SPATIOTEMPORAL PREDICTIVE MODELS OF MEDITERRANEAN VEGETATION DYNAMICS

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Abstract. Empirical modeling of vegetation dynamics can be used for predictive purposes. The goal of the present study is to construct and evaluate possible approaches for empirical modeling of vegetation dynamics, and to investigate their potential use in planning and management.

An empirical model of mediterranean vegetation dynamics was constructed using a case study of vegetation change in an area in the Galilee mountains, northern Israel, between 1964 and 1992. Present vegetation in any location was modeled as a function of past vegetation and environmental factors (e.g., topography and various disturbances); future vegetation was then modeled as a function of current vegetation and effects of environmental factors. In order to assess model performance, we compared the actual vegetation map with maps representing model realizations for the study area and for an external validation area. Three types of measures were used to compare the predicted and actual vegetation maps: overall vegetation composition, pattern indices, and cell-by-cell match. We compared the performance of logistic vs. linear models and of stochastic vs. deterministic realizations of a logistic model.

Our results indicate that landscape-scale vegetation dynamics can be fairly well modeled using a few biologically important variables. The logistic and linear models had similar performance, in spite of the reduced information on which the logistic models were based. The use of only a 4% sample of the database resulted in a negligible reduction in model performance. Model performance was reduced, but was still fair, when applied to an external area. The merits and limitations of this modeling approach are discussed in comparison with other approaches for modeling vegetation dynamics.

Key words: aerial photographs; empirical model; GIS; mediterranean vegetation; polychotomous logistic model; predictive modeling; spatiotemporal models; succession; vegetation dynamics.

INTRODUCTION

Destruction and fragmentation of natural areas are now becoming a worldwide concern. As the remaining natural areas become smaller and more fragmented, it is increasingly important to manage them wisely (Soulé and Wilcox 1980). Ecological systems are inherently dynamic and change over a variety of spatial and temporal scales. Therefore, planning and management must be based on predictions of future dynamics, rather than on detailed descriptions of current states (Western et al. 1989). Spatially explicit dynamic models are useful tools for decision-making processes (Boumans and Sklar 1990, Turner et al. 1995). Currently, most spatially explicit, dynamic models for land management have been developed for one or a few species (Turner et al. 1995). Extrapolating from such models to ''biodiversity'' is problematic. In the absence of models for each species of interest, the development of spatial models of vegetation changes could assist managers seeking to maintain biodiversity (Turner et al. 1995).

Both mechanistic and empirical approaches are widely used in modeling vegetation dynamics. The mechanistic approach assumes that the factors underlying the process are known, and explicit functions are used to connect these independent factors with the modeled variable (Levin 1997). Prevailing in this category are the individual-based forest simulators (for a short review, see Holt et al. 1995). Recent models of this kind are spatially explicit (Acevedo et al. 1995, Pacala et al. 1996). In empirical models, future changes in vegetation are extrapolations of past changes. In a pure empirical model, no ecological assumptions are built into the modeling processes, which are based on observations only. Transition models (also called Markov models, reviewed by Usher 1992) are the most common empirical models of vegetation dynamics, and are often used to predict expected future vegetation (e.g., Hall et al. 1991, Scanlan and Archer 1991, Callaway and Davis 1993). Transition models are not spatial, and even when based on spatially explicit data (e.g., vegetation maps; Hall et al. 1991), typically predict only the regional totals for each class of vegetation

(but see Wu et al. [1997] for a spatially explicit version of a transition model).

The goal of the present study is to develop and evaluate a modeling approach for predicting vegetation dynamics that may serve as a tool for planning and management. Present vegetation in any location is modeled as a function of past vegetation and site factors (such as topography and various disturbances); future vegetation pattern is then modeled as a function of current vegetation and site factors. This is basically an empirical model, but unlike transition models, in which change is randomly driven, here specific environmental factors drive vegetation change and ecological considerations determine the choice of the relevant factors for the model.

Specifically, we discuss the following aspects of this modeling approach: (1) a comparison between alternative models and model realizations; (2) spatial autocorrelation in such spatiotemporal models; (3) indices for performance of a spatially explicit model; and (4) merits and limitations of this approach in the context of tools for planning and management.

Logistic and linear models, stochastic and deterministic realizations

Logistic regression is often used to predict probabilities for presence/absence of a specific vegetation type (or species) in each point (e.g., Toner and Keddy 1997). A vegetation map may be constructed using a realization of these probabilities. When more than two vegetation types are mapped, polychotomous logistic regression (Hosmer and Lemeshow 1989) may be used to predict the respective probabilities (Davis and Goetz 1990). Often, however, the raw data consist of the proportion of cover of different vegetation types in each cell. In this case, a reduction of the data into few vegetation categories is needed before logistic regression can be used. This involves a loss of information. An alternative approach is a linear model, in which the proportion of cover in each cell is the dependent variable. In this study, we compare these two modeling approaches in terms of statistical adequacy and forecasting performance.

To create a predicted vegetation map based on such models, two types of realizations can be used (Buckland and Elston 1993). In a deterministic realization, the predicted value for a given cell is determined on the basis of the regression coefficients (in a linear model), or by assigning the cell to the class of its highest probability (in a logistic model). In a stochastic realization, a value is drawn randomly using the multinomial probabilities from the logistic model to determine a cell's status. Stochastic realization can be applied to a linear regression model as well, but the logistic model is more appropriate to represent a stochastic process with discrete states (Buckland and Elston 1993). In the present study, only deterministic realizations were considered for the linear model.

METHODS

Study area

An area of 4 km² (400 ha) on the northern slopes of Mt. Meron, Upper Galilee Mountains, Israel (32° N, 35° E) was chosen for the study. The area is heterogeneous in terms of topography (Fig. 1) and the mixture of vegetation types, but homogenous in its bedrock conditions (brown rendzina on dolomite rocks; O. Salmon, *personal communication*). The dominant tree, shrub, and dwarf shrub species are *Quercus calliprinos, Calicotome villosa,* and *Sarcopoterium spinosum,* respectively. The entire area was subject to intensive grazing and tree harvesting until 1948, when the nearby Arab village Sasa was abandoned. These practices have been largely reduced since then, and a rapid process of vegetation recovery is taking place in the region. Starting in the early 1960s, different parts of the area experienced different grazing regimes, in terms of both the type of livestock (goats vs. cattle), and grazing intensity. These regimes were kept relatively constant from 1964 to the present. The regional water divide bisects the study area into two distinct units, belonging to different drainage basins. The eastern unit (65% of the study area) was allocated to the construction of the models and the western unit (35% of the study area) served as a validation area. The western unit had no plots with cattle; therefore, an adjacent cattle-grazing plot was added to the validation area. These two units are shown in Fig. 1.

Vegetation maps

The methods used to produce vegetation maps from pan-chromatic aerial photographs are described in detail by Carmel and Kadmon (1998). The main steps of the procedure are described here briefly. Two aerial photographs of the study area (1964 and 1992) were chosen as a basis for the analysis. Diapositives of the photos were scanned, ortho-rectified, and geo-referenced to a planimetric coordinate system. Spatial resolution (pixel size) in both photomaps was 0.3 m. The combined RMS (root-mean-square) positional error between the photomaps was 1.13 m. The vegetation was classified based on its height: woody vegetation > 2.5 m ("trees"); woody vegetation < 2.5 m, including shrubs, semi-shrubs, and low trees ("shrubs"); and herbaceous vegetation, including bare ground ("herbs"). Classification accuracy was 89% in the 1992 image and 82% in the 1964 image (Carmel and Kadmon 1998). Anthropogenic elements (settlements, agricultural areas, etc.) were manually digitized on the photos and excluded from further analyses.

