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THE DECLINE OF CORK OAK WOODLANDS: BIOTIC AND ABIOTIC INTERACTIONS IN PORTUGUESE *MONTADOS*

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The decline of cork oak woodlands: biotic and abiotic interactions in Portuguese *montados*

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A Rafael,

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ABSTRACT

Cork oak (*Quercus suber* L.) is an evergreen tree species restricted to the western Mediterranean basin. The largest cork oak woodlands are found in southern Portugal where they are known as *montados*. This Mediterranean ecosystem has a distinctive patchy appearance, which is the result of long-term ecological and land use dynamics that have shaped the landscape. In some cases, overexploitation of the land has led to soil degradation and lack of cork oak natural regeneration which is putting at risk the conservation of this ecosystem. This thesis studied the factors implicated in the decline of the *montado*, most particularly those which can have an effect on cork oak regeneration paying special attention to management. The initial evaluation of cork oak nutritional dynamics showed that the amount of leaf fall was identical in different land uses, there was a delayed decomposition rate in exposed soils (shrubs absent), and litter quality varied according to land use, which probably had an effect in soil microbial dynamics and in resultant nutrient release. Soil nematode communities were thus studied in order to test for differences among land uses. Nematode composition was a good predictor of changes in decomposition in the soil food web and plant succession in the *montado*, however temporal variations had a greater influence on results rather than land uses. Additionally, plant-parasitic nematodes were highly abundant in the soil but were not found in roots of cork oak seedlings, and therefore are not likely a limitation to cork oak regeneration. The lack of regeneration in cork oak populations severely affects the future of the *montado,* and on the third chapter of this thesis the most important limitations to cork oak during the early stages of regeneration (seedling emergence and survival to the first summer) were identified and related to management practices. Temperature and relative humidity regulated seedlings emergence and survival, and early-emerging seedlings showed higher drought tolerance and resprouting ability. Bigger acorns and higher plant cover significantly assisted emergence, survival and resprouting of seedlings, putting forward the preservation of the shrub layer and the reforestation by direct sowing as important strategies to overcome the lack of cork oak regeneration in *montados* in the short-term. To better support these conclusions, a System Dynamics Model was developed to recreate the management practices associated with cork oak *montado* and the main environmental factors influencing this ecosystem, *i.e.* acorn germination, competition, fire, drought, livestock damage, shrub clearing, and cork oak death. Model predictions confirmed that the long-term sustainability of this ecosystem seems to be guaranteed if we limit the quantity and quality of livestock and if we extend the shrub clearing period. This thesis presents evidence that the future of the cork oak *montado* is severely threatened while inadequate management practices are common.

Key-words: litter decomposition, natural regeneration, management, modelling, *Quercus suber*, soil nematodes.

RESUMO

O sobreiro (*Quercus suber* L.) é uma espécie arbórea perenifólia cuja distribuição mundial se restringe à parte ocidental da bacia mediterrânica. Os maiores bosques de sobreiro encontram-se no Sul de Portugal onde são conhecidos como montados. Este ecossistema mediterrânico tem a aparência característica de uma savana, que é o resultado de longas dinâmicas ecológicas e de uso do território que moldaram a paisagem. Em alguns casos, a sobreexploração destes territórios causou a degradação do solo e a ausência de regeneração natural de sobreiro que estão a pôr em risco a conservação deste ecosistema de elevada importância ecológica e económica. Nesta tese foram estudados os factores envolvidos no declínio do montado, em particular aqueles que podem ter um efeito na regeneração de sobreiro atendendo especialmente às prácticas de gestão. A avaliação inicial das dinâmicas nutricionais do sobreiro demonstrou que a quantidade de folhas caídas é idêntica em diferentes usos de solo, existe uma lenta taxa de decomposição em solos expostos (ausência de arbustos), e a qualidade da folhada apresenta diferenças entre usos de solo. Estes parâmetros têm provavelmente um efeito nas dinâmicas da microfauna do solo e consequente libertação de nutrientes. As comunidades de nemátodes do solo foram então estudadas para testar diferenças entre usos de solo. A composição de nemátodes foi um bom predictor de alterações no processo de decomposição nas cadeias tróficas do solo e na sucessão de plantas no montado, no entanto as variações temporais exerceram uma maior influência nos resultados que os usos de solo. Adicionalmente, o grupo de nemátodes parasitas de plantas foi muito abundante no solo mas não foram registados em raízes de plântulas de sobreiro, e daí não são provavelmente uma limitação à regeneração de sobreiro. A ausência de regeneração em populações de sobreiro é a maior ameaça ao futuro do montado e, no terceiro capítulo desta tese, os factores mais importantes que limitam o sobreiro durante as fases iniciais de regeneração foram identificados e relacionados com as práticas de gestão. A temperatura e a humidade relativa regulou a emergência e a sobrevivência das plântulas, e plântulas que emergiram mais cedo demonstraram maior tolerância à seca e capacidade de rebentar. Bolotas maiores e maior cobertura de plantas beneficiaram significativamente a emergência, sobrevivência e rebentação das plântulas, sugerindo que a preservação de um estrato arbustivo e a reflorestação por sementeira directa podem ser estratégias importantes para suplantar a ausência de regeneração nos montados a curto prazo. De modo a suportar estas conclusões, foi desenvolvido um

Modelo de Dinâmicas de Sistema para recriar as prácticas de gestão associadas ao montado de sobro e os principais factores ambientais que influenciam este ecossistema, *i.e.* germinação de bolotas, competição, fogo, seca, danos por gado, remoção de arbustos, e morte de árvores. As previsões do modelo confirmaram que a sustentabilidade deste ecossistema pode ser garantida se a quantidade e qualidade de gado forem limitadas e o período entre sucessivas limpezas do estrato arbustivo for alargado. Esta tese apresenta evidências de que o futuro do montado de sobro está bastante ameaçado enquanto práticas de gestão inadequadas forem comuns.

Palavras-chave: decomposição da folhada, gestão do montado, modelação, nemátodes do solo, *Quercus suber*, regeneração natural.

GENERAL INTRODUCTION

ECOLOGY OF A MEDITERRANEAN-TYPE ECOSYSTEM

THE *MONTADO* ECOSYSTEM

Cork oak woodlands are a Mediterranean-type ecosystem which has evolved through major geological and climatic changes that took place during the Pleistocene period and is a special mixture of nature and nurture in the Mediterranean region (Pereira & Pires da Fonseca 2003). Long-term human presence and related activities resulted in an agro-silvo-pastoral system typically adaptated to generally poor productive areas. The largest cork oak woodlands extend over an area of 3.1–6.3 million hectares in the southern Iberian Peninsula (Campos 1992, 1993, Joffre *et al.* 1999, Pereira & Pires da Fonseca 2003, Olea & Miguel-Ayanz 2006), where they are known as *montados* or *dehesas* (the Portuguese and Spanish names, respectively, hereafter referred to as *montados*).

Figure 1. View of a *montado* with its typical physiognomy of scattered trees distributed on extensive flat or hilly areas (photograph by R. Ceia).

The successive clearing of evergreen oak forests and shrublands, composed mainly by cork oak (*Quercus suber* L.) and holm oak (*Q. rotundifolia* Lam.) transformed the ecosystem into a physiognomy of scattered tree cover with densities varying from 20 to 80 trees per hectare (Joffre *et al.* 1999, Pinto-Correia & Mascarenhas 1999, Plieninger 2007; Fig. 1). Human management has favored habitat heterogeneity and biodiversity, creating a multiplicity of ecotones that resulted from the coevolution of man and nature, both acting as main drivers of biodiversity distribution in this ecosystem (di Castri 1981, Blondel & Aronson 1999, Pereira & Pires da Fonseca 2003, Blondel 2006). Even though *montados* show up as cork-holm oak ecosystems, their floristic composition (Ojeda *et al.* 1995, Pérez-Latorre 1996, Lourenço *et al.* 1998, Pereira & Pires da Fonseca 2003) is identical to that of the mid-Holocene Mediterranean forests (Carrión *et al.* 2000), but many of those plants are nowadays restricted to streamside tracks of land, stony uncultivated areas or quickset hedges. Indeed, of the total Iberian fauna and flora, *montados* support approximately 30 % of the plant species, 40 % of the bird species and 60% of both mammal and reptile species (Pineda & Montalvo 1995). Given their wide geographical range, biodiversity distribution patterns vary among *montados* (Pereira & Pires da Fonseca 2003). The ecological importance of the *montados* was stated with their classification as protected habitats in the framework of the European Union Natura 2000 Network (92/43/EEC Habitats Directive) and they are considered high nature value farming systems, according to the classification proposed by the European Environmental Agency (Paracchini *et al.* 2008). *Montados* are also biodiversity hotspots for conservation priorities, defined as areas featuring exceptional concentrations of endemic species and experiencing exceptional loss of habitat (Myers *et al.* 2000).

THE CORK OAK TREE

Cork oak is a sclerophyllous evergreen oak that occurs in non-carbonated soils in the western part of the Mediterranean Basin (Natividade 1950, Pausas *et al.* 2009a; Fig. 2). It occupies about 1.7 million hectares, to a great extent shared by seven countries located in south Europe and north Africa: Morocco, Algeria, Tunisia, Italy, France, Spain and Portugal (Mendes & Graça 2009; Fig. 3). In particular, Portugal holds > 40 % of the species area worldwide, approximately 737 000 hectares (DGRF 2007).

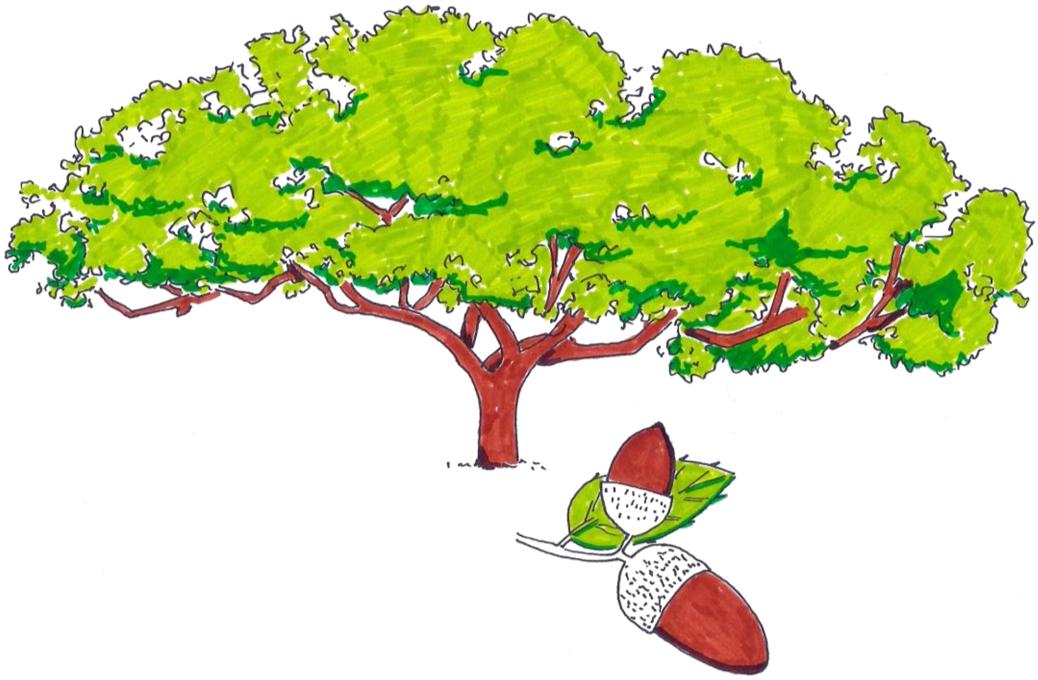

Figure 2. Cork oak tree with detail of leaf and acorns (drawing by M. Nunes).

The optimal climate for cork oak is a Mediterranean climate tempered by Atlantic influence, with annual precipitation between 600 and 800 mm and temperature ranging from 15 to 19 ºC. Trees can survive in drought years with less than 500 mm of annual precipitation due to their extensive and deep root systems. Cork oaks are almost entirely restricted to soils derived from siliceous rocks, being commonly considered acidophilus and calcifugous or lime intolerant (Natividade 1950, Montero & Cañellas 2003). Cork oak is a slow-growing tree with a lifespan of 250–300 years. During winter tree growth stops until temperatures rise again in spring and the increase of soil moisture by winter rainfall contributes to the next year’s spring growth; growth slows down or even stops in summer due to high temperatures (Costa & Pereira 2007).

Cork oak has a thick insulating bark where the same cork cambium remains active throughout the whole life and is formed of continuous layers of suberized cells, making it very different from other trees (Graça & Pereira 2000). The only other oak known to develop cork is the Chinese cork oak (*Quercus variabilis* Blume), however its cork yield is lower. Cork bark is considered a fire protection mechanism, product of evolution (Pausas 1997, Pausas *et al.* 2009a, Catry *et al.* 2012). The bark increases its thickness by about 2–5 mm per year, up to 20 cm, although the thickness depends mainly on genetical variation, tree age, climatic conditions and soil type (Pereira 2007). Because of its impermeability, the cork bark functions as a protective barrier between the living tissues inside the tree and the exterior environmental conditions, for example, preventing water loss and protecting against high temperatures. This bark is usually harvested and regrows after extraction, a traditional practice that does not harm the tree (Fig. 4). The cork cambium cell layer dies and a new cambium forms, the new cork cambium starts cell division, and a new layer is formed (Pereira & Tomé 2004, Pausas *et al.* 2009a).

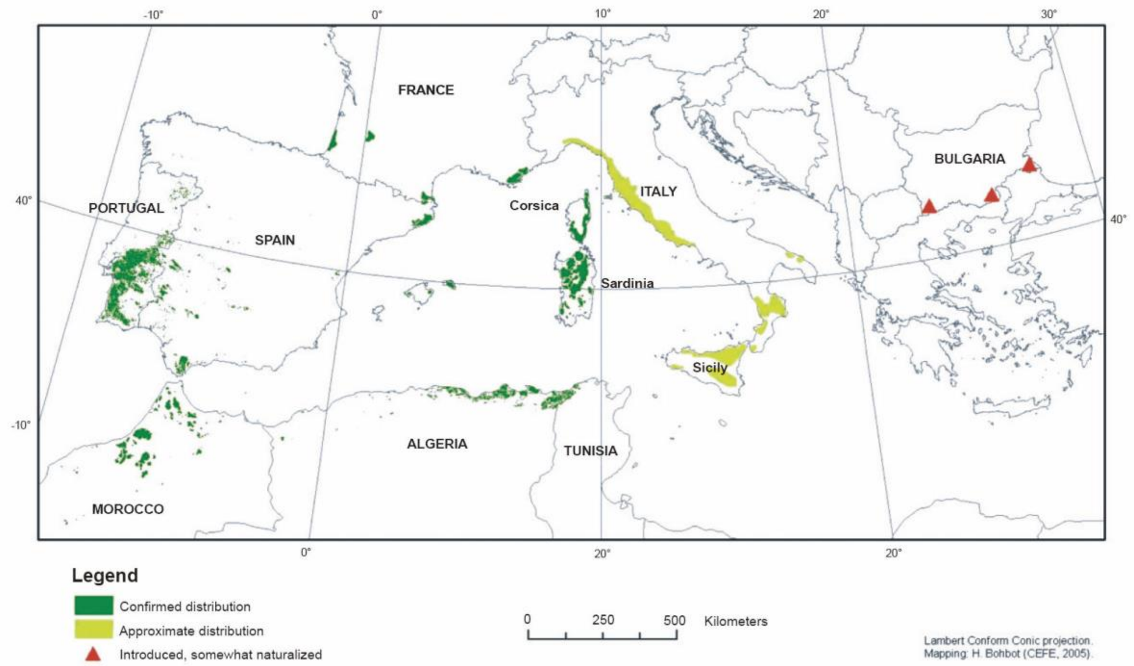

Figure ´25. Distribution of cork oak in the western Mediterranean Basin (reproduced from Bohbot *et al.* 2005).

Cork oak begins fructifying at an age of 15–20 years. This species produces male and female (unisexual) flowers in different inflorescences on the same individual (monoecy). Most trees have flowers of both sexes, with a high degree of self-incompatibility and the development of male and female flowers is asynchronous in each tree. Florescence occurs during a prolonged period from March to June. The vector for pollination is wind, and fertilised flowers mature into acorns. Cork oak produces both annual and biennial acorns; this heterogeneous acorn maturation pattern is an oddity among oaks. Annual acorns mature the same year as the flowers which produced them, while biennial acorns grow and mature in the autumn of the following year (Elena-Roselló *et al.* 1993). The proportion of annual and biennial acorns varies in response to environmental factors and meteorological conditions, limited by cold or drought (Díaz-Fernández *et al.* 2004, Pausas *et al.* 2009a). Cork oak is a mast-seeding tree meaning that each ten-year period there are two or three more abundant acorn harvests, which usually coincide with rainy springs. Production can vary greatly between individual trees within a population in any given year (Natividade 1950, Pausas *et al.* 2009a). Acorns fall to the ground from mature trees between October and February (Pérez-Ramos & Marañón 2008). They can be lost due to predation or be dispersed by animals (Fig. 5). The main seed dispersers are the European jay (*Garrulus glandarius*), dung beetles and mice. Jays promote long-distance dispersal, whereas dung beetles and mice promote short-distance dispersal (Acácio *et al.* 2007, Pons & Pausas 2007a, 2007b, Pérez-Ramos *et al.* 2013). They are often effective dispersal agents of oak species, with recruitment originating from unrecovered cached seeds (Herrera 1995). The acorn predators are mainly insects, such as the acorn weevil (*Curculio* spp., Coleoptera) and the acorn moth (*Cydia* spp., Lepidoptera), wood mouse (*Apodemus sylvaticus*), jay, red and roe deer (*Cervus elaphus* and *Capreolus capreolus*, respectively), and wild boar (*Sus scrofa*) (Herrera 1995, Branco *et al.* 2002, Pons & Pausas 2007b, Pérez-Ramos & Marañón 2008, Arosa *et al.* 2015). Livestock (pigs, cows, goats and sheep) also eat the acorns (Pausas *et al.* 2009b, Arosa *et al.* 2015).

Figure 4. Cork bark stripping and piles of cork (photographs by R. Ceia).

When temperature, canopy and soil moisture conditions are favourable, fallen acorns germinate during December–January and emerge from March to July (Arosa *et al.* 2015). Although cork oak seedling survival and growth may be severely limited by competition for light deficit under dense canopies, by summer water deficits, and by nutrients (Callaway 1992, Holmgren *et al.* 1997), the facilitative effect of shrubs over seedling survival may be necessary, due to the nurse effects associated with shading that may reduce the drought stress in seedlings and the protection from hervivores (Quero *et al.* 2006, Pérez-Ramos *et al.* 2008, Smit *et al.* 2008, Pulido *et al.* 2010, Arosa *et al.* 2015). Also, the protective shrub cover promotes soil rehabilitation and prevents erosion, especially after fire events (Acácio *et al.* 2009, Simões *et al.* 2009, Nunes *et al.* 2011). Cork oak seedlings have the extraordinary ability of resprouting from stems and basal buds after leaf consumption or summer drought, mainly influenced by early emergence and later drying of seedlings (Urbieta *et al.* 2008, Arosa *et al.* 2015; Fig. 5). This capacity is related to the root system of cork oak, after germination there is a clear priority for root growth, and seedling survival cannot be guaranteed before roots reach a soil depth that holds water in the summer (Maroco *et al.* 2002).

Figure 5. Types of damages inflicted by animals on seeds and seedlings: acorn damage by insect (upper left), acorn damaged by wild boar (upper right), acorn damaged by rodent (lower left), and resprouting second year seedling after livestock consumption (lower right) (photographs by M.L. Arosa).

HUMAN USE AND SOCIOECONOMIC PERSPECTIVES OF *MONTADOS* IN PORTUGAL

The origin of the Portuguese word *montado* goes back to the Middle Ages, when *montar* was the term for exploiting communal hills, either for pasturing, timber harvesting, wooding and hunting (Fonseca 2004, Coelho 2007). Past human use of the *montados* (Romans likely used it to rear pigs) shaped this ecosystem to the present days (Joffre *et al.* 1999, Rey Benayas & Scheiner 2002). The traditional management of the *montado* consisted of selective tree clearing to enhance herb growth and to increase tree crown coverage in order to provide a regular yield of edible, high-quality acorns (Rupérez 1957). Poor or non-agricultural lands were mostly cultivated to prevent shrub invasion of grasslands and to supply fodder and grain for livestock (San Miguel 1994, Montero *et al.* 2000, San Miguel 2005).

The management system in *montado* has been developed for extensive livestock rearing, originally Iberian pigs but nowadays also sheep and bovine cattle, which feed on acorns, from early autumn to late spring, and grasses, in the rest of the year (Campos 1984, Campos & Martín 1987; Fig. 6). Forestry is not aimed for timber production but for increasing the crown coverage per tree to increase the acorns productivity, the exploitation of cork oaks results in the most economically significant product which is the cork. Portugal is the leader-country in cork production and exportation, being responsible for 54 % (at a mean annual production of 157 000 T) of the world production of this good (APCOR 2007). Cork industry has a very important role in the Portuguese economy, representing 3 % of the Gross Domestic Product (Tinoco *et al.* 2009) and employing around 15 000 persons just in the transformation sector (APCOR 2007).

Instead of taking full advantage of the output of a particular product, the *montado* optimizes the use of every natural resource within its environment with a minimum input of energy and materials. It is due to this versatility that the *montado* has been able to successfully satisfy human requirements from the Middle Ages up to the 21st century (Olea & Miguel-Ayanz 2006). Notwithstanding its direct socioeconomic value, the *montado* also provides other economical incomes and a wide variety of services, or environmental benefits: structural and biological diversity, environmental stability (erosion, climate, nutrient and water cycles, fire, carbon storage), landscape, leisure activities, hunting, tourism, and cultural heritage, among others (Belo *et al.* 2009).

Figure 6. Different types of livestock grazing: black Iberian pigs (above), sheep (middle) and cattle (below) (photographs by R. Ceia).

LIMITING FACTORS TO CORK OAK NATURAL REGENERATION

The lack of tree health and low natural regeneration rates of cork oak are the main causes of the *montado* decline. Intensive pruning, exaggerated cork harvesting and the influence of pests and diseases affect tree health (Camilo-Alves *et al.* 2013, Acácio & Holmgren 2014). Also, the limitations to natural regeneration in Mediterranean evergreen oak systems have been attributed to various causes, including poor dispersal and shortage of viable acorns (Siscart *et al.* 1999, Branco *et al.* 2002, Pulido & Díaz 2005, Acácio *et al.* 2007), high post-dispersive acorn losses and seedling mortality due to predation by livestock and wild animals (Herrera 1995, Santos & Tellería 1997, Plieninger *et al.* 2004, Acácio *et al.* 2007, Plieninger 2007, Pérez-Ramos *et al.* 2008, Smit *et al.* 2008, Pulido *et al.* 2013), and low seedling survival to summer drought (Retana *et al.* 1999, Marañón *et al.* 2004, Plieninger *et al.* 2004, Acácio *et al.* 2007, Gómez-Aparicio *et al.* 2008, Smit *et al.* 2008, Gimeno *et al.* 2009, Smit *et al.* 2009).

The increase in fire frequency in the last few decades in the Mediterranean basin (Pausas & Vallejo 1999) should be taken into account. Although cork oak is able to resist fire due to the bark insulation and to the mechanism of resprouting afterwards, frequent or intense wildfires may kill adult trees, specially if wildfires occur immediately after cork extraction and this has become an additional obstacle to cork oak survival and recruitment (Moreira *et al.* 2007, Acácio *et al.* 2009, 2010, Catry *et al.* 2012). Also, extreme droughts that affect the species are phenomena whose occurrence or frequency is not possible to be predicted with sufficient anticipation, due to its dependence on meteorological conditions (Vivas & Maia 2007).

Successive intensification practices and a later extensification over the second half of the 20th century have contributed to *montado* degradation and greatly affected the present condition of the vegetation, sometimes jeopardizing its resilience (Pinto-Correia & Mascarenhas 1999). The development of the generalised use of wide plows, disc harrows and scarifiers destroy young trees, damage roots and deteriorate established trees, increasing their vulnerability to the attack of pests and diseases (Branco & Ramos 2009, Arosa *et al.* 2015). In the traditional *montado*, the ground cover is a rotation of culture/fallow/pasture, with periods depending on soil quality and on the main objectives of the *montado* exploitation. Natural pastures were used for sheep and pig grazing and browsing but, in the last years, cattle populations increased with serious consequences to the *montado* ecosystem (Pinto-Correia & Godinho 2013;

Fig. 6). Cattle tend to damage young trees, compact soil and decrease both water infiltration and biodiversity (Plieninger *et al.* 2004, Plieninger 2006). Also, soil erosion increases as the shrub undercover is substituted by pastures. The effect climate change with extreme heat, drought and rain events led to an overall decline in the tree condition and a higher susceptibility to pest and diseases (*e.g. Phytophtora cinnamomi*) that spread through those degraded soils and will also deplete the system (Diffenbaugh *et al.* 2007, Marañón 2008, Pinto-Correia & Fonseca 2009, Azul *et al.* 2011, Hoerling *et al.* 2012). If on the one hand overgrazing exposes plants without sufficient recovery periods, on the other hand grazing has a role in soil fertilisation, and contributes to shrub control (Plieninger *et al.* 2004, Plieninger 2006).

THESIS OBJECTIVES

The broad framework of this thesis is centered on the role of biotic and abiotic factors implicated in the ecosystem functioning of the *montado*. The main focus was to understand the general decline of this ecosystem, particularly the alarming lack of regeneration in many cork oak populations throughout the western Mediterranean.

This thesis addresses the following specific questions:

1) Do cork oak leaf fall, litter decomposition and quality differ according to land uses in the *montado*?
2) Which is the functional interpretation of soil nematode community in *montados* due to management practices through time?
3) Can plant-parasitic nematodes affect cork oak seedlings and therefore reduce natural regeneration?
4) Which biotic and abiotic factors can restrict cork oak during the early stages of regeneration?
5) What is the role of management and environmental factors in the long-term sustainability of the *montado*?

In Chapter 1 it was evaluated if differences in land use and its plant community influenced decomposition through changes in the quality of the produced litter by the cork oak (question 1). Foliar nutrient content, litter decomposition and its dynamics are widely recognized as an effective measure of the nutritional status of plants and are key processes in nutrient cycling and energy transfer of terrestrial ecosystems, influencing their stability (Chapin 1980, Maguire 1994, Vitousek *et al.* 1994, Aerts & Chapin 2000). Understanding cork oak nutritional dynamics would help the conservation and management of trees as reduced fitness will unfavorably affect their mineral nutrition (Robert *et al.* 1996).

Nematodes are the most abundant (millions per m^2) and diverse (over 30 taxa per kg of soil) metazoans in soils (Yeates 1979). Belowground, plant-parasitic nematodes are often a hidden enemy to human land uses (Yeates 1996), undetected until they reach large population densities. Given the ease of extracting soil nematodes and their identification to functional groups, the nematode communities were assessed in Chapter 2 to test for differences among management types of the *montado* and to understand nematode role in the establishment of cork oaks. Samples from cork oak rhizosphere (soil and roots) were collected as they offer great potential for use as indicators of biodiversity and for assessing the consequences of changing land use on soil conditions (Tomar & Ahmad 2009). Results can provide information on the soil food-web and also on plant-parasitic nematodes burden of cork oaks (questions 2 and 3).

Limitations to cork oak natural regeneration were further studied in Chapter 3. This experimental study investigated the effect of biotic and abiotic factors on cork oak establishment and survival (question 4), namely cache survival, seedling emergence, survival and resprouting, and results were compared among land uses. This approach mimicked successfully dispersed seeds by experimentally caching acorns at increasing distances from mother trees. Seedlings were monitored during one year and losses due to herbivory and desiccation were recorded, as recruitment does not guarantee successful regeneration.

Finally, question 5 was addressed in Chapter 4 by integrating in a single approach the multifactorial causes implicated in cork oak decline across the Iberian Peninsula. We proposed the development of a dynamic model to predict the future trends and factors influencing the sustainability of the *montado* ecosystem (Sterman 2001). Tested hypotheses aim to improve the comprehension of management and environmental factors as the most determinant limiting factors influencing cork oak population dynamics. The consequences of different management practices for cork oak regeneration will be discussed, and the ecological and economic added value that the conservation of this ecosystem can provide.

STUDY AREA – HERDADE DO FREIXO DO MEIO

All fieldwork was carried out in Montemor-o-Novo, south Portugal, in the Herdade do Freixo do Meio (38º 42’ N, 8º 19’ W), a farm that manages 1 140 ha of *Quercus suber* – *Q. rotundifolia* cork-holm oak *montado* (Fig. 7). The Herdade do Freixo do Meio was converted into organic farming in 2001 and has been developing a sustainable agriculture, valuing the existing natural resources and the cycles of nature. This region has a Mediterranean climate with hot and dry summers and rainfall mostly in autumn and winter (mean annual rainfall = 660 mm, mean annual temperature = 15.4 ºC, mean annual evaporation = 1 760 mm; INMG 1991). The landscape is a mosaic of various densities of trees, the dominant species being cork oak, holm oak and *Pinus* spp., with cleared areas consisting of pastures and agricultural fields (clover, wheat, barley, oat) as undercover, usually in a rotation scheme that includes fallows and some areas with a shrub undergrowth of *Cistus* spp., *Asparagus acutifolius, Ulex australis* subsp. *welwitschianus*, *Pistacia lentiscus*, *Arbutus unedo*, *Phillyrea angustifolia*, *Crataegus monogyna*, *Quercus coccifera* and *Lavandula pedunculata*. As the entire area is managed principally for extensive rearing of sheep and Iberian pigs, shrubby understories are cut periodically to enhance pasture growth while some areas are cultivated to supply fodder and grain for livestock. Forestry is aimed at cork harvesting, which takes place at ca. nine years intervals in mature cork oak trees, but fuelwood is also periodically obtained from canopy pruning and cutting of dead and decaying trees.

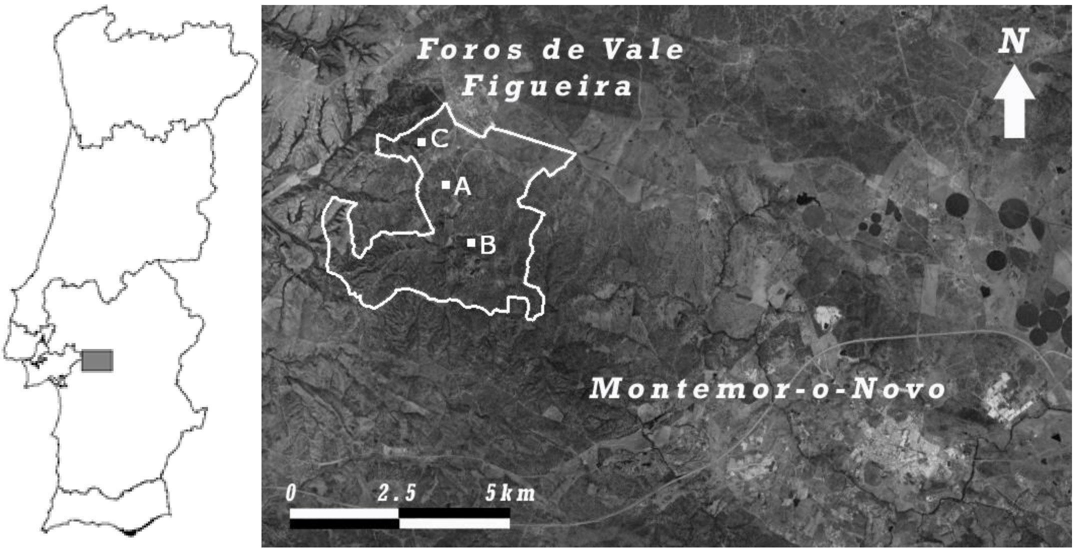

Figure 7. Map of the study area in south Portugal showing the limits of the Herdade do Freixo do Meio (white line) (adapted from Google Inc. 2013).

All field collection data for this thesis was carried out at three sites within the study area (Table 1). Sites were selected in order to represent different management precedents and cork oak was the dominant tree species in each site.

Table 1. Description of the three sites (A, B and C) concerning locality, soil, forest structure and land uses. DBH – diameter at breast height.

	Site A	**Site B**	**Site C**
Locality			
Latitude	38° 41'	38° 42'	38° 42'
Longitude	8° 19'	8° 19'	8° 20'
Altitude (m)	150	175	150
Size (ha)	32	35	29
Slope exposure	SSO	SO	O
Soil			
Bedrock type	Granite	Granite	Granite
pH (H_2O)	4.90	5.15	5.05
Organic matter (%)	1.82	1.85	1.70
Carbon (%)	1.06	1.07	0.98
Nitrogen (%)	0.09	0.09	0.08
Forest structure			
Density (trees.ha^{-1})	25	40	45
Cork oak trees (%)	69	76	93
Crown diameter (m)	11.1	10.8	9.2
DBH (cm)	163	164	138
Shrub density	Low	Medium	High
Land uses			
Agriculture	Yes	No	No
Livestock	Yes	Yes	No
Forestry	Yes	Yes	Yes

CHAPTER 1

Cork oak leaf fall, litter quality and decomposition in three different land uses within a *montado* of southern Portugal

ABSTRACT

To understand the effects of different land uses on cork oak (*Quercus suber*) leaf litter fall, quality and decomposition, three differently managed areas were evaluated in a *montado* ecosystem in southern Portugal. Leaf fall was determined by means of litter traps while the litterbag technique was used for the decomposition experiment, leaf thickness was calculated and litter chemical composition was determined before the decomposition process started and after 18 months in the soil. The estimated amount of cork oak leaf fall per site showed no significant differences, despite of the positive influence of tree crown size on leaf fall. Lower leaf thickness and leaf content of cellulose, hemicellulose and lignin were associated with higher decomposition rates found on less disturbed sites. Differences in land use which exposed soil to harsh climate conditions, and thus negatively affected soil microbial dynamics, resulted in lower decomposition rates in the more disturbed site.

INTRODUCTION

Cork oak (*Quercus suber*) is an evergreen tree species of the western part of the Mediterranean Basin (Pausas *et al.* 2009a). The largest cork oak woodlands are found in the Iberian Peninsula, and were used for agricultural, pastoral and forestry uses at least since the Middle Age (Joffre *et al.* 1999, Olea *et al.* 2005, Bugalho *et al.* 2011a). In Portugal, this ecosystem is known as *montado* and it is characterised by open woodlands (20–80 trees.ha^{-1}) with only one or a few tree species besides cork oak, mainly holm oak (*Quercus rotundifolia*) and pines (*Pinus* spp.). Since *montados* are found in different environmental (climatic and edaphic) conditions, their structure and understory composition are variable (Joffre *et al.* 1999, Pinto-Correia & Mascarenhas 1999), and human management has favored habitat heterogeneity and biodiversity at local and regional levels, creating a multiplicity of ecotones (Blondel 2006). This ecosystem is a protected habitat within the EU Habitats Directive (92/43/EEC) but the long term persistence of cork oak in *montados* is a subject of serious concern among both the public and scientific community. The main causes of degradation are lack of cork oak health, mainly due to pests and pathogens, and low natural regeneration rates (Díaz *et al.* 1997, Pulido & Díaz 2005, Acácio *et al.* 2007, Camilo-Alves *et al.* 2013, Acácio & Holmgren 2014, Arosa *et al.* 2015). Reduced fitness of cork oak trees will unfavorably affect their mineral nutrition (Robert *et al.* 1996), thus understanding of cork oak nutritional dynamics can help the management of this ecosystem.

Foliar nutrient content, litter decomposition and its dynamics are widely recognized as an effective measure of the nutritional status of plants and are key processes in nutrient cycling and energy transfer of terrestrial ecosystems, influencing their stability (Chapin 1980, Maguire 1994, Vitousek *et al.* 1994, Aerts & Chapin 2000). Litter fall is a principal pathway to return carbon and nutrients (particularly nitrogen and phosphorus) to the soil, and litter decomposition contributes with 70 % of the total annual carbon flux (Miller 1984, Raich & Schlesinger 1992, Cadish & Giller 1997, Piatek & Allen 2000). Litter decomposition involves the mineralization and humification of lignin, cellulose and hemicellulose, and the leaching of soluble compounds while carbon (C), nitrogen (N), and phosphorus (P) are mineralised or immobilised in the soil (Aber & Melillo 1982, Gallardo & Merino 1993, Coûteaux *et al.* 1995). There are three main factors controlling litter decomposition, (i) climate, (ii) litter chemistry, and (iii) soil organisms, with litter chemistry being the strongest determinant of the decomposition processes within the same climate region (Hart *et al.* 1992, Lavelle *et al.* 1993, Lisanework & Michelsen 1994). Nevertheless, Mediterranean ecosystems have long dry summers and the decomposition rate is affected by limited moisture in these periods, corresponding to high mortality of decomposer soil organisms (Arosa *et al.* 2014). Moreover, the degradation of vegetation and soils by wildfires, land abandonment and overgrazing, as well as the sclerophyllous leaves with a high content of structural compounds can all affect decomposition (Gallardo & Merino 1993, Coûteaux *et al.* 1995, Kavvadias *et al.* 2001).

This study evaluated cork oak leaf fall, litter quality and decomposition in three *montados* subjected to different land uses. We estimated the amount of foliar litter fall per site and analysed how it was influenced by tree crown size and tree density. As the presence of cutin in leaves of Mediterranean species confers impermeability and resistance to microbial degradation (Kolattukudy 1980), we compared leaf thickness and tested for differences in litter decomposition rates among sites. Furthermore, the concentrations of N, C, P, lignin, cellulose and hemicellulose in foliar litter were determined before the decomposition process started and after 18 months in the soil, in order to better understand nutrient cycling in the *montado*.

METHODS

STUDY AREA

Fieldwork was carried out from March 2011 to May 2014 in Montemor-o-Novo, southern Portugal, in the Herdade do Freixo do Meio (38º 42’ N, 8º 19’ W), a farm that manages 1 140 ha of cork-holm oak *montado*. The area has a Mediterranean climate with hot and dry summers and rainfall mostly in autumn and winter (mean annual rainfall = 660 mm, mean annual temperature = 15.4 ºC, mean annual evaporation = 1 760 mm; INMG 1991). Three sites within the study area were selected, cork oak was the dominant tree species and each site corresponded with a land use that had been historically subjected to different types of management. A detailed description of the three sites (A, B and C) is provided in Table 1 in General Introduction.

Site A had a density of 25 trees.ha^{-1} and the mean crown diameter of cork oak trees was 11.1 m. As soil ploughing was carried out every 1–2 years to enhance pasture growth for livestock rearing or to produce fodder and grain, shrubs were almost absent from this site.

Site B had a density of 40 trees.ha^{-1} and the mean crown diameter of cork oak trees was 10.8 m. There were no agricultural uses in this site, although it was used for extensive livestock rearing. Encroaching shrubs are periodically cut with chains in this site to allow livestock grazing and browsing and during this study there was a dense scrubby undergrowth of *Cistus* spp. and *Asparagus acutifolius*.

Site C had a density of 45 trees.ha^{-1} and the mean crown diameter of cork oak trees was 9.2 m. This site comprised only forestry uses and it had a dense heterogeneous shrubby understorey composed by *Cistus* spp., *A. acutifolius, Ulex australis* subsp. *welwitschianus, Pistacia lentiscus, Arbutus unedo, Phillyrea angustifolia, Crataegus monogyna, Quercus coccifera* and *Lavandula pedunculata*.

LEAF FALL

Leaf fall was determined by means of litter traps. Traps were constructed of circular nets of 0.25 m^2 attached to the canopy with a string. Three traps per tree were installed in a total of 20 cork oak trees per site, with a grand total of 180 traps in the three sites. The contents of each trap were inspected every 15 days from January to

December 2011 and leaf fall was restricted to the period between May and mid-July. Litter was collected, dried at 60 °C and leaves were weighed for each litter trap. Tree crown projection area was calculated for each selected tree, by measuring maximum and minimum crown diameters, in order to estimate foliar litter fall per tree (kg.tree^{-1}). To predict the amount of foliar litter fall per site (kg.ha^{-1}) we multiplied the foliar litter fall per tree by tree density in each site.

LITTER QUALITY AND DECOMPOSITION

Litter decomposition rates were evaluated using the litterbag technique (Garnier *et al.* 2007). Leaves were collected in June 2012, *i.e.* the peak of leaf senescence, and dried at room temperature for 3–4 days until weight stabilization. A standard 1 mm mesh fabric was used to make flat polyester bags of about 10 × 10 cm and 2.0 ± 0.1 g of leaves were placed in each bag. Thirty litterbags were placed under the canopy of 10 cork oak trees per site. The experiment began in November 2012 and lasted for 18 months with three harvests: April 2013 (6 months), November 2013 (12 months) and April 2014 (18 months). After harvesting, bags were cleaned and dried out at 60 ºC for 3 days, and the clean litter weighed.

Litter chemical composition for the cork oak leaf litter was determined at time 0 and after harvesting litterbags in the soil for 18 months. All this leaf material was oven dried at 60 ºC. Total concentrations of C and N were determined with CHN elemental analyser (FlashEA1112, ThermoFinnigan elemental analyser). Total concentration of P was determined using an ICP-MS (ELEMENTXR, ThermoFinnigan). Lignin and cellulose were determined following AOAC (1993) methods and hemicellulose following the procedures described by Van Soest & Wine (1967). Also, these results were used to calculate two indices, the ratios C/N and the lignin/N. The C/N ratio expresses the N concentration in organic matter, a low C/N suggest a high decomposition rate in the early stages of decomposition (Berg & Ekbohm 1983). The lignin/N ratio assumes that N and lignin have opposite effects on the decomposition rate, and is a good predictor of mass loss during the initial stages of decay (Melillo *et al.* 1982).

Leaf thickness (LT) was calculated using measurements of Specific Leaf Area (SLA) and Leaf Dry Matter Content (LDMC), given that LT = 1/(SLA x LDMC) (Gallardo & Merino 1993, Pérez-Harguindeguy *et al.* 2000, Vile *et al.* 2005). Following standard methodologies (Pérez-Harguindeguy *et al.* 2013), SLA ($cm^2.kg^{-1}$) was determined on 15 full-grown cork oak fresh leaves per site, while LDMC ($mg.g^{-1}$) was measured after drying those leaves.

DATA ANALYSIS

Data exploration was completed with Brodgar 2.6.6 (Highland Statistics Ltd. 2009), an interface supported by software R version 2.9.1 (R Development Core Team 2009).

Analyses of Variance (ANOVA), followed by post-hoc Tukey tests ($\alpha = 0.05$), were carried out with Statistica 8.0 (StatSoft Inc. 2007) in order to test for the effect of site in leaf fall, leaf thickness and remaining litter mass. Data were firstly examined with Levene's tests, and the arcsine transformation was applied to remaining litter mass data for homogeneity of variances.

Principal Components Analyses (PCA) were performed using CANOCO for Windows version 4.5 (ter Braak & Smilauer 2002) to describe correlations between litter quality variables (N, C, P, cellulose, hemicellulose, lignin) and also the ratios C/N and lignin/N at the beginning of the study and 18 months later.

Results are indicated as mean ± standard error.

RESULTS

LEAF FALL

Foliar litter fall recorded in litter traps during 2011 was 289.9 ± 42.7, 221.9 ± 42.4 and 187.2 ± 22.2 $g.m^{-2}$ in sites A, B and C, respectively (232.4 ± 21.4 $g.m^{-2}$ for the study area). There were nearly significant differences among sites in the estimated foliar litter fall per tree (A: 34.4 ± 8.0 $kg.tree^{-1}$, B: 22.6 ± 5.3 $kg.tree^{-1}$, C: 14.9 ± 2.9 $kg.tree^{-1}$; $F_{2,\ 57} = 2.97$, $p = 0.060$) but none were found in foliar litter fall per site (A: 859.7 ± 201.2 $kg.ha^{-1}$, B: 903.0 ± 211.8 $kg.ha^{-1}$, C: 671.9 ± 131.3 $kg.ha^{-1}$; $F_{2,\ 57} = 0.46$, $p = 0.633$).

Remaining litter mass percentages at 6, 12 and 18 months were, respectively, 51 %, 49 % and 27 % in site A, 28 %, 23 % and 14 % in site B and 44 %, 35 % and 24 % in site C (Fig. 8). Overall, litter decomposition rates were lowest in the spring-summer period (6–12 months) while the highest decomposition rates occurred during the initial autumn-winter period (0–6 months) (Fig. 8). There were significant differences between site B and sites A and C in the remaining litter mass at 6 months ($F_{2, 27} = 4.82$, $p = 0.019$) and 12 months ($F_{2, 27} = 9.67$, $p = 0.010$). Although, no significant differences were found among sites in remaining litter mass at 18 months ($F_{2, 27} = 1.49$, $p = 0.251$).

