

Predicting Landscape Vegetation Dynamics Using State-and-Transition Simulation Models

Colin J. Daniel and Leonardo Frid

Authors

Colin J. Daniel is an ecologist with Apex Resource Management Solutions Ltd., 937 Kingsmere Ave, Ottawa, Ontario, Canada K2A 3K2, colin.daniel@apexrms.com. **Leonardo Frid** is an ecologist with Apex Resource Management Solutions Ltd., 1110 Lenora Drive, Bowen Island, British Columbia, Canada V0N 1G1, leonardo.frid@apexrms.com.

Abstract

This paper outlines how state-and-transition simulation models (STSMs) can be used to project changes in vegetation over time across a landscape. STSMs are stochastic, empirical simulation models that use an adapted Markov chain approach to predict how vegetation will transition between states over time, typically in response to interactions between succession, disturbances and management. With STSMs a landscape is divided into a set of simulation cells, each cell is assigned to an initial vegetation state, and the model then predicts how each cell may change from one vegetation state to another over time. Over the years an extensive suite of features have been added to STSMs that allow them to represent a range of dynamics important to landscape modeling, including tracking age-structure, triggering transitions based on past events, setting targets for certain transitions, and varying transition rates over time. STSMs are also now able to represent spatial variability in two different ways: by dividing the landscape into spatial strata, typically defined by one or more important drivers of vegetation change, or alternatively by developing a spatially-explicit STSM, whereby transition events, such as fire or invasion by non-native vegetation, can be simulated to spread across the landscape.

Since their introduction in the early 1990s, STSMs have been applied to a wide range of landscapes and

management questions, including forests, rangelands, grasslands, wetlands and aquatic communities, over spatial extents ranging from thousands to millions of hectares. Several software tools currently exist to support the development of STSMs; the most recent of these products, called the Path Landscape Model, is the latest in a lineage of STSM development tools that includes both the Vegetation Dynamics Development Tool (VDDT) and the Tool for Exploratory Landscape Analysis (TELSA).

Keywords: state-and-transition simulation model, STSM, ecological model, ecological restoration, ecosystem management, landscape ecology, vegetation dynamics, Path Landscape Model, TELS, VDDT.

Introduction

Models are often used to predict vegetation conditions across a landscape over time. Since the early 1970's a wide range of models have been developed for this purpose. As one might expect these models vary considerably in their approach; over the years several authors have attempted to classify these models, each using a slightly different set of criteria for distinguishing between approaches (Baker 1989; Keane et al. 2004; Scheller and Mladenoff 2006; Xi et al. 2009). Common criteria that emerge from these reviews for distinguishing between models include:

1. Degree to which ecosystem processes, such as succession and disturbance, are simulated mechanistically (as opposed to being developed empirically);
2. Whether or not the models are deterministic (i.e. predict a single future) or stochastic (i.e. predict a distribution of possible futures);
3. Scale at which ecosystem processes are represented—e.g. gap (m^2), stand (ha), region (km^2);
4. Extent to which the spatial dynamics of ecosystem processes are represented explicitly (e.g. disturbance spread over time);

5. Range of ecosystems to which the models can be applied (the majority of landscape models have been developed for forest ecosystems).

One technique for predicting landscape-level vegetation change is to use *state-and-transition models*, a term first introduced by Westoby et al. (1989) in reference to conceptual models describing the successional dynamics of rangeland vegetation over time. Through the use of box-and-arrow diagrams, these models describe a series of discrete states in which a parcel of land can find itself at any point in time, along with transitions, both natural and anthropogenic, that can move land between these states. Conceptual state-and-transition models provide a simple, flexible approach for describing and documenting one's understanding of the vegetation dynamics associated with a particular ecosystem (for example, see Grant 2006; Bestmeyer et al. 2009; Knapp et al. 2011).

A second form of state-and-transition models exists that extend the conceptual models described above by assigning probabilities to each of the transition pathways, leading to models that can simulate the states and transitions that might occur over time across a landscape. To distinguish these models from their conceptual counterparts we refer to them more specifically as *state-and-transition simulation models* (STSM).

Using the criteria outlined above, STSMs can be considered:

1. Strongly empirical: model relationships are typically fitted to data and/or understanding (including output from other models);
2. Stochastic: model dynamics involve probabilities, allowing for predictions that are distributions, rather than single values;
3. Stand or regional scale: models are typically developed to represent processes occurring at either a stand or regional scale;
4. Optionally spatially-explicit: a unique feature of STSMs is that models can be developed and run either with or without explicitly representing spatial processes;
5. Suitable for any ecosystem: due to their empirical nature, STSMs can be developed for any vegetation community.

In this article we provide an introduction to the STSM approach for simulating vegetation change across a landscape. We first explain the theory and concepts behind the approach, including definitions and terminology for some of the most commonly used STSM features. We then review software currently available for constructing and running STSMs, including a simple example of how the software can be used. Finally we provide an overview of some of the questions and landscapes to which STSMs have been applied.

Modeling Approach

STSMs are stochastic, empirical simulation models, whereby the vegetation across a landscape is classified into states, probabilities are assigned to possible transitions between states, and the landscape is then simulated through time using Monte Carlo simulation methods. Technically an STSM can be considered a Markov chain, whereby the probability of transitioning from one state to another at any given time depends only on the present state (Baker 1989). However, as we shall see later in this section, current STSMs tend to push the Markov chain definition well beyond its usual "textbook" formulation.

For simple STSMs, a landscape is first divided into a set of n simulation cells; these cells can be any geometric shape and size (e.g. either raster pixels or polygons). The model then defines a discrete set of r states, $S = \{s_1, s_2, \dots, s_r\}$, in which each simulation cell can be found over time, and a discrete set of m transition types, $U = \{u_1, u_2, \dots, u_m\}$, through which each state s_i can transition to s_j . Transition probabilities, $p_{m,i,j}$, specify the probability that state s_i transitions to s_j via transition type m in a single timestep of the simulation. Each non-zero transition probability is referred to as a *transition pathway*.