The vegetation maps were in raster format, i.e., consisting of grid cells. Accurate assessment of vegetation changes requires that comparisons of vegetation in different points in time are made between grid cells that actually represent the same area (Townshend et al. 1992). Using a cell size of 15 × 15 m, we achieved a
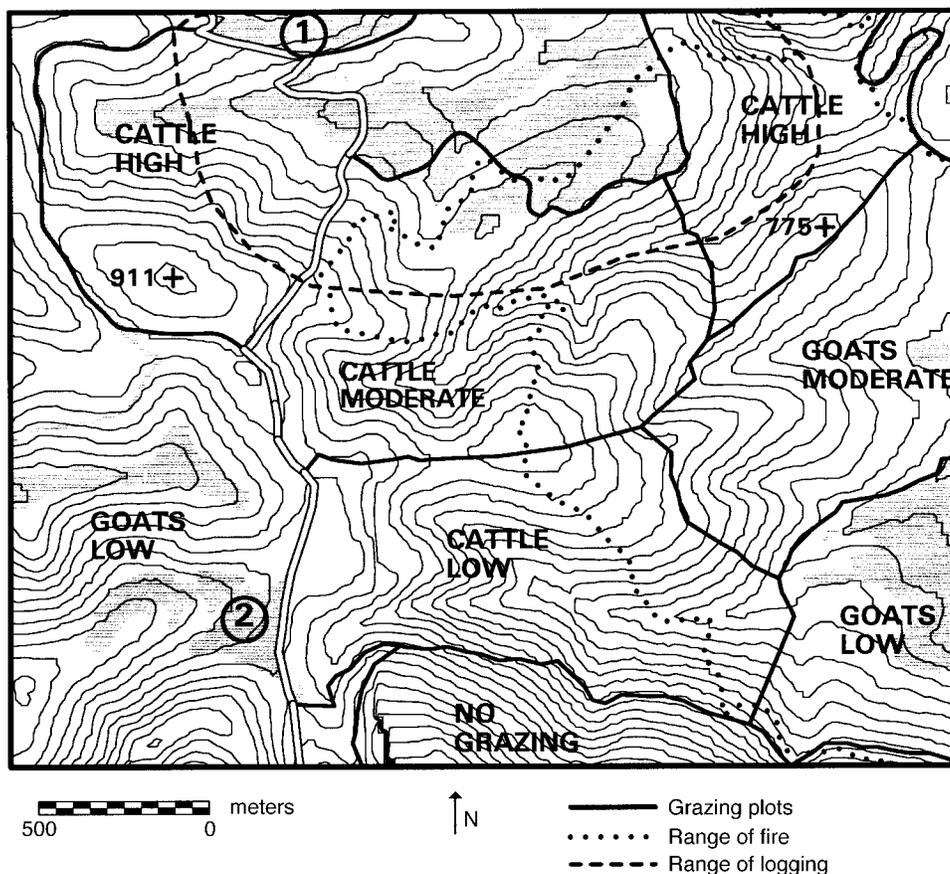
FIG. 1. A map of the study area, showing the topography and the distribution of grazing regimes (modified from Carmel and Kadmon [1999]). Contour intervals represent 10 m in elevation. Shaded portions are agricultural areas or villages. Circled numbers are the locations of (1) Kibbutz Sasa and (2) Mt. Meron field study center. The double line separates the model area (east) and validation area (west).

minimum spatial overlap of 90% between identical grid cells in 1964 and 1992 maps. The proportion of cover of each vegetation type (trees, shrubs, and herbs) in each grid cell was calculated based on the vegetation maps with the 0.3-m resolution. All other digital maps in the database were rescaled to the same resolution.

Disturbance and topography maps

The major disturbance factors in this area (grazing, logging, and fire) were documented, and maps of their intensities across the study area were produced. This part is described in detail in Carmel and Kadmon (1999), and is briefly reviewed here. The study area consists of areas grazed by cattle and areas grazed by goats. Fences divide those areas into plots of three distinct grazing intensities for cattle (high, moderate, and low), two levels of goat grazing (moderate and low), and a plot that was not grazed at all. A single low-intensity fire occurred in the area during the period studied, in 1978. The spatial range of the fire was delimited on an aerial photo taken several weeks after the fire. A single logging event occurred in 1980, and the range of that event was also delimited.

A digital terrain model (DTM, which denotes the elevation at each point in the area) was produced in the photo-rectification process, (Fig. 1 illustrates its contour representation). This DTM was used to derive digital maps of elevation, slope, and aspect for the study area. Aspect is represented by angular data (0–360°), and it was decomposed to north–south and east–west linear components (Periera and Itami 1991).

The models

Two types of multiple regression models were constructed: a linear regression model and a polychotomous logistic regression model. Each of these models was constructed twice, using the whole data set and using a small sample. The SPSS package (SPSS 1993) and the SAS package, procedure CATMOD (SAS Institute 1990), were used for building the linear regression and the polychotomous logistic regression, respectively.

Dependent variables

In the linear model, 1992 cell-specific tree cover (TREE92) and cell-specific herbaceous cover (HERB92)

were the dependent variables. The third component, 1992 shrub cover, was calculated as $1 - (\text{TREE92} + \text{HERB92})$. Linear regression assumptions maintain that the error terms are independent, have zero mean and constant variance, and follow a normal distribution. When the dependent variable Y is a proportion, as in our case, the error variance is not constant but proportional to $E(Y)\{1 - E(Y)\}$, where $E(Y)$ is the expected value of the dependent variable Y. We followed a common remedy in this case, and used the transformation arcsine $\sqrt{Y}$ to stabilize the error variance (Weisberg 1985). Plots of the studentized residuals against predictions and against predictors confirmed compliance with model assumptions.

For the polychotomous logistic regression, the vegetation data were reduced: each cell was assigned its dominant vegetation type (the one with the largest cover). The dependent variable was the 1992 vegetation category.

Independent variables

In this study, an attempt was made to construct a model that would be general, and applicable to other mediterranean regions. Thus, only variables that are known to causally affect mediterranean vegetation were included as potential predictors. These predictors were classified into three groups (Table 1): characteristics of 1964 vegetation, topography variables, and disturbance characteristics (grazing, logging, and fire).

Vegetation change in a specific cell may be affected by initial vegetation in neighboring cells (for example, cells with no woody vegetation in their neighborhood may show little change in woody vegetation, compared to cells surrounded by woody vegetation). Therefore, the first group, 1964 vegetation characteristics, included variables describing the vegetation in each cell, as well as indices for 1964 vegetation in neighboring cells (Table 1). Preliminary analysis (using univariate regression) revealed that indices based on the nearest four neighbors were the only ones that had a detectable effect on 1992 vegetation pattern (as opposed to indices based on a larger neighborhood size). Three such indices (for trees, shrubs, and herbs) were calculated for each model. In the linear models, these terms were the mean of cover proportions of the respective vegetation type in the four nearest neighbors; in the logistic models, these terms were the sum of cells dominated by the respective vegetation type.

