

Research article

Comparing landscape scale vegetation dynamics following recent disturbance in climatically similar sites in California and the Mediterranean basin

Yohay Carmel^{1,*} and Curtis H. Flather²

¹*Faculty of Civil and Environmental Engineering, The Technion – Israel Institute of Technology, Haifa 32000 Israel;* ²*USDA Forest Service, Rocky Mountain Research Station, Fort Collins, CO, USA;* *Author for correspondence (e-mail: yohay@tx.technion.ac.il)

Received 15 June 2003; accepted in revised form 11 November 2003

Key words: California, Convergent evolution, Disturbance history, Israel, Landscape dynamics, Mediterranean-type ecosystems, Vegetation change

Abstract

A long line of inquiry on the notion of ecological convergence has compared ecosystem structure and function between areas that are evolutionarily unrelated but under the same climate regime. Much of this literature has focused on quantifying the degree to which animal morphology or plant physiognomy is alike between disjunct areas. An important property of ecosystems is their behavior following disturbance. Yet, this aspect of ecosystems has not been investigated in a comparative study of convergence. If different ecosystems are under similar environmental controls, then one would predict that the rates and patterns of response to disturbance would also be similar. The objective of this study is to compare landscape dynamics following disturbance using spatiotemporal models to quantify vegetation change in Mediterranean ecosystems found in California and Israel. We model the process of tree and shrub regeneration at the landscape scale in two similar study sites in Israel (Mount Meron) and California (Hasting Nature Reserve). During the periods studied (1964–1992 for Israel and 1971–1995 for California), average annual change in tree cover was 5 times larger in Israel than in California. Based on multiple regression models, differences were found in the relative importance of specific variables predicting vegetation change. In Hastings (California), initial tree cover accounted for most of the explained variability in 1995 tree cover (partial $R^2 = 0.71$), while in Meron (Israel), grazing type and intensity, topography indices, and initial vegetation each accounted for about a third of the explained variability. These findings support the notion that traits such as regeneration pattern and rate, both at the individual level and at the landscape level, were largely affected by the human land use history of the region.

Introduction

Ecological convergence is commonly defined as the expression of similar ecosystem characteristics between areas that are evolutionarily unrelated but whose biota have been subject to similar environmental controls (Cody and Mooney 1978). Evidence bearing on the legitimacy of convergence is typically sought through intercontinental comparisons of eco-

system structure and function among areas with similar climates. Much of this literature has focused on quantifying the commonality in animal morphology (Cody 1973; Karr and James 1975; Pianka 1986; Losos et al. 1998) or plant physiognomy (Kummerow 1973; Naveh and Whittaker 1979; Martinez and Fuentes 1993; Cowling et al. 1996) among species inhabiting these geographically disjunct areas. There also is a growing literature that examines the ques-

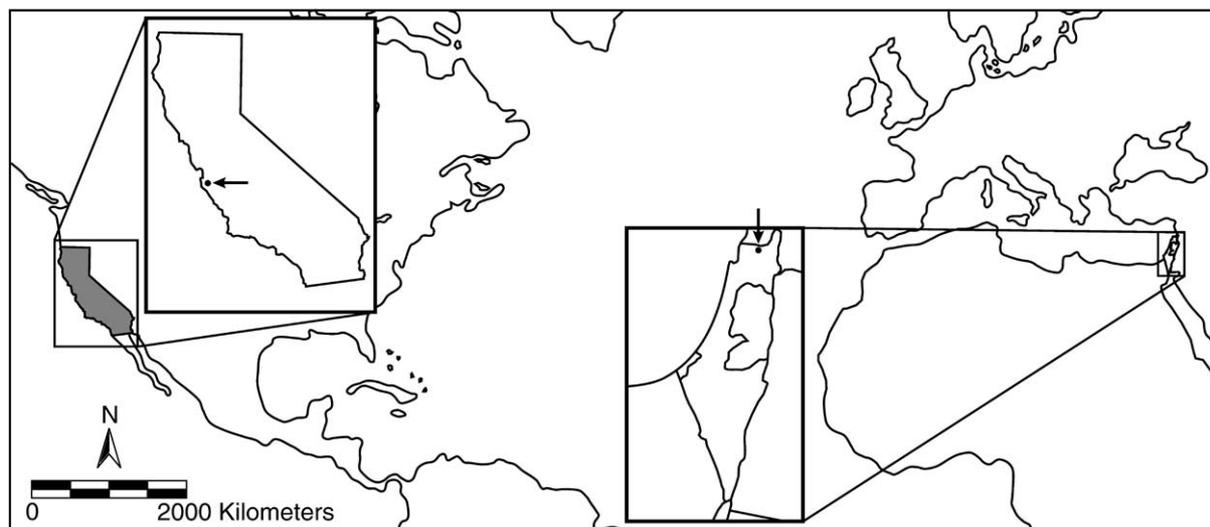


Figure 1. Locations of the study areas in California and Israel. Arrows pointing to Mount Meron Nature Reserve, Israel, and Hastings Nature Reserve, California, respectively.

tion of convergence functionally by comparing soil-vegetation relationships (Zinke 1973), successional trajectories (Armesto et al. 1995), and aboveground net primary productivity (Paruelo et al. 1998).

The recurrent focus on convergence in the ecological literature is related to a number of factors. If convergence exists it implies a certain degree of determinism in evolutionary pathways and community assembly (Pianka 1975; Tilman 1989). From an applied perspective, convergence suggests that data from well-studied ecosystems could provide the necessary information or models to evaluate large-scale ecosystem properties for similar, data-poor ecosystems (Paruelo et al. 1998). In either case, convergence is one concept under which ecologists seek to derive general principles that govern the structure and function of ecosystems.

An important property of ecosystems is their resilience (*sensu* Likens 1992) – that is, their behavior following disturbance. For example, vegetation changes on agricultural landscapes following farm abandonment can show characteristic rates and spatial pattern within different ecosystems (Glenn-Lewin and van der Maarel 1992). This aspect of ecosystem behavior has not been assessed quantitatively within the framework of a comparative study of convergence. If different ecosystems are in fact under similar environmental controls, then one would predict that the rates and patterns of response to disturbance would also be similar. The objective of the present study is to compare the landscape dynamics, using

spatiotemporal models, of vegetation change after disturbance (agricultural practices, fire, and grazing) occurring in similar Mediterranean ecosystems in California and Israel (Figure 1). A criticism of past paired-ecosystem studies is that the degree of environmental similarity between study sites is not quantified directly but based on classifications of ecological attributes that broadly lump geographic areas (Schluter 1986; Wiens 1991). To overcome this criticism we purposefully selected a pair of sites that attempted to maximize inter-site similarity across a set of predefined environmental variables. By doing so, we hope to control for the environmental heterogeneity that exists within broadly classified climatic zones that are often used as the basis for selecting sites for comparative studies of convergence.

Part A: Site selection

Methods

Because a detailed quantitative study of vegetation dynamics had already been completed for a site in Israel (Carmel and Kadmon 1999; Carmel et al. 2001*b*), we used the environmental characteristics of that site as the target to match with a site in California. Our primary quantitative criterion was climate similarity, since climate is known to be the major determinant of vegetation at regional and global scales (Prentice 1990) and is considered the major factor driving con-

vergence in Mediterranean-type ecosystems (Di Castri and Mooney 1973). However, we also considered vegetation composition and structure, physiography, land use and disturbance history, and land ownership in making the final site selection in California.

Phase I: Combining climate, vegetation, and physiography to identify candidate sites.

Mediterranean climates are characterized by a bi-seasonality in temperature and precipitation – cool wet winters with low solar irradiance and hot dry summers with high solar irradiance (Hobbs et al. 1995). A climate hythergraph for Mount Meron generated from data collected in Meron Field Center meteorological station during the 1964-1993 period (Mount Meron Field Center, unpublished data) served as the target pattern to match in selecting our California site. Mean monthly temperature and precipitation surfaces were generated for California using the PRISM software (Daly et al. 1994). PRISM uses point measurements of climate data and a digital elevation model to spatially interpolate estimates of mean monthly temperature and precipitation at a 10 km resolution. State-wide monthly temperature and precipitation surfaces for California were used to generate hythergraphs to compare with the Mount Meron climatic data. A monthly matching score between each 10 km grid and Mount Meron was calculated as the absolute difference in monthly means between California and Israel. We then constructed maps of the overall precipitation and temperature match by summing the matching scores over all monthly estimates and normalizing the scores to vary between 0 (poor match) and 100.

In order to select candidate sites, we used the California Ecological Units classification (Miles and Goudey 1997), and land ownership, land use and vegetation types data (Davis et al. 1998) together with the results of the climatic match, to mark areas that satisfied the following criteria: 1) Matched Mount Meron's climatic patterns. 2) Mediterranean-type vegetation (oak woodland and chaparral) was present. 3) Public land ownership or research reserves were present (to ensure site access). 4) Matched Mount Meron's topography (mountains or hills, moderate to steep slopes).

Phase II: final site selection.

Final site selection was based on field visits and interviews with local biologists. For each potential site we (1) documented its current vegetation structure and its history in past decades, and (2) inspected availability of historic air photos. In addition to the criteria specified in Phase I, we also evaluated sites according to the following criteria: 1) Resembled Mount Meron's vegetation structure (oak forest, various stand densities, existing shrub, dwarf-shrub and herbaceous layers, where all these formations often intermingle to form a complicated mosaic at a very fine scale). Ranking the sites for this criterion was based on our own perception, and was entirely subjective. 2) Vegetation formations that are not found in the Meron site, such as conifers, were absent. 3) Matched Mount Meron's disturbance history (cessation or significant reduction of cultivation practices and grazing intensity half a century ago).

