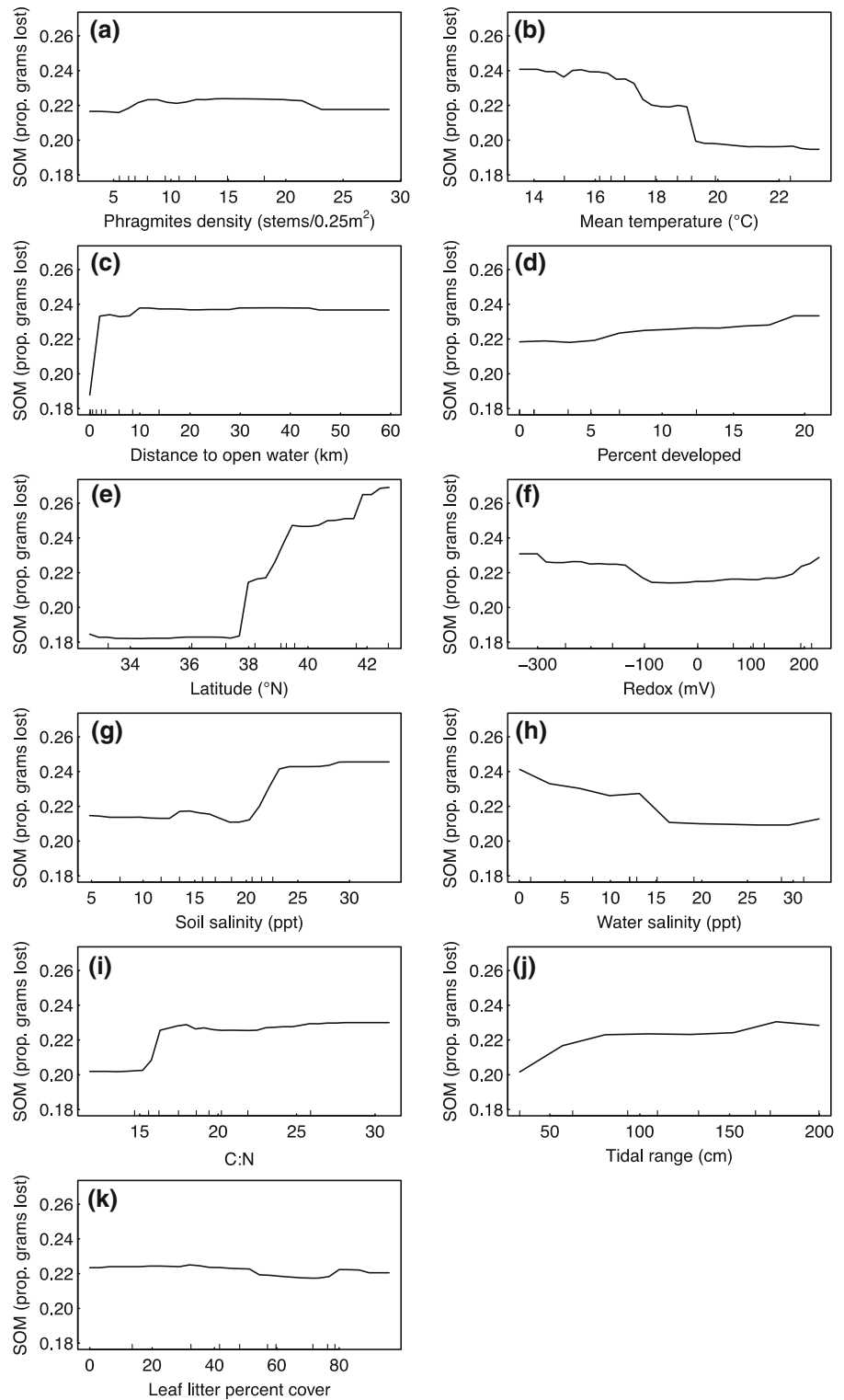
Variables operating at multiple spatial scales explained 80–95 % of the observed biogeographic variation in invasive *P. australis* across our sites (see  $R^2$  values in Table 1). Latitude itself was the primary predictor in terms of average rank across all responses (Table 1). The positive relationship between *P. australis* density and latitude is counter to the negative relationship between latitude and primary production in coastal marshes dominated by the native species *Spartina alterniflora* (Kirwan et al. 2009). Species richness of the benthic macroinvertebrates that utilize *P. australis* as habitat also increased with latitude (Fig. 8e), mirroring the gradient in *P. australis* density rather than widespread gradients of decreasing species richness with increasing latitude in other ecosystems

