



A model of plant community dynamics based on replacement networks

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Keywords

Aleppo pine; Complex systems; Disturbance; Ecological networks; Facilitation; Forest dynamics; Holm oak; *Pinus halepensis*; *Quercus ilex*; Species co-existence

Nomenclature

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Introduction

Natural vegetation plays a central role in key ecosystem services, such as climate control, soil fertility or biodiversity conservation (Isbell et al. 2011). The fast transformations of vegetation under the current global change scenario challenge the ability of community ecology to anticipate how plant assemblages change under natural or

Abstract

Questions: When a tree or a shrub dies, the space it occupied can be overtaken by plants that were recruiting beneath it or colonized by new species. Such replacement processes can drive the temporal change in species abundance in a plant community. Can we predict the dynamics of a real plant community using observational data on plant–plant recruitment interactions? What would be the relative importance of recruitment interactions vs life-history traits in determining community dynamics?

Location: Forest communities dominated by *Pinus halepensis* and *Quercus ilex* in SE Spain.

Methods: We develop a continuous time non-linear model that can be easily parameterized with empirical data for the interactions between adult and juvenile plants recruiting beneath them. These interactions form a complex replacement network (or matrix) that is the backbone of the model. We parameterize the model with life-history data from the literature and from recruitment interactions observed in a successional community 12 yr after a forest fire. We explore the behaviour of the model under different intensities of chronic disturbance, and after modifications of the structure of the replacement network and the values of the parameters.

Results: The model predicts that the current community of the burned area will develop into a forest very similar quantitatively to the surrounding mature forests, as long as the rates of chronic disturbance remain very low. For increasingly higher levels of chronic disturbance, the community would reach stable states resembling a mixed pine–oak forest, a degraded oak forest, an oak dehesa and, finally, a steppe-like vegetation. All these types of plant assemblages can currently be found throughout the study area. These predictions are less sensitive to variation in the estimates of species' life history (i.e. growth, death and colonization rates) than to variation in the structure of the recruitment matrix.

Conclusions: The model projects realistic community dynamics. The analysis of the model suggest that understanding the structure of replacement networks and how they are assembled can contribute significantly to our knowledge of the dynamics and stability of forest plant communities.

human-induced disturbances (Chazdon 2008). Even though there have been many theoretical advances and syntheses on the mechanisms promoting species co-existence (Chesson 2000; Silvertown 2004; Siepielski & McPeck 2010), we still need to improve our ability to predict real community dynamics (Agrawal et al. 2007).

Plant community dynamics (i.e. the patterns of temporal change in the relative abundance of species in local

plant communities) is usually modelled as a process of replacement, whereby the death of one plant, or large parts of it, releases space where individuals of the same or a different species can grow or recruit (e.g. Horn 1976; Grubb 1977; Pacala et al. 1998; Hubbell 2001). Current models of plant community dynamics assume that any species can grow or recruit in the space released by individuals of any other species (typically, a dead plant is replaced in the models by choosing a new recruit among all the species in the community). Thus, in such models, the species of a local community are involved in a sort of panmictic replacement (all-replacing-all) process. However, many field studies have documented mechanisms that can prevent replacement from being panmictic. There is ample evidence that seed dispersal limitation or biases (Rother et al. 2013; Rey & Alcántara 2014), allelopathy (Inderjit et al. 2011), specialized pathogens or parasites (Janzen 1970) or plant soil legacies (Van der Voorde et al. 2011) can prevent the recruitment of some plant species in the presence of some other species or in the space formerly occupied by other species. Moreover, field studies that have documented the interactions between recruiting individuals and adult plants at the community level strongly suggest that recruitment is not even close to panmictic (Verdú & Valiente-Banuet 2008; Alcántara & Rey 2012). For example, in Mexican arid and semi-arid communities, plant species recruit only 15–35% of the species available in the community (Verdú & Valiente-Banuet 2008). Recognition that recruitment is not panmictic at the community level can have important consequences for our understanding of plant community dynamics. For example, George & Bazzaz (1999) found that understory ferns can filter the sapling bank, favouring the recruitment of certain canopy tree species against others, so the presence or absence of ferns in the forest floor can drive the relative abundance of canopy trees in the forest. A similar effect has recently been documented in the case of bamboos and several tree species in a tropical forest (Rother et al. 2013).

Although the concept of replacement dynamics is not new, it has not been used as the central focus in developing mechanistic models of community dynamics (Myer 2012). Horn's (1976) use of Markovian models (see also Siles et al. 2008) was close to it, but such models subsume many processes (e.g. recruitment, growth and survival) under a single parameter (the transition probability), so they do not allow investigating the role of these processes as drivers of the dynamics. We propose a compartmental model based on the concept of replacement dynamics. Compartmental models are used to characterize systems whose dynamics are driven by the interchange of resources between its components. For example, compartmental models have been used to study the dynamics and

stability of food webs (Yodzis & Innes 1992) and peatlands (Pastor et al. 2002). In the case of a plant assemblage, the compartments of the model would be the groups of individuals of each species, and space can be considered as the resource that is interchanged between them through replacement processes (Grubb 1977; Alcántara & Rey 2012; Myer 2012). Living space is not by itself a resource, but it provides access to essential resources, so it can be considered as a surrogate for resources (Van Hulst 1992). The backbone of the model is the replacement network represented by a matrix of interactions between adult and juvenile plants recruiting beneath them. This network describes which species recruit under which other species, and the corresponding matrix describes the density of recruitment of each species under every species in the assemblage.

A network approach can improve our understanding of plant community dynamics; moreover, it can also make the analysis of plant community dynamics more easily comparable and complementary with the analysis of ecosystem or food web models, so that both fields can share analytical and theoretical developments (e.g. Alcántara & Rey 2012, 2014). The recognition that the network of interactions between species is key to understand community dynamics spurred research on food web properties over the last decades. For example, it has allowed progress in understanding how real food webs are assembled, how the strength of interactions affect food web or ecosystem stability and how the very structure of predator–prey interaction networks affects food web persistence and resistance to disturbance (see Pascual & Dunne 2006; Moore & de Ruiter 2012 and references therein). Such topics are of great relevance for conservation and management purposes. These advances rely on two key instruments: (1) incorporation of graph theory in the analysis of food web structure (Roberts 1978; Dunne et al. 2002; Allesina & Bodini 2005), and (2) use of dynamic models that can be easily parameterized with real-world data (e.g. Gal et al. 2009; Boit et al. 2012) and that allow explicit consideration of food web structure (Brose et al. 2006; Williams 2008; Stouffer & Bascompte 2010, 2011). Plant community ecology has not yet incorporated these instruments within its research agenda, although the few attempts made so far are promising. For example, Bohn et al. (2011) explored the role of competition and disturbance on the structure of communities in a model that included populations with different theoretically derived plant life strategies. On the other hand, recent studies (Verdú & Valiente-Banuet 2008, 2011) show that the structure of plant–plant facilitation networks is influenced by the phylogenetic distance between nurse plants and the recruits beneath them, and that this structure prevents

species extinction, thus preserving biodiversity. In Alcántara & Rey (2012) we showed that replacement networks seem to have a simple functional structure, and that such structure allows the long-term co-existence of most species in the assemblage, even if one of them were forced to extinction.