This phase culminated in a Table of scores assigned to each of the sites for each criterion, and the site that scored highest was chosen.

Results

Maps comparing mean monthly precipitation and temperature patterns from California with Mount Meron were very different (Figure 2). Mount Meron precipitation pattern (wet winter and dry summer) corresponds well to the Mediterranean vegetation region of California, particularly along the coastal range and the Sierra Foothills. In contrast, areas of best match with Meron temperature pattern are on agricultural lands in the Central Valley. Given these results, we searched the entire Mediterranean region of California, to select several candidate sites that satisfied our Phase II criteria. We ended up with eight candidate sites. These sites are marked in Figure 2, and listed in Table 1.

The matching scores for the eight candidate California sites revealed two sites (South Cow Mountain near Hopland and Hastings Nature Reserve) that compared relatively well with Mount Meron across most criteria (Table 1). The South Cow Mountain site scores better than Hastings Nature Reserve in matching vegetation structure, and slightly less than Hastings in resembling Meron climatic patterns. However, Hastings was the only site that had a site history similar to Mount Meron (i.e., subject to agricultural

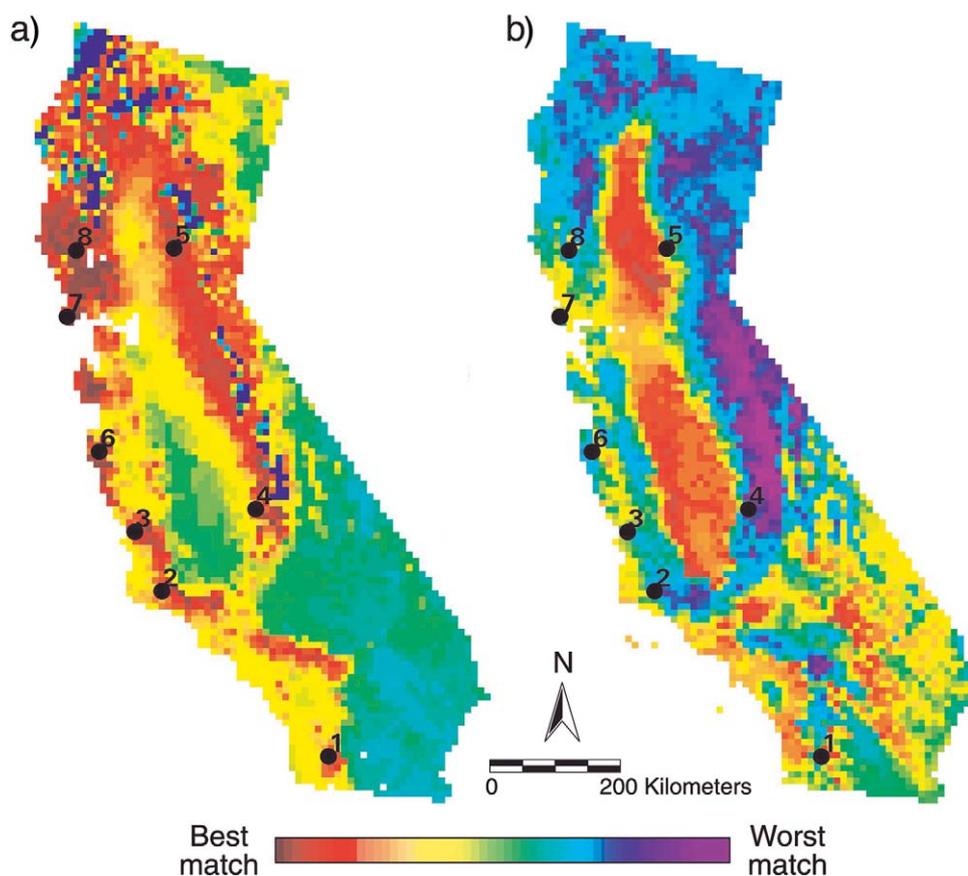


Figure 2. Climatic match between Meron and California on a monthly basis (see text for details). Californian climatic data are based on PRISM data (Daly et al 1994). (a) Match in precipitation. (b) Match in temperature.

practices and livestock grazing during the first half of the 20th century, after which these practices ceased). We thus selected Hastings Nature Reserve as the study area for a detailed vegetation dynamics study. The sizes of study sites were 394 hectares and 588 hectares, for Meron and Hastings respectively.

A more detailed environmental comparison of the Hastings Nature Reserve and Mount Meron sites further supports their selection for a comparative study of convergence in vegetation dynamics. Both sites share a similar geographic position (< 50 km east of the sea/ocean), topographic structure (both sites occur within a distinct mountain ridge that is hilly with moderate slopes), and vegetation formations (a mosaic of herbaceous vegetation, shrubs, and woodlands, with tree species composition being dominated by a mixture of evergreen and deciduous oaks). In addition, both sites share a similar 'disturbance history', with respect to cultivation, grazing and fire (Figure 3). Cultivation and livestock grazing ceased

in Hastings in 1937, following establishment of the nature reserve (Davis 1967; Griffin 1988). Domestic grazing continued in the areas surrounding the reserve at moderate levels. Deer grazing in the reserve continued through the entire period (M. Stromberg, personal communication). In Meron, until 1948 large parts of the study area were cultivated fields (Markus 1994), and since 1948 cultivation was restricted to few areas within the study area (Figure 3b), and those parts were excluded from the analysis (Carmel and Kadmon 1999). Grazing in Mount Meron study area decreased gradually since 1948, and moderate to low levels of grazing (either cattle or goats) dominated most of the study area (Figure 3b).

In Meron, one large fire burned almost a quarter of the study area. Other fire events had a very small spatial extent. Similarly, in Hastings, 25% of the area was burned in two fire events, one in the woodland and one in the chaparral, while other fire events were small.

Table 1. Site scores (and ranks) for matching Meron conditions. Precipitation and temperature patterns: the scores are the cumulative monthly differences between Meron and each site (see text for details). Scores are normalized to 0 (worst match) through 100. General similarity with Meron's vegetation structure (oak forest, various stand densities, existing shrub, dwarf-shrub and herbaceous layers, where all these formations often intermingle to form a complicated mosaic at a very fine scale). Ranking the sites for this criterion is based on our own perception, is entirely subjective and non-quantitative. Scores are in the range of 0 (least match) to 5. Presence of Meron vegetation formations, namely evergreen and deciduous sclerophyllous trees, evergreen shrubs, dwarf shrubs and herbaceous vegetation. Scores are the # of different formations in the site, and are in the range of 0-4. Absence of vegetation formations not present in Meron, such as large conifer stands. Scores are either 1 (no such vegetation formations) or 0. Site history, with the goal of matching Meron's disturbance regime (cessation or significant reduction of agricultural practices and grazing intensity half a century ago). Scores are either 0 (no match) or 1. The cumulative ranking is the simple sum of rank scores across criteria.

#	Site	Location	Precipitation match	Temperature match	General similarity with Meron vegetation structure	Presence of Meron vegetation formations	Absence of vegetation formations not present in Meron	Site history	Cumulative ranking
1	Cuyacama Mountains	East of San Diego	86 (2)	66 (2)	3 (4.5)	3 (6.5)	0 (3)	0 (4)	22
2	Santa Ynez Mountains	North of Santa Barbara	83 (1)	73 (4)	3 (4.5)	3 (6.5)	0 (3)	0 (4)	23
3	Los Padres National Forest	North of San Luis Obispo	85 (3)	77 (5.5)	2 (2)	2 (2.5)	0 (3)	0 (4)	20
4	Sequoia National Forest	East of Porterville	87 (4)	34 (1)	2 (2)	2 (2.5)	0 (3)	0 (4)	16.5
5	Sierra Foothills Research Center	East of Marisville	92 (5)	87 (8)	2 (2)	2 (2.5)	1 (7)	0 (4)	28.5
6	Hastings Reserve	Carmel Valley	97 (7.5)	77 (5.5)	4 (6.5)	3 (6.5)	1 (7)	1(8)	41
7	Mt Tamalpais	North of San Francisco	95 (6)	83 (7)	4 (6.5)	2 (2.5)	0 (3)	0 (4)	29
8	South Cow Mountain	East of Hopland	97 (7.5)	67 (3)	5 (8)	3 (6.5)	1 (7)	0 (4)	36

The major difference between these two sites is the soil type. Meron soils are Terra Rosa derived from hard limestone and dolomites, and small patches of marl (Rabinovitch-Vin 1983). Hastings soils are sandy loam and clay loam, derived from Mesozoic granitics and sedimentary rocks (Griffin 1988). This mismatch occurs generally state-wide, and California's granite and metamorphic bedrock are not a good match to the limestone and dolomites prevailing in the eastern Mediterranean (Naveh 1967).