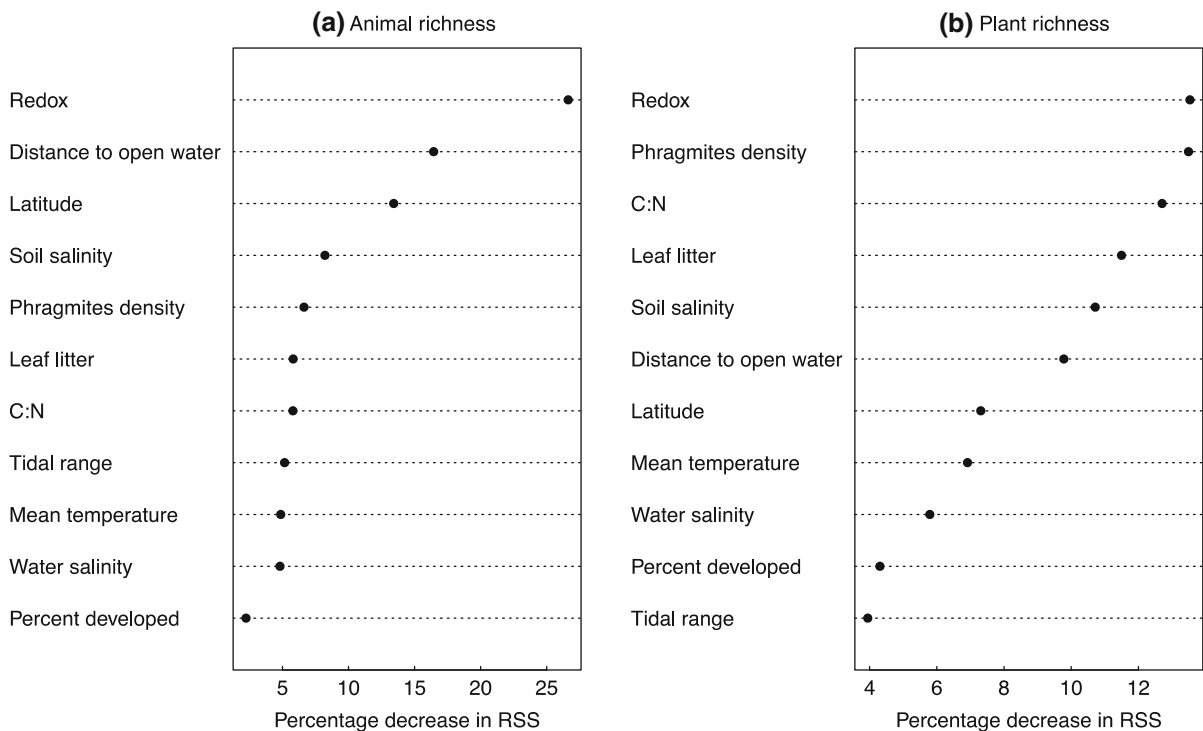
(Hillebrand 2004). In contrast, species richness of co-occurring plant species did not show a strong relationship with latitude (Figs. 1c, 7b, 9e). Rather, *P. australis* density was one of the top two predictors of plant species richness, and this relationship was strongly negative, consistent with expectations if *P. australis* is the competitive dominant in this plant community (Silliman and Bertness 2004).

In contrast to the relative importance of *P. australis* density for animal and plant richness, sediment organic matter across our sites was best predicted by latitude and sediment temperature, with little variation explained by *P. australis* (Fig. 5). SOM increased with increasing latitude and decreasing temperature, consistent with higher decomposition rates in lower latitudes (Zhang et al. 2008; Kirwan et al. 2014). However, because our data are limited to a single sampling period at each site, we may have detected different relationships between SOM and our predictors had we sampled in a different season (e.g., mid-summer, when temperature variation across sites is likely reduced). Further, although neither *P. australis* density nor leaf C:N were important predictors of SOM in our analysis relative to latitude and temperature, invasive *P. australis* can alter decomposition and sediment C storage relative to native marsh species due to elemental or lability differences in the plant tissue (Meyerson 2000; Windham 2001; Liao et al. 2008). For instance, in the Yangtze estuary in China, where *P. australis* is native and *Spartina alterniflora* is invasive, decomposition rates of *S. alterniflora* litter were twice as fast as *P. australis* litter (Liao et al. 2008). The same pattern of faster decomposition in *S. alterniflora* was also observed in a New England marsh (Warren et al. 2001). Field experiments that manipulate temperature and litter identity at multiple sites across a broad biogeographical range would generate a more precise understanding of the effects of *P. australis* on SOM across a latitudinal gradient but were beyond the scope of this study.