The compartmental model of plant community dynamics we introduce here can be easily parameterized with real-world data, so it can be coupled to theoretical or empirical replacement networks to explore their dynamics or to assess different aspects of their stability. To introduce the model, we use it to study the successional dynamics of a woody plant assemblage dominated by Aleppo pine (*Pinus halepensis*) in southern Spain, and how the process can vary depending on the level of chronic disturbance. Provided the model reproduced realistic patterns of change in the studied vegetation, we further explore the influence of life-history traits (i.e. the rates of growth, death and colonization of disturbed space) and the structure of the recruitment network on the dynamics of the community.

Methods

Study area

The field study was conducted in a *Pinus halepensis* forest in southern Spain (UTM 30S 4168N, 434E; 680–875 m a.s.l.). This type of forest is protected under the type '9540 – Mediterranean pine forests with endemic Mesogeian pines' in the EU Habitats Directive, covering 3.37×10^6 ha in Spain, of which 1.05×10^6 ha are dominated by *P. halepensis* (Ruiz Benito et al. 2009). Forests dominated by *P. halepensis* in dry Mediterranean environments occur from southeast Spain through the Balearic Islands to southern France, are particularly rich in shrub species and present a favourable conservation status throughout (Ruiz Benito et al. 2009). In September 2009 we collected data on the natural recruitment of woody plants in a 6-ha forest stand affected by fire in 1997 (building phase area hereafter), and nearby forested areas not affected by fire (forest area hereafter). This pair of areas was appropriate for modelling and validation since, according to aerial photographs, the pair had the same vegetation before the fire and had not been severely disturbed after fire. Therefore, we will assume that building phase and nearby forest areas are successional stages of the same type of community, so that vegetation currently in the building phase will eventually transform into the vegetation we can observe today in the forest. It is widely accepted that in Mediterranean forests, in the absence of relevant ecological changes, the same pre-disturbance community develops spontaneously only a few decades after fire (Trabaud 1994; Whelan 1995). Indeed,

Rodrigo et al. (2004) showed that this is the case in forests dominated by *P. halepensis*.

Replacement model of plant community dynamics

The model defines the dynamics of plant cover over time in a local plant assemblage. For the purpose of our model, we define a local assemblage as a group of plants of different species living within an area whose extension would potentially allow the seeds of any of these species to reach a spot under the canopy of an individual of any species in the assemblage. Each compartment comprises all the individual plants of the same species present in the assemblage (for simplicity, hereafter we will refer to the compartments as 'species'). Each species is characterized by its cover and is connected to other species by interchanges of space (Fig. 1). The rate of variation in cover of a species (x_i) in a local assemblage formed by n species is given by:

$$\frac{dx_i}{dt} = x_i G_i + \sum_{j=1}^n R_{ij(i \neq j)} - x_i D_i + C_i \quad (1)$$

The first term in Eq. 1 is the increase in cover through vegetative growth. We will assume that the vegetative growth rate (G_i) of the local population of species i decreases as total cover in the community approaches its maximum (K):

$$G_i = g_i \left(1 - \frac{\sum_{j=1}^n x_j}{K} \right) \quad (2)$$

where g_i is the average rate of increase in cover of adult plants of species i . This term incorporates the effects of intra- and interspecific competition between adult plants on growth.

The second term in Eq. 1 is the capture of space through the replacement of dead individuals. This replacement occurs at a rate that depends on the death rate of adult plants (d_j), on the input density (α_{ij}) of saplings of species i under species j (i.e. the input of seeds and their survival to reach the sapling stage) and on the average size of saplings of species i (s_i):

$$R_{ij} = x_j d_j s_i \alpha_{ij}; \text{ with } i \neq j \quad (3)$$

The third term in Eq. 1 represents the rate of space loss, which can be caused by the death of adult individuals of species i through aging (d_i) or by external chronic disturbances (u), which constantly create new free space. This chronic disturbance would be the compound result of factors operating continuously, like strong winds or

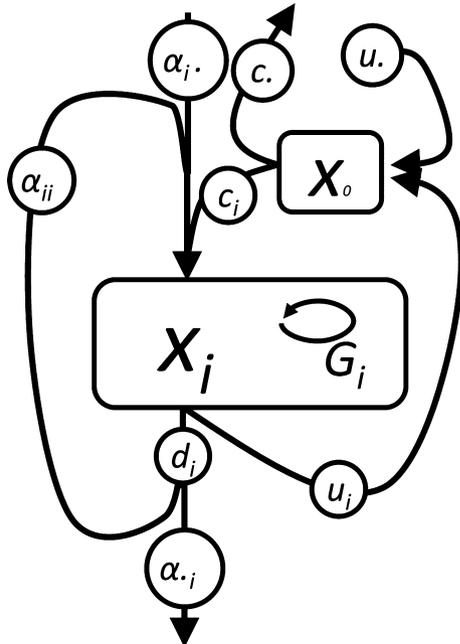


Fig. 1. Basic structure of flows in the compartmental model determining the variation in cover of species i (x_i). The population of species i is represented as a compartment that can increase in size through growth (G_i) or through recruitment. The input of space through recruitment can be the result of the recruitment of species i under other nurse species (α_{ij} ; note that ‘ i ’ in the suffix means ‘any other species’), under conspecific individuals (α_{ii}) or in open spaces created by disturbances (c_i). In turn, a decrease in cover of species i can be a consequence of the death of individuals (d_i) or of the action of external disturbances (u) that create new open space (x_o). Part of the space lost after the death of individuals of species i , or parts of individuals (e.g. branches or shoots), will be overtaken by individuals of different species growing beneath (α_{ij}), but part of this space can be regained by species i if its seedlings can recruit under conspecific plants ($\alpha_{ii} > 0$). Similarly, part of the space lost through disturbance can be regained through colonization if seedlings can recruit in newly opened spaces ($c_i > 0$). Other species can reduce available open spaces by recruiting there (c_j) or may release space by disturbance (u).