Discussion

Studies of convergent evolution often implicitly assume that ecosystem characteristics are unaffected by within-region heterogeneity. This heterogeneity may result from local environmental determinants (soil, topography etc.), or from local history. When whole ecosystems are compared, within-region variability may mask similarities between regions. It is typically not feasible to study multiple sites in each region, and thus the choice of sites for between-regions comparison becomes crucial. Yet, the issue of choosing the best matching sites is seldom dealt with

in studies of convergence and may explain, in part, why after decades of comparative research, the literature still equivocates widely on whether convergence has any basis in ecological reality (see Shmida 1981; Barbour and Minnich 1990). In this study we constructed a quantitative protocol for matching a site for ecological comparison, when many factors are to be considered. Matching the climate of a particular site was our first priority, assuming that climate is the primary abiotic determinant of convergence in terrestrial ecosystems (Cody and Mooney 1978). In the present case, several sites across California were found to match the monthly precipitation and temperature pattern of the site in Israel fairly well. A second set of criteria that accounted for physical factors (e.g., topography), ecological considerations (vegetation composition, recent history of disturbance) and practical matters (land ownership, air photo availability), were used to rank the climatically-defined candidates. When the candidate sites were evaluated against all criteria, a clear ranking emerged, and the best match was selected.

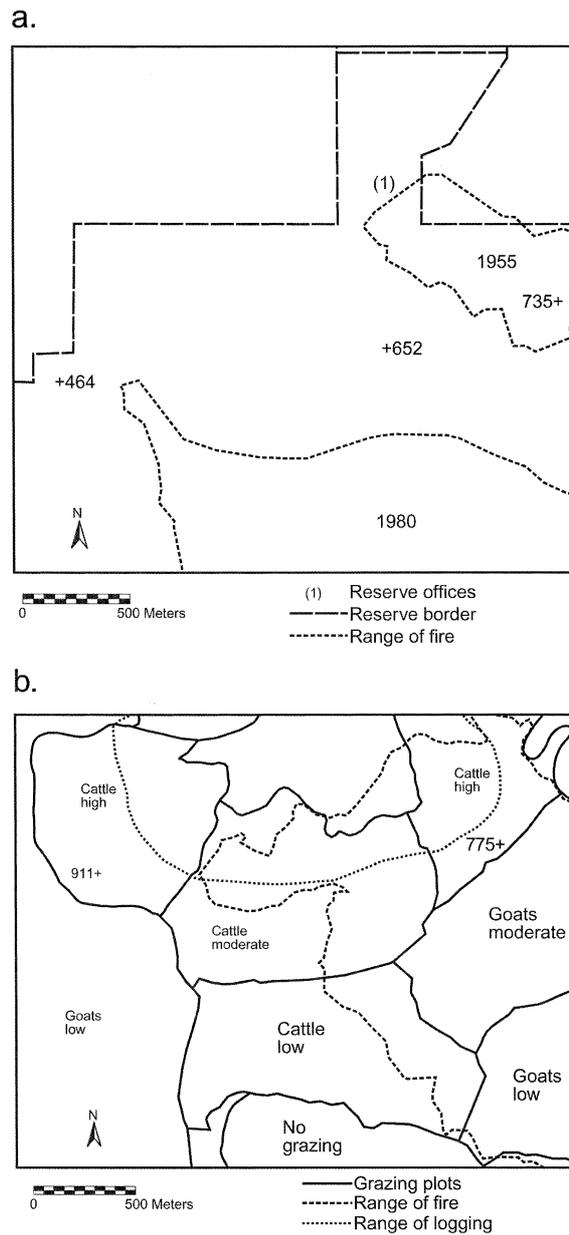


Figure 3. The study sites. (a) Hastings study area, showing the ranges of major fires since 1920, with year of event. The central area delimited by the broken lines is the nature reserve area. (b) Meron study area, showing ranges of fire (right side of line), grazing type and intensity, and logging. Selected elevation points are marked by + signs.

Part B: Landscape scale vegetation changes

Methods

Database construction

Vegetation changes

A temporal set of historical air photos for the California site were located by searching the University of California libraries, private companies, and the National Archives. A set of five air photos (for the years 1939, 1949, 1956, 1971 and 1995) formed the raw spectral database from which vegetation dynamics in California were to be quantified. The methods used to classify the California vegetation follow the procedure used for Mount Meron (Carmel and Kadmon 1998), and are described in detail elsewhere (Carmel et al. 2001a). The photos were scanned, ortho-rectified, and geo-referenced to a planimetric coordinate system. Spatial resolution (pixel size) in all photomaps was set to 0.6 m. The classification method was a hybrid supervised / unsupervised classification, followed by a spatial filter. The classification scheme distinguished three vegetation classes: oak woodland, chaparral, and grassland as in Griffin (1988). Location error (RMSE) was 2.42 and 2.51 m for the 1971, and 1995 photomaps, respectively. Classification accuracy (PCC, proportion of classified correctly pixels) was 0.94, and 0.91, respectively. The cumulative effects of classification error and especially location error may largely affect the accuracy of the dataset as a whole (Carmel et al. 2001a). To reduce uncertainty, we reduced the spatial resolution of the classified image from 0.6 m to 15 m. Percent cover of each vegetation type in each 15×15 m grid cell was calculated based on the vegetation maps with the 0.6 m resolution. All other digital maps in the database were re-scaled to the same resolution. The average annual rate of change was calculated as $[(\text{cover in } t_2 - \text{cover in } t_1) / (t_2 - t_1)]$, where t_1 is the beginning year of the time period and t_2 is the ending year of the time period.

Environmental factors

The major disturbance factors in both ecosystems are thought to be cultivation, grazing, logging, and fire (Griffin 1988; Naveh 1994). All of these factors were documented for both study areas, and maps of their intensities were produced. Logging was not considered in this study. In Mt. Meron a single logging event occurred in a small part of the area, that was excluded

from the analysis (Carmel and Kadmon 1999), while in Hastings Reserve no logging occurred since the establishment of the reserve in 1937 (Griffin 1988).

In Meron three distinct grazing regimes were identified (Carmel and Kadmon 1999), high, moderate and low, corresponding to 340, 110, and 30 cattle grazing days per ha per year, CGD/HY (Noy-Meir et al. 1989). Livestock grazing was excluded from Hastings Reserve shortly after its establishment in 1937, although it did continue in areas neighboring the reserve. Typical cattle density during the first half of the 20th century was 90 to 120 CGD/HY (Lindsay 1943). During the second half of the century, grazing intensity around the reserve decreased, and was estimated to be ~60 CGD/HY (M. Stromberg, personal communication). Based on these historical data, we classified the Hastings Reserve area into the 'no grazing' category, and assigned the surrounding area into the 'moderate' class. Wild ungulate grazing in Mount Meron (by gazelles, *Gazella gazella*) is very uncommon (Markus 1994). In contrast, deer (*Odocoileus hemionus*) are common both in and outside the Hastings Reserve (Davis 1967; Griffin 1988). Wild pigs (*Sus scrofa*), that were found to affect acorn and seedling survival in California (Sweitzer and Van Vuren 2002), are quite common on both study sites. We found no data that would permit inclusion of wild ungulate grazing in our analysis.

Fire records were available for the last 80 years for Hastings Reserve (Griffin 1988) and for the last 60 years for Meron (Markus 1994). All fires in the two sites were documented using air photos for Mount Meron, and maps in Griffin (1988) for Hastings. Fire ranges were delimited and digitized. Each fire event was coded as an independent binary variable, with '1' for burnt areas and '0' for non burnt areas.

A digital elevation model (DEM) was produced in the photo-rectification process for both study areas at a spatial resolution of 0.6 m. This DEM was used to derive digital maps of elevation, slope, and aspect for the study area. Aspect is represented by angular data ($0^\circ - 360^\circ$), and it was decomposed to north-south and east-west linear components.

Statistical analysis

A multiple regression approach was used to model vegetation dynamics, where cell-specific vegetation cover was predicted from information on its past vegetation condition, topographic variables, and disturbance characteristic. The statistical models were

estimated only for the two most recent time periods: 1971-1995 for Hastings and 1964-1992 for Meron.

The digital maps were translated to a database in which each record corresponded to a grid cell in the study area. Preliminary investigations of the spatial structure of the data revealed that spatial autocorrelation diminished with distance; for distances of 6 cells (90 m) the autocorrelation values in the residuals of a preliminary model were below 0.05. We therefore employed a systematic sampling scheme and selected every sixth cell in both row and column directions (Legendre and Legendre 1998). This resulted in a sample size of ~ 3% of the data ($n = 718$).

The dependent variables were 1995 cell-specific percentage cover of woodland, and 1995 cell-specific percentage cover of chaparral. Both variables were arcsin-square-root transformed to stabilize the error variance. Candidate predictor variables for the regression models were classified into three groups: historic vegetation conditions (i.e., vegetation types in 1971), topographic variables, and disturbance characteristics (grazing and fire). Vegetation change in a specific cell may be affected by vegetation characteristics in that cell's neighborhood (Frelich et al. 1998). Therefore, indices for initial vegetation in adjacent cells (i.e., first-order neighbors) were also included in the model. Dummy variables were created to represent the disturbance categorical data; for example, the variable FIRE1980 accepted value of 1 for cells inside the range of the 1980 fire event and 0 for all other cells. Because environmental variables may be related to vegetation non-linearly, we also included the square of each variable as candidate regressors into the model (Carmel and Kadmon 1999). All possible combinations of first-order interactions between the candidate variables were also tested for inclusion in the final model.

Model selection was accomplished using a stepwise variable selection procedure. Model fit was evaluated using R^2 . Partial R^2 was calculated (Legendre and Legendre 1998) to assess the roll of each predictor or group of predictors in explaining variation in woodland or chaparral cover. Plots of the studentized residuals against predictions and against predictors confirmed compliance with model assumptions. The error independence assumption was inspected by mapping the distribution of residuals in the study area.

