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State-Space Modeling Indicates Rapid Invasion of an Alien Shrub in Coastal Dunes

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ABSTRACT

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Invasion by alien plants has negative effects on coastal dunes. Monitoring local spread of invasive species depends on long-term data with sufficient spatial resolution. Bayesian state-space models are a new method for monitoring invasive plants based on unbalanced permanent-plot data. The method allows separation of process and sampling variance, thus enabling ecological predictions with a known degree of uncertainty. The method is applied for the invasive shrub *Rosa rugosa* (Japanese rose) in Danish fixed dunes. The probability of observing *R. rugosa* increased significantly from 0.18 to 0.28 during the period 2004–2007. The species was found in all Danish coastal regions, albeit slightly less common in northern Denmark. We discuss the advantages and limitations of using Bayesian state-space models for monitoring and predicting plant invasions using presence–absence data.

ADDITIONAL INDEX WORDS: *Denmark, invasive alien plant, monitoring, permanent plots,* Rosa rugosa*, time-series analysis.*

INTRODUCTION

Coastal dunes are endangered ecosystems in many countries (Martínez and Psuty, 2004), and dune biodiversity is negatively affected by coastal protection, forestation, eutrophication, and recreation (Grunewald, 2006; Jones *et al.*, 2004; Oliveira and Souza, 2009; Remke *et al.*, 2009). During the past decades, there has been a documented loss of open species-rich dune vegetation and a widespread invasion by tall grasses and woody species (Lamoot, Meert, and Hoffmann, 2005; Veer and Kooijman, 1997). In some regions, alien species have been planted to stabilize dunes, and these plants have subsequently become invasive, *e.g.*, *Ammophila arenaria* in California, and *Pinus nigra* at Lake Michigan (Leege and Murphy, 2001; Wiedemann and Pickart, 1996). Coastal dunes are more susceptible to plant invasions under nutrient-rich conditions and changed disturbance regime (Acosta, Carranza, and Izzi, 2008; Kim, 2005; Rodgers and Parker, 2003).

Invasive alien plants have become a problem for coastal ecosystems (*e.g.*, Bar, Cohen, and Shoshany, 2004; Kollmann *et al.*, 2009) because of their negative effects on biodiversity and ecosystem services (Nentwig, 2007). The disentangling of interactive effects of land use change, eutrophication, reduced dune dynamics, and plant invasions is an active field of coastal research and management, but more studies are needed on monitoring the invasion process over long periods (Strayer *et al.*, 2006). On regional or continental scales, the invasion history of plants species can be reconstructed using herbarium records (Fuentes *et al.*, 2008; Mihulka and Pyšek, 2001), but few studies exist on long-term patterns of local spread based on permanent plots (*e.g.*, Foxcroft *et al.*, 2004). This method would be more accurate than using aerial photographs (Buell, Pickart, and Stuart, 1995), but it has the problem of small and often unbalanced sample size. Thus, new analytical approaches are needed to deal with this problem.

A significant proportion of the northwestern European dunes are situated in Denmark, primarily along the west coast (Doody, 1994), and Denmark hosts 20% of the total dune area in northern Europe. One of the most obvious threats, especially to coastal fixed dunes, is invasion by alien trees and shrubs, particularly *Pinus mugo* and *Rosa rugosa* (Thiele, Kollmann,

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and Andersen, 2009). *Rosa rugosa* constitutes a considerable threat to dune habitats, because it suppresses natural vegetation of high conservation value (Isermann, 2008a, 2008b). The shrub has been a popular ornamental in gardens and parks, and only recently its problematic traits have been identified (Bruun, 2005). To improve local control efforts, it is urgent to analyze *R. rugosa* invasions in coastal dunes as done by Jørgensen and Kollmann (2009) on a landscape scale using aerial photographs, whereas no regional analysis exists on the invasion rate of the species based on permanent plots.

This study suggests Bayesian state-space models as a new method for monitoring the spread of invasive plants based on unbalanced plot data (Clark and Bjørnstad, 2004). This approach for reconstructing the regional spread of invasive species is applied for the first time using the instructive example of *R. rugosa* in Danish fixed dunes. More specifically, the rate of local spread in dunes is measured by the annual increase in the probability of observing the species in a plot. In addition, the regional distribution of the species in Danish coastal dunes is described.

