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Modelling Mediterranean landscape succession-disturbance dynamics: A landscape fire-succession model

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ABSTRACT

We present a spatially explicit Landscape Fire-Succession Model (LFSM) developed to represent Mediterranean Basin landscapes and capable of integrating modules and functions that explicitly represent human activity. Plant-functional types are used to represent spatial and temporal competition for resources (water and light) in a rule-based modelling framework. Vegetation dynamics are represented using a rule-based community-level modelling approach that considers multiple succession pathways and vegetation climax states. Wildfire behaviour is represented using a cellular-automata model of fire spread that accounts for land-cover flammability, slope, wind and vegetation moisture. Results show that wildfire spread parameters have the greatest influence on two aspects of the model: land-cover change and the wildfire regime. This sensitivity highlights the importance of accurately parameterising this type of grid-based model for representing landscape-level processes. We use a pattern-oriented modelling approach in conjunction with wildfire power-law frequency-area scaling exponent β to calibrate the model. Parameters describing the role of soil moisture on vegetation dynamics are also found to significantly influence land-cover change. Recent improvements in understanding the role of soil moisture and wildfire fuel loads at the landscape-level will drive advances in Mediterranean LFSMs.

1. Introduction

Landscape Fire-Succession Models (LFSMs) simulate the dynamic interaction of fire, vegetation, and often climate, in a spatially explicit manner (Keane et al., 2004). LFSMs have been used to model many different (mainly forest) ecosystems, including boreal (Pennanen et al., 2004), mixed broadleaf-conifer (He and Mladenoff, 1999), and maquis-forest mosaics (Perry and Enright, 2002), across extents of 10^1–10^4 km^2 and durations of 10^1–10^3 yr. Being spatially explicit, LFSMs are able to examine the spatial interaction of ecological processes through time (e.g., wildfire occurrence and vegetation regeneration). This is particularly important in spatially heterogeneous environments, such as those found in the Mediterranean Basin. The characteristic complexity and heterogeneity of Mediterranean Basin landscapes have led some to doubt the feasibility of spatially explicit, physiologically based forest modelling that has been possible in other ecosystems (e.g., more temperate regions Zavala et al., 2000). Consequently, vegetation functional types have generally been adopted in recent models of Mediterranean forest succession-disturbance dynamics (e.g., Zavala and Zea, 2004; Pausas, 2006). Some authors have advocated the use of rule-based modelling frameworks that can incorporate quantitative and qualitative understanding to negotiate the relatively poor process understanding in regions such as the Mediterranean (McIntosh, 2003; McIntosh et al., 2003). This paper presents the development and testing of a LFSM that utilises plant-functional types in a rule-based framework to examine vegetation-wildfire dynamics for a Mediterranean landscape.

Human activity has a long history in the Mediterranean Basin. Evidence of human modification of landscape patterns and processes is widespread across the region (Wainwright and Thornes, 2004). Changes in the pattern of human activity can have marked impacts upon landscape dynamics. For example, abandonment of low-intensity agricultural land has contributed to increased forest cover around the northern rim of the Mediterranean Sea in recent decades (Mazzoleni et al., 2004). If the consequences of such change(s) are to be understood models that explicitly consider human activity as a component of landscape dynamics will be required. The LFSM

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presented in this paper is constructed with the intention of subsequently integrating an agent-based model of human land-use decision-making (Millington et al., 2008).

2. Spatial modelling of Mediterranean succession-disturbance dynamics

2.1. Mediterranean vegetation dynamics

The deterministic, equilibrium-based Clementsian view of succession (progressing toward a stable climax community) has been intensely debated by ecologists (Perry, 2002). We use the term 'succession' to describe vegetation distribution and change due to competition across shifting spatio-temporal resource gradients. The traditional conceptualisation of succession in Mediterranean landscapes is one where shade-intolerant pines are replaced by shade-tolerant oaks that establish themselves in the pine understorey (e.g., Barbero et al., 1990; Zavala et al., 2000). However, this pathway does not consider the role of disturbance and spatial variation of resources in preventing this oak climax from being reached. Vegetation establishment and succession in Mediterranean-type ecosystems are dependent, in both time and space, on resource gradients (moisture and light), disturbance type and frequency, previous land-use/cover, and the vegetation of adjacent land areas (via seed dispersal). Competition for water and light following disturbance (such as wildfire) and along gradients of these resources is the predominant cause of characteristic Mediterranean community structures (Vila and Sardans, 1999; Zavala et al., 2000). Consequently, it is vital that models of Mediterranean forest vegetation-dynamics consider the processes generated and produced by disturbance and succession (Zavala et al., 2000).

2.2. Issues of scale and representation

The implementation of detailed models of wildfire-vegetation dynamics at the landscape level (i.e., extents of 10^2–10^4 km^2 over decades) is hampered by the difficulties of scaling process knowledge and information from fine grains to large extents and the associated high levels of parameterisation that this scaling requires (Keane et al., 2004). In Mediterranean forest landscapes, efforts to develop Individual-Based Models (IBMs) of vegetation dynamics (representing the establishment, growth and senescence of individual organisms) are confronted by several problems. These problems are primarily related to the morphological and behavioural characteristics of Mediterranean-type species. For instance, Pausas (1999a) suggests that the use of the same allometric equations for all species is not acceptable in Mediterranean-type vegetation, whereas it may be for models representing temperate regions. Furthermore, it is often difficult to establish the growth rates or life span of Mediterranean-type vegetation species (Pausas, 1999a; Mouillot et al., 2001). Growth rates often vary in time according to resource availability (especially due to water availability and temperature) and it is difficult to establish these rates empirically (e.g., from tree rings) in Mediterranean-type species (Pausas, 1999a). Root networks of species that resprout following disturbance may be hundreds of years old while the above-ground vegetation appears in a juvenile state (Grove and Rackham, 2001). Underground structures further impede the use of IBMs in these regions, as it is difficult to estimate parameters for underground growth and competition (Pausas, 1999a).

The use of Plant-Functional Types (PFTs) overcomes many of these problems and enables systematic analysis of ecosystem function and sensitivity to environmental change (McIntyre and Hobbs, 1999). PFTs classify plants by common responses to environmental conditions in terms of growth, reproduction strategies and resource competition, thereby providing a simplified representation of numerous plant species within an ecosystem (McIntyre and Hobbs, 1999; Rusch et al., 2003). Using PFTs to simulate coarse land-cover classes reduces model complexity compared with an individual-based approach, but allows realistic representation of plant competition, growth and response to disturbance. The obligate seeder and resprouter PFTs have been widely used to describe the life-history strategies adopted by Mediterranean-type vegetation to survive in the face of frequent disturbance (e.g., Keeley and Zedler, 1978; Barbero et al., 1990; Enright et al., 1998a,b). Resprouters (e.g., *Quercus ilex*) rely on large underground biomass stores (lignotubers) and root systems or protection of above-ground biomass to survive disturbance and resprout vegetatively (Enright et al., 1998b; Bellingham and Sparrow, 2000). Obligate seeders (e.g., *Pinus pinea* and *Pinus pinaster*) die in the event of disturbance but populations are maintained by rapid recolonisation of a disturbed area from seeds in the canopy (Enright et al., 1998a; Tapias et al., 2004).

2.3. Representation of wildfire in landscape fire-succession models

The wildfire 'regime' is the frequency, timing, and burned area of all fires in a region (Whelan, 1995). Most previous LFSMs have taken a stochastic approach to represent fire ignition, igniting fires in each time step as a function of probability distribution functions parameterised by empirical data (Keane et al., 2004). Once alight, the burned area of a fire is related to the subsequent spread of that fire. Fire-shape and Cellular Automata (CA) approaches have been used previously to represent fire spread in LFSMs. Given an ignition location, wind direction and speed it is possible to reasonably estimate the size and shape of a wildfire from a set of fire-shape templates, the most commonly used being the ellipse (e.g., Anderson et al., 1982; Catchpole et al., 1992). However, these fire-shape models often assume fire spread across uniform fuel, topography and microclimatic conditions, variation in any of which will cause variation in rate and direction of spread. This is a major drawback in spatially heterogeneous landscapes. To overcome these problems the CA approach considers the landscape as a grid of finite cells, each of which is assumed to have a uniform internal state. Each cell may possess several attributes, which may be constant (e.g., slope) or dynamic (e.g., fuel load). The probability of fire spreading between cells is then dependent on these attributes.

2.4. Previous Mediterranean landscape fire-succession models

Spatially explicit modelling of vegetation and fire dynamics at the landscape level has a short history in Mediterranean-type ecosystems (Zavala et al., 2000). Early models used PFTs to examine Mediterranean-type vegetation-dynamics non-spatially (e.g., Pausas, 1999b). Several attempts have been made to model Mediterranean-type vegetation-dynamics spatially, with varying degrees of mechanistic representation. The process-based SImulator for meditERRnean landscApes (SIERRA Mouillot et al., 2001, 2002) was developed to examine the interaction(s) between vegetation-dynamics and fire regimes for landscapes with Mediterranean-type vegetation communities. Taking a PFT approach, with stands of vegetation on a 30-m resolution grid, SIERRA represents spatial heterogeneity in landscape patterns and processes. Seed dispersal, surface water flow and fire spread are simulated spatially, with the assumption that water availability and solar radiation are critical constraints on vegetation productivity and competition. Fire is represented using a fire-shape approach. A large number of parameters are needed to drive this physiological, mechanistic model that uses numerous equations to simulate processes such as infiltration, root water uptake and net primary production. Consequently, the high data demands of this approach limit the widespread application of such a model.

