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Spatial prediction of invasion success across heterogeneous landscapes using an individual-based model

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Abstract

The limited resources available for managing invasive plant species in native ecosystems and the magnitude of the problem make it essential that we develop methods to prioritize sites for management efforts. We used the individual-based simulation model ECOTONE in conjunction with climate and soil texture data to identify grassland site types where the invasive perennial forb *Acroptilon repens* is likely to be successful, and to create a threat map indicating the most vulnerable regions of Colorado. *Acroptilon repens* has the potential to become most abundant in dry areas with fine-textured soils. This information can be used to direct management efforts towards the areas at greatest risk, allowing the most effective use of limited resources. The most common approach for identifying invasible regions has been to extrapolate from the locations of existing invasions to find similar sites. Two major drawbacks to this method are the lack of consideration of the role of the existing plant community in inhibiting or facilitating invasion, and the assumption that the invading species is at equilibrium with the environment. The combination of an individual-based simulation model and a geographic information system provides a flexible tool to investigate the community and regional dynamics of invasive plant species.

Introduction

Limited resources are available for the control of invasive species. Given this constraint, it is necessary to allocate scarce resources where they will be the most effective. One approach is to focus most monitoring efforts on site types where a given species is likely to be successful, and spend less effort on areas where it will not do well. Predictions of potential geographic distributions of invasive species have been almost entirely based on climatic variables, using logistic regression to identify environmental envelopes for particular species which can be used to identify their potential ranges in novel areas (e.g., Panetta and Dodd 1987; Franklin 1995; Higgins et al. 1999). This approach has two main drawbacks. First, it assumes that existing invasion sites represent the entire range of sites that can be occupied by the target species. If the range of a species is still actively expanding, this is unlikely to be a valid assumption. The other limitation of envelope methods is that they do not incorporate any information about native plant communities. Competition between native and introduced species can act to limit the spread of the invader.

An alternative approach is to use a simulation model to identify suitable site types, and then use that information with a geographic information system (GIS) to identify similar site types on the landscape. An individual-based simulation model incorporates traits of the invasive species, characteristics of the existing plant community and abiotic factors. Simulation modeling is a flexible tool that can be used to study both current and potential invasive species over a wide range of environmental conditions and plant community types. Equivalent experimental field studies are very difficult, and may involve the risk of increasing the range of the invasive species (Mack 1996).

Although simulation modeling can produce range maps similar to those resulting from logistic regression of environmental envelopes, it is a much more sophisticated tool. In particular, it avoids the problems inherent in extrapolating from known infestations, such as the bias towards identified habitat types, and can include the effects of ecological factors such as competition and disturbance (Chicoine et al. 1986; Higgins et al. 1999). Simulation modeling also avoids the often invalid equilibrium assumption necessary to extrapolate from current to future distributions. Modeling provides a dynamic response, so that if environmental conditions or the species present change, the results will change accordingly. Simulation modeling can be used to predict future dynamics, and can be used to generate testable hypotheses about key processes or abiotic factors affecting invasion. Simulation modeling may not be an appropriate tool in every case, since effective use requires extensive knowledge about the autecology and physiology of both the introduced and native species. The applicability of the results depends on the accuracy of this information as well as the spatial resolution of available data on soils, climate and other important environmental variables.

We illustrate the simulation modeling approach using a version of the ECOTONE model (Peters and Herrick 2001; Peters 2002) that has been modified to simulate the dynamics of the extremely invasive forb *Acroptilon repens* (L.) DC. (Goslee et al. 2001). *Acroptilon repens* is a long-lived perennial with the ability to form dense stable monocultures. This species has become a serious problem in grasslands of the western US and Canada since its introduction from Eurasia in contaminated alfalfa seed during the early 1900s (Rogers 1928; Watson 1980; Roché and Roché 1988, 1991). *Acroptilon repens* is probably not dispersal limited in Colorado because it was introduced a century ago and dispersed widely in agricultural seed. Like many other invasive species, *A. repens* can suppress the growth of both crop species and native grasses, resulting in economic losses and decreases in biodiversity. Allelopathy has been implicated in the success of this species (Stevens 1986; Kelsey and Bedunah 1989; Goslee et al. 2001; Grant et al. 2003).

