



# The effects of disturbance based management on the dynamics of Mediterranean vegetation: A hierarchical and spatially explicit modeling approach

Avi Bar Massada<sup>a,\*</sup>, Yohay Carmel<sup>a</sup>, Gili Koniak<sup>b</sup>, Imanuel Noy-Meir<sup>b</sup>

<sup>a</sup> Faculty of Civil and Environmental Engineering, Technion-Israel Institute of Technology, Technion City, Haifa 32000, Israel

<sup>b</sup> Institute of Plant Sciences, The Robert H. Smith Faculty of Agriculture, Food, and Environment, The Hebrew University of Jerusalem, Rehovot 76100, Israel

## ARTICLE INFO

### Article history:

Received 18 March 2009  
Received in revised form 2 June 2009  
Accepted 3 June 2009  
Available online 2 July 2009

### Keywords:

Spatially explicit  
Mediterranean  
Disturbances  
Plant functional types

## ABSTRACT

The eastern Mediterranean region has been subjected to intensive human disturbance in the past 10,000 years, mainly in the forms of agro-pastoral activities such as grazing, shrub clearing, and prescribed burning. This disturbance history resulted in the formation of highly heterogeneous landscapes, characterized by high biodiversity. Recent changes in human activities have resulted in a decrease of landscape heterogeneity, leading to decreasing biodiversity and increasing fire risk. To conserve heterogeneity, land managers apply disturbance based management practices, using the same activities that created and maintained landscape heterogeneity in the past. However, the long-term and large-scale outcomes of these disturbances are often unknown, due to the complex response of Mediterranean vegetation to disturbance. Here we report on a spatially explicit, hybrid, and spatially hierarchical ecological model developed by us. The model attempts to predict the outcome of various disturbance based management activities on the long-term spatio-temporal dynamics of five common Mediterranean vegetation types. The model uses a spatially explicit state and transition formulation, with continuous transition functions. Model simulations were conducted on a Mediterranean landscape in Northern Israel, incorporating various disturbance practices that are common in the region. Simulation results highlight the potential of disturbance based management as a tool for conserving landscape heterogeneity, as well as the complex interactions between disturbances and the spatial structure of the landscape in Mediterranean regions.

© 2009 Elsevier B.V. All rights reserved.

## 1. Introduction

Human agro-pastoral activities have been shaping the vegetation of eastern Mediterranean landscapes for the past 10,000 years through grazing, clear cutting, and burning (Naveh and Dan, 1973). The long-term results of these activities are vegetation mosaics, which are fine-grained landscapes consisting of different vegetation types interlaced at small spatial scales. Vegetation mosaics are characterized by high biodiversity, since they consist of many microhabitats that support different life forms and species (Perevolotsky and Seligman, 1998).

Socio-economic changes in many countries in the Mediterranean basin resulted in the abandonment of traditional agro-pastoral activities (Naveh and Dan, 1973; Rundel, 1998), leading to a sharp decrease in the areas being grazed regularly (Naveh and Kutiel, 1986) and clear cut. As a result, many mosaic landscapes have been converted into dense scrublands and woodlands (Naveh and Kutiel, 1986; Carmel and Kadmon, 1999). These pro-

cesses have decreased landscape heterogeneity (Lavorel, 1999), and engendered some undesired consequences, such as a decrease in biodiversity and scenic diversity, and an increase of fire risk (Pausas and Vallejo, 1999). It is therefore important to conserve vegetation mosaics and landscape heterogeneity (Perevolotsky and Seligman, 1998; Pausas, 1999a,b). This is possible by re-applying the traditional disturbances that created and sustained these landscapes in the past: grazing, clear cutting, and prescribed burning (Perevolotsky and Seligman, 1998). However, the feasibility and efficiency of such “management for heterogeneity” techniques are not straightforward. Woody vegetation recovery following disturbances is rapid, and within 5–10 years complete woody cover is restored (Henkin et al., 1999; Perevolotsky et al., 2003). Species composition and distribution of individuals is often similar to that before the disturbance (Hadar et al., 1999). A complex of several management practices in a precise sequence may be required to maintain open patches with herbaceous vegetation for longer periods (Seligman, 1996; Henkin et al., 1999).

How can active intervention channel vegetation dynamics to restore and maintain spatially heterogeneous mosaic landscapes in Mediterranean environments? The working hypothesis assumed here is that management can do so. The ‘how’ is yet largely unknown. The approach chosen here is the development

\* Corresponding author. Present address: Department of Forest and Wildlife Ecology, University of Wisconsin, Madison 53706, WI, USA. Tel.: +1 608 261 1050.

E-mail address: [barmassada@wisc.edu](mailto:barmassada@wisc.edu) (A. Bar Massada).

of a dynamic mathematical model that describes and predicts long-term changes in Mediterranean vegetation in response to disturbances and management events.

Mathematical models can be useful tools for managers who want to explore the possible consequences of their decisions. Models of vegetation dynamics can be classified into several types. Many of these models define a basic unit that can be in one of several vegetation states, and can transit from one vegetation state to another (Westoby et al., 1989). In Markov models (Usher, 1992; Rego et al., 1993; Caswell, 2001) the transition is defined by a matrix of transition probabilities, while in semi-Markov models (Acevedo et al., 1995) the transition probability depends on the period the unit area has been in its present state. In cellular automata models (Silvertown et al., 1992; Hogeweg, 1988; Balzter et al., 1998), the transition is governed by deterministic transition rules that depend on the states of neighboring units. In gap models (Shugart and West, 1980; Botkin, 1993), the patch is defined by the identity (and optionally age) of the dominant adult tree and the presence of seedlings and saplings of trees of the same and other species. The changes in the state of a gap may include a variety of factors and processes (Urban et al., 1991; Pacala et al., 1996). In individual based models (Urban and Shugart, 1992) the basic unit is not an area but an individual plant, and the model can describe life cycle, growth, reproduction and dispersal as a function of environmental conditions and neighboring individuals. In addition to the traditional modeling approaches, hybrid models merge procedures or sub-models of different types, often in a spatially hierarchical structure (Acevedo et al., 2001; Pausas, 2003). Models of these different types have been developed mainly for forest ecosystems (Shugart and West, 1980), but there have also been applications to savanna or wooded grasslands (Jeltsch et al., 1997) and structurally more complex Mediterranean-type vegetation.

A central conceptual and technical challenge in studying and modeling vegetation dynamics is the necessity to span a range of spatial scales (Coughenour, 1991; Levin, 1992; Noy-Meir, 1996). The basic processes of vegetation change – the birth, growth and death of individual plants – occur at a scale of one to a few meters, commonly referred to as the “patch” or “gap” scale (Pickett and White, 1985). The basic spatial unit most commonly used in the analysis of plant communities and vegetation dynamics is the “site”, which represents an area characterized by specific microclimate, topography and rock soil conditions, and by a specific disturbance history. A site is an assemblage of adjacent and interacting individuals of different species and of vegetation patches and gaps of different structure and composition. The typical scale at which decisions on ecosystem management are taken is larger, usually several square kilometers, i.e. the “landscape” scale. A landscape thus consists of a large number of sites that may differ in habitat conditions and land use history as well as in vegetation structure and composition.

The scale problem in management-oriented ecological models is: producing predictions, at the landscape scale, of changes in plant communities observed at site scale, but generated by processes at the patch or individual scale. One approach to this problem is to ignore the local scale, and model only the larger scales: site and landscape (Carmel et al., 2001; Franklin et al., 2001). A second approach involves mere multiplication of the process at the local scale, to construct artificial landscapes (Jeltsch et al., 1996; Balzter et al., 1998; Pausas, 2003). The former approach was criticized as being case-specific and not general (Higgins and Richardson, 1996) while the latter approach was seen as being unrealistic (van Tongeren, 1995). A third approach is hierarchical models that operate on a real landscape at two or three scales simultaneously (e.g. Acevedo et al., 1996, 2001; Koniak and Noy-Meir, 2009). Hierarchical models have been developed for the modeling of forest dynamics in boreal forests (Pacala et al., 1996). Such a model could predict the future vegetation structure at the landscape scale, based on pro-

cesses operating at the site scale (namely grazing, clearing, fire, and seed dispersal), which in turn affect the development at the patch scale (plant growth, mortality, expansion, and takeover by a colonizer).