MATERIALS AND METHODS

Study Species

Rosa rugosa Thunb. (Rosaceae) is a multistemmed deciduous shrub forming dense, 1- to 2-m-tall stands. *Rosa rugosa* shrubs have a lateral clonal spread rate of 0.4 to 0.5 m year^{-1} (Kollmann *et al.*, 2009) due to suckers that develop from rhizomes or roots, and rhizome fragments are a potential mode of dispersal. In addition to vegetative dispersal, seeds are effectively spread by birds and water, while the seed bank of the species is short lived; for a review, see Bruun (2005).

Rosa rugosa was introduced to Europe from East Asia between the late-19th century and mid-20th century. In the 1950s, it became a popular ornamental around summer houses, roads, and parking places due to its resistance to wind and its tolerance of nutrient-poor soil conditions (Bruun, 2005). More recently, the species has invaded species-rich coastal ecosystems in northwestern Europe, transforming them into monospecific scrub with reduced biodiversity (Isermann, 2008a, 2008b).

Within the past decades, the distribution and local cover of *R. rugosa* have increased markedly along the Danish coast (*e.g.*, Kollmann *et al.*, 2009). Still, little quantitative information is available at a national scale. Based on aerial photographs of a coastal heath in Denmark, Didriksen (1999) found that *R. rugosa* had spread from a few patches to a more or less contiguous cover of 3.5 ha within less than 50 years, most likely by means of clonal growth. Distribution of the species is positively correlated with houses, roads, and tracks (Jacobsen and Ejrnæs, 2004; Jørgensen and Kollmann, 2009). However, seeding and transplant experiments have shown that *R. rugosa* is able to establish in all dune communities once seeds have arrived, and small-scale soil disturbance promotes seedling emergence and survival (Kollmann *et al.*, 2007).

Distribution Data

The distribution data on *R. rugosa* were collected from 2004 to 2007 as part of a national Danish monitoring scheme on trends in biodiversity (Svendsen *et al.*, 2005), including 574 permanent plots from 40 coastal sites (Figure 1). The sites were randomly selected, albeit stratified with respect to size and quality of habitat types in Denmark. The sites used within this study are those within the category "fixed dunes with herbaceous vegetation" (EU habitat code 2130). At each site, 20 to 60 circular plots with a 5-m radius (78.9 m^2) were randomly placed in 2004; the plots were revisited in the following 3 years within global positioning system accuracy (<10 m), and presence–absence of all vascular plants was recorded. In total, 2199 plot surveys were included, with 491 plots recorded four times, 69 plots recorded three times, and 14 plots recorded twice.

The aim of the present study was to predict local spread of the invasive alien *R. rugosa*. In 26 of the 40 sites, *R. rugosa* was not observed in any plot sampled during the 4-year monitoring period; thus, these sites were omitted from the time-series analysis (Figure 1). The data from the 14 sites with *R. rugosa* were somewhat irregular; in 2 sites the permanent plots were only sampled in 3 of the 4 years, and the number of plots varied both across sites and years. The uneven numbers reflect that in some sites only few plots qualified for the habitat type studied.

