Universidade de Lisboa
Faculdade de Ciências
Departamento de Biologia Vegetal

Management of multi-ownership Mediterranean forest landscapes: balancing biodiversity conservation and fire risk reduction

Miguel Porto Bértolo Adão Pereira

Doutoramento em Biologia - Especialidade de Ecologia
2012

Universidade de Lisboa
Faculdade de Ciências
Departamento de Biologia Vegetal

Management of multi-ownership Mediterranean forest landscapes: balancing biodiversity conservation and fire risk reduction

Miguel Porto Bértolo Adão Pereira

Tese orientada por:
Profª Doutora Otília Correia
Prof. Doutor Pedro Beja
especialmente elaborada para a obtenção do grau de doutor em Biologia, especialidade de Ecologia
2012

Resumo

A gestão de ecossistemas humanizados é complexa, dado que cada serviço ou produto explorado pelo homem requer medidas de gestão adequadas, as quais são muitas vezes contraditórias entre si. Esta gestão tem de ser planeada ao nível da paisagem, uma vez que muitos dos serviços prestados dependem da estrutura espacial, principalmente aqueles que advêm do funcionamento dos ecossistemas e da biodiversidade. Conciliar os diferentes regimes de gestão para que se maximize o proveito dos serviços é particularmente difícil quando a paisagem está dividida por muitos proprietários privados com diferentes expectativas e não há uma entidade gestora que coordene as acções de gestão, cada proprietário tomando as suas próprias opções. As abordagens clássicas para os problemas de conservação ou gestão ao nível da paisagem são em geral desadequadas para um cenário como este, pois implicitamente partem do princípio que há uma entidade responsável pela gestão, e não integram a incerteza associada às opções individuais de gestão nem a dinâmica temporal da paisagem típica das paisagens humanizadas, encarando muitas vezes as paisagens como estáticas.

Neste estudo procura-se desenvolver um método de optimização da gestão da paisagem adequado a este tipo de cenários. Além da complexidade inerente à própria definição de um regime de gestão adequado, uma das principais limitações práticas é a dificuldade em implementar esse regime de gestão de forma rigorosa em paisagens de múltipla propriedade. Assim, o conceito que subjaz ao método consiste em encontrar regras simples e não espaciais de gestão que, mesmo que não sejam implementadas correctamente, consigam cumprir objectivos múltiplos e contraditórios à escala da paisagem cumulativamente ao longo do tempo. O esquema geral consiste na integração de um simulador e analisador de paisagem dentro de um algoritmo de optimização multi-objectivo. Assim, neste método: a) é dada especial importância à simplicidade dos regimes de gestão, partindo do princípio que quanto mais simples forem as regras, mais correctamente serão cumpridas; b) é incorporada a incerteza associada ao não cumprimento das regras por parte dos proprietários, bem como a ausência de coordenação entre eles, através da introdução de estocacidade nas simulações; c) os objectivos da optimização podem ser formulados tendo em conta o efeito da gestão na dinâmica da paisagem ao longo de todo o período simulado e não apenas o resultado final dessa gestão; d) podem ser formulados objectivos respeitantes ao padrão espacial, usando métricas de paisagem. Com esta abordagem, pretende-se que as soluções de gestão obtidas sejam robustas aos desvios expectáveis aquando da implementação no terreno e que satisfaçam os objectivos de uma forma continuada no tempo.

O método foi testado numa paisagem do sul de Portugal, onde o coberto vegetal dominante são florestas de sobreiro. Nesta área, a principal actividade económica é a extracção de cortiça, o que leva os proprietários a desmatar periodicamente os sobreirais de forma a minimizar o risco de incêndio e facilitar a extracção. A gestão é, contudo, efectuada pelos proprietários em propriedades pequenas, segundo decisões individuais, o que se traduz numa grande variabilidade na frequência com que é efectuada e na ausência de um padrão espacial definido. A baixa preditibilidade da gestão não planeada e das suas consequências ao nível da paisagem coloca questões relativamente a) ao impacto que tal gestão poderá ter a longo prazo na biodiversidade ao nível da paisagem e b) à eficácia desta gestão não planeada a reduzir risco de incêndio, comparativamente ao custo total. Este problema é especialmente importante num cenário onde a disponibilidade de subsídios comunitários tem levado a um aumento generalizado das frequências de desmatação, o que pode ter consequências graves para a biodiversidade.

Para abordar este problema, o trabalho divide-se em duas grandes etapas: modelação e simulação-optimização. Na primeira parte (Capítulos 2 a 4) procurou-se perceber, através de modelação estatística, a

influência da desmatação nas comunidades arbustivas, herbáceas, e na acumulação de biomassa combustível. Na segunda (Capítulo 5), este conhecimento foi usado para obter soluções de gestão que garantam objectivos relativos à biodiversidade, risco de incêndio e custo.

Nos Capítulos 2 e 3 da tese foram analizados os impactos da desmatação nas comunidades arbustivas (Capítulo 2) e herbáceas (Capítulo 3) com base numa cronosequência de 48 parcelas de amostragem com diferentes idades (i.e., tempo decorrido desde a última limpeza de matos) até cerca de 70 anos. As respostas das comunidades foram analizadas agrupando as espécies em grupos funcionais de acordo com características relevantes para a resposta à perturbação. Os resultados apontam para uma influência bastante evidente da desmatação sobre a estrutura e composição das comunidades arbustivas e herbáceas, sendo possível detectar os seus efeitos até 70 anos após desmatação em alguns grupos funcionais. Em particular, a gestão recorrente leva ao declínio ou quase eliminação de grupos de plantas como os arbustos produtores de frutos carnudos, ervas clonais e perenes com formas de crescimento em tufo ou roseta, o que pode levar ao desaparecimento de algumas funções do ecossistema e outros grupos biológicos associados. Estes padrões têm implicações para um adequado planeamento da gestão, pois a subsistência destes grupos deverá ser garantida ao nível da paisagem, o que requer medidas de gestão pensadas a longo prazo, que resultem em estruturas de paisagem compatíveis com a sua manutenção continuada ao longo do tempo. Tal passará, no mínimo, por: a) garantir que existe suficiente representação espacial de todo o espectro de idades ao longo do tempo, e b) reservar algumas áreas da paisagem fixas que são mantidas sem gestão, as quais servirão de fontes de propágulos ou de bancos de espécies de baixa mobilidade. Um cuidadoso planeamento espacial da gestão permitiria manter esta estrutura sem um significativo acréscimo no risco global de incêndio e possivelmente com um menor custo.

No Capítulo 4 fez-se uma análise da acumulação de biomassa combustível ao longo do tempo desde a última desmatação, de forma a perceber a influência da gestão no risco de incêndio local. O objectivo principal reside em caracterizar a relação custo-benefício da gestão de matos. Embora não haja dúvida que o menor risco de incêndio está associado a desmatações muito frequentes, o custo implicado não é comportável, pelo que importa saber até que ponto o investimento no aumento da frequência de desmatação compensa em termos de redução de risco a nível local. Os resultados mostraram um aumento não linear de ritmo decrescente da biomassa combustível ao longo do tempo desde a última desmatação, sendo que a partir de uma determinada altura o aumento da biomassa já pouco se faz sentir. O facto de a curva não ser linear e tender para a estabilização cria alguma margem aquando da procura de compromissos de gestão que não sejam demasiado dispendiosos mas que cumpram os seus objectivos (Capítulo 5).

No Capítulo 5, foram procurados os regimes de gestão que melhor cumprissem um conjunto de objectivos formulados com base nos conhecimentos adquiridos nos capítulos anteriores. Dado que não existe uma solução única que satisfaça todos os objectivos, foi usado um algoritmo genético multi-objectivo baseado na aproximação da fronteira de Pareto - o conjunto de soluções que representam os melhores compromissos possíveis entre objectivos. Para este caso de estudo foram formulados seis objectivos que traduzem as principais preocupações existentes na área: minimizar o risco de incêndio, minimizar o custo das operações de limpeza e maximizar o potencial de biodiversidade. Dado que tanto o risco de incêndio como a biodiversidade são factores que se desenvolvem à escala da paisagem, os objectivos a eles relativos foram directa ou indirectamente calculados a partir de métricas espaciais. Os resultados permitiram concluir que não é necessário um plano de gestão rígido para que se obtenham configurações de paisagem adequadas à manutenção de todos os objectivos. Com regras muito simples, baseadas apenas na divisão dos proprietários em grupos aos quais são prescritos diferentes frequências de desmatação, a paisagem foi gradualmente adquirindo características favoráveis ao baixo risco de incêndio e maior biodiversidade, com um baixo custo

total. A abordagem usada permitiu também que pudessem ser seleccionadas *a posteriori* soluções de acordo com preferências ou constrangimentos que possam existir, por exemplo, impondo limitações rígidas ao orçamento, ou dando preferência aos objectivos de risco de incêndio em desfavor dos restantes.

No Capítulo 6 é feita uma discussão integrada das principais conclusões. A abordagem proposta mostrou ser adequada ao caso de estudo, dando resposta ao problema de como gerir uma paisagem eficazmente com o mínimo de recursos e realçando o potencial da gestão não coordenada enquanto ferramenta de gestão da paisagem. É também uma abordagem suficientemente flexível para ser aplicada em muitas situações, sendo especialmente adequada, com alguns melhoramentos, para casos de elevada incerteza e baixos recursos. Porém, é importante ensaiar a abordagem em casos de estudo mais complexos que envolvam objectivos mais particulares, bem como aproveitar a elevada flexibilidade do método para incorporar modelos mais realistas dos vários componentes.

Palavras-chave: paisagens multifuncionais, gestão sustentável, simulação-optimização da paisagem, conservação da biodiversidade

Abstract

1. The sustainable management of human-dominated landscapes often requires the spatial and temporal allocation of local management regimes in order to support biodiversity and ecosystem services, but satisfactory schedules are often difficult to design and implement. Classical optimization approaches to this problem are generally unfeasible in multi-ownership landscapes, because they disregard uncertainties and lack of coordination in landowners' actions, and they rarely incorporate temporal dynamics.
2. We addressed this problem in a cork oak forest landscape in southern Portugal, where understory clearing to reduce fire risk is the main management action, and there is no coordination among multiple landowners. First, we quantified the consequences of management for biodiversity and fire risk, modelling plant community dynamics and fuel accumulation along a 70-year chronosequence. Second, we developed an approach integrating a multi-objective optimization algorithm coupled with a landscape simulator and analyser, which were designed to find and evaluate non-spatial management rules that best achieve landscape-level objectives under uncoordinated and imperfect implementation by individual landowners.
3. After management, pioneer plants such as most annual herbs and dry-seeded shrubs recovered rapidly (<10 years), whereas some perennial herbs and fleshy fruited and resprouter shrubs only approached pre-disturbance levels after >50 years. Fuel accumulation was rapid during the first 10-20 years, levelling off thereafter. Structural vegetation complexity and vertical fuel continuity increased through the chronosequence.
4. The simulation-optimization approach converged to solutions involving one dominant group of landowners clearing the understory at short intervals (about 10 years), and the remaining managing at very long intervals (>50 years), providing a reasonable compromise between biodiversity maximization, and minimization of fire risk and cost, during a simulation period of 100 years.
5. The approach developed in this thesis may find wide application in a range of multi-ownership landscapes, helping to achieve contrasting landscape-level objectives even under uncoordinated and imperfect management.

Keywords: multifunctional landscapes, sustainable management, landscape simulation-optimization, biodiversity conservation

Agradecimentos

Ao meu orientador Pedro Beja por me ter recebido de surpresa, pelos ensinamentos do pragmatismo, as tempestades de ideias e pela crucial ajuda a pôr as ideias no papel.

À minha orientadora Otília Correia também por me ter acolhido sem hesitar, o apoio e confiança em todo e qualquer campo, já desde longe.

Ao Rui Guerreiro e Ricardo Silva pela preciosa ajuda na amostragem de campo e os belos tempos passados dentro do Caldeirão.

A todos os meus amigos (que não vou nomear pela dificuldade que tenho em definir um *threshold*), pela amizade, as pedras empilhadas ao longo do caminho, e pelos inúmeros dias de campo que movem as mãos.

À minha família, os meus pais "papá zé e mamã", o mano (o melhor compositor), o "vô bértolo" e a "votó" por me ter mostrado as plantas.

à júlia pelas manhãs de abrir a janela e sair a voar
e por si.

This thesis was supported by the Portuguese Foundation for Science and Technology - fellowship BD/28974/2006 and IFADAP-Program AGRO 8.1 (project 458 - 2003.09.002326.2).

FCT
Fundação para a Ciência e a Tecnologia
MINISTÉRIO DA EDUCAÇÃO E CIÊNCIA

Table of contents

1

General Introduction

Serra do Caldeirão

General introduction

Setting the scene

The classical land use paradigm segregates human activities from biodiversity conservation (Margules and Pressey, 2000; Scherr and McNeely, 2008), defending that landscapes should comprise areas dedicated to conservation and areas dedicated to human activities separately. In this context, a whole body of theory has been developed around the topics of where and how should natural reserves be established - e.g. what would be the size, shape and spatial configuration that maximizes the success in fulfilling conservation objectives with the least cost (Cabeza and Moilanen, 2003; Meir *et al.*, 2004; Fischer *et al.*, 2009) - disregarding the potential role of the remaining landscape in contributing to conservation. This paradigm, known as Systematic Conservation Planning (Margules and Pressey, 2000) has been changing, as the importance of human-dominated habitats in conservation is increasingly being recognized.

Implicitly, the systematic conservation planning framework was based on the premises that the worldwide network of protected areas could provide a good representation of the whole variety of biodiversity on the planet, and that these areas were able to conserve, in the long-term, on-going natural processes and viable biological populations (Margules and Pressey, 2000). None of these premises can be guaranteed to be true, however. In one hand, reserves will never be sufficiently large to ensure that a significant part of biodiversity is protected (Franklin, 1993; Wear *et al.*, 1996). On the other hand, the scales at which species and populations respond extend in many cases well beyond the size of reserves. In fact, the characteristics of the non-reserve area can have strong effects on the persistence of populations within reserves, as they influence for instance the connectivity between them (Franklin, 1993; Fischer and Lindenmayer, 2007). Therefore, in human-dominated landscapes it becomes important to include the non-reserve area as a part of the conservation problem (Wear *et al.*, 1996; Fischer and Lindenmayer, 2007) so that management outside reserves is planned having in account its impacts on the whole landscape biodiversity.

In human-dominated landscapes, one of the main problems faced by species and communities is to adapt and survive in face of the novel disturbance regimes imposed by modern human activities (McIntyre and Hobbs, 1999; White and Jentsch, 2001). Species and communities have co-evolved with natural disturbances and, in some regions of the world, with past, moderate human disturbances (Di Castri *et al.*, 1981; Lavorel, 1999). As a consequence, they have acquired traits that confer them resistance and resilience to those disturbances (White and Jentsch, 2001). However, modern human disturbances can be markedly different in magnitude, periodicity and extent, due, for example, to mechanization of agricultural and silvicultural practices (Benton *et al.*, 2003; Scherr and McNeely, 2008). Hence, species may not be able to respond to these novel forms of disturbance. Landscape homogenization and/or fragmentation as a consequence of alterations in the past traditional or natural disturbance regimes are among the most influent negative factors on species long-term persistence. Adequately managing landscapes at landscape level in the long term is, hence, a key point in the whole problem (Macfarlane, 2000).

Landscape management to achieve multiple objectives is a complex problem *per se* because of the often contrasting nature of the objectives that are to be achieved (Mander *et al.*, 2007). For example, biodiversity conservation objectives usually demand different or opposite management practices than those required to achieve production objectives of human activities (Young *et al.*, 2005; Eriksson and Hammer, 2006; O'Farrell and Anderson, 2010). The difficulty in devising management regimes that reconcile all objectives further increases when landscapes are managed by private owners who take their own individual and independent management decisions (Wear *et al.*, 1996; Lewis *et al.*, 2011). Because some ecosystem processes and functions respond at a landscape/regional scale, objectives related to those functions (e.g. maintain viable populations of species X, guarantee pollination services for adjacent crops (Ricketts *et al.*, 2008), etc.) require management planning in a landscape integrated manner. Therefore, there appears to be some contradiction between the so-called multi-ownership landscapes and biodiversity conservation.

In this thesis, we aim to develop a framework to solve landscape management problems overcoming the limitations related to land multi-ownership and contradictory objectives. Our framework integrates a landscape simulation module nested within a multi-objective optimization algorithm, thereby allowing the optimization procedure to progressively select the most adequate management regimes based on the actual effects that they have on a simulated landscape. We take a particular case study as a model - a forest landscape where biodiversity and production objectives potentially collide - and start by doing a series of statistical analyses to investigate the long term responses of plant communities to forest management and the patterns of biomass accumulation after management. These will serve as a basis to guide the formulation of objectives related to biodiversity and fire risk in the simulation-optimization component. Finally, we discuss the limitations and opportunities associated with a multi-ownership land organization in fulfilling landscape-wide goals.

Disturbance as a promoter of landscape heterogeneity

Disturbance-succession dynamics

Natural and anthropogenic disturbances are a primary cause of landscape heterogeneity (White and Jentsch, 2001 and references therein). In one hand, disturbances that are small and/or patchy (e.g. treefall gaps or windblows; Wiens, 2000), in a short period of time will produce a mosaic of disturbed versus undisturbed areas that are crucially different in biotic and abiotic conditions due to the usually dramatic structural changes incurred. On the other hand, large, intense and/or apparently spatially homogeneous disturbances (e.g. large fires) are also capable of creating heterogeneity in the longer term even though one might expect the opposite. The same disturbance event can show quite different effects in the long term among sites (Turner *et al.*, 1998), depending on the pre-existing abiotic or biotic heterogeneity in the system itself (e.g. variations in species composition) or spatial variation in severities within disturbed areas (Turner, 2005), which may also depend on the former. Pre-existing heterogeneity may be related to intrinsic environmental heterogeneity *per se* or may be the result of a previous smaller and patchy disturbance event (White and Jentsch, 2001). The interplay between disturbance and ecological succession is the main cause of this phenomenon.

Succession is rarely, if ever, a homogeneous and predictable (deterministic) process in space and time, as classic models suggest (Connell and Slatyer, 1977). The course of succession after disturbance, besides being affected by the properties of the disturbance itself, is also strongly affected by local conditions, previous vegetation, landscape context, and colonization chance. This can lead to multiple succession trajectories and rates happening in otherwise similar places, causing spatial and temporal successional heterogeneity (Turner *et al.*, 1998; Kashian *et al.*, 2005). Therefore, even an isolated disturbance event (in time) may span its effects for centuries, eventually propagating its effects to the next event (Kashian *et al.*, 2005), thus creating long-term "perennial" heterogeneity in community structure, composition, and, therefore, local environmental conditions (Stewart *et al.*, 2000). Hence, the relationship between disturbance and heterogeneity may become quite complex and the underlying mechanisms, which are little known, are a basic knowledge required in the field of landscape management (White and Jentsch, 2001).

Importance of heterogeneity to biodiversity

There is general agreement that heterogeneity creates conditions to support diversity (Lindenmayer *et al.*, 2006). Environmental heterogeneity widens the range of existing habitat types; a more heterogeneous environment provides more ecological opportunities for more species (Lindenmayer *et al.*, 2006), and results in a more complete use of available resources (Stewart *et al.*, 2000). Heterogeneity has long been known to promote species coexistence through resource partitioning (Tilman and Kareiva, 1997; Griffin *et al.*, 2009), therefore increasing the number of species that can survive in an area by reducing competition processes (Tylianakis *et al.*, 2008). However, as Wiens (2000) state, too simple generalizations about the biological effects of heterogeneity are meaningless, since the type of heterogeneity, the response of each organism to it and the scale at which they respond are all crucial factors to consider as part of the equation, and differ according to the source of heterogeneity. Further, for some organisms, heterogeneity might not even be beneficial (Lindenmayer *et al.*, 2000).

In fact, human-induced heterogeneity *per se* is usually quite different from natural heterogeneity in its properties, irrespective of their causes being different. Spatial patterns of human-induced heterogeneity normally develop at a larger scale, so that organisms that perceive space at smaller scales may actually be experiencing homogeneity instead. Understanding the responses of a given organism to a given natural heterogeneity pattern is therefore not sufficient to predict its response to anthropogenic heterogeneity, which may well have negative consequences (Stewart *et al.*, 2000) as opposed to natural heterogeneity. Nowadays, however, a significant part of heterogeneity is human-induced large-scale heterogeneity, so it is of great importance to further explore its effects on organisms.

Heterogeneity in human-dominated landscapes

Human disturbances: different patterns, scale and intensity

Direct destruction of habitats is undoubtedly the most conspicuous form of negative human impacts on natural systems. However, in most cases, the situation is less extreme, with human activities impacting habitats to a certain degree without their total elimination. Human activities can cause impacts by a) altering natural disturbance regimes (e.g. frequency and intensity); and b) creating new forms of disturbance (White and Jentsch, 2001). Disturbance exclusion is one classical example of an impact associated with altering natural disturbance regimes. For example, by managing forests to avoid natural fires, man is changing the frequency (from high to low) and severity (from low to high) of natural fires (Piñol *et al.*, 2005). Simultaneously, a new type of disturbance (fuel management) is created, which has no direct parallel within natural disturbances, hence, knowledge about organism responses to apparently similar natural disturbances may not apply.

Novel forms of disturbance or altered disturbance regimes may cause significant changes in landscapes (Turner, 2005), to which species may not be able to respond positively. In the past, many traditional practices maintained a certain degree of heterogeneity in human landscapes by using, for example, extensive grazing and fire (Lavorel, 1999; Grove and Rackham, 2001; Altieri, 2004; Bar Massada *et al.*, 2009), in such a way that some species actually became dependent on traditional human activities to persist. Recent agricultural and forestry intensification as well as other modern human-related disturbances, in contrast, often lead to an almost complete homogenization of the landscape over vast areas (Altieri, 1999; Lavorel, 1999; Wiens, 2000; Bar Massada *et al.*, 2009) at both local and landscape scale, causing generalized species declines.

However, recent trends suggest that it shall be possible to reconcile, to some extent, human production activities and biodiversity, sometimes with positive effects for production activities (Scherr and McNeely, 2008; Keitt, 2009), by means of heterogeneity. Heterogeneity has been shown to be of major importance both in farmed landscapes (Benton *et al.*, 2003; Groot *et al.*, 2010) and in forested landscapes (Bengtsson *et al.*, 2000). Hence, management solutions that recreate heterogeneity are the key to restore and sustain biodiversity (Benton *et al.*, 2003; Fischer *et al.*, 2006; Fuhlendorf *et al.*, 2006). Some studies defend that the landscape organization paradigm in production landscapes must change from monocultures occupying extensive areas of land to heterogeneous multifunctional production systems (Altieri, 1999, 2004; O'Farrell and Anderson, 2010). Heterogeneity in these systems must be viewed both at a small scale (e.g. intercropping) and at the landscape scale (land use heterogeneity). In parallel, the concept of pattern-oriented management strategies (Fischer *et al.*, 2006) and the idea of emulating natural disturbances (Bengtsson *et al.*, 2000; Lindenmayer *et al.*, 2006; Torras and Saura, 2008) emerges also as a way to counteract landscape simplification (especially in forests) by suggesting a set of general management principles that promote heterogeneity.

Heterogeneity versus fragmentation

Given the widespread use of the term "heterogeneity", however, it is important to distinguish this concept from the concept of "fragmentation" because the latter has a negative reputation in conservation, while the former is generally accepted as beneficial, hence, might be misused. The negative impacts of fragmentation and homogenization on biodiversity have been a topic of many studies (Fahrig, 2003) which highlight the need to conserve the "true" heterogeneity. The typical case where certain areas of a landscape are set aside for conservation but the remaining is devoted to intensive production activities may not actually fit in the concept of heterogeneity. Rather, in such landscapes the process is better described as fragmentation associated to habitat loss (Fahrig, 2003).

Although subtle, there are key differences between these concepts, even though in the real world, a continuum of situations from fragmented to heterogeneous landscapes exists. The classical definitions state that a fragmented landscape is composed of patches which are isolated from each other by a matrix of habitats unlike the original (Wilcove *et al.*, 1986; Faaborg *et al.*, 1995; McIntyre and Hobbs, 1999; Fahrig, 2003; Fischer and Lindenmayer, 2006). From this, we can infer that a) in a fragmented landscape, there are extreme differences between the "patches" and the "matrix" so that the patches are suitable habitat but the matrix is not; b) the "patches" are not connected to each other. Further, we can add that, generally but not necessarily, the "matrix" is a homogeneous, continuous and large expanse of land. A fragmented landscape, in this sense, is made of discrete units, as opposed to an heterogeneous landscape, made of a continuum of environmental gradients (Fischer and Lindenmayer, 2007). Even though there may exist situations where the "fragmentation model" applies, these authors emphasize that in many cases it is not possible to clearly separate the matrix from the patches, and the role of the "matrix" in contributing to biodiversity has been neglected in the literature.

Dichotomic views of the landscape, which have their roots in the Theory of Island Biogeography (MacArthur and Wilson, 1967), are actually oversimplifications of limited use and still exist mainly because of the ease of practical implementation, being relatively simple to set aside a percentage of land as biological reserves and leave the remaining to the free will of its owners. But, as Fischer and Lindenmayer (2006) suggest, a paradigm shift should take place, from the "fragmentation model" to the "continuum model". This shift, however, to be successfully applied in the real world, assumes that it is feasible to reconcile human activities with heterogeneity at all scales; therefore implying an integrated action involving many owners, decision-makers and interests. This is the concept behind the so-called multifunctional landscapes.

Multifunctional landscapes and sustainability

The main idea behind multifunctional landscapes resides precisely in safeguarding heterogeneity, which confers them the ability to support various, sometimes contradictory, functions (Mander *et al.*, 2007). This concept is strongly linked to sustainability (O'Farrell and Anderson, 2010), as the idea of *maintenance* of functions implies. Sustainable management of such landscapes requires thinking and planning at the regional level (Groot *et al.*, 2010). However, in real landscapes, existing management practices resulting from the ensemble of individual decisions of landowners may not be sustainable in the long term, as it was discussed by Hardin (1968) in "the tragedy of the commons".

Managing landscapes towards sustainability poses problems at various levels. In the first place, devising management solutions that are able to fulfil the specific requirements of a landscape is not trivial due to the inherent complexity of natural systems (Spies *et al.*, 2007; Groot *et al.*, 2010; O'Farrell and Anderson, 2010), and general guidelines don't provide enough detail for all situations (Fischer *et al.*, 2006). Secondly, it requires reconciling the needs posed by each of the landscape functions of interest, some of which may require opposite management practices (Young *et al.*, 2005), while accounting for the dynamic nature of landscapes. Finally, coordinating management actions in the field in order to accomplish whatever management plan is desired may pose several difficulties when landscape is divided into many private owners often with different expectations (Macfarlane, 2000; Groot *et al.*, 2010; Lewis *et al.*, 2011), which often happens in multifunctional landscapes. In these so-called multi-ownership landscapes, management strategies will significantly gain if designed having in account the practical limitations related to implementation (Polasky *et al.*, 2005), which represents a significant challenge.

Disturbance in the context of Mediterranean landscapes

Fire is one of the major disturbance factors that characterizes Mediterranean landscapes worldwide (Blondel and Aronson, 1999; Grove and Rackham, 2001). It is of paramount importance in shaping landscape structure by creating heterogeneous mosaics of different ecological situations inhabited by different sets of species, therefore increasing diversity (Bar Massada *et al.*, 2009). In parallel, in the Euro-Mediterranean region, man has also been an important selection pressure over ecosystems, mainly by the use of fire and grazing in ancient times (White and Jentsch, 2001; Bar Massada *et al.*, 2009). As a consequence, species and communities have evolved response mechanisms to cope with various disturbances, as well as with environmental instability typical of the climate (Rundel, 1998). Altogether, these facts confer a high resilience of many Mediterranean vegetation types to disturbances (Lavorel, 1999; Acácio and Holmgren, 2012). This view is not, however, unanimous (Bradshaw *et al.*, 2011) and should not be generalized to all species and vegetation types (Lavorel, 1999; Rodrigo *et al.*, 2004; Bradshaw *et al.*, 2011), being incautious to suppose that the increased use of disturbances such as fire as a regular management practice will not degrade ecosystems (Rodrigo *et al.*, 2004; Bradshaw *et al.*, 2011).

At landscape scale, several studies report the importance of fire in contributing to overall landscape biodiversity. Burnt areas represent important opportunities for early-successional pioneer plant species (Capitanio and Carcaillet, 2008) and animal species typical of open and low shrublands (Herrando *et al.*, 2003), which are not found in late successional habitats. Findings of these and other authors (Blondel and Farré, 1988) suggest that the contribution of early successional habitats to overall species richness is larger than that of late successional habitats due to a higher heterogeneity between burnt areas caused by dispersal limitation

(Brotons *et al.*, 2005). Similarly, other disturbances with similar effects to fire have also been shown to be crucial for promoting overall diversity (Verdasca *et al.*, 2012). However, when pioneer species are not dispersal-limited, as is the case of many ruderal herbs, and late-successional species possess persistence traits (e.g. resprouter shrubs), the opposite trend may be seen, i.e., fire will reduce beta diversity (Reilly *et al.*, 2006). Despite this, it is reasonable to suppose that overall, in Mediterranean habitats, a significant part of landscape species diversity may be attributable to fire.

Nowadays, however, fire is not socially acceptable and a great effort is spent in managing highly-flammable Mediterranean forests in order to reduce fire risk (Pérez-Ramos *et al.*, 2008). Such practices could have the potential to emulate the ecological role of natural fires by creating heterogeneity (Crow and Perera, 2004; Quilchano *et al.*, 2007), but the pattern, frequency, extent and severity in which they are applied seldom resembles the natural disturbance regimes (Crow and Perera, 2004), acting like a simplifying factor instead. As such, these practices fail to emulate natural disturbance regimes if not adequately planned in that direction.

The high resilience of Mediterranean shrub vegetation, which has the ability to recover quickly after disturbances, is both an opportunity and a limitation. In one hand, managers have a wider range of options to schedule management operations in space and time without deleterious consequences to natural systems. On the other hand, in order to maintain heterogeneity and a low fire risk, management practices must be applied frequently at least in some areas, otherwise natural succession will rapidly lead to homogenization (Bar Massada *et al.*, 2009) and very high fire risk vegetation, unless extreme abiotic conditions hinder the recovery process.

The study system

Cork oak forests are a habitat restricted to the western Mediterranean basin, which hosts high levels of biodiversity (Marañón *et al.*, 1999; Bugalho *et al.*, 2009; Blondel *et al.*, 2010). Structurally, these are short and closed forests dominated mostly by sclerophyllous species with a complex multi-layered understory. Shrub and herb species account for the greater part of plant species richness, whereas the tree layer is mostly dominated by *Quercus suber* L. alone, probably due to human selection through ages (Urbieta *et al.*, 2008). These forests have been chiefly exploited for cork extraction, which is a highly valued product with a variety of industrial uses (Aronson *et al.*, 2009).

Cork is among the most sustainable forest productions in the world since its exploitation does not kill, and barely harms the trees (Aronson *et al.*, 2009; but see Moreira *et al.*, 2007). Yet, these forests present a very high fire risk (Moreira *et al.*, 2007) that leads to the implementation of fuel reduction practices which severely alter the structure of these forests (Barbero *et al.*, 1990) by eliminating the shrub layer, potentially having negative impacts on biodiversity. Ultimately, if shrub clearing practices are too frequent and/or are complemented with other human-induced disturbances such as grazing, the system is likely to change to a cork oak "savanna" (Quilchano *et al.*, 2007), locally known as "montado" (spanish "dehesa"), characterized by scattered trees with herbaceous understory and nearly absence of the shrub layer (Joffre *et al.*, 1999).

The montado system is highly valued for its multifunctional nature (agro-silvo-pastoral) that is paralleled by high levels of biodiversity (Bugalho *et al.*, 2011), which is partly attributable to the diversity of management practices that these areas are subjected to (Bugalho *et al.*, 2009, 2011). Abandonment of montado systems is accompanied by a decrease in species richness (Castro *et al.*, 2010) due to shrub encroachment (Acácio *et al.*, 2009; Bugalho *et al.*, 2011 and references therein) and consequent decline in herbaceous light-demanding species that comprise an important part of species richness. In contrast with forests, however, montados and recurrently cleared cork oak forests are impoverished in specialist forest plant species often of high conservation value due to their regional scarcity, while enriched in widespread generalist weedy species (Ojeda *et al.*, 2001; Quilchano *et al.*, 2007; Pérez-Ramos *et al.*, 2008). Similarly, the majority of shrub and tree species (other than the cork oak) are absent in the montado system, which results in a very simplified structure compared to forests, therefore a markedly different habitat. Taking into account responses of the various biological groups to this duality (Moreira *et al.*, 2005; Taboada *et al.*, 2006; Santana *et al.*, 2012; Verdasca *et al.*, 2012), the whole picture calls for the need that an adequate balance is maintained at the landscape scale between different successional stages, from the early-successional grazed montado to the unmanaged cork oak forest, so to maximize species diversity at landscape level.

Our study focuses on the cork oak forests of "Serra do Caldeirão" as the case study. This is a hilly region in southern Portugal whose vegetation is comprised by cork oak forest as the primary cover type, within which patches of shrublands and riparian vegetation persist. Forest patches range from recurrently disturbed areas (structurally similar to montado) that are nearly pure stands of cork oak, to dense thickets of Mediterranean maquis where several other shrub and tree species co-dominate, like the strawberry tree (*Arbutus unedo* L.), tree heath (*Erica arborea* L.) and a variety of low shrubs of the genera *Cistus*, *Erica*, *Lavandula*, *Calluna*, *Genista, Ulex* and others (Acácio *et al.*, 2009). Shrubland patches present a similar shrub composition, but are mostly dominated by the rockrose (*Cistus ladanifer* L.), which may form, in some areas, nearly monospecific stands with a few scattered cork oak trees. These vegetation types are likely to be different stages of the same successional gradient (Natividade, 1950), but some studies have shown that *C. ladanifer*-dominated shrublands are probably a dead-end from which community may not be able to evolve further without external help (Acácio *et al.*, 2007, 2009).

In the first half of the 20th century, landscape in this region was far more agricultural than nowadays, with little natural vegetation remaining (Krohmer and Deil, 2003). However, from 1950 onwards, land abandonment led to a progressive change, with shrublands dramatically increasing and occupying the understory of cork oak forests. Simultaneously, cork exploitation became the most important economic activity (Moreira *et al.*, 2007), hence, forests have started to be subject to shrub clearing operations undertaken by private landowners aiming at minimizing fire risk. Since landscape ownership is severely fragmented by many independent landowners (Moreira *et al.*, 2007), management decisions are taken at the individual level. The consequent diversity in management regimes has created a constantly changing heterogeneous mosaic of different successional stages. However, in recent years, availability of EU subsidies (WWF, 2006) and the high incidence of large fires (Moreira *et al.*, 2007) led to an increase in management frequency, with consequent decline of the area occupied by late successional vegetation. Such trend is expected to have negative impacts on biodiversity by increasing landscape homogeneity, fragmentation and habitat loss.

More details of the study area can be found in Chapters 2-4.

Objectives and expected achievements

The main question that guides our study is whether it is possible to implement a management regime that fulfils landscape-level objectives working only with small adjustments undertaken in largely uncoordinated actions of individual landowners. Under the umbrella of this general objective, a series of partial objectives will be addressed:

- Understand the long term impacts of forest management on different groups of plant species and plant communities
- Characterize the long term fuel succession in a Mediterranean forest

- Analyze the implications of the above findings to the design of landscape management regimes
- Explore the potentials and limitations of uncoordinated management in achieving landscape and biodiversity objectives

Even though we illustrate our approach in a specific case study, it may be widely applied to many situations due to its flexibility, being especially suited for complex problems with many objectives and trade-offs to be accomplished.

Organization of the thesis

This thesis is organized in 6 chapters. Chapter 1 provides the context, general theoretical introduction of the topics and motivation. Chapters 2 to 5 correspond to published scientific papers (2 and 3) or papers in the submission stage (4 and 5). Chapter 6 integrates all conclusions and discusses their implications to forest management.

The overall rationale has two components - a statistical modelling component (Chapters 2 to 4) and an optimization component (Chapter 5). The statistical modelling component aims to explore the trends exhibited by shrub communities (Chapter 2), herbaceous communities (Chapter 3) and fuel accumulation (Chapter 4), in relation to a gradient of time since last disturbance event (shrub clearing) and disturbance frequency in cork oak forests. Models and conclusions from these papers serve as a basis to Chapter 5, in which we develop an optimization framework to deal with a multi-ownership management problem that integrates biodiversity and fire risk objectives.

In Chapter 2, we explore the shrub layer dynamics in relation to the frequency and time since last forest management operation. We analyze the patterns of key shrub and tree species and functional groups in terms of total cover, cover by vertical strata and diversity measures using Generalized Additive Models. Overall, we aim to understand how forest management affects vegetation structure, complexity and diversity patterns, and assess whether these effects are long-term.

Chapter 3 uses a similar methodology to Chapter 2 applied to herbaceous communities, but explores in further detail the responses of different *a priori* functional groupings of species, based on life history traits and dispersal strategies. The general aim is to understand the long-term impacts of forest management on functional and compositional diversity, with focus on the number of functional groups and richness within each functional group.

Chapter 4 combines the data on vegetation structure with species-specific fire-related traits to produce a picture of fuel succession along time since last management operation. By understanding the evolution of fuel properties, we aim to make the link between vegetation composition and structure along successional time, and fire risk in our study system. This knowledge is one of the building blocks of the next chapter, by providing a measure of fire risk along time since management.

Chapter 5 examines the implications of the previous chapters for landscape-level management planning, using a multi-objective optimization algorithm to devise the best management solutions that fulfil biodiversity and fire risk objectives. This is an integrating chapter, which aims to implement in practice the guidelines obtained from the ecological modelling component. This is achieved by means of simulation of scenarios and aims to approximate the real world by accounting for all kinds of limitations associated with the private ownership of landscapes, uncoordination and limitation of funds.

Chapter 6 picks results and conclusions from previous chapters and draws the general findings in the context of the dynamics of Mediterranean vegetation after disturbance, and of management in multi-ownership landscapes. We conclude by highlighting the influence of limitations and opportunities of uncoordinated management to conservation and propose some general management guidelines - although tentative - to reconcile biodiversity and human activities in these systems.

REFERENCES

Acácio, V., Holmgren, M., 2012. Pathways for resilience in Mediterranean cork oak land use systems. Annals of Forest Science.

Acácio, V., Holmgren, M., Jansen, P. a., Schrotter, O., 2007. Multiple Recruitment Limitation Causes Arrested Succession in Mediterranean Cork Oak Systems. Ecosystems 10, 1220–1230.

Acácio, V., Holmgren, M., Rego, F.C., Moreira, F., Mohren, G.M.J., 2009. Are drought and wildfires turning Mediterranean cork oak forests into persistent shrublands? Agroforestry Systems 76, 389–400.

Altieri, M.A., 1999. The ecological role of biodiversity in agroecosystems. Agriculture, Ecosystems & Environment 74, 19–31.

Altieri, M.A., 2004. Linking ecologists and traditional farmers in the search for sustainable agriculture. Frontiers in Ecology and the Environment 2, 35–42.

Aronson, J., Pereira, J.S., Pausas, J.G., 2009. Cork Oak Woodlands on the Edge: Ecology, Biogeography, and Restoration of an Ancient Mediterranean Ecosystem. Island Press, Washington DC, USA.

Bar Massada, A., Carmel, Y., Koniak, G., Noy-Meir, I., 2009. The effects of disturbance based management on the dynamics of Mediterranean vegetation: A hierarchical and spatially explicit modeling approach. Ecological Modelling 220, 2525–2535.

Barbero, M., Bonin, G., Loisel, R., Quézel, P., 1990. Changes and disturbances of forest ecosystems caused by human activities in the western part of the mediterranean basin. Vegetatio 87, 151–173.

Bengtsson, J., Nilsson, S.G., Franc, A., Menozzi, P., 2000. Biodiversity, disturbances, ecosystem function and management of European forests. Forest Ecology and Management 132, 39–50.

Benton, T.G., Vickery, J.A., Wilson, J.D., 2003. Farmland biodiversity: is habitat heterogeneity the key? Trends in Ecology & Evolution 18, 182–188.

Blondel, J., Aronson, J., 1999. Biology adn Wildlife of the Mediterranean Region. Oxford University Press, Oxford, UK.

Blondel, J., Aronson, J., Bodiou, J.-Y., Boeuf, G., 2010. The Mediterranean Region. Biological diversity in space and time. Oxford University Press, Oxford, UK.

Blondel, J., Farré, H., 1988. The convergent trajectories of bird communities along ecological successions in european forests. Oecologia 75, 83–93.

Bradshaw, S.D., Dixon, K.W., Hopper, S.D., Lambers, H., Turner, S.R., 2011. Little evidence for fire-adapted plant traits in Mediterranean climate regions. Trends in plant science 16, 69–76.

Brotons, L., Pons, P., Herrando, S., 2005. Colonization of dynamic Mediterranean landscapes: where do birds come from after fire? Journal of Biogeography 32, 789–798.

Bugalho, M.N., Caldeira, M.C., Pereira, J.S., Aronson, J., Pausas, J.G., 2011. Mediterranean cork oak savannas require human use to sustain biodiversity and ecosystem services. Frontiers in Ecology and the Environment 9, 278–286.

Bugalho, M.N., Plieninger, T., Aronson, J., Ellatifi, M., Crespo, D.G., 2009. Open woodlands: a diversity of uses (and overuses). In: Aronson, J., Pereira, J.S., Pausas, J.G. (Eds.), Cork Oak Woodlands on the Edge: Ecology, Biogeography, and Restoration of an Ancient Mediterranean Ecosystem. Island Press, Washington DC, USA., pp. 33–45.

Cabeza, M., Moilanen, A., 2003. Site-Selection Algorithms and Habitat Loss. Conservation Biology 17, 1402–1413.

Capitanio, R., Carcaillet, C., 2008. Post-fire Mediterranean vegetation dynamics and diversity: A discussion of succession models. Forest Ecology and Management 255, 431–439.

Di Castri, F., Goodall, W., Specht, R.L., 1981. Mediterranean-type shrublands. In: Ecosystems of the World. Elsevier, Amsterdam.

Castro, H., Lehsten, V., Lavorel, S., Freitas, H., 2010. Functional response traits in relation to land use change in the Montado. Agriculture, Ecosystems & Environment 137, 183–191.

Connell, J.H., Slatyer, R.O., 1977. Mechanisms of Succession in Natural Communities and Their Role in Community Stability and Organization. The American Naturalist 111, 1119–1144.

Crow, T.R., Perera, A.H., 2004. Emulating natural landscape disturbance in forest management – an introduction. Landscape Ecology 19, 231–233.

Eriksson, S., Hammer, M., 2006. The challenge of combining timber production and biodiversity conservation for long-term ecosystem functioning—A case study of Swedish boreal forestry. Forest Ecology and Management 237, 208–217.

Faaborg, J., Brittingham, M., Donovan, T., Blake, J., 1995. Habitat fragmentation in the temperate zone. In: Martin, T.E., Finch, D.M. (Eds.), Ecology and Management of Neotropical Migratory Birds. Oxford University Press, New York, pp. 357–380.

Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics 34, 487–515.

Fischer, J., Lindenmayer, D.B., 2006. Beyond fragmentation: the continuum model for fauna research and conservation in human-modified landscapes. Oikos 112, 473–480.

Fischer, J., Lindenmayer, D.B., 2007. Landscape modification and habitat fragmentation: a synthesis. Global Ecology and Biogeography 16, 265–280.

Fischer, J., Lindenmayer, D.B., Manning, A.D., 2006. Biodiversity, ecosystem function, and resilience: ten guiding principles for commodity production landscapes. Frontiers in Ecology and the Environment 4, 80–86.

Fischer, J., Peterson, G.D., Gardner, T. a, Gordon, L.J., Fazey, I., Elmqvist, T., Felton, A., Folke, C., Dovers, S., 2009. Integrating resilience thinking and optimisation for conservation. Trends in ecology & evolution 24, 549–54.

Franklin, J.F., 1993. Preserving biodiversity: species, ecosystems, or landscapes? Ecological Applications 3, 202–205.

Fuhlendorf, S.D., Harrell, W.C., Engle, D.M., Hamilton, R.G., Davis, C. a, Leslie, D.M., 2006. Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. Ecological applications 16, 1706–16.

Griffin, J.N., Jenkins, S.R., Gamfeldt, L., Jones, D., Hawkins, S.J., Thompson, R.C., 2009. Spatial heterogeneity increases the importance of species richness for an ecosystem process. Oikos 118, 1335–1342.

Groot, J.C.J., Jellema, A., Rossing, W. a. H., 2010. Designing a hedgerow network in a multifunctional agricultural landscape: Balancing trade-offs among ecological quality, landscape character and implementation costs. European Journal of Agronomy 32, 112–119.

Grove, A.T., Rackham, O., 2001. The Nature of Mediterranean Europe. An Ecological History. Yale University Press, New Haven, USA.

Hardin, G., 1968. The tragedy of the Commons. Science 162, 1243–1248.

Herrando, S., Brotons, L., Llacuna, S., 2003. Does fire increase the spatial heterogeneity of bird communities in Mediterranean landscapes? Ibis 145, 307–317.

Joffre, R., Rambal, S., Ratte, J.P., 1999. The dehesa system of southern Spain and Portugal as a natural ecosystem mimic. Agroforestry Systems 45, 57–79.

Kashian, D.M., Turner, M.G., Romme, W.H., Lorimer, C.G., 2005. Variability and convergence in stand structural development on a fire-dominated subalpine landscape 86, 643–654.

Keitt, T.H., 2009. Habitat conversion, extinction thresholds, and pollination services in agroecosystems. Ecological Applications 19, 1561–73.

Krohmer, J., Deil, U., 2003. Dynamic and conservative landscapes? Present vegetation cover and land-use changes in the Serra de Monchique (Portugal). Phytocoenologia 33, 767–799.

Lavorel, S., 1999. Ecological diversity and resilience of Mediterranean vegetation to disturbance. Diversity and Distributions 5, 3–13.

Lewis, D.J., Plantinga, A.J., Nelson, E., Polasky, S., 2011. The efficiency of voluntary incentive policies for preventing biodiversity loss. Resource and Energy Economics 33, 192–211.

Lindenmayer, D.B., Franklin, J.F., Fischer, J., 2006. General management principles and a checklist of strategies to guide forest biodiversity conservation. Biological Conservation 131, 433–445.

Lindenmayer, D.B., Margules, C.R., Botkin, D.B., 2000. Indicators of Biodiversity for Ecologically Sustainable Forest Management. Conservation Biology 14, 941–950.

MacArthur, R.H., Wilson, E.O., 1967. The theory of island biogeography. Princeton University Press, New Jersey.

Macfarlane, R., 2000. Achieving Whole-Landscape Management across Multiple Land Management Units: A case study from the Lake District Environmentally Sensitive Area. Landscape Research 25, 229–254.

Mander, Ü., Wiggering, H., Helming, K., 2007. Multifunctional land use: meeting future demands for landscape goods and services, Landscape. Springer, Berlin.

Marañón, T., Ajbilou, R., Ojeda, F., Arroyo, J., 1999. Biodiversity of woody species in oak woodlands of southern Spain and northern Morocco. Forest Ecology and Management 115, 147–156.

Margules, C.R., Pressey, R.L., 2000. Systematic conservation planning. Nature 405, 243–53.

McIntyre, S., Hobbs, R.J., 1999. A Framework for Conceptualizing Human Effects on Research Models. Conservation Biology 13, 1282–1292.

Meir, E., Andelman, S., Possingham, H.P., 2004. Does conservation planning matter in a dynamic and uncertain world? Ecology Letters 7, 615–622.

Moreira, F., Beja, P., Morgado, R., Reino, L., Gordinho, L., Delgado, A., Borralho, R., 2005. Effects of field management and landscapecontext on grassland wintering birds in Southern Portugal. Agriculture, Ecosystems & Environment 109, 59–74.

Moreira, F., Duarte, I., Catry, F.X., Acácio, V., 2007. Cork extraction as a key factor determining post-fire cork oak survival in a mountain region of southern Portugal. Forest Ecology and Management 253, 30–37.

Natividade, J.V., 1950. Subericultura. Direcção Geral das Florestas, Lisboa, Portugal.

Ojeda, F., Marañón, T., Arroyo, J., 2001. Plant diversity patterns in the Aljibe Mountains (S. Spain): a comprehensive account. Ecography 24, 683–695.

O'Farrell, P.J., Anderson, P.M., 2010. Sustainable multifunctional landscapes: a review to implementation. Current Opinion in Environmental Sustainability 2, 59–65.

Piñol, J., Beven, K., Viegas, D.X., 2005. Modelling the effect of fire-exclusion and prescribed fire on wildfire size in Mediterranean ecosystems. Ecological Modelling 183, 397–409.

Polasky, S., Nelson, E., Lonsdorf, E., Fackler, P., Starfield, A., 2005. Conserving species in a working landscape: land use with biological and economic objectives. Ecological Applications 15, 1387–1401.

Pérez-Ramos, I.M., Zavala, M.A., Marañón, T., Díaz-Villa, M.D., Valladares, F., 2008. Dynamics of understorey herbaceous plant diversity following shrub clearing of cork oak forests: A five-year study. Forest Ecology and Management 255, 3242–3253.

Quilchano, C., Marañón, T., Pérez-Ramos, I.M., Noejovich, L., Valladares, F., Zavala, M.A., 2007. Patterns and ecological consequences of abiotic heterogeneity in managed cork oak forests of Southern Spain. Ecological Research 23, 127–139.

Reilly, M.J., Wimberly, M.C., Newell, C.L., 2006. Wildfire effects on beta diversity and species turnover in a forested landscape. Journal of Vegetation Science 17, 447–454.

Ricketts, T.H., Regetz, J., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Bogdanski, A., Gemmill-Herren, B., Greenleaf, S.S., Klein, A.M., Mayfield, M.M., Morandin, L.A., Ochieng', A., Potts, S.G., Viana, B.F., 2008. Landscape effects on crop pollination services: are there general patterns? Ecology letters 11, 499–515.

Rodrigo, A., Retana, J., Picó, F.X., 2004. Direct regeneration is not the only response of Mediterranean forests to large fires. Ecology 85, 716–729.

Rundel, P.W., 1998. Landscape disturbance in Mediterranean-type ecosystems: an overview. In: Rundel, P.W., Montenegro, G., Jaksic, F.M. (Eds.), Landscape Disturbance and Biodiversity in Mediterranean-Type Ecosystems. Springer-Verlag, Berlin, pp. 3–22.

Santana, J., Porto, M., Gordinho, L., Reino, L., Beja, P., 2012. Long-term responses of Mediterranean birds to forest fuel management. Journal of Applied Ecology 49, 632–643.

Scherr, S.J., McNeely, J. a, 2008. Biodiversity conservation and agricultural sustainability: towards a new paradigm of "ecoagriculture" landscapes. Philosophical transactions of the Royal Society of London. Series B, Biological sciences 363, 477–94.

Spies, T. a, McComb, B.C., Kennedy, R.S.H., McGrath, M.T., Olsen, K., Pabst, R.J., 2007. Potential effects of forest policies on terrestrial biodiversity in a multi-ownership province. Ecological applications 17, 48–65.

Stewart, A.J.A., John, E.A., Hutchings, M.J., 2000. The world is heterogeneous; ecological consequences of living in patchy environment. In: Hutchings, M.J., John, E.A., Stewart, A.J.A. (Eds.), Ecological Consequences of Environmental Heterogeneity. Blackwell Science, pp. 1–8.

Taboada, A., Kotze, J.D., Tárrega, R., Salgado, J.M., 2006. Traditional forest management: do carabid beetles respond to human-created vegetation structures in an oak mosaic landscape? Forest Ecology and Management 237, 439–449.

Tilman, D., Kareiva, P.M., 1997. Spatial ecology: the role of space in population dynamics and interspecific interactions. Princeton University Press, New Jersey.

Torras, O., Saura, S., 2008. Effects of silvicultural treatments on forest biodiversity indicators in the Mediterranean. Forest Ecology and Management 255, 3322–3330.

Turner, M.G., 2005. Landscape Ecology: What is the state of the Science? Annual Review of Ecology, Evolution, and Systematics 36, 319–344.

Turner, M.G., Baker, W.L., Peterson, C.J., Peet, R.K., 1998. Factors Influencing Succession: Lessons from Large, Infrequent Natural Disturbances. Ecosystems 1, 511–523.

Tylianakis, J.M., Rand, T. a., Kahmen, A., Klein, A.-M., Buchmann, N., Perner, J., Tscharntke, T., 2008. Resource Heterogeneity Moderates the Biodiversity-Function Relationship in Real World Ecosystems. PLoS Biology 6, e122.

Urbieta, I.R., Zavala, M.A., Marañón, T., 2008. Human and non-human determinants of forest composition in southern Spain: evidence of shifts towards cork oak dominance as a result of management over the past century. Journal of Biogeography 35, 1688–1700.

Verdasca, M.J., Leitão, A.S., Santana, J., Porto, M., Dias, S., Beja, P., 2012. Forest fuel management as a conservation tool for early successional species under agricultural abandonment: The case of Mediterranean butterflies. Biological Conservation 146, 14–23.

WWF, 2006. Conflicting EU Funds: Pitting Conservation against unsustainable development. WWF Global Species Programme. Wien.

Wear, D.N., Turner, M.G., Flamm, R.O., 1996. Ecosystem Management with Multiple Owners: Landscape Dynamics in a Southern Appalachian Watershed. Ecological Applications 6, 1173–1188.

White, P.S., Jentsch, A., 2001. The Search for Generality in Studies of Disturbance and Ecosystem Dynamics. Progress in Botany 62.

Wiens, J.A., 2000. Ecological heterogeneity: an ontogeny of concepts and approaches. In: The Ecological Consequences of Heterogeneity. Blackwell Science, pp. 9–31.

Wilcove, D.S., McLellan, C.H., Dobson, A.P., 1986. Habitat fragmentation in the temperate zone. In: Soulé, M.E. (Ed.), Conservation Biology: The Science of Scarcity and Diversity. Sinayer Associates, Inc., Sunderland, MA., pp. 237–256.

Young, J., Watt, A., Nowicki, P., Alard, D., Clitherow, J., Henle, K., Johnson, R., Laczko, E., McCracken, D., Matouch, S., Niemelä, J., Richards, C., 2005. Towards sustainable land use: identifying and managing the conflicts between human activities and biodiversity conservation in Europe. Biodiversity and Conservation 14, 1641–1661.