vertebrate herbivores. These losses can be partially compensated for by recruitment and growth of conspecific saplings under dead plants ($d_i s_i \alpha_{ii}$), so:

$$D_i = u + d_i - d_i s_i \alpha_{ii} \tag{4}$$

The last term in Eq. 1 (C_i) represents the colonization of disturbed space. Colonization rate depends on density of recruitment ($s_i c_i$) of saplings in spaces not covered by a plant, and the rate at which such spaces are created through chronic disturbances (u):

$$C_i = c_i s_i u \tag{5}$$

These assumptions result in the model specified as:

$$x'_i = x_i \left(g_i \left(1 - \frac{\sum_{j=1}^n x_j}{K} \right) - d_i + d_i s_i \alpha_{ii} - u \right) + \sum_{j=1}^n (i \neq j) x_j d_j s_i \alpha_{ij} + c_i s_i u \tag{6}$$

The term on the left side (x'_i) is the derivative of cover with respect to time. The first term on the right side contains the balance of vegetative growth, recruitment under conspecifics and death in each species; the second term contains recruitment through replacement of other species; and the third term is the recruitment through colonization of disturbed space. Table 1 summarizes the parameters required to implement the model.

Equation 6 has the general form of a complex non-linear (density-dependent) system:

$$x' = Ax(t) + CU \tag{6'}$$

A is a $n \times n$ square matrix with main diagonal elements:

$$a_{ii} = \left(g_i \left(1 - \frac{\sum_{j=1}^n x_j}{K} \right) - (1 - s_i \alpha_{ii}) d_i - u \right)$$

and off-diagonal elements:

$$a_{ij} = d_j s_i \alpha_{ij}$$

Matrix A is the replacement matrix that is at the heart of the model. It is the mathematical description of the

Table 1. Summary of the variables and constants in the model.

Symbol	Meaning	Source	Unit
n	Number of species	Observed	
x_i	Cover of species i	Observed	$m^2 \cdot ha^{-1}$
α_{ij}	Input density of saplings of species i under adult plants of species j	Observed	saplings $\cdot m_j^{-2}$
g_i	Average rate of increase in density cover of adult plants of species i	Estimated	yr^{-1}
s_i	Average size of juvenile plants of species i	Estimated	$m_i^2 \cdot sapling_i^{-1}$
d_i	Annual death rate of species i	Estimated	yr^{-1}
c_i	Input density of saplings of species i in free space	Observed	saplings $\cdot m_o^{-2}$
u	External disturbance rate: constant annual rate of creation of free space through disturbance	Assumed	yr^{-1}
K	Maximum density of the set of modelled species in the reference community	Observed	$m^2 \cdot ha^{-1}$
am_i	Age at maturity	Estimated	yr

community's replacement network. $x(t)$ is a vector of size n with elements x_i representing the cover of each species at time t . C is a n vector formed by c_i s_i elements. We assume that vector C is time-invariant. Finally, U represents the constant input of new open space through disturbance (u).

The model incorporates many assumptions largely enforced by the lack of data required to incorporate more realistic details, so there is plenty of room for refinements, as in every model. Most of our assumptions have to do with the variability among species, or the lack thereof, in their responses to the environment. For example, we assume that the effect of intra- and interspecific competition on growth is the same for all species, and that chronic disturbance affects all species with the same intensity. Another relevant set of assumptions is related to the temporal invariance of most model parameters. It is possible to incorporate species-specific differences and temporal variability in these parameters to gain realism, but it would be at the expense of complicating considerably the process of parameterization of the model, thus decreasing its ease of use.

Data collection

In the building phase area we surveyed four parallel 50 m \times 5-m transects spaced at least 50 m from each other. In each transect we recorded the presence of saplings of woody species, noting in each case the species recruiting and the species growing directly above it. Plants less than 1 yr old were not considered. Data from the four transects were pooled to estimate the values of α_{ij} and c_i . To estimate species cover we used the four transects of the building phase area and another four transects conducted in the forest area. In each transect we estimated the cover of each species by placing a 5-m pole (divided in ten 0.5-m segments) horizontally at 1-m intervals along the transect. We recorded the species (plus open ground and bedrock when present) contacting the pole in every segment at ground level, 1 m above ground and in the tree canopy stratum. The cover of each species (x_i) was obtained as the number of contacts with the species relative to the total number of points sampled along transects expressed on a per hectare basis. We used, for modelling purposes, only species covering more than 5 m² in transects of building phase area.

Model parameterization

Full details on the procedures used to parameterize the model are shown in Appendix S1. Briefly, estimates of recruitment rates (α_{ij} and c_i) were obtained from transects

conducted in the building phase area. To obtain estimates of life-history traits we used allometric relationships, following the approach used in food-web models (e.g. Yodzis & Innes 1992). We used a Gompertz function (Zeide 2004; Caplat et al. 2008) to obtain g_i and s_i . The age of maturity was obtained from the literature and from our own observations (Table 2). We also collected information from the literature on the typical life span and height of 84 species of shrubs and trees from 33 families, and used a general linear model to estimate the life span of the species in the model. We used the reciprocal of life span as a constant intrinsic mortality rate (d_i) that represents all causes of mortality related to aging.

Analysis of the model

Unless otherwise stated, we used the species cover of the building phase area as initial state vector in the simulations. To simulate the post-fire successional dynamics we need to account for delays of recruitment occurring in the years immediately after fire. Thus, in the simulations we imposed two conditions: (i) that recruitment occurs in the first year after fire through resprouting and fire-stimulated seed germination; (ii) subsequently, recruitment is absent for a few years, until the first generation of plants of each species reach the age of maturity. To implement these conditions we multiplied the α_{ij} and c_i terms by the unit step function defined so that it takes values of 0 from $t = 0$ to $t = \text{age at maturity of species } i$, and 1 thereafter.