Of the regional variables included in our study, distance to open coastal water had the greatest predictive power, particularly for the community and ecosystem responses (Table 1). While distance to open coastal water was not uniformly distributed across our sites, most of the effect of this variable occurred within the first 10 km from the open coast, which is the range of distances represented by all but

**Fig. 6** Partial dependency plots showing the marginal effect of each explanatory variable on sediment organic matter (SOM) in the Random Forest model. The partial dependency plots show the average trend in the response variable as a function of the focal explanatory variable, while keeping all other explanatory variables fixed; thus, the values of the y-axis do not represent the raw data. Ticks on the x-axis indicate the raw data





**Fig. 7** Importance of each explanatory variable for explaining **a** animal (benthic macroinvertebrate) and **b** plant species richness in the Random Forest model

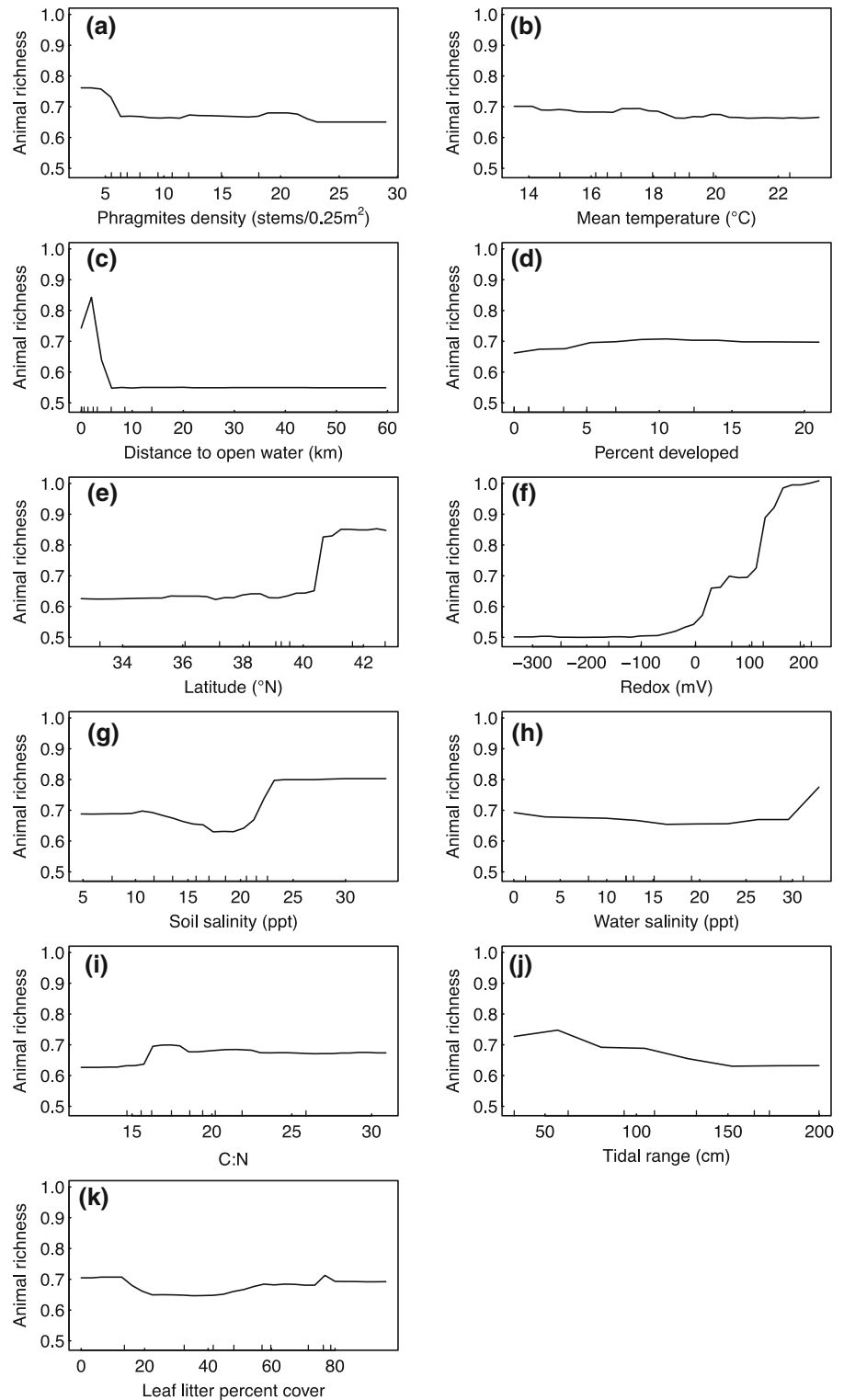
one of our sites. For example, both animal (Fig. 8c) and plant (Fig. 9c) species richness declined in *P. australis* subsites from 0 to 10 km of the coast in our study. The more dramatic decline for animal richness is consistent with most of the macroinvertebrate species being of marine origin (e.g., fiddler crabs, snails, mussels, and amphipods) and thus being more abundant lower down in the estuary. Contrary to species richness, SOM increased from 0 to 10 km from the coast and then plateaued (Fig. 6c), consistent with results showing that the pool of organic material toward the head of estuaries increasingly consists of aged and refractory riverine organic material (Middelburg et al. 1996). Future studies designed specifically to test relationships with distance to open coastal water will help clarify the mechanisms underlying these patterns. The regional-level variables of tidal range and water salinity had consistently low explanatory power in our analyses.