Existing model types are difficult to apply in Mediterranean systems, due to its high spatial and structural heterogeneity. State-and-transition models are non-spatial, and use constant transition probabilities, which also characterize cellular automata models. Gap models were developed for more homogeneous forests with a clear vertical stratification, which do not exist in the majority of Mediterranean shrublands and woodlands. Therefore, in this research a hybrid modeling approach was taken, combining sub-processes from different model types. The core functions of the model are based on the non-spatial model by Koniak and Noy-Meir (2009). The dynamic process behind the model is based on state-and-transition models (Westoby et al., 1989), where transitions between dominant plant functional types (PFT) are depicted as stochastic processes, with probabilities governing the transitions between them. Traditionally, these models are non-spatial and use constant transition probabilities. Here, following Koniak and Noy-Meir (2009), a different approach was taken using continuous transition functions as an alternative to the constant transition probabilities. These functions depend on the spatial configuration of the vegetation, making them spatially explicit transition functions (Perry and Enright, 2008). Colonization and growth of two PFTs in the same patch, one as dominant and one as colonizer, originated from gap models (reviewed by Bugmann, 2001).

The objectives of the present work were: (1) to develop, on the basis of the non-spatial model by Koniak and Noy-Meir (2009), a spatially explicit model at multiple hierarchical scales, from patch (cell) through site to landscape, incorporating ecological processes that operate at various scales. (2) To explore and validate model predictions regarding the spatio-temporal dynamics of Mediterranean vegetation under various disturbance and management activities. Model parameterization, development and validation were conducted for a Mediterranean mosaic landscape in northern Israel.

## 2. Methods

### 2.1. Model structure

The model is a spatially explicit expansion of the non-spatial model by Koniak and Noy-Meir (2009). The model simulates the spatio-temporal dynamics of five plant functional types (PFTs hereafter), which correspond to groups of species with common structural and functional characteristics common to many Mediterranean regions: [1] herbaceous vegetation; [2] dwarf shrubs; [3] low shrubs; [4] tall shrubs; [5] low trees (Fig. 1). At each time step of the model, which is one year, PFTs in different locations can change according to a set of transition functions (details below). The model depicts the study area as a regular grid consisting of equal sized cells, each dominated by a single PFT. The model consists of three spatially hierarchical levels that are nested: [1] cell (patch), which is a square unit area of 1 m<sup>2</sup> (approximately the size of an adult dwarf shrub), which is dominated by a single PFT, but can have an additional colonizer PFT growing beneath the dominant PFT. This is the lowest level, where the majority of ecological processes occur. [2] Site, which is a square collection of cells (area of 100 m<sup>2</sup>), which are subjected to the same disturbances. In other words, a specific disturbance is assumed to be acting identically on all cells in the site. [3] Landscape, which is the entire area of model operation, consisting of many entities of the lower hierarchical levels. The general flowchart of the model is depicted in Fig. 2.

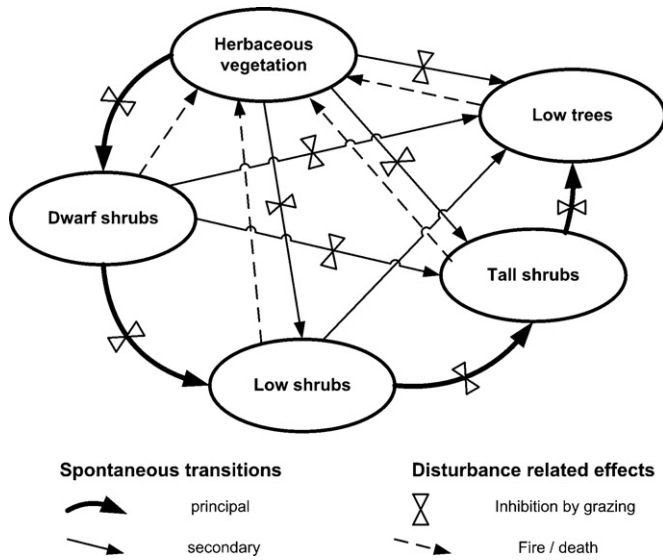


Fig. 1. The transition processes (arrows) between the five PFTs (ellipses) in the study area.

2.2. State variables and parameters

Each hierarchical level has its own state variables. At the cell level, there are five state variables: type, age, and height of the dominant PFT, and type and age of the colonizer PFT (if any). At the site level there are two state variables: percent cover of each PFT and seed availability per PFT. At the landscape scale, percent cover of each PFT is the only state variable. All PFT variables are arrays of five values, since there are five different PFTs.

The model includes three types of parameters: [1] Probabilities of events (e.g. maximal colonization and expansion probabilities, probabilities of seed production and dispersal); [2] Age effects (e.g. maximum age of a PFT, reproductive age, etc); [3] Growth parameters (e.g. growth rate, maximum height). Each parameter has a specific value per PFT. The majority of model parameters were obtained from Koniak and Noy-Meir (2009). The remaining parameter values were derived from field data, the literature, and expert opinions.

2.3. Transitions between PFTs

The model simulates spatio-temporal change using a spatially explicit state and transition process (Perry and Enright, 2008) with continuous transition functions between the PFTs. The type  $D$  of the dominant PFT in a specific cell  $(x,y)$  in the landscape next year  $(t + 1)$  is a function of a transition function  $P$  between the dominant PFT at present  $(t)$  to the dominant PFT in the following year:

$$D(x, y, t + 1) = f\{P(x, y, t), D(x, y, t)\} \tag{1}$$

2.4. Transition sub-processes

There are three transition processes in the model: seed colonization, vegetative expansion, and death. In seed colonization, seeds from neighboring cells enter a cell and establish in it. These seeds form a colonizer PFT that grows under the dominant PFT. After a time lag, a deterministic takeover occurs, in which the colonizer PFT replaces the dominant PFT and becomes the new dominant PFT in the cell. The second transition process, vegetative expansion, is the replacement of the dominant PFT in a cell by the canopy growth of a PFT from an immediate neighboring cell (one of its eight surrounding neighbors). In the third process, death, the domi-

nant PFT is replaced by herbaceous vegetation, assuming that there is a constant seed bank of herbaceous species everywhere in the landscape.

2.5. Colonization

It is assumed here that a PFT can only be replaced by a “taller” PFT (a PFT that is of a higher successional level, Fig. 1). Consequently, colonization of a PFT into itself or a lower PFT into a taller PFT is not allowed in the model. The probability that colonization of a different PFT  $k$  will occur in a cell dominated by PFT  $j$  (only possible when  $k > j$ ) is the product of three components: [1] the maximal colonization probability (a parameter); [2] the availability of seeds of PFT  $k$  in the cell vicinity; and [3] the grazing intensity in the site (Koniak and Noy-Meir, 2009):

$$C_{j,k} = c_{\max,j,k} \times S_{k,t} \times (1 - r_{c,k} \cdot G_t) \tag{2}$$

where  $C_{j,k}$  is the actual probability of colonization of PFT  $k$  into PFT  $j$ ,  $c_{\max,j,k}$  is a parameter representing maximal probability of colonization (under ideal conditions, e.g. there is no limit on seed availability),  $S_{k,t}$  is the availability of seeds of type  $k$  in the area (see below),  $r_{c,k}$  is a parameter representing the effect of grazing on recruitment of seeds of PFT  $k$ , and  $G_t$  is the grazing intensity at the site at time  $t$  (between 0 and 1, defined by the user).

The determination of the availability of seeds of PFT  $k$  ( $S_{k,t}$ ) is based on the approximate mechanisms of dispersal of the different PFTs used in the model, and on the location of the cell and the site in the landscape. The woody PFTs used in this model were divided into two groups based on their dispersal mechanisms: [1] Tall shrubs and low trees have fleshy fruits, dispersed by birds. [2] Low shrubs and dwarf shrubs have other means of dispersal, which are unknown, but are limited in distance compared to the bird-dispersed PFTs. Therefore, two different procedures for calculating local seed availability were created, accounting for the different mechanisms described above.

2.6. Tall shrub and low tree seed production and availability

The rationale that governed the development of this mechanism was based on the data on behavior of the common bird species involved in the dispersal of fleshy fruited species. These bird species have small territories, of about 1 ha (Izhaki et al., 1991). They spend the majority of time in the densely vegetated areas within their territory, in order to avoid predation (PFTs that supply such protection are low shrubs, tall shrubs, and low trees). The vast majority of seeds are dispersed and deposited in the denser areas of the territory, which are also the areas where more fruit is available (Debussche and Iseemann, 1994; Herrera et al., 1994; Herrera, 1995, 1998; Rey and Alcantara, 2000). Open cells will receive smaller amounts of seeds. Thus, determination of seed availability in a specific site needs to account for its relative shrub cover when compared to its overall neighborhood, which represents the territory of seed-dispersing birds. Here, the size of this neighborhood is assumed to be a rectangular block of  $10 \times 10$  sites (corresponding to 1 ha, similar to the average territory size of the dispersing bird species).