A simulation then tracks the state of each simulation cell, $C = \{c_1, c_2, \dots, c_n\}$, over a series of discrete timesteps; the duration of each timestep is user-defined (e.g. day, year, decade). A simulation begins by assigning each cell to an initial state for the first timestep. Each cell's state is then

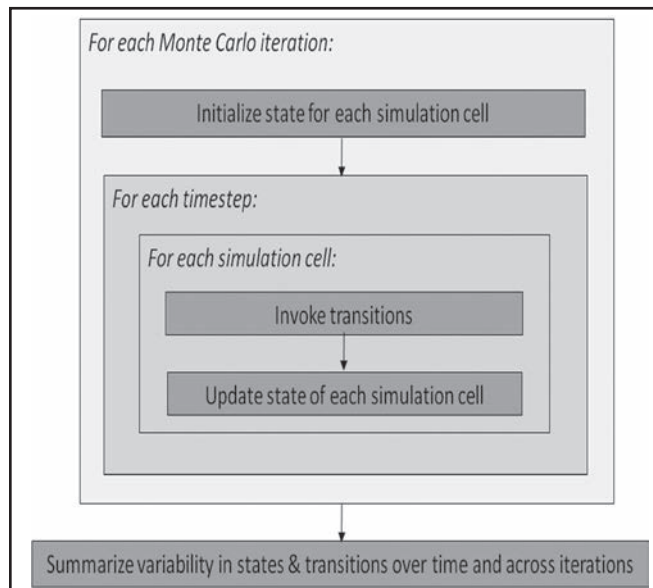


Figure 1—Flowchart showing the STSM algorithm.

subject to change from one timestep to the next according to the transition probabilities defined between states; a maximum of one transition can occur per cell in each timestep. A single iteration of a simulation is complete once the state of every simulation cell is calculated for a specified number of successive timesteps. Because the model uses probabilities to determine when and where transitions occur, the model's predictions are stochastic, and the fate of any one simulation cell can vary from one run of the model to the next. Consequently, model runs are repeated for several iterations (i.e., Monte Carlo simulations), with the result being a distribution of projected outcomes for the state of each simulation cell over time (fig. 1).

There is a common misconception that Markov chains are too simple to represent many of the processes important to landscape vegetation modelling. However, as described in detail by Baker (1989), it is possible to represent a rich suite of dynamics using Markov chains by simply defining the state space appropriately. For example if transition probabilities for a particular state depend upon the time since a previous event, one can expand the state space to include a new state for each possible time since the event; with enough states any number of preceding events can be represented as a Markov chain. Markov chains can also be non-stationary, allowing probabilities to change over space and time; in

this way external drivers, such as climate change or harvest demand, can be represented through changing probabilities; any non-stationary Markov chain can be made stationary by including enough new states to represent all the conditions across which the probabilities vary. Spatial processes, such as contagion of transitions between neighbouring simulation cells, can also be represented by allowing the transition probabilities to vary according to both the cell location and the previous state of neighbouring cells. Again, with a sufficiently large state space, these dynamics can ultimately be represented as a Markov chain: in the limit a model could be disaggregated such that each simulation cell and year is defined as a unique "state," allowing complete control over how the transition probabilities vary across both space and time.

So while it is possible, in theory, to model quite complex dynamics using a Markov chain, the number of states required rises geometrically once the model includes one or more of the features outlined above; formulating a model as a traditional Markov chain can quickly overwhelm even the most proficient modeller. STSMs have been designed specifically to overcome these challenges: since the development of the first STSMs in the early 1990's, features have been steadily added to the basic Markov chain formulation to shield modellers from this complexity. Over the years a number of features have been added to STSMs to allow users to rapidly and simply incorporate many of the complex dynamics outlined above, without the need to explicitly specify and track the full state space; some of these key features are described below.

State Age and Deterministic Transitions

In addition to tracking the state (S) of each simulation cell, STSMs can also track a second state variable: the age, $A = \{a_1, a_2, \dots, a_n\}$, of each cell. Each simulation cell is assigned an age at the start of the simulation (in addition to its state); by incrementing this age by one for each timestep of the simulation, the age of each simulation cell can be tracked over time. In addition, an upper and lower age limit can be specified for each state. Once the age for a simulation cell reaches the upper limit for its current state, the age is no longer incremented in future timesteps. A special form of

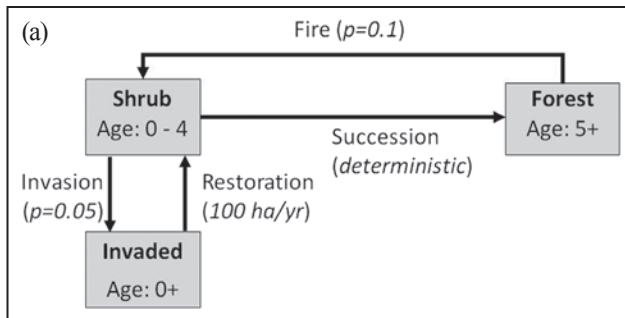
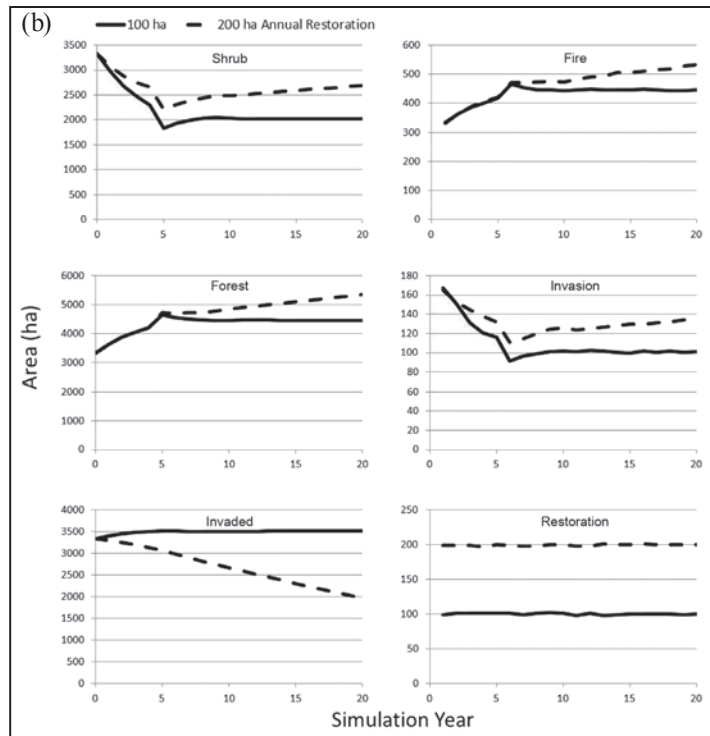


Figure 2—Example of a simple STSM, illustrating (a) Pathway diagram and (b) Simulation results showing area over time in each state class (Shrub, Forest, Invaded) and area over time undergoing transitions (Fire, Invasion, Restoration) for 2 scenarios: 100 ha/yr restoration (solid) and 200 ha/yr restoration (dashed). Model was run for 20 years and 100 Monte Carlo iterations over a 10,000 ha landscape, divided into 1ha simulation cells, assuming equal area in each state and age class initially; graphs display the average values over all iterations.



transition pathway, referred to as a *deterministic transition pathway*, can be specified for each state, causing a transition to occur automatically to a new state once the age of the cell exceeds the state's upper age limit; only one deterministic transition pathway is allowed per state. The lower age limit of the destination state associated with a deterministic transition pathway is then used to reset the age for the cell after a deterministic transition. Deterministic transitions are typically used to represent age-based vegetation succession in STSMs.