Previous work documented a positive relationship between regional shoreline development and *P. australis* abundance (King et al. 2007; Bertness et al. 2002; Silliman and Bertness 2004), and Lambert et al. (this

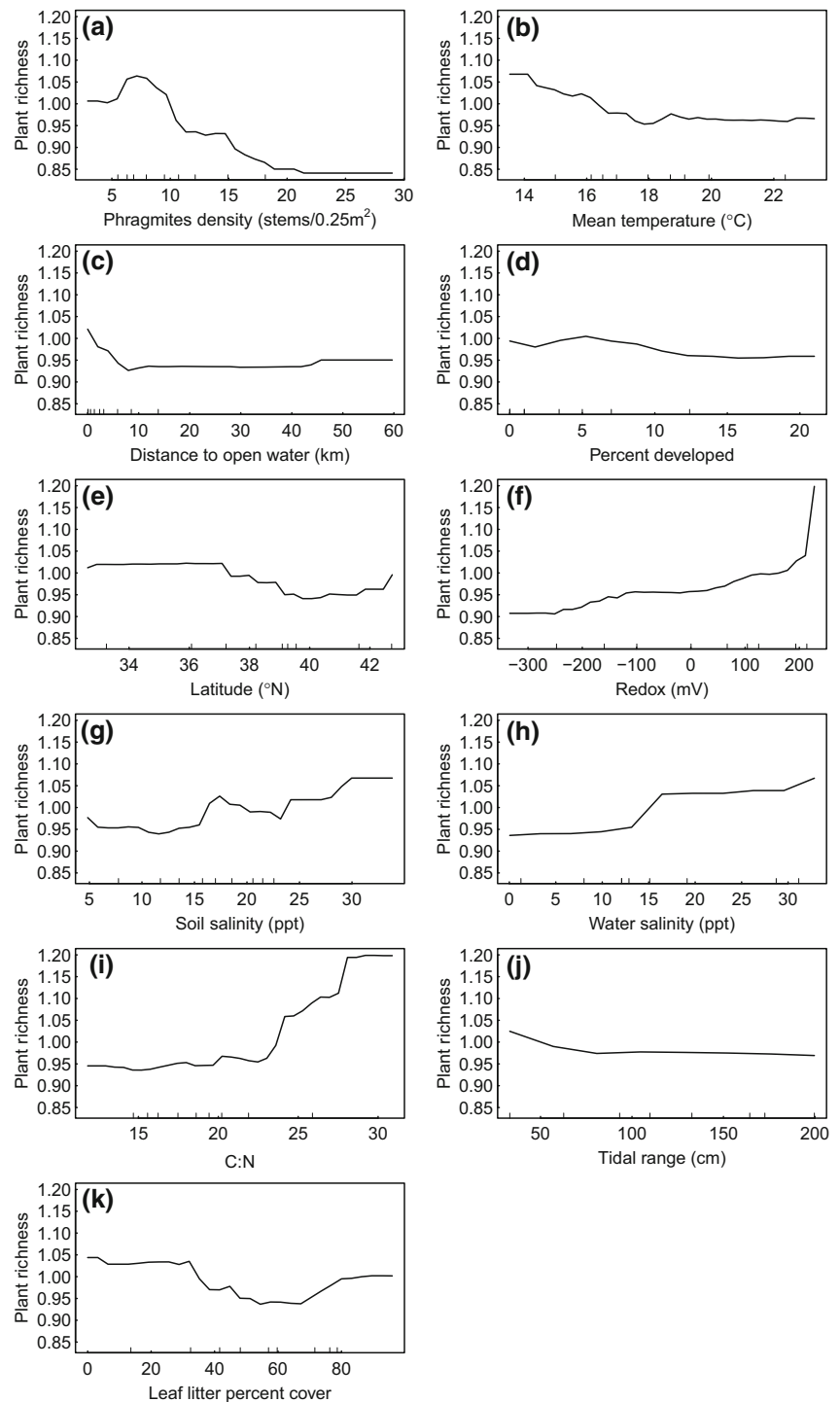
volume) found an association between invasive *P. australis* and wetland disturbance in or near urban centers. We also found generally positive relationships between the percent of developed land and *P. australis* stem density and stem height at the sites we sampled (Figs. 3c, 4c). Yet relative to the suite of predictor variables we analyzed, percent developed land had low predictive power for the plant responses (Fig. 2) and even less explanatory capability for the community and ecosystem responses (Figs. 5, 7). This low predictive power may have resulted from the relatively low average development and/or the relatively small range of developed lands (0–21 %) adjacent to our study sites. Alternatively, the importance of development may vary across regions within our study area. Examination of sites varying across a greater range of percent developed land along a latitudinal gradient is needed to provide a more robust test of potential regional variation in the effects of development.

