Mapping and Modeling the dynamics of Mediterranean vegetation under various management activities

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Mapping and Modeling the dynamics of Mediterranean vegetation under various management activities

Research Thesis

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Table of contents

List of tables

List of figures

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 and scenic diversity. Recent changes in human activities 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. In this research, the effects of disturbances on the spatio-temporal dynamics of vegetation in Mediterranean landscapes were studied.

The major component of the research consisted of the development of a spatially explicit, hybrid, and spatially hierarchical ecological model, in attempt 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 two types of landscapes, random-generated and actual, and 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.

Spatially explicit models require vegetation maps in order to be applied on actual landscapes. The task of mapping Mediterranean vegetation is complex, due to its fine scale spatial heterogeneity, coupled with the high spectral similarity of many of the common woody species. In the second component of the research, a novel mapping approach was developed for this task, based on data fusion of LiDAR and aerial photography. A continuous map of height and woody cover is created, and then categorized in order to generate the required vegetation map that serves as the input for the model.

The third component of the research was empirical quantification of the effects of two common disturbances – goat grazing and shrub clearing, on the fine scale spatial structure of woody vegetation. This part of the work coupled data from a large scale field experiment with the analysis of low altitude aerial photography. Landscape metrics that are commonly used in the assessment of large-scale landscape structure were successfully employed here to quantify the very fine scale structure of vegetation following disturbances.

Together, the three components of this work enhanced the understanding, methodology, and predictive capability of the outcomes of disturbance based management on the structure, configuration, and composition of a Mediterranean landscape at various spatial and temporal scales. This field of research is becoming increasingly important due to the wide-spread land use and land cover changes in many Mediterranean regions, that can be moderated and controlled through disturbance based management.

Symbols and abbreviations

PFT – Plant functional type

C(x,y) – dominant PFT at location *(x,y)*

P – Transition function between different PFT

t – Time in years

HE – Herbaceous vegetation

DS – Dwarf shrubs

LS – Low shrubs

TS – Tall shrubs

LTR – Low trees

$Ageest_j$ - Age of establishment of PFT j

$Ageregrow_{clear}$ – Presumed age of regrowth following clearing event

$Ageregrow_{fire}$ - Presumed age of regrowth following fire event

$Agerep_j$ – Reproductive age

$Agemat_j$ - Age of maturity

$Agemax_j$ – Maximal age

$hgtescape_j$ – Height above grazing limit

$hgrow_j^{\max}$ - Maximal height growth rate

$h_j^{\max}$ - Maximum height

$Hregrow_{fire}$ – Height one year after fire

$Hregrow_{clear}$ - Height one year after clearing

$Seedprodmx_j$ - Maximal seed production (as probability)

$Seedprodmx_j^{short}$ - Maximal seed production at the short range (as probability)

$Seedprodmx_j^{long}$ - Maximal seed production at the long range (as probability)

$Ssurv_j$ - Proportion of seed survival per year

$pmort_j$ – Probability of mortality

$Pregrow_{clear}$ – Probability of regrowth following clearing

$Pregrow_{fire}$ - Probability of regrowth following fire

$rhgrz_j$ – Probability of death due to grazing

$\downarrow Egrz_j$ - Effect of grazing on expansion probability

$\downarrow Cgraz_j$ - Effect of grazing on colonization probability

$P^{j\rightarrow i}_{expansion\,\max}$ - Maximal expansion probability

$P^{j\rightarrow i}_{colonization\,\max}$ - Maximal colonization probability

$P^{j\rightarrow i}_{expansion}$ - Actual expansion probability

$P^{j\rightarrow i}_{colonization}$ - Actual colonization probability

$Seed_{j,t}$ – Seed availability

$Seedprod_{j,t}$ – Seed production

N – Number of patches in a site

$N^{*}_{j,t}$ – Number of patches dominated by PFT j

$HCover_{site}$ – Relative cover of low shrubs, tall shrubs, and trees in a site

$h_{j,t}$ – PFT height

SIDI – Simpson's index of diversity

ED – Edge density

SA – Sensitivity analysis

LiDAR – Light detection and ranging

SAR – Synthetic aperture radar

DEM – Digital elevation model

DTM – Digital terrain model

DSM – Digital surface model

RGB – Red, green, blue

AVHRR – Advanced very high resolution radiometer

PLAND – Proportion of landscape

PD – Patch density

AREA – Mean patch area

GYRATE – Mean radius of gyration

SHAPE – Mean shape index

PROXIM – Mean proximity index

Introduction

The Mediterranean mosaic landscapes

The vegetation of Israel and other Mediterranean countries has been shaped over thousands of years by the dynamic interactions between the traditional human agro-pastoral land use (clearing, grazing, and burning) and regeneration processes of the natural vegetation (Naveh and Dan 1973, Barbero et al. 1990, Perevolotsky and Seligman 1998). The typical Mediterranean mountain landscape created by these processes is a spatially heterogeneous “mosaic” formed of patches of different vegetation formations due to different histories of disturbance and regeneration (Zohary 1973, Naveh and Kutiel 1986). The size of elements (or patches) in this mosaic is not large, typically in the order of tens to hundreds meters (Shoshany 2000, Dufor Dror 2002). This spatial scale, or grain, of the landscape has important ecological consequences, both for plants (dispersal, gene flow, diversity) and for animals (diversity within foraging and home ranges).

Over the past decades, socio-economic processes have caused substantial changes in the land use of Mediterranean upland in Israel and other Mediterranean countries (Naveh and Dan 1973, Rundel 1998). Most small cultivation patches and even larger terraces have been abandoned. Clearing and cutting of woody vegetation has been restricted. Goat herding has been discontinued or reduced in large areas, and in some cases replaced by cattle grazing. As a result of these changes in land use, there have been substantial alterations in the vegetation, towards dense, closed woody formations over large areas. This, in turn, resulted in reduced landscape and species diversity and an increase in the extent and intensity of wild fires (Perevolotsky and Seligman 1998).

In the absence of disturbance, the vegetation tends to converge to a formation of tall dense scrub forest (maquis) dominated by multi-stem trees or tall shrubs (e.g. *Quercus calliprinos, Pistacia palaestina, Phillyrea media*) which is the presumed climax community on Terra-Rossa soils developed on hard limestone rock, prevalent in mountain landscapes in Israel (Zohary 1973). In areas with more than 700 mm annual rainfall and on north-facing slopes, the development of a complete cover of close tall maquis is observed after 30 years without disturbance (Carmel and Kadmon

1999). In drier habitats the process is slower (Kadmon and Harari-Kremer 1999). There is a growing awareness among ecologists and land managers that the conversion of a formerly diverse heterogeneous mosaic landscape to a uniformly closed, tall forest landscape involves significant losses of biodiversity, scenic diversity, and an increase in fire risk. The ecological and social benefits inherent in the Mediterranean mosaic landscape are increasingly recognized and valued. How can this heterogeneous landscape be sustained, in areas where it is disappearing by spontaneous or human-induced processes? How can landscape heterogeneity be restored in areas where these processes have already advanced to produce a uniform landscape of closed woody vegetation?

The role of management in preserving the mosaic landscapes

Grazing (especially by goats), clearing or thinning of woody plants, and fire in patches have been the main factors that created and maintained historically the Mediterranean mosaic landscape (Naveh and Dan 1973, Rundel 1998). In principle, the same factors could be managed in the present and future to sustain and restore landscape heterogeneity, even though the socio-economic rationale for such management is different from the historic one. However, the feasibility and efficiency of such "management for heterogeneity" techniques are not straightforward. Experiments reveal that woody vegetation recovery, even following extreme disturbance, is very rapid, and within 5 to 10 years complete woody cover is restored (Henkin et al. 1999, Perevolotsky et al. 2003). A recent study found this phenomenon to be common in other Mediterranean countries as well (Carmel and Flather 2004). The species composition and distribution of individuals is often similar to that previous to the disturbance. 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).

Research questions

The central research question, scientific and applied, that motivated this research is: How can active human intervention channel natural vegetation dynamics so as to effectively restore and maintain in the long term (decades) spatially heterogeneous “mosaic” landscapes in Mediterranean upland environments, in order to conserve biodiversity. The underlying assumption is that high landscape heterogeneity supports high biodiversity (ultimately, the major target for conservation) since it consists of many habitats, corresponding with many ecological niches. Landscape heterogeneity, therefore, is used here as a surrogate to biodiversity. The working hypothesis assumed here is that management can, in principle, conserve and restore landscape diversity. The 'how' is yet largely unknown. Questions such as 'what sequence of means could the manager employ in order to maintain a dynamic mosaic of the landscape for the next 50 years?' are yet unanswered. The approach chosen in this research is the development of a dynamic mathematical model to describe and predict long-term changes in Mediterranean vegetation in response to disturbances and management events. The model utilizes and integrates a body of empirical information and theoretical insight on the ecological processes in these systems that have been obtained by field research in Israel.

A second research question, which is intermixed with the major research question, is how to map the structure of vegetation in Mediterranean landscapes. This question has emerged from the modeling process, since spatially explicit models go side-by-side with spatial data about the type, structure, or formation of vegetation, usually in form of a vegetation map. Such a map is often incorporated to two aspects of model development and implementation: model validation (is the predicted vegetation dynamics generated by the model similar to actual vegetation dynamics? how accurate is the model?), and model simulations (using a vegetation map as the starting conditions of the landscape for simulations of future vegetation dynamics). Due to many existing limitations in mapping Mediterranean vegetation, a new approach for mapping vegetation structure was developed, using data fusion of light detection and ranging (LiDAR) data and aerial photography. The product of the process is a continuous map of vegetation structure that can be categorized into thematic vegetation maps according to the requirements of specific studies, in this case the starting conditions for simulations of future vegetation dynamics.

The third research question deals with another perspective of the interaction between disturbance and spatial vegetation dynamics, this time through an empirical assessment using remote sensing. The research question of this part was how two types of disturbance (goat grazing and shrub clearing) affect the fine-scale spatial structure of woody vegetation. This was assessed empirically by mapping the vegetation in a set of experimental plots exposed to those disturbances. In contrast to previous studies, a very high resolution mapping approach was taken, using balloon-based aerial photography. The motivation to study vegetation at a fine scale was that many fundamental ecological processes (especially in Mediterranean type ecosystems) occur at the fine scale, and are impacted by the fine scale structure of the woody vegetation. Such processes include seed dispersal, pollination, competition for sunlight and resources, and alteration of fine scale biogeochemical pathways.

Research objectives

1. To develop, explore and validate a spatially explicit mathematical model of Mediterranean vegetation dynamics, focusing on the responses to anthropogenic disturbance and land use factors.
2. To implement this model in a Mediterranean mosaic landscape, Ramat Hanadiv Nature Park, and to predict the effect of various management operations on the future vegetation structure in the landscape.
3. To develop a data-fusion approach for mapping Mediterranean vegetation using a combination of LiDAR and color aerial photography. The approach used to generate two types of maps: vegetation structure and plant functional types. The latter is incorporated as the starting conditions of the modeling process (objective 2).
4. To quantify the effects of goat grazing and shrub clearing on the fine scale spatial structure of woody vegetation in a Mediterranean landscape.

Modeling vegetation dynamics[1]

Background

Ecological models for vegetation change

In complex systems, such as the ecosystems studied here, mathematical models are useful scientific tools for exploring the consequences of different hypotheses on the functioning of the system or its components. They can also be useful as a practical tool for managers to explore the possible consequences of their decisions. Models of vegetation dynamics can be classified into several main types. Common to many of these models is a basic unit that can be in one of several vegetation states and the dynamic model generates transitions of units from one vegetation state to another (Westoby et al. 1989). In Markov type models (Usher 1992, Rego et al. 1993) the transition of a unit area from one vegetation state to another 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, Balzter et al. 1998), the transition of a unit area from one vegetation state to another is governed by deterministic transition rules that depend on the states of neighboring units. These models depict the landscape as a binary grid, and changes of the spatial pattern of both the foreground (vegetation) and background (non vegetation) can by analyzed through time (Shoshany and Kelman 2006, Shoshany 2008). In gap models, originally developed for forests (Shugart and West 1980, Botkin 1993), the patch is defined by the identity (and optionally age) of the dominant adult tree and the presence (optionally number and age) 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 models (Urban and Shugart 1992, Grimm and Railsback 2005) 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. Models of these different types

[1]Based on: Bar Massada, A., Koniak, G., Noy-Meir, I., and Carmel, Y. The effects of disturbance based management on the spatio-temporal dynamics of Mediterranean vegetation: A spatially hierarchical modeling approach. Submitted to *Ecological Applications*.

have been developed and applied 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 (Standiford and Howitt 1993, Pausas 1999, Carmel et al. 2001, Pausas 2003).

In recent years, the historical distinctions between the different types of dynamic vegetation models have become blurred. The increase in computer power and speed has allowed the development and implementation of hybrid models that merge procedures or sub-models of different types, often in a spatially hierarchical structure (Acevedo et al. 2001, Pausas 2003). The limiting factor for model complexity is no longer computation power but rather the ability to parameterize the model, i.e. to assign realistic values to an increasing number of parameters.

Scale in ecological modeling

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 monitoring, description and analysis of plant communities and vegetation dynamics is the "site". The definition of a site usually presumes a given "habitat", characterized by specific micro-climate, topography and rock-soil conditions, and by 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 evaluation and management are taken is larger, 10^3 to 10^4 m, i.e. the "landscape" scale (Naveh and Lieberman 1994). 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 ecological modeling then 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 criticized as being unrealistic (van Tongeren 1995). A third approach is hierarchical models that operate on a real landscape at two or three scales simultaneously. In this case, ecological processes can be represented in different spatial scales, according to their inherent properties or model requisites. Hierarchical models have been developed for the modeling of forest dynamics in other systems (Pacala et al. 1996). Such a model, for example, could predict the future vegetation structure at the landscape scale, based on processes operating at the site scale (namely grazing, clearing, fire, and seed dispersal) which in turn effect the development at the patch scale (plant growth, mortality, expansion, and takeover by a colonizer).

Existing models for Mediterranean vegetation dynamics

In the past decades, there have been several attempts to model different aspects of Mediterranean vegetation, using various approaches. Pausas (1999) reviewed the main problems of applying gap models for Mediterranean systems, mainly the interactions and regeneration traits following disturbance (especially fire) that vary between two major life forms (seeders and resprouters). Additionally, Mediterranean vegetation dynamics are affected by environmental factors such as climate, soils, and topography. Carmel et al (2001) accounted for the effect of environmental factors via an empirical model that simulates the dynamics of three common vegetation types (trees, shrubs, and herbaceous vegetation) under grazing and fire over a decadal time scale in Northern Israel. A different modeling approach, using Markov chains, also accounted for the effects of grazing, fire, and topography on the changes of vegetation formations in California (Callaway and Davis 1993). Markov chains were also used by Rego et al (1993) for modeling the temporal dynamics of an Oak dominated shrubland. In the same region, the spatio-temporal dynamics of six functional types, under varying fire regimes, in four different landscape types were modeled using LANDIS (Mladenoff et al. 1996, Mladenoff and He 1999), adopted to the Mediterranean system by Franklin et al (2001). Initial landscape pattern was found to have a pronounced impact on vegetation dynamics. This was modeled explicitly by Pausas (2003) but also reported empirically by Carmel et al (2001).

The present approach

Accounting for all the above, in this research the following modeling approach was taken. A hybrid, stochastic, hierarchical, and spatially explicit vegetation model was developed. The model simulates the spatio-temporal dynamics of five plant functional types (PFTs hereafter) common to Mediterranean landscapes, under various disturbance regimes (that are controlled by the user of the model). Three general types of disturbances exist in the model: grazing (either by goats or by cattle), shrub clearing, and prescribed burning.

The mechanism of change in the model is based on a spatially explicit state-and-transition process, where in each time step (one year), the dominant PFT in the basic modeling unit can be replaced by a different PFT according to a specific transition probability (Figure 1). Unlike Markov models, the transition probabilities are not constant, but rather are spatially explicit continuous transition functions. The process of change in the model is directional, assuming that taller PFT succeed lower PFT over time (Figure 1). This is the main assumption behind the model. Transitions in the opposite direction (tall to low) can not occur except in the case of death of a woody PFT, after which it is replaced deterministically by herbaceous vegetation (assuming that there is a constant seed bank or seed deposition of herbaceous vegetation across the landscape). Disturbances (grazing by goats or cattle, fire, and clear cutting) have various impacts on transition processes, including alternation of rates of change (by grazing) and death (by fire or clear cutting).

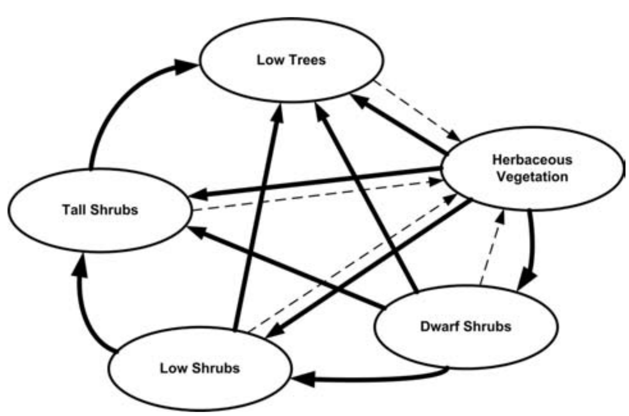


Figure 1. The possible transitions between the five PFT in the model. Solid arrows represent processes of colonization from seeds or vegetative expansion. Dashed lines represent the outcome of death of a woody PFT.

The model accepts as an input a high resolution vegetation map, consisting of the five PFTs that are represented in the model. In addition, the operator determines the disturbance scenario to be applied, detailing what (type of disturbance), where (which sites), and when (which years) disturbance management will be applied. The model incorporates the disturbance regime with the natural transition process, and yields the vegetation map for each year of the simulation. The model is typically run for periods of 50-100 years, depending on the scenario of interest.

Methods

Model structure

The model simulates the spatio-temporal dynamics of five PFTs, which correspond to groups of species with common structural and functional characteristics common to many Mediterranean regions: [1] Herbaceous vegetation (regardless of species); [2] Dwarf shrubs (e.g. *Sarcopoterium spinosum*); [3] Low deciduous shrubs (e.g. *Calyicotome villosa*); [4] Tall evergreen shrubs (e.g. *Pistacia lentiscus*); [5] Low trees (e.g. *Phillyrea media*). 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 nested spatially hierarchical levels (Figure 2): [1] Patch (cell), which is a square cell with an area of 1 m^2 (approximately the size of an adult 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, that is a square collection of patches (area of 100 m^2), that have the same disturbance history. That is, a specific disturbance is assumed to be acting identically on all patches in the site. [3] Landscape, which is the entire area of model operation, consisting of many entities of the lower hierarchical levels.

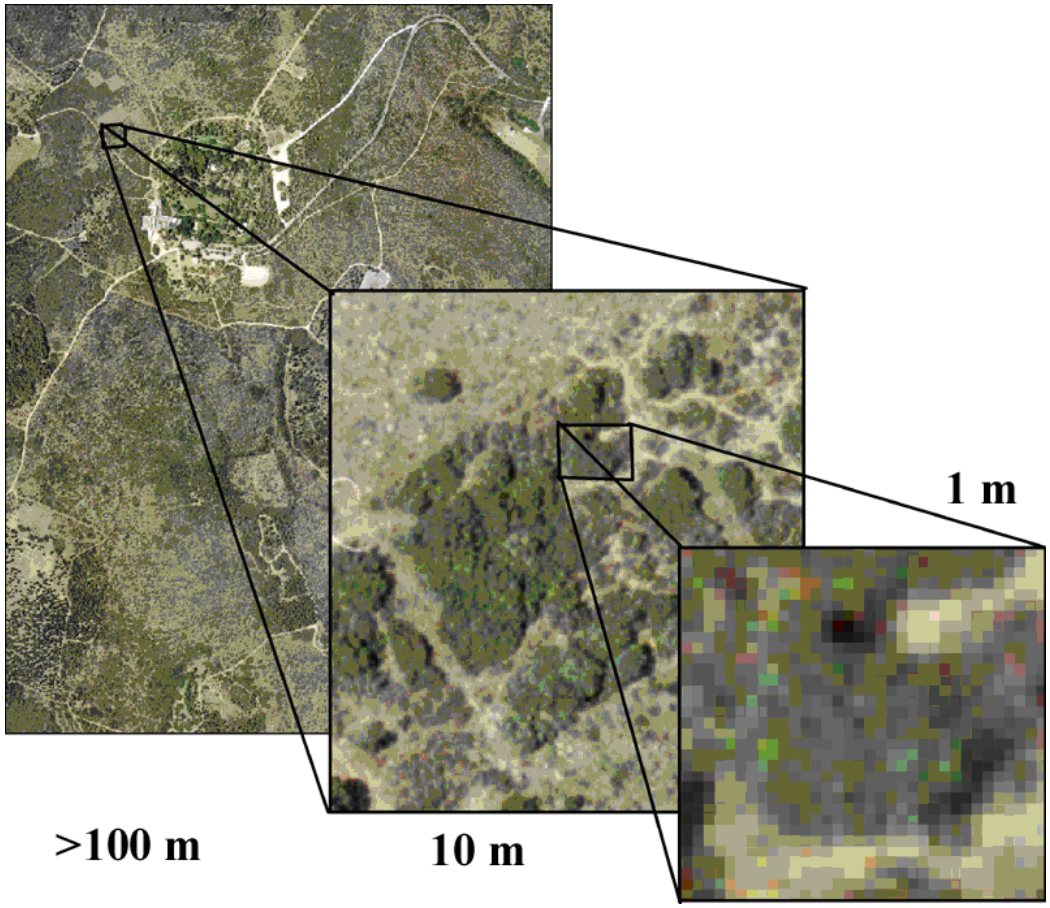


Figure 2. The hierarchical levels of the model. From left to right: landscape, site, and patch.