Other recent spatially explicit but less mechanistic (and therefore less data-demanding) models of Mediterranean-type vegetation-dynamics have been developed by Pausas (1999a, 2003, 2006) and Zavala and Zea (2004). These models are largely abstract and independent of specific study areas. For example, Pausas (1999b, 2006) has developed abstract CA models of Mediterranean forest succession and disturbance that consider PFTs and disturbance regime characteristics. The spatially explicit FATELAND model (Pausas, 2006) represents species competition in grid cells as a function of their life-history characteristics and the fire regime. Use of FATELAND suggested that not only do species respond differentially to altered fire regimes, but that the nature of their response varies with landscape pattern. Using a similar approach, Zavala and Zea (2004) examined the spatial dynamics of two PFTs (oak 'resprouters' and pine 'seeders'), varying soil moisture and disturbance occurrence across a hypothetical landscape. They found that the spatial distribution of soil-moisture and the presence/absence of disturbance influenced both the spatial distribution of species and the temporal variation in size of the modelled populations. Most recently, Syphard et al. (2007) modified the LANDIS model for application in southern California. They found that the model was able to reproduce expected responses of 'seeder' and 'resprouter' PFTs to variation in fire return intervals.

Models such as FATELAND are not direct representations of specific landscapes or study areas but they do bridge the gap between highly abstract succession-disturbance models and the mechanistic site-specific simulation models that are highly demanding in both data and computational resources (Millington et al., 2006; Perry and Millington, 2008). Finding the appropriate level of representation remains an important issue for ecological modellers (Perry, 2009). Furthermore, the major disturbance agent in this region, human activity, is conspicuously absent from the discussion above and from previous LFSMs constructed for the Mediterranean region. The model presented here is the ecological component of a wider modelling project that aims to represent human activity explicitly in a LFSM. Consequently, a PFT approach that considers coarse land-cover classes is most appropriate for our purposes.

3. Methods

3.1. Study area

Our model was developed using data for EU Special Protection Area number 56, 'Encinares del río Alberche y Cofio' (SPA 56) in central Spain near Madrid. SPA 56 covers approximately 83,000 ha (830 km^2) on the southern slopes and foothills of the Sierra de Guadarrama (altitudinal range 600–1300 m a.s.l). The region is characterized by a Mediterranean-type climate (mean annual rainfall 700 mm and mean daytime temperature 19 °C) and flora (dominated by *Pinus* and *Quercus* species). Romero-Calcerrada and Perry (2004) and Millington et al. (2007) describe SPA 56 and data available for the construction of this model. In this paper we present initial results for the entire area, but focus our detailed analyses on a representative sub-section of SPA 56 covering approximately 20,000 ha (200 km^2, outlined on year 25 in Fig. 5).

3.2. Vegetation state-and-transition model

To represent vegetation dynamics our LFSM adopts an approach similar to the Rule-Based Community-Level Modelling (RBCLM) system developed by McIntosh (2003) and McIntosh et al. (2003). The RBCLM system was developed for vegetation modelling with qualitative knowledge, where quantitative data for model parameterisation are lacking. Changes in categorical state variables such as land-cover classes are represented by rules based on a qualitative understanding that links state variables and environmental descriptors. The key attributes of vegetation change addressed by the RBCLM approach are (McIntosh, 2003):

1. *direction of transition* between land-cover classes
2. *rate of transition* between these land-cover classes.

Considering vegetation change at a categorical level in this way allows qualitative understanding of vegetation dynamics to be translated into a formal, spatial model at the landscape level. Our LFSM adopts this approach, with rules for change based on the behaviour of seven land-cover classes (Table 1) and their interaction with key environmental resource constraints (water and light availability) and disturbance (fire and agriculture). These land-cover classes consist of two dominant vegetation types that have distinct life-history traits and reproductive strategies (pine and oak), three mixed land-cover types (transition forest, deciduous and shrubland), and two non-vegetated land covers (water/quarry and a 'burnt' land-cover class).

The 'pine' land cover is dominated by *P. pinea* and *P. pinaster*. The 'oak' land cover is predominantly *Q. ilex*. These classes are considered as 'seeder' and 'resprouter' PFTs respectively. All species in each of these classes are assumed to belong to the same PFT (i.e., all have the same life-history traits and functional responses to environmental resources and disturbances). The 'transition forest' land-cover does not represent a single species, rather it encompasses the mixed state between an idealised pine–oak transition and other mixed land-cover conditions (i.e., mixed pine-deciduous forest). The deciduous forest land cover is also composed of mixed species (Table 1), and is found in the relatively cooler, more moist areas of the study area. Deciduous species (e.g., *Castanea sativa*) in SPA 56 exhibit both resprouter and obligate seeder responses to fire and are represented as a combination of these functional types (by considering different 'successional trajectories' – see below). If burnt, *all* land-cover classes become shrubland soon after burning. Unlike the other vegetation land-covers, the shrubland class can transit directly to all other vegetation land-covers.

These coarse classes of vegetation (Classes 1–5, Table 1) are appropriate for the 30 m spatial resolution of the lattice that represents the landscape. Temporal resolution of the model is one year (Fig. 1). For each pixel, at each simulated year, a rule-set defines a direction of transition and the duration over which this transition will take to occur. Specifically, four pixel-variables are considered in this process (McIntosh et al., 2003):

1. *Class*, C: current land-cover class (as defined in Table 1, Classes 1–7)
2. *Total time in class*, Tin: length of time [yr] pixel has been in current class C at present time t ($C(t)$)
3. *Direction of transition*, ΔD: the resulting class of a pixel on completion of its current transition trajectory, as a function of $C(t)$ and environmental conditions
4. *Total time required to complete transition*, ΔT [yr]: a function of ΔD and environmental conditions.

Values for Tin, are derived from a set of logical statements:

- IF $C(t) \neq C(t-1)$ THEN $Tin(t) = 1$ Statement 1

- IF $C(t) = C(t-1)$ AND $\Delta D(t) = \Delta D(t-1)$ THEN $Tin(t) = Tin(t-1) + 1$ Statement 2

- IF $C(t) = C(t-1)$ AND $\Delta D(t) \neq \Delta D(t-1)$ THEN $Tin(t) = 1$ Statement 3

To derive ΔD and ΔT, the set of pixel physical attributes is compared to a look-up table (see online supplementary material) in which a value for ΔD and ΔT for every possible combination of pixel physical attributes, is listed.

Table 1
Land-cover classes considered in the model. Potential transitions (direction indicated by →) between land-cover classes are shown with the duration over which they occur. Land-cover flammability values are used to simulate wildfire spread (*LCF* in Eq. (8)).

Class	Land-Cover	Description	Class Change
1	Pine	Primarily *Pinus pinea* and *Pinus pinaster*	→2; 15–40 yr →3; 20 yr
2	Transition Forest	Mixed *Pinus*, *Quercus* and *Juniperus* species	→1; 20–30 yr →3; 20–25 yr →4; 20–50 yr
3	Deciduous	Primarily chestnut (*Castanea sativa*), oak (*Quercus pyrenaica*) and alder (*Alnus glutinosa*) but also *Populus* species	→1; 20–30 yr →2; 30–40 yr
4	Oak	Predominantly *Quercus ilex*	→2; 30 yr
5	Shrubland	*Cistus*, *Lavandula* and *Genista* species with juvenile *Pinus* and *Quercus* in shrub state	→1; 10–15 yr →2; 15 yr →3; 15–20 yr →4; 30–50 yr
6	Water/Quarry	River, reservoir or open stone quarry	Unchanging
7	Burnt	Post-fire condition of states 1–5	→5; 3 yr

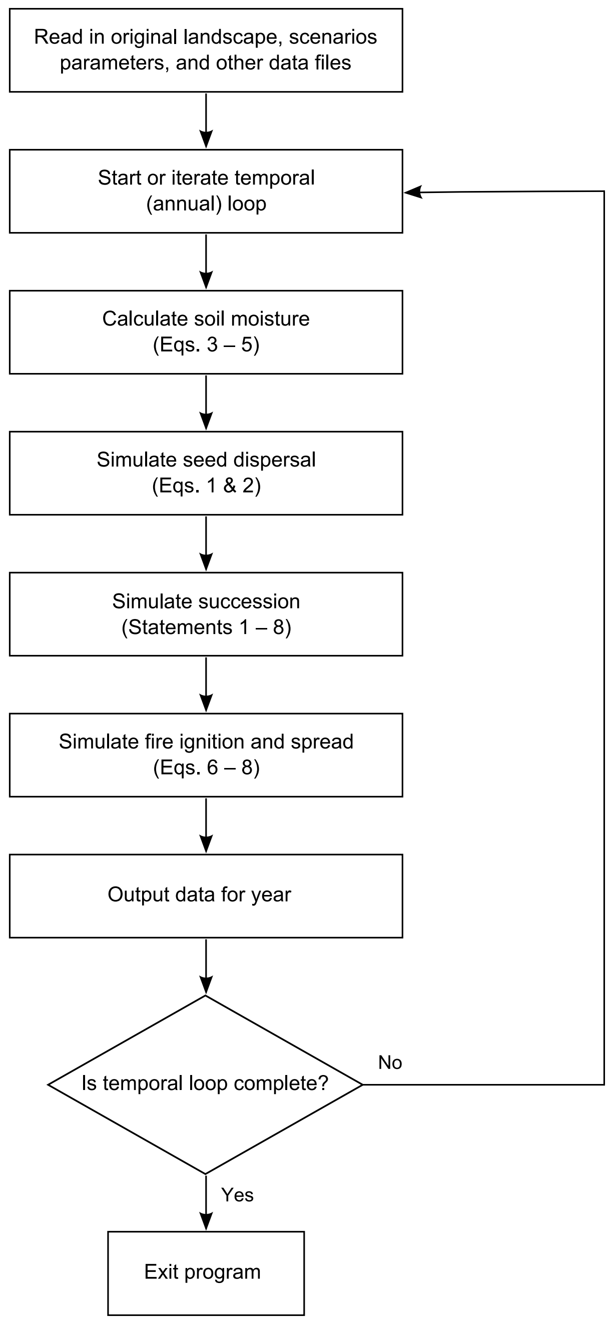

Fig. 1. Schematic diagram of the model. Starting from the top of the diagram, this process is iterated for as many annual time-steps as required.

