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Selection of Models of Invasive Species Dynamics[1]

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Abstract: Mathematical and process-based simulation models are powerful tools for synthesizing information about invasive species. However, there are a number of different types of models, ranging from simple to complex that can be selected for any given application. In this article, a model classification framework of three types of models is applied to studies of invasive species that allows the objective selection of a model type on the basis of its ability to capture key processes and dynamics, yet minimize the errors in prediction. Model selection is illustrated using a series of increasingly complex models.
Additional index words: Nonspatial models, spatially explicit models, spatially implicit models.

INTRODUCTION

Biotic invasions remain a critical challenge to ecologists, weed scientists, and land managers despite efforts to restrict the introduction of alien species and to minimize the amount of area infested. Although many studies have been conducted on various aspects of invasive species, we still lack the ability to successfully predict three main aspects of biotic invasions: (1) the conditions under which a species will become invasive, (2) the attributes that make some species more invasive than others, and (3) the dynamics of invasions (Mack et al. 2000). Mathematical and process-based simulation models with an ecological conceptual foundation are a powerful tool for synthesizing known information about invasive species and can be used to examine these three aspects of biotic invasions (Higgens and Richardson 1996; Higgens et al. 1996). However, there are a number of different types of models ranging from simple to complex that can be selected for any given application. The decision as to which type of model to select is not always obvious, yet the consequences in terms of errors in prediction of selecting an inappropriate model can be serious (Peters et al. 2004). An objective decision-making framework based on study goals relative to trade-offs in the strengths and weaknesses of different types of models is needed. The objective of this article is to apply a model classification framework and selection procedure to studies of invasive species. This framework will allow the

objective selection of a model type on the basis of its ability to capture key processes and dynamics, yet minimize the errors in prediction.

TYPES OF MODELS AND ERRORS

There is a broad range of models available for simulating invasive species dynamics. These models range from simple models with very few parameters to complex models with many parameters. The ability of models to represent complex ecological dynamics as well as the errors in prediction varies by model type. There are two classes of errors that typically occur: "errors of omission" refer to those errors associated with missing parameters that are potentially important to dynamics, and "errors of commission" refer to errors associated with including parameters that are not necessary as well as to the accumulation of small errors associated with each parameter as the number of parameters increases (Gardner et al. 1980; O'Neill 1973; Peters et al. 2004; Reynolds and Acock 1985).

In selecting a model type, there is a trade-off between simple and complex models in terms of the class of error. Simple models with few parameters have small errors of commission and yet have limited predictive ability because of large errors of omission associated with missing processes that are critical to system dynamics. As model complexity increases, errors of omission decrease and errors of commission increase as more parameters are added. The challenge is to select a model that is sufficiently complex to represent the key processes and yet does not include unnecessary parameters.

Several classifications for distinguishing simple and

complex models have been proposed (e.g., Higgens and Richardson 1996; Peters et al. 2004). One classification is particularly relevant to modeling invasive species dynamics because it distinguishes three types of models based on the degree of spatial interactions, the processes often cited as important to the spread of invasives: nonspatial, spatially implicit, and spatially explicit models (Peters et al. 2004). The models are differentiated by their inclusion or exclusion of spatial location of simulated plots and spatially contagious or neighborhood processes that connect simulated plots. Both these characteristics are often included in studies of invasive species. In general, complexity increases from nonspatial to spatially implicit and spatially explicit models (Peters et al. 2004), although exceptions are possible (e.g., Cummings 2002).

Nonspatial Models. The simplest models are often nonspatial where neither spatial location nor contagious processes are included in the input parameters (Peters et al. 2004). These models are often used to represent specific aspects of ecological systems, such as population growth and mortality using exponential growth and logistic models (Higgens and Richardson 1996). Nonspatial simulation models are used to account for variation among individuals without regard to spatial variation in the environment. For example, plots containing individual plants of perennial grasses have been simulated using within-plot parameters, such as local recruitment, competition, and mortality, to successfully represent the average dynamics of a large homogeneous grassland (e.g., Symstad et al. 2003). Nonspatial models generally require the fewest number of parameters and are expected to have the smallest errors of commission of the three types of models (see Crawley 1986; Williamson 1989 for exceptions). However, these models can have the highest errors of omission if important spatial processes are not represented.