State variables

Each hierarchical level has its own state variables. At the patch 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 combined percent cover of the woody PFTs except dwarf shrubs. At the landscape level there is one state variable: total percent cover of each PFT. Notice that the PFT variables are essentially arrays of five values, since there are five different PFTs.

Model parameters

The model consists of three types of parameters (Table 1): [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] height parameters (e.g. growth rate, maximum height). Each parameter has a specific value per PFT. Parameters values were derived from field data, the literature, and expert opinions (Table 1).

Transitions between PFTs

The dynamic framework of the model is based on a spatially explicit state and transition process with continuous transition functions between the PFTs (rather than constant transition probabilities as in classic Markov models). Therefore, the identity of the dominant PFT in a specific patch in the landscape in the next year is a function of a transition function between the dominant PFT at present to the dominant PFT at the next year:

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

where *C* is the identity of the dominant PFT in the cell at location (*x,y*) in the landscape at time *t*, and *P* is a transition function between different possible PFTs in each location at time *t*. The transition function *P* is a product of various sub-processes detailed below.

Transition sub processes

There are three major transition processes in the model: colonization from seeds, vegetative expansion, and death. In seed colonization, seeds from neighboring patches (at various distances) can enter a patch and establish in it. These seeds form a colonizer PFT that grows under the dominant PFT. After a time lag (denoted by the parameter *Ageest*), a deterministic takeover occurs, in which the colonizer PFT replaces the dominant PFT and becomes the new dominant PFT in the patch. The second transition process, vegetative expansion, is the replacement of the dominant PFT in a patch by the canopy growth of a PFT from an immediate neighboring patch (one of its eight surrounding neighbors). In the third process, death, the dominant PFT is replaced by herbaceous vegetation. It is assumed that there is a constant seed bank of herbaceous species everywhere in the landscape, therefore the elimination of a woody PFT essentially leads to the regrowth of herbaceous vegetation in the same spot.

Table 1. Model parameters. Abbreviations: HE – herbaceous vegetation, DS - dwarf shrubs, LS - low shrubs, TS - tall shrubs, and TR – low trees. EO is expert opinion.

Parameter	***HE***	***DS***	***LS***	***TS***	***TR***	***Source***
$Ageest_j$		4.00	6.00	8.00	10.00	Koniak and Noy Meir
$Ageregrow_{clear}$	1.00	4.00	6.00	8.00	10.00	Koniak and Noy Meir
$Ageregrow_{fire}$	1.00	4.00	6.00	8.00	10.00	EO (Neeman, G)
$Agerep_j$	1.00	6.00	8.00	12.00	25.00	Herrera et al (1994)
$Agemat_j$		20.00	25.00	60.00	80.00	Koniak and Noy Meir
$Agemax_j$	1.00	30.00	40.00	80.00	100.00	EO (Perevolotsky, A)
$hgtescape_j$	2.00	2.00	1.50	2.00	2.00	EO (Glasser, Z)
$hgrow_j^{\max}$		0.05	0.10	0.15	0.15	Koniak and Noy Meir
$h_j^{\max}$	0.20	0.50	2.00	2.70	4.00	Approx. field measurements
$Hregrow_{fire}$	0.20	0.20	0.40	0.60	0.80	EO (Neeman, G)
$Hregrow_{clear}$	0.20	0.20	0.40	0.60	0.80	Koniak and Noy Meir
$Seedprodmx_j$				0.45	0.45	Herrera (1998)
$Seedprodmx_j^{short}$		0.95	0.95			EO (Henkin, Z)
$Seedprodmx_j^{long}$		0.80	0.40			EO (Henkin, Z)
$Ssurv_j$			0.50			EO (Naveh, Z)
$pmort_j$		0.05	0.05	0.01	0.01	Koniak and Noy Meir
$Pregrow_{clear}$	1.00	0.40	0.40	0.40	0.40	Filed measurements
$Pregrow_{fire}$	1.00	0.20	0.40	0.40	0.40	EO (Neeman, G)
$rhgrz_j$ (goats)		-0.85	-0.90	-0.80	-0.90	EO (Glasser, Z)
$rhgrz_j$ (cattle)		0.00	0.00	-0.30	-0.90	EO (Hadar, L)
$\downarrow Egrz_j$ (goats)		-0.70	-0.90	-0.80	-0.90	Koniak and Noy Meir
$\downarrow Egrz_j$ (cattle)		-0.10	-0.10	-0.30	-0.90	Koniak and Noy Meir

$\downarrow Cgraz_j$ (goats)			-0.90	-0.95	-0.90	-0.90	Koniak and Noy Meir
$\downarrow Cgraz_j$ (cattle)			-0.10	-0.10	-0.50	-0.80	Koniak and Noy Meir
$P^{j \to i}_{expansion\,\max}$							
	HE	0	0.2	0.05	0.05	0.05	Koniak and Noy Meir
	DS	0	0	0.05	0.05	0.05	Koniak and Noy Meir
	LS	0	0	0	0.05	0.05	Koniak and Noy Meir
	TS	0	0	0	0	0.05	Koniak and Noy Meir
	TR	0	0	0	0	0	Koniak and Noy Meir
$P^{j \to i}_{colonization\,\max}$							
	HE	0	0.15	0.15	0.05	0.01	Reisman Berman (2004), Koniak and Noy Meir
	DS	0	0	0.07	0.1	0.02	EO (Noy Meir, I, Henkin, Z)
	LS	0	0	0	0.15	0.15	EO (Noy Meir, I, Henkin, Z)
	TS	0	0	0	0	0.08	Herrera (1998)
	TR	0	0	0	0	0	Herrera (1998)

Colonization

It is assumed that a PFT can only be replaced by a "taller" PFT (a PFT that is of a higher successional level, Figure 1), therefore 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 *j* will occur in a patch dominated by PFT *i* (only possible when $j>i$) is the product of three components: [1] the maximal colonization probability (a parameter); [2] the availability of seeds of PFT j in the patch vicinity; and [3] the grazing intensity in the site:

$$P^{j \to i}_{colonization} = P^{j \to i}_{colonization\,\max} \cdot Seed_{j,t} \cdot (1 + \downarrow Cgraz_j \cdot Grazing_t) \qquad (2)$$

where $P^{j \to i}_{colonization}$ is the actual probability of colonization of PFT *j* into PFT *i*, $P^{j \to i}_{colonization\,\max}$ is a parameter representing maximal probability of expansion (under ideal conditions, e.g. there is no limit on seed availability), $Seed_{j,t}$ is the availability of seeds of type *j* in the area (see below), $\downarrow Cgraz_j$ is a parameter representing the effect of grazing on recruitment of seeds of PFT *j*, and $Grazing_t$ is the grazing intensity at the site at time t (between 0-1, defined by the user).

The determination of the availability of seeds of PFT *j* ($Seed_{j,t}$) is based on the approximate mechanisms of dispersal of the different PFTs used in the model, and on the location of the patch and the site in the landscape. The woody PFTs used in this model can be divided into two groups based on their dispersal mechanisms: [1] Tall shrubs and trees are characterized by fleshy fruits, dispersed by birds. [2] Low shrubs and dwarf shrubs have other means of dispersal, which are not known, but are limited in distance compared to the bird-dispersed PFTs. Therefore, two different mechanisms for seed production were created, accounting for the different mechanisms described above.

Tall shrubs and trees seed production and availability

The rational 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 hectare on average (Izhaki et al. 1991). They spend the majority of their time in the more densely vegetated areas within their territory, in order to avoid predation (plant types that supply this sort of protection include low shrubs, tall shrubs, and low trees). Therefore, the vast majority of seeds are dispersed and deposited in the denser areas of the territory, which are also the areas where more fruit are available (Debussche and Isenmann 1994, Herrera et al. 1994, Herrera 1995, 1998, Rey and Alcantara 2000). Open patches will therefore receive smaller amounts of seeds. Thus, determination of seed availability to a specific site needs to account for its relative shrub cover when compared to its neighborhood that represents the territory of seed-dispersing birds. Here, the size of this neighborhood is assumed to be a rectangular block of 10 × 10 sites (corresponding to 100 × 100 m^2, or 1 hectare, similar to the approximate 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:

$$Seedprod_{j,t} = Seedprodmx_j \cdot \frac{N^*_{j,t}}{N} \tag{3}$$

where $Seedprod_{j,t}$ represents the amount of seeds of PFT *j* that will be produced in time *t* at the site, $Seedprodmx_j$ represents the maximal amount of seeds that are produced by a patch dominated by PFT *j*, $N^*_{j,t}$ is the number of patches dominated by PFT *j* with plants older than their reproductive age (the parameter $Agerep_j$), and *N* is the total amount of patches in the site (100). *j* can be only tall shrubs or shrub-trees, for mechanism [1] above.

The combined cover of low shrubs, tall shrubs, and tree-shrubs is calculated, representing the "hiding cover", or the percent of area available for safe bird movements in the site:

$$HCover_{site} = \frac{N_{low} + N_{tall} + N_{tree}}{N} \tag{4}$$

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

For a specific site, the average $Seedprod_{j,t}$ in the 100 neighboring sites $\overline{Seedprod_{j,block}}$ was calculated for each block (10 × 10 site neighborhood). This was done also for the "hiding cover", yielding $\overline{HCover_{block}}$. Then, the actual seed availability $Seed_{j,t}$ for all patches in the site is:

$$Seed_{j,t} = Seed_{j,t-1} \cdot Ssurv_j + \overline{Seedprod_{j,block}} \cdot \frac{HCover_{site}}{\overline{HCover_{block}}} \tag{5}$$

where $Ssurv_j$ 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 equation 2.

Low shrubs and dwarf shrubs seed production and availability

The majority of seed dispersal events observed for these two PFTs occur at the very short range, but there is a small quantity of longer-distance events (Henkin et al. 1999, Henkin et al. 2007b). Seed production was divided into two stages, or distances. Short range dispersal enables seeds to arrive to the neighboring patch, representing the fall of fruits from the mother plant by gravity. Long range dispersal accounts for unknown dispersal mechanisms operating at the 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 equation 3:

$$Seedprod_{j,t}^{short} = Seedprodmx_{j}^{short} \cdot \frac{N_{j,t}^{*}}{8} \tag{6}$$

where $Seedprod_{j,t}^{short}$ represents the probability of seed arrival from the short range, $Seedprodmx_{j}^{short}$ is a parameter that expresses the maximal seed production, (when all 8 neighboring patches are in state *j* and reproductive).

The probability of long range seed arrival depends on the production of seeds in a nine site rectangular neighborhood:

$$Seed_{j}^{long} = \frac{1}{9}\sum_{site=1}^{9} Seedprodmx_{j}^{long} \cdot \frac{N_{j,site}^{*}}{N} \tag{7}$$

where $Seed_{j}^{long}$ is the probability of arrival of seeds from the long range (represented by a 9 site neighborhood). For the sake of simplicity, equation 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 equations 6 and 7, plus the component of seed survival from the previous year (as in equation 3):

$$Seed_{j,t} = Seed_{j,t-1} * Ssurv_j + Seed_j^{short} + Seed_j^{long} \quad (8)$$

Expansion

The probability of the dominant PFT in a patch changing from PFT *i* to a "higher" PFT *j* as a result of expansion of adult plants is a function of the number of patches in state *j* located in its immediate neighborhood, i.e. the 8 neighboring patches, the ages of the PFT in the neighboring patches, and the grazing intensity.

$$P_{expansion}^{j \to i} = P_{expansion\max}^{j \to i} \cdot \frac{N_{j,8}}{8} \cdot \left(\frac{Agemat_j - \overline{Age}_{j,t}}{Agemat_j - Ageest_j} \right) \cdot \left(1 + \downarrow Egrz_j \cdot Grazing_t \right) \quad (9)$$

where $P_{expansion}^{j \to i}$ is the probability that a patch dominated by PFT *i* will be invaded by PFT *j*, $P_{expansion\max}^{j \to i}$ is parameter that represents the maximal probability of expansion (when all neighbors are of type *j*), $N_{j,8}$ is the number of patches in state *j* in the rectangular 8 patches neighborhood, $Agemat_j$ (parameter) is the maturity age of PFT *j*, $Ageest_j$ (parameter) is the establishment age of PFT *j*, $\overline{Age}_{j,t}$ is the average age of PFTs in the neighboring patches at time *t*, and $\downarrow Egrz_j$ is a parameter that represents the negative effect of grazing on the rate of expansion.

Natural death

Once the age of the dominant PFT *j* in a patch exceeds a threshold age, denoted by the parameter $Agemax_j$, the parameter $pmort_j$ denotes its probability of dying and being replaced by the lowest PFT, herbaceous vegetation. If there is a colonizer PFT underneath the dominant PFT, is remains alive, and will become the new dominant the next year.

Height growth

The dominant PFT in a patch increases its height each year, with the rate of growth slowing as the plant becomes taller. Additionally, grazing can reduce the rate of height growth of certain PFTs depending on the grazing intensity. The height growth of PFT *j* is denoted by:

$$h_{j,t+1} = h_{j,t} + hgrow_j^{\max} \cdot \left(1 - \frac{h_{j,t}}{h_j^{\max}}\right) \cdot \left(1 + rhgrz_j \cdot G_t\right) \tag{10}$$

where $h_{j,t}$ is plant height at time *t*, $hgrow_j^{\max}$ is the maximal possible growth rate (a parameter), $h_j^{\max}$ is the maximal plant height for PFT *j*, and $rhgrz_j$ (a parameter) is a height reduction factor accounting for the effect of grazing (the relative reduction of height growth per unit of grazing intensity). Grazing effect on height is zero when grazers can not reach the top of the plant, i.e. when $h_{j,t} > hgtescape_j$, where *hgtescape* is a parameter.

Grazing

The model accounts for two types of grazing, by goats or by cattle. Grazing intensity is represented by a value between 0 – 1 (0 - no grazing, 1 - intense grazing). The user defines prior to the model simulation the following parameters: location (which sites), period (which years), grazing agent (goat, cattle, or both) and intensity (0-1), according to the desired management schedule. Grazing affects model behavior via modification of the probabilities of colonization and expansion (equations 3 and 9, respectively), and through its impact on the height of the dominant PFT in a patch (equation 10).

Fire and clearing

Fire and clearing are user-controlled events that operate similarly in this model. The occurrence and location of fire and clearing events is defined by the user as discrete events, since they are treated as management activities (there are no random fires in the model). Each PFT has a probability of regenerating following these disturbances (the parameters $Pregrow_{fire}$ and $Pregrow_{clear}$). If a PFT in a patch fails to survive following fire or clearing, it is replaced by herbaceous vegetation. If it survives, its height becomes lower (denoted by the parameter $Hregrow_{fire}$ and $Hregrow_{clear}$), representing the regeneration of branches from the top of the root system. Additionally, it is considered that the physiological age of the regrowth (in terms of time till reproductive stage, expansion, mortality, etc.) is greater than that of a seedling, but less than that of the pre-fire mature plant (denoted by the parameters $Ageregrow_{fire}$ and $Ageregrow_{clear}$). In a year when fire or clearing occurs, no other transitions are allowed to take place.

Starting and ending conditions

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

The standard outputs of the models are: maps of dominant PFTs, their ages, and their heights; 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.

Sensitivity analysis

The effect of model parameters on model output was assessed via a global sensitivity analysis using a Monte Carlo approach. In this approach, appropriate for models with a large number of parameters, sensitivity analysis is performed on groups of parameters, rather than on one parameter at a 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 value. All other parameters are kept unchanged. The model was run a large number of times, once per each group. The output of a simulation with no changes in any parameter values served as a reference. The sensitivity score of each run (or each set of parameters) was the absolute difference between its output and the reference output. For each parameter, we computed the average and standard deviation of the sensitivity scores of the simulations where it was altered. The average represents the overall effect of a specific parameter, and the standard deviation represents its interactions with other parameters. Parameters with high scores of average and standard deviation are those that the model is highly sensitive to.

In each run of the model, we used only the output of year 50 for calculating sensitivity scores, and ignored other outputs of previous years (in order to avoid dependence between outputs). Model output was defined as the total number of patches of each PFT at year 50 (i.e. there are five analysis results). Due to the heavy computational price of model runs on large landscapes, sensitivity analysis was conducted at a small, random landscape, consisting of 100×100 patches (corresponding with 10×10 sites, or 1 ha). Initial conditions represent an open landscape, with percent cover of 73% herbaceous vegetation, 12% dwarf shrubs, 7% low shrubs, 5% tall shrubs, and 3% low trees.

Model validation

Validation of spatio-temporal models is a complicated task, since the necessary ground truth data is seldom available. Here, validation requires 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 is 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 is possible, however, to differentiate herbaceous vegetation from woody vegetation at high accuracy. Therefore, it is possible to evaluate the model using the dynamics of woody vegetation.

Since the initial conditions are 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. In addition, one aspect of landscape structure, edge density of the herbaceous patches, was also calculated.

The validation was conducted using a 500×350 m^2 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 validation area was burned in a wildfire in 1980, and subjected to medium intensity cattle grazing since 1989. The starting conditions were randomly generated 30 times.

Example simulations

The effects of various management activities on the long term (50 years) structure and composition of vegetation were simulated on two landscapes: [1] a random landscape with initial herbaceous dominance, and scarce woody cover. A random landscape portrays more clearly the effects of disturbances, since the effect of initial landscape configuration is normalized. The random landscape simulations were conducted with

30 repetitions to minimize the effects of stochasticity; [2] an actual landscape, which is Ramat Hanadiv Nature Park in Northern Israel (Figure 3). In [1], the landscape area is 233 ha, and initial PFTs cover percentages are 70.5, 15, 8.5, 4, and 2 for herbaceous vegetation, dwarf shrubs, low shrubs, tall shrubs, and low trees, respectively. The PFTs are randomly distributed across the landscape according to the initial percentage cover. During the simulations, the entire landscape was undisturbed, or subjected to various combinations of grazing at different intensities and fire (Table 2). In [2], the initial conditions (dominant PFTs and PFTs height) were mapped from remotely sensed data that included a fusion of aerial photography and LiDAR. Detailed description on the preparation of the vegetation map is provided in the next section. The size of the modeled area is 233 ha, and its topography is relatively flat. The area was divided into 10 management units (based on actual units), each subjected to different management scenarios. The overall objective of the management treatments is to preserve the mosaic structure of the landscape.

Since there is no concise way to quantify the structure of the mosaic (i.e. the degree of 'mosaicness'), I used a combination of Simpson index of diversity (SIDI) and the edge density (ED) index to account for thematic diversity and spatial diversity, respectively. The Simpson index of diversity portrays the probability that two randomly selected cells will not belong to the same PFT:

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

where *SIDI* is 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 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, divided by total landscape area. For simple landscape configurations, and when the total number of patches is small, the amount of edge is small. As the landscape becomes more convolved, and the amount of small patches 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 2). Initial conditions where 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.

Table 2. Management scenarios.

Landscape type	*Scenario name*	*Description*
Random	None	Entire landscape undisturbed
	G	Intensive goat grazing, entire landscape
	C	Intensive cattle grazing, entire landscape
	GC	Intensive goat and cattle grazing, entire landscape
	GC_{med}	Intermediate goat and cattle grazing, entire landscape
	F	Fire at year 25, no grazing
	GF	Fire at year 25, intensive goat grazing
	CF	Fire at year 25, intensive cattle grazing
	GCF	Fire at year 25, intensive goat and cattle grazing
	$GC_{med}F$	Fire at year 25, intermediate goat and cattle grazing
Actual	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_{med}	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
	$GC_{med}F$	Same as GC_{med}, with fire in year 1

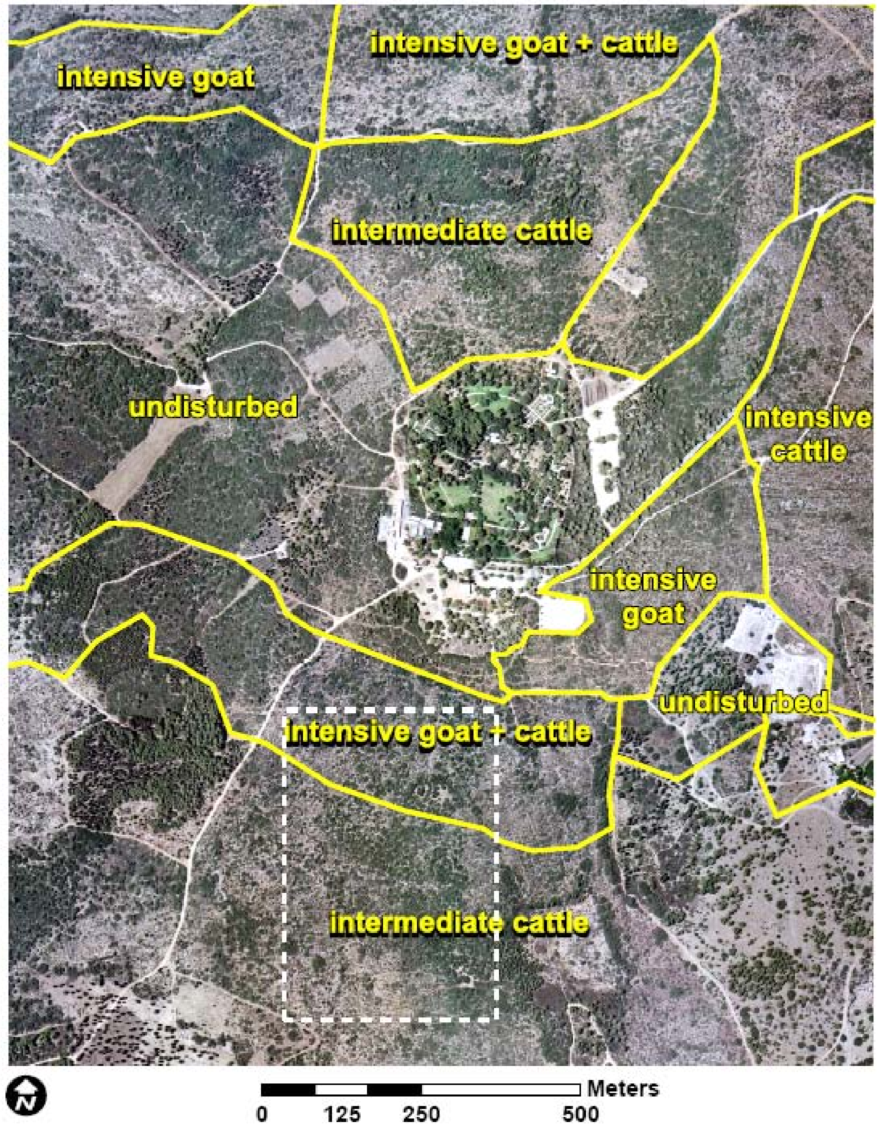


Figure 3. An aerial image of the study area, which is a subset of the Ramat Hanadiv Nature Park (Northern Israel). The existing management units are marked by yellow lines. The validation area is marked by a dashed white rectangle.