Values for ΔT represent the duration for a transition of type ΔD to occur given a pixel's physical attributes. Values for ΔD and ΔT will vary if a pixel's attributes change, however. Specifically, these values will vary depending upon seed, light and water availability (as discussed below). For example, if a seed source becomes available that was not present previously, the transition may change toward the vegetation represented by the seed source (e.g., transition from shrubland to pine may change to transition from shrubland to deciduous if seeds become available for the latter and conditions are hydric, Fig. 2). Because ΔT is dependent on both ΔD and pixel physical attributes however, a rule is required for the situation in which ΔD changes before a transition has successfully been completed:

- IF $\Delta D(t) \neq \Delta D(t-1)$ AND $C(t) = C(t-1)$ THEN $\Delta T = [\Delta T(t-1) + \Delta T(t)]/2$ Statement 4

where $\Delta T(t)$ is newly established for time t. Finally, at each time step, rules are checked to establish whether a state transition occurs:

- IF $Tin(t) \geq \Delta T(t)$ THEN $C(t+1) = \Delta D$ Statement 5

- IF $Tin(t) < \Delta T(t)$ THEN $C(t+1) = C(t)$ Statement 6

Vegetation age is monitored for each pixel to determine whether reproductive maturity has been achieved. Oak vegetation is assumed to reach reproductive maturity at 15 years, and pine and deciduous at 12 years (Pausas, 1999b). If vegetation is immature, resprouter material or seeds will not be present in the pixel unless dispersed from another source of mature vegetation via seed dispersal (Section 3.3). For each simulated year, pixels are classified as either being on a 'regeneration' or 'secondary' ('old-field') succession pathway (Fig. 2). Regeneration succession occurs where mature resprouter vegetation is present. Secondary succession occurs where mature resprouter vegetation is not present. A pixel will switch from secondary to regeneration succession when reprouter vegetation becomes mature. Mature resprouter vegetation is assumed to survive burning, while (obligate) seeder species of all ages die (their seeds surviving if they were mature). However, if burning is particularly frequent resprouters will not survive (Zavala et al., 2000) and a pixel will switch from regeneration succession to secondary succession (Fig. 2). Thus, the succession pathway that a pixel is following depends upon the type of vegetation present and whether it is reproductively mature.

Our model does not consider the intensity of burning (e.g., ground fire *versus* crown fire) and simply assumes that all fires are stand-replacing (all burned pixels are reset to the 'burnt' state). This assumption is suitable given the coarse land-cover classes considered (Pausas, 1999b). Fire return times to each pixel are used to assess the survival of resprouter vegetation following disturbance. Probability of mortality due to fire has an inverse relationship with organism biomass and trunk diameter (Moreno and Oechel, 1993; Pausas, 1997; Hodgkinson, 1998). As vegetation biomass is not considered here, age is used as a proxy for biomass, with biomass increasing with age until a maximum. Thus, mortality occurs if:

$mf > Age/OM$, for $Age < 100$ Statement 7a

$mf > 100/OM$, for $Age \geq 100$ Statement 7b

where mf is fire frequency (fires yr^{-1}) and mortality-scaling parameter $OM = 200$ ($\mathrm{yr}^2\ \mathrm{fire}^{-1}$). This value for OM is based on qualitative understanding as insufficient data have prevented empirical studies from quantitatively establishing the disturbance frequency causing mortality (Trabaud and Galtie, 1996). We assume that at an age of 100 years the relationship between vegetation biomass and age becomes weak enough to be considered constant (i.e., the tree is assumed to be fully grown).

3.3. *Seed dispersal*

Key to the accurate representation of seed-dispersal dynamics is selection of appropriate seed-dispersal kernels to represent vegetation types and species (Greene et al., 2004; Jongejans et al., 2008). Pons and Pausas (2007) found that the lognormal distribution best described the distance distribution of acorns from *Quercus* species by birds in Spain. We use the lognormal distribution (mean of 46.7 m, standard deviation of 2.34, Pons and Pausas, 2007) to model the probability of acorn presence in a non-oak pixel:

$$P = \frac{1}{x\sigma\sqrt{2\pi}}\exp\left[-\frac{(\ln(x)-\mu)^2}{2\sigma^2}\right] \tag{1}$$

where x is the distance (m) to the nearest pixel containing mature oak vegetation. Pons and Pausas (2007) found a maximum acorn dispersal distance (Oak MD) of 545.4 m. To speed simulation time, for $x > 550$ m we assume the probability of acorn presence to be 0.001. We use an exponential distribution to model seed dispersal from vegetation types for which wind is the primary dispersal mechanism (i.e., pine and deciduous types):

$$P = e^{-b\cdot\left(\frac{x}{MD}\right)} \tag{2}$$

where x is the distance (m) to nearest seed source (i.e., pixel containing mature pine or deciduous vegetation) and $MD > x > ED$, MD is the maximum seeding distance and the distance-decrease parameter $b = 5$. The exponential distribution has been used to model seed dispersal for these vegetation types in previous models (Pausas, 2006; Syphard et al., 2007). We assume $MD = 100$ m and $ED = 75$ m, consistent with these previous models. For $x \leq ED$ we assume the probability of a pixel containing seeds for germination that year is 0.95 and for $x > MD$ we assume a probability of 0.001. We use a 'Quad-Tree' data structure (Govindarajan et al., 2004) to facilitate efficient computation of seed probabilities for each pixel in the landscape.

At model initialization the three land-cover maps available for the study area (for 1984, 1991 and 1999, see Romero-Calcerrada and Perry, 2002; Millington et al., 2007) are used to assign initial seed locations and vegetation ages (using the rules specified in Table 2). As the original land-cover maps do not specify the mature vegetation types present in each transition forest pixel, transition forest in the initial land-cover map is assumed to contain *all* seed sources (as transition forest must contain at least

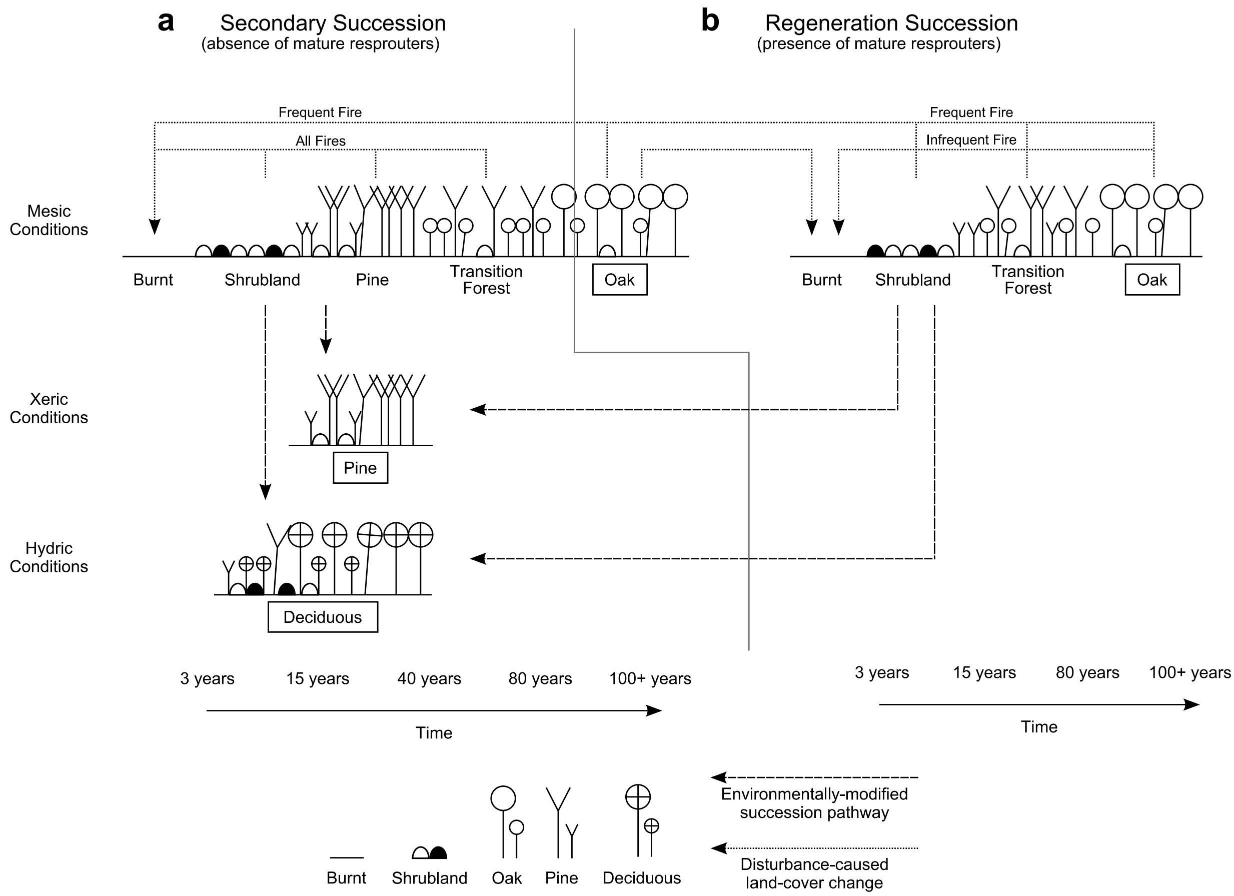

Fig. 2. Succession pathways used in the vegetation-dynamics model for a) secondary succession and b) regeneration succession. Directions and rates of transition are shown for various environmental conditions. Succession pathways may be modified from the default pathway (at top) by changes in environmental conditions (dashed arrows). Potential 'climax' vegetation covers (i.e., final cover given the current environmental conditions) are highlighted by boxes around their respective labels. Disturbance by fire (dotted arrows) converts land cover to the burnt state. Frequent fire (see Statement 7) results in secondary succession. Predominant pathways are shown; for all pathways see supporting online material.