Transition Targets

Not all transition pathways are best represented in STSMs using probabilities. One example of this is the deterministic transition pathways that handle the dynamics of ageing between states. A second situation occurs frequently for management-oriented transition pathways, where the level of a transition is more appropriately expressed as a fixed target for the area treated each timestep, rather than as a probability of occurrence. Transition targets are typically specified by transition type for some portion of the landscape, and can vary over time (e.g. target for area harvested each year). To reformulate these transitions as a

Markov chain, STSMs dynamically convert these targets to an equivalent probability for each transition pathway and timestep, based on the number of simulation cells eligible for the transition pathway during each timestep of the simulation.

Figure 2a shows an example of a very simple STSM. The pathway diagram defines the suite of possible states and transitions between states for the modelled system, where boxes represent states and arrows represent transition pathways. In this example “Fire” and “Invasion” are represented as probabilistic transitions (with annual probabilities), “Succession” is modelled as a deterministic transition (i.e. occurring with a probability of 1 once the age of the Shrub state reaches 4), and “Restoration” is set to have a transition target of 100 ha/yr. To begin the simulation the landscape is divided into simulation cells, with each cell being assigned an initial state and age. A single iteration of the model involves predicting the state of each simulation cell for a series of timesteps. Repeating the simulation for multiple iterations generates a distribution of predicted results for the state of each cell (fig. 2b).

While already more complicated than a basic Markov chain, the model shown in fig. 2 would still be considered

a very simple STSM; additional advanced features, which are commonly found in most applied STSMs, are described below.

Transition Pathway Age Range

By default a transition pathway specified for a particular state acts on all simulation cells in that state, regardless of the cell's age. One exception is a deterministic transition, which is triggered only for cells that have exceeded the state's upper age limit (and does so with a probability of 1). For all other probabilistic transition pathways, however, it is possible in STSMs to change the default settings to constrain a particular transition pathway such that it only applies to those simulation cells that fall within a specified age range. For example, in a forest-based landscape one might specify a transition pathway called “thinning” that applies to a particular state (e.g., Forest), but only to those simulation cells within a specified age range (e.g., 70–90 years old).

Post-Transition Age

When a probabilistic transition occurs for a simulation cell, both the state and the age of the cell are updated according to the associated transition pathway. By default the age of the cell is set to the start age of the pathway's new destination state; however it is possible to specify alternative behaviours for the post-transition age: transition pathways can be specified to retain the age of the cell prior to the transition; they can also shift the age forward or backward. For example a transition pathway called “stand-replacing fire” might reset the age of the simulation cell to age 0, while a “surface fire” transition pathway might maintain the current age of the simulation cell.

Time-Since-Transition

In addition to tracking the current state (S) and age (A) of each simulation cell over the course of the simulation, STSMs can optionally track a third state variable: the number of timesteps since each type of transition last occurred for each simulation cell. This state variable is referred to as the *time-since-transition* (TST) for the cell, $tst_{m,n}$, which is tracked for every simulation cell n and transition type m . Similar to the option to specify age ranges

for transition pathways, TST can also be used to constrain which simulation cells are eligible for each transition pathway. For example, STSMs can represent the changing fire dynamics that occur on a landscape through the implicit build-up of fuels using the TST feature: simulation cells burned in a high severity wildfire can be modelled to not experience another high severity wildfire for the following 20 years, the assumed time needed for sufficient fuels build up.

Temporal Heterogeneity

Because STSMs are stochastic, using probabilities to determine when and where transition occur, there will always be some variability between timesteps in the number of transitions that occur during a particular simulation. However there are often situations in which additional temporal variability is required in order to adequately capture landscape dynamics. For example, weather conditions and/or climate change may result in different patterns or trends of high and low fire risks from one year to the next, or insect outbreaks may show a cyclical pattern over many years. From an STSM perspective, capturing this kind of temporal variability involves varying the probabilities for certain transition pathways over time. This can be accomplished using *transition multipliers*, which scale the base probabilities associated with one or more transition pathways up and down over the course of a simulation according to an externally driven pattern.

Spatial Heterogeneity

Often there is a requirement for STSMs to capture the spatial heterogeneity across a landscape. Biophysical factors, such as climate and soils, are often key determinants of vegetation dynamics; many disturbances, both natural and anthropogenic, tend to be aggregated spatially. Depending upon the requirements of any particular analysis, the amount of spatial variability that the model must capture will vary.

STSMs can represent three different forms of spatial variability. Firstly, as illustrated in fig. 2, a single set of pathway diagrams can be developed for the landscape as a whole—we refer to this as a *whole landscape* STSM.

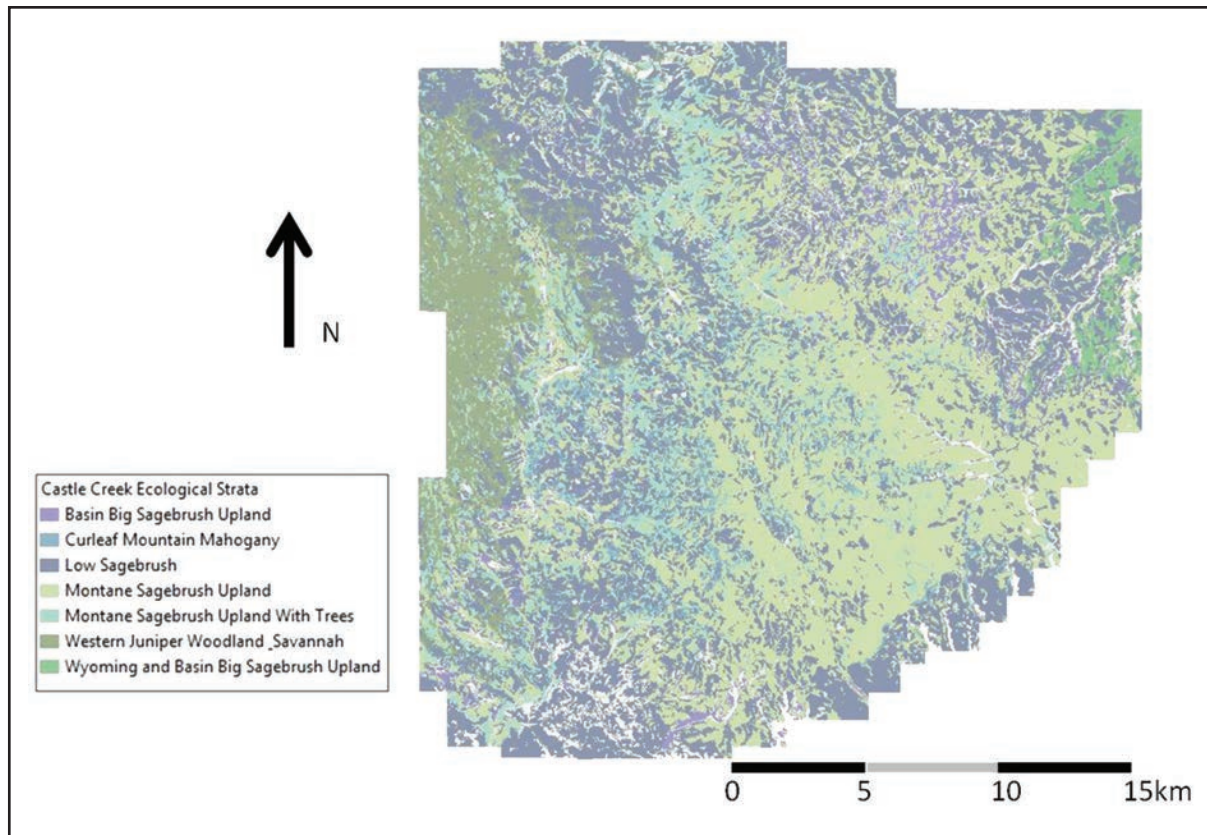


Figure 3—Map showing ecological strata for the 46,000 ha Castle Creek landscape in Idaho. In a spatially stratified STSM, each stratum can be represented by a different pathway diagram.