For each site in the landscape, in each year, a preliminary seed production value is calculated as follows (Koniak and Noy-Meir, 2009):

$$S_{k,t}^0 = S_k^{\max} \times \frac{N_{k,t}^*}{N} \tag{3}$$

where  $S_{k,t}^0$  represents the amount of seeds of PFT  $k$  that will be produced in time  $t$  at the site,  $S_k^{\max}$  represents the maximal amount of seeds that are produced by a cell dominated by PFT  $k$ ,  $N_{k,t}^*$  is the

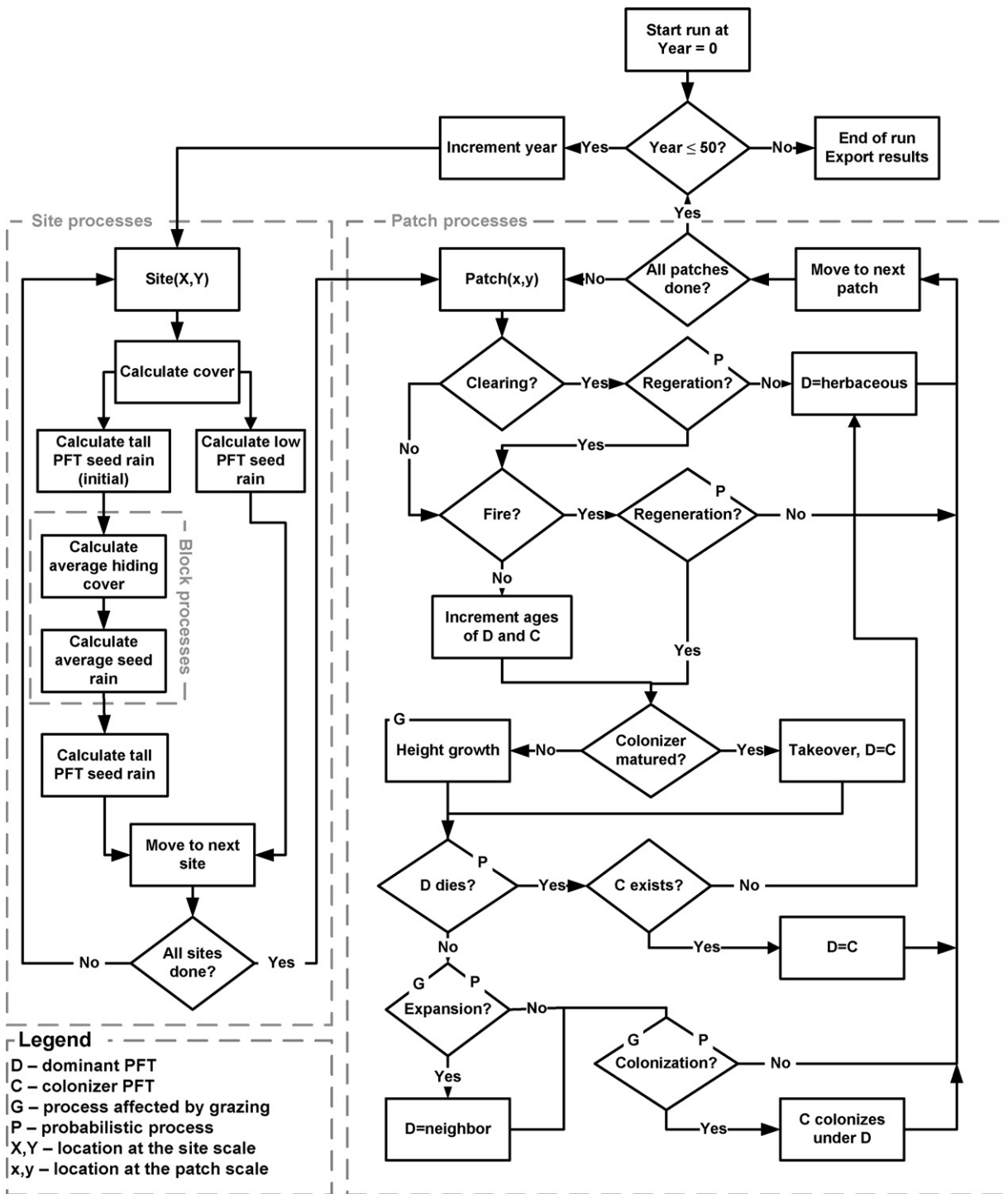


Fig. 2. Model flowchart.

number of cells dominated by PFT  $k$  with plants older than their reproductive age (the parameter  $a_{r,k}$ ), and  $N$  is the total amount of cells in the site (100). For mechanism [1] above,  $k$  can be only tall shrubs or low trees.

The combined cover of low shrubs, tall shrubs, and low trees representing the “hiding cover”, or the percent of area available for safe bird movements in the site, is calculated as (Izhaki et al., 1991):

$$P_{h,site} = \frac{N_{low} + N_{tall} + N_{tree}}{N} \quad (4)$$

where  $N_{low}$ ,  $N_{tall}$  and  $N_{tree}$  are the number of cells that are dominated by low shrubs, tall shrubs, and low trees, respectively.

For a specific site, the average  $S_{k,t}^0$  in the 100 neighboring sites  $\bar{S}_{k,block}$  was calculated for each block ( $10 \times 10$  site neighborhood). This was also done for the “hiding cover”, yielding  $\bar{P}_{h,block}$ . Then, the actual seed availability  $S_{k,t}$  for all cells in the site is calculated using the equation from Koniak and Noy-Meir (2009), but replacing the single-site scale terms with a multi-site term based on the average seed production in the block, the average hiding cover in the block, and the hiding cover in the current site. Thus, seeds are produced at the block scale, but dispersed mainly into sites that have more

protective cover for birds:

$$S_{k,t} = S_{k,t-1} \times u_k + \bar{S}_{k,block} \times \frac{P_{h,site}}{\bar{P}_{h,block}} \quad (5)$$

where  $u_k$  is a parameter representing the fraction of seeds that persisted through the passing year (as a seed bank). The output of this equation is then inserted into Eq. (2).

### 2.7. Low shrub and dwarf shrub seed production and availability

The majority of seed dispersal events observed for these two PFTs occurs in the very short range, but there is a small quantity of longer distance events (Henkin et al., 1999, 2007). Seed production was divided into two stages, or distances. Short range dispersal enables seeds to reach the neighboring cell, representing the fall of fruits from the mother plant. Long range dispersal accounts for unknown dispersal mechanisms operating at scales of up to few tens of meters observed in the field. The probability of short range arrival of seeds uses a revised version of Eq. (3), which is based on Koniak and Noy-Meir (2009) but incorporates an 8-cell neighborhood instead of a full site neighborhood:

$$S_{short,k,t} = S_{short,k}^{max} \times \frac{N_{k,t}^*}{8} \quad (6)$$

where  $S_{short,k,t}$  represents the probability of seed arrival from the short range,  $S_{short,k}^{max}$  is a parameter that expresses the maximal seed production (when all eight neighboring cells are in state  $k$  and reproductive).

The probability of long range seed arrival depends on the production of seeds in a nine-site rectangular neighborhood, and replaces the constant term of seed import from outside the site used by Koniak and Noy-Meir (2009):

$$S_{long,k} = \frac{1}{9} \times \sum_{site=1}^9 \left( S_{long,k}^{max} \times \frac{N_{k,site}^*}{N} \right) \quad (7)$$

where  $S_{long,k}$  is the probability of seeds arriving from the long range (represented by a nine-site neighborhood). For the sake of simplicity, Eq. (7) has only a single summation, but in the actual code, there is a double summation that generates a rectangular neighborhood.

The actual availability of seeds of dwarf shrubs and low shrubs is the sum of the probabilities from Eqs. (6) and (7), plus the component of seed survival from the previous year (as in Eq. (3) and Koniak and Noy-Meir (2009)):

$$S_{k,t} = S_{k,t-1} \times u_k + S_{short,k} + S_{long,k} \quad (8)$$

The output of this equation is then inserted into Eq. (2).

### 2.8. Expansion

The probability of the dominant PFT in a cell changing from PFT  $j$  to a “higher” PFT  $k$  as a result of expansion of adult plants is a function of the number of cells in state  $k$  located in its immediate neighborhood, i.e. the eight neighboring cells, the ages of the PFTs in the neighboring cells, and the grazing intensity. The difference from the original equation from Koniak and Noy-Meir (2009) is the usage of an eight-cell neighborhood rather than the entire site:

$$e_{j,k} = e_{max,j,k} \times \frac{N_{k,8}}{8} \times \left( \frac{a_{s,k} - A_{k,t}}{a_{s,k} - a_{e,k}} \right) \times (1 - r_{e,k} \times G) \quad (9)$$

where  $e_{j,k}$  is the probability that a cell dominated by PFT  $j$  will be invaded by PFT  $k$ ,  $e_{max,j,k}$  is the parameter that represents the maximal probability of expansion (when all neighbors are of type

$k$ ),  $N_{k,8}$  is the number of cells in state  $k$  in the rectangular eight-cell neighborhood (parameter) is the maturity age of PFT  $k$ ,  $a_{s,k}$  (parameter) is the establishment age of PFT  $k$ ,  $A_{k,t}$  is the average age of the PFTs in the neighboring cells at time  $t$ , and  $r_{e,k}$  is a parameter that represents the negative effect of grazing on the rate of expansion.

