

Original Articles

Modeling spatial and temporal dynamics of plant species richness across tidal creeks in a temperate salt marsh

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ABSTRACT

In salt marsh ecology, various indicators, including environmental, biological, and anthropogenic factors, have been used to predict the patterns of plant species richness. The potential impact of spatial autocorrelation on this prediction, however, has yet to receive much attention. In this paper, two sets of regression models were developed to predict spatial patterns (in 2006) and temporal changes (from 2006 to 2012) of richness across selected tidal creeks at a Danish salt marsh: (1) traditional ordinary least squares (OLS) using soil and topographic parameters as independent variables and (2) spatial regressions in which spatial filters produced by spatial eigenvector mapping were included into the non-spatial OLS as additional independent variables. Such incorporation led to a general improvement of model outcomes, that is, increases in R^2 and decreases in both Akaike's information criterion and residual autocorrelation. Notably, only spatial filters were always significant independent variables for both the spatial and temporal dynamics of species richness. In contrast, no environmental variables were consistently significant because of the substantial reduction in their regression coefficients after spatial regression. These results imply that identifying the relevant indicators of richness patterns in salt marshes may be a much more complicated job than previously thought. By revealing the new and statistically more rigorous predictive power of these environmental (i.e., non-spatial) variables, the spatially explicit modeling employed in this paper will provide benefits to the literature on ecological indicators.

1. Introduction

Over the past three decades, ecologists have made substantial progress in the study of environmental, biological, and anthropogenic factors that potentially influence the patterns of plant species richness in salt marshes (Gough et al., 1994; Grace and Pugeseck, 1997; Ungar, 1998; Silliman and Bertness, 2004; Suchrow et al., 2015). These factors include, but are not limited to, surface elevation (Sánchez et al., 1996; Funk et al., 2004; Suchrow and Jensen, 2010), salinity (Brewer et al., 1997; Silvestri et al., 2005), disturbance (Valiela and Rietsma, 1995), herbivory (Andresen et al., 1990; Kiehl et al., 1996; Olf and Ritchie, 1998), biomass productivity (Moore and Keddy, 1989; García et al., 1993), biotic interactions (Hacker and Bertness, 1999; Ewanchuk and Bertness, 2004), and restoration (Mossman et al., 2012). These components, often treated as independent variables in the regression framework, have proven to be significant indicators of species richness (i.e., a dependent variable) across many different salt marsh systems. In contrast, in this paper, I explicitly address two underrepresented topics in this line of research: (1) incorporation of spatial variables into species richness modeling and (2) investigation of changing species richness through time (hereafter, Δ richness).

First, most of the studies mentioned above, whether conducted at local or regional scales, are concerned with *spatial* data (i.e., vegetation plots are distributed across space). In such a case, both independent and dependent variables that are involved in the associated modeling are most likely to possess inherent spatial autocorrelation with varying degrees (Legendre, 1993; Franklin, 2009). This is because, for example, the dispersal of seeds and the movement of moisture, nutrients, and sediments from one location to another are all spatially diffusive processes, making the biological and physical conditions of different sites more related (or dependent) than expected by chance. Spatial autocorrelation is widely known to profoundly affect the outcomes of ecological and biogeographical modeling, and hence, there have been considerable efforts to account for such impacts in statistically appropriate ways (Araújo and Guisan, 2006; Guisan et al., 2006; Austin, 2007; Dormann, 2007; Dray et al., 2012; Miralha and Kim, 2018). One possible approach of this sort, which has increasingly been used in the last 15 years, though not in salt marsh ecology yet, is to include spatial terms (e.g., trend surface, autocovariate, and spatial filter) as additional independent variables into traditional species distribution modeling (Borcard and Legendre, 2002; Lichstein et al., 2002; Miller et al., 2007; Kim and Shin, 2016; Malanson et al., 2017).

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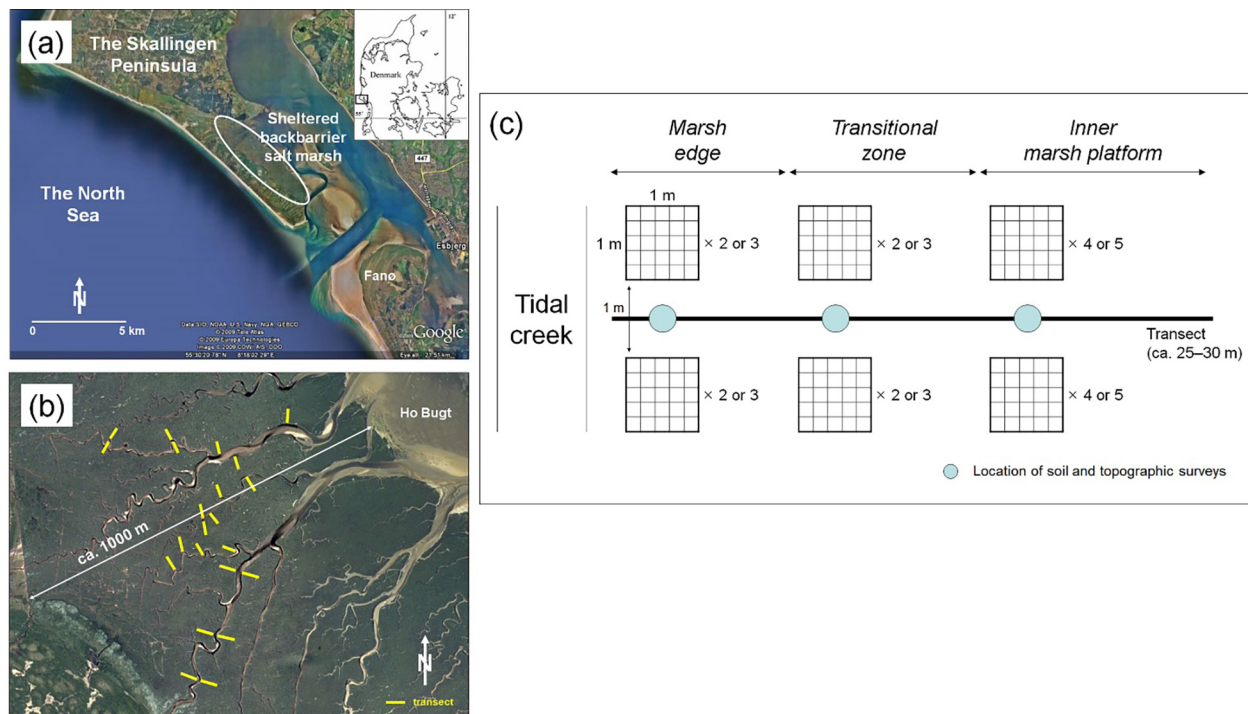