We found numerical solutions to the model with the species-specific parameters obtained for the building phase area, using Mathematica (v 8.0; Wolfram Research, Champaign, IL, US). Life history and abundance parameters of the species in the model are shown in Table 2, while the recruitment matrix (α_{ij}) and colonization vector (c_i) are presented in Table 3 (see also Appendix S2). Every run of the model spanned 2000 yr. The projection of our model depicts the general dynamics of the community in the very long term, under constant life history, interaction and disturbance rates. Obviously, many forces can modify this general trend: temporal fluctuations in the levels of disturbance will occur, climate change may modify the result of interactions and the life-history traits, and we did not consider the possibility of colonization of the local community by new species from the regional species pool. These and other processes can be incorporated into the model, but in the present study we focus on the inertia that life history and replacement interactions impose on vegetation dynamics. For this reason we chose a very long projection time, because it takes several cycles of replacement to reach stability in the relative abundance of species, and each cycle lasts the life span of the longest-lived species in the community (284 yr in *Q. ilex*). In fact, it takes more

Table 2. Life-history traits and cover of the species included in the models. Typical height of adult plants (H), age at maturity (am), life span (LS), average size of juvenile plants (s), average annual growth rate of adult plants (g), and annual death rate (d). See main text for the methods used to estimate the parameters. Sources of data for life span are indicated in Appendix S1.

Species	Life-history Traits						Cover (x_i) (m ² ·ha ⁻¹)			
	H_i (m)	am_i (yr)	LS_i (yr)	s_i (m ²)	g_i (m ² ·yr ⁻¹)	d_i (yr ⁻¹)	Building Phase		Forest	
							Mean	SD	Mean	SD
<i>Cistus albidus</i>	1	2.5 ^a	33.64	0.116	0.016	0.03	2722.7	919.9	225.8	102.6
<i>Cistus salvifolius</i>	0.6	2.5 ^a	26.73	0.042	0.007	0.037	334.4	159.4	3.4	6.8
<i>Daphne gnidium</i>	2	2 ^b	45.96	0.577	0.045	0.022	117.3	27.0	34.7	59.5
<i>Genista cynerea</i>	1.5	2 ^b	20.24	0.325	0.061	0.049	136.2	170.7	0.25*	0.5
<i>Phillyrea angustifolia</i>	3	10 ^c	79.45	0.413	0.102	0.013	343.8	157.7	460.2	360.1
<i>Phlomis purpurea</i>	1	2 ^b	20.71	0.144	0.027	0.048	631.1	558.9	206.1	140.1
<i>Pinus halepensis</i>	20	10 ^d	206.84	2.51	0.219	0.005	166.1	109.4	2997.5	752.9
<i>Pistacia lentiscus</i>	4	10.3 ^b	96.57	0.528	0.108	0.01	717.0	329.7	960.4	820.8
<i>Pistacia terebinthus</i>	5	10.3 ^b	106.78	0.674	0.124	0.009	922.6	618.4	807.7	490.1
<i>Quercus coccifera</i>	3	21.1 ^b	120.94	0.123	0.045	0.008	211.3	222.6	439.1	734.9
<i>Quercus ilex</i>	20	21.1 ^b	284.16	2.422	0.334	0.004	85.4	78.0	59.7	81.4
<i>Rhamnus lycioides</i>	2.5	2 ^b	95.07	0.901	0.033	0.011	182.4	113.8	255.7	116.3
<i>Rosmarinus officinalis</i>	2	2 ^b	28.3	0.577	0.076	0.035	2368.8	752.2	2134.9	916.4
<i>Thymus mastichina</i>	0.5	2 ^b	15.16	0.144	0.038	0.066	49.8	99.5	3.9	7.8
<i>Ulex parviflorus</i>	1.2	2 ^b	18.31	0.831	0.175	0.055	230.3	396.6	37.7	75.3

**Genista cynerea* was present in the forest at very low density, and it did not occur in transects. To allow calculation of SDIs for this species, we assigned it 0.25 m² (the smallest cover possible through our sampling method) in one transect.

^aPapió (1988); ^bVerdú (2002); ^cPers. obs.; ^dLloret et al. (2003).

Table 3. Recruitment matrix (α_{ij}) showing the input density of saplings of species i (rows) under plants of species j (columns). Full species names are given in Table 2. The order of species is the same in rows and columns. The main diagonal indicates recruitment under conspecific plants. The last column represents the colonization vector (recruitment density in open space) c_i . A standardized form of this table is shown in Appendix S2, where we also show the percentage of recruits under nurse species not included in the model.

	<i>C. alb.</i>	<i>C. sal.</i>	<i>D. gni.</i>	<i>G. cyn.</i>	<i>P. ang.</i>	<i>P. pur.</i>	<i>P. hal.</i>	<i>P. len.</i>	<i>P. ter.</i>	<i>Q. coc.</i>	<i>Q. ile.</i>	<i>R. lyc.</i>	<i>R. off.</i>	<i>T. mas.</i>	<i>U. par.</i>	c_i
<i>C. alb.</i>	0.181	0	0.005	0.005	0.011	0.011	0.027	0.450	0.044	0.011	0	0.005	0.582	0	0.005	0.252
<i>C. sal.</i>	0.578	0	0.048	0	0	0	0.193	0.193	0.048	0.096	0	0	1.494	0	0	0.771
<i>D. gni.</i>	0.138	0	0	0	0	0	0	0	0	0	0	0.138	0.828	0	0	0
<i>G. cyn.</i>	0.111	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>P. ang.</i>	0.188	0	0	0	0	0	0	0.141	0.329	0	0	0.047	0.047	0	0	0
<i>P. pur.</i>	0.643	0	0	0.048	0.071	0.048	0.238	0.238	1.000	0.024	0	0.024	0.810	0	0.024	1.238
<i>P. hal.</i>	0.933	0	0.067	0	0.067	0.200	0.667	0.200	0.733	0.067	0	0	0.933	0	0	0.533
<i>P. len.</i>	0	0	0	0	0	0	0.023	0	0	0	0	0	0	0	0	0
<i>P. ter.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0.035	0	0	0
<i>Q. coc.</i>	0.078	0	0	0	0	0	0.157	0.078	0.314	0	0	0	0.314	0	0	0
<i>Q. ile.</i>	1.400	0	0	0	0	0	0.200	1.200	0	0	0	0	0.600	0	0	0
<i>R. lyc.</i>	0.087	0	0	0	0.087	0	0	0.348	0.609	0.087	0	0	0.435	0	0	0.087
<i>R. off.</i>	0.103	0	0.007	0	0	0.007	0.007	0	0.007	0	0	0	0.096	0	0	0.068
<i>T. mas.</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.615
<i>U. par.</i>	0	0	0	0	0	0	0	0	0	0	0	0.073	0	0	0	0

than 600 yr to reach a relative stability of the model's projections.