A model in this form does not capture any of the spatial variability across the landscape; rather, it provides only predictions for the total area in each state over time. Information on the location and configuration of the simulation cells is not used: each cell is simulated independently of all others, essentially acting as a spatial “replicate” in a Monte Carlo simulation.

A second and more commonly used approach for STSM development is to stratify the landscape according to one or more criteria that are considered to be important external drivers of vegetation change, and then to develop a separate pathway diagram for each of these strata—we refer to this as a *spatially-stratified STSM*. As with whole landscape STSMs, each simulation cell within a stratum is simulated independently of its neighbours; however each simulation cell is assigned to a particular stratum at the start of the simulation. Strata are typically defined according to one or more important drivers of vegetation change. Biophysical

drivers, such as soils, climate and topography are the most common: here the strata often follow existing ecological classification systems, examples of which include potential vegetation types (Chiarucci et al. 2010), biophysical settings (Long et al. 2006), ecological sites (Bestelmeyer et al. 2009) and biogeoclimatic zones (MacKenzie 2012). Stratification also often reflects differences in anthropogenic activity across the landscape, by dividing the landscape into zones with differing management practices (e.g., protected vs. unprotected, private vs. public).

Stratifying the landscape allows the modeller to specify different assumptions—such as states, transitions, pathway probabilities and management targets—for each of the landscape strata, thus capturing some of the spatial variability in vegetation dynamics across the landscape (fig. 3). Model projections, in turn, can be displayed spatially across the entire landscape, classified according to the original strata polygons. Recently, modellers have begun to relax the

assumption that the stratum to which each simulation cell is assigned is static, and instead allow simulation cells to shift from one stratum to another over the course of a simulation (e.g., Provencher and Anderson 2011). This option has become an increasingly important tool for representing shifts over time in biophysical boundaries (e.g. due to climate change) that were historically considered fixed.

The third and final approach for representing spatial variability is to develop what we refer to as a *spatially-explicit* STSM. These models typically begin as a spatially-stratified STSM with a number of important additions. Firstly, transition probabilities can be made specific to each simulation cell; for example an external driver, such as topography or climate, could influence the probability of a particular transition (e.g., fire) for each cell on the landscape. Secondly, in a spatially-explicit STSM each simulation cell is aware of the location and state of other cells; as a result the transition probabilities for any cell can be influenced by the past and present state of its neighbours (i.e. simulation cells are no longer independent). This feature is commonly used to “spread” transitions across a landscape, both within a timestep (e.g., fire) or between timesteps (e.g., invasives). Finally, a target frequency distribution of sizes for transition events on the landscape can be specified as a model input, guiding the number and size of contiguous transition “patches” that occur across the landscape. Figure 4 shows the typical output of a spatially-explicit STSM: the result of a single Monte Carlo iteration is a prediction for the state of each simulation cell in every timestep; repeating simulations for multiple iterations results in distribution of predictions for the state of each cell.

On the surface it would seem that spatially-explicit models would always be a modeller’s first choice, as they appear to produce the most ecologically relevant predictions. However there are important trade-offs to consider when deciding on the approach to use for capturing spatial variation (Mladenoff 2004). Firstly, the time and resources required to prepare and run a spatially-explicit model are generally much greater than that of a simpler spatially-stratified model. Deciding to use a spatially-explicit model often means making sacrifices in other areas of an overall modeling project: extra time spent preparing, running and

analysing these models takes away from time available for exploring model behaviour in greater depth, particularly over larger landscapes. Secondly, the data and additional model parameters required to run a spatially-explicit STSM are not always available. Finally, many modelling projects do not require predictions be spatially disaggregated to the level of a simulation cell, in which case the added complexity of a spatially-explicit model may be of no value to the modeller.

Software

While many landscape vegetation models include some capabilities to represent Markov chains (Keane et al. 2004), over the past 20 years three software tools have been developed to support the STSM features described in this paper. The first of these is the Vegetation Dynamics Development Tool (VDDT; ESSA Technologies Ltd. 2007). Originally developed to support landscape modeling for a project in the Interior Columbia River Basin of the U.S. in the early 1990’s (Hann et al. 1997), VDDT was the first software tool designed specifically to develop and run STSMs, and includes a simple visual editor for STSM pathway diagrams, a simulation engine for running models, and a graphics module for viewing model output. VDDT was originally designed to support the development of whole landscape STSMs, although with some effort technically adept users are able to adapt the software to run spatially-stratified STSMs. While the software is still available for free download, and support for using the software is still available, development of the product was discontinued in 2011.

A second software tool available for developing STSMs is the Tool for Exploratory Landscape Analysis (TELSA; Kurz et al. 2000; ESSA Technologies 2008). Originally developed to support forest management in British Columbia, Canada, TELSAs provides the capability to run polygon-based spatially-explicit STSMs. TELSAs was designed to work in conjunction with VDDT—typically users develop their STSM pathway diagrams first using the visual editor in VDDT, then import this information into TELSAs. Within the TELSAs software, users are able to prepare additional model inputs (including GIS maps using an ArcGIS extension), run Monte Carlo simulations, and view model