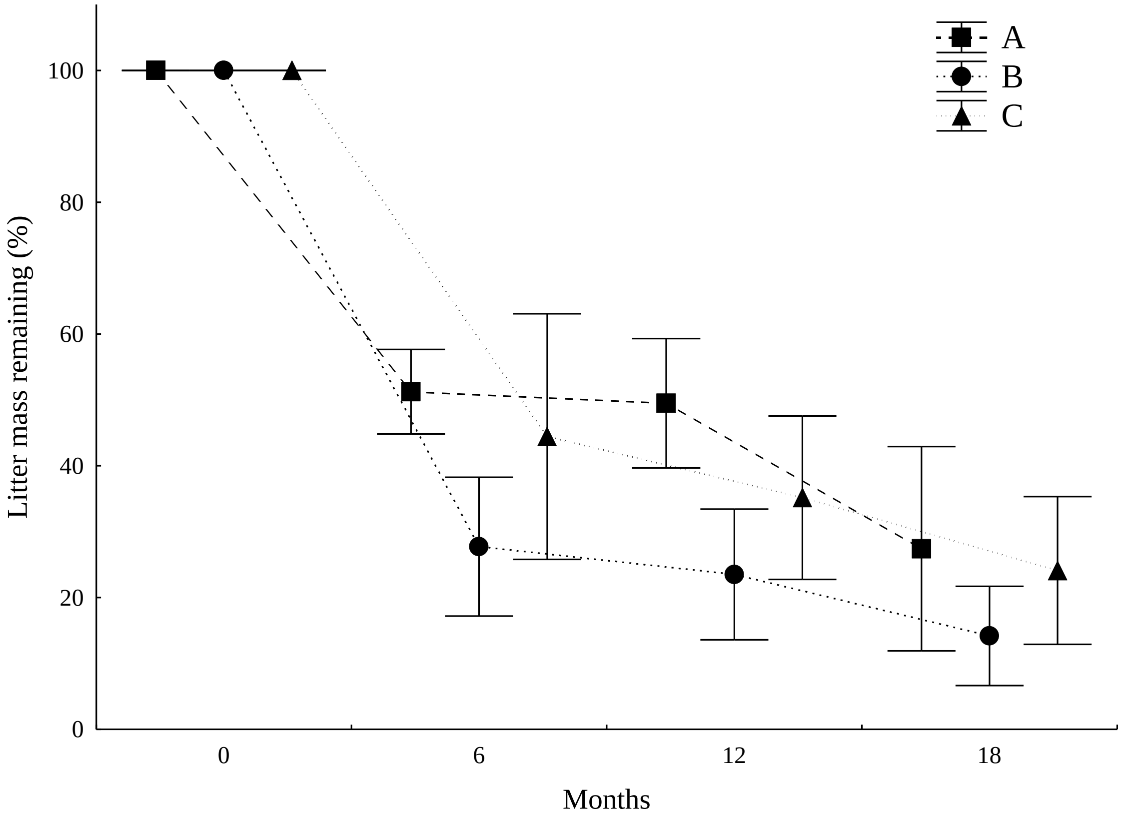

Figure 8. Litter mass remaining in litterbags placed under the canopy of cork oaks in the three sites (A, B and C). The experiment started in November 2012 (0 months) and litterbag harvesting was carried out in April 2013 (6 months), November 2013 (12 months) and April 2014 (18 months). Values are mean ± SE of 10 replicates per site.

The PCA (Fig. 9) reduced the original 8 x 3 matrices from the analysis of litter quality in each sampling period (Table 2) to two independent principal components that explained 62.7 % and 37.3 % (0 months), and 71.9 % and 28.1 % (18 months) of the variation, respectively. Both at the initial and late stages, site B is separated from sites A and C on the first axis (Fig. 9).

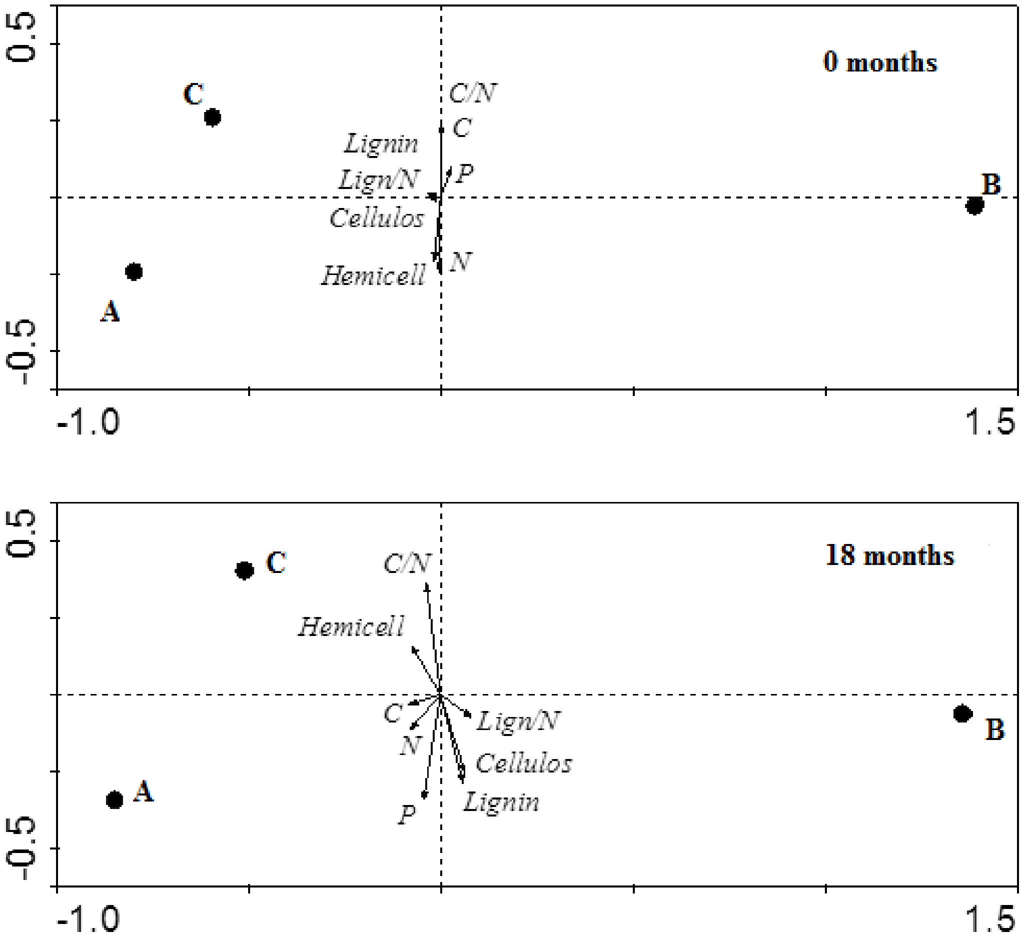

Figure 9. Correlation biplots with values of litter chemical composition (N, P, C, cellulose, hemicellulose and lignin, C/N and lignin/N) in the three sites (A, B and C) at the beginning of the study (above) and 18 months later (below).

At an initial stage, values of N, C and P, and the C/N ratio, are only slightly different among sites (Table 2). On the other hand, leaves from site B had very low values of cellulose and lignin, and lignin/N ratio, while the highest values for these paramenters, as well as hemicellullose, were found on leaves from site A (Table 2).

After 18 months in the soil, litter content of N, C and P is variable among sites. The C/N ratio shows small differences among sites, although the lignin/N ratio is very high in site B (Table 2). Site B also presents the highest concentration of cellulose on remaining litter mass at 18 months.

Table 2. Litter chemical composition (mg) in decomposition bags (each bag with 2.0 ± 0.1 g of cork oak leaves) placed in the three sites (A, B and C) at the beginning of the decomposition experiment (0 months) and after 18 months in the soil. Results correspond to the mean of three replicates.

	N	C	P	Cellulose	Hemicellulose	Lignin	C/N	Lignin/N
0 months								
A	35.20	989.60	3.00	465.80	191.80	167.20	28.11	4.75
B	35.00	995.60	3.40	362.80	175.00	122.80	28.45	3.51
C	34.80	1001.40	3.20	457.40	173.80	164.00	28.78	4.71
18 months								
A	15.53	271.31	0.85	81.38	65.51	54.23	17.47	3.49
B	8.18	141.09	0.18	97.19	44.37	66.82	17.25	8.17
C	12.47	241.47	0.10	57.46	73.21	40.93	19.36	3.28

Leaf thickness was 0.228 ± 0.001, 0.205 ± 0.001, 0.184 ± 0.001 mm in sites A, B and C, respectively. In site C, leaf thickness was significantly lower than in sites A and B ($F_{2, 42} = 6.99$, $p = 0.002$).

DISCUSSION

Differences in land use and its plant community can influence decomposition through changes in the quality of the produced litter by the community and alterations of the temperature and moisture regime at the soil surface (Castro *et al.* 2010). Our study highlights important differences in cork oak leaf fall, litter quality and decomposition according to the main land uses in the *montado*. Because tree density and tree crown size show a strong inverse relationship in *montados*, the estimated amount of cork oak leaf fall in each site was identical, even though wider crowns provided more leaf fall. Furthermore, lower values of leaf thickness were associated with a higher tree density which, together with a lower content of cellulose, hemicellulose and lignin, is likely related with the higher decomposition rates found in sites B and C. Litter quality and deficient soil microbial activity, due to soil exposition to severe climate conditions in the absence of shrubs, were the probable causes of the lowest decomposition rates in site A. Overall, our results demonstrate that a faster nutrient cycling can occur in *montados* with high tree density and dense shrub layer.

LEAF FALL

In the Mediterranean region, leaf fall can be an adaptation to the water deficit that occurs during the summer dry period (Rodrigues *et al.* 1995) and evergreen cork oaks shed their old leaves mainly during spring in order to reduce transpiration surface (Andivia *et al.* 2010). Mean values of cork oak leaf fall in our study (0.23 $kg.m^{-2}.yr^{-1}$) were lower than 0.51 $kg.m^{-2}.yr^{-1}$ obtained by Sá *et al.* (2001), but were consistent with other previous calculations for cork oak: 0.23 $kg.m^{-2}.yr^{-1}$ (Andivia *et al.* 2010), 0.26 $kg.m^{-2}.yr^{-1}$ (Caritat *et al.* 2006), 0.29 $kg.m^{-2}.yr^{-1}$ (Aponte *et al.* 2013). The amount of litter fall shows a direct relationship with the aerial biomass in the canopy (Chertov *et al.* 1999) and we found marked differences among sites in leaf fall per tree given that wider tree crowns provided a higher amount of foliar litter fall. Nevertheless, these differences did not stand for an overall increase in foliar litter fall per site because tree crowns were wider where tree density was lower.

LITTER QUALITY AND DECOMPOSITION

Litter decomposition rates were significantly different among the three sites. The chemical composition of the litter, the environmental conditions, soil animals and microorganisms affect the rate of decomposition (Singh & Gupta 1977, Berg & McClaugherty 2008). Also, leaf thickness can help to explain decomposition rates of sclerophyllus leaves, negatively affecting litter mass loss (Gallardo & Merino 1993, Pérez-Harguindeguy *et al.* 2000, Cornwell *et al.* 2008).

Lower initial concentrations of lignin and cellulose in cork oak leaves from site B might have facilitated decomposition in relation to the other two sites. The leaves are structurally organised so that cellulose and hemicellulose are found in the primary cell wall and lignin in the secondary, thus the decomposition process occurs in different stages as these larger lignin macromolecules difficult leaf decomposition (Berg & McClaugherty 2008). At the end of the study, lignin and cellulose were slowly degraded in site B and seem to negatively affect the decomposition progress. The presence of a pond near this site may have interfered in the process of decomposition, affecting litter quality during winter. This pond increased its water level in winter, resulting in an increase of humidity that may have influenced the mineralization and leaching of soluble compounds, resulting on the death of some microbial communities and incomplete mineralization (Coûteaux *et al.* 1995). Values of lignin are presumably altered in wet soils (Berg *et al.* 1993a) and this can explain the observations at this late decomposition stage, where cellulose and lignin decomposition slow down relatively to the other two sites, also affecting results of the lignin/N ratio.

On the other hand, initial concentrations of cellulose, hemicelluloses and lignin and leaf thickness were highest in site A, hampering the early decomposition process. Moreover, tree density was low (25 trees.ha^{-1}) and, in the absence of shrubs, soil exposition to harsh climate conditions during summer can have a large negative impact on soil microbial activity and nutrient cycling (Corre *et al.* 2002, Quilchano & Marañón 2002, Gaxiola & Armesto 2015). The cycling of nutrients in the soil during decomposition is mainly controlled by soil nematodes communities, stimulating microbial growth when feeding on them (Ingham *et al.* 1985, Hunt *et al.* 1987). The limited plant cover in site A can largely explain the lowest rates of litter mass loss, since the disturbance of decomposing communities can significantly slow down the decomposition process (Gurlevik *et al.* 2003, Blanco *et al.* 2011).

Climate variables can have greater influence than leaf quality on litter decomposition, at least in an early decomposition stage when substances are more easily degradable (Berg *et al.* 1993b). In Mediterranean oak forests, soil microbial biomass is affected by season, vegetation cover type and structure, and soil depth, with maxima occurring mainly during the rainy season (Aponte *et al.* 2010, Costa *et al.* 2013, Arosa *et al.* 2014). Those seasonal variations associated to the summer drought in the Mediterranean, are especially important for ecosystem functioning and are reflected in soil microbial dynamics by the nutrient release and immobilization cycles and in the nutrient availability for plants (Aponte *et al.* 2010, Matías *et al.* 2011).

CHAPTER 2

Temporal effects dominate land use as factors affecting soil nematode communities in Mediterranean oak woodlands

ABSTRACT

We analysed the soil nematode community within three different *montados* (agricultural, pastoral and forestry uses), focusing on temporal variation. Nematodes were classified into trophic groups [bacterivores, fungivores, omnivores, predators and plant-parasitic nematodes (PPN)] and we calculated the maturity index for free-living taxa (MI), maturity index for plant-parasitic taxa (PPI) and the nematode channel ratio (NCR). Temporal variations were most evident during winter when there was a rise in the abundance of the five functional groups. Concordantly, there was a simultaneous increase of soil moisture and organic matter, due to litter decomposition. Fungivore abundance was highest in the forest and the temporal occurrence and abundance of many PPN genera was largely determined by land use. Land management was responsible for differences in plant community structure and composition, thus plant diversity increased from the agricultural to the forestry use. Because the *montado* shows great temporal variability in vegetation structure our results of MI, PPI and PPI/MI ratio explain the significant changes in the nutritional status over time, with the highest values recorded in the spring. NCR is a good indicator of energy efficiency in the soil decomposition process. Its lowest values were attained in the forest, where the slow-growing plant species favoured a lower activity of the bacterial energy channel and a prevalence of the fungal-based decomposition energy channel. Nematode composition reflected plant succession, changes in decomposition in the soil food web and temporal variations in the structure of soil. Altought the soil was rich in PPN they were not found in roots of cork oak seedlings, not being a limitation to cork oak regeneration.

INTRODUCTION

In the southern Iberian Peninsula, Mediterranean forests were dominated by cork oak (*Quercus suber*) and holm oak (*Q. rotundifolia*) trees. However, since the late Middle Ages and especially between 1850 and 1950, many of these forests have been lost by human activities such as shrub clearing, ploughing, tree thinning and conversion to agricultural land (Díaz *et al.* 1997). Presently, these ecosystems, known as *montados* in Portugal, consist of an open tree layer with a shrub or annual herbaceous understory and are characterised by a systematic combination of agricultural, pastoral, and forestry uses (Pinto-Correia 1993, Joffre *et al.* 1999, Costa *et al.* 2009). Cork oaks trees are of major economical importance in *montados* as their bark (*i.e.* cork) can be harvested every nine years, a process that does not harm the trees because the cork layer regenerates after extraction (Pausas *et al.* 2009a). Moreover, *montados* are protected habitats within the EU Habitats Directive (92/43/EEC) and are considered High Nature Value Farming Systems, according to the classification proposed by the European Environmental Agency (Paracchini *et al.* 2008). This ecosystem has evolved over centuries as a consequence of management activities but, at present, *montados* are undergoing an unprecedented rate of change. The intensification of grazing and ploughing activities in the undercover hampers tree regeneration and at the same time it disrupts the physical properties of soils, putting at risk the maintenance of this ecosystem in the long-term (Plieninger & Wilbrand 2001, Plieninger 2007, Bugalho *et al.* 2011a, 2011b). Therefore, the preservation of the *montado* depends on the consistent application of a management strategy that promotes tree regeneration and soil protection (Pulido & Díaz 2005, Bugalho *et al.* 2011a, Arosa *et al.* 2015).

Nematodes constitute the most abundant group within the soil mesofauna, with free-living nematodes playing an indispensable role in decomposing processes occurring in soil ecosystems (Yeates 1979). The cycling of nutrients below ground is controlled by herbivores, including nematodes, mainly by stimulating soil microbial activity, nutrient recycling and increased nutrient acquisition by plants from soil (McNaughton *et al.* 1997, Bardgett *et al.* 1998). Trophic interactions can be assigned to nematodes in the majority of soils (*e.g.* Moorhead *et al.* 2002) and these can be classified into five functional groups: bacterivores, fungivores, plant-feeders, predators and omnivores. Bacterivores and fungivores are indirectly involved in decomposition and nitrogen and carbon mineralization by feeding on bacteria and fungi, including mycorrhiza (Yeates & Coleman 1982, Ferris *et al.* 2004). Plant-parasitic nematodes (hereafter referred to using the abbreviation PPN) interact with flora by feeding on plant roots or shoots (Ingham *et al.* 1985). Predator nematodes feed upon soil invertebrates including other nematodes, enchytraeids, tardigrades and protozoa (Moore & de Ruiter 1991). Omnivores do not hold a separate position in the food chain but may add connectedness to the food web (Coleman *et al.* 1993) by feeding on more than one food source, including bacteria, fungi, algae, protozoa and rotifers. Nematode analysis is currently gaining interest in ecological studies in order to assess the functioning of soils (Wilson & Kakouli-Duarte 2009). Nematode community indices are a useful tool for monitoring environmental conditions and soil ecosystem function (Bongers & Ferris

1999, Ferris *et al.* 2001, Neher 2001, Berkelmans *et al.* 2003). The nematode community can be characterised by the maturity index for free-living taxa (MI) and the maturity index for plant-parasitic taxa (PPI) (Bongers 1990, Bongers & Ferris 1999). For the calculation of maturity indices, soil nematodes are categorized into a 1–5 coloniser (r-strategists) and persister (k-strategists) ranking, termed as cp value, following the assumption of a shift toward opportunistic species under stress conditions (Odum 1985, Bongers 1990). The maturity index is the weighted mean cp value of the number of individuals in a representative soil sample. The index values vary according to the levels of disturbance, from less than 2.0 in nutrient-enriched disturbed systems to ± 4.0 in pristine environments. Nematodes that feed on higher plants are omitted from the calculation of the MI because their occurrence and abundance is largely determined by the community structure, host status and vigour of plants growing in the soil. Consequently, the equivalent of the MI for plant-feeding nematodes (the plant-parasite index, PPI) is calculated separately (Bongers 1990, Bongers & Ferris 1999). The ratio PPI/MI (Bongers *et al.* 1997) is a sensitive indicator of enrichment. Moreover, the nematode channel ratio (NCR) expresses the energy efficiency in soil decomposition processes, providing information on the relative dominance of the bacterial or fungal energy channel based on the abundance of bacterial and fungal feeding nematodes in the soil ecosystem (Yeates 2003). These energy channels represent two lines of dead biomass consumption: the fungal energy channels predominate when organic material is of high C/N ratio, when organic material is of low C/N ratio bacterial decomposition channels predominate (Moore & Hunt 1988, Ferris & Bongers 2006, Costa *et al.* 2011).

The main objective of this study is to provide a functional interpretation of the soil nematode community structure in *montados* in three sites due to land management practices and through time. We assess if differences in the nematode communities reflect differences in management of *montados* regarding agricultural, pastoral and forestry uses. Sites with high levels of grazing and soil ploughing for agriculture, are believed to be occupied by organisms that are less able to colonize and become established, thus presenting lower values of maturity indices. On the other hand, we consider the effect of time which, by modifying soil physical-chemical properties, can also affect nematode densities (Yeates *et al.* 1997, Bardgett & Cook 1998, Costa *et al.* 2011). Additionally, we will evaluate the potential burden of PPN in the different types of *montado* to estimate whether these can affect cork oak seedlings, therefore representing a limitation to regeneration.

METHODS

STUDY AREA

Our study area was set in Montemor-o-Novo, Portugal, most specifically in the Herdade do Freixo do Meio (38º 42’ N, 8º 19’ W), an organic farm that manages 1 140 ha of cork-holm oak *montado*. Within the study area, we selected three sites of approximately 30 ha each representing different management precedents concerning agricultural, pastoral and forestry uses. Cork harvesting and tree pruning were the main forestry activities undertaken in the three sites, despite the fact that they did not take place every year.

Site A was a grassland with scattered cork and holm oaks (25 trees.ha^{-1}). This site was mechanically disc ploughed in autumn for the sowing of clover (*Trifolium* spp.) and intensive sheep grazing occurred during part of the year (winter, spring and autumn).

Site B was a dense cork-holm oak *montado* (40 trees.ha^{-1}) with shrub undergrowth of *Cistus* spp. and *Asparagus acutifolius*. There were no agricultural uses in this site, although it was moderately used by livestock (pigs in winter and sheep in autumn).

Site C was a dense cork oak *montado* (45 trees.ha^{-1}), including a minor number of holm oaks and stone pines (*Pinus pinea*), and a high density heterogeneous understory composed by shrub formations of *Cistus* spp., *A. acutifolius, Ulex australis* subsp. *welwitschianus, Pistacia lentiscus, Arbutus unedo, Phillyrea angustifolia, Crataegus monogyna, Quercus coccifera* and *Lavandula pedunculata*. This site management comprised only forestry uses.

To account for climatic differences among sites, temperature and relative humidity measures were obtained with a thermohygrometer (HOBO Pro v2 logger, Onset Computer Corporation, USA) at each site. These thermohygrometers were placed 1.5 m above the ground under tree canopy and data were hourly recorded for one year starting in January 2012. Soil chemical properties and moisture content were also examined in the three sites twice, coinciding with spring and autumn.

NEMATODE SAMPLING, EXTRACTION AND IDENTIFICATION

Nematode sampling was carried out in the three sites four times during 2012. As each sampling coincided with a season, to simplify the text sampled time will be named as winter, autumn, spring and summer. Samples of rhizosphere soil (10 samples per site per season) were collected at a depth of 10–20 cm, placed in individual plastic bags (1 000 cm^3) and kept in cold storage at 4 ºC until processed. Soil samples were collected within sites at random but the presence of a cork oak seedling was mandatory in order to use its root for the extraction of endoparasitic nematodes. We used an adaptation of the generalist tray method for nematode extraction: living mobile nematodes were extracted from 100 cm^3 sieved soil samples for 72 hours and endoparasitic nematodes were extracted from sieved root samples for 240 hours (Whitehead & Hemming 1965). Preparations were observed under an inverted microscope at 100–400 x magnification. We counted all extracted nematodes in the sample. For the determination of the feeding group we counted a subsample of 100 nematodes that were classified into functional groups (bacterivores, fungivores, PPN, predators and omnivores) according to their digestive system structure (Tarjan & Hopper 1974, Bongers & Bongers 1998). With these results both maturity indices (MI and PPI) and NCR were calculated. In order to describe PPN community and to determine if these should have an effect on cork oaks, we further identified PPN to genus level (Mai & Mullin 1996).

DATA ANALYSIS

Analyses of Variance (ANOVA), followed by post-hoc Tukey tests ($\alpha = 0.05$), were used to test for temporal differences among sites in the number of individuals of each functional group per preparation. Data were log-transformed for normality and homogeneity of variances. To test for differences in the number of bacterivores, PPN and total number of nematodes per preparation we used Kruskal-Wallis tests, followed by multiple comparisons of mean ranks for all groups, because variance was not homogeneous, even after data transformation. ANOVAs were also performed to test for differences among sites in mean daily temperature and relative humidity. All analyses were conducted using Statistica version 8.0 (StatSoft Inc. 2007).

Principal Components Analyses (PCA) were performed using CANOCO for Windows version 4.5 (ter Braak & Smilauer 2002) to describe temporal patterns in PPN genera composition among sites. These analyses reduce the dimensionality of the PPN genera while retaining most of the variation in the data set. Samples can be plotted allowing us to visually assess similarities and differences between PPN genera. The number of individuals of each PPN genera per preparation (log-transformed) were used as dependent variables through time.

Generalised Linear Models (GLM) were used to test the temporal and site effects for the indices of ecosystem function (MI, PPI, PPI/MI and NCR). Significant differences among groups were further elucidated through the post-hoc Tukey test ($\alpha = 0.05$). GLM were performed with Statistica version 8.0 (StatSoft Inc. 2007).

RESULTS

SOIL NEMATODES

A mean of 751 ± 660 nematodes were counted per preparation extracted from the soil (100 cm^3). The most abundant nematodes were bacterivores followed by fungivores, especially in site A and B while in site C the abundance of fungivore was higher than the other functional groups (bacterivores, PPN, predators and omnivores). Predators and omnivores were considerably less abundant in all sites (Fig. 10). There were no significant differences in the total number of nematodes among sites ($H_{2, 117} = 0.84$, $p = 0.656$), however, it was significantly highest in winter ($H_{3, 116} = 68.35$, $p < 0.001$) (Fig. 10). Significant differences in nematodes abundance among sites were only found in fungivores ($F_{2, 117} = 4.15$, $p = 0.018$), although these did not occur through time. Nevertheless, an increasing gradient of fungivore abundance was found every sampled time from site A to site C (Fig. 10). All functional groups showed significant or nearly significant differences over time (bacterivores: $H_{3, 116} = 59.37$, $p < 0.001$; fungivores: $F_{3, 116} = 32.17$, $p < 0.001$; PPN: $H_{3, 116} = 40.82$, $p < 0.001$; predators: $F_{3, 116} = 43.92$, $p < 0.001$; omnivores: $F_{3, 116} = 2.65$, $p = 0.053$) and higher abundances were found in winter. Fungivore abundance was significantly lower in summer (sites A and C) and autumn (sites A, B and C), as was the abundance of predators in the three sites.

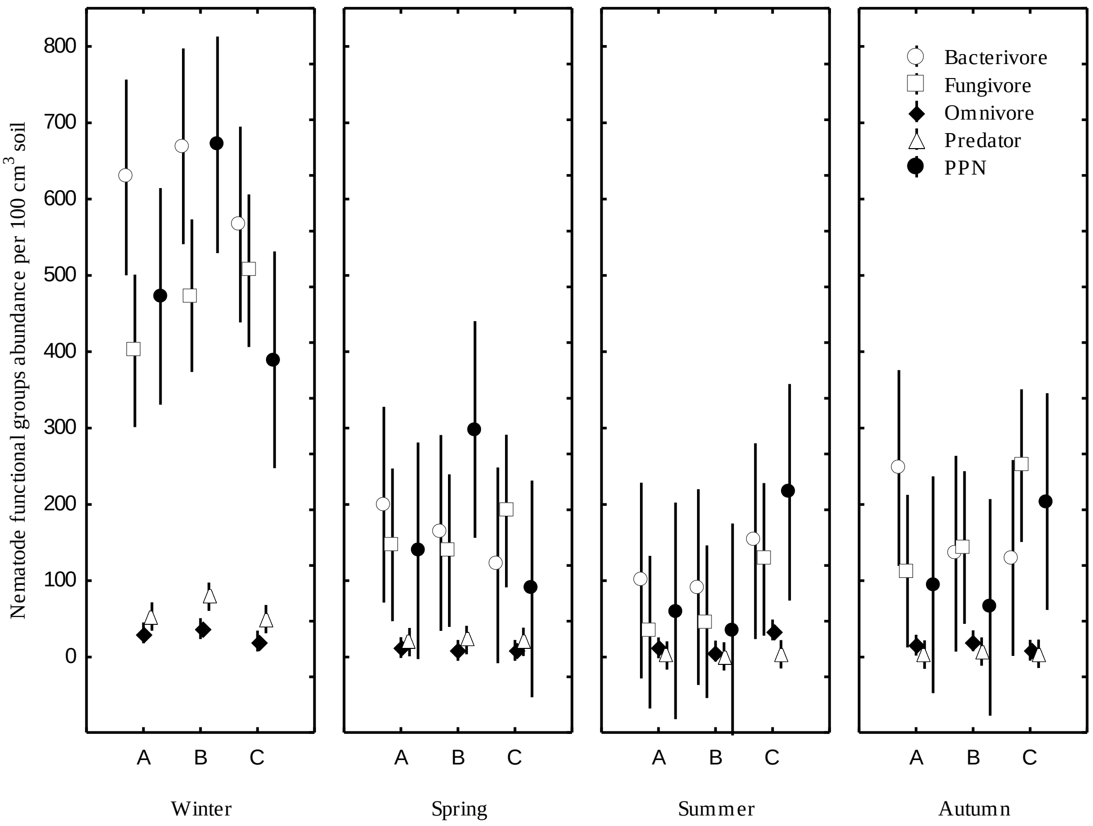

Figure 10. Temporal abundance of soil nematodes, classified into functional groups, detected in the three sites (see methods for information on experimental sites). Data correspond to the means ± SD of 10 replicates per site.

The GLM applied to the indices of ecosystem function showed the highest values of MI ($F_{12,\ 278.1} = 5.88$, $p < 0.050$), PPI ($F_{12,\ 278.1} = 7.79$, $p < 0.010$) and PPI/MI ($F_{12,\ 278.1} = 6.06$, $p < 0.010$) in spring. Within sites, only the NCR was significantly lower in site C ($F_{8,\ 210} = 4.32$, $p < 0.050$) (Table 3).

ENDOPARASITIC AND LIVING MOBILE PPN

Endoparasitic nematodes were not found in any of the preparations extracted from sieved roots of cork oak seedlings (n = 120). On the contrary, PPN extracted from soil samples consisted of 11 genera (number of samples where present): *Criconemella* (31), *Gracilacus* (60), *Helicotylenchus* (98), *Hemicycliophora* (2), *Heterodera* (16), *Longidorus* (42), *Pratylenchus* (92), *Rotylenchus* (74), *Trichodorus* (5), *Tylenchorhynchus* (70) and *Xiphinema* (41).

Table 3. Indices of ecosystem function (MI – maturity index for free-living nematodes, PPI – maturity index for plant-parasitic nematodes, NCR – nematode channel ratio) calculated per season in the three sites (A, B and C) (see methods for information on experimental sites). Data correspond to the mean ± SD of 10 replicates.

	MI	PPI	PPI/MI	NCR
Winter				
A	1.68 ± 0.25	2.99 ± 0.22	1.83 ± 0.34	0.58 ± 0.19
B	1.60 ± 0.14	3.13 ± 0.31	1.96 ± 0.21	0.60 ± 0.14
C	1.61 ± 0.17	3.00 ± 0.34	1.87 ± 0.18	0.53 ± 0.16
Spring				
A	1.71 ± 0.29	3.37 ± 0.21	2.03 ± 0.43	0.53 ± 0.17
B	1.74 ± 0.26	3.54 ± 0.25	2.07 ± 0.28	0.52 ± 0.17
C	1.83 ± 0.26	3.63 ± 0.36	2.00 ± 0.21	0.39 ± 0.17
Summer				
A	1.52 ± 0.15	3.01 ± 0.29	2.00 ± 0.25	0.66 ± 0.14
B	1.57 ± 0.18	2.92 ± 0.09	1.87 ± 0.18	0.73 ± 0.11
C	1.80 ± 0.26	3.07 ± 0.51	1.71 ± 0.21	0.55 ± 0.19
Autumn				
A	1.79 ± 0.26	3.10 ± 0.49	1.78 ± 0.46	0.51 ± 0.13
B	1.44 ± 0.25	3.11 ± 0.40	2.23 ± 0.58	0.68 ± 0.19
C	1.85 ± 0.26	2.79 ± 1.04	1.55 ± 0.61	0.32 ± 0.20

The PCA (Fig. 11) reduced the original 30 x 11 matrices, one for each sampling, to two independent principal components that explained 24.2 % and 21.8 % (winter), 30.2 % and 18.7 % (spring), 24.5 % and 18.1 % (summer), and 24.8 % and 18.3 % (autumn) of the variation, respectively. Every sampling showed a regular discrimination between site A and samples from the two other sites, according to PPN variability. The genera that most contributed for this segregation were *Gracilacus*, *Helicotylenchus*, and to a lesser extent *Criconemella* and *Rotylenchus*. In spring, the variability of the genus *Rotylenchus* did not stand for that distinction, supporting instead the separation of samples from site B. Samples from site B were generally discriminated by the variability of the genus *Xiphinema*, although most noticeably in spring. Moreover, in summer, samples from site B showed an inverse relationship with the variability of *Longidorus* and *Tylenchorhynchus*. Overall, no particular PPN genus fomented the segregation of samples from site C, except in autumn when it was determined by the variability of *Criconemella*.

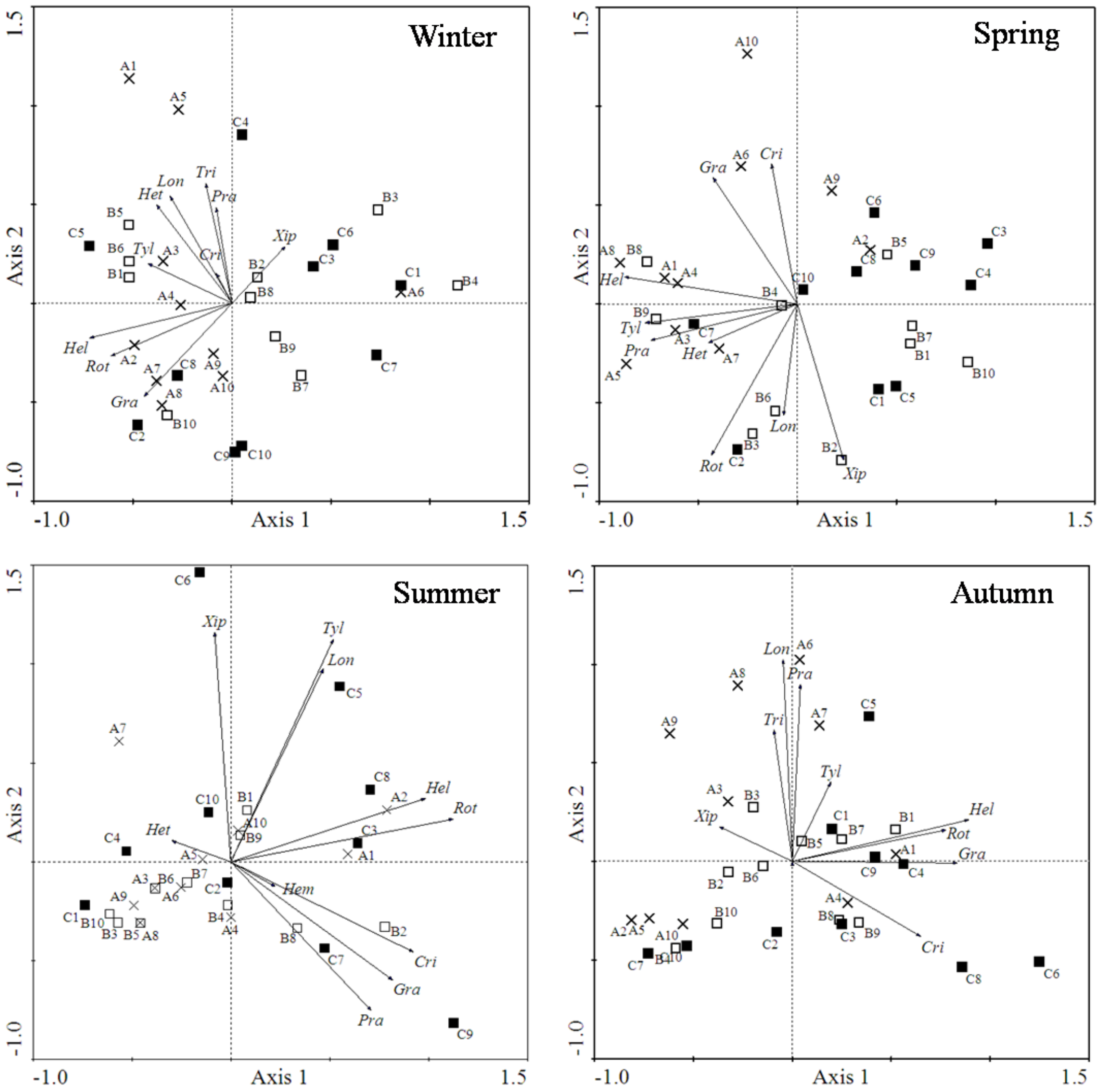

Figure 11. Biplots with PPN genera temporal variability and sample scores, according to site (A: X-mark, B: empty square, C: filled square). Codes for genera are *Cri* – *Criconemella*, *Gra* – *Gracilacus*, *Hel* – *Helicotylenchus*, *Hem* – *Hemicycliophora*, *Het* – *Heterodera*, *Lon* – *Longidorus*, *Pra* – *Pratylenchus*, *Rot* – *Rotylenchus*, *Tri* – *Trichodorus*, *Tyl* – *Tylenchorhynchus*, and *Xip* – *Xiphinema*.

SOIL AND CLIMATIC DATA

Temperature and relative humidity data recorded during this study agree with the Mediterranean climate of long, hot, dry summer and a mild, humid winter (mean annual temperature = 15.5 ºC, mean annual relative humidity = 73.6 %). Among sites, mean daily temperature was lowest in site B and relative humidity was highest in site B (temperature: $F_{2,\ 1095} = 2.96$, $p > 0.050$; relative humidity: $F_{2,\ 1095} = 5.06$, $p < 0.010$). The three sites showed no differences with respect to soil chemical properties and soil moisture content (Table 4). All tested soils were dry and acidic, which compromises the uptake of macronutrients, and had low levels of stable organic matter. These types of soils are prone to erosion and plant cover and soil biota may play crucial roles in the maintenance of a functioning soil layer. The organic matter content increased in the autumn, possibly due to the accumulation of dead plant material in the previous summer, without a correspondent decrease in soil pH. The increased levels of stable organic matter in the autumn may improve soil structure and provide nutrients, after the water and temperature stresses of the previous summer.

Table 4. Soil chemical properties and soil moisture content (mean ± SD of 10 replicates, measured *in situ*) in the three sites (A, B and C) in spring and autumn. C – Carbon, N – Nitrogen.

	pH (H_2O)	Organic matter (%)	C (%)	N (%)	C/N	Soil moisture (%)
Spring						
A	4.6	1.32	0.77	0.08	9.57	28.91 ± 5.86
B	4.7	1.27	0.74	0.07	10.52	22.94 ± 5.78
C	5.1	1.88	1.09	0.09	12.12	26.70 ± 4.35
Autumn						
A	5.2	2.33	1.35	0.11	12.29	22.39 ± 3.06
B	5.6	2.43	1.41	0.12	11.75	17.30 ± 2.79
C	5.0	1.52	0.88	0.08	11.02	18.30 ± 2.79

DISCUSSION

Temporal variations in nematode communities were most evident during winter when there was a rise in the abundance of the five functional groups in every experimental site. The high availability of food sources, *e.g.* fungi, plant roots or shoots and microbial communities, during that period may explain these differences (Ferris *et al.* 2004). Concordantly, there is a simultaneous increase of soil moisture and organic matter in winter, due to litter decomposition (Sohlenius *et al.* 2011). Although temperatures are more favourable to decomposition processes in the spring for *montado* ecosystems, microbial activity peaks in the rainy season (autumn and winter), after the litter inputs resulting from the summer drought (Costa *et al.* 2013). The increased organic matter content of soil between the spring and the autumn may result from litter inputs from the understory shrub vegetation (Correia *et al.* 2014), however in site C, which had the most dense and diverse shrub understory, an increase in organic matter and macronutrients was not observed. In fact, the herbaceous vegetation of site A may have had a larger contribution to the soil organic matter pool after the summer senescence than the dense shrub understory of site C (Otieno *et al.* 2011). Litter origin (shrub *vs.* herbaceous) and hence litter quality is also known to affect decomposition rates, with the former being decomposed at slower rates than the latter (Castro *et al.* 2010). The soil C/N ratio and soil pH increased with site disturbance (from site A to site C) in spring, which agrees with results obtained elsewhere for areas under increasing cattle grazing regimes (Bardgett *et al.* 2001), but not in autumn. None of the measured soil parameters could be related to populations of any of the nematode trophic groups or genera. Even if it is widely assumed that soil properties influence nematode distribution and damage to crops in agricultural systems, a direct relationship cannot often be found between presence and/or abundance of given genera and soil physic-chemical parameters (Chen *et al.* 2012). However, the cycling of nutrients in the soil is controlled mainly by nematodes, by stimulating microbial growth when feeding on them, based on the comparative estimates of other studies (*e.g.* Ingham *et al.* 1985, Hunt *et al.* 1987, Ferris *et al.* 1998). Bacterivorous and fungivorous nematodes appear to be the major contributors to N mineralisation. Increases in mineral N may follow the irrigation of dry soil (Sparling & Ross 1988, Lundquist *et al.* 1999) and consequently N mineralisation is probably offset by the considerable leaching of N that occurs during winter months (Poudel *et al.* 2001). However, grazing by aboveground herbivores can interfere over rates of vegetation succession, altering the quantity and quality of litter inputs to soil, which in turn affects soil biota and rates of soil nutrient cycling (Bardgett & Wardle 2003, Wardle *et al.* 2004).

Contrary to our expectations, distinct land uses had a small effect on nematode communities in *montados* while concerning functional assemblages. Nevertheless, there were noteworthy differences concerning fungivore abundance. This result is in agreement with the prominent role of fungi in ecosystem processes under low grazing, or completely unmanaged systems (Bardgett *et al.* 2001) and could be related to the input of lignin-rich, fungal-decomposition based litter originating from the understory shrubs (Castro *et al.* 2010). The temporal occurrence and abundance of many PPN genera was largely determined by land use. The genera *Gracilacus* and *Helicotylenchus* were associated to agriculture and livestock grazing (site A). Management was responsible for differences in plant community structure and composition among land uses, thus plant diversity increased from site A to site C. Given that PPN genera may have different levels of specificity to their hosts, it would be predictable that site C was the one with higher PPN diversity (Wardle *et al.* 2003, De Deyn *et al.* 2004, Viketoft *et al.* 2005). In our study, the number of PPN genera was identical in the three land uses; nonetheless, their variability was more homogeneous in site C.

Despite PPN being one of the most representative groups in the soil, endoparasitic nematodes were not found in roots of cork oak seedlings. As a significant number of root samples were sampled in the three land uses, we assume that PPN are not likely a limitation to cork oak regeneration since they did not affect seedling establishment.

Whilst data of nematode abundance was useful, the indices of maturity and trophic diversity are less variable than populations of individual trophic groups and thus may be more useful to detect trends in the ecological condition of soils (Neher & Darby 2009), providing a more structured ordination. Our results of MI, PPI and PPI/MI ratio explained the significant changes in the nutritional status over time following modifications in the dynamics of vegetation (Bongers *et al.* 1997), because the *montado* shows great variability in vegetation structure through time. Highest values of MI, PPI and PPI/MI were obtained in spring. An increasing population of bacterial feeders, with high reproduction rates, results in a decreasing MI. The persister nematodes (with higher cp values) are more resistant to disturbances and higher values of MI represent a less disturbed site. The PPI is comparable to MI but based on plant parasitic nematodes; PPI may increase with increasing soil fertility, whereas the MI decreases (Bongers 1990, Bongers & Ferris 1999). This inverse relationship is not shown by our data, which supports previous data suggesting organic farming systems are more sustainable due to the lack of synthetic pesticide and fertilizer use providing better closed nutrient cycles (Mulder *et al.* 2005). As the MI and the PPI may show diverging trends, a merging of the information provided by the life strategy (MI) and the functional information given by the PPI is the PPI/MI ratio (Bongers *et al.* 1997). We used this ratio as a useful additional parameter to detect differences through time. This ratio significantly varied with the highest values reached in spring. These ratios were higher than 1.6 in several of our observations, suggesting that resource utilization by plants may be far from optimal (Bongers *et al.* 1997). Significant differences among sites were only found concerning the NCR. NCR is a good indicator to express the energy efficiency in soil decomposition process (Moore *et al.* 1988, Yeates 2003), providing information on the dominant way in which the breakdown of organic matter proceeds with the participation of bacteria or fungi. Values for this ratio are constrained between 0 (totally fungi mediated) to 1 (totally bacteria mediated). Highest values were attained in sites A and B, suggesting a higher activity of the bacterial energy channel in these sites with fast-growing plant species, which dominate in early succession and produce high quality litter (*i.e.* N-rich) promoting bacterial-dominated food webs. NCR values were lowest in autumn and in site C (0.37 ± 0.18) evidencing a prevalence of the fungal-based decomposition energy channel, where slow-growing plants dominate in late succession and produce low-quality, phenolic-rich litter that favours fungal dominated food webs (Wardle 2002, Bardgett 2005). In addition, sites A and B are areas where the soil is regularly mechanized and grazed, and the detected differences among sites could indicate that soil conditions in site C are more stable (Viketoft *et al.* 2011).

This work is the first to use the soil nematodes as indicators of disturbance in the *montado* ecosystem. Nematode composition provided information on plant succession and changes in decomposition pathways in the soil food web. Our results stressed temporal variations in the structure of soil nematodes communities despite the effect of disturbance caused by land use. Future studies should be carried out in other areas of *montado* in order to confirm these patterns on a broad scale. Also, routine analysis of nematode fauna in different agroforestry systems affords rapid assessment of response to soil management practices and levels of stressors, so that sustainable optimal yields can be achieved.

CHAPTER 3

Factors affecting cork oak (*Quercus suber*) regeneration: acorn sowing success and seedling survival under field conditions

ABSTRACT

The lack of regeneration in many Iberian cork oak (*Quercus suber*) populations is putting at risk the conservation of the *montado* ecosystem. Biotic and abiotic factors as well as management are thought to constrain cork oak regeneration at multiple stages. The aim of this work was to identify limitations to cork oak during the early stages of regeneration (seedling emergence and survival to the first summer) and relate them to management practices undertaken at three sites in southwestern Iberian Peninsula. Experimentally burying of acorns was carried out at three distinctly managed *montados*. Cache predation, seedling emergence, survival and resprouting were monitored during the first year after germination. Regeneration was evaluated at individual and local level by testing the effect of biotic and abiotic factors in each stage. The regeneration processes were determined by temperature and relative humidity, seedlings that emerged earlier showed higher drought tolerance and resprouting ability whereas those drying later had enhanced resprouting probabilities. Bigger acorns and higher plant cover significantly assisted emergence, survival and resprouting of seedlings. Main mortality causes were drought (38 %) and mechanical ploughing (33 %) while cache predation and browsing on seedlings were low (1.7 % when excluding tag effect on cache predation and 0.6 %, respectively). Seedling emergence and survival to drought were significantly lower in the most disturbed site than in the other two sites. Abiotic factors restrain early regeneration processes while acorn size and plant cover are key factors determining seedling emergence and survival. The lack of cork oak regeneration may be overcome in the short-term by preserving the shrub layer. Moreover, reforestation by direct sowing should be also considered.

