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A new model to simulate climate-change impacts on forest succession for local land management

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Abstract. We developed a new climate-sensitive vegetation state-and-transition simulation model (CV-STSM) to simulate future vegetation at a fine spatial grain commensurate with the scales of human land-use decisions, and under the joint influences of changing climate, site productivity, and disturbance. CV-STSM integrates outputs from four different modeling systems. Successional changes in tree species composition and stand structure were represented as transition probabilities and organized into a state-and-transition simulation model. States were characterized based on assessments of both current vegetation and of projected future vegetation from a dynamic global vegetation model (DGVM). State definitions included sufficient detail to support the integration of CV-STSM with an agent-based model of land-use decisions and a mechanistic model of fire behavior and spread. Transition probabilities were parameterized using output from a stand biometric model run across a wide range of site productivities. Biogeographic and biogeochemical projections from the DGVM were used to adjust the transition probabilities to account for the impacts of climate change on site productivity and potential vegetation type. We conducted experimental simulations in the Willamette Valley, Oregon, USA. Our simulation landscape incorporated detailed new assessments of critically imperiled Oregon white oak (*Quercus garryana*) savanna and prairie habitats among the suite of existing and future vegetation types. The experimental design fully crossed four future climate scenarios with three disturbance scenarios. CV-STSM showed strong interactions between climate and disturbance scenarios. All disturbance scenarios increased the abundance of oak savanna habitat, but an interaction between the most intense disturbance and climate-change scenarios also increased the abundance of subtropical tree species. Even so, subtropical tree species were far less abundant at the end of simulations in CV-STSM than in the dynamic global vegetation model simulations. Our results indicate that dynamic global vegetation models may overestimate future rates of vegetation change, especially in the absence of stand-replacing disturbances. Modeling tools such as CV-STSM that simulate rates and direction of vegetation change affected by interactions and feedbacks between climate and land-use change can help policy makers, land managers, and society as a whole develop effective plans to adapt to rapidly changing climate.

Key words: agent-based model; disturbance; dynamic global vegetation model; Envision; fire; MCI; Oregon; state-and-transition simulation model; Willamette Valley.

INTRODUCTION

Human activities dominate and alter terrestrial ecosystem dynamics through both anthropogenic climate change and land-use change, among other factors (Vitousek et al. 1997). Changes in land use and land

cover contribute to complex feedbacks between human activities and ecosystems in space and time (Farber et al. 2006). Projecting the interactive effects of climate change and land-use decisions is therefore crucial to managing ecosystems (Keane et al. 2004). To do so effectively requires mechanistic simulations of climate change, land management, ecological succession, and disturbance at a fine spatial grain commensurate with the scales at which human decision-making takes place (Bone et al. 2013, Keane et al. 2013, King et al. 2013).

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Dynamic global vegetation models (DGVMs) are a leading way to evaluate the potential for changes in vegetation under future climate-change scenarios (Kucharik et al. 2006, Gavin et al. 2007, Littell et al. 2010). These models are diverse, but in general include biogeochemical, physiological, and disturbance mechanisms to simulate changes in vegetation (Moorcroft 2006). DGVMs have also been used at regional scales to provide public and private land managers better information on how climate affects vegetation (Koca et al. 2006, Rogers et al. 2011). To be globally applicable, however, DGVMs must simplify their representation of vegetation and landscapes. Most DGVMs describe vegetation in broad plant functional types and physiognomic groups, rather than specifying individual plant species and vegetation communities (Bachelet et al. 2001). While some DGVMs may include management (Albani et al. 2006), management is not simulated mechanistically based on human decision processes. In addition, most DGVMs use a spatial grain that is coarser than the spatial grain at which land-use decisions are made (Hurtt et al. 1998). Successful modeling projects have incorporated land-management changes into climate-sensitive vegetation modeling (Scheller and Mladenoff 2005, Scheller et al. 2007), but these projects are limited by having gridded spatial units that do not conform to underlying topographic variation, and are not able to move dynamically between “natural” and “developed” land cover. Plant community structure and composition are the dynamic products of species-specific plant growth and mortality as determined by local environmental conditions, nonanthropogenic disturbances, and human influences. To the extent that DGVMs limit the dynamic representation of these processes, and simulate them coarsely, nonmechanistically, or not at all, their projections are unlikely to predict future vegetation dynamics accurately.

Furthermore, DGVMs must “spin-up” to equilibrate carbon and nutrient pools, and then predict potential vegetation dynamics from the specified climate and soil inputs. Current vegetation, however, is often strongly determined by the legacy of previous land use and land cover. Priority effects can be important determinants of future successional dynamics (Pfeifer-Meister et al. 2012). Thus, DGVMs may provide projections that further diverge from current and future conditions if their assessment of growing conditions does not match that of the current landscape (Van Vuuren et al. 2011).

For these reasons, three ecological modeling innovations would substantially advance simulations of climate-change impacts on vegetation in human-dominated landscapes. The first is to couple DGVM projections with models that operate at sufficiently fine spatial grains to incorporate land-use decisions and disturbances. The second is to use current vegetation as a starting point for future simulations. The third is to

integrate mechanistic models of land management and wildfire with a vegetation model at the same high-resolution spatial scale.

To investigate how changes in climate and policy might interact to influence vegetation dynamics, we developed a new modeling tool, the Climate-sensitive Vegetation State-and-Transition Simulation Model (CV-STSM). Our implementation of CV-STSM achieves the three innovations identified above. The new model integrates components and outputs from four modeling systems to simulate the interactions of climate change and human land-use decisions on vegetation succession. CV-STSM (1) simulates changes in vegetation productivity and plant physiognomic type based on changes in climate using a DGVM, (2) links the resultant plant physiognomic types to locally relevant plant community types in terms of species composition and vegetation structure as defined within a state-and-transition simulation model (STSM), (3) allows for growth of, and competition among, tree species to drive vegetation succession using a stand biometric model, and (4) supports mechanistic simulations of human land-use decision-making through a spatially explicit agent-based model. The resulting model is spatially explicit and probabilistic, allowing for examination of changes in land cover over decades, while retaining deterministic changes in future climate and the DGVM’s vegetation classes.

Repeated simulations with the model allowed exploration of a broad range of potential future conditions. In the following section, we describe the development of CV-STSM and its components. We then describe a series of simulations using CV-STSM in the southern Willamette Valley, Oregon, USA, where regional planning efforts have recently focused on climate change and the conservation of critically imperiled savanna and prairie ecosystems. The simulations demonstrate CV-STSM’s functionality across a range of climate-change scenarios and levels of landscape disturbance for the coming century.

MATERIALS AND METHODS

Model design

CV-STSM integrates inputs and outputs from existing models and incorporates them within a highly adaptable state-and-transition simulation-modeling framework (Fig. 1A). In the following subsections, we describe the general model structure, and then describe modifications and parameterizations for our study area (see *Model parameterization* and Appendices A and B). There are numerous facets to our larger modeling framework (Fig. 1B). In this paper, we focus on the vegetation-modeling component, which can run independently from the other components.

Spatial framework.—To include mechanistic and spatially explicit land-use decision-making, we built CV-STSM as a vegetation module within the agent-

based model Envision (*available online*).¹¹ Envision operates in a geographic information system (ArcGIS; Esri 2009) environment (Bolte et al. 2006, Guzy et al. 2008). The central feature of Envision is a spatially explicit model of human decisions that can be linked to other models.

The spatial grain at which agents make decisions in Envision is referred to as an integrated decision unit (IDU). Agents make choices based on a set of actions (termed policies) that are available to them, their propensities for different types of actions, and feedbacks from the changing landscape, thus allowing for the emergence of complex model behavior. An IDU's vegetation can change due to agent decisions, ecological succession, or disturbance.

Plant community state definitions.—State-and-transition simulation models (STSMs) are relatively simple conceptual depictions of dynamic systems that can be reduced to a finite number of discrete conditions and transitions among them (Daniel and Frid 2012). STSMs are commonly used in highly applied settings, such as forestry (Haefner 2005). One advantage of STSMs is that they are highly adaptable. For example, users may define plant communities by the specific features they deem important, and for which data are available. For this project, we modified an existing STSM framework developed for classifying vegetation types in the program VDDT (Vegetation Dynamics Development Tool; ESSA Technologies, Vancouver, British Columbia, Canada), which is widely used in ecological management. We defined plant community states based on four characteristics: dominant and subdominant tree species, quadratic mean stem diameter, canopy closure, and canopy layering, as is common in forestry applications.