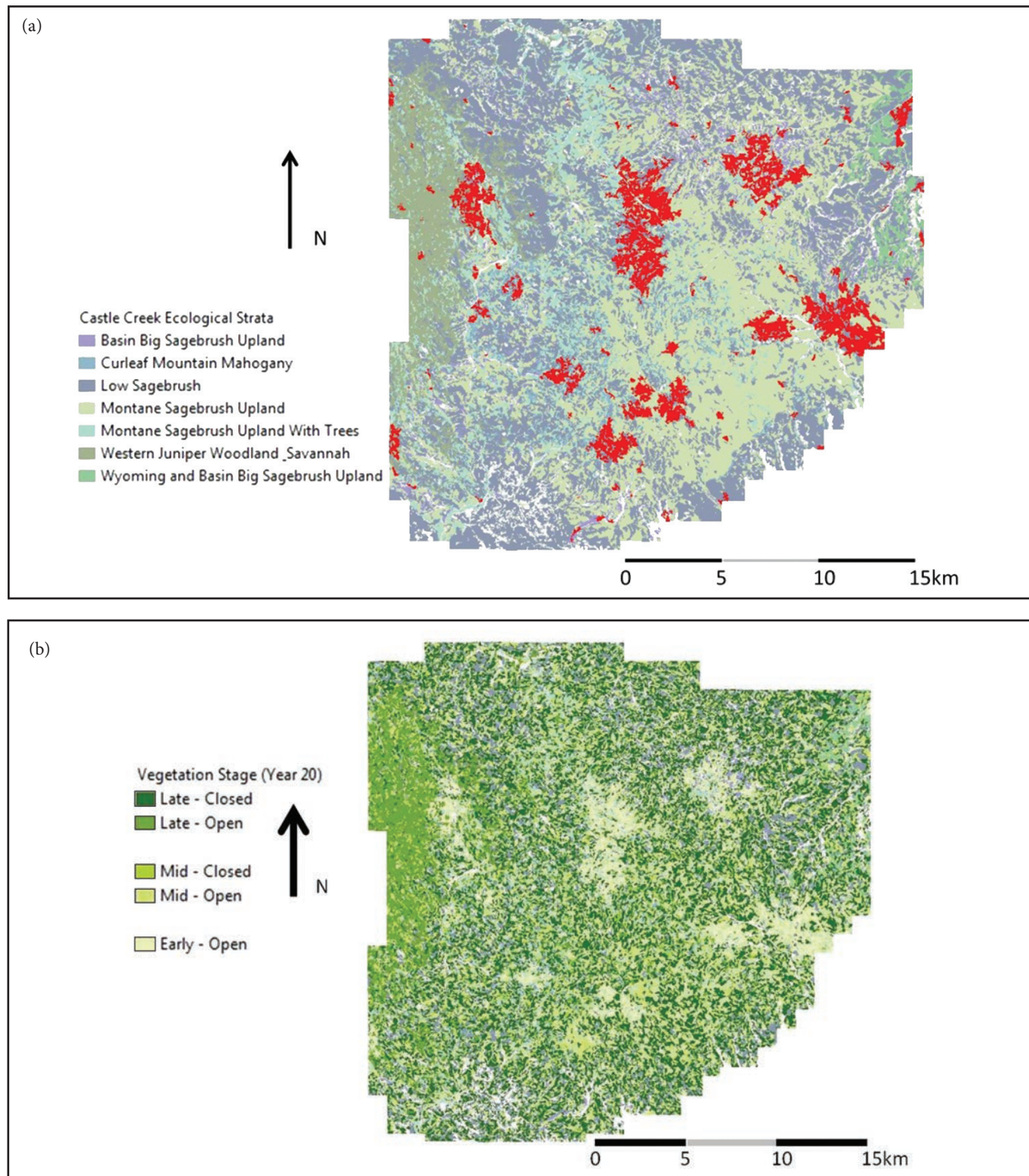


Figure 4—Sample output from a spatially-explicit STSM for the Castle Creek landscape of fig. 3. Results are shown for a single Monte Carlo iteration of a 20-year simulation. (a) Map showing cumulative area burned (in red) from year 0-20, superimposed upon ecological strata. (b) Map showing projected vegetation state in year 20.

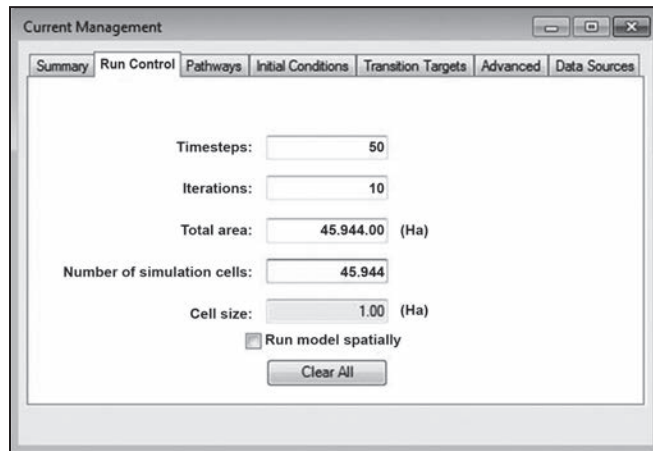


Figure 5—Sample run control settings for a STSM, as specified using the Path Landscape Model.

outputs (including maps in ArcGIS). Like VDDT, TELSA is available for free download, and continues to be supported and developed.

The last software tool for developing STSMs is the Path Landscape Model (Apex Resource Management Solutions 2012). First released in 2009, Path was designed to merge the functionality of both VDDT and TELSA, allowing users to develop and run whole landscape, spatially-stratified, and spatially-explicit STSMs all from a single platform. One of the major objectives of Path was to simplify the process of developing models and analyzing the results. Some of the important new features found in Path include the ability to develop and run spatially-stratified STSM models, including an option to specify transitions between strata, and the ability to create and run spatially-explicit STSMs using an automated connection to the TELSA simulation engine. At present, Path is being actively developed and supported, and is available for free download.

Using a software tool such as the Path Landscape Model to develop and run a spatially-stratified STSM is relatively straightforward, and typically involves the following steps:

1. Specify a number of run control parameters for the simulation, including the total number of timesteps, the number of Monte Carlo iterations, the total area of the landscape and the number of simulation cells (fig 5).

2. Divide the landscape into one or more ecological and/or land management strata and define a suite of possible states and transitions for each stratum. The list of possible strata, states and transitions is fully configurable by the user. Possible transitions between states are typically displayed as a pathway diagram for each strata. As discussed previously, there are three types of transition pathways that can be defined in STSMs: deterministic, probabilistic, and targets (fig. 6).
3. Specify the proportion of the landscape in each stratum and state (and optionally age) at the beginning of the simulation (fig. 7). For spatially-explicit simulations this information is derived directly from a user-specified polygon GIS map layer.
4. Run the simulation to generate model output. There are two basic outputs generated for every run: the area in each state over time, and the area undergoing each type of transition over time (fig. 8). If multiple Monte Carlo iterations are simulated then a range of variability around each of these model outputs can also be calculated.

In addition to the model inputs described above, running a spatially-explicit STSM in Path involves specifying the following:

1. A polygon GIS shapefile dividing the landscape into simulation cells, with an initial STSM stratum, state and age assigned to each polygon;
2. A frequency distribution for the size of STSM transition events.

With these additional model inputs, Path is then able to automatically configure and run a spatially explicit TELSA simulation. Additional details on the TELSA model algorithms can be found in Kurz et al. (2000) and ESSA Technologies (2008).