2

Long-term understory recovery after mechanical fuel reduction in Mediterranean cork oak forests

J. Santana, M. Porto, L. Reino, P. Beja

published in
Forest Ecology and Management
261 (2011) 447-459

Deschampsia stricta
perennial grass restricted to a few scattered locations in the study area, rare in its entire range, associated with open shrublands
(endemic to Portugal)

Long-term understory recovery after mechanical fuel reduction in mediterranean cork oak forests

Joana Santana[a,b], Miguel Porto[a,d], Luís Reino[a,b,c], Pedro Beja[b]

[a] ERENA, Rua Robalo Gouveia, 1-1A, 1900-392 Lisboa, Portugal
[b] CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Campus Agrário de Vairão, Universidade do Porto, 4485-601 Vairão, Portugal
[c] Centro de Estudos Florestais, Instituto Superior de Agronomia, Universidade Técnica de Lisboa, Tapada da Ajuda, 1349-017 Lisboa, Portugal
[d] Centro de Biologia Ambiental, Departamento de Biologia Vegetal, Faculdade de Ciências de Lisboa, Universidade de Lisboa, C2 Campo Grande, 1749-016 Lisboa, Portugal

ABSTRACT

In the Euro-Mediterranean region, mechanical fuel reduction is increasingly used in response to the mounting occurrence of catastrophic wildfires, yet their long-term ecological effects are poorly understood. Although Mediterranean vegetation is resilient to a range of disturbances, it is possible that widespread fuel management at short intervals may threaten forest structural complexity and the persistence of some plant species and functional types, with overall negative consequences for biodiversity. We used a chronosequence approach to infer woody vegetation changes in the first 70 years after understory clearing in upland cork oak (*Quercus suber*) forests, and to assess how these are affected by treatment frequency. Across the chronosequence there was a shift between plant communities with contrasting composition, structure and functional organization. Understory cover increased quickly after disturbance and a community dominated by pioneer seeder and dry-fuited shrubs (*Cistus ladanifer*, *C. populifolius*, *Genista triacanthos*, and *Lavandula stoechas*) developed during about 15 years, but this was slowly replaced by a community dominated by resprouters and fleshy-fruited species (*Arbutus unedo*, *Erica arborea*) > 40 years after disturbance. During the first 15 years there were rapid increases in woody species richness, vertical structural diversity, cover by *Q. suber* juveniles and saplings, and shrub cover at <1.5 m strata, which levelled off or slightly declined thereafter. In contrast, tree species richness, tree density and density of arboreal *A. unedo* and *E. arborea*, vertical structural evenness, and cover at >1.5m strata increased slowly for >50 years. Treatment frequency showed strongly negative relationships with species richness, structural diversity and evenness, and horizontal and vertical understory cover, particularly that of slowly recovering species. These findings suggest that fuel reduction programs involving widespread and recurrent understory clearing may lead to the elimination at the landscape scale of stands with complex multi-layered understory occupied by large resprouters and fleshy-fruited species, which take a long time to recover after disturbance. Fuel management programs thus need to balance the dual goals of fire hazard reduction and biodiversity conservation, recognizing the value of stands untreated for >50 years to retain ecological heterogeneity in Mediterranean forest landscapes.

Keywords: biodiversity conservation; disturbance ecology; ecological succession; forest management; landscape mosaics; Mediterranean plant communities; structural complexity.

INTRODUCTION

Fire is one of the most important natural disturbances shaping the composition and structure of forest ecosystems (Thomas and Packham, 2007), but the occurrence of natural fire regimes in many landscapes is no longer possible, acceptable or even desirable due to social, economical or historical constraints (Foster and Motzkin, 2003; Ager *et al.* 2010). As a consequence, there is interest among land managers and scientists in developing and applying forest fuel management strategies that reduce the risk of wildfires, while retaining the structural and functional attributes of forest ecosystems, and promoting the sustainable use of their goods and services (Crow and Perera, 2004; Agee and Skinner, 2005; Lehmkuhl *et al.* 2007). Thus, understanding the consequences of fuel reduction treatments on forest ecology is increasingly important to inform forest management decision-making (Stephens *et al.*, 2009).

Management of forest fuels is a particularly acute problem in the Euro-Mediterranean region (Xanthopoulos *et al.*, 2006), where the incidence of fire is high and fire is one of the major ecological factors shaping forest landscapes into their present mosaic-like regeneration and disturbance patterns (Grove and Rackham, 2001; Blondel *et al.*, 2010). Spatial heterogeneity created by fire and other disturbance events may be important for the conservation of a diverse array of species with contrasting habitat specializations (Palma *et al.*, 1999; De La Montaña *et al.*, 2006; Taboada *et al.*, 2006). However, fire in these forests is increasingly considered unacceptable, due to the mounting occurrence of catastrophic wildfires causing significant losses of human lives and livelihood (Pausas *et al.*, 2008). Increases in fire frequency, intensity and extent are largely a consequence of ongoing rural depopulation and land abandonment normally followed by shrub encroachment and afforestation of former pastures and cultivated fields (Krohmer and Deil, 2003; Acácio *et al.*, 2009; Bugalho *et al.*, 2009), which may be exacerbated in the future by global warming (Moriondo *et al.*, 2006). Because of this, fire suppression is at present the main tenet of forest management policies in Mediterranean Europe, involving the regular removal of forest understory to reduce fuel accumulation, aiming to prevent the violent progression of wildfires and to attain efficiency of suppression operations and safety of fire crews (Xanthopoulos *et al.*, 2006). Fuel reduction is often achieved by mechanical cutting of shrubs and small trees, while prescribed burning tends to be much less used due to logistical and technical difficulties (Xanthopoulos *et al.*, 2006). Despite its widespread use, there is still limited understanding on the ecological effects of mechanical fuel reduction in Mediterranean forests (e.g., Pérez-Ramos *et al.*, 2008).

Recovery of Mediterranean vegetation after disturbance is widely believed to follow a direct regeneration pattern, in which the source of regeneration is the species pool existing immediately prior to disturbance, and the same predisturbance community is restored rapidly after disturbance (Calvo *et al.*, 2002, 2005; Rodrigo *et al.*, 2004). Direct regeneration has been inferred primarily from studies on vegetation recovery after fire, though there is also evidence for broadly similar rates and pathways of recovery after fire and mechanical disturbances, with communities tending to reach predisturbance diversity, composition and structure in just a few years (Calvo *et al.* 2002, 2005; Potts *et al.* 2010). These patterns are often taken to imply that Mediterranean systems are highly resilient because plants are adapted to disturbance, and so the risk of losing species after disturbance should be low (Rodrigo *et al.*, 2004; Blondel *et al.*, 2010). However, most extant studies have been relatively short-term (< 15 years) and they have focused on shrubland communities recurrently affected by fire or anthropogenic disturbance, which may thus be particularly resilient to further disturbances (Calvo *et al.*, 2002, 2005; Potts *et al.*, 2010). In contrast, plant communities associated with less disturbed environments, such as those of mature forests, may take more time to recover after disturbance and they may lose species if repeatedly disturbed (Marañon *et al.*, 1999; Díaz-Delgado *et al.*, 2002; Hampe and Arroyo 2002). Also, the structural complexity of these communities may be lost and take a long time to recover after disturbance, which in turn may affect habitat conditions for a range of forest organisms (De La Montaña *et al.*, 2006; Taboada *et al.*, 2006). Information is thus needed on the long-term recovery dynamics of vegetation after fuel reduction treatments, which would be important in management planning to define treatment frequencies and spatial patterns assuring the representation of different successional stages at the landscape scale (Lindenmayer *et al.*, 2006).

This study examined the long-term consequences of fuel reduction treatments on understory vegetation in Mediterranean cork oak (*Quercus suber*) forests. These forests cover about 2.5 million hectares in the Mediterranean Basin, where they are exploited chiefly for the production of cork used in wine bottle stoppers and insulation materials, among other industrial uses (Aronson *et al.*, 2009). This is one of the most sustainable forest productions in the world, because cork exploitation involves striping the tree bark about every nine years while keeping the trees alive (Aronson *et al.*, 2009). Cork oak forests under exploitation retain high levels of biodiversity (Marañon *et al.*, 1999; Bugalho *et al.*, 2009; Blondel *et al.*, 2010), and they are representative of native mixed oak forests that occurred within their range, albeit with a much greater dominance and density of cork oaks than in original forests due to anthropogenic selection (Urbieta *et al.*, 2008). Vast areas covered by cork oak forests are classified as National Protected Areas or Sites of Community Importance under European Union Directive 92/43/EEC, legally requiring forest managers to meet biodiversity conservation goals while maximizing socio-economic benefits (Berrahmouni *et al.*, 2009). Understory clearing is a long-standing management prescription in these forests, aiming at reducing fire hazards, easing cork extraction and reducing competition between trees and shrubs, thereby maximizing the economic return from cork exploitation (Natividade, 1950; Montero and Cañellas, 1999). Preliminary evidence suggests that early-successional plant communities are rapidly restored after mechanical fuel reduction in cork oak forests, while more mature communities may be severely depleted where treatments are carried out frequently and over large spatial scales (Marañon *et al.*, 1999; Pérez-Ramos *et al.*, 2008). Here we used a chronosequence approach to infer woody vegetation recovery rates and pathways during the first 70 years after understory clearing. Specifically, we analyzed how woody plant communities changed over time since the last mechanical treatment and with treatment frequency, in terms of (i) tree species richness and density of dominant species, (ii) species richness of woody plants and cover by dominant species, (iii) vertical cover per stratum and structural complexity of understory vegetation, and (iv) species richness and cover of woody plant functional types. Results were then used to discuss the implications of mechanical fuel reduction treatments to the conservation of biodiversity in Mediterranean oak forests.

METHODS

Study area

The study was conducted in the Caldeirão hills (southern Portugal), within an area of about 30,000 ha situated at 200-580 m above sea level (a.s.l.) around the village of Barranco do Velho (37º 14' N, 7º 56' W) (Figure 1). Climate is Mediterranean, with annual rainfall varying markedly from year to year (415–1903 mm); about 80% of the annual rain occurs in October–March and < 5% in the hot, dry months of June–August (Barranco do Velho weather station, 467 m a.s.l.; http://snirh.pt). Mean monthly temperature ranges from 10.3ºC (January) to 24ºC (August) (São Brás de Alportel weather station, 334 m a.s.l.; http://snirh.pt). The geological substrate consists of Paleozoic shale and greywacke. Soils are generally shallow shale lithosols, with low fertility and prone to erosion. The landscape is covered by vast expanses of evergreen oak forests, ranging from almost pure cork oak stands to complex Mediterranean maquis with dominating cork oaks surrounded by tall strawberry trees (*Arbutus unedo*) and tree heath (*Erica arborea*) (Acácio *et al.*, 2009). Forest stands are often interspersed with nearly monospecific *Cistus ladanifer* shrublands or more diverse Mediterranean heathland dominated by *Calluna vulgaris* and species of *Genista*, *Cistus*, *Erica*, *Lavandula* and *Ulex* (Acácio *et al.*, 2009). Pastoral activities are largely restricted to a very few and small herds of goat and sheep, and the main Mediterranean wild herbivores, such as the European rabbit (*Oryctolagus cuniculus*) and red deer (*Cervus elaphus*) are very scarce or absent, though wild boars (*Sus scrofa*) are abundant. The main economic activity is the production of cork, which is generally conducted on small private properties (<10 ha) by aged landowners (often > 60 years old).

The landscape was far more agricultural during the first half of the 20th century, when national policies of food self-sufficiency (Wheat Campaign; 1929-1938) conducted to large-scale clearing of natural vegetation for cereal cultivation (Krohmer and Deil, 2003). Since the 1950s, human population has declined along with the abandonment of agricultural and pastoral activities, and the concurrent increase in shrubland cover (Krohmer and Deil, 2003; Acácio *et al.*, 2009). Cover by cork oak forests has remained fairly stable over this period (Acácio *et al.*, 2009), though management has largely changed from a traditional agro-silvo-pastoral system including cereal cultivation and livestock grazing under the tree canopy, to a purely forestry system including mechanical clearing of understory woody vegetation as the main silvicultural operation (Bugalho *et al.*, 2009). The periodicity of shrub clearing is variable and depends on the decisions of individual landowners, but it often occurs at about 9-year intervals in association with the cork extraction cycle. However, in many stands the management of understory vegetation is either absent or very sporadic. As a consequence, the landscape is composed of a complex mosaic of forest stands with understory vegetation at different successional stages, ranging from stands with herbaceous understory to stands with dense cover by tall shrubs and small trees.

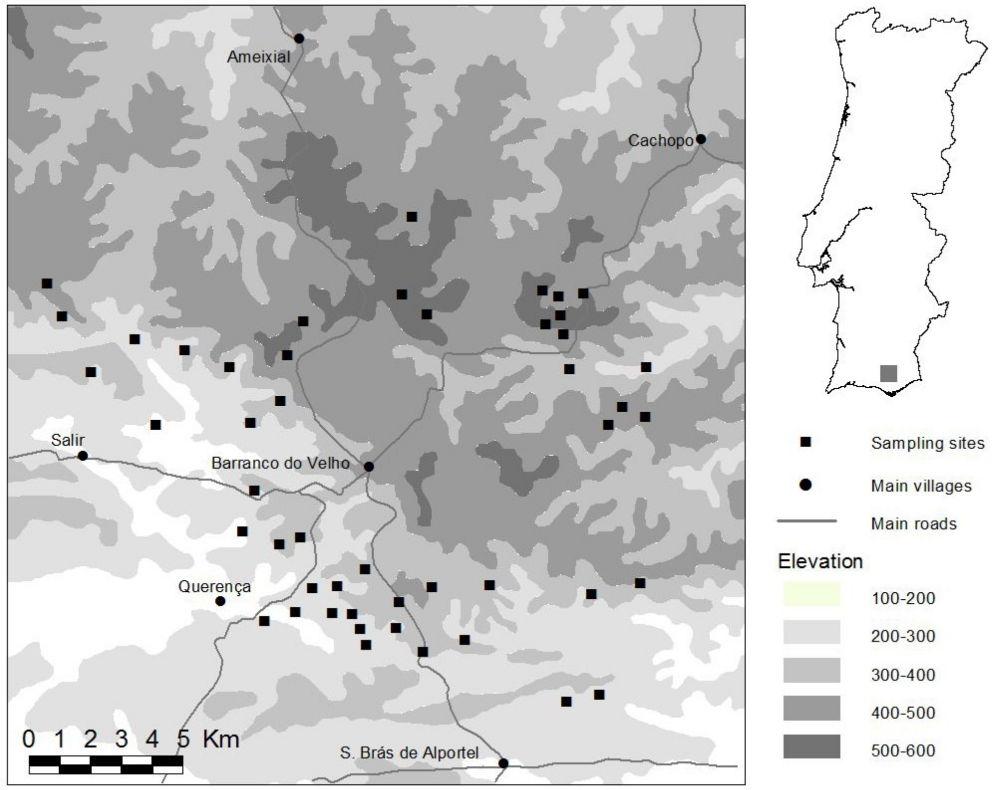


Figure 1: Location of cork oak (*Quercus suber*) forest stands sampled for vegetation composition and structure in the Caldeirão hills (southern Portugal).

Study design

The study was based on the space-for-time substitution method (e.g., Foster and Tilman, 2000), using a chronosequence of 48 cork oak forest stands ranging from zero to about 70 years since the last clearing of understory vegetation (Fig. 2). This method inferred the sequence of vegetation development since the last disturbance, from contemporary spatial variation in understory vegetation among forest stands with different management histories. Because it was not possible to fully meet the assumption that sites differed only in understory age and that each site traced exactly the same history in both its biotic and abiotic components, due for instance to differences in aspect, elevation, slope and management, this approach is unlikely to provide detailed information on temporal changes that occur in any given site (Johnson and Miyanishi, 2008). However, examination of this chronosequence was expected to reveal broad, regional-scale successional trends by averaging across site-to-site differences in vegetation structure that occur because of differences in environmental conditions and site history (Foster and Tilman, 2000).

Forest stands were selected according to a stratified random procedure, with each stratum corresponding to one of six categories of increasing structural complexity of understory vegetation. Structural categories were used instead of the actual age of understory vegetation, because the management history of forest stands could only be assessed *a posteriori* from enquiries and historical sequences of aerial photographs (see below). To obtain a full sample of understory ages represented in the region, the definition of sampling strata was based on a putative sequence of successional vegetation development in the uplands of southern Portugal (Rivas-Martinez *et al.*, 1990; Seng and Deil, 1999; Seng, 2003): 1) bare soil or covered by an herbaceous layer, with <5% woody cover; 2) sparse shrub layer composed chiefly by seedlings or saplings up to 20 cm high, or with sprouting stools up to 40 cm; 3) homogeneous, even-aged shrub layer, with heights generally between 40 cm and 1.5 m; 4) homogeneous, even-aged shrub layer, with at least some stems > 1.5 m high but with diameter at breast height (dbh) < 5 cm; 5) shrub layer with many stems > 2 m high but with dbh < 8 cm; 6) heterogeneous, uneven-aged shrub layer, with several stems with dbh > 8 cm. Although recognition of these types in the field could be prone to some subjectivity, this was unlikely to affect the results because subsequent analyses were based on estimated ages and not on structural categories.

Random locations were distributed across the study area at > 800 m from each other, within forest stands with > 30 % canopy cover by *Quercus suber*. Forests affected by fire were excluded, to avoid confounding the effects of shrub clearing and burning. Although detailed cartography of burned areas were only available from 1990 onwards (http://www.afn.min-agricultura.pt), confirmation that the selected cork oak forest stands had not burnt in earlier decades was obtained from local landowners. At each random location, a homogeneous 1-ha plot representative of one structural category was chosen and demarcated in the field. The procedure was repeated until all plots of all structural categories were selected.

Figure 2: Examples of cork oak forest stands at different times after mechanical fuel reduction treatments (Caldeirão hills, southern Portugal): (A) two years, (B) 15 years, (C) 40 years and (D) 70 years.

Management history

Understory management history was inferred primarily from a sequence of orthorectified and georeferenced digital aerial photographs covering a 45-year period: 1958 (scale 1:26,000), 1972 (scale 1:8,000), 1985 (scale 1:5,000), 1995 (scale 1:40,000) and 2002 (scale 1:5,000) (see Acácio *et al.*, 2009 for details). Information on the woody understory could be obtained from aerial photographs, due to the relatively open canopy of cork oak forest stands and because clearing affected arboreal plants such as *Arbutus unedo* and *Erica arborea*. For each image year, the condition of the understory vegetation in each sampling plot was classified in three broad classes: 1) shrub layer sparse or absent; 2) cover by Mediterranean shrublands; 3) cover by tall Mediterranean maquis with *Arbutus unedo* and *Erica arborea*. This information was used to estimate the approximate dates of shrub clearing events, assuming that: 1) class 1 indicates that a clearing event occurred < 2 years before the image year; 2) other obvious reductions in understory woody vegetation cover, including changes from classes 3 to 2, indicate that shrub clearing occurred at the middle of the time interval between two consecutive aerial photographs. Otherwise, we assumed that no clearing event took place between the two consecutive aerial photographs.

Understory clearing events before the period covered by aerial photographs were estimated using 1958 images assuming that: 1) class 2 indicates the clearing of understory < 10 years of image year; 2) class 3 indicates the clearing of understory at about 1935, because this was the historical peak of shrub clearing for cereal cultivation and livestock grazing during the Wheat Campaign. The latter assumption was based on historical sources documenting a nearly complete clearing of woody vegetation for cereal cultivation and livestock grazing at the peak of the Wheat Campaign in the 1930s (Feio, 1949; Guerreiro, 1951). Although this was a relatively crude approximation to the age of the oldest understory vegetation, it affected only four parcels that did not appear to behave as outliers or influential points in subsequent data analysis (see Results section).

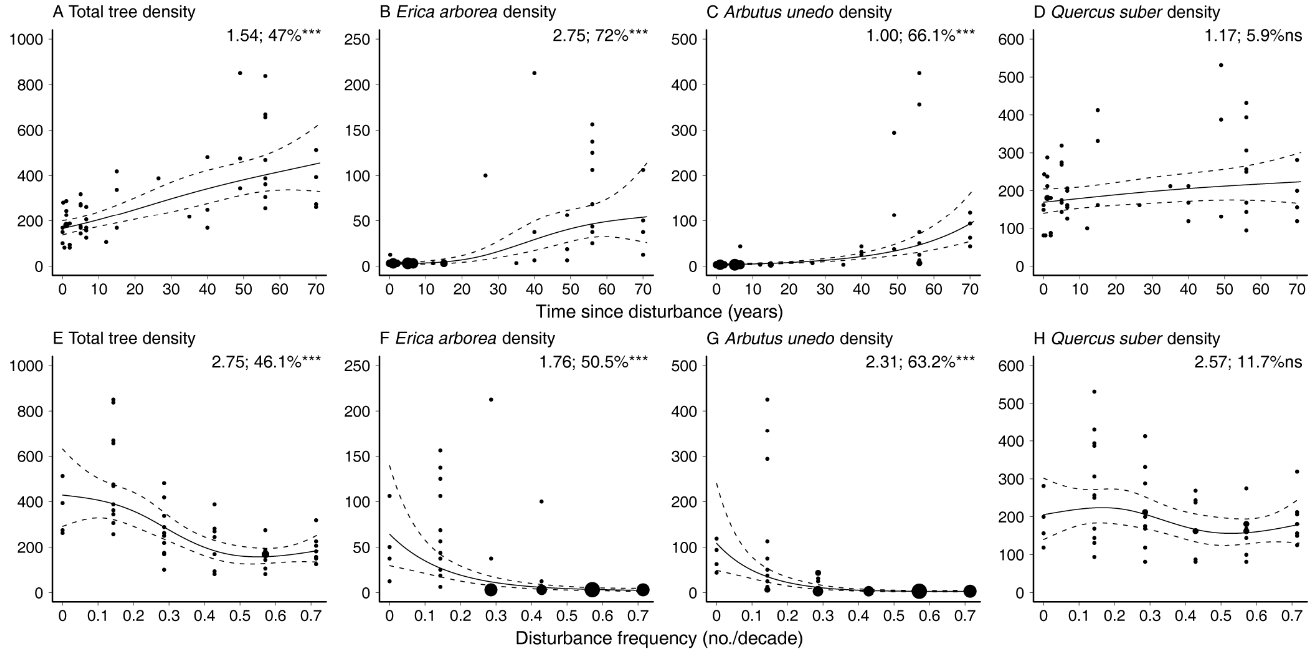


Figure 3: GAM fits (solid lines) between tree densities and management variables reflecting the time since disturbance (A-D) and disturbance frequency (E-H), and 95% Bayesian "credible intervals" (shaded area). Dot sizes are proportional to the number of observations (· 1, • 2, ● 3, ● 4, ● 5, ● 6, ● 7, ● 8, ● 9). Effective degrees of freedom, % variance explained and *P*-value are provided for each model (* *P* <0.001, ** *P* <0.01, * *P* <0.05, § *P* <0.1, ns *P* ≥ 0.1).**

Photo interpretation of vegetation classes and assumptions regarding the identification and dating of understory clearing events were based on comparisons between patterns of aerial photos of 2002 and vegetation types recognized in the field during several visits to the study area (2004). All field work and photo interpretation were made by the same person (MP), thus avoiding observer bias. Historical management regimes derived from aerial photographs were also cross-checked with information obtained from enquiries to the landowner of each forest stand. However, landowners did not maintain systematic registers of silvicultural operations, and so they sometimes missed to report earlier shrub clearing events that were evident from aerial photographs. Therefore, enquiries were only considered a reliable source of information for relatively recent events (< 10 years), though they often confirmed the interpretation of aerial photographs over more extend periods.

Information from aerial photographs and enquiries was combined to derive two variables reflecting: (1) the time since disturbance – number of years elapsed between the last shrub clearing event and the time of vegetation sampling; and (2) disturbance frequency – number of shrub clearing events occurring per decade. Although the two variables tend to be correlated, this was not the case in parcels cleared at ≤ 15 years (R=0.03, n=28), because some recently treated parcels were under recurrent understory clearing regimes, whereas others had not suffered any significant disturbance for several decades.

Vegetation sampling

Variables characterizing stand structure and understory woody vegetation attributes were sampled once in each 1-ha plot, between November 2004 and March 2005 (Supplementary Table S1). Species and diameter at breast height (dbh) were recorded for every tree (stem ≥ 6 cm dbh) on four 20 x 20 m quadrats located at regular intervals on alternate sides of a primary 100-m transect, oriented along the central portion of each sampling plot. These data were then used to estimate the density of trees of each species (trees/ha), as well as the density of large (dbh > 60cm) cork oaks.

The horizontal percentage cover of each shrub (woody stems < 6 cm dbh) species was estimated by the linear intercept method (Hays *et al.*, 1981), along four 20-m transects perpendicular to the primary transect crossing the centre of each quadrat. Woody vines such as *Smilax aspera*, *Lonicera implexa* and *L. periclymenum* were excluded, due to poorly defined boundaries of plant growth. Cover was estimated in terms of both species and broad plant functional types, because the latter may uncover responses to forest management independent of species composition (e.g., Decoq *et al.*, 2004). Shrub species were grouped according to the resprouter vs. seeder dichotomy (Supplementary Table S2), reflecting whether recovery after disturbance occurs primarily through vegetative resprout or seed regeneration (Verdú, 2000), and the dry vs. fleshy fruit dichotomy, reflecting the potential for large-scale dispersal by avian and mammalian frugivores (Herrera and Pellmyr, 2002).

Vertical shrub cover was estimated by approximating the foliage crown of each shrub to an ellipse (Nelson, 1997), centred in $(C_x,C_y)=[(X_1+X_2)/2, (Y_1+Y_2)/2]$, with X_1 and X_2 = distance from the beginning of the transect to the start and end of the intercepts with the foliage crown of a given shrub; and Y_1 and Y_2 = height of the basis and the top of the foliage crown, respectively. To estimate the vertical percentage cover by foliage crowns, the ellipses corresponding to all shrubs recorded along each transect were merged and subdivided into height strata: <0.30, 0.30-0.60, 0.60-1, 1.0-1.5, 1.5-2.0, 2.0-3.0, 3.0-4.0 m, >4.0 m.

Diversity measures

Species richness (*S*) of shrubs and trees was estimated as the total number of species recorded on the four sampling units in each plot. Spatial heterogeneity in species richness within plots was based on the average of pairwise comparisons between sampling units based on the Sørensen's similarity index (*SI*, Magurran, 1988), calculated as $SI=(2a)/(b+c)$, where *a* is the number of species shared by two sampling units, and *b* and *c* the number of species in each of the two units. Shannon diversity index (H', Shannon and Weaver, 1949) was calculated for shrubs as $H' = -\Sigma\ p_i.\ln\ p_i$, where $p_i=C_i/\ \Sigma C_i$, C_i is the percentage cover of species *i*, and ΣC_i is the sum of all cover values of all species. The Shannon index was also used to estimate foliage height diversity, with each of the eight vertical strata acting as "species". Evenness (*J'*, Pielou, 1966) was calculated as $J'=H'/\log_2 S$, where *H'* and *S* are the values as calculated above.

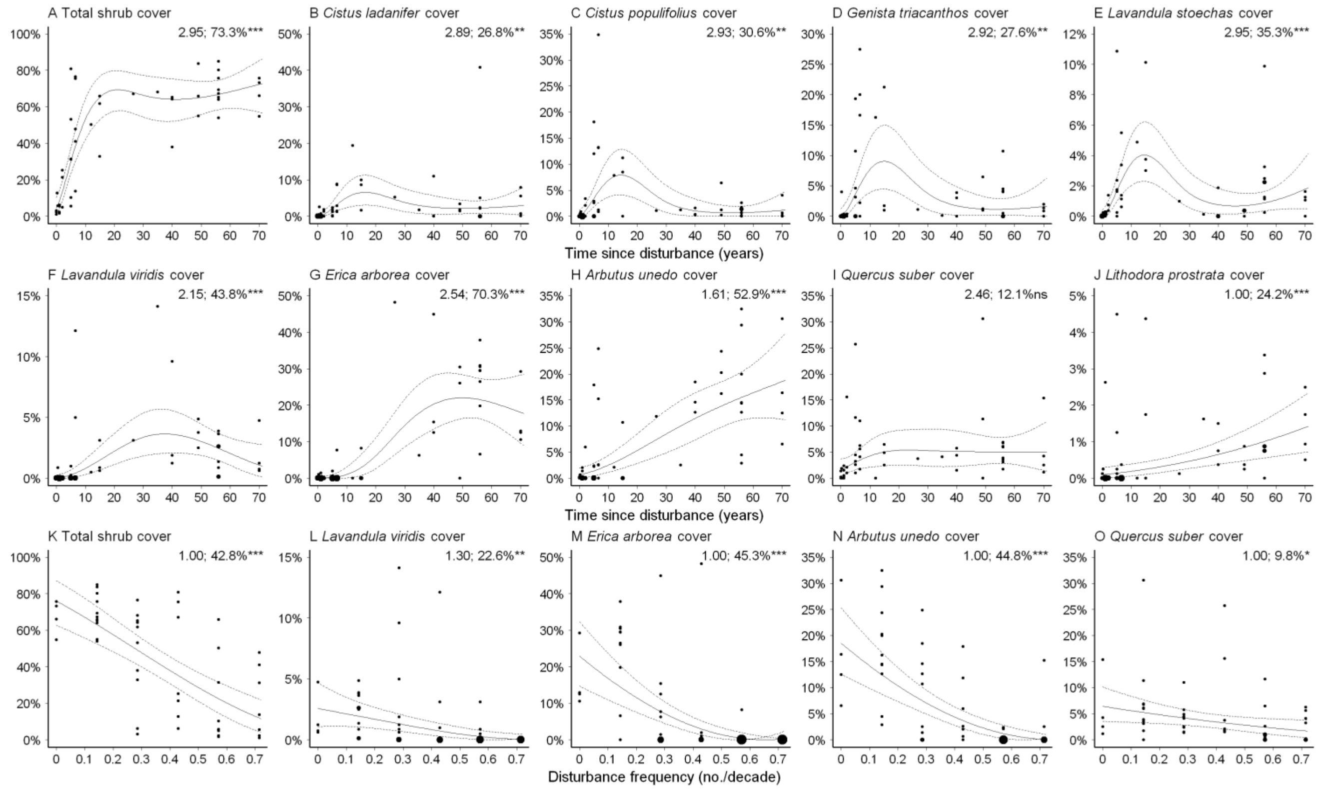


Figure 4: GAM fits (solid lines) between understory vegetation cover and management variables reflecting the time since disturbance (A-J) and disturbance frequency (K-O), and 95% Bayesian "credible intervals" (shaded area). Dot sizes are proportional to the number of observations (· 1, • 2, • 3, ● 4, ● 5, ● 6, ● 7). Effective degrees of freedom, % variance explained and *P*-value are provided for each model (* *P* < 0.001, ** *P* < 0.01, * *P* < 0.05, § *P* < 0.1). GAM fits with *P* > 0.10 are not shown.**

Statistical analysis

Vegetation data were related to management variables using Generalized Additive Models (GAMs) (Hastie & Tibshirani, 1990) fitted in R 2.7.2 (R Development Core Team, 2008) software using 'mgcv' package (Wood, 2006). A penalized cubic regression spline was chosen to smooth explanatory variables by Generalized Cross Validation (GCV). The basis dimension (k; k=4) less one degree of freedom, due to the identifiability constraint on each smooth term, was defined as upper limit to smooth estimation by GCV (Wood, 2006). We defined k=4 to allow some complexity in the functions, while avoiding over-fitting the data. Continuous variables were modelled using GAMs with a normal error with an identity link. Before analysis, the angular transformation was used to overcome the unity sum constraint of percentage cover variables (Crawley, 2007). A quasi-Poisson error with a log link function was used for species richness data, thereby ensuring that fitted values are positive. Quasi-Poisson was used rather than Poisson due to overdispersion (variance > mean) of the response variable (Crawley, 2007). Confidence (credible) regions for each function were estimated based on 95% Bayesian "credible intervals" (Wood, 2006).

RESULTS

Overstory composition and density

The dominant tree in all stands was *Q. suber*, while arboreal *Erica arborea* and *Arbutus unedo* were the only other abundant trees. The overall density of trees increased with time since disturbance (Fig. 3A), and declined with increasing disturbance frequency (Fig. 3E). Density of *Q. suber* did not vary with either disturbance timing (Fig. 3D) or frequency (Fig. 3H). The density of large *Q. suber* was not affected by understory clearing. The densities of arboreal *Erica arborea* and *Arbutus unedo* increased after disturbance during about 40-50 years and leveled off thereafter (Fig. 3B-C), whereas they declined sharply in frequently cleared stands (Fig. 3F-G).

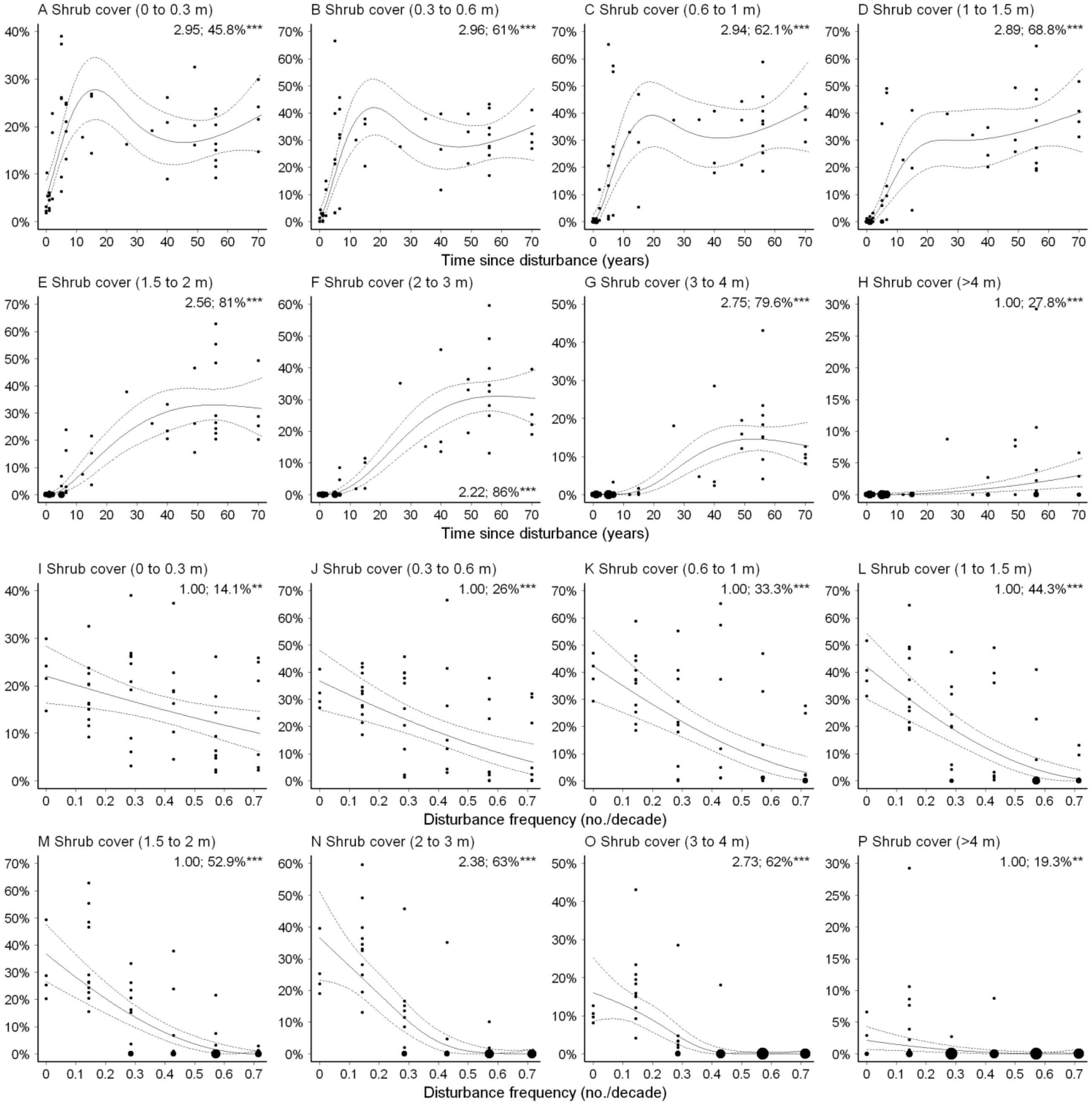


Figure 5: GAM fits (solid lines) between vertical understory structure and management variables reflecting the time since disturbance (A-H) and disturbance frequency (I-P), and 95% Bayesian "credible intervals" (shaded area). Dot sizes are proportional to the number of observations (· 1, • 2, • 3, ● 4, ● 5, ● 6, ● 7, ● 8, ● 9). Effective degrees of freedom, % variance explained and *P*-value are provided for each model (* *P* < 0.001, ** < 0.01, * *P* < 0.05, § *P* < 0.1). GAM fits with *P* > 0.10 are not shown.**

Horizontal understory vegetation cover

Overall horizontal cover by woody understory was very low in recently cleared stands, but it increased sharply with time since disturbance for about 20 years, appearing to level off thereafter (Fig. 4A). Among the most widespread species (frequency of occurrence >50%), the quickest recovery was estimated for *C. ladanifer*, *C. populifolius*, *Genista triacanthos*, and *Lavandula stoechas*, reaching maximum cover at about 15 years after clearing disturbance and declining thereafter (Fig. 4B-E). A comparable pattern was found for *Lavandula viridis*, though it showed a slower recovery and peaked at about 30-40 years after disturbance (Fig. 4F). The slowest recovery was found for *E. arborea*, with cover levelling off or slightly declining after about 50 years (Fig. 4F), and for *A. unedo* and *Lithodora prostrata*, with cover increasing continuously across the chronosequence (Fig. 4H,J). Cover by *Q. suber* increased for about 15 years and levelled off thereafter (Fig. 4I). Disturbance frequency was negatively related to the overall woody cover and that of *L. viridis*, *Q. suber*, *E. arborea* and *A. unedo* (Fig. 4K-O), but no significant relationship was found for quickly recovering species (P > 0.10; graphs not shown). Negative relationships were strongest for *E. arborea* and *A. unedo* (Fig. 4M-N), which were among the slowest recovering species.

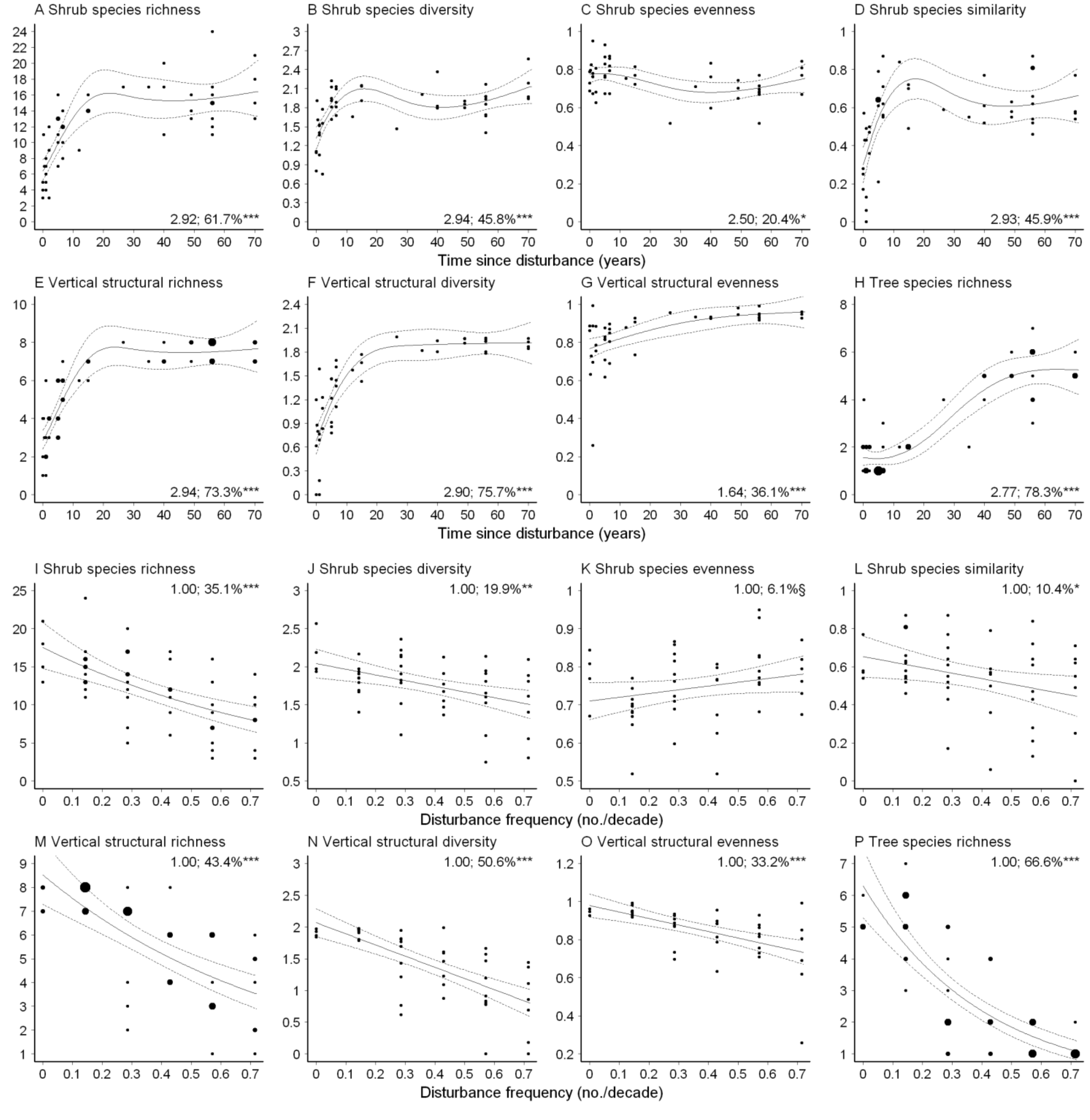


Figure 6: GAM fits (solid lines) between species and vertical structure diversity indexes and management variables reflecting the time since disturbance (A-H) and disturbance frequency (I-P), and 95% Bayesian "credible intervals" (shaded area). Dot sizes are proportional to the number of observations (· 1, • 2, ● 3, ● 4, ● 5, ● 6). Effective degrees of freedom, % variance explained and *P*-value are provided for each model (* *P* < 0.001, ** *P* < 0.01, * *P* < 0.05, § *P* < 0.1). GAM fits with *P* > 0.10 are not shown.**

Vertical understory structure

Cover at the lowest vertical strata (< 1 m) increased sharply for about 15 years, declining slightly thereafter to a minimum at about 40 years after disturbance (Fig. 5A-C). Cover in intermediate strata also increased sharply for about 20 years after disturbance, keeping an increasing trend thereafter, though at a much slower rate (Fig. 5D). At the upper strata (> 1.5 m), cover increased for about 50 years after disturbance, levelling off or slightly decreasing thereafter (Fig. 5E-G). The only exception was the > 4 m strata, where cover increased linearly with time since disturbance (Fig. 5H). The frequency of clearing events was negatively related with understory cover at all vertical strata, though lower strata tended to be less affected than upper strata, except for the > 4 m level (Fig. 5I-P).

The number of strata occupied by woody understory vegetation and the vertical structural diversity (H') increased in the first 20 years after disturbance and then levelled off (Fig. 6E-F), whereas they both declined linearly with increasing disturbance frequency (Fig. 6M-N). Vertical evenness tended to increase with time since disturbance (Fig. 6G) and declined with disturbance frequency (Fig. 6O).

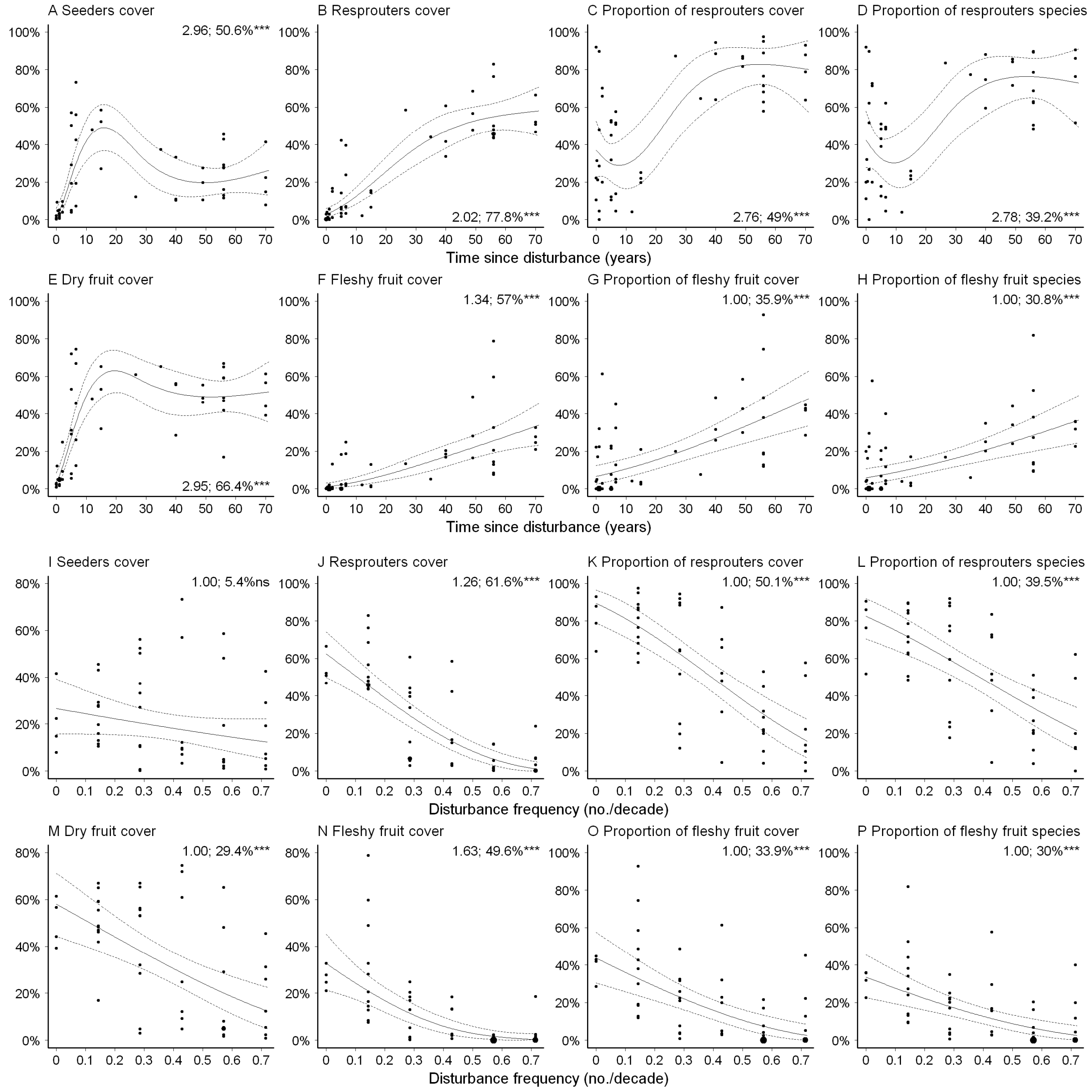


Figure 7: GAM fits between functional organization and management variables reflecting the time since disturbance (A-H) and disturbance frequency (I-P) (solid lines), and 95% Bayesian "credible intervals" (shaded area). Dot sizes are proportional to the number of observations (· 1, • 2, ● 3, ● 4). Effective degrees of freedom, % variance explained and *P*-value are provided for each model (* $P < 0.001$, ** $P < 0.01$; * $P < 0.05$; § $P < 0.1$). GAM fits with $P > 0.10$ are not shown.**

Species diversity

Tree species richness was very low in recently cleared stands and it increased thereafter to a plateau about 50 years after disturbance (Fig. 6H). Richness of woody understory species increased after disturbance for about 20 years and then tended to level off (Fig. 6A). Both diversity (H') and Sorensen's index reflecting spatial homogeneity in woody understory species composition increased for about 15 years after disturbance, and then declined to a lower plateau about 40 years after disturbance (Fig 6B,D). In contrast, the evenness of woody understory species declined after disturbance for about 40 years and increased thereafter (Fig. 6C). All diversity parameters tended to decline linearly with increasing disturbance frequency, whereas evenness showed the opposite pattern (Fig. 6I-P).

Functional types

Cover by seeder and dry-fruit producing shrubs increased sharply after understory clearing, showing a peak at about 20 years and declining thereafter to a lower plateau at about 50 years (Fig. 7A,E). The overall cover by resprouter species, as well as the ratio of resprouters to seeders, increased slowly up to a maximum about 50 years after disturbance and then tended to level off (Fig. 7B-D). The overall cover by fleshy-fruit producing species, as well as the ratio of fleshy- to dry-fruit producing species, increased slowly throughout the study period (Fig. 7F-G). Cover by seeders was not influenced by the frequency of disturbance events, whereas cover by resprouters, and that of dry- and fleshy fruit producers, as well as the ratios of resprouters to seeders, and that of fleshy- to dry-fruit producers, showed significantly negative linear relations with disturbance frequency (Fig. 7I-P).

DISCUSSION

Overall patterns

Fuel reduction treatments in cork oak forests reflected a strong specialization on cork production, generally involving full elimination of potential tree and shrub competitors (Natividade, 1950; Montero and Cañellas, 1999). During treatments, the soil was often ploughed using disc harrows which eliminated both aerial and underground parts of the plants, destroying the root systems and the bud bank of resprouting species, and generally leaving only *Q. suber* trees. Despite this major disturbance, regeneration of pioneer shrubs occurred in just a few years and species richness was restored in about 15 years, though a far longer period (> 50 years) appeared to be required for significant increases in tree species richness, in cover by large resprouters and fleshy-fruited species, and in the development of a complex multi-layered understory. There was thus evidence that full recovery of understory composition and structure may be slow after mechanical treatments, particularly in frequently treated stands. Widespread and recurrent fuel reduction may thus drive a process of simplification, similar to that resulting over historical times in the replacement of mixed oak woods by nearly monospecific cork oak forests and savannas (Urbieta *et al.*, 2008).

Potential shortcomings and limitations

Interpretation of the main patterns observed in this study need to consider the potential limitations and constraints of the chronosequence approach (Foster and Tilman, 2000; Johnson and Miyanishi, 2008). In particular, variation among sites in some physical characteristics and historical management makes it necessary to infer only broad, regional-scale successional trends (Foster and Tilman, 2000), rather than temporal changes occurring at any specific site (Johnson and Miyanishi, 2008). One of the main constraints was that understory clearing was less likely in steep slopes due primarily to higher economic costs (Acácio *et al.*, 2009), and so recurrently cleared stands tended to be located in relatively flat areas. This could not be controlled through sampling design and it may have resulted in underestimates of understory recovery rates in flat areas, because soil erosion in steep slopes tends to delay the development of Mediterranean vegetation after disturbance (Bochet *et al.*, 2009). Inferring the history of understory management from aerial photographs may also produce underestimates of recovery rates, at least in principle, because vegetation may be cleared and then recover without leaving obvious signs in consecutive photographs. This problem was probably minimal, however, because fuel treatments affected areas much larger than our study parcels and they produced long-lasting changes in vegetation cover and pattern that were obvious in aerial photographs over long time frames. In general, these problems are unlikely to affect significantly the inferences drawn on vegetation successional dynamics, though they probably contributed for scatter around the estimated average response curves.

Another problem was the high correlation between the time since clearing and clearing frequency for understory ages > 15 years, which made it difficult to isolate the unique effects of each variable. Nevertheless, there were some ecologically meaningful cases in which only one of the variables showed significant effects, suggesting that disturbance timing and frequency had indeed distinct effects on understory vegetation. For instance, *Cistus* species tended to be strongly influenced by disturbance timing but not frequency, strongly increasing in recently disturbed stands irrespective of past disturbance history.

Finally, although this study encompassed a time interval far longer than that of other studies addressing the consequences of fuel management (e.g., Decocq *et al.*, 2004, Calvo *et al.*, 2005, Pérez-Ramos *et al.*, 2008a), this was still shorter than the long time frames usually required for appreciating the dynamics of forest ecosystems (Frelich, 2002; Thomas and Packham, 2007). This was unavoidable due to the relatively young age of the studied cork oak forests (< 100 years) and to the lack of adequate historical data.

Long-term understory recovery

Changes in understory vegetation observed in this study support the idea of mechanical fuel reduction causing a shift between plant communities with contrasting composition, structure and functional organization, as already suggested for fire disturbances (Zedler *et al.*, 1983; Díaz-Delgado *et al.*, 2002; Rodrigo *et al.*, 2004). During the first 20 years of the chronosequence the understory was dominated by pioneer seeder and dry-fruit producing species such as *C. ladanifer*, *C. populifolius*, *G. triachantos*, and *L. stoechas*, which are associated with repeatedly disturbed environments (Herrera, 1997; Seng and Deil, 1999; Tárrega *et al.*, 2001; Acácio *et al.*, 2007). This was followed in the next 20 years by a transition phase with a mixed composition of pioneer seeders and resprouters, eventually reaching after > 50 years a plant community structurally dominated by large resprouters such as *Erica arborea* and *Arbutus unedo*. These changes were matched by strong increases in diversity and cover of fleshy-fruited species, and by the development of complex multi-layered understory vegetation structure across the chronosequence, because Mediterranean seeder shrubs tend to be anemochorous, dry-fruited, and mostly small (<1.5 m) species, whereas resprouters tend to be vertebrate-dispersed, fleshy-fruited and often tall (>2 m) species (Herrera, 1992; Verdú, 2000).

Recovery of pioneer seeder shrubs likely occurred through germination from the local seed bank, as they started to regenerate immediately after clearing and reached high cover in 15 years. Although pioneer Mediterranean shrubs are most often associated with the occurrence of fire and heat stimulation (Roy *et al.*, 1992; Trabaud, 2000), seed germination is also stimulated by mechanical disturbances (Tárrega *et al.*, 2001; Calvo *et al.*, 2005). Recruitment only occurs during the first few years after disturbance, and so subsequent shrubland development probably resulted primarily from the growth of plants recruited shortly after clearing (Roy *et al.*, 1992; Calvo *et al.*, 2002). Pioneer Mediterranean seeder shrubs are relatively short-lived (Roy *et al.*, 1992), and so their senescence and death probably caused the observed decline beginning at around 15 years after clearing. Reduction of cover by pioneer shrublands at about this age probably provided colonization and growth opportunities for other woody plants (Calvo *et al.*, 2002), including other seeder shrubs characteristic of mid and late-successional stages, such as *Lavandula viridis* and *Lithodora prostrata*, respectively. Recovery of dominant resprouters also occurred after the decline of pioneer shrubs, which agrees with their association with late successional stages in Mediterranean ecosystems (Verdú, 2000). In our particular case it is likely that recovery was particularly slow because ploughing depleted the bud bank, whereas a quicker colonization could be expected after disturbances not affecting the root system, such as fire or mechanical cutting of aboveground phytomass (Calvo *et al.*, 2002). When the root system is preserved, resprouting can occur immediately after disturbance, taking advantage of the nutrients and water accumulated in the roots (Verdú, 2000), but is slow when the bud bank is depleted, probably involving resprouting from bud remnants or seed germination. Dense vegetation is required for the establishment of most Mediterranean resprouters from seeds, including *A. unedo* (Mesléard and Lepart, 1991), which may have further delayed recovery after recurrent ploughing. This may have contributed for the scarcity in our chronosequence of many late-successional resprouters and fleshy-fruited species that are relatively common in evergreen oak forests elsewhere in south-western Iberia (Marañon *et al.*, 1999; Seng and Deil, 1999; Seng, 2003; Krohmer and Deil, 2003), such as, e.g., *Viburnum tinus*, *Rhamnus alaternus*, and *Phillyrea latifolia*, suggesting that a period longer than 70 years is required for their full recovery after recurrent disturbance.

Recovery of understory *Q. suber* was in marked contrast with the other dominant resprouters, as it increased from almost complete absence to maximum cover in just about 15 years after mechanical clearing, largely corresponding to increases in juvenile and sapling densities, and it was little affected by treatment frequency. This was probably a consequence of basal sprouting of mature trees (Moreira *et al.*, 2009), which may be an induced response to injury of superficial roots or changes in environmental conditions associated with understory clearing (Paysen *et al.*, 1991; Del Tredici, 2001). The initial contribution of seeding to *Q. suber* regeneration was probably low, due to high acorn predation, low rates of germination, and high seedling mortality in herbaceous habitats and early-successional shrublands prevailing in the understory of recently and recurrently cleared stands (Pons and Pausas, 2006; Acácio *et al.*, 2007). Regeneration through seeding may have been higher in late-successional forest habitats (Acácio *et al.*, 2007), though understory cover of *Q. suber* remained essentially stable across the chronosequence after the first decade following clearing. This probably resulted from the formation of a typical seedling and sapling bank (*sensu* Pons and Pausas, 2006), corresponding to a pool of suppressed slow-growing individuals waiting for improved conditions for resuming growth to maturity, often requiring the formation of canopy gaps through small or large scale disturbances (Espelta *et al.*, 1995; Gracia *et al.*, 2001; Pons and Pausas, 2006). Although mechanical fuel management could open such gaps through, e.g., the removal of large *A. unedo* and *E. arborea*, this was unlikely to result in tree recruitment under current practices due to virtual destruction of the “seedling bank” during treatments. The seedling and sapling bank may thus contribute little to tree recruitment under current management practices, as it was found in other Mediterranean oak forests (Gracia *et al.*, 2001). This view is supported by the constancy of *Q. suber* tree densities across the chronosequence, irrespective of fuel reduction timing and frequency, and the general shortage of small trees in size-frequency distributions (M. Porto and P. Beja, Unpublished Data).