Transition probability initialization.—Empirical data and expert judgment may be used to initialize transitions in an STSM (Scanlan 1994, Czembor and Vesk 2009, Daniel and Frid 2012, Kerns et al. 2012). Additionally, transitions may be deterministic or probabilistic. In CV-STSM, all transitions are probabilistic. We used the Forest Vegetation Simulator (FVS; Crookston and Dixon 2005) to generate the initial transition probabilities for CV-STSM based on plot-level data from a large number of forest stands (Moeur and Vandendriesche 2010, Weisz and Vandendriesche 2012; FVS is *available online*).¹² FVS was developed by the United States Forest Service and is widely used throughout the United States. FVS projects forest development based on regionally derived statistical relationships, using lists of trees (species, size, and condition) as both input and output. Tree growth and mortality projections are largely deterministic for any given tree list. We assembled tree lists from multiple existing data sources to capture variability within each vegetation state; these yielded different stand developmental trajectories and

allowed us to calculate transition probabilities into other states. The tree lists capture existing vegetation as well as representations of potential future stand types and growth conditions. FVS represents site productivity using site index (SI), which is the height to which a tree of a representative species grows in 50 years. For our study area, the representative species is Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). SI is used to predict the effects of productivity on tree growth, competition, and mortality. We varied SI in our parameterization simulations to account for spatial differences in SI and changes in productivity due to climate change, as described briefly in Kerns et al. (2012) and in the following section.

Transition probability modifications and emergence of novel communities.—Because FVS assumes an unchanging climate, we used estimates of site productivity and plant community types from the DGVM MC1, a dynamic vegetation model developed by the USDA (Bachelet et al. 2001, Lenihan et al. 2008), to adjust transition probabilities in CV-STSM over time (Kerns et al. 2012, Yospin 2012; *available online*).¹³ MC1's projections are sensitive to changes in input variables (e.g., climate and soils data), model parameters (e.g., sensitivity of productivity to changing atmospheric CO₂ concentration), and emergent properties (e.g., fire disturbance regime and nutrient availability). The current implementation of MC1 in the northwest United States is on a 30-arc-second grid, which translates to approximately 800-m grid cells (Rogers et al. 2011). A potential vegetation map, constrained by long-term biogeographic and hydrologic averages to avoid transient anomalies, initializes vegetation cover in MC1. A spin-up phase with detrended historic climate data initializes carbon pools under a variety of fire regimes. MC1 then runs through a 100-year historical period with observed climate data. Finally, MC1 provides projections of biogeochemical cycling and vegetation dynamics for each pixel (grid cell) in the landscape on a monthly time step in the future based upon downscaled output from general circulation models. The fire sub-model within MC1 (Lenihan et al. 1998) distributes the carbon pools into fuel categories, calculates the moisture content of these fuels, and then removes carbon from the appropriate pools on a cell-by-cell basis after a fire. MC1's projection of potential vegetation types (PVT) is based on broad physiognomic types (e.g., temperate maritime evergreen needleleaf forest), which we were able to interpret in terms of community types and dominant tree species already in our study area. We used these projections of PVT to constrain the STSM to those species and community types that might become dominant locally under climate change. We also used correlations between MC1 output and SI to dynamically adjust SI annually, thus allowing climate-driven changes

¹¹ <http://envision.bioe.orst.edu>

¹² <http://www.fs.fed.us/fmsc/fvs/>

¹³ <http://www.fsl.orst.edu/dgvm/>

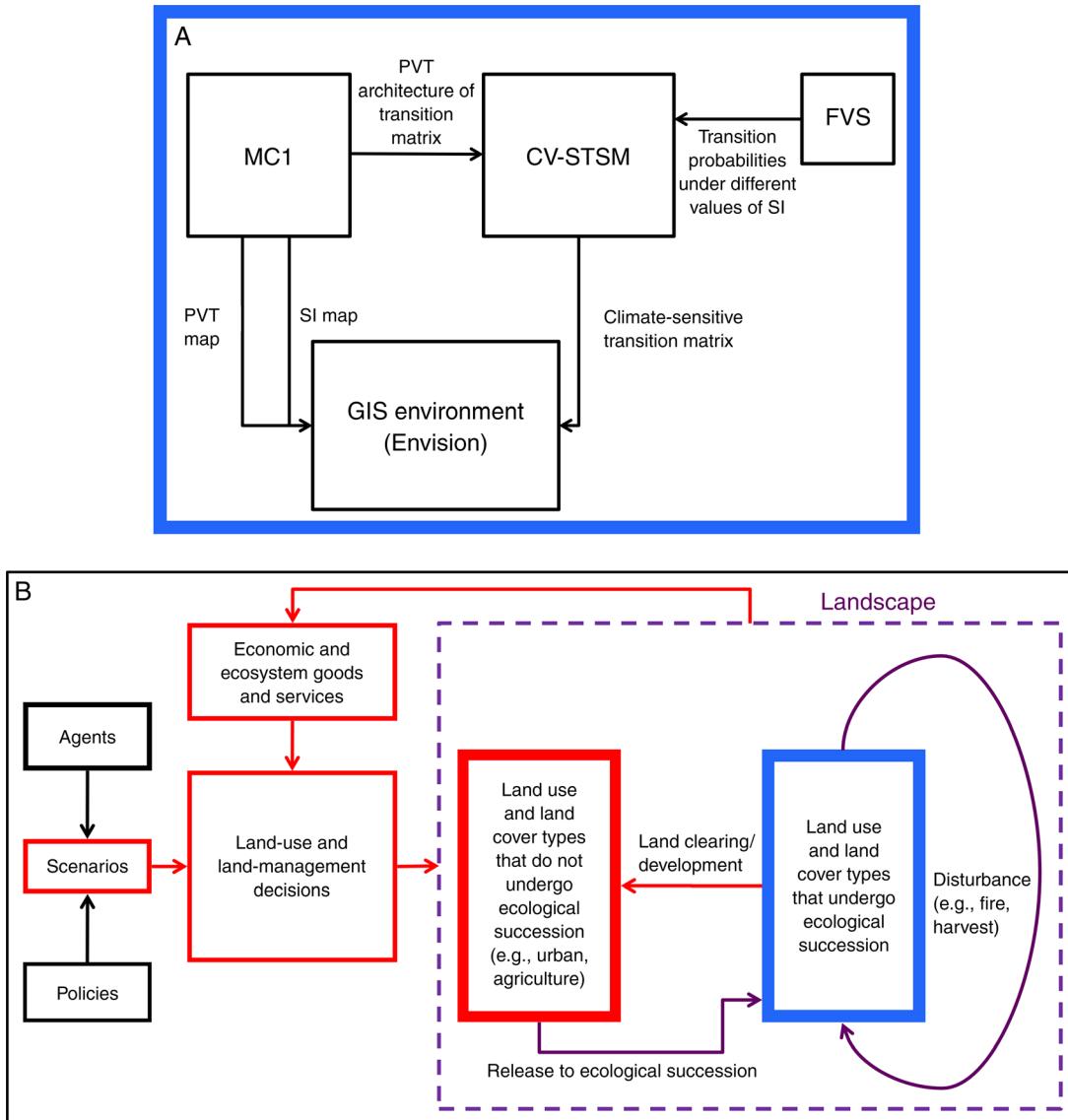


FIG. 1. (A) Schematic diagram of climate-sensitive vegetation state-and-transition simulation model (CV-STSM) coupled with MC1, Forest Vegetation Simulator (FVS), and Envision. (B) The role of the coupled vegetation modeling from panel (A) (contained within the purple box) within the larger land-use decision model. Abbreviations are PVT, potential vegetation type; SI, site index; GIS, geographic information system. FVS, MC1, and Envision are existing computer models. The arrows show data moving from one module to another, within Envision modules governing land use and land cover types that undergo ecological succession (Fig. 1A) and within all Envision modules (Fig. 1B).

in successional rates for each Envision IDU. While STSMs are generally used for nonchanging climates, by coupling transition probabilities and an expanded range of possible states to the dynamics of a climate-sensitive DGVM, we combined the utilities of both types of technology.