Spatially Implicit Models. The inclusion of spatially structured data into nonspatial models results in spatially implicit models (Peters et al. 2004). This type of model is most appropriately used when spatial location is important, but spatial processes and the landscape context are not important to plot dynamics. These models are often used in ecology because the physical environment is spatially structured and ecological processes are frequently correlated with spatial variation in the environment (Legendre et al. 1989). Examples include regression models used to predict potential range distributions of invasive trees on the basis of current habitat prefer-

ences (e.g., Lee et al. 1991). Spatially implicit simulation models have been used for the invasion dynamics of Russian knapweed [*Acroptilon repens* (L.) DC], where variation in soil texture and native grass sensitivity to allelochemicals were examined (e.g., Goslee et al. 2001). This type of model often combines a simulation model with spatial databases in a geographic information system. Model assumptions include a readily available seed source and no net movement of water onto or away from a plot. Thus, these models are most useful when local, yet spatially variable, plant–scale processes dominate system dynamics rather than connectivity among plots, such as seed dispersal and water runon–runoff patterns.

Spatially Explicit Models. The third type of model includes both spatial location and contagious or neighborhood processes to determine dynamics for a specific plot. Contagious processes are important under three conditions: (1) transfers of materials, organisms, energy, etc. among sites are large, (2) rates of transfer are determined by local conditions, and (3) variables governing local scale transfers are spatially heterogeneous (Peters et al. 2004). Reaction–diffusion models are the simplest form used for invasive species. These models have been used successfully to represent range expansion of a number of animal species and diseases (Hengeveld 1989; Holmes et al. 1994; With 2002). However, in some cases, these models can underestimate rates of spread by an order of magnitude (Andow et al. 1990). Although spatial location of individual modeling elements is not tracked explicitly, these models fit best under the spatially explicit type of model.

Simulation models have been developed to represent variation in plant attributes, environmental heterogeneity, and stochasticity that cannot be addressed in analytical models (Higgens et al. 1996, 2000; Kriticos et al. 2003; Rastetter et al. 2003). For example, the spread of wild oats (*Avena fatua* L.) in New South Wales was simulated based on seed dispersal, a spatial process that connects simulated cells, and local population processes, such as seedling establishment (Auld and Coote 1990). Cellular automaton models provide another familiar example for invasive species (Tilman and Kareiva 1997) that have been used to examine how habitat shape affects rates of colonization (Cummings 2002). Although these models are appealing because of the complexity of processes included, they also often have the highest errors of commission and highest prediction error of the three model types.

MODEL SELECTION

An appropriate model should successfully meet the goals of the study by including only the key processes and driving variables with important influences on system dynamics. One approach to model selection that is often invoked is to start with the simplest model possible that includes the key processes expected to be important and then add parameters until the model output is similar to field observations. An example of this approach is provided by research conducted on the recovery of a perennial grass across disturbed areas, a process similar to the spread of an invasive species. The objective of the modeling exercise was to predict recovery times after disturbance and to identify the key processes influencing recovery. This example also illustrates the close connection between modeling and experiments that is required for successful problem solving.

Initial simulations were conducted using a nonspatial individual plant–based gap dynamics model (STEPPE) for one disturbance size (<1 m^2, Coffin and Lauenroth 1990). Plots were simulated with the same environmental input parameters; however, each plot had slightly different species parameters for recruitment and mortality because STEPPE is stochastic for these processes. Seeds were assumed to always be available, thus recruitment was controlled by the probability of seedling establishment. Because simulated recovery times were faster than expected on the basis of field observations, additional runs were conducted where seed availability was related to annual precipitation. These model results were similar to field observations on small disturbances and led to new experiments on seed production and presence in the soil (Coffin and Lauenroth 1989, 1992).

Because many disturbances are larger than 1 m^2 and occur across a range of soils with properties that influence seedling establishment, additional simulations were conducted for disturbances ranging in size from 1 to 16 m^2 with one of five soil textures (Coffin and Lauenroth 1994). In one set of simulations, independent plots were simulated using a spatially implicit model that accounted for variation in soil type and the range in disturbance sizes. In the other set, the contagious process of seed dispersal by wind was simulated using a grid of connected plots in a spatially explicit model. Results showed that the spatially implicit model was able to capture recovery dynamics on different soils for small, disturbed areas where seed availability is not limiting. However, the spatially explicit model provided better predictive ability as disturbance size increased beyond the seed dispersal distance of the recovering grass.

In conclusion, the sequential addition of parameters and increase in model complexity can allow the identification of key parameters and processes, both for inclusion into the model and as hypotheses to be tested by new experiments. This approach minimizes the error of commission by only adding parameters when needed and minimizes the error of omission by adding new parameters when model results have low predictive ability. A similar approach of sequential model development and selection, from simple to complex, can be used for simulating invasive species dynamics. Objective selection of a model is particularly important in invasive species studies where errors of prediction need to be minimized when predicting dynamics and making management decisions.

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