### 2.9. Other processes

The model simulates height growth, disturbances, and death in the same manner as the model by Koniak and Noy-Meir (2009). Height growth assumes a saturation growth curve model, in which growth rate decreases as plants become older. Grazing by goats or cattle are management actions controlled by the user, which defines their intensity (between 0 and 1), location (which sites), and timing (which years). Grazing affects model behavior via modification of the probabilities of colonization and expansion (Eqs. (3) and (9), respectively), and through its impact on height change. Fire and clearing are user-defined events as well, and each PFT subjected to them has a probability of regenerating via regrowth, though it is assigned a lower height. Death is a probabilistic event, and its probability is constant once a dominant PFT  $k$  reaches a certain age. A dead PFT is replaced by herbaceous vegetation.

### 2.10. Starting and ending conditions

The model requires the following data for initializing a simulation: [1] initial conditions: maps of dominant PFTs, their ages and heights; maps of colonizer PFTs and their ages; [2] management protocols: fire and clearing locations and times (years); grazing types (goat/cattle/both), intensities (0–1), locations (site serial numbers), and times (years). Typically, we ran simulations of 100 years.

The standard output of the models is: maps of dominant PFTs, their ages, and their heights; and maps of colonizer PFTs and their ages. These maps are generated for each year separately. Additionally, the percent cover of the different dominant PFTs (per each year) is generated for each site and for the entire landscape. The model runs in a C++ environment with all input and output data files stored in ASCII format.

### 2.11. Sensitivity analysis

The effect of model parameters on model output was assessed by a Monte Carlo sensitivity analysis approach. Sensitivity analysis was performed on groups of parameters, rather than on one parameter each time. In each run, a group of 10 parameters was randomly selected, and their initial value was multiplied by a constant value that represents the percentage of deviation from their original values. All other parameters were kept unchanged. The model was run a large number of times, and in each run a different group of parameters was modified. Model output was defined as the total number of cells of each PFT at year 50 (i.e., there were five analysis results). The reference for calculating sensitivity scores was the output of a simulation with no changes in any parameter. The sensitivity score of a simulation run was assigned to all the parameters that were modified in that run, and was calculated as the absolute difference between its output and the reference output. For each parameter, the average and standard deviation of the sensitivity scores of simulations in which it was altered were calculated. The average represents the overall effect of a specific parameter, and the standard deviation represents its interactions with other parameters. Parameters with high average and standard deviation were those to which the model is highly sensitive.

In each run of the model, we used only the output of year 50 for calculating sensitivity scores, and ignored the output of

previous years (in order to avoid temporal autocorrelation). Due to long computation times in large model landscapes, sensitivity analysis was conducted on a small, random landscape, consisting of  $100 \times 100$  cells (corresponding to  $10 \times 10$  sites, or 1 ha). Initial conditions represented an open landscape, with 73% herbaceous vegetation, 12% dwarf shrubs, 7% low shrubs, 5% tall shrubs, and 3% low trees.

### 2.12. Model validation

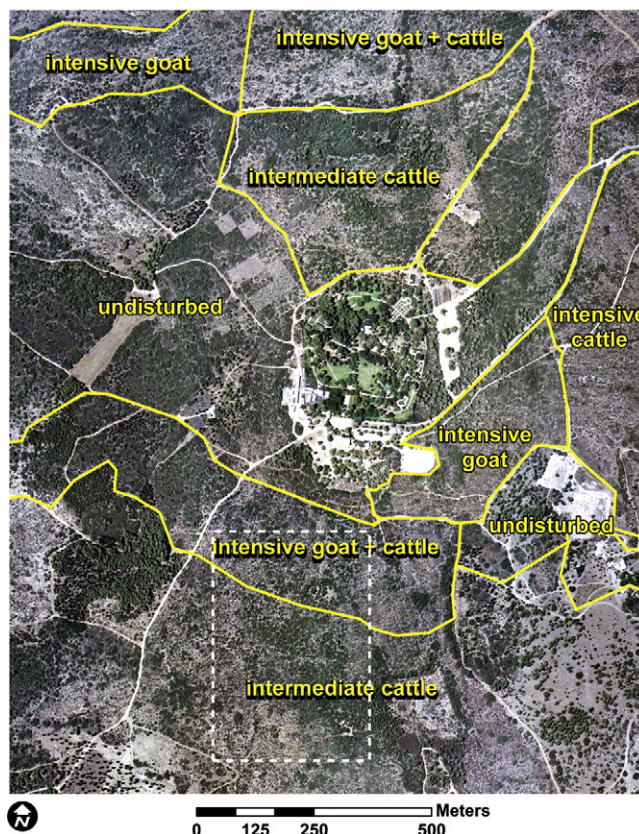
Validation of spatio-temporal models is a complicated task, since the necessary field data is seldom available. Here, validation required a comparison of model simulations to actual vegetation dynamics, accounting for the disturbance history. A full validation of a spatially explicit dynamic model requires actual vegetation maps of several points in time, at the relevant spatial scale (1 m), temporal resolution (every decade), and thematic detail (five vegetation types), as well as a detailed documentation of disturbance history for each site during the studied period. The best available source of spatio-temporal data for the purpose of this study is aerial photographs, due to their high spatial resolution and large temporal cover. However, it was impossible to generate reliable vegetation maps of all five vegetation types from aerial photography (especially in panchromatic photos, which are the only ones available for the earlier years). It was possible, however, to differentiate herbaceous vegetation from woody vegetation at high accuracy. Therefore, the model was evaluated using the dynamics of woody vegetation.

Since the initial conditions were only partially known (map of woody and herbaceous vegetation), a multiple simulations approach was taken. In each simulation, the relative cover of each woody vegetation type was randomly selected, and each woody pixel in the vegetation map was randomly assigned to a single vegetation type, so that the overall cover of each PFT in the simulation corresponds to the selected value. The process was repeated 30 times, and the average cover of herbaceous vegetation in each year was calculated.

The validation was conducted using a  $500 \text{ m} \times 350 \text{ m}$  area in the center of the study area. Five vegetation maps were generated by classifying aerial photographs from 1974 (starting conditions), 1984, 1997, 2004, and 2007 into two classes: woody and herbaceous vegetation, using Isodata unsupervised classification (Campbell, 1996). For each photograph, classification accuracy was assessed using a set of 30 randomly located control points that were visually interpreted as being woody or herbaceous. The overall classification accuracy was 91%. The validation area was burned in a wildfire in 1980, and has been subjected to medium intensity cattle grazing since 1989. The starting conditions were randomly generated 30 times.

### 2.13. Example simulations

The effects of various management activities on the long-term (50 years) structure and composition of vegetation were simulated at Ramat Hanadiv Nature Park in northern Israel (Fig. 3). The initial conditions (dominant PFT and PFT height) were mapped from remotely sensed data that included a fusion of aerial photography and LiDAR (Bar Massada, 2008). The size of the modeled area is 233 ha, and its topography is relatively flat. The area of the Park is covered by various types of Mediterranean vegetation, in varying successional stages. The area was divided into 10 management units (based on actual units), each subjected to different management scenarios (Table 1) that exist or are proposed for the study area. The overall objective of the management treatments is to preserve landscape heterogeneity and specifically the mosaic structure of the landscape by maintaining a wide array of habitats, supporting



**Fig. 3.** An aerial image of the study area, which is a subset of the Ramat Hanadiv Nature Park (northern Israel). The existing management units are marked by yellow lines. The validation area is marked by a dashed white rectangle. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

high species richness and diversity (Hadar L., personal communication).

Since there are many ways to quantify the structure of the mosaic (Gustafson, 1998), we used a combination of Simpson index of diversity (SIDI) and the edge density (ED) index to account for thematic diversity and spatial diversity, respectively. Simpson index of diversity indicates heterogeneity in the composition of PFTs. It portrays the probability that two randomly selected cells will not belong to the same PFT:

$$\text{SIDI} = 1 - \sum_{i=1}^S \left( \frac{N_i}{N_t} \right)^2 \quad (11)$$

where SIDI is the Simpson index of diversity,  $S$  is the total number of PFTs,  $N_i$  is the number of cells dominated by PFT  $i$ , and  $N_t$

**Table 1**  
Management scenarios.

Scenario name	Description
None	Entire landscape undisturbed
Present	Different management in each unit. Includes intensive goat grazing, intensive cattle grazing, intermediate intensity goat and cattle grazing, and no disturbance
G	Intensive goat grazing, entire landscape
C	Intensive cattle grazing, entire landscape
GC	Intensive goat and cattle grazing, entire landscape
GC <sub>half</sub>	Intermediate goat and cattle grazing, entire landscape
GF	Same as G, with fire in year 1
CF	Same as C, with fire in year 1
GCF	Same as GC, with fire in year 1
GC <sub>half</sub> F	Same as GC <sub>half</sub> , with fire in year 1

is the total number of cells in the landscape. *SIDI* ranges between zero (all cells in the landscape are of the same PFT) to  $1-1/S$ . Edge density is a measure of landscape complexity, and equals the sum of lengths of all edge pixels in the landscape (edges between cells of different classes) divided by the total landscape area. For simple landscape configurations, and when the total number of cells is small, the amount of edge is small. As the landscape becomes more convoluted, and the amount of small cells increases, edge density increases.