Design summary.—Our model (CV-STSM) integrates climate-driven changes in tree growth potential and broad plant physiognomic groups from a DGVM (MC1) with a model of tree growth rates and successional trajectories for regional plant community types (FVS) through a state-and-transition framework

(VDDT) to create vegetation transition probabilities that are functions of time, SI, and PVT. CV-STSM allows for finer description of local plant communities than DGVMs, uses current vegetation as the starting point for future projections, uses large local data sets for parameterization of transitions, allows for the incorporation of specified types of land-use decisions, and achieves this at a fine spatial grain that is appropriate for informing local management decisions (Fig. 1). Transitions within CV-STSM were trained by FVS using existing regional data. With space- and time-filling maps of MC1 output for projected PVTs and SI, CV-STSM

can modify and constrain transitions to incorporate spatially and temporally explicit effects of climate change on successional trajectories.

In this paper, CV-STSM uses Envision solely as a GIS framework to provide climate-sensitive spatial input data. However, if the full capabilities of Envision are used, simulations of vegetation change in CV-STSM can be coupled to mechanistic simulations of wildland fire behavior, other ecological disturbance processes, and to agent-based human decision modeling (Fig. 1B).

Study area

Our study area is located in the southern Willamette Valley, Oregon, USA (Fig. 2). The 820-km² study area is bounded by the Eugene-Springfield metropolitan area's urban growth boundary (population 256 000) and the edges of the Willamette Valley ecoregion (Hulse et al. 2002). It encompasses three incorporated towns ranging from 1000–8000 people each, as well as extensive wildland–urban interface. The study area includes approximately 89 000 IDUs; the maximum mapping unit is 5 ha and the majority of IDUs are 1 ha or less. Elevation ranges from 115 m on the Willamette Valley floor to 630 m in the Cascade Mountain foothills. Extant vegetation is diverse and includes prairie, savanna, woodland and forest, as well as agricultural lands. The dominant conifer forest type, both now and in the late 19th century, is Douglas-fir forest. Plant communities that contain Oregon white oak (*Quercus garryana* Douglas ex Hook.) are particularly valued in the Pacific Northwest, and conservation and restoration of open Oregon white oak habitats is emerging as a conservation priority (Ulrich 2010, Michalak 2011). Accordingly, we took extensive efforts to accurately map oak communities in the current landscape and to model their successional trajectories.

When we performed simulations for the future period, we did so only for areas that had “natural” vegetation at the beginning of the simulation (2007). Many of the areas that were the highest-quality oak habitat prior to Euro-American settlement have been converted to agricultural uses or urbanized, and are therefore not included in any future simulations.

Model parameterization

State-and-transition simulation model.—We created a customized STSM to describe both current and potential future vegetation at a level of detail that would allow us to simulate the successional trajectories of plant communities within the study area. We classified species assemblages into eight ecologically related cover types defined by dominant and subdominant tree species, relying on previous fieldwork (Day 2005, Sonnenblick 2006, Murphy 2008) and knowledge of these communities. Based on the projections of potential vegetation from previous work with MC1, we added four cover types to the STSM to represent future PVTs not present in the contemporary landscape: (1) ponderosa pine (*Pinus*

ponderosa Lawson and C. Lawson) savanna, (2) ponderosa pine woodland, (3) Pacific madrone (*Arbutus menziesii* Pursh) woodland and forest, and (4) Pacific madrone and Douglas-fir forest. The four new cover types contain tree species that are present but not dominant in the current landscape (Table 1). New species could migrate into the study area (or escape from horticultural plantings) to form other cover types, but tree species that could represent future MC1 PVTs already exist in the landscape. We therefore assumed that the immigration and emerging dominance of new tree species was not necessary to simulate during the relatively short (93 year) time frame of our simulations.

We defined 111 discrete states in 12 cover types, and linked each cover type to corresponding potential vegetation types from MC1 (Table 1). To define states, we used four parameters: dominant tree species (the cover type), quadratic mean stem diameter (five classes), canopy closure (three levels), and canopy layering (one or two layers). Quadratic mean diameter is a weighted mean that emphasizes larger trees in a stand. To assign initial states to the landscape, we collected descriptions of vegetative cover from five existing data sources and used them to generate the four parameters needed to assign a vegetation state to each IDU. We especially scrutinized these data sets to describe prairie and oak savanna habitats, which currently have limited distributions.

Transition probability initialization.—To generate transition probabilities for our STSM, we applied the rates of tree growth and successional changes projected by a newly revised version of the Pacific Northwest variant of FVS (Gould et al. 2011). The revisions incorporate modifications to the height, growth rate, competitive dynamics, and mortality of Oregon white oak that were assessed as part of our larger research effort. We ran FVS using multiple tree lists to initialize and train the transition probabilities in our STSM. Tree lists came from over 2000 plots from several data sets in southern and western Oregon, principally from the Forest Inventory and Analysis database (Woudenberg et al. 2010; *available online*).¹⁴ The tree lists were binned into STSM states based on the four parameters described above. Plot data from western Oregon (Willamette Valley to southwestern Oregon) provided sufficient replicates of each current and future state. To simulate tree regeneration, we used averaged data from over 1000 plots that included seedling data. FVS runs were performed with and without tree regeneration. We ran each of these tree lists for 100 years at a wide enough range of SI values to describe current and future landscapes, and then re-binned the output tree lists into STSM states. Our use of multiple tree lists for each state resulted in many possible successional trajectories in FVS, from which we calculated the values of annual transition probabilities.

¹⁴ <http://www.fia.fs.fed.us/>

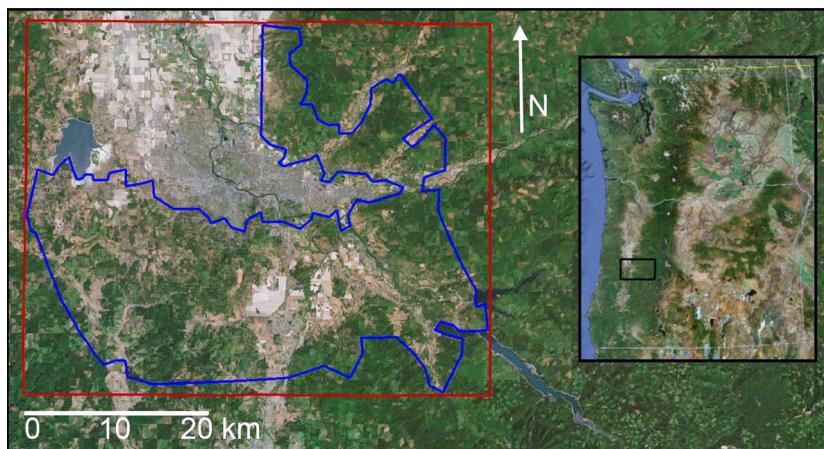


FIG. 2. Satellite imagery of the study area location in the Willamette Valley, Oregon, USA. The red rectangle represents the bounding box for the MC1 simulations. The blue line surrounds the study area. Source: Google Earth; 43°59'22.69" N, 122°53'05.26" W. Image made on 1 August 2011.

Transition probability adjustments and constraints.—

1. *MC1 customization*—A major goal of our project was to develop a way to begin our simulations on the present landscape with a version of MC1 that matched observed historical vegetation, rather than providing estimates of potential natural vegetation. Doing so would avoid undesirable sudden changes between the historical future simulation periods (Van Vuuren et al. 2011). In previous simulations with MC1 (Rogers et al. 2011), the historical period (1895–2006) yielded a temperate maritime evergreen needleleaf forest (which we equate to Douglas-fir forest in our study domain), instead of the prairie and savanna habitats that existed within the study

area in the mid-to-late 19th century (Habeck 1961). It is likely that the emergent fire behavior regime in MC1 drastically underestimated historical fire frequency, which was influenced by recurring burning by indigenous people (Christy and Alverson 2011). To explore the consequences of this underestimation, we built new adjustable parameters into MC1 that allowed us to specify the fire return interval and the burn date during the spin-up phase. We then examined MC1 output variables using fire return intervals of 3, 5, 10, 15, and 20 years, from the 150th to the 300th day of the year, by steps of 25 days (appropriate for the fire season of the region's Mediterranean climate) during the spin-up phase.

TABLE 1. State-and-transition simulation model (STSM) tree cover types with dominant and associated local species.