Dummy variables were created to represent the categorical indices for disturbance (for example, the variable LOWCATTLE was assigned the value 1 for cells in plots with low-intensity cattle grazing and 0 in all other cells). Environmental variables may be related to vegetation nonlinearly. Hence, the square of each variable, as well as the variable itself, was considered for inclusion in the models (Gates et al. 1994). Because interactions between topography components were expected (Brown 1994), all first-order interactions be-

TABLE 1. List of potential predictors for the regression models.

Variable, by group	Description
1964 vegetation for linear models	
TREE64	Proportion of trees in a grid cell in 1964
SHRUB64	Proportion of shrubs in a grid cell in 1964
HERB64	Proportion of herbs in a grid cell in 1964
1964 vegetation for logistic models	
VEGET64	Cell-specific dominant vegetation type in 1964.
Neighbor indices for 1964 vegetation	
NEIBORHERB64	Index of 1964 herbaceous cover in the cell's neighborhood
NEIBORSHRUB64	Index of 1964 shrub cover in the cell's neighborhood
NEIBORTREE64	Index of 1964 tree cover in the cell's neighborhood
Topography variables	
ASPECT-NS	North–south linear component of aspect angle, in 0°–180° scale, where N = 0°, S = 180°, and E = W
ASPECT-EW	East–west linear component of aspect angle, in 90°–270° scale, where E = 90°, W = 270°, and N = S
SLOPE	Slope inclination
Z	Elevation in meters above sea level
Disturbance indices	
LOWCATTLE	Value = 1 for cells in areas with low cattle grazing regime; 0 for all other cells
MODCATTLE	1, moderate cattle grazing; 0, other
HIGHCATTLE	1, high cattle grazing; 0, other
LOWGOAT	1, low goats grazing; 0, other
MODGOAT	1, moderate goats grazing; 0, other
FIRE	1, inside the range of fire; 0, other
LOGGING	1, inside the range of logging; 0, other

tween topography variables were included as potential predictors.

Predictors were chosen using a forward stepwise procedure, with $p(\text{in}) = 0.05$ and $p(\text{out}) = 0.1$. In order to compare all models (logistic/linear, all data/sample) on an equal basis, we constructed them using the same set of potential predictors. Exceptions to this rule were 1964 vegetation variables, which were entered as proportion of cover in the linear models and as the cell's dominant category in the logistic models.

Constructing a sample database

Spatial autocorrelation is a general statistical property of variables measured across geographic space. It presents a problem for statistical analysis because autocorrelated data violate the assumption of independence made in most common statistical procedures (Cliff and Ord 1981). A commonly used solution to this problem is to select only a subset of the data, thus

reducing the extent of autocorrelation (Periera and Itami 1991, Buckland and Elston 1993, Brown 1994, Gates et al. 1994). Such a solution involves a massive loss of information (Legendre 1993). Here, we consider the question of how much we lose in model performance, using only a small fraction of the data instead of the whole database. Looking at this issue from a different aspect, one may ask how much one gains by mapping the whole area, as opposed to sampling at specific locations.

In order to compare the performance of a model based on the complete database with that of a model based on a sample of the data, we looked for a sample in which spatial autocorrelation was negligible. Preliminary analyses of the residuals of the linear model indicated that for distances of five cells (75 m) and more, the spatial autocorrelation was below 0.1. To obtain a sample of the data, we therefore employed a systematic sampling scheme, and selected every fifth cell in both row and column directions. This resulted in a sample size of ~4% of the data ($n = 547$). This subsample was used to construct linear and logistic models, similar to those based on the complete data set.

The error independence assumption was inspected via maps of the residuals. Moran's coefficient was used to measure the degree of spatial autocorrelation in the continuous variables (Cressie 1991). It was calculated for the original vegetation maps and for maps of model residuals.

Model realizations

Predicted vegetation maps for 1992 were constructed for the different models, indicating the dominant vegetation type for each grid cell. Maps were produced for the area that served to calibrate the model (''model area'') and for the external area allocated for model validation (''validation area''). In the linear models, proportion cover of trees and herbaceous vegetation for each grid cell were determined based on the respective regression coefficients. The shrub cover was calculated as the remaining proportion. Each cell was then assigned its dominant vegetation type. We name this type of realization ''deterministic,'' to indicate that once the proportion is estimated, the respective realization is determined.

In the polychotomous logistic models, the cell-specific probabilities associated with each vegetation type were used to construct two types of realizations. In the first type, a number in the interval [0,1] was drawn at random and was compared to the probabilities derived from logistic model for each class (p_1, p_2, and p_3, are the probabilities for trees, shrubs and herbs, respectively). If a number between zero and p_1 was drawn, then category 1 (trees) was assigned to this cell. If the random number was in the interval [p_1, $p_1 + p_2$], then category 2 (shrubs) was assigned to the cell. Category 3 (herbaceous vegetation) was assigned if the random number exceeded [$p_1 + p_2$]. We refer to this type as

''stochastic realization.'' In the second type, a deterministic realization, the highest probability determined the cell type.

Model performance

Model performance was evaluated independently for the model area and for the validation area, using the following measures.

1) Overall vegetation composition: proportions of each vegetation type in the relevant area were calculated and compared to the actual proportions.

2) Vegetation pattern: patterns in the predicted maps were assessed using three indices, the number of patches, the average patch size, and the contagion index (Li and Reynolds 1993). The latter index measures the extent to which the vegetation types are clumped or aggregated (Turner et al. 1989).

3) Cell-by-cell match: each predicted vegetation map was compared with the actual map on a cell-by-cell basis.

An error matrix was created for each comparison, and the significance of the κ coefficient of agreement, which controls for the match expected by chance alone (Cohen 1960), was tested. To test for the differences between predictive accuracy of alternative models, we applied McNemar's test (Fleiss 1981) a two-by-two table of correctly vs. incorrectly predicted cells. Because these tests require independence between observations, we applied them to a systematic subsample of the data. This subsample was constructed using the same method previously described.

Model applicability for planning and management

We illustrate the potential of the model in relation to an actual management problem. The Israeli Nature Reserve Authority plans to proclaim this area as part of the adjacent Mt. Meron Nature Reserve, and to prohibit grazing in the whole area. The implications of excluding grazing from the area were examined by creating two predicted vegetation maps for the year 2020, one under the scenario of no grazing in the whole area, and the other under the scenario of ''Status Quo,'' i.e., no change in grazing regimes across the study area. Model limitations and implicit assumptions will be discussed.

RESULTS

Regression models

Table 2 summarizes the results of model building for the linear models of (a) tree and (b) herbaceous cover, respectively. Similar sets of predictors were found to be significant for the logistic models. Initial vegetation, topography, and the ''disturbances'' (fire, logging, and grazing) all had significant impacts on present vegetation cover. These factors together explained 54% and 76% of the observed variability in herbaceous cover and tree cover, respectively, in the linear model based

TABLE 2. Regression results for the linear models for (a) tree cover and (b) herbaceous cover.