INTRODUCTION

Cork oak (*Quercus suber*) is an evergreen tree species restricted to the western part of the Mediterranean Basin (Tutin *et al.* 1964). This species has the rare ability of producing a thick cork layer in the outer bark which is periodically harvested bringing in an important income to landowners (Pinto-Correia & Mascarenhas 1999, Berrahmouni *et al.* 2007, Pereira 2007, Ribeiro *et al.* 2010, Bugalho *et al.* 2011a). The largest cork oak woodlands are found in the Iberian Peninsula, where, along with cork harvesting, agricultural, pastoral and other forestry uses have been practiced at least since the Middle Age (Joffre *et al.* 1999, Olea *et al.* 2005, Bugalho *et al.* 2011a). In this agro-silvo-pastoral ecosystem, known as *montado* or *dehesa* (the Portuguese and Spanish names, respectively; hereafter referred using the Portuguese word), cork oak trees have been selected and shaped by people through the centuries. In the present days, *montados* are typically open woodlands (20–80 trees.ha^{-1}) with only one or a few tree species besides cork oak, mainly holm oak (*Quercus rotundifolia*) and pines (*Pinus* spp.) (Joffre *et al.* 1999, Pinto-Correia & Mascarenhas 1999). Understoreys are traditionally used for cultivation and grazing by sheep and pigs, and despite shrubs sprout frequently (*e.g. Cistus*, *Asparagus, Erica, Lavandula* and *Ulex* ssp.) these are either cleared out or artificially kept at low densities (Díaz *et al.* 1997, Lourenço *et al.* 1998, Joffre *et al.* 1999, Pinto-Correia & Mascarenhas 1999).

A sustainable human use of *montados* has taken place over generations, by supporting the regulatory functions of the ecosystem (biotic and abiotic) while allowing for profitable economic activities (Barret 1992, Bugalho *et al.* 2011a). However, *montados* are undergoing an unprecedented rate of change. Despite cork oaks are long-lived trees, up to 200 years or more, the long-term persistence of the *montado* is seriously at risk due to a general decline and an distressing lack of natural regeneration in many Iberian cork oak populations (Montero *et al.* 1994, Pausas *et al.* 2009b).

Natural regeneration is a dynamic process where new individuals are recruited into the mature population compensating population losses due to mortality (Harper 1977). It is the product of distinct reproductive stages (*e.g.* flowering, seed dispersal, seedling emergence and seedling survival) which are restricted by several biotic and abiotic factors (*e.g.* Schrupp 1990, Jordano & Herrera 1995, Holmgren *et al.* 1997, Pulido & Díaz 2005, Fei & Steiner 2008, Pastur *et al.* 2013). In Mediterranean evergreen oak systems, limitations to regeneration have been attributed to various causes, including poor dispersal and shortage of viable acorns (Siscart *et al.* 1999, Branco *et al.* 2002, Pulido & Díaz 2005, Acácio *et al.* 2007), high post-dispersive acorn losses and seedling mortality due to predation by livestock and wild animals (Herrera 1995, Santos & Tellería 1997, Plieninger *et al.* 2004, Acácio *et al.* 2007, Plieninger 2007, Pérez-Ramos *et al.* 2008, Smit *et al.* 2008, Pulido *et al.* 2013), and low seedling survival to summer drought (Retana *et al.* 1999, Marañón *et al.* 2004, Plieninger *et al.* 2004, Acácio *et al.* 2007, Gómez-Aparicio *et al.* 2008, Smit *et al.* 2008, Gimeno *et al.* 2009, Smit *et al.* 2009). Nevertheless, little is known about natural regeneration processes in cork oaks and a few of the published studies on this subject focused on areas with an extremely low tree density (Herrera 1995) or fragmented peripheral populations (Pausas *et al.* 2006, Pons & Pausas 2006). Furthermore, the intensification of grazing and ploughing activities in the understorey has long been indicated as a setback to regeneration in *montados* (Pinto-Correia & Mascarenhas 1999) but the effect of management on regeneration is normally missing from this sort of studies (Marañón *et al.* 2004, Acácio *et al.* 2007, Maltez-Mouro *et al.* 2007, 2009).

In this study, we aim to identify biotic and abiotic factors that critically affect cork oak during the early stages of regeneration and to relate these limitations to management practices undertaken at three sites in southwestern Iberian Peninsula. Our approach was to mimic seed dispersal by experimentally burying acorns of the same cohort and monitor cache predation, seedling emergence, survival, and resprouting after summer drought during the first year following germination. Regeneration was evaluated at individual (seedling) and local (site) levels and the following hypotheses were tested: (i) post-dispersal predation of acorns (*i.e.* cache predation) is higher in livestock grazing regimes but also in shrubby areas, considering the positive correlation between shrub cover and acorn removal by rodents (Pons & Pausas 2007b, Smit *et al.* 2008); (ii) seedling emergence probability is higher for larger acorns, in accordance with recently published laboratory work (Ramos *et al.* 2013); (iii) seedling establishment and survival against summer drought is facilitated by shrub and canopy cover, as verified in other Mediterranean evergreen oak systems (Espelta *et al.* 1995, Smit *et al.* 2008, 2009); (iv) drought tolerance and resprouting are assisted by early emergence and later drying of seedlings, respectively, as well as by larger seedling sizes, because an enhanced physiological performance during establishment is expected to outcome from these factors (Schwilk & Ackerly 2005, Verdú & Traveset 2005); and (v) livestock browsing and intensive management practices involving mechanical soil disturbance during early stages of regeneration significantly reduce the number of seedlings. Overall, we expect that the multiple-staged limitations to cork oak regeneration are associated with chronic management differences among sites. Our study is particularly important in the context of climate warming (Christensen *et al.* 2007), in which it is expected that increased droughts and variability of rainfall regime in Mediterranean-type ecosystems will impose stronger constraints to germination and survival of cork oak seedlings.

MATERIALS AND METHODS

STUDY AREA

We carried out fieldwork in Montemor-o-Novo, southern Portugal, in the Herdade do Freixo do Meio (38º 42’ N, 8º 19’ W), a farm that manages 1 140 ha of cork-holm oak *montado*. This region has a Mediterranean climate with hot and dry summers and rainfall mostly in autumn and winter (mean annual rainfall = 660 mm, mean annual temperature = 15.4 ºC, mean annual evaporation = 1 760 mm; INMG 1991). In order to test our hypotheses, we selected three sites within the study area where cork oak was the dominant tree species and which had been historically subjected to different types of management.

Site A was characterised by a scattered tree cover (25 trees.ha^{-1}, 69 % cork oak) and by the absence of a shrub layer. Selective tree clearing occurred in the past to enhance crop cultivation in this site. Crop cultivation is regularly continued to produce fodder for livestock at the end of summer. Except in summer, this site was used as pasture for sheep (3.5 heads.ha$^{\mathbf{-1}}$) during the period of this study. In autumn, it was disc-ploughed and seeded with forage species (*Trifolium* spp.) to benefit the growth of pasture.

Site B was a dense cork-holm oak *montado* (40 trees.ha^{-1}, 76 % cork oak) with scrubby undergrowth of *Cistus* spp. and *Asparagus acutifolius*. Encroaching shrubs are periodically (4–5 years) cut with chains in this site to allow livestock grazing and browsing. During our study, this site was used by black Iberian pigs in early winter 2011/2012 (2.5 heads.ha^{-1}) and by sheep in autumn 2012 (2.5 heads.ha^{-1}).

Site C had a density of 45 trees.ha^{-1}, mainly cork oak (93 %) but also some holm oak and stone pine (*Pinus pinea*) (5 % and 2 %, respectively), and a dense heterogeneous shrubby understorey comprising *Cistus* spp., *A. acutifolius*, *Ulex australis* subsp. *welwitschianus*, *Pistacia lentiscus*, *Arbutus unedo*, *Phillyrea angustifolia*, *Crataegus monogyna*, *Quercus coccifera* and *Lavandula pedunculata*. This site was the most analogous to non-managed cork oak woodlands.

All sites had approximately 30 ha, ranging from 150–175 m a.s.l., and were located less than 3 km apart. Cork harvesting had taken place more than 3 years prior to our study in every cork oak tree in the study area.

EXPERIMENTAL DESIGN

In mid-November 2011, after mature acorns have fallen, we collected a number of acorns under the canopy of 20 randomly selected cork oak trees in each site. After confirming acorn viability with the flotation method (Gribko & Jones 1995), we retained 15 healthy acorns per tree. Following Johnson (1981) and Nilsson *et al.* (1996) we buried the acorns horizontally at a depth of 2 cm, simulating a successful cache, at five distances from the parent tree (next to the trunk, 5, 10, 15 and 20 m) along a randomly oriented transect. At each distance we cached three acorns, separated by 40 cm, and we tagged the central one with an orange vinyl flag set on top of a 45 cm stake wire which was buried 20 cm deep. We tested the effect of this tag on cache predation, based on the hypothesis that animals could be more attracted to tagged caches. All acorn handling was conducted wearing gloves and minimising soil disturbance to avoid attracting seed pilferers.

We monitored transects every two weeks until March 2013 and, for each cached acorn (n = 900), we considered four binomial (presence/absence) responses: cache predation, seedling emergence, seedling survival (from herbivory and first summer drought), and seedling resprouting (of dry seedlings after summer drought). Simultaneously, we recorded nine variables which we related to the previous responses: tag, cache predator, plant cover, acorn size (fresh weight, without cap, of the collected acorns measured before caching), seedling size (seedling height at emergence), time to seedling emergence (number of days since caching to emergence), time to seedling drying out (number of days since the seedling emerged until it dried out), temperature and relative humidity.

We determined plant cover by taking hemispherical photographs, using a digital camera (Canon EOS 350D, Canon, Japan) with a Fisheye converter (8 mm F3.5 EX DG Circular Fisheye Sigma, Japan). Photographs were taken at 0.25 m over each cache, orientated to the magnetic north and horizontally located using a bubble-level, and processed with Gap Light Analyzer 2.0 (Frazer *et al.* 1999). Plant cover (%) was calculated as 100 – openness, the latter being the percentage of open sky seen from beneath a forest canopy.

Temperature and relative humidity data were hourly recorded in the three sites with thermohygrometers (HOBO Pro v2 logger, Onset Computer Corporation, USA) placed 1.5 m above-ground. The values of temperature and relative humidity used in data analyses corresponded to the mean of the three sites calculated for each monitoring period. We additionally calculated vapour pressure deficit (VPD) from saturation vapour pressure, obtained from temperature based on Tetens formula, and relative humidity (Murray 1967, Monteith & Unsworth 1990).

In order to compare the three sites in terms of soil characteristics, we determined soil chemical properties and moisture content at the three sites in spring and autumn 2012. Soil moisture content was measured *in situ* at ten stations with a ThetaProbe ML2x (Delta-T devices Ltd., England). In summer, we failed to measure soil moisture content because soil was completely dry and the device was not able to obtain records.

DATA ANALYSIS

Because sampled acorns/seedlings were not independent from site, these were considered as pseudoreplicates and the effect of measured variables was tested on each response variable (cache predation, seedling emergence, seedling survival, and seedling resprouting) using nested Analysis of Variance (ANOVA). Cache predation was tested for the effects of tag; seedling emergence was tested for the effects of plant cover and acorn size; seedling survival was tested for the effects of plant cover, acorn size, seedling size and time to seedling emergence; and seedling resprouting was tested for the effects of plant cover, acorn size, seedling size, time to seedling emergence and time to seedling drying out.

We ran Generalised Linear Models (GLM) to explore the relationship between site management and the four response variables assuming a binomial distribution and logit link function. We computed models using the Drop 1 option, which starts with a model using all selected explanatory variables and then drops one explanatory variable based on its significance using a ANOVA. We carried out ANOVAs, followed by post-hoc Tukey tests ($\alpha = 0.05$), to test for differences among sites in the values of temperature, relative humidity, soil moisture, plant cover and acorn size.

We used Brodgar 2.6.6 (Highland Statistics Ltd. 2009), an interface supported by software R version 2.9.1 (R Development Core Team 2009), for data exploration and GLM analyses whereas nested ANOVAs were performed with Statistica 8.0 (StatSoft Inc. 2007). Results are presented as mean ± standard deviation.

RESULTS

CACHE PREDATION

From the 900 acorns cached, a total of 66 were predated (7.3 %). Most predation records (n = 56) corresponded to tagged caches and tag showed a significant effect on cache predation ($F_{1,\ 899} = 32.19$, $p < 0.001$; Table 5). Rodents and wild boar were the most relevant cache predators (56.1 % and 39.4 % of predation records, correspondingly; Fig. 12) identified by signs of shallow digging marks with acorn removal for rodents and soil uprooting for wild boar. Less important cache predators were pigs (two records) and a dung beetle (one record). In addition, we recorded one unviable cache in consequence of the establishment of an ant colony which we do not consider here as a predation record.

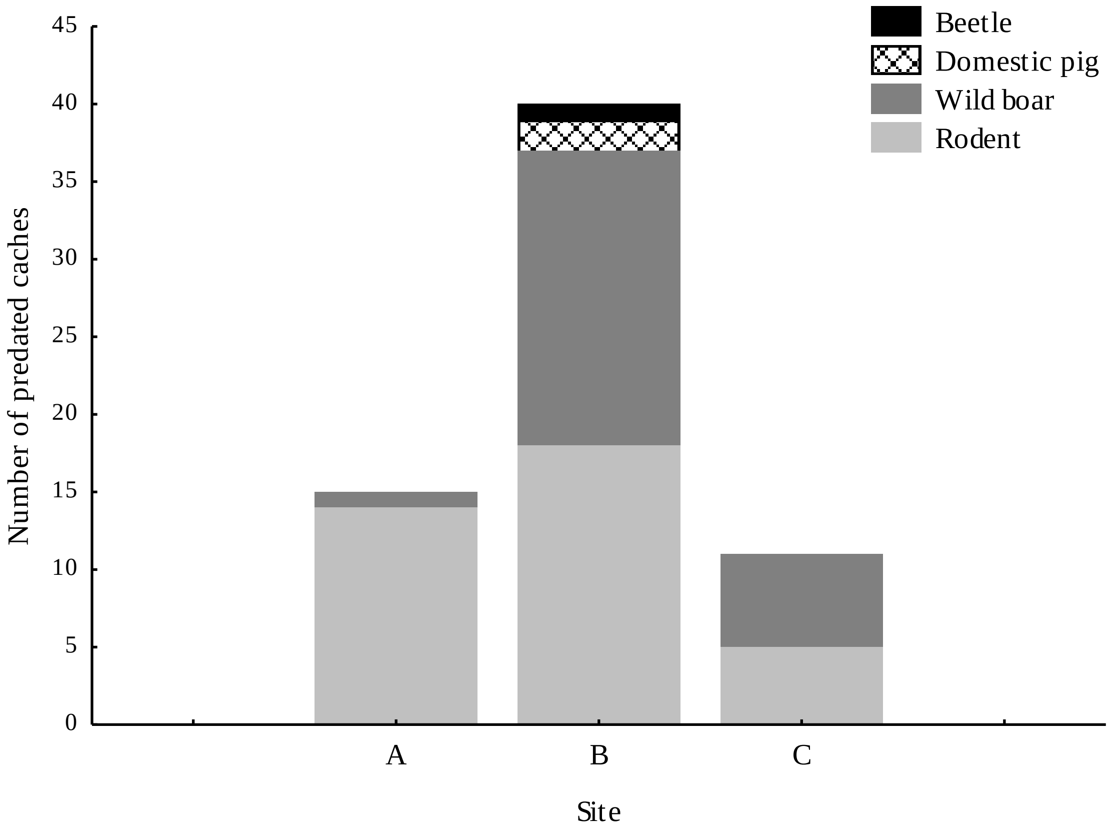

Figure 12. Cache predation in the three sites according to predator type. The number of predated caches reports to a total of 300 caches per site.

Seedlings emerged in 55.5 % of the caches (n = 462), excluding the predated ones. Emergence occurred 4–8 months after the caching date, *i.e.* started in early March, when the mean temperature in the understorey rose from 8.6 to 12.7 ºC, and went on until mid-July, when the highest annual mean temperature was recorded (24.0 ºC) (Fig. 13). The highest emergence rates occurred in April and May, following an increase in mean relative humidity from 58.9 to 83.9 % whilst mean temperatures were above 11.7 ºC. Mean values of VPD in April and May were 0.25 kPa in April and 0.54 kPa in May.

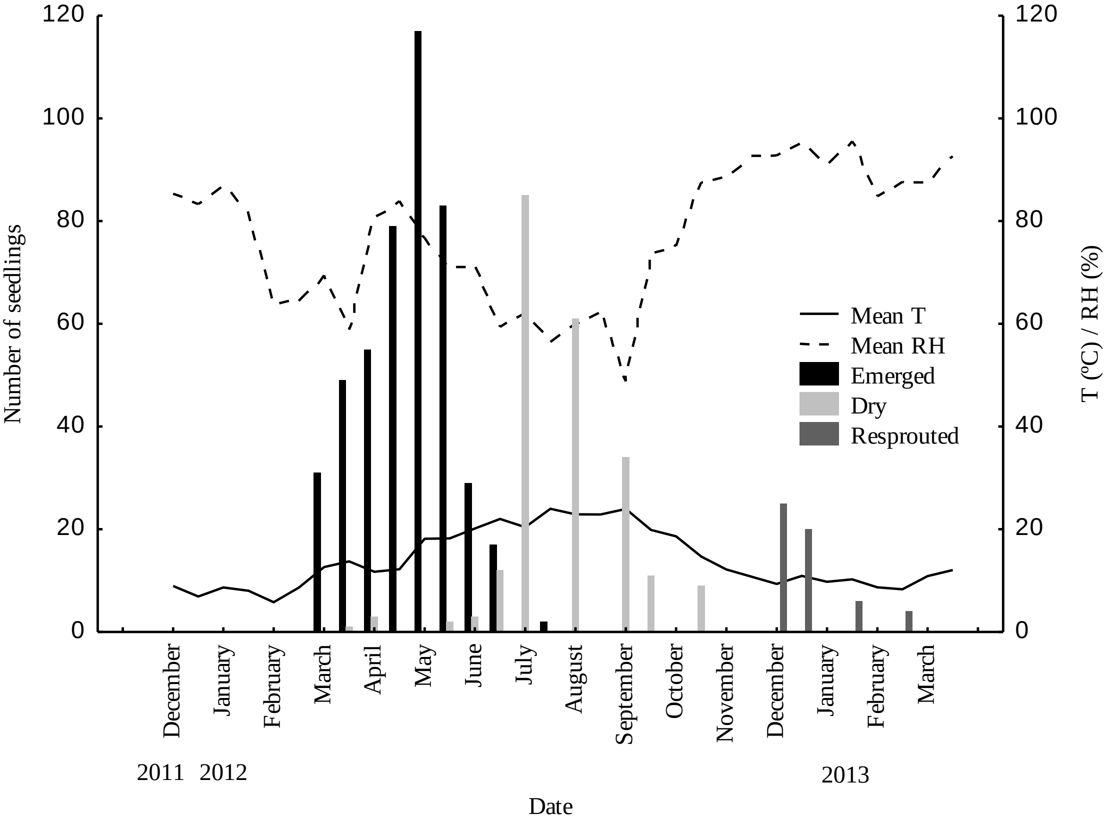

Figure 13. Seedling emergence, drying and resprouting throughout the study period and its relationship with temperature (T) and relative humidity (RH). Columns present the number of emerged, dry and sprouted seedlings for each monitoring period. Temperature and relative humidity values correspond to the mean of the three sites calculated for each monitoring period.

Plant cover had a significant effect on seedling emergence ($F_{1,\ 832} = 6.50$, $p < 0.001$; Table 5) and emergence probability increased for higher plant cover percentages. Also, bigger acorns had a significant positive effect on seedling emergence ($F_{1,\ 832} = 4.71$, $p < 0.001$; Table 5).

Mortality caused by herbivory was recorded in three seedlings, representing just 0.6 % of the 462 emergences. The percentage of dry seedlings after summer drought was 74.0 % (n = 342). We recorded 18 dry seedlings during spring, only a few weeks after emergence (41 ± 21 days), but the majority (n = 324) dried out from July to October, more than two months after emergence (97 ± 36 days) (Fig. 13). Nearly no drying happened when the mean relative humidity was higher than 75.7 % (VPD < 1.16 kPa). The highest drying rate occurred between July and September, when mean relative humidity dropped below 62.7 % (VPD > 1.84 kPa). This period coincided also with high mean temperatures, above 19.9 ºC.

Table 5. ANOVA results (parameter estimates with their F and p) showing the relationship between the four response variables (cache predation, seedling emergence, seedling survival and seedling sprouting) and tested explanatory variables.

	Cache predation (n = 900)	**Seedling emergence (n = 833)**	**Seedling survival (n = 459)**	**Seedling sprouting (n = 230)**
Tag	F = 32.19, p < 0.001	–	–	–
Plant cover	–	F = 6.50, p < 0.001	F = 11.71, p < 0.001	F = 5.73, p < 0.010
Acorn size	–	F = 4.73, p < 0.010	F = 5.71, p < 0.001	F = 12.32, p < 0.001
Seedling size	–	–	F = 0.90, p = 0.443	F = 1.47, p = 0.233
Time to seedling emergence	–	–	F = 4.15, p < 0.010	F = 10.06, p < 0.001
Time to seedling drying out	–	–	–	F = 23.11, p < 0.001
Site	F = 22.86, p < 0.001[a]	F = 9.75, p < 0.001[b]	F = 11.35, p < 0.001[b]	F = 0.001, p = 0.975[c]

[a] significantly higher in site B; [b] significantly lower in site A; [c] tested without site A.

Similarly to seedling emergence results, plant cover and acorn size showed very significant direct relationships with seedling survival ($F_{1, 458} = 6.50$, $p < 0.001$ and $F_{1, 458} = 4.71$, $p < 0.001$, respectively; Table 5). In addition, seedling survival probabilities were higher for earlier seedling emergence ($F_{1, 458} = 4.15$, $p < 0.010$; Table 5) but there was no significant effect of seedling size ($F_{1, 458} = 0.90$, $p = 0.443$; Table 5).

SEEDLING RESPROUTING

We evaluated seedling resprouting from a sample of 230 dry seedlings, corresponding just to plants in sites B and C. Overall, resprouting was recorded in 23.9 % of the sampled dry seedlings (*n* = 55). Resprouting occurred mainly in December (n = 45, 108 ± 25 days after drying out), when the monthly means of temperature and relative humidity in the understorey were 10.1 ºC and 94.1 % (VPD = 0.07 kPa) (Fig. 13). Resprouting was also recorded in January (n = 6, 147 ± 39 days after drying out) and February (n = 4, 212 ± 34 days after drying out), associated respectively with monthly means of temperature and relative humidity of 10.0 ºC and 93.2 % (VPD = 0.08 kPa), and 8.5 ºC and 86.2 % (VPD = 0.15 kPa). No further resprouting was seen when mean temperature rose to 11.5 ºC in March, although mean relative humidity was 90.0 %.

In agreement with seedling survival results, there was a significant positive effect of plant cover, acorn size, and time to seedling emergence on seedling resprouting (plant cover: $F_{1, 229} = 5.73$, $p < 0.010$; acorn size: $F_{1, 229} = 12.32$, $p < 0.001$; time to seedling emergence: $F_{1, 229} = 10.06$, $p < 0.001$; Table 5) and there was also no significant effect of seedling size on this response variable ($F_{1, 229} = 1.47$, $p < 0.233$; Table 5). Moreover, seedling resprouting showed a significant direct relationship with time to seedling drying out ($F_{1, 229} = 23.11$, $p < 0.001$; Table 5).

In late March 2013 we recorded 160 seedlings resultant of the 900 experimentally buried acorns in November 2011. These consisted of 105 seedlings which did not dry out and 55 seedlings which resprouted in winter after drying out mainly in summer.

The three sites were much similar with respect to temperature ($F_{2,\ 48} = 0.14$, $p = 0.873$) and relative humidity ($F_{2,\ 48} = 0.33$, $p = 0.719$). All tested soils were dry and acidic, and had low levels of stable organic matter (Table 4 in Chapter 2). Soil moisture content was highest in site A and it showed significant differences in autumn ($F_{2,\ 28} = 8.76$, $p < 0.001$; Table 4 in Chapter 2) while in spring differences among sites were nearly significant ($F_{2,\ 28} = 3.15$, $p = 0.059$; Table 4 in Chapter 2). Plant cover and acorn size also showed significant differences among sites ($F_{2,\ 897} = 3.91$, $p < 0.050$ and $F_{2,\ 897} = 7.70$, $p < 0.001$). Mean percentages of plant cover over each cache were significantly higher in site C (42.5 ± 18.1 %) than in sites A and B (41.4 ± 19.7 % and 37.5 ± 20.3 %, respectively) and acorn size was significantly lower in site A (5.3 ± 2.1 g) than in sites B and C (7.7 ± 2.9 g and 7.3 ± 2.8 g, respectively).

Significant differences among sites were found in every response variable except seedling resprouting (Table 5). Cache predation was significantly higher in site B than in the other two sites ($F_{1,\ 899} = 22.86$, $p < 0.001$; Table 5). Site B was the only site to have foraging pigs yet these animals were responsible for the predation of no more than two caches (Fig. 12). Rodents were the main cache predators in site A while in sites B and C the proportion of caches predated by rodents and wild boars was almost identical (Fig, 12). Excluding predated caches, seedling emergence percentages were 43.5 %, 59.2 %, and 63.9 % in sites A, B and C, respectively (Fig. 14), being significantly lower in site A than in the other two sites ($F_{1,\ 832} = 9.75$, $p < 0.001$; Table 5). Sites also differed in seedling survival probabilities ($F_{1,\ 458} = 11.35$, $p < 0.001$; Table 5), showing significantly lower values in site A (9.7 %) than in sites B and C (29.9 % and 32.1 %, respectively) (Fig. 14). Despite livestock pressure being higher on site A, herbivory was the mortality cause of only two seedlings in this site (plus another one in site B), and seedling mortality depended on a greater extent on summer drought than it did on herbivory. We did not evaluate resprouting in site A because this site was mechanically disc ploughed for pasture renewal in autumn, an operation which destroyed or seriously damaged all seedlings, dry or not. Resprouting percentages of dry seedlings in sites B and C were identical (23.8 % and 24.0 %, respectively; $F_{1,\ 229} = 0.001$, $p = 0.975$; Table 5).

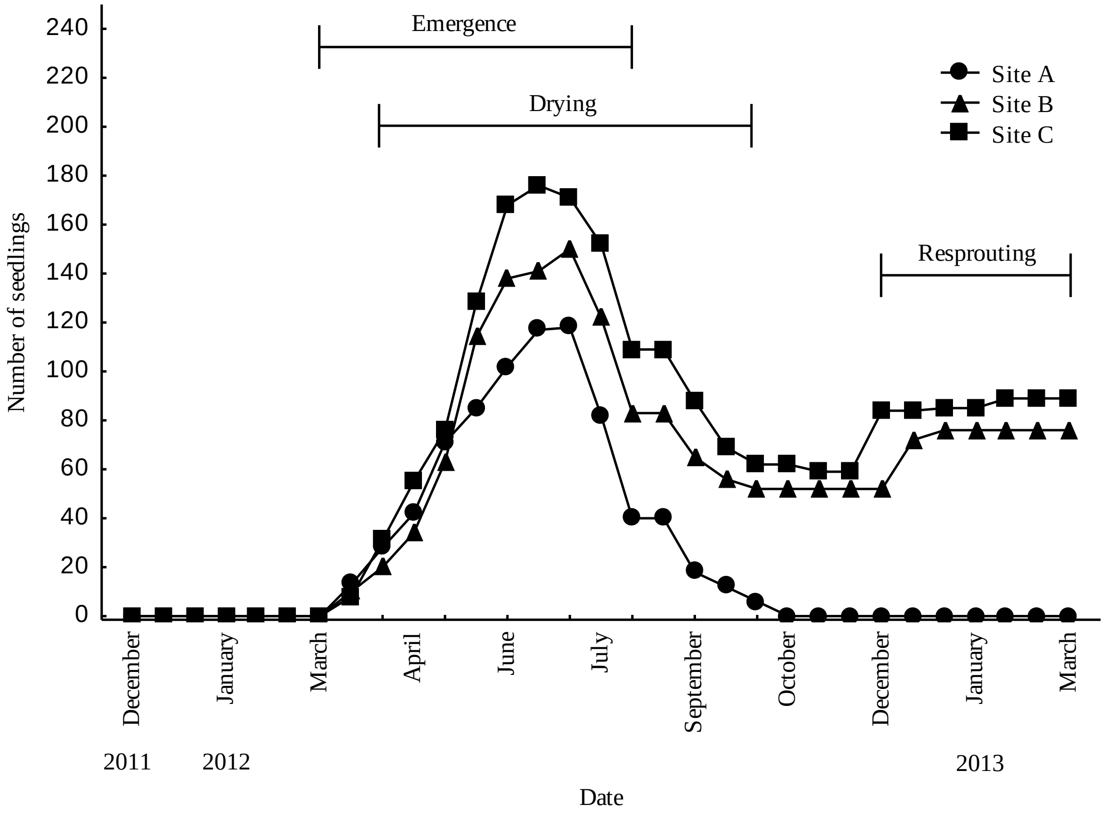

Figure 14. Seedling establishment and survival in the three sites during the study period. Results were obtained from a total of 900 acorns cached in the study area (300 acorns/site).

DISCUSSION

In this study we followed a cohort of nine hundred individuals during the initial stages of plant life, a key bottleneck for cork oak regeneration (Acácio *et al.* 2007), and identified important biotic and abiotic factors which hampered caches to succeed and seedlings to survive. As predicted by our hypothesis one, post-dispersal predation of acorns was highest in the management system which combined free-range livestock with a shrubby understorey (site B). However, cache predation by livestock was very low and most post-dispersal predation of acorns was due to wild animals, in particular rodents and wild boars. In agreement with hypotheses two and three, acorn size and plant cover had a major influence on seedling emergence and survival. Moreover, seedling tolerance to drought and resprouting were also influenced by early emergence and later drying of seedlings but, contrary to our expectation, seedling size had no significant effect on seedling responses (hypothesis four). On the other hand, cork oak regeneration was severely reduced by ploughing activities carried out in the most intensively managed area (site A), but, contrary to the predictions of our hypothesis five, livestock browsing had a small impact on the early stages of regeneration. In this section we analyse in detail our hypotheses and discuss the limitations of our approach as well as the implications of our results for the conservation of the *montado*.

STUDY LIMITATIONS

Montados are complex agro-silvo-pastoral systems, in which complexity increases with the variety of land tenure and land uses (Joffre *et al.* 1999, Pinto-Correia & Mascarenhas 1999, Plieninger & Wilbrand 2001, Bugalho *et al.* 2011a). A common problem of assessing management impacts in this ecosystem is that it is difficult to follow rules of good experimental design, such as randomization and replication, in a landscape characterised by site variability, especially at the topography, climate and soil levels (Pinto-Correia 1993). In our study, we were not able to replicate treatments due to the absence of nearby analogous sites during the period of study. Nonetheless, the three chosen sites were identical in soil properties, climate and topography and were sufficiently large to test our hypotheses at a local level. Land management systems were the probable reason for most differences found among sites and our results are consistent at showing management influence on biotic and abiotic factors affecting cork oak regeneration. In addition, this is the first comprehensive evaluation of multiple-staged limitations to cork oak regeneration which accounts for the effects of management.

THE EFFECT OF ABIOTIC FACTORS

The influence of abiotic factors on the early stages of cork oak regeneration was determinant given that seedling emergence and survival were highly synchronized with temporal variations of temperature and relative humidity. Dry acidic soils, such as those found in our study area, are prone to erosion and plant cover as well as soil biota may play crucial roles in the maintenance of a functioning soil layer (Aponte *et al.* 2011). The increase of stable organic matter in autumn due to the accumulation of dead plant material may improve soil structure and provide nutrients for seedlings after the water and temperature stresses of summer.

Temperature and soil moisture can be the reasons for the failure of seedling emergence (Burton & Bazzaz 1991) and we found a significant positive effect of early seedling emergence on survival probabilities at the end of the first year after germination. Also, seedlings drying later in the season had a selective advantage over those drying earlier, as they were more susceptible to resprout. Soil moisture content was higher in site A than in sites B and C, suggesting a lower competition for water in the absence of shrubs. Despite competition for water with shrubs and trees can potentially exacerbate drought effects of seedlings in the understorey (Holmgren *et al.* 1997, Valladares & Pearcy 2002, Sack *et al.* 2003), this was apparently no constraint to cork oak as drought tolerance of seedlings was highest in sites B and C.

THE EFFECT OF BIOTIC FACTORS

Previous studies analysing the consumption of fallen acorns in Mediterranean oak landscapes have documented very high removal rates (Herrera 1995, Santos & Tellería 1997, Gómez *et al.* 2003, Pons & Pausas 2007b, Pérez-Ramos *et al.* 2008). Higher recruitment rates, due to improved emergence and reduced predation (Shaw 1968, Borchert *et al.* 1989, Pulido & Díaz 2005, Smit *et al.* 2009), can be achieved by burying acorns to assist natural regeneration. In our study, cached acorns underwent very low removal rates and were almost exclusively consumed by rodents and wild boars. On the other hand, when acorns are lying on soil surface, they are consumed not only by wild boars and rodents but also by a range of ungulates, lagomorphs and avian predators (Herrera 1995, Díaz *et al.* 1996, Gómez *et al.* 2003, Pulido & Díaz 2005, Pons & Pausas 2007b). Additionally, an invertebrate (a dung beetle) predated one of our caches, widening the conclusions of Pérez-Ramos *et al.* (2007) to cached acorns. These authors showed that dung beetles bury and feed on fallen acorns in autumn acting as secondary seed dispersers given that some buried acorns can be abandoned without predating and emerge as seedlings. Even though post-dispersal predation was not an important limitation to regeneration in our study, we observed that the presence of tags marking buried acorns had a very significant effect on cache predation. If we discard that influence and consider only the caches that were not tagged, cache predation percentage was only 1.7 %.

Desiccation was the most important cause of cork oak mortality during the first year (37.9 % of total emerged seedlings), due to the correlation between low water availability and overheating (Valladares 2003). In Mediterranean communities, most woody plants resprout after disturbance, often from subterranean structures (James 1984, Bond & Midgley 2001). Cork oak has an extraordinary capacity of resprouting from stems and basal buds, and, under severe drought, the plant may shed its leaves and resprout when the drought is over, mainly in winter (Urbieta *et al.* 2008).

In agreement with studies on holm oak *montados*, the presence of a protective shrub layer and tree canopy significantly promoted emergence (Pulido & Díaz 2005, Smit *et al.* 2009) and assisted seedling survival, mainly by shading seedlings against summer drought (Espelta *et al.* 1995, Gómez-Aparicio *et al.* 2008, Smit *et al.* 2008). A high plant cover also promoted seedling resprouting in our study, probably through changes in the understorey which probably relate to decreasing radiation and water evaporation. Seedling emergence and survival probabilities also increased with acorn size. Seedling emergence relies on seed resources (Roach & Wulff 1987) and recent laboratory research showed a positive relationship between acorn size and germination in cork oak (Ramos *et al.* 2013). Nevertheless, our study demonstrated that acorn size has an additional and even more significant influence on seedling survival and resprouting. Differences in maternally provisioned resources can be vital for seedlings since these reserves are directed mainly to the root (Grime & Jeffrey 1965). There is a clear priority for root growth in cork oaks during the early stages of plant life and seedling survival cannot be guaranteed before roots reach a soil depth that holds water in the summer (Maroco *et al.* 2002). That should also be the reason for seedling size showing no significant effect on the survival of cork oak seedlings. Furthermore, cork oak seedlings from larger acorns have slower relative growth rates and a seedling-size effect (*i.e.* larger seeds produce larger seedlings) was only verified for this species under low light conditions (Quero *et al.* 2007).

THE EFFECT OF MANAGEMENT

In our study, stronger limitations to cork oak regeneration were imposed by management systems, particularly by ongoing practices involving mechanical soil disturbance. Our conclusions are supported by recent research in cork oak forests (Acácio *et al.* 2007, Maltez-Mouro *et al.* 2007, 2009), where management was restricted to periodic cork harvesting (at *ca.* 9-year intervals) in mature trees, which found no major constrains to cork oak regeneration. Notwithstanding, regeneration was seriously restricted/significantly held back in the most intensive management system (site A), which sustains the general concern about cork oak regeneration (Montero *et al.* 1994, Pausas *et al.* 2009b).

Management practices prior to our study probably caused marked differences in the three sites, which included acorn size and plant cover, the two factors which we found to have greater influence on the early stages of regeneration.

Acorn size is driven, above all, by climate conditions and the production of smaller acorns is more frequent in climatically restricted sites (Díaz-Fernández *et al.* 2004, Gómez 2004, Gimeno *et al.* 2009). Local adaptation through natural selection chiefly favours bigger acorns (Díaz-Fernández *et al.* 2004, Gómez 2004), although our sites were under the same climate influence since they were relatively close to each other (*ca.* 3 km) and, furthermore, measures of temperature and relative humidity taken in the three sites were not significantly different during the period of our study. Therefore, we believe that site management was the source of the discrepancy we found in acorn size. Although our results do not provide any indication regarding which particular practice was the reason of such differences, we found the smaller acorns in the most disturbed site.

Vegetation structure, mainly tree density and shrub cover, should account for part of site variations in cache predation rates and type of predator, where predation increased under denser plant cover (Gómez *et al.* 2003, Pulido & Díaz 2005, Pons & Pausas 2007b, Pérez-Ramos *et al.* 2008). Likewise, plant cover percentages contributed to differences in seedling emergence and survival among sites.

Ongoing management practices during our study concerned domestic livestock, grazing pressure and ploughing activities. Overall, livestock impact on cache and seedling survival was practically nil (0.6%). It is generally established that pigs reared extensively in the *montado* forage under trees after acorn fall, improving the quality of their meat by largely feeding on acorns. Given that in our study acorns were cached, predation by pigs was insignificant (0.2%) when compared with other studies carried out with superficial acorns (*e.g.* 6–14%; Pulido & Díaz 2005). Sheep grazing following acorn fall in our study area had no associated cache losses, and, although sheep grazed after emergence, these herbivores killed only three seedlings. However, we recorded drastic seedling mortality as a consequence of mechanical ploughing. This manoeuvre was carried out in the site with most significant regeneration limitations, cutting down a whole cohort of 112 seedlings before seedling resprouting (32.7% of total emerged seedlings).

ECOLOGICAL AND MANAGEMENT IMPLICATIONS

The *montado* ecosystem generally experiences environmental perturbations including periodic fires and recurring droughts (Aschmann 1973). In this scenario, regeneration establishment depends on improved seedling emergence and the growth of vigorous seedlings with longer roots to increase the chances of survival against summer drought. Our study suggests that the early performance of cork oak seedlings is primarily induced by parental effects mediated by acorn size. However, management measures are needed to uphold cork oak regeneration in the *montado*. The maintenance or increase of the protective shrub layer, for example, by temporary fallow management, would ease establishment in shady environments. Facilitation by shrubs may hold an increasingly importance in the *montado* given the expected changes in drought occurrence due to climate change (Christensen *et al.* 2007). Chain and disc ploughing for shrub cutting and enhanced pasture growth are common practices that do not benefit cork oaks at all, damaging seedlings and tree roots, spreading diseases and modifying the physical properties of soils (Ferreira 2000, Bugalho *et al.* 2009). Mechanical management in *montados* should be minimal in order to retain their ecological heterogeneity (Santana *et al.* 2011). Our results advocate that extensive livestock rearing does not put cork oak regeneration at risk. However, this postulate does not stand for cattle systems, as these may add other causes of cache/seedling mortality (*e.g.* trampling; Gómez *et al.* 2003).

The fact that seedling emergence rates were relatively high (55.5 %), suggests that reforestation through direct sowing of fallen acorns can be a low-cost highly valuable measure to increase cork oak regeneration in *montados*. As bigger acorns had a positive significant effect on emergence, we recommend sowing acorns with more than 7 g. Also, caches can be placed under the canopy of pre-existing shrubs since these can have a strong facilitative effect on seedling establishment, survival and growth in Mediterranean ecosystems (Castro *et al.* 2002, Gómez-Aparicio *et al.* 2004, Smit *et al.* 2008). Nonetheless, we recommend the preventive practices of acorn handling with gloves and reducing soil disturbance before manual sowing (Duncan *et al.* 2002). We additionally recommend dismissing the use of marking tags or any kind of enclosures, to avoid attracting seed pilferers. This recommendation should further be considered in seed removal studies as our results showed that removal rates involving label placement *in situ* can be biased.

Taken altogether, our results support the view that balanced management measures are the key to overcome the multiple-staged regeneration limitations and to promote a long-term persistence of the *montado*.

CHAPTER 4

Long-term sustainability of cork oak *montados* in the Iberian Peninsula: a model-based approach for assessing the effects of management options in a declining ecosystem

ABSTRACT

The future of the *montado* is questioned because the lack of cork oak health and low natural regeneration rates. We developed a System Dynamics Model to predict the long-term sustainability of the cork oak *montado* by recreating the management practices and the main environmental factors associated with this ecosystem (*i.e.* acorn germination, competition, fire, drought, livestock damage, shrub clearing, and cork oak death). Results indicated that the main limitations to cork oak regeneration in *montados* outcome from land management practices, being the main stressors livestock density and the intensive use of heavy machinery. The main conclusions were that limiting the quantity and type of livestock and extending shrub clearing for longer periods would invert the present decreasing trend of cork oak populations thus allowing the long-term sustainability of this ecosystem.

INTRODUCTION

The largest cork oak woodlands are found in the Iberian Peninsula, where cork harvesting, agricultural, pastoral and other forestry uses have been practiced at least since the Middle Age (Joffre *et al.* 1999, Olea *et al.* 2005, Bugalho *et al.* 2011a). In this agro-silvo-pastoral ecosystem, known as *montado* or *dehesa* (the Portuguese and Spanish names, respectively), human management has favored habitat heterogeneity and biodiversity at local and regional levels, creating a multiplicity of ecotones (Blondel 2006), and *montados* are considered both a protected habitat within the EU habitats directive (92/43/EEC) and a high nature value farming system, according to the classification proposed by the European Environmental Agency (Paracchini *et al.* 2008).

Cork oak (*Quercus suber*) is an evergreen tree species restricted to the western part of the Mediterranean Basin (Tutin *et al.* 1964). The long-term persistence of cork oak in *montados* is a subject of serious concern among both the public and scientific community, given the even-agedness of many *montado* areas. The main causes for this concern are the lack of cork oak health and low natural regeneration rates. Tree health has been affected by intensive pruning, exaggerated cork harvesting and the influence of pests and diseases (Camilo-Alves *et al.* 2013, Acácio & Holmgren 2014). The limitations to natural regeneration have been attributed to various causes, including poor dispersal and shortage of viable acorns (Siscart *et al.* 1999, Branco *et al.* 2002, Pulido & Díaz 2005, Acácio *et al.* 2007), high post-dispersive acorn losses associated with seedling mortality due to over-predation by livestock and wild animals (Herrera 1995, Santos & Tellería 1997, Plieninger *et al.* 2004, Acácio *et al.* 2007, Plieninger 2007, Pérez-Ramos *et al.* 2008, Smit *et al.* 2008, Pulido *et al.* 2013), and low seedling survival to summer drought (Retana *et al.* 1999, Marañón *et al.* 2004, Plieninger *et al.* 2004, Acácio *et al.* 2007, Gómez-Aparicio *et al.* 2008, Smit *et al.* 2008, Gimeno *et al.* 2009, Smit *et al.* 2009). Besides, the development of farm mechanization, including the generalised use of wide plows, disc harrows, and scarifiers destroys young trees and may damage roots and weaken established trees, creating more susceptibility to the attack of pest and diseases (Branco & Ramos 2009, Arosa *et al.* 2015). The increasing fire frequency in the last few decades in the Mediterranean region (Pausas & Vallejo 1999) has also become an additional obstacle to cork oak survival and recruitment (Acácio *et al.* 2009, 2010). Although cork oak is able to resist fire due to the bark insulation and to the mechanism of resprouting afterwards, frequent or intense wildfires may kill adult trees, especially if wildfires occur immediately after cork extraction (Moreira *et al.* 2007). Also, extreme droughts consequence of the increase of mean annual temperature and rainfall extremes during the last decades will reduce the forest cover and limit cork oak regeneration (Vivas & Maia 2007, Acácio *et al.* 2009).

Cork oak represents an important resource of high economic value in the Iberian Peninsula. In fact, the high economic value of cork oak lies in its ability to produce a thick bark with a continuous layer of cork tissue on the outside, a differentiation characteristic from the other evergreen oaks. Cork thickness and properties make it valuable raw material for industry. After the removal of the outer bark, a traditional practice that does not harm the tree and occurs every 9 year, the tree has the capacity to produce a new cork bark by adding new layers of cork every year and this may be repeated throughout the tree lifetime (Pausas *et al.* 2009a). The annual production of cork is about 370 000 T, mostly from the cork oaks of Portugal and Spain, that produce respectively 51 % and 23 % of the world total (Pereira & Tomé 2004). Therefore, the conservation of this complex ecosystem requires considering its ecological and economic sustainability, *i.e.* understanding its capacity to withstand and recover from disturbances imposed by natural and anthropogenic factors (Müller 2005, Kandziora *et al.* 2013, Stoll *et al.* 2015).

Modelling is a useful tool to study complex systems by predicting the outcome of alternative scenarios, and might help guiding current management options from projected future outcomes (Bastos *et al.* 2012, Bastos *et al.* 2015). Actually dynamic models can be used to improve the understanding of complex multifactorial mechanistic processes as they simultaneously integrate the structure and the composition of systems for a specific period (Jørgensen 1994, 2001). When properly developed, tested and applied with insight and with respect for their underlying assumptions, dynamic models are capable of simulating conditions that are difficult or impossible to produce otherwise (Jørgensen 2001).

We have developed a System Dynamics Model to recreate the management practices associated with cork oak *montado* and the main environmental factors influencing this semi-natural ecosystem, in order to predict its sustainability (Sterman 2001). The hypothesis associated considers that the different biotic and abiotic factors act interrelated, influencing the cork oak population dynamics. Overall, this study aims to integrate in a single approach the multifactorial factors associated with cork oak population dynamics, particularly the ones implicated in its decline across the Iberian Peninsula, improving the comprehension of the most determinant and highlighting the implications for the long-term sustainability of the *montado* system.