Results

The major change that took place at Hastings during the study period was the growth of trees (Figure 4a-b). This change was smaller than its equivalent in the Israeli site by an order of magnitude (Figure 4c-d). Table 2 describes the change in vegetation formations composition during the respective periods. Herbaceous vegetation / grassland in both sites decreased, reflecting the increase in woodland. Both Californian chaparral and Mediterranean shrubs changed very little during the studied periods. In both sites, the rate of change was not homogenous across the area. In Meron, increase in tree cover was concentrated in the south-central part of the area, whereas change in Hastings did not have any clear spatial pattern (Figure 5).

The rate of vegetation change is dependant on various environmental factors. Controlling for similarity in topographic conditions, protection from cattle grazing, and initial vegetation cover, a trend of a three- to twelve-fold difference between the two ecosystems in the average annual rate of change, was observed for most groups (Figure 6). In particular, for similar initial vegetation cover, the rate of change in tree cover in Meron was consistently higher than in California.

The annual rate of change in woodland at Hastings was affected strongly by initial woodland cover in a non-linear fashion (Figure 7a). The equivalent results for Meron (Figure 7b) show a similar hump-shaped curve. Such a shape is to be expected: when initial tree cover is low, tree growth is also low. As tree cover approaches 100%, there is little space left for further increase. Thus, maximum increase in tree cover is expected for intermediate values of initial tree cover. The Y axis in Figure 7 exemplifies the difference in the rate of change between the two systems: in Meron the change varies over 0.1 to 0.55 while in Hastings it varies from 0.00 to 0.08.

In Hastings, both 1971 woodland cover and 1995 woodland cover were positively correlated with slope angle, and with the north-south component of the aspect (Table 3). In contrast, in Mount Meron, initial vegetation is not correlated with topographic indices, while current vegetation is strongly correlated with topography (Table 4). Protection from cattle grazing did not seem to affect vegetation change at Hastings, in strong contrast to its effects in Israel (Table 3, Table 4). Neighborhood effects (indices for initial vegeta-

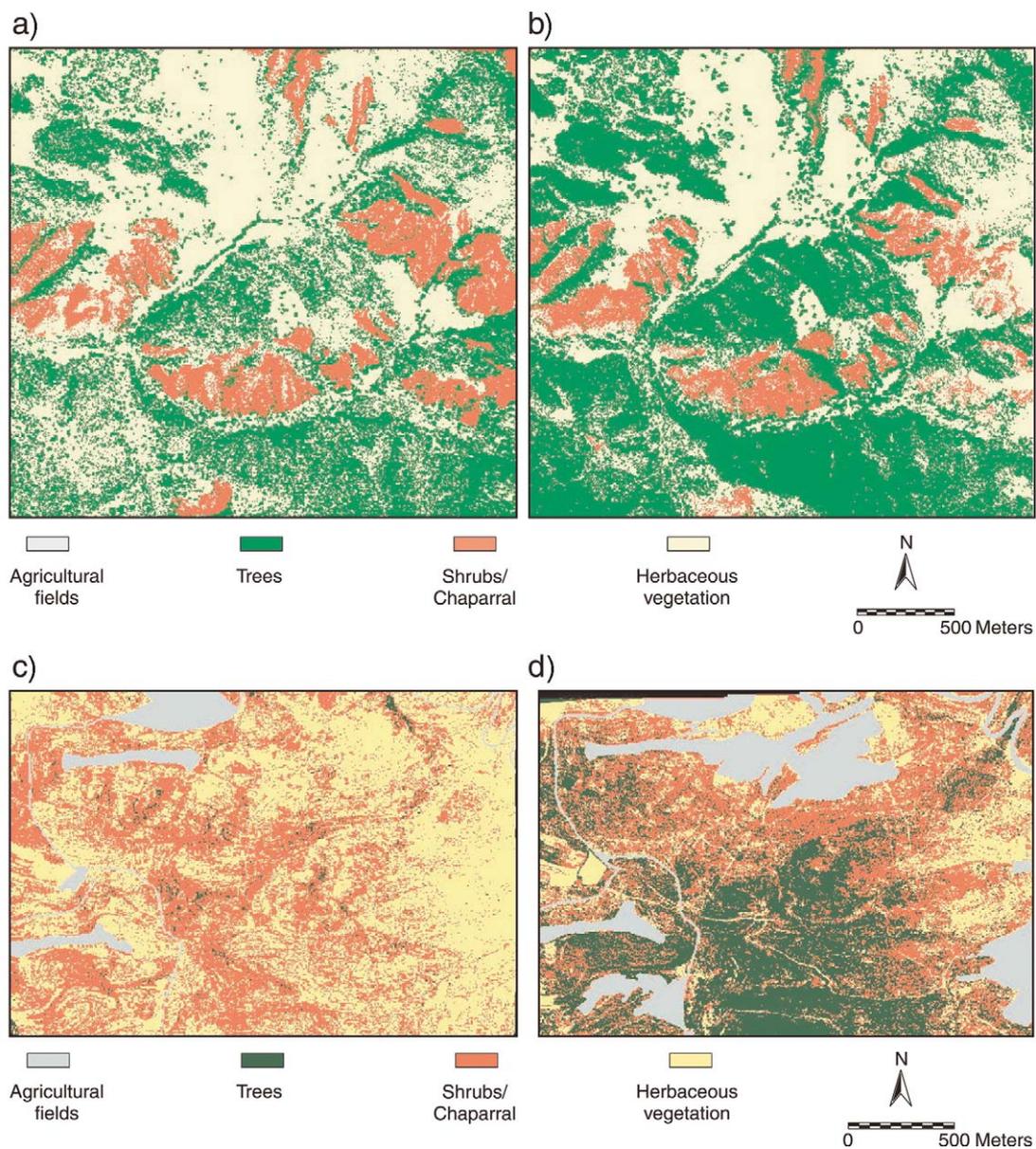


Figure 4. Vegetation maps of Hastings Nature Reserve in (a) 1971 and (b) 1995, and Mount Meron in (c) 1964 and (d) 1992.

Table 2. Proportional composition of vegetation formations during the studied periods.

	Meron		Hastings	
	1964	1992	1971	1995
Trees / woodland	0.02	0.41	0.46	0.51
Shrubs / Chaparral	0.42	0.35	0.12	0.11
Herbaceous vegetation / grassland	0.56	0.24	0.42	0.38

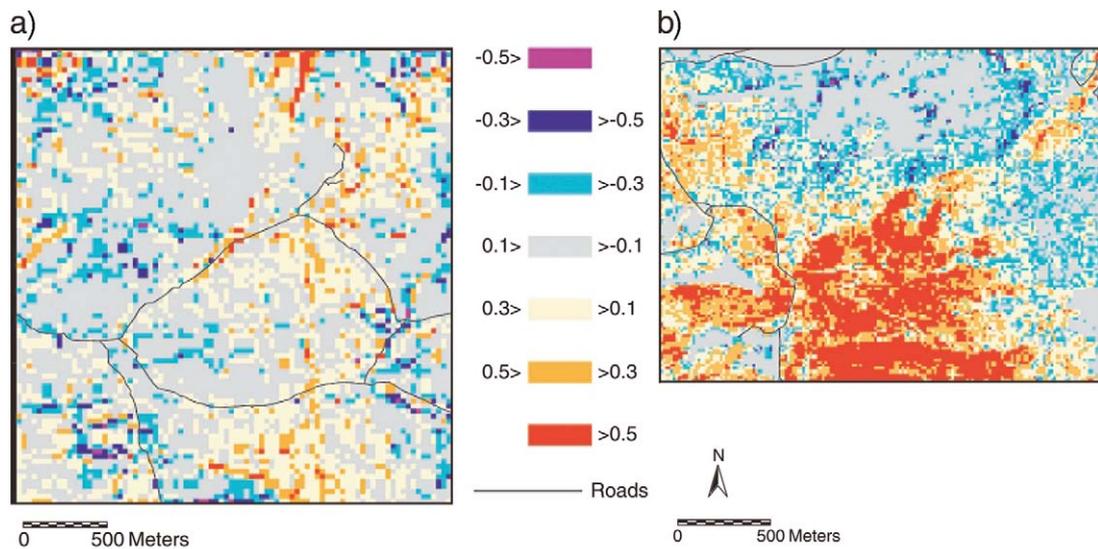


Figure 5. Change in tree cover for (a) Hastings (1971 to 1995) and (b) Meron (1964 to 1992). Change is calculated as $[TREES_{t_2} - TREES_{t_1}]$ where TREES is the cell-specific proportion cover of trees; t_1 and t_2 are the former and latter time steps, respectively. Cell size in both images is 30 m. Main roads are given for orientation.