	B†	
Variable, by group	Model based on subsample ($n = 547$)	Model based on all data ($n = 13\,855$)
a) Models for tree cover		
Constant	1.127***	0.954***
1964 vegetation		
HERB64	−0.457**	−0.264***
(HERB64)²	−0.388**	−0.462***
Topography variables		
ASPECT-NS	NS	0.001*
ASPECT-EW	0.003***	0.002***
SLOPE	1.062**	1.205***
ASPECT-NS × SLOPE	−0.011**	−0.012***
Disturbance indices		
MODCATTLE	−0.502*	−0.348***
HIGHCATTLE	−0.496*	−0.395***
LOWGOAT	NS	−0.293***
MODGOAT	−0.483*	−0.371***
FIRE	NS	−0.055***
LOGGING	−0.357***	−0.334***
b) Models for herbaceous cover		
Constant	0.373*	0.430***
1964 vegetation		
HERB64	NS	0.013*
(HERB64)²	0.506**	0.514***
Topography variables		
ASPECT-NS	0.0015*	0.004***
ASPECT-EW	−0.0015***	−0.0015***
SLOPE	NS	−0.582***
ASPECT-NS × SLOPE	−0.0034*	−0.022**
Disturbance indices		
MODCATTLE	0.066*	0.078***
HIGHCATTLE	NS	0.161***
LOWGOAT	NS	0.183***
MODGOAT	0.302*	0.226***

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; NS, not significant.
† B is the unstandardized regression coefficient, which denotes the impact of each specific variable on the slope of the regression line.

on the complete database. Grazing by both cattle and goats inhibited the expansion of trees and reduced the rate of herbaceous withdrawal. Logging and fire affected tree cover negatively, whereas herbaceous cover was not significantly affected by these factors. Tree cover increased and herbaceous cover decreased with increasing slope. Tree cover increased, whereas herbaceous cover decreased from south- to north-facing slopes, and from east- to west-facing slopes. The interaction terms between the north–south component of aspect angle and slope inclination were also significant. Effects of all neighborhood indices of 1964 vegetation on 1992 vegetation were nonsignificant. In general, the regression coefficients of the subsample-based models were not very different from those of the all-data based models (see Table 2 for the linear model).

Spatial autocorrelation in the actual vegetation maps was high, with Moran's coefficient being 0.77 and 0.85 for maps of the 1992 herbaceous and tree cover, respectively. The values for the linear model residuals for herbaceous and tree cover were reduced to 0.57 and 0.58, respectively ($P < 0.05$ in all cases). Some patchiness of model residuals was evident in the models (Fig. 2).

Model predictions

All predicted maps had a significantly better match to the actual vegetation map then expected by chance, for both the model area and the validation area (κ was significant at the $P < 0.01$ level in all cases). The general patterns of the actual vegetation map of the model area are well depicted by the model maps, yet there are some important differences between the models (Fig. 3), which are documented in the following subsections.

Complete vs. sample data sets

In general, the use of 4% of the data yielded results very similar to those obtained using the whole data set. Cell-by-cell match between model maps derived from
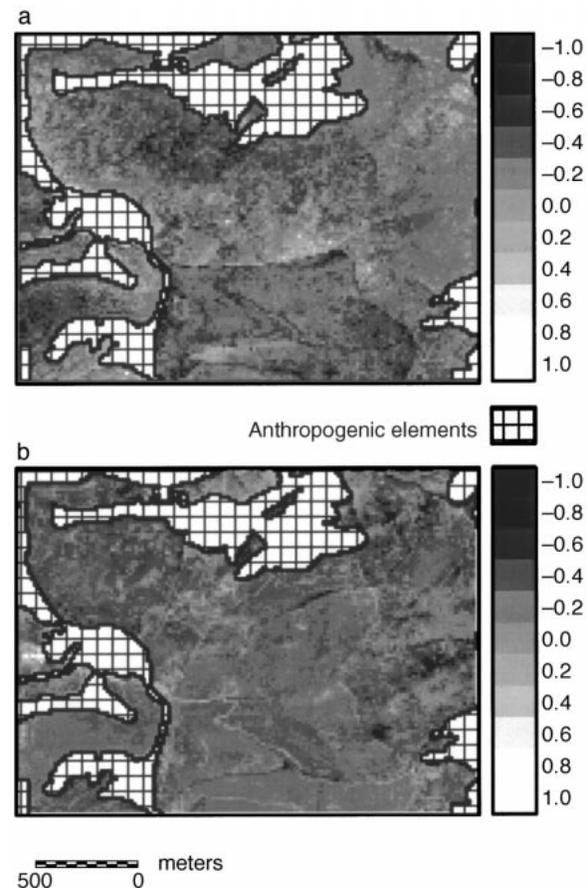
FIG. 2. Residuals of the linear models predicting the proportion of cover of (a) trees and (b) herbaceous vegetation in each grid cell.