Of the local-scale variables, *P. australis* leaf C:N, sediment oxygen (redox), sediment salinity, and leaf litter percent cover had substantial explanatory power for *P. australis* production, associated plant and animal

**Fig. 8** Partial dependency plots showing the marginal effect of each explanatory variable on animal richness (number of benthic macroinvertebrate taxa) in the Random Forest model. The partial dependency plots show the average trend in the response variable as a function of the focal explanatory variable, while keeping all other explanatory variables fixed; thus, the values of the y-axis do not represent the raw data. Ticks on the x-axis indicate the raw data



**Fig. 9** Partial dependency plots showing the marginal effect of each explanatory variable on plant richness (number of taxa) in the Random Forest model. The partial dependency plots show the average trend in the response variable as a function of the focal explanatory variable, while keeping all other explanatory variables fixed; thus, the values of the y-axis do not represent the raw data. Ticks on the x-axis indicate the raw data



species richness, and SOM (Table 1). Interestingly, these local variables can be a response to *P. australis* as well as a predictor, complicating their interpretation.

For instance, species-specific tolerances to sediment oxygen and salinity can influence plant species distributions in coastal wetlands (Pennings and Bertness

2001). However, plant species can also alter sediment salinity and oxygen through root and rhizome activity belowground, and *P. australis* in particular appears to have a strong effect on these variables, lowering sediment salinity and increasing sediment oxygen (Windham and Lathrop 1999). We did not manipulate *P. australis* in this study, and so we cannot tease apart the direction of the relationship driving strong associations of high *P. australis* density and stem height with high sediment oxygen, or increased *P. australis* stem height with decreased sediment salinity. Future experiments examining the relative importance of these factors could help clarify this gap in our understanding.

Leaf C:N was the second most important predictor for *P. australis* responses and the fourth most important predictor for community and ecosystem processes (Table 1). Although variation in this ratio can result from changes in either C or N content, increases in leaf percent N were strongly correlated with decreases in C:N ( $R^2 = 0.81$ ;  $y = -7.16x + 37.49$ ), while leaf percent C showed no relationship with leaf C:N ( $R^2 = 0.03$ ). Thus, lower C:N values indicate higher tissue N in our study. As expected, *P. australis* was positively correlated with this increased N availability, with higher stem density at lower C:N values (Fig. 2h). Although *P. australis* density increased with latitude, and a prior study found an increase in *P. australis* tissue N content with latitude (Cronin et al. 2015), we found a weak negative relationship between latitude and percent N ( $R^2 = 0.17$ ;  $y = -0.07x + 5.13$ ). Interestingly, plant species richness increased with increasing *P. australis* leaf C:N (and decreasing percent N; Fig. 9i), even after accounting for the effects of *P. australis* density, suggesting increased plant species coexistence with lower nutrient availability. Alternatively, this pattern may result from complementary resource use and increased N uptake in species rich subsites (c.f., Tilman et al. 2001); the understory plant community often consisted of diverse, mostly native flowering species, including grasses, sedges, rushes, forbs, and vines, suggesting that complementarity may also be playing a role in maintaining plant species diversity. These alternative explanations illustrate the bi-directional relationship between *Phragmites* leaf C:N and plant response variables. Such reciprocal effects may also explain the complex relationship between C:N and *P. australis* stem height (Fig. 4h)—i.e., increased N availability may lead to increased stem height, thereby increasing tissue C:N values.

Percent cover of leaf litter had high explanatory power for *P. australis* density and stem height (Fig. 2): increasing cover of leaf litter had a negative effect on both responses. Previous work has shown that litter removal causes an increase in *P. australis* stem density, but no change in stem height (Holdredge et al. 2011). Increasing leaf litter cover was also associated with a general decline in the richness of the primarily native neighboring plant species assemblage, consistent with negative effects of litter on plant species that co-occur with *P. australis*, most likely due to light limitation (Holdredge et al. 2011). Although leaf litter may increase habitat complexity and influence interactions among associated animal species (Finke and Denno 2006), it was not a strong predictor of benthic macroinvertebrate richness in our study.

Examining the relative importance of local- and regional-scale variables across a latitudinal gradient can enhance understanding of the key factors determining invasive species success and the resultant effects on community and ecosystem processes. While studies of *P. australis* within regions of our larger study area have documented a positive relationship between shoreline development and *P. australis* abundance (Bertness et al. 2002; Silliman and Bertness 2004), percent developed land was a relatively weak predictor of *P. australis* density and height across the sites and biogeographic scale examined here. However, the negative effects of leaf litter on *P. australis* and the associated plant community were consistent from a local-scale experiment (Holdredge et al. 2011) to our broad biogeographic survey. Thus, it is not simply that larger-scale variables are more important at larger spatial scales; rather, some local-scale variables (e.g., leaf litter, leaf C:N, sediment oxygen) are important across latitudinal scales. These results can inform the management of invasive *P. australis* by identifying a common suite of variables likely to be strongly associated with key population, community, and ecosystem processes.