To assess the fit of the model with different parameterizations we calculated, for each species every year in the simulations, the absolute value of the difference between its observed cover in the forest area and its predicted

cover, divided by the SD of its cover in the forest area. We will use the acronym SDIs for this standardized distance averaged across species at a given time in the simulations. SDIs <1.96 indicates that the predicted cover of species in the model falls, on average, within the 95% confidence interval of their observed abundances (see

Boit et al. 2012 for a similar analysis). Since cover varied by orders of magnitude among species, we log-transformed the observed and predicted cover, so that rare and dominant species contribute similarly to these indices of goodness of fit.

We conducted three sets of simulations to explore the dynamics of the model and the role of its different elements on the model's output.

1 *Effect of chronic disturbance (u) on the stable state of the community*: Chronic disturbance rate is measured as the proportion of cover that is affected by disturbances every year. Since we lack direct estimates of this rate and it can show a large spatial and temporal variability, we conducted independent runs of the model for values of u between 0 and 1 at steps of 0.01 to assess the general effect of u , and then for u between 0 and 0.1 at steps of 0.002. We will refer to the model run with the value of u that produced the best fit ($u = 0.03$; see Results) as the 'basal model'.

2 *Sensitivity to parameter variation*: Sensitivity analysis evaluates which parameters govern model output more significantly. Basically, we modified the values of each component of the basal model (i.e. initial state vector, life history vectors, colonization vector and recruitment matrix) in independent sets of 100 simulations. In each set, the elements of the corresponding vectors or matrix were multiplied by a vector or matrix of values randomly chosen from a uniform distribution between 0.75 and 1.25 (i.e. we assumed up to 25% variability around the nominal estimates of each parameter) while the rest of elements were held at their nominal values. In the case of life history (i.e. vectors of sapling size and adult growth rate, age at maturity and life span) the vectors were multiplied in each run by the same vector of random values so that the within-species covariance among life-history traits was preserved. Application of these random vectors and matrices preserved the structure of the original ones (i.e. the position of the non-zero entries in each vector or matrix) as well as the mean and variance of the parameters, but changed their relative values among species.

3 *Sensitivity to matrix structure*: The last set of simulations explored the effect of the structure of the recruitment matrix (i.e. the distribution of the non-zero values within the matrix) on the long-term community predicted by the basal model. First, we ran 100 simulations of the basal model but in each run we used a random permutation of the recruitment matrix (with rows and columns independently permuted), so that the mean and variance of matrix elements was preserved but their distribution across the matrix varied. We also conducted this procedure but using non-zero values randomly generated from a probability distribution with the same mean and variance as the original recruitment matrix. The results of this last simulation were qualitatively the same as those obtained from the

random permutation of the original recruitment matrix, so we do not report these results.

Most models of forest dynamics assume explicitly or implicitly that every species can potentially recruit under, and thus eventually replace, dead individuals of any other species (Purves et al. 2008; Adler et al. 2010). In other words, all the replacements of individuals of one species by individuals of the same or another species are allowed. This assumption would imply that all the α_{ij} elements of the recruitment matrix would be larger than zero (i.e. the matrix would be saturated). We explored two of such saturated matrices, one where unobserved links are assumed to be there at a low density ($\alpha_{ij} = 0.005$ saplings·m⁻², the minimum observed recruitment density), and one where all α_{ij} were assumed to be equal ($\alpha_{ij} = 0.268$ saplings·m⁻², the mean observed recruitment density).

We also explored the influence of each individual element of the matrix on the output of the basal model. To this end, we ran simulations of the basal model but each time using a recruitment matrix with one of its non-zero elements reset to zero. Finally, we explored the possible effect of adding individual elements to the recruitment matrix. In this case, in each run we used the original recruitment matrix but setting one of its zero entries to the minimum observed recruitment density.

Results

Observed woody communities in the building phase and forest areas

The building phase had 24 species of woody plants, with a total cover of 79.0% (Appendix S3). The dominant species were the shrubs *Cistus albidus* (30.6%) and *Rosmarinus officinalis* (24.5%). We chose for the model 15 species (Table 2), which summed 98.6% of the total cover of woody plants. The forest area had also 24 species with a total cover of 87.4% (Appendix S3), and was dominated by *P. halepensis* (33.8%) and *R. officinalis* (22.4%). The 15 species chosen for the model represented 94.3% of the woody species cover in the forest (Table 2). There were 17 species common to both areas, seven species were found only in the building phase and seven only in the forest. *Genista cynerea* was the only species in the model that occurred in the building phase but not in the forest.

Effect of chronic disturbance on the community

Changing the value of u would produce a strong impact on the community (Fig. 2). Most species could be able to tolerate u values below 0.012 with decreases in their long-term cover of around 42%, but would decline abruptly under more intense disturbance, settling at extremely small long-term cover (<1 m²·ha⁻¹) if u were above 0.03.