Applications

STSMs have been applied to a wide range of questions and ecological systems. While most other landscape simulation models are designed to work with only forested ecosystems, due to their empirical nature STSMs have no predetermined

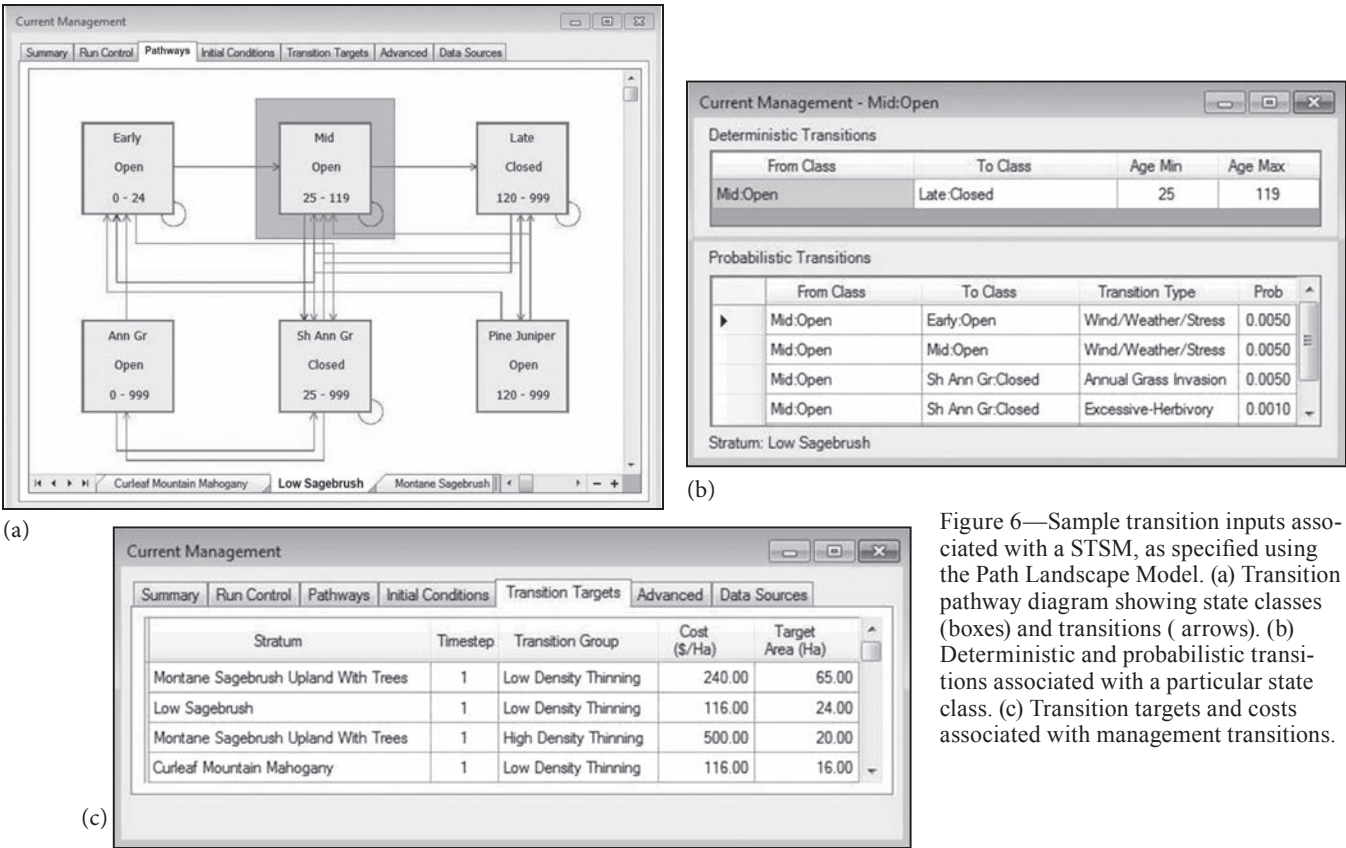


Figure 6—Sample transition inputs associated with a STSM, as specified using the Path Landscape Model. (a) Transition pathway diagram showing state classes (boxes) and transitions (arrows). (b) Deterministic and probabilistic transitions associated with a particular state class. (c) Transition targets and costs associated with management transitions.

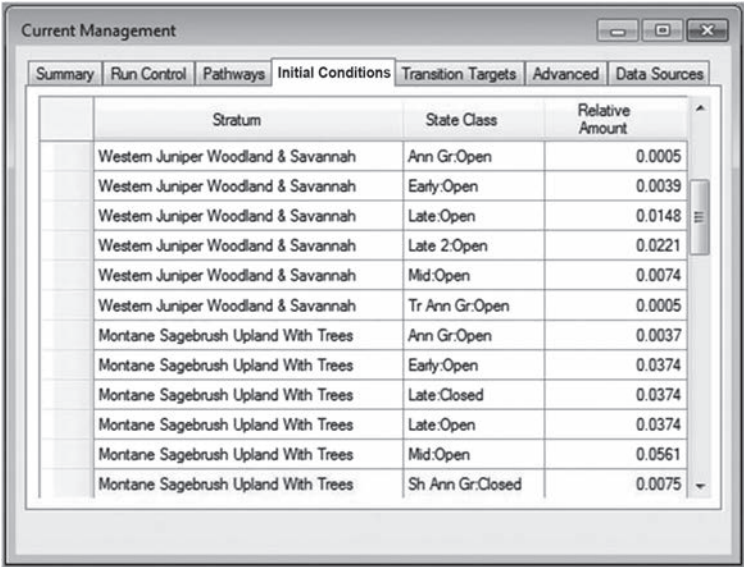


Figure 7—Sample STSM initial conditions, as specified using the Path Landscape Model.

relationships and as such can be parameterized for any suite of vegetation communities. STSMs are often used in situations where landscapes include some non-forest vegetation

types; they are also often used in situations where landscapes include non-native exotic vegetation (e.g., Forbis et al. 2006; Provencher et al. 2007; Frid and Wilmshurst 2009).