one mature species by definition). Transition Forest that subsequently appears in the simulated landscape is assumed to contain only those seed sources for the mature vegetation types that are known to be present (via simulation). Initial shrubland pixels are assumed to contain no seed sources, as original land-cover maps do not specify vegetation types present, and shrubland does not necessarily contain any mature vegetation. Shrubland that subsequently appears in the landscape may contain mature oak vegetation that has survived previous burning.

3.4. Soil moisture

Soil-moisture availability (*SM*, mm) in a pixel is calculated as a function of total volume of incoming precipitation and overland flow and outgoing overland flow per time step:

$$SM = P + R_i - R_o \tag{3}$$

where P is precipitation, R_i is incoming overland flow and R_o is outgoing overland flow (all in units of mm). The Soil Conservation Service Curve Number (SCS-CN) method (SCS, 1985) is a commonly used method for calculating overland flow in agricultural,

Table 2
Rules to establish initial age of the four forest land-cover classes. LC denotes any one of pine, deciduous or oak land-cover (Classes 1, 3, 4, Table 1). Transition forest is land-cover Class 2. If the rule is satisfied the corresponding initial age of the given land-cover is assigned at model initialization.

Rule	Age of *LC* (yr)
IF 1984 AND 1991 AND 1999 = *LC*	16
IF 1984 AND 1991 = *LC* AND 1999 ≠ *LC*	8
IF 1999 AND 1991 ≠ *LC*	1
IF 1999 = Transition Forest	1
IF 1999 ≠ *LC* AND 1999 ≠ Transition Forest	0

forest and urban watersheds. The SCS-CN approach has relatively low data and parameterisation requirements and is used here in preference to other more mechanistically detailed (and data-demanding) approaches. This method calculates the total volume of overland flow per time step (*R*, whether incoming or outgoing) as:

$$R = \frac{(P - 0.02S)^2}{(P + 0.08S)} \tag{4}$$

where the 'initial abstraction rate' *S* is given by:

$$S = 2.54\left(\frac{1000}{CN} - 10\right) \tag{5}$$

and where *CN* is a curve number (dimensionless). The curve number is a function of vegetation, slope and soil type. Curve numbers have been calculated for numerous vegetation and soil types and the values used in the LFSM are presented in Appendix 1.

To apply this method spatially a flow-routing algorithm is used to distribute moisture around the landscape as a function of its topography. The RUNOFF function in IDRISI (Jenson and Domingue, 1988; Clark Labs, 2004) is used to produce a flow-routing map. As soil erosion and other geomorphologic processes are not considered in the model, the flow-routing map is assumed to be static. Moisture availability is classified into three classes (xeric ≤ 500 mm, 500 mm < mesic ≤ 1000 mm, and hydric > 1000 mm), consistent with those used in previous similar models (e.g., Zavala and Zea, 2004; Zavala and Bravo de la Parra, 2005).

3.5. Solar radiation

The availability of solar radiation is modelled as a function of the aspect of a pixel, with south-facing slopes receiving greater insolation than north-facing slopes annually. This situation is reflected in the transitions look-up table (online material), with deciduous vegetation favouring north-facing slopes, and pine vegetation favouring south-facing slopes. The shade-tolerance of evergreen oak and its preference to establish in the understorey of other species are reflected in the conceptualisation of the landscape successional dynamics (Fig. 2).

3.6. Wildfire model

Our LFSM represents the wildfire regime by integrating a cellular-automata (CA) model of fire spread with the vegetation-dynamics model described above. The coarse representation of vegetation in the model precludes the use of a detailed fire behaviour model (e.g., BEHAVE Burgan and Rothermel, 1984; Andrews, 1986). Constructing the model using a CA-type approach allows direct integration with the vegetation-dynamics component of the model and also allows the consideration of how environmental variables such as topography and climate influence spread.

We use the Poisson distribution to generate the number of individual wildfire events during each model time step. The number of fires per year in northeast Spain was found to follow a Poisson process for 1975–1998 (Diaz-Delgado et al., 2004). Using the Poisson distribution, the probability p of the occurrence of exactly x events during a specified time interval is given by:

$$p(x) = \frac{e^{-\lambda}\lambda^{x}}{x!} \tag{6}$$

where λ is the shape parameter (i.e., mean occurrence for the time interval specified). The parameter λ is estimated in our model by:

$$\lambda = m \times \frac{MAT}{MAP} \tag{7}$$

where MAT is mean annual temperature (°C), MAP is mean annual precipitation (mm) and climate ignition scaling parameter $m = 12$. Short-term (i.e., daily, weekly) climatic conditions are known to influence wildfire ignition risk more than mean annual conditions and are used by several major wildfire risk models (e.g., the US NFDRS, Deeming et al., 1977; Burgan, 1988). However, our model assumes that changes in mean annual conditions correspond with changes in intra-annual conditions. For example, De Luis et al. (2000, 2001) found that decreases in mean annual precipitation correspond with increases in the number/intensity of intra-annual drought periods in Spain, and suggested it was one factor causing observed increases in frequency in the region recently. The value for parameter m was estimated by comparing observed fire frequencies (6.0 fire yr^{-1}) with observed temperature and precipitation data for SPA 56 for 1989–2000. Fires ignite at random locations in all analyses considered in this paper.

In our CA model, fire may spread into any of a burning cell's eight neighbouring cells that contain a flammable land-cover (i.e., all land-cover classes except water/quarry and burnt – see supplementary online material for a movie illustrating fire spread in the model). The probability of fire spreading into an adjacent cell is calculated as a function of the vegetation flammability probability, modified by slope and climate conditions:

$$P = LCF \cdot SR \cdot FMR \cdot W \tag{8}$$

where LCF is land-cover flammability, SR is slope risk, FMR is fuel-moisture risk, and W is wind risk. A uniform random deviate in the interval [0, 1] is compared with this probability to determine if spread occurs. The flammabilities of land-cover classes (LCF in Eq. (8), default values in Table 6) are interpreted as the probability of a cell with the given land-cover being ignited by a burning adjacent cell on flat ground (between −5% and 5% slope, negative values represent movement downslope), with vegetation moisture in the range 0.5–0.6, and no wind. Wildfire is known to spread preferentially upslope due to flame height and vertical heat convection effects (Viegas, 1998). Categories of slope (%) are classified into risk classes (SR in Eq. (8)) following Perry and Enright (2002, Table 3).

Alongside vegetation type, fuel-moisture content (especially in fine fuel, such as small branches and leaves) is an important determinant of flammability, and is considered in many fire danger rating systems (e.g., the US NFDRS) and fire simulation models (e.g., BEHAVE). Vegetation moisture is considered here by classifying cell values derived from Eq. (7) into five classes and assigning appropriate multipliers (FMR in Eq. (8), Table 4). Wind data for the study area are not available, so conditions (direction and strength) are generated at random for each simulated fire. Three possible wind strength classes are simulated (W in Eq. (8), Fig. 3) based on the results of similar models of wildfire spread (Karafyllidis et al., 1997; Perry and Enright, 2002).

Table 3
Slope Risk. Classification of SR values (dimensionless) used in Eq. (8).

Slope (%)	SR
slope < −25	0.80
−25 ≤ slope < −15	0.90
−15 ≤ slope < −5	0.95
−5 ≤ slope < 5	1.00
5 ≤ slope < 15	1.05
15 ≤ slope < 25	1.10
slope ≥ 25	1.20

Table 4
Fuel-Moisture Risk. Classification of FMR values (dimensionless) used in Eq. (8).

Moisture Class	FMR
moisture < 0.2	0.8
0.2 ≤ moisture < 0.3	0.9
0.3 ≤ moisture < 0.5	1.0
0.5 ≤ moisture < 0.6	1.1
Moisture ≥ 0.6	1.2

3.7. Model calibration

Parameter values have been derived from several sources: (i) literature on vegetation change in forest ecosystems in the western Mediterranean Basin (e.g., Barbero et al. (1990)); (ii) previous landscape fire-succession models (e.g., Perry and Enright, 2002; Pausas, 2006; Syphard et al., 2007); (iii) anecdotal evidence collected from other sources (e.g., Grove and Rackham, 2001); (iv) knowledge of the study region and its dynamics gathered from 'experts' (i.e., scientists, forestry managers etc. in a similar fashion to that used by McIntosh et al., 2003).