STSM cover type	Dominant species description	Dominant species	Associated species
Oak savanna	drought-tolerant broadleaf deciduous	<i>Quercus garryana</i>	<i>Quercus kelloggii</i>
Oak woodland	drought-tolerant broadleaf deciduous	<i>Quercus garryana</i>	
Oak and Douglas-fir woodland	drought-tolerant broadleaf deciduous and needleleaf evergreen	<i>Quercus garryana</i> , <i>Pseudotsuga menziesii</i>	
Douglas-fir and oak woodland	drought-tolerant broadleaf deciduous and needleleaf evergreen	<i>Pseudotsuga menziesii</i> , <i>Quercus garryana</i>	
Douglas-fir forest	less mesic needleleaf evergreen	<i>Pseudotsuga menziesii</i>	<i>Calocedrus decurrens</i> , <i>Pinus ponderosa</i>
Douglas-fir and maple forest	mesic needleleaf evergreen and broadleaf deciduous	<i>Pseudotsuga menziesii</i> , <i>Acer macrophyllum</i>	<i>Thuja plicata</i> , <i>Tsuga heterophylla</i>
Douglas-fir and grand fir forest	more mesic needleleaf evergreen	<i>Pseudotsuga menziesii</i> , <i>Abies grandis</i>	
Bigleaf maple forest	mesic broadleaf deciduous	<i>Acer macrophyllum</i>	<i>Alnus rubra</i> and <i>A. rhombifolia</i> , <i>Fraxinus latifolia</i> , <i>Populus balsamifera</i>
Pine savanna	xeric evergreen needleleaf	<i>Pinus ponderosa</i>	
Pine woodland	xeric evergreen needleleaf	<i>Pinus ponderosa</i>	
Madrone woodland and forest	evergreen broadleaf	<i>Arbutus menziesii</i>	
Madrone and Douglas-fir forest	evergreen broadleaf and needleleaf	<i>Arbutus menziesii</i> , <i>Pseudotsuga menziesii</i>	

Many combinations of fire return interval and burn day created vegetation conditions that were similar to observed vegetation in the study area prior to Euro-American settlement. We chose to use a 10-year fire return interval, burning on day 197, during the spin-up phase. We then simulated the historical period with fire disabled in MC1 to mimic both the loss of indigenous burning and active fire suppression that occurred in the study area. Only a few years after removing fire from the system, vegetation in the MC1-simulated study area quickly approached values associated with a dense Douglas-fir forest, matching observations of the directions of successional change, albeit with changes occurring more rapidly in the model than in reality.

We turned off the fire model in MC1 to simulate the future period, except when we wanted to explore the full range of MC1 outputs. We did so (1) to distinguish direct climate effects on vegetation from interactive effects with disturbance and (2) to allow the incorporation of a different mechanistic fire model, FlamMap (Finney 2006), in Envision (G. I. Yospin, *unpublished data*; FlamMap *available online*).¹⁵

2. *MC1 future projections.*—We explored MC1's dynamics under three general circulation models (GCMs), Hadley (Met Office Hadley Centre for Climate Prediction and Research, Devon, UK [Johns et al. 2003]), MIROC (model for interdisciplinary research on climate; Center for Climate System Research, University of Tokyo, Japan [Hasumi and Emori 2004]), and CSIRO (Commonwealth Scientific and Industrial Research Organisation, Clayton South, Australia [Gordon et al. 2002]), all run under the A2 emissions scenario (Nakićenović et al. 2000), because it is unlikely that human emissions will be less than this scenario (Raupach et al. 2007). The land-use changes inherent in these scenarios are at present the only land-use changes explicitly represented in the CV-STSM. To explore the effect of CO₂ fertilization in MC1 on future vegetation dynamics, we examined six future climate scenarios, three GCMs crossed with two CO₂ fertilization parameterizations. Analysis of the output under varying CO₂ fertilization scenarios indicated that, for our study area, MC1 was insensitive to changing vegetation sensitivity to CO₂ fertilization (see Appendix C). Thus, despite findings showing the importance of CO₂ fertilization in many regions (Norby et al. 2005), further analyses in this manuscript consider only the three GCMs using the A2 emissions scenarios and moderate vegetation sensitivity to atmospheric CO₂.

MC1 output showed modest trends over time in variables associated with productivity. Over 93 years of simulation time, carbon pools generally changed by only 5–10%. In contrast, MC1 showed large changes in potential vegetation types. At simulation year 0 (2007 AD), the study area was a mix of three PVTs. The dominant PVT (~85% of the landscape) was temperate

maritime evergreen needleleaf forest in the bounding rectangle around the study area, which we interpret as representing Douglas-fir forest (Table 1). About 15% of the area began in the subtropical mixed broadleaf and needleleaf evergreen forest, which can be interpreted as representing mixed Douglas-fir and oak or madrone forest. There were also six grid cells (~0.2% of the landscape) that were projected to be C₃ grassland. According to MC1, these remained C₃ grassland for all climate scenarios at all time points, most likely due to their shallow soils.

The time to reach the final PVT in MC1 depended on the GCM. All simulations showed some degree of switching between the subtropical mixed broadleaf and the maritime evergreen needleleaf forest potential vegetation types. When using the Hadley model, the landscape also included the continental needleleaf evergreen forest potential vegetation type (similar to interior ponderosa pine forests/savannas) across a substantial area, mostly between simulation years 30 and 50. All simulations agreed on the ultimate dominance of subtropical mixed broadleaf and needleleaf evergreen forest PVT, which was essentially the only PVT present by the end of the simulation period in 2099. The rapid and dynamic shift between vegetation types over the course of the simulations stems from the study area location, near the confluence of the three bioclimatic zones (maritime temperate, continental temperate, and subtropical; Kuchler 1964) and from the sensitivity of MC1 to projected climate changes in the study area.

With fire turned on, MC1 simulated three spatially large, low-intensity fires near the end of the simulation period (2077–2099) for all climate scenarios. These fires did not alter MC1's projections of PVT, and had only minor effects on MC1 output variables. These findings indicate that turning off the fire model in MC1 had only a minor effect on projections of MC1 output variables. Because we turned off the fire model in MC1, however, our reported results with MC1 will disagree with previous research using MC1 for regions that include our study area (e.g., Rogers et al. 2011).

3. *Transition probability adjustments.*—MC1 output does not include SI, which is needed by FVS, but it includes numerous outputs related to vegetation productivity, soils, and climate. To relate MC1 output variables to SI values, we correlated averaged MC1 output from 1982–2006 with available SI data (Gould et al. 2011). We performed this correlation for 1790 MC1 cells, ranging from central to southern Oregon, in the Coast Range and valleys. This geographic choice brackets the range of expected SI in the study area from the present until 2099, based on the prediction that future climate in the Willamette Valley may resemble current climate in southwestern Oregon (Rogers et al. 2011). We used Akaike's information criterion (AIC; Akaike 1974) to select a final model with an overall adjusted $r^2 = 0.55$ (Table 2) to produce space- and time-filling maps of SI for our study area.

¹⁵ <http://www.firelab.org/project/flammap>

TABLE 2. Variables used in the regression equation relating MC1 variables to site index.

Variable	Coefficient	Standardized coefficient
Total soil carbon	9.081×10^{-4}	0.482
Forest net primary productivity	1.699×10^{-2}	0.229
Average June temperature	2.158	0.183
Aboveground live forest carbon	1.962×10^{-4}	0.120
Leaf shape index†	-0.1989	-0.0551
Intercept	75.6	

† Leaf shape index ranges continuously from 0 to 1, where 0 corresponds to needle-shaped leaves and 1 corresponds to broad leaves.