Analyses in this study focused on the stand scale, though local recovery pathways may be influenced by the distribution of colonization sources and dispersal agents across the landscape, which may for instance filter out species that are regionally unavailable or rare due to environmental or historical factors (Bellemare *et al.*, 2002). Limitation of colonization sources may have determined the shortage of late-successional resprouters and fleshy-fruited species in our study area, where populations of these species were probably strongly depleted during the first half of the 20th century, due to very extensive deforestation, and cereal cultivation and grazing under the tree canopy of remaining, savanna-like forests (Feio, 1949; Guerreiro, 1951; Acácio *et al.*, 2009; Bugalho *et al.*, 2009). During the same period, however, *A. unedo* was likely protected in remnant forest stands because its fruit was highly prized for the traditional production of a distilled beverage, which may have favoured its subsequent expansion in late-successional understory after agricultural abandonment. Past (> 50 years) management decisions taken at the stand scale thus seemed to have shaped the colonization pool at the landscape scale, which then likely influenced the rates and pathways of understory recovery after disturbance at the stand scale. These feed-back loops between the stand and landscape scales deserve further attention by researchers, as this may generate a complex disturbance-succession dynamics, with consequences for the management and conservation of Mediterranean forest landscapes.

Management implications

Developing and maintaining landscape heterogeneity through management emulating natural disturbance patterns and processes is generally considered essential for the conservation of forest biodiversity (Crow and Perera, 2004; Lindenmayer *et al.*, 2006; Lehmkuhl *et al.*, 2007). However, in forest landscapes which have long since lost their natural disturbance regimes and natural patterns of heterogeneity, such as Euro-Mediterranean forests, mechanical fuel reduction may provide a practical alternative to create the spatial heterogeneity needed to sustain high biodiversity levels. For instance, in cork oak landscapes the pioneer *C. ladanifer* shrublands associated with recurrent fuel management are key habitats for European rabbits (*Oryctolagus cuniculus*) (Beja *et al.*, 2007), which are important food resources for the endangered Iberian lynx (*Lynx pardinus*) and Bonelli's eagle (*Aquila fasciata*), that tend to shelter and reproduce in little disturbed forest patches (Palma *et al.*, 1999, 2006). This type of spatial heterogeneity can be restored in the absence of fire through the spatial distribution of forest stands with different timings and recurrence of fuel reduction treatments, thereby creating a landscape mosaic of patches in different successional stages.

Currently, widespread efforts to reduce fire risk may contribute to over-dominance at the landscape scale of forest stands with early-successional understory, characterized by reduced richness of woody species and low structural complexity. This may result in the decline of specialized species associated with relatively undisturbed forests (Marañon *et al.*, 1999; Hampe and Arroyo, 2002; De La Montaña *et al.*, 2006). These negative consequences are probably worsened by the use of treatments such as disc harrowing, which delay the recovery of resprouters typical of little disturbed forests, including fleshy-fruited species and probably also their bird and mammal dispersal agents (Herrera and Pellmyr 2002). These negative effects might be minimised through the use of brush cutting devices preserving the root system, which may foster a quicker recovery of resprouters and thus higher species diversity in early-successional stages. Spatial variation in the use of fuel reduction techniques might contribute for creating spatial heterogeneity of early-successional understory habitats, given the contrasting response of overall plant communities to different anthropogenic disturbances (e.g., Tárrega *et al.*, 2001; Calvo *et al.*, 2002, 2005).

Maintaining patches with well-developed multi-layered understory may be particularly challenging in Mediterranean forests, as they are particularly hazardous for the spread of damaging wildfires. For instance, postfire survival of cork oaks is negatively related with shrub cover, thereby justifying a recommendation for understory clearing some time before cork stripping, to reduce fire severity and tree mortality (Moreira *et al.*, 2007). Considering that well-developed multi-layered understory, as well as cover by resprouters and fleshy-fruited species, may take decades to recover after recurrent mechanical disturbance, we should expect these to be largely lost under the typical 9-year cycle of cork exploitation. Conservation strategies should thus strive to safeguard some forest stands from mechanical disturbance, where natural development of understory vegetation should be allowed. These stands should be interspersed with patches where fuel reduction treatments are carried out regularly, thereby reducing fire hazard at the landscape scale (Loehle, 2004; Lehmkuhl *et al.*, 2007). Defining the type, number, area and distribution of patches to be retained, however, is a complex optimization problem that should be the subject of future research, requiring the integration of

Mediterranean landscape succession disturbance-dynamics (e.g., Millington *et al.*, 2009) and accounting for multiple management objectives such as biodiversity conservation, fire hazard reduction, and sustainable forest use (Bugalho *et al.*, 2009; Santos and Thorne, 2010).

ACKNOWLEDGEMENTS

This study was funded by IFADAP-Program AGRO 8.1 (project 458 - 2003.09.002326.2), and by the Portuguese Science and Technology Foundation through grants SFRH/BPD/62865/2009 to LR and SFRH/BD/28974/2006 to MP. We thank researchers and technicians of the Forest Producers Association of Barranco do Velho, the Association In Loco, the Association for the Defence of Mértola Heritage, and the Centre for Applied Ecology “Baeta Neves”, for collaboration in the development of this project. We also thank R. Guerreiro and R. Silva for help in field work, and F. Moreira and M. Bugalho for critical reading of the manuscript.

REFERENCES

Agee, J.K., Skinner, C.N., 2005. Basic principles of forest fuel reduction treatments. Forest Ecology and Management 211, 83–96.

Ager, A.A., Vaillant, N.M., Finney, M.A., 2010. A comparison of landscape fuel treatment strategies to mitigate wildland fire risk in the urban interface and preserve old forest structure. Forest Ecology and Management 259, 1556-1570.

Acácio, V., Holmgren, M., Jansen, P.A. , Schrotter, O., 2007. Multiple recruitment limitation causes arrested succession in Mediterranean cork oak systems. Ecosystems 10, 1220-1230.

Acácio, V., Holmgren, M., Rego, F., Moreira, F., Mohren, G.M.J., 2009. Are drought and wildfires turning Mediterranean cork oak forest into persistent shrublands? Agroforestry Systems 76, 389-400.

Aronson, J., Pereira, J.S., Pausas, J. (Eds.), 2009. Cork oak woodlands on the edge: Ecology, biogeography, and restoration of an ancient Mediterranean ecosystem. Island Press, Washington DC, USA.

Beja, P., Pais, M., Palma, L., 2007. Rabbit *Oryctolagus cuniculus* habitats in Mediterranean scrubland: the role of scrub structure and composition. Wildlife Biology 13, 28-37.

Bellemare, J., Motzkin, G., Foster, D.R., 2002. Legacies of the agricultural past in the forested present: an assessment of historical land-use effects on rich mesic forests. Journal of Biogeography 29, 1401-1420.

Berrahmouni, N., Regato, P., Ellatifi, M., Daly-Hassen, H., Bugalho, M.N., Bensaid, S., Díaz, M., Aronson, J., 2009. Ecoregional Planning for Biodiversity Conservation. In: Aronson, J., Pereira, J.S., Pausas, J. (Eds.), Cork oak woodlands on the edge: Ecology, biogeography, and restoration of an ancient Mediterranean ecosystem. Island Press, Washington DC, pp. 213-216.

Blondel, J., Aronson, J., Bodiou, J.-Y., Boeuf, G., 2010. The Mediterranean Region. Biological Diversity in Space and Time. Oxford University Press, Oxford, UK.

Bochet, E., García-Fayos, P., Poesen, J., 2009. Topographic thresholds for plant colonization on semi-arid eroded slopes. Earth Surface Processes and Landforms 34, 1758–1771.

Bugalho M.N., Plieninger, T., Aronson, J., Ellatifi, M., Crespo, D.G., 2009. Open woodlands: a diversity of uses (and overuses). In: Aronson, J., Pereira, J.S., Pausas, J. (Eds.), Cork oak woodlands on the edge: Ecology, biogeography, and restoration of an ancient Mediterranean ecosystem. Island Press, Washington DC, pp. 33-45.

Calvo, L., Tárrega, R., Luis, E. 1999. Post-fire succession in two Quercus pyrenaica communities with different disturbance histories. Annals of Forest Science 56, 441-447.

Calvo, L., Tárrega, R., Luis, E., 2002. Secondary succession after perturbations in a shrubland community. Acta Oecologica 23, 393-404.

Calvo, L., Tárrega, R., Luis, E., Valbuena, L., Marcos, E., 2005. Recovery after experimental cutting and burning in three shrub communities with different dominant species. Plant Ecology 180, 175–185.

Crawley, M.J., 2007. The R book, John Wiley & Sons, Ltd, Chichester.

Crow, T. R., Perera, A.H., 2004. Emulating natural landscape disturbance in forest management: an introduction. Landscape Ecology 19, 231-233.

Decocq, G., Aubert, M., Dupont, F., Alard, D., Saguez, R., Wattez-Franger, A., De Foucault, B., Delelis-Dusollierand, A., Bardat, J., 2004. Plant diversity in a managed temperate deciduous forest: understory response to two silvicultural systems. Journal of Applied Ecology 41, 1065-1079.

Del Tredici, P., 2001. Sprouting in temperate trees: a morphological and ecological review. Botanical Review 67, 121–140.

Díaz-Delgado, R., Lloret, F., Pons, X., Terradas, J. 2002. Satellite evidence of decreasing resilience in Mediterranean plant communities after recurrent wildfires, Ecology 83, 2293-2303.

Espelta, J.M., Riba, M., Retana, J., 1995. Pattern of seedling recruitment in West-Mediterranean Quercus ilex forests influenced by canopy development. Journal of Vegetation Science 6, 465–472.

Feio, M., 1949. Le Bas Alentejo et l’Algarve (Livret-Guide de l’Excursion E). XVI Congrès Internationale de Géographie, CEG, Lisbon.

Foster, B.L., Tilman, D., 2000. Dynamic and static views of succession: testing the descriptive power of the chronosequence approach, Plant Ecology 146, 1-10.

Foster, D.R., Motzkin, G., 2002. Interpreting and conserving the openland habitats of coastal New England: insights from landscape history. Forest Ecology and Management 185, 127-150.

Frelich, L.E., 2002. Forest dynamics and disturbance regimes. Studies from temperate evergreen-deciduous forests. Cambridge University Press, Cambridge, UK.

Gracia, M., Retana, J., Pico, F.X., 2001. Seedling bank dynamics in managed holm oak (Quercus ilex) forests. Annals of Forest Science 58, 843–852.

Grove, A. T., Rackham, O., 2001. The nature of Mediterranean Europe: an ecological history. Yale University Press, London, UK.

Guerreiro, M.G., 1951. Valorização da Serra Algarvia : a erosão, a cobertura vegetal e a água. Direcção Geral dos Serviços Florestais e Aquícolas, Lisbon.

Hampe, A., Arroyo, J., 2002. Recruitment and regeneration in populations of an endangered South Iberian Tertiary relict tree. Biological Conservation 107, 263-271.

Hastie, T.J., Tibshirani, R.J., 1990. Generalized Additive Models. Chapman & Hall, London, UK.

Hays, R.L., Summers, C., Seitz, E., 1981. Estimating wildlife habitat variables. FWS/OBS-81/47, U.S.D.I. Fish and Wildlife Service. USA.

Herrera, C.M. 1992. Historical effects and sorting processes as explanations for contemporary ecological patterns: character syndromes in Mediterranean woody plants. American Naturalist 140, 421-446.

Herrera, C.M., Pellmyr, O. (Eds.), 2002. Plant-Animal Interactions. An Evolutionary Approach. Blackwell Publishing, Oxford, UK.

Herrera, J. 1997. Effects of disturbance on the reproductive potential of Lavandula stoechas, a Mediterranean sclerophyllous shrub. Ecography 20, 88-95.

Johnson, E.A., Miyanishi, K., 2008. Testing assumptions of chronosequences in succession. Ecology Letters 11, 419-431.

Krohmer, J., Deil, U., 2003. Dynamic and conservative landscapes? Present vegetation cover and land-use changes in the Serra de Monchique (Portugal). Phytocoenologia 33, 767-799.

Lehmkuhl, J. F., Kennedy, M., Ford, E.D., Singleton, P.H., Gaines, W.L., Lind, R.L., 2007. Seeing the forest for the fuel: Integrating ecological values and fuels management. Forest Ecology and Management 246, 73–80.

Lindenmayer, D.B., Franklin, J.F., Fischer, J., 2006. General management principles and a checklist of strategies to guide forest biodiversity conservation. Biological Conservation 131, 433-445.

Lloret, F. Vilà, M., 1997. Clearing of vegetation in Mediterranean garrigue: response after a wildfire. Forest Ecology and Management 93, 227-234.

Magurran, A. E., 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, NJ, USA.

Marañon, T., Ajbilou, R., Ojeda, F., Arroyo, J., 1999. Biodiversity of woody species in oak woodlands of southern Spain and northern Morocco. Forest Ecology and Management 115, 147-156

Mesléard, F., Lepart, J., 1991. Germination and seedling dynamics of Arbutus unedo and Erica arborea on Corsica. Journal of Vegetation Science 2, 155-164.

Millington, J.D.A., Wainwright, J., Perry, G.L.W., Romero-Calcerrada, R., Malamud, B.D., 2009. Modelling Mediterranean landscape succession-disturbance dynamics: A landscape fire-succession model. Environmental Modelling & Software 24, 1196-1208.

De La Montaña, E., Rey-Bernayas, J.M., Carrascal, L.M., 2006. Response of bird communities to silvicultural thinning of Mediterranean maquis. Journal of Applied Ecology, 43, 651-659.

Montero, G., Cañellas, I., 1999. Manual de reforestación y cultivo de alcornoque (Quercus suber L.). Ministerio de Agricultura, Pesca y Alimentación, Instituto Nacional de Investigación y Tecnologia Agrária y Alimentaria, Madrid, Spain.

Moreira, F., Catry, F., Duarte, I., Acácio, V., Silva, J.S., 2009. A conceptual model of sprouting responses in relation to fire damage: an example with cork oak (Quercus suber L.) trees in Southern Portugal. Plant Ecology 201, 77–85.

Moreira F, Duarte, I., Catry, F., Acácio, V., 2007. Cork extraction as a key factor determining post-fire cork oak survival in a mountain region of southern Portugal. Forest Ecology and Management 253, 30–37.

Moriondo, M., Good, P., Durao, R., Bindi, M., Giannakopoulos, C., Corte Real, J., 2006. Potential impact of climate change on forest fire risk in Mediterranean area, Climate Research 31, 85-95.

Natividade, J.V., 1950. Subericultura. Direcção Geral das Florestas, Lisboa, Portugal.

Nelson, R., 1997. Modeling forest canopy heights: the effects of canopy shape. Remote Sensing of Environment 60, 327-334.

Onaindía, M., Dominguez, I., Albizu, I., Garbisu, C., Amezaga, I., 2004. Vegetation diversity and vertical structure as indicators of forest disturbance. Forest Ecology and Management 195, 341-354.

Palma, L., Beja, P., Rodrigues, M., 1999. The use of sighting data to analyse Iberian lynx habitat and distribution. Journal of Applied Ecology 36, 812–824.

Palma, L., Beja, P., Pais, M., Fonseca, L.C., 2006. Why do raptors take domestic prey? The case of Bonelli's eagles and pigeons. Journal of Applied Ecology 43, 1075-1086.

Pausas, J.G., Llovet, J., Rodrigo, A., Vallejo, R., 2008. Are wildfires a disaster in the Mediterranean basin? – A review. International Journal of Wildland Fire 17, 713–723.

Paysen, T. E., Narog, M.G., Tissell, R.G., Lardner, M.A., 1991. Trunk and root sprouting on residual trees after thinning a Quercus chrysolepis stand. Forest Science 37, 17-27

Pérez-Ramos, I.M., Zavala, M.A., Marañón, T., Díaz-Villa, M.D., Valladares, F., 2008. Dynamics of understorey herbaceous plant diversity following shrub clearing of cork oak forests: a five-year study. Forest Ecology and Management 255, 3242-3253.

Pielou, E.C., 1966. The measurement of diversity in different types of biological collections. Journal of Theoretical Biology 13, 131-144.

Pons, J., Pausas, J.G., 2006. Oak regeneration in heterogeneous landscapes: the case of fragmented Quercus suber forests in the eastern Iberian Peninsula. Forest Ecology and Management 231, 196–204.

Potts, J.B., Marino, E., Stephens, S.L., 2010. Chaparral shrub recovery after fuel reduction: a comparison of prescribed fire and mastication techniques. Plant Ecology 210, 303-315.

R Development Core Team, 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Rivas-Martínez, S., Lousã, M., Díaz, T.E., Fernández-González, F., Costa, J.C., 1990. La vegetatión del Sur de Portugal (Sado, Alentejo y Algarve). Itinera Geobotánica 3, 5-126.

Roy, J., Sonié, L., 1992. Germination and population dynamics of Cistus species in relation to fire. Journal of Applied Ecology 29, 647-655.

Rodrigo, A., Retana, J., Picó, F.X., 2004. Direct regeneration is not the only response of Mediterranean forests to large fires. Ecology 85, 716–729.

Santos, M.J., Thorne, J.H., 2010. Comparing culture and ecology: conservation planning of oak woodlands in Mediterranean landscapes of Portugal and California. Environmental Conservation 37, 155-168.

Shannon, C., Weaver, W., 1949. The mathematical theory of communication. University of. Illinois Press, Urbana, Illinois, USA.

Seng, M., 2003. The use of understorey heterogeneity, species diversity and stand structure for characterizing Quercus suber forests in south-western Spain and Portugal - a methodological approach. Phytocoenologia 33, 749-766.

Seng, M., Deil, U., 1999. Forest vegetation types in the serra de Monchique (Portugal): Anthropogenic changes of oak forests. Silva Lusitana 7, 71-92.

Stephens, S.L., Moghaddas, J.J., Ediminster, C., Fiedler, C.E., Hasse, S., Harrington, M., Keeley, J.E., McIver, J.D., Metlen, K., Skinner, C.N., Youngblood, A., 2009. Fire treatment effects on vegetation structure, fuels, and potential fire severity in western U.S. forests. Ecological Applications 19, 305–320.

Taboada, A., Kotze, D.J., Tárrega, R., Salgado, J.M., 2006. Traditional forest management: do carabid beetles respond to human-created vegetation structures in an oak mosaic landscape? Forest Ecology and Management 237, 436-449.

Tárrega, R., Luis-Calabui, E., Valbuena, L., 2001. Eleven years of recovery dynamic after experimental burning and cutting in two Cistus communities. Acta Oecologica 22, 277-283.

Thomas, P.A., Packham, J.R., 2007. Ecology of woodlands and forests. Description, dynamics and diversity. Cambridge University Press, Cambridge.

Trabaud, L., 2000. Seeds: their soil bank and their role in postfire recovery of ecosystems of the Mediterranean basin. In: Trabaud, L. (Ed.), Life and environment in the Mediterranean. WIT Press, Southampton, pp. 229-259.

Urbieta, I.R., Zavala, M.A., Marañón, T., 2008. Human and non-human determinants of forest composition in southern Spain: evidence of shifts towards cork oak dominance as a result of management over the past century. Journal of Biogeography 35, 1688-1700.

Verdú, M., 2000. Ecological and evolutionary differences between Mediterranean seeders and resprouters. Journal of Vegetation Science 11, 265-268.

Wardell-Johnson, G.W., Williams, M.R., Mellican, A.E., Annels, A., 2004. Floristic patterns and disturbance history in karri forest, south-western Australia. 1. Environment and species richness. Forest Ecology and Management 125, 297-307.

Wood, S.W., 2006. Generalized additive models. An introduction with R. Champman & Hall/CRC, Boca Raton.

Xanthopoulos, G., Caballero, D., Galante, M., Alexandrian, D., Rigolot, E., Marzano, R., 2006. Forest fuels management in Europe. In: Andrews, P.L., Butler, B.W. (Eds.), Fuels management-how to measure success: Conference Proceedings. USDA Forest Service, Portland, pp. 29-46.

Zedler, P.H., Gautier, C.R., McMaster, G.S., 1983. Vegetation change in response to extreme events: the effect of a short interval between fires in California chaparral and coastal scrub. Ecology 64, 809-818.

SUPPLEMENTARY MATERIAL

Supplementary Table S1: Summary statistics (mean±standard deviation [minimum – maximum]) of variables used to characterize 48 1-ha cork oak (*Quercus suber*) stands in the Caldeirão hills (southern Portugal).

Variables description	**Mean±SD (Min-Max)**
Explanatory variables	
Time since disturbance (years)	24.7±25.4 (0-70)
Disturbance frequency (no./decade)	0.4±0.2 (0-0.7)
Response variables	
Tree density (dbh ≥ 6 cm, trees/ha)	
Total tree density	294.3±180.2 (81.2-850.0)
Quercus suber density	210.4±100.6 (81.3-531.3)
Large *Quercus suber* density (dbh > 60 cm)	37.1±32.6 (6.3-162.5)
Erica arborea density	28.3±49.7 (0-212.5)
Arbutus unedo density	39.2±89.6 (0-425)
Understory vegetation cover	
Erica arborea cover (%)	10±14.0 (0-48.3)
Arbutus unedo cover (%)	8.5±9.6 (0-32.5)
Quercus suber cover (%)	5.0±6.2 (0-30.6)
Genista triacanthos cover (%)	4.1±6.8 (0-27.5)
Cistus ladanifer cover (%)	3.5±6.7 (0-40.9)
Calluna vulgaris cover (%)	3.4±5.7 (0-25.2)
Cistus populifolius cover (%)	3.3±6.3 (0-34.9)
Cistus salvifolium cover (%)	2.1±4.0 (0-22.0)
Lavandula viridis cover (%)	1.8±3.1 (0-14.1)
Lavandula stoechas cover (%)	1.8±2.6 (0-10.9)
Lithodora prostata cover (%)	0.8±1.1 (0-4.5)
Total woody understory cover (%)	44.1±28.8 (1.1-85)
Vertical understory structure	
Shrub cover (0 to 0.3 m; %)	16.8±9.5 (1.8-39)
Shrub cover (0.3 to 0.6 m; %)	22.9±16.3 (0-66.5)
Shrub cover (0.6 to 1 m; %)	23.1±19.7 (0-65.2)
Shrub cover (1 to 1.5 m; %)	20.1±19.0 (0-64.6)
Shrub cover (1.5 to 2 m; %)	15.6±17.3 (0-62.9)
Shrub cover (2 to 3 m; %)	13.4±16.6 (0-59.6)
Shrub cover (3 to 4 m; %)	6.3±9.5 (0-43.1)
Shrub cover (>4 m; %)	1.7±4.9 (0.0-29.2)
Shrub vertical structural richness (no.)	5.6±2.2 (1-8)
Shannon's diversity of shrub vertical structure	1.4±0.6 (0-2)
Evenness of shrub vertical structure	0.9±0.1 (0.3-1)
Species diversity	
Tree species richness (dbh >6 cm, no.)	3.0±1.9 (1-7)
Shrub species richness (dbh < 6 cm, no.)	12.0±4.8 (3-24)
Shrub Shannon's diversity index	1.8±0.4 (0.7-2.6)
Shrub Pielou's evenness index	0.7±0.1 (0.5-1)
Shrub Sørensen´s similarity index	0.5±0.2 (0-0.9)
Functional organization	
Total seeders shrub cover (%)	22.1±19.2 (0.3-73.3)
Total resprouters shrub cover (%)	27.3±25.0 (0-82.9)
Proportion of resprouters shrub cover (%)	53.2±30.9 (0-97.5)
Proportion of resprouters shrub species (%)	52.4±28.2 (0-92.0)
Total dry fruit shrub cover (%)	36.0±24.2 (0.9-74.6)
Total fleshy fruit shrub cover (%)	12.9±16.7 (0-78.9)
Proportion of fleshy fruit shrub cover (%)	22.7±21.8 (0-92.8)
Proportion of fleshy fruit shrub species (%)	18.4±17.8 (0-81.9)

Supplementary Table S2: Percentage occurrence and mean percent cover (±standard deviation; minimal and maximal) where the species occur, of understory shrubs, in 48 cork oak (*Quercus suber*) forest stands in the Caldeirão hills (southern Portugal). Species are classified according to type of fruit and response to disturbance.

Species	Type of fruit	Response to disturbance	%Occurrence (n=48)	Mean±SD (min-max)
Quercus suber	Dry	Resprouter	89.6	5.6±6.3 (0.2-30.6)
Lavandula stoechas	Dry	Seeder	81.3	2.2±2.7 (0.1-10.9)
Cistus ladanifer	Dry	Seeder	75.0	4.7±7.4 (0.1-40.9)
Cistus populifolius	Dry	Seeder	75.0	4.4±7.0 (0.1-34.9)
Arbutus unedo	Fleshy	Resprouter	72.9	11.7±9.5 (0.1-32.5)
Genista triacanthos	Dry	Seeder	72.9	5.6±7.4 (0.1-27.5)
Calluna vulgaris	Dry	Seeder	70.8	4.8±6.3 (0.2-25.2)
Lavandula viridis	Dry	Seeder	64.6	2.9±3.4 (0.1-14.1)
Cistus salvifolius	Dry	Seeder	60.4	3.5±4.7 (0.1-22.0)
Lithodora prostrata	Dry	Seeder	60.4	1.3±1.2 (0.1-4.5)
Erica arborea	Dry	Resprouter	54.2	18.5±14.3 (0.2-48.3)
Daphne gnidium	Fleshy	Resprouter	39.6	0.5±0.4 (0.1-1.8)
Ulex argenteus	Dry	Seeder	37.5	6.9±7.7 (0.1-25.0)
Helichrysum stoechas	Dry	Seeder	35.4	0.8±0.8 (0.1-3.0)
Genista hirsuta	Dry	Seeder	27.1	4.0±5.4 (0.7-20.1)
Myrtus communis	Fleshy	Resprouter	27.1	2.6±2.7 (0.1-8.5)
Phlomis purpurea	Dry	Seeder	27.1	1.0±0.9 (0.1-2.9)
Quercus coccifera	Dry	Resprouter	22.9	7.9±7.5 (0.1-21.3)
Phillyrea angustifolia	Fleshy	Resprouter	16.7	1.5±1.1 (0.2-3.8)
Cistus crispus	Dry	Seeder	14.6	2.2±3.3 (0.2-9.5)
Pistacia lentiscus	Fleshy	Resprouter	14.6	1.6±1.5 (0.2-4.4)
Pinus pinaster	Dry	Seeder	12.5	0.6±0.5 (0.1-1.4)
Quercus rotundifolia	Dry	Resprouter	12.5	2.3±2.1 (0.1-5.9)
Rubus ulmifolius	Fleshy	Resprouter	12.5	2.2±2.6 (0.2-7.1)
Viburnum tinus	Fleshy	Resprouter	12.5	25.9±26.1 (0.6-70.8)
Olea europaea	Fleshy	Resprouter	8.3	0.4±0.3 (0.1-0.7)
Phillyrea latifolia	Fleshy	Resprouter	8.3	0.5±0.1 (0.4-0.6)
Phagnalon saxatile	Dry	Seeder	8.3	0.8±0.5 (0.1-1.1)
Quercus lusitanica	Dry	Resprouter	8.3	2.1±2.1 (0.5-5.2)
Calamintha baetica	Dry	Seeder	6.3	0.3±0.3 (0.1-0.6)
Erica lusitanica	Dry	Resprouter	6.3	0.5±0.4 (0.2-1.0)
Ruscus aculeatus	Fleshy	Resprouter	6.3	1.0±0.9 (0.1-2.0)
Teucrium scorodonia	Dry	Seeder	6.3	1.4±1.3 (0.2-2.9)
Adenocarpus complicatus	Dry	Resprouter	4.2	15.4±16.4 (3.7-27.0)
Cistus albidus	Dry	Resprouter	4.2	1.4±1.9 (0.1-2.7)
Osyris lanceolata	Fleshy	Resprouter	4.2	0.4±0.4 (0.1-0.7)
Quercus faginea	Dry	Resprouter	4.2	4.0±1.4 (3.0-5.0)
Rhamnus alaternus	Fleshy	Resprouter	4.2	0.1±0.0 (0.1-0.1)
Thymus mastichina	Dry	Seeder	4.2	0.3±0.1 (0.2-0.4)
Thymelaea villosa	Dry	Resprouter	4.2	0.1±0.0 (0.1-0.1)
Acacia saligna	Dry	Seeder	2.1	0.2 (0.2-0.2)
Dittrichia viscosa ssp. *revoluta*	Dry	Seeder	2.1	0.1 (0.1-0.1)
Erica australis	Dry	Resprouter	2.1	0.1 (0.1-0.1)
Euphorbia paniculata	Dry	Seeder	2.1	1.1 (1.1-1.1)
Erica umbellata	Dry	Seeder	2.1	1.0 (1.0-1.0)
Halimium lasianthum ssp. *lasianthum*	Dry	Seeder	2.1	0.2 (0.2-0.2)
Halimium ocymoides	Dry	Seeder	2.1	0.1 (0.1-0.1)
Hypericum perfoliatum	Dry	Resprouter	2.1	0.7 (0.7-0.7)

Species	**Type of fruit**	**Response to disturbance**	**%Occurrence (n=48)**	**Mean±SD (min-max)**
Lonicera implexa	Fleshy	Resprouter	2.1	0.1 (0.1-0.1)
Lavatera olbia	Dry	Resprouter	2.1	0.2 (0.2-0.2)
Stahelina dubia	Dry	Seeder	2.1	0.1 (0.1-0.1)
Teucrium haenseleri	Dry	Resprouter	2.1	1.9 (1.9-1.9)
Tuberaria lignosa	Dry	Seeder	2.1	0.2 (0.2-0.2)

3

Long-term consequences of mechanical fuel management for the conservation of Mediterranean forest herb communities

M. Porto, O. Correia, P. Beja

published in
Biodiversity Conservation
20 (2011) 2669-2691

Doronicum plantagineum* subsp. *tournefortii
one of the rarest herb species found in the study area, known only from one site within nearly undisturbed forest
(endemic to Portugal)

Long-term consequences of mechanical fuel management for the conservation of mediterranean forest herb communities

Miguel Porto[a], Otília Correia[a], Pedro Beja[b]

[a]Departamento de Biologia Vegetal, Faculdade de Ciências de Lisboa, Centro de Biologia Ambiental, Universidade de Lisboa, C2 Campo Grande, 1749-016 Lisboa, Portugal
[b]CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Campus Agrário de Vairão, Universidade do Porto, 4485-601 Vairão, Portugal

ABSTRACT

Mechanical understory clearing is increasingly used in Euro-Mediterranean forests to reduce fire hazard, yet its long-term consequences for biodiversity conservation remain poorly understood. This study analysed the influence of fuel reduction timing and frequency on herbaceous species richness, cover and composition, functional richness and composition, and richness and cover within functional groups (life and growth forms, dispersal strategy, clonality, and plant height), using a chronosequence of cork oak (*Quercus suber*) stands spanning about 70 years since understory clearing. Overall species richness was virtually constant over time, but the richness of annual and versatile (plant height) species was much higher in recently and recurrently treated stands; the opposite was found for perennial (mainly hemicryptophytes and chamaephytes), tussock-forming and clonal species richness, and functional richness. Overall herbaceous cover and that of annual, semi-basal, non-clonal and versatile species were favoured by recent and recurrent fuel treatments; cover by perennial (hemicryptophytes and chamaephytes), short basal, tussock-forming, and clonal species tended to increase for > 10-20 years after disturbance, and declined with disturbance frequency. There was a marked long-term shift in species and functional composition associated with the timing and frequency of fuel reduction treatments. These findings suggest that widespread fuel reduction treatments at < 10 year intervals may shift understory herb communities to early-successional stages, impairing the persistence of species and functional types recovering slowly after disturbance. Fuel management needs to balance the dual goals of fire hazard reduction and biodiversity conservation, retaining undisturbed patches in landscapes otherwise managed to reduce fuel accumulation.

Keywords: Disturbance ecology, Ecological succession, Forest management, Landscape mosaics, Mediterranean plant communities

INTRODUCTION

Natural disturbances play a key role in maintaining forest structure and function by promoting spatial and temporal heterogeneity in environmental conditions (Frelich 2002; Thomas and Packham 2007). In contrast, anthropogenic disturbances may negatively affect forest ecosystems because they often are of a different nature, intensity, periodicity and scale (Torras and Saura 2008; von Oheimb and Härdtle 2009). Approximating forest management practices to natural disturbance regimes is thus one of the major challenges in modern forestry, in order to maintain both biodiversity and economic outputs (Bengtsson *et al.* 2000; Lindenmayer *et al.* 2006).

Clearing of understory vegetation to reduce fire hazard is a common anthropogenic disturbance affecting forests in temperate and dry regions worldwide (Agee and Skinner 2005; Xanthopoulos *et al.* 2006, pp. 29-46; Stephens *et al.* 2009). Fuel reduction is often achieved through prescribed burning, which is believed to emulate natural disturbance regimes, thus contributing to the conservation of ecosystem structure and function (Stephens *et al.* 2009). In many cases, however, the implementation of prescribed burning is impossible or impractical, and so fuel reduction is achieved through the mechanical removal of understory shrubs and smaller trees whose branches carry fire into forest canopies, while retaining larger trees (Agee and Skinner 2005). The consequences of this practice for biodiversity remain poorly understood, though it is possible that rotational understory clearing may create heterogeneity at the landscape scale, thereby providing conditions for species with distinct habitat requirements (Converse *et al.* 2006; Santana *et al.* In Press). In contrast, clearing may also be negative because high recurrence of stand management across the landscape may eliminate species recovering slowly after disturbance (Decocq *et al.* 2004b; Santana *et al.* In Press).

Developing mechanical fuel reduction programs compatible with biodiversity conservation is a particularly acute problem in Euro-Mediterranean forests, where this technique has been used ever more in response to increases in fire frequency, intensity and extent (Xanthopoulos *et al.* 2006). The accumulation of fuels in these forests was largely prevented by traditional pastoral and agricultural activities, but these have strongly declined due to ongoing rural depopulation and land abandonment, normally followed by shrub encroachment (Acácio *et al.* 2009; Aronson *et al.* 2009; Blondel *et al.* 2010). In this context, mechanical understory clearing became widely used to reduce the accumulation of combustible materials, in the attempt to reduce fire hazard while restoring landscape heterogeneity (Xanthopoulos *et al.* 2006). This management approach assumes, often implicitly, that Mediterranean vegetation is highly resilient because plants are adapted to disturbance, and so the risk of losing species after disturbance should be low (but see, e.g., Rodrigo *et al.* 2004). However, most studies have been relatively short-term (< 15 years) and focused primarily on shrublands recurrently affected by fire or anthropogenic disturbance, which may thus be particularly resilient to further disturbances (Calvo *et al.* 2002, 2005; Potts *et al.* 2010). In contrast, plant communities associated with less disturbed environments, such as those of mature forests, may have longer recovery times and so they may loose species if repeatedly disturbed (Marañon *et al.* 1999; Díaz-Delgado *et al.* 2002; Hampe and Arroyo 2002). Information is thus needed on the long-term recovery dynamics of vegetation after mechanical fuel treatments, which would be important to define treatment frequencies and spatial patterns assuring the representation of different successional stages at the landscape scale (Lindenmayer *et al.* 2006).

This study used a chronosequence approach to examine the consequences over about 70 years of mechanical fuel treatments on the herbaceous understory of Mediterranean cork oak (*Quercus suber*) forests. These forests cover about 2.5 million hectares in the Mediterranean Basin, where they are exploited chiefly for the production of cork used in wine bottle stoppers and insulation materials (Aronson *et al.* 2009). In a previous study we showed that after understory clearing there is a quick recovery of pioneer seeder and dry-fruited shrubs, which are then slowly replaced by large resprouters and fleshy-fruit producing species, eventually leading to the development of a complex multi-layered understory > 50 years after disturbance (Santana *et al.* In Press). We now hypothesize that herbaceous communities may show a comparable shift in composition and structure over time, as there is some evidence that although herbaceous diversity recovers rapidly after fuel management in Mediterranean systems (Calvo *et al.* 2002, 2005; Peréz-Ramos *et al.* 2008), at least some species and functional types are strongly associated with undisturbed habitats (Ojeda *et al.* 2000; Bonet and Pausas 2004). This hypothesis was tested by examining how the timing and frequency of understory clearing affects herbaceous understory communities, in terms of (i) species and functional group richness; (ii) richness of species within functional groups; (iii) overall herbaceous cover and cover per functional group; and (iv) species and functional composition. Results were then used to discuss the implications of fuel management for the conservation of Mediterranean forest herb communities.

METHODS

Study area

The study was conducted in southern Portugal, within about 30 000 ha situated in the Caldeirão hills (37º08'-37º22' N, 8º03'-7º49' W; 200-580 m a.s.l.). Climate is Mediterranean, with marked variation in annual rainfall (415–1903 mm), about 80% of which occurs in October-March and <5% in June-August. Mean monthly temperature ranges from 10.3ºC (January) to 24ºC (August). Soils are generally shallow shale lithosols, with low fertility and high erodability. Cork oak forests dominate the landscape, ranging from almost pure stands to complex Mediterranean maquis with cork oaks surrounded by tall strawberry trees (*Arbutus unedo*) and tree heath (*Erica arborea*) (Acácio *et al.* 2009). There are also nearly monospecific *Cistus ladanifer* shrublands and more diverse Mediterranean heathland dominated by *Calluna vulgaris* and species of *Genista*, *Cistus*, *Erica*, *Lavandula* and *Ulex* (Acácio *et al.* 2009). Domestic and wild vertebrate grazers are scarce. The main economic activity is the production of cork, generally conducted on small private properties (<10 ha) by aged landowners (often >60 years old). Mechanical understory clearing is the main silvicultural operation, which is often carried out at 9-year intervals in association with the cork extraction cycle. Understory management in some stands is absent or very sporadic, and so the landscape is composed of a complex forest mosaic with understory vegetation at different successional stages. See Santana *et al.* (In Press) for details.

Study design

The study was based on a chronosequence of 48 cork oak stands spanning about 70 years since the last understory clearing, inferring herbaceous community dynamics from contemporary spatial variation among stands with different management histories (Foster and Tilman 2000). Because it was not possible to fully meet the assumption that stands differed only in understory age and that each site traced exactly the same history in both its biotic and abiotic components, due for instance to differences in aspect, elevation, slope and management, this approach is unlikely to provide detailed information on temporal changes that occur in any given stand (Johnson and Miyanishi 2008). However, examination of this chronosequence was expected to reveal broad, regional-scale successional trends by averaging across site-to-site differences in herbaceous communities that occur because of differences in environmental conditions and site history (Foster and Tilman 2000).

Forest stands were selected according to the stratified random procedure detailed by Santana *et al.* (In Press). Six strata corresponding to categories of increasing structural complexity of understory vegetation were defined, based on a putative successional sequence in the uplands of southern Portugal (Rivas-Martinez *et al.* 1990; Seng and Deil 1999). Structural categories were used instead of actual understory ages, because management histories could only be assessed *a posteriori* from enquiries and aerial photographs (see below). Random locations were distributed across the study area at >800 m from each other, within forest stands with >30% canopy cover by cork oaks. Forests affected by fire were excluded, to avoid confounding the effects of shrub clearing and burning. At each random location, a homogeneous 1-ha plot representative of the dominant structural category was chosen and demarcated in the field. The procedure was repeated until all plots of all structural categories were selected.

Understory management history was inferred primarily from a sequence of orthorectified and georeferenced digital aerial photographs: 1958 (scale 1:26,000), 1972 (scale 1:8,000), 1985 (scale 1:5,000), 1995 (scale 1:40,000) and 2002 (scale 1:5,000) (see Santana *et al.* In Press for details). This procedure was feasible due to the relatively open canopy of cork oak forests and because arboreal plants were often removed during mechanical clearing. For each image year, understory condition in each stand was classified in three broad classes: 1) shrub layer sparse or absent; 2) cover by shrublands; 3) cover by tall maquis with *A. unedo* and *E. arborea*. This information was used to estimate the approximate dates of shrub clearing events, assuming that: 1) class 1 indicates that clearing occurred < 2 years before the image year; 2) other obvious reductions in understory woody vegetation cover, including changes from classes 3 to 2, indicate that clearing occurred at the middle of the time interval between two consecutive aerial photographs. Understory clearing events before the period covered by aerial photographs were estimated using 1958 images assuming that: 1) class 2 indicates the clearing of understory < 10 years of image year; and 2) class 3 indicates the clearing of understory in 1935, corresponding approximately to the historical peak of cereal cultivation and livestock grazing (Feio 1949; Guerreiro 1951).

Assumptions regarding the identification and dating of clearing events were based on comparisons between patterns of aerial photos of 2002 and vegetation types recognized in the field during several visits to the study area (2004), and they were cross-checked with enquiries to the landowner of each forest stand (Santana *et al.* In Press). Data from aerial photographs and enquiries were combined to estimate: (1) the time since disturbance – number of years elapsed between the last shrub clearing event and the time of vegetation sampling; and (2) disturbance frequency – number of shrub clearing events occurring per decade.

Herbaceous understory characterization

Herbaceous understory composition and structure was estimated in four 2-m radius circles (12.6 m^2) within each 1-ha plot, once between 10 and 15 May 2005. Each plot was divided into four quadrants, and each circle was located at the centre of each quadrant. Herbaceous species occurring within each circle were identified and the percentage cover of each species was visually estimated. Percentage cover per species was then computed by averaging the four estimates within each plot. Additionally, the entire 1-ha plot was systematically surveyed for species not recorded within the four circles. Autumnal herbs, which correspond to a relatively small fraction of species richness, were not included in this study (e.g., Pérez-Ramos *et al.* 2008).

Species were classified into basic functional groups based on life form, growth form, plant height, clonality and dispersal strategy (Supplementary Table S1), all of which are known to influence the response to disturbance through their influence on survival or colonization abilities (Cornelissen *et al.* 2003). Categorization was based on direct observation of plants and bibliographic sources (Malo and Suárez 1995; Bonet and Pausas 2004; Paula *et al.* 2009). Cover by a functional group was calculated as the sum of covers of all species belonging to that group.

Data analysis

Prior to statistical analysis, the time since disturbance was log-transformed to allow for greater resolution in the early years after disturbance, when herbaceous communities tend to change at a faster rate (Calvo *et al.* 2002; Bonet and Pausas 2004; Pérez-Ramos *et al.* 2008). The square-root transformation was used for percentage data to reduce the influence of a few large values and to minimise problems associated with the unity sum constraint. Gradients in herbaceous community composition were then extracted with Detrended Correspondence Analysis (DCA), using the 'VEGAN' software package (Oksanen *et al.* 2009). Separate analyses were carried out in terms of species composition and functional traits. In each case, species or functional groups with <6 occurrences were removed from analysis, and other rare species/groups were downweighted (Oksanen *et al.* 2009).

Species and functional group richness and percentage cover, and community gradients derived from DCA, were related to management variables using Generalized Additive Models (GAMs) (Hastie & Tibshirani 1990) fitted in R software with 'mgcv' package (Wood 2006). Count data were modelled with a quasi-Poisson distribution and logarithmic link function, thereby accounting for overdispersion, while continuous variables were modelled with a Gaussian distribution with identity link. We used thin plate regression splines and chose the basis dimension of the spline which yielded the model with the lowest Akaike Information Criterion (quasi-AIC for count models), within three possible dimensions (3 to 5). Higher dimensions allow greater complexity of the fitted curves but may result in overfitting. Confidence intervals (95%) of the predicted curves were estimated by predicted mean ± 2*standard error of the prediction.

In analyses based on functional groups, explanatory power of models may be spuriously influenced by grouping *per se*, independently of which species fall into which group (Wright *et al.* 2006). This problem was addressed using a permutation procedure, comparing the explanatory power (R^2) of the model of interest with that of 50 000 models computed from random data sets (Petchey and Gaston 2006). In the case of richness and percentage cover variables, we randomly assigned species to functional groups, using the same number of groups defined *a priori* and the same overall number of species per group. The species richness and percentage cover of each target group were then computed per plot and new GAM models were estimated using the permuted data set. The permutation procedure for models based on DCA axes was similar, except that the site scores were re-calculated each time by repeating the DCA with each random classification of species.

RESULTS

Species and functional group richness

Altogether, 178 species were recorded (Supplementary Table S1), with an average of 25.5 ± 10.2 (SD) species per plot. A total of 65 species (36.5%) occurred in a single plot, while only 14 species (7.8%) occurred in at least half the plots. Overall species richness was unrelated ($P > 0.10$) to disturbance timing and frequency (Figure 1a,c), though strong relationships were found for species richness within functional groups (Table 1). In terms of life forms, the richness of annual species (therophytes) declined with time since disturbance. In contrast, the richness of perennial and hemicryptophyte species increased after disturbance during the first 10-20 years, and then converged slowly to a plateau, while the richness of chamaephytes increased almost linearly over the chronosequence (Figure 2a,e,m,q). Richness of perennials, hemicryptophytes, chamaephytes and geophytes declined with disturbance frequency (Figure 2g,o,s,k). Permutation tests supported (percentiles > 95%) all significant relationships derived from GAMs, except that of geophytes (Table 1).

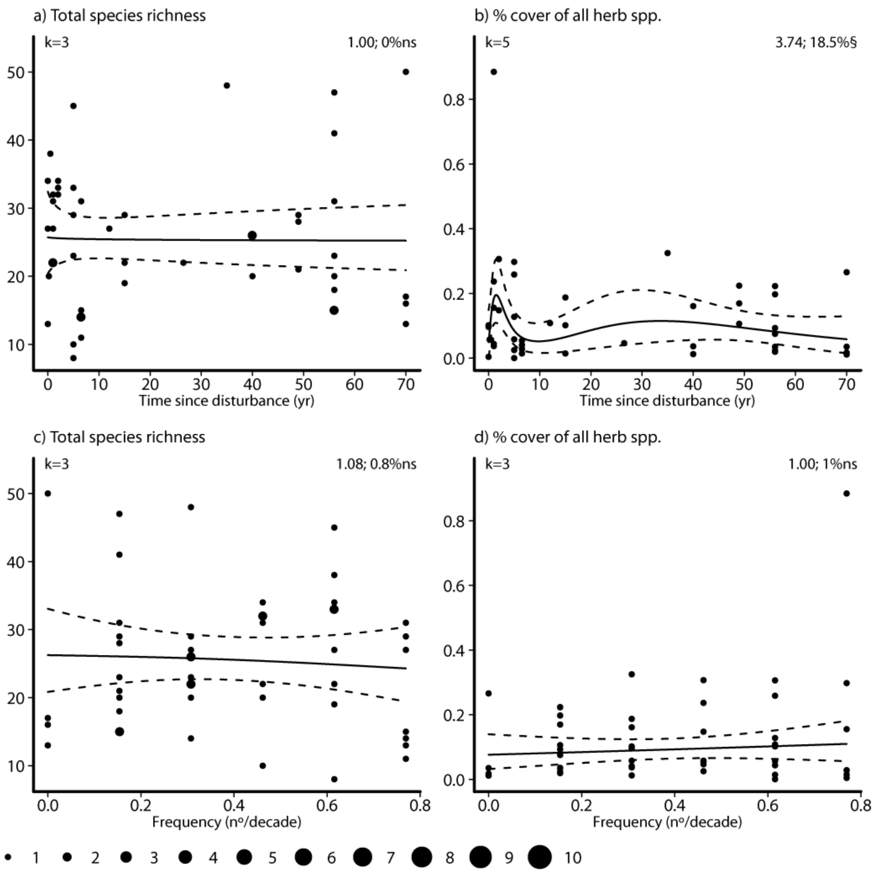


Figure 1: Generalized Additive Model fits (solid lines) and 95% confidence intervals (hatched lines), of relationships between total richness and cover of herbaceous species, and the timing and frequency of understory clearing disturbances. Dot sizes are proportional to the number of observations. Dimension of the fitted spline (k), effective degrees of freedom, percentage variance explained, and significance-level (* *P* <0.001, ** *P* <0.01, * *P* <0.05, § *P* <0.1, ns *P* ≥ 0.1) are provided for each model.**

Responses to disturbance recorded for other functional traits were broadly similar to that observed for the life forms (Supplementary Figures S1-4), though their strength strongly varied among groups (Table 1). Richness of tussock-forming species increased with time since disturbance and strongly declined with disturbance frequency (Table 1; Supplementary Figure S1m,o). Richness of erect leafy species slightly declined with time since disturbance, while weak negative effects of disturbance frequency were found for short basal and climber/scrambler species (Table 1; Supplementary Figure S1i,c,w). No significant relationships were found for dispersal strategy groups (Table 1; Supplementary Figure S2). The richness of species with vegetative spread (with stolons or rhizomes) strongly increased with time since disturbance and declined with disturbance frequency (Table 1; Supplementary Figure S3b,j). The richness of species with versatile height declined with time since disturbance, while an inverse tendency, albeit weaker, was found for tall species (Table 1; Supplementary Figure S4b,c). There was strong support (percentiles > 98%) by permutation tests for tussock-forming species and species with vegetative spread (Table 1).

Number of different life forms increased linearly with time since disturbance, and declined linearly with disturbance frequency (Figure 3a,b). The number of growth form groups tended to increase for about 10-20 years, but subsequently converged to a plateau (Figure 3c). At low disturbance frequency the richness of growth forms was high and remained essentially stable, but it strongly declined in the most frequently disturbed sites (Figure 3d). Life and growth form results were supported by permutation tests (percentile > 95%). For the remaining groups there was no evidence that functional richness was affected by disturbance timing or frequency.

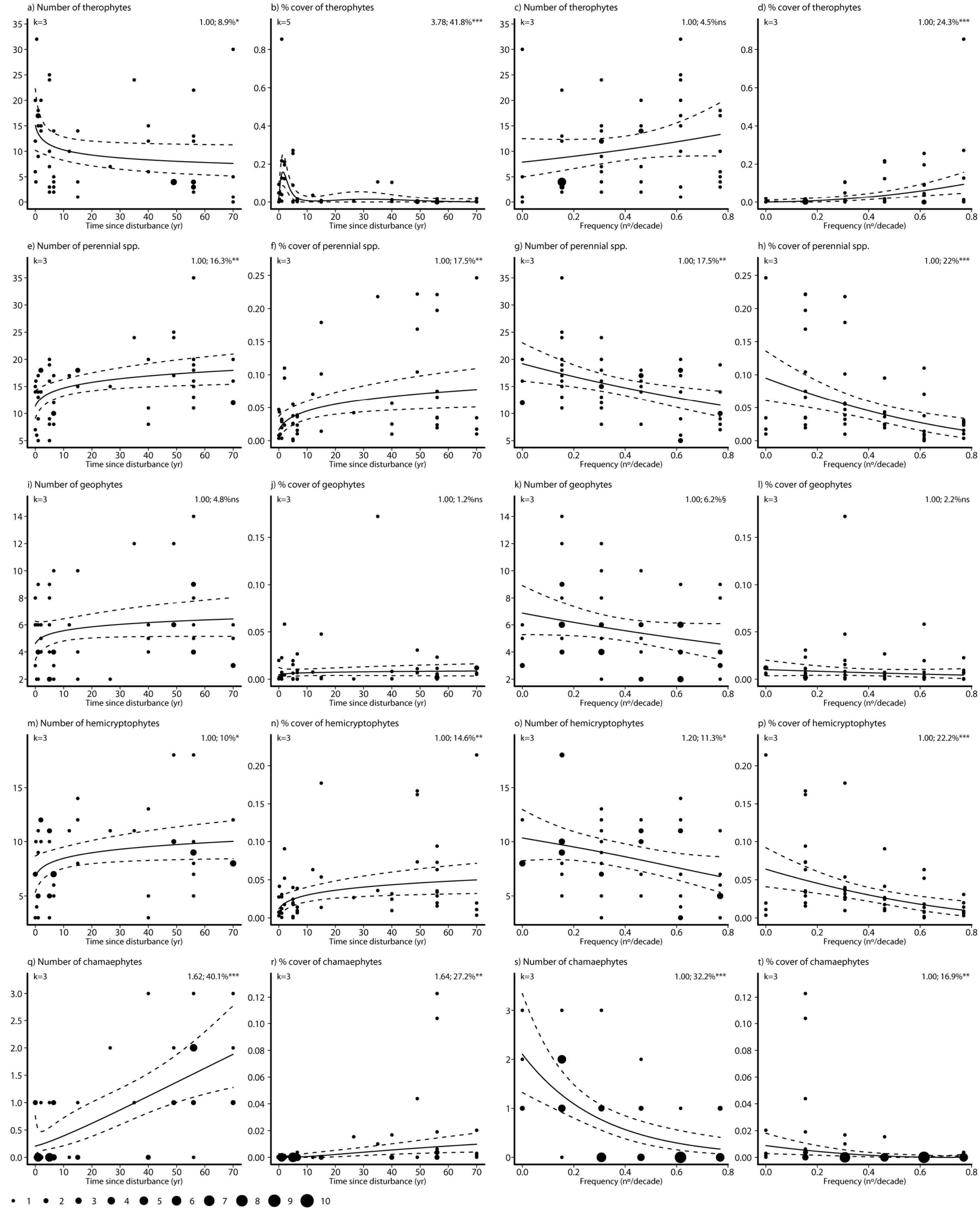


Figure 2: Generalized Additive Model fits (solid lines) and 95% confidence intervals (hatched lines), of relationships between species richness and cover within life form functional groups, and the timing and frequency of understory clearing disturbances. Dot sizes are proportional to the number of observations. Dimension of the fitted spline (k), effective degrees of freedom, percentage variance explained, and significance-level (* P <0.001, ** P <0.01, * P <0.05, § P <0.1, ns P ≥ 0.1) are provided for each model.**

Table 1: Summary of Generalized Additive Models relating the richness and percentage cover of species within functional groups to the timing and frequency of understory clearing disturbances, including the percentage of explained variance (R^2) the main direction of the trend ([+] positive; [-] negative), and the significance level (* P < 0.001; ** P < 0.01; * P < 0.05; § P < 0.10; ns P > 0.10). For each model, the table presents the percentile of the estimated R^2 in relation to the R^2 distribution of 50 000 random models, computed by permuting species assignment to functional groups. [a] Myrmecochory and hoarding were excluded from analyses due to the very low number of occurrences.**

	Species Richness				Percentage cover			
	Timing		Frequency		Timing		Frequency	
	GAM	Perc	GAM	Perc	GAM	Perc	GAM	Perc
All herb species	ns	-	ns	-	18.5%(-)§	-	ns	-
Life forms								
Therophyte	8.9%(-)*	99.5	ns	84.0	41.8%(-)***	100	24.3%(+)***	99.8
Perennial	16.3%(+)**	100	17.5%(-)**	100	17.5%(+)**	98.8	22.0%(-)***	99.4
Geophyte	ns	70.9	6.2%(-)§	76.4	ns	20.8	ns	27.1
Hemicryptophyte	10.0%(+)*	95.0	11.3%(-)*	95.3	14.6%(+)**	85.0	22.2%(-)***	94.0
Chamaephyte	40.1%(+)***	100	32.2%(-)***	99.7	27.2%(+)**	98.7	16.9%(-)**	88.7
Growth forms								
Short basal	ns	92.0	9.1%(-)*	88.9	16.2%(+)*	86.9	29.4%(-)**	97.4
Semi-basal	ns	39.7	ns	24.1	41.8%(-)***	99.8	17.7%(+)**	89.3
Erect leafy	8.3% (-)*	93.2	ns	76.7	13.6%(-)**	83.0	11.5%(+)*	67.2
Tussock	24.0%(+)**	98.7	32.0%(-)**	99.8	14.2%(+)**	76.5	17.1%(-)**	84.3
Parasite	ns	67.2	ns	35.6	ns	14.4	ns	15.8
Climber/scrambler	ns	60.5	11.7%(-)§	86.2	6.0%(+)§	49.0	7.7%(-)§	59.0
Dispersal strategy[a]								
Anemochory	ns	52.5	ns	78.2	20.0%(-)§	55.3	ns	15.3
Barochory	ns	35.1	ns	18.5	ns	44.9	ns	26.5
Ectozoochory	ns	11.3	ns	15.6	28.4%(-)**	84.2	12.3%(+)*	69.6
Endozoochory	ns	40.3	ns	35.4	ns	13.4	ns	0.3
Clonality								
Non-clonal	ns	94.7	ns	51.0	27.5%(-)**	99.5	10.0%(+)*	97.6
Vegetative spread	25.9%(+)**	99.7	22.3%(-)***	98.9	26.1%(+)**	98.9	31.2%(-)***	98.4
Stolons/long rhizomes	18.8%(+)*	95.7	10.2%(-)*	82.1	14.8%(+)§	78.3	10.2%(-)*	69.3
Short rhizomes	16.2%(+)**	95.1	15.5%(-)**	93.7	26.0%(+)***	98.4	36.9%(-)***	99.6
Plant height								
Short (<40 cm)	ns	28.6	ns	10.8	ns	61.1	6.8%(-)§	61.7
Tall (> 40 cm)	6.6%(+)§	88.4	8.2%(-)§	90.0	ns	48.8	6.0%(-)§	48.5
Versatile	12.8%(-)*	93.0	ns	78.8	45.9%(-)***	100	25.5%(+)***	94.7

Herbaceous cover

The overall herbaceous cover showed a weak bimodal response to the time since disturbance, with a first peak at about two years and a second shallower peak at about 30 years, while there was no relationship with disturbance frequency (Figure 1b,d). In terms of functional groups, there was also a pronounced early peak in cover by annual (life form), semi-basal (growth form), non-clonal (clonality), and versatile (plant height) species (Figure 2b; Supplementary Figures S1f, S3e, S4e), which was strongly supported by GAM significance and permutation tests (Table 1). Similar responses were found for anemochorous and ectozoochorous (dispersal strategy) species (Supplementary Figure S2e,f), but they were little supported by permutation tests (Table 1). Cover by erect leafy species (growth form) also peaked just after disturbance, declining thereafter across the chronosequence (Supplementary Figure S1j), though permutation tests provided weak support to this relationship (Table 1). Functional groups with an early peak in percentage cover tended to be positively affected by disturbance frequency (Figure 2; Supplementary Figures S1-4), but effects for the dispersal strategy groups were little supported by permutation tests (Table 1).