Parameters influencing the wildfire model are calibrated to reproduce characteristics of the observed SPA 56 wildfire regime. To establish suitable parameter values, an appropriate measure to characterise wildfire regimes is required. From a wide number of possible heavy tailed frequency-area distributions (e.g., Schoenberg et al., 2003) the power-law distribution is the most parsimonious model (Millington et al., 2006). This distribution has also been found to be an accurate descriptor of wildfire regimes for events over a large range of orders of magnitude and across many ecosystems (Malamud et al., 1998; Ricotta et al., 1999, 2001; Song et al., 2001). Power-law distributions follow:

$$f(A) \sim A^{-\beta} \tag{9}$$

where $f(A)$ is the frequency of fires with size A and scaling constant β. It has been suggested previously that the distribution, and the use of the exponent β, is an efficient and effective measure for comparing wildfire regimes if frequency densities normalised by the temporal and spatial extents of the data set are used (Malamud et al., 2005; Millington et al., 2006). The scaling exponent β is a measure of the number of small *versus* medium *versus* large fires. Larger β values indicate 'large' fires are rarer relative to smaller fires, and *vice versa*. We tested multiple combinations of LCF values (ten 250-year model replicates for each set) and compared the resulting β value with β values for empirical wildfire data.

3.8. Sensitivity analysis

We use sensitivity analysis to verify that the model behaves as expected and to assess how the model's dynamics are affected by parameter uncertainty. We use simple univariate and incomplete multivariate permutation sensitivity analyses to test our model. For univariate analyses each input parameter is varied by ±10% of its 'default' value, while all other parameters are held at their default value (Table 5). A complete multivariate permutation analysis examines the result of holding each input parameter at its default value while varying all other parameters (±10%). We use an incomplete test that holds the default values of associated input parameters (e.g., all those controlling soil moisture, those controlling seed dispersal, etc.), while varying all other parameters. An incomplete test reduces the number of simulations required but allows the interpretation of the influence and interaction of different components of the model. To understand the influence of each parameter (set) we

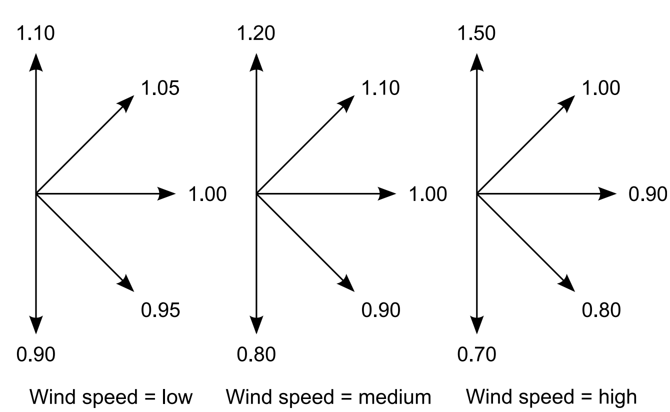

Fig. 3. Fire Risk as a function of wind strength and direction. Classification of values used in Eq. (8).

examine the proportional change in the state variable for a given change in the parameter(s) in question.

We consider two state variables, one that measures land-cover composition and a second that reflects the wildfire regime. To examine land-cover composition we consider the proportion of landscape in the shrubland land-cover class after 250 simulated years. This measure represents (in the model at least) the initial 'coloniser' vegetation, appearing immediately following disturbance, and thus gives an indication of the 'immaturity' of the landscape. Other landscape measures (e.g., the number of vegetation patches and Shannon's index of diversity for vegetation classes) are strongly correlated with the abundance of shrubland. To examine changes in the wildfire regime we examine the wildfire power-law frequency-area scaling exponent β (as described above in Section 3.7). Ten model repetitions are made for each parameter set (Table 5), and the mean proportion of the landscape occupied by shrubland is compared with the value for the base parameter set. We use a *t*-test to assess if the land-cover composition for each set of model repetitions is statistically significantly different from the default parameter set. Fires from the ten repetitions are combined to form a single data set for wildfire-regime analyses. Malamud et al. (2005) suggest that β values for datasets with less than 100 fires should be treated cautiously. Combining results from the 10 runs ensures sufficient data points to produce robust estimates of the 95% confidence limit for β. Consequently, we are unable to test for significant differences between β in sensitivity analyses. Two other state variables are used to characterise the simulated wildfire regimes (Eq. (6)): largest burned area for a single event and total burned area for the duration of simulation replicates. Mean fire size is not considered as a state variable because the power-law distribution does not have any defined moments (where the first moment is the 'average').

4. Results

4.1. Model calibration

Using parameter values specified in Table 5 (also see Appendix 1 and online supplementary material), output from the vegetation state-and-transition model (in an absence of disturbance) shows model behaviour consistent with the basic model construction (Figs. 4 and 5). From an initial landscape dominated by shrubland (all human land uses initially replaced with shrubland), succession-type changes shift landscape composition toward the hypothetical evergreen oak climax (Fig. 4). Spatially, deciduous species are found in the bottoms of river valleys and pine forest tends to be found in drier, more exposed areas (Fig. 5).

Millington et al. (2006) showed that the β values for all studies using the power-law distribution to describe empirical wildfire regimes fell in the range 1.1–2.2. Malamud et al. (2005) found β values for fires on United States Forestry Service (USFS) during 1970–2000 for Bailey's (1995) Mediterranean and Mediterranean Mountains ecoregions were 1.30 and 1.46, respectively. Ricotta et al. (2001) found that fire regimes for regions of Spain between 1974 and 1999 fell in the range 1.1–1.5. Combined results for ten 250-year model replicates with default *LCF* values (Table 6) produce $\beta = 1.32 \pm 0.09$ (95% confidence interval, Fig. 6a). These values are consistent with the range of empirical values found by Malamud et al. (2005) and Ricotta et al. (2001). The poisson probability distribution (Eq. (6)) using climate ignition scaling parameter $m = 12$ (Eq. (7)) results in zero, one or two fires per year for an example 250-year replicate with default *LCF* values (Fig. 7).

4.2. Sensitivity analysis

Sensitivity analysis suggests that (i) increases in parameter values cause greater changes in the state variable than decreases, and (ii) that the most sensitive parameters are related to wildfire spread and soil moisture (Table 5). Parameters for seed dispersal have limited

Table 5
Sensitivity Analysis Results. Default parameter values are shown with the corresponding ±10% values used in analyses. Multivariate permutations are shown at bottom. Results are shown for each univariate and multivariate analysis for two state variables; mean final proportion of the landscape in shrubland cover for 10 simulation replicates (Shrubland) and wildfire frequency-area power-law distribution exponent β (Wildfire β, see Eq. (9)). Asterisks denote shrubland proportions that are statistically different from results for default parameters (0.026). Values in brackets for shrubland are percentage change relative to the default results. Results in bold indicate a change in shrubland area greater than 15%. Wildfire β results are for all fires from the 10 simulation replicates. Values in brackets for Wildfire β values are 95% confidence intervals.

Parameter	Value	Value (+10%)	Value (−10%)	Shrubland (+10%)	Shrubland (−10%)	Wildfire β (+10%)	Wildfire β (−10%)
Univariate Analyses							
Xeric Soil Moisture Class (mm, Eq. (3))	500	550	450	**0.038*** **(46%)**	**0.012***(**−55%)**	1.31 (±0.10)	1.33 (±0.09)
Hydric Soil Moisture Class (mm, Eq. (3))	1000	1100	900	**0.019*** (**−28%)**	**0.036*** **(35%)**	1.34 (±0.09)	1.30 (±0.09)
Land-Cover Flammability (probability, Eq. (8))	0.23, 0.23, 0.22, 0.24, 0.22	0.253, 0.253, 0.242, 0.264, 0.242	0.207, 0.207, 0.198, 0.216, 0.198	**0.063*** **(142%)**	**0.021** (**−21%)**	1.17 (±0.04)	1.45 (±0.13)
Slope Risk (dimensionless, Eq. (8))	0.80, 0.90, 0.95, 1.00, 1.05, 1.10, 1.20	0.880, 0.990, 1.045, 1.100, 1.155, 1.210, 1.320	0.720, 0.810, 0.855, 0.900, 0.945, 0.990, 1.080	**0.090*** **(244%)**	**0.022** (**−16%)**	1.14 (±0.04)	1.42 (±0.12)
Fuel-Moisture Risk (dimensionless, Eq. (8))	0.8, 0.9, 1.0, 1.1, 1.2	0.88, 0.99, 1.10, 1.21, 1.32	0.72, 0.81, 0.90, 0.99, 1.08	**0.091*** **(248%)**	**0.020*** (**−24%)**	1.18 (±0.04)	1.40 (±0.14)
Climate Ignition Scaling, m (dimensionless, Eq. (7))	12	14	10	0.025 (−4%)	0.024 (−10%)	1.37 (±0.09)	1.30 (±0.08)
Oak Mortality, OM (yr^2 $fire^{-1}$, Statement 7)	200	220	180	0.024 (−7%)	0.029 (12%)	1.34 (±0.09)	1.34 (±0.09)
Oak MD (m, Eq. (1))	500	550	450	0.023 (−12%)	0.025 (−4%)	1.33 (±0.09)	1.36 (±0.09)
Oak Mean (m, Eq. (1))	46.7	51.37	42.03	0.024 (−9%)	0.027 (3%)	1.35 (±0.09)	1.34 (±0.08)
Oak SD (m, Eq. (1))	2.34	2.574	2.106	0.024 (−9%)	0.023 (−11%)	1.29 (±0.10)	1.33 (±0.09)
Wind ED (m, Eq. (2))	75	82.5	67.5	0.024 (−8%)	0.026 (0%)	1.29 (±0.09)	1.31 (±0.08)
Multivariate Analysis							
Wind MD (m, Eq. (2))	100	110	90	0.024 (−8%)	0.023 (−12%)	1.33 (±0.09)	1.28 (±0.10)
Moisture (Eq. (3))	Xeric & Hydric Soil Moisture	550, 1100	450, 900	**0.042*** **(61%)**	0.024 (−7%)	1.29 (±0.09)	1.32 (±0.09)
Vegetation (Eq. (8))	Land-Cover Flammability, Slope, Fuel Moisture, Climate Ignition & Oak Mortality	Values as above	Values as above	**0.611*** **(2231%)**	**0.018*** **(33%)**	0.98 (±0.12)	1.66 (±0.22)
Oak (Eq. (1))	Oak MD, Mean & SD	550, 51.37, 2.574	450, 42.03, 2.106	0.025 (−6%)	0.024 (−9%)	1.35 (±0.10)	1.37 (±0.09)
Wind (Eq. (2))	Wind ED & MD	82.5, 110	67.5, 90	0.028 (8%)	**0.018*** (**−30%)**	1.32 (±0.08)	1.33 (±0.08)