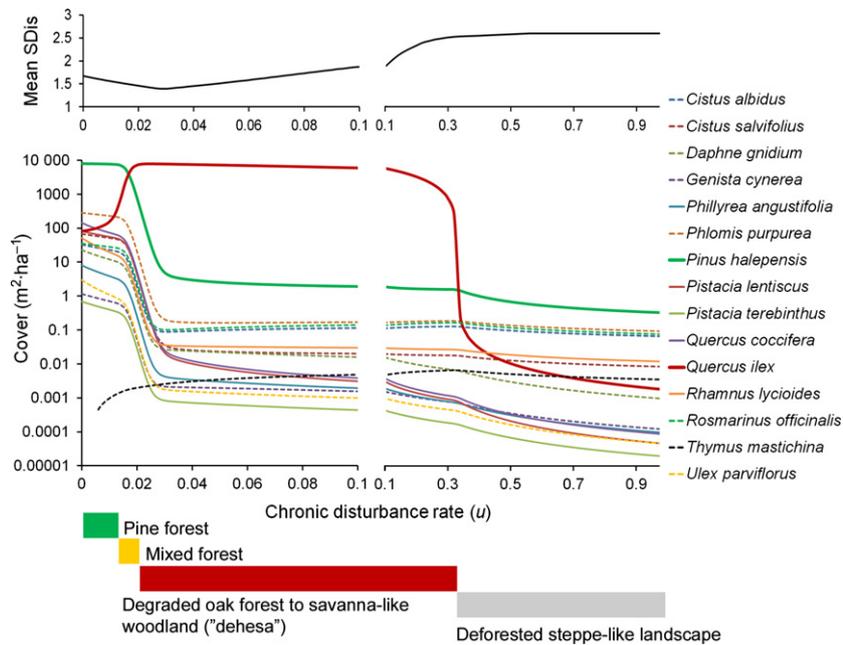


Fig. 2. Effect of chronic disturbance rate (u) on long-term species cover. Top panel: Goodness of fit between predicted and observed species cover. For each value of u , the line indicates the best value of the mean standardized distance (SDIs) obtained along the 2000 yr spanned by the corresponding simulation. SDIs below 1.96 indicates that the predicted cover for a species is, on average, within the 95% confidence interval of its cover observed in real forest area (i.e. lower values indicate a better fit between predicted and observed cover). Middle panel: cover of each species predicted at the end of the simulations (2000 yr) for every value of u . Small shrubs are represented with dashed lines, tall shrubs and small trees with thin continuous lines, and trees with thick continuous lines. Cover is in log-scale for clearer display of the rarer species. Lower panel: four main types of community that can be described along the gradient of habitat degradation represented by increasing levels of u . Note that there is a scale change in the u -axis at $u = 0.1$ to show the effect of small values of u in more detail.

On the other hand, *Quercus ilex* would increase in cover for u between 0 and 0.024, declining continuously thereafter to reach extremely small values for $u > 0.32$. SDIs was lower than 1.96 for u values between 0 and 0.1, with the best value (SDIs = 1.416) for $u = 0.03$.

The gradient of degradation caused by chronic disturbance can be interpreted as a continuum of possible communities, with three main points of change occurring at u values around 0.016, 0.018 and 0.32. For u between 0 and 0.016 the long-term community would be a pine forest with total cover of woody plants between 8764 and 8207 $\text{m}^2\cdot\text{ha}^{-1}$, *P. halepensis* being the dominant tree, representing 86–92% of the woody plant cover, *Q. ilex* 1–8.6%, and shrubs 5–8%. For $u = 0$, *P. halepensis* will be the dominant species from year 47 onwards, while *Q. ilex* would reach its maximum cover in year 137, declining thereafter (Fig. 3). The maximum similarity with the current forest (SDIs = 1.672) would be reached in year 109.

For u in the range 0.016–0.018 the long-term community would be a mixed pine–oak forest with total cover of woody plants around 8067–8129 $\text{m}^2\cdot\text{ha}^{-1}$, *P. halepensis* and *Q. ilex* representing between 30% and 67% of the woody plant cover, respectively, and shrubs 2–4%. For

$u = 0.017$, the maximum similarity to the forest (SDIs = 1.480) would occur in year 74 (Fig. 3).

For values of u between 0.018 and 0.32, total cover of woody plants would decrease from 8016 to 267 $\text{m}^2\cdot\text{ha}^{-1}$ and would always be strongly dominated by *Q. ilex* (>90% of the woody plant cover). This gradient resembles the transition from a degraded oak forest to an oak savanna (dehesa). For $u = 0.03$ (the value of u that produced the best fit of the model), *P. halepensis* will dominate the vegetation in the short term (from year 39 to year 109), but will start declining and be replaced as the dominant species by *Q. ilex* from year 121 (Fig. 3). Under this level of chronic disturbance, the current vegetation of the building phase should reach a maximum similarity to the forest (SDIs = 1.416) after 60 yr, with a predicted cover within 1.96 SD of the observed values in 13 species, but overestimated for *G. cynerea* (SDIs = 6.456) and underestimated for *R. officinalis* (SDIs = -5.016). At this time, the total predicted tree cover would be 40.67%, and 28.89% for total cover of shrubs.

Finally, for u above 0.32 total cover of woody plants would be less than 100 $\text{m}^2\cdot\text{ha}^{-1}$, representing a deforested vegetation with very few and scattered pines (ca. 60% of

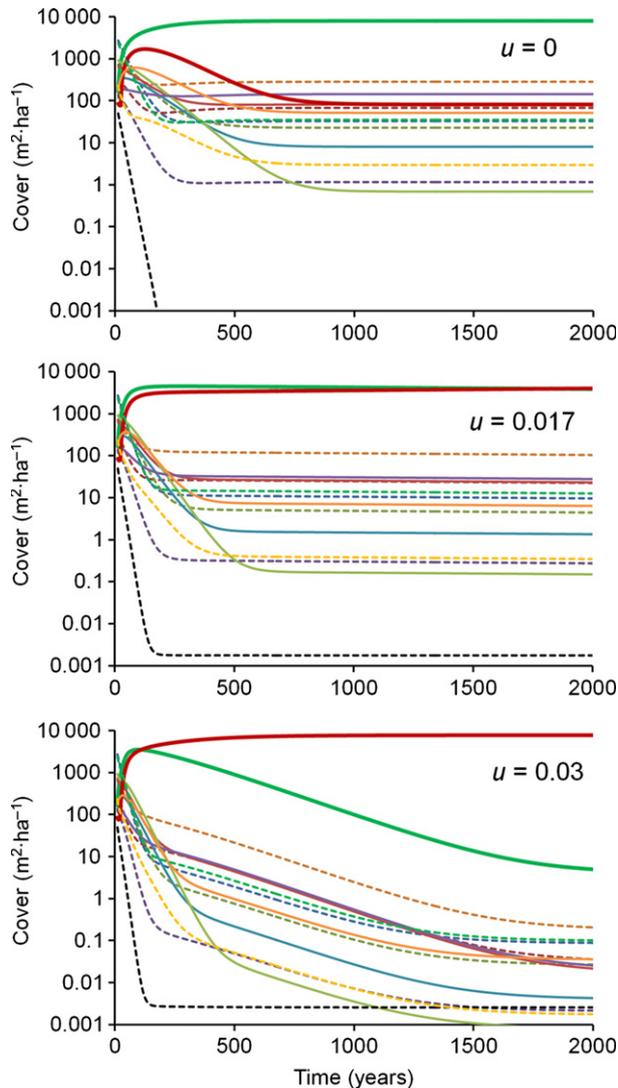


Fig. 3. Projection of the successional dynamics expected for the current vegetation under three intensities of chronic disturbance rate ($u = 0, 0.017$ and 0.03) that result in different types of forest community (pine forest, mixed pine–oak forest and a degraded oak woodland or dehesa, respectively; see Fig. 2). The initial state vector was the same in the three simulations and was set as the observed current state of the building phase area (12 yr after fire). Lines are coded as in Fig. 2.

the woody plant cover), oaks (ca. 1% of the woody plant cover) and shrubs (ca. 39% of the woody plant cover).