Cover tended to increase with time since disturbance and decline with disturbance frequency for perennials, hemicryptophytes and chamaephytes (life form), short basal and tussock-forming species (growth form), and species with vegetative spread (clonality), especially those with short rhizomes (Table 1). In general, cover increased rapidly in the first 10-20 years after disturbance, followed by a slow convergence to a plateau in later years (Figure 2; Supplementary Figures S1-4). Permutation tests strongly supported the models of perennials, hemicryptophytes (disturbance frequency), chamaephytes (disturbance timing), short basal (frequency) and species with vegetative spread (Table 1). The remaining functional groups showed relationships with disturbance variables that were either not statistically significant or very weakly supported by permutation tests (e.g., climbers/scramblers and plant height groups) (Table 1).

Herbaceous community structure

The DCA of herbaceous species cover extracted two dominant axes that together accounted for 68% of variability in the original data (Figure 4a). The gradient described by the first axis (47% of variability) was very strongly related with time since disturbance, showing a rapid variation in community composition in the first 10-20 years, followed by a slow tendency for stabilization in later years (Figure 4b). This gradient had an S-shaped relationship with disturbance frequency, underlining a tendency for a shift in community composition between regularly and rarely disturbed sites (Figure 4c). Widespread species (frequency of occurrence >40%) mostly associated with recently and regularly disturbed stands included *Andryala integrifolia*, *Briza maxima*, *Gladiolus illyricus, Jasione montana* and *Leontodon longirrostris*, whereas *Dactylis glomerata*, *Picris algarbiensis*, *Pulicaria odora*, *Tamus communis* and *Urginea maritima* were mostly associated with undisturbed stands (Figure 4a).

In all DCAs based on cover by functional groups, a large proportion of variation in community structure was accounted for by the first axis (33%-48%), which was strongly related to the time since disturbance and disturbance frequency in every case except the dispersal strategy groups (Figure 5). Variation in terms of life form, growth form, and plant height was rapid in the first 10-20 years, tending to slowly stabilize in later years (Figure 5f,g,i). In contrast, functional variation in clonality was nearly linear across the chronosequence (Figure 5h). Responses to frequency of disturbance were S-shaped in the case of life form, growth form and plant height, underlining a shift in community functional organization, and linear in the case of clonality (Figure 5k-n). Recently and regularly disturbed stands were dominated by annual life forms, parasite and semi-basal growth forms, non-clonal species, and species with versatile plant height. In contrast, in undisturbed stands there was increased dominance of perennial life forms (mainly chamaephytes), short basal, climber/scrambler and tussock growth forms, and species with vegetative spread and non-versatile plant height (Figure 5). These patterns were strongly supported by permutation tests (Figure 5).

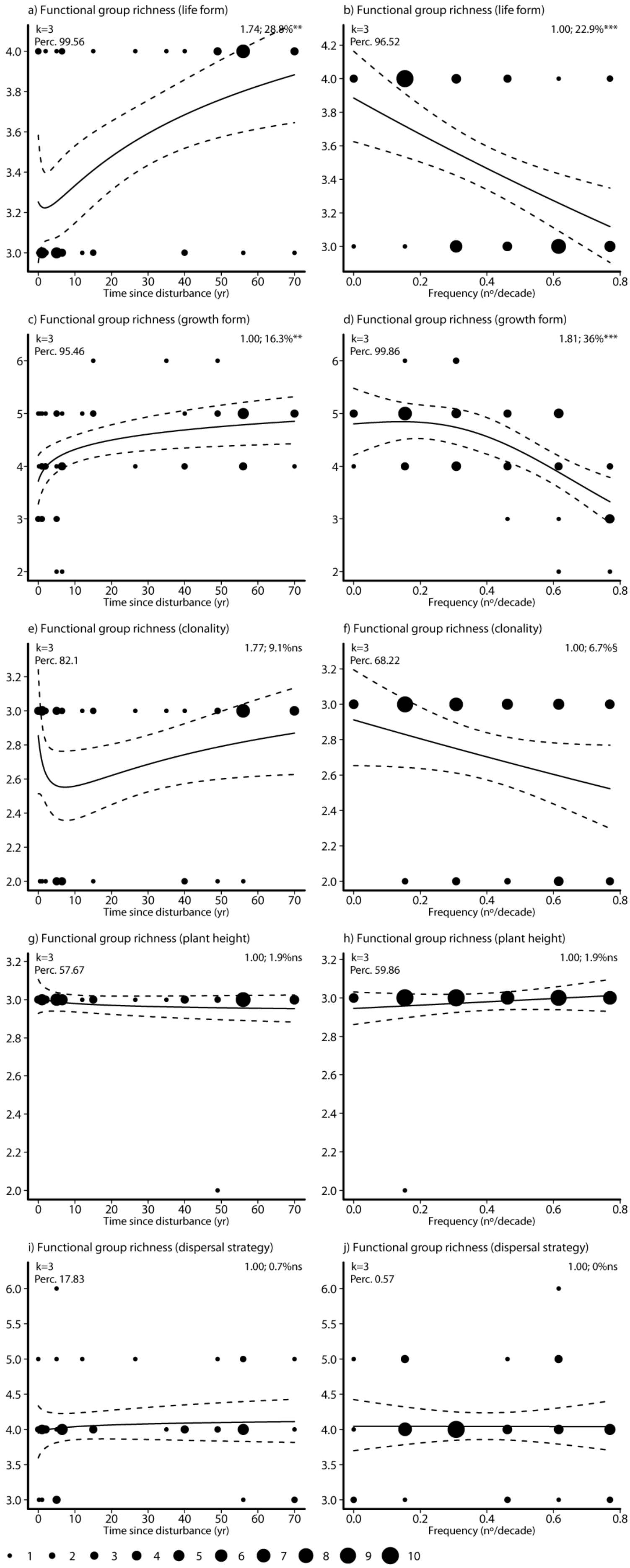


Figure 3: Generalized Additive Model fits (solid lines) and 95% confidence intervals (hatched lines), of relationships between functional richness and the timing and frequency of understory clearing disturbances. Dot sizes are proportional to the number of observations. Dimension of the fitted spline (k), effective degrees of freedom, percentage variance explained, and significance-level (* P <0.001, ** P <0.01, * P <0.05, § P <0.1, ns P ≥ 0.1) are provided for each model.**

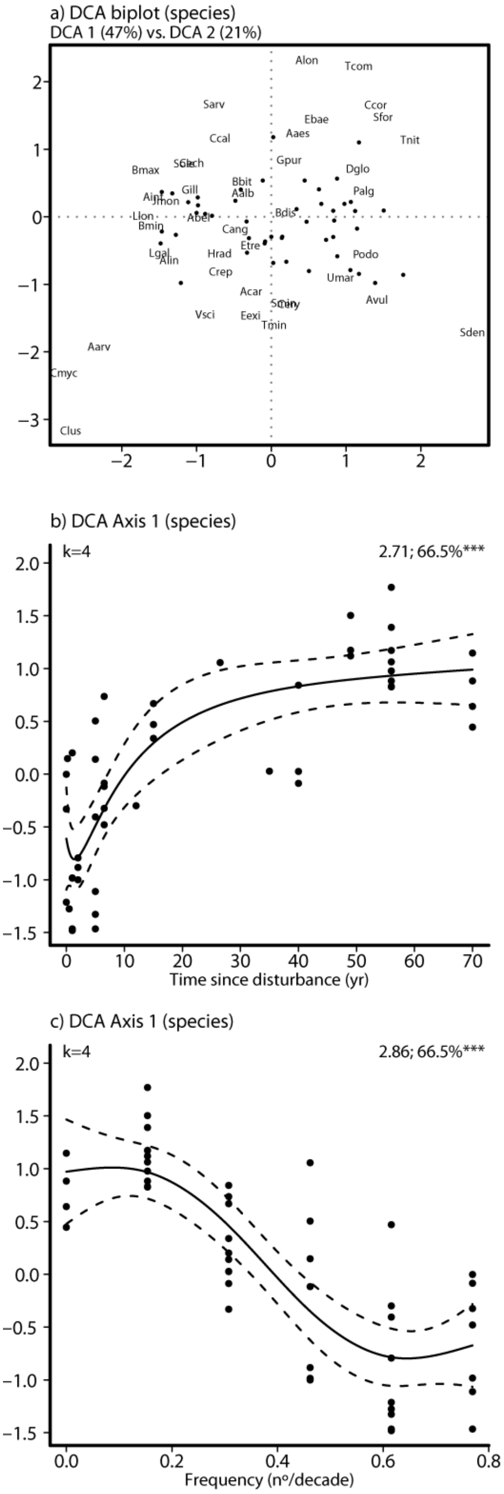


Figure 4: Ordination biplots of Detrended Correspondence Analyses (DCA) of herbaceous species composition data (a), and Generalized Additive Model fits (solid lines) and 95% confidence intervals (hatched lines) of relationships between the dominant gradient (DCA 1) and the timing (b) and frequency (c) of understory clearing disturbances. Dimension of the fitted spline (k), effective degrees of freedom, percentage variance explained, and significance-level (* P <0.001, ** P <0.01, * P <0.05, § P <0.1, ns P ≥ 0.1) are provided for each model. The biplot represents species with frequency of occurrence > 12.5%: Acar: *Aira caryophyllea*; Amas: *Allium massaesylum*; Aarv: *Anagallis arvensis*; Abel: *Anarrhinum bellidifolium*; Aint: *Andryala integrifolia*; Avul: *Anthyllis vulneraria* subsp. *gandogeri*; Alon: *Aristolochia longa*; Aalb: *Arrhenaterum album*; Aaes: *Asphodelus aestivus*; Alin: *Asterolinon linum-stellatum*; Bsyl: *Bellis sylvestris*; Bbit: *Bituminaria bituminosa*; Bdis: *Brachypodium distachyon*; Bmax: *Briza maxima*; Bmin: *Briza minor*; Clus: *Campanula lusitanica*; Ccor: *Carlina corymbosa*; Ccal: *Centranthus calcitrapae*; Cery: *Centaurium erythraea* subsp. *grandiflorum*; Cmyc: *Coleostephus myconis*; Crep: *Coronilla repanda* subsp. *dura*; Cves: *Crepis vesicaria*; Cang: *Crucianella angustifolia*; Cech: *Cynosurus echinatus*; Chyp: *Cytinus hypocistis*; Dglo: *Dactylis glomerata*; Dpur: *Digitalis purpurea*; Efoe: *Elaeoselinum foetidum*; Etre: *Epipactis tremolsii*; Ebae: *Erophaca baetica*; Eexi: *Euphorbia exigua*; Gpar: *Galium parissiense*; Gpur: *Geranium purpureum*; Gill: *Gladiolus illyricus*; Hhis: *Hyacinthoides hispanica*; Hper: *Hypericum perfoliatum*; Hrad: *Hypochaeris radicata*; Jmon: *Jasione montana*; Llon: *Leontodon longirrostris*; Lgal: *Logfia gallica*; Palg: *Picris algarbiensis*; Podo: *Pulicaria odora*; Rmed: *Reseda media*; Rind: *Rumex induratus*; Shyb: *Sanguisorba hybrida*; Smin: *Sanguisorba minor*; Sfor: *Sedum forsterianum*; Sden: *Selaginella denticulata*; Sliv: *Senecio lividus*; Sarv: *Sherardia arvensis*; Sole: *Sonchus oleraceus*; Tcom: *Tamus communis*; Tmin: *Thapsia minor*; Tnit: *Thapsia nitida*; Tbar: *Tolpis barbata*; Tarv: *Torilis arvensis* subsp. *purpurea*; Tcam: *Trifolium campestre*; Urup: *Umbilicus rupestris*; Umar: *Urginea maritima*; Upic: *Urospermum picroides*; Vsci: *Vulpia myurus* subsp. *sciuroides*.**

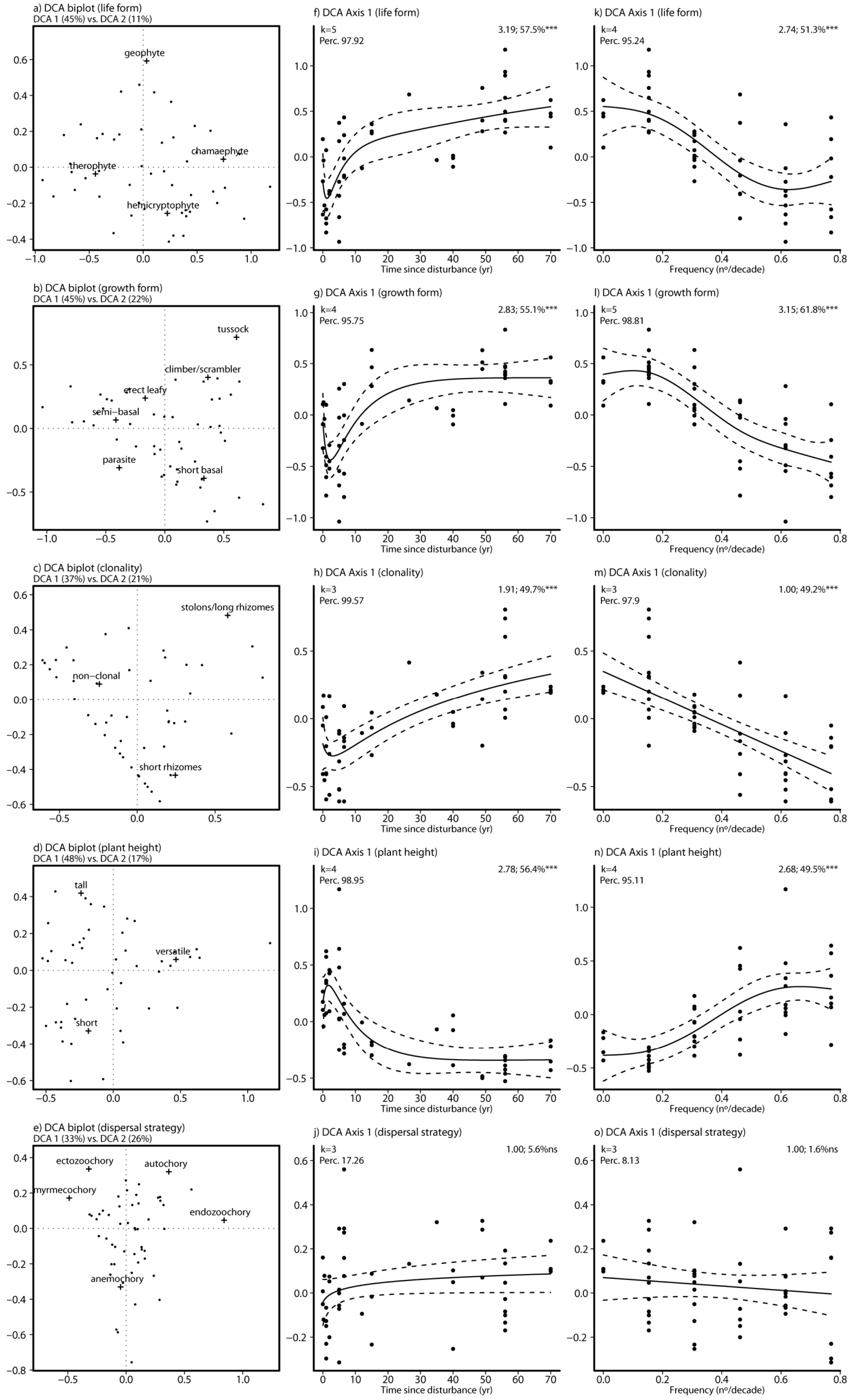


Figure 5: Ordination biplots of Detrended Correspondence Analyses (DCA) of herbaceous functional composition data (a-e), and Generalized Additive Model fits (solid lines) and 95% confidence intervals (hatched lines) of relationships between the dominant gradients (DCA 1) and the timing (f-j) and frequency (k-o) of understory clearing disturbances. Dimension of the fitted spline (k), effective degrees of freedom, percentage variance explained, and significance-level (* P <0.001, ** P <0.01, * P <0.05, § P <0.1, ns P ≥ 0.1) are provided for each model.**

DISCUSSION

Overall patterns

Mechanical shrub clearing showed pronounced effects on forest herb communities, which were stronger during the first 10-20 years after disturbance. However, effects were still noticeable after about 70 years and would probably be felt for longer, as some community attributes did not appear to stabilise within the chronosequence. Understanding the ecological consequences of fuel management, even when the studied biological group has short life cycles, may thus require study periods much longer than that normally analysed (e.g., Calvo *et al.* 2005; Perchemlides *et al.* 2008; Pérez-Ramos *et al.* 2008), which is in line with the long time frames usually required for appreciating the dynamics of forest ecosystems (Bellemare *et al.* 2002; Frelich 2002; Thomas and Packham 2007).

Changes in the herbaceous understory across the chronosequence shared some similarities to the successional patterns after land abandonment (Bonet and Pausas 2004), and supported the idea of disturbances such as mechanical fuel reduction causing a long-term shift between communities with contrasting composition, structure and functional organization (Díaz-Delgado *et al.* 2002; Rodrigo *et al.* 2004; Santana *et al.* In Press). These results are in marked contrast with the rapid recovery of herbaceous communities after mechanical clearing previously reported in Mediterranean shrublands and forests (e.g. Calvo *et al.* 2002, 2005; Pérez-Ramos *et al.* 2008). For instance, Pérez-Ramos *et al.* (2008) found that pre-disturbance herbaceous diversity in cork oak stands was approximately restored in just five years after shrub clearing, whereas Calvo *et al.* (2002) reported recovery times of about 10-15 years in Mediterranean shrublands. These contrasting patterns may partly be reconciled by considering that rapid restoration of community attributes may be found most often in short-term studies (< 15 years) or in recurrently disturbed habitats, which may be particularly resilient to further disturbances (Calvo *et al.* 2002, 2005; Potts *et al.* 2010), whereas long-term studies (> 50 years) or studies analysing more stable forest communities may tend to report much slower recovery rates (Bonet and Pausas 2004; this study).

Perception of herbaceous recovery rates may also be strongly influenced by the attributes used to assess community dynamics. Although some community attributes recovered over long time frames, species richness appeared essentially constant through the chronosequence, while herbaceous cover reached a peak in just about two years. In common with other studies, patterns derived from these relatively coarse attributes masked complex responses that could only be uncovered and interpreted by using finer attributes, such as, for instance, the variation in richness and cover within functional groups (Bonet and Pausas 2004; Decocq *et al.* 2004a; Perchemlides *et al.* 2008; von Oheimb and Härdtle 2009; this study).

Disturbance-favoured herbaceous communities

Some herbaceous species recovered quickly after mechanical clearing, showing a marked peak in cover about two years after disturbance and declining afterwards, either rapidly or progressively, to a nearly constant level. These species thus appeared to be favoured by mechanical disturbance, dominating the understory in recently and recurrently disturbed stands. Groups of species showing this pattern shared some traits like a terophytic life form (annuals), a semi-basal growth form (i.e. partial rosettes), no clonal ability, and versatility in height. Similar short-term positive effects of shrub clearing on the herbaceous layer, particularly on annual herbs, have often been reported in Mediterranean-type systems (Calvo *et al.* 2005; Perchemlides *et al.* 2008; Pérez-Ramos *et al.* 2008), probably resulting from the higher light availability at the ground level, and to decreases in the amount of litterfall and in physical obstruction by woody plants (Quilchano *et al.* 2008, Santana *et al.* In Press). These changes are expected to stimulate the germination of both seeds dispersing from nearby grassland patches and the local soil seed banks (Díaz-Villa *et al.* 2003, Pérez-Ramos *et al.* 2008). Subsequent declines in overall herbaceous cover and in richness and cover of annual species were coincident with the recovery of understory shrubs (Santana *et al.* In Press), which likely degraded again the habitat conditions for a large set of annual herbs (Calvo *et al.* 2005; Perchemlides *et al.* 2008).

Disturbance also appeared to favour species versatile in height, which were prevalent during about the first decade and increased in cover along with disturbance frequency. Reasons for this pattern are uncertain, though phenotypic plasticity of traits allows species to adapt to different environments and communities and confers competitive advantage in fluctuating environments (Poorter and Lambers 1986, Callaway *et al.* 2003). Furthermore, versatility in plant height and in other functional traits may be correlated (Lavorel *et al.* 1997), which may further favour the ability of species to colonise recently and recurrently disturbed environments.

Long-term herbaceous understory recovery

Species with perennial life form (especially chamaephytes), tussock habit and vegetative spread tended to be eliminated by mechanical clearing, slowly reappearing along the chronosequence. These results are in line with studies showing that recovery after major disturbances of typical forest herbs, mainly perennials, may take several decades or even centuries (Bellemare *et al.* 2002; Flinn and Vellend 2005), probably because they require particular regeneration niches that may take a long time for developing (Albrecht and McCarthy 2009), they often lack a persistent seed bank (Decocq *et al.* 2004b; Dölle & Schmidt 2009) and they have low colonization rates from external sources due to limited dispersal capacity (Bellemare *et al.* 2002; Brunet 2007).

Early elimination and subsequent slow recovery, in our case, was probably mediated by physical destruction of the perennating tissue, since the higher up it is located (chamaephytes > hemicryptophytes > geophytes), the more exposed plants are to disturbance (Cornelissen *et al.* 2003). Vegetative spread, however, should promote persistence under disturbance because clonality organs are often linked with resource storage (Cornelissen *et al.* 2003) and hence, capacity to resprout. Moreover, species with a high degree of vegetative spread, as long as they persist, are in advantage when colonizing open space (Cornelissen *et al.* 2003), being able to immediately take advantage of it (Aikens *et al.* 2007), but neither of these views was supported by this and other studies (McIntyre *et al.* 1995; Mabry and Fraterrigo 2009). This may be a consequence of disturbance intensity, which plays a crucial role in determining the fate of the disturbed site, by controlling the relative importance of persistence versus immigration/regeneration from seed bank (Aikens *et al.* 2007). Mechanical clearing in our study area generally involved deep ploughing with disc harrows, which may result in the elimination of storage organs of plants with resprouting capacity, and thus their elimination from early-successional stages (Santana *et al.* In Press).

Contrary to other studies, we did not find any evidence for the type of dispersal mechanism significantly affecting recovery of the herbaceous understory. Species with poor dispersal capacity are usually expected to take a long time to recolonize disturbed sites (Bellemare *et al.* 2002) and to be negatively influenced by habitat fragmentation (Aparicio *et al.* 2008), so that species that recolonize isolated suitable patches tend to have adaptations for long dispersal (Brunet 2007). It might thus be expected that short distance dispersal (autochorous and myrmecochorous) should appear only in late successional stages. The absence of this pattern in our particular case may indicate that either the regional species pool was already depleted of forest herbs or the time frame analysed was not long enough to allow recolonization by herbs with short distance dispersal. This may also correspond to a failure in the detection of a pattern due to uncontrolled variation related to landscape variables, such as distance to the late-successional population sources (Brunet 2007).

Conservation implications

This study suggests that mechanical fuel management may have long-term negative consequences for species and functional diversity of Mediterranean forest herbs. To control the development of the woody understory and thus reduce fire hazard, fuel management is often carried out at relatively short intervals (typically 9 years in the case of cork oak forests), which are much shorter than recovery times of herbaceous communities. In these circumstances, communities dominated by early-successional species tend to be maintained, while species and functional groups associated with late-successional stages may strongly decline or even be eliminated (Decocq *et al.* 2004a; Santana *et al.* In Press; this study). To solve this problem, patches with old understory need to be kept undisturbed for extended periods (> 50 years), as they may act as repositories of forest herb diversity and sources of colonisation for other, more frequently disturbed patches.

Despite its value for biodiversity conservation, it cannot be ignored that accumulation of woody materials in forest stands excluded from fuel reduction treatments may represent an increased risk of high-intensity fires. Fuel management thus needs to be planned at the landscape scale, so as to create heterogeneous mosaics of patches in different successional stages and to create discontinuities between late-successional patches with high fire risk. These mosaic landscapes may be essential for the conservation of Mediterranean forest biota requiring a range of contrasting ecological conditions, including for instance plants (Santana *et al.* In Press; this study), birds (de la Montaña 2006), and top predators (Palma *et al.* 1999, 2006; Beja *et al.* 2007). Defining the characteristics of such mosaic landscape, particularly the number, area and distribution of late-successional patches to be retained, should be the subject of future research, requiring the integration of Mediterranean landscape succession disturbance-dynamics (e.g., Millington *et al.* 2009) and accounting for multiple management objectives such as biodiversity conservation, fire hazard reduction, and sustainable forest use (Aronson *et al.* 2009; Santos and Thorne 2010).

ACKNOWLEDGEMENTS

This study was funded by IFADAP-Program AGRO 8.1 (project 458 - 2003.09.002326.2), and by the Portuguese Science and Technology Foundation through grant SFRH/BD/28974/2006 to MP. We thank researchers and technicians of the Forest Producers Association of Barranco do Velho, the Association In Loco, the Association for the Defence of Mértola Heritage, and the Centre for Applied Ecology “Baeta Neves”, for collaboration in the development of this project. We also thank Ricardo Silva and Rui Guerreiro for their valuable assistance in the field work.

REFERENCES

Acácio V, Holmgren M, Rego F, Moreira F, Mohren GMJ (2009) Are drought and wildfires turning Mediterranean cork oak forest into persistent shrublands? Agroforestry Systems 76:389–400

Agee JK, Skinner CN (2005) Basic principles of forest fuel reduction treatments. Forest Ecology and Management 211:83–96

Aikens ML, Ellum D, McKenna JJ, Kelty MJ, Ashton MS (2007) The effects of disturbance intensity on temporal and spatial patterns of herb colonization in a southern New England mixed-oak forest. Forest Ecology and Management 252:144–158

Albrecht MA, McCarthy BC (2009) Seedling establishment shapes the distribution of shade-adapted forest herbs across a topographical moisture gradient. Journal of Ecology 97:1037–1049

Aparicio A, Albaladejo RG, Olalla-Tárraga MA, Carrillo LF, Rodríguez MA (2008) Dispersal potentials determine responses of woody plant species richness to environmental factors in fragmented Mediterranean landscapes. Forest Ecology and Management 255:2894–2906

Aronson J, Pereira JS, Pausas J (2009) Cork oak woodlands on the edge: Ecology, biogeography, and restoration of an ancient Mediterranean ecosystem. Island Press, Washington DC, USA

Beja P, Pais M, Palma L (2007) Rabbit Oryctolagus cuniculus habitats in Mediterranean scrubland: the role of scrub structure and composition. Wildlife Biology 13:28–37

Bellemare J, Motzkin G, Foster DR, Forest H (2002) Legacies of the agricultural past in the forested present: an assessment of historical land-use effects on rich mesic forests. Journal of Biogeography 29:1401–1420

Bengtsson J, Nilsson SG, Franc A, Menozzi P (2000) Biodiversity, disturbances, ecosystem function and management of European forests. Forest Ecology and Management 132:39–50

Blondel J, Aronson J, Bodiou J-Y, Boeuf G (2010) The Mediterranean Region. Biological Diversity in Space and Time. Oxford University Press, Oxford, UK.

Bonet A, Pausas J (2004) Species richness and cover along a 60-year chronosequence in old-fields of southeastern Spain. Plant Ecology 174:257–270

Brunet J (2007) Plant colonization in heterogeneous landscapes: an 80-year perspective on restoration of broadleaved forest vegetation. Journal of Applied Ecology 44:563–572

Callaway RM, Pennings SC, Richards CL (2003) Phenotypic plasticity and interactions among plants. Ecology 84:1115–1128

Calvo L, Tárrega R, Luis E (2002) Secondary succession after perturbations in a shrubland community. Acta Oecologica 23:393–404

Calvo L, Tárrega R, Luis E, Valbuena L, Marcos E (2005) Recovery after experimental cutting and burning in three shrub communities with different dominant species. Plant Ecology 180:175–185

Converse SJ, White GC, Farris KL, Zack S (2006) Small mammals and forest fuel reduction: National-scale responses to fire and fire surrogates. Ecological Applications 16:1717–1729

Cornelissen JH, Lavorel S, Garnier E, Díaz S, Buchmann N, Gurvich DE, Reich PB, Steege HT, Morgan HD, Heijden MG, Pausas JG, Poorter H (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. Australian Journal of Botany 51:335–380

De La Montaña E, Rey-Bernayas JM, Carrascal LM (2006) Response of bird communities to silvicultural thinning of Mediterranean maquis. Journal of Applied Ecology 43:651–659

Decocq G, Aubert M, Dupont F, Alard D, Saguez R, Wattez-Franger A, Foucault B, Delelis-Dusollier A, Bardat J (2004a) Plant diversity in a managed temperate deciduous forest: understorey response to two silvicultural systems. Journal of Applied Ecology 41:1065–1079

Decocq G, Valentin B, Toussaint B, Hendoux F, Saguez R, Bardat J (2004b) Soil seed bank composition and diversity in a managed temperate deciduous forest. Biodiversity and Conservation 13:2485–2509

Díaz-Delgado R, Lloret F, Pons X, Terradas JJ (2002) Satellite evidence of decreasing resilience in Mediterranean plant communities after recurrent wildfires. Ecology 83:2293–2303

Díaz-Villa MD, Marañón T, Arroyo J, Garrido B (2003) Soil seed bank and floristic diversity in a forest-grassland mosaic in southern Spain. Journal of Vegetation Science 14:701–709

Dölle M, Schmidt W (2009) The relationship between soil seed bank, above-ground vegetation and disturbance intensity on old-field successional permanent plots. Applied Vegetation Science 12:415–428

Feio M (1949) Le Bas Alentejo et l'Algarve (Livret-Guide de l'Excursion E). XVI Congrès Internationale de Géographie, CEG, Lisbon

Flinn KM, Vellend M (2005) Recovery of forest plant communities in post-agricultural landscapes. Frontiers in Ecology and the Environment 3:243–250

Foster BL, Tilman D (2000) Dynamic and static views of succession: testing the descriptive power of the chronosequence approach. Plant Ecology 146:1–10

Frelich LE (2002) Forest dynamics and disturbance regimes. Studies from temperate evergreen-deciduous forests. Cambridge University Press, Cambridge, UK

Guerreiro MG (1951) Valorização da Serra Algarvia: a erosão, a cobertura vegetal e a água. Direcção Geral dos Serviços Florestais e Aquícolas, Lisbon

Hampe A, Arroyo J (2002) Recruitment and regeneration in populations of an endangered South Iberian Tertiary relict tree. Biological Conservation 107:263–271

Hastie TJ, Tibshirani RJ (1990) Generalized Additive Models. Chapman & Hall, London, UK

Johnson EA, Miyanishi K (2008) Testing assumptions of chronosequences in succession. Ecology Letters 11:419–431

Lavorel S, McIntyre S, Landsberg J, Forbes TDA (1997) Plant functional classifications: from general groups to specific groups based on response to disturbance. Trends in Ecology & Evolution 12:474–478

Lindenmayer DB, Franklin JF, Fischer J (2006) General management principles and a checklist of strategies to guide forest biodiversity conservation. Biological Conservation 131:433–445

Mabry CM, Fraterrigo J (2009) Species traits as generalized predictors of forest community response to human disturbance. Forest Ecology and Management 257:723–730

Malo JE, Suárez F (1995) Herbivorous mammals as seed dispersers in a Mediterranean dehesa. Oecologia 104:246–255

Marañon T, Ajbilou R, Ojeda F, Arroyo J (1999) Biodiversity of woody species in oak woodlands of southern Spain and northern Morocco. Forest Ecology and Management 115:147–156

McIntyre S, Lavorel S, Tremont R (1995) Plant life-history attributes: their relationship to disturbance response in herbaceous vegetation. Journal of Ecology 83:31–44

Millington JDA, Wainwright J, Perry GLW, Romero-Calcerrada R, Malamud BD (2009) Modelling Mediterranean landscape succession-disturbance dynamics: A landscape fire-succession model. Environmental Modelling & Software 24:1196–1208

Ojeda F, Marañón T, Arroyo J (2000) Plant diversity patterns in the Aljibe Mountains (S.Spain): a comprehensive account. Biodiversity and Conservation 9:1323–1343

Oksanen J, Kindt R, Legendre P, O'Hara B, Simpson GL, Solymos P, Stevens MHH, Wagner H (2009) Vegan: Community Ecology Package. R package version 1.15-2. http://cran.r-project.org/web/packages/vegan/index.html. Cited 9 Dec 2010

Palma L, Beja P, Rodrigues M (1999) The use of sighting data to analyse Iberian lynx habitat and distribution. Journal of Applied Ecology 36:812–824

Palma L, Beja P, Pais M, Fonseca LC (2006) Why do raptors take domestic prey? The case of Bonelli's eagles and pigeons. Journal of Applied Ecology 43:1075–1086

Paula S, Arianoutsou M, Kazanis D, Tavsanoglu Ç, Lloret F, Buhk C, Ojeda F, Luna B, Moreno JM, Rodrigo A, Espelta JM, Palacio S, Fernández-Santos B, Fernandes PM, Pausas JG (2009) Fire-related traits for plant species of the Mediterranean Basin. Ecology 90:1420–1420

Perchemlides KA, Muir PS, Hosten PE (2008) Responses of chaparral and oak woodland plant communities to fuel-reduction thinning in Southwestern Oregon. Rangeland Ecology & Management 61:98–109

Pérez-Ramos IM, Zavala MA, Marañón T, Díaz-Villa MD, Valladares F (2008) Dynamics of understorey herbaceous plant diversity following shrub clearing of cork oak forests: A five-year study. Forest Ecology and Management 255:3242–3253

Petchey OL, Gaston KJ (2006) Functional diversity: back to basics and looking forward. Ecology Letters 9:741–58

Poorter H, Lambers H (1986) Growth and competitive ability of a highly plastic and marginally plastic genotype of *Plantago* major in a fluctuating environment. Physiologia Plantarum 67:217–222

Potts JB, Marino E, Stephens SL (2010) Chaparral shrub recovery after fuel reduction: a comparison of prescribed fire and mastication techniques. Plant Ecology 210:303–315

Quilchano C, Marañón T, Pérez-Ramos IM, Noejovich L, Valladares F, Zavala MA (2008) Patterns and ecological consequences of abiotic heterogeneity in managed cork oak forests of Southern Spain. Ecological Research 23:127–139

Rivas-Martínez S, Lousã M, Díaz TE, Fernández-González F, Costa JC (1990) La vegetatión del Sur de Portugal (Sado, Alentejo y Algarve). Itinera Geobotánica 3:5–126

Roberts MR (2004) Response of the herbaceous layer to natural disturbance in North American forests. Canadian Journal of Botany 82:1273–1283

Rodrigo A, Retana J, Picó FX (2004) Direct regeneration is not the only response of Mediterranean forests to large fires. Ecology 85:716–729

Santana J, Porto M, Reino L, Beja P (in press) Long-term understory recovery after mechanical fuel reduction in Mediterranean cork oak forests. Forest Ecology and Management

Santos MJ, Thorne JH (2010) Comparing culture and ecology: conservation planning of oak woodlands in Mediterranean landscapes of Portugal and California. Environmental Conservation 37:155–168

Seng M, Deil U (1999) Forest vegetation types in the serra de Monchique (Portugal): Anthropogenic changes of oak forests. Silva Lusitana 7:71–92

Stephens SL, Moghaddas JJ, Ediminster C, Fiedler CE, Hasse S, Harrington M, Keeley JE, McIver JD, Metlen K, Skinner CN, Youngblood A (2009) Fire treatment effects on vegetation structure, fuels, and potential fire severity in western U.S. forests. Ecological Applications 19:305–320

Thomas PA, Packham JR (2007) Ecology of woodlands and forests. Description, dynamics and diversity. Cambridge University Press, Cambridge

Thomas SC, Halpern CB, Falk DA, Liguori DA, Austin KA (1999) Plant diversity in managed forests: understory responses to thinning and fertilization. Ecological Applications 9:864–879

Torras O, Saura S (2008) Effects of silvicultural treatments on forest biodiversity indicators in the Mediterranean. Forest Ecology and Management 255:3322–3330

von Oheimb G, Härdtle W (2009) Selection harvest in temperate deciduous forests: impact on herb layer richness and composition. Biodiversity Conservation 18:271–287

Wood SN (2006) Generalized additive models: An introduction with R. Champman and Hall/CRC, Boca Raton

Wright JP, Naeem S, Hector A, Lehman C, Reich PB, Schmid B, Tilman D (2006) Conventional functional classification schemes underestimate the relationship with ecosystem functioning. Ecology Letters 9:111–120

Xanthopoulos G, Caballero D, Galante M, Alexandrian D, Rigolot E, Marzano R (2006) Forest fuels management in Europe. In: Andrews PL, Butler BW (eds) Fuels management-how to measure success: Conference Proceedings. USDA Forest Service, Portland, OR, USA, pp29–46

SUPPLEMENTARY MATERIAL

Supplementary Table S1: List of herbaceous species recorded in 48 1-ha cork oak parcels sampled in the Caldeirão hills (southern Portugal). Species are classified in terms of five functional traits.

Taxon[a]	Life form[b]	Growth form[c]	Clonality[d]	Plant height[e]	Dispersal strategies[f]
Aetheorhiza bulbosa	G	r	S	s	a
Agrostis castellana	H	t	S	t	a
Aira caryophyllea	T	s	N	s	a
Aira cupaniana	T	s	N	s	a
Airopsis tenella	T	s	N	s	a
Allium massaessylum	G	r	N	s	b
Allium sp.	G	e	N	t	b
Anagallis arvensis	T	e	N	s	b
Anarrhinum bellidifolium	H	s	N	v	b
Andryala arenaria	T	s	N	v	b
Andryala integrifolia	H	e	N	t	b
Anemone palmata	G	r	N	s	a
Anthoxanthum aristatum subsp. *macranthum*	T	s	N	s	ae
Anthoxanthum ovatum	T	s	N	s	ae
Anthyllis vulneraria subsp. *gandogeri*	H	s	N	s	ae
Arisarum vulgare	G	r	R	s	nh
Aristolochia longa	G	e	N	t	b
Arrhenaterum album	G	s	S	t	a
Asphodelus aestivus	G	r	N	t	b
Asplenium billotii	H	r	N	s	a
Asplenium onopteris	H	r	N	s	a
Asplenium trichomanes	H	r	N	s	a
Asterolinum linum-stellatum	T	e	N	s	b
Avena barbata subsp. *barbata*	T	s	N	t	ea
Avena barbata subsp. *lusitanica*	T	s	N	t	ea
Avena sterilis	T	s	N	t	ea
Bellis sylvestris	H	r	N	s	ea
Bituminaria bituminosa	H	s	N	t	eabn
Brachypodium distachyon	T	s	N	s	ae
Brachypodium sylvaticum	H	t	N	t	ae
Briza maxima	T	s	N	v	ae
Briza minor	T	s	N	s	a
Bromus diandrus	T	s	N	t	a
Bromus hordeaceus	T	s	N	s	ae
Bromus madritensis	T	s	N	v	ae
Bromus rubens	T	s	N	v	ae
Campanula lusitanica	T	e	N	s	b
Campanula rapunculus	H	s	N	t	b
Carduus tenuiflorus	T	e	N	t	ae
Carex divulsa	H	t	R	s	b
Carex sp.	H	t	R	s	b
Carlina corymbosa	H	s	N	s	ae
Centaurium erythraea subsp. *grandiflorum*	H	s	N	s	a
Centranthus calcitrapae	T	e	N	v	a
Cerastium glomeratum	T	e	N	s	bn
Chamaemelum mixtum	T	e	N	v	ae
Clinopodium vulgare	H	e	R	s	eb
Coleostephus myconis	T	e	N	v	ae
Conopodium majus subsp. *marizianum*	G	r	N	s	ab
Conopodium marianum	G	r	N	s	ab
Coronilla repanda subsp. *dura*	T	e	N	s	ea
Crepis vesicaria	H	s	N	v	a
Crucianella angustifolia	T	e	N	s	ba

Taxon[a]	**Life form**[b]	**Growth form**[c]	**Clonality**[d]	**Plant height**[e]	**Dispersal strategies**[f]
Cynosurus echinatus	T	s	N	s	ae
Cynosurus elegans	T	s	N	s	ae
Cytinus hypocistis	G	p	N	s	n
Dactylis glomerata	H	t	N	t	ae
Daucus carota subsp. maximus	H	s	N	t	e
Daucus crinitus	H	s	N	t	e
Daucus sp.	H	s	N	t	e
Deschampsia stricta	H	t	R	t	a
Digitalis purpurea	H	s	N	t	b
Distichoselinum tenuifolium	G	s	R	t	a
Dorycnopsis gerardi	H	e	N	t	bn
Drosophyllum lusitanicum	C	r	N	s	b
Elaeoselinum foetidum	H	r	N	t	a
Epipactis tremolsii	G	e	R	t	a
Erodium cicutarium	T	s	N	s	e
Erophaca baetica	G	e	R	t	b
Eryngium dilatatum	H	s	N	s	a
Euphorbia exigua	T	e	N	s	m
Filago lutescens	T	e	N	s	a
Fritillaria lusitanica	G	e	N	t	b
Fumaria capreolata	T	c	N	v	b
Galactites tomentosa	T	s	N	v	a
Galium divaricatum	T	c	N	s	b
Galium parissiense	T	c	N	s	bn
Gastridium ventricosum	T	s	N	s	a
Geranium molle	T	s	N	s	b
Geranium purpureum	T	s	N	s	b
Gladiolus illyricus	G	e	N	t	a
Holcus lanatus	H	t	N	t	a
Holcus setiglumis	T	s	N	s	a
Hyacinthoides hispanica	G	r	N	s	b
Hymenocarpus lotoides	T	e	N	s	bn
Hyparrhenia hirta	H	t	N	t	ea
Hypericum humifusum	H	e	R	s	b
Hypericum perfoliatum	H	e	R	t	a
Hypochaeris glabra	T	r	N	s	ae
Hypochaeris radicata	H	r	N	t	a
Jasione montana	T	e	N	s	b
Lactuca sp.	H	s	N	t	a
Lathyrus clymenum	T	c	N	t	nb
Leontodon longirrostris	T	r	N	s	a
Limodorum abortivum	G	p	R	t	a
Logfia gallica	T	e	N	s	ae
Lolium rigidum	T	s	N	s	a
Lolium temulentum	T	s	N	s	a
Lotus parviflorus	T	e	N	s	b
Lupinus luteus	T	e	N	v	b
Lupinus micranthus	T	e	N	v	b
Luzula forsteri	H	t	S	s	a
Malva hispanica	T	e	N	s	b
Melica minuta	H	t	N	t	a
Mentha pulegium	H	e	S	s	b
Mercurialis ambigua	T	e	N	v	ae
Micromeria graeca	C	e	N	s	b
Micropyrum tenellum	T	s	N	s	a
Misopates orontium	T	e	N	v	a
Muscari comosum	G	r	N	s	hb

Taxon[a]	**Life form**[b]	**Growth form**[c]	**Clonality**[d]	**Plant height**[e]	**Dispersal strategies**[f]
Narcissus calcicola	G	r	N	s	b
Oenanthe crocata	G	s	N	t	b
Oenanthe pimpinelloides	H	s	N	t	b
Orchis sp.	G	r	N	s	a
Ornithogalum broteroi	G	r	N	s	b
Ornithogalum pyrenaicum	G	r	N	t	b
Ornithopus compressus	T	s	N	s	b
Orobanche artemisiae-campestris	G	p	N	s	a
Orobanche gracilis	G	p	N	s	a
Picris algarbiensis	H	r	N	t	a
Piptatherum miliaceum	H	t	N	t	ae
Plantago coronopus	T	r	N	s	a
Polypodium interjectum	H	r	R	s	a
Pteridium aquilinum	G	r	S	t	a
Pulicaria odora	H	r	R	s	a
Pulicaria paludosa	T	e	N	t	a
Radiola linoides	T	e	N	s	b
Ranunculus bulbosus	G	r	N	v	b
Ranunculus gregarius	G	r	R	s	eb
Raphanus raphanistrum	T	s	N	s	b
Reseda media	T	s	N	s	a
Rumex angiocarpus	H	s	S	s	a
Rumex bucephalophorus	T	s	N	s	ae
Rumex induratus	C	e	R	t	a
Ruta angustifolia	C	e	N	t	b
Ruta montana	C	e	N	t	b
Sanguisorba hybrida	H	s	N	t	a
Sanguisorba minor	H	s	N	s	a
Scilla monophyllus	G	r	N	s	b
Scorpiurus sulcatus	T	s	N	s	enb
Scorpiurus vermiculatus	T	s	N	s	nb
Scrophularia scorodonia	H	e	R	t	b
Sedum forsterianum	C	r	S	s	ab
Selaginella denticulata	C	r	S	s	a
Senecio lividus	T	e	N	v	a
Serapias cordigera	G	r	N	s	a
Serapias sp.	G	r	N	s	a
Sherardia arvensis	T	e	N	s	b
Silene gallica	T	s	N	s	ae
Sonchus asper	T	e	N	v	a
Sonchus oleraceus	T	e	N	v	a
Stachys arvensis	T	e	N	s	b
Tamus communis	G	c	N	t	n
Teucrium haenseleri	C	e	N	s	b
Thapsia minor	H	r	N	v	a
Thapsia nitida	H	r	N	t	a
Tolpis barbata	T	s	N	s	eb
Torilis arvensis subsp. *purpurea*	T	s	N	v	ea
Trifolium angustifolium	T	e	N	v	e
Trifolium arvense	T	e	N	s	e
Trifolium campestre	T	e	N	s	eb
Trifolium ligusticum	T	e	N	s	e
Trifolium stellatum	T	e	N	s	e
Tuberaria guttata	T	s	N	s	bn
Tuberaria lignosa	H	r	N	s	b
Umbilicus rupestris	G	s	N	s	ab
Urginea maritima	G	r	N	s	a

Taxon[a]	**Life form**[b]	**Growth form**[c]	**Clonality**[d]	**Plant height**[e]	**Dispersal strategies**[f]
Urospermum picroides	T	e	N	v	a
Vicia benghalensis	T	c	N	s	nb
Vicia disperma	T	c	N	t	nb
Vicia lutea	T	c	N	s	nb
Vicia peregrina	T	c	N	s	nb
Vicia sativa	T	c	N	s	nb
Vulpia ciliata	T	s	N	s	ae
Vulpia geniculata	T	t	N	v	a
Vulpia myurus subsp *sciuroides*	T	s	N	s	an
Vulpia myurus subsp. *myurus*	T	s	N	s	an
Vulpia sp.	T	s	N	s	an

[a] Plant species nomenclature follows Flora Iberica (Castroviejo, S. *et al.* (eds), 1986–2008. Flora Iberica, Vols. I, II, III, IV, V, VI, VII (I/II), VIII, X, XIV, XV, XVIII, XXI. Real Jardín Botánico, CSIC, Madrid) and Nova Flora de Portugal (Franco, J.A., 1971-1984. Nova Flora de Portugal (Continente e Açores), Vols. I, II). Edition of the Author, Lisbon; Franco, J.A. Rocha-Afonso, M.L. 1994-2003, Nova Flora de Portugal (Continente e Açores), Vol. III (I/II/III). Escolar Editora, Lisbon).

