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C. Puerta-Piñero, L. Brotons, L. Coll & J. R. González-Olabarría

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Valuing acorn dispersal and resprouting capacity ecological functions to ensure Mediterranean forest resilience after fire

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Abstract Ecological processes within forests provide vital ecosystem services to society, most of which depend on the persistence of tree cover that can be altered after the impact of a disturbance. The aim of the present study was to examine the role of seed dispersal and resprouting that mediate resilience to large fires and evaluate the economic costs that these ecological functions provide. We used field data from 412 plots of the Spanish National Forest Inventory providing information on pre- and post-fire conditions of Mediterranean *Pinus* spp. and *Quercus* spp.-dominated forests. Then, we determined the need for restoration (N_{Rest}) and estimated the minimum pre-fire densities needed to ensure adequate post-fire cover. Economic valuations were assessed through three different scenarios (Sc) of possible human-management actions aimed at ensuring proper post-fire tree cover: Sc. 1) a pre-fire management scenario evaluating the costs of planting *Quercus* spp. seedlings in the understory, mimicking the whole dispersal function; Sc. 2) a pre-fire scenario in which enrichment plantations increased the densities of natural oaks; and Sc. 3) a post-fire scenario where the restoration is done through planting pines within the burned area. Approximately 90% of the burned area (371 out of 412 plots) was able to recover after fire supporting the view that Mediterranean forests are resilient to fire. This resilience was primarily mediated by biotic seed dispersal and posterior resprouting of tree species. These ecological functions saved between 626 and 1,326 €/ha compared to the human-management actions. Ensuring key ecological processes within forests increases forest resilience and recovery after fire leading to a generally significant saving of economic resources. In a perspective of increased future impact of disturbances and decrease availability of economic resources for forest management, the implications of the present study can be far reaching and extended to other forest planning exercises.

Keywords Disturbance · Ecosystem services · *Garrulus glandarius* · *Pinus* spp · *Quercus* spp · Resprouters

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C. Puerta-Piñero · L. Brotons · L. Coll · J. R. González-Olabarría
Centre Tecnològic Forestal de Catalunya (CTFC), Crta. St. Llorenç de Morunys, km 2, 25280 Solsona, Spain

Present Address:
C. Puerta-Piñero (✉)
Smithsonian Tropical Research Institute, Unit 0948 DPO AA, Washington, DC 34002-0948, USA
e-mail: puertac@si.edu

Introduction

Understanding the social value of ecological functions and the services provided to society is now a key focus within the framework of policy makers and ecosystem managers (Daily 1997; Kremen 2005; Huberman 2009; Luck et al. 2009; Thompson et al. 2009). A commonly accepted definition of ecosystem services is the one proposed by the Millennium Ecosystem Assessment (MA 2005), defined simply as the benefits that people obtain from ecosystems. The MA further classifies ecosystem services into provisioning, regulating, supporting or cultural services (Huberman 2009). The attractiveness of the 'ecosystem services' concept is mostly due to its capacity to provide a link between management policies and environmental conservation strategies. Although the contribution of organisms to ecosystem dynamics is now generally well

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described, still little is known about the relationships between these processes within a social context (Kremen 2005; Kremen et al. 2007; Luck et al. 2009). Ecosystem services such as carbon storage, water depuration, ground cover undertaking, pest control, pollination or seed dispersal range from global to local impacts on society (Hougner et al. 2006; Naidoo and Ricketts 2006; Kremen 2005; Kremen et al. 2007). Therefore, it is vital to quantify the supply of ecological functions relative to social demands and assess the relative contributions of different species and their respective role (Kremen 2005; Huberman 2009).

Some recent efforts at understanding the linkages between biodiversity, ecosystem processes, ecosystem services and human well-being relate to the concept of resilience (Mäler et al. 2008; Huberman 2009). A system's resilience can be described as its capacity to absorb external shocks without suffering a posterior change in state, and its ability to then recover from a wide range of environmental stresses and disturbances (Holling 1973). Because of the different services forests provide to societies, forest resilience as well as the ecological factors determining that resilience become priority targets to ensure provision of those services in a rapidly changing context dominated by environmental disturbances (SCBD 2001; Thompson et al. 2009).

Critical services associated with forest systems are dependent on the persistence of an adequate tree cover providing the vertical structure allowing different ecological processes to occur. The possibility of recovering tree overstory after a disturbance allows the system to rapidly recover ecosystem services of high social value including better soil protection and water quality, carbon (CO_2) fixation, possibility of hunting or simply encompassing scenic beauty (Luck et al. 2009). Thus, understanding and managing ecological interactions, and ensuring that forests are