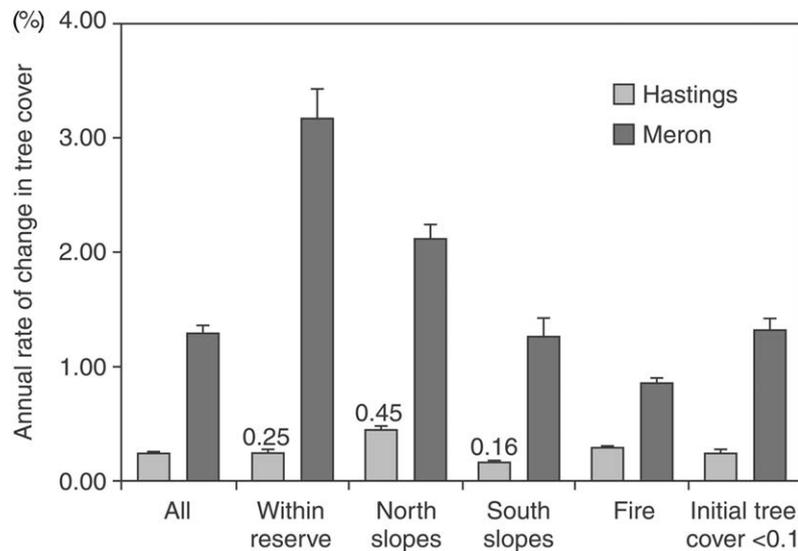


Figure 6. Annual rate of change in tree cover in Hastings and Meron, under various conditions. The bars indicate ± 1 standard error.

tion cover in neighboring cells) were found insignificant in both study sites.

A single fire event occurred in 1980 in the southern part of the Hastings Reserve (Griffin 1988), burning dense oak woodland. The effects of that fire on 1995 vegetation at Hastings were insignificant. The trees recovered completely, and woodland cover in 1995 is higher than in 1971 in the burnt area. Although we did not use pre-1971 data to model veg-

etation dynamics, vegetation composition in our historical air photos indicate that chaparral recovery after a 1955 chaparral fire was slower than forest recovery, and was still incomplete in 1995 (Figure 8). The 1978 fire in Mount Meron encompassed about a quarter of the study area, burning grassland, shrubland and forest. Similar to California, vegetation recovery was swift, and the effects of fire on 1992 vegetation were minor (Carmel and Kadmon 1999).

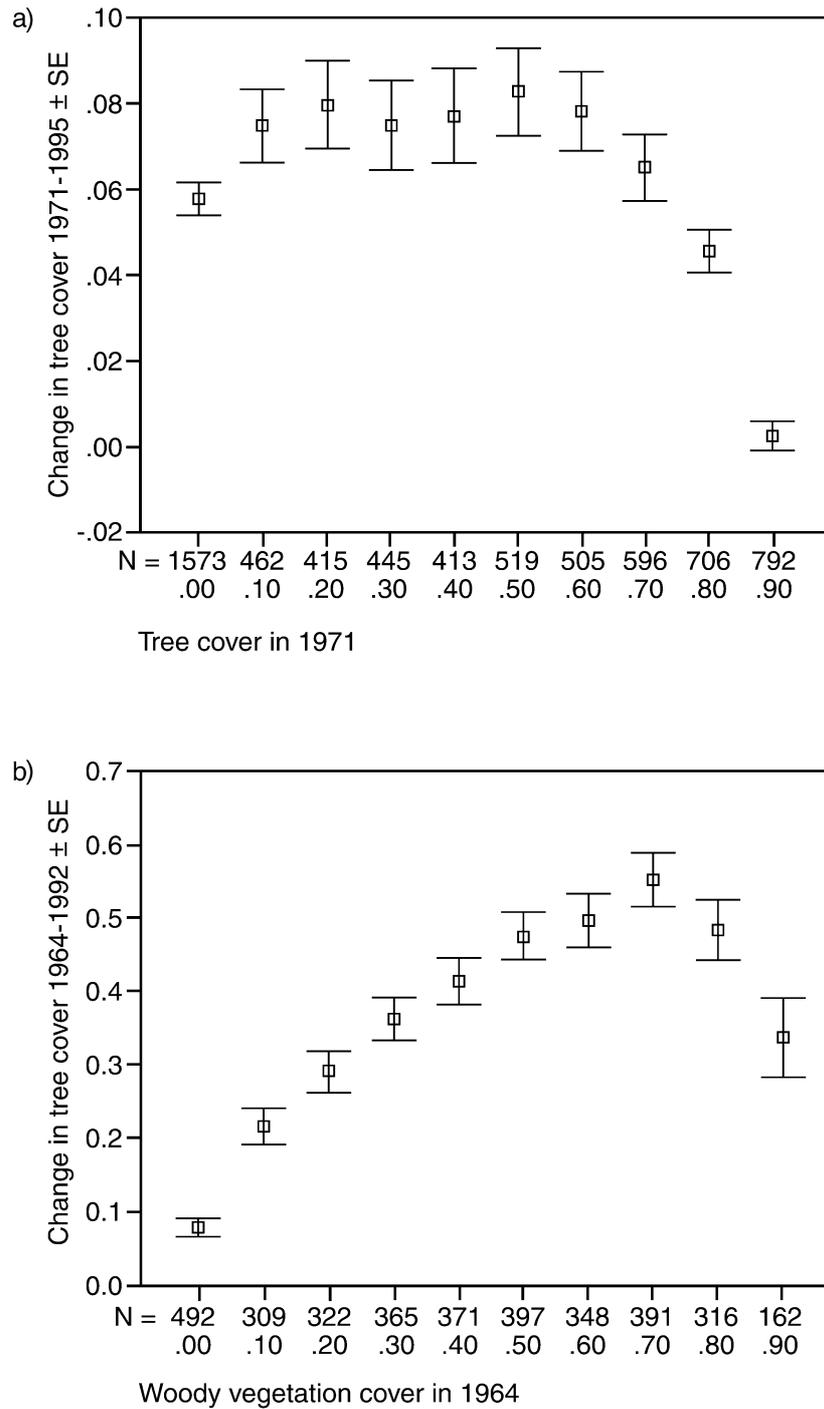


Figure 7. Change in tree cover as a function of initial vegetation cover, for (a) Hastings and (b) Meron. Bars indicate ± 1 standard error.

When all predictors were entered into a multiple regression, similar proportions of explained variability in tree cover were found in both study sites (Table 3, Table 4, Figure 9). However, obvious differences

were found between the sites, regarding the contributions of specific predictors and groups of predictors. Woodland cover in 1971 accounted for most of the total explained variability in 1995 woodland cover in

Table 3. Regression models predicting recent woodland and chaparral cover changes (1971 to 1995) for Hastings Nature Reserve, California. Significance level for each predictor is indicated by * for $p < 0.05$, ** for $p < 0.01$, *** for $p < 0.001$, and NS for $p > 0.05$.

Estimated Parameters	Dependent Variable	
	1995 proportion cover of woodland in cell	1995 proportion cover of chaparral in cell
Constant	- 5.92E-02**	- 3.73E-03*
TREE71 (proportion cover of trees in cell in 1971)	0.910***	NS
CHAPA71 (proportion cover of chaparral in cell in 1971)	NS	1.22***
ASPECT-NS (north-south component of aspect angle, 0°-180° scale, N=0°, S=180°)	- 7.94E-04***	2.7E-03*
SLOPE (slope inclination)	1.63E-04*	NS
Adjusted Multiple R ²	0.79	0.85

Table 4. Regression models predicting recent tree and shrub cover changes (1964 to 1992) for Mount Meron, Israel. Significance level for each predictor is indicated by * for $p < 0.05$, ** for $p < 0.01$, *** for $p < 0.001$, and NS for $p > 0.05$.

Estimated Parameters	Dependent Variable	
	1995 proportion cover of trees in cell	1995 proportion cover of shrubs in cell
Constant	1.027	0.306***
HERB64 (proportion cover of herbaceous vegetation in cell in 1971)	- 0.423**	0.451*
HERB64 ² (the square term for HERB64)	- 0.310*	- 0.295*
ASPECT-NS (north-south component of aspect angle, 0°-180° scale, N=0°, S=180°)	- 1.426E-03***	- 3.0E-03*
ASPECT-EW (east-west component of aspect angle, 0°-180° scale, E=0°, W=180°)	3.146E-03***	- 8.26E-04*
SLOPE (slope inclination)	0.883*	- 0.625*
ASPECT-NS*SLOPE (the interaction term between slope and N-S component of aspect)	- 4.123E-03***	- 1.257E-03***
LOWCATTLE (1 for cells in areas with low cattle grazing regime, 0 for all other cells)	NS	- 0.131***
MODCATTLE (1 - moderate cattle grazing, 0 - other)	- 0.356***	0.141***
HIGHCATTLE (1 - high cattle grazing, 0 - other)	- 0.533***	0.221***
LOWGOAT (1 - low goat grazing, 0 - other)	- 0.296***	7.499E-02*
MODGOAT (1 - moderate goat grazing, 0 - other)	- 0.356***	NS
Adjusted Multiple R ²	0.72	0.32

Hastings, while topographic indices were strongly correlated with initial woodland cover (Figure 9a). In contrast, in Meron, topography was not correlated with 1964 tree cover, and had its own independent contribution to the total explained variability in tree cover. Disturbance in Meron affected tree cover largely and significantly. The major disturbance factor in Meron was grazing, accounting for 0.4 of the explained variability in tree cover (Figure 9a). In contrast, both fire and the grazing surrogate (reserve border) did not have any significant effects on woodland cover in Hastings. In both study sites, slope, aspect and an interaction term between them affected tree cover, while elevation was insignificant (Table 3, Table 4).

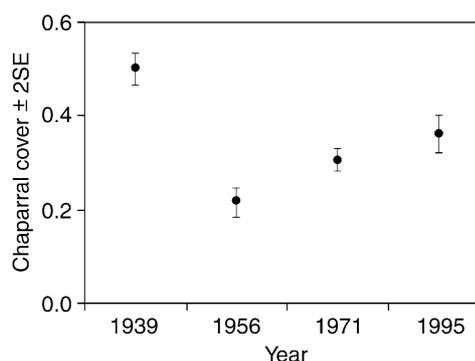


Figure 8. Chaparral cover in 1939, 1956, 1971, for the area burnt in 1955 chaparral fire. Bars indicate ± 2 standard errors.