METHODS

STUDY SPECIES

Cork oak is a sclerophyllous evergreen oak that occurs in non-carbonated soils in the western part of the Mediterranean Basin (Pausas *et al.* 2009a). The main distinctive feature of this species is its thick insulating bark which evolved as a fire protection mechanism (Pausas 1997, Catry *et al.* 2012) and which regrows after extraction for cork production (Pausas *et al.* 2009a). This is a slow-growing tree with a high longevity like other oaks, with a lifespan of 250–300 years. Flowering and fructification occur at around 15–20 years of age (Pereira & Tomé 2004) producing both annual and biennial acorns. This heterogeneous acorn maturation pattern is a peculiarity among oaks, annual acorns mature the same year as the flowers which produced them, while biennial acorns grow and mature in the autumn of the following year (Natividade 1950, Elena-Roselló *et al.* 1993, Díaz-Fernández *et al.* 2004, Pereira &

Tomé 2004). Acorns can be dispersed by animals or predated. The main seed dispersers are wood mouse (*Apodemus sylvaticus*) and European jay (*Garrulus glandarius*), which are involved in short- and long-distance dispersal, respectively (Herrera 1995, Pausas *et al.* 2009b). Acorn predators are mainly seed-boring insects, such as the acorn weevil (*Curculio* spp., Coleoptera) and the acorn moth (*Cydia* spp., Lepidoptera). In open areas, predators can also be livestock, deer, wild boar, birds and rabbits whereas under a shrub canopy acorn predation is mostly carried out by small rodents, since neither large mammals nor birds will penetrate the dense vegetation (Herrera 1995). Cork oak trees grow in areas with strong seasonal water deficits by surviving to droughts in part due to their extensive and deep root system and in some cases seedlings shed leaves and resprout when the drought is over (Acácio 2007, Gómez-Aparicio *et al.* 2008, Arosa *et al.* 2015).

THE *MONTADO* ECOSYSTEM

Montados are typically open woodlands (20–80 trees ha^{-1}) with only one or a few tree species such as cork oak, holm oak (*Quercus rotundifolia*) and pines (*Pinus* spp.) (Joffre *et al.* 1999, Pinto-Correia & Mascarenhas 1999, Pinto-Correia & Fonseca 2009). This ecosystem consists of a landscape that has evolved over centuries as a special mix of nature and nurture in the Mediterranean region (Pereira & Pires da Fonseca 2003). Since the late Middle Ages and especially between 1850 and 1950, human activities such as shrub clearing, ploughing, tree thinning and conversion to agricultural land might disrupt the species population dynamics, jeopardizing the cork oak trees and impacting also the ecological and economic systems associated (Díaz *et al.* 1997).

DYNAMIC MODEL CONCEPTUALIZATION

Cork oak population dynamics were modelled to understand the effects of specific management practices on the sustainability of the cork oak *montado* under the environmental trends expected for the 21st century. Natural regeneration is a dynamic process where new individuals are recruited into the mature population, compensating population losses due to mortality (Harper 1977). It is the product of distinct reproductive stages which are constrained by several biotic and abiotic factors

(Holmgren *et al.* 1997, Pulido & Díaz 2005, Fei & Steiner 2008). Therefore, we created a System Dynamics Model with four sub-models concerning the cork oak population dynamics based on cork oak age stratification, represented by the sum of different life stage cohorts (seedlings, saplings, immature trees and adult trees), and one additional sub-model to assess the economic balances associated (Fig. 15).

Year was chosen as time unit and the simulation period was established for 300 years. This period was considered suitable to capture the influence of main factors influencing the cork oak regeneration, namely those induced by management options. Also, this delayed period of simulation represented the whole life-cycle of cork oak tree (*i.e.* 250–300 years; Costa & Pereira 2007). All modelling was performed with the software STELLA version 10.0.5 (Isee Systems, Inc.). The original conceptual diagram of the overall sub-models and full explanation of the variables included in the model construction are available as Appendix I, II, III and IV

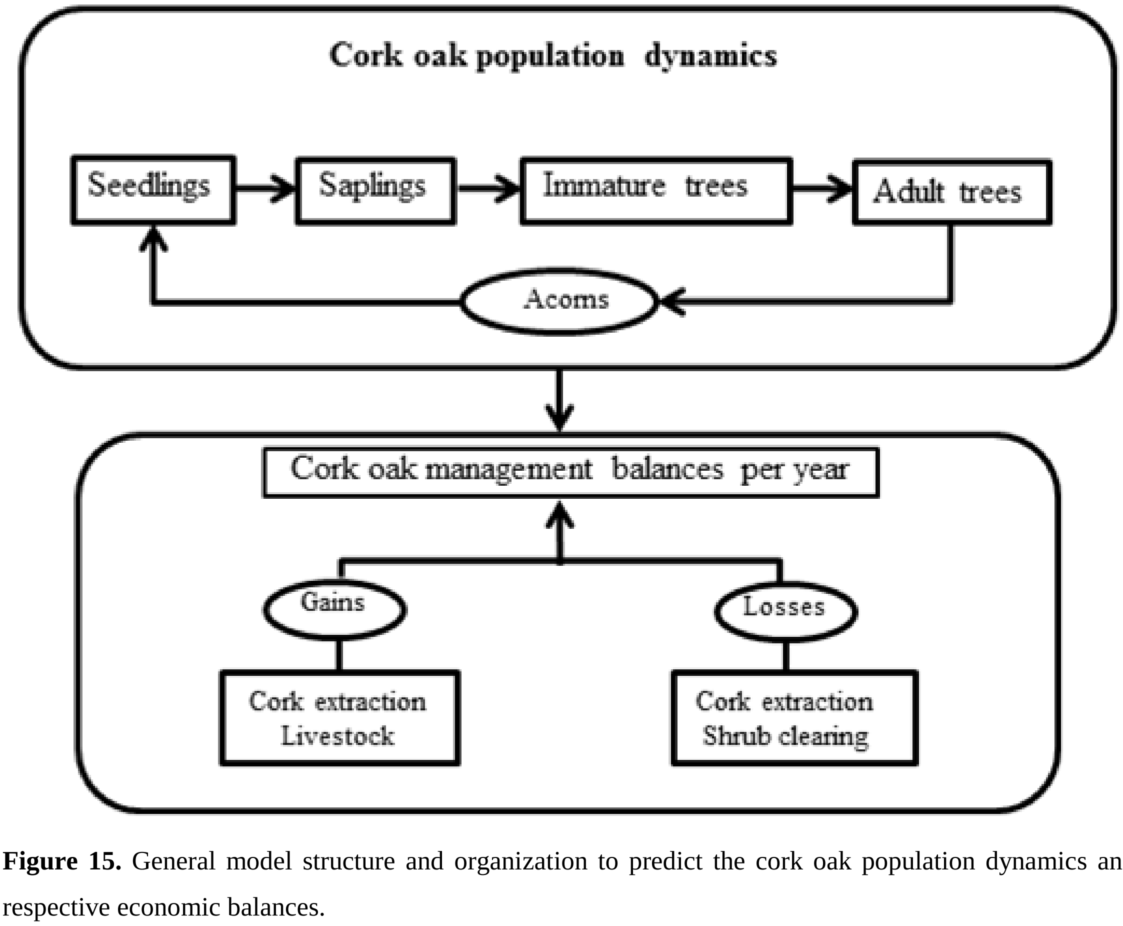

Figure 15. General model structure and organization to predict the cork oak population dynamics and respective economic balances.

The model structure included four sub-models that were developed to reproduce the dynamics of (i) seedlings, (ii) saplings, (iii) immature trees, and (iv) adult trees (Fig. 15, Appendix I). For each sub-model, cork oak trees were grouped into classes, considering their stage, size and diameter at breast height (DBH): seedlings (acorn or cotyledon scatters still attached, height < 50 cm), saplings (height > 50 cm, DBH < 10 cm), juvenile tree (height > 50 cm, DBH > 10 cm) and adult tree (DBH > 25 cm) (Muick & Bartolome 1987, Montero & Cañellas 2003). To initiate the simulation (t = 0), a mean number of 50 adult trees.ha^{-1} was considered (Joffe *et al.* 1999). Transitions between life stages were affected by biotic and abiotic factors that implicate cause-effect relations. Data used in the model was compiled from publications regarding cork oak and cork oak *montados* in the Iberian Peninsula, with specific conditions ranging from inland regions with lower annual precipitation (550 mm) and higher temperature (17 ºC), to coastal regions with higher rainfall (1 800 mm) and milder temperatures (14 ºC).

1. Biotic and abiotic processes influencing natural regeneration

Several biotic and abiotic processes were considered to have an influence on the species regeneration cycle: seedlings and saplings were affected by dry out, fire occurrence, livestock type and presence, and shrub clearing and timing (Fig. 16). On the other hand, immature trees and adult trees were affected by fire and natural death by aging. The progression of trees to the next life stage within the model will be firstly limited by intraspecific competition, and then by the availability of cork oak plants.

Acorn germination

To model the germination of acorns, each adult tree in the system was assumed to produce an average of 16.46 kg acorns per year (Herrera 1995, Cañellas *et al.* 2007, Pérez-Ramos & Marañón 2008). Since the germination of acorns is limited by biotic factors related with predation and insect damage, the effective number of acorns that enter the system was dependent on the predation survival rate and quantity of intact acorns. Furthermore, acorns that do not germinate and remain in the understory, dry out before the beginning of a new year.

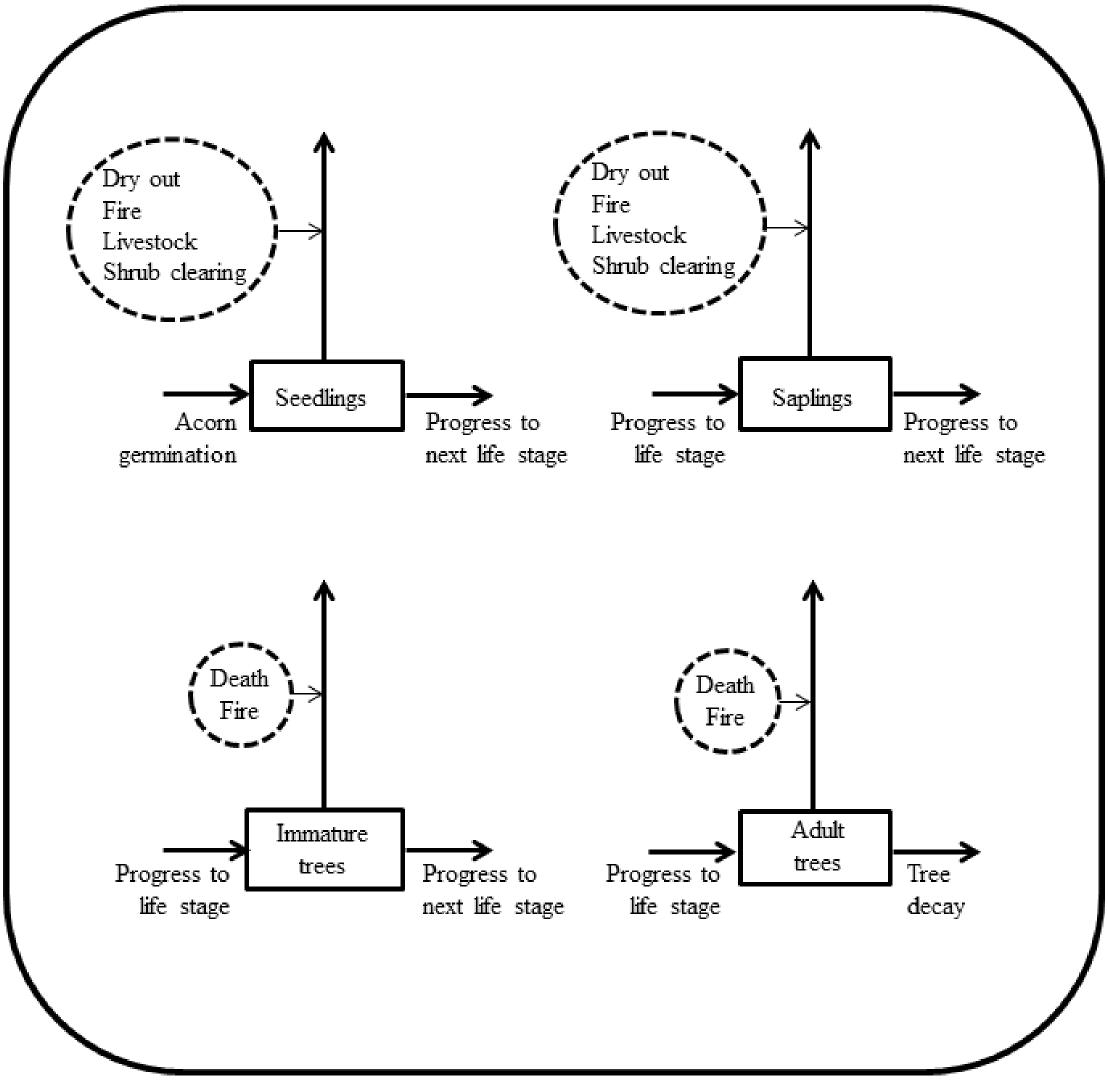

Figure 16. General structure of the four sub-models relative to the main cork oak life stages and the processes influencing each cohort of individuals. Individuals of a specific cohort transit to the next life stage when completing their development.

Competition

Competition involves a struggle to preempt resources such as light, water or nutrients that control carbon sequestration (Flores-Martínez *et al.* 1994, Holmgren *et al.* 1997, Callaway & Walker 1997). Our dynamic model was designed to recreate intraspecific competition by the different stages within the sub-models, from the sapling to the adult trees stage, considering the amount of growing space occupied by each tree. During tree development the interactions vary from early stages competition for soil resources and light to later stages of competition for light and affect the shape and size of crowns (Kenkel 1988, Deleuze *et al.* 1996). With increasing tree cover and light limitation, the older individuals begun to disproportionately obstruct the incoming solar radiation because of its unidirectional nature, thereby suppressing the growth of younger trees (Dolezal *et al.* 2004). In this context, Assman & Gardiner (1970) defined that the area available for a tree is represented by its crown projection and the corresponding fraction not occupied, thus we used the Di Bérenger´s method for calculating average crown projection using the diameter at breast height (DBH). This method enables the calculation of the distribution of trees within an area that can be developed as an intimate mixture of trees belonging to all age classes. Through the function $y = 0.0431 \bullet x^{1.6025}$ (x is DBH in cm) we limited the total cork oak trees.ha^{-1} belonging to each size class (Natividade 1950, Marín-Pageo & Camacho 2011).

Fire

Fires are common events in southern Europe and cork oaks are vulnerable to fires, especially seedlings, saplings, immature trees and adult trees when burning occurs immediately after cork extraction (Cabezudo *et al.* 1995, Pausas 1997, Moreira *et al.* 2007, Catry *et al.* 2012). We used fire data (1968–2012) from the Spanish Forest Service (magrama.gob.es) to parametrize the fire frequency in model but also the consequences of fires for each cork oak life stage, adjusted according to the respective tree diameters (DBH) (Catry *et al.* 2012). The average number of 0.013 ± 0.017 fires.ha^{-1} (mean ± SD), obtained from 100 independent stochastic simulations, was considered a reliable replica of the regional historical trends.

Drought

Droughts contribute to cork oak loss as it hampers regeneration and increases tree mortality (Acácio & Holmgren 2014). Drought effects were considered over seedlings and saplings, the more vulnerable life stages to this factor, reproduced in the model considering the historical trends of droughts in mainland Portugal from 1976–2007 (INAG 2007). The average number of 0.24 ± 0.078 droughts.ha^{-1} (mean ± SD), obtained from 100 independent stochastic simulations, was considered a reliable reproduction of the regional historical trends of droughts events.

Livestock damage

Livestock damage over seedlings and saplings was included in the model using the browsing index, *i.e.* browsing damages > 50 % of leaf area including the apical shoot (Reimoser 2000). The consequences of intense grazing are the death of young trees, soil compaction and decrease of both water infiltration and biodiversity (Plieninger *et al.* 2004, Plieninger 2006). Grazing pressure equals the ratio between stocking rate, *i.e.* the number of livestock units (LU) per unit area per unit time, and biomass (total dry weight of vegetation per unit area per unit time) (Allen *et al.* 2011, Sales-Baptista *et al.* 2015). From the 50's to present times, stocking rates in *montados* increased from 0.10–0.15 to 0.24–0.40 LU.ha^{-1} and the dynamic model tried to recreate this effect over seedlings and saplings, using the livestock damage rate (Plieninger & Wilbrand 2001, Plieninger *et al.* 2004, Plieninger 2006, Milán *et al.* 2006).

Shrub clearing

We included the effect of shrub clearing over seedlings and saplings in the dynamic model since this is a common practice in *montados* to control shrub invasion and to promote pasture growht (Pignatti 1983, Pulido *et al.* 2001, Plieninger *et al.* 2003, 2004, Calvo *et al.* 2005). Contrary to the effect of shrub encroachment that enhances oak regeneration, promotes soil rehabilitation and prevents erosion, shrub clearing increases soil erosion and can kill the regenerating cork oak seedlings and saplings (Plieninger *et al.* 2004, Pulido & Díaz 2005, Pérez-Ramos *et al.* 2008, Simões *et al.* 2009, Nunes *et al.* 2011, Arosa *et al.* 2015). Mortality due to shrub clearing was included in our model based on the results of Arosa *et al.* (2015).

Cork oak death

Tree death often represents a sum of a continuous process with multiple contributors, interplaying conspicuous factors such as age, insect damage or diseases, with unobvious factors such as management and climate (Franklin *et al.* 1987, Branco *et* *al.* 2002, Camilo-Alves *et al.* 2013). In the model, we considered the effect of tree death over immature and adult cork oak trees using data from Ribeiro & Surový (2008) who determined the mortality of cork oak (trees.ha^{-1}) using aerial photographs covering the entire distribution of cork oak in Portugal.

2. *Economic balance*

Cork oak *montado* is a multifunctional production ecosystem that can benefit society with many goods and services (Fig. 15), although the economic sustainability of cork oak *montado* depends mainly on the price of cork, associated with its quality and final use. Cork oak trees may live 250–350 years but cork thickness decreases and the limit to useful cork production is 150–200 years. Trees with circumference at breast height > 70 cm can be debarked, which corresponds to trees > 25–40 years of age, depending on site productivity and tree density. After the first cork debarking, the minimum period allowed between cork extractions is 9 years (Pereira & Tomé 2004, Pinheiro *et al.* 2008). Furthermore, depending of the management and *montado* land uses profits can be also increased mainly by livestock production and crop cultivation. On the other hand, shrub clearing and cork extractions represent the main costs associated with the management of *montados*. Overall, the cork oak dynamics under different management practices were used to assess the economic incomes from *montado* by balancing the financial gains and losses between scenarios.

SCENARIOS

Our System Dynamics Model was constructed in order to simulate realistic environmental conditions and management options concerning cork production besides addressing its influence on the cork oak population dynamics. Four scenarios were designed considering the influence of periodic fires, droughts and cork extraction.

Scenario 1 recreated the actual management of the *montados*, with shrub clearing every 4 years and annual presence of livestock with values ranging between 0.24–0.40 LU.ha^{-1} (the browsing index varied between 0.278–0.651 on seedlings and between 0.574–0.875 on saplings). Scenario 2 was based on the previous scenario, however shrub clearing occurs every 5 years. This allowed us to test the effects of a simple management change on the population dynamics as we maintained the density of livestock. Scenario 3 represented a situation where the livestock density was 0.40 $LU.ha^{-1}$. The browsing index corresponded to 0.651 and 0.875 on seedlings and saplings, respectively. Shrub clearing occurred every 5 years. Scenario 4 simulated the reconversion to agroforestry with annual crops on the understory.

The environmental conditions considered for all scenarios were similar. Cork oak life stages were grouped by scenario, considering periods of 100 years, in order to identify the critical developing stages involved in the regeneration.

We used Kruskal-Wallis tests to assess the effects of different management practices on the dynamics of cork oak populations and on the income from cork oak activities. This non-parametric test was used to detect differences among scenarios since the variables did not meet the normality assumption, even after data transformation. For post hoc tests, Tukey tests were used. Statistical analyses were carried out using the software Statistica version 8.0 (StatSoft Inc. 2007).

RESULTS

Scenario 1 predicted a decrease for all life stages (acorns, seedlings, saplings, immature and adult trees) throughout the simulation, the decrease in the number of adult trees will restrict the amount of acorns available each year, and consequently the number of seedlings and saplings (Fig. 17). In fact, the number immature trees is expected to be largely reduced by the effect of heavy machinery associated with shrub clearing while fire, drought, livestock browsing and cork extraction seem to play a minor role. The initial density of 50 adult $trees.ha^{-1}$ is expected to decrease to 16 $trees.ha^{-1}$ in the 300 years of simulation (– 22.29 % of adult trees per 100 years).

On the other hand, the initial density of adult trees in scenario 2 is expected to increase to 70 $trees.ha^{-1}$ in the 300 years of simulation (+ 13.66% adult trees per 100 years) (Fig. 18). The progressive increase in the number of adult trees will raise the number of acorns and consequently the number of seedlings and saplings. Also, the predicted revenue from cork oak *montado* was significantly higher in scenario 2 (768.25 ± 195.22 $€.ha^{-1}$ per year) than in scenario 1 (409.64 ± 147.36 $€.ha^{-1}$ per year) ($H_{1,\ 298} = 345.52$, $p < 0.001$; Fig. 22).

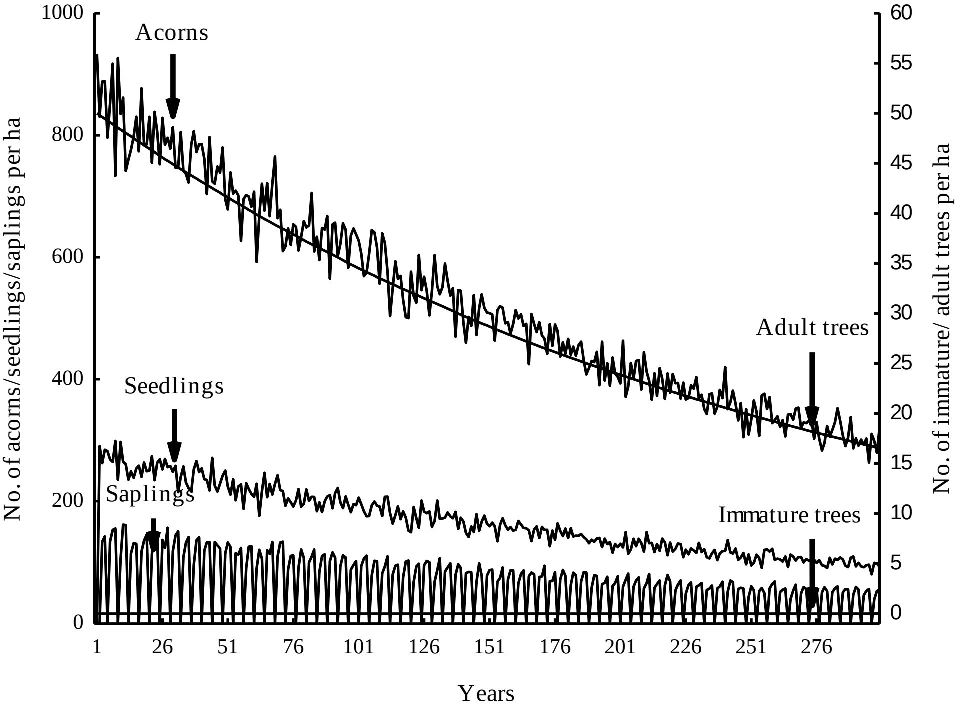

Figure 17. Cork oak population dynamics (acorns, seedlings, saplings, immature, and adult trees) in scenario 1, using 100 independent simulations throughout 300 years of simulation. This simulation included the random occurrence of fires and droughts, shrub clearing every 4 years, the presence of livestock (0.24–0.40 LU.ha^{-1}) and cork extraction every 9 years.

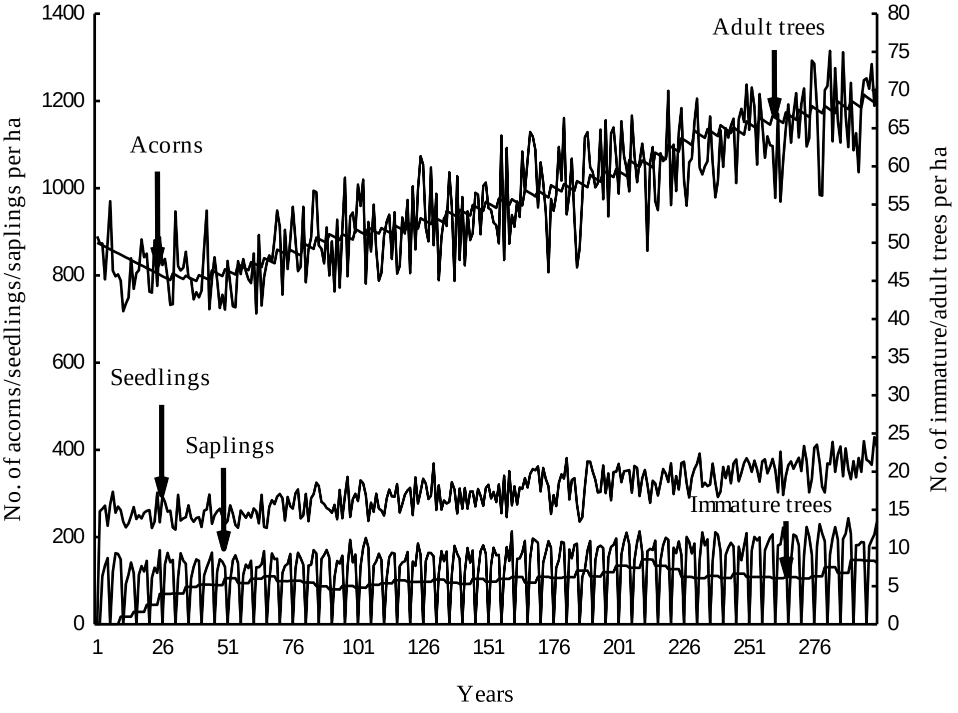

Figure 18. Cork oak population dynamics (acorns, seedlings, saplings, immature, and adult trees) in scenario 2, using 100 independent simulations throughout 300 years of simulation. This simulation included the random occurrence of fires and droughts, shrub clearing every 5 years, the presence of livestock (0.24–0.40 LU.ha^{-1}) and cork extraction every 9 years.

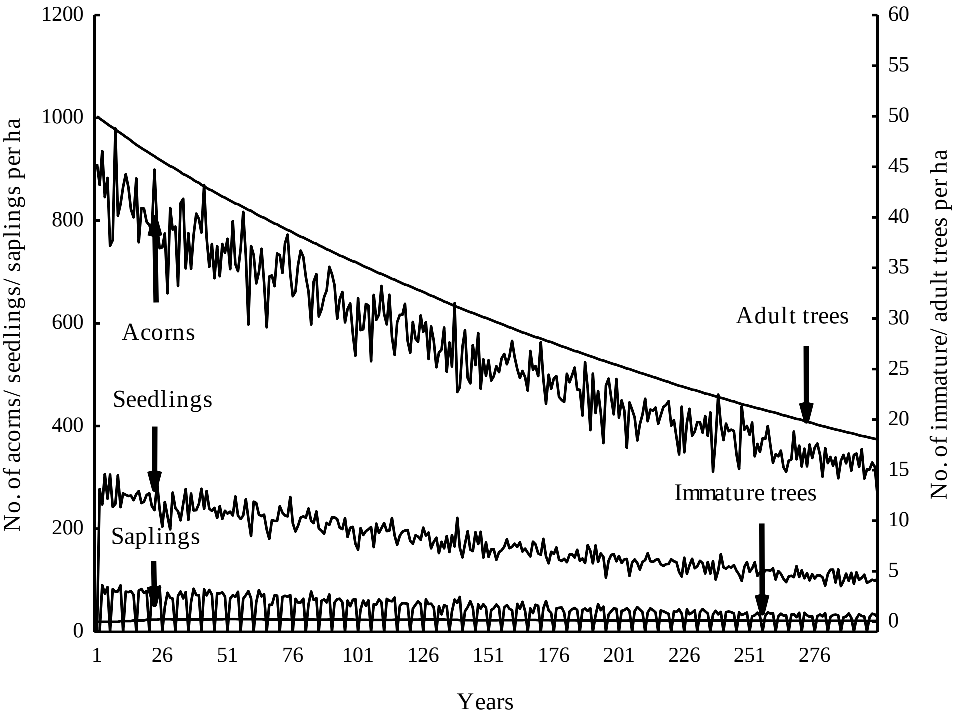

Figure 19. Cork oak population dynamics (acorns, seedlings, saplings, immature, and adult trees) in scenario 3, using 100 independent simulations throughout 300 years of simulation. This simulation included the random occurrence of fires and droughts, shrub clearing every 5 years, the presence of livestock (0.40 LU.ha^{-1}) and cork extraction every 9 years.

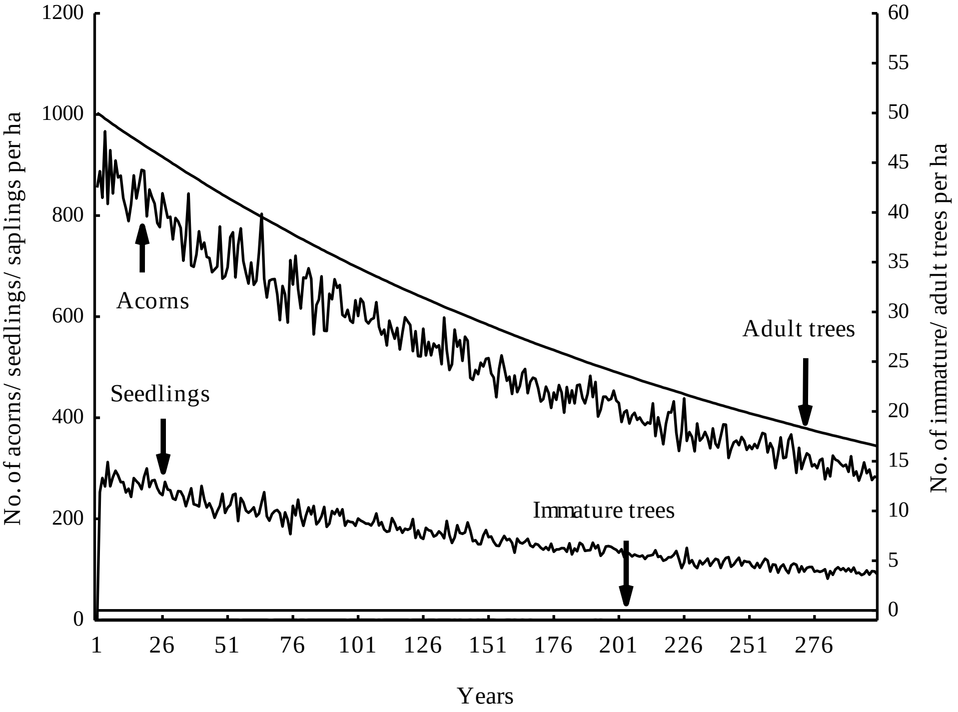

Figure 20. Cork oak population dynamics (acorns, seedlings, saplings, immature, and adult trees) in scenario 4, using 100 independent simulations throughout 300 years of simulation. This simulation included the random occurrence of fires and droughts, shrub clearing every year, and cork extraction every 9 years, while livestock was absent.

Even though shrub clearing is carried out every 5 years, by increasing livestock pressure in scenario 3 there is an overall decrease in acorns, seedlings, saplings, immature and adult trees (Fig. 19). The estimated density of adult trees in 300 years from present decreased to 18 trees.ha^{-1} (– 21.30% of adult trees per 100 years).

According to scenario 4, there is an estimated decrease in the density of adult trees, which would be 16 trees.ha^{-1} at the end of 300 years of simulation (– 22.32% of adult trees per 100 years) (Fig. 20).

Kruskal-Wallis tests, complemented by the Tukey multiple comparison test, analysed the cork oak population dynamics of seedlings (A), saplings (B), immature trees (C) and adult trees (D) per hectare grouped in periods of 100 years per scenario. Significant differences were found between scenario 2 and scenarios 1, 3 and 4 in the number of seedlings.ha^{-1} ($H_{3,\,1196}$ = 583.98, $p < 0.001$; Fig. 21A), saplings.ha^{-1} ($H_{3,\,1196}$ = 362.94, $p < 0.001$; Fig. 21B), immature trees.ha^{-1} ($H_{3,\,1196}$ = 1055.98, $p < 0.001$; Fig. 21C) and adult trees.ha^{-1} ($H_{3,\,1196}$ = 636.41, $p < 0.001$; Fig. 21D).

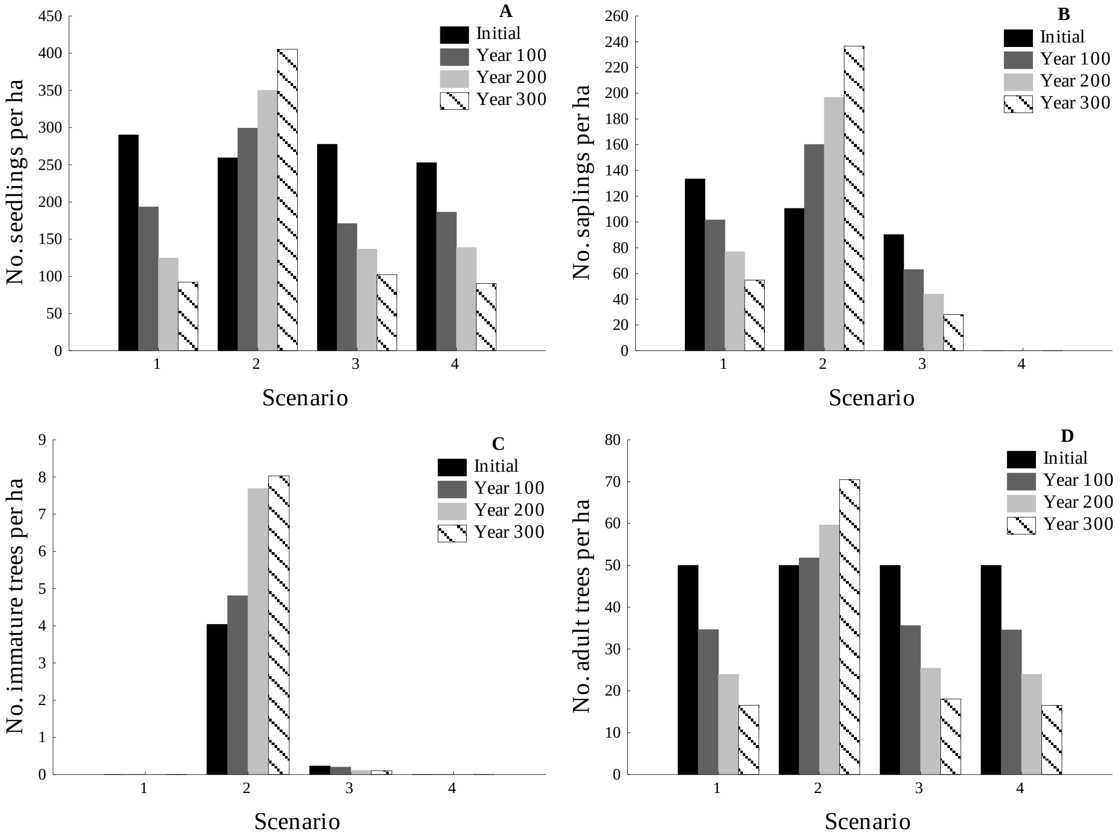

Figure 21. Cork oak population dynamics of seedlings (A), saplings (B), immature trees (C) and adult trees (D) per hectare, grouped in periods of 100 years per scenario.

The economic balances associated with each scenario (Fig. 22) showed also that scenario 2 had the highest predicted revenue from cork oak (768.25 ± 195.22 €.ha^{-1} per year). The profits associated with scenarios 1 and 3 were identical (409.64 ± 147.36 and 425.29 ± 145.93 €.ha^{-1} per year, respectively) while scenario 4 generated the lowest income (114.06 ± 147.78 €.ha^{-1} per year).

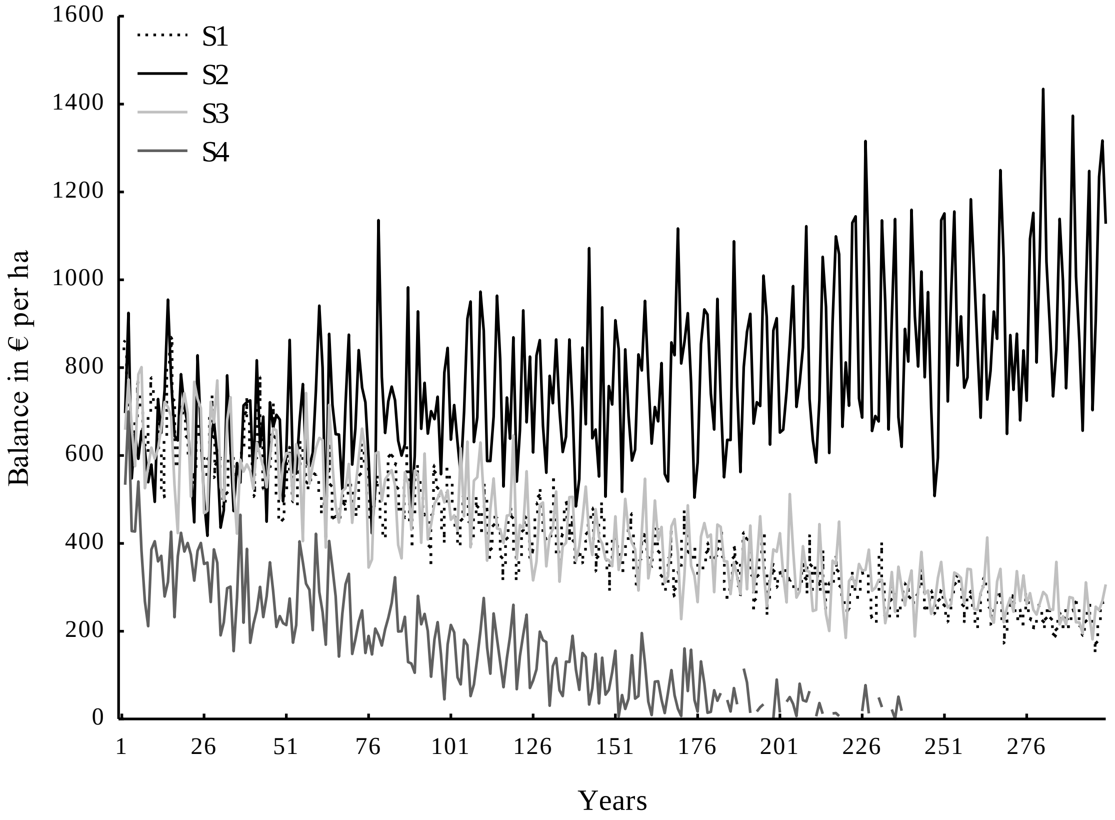

Figure 22. Predicted economic revenue (€.ha^{-1}) for scenarios 1, 2, 3 and 4 throughout 300 years of simulation.

DISCUSSION

In the *montado* ecosystem, a dramatic mortality of cork oak happened when trees were thinned to ease the use of farm machinery and promote wider crowns that yield more acorns (Pulido *et al.* 2001, Moreno-Marcos 2007, Plieninger 2007). As cork oaks are coming close to the end of their natural life, strategies were created to preserve the *montado* and enhance its cultural and natural values. Legal protection of the trees and agro-environmental schemes have been implemented to protect and promote tree plantation in the *montado* (Pinto-Correia *et al.* 2011). On the other hand, most *montados* in Spain and Portugal are private and changes in the rural socioeconomic condition, in part induced by the Common Agricultural Policy (CAP), have contributed to the rural exodus due to poor conditions for agriculture, the peripheral location of the rural areas and the lack of employment (Van Doorn & Bakker 2007). Therefore, the importance of the socioeconomic situation in relation to land use change is generally recognized (Brandt *et al.* 1999): the direct aid to cereal areas and to some grazing animals into single payments to farmers, which are decoupled from production, resulted in land owners that have tended to replace sheep and goats with cattle, which in last 16 years increased its numbers by 2.5 times due to CAP support (Dýrmundsson 2004, Pinto-Correia & Godinho 2013, Pinto-Correia *et al.* 2014, Viegas *et al.* 2014). After the abandonment of cereal crops and livestock rearing, during the 70's, shrub clearing and rotational ploughing became common practices to control shrub invasion, to promote pasture production and prevent fire (Pignatti 1983, Pulido *et al.* 2001, Plieninger *et al.* 2003, 2004, Calvo *et al.* 2005). The heavy cattle breeds or higher livestock rates together with deep ploughing of cultivated crops is undoubtedly affecting natural regeneration and many authors estimate these factors as a major threat to the *montado* ecosystem (Pinto-Correia & Mascarenhas 1999, Bugalho *et al.* 2011a, Moreno & Pulido 2013).

This is in accordance to our results that indicate that high livestock density and/or the use of heavy machinery compromise the future sustainability and the consequent revenue for farmers in the long-term. Our findings indicate that the main limitations to the lack of cork oak regeneration in *montados* rise from land management practices, rather than environmental factors. In fact, the obtained results suggest that delaying shrub clearing and limiting the quantity of livestock units might constitute a suitable measure to allow the long-term sustainability of the *montado*. A minimal delay of one year in soil ploughing (scenario 2) was enough for landowners to ensure an increase in the number of adult trees and the long-term sustainability of the *montado* ecosystem. Since cork is the most profitable product obtained from the *montado*, an increase in the density of adult trees would have also a direct positive effect on potential incomes. Although, by increasing livestock densities (scenario 3), cork oak regeneration is severely constrained due to the consumption of seedlings and saplings, and the regeneration cycle would eventually collapse just like when there is a continuous use of heavy machinery (scenarios 1 and 4).

Our results are in accordance with other authors who argued that livestock pressure determines the rates of *montado* loss (Blondel 2006, Plieninger 2007, Gaspar *et al.* 2008, Bugalho *et al.* 2011b). Acorn predation and browsing, as well as trampling of seedlings are the main pressures of overgrazing, associated with the intensity and type of grazing (livestock type, breeds, density, length of time in pasture) (Pulido & Díaz 2005). Despite some authors limit the carrying capacity of the *montado* near 1.00 $LU.ha^{-1}$ (Baeza 2004, Calvo *et al.* 2012), our results indicate that livestock pressure is at its maximum in 0.40 $LU.ha^{-1}$ and by increasing this number we would seriously compromise the future of the *montado* ecosystem.

Results relative to shrub clearing are in accordance with Godinho *et al.* 2014 who demonstrated that most of the *montado* loss is associated with land management practices. Shrub clearing increases plant diversity whereas shrub encroachment might promote landscape heterogeneity and benefit the fungal community in *montado*, increasing the mycorrhizal community which is part of the symbiosis most intimately connected to the soil and most directly involved in uptaking nutrients and influencing soil properties (Azul 2002, Azul *et al.* 2010). The period between consecutive shrub clearings supports different management objectives: intensive shrub clearing every three years will favor pastureland for livestock grazing and decreasing shrub growing will neglect its positive protector effect over regeneration (Canteiro *et al.* 2011, Simões *et al.* 2015). This agrees with our results, where short periods between clearings would inhibit the regeneration of trees, since mechanical clearing is a non-selective tool which destroys most seedlings (Arosa *et al.* 2015). According to our results, we assume that extending shrub clearing for longer periods would benefit natural regeneration in agreement with other studies (Canteiro *et al.* 2011, Simões *et al.* 2015). Their conclusions suggest maintaining the shrub cover for a period between 7-12 years, this would help save cork oak regeneration, and promote tree nursery and soil rehabilitation. Conversely, longer periods than 12 years could facilitate fire spread due to the accumulation of dead material (Canteiro *et al.* 2011). EU programs have only been subsidizing planting young cork oak trees but results obtained by Arosa *et al.* (2015) confirmed that direct seeding of cork oak is a good alternative to facilitate regeneration, because emergence success ranged between 43.5 % and 63.9 %. Subsidies play an important role in management decision and can contribute to further degradation of tree cover (Pinto-Correia & Vos 2004).

The capacity to accurately forecast responses of indicator species to landscape changes is crucial for conservation planning and to support key ecosystems management (Kandziora *et al.* 2013). In *montado* systems, there is a lack of evaluation on the long-term ecological changes associated with management practices, whose consequences might represent major limiting factors to the ecological and economic sustainability of this valuable agro-ecosystem. Furthermore, studies have been directed at local scales, however large-scale analyses are mandatory to fully understand the role of multi-scale cumulative drivers influencing the regeneration process and the role of policies in managing this ecosystem (Godinho *et al.* 2014). In this context, the combination of local population dynamics (temporal) and regional distributional (spatial) models can help to assess and predict how anthropogenic and environmental changes will affect the abundance and displacement of vulnerable species or communities in disturbed ecosystems and regions (Guisan & Thuiller 2005). As demonstrated in this study, dynamic models allow prediction of trends in the local population dynamics, including those attributable to changes in habitat due to different sources of perturbation (Winkler 2006). Complementarily, spatial models are useful to identify areas where the conflict between the previous forecasted trends and drivers of pressure are of major conservationist concern, by allowing the integration of the ecological consequences from local to regional levels (Bjørnstad *et al.* 1999, Vicente *et al.* 2011). Therefore, these kind of new model-based methodologies represent an early step to support strategic options for impact mitigation and management by providing projections of long-term indicator trends under realistic social–ecological change scenarios (Bastos *et al.* 2015). Additionally, in support of technical and political decision, modelling can be very useful as an investigative tool to forecast the outcome of alternative scenarios, guiding current management options from predicted future targets (Bastos *et al.* 2012).

GENERAL DISCUSSION

Since the Middle Ages, Mediterranean cork oak ecosystems have been shaped by their exploitation either for pasturing, timber harvesting, wooding or hunting, in a combination of human management and ecological drivers that affect vegetation dynamics. The result of this interaction of nature and nurture is the current cork oak *montado* landscape in southern Portugal. The overexploitation of the land has led to soil degradation and erosion, loss of woodlands and failures in cork oak regeneration. In this thesis we tested the main biotic and abiotic factors that, not acting isolated, have been influencing the cork oak population dynamics. The main focus was on the issue of lack of cork oak natural regeneration.