Overall landscape heterogeneity was assessed as an outcome of different management scenarios, applied to different management units independently, or to the entire landscape as a whole (Table 1). Initial conditions were identical for all scenarios, and were based on the vegetation map of 2004. The simulation was conducted for a period of 50 years, and repeated five times per scenario. Diversity indices were calculated for the entire landscape at year 0 and year 50.

2.14. Comparison with a non-spatial model

The model developed here is a multi-scale spatially explicit version of the non-spatial model by Koniak and Noy-Meir. To assess the difference in model predictions, we simulated two sets of model runs, depicting random and actual initial conditions, in both models and compared the temporal dynamics of PFT cover. In the random set, landscape area was 233 ha, and initial PFT cover percentages were 70.5, 15, 8.5, 4, and 2 for herbaceous vegetation, dwarf shrubs, low shrubs, tall shrubs, and low trees, respectively. The PFTs were randomly distributed across the landscape according to the initial percentage cover. During the simulations, the entire landscape was undisturbed. In the non-spatial model there are no interactions between sites, so the simulation consisted of 27 repetitions of the same initial conditions vector, for which the average cover of each PFT in every year was calculated.

The actual initial conditions were identical to the ones used for predicting the future of the study area (see previous section), with initial PFT cover percentages of 54.5, 15.5, 3.25, 15.75, and 11 for herbaceous vegetation, dwarf shrubs, low shrubs, tall shrubs, and low trees, respectively. We assumed there were no disturbances over the entire period.

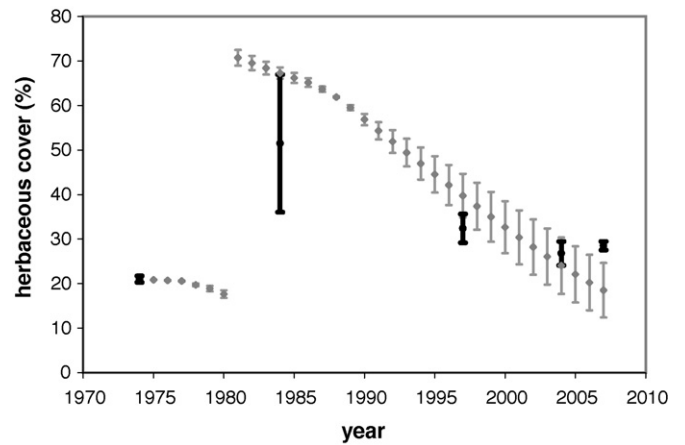


Fig. 5. Results of model validation. A comparison of 33 years of changes in herbaceous vegetation cover (gray dots), as predicted by 30 model runs with varying configurations of woody PFTs, with five values of cover measured from classified aerial photographs (black dots). The error bars of the aerial photography data represent the classification error, while the error bars of the model data represent the standard deviation of herbaceous cover. The leap in herbaceous cover in 1981 is a result of a wildfire that burned the entire validation area.

3. Results

3.1. Sensitivity analysis

The global sensitivity analysis process revealed that six parameter types (i.e., each parameter type consists of up to five parameters having the same role, one per PFT, so for example, there are five maximal ages) were more influential on model output than others (Fig. 4): maximal age, age of maturity, maximal colonization probability, maximum seeding probability, and maximum seeding probability at short distances. For each PFT, the three most influential parameters were always a subset of these parameter types. All these parameters are related to the processes of colonization and expansion in the model, thus their impact on model output is the result of their role in the two major transition processes that move the chains of vegetation change in the model.

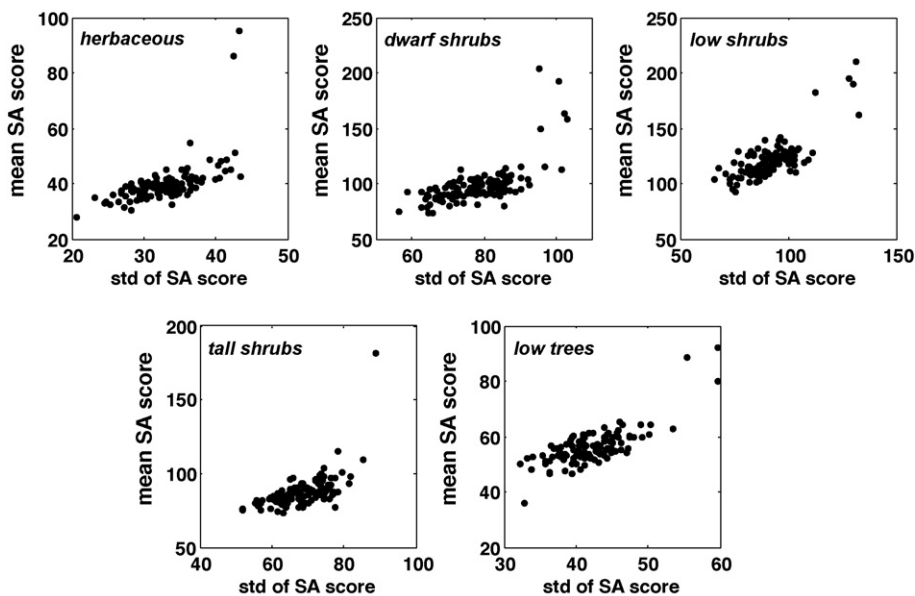


Fig. 4. Results of the sensitivity analysis. Plots show the averages and standard deviations of the sensitivity scores for each parameter (black dot). Each plot corresponds with a single output variable, which is the percent cover of a certain PFT at year 50. Points with large mean values are those to which the model is the most sensitive. Points with large standard deviations correspond to parameters that have a high degree of interaction with other parameters.

### 3.2. Model validation

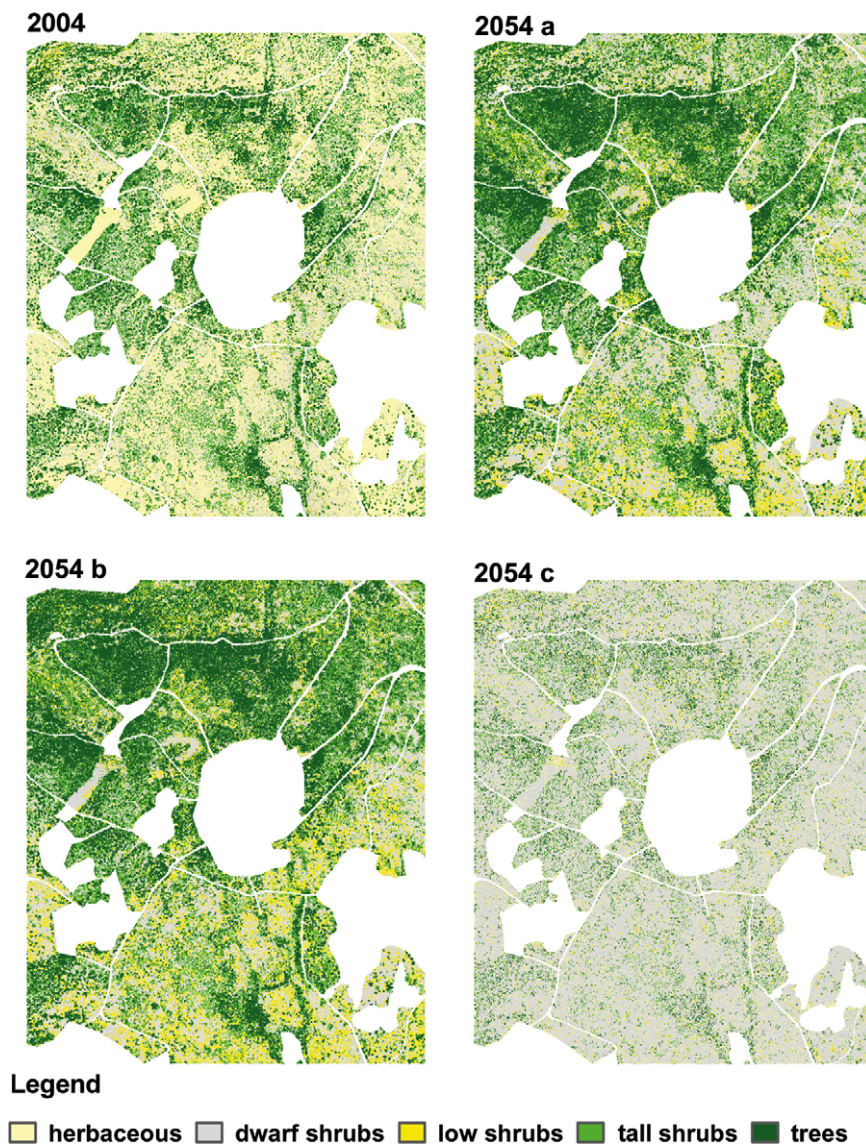
In general, the model reconstructed temporal dynamics of herbaceous vegetation cover that are quite similar to those that were mapped from the aerial photographs (Fig. 5). The rate of decline in herbaceous cover seemed to be higher in the model than in reality, but the difference is not overwhelming. The amount of woody cover that was destroyed by the wildfire of 1981 was lower than what the model predicted, but the general trend is similar.