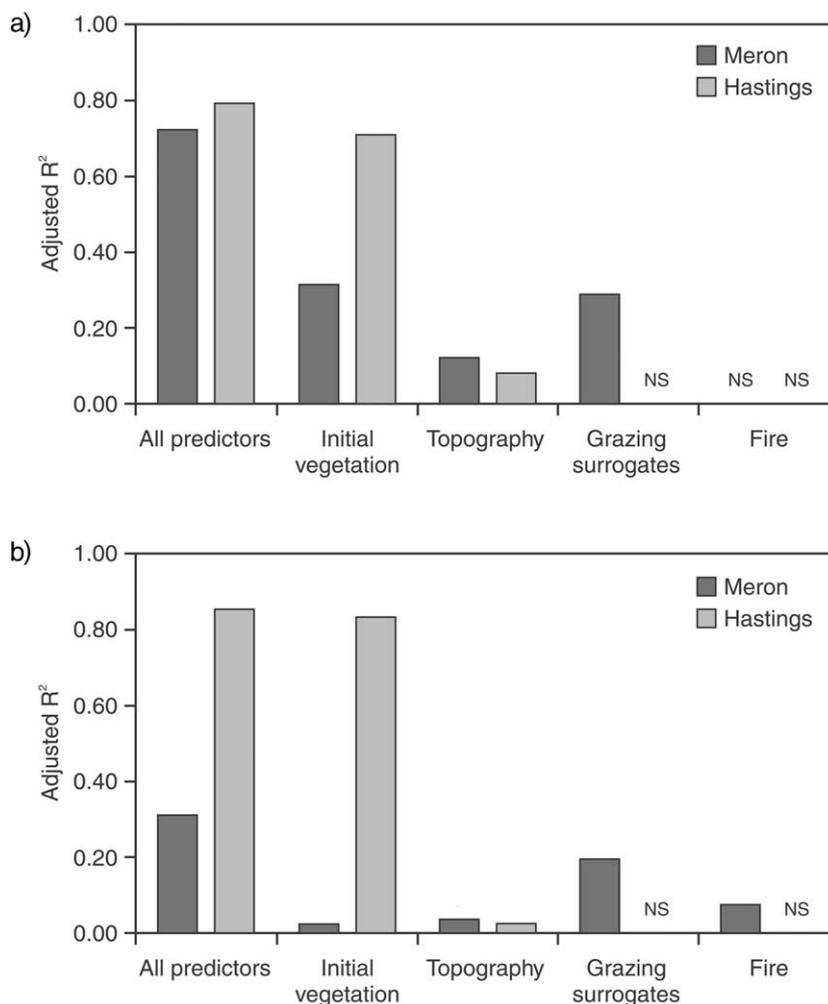


Figure 9. Factors affecting (a) tree cover and (b) shrub/chaparral cover in Meron (1992) and Hastings (1995). The left column represents the adjusted R² in the multiple regression, where values in the other columns represent the partial R² for the respective group of predictors.

When the same analysis was run for shrubs/chaparral, results for Hastings were similar to those for woodland, in which 1971 chaparral cover explained 0.86 of the total variability in 1995 chaparral cover, while effects of all other predictors were negligible (Table 4, Figure 9). For Meron, grazing surrogates were the most important predictors of 1992 shrub cover, while initial vegetation, topography, and fire all contributing significantly to the total explained variability (which was relatively low, only 0.31).

Discussion

Results of this study reveal a major difference in vegetation dynamics between the Californian and the Is-

raeli sites. Changes in Hastings were limited, and apparently consisted of growth of existing adult trees only. Changes in Meron were extensive. Even expanses of open areas became largely covered by woodland within three decades. Given that the two sites are similar in many ways, including vegetation structure and disturbance history, our original expectation was that vegetation dynamics in both systems would also be similar. What sort of explanations can be offered for such disparate dynamics in these two ecosystems? And to what degree do the differences in these two specific systems represent differences in vegetation dynamics between the Mediterranean basin and California? These two questions are not independent and will be treated here simultaneously.

The major vegetation formations in Israel and in California are generally similar (Naveh 1967), yet, at least one difference is notable: (1) In Meron, the 'shrubs' class was defined as a physiognomic group of woody vegetation > 2.5 m (following Tomaselli 1977). This class includes typical shrub species such as *Calicotome villosa* and *Cistus creticus*, but also low trees. In contrast, the chaparral formation in Hastings is a distinct physiognomic group, but it turned out that in most cases to represent also a particular community of species. One reason for this is the scarcity of low trees (= regenerating trees, saplings) in Hastings. In spite of similarity in vegetation formations, these two ecosystems had very different initial conditions at the landscape scale. At the beginning of the study period, almost half of the area of Hastings was covered by mature oak stands, while the entire area of Meron was covered by herbaceous vegetation and shrubs. Thus, the finding that overall increase in woodland cover in Hastings was much smaller than in Meron is partially explained by the fact that it had more woodland cover to begin with. Thus, it could be claimed that in Hastings the vegetation reached some sort of equilibrium with the environment, and that areas not covered by trees can not support trees. However, in Hastings there are several areas where the forest was cleared, and the land was cultivated for a few decades. These areas were abandoned in 1937, when the reserve was established (Lindsdale 1943), and were still devoid of woody vegetation 68 years later. In Meron, areas where agricultural practices ceased in 1948 were 80%-100% covered by trees in 1992. Also, our results show that even when controlling for similar initial vegetation cover, there is still a big difference in vegetation change between Meron and Hastings.

Another potential explanation that could partially account for the lower regeneration rates in California, relates to the nature of agricultural practices. In the early part of the 20th century, the Israeli system of small-plot pastoral cultivation in the Mount Meron region was possibly a less intensive form of disturbance than that which occurred in some parts of California. Pavlik et al. (1992) recount the use of machinery and explosives to harvest and clear oak woodlands for farmland. However, in the vicinity of Hastings, these practices were not used before the onset of the reserve (Lindsdale 1943, M. Stromberg, personal communication). Trees were cut using hand saws and stumps were left to rot, or were burnt. In Meron, the root system of trees at the edges of the

cultivated plots were often left untouched, and the tree could survive for decades assuming the formation of a small shrub. The same formations of shrubby oaks were also common in areas that were not cultivated, but heavily grazed. These oaks could regenerate rather rapidly when agricultural lands were abandoned or grazing was reduced. Thus, the regeneration in Meron was partly vegetative. However, the observed change in Meron oak cover can not be entirely attributed to vegetative regeneration. Trees became established in large fields, where back in 1945 no woody vegetation existed anywhere nearby (unpublished data). In conclusion, the landscape changes in Meron are a combination of regeneration from seeds and vegetative regeneration. In Hastings, there was practically no regeneration from seeds (White 1966; Griffin 1971), while expansion of woodland cover was limited to growth of adult trees, but not vegetative regeneration from stumps (M. Stromberg, personal communication).

A legitimate criticism of the current study is that it only compares two sites. It could be argued that the deviation in system dynamics we observed is attributable to some random effect. To address this concern we searched the literature for studies that quantified vegetation change in California and Mediterranean systems. Quantitative studies of vegetation change at the landscape scale, and across several decades are not common. The studies we found varied in their spatial and temporal scales, and reported results in ways that often differed from our study. Yet, for four studies from California and five studies from the Mediterranean Basin we were able to calculate a common system attribute – the average annual change in tree cover (as defined earlier). The studies of Mediterranean ecosystems that provide quantitative data on vegetation change at the landscape scale, indicate rates larger than those in California by a factor of 2 to 20 (Table 5). It appears that the deviation in vegetation dynamics between Hastings and Meron can not be attributed to some random effect – comparisons with the literature suggest that the pattern we observed may generally hold across sites in the Mediterranean Basin and California.

How can these disparate dynamics be interpreted in view of existing literature on convergence in Mediterranean-type ecosystems? Our results suggest that historical factors may have had a stronger effect in shaping contemporary vegetation dynamics than the abiotic controls. This explanation is consistent with the theory of historical contingency (Cadle and

Table 5. Average annual change in tree cover, calculated using data from different studies of vegetation dynamics in California and in the Mediterranean basin.

Region	Source	Site name	Precipitation	Study period (in years)	Average annual change in tree cover
California	Brooks and Merenlender 2001	Hopland area	900	28	0.11%
California	Scheidlinger and Zedler 1979	San Diego County		42	-0.05%
California	Callaway and Davis 1993	Gaviota State Park, non-grazed	600	42	0.43%
California	Callaway and Davis 1993	Gaviota State Park, grazed	600	42	0.20%
California	This study	Hastings Nature Reserve	600	56	0.25%
Mediterranean	Paraskevopoulos et al 1994	Mt. Pilon, Greece	475	30	2.03%
Mediterranean	Samocho et al 1980	Adulam, Israel	450	22	1.59%
Mediterranean	Samocho et al 1980	Bar Giora, Israel	550	22	0.92%
Mediterranean	Preiss et al 1997	Montpelier, France	1150	33	0.95%
Mediterranean	Kadmon and Harari-Kremer 1999	Mt. Carmel, Israel	700	32	1.06%
Mediterranean	Carmel and Kadmon 1999	Mt. Meron, Israel	900	28	1.3%

Greene 1993; Losos et al. 1998; Lawton 1999). Historical contingency predicts that unique past events (e.g., different land use histories), or the idiosyncrasies of environment that remain even in similar climates, have a large, and perhaps overriding, influence on ecosystem structure and function.