Our study also illustrates the value of a biogeographic approach for understanding the establishment of latitudinal gradients in production and species richness. Latitude most strongly predicted *P. australis* density, but local- and regional-scale variables were also good predictors of *P. australis* density and height at our sampled subsites, consistent with other studies showing that both small- and large-scale factors shape biogeographic patterns (Gotelli et al. 2010; Gouhier



et al. 2010; McGill 2010). In addition, the direction of this relationship was the reverse of expectations based on the dominant native plant species *Spartina alterniflora* in these same coastal marsh habitats (Kirwan et al. 2009), suggesting that these two foundation plant species may respond differently to environmental variation across latitude, and/or that longer-term evolutionary processes are contributing to biogeographic patterns in *S. alterniflora*. Further, we show that invasive ecosystem engineers such as *P. australis*, which often shape the structure and function of communities and ecosystems, can alter the effects of latitudinal variables on community and ecosystem properties like species diversity. Thus, invasive engineering species may cause regional and biogeographic patterns that fundamentally differ from those of native species and/or non-engineering species.

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## References

- Berke SK, Jablonski D, Krug AZ, Valentine JW (2014) Origination and immigration drive latitudinal gradients in marine functional diversity. *PLoS ONE* 9:e101494
- Bertness MD, Ewanchuk PJ, Silliman BR (2002) Anthropogenic modification of New England salt marsh landscapes. *Proc Natl Acad Sci USA* 99:1395–1398
- Breiman L (2001) Random forests. *Mach Learn* 45:5–32
- Breiman L, Friedman J, Stone CJ, Olshen RA (1984) Classification and regression trees. Chapman and Hall, London
- Caplan JS, Wheaton CN, Mozdzer TJ (2014) Belowground advantages in construction costs facilitate a cryptic plant invasion. *AoB Plants* 6:plu020
- Christian JM, Wilson SD (1999) Long-term ecosystem impacts of an introduced grass in the northern Great Plains. *Ecology* 80:2397–2407
- Crain CM, Silliman BR, Bertness SL, Bertness MD (2004) Physical and biotic drivers of plant distribution across estuarine salinity gradients. *Ecology* 85:2539–2549
- Cronin JT, Bhattarai GP, Allen WJ, Meyerson LA (2015) Biogeography of a plant invasion: plant-herbivore interactions. *Ecology* 96:1115–1127
- Cutler DR, Edwards TC, Beard KH, Cutler A, Hess KT, Gibson J, Lawler JJ (2007) Random forests for classification in ecology. *Ecology* 88:2783–2792
- Dormann CF, Elith J, Bacher S, Buchmann C, Carl G, Carre G, Garcia Marquez JR, Gruber B, Lafourcade B, Leitao PJ, Munkemuller T, McClean C, Osborne PE, Reineking B, Schroder B, Skidmore AK, Zurell D, Lautenbach S (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36:27–46
- Fenbergh PB, Menge BA, Raimondi PT, Rivadeneira MM (2015) Biogeographic structure of the northeastern Pacific rocky intertidal: the role of upwelling and dispersal to drive patterns. *Ecography* 38:83–95
- Finke DL, Denno RF (2006) Spatial refuge from intraguild predation: implications for prey suppression and trophic cascades. *Oecologia* 149:265–275
- Gilchrist GW, Huey RB, Balanya J, Pascual M, Serra L (2004) A time series of evolution in action: a latitudinal cline in wing size in South American *Drosophila subobscura*. *Evolution* 58:768–780
- Gotelli NJ, Graves GR, Rahbek C (2010) Macroecological signals of species interactions in the Danish avifauna. *Proc Natl Acad Sci* 107:5030–5035
- Gouhier TC, Guichard F, Menge BA (2010) Ecological processes can synchronize marine population dynamics over continental scales. *Proc Natl Acad Sci* 107:8281–8286
- Grosholz ED, Levin LA, Tyler AC, Neira C (2009) Changes in community structure and ecosystem function following *Spartina alterniflora* invasion of Pacific estuaries. In: Silliman BR, Grosholz ED, Bertness MD (eds) Human impacts on salt marshes: a global perspective. University of California Press, Berkeley
- Guo W-Y, Lambertini C, Li X-Z, Meyerson LA, Brix H (2013) Invasion of Old World *Phragmites australis* in the New World: precipitation and temperature patterns combined with human influences redesign the invasive niche. *Glob Change Biol* 19:3406–3422
- Hillebrand H (2004) On the generality of the latitudinal diversity gradient. *Am Nat* 163:192–211
- Holdredge C, Bertness MD, Von Wettberg E, Silliman BR (2011) Nutrient enrichment enhances hidden differences in phenotype to drive a cryptic plant invasion. *Oikos* 119:1776–1784
- Homer CG et al (2015) National Land Cover Database for the conterminous United States—representing a decade of land cover change information. *Photogramm Eng Remote Sens* 81:345–354
- Howard J, Hoyt S, Isensee K, Telszewski M, Pidgeon E (eds) (2014) Coastal blue carbon: methods for assessing carbon stocks and emissions factors in mangroves, tidal salt marshes, and seagrasses. Conservation International, Intergovernmental Oceanographic Commission of UNESCO, International Union for Conservation of Nature. Arlington, VA
- Jones CG, Lawton JH, Shachak M (1996) Organisms as ecosystem engineers. In: Samson FB, Knopf FL (eds) Ecosystem management. Springer, New York, pp 130–147