The spatial grain for MC1 (approximately 800-m grid cells) is much larger than the IDUs, and thus the MC1-projected values for SI needed to be downscaled to individual IDUs. To do this, we adjusted the future SI of each IDU (SI_{IDU_t}) proportionally over time, based on that IDU's initial SI (SI_{IDU_0}), the MC1 cell's initial SI (SI_{MC1_0}), and the MC1 cell's projected future SI (SI_{MC1_t}) at time t

$$SI_{IDU_t} = SI_{IDU_0} \left(\frac{SI_{MC1_t}}{SI_{MC1_0}} \right).$$

4. *Transition probability constraints.*—Since the STSM contains all vegetation types and transitions needed for multiple future climate scenarios, as well as the present climate, we limited the possible transitions as follows: (1) we determined which cover types and associated states and species would be compatible with each MC1 PVT and (2) we constrained the STSM to allow transitions only to compatible states (Table 3). For example, under the subtropical mixed broadleaf and needleleaf evergreen forest PVT, no transitions to pine savanna or woodland are allowed, because MC1 would not infer the occurrence of a vegetation type similar to ponderosa pine savanna or woodland under this PVT; for the same reason, existing pine savanna or woodland states can only remain unchanged, or transition to other states via allowed transitions. Within each PVT, transition probabilities for each state were proportionally adjusted to compensate

for the transitions that were disallowed so that the sum of allowed probabilities was always unity. As PVTs change in the future, we permit all existing states to persist in the landscape until changed by succession or a stand-replacing disturbance. It is clear that climate change has increased rates of tree mortality in some locations (Allen et al. 2010). MC1 output, however, showed no evidence of large-scale tree mortality (e.g., large future losses of tree carbon due to drought). Because individual trees are long-lived and can acclimate to new conditions, they can survive for many years in suboptimal growth conditions, leading to time lags and nonlinear responses to drought. Following a stand-replacing disturbance, however, only transitions allowed under the current PVT may occur. If the dominant tree species in the pre-disturbance state is compatible with the current PVT (Table 3) and is capable of resprouting following disturbance (i.e., oaks, bigleaf maple, and madrone), then the IDU will regenerate as a young tree state of the cover type corresponding to that species. If the pre-disturbance state did not contain any compatible species that resprout following disturbance, then the IDU regenerates as an open, grass/forb state of the dominant cover type for that PVT. For example, within the subtropical mixed broadleaf and needleleaf evergreen forest PVT, an IDU that was mixed oak and Douglas-fir woodland pre-disturbance will regenerate as a young oak state. Under that same PVT, however, an IDU that was mixed Douglas-fir and grand fir forest will regenerate as a madrone grass/forb state and then undergo probabilistic succession. We address the limitations of this approach in *Discussion*.

MODEL BEHAVIOR AND RESULTS

STSM probabilistic behavior

First, we performed (nonspatial) simulations outside of Envision to examine the probabilistic nature of CV-STSM. Starting from either an oak savanna state or a Douglas-fir state, we ran repeated simulations in CV-STSM for 500 years, with SI = 30.48 m under the maritime evergreen needleleaf forest PVT (Fig. 3). We

TABLE 3. State-and-transition simulation model (STSM) tree cover types to which transitions are allowed under each MC1-derived potential vegetation type (PVT).

STSM cover type	Temperate maritime evergreen needleleaf forest	Temperate continental evergreen needleleaf forest	Subtropical mixed evergreen forest	C ₃ grassland
Oak savanna	allowed	allowed	allowed	allowed
Oak woodland	allowed	allowed	allowed	
Oak and Douglas-fir woodland	allowed	allowed	allowed	
Douglas-fir and oak woodland	allowed	allowed	allowed	
Douglas-fir forest	allowed		allowed	allowed†
Douglas-fir and maple forest	allowed			
Douglas-fir and grand fir forest	allowed			
Bigleaf maple forest	allowed			
Pine savanna		allowed		allowed
Pine woodland		allowed		
Madrone woodland and forest			allowed	allowed†
Madrone and Douglas-fir forest			allowed	

† Open-canopied grassland states are the only states allowed for this cover type and PVT.

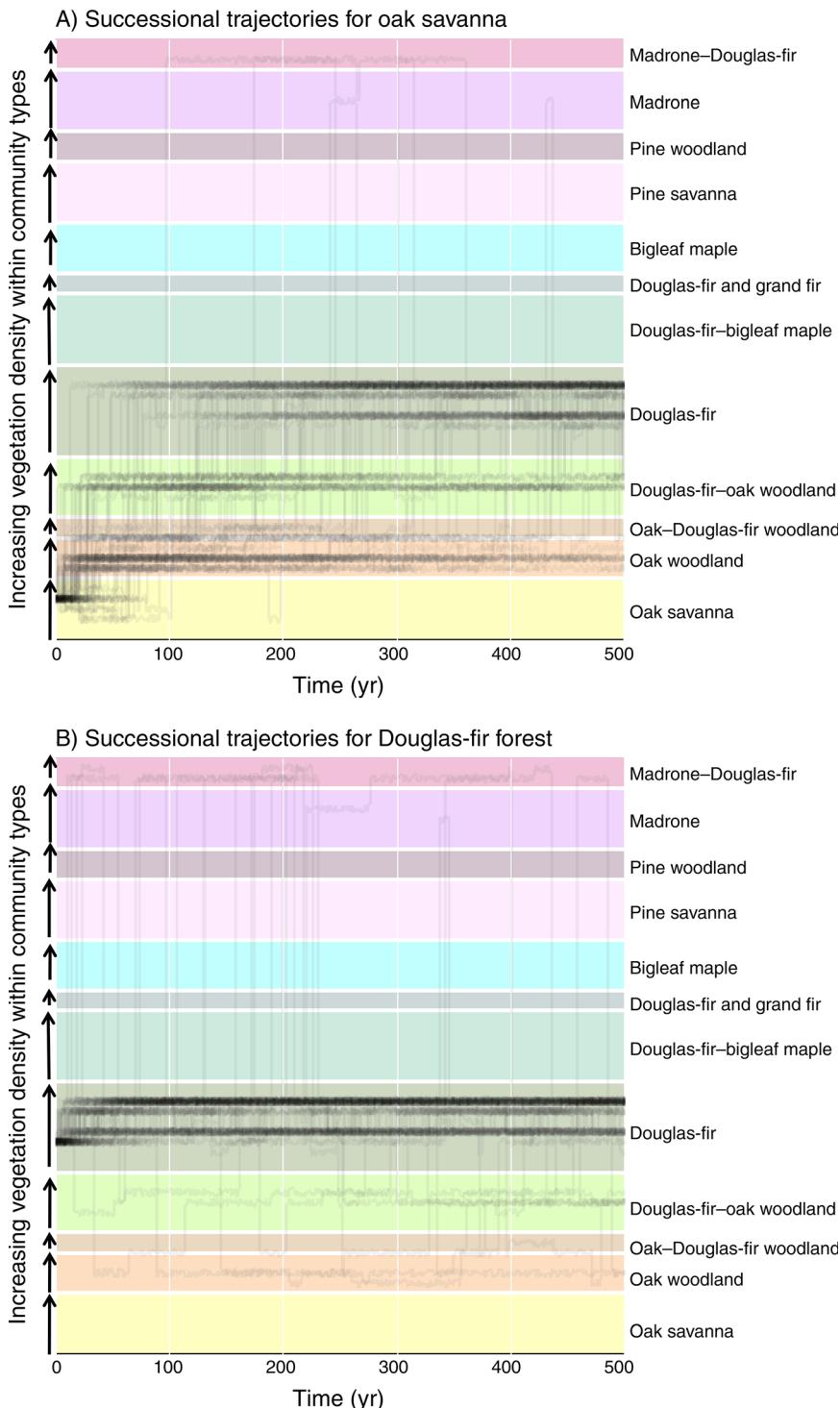


FIG. 3. Changes in state-and-transition simulation model (STSM) cover types over time. Each panel shows 100 probabilistic simulations run for 500 years, each from two different starting states. Panel A begins in an oak savanna state and ends with substantial proportions of large-diameter, closed-canopy, one- and two-canopy-layer Douglas-fir states, medium-diameter Douglas-fir–oak woodland states, and medium-diameter oak woodland states. Panel B begins in a medium-diameter, one-canopy-layer Douglas-fir state, and ends with substantial proportions of large-diameter, closed-canopy, one- and two-canopy-layer Douglas-fir states. Colored boxes correspond to the 12 different cover types used in the STSM, each of which contains all associated states; the height of the colored box corresponds to the number of states specified in the STSM. Within each cover type, moving higher on the y-axis corresponds to increased vegetation density, either in terms of stem diameter, canopy closure, canopy layering, or a combination of the three. Darker traces indicate a greater proportion of simulations in a particular cover type at a particular

implemented these simulations in the computer language R (R Development Core Team 2008) (see Supplement). The patterns of change in Fig. 3 demonstrate the variability in CV-STSM behavior that is due to the transition probabilities themselves. The precise modifications of transition probabilities, as changing climate affects SI, are available in the model code (see Appendix B). Results were consistent with observed successional trajectories in the region (Habeck 1961, Thilenius 1968, Johannessen et al. 1971, Day 2005). Under the maritime evergreen needleleaf forest PVT, all simulations tended to converge on Douglas-fir forest as the final state. Oak savanna largely transitioned to oak woodland within 50 years, but while oak woodlands diminished in extent, they were able to persist throughout the simulation. Our field data and other research in this region suggest that succession from oak woodland to Douglas-fir forest may typically be somewhat faster than simulated by the model (Thilenius 1968, Johannessen et al. 1971, Day 2005). For all starting states, the tendency was to move toward a few different Douglas-fir forest states, differentiated by tree size and canopy layering. Some small amount of grand fir was usually present following the first 100 years of simulation time. Bigleaf maple and madrone types appeared infrequently and ephemerally. The model showed the capacity for states to both increase and decrease in mean stem size. These changes in quadratic mean diameter reflect either infill with small trees, tree mortality, or individual tree growth, as projected by FVS.