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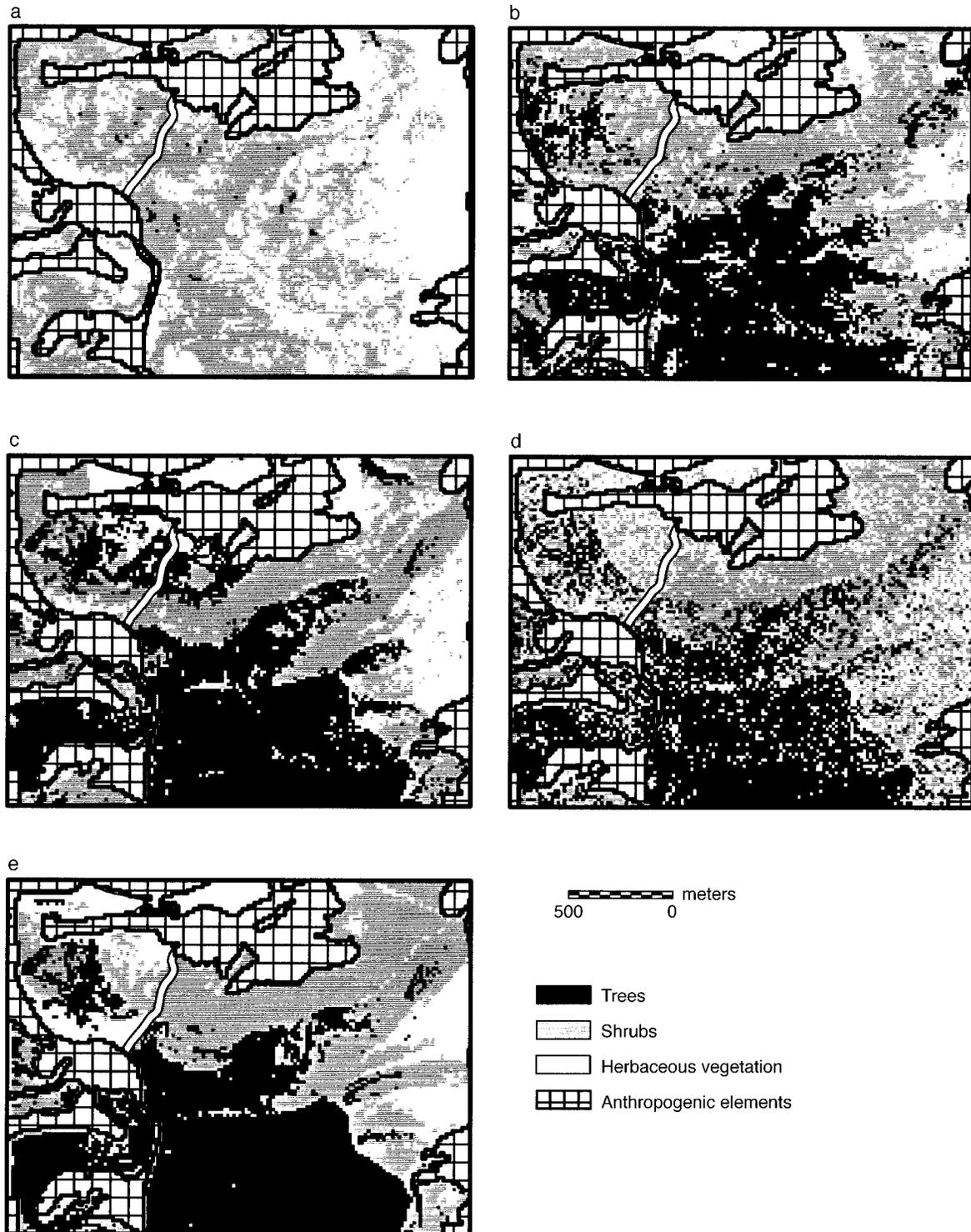
FIG. 3. Actual and model prediction maps: (a) actual 1964 vegetation map, which was the model input; (b) actual 1992 vegetation map; (c) linear model map; (d) logistic model, stochastic realization; (e) logistic model deterministic realization. The double line separates the model area (east) and validation area (west).
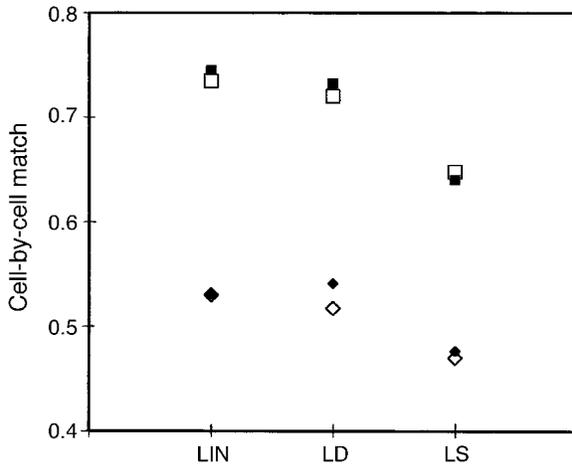
FIG. 4. Match between actual and predicted vegetation maps on a cell-by-cell basis. Abbreviations are: LIN, linear model; LD, logistic model, deterministic realization; and LS, logistic model, stochastic realization. Open markers represent models based on the sample data set, and solid markers represent models based on the complete data set. Squares represent results for the model area, and diamonds represent results for the validation area.

TABLE 3. Actual and predicted proportions of trees, shrubs, and herbaceous vegetation in 1992, in (a) the model area and (b) the validation area. Predicted proportions were calculated from the respective model realizations.

Vegeta-tion type	Actual vegetation map	Models		
		Linear	Logistic, deter-ministic	Logistic, stochastic
a) Model area				
Trees	0.51	0.46	0.44	0.50
Shrubs	0.32	0.33	0.41	0.33
Herbs	0.17	0.21	0.15	0.16
b) Validation area				
Trees	0.45	0.42	0.42	0.35
Shrubs	0.41	0.39	0.35	0.33
Herbs	0.14	0.19	0.23	0.31

the whole data and their subsample-based counterparts was between 0.92 and 0.96 in all cases. The match between model maps and actual vegetation maps was slightly higher in the all-data based models than in the subsample-based models in most cases (Fig. 4), but these differences were not significant (McNemar's test, $P > 0.05$). In the following sections, we present the results for the models based on the complete data, given that results for their subsample-based counterparts are similar.

Stochastic vs. deterministic realizations

Vegetation composition.—The stochastic realization of the polychotomous logistic model predicted vegetation composition in the model area rather precisely (with differences of 1% between actual composition and model estimation; Table 3), which is a natural outcome of its statistical properties. Vegetation composition was predicted less successfully by the deterministic realizations of both the logistic and the linear models (with differences of 2–8%; Table 3).

Spatial patterns.—The stochastic realizations were consistently more fragmented than the actual ones, whereas the deterministic realizations were more clumped than the actual ones (Figs. 3 and 5).

Cell-by-cell match.—The match between model and actual maps was significantly higher in the deterministic realizations of both the logistic and linear models than in the stochastic realizations of the logistic model (McNemar's test, $P < 0.05$ for all comparisons; see also Fig. 4). The slight differences between the deterministic realizations of the logistic and linear models were not significant (McNemar's test, $P > 0.05$).

FIG. 5. Landscape pattern indices calculated for the actual 1992 vegetation map and for 1992 model maps, for the model area: (a) contagion; (b) total number of patches; (c) mean patch size. Abbreviations are: VM, actual vegetation map (square); LIN, linear model; LD, logistic model, deterministic realization; and LS, logistic model, stochastic realization. A very similar trend was found for the validation area (not presented).
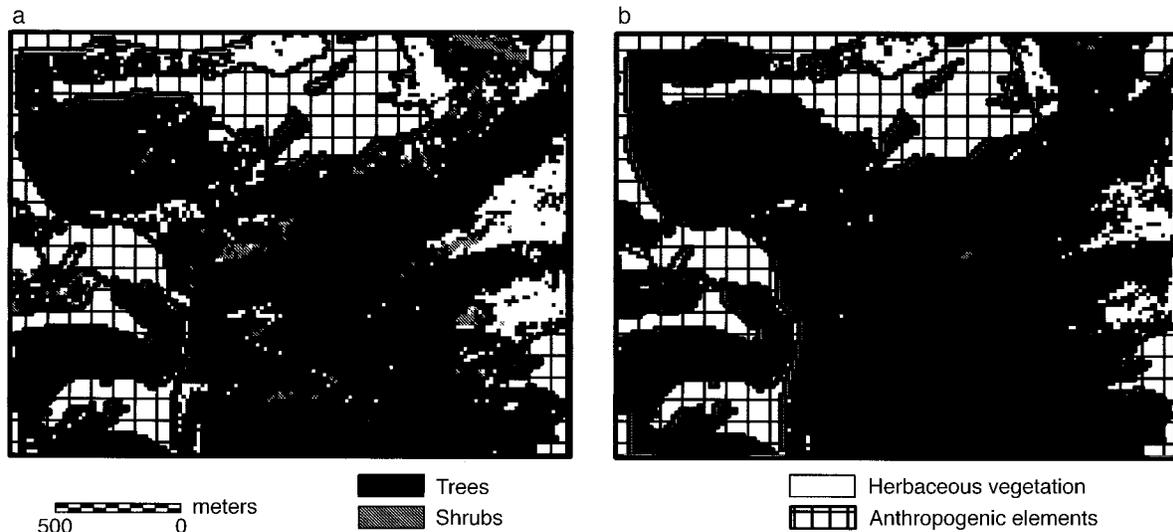
Fig. 6.   Predicted vegetation maps for 2020. Maps were constructed using the linear model, based on the actual 1992 vegetation map and regression coefficients. Two scenarios were considered: (a) grazing regimes would be the same as in the last 30 yr across the study area, and (b) both goats and cattle grazing would be halted in the whole area. Both scenarios assume that no other disturbance (e.g., fire, logging) occurs in the area during the period 1992–2020.