What might be some of the sources of these historical contingencies? The first explanation relates to the poor recruitment of Californian oaks. The lack of oak regeneration in many Mediterranean regions in California was noted early in the 20th century (Sudworth 1908) and has been a subject of much concern in ecological studies since the 1960's (White 1966; Griffin 1971). Possible hypothesized causes of these phenomena from the literature include the following:

1) Cattle grazing has increased the pressure on oak woodlands, and reduced recruitment (McClaran 1987; Phillips et al. 1996; Jansen et al. 1997; Standiford et al. 1997).

2) Deer and /or pocket gopher (*Thomomys* spp.) populations, and possibly other predator populations have increased as a result of general changes in Californian ecosystems, thus acorns and seedlings are more heavily preyed upon (McCreary 1989).

3) Combination of long-term ecosystem changes, such as fire suppression, tree clearing, and grazing during the last two centuries have affected ecosystem conditions (e.g., soil properties) in a way that they are less favorable for oak seedlings (McCreary 1989; Mensing 1992).

4) Soil moisture, the major factor that determines seedling survival, is heavily depleted by grasses. According to proponents of this hypothesis, annual

grasses, which largely displaced perennials in the last century, deplete soil moisture earlier and faster. Seedlings, therefore, face much harsher conditions than 200 years ago (Muick 1991; Momen et al. 1994).

It is generally agreed among Californian ecologists, that poor regeneration is caused by some combination of several factors that can vary from place to place. All these potential causes can be grouped under the title of 'local ecological conditions'. In the context of this comparative study, the slow change in vegetation in Hastings could be representative of larger regions in California, and is a direct result of these 'local ecological conditions'. Thus, it could be hypothesized that the potential for woodland regeneration in California is not much different than in the Mediterranean basin and the observed vegetation stability results from the specific ecological circumstances of California in the 20th century. According to this explanation, results of this study do not necessarily reject possible convergence in vegetation dynamics in Mediterranean-type ecosystems.

A longer term source of historical contingency is that disjunct Mediterranean-type ecosystems may have been subject to entirely different evolutionary histories. In the Mediterranean basin, the vegetation has evolved under heavy human exploitation, including grazing and harvesting during the entire Holocene (Di Castri and Mooney 1973; Naveh and Dan 1973; Naveh and Kutiel 1986; Seligman and Perevolotsky 1994). In contrast, Californian Mediterranean systems have only recently (< 200 years ago) come under anthropogenic pressures of a similar magnitude (Axelrod 1977; Mensing 1998).

In conclusion, the comparison of vegetation dynamics following disturbance between Mediterranean-type ecosystems in California and Israel reveals vast differences. Possibly, these differences are attributable to disparate historical contingencies, either in the short term (differences in recent land use histories, both site-specific and regional) or in the long term (possible differences in inherent regeneration capabilities that reflect adaptations to differing human impacts in the two regions that have occurred over several millennia).

Which of these sources of historical contingencies explains the discrepant pattern of vegetation change that we observed? This question can not be answered within the framework of an observational study. A controlled experiment, in which species from both regions are growing in the same controlled environment, under treatments that mimic various natural disturbances, may have better chances of yielding indications. Yet even then, untangling the causative pathways within the experimental design will be complicated by the many potential factors (and their interactions) that appear to be contributing to the geographic discrepancies in oak woodland response to disturbance. In an effort to address this question, we have recently initiated a mutual transplant experiment involving acorns from several Mediterranean and Californian species, in order to compare seedling growth rate and responses to various types of experimental disturbance. This study may help determine whether Mediterranean species are inherently capable of more vigorous regeneration than Californian species, in response to various disturbance types.

Acknowledgements

Mark Stromberg, Director of Hasting Nature Reserve, provided a wealth of information on the Hastings area. We would also like to thank Tom White (Cleveland National Forest), Mark Borchert (Los Padres National Forest), Don Potter (Stanislaus National Forest), Brooks Smith (Mendocino National Forest), Adina Merenlender and Colin Brooks (Hopland Extension and Research Center), and Frank Davis, Bill Kuhn and David Stoms (UCSB Department of Geography), for their assistance in the site selection process for California. Denis Dean of Colorado State University and Ronen Kadmon of the Hebrew University helped us throughout this study. We also acknowledge Zev Naveh and two anonymous reviewers

for their constructive comments on previous versions of the manuscript.

References

- Armesto J.J., Vidiella P.E. and Jimenez H.E. 1995. Evaluating causes and mechanisms of succession in the Mediterranean regions in Chile and California. In: Kalin Arroyo M.T., Zedler P.H. and Fox M.D. (eds), *Ecology and Biogeography of Mediterranean Ecosystems in Chile, California and Australia*. Springer-Verlag, New York, New York, USA, pp. 418–435.
- Axelrod D.I. 1977. Outline history of California vegetation. In: Barbour M.G. and Major J. (eds), *Terrestrial Vegetation of California*. John Wiley & Sons, New York, New York, USA, pp. 139–193.
- Barbour M.G. and Minnich R.A. 1990. The myth of chaparral convergence. *Israel Journal of Botany* 39: 453–463.
- Brooks C.N. and Merenlender A. 2001. Determining the pattern of oak woodland regeneration for a cleared watershed in northwest California: A necessary first step for restoration. *Restoration Ecology* 9: 1–12.
- Cadle J.E. and Greene H.W. 1993. Phylogenetic patterns, biogeography, and the ecological structure of neotropical snake assemblages. In: Ricklefs R.E. and Schluter D. (eds), *Species Diversity in Ecological Communities*. University of Chicago Press, Chicago, Illinois, USA, pp. 281–293.
- Callaway R.M. and Davis F.W. 1993. Vegetation dynamics, fire, and the physical environment in coastal central California. *Ecology* 74: 1567–1578.
- Carmel Y., Dean D.J. and Flather C.H. 2001a. Combining location and classification error sources for estimating multi-temporal database accuracy. *Photogrammetric Engineering & Remote Sensing* 67: 865–872.
- Carmel Y. and Kadmon R. 1998. Computerized classification of Mediterranean vegetation using panchromatic aerial photographs. *Journal of Vegetation Science* 9: 445–454.
- Carmel Y. and Kadmon R. 1999. Grazing, topography, and long-term vegetation changes in a Mediterranean ecosystem. *Plant Ecology* 145: 239–250.
- Carmel Y., Kadmon R. and Nirel R. 2001b. Spatio-temporal predictive models of Mediterranean vegetation dynamics. *Ecological Applications* 11: 268–280.
- Cody M.L. 1973. Parallel evolution in bird niches. In: Di Castri F. and Mooney H.A. (eds), *Mediterranean Type Ecosystems: Origin and Structure*. Springer-Verlag, New York, New York, USA, pp. 306–338.
- Cody M.L. and Mooney H.A. 1978. Convergence versus nonconvergence in Mediterranean-climate ecosystems. *Annual Review of Ecology and Systematics* 9: 265–321.
- Cowling R.M., Rundel P.W., Lamont B.B., Aroyo M.K. and Arino M. 1996. Plant diversity in Mediterranean-climate regions. *Trends in Ecology and Evolution* 11: 362–366.
- Daly C., Neilson R.P. and Phillips D.L. 1994. A statistical-topographic model for mapping climatological precipitation over mountainous terrain. *Journal of Applied Meteorology* 33: 140–158.
- Davis F.W., Stoms D.M., Hollander A.D., Thomas K.A., Stine P.A., Odion D., Borchert M.I., Thorne J.H., Gray M.V., Walker R.E., Warner K. and Graae J. 1998. *The California Gap Analysis*