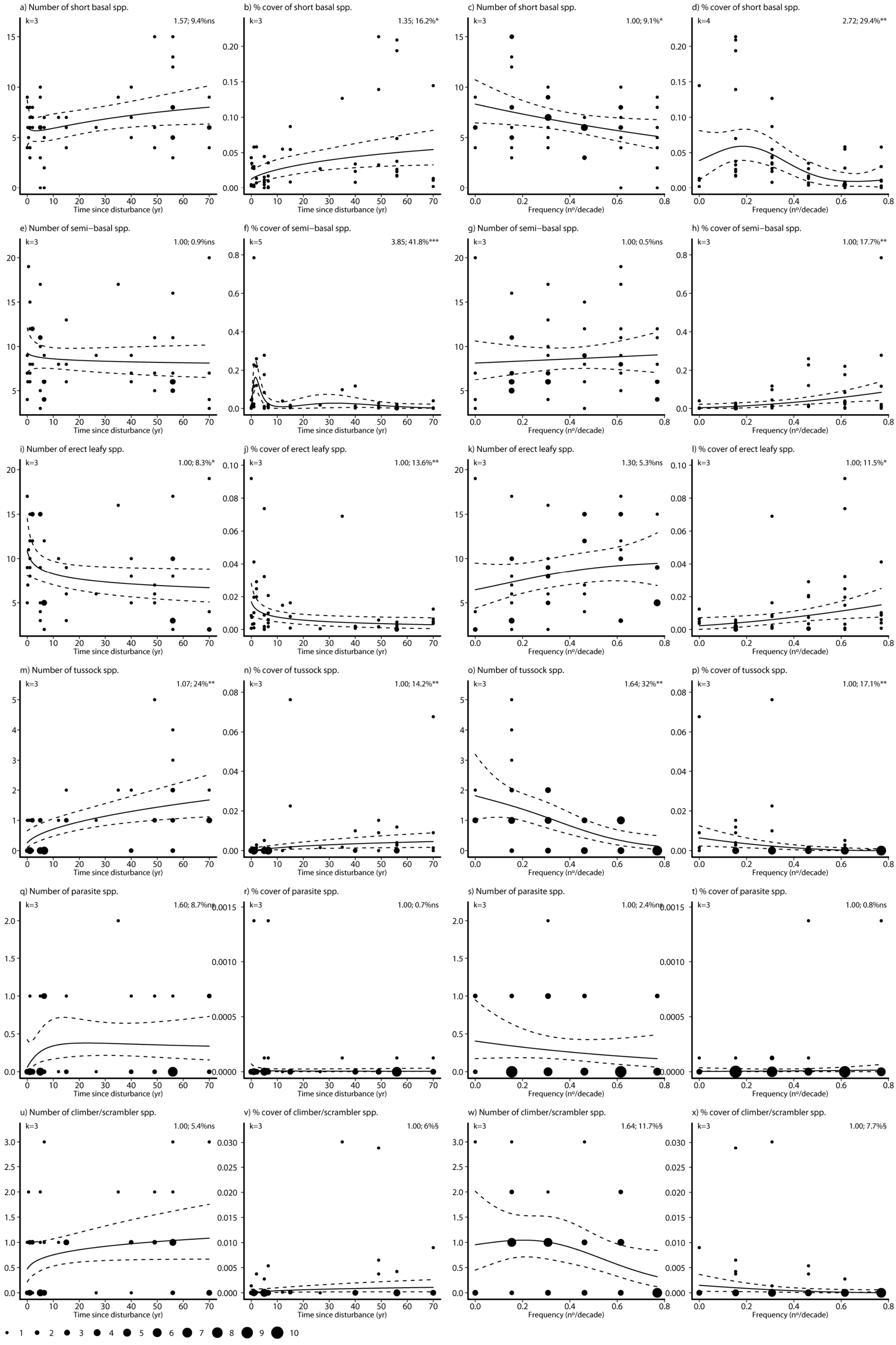
[b] Life form: T - therophyte, H - hemicryptophyte, G - geophyte, C - chamaephyte;

[c] Growth form: r - short basal (rosettes), s - semi-basal (partial rosettes), e - erect leafy, t - tussock forming, c - climber or scrambler, p - parasite;

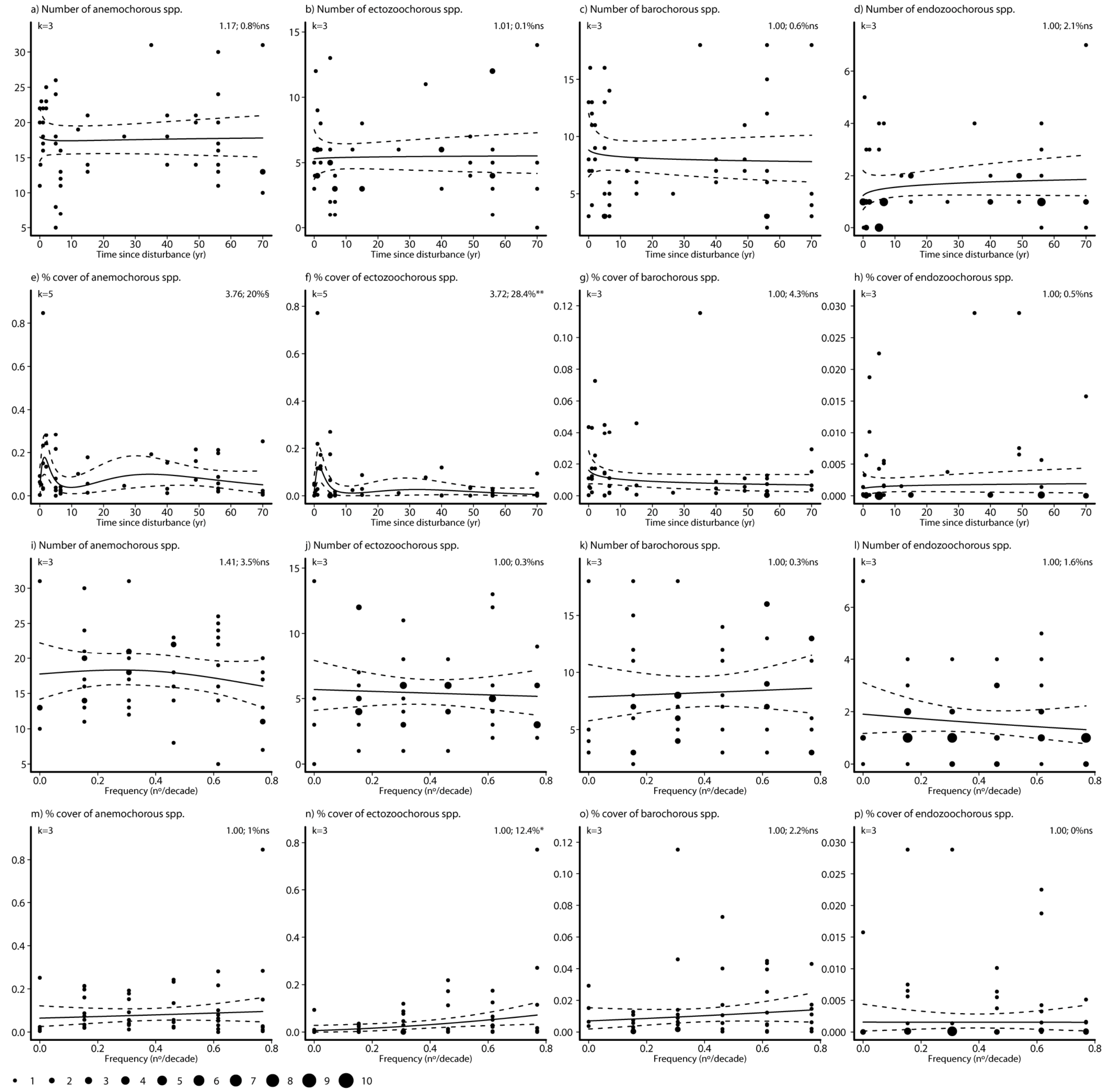
[d] Clonality: N - non-clonal, R - short rhizomes, S - stolons or long rhizomes;

[e] Plant height: s - short (<40 cm), t - tall (>40 cm), v - versatile;

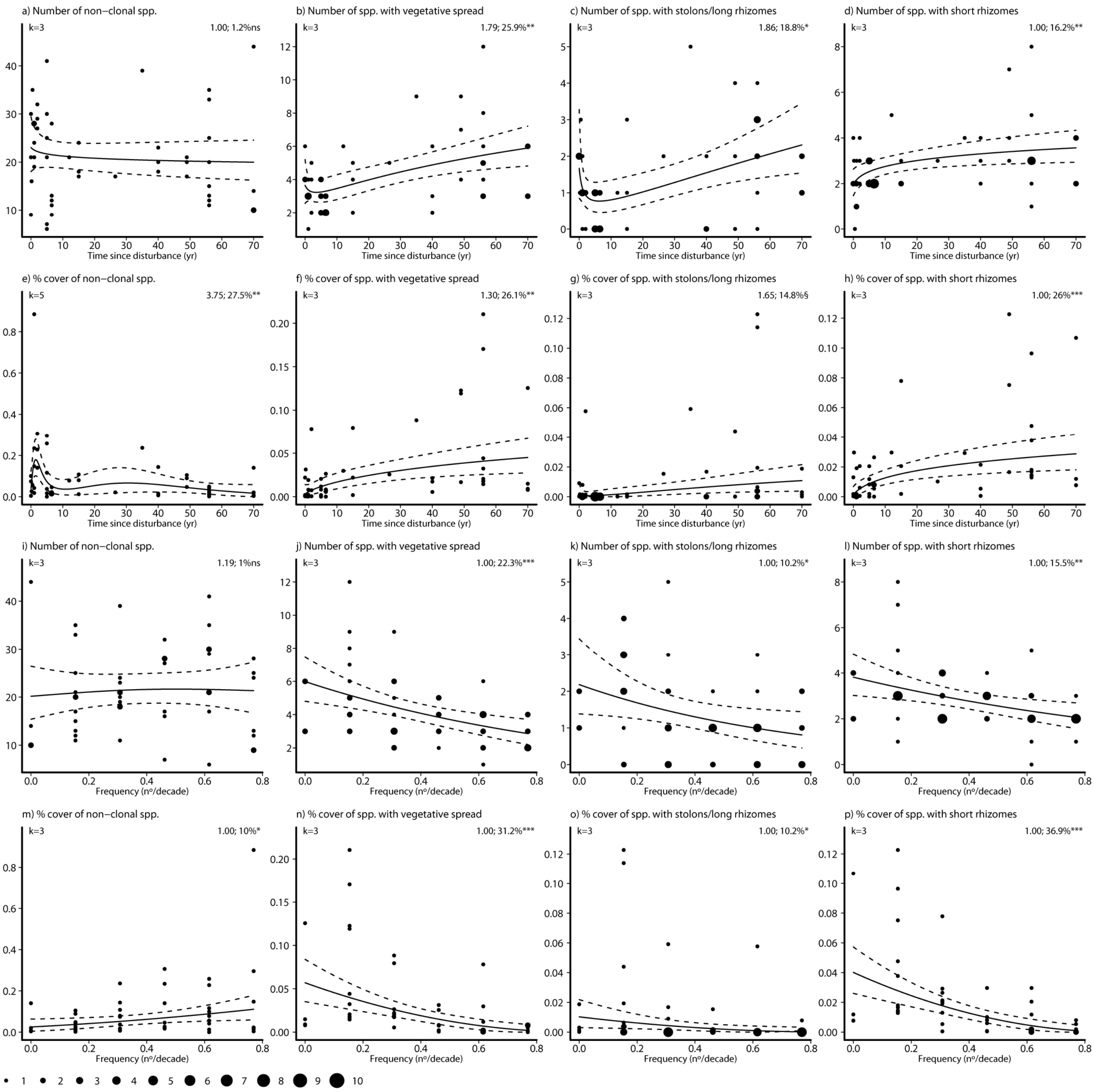
[f] Dispersal strategy: a - anemochory, b - barochory, e - ectozoochory, n - endozoochory, m - myrmecochory, h - hoarding. Species with multiple dispersal strategies were classified in more than one group.



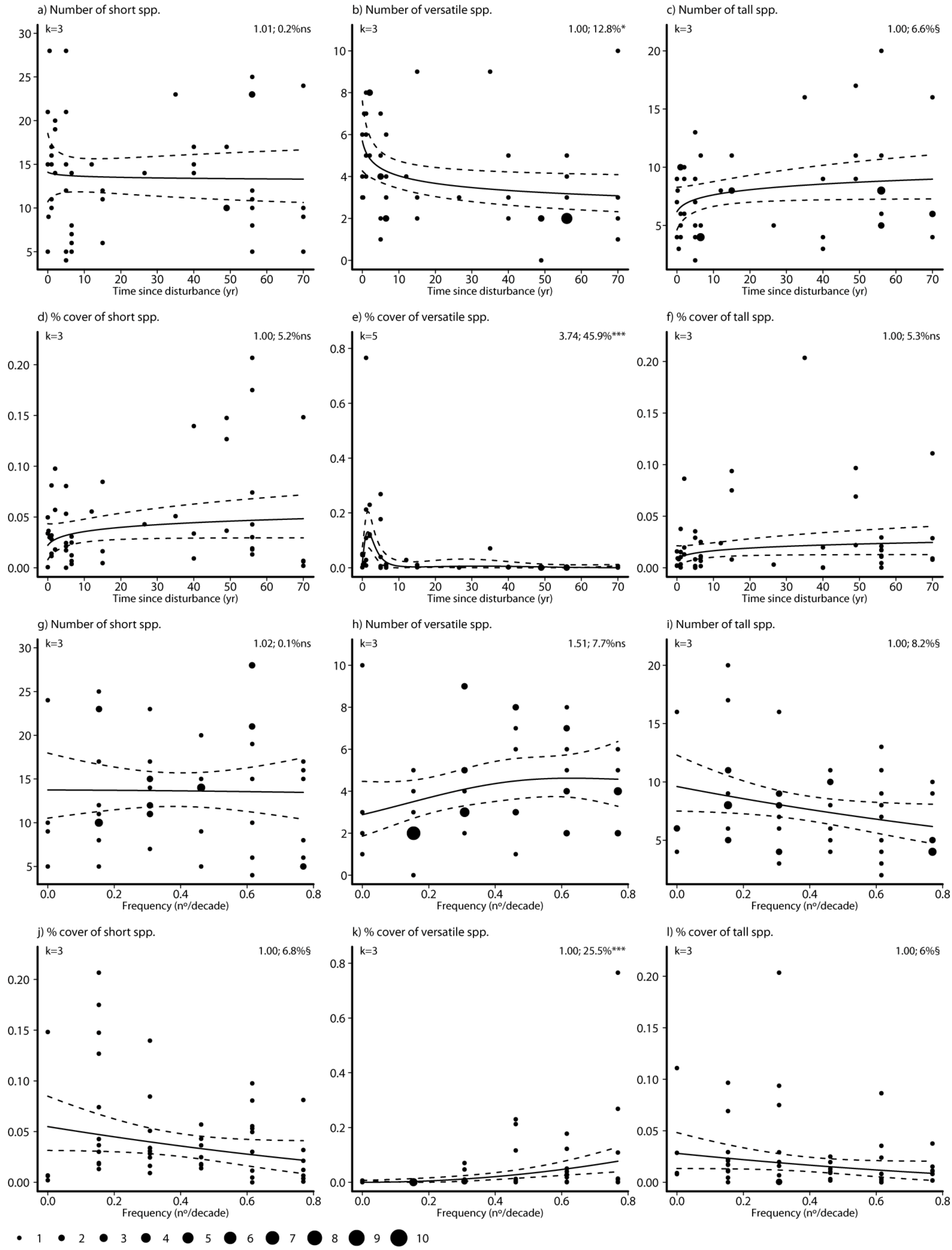
Supplementary Figure S1: Generalized Additive Model fits (solid lines) and 95% confidence intervals (hatched lines), of relationships between species richness and cover within growth form types, and the timing and frequency of understory clearing disturbances. Dot sizes are proportional to the number of observations. Dimension of the fitted spline (k), effective degrees of freedom, percentage variance explained, and significance-level (* *P* <0.001, ** *P* <0.01, * *P* <0.05, § *P* <0.1, ns *P* ≥ 0.1) are provided for each model.**



Supplementary Figure S2: Generalized Additive Model fits (solid lines) and 95% confidence intervals (hatched lines), of relationships between species richness and cover within dispersal strategy types, and the timing and frequency of understory clearing disturbances. Dot sizes are proportional to the number of observations. Dimension of the fitted spline (k), effective degrees of freedom, percentage variance explained, and significance-level (* *P* <0.001, ** *P* <0.01, * *P* <0.05, § *P* <0.1, ns *P* ≥ 0.1) are provided for each model.**



Supplementary Figure S3: Generalized Additive Model fits (solid lines) and 95% confidence intervals (hatched lines), of relationships between species richness and cover within clonality types, and the timing and frequency of understory clearing disturbances. Dot sizes are proportional to the number of observations. Dimension of the fitted spline (k), effective degrees of freedom, percentage variance explained, and significance-level (* *P* <0.001, ** *P* <0.01, * *P* <0.05, § *P* <0.1, ns *P* ≥ 0.1) are provided for each model.**



Supplementary Figure S4: Generalized Additive Model fits (solid lines) and 95% confidence intervals (hatched lines), of relationships between species richness and cover within plant height types, and the timing and frequency of understory clearing disturbances. Dot sizes are proportional to the number of observations. Dimension of the fitted spline (k), effective degrees of freedom, percentage variance explained, and significance-level (* *P* <0.001, ** *P* <0.01, * *P* <0.05, § *P* <0.1, ns *P* ≥ 0.1) are provided for each model.**

4

Modeling fuel succession in Mediterranean cork oak forests along a 70-year chronosequence

M. Porto, O. Correia, P. Beja

submitted

Drosophyllum lusitanicum
one of the most unique carnivorous plants in the world, associated with early successional, transient habitats (e.g. after fire or clearing)

Modeling fuel succession in mediterranean cork oak forests along a 70-year chronosequence

Miguel Porto[a], Otília Correia[a], Pedro Beja[b]

[a]Departamento de Biologia Vegetal, Faculdade de Ciências de Lisboa, Centro de Biologia Ambiental, Universidade de Lisboa, C2 Campo Grande, 1749-016 Lisboa, Portugal
[b]CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Campus Agrário de Vairão, Universidade do Porto, 4485-601 Vairão, Portugal

ABSTRACT

Mechanical removal of understory vegetation is increasingly used in Euro-Mediterranean forests to reduce fire hazard, but little is known about the long-term patterns of fuel change after management. We used a 70-year post-management chronosequence to investigate fuel succession in cork oak *Quercus suber* forests. Shrub cover increased rapidly during the first 10 years, stabilising after about 30 years. Mean shrub height, crown volume, total standing biomass, and biomass of leaves, and coarse and fine materials, also increased rapidly during the first 10 years, but then converged slowly to a plateau that was not reached within the chronosequence. A high vertical continuity of fuels from the ground level to the tree canopy (0-2 m) was reached in just about 10-20 years, but peak understory cluttering occurred only at 50-70 years. Fine materials accumulated primarily at lower strata (<1 m) throughout the chronosequence, whereas leaves and coarse materials accumulated first at lower strata, and then progressively occupied the upper strata (>1.5 m). Results suggest that recurrent fuel management may promote highly flammable pioneer shrublands, whereas lack of management promotes late-successional vegetation with high risk of intense wildfires. Solving this conundrum requires careful planning of the spatial and temporal distribution of treatments to reduce the risk of fire spread at the landscape scale.

Keywords: fuel succession, *Quercus suber* forests, fuel management, Portugal

INTRODUCTION

Fuel, weather and topography are the main factors influencing wildfire intensity, severity and behaviour (Peterson *et al.* 2005). From these, only fuel can be controlled, making it the main target of management efforts for fire prevention, even though it may not be the most important factor in conditioning fire (Bessie and Johnson 1995). Fuel management, however, does not aim to avoid the occurrence of fire, but to reduce its intensity, thereby facilitating fire suppression and minimizing damages (Fernandes *et al.* 2004). Understanding fuel dynamics in space and time is thus a basic prerequisite for fire prediction and it is of great interest to land managers (Bilgili 2003; Baeza *et al.* 2006) as a basis for prioritizing management activities (He *et al.* 2004).

Fire risk is often assumed to be directly related to age since last fire or other disturbance, through the accumulation of dead biomass (e.g. leaf litter, down branches and logs) (Keane *et al.* 2004), eventually reaching steady-state conditions (Plucinski 2006). This is based on the view that continuing fuel accumulation and an increased fraction of dead material will result in an increasing probability of fire (Bond and van Wilgen 1996; Bond and Keeley 2005), which might be true for some types of forests where dead fuels are the main combustible material (Plucinski 2006). However, in shrub dominated communities, living vegetation constitutes the bulk of fuel available (Plucinski 2006), and so fuel accumulation through time may not be characterized by a constant increase because of the inherent dynamics of vegetation communities and the role of ecological succession processes (Baeza *et al.* 2011), which may strongly alter species composition, abundance and organization (Tilman 1985; Huston and Smith 1987). These alterations will be reflected in fuel properties, in a process called ‘fuel succession’, and ultimately affect fire behaviour (Schwilk and Caprio 2011).

The drivers of fuel succession are several plant traits that influence flammability (e.g. chemistry and arrangement of fuel particles, structure and architecture of plant species, etc.) (Rundel 1981; Schwilk 2003; Ormeño *et al.* 2009; Baeza *et al.* 2011). For example, high surface/volume ratios, large amounts of fine materials and the retention of standing dead biomass are among the most influent characteristics that facilitate fire initiation and propagation (Papió and Trabaud 1990; Fernandes and Pereira 1993; Baeza *et al.* 2006). Thus, alterations in the abundance and proportion of species possessing such traits, which are part of the natural succession process, are likely to have an impact in overall fuel properties (Clemente *et al.* 1996; De Luís *et al.* 2004; Baeza *et al.* 2006). However, even though it is simple to relate species traits to species flammability (Ormeño *et al.* 2009; Saura-Mas *et al.* 2010; Liodakis *et al.* 2011), predicting the flammability at the community level is not straightforward due to the complex interactions among species (Lavorel and Garnier 2002; Baeza *et al.* 2011). Furthermore, vegetation development affects both micro-climate and soil physical properties, which in turn influence live and dead fuel moisture dynamics and subsequent fire behaviour (Keane *et al.* 2004). The fire risk associated with a plant community is, therefore, considered an emergent property of the community (Baeza *et al.* 2011). In these circumstances, understanding the interrelationships between vegetation dynamics and fuel succession is fundamental to predict the behaviour of fires (Krivtsov *et al.* 2009) and to plan wildfire control strategies (Baeza *et al.* 2006).

Gaining a better understanding of fuel dynamics is particularly important in the Euro-Mediterranean region, where land abandonment and the associated processes of shrub encroachment and afforestation are leading to an increasing frequency of catastrophic wildfires causing significant losses of human lives and livelihood (Pausas *et al.* 2008; Moreira *et al.* 2011). Because of this, fire suppression is at present the main tenet of forest management policies in this region, often involving mechanical silvicultural treatments to remove understory woody vegetation and decrease tree density (thinning), thereby preventing the violent progression of wildfires (Moreira *et al.* 2011). It is uncertain, however, how management will affect fuel succession in the long run, due to complex and species-specific effects of disturbance (Plucinski 2006). For instance, while fuel management may eliminate resprouter species for long periods by destroying persistent regenerative buds, it may also act like fire in stimulating mass germination of highly flammable species which rely on persistent seed banks to survive (Hanley *et al.* 2001; Santana *et al.* 2011). Despite a few recent studies (Baeza *et al.* 2006, 2011; Saura-Mas *et al.* 2010; Schwilk and Caprio 2011), information is still needed on the long-term post-management succession of fuels, in order to develop strategies for reducing fire risk with maximum effectiveness and minimal cost (Loehle 2004; Rytwinski and Crowe 2010; González-Olabarria and Pukkala 2011).

This study used a 70-year post-management chronosequence to examine fuel succession after complete mechanical clearing of understory woody vegetation in Mediterranean cork oak (*Quercus suber*) forests, which are particularly valuable from both socio-economic and ecological standpoints (Bugalho *et al.* 2011).These forests naturally present a very high fire risk since cork oaks are low stature trees whose crown is frequently in contact with those of understory shrubs, which are themselves very flammable. As a consequence, mechanical clearing of understory vegetation is a long-standing practice in cork oak forests (Natividade 1950; Montero and Cañellas 1999), which reduces the risk of high-intensity fires and may improve tree survival and resprouting ability in the case of fire occurrence (Moreira *et al.* 2007). In a previous study, we showed that after management operations which virtually eliminate woody understory vegetation and destroy its root system and the bud bank of resprouter species, there is a quick recovery of pioneer seeder and dry-fruited shrubs, which are then slowly replaced by large resprouters and fleshy-fruit producing species, eventually leading to the development of a complex multi-layered understory >50 years after disturbance (Santana *et al.* 2011). We now examine how these changes in woody community composition and structure translate into temporal patterns of fuel succession, in terms of: (i) total vegetation biomass; (ii) biomass of leaves, and fine and coarse materials; and (iii) vertical distribution of fuels. Results were then used to discuss the management of fuels in Mediterranean oak forests.

MATERIALS AND METHODS

Study area

The study was conducted in southern Portugal, within about 30 000 ha situated in Serra do Caldeirão (37º08'–37º22' N, 8º03'–7º49' W; 200–580 m a.s.l.). Climate is Mediterranean, with marked variation in annual rainfall (415–1903 mm), about 80% of which occurs in October–March and <5% in June–August. Mean monthly temperature ranges from 10.3ºC (January) to 24ºC (August). Soils are generally shallow shale lithosols, with low fertility and high erodibility. Cork oak forests dominate the landscape, ranging from almost pure stands to complex Mediterranean maquis with cork oaks surrounded by tall strawberry trees (*Arbutus unedo*) and tree heath (*Erica arborea*) (Acácio *et al.* 2009). There are also nearly monospecific *Cistus ladanifer* shrublands and more diverse Mediterranean heathland dominated by *Calluna vulgaris* and species of *Genista*, *Cistus*, *Erica*, *Lavandula* and *Ulex* (Acácio *et al.* 2009). Agriculture is nearly absent and pastoral activities are largely restricted to a very few and small herds of goat and sheep. Economic activity is dominated by cork production which is generally conducted on small private properties (<10 ha) by aged landowners (often >60 years old).

The landscape was far more agricultural during the first half of the 20th century, when national policies of food self-sufficiency (Wheat Campaign 1929–1938) conducted to large-scale clearing of natural vegetation for cereal cultivation (Krohmer and Deil 2003). Since the 1950s, human population has declined along with the abandonment of agricultural and pastoral activities, and the concurrent increase in shrubland cover (Krohmer and Deil 2003; Acácio *et al.* 2009). Cover by cork oak forests has remained fairly stable, though management largely changed from a traditional agroforestry system, with cereal cultivation and livestock grazing under the tree canopy, to a purely forestry system, with thinning and the removal of understory shrubs as the main silvicultural operations (Feio 1949; Guerreiro 1951; Acácio *et al.* 2009). This is generally carried out using tractor-towed disc harrows, which revolve the top soil while greatly modifying the structure and arrangement of fuels. The periodicity of understory management is variable and depends on the decisions of individual landowners, but it often occurs at about 9-year intervals in association with the cork extraction cycle, though it is either absent or very sporadic in many stands. As a consequence, the landscape is a mosaic of stands with understory vegetation at different successional stages (Santana *et al.* 2011).

Study design

The study was based on the space-for-time substitution method (e.g., Foster and Tilman 2000), using a 70-year post-management chronosequence of 48 cork oak stands. The chronosequence approach inferred temporal fuel succession from contemporary spatial variation in forest stands at different times since the last management event (Haslem *et al.* 2011). Since stands differed in biotic, environmental and management factors other than understory age (e.g. slope, aspect, elevation, type of management), this approach was not expected to provide information on temporal changes that occur at a given site (Johnson and Miyanishi 2008). However, this chronosequence was expected to reveal broad, regional-scale successional trends by averaging across site-to-site differences in fuel amount and structure that occur because of differences in environmental conditions and site history (Foster and Tilman 2000). The limitations of this approach are discussed is more detail in Santana *et al.* (2011).

Forest stands were selected according to a stratified random procedure (Santana *et al.* 2011). Random locations were distributed across the study area at >800 m from each other, within forest stands with >30% canopy cover by cork oaks. Forests affected by fire were excluded, to avoid confounding the effects of mechanical fuel management and burning. Each random location was classified into one of six structural strata, corresponding to categories of increasing structural complexity of understory woody vegetation, which were based on a putative sequence of successional vegetation development in the uplands of southern Portugal (Rivas-Martinez *et al.* 1990; Seng and Deil 1999). Structural categories were used instead of actual understory ages, because management histories could only be assessed a posteriori from enquiries and aerial photographs (see below). At each random location, a homogeneous 1-ha plot representative of the dominant structural stratum was chosen, and demarcated in the field. The procedure was repeated until eight plots in each stratum were selected. Stratification based on structural understory vegetation features served solely to guarantee a wide range of variation of understory ages in the sampled stands, and was not used in any analysis.

Management history

Understory management history was inferred primarily from a sequence of orthorectified and georeferenced digital aerial photographs: 1958 (scale 1:26,000), 1972 (scale 1:8,000), 1985 (scale 1:5,000), 1995 (scale 1:40,000) and 2002 (scale 1:5,000) (Santana *et al.* 2011). This procedure was feasible due to the relatively open canopy of cork oak forests and because large *A. unedo* and *E. arborea* trees were often removed during mechanical clearing. For each image year, understory condition in each stand was classified in three broad classes: 1) shrub layer sparse or absent; 2) cover by shrublands; 3) cover by tall maquis with *A. unedo* and *E. arborea*. Class 1 was assumed to indicate that shrub clearing occurred <2 years before the image year. Other obvious reductions in understory woody vegetation cover, including changes from classes 3 to 2, were assumed to indicate that clearing occurred at mid time between two consecutive aerial photographs. Understory clearing events before the period covered by aerial photographs were estimated using 1958 images assuming that: 1) class 2 indicates a management event <10 years of image year; and 2) class 3 indicates a management event in 1935. The latter assumption was based on historical sources documenting a nearly complete clearing of woody vegetation for cereal cultivation and livestock grazing at the peak of the Wheat Campaign in the mid 1930s (Feio 1949; Guerreiro 1951). Although this was a relatively crude approximation to the age of the oldest understory vegetation, it affected only four parcels that did not appear to behave as outliers or influential points in subsequent data analysis.

Assumptions regarding the identification and dating of fuel management events were based on comparisons between patterns of aerial photos of 2002 and vegetation types recognized in the field during several visits to the study area (2004), and they were cross-checked with enquiries to the landowner of each forest stand (Santana *et al.* 2011). Data from aerial photographs and enquiries were then combined to estimate the number of years elapsed between the last fuel management event and the time of vegetation sampling.

Fuel characterization

Understory woody vegetation was characterized once in each 1-ha plot, between November 2004 and March 2005 (Santana *et al.* 2011). In each plot, four 20 m transects were distributed regularly on alternate sides of a 100 m line along the central axis of the plot, where shrub cover was estimated using the linear intercept method (Hays *et al.* 1981). The study focused on plants with woody stems <6 cm diameter at breast height (dbh), because these were the most frequently removed during fuel management. Woody or perennial vines such as *Lonicera* spp. and *Smilax aspera* were excluded due to the diffuse and irregular shape of their crown, which would yield non-meaningful cover estimates.

For each shrub intercepted by the transect, we recorded the species identity, the distance from the transect beginning to the start (X1) and end (X2) of the intercepts with the foliage crown, and the height of the base (Y1) and the top (Y2) of the foliage crown. Percent cover by shrubs was computed by summing the lengths (X2-X1) of the vertical projection of the crowns of each species in the four transects, discarding overlapping crowns, and dividing by total transect length. Total area covered by shrubs and by each shrub species were then computed by multiplying the corresponding percent covers by the area of the plot. Volumes were calculated by multiplying the total area covered by each species in a plot by the mean height (Y2-Y1) of all individuals of that species in the plot (Fernandes *et al.* 2004). Biomasses were computed by multiplying the volume of each species by the species-specific dry weight per unit of crown volume (bulk density; kg/m3), and summing the results across species to yield the total standing biomass. For each species recorded in our study, we used the bulk densities reported in Fernandes and Pereira (1993) for that species or for the most structurally similar. In each case, values were computed for three fuel classes: fine materials (twigs <6 mm in diameter), coarse materials (>6 mm) and leaves.

To estimate the vertical structure of plant biomass, the foliage crowns of each shrub were approximated to an ellipse (Nelson 1997), centred in (Cx,Cy)=[(X1+X2)/2, (Y1+Y2)/2] with radii (X2-X1)/2 and (Y2-Y1)/2, and the ellipses corresponding to all shrubs of a given species recorded along each transect were merged and subdivided into 50cm strata. The volume occupied by each species in each vertical stratum was then estimated, and multiplied by the species-specific bulk density to compute its biomass per stratum. Total biomass per stratum and fuel class was then estimated by summing the corresponding values across species.

Data analysis

Patterns of variation in the composition of understory woody vegetation were first examined using Detrended Correspondence Analysis (DCA), using the 'vegan' software package (Oksanen *et al.* 2009). The DCA was computed with the mean percentage cover of each species in each plot. Species occurring in less than six plots were excluded from analysis and the remaining rare species were downweighted. Community gradients derived from DCA and global (plot-level) fuel variables were then related to time since fuel management using Generalized Additive Models (GAM) (Hastie and Tibshirani 1990), fitted with the 'mgcv' software package (Wood 2006a). Percent cover data were modelled with quasi-binomial family with a logit link, thereby accounting for overdispersion, while continuous variables were modelled with Gaussian family. In the latter case, an identity link was used for community gradient data, whereas a log link was used for biomass to ensure positive fitted values. A thin plate spline was chosen to smooth explanatory variables by Generalized Cross Validation (GCV). We defined the basis dimension as k=4 to allow some complexity in the functions, while avoiding over-fitting the data. Confidence intervals (95%) of the predicted curves were estimated by predicted mean ± 2*standard error of the prediction. These procedures have previously shown to provide adequate descriptions of complex non-linear patterns of successional variation of understory vegetation after disturbance (Porto *et al.* 2011; Santana *et al.* 2011).

To model temporal changes in the vertical distribution of fuels, biomass variables computed per stratum were related to both time since management and mean stratum height. Because data points in this case are grouped by the sampling plot and, within it, are spatially correlated in the vertical direction (stratum height), we used Generalized Additive Mixed Models (GAMM) instead of simple GAMs (Lin and Zhang 1999), using package 'mgcv' in conjunction with 'nlme' (Pinheiro *et al.* 2010). GAMMs are especially designed for the inference of relationships of clustered and correlated data by adding random effects to the additive predictor, which account for that correlation. In this case, we specified as random effects the grouping structure of the data defined by the sampling plot, allowing model intercepts to vary between plots, and we specified a spatial (one-dimensional) correlation structure in the residuals based on the empirical semi-variogram (Pinheiro and Bates 2000), which used the mean stratum height as spatial covariate. This was necessary since adjacent horizontal strata are more likely to share the crowns of the same shrubs, thus, per-stratum variables are autocorrelated. In all GAMMs, the fixed effects were fitted as a tensor product smoother function of the two independent variables, since it allows the use of variables with different scales as terms of the same function (Wood 2006a, 2006b), and basis dimension was fixed at k=4 for both variables.

RESULTS

The understory woody plant community was strongly affected by fuel management, showing major temporal changes in composition for the entire duration of the chronosequence (Figure 1). During about the first 15 years, the community was dominated by a range of pioneer shrubs such as *Cistus crispus*, *C. populifolius*, *Helichrysum stoechas*, *Genista triacanthos*, *C. salvifolius* and *Ulex argenteus*, among others, which appeared to be replaced by a more mature community dominated by *Viburnum tinus*, *Myrtus communis*, *Pistacia lentiscus*, *Quercus coccifera*, *Erica arborea*, *Quercus rotundifolia*, *Genista hirsuta*, *Phlomis purpurea*, *Phillyrea angustifolia* and *Arbutus unedo*.

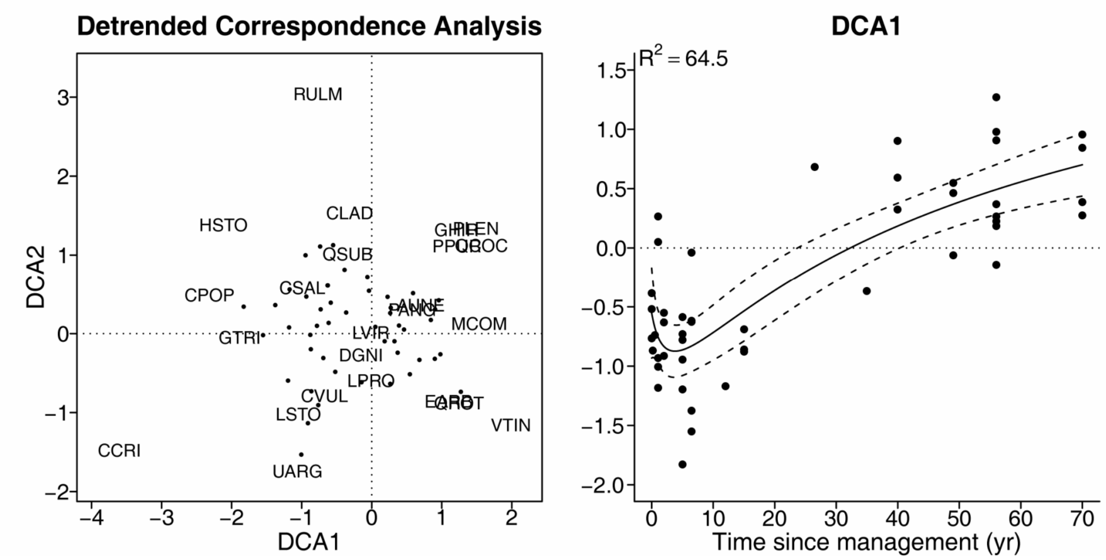


Figure 1: Detrended Correspondence Analysis (DCA) biplot of shrub species cover (left) and Generalized Additive Model between sampling plot scores in DCA axis 1 and time since last fuel management (right). Species occurring in less than 6 plots were excluded from DCA. Dashed lines limit the 95% confidence interval of the estimated mean. AUNE - *Arbutus unedo*, CCRI - *Cistus crispus*, CLAD - *Cistus ladanifer*, CSAL - *Cistus salviifolius*, CPOP - *Cistus populifolius*, CVUL - *Calluna vulgaris*, DGNI - *Daphne gnidium*, EARB - *Erica arborea*, GTRI - *Genista triacanthos*, HSTO - *Helichrysum stoechas*, LPRO - *Lithodora prostrata*, LSTO - *Lavandula stoechas*, LVIR - *Lavandula viridis*, MCOM - *Myrtus communis*, PANG - *Phillyrea angustifolia*, PLEN - *Pistacia lentiscus*, PPUR - *Phlomis purpurea*, QCOC - *Quercus coccifera*, QROT - *Quercus rotundifolia*, QSUB - *Quercus suber*, RULM - *Rubus ulmifolius*, UARG - *Ulex argenteus*, VTIN - *Viburnum tinus*.

Temporal changes in species composition after management went along major changes in shrub cover, crown volume, mean shrub height and standing biomass (Figures 2, 3). Shrub cover increased very rapidly during the first 10 years, but then nearly stabilised in a plateau after about 30 years (Figure 2). The increase in shrub volume was more gradual, though there was also a faster increase during the first 10-20 years, followed by a slow convergence to a plateau, which was not reached during the time frame of the chronosequence (Figure 2). Mean shrub height followed a pattern broadly similar to that of the volume, with the shrub layer ranging from <50 cm to >120 cm across the chronosequence (Figure 3). Total standing biomass, as well as that of leaves, and fine and coarse materials, also showed an overall increase throughout the chronosequence, albeit at faster rate during about the first 20 years, particularly in the case of fine materials (Figure 3). Afterwards there was a slow convergence to a plateau, which was not reached during the time frame of the chronosequence (Figure 3). Most biomass accumulated as coarse materials and, to a lesser extent, fine materials (Figure 3).

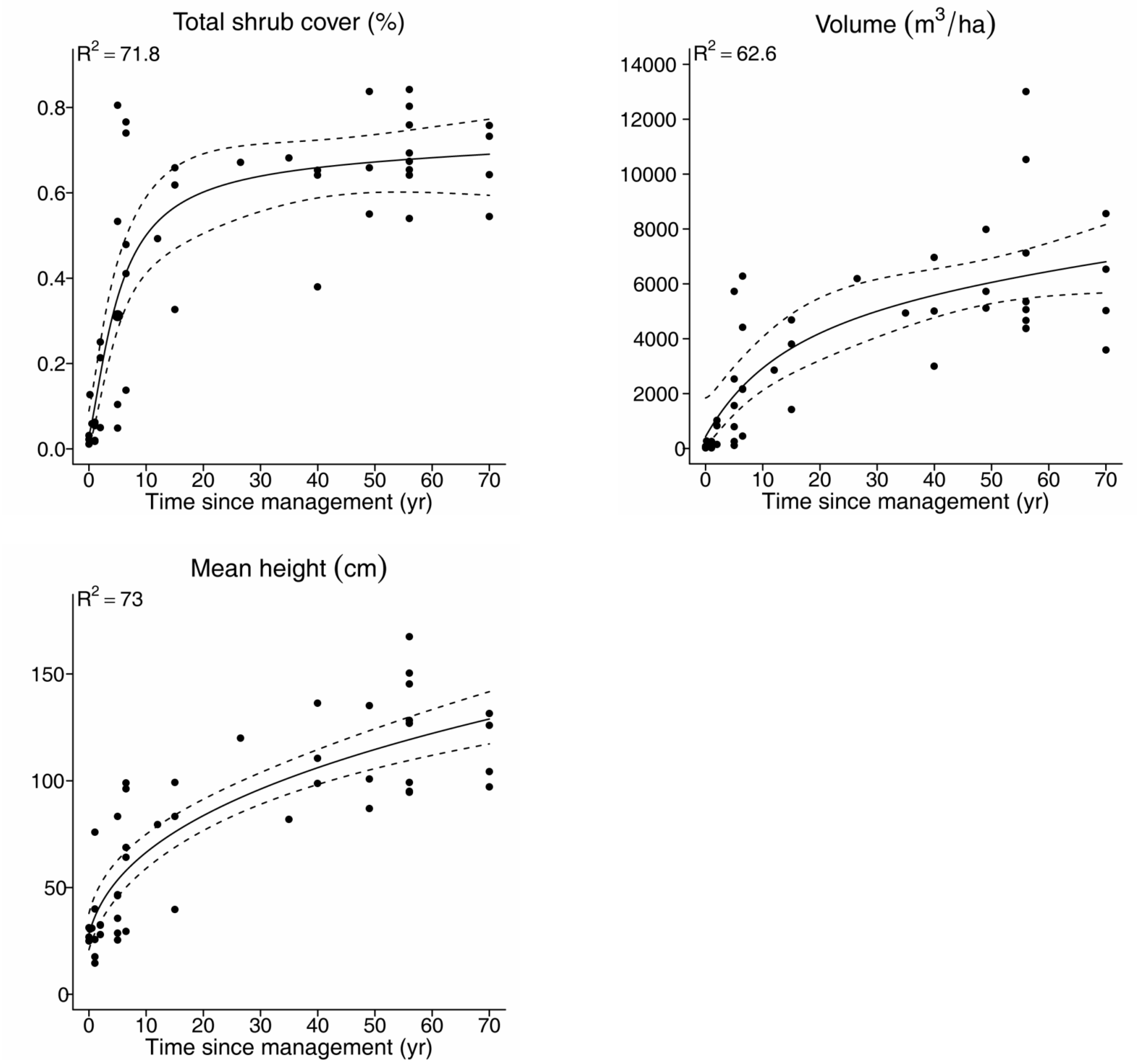


Figure 2: Generalized Additive Models relating total shrub cover, volume and mean height, to time since fuel management. Dashed lines limit the 95% confidence interval of the estimated mean.

Patterns of biomass accumulation after management showed a strong vertical variation (Figure 4). Total standing biomass accumulated first in the lower strata, showing a maximum at about 20-30 years in the <50 cm stratum (Figure 4). Biomass accumulated progressively over the years in the upper strata, with a peak in the 1-2 m strata appearing about 50 years after management (Figure 4). A high vertical continuity from the ground level to the tree canopy was reached in just about 10-20 years, but it peaked at about (50-70 years) (Figure 4). The coarse materials and leaves behaved similarly to each other along the chronosequence, with a peak at the 100 cm stratum about 10 years after disturbance, and another at the 150 cm stratum from 60 years onwards. This contrasts markedly with the pattern of fine materials, where the major biomass accumulation is in the lowest stratum all throughout the chronosequence, which rapidly attains nearly its maximum at about 15 years, being approximately steady thereafter.

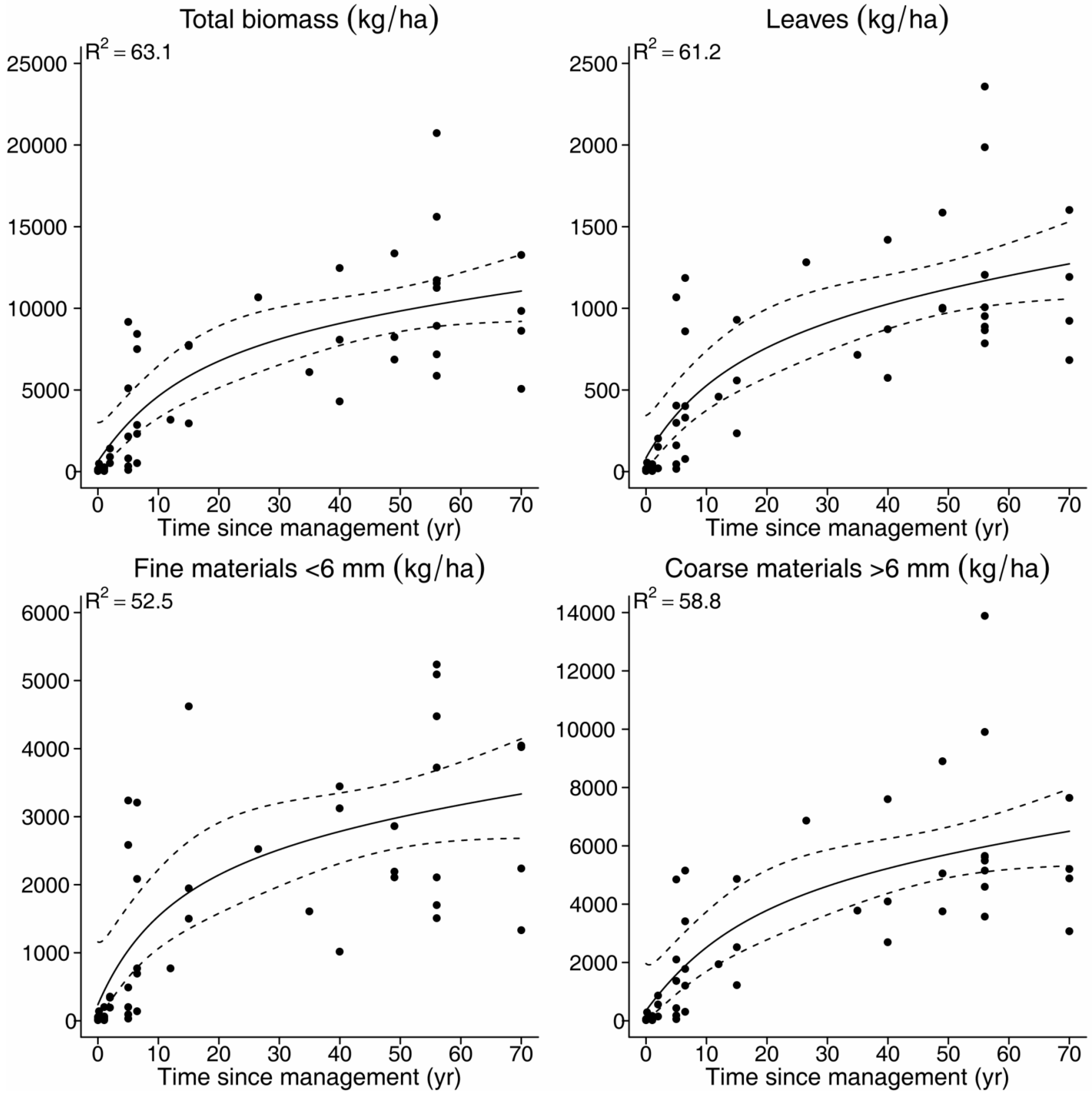
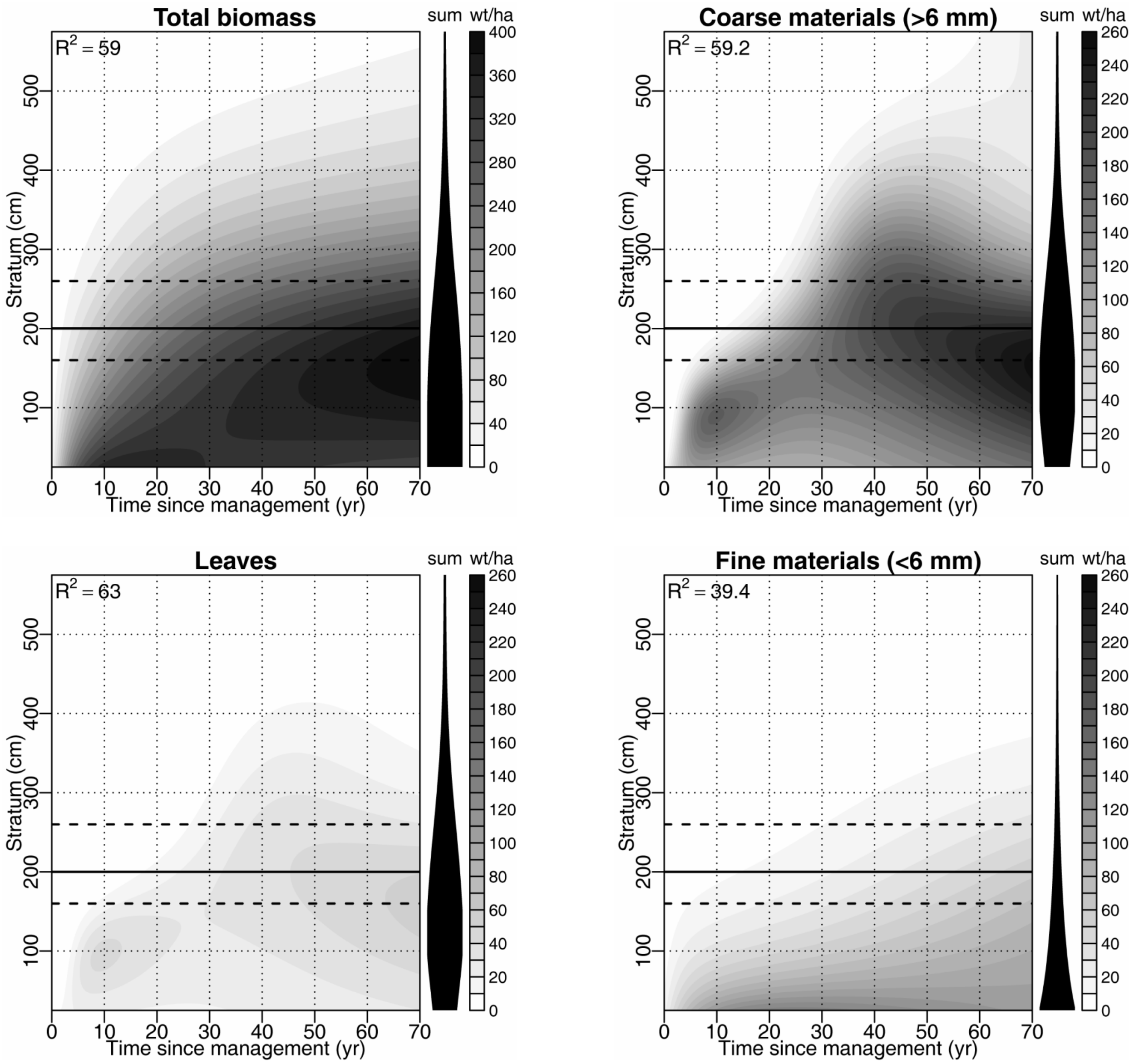


Figure 3: Generalized Additive Models relating total plant biomass, and biomass of leaves, and coarse and fine materials, to time since fuel management. Dashed lines limit the 95% confidence interval of the estimated mean.


Total biomass

Coarse materials (>6 mm)

Leaves

Fine materials (<6 mm)

Figure 4: Generalized Additive Mixed Models relating per-stratum total plant biomass, and biomass of leaves, and coarse and fine materials, to time since fuel management and vertical stratum height. Shades represent the predicted biomass per area at a given stratum and time since disturbance. Horizontal black lines indicate the quartiles (dashed lines) and median (solid line) of the mean height of the base of Quercus suber crowns. Side diagram represents the cumulative predicted biomass per stratum, summed across all years (relative scale). Shading scale is in arbitrary mass/area units (same units used across all plots). Note: shade levels are equivalent in all plots except total biomass.

DISCUSSION

The study supported the view that successional vegetation dynamics significantly influences the amount and structure of fuels in Mediterranean forests, mainly through: i) nonlinear changes in total shrub cover and volume; and ii) differential changes in cover by species with different fuel properties. As a consequence, fire risk may be dependent on the successional stage rather than showing a simple relationship with understory age as it is often assumed by some general fire spread models (Keane *et al.* 2004). These results are in line with other studies developed in Mediterranean climates, pointing to the idea that Mediterranean communities share a specific pattern of biomass accumulation and structure after disturbance (Moritz 2003; Moritz *et al.* 2004; Nunes *et al.* 2005; Baeza *et al.* 2011).

Vegetation succession and fuel load dynamics

During understory fuel management, the soil was often ploughed using disc harrows which eliminated both aerial and underground parts of the plants, destroying the root systems and the bud bank of resprouting species (Santana *et al.* 2011). Despite these very invasive treatments, the woody vegetation recovered quickly, with shrub cover, volume and biomass reaching nearly pre-disturbance levels in just 10-20 years, though they tended to continue increasing throughout the chronosequence, albeit at much lower rates. Recovery in the first two decades after management was mostly due to the rapid development of pioneer seeder shrub species (Santana *et al.* 2011; this study), for which germination may be stimulated by mechanical soil disturbance (Tárrega *et al.* 2001; Calvo *et al.* 2005). These species tend to have a high proportion of fine materials (Saura-Mas *et al.* 2010; Baeza *et al.* 2011) which may explain the particularly high rates of fine material accumulation during the first years after management.

Resprouter species in the study area were dominated by *Arbutus unedo* and *Erica arborea*, which recovered much slower than seeder species due to the elimination of bud banks during fuel management (Santana *et al.* 2011). The slow recovery of these species probably caused the observed increase in mean shrub height, and the progressive increases in crown volume and accumulation of biomass during many decades. Although these variables tended to converge to a plateau, they did not reach it within the time frame of the chronosequence, suggesting that fuel loads continue to increase for >70 years, though at a relatively slow rate. This is in line with recent studies suggesting that long time frames are required to understand the dynamics of forest fuel accumulation (Haslem *et al.* 2011). In particular, long time frames are needed to assess the possibility of fuel loads actually declining later in the succession (Hanes 1971; Haslem *et al.* 2011), which was not observed in our study.

Vertical fuel continuity

The vertical continuity of plant biomass was high all through the chronosequence except during the first few years (<10 years) after management, though nearly complete cluttering of the understory only occurred >50 years after management. This pattern was largely a consequence of the low stature of the cork oaks, causing a continuum of fuels from the ground level to the tree canopy even with moderate increases in shrub height (<2 m). However, there was an uneven behaviour of different fuel classes, with continuity mostly resulting from increases in the biomass of coarse materials and, to a much lesser extent, leaves, while fine materials mostly accumulated at <1 m throughout the choronosequence. This is particularly relevant because leaves and fine materials are considered the most determinant fuel classes in fire propagation (Andrews 1986; Papió and Trabaud 1990; Fernandes and Botelho 2003), while the importance of coarse fuels may be considered marginal, since they need higher temperatures to ignite because of the very low surface/volume ratio (Saura-Mas *et al.* 2010).

Differences between fine and coarse materials in the patterns of temporal variation in vertical continuity were probably a consequence of the uneven successional development of species with contrasting life history strategies. The pattern for fine materials was probably driven to a large extent by the seeder shrub species, which have a high proportion of fine materials and tend to maintain a low stature during the chronosequence. Although most seeder shrubs were pioneer species that developed rapidly after management and had peak cover after about 10-20 years, others such as *Genista hirsuta* occurred later in the succession, thereby explaining the high concentration of fine materials at lower strata across the chronosequence. In contrast, biomass accumulation at the upper strata was probably related with the development of large resprouters such as *A. unedo*, which were absent from recently cleared stands, progressively growing and occupying the higher levels in later decades. These species tend to have a larger proportion of coarse materials and leaves, which justify the peaks in these fuel classes at 1-2 m about 50-70 years after management. However, at least one large resprouter species (*E. arborea*) also has a high amount of fine materials (Supplementary Table 1), which may have contributed to the progressive but slow increase of fine materials in upper strata.

Implications for fire risk management

In the Mediterranean region, major efforts are carried out every year to reduce forest fuel accumulation through mechanical removal of understory woody vegetation, aiming to reduce the likelihood of fire occurrence and severity (Moreira *et al.* 2011). In our study we showed that this method effectively reduced fuel accumulation in cork oak forests, but also that these effects were short term. Indeed, high fuel loads built rapidly in just about 10 years, while high vertical continuity in plant biomass from the ground level to the tree canopy was reached in just about 10-20 years. The lower understory layer of seeder shrubs that develops shortly after management was made up of species with a high proportion of fine materials and high flammability, and it is akin to shrublands that are the most susceptible to fire in Portugal (Nunes *et al.* 2005; Moreira *et al.* 2009). This is in line with the existence of a positive feedback effect between disturbances and vegetation flammability, with frequent disturbances (fires or fuel management) moving the equilibrium towards more flammable species, which therefore increases the probability of fire occurrence (Grigulis *et al.* 2005; Valdecantos *et al.* 2009; Saura-Mas *et al.* 2010; Schwilk and Caprio 2011). As a consequence, unless the efforts of fuel elimination are intensive and sustained at short intervals (<<10 years) over large areas, they may have the undesirable effect of actually promoting highly flammable shrublands under the tree canopy.

Given the high flammability of Mediterranean pioneer shrublands, it has been argued that management should strive to increase ecosystem resilience by redirecting vegetation to later successional stages (e.g. Vallejo and Alloza 1998; Valdecantos *et al.* 2009). This is based on the view that late-successional stages are dominated by resprouters (e.g. *A. unedo*, *Phillyrea* spp., *Pistacia lentiscus*, etc.) (Verdú 2000, Valdecantos *et al.* 2009; Santana *et al.* 2011), in which a considerably large proportion of biomass is in the form of coarse fuels, which are not readily available for rapid combustion (Saura-Mas *et al.* 2010). At the same time, highly flammable pioneer shrubs tend to decline in later stages of succession (Clemente *et al.* 2007; Baeza *et al.* 2011; Santana *et al.* 2011) due to usually short life spans (Pausas 1999; Lloret 2004; Baeza *et al.* 2011). Although this strategy seems attractive and it has positive side effects for biodiversity conservation by providing habitat conditions for late-successional biota (Palma *et al.* 1999, Porto *et al.* 2011, Santana *et al.* 2011, Verdasca *et al.* in press), it may also have a number of potential shortcomings. In particular, this study showed that the fuel load at all but the lowest vertical strata (<50 cm), including the fine materials, increased throughout the chronosequence, albeit at lower rates about 20-30 years after management. As a consequence, in our particular study system the risk of rapid combustion probably remained high for 70 years after management. This is corroborated by the outcome of large fires that occurred in the study area in the summer of 2004 (28,624 ha), which burned vast areas of cork oak forest with late-successional understory. Fires affecting forests with old understory may be particularly damaging, because they burn at high temperature and may contribute for lower post-fire survival of cork oak trees (Moreira *et al.* 2007). Redirecting the vegetation to late-successional stages may thus be in at least some circumstances an inadequate strategy to reduce the risk of catastrophic wildfires in Mediterranean forest landscapes. It should be noted, however, that our study used a relatively short chronosequence (70 years), and so it could not rule out the possibility of fine fuels and overall fire risk declining over longer time frames (Hanes 1971; Haslem *et al.* 2011; Baeza *et al.* 2011).

Results from our study illustrate the problems associated with the local management of fuels, with recurrent management favouring the development of highly flammable shrublands, while lack of management favours biomass accumulation and the risk of very intense fires. These problems are particularly serious in landscapes such as our study area, where fuel management is carried out opportunistically by private landowners on their small estates (often <10 ha), often depending on the sporadic availability of governmental subsidies, and thus creating a largely random patchwork of treated and untreated stands in different successional stages, which may not contribute to the overall reduction of fire risk. This problem can only be solved if the planning of fuel management is scaled up (González *et al.* 2005; González-Olabarria and Pukkala 2011), involving the definition of optimal distributions of fuel treatments in space and time that contribute for achieving a so-called "firesafe landscape" (e.g. Loehle 2004; González *et al.* 2005; Ryu *et al.* 2007; Rytwinski and Crowe 2010; González-Olabarria and Pukkala 2011).