Performance in model area and validation area

Vegetation composition.—The stochastic realization was considerably less accurate in predicting vegetation composition in the external validation area, compared to its performance in the study area (Table 3). In contrast, predictions of vegetation composition in deterministic realizations of both model types were not less accurate for the validation area than for the model area (Table 3).

Spatial pattern.—There were no differences in prediction quality between the model and the validation areas.

Cell-by-cell match.—The match between model and actual maps was significantly lower for the validation area than for the model area (McNemar's test, $P < 0.01$

TABLE 4.   Proportions of vegetation types in 2020 in the whole study area, predicted by different models, for (a) continuation of grazing under the same regimes across the study area, and (b) no grazing at all in study area.

Vegetation type	Predicted proportions (2020)			Actual proportions (1992)
	LIN	LD	LS	
a) Grazing in study area				
Trees	0.74	0.79	0.68	0.49
Shrubs	0.08	0.06	0.15	0.34
Herbs	0.18	0.15	0.16	0.16
b) No grazing in study area				
Trees	0.86	0.96	0.90	0.49
Shrubs	0.02	0.001	0.05	0.34
Herbs	0.12	0.04	0.06	0.16

Notes: Abbreviations are: LIN, linear model; LD, logistic model, deterministic realization; and LS, logistic model, stochastic realization. Actual proportions in 1992 are also presented.

for all comparisons). Extrapolating the models to fit an external area reduced their match by 19–21% (Fig. 4).

Model applicability for planning and management

Predicted vegetation maps for 2020 were created based on (1) a scenario of no change in grazing regime across the study area, and (2) a scenario of no grazing in the whole area. Both scenarios assumed no fire and no logging in the area during the period 1992–2020. Predicted maps resulting from the deterministic realization of the logistic model are portrayed in Fig. 6. Predicted vegetation composition under all three realizations is presented in Table 4. The predicted vegetation maps for these two scenarios show that a further increase in tree cover in the area is expected, even if grazing continues (Fig. 6). If grazing is eliminated from the area, trees are predicted to dominate the whole study area, whereas shrubs and herbaceous vegetation are expected to disappear almost entirely (Fig. 6, Table 4). Remaining patches of these two vegetation types are predicted to be small and isolated. Note that this major prediction is consistent in all realizations, in spite of some differences between them (Table 4). Under the "status quo" scenario, trees are predicted to cover 68–79% of the area; under the "no grazing" scenario, trees are projected to cover 86–96% of the area.

DISCUSSION

Prediction is a principal means of testing fit between theory and observed phenomena (Pickett and Kolasa 1989). However, another important aspect of prediction is its use for planning and management (Glenn-Lewin et al. 1992). The variety of models for vegetation dynamics is large, and there is no one "best modelling

approach'' (Urban and Shugart 1992). The pros and cons of each modeling approach should be considered in the context of its purpose. In the context of forecasting, both empirical and mechanistic approaches have been criticized (for a short review, see Koehl 1989).

Van Tongeren (1995) argues that when general mechanistic ecosystem models are used to predict specific situations, the probability for a good prediction is low. Some individual-based mechanistic models have had good fit between model predictions and independent validation data (e.g., Pacala et al. 1996). Yet, in order to achieve accurate mechanistic models, demographic parameters have to be calibrated based on field experiments (Pacala et al. 1996). For widespread use in planning and management, construction of such experiments often may not be feasible. The mechanistic approach has also been used to construct large-scale stochastic models of vegetation dynamics (Jeltsch et al. 1997, He and Mladenoff 1999). These models emphasize the general nature of patterns and dynamics produced at large scales, rather than predictive ability for specific local situations (He and Mladenoff 1999). Additionally, validation of such models against independent data often is not feasible (He and Mladenoff 1999).

The use of empirical models for predictive purposes has also been questioned (Lehman 1986, Higgins and Richardson 1996). It is argued that, underpinned by empirical data, these models would only fit the area upon which they were calibrated (Verbyla and Fisher 1989). Another serious limitation of most empirical models is that they are not spatially explicit, which is an important property for a model intended to apply to land management (Boumans and Sklar 1990).

In the present study, we chose an intermediate approach to model vegetation dynamics. Unlike common empirical models, specific environmental and biological factors are assumed to have causal roles in the observed dynamics, and are used to drive the changes in the model. Unlike mechanistic models, these causal relationship are not expressed as a set of specific functions, but are calculated directly from the available data. Multiple regression is used to identify and quantify effects of environmental factors on vegetation change in past decades. Present vegetation in any location is modeled as a function of past vegetation and the effects of environmental factors (i.e., site factors such as topography and disturbances); future vegetation pattern is then modeled as a function of current vegetation and effects of environmental factors. We believe that this approach integrates some of the advantages of mechanistic models (namely, the explicit use of causal factors renders generality in the model) and empirical models (simplicity, precision, and realism). Additionally, it is particularly suitable to accommodate imagery-derived data, which become ever more available and affordable.

Recent models of vegetation dynamics (Wu et al. 1997) and land-use change (Wear and Bolstad 1998) used a similar approach. Wu et al. (1997) developed a spatially explicit version of a transition model for vegetation dynamics between cattail and sawgrass in Florida wetlands. The probability that a grid cell would change into a specific vegetation type is the weighted sum of probabilities associated with its specific environmental characteristics. That model has three characteristics in common with the models of the present study: aerial photographs are the source of data, it achieves a fine resolution (20×20 m grid cell), and it has the capability of creating predicted future vegetation maps for use in planning and management. Wear and Bolstad (1998) developed an approach for modeling land-use change that makes use of a multiple regression in which economical, as well as environmental, factors are explanatory variables. The model is calibrated using remote-sensing data, and is capable of forecasting land-use maps.

Several issues associated with the approach presented here, and its various possible versions, will be discussed, followed by an evaluation of this approach in the context of planning and management. Carmel and Kadmon (1999) provide a discussion of the ecological factors that were found to drive vegetation dynamics in this mediterranean ecosystem.

Linear vs. logistic models

The input of the linear model was the proportion of cover of each vegetation type in a 15×15 m grid cell, which consisted of 2500 pixels of 30×30 cm in the original vegetation map. In the logistic model, this information was reduced to a single value for each grid cell, its dominant vegetation type. In spite of this reduction, performance of the logistic models was similar to that of their linear counterparts. This result may be explained by a trade-off between model adequacy and loss of information. The underlying assumptions in the linear model, such as variance homogeneity, were not completely satisfied. The logistic model, in contrast, was fully adequate for probability predictions, but used reduced data.

Deterministic vs. stochastic realizations

In a previous study, stochastic realizations of a logistic model outperformed deterministic realizations of the same model in predicting the general pattern of deer distribution in Scotland (Buckland and Elston 1993). In the present study, in which models were assessed using three different aspects of performance, determining which realization was better depended on the aspect of performance considered. The stochastic realizations performed better than the deterministic ones in predicting the vegetation composition in the model area, but this trend was reversed in the external validation area. Deterministic realizations outperformed their stochastic counterparts in matching the actual map. Both the stochastic and deterministic re-

alizations failed to predict spatial patterns accurately; the stochastic realizations were more fragmented than the actual ones, whereas the deterministic realizations were more clumped than the actual ones. One possible conclusion is that both types should be constructed to bracket the actual range of pattern. The actual vegetation is expected to be less fragmented than the stochastic realization and more fragmented than the deterministic realization.