### 3.3. Model simulations—general trends

Model results portrayed vegetation dynamics that are qualitatively similar to actual dynamics of Mediterranean vegetation that were previously reported (Carmel and Kadmon, 1999). Under the present disturbance scenario, the south central area which is being moderately grazed by both cattle and goats, will transform from a semi open area with many herbaceous cells into a dwarf shrub dominated area (Fig. 6a). The southern area of the landscape, being grazed by cattle, will gradually transform into a denser combination of the taller PFTs. The cessation of disturbance (Fig. 6b) results in a transformation of many areas in the landscape to the domi-

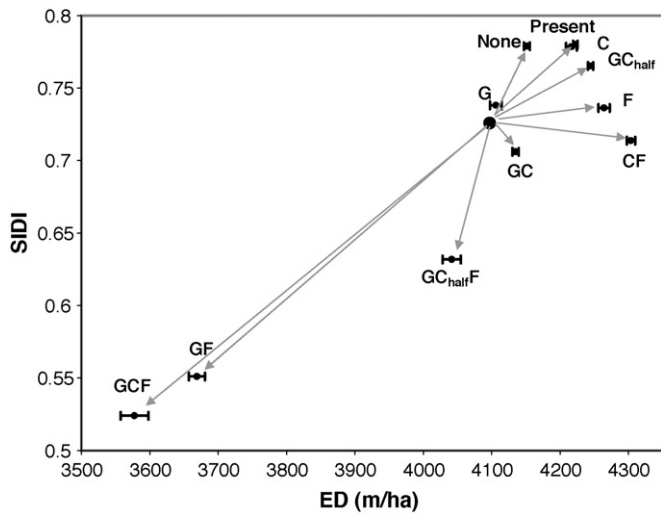
nance of taller PFTs, with increased shrub density, and a pronounced decrease in the cover of herbaceous cells, especially in the northern part of the landscape. Fire followed by intensive grazing by both goats and cattle over the entire landscape results in the transformation of the heterogeneous vegetation mosaic into a dwarf shrub dominated landscape, with a limited number of scattered and mostly isolated cells of taller PFTs (Fig. 6c). This form of landscape is indeed common in the eastern Mediterranean, where intensive goat grazing has formed a dwarf shrub dominated landscape.

In terms of landscape heterogeneity, four of the five scenarios that included fire resulted in a decrease of Simpson's index of PFT diversity, with the combination of fire and intensive goat and cattle grazing showing the most pronounced decrease, and the combination of cattle and fire showing the least decrease (Fig. 7). Fire without further disturbance resulted in an increase of both Simpson's index and edge density. In contrast, five of the six scenarios that excluded fire showed an increase in Simpson's index, with the intensive goat with cattle combination resulting in a decrease of Simpson's index. The undisturbed, present management, fire, intermediate goat and cattle grazing, and cattle grazing resulted in similar Simpson's index values, but their edge density values increased. In all cases, the intensive goat grazing scenarios resulted



**Fig. 6.** Actual and projected vegetation maps. The starting condition map is top left; Vegetation after 50 years, assuming continuation of the present management scenario (top right); Vegetation after 50 years, undisturbed (bottom left); Vegetation after 50 years, fire in 2005 and intensive goat and cattle grazing ever after (bottom right).





**Fig. 7.** The effect of management scenarios on landscape heterogeneity, expressed by Simpson's index of diversity (SIDI) and edge density (ED), in 2054. Values shown are averages of five simulations per scenario, with error bars representing standard deviations (the SIDI standard deviations were negligible; therefore the x-axis error bars are not shown). The large black dot in the center represents landscape heterogeneity in 2004. C is intensive cattle grazing, G is intensive goat grazing, F is fire in year 1, None is no disturbance, Present is the actual disturbances in the landscape at present, the subscript <sub>half</sub> that follows G, C, or both represents intermediate grazing intensity.

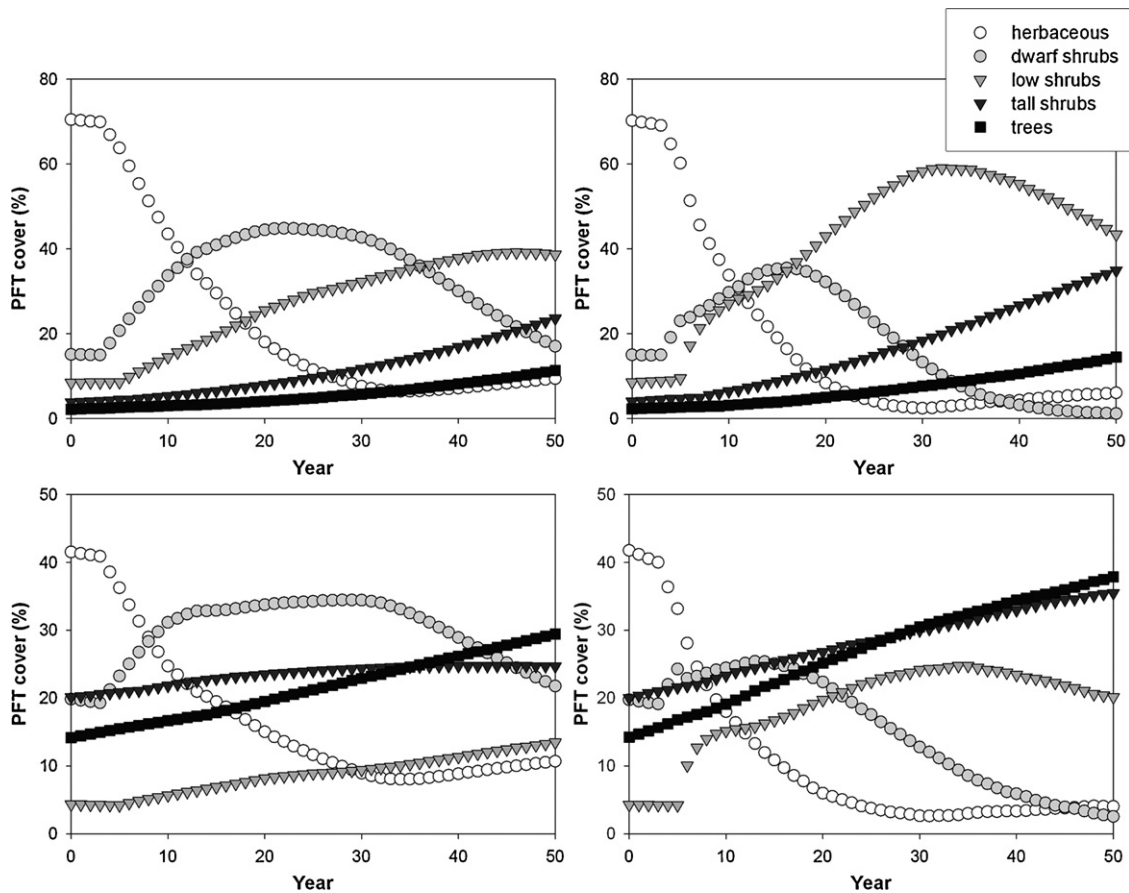
in lower edge density values compared to the other scenarios, especially in the case of grazing that followed fire in year 1.