Results

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 (Figure 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 of these parameters are related to the processes of colonization and expansion in the model, thus their impact on model output are outcomes of their role in the two major transition processes that move the chains of vegetation change in the model.

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 (Figure 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 destructed by the wildfire of 1981 was lower than what the model predicted, but the general trend is similar. For 2004 and 2007, the values of model derived edge density were similar to those observed from the aerial photography, while there was a difference between the corresponding values in 1984 and 1997 (Figure 5), although that the general trend of the graph was consistent.

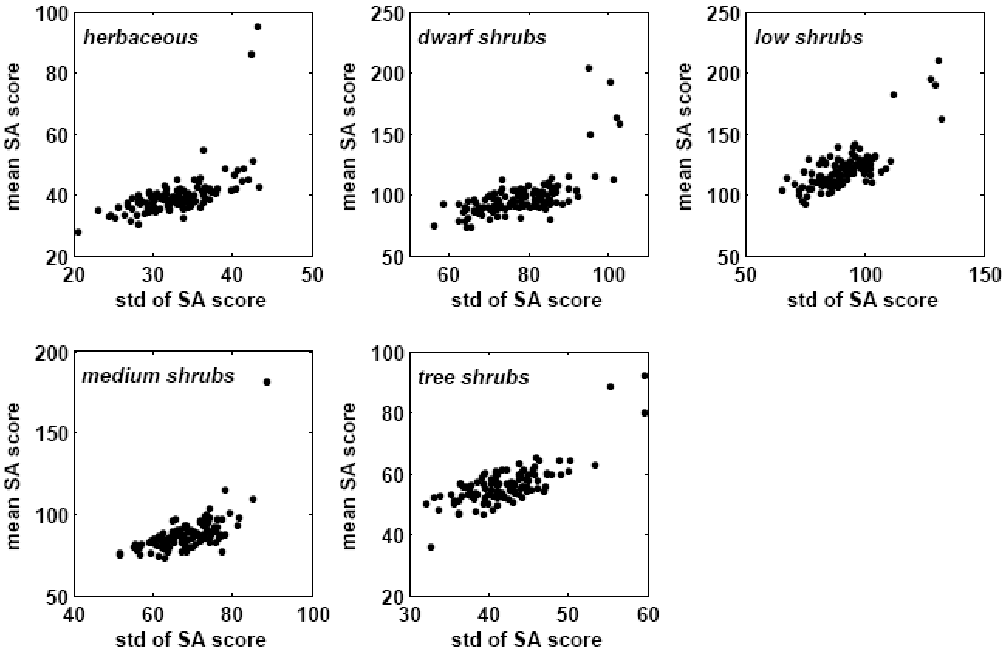
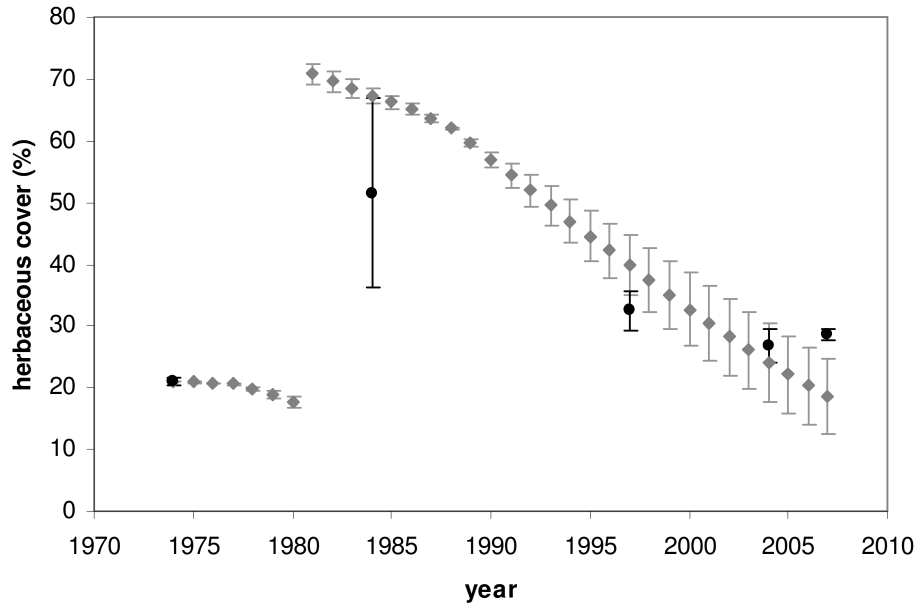


Figure 4. Results of the sensitivity analysis. Plots show the average and standard deviation of the sensitivity scores for each parameter (black dot). Each plot corresponds with a single output variable, which is percent cover of a certain PFT at year 50. Points with large mean values are those which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

Model simulations – general trends on a random landscape

In general, model results that were based on the random landscape portrayed dynamics that are qualitatively similar to actual dynamics of Mediterranean vegetation that were reported before (Carmel and Kadmon 1999). Left undisturbed, the vegetation goes a classic succession process, with taller PFTs replacing lower PFTs over time. When starting conditions consist of a mainly open landscape, dominated by herbaceous vegetation, dominance of the taller woody PFTs becomes apparent only after more than 50 years (Figure 6). Grazing disturbances slow down the process, depending on their intensity and the type of grazing. Goat grazing has a stronger effect on vegetation change, since it almost halts completely the growth and transitions from the lower PFTs to the taller PFTs. This is in accord with empirical



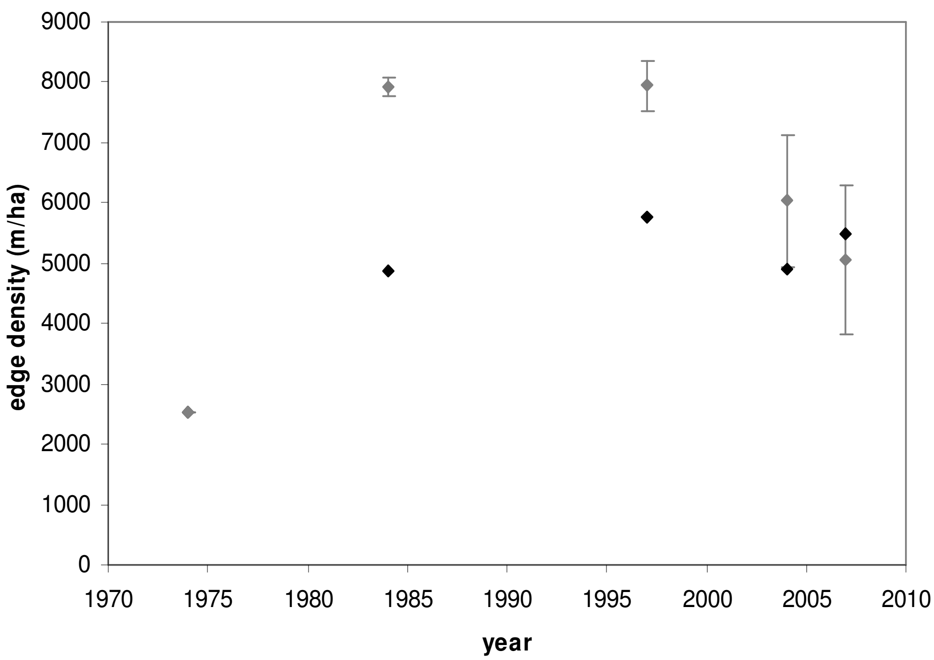


Figure 5. Results of model validation. A comparison of 33 years of changes in herbaceous cover (gray dots, top), and edge density (bottom) as predicted by 30 model runs with varying configurations of woody PFTs, with five values of cover and edge density measured from classified aerial photographs (black dots). The error bars of the aerial photography points represent the classification error of the photo interpretation process (only at the top figure). The leap in herbaceous cover in 1981 is a result of a wildfire which burned the entire validation area.

results of a study of 28 years in the Mediterranean region of Israel (Carmel and Kadmon 1999). After an unstable period of transition, goat grazing yields a landscape dominated by dwarf shrubs and herbaceous vegetation. This form of landscape is indeed common in the eastern Mediterranean, where intensive goat grazing form a dwarf shrub dominated landscape. Cattle grazing has a more subtle effect on the woody PFTs, since cattle tends to prefer the herbaceous vegetation. Nevertheless, cattle may browse the leaves of the tallest PFT, slowing its encroachment into the lower PFT. Additionally, cattle may impact the woody PFTs by trampling. However, this impact has a limited effect on the succession as depicted by model simulations.

Fire and clearing have a stronger effect on the woody PFTs (Figure 6e-f). Following a fire or clearing event, the majority of woody vegetation dies, and is replaced by herbaceous vegetation. However, a portion of the original woody vegetation survives the disturbance by re-growing back in the following year, since many of the woody PFTs used in this model can regenerate from the root system after fire of clearing events.

Scenario simulations on the actual landscape and the mosaic pattern

Four of the five scenarios that included fire resulted in a decrease of Simpson's index, 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 minimal decrease (Figure 7a). Fire without further disturbance resulted in an increase of Simpson's index and edge density. In contrast, five of the six scenarios that excluded fire showed an increase in Simpson's index (Figure 7b), with intensive goat with cattle combination resulting in a decrease of Simpson's index (Figure 7a). 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 in lower edge density values compared to the other scenarios, especially in the case of grazing that followed fire in year 1. This may be because the vegetation is unable to regenerate following the fire, since it is browsed by the goats (and to a lesser extent by cattle). Therefore, succession does not proceed as long as the grazing continues. The spatial configuration of the vegetation at the beginning of the simulation and after 50 years of management (three scenarios) is shown in figure 8.

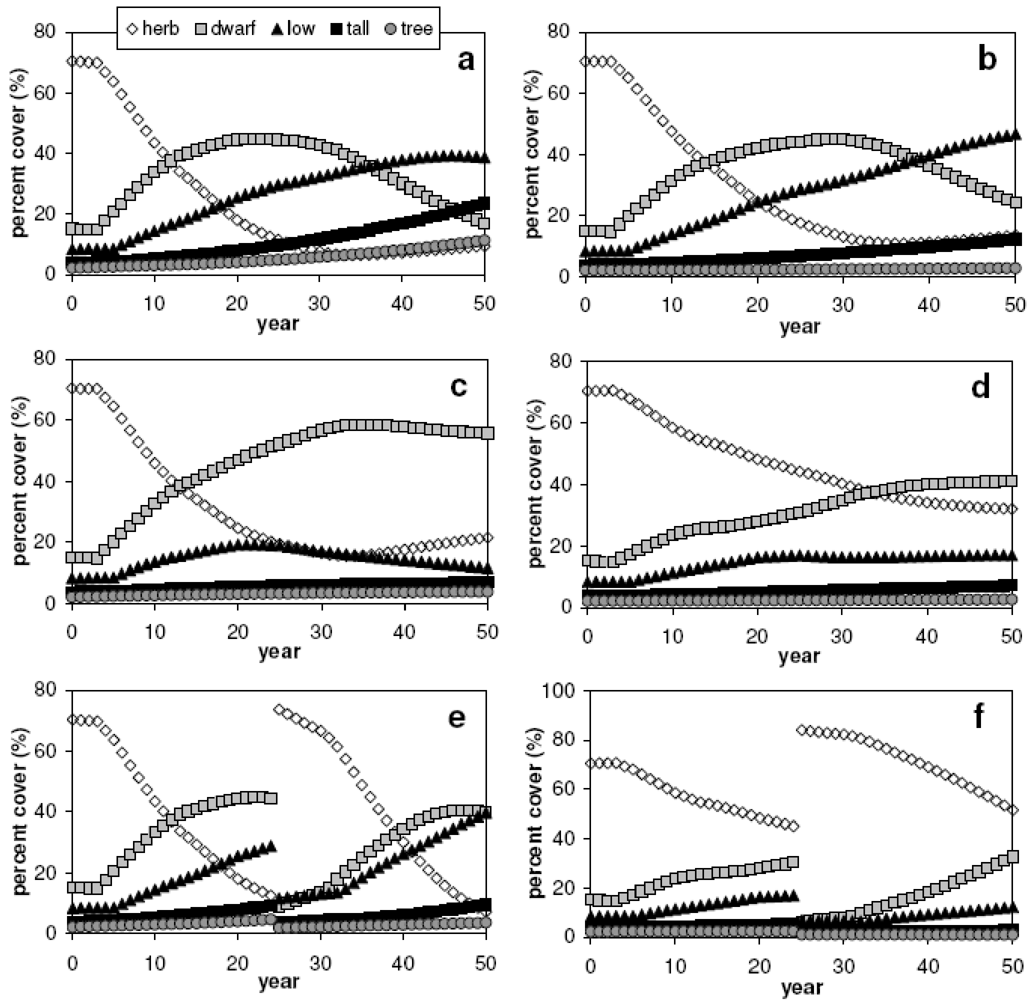


Figure 6. Temporal dynamics of the different PFTs, starting from an open (herbaceous dominated) landscape, with a random spatial configuration of PFTs, and different disturbances: control (a), cattle grazing (b), goat grazing (c), goat with cattle grazing (d), fire in year 25 (e), and goat with cattle grazing coupled with fire at year 25 (f). All grazing pressures are maximal

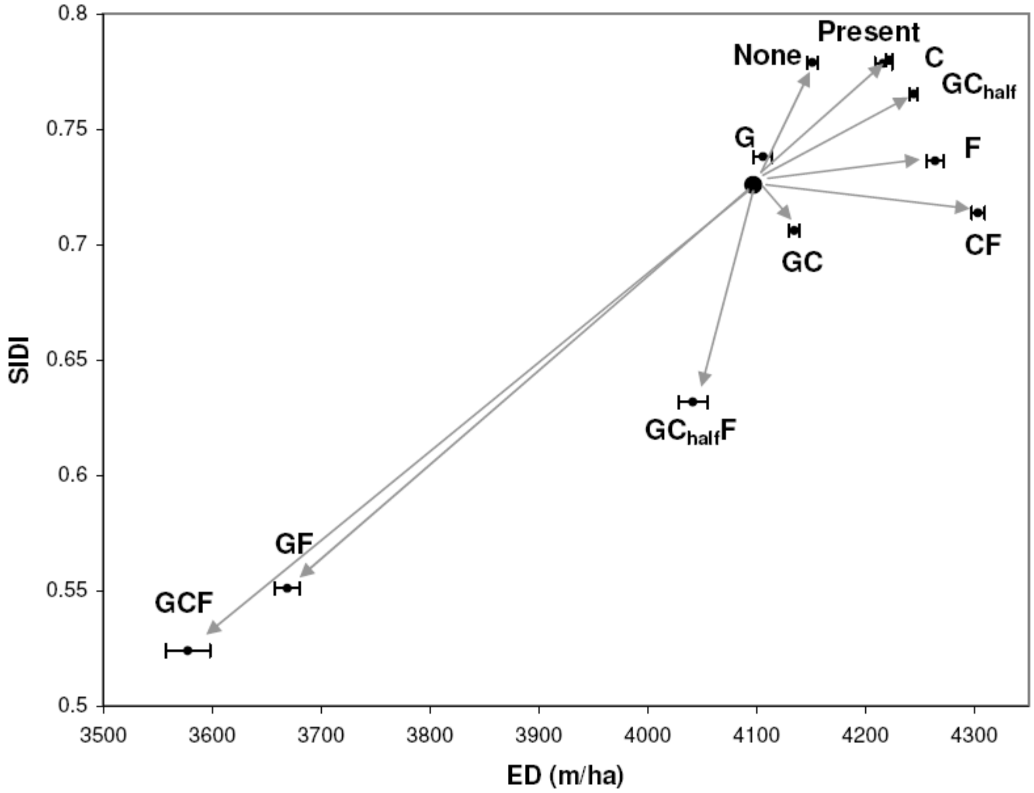


Figure 7. The effect of management scenarios on Simpson's index of diversity (SIDI) and on edge density (ED). Values shown are averages of five simulations per scenario, with error bars representing standard deviations (the SIDI standard deviations were negligible; therefore the y-axis error bars are not shown). 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 $_{half}$ that follows G, C, or both represents intermediate grazing intensity.

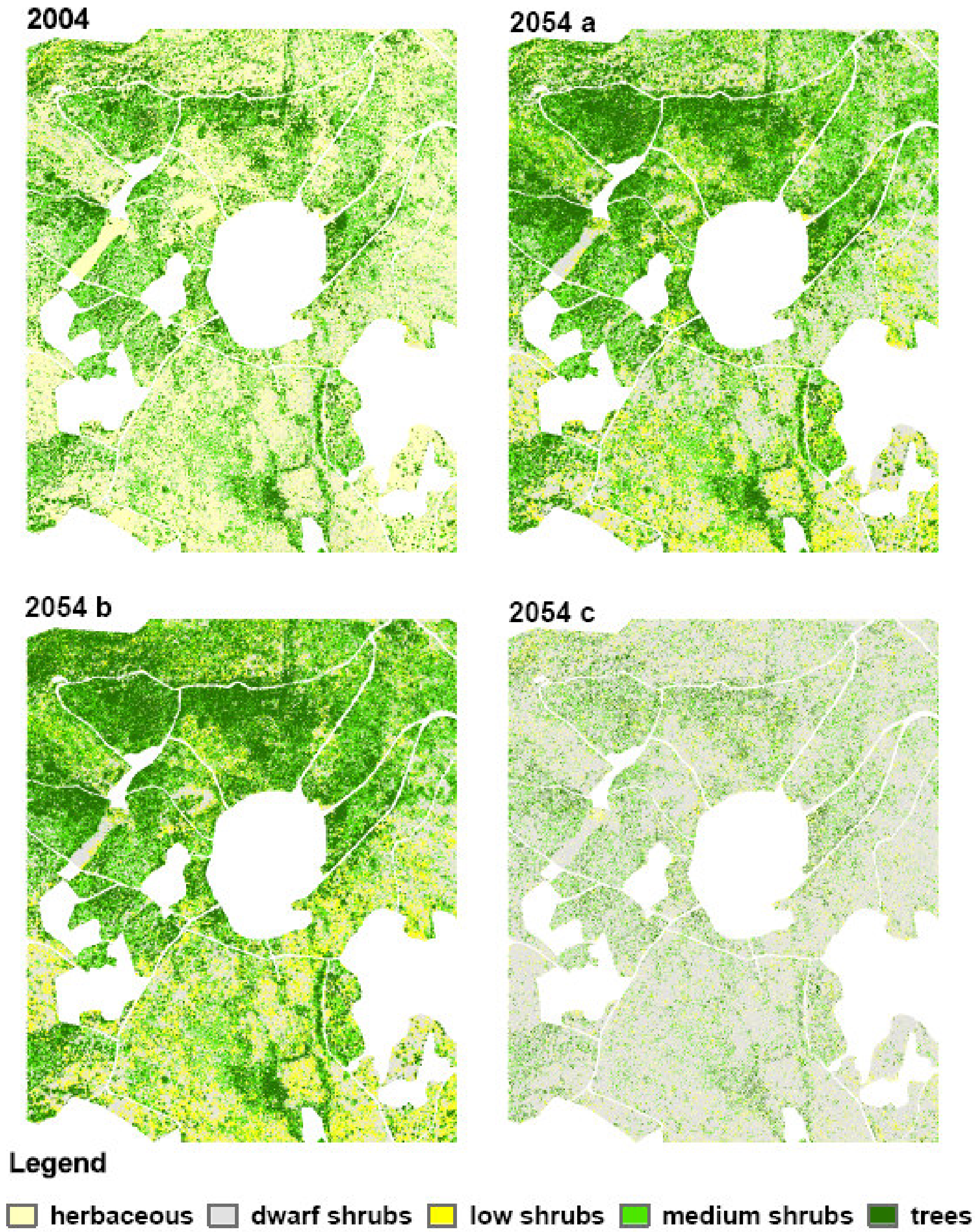


Figure 8. Actual and projected vegetation maps: The starting condition map (based on data fusion of LiDAR and aerial photography) is top left; Vegetation after 50 years, assuming continuation of the present management scenario (top right); Vegetation after 50 years, undisturbed (bottom left); Vegetation after 50 years, fire in 2005 and intensive goat and cattle grazing ever after (bottom right).