Statistical considerations

The parameter estimates of the subsample-based models are only slightly different from those of the all-data-based models. When these estimates are used to reconstruct a map for the entire area, the result is very similar to that of the all-data-based map. This indicates that, for a proper sample size (in this case, $n = 547$), the additional information gained by mapping the whole area results in a negligible improvement in model performance.

Maps of residuals of the models suggested that model errors were patchily distributed in space, probably pointing to latent environmental factors such as small-scale differences in soil type and local differences in grazing intensity that were not accounted for by the grazing plots. The fact that there are missing variables in the model reduces its performance; yet this should not prevent us from using it (cautiously) for predictive purposes.

An alternative approach to the problem of spatial autocorrelation is to accommodate it into the model (Legendre 1993). For example, Augustin et al. (1998) used values of the response variable at neighboring cells (autocovariates), in addition to environmental variables, as predictors in a spatial model, and found this to significantly improve model predictions. However, this approach is not applicable in the case of spatiotemporal models of the type presented here because they are typically calculated from the actual map, which is, in the case of a spatiotemporal dynamic model, the future map to be predicted (Cliff and Ord 1981). Investigating the consequences of ignoring spatial structure for the performance of the models, we compared our predictive model (in which spatial autocorrelation is ignored) with a similar model that incorporates spatial structure in the form of autocovariates (Y. Carmel, R. Kadmon, and R. Nirel, *unpublished data*). It was found that a considerable improvement in model performance was gained when autocovariates were included in the model. A possible direction for future effort to integrate spatial autocorrelation into spatiotemporal models may include iterative simulations of expected spatial structure, similar to those applied in predicting current distribution of species (Augustin et al. 1998).

Indices of 1964 neighbor vegetation were nonsignificant in all regression models. This may be a result of the specific structure of 1964 vegetation. At a res-

olution of 15 m, vegetation in the cell's neighborhood was generally similar to vegetation in the cell itself, and thus provided no additional information.

Using the model for extrapolations

Measuring model performance in an external area is a strict test for its generality. Often, models that fit well to the sites on which they are based fail to predict external sites (Verbyla and Fisher 1989, Buckland and Elston 1993). For example, Mcquilkin (1976) reported a vegetation model with R^2 of 0.66 that dropped to 0.01 when tested against independent data. In the present study, the model and validation areas, although adjacent, are distinct units. For the most part, they belong to different drainage basins. They are characterized by different combinations of slope and aspect, and are grazed by different goat herds. Taking these differences into account, a reduction in model performance when predictions were made for the external area was expected. However, the general vegetation pattern in the validation area was still well depicted by the model maps. Cell-by-cell match between model maps and the actual map was significantly reduced when models were applied to the validation area; in contrast, the quality of predictions of pattern indices and vegetation composition was similar to that of the model area (except the stochastic prediction for vegetation composition).

Model applicability for planning and management

The potential of such models to relate to actual management decisions is exemplified, for the case of grazing, in Mt. Meron Nature Reserve. Our results predict that exclusion of grazing from the study area (as planned by the Israel Nature Reserve Authority) would result in trees becoming the sole vegetation type, while shrubs and herbaceous vegetation would almost disappear by the year 2020. Remaining patches of these vegetation types would be small and isolated. Thus, the exclusion of grazing would decrease variability in vegetation types, and the entire biota dependent on the shrubs and herbaceous vegetation would be eliminated. Successional processes similar to those described here are occurring across the Galilee mountains and in other parts of the mediterranean region of Israel (Samocha et al. 1980, Kadmon and Harari-Kremer 1999a). Thus, in the long term, the proposed exclusion of grazing would result in loss of biodiversity. In contrast, the continuation of grazing may serve as a means of management that may decelerate these processes and may help to conserve landscape heterogeneity and biodiversity.

Model predictions assume that the rate of vegetation change is constant. This assumption is conditioned upon several factors. (1) No other disturbances (fire, logging, etc.), would occur in the study area in the next 28 yr. This may be an unrealistic assumption. However, the model framework could be adjusted to include dis-

turbances of the sort that took place in the area during the period studied, in the same way that grazing was altered in the previously mentioned scenarios. (2) No anthropogenic land-use change would occur in the study area. This, too, is an unlikely scenario for the mediterranean region. Yet, hypothetical or planned land-use change could be accounted for by the model by simply altering the scenario of land use in the simulation input. (3) No climate change would occur in the study area in the next 28 yr. This assumption may not hold, given our current knowledge about global and local climate shifts. If the model is calibrated for other mediterranean sites with different climatic conditions, as previously suggested, it would be possible to run sensitivity analyses for scenarios of climate shifts.

Turner et al. (1995) mention some properties for a spatially explicit model aiming to aid land management decision making. Although they refer specifically to population models, we believe that this list is relevant for models of vegetation dynamics as well. The modeling approach presented here seems to match each one of the characteristics mentioned by Turner et al. (1995). (1) The model should operate on spatial and temporal scales relevant to management decisions. Vegetation maps based on aerial photographs can cover a range of 1–100 km^2 (Kuechler and Zonneveld 1988) and span 4–5 decades (Carmel and Kadmon 1998). These dimensions correspond to many actual management questions (Turner et al. 1995). (2) Measurement of input variables should be affordable. Black and white aerial photographs have been available (and affordable) for the last 50–60 yr for many parts of the world (Kadmon and Harari-Kremer 1999b). Measurement of other variables is also relatively simple, although detailed data for disturbance history may not always exist. (3) Effects of alternative management scenarios may be foreseen. The approach presented here is particularly amenable for such ''scenario-analysis.'' (4) The visualization of spatially explicit model outputs may be very useful for managers. Fig. 6 is a good example of this point.

Considering the merits and limitations of the modeling approach presented here, we believe that it may serve as a valuable tool for planning and management. Management programs based on expected vegetation dynamics would be more realistic than those based on current vegetation maps. The approach presented here offers a step forward in this direction.

Literature Cited

Acevedo, M. F., D. L. Urban, and M. Ablan. 1995. Transition and gap models of forest dynamics. Ecological Applications **5**:1040–1055.

Augustin, N. H., M. A. Muggleston, and S. T. Buckland. 1998. The role of simulation in modelling spatially correlated data. Environmetrics **9**:175–196.

Boumans, R. M. J., and F. H. Sklar. 1990. A polygon-based spatial (PBS) model for simulating landscape change. Landscape Ecology **4**:83–98.

Brown, D. G. 1994. Predicting vegetation types at treeline using topography and biophysical disturbance variables. Journal of Vegetation Science **5**:641–656.

Buckland, S. T., and D. A. Elston. 1993. Empirical model for the spatial distribution of wildlife. Journal of Applied Ecology **30**:478–495.

Callaway, R. M., and F. W. Davis. 1993. Vegetation dynamics, fire, and the physical environment in coastal central California. Ecology **74**:1567–1578.

Carmel, Y., and R. Kadmon. 1998. Computerized classification of Mediterranean vegetation using panchromatic aerial photographs. Journal of Vegetation Science **9**:445–454.