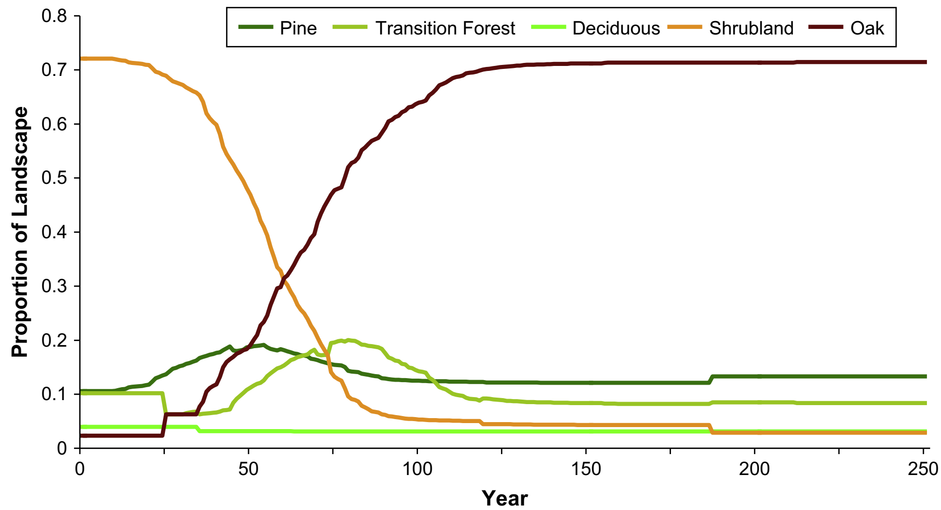

Fig. 4. Time series of landscape land-cover composition from the vegetation-dynamics model. This result is for a single 'no disturbance' model run and demonstrates the conceptual model of succession toward different 'climax' vegetation covers dependent on environmental conditions and seed availability (Fig. 2). Units on the *x* axis are in years from the start of the model run.

effects on the state variables. Individual parameters (univariate analysis) with statistically significant effects on land-cover composition are xeric and hydric soil-moisture classes, land-cover flammability (increase only), slope risk (increase only), and fuel-moisture risk. Multivariate permutation analyses show that land-cover composition is sensitive to moisture parameters (increase only), vegetation parameters, and wind seed dispersal (decrease only). Increases in all vegetation parameters (multivariate analysis) have by far the largest effect on land-cover composition, causing an order of magnitude greater proportional increase in shrubland cover.

Only three individual parameters in the univariate analysis cause noticeable changes in β values (relative to 95% confidence limits). These parameters are all controls on modelled wildfire spread: vegetation flammability, slope risk, and fuel-moisture risk. Other parameters with significant effects on land-cover composition (e.g., soil-moisture classes) do not produce changes in β. The only parameter set to cause large changes in β values in the multivariate analysis is the vegetation parameter set. However, changes in these parameters also result in weaker power-law relationships between wildfire frequency and area (r^2 values, not shown, decrease with corresponding increases in 95% error limits). In the case of increases in vegetation parameters the power-law relationship collapses at large fire sizes (Fig. 6b).

A strong negative relationship between total flammability and values of β is evident (Fig. 8). This relationship indicates that as total land-cover flammability decreases, large fires become rarer relative to smaller fires. This behaviour is also indicated by trends in maximum fire size and mean total burned area, which increase with total flammability (Table 6). An increase in the frequency of fires with large area is not unexpected and highlights that while the frequency-area relationship remains a power-law, its exponent β value changes markedly.

5. Discussion and conclusions

5.1. Sensitivity analysis

The sensitivity analyses indicate several model parameters have a significant influence on land-cover change. Using two state variables, one a measure of land-cover composition and the second a measure of the wildfire regime (the frequency-area power-law distribution exponent, β), we are able to examine which aspects of the model these parameters influence. Parameters controlling soil moisture have a significant effect on land-cover composition (with greater proportional changes in the state variable than the parameter) but had limited influence on β values (Table 5). This behaviour indicates that these variables influence land-cover composition via vegetation succession processes rather than wildfire, and is consistent with the structure of the model and conceptualisation of succession trajectories and vegetation change (Fig. 2). The multivariate permutation analysis for moisture parameters caused significant change in land-cover composition in one direction (Table 5). Moisture gradients are known to be an important control on vegetation dynamics in Mediterranean environments (Zavala et al., 2000) and have been found to explain landscape patterns of resprouting better than disturbance frequency models (Clarke et al., 2005). Although LFSMs for Mediterranean environments have examined the effects of seed dispersal (Pausas, 1999b; Syphard et al., 2007), spatial patterns of vegetation types (Pausas, 2003, 2006) and fire return interval (Pausas, 2006; Syphard et al., 2007) on landscape dynamics, to the best of our knowledge no Mediterranean LFSMs have examined the effects of (soil) moisture availability. Recent analyses of the relationship between soil moisture and fertility at the landscape level (Svoray et al., 2007, 2008) mean that this is an aspect of Mediterranean landscape dynamics that can now be investigated in more detail with LFSMs. Future application of Mediterranean LFSMs (including the model presented here) will need to investigate these relationships at the landscape level in more detail, particularly with regards spatial patterns of moisture gradients.

In contrast to soil-moisture parameters, parameters controlling wildfire spread (land-cover flammability, slope risk, and fuel-moisture risk, Eq. (8)) affect both land-cover composition and wildfire β values. This fact indicates that these parameters are important controls on the representation of the wildfire regime, likely associated with critical threshold behaviour found in CA-type models (e.g., Ratz, 1995). Changes in the simulated wildfire regime subsequently effect land-cover composition; decreased β values result in significant increases in shrubland area (Table 5). In particular, shrubland area dramatically increases (from 3% to 61% of the landscape) when all 'vegetation' parameters are increased in the multivariate sensitivity analysis. Furthermore, this multivariate permutation results in the collapse of the wildfire frequency-area power-law relationship which has been shown empirically to be