Discussion

Model objective and structure

Mediterranean landscapes are characterized by spatial heterogeneity of vegetation types at extremely fine scales, presumably resulting from thousands of years of human disturbance (Naveh and Dan 1973, Naveh and Kutiel 1986). It is desirable to conserve this heterogeneity, since the open patches are home to rich herbaceous communities, consisting of many hundreds of species. This conservation should be based on carefully planned management programs that use the disturbance agents that have maintained its diversity over the years (Perevolotsky and Seligman 1998, Perevolotsky 2006). In principal, dynamic ecological models can be used for this purpose. Existing model types, however, have several limitations regarding their applicability to Mediterranean systems. State-and-transition models (e.g. Markov) are non spatial and use constant transition probabilities, thus are too simple in comparison to the complexity of these landscapes, as are cellular automata models. Gap models were developed for more homogeneous forests with a clear vertical stratification, which does 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 (in review). The dynamic process behind the model is based on state-and-transition models (Westoby et al. 1989), where transitions between PFT are depicted as stochastic processes, with probabilities governing the transitions between them. Most of these models are non-spatial, and use constant transition probabilities. Here, a different approach was taken, that is based on 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. The spatial explicitness of the model (neighborhood rules) was derived from cellular automata models (Hogeweg 1988). Colonization and growth of two PFT in the same patch, but in different layers, originated from gap models (Urban et al. 1991, Bugmann 2001).

The model relies on several assumptions. The major assumption is that succession proceeds always from low species towards tall species (i.e. a PFT can only be replaced by a taller PFT unless it dies). Although that in nature, there are cases where lower PFTs continue to grow beneath taller PFTs, replacing them if they die. In the majority of cases, however, the forward transition holds true. A second assumption is the transitions are abrupt; meaning that once a colonizer takes over a dominant, the old dominant disappears. In reality, there are cases where the two PFTs share the patch for a long period of time, without a clear distinction between a true dominant and a true colonizer. This is a valid assumption in vegetation modeling, since often it is impossible to describe spatially explicit succession in a continuous manner without introducing further noise into the model. A third major assumption is the occurrence of seed dispersal and colonization events in the intermediate hierarchical level, without explicit consideration of the actual dispersal kernel. This is because in Mediterranean PFTs modeled here, the actual dispersal mechanisms are not known explicitly. While the dispersal kernel of tall shrubs and trees were studied in the past, and are generally understood (Izhaki et al 1991), there is almost no knowledge about the long distance dispersal mechanisms of low shrubs and dwarf shrubs (although that the clonally growth of dwarf shrubs is well studied, Reisman-Berman 2004).

While the above assumption might distance the model from reality, making it complex beyond valuable interpretation, its qualitative and quantitative validation steps show that it portrays patterns that 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 the decrease in cover of herbaceous species in the absence of disturbance, and the 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 the lack of sufficient data, showed that the model predicts vegetation dynamics similar to actual dynamics observed by means of remote sensing. Therefore, the model may be used in order to predict the general trends of vegetation changes as a result of management actions.

The model ignores three components that have a major role in the dynamics of Mediterranean vegetation, namely climate, topography, and soils (Zohary 1973). In order to incorporate their effects in the model, additional parameters are needed (the impacts of these variables on the maximal transition probabilities). These are difficult to obtain due to the scarce amount of data available.

The model operates at a very high spatial resolution due to the high spatial heterogeneity of the landscape. This imposes several difficulties on model application. A pre-requisite for running the model on actual landscapes is the availability of vegetation data of a sufficient spatial resolution. Since the model consists of five PFTs, input data should consist of vegetation maps that include all of these types. At present, vegetation maps that combine this thematic and spatial detail are scarce (due to technical and methodological limitations); therefore new means for generating them need to be developed. For the purpose of this study, a newly developed vegetation map that was generated by fusion of LiDAR and aerial photography was used (Bar Massada et. al, in review, and the next section of this thesis). This map covers a small geographical extent, thus the application of the model as an actual management-aid tool for large areas is constrained by the lack of sufficient input data. Such data may be available in the future, enabling the application of the model over larger areas.

The impact of disturbances

The disturbances that were applied to the virtual landscape had varying effects on its heterogeneity. Without disturbance, the landscape will eventually be dominated by the taller PFTs, as it usually happens in reality. Grazing (either by goats or by cattle) slows down the successional process, since browsing by goats prevents the lateral growth of woody vegetation by consuming the leaves on the peripheral branches, increasing edge density. In small shrubs, height growth is also prevented since the top branches are accessible to the browsing animal. Cattle has a less pronounced impact, since the dietary preferences of cows consists of mainly herbaceous vegetation, and to a lesser extent low trees (Seligman and Perevolotsky 1994). In contrast to the effect of grazing, which seldom reduces the cover of existing woody vegetation, fire and clearing transform the vegetation into a lower successional level, by decreasing woody cover and enabling the re-expansion of herbaceous vegetation over the newly opened patches. The majority of woody species in the Mediterranean have regeneration capabilities to cope with the impact of fire and clearing. These are based on rapid re-sprouting from the root system, or developing a long-lasting seed bank. Therefore, even after intense fire or clearing events, a certain proportion of the original vegetation reappears in the landscape in the following growing season, and the overall rate of regeneration to the pre-disturbance state of vegetation is rapid. The model accounts for these traits by allowing regeneration of the woody PFTs following disturbances. The rate of 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).

The vegetation mosaic and landscape heterogeneity

The main motivation for the development of this model was to aid the attempts to conserve the Mediterranean vegetation mosaic by conserving landscape heterogeneity, which is a surrogate to biodiversity. A measure of landscape heterogeneity was required for assessing the results of the model. Many studies, especially in the field of landscape ecology, dealt with the quantification of landscape pattern through the usage of landscape metrics (Turner and Gardner 1991, Gustafson 1998). No single landscape metric can be used as a measure of landscape 'mosaicness', since the mosaic consists of a mixture of different patch types, with varying sizes and spatial configurations in the entire spectrum of spatial scales. Therefore, 'mosaicness' consists of at least three elements: diversity of patch types (thematic diversity), diversity of patch sizes (scale), and diversity of spatial complexity (fragmentation). It was attempted to simplify this problem by using a combination of two measures of landscape heterogeneity. Simpson's index of diversity was used in order to portray the relative abundance of each patch type (thematic diversity), and edge density was used as a surrogate of the spatial complexity of the landscape. While there are many other indices that can yield similar results, the focus was on these two due to their straightforward meaning. A combination of these metrics formed a parametric space in which it was easier to visualize the impact of the various disturbance scenarios, accounting for patch type diversity and its shape complexity. Further research may find better means for quantifying landscape mosaic.

Mapping the structure of Mediterranean vegetation using data fusion of LiDAR and aerial photography[2]

Motivation

Landscape scale models require not only a mathematical or functional basis, but also an extensive spatial basis (especially in the case of spatially explicit models). The spatial basis requires accurate representation (vegetation mapping) of the landscape to be modeled. The basic mapping unit (pixel size in raster maps, scale in vector maps) needs to be equivalent to the basic spatial unit of the model. In this study, the basic mapping unit is the patch.

Background

Since its earliest days, vegetation mapping is divided between two major schools, floral mapping, where taxonomic composition is a major criterion, and structural mapping, which largely ignores species composition (Richards et al. 1943, Wagner 1957, Mucina 1997). Common to both schools, however, is the subjective and arbitrary decisions made in the grouping of vegetation into several types.

Structural vegetation mapping is often used in ecological models, particularly at coarse scales (landscape-, regional-, and global scales). Vegetation maps at these scales are conveniently constructed using computerized classification of remotely sensed images (de Jong and Burrough 1995, Carmel and Kadmon 1998, Kadmon and Harari-Kremer 1999, Shoshany 2000, Alados et al. 2004), where the vegetation is classified into several groups according to a pre-defined, discrete classification scheme. In these schemes, the classes are typically determined using the nature of the dominant species (Verheyden et al. 2002) or the dominant vegetation formation (Alados et al. 2004). Numerous classification schemes have been proposed, including regional systems such as Mediterranean vegetation schemes (Naveh and Whittaker 1979, Tomaselli 1981a), or European vegetation classification (Davies et al. 2004), habitat-specific schemes (Aaviksoo 1995), and several global classification systems

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[2]Based on: Bar Massada, A., Kent, R., Blank, L., Perevolotsky, A., Hadar, L., and Carmel, Y. Mapping Mediterranean vegetation using continuous structural characteristics. Submitted to *Remote Sensing of Environment*.

(Matthews 1983, Running et al. 1995). A single continuous classification scheme was proposed for global climate models by (Brovkin et al. 1997), in which the vegetation was characterized by the proportion cover of trees in each cell.

Continuous versus thematic vegetation maps

Land cover and vegetation maps are generally thematic. This is because humans have difficulties interpreting continuous spatial data, due to our perception of the natural world. In the case of structural vegetation maps, for example, the actual structure is continuous, while our human perception often favors some sort of grouping into thematic classes that makes it easier to visualize and interpret. However, continuous vegetation maps may have some advantages over thematic maps. Vegetation maps are often used for the analysis of species distribution and abundance (Seto et al. 2004). Each species perceives the landscape differently (von Uexkull 1957, Manning et al. 2004). Our subjective classification of the vegetation is likely to be an inferior predictor of other species' habitat, compared to raw, unclassified, continuous representation of the vegetation. This is particularly important where management actions for conservation are proposed based on the human perception of the landscape, while the species of interest may view the landscape in a completely different way (McIntyre and Hobbs 1999). Moreover, a thematic map is a single, non-flexible final product, while continuous vegetation mapping has the potential to be realized into numerous thematic maps, depending on the specific requirements of a specific application, as shown below.

Classifying the vegetation of Mediterranean regions

In the past decades, several qualitative approaches (and terminologies) for the classification of Mediterranean vegetation units have been in use, depending on the specific sub-region in which they were originated (Naveh and Whittaker 1979, Dufour Dror 2002). Naveh and Wittaker (1979) proposed a general classification of all Mediterranean vegetation units using height only, which includes four classes: [1] 0 - 0.5 m; [2] 0.5 - 1.5 m; [3] 1.5 - 5 m; and [4] 5 - 10 m (Table 3). Tomaselli (1981) developed a widely used physiognomic classification of Mediterranean shrubland vegetation (or matorral) that is based on three components: [1] height (Table 3), which consists of high (> 2 m), medium (0.6 – 2 m), and low (<0.6 m) matorral; [2] cover (Table 4), which consists of dense (cover>75%), discontinuous (50 – 75% cover), and scattered (<50% cover) matorral; and [3] the morphology of the predominant species – trees, low and dense vegetation, and matorral consisting of thorny xerophytes.

Numerous other classification schemes of Mediterranean vegetation exist, reflecting the large variability of vegetation structures and the identity of the dominant species that varies between sub-regions (Davies et al. 2004). The abundance of classes and sub classes, each fitted to a specific sub-region, essentially causes confusion when one attempts to compare different vegetation units in different areas in Mediterranean regions (Dufour Dror 2002).

Table 3. Height categories.

Height category	*Tomaselli (1981)*	*Naveh and Whittaker (1979)*
Herbaceous / dwarf shrubs	<0.6	<0.5
Tall shrubs	0.6 - 2	0.5 - 1.5
Tall shrubs	>2	1.5 - 5
Trees		5 - 10

Table 4. Cover categories*.

Cover category	*Tomaselli (1981)*
Scattered (sparse)	<50%
Discontinuous	50-75%
Dense	>75%

* Values represent the percent of woody sub pixels within a $2 \times 2\ m^2$ square pixel.

Mapping the vegetation of Mediterranean regions

Land cover maps that use the above mentioned terminologies vary in the level of thematic and spatial detail. General land cover maps, such as the European CORINE land cover methodology (Bossard et al. 2000), consist of broad classes (e.g. all classes discussed above are termed 'Sclerophyllous vegetation') and a large spatial grain (minimal mapping unit is 25 ha). Even more detailed cover maps, such as the Spanish SINAMBA (Seonane et al. 2004) seldom portray spatial detail finer than 30 m (which is the spatial resolution of Landsat satellite platform, often used as the main data source for such regional maps). In Mediterranean regions, the vegetation is heterogeneous at much finer scales (Zohary 1973, Bar Massada et al. 2008), and large grain size is often inadequate. While large grain (pixel size) is a necessary compromise for land cover maps of large areas, practical management activities often require more detailed maps, both spatially and thematically, in order to devise optimal management decisions (Perevolotsky 2006). Additionally, attempts to relate species richness and abundance to the structure of vegetation might also require more detailed data.

The major challenge of Mediterranean vegetation mapping is therefore to produce a map that would be geographically robust (relevant for all sub regions), spatially realistic (captures the inherent spatial heterogeneity that exists in Mediterranean mosaic landscapes), automated (prevents biased mapping resulting from subjective human interpretation), and cost-effective. A possible approach would be to ignore the subjective, often fuzzy definitions of vegetation units that are based on botanical terminology, and focus on the actual structure of vegetation, in a manner that is robust over the entire Mediterranean region. Such an approach needs to account only for the measurable characteristics of vegetation that will either allow its segregation into different structural classes, or describe its structure as a continuous phenomenon. Two basic structural traits of vegetation are height and cover (Tomaselli 1981b, Kuchler 1988). Since both height and cover are continuous variables, a continuous structure map can be generated, instead of the traditional thematic cover maps. For other applications, such as the model that was developed in this research, the continuous map can then be categorized by a height/cover classification scheme into a PFT map that can supply the initial vegetation map for model simulations.

Previous studies that applied thematic classification approaches mapped the vegetation classes by means of human interpretation of aerial photographs, both for height and cover (Dufour Dror 2002, Sluiter and de Jong 2007). Sluiter and de Jong (2007) mapped land cover changes in Southern France using height, cover, and species composition, based on Tomaselli's scheme, yielding 18 cover classes. Dufour Dror (2002) proposed a three component classification based on height, cover, and vegetation stratification (the number of layers), resulting in 55 vegetation classes. Both studies mapped the landscape with a minimal mapping unit that is larger than the grain size of heterogeneity in Mediterranean regions, as an inherent byproduct of the polygon-based human interpretation process. Additionally, height measurements were not carried out in a systematic manner across the landscape. This, coupled with the subjective manner of the human interpretation process, might result in non-robust mapping products. At present, I am unaware of any studies that have generated continuous structural maps based on height and cover.

Generating a fine spatial scale map of height and cover requires two data sources: a vegetative cover map and a vegetation height map. The generation of vegetation cover maps is common, and uses a set of tools that have become standard practice in remote sensing in the past decades. In contrast, the generation of vegetation height maps is more complicated. The classic method for measuring heights over large areas involves stereoscopic analysis of remotely sensed imagery (Kraus 1993). In spite of recent advances in the field (Heiskanen 2006), it is still difficult to apply automated 3D mapping to large areas at high resolution.

Active sensors

An entirely different remote sensing approach that is rapidly emerging for vegetation mapping in is based on active sensors, such as synthetic aperture radar (SAR) and light detection and ranging (LiDAR). LiDAR sensors emit a short duration laser pulse (typically in the wavelength range of 900-1064 nm if the target is vegetation) towards a target surface, which returns a reflection of the pulse to the sensor's receiver (Lefsky et al. 2002). The elapsed time between the emission of the pulse and the reception of its reflection enables the determination of the distance between the sensor and the target surface, since the laser pulse travels at the speed of light. Airborne LiDAR sensors repeatedly measure these distances along transects that are perpendicular to the flight line of the carrying airplane (scanning mode), generating a set of samples that represents the 3D structure of the measured surface. This set can be interpolated into a continuous grid of the surface.

In the past decade, these sensors have been used successfully for various mapping applications, such as measurements of vegetation height (Hinsley et al. 2002, Goodwin et al. 2006, Straatsma and Middelkoop 2006, Bergen et al. 2007), canopy structure (Hinsley et al. 2002, Goodwin et al. 2006, Hyde et al. 2006, Tickle et al. 2006), biomass (Bergen et al. 2007), and leaf area index (Lefsky et al. 1999).

Data fusion

Mapping products of SAR or LiDAR alone are not always better than classification of spectral remote sensing imagery. However, combining them with spectral sensors yields superior results (Hyde et al. 2006, Geerling et al. 2007, Wallerman and Holmgren 2007). LiDAR, combined with spectral imagery, has been used for mapping detailed structural classes and species composition in forests (Hill and Thomson 2005, Tickle et al. 2006, Wallerman and Holmgren 2007, Wulder et al. 2007), wetlands (Geerling et al. 2007), and rangeland vegetation (Bork and Su 2007), and the results were characterized by high map accuracy.

Present approach

A data-fusion approach incorporating LiDAR and high resolution color aerial photography was developed in order to produce a continuous map of PFTs in Mediterranean regions. The map was created by overlaying data layers of vegetation height and cover in a 2 m spatial resolution, which were categorized into a thematic vegetation map of the five PFT needed as an input for the newly developed vegetation model, using ancillary data. The method was applied and tested in the Ramat-Hanadiv Nature Park, Northern Israel, which is also the test site for the simulations of the vegetation model. The resulting high resolution thematic vegetation map was used as the starting conditions for model simulations that predicted the future effect of different management scenarios.

Methods

Study area

The study was conducted at Ramat Hanadiv Nature Park, located at the Southern tip of Mt. Carmel, Northern Israel (32°30' N, 34°57' E). The area is a plateau with an elevation of 120 m a.s.l., descending steeply towards the coastal plain in the west via a series of rock cliffs, and descending gently towards the Nadiv Valley in the east. The parent rock formations consist of limestone and dolomite, with a volcanic marly tuff layer below the upper limestone layer. The soil in the area is mainly Xerochreps, developed on hard limestone or dolomite (Kaplan 1989). The climate is eastern Mediterranean, with an average annual rainfall of 600 mm, occurring mostly between November-March. The vegetation is mostly Eastern Mediterranean scrubland and shrublands, dominated by dwarf shrubs (*Sarcopoterium spinosum*), low summer deciduous shrubs (*Calycotome villosa*), evergreen tall shrubs (*Pistacia lentiscus*), and evergreen tall shrubs (*Phillyrea media*). Additionally, several scattered forest groves exist in the area, consisting mostly of conifer plantations (mainly *Pinus halepensis*, *Pinus brutia*, and *Cupressus sempervirens*). The area has a very rich flora of annuals and geophytes in open patches (Hadar et al. 1999, Hadar et al. 2000). Landscape structure is a fine-grained mosaic of woody patches at different heights and sizes, herbaceous clearings, exposed rocks, and bare ground (Perevolotsky et al. 2003).

A conventional polygonal vegetation map of Ramat Hanadiv park (Sagie et al. 2000) consists of 21 classes of vegetation formations and other, human-made, cover types. Natural vegetation is described either by the dominant species or by the traditional Mediterranean classification, in addition to the density of the vegetation (e.g. dense garrigue, open park woodland, sparse pine). The map was generated by manual classification of aerial photographs coupled with field surveys.

Mapping process

The mapping process consisted of two steps: mapping cover and height, and data fusion. The first step consisted of two components: [1] classifying an aerial photograph, generating a woody cover map; [2] processing and analysis of LiDAR data, generating a height map. These two layers were then overlayed in the second step to derive two distinct products: a continuous height/cover visualization, which was then categorized into a PFT map, consisting of five PFT, which was used in order to generate the starting conditions of the vegetation model scenario simulations.

Generation of the woody cover map

A digital color orthophoto of the study area was generated by Ofek™ aerial photography, in the summer of 2004 at a spatial scale of 0.25m (Figure 9). The image was classified into two classes using unsupervised IsoData classification (Campbell 1996). Following the classification, 'salt-and-pepper' noise was removed by median filtering with a 3 by 3 pixels window size. The agreement between these classes and the two predominant cover types in the study area - woody vegetation and non-vegetation - was assessed in the field. Sixty six points were selected in random locations across the image, and were further identified in the field. The agreement between the classification and the filed data was 92.42%. A map of the relative woody cover in 2 m blocks was generated by recording the number of woody pixels within a 2 m grid superimposed on the image, normalized to a percent cover image (0-100% cover).

Generation of the height map

Vegetation height was assessed by Ofek™ aerial photography in 2005 with an Optech™ ALTM2050 LiDAR, using the single return method with horizontal spacing of 1-2 m between points. Flight altitude was 1500 m. Following geocorrection, the vertical accuracy of the LiDAR points was 0.15 m, and the planimetric (XY) accuracy was 0.75 m. A digital elevation model (DEM) of the ground was generated by overlaying the LiDAR on the orthophoto, and identifying points located on the ground. A continuous DTM was then generated by extrapolating the data from the points, resulting in a 2 m grid. To convert the values of the LiDAR points from elevation above sea level to height above ground, the DEM value underneath each point was subtracted from the point's elevation. A digital surface model (DSM) of the landscape was derived by calculating the average height of points within a grid of 2 m pixel size that fits spatially to the grid of woody cover. The average number of LiDAR samples per pixel was 5.47±2.

Continuous vegetation structure visualization

The height and cover maps were overlaid in order to locate pixels that have invalid values, such as zero cover and non-zero height, or vice versa. Such mismatches can result from errors in a single map or in both maps. Therefore, in all pixels where either height or cover was zero, the other value was set to zero as well. Since height and cover values are possibly dependant (implying that it is unnecessary to use both for mapping purposes), their correlation was assessed based on 1000 randomly selected pixels (a subset was used since the total number of pixels in the image was very large).