Cork oak leaf fall, litter decomposition and quality at three *montado* land uses in southern Portugal were evaluated (Chapter 1). Decomposition rates showed seasonal variations associated to the summer drought in the Mediterranean, which are especially important for ecosystem functioning and are reflected in soil microbial dynamics by the nutrient release and immobilization cycles and in the nutrient availability for plants (Aponte *et al.* 2010, Matías *et al.* 2011). Also, leaf thickness revealed to be a good index to explain decomposition rates of sclerophyllus leaves, negatively affecting cork oak litter mass loss.

Here we presented the first work to use the soil nematodes as indicators of different levels of disturbance in a cork oak *montado* ecosystem (Chapter 2). Our results stress seasonal and site fluctuations in the structure of soil nematode communities. The study of the effect of soil nematodes over seedlings concluded that the former did not harm young cork oak plants. A one year sampling over 120 cork oak seedling roots returned only residual numbers of plant parasitic nematodes.

In Chapter 3, we followed a cohort of nine hundred individuals during the initial stages of plant life, a key bottleneck for cork oak regeneration and identified important biotic and abiotic factors which hampered caches to succeed and seedlings to survive. The presence of livestock and shrubs negatively affected post-dispersal predation of acorns, however cache predation was very low and most post-dispersal predation of acorns was due to wild animals, in particular rodents and wild boars. We identified acorn size and plant cover as the main factors positively influencing seedling emergence and survival. Furthermore, seedling tolerance to drought and resprouting were also influenced by early emergence and later drying of seedlings, this capacity being likely related with the prioritary development of cork oak root system after germination.

Notwithstanding, regeneration was most constrained due to current management practices, such as soil ploughing which severely hacked seedlings.

To integrate in a simple approach the multifactorial causes implicated in the cork oak decline across the Iberian Peninsula, considering both lack of natural regeneration and lack of tree health, we developed a System Dynamics Model (Chapter 4). This was a tool to improve the comprehension of the most determinant factors affecting the long-term sustainability of the *montado* system. Also, we assessed the economic revenue from *montado* relatively to the cork oak dynamics under different management practices by balancing the financial gains and losses. The findings of this study indicated that the main limiting factors driving the lack of regeneration of cork oak trees in *montados* seem to rise from the land management practices, rather than environmental factors. The main stressors over cork oak *montado* natural regeneration were the increasing numbers of livestock units per area and the intensive use of heavy machinery. Also, and agreeing with the results, extending shrub clearing for longer periods would benefit cork oak regeneration by promoting tree nursery and soil rehabilitation while allowing the growth of seedlings and saplings.

The management approaches would vary between different *montados* and with different socioeconomic and ecological conditions. Thus, we combined our studies on leaf fall, litter decomposition, litter quality, nematodes communities and cork oak early stages of regeneration in three *montado* sites considering a decreasing gradient of tree cover and undercover (meaning a degradation gradient from site C to site A) to test differences between land uses. Associating the values of the energy efficiency in soil decomposition process (Chapter 1) with the values of the Nematode Chaennel Ratio obtained after nematode identification (Chapter 2) we provided information on the way the breakdown of organic matter proceeds with the participation of bacteria or fungi (Moore *et al.* 1988, Yeates 2003). This resulted in domination of the bacterial energy channel and production of high quality litter in site A, but the absence of undercover decreased litter moisture and litter input to the soil, resulting in an increase of light, exposing areas to summer desiccation, altering the decomposing communities and reducing the decomposition rates. Throughout the nematode survey, the most disturbed habitat was site A while site C was characterised as the most natural undisturbed site (Chapter 2). This degradation resulted in low resource utilization by plants. Relative to the whole regeneration process (Chapter 3), plant cover percentages contributed to differences in seedling emergence and survival among sites, the regeneration process was significantly held back in site A, as desiccation was the most important cause of cork oak mortality during the first year (Valladares 2003, Arosa *et al.* 2015). We also recorded extreme seedling mortality as a consequence of mechanical ploughing. This manoeuvre was carried out in site A to improve the growing of pasture, cutting down a whole cohort of seedlings.

IMPLICATIONS FOR MANAGEMENT AND RESTORATION

Our findings can be transferred to cork oak *montado* managers to support practices and recommendations, to facilitate the cork oak conservation and the sustainable management of this ecosystem. The sustainability of an ecosystem can happen when, over generations, it supports the natural regulatory functions of ecosystems (biotic and abiotic) while allowing for profitable economic activities and providing an environment that enhances the physical and mental well-being of the people who live in it (Barret 1992) and *montados* seem to fit the description when land is used with care. Results from Chapter 4 indicated that the problem arises mainly when the number of livestock units increases and when shrub clearing with heavy machinery is done with high frequencies. These results were clear about the future of the cork oak *montado*: the forest ecosystem is now threatened mainly by anthropogenic factors. Management actions must be implemented at landscape scale to have a positive effect over the multiple constraints on cork oak recruitment. The lack of regeneration is a common failure in *montados* throughout the Iberian Peninsula, and the restoration practices for cork oak montado recovery should consider actions regarding all the threats affecting cork oak *montados* (Fig. 23).

The restoration practices can begin from site amelioration to improve soil properties and reduce soil losses and regulating water and nutrient fluxes (Young *et al.* 2005, Vallejo *et al.* 2012). To increase the amount of soil nutrients and organic matter the presence of woody species should be promoted because of the accumulation of litter beneath their canopies, trapping of windblown particles or symbiotic associations with N-fixing micro-organisms (Escudero *et al.* 1985, Aguiar & Sala 1994, Chapin *et al.* 1994, Alpert & Mooney 1996, Young *et al.* 2005). Nematode sampling is recommended in the context of restoration as they can provide decision criteria for conservation and remediation in different *montados*. Extraction of nematodes is simple and they can be easily preserved, sampling is possible with a small soil sample and also does not harm the sampling site. They inform on succession and changes in the decomposition process in the soil food web, nutrient status, fertility and acidity of soil, and the effects of soil contaminants (Bongers & Ferris 1999, Ruess & Ferris 2004).

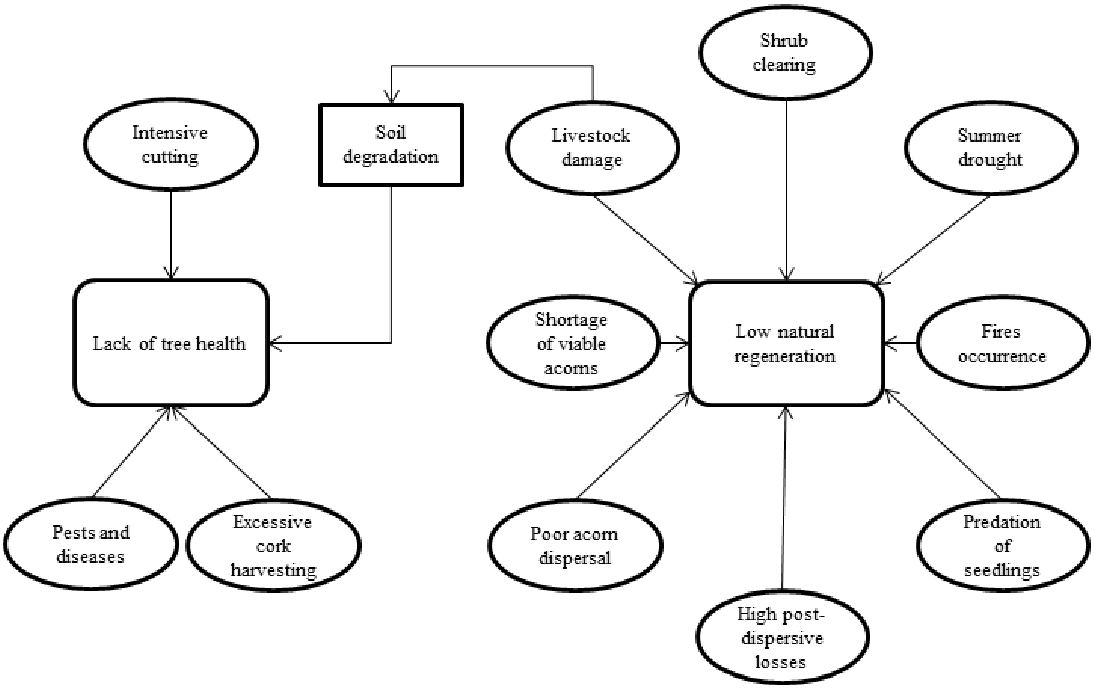

Figure 23. Main threats to cork oak in *montados.* In circles are the main factors affecting the lack of tree health and the low natural regeneration. Soil degradation is a consequence of livestock damage that also affects the lack of tree health.

The management actions would need to simultaneously address the shortage of viable acorns, poor acorn dispersal, post-dispersal loses and low rates of seedling survival. The concrete actions that could be taken include the maintenance or promotion of nurse-plants to facilitate cork oak seed germination and seedling survival (Callaway & Pugnaire 1999, Caldeira *et al.* 2014). The maintenance of mosaics including shrubland patches would conserve and increase the cork oak population size, protect from herbivory and alleviate abiotic stress (Gómez-Aparicio *et al.* 2004, Pulido & Díaz 2005, Smit *et al.* 2008, Arosa *et al.* 2015). Furthermore, shrub encroachment might promote landscape heterogeneity and benefit the fungal community in *montado*, the presence of mycorrhizas improve water uptake of seedlings and trees, minimizing the effects of drought (Azul 2002, Azul *et al.* 2010). These mosaics must be managed with caution and the shrub clearing must be well planned to help safe cork oak regeneration and promote tree nursery and soil rehabilitation. The shrub cover should be maintained for minimum period of 7 years and maximum of 12 years (Canteiro *et al.* 2011, Simões *et al.* 2015). Longer periods would facilitate fire spread due to the accumulation of dead material (Canteiro *et al.* 2011). Chain and disc ploughing for shrub cutting and enhanced pasture growth are common practices that damages cork oak seedlings and tree roots, spreading diseases and modifying the physical properties of soils (Ferreira 2000, Bugalho *et al.* 2009). Mechanical management in *montados* should be minimal in order to retain their ecological heterogeneity (Santana *et al.* 2011).

Direct seeding of acorns is a good alternative to facilitate regeneration because of emergence success (Young *et al.* 2005, Arosa *et al.* 2015) and protection of acorns and seedlings from livestock grazing or wild herbivores in *montados* with high stocking rates. Acorn predation and browsing, trampling of seedlings and soil compaction are the main pressures by overgrazing, from where damages are mostly associated with the intensity and type of grazing (Pulido & Díaz 2005). The exclusion of grazers, permanent or temporary, from some areas with high livestock pressure, would allow young stages of regeneration to reach sufficient height above the browsing line to become reproductive trees (Vallejo *et al.* 2012, Carmona *et al.* 2013). Our results show that extensive livestock rearing had a small impact on the early stages of regeneration. However, this result does not stand for cattle systems, as these may increase seedling mortality (Gómez *et al.* 2003). Land owners suggest that direct oak seeding should be used instead of planting because it would allow higher seedling survival, thus EU programs have only been funding planting young cork oak trees (Acácio *et al.* 2010). Meanwhile, drought is the main threat to the survival of nursery-raised seedlings in Mediterranean regions and restoration projects fail because of post-planting water deficits (Vallejo 2009). Subsidies can contribute to degradation of *montados* as they have an important role in management decision (Pinto-Correia & Vos 2004).

Fire regimes are strongly linked to climate, but there are some examples in which most of the variability in fire regimes changes are better attributed to vegetation (fuel structure and continuity) and to socioeconomic and policy changes (Pausas 2004, Pausas & Keeley 2014). All these causes might generate landscape changes in fuel structure and can drastically change fire activity. In the event of a wildfire the post-fire restoration techniques should be considered in order to prevent soil loss and erosion and increase the post-fire survival of cork oaks. Also, the presence of livestock can have a negative impact on the post-fire recovery, even if it does not kill the trees, hindering the natural regrowth (Catry *et al.* 2010). Only when active restoration is needed should we consider plantation or direct seeding (Duyea 2000, Vallejo *et al.* 2012). Alternatively, the passive restoration that protects areas from further disturbances and allows natural colonization, regrowth and successional processes is considered a less costly intervention with faster recovery rates (Espelta *et al.* 2003, Lamb & Gilmour 2003, Moreira *et al.* 2009, Vallejo *et al.* 2012).

Some indicators exist to evaluate the restoration practices. The monitoring of these ecological actions should be implemented to evaluate the ecological restoration success (Aronson & Le Floch 1996, Whisenant 1999).

FINAL CONSIDERATIONS ABOUT THE FUTURE OF CORK OAK *MONTADOS*

This study presents evidence that the future of the cork oak *montado* is severely threatened by loss of ecological resilience (a decrease in the density of mature trees thus requiring an additional effort to increase regeneration) and loss of social and economic resilience (land abandonment and lack of adequate management). In many *montado* ecosystems, degradation processes are not local thus large heterogeneous areas need to be restored (Vallejo *et al.* 2012). Different combinations of the above-mentioned restoration techniques may be required for different purposes and also for different parts of the landscape.

The decline of the cork oak *montado* could be mitigated by combining scientific knowledge with traditional local knowledge because land managers need practical guidance from ecologists in effectively achieving restoration goals (Clewell & Rieger 1997, King & Whisenant 2009). However, much real-world restoration largely takes place independently of the interchange with the academic field of restoration ecology. The main problems in both restoration and conservation, is formed between academic research, time and resource-limited implementation (Young *et al.* 2005). Nevertheless, we should identify the most urgent research lines and involve the multiple stakeholders in management, meaning that ecologists need to come together with land owners and governments to develop a strategy for the future of this ecosystem.

Future work should be directed to develop the restoration strategies of cork oak *montados*, which will then contribute to fight desertification, protect biodiversity, mitigate climate change and promote the sustainable develop of human communities. These restoration programs would affect the economic development of local people, and therefore an important policy and planning effort over these affected communities should be done, with development of multipurpose businesses, which generate additional income, and sometimes by the direct payment for ecosystem services, paying to farm for nature´s services so that ecological and socioeconomic thresholds can be overcome.

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APPENDICES

Appendix I – Stella conceptual diagram.

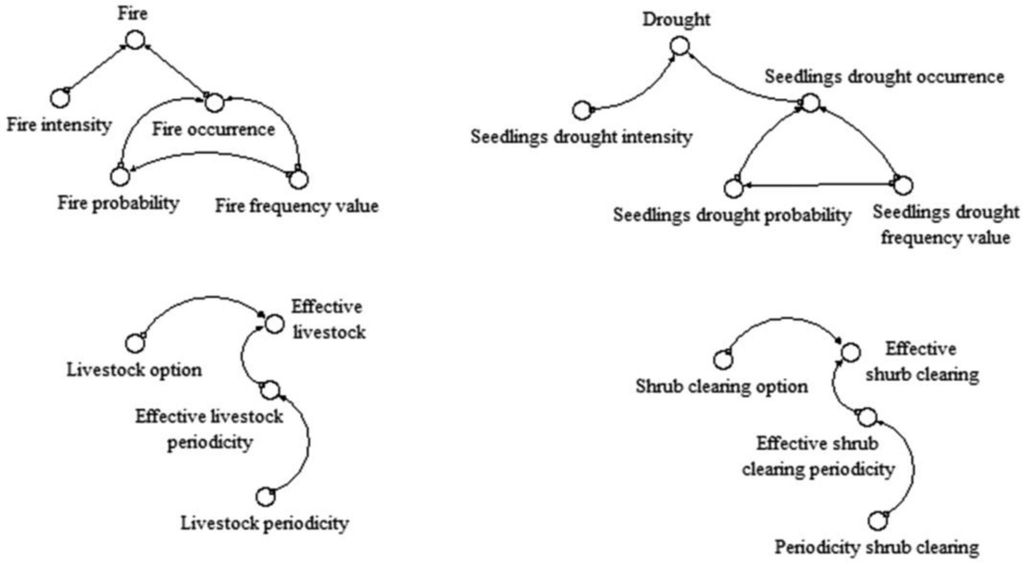


Figure 24. Stella software conceptual diagram of the sub-model of fire, drought and land use. Small circles are variables, parameters or constants; all the relations between variables are fine arrows. The specification of all variable codes is expressed in Appendix II and Table 6.

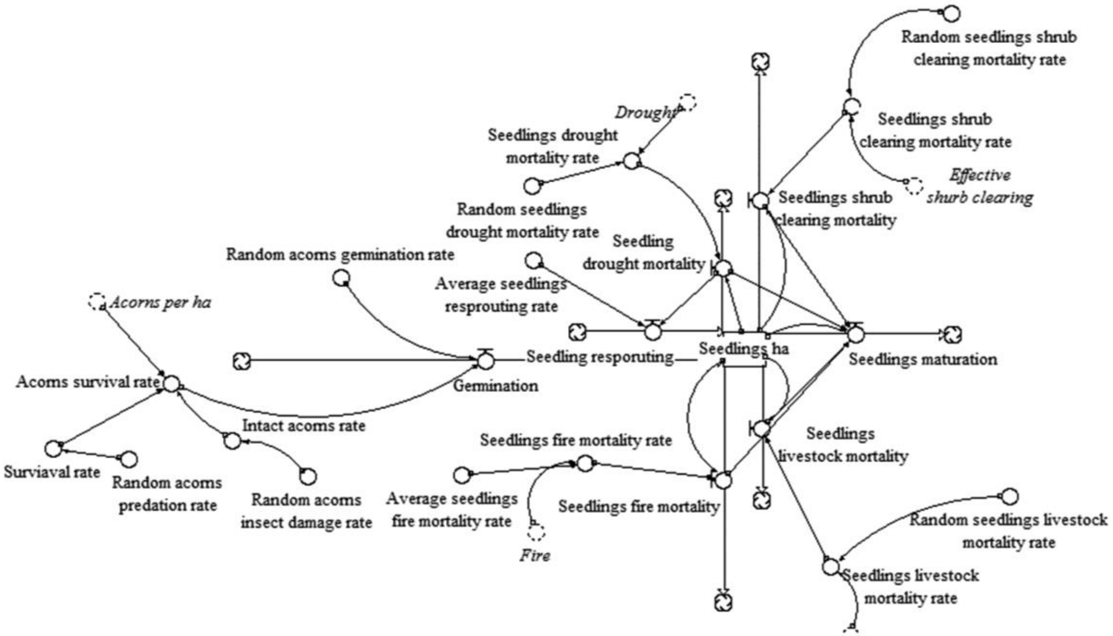
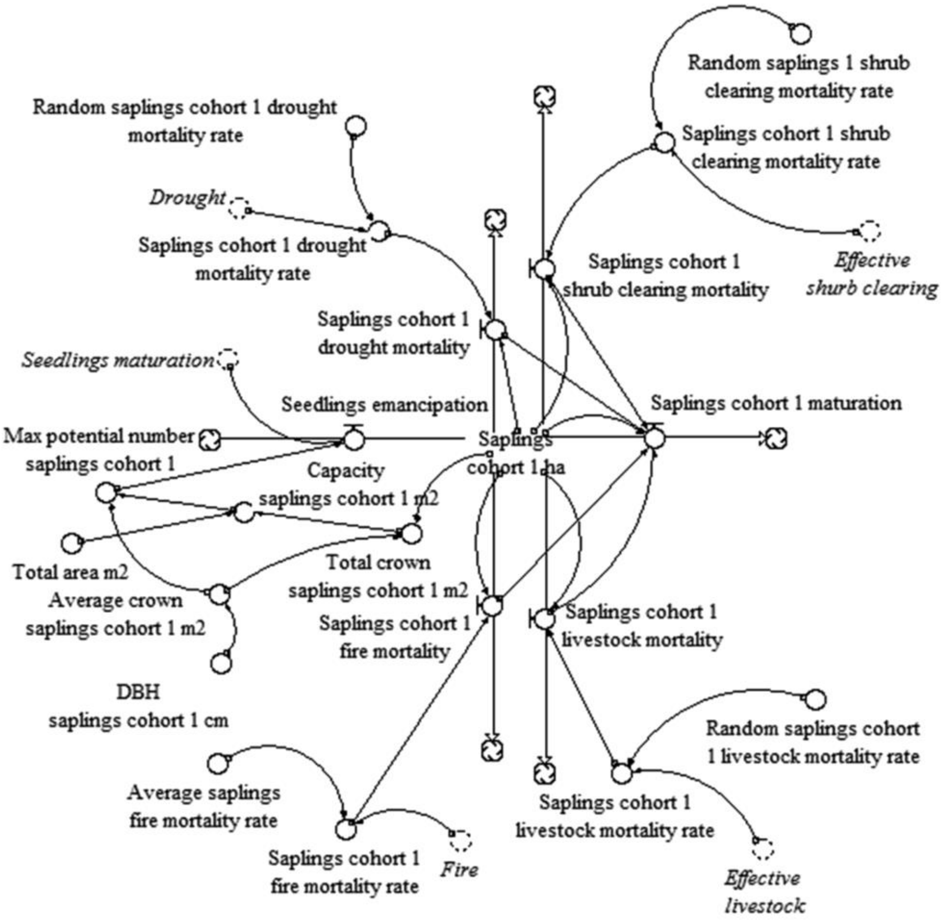
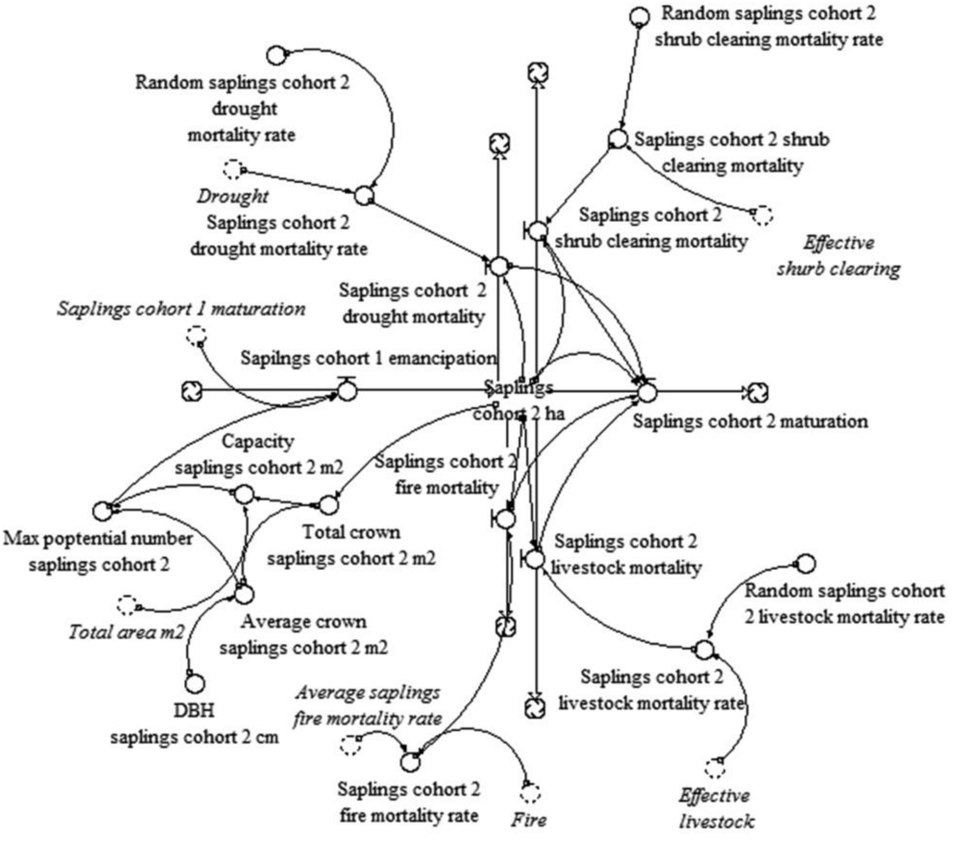


Figure 25. Stella software conceptual diagram of the sub-model of seedlings. Rectangles represent the state variables, seedlings; other variables, parameters or constants are small circles; sinks and sources are cloudlike symbols; flows are thick arrows; all the relations between state variables and other variables are fine arrows. The specification of all variable codes is expressed in Appendix II and Table 6.


Random saplings 1 shrub clearing mortality rate
Random saplings cohort 1 drought mortality rate
Saplings cohort 1 shrub clearing mortality rate
Drought
Saplings cohort 1 drought mortality rate
Saplings cohort 1 shrub clearing mortality
Effective shurb clearing
Saplings cohort 1 drought mortality
Seedlings maturation
Seedlings emancipation
Saplings cohort 1 maturation
Max potential number saplings cohort 1
Saplings cohort 1 ha
Capacity saplings cohort 1 m2
Total crown saplings cohort 1 m2
Total area m2
Average crown saplings cohort 1 m2
Saplings cohort 1 fire mortality
Saplings cohort 1 livestock mortality
DBH saplings cohort 1 cm
Random saplings cohort 1 livestock mortality rate
Average saplings fire mortality rate
Saplings cohort 1 livestock mortality rate
Saplings cohort 1 fire mortality rate
Fire
Effective livestock


Random saplings cohort 2 shrub clearing mortality rate
Random saplings cohort 2 drought mortality rate
Saplings cohort 2 shrub clearing mortality
Drought
Saplings cohort 2 drought mortality rate
Saplings cohort 2 shrub clearing mortality
Effective shurb clearing
Saplings cohort 2 drought mortality
Saplings cohort 1 maturation
Sapilngs cohort 1 emancipation
Saplings cohort 2 ha
Saplings cohort 2 maturation
Capacity saplings cohort 2 m2
Saplings cohort 2 fire mortality
Total crown saplings cohort 2 m2
Max poptential number saplings cohort 2
Saplings cohort 2 livestock mortality
Total area m2
Average crown saplings cohort 2 m2
Random saplings cohort 2 livestock mortality rate
DBH saplings cohort 2 cm
Average saplings fire mortality rate
Saplings cohort 2 livestock mortality rate
Saplings cohort 2 fire mortality rate
Fire
Effective livestock

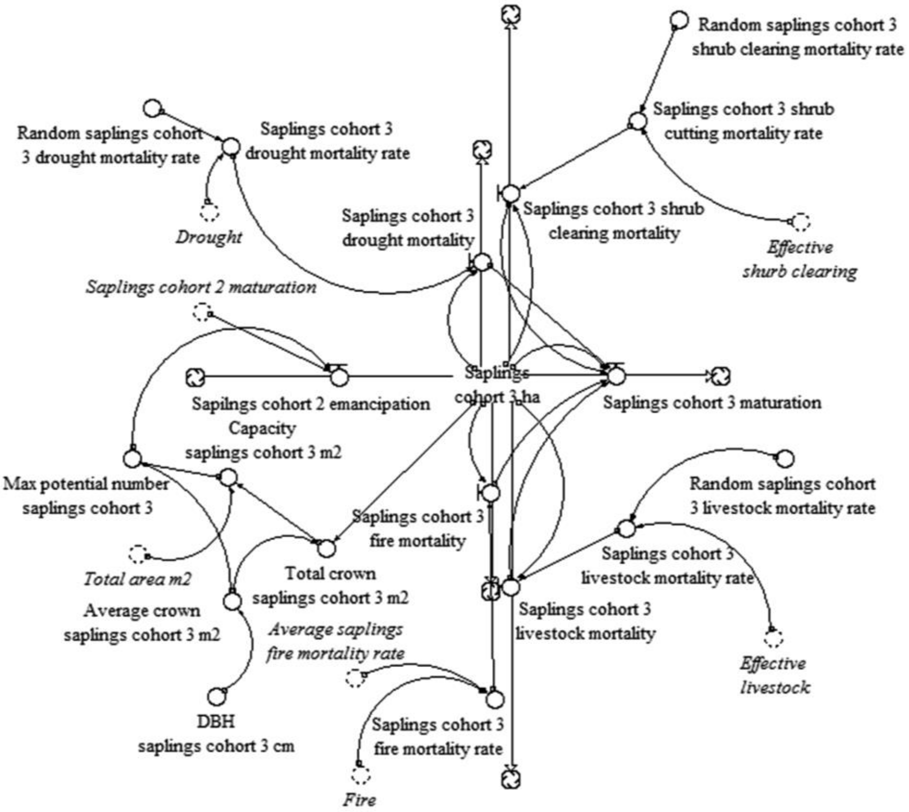
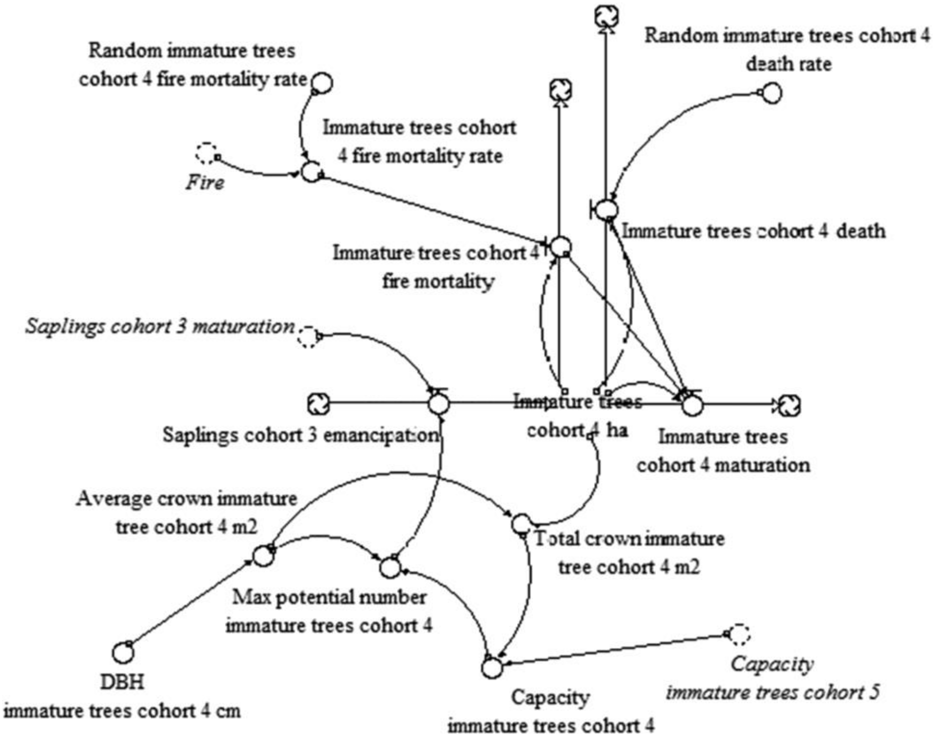
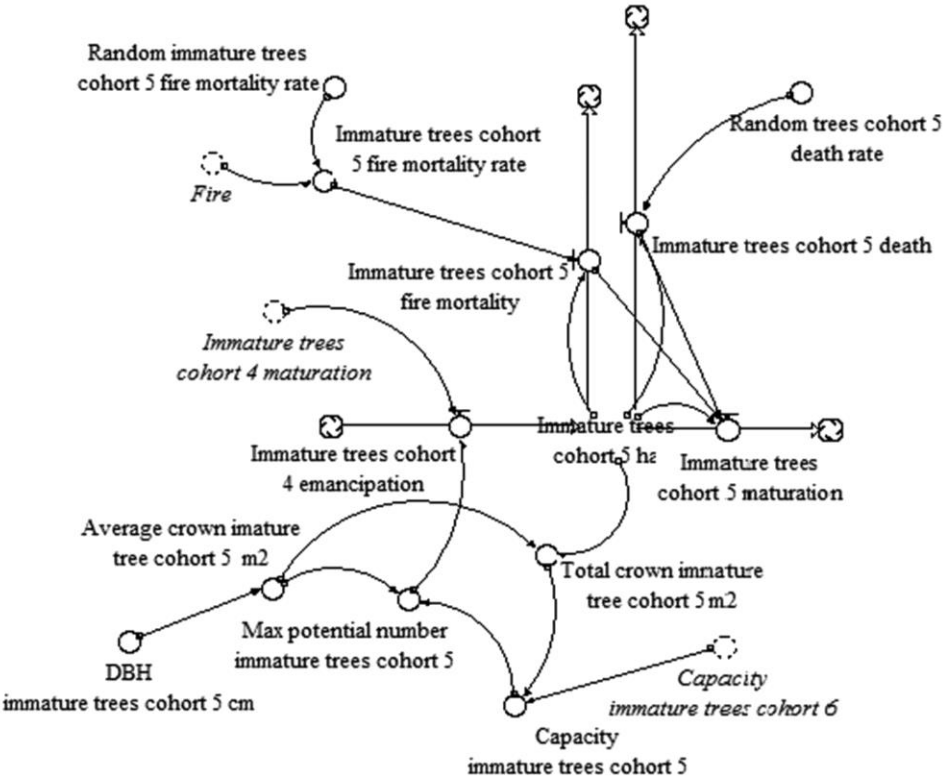
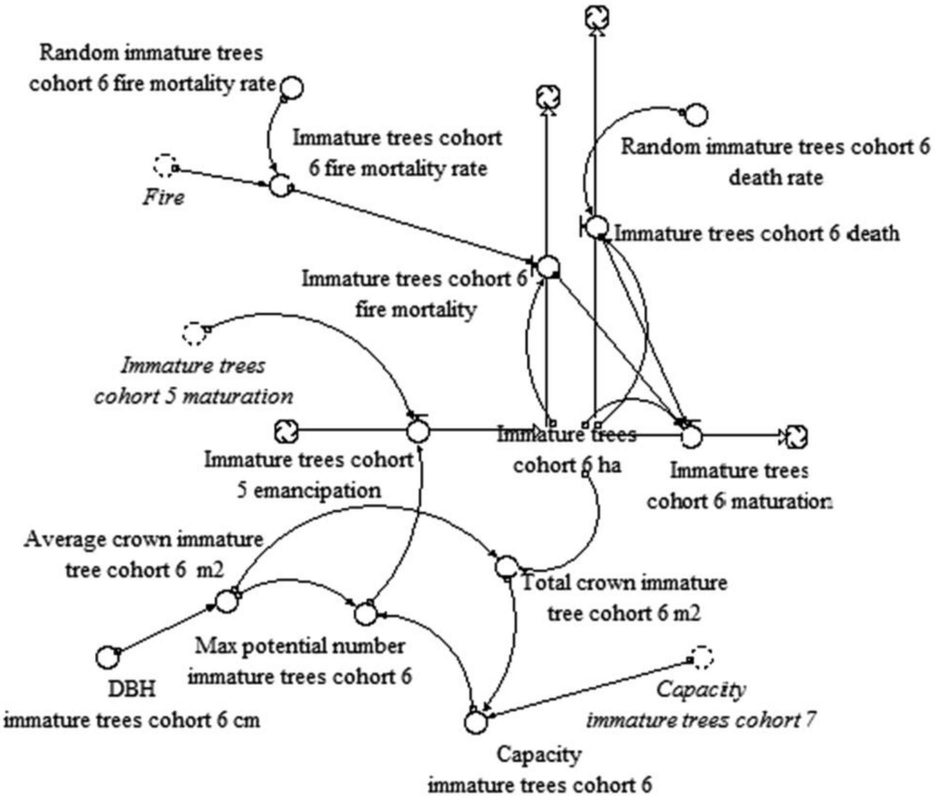
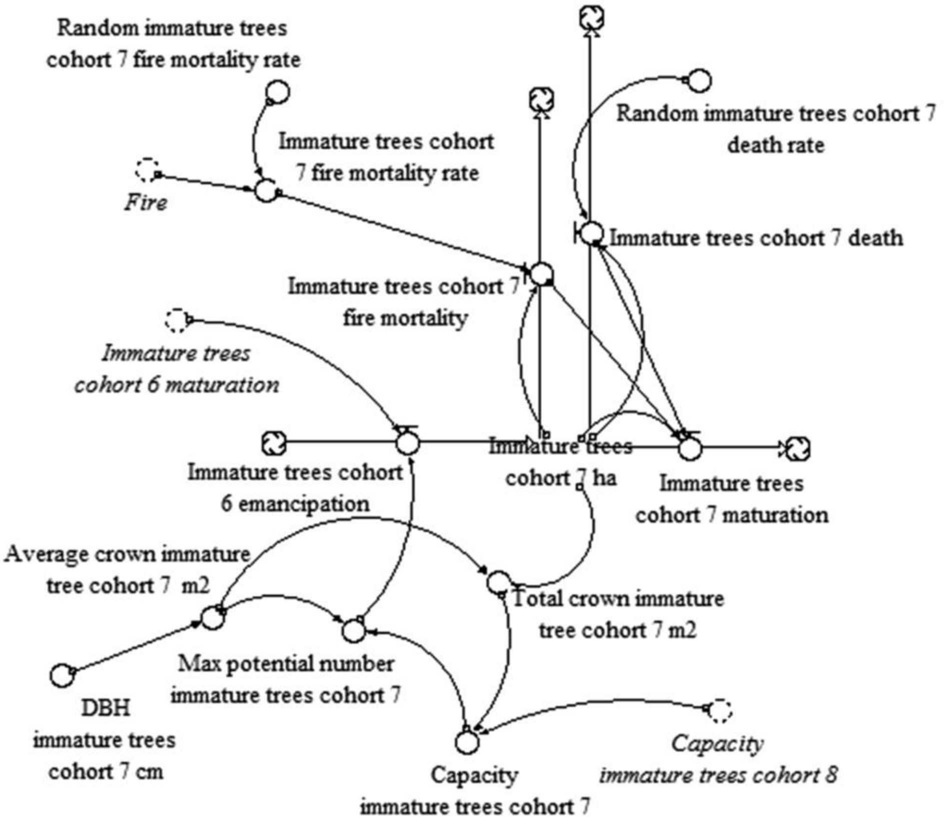


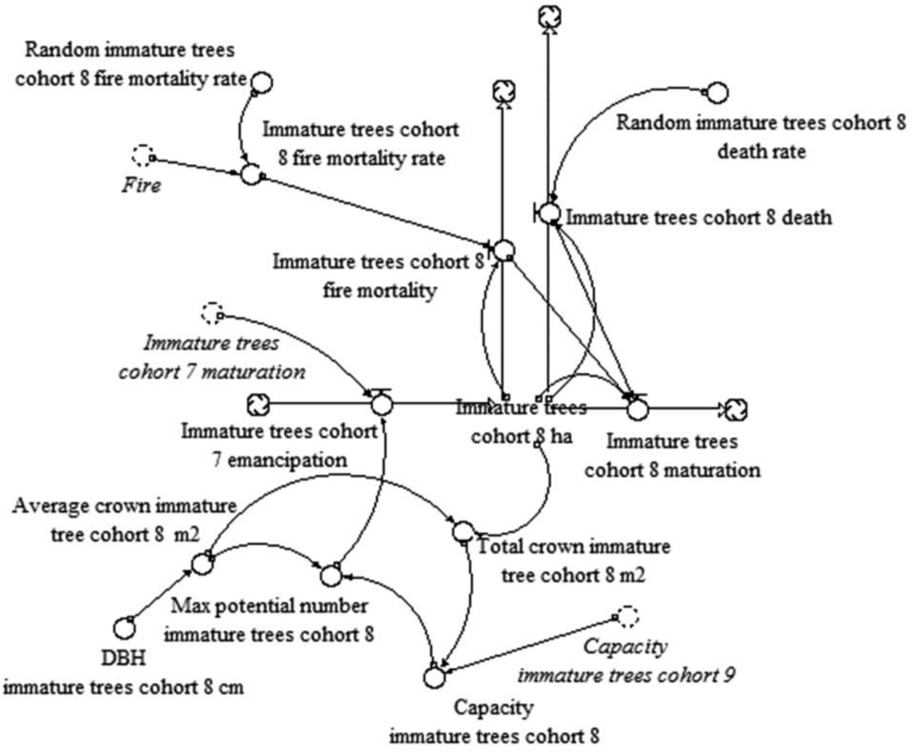
Figure 26. Stella software conceptual diagram of the sub-model of saplings. Rectangles represent the state variables, saplings; other variables, parameters or constants are small circles; sinks and sources are cloudlike symbols; flows are thick arrows; all the relations between state variables and other variables are fine arrows. The specification of all variable codes is expressed in Appendix II and Table 6.