Fig. 1. (a) Geographic location of the study site, the Skallingen salt marsh in southwestern Denmark. (b) Twenty-two transects established across various tidal creeks of the marsh. (c) Field design for vegetation, soil, and topographic surveys.

Second, whereas many advances have been made in identifying the spatial patterns and determinants of species richness at a point in time, the same identification has rarely been attempted for Δ richness over a given period. Predicting how species richness changes is a timely task in salt marsh ecology, especially in this era of rapid climate change, the melting of polar ice, and development pressure by humans (Morris et al., 2002; Scavia et al., 2002; Craft et al., 2009; Feagin et al., 2010; Kirwan et al., 2010). In particular, it should be a high priority to perform a detailed survey on the patterns of Δ richness across a wide range of environmental gradients within a marsh to facilitate an informed prediction of the circumstances under which an increase or reduction in richness is likely (e.g., Wanner et al., 2014).

The purpose of this paper was to predict plant species richness and its change over time (Δ richness) using environmental and spatial factors across various selected tidal channels at a temperate salt marsh of the Danish Wadden Sea. I hereby performed a set of traditional (non-spatial) regression and spatial regression (see Section 3.5), the latter explicitly incorporating the presence and effect of spatial autocorrelation. Then, the outcomes of these two approaches were compared to address the following questions:

- (1) What is the relative importance of environmental and spatial factors to species richness and Δ richness? Is the influence of spatial factors on richness patterns negligible enough to justify past studies that did not explicitly consider the potential impact of spatial autocorrelation within models?
- (2) Comparing the original partial regression coefficients (i.e., β values of environmental variables) yielded by non-spatial regression and the new coefficients produced by spatial regression, are there noticeable differences between the two groups? Again, is the influence of spatial factors so negligible that the predictive power of the environmental variables exhibit minimal shifts before and after spatial regression?

2. Statistical and ecological background

One critical issue, arising from the presence of spatial autocorrelation in the data used for species–environment modeling, is the violation of the assumption of independently and identically distributed errors (Cliff and Ord, 1972; Griffith, 2000). If ignored, this will further induce an underestimation of the standard errors, inflating the Type I error rate (Legendre, 1993; Lichstein et al., 2002; Anselin, 2003). Moreover, one is most likely to observe a bias in the resulting model estimates, such as the coefficient of determination (R^2), F -statistic, and partial regression coefficients. Taken together, these side effects prevent a proper interpretation of ecological patterns and associated processes. For more statistical explanations of this kind, see Legendre (1993), Griffith (2003), and Dormann et al. (2007, 2013).

To produce the spatial factors to be included in spatial regression, spatial eigenvector mapping (SEVM) was employed in this research (Griffith, 2003; Dray et al., 2006; Rangel et al., 2010; Thayn and Simanis, 2013). The power of SEVM lies in its capability of characterizing spatial autocorrelation at multiple scales simultaneously, as evidenced by many successful applications in macroecology and biogeography (Diniz-Filho and Bini, 2005; de Marco et al., 2008; Peres-Neto and Legendre, 2010; Gouveia et al., 2013; Bailly et al., 2016). This aspect is certainly a benefit to this paper because the structure of environment and species data can originate from different sources of spatial autocorrelation, each detected at a distinct scale (Borcard and Legendre, 2002; Griffith, 2003; Václavík et al., 2012; Kim and Shin, 2016). At small spatial scales, spatial autocorrelation can be driven by, for example, contagious biological processes, including short-range propagule dispersal, vegetative reproduction, disturbance history, and inter-species competition (Callaway and Josselyn, 1992; Rand, 2000; Pennings et al., 2005; Silvestri et al., 2005; McKee and Rooth, 2008). At larger scales, exogenous environmental factors, such as sea-level variations, fluvial-geomorphic creek processes, and managed coastal realignment, should be dominant controls on the spatial structure of diversity and composition because the associated water flow can actively exchange materials and energy among localities (Warren and Niering,

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