Our objectives were: (1) to use simulation modeling to identify the site types where *Acroptilon repens* is able to succeed based on soil texture, climate and the native plant community, and (2) to create a coarse-scale threat map identifying the locations of these site types across Colorado. This information can be used to direct management efforts towards the areas at greatest risk, allowing the most effective use of limited resources, and as the background for more intensive research at a finer spatial scale.

Materials and methods

The most accurate approach would be to simulate each GIS grid cell individually. Unfortunately, the ECOTONE model requires daily weather data for long periods to calibrate the weather simulator, and these data are neither available for all grid cells nor accurately extrapolated across large regions. An intermediate regression step is needed to expand the model results to large areas because the data necessary to model each grid cell directly are not available. The general procedure involves first choosing representative site types from the range of environmental conditions present in Colorado. An individual-based simulation model is used to predict the percentage of the biomass of an invasive species on each of the existing site types. Regression (linear or nonlinear as appropriate) is then used to relate predicted success from the model output to environmental variables for which data are available over the entire geographic area of interest. Finally, the GIS database provides the spatially-referenced information needed to create a map predicting invasion success across a region.

Simulation model

ECOTONE is an individual-based below-ground gap dynamics model developed for arid and semiarid grasslands and shrublands, and has been modified for use with allelopathic invasive species (Peters and Herrick 2001; Goslee et al. 2001; Peters 2002). This model simulates recruitment, growth and mortality of each plant on a small plot (0.12 m^2) at an annual timestep. Recruitment probability is determined by the relative availability of seeds of each species. Growth is determined by competition for water by soil layer among plants on a daily timestep, and aggregated to grow plants annually. Probability of mortality depends on species longevity and slow growth constraints for each individual. Driving variables include daily precipitation and temperature and soil texture. The focus of the model is on water availability because of its importance for semiarid systems in Colorado. Further details are provided in Peters (2002); Goslee et al. (2001) describe the allelopathic component.

The major species parameters for ECOTONE include maximum growth rate, photosynthetic pathway and associated traits such as water-use efficiency, maximum plant biomass and aboveground and belowground biomass distributions. Model parameters for 15 plant functional groups common to the grasslands of Colorado were derived from previous research and from the literature, and are described in detail in Goslee et al. (2001).

Representative site types

We located Colorado weather stations with a continuous record of daily precipitation and temperature for the past 30 years, a time period sufficient to generate long-term weather data using first-order Markov analysis (Colorado Climate Center 2001). After eliminating all areas of the state which receive > 50 cm of precipitation per year, the approximate limit of grassland ecosystems in Colorado, we had 132 stations available. For each weather station, we simulated *Acroptilon repens* invasion over a 250-year timespan on four soil textures that represent commonly occurring soils in the state (USDA 1993): clay (58% clay, 22% sand), clay loam (34% clay, 32% sand), loam (18% clay, 43% sand) and loamy sand (6% clay, 82% sand). Soil layer structure was the same as used in Goslee et al. (2001), and soil texture was assumed to be the same for all layers. The same set of plant functional groups was used for each soil texture and weather station. We had a total of 528 separate parameter sets (132 weather stations $\times$ four soil texture classes).

Each parameter set was used for 25 replicate model runs, each of 250 years of different simulated weather. Replicate runs are needed because recruitment and mortality have stochastic elements. To avoid bias associated with initial conditions, all plots started with no vegetative cover. The model output contained above- and belowground biomass for each species in each year. Because we were interested in long-term invasion success, we chose to summarize these results using the mean percentage of *A. repens* aboveground biomass during the last 50 years of the simulation, the time at which the initially bare plot has reached a pseudo-equilibrium (*sensu* Shugart 1984). The combination of long simulations and initially bare plots allowed us to identify site types with physical conditions where *A. repens* is expected to become established and grow, and where it can compete successfully with native species over many years.

Map creation

Linear regression analysis related simulated percentage *A. repens* biomass to mean annual temperature and total annual precipitation individually and in combination for each soil texture class (S-Plus 3.4; Insightful, Inc.). Three different regression models, mean annual temperature only, annual precipitation only, and temperature and precipitation with an interaction term, were fitted. If detailed weather input parameters had been available for all locations in Colorado, the entire state could have been simulated directly and this step would not have been required.