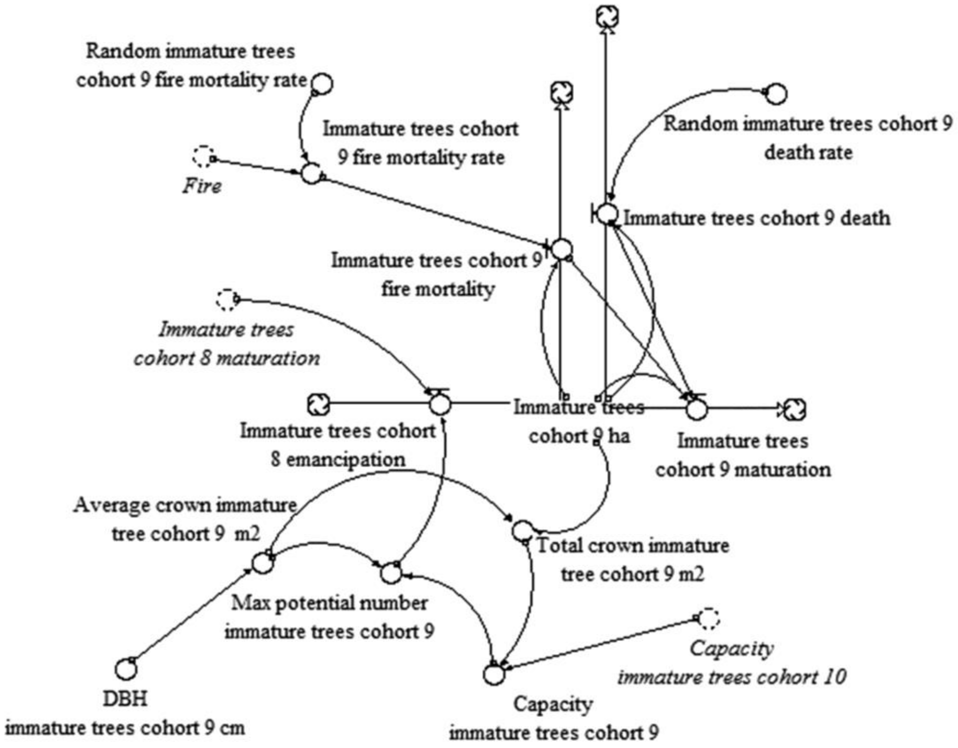


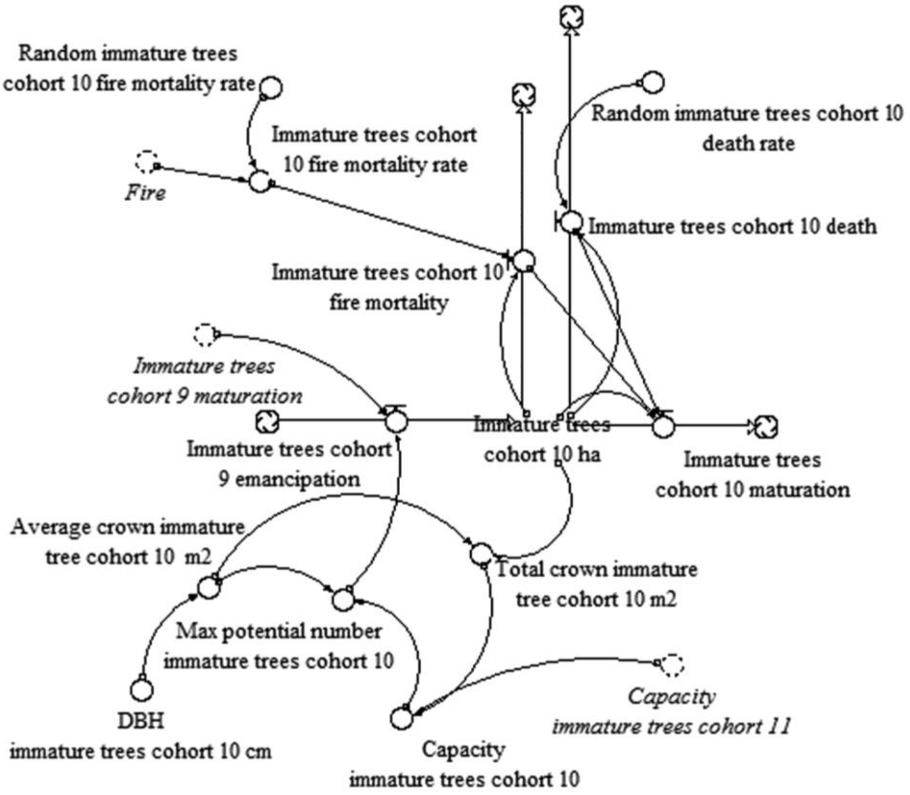

Random immature trees cohort 5 fire mortality rate
Immature trees cohort 5 fire mortality rate
Fire
Random trees cohort 5 death rate
Immature trees cohort 5 death
Immature trees cohort 5 fire mortality
Immature trees cohort 4 maturation
Immature trees cohort 5 ha
Immature trees cohort 4 emancipation
Immature trees cohort 5 maturation
Average crown imature tree cohort 5 m2
Total crown immature tree cohort 5 m2
Max potential number immature trees cohort 5
DBH immature trees cohort 5 cm
Capacity immature trees cohort 6
Capacity immature trees cohort 5

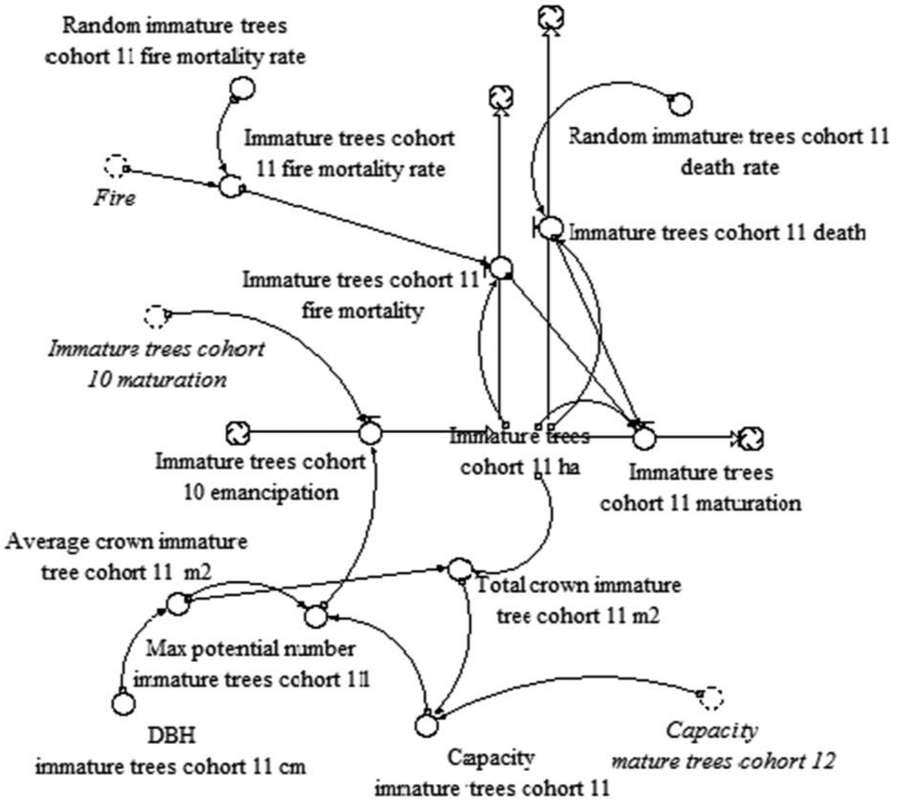

Random immature trees cohort 6 fire mortality rate
Immature trees cohort 6 fire mortality rate
Fire
Random immature trees cohort 6 death rate
Immature trees cohort 6 death
Immature trees cohort 6 fire mortality
Immature trees cohort 5 maturation
Immature trees cohort 6 ha
Immature trees cohort 5 emancipation
Immature trees cohort 6 maturation
Average crown immature tree cohort 6 m2
Total crown immature tree cohort 6 m2
Max potential number immature trees cohort 6
DBH immature trees cohort 6 cm
Capacity immature trees cohort 7
Capacity immature trees cohort 6

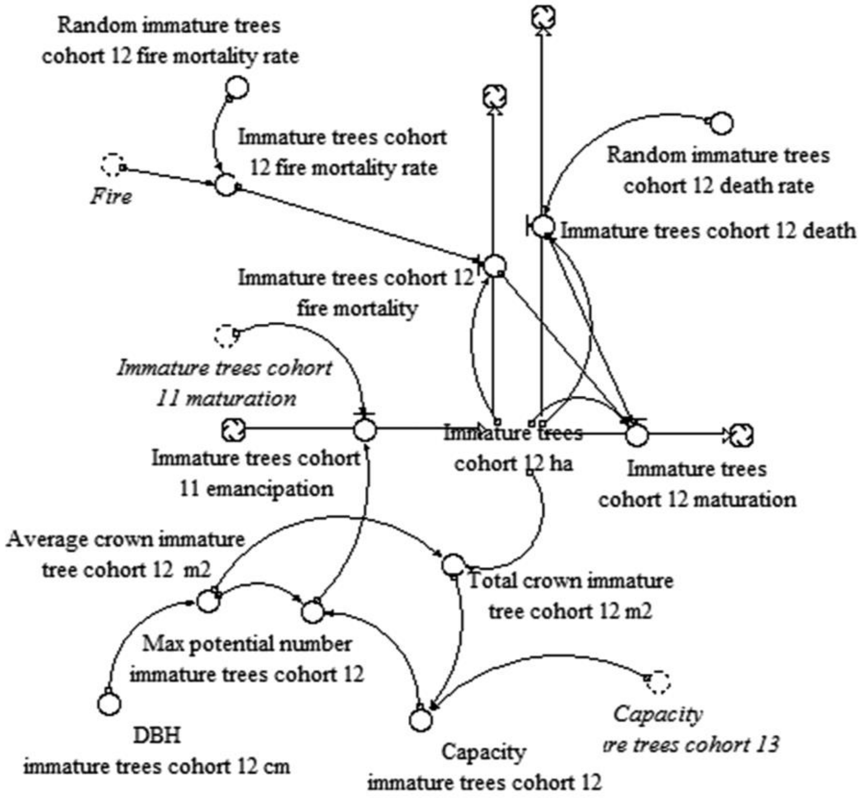

Random immature trees cohort 7 fire mortality rate
Immature trees cohort 7 fire mortality rate
Fire
Random immature trees cohort 7 death rate
Immature trees cohort 7 death
Immature trees cohort 7 fire mortality
Immature trees cohort 6 maturation
Immature trees cohort 6 emancipation
Immature trees cohort 7 ha
Immature trees cohort 7 maturation
Average crown immature tree cohort 7 m2
Total crown immature tree cohort 7 m2
Max potential number immature trees cohort 7
DBH immature trees cohort 7 cm
Capacity immature trees cohort 7
Capacity immature trees cohort 8

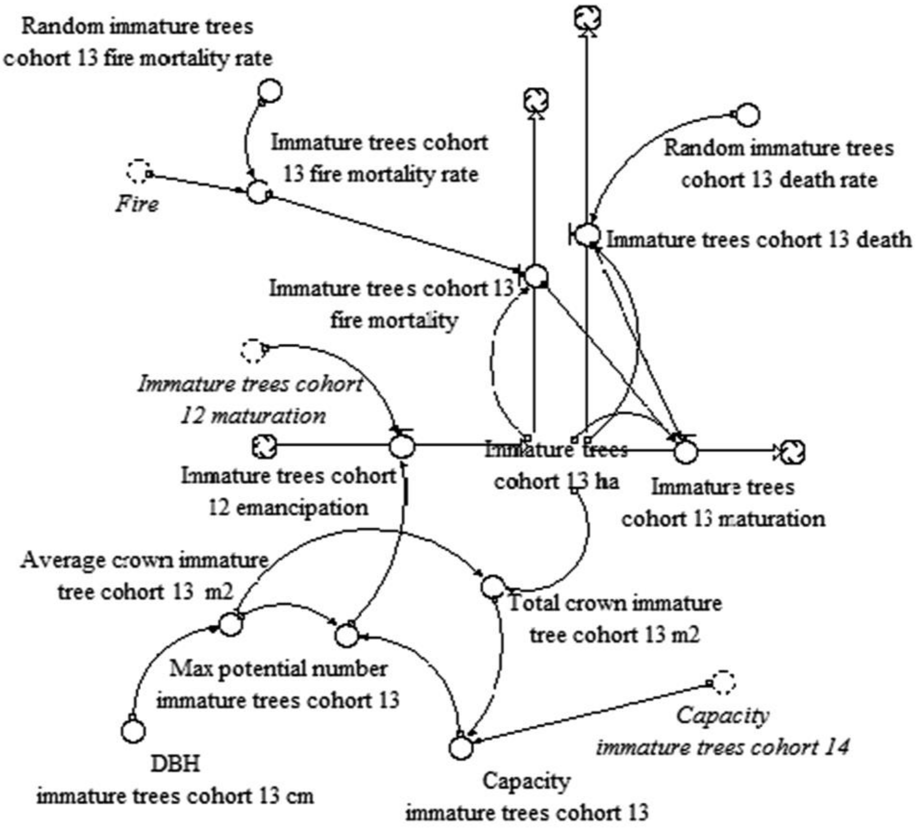

Random immature trees cohort 8 fire mortality rate
Immature trees cohort 8 fire mortality rate
Fire
Random immature trees cohort 8 death rate
Immature trees cohort 8 death
Immature trees cohort 8 fire mortality
Immature trees cohort 7 maturation
Immature trees cohort 7 emancipation
Immature trees cohort 8 ha
Immature trees cohort 8 maturation
Average crown immature tree cohort 8 m2
Total crown immature tree cohort 8 m2
Max potential number immature trees cohort 8
DBH immature trees cohort 8 cm
Capacity immature trees cohort 9
Capacity immature trees cohort 8

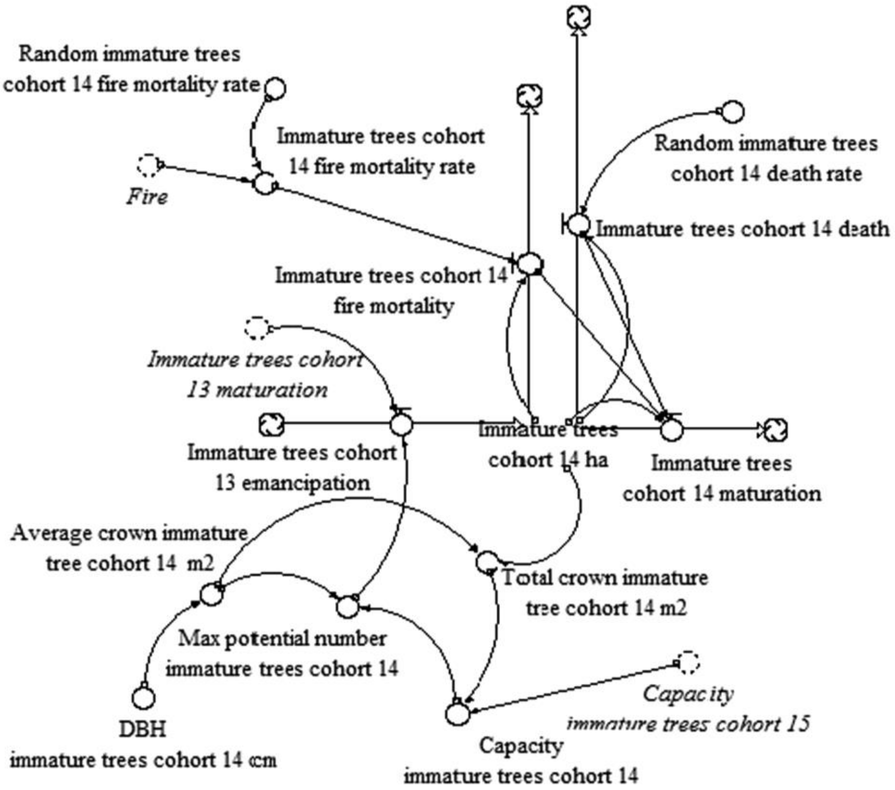

Random immature trees cohort 9 fire mortality rate
Immature trees cohort 9 fire mortality rate
Fire
Random immature trees cohort 9 death rate
Immature trees cohort 9 death
Immature trees cohort 9 fire mortality
Immature trees cohort 8 maturation
Immature trees cohort 8 emancipation
Immature trees cohort 9 ha
Immature trees cohort 9 maturation
Average crown immature tree cohort 9 m2
Total crown immature tree cohort 9 m2
Max potential number immature trees cohort 9
Capacity immature trees cohort 10
DBH immature trees cohort 9 cm
Capacity immature trees cohort 9

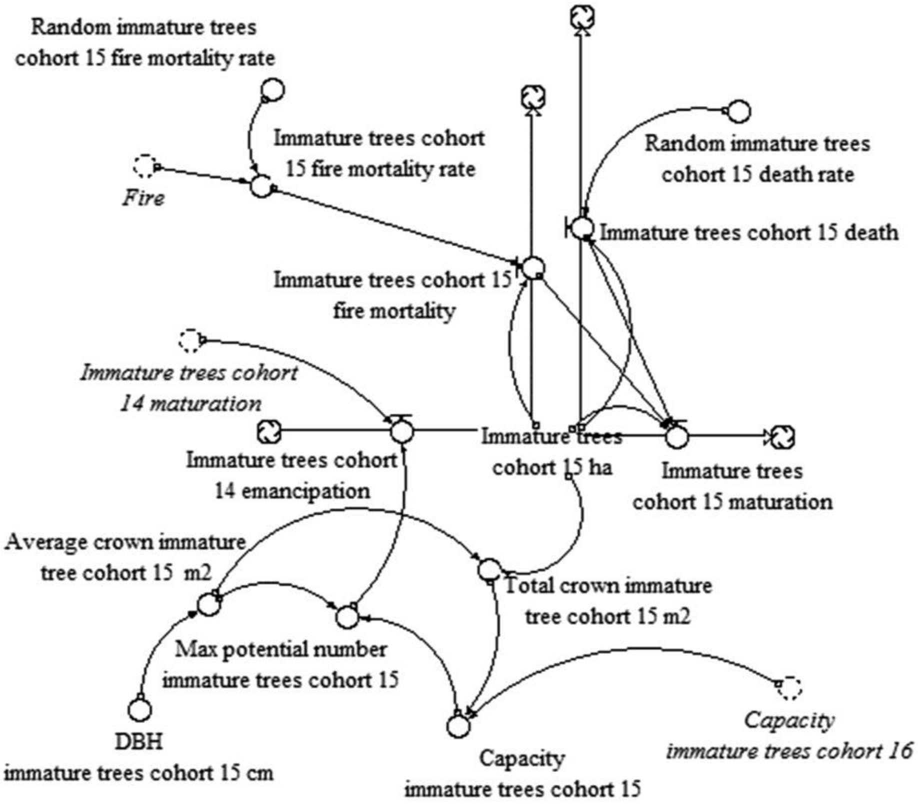

Random immature trees cohort 10 fire mortality rate
Immature trees cohort 10 fire mortality rate
Fire
Random immature trees cohort 10 death rate
Immature trees cohort 10 death
Immature trees cohort 10 fire mortality
Immature trees cohort 9 maturation
Immature trees cohort 9 emancipation
Immature trees cohort 10 ha
Immature trees cohort 10 maturation
Average crown immature tree cohort 10 m2
Total crown immature tree cohort 10 m2
Max potential number immature trees cohort 10
DBH immature trees cohort 10 cm
Capacity immature trees cohort 11
Capacity immature trees cohort 10

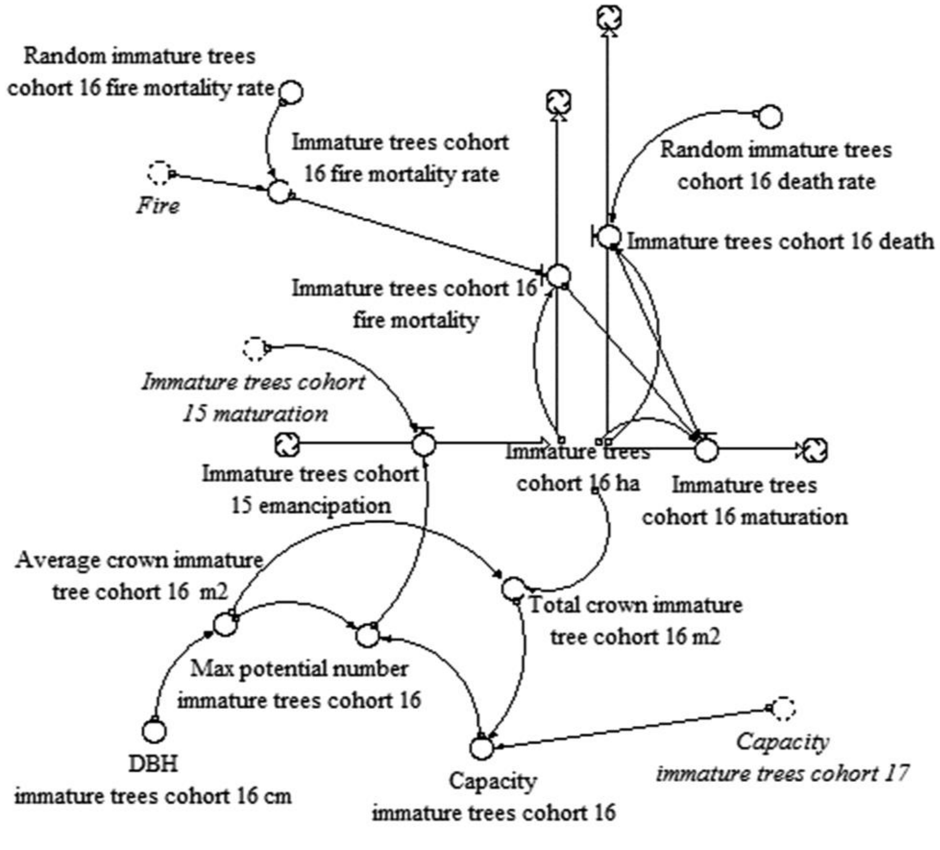

Random immature trees cohort 11 fire mortality rate
Immature trees cohort 11 fire mortality rate
Fire
Random immature trees cohort 11 death rate
Immature trees cohort 11 death
Immature trees cohort 11 fire mortality
Immature trees cohort 10 maturation
Immature trees cohort 10 emancipation
Immature trees cohort 11 ha
Immature trees cohort 11 maturation
Average crown immature tree cohort 11 m2
Total crown immature tree cohort 11 m2
Max potential number immature trees cohort 11
DBH immature trees cohort 11 cm
Capacity immature trees cohort 11
Capacity mature trees cohort 12

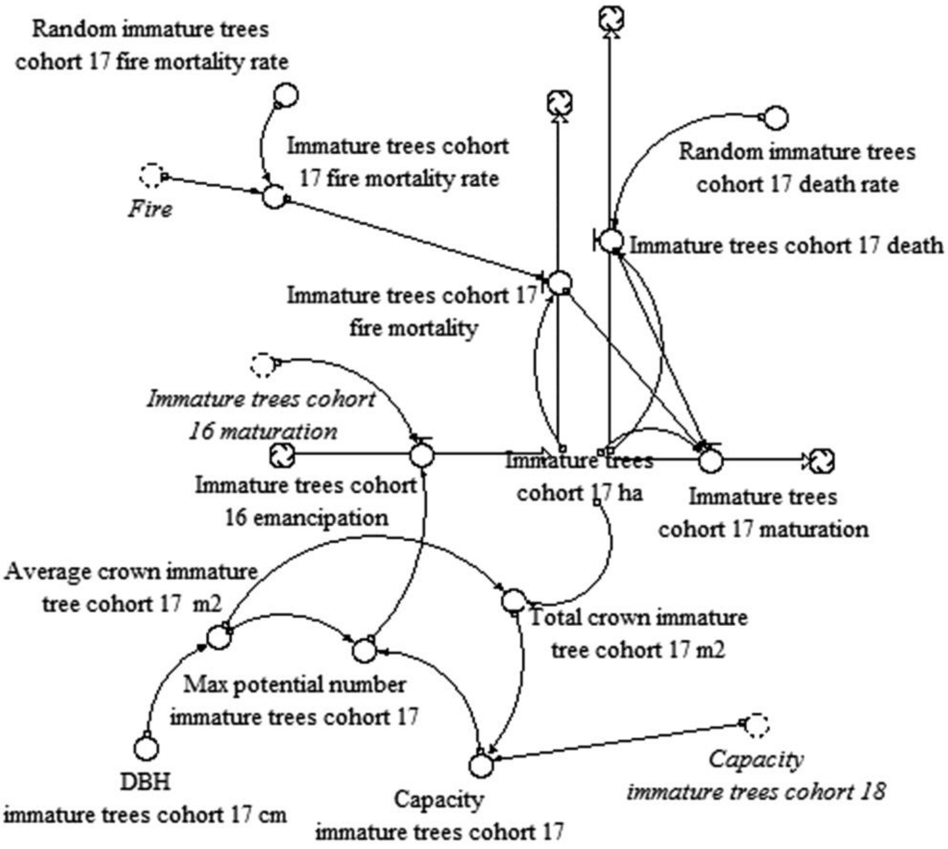

Random immature trees cohort 12 fire mortality rate
Immature trees cohort 12 fire mortality rate
Fire
Random immature trees cohort 12 death rate
Immature trees cohort 12 death
Immature trees cohort 12 fire mortality
Immature trees cohort 11 maturation
Immature trees cohort 11 emancipation
Immature trees cohort 12 ha
Immature trees cohort 12 maturation
Average crown immature tree cohort 12 m2
Total crown immature tree cohort 12 m2
Max potential number immature trees cohort 12
DBH immature trees cohort 12 cm
Capacity immature trees cohort 12
Capacity re trees cohort 13

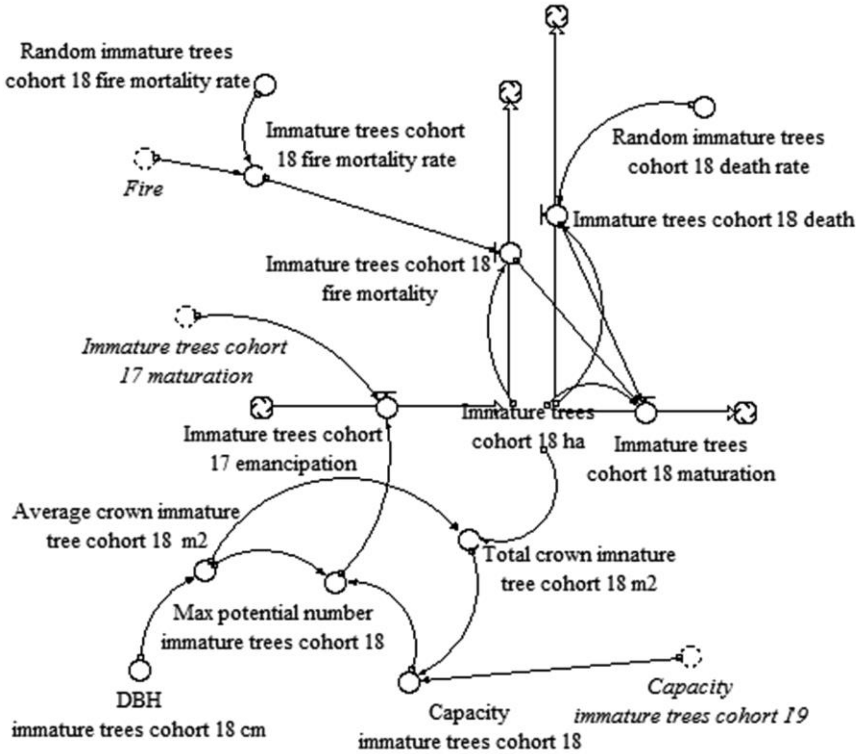

Random immature trees cohort 13 fire mortality rate
Immature trees cohort 13 fire mortality rate
Fire
Random immature trees cohort 13 death rate
Immature trees cohort 13 death
Immature trees cohort 13 fire mortality
Immature trees cohort 12 maturation
Immature trees cohort 12 emancipation
Immature trees cohort 13 ha
Immature trees cohort 13 maturation
Average crown immature tree cohort 13 m2
Total crown immature tree cohort 13 m2
Max potential number immature trees cohort 13
Capacity immature trees cohort 14
DBH immature trees cohort 13 cm
Capacity immature trees cohort 13

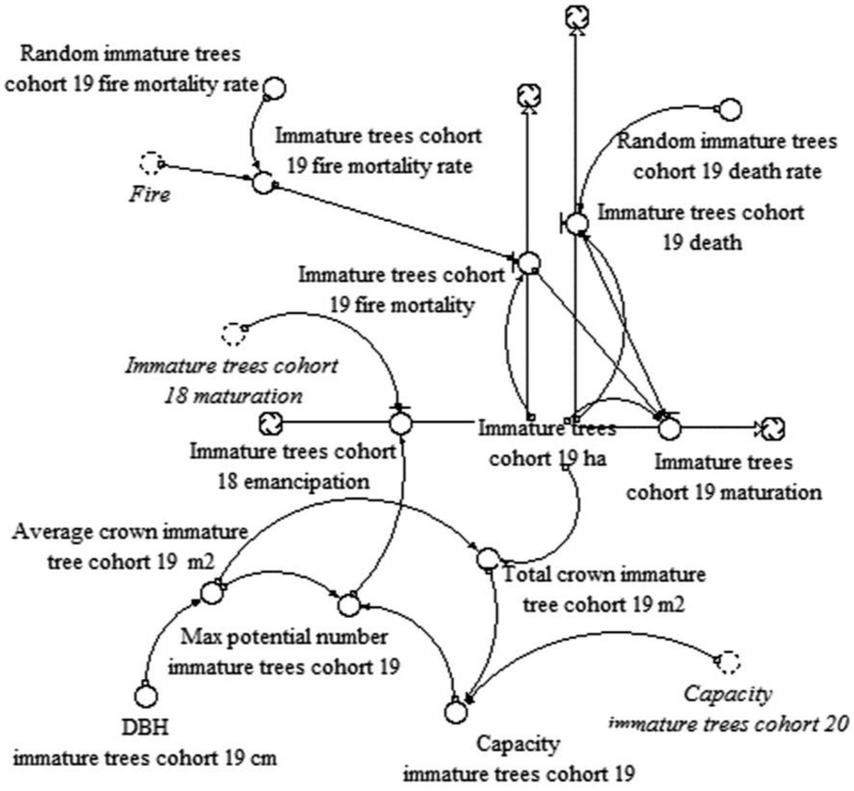

Random immature trees cohort 14 fire mortality rate
Immature trees cohort 14 fire mortality rate
Fire
Random immature trees cohort 14 death rate
Immature trees cohort 14 death
Immature trees cohort 14 fire mortality
Immature trees cohort 13 maturation
Immature trees cohort 13 emancipation
Immature trees cohort 14 ha
Immature trees cohort 14 maturation
Average crown immature tree cohort 14 m2
Total crown immature tree cohort 14 m2
Max potential number immature trees cohort 14
Capacity immature trees cohort 15
DBH immature trees cohort 14 cm
Capacity immature trees cohort 14

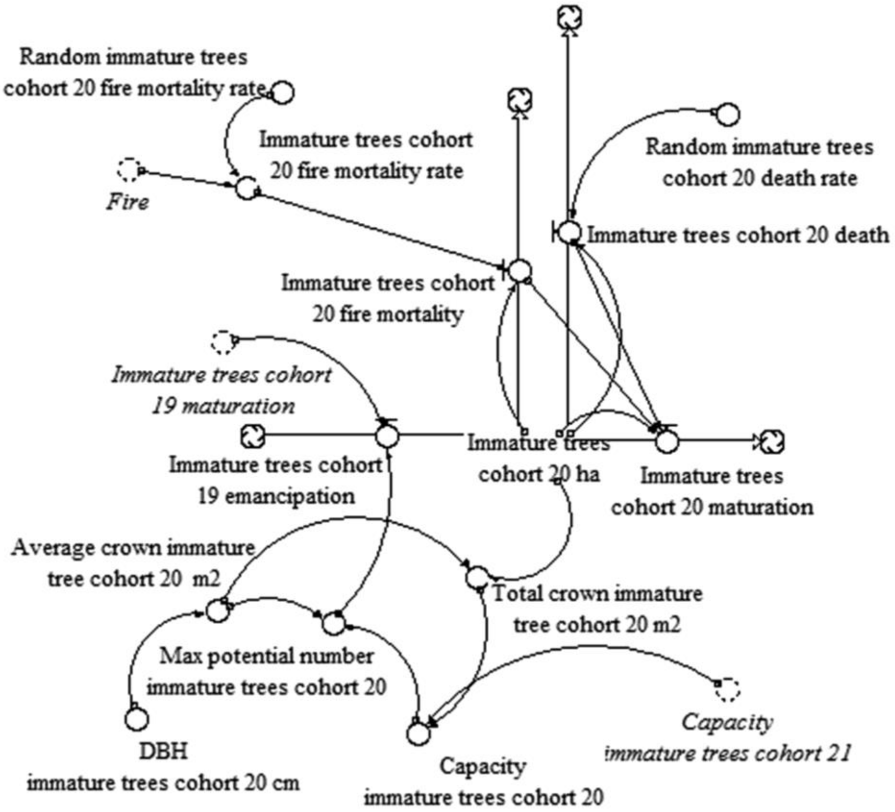

Random immature trees
cohort 15 fire mortality rate
Immature trees cohort
15 fire mortality rate
Fire
Random immature trees
cohort 15 death rate
Immature trees cohort 15 death
Immature trees cohort 15
fire mortality
Immature trees cohort
14 maturation
Immature trees
cohort 15 ha
Immature trees cohort
14 emancipation
Immature trees
cohort 15 maturation
Average crown immature
tree cohort 15 m2
Total crown immature
tree cohort 15 m2
Max potential number
immature trees cohort 15
DBH
immature trees cohort 15 cm
Capacity
immature trees cohort 15
Capacity
immature trees cohort 16


Random immature trees
cohort 16 fire mortality rate
Immature trees cohort
16 fire mortality rate
Fire
Random immature trees
cohort 16 death rate
Immature trees cohort 16 death
Immature trees cohort 16
fire mortality
Immature trees cohort
15 maturation
Immature trees
cohort 16 ha
Immature trees cohort
15 emancipation
Immature trees
cohort 16 maturation
Average crown immature
tree cohort 16 m2
Total crown immature
tree cohort 16 m2
Max potential number
immature trees cohort 16
DBH
immature trees cohort 16 cm
Capacity
immature trees cohort 16
Capacity
immature trees cohort 17


Random immature trees
cohort 17 fire mortality rate
Immature trees cohort
17 fire mortality rate
Fire
Random immature trees
cohort 17 death rate
Immature trees cohort 17 death
Immature trees cohort 17
fire mortality
Immature trees cohort
16 maturation
Immature trees cohort
16 emancipation
Immature trees
cohort 17 ha
Immature trees
cohort 17 maturation
Average crown immature
tree cohort 17 m2
Total crown immature
tree cohort 17 m2
Max potential number
immature trees cohort 17
DBH
immature trees cohort 17 cm
Capacity
immature trees cohort 17
Capacity
immature trees cohort 18


Random immature trees
cohort 18 fire mortality rate
Immature trees cohort
18 fire mortality rate
Fire
Random immature trees
cohort 18 death rate
Immature trees cohort 18 death
Immature trees cohort 18
fire mortality
Immature trees cohort
17 maturation
Immature trees cohort
17 emancipation
Immature trees
cohort 18 ha
Immature trees
cohort 18 maturation
Average crown immature
tree cohort 18 m2
Total crown imnature
tree cohort 18 m2
Max potential number
immature trees cohort 18
DBH
immature trees cohort 18 cm
Capacity
immature trees cohort 18
Capacity
immature trees cohort 19


Random immature trees cohort 19 fire mortality rate
Immature trees cohort 19 fire mortality rate
Fire
Random immature trees cohort 19 death rate
Immature trees cohort 19 death
Immature trees cohort 19 fire mortality
Immature trees cohort 18 maturation
Immature trees cohort 18 emancipation
Immature trees cohort 19 ha
Immature trees cohort 19 maturation
Average crown immature tree cohort 19 m2
Total crown immature tree cohort 19 m2
Max potential number immature trees cohort 19
Capacity immature trees cohort 20
DBH immature trees cohort 19 cm
Capacity immature trees cohort 19


Random immature trees cohort 20 fire mortality rate
Immature trees cohort 20 fire mortality rate
Fire
Random immature trees cohort 20 death rate
Immature trees cohort 20 death
Immature trees cohort 20 fire mortality
Immature trees cohort 19 maturation
Immature trees cohort 19 emancipation
Immature trees cohort 20 ha
Immature trees cohort 20 maturation
Average crown immature tree cohort 20 m2
Total crown immature tree cohort 20 m2
Max potential number immature trees cohort 20
Capacity immature trees cohort 21
DBH immature trees cohort 20 cm
Capacity immature trees cohort 20

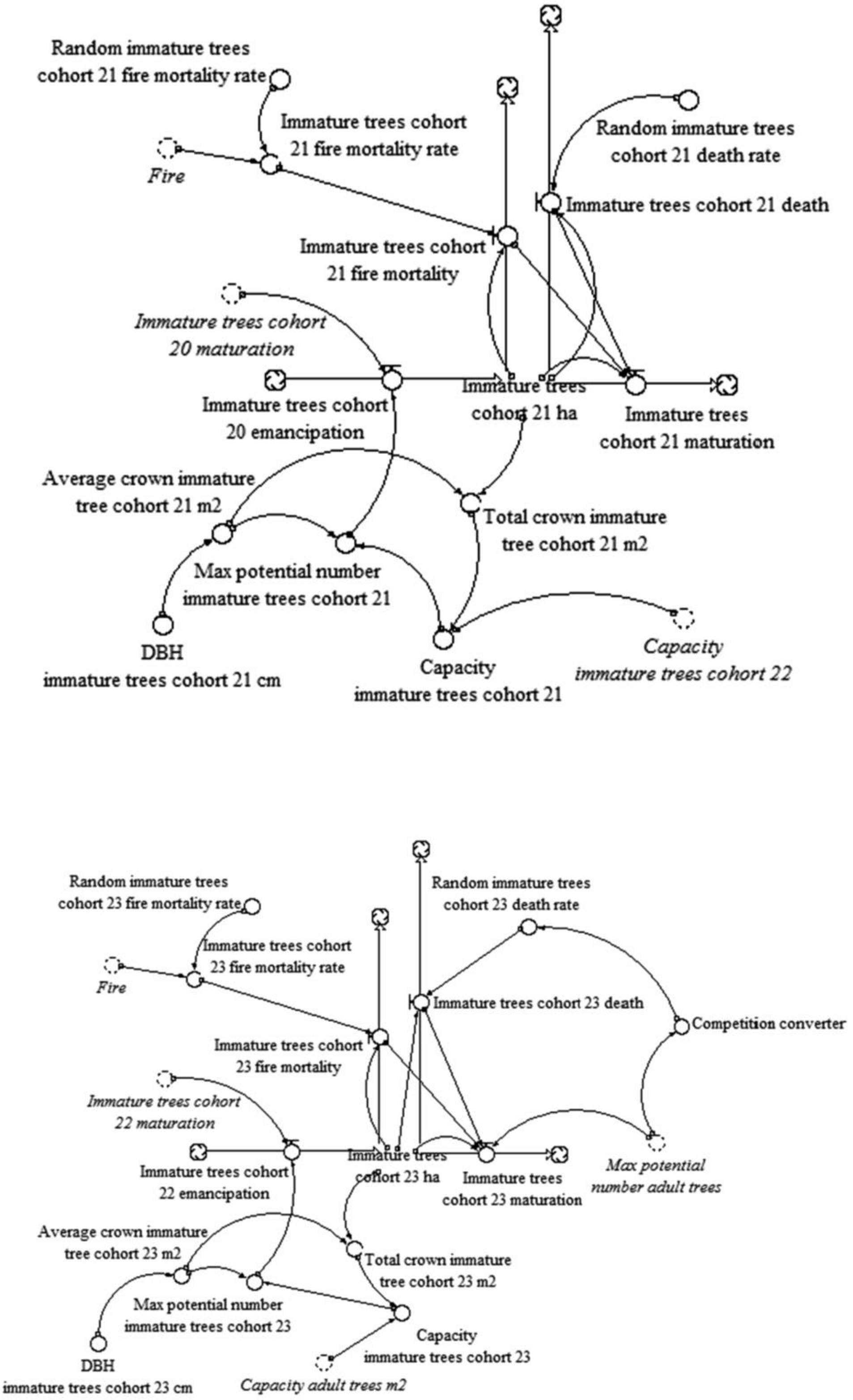


Figure 27. Stella software conceptual diagram of the sub-model of immature trees. Rectangles represent the state variables, immature trees; other variables, parameters or constants are small circles; sinks and sources are cloudlike symbols; flows are thick arrows; all the relations between state variables and other variables are fine arrows. The specification of all variable codes is expressed in Appendix II and Table 6.

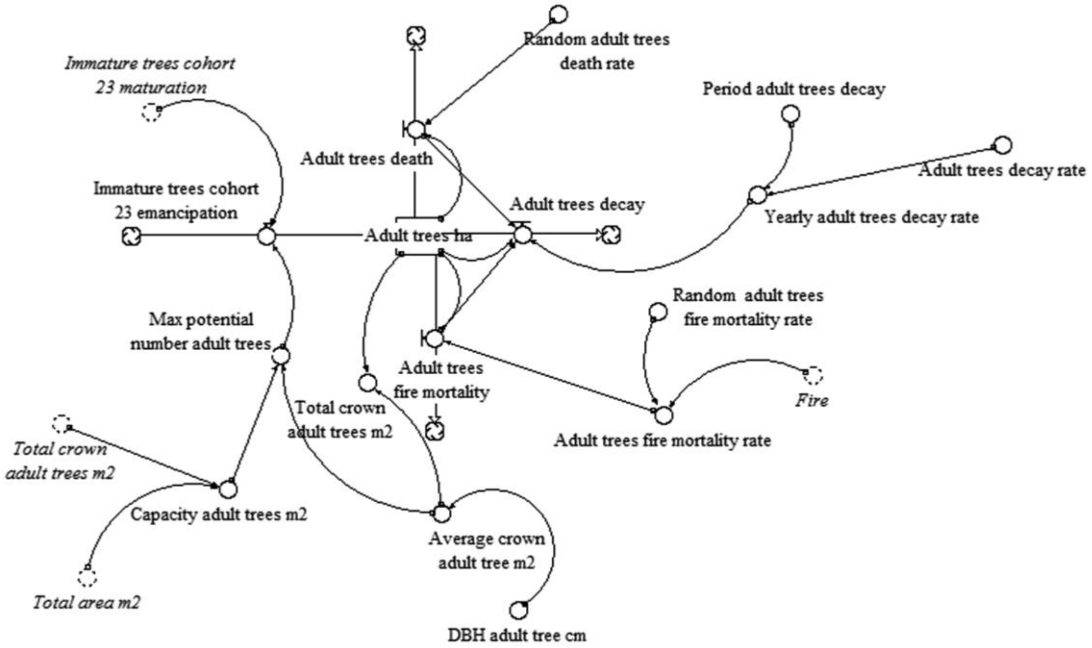


Figure 28. Stella software conceptual diagram of the sub-model of adult trees. Rectangles represent the state variables, adult trees; other variables, parameters or constants are small circles; sinks and sources are cloudlike symbols; flows are thick arrows; all the relations between state variables and other variables are fine arrows. The specification of all variable codes is expressed in Appendix II and Table 6.

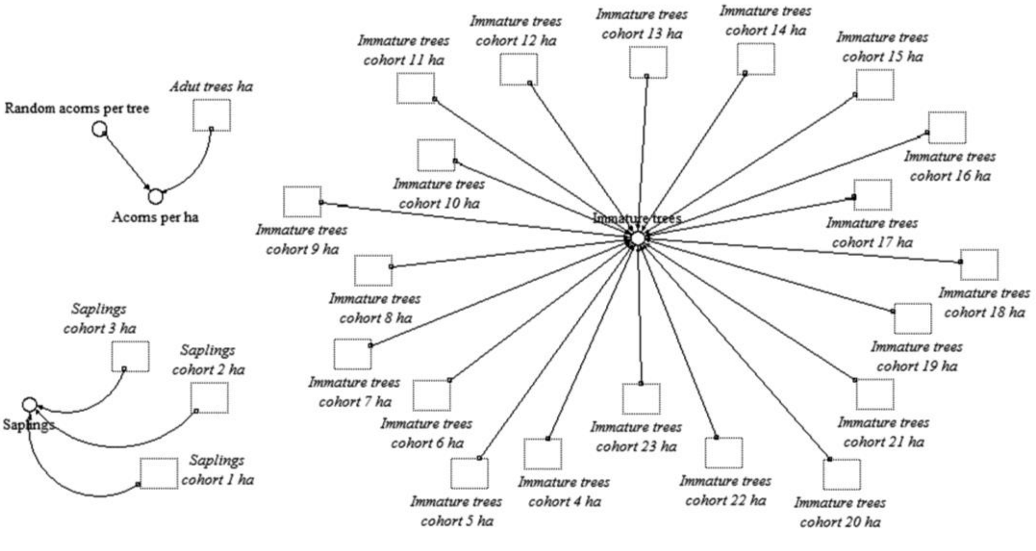


Figure 29. Stella software conceptual diagram of the sub-model of population dynamics metrics. Rectangles represent the state variables; other variables, parameters or constants are small circles; sinks and sources are cloudlike symbols; flows are thick arrows; all the relations between state variables and other variables are fine arrows. The specification of all variable codes is expressed in Appendix II and Table 6.

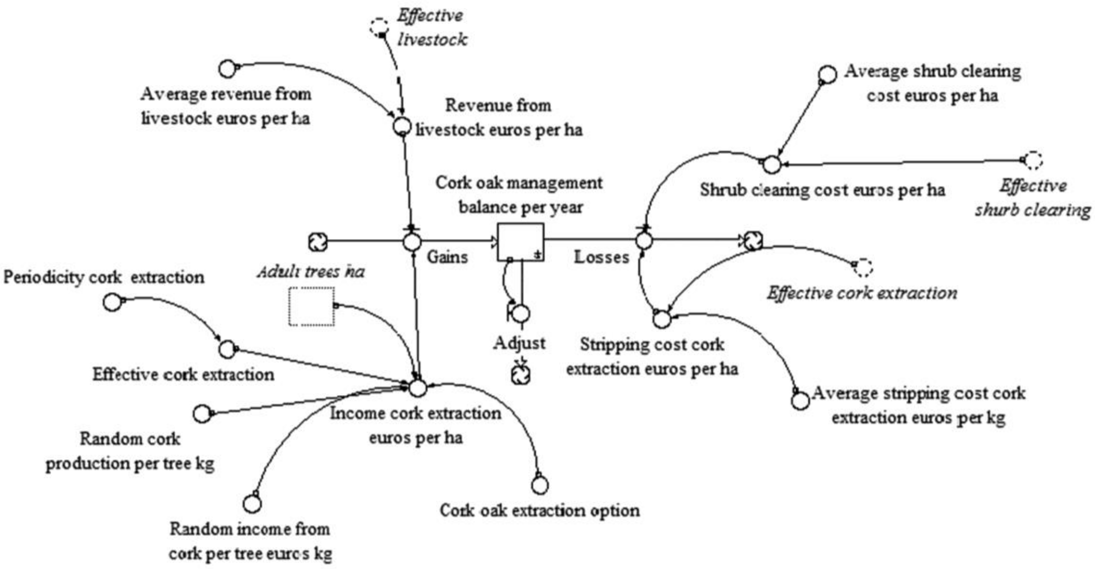


Figure 30. Stella software conceptual diagram of the sub-model of cork oak management income per year. Rectangles represent the state variables, seedlings; other variables, parameters or constants are small circles; sinks and sources are cloudlike symbols; flows are thick arrows; all the relations between state variables and other variables are fine arrows. The specification of all variable codes is expressed in Appendix II and Table 6.

Appendix II – Cork oak population dynamics variables included in the five sub-models, respective description, measure units and reference.

Table 6 - Specification of the main variables included in the model, respective description, measure units and references.

Cork oak population dynamics			
Variable	**Description**	**Unit**	**Source**
Seedlings			
Random acorns per tree	Average kg of acorns per tree Minimum acorns per tree= 1.32 Maximum acorns per tree= 33.6	kg of acorns	Herrera 1995, Canellas et al 2007, Pérez- Ramos and Marañón 2008
Random acorns Predation rate	Proportion of predated acorns before germination Minimum acorns predation rate = 0.36 Maximum acorns predation rate = 0.83	rate	Acacio et al 2007
Random acorns insect damage rate	Proportion of acorns damaged by insects before germination Minimum acorns insect damage rate = 0.09 Maximum acorns insect damage rate = 0.68	rate	Branco et al 2002, Acacio et al 2007
Random acorns Acorn germination rate	Proportion of acorns successfully germinated Minimum acorns germination rate = 0.38 Maximum acorns germination rate = 0.84	rate	Herrera 1995, Acacio et al 2007, Arosa et al 2015
Average seedlings fire mortality rate	Proportion of seedling mortality by fire Fire seedlings mortality = 0.0008	rate	Catry et al 2012
Random seedling drought mortality rate	Proportion of seedling mortality by drought Minimum seedlings drought mortality rate= 0.68 Maximum seedlings drought mortality rate = 0.70	rate	Arosa et al 2015
Random seedlings livestock mortality rate	Proportion of seedling mortality by livestock Minimum seedlings livestock mortality rate = 0.28 Maximum seedlings livestock mortality rate = 0.65	rate	Plieninger et al 2004
Random seedlings shrub clearing mortality rate	Proportion of seedling mortality by shrub clearing Minimum seedlings shrub clearing mortality rate = 0 Maximum seedlings shrub clearing mortality rate= 1	rate	Arosa et al 2015
Average seedlings resprouting rate	Proportion of seedling successfully resprouted = 0.239	rate	Arosa et al 2015
Saplings			
Average saplings fire mortality rate	Proportion of saplings mortality by fire Fire saplings mortality = 0.0008	rate	Catry et al 2012
Random saplings cohort x drought mortality rate	Proportion of saplings mortality by drought Minimum saplings drought mortality rate= 0.68 Maximum saplings drought mortality rate= 0.70	rate	Arosa et al 2015
Random saplings cohort x livestock mortality rate	Proportion of saplings mortality by livestock Minimum saplings livestock mortality rate = 0.57 Maximum saplings livestock mortality rate = 0.87	rate	Plieninger et al 2004
Random saplings cohort x shrub clearing mortality rate	Proportion of saplings mortality by shrub clearing Minimum saplings shrub clearing mortality rate = 0 Maximum saplings shrub clearing mortality rate = 1	rate	Arosa et al 2015
DBH saplings	Saplings average diameter at breast height = 6	cm	Pulido et al. 2013
Immature tres			
Random immature trees cohort x fire mortality rate	Proportion of immature trees mortality by fire Minimum immature trees cohort x fire mortality rate = 0.06 Maximum immature trees cohort x fire mortality rate = 0.08	rate	Catry et al 2012
Random immature trees cohort x death rate	Proportion of immature trees death Minimum immature trees cohort x death rate = 0 Maximun immature trees cohort x death rate = 0.000092	rate	Ribeiro and Surový 2008
DBH immature trees	Immature trees average diameter at breast height = 10	cm	Pulido et al. 2013
Adult trees			
Adult trees per ha	Initial density of adult trees = 50	trees ha^{-1}	Joffre et al 1999
Random adult trees fire mortality rate	Proportion of adult trees mortality by fire Minimum adult trees fire mortality rate = 0.038214 Maximum adult trees fire mortality rate = 0.04465	rate	Catry et al 2012
Random adult trees death rate	Proportion of adult trees death Minimum adult trees death rate = 0 Maximum adult trees death rate = 0.000092	rate	Ribeiro and Surový 2008

DBH adult trees	Adult trees average diameter at breast height = 89	cm	Pulido et al. 2013
Cork oak management income per year			
Random cork production per tree kg	Average kg of cork produced per tree Minimum cork production per tree = 35.95534 Maximum cork production per tree = 69.56406	kg tree^{-1}	Pereira and Tomé 2004
Random income from cork per tree euros kg	Average income in € per kg of produced cork Minimum income from cork per tree = 1.33 Maximum income from cork per tree = 3.33	€ kg^{-1}	Pinheiro and Ribeiro 2013
Average stripping cost cork extraction euros per kg	Average cost of cork extraction in € per kg Stripping cost cork extraction = 0.23	€ kg^{-1}	Pinheiro and Ribeiro 2013
Periodicity cork extraction	Average years between cork extraction Periodicity cork extraction = 9	years	Pereira and Tomé 2004
Average shrub clearing cost euros per ha	Average cost in € per cleared ha Shrub clearing cost = 120	€ ha^{-1}	Pinheiro et al 2008
Average revenue from livestock euros per ha	Average income in € of livestock per ha Revenue form livestock = 22.4	€ ha^{-1}	Pinheiro et al 2008

Appendix III – Mathematic equations included in the model.