### 3.4. Comparison to a non-spatial model

In both initial conditions (random and actual landscapes) there were pronounced differences between the spatial and the non-spatial models (Fig. 8). The successional dynamics were more rapid in the non-spatial model, i.e. the transitions between lower PFTs to taller PFTs at the landscape scale occurred faster in the non-spatial model. Under random initial conditions, tall shrubs are about to replace low shrubs after 50 years in the non-spatial model, while low shrubs are in their peak of cover in the spatial model at the same time. In addition, the cover of tall shrubs and low trees changes much slower in the spatial model. Both models, however, show similar rates of decrease of herbaceous cover. Under actual starting conditions, differences were more pronounced (Fig. 8). While low trees exhibited similar dynamics, herbaceous vegetation cover decreased slower in the spatial model, while dwarf shrubs grew faster and were the dominant cover type for thirty years, to be surpassed later by low trees. In the non-spatial model, the increase in dwarf shrubs was inhibited by the increase in the low shrubs, which rose fast between the fifth and tenth year. In contrast, low shrubs increased much slower in the spatial model.

## 4. Discussion

Mediterranean landscapes are characterized by fine scale spatial heterogeneity of vegetation, resulting from thousands of years of human disturbance (Naveh and Dan, 1973; Naveh and Kutiel,



**Fig. 8.** Temporal dynamics of five PFTs for the spatial model (left) and the non-spatial model by Koniak and Noy-Meir (2009) (right). The top graphs depict random initial conditions, and the bottom graphs depict actual initial conditions which correspond with those depicted in Fig. 6 for the undisturbed scenario.

1986). This heterogeneity supports high species diversity, and as such is a major conservation target that may be conserved by disturbance-based management (Perevolotsky and Seligman, 1998; Perevolotsky, 2006). In principal, dynamic ecological models may aid this purpose. In order to better understand the long-term and large scale interactions between disturbance-based management and landscape heterogeneity, we developed a spatially explicit, hybrid, and hierarchical ecological model, that is based on continuous state and transition functions.

The model relies on several assumptions. The major assumption is that change proceeds from low species to tall species (a PFT can only be replaced by a taller PFT unless it dies). In reality, there are cases where lower PFTs continue to grow underneath taller PFTs, replacing them if they die. In the majority of cases, however, the forward transition assumption holds true. A second assumption is that transitions are abrupt; once a colonizer takes over a dominant, the old dominant disappears. In reality, two PFTs may share the cell for a long period of time, without a clear distinction between a true dominant and colonizer. However, it is impossible to describe spatially explicit succession in a continuous manner without greatly increasing model complexity. Another assumption is the occurrence of seed dispersal and colonization events in the intermediate hierarchical level, without consideration of the actual dispersal kernel. This is because the dispersal mechanisms of the PFTs modeled here are unknown. While the dispersal kernels of tall shrubs and low trees were studied in the past, and are generally understood (Izhaki et al., 1991), there is scarce knowledge about long distance dispersal mechanisms of low shrubs and dwarf shrubs.

The above assumptions might distance the model from reality; yet, its qualitative and quantitative validation shows that its patterns are similar to actual spatio-temporal dynamics of vegetation. Model results are in agreement with the present knowledge regarding succession and change in the eastern Mediterranean region, which include decrease in cover of herbaceous species in the absence of disturbance, and transitions from lower woody species to taller woody species in a decadal time (Broide et al., 1996; Carmel and Flather, 2004). Model validation, although limited due to lack of data, showed that model predictions are similar to actual dynamics.

The model further ignores three components that have a major role in the dynamics of Mediterranean vegetation: climate, topography, and soils (Zohary, 1973). In the present case study, this simplification is justified by the relative homogeneity of these factors across the landscape, while applying the model to other areas would require additional parameters.

The high spatial resolution of the model imposes several difficulties on its application. A pre-requisite for running the model on actual landscapes is the availability of high resolution vegetation data. At present, vegetation maps that combine this thematic and spatial detail are scarce (due to technical and methodological limitations), thus the application of the model as an actual management-aid tool for large areas is constrained by the lack of sufficient input data (but this may change in the future).

Model simulations revealed that disturbances had varying effects on landscape heterogeneity. Without disturbance, the landscape was eventually dominated by the taller PFT. Grazing slowed down the successional process, since browsing by goats prevented the lateral growth of woody vegetation. In small shrubs, height growth was also prevented since the top branches were accessible to the browsing animal. Cattle had a less pronounced impact, since cows feed mainly on herbaceous vegetation, and to a lesser extent low trees (Seligman and Perevolotsky, 1994). In contrast to the effect of grazing, which seldom reduced the cover of existing woody vegetation, fire and clearing transformed the vegetation to a lower successional level by decreasing woody cover and enabling the re-expansion of herbaceous vegetation over the newly opened cells. The rate of woody regeneration to the pre-disturbance state

depends on the initial configuration of the community; the higher the original cover of a PFT, the more of it will regenerate, and through a feed-forward mechanism, it will regain its past cover faster (since the transitional processes in the model, both colonization and expansion, depend on the relative cover of each PFT).

Current landscape heterogeneity is apparently moderate, and may either increase or decrease, conditioned on the nature of management actions to be taken (Fig. 7). An increase in landscape heterogeneity was projected under the no disturbance scenario (Fig. 7). A possible explanation is that the study area is in a mixed successional stage that still reflects the outcomes of past disturbances (large wildfire, ongoing cattle grazing). A period of increasing heterogeneity is expected to occur, before the landscape transforms into a denser form, with decreased heterogeneity. Therefore, the change in landscape heterogeneity depends on the initial conditions of the landscape, and the disturbance history.

The spatial model developed here generated different temporal dynamics than those created by its predecessor non-spatial model by Koniak and Noy-Meir (2009), both for random and actual initial conditions, though in the case of random initial conditions differences were smaller. In both cases, successional dynamics were faster in the non-spatial model. This difference was probably caused by the effect of spatial configuration on transition probabilities, which exists only in the spatial model. Same initial PFT cover may have multiple configurations across the landscape, and this is known to affect the spatio-temporal dynamics of PFT cover (Pausas, 2003). Therefore, spatially explicit vegetation models are expected to generate more realistic results in cases where vegetation has a stronger non-random spatial pattern.

The models developed in this study and in a previous research (Koniak and Noy-Meir, 2009) are preliminary steps in the research of the interactions among management and vegetation dynamics in Mediterranean landscapes. Such models are powerful tools for assessing the long-term impact of management for mosaic conservation. At present, due to the lack of long-term field data, models may be the only available tools for reaching this goal. Further development of the model may include the incorporation of additional environmental variables and climatic conditions, provided that they are based on sufficient empirical data, which at present is unavailable.

## Acknowledgment

The research was funded by the Israel Science Foundation grant 625/05.

## References

- Acevedo, M.F., Urban, D.L., Shugart, H.H., 1996. Models of forest dynamics based on roles of tree species. *Ecol. Model.* 87, 267–284.
- Acevedo, M.F., Ablan, M., Urban, D.L., Pamarti, S., 2001. Estimating parameters of forest patch transition models from gap models. *Environ. Modell. Softw.* 16, 649–658.
- Acevedo, M.F., Urban, D.L., Ablan, M., 1995. Transition and GAP models of forest dynamics. *Ecol. Appl.* 5, 1040–1055.
- Balster, H., Braun, P.W., Kohler, W., 1998. Cellular automata models for vegetation dynamics. *Ecol. Model.* 107, 113–125.
- Bar Massada, A., 2008. Mapping and modeling the dynamics of Mediterranean vegetation under various management activities. Ph.D. Thesis. Technion, Israel Institute of Technology.
- Botkin, D.B., 1993. *Forest Dynamics*. Oxford University Press, Oxford, 309 pp.
- Broide, H., Kaplan, M., Perevolotsky, A.E., 1996. The development of woody vegetation in the Ramat Hanadiv Park and the impact of fire. *Ecol. Environ.* (in Hebrew, English abstract) 3, 127–132.
- Bugmann, H.C., 2001. A review of forest gap models. *Clim. Change* 51, 259–305.
- Campbell, J.B., 1996. *Introduction to Remote Sensing*. Taylor & Francis, London.
- Carmel, Y., Flather, C.H., 2004. Comparing landscape scale vegetation dynamics following recent disturbance in climatically similar sites in California and the Mediterranean basin. *Landsc. Ecol.* 19, 573–590.
- Carmel, Y., Kadmon, R., 1999. Effects of grazing and topography on long-term vegetation changes in a Mediterranean ecosystem in Israel. *Plant. Ecol.* 145, 243–254.