Our GIS database for Colorado contained soil texture and climate data. We extracted soil texture data (percentage sand, silt and clay) from

Table 1. Analysis of variance results for simulated percentage *A. repens* aboveground biomass against percentage soil clay, mean annual temperature and annual precipitation.

	df	Sum of Sq	Mean Sq	*F* value	Pr (*F*)
Clay	1	2629547	2629547	24185.45	0.0000
Precipitation	1	507386	507386	4666.72	0.0000
Temperature	1	137128	137128	1261.25	0.0000
Residuals	11696	1271640	109		

STATSGO soils maps (USDA 1991). PRISM temperature and precipitation maps for Colorado were used as a source for minimum and maximum monthly temperature and monthly precipitation, which were used to calculate annual averages and totals (Daly et al. 1994). All GIS data were imported into ArcInfo (ArcInfo 7.2, ESRI, Inc), and rescaled to a consistent pixel size (5 km). The best-fit linear regression equation describing simulated *A. repens* biomass for each soil texture class was used within ArcInfo to create a map of Colorado indicating the predicted *A. repens* percentage biomass for each grid cell.

Model testing

The model was tested for *A. repens* in eastern Colorado as part of previous work (Goslee et al. 2001). Although formal sensitivity analyses were not conducted, preliminary analyses suggest that model output is most sensitive to parameters associated with competition for water. However, changing these parameters within a reasonable range of values did not change the results presented here. Results of the simulation model were compared to known *A. repens* locations. A survey of state county extension agents and weed supervisors identified 528 locations in Colorado where *A. repens* is found (Goslee et al. 2003). Cover data were not available for these sites. All locations were incorporated into the GIS database for comparison with the simulation results.

Results

Prediction of A. repens *abundance*

ECOTONE predicted a wide range of *A. repens* success across Colorado, from 3.4 to 99.6% of the total aboveground plant biomass, with a median value of 44%. The performance of *A. repens* was related to all three environmental factors chosen for analysis (Table 1). Soil clay content showed the strongest effect on *A. repens* percentage biomass, followed by precipitation and temperature. The percentage of *A. repens* biomass was highest at low precipitations and high temperatures. Simulated percentage biomass was significantly different among the four soil classes (Figure 1). *Acroptilon repens* was most abundant on fine-textured soils (clay and clay loam). Success of *A. repens* on clay and clay loam soils was more variable than success of coarser-textured loam and loamy sand soils.

Development of threat map

Of the three regression models tested, the interaction models had the greatest explanatory power. A separate regression equation was calculated for each soil texture class, and used with the GIS soil and climate data to create the threat map for

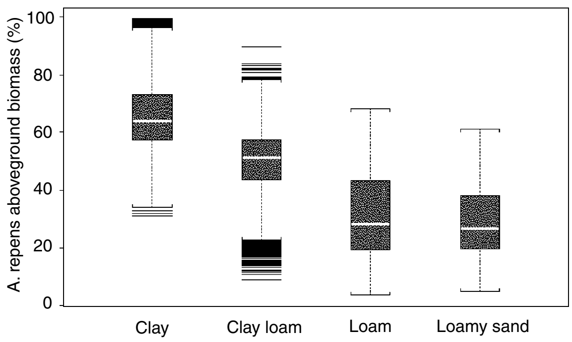

Figure 1. Simulated percentage *A. repens* aboveground biomass for each of four soil textures. All means are highly significantly different (*t*-test; $P < 0.001$). The box area contains the middle 50% of the data, and the median is voided from the box so that skewness can be assessed. Outliers are shown as lines beyond the whiskers, which indicate 1.5 times the interquartile range (S-Plus defaults; Insightful, Inc.).

Table 2. Regression coefficients for simulated percentage *A. repens* aboveground biomass against temperature and precipitation for each of four soil texture classes. The temperature coefficient was not significant for loamy sand, while the precipitation coefficient was not significant for clay loam, but in both cases the interaction of temperature : precipitation was highly significant. All other coefficients were significant.