Carmel, Y., and R. Kadmon. 1999. Grazing, topography, and long term vegetation changes in a Mediterranean ecosystem. Plant Ecology **145**:239–250.

Cliff, A. D., and J. K. Ord. 1981. Spatial processes: models and applications. Pion, London, UK.

Cohen, J. 1960. A coefficient of agreement for nominal scales. Educational and Psychological Measurement **20**: 37–46.

Cressie, N. 1991. Statistics for spatial data. John Wiley, New York, New York, USA.

Davis, F. W., and S. Goetz. 1990. Modeling vegetation pattern using digital terrain data. Landscape Ecology **4**:69–80.

Fleiss, J. L. 1981. Statistical methods for rates and proportions. Second edition. John Wiley, New York, New York, USA.

Gates, S., D. W. Gibbons, P. C. Lack, and R. J. Fuller. 1994. Declining farmland bird species: modelling geographical patterns of abundance in Britain. Pages 153–177 *in* P. J. Edwards, R. M. May, and N. R. Webb, editors. Large scale ecology and conservation biology. Blackwell Science, Oxford, UK.

Glenn-Lewin, D. C., P. K. Peet, and T. T. Veblen, editors. 1992. Plant succession: theory and prediction. First edition. Chapman and Hall, Cambridge, UK.

Hall, F. G., D. B. Botkin, D. E. Strebel, K. D. Woods, and S. J. Goetz. 1991. Large-scale patterns of forest succession as determined by remote sensing. Ecology **72**:628–640.

He, H. S., and D. J. Mladenoff. 1999. Spatially explicit and stochastic simulation of forest-landscape fire disturbance and succession. Ecology **80**:81–99.

Higgins, S. I., and D. M. Richardson. 1996. A review of models of alien plant spread. Ecological Modelling **87**: 249–265.

Holt, R. D., S. W. Pacala, T. W. Smith, and J. Liu. 1995. Linking contemporary vegetation models with spatially explicit animal population models. Ecological Applications **5**:20–27.

Hosmer, D. W., and S. Lemeshow. 1989. Applied logistic statistics. John Wiley, New York, New York, USA.

Jeltsch, F., S. J. Milton, W. R. J. Dean, and N. Van Rooyen. 1997. Analyzing shrub encroachment in the southern Kalahari: a grid-based modelling approach. Journal of Applied Ecology **34**:1497–1508.

Kadmon, R., and R. Harari-Kremer. 1999a. Landscape-scale regeneration dynamics of disturbed Mediterranean maquis. Journal of Vegetation Science **10**:383–402.

Kadmon, R., and R. Harari-Kremer. 1999b. Studying long-term vegetation dynamics using digital processing of historical aerial photographs. Remote Sensing of Environment **68**:164–176.

Koehl, M. A. R. 1989. Discussion: from individuals to populations. Pages 39–53 *in* J. Roughgarden, R. M. May, and

S. A. Levin, editors. Prespectives in ecological theory. Princeton University Press, Princeton, New Jersey, USA.

Kuchler, A. W., and I. S. Zonneveld, editors. 1988. Vegetation mapping. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? Ecology **74**:1659–1673.

Lehman, J. T. 1986. The goal of understanding in limnology. Limnology and Oceanography **31**:1160–1166.

Levin, S. A. 1997. Mathematical and computational challenges in population biology and ecosystems science. Science **275**:334–343.

Li, H., and F. Reynolds. 1993. A new contagion index to quantify spatial patterns of landscapes. Landscape Ecology **8**:155–162.

Mcquilkin, R. A. 1976. The necessity of independent testing of soil–site equations. Soil Science Society of America Journal **40**:783–785.

Pacala, S. W., C. D. Canham, J. Saponara, J. A. Silander, R. K. Kobe, and E. Ribbens. 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. Ecological Monographs **66**:1–43.

Periera, J. M. C., and R. M. Itami. 1991. GIS-based habitat modeling using logistic multiple regression: a study of the Mt. Graham red squirrel. Photogrammetric Engineering & Remote Sensing **57**:1475–1486.

Pickett, S. T. A., and J. Kolasa. 1989. Structure of theory in vegetation science. Vegetatio **83**:7–15.

Samocha, Y., M. Litav, P. Fine, and Y. Vizel. 1980. Development rate of woodland trees in the Judea Mountains. Layaaran **30**:6–15 [In Hebrew.].

SAS Institute. 1990. SAS/STAT user's guide. Version 6, Fourth edition. Volume 2. SAS Institute, Cary, North Carolina, USA.

Scanlan, J. C., and S. Archer. 1991. Simulated dynamics of succession in a North American subtropical *Prosopis* savanna. Journal of Vegetation Science **2**:625–634.

Soulé, M. E., and B. A. Wilcox, editors. 1980. Conservation biology: an evolutionary–ecological perspective. Sinaur Associates, Sunderland, Massachusetts, USA.

SPSS. 1993. SPSS for Windows-based system. User's guide 6.0. SPSS, Chicago, Illinois, USA.

Toner, M., and P. Keddy. 1997. River hydrology and riparian wetlands: a predictive model for ecological assembly. Ecological Applications **7**:236–246.

Townshend, J. R. G., C. O. Justice, C. Gurney, and J. McManus. 1992. The impact of misregistration on change detection. IEEE Transactions in Geoscience and Remote Sensing **30**:1054–1060.

Turner, M. G., G. J. Arthaud, R. T. Engstrom, S. J. Hejl, J. Liu, S. Loeb, and K. McKelvey. 1995. Usefulness of spatially explicit population models in land management. Ecological Applications **5**:12–16.

Turner, M. G., R. Costanza, and F. H. Sklar. 1989. Methods to evaluate the performance of spatial simulation models. Ecological Modelling **48**:1–18.

Urban, D. L., and H. H. Shugart. 1992. Individual-based models of forest succession. Pages 249–292 *in* D. C. Glenn-Lewin, R. K. Peet, and T. T. Veblen, editors. Plant succession. Chapman and Hall, London, UK.

Usher, M. B. 1992. Statistical models of succession. Pages 225–247 *in* D. C. Glenn-Lewin, R. K. Peet, and T. T. Veblen, editors. Plant succession. Chapman and Hall, London, UK.

van Tongeren, O. F. R. 1995. Data analysis or simulation model: a critical evaluation of some methods. Ecological Modelling **78**:51–60.

Verbyla, D. L., and R. F. Fisher. 1989. An alternative approach to conventional soil–site regression modeling. Canadian Journal of Forest Research **19**:179–184.

Wear, D. N., and P. V. Bolstad. 1998. Land-use changes in Southern Appalachian landscapes: spatial analysis and forecast evaluation. Ecosystems **1**:575–594.

Weisberg, S. 1985. Applied linear regression. Second edition. John Wiley, New York, New York, USA.

Western, D., M. C. Pearl, S. L. Pimm, B. Walker, I. Atkinson, and D. S. Woodruff. 1989. An agenda for conservation action. Pages 304–322 *in* D. Western and M. C. Pearl, editors. Conservation for the twenty-first century. Oxford University Press, New York, New York, USA.

Wu, Y., F. H. Sklar, and K. Rutchey. 1997. Analysis and simulations of fragmentations of patterns in the Everglades. Ecological Applications **7**:268–276.