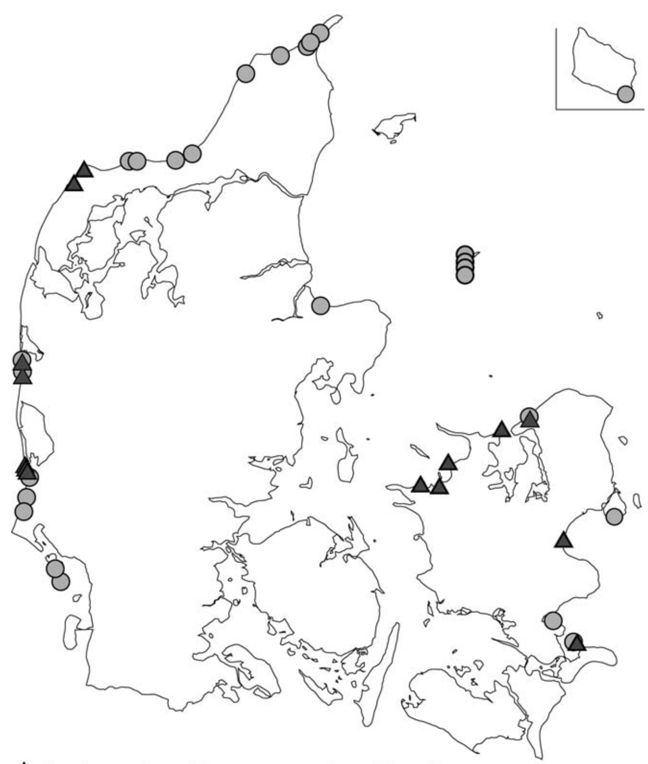

Figure 1. Map of the 40 coastal monitoring sites in Denmark situated in fixed dunes with herbaceous vegetation (EU habitat code 2130). In 14 sites, the invasive shrub *Rosa rugosa* was recorded in at least one of the sample plots during 2004–2007; in the remaining 26 sites, the plant was not recorded in the study period.

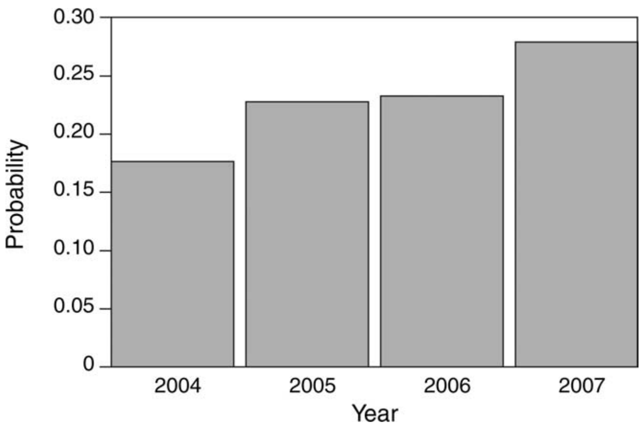

Figure 2. Mean probabilities of observing *Rosa rugosa* in 574 plots sampled in coastal dunes in Denmark from 2004 to 2007.

State-Space Modeling

Since the data structure was irregular (as in many other field studies), it was decided to model the change in probability of observing a *R. rugosa* plant using a Bayesian state-space model, where the probability of species presence in a plot at a specific site is modeled by a latent variable. The state-space modeling approach is not sensitive to missing values in the time series (Clark and Bjørnstad, 2004). Furthermore, it is possible to separate the observed variance into the sampling variance and the (more interesting) variance of the annual change of the probability of observing *R. rugosa*.

The probability of observing a *R. rugosa* plant in a plot at site i and time t was calculated by the latent variables $X_{i,t}$, and the observed event at site i in plot j at time t was denoted by $Y_{i,j,t}$. If a *R. rugosa* plant was recorded at site i in plot j at time t, then $Y_{i,j,t} = 1$; otherwise, $Y_{i,j,t} = 0$. The change in the probability of observing *R. rugosa* was then modeled using a state-space model.

It was assumed that all sites had a similar change in the logit-transformed probability of observing a *R. rugosa* plant during the years and that the change in the logit-transformed probability was normally distributed, *i.e.*,

$$\text{logit}(X_{i,t}) = \text{logit}(X_{i,t-1}) + \alpha + \varepsilon, \text{ with } \varepsilon \sim N(0, \sigma^2) \quad (1)$$

where α is the mean annual change and σ^2 is the variance of the annual change. The events of observing a *R. rugosa* plant at site i in plot j at time t was assumed to be Bernoulli distributed with the probability parameter $X_{i,t}$, *i.e.*,

$$Y_{i,j,t} \sim \text{Bernoulli}(X_{i,t}) \quad (2)$$

The model was parameterized using numerical Bayesian methods, where the joint posterior distribution of the two parameters of interest, α and σ, and all the latent variables, $X_{i,t}$, was calculated using a Markov chain Monte Carlo method (MCMC) with a Metropolis-Hastings algorithm (Carlin and Louis, 1996). A multivariate normal candidate distribution was used, including a MCMC run of 100,000 iterations with a burn-in period of 1000 iterations. The prior distributions of all parameters and latent variables were assumed to be uniformly distributed in their domains, except for σ, which was assumed to be larger than 0.05 to ensure adequate mixing properties of the sample of the posterior distribution. Plots of the sampling chains of all parameters and latent variables were inspected to check the mixing properties of the sampling procedure used.