ACKNOWLEDGEMENTS

This study was funded by IFADAP-Program AGRO 8.1 (project 458 – 2003.09.002326.2), and by the Portuguese Science and Technology Foundation through grant SFRH/BD/28974/2006 to MP. We thank researchers and technicians of the Forest Producers Association of Barranco do Velho, the Association In Loco, the Association for the Defence of Mértola Heritage, and the Centre for Applied Ecology 'Baeta Neves', for collaboration in the development of this project. We also thank R. Guerreiro and R. Silva for their valuable assistance in the field work.

REFERENCES

Acácio V, Holmgren M, Rego F, Moreira F, Mohren GMJ (2009) Are drought and wildfires turning Mediterranean cork oak forests into persistent shrublands? Agroforestry Systems 76, 389-400.

Andrews PL (1986) BEHAVE: Fire behavior prediction and fuel modeling system - BURN subsystem, part 1. USDA Forest Service, Intermountain Forest and Range Experiment Station General Technical Report GTR-INT-194. (Ogden, UT)

Baeza MJ, Raventós J, Escarré A, Vallejo VR (2006) Fire risk and vegetation structural dynamics in mediterranean shrubland. Plant Ecology 187(2), 189-201.

Baeza MJ, Santana VM, Pausas JG, Vallejo VR (2011) Successional trends in standing dead biomass in Mediterranean basin species. Journal of Vegetation Science 22, 467-474.

Bessie WC, Johnson EA (1995) The relative Importance of fuels and weather on fire behavior in subalpine forests. Ecology 76(3), 747-762.

Bilgili E (2003) Stand development and fire behavior. Forest Ecology and Management 179, 333-339.

Bond WJ, Keeley JE (2005) Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. Trends in ecology & evolution 20(7), 387-94.

Bond WJ, van Wilgen BW (Eds) (1996) 'Fire and plants.' (Chapman & Hall: London)

Bugalho MN, Caldeira MC, Pereira JS, Aronson JJ, Pausas JG (2011) Mediterranean cork oak savannas require human use to sustain biodiversity and ecosystem services. Frontiers in Ecology and the Environment 9, 278-286.

Calvo L, Tárrega R, Luis E, Valbuena L, Marcos E (2005) Recovery after experimental cutting and burning in three shrub communities with different dominant species. Plant Ecology 180, 175–185.

Clemente AS, Rego FC, Correia O (1996) Demographic patterns and productivity of post-fire regeneration in Portuguese Mediterranean maquis. International Journal of Wildland Fire 6(1), 5-12.

Clemente AS, Rego FC, Correia O (2007) Seed bank dynamics of two obligate seeders, Cistus monspeliensis and Rosmarinus officinalis, in relation to time since fire. Plant Ecology 190(2), 175-188.

De Luís M, Baeza MJ, Raventós J, González-Hidalgo JC (2004) Fuel characteristics and fire behavior in mature Mediterranean gorse shrublands. International Journal of Wildland Fire 13(1), 79-87.

Feio M (1949) Le Bas Alentejo et l'Algarve. In 'Livret-Guide de l'Excursion E'. (XVI Congrès Internationale de Géographie, CEG: Lisbon)

Fernandes PAM, Botelho HS (2003) A review of prescribed burning effectiveness in fire hazard reduction. International Journal of Wildland Fire 12, 117-128.

Fernandes PAM, Loureiro CA, Botelho HS (2004) Fire behaviour and severity in a maritime pine stand under differing fuel conditions. Annals of Forest Science 61, 537-544.

Fernandes PAM, Pereira JP (1993) Caracterização de Combustíveis na Serra da Arrábida. Silva Lusitana 1(2), 237-260.

Foster BL, Tilman D (2000) Dynamic and static views of succession: testing the descriptive power of the chronosequence approach. Plant Ecology 146, 1-10.

González JR, Palahí M, Pukkala T (2005) Integrating Fire Risk Considerations in Forest Management Planning in Spain – A Landscape Level Perspective. Landscape Ecology 20(8), 957-970.

González-Olabarria J-R, Pukkala T (2011) Integrating fire risk considerations in landscape-level forest planning. Forest Ecology and Management 261(2), 278-287.

Grigulis K, Lavorel S, Davies ID, Dossantos A, Lloret F, Vila M (2005) Landscape-scale positive feedbacks between fire and expansion of the large tussock grass, Ampelodesmos mauritanica in Catalan shrublands. Global Change Biology 11(7), 1042-1053.

Guerreiro MG (1951) 'Valorização da Serra Algarvia: a erosão, a cobertura vegetal e a água.' (Direcção Geral dos Serviços Florestais e Aquícolas: Lisbon)

Hanes TL (1971) Succession after Fire in the Chaparral of Southern California. Ecological Monographs 41(1), 27-52.

Hanley ME, Fenner M, Ne'eman G (2001) Pregermination heat shock and seedling growth of fire-following Fabaceae from four Mediterranean-climate regions. Acta Oecologica 22, 315-320.

Haslem A, Kelly LT, Nimmo DG, Watson SJ, Kenny SA, Taylor RS, Avitabile SC, Callister KE, Spence-Bailey LM, Clarke MF, Bennett AF (2011) Habitat or fuel? Implications of long-term, post-fire dynamics for the development of key resources for fauna and fire. Journal of Applied Ecology 48, 247-256.

Hastie TJ, Tibshirani RJ (1990) 'Generalized Additive Models.' (Chapman & Hall: London)

Hays RI, Summers C, Seitz E (1981) 'Estimating Wildlife Habitat Variables.' (USDI Fish and Wildlife Service: USA)

He HS, Shang B, Crow T, Gustafson E, Shifley S (2004) Simulating forest fuel and fire risk dynamics across landscapes - LANDIS fuel module design. Ecological Modelling 180(1), 135-151.

Huston M, Smith T (1987) Plant succession: life history and competition. The American Naturalist 130, 168-198.

Johnson EA, Miyanishi K (2008) Testing assumptions of chronosequences in succession. Ecology Letters 11, 419-431.

Keane RE, Cary GJ, Davies ID, Flannigan MD, Gardner RH, Lavorel S, Lenihan JM, Li C, Rupp TS (2004) A classification of landscape fire succession models: spatial simulations of fire and vegetation dynamics. Ecological Modelling 179(1), 3-27.

Krivtsov V, Vigy O, Legg C, Curt T, Rigolot E, Lecomte I, Jappiot M, Lampin-Maillet C, Fernandes P, Pezzatti GB (2009) Fuel modelling in terrestrial ecosystems: An overview in the context of the development of an object-orientated database for wild fire analysis. Ecological Modelling 220(21), 2915-2926.

Krohmer J, Deil U (2003) Dynamic and conservative landscapes? Present vegetation cover and land-use changes in the Serra de Monchique (Portugal). Phytocoenologia 33, 767-799.

Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Functional Ecology 16(5), 545-556.

Lin X, Zhang D (1999) Inference in generalized additive mixed models by using smoothing splines. Journal of the Royal Statistical Society: Series B (Statistical Methodology) 61(2), 381-400.

Liodakis S, Agiovlasitis IP, Kakardakis T, Tzamtzis N, Vorisis D, Lois E (2011) Determining hazard risk indices for Mediterranean forest species based on particle flammability properties. Fire Safety Journal 46(3), 116-124.

Lloret F (2004) Régimen de incendios y regeneración. In 'Ecología del bosque mediterráneo en un mundo cambiante'. (Ed F Valladares) pp. 249-277. (Ministerio de Medio Ambiente. EGRAF SA: Madrid)

Loehle C (2004) Applying landscape principles to fire hazard reduction. Forest Ecology and Management 198(1-3), 261-267.

Montero G, Cañellas L (1999) 'Manual de reforestación y cultivo de alcornoque (Quercus suber L.)' (Ministerio de Agricultura, Pesca y Alimentación, Instituto Nacional de Investigación y Tecnologia Agrária y Alimentaria: Madrid)

Moreira F, Duarte I, Catry FX, Acácio V (2007) Cork extraction as a key factor determining post-fire cork oak survival in a mountain region of southern Portugal. Forest Ecology and Management 253(1-3), 30-37.

Moreira F, Vaz P, Catry FX, Silva JS (2009) Regional variations in wildfire susceptibility of land-cover types in Portugal: implications for landscape management to minimize fire hazard. International Journal of Wildland Fire 18, 563-574.

Moreira F, Viedma O, Arianoutsou M, Curt T, Koutsias N, Rigolot E, Barbati A, Corona P, Vaz P, Xanthopoulos G, Mouillot F, Bilgili E. (2011) Landscape wildfire interactions in southern Europe: Implications for landscape management. Journal of Environmental Management 92, 2389-2402.

Moritz MA (2003) Spatiotemporal analysis of controls on shrubland fire regimes: age dependency and fire hazard. Ecology 84, 351-361.

Moritz MA, Keeley JE, Johnson EA, Schaffner AA (2004) Testing a basic assumption of shrubland fire management: how important is fuel age? Frontiers in Ecology and the Environment 2(2), 67-72.

Natividade JV (1950) 'Subericultura.' (Direcção Geral das Florestas: Lisboa) Nelson R (1997) Modeling forest canopy heights: the effects of canopy shape. Remote Sensing of Environment 60(3), 327-334.

Nunes MCS, Vasconcelos MJ, Pereira JMC, Dasgupta N, Alldredge RJ, Rego FC (2005) Land cover type and fire in Portugal: do fires burn land cover selectively? Landscape Ecology 20(6), 661-673.

Oksanen J, Kindt R, Legendre P, O'Hara B, Simpson GL, Solymos P, Stevens MHH, Wagner H (2009) Vegan: community ecology package. R package version 1.15-2.

Ormeño E, Céspedes B, Sánchez IA, Velasco-García A, Moreno JM, Fernandez C, Baldy V (2009) The relationship between terpenes and flammability of leaf litter. Forest Ecology and Management 257(2), 471-482.

Palma L, Beja P, Rodrigues M. (1999) The use of sighting data to analyse Iberian lynx habitat and distribution. Journal of Applied Ecology 36, 812–824.

Papió C, Trabaud L (1990) Structural characteristics of fuel components of five Meditarranean shrubs. Forest Ecology and Management 35(3-4), 249-259.

Pausas JG (1999) Mediterranean vegetation dynamics: modelling problems and functional types Plant Ecology 140(1992), 27-39.

Pausas JG, Llovet J, Rodrigo A, Vallejo R (2008) Are wildfires a disaster in the Mediterranean basin? – a review. International Journal of Wildland Fire 17, 713-723.

Peterson DL, Johnson MC, Agee JK, Jain TB, Mckenzie D, Reinhardt ED (2005) Forest Structure and Fire Hazard in Dry Forests of the Western United States. USDA Forest Service, Pacific Northwest Research Station General Technical Report PNW-GTR-628.

Pinheiro JC, Bates DM (2000) 'Mixed-Effects Models in S and S-PLUS.' (Springer-Verlag)

Pinheiro J, Bates D, DebRoy S, Sarkar D, R Development Core Team (2010) nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-97.

Plucinski MP (2006) Fuel dynamics in shrub-dominated landscapes. In ‘Bushfire Conference’, 6-9 June 2006, Brisbane.

Porto M, Correia O, Beja P (2011) Long-term consequences of mechanical fuel management for the conservation of Mediterranean forest herb communities. Biodiversity and Conservation 20, 2669-2691.

Rivas-Martínez S, Lousã M, Díaz TE, Fernández-González F, Costa JC (1990) La vegetatión del Sur de Portugal (Sado, Alentejo y Algarve). Itinera Geobotánica 3, 5–126.

Rundel P (1981) Structural and chemical components of flammability. In ‘Proceedings of the Conference on fire regimes and ecosystem properties.’ (Eds H Mooney, N Bonicksen, JL Christensen, W Reiners) pp. 183-207. (USDA Forest Service General Technical Report WO-86)

Rytwinski A, Crowe KA (2010) A simulation-optimization model for selecting the location of fuel-breaks to minimize expected losses from forest fires. Forest Ecology and Management 260(1), 1-11.

Ryu S, Chen J, Zheng D, Lacroix J (2007) Relating surface fire spread to landscape structure: An application of FARSITE in a managed forest landscape. Landscape and Urban Planning 83(4), 275-283.

Santana J, Porto M, Reino L, Beja P (2011) Long-term understory recovery after mechanical fuel reduction in Mediterranean cork oak forests Forest Ecology and Management 261(3), 447-459.

Saura-Mas S, Paula S, Pausas JG, Lloret F (2010) Fuel loading and flammability in the Mediterranean Basin woody species with different post-fire regenerative strategies. International Journal of Wildland Fire 19, 783-794.

Schwilk DW (2003) Flammability is a niche construction trait: canopy architecture affects fire intensity. The American Naturalist 162(6), 725-33.

Schwilk DW, Caprio AC (2011) Scaling from leaf traits to fire behaviour: community composition predicts fire severity in a temperate forest. Journal of Ecology 99(4), 970-980.

Seng M, Deil U (1999) Forest vegetation types in the serra de Monchique (Portugal): Anthropogenic changes of oak forests. Silva Lusitana 7, 71–92.

Tárrega R, Luis-Calabuig E, Valbuena L (2001) Eleven years of recovery dynamic after experimental burning and cutting in two Cistus communities. Acta Oecologica 22, 277-283.

Tilman D (1985) The resource-ratio hypothesis of plant succession. The American Naturalist 125, 827-852.

Valdecantos A, Baeza MJ, Vallejo VR (2009) Vegetation management for promoting ecosystem resilience in fire-prone Mediterranean shrublands. Restoration Ecology 17(3), 414-421.

Vallejo R, Alloza JA (1998) The restoration of burned lands: the case of Eastern Spain. In ‘Large forest fires’. (Ed JM Moreno) pp.91-108. (Backhuys Publishing: Leiden)

Verdasca MJ, Leitão AS, Santana J, Porto M, Dias S, Beja P (in press) Forest fuel management as a conservation tool for early successional species under agricultural abandonment: the case of Mediterranean butterflies. Biological Conservation.

Verdú M (2000) Ecological and evolutionary differences between Mediterranean seeders and resprouters. Journal of Vegetation Science 11, 265-268.

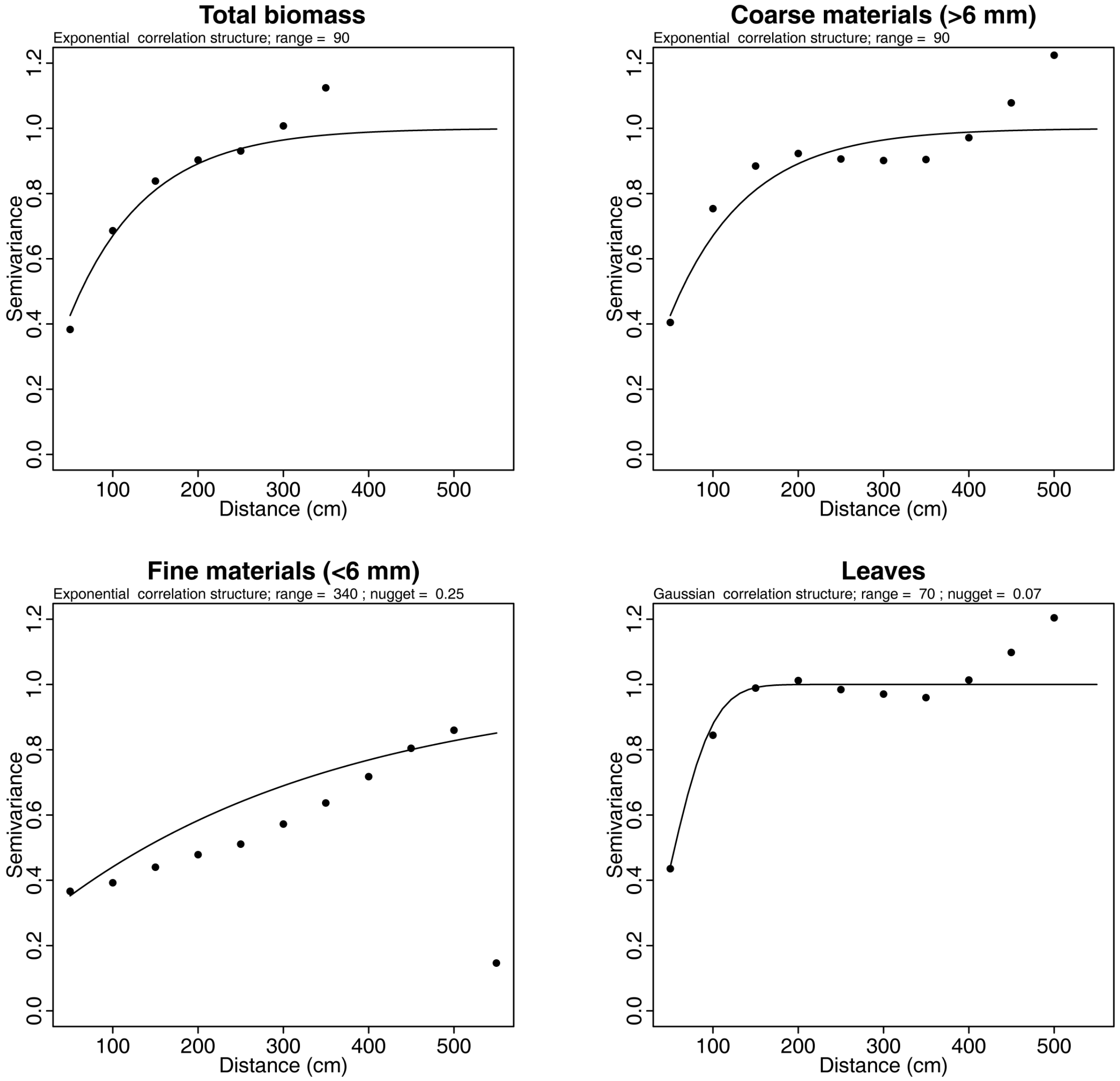
Wood SN (2006a) ‘Generalized Additive Models: an Introduction with R.’ (Chapman & Hall/CRC, Boca Raton)

Wood SN (2006b) Low-rank scale-invariant tensor product smooths for generalized additive mixed models. Biometrics 62(4), 1025-36

SUPPLEMENTARY MATERIAL

Supplementary Table 1: Bulk density values used (kg of biomass / m3 of crown volume) for the shrub species occurring in the sampling plots. Values of species marked with an asterisk (*) were obtained from Fernandes and Pereira (1993), other species were approximated to the most structurally similar.

Species	Leaves	Fine materials	Coarse materials	Total
Adenocarpus complicatus	0.11	0.28	0.89	1.27
*Arbutus unedo**	0.17	0.22	0.57	0.96
Calaminha baetica	0.15	0.35	0.21	0.71
Calluna vulgaris	0.21	0.48	1.29	1.98
Cistus albidus	0.12	0.17	0.43	0.72
Cistus crispus	0.15	0.35	0.21	0.71
*Cistus ladanifer**	0.12	0.17	0.43	0.72
Cistus populifolius	0.23	0.17	0.43	0.83
Cistus salviifolius	0.15	0.35	0.21	0.71
*Daphne gnidium**	0.01	0.05	0.08	0.14
*Erica arborea**	0.22	0.46	1.25	1.93
Erica lusitanica	0.22	0.46	1.25	1.93
Erica umbellata	0.21	0.48	1.29	1.98
Genista hirsuta	0.10	4.47	1.13	5.71
Genista triacanthos	0.21	0.48	1.29	1.98
Helichrysum stoechas	0.12	0.38	0.58	1.08
*Lavandula stoechas**	0.12	0.38	0.58	1.08
Lavandula viridis	0.12	0.38	0.58	1.08
Lithodora prostrata	0.15	0.35	0.21	0.71
*Myrtus communis**	0.13	0.32	0.27	0.72
*Olea europaea**	0.11	0.32	0.73	1.17
Phagnalon saxatile	0.12	0.38	0.58	1.08
*Phillyrea angustifolia**	0.21	0.36	0.51	1.08
*Phillyrea latifolia**	0.19	0.27	1.26	1.71
Phlomis purpurea	0.12	0.17	0.43	0.72
*Pistacia lentiscus**	0.18	0.34	1.09	1.61
*Quercus coccifera**	0.21	0.47	0.90	1.58
Quercus faginea	0.21	0.47	0.90	1.58
Quercus lusitanica	0.25	0.57	0.73	1.54
*Quercus rotundifolia**	0.21	0.25	0.93	1.39
Quercus suber	0.21	0.25	0.93	1.39
Rubus ulmifolius	0.21	0.25	0.93	1.39
Teucrium haenseleri	0.12	0.38	0.58	1.08
Teucrium scorodonia	0.15	0.35	0.21	0.71
Thymus mastichina	0.21	0.48	1.29	1.98
Ulex argenteus	0.10	4.47	1.13	5.71
Viburnum tinus	0.19	0.27	1.26	1.71



Supplementary Figure 1. Adjusted and empirical semivariograms of the spatial correlation structures used in the Generalized Additive Mixed Models relating per-stratum biomass values to time since fuel management and vertical stratum height. Distance is the one-dimensional vertical distance between strata.

5

Optimization of landscape services under uncertain management by multiple landowners

M. Porto, O. Correia, P. Beja

submitted

Thymelaea villosa
a small resprouting shrub inhabiting low heathlands, apparently favored by clearing despite this, it's fairly uncommon throughout its range

Optimization of landscape services under uncertain management by multiple landowners

Miguel Porto[a], Otília Correia[a], Pedro Beja[b]

[a]Departamento de Biologia Vegetal, Faculdade de Ciências de Lisboa, Centro de Biologia Ambiental, Universidade de Lisboa, C2 Campo Grande, 1749-016 Lisboa, Portugal
[b]CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, Campus Agrário de Vairão, Universidade do Porto, 4485-601 Vairão, Portugal

ABSTRACT

Landscapes are often patchworks of private properties, where composition and configuration patterns result from cumulative effects of the actions of multiple landowners. Securing the delivery of services in such multi-ownership landscapes is challenging, because it is difficult to assure tight compliance to spatially explicit management rules at the level of individual properties, which may hinder the conservation of critical landscape features. To deal with these constraints, a multi-objective simulation-optimization procedure was developed to select non-spatial management regimes that best meet landscape-level objectives, while accounting for uncoordinated and uncertain response of individual landowners to management rules. Optimization approximates the non-dominated Pareto frontier, combining a multi-objective genetic algorithm and a simulator that forecasts trends in landscape pattern as a function of management rules implemented annually by individual landowners. The procedure was demonstrated with a case study for the optimum scheduling of fuel treatments in cork oak, *Quercus suber*, forest landscapes, involving six objectives related to reducing management costs (1), reducing fire risk (3), and protecting biodiversity associated with mid- and late-successional understories (2). There was a trade-off between fire risk and biodiversity objectives, that could be minimised by selecting management regimes involving a large group of landowners clearing the understory at short intervals (<10 years), and the remaining managing at long intervals (>80 years). The optimal management regimes produces a mosaic landscape dominated by stands with herbaceous and low shrub understories, but also with a satisfactory representation of old understories, that was favourable in terms of both fire risk and biodiversity. The simulation-optimization procedure presented can be extended to incorporate a wide range of landscape dynamic processes, management rules and quantifiable objectives. It may thus be adapted to other socio-ecological systems, particularly where specific patterns of landscape heterogeneity are to be maintained despite imperfect management by multiple landowners.

Keywords: biodiversity, cork oak, fire management, fuels management, landscape management, Mediterranean forest, Pareto optimization

INTRODUCTION

In its seminal paper, Hardin (1968) hypothesized that a system based on a common resource that is not managed will inevitably tend to exhaustion as a consequence of every user maximizing its own benefit. A landscape used by multiple landowners can be viewed as such a common resource (Hudson, 1986), where the resource units may be equated to the products and services the landscape provides (Polasky *et al.*, 2005; Gustafson *et al.*, 2007). Many of these products and services, including those of direct interest to the landowners such as fire risk regulation (Loehle, 2004; González *et al.*, 2005; González-Olabarria and Pukkala, 2011) and water quality regulation (Nelson *et al.*, 2009), are dependent on whole-landscape structure (Gustafson *et al.*, 2007; O'Farrell and Anderson, 2010). However, landowners maximizing their own benefit at the scale of individual private properties may fail to maintain key structural features at the landscape scale, thus compromising the delivery of valuable ecosystem services (Parkhurst *et al.*, 2002; Gustafson *et al.*, 2007).

Achieving favourable patterns of landscape composition and configuration is often regarded as a problem of optimising the spatial distribution and temporal scheduling of management activities, so as to fulfil a given set of objectives (Lu and Eriksson, 2000; Baskent and Keles, 2005; Kennedy *et al.*, 2008; Costa *et al.*, 2009; Rytwinski and Crowe, 2010). For instance, optimization of forest landscape management often involves the development of management schedules maximising sustainable yields, maintaining successional heterogeneity or increasing fire resistance (Van Deusen, 2001; Bettinger *et al.*, 2003; Kurttila and Pukkala, 2003). Although this approach is feasible where landscapes are closely managed by a single or a very few institutions, either public or private, it may be impossible to implement in multi-ownership landscapes, i.e. patchworks of private properties with different owners, where there is little direct control over each landowner's management decisions (Sturtevant *et al.*, 2009). Avoiding a landscape level “tragedy of the commons” (Hardin, 1968) may thus require landowners to follow a set of prescribed rules, which may be implemented through governmental land use restrictions and management regulations (Wear *et al.*, 1996), voluntary incentive schemes (Parkhurst *et al.*, 2002; Nelson *et al.*, 2008; Hartig and Drechsler, 2009; Juutinen *et al.*, 2009; Lewis *et al.*, 2011), or even self-regulation (Ostrom, 2009). Whatever the implementation mechanism, however, a key challenge is to optimize rules that once implemented by landowners will contribute for successufully achieving landscape scale objectives that are relevant at the individual and societal levels (Sturtevant *et al.*, 2009; Moreira *et al.*, 2011).

Designing management rules for multi-ownership landscapes is particularly difficult, mainly because individual landowners may vary widely in their response to a common set of rules (Macfarlane, 2000; Johnson *et al.*, 2007), and this variation cannot be controlled or accurately predicted (Johnson *et al.*, 2007; Lewis *et al.*, 2011). The inherent unpredictability of the system thus precludes the use of most methods designed to optimise landscape management, which assume that rules will be strictly implemented according to a fixed plan (e.g. Bettinger *et al.*, 2005; Kennedy *et al.*, 2008; González-Olabarria and Pukkala, 2011). In reality, however, individual landowners may decide to ignore the rules altogether due to poor enforcement, or they may vary in the rigour of their implementation due to individual preferences or economic constraints (Stranlund, 1995; Chomitz *et al.*, 2006; Lewis *et al.*, 2011). As a consequence, the spatial and temporal scheduling of management activities designed through conventional optimization approaches would be only loosely implemented by individual landowners, which may result in landscapes widely different from those initially foreseen. Furthermore, these landscapes would be dynamic due to the spatial and temporal variations in landowners' decisions, making it unlikely that an optimal landscape composition and configuration can realistically be achieved, in marked contrast to the solutions normally reached by landscape optimization methods. Solving these problems requires optimization approaches that explicitly integrate the stochasticity inherent to landowners' decisions, and the concurrent dynamics in landscape structure, in the process of designing solutions.

This paper describes an approach for optimising management rules under the constraint of stochastic landowners’ decisions in a dynamic landscape, illustrating its application to a problem of Mediterranean forest landscape management for increasing fire resistance and promoting biodiversity conservation. The problem was based on a well-studied upland cork oak, *Quercus suber*, landscape in southern Portugal (Acácio *et al.*, 2009; Porto *et al.*, 2011, 2012; Santana *et al.*, 2011, 2012; Verdasca *et al.*, 2012), where cork is the main forest product and mechanical clearing of understory vegetation to reduce fire risk is the main management action. Management is undertaken at the scale of individual properties depending on landowner decisions, usually occurring at 9-year intervals in association with the cork extraction cycle, though in many stands it may either be absent or very sporadic. Fuel management is thus rather inefficient in this fine-grained (< 10 ha) multi-ownership landscape, because it is conducted at the scale of individual properties, with little or no coordination among neighbours, and there is accumulation of fuel materials in properties that are unmanaged for long periods. On the other hand, although unmanaged stands increase fire risk, they are critical for the conservation of biodiversity, which benefits from complex mosaics of forest stands with understory vegetation in different successional stages (Porto *et al.*, 2011; Santana *et al.*, 2011, 2012; Verdasca *et al.*, 2012). Consideration of biodiversity conservation is mandatory in this landscape, because it is included in a Site of Community Importance classified under the European Directive 92/43/EEC. The problem is thus to design a management regime of understory vegetation clearing that increases landscape resistance to fire propagation, while maintaining the heterogeneous mosaic required for biodiversity conservation. Although the optimization approach presented here was designed to solve a particular problem, it may be applicable to other multi-ownership forest landscapes, as well as other socio-ecological systems where the conservation of common landscape resources is influenced by the uncoordinated decisions of multiple landowners.

METHODS

The approach

The problem addressed in this study involves the design of simple management rules that during N years of implementation by individual landowners in a multi-ownership landscape, cumulatively result in the best compromise in optimizing multiple objectives simultaneously. Variation in the responses of individual landowners to management rules causes uncertainties on the spatial pattern and temporal dynamics of landscape composition and configuration, thus making the problem inherently stochastic. To explicitly integrate the stochasticity in landowners decisions, the study used a simulation-optimization approach (Liu *et al.*, 2000; Baskent and Keles, 2005; Rytwinski and Crowe, 2010), where the objective function of an optimization algorithm integrates a landscape simulator and analyser. Simulation-optimization finds the best configurations of decision variables for a given system, where the performance is evaluated based on the output of a computer simulation model of the system (Rytwinski and Crowe, 2010). The optimization is achieved through a iterative process, which involves (a) choosing a solution, which is then (b) evaluated through simulation, and then (c) passed back to the optimization procedure which acts on the solution according to the simulation results (Rytwinski and Crowe, 2010). The details of the latter step depend on the optimization algorithm that is used.

The multi-objective optimization approach used in this study was based on the concept of Pareto optimality (Fonseca and Fleming, 1995), thus explicitly recognising that there is no single solution for problems requiring the simultaneous optimization of multiple objectives (e.g. Kennedy *et al.*, 2008; Groot *et al.*, 2010). This was considered more adequate than the conventional weighting of objectives and their subsequent conversion into a scalar-valued function that is optimized (e.g. Kurttila and Pukkala, 2003; González *et al.*, 2005; González-Olabarria and Pukkala, 2011), because objectives often conflict and because weighting the relative importance of different objectives involves a large degree of subjectivity and is generally difficult to justify (Naidoo *et al.*, 2006; Kennedy *et al.*, 2008), being a decision that should be left to the land manager rather than be taken by the investigator.

The concept of Pareto optimality is based on finding the Pareto frontier, which is the set of non-dominated solutions to the problem (Kennedy and Ford, 2011). A solution is defined to be non-dominated if there exists no other feasible solution that will give an improvement in one objective without a subsequent degradation in at least one other objective (Coello Coello *et al.*, 2007). The method thus provides a range of multiple alternatives before the relative importance of the objectives are specified, which can then be used by decision makers to set preferences and re-examining both them and the proposed management model (e.g. Blasco *et al.*, 2008; Kennedy *et al.*, 2008).

Calculating the entire non-dominated Pareto frontier by systematically evaluating the entire feasible solution space is computationally prohibitive due to the very large number of combinations of values for the decision variables. Therefore, a genetic algorithm was used as a search process to converge to an approximation of the non-dominated Pareto frontier (e.g. Ducheyne *et al.*, 2006; Holzkämper *et al.*, 2006; Kennedy *et al.*, 2008). This is achieved through simultaneous optimization of a vector-valued objective function in order to find the groups of decision variable values (the optimal set) that optimize the management objectives (Kennedy *et al.*, 2008). Genetic algorithms search for the best solutions to a given problem by applying evolutionary principles to a population of candidate solutions over N generations, giving “competitive advantage” to those solutions that best fulfil the objectives as a whole (Coello Coello, 2007). Each solution is described by a set of parameters, which are progressively optimized throughout the process. The core of a genetic algorithm is its objective function, which calculates the values of the objectives based on the parameters that are being optimized.

Definition of objectives

The landscape level objectives considered in this study for upland cork oak forests of southern Portugal were (1) fire risk minimization, (2) maximization of biodiversity value, and (3) minimization of management costs. Fire risk was estimated from three surrogate variables related to the amount and spatial distribution of forest fuels across the landscape, which are known to influence fire initiation, propagation and severity. It was thus assumed that minimization of fire risk over a given period implies (1.1) minimization of the maximum annual fuel load across the landscape; (1.2) maximization of the minimum annual edge contrast between areas with different fuel loads, i.e. increase fuel discontinuities (Viedma *et al.*, 2009) and compartmentation (Loehle, 2004); and (1.3) maximization of the minimum annual fuel concentration in a few small areas (Loehle, 2004; González *et al.*, 2005). These three surrogate variables were summarized along the given period with their overall minimum/maximum so to avoid years of extreme fire risk, whose disproportional importance would be diluted if using a mean value. Total fuel load (1.1) was quantified simply by computing the amount of understory biomass of fine materials and leaves (kg/ha) across the landscape, ignoring tree biomass because this was not affected by fuel management. Edge contrast (1.2) and concentration (1.3) of fuel loads across the landscape were estimated using continuous surface metrics (McGarigal *et al.*, 2009), which are extensions of the classical patch-based metrics that do not require discretization into patches whose boundaries are often arbitrary (González *et al.*, 2005). Edge contrast (1.2) was quantified using the variance of edge contrast metric ("root mean square slope", McGarigal *et al.*, 2009), which was computed as the variance of the absolute differences in understory biomass between all pairs of adjacent 1-ha cells, showing the highest values when there is strong spatial heterogeneity in biomass distribution (i.e. spatial fragmentation). Fuel concentration (1.3) was estimated using the surface skewness metric (McGarigal *et al.*, 2009), which was quantified as the skewness coefficient of understory biomass across all 1-ha cells. This is a non-spatial measure of asymmetry about the mean, showing the highest values when the majority of cells have low biomass and just a few have high biomass. These surrogate variables were used instead of fire spread simulations due to the computational burden of coupling stochastic landscape dynamics with stochastic fire spread simulations (e.g. Kennedy *et al.*, 2008).

Biodiversity impacts were estimated from two surrogate variables quantifying the area occupied by cork oak stands with mid- (30-60 years) and late-successional (>60 years) understories. These variables were based on the observation that a range of plant and animal species are associated with complex and multi-layered understories, which take a long time to recover after management (Porto *et al.*, 2011; Santana *et al.*, 2011, 2012; Verdasca *et al.*, 2012). Therefore, there is a risk that widespread and recurrent fuel management across the landscape might eliminate habitat conditions for these species, with negative consequences for biodiversity. A variable reflecting habitat availability for early-successional and edge species was not considered, because it was assumed that the objective of maximizing habitat for these species was equivalent to minimising fire risk, as both involve the clearing of understory vegetation. It was thus assumed that minimization of biodiversity impacts implies the maximization of the minimum area attained by stands with mid- and late-successional understories across the simulation period.

Minimizing the cost of management was also included as an objective, because an optimal solution for increasing landscape resistance to fire risk would be to manage the entire landscape, but this was unfeasible due to economic constraints, besides having strongly negative ecological consequences. The total area managed each year was used as a surrogate of management cost, assuming that costs are constant across the landscape. Although this is a simplification, it was considered reasonable because the optimization exercise was based on simulated landscapes that were homogeneous in all respects except understory age.

Definition of optimization decision variables

The interval in years that a given landowner should leave between two consecutive operations of understory clearing was the basic decision variable used in optimization. This parameter was selected because it can be easily prescribed and then controlled by an external or internal authority, it reflects the main management decision taken by landowners in the study area, and it has major direct consequences for the landscape level objectives. Management intervals were constrained to vary between 3 and 100 years, with the lower limit corresponding to a value rarely observed in the study area, and the upper limit corresponding to lack of management during the simulation period.

Based on the management interval, five strategies of increasing organizational complexity were defined, in order to explore the trade-off between strategy complexity and performance in achieving objectives: i) a single group strategy, where all landowners are asked to manage with a given interval; and multiple group strategies, where landowners are divided in (ii) two, (iii) three, (iv) four, and (v) five groups according to given proportions, each of which is asked to manage with a different given interval. The decision variables for the more complex scenarios thus included the management interval to be implemented by each group of landowners, and the proportions of landowners in each management group, thus corresponding to optimize 1, 3, 5, 7, and 9 parameters, respectively. Division in groups was used because observations from the study area suggest that groups of landowners manage their land differently, probably depending on personal interests and social and economic constraints. For instance, many landowners live in coastal towns far from their property, and so they are likely to undertake management operations less frequently than landowners living in small parishes close to their land. In practical terms, a more complex scenario is less likely to be implemented correctly, given the social context of multi-ownership landscapes, though it was considered worth evaluating to what extent this increased complexity compensates in achieving the landscape-level objectives.

Landscape simulation

The study focused on a simulated landscape that was based on the ecological and socio-economic characteristics of cork oak forest landscapes in Serra do Caldeirão, Southern Portugal (for details see Porto *et al.*, 2011; Santana *et al.*, 2011, 2012; Verdasca *et al.*, 2012). The simulated landscape was an 18x18 km square of 1-ha hexagonal cells, which was randomly partitioned by different landowners into landholdings, with areas approximately following a Gamma distribution with mean=20 and variance=100. Gamma distribution was used because there is no *a priori* knowledge about the expected distribution of the landholding area except that it is strictly positive. To simulate the heterogeneous vegetation mosaic characteristic of the study area, each landholding was assigned an age since the last understory clearing event, which was sampled from a uniform distribution between 0 and 70 years. Each landholding was thus considered a management unit, assuming that every landowner will manage his entire property at once. This simulated landscape was used instead of a real landscape, due to practical difficulties in assessing the boundaries of individual properties and to lack of data on the management history of every property. Furthermore, the use of a simplified simulated landscape was expected to enhance the generality of the results and thus its application to other socio-ecological systems.

Landscape dynamics were simulated by incorporating the disturbance-succession processes associated with fuel management by individual landowners. According to each management scenario, each landowner cleared the understory vegetation at specified time intervals, independently of other landowners. Uncertainty in landowner responses to management rules was introduced by specifying the management interval of each landowner as a random variable instead of a fixed value, following a Gamma distribution with mean equal to the specified management rule and variance computed such that the shape parameter was kept constant and equal to 100. The purpose was to make uncertainty larger at larger intervals. It was assumed that mechanical fuel management removes all understory woody vegetation except cork oaks, and that after management the vegetation recovers following the successional pathway described by (Santana *et al.*, 2011), with biomass accumulation following the curve described by (Porto *et al.*, 2012). Although this curve was based on data for the first 70 years after understory clearing, we deemed reasonable to extrapolate up to 100 years, because variation after about the first 50 years was very slight. Assumptions regarding the biomass accumulation curve could also be considered simplistic due to spatial and temporal heterogeneities in vegetation successional pathways (Turner *et al.*, 1998; Kashian *et al.*, 2005). However, it was expected that they still provide a useful approximation to the landscape-scale disturbance-succession dynamics resulting from the cumulative effects of management actions undertaken by individual landowners.

During the simulation period, the objective variables were computed each year and retained for calculation of the objectives. In all objectives but the managed area per year, the first 20 years of simulation were discarded to allow for landscape "adaptation" to the new regime. The landscape simulator and analyser was implemented using software written in the C programming language for performance reasons.

Simulation-optimization procedure

For each management scenario, the simulation-optimization procedure was initialised by randomly generating 800 decision variable combinations (a population). Each combination (an individual) was implemented in the simulated landscape for a period of 100 years, and the values of the six objective variables were computed. Each individual in the current population was ranked according to how well it achieves the optimization objectives relative to the population, with non-dominated individuals assigned Rank 1. Rank 2 individuals are the non-dominated individuals after removing Rank 1 individuals, and so on. Individuals were then chosen randomly to enter the breeding stage of the genetic algorithm, based on both their non-dominated ranking and their uniqueness. These individuals (the parents) were used to generate the next population, either through mutation of the parent vector (i.e. small changes in randomly chosen decision variable values), or through cross-over between two vectors (i.e., exchange of decision variables between two parents). The cycle (generation) was then resumed, by implementing each individual in the simulated landscape, computing the objective variables, evaluating the effectiveness of individuals in the current population, and randomly choosing the parents of the next generation. The process was repeated until a unique optimum was reached or after 150 generations. The final output of the search was the approximated non-dominated Pareto frontier, corresponding to the alternative solutions to the optimization problem.

The procedure as described above (some details omitted) was introduced by (Deb *et al.*, 2002) as the Nondominated Sorting Genetic Algorithm II, implemented in the R environment (R Development Core Team, 2008) in the package "mco" (Trautmann *et al.*, 2010). This algorithm was considered particularly adequate because it includes a mechanism to avoid crowding of solutions, that is, to maintain diversity among the population of solutions in every iteration. The direct consequence is that, upon finishing, optimal solutions are maximally spread in the objective space, thus covering the widest possible range of situations. This allows a decision-maker to be able to choose the solutions that best suit his needs, by picking the subset that varies within the intervals of the objectives that he considers the most adequate.

Post-processing of optimization results

The Pareto frontier was visualized using level diagrams, where the objective vectors of the optimization solutions are represented in relation to the values of each objective variable (Blasco *et al.*, 2008). To reduce dimensionality of the objective vectors and thus allow representation in a bi-dimensional plot, each vector was scored with its Euclidean multivariate distance (after standardization) to the theoretical point where all the objectives are at their lowest (or highest) possible value simultaneously (ideal but unachievable solution). A level diagram was produced for each objective, with the position of each optimization solution in the Y axis being constant across diagrams (Blasco *et al.*, 2008). Level diagrams were then used to assess the performance of each individual solution in meeting each objective within the global quality space of all solutions in all scenarios.

To explore the consequences of decision-maker preferences for achieving landscape level objectives, optimization results were further processed by restricting solutions to those meeting a set of objective constraints, according to what could be considered feasible in practical terms (implementation cost) and reasonable in objective outcomes (fire risk and biodiversity). Restrictions were imposed considering the potential preferences of: a (i) funding agency, limiting management area to 5% or 10% (± 0.25%) of the landscape each year; a (ii) forest management agency, requiring that each fire risk objective should lie within the 25% best results observed in simulations; and a conservation agency, requiring that a minimum area of 10% should be maintained over time for both the 30-60 years and the > 60 years age classes. The consequences of these restrictions on the solution space were visualised using level diagrams.

In order to analyse in detail the temporal variation in the landscape level objectives resulting from feasible solutions, the management parameters of some of the best solutions were implemented in the initial landscape and simulated during 100 years. The values of the objectives, as well landscape composition in terms of 10-year understory age classes, were then plotted in relation to simulation year. Because the simulator accounts for uncertainty when implementing management, the consequences of each solution were plotted as the mean value assessed through 100 simulations.

RESULTS

Overall simulation-optimization results

Results from the simulation-optimization procedure indicated that the single group strategy always performed poorly in achieving the overall landscape level objectives (Fig. 1). The best solutions for this strategy indicated that all landowners should clear the understory at about 70-year intervals (Supplementary Figure 1), but this leads to landscapes where the fuel load tends to be too high, and its distribution across the landscape tends to be too continuous, as indicated by the low edge contrast of fuel loads (Fig. 1). The strategy was more satisfactory in terms of cost, as the total area managed per year was lowest, and in terms of mid- and late-successional biodiversity, as the conservation objectives were often achieved (Fig. 1).

In contrast to the single interval strategy, there was much higher overall quality of solutions for the multiple group strategies, with little variation in performance between strategies involving different groups of landowners (Fig. 1). Most of the best solutions were associated with the two group strategy, with about 50-60% of landowners clearing the understory at short intervals (4-6 years), and the remaining clearing the understory at very long intervals (80-100 years) (Fig. 2a). Solutions involving a larger number of groups largely maintained the same pattern, with a dominant group managing at short intervals and two or more groups managing at different intervals within the 70-100 year time frame (Fig. 2a). Optimizations for a given number of groups often converged to solutions with a smaller number of groups (i.e., < 1% of landowners in a given group or differences between management intervals < 1 year). It is also noteworthy that there were very few solutions involving landowners managing at 10-50 years intervals (Supplementary Figure S1).

Objective trade-offs in the Pareto frontier

There were strong relations between objectives for all management strategies, pointing to the presence of major trade-offs (Fig. 3). Solutions with low fuel loads and high fuel concentration in a few areas always required high proportions of the landscape treated annually (Fig. 3a,c), thereby underlining a trade-off between management cost and fire risk reduction. Edge contrast declined with increasing proportion of the landscape treated annually in the single group strategy, but not in the multiple group strategies (Fig. 3b).

In general, there were trade-offs between fire reduction objectives and the conservation of mid- and late-successional biodiversity, as there was a strong tendency for solutions with low fuel loads and high fuel concentration, also having low proportions of mid- and late-successional understories (Fig. 3h,i,m,n). This effect, however, was stronger for single than for multiple group strategies, and it was also weaker for mid-successional understories in multiple group strategies. Edge contrast and the proportion of mid- and late-successional stands were positively related (Fig. 3k,l), underlining the greater variability of biomass distribution across landscapes with higher biomass density, particularly in the single group strategy.

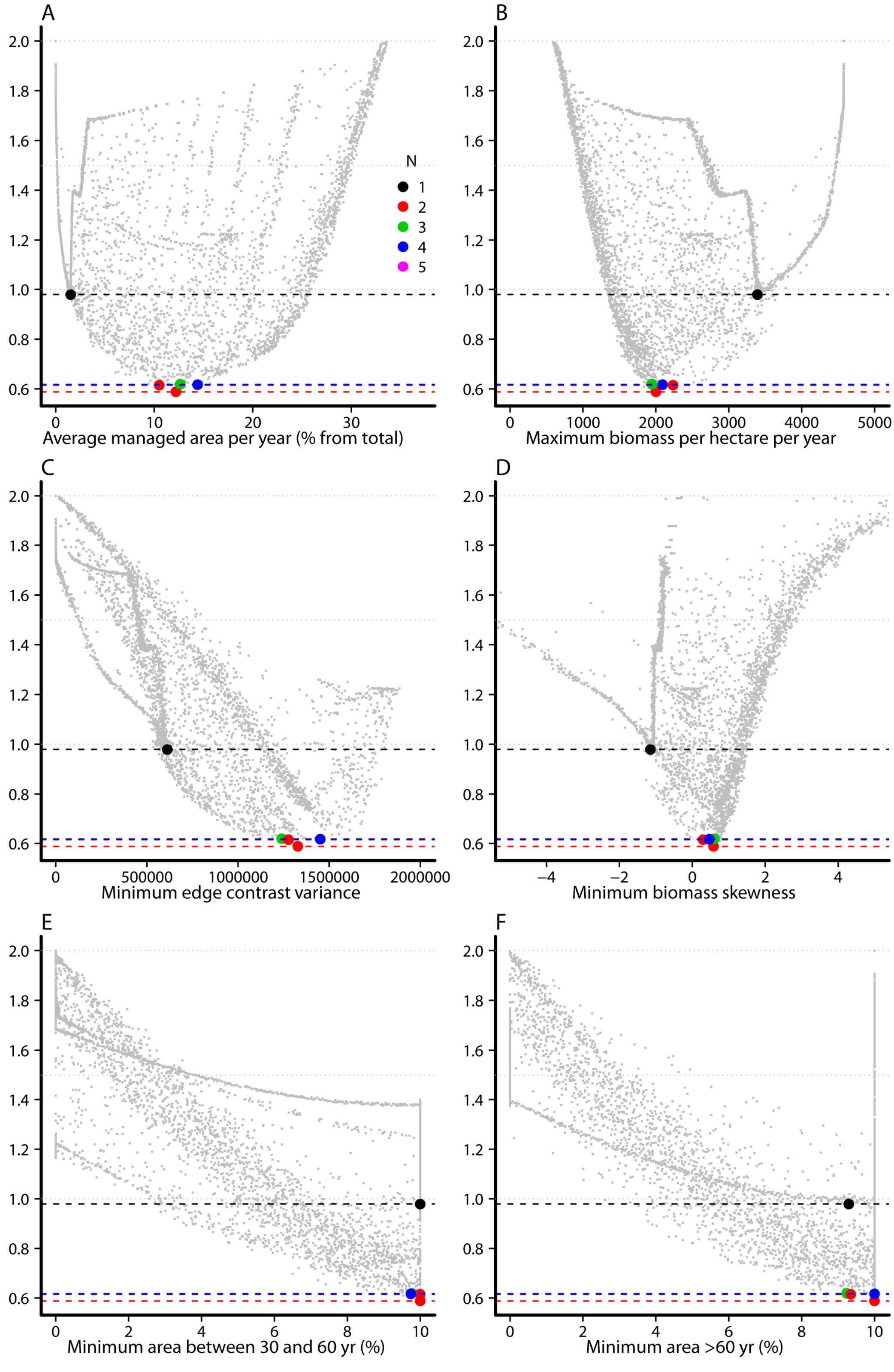


Figure 1: Level diagrams of optimization solutions for the six objectives (A-F, x axis), each plot showing the five management strategies. The best solution in each strategy in terms of its distance to the ideal overall solution (y axis, the same across all plots) is highlighted. Colours refer to the number of effective management groups in the solution, i.e. after discarding groups with < 1% of landowners and merging groups differing < 1 year in management intervals.

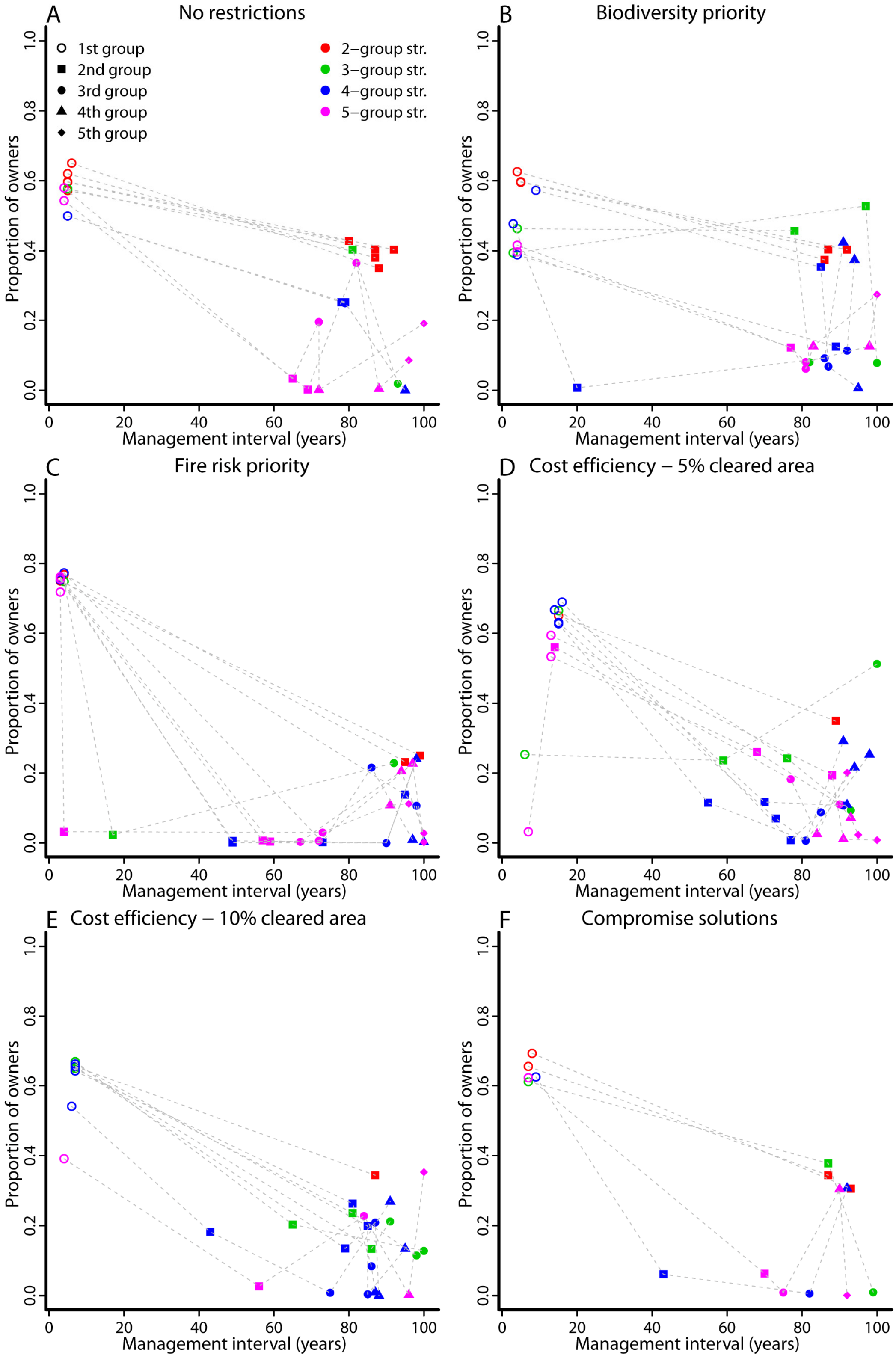


Figure 2: Plots representing the details of the ten overall best management solutions (across strategies) in each restriction scenario (A-F). Each solution is represented by a set of connected points, each point representing a group with a given assigned management interval (x axis) and given proportion of landowners belonging to it relative to the total of landowners (y axis). Colours refer to the strategy of each solution (i.e. how many groups were considered).

Consequences of management preferences

Constraining the total area managed each year to approximately 5% or 10% of the landscape strongly reduces the overall quality of the optimization solutions (Supplementary Figures S2 and S3). For the 5% constraint, the best solutions would generally involve a group of 50%-70% of landowners clearing the understory at about 13-16 year intervals, and one or more groups managing with different intervals within the 50-100 year time frame (Fig. 2). Irrespective of the solution, however, this constraint would imply a high fire risk, due to a high fuel load and high fuel continuity across the landscape, though the objectives for the mid- and late-successional biodiversity could reasonably be achieved (Supplementary Figure S2). For the 10% constraint, most of the best solutions would involve a group of 50-70% of landowners managing at 6-7 year intervals, and the remaining managing at different intervals within the 80-100 year time frame. Despite this constraint, these solutions would produce reasonable results in terms of fire risk and biodiversity objective variables (Supplementary Figure S3).

If management is focused on fire risk, assuming very ambitious goals for the corresponding objective variables (i.e., the 25% best outcomes for each of the three fire risk objectives), then the best solutions would involve most landowners (about 75%) clearing the understory at very short intervals (3-4 years), and the remaining mostly managing at one or more intervals in the 70-100 year time frame. Irrespective of the solution, the costs would always be very high, because over 25% of the area would have to be managed annually (Supplementary Figure S4). Furthermore, the proportion of area occupied by stands with either mid- or late-successional understory would fall below 10% during the simulation period, and thus the biodiversity objectives would never be achieved.

Focusing on biodiversity objectives provides a large number of alternative solutions, most of which perform very poorly due to its high cost and fire risk (Supplementary Figures S1 and S5). However, the best biodiversity solutions are globally similar to some of the best overall solutions, involving one group of about 60% of landowners managing at 5 year intervals, and the remaining managing at about 90 year intervals (Fig. 2). There are, however, variants to this pattern, with the short interval group varying from 40% to 60% of landowners, and from 3 to 9 year management intervals, whereas the long interval group may include one to four sub-groups managing at different intervals in the 70-100 year time frame.

There was no overall optimization solution achieving simultaneously all the most ambitious goals in terms of cost, fire risk and biodiversity. However, relaxing these goals to targets of less than 10% of the landscape managed each year, of fire risk objectives within the 50% best solutions obtained in the optimizations, and a minimum representation of 9-10% of mid- and late-successional understory ages, produced solutions with reasonable overall quality (Supplementary Figure S6). These compromise solutions involved a group of about 60-70% of landowners clearing the understory at about 7-9 year intervals, whereas most of the others manage at about 90 year intervals (Fig 2).