A continuous map that represents the structure of vegetation in the landscape was then created by stacking the corrected height map, the cover map, and a blank map with the same extent into a RGB image (for the sake of visualization). The height and cover maps were assigned to the green and blue layers of the RGB image, respectively, with inverted color scales.

Comparison with a polygonal vegetation formations map

The polygonal vegetation formations map that has been used for management purposes in the study area was compared to the vegetation structure maps created here. For the sake of simplicity, only the most abundant formation in the polygonal map, sparse maquis (covering 41% of the map), was further analyzed in detail. First, a visual comparison was carried out to identify whether the continuous vegetation structure inside the sparse maquis polygons was indeed homogeneous. Then, three rectangular polygonal subsets (150×150 m^2) were overlaid on three areas within the sparse maquis class in the vegetation formations map that were visually identified as having different structures. In each subset, descriptive statistics of height and cover were derived from the corresponding maps. Additionally, height and cover were randomly sampled at 30 points inside each subset, to test whether there are significant differences between the distributions of height and cover in the three subsets.

Generation of the PFT map

The vegetation model that was developed in this research requires a PFT map in order to conduct simulations of actual landscapes. A suitable PFT map of Ramat Hanadiv Nature Park was generated by categorizing the height and cover layers according to a set of a-priori decisions, based on the characteristics of the PFTs. Each PFT was assigned to a typical combination of ranges of height and cover (Table 5) forming the final fusion product.

Figure 9. An aerial photograph of the study area.

Table 5. Height and cover combinations for classifying PFT.

PFT	*Height (m)*	*Cover (%)*
Herbaceous	<0.25	
Dwarf shrubs	0.25-0.5	
Low shrubs	0.5-1.5	<33
Tall shrubs	0.5-1.5	>33
Low trees	>1.5	>33

Results

Height and cover

The distribution of cover in the study area had two distinctive peaks, one at zero cover (open areas) and one at maximal cover (continuous vegetation, Figure 10). The distribution of heights had a peak at zero, from which the height decreased in a negative exponential form (Figure 10).

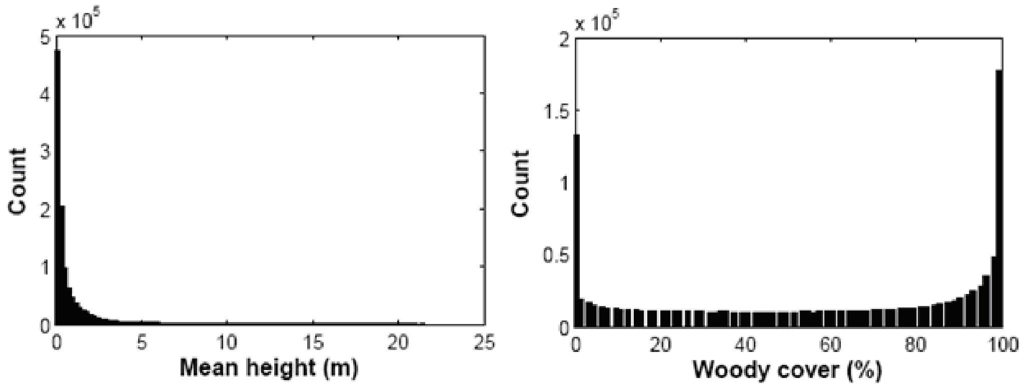

Figure 10. Histograms of mean height (left) and woody cover (right) for the study area.

Vegetation structure maps

The continuous vegetation structure map that was generated by fusing the height and cover maps (Figure 11) portrays clearly the large structural heterogeneity of the vegetation in the study area (Figure 12). The continuum of height/cover combinations ranges from low-open pixels, representing herbaceous patches (as well as roads and other man made surfaces) to tall-dense pixels, usually corresponding with pine and cypress plantations. The correlation between 1000 random samples of height and cover in the continuous data was low ($r=0.294$) but significant ($p<0.01$, probably due to the large sample size), confirming the need for using both height and cover as descriptors of the vegetation type (i.e. rather than using only one of them).

There was a considerable amount of structural variation within any single thematic class in the polygonal vegetation formations map. Even by visual inspection it was clear that the sparse maquis class can be further classified into at least three additional structural classes. This is evident regardless of whether the comparison is made with the continuous structure map or the classified structure map. Each of the three rectangular subsets has different mean height and cover values from the others, with one being characterized by low, open vegetation, and the others being more dense and tall (Table 6, Figure 13). Both height and cover differed significantly between the three subsets (Kruskal Wallis tests, $P<0.001$ in both cases). Additional heterogeneity was found in other classes in the vegetation formations map.

The PFT map (Figure 14) follows the general shape of the continuous map. The different vegetation units in the study area emerge clearly from the map. The most abundant PFT (in terms of cover) is herbaceous vegetation, followed by dwarf shrubs, tall shrubs, low trees, and low shrubs (Figure 15). Other cover types (e.g. pine plantations, cypress plantations, gardens, and other) consist of 20% of the area.

Table 6. Descriptive statistics of height and cover in three blocks inside the sparse maquis category of the thematic vegetation formation map.

block number	*mean cover (±std)*	*mean height (±std)*	*maximum height*
1	28.82 (28.43)	0.22 (0.3)	3.26
2	51.36 (32.47)	0.74 (0.76)	4.22
3	77.55 (25.51)	0.52 (0.45)	2.92

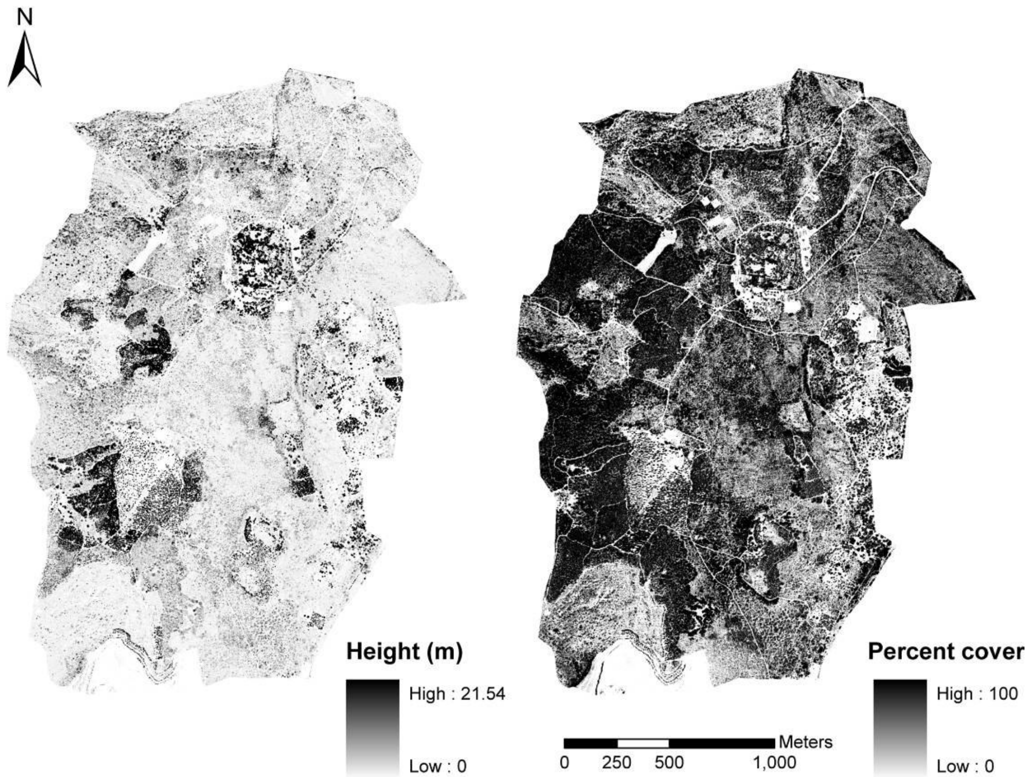

Figure 11. Maps of the study area: woody cover (left), and mean height (right).

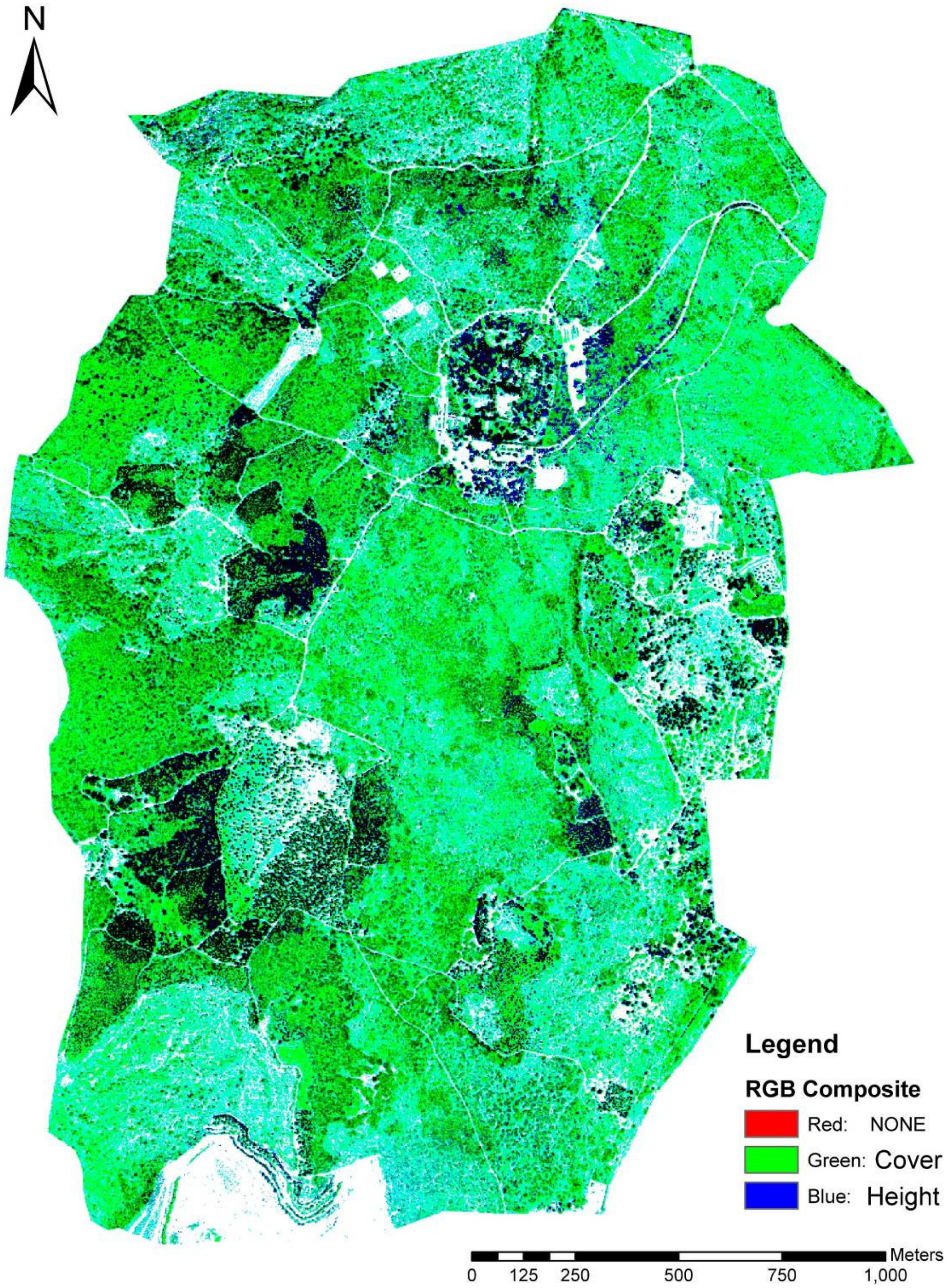

Figure 12. The continuous map of vegetation structure (inverted RGB). Darker pixels represent tall and dense vegetation, while brighter pixels represent low and sparse vegetation. Green pixels represent low and dense vegetation, while blue pixels represent tall and sparse vegetation (usually tall individual trees with no understorey vegetation).

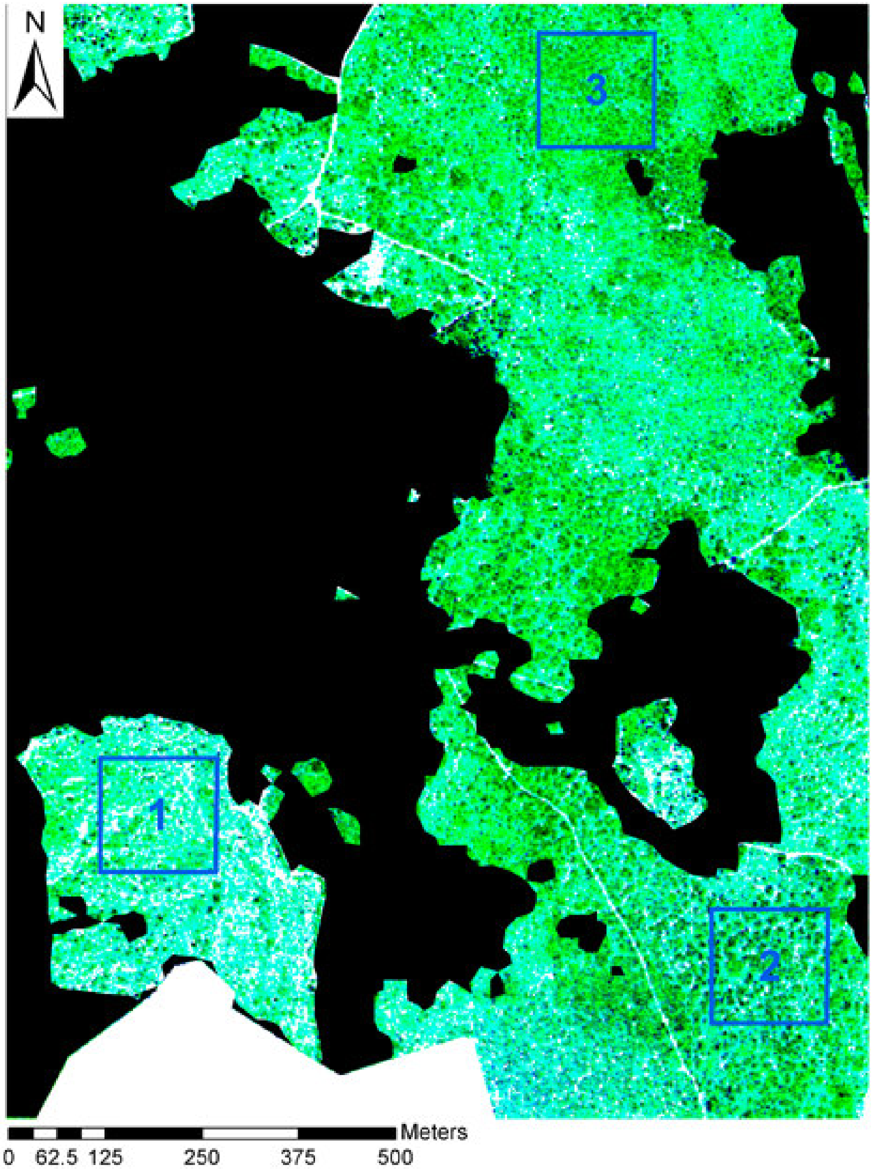

Figure 13. A subset of the polygonal vegetation formation map, overlaid on the vegetation structure map. Black areas represent classes other than sparse maquis. Colored areas represent sparse maquis, with the heterogeneity derived from the structure map (the formation map being transparent). The three blue rectangles are blocks in which the statistics of the structure map were derived. Notice the difference structures within each block (and additional heterogeneity in their surroundings), which presumably represent the same formation, sparse maquis.

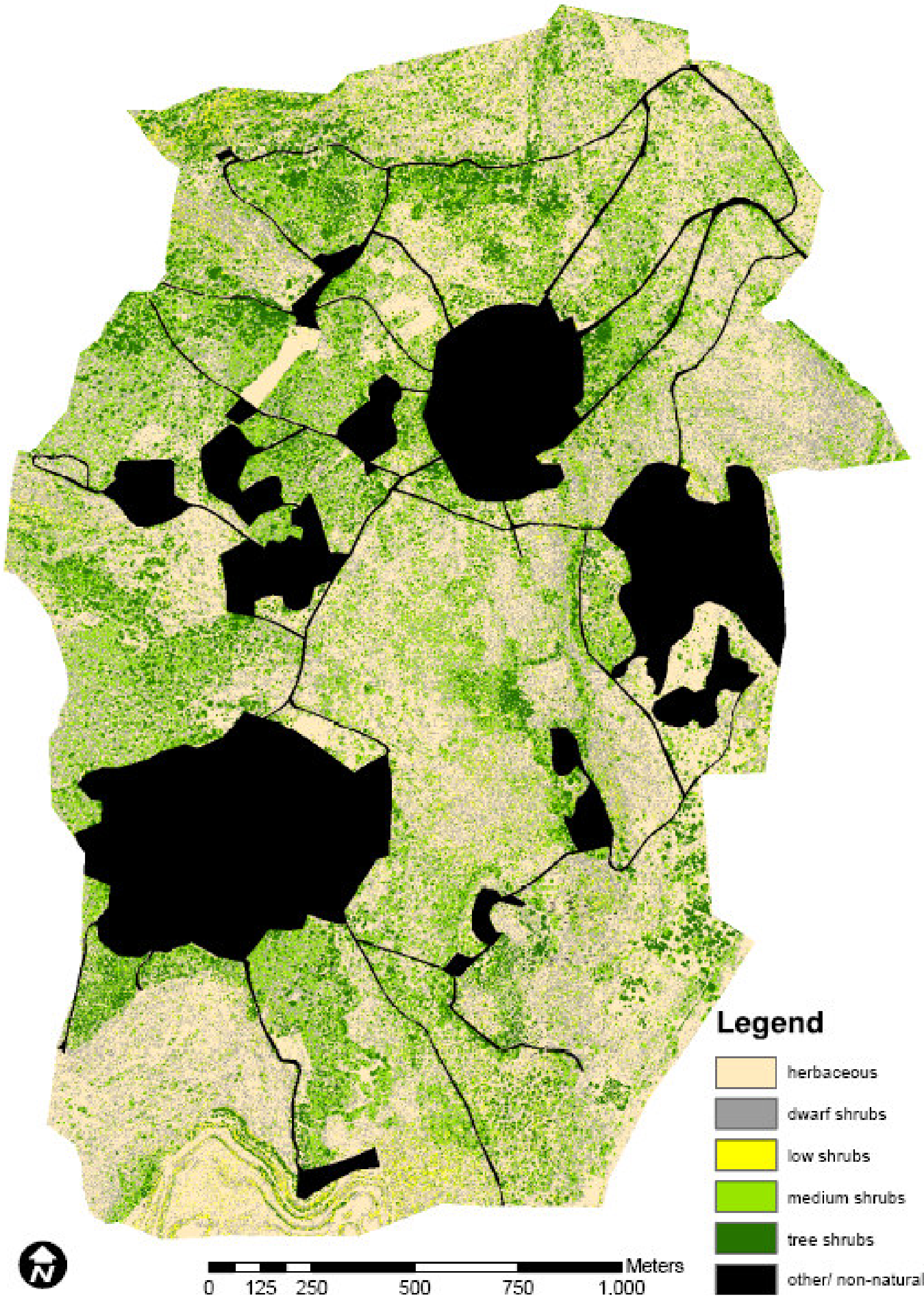

Figure 14. The PFT map. Black areas (representing other types of vegetation and non-natural areas) were digitized manually and omitted from further analyses.

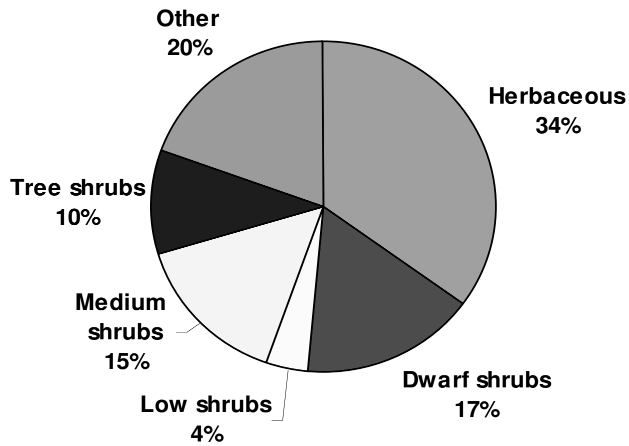

Figure 15. The relative cover of the PFT in the study area, based on data fusion of LiDAR and aerial photography.

Discussion

Mapping vegetation in Mediterranean regions is a complicated task, since these landscapes are characterized by highly heterogeneous and spatially complex vegetation. This heterogeneity occurs at many spatial scales simultaneously, further complicating attempts of mapping the vegetation in a manner that is both geographically robust and spatially realistic. Previous approaches for mapping Mediterranean vegetation tended to incorporate human subjective decisions, either in the mapping technique (manual delineation of polygonal semi-homogeneous units) or the concept (using the dominant species as surrogates of vegetation formation), or both. Due to fine scale heterogeneity, it is not possible to manually map vegetation units in a robust manner over large areas. The dominant species vary between different sub-regions of the Mediterranean, and the existing naming conventions for vegetation formations are general and vary between countries. Therefore, much detail is lost in the attempts to map the vegetation using existing thematic classes. As a result, many existing vegetation maps have thematic classes that are too general or consist of classes that are locally specific, and therefore can not be directly compared to maps from other regions. Vegetation maps that would be thematically consistent over large areas would facilitate comparisons between different sub-regions.

In this study, Mediterranean vegetation was mapped using a different approach, accounting only for the structural characteristics of vegetation that can be objectively measured. Initially, no subjective assumptions were made regarding the classification of vegetation into different groups using its structural traits, in order to preserve an unbiased description of the landscape, regardless of the location of the mapped area. The result of this stage is a continuous vegetation map that describes the spatial structure of woody vegetation as an almost continuous phenomenon. Based on the continuous map, one may use any desired classification scheme that is based on the relevant ancillary data and additional knowledge in order to generate a thematic vegetation map according to its needs. This was exemplified by mapping Mediterranean plant functional types based on ancillary data about the distributions of height and cover of those types in the study area. Additionally, it was shown here that in a traditional vegetation formations map that is based on the classical approach for describing Mediterranean vegetation, a considerable amount of structural heterogeneity is lost in comparison to the actual, fine scale heterogeneity that exists in the area, mapped by the height/cover method.

Height and cover are the most straightforward descriptors of vegetation structure (Kuchler 1988). While mapping cover is a common practice since the earliest air photography, mapping height in detail and in large spatial extents was less common until recent years due to technical limitations. Mapping height, or the 3D structure of vegetation, is greatly aided if active remote-sensing instruments (LiDAR, SAR etc.) are used. The availability of such sensors is increasing, and their application for mapping vegetation structure is likely to become more and more widespread. In Mediterranean vegetation, there will always be a need for maintaining a high density of height samples per unit area due to the fine scale spatial heterogeneity in comparison to other biomes. This may pose a limitation on the overall extent that can be mapped, since the volume of data that is generated by LiDAR is large, making computer analysis of the results cumbersome and time consuming. With the advancement in computing power, however, this may become a less limiting factor in the future.

In this study, it was attempted to overcome the problem of subjectivity in mapping the structure of vegetation, and to present a continuous mapping approach as an alternative to the widely used polygonal mapping approach. The method was based on high-resolution measurements of vegetation height and cover, both being characteristics of vegetation that can be readily measured using existing remote sensing technology. The structure of vegetation was portrayed by a continuous height – cover space, rather than using a pre-defined, subjective categorization of the vegetation structure. A comparison of the newly generated map with an existing polygonal map of vegetation formations showed that the proposed method portrays much more of the actual structural variability existing in the field, compared to the traditional polygonal map. This implies that using thematic polygon maps for the description of vegetation structure in Mediterranean regions might be hindered by the minimal mapping unit of those maps, which needs to be small enough to portray the fine scale structural heterogeneity that characterizes these landscapes. Therefore, the proposed method might serve to construct robust vegetation structure maps that can be used to compare landscapes in different regions. Additionally, the continuous map may be classified into any form of thematic map, depending of the specific needs and requirements of its creator. Here, the thematic map of plant functional types that was created from the continuous map was used as the starting conditions map for the vegetation model that was described in the previous chapter.

Quantifying the effects of goat grazing and shrub clearing of the fine scale pattern of woody vegetation[3]

Motivation

Goat grazing and shrub clearing are common land use / disturbance practices in the Mediterranean region. In addition to their impact at the landscape scale, they may alter the fine scale spatial pattern of woody vegetation. In Mediterranean type ecosystems, the spatial pattern of woody vegetation affects various ecological and physical processes that occur at the micro-habitat scale, such as pollination, seed dispersal, availability of sunlight and competition for resources. Therefore, it is desirable to develop means for quantifying the impact of those disturbances on the fine scale spatial structure of woody vegetation.

Background

Large scale fragmentation versus fine scale fragmentation

The concept of habitat fragmentation has been central to conservation research and practice in recent decades (Haila 2002). Fragmentation is typically viewed as a spatial phenomenon that takes place at the landscape scale or at larger spatial scales (Lindenmayer and Fischer 2006). Fragmentation is a result of various disturbances, such as wildfire, windstorms, forest-clearing, urban sprawl, etc., that are relatively homogeneous at large scales. Some types of disturbance, such as grazing, tree-clearing, low-intensity fires and invading species, affect the ecosystem at a variety of scales, including spatial scales smaller than the landscape scale (Naveh and Kutiel 1986, Adler et al. 2001, Henkin et al. 2007a). However, these small scale effects are traditionally conceived as 'modifying' the land, rather than fragmenting it.

Lord and Norton (1990) noted that these fine-scale processes can also be considered as fragmentation, and termed it 'structural fragmentation', as oppose to 'geographical fragmentation', which they assigned to fragmentation at landscape scale

[3]Based on: Bar Massada, A., Gabay, O., Perevolotsky, A., and Carmel, Y. (2008). Quantifying the effects of grazing and shrub clearing on the small scale spatial pattern of vegetation. *Landscape Ecology*, 23(4) 327-339.

or larger scales. Here, I refer to these two types as fine-scale fragmentation vs. geographical fragmentation. In geographical fragmentation, the scale of the process is much larger than the scale of the individual plants, while in fine scale fragmentation, the scale of the process is close to the scale of the individual plants. Invasion of exotic plants, and heavy grazing, were both described as inflicting fine scale fragmentation on ecosystems.

Lord and Norton (1990) highlighted the potential differences between geographical and fine scale fragments. These include lack of intact core area in the fine scale fragments, resulting from their overall small area. This essentially leads to lack of difference between the edge and the core, making the entire patch an "edge" patch, and thus increasing its susceptibility to disturbances (in contrast to geographical fragments where the edge can absorb external disturbance, leaving the core area undisturbed). Additionally, functional interactions between organisms are more likely to be disrupted in fine scale fragments since only a fraction of the original species assemblage is retained.

The changes in spatial heterogeneity of landscape are important because they may imply on changes in habitat diversity and influence the diversity of organisms ranging from insects to birds and mammals (Bock and Bock 1984, Dennis et al. 1998) and interactions among them. Activities of many organisms depend on the structure of their immediate environment, and thus are expected to be affected by changes in spatial heterogeneity of landscape caused by fine scale fragmentation. For example, the shape of a shrub can affect movement and browsing patterns of large herbivores (Etzenhouser et al. 1998), beetle movements (Crist et al. 1992), and foraging behavior of seed harvesting ants (Crist and Wiens 1994). It was found that habitat alteration affects individual movements and patch selection of insect species, and thus change species richness, guild structure and species distributions (Golden and Crist 1999).

Fine scale fragmentation may affect processes that occur at small spatial scale but have also considerable impact on the ecosystem, through their effect on interaction such as pollination (Ghazoul 2005) or seed consumption (Crist and Wiens 1994). In a meta-analysis of independent fragmentation studies, it was found that fragmentation has an overall large and negative effect on pollination and on plant reproduction (Goverde et al. 2002, Aguilar et al. 2006).

Typifying small scale impacts of disturbance as 'fragmentation' has important implications, since there exist a whole set of well studied tools for evaluating, quantifying, and analyzing fragmentation, namely landscape metrics (McGarigal and Cushman 2002, Li and Wu 2004, Neel et al. 2004). In contrast, the quantification of the current concept of 'land modification' as a result of local disturbance is not straightforward, and tools equivalent to landscape metrics are not available to assess the degree of modification that results from such disturbances.

However, to this date, I am unaware of any attempt to analyze and quantify fine scale fragmentation in a manner similar to the ubiquitous analyses of geographical fragmentation, where the grain size is much larger. This is unfortunate, since rapid fine scale fragmentation is taking place in vast parts of the world, where grazing, wood cutting and invading species have strong impact on local ecosystems, and precise measurements and analyses of these phenomena are of utmost importance. Moreover, active management based on landscape manipulation is suggested for various ecosystems in order to maintain biodiversity (Perevolotsky 2006). If this practice becomes widespread, a quantitative tool to assess the intervention (or management) impact would be required. Landscape metrics may serve as such quantitative tools.

Landscape metrics

Over the past 20 years, much research was directed to landscape metrics, highlighting their potential applications but also their limitations (Li and Wu 2004). Landscape metrics react in complex manners to changes in landscape patterns (Neel et al. 2004) and analysis scale (Wu et al. 2002, Saura 2004, Wu 2004). Different metrics respond differently to changes in class aggregation and abundance, ranging from simple linear responses to complex, non-linear responses (Neel et al. 2004). Therefore, vegetation patterns can not be described adequately by a single landscape metric, and it is recommended to use an entire set of metrics from different classes instead (Li and Wu 2004). Additionally, scale and extent of the analysis are well known to affect the behavior of landscape metrics (Turner et al. 1989, Wu et al. 2002, Saura 2004, Wu 2004, Garci'a-Gigorro and Saura 2005). It is important to define and account for three different scales in studies that use landscape metrics: [1] the scale of observation, in which the landscape pattern is captured by the remote sensing platform or the field data gathered; [2] the scale of analysis, in which the landscape metrics analysis is actually performed, usually following some sort of filtering, aggregation, or resampling of the original data (Li and Wu 2004); [3] the actual scale (or scales) of the ecological patterns and processes of interest (Levin 1992). In order to better tackle the problem of scale, multiple-scale analysis is often performed, either by directly comparing data from different sensors (Benson and MacKenzie 1995, Saura 2004), or by synthetically rescaling the data by means of aggregation techniques (Wu et al. 2002, Saura 2004, Wu 2004). A comparison that would include different sensors for each scale would be a better representative of reality than aggregation, due to the different physical properties of different sensors (Saura 2004). However, the majority of multi-scale studies used aggregation due to limitations on image availability.

Mapping fine scale fragmentation

The lack of studies quantifying fine scale fragmentation may be attributed, at least partly, to technical challenges. In order to analyze spatial phenomena, the resolution of the data needs to be finer than the scale of the phenomenon of interest (Campbell 1996). Thus, for example, forest fragmentation in the continental United States (Riitters et al. 2002), where the units of interest were forest stands, was studied using Landsat TM images, at a spatial resolution of 30 m. Global forest fragmentation was assessed using land cover maps derived from AVHRR imagery at a spatial resolution of 1 Km (Riitters et al. 2000). In fine scale fragmentation, the units of interest are single plants – trees, shrubs, and dwarf shrubs, sometimes smaller than 1 m^2. The spatial resolution required to study fine scale fragmentation should therefore be much higher, at the order of centimeters.

Currently, most vegetation maps derived from satellite images and air photos have coarser spatial resolutions. The highest spatial resolutions used for mapping spatial pattern were 0.125 m, where aerial photographs were used to map shrubby patches within an agricultural matrix in the Negev desert , Israel (Svoray et al. 2007); 0.13 m, where a color infrared aerial photo was used to map serpentine grassland in California (Lobo et al. 1998); and 0.15 m, where wetland vegetation was mapped from an aerial photo acquired from a low-altitude balloon platform, in Japan (Miyamoto et al. 2004). In this study, I employ a very low altitude balloon platform, combined with meticulous mapping techniques, in order to achieve an extremely high resolution vegetation map, with a pixel size of 0.04 m. This technique enables quantitative analysis of fine scale fragmentation of woody vegetation composed of small patches, among other structures.

Present approach

The major goal of this part of the thesis is to describe local effects of grazing and tree clearing in terms of fine scale fragmentation (structural fragmentation, sensu Lord & Norton 1990). Quantifying various landscape metrics for areas that are subject to different disturbance regimes will enable us to quantify the magnitude of their impact on the landscape, and to determine whether such impacts are significantly different for different types of disturbance. A secondary objective of this study is to assess the effect of analysis scale (in the range between high and very high spatial resolutions) on the behavior of the metrics and their ability to differentiate between the effects of different disturbances. The study combines high-resolution mapping of the natural woody vegetation in experimental plots, followed by a multi-scale analysis of the fine scale structure of the vegetation using a set of landscape metrics.

Methods

Experimental design

The study was conducted in an existing field experiment at Ramat Hanadiv Nature Park. The field experiment was erected in 2004, and it consists of twenty rectangular plots of ca. 1200 m^2 each, that were set up in a small watershed at the northern part of the park (Figure 16). The plots were divided into four groups of five plots, each group subjected to a different treatment, applied annually since the beginning of the experiment. The treatments were (1) goat grazing (approximately 400 goat days/1000 m^2/year), (2) shrub clearing (shrubs were cut mechanically every fall to ground level; rapid spontaneous regeneration was uninhibited), (3) shrub clearing combined with goat grazing (goats enter the plots 6 months after the clearing treatment and consume the regenerating shrubs), and (4) control (no disturbance). Thus, the experiment consisted of four treatments with five repetitions.

Several isolated trees of species that are rare in the park were left in three clearing + grazing plots (with percent cover of 15.7%, 3.68%, and 1.69%) and one clearing plot (with percentage cover of 33.27%). These trees were digitized and omitted from all further analyses.

Vegetation photography and mapping

An aerial survey of the 20 study plots was performed in July 2006 by Sky Balloons™, using a digital camera (Minolta dimage™) mounted on a helium balloon. The camera was operated manually from the ground with a remote control. The operator controlled all camera functions, and its tilt relative to the balloon platform. The altitude of the survey was 110 meter above ground surface. More than 100 images of the study plots were acquired from varying angles and locations. A subset of 9 images was selected for geo-correction, based on a visual evaluation of image quality, contrast, and proximity to nadir angle. Prior to the aerial survey, 36 ground control points were marked in the field using calibration marks. The images were geo-corrected using the linear rubber sheeting method (Saalfeld 1985, White and Griffin 1985), based on the locations of the control points visible in each image. A set of 4-9 control points was used per image. The spatial resolutions of the geo-corrected images ranged between 0.0209 and 0.038 m, depending on the exact altitude of the balloon at the time of photo acquisition.

Vegetation classification

The images were classified into three thematic classes, (1) woody vegetation, (2) bare ground + herbaceous vegetation, and (3) rocks, using a maximum likelihood supervised classification in ERDAS IMAGINE 8.6 (ERDAS 1999). Bare ground and herbaceous vegetation were assigned into the same class since the photos were taken in the dry season, when dry herbaceous vegetation is inseparable from bare ground. Spectral signatures of the three classes were acquired separately for each image since there was a large variation in the overall brightness of different images.

We assessed the overall classification accuracy of the image, and calculated Cohen's kappa and user accuracy for each class (Congalton and Green 1999). Classification accuracy was assessed with 100 reference points (interpreted manually) selected in a stratified random scheme. To reduce edge effects, only pixels that were located in homogeneous regions of the classified image (defined by a neighborhood of seven by seven pixels of the same class) were used as reference points (Verbyla and Hammond 1995). A subset of 30 reference points was selected and validated in the field, in order to evaluate the quality of the manual interpretation.

Landscape metrics analysis

In order to standardize the spatial resolution of the classified images, all images were resampled to the largest pixel size, 0.038 m, and merged into a single mosaic. A clumping algorithm (ERDAS 1999) was then applied to the image using a 8-pixels neighborhood rule, and a map of individual patches was constructed. Patches < 10 pixels (corresponding to an area of ca. 0.014 m^2) were typically artifacts of the classification process, and were therefore eliminated using a focal majority filter (ERDAS 1999). The resulting image was divided into 20 images, one per study plot, and imported into Fragstats 3.3 software (McGarigal et al. 2002).

Only a few basic metrics of more than a hundred that appear in the literature were used in this study. Landscape metrics are frequently strongly correlated, and can be confounded (McGarigal and McComb 1995, Riitters et al. 1995, Gustafson 1998, Hargis et al. 1998, Tinker et al. 1998). Analysis of these authors' recommendations revealed reasonable agreement on a core set of metrics (Botequilha Leitão and Ahern 2002). Therefore, seven basic metrics for the spatial analysis of the woody patches in each of the 20 study plots were selected (Table 7): proportion of landscape, mean patch area, edge density, mean proximity index, patch density, mean radius of gyration, and mean shape index. These metrics capture the basic spatial processes studied here (decrease in woody cover and patch size, increase of edge and spacing between patches, and change in patch shape).

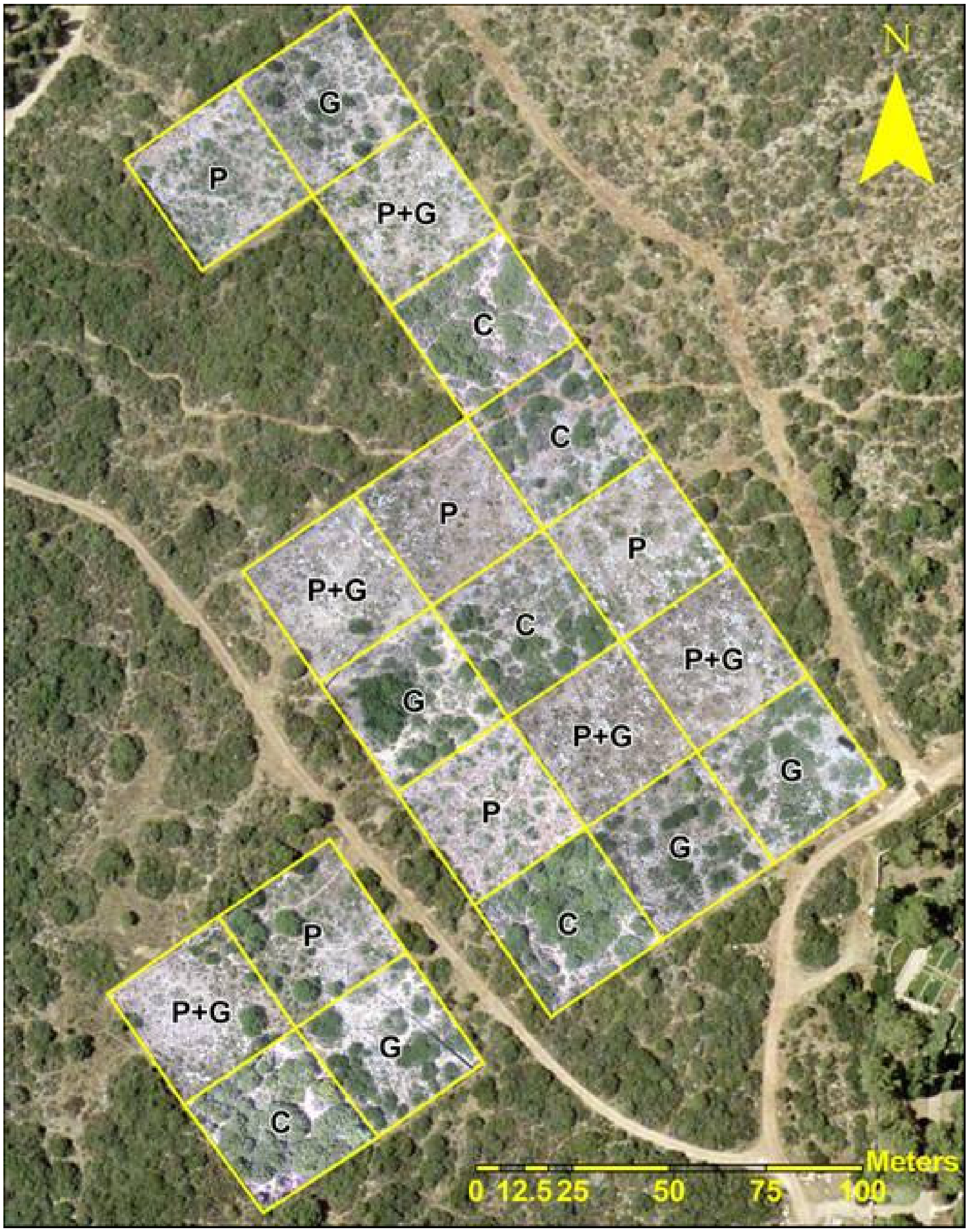

Figure 16. Aerial photo of the experimental setup, comprised of 9 geo-corrected balloon images (spatial resolutions ranging between 2-4 cm) overlaid on an orthophoto of the study area (spatial resolution of 25 cm). The study plots are marked by yellow rectangles, with the corresponding treatment type written inside. C – Control, G Goat grazing, P – shrub clearing, P+G – clearing with Grazing.

The seven landscape metrics derived from the four treatments in the 20 study plots were analyzed in the following manner. First, one way analysis of variance (ANOVA) was performed separately for each metric to find whether at least one of the treatments had a significantly different mean metric value than the others. Some replicate plots had common boundaries, and the assumption of spatial independence may have been very slightly violated, yet its effect was considered to be minor, still allowing the conduction of ANOVA. For cases where the one way ANOVA was revealed significant differences, multiple comparisons were performed to detect pairs of treatments that resulted in different metric values, using Tukey's HSD. As an additional indication of small scale effects of fine scale fragmentation on vegetation structure, a principal component analysis was performed using the entire set of landscape metrics combined.

Table 7. A list of landscape metrics used in this work. Description follows McGarigal et al. (2002).

Metric name	*Description*	*Range*
Proportion of landscape (PLAND)	A measure of landscape composition: the proportional abundance of each patch type in the landscape.	PLAND≥0
Patch density (PD)	Number of patches per unit area	PD≥0
Edge density (ED)	Total patch edge lengths per unit area	ED≥0
Mean patch area (AREA)	Mean area of patches in the landscape in m^2	AREA≥0
Mean radius of gyration (GYRATE)	Radius of gyration is a measure of patch extent: the mean distance between each cell (pixel) in the patch and the patch centroid in meters	GYRATE≥0, Equals 0 when the patch consists of a single cell; increases with patch growth.
Mean shape index (SHAPE)	Shape index is a measure of patch shape complexity: how close is the patch shape to a square	SHAPE≥1, Approaches 1 when the shape is close to a square; grows as the shape is more irregular
Mean proximity index (PROXIM)	Proximity index is a measure of landscape fragmentation, based on the distribution of distances between patches and patch sizes in a defined neighborhood size with *N'* patches.	PROXIM≥0, Approaches 0 when the landscape consists of small, isolated patches; increases as the landscape consists of large, continuous patches

Data rescaling

The original vegetation maps (~4 cm pixel size) were rescaled to four coarser scales, with pixel sizes of 25 cm, 50 cm, 75 cm, and 100 cm. Each new map was derived directly from the original vegetation map using a majority rule, where the new pixel value is set to the value of the most abundant class in the corresponding area in the original map. Maps with pixel sizes larger than 100 cm were not evaluated since the small number of pixels in each study plot, makes the landscape metric analysis inappropriate. Following the rescaling, the statistical analyses described above were applied to each rescaled data set. In addition, a scaling function was fitted to each metric in each treatment, from one of the following possibilities: logarithmic, power, exponential, linear, or none. One scaling function per metric was selected based on its coefficient of determination (R^2). The function was fitted to the raw data that included 25 points per treatment (5 scales × 5 repetitions) for each metric.

Results

Classification results and accuracy

The classified vegetation maps followed closely the fine spatial patterns of woody vegetation and of rocks (Figure 17). Classification accuracy was 90%, and the overall kappa statistic was 0.82. User accuracy for the woody class was 90.2% and producer accuracy was 93.88%. The conditional kappa statistics were 0.81, 0.87, and 0.73, for woody vegetation, bare ground, and rocks, respectively. There was a complete agreement between the 30 field measured reference points and their manually interpreted counterparts.

Landscape metrics

Generally speaking, disturbance increased fine scale fragmentation at all spatial scales (Figure 18). Analysis of variance revealed that for six of the seven landscape metrics, at least one of the treatments had a significantly different mean metric value than the others ($P<0.05$). These results were consistent at all spatial scales (Figure 19). The impact of clearing was consistently stronger than the impact of grazing, and clearing followed by grazing had yet a stronger impact (Figure 18, 20). The effect of disturbance was expressed in several ways: the proportion cover of woody vegetation decreased with increased disturbance, (Figure 18a) while patch density increased (Figure 18b), in agreement with a major reduction in mean patch area (Figure 18c). Edge density also increased, providing additional indication that disturbance results in

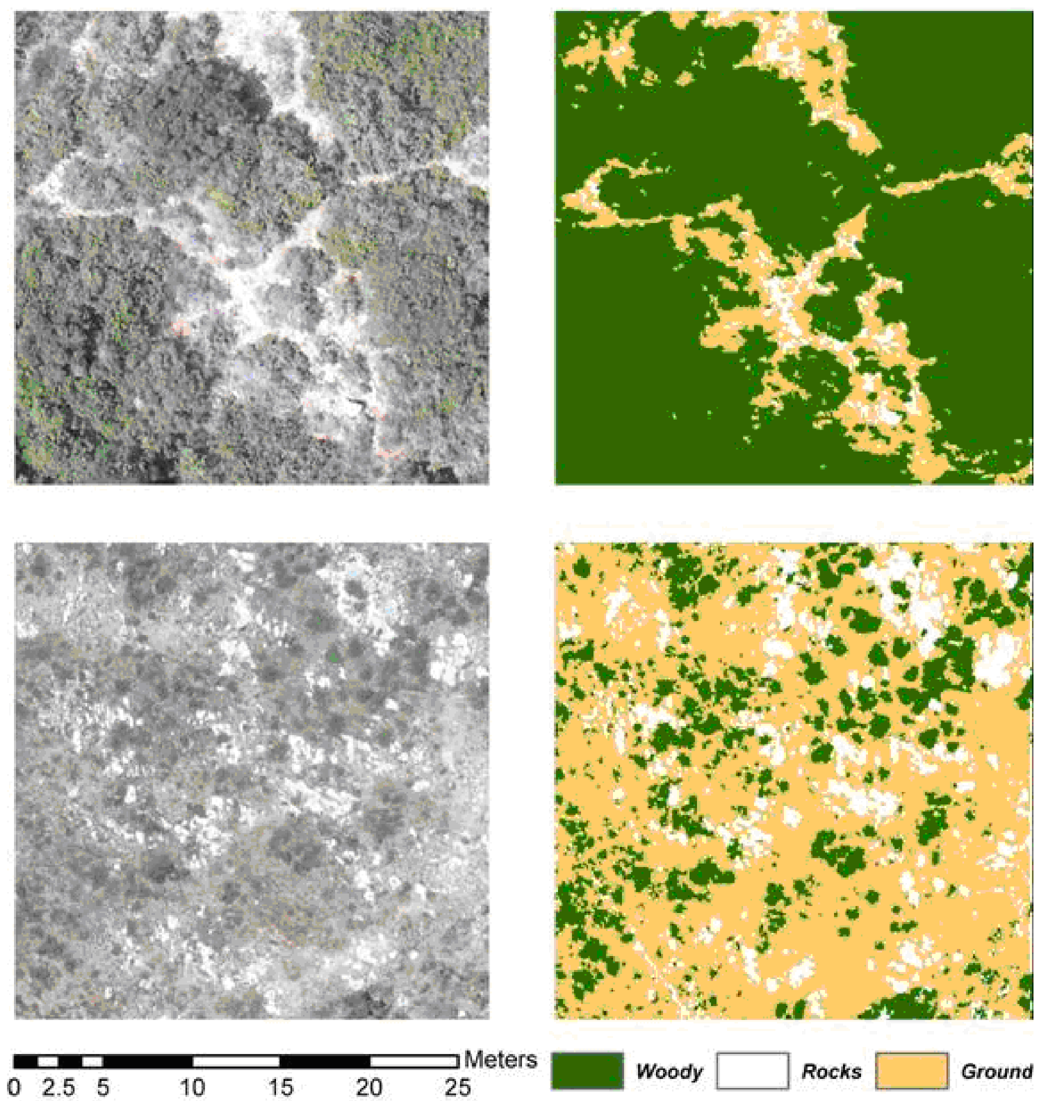

Figure 17. Aerial images (left) and their corresponding classifications (right), of a control area (top) and a grazed + cleared area (bottom).

fine scale fragmentation (Figure 18d). Mean proximity index decreased following disturbance (Figure 18f), corresponding to an increased spacing between patches. Mean shape index was the only metric for which differences between treatments were not significant at the four finer scales, although differences were significant at the coarsest scale (Figure 18g, Figure 19).

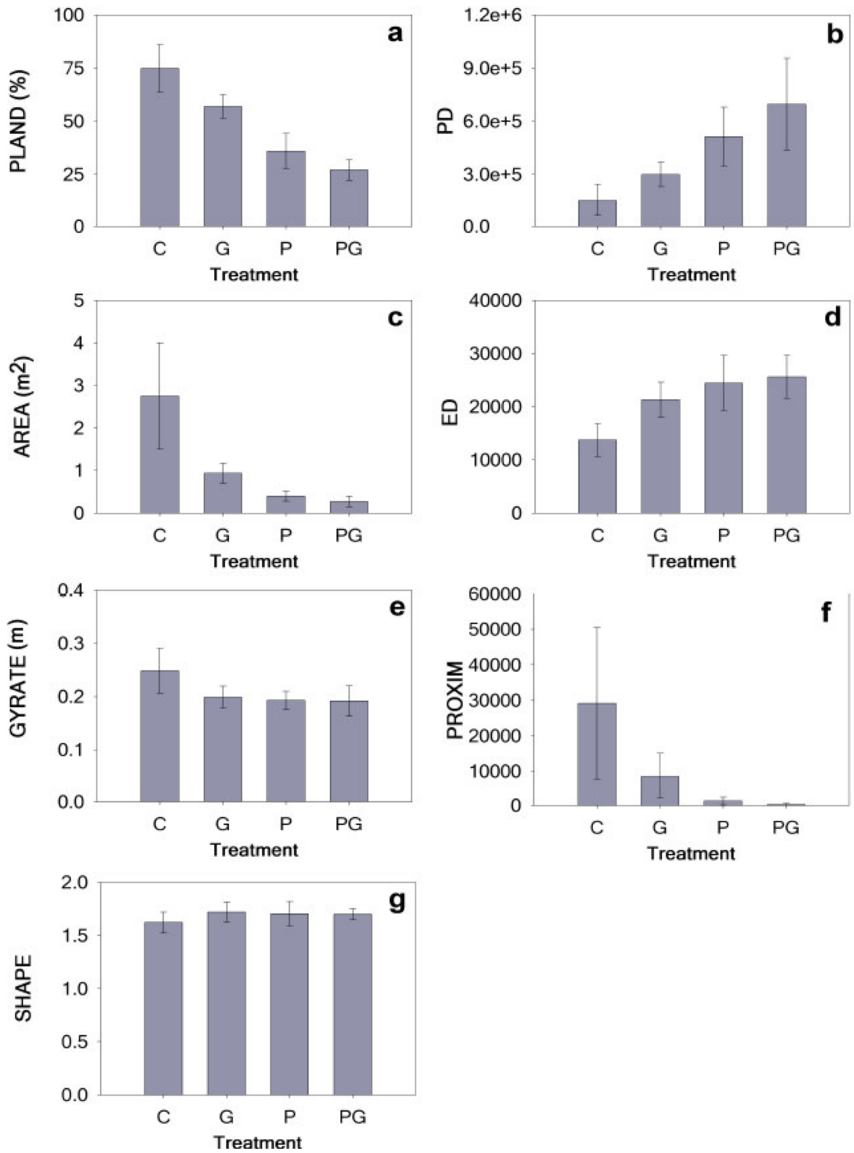

Figure 18. Average values of landscape metrics for woody patches in the different treatments at the finest scale. PLAND is proportion of landscape, PD is patch density, AREA is mean patch area, ED is edge density, GYRATE is mean radius of gyration, PROXIM is mean proximity index, and SHAPE is mean shape index. The category axis lists the types of treatments: C – Control, G – Goat grazing, P – shrub clearing, PG – clearing with Grazing.

The various metrics exhibited five types of scaling relations (Figure 19). Edge density exhibited a logarithmic scaling relation ($y=a\ln x+b$, where a and b are parameters) in the majority of treatments, with an average R^2 of 0.87. Mean patch area and mean proximity index exhibited a power law scaling relation ($y=ax^b$) in the majority of the treatments, with an average R^2 of 0.85 and 0.82, respectively. Patch density and mean radius of gyration exhibited an exponential scaling relation ($y=ae^{bx}$) in all treatments, with an average R^2 of 0.88 and 0.91, respectively. Proportion of landscape was relatively constant at different scales, and mean shape index did not exhibit any consistent scaling relation. Accounting for the different disturbances, the control plots were the most sensitive to changing scales in all metrics except patch density and edge density (where the clearing with grazing treatment was the most sensitive), and proportion of landscape (where all treatments were insensitive to changing scales). Scale had mixed effects on the degree of difference between treatments. In patch density, edge density, and mean proximity index, the differences between treatments decreased with increasing scale, corresponding to a negative exponential coefficient. In proportion of landscape, the differences between treatments were consistent over the entire range of scales. In all other metrics, the differences between treatments increased with increasing scale.

The majority of landscape metrics captured significantly the effects of grazing and of clearing on vegetation structure when compared to the undisturbed control plots (Table 8). The multiple comparisons showed that in four landscape metrics -- the grazing treatment differed significantly from the control at the finest scale. At the coarsest scale, only proportion of landscape differentiated between grazing and control plots. Edge density differentiated between them only at the finest scale, while patch density and mean shape index failed to do so at any scale. In six metrics, the clearing and the clearing + grazing treatments differed significantly from the control, and these differences were consistent over the entire range of scales except for mean proximity index at the coarsest scale. In contrast, mean shape index differentiated between control plots and clearing plots only at the coarsest scale. The grazing and clearing plots differed only in the proportion of woody vegetation cover. The clearing + grazing plots differed from the grazing plots in the proportion of woody cover and in patch density. The clearing and the clearing + grazing plots differed only in the value of patch density at the pixel size of 50 cm.

A PCA on the original data set showed that the first three principal components of the multi-metric data contributed to 60.12%, 17.1%, and 12.3% of the variation in the data, respectively. The first component corresponds well to the different treatments (Figure 20). The control treatment is clearly different than the other treatments, and the effects of clearing and clearing + grazing are hard to distinguish.

Table 8. Multiple comparisons of the effect of treatments on the value of the landscape metrics at various spatial scales. Significant differences (at the 0.05 level) are marked by a number between 1 and 5, where 1 represents the smallest scale (pixel size of 4 cm), and 5 represents the largest spatial scale (pixel size of 100 cm). C is control, G is grazing, P is clearing, PG is clearing with grazing.

Treatment pair	*Proportion of landscape*	*Patch density*	*Edge density*	*Mean patch area*	*Mean radius of gyration*	*Mean proximity index*	*Mean shape index*
C-G	1 2 3 4 5		1	1 2 3 4	2 3	1 2 3 4	
C-P	1 2 3 4 5	1 2 3 4 5	1 2 3 4 5	1 2 3 4 5	1 2 3 4 5	1 2 3 4	5
C-PG	1 2 3 4 5	1 2 3 4 5	1 2 3 4 5	1 2 3 4 5	1 2 3 4 5	1 2 3 4	5
G-P	1 2 3 4 5	5				4	
G-PG	1 2 3 4 5	1 2 3 4 5				4	
P-PG		3					

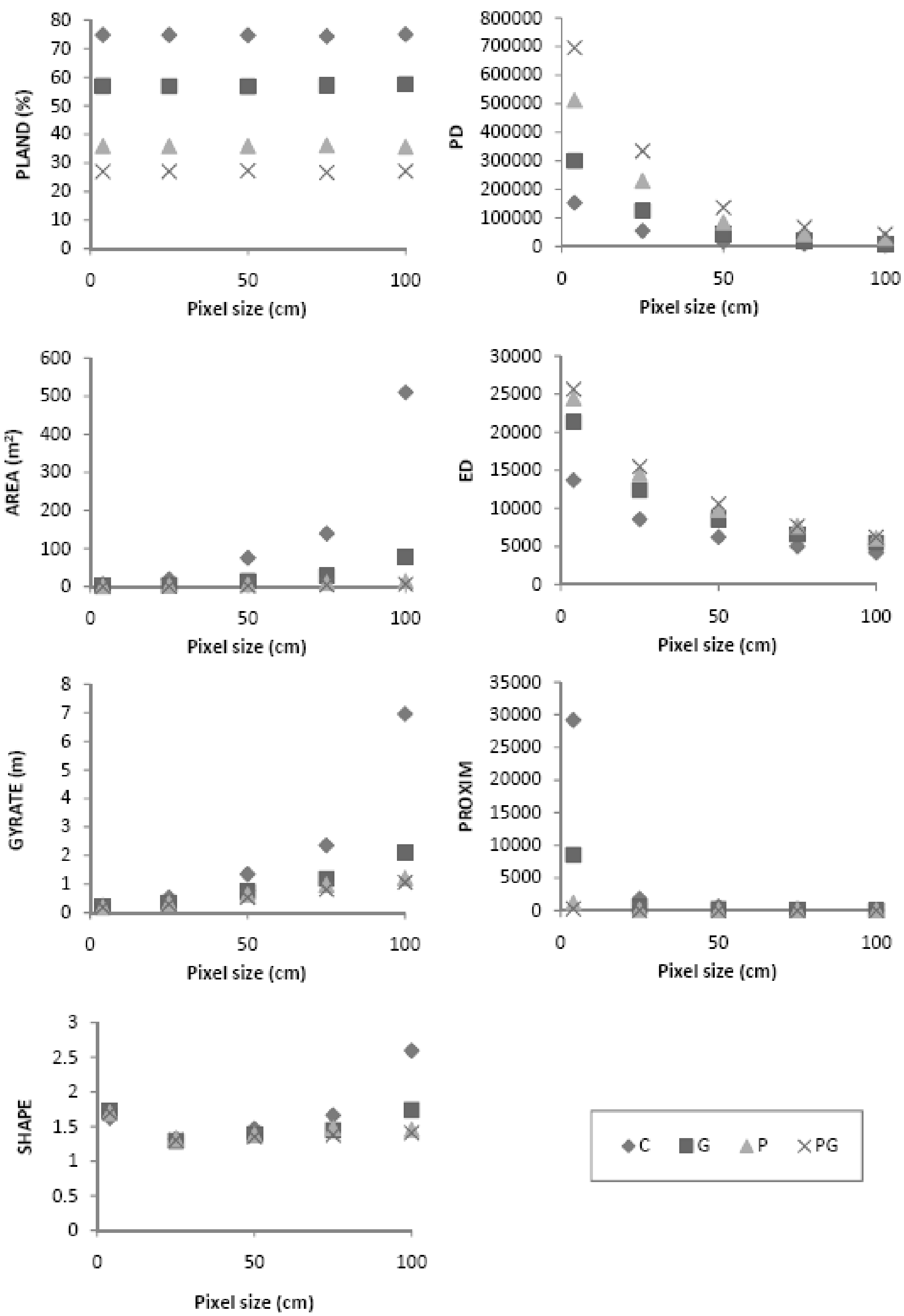

Figure 19. The effect of changing scale on the average values of the landscape metrics of the four treatments: C – Control, G – Goat grazing, P – shrub clearing, PG – clearing with Grazing.

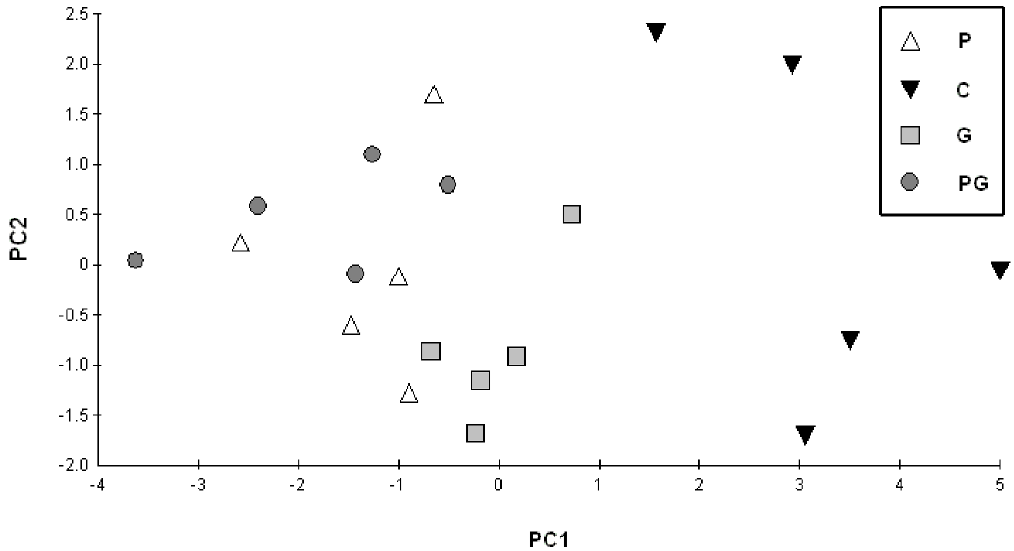

Figure 20. The first two principal components of the multi-metric data in the four treatments at the finest scale.

Discussion

Impact of disturbances on vegetation structure

Landscape metrics that are commonly applied to describe large-scale vegetation structure were successfully employed for the analysis of fine scale fragmentation resulting from small-scale disturbances.

At the finest scale of analysis, the first four parameters of the seven examined metrics revealed significantly the effect of grazing. This is not surprising, since goat grazing alters the shape of the woody patch mainly by browsing on its edges (leaves and twigs), which are accessible to the animal. Moreover, goats climb on the trees/shrubs with their front legs and break branches. As a result, woody patch area decreases while edge area increases. This tendency explains also the decrease in proportion of landscape. Patch density was higher in the grazing treatment, but not significantly. Increase in the number of patches following grazing is expected, since grazing can divide large woody patches into smaller sub-patches, but rarely eliminates entire patches. In our study, however, this trend is not significant. The decrease in patch area has lead to a decrease in the mean proximity index (corresponding to increased fragmentation between patches). The non-significant change in mean radius of gyration is probably a consequence of the grazer's inability to penetrate the patch core, thus the majority of feeding occurs at the edges – leading to an increased edge density while the changes in the mean radius of gyration are minor. In contrast to the expectations, mean shape index was not altered significantly by grazing, although patch perimeter increased and patch area decreased.

The effects of scale

The scaling laws for five of the metrics in this study were compared to previously reported laws for the same metrics (Wu 2004, Wu et al. 2002). Three of the metrics (mean shape index, mean patch area, and proportion of landscape) were consistent between the studies, but two other (patch density and edge density) were inconsistent. Here, the scaling relations for edge density and patch density were logarithmic and exponential, respectively, while in Wu (2002) the relations were power law, although that he reported that an exponential relation was almost as good as the power law. Differences in scaling relations between studies might be a result of the small number of scales used in this study (five), compared to the 24 scales used by Wu (2004). Here, relations were selected according to the coefficient of determination (R^2), which is dependant on the number of observations, and is possibly inflated by logarithmic transformations of the data used for fitting the linear regression line (Saura 2004). Consequently, differences between the coefficients of determination of different functions were rather small, with an average difference over all treatments of 0.037 for patch density and 0.083 for edge density. Another possibility is that scaling relations may vary over large range of scales (Garci'a-Gigorro and Saura 2005) and are consistent only for a small range of scales (Saura and Castro 2007). This might explain the differences in scaling relations, since the finest scale studied by Wu (2004), is much coarser than the coarsest scale of the present study.

The sensitivity of the different metrics to changing scales was probably overestimated since re-scaling via aggregation yields different results than using data sets from different sensors (Benson and MacKenzie 1995, Saura 2004). This is important, since statistically there were not many differences in the ability of the landscape metrics to distinguish between different disturbances at the pixel size range of 4-75 cm (edge density was the sole metric where a 4 cm resolution was superior to all coarser resolutions for distinguishing between control and grazing plots).

Therefore, using small pixel sizes for capturing subtle differences in vegetation structure through landscape metrics may be superior to using larger pixel sizes.

Mapping considerations

The performance of the landscape metrics was generally satisfactory. However, a major limitation of using conventional landscape metrics for quantification of fine scale fragmentation is the lack of a vertical dimension. Fine scale fragmentation often involves reduction of vegetation height (clear-cutting, grazing of medium-low woody species), which cannot be captured by the existing landscape metrics. Vegetation height has an important role, since it affects light availability to neighboring vegetation patches and understorey vegetation, and also contributes to the ability of the plant to withstand grazing by preventing access to its core. Mapping the vertical dimension of vegetation is harder than the horizontal dimension, due to technical limitations of automated height measurements, and the complicated crown structure (Ogunjemiyo et al. 2005).

Low altitude aerial photography may serve as an effective tool for the study of vegetation structure at small spatial scales. The high spatial resolution achieved by static low altitude platforms such as balloons enables the mapping of woody vegetation in precise details, which in the case of this study, reveals the fine scale fragmentation resulting from management. The method is especially appropriate for studies of fine scale fragmentation and small-scale vegetation structure. A practical benefit of this approach is the low cost of a balloon-based survey, compared to an airplane-based survey. On the other hand, the method is impractical for coarse-scale studies, due to the large number of photos needed on order to cover larger areas.

Grazing and clear-cutting affect the spatial pattern of vegetation (Sal et al. 1999, Palmer et al. 2004, Adler and Hall 2005, Henkin et al. 2007a). I am not aware of any attempts to analyze and quantify these impacts at small scales. Typifying small scale impact of disturbance as fine scale fragmentation enables us to apply metrics usually used for quantifying large-scale fragmentation. The results reported hereby suggest that common landscape metrics used for measuring large-scale landscape-heterogeneity can also capture small-scale changes in landscape resulting from local disturbance or proactive management.

Grazing and clear-cutting may consist important tools in management for conservation because of their influence on habitat structure and biodiversity (Collins et al. 1998), changing physical and biological conditions (Dzwonko and Loster 1998, Woodcock et al. 2005) and increasing environmental heterogeneity at different spatial scales (Mcnaughton 1983, Sal et al. 1999). In order to use grazing and clear-cutting as management tools, it is necessary to study the ways they affect landscape patterns. Using small-scale landscape metrics to quantify the effects of such management on the landscape at fine scales offers a powerful means towards this end.

Synthesis

The Eastern Mediterranean region has been subjected to intensive human land use in the past 10000 years, possibly much more (Rundel 1998, Naveh 1973). The major forms of land use have been agro-pastoral activities such as grazing, either by goats or by cattle, fire, and clear cutting. The long term application of these disturbances on landscape structure created and maintained vegetation mosaics, which are highly heterogeneous landscapes, consisting of a mixture of different vegetation formations intermixed across the landscape. Land use changes in the past century resulted in land abandonment and the cessation of many agro-pastoral activities in many places around the Mediterranean basin (Alados 2004). As a result, heterogeneous landscapes have been gradually transformed (at a decadal rate) into more homogeneous landscapes, consisting of dense shrublands and woodlands. From the ecological point of view, this has some undesired consequences, such as a sharp decrease of biodiversity of many groups, a decrease of scenic diversity, and an increase of fire risk. In order to conserve landscape heterogeneity, land managers often apply disturbance based management, which uses the same types of disturbances that have been predominant in the region in the past (Perevolotsky 1998). However, Mediterranean ecosystems evolved under disturbance, and species have complex defense and regeneration mechanisms to cope with various disturbances. As a result, the long term interactions between disturbance and vegetation dynamics are not fully understood. This knowledge gap has motivated the search for alternative approaches and additional tools that will increase the understanding of these interactions, and was the driving force behind this research.

In this research, the complex interactions between disturbance based management and the woody vegetation in Mediterranean regions was studied in three ways: modeling, mapping, and field experiments. The models developed in this study and in a previous research (Koniak and Noy-Meir, in review) are preliminary steps in the research of the interactions between management and long term vegetation dynamics in Mediterranean landscapes, both spatially and temporally. The majority of vegetation models that have been widely used for studying vegetation dynamics were developed for boreal forests in the Northern United States (Botkin 1993, Bugmann 2001). As such, their characteristics (e.g. basic modeling entity or grain size, disturbances accounted for and ability to generate high spatial heterogeneity) make them ill-suited for application in the highly-heterogeneous Mediterranean type ecosystems. Therefore, a hybrid modeling approach, combining several modeling techniques was developed here, to custom tailor the model to the complex array of characteristics that define the disturbance versus vegetation dynamics problem studied here. The importance of this model relies on the fact that it succeeded in reconstructing spatial and temporal dynamics of Mediterranean vegetation (compared to empirically derived data) in a manner that suggests that it can be used for studying the complex interactions between disturbance and vegetation dynamics. Such models are powerful tools towards 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 achieving this goal.

Both research and management planning require extensive knowledge regarding the spatial characteristics (structure, composition, and configuration) of the woody vegetation, since it has a strong impact on other components of the landscape (Shachak et al. 2008). This can be acquired by means of remote sensing techniques. Here, two approaches for achieving this objective were developed, based on data fusion of standard aerial photography and LiDAR to describe fine scale structure, and using low altitude balloon photography to describe very fine scale structure. The former was incorporated into the study in order to supply the starting conditions of the model for the simulations that attempt to predict the future vegetation dynamics. The latter was used indirectly, as an ancillary data source that enhances the understanding of the spatial patter of vegetation under disturbance. The results of the application of these methods on a landscape in Northern Israel portray clearly the characteristics of this complex system, and furthermore the interactions of its structure with external disturbances.

A combination of three research approaches has been used here in order to attempt and enhance our understanding of the complex interactions between disturbances and landscape structure in the long temporal scale and the small to intermediate spatial scale. The three approaches (mapping, field experiments, and predictive modeling) are intermixed and required to better tackle the challenges that were raised by the research question (Figure 21). The fine scale study of vegetation structure in experimental plots produced valuable ancillary data and understanding about the impact of disturbances on the small scale, and aided the qualitative validation of some of the model results. Knowledge obtained from the fine scale mapping was incorporated into the development of large scale mapping approach, in terms of which grain size should be used, and the importance of inclusion of vegetation height as a valuable descriptor of vegetation structure (since its lacking hindered the fine scale mapping). The large scale map, in turn, was used to produce the PFT map that was the spatial basis for model simulations on an actual landscape.

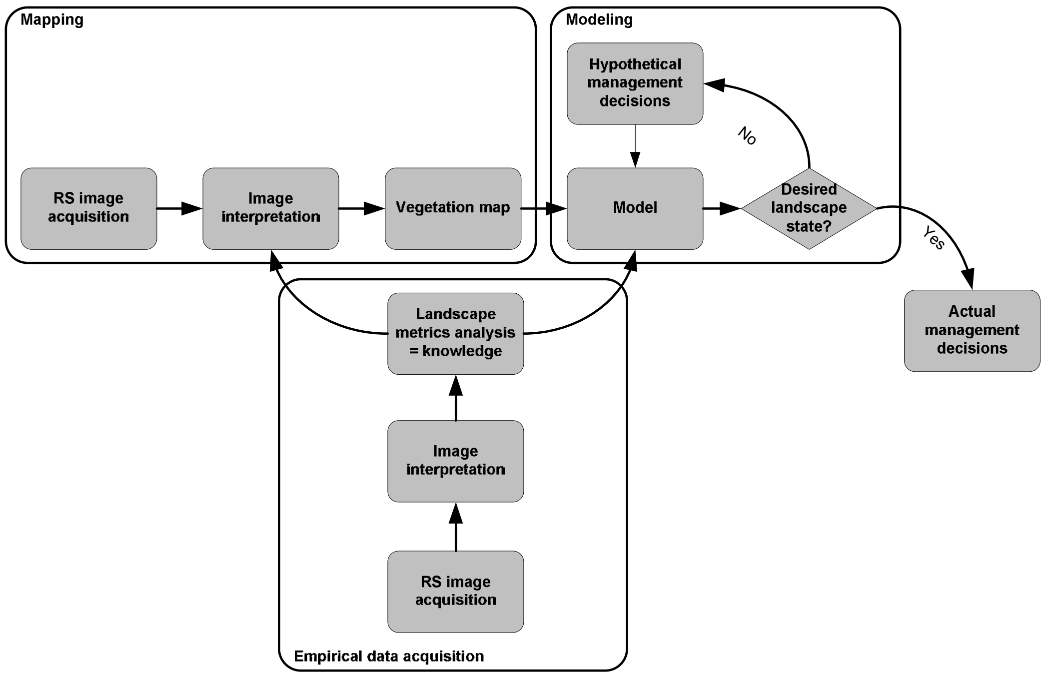

Figure 21. The three components of the research, their interactions, and their corresponding sub-processes.

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מיפוי ומידול הדינאמיקה של צומח ים תיכוני

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לשם מילוי חלקי של הדרישות לקבלת התואר דוקטור לפילוסופיה

אבי בר מסדה

הוגש לסנט הטכניון – מכון טכנולוגי לישראל

סיון תשס"ח   חיפה   יוני 2008

המחקר נעשה בהנחיית פרופסור יוחאי כרמל בפקולטה להנדסה

אזרחית וסביבתית

אני מודה לטכניון על התמיכה הכספית הנדיבה בהשתלמותי

תקציר

אזור מזרח אגן הים התיכון הושפע על ידי פעילות אנושית אינטנסיבית במהלך 10000 השנה האחרונות לפחות. השפעה זו כללה שימושי קרקע מסורתיים כגון רעייה על ידי בקר ועזים, כריתת צומח מעוצה ושריפות. לאורך השנים, התוצר המצטבר של הפרעות האלה על מבנה הנוף היה יצירת פסיפסי צומח, אשר הם טיפוסי נוף מגוונים ביותר, המורכבים מאוסף של טיפוסי צומח שונים המפוזרים במרחב בסקאלות מרובות. המגוון הנופי של פסיפסי הצומח מכיל מגוון בתי גידול התומכים בעושר ומגוון מינים גדול של קבוצות שונות של אורגניזמים.

במהלך העשורים האחרונים חלו שינויים בשימושי קרקע באזורים רבים סביב אגן הים התיכון, הכוללים בעיקר נטישת אדמות מרעה והפסקת פעולות חקלאות מסורתית. כתוצאה מכך, הצומח המעוצה החל להתפשט באין מפריע ונופים מגוונים של פסיפסי צומח החלו להפוך בהדרגה לנופים אחידים יותר, הכוללים בעיקר צורות צומח גבוהות וצפופות כגון גריגה וחורש. הירידה במגוון הנופי בשל תהליך זה מביאה לירידה במגוון המינים של קבוצות רבות בשל היעלמות הכתמים העשבוניים הפתוחים מהנוף ולעליה בסכנה של התפשטות שריפות בשל היווצרות שכבת דלק רציפה על פני השטח.

מנהלי שטחים פתוחים המעוניינים לשמר את ההטרוגניות של הנוף יכולים לעשות זאת על ידי הפעלת ממשק הפרעות. ממשק הפרעות מתבסס על הפעלת אותן פעולות ההפרעה המסורתיות אשר יצרו ושימרו את פסיפס הצומח הים תיכוני בעבר. מרעה עזים ובקר הן שיטות ההפרעה הנפוצות ביותר בשל התועלת הכלכלית שבהן. כריתה ודילול של צומח מעוצה שכיחות פחות בשל העלות הגבוהה, ושימוש בשריפות מבוקרות כממשק הפרעה אינו מתבצע בישראל, אך מקובל בארצות אחרות.

הבעיה העקרונית בשימוש בממשק הפרעות לצורך שימור המגוון הנופי היא הקושי לחזות את ההשלכות שלו בזמן ובמרחב. רוב מיני הצומח המעוצה באזור עברו אבולוציה תחת הפרעות, ופיתחו מגוון של מנגנוני הגנה והתחדשות להפרעה. התחדשות לאחר הפרעה יכולה להתבצע על ידי צימוח חוטרים או גידול מחודש מתוך צוואר השורש תוך הסתמכות על מאגרי חומרים מזינים מבית השורשים. דרך נוספת היא הפצת זרעים מסיבית לאחר ההפרעה, אשר מעודדת נביטה של פרטים חדשים כתחליף לצמח האם.

לפיכך, השפעת הפרעות על הצומח המעוצה היא זמנית בלבד, והתוצר המרחבי של ההפרעות הוא במקרים רבים עלייה במגוון הנופי כתלות במקום, זמן, סוג ועוצמת ההפרעה. מנהלי שטחים פתוחים המעוניינים לאמוד את ההשלכות של פעולות הממשק שלהם על הנוף הצמחי בטווח הארוך ובמרחב חסרים כיום ידע וכלים, בשל פער ידע מדעי בנוגע לתהליכים אלה.

פתרון מעשי לפער הידע הקיים הוא שימוש במודלים אקולוגים של שינוי צומח. מודלים אלה מאפשרים לאמוד או לחזות את מאפייני הנוף הצמחי בעתיד כתלות בתהליכים שונים, ובתקופות זמן שונות, וכוללים במקרים רבים גם את התרחשותן של הפרעות. רוב המודלים הללו פותחו עבור מערכות של יערות ממוזגים, אשר שונים מאוד בתכונותיהם מהמערכת המורכבת של הצומח הים תיכוני. למשל, הסקאלה המפורטת ביותר של השונות המרחבית בין טיפוסי צומח שונים ביער הממוזג גדולה במספר סדרי גודל מזו המאפיינת צומח ים תיכוני. לכן, שימוש במודלים הקיימים אינו אפשרי עבור צומח ים תיכוני, ונדרש לפתח סוג חדש של מודלים אשר יתאים בצורה טובה יותר לתכונות הייחודיות של המערכת הזו.

מטרת עבודה זו היא לחקור מספר היבטים של הקשר בין ממשק הפרעות לבין הדינאמיקה של הצומח המעוצה בזמן ובמרחב. המטרה המרכזית היא פיתוח ובחינה של מודל אקולוגי דינאמי אשר מנסה חזות את ההשפעה של ממשק הפרעות על השתנות של חמישה טיפוסי צומח בזמן ובמרחב. מטרה נוספת היא פיתוח של שיטה למיפוי צומח ים תיכוני, אשר מספקת את תנאי ההתחלה של המודל. המטרה השלישית היא כימות אמפירי של ההשפעה של שתי הפרעות – רעיית עזים וכריתה על הדפוס המרחבי של הצומח המעוצה בקנה מידה מרחבי מפורט.

המודל שפתוח כאן הוא מודל סטוכאסטי, היירארכי ומרחבי מפורט החוזה את ההשתנות בזמן ובמרחב של חמישה טיפוסי צומח נפוצים במערכות ים תיכוניות (צומח עשבוני, בני שיח, שיחים נמוכים, שיחים גבוהים ועצים נמוכים) תחת ממשק הפרעות. המודל הוא היברידי, כלומר בנוי ממספר שיטות מידול צומח שונות המשולבות יחדיו על מנת להתאים בצורה המיטבית את המודל למורכבות המערכת הים תיכונית. המרחב מתואר בו כמטריצה של תאים בשלוש רמות היירארכיות מקוננות: [1] כתם (patch), המייצג שטח של מ"ר ונתון לשליטה של טיפוס צומח יחיד; [2] אתר (site), המורכב ממאה כתמים (ריבוע של 100 מ"ר) החשופים להיסטוריית הפרעות אחידה; [3] נוף (landscape), המכיל אתרים רבים בעלי היסטוריית הפרעות מגוונת. ההשתנות של טיפוסי הצומח בזמן ובמרחב מבוססת על תהליך סטוכאסטי של

מצבים ומעברים (state and transition), בו טיפוסי הצומח בכתם משתנים עם הזמן כפונקציה של הסתברויות מעבר. הסתברויות אלה תלויות במאפייני הכתם, סביבתו והתרחשות אירועי הפרעה.

המודל הופעל על שתי מערכות: [1] וירטואלית אקראית; [2] אמיתית, המבוססת על מפת צומח של פארק הטבע רמת הנדיב (אשר הופקה בשלב השני של המחקר). בכל מערכת נבחנו ההשפעות של מספר פעולות ממשק על השפע היחסי של טיפוסי הצומח השונים, על פיזורם המרחבי, ועל ההטרוגניות הכוללת של המרחב.

מתוך הרצות המודל עולה כי לממשק ההפרעות יש השפעה רבה על כל מאפייני המערכת שנבדקו, כך שלסוג ועוצמת ההפרעה הספציפית, ביחד עם שילוב של הפרעות שונות בזמן ובמרחב יש יכולת ליצור מרחבים שונים לחלוטין. באופן יותר פרטני, המודל חוזה כי ללא כל הפרעה, שטחים פתוחים יחסית (בעלי כיסוי מעוצה נמוך) הופכים תוך מספר עשורים לשטחים בשליטת המינים המעוצים הגבוהים, בעוד שהכתמים הפתוחים כמעט ונעלמים. רעיית עיזים הופכת את השטח לבתת בני שיח ושומרת על כיסוי עשבוני נמוך עד בינוני, בעוד שרוב המעוצים מדוכאים. לרעיית בקר יש השפעה פחותה על רוב המעוצים מלבד העצים מאחר ופרות מעדיפות לצרוך בעיקר את המרכיב העשבוני של הנוף. שריפות פותחות את השטח ומביאות אותו לשליטה עשבונית, אולם לפרק זמן מוגבל אם אין הפרעה נוספת מאחר והצומח המעוצה מתחדש ומחלף בהדרגה את הצומח העשבוני. מבחינת ההטרוגניות הכוללת ברמת הנוף של רמת הנדיב, נמצא כי רעיית עזים אינטנסיבית משמרת את המגוון הנופי כאשר היא מופעלת בכלל המרחב, בעוד שמרעה בקר, המשך ממשק ההפרעות הנוכחי (המבוסס ברובו על בקר) או אף אי הפרעה גורמים לעלייה במגוון הנופי. שריפה אחידה בכל השטח מורידה את המגוון הנופי ברמות שונות, כתלות בקיומן של הפרעות נוספות באותה התקופה.

בחלק השני של העבודה פותחה שיטה למיפוי רציף של הנוף הצמחי. שיטה זו מבוססת על תיאור המרחב בסקאלה רציפה של גובה ממוצע וכיסוי צומח. היתרון המרכזי של גישה זו הוא שהיא אובייקטיבית כמעט לחלוטין, מאחר ואינה דורשת כל הנחה מוקדמת לגבי זהות \ מאפייני האובייקטים הקיימים במרחב. את המפה הרציפה אפשר לסווג לאחר מכן לקטגוריות תמאטיות לפי הצורך. במקרה זה, היא סווגה למפת טיפוסי צומח הכוללת את חמשת טיפוסי הצומח עליהם פועל המודל. עדיפותה של מפת הצומח הרציפה על מפת צומח סטנדרטית (תמאטית) של איזור המחקר נבחנה סטטיסטית והוכחה.

בחלק השלישי של העבודה נבדקה השפעת שתי צורות הפרעה נפוצות (רעיית עזים וכריתה) על הדפוס המרחבי המפורט של הצומח המעוצה. במחקר זו בוצע מיפוי של הצומח המעוצה בחלקות ניסוי שטח ברמת הנדיב, הכולל 20 חלקות של דונם. כל חלקה נתונה לאחת מארבע הפרעות: [1] רעיית עזים אינטנסיבית; [2] כריתה; [3] כריתה ורעייה; [4] ביקורת. מפת צומח ברזולוציה מרחבית גבוהה מאוד (4 ס"מ לפיקסל) הופקה על ידי סיווג ממוחשב של צילומי אוויר בגובה נמוך של החלקות, אשר צולמו מתוך בלון הליום שריחף מעל פני השטח. המבנה המרחבי של הצומח כומת על ידי חישוב מדדי הנוף של כל חלקה, ולאחר מכן נערך ניתוח סטטיסטי של מדדי הנוף בטיפולים השונים. נמצא כי במקרים רבים, לטיפולים השונים יש השפעה מובהקת על מבנה הצומח בחלקות כפי שהוא מתבטא על ידי מדדי הנוף. השפעת סקאלת הניתוח (גודל הפיקסל של מפת הצומח) על התוצאה נבחנה גם כן, ונמצא כי מדדי הנוף (ויכולתם לזהות את השפעות ההפרעות באופן מובהק) תלויים בסקאלה בה הם מחושבים.

מכלול התוצאות שהתקבלו במחקר זה ממחיש את המורכבות הרבה של יחסי הגומלין בין הפרעות מסורתיות לבין השתנות הצומח בזמן ובמרחב. לממשק הפרעות אכן ישנה יכולת לעצב את המרחב ולהשפיע על מידת ההטרוגניות של הנוף הצמחי, וזאת בסקאלות מרובות, החל מהרמה המפורטת (עשרות סנטימטרים רבועים) ועד לרמת הנוף (אלפי דונמים). להפרעות שונות ולשילובים שונים של הפרעות בזמן ובמרחב יש השפעה רבה על מראה הנוף בעתיד, בסדר גודל של עשרות שנים. תכנון ממשק הפרעות מיטבי הוא משימה מורכבת, המחייבת הבנה מעמיקה של ההשלכות של פעולות הממשק על הנוף הצמחי. מחקר זה סיפק תוצאות ראשוניות לגבי מורכבות התהליכים, ופותח דרך למחקרים נוספים אשר יוכלו לנצל את המודל שפותח כאן על מנת לבחון שאלות אלה ואחרות לפי הצורך.