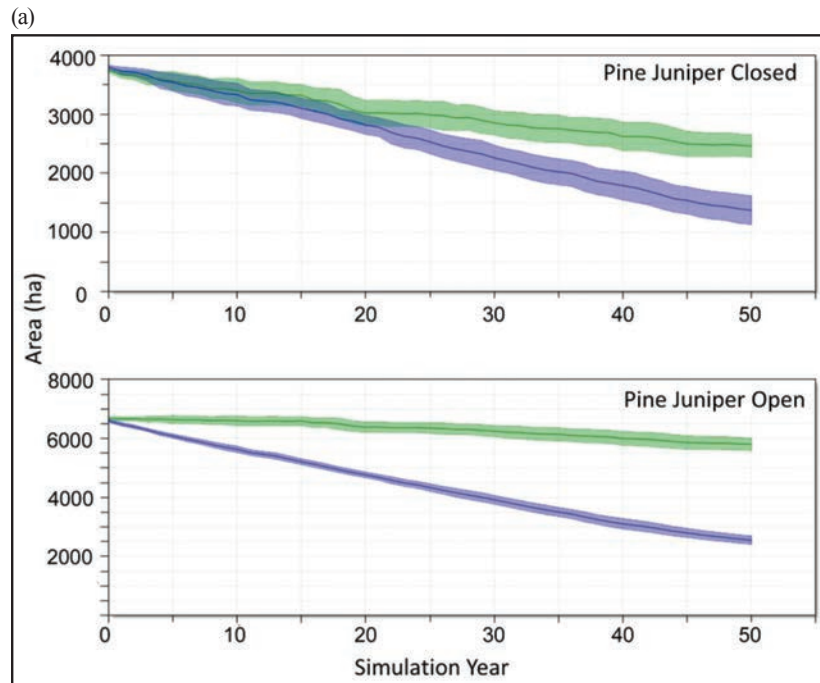
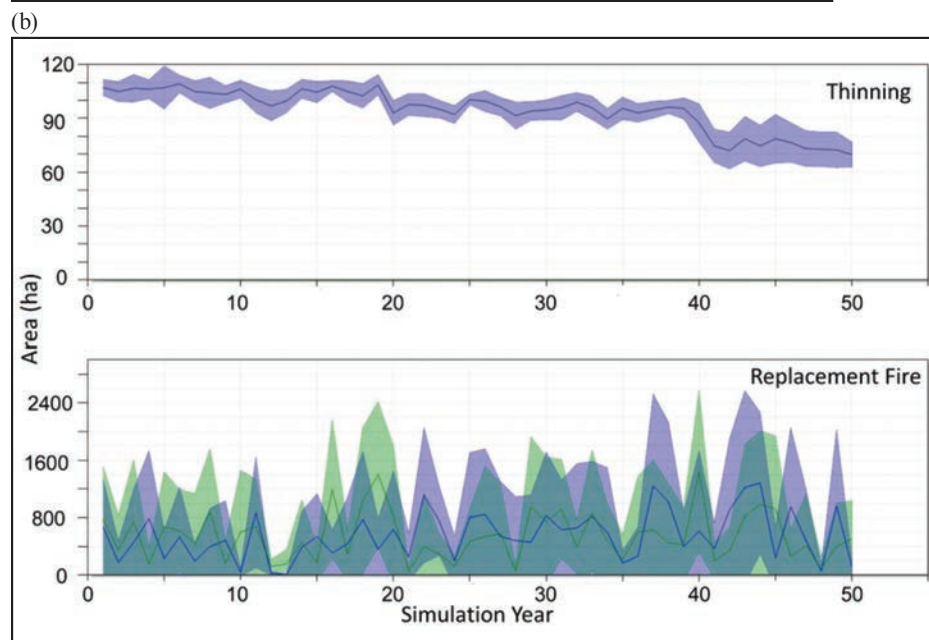


Figure 8—Sample STSM output for the Castle Creek landscape of fig. 3, comparing two simulation scenarios: No Management (green) and Current Management (blue). Shading shows 1.96 standard errors around the mean across 10 Monte Carlo iterations. (a) Area over time, across the entire landscape, in two of the model's state classes: Pine Juniper Closed and Pine Juniper Open. (b) Area over time, across the entire landscape, undergoing two of the model's transitions: Low Density Thinning and Replacement Fire.



Typically, the pathways and probabilities in STSMs are determined through analysis of historical data regarding rates of succession, disturbance and management; in situations where data is lacking, however, STSMs can be readily parameterized using literature and/or expert opinion (e.g., Czembor et al. 2011, Price et al. 2012), making the approach suitable for projects that contain at least some vegetation communities for which data and/or knowledge is limited.

Finally with STSMs there are no hidden assumptions or relationships in the models, particularly when developed using software such as the Path Landscape Model, although, as with all models, it becomes increasingly challenging to keep track of all of the relationships as the complexity of the model increases. This makes the models well-suited for decision making in situations where stakeholder engagement and consensus are important.

STSM modeling projects usually begin by developing a whole-landscape or spatially-stratified STSM; avoiding a spatially-explicit model in the early stages of a modeling project makes it much simpler to parameterize and validate an initial model. Many, but not all, modeling projects eventually convert their STSMs to a spatially-explicit form. Factors that tend to limit the development of spatially-explicit STSMs include: (1) the objectives of the analysis not requiring spatially-explicit predictions; (2) the spatial extent of the landscape being too large to run in a spatially-explicit form; (3) a shortage of spatial data and/or resources required to develop and run the more complicated spatially-explicit models.

The first known use of STSMs was in support of landscape-level vegetation modeling for the Interior Columbia River Basin Ecosystem Management Project in the U.S. Pacific Northwest (Hann et al. 1997). In this project, a spatially-stratified STSM was developed using the VDDT software. The STSM approach provided two key benefits to this project: firstly, it provided a modelling platform that could handle both forests and rangelands across a single landscape; secondly, it allowed input from both stakeholders and experts to be incorporated into the models (Kurz et al. 1999).

Since this first project, STSMs have been applied to a wide range of management questions across a variety of ecological settings (table 1). The remainder of this section provides an overview of some of the questions for which the STSM approach has been used; additional examples can be found in Kerns et al. (2012b).

Forest Ecosystems

STSMs have been used extensively to inform the management and ecology of forest ecosystems. Klenner et al. (2000) were the first to develop a spatially-explicit STSM, using it to predict the combined effects of management actions and natural disturbances on old-growth habitat and patch size changes in British Columbia, Canada. Carlson and Kurz (2007) used a spatially-explicit STSM to explore the ability of alternative timber harvest strategies to approximate natural fire patterns in a boreal mixedwood

forest of Alberta, Canada. Hemstrom et al. (2007) and Strand et al. (2009) used spatially-explicit STSMs to simulate the effects of alternative fire suppression and prescribed burning strategies on the structure and composition of forested systems in Idaho and Oregon. Klenner and Walton (2009) used a spatially-explicit STSM to predict the effects of alternative forest management treatments, such as partial cutting and fuel management treatments, on indicators of wildlife habitat, including understory productivity. Finally, a spatially-explicit STSM analysis was used to recreate the pre-European settlement structure and composition of the 12 million hectare Great Lakes St. Lawrence forest region of Ontario (Ontario Ministry of Natural Resources 2010).

Ecological Restoration

A second major application area for STSMs has been their use in supporting ecological restoration, particularly in rangeland and grassland vegetation communities. Forbis et al. (2006) developed a spatially-stratified STSM to explore the effects of alternative restoration scenarios across a 4.6 million hectare landscape of desert scrub (*Atriplex* spp. and others) and sagebrush (*Artemisia* spp.) communities in the Great Basin ecoregion of the western U.S. The model compared the effects of varying levels of fire suppression, livestock grazing, and restoration treatments on the predicted vegetation cover of native perennial understory and tree-invaded and weed-dominated states. Provencher et al. (2007) developed a spatially-explicit STSM to compare the cost and effectiveness of varying levels of managed fire, livestock grazing, and non-native species management in an effort to restore degraded vegetation types for a 140,000 hectare rangeland landscape in eastern Nevada. An STSM was developed to explore the effectiveness of alternative control strategies for the management of the invasive crested wheatgrass (*Agropyron cristatum*) in Grasslands National Park of Canada (Frid and Wilmschurst 2009); this spatially-explicit STSM included an explicit representation of the inter-annual spread of invasive vegetation across a landscape.