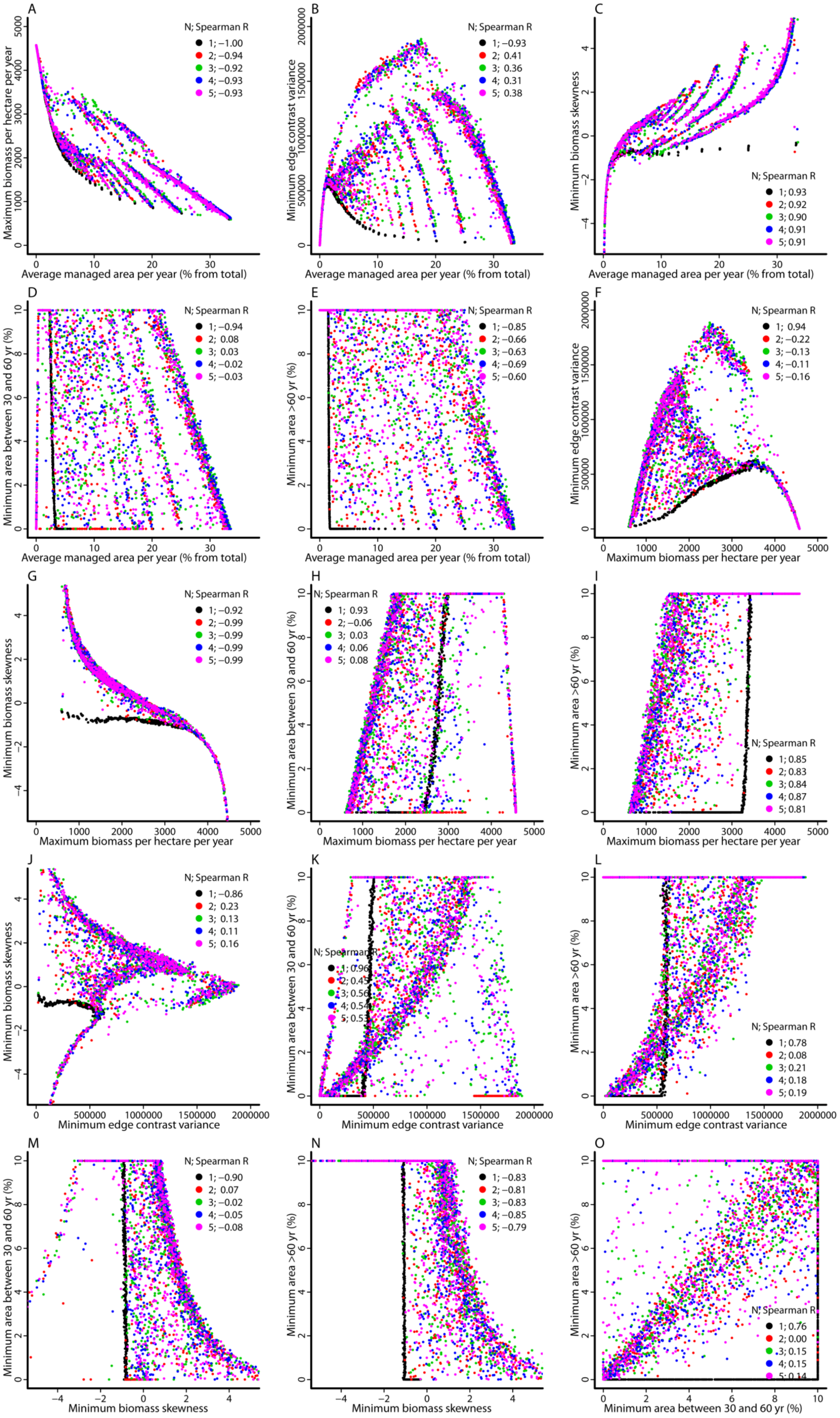


Figure 3: Scatterplots between all pairs of objective values of all the solutions in the Pareto front of all strategies. Spearman rank correlations per strategy are indicated. Colours refer to the strategy of each solution (N=1 to 5 groups).

Landscape dynamics under optimal management

The best compromise solution resulted in a landscape largely dominated (> 60%) by stands with young understory ages (<10 years), whereas both mid- (30-60 years) and late-successional (>60 years) understories were represented by about 10-20% of the landscape (Fig. 4). This pattern of landscape composition was approximately the same for all compromise solutions (Supplementary Figure S7). Trends in cost and fire risk management objectives showed a cyclic component, with large fluctuations in the first decades and a subsequent convergence to rather stable values (Figure 5). The proportion of mid- and late-successional ages showed a large decline towards the mid and the end of the simulation period (respectively), but recovered and, as far as it can be observed, seemed to approach a stable level above the 10% threshold (Figure 5)

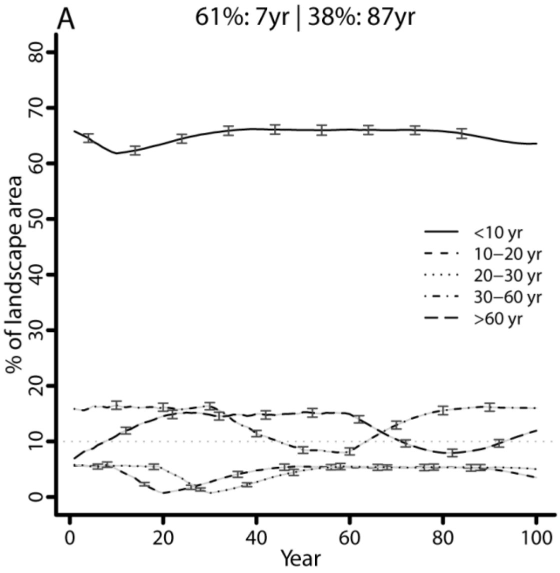


Figure 4: Percentage area (y axis) of landscape in each age class throughout the simulation period (x axis) in landscapes managed according to the best regime obtained in the compromise solutions (Supplementary Figure 6), in terms of its distance to the ideal overall solution. Lines depict the values averaged over 100 simulations of the same landscape subjected to the management regime, and error bars the standard deviation.

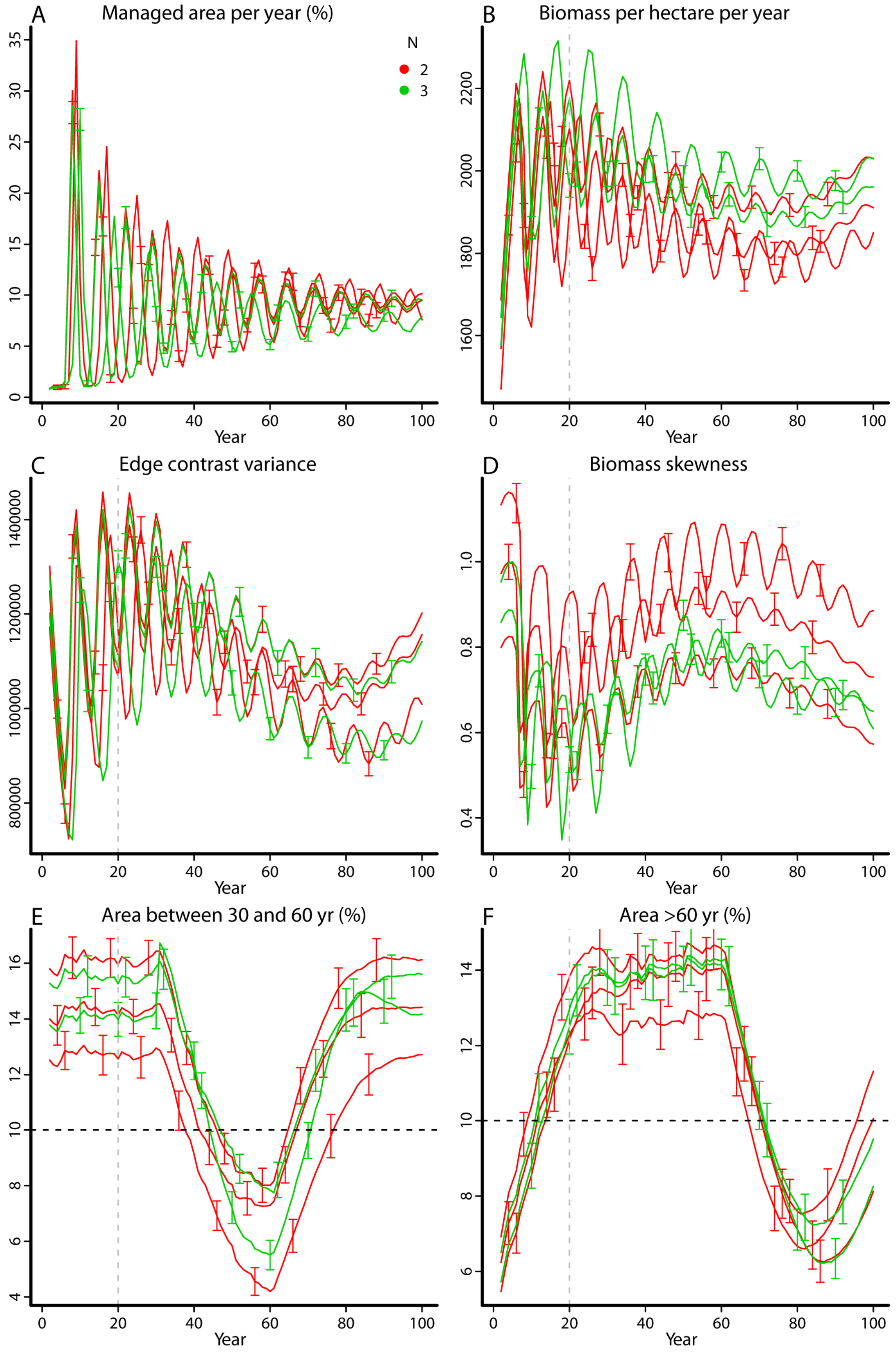


Figure 5: Values taken by the six objectives (A-F) along the simulation period (x axis) of the five compromise solutions (Supplementary Figure 6). Each line corresponds to a solution and depicts the values averaged over 100 simulations of the same landscape subjected to the management regime of the solution. Error bars represent the standard deviation. Colours refer to the number of effective management groups in the solution, i.e. after discarding groups with < 1% of landowners and merging groups differing < 1 year in management intervals. Objective values used in the optimization algorithm correspond to the average (A) or the minimum (B-F) taken along the whole simulation period (A) or discarding the first 20 years (B-F, vertical dashed line).

DISCUSSION

Designing management strategies to secure the services provided by landscapes made up of patchworks of private properties is challenging, due to the inherent stochasticity in landowners' responses to management rules, which in turn result in temporal and spatial variations in landscape composition and configuration that are hard to predict. The multi-objective simulation-optimization approach described in this study provides a tool to deal with these challenges, by explicitly integrating uncertainty in the implementation of management rules by individual landowners. Furthermore, this approach based on Pareto optimality provides a range of potential solutions to each optimization problem, allowing detailed examination of trade-offs between management objectives and identification of the consequences of management preferences by decision makers (e.g. Kennedy *et al.*, 2008). Although the approach was described using a particular case, it may be sufficiently flexible to deal with other socio-ecological systems where the provision of landscape services results from the cumulative effects of individual decisions by multiple landowners (e.g. Gustafson *et al.*, 2007). It is thus expected that this approach may find wide applicability to help solve management problems in multi-ownership landscapes.

Management strategies for upland cork oak landscapes

Despite a number of simplifications and assumptions taken in the development of the simulation-optimization approach for the management of cork oak upland landscapes, the study provided valuable guidelines for reducing fire risk and conserving mid- and late-successional biodiversity, while controlling for management costs. These guidelines should be taken as tentative, because the development of detailed management recommendations would require the incorporation of a great deal of additional realism in the landscape simulation conditions.

A key result of the simulation-optimization is that there should be two or more groups of landowners, each associated with a given management regime, whose cumulative action contributes for achieving the landscape-level objectives. Most management solutions involved a group of about 50%-70% of landowners clearing the understory at short intervals (3-9 years), though the exact proportions and intervals depended on management preferences. If reducing fire risk was the overarching goal then the percentage of landowners in the short rotation cycle was highest and the management interval was about 3-4 years, whereas a focus on biodiversity yielded the lowest proportion of landowners in the short rotation cycle and management intervals of up to 9 years. Irrespective of the details of the management regime, however, there was a very clear indication that a large proportion (>50%) of the landscape needs to be recurrently managed if the accumulation of fuel load is to be prevented. These management guidelines clearly contrast with current practice, though traditional understory clearing in association with the 9-year cork extraction cycle is within the optimal management intervals emerging from this study. However, ongoing processes of rural depopulation and land abandonment have resulted in a declining proportions of the landscape managed with this rotation cycle, which thus results in overly accumulation of biomass and increasing fire risk (Pausas *et al.*, 2008; Román-Cuesta *et al.*, 2009; Moreira *et al.*, 2011; Porto *et al.*, 2012).

Besides the short rotation cycle, most management solutions also involved a group of landowners clearing the understory with a long rotation cycle (about 80-100 years), whereas very few solutions involved management at intervals of about 20-60 years. Considering that the time frame of the landscape dynamics simulation was 100 years, the longest intervals should probably be interpreted as absence of understory management. The proportion of landowners associated with the long rotation cycle is largest if management focuses on biodiversity conservation, and smallest if the main focus is fire risk reduction. Within the long rotation cycle, there were management solutions that involved a single group managing with the same recurrence interval, where others involved two or more groups managing at different intervals within this time frame. The emergence of long rotation management schedules in the optimization process are probably a consequence of the biodiversity objectives, being necessary to maintain a sufficient representation of stands with mid- and late-successional understory. Irrespective of the management details, the key result is that areas with old understory can only be maintained if there is a distinct group of landowners that are required to clear the understory at long intervals or even not manage at all. As in the case of the short rotation cycle, these management guidelines contrast with current practice, due to uncoordinated management among landowners. In these circumstances, mid- and late-successional understories are cleared at irregular intervals, and so they may disappear from the landscape if the average recurrence interval is less than about 30 and 60 years, respectively.

Combining a large proportion of landowners under the short rotation cycle regime, with a smaller group under the long rotation cycle, results in a landscape with low fire risk while maintaining biodiversity associated with mid- and late-successional understories. The implementation of this management regime would result in a heterogeneous landscape dominated by a patchwork of stands with herbaceous or small shrubland understory, though maintaining a reasonable representation of patches with complex and multi-layered understory (Santana *et al.*, 2011). This landscape would likely contribute for the conservation of Mediterranean forest biodiversity, by providing conditions for a wide range of species associated with early, mid and late successional habitats (Porto *et al.*, 2011; Santana *et al.*, 2011, 2012; Verdasca *et al.*, 2012). Furthermore, this mosaic landscape would be suitable for endangered species requiring complementary habitats, including for instance top predators that breed or shelter in undisturbed stands with late-successional understories, while feeding on prey such as rabbits that are associated with patchworks of shrublands and herbaceous habitats (Palma *et al.*, 1999, 2006; Beja *et al.*, 2007). The simulation-optimization procedure thus converged to a management regime promoting landscape heterogeneity, which is an overarching goal in forest landscapes (Lindenmayer *et al.*, 2006; Turner *et al.*, 2012)

Improving the simulation-optimization approach

While the simulation-optimization approach used in this study was useful to generate insights on the optimal management of upland cork oak landscapes, its use for guiding the actual management of real landscapes would require introducing far more realism in landscape conditions and simulation parameters. One key limitation was that initial simulation conditions were based on a virtual landscape, rather than in an actual landscape. Although this was necessary due to the shortage of information on the boundaries of private properties and on the initial distribution of understory ages, it should be stressed that making detailed management prescriptions would require simulations based on the actual characteristics of a real landscape (Piñol *et al.*, 2005). Another problem was that the simulated landscape assumed homogeneity of environmental conditions, though this was a simplification since natural heterogeneities associated with, for instance, slope, exposure and soil type, may strongly influence vegetation successional pathways, biomass accumulation and management costs (Porto *et al.*, 2011; Santana *et al.*, 2011). Furthermore, in this study we have only considered a biomass accumulation curve of fine fuels and leaves , though there may be some differences in the accumulation of different fuel types (e.g. coarse and overall fuels), with consequences for fire risk (Porto *et al.*, 2012). All or part of these additional complexities could be easily incorporated in the landscape simulation algorithm, depending on the amount of ecological data available. This would require the association of management units with a set of environmental variables, which could then be used to modify biomass accumulation curves and management cost as a function of relevant environmental conditions (Naidoo *et al.*, 2006; Román-Cuesta *et al.*, 2009). Undertaking these exercises was beyond the scope of the present study, due to limitations in the information available.

In contrast to most other studies dealing with the optimization of landscapes to increase fire resistance, the decision variables used in optimization were not spatially explicit, which may be regarded as a shortcoming of our approach. Indeed, while this type of studies normally focus on the optimal spatial distribution of fuel treatments (e.g. Loehle, 2004; Kennedy *et al.*, 2008; Rytwinski and Crowe, 2010), our approach dealt with the temporal distribution of fuel treatments by groups of landowners, without considering explicitly any spatial component. In fact, the spatial component in our procedure was specified only in terms of landscape configuration objectives, by optimizing variables related to spatial fuel continuity and concentration. This option was purposefully taken to better incorporate the inherently stochastic character of decisions by landowners in multi-ownership landscapes, where it is nearly impossible to guarantee that a given treatment will be allocated to a given spatial location. Because of this, our approach produced solutions indicating, for instance, that there should be at least two groups of landowners involved in either in short or long management cycles, but not where in the landscape should these differential management regimes should better be assigned. Future research efforts should be devoted to extend our simulation-optimization approach in order to consider decision variables with both temporal and spatial components, introducing uncertainty associated with both the timing and the location of fuel treatments.

Biodiversity objectives considered in this study were very simple, specifying only that a given minimum percentage of mid- and late-successional habitats should be retained in the landscape over 100 years. More complex goals could be incorporated within our framework by using species-specific habitat and/or metapopulation models to estimate variation in species diversity and abundance over the simulation period (e.g. Wintle *et al.*, 2005; Gustafson *et al.*, 2007; Hartig and Drechsler, 2009), and then specifying optimization objectives such as the maximization of species diversity or habitat quantity for particular species or groups of species. This procedure could be particularly useful to design landscapes for species of conservation concern (e.g. Kurttila and Pukkala, 2003; Kennedy *et al.*, 2008), in the context of multi-objective optimization and duly accounting for stochasticity inherent to multi-ownership landscapes. Combining our simulation-optimization approach with species-specific habitat models will be the subject of future papers.

Optimizing the management of multi-ownership landscapes

The approach to the management planning of multi-ownership landscapes developed in this study differed in a number of significant ways and it is expected to overcome some of the practical problems associated with previous approaches. In the first place, previous approaches assumed that there is an optimal landscape configuration, but give little consideration on how such landscape can be produced in practice, assuming that there are no impediments to implementation (Meir *et al.*, 2004; Visconti *et al.*, 2010). Secondly, they assume that the optimal configuration is static and can be maintained through a spatial and temporal scheduling of management activities rigorously implemented by individual landowners (e.g. Kurttila and Pukkala, 2003), failing to account for landscape dynamics (Meir *et al.*, 2004; Drechsler *et al.*, 2009; Visconti *et al.*, 2010). Finally, they assume, often implicitly, that there is coordination among landowners in the implementation of the management plan (e.g. Kurttila and Pukkala, 2003; Visconti *et al.*, 2010). These assumptions make it doubtful whether these approaches can find wide applicability in real landscapes, because management rules are often poorly enforced and thus may not be strictly respected by landowners (Lewis *et al.*, 2011). Furthermore, allocating specific management regimes to particular spatial locations may have high social and economic costs, which may be hard to support (Polasky *et al.*, 2001; Chomitz *et al.*, 2006; Naidoo *et al.*, 2006; Visconti *et al.*, 2010).

To solve previous limitations, our approach was based on the idea that landscape-level objectives can emerge from uncoordinated and uncertain responses of individual landowners to management rules, without explicit spatial planning (Chomitz *et al.*, 2006; Gustafson *et al.*, 2007). This led to the development of a simulation-optimization approach that incorporates some of the complexities and uncertainties associated with the management of real landscapes, recognizing that a static landscape configuration may never be achieved due to the inherent stochasticity in landowners' decisions and their imperfect compliance with management rules as well as to natural succession. Despite these problems associated with the management of multi-ownership landscapes, our approach was able to show that landscape-level objectives can indeed be obtained by defining simple, non-spatial management rules that are implemented individually by each landowner, subject to uncertainty, and without the need for coordination among them. The approach provided dynamic landscape configurations that optimized the landscape-level objectives, without requiring a precise spatial allocation of management activities. The mechanism for producing such optimal landscapes is inherent in the simulation-optimization procedure, because the optimization of management rules is conditional on the degree to which they achieve the landscape-level objectives from the beginning to the end of the simulation period.

The extent to which our approach can be applicable to other socio-ecological systems is uncertain, but is likely that it could provide valuable insights for the management of a range of different multi-ownership landscapes. In particular, the approach may be useful where management involves the creation and maintenance of spatial heterogeneity in ecological conditions, which is often a key management goal in a range of forest (Bengtsson *et al.*, 2000; Lindenmayer *et al.*, 2006; Turner *et al.*, 2012) and agricultural (Benton *et al.*, 2003; Groot *et al.*, 2010) landscapes. There are cases, however, where the application of this approach may be inappropriate, requiring a more conventional spatially explicit landscape planning (e.g. Kurttila and Pukkala, 2003). This may be the case, for instance, where the conservation of biodiversity or environmental functions is strongly associated with particular locations, and so there is no flexibility in the spatial allocation of management regimes. Exploring the limits of applicability of the approach outlined in here, as well as eventual improvements that may make it more widely applicable, should be the subject of future research. Comparative evaluation of the cost-effectiveness of spatial versus non-spatial solutions to a wide range of management problems could prove particularly valuable.

ACKNOWLEDGEMENTS

This study was funded by IFADAP-Program AGRO 8.1 (project 458 - 2003.09.002326.2), and by the Portuguese Science and Technology Foundation through grant SFRH/BD/28974/2006 to MP. We thank researchers and technicians of the Forest Producers Association of Barranco do Velho, the Association In Loco, the Association for the Defence of Mértola Heritage, and the Centre for Applied Ecology "Baeta Neves", for collaboration in the development of this project.

REFERENCES

Acácio, V., Holmgren, M., Rego, F.C., Moreira, F., Mohren, G.M.J., 2009. Are drought and wildfires turning Mediterranean cork oak forests into persistent shrublands? Agroforestry Systems 76, 389–400.

Baskent, E.Z., Keles, S., 2005. Spatial forest planning: A review. Ecological Modelling 188, 145–173.

Beja, P., Pais, M., Palma, L., 2007. Rabbit Oryctolagus Cuniculus Habitats in Mediterranean Scrubland: The Role of Scrub Structure and Composition. Wildlife Biology 13, 28.

Bengtsson, J., Nilsson, S.G., Franc, A., Menozzi, P., 2000. Biodiversity, disturbances, ecosystem function and management of European forests. Forest Ecology and Management 132, 39–50.

Benton, T.G., Vickery, J.A., Wilson, J.D., 2003. Farmland biodiversity: is habitat heterogeneity the key? Trends in Ecology & Evolution 18, 182–188.

Bettinger, P., Graetz, D., Sessions, J., 2005. A density-dependent stand-level optimization approach for deriving management prescriptions for interior northwest (USA) landscapes. Forest Ecology and Management 217, 171–186.

Bettinger, P., Johnson, D.L., Johnson, K.N., 2003. Spatial forest plan development with ecological and economic goals. Ecological Modelling 169, 215–236.

Blasco, X., Herrero, J.M., Sanchis, J., Martínez, M., 2008. A new graphical visualization of n-dimensional Pareto front for decision-making in multiobjective optimization. Information Sciences 178, 3908–3924.

Chomitz, K.M., Fonseca, G.A.B., Alger, K., Stoms, D.M., Honzák, M., Landau, E.C., Thomas, T.S., Thomas, W.W., Davis, F., 2006. Viable Reserve Networks Arise From Individual Landholder Responses To Conservation Incentives. Ecology And Society 11, 40.

Coello Coello, C.A., Lamont, G.B., van Veldhuizen, D.A., 2007. Evolutionary Algorithms for Solving Multi-Objective Problems, 2nd ed. Springer.

Costa, A., Oliveira, A.C., Vidas, F., Borges, J.G., 2009. An approach to cork oak forest management planning: a case study in southwestern Portugal. European Journal of Forest Research 129, 233–241.

Deb, K., Pratap, A., Agarwal, S., Meyarivan, T., 2002. A Fast and Elitist Multiobjective Genetic Algorithm: NSGA-II. IEEE Transactions on Evolutionary Computation 6, 182–197.

Van Deusen, P.C., 2001. Scheduling Spatial Arrangement and Harvest Simultaneously. Silva Fennica 35, 85–92.

Drechsler, M., Lourival, R., Possingham, H.P., 2009. Conservation planning for successional landscapes. Ecological Modelling 220, 438–450.

Ducheyne, E.I., de Wulf, R.R., de Baets, B., 2006. A spatial approach to forest management optimization: linking GIS and multiple objective genetic algorithms. International Journal of Geographical Information Science 20, 917–928.

Fonseca, C.M., Fleming, P.J., 1995. An Overview of Evolutionary Algorithms in Multiobjective Optimization. Evolutionary Computation 3, 1–16.

González, J.R., Palahí, M., Pukkala, T., 2005. Integrating Fire Risk Considerations in Forest Management Planning in Spain – A Landscape Level Perspective. Landscape Ecology 20, 957–970.

González-Olabarria, J.-R., Pukkala, T., 2011. Integrating fire risk considerations in landscape-level forest planning. Forest Ecology and Management 261, 278–287.

Groot, J.C.J., Jellema, A., Rossing, W. a. H., 2010. Designing a hedgerow network in a multifunctional agricultural landscape: Balancing trade-offs among ecological quality, landscape character and implementation costs. European Journal of Agronomy 32, 112–119.

Gustafson, E.J., Lytle, D.E., Swaty, R., Loehle, C., 2007. Simulating the cumulative effects of multiple forest management strategies on landscape measures of forest sustainability. Landscape Ecology 22, 141–156.

Hardin, G., 1968. The tragedy of the Commons. Science 162, 1243–1248.

Hartig, F., Drechsler, M., 2009. Smart spatial incentives for market-based conservation. Biological Conservation 142, 779–788.

Holzkämper, A., Lausch, A., Seppelt, R., 2006. Optimizing landscape configuration to enhance habitat suitability for species with contrasting habitat requirements. Ecological Modelling 198, 277–292.

Hudson, B.J., 1986. Landscape as resource for national development: a Caribbean view. Geography 71, 116–121.

Johnson, K.N., Bettinger, P., Kline, J.D., Spies, T. a, Lennette, M., Lettman, G., Garber-Yonts, B., Larsen, T., 2007. Simulating forest structure, timber production, and socioeconomic effects in a multi-owner province. Ecological applications 17, 34–47.

Juutinen, A., Mönkkönen, M., Ylisirniö, A.-L., 2009. Does a voluntary conservation program result in a representative protected area network?The case of Finnish privately owned forests. Ecological Economics 68, 2974–2984.

Kashian, D.M., Turner, M.G., Romme, W.H., Lorimer, C.G., 2005. Variability and convergence in stand structural development on a fire-dominated subalpine landscape 86, 643–654.

Kennedy, M.C., Ford, E.D., 2011. Using Multicriteria Analysis of Simulation Models to Understand Complex Biological Systems. BioScience 61, 994–1004.

Kennedy, M.C., Ford, E.D., Singleton, P., Finney, M., Agee, J.K., 2008. Informed multi-objective decision-making in environmental management using Pareto optimality. Journal of Applied Ecology 45, 181–192.

Kurttila, M., Pukkala, T., 2003. Combining holding-level economic goals with spatial landscape-level goals in the planning of multiple ownership forestry. Landscape Ecology 18, 529–541.

Lewis, D.J., Plantinga, A.J., Nelson, E., Polasky, S., 2011. The efficiency of voluntary incentive policies for preventing biodiversity loss. Resource and Energy Economics 33, 192–211.

Lindenmayer, D.B., Franklin, J.F., Fischer, J., 2006. General management principles and a checklist of strategies to guide forest biodiversity conservation. Biological Conservation 131, 433–445.

Liu, G., Nelson, J.D., Wardman, C.W., 2000. A target-oriented approach to forest ecosystem design — changing the rules of forest planning. Ecological Modelling 127, 269–281.

Loehle, C., 2004. Applying landscape principles to fire hazard reduction. Forest Ecology and Management 198, 261–267.

Lu, F., Eriksson, L.O., 2000. Formation of harvest units with genetic algorithms. Forest Ecology and Management 130, 57–67.

Macfarlane, R., 2000. Achieving Whole-Landscape Management across Multiple Land Management Units: A case study from the Lake District Environmentally Sensitive Area. Landscape Research 25, 229–254.

McGarigal, K., Tagil, S., Cushman, S.A., 2009. Surface metrics: an alternative to patch metrics for the quantification of landscape structure. Landscape Ecology 24, 433–450.

Meir, E., Andelman, S., Possingham, H.P., 2004. Does conservation planning matter in a dynamic and uncertain world? Ecology Letters 7, 615–622.

Moreira, F., Viedma, O., Arianoutsou, M., Curt, T., Koutsias, N., Rigolot, E., Barbati, A., Corona, P., Vaz, P., Xanthopoulos, G., Mouillot, F., Bilgili, E., 2011. Landscape--wildfire interactions in southern Europe: implications for landscape management. Journal of environmental management 92, 2389–402.

Naidoo, R., Balmford, A., Ferraro, P.J., Polasky, S., Ricketts, T.H., Rouget, M., 2006. Integrating economic costs into conservation planning. Trends in ecology & evolution 21, 681–7.

Nelson, E., Mendoza, G., Regetz, J., Polasky, S., Tallis, H., Cameron, D.R., Chan, K.M., Daily, G.C., Goldstein, J., Kareiva, P.M., Lonsdorf, E., Naidoo, R., Ricketts, T.H., Shaw, M.R., 2009. Modeling multiple ecosystem services, biodiversity conservation, commodity production, and tradeoffs at landscape scales. Frontiers in Ecology and the Environment 7, 4–11.

Nelson, E., Polasky, S., Lewis, D.J., Plantinga, A.J., Lonsdorf, E., White, D., Bael, D., Lawler, J.J., 2008. Efficiency of incentives to jointly increase carbon sequestration and species conservation on a landscape. Proceedings of the National Academy of Sciences of the United States of America 105, 9471–6.

Ostrom, E., 2009. A general framework for analyzing sustainability of social-ecological systems. Science 325, 419–422.

O'Farrell, P.J., Anderson, P.M., 2010. Sustainable multifunctional landscapes: a review to implementation. Current Opinion in Environmental Sustainability 2, 59–65.

Palma, L., Beja, P., Pais, M., Cancela Da Fonseca, L., 2006. Why do raptors take domestic prey? The case of Bonelli's eagles and pigeons. Journal of Applied Ecology 43, 1075–1086.

Palma, L., Beja, P., Rodrigues, M., 1999. The use of sighting data to analyse Iberian lynx habitat and distribution. Journal of Applied Ecology 36, 812–824.

Parkhurst, G.M., Shogren, J.F., Bastian, C., Kivi, P., Donner, J., Smith, R.B.W., 2002. Agglomeration bonus: an incentive mechanism to reunite fragmented habitat for biodiversity conservation. Ecological Economics 41, 305–328.

Pausas, J.G., Llovet, J., Rodrigo, A., Vallejo, R., 2008. Are wildfires a disaster in the Mediterranean basin? – A review. International Journal of Wildland Fire 17, 713–723.

Piñol, J., Beven, K., Viegas, D.X., 2005. Modelling the effect of fire-exclusion and prescribed fire on wildfire size in Mediterranean ecosystems. Ecological Modelling 183, 397–409.

Polasky, S., Camm, J.D., Garber-yonts, B., 2001. Selecting Biological Reserves Cost-Effectively: An Application to Terrestrial Vertebrate Conservation in Oregon. Land Economics 77, 68–78.

Polasky, S., Nelson, E., Lonsdorf, E., Fackler, P., Starfield, A., 2005. Conserving species in a working landscape: land use with biological and economic objectives. Ecological Applications 15, 1387–1401.

Porto, M., Correia, O., Beja, P., 2011. Long-term consequences of mechanical fuel management for the conservation of Mediterranean forest herb communities. Biodiversity and Conservation 20, 2669–2691.

Porto, M., Correia, O., Beja, P., 2012. Modelling fuel succession in Mediterranean cork oak forests along a 70-year chronosequence. In: Management of Multi-ownership Mediterranean Forest Landscapes: Balancing Biodiversity Conservation and Fire Risk Reduction. Faculdade de Ciências, Universidade de Lisboa, Lisboa.

R Development Core Team, 2008. R: A Language and Environment for Statistical Computing. Vienna Austria R Foundation for Statistical Computing.

Román-Cuesta, R.M., Gracia, M., Retana, J., 2009. Factors influencing the formation of unburned forest islands within the perimeter of a large forest fire. Forest Ecology and Management 258, 71–80.

Rytwinski, A., Crowe, K.A., 2010. A simulation-optimization model for selecting the location of fuel-breaks to minimize expected losses from forest fires. Forest Ecology and Management 260, 1–11.

Santana, J., Porto, M., Gordinho, L., Reino, L., Beja, P., 2012. Long-term responses of Mediterranean birds to forest fuel management. Journal of Applied Ecology 49, 632–643.

Santana, J., Porto, M., Reino, L., Beja, P., 2011. Long-term understory recovery after mechanical fuel reduction in Mediterranean cork oak forests. Forest Ecology and Management 261, 447–459.

Stranlund, J.K., 1995. Public mechanisms to support compliance to an environmental norm. Journal of Environmental Economics and Management 28, 205–222.

Sturtevant, B.R., Miranda, B.R., Yang, J., He, H.S., Gustafson, E.J., Scheller, R.M., 2009. Studying Fire Mitigation Strategies in Multi-Ownership Landscapes: Balancing the Management of Fire-Dependent Ecosystems and Fire Risk. Ecosystems 12, 445–461.

Trautmann, H., Steuer, D., Mersmann, O., 2010. mco: Multicriteria optimization algorithms and related functions.

Turner, M.G., Baker, W.L., Peterson, C.J., Peet, R.K., 1998. Factors Influencing Succession: Lessons from Large, Infrequent Natural Disturbances. Ecosystems 1, 511–523.

Turner, M.G., Donato, D.C., Romme, W.H., 2012. Consequences of spatial heterogeneity for ecosystem services in changing forest landscapes: priorities for future research. Landscape Ecology.

Verdasca, M.J., Leitão, A.S., Santana, J., Porto, M., Dias, S., Beja, P., 2012. Forest fuel management as a conservation tool for early successional species under agricultural abandonment: The case of Mediterranean butterflies. Biological Conservation 146, 14–23.

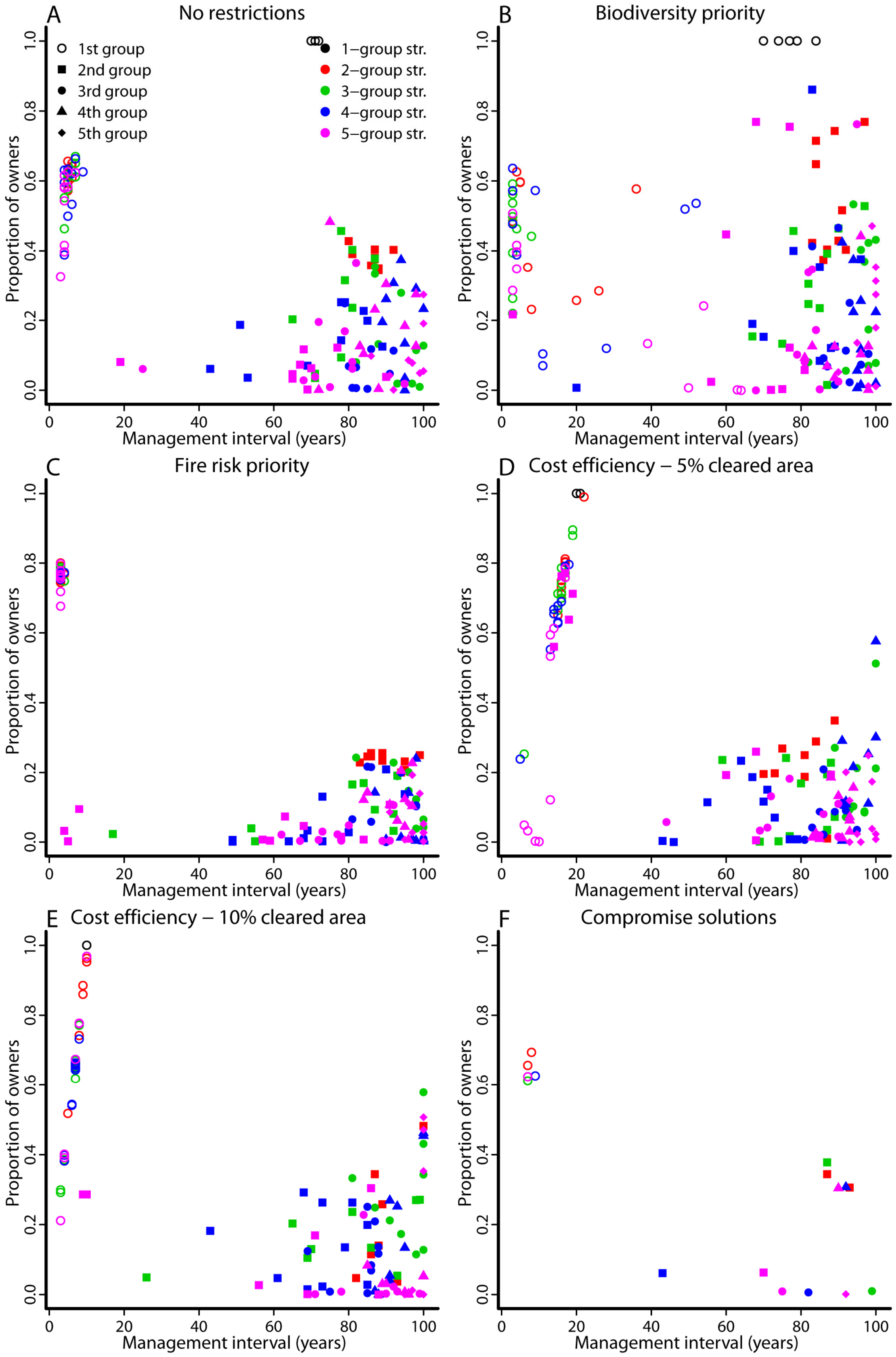
Viedma, O., Angeler, D.G., Moreno, J.M., 2009. Landscape structural features control fire size in a Mediterranean forested area of central Spain. International Journal of Wildland Fire 18, 575–583.

Visconti, P., Pressey, R.L., Segan, D.B., Wintle, B. a., 2010. Conservation planning with dynamic threats: The role of spatial design and priority setting for species' persistence. Biological Conservation 143, 756–767.

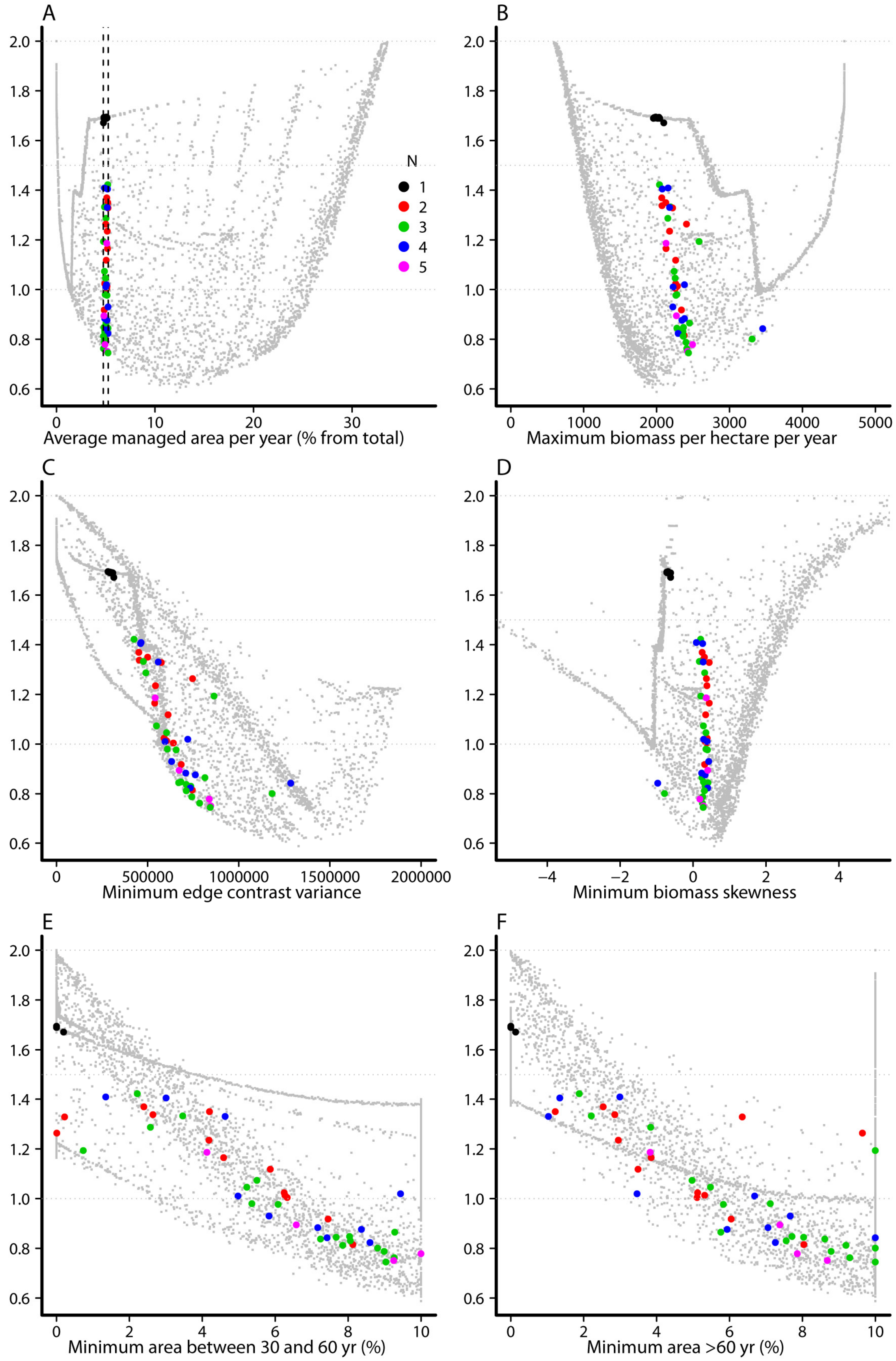
Wear, D.N., Turner, M.G., Flamm, R.O., 1996. Ecosystem Management with Multiple Owners: Landscape Dynamics in a Southern Appalachian Watershed. Ecological Applications 6, 1173–1188.

Wintle, B.A., Bekessy, S.A., Venier, L.A., Pearce, J.L., Chisholm, R.A., 2005. Utility of Dynamic-Landscape Metapopulation Models for Sustainable Forest Management. Conservation Biology 19, 1930–1943.

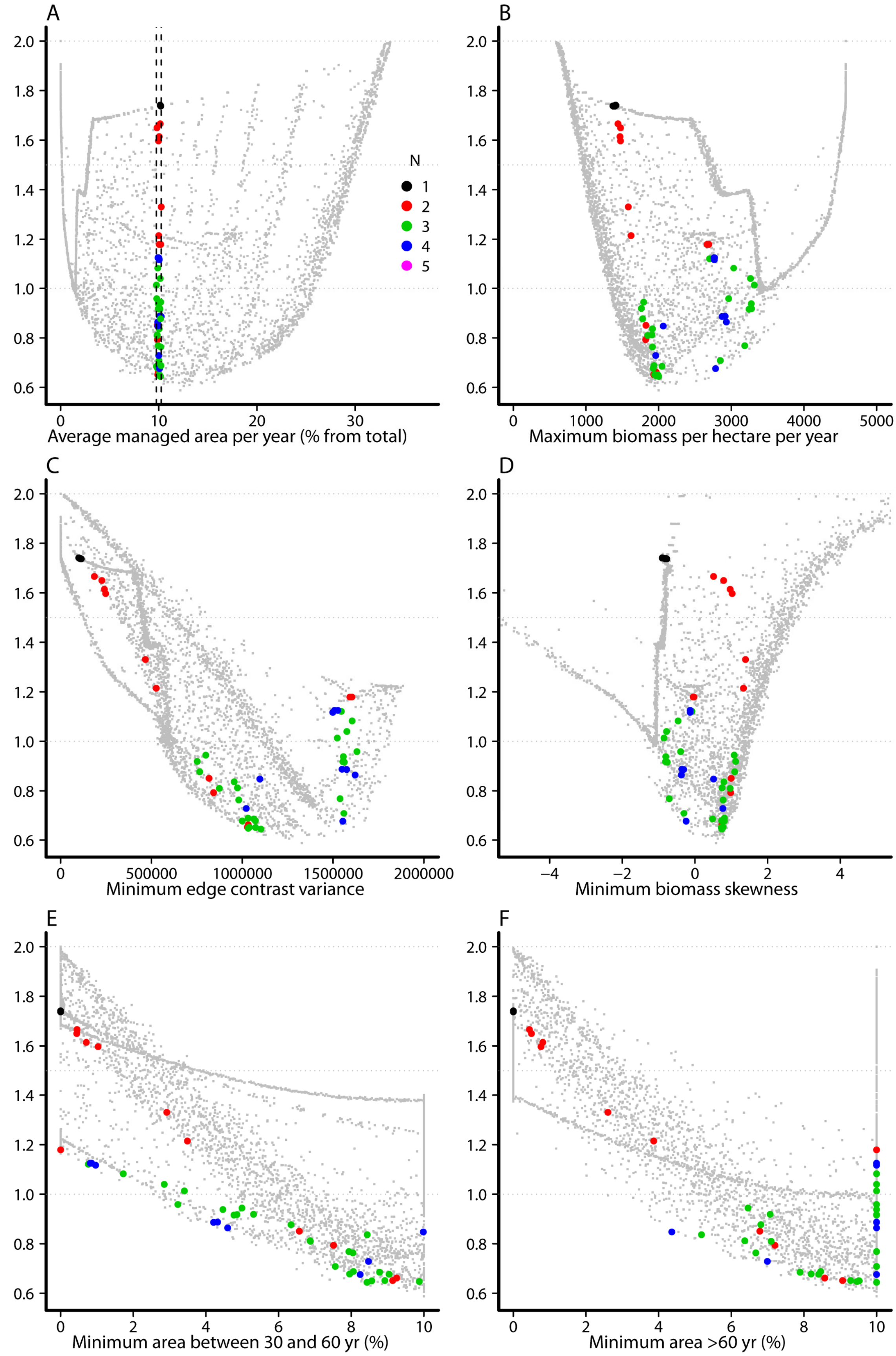
SUPPLEMENTARY MATERIAL



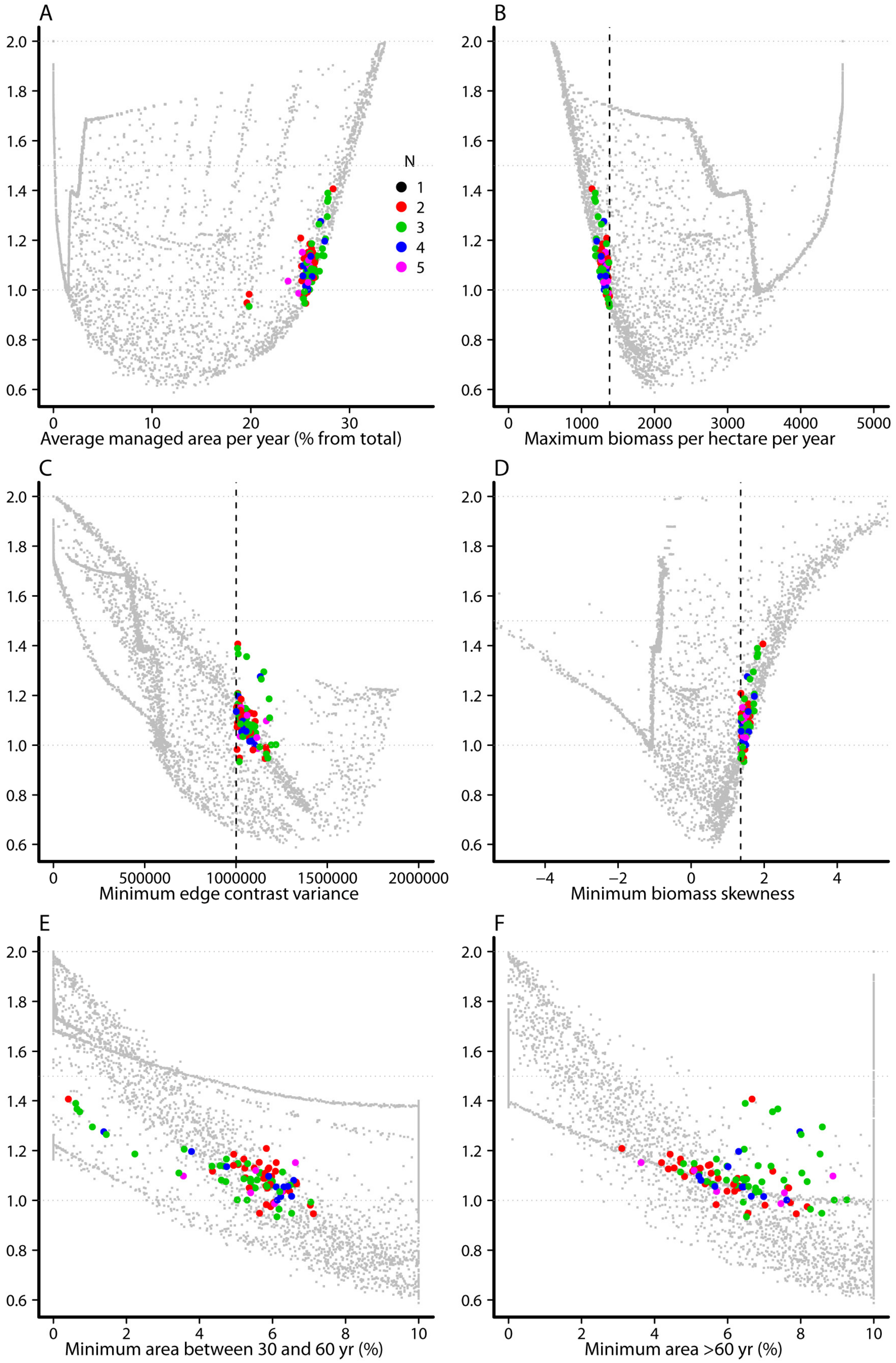
Supplementary Figure S1: Plots representing management groups as a function of assigned management interval (x axis) and proportion of landowners in the group (y axis), of the ten overall best management solutions of each strategy (when available), in each scenario (A-F). Colours refer to the strategy to which each group belongs. For the sake of clarity, points of the same solution are not connected.



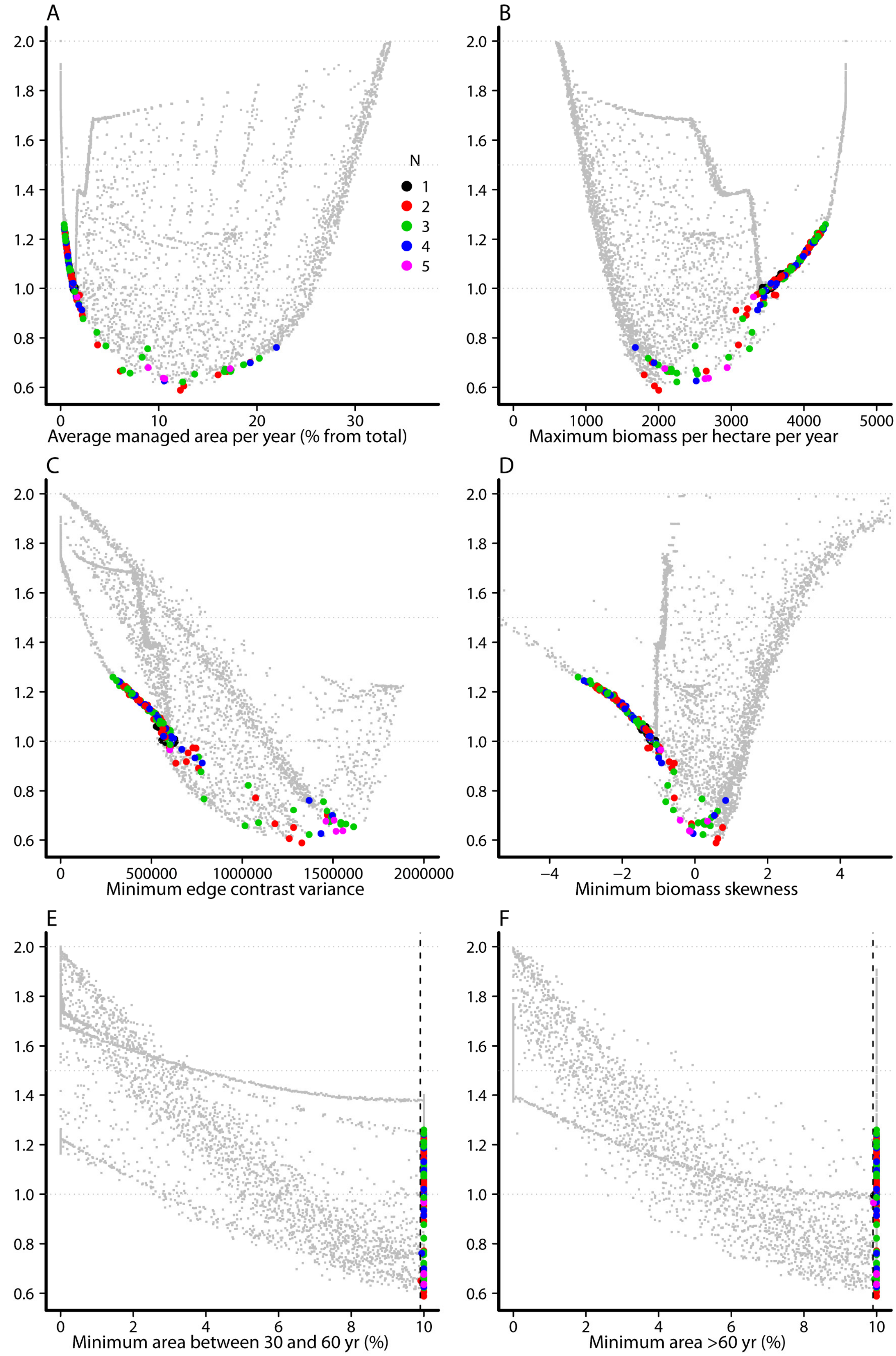
Supplementary Figure S2: Level diagrams of optimization solutions for the six objectives (A-F, x axis), each plot showing the five management strategies. Solutions that have approximately the same implementation cost (A) falling within 5% ± 0.25% (vertical dashed lines) are highlighted. The y axis represents the distance between each observed solution and the ideal overall solution, which is the same across the six plots. Colours refer to the number of effective management groups in the solution, i.e. after discarding groups with < 1% of landowners and merging groups differing < 1 year in management intervals.