	Clay	Clayloam	Loam	Loamy sand
Intercept	115.49	54.47	53.43	55.91
Temprature	−0.92	1.37	0.96	−0.05
Precipitation	−1.47	0.08	−0.15	−0.41
Temp : Precip	0.04	−0.07	−0.09	−0.04

Colorado (Table 2). This extrapolation showed that *A. repens* could potentially be found throughout the state in varying amounts due to interactions between temperature, precipitation and soil texture (Figure 2). The least susceptible sites were located along the eastern border; much of the eastern plains had a low likelihood of *Acroptilon repens* success (<35% aboveground biomass). The exceptions were patches associated with fine-textured soils generally located in river valleys, particularly along the Platte River in the north-east and the Arkansas River in the southeast. There were two main susceptible areas in the central portion of the state: one around Alamosa in south-central Colorado and the other in Park County in the center of the state. There were also scattered invasion cells throughout the mountains at lower elevations and in valleys. In the western part of the state, *A. repens* was most successful in river basins, along the Colorado River in west-central Colorado and the White River in the northwest. Scattered invasion sites were predicted in the southwestern portion of Colorado as well.

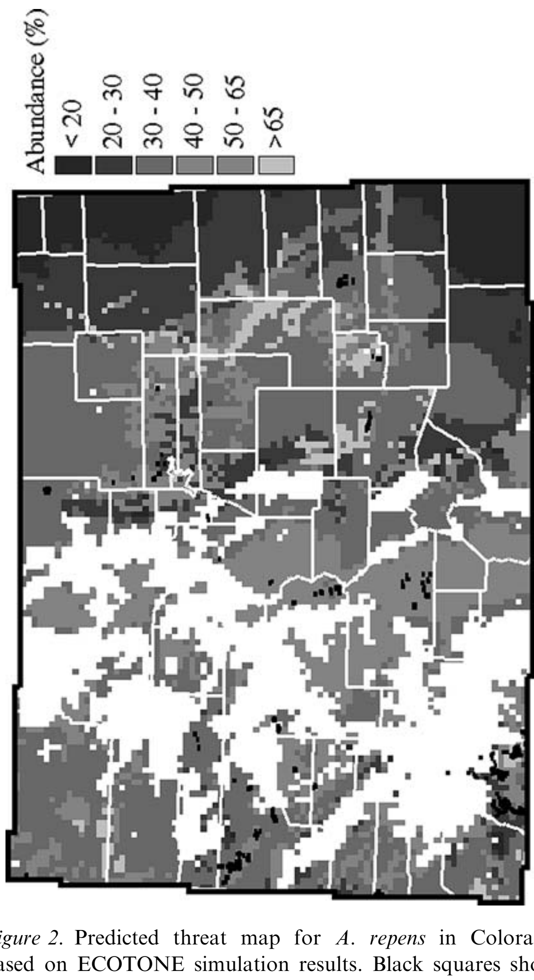

Figure 2. Predicted threat map for *A. repens* in Colorado based on ECOTONE simulation results. Black squares show the locations of known *A. repens* patches. White areas are outside the ecological bounds of the model (>50 cm precipitation per year).

Known *A. repens* locations overlain on the threat map showed a good correspondence with predicted areas of greatest biomass proportion. The most notable exceptions were two clusters of actual *A. repens* patches, one near the eastern border of the state in Kiowa County, and the other near the northern border in Larimer County. Both of these clusters were around reservoirs, which are artificial features below the resolution of the GIS layers used, and so would not be expected to be identified as threatened areas by the model.

Discussion

The individual components of our analysis strategy have been previously applied to the study of invasive exotics. GIS methods have been used to investigate weed ranges, and to simplify the process of identifying environmental envelopes for individual species (Burkart and Buhler 1997; Goslee et al. 2003). Various types of simulation models have also been used. Spatial models, such as the common diffusion model, often do not consider spatial heterogeneity or ecological processes other than dispersal (Higgins et al. 1999). While this class of model can be used to predict an overall range expansion area (e.g., Smith et al. 1999), it cannot predict the fate of an individual site. Individual-based models allow for the inclusion of both spatial heterogeneity and ecological processes, and can be used to make predictions for a particular location. Higgins and Richardson (1996) point out the potential utility of individual-based models, but note that they have been used little in the study of invasive species (see Goslee et al. 2001 for an exception). The major advantages of individual-based simulation models for predicting invasive species abundance include their ability to consider particular processes and interactions, their predictive capability, and their ability to incorporate alterations in local disturbance regimes or climate patterns.