Effects of disturbance and climate change

Simulations were also conducted with CV-STSM running as a module within Envision to explore the effects and interactions of climate and disturbance scenarios at the landscape scale. We simulated four climate scenarios (no climate change, Hadley A2, MIROC A2, CSIRO A2) and three levels of generic, stand-replacing disturbance (no disturbance [0%], 5%, or 17% of the IDUs disturbed per year). Regionally, all three A2 climate scenarios indicate increasing temperatures, especially in the summer. Precipitation is more variable, but all scenarios indicate increasing precipitation in the winter and decreasing precipitation in the summer. Within these constraints, CSIRO A2 is relatively cool and wet, MIROC A2 is warm and wet, and Hadley A2 is hot and dry (Rogers et al. 2011). The disturbance levels yield disturbance return intervals of 20 years and six years, which bracket the estimates of the pre-Euro-American fire return interval for the Willamette Valley Ecoregion (Morris 1934, Weisberg and Swanson 2001, Walsh et al. 2010), and are therefore appropriate limits for a sensitivity analysis. We implemented disturbance in a spatially random and disaggre-

gated fashion, unlike any disturbance the landscape is likely to experience, in order to explore a wide range of potential model behavior. The interactions of this vegetation model with a mechanistic fire model and a mechanistic model of human land-management decisions in fully coupled Envision runs will be the subject of future papers (G. I. Yospin, *unpublished data*). This implementation of generic disturbance, however, allowed us to explore the range of behavior that CV-STSM produces when specific disturbance frequencies are associated with different climate scenarios.

Disturbance and climate interacted strongly to drive vegetation change in CV-STSM (Fig. 4). By aggregating across the entire landscape, Fig. 4 shows both the range and central tendency of CV-STSM over thousands of independent simulations. Without disturbance or climate change (Fig. 4A), there was an overall trend in the landscape toward Douglas-fir forest at the expense of oak savanna, while oak woodland initially increased and then stabilized until the end of the 93-yr model run. As CV-STSM runs probabilistically for longer periods of time, losses begin to accrue in oak woodland once the pool of oak savanna is exhausted (e.g., as in Fig. 3), until most of the landscape becomes various types of Douglas-fir forest, consistent with the theoretical climatic-climax vegetation for this area (Franklin and Dyrness 1988). With sufficient disturbance, however, there was a stabilization or increase in oak savanna and an increase in bigleaf maple, accompanied by reduced increases to Douglas-fir forest and losses to oak woodland, consistent with the theoretical fire climax for this area (Habeck 1961, Franklin and Dyrness 1988).

The effect of climate change was heavily dependent on disturbance, and in general, all climate scenarios produced similar changes in vegetation for any given disturbance scenario by yr 90, near the end of the simulation (Fig. 4). Without disturbance, the climate-change scenarios had little impact on vegetation. In contrast, under the shortest disturbance return interval all of the climate-change scenarios generated a large reduction in the amount of Douglas-fir forest by the end of the model run and increased the amount of novel local cover types (e.g., madrone forest). Oak savanna habitats increased with increasing disturbance regardless of projected climate change and achieved somewhat higher quantities than under no climate change at comparable disturbance levels.

The interaction between disturbance and climate change also showed some of the nuances differentiating how the GCMs project climate change for the study area (Bachelet et al. 2011, Rogers et al. 2011). While all three GCMs projected warming in the study area, Hadley and MIROC projected substantial and comparable warming (~4.2°C), while CSIRO projected the least warming

←

point in time. Simulations were conducted with a site index of 30.48 m under the maritime evergreen needleleaf forest potential vegetation type.

($\sim 2.6^{\circ}\text{C}$). CSIRO projected a larger increase in mean annual precipitation than MIROC, while Hadley projected small decreases in mean annual precipitation (Rogers et al. 2011). Hadley produced the most rapid changes in vegetation when disturbance occurred in the landscape, with the largest increases in oak and madrone cover types. By the end of the simulations, however, vegetation grown under the three GCMs tended to converge. MIROC produced little change for most of the simulation time. The rate of vegetation change at the end of the MIROC simulations with disturbance, however, far exceeded the rates of change seen under the other combinations of climate and disturbance scenarios. Ponderosa pine appeared, but only very briefly, in two episodes during the simulation (see Appendix C). At its greatest extent (under Hadley and the 17% disturbance regime), ponderosa pine cover types occupied approximately 2.8% of the IDUs in the study area.

Spatial output

Given the spatially random and disaggregated nature of the disturbance used in these simulations, it is inappropriate to over-interpret the spatial output from the disturbance simulations. With this caveat in mind, however, the spatial output reveals important model dynamics (Fig. 5). Because the implementation of CV-STSM in Envision is based on transition probabilities operating in thousands of IDUs, the spatial output shown in Fig. 5 reflects the outcomes of thousands of independent simulations. The initial landscape contained a mixture of oak, Douglas-fir, and bigleaf maple cover types (Fig. 5A). With a disturbance return interval of six yrs and no climate change, oak occurred largely on the lower slopes of the valley foothills, while maple largely occurred further upslope (Figs. 2 and 5B). Contemporary observations show a strong maple presence and occasional dominance in uplands following disturbance by timber harvest (Johannessen et al. 1971); CV-STSM matches these observations. On the other hand, vegetation maps from 1851 do not show maple-dominated stands in the uplands, likely because wildfire was less frequent at higher elevations away from the valley floor, and the climate was likely somewhat cooler at the end of “The Little Ice Age.”

The strong interactions between climate change and disturbance were also apparent spatially. Areas of the landscape that existed as Douglas-fir forest without a substantial oak component at the start of the simulation were almost entirely converted to madrone cover types under the high disturbance regime (Fig. 5C). Much of the landscape, again, especially in the lowlands, remained in or changed to open oak savanna cover types. This was most likely due to the oak's ability to resprout following stand-replacing disturbance.

DISCUSSION

The likelihood that DGVMs can accurately predict vegetation dynamics and disturbance in intensively human-managed landscapes such as the wildland–urban interface is remote. DGVMs are not designed to mechanistically simulate anthropogenic disturbance or realistic land-use decision-making at a fine spatial grain and lack time lags conferred by tree longevity. In heavily managed landscapes, future simulations with DGVMs that project potential natural vegetation may not be relevant to managers interested in changes to existing land cover over the next several decades. Other modeling projects that have incorporated management into DGVMs are often unable to deliver detailed assessments of land-cover change over the short time horizons at which land-use decisions are made (Scheller et al. 2007). CV-STSM, therefore, provides a necessary bridge between DGVMs and land-use decision models that wish to simulate changes to existing land cover.

CV-STSM produces expected dynamics with or without disturbance under current climate, suggesting that it appropriately depicts current vegetation dynamics. Without disturbance, states from many starting conditions converged to the dominant current cover type, Douglas-fir forest, under both current and future climate. The particular climate-change scenarios affected these trajectories only marginally. Because CV-STSM assumes that established forest stands persist under future climate, there are no dramatic changes in vegetation due to climate change without disturbance. However, there was a strong interaction in CV-STSM between disturbance and climate-change effects on vegetation. With stand-replacing disturbances, climate change results in increasing dominance of established resprouting species, and the emergence of novel vegetation types. The increases are especially pronounced with the higher frequency disturbance regime under the hot, dry Hadley scenario, as well as at the end of the warm, wet MIROC scenario. Because the model is sensitive to the sprouting capabilities of dominant tree species, we encourage future fieldwork that could help support, refute, or reformulate how we have parameterized tree sprouting and transition probabilities, including the ability of subdominant tree species that currently are present at only low levels in the landscape to emerge as community dominants due to climate forcing. CV-STSM suggests the potential for rapid and pronounced changes in land cover under more severe future climate change.