Table 7: Specification of all mathematic equations included in the model. The description of the main variables is expressed in Appendix II.

DIFFERENCE EQUATIONS
Cork oak population dynamics
1.Seedlings
Seedlings_ha(t) = Seedlings_ha(t - dt) + (Germination + Seedling_resporuting - Seedlings_shrub_clearing_mortality - Seedlings__livestock_mortality - Seedlings_fire_mortality - Seedling__drought_mortality - Seedlings_maturation) * dt
2.Saplings
Saplings_cohort_1_ha(t) = Saplings_cohort_1_ha(t - dt) + (Seedlings_emancipation - Saplings_cohort_1__livestock_mortality - Saplings_cohort_1_maturation - Saplings_cohort_1__fire_mortality - Saplings_cohort_1__shrub_clearing_mortality - Saplings_cohort_1__drought_mortality) * dt
Saplings__cohort_2_ha(t) = Saplings__cohort_2_ha(t - dt) + (Sapilngs_cohort_1_emancipation - Saplings_cohort_2_livestock_mortality - Saplings_cohort_2_maturation - Saplings_cohort_2__fire_mortality - Saplings_cohort_2__shrub_clearing_mortality - Saplings_cohort__2_drought_mortality) * dt
Saplings_cohort_3_ha(t) = Saplings_cohort_3_ha(t - dt) + (Sapilngs_cohort_2_emancipation - Saplings_cohort_3_livestock_mortality - Saplings_cohort_3_maturation - Saplings_cohort_3__fire_mortality - Saplings_cohort_3_shrub_clearing_mortality - Saplings_cohort_3_drought_mortality) * dt
3.Immature trees
Immature_trees__cohort_4_ha(t) = Immature_trees__cohort_4_ha(t - dt) + (Saplings_cohort_3_emancipation - Immature_trees_cohort_4__fire_mortality - Immature_trees_cohort_4_maturation - Immature_trees_cohort_4_death) * dt
Immature_trees__cohort_5_ha(t) = Immature_trees__cohort_5_ha(t - dt) + (Immature_trees_cohort_4_emancipation - Immature_trees_cohort_5__fire_mortality - Immature_trees_cohort_5_maturation - Immature_trees_cohort_5_death) * dt
Immature_trees__cohort_6_ha(t) = Immature_trees__cohort_6_ha(t - dt) + (Immature_trees_cohort_5_emancipation - Immature_trees_cohort_6__fire_mortality - Immature_trees_cohort_6_maturation - Immature_trees_cohort_6_death) * dt
Immature_trees__cohort_7_ha(t) = Immature_trees__cohort_7_ha(t - dt) + (Immature_trees_cohort_6_emancipation - Immature_trees_cohort_7__fire_mortality - Immature_trees_cohort_7_maturation - Immature_trees_cohort_7_death) * dt
Immature_trees__cohort_8_ha(t) = Immature_trees__cohort_8_ha(t - dt) + (Immature_trees_cohort_7_emancipation - Immature_trees_cohort_8__fire_mortality - Immature_trees_cohort_8_maturation - Immature_trees_cohort_8_death) * dt
Immature_trees__cohort_9_ha(t) = Immature_trees__cohort_9_ha(t - dt) + (Immature_trees_cohort_8_emancipation - Immature_trees_cohort_9__fire_mortality - Immature_trees_cohort_9_maturation - Immature_trees_cohort_9_death) * dt
Immature_trees__cohort_10_ha(t) = Immature_trees__cohort_10_ha(t - dt) + (Immature_trees_cohort_9_emancipation - Immature_trees_cohort_10__fire_mortality - Immature_trees_cohort_10_maturation - Immature_trees_cohort_10_death) * dt
Immature_trees__cohort_11_ha(t) = Immature_trees__cohort_11_ha(t - dt) + (Immature_trees_cohort_10_emancipation - Immature_trees_cohort_11__fire_mortality - Immature_trees_cohort_11_maturation - Immature_trees_cohort_11_death) * dt
Immature_trees__cohort_12_ha(t) = Immature_trees__cohort_12_ha(t - dt) + (Immature_trees_cohort_11_emancipation - Immature_trees_cohort_12__fire_mortality - Immature_trees_cohort_12_maturation - Immature_trees_cohort_12_death) * dt
Immature_trees__cohort_13_ha(t) = Immature_trees__cohort_13_ha(t - dt) + (Immature_trees_cohort_12_emancipation - Immature_trees_cohort_13__fire_mortality - Immature_trees_cohort_13_maturation - Immature_trees_cohort_13_death) * dt
Immature_trees__cohort_14_ha(t) = Immature_trees__cohort_14_ha(t - dt) + (Immature_trees_cohort_13_emancipation - Immature_trees_cohort_14__fire_mortality - Immature_trees_cohort_14_maturation - Immature_trees_cohort_14_death) * dt
Immature_trees__cohort_15_ha(t) = Immature_trees__cohort_15_ha(t - dt) + (Immature_trees_cohort_14_emancipation - Immature_trees_cohort_15__fire_mortality - Immature_trees_cohort_15_maturation - Immature_trees_cohort_15_death) * dt
Immature_trees__cohort_16_ha(t) = Immature_trees__cohort_16_ha(t - dt) + (Immature_trees_cohort_15_emancipation - Immature_trees_cohort_16__fire_mortality - Immature_trees_cohort_16_maturation - Immature_trees_cohort_16_death) * dt

Immature_trees__cohort_17_ha(t) = Immature_trees__cohort_17_ha(t - dt) + (Immature_trees_cohort_16_emancipation - Immature_trees_cohort_17__fire_mortality - Immature_trees_cohort_17_maturation - Immature_trees_cohort_17_death) * dt

Immature_trees__cohort_18_ha(t) = Immature_trees__cohort_18_ha(t - dt) + (Immature_trees_cohort_17_emancipation - Immature_trees_cohort_18__fire_mortality - Immature_trees_cohort_18_maturation - Immature_trees_cohort_18_death) * dt

Immature_trees__cohort_19_ha(t) = Immature_trees__cohort_19_ha(t - dt) + (Immature_trees_cohort_18_emancipation - Immature_trees_cohort_19_fire_mortality - Immature_trees_cohort_19_maturation - Immature_trees_cohort_19_death) * dt

Immature_trees__cohort_20_ha(t) = Immature_trees__cohort_20_ha(t - dt) + (Immature_trees_cohort_19_emancipation - Immature_trees_cohort_20_fire_mortality - Immature_trees_cohort_20_maturation - Immature_trees_cohort_20_death) * dt

Immature_trees__cohort_21_ha(t) = Immature_trees__cohort_21_ha(t - dt) + (Immature_trees_cohort_20_emancipation - Immature_trees_cohort_21_fire_mortality - Immature_trees_cohort_21_maturation - Immature_trees_cohort_21_death) * dt

Immature_trees__cohort_22_ha(t) = Immature_trees__cohort_22_ha(t - dt) + (Immature_trees_cohort_21_emancipation - Immature_trees_cohort_22_fire_mortality - Immature_trees_cohort_22_maturation - Immature_trees_cohort_22_death) * dt

Immature_trees__cohort_23_ha(t) = Immature_trees__cohort_23_ha(t - dt) + (Immature_trees_cohort_22_emancipation - Immature_trees_cohort_23_fire_mortalit1 - Immature_trees_cohort_23_maturation - Immature_trees_cohort_23_death) * dt

4.Adult trees

Adut_trees_ha(t) = Adut_trees_ha(t - dt) + (Immature_trees_cohort_23_emancipation - Adult_trees__fire_mortality - Adult_trees_death - Adult_trees_decay) * dt

Economic balances

Cork_oak_management_balance_per_year(t) = Cork_oak_management__balance_per_year(t - dt) + (Gains - Losses - Adjust) * dt

PROCESS EQUATIONS

Cork oak population dynamics

1.Seedlings

INIT Seedlings_ha = 0

INFLOWS:

Germination = Random_acorns_germination_rate*Acorns_survival_rate

Seedling_resporuting = Average_seedlings_resprouting_rate*seedling__drought_mortality

OUTFLOWS:

Seedlings_shrub_clearing_mortality = Seedlings_ha*Seedlings_shrub_clearing_mortality_rate

Seedlings__livestock_mortality = Seedlings_livestock_mortality_rate*Seedlings_ha

Seedlings_fire_mortality = Seedlings_fire_mortality_rate*Seedlings_ha

Seedling__drought_mortality = seedlings_drought__mortality_rate*Seedlings_ha

Seedlings_maturation = Seedlings_ha-(seedlings_shrub_clearing_mortality+seedling__drought_mortality+seedlings_fire_mortality+seedlings__livestock_mortality)

2.Saplings

INIT Saplings_cohort_1_ha = 0

INFLOWS:

Seedlings_emancipation = if Seedlings_maturation <= Max_potential_number__saplings_cohort_1 then Seedlings_maturation ELSE Max_potential_number__saplings_cohort_1

OUTFLOWS:

Saplings_cohort_1__livestock_mortality = Saplings_cohort_1_livestock_mortality_rate*Saplings_cohort_1_ha

Saplings_cohort_1_maturation = Saplings_cohort_1_ha-(saplings_cohort_1__shrub_clearing_mortality+saplings_cohort_1__drought_mortality+Saplings_cohort_1__fire_mortality+saplings_cohort_1__livestock_mortality)

Saplings_cohort_1__fire_mortality = Saplings_cohort_1_fire_mortality_rate*Saplings_cohort_1_ha

Saplings_cohort_1__shrub_clearing_mortality = Saplings_cohort_1_shrub_clearing_mortality_rate*Saplings_cohort_1_ha

Saplings_cohort_1__drought_mortality = Saplings_cohort_1_drought__mortality_rate*Saplings_cohort_1_ha

INIT Saplings__cohort_2_ha = 0

INFLOWS:

Sapilngs_cohort_1_emancipation = if Saplings_cohort_1_maturation <= Max_poptential_number_saplings_cohort_2 then Saplings_cohort_1_maturation ELSE Max_poptential_number_saplings_cohort_2

OUTFLOWS:

Saplings_cohort_2_livestock_mortality = Saplings_cohort_2_livestock_mortality_rate*Saplings__cohort_2_ha

Saplings_cohort_2_maturation = Saplings__cohort_2_ha-(saplings_cohort_2__shrub_clearing_mortality+saplings_cohort__2_drought_mortality+saplings_cohort_2__fire_mortality+saplings_cohort_2_livestock_mortality)

Saplings_cohort_2__fire_mortality = saplings_cohort_2_fire_mortality_rate*Saplings__cohort_2_ha

Saplings_cohort_2__shrub_clearing_mortality = Saplings_cohort_2_shrub_clearing_mortality*Saplings__cohort_2_ha

Saplings_cohort__2_drought_mortality = Saplings_cohort_2_shrub_clearing_mortality_rate*Saplings__cohort_2_ha

INIT Saplings_cohort_3_ha = 0

INFLOWS:

Sapilngs_cohort_2_emancipation = if Saplings_cohort_2_maturation <= Max_potential_number__saplings_cohort_3 then Saplings_cohort_2_maturation ELSE Max_potential_number__saplings_cohort_3

OUTFLOWS:

Saplings_cohort_3_livestock_mortality = Saplings_cohort_3_livestock_mortality_rate*Saplings_cohort_3_ha

Saplings_cohort_3_maturation = Saplings_cohort_3_ha-(Saplings_cohort_3_shrub_clearing_mortality+Saplings_cohort_3_drought_mortality+saplings_cohort_3__fire_mortality+saplings_cohort_3_livestock_mortality)

Saplings_cohort_3__fire_mortality = Saplings_cohort_3__fire_mortality_rate*Saplings_cohort_3_ha

Saplings_cohort_3_shrub_clearing_mortality = Saplings_cohort_3_shrub_cutting_mortality_rate*Saplings_cohort_3_ha

Saplings_cohort_3_drought_mortality = Saplings_cohort_3_ha*Saplings_cohort_drought_mortality_rate

3.Immature trees

INIT Immature_trees__cohort_4_ha = 0

INFLOWS:

Saplings_cohort_3_emancipation = IF Saplings_cohort_3_maturation <= Max_potential_number_immature_trees_cohort_4 THEN Saplings_cohort_3_maturation ELSE Max_potential_number_immature_trees_cohort_4

OUTFLOWS:

Immature_trees_cohort_4__fire_mortality = immature_trees_cohort_4_fire_mortality_rate*Immature_trees__cohort_4_ha

Immature_trees_cohort_4_maturation = Immature_trees__cohort_4_ha-(immature_trees_cohort_4_death+immature_trees_cohort_4__fire_mortality)

Immature_trees_cohort_4_death = Random_immature_trees_cohort_4__death_rate*Immature_trees__cohort_4_ha

INIT Immature_trees__cohort_5_ha = 0

INFLOWS:

Immature_trees_cohort_4_emancipation = IF Immature_trees_cohort_4_maturation <= Max_potential_number_immature_trees_cohort_5 THEN Immature_trees_cohort_4_maturation ELSE Max_potential_number_immature_trees_cohort_5

OUTFLOWS:

Immature_trees_cohort_5__fire_mortality = Immature_trees_cohort_5_fire_mortality_rate*Immature_trees__cohort_5_ha

Immature_trees_cohort_5_maturation = Immature_trees__cohort_5_ha-(Immature_trees_cohort_5_death+Immature_trees_cohort_5__fire_mortality)

Immature_trees_cohort_5_death = Random_trees_cohort_5__death_rate*Immature_trees__cohort_5_ha

INIT Immature_trees__cohort_6_ha = 0

INFLOWS:

Immature_trees_cohort_5_emancipation = IF Immature_trees_cohort_5_maturation <= Max_potential_number_immature_trees_cohort_6 THEN Immature_trees_cohort_5_maturation ELSE Max_potential_number_immature_trees_cohort_6

OUTFLOWS:

Immature_trees_cohort_6__fire_mortality = Immature_trees_cohort_6_fire_mortality_rate*Immature_trees__cohort_6_ha

Immature_trees_cohort_6_maturation = Immature_trees__cohort_6_ha-(Immature_trees_cohort_6_death+Immature_trees_cohort_6__fire_mortality)

Immature_trees_cohort_6_death = Random_immature_trees_cohort_6__death_rate*Immature_trees__cohort_6_ha

---

INIT Immature_trees__cohort_7_ha = 0

INFLOWS:

Immature_trees_cohort_6_emancipation = IF Immature_trees_cohort_6_maturation <= Max_potential_number_immature_trees_cohort_7 THEN Immature_trees_cohort_6_maturation ELSE Max_potential_number_immature_trees_cohort_7

OUTFLOWS:

Immature_trees_cohort_7__fire_mortality = Immature_trees_cohort_7_fire_mortality_rate*Immature_trees__cohort_7_ha

Immature_trees_cohort_7_maturation = Immature_trees__cohort_7_ha-(Immature_trees_cohort_7_death+Immature_trees_cohort_7__fire_mortality)

Immature_trees_cohort_7_death = Random_immature_trees_cohort_7__death_rate*Immature_trees__cohort_7_ha

---

INIT Immature_trees__cohort_8_ha = 0

INFLOWS:

Immature_trees_cohort_7_emancipation = IF Immature_trees_cohort_7_maturation <= Max_potential_number_immature_trees_cohort_8 THEN Immature_trees_cohort_7_maturation ELSE Max_potential_number_immature_trees_cohort_8

OUTFLOWS:

Immature_trees_cohort_8__fire_mortality = Immature_trees_cohort_8_fire_mortality_rate*Immature_trees__cohort_8_ha

Immature_trees_cohort_8_maturation = Immature_trees__cohort_8_ha-(Immature_trees_cohort_8_death+Immature_trees_cohort_8__fire_mortality)

Immature_trees_cohort_8_death = Random_immature_trees_cohort_8__death_rate*Immature_trees__cohort_8_ha

---

INIT Immature_trees__cohort_9_ha = 0

INFLOWS:

Immature_trees_cohort_8_emancipation = IF Immature_trees_cohort_8_maturation <= Max_potential_number_immature_trees_cohort_9 THEN Immature_trees_cohort_8_maturation ELSE Max_potential_number_immature_trees_cohort_9

OUTFLOWS:

Immature_trees_cohort_9__fire_mortality = Immature_trees_cohort_9_fire_mortality_rate*Immature_trees__cohort_9_ha

Immature_trees_cohort_9_maturation = Immature_trees__cohort_9_ha-(Immature_trees_cohort_9_death+Immature_trees_cohort_9__fire_mortality)

Immature_trees_cohort_9_death = Random_immature_trees_cohort_9_death_rate*Immature_trees__cohort_9_ha

---

INIT Immature_trees__cohort_10_ha = 0

INFLOWS:

Immature_trees_cohort_9_emancipation = IF Immature_trees_cohort_9_maturation <= Max_potential_number_immature_trees_cohort_10 THEN Immature_trees_cohort_9_maturation ELSE Max_potential_number_immature_trees_cohort_10

OUTFLOWS:

Immature_trees_cohort_10__fire_mortality = Immature_trees_cohort_10_fire_mortality_rate*Immature_trees__cohort_10_ha

Immature_trees_cohort_10_maturation = Immature_trees__cohort_10_ha-(Immature_trees_cohort_10_death+Immature_trees_cohort_10__fire_mortality)
Immature_trees_cohort_10_death = Random_immature_trees_cohort_10_death_rate*Immature_trees__cohort_10_ha

INIT Immature_trees__cohort_11_ha = 0
INFLOWS:
Immature_trees_cohort_10_emancipation = IF Immature_trees_cohort_10_maturation <= Max_potential_number_immature_trees_cohort_11 THEN Immature_trees_cohort_10_maturation ELSE Max_potential_number_immature_trees_cohort_11
OUTFLOWS:
Immature_trees_cohort_11__fire_mortality = Immature_trees_cohort_11_fire_mortality_rate*Immature_trees__cohort_11_ha
Immature_trees_cohort_11_maturation = Immature_trees__cohort_11_ha-(Immature_trees_cohort_11_death+Immature_trees_cohort_11__fire_mortality)
Immature_trees_cohort_11_death = Random_immature_trees_cohort_11_death_rate*Immature_trees__cohort_11_ha

INIT Immature_trees__cohort_12_ha = 0
INFLOWS:
Immature_trees_cohort_11_emancipation = IF Immature_trees_cohort_11_maturation <= Max_potential_number_immature_trees_cohort_12 THEN Immature_trees_cohort_11_maturation ELSE Max_potential_number_immature_trees_cohort_12
OUTFLOWS:
Immature_trees_cohort_12__fire_mortality = Immature_trees_cohort_12_fire_mortality_rate*Immature_trees__cohort_12_ha
Immature_trees_cohort_12_maturation = Immature_trees__cohort_12_ha-(Immature_trees_cohort_12_death+Immature_trees_cohort_12__fire_mortality)
Immature_trees_cohort_12_death = Random_immature_trees_cohort_12_death_rate*Immature_trees__cohort_12_ha

INIT Immature_trees__cohort_13_ha = 0
INFLOWS:
Immature_trees_cohort_12_emancipation = IF Immature_trees_cohort_12_maturation <= Max_potential_number_immature_trees_cohort_13 THEN Immature_trees_cohort_12_maturation ELSE Max_potential_number_immature_trees_cohort_13
OUTFLOWS:
Immature_trees_cohort_13__fire_mortality = Immature_trees_cohort_13_fire_mortality_rate*Immature_trees__cohort_13_ha
Immature_trees_cohort_13_maturation = Immature_trees__cohort_13_ha-(Immature_trees_cohort_13_death+Immature_trees_cohort_13__fire_mortality)
Immature_trees_cohort_13_death = Random_immature_trees_cohort_13_death_rate*Immature_trees__cohort_13_ha

INIT Immature_trees__cohort_14_ha = 0
INFLOWS:
Immature_trees_cohort_13_emancipation = IF Immature_trees_cohort_13_maturation <= Max_potential_number_immature_trees_cohort_14 THEN Immature_trees_cohort_13_maturation ELSE Max_potential_number_immature_trees_cohort_14
OUTFLOWS:
Immature_trees_cohort_14__fire_mortality = Immature_trees_cohort_14_fire_mortality_rate*Immature_trees__cohort_14_ha
Immature_trees_cohort_14_maturation = Immature_trees__cohort_14_ha-(Immature_trees_cohort_14_death+Immature_trees_cohort_14__fire_mortality)
Immature_trees_cohort_14_death = Random_immature_trees_cohort_14_death_rate*Immature_trees__cohort_14_ha

INIT Immature_trees__cohort_15_ha = 0
INFLOWS:
Immature_trees_cohort_14_emancipation = IF Immature_trees_cohort_14_maturation <= Max_potential_number_immature_trees_cohort_15 THEN Immature_trees_cohort_14_maturation ELSE Max_potential_number_immature_trees_cohort_15

OUTFLOWS:

Immature_trees_cohort_15__fire_mortality = Immature_trees_cohort_15_fire_mortality_rate*Immature_trees__cohort_15_ha

Immature_trees_cohort_15_maturation = Immature_trees__cohort_15_ha-(Immature_trees_cohort_15_death+Immature_trees_cohort_15__fire_mortality)

Immature_trees_cohort_15_death = Random_immature_trees_cohort_15_death_rate*Immature_trees__cohort_15_ha

---

INIT Immature_trees__cohort_16_ha = 0

INFLOWS:

Immature_trees_cohort_15_emancipation = IF Immature_trees_cohort_15_maturation <= Max_potential_number_immature_trees_cohort_16 THEN Immature_trees_cohort_15_maturation ELSE Max_potential_number_immature_trees_cohort_16

OUTFLOWS:

Immature_trees_cohort_16__fire_mortality = Immature_trees_cohort_16_fire_mortality_rate*Immature_trees__cohort_16_ha

Immature_trees_cohort_16_maturation = Immature_trees__cohort_16_ha-(Immature_trees_cohort_16_death+Immature_trees_cohort_16__fire_mortality)

Immature_trees_cohort_16_death = Random_immature_trees_cohort_16_death_rate*Immature_trees__cohort_16_ha

---

INIT Immature_trees__cohort_17_ha = 0

INFLOWS:

Immature_trees_cohort_16_emancipation = IF Immature_trees_cohort_16_maturation <= Max_potential_number_immature_trees_cohort_17 THEN Immature_trees_cohort_16_maturation ELSE Max_potential_number_immature_trees_cohort_17

OUTFLOWS:

Immature_trees_cohort_17__fire_mortality = Immature_trees_cohort_17_fire_mortality_rate*Immature_trees__cohort_17_ha

Immature_trees_cohort_17_maturation = Immature_trees__cohort_17_ha-(Immature_trees_cohort_17_death+Immature_trees_cohort_17__fire_mortality)

Immature_trees_cohort_17_death = Random_immature_trees_cohort_17_death_rate*Immature_trees__cohort_17_ha

---

INIT Immature_trees__cohort_18_ha = 0

INFLOWS:

Immature_trees_cohort_17_emancipation = IF Immature_trees_cohort_17_maturation <= Max_potential_number_immature_trees_cohort_18 THEN Immature_trees_cohort_17_maturation ELSE Max_potential_number_immature_trees_cohort_18

OUTFLOWS:

Immature_trees_cohort_18__fire_mortality = Immature_trees_cohort_18_fire_mortality_rate*Immature_trees__cohort_18_ha

Immature_trees_cohort_18_maturation = Immature_trees__cohort_18_ha-(Immature_trees_cohort_18_death+Immature_trees_cohort_18__fire_mortality)

Immature_trees_cohort_18_death = Random_immature_trees_cohort_18_death_rate*Immature_trees__cohort_18_ha

---

INIT Immature_trees__cohort_19_ha = 0

INFLOWS:

Immature_trees_cohort_18_emancipation = IF Immature_trees_cohort_18_maturation <= Max_potential_number_immature_trees_cohort_19 THEN Immature_trees_cohort_18_maturation ELSE Max_potential_number_immature_trees_cohort_19

OUTFLOWS:

Immature_trees_cohort_19_fire_mortality = Immature_trees_cohort_19_fire_mortality_rate*Immature_trees__cohort_19_ha

Immature_trees_cohort_19_maturation = Immature_trees__cohort_19_ha-(Immature_trees_cohort_19_death+Immature_trees_cohort_19_fire_mortality)

Immature_trees_cohort_19_death = Random_immature_trees_cohort_19_death_rate*Immature_trees__cohort_19_ha

---

INIT Immature_trees__cohort_20_ha = 0

INFLOWS:

Immature_trees_cohort_19_emancipation = IF Immature_trees_cohort_19_maturation <= Max_potential_number_immature_trees_cohort_20 THEN Immature_trees_cohort_19_maturation ELSE Max_potential_number_immature_trees_cohort_20

OUTFLOWS:

Immature_trees_cohort_20_fire_mortality = Immature_trees_cohort_20_fire_mortality_rate*Immature_trees__cohort_20_ha

Immature_trees_cohort_20_maturation = Immature_trees__cohort_20_ha-(Immature_trees_cohort_20_death+Immature_trees_cohort_20_fire_mortality)

Immature_trees_cohort_20_death = Random_immature_trees_cohort_20_death_rate*Immature_trees__cohort_20_ha

INIT Immature_trees__cohort_21_ha = 0

INFLOWS:

Immature_trees_cohort_20_emancipation = IF Immature_trees_cohort_20_maturation <= Max_potential_number_immature_trees_cohort_21 THEN Immature_trees_cohort_20_maturation ELSE Max_potential_number_immature_trees_cohort_21

OUTFLOWS:

Immature_trees_cohort_21_fire_mortality = Immature_trees_cohort_21_fire_mortality_rate*Immature_trees__cohort_21_ha

Immature_trees_cohort_21_maturation = Immature_trees__cohort_21_ha-(Immature_trees_cohort_21_death+Immature_trees_cohort_21_fire_mortality)

Immature_trees_cohort_21_death = Random_immature_trees_cohort_21_death_rate*Immature_trees__cohort_21_ha

INIT Immature_trees__cohort_22_ha = 0

INFLOWS:

Immature_trees_cohort_21_emancipation = IF Immature_trees_cohort_21_maturation <= Max_potential_number_immature_trees_cohort_22 THEN Immature_trees_cohort_21_maturation ELSE Max_potential_number_immature_trees_cohort_22

OUTFLOWS:

Immature_trees_cohort_22_fire_mortality = Immature_trees_cohort_22_fire_mortality_rate*Immature_trees__cohort_22_ha

Immature_trees_cohort_22_maturation = Immature_trees__cohort_22_ha-(Immature_trees_cohort_22_death+Immature_trees_cohort_22_fire_mortality)

Immature_trees_cohort_22_death = Random_immature_trees_cohort_22_death_rate*Immature_trees__cohort_22_ha

INIT Immature_trees__cohort_23_ha = 0

INFLOWS:

Immature_trees_cohort_22_emancipation = IF Immature_trees_cohort_22_maturation <= Max_potential_number_immature_trees_cohort_23 THEN Immature_trees_cohort_22_maturation ELSE Max_potential_number_immature_trees_cohort_23

OUTFLOWS:

Immature_trees_cohort_23_fire_mortalit1 = Immature_trees_cohort_23_fire_mortality_rat_1*Immature_trees__cohort_23_ha

Immature_trees_cohort_23_maturation = if Immature_trees__cohort_23_ha <= Max_potential__number_adult_trees then Immature_trees__cohort_23_ha-(Immature_trees_cohort_23_death+Immature_trees_cohort_23_fire_mortalit1) ELSE Max_potential__number_adult_trees

Immature_trees_cohort_23_death = Immature_trees_cohort_23_death_rate*Immature_trees__cohort_23_ha

4.Adult trees

INIT Adut_trees_ha = 0

INFLOWS:

Immature_trees_cohort_23_emancipation = if Immature_trees_cohort_23_maturation <= Max_potential_number_adult_trees then Immature_trees_cohort_23_maturation ELSE Max_potential_number_adult_trees

OUTFLOWS:

Adult_trees_fire_mortality = Adult_trees_fire_mortality_rate*Adut_trees_ha

Adult_trees_death = Random_adult_trees_death_rate*Adut_trees_ha

Adult_trees_decay = yearly_adult_trees_decay_rate*Adut_trees_ha-(Adult_trees_death+Adult_trees_fire_mortality)
Economic balances
INIT Cork_oak_management_balance_per_year = 0 INFLOWS: Gains = Revenue_from_livestock_euros_per_ha+income_cork_extraction_euros_per_ha OUTFLOWS: Losses = stripping_cost_cork_extraction_euros_per_ha+shrub_clearing_cost_euros_per_ha Adjust = Cork_oak_management_balance_per_year
COMPOSED VARIABLES
Fires
Fire = IF fire_occurrence=1 THEN fire_intensity ELSE 0
Fire_occurrence = IF Fire_probability=fire_frequency_value THEN 1 ELSE 0
Adult_trees_fire_mortality_rate = IF fire =1 THEN fire*Random__adult_trees__fire_mortality_rate ELSE 0
Droughts
Drought = IF Seedlings_drought_occurrence=1 THEN Seedlings_drought_intensity ELSE 0
Seedlings_drought_occurrence = IF Seedlings_drought_probability=Seedlings_drought_frequency_value THEN 1 ELSE 0
Saplings_cohort_1_drought__mortality_rate = IF DROUGHT=1 THEN DROUGHT*Random_saplings_drought_mortality_rate ELSE 0*0
Saplings_cohort_3_drought__mortality_rate = IF DROUGHT=1 THEN DROUGHT*Random_saplings_drought_mortality_rate ELSE 0
Saplings_cohort_3_drought__mortality_rate = IF DROUGHT=1 THEN DROUGHT*Random_saplings_drought_mortality_rate ELSE 0
Land use management
Effective_livestock = IF Livestock_option=1 AND effective_livestock__periodicity=0 THEN 1 ELSE 0
Seedlings_livestock_mortality_rate = IF Effective__livestock =1 THEN Random_seedlings_livestock_mortality_rate ELSE 0
Saplings_cohort_1_livestock_mortality_rate = IF Effective__livestock =1 THEN Random_saplings_livestock_mortality_rate ELSE 0
Saplings_cohort_2_livestock_mortality_rate = IF Effective__livestock =1 THEN Random_saplings_livestock_mortality_rate ELSE 0
Saplings_cohort_3_livestock_mortality_rate = IF Effective__livestock =1 THEN Random_saplings_livestock_mortality_rate ELSE 0
Effective_shurb_clearing = IF shrub_clearing_option = 1 AND effective_shrub_clearing_periodicity = 0 THEN 1 ELSE 0
Seedlings_shrub_clearing_mortality_rate = IF Effective__shurb_clearing = 1 THEN Random_seedlings_shrub_clearing_mortality_rate ELSE 0
Saplings_cohort_1_shrub_clearing_mortality_rate = IF Effective__shurb_clearing = 1 THEN Random_saplings_shrub_clearing_mortality_rate ELSE 0
Saplings_cohort_2_shrub_clearing_mortality = IF Effective__shurb_clearing = 1 THEN Random_saplings_shrub_clearing_mortality_rate ELSE 0
Saplings_cohort_3_shrub_cutting_mortality_rate = IF Effective__shurb_clearing = 1 THEN Random_saplings_shrub_clearing_mortality_rate ELSE 0
Competition_converter = IF Max_potential__number_adult_trees > 0 THEN (1/ Max_potential__number_adult_trees)*174.3 ELSE 174.3
Economic balances
Income_cork_extraction_euros_per_ha = IF Cork_oak_extraction_option=1 AND effective_cork_extraction =0 THEN Adut_trees_ha*Random_cork_production_per_tree_kg*Random_income_from_cork_per_tree_euros_kg ELSE 0
Revenue_from_livestock_euros_per_ha = IF Effective__livestock=1 THEN Average_revenue_from_livestock_euros_per_ha ELSE 0
Shrub_clearing_cost_euros_per_ha = IF Effective__shurb_clearing=1 THEN Average_shrub_clearing_cost_euros_per_ha ELSE 0

Stripping_cost_cork_extraction_euros_per_ha = IF effective_cork_extraction=0 THEN Average_stripping_cost_cork_extraction_euros_per_kg ELSE 0

Cork oak population dynamics

1.Seedlings

Acorns_per_ha = Adut_trees_ha*Random_acorns_per_tree

Acorns_survival_rate = Acorns_per_ha*(Surviaval_rate+Intact_acorns_rate)/2

Intact_acorns_rate = 1-Random_acorns_insect_damage_rate

Surviaval_rate = 1-Random_acorns_predation_rate

Seedlings_drought_mortality_rate = DROUGHT*Random_seedlings_drought_mortality_rate

Seedlings_fire_mortality_rate = Fire*Average_seedlings_fire_mortality_rate

2.Saplings

Capacity_saplings_cohort_1_m2 = Total_area_m2-Total_crown__saplings_cohort_1_m2

Capacity_saplings_cohort_2_m2 = Total_area_m2-Total_crown__saplings_cohort_2_m2

Capacity_saplings_cohort_3_m2 = Total_area_m2-Total_crown__saplings_cohort_3_m2

Average_crown_saplings_cohort_1_m2 = 0.0431*DBH __saplings_cohort_1_cm^1.6025

Average_crown_saplings_cohort_2_m2 = 0.0431*DBH__saplings_cohort_2_cm^1.6025

Average_crown_saplings_cohort_3_m2 = 0.0431*DBH__saplings_cohort_3_cm^1.6025

Saplings_cohort_1_fire_mortality_rate = fire*Average_saplings_fire_mortality_rate

Saplings_cohort_2_fire_mortality_rate = fire*Average_saplings_fire_mortality_rate

Saplings_cohort_3_fire_mortality_rate = fire*Average_saplings_fire_mortality_rate

Max_potential_number_saplings_cohort_1 = Capacity__saplings_cohort_1_m2/average_crown_saplings_cohort_1_m2

Max_poptential_number_saplings_cohort_2 = capacity_saplings_cohort_2_m2/average_crown_saplings_cohort_2_m2

Max_potential_number_saplings_cohort_3 = capacity_saplings_cohort_3_m2/average_crown_saplings_cohort_3_m2

Total_crown__saplings_cohort_1_m2 = Saplings_cohort_1_ha*average_crown_saplings_cohort_1_m2

Total_crown__saplings_cohort_2_m2 = Saplings__cohort_2_ha*average_crown_saplings_cohort_2_m2

Total_crown__saplings_cohort_3_m2 = Saplings_cohort_3_ha*average_crown_saplings_cohort_3_m2

Saplings = Saplings_cohort_1_ha+Saplings__cohort_2_ha+Saplings_cohort_3_ha

3.Immature trees

Capacity_immature_trees_cohort_4 = Capacity_immature_trees_cohort_5-Total_crown_immature_tree_cohort_4_m2

Capacity_immature_trees_cohort_5 = Capacity_immature_trees_cohort_6-Total_crown_immature_tree_cohort_5_m2

Capacity_immature_trees_cohort_6 = Capacity_immature_trees_cohort_7-Total_crown_immature_tree_cohort_6_m2

Capacity_immature_trees_cohort_7 = Capacity_immature_trees_cohort_8-Total_crown_immature_tree_cohort_7_m2

Capacity_immature_trees_cohort_8 = Capacity__immature_trees_cohort_9-Total_crown_immature_tree_cohort_8_m2

Capacity_immature_trees_cohort_9 = Capacity_immature_trees_cohort_10-Total_crown_immature_tree_cohort_9_m2

Capacity_immature_trees_cohort_10 = Capacity_immature_trees_cohort_11-Total_crown_immature_tree_cohort_10_m2

Capacity_immature_trees_cohort_11 = Capacity_immature_trees_cohort_12-Total_crown_immature_tree_cohort_11_m2

Capacity_immature_trees_cohort_12 = Capacity_immature_trees_cohort_13-Total_crown_immature_tree_cohort_12_m2

Capacity_immature_trees_cohort_13 = Capacity_immature_trees_cohort_14-Total_crown_immature_tree_cohort_13_m2

Capacity_immature_trees_cohort_14 = Capacity_immature_trees_cohort_15-Total_crown_immature_tree_cohort_14_m2

Capacity_immature_trees_cohort_15 = Capacity_immature_trees_cohort_16-Total_crown_immature_tree_cohort_15_m2

Capacity_immature_trees_cohort_16 = Capacity_immature_trees_cohort_17-Total_crown_immature_tree_cohort_16_m2

Capacity_immature_trees_cohort_17 = Capacity_immature_trees_cohort_18-Total_crown_immature_tree_cohort_17_m2

Capacity_immature_trees_cohort_18 = Capacity_immature_trees_cohort_19-Total_crown_imnature_tree_cohort_18_m2

Capacity_immature_trees_cohort_19 = Capacity_immature_trees_cohort_20-Total_crown_immature_tree_cohort_19_m2

Capacity_immature_trees_cohort_20 = Capacity_immature_trees_cohort_21-Total_crown_immature_tree_cohort_20_m2

Capacity_immature_trees_cohort_21 = Capacity_immature_trees_cohort_22-Total_crown_immature_tree_cohort_21_m2

Capacity_immature_trees_cohort_22 = Capacity_immature_trees_cohort_23-Total_crown_immature_tree_cohort_22_m2

Capacity_immature_trees_cohort_23 = Capacity_adult_trees_m2-Total_crown_immature_tree_cohort_23_m2

Average_crown_immature_tree_cohort_4_m2 = 0.0431*DBH__immature_trees_cohort_4_cm^1.6025

Average_crown_imature_tree_cohort_5_m2 = 0.0431*DBH__immature_trees_cohort_5_cm^1.6025

Average_crown_immature_tree_cohort_6__m2 = 0.0431*DBH__immature_trees_cohort_6_cm^1.6025

Average_crown_immature_tree_cohort_7__m2 = 0.0431*DBH__immature_trees_cohort_7_cm^1.6025

Average_crown_immature_tree_cohort_8__m2 = 0.0431*DBH__immature_trees_cohort_8_cm^1.6025

Average_crown_immature_tree_cohort_9__m2 = 0.0431*DBH__immature_trees_cohort_9_cm^1.6025

Average_crown_immature_tree_cohort_10__m2 = 0.0431*DBH_immature_trees_cohort_10_cm^1.6025

Average_crown_immature_tree_cohort_11__m2 = 0.0431*DBH_immature_trees_cohort_11_cm^1.6025

Average_crown_immature_tree_cohort_12__m2 = 0.0431*DBH_immature_trees_cohort_12_cm^1.6025

Average_crown_immature_tree_cohort_13__m2 = 0.0431*DBH_immature_trees_cohort_13_cm^1.6025

Average_crown_immature_tree_cohort_14__m2 = 0.0431*DBH_immature_trees_cohort_14_cm^1.6025

Average_crown_immature_tree_cohort_15__m2 = 0.0431*DBH_immature_trees_cohort_15_cm^1.6025

Average_crown_immature_tree_cohort_16__m2 = 0.0431*DBH_immature_trees_cohort_16_cm^1.6025

Average_crown_immature_tree_cohort_17__m2 = 0.0431*DBH_immature_trees_cohort_17_cm^1.6025

Average_crown_immature_tree_cohort_18__m2 = 0.0431*DBH_immature_trees_cohort_18_cm^1.6025

Average_crown_immature_tree_cohort_19__m2 = 0.0431*DBH_immature_trees_cohort_19_cm^1.6025

Average_crown_immature_tree_cohort_20__m2 = 0.0431*DBH_immature_trees_cohort_20_cm^1.6025

Average_crown_immature_tree_cohort_21_m2 = 0.0431*DBH__immature_trees_cohort_21_cm^1.6025

Average_crown_immature_tree_cohort_22_m2 = 0.0431*DBH__immature_trees_cohort_22_cm^1.6025

Average_crown_immature_tree_cohort_23_m2 = 0.0431*DBH__immature_trees_cohort_23_cm^1.6025

Max_potential_number_immature_trees_cohort_4 = Capacity__immature_trees_cohort_4/Average_crown_immature_tree_cohort_4_m2

Max_potential_number_immature_trees_cohort_5 = Capacity__immature_trees_cohort_5/Average_crown_imature_tree_cohort_5__m2

Max_potential_number_immature_trees_cohort_6 = Capacity__immature_trees_cohort_6/Average_crown_immature_tree_cohort_6__m2

Max_potential_number_immature_trees_cohort_7 = Capacity__immature_trees_cohort_7/Average_crown_immature_tree_cohort_7__m2

Max_potential_number_immature_trees_cohort_8 = Capacity__immature_trees_cohort_8/Average_crown_immature_tree_cohort_8__m2

Max_potential_number_immature_trees_cohort_9 = Capacity__immature_trees_cohort_9/Average_crown_immature_tree_cohort_9__m2

Max_potential_number_immature_trees_cohort_10 = Capacity__immature_trees_cohort_10/Average_crown_immature_tree_cohort_10__m2

Max_potential_number_immature_trees_cohort_11 = Capacity__immature_trees_cohort_11/Average_crown_immature_tree_cohort_11__m2

Max_potential_number_immature_trees_cohort_12 = Capacity__immature_trees_cohort_12/Average_crown_immature_tree_cohort_12__m2

Max_potential_number_immature_trees_cohort_13 = Capacity__immature_trees_cohort_13/Average_crown_immature_tree_cohort_13__m2

Max_potential_number_immature_trees_cohort_14 = Capacity__immature_trees_cohort_14/Average_crown_immature_tree_cohort_14__m2

Max_potential_number_immature_trees_cohort_15 = Capacity__immature_trees_cohort_15/Average_crown_immature_tree_cohort_15__m2

Max_potential_number_immature_trees_cohort_16 = Capacity__immature_trees_cohort_16/Average_crown_immature_tree_cohort_16__m2

Max_potential_number_immature_trees_cohort_17 = Capacity__immature_trees_cohort_17/Average_crown_immature_tree_cohort_17__m2

Max_potential_number_immature_trees_cohort_18 = Capacity__immature_trees_cohort_18/Average_crown_immature_tree_cohort_18__m2

Max_potential_number_immature_trees_cohort_19 = Capacity__immature_trees_cohort_19/Average_crown_immature_tree_cohort_19__m2

Max_potential_number_immature_trees_cohort_20 = Capacity__immature_trees_cohort_20/Average_crown_immature_tree_cohort_20__m2

Max_potential_number_immature_trees_cohort_21 = Capacity__immature_trees_cohort_21/Average_crown_immature_tree_cohort_21_m2

Max_potential_number_immature_trees_cohort_22 = Capacity__immature_trees_cohort_22/Average_crown_immature_tree_cohort_22_m2

Max_potential_number_immature_trees_cohort_23 = Capacity__immature_trees_cohort_23/Average_crown_immature_tree_cohort_23_m2

Total_crown_immature_tree_cohort_4_m2 = Immature_trees__cohort_4_ha*Average_crown_immature_tree_cohort_4_m2

Total_crown_immature_tree_cohort_5_m2 = Immature_trees__cohort_5_ha*Average_crown_imature_tree_cohort_5__m2

Total_crown_immature_tree_cohort_6_m2 = Immature_trees__cohort_6_ha*Average_crown_immature_tree_cohort_6__m2

Total_crown_immature_tree_cohort_7_m2 = Immature_trees__cohort_7_ha*Average_crown_immature_tree_cohort_7__m2

Total_crown_immature_tree_cohort_8_m2 = Immature_trees__cohort_8_ha*Average_crown_immature_tree_cohort_8__m2

Total_crown_immature_tree_cohort_9_m2 = Immature_trees__cohort_9_ha*Average_crown_immature_tree_cohort_9__m2

Total_crown_immature_tree_cohort_10_m2 = Immature_trees__cohort_10_ha*Average_crown_immature_tree_cohort_10__m2

Total_crown_immature_tree_cohort_11_m2 = Immature_trees__cohort_11_ha*Average_crown_immature_tree_cohort_11__m2

Total_crown_immature_tree_cohort_12_m2 = Immature_trees__cohort_12_ha*Average_crown_immature_tree_cohort_12__m2

Total_crown_immature_tree_cohort_13_m2 = Immature_trees__cohort_13_ha*Average_crown_immature_tree_cohort_13__m2

Total_crown_immature_tree_cohort_14_m2 = Immature_trees__cohort_14_ha*Average_crown_immature_tree_cohort_14__m2

Total_crown_immature_tree_cohort_15_m2 = Immature_trees__cohort_15_ha*Average_crown_immature_tree_cohort_15__m2

Total_crown_immature_tree_cohort_16_m2 = Immature_trees__cohort_16_ha*Average_crown_immature_tree_cohort_16__m2

Total_crown_immature_tree_cohort_17_m2 = Immature_trees__cohort_17_ha*Average_crown_immature_tree_cohort_17__m2

Total_crown_imnature_tree_cohort_18_m2 = Immature_trees__cohort_18_ha*Average_crown_immature_tree_cohort_18__m2

Total_crown_immature_tree_cohort_19_m2 = Immature_trees__cohort_19_ha*Average_crown_immature_tree_cohort_19__m2

Total_crown_immature_tree_cohort_20_m2 = Immature_trees__cohort_20_ha*Average_crown_immature_tree_cohort_20__m2

Total_crown_immature_tree_cohort_21_m2 = Immature_trees__cohort_21_ha*Average_crown_immature_tree_cohort_21_m2

Total_crown_immature_tree_cohort_22_m2 = Immature_trees__cohort_22_ha*Average_crown_immature_tree_cohort_22_m2

Total_crown_immature_tree_cohort_23_m2 = Immature_trees__cohort_23_ha*Average_crown_immature_tree_cohort_23_m2

Immature_trees_cohort_4_fire_mortality_rate = fire*Random_immature_trees_cohort_4_fire_mortality_rate

Immature_trees_cohort_5_fire_mortality_rate = fire*Random_immature_trees_cohort_5_fire_mortality_rate

Immature_trees_cohort_6_fire_mortality_rate = fire*Random_immature_trees_cohort_6_fire_mortality_rate