Simulation model results showed that *A. repens* has the potential to become most abundant in dry areas of Colorado with fine-textured soils. The interaction between precipitation, temperature and soil texture led to high spatial heterogeneity in *A. repens* distribution across the state. The threat map of Colorado showing predicted *A. repens* percentage biomass can be used to target resources (money and effort) to regions where *A. repens* is likely to be a serious problem. Because we were interested in creating a coarse-scale threat map, we chose not to incorporate the effects of disturbance or seed dispersal. Our objective was to identify regions that require more (or less) intensive monitoring, and not to understand invasion dynamics at a fine scale. It is difficult or impossible to predict seed dispersal or disturbance events at a regional scale. Instead we tried to identify areas where *A. repens* will be successful if it becomes established. These are the regions that should be watched, so that if disturbance conditions and propagule availability allow *A. repens* to become established it will be detected early.

The simulation model-GIS approach allowed us to use all information on this species available in the literature and from our own research in conjunction with detailed climate and soils data. This process-based method more closely duplicates our understanding of the ecological functioning of plant communities than any other technique which has been used to describe potential ranges of introduced invasive species. Using an individual-based simulation model to examine the success of invasive species allows the isolation of environmental and climatic factors and plant community traits that facilitate or retard the spread of a particular species. The simulation model indicated that soil texture and precipitation were more important than temperature as determinants of *A. repens* success. Simulation results were supported by analysis of known *A. repens* locations (Goslee et al. 2003).

The predicted *A. repens* distribution did not match all known locations. In cases where the simulation model failed to identify groups of known patches as a threatened area (errors of omission), the main reason is probably the coarse resolution of soils and climate data. The scale used completely missed small artificial features such as reservoirs. This could be remedied by more detailed modeling of areas of particular interest, if sufficiently fine-grained data were available. Errors could also be due to lack of complete understanding of the ecology and physiology of *A. repens*, although previous work suggests that our methods are accurate at the site level for grassland vegetation (Goslee et al. 2001). A third potential source of error is our assumption that a particular group of functional types adequately represents the existing vegetation over a wide geographic area. Our predictions for eastern Colorado shortgrass steppe areas are more accurate than our extrapolation to other grassland types in the western part of the state because ECOTONE was originally developed and parameterized here. The latter two sources of error also contribute to the likelihood of errors of commission, where areas are predicted to be high-risk for *A. repens*, but none is known. It is important to make the distinction between potential habitat and actual habitat. These areas may actually be unoccupied by *Acroptilon repens* because seeds were never transported to the vicinity. It is likely that our knowledge of *Acroptilon repens* locations is incomplete, and a detailed survey may well locate infestations within those areas.

Simulation models require considerable information about both the invasive species and the existing community. For systems where these data are available, simulation models have a number of advantages, including the ability to take into account existing vegetation type, to incorporate ecological processes, and to predict the success of an invasive species at a much finer scale than the regression model. The coarse resolution of the soils and weather data available restricted us to a regional approach, but the approach presented here will become increasingly valuable for site prediction as data resolution and availability improve. The simulation model approach has many more applications than simply range prediction. Once a model has been developed, parameterized and tested for a particular community type, it can be used to examine traits of actual or hypothetical species that allow them to become invasive. The combination of simulation model and GIS provides the ability to examine geographic patterns, species traits and community dynamics. Simulation modeling can be used to identify key processes and to generate hypotheses about species distributions. This approach can evaluate the success of an invasive plant species under hypothetical conditions. These include climate change scenarios, management plans, disturbance regimes, and many more. Thus, the simulation model-GIS approach can be of great benefit to ecologists, planners and policymakers because it allows estimates of risk to be made for particular species in a wide variety of situations. Even without the need for prediction under different hypothetical conditions, a threat map such as that presented here is quite useful for allocating limited management resources towards those areas where the invasive exotic perennial *A. repens* is most likely to thrive.

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