One of the major technical challenges in coupling different classes of models is bringing outputs and inputs from various models and data sources into congruence (Kerns et al. 2012). We correlated a metric of productivity from a global model of projected vegetation with one based on empirical measurements of local conditions. This relationship was incorporated into CV-STSM by downscaling information from the 800-m grid cells in MC1 to smaller, irregular polygons in our study

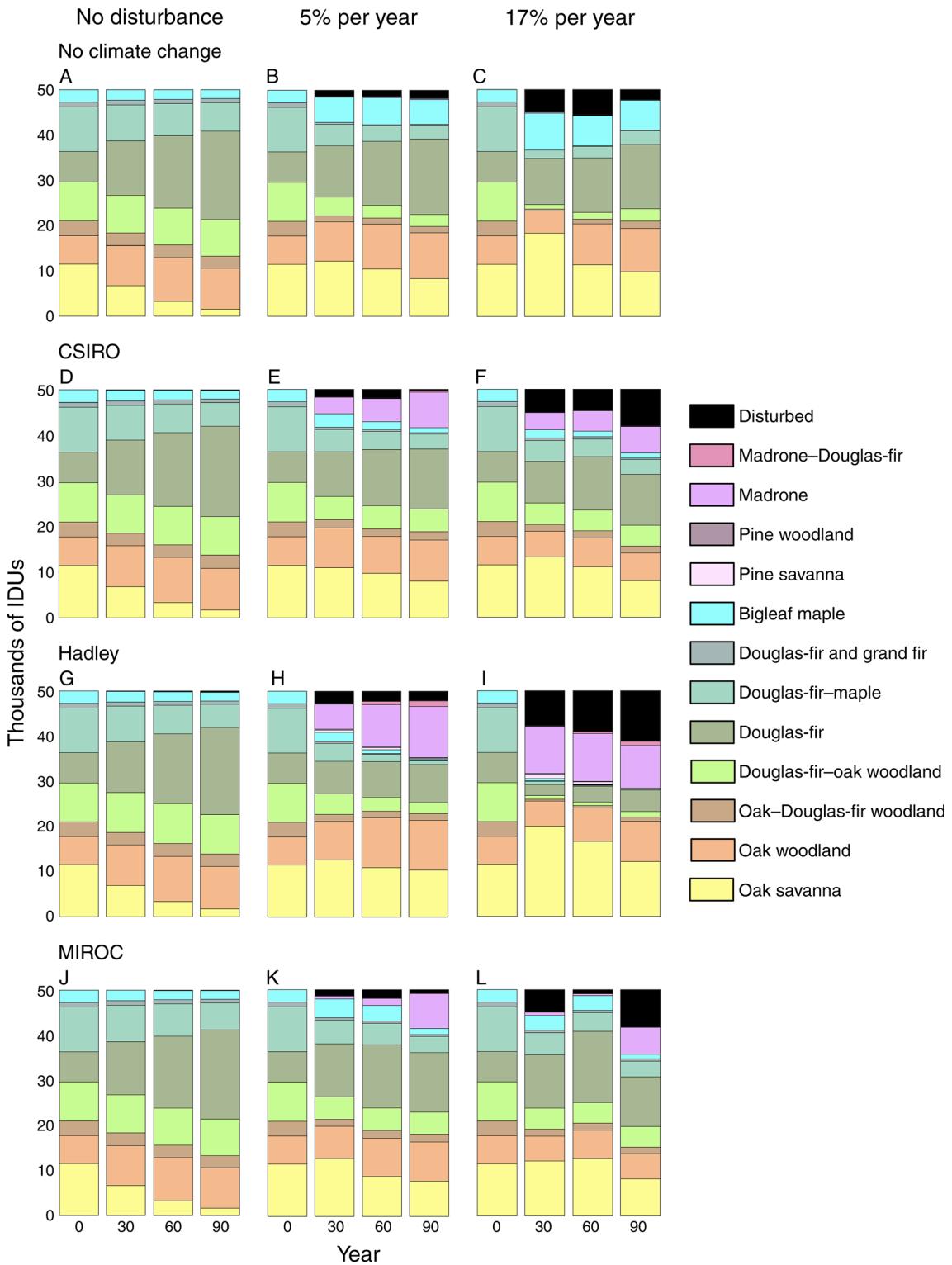


FIG. 4. Projected state-and-transition simulation model (STSM) cover types in number of integrated decision units (IDUs) at four time points with three global circulation models. Descriptions of the cover types are in Table 1. Climate scenarios are (A–C) no climate change, (D–F) CSIRO A2, (G–I) Hadley, and (J–L) MIROC A2. Disturbance regimes are (A, D, G, J) no disturbance, (B, E, H, K) 5% disturbance per year, and (C, F, I, L) 17% disturbance per year. The most common purple hue in panels E, F, H, I, K, and L corresponds to the madrone (M) cover type.

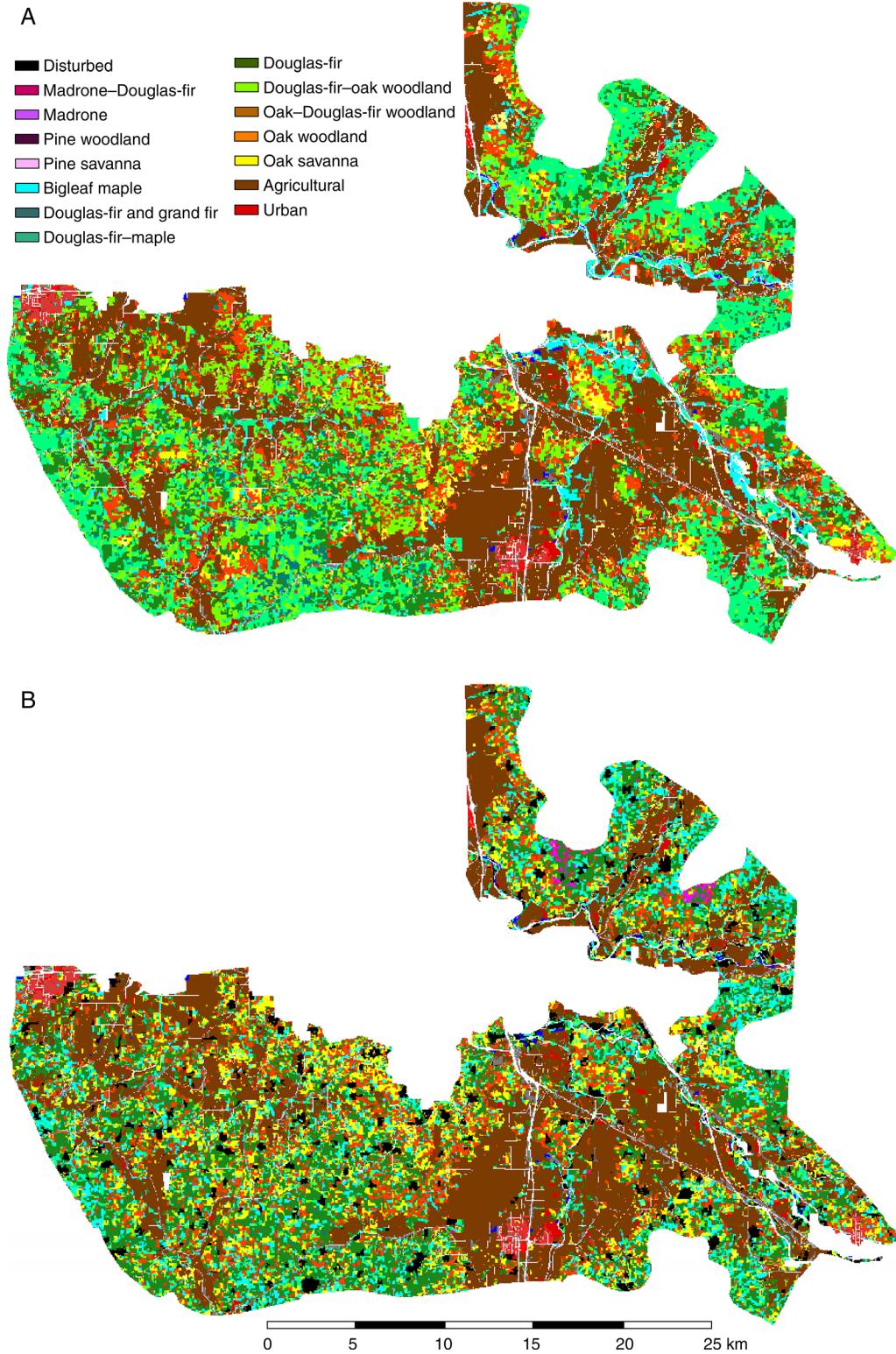


FIG. 5. Simulated plant cover types shown spatially for the study area for (A) year 0; (B) no climate change, 17% disturbance, year 90; (C) Hadley A2, 17% disturbance, year 90.