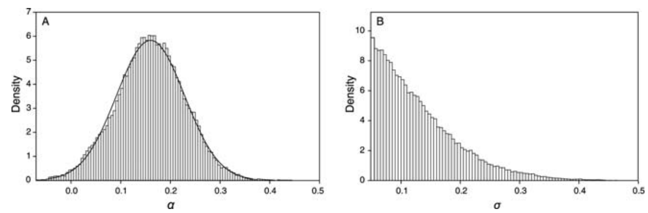

Figure 3. Marginal posterior distribution of the mean (A, with fitted normal distribution), and standard deviation (B) of annual change in logit-transformed probabilities of observing *Rosa rugosa* in coastal dunes.

RESULTS

Changes in Invasion

The mean probability of observing *R. rugosa* in a 79-m^2 plot increased from 0.18 to 0.28 during the 4 years for all fixed dune sites (Figure 2). When the hierarchical sampling design was taken into account using the state-space model, the estimated annual change in probability of observing *R. rugosa* in a plot was significantly higher than zero ($p = 0.011$). The estimated marginal posterior distributions of the mean (α) and the standard deviation (σ) of the annual change in the logit-transformed probabilities are shown in Figure 3. The 95% credible interval of the annual change was 0.024 to 0.292, and the estimated mean and standard deviation of the annual change were of the same order, *i.e.*, the median coefficient of variation was 0.73.

Regional Distribution

Rosa rugosa was found in all Danish coastal regions (Figure 1). However, the regional absence–presence pattern indicates that the species was less common in northern Denmark (18%; found in 2 of 11 sites), compared with western and eastern Denmark (41%; 5 of 12 sites and 7 of 17 sites, respectively).

DISCUSSION

Bayesian state-space models are suitable for dealing with unbalanced historical data as used in this methodological study since the estimated parameters of interest (α and σ) are not influenced by irregular data structure (Clark and Bjørnstad, 2004). Furthermore, the method allows separation of process and sampling variance, which enables ecological predictions with a known degree of uncertainty (Clark, 2007). Thus, we could make for the first time predictions of the annual change of an invasive species at a specific site, including an evaluation of the uncertainty. For example, if the probability of observing the invasive *R. rugosa* in a plot is 0.2, then this probability is expected to have increased to 0.23 in 1 year, with a 95% credible interval between 0.18 and 0.29. We recommend state-space models for similar investigations of biodiversity change in coastal habitats based on time series of plot data.

The regional distribution patterns of *R. rugosa* support the results by Thiele, Kollmann, and Andersen (2009) for Danish inland sites, showing that it is the most common invasive alien plant species in the country. The lower frequency in northern Denmark might be related to potential negative effects of a harsher regional climate (*cf.* Bruun, 2005), although the species is able to regenerate from seedlings in the dune habitats of this region (Kollmann *et al.*, 2007). Another explanation might be that the dune areas in northern Denmark are larger and more remote from roads, tracks, or houses (*cf.* Jørgensen and Kollmann, 2009).

A recent review by Pyšek and Hulme (2005) described rates in spread of invasive species. Comparing with these data it is surprising that the local spread of *R. rugosa* is so fast that it can be detected by the rather insensitive method used in this study within a period of only 4 years. The success might be due to a combination of efficient seed dispersal (Bruun, 2005), a positive response of seedling establishment to small-scale disturbance and soil nutrients (Kollmann *et al.*, 2007), and efficient lateral clonal growth (Kollmann *et al.*, 2009). The rapid expansion of the species suggests further research into the mechanisms of the colonization process and into possible ecological factors promoting or counteracting the invasion. Long-term monitoring of the spread of *R. rugosa* and new experiments are necessary to understand direct and indirect effects of global warming and the consequences of changed dune dynamics, including grazing by large herbivores. Although management of the species is difficult (Kollmann *et al.*, in press), immediate and appropriate control measures have to be developed based on best knowledge on the biology of *R. rugosa* to benefit conservation of coastal dunes in a changing world.

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