- Kettenring KM, McCormick MK, Baron HM, Whigham DF (2011) Mechanisms of *Phragmites australis* invasion: feedbacks among genetic diversity, nutrients, and sexual reproduction. *J Appl Ecol* 48:1305–1313
- King RS, Deluca WV, Whigham DF, Marra PP (2007) Threshold effects of coastal urbanization on *Phragmites australis* (common reed) abundance and foliar nitrogen in Chesapeake Bay. *Estuaries Coasts* 30:469–481
- Kirwan ML, Guntenspergen GR, Morris JT (2009) Latitudinal trends in *Spartina alterniflora* productivity and the response of coastal marshes to global change. *Glob Change Biol* 15:1982–1989
- Kirwan ML, Guntenspergen GR, Langley JA (2014) Temperature sensitivity of organic-matter decay in tidal marshes. *Biogeosciences* 11:4801–4808
- Kleinhesselink AR, Magnoli SM, Cushman JH (2014) Shrubs as ecosystem engineers across an environmental gradient: effects on species richness and exotic plant invasion. *Oecologia* 175:1277–1290
- Lambertini C, Gustafsson MHG, Frydenberg J, Lissner J, Speranza M, Brix H (2006) A phylogeographic study of the cosmopolitan genus *Phragmites* (Poaceae) based on AFLPs. *Plant Syst Evol* 258:161–182
- Lambertini C, Mendelssohn IA, Gustafsson MHG, Olesen B, Riis T, Sorrell BK, Brix H (2012) Tracing the origin of the Gulf Coast *Phragmites* (Poaceae): a story of long-distance dispersal and hybridization. *Am J Bot* 99:538–551
- Lavergne S, Molofsky J (2010) Reed Canary Grass (*Phalaris arundinacea*) as a biological model in the study of plant invasions. *Crit Rev Plant Sci* 23:415–429
- Liao CZ, Luo YQ, Fang CM, Chen JK, Li B (2008) Litter pool sizes, decomposition, and nitrogen dynamics in *Spartina alterniflora*-invaded and native coastal marshlands of the Yangtze Estuary. *Oecologia* 156:589–600
- McCormick MK, Kettenring KM, Baron HM, Whigham DF (2010) Spread of invasive *Phragmites australis* in estuaries with differing degrees of development: genetic patterns, Allee effects, and interpretation. *J Ecol* 98:1369–1378
- McGill B (2010) Matters of scale. *Science* 328:575–576
- Meyerson LA (2000) Ecosystem-level effects of invasive species: a *Phragmites* case study in two freshwater tidal marsh ecosystems on the Connecticut River. Ph.D. Thesis, Yale University
- Meyerson LA, Cronin JT (2013) Evidence for multiple introductions of *Phragmites australis* to North America: detection of a new non-native haplotype. *Biol Invasions* 15:2605–2608
- Meyerson LA, Saltonstall K, Chambers RM, Silliman BR, Bertness MD, Strong D (2009) *Phragmites australis* in Eastern North America: a historical and ecological perspective. In: Silliman BR, Grosholz ED, Bertness MD (eds) *Human impacts on salt marshes: a global perspective*. University of California Press, Berkeley
- Middelburg JJ, Klaver G, Nieuwenhuize J, Wielemaker A, de Haas W, Vlug T, van der Nat JFWA (1996) Organic matter mineralization in intertidal sediments along an estuarine gradient. *Mar Ecol Prog Ser* 132:157–168
- Minchinton TE, Bertness MD (2003) Disturbance-mediated competition and the spread of *Phragmites australis* in a coastal marsh. *Ecol Appl* 13:1400–1416
- Minchinton TE, Simpson JC, Bertness MD (2006) Mechanisms of exclusion of native coastal marsh plants by an invasive grass. *J Ecol* 94:342–354
- Mozdzer TJ, Megonigal JP (2012) Jack-and-Master trait responses to elevated CO<sub>2</sub> and N: a comparison of native and introduced *Phragmites australis*. *PLoS ONE* 7:e42794
- Mozdzer TJ, Megonigal JP (2013) Increased methane emissions by an introduced *Phragmites australis* lineage under global change. *Wetlands* 33:609–615
- Mozdzer TJ, Zieman JC (2010) Ecophysiological differences between genetic lineages facilitate the invasion of non-native *Phragmites australis* in North American Atlantic coast wetlands. *J Ecol* 98:451–458
- Mozdzer TJ, Zieman JC, McGlathery KJ (2010) Nitrogen uptake by native and invasive temperate coastal macrophytes: importance of dissolved organic nitrogen. *Estuaries Coasts* 33:784–797
- Mozdzer TJ, McGlathery KJ, Mills AL, Zieman JC (2014) Latitudinal variation in the availability and use of dissolved organic nitrogen in Atlantic coast salt marshes. *Ecology* 95:3293–3303
- Neira C, Grosholz ED, Levin LA, Blake R (2006) Mechanisms generating modification of benthos following tidal flat invasion by a *Spartina* hybrid. *Ecol Appl* 16:1391–1404
- Neubauer SC, Miller WD, Anderson IC (2000) Carbon cycling in a tidal freshwater marsh ecosystem: a carbon gas flux study. *Mar Ecol Prog Ser* 199:13–30
- Pennings SC, Bertness MD (2001) Salt marsh communities. In: Bertness MD, Gaines SD, Hay ME (eds) *Marine community ecology*. Sinauer Associates, Sunderland
- Pennings SC, Silliman BR (2005) Linking biogeography and community ecology: latitudinal variation in plant-herbivore interaction strength. *Ecology* 86:2310–2319
- Pennings SC, Ho C-K, Salgado CS, Wieski K, Dave N, Kunza AE, Wason EL (2009) Latitudinal variation in herbivore pressure in Atlantic Coast salt marshes. *Ecology* 90:183–195
- Prasad AM, Iverson LR, Liaw A (2006) Newer classification and regression tree techniques: bagging and random forests for ecological prediction. *Ecosystems* 9:181–199
- R Development Core Team (2015) R: a language and environment for statistical computing. Vienna, Austria
- Rohde K (1992) Latitudinal gradients in species diversity: the search for the primary cause. *Oikos* 65:514–527
- Romero GQ, Goncalves-Souza T, Vieira C, Koricheva J (2014) Ecosystem engineering effects on species diversity across ecosystems: a meta-analysis. *Biol Rev*. doi:10.1111/brv.12138
- Rooth JE, Stevenson JC, Cornwell JC (2003) Increased sediment accretion rates following invasion by *Phragmites australis*: the role of litter. *Estuaries* 26:475–483
- Saltonstall K (2002) Cryptic invasion by a non-native genotype of the common reed, *Phragmites australis* into North America. *Proc Natl Acad Sci USA* 99:2445–2449
- Saltonstall K (2003) Microsatellite variation within and among North American lineages of *Phragmites australis*. *Mol Ecol* 12:1689–1702
- Sax DF, Stachowicz JJ, Gaines SD (eds) (2005) *Species invasions: insights into ecology, evolution, and biogeography*. Sinauer Associates, Sunderland