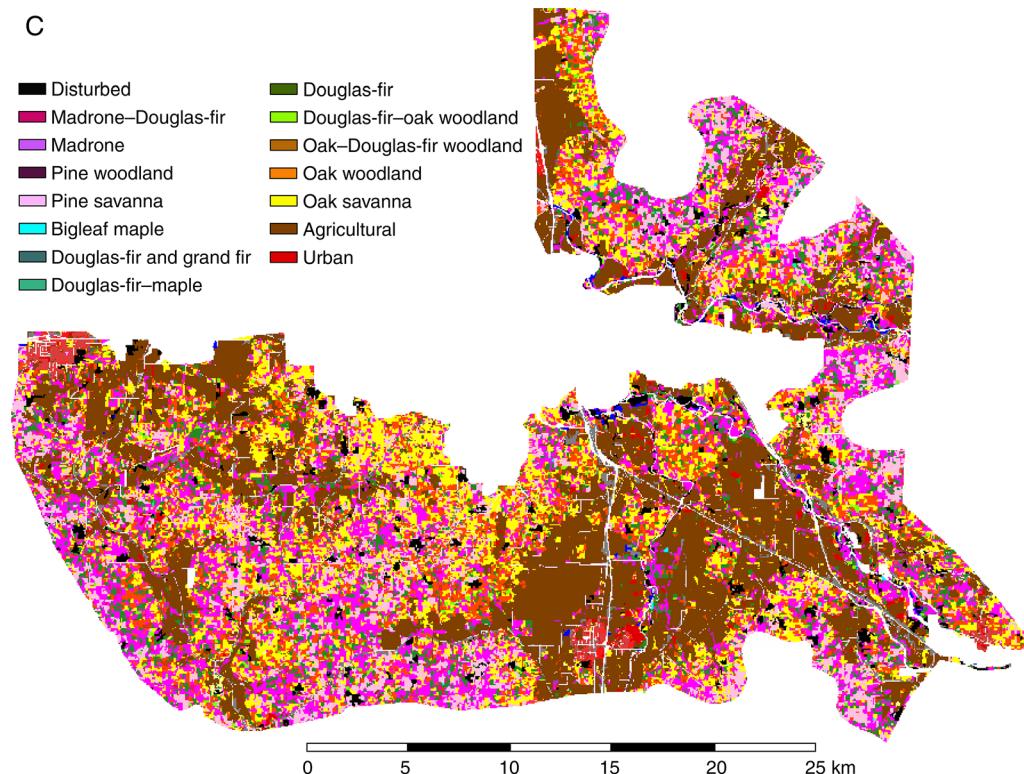


FIG. 5. Continued.

area that conformed to soil-type boundaries and projecting changes in site productivity into the future. Finally, we developed a means to match broad descriptions of potential vegetation types from a DGVM to plant communities of known species composition, including both current and potential future vegetation types. Through all these steps we were able to train and constrain an STSM that was parameterized with results from a biometric forest stand model of vegetation change to be congruent with the vegetation responses to climate change projected by a DGVM. This congruency is to both the thresholds between vegetation types in MC1 and the continuous output variables from MC1. While some changes in PVTs in MC1 may be faster than changes in cover type in CV-STSM, this was a design choice that allowed us to describe vegetation in detail, while still allowing for trends in biogeochemical processes to direct successional trajectories. In this way, our work is a major step forward relative to other, previous modeling projects (e.g., Scheller et al. 2007), because CV-STSM can facilitate accounting for the dynamic consequences of land management on land cover.

We have translated an increasing dominance of new MC1 PVTs as representing increasing dominance of Pacific madrone and ponderosa pine cover types, as these species occur in the current study area at low abundances and these cover types represent the nearest

species assemblages that are representative of the new PVTs. Our reliance on extant regional species assemblages to parameterize successional transitions that include novel future vegetation types allowed us to incorporate empirically based rates of successional change that begin from the current vegetation without mandating new dominant tree species in the near future. This decision rests on a relatively conservative assumption that species that do not currently occur locally are unlikely to immigrate, establish, and become dominant in the next 90 years. The STSM framework, however, is sufficiently adaptable that truly novel species assemblages could be incorporated should the user be prepared to define and parameterize transitions among these states.

Rates of change in vegetative cover were much slower in CV-STSM simulations than in MC1 simulations. There are two reasons for this. First, MC1 assumes that vegetation quickly reaches its maximum leaf area index. This is due principally to temperature and water limitation, and, to a lesser extent, nitrogen dynamics. Transition rates in CV-STSM, however, were determined in FVS based upon regionally derived statistical relationships of tree growth, competition, and mortality. Transition rates from the observed dynamics that parameterize FVS are much lower than those imposed by physiological limitations in MC1. Second, MC1 outputs showed no evidence of substantial drought-

related mortality events in the study area. Because of this, CV-STSM's assumption that established forest stands can otherwise persist under future climate meant that it projected no dramatic changes in vegetation without disturbance. The long lifespans of many of the tree species (e.g., >500 years for Douglas-fir) and paleoecological reconstructions (Rollinson et al. 2012) help justify this assumption. Higher levels of disturbance increased the convergence between predictions from CV-STSM and MC1 because disturbance allowed more rapid successional changes as informed by MC1. If climate change is severe enough to kill dominant tree species or prevent seedling establishment, then CV-STSM will underrepresent climate effects on rates of vegetation change. We consider this unlikely in the near future (i.e., until 2050, at which point future climate projections begin diverging rapidly), given the current mild climate and projected limited change in climate averages in the study area, as well as the broad regional distribution of all of our dominant and subdominant tree species. Climate change could increase dominant tree species' susceptibilities to stand-replacing disturbances, such as insect or pathogen outbreaks. If that were the case, the interaction of disturbance and tree replacement would bring the rates of vegetation change projected in CV-STSM and MC1 into closer alignment.

The imposition of spatially random disturbances at regular intervals allowed us to directly test the effects of disturbance on model dynamics. The timing of vegetation changes projected by MC1 has the potential to substantially alter successional trajectories in the model when a mechanistic fire model and vegetation management are coupled with CV-STSM in Envision. For example, under the Hadley projections with MC1 there were two periods during the 21st century that were favorable for continental evergreen needleleaf forest growth (see Appendix C). If large stand-replacing fires were to occur during one of these periods, ponderosa pine could increase in dominance in these areas, with effects that last for decades.

Other modeling efforts have included detailed descriptions of vegetation, human land management, and disturbance under projected climate change (Keane et al. 1996, Bachelet et al. 2001, Scheller et al. 2007, Medvigy et al. 2009, Moeur and Vandendriesche 2010). However, CV-STSM addresses central issues needed to link models of climate-change impacts to simulations of human land use. It incorporates key dynamics of a DGVM, while addressing crucial limitations. These include using current vegetation as a starting point for simulations and attenuating rates of successional change to those supported by realistic rates of tree growth and replacement. Although land-use scenarios are at present only explicitly considered as components of the emissions scenarios driving the simulations (Moss et al. 2010), CV-STSM allows human land management to be incorporated mechanistically by modeling vegetation at a spatial grain and taxonomic resolution commensurate

with the ways in which people manage landscapes. Modeling tools like CV-STSM are among the many next steps needed to help planners and land managers develop effective, adaptive plans of action that can reflect the expected broad-scale responses of vegetation to rapid changes in regional climate.

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SUPPLEMENTAL MATERIAL

Ecological Archives

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