Sensitivity to parameter variation

Adding random variability in the elements of the initial state vector resulted in a mean SDis of 1.474 (range: 1.305–1.961). Variation in the positive entries of the recruitment matrix also had a small effect on model performance, with mean SDis across runs of 1.417 (range:

1.352–1.469). Similarly, variation in the colonization vector scarcely affected model performance, with a mean SDis of 1.413 (range: 1.372–1.470). Finally, variation in the life-history traits also had a small effect on model performance, with a mean SDis of 1.454 (range: 1.264–1.667). Thus, model performance was scarcely affected by 25% random variation in its parameters, since the mean values of SDis obtained in all simulations were only slightly larger than the SDis of the basal model, and the values of SDis in each set of simulations were mostly lower than 1.96.

Sensitivity to matrix structure

Random permutations of the elements of the recruitment matrix had a very strong effect on model performance. Randomly permuted matrices had a mean SDis of 2.344, with a range between 1.552 and 2.599, so all the permutations performed worse than the basal model. Similarly, a saturated recruitment matrix resulted in worse performance than the basal model, both when we added the minimum observed recruitment density to all the entries on the original matrix (SDis = 2.09), or when we set all the entries of the matrix to the mean observed recruitment density (SDis = 2.599). Addition of single entries in the matrix tended to decrease model performance (mean SDis = 1.514; range: 1.385–2.599). The strongest decrease occurred when we added the possibility of recruitment of *Cistus salvifolius* (SDis = 2.599) or *Q. coccifera* (SDis = 2.064) under other species. In contrast, removal of some entries tended to improve the model's predictions (mean SDis = 1.410; range: 1.193–1.472). The largest improvement was observed after removing the recruitment of *G. cynerea* under *C. albidus*.

Discussion

Quantitative and qualitative validation of the model

The results of the model reproduce the expected state of the vegetation in the studied plot some decades after fire. Ideally, one would compare the temporal trajectory of each species in the model against the trajectory observed along the succession in the real community. Unfortunately, it would take several decades, even a few hundred years in the case of forest communities, to collect such information (see Spencer & Tanner 2008 or Boit et al. 2012 for examples in communities with faster dynamics), and there are not published chronosequences of the succession in this type of forest in the study area. Although we lack direct quantitative information about the successional development of the vegetation in the study site, our model renders a set of predictions that a realistic model of the successional dynamics should achieve. On the one hand, the projected community reaches a state very similar to the

studied forest: the predicted cover of 13 out of 15 species modelled was within the 95% confidence interval of the observed mean. On the other hand, the model predicts that the current burned area will reach its maximum similarity with the studied forest in 60 yr. This time scale is congruent with the fact that the study area was largely deforested in 1956 (according to aerial photographs), so the vegetation of the studied forest has been growing without major disturbance for more than 50 yr.

Additionally, the projections of our model depict alternative states of the vegetation that agree with vegetation types occurring under different intensities of disturbance in the study area. Alternative successional trajectories can be driven by the chronic action of large herbivores (Hidding et al. 2013; Sankaran et al. 2013). Under the environmental conditions of the study site, our results suggest the next sequence of vegetation change in response to chronic disturbance: (1) forests dominated by *P. halepensis* should occur under negligible levels of chronic disturbance ($u < 0.016$); as disturbance increases, the cover of *Q. ilex* increases, so (2) a mixed oak–pine forest develops for disturbance rates between 0.016 and 0.018, until pines start declining and the oaks become the dominant trees. In (3), a degraded oak forest with scarce shrub cover occurs at disturbance rates between 0.018 and 0.32; finally, for disturbance rates above 0.32, the cover of woody vegetation would almost disappear, leaving (4) a landscape dominated by bare ground (possibly covered with annuals or non-woody perennials, which were not included in the model) with scarce patches of small shrubs and occasionally some scattered solitary pines or oaks. This prediction assumes a very large recurrence time for major disturbance events. With recurrence times of major fire events in the range of 100–200 yr (as documented for southern Spain by Carrión et al. 2003), oaks would not reach dominance even under moderate levels of chronic disturbance, so pine and mixed pine–oak forests would prevail in the landscape (Fig. 3), as occurs in the study area. On the other hand, with shorter recurrence times, fire would become a strong and chronic disturbance, giving rise to the type of largely deforested landscapes we found for u values above 0.3.

The four types of vegetation predicted by the model for the study site are common in southeast Spain, and usually appear mixed, forming a mosaic landscape (Mapa Forestal de España 1997–2006). According to our results, this landscape could be a consequence of spatially heterogeneous levels of chronic disturbance, as could be expected in a region that has been anthropogenically altered for centuries. Unfortunately, there is hardly any published data on the disturbance rates caused by chronic biotic or abiotic agents in Mediterranean vegetation. Mancilla-Leytón et al. (2013) found, in a *Pinus pinea* forest of southern Spain, that domestic goats, at $2.7 \text{ ind}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$, increased

the extent of bare ground by approximately 6.7% per year. The wild goat (*Capra pyrenaica*) and the wild boar (*Sus scrofa*) are currently the only wild free-ranging large herbivores in the study area. The density of wild goats in the study area in the year 1996 was estimated between 0.031 and $0.044 \text{ ind}\cdot\text{ha}^{-1}$ (Pérez et al. 2002). Also in the study area, the density of wild boar has been estimated at between 0.008 and $0.022 \text{ ind}\cdot\text{ha}^{-1}$ (Bosch et al. 2012). Assuming that individuals of wild goat, wild boar and domestic goat have similar impacts on vegetation cover, the rate of disturbance caused by wild herbivores in the study area would be lower than $u = 0.002$, which would allow, according to our model, the persistence of Aleppo pine forests in these mountains in places not managed by man. However, domestic cattle (goats and sheep) abound in the study area, so we can expect a higher value of u in the burned plot, likely within the range of $u = 0.03$ (i.e. disturbance affecting $300 \text{ m}^2\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$) suggested by our model. At this level of disturbance, our model predicts a shift in dominance from pines to oaks in 109 yr. This shift in dominance has been also suggested to occur in 110–120 yr in a chronosequence study by Capitanio & Carcaillet (2008) in *P. halepensis* forests of southern France.