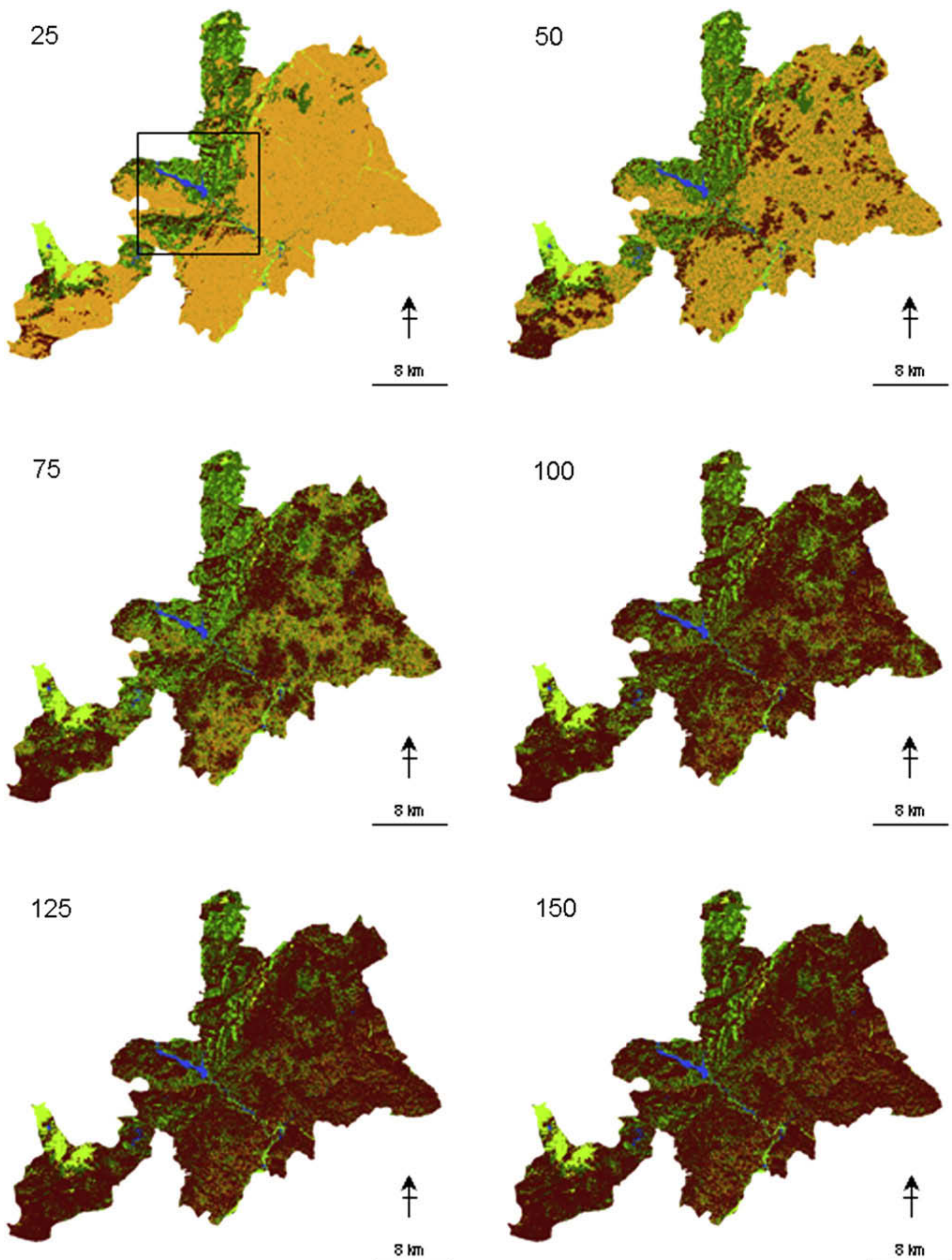

Fig. 5. Spatial representation of landscape change for the vegetation-dynamics model. These simulated land-cover maps for SPA 56 present a spatial representation of the time series shown in Fig. 4 (for 25 year intervals). The box on year 25 is the outline of the sub-section of the landscape on which we perform our sensitivity analyses. Colour legend as for Fig. 4.

robust across many regions of world (Millington et al., 2006). We observe deviation from the power-law relationship at larger fire areas for this vegetation permutation because fires spread to span the entire landscape (also see Malamud et al., 1998). This result suggests that the parameter values used for this multivariate permutation do not appropriately represent relationships between the variables as they exist in the study area. The use of the power-law relationship to parameterise the model is discussed in more detail below (Section 5.2).

Variation in seed-dispersal parameters did not result in significant differences in land-cover composition and did not influence wildfire β values. Proportional change in the state variable was generally equal to proportional change in the parameter. This behaviour indicates seed-dispersal parameters have less influence on landscape dynamics than moisture gradients and wildfire. However, decreasing both effective and maximum seed-dispersal distance parameters (Eq. (2)) in the multivariate permutation analyses did result in a significant effect on land-cover composition consistent with expectations (i.e., an increase in non-Forest land cover, Table 5). Our results are similar to the implementation of the LANDIS LFSM in a Mediterranean environment (Syphard et al., 2007). Although the significance of changes in land-cover composition between seed-dispersal scenarios was not reported, LANDIS results for effective wind dispersal distances of 50 m and 75 m were very similar (but did decrease noticeably when effective distance was reduced to 5 m – Fig. 7 in Syphard et al., 2007). Obligate seeders did not respond to changes in seed-dispersal distances (Syphard et al., 2007), again consistent with the behaviour

Table 6
Total Land-Cover Flammability Analysis Results. Values for *LCF* (see Eq. (8)) for each replicate analysed are presented for each land cover along with default values. Results are for all fires from 10 simulations for each replicate. Results indicate that increases in total *LCF* for all land-cover types result in decreases in wildfire power-law frequency-area distribution exponent β (see Eq. (9)), and increases in maximum area of a single fire and the sum of all fire areas. r^2 values are for the best fit line for the power-law frequency-area distribution.

Replicate	LCF (dimensionless)						Number of Fires	Max. Fire Area (km^2)	Sum Fire Area (km^2)	Wildfire β (dimensionless)	r^2
	Pine	T. Forest	Deciduous	Shrubland	Oak	Total					
TF1	0.19	0.19	0.18	0.20	0.18	**0.94**	892	0.25	12.4	1.52 (±0.16)	0.95
TF2	0.20	0.20	0.19	0.21	0.19	**0.99**	933	0.34	15.3	1.51 (±0.16)	0.95
TF3	0.21	0.21	0.20	0.22	0.20	**1.04**	962	0.61	26.8	1.42 (±0.11)	0.97
TF4	0.22	0.22	0.21	0.23	0.21	**1.09**	966	2.75	47.4	1.36 (±0.12)	0.96
Default	0.23	0.23	0.22	0.24	0.22	**1.14**	916	3.23	76.1	1.32 (±0.09)	0.97
TF5	0.24	0.24	0.23	0.25	0.23	**1.19**	947	11.27	206.9	1.26 (±0.06)	0.98
TF6	0.25	0.25	0.24	0.26	0.24	**1.24**	914	50.62	858.4	1.21 (±0.05)	0.98
TF7	0.26	0.26	0.25	0.27	0.25	**1.29**	931	135.23	4682.6	1.11 (±0.03)	0.99
TF8	0.27	0.27	0.26	0.28	0.26	**1.34**	952	162.01	20393.4	0.99 (±0.04)	0.98

observed in our model. Using an abstract Mediterranean LFSM, Pausas (1999b) showed variation in vegetation dynamics for different fire frequencies. Future use and refinement of our model will examine the interaction of different wildfire regimes with variations in seed-dispersal distance parameters.

5.2. Landscape model construction

Perry and Millington (2008) distinguish the complementary approaches of predictive and exploratory spatial modelling of succession-disturbance dynamics in forest ecosystems. The former combines understanding and data to predict system dynamics, whereas the latter aims to improve understanding of systems where uncertainty is high. Previous spatially explicit models of Mediterranean succession-disturbance dynamics at the landscape level have usually been exploratory and independent of empirical study areas (e.g., Zavala and Zea, 2004; Pausas, 2006). Recently Syphard et al. (2007) modified the LANDIS simulation model for use in California, but no LFSMs have been developed to represent actual landscapes in the Mediterranean Basin. The challenges of representing existing landscapes in the Mediterranean Basin using empirical data, highlight many of the aspects of Winsberg's (1999) 'epistemology of simulation'. That is, the development of our LFSM has required approximations, idealisations and transformations to confront an analytically intractable spatial and temporal problem in the face of sparse data. In turn, these have been justified on the basis of existing theory, available data, empirical generalisations, and the modellers' experience of the system and other attempts made to model it. The use of plant-functional types within a rule-based framework (derived largely from the RBCLM approach of McIntosh et al., 2003) is indicative of the qualitative simulation modelling approach necessitated by the current state of knowledge regarding Mediterranean vegetation dynamics over large spatial and temporal extents.

This current state of knowledge requires that models of Mediterranean succession-disturbance dynamics represent these phenomena at a coarser resolution than has been possible in other regions of the world (such as the northern hardwood forests of the Great Lakes region using LANDIS, He and Mladenoff, 1999). Nevertheless, the task of parameterising models that scale process knowledge and information from fine grains to large extents to represent empirical landscapes remains challenging. For example, studies have examined the flammability of Mediterranean vegetation (individual species) according to calorific value (Dimitrakopoulos and Panov, 2001), time-to-ignition (Dimitrakopoulos and Mateeva, 1998), and have classified flammability more

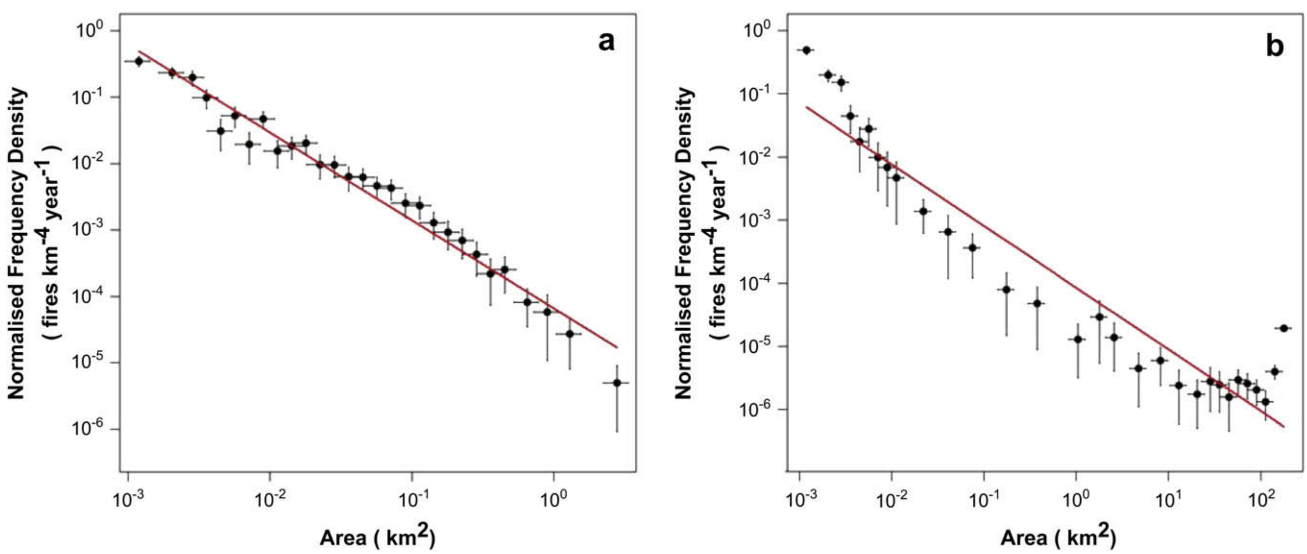

Fig. 6. Example model wildfire frequency-area distributions a) Default parameter values and b) +10% vegetation parameters (Table 5). Each plot is for data for ten 250-year model replicates. Points are normalised frequency densities $f(A)$ (number of fires per 'unit bin' of 1 km^2, normalised by the length of the model run in years and area of the study area in km^2) plotted as a function of wildfire area A. The solid line is the best least-squares fit to $\log[f(A)] = -\beta \cdot \log[A] + \log \alpha$ where β and α are constants. Vertical error bars (approximately 95% confidence) are two standard deviations of the normalised frequency densities $f(A)$ calculated as $\pm 2\sqrt{\delta N}$, where $\sqrt{\delta N}$ is the number of wildfires in a 'unit bin' of width δA. Note how the power-law relationship collapses at large fire sizes in b) as fires spread to span the entire sub-section of the landscape we analyse.