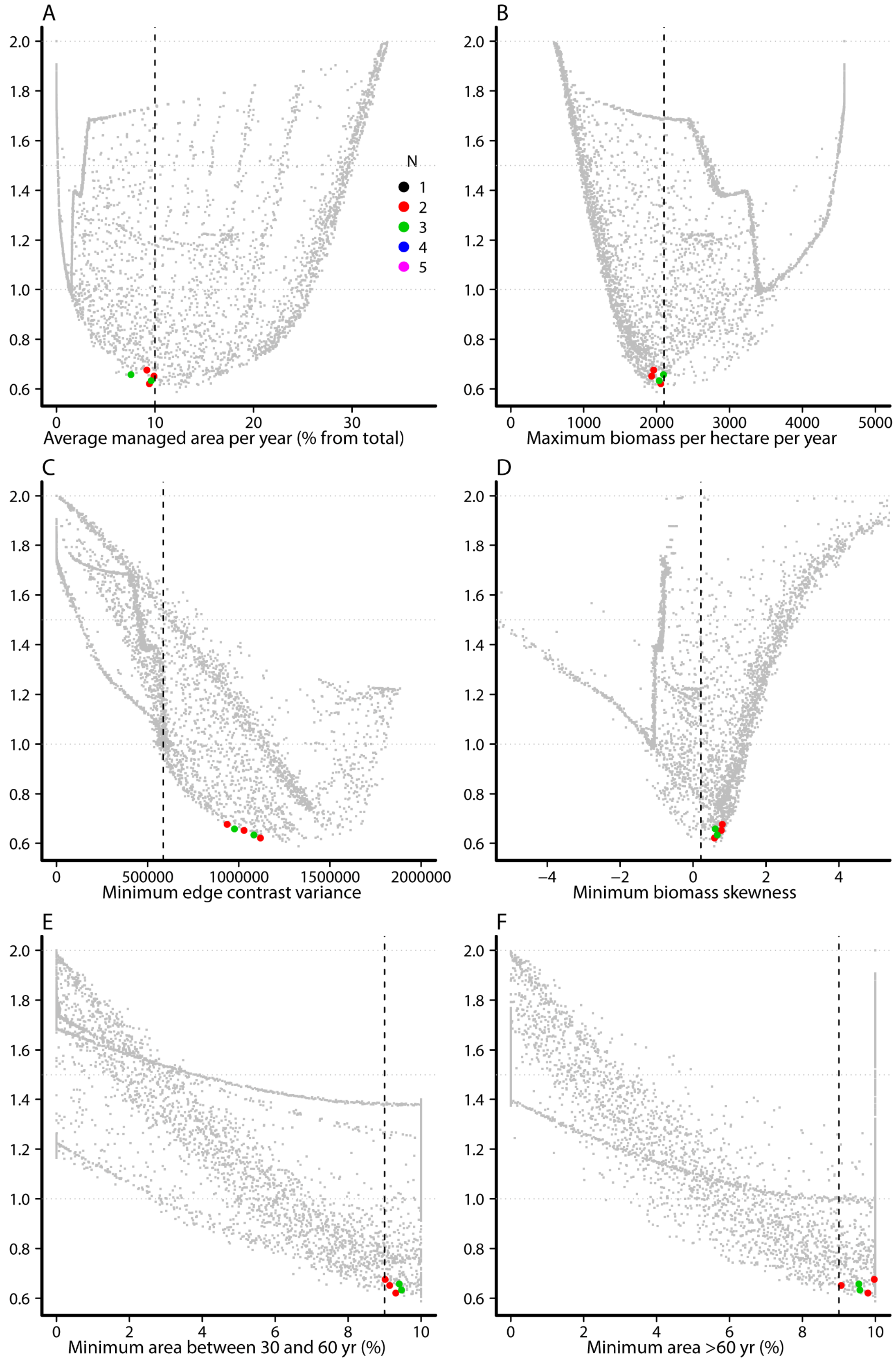
Supplementary Figure S3: Level diagrams of optimization solutions for the six objectives (A-F, x axis), each plot showing the five management strategies. Solutions that have approximately the same implementation cost (A) falling within 10% ± 0.25% (vertical dashed lines) are highlighted. The y axis represents the distance between each observed solution and the ideal overall solution, which is the same across the six plots. Colours refer to the number of effective management groups in the solution, i.e. after discarding groups with < 1% of landowners and merging groups differing < 1 year in management intervals.



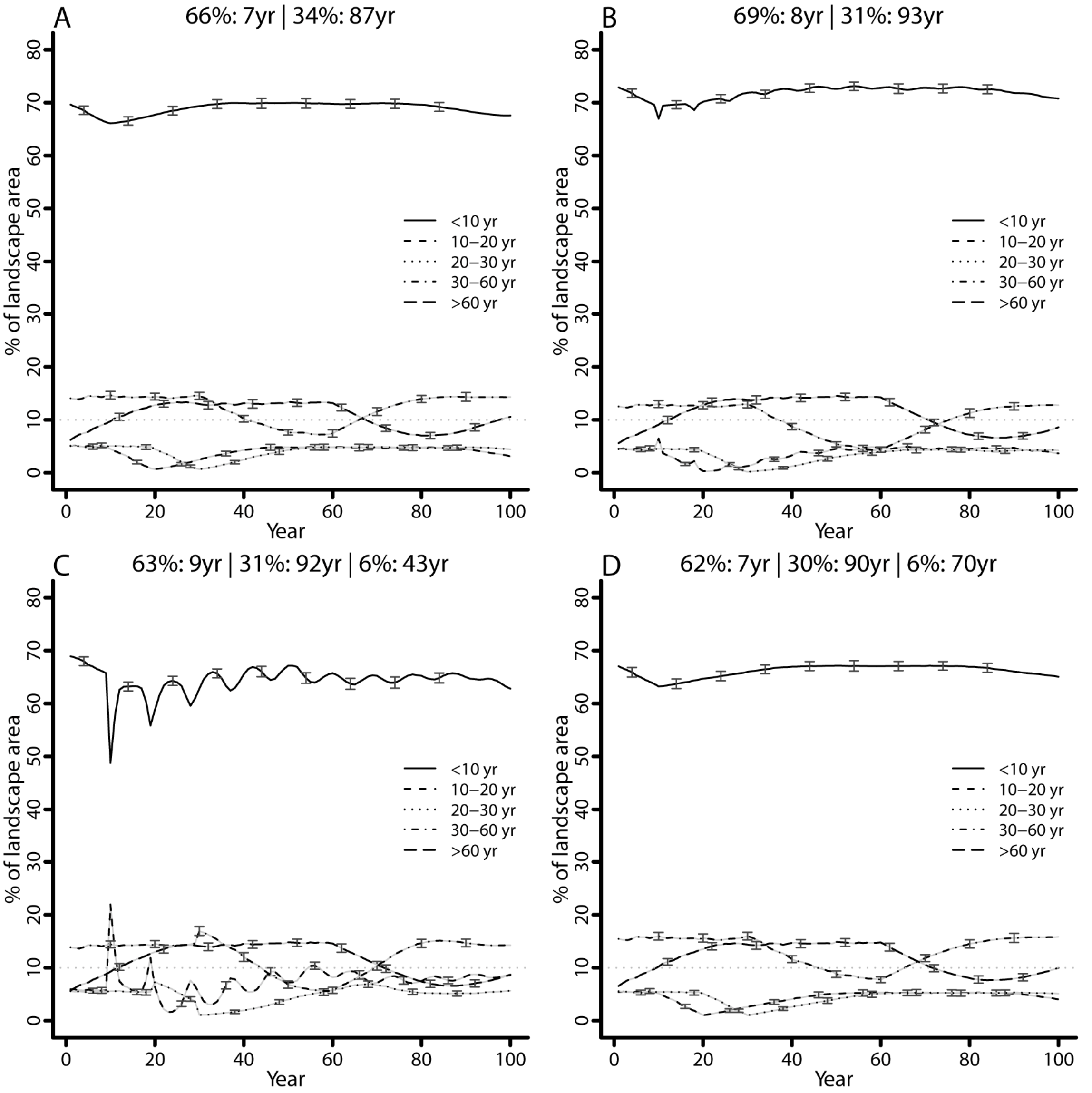
Supplementary Figure S4: Level diagrams of optimization solutions for the six objectives (A-F, x axis), each plot showing the five management strategies. Solutions that best fulfil the three fire risk objectives simultaneously (B-D), i.e., those that fall below the 25% percentile (in B) and above the 75% percentile (in C, D) are highlighted. Percentiles are depicted by vertical dashed lines. The y axis represents the distance between each observed solution and the ideal overall solution, which is the same across the six plots. Colours refer to the number of effective management groups in the solution, i.e. after discarding groups with < 1% of landowners and merging groups differing < 1 year in management intervals.



Supplementary Figure S5: Level diagrams of optimization solutions for the six objectives (A-F, x axis), each plot showing the five management strategies. Solutions that fulfil both biodiversity objectives simultaneously (E, F), i.e., resulting at least in 9.9% (vertical dashed lines) of the area maintained in each age class throughout the simulation period, are highlighted. The y axis represents the distance between each observed solution and the ideal overall solution, which is the same across the six plots. Colours refer to the number of effective management groups in the solution, i.e. after discarding groups with < 1% of landowners and merging groups differing < 1 year in management intervals.



Supplementary Figure S6: Level diagrams of optimization solutions for the six objectives (A-F, x axis), each plot showing the five management strategies. Solutions that perform reasonably in all objectives simultaneously, i.e., that fall below (A, B) or above (C-F) the vertical dashed lines are highlighted. Lines correspond to 10% of landscape managed each year (A), the percentile 50 of the fire risk objectives (B-D) and a minimum of 9% of the area maintained in the two age classes (E, F). The y axis represents the distance between each observed solution and the ideal overall solution, which is the same across the six plots. Colours refer to the number of effective management groups in the solution, i.e. after discarding groups with < 1% of landowners and merging groups differing < 1 year in management intervals.



Supplementary Figure S7: Percentage area (y axis) of landscape in each age class throughout the simulation period (x axis) in landscapes managed according to the regimes obtained in the compromise solutions (Supplementary Figure 6). Each plot corresponds to one of the 4 solutions (excluding the best, see Figure 5). Lines depict the values averaged over 100 simulations of the same landscape subjected to the same management regime, and error bars the standard deviation.

6

General Discussion

Adenocarpus anisochilus
large shrub typical of the cork oak forest understory in the few little disturbed patches (endemic to the mountains of Algarve)

General discussion

Overall patterns

The main goal of this thesis was to understand if and to what extent it is possible to achieve management objectives at the landscape scale through the uncoordinated management of individual properties, using as case study a cork oak forest landscape in southern Portugal. Management of this landscape is challenging, because it involves apparently incompatible objectives of fire risk reduction and biodiversity conservation, and management is undertaken by individual landowners, within their small properties, with no landscape scale coordination. To address this issue, we started by analyzing the long-term consequences for vegetation communities (Chapters 2 and 3) and fire risk (Chapter 4) of mechanical clearing of the woody understory, which was the main management action carried out by landowners in this landscape. After that, we used computer simulations to assess the consequences at the landscape scale of local and independent management actions, which was embedded in an optimization procedure to design management strategies that could achieve landscape level objectives despite uncoordinated and local management (Chapter 5).

Plant community succession after mechanical disturbance in the studied cork oak forests was characterized by a fast, short-term recovery of herbaceous and woody plant communities, which was followed by an increasingly slower change in all plant descriptors in the longer term (>20 years). However, finer analyses revealed different sets of species making their appearance at different successional times, so that after ca. 70 years, communities were markedly different both in herb and shrub composition from early successional communities, suggesting that forest management practices have long term effects on plant communities, namely in the herbaceous species. This fact has implications not only on other biological groups that are strongly dependent on vegetation (Santana *et al.*, 2012; Verdasca *et al.*, 2012) but also on forest management planning, if sustainability is one of the aims to be achieved. Changes in vegetation were accompanied by a change in the amount and type of fuel, which increased rapidly in the short term but tended to accumulate at a lower rate thereafter. This pattern is in close association with the shrub community not only due to changes in total cover, but also because different species appearing at different successional times, possess different physical traits that influence flammability.

The comparative analysis of vegetation and fuel successional patterns highlighted the management conundrum in this landscape. In the one hand, the long term effects of management on plant communities suggest that it is important to maintain the full spectrum of successional ages so that landscape biodiversity is maximized. On the other hand, however, maintaining late successional understory ages increases fire risk, which may be socially and economically unacceptable. This was the problem tackled with the simulation-optimization approach, which aimed to produce management regimes that were simple enough not to require coordination, but powerful enough to accomplish landscape-scale objectives. Results suggested that the solution to the biodiversity-fire risk conundrum must reside in a careful spatial planning of forest management practices, so that both components are satisfied at landscape scale, albeit not necessarily at a local scale. Given the strongly spatial nature of fire, a fire-safe landscape can be achieved, for example, by breaking continuity between high fire risk patches. However, the inherent ecosystem dynamics require a continuous effort to keep the risk reasonably low at all times, and simultaneously maintaining a temporal continuity (stability) of suitable habitat for as much species as possible. Such landscape organization may not be straightforward to achieve when land ownership is divided into many private owners that lack coordination.

We have shown, however, that if landowners follow some simple rules, irrespective of those followed by their neighbours, it is possible to achieve positive landscape outcomes.

Taken together, the results thus suggest that, at least in some circumstances, uncoordinated management actions taken at the individual landholding level are indeed able to produce quite satisfactory combined results in a larger scale of analysis (landscape), fulfilling objectives that would expectedly demand coordination. Although these results are specific to the particular landscape analyzed in this thesis, it is possible that they are applicable to similar landscapes elsewhere, where achieving landscape level goals requires the maintenance of successional heterogeneity.

Mediterranean vegetation dynamics after disturbance

Long-term effects of forest management

Human activities on ecosystems may have impacts that are still noticeable centuries after disturbance has ceased (Bellemare *et al.*, 2002; Dupouey *et al.*, 2002; Josefsson *et al.*, 2009). Mediterranean vegetation, however, is generally believed to be highly resilient to disturbances (Zavala *et al.*, 2000; Rodrigo *et al.*, 2004) due to its evolutionary history (Rundel, 1998; Bar Massada *et al.*, 2009). Our results suggest that this view cannot be generalized, since many of the effects of disturbance on community structure and composition spanned for many decades. As Rodrigo *et al.* (2004) and Baeza *et al.* (2007) state, resilience depends on the type of community, so that communities that are naturally adapted to disturbance (e.g. some types of shrublands and of grasslands) will show higher resilience than those that are not (e.g. mature forests) (Calvo *et al.*, 2002, 2005; Baeza *et al.*, 2007; Potts *et al.*, 2010). As such, it was expected that in our study system the structure and composition of late successional communities would not be reestablished in the short term. In fact, results from chapters 2-3 show that several species and groups of species are absent from the "pioneer" communities and only start appearing many decades after disturbance, including some herbaceous species. Resprouting and fleshy-fruited shrubs were nearly eliminated in frequently disturbed sites, and richness of some herbaceous groups - namely perennial life forms - was severely depleted after disturbance, taking a long time to recover. Unlike (Pérez-Ramos *et al.*, 2008) who studied a very similar system and disturbance (albeit in the short term), finding a rapid recovery of herbaceous communities, our data shows that a full recovery of cork oak forest vegetation - including understory herbaceous communities - only takes place in the long term.

Reasons for these long term effects could be due, for example, to limitations in persistence, recruitment (Hermy *et al.*, 1999), dispersion (Hermy *et al.*, 1999; Verheyen *et al.*, 2003; Brunet, 2007) and establishment (Peterken and Game, 1984) of the so-called "forest species" (Hermy *et al.*, 1999). Forest species share a particular set of traits that renders them unable to quickly recover or colonize a disturbed forest patch (Bierzychudek, 1982; Bellemare *et al.*, 2002). They usually require a long continuous history of forest habitat in a given place in order to persist (Hermy *et al.*, 1999; Verheyen *et al.*, 2004), and are unable to withstand high intensity management operations (Oheimb and Härdtle, 2009) or even temporary land use changes (Hermy *et al.*, 1999), namely because they usually take several years to reach sexual maturity (Bierzychudek, 1982) and do not have a persistent seed bank (Hermy *et al.*, 1999; Dölle and Schmidt, 2009). Some results, but not all, from Chapters 2 and 3 are in accordance with these patterns, showing a differential response of dry-fruited vs. fleshy-fruited shrubs, as well as annual vs. perennial herbs. These groups differ in dispersion, persistence and reproductive abilities, which is partly due to trait syndromes (Herrera, 1992; Aparicio *et al.*, 2008), so that fleshy-fruited shrubs and perennial herbs prevail in later stages of succession and vice-versa, which is expected if we take into account the trait syndromes that these groups represent (Bierzychudek, 1982). However, the most relevant findings in herbaceous species were the absence of a differential response among dispersal groups, which is not expected. Although theory predicts (Aparicio *et al.*, 2008) and some studies show (Houssard *et al.*, 1980; Bellemare *et al.*, 2002) that there should be a relationship between dispersion abilities and successional time, even though there is no consensus as to the details of the relationship (Houssard *et al.*, 1980; Bonet and Pausas, 2004; Aparicio *et al.*, 2008), we did not detect any trend in our results for herbaceous species. Possible reasons may be related to other correlated traits masking the response of dispersal traits, or incomplete classification of species whose seeds, albeit apparently not possessing adaptations to endozoochory (e.g. grasses), are in fact dispersed by herbivores in addition to wind, including large grazers (Malo and Suárez, 1995).

Fire versus mechanical disturbances

The lower resilience of the studied communities to mechanical disturbance in our study is probably linked with the different type of disturbance, compared to the natural disturbances with which communities have evolved (Zavala *et al.*, 2000). Although it is controversial that what we call adaptations to fire have indeed evolved in response to it (Bond and Keeley, 2005; Bradshaw *et al.*, 2011), there is no doubt that Mediterranean vegetation possesses a set of traits that greatly increase species fitness in fire-prone systems (Bradshaw *et al.*, 2011). This does not, however, guarantee resilience in altered fire regimes or under other types of biomass-destructive disturbances. Indeed, the type of disturbance determines the structure and composition of the initial stages of succession (Turner *et al.*, 1998; Tárrega *et al.*, 2001), which influences that of later stages (Connell and Slatyer, 1977; Capitanio and Carcaillet, 2008), and therefore can affect the successional pathway of a disturbed community (Bond and Midgley, 2001) especially when keystone species are involved (Valdecantos *et al.*, 2009), although convergence along time has also been found in some studies (Tárrega *et al.*, 2001). Two major processes are directly involved in shaping the post-disturbance community: persistence and regeneration of component species (Bond and Midgley, 2001) subjected to disturbance. These are imprinted in Mediterranean vegetation in the resprouter-seeder dichotomy, which may (Zavala *et al.*, 2000), or may not (Vesk and Westoby, 2004), be extremes of a gradient of resource allocation strategies that determine the extent to which a species is able to persist (Hodgkinson, 1998) or solely recruit from seed following severe disturbance (Bond and Midgley, 2001). Results from Chapter 2 show an important difference between the responses of species in these two extremes. Seeder shrubs, i.e. those that entirely rely on mass seed germination to recover after disturbance, were clearly in advantage over resprouters for many years, which contrasts with the usual patterns following fire documented at least in some studies (Clemente *et al.*, 1996; Pausas *et al.*, 1999; Calvo *et al.*, 2002). This maintained a distinct community, both in composition and in structure, which dominated before resprouters could establish. The way a particular disturbance affects propagules and regenerative tissues is the key factor behind the differential response of these groups (Baeza *et al.*, 2007). For example, it is expected that purely above ground disturbances (such as fire) will not significantly affect regeneration of resprouting species (Vesk and Westoby, 2004) except for juveniles (Hodgkinson, 1998), whereas disturbances that mechanically affect the soil will "postpone" the increase of resprouters, since they must regenerate from seed (Calvo *et al.*, 2002) due to destruction of their perennating organs (Baeza *et al.*, 2007), a process which is significantly slower than regeneration of seeder species (Vallejo and Alloza, 1998; Baeza *et al.*, 2007). Additionally, fire has several other effects on recruitment processes that mechanical disturbance can only partially mimic (Calvo *et al.*, 2005; Bradshaw *et al.*, 2011) and that will further increase the differences between fire and mechanical disturbances (Peltzer *et al.*, 2000; Potts *et al.*, 2010). Our results then suggest that mechanical disturbances reduce the resilience of communities even if infrequent by reducing the expression of resprouters (Valdecantos *et al.*, 2009), and, if recurrent, will probably eliminate entire functional groups from the system (Hobbs and Norton, 1996), which may impact organisms that depend on some specific species or groups of species, like birds (Santana *et al.*, 2012), butterflies (Verdasca *et al.*, 2012) and herbaceous plants (Chapter 3).

Forest management and fire risk

The differential responses of different groups of species to management suggest that it is not straightforward to assess the efficiency of management in reducing fire risk as a simple linear function of management frequency, since biomass accumulation is heterogeneous along time. Results from Chapter 4 show that just about 10-20 years after management, the shrub cover and biomass continuity is reestablished at very high levels similar to the pre-disturbance community. This pattern is in accordance with the facts that seeder shrubs rapidly regenerate a few years after disturbance (see previous sections) and are highly flammable, in particular more flammable than resprouters (Valdecantos *et al.*, 2009; Saura-Mas *et al.*, 2010). Because seeder species are favoured by frequent fires, such high-frequency management may lead the system to enter a positive feedback fire degradation loop (Valdecantos *et al.*, 2009) where the occurrence of fire promotes the appearance of a more flammable community, which in turn increases the risk of a subsequent fire and calls for even more frequent management operations to be undertaken. This positive feedback is suggested by many studies (Grigulis *et al.*, 2005; Valdecantos *et al.*, 2009; Saura-Mas *et al.*, 2010) and is not exclusive to Mediterranean-type communities (Schwilk and Caprio, 2011). Such results suggest a trade-off between management cost and actual fire risk reduction. For example, the gain in accumulated fire risk reduction when shifting from a 20-year interval regime to a 10-year regime may not pay off the doubling of the cost. However, it is important to note the fire risk in a given area is not just a local scale property (Loehle, 2004). It is empirically evident that the distribution of fuels in a landscape will strongly determine the behaviour of fire in that landscape (González *et al.*, 2005; Ryu *et al.*, 2007), namely their spatial continuity (González-Olabarria and Pukkala, 2011), hence, the fire risk of a given area is moderated by its landscape context. The problem thus demands scaling up to a spatially explicit analysis at the landscape level starting with the local scale data. Achieving a landscape with intrinsic low fire risk eventually reduces the costs of aggressive fire suppression by reducing its severity (Stephens *et al.*, 2009).

Management of complex multifunctional landscapes

Multifunctional landscapes, being a human "construction" upon natural systems, need adequate management to be undertaken in order to sustain in the long term their functions, services and the ecological balance (O’Farrell and Anderson, 2010). Such adequate management regime may not, however, be easily achieved under the practical constraints of fragmented, privately owned landscapes. Our hypothesis explored in Chapter 5 was that an adequate management regime needs not to be a strict plan to be followed exactly as prescribed, but can be a loose, somewhat vague plan, that is thus able to cope with this and other practical limitations related to implementation - by integrating them - so that the objectives are not compromised even in far-from-ideal situations. The main point behind our hypothesis is that landscape-level objectives can emerge from uncoordinated and uncertain management practices (Chomitz *et al.*, 2006; Gustafson *et al.*, 2007).

Spatial and temporal heterogeneity

Spatial heterogeneity is a highly valued landscape feature that is widely viewed as a solution for a large variety of problems posed by man in natural systems (Lindenmayer *et al.*, 2006), even though its mechanisms are far from being understood given the diversity and complexity of species responses to it (Wiens, 2000). Temporal heterogeneity may be, however, far more harmful because it generally means breaking the temporal continuity of habitats, which is especially negative for sessile organisms or organisms with limited dispersal and colonization abilities (Verheyen *et al.*, 2004).

Results from Chapter 5 suggest that uncoordinated management is not necessarily an impediment to achieve landscape level objectives based on maintaining spatial heterogeneity, since the inherent randomness associated with uncoordination will naturally produce some degree of heterogeneity. This is supported by the fact that it was possible to achieve fairly good results with minimal management constraints - by randomly dividing landowners in just two groups with different prescriptions, but without the need to spatially allocate management operations or to specify criteria to divide the groups. This approach is largely based on randomness, hence contrasting with management scheduling approaches, that impose rigid management schemes, with precise locations (Kennedy *et al.*, 2008; Rytwinski and Crowe, 2010) and dates (Baskent and Keles, 2005; Costa *et al.*, 2009). While scheduling approaches have the potential to yield superior results, as they are optimized for each particular case, the feasibility of their implementation in the real world is very limited to landscapes where a full control over landscape management exists.

Simulation of optimal management solutions yielded, however, a high amount of temporal heterogeneity (i.e. instability), which is depicted in the large fluctuations of some objective values from year to year. This is normally not desired in the context of landscape management since large fluctuations of landscape properties or objectives may have severe impacts, for example, on biological populations that demand some stability (Verheyen *et al.*, 2004; Wintle *et al.*, 2005; Fischer and Lindenmayer, 2007; Keitt, 2009). Hence, in many cases, more than achieving given objectives at a given point in time or averaged values along a period, it is important to guarantee that those objective values do not fall outside a given interval anywhere in time (i.e. are evenly distributed in time); the so-called "even flow" objectives. Even flow objectives are traditionally used in forest management scheduling problems (Baskent and Keles, 2005; Costa *et al.*, 2009), and are an example of the practical importance that guaranteeing a low temporal heterogeneity has in some situations. In our case study, conservation objectives can be seen as even flow objectives - they ensure an "even habitat flow" for different species groups - by being required not to go below a certain level during the whole simulation period, in an attempt to minimize the likelihood of phenomena like extinction thresholds and cascades (Fischer and Lindenmayer, 2007; Keitt, 2009) of specialist species. Even though our scenarios were very simplified, it was possible to keep these objectives relatively stable, and this was due to the existence of landowner groups with different management frequencies. Hence, even flow objectives do not necessarily require to schedule in detail every management operation, being at least partly compatible with uncoordinated management.

Under our management scenarios, however, we could not fully separate temporal heterogeneity from spatial heterogeneity. All objectives except the conservation objectives showed a strong cyclical instability that was a consequence of the synchronization of owners with high management frequencies. Since high management frequencies were required to achieve spatial heterogeneity, having a long term spatially heterogeneous landscape that is relatively stable in its properties, for example, by avoiding temporary peaks in fire risk or periods of low habitat availability, could not be accomplished in these scenarios. This would probably require including more complex constraints to the problem formulation (e.g. neighbourhood constraints) leaving less variation at random, but such option would render the implementation in a multi-ownership landscape less feasible.

Integrating uncertainty

Problems that develop in the socio-ecological realm suffer in general from high uncertainty that is not easily controlled (Fischer *et al.*, 2009). Traditional analytical experimental ecology works on the basis of eliminating uncertainty when possible (Holling, 1998), whereas applied ecology should endeavour to incorporate it (Peterson *et al.*, 2003; Fischer *et al.*, 2009), thus increasing the chances of achieving the goals in highly uncertain systems (Halpern *et al.*, 2006). Not incorporating uncertainty in optimization problems may lead to sub-optimal solutions being selected because their fitness may be overestimated (McCarthy and Burgman, 1995; Kangas and Kangas, 1999). Further, exact solutions may not be robust enough to produce acceptable outcomes under the natural limits of variation of real-world variables under uncertainty (Regan *et al.*, 2005). Robustness estimation through *a posteriori* analyses to estimate uncertainty (González *et al.*, 2005) while ignoring it during optimization, may actually be providing just a local measure of robustness (Sniedovich, 2012) which may be insufficient because it does not account for the entire uncertainty space but only that centred on given solutions which may be biased.

We considered human behaviour as the major source of uncertainty in our study system, by purposefully introducing a stochastic component in management, hence, placing stochasticity within the optimization objective function. Uncertainty is not new to landscape management studies, many widespread landscape simulators and fire spread simulators are primarily based on stochasticity (McCarthy and Burgman, 1995; He *et al.*, 1999; see review in Keane *et al.*, 2004). However, optimization studies that include uncertainty during the process of optimization are scarce (Kennedy *et al.*, 2008; Rytwinski and Crowe, 2010). Many studies use deterministic objective functions (Turner *et al.*, 2002; González *et al.*, 2005; Holzkämper *et al.*, 2006; Bauer *et al.*, 2010) or, more recently, separate the stochastic component from the optimization process (Venema *et al.*, 2005; Gustafson *et al.*, 2006; González-Olabarria and Pukkala, 2011). In our study, uncertainty was introduced within optimization both in space - management operations were not spatially allocated - and in time - intervals between consecutive management operations were taken from a random distribution with known mean, so that optimized solutions were ready to cope with unpredictable deviations from what is desired. The idea can be summarized as "we do not know where and when the next management operation is going to take place, but we know that the resulting landscape pattern and consequent effects will meet our objectives along time". Hence, a given solution produces always different outcomes each time it is evaluated, that is, the objective function is subject to noise. Various solutions were proposed to overcome the problems related to "noisy fitness functions" (Jin and Branke, 2005). As Fitzpatrick and Grefenstette (1988) suggest, one simple way to cope with this is to increase population size of the optimization algorithm, since in a large population, the influence of noise in a given individual is compensated by the existence of more similar individuals - i.e., there is an "implicit averaging" (Jin and Branke, 2005) of the objective function values.

Under uncertainty, robust decision-making must have into account the whole possible range of variation of real-world variables in order to produce solutions that best perform under the worst scenario (Sniedovich, 2012). In this context, our optimization procedure, by having a large population and a large number of generations for relatively simple problems, sampled a wide range of random variation around each candidate solution. This, however, is still a very limited approach to handle uncertainty and represents one of the shortcomings to be futurely addressed (see general conclusions below). Further, other sources of uncertainty were not accounted for in our study, such as that related to the error present in the model of biomass accumulation used for fire risk estimation. Despite the fact that this represents an important source of uncertainty, relative comparisons between scenarios shall still be robust, since the error is consistent among scenarios (Larson *et al.*, 2004).

Conservation implications

One of the key challenges in modern forestry is to reconcile biodiversity with production activities (Eriksson and Hammer, 2006), which has led to the paradigm that forest management practices should emulate natural disturbances, in an attempt to minimize its impacts on ecosystems (Crow and Perera, 2004; Long, 2009) and approximate human-modified landscapes to natural landscapes. Our results, however, show that the best management practices that satisfy conservation and economic objectives are not similar to natural disturbance regimes, both at the local and landscape scale, hence raising the question of whether emulating natural disturbances is the most adequate option in these systems. Indeed, as Stephens *et al.* (2009) state, reverting back to a past condition may not always be desirable given the present and future context, or we may not even know how would the past natural communities look like (Niemelä, 1999), especially in regions that have had human influence for millennia such as the Euro-Mediterranean region (White and Jentsch, 2001; Bar Massada *et al.*, 2009). Further, natural disturbance regimes may not be socially acceptable because they often involve fire (Pausas *et al.*, 2008). Hence, rather than just seeking an ecosystem state that is not known by applying a management "black box" inspired in the supposed natural disturbance regime - the "coarse-filter approach" (Lehmkuhl *et al.*, 2007) -, this should be complemented with practical ecological knowledge, and goals should be adapted to the present and future context. A simulation-optimization approach is especially helpful in this respect (Lehmkuhl *et al.*, 2007).

Uncoordinated management in conservation

Uncoordinated management was shown to be effective in fulfilling a variety of contradictory objectives at local and landscape scale, despite the practical limitations that are inherent to it. Uncoordination means that a landowner's management decision is not dependent on his neighbours' decisions, which is likely the case of many multi-ownership landscapes and is a major limitation when biodiversity objectives are targeted (Gustafson *et al.*, 2007; Hartig and Drechsler, 2009). Approaches to deal with this situation include monetary incentives paid to landowners that take into account spatial criteria like agglomeration (Parkhurst *et al.*, 2002; Hartig and Drechsler, 2009; Lewis *et al.*, 2011). However, the existence of conservation funds for implementing such approach is unlikely in many cases. Still, assuming a total absence of monetary input towards conservation and total independence among landowners' actions, we showed that it was possible to fulfil spatial objectives aimed at conservation. It is, however, likely that this is not achievable in all cases, depending on the specific objectives. For example, maximizing heterogeneity may be compatible with uncoordination whereas minimizing fragmentation may not. In any case, the value of uncoordinated management as a landscape management tool should not be disregarded but explored in more detail, not only because heterogeneity is generally desirable (Lindenmayer *et al.*, 2006) but also because it may be the only tool in many landscapes.

So, what to do?

The key point that we aim to highlight from our results is the simplicity of the optimized management regimes. Although the algorithm was given enough flexibility to produce complex management solutions, the best options to manage landscape with the given objectives were generally simple, yet efficient. Some general guidelines can be devised, despite the limitations and oversimplifications associated with this study (see discussion in Chapter 5), but should be considered no more than tentative, as the limitations of some objectives we used in optimization might be causing some bias. Landscape heterogeneity was shown to be an important feature at all levels, and it could be maintained in the long term by splitting landowners in groups with contrasting management frequencies. In general, in order to keep fire risk low, about half of the landscape should be managed frequently. The remainder area should be either not managed or managed very occasionally (depending on the objective preferences), so to assure both heterogeneity and the maintenance of late successional vegetation, which is irreplaceable in terms of plant community structure and composition. Thus, a division of landowners in two groups, with about half of them managing frequently (every 3-9 years) and the other half not managing, seemed to be the main basic pattern arising from our results, with minor variations.

Conclusions and future prospects

Biodiversity conservation in dynamic landscapes has only recently started to be addressed in conservation studies (Pressey *et al.*, 2007; Drechsler *et al.*, 2009). The majority of studies under the framework of systematic conservation planning (Margules and Pressey, 2000) did not incorporate either the natural or human-induced dynamics (dynamic threats) that landscapes undergo, treating socio-ecological systems as static (Meir *et al.*, 2004; Holzkämper *et al.*, 2006; Drechsler *et al.*, 2009; Visconti *et al.*, 2010). Further, studies often assume that there are no impediments to implement conservation actions (Meir *et al.*, 2004; Visconti *et al.*, 2010) and that those can be implemented all at once, which is unrealistic (Faith *et al.*, 2003). Our work, despite its shortcomings (see below), tries to overcome these limitations: a) it explicitly integrates landscape dynamics, which are produced by management regimes and succession, within the optimization procedure and uses the whole output of simulations to evaluate the long term continued impacts of different management prescriptions; b) it incorporates implementation limitations in two ways - by integrating management uncertainty related to landowners' choices and by limiting total implementation cost to user-defined values and c) the whole framework is oriented towards adjusting existing landscape dynamics to achieve objectives cumulatively along time, rather than obtain desired results in one given moment. Our study is therefore in line with the conservation planning challenge of evaluating the long term impacts of different disturbance regimes arising from alternative management prescriptions (Pressey *et al.*, 2007).

The most important contribution of this study, hence, does not reside in the particular conclusions related to the study system, but in the different approach we took to a classical problem - at the methodological and at the conceptual level. Methodologically, the tight parallel combination between four modules that are usually separated (statistical modelling, simulation, landscape analysis and optimization) in a single module greatly increased the ability to adequately address the progressive effects of ongoing landscape dynamics on the desired objectives, and use this data during optimization. Conceptually, our approach was formulated under the idea that multiple owners acting independently from each other can produce, progressively, an outcome that satisfies landscape objectives, hence, regards landowners' actions, which are largely uncoordinated, as an opportunity rather than a limitation. It is, thus, a merging between a simplified agent-based framework (Valbuena *et al.*, 2009) and an optimization algorithm.

We recognize, however, that our approach can be explored much further, both in regards to improving the general framework, and also within the particular case of forest management towards reconciling biodiversity and fire risk reduction. A few examples of possible improvements follow:

- Include species occurrence and/or metapopulation and/or habitat suitability models (Wintle *et al.*, 2005; Hartig and Drechsler, 2009) within the simulation, in order to better estimate/predict the responses of biological populations to management along time;
- Substitute indirect indicators of fire risk by fire propagation models that evaluate fire risk by stochastic simulation of fire spread (Rytwinski and Crowe, 2010). This would obviate the limitations - and eventual biasing - of landscape surface metrics discussed in Chapter 5 by using a more realistic view of the influence of management on fire risk.
- Better cope with uncertainty within the optimization algorithm by, for example, resampling each candidate solution N times and using the worst outcomes as the ranking criterion (Sniedovich, 2012).

- Explore the potential of uncoordinated management in obtaining landscapes with more specific/complex patterns, for example, with aggregate habitat patterns or with minimum continuous area requirements. This would probably require to increase the complexity of the management rules/constraints used in the algorithm in such a way that they remain sufficiently simple to be followed by landowners, but effective enough to produce such patterns;

We highlight the importance of more thoroughly explore the last statement. If uncoordinated management has the power to act as stated, it would represent an important advance in conservation science, by emphasizing the role - and providing solutions - that local people may have in biodiversity conservation in human-dominated landscapes with little overhead effort, even when conservation funds are not available. The classical view that puts all conservation effort into well defined reserves should be seen as a complementary approach, which is indeed useful in cases where biodiversity values have a precise spatial location - and there are many -, but does not solve the problems when target species use landscape as a whole.

REFERENCES

Aparicio, A., Albaladejo, R.G., Olalla-Tárraga, M.A., Carrillo, L.F., Rodríguez, M.A., 2008. Dispersal potentials determine responses of woody plant species richness to environmental factors in fragmented Mediterranean landscapes. Forest Ecology and Management 255, 2894–2906.

Baeza, M.J., Valdecantos, A., Alloza, J.A., Vallejo, V.R., 2007. Human disturbance and environmental factors as drivers of long-term post-fire regeneration patterns in Mediterranean forests. Journal of Vegetation Science 18, 243–252.

Bar Massada, A., Carmel, Y., Koniak, G., Noy-Meir, I., 2009. The effects of disturbance based management on the dynamics of Mediterranean vegetation: A hierarchical and spatially explicit modeling approach. Ecological Modelling 220, 2525–2535.

Baskent, E.Z., Keles, S., 2005. Spatial forest planning: A review. Ecological Modelling 188, 145–173.

Bauer, D.M., Swallow, S.K., Paton, P.W.C., 2010. Cost-effective species conservation in exurban communities: A spatial analysis. Resource and Energy Economics 32, 180–202.

Bellemare, J., Motzkin, G., Foster, D.R., Forest, H., 2002. Legacies of the agricultural past in the forested present: an assessment of historical land-use effects on rich mesic forests. Journal of Biogeography 29, 1401–1420.

Bierzychudek, P., 1982. Life histories and demography of shade-tolerant temperate forest herbs: a review. New Phytologist 90, 757–776.

Bond, W.J., Keeley, J.E., 2005. Fire as a global “herbivore”: the ecology and evolution of flammable ecosystems. Trends in ecology & evolution 20, 387–94.

Bond, W.J., Midgley, J.J., 2001. Ecology of sprouting in woody plants: the persistence niche. Trends in ecology & evolution 16, 45–51.

Bonet, A., Pausas, J.G., 2004. Species richness and cover along a 60-year chronosequence in old-fields of southeastern Spain. Plant Ecology 174, 257–270.

Bradshaw, S.D., Dixon, K.W., Hopper, S.D., Lambers, H., Turner, S.R., 2011. Little evidence for fire-adapted plant traits in Mediterranean climate regions. Trends in plant science 16, 69–76.

Brunet, J., 2007. Plant colonization in heterogeneous landscapes: an 80-year perspective on restoration of broadleaved forest vegetation. Journal of Applied Ecology 44, 563–572.

Calvo, L., Tárrega, R., Luis-Calabuig, E., 2002. Secondary succession after perturbations in a shrubland community. Acta Oecologica 23, 393–404.

Calvo, L., Tárrega, R., Luis-Calabuig, E., Valbuena, L., Marcos, E., 2005. Recovery after Experimental Cutting and Burning in Three Shrub Communities with Different Dominant Species. Plant Ecology 180, 175–185.

Capitanio, R., Carcaillet, C., 2008. Post-fire Mediterranean vegetation dynamics and diversity: A discussion of succession models. Forest Ecology and Management 255, 431–439.

Chomitz, K.M., Fonseca, G.A.B., Alger, K., Stoms, D.M., Honzák, M., Landau, E.C., Thomas, T.S., Thomas, W.W., Davis, F., 2006. Viable Reserve Networks Arise From Individual Landholder Responses To Conservation Incentives. Ecology And Society 11, 40.

Clemente, A.S., Rego, F.C., Correia, O., 1996. Demographic patterns and productivity of post-fire regeneration in portuguese Mediterranean maquis. International Journal of Wildland Fire 6, 5–12.

Connell, J.H., Slatyer, R.O., 1977. Mechanisms of Succession in Natural Communities and Their Role in Community Stability and Organization. The American Naturalist 111, 1119–1144.

Costa, A., Oliveira, A.C., Vidas, F., Borges, J.G., 2009. An approach to cork oak forest management planning: a case study in southwestern Portugal. European Journal of Forest Research 129, 233–241.

Crow, T.R., Perera, A.H., 2004. Emulating natural landscape disturbance in forest management – an introduction. Landscape Ecology 19, 231–233.

Drechsler, M., Lourival, R., Possingham, H.P., 2009. Conservation planning for successional landscapes. Ecological Modelling 220, 438–450.

Dupouey, J.L., Dambrine, E., Laffite, J.D., Moares, C., 2002. Irreversible impact of past land use on forest soils and biodiversity. Ecology 83, 2978–2984.

Dölle, M., Schmidt, W., 2009. The relationship between soil seed bank, above-ground vegetation and disturbance intensity on old-field successional permanent plots. Applied Vegetation Science 12, 415–428.

Eriksson, S., Hammer, M., 2006. The challenge of combining timber production and biodiversity conservation for long-term ecosystem functioning—A case study of Swedish boreal forestry. Forest Ecology and Management 237, 208–217.

Faith, D.P., Carter, G., Cassis, G., Ferrier, S., Wilkie, L., 2003. Complementarity, biodiversity viability analysis, and policy-based algorithms for conservation. Environmental Science & Policy 6, 311–328.

Fischer, J., Lindenmayer, D.B., 2007. Landscape modification and habitat fragmentation: a synthesis. Global Ecology and Biogeography 16, 265–280.

Fischer, J., Peterson, G.D., Gardner, T. a, Gordon, L.J., Fazey, I., Elmqvist, T., Felton, A., Folke, C., Dovers, S., 2009. Integrating resilience thinking and optimisation for conservation. Trends in ecology & evolution 24, 549–54.

Fitzpatrick, J.M., Grefenstette, J.J., 1988. Genetic algorithms in noisy environments. Machine Learning 3, 101–120.

González, J.R., Palahí, M., Pukkala, T., 2005. Integrating Fire Risk Considerations in Forest Management Planning in Spain – A Landscape Level Perspective. Landscape Ecology 20, 957–970.

González-Olabarria, J.-R., Pukkala, T., 2011. Integrating fire risk considerations in landscape-level forest planning. Forest Ecology and Management 261, 278–287.

Grigulis, K., Lavorel, S., Davies, I.D., Dossantos, A., Lloret, F., Vila, M., 2005. Landscape-scale positive feedbacks between fire and expansion of the large tussock grass, Ampelodesmos mauritanica in Catalan shrublands. Global Change Biology 11, 1042–1053.

Gustafson, E.J., Lytle, D.E., Swaty, R., Loehle, C., 2007. Simulating the cumulative effects of multiple forest management strategies on landscape measures of forest sustainability. Landscape Ecology 22, 141–156.

Gustafson, E.J., Roberts, L.J., Leefers, L. a, 2006. Linking linear programming and spatial simulation models to predict landscape effects of forest management alternatives. Journal of environmental management 81, 339–50.

Halpern, B.S., Regan, H.M., Possingham, H.P., McCarthy, M. a, 2006. Accounting for uncertainty in marine reserve design. Ecology letters 9, 2–11; discussion 11–4.

Hartig, F., Drechsler, M., 2009. Smart spatial incentives for market-based conservation. Biological Conservation 142, 779–788.

He, H.S., Mladenoff, D.J., Crow, T.R., 1999. Object-oriented design of LANDIS, a spatially explicit and stochastic forest landscape model. Ecological Modelling 119, 1–19.

Hermy, M., Honnay, O., Firbank, L., Grashof-Bokdam, C., Lawesson, J.E., 1999. An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. Biological Conservation 91, 9–22.

Herrera, C.M., 1992. Historical effects and sorting processes as explanations for contemporary ecological patterns: character syndromes in mediterranean woody plants. The American Naturalist 140, 421–446.

Hobbs, R.J., Norton, D.A., 1996. Towards a conceptual framework for Restoration Ecology. Restoration Ecology 4, 93–110.

Hodgkinson, K.C., 1998. Sprouting success of shrubs after fire: height-dependent relationships for different strategies. Oecologia 115, 64–72.

Holling, C.S., 1998. Two cultures of Ecology. Conservation Ecology 2.

Holzkämper, A., Lausch, A., Seppelt, R., 2006. Optimizing landscape configuration to enhance habitat suitability for species with contrasting habitat requirements. Ecological Modelling 198, 277–292.

Houssard, C., Escarré, J., Romane, F., 1980. Development of species diversity in some Mediterranean plant communities. Vegetatio 43, 59–72.

Jin, Y., Branke, J., 2005. Evolutionary Optimization in Uncertain Environments - A Survey. IEEE Transactions on Evolutionary Computation 9, 303–317.

Josefsson, T., Hörnberg, G., Östlund, L., 2009. Long-Term Human Impact and Vegetation Changes in a Boreal Forest Reserve: Implications for the Use of Protected Areas as Ecological References. Ecosystems 12, 1017–1036.

Kangas, A.S., Kangas, J., 1999. Optimization bias in forest management planning solutions due to errors in forest variables. Silva Fennica 33, 303–315.

Keane, R.E., Cary, G.J., Davies, I.D., Flannigan, M.D., Gardner, R.H., Lavorel, S., Lenihan, J.M., Li, C., Rupp, T.S., 2004. A classification of landscape fire succession models: spatial simulations of fire and vegetation dynamics. Ecological Modelling 179, 3–27.

Keitt, T.H., 2009. Habitat conversion, extinction thresholds, and pollination services in agroecosystems. Ecological Applications 19, 1561–73.

Kennedy, M.C., Ford, E.D., Singleton, P., Finney, M., Agee, J.K., 2008. Informed multi-objective decision-making in environmental management using Pareto optimality. Journal of Applied Ecology 45, 181–192.

Larson, M. a., Thompson, F.R., Millspaugh, J.J., Dijak, W.D., Shifley, S.R., 2004. Linking population viability, habitat suitability, and landscape simulation models for conservation planning. Ecological Modelling 180, 103–118.

Lehmkuhl, J., Kennedy, M., Ford, E., Singleton, P., Gaines, W., Lind, R., 2007. Seeing the forest for the fuel: Integrating ecological values and fuels management. Forest Ecology and Management 246, 73–80.

Lewis, D.J., Plantinga, A.J., Nelson, E., Polasky, S., 2011. The efficiency of voluntary incentive policies for preventing biodiversity loss. Resource and Energy Economics 33, 192–211.

Lindenmayer, D.B., Franklin, J.F., Fischer, J., 2006. General management principles and a checklist of strategies to guide forest biodiversity conservation. Biological Conservation 131, 433–445.

Loehle, C., 2004. Applying landscape principles to fire hazard reduction. Forest Ecology and Management 198, 261–267.

Long, J.N., 2009. Emulating natural disturbance regimes as a basis for forest management: A North American view. Forest Ecology and Management 257, 1868–1873.

Malo, J.E., Suárez, F., 1995. Herbivorous mammals as seed dispersers in a Mediterranean dehesa. Oecologia 104, 246–255.

Margules, C.R., Pressey, R.L., 2000. Systematic conservation planning. Nature 405, 243–53.

McCarthy, M.A., Burgman, M.A., 1995. Coping with uncertainty in forest wildlife planning. Forest Ecology and Management 74, 23–36.

Meir, E., Andelman, S., Possingham, H.P., 2004. Does conservation planning matter in a dynamic and uncertain world? Ecology Letters 7, 615–622.

Niemelä, J., 1999. Management in relation to disturbance in the boreal forest. Forest Ecology and Management 115, 127–134.

Oheimb, G., Härdtle, W., 2009. Selection harvest in temperate deciduous forests: impact on herb layer richness and composition. Biodiversity and Conservation 18, 271–287.

O'Farrell, P.J., Anderson, P.M., 2010. Sustainable multifunctional landscapes: a review to implementation. Current Opinion in Environmental Sustainability 2, 59–65.

Parkhurst, G.M., Shogren, J.F., Bastian, C., Kivi, P., Donner, J., Smith, R.B.W., 2002. Agglomeration bonus: an incentive mechanism to reunite fragmented habitat for biodiversity conservation. Ecological Economics 41, 305–328.

Pausas, J.G., Carbó, E., Neus Caturla, R., Gil, J.M., Vallejo, R., 1999. Post-fire regeneration patterns in the eastern Iberian Peninsula. Acta Oecologica 20, 499–508.

Pausas, J.G., Llovet, J., Rodrigo, A., Vallejo, R., 2008. Are wildfires a disaster in the Mediterranean basin? – A review. International Journal of Wildland Fire 17, 713–723.

Peltzer, D.A., Bast, M.I., Wilson, S.D., Gerry, A.K., 2000. Plant diversity and tree responses following contrasting disturbances in boreal forest. Forest Ecology and Management 127, 191–203.

Peterken, G.F., Game, M., 1984. Historical factors affecting the number and distribution of vascular plant species in the woodlands of central Lincolnshire. Journal of Ecology 72, 155–182.

Peterson, G.D., Cumming, G.S., Carpenter, S.R., 2003. Scenario Planning: a Tool for Conservation in an Uncertain World. Conservation Biology 17, 358–366.

Potts, J.B., Marino, E., Stephens, S.L., 2010. Chaparral shrub recovery after fuel reduction: a comparison of prescribed fire and mastication techniques. Plant Ecology 210, 303–315.

Pressey, R.L., Cabeza, M., Watts, M.E., Cowling, R.M., Wilson, K. a, 2007. Conservation planning in a changing world. Trends in ecology & evolution 22, 583–92.

Pérez-Ramos, I.M., Zavala, M.A., Marañón, T., Díaz-Villa, M.D., Valladares, F., 2008. Dynamics of understorey herbaceous plant diversity following shrub clearing of cork oak forests: A five-year study. Forest Ecology and Management 255, 3242–3253.

Regan, H.M., Ben-Haim, Y., Langford, B., Wilson, W.G., Lundberg, P., Andelman, S.J., Burgman, M., 2005. Robust decision-making under severe uncertainty for conservation management. Ecological Applications2 15, 1471–1477.

Rodrigo, A., Retana, J., Picó, F.X., 2004. Direct regeneration is not the only response of Mediterranean forests to large fires. Ecology 85, 716–729.

Rundel, P.W., 1998. Landscape disturbance in Mediterranean-type ecosystems: an overview. In: Rundel, P.W., Montenegro, G., Jaksic, F.M. (Eds.), Landscape Disturbance and Biodiversity in Mediterranean-Type Ecosystems. Springer-Verlag, Berlin, pp. 3–22.

Rytwinski, A., Crowe, K.A., 2010. A simulation-optimization model for selecting the location of fuel-breaks to minimize expected losses from forest fires. Forest Ecology and Management 260, 1–11.

Ryu, S., Chen, J., Zheng, D., Lacroix, J., 2007. Relating surface fire spread to landscape structure: An application of FARSITE in a managed forest landscape. Landscape and Urban Planning 83, 275–283.

Santana, J., Porto, M., Gordinho, L., Reino, L., Beja, P., 2012. Long-term responses of Mediterranean birds to forest fuel management. Journal of Applied Ecology 49, 632–643.

Saura-Mas, S., Paula, S., Pausas, J.G., Lloret, F., 2010. Fuel loading and flammability in the Mediterranean Basin woody species with different post-fire regenerative strategies. International Journal of Wildland Fire 19, 783–794.

Schwilk, D.W., Caprio, A.C., 2011. Scaling from leaf traits to fire behaviour: community composition predicts fire severity in a temperate forest. Journal of Ecology 99, 970–980.

Sniedovich, M., 2012. Fooled by local robustness: an applied ecology perspective. Ecological Applications 22, 1421–1427.

Stephens, S.L., Moghaddas, J.J., Edminster, C., Fiedler, C.E., Haase, S., Harrington, M., Keeley, J.E., Knapp, E.E., McIver, J.D., Metlen, K., Skinner, C.N., Youngblood, A., 2009. Fire treatment effects on vegetation structure, fuels, and potential fire severity in western U.S. forests. Ecological Applications 19, 305–20.

Turner, B.J., Chikumbo, O., Davey, S.M., 2002. Optimisation modelling of sustainable forest management at the regional level: an Australian example. Ecological Modelling 153, 157–179.

Turner, M.G., Baker, W.L., Peterson, C.J., Peet, R.K., 1998. Factors Influencing Succession: Lessons from Large, Infrequent Natural Disturbances. Ecosystems 1, 511–523.

Tárrega, R., Luis-Calabuig, E., Valbuena, L., 2001. Eleven years of recovery dynamic after experimental burning and cutting in two Cistus communities. Acta Oecologica 22, 277–283.

Valbuena, D., Verburg, P.H., Bregt, A.K., Ligtenberg, A., 2009. An agent-based approach to model land-use change at a regional scale. Landscape Ecology 25, 185–199.

Valdecantos, A., Baeza, M.J., Vallejo, V.R., 2009. Vegetation Management for Promoting Ecosystem Resilience in Fire-Prone Mediterranean Shrublands. Restoration Ecology 17, 414–421.

Vallejo, V.R., Alloza, J.A., 1998. The restoration of burned lands: the case of eastern Spain. In: Moreno, J.M. (Ed.), Large Forest Fires. Backhuys, Leiden, NL, pp. 91–108.

Venema, H., Calamai, P., Fieguth, P., 2005. Forest structure optimization using evolutionary programming and landscape ecology metrics. European Journal of Operational Research 164, 423–439.

Verdasca, M.J., Leitão, A.S., Santana, J., Porto, M., Dias, S., Beja, P., 2012. Forest fuel management as a conservation tool for early successional species under agricultural abandonment: The case of Mediterranean butterflies. Biological Conservation 146, 14–23.

Verheyen, K., Honnay, O., Motzkin, G., Hermy, M., Foster, D.R., 2003. Response of forest plant species to land-use change: a life-history trait-based approach. Journal of Ecology 91, 563–577.

Verheyen, K., Vellend, M., Van Calster, H.V., Peterken, G.F., Hermy, M., 2004. Metapopulation dynamics in changing landscapes: a new spatially realistic model for forest plants. Ecology 85, 3302–3312.

Vesk, P.A., Westoby, M., 2004. Sprouting ability across diverse disturbances and vegetation types worldwide. Journal of Ecology 92, 310–320.

Visconti, P., Pressey, R.L., Segan, D.B., Wintle, B. a., 2010. Conservation planning with dynamic threats: The role of spatial design and priority setting for species' persistence. Biological Conservation 143, 756–767.

White, P.S., Jentsch, A., 2001. The Search for Generality in Studies of Disturbance and Ecosystem Dynamics. Progress in Botany 62.

Wiens, J.A., 2000. Ecological heterogeneity: an ontogeny of concepts and approaches. In: The Ecological Consequences of Heterogeneity. Blackwell Science, pp. 9–31.

Wintle, B.A., Bekessy, S.A., Venier, L.A., Pearce, J.L., Chisholm, R.A., 2005. Utility of Dynamic-Landscape Metapopulation Models for Sustainable Forest Management. Conservation Biology 19, 1930–1943.

Zavala, M.A., Espelta, J.M., Retana, J., 2000. Constraints and Trade-Offs in Mediterranean plant communities: the case of holm oak-Aleppo pine forests. The Botanical Review 66, 119–149.