Our results agree with the conclusions of recent palynological studies in southern Spain. Changes in community composition after the Last Glacial Maximum in Southern Europe are characterized by the alternation and co-dominance of oaks and pines (Zabala et al. 2000; Carrión et al. 2010). This co-dominance has been interpreted as a complex mosaic of pure monospecific stands and patches of mixed species, with decreasing pine associated with increasing oak abundance (Zabala et al. 2000). Our model not only predicts that such a mosaic could be caused by spatial heterogeneity in disturbance levels, it also predicts that pines and oaks will tend to co-vary negatively in the long term: as Fig. 3 shows, the abundance of pines and oaks would co-vary positively during, approximately, the first 100 yr after major disturbance, and would thereafter co-vary negatively for centuries. On the other hand, Carrión et al. (2001, 2010) concluded that in the absence of the last millennium of human activity, many areas of natural vegetation currently dominated by oak woodlands would likely be dominated by some species of *Pinus*. The study of a pollen sequence in southeast Spain (Carrión & van Geel 1999) indicates that pine forests dominated the post-glacial landscape, resisting the invasion by oaks; but these pine forests were finally replaced by evergreen oak scrub after local fire disturbance by the Neolithic populations settled in the vicinity of the study site. Accordingly, our model shows that pine forest would dominate our study site at very low levels of disturbance, but sustained disturbance of low or moderate intensity after fire, as can be expected from domestic cattle and fuelwood extraction,

can transform the pine forest into oak woodland in a few generations.

Model sensitivity

Random variation in the model's parameters did not result in a strong change of its predictions (the largest SDIs in the sensitivity simulations was 1.96). Thus, the model's predictions are very robust against moderate errors in the estimation of its parameters. Nevertheless, the fact that some sensitivity runs achieved slightly better performance than the basal model indicates that there is room for improvement in parameter estimation. The largest improvement would likely be obtained through a better estimation of the life-history parameters, for which some sensitivity runs achieved mean SDIs of 1.26. On the one hand, this result is not surprising since we used very indirect estimates of life-history parameters while the rest of parameters were obtained directly in the field. On the other hand, this same result also suggests that our allometric estimates of life-history traits provide a very good approximation to the real parameter values. In fact, allometric estimates of species physiological and behavioural traits have proven their utility in ecosystem and food web models (Brose et al. 2006; Boit et al. 2012).

Model predictions are sensitive to changes in the structure of the recruitment matrix. Both saturated and randomly permuted matrices reduced model performance. Single element additions also decreased model performance, particularly when we added the possibility of recruitment of *C. salvifolius* or *Q. coccifera* under other species. This suggests that environmental conditions promoting the recruitment of these species under other plants could divert vegetation dynamics towards a different state. This possibility seems unlikely in the case of *C. salvifolius* since species of *Cistus* tend to recruit in open spaces, making it difficult to envisage environmental conditions enforcing its recruitment under other plants. However, *Q. coccifera* usually recruits under other plants, so this species could become co-dominant in Aleppo pine forests where the environmental conditions improved its recruitment. For example, *Q. coccifera* is the dominant understorey species in some Aleppo pine forests located in Mediterranean coastal areas of Spain (Rivas-Martínez 1987) and France (Trabaud et al. 1985).

Removal of some elements of the matrix contributed to improve model performance more than single element additions. The largest improvement occurred after removal of the recruitment of *G. cynerea* under *C. albidus*, implying the extinction of the former species, which is actually absent from the forest area. This result suggests that not all observed recruitment interactions would actually lead to replacement events. It is possible that some recruitment

interactions are so infrequent ($\alpha_{ij} \approx 0$) that their chances of participating in a replacement event are effectively zero. It is also possible that the death rate of some species is so small that very few replacement events have occurred in the studied forest. Whatever the reason, this result suggests that more detailed knowledge of species-specific replacement processes can improve the accuracy of the model.

Focus should be placed on replacement network structure

Analysis of the replacement dynamics model suggests that inaccuracy in the structure of the matrix is more detrimental for model performance than inaccuracy in the values of the matrix elements or in the life-history components of the model. Obviously, accuracy in all components of the model is necessary, but the emphasis of empirical studies on plant communities has been biased towards the accurate estimation of life-history parameters (Sheil & May 1996; Zens & Peart 2003) or interaction coefficients (Freckleton & Watkinson 2001), while accuracy in the structure of the interactions matrix has been largely neglected. Markov chain models of plant community dynamics (Horn 1976; Siles et al. 2008) are based on a transition probability matrix, so their results certainly depend strongly on the structure of the matrix. However, these studies have not addressed the effect of matrix structure on their results. Forest models assume 'panmictic recruitment', which amounts to using a saturated recruitment matrix. For assemblages formed by very few species, as is the case in the above-mentioned studies, the assumption of matrix saturation is likely appropriate. But many real assemblages are species-rich, and there is ample evidence that not all species recruit under any other, which indicates that real plant communities present structured recruitment matrices (Verdú & Valiente-Banuet 2008; Alcántara & Rey 2012). The disregard of the structure of the recruitment matrix in plant community models is unfortunate, because theoretical studies have shown that the structure of the interactions matrix can determine the co-existence of species in communities of competitors (Calcagno et al. 2006; Laird & Schamp 2006; Allesina & Levine 2011; Rojas-Echenique & Allesina 2011). Under the framework of replacement dynamics, the study of plant community dynamics could seek new advances (Myster 2012) similar to those achieved in the last decades in the study of ecosystem and food web dynamics (Pascual & Dunne 2006; Moore & de Ruiter 2012). For example, we can address questions like: does the structure of replacement networks differ between plant communities; what processes (e.g. seed dispersal, seed survival, germination, seedling establishment and survival) determine the structure of replacement networks; and does variation in these

processes affect the dynamic properties of plant communities (e.g. their resilience, resistance to invasion, equilibrium states)? By developing a mathematical model that can accommodate a large number of species and yet is easily parameterized, we seek to provide a new tool for the theoretical and empirical study of plant community dynamics, a tool that can be readily used in the management of environmental problems at the level of plant communities, and that, by the same token, can help to move this field towards the important advances that are taking place in the study of complex ecological networks.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Methods used to parameterize the model.

Appendix S2. Standardized form of recruitment matrix and colonization vector.

Appendix S3. Current cover of species in the study sites.