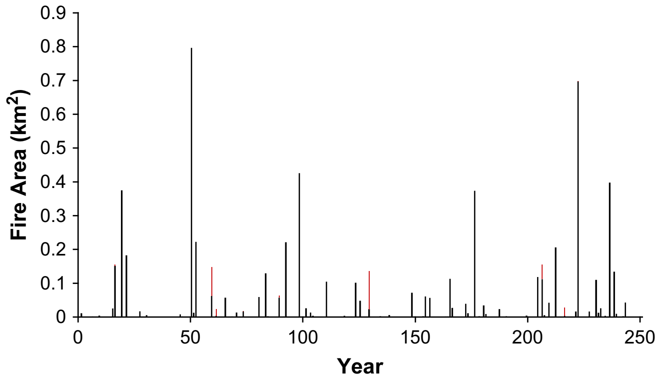

Fig. 7. Wildfire areas for a single 250-year model replicate with default parameter values. In this instance, the Poisson probability distribution for default climate parameters results in zero, one or two fires per year (multiple fires in a single year are represented by different coloured bars in the stacked plot) with fires ranging in size from 0.0009 (a single pixel) to 0.7965 km^2.

generally (Dimitrakopoulos and Papaioannou, 2001). However, no studies are known to have considered the explicit probability of spread at the scale considered here (coarse land-cover vegetation classes at the landscape level) for the CA approach. Consequently, we ranked land-covers in order of flammability according to these previous studies (Dimitrakopoulos and Mateeva, 1998; Dimitrakopoulos and Panov, 2001; Dimitrakopoulos and Papaioannou, 2001). Multiple sets of flammability probabilities using this ranking were then tested to find the set that reproduced empirical wildfire-regime characteristics (i.e., similar β values). Thus, the wildfire component of the model is parameterised by examining how changes in fine-scale parameters influence the broad-scale patterns produced by the model, which in turn are compared to those observed empirically. This 'pattern-oriented modelling' approach (Grimm et al., 1996, 2005) examines the influence of fine-scale parameters on broad-scale measures of system behaviour to select appropriate values for the fine-scale parameters. This is particularly useful in our case where poor understanding of the more fine-scale processes driving broader-scale system dynamics and patterns makes it difficult to parameterise the mechanistic model. Recently, Grimm et al. (2005) emphasised the use of the pattern-oriented approach for agent-based modelling, but the approach has also been used for cellular-automata models (Grimm et al., 1996; Wiegand et al., 2003). We suggest our approach, utilising β, is useful for the parameterisation of cellular-automata-based wildfire behaviour models used in landscape succession-disturbance models in that it captures the overall behaviour and pattern of fire spread in the landscape.

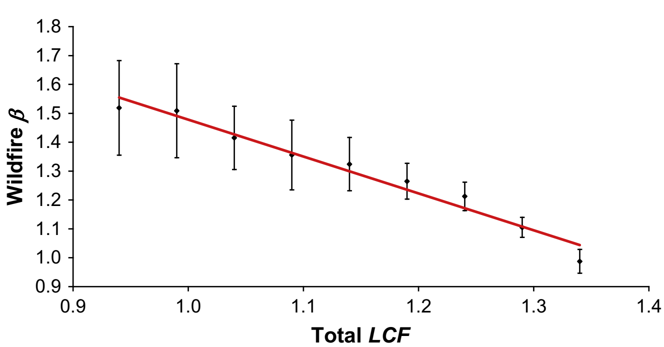

Fig. 8. Relationship between β and total *LCF*. Error bars are lower/upper 95% confidence intervals, calculated from the standard error. The trend line has $r^2 = 0.97$.

5.3. Future model development and use

In this paper we have presented the initial steps to conceptualise, construct and verify a Mediterranean landscape fire-succession model. Our results show that this version of the model is functioning as intended and have highlighted which parameters have greatest influence on two aspects of the model; land-cover change and the wildfire regime. There are several aspects of our modelling that could be improved to ensure appropriate representation of Mediterranean landscape-level patterns and processes. For example, as highlighted above, Mediterranean LFSMs (including ours) need to consider the importance of soil-moisture gradients for vegetation in more detail. Our model will also be refined and used to examine the interaction of wildfire regimes and seed-dispersal parameters. Furthermore, this analysis will need to be explicitly spatial as we have focused in this paper on the aggregated, landscape-level response of land-cover composition and wildfire-regime characteristics.

Understanding about the flammability of vegetation is improving for Mediterranean environments and will allow a more detailed representation of fire intensity and fire effects in the future. For example, recent progress on the understanding of fuel loads and canopy-fire characteristics for typical Mediterranean-type vegetation (e.g., Dimitrakopoulos et al., 2007; Mitsopoulos and Dimitrakopoulos, 2007) will aid our development of a vertically layered (three-dimensional) CA wildfire spread model. This would help overcome the limitations of our current model which is unable to distinguish between ground and crown fires, and only considers stand-replacing wildfire events. Incorporating these processes will in turn allow us to examine the effects of different intensities of wildfires for landscape-level vegetation dynamics.

Future versions of the model may also need to consider the introduction (via afforestation of abandoned agricultural land) of non-native tree species such as Eucalyptus (*Eucalyptus globulus*). Eucalyptus has been introduced in Spain since the 1940s for timber production because it is fast-growing (Chas Amil, 2007). However, because this species is also highly flammability its introduction may also be partly responsible for the increases in wildfire frequency and extent in the Mediterranean Basin during recent decades (Shakesby et al., 1996). Although not currently an issue in the region we have considered here, including a 'eucalyptus' land cover in the model may be necessary for its application in other areas of the Mediterranean Basin.

We intend to use our model to investigate potential impacts of climate change on Mediterranean landscape wildfire and vegetation dynamics. Currently, our ability to do this is restricted by the annual temporal resolution of the model which is unable to represent the strong seasonality of the Mediterranean-type climate (Wainwright and Thornes, 2004). In Mediterranean environments vegetation flourishes in spring following high rainfall during late autumn/early winter months, but has dried and reaches its most flammable condition in late summer/early autumn after the long hot, dry summers. Appropriate representation of seasonal climate will be vital to ensure LFSMs are able to accurately account for impacts of climate change on wildfire and vegetation dynamics in Mediterranean environments. Furthermore, achieving this representational fidelity would allow investigation of post-fire effects that result from the interaction of climate, vegetation and wildfire. For example, Pausas (1999a) has highlighted the importance of considering the potential for soil erosion as a result of torrential rainfall in late autumn following summer wildfire that removes stabilising vegetation.

The most important development we intend for this model, however, is the added representation of human activity as a disturbance. Other than wildfire, the main impediment to vegetation succession-type processes in our study area, and other areas in the

Mediterranean Basin, is agriculture (both arable and pastoral). However, in recent years SPA 56 has experienced agricultural decline leading to land abandonment and decreases in agricultural land covers with commensurate increases in shrub and forest land covers (Romero-Calcerrada and Perry, 2004). Our model has been developed with the intention of integrating modules that explicitly represent human land-use activity to examine these dynamics. Understanding the interaction of wildfire and vegetation dynamics with potential future land-use change due to changing social and economic activity will benefit natural resources managers and local planning officials. One of the next steps with our modelling research is to integrate our agent-based model of traditional Mediterranean agricultural decision-making (Millington et al., 2008) with the model presented here to investigate how human land-use influences the wildfire regime and, consequently, vegetation dynamics. This integrated model will allow us to investigate the relative importance of climate change *versus* changes in human socio-economic activity, and specifically lightning- *versus* human-caused fires. Accounting for the influence of human activity on succession-disturbance dynamics is particularly important in regions such as the Mediterranean Basin where humans are a pervasive presence in the landscape and have been for many generations, but which are now undergoing social and economic change.

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Appendix 1. Soil Conservation Service Curve Numbers. Values used for CN (dimensionless) in Eq. (5). Infiltration capacity decreases from soil A to soil D. Sources: Ferrér et al. (1995), Symeonakis et al. (2004).

Soil	Pine	T. Forest	Pasture	Deciduous	Shrubland	Oak	HOP	Crops	Urban	Burnt
Slope < 3%										
A	35	35	71	35	46	35	56	62	93	91
B	54	54	78	54	68	54	75	72	93	91
C	69	69	82	69	78	69	86	78	93	91
D	77	77	86	77	83	77	91	82	93	91
Slope ≥ 3%										
A	39	39	76	39	46	39	56	65	96	94
B	60	60	82	60	68	60	75	76	96	94
C	73	73	88	73	78	73	86	84	96	94
D	78	78	91	78	83	78	91	87	96	94

Appendix. Supplementary information

Supplementary information associated with this article can be found, in the online version, at doi:10.1016/j.envsoft.2009.03.013

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