Immature_trees_cohort_7_fire_mortality_rate = fire*Random_immature_trees_cohort_7_fire_mortality_rate

Immature_trees_cohort_8_fire_mortality_rate = fire*Random_immature_trees_cohort_8_fire_mortality_rate

Immature_trees_cohort_9_fire_mortality_rate = fire*Random_immature_trees_cohort_9_fire_mortality_rate

Immature_trees_cohort_10_fire_mortality_rate = fire*Random_immature_trees_cohort_10_fire_mortality_rate

Immature_trees_cohort_11_fire_mortality_rate = fire*Random_immature_trees_cohort_11_fire_mortality_rate

Immature_trees_cohort_12_fire_mortality_rate = fire*Random_immature_trees_cohort_12_fire_mortality_rate

Immature_trees_cohort_13_fire_mortality_rate = fire*Random_immature_trees_cohort_13_fire_mortality_rate

Immature_trees_cohort_14_fire_mortality_rate = fire*Random_immature_trees_cohort_14_fire_mortality_rate

Immature_trees_cohort_15_fire_mortality_rate = fire*Random_immature_trees_cohort_15_fire_mortality_rate

Immature_trees_cohort_16_fire_mortality_rate = fire*Random_immature_trees_cohort_16_fire_mortality_rate

Immature_trees_cohort_17_fire_mortality_rate = fire*Random_immature_trees_cohort_17_fire_mortality_rate

Immature_trees_cohort_18_fire_mortality_rate = fire*Random_immature_trees_cohort_18_mortality_rate

Immature_trees_cohort_19_fire_mortality_rate = fire*Random_immature_trees_cohort_19_mortality_rate

Immature_trees_cohort_20_fire_mortality_rate = fire*Random_immature_trees_cohort_20_mortality_rate

Immature_trees_cohort_21_fire_mortality_rate = fire*Random_immature_trees_cohort_21_mortality_rate

Immature_trees_cohort_22_fire_mortality_rate = fire*Random_immature_trees_cohort_22_mortality_rate

Immature_trees_cohort_23_fire_mortality_rat_1 = fire*Random_immature_trees_cohort_23_mortality_rate

Immature_trees = Immature_trees__cohort_4_ha+Immature_trees__cohort_5_ha+Immature_trees__cohort_6_ha+Immature_trees__cohort_7_ha+Immature_trees__cohort_8_ha+Immature_trees__cohort_9_ha+Immature_trees__cohort_10_ha+Immature_trees__cohort_11_ha+Immature_trees__cohort_12_ha+Immature_trees__cohort_13_ha+Immature_trees__cohort_14_ha+Immature_trees__cohort_15_ha+Immature_trees__cohort_16_ha+Immature_trees__cohort_17_ha+Immature_trees__cohort_18_ha+Immature_trees__cohort_19_ha+Immature_trees__cohort_20_ha+Immature_trees__cohort_21_ha+Immature_trees__cohort_22_ha+Immature_trees__cohort_23_ha

4.Adult trees

Capacity_adult_trees_m2 = Total_area_m2-Total_crown__adult_trees_m2

Average_crown_adult_tree_m2 = 0.0431*DBH_adult_tree_cm^1.6025

Max_potential_number_adult_trees = Capacity_adult_trees_m2/Average_crown_adult_tree_m2

Total_crown_adult_trees_m2 = Adut_trees_ha*Average_crown_adult_tree_m2

Yearly_adult_trees_decay_rate = (1+Adult_trees_decay_rate)^(1/period_adult_trees_decay)-1

RANDOM VARIABLES

Fires

Fire_intensity = Random (0,1)

Fire_probability = Round(Random (1,fire_frequency_value))

Random_immature_trees_cohort_4_fire_mortality_rate = Random(0.063154,0.080048)

Random_immature_trees_cohort_5_fire_mortality_rate = Random(0.063154,0.080048)

Random_immature_trees_cohort_6_fire_mortality_rate = Random(0.063154,0.080048)
Random_immature_trees_cohort_7_fire_mortality_rate = Random(0.063154,0.080048)
Random_immature_trees_cohort_8_fire_mortality_rate = Random(0.063154,0.080048)
Random_immature_trees_cohort_9_fire_mortality_rate = Random(0.063154,0.080048)
Random_immature_trees_cohort_10_fire_mortality_rate = Random(0.063154,0.080048)
Random_immature_trees_cohort_11_fire_mortality_rate = Random(0.063154,0.080048)
Random_immature_trees_cohort_11_fire_mortality_rate = Random(0.063154,0.080048)
Random_immature_trees_cohort_13_fire_mortality_rate = Random(0.063154,0.080048)
Random_immature_trees_cohort_14_fire_mortality_rate = Random(0.063154,0.080048)
Random_immature_trees_cohort_15_fire_mortality_rate = Random(0.063154,0.080048)
Random_immature_trees_cohort_16_fire_mortality_rate = Random(0.063154,0.080048)
Random_immature_trees_cohort_17_fire_mortality_rate = Random(0.063154,0.080048)
Random_immature_trees_cohort_18_fire_mortality_rate = Random(0.063154,0.080048)
Random_immature_trees_cohort_19_fire_mortality_rate = Random(0.063154,0.080048)
Random_immature_trees_cohort_20_fire_mortality_rate = Random(0.063154,0.080048)
Random_immature_trees_cohort_21_fire_mortality_rate = Random(0.063154,0.080048)
Random_immature_trees_cohort_22_fire_mortality_rate = Random(0.063154,0.080048)
Random_immature_trees_cohort_23_fire_mortality_rate = Random(0.063154,0.080048)
Random_adult_trees_fire_mortality_rate = Random(0.038214,0.04465)

Droughts

Seedlings_drought_intensity = Random(0,1)
Seedlings_drought_probability = Round(Random(1,Seedlings_drought_frequency_value))

Cork oak population dynamics

1.Seedlings

Random_acorns_per_tree = Random(1.32,33.6)
Random_acorns_germination_rate = Random(0.38,0.84)
Random_acorns_insect_damage_rate = Random(0.09,0.68)
Random_acorns_predation_rate = Random(0.36,0.83)
Random_seedlings_drought_mortality_rate = Random(0.679,0.701)
Random_seedlings_livestock__mortality_rate = Random (0.28,0.65)
Random_seedlings_shrub_clearing_mortality_rate = Random (0,1)

2. Saplings

Random_saplings_cohort_1_drought_mortality_rate = Random(0.679,0.701)
Random_saplings_cohort_2_drought_mortality_rate = Random(0.679,0.701)
Random_saplings_cohort_3_drought_mortality_rate = Random(0.679,0.701)
Random_saplings_cohort_1_livestock_mortality_rate = Random (0.57,0.87)
Random_saplings_cohort_2_livestock_mortality_rate = Random (0.57,0.87)
Random_saplings_cohort_3_livestock_mortality_rate = Random (0.57,0.87)
Random_saplings_cohort_1_shrub_clearing_mortality_rate = Random (0,1)
Random_saplings_cohort_2_shrub_clearing_mortality_rate = Random (0,1)
Random_saplings_cohort_3_shrub_clearing_mortality_rate = Random (0,1)

3.Immature trees

Random_immature_trees_cohort_4__death_rate = Random(0,0.0000092)
Random_immature_trees_cohort_5__death_rate = Random(0,0.0000092)
Random_immature_trees_cohort_6__death_rate = Random(0,0.0000092)
Random_immature_trees_cohort_7__death_rate = Random(0,0.0000092)
Random_immature_trees_cohort_8__death_rate = Random(0,0.0000092)
Random_immature_trees_cohort_9_death_rate = Random(0,0.0000092)

Random_immature_trees_cohort_10_death_rate = Random(0,0.0000092)
Random_immature_trees_cohort_11_death_rate = Random(0,0.0000092)
Random_immature_trees_cohort_12_death_rate = Random(0,0.0000092)
Random_immature_trees_cohort_13_death_rate = Random(0,0.0000092)
Random_immature_trees_cohort_14_death_rate = Random(0,0.0000092)
Random_immature_trees_cohort_15_death_rate = Random(0,0.0000092)
Random_immature_trees_cohort_16_death_rate = Random(0,0.0000092)
Random_immature_trees_cohort_17_death_rate = Random(0,0.0000092)
Random_immature_trees_cohort_18_death_rate = Random(0,0.0000092)
Random_immature_trees_cohort_19_death_rate = Random(0,0.0000092)
Random_immature_trees_cohort_20_death_rate = Random(0,0.0000092)
Random_immature_trees_cohort_21_death_rate = Random(0,0.0000092)
Random_immature_trees_cohort_22_death_rate = Random(0,0.0000092)
Random_immature_trees_cohort_23_death_rate = Random(0,0.0000092)*Competition_converter

4.Adult trees

Random_adult_trees__death_rate = Random(0,0.0000092)

Economic balances

Random_cork_production_per_tree_kg = Random(35.95534,69.56406)
Random_income_from_cork_per_tree_euros_kg = Random(1.33,3.33)

CONSTANTS

Fires

Fire_option = 1
Fire_frequency_value = 40
Average_seedlings_fire_mortality_rate = 0.000805
Average_saplings_fire_mortality_rate = 0.000805

Droughts

Seedlings_drought_frequency_value = 3

Land use management

Livestock_periodicity = 1
Effective_livestock_periodicity = Counter(0,Livestock_periodicity)
Shrub_clearing_option = 1
Periodicity_shrub_clearing = 5
Effective_shrub_clearing_periodicity = Counter(0,periodicity_shrub_clearing)
Cork_extraction_option=1
Periodicity_cork_oak_extraction = 9
Effective_cork_extraction = Counter (0,periodicity_cork_oak_extraction)

Cork oak population dynamics

Total_area_m2 = 10000

1.Seedlings

Average_seedlings_resprouting_rate = 0.239

2.Saplings

DBH_saplings_cohort_1_cm = 3
DBH_saplings_cohort_2_cm = 6
DBH_saplings_cohort_3_cm = 9

3.Immature trees

DBH__immature_trees_cohort_4_cm = 10
DBH__immature_trees_cohort_5_cm = 10.5
DBH__immature_trees_cohort_6_cm = 11

DBH__immature_trees_cohort_7_cm = 11.5
DBH__immature_trees_cohort_8_cm = 12
DBH__immature_trees_cohort_9_cm = 12.5
DBH__immature_trees_cohort_10_cm = 13
DBH__immature_trees_cohort_11_cm = 13.5
DBH__immature_trees_cohort_12_cm = 14
DBH__immature_trees_cohort_13_cm = 14.5
DBH__immature_trees_cohort_14_cm = 15
DBH__immature_trees_cohort_15_cm = 16
DBH__immature_trees_cohort_16_cm = 17
DBH__immature_trees_cohort_17_cm = 18
DBH__immature_trees_cohort_18_cm = 19
DBH__immature_trees_cohort_19_cm = 20
DBH__immature_trees_cohort_20_cm = 21
DBH__immature_trees_cohort_21_cm = 22
DBH__immature_trees_cohort_22_cm = 23
DBH__immature_trees_cohort_23_cm = 24

4. Adult trees

DBH_adult_tree_cm = 89
Adult_trees_per_ha = 50
Period_adult_trees_decay = 200
Adult_trees_decay_rate = 1

Economic balances

Cork_oak_extraction_option = 1
Average_shrub_clearing_cost_euros_per_ha = 120
Average_revenue_from_livestock_euros_per_ha = 22.4
Average_stripping_cost_cork_extraction_euros_per_kg = 0.23

Appendix IV – Cork oak population dynamics and economic incomes.

CORK OAK POPULATION DYNAMICS AND ECONOMIC INCOMES FROM MANAGEMENT

A) PURPOSE

The sub-model was designed to simulate the cork oak population dynamics, based on the species reproductive biology and mechanisms regulating their intrinsic dynamics (Figure 1, 2, 3, 4, 5 and 6). Additionally, a sub-model concerning the economic incomes from the *montados* management was also considered (Figure 29).

B) STRUTURE AND FUNTIONING

1. FIRES
2. DROUGHTS
3. LAND USE MANAGEMENT
4. CORK OAK POPULATION DYNAMICS
5. CORK OAK POPULATION DYNAMICS METRICS
6. ECONOMIC BALANCES

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1. FIRE

Fire events were included in the model as stochastic occurrences, in order to simulate fire regimes that represent typical phenomenon shaping the landscape in the region (magrama.gob.es).

Modelling elements

• *Fire* (Figure 1 and Table 7 – "Composed variables")

1.1. Fire occurrence

Fire events were simulated by generating random probabilities of fire occurrence. After the calibration procedures, the average number of 0.013 ± 0.017 fires.ha-1 (mean ± standard deviation) obtained per study unit in 44 years, from 100 independent stochastic simulations, was considered a reliable reproduction of the regional historical trends of fire events (0.016 ± 0.021 fires.ha-1) (magrama.gob.es).

Modelling elements

- *Fire occurrence* (Figure 1 and Table 7 – "Composed variables")
- *Fire probability* (Figure 1 and Table 7 – "Random variables")
- *Fire frequency value* (Figure 1 and Table 7 – "Constant")

1.2. *Fire intensity*

The overall possible range concerning the percentage of area liable to be burnt was considered (i.e. from 0% to 100%), assuming that the correspondent area being modelled (i.e. 1ha) is prone to be burned totally.

Modelling elements

- *Fire intensity* (Figure 1 and Table 7 – "Random variables")

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2. DROUGHT

Drought events were included in the model as stochastic occurrences, in order to recreate droughts regimes that are typical phenomenon in the region (INAG 2007).

Modelling elements

- *Drought* (Figure 1 and Table 7 – "Composed variables")

2.1. *Drought probability*

Drought events were simulated by generating random probabilities of drought occurrence. After the calibration procedures, the average number of 0.24 ± 0.078 droughts.ha^{-1} (mean ± standard deviation) obtained per study unit in 31 years, from 100 independent stochastic simulations, was considered a reliable reproduction of the regional historical trends of drought events (0.24 ± 0.43 droughts.ha-1) (INAG 2007).

Modelling elements

- *Drought occurrence* (Figure 1 and Table 7 – “Composed variables”)
- *Drought probability* (Figure 1 and Table 7 – “Random variables”)
- *Drought frequency value* (Figure 1 and Table 7 – “Constant”)

2.2. *Drought intensity*

The overall possible range concerning the intensity of droughts was considered (i.e. from 0% to 100%), assuming that the correspondent area being modelled (i.e. 1ha) is prone to totally be affected by droughts.

Modelling elements

- *Drought intensity* (Figure 1 and Table 7 – “Random variables”)

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3. LAND USE MANAGEMENT

Several abiotic factors related with land use management were considered to have influence on the cork oak regeneration cycle, including livestock and shrub clearing.

Modelling elements

- *Livestock option* (Figure 1 and Table 7 – “Constants”)
- *Shrub clearing option* (Figure 1 and Table 7 – “Constants”)

3.1. Livestock

The Livestock option was included in the model in order to simulate the presence of livestock in *montados*, which is a common practice that damage young trees, compact soil and decrease both water infiltration and biodiversity (Plieninger et *al.* 2004, Plieninger 2006).

Modelling elements

- *Livestock periodicity* (Figure 1 and Table 7 – “Constants”)
- *Effective livestock periodicity* (Figure 1 and Table 7 – “Constants”)
- *Effective livestock* (Figure 1 and Table 7 – “Composed variables”)

3.1.1. *Livestock Periodicity*

Since livestock might be yearly present in a *montado*, especially when there is scarcity of forage and animals are feed with fodder concentrates, hay and straw, the livestock periodicity was assumed to possibly start in 1 (i.e. yearly livestock presence) (Blanco et *al.* 1997, Plieninger et *al.* 2004).

3.2. Shrub clearing

The shrub clearing option was included in the model in order to simulate a common non-selective mechanical practice in *montados*, used to control shrub invasion, promote pasture production and to prevent against fires (Arosa et *al.* 2015).

Modelling elements

- *Shrub clearing periodicity* (Figure 1 and Table 7 – “Constants”)
- *Effective shrub clearing periodicity* (Figure 1 and Table 7 – “Constants”)
- *Effective shrub clearing* (Figure 1 and Table 7 – “Composed variables”))

3.2.1. *Shrub clearing periodicity*

Since shrub clearing might be yearly implemented in *montados* to control shrub invasion, promote pasture production and to prevent fires spreading (Pignatti 1983, Pulido et *al.* 2001, 2005, Calvo et *al.* 2005), the shrub clearing periodicity was assumed, based on expert knowledge, to range from 1 (yearly) to every 5 years.

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4. CORK OAK POPULATION DYNAMICS

To model the cork oak natural regeneration where new individuals are recruited into the mature population compensating population losses due to mortality, four phases of the species' life-cycle were considered: seedlings, saplings, immature trees and adult trees. The cork oak population dynamics were based on cork oak age stratification (seedlings, saplings, immature trees and adult trees), represented by the sum of different life stage cohorts, expressed in densities (number of individuals per hectare).

STATE VARIABLES:

4.1.SEEDLINGS: (*Seedlings ha*) (Figure 24 and Table 7 – "Difference equations")
4.2.SAPLINGS: (*Saplings cohort x ha*) (Figure 25 and Table 7 – "Difference equations")
4.3.IMMATURE TREES: (*Immature trees cohort x ha*) (Figure 26 and Table 7 – "Difference equations")
4.4.ADULT TREES: (*Adult trees ha*) (Figure 27 and Table 7 – "Difference equations")

4.1.SEEDLINGS

The dynamics of seedlings result from the balance between the successfully germinated acorns and the mortality of seedlings.

PROCESSES

4.1.1. ACORN GERMINATION
Germination (Figure 24 and Table 7 – "Process equations")
4.1.2. DROUGHT MORTALITY
Seedling drought mortality (Figure 24 and Table 7 – "Process equations")
4.1.3. SEEDLING RESPORUTING
Seedlings resprouting (Figure 24 and Table 7 – "Process equations")
4.1.4. FIRE MORTALITY
Seedlings fire mortality (Figure 24 and Table 7 – "Process equations")
4.1.5. LIVESTOCK MORTALITY
Seedlings livestock mortality (Figure 24 and Table 7 – "Process equations")
4.1.6. SHRUB CLEARING MORTALITY
Seedlings shrub clearing mortality (Figure 24 and Table 7 – "Process equations")
4.1.7. SEEDLING MATURATION
Seedlings maturation (Figure 24 and Table 7 – "Process equations")

4.1.1. ACORN GERMINATION

Acorns developing to the seedlings stage. Since the germination of acorns is limited by biotic factors related with predation and insect damage, the effective number of acorns that enter the system is dependent on the acorns predation survival rate and the quantity of acorns that remain undamaged by insects. Furthermore, acorns that do not germinate remaining in the understory were assumed to dry out before the beginning of a new year.

Modelling elements

- *Acorns survival rate* (Figure 24 and Table 7 – "Composed variables")
- *Random acorns germination rate* (Figure 24 and Table 7 – "Random variables")

4.1.1.1. *Acorns survival rate*

The acorns survival rate is determined by the proportion of acorns that effectively germinates, taking into account losses by predation and damage by insects.

Modelling elements

- *Acorns per ha* (Figure 24 and Table 7 – "Composed variables")
- *Acorns insect damage survival rate* (Figure 24 and Table 7 – "Constants")
- *Acorns predation survival rate* (Figure 24 and Table 7 – "Constants")

Acorns insect damage survival rate

The acorns survival rate from insects damage is determined by the proportion of acorns expected to be undamaged by insects per year of simulation, ranging from (1-0.91) to (1-0.22) (Branco et *al.* 2002).

Modelling elements

- *Random acorns insect damage rate* (Figure 24 and Table 7 – “Random variables”)

Acorns predation survival rate

The acorns predation survival rate is determined by the proportion of acorns expected to keep viable from predation per year of simulation, ranging from (1-0.64) to (1-0.17) (Branco et *al.* 2002).

Modelling elements

- *Random acorns predation rate* (Figure 24 and Table 7 – “Random variables”)

4.1.1.2. Random acorns *germination rate*

The acorns germination rate is determined by the proportion of acorns expected to successfully germinate per year of simulation, ranging from 0.38 to 0.84 (Branco et *al.* 2002).

4.1.2. DROUGHT MORTALITY

Seedlings drying out due to droughts. Since droughts affect the survival of seedlings due to a poorer plant water status, photoinhibition and overheating (Valladares 2003), mortality from drought was taken into account.

Modelling elements

- *Seedlings drought mortality rate* (Figure 24 and Table 7 – “Composed variables”)

4.1.2.1. *Seedlings drought mortality rate*

Whenever a drought is generated, the seedlings drought mortality rate is determined by the proportion of seedlings expected to die due to droughts per year of simulation, ranging from 0.68 to 0.70 (Arosa et *al.* 2015), influenced by the generated drought intensity.

- *Drought* (Figure 24 and Table 7 – “Composed variables”)
- *Random seedlings drought mortality rate* (Figure 24 and Table 7 – “Random variables”)

4.1.3. SEEDLING RESPROUTING

Seedlings resprouting from droughts. Since cork oak trees survive to droughts due to their extensive and deep root system, and in some cases because the trees may shed its leaves and resprout when the drought is over (Acácio 2007, Gómez-Aparicio et *al.* 2008, Arosa et *al.* 2015), seedling resprouting from drought were taken into account.

Modelling elements

- *Average seedlings resprouting rate* (Figure 24 and Table 7 – “Constants”)
- *Seedlings drought mortality* (Figure 24 and Table 7 – “Process equations”)

4.1.3.1. Average *seedlings resprouting rate*

The seedlings resprouting rate is given by the proportion of seedlings expected to resprout after droughts per year of simulation (Arosa et *al.* 2015).

4.1.4. FIRE MORTALITY

Seedlings mortality due to fire. Since fires affect the survival of seedlings due to direct mortality and also, indirectly, the availability of below-ground carbohydrate reserves that facilitate resprouting (Moreira et al. 2009), seedlings mortality from fire was taken into account.

Modelling elements

- *Seedlings fire mortality rate* (Figure 24 and Table 7 – “Composed variable”)

4.1.4.1. *Seedlings fire mortality rate*

Whenever a fire is generated, the seedlings fire mortality rate is determined by the proportion of seedlings expected to die due to fire per year of simulation (Catry et *al.* 2012), influenced by the generated fire intensity.

Modelling elements

- *Fire* (Figure 24 and Table 7 – "Composed variables variables")
- *Average seedlings fire mortality rate* (Figure 24 and Table 7 – "Constants")

4.1.5. LIVESTOCK MORTALITY

Seedlings mortality due to livestock grazing. Since the presence of livestock affects the survival of saplings due to stem consumption (Plieniger et *al.* 2004), mortality from livestock grazing was taken into account.

Modelling elements

- *Seedlings livestock mortality rate* (Figure 24 and Table 7 – "Composed variables")

4.1.5.1. *Seedlings livestock mortality rate*

The seedlings livestock mortality rate is determined by the proportion of seedlings expected to die due to livestock grazing per year of simulation, ranging from 0.28 to 0.65 (Plieninger et *al.* 2004).

Modelling elements

- *Effective livestock* (Figure 24 and Table 7 – "Constants")
- *Random seedlings livestock mortality rate* (Figure 24 and Table 7 – "Random variables")

4.1.6. SHRUB CLEARING MORTALITY

Seedlings mortality due to management practices. Since heavy machinery affects the survival of seedlings due to stem cutting (Arosa et *al.* 2015), mortality from shrub clearing was taken into account.

Modelling elements

- *Seedlings shrub clearing mortality rate* (Figure 24 and Table 7 – "Constants")

4.1.6.1. *Seedlings shrub clearing mortality rate*

The seedlings shrub clearing mortality rate is determined by the proportion of seedlings expected to die due to shrub clearing per year of simulation, ranging from 0 and 1 (Arosa et *al.* 2015).

Modelling elements

- *Effective shrub clearing* (Figure 24 and Table 7 – "Constants")
- *Random seedlings shrub clearing mortality rate* (Figure 24 and Table 7 – "Random variables")

4.1.7. SEEDLING MATURATION

Seedlings developing to the saplings stage. At the end of the first year, the successfully developed seedling individuals are able to transit to saplings (Pulido et *al.* 2013).

Modelling elements

- *Seedling shrub clearing mortality* (Figure 24 and Table 7 – "Process equations")
- *Seedlings drought mortality* (Figure 24 and Table 7 – "Process equations")
- *Seedlings fire mortality* (Figure 24 and Table 7 – "Process equations")
- *Seedlings livestock mortality* (Figure 24 and Table 7 – "Process equations")

4.2.SAPLINGS

The dynamics of saplings result from the balance between the successfully maturated seedlings and the mortality of saplings. Sapling stage was assumed to take three years before individuals reach immature trees stage (Pulido et *al.* 2013). The processes included in the saplings dynamics were replicated for each cohort of individuals (i.e. from cohort 1 to cohort 3).

PROCESSES

4.2.1. SAPLINGS EMANCIPATION
Seedlings emancipation (Figure 25 and Table 7 – “Process equations”)
Saplings cohort x emancipation (Figure 25 and Table 7 – “Process equations”)
4.2.2. DROUGHT MORTALITY
Saplings cohort x drought mortality (Figure 25 and Table 7 – “Process equations”)
4.2.3. FIRE MORTALITY
Saplings cohort x fire mortality (Figure 25 and Table 7 – “Process equations”)
4.2.4. LIVESTOCK MORTALITY
Saplings cohort x livestock mortality (Figure 25 and Table 7 – “Process equations”)
4.2.5. SHRUB CLEARING MORTALITY
Saplings cohort x shrub clearing mortality (Figure 25 and Table 7 – “Process equations”)
4.2.6. SAPLINGS MATURATION
Saplings cohort x maturation (Figure 25 and Table 7 – “Process equations”)

4.2.1. SAPLINGS EMANCIPATION

Seedlings developing to the stage of saplings, including developing of saplings between cohorts of individuals. Since the density of individuals is limited due to resources availability (Oliveira et *al.* 1994), competition between sapling individuals was included in the saplings maturation between cohort of individuals.

Modelling elements

- *Seedlings maturation* (Figure 25 and Table 7 – “Process equations”) or *Saplings cohort x maturation* (Figure 25 and Table 7 – “Process equations”)
- *Max potential number saplings cohort x* (Figure 25 and Table 7 – “Composed variables”)

4.2.1.1. *Max potential number saplings cohort x*

The effective number of new potential individuals, taking into account space availability.

Modelling elements

- *Average crown saplings cohort x m2* (Figure 25 and Table 7 – “Composed variables”)
- *Capacity cohort x saplings m2* (Figure 25 and Table 7 – “Composed variables”)

Average crown saplings cohort x m2

The saplings average crown area in m2, calculated by:
y = 0.0431•x1.6025 (x is DBH in cm) (Natividade 1950, Marín-Pageo & Camacho 2011).

Modelling elements

- *DBH saplings cohort x cm* (Figure 25 and Table 7 – “Constants”)

DBH saplings cohort x cm

The average diameter at breast height of saplings, assumed as 6 cm (Pulido et *al.* 2013).

Capacity cohort x saplings m2

Area available for regeneration of new individuals, taking into account the total area occupied by the already established individuals (in crown area).

Modelling elements

- *Total area m2* (Figure 25 and Table 7 – “Composed variables”)
- *Total crown saplings cohort x m2* (Figure 25 and Table 7 – “Composed variables”)

Total area m2

Total area being modeled (1ha = 10 000 m2).

Total crown saplings cohort x m2

The total area occupied by saplings (in crown area), taking into account the effective number of individuals established in the system.

Modelling elements

- *Saplings ha* (Figure 25 and Table 7 – "Difference equations")
- *Average crown saplings cohort x m2* (Figure 25 and Table 7 – "Composed variables")

4.2.2. DROUGHT MORTALITY

Saplings drying out due to droughts. Since droughts affect the survival of saplings due to a poorer plant water status, photoinhibition and overheating (Valladares 2003), mortality from drought was taken into account.

Modelling elements

- *Saplings cohort x drought mortality rate* (Figure 25 and Table 7 – "Composed variables")

4.1.2.1. *Saplings cohort x drought mortality rate*

Whenever a drought is generated, the saplings drought mortality rate is determined by the proportion of saplings expected to die due to droughts per year of simulation, ranging from 0.68 to 0.70 (Arosa et *al.* 2015), influenced by the generated drought intensity.

- *Drought* (Figure 24 and Table 7 – "Composed variables")
- *Random saplings cohort x drought mortality rate* (Figure 24 and Table 7 – "Random variables")

4.2.3. FIRE MORTALITY

Saplings mortality due to fire. Since fires affect the survival of seedlings due to direct mortality and also, indirectly, the availability of below-ground carbohydrate reserves that facilitate resprouting (Moreira et *al.* 2009), mortality from fires was taken into account.

Modelling elements

- *Saplings cohort x fire mortality rate* (Figure 25 and Table 7 – "Composed variable")

4.2.4.1. *Saplings cohort x fire mortality rate*

Whenever a fire is generated, the saplings fire mortality rate is determined by the proportion of saplings expected to die due to fire per year of simulation (Catry et al 2012), influenced by the generated fire intensity.

Modelling elements

- *Fire* (Figure 25 and Table 7 – "Composed variables variables")
- *Average saplings fire mortality rate* (Figure 25 and Table 7 – "Constants")

4.2.4. LIVESTOCK MORTALITY

Saplings mortality due to livestock grazing. Since the presence of livestock affects the survival of saplings due to stem consumption (Plieninger et *al.* 2004), mortality from livestock grazing was taken into account.

Modelling elements

- *Saplings cohort x livestock mortality rate* (Figure 25 and Table 7 – "Composed variable")

4.2.5.1. *Saplings cohort x livestock mortality rate*

The saplings livestock mortality rate is determined by the proportion of saplings expected to die due livestock grazing per year of simulation, ranging from 0.57 to 0.87 (Plieninger *et al.* 2004).

Modelling elements

- *Effective livestock* (Figure 25 and Table 7 – “Constants”)
- *Random saplings cohort x livestock mortality rate* (Figure 25 and Table 7 – “Random varables”)

4.2.5. SHRUB CLEARING MORTALITY

Saplings mortality due to management practices. Since heavy machinery affects the survival of saplings due to stem cutting (Arosa et *al.* 2015), mortality from shrub clearing was taken into account.

Modelling elements

- *Saplings cohort x shrub clearing mortality rate* (Figure 25 and Table 7 – “Composed variable”)

4.2.5.1. *Saplings cohort x shrub clearing mortality rate*

The saplings shrub clearing mortality rate is determined by the proportion of saplings expected to die due to shrub clearing per year of simulation, ranging from 0 to 1 (Arosa et *al.* 2015).

Modelling elements

- *Effective shrub clearing* (Figure 25 and Table 7 – “Constants”)
- *Random saplings cohort x shrub clearing mortality rate* (Figure 25 and Table 7 – “Random variables”)

4.2.6. SAPLINGS MATURATION

Developing of saplings between cohorts of individuals. At the end of the third year, the successfully developed sapling individuals are able to transit to immature trees (Pulido et *al.* 2013).

Modelling elements

- *Saplings cohort x shrub clearing mortality* (Figure 25 and Table 7 – “Process equations”)
- *Saplings cohort x drought mortality* (Figure 25 and Table 7 – “Process equations”)
- *Saplings cohort x fire mortality* (Figure 25 and Table 7 – “Process equations”)
- *Saplings cohort x livestock mortality* (Figure 25 and Table 7 – “Process equations”)

4.3.IMMATURE TREES

The dynamics of immature trees result from the balance between the successfully maturated saplings and the mortality of immature trees. Immature trees stage was assumed to take twenty years before individuals reach adult trees stage (Pulido et *al.* 2013). The processes included in the immature trees dynamics were replicated for each cohort of individuals (i.e. from cohort 4 to cohort 23).

PROCESSES

4.3.1. IMMATURE TREES EMANCIPATION
Saplings cohort 3 emancipation (Figure 26 and Table 7 – “Process equations”)
Immature trees cohort x emancipation (Figure 26 and Table 7 – “Process equations”)
4.3.2. FIRE MORTALITY
Immature trees cohort x fire mortality (Figure 26 and Table 7 – “Process equations”)
4.3.3. DEATH
Immature trees cohort x death (Figure 26 and Table 7 – “Process equations”)
4.3.4. IMMATURE TREES MATURATION
Immature trees cohort x maturation (Figure 26 and Table 7 – “Process equations”)

4.3.1. IMMATURE TREES EMANCIPATION

Saplings developing to the stage of immature trees, including developing of immature trees between cohorts of individuals. Since the density of individuals is limited due to resources availability (Oliveira et *al.* 1994), competition between immature trees was included in the saplings maturation between cohort of individuals.

Modelling elements

- *Saplings cohort 3 maturation* (Figure 26 and Table 7 – “Process equations)
- *Immature trees cohort x maturation* (Figure 26 and Table 7 – “Process equations”)

- *Max potential number immature trees cohort x* (Figure 26 and Table 7 – “Composed variables”)

4.2.1.1. *Max potential number immature trees cohort x*

The effective number of new potential immature individuals, taking into account space availability.

<u>Modelling elements</u>

- *Average crown immature trees cohort x m2* (Figure 26 and Table 7 – “Composed variables”)
- *Capacity immature trees cohort x m2* (Figure 26 and Table 7 – “Composed variables”)

Average crown immature trees cohort x m2

The immature trees average crown area in m2, calculated by:
y = 0.0431•x1.6025 (x is DBH in cm) (Natividade 1950, Marín-Pageo & Camacho 2011).

<u>Modelling elements</u>

- *DBH immature trees cohort x cm* (Figure 26 and Table 7 – “Constants”)

DBH immature trees cohort x cm

The average diameter at breast height of immature trees, assumed as 17.5 cm (Pulido et *al.* 2013)

Capacity immature trees cohort x m2

Area available for regeneration of new individuals, taking into account the total area occupied by established immature individuals (in crown area).

<u>Modelling elements</u>

- *Total area m2* (Figure 26 and Table 7 – “Composed variables”)
- *Total crown immature trees cohort x m2* (Figure 26 and Table 7 – “Composed variables”)

Total area m2

Total area being modeled (1ha = 10 000 m2).

Total crown immature trees cohort x m2

The total area occupied by immature trees (in crown area), taking into account he effective number of individuals established in the system.

<u>Modelling elements</u>

- *Immature trees cohort x ha* (Figure 26 and Table 7 – “Composed variables”)
- *Average crown immature trees cohort x m2* (Figure 26 and Table 7 – “Composed variables”)

4.3.2. FIRE MORTALITY

Immature trees mortality due to fire. Since fires affect the survival of immature trees due to tree height, tree health and bark thickness (Moreira et *al.* 2007), mortality from fires was taken into account.

<u>Modelling elements</u>

- *Immature trees cohort x fire mortality rate* (Figure 26 and Table 7 – “Composed variable”)

4.3.4.1. *Immature trees cohort x fire mortality rate*

Whenever a fire is generated, the immature trees fire mortality rate is determined by the proportion of immature trees expected to die due to fire per year of simulation, ranging from 0.063 to 0.080 (Catry et *al.* 2012), influenced by the generated fire intensity.

<u>Modelling elements</u>

- *Fire* (Figure 26 and Table 7 – “Constants”)
- *Random immature trees cohort x fire mortality rate* (Figure 26 and Table 7 – “Random variables”)

4.3.3. IMMATURE TREES DEATH

Mortality of immature trees. The mortality of immature trees cohort 23 is influenced by the density of adult trees present in the system.

Modelling elements

- *Random immature trees cohort x death rate* (Figure 26 and Table 7 – “Random variables”)
- *Competition converter* (Figure 26 and Table 7 – “Constants”)

4.3.3.1. *Random immature trees cohort x death rate*

The immature trees death rate is determined by the proportion of immature trees expected to die per year of simulation, ranging from 0 to 0.0000092 (Ribeiro and Surový 2008). This rate include multiple factors influencing immature trees survival, such as mortality by insects damage, diseases, management or climate (Franklin et *al.* 1987, Branco et *al.* 2002, Camilo-Alves et *al.* 2013).

4.3.3.2. *Competition converter*

The competition converter determines an intensification in the immature trees cohort 23 death rate depending on the increasing density of adult trees in the system, assuming an average maximum potential of 174.3 adult trees per hectare (Natividade 1950, Marín-Pageo & Camacho 2011, Pulido et al., 2013).

4.3.4. IMMATURE TREES MATURATION

Developing of immature trees between cohorts of individuals. At the end of the twentieth year, the successfully developed immature trees are able to transit to adult trees (Pulido et *al.* 2013) , taking into account the average maximum potential of 174.3 adult trees per hectare (Natividade 1950, Marín-Pageo & Camacho 2011, Pulido et al., 2013).

Modelling elements

- *Immature trees cohort x death* (Figure 26 and Table 7 – “Process equations”)
- *Immature trees cohort x fire mortality* (Figure 26 and Table 7 – “Process equations”)
- *Max potential number adult trees* (Figure 26 and Table 7 – “Composed variables”)

4.4. ADULT TREES

The dynamics of mature trees result from the balance between the successfully immature trees maturation and the mortality of adult trees.

PROCESSES

4.4.1. ADULT TREES EMANCIPATION
Immature trees cohort 23 emancipation (Figure 27 and Table 7 – “Process equations”)
4.4.2. ADULT TREES FIRE MORTALITY
Adult trees fire mortality (Figure 27 and Table 7 – “Process equations”)
4.4.3. ADULT TREES MORTALITY
Adult trees death (Figure 27 and Table 7 – “Process equations”)
4.4.4. ADULT TREES DECAY
Adult trees decay (Figure 27 and Table 7 – “Process equations”)

4.4.1. ADULT TREES EMANCIPATION

Developing of immature trees to adult stage. Since the density of adult individuals is limited due to resources availability (Oliveira et al. 1994), competition between individuals was included in the immature trees emancipation to reach adult stage.

Modelling elements

- *Immature trees cohort 23 maturation* (Figure 27 and Table 7 – “Process equations)
- *Max potential number adult trees* (Figure 27 and Table 7 – “Constants”)

4.2.1.1. *Max potential number adult trees*

The effective number of new potential individuals, taking into account space availability.

<u>Modelling elements</u>

- *Average crown adult trees m2* (Figure 27 and Table 7 – “Composed variables”)
- *Capacity adult trees m2* (Figure 27 and Table 7 – “Composed variables”)

Average crown adult trees m2

The adult trees average crown area in m2, calculated by:
$y = 0.0431 \bullet x1.6025$ (x is DBH in cm) (Natividade 1950, Marín-Pageo & Camacho 2011).

<u>Modelling elements</u>

- *DBH adult trees cm* (Figure 27 and Table 7 – “Constants”)

DBH adult trees cm

The average diameter at breast height of adult individuals, assumed as 57 cm (Pulido et *al.* 2013).

Capacity adult trees m2

Area available for regeneration of new individuals, taking into account the total area occupied by established adult individuals (in crown area).

<u>Modelling elements</u>

- *Total area m2* (Figure 27 and Table 7 – “Composed variables”)
- *Total crown adult trees m2* (Figure 27 and Table 7 – “Composed variables”)

Total area m2

Total area being modeled (1ha = 10 000 m2).

Total crown adult trees m2

The total area occupied by adult trees (in crown area), taking into account he effective number of individuals established in the system.

<u>Modelling elements</u>

- *Adult trees ha* (Figure 27 and Table 7 – “Composed variables”)
- *Average crown adult trees m2* (Figure 27 and Table 7 – “Composed variables”)

4.4.2. FIRE MORTALITY

Adult trees mortality due to fire. Since fires affect the survival of adult trees due to tree height, tree health and bark thickness (Moreira et *al.* 2007), mortality from fires was taken into account.

<u>Modelling elements</u>

- *Adult trees fire mortality rate* (Figure 27 and Table 7 – “Composed variable”)

4.4.4.1. *Adult trees fire mortality rate*

Whenever a fire is generated, the adult trees fire mortality rate is determined by the proportion of adult trees expected to die due to fire per year of simulation, ranging from 0.038 to 0.045 (Catry et *al.* 2012), influenced by the generated fire intensity.

<u>Modelling elements</u>

- *Fire* (Figure 27 and Table 7 – “Composed variables variables”)

- *Random adult trees fire mortality rate* (Figure 27 and Table 7 – “Random variables”)

4.4.3. ADULT TREES MORTALITY

Mortality of adult trees.

Modelling elements

- *Random adult trees death rate* (Figure 27 and Table 7 – “Random variables”)

4.4.3.1. Random *adult trees death rate*

The adult trees death rate is determined by the proportion of adult trees expected to die per year of simulation, ranging from 0 to 0.0000092 (Ribeiro and Surový 2008). This rate include multiple factors influencing cork oak adult trees survival, such as mortality by insects damage, diseases, management or climate (Franklin et al. 1987, Branco et al. 2002, Camilo-Alves et *al.* 2013).

4.4.4. ADULT TREES DECAY

Adult trees decaying due to age.

Modelling elements

- *Adult trees decay* (Figure 27 and Table 7 – “Composed variables”)

4.4.4.1. *Adult trees decay*

The proportion of adult individuals that leave the system due to age decay per year of simulation.

Modelling elements

- *Period adult trees decay* (Figure 27 and Table 7 – “Constants”)
- *Adult trees decay rate* (Figure 27 and Table 7 – “Constants”)

Period adult trees decay

The period assumed to incorporate the maximum trees decay, assuming 200 years as the species life span (Montero & Canellas 2003).

Adult trees decay rate

The maximum trees decay.

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5. CORK OAK POPULATION DYNAMICS METRICS

5.1. SAPLINGS
Saplings cohort x ha (Figure 28 and Table 7 – “Difference equations”)
5.2. IMMATURE TREES
Immature trees cohort x ha (Figure 28 and Table 7 – “Difference equations”)
5.3. ACORNS
Acorns ha (Figure 28 and Table 7 – “Composed variables”)

5.1. SAPLINGS

Total number of saplings per hectare.

Modelling elements

Saplings cohort x ha (Figure 28 and Table 7 – “Difference equations”)

5.2. IMMATURE TREES

Total number of immature trees per hectare.

Modelling elements

Immature trees cohort x ha (Figure 28 and Table 7 – “Difference equations”)

5.3. ACORNS

Total number of acorns per hectare.

Modelling elements

Adult trees ha (Figure 28 and Table 7 – “Difference equations”)
Random acorns per tree (Figure 28 and Table 7 – “Random variables”)

5.3.1. Random *acorns per tree*

The density of acorns is determined by the average kg of acorns produced per cork oak tree, ranging from 1.32 to 33.6 kg of acorns per tree (Canellas et *al.* 2007, Pérez- Ramos and Marañón 2008).

6. ECONOMIC BALANCES

Economic incomes from *montado*. This sub-model takes into account the financial balance between revenues from livestock and cork production and costs associated with soil management and stripping of cork oak extraction.

PROCESSES

6.1. GAINS
Gains (Figure 30 and Table 7 – “Process equations”)
6.2. LOSSES
Losses (Figure 30and Table 7 – “Process equations”)

6.1. GAINS

Incomes from livestock production and cork production.

Modelling elements

- *Revenue from livestock euros per ha* (Figure 30 and Table 7 – “Composed variables”)
- *Income cork extraction euros per ha* (Figure 30 and Table 7 – “Composed variables”)

6.1.1. *Revenue from livestock euros per ha*

Since the livestock presence is common in *montados*, representing financial profits in terms of food (black pigs, cattle, merino sheep and goats) and direct payments to farmers enrolled under the Common Agricultural Policy (CAP) (Pinheiro et *al.* 2008), the effective revenue from livestock was taken into account.

Modelling elements

- *Effective livestock* (Figure 30 and Table 7 – “Composed variables”)
- *Average revenue from livestock euros per ha* (Figure 30 and Table 7 – “Constant”)

6.1.1.1. *Average revenue from livestock euros per ha*

Benefits, in euros per hectare, obtained by the presence of livestock (Pinheiro et *al.* 2008)

6.1.2. *Income cork extraction euros per ha*

Since the cork has the largest economic impact in *montados*, representing financial profits in terms of cork oak management (Pinheiro et *al.* 2008), the income from cork oak extraction in *montado* was taken into account.

Modelling elements

- *Cork oak extraction option* (Figure 30 and Table 7 – “Constants”)
- *Effective cork extraction* (Figure 30 and Table 7 – “Composed variables”)
- *Random cork production per tree kg* (Figure 30 and Table 7 – “Random variables”)
- *Random income from cork per tree euros kg* (Figure 30 and Table 7 – “Random variables”)

6.1.2.1. *Effective cork extraction*

Since cork extraction is a common practice implemented in *montados* every 9 years, a 9 years cyclic periodicity was taken into account (Pereira and Tomé 2004, Pinheiro et *al.* 2008).

Modelling elements

- *Periodicity cork extraction* (Figure 30 and Table 7 – “Constants”)

6.1.2.2. Random *cork production per tree kg*

The amount of kilograms produced per tree, ranging from 35.95 to 69.56 kg/tree (Pereira and Tomé 2004).

6.1.2.3. Random i*ncome from cork per tree euros kg*

Benefits, in euros per kilograms of cork, ranging from 1.3 to 3.3 euros/kg (Pinheiro and Ribeiro 2013).

6.2. LOSSES

The losses from soil management and cork extraction.

Modelling elements

- *Shrub clearing cost euros per ha* (Figure 30 and Table 7 – “Composed variables”)
- *Stripping cost cork extraction euros per ha* (Figure 30 and Table 7 – “Composed variables”)

6.2.1. *Shrub clearing cost euros per ha*

The costs, in euros per hectare, associated to the periodic shrub clearing.

Modelling elements

- *Effective shrub clearing periodicity* (Figure 30 and Table 7 – “Constants”)
- *Average shrub clearing euros per ha* (Figure 30 and Table 7 – “Random variables”)

6.2.1.1. Average *shrub clearing euros per ha*

The costs, in euros per hectare, associated to shrub clearing (Pinheiro et *al.* 2008).

6.2.2. *Stripping cost cork extraction euros per ha*

The costs, in euros per hectare, associated to the periodic cork oak extraction.

Modelling elements

- *Effective cork extraction* (Figure 30 and Table 7 – “Constants”)
- *Average stripping cost cork extraction euros per kg* (Figure 30 and Table 7 – “Constants”)

6.2.2.1. Average *stripping cost cork extraction euros per kg*

The costs, in euros per kilogram, associated to cork oak extraction (Pinheiro et *al.* 2008).