- Schemske DW, Mittelbach GG, Cornell HV, Sobel JM, Roy K (2009) Is there a latitudinal gradient in the importance of biotic interactions? *Annu Rev Ecol Evol Syst* 40:245–269
- Silliman BR, Bertness MD (2004) Shoreline development drives invasion of *Phragmites australis* and the loss of plant diversity in New England salt marshes. *Conserv Biol* 18:1424–1434
- Simley J, Doumbouya A (2012) National hydrography dataset—linear referencing. US Geological Survey Fact Sheet 3068
- Strayer DL, Beighley RE, Thomopson LC, Brooks S, Nilsson C, Pinay G, Naiman RJ (2003) Effects of land cover on stream ecosystems: roles of empirical models and scaling issues. *Ecosystems* 6:407–423
- Tilman D, Reich PB, Knops J, Wedin D, Mielke T, Lehman C (2001) Diversity and productivity in a long-term grassland experiment. *Science* 294:843–845
- Turner RE (1976) Geographic variations in salt marsh macrophyte production: a review. *Contrib Mar Sci* 20:47–68
- Vitousek PM, Walker LR (1989) Biological invasion by *Myrica faya* in Hawaii: plant demography, nitrogen fixation, ecosystem effects. *Ecol Monogr* 59:247–265
- Warren RS, Fell PE, Grimsby JL, Buck EL, Rilling GC, Fertik RA (2001) Rates, patterns, and impacts of *Phragmites australis* expansion and effects of experimental *Phragmites* control on vegetation, macroinvertebrates, and fish within tidelands of the lower Connecticut River. *Estuaries* 24:90–107
- Willig MR, Kaufman DM, Stevens RD (2003) Latitudinal gradients of biodiversity: pattern, process, scale and synthesis. *Annu Rev Ecol Evol Syst* 34:273–309
- Windham L (2001) Comparison of biomass production and decomposition between *Phragmites australis* (Common Reed) and *Spartina patens* (Salt Hay Grass) in brackish tidal marshes of New Jersey, USA. *Wetlands* 21:179–188
- Windham L, Ehrenfeld JG (2003) Net impact of a plant invasion on nitrogen-cycling processes within a brackish tidal marsh. *Ecol Appl* 13:883–896
- Windham L, Lathrop RG Jr (1999) Effects of *Phragmites australis* (Common Reed) invasion on aboveground biomass and soil properties in brackish tidal marsh of the Mullica River, New Jersey. *Estuaries* 22:927–935
- Wright JP, Jones CG (2004) Predicting effects of ecosystem engineers on patch-scale species richness from primary productivity. *Ecology* 85:2071–2081
- Zhang D, Hui D, Luo Y, Zhou G (2008) Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. *J Plant Ecol* 1:85–93