- Carmel, Y., Kadmon, R., Nirel, R., 2001. Spatiotemporal predictive models of Mediterranean vegetation dynamics. *Ecol. Appl.* 11, 268–280.
- Caswell, H., 2001. *Matrix Population Models: Construction, Analysis, and Interpretation*. Sinauer Associates, Sunderland, USA, 722 pp.
- Coughenour, M.B., 1991. Spatial components of plant–herbivore interactions in pastoral, ranching and native ungulate systems. *J. Range Manage.* 44, 530–542.
- Debussche, M., Iseemann, P., 1994. Bird-dispersed seed rain and seedling establishment in patchy Mediterranean vegetation. *Oikos* 69, 414–426.
- Franklin, J., Syphard, A.D., Mladenoff, D.J., He, H.S., Simons, D.K., Martin, R.P., Deutschman, D., O'Leary, J.F., 2001. Simulating the effects of different fire regimes on plant functional groups in Southern California. *Ecol. Model.* 142, 261–283.
- Gustafson, E., 1998. Quantifying landscape spatial pattern: what is the state of the art. *Ecosystems* 1, 143–156.
- Hadar, L., Noy-Meir, I., Perevolotsky, A., 1999. The effect of shrub clearing and grazing on the composition of a Mediterranean plant community: functional groups versus species. *J. Veg. Sci.* 10, 673–682.
- Henkin, Z., Seligman, N.G., Noy-Meir, E., 2007. Successional transitions and management of a phosphorus-limited shrubland ecosystem. *Rangeland Ecol. Manage.* 60, 453–463.
- Henkin, Z., Seligman, N.G., Noy-Meir, I., Kafkafi, U., 1999. Secondary succession after fire in a Mediterranean dwarf-shrub community. *J. Veg. Sci.* 10, 503–514.
- Herrera, C.M., 1995. Plant–vertebrate seed dispersal systems in the Mediterranean: ecological, evolutionary, and historical determinants. *Annu. Rev. Ecol. Syst.* 26, 705–727.
- Herrera, C.M., 1998. Long-term dynamics of Mediterranean frugivorous birds and fleshy fruits: a 12-year study. *Ecol. Monogr.* 68, 511–538.
- Herrera, C.M., Jordano, P., Lopez-Soria, L., Amat, J.A., 1994. Recruitment of a mast-fruiting, bird-dispersed tree: bridging frugivore activity and seedling establishment. *Ecol. Monogr.* 64, 315–344.
- Higgins, S.I., Richardson, D.M., 1996. A review of models of alien plant spread. *Ecol. Model.* 87, 249–265.
- Hogeweg, P., 1988. Cellular automata as a paradigm for Ecological modeling. *Appl. Math. Comput.* 27, 81–100.
- Izhaki, I., Walton, P.B., Safrieli, U.N., 1991. Seed shadows generated by frugivorous birds in an eastern Mediterranean scrub. *J. Ecol.* 79, 575–590.
- Jeltsch, F., Milton, S.J., Dean, W.R.J., Van Rooyen, N., 1996. Tree spacing and coexistence in semiarid savannas. *J. Ecol.* 84, 583–595.
- Jeltsch, F., Milton, S.J., Dean, W.R.J., Van Rooyen, N., 1997. Analysing shrub encroachment in the southern Kalahari: a grid-based modelling approach. *J. Appl. Ecol.* 34, 1497–1508.
- Koniak, G., Noy-Meir, I., 2009. A hierarchical, multi-scale, management-responsive model of Mediterranean vegetation dynamics. *Ecol. Model.* 220, 1148–1158.
- Lavorel, S., 1999. Ecological diversity and resilience of Mediterranean vegetation to disturbance. *Divers. Distribut.* 5, 3–13.
- Levin, S.A., 1992. The problem of pattern and scale in ecology: The Robert H. MacArthur award lecture. *Ecology* 73, 1943–1967.
- Naveh, Z., Dan, J., 1973. The human degradation of Mediterranean landscapes in Israel. In: Di Castri, F., Mooney, H.A. (Eds.), *Mediterranean Type Ecosystems (Origin and Structure)*. Springer-Verlag, Berlin, pp. 373–390.
- Naveh, Z., Kutiel, P., 1986. Changes in the Mediterranean vegetation of Israel in response to human habitation and land use. In: Woodwell, G.M. (Ed.), *The Earth in Transition, Patterns and Processes of Biotic Impoverishment*. Cambridge University Press, Cambridge, pp. 259–296.
- Noy-Meir, I., 1996. The spatial dimensions of plant–herbivore interactions. In: West, N.E. (Ed.), *Rangelands in a sustainable biosphere. Proceedings of the 5th International Rangeland Congress. Society for Range Management, Denver*, pp. 152–154.
- Pacala, S.W., Canham, C.D., Saponara, J., Silander Jr., J.A., Kobe, R.K., Ribbens, E., 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. *Ecol. Monogr.* 66, 1–43.
- Pausas, J.G., 1999a. Mediterranean vegetation dynamics: modelling problems and functional types. *Plant. Ecol.* 140, 27–39.
- Pausas, J.G., 1999b. Response of plant functional types to changes in the fire regime in Mediterranean ecosystems: a simulation approach. *J. Veg. Sci.* 10, 717–722.
- Pausas, J.G., Vallejo, R., 1999. The role of fire in European Mediterranean ecosystems. In: Chuvieco, E. (Ed.), *Remote Sensing of Large Wildfires in the European Mediterranean Basin*. Springer Verlag, New York, pp. 3–16.
- Pausas, J.G., 2003. The effect of landscape pattern on Mediterranean vegetation dynamics: a modelling approach using functional types. *J. Veg. Sci.* 14, 365–374.
- Perevolotsky, A., 2006. Integrating landscape ecology in the conservation of Mediterranean ecosystems: the Israeli experience. *Isr. J. Plant. Sci.* 53, 203–213.
- Perevolotsky, A.E., Ettinger, S.Z.R., Yonatan, R., 2003. Management of fuel brakes in the Israeli Mediterranean ecosystems: the case of Ramat-Hanadiv Park. *J. Mediterr. Ecol.* 3, 13–22.
- Perevolotsky, A.E., Seligman, N.G., 1998. Role of grazing in Mediterranean rangeland ecosystems. *Bioscience* 48, 1007–1017.
- Perry, G.L.W., Enright, N.J., 2008. Contrasting outcomes of spatially implicit and spatially explicit models of vegetation dynamics in a forest-shrubland mosaic. *Ecol. Model.* 207, 327–338.
- Pickett, S.T.A., White, R.S., 1985. *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, London, 472 pp.
- Rego, F., Pereira, J., Trabaud, L., 1993. Modelling community dynamics of a *Quercus coccifera* L. garrigue in relation to fire using Markov chains. *Ecol. Model.* 66, 251–260.
- Rey, P.J., Alcantara, J.M., 2000. Recruitment dynamics of a fleshy-fruited plant (*Olea europaea*): connecting patterns of seed dispersal to seedling establishment. *J. Ecol.* 88, 622–633.
- Rundel, P.W., 1998. Landscape disturbance in Mediterranean-type ecosystems: an overview. In: Rundel, P.W., Montenegro, G., Jaksic, F.M. (Eds.), *Landscape Disturbance and Biodiversity in Mediterranean Type Ecosystems*. Springer, Berlin, pp. 3–22.
- Seligman, N.G., 1996. Management of Mediterranean grasslands. In: Hodgson, J., Illius, A.W. (Eds.), *The Ecology and Management of Grazing Systems*. CAB International, Wallingford, UK, pp. 359–392.
- Seligman, N.G., Perevolotsky, A., 1994. Has intensive grazing by domestic livestock degraded Mediterranean Basin rangelands? In: Arianoutsou, M., Groves, R.H. (Eds.), *Plant–Animal Interactions in Mediterranean-Type Ecosystems*. Kluwer Academic Publishers, Netherlands, pp. 93–103.
- Shugart, H.H., West, D.C., 1980. Forest succession models. *Bioscience* 30, 308–313.
- Silvertown, J., Holtier, S., Johnson, J., Dale, P., 1992. Cellular automation models of interspecific competition for space—the effect of pattern on process. *J. Ecol.* 80, 527–533.
- Urban, D.L., Bonan, G.B., Smith, T.M., Shugart, H.H., 1991. Spatial applications of gap models. *For. Ecol. Manage.* 42, 95–110.
- Urban, D.L., Shugart, H.H., 1992. Individual-based models of forest succession. In: Glenn-Lewin, D.C., Peet, R.K., Veblen, T.T. (Eds.), *Plant Succession*. Chapman & Hall, London, pp. 249–292.
- Usher, M.B., 1992. Statistical models of succession. In: Glenn-Lewin, D.C., Peet, R.K., Veblen, T.T. (Eds.), *Plant Succession*. Chapman & Hall, London, pp. 225–247.
- van Tongeren, O.F.R., 1995. Data analysis or simulation model: a critical evaluation of some methods. *Ecol. Model.* 78, 51–60.
- Westoby, M., Walker, B., Noy-Meir, I., 1989. Opportunistic management for rangelands not at equilibrium. *J. Range Manage.* 42, 266–274.
- Zohary, M., 1973. *Geobotanical Foundations of the Middle East*. Gustav Fischer Verlag, Amsterdam.