The Nature Conservancy (TNC) has extended the application of STSMs for ecosystem restoration to help

Table 1—Examples of past STSM applications

Reference	Ecosystems	Application	Geographic area	Spatial extent (ha)	Spatially-explicit?
Provencher et al. 2008	Rangeland	Natural range of variability	Nevada USA	18,000	No
Strand et al. 2009	Forest	Fire and aspen management	Idaho USA	37,000	Yes
Frid and Wilmschurst 2009	Grassland	Grassland invasive management	Saskatchewan Canada	42,000	Yes
Miller 2007	Forest	Wildfire regimes	Idaho USA	50,000	Yes
Wondzell et al. 2007	Aquatic/Riparian	Disturbances and salmonid habitat	Oregon USA	54,000	No
Klenner et al. 2000	Forest	Management and wildlife habitat	British Columbia Canada	63,000	Yes
Low et al. 2010	Rangeland/Forest	Conservation planning	California USA	76,000	No
Klenner and Walton 2009	Forest	Management and wildlife habitat	British Columbia Canada	100,000	Yes
Provencher et al. 2007	Rangeland	Restoration and invasive management	Nevada USA	142,000	Yes
Hemstrom et al. 2007	Forest/Rangeland	Fuel and wildfire management	Oregon USA	178,000	No
Zweig and Kitchens 2009	Wetland	Wetland hydrology management	Florida USA	200,000	No
Czembor and Vesik 2009, Czembor et al. 2011	Forest	Restoration	Victoria Australia	250,000	No
Carlson and Kurz 2007	Forest	Harvest and landscape pattern	Alberta Canada	270,000	Yes
Price et al. 2012	Forest	Forest management and climate change	Michigan USA	272,000	Yes
Forbis et al. 2006	Rangeland	Restoration and invasive management	Great Basin USA	4.3 million	No
Ontario Ministry of Natural Resources 2010	Forest	Pre-European settlement conditions	Ontario Canada	11.9 million	Yes
Rollins 2009, Swaty et al. 2011	Terrestrial	Assessment of ecological departure	Entire USA	~900 million	No
Kerns et al. 2012b	Various	12 papers covering a range of applications	Worldwide	Various	Yes and no

them determine how to get the best return on the restoration investment (Low et al. 2010). As part of their conservation planning process, TNC first uses an STSM approach to help predict how far departed a landscape is from “desired” condition; they then extend this reference STSM to explore how alternative future management actions will change the vegetation composition and structure of the landscape, and use this to predict which combination of management actions, on a per unit cost basis, will move the landscape most cost-effectively towards their desired condition.

Aquatic/Riparian Ecosystems

In addition to their long-standing application to upland vegetation communities, STSMs have also been developed for use in aquatic and riparian systems. A spatially-stratified STSM was developed to evaluate the effects of disturbances and land management practices, such as grazing, flooding, debris flows and wildfire disturbances, on riparian and aquatic vegetation for a river system in Oregon (Wondzell et al. 2007). In this STSM the states were defined by channel morphology and riparian vegetation, and model output was interpreted in terms of its suitability as habitat for anadromous salmonids. As a second example, Zweig and Kitchens (2009) developed a non-spatial STSM for predicting the effects of alternative hydrological regimes on wetland vegetation in the Florida Everglades.

Regional Land Management

Finally, because of their flexibility in handling a wide range of vegetation types and varying data availability, STSMs are well suited for use in regional and national land management initiatives. For example, the LANDFIRE program, a 5-year national, multi-agency project, developed over 1200 STSM models to predict the pre-European settlement conditions for all of the major ecosystems of the United States (Rollins 2009, Swaty et al. 2011). The Integrated Landscape Assessment Project (ILAP), a 3-year project to prioritize land management actions in the western U.S., developed over 200 STSMs, one for every potential vegetation type (PVT) found across all lands in Arizona, New Mexico, Oregon and Washington (Hemstrom et al. 2012).

Conclusions

STSMs provide a simple, flexible approach for predicting landscape-level vegetation change in response to both natural disturbances and management actions. They are stochastic, empirical simulation models, based on a Markov chain approach, that predict how vegetation will transition between states over time across a landscape. With STSMs a landscape is divided into a set of simulation cells (e.g. either raster pixels or polygons), each cell is assigned an initial vegetation state, and then the model predicts how the state of each cell changes over time. Spatial processes are typically represented in STSMs in one of two ways: by stratifying the landscape into zones that behave similarly with respect to vegetation change, and then representing each of these strata with its own non-spatial STSM; or alternatively, by creating a spatially-explicit STSM for the landscape in which the dynamics of every simulation cell is potentially dependent on its neighbours.

Over the past 20 years, the software available for developing STSMs has evolved considerably. Modellers are now able to represent an array of complex dynamics, including tracking and modifying the age-structure of the landscape, setting transitions to be contingent on past events, providing targets for transition areas (e.g. for forest harvest and management treatments), changing transition probabilities over time (e.g., due to climate change), and spreading disturbances across a landscape (e.g., for fire and invasive species).

As with all models, there are limitations to the use of STSMs for predicting vegetation change. Likely the most significant limitation is their purely empirical nature, whereby model relationships are typically fitted to existing knowledge and data. This makes it challenging to use the models to make predictions under novel conditions, as knowledge and data may not exist upon which to base the input parameters. To overcome this limitation users are increasingly turning to other, more specialized models to inform the model inputs for STSMs; for example Kerns et al. (2012a) have used the MC1 dynamic global vegetation model to incorporate climate change effects into STSMs, while others have used output from the Forest Vegetation

Simulator (FVS) to calibrate transition probabilities in STSMs (Shlisky and Vandendriesche 2012; Weisz and Vandendriesche 2012). This approach allows modellers to combine the integrative capabilities of STSMs with the mechanistic capabilities of other models. A second limitation with STSMs is that all relationships must be ultimately be expressed in terms of a Markov chain. This restriction can be limiting in certain circumstances: for example while it might be desirable to represent post-fire succession as a Markov chain, the fire spread component of the model might be better represented using a more mechanistic simulation approach. At present it is not possible to create such hybrid modeling approaches with STSMs. Efforts are underway, however, to extend the capabilities of STSM software (i.e. the Path Landscape Model) so that it can dynamically link to other models; this would provide the capability to generate hybrid modelling approaches, whereby external models could be called upon to provide specialized predictions within an STSM model run.

The STSM approach has been applied to a wide range of management questions and vegetation communities. Because STSMs can be developed for any vegetation community, they are well suited for landscapes that include a range of vegetation types. Examples of ecosystems in which STSMs have been developed include those with forest, rangeland and wetland components; they have also been used extensively to represent the dynamics of non-native (i.e., invasive) species. The spatial extent over which STSMs have been applied ranges from a few thousand to millions of hectares. Finally, STSMs are well suited for use in situations with imperfect knowledge or data, as the models can be parameterized, when necessary, using expert opinion, and a wide range of scenarios can be simulated to represent uncertainty in model inputs.

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