- Project--Final Report. University of California, Santa Barbara, California, USA.
- Davis J. 1967. Some effects of deer browsing on Chamise sprouts after fire. *The American Midland Naturalist* 77: 234–238.
- Di Castri F. and Mooney H.A., eds. 1973. *Mediterranean Type Ecosystems: Origin and Structure*. Springer-Verlag, New York, New York, USA.
- Frellich L.E., Sugita S., Reich P.B., Davis M.B. and Friedman S.K. 1998. Neighborhood effects in forests: implications for within-stand patch structure. *Journal of Ecology* 86: 149–161.
- Glenn-Lewin D.C. and van der Maarel E. 1992. Patterns and processes of vegetation dynamics. In: Glenn-Lewin D.C., Peet R.K. and Veblen T.T. (eds), *Plant Succession*. Chapman & Hall, London, UK, pp. 11–58.
- Griffin J.R. 1971. Oak regeneration in the upper Carmel valley, California. *Ecology* 52: 862–868.
- Griffin J.R. 1988. *A natural history of Hastings Reservation, Carmel Valley, California*. Report No. 1. Hastings Natural History Reservation, University of California, Berkeley, California, USA.
- Hobbs R.J., Richardson D.M. and Davis G.W. 1995. Mediterranean-type ecosystems: opportunities and constraints for studying the function of biodiversity. In: Davis G.W. and Richardson D.M. (eds), *Mediterranean-type Ecosystems: The Function of Biodiversity*. Springer-Verlag, New York, New York, USA, pp. 1–42.
- Jansen H.C., Snow R.R., Treber G.A. and Bell F.L. 1997. Effects of livestock grazing on Blue Oak saplings. In: Pillsbury N.H., Verner J. and Tietje W.D. (eds), *Proceedings of a symposium on oak woodlands: ecology, management, and urban interface issues*. General Technical Report PSW-GTR-160. USDA, Forest Service, Pacific Southwest Research Station, Berkeley, California, USA, pp. 313–320.
- Kadmon R. and Harari-Kremer R. 1999. Landscape-scale regeneration dynamics of disturbed Mediterranean maquis. *Journal of Vegetation Science* 10: 383–402.
- Karr J.R. and James F.C. 1975. Ecomorphological configurations and convergent evolution in species and communities. In: Cody M.L. and Diamond J.M. (eds), *Ecology and Evolution of Communities*. Harvard University Press, Cambridge, Massachusetts, USA, pp. 258–291.
- Kummerow J. 1973. Comparative anatomy of sclerophylls of Mediterranean climatic areas. In: Di Castri F. and Mooney H.A. (eds), *Mediterranean Type Ecosystems: Origin and Structure*. Springer-Verlag, New York, New York, USA, pp. 157–169.
- Lawton J.H. 1999. Are there general laws in ecology? *Oikos* 84: 177–192.
- Legendre P. and Legendre L. 1998. *Numerical ecology*, 2 edition. Elsevier, Amsterdam, The Netherlands.
- Likens G.E. 1992. *The ecosystem approach: its use and abuse*. Excellence in ecology Vol. 3. Ecology Institute, Oldendorf/Luhe, Germany.
- Lindsay J.M. 1943. *Human relations to the Hastings Reservation in the past (with information on land use and its influence on vegetation)*. Unpublished document. Hastings Natural Reservation, Carmel Valley, California, USA.
- Losos J.B., Jackman T.R., Larson A., de Queiroz K. and Rodríguez-Schettino L. 1998. Contingency and determinism in replicated adaptive radiations of island lizards. *Science* 279: 2115–2118.
- Markus M. 1994. *Meron Mountain – a landscape survey*. Nature Reserve Authority, Jerusalem (In Hebrew).
- Martinez E. and Fuentes E. 1993. Can we extrapolate the California model of grassland-shrubland ecotone? *Ecological Applications* 3: 417–423.
- McClaran M.P. 1987. Blue oak age structure in relation to livestock grazing history in Tulare county, California. In: Plumb T.R. and Pillsbury N.H. (eds), *Proceedings of the symposium on multiple-use management of California's hardwood resources*. General Technical Report PSW-GTR-100. USDA, Forest Service, Pacific Southwest Research Station, Berkeley, California, USA, pp. 358–366.
- McCreary D.D. 1989. Regenerating native oaks in California. *California Agriculture* 43(4-6): 358–360.
- Mensing S. A. 1992. The impact of European settlement on blue oak (*Quercus douglasii*) regeneration and recruitment in the Tehachapi Mountains, California. *Madrono* 39: 36–46.
- Mensing S. 1998. 560 years of vegetation change in the region of Santa Barbara. *Madrono* 45: 1–11.
- Miles S.R. and Goudey C.B. 1997. *Ecological subregions of California*. Publication No. R5-EM-TP-005, Pacific South-west Region, USDA Forest Service. USDA Forest Service, San Francisco, California, USA.
- Momen B., Menke J.W., Welker J.M., Rice K.J. and Chapin F.S., III. 1994. Blue oak regeneration and seedling water relations in four sites within a California oak savanna. *International Journal of Plant Sciences* 155: 744–749.
- Muick P.C. 1991. Effects of shade on blue oak and coast live oak regeneration on California annual grassland. In: Standiford R. (ed.), *Proceedings of the symposium on oak woodlands and hardwood rangeland management*. General Technical Report PSW-GTR-126. USDA, Forest Service, Pacific Southwest Research Station, Berkeley, California, USA, pp. 21–24.
- Naveh Z. 1967. Mediterranean ecosystems and vegetation types in California and Israel. *Ecology* 48: 445–459.
- Naveh Z. 1994. The role of fire in the Mediterranean landscape of Israel. In: Moreno J.M. and Oechel W.C. (eds), *The Role of Fire in the Mediterranean-type Ecosystems*. Springer-Verlag, New York, New York, USA, pp. 163–185.
- Naveh Z. and Dan J. 1973. The human degradation of Mediterranean landscapes in Israel. In: Di Castri F. and Mooney H.A. (eds), *Mediterranean Type Ecosystems: Origin and Structure*. Springer-Verlag, New York, New York, USA, pp. 273–390.
- Naveh Z. and Kutiel P. 1986. Changes in the Mediterranean vegetation of Israel in response to human habitation and land use. In: Woodwell, G. (ed.), *The Earth in Transition: Patterns and Processes of Biotic Impoverishment*. Cambridge University Press, Cambridge, UK, pp. 259–296.
- Naveh Z. and Whittaker R.H. 1979. Structural and floristic diversity of shrublands and woodlands on northern Israel and other Mediterranean areas. *Vegetatio* 41: 171–190.
- Noy-Meir I., Gutman M., Kaplan Y. 1989. Responses of Mediterranean grassland plants to grazing and protection. *Journal of Ecology* 77: 290–310.
- Paraskevopoulos S.P., Iatrou G.D. and Pantis J.D. 1994. Plant growth strategies in evergreen-sclerophyllous shrublands (Maquis) in central Greece. *Vegetatio* 115: 109–114.
- Paruelo J.M., Jobbagy E.G., Sala O.E., Lauenroth W.K. and Burke I.C. 1998. Functional and structural convergence of temperate grassland and shrubland ecosystems. *Ecological Applications* 8: 194–206.

- Pavlik B., Muick P.C. and Johnson S.G. 1992. Oaks of California. Cachuma Press, Los Olivos, California, USA.
- Phillips R.L., McDougald N.K., Standiford R. and Frost W.E. 1996. Blue oak seedlings may be older than they look. *California Agriculture* 50: 17–19.
- Pianka E.R. 1975. Do ecosystems converge? *Science* 188: 847–848.
- Pianka E.R. 1986. Ecology and natural history of desert lizards. Princeton University Press, Princeton, New Jersey, USA.
- Preiss E., Martin J.L. and Debussche M. 1997. Rural depopulation and recent landscape changes in a Mediterranean region: consequences to the breeding avifauna. *Landscape Ecology* 12: 51–61.
- Prentice C. 1990. Bioclimatic distribution of vegetation for general circulation model studies. *Journal of Geophysical Research* 95: 11811–11830.
- Rabinovitch-Vin A. 1983. Influence of nutrients on the composition and distribution of plant communities in Mediterranean-type ecosystems of Israel. In: Kruger F.J., Mitchell D.T. and Jarvis J.U.M. (eds), *Mediterranean-type Ecosystems – the Role of Nutrients*. Springer-Verlag, Berlin, Germany, pp. 74–85.
- Samocho Y., Litav M., Fine P. and Vizel Y. 1980. Development rate of woodland trees in the Judea Mountains. *Layaaran* 30: 6–15 (In Hebrew).
- Scheidlinger C.R. and Zedler P.H. 1979. Change in vegetative cover of oak stands in southern San Diego County: 1928-1970. In: Plumb T.R. (ed.), *Proceedings of the symposium on the ecology, management and utilization of California oaks*, pp. 81-85. USDA, Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, California, USA.
- Schluter D. 1986. Tests for similarity and convergence of finch communities. *Ecology* 67: 1073–1085.
- Seligman N.G. and Perevolotsky A. 1994. Has intensive grazing by domestic livestock degraded Mediterranean Basin range-lands? In: Arianoutsou M. and Groves R.H. (eds), *Plant-animal Interactions in Mediterranean-type Ecosystems*. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 93-103.
- Shmida A. 1981. Mediterranean vegetation in California and Israel: similarities and differences. *Israel Journal of Botany* 30: 105–123.
- Standiford R., McDougald N.K., Frost W.E. and Phillips R.L. 1997. Factors influencing the probability of oak regeneration on Southern Sierra Nevada woodlands in California. *Madrono* 44: 170–183.
- Sudworth G.B. 1908. *Forest trees of the Pacific slope*. U.S. Department of Agriculture, Government Printing Office, Washington, DC, USA.
- Sweitzer R.A. and Van Vuren D.H. 2002. Rooting and foraging effects of wild pigs on tree regeneration and acorn survival in California's oak woodland ecosystems. In: Standiford R.B., McCreary D. and Purcell K.L. (eds), *Proceedings of the fifth symposium on oak woodlands: oaks in California's changing landscape*, pp. 219-231. General Technical Report PSW-GTR-184. USDA, Forest Service, Pacific Southwest Research Station, Berkeley, California, USA, pp. 219–231.
- Tilman D. 1989. Discussion: population dynamics and species interactions. In: Roughgarden J., May R.M. and Levin S.A. (eds), *Perspectives in Ecological Theory*. Princeton University Press, Princeton, New Jersey, USA, pp. 89–100.
- White K.L. 1966. Structure and composition of foothill woodland in Central Coastal California. *Ecology* 47: 229–237.
- Wiens J.A. 1991. Ecological similarity of shrub-desert avifaunas of Australia and North America. *Ecology* 72: 479–495.
- Zinke P.J. 1973. Analogies between the soil and vegetation types of Italy, Greece, and California. In: Di Castri F. and Mooney H.A. (eds), *Mediterranean-type Ecosystems: Origin and Structure*. Springer-Verlag, New York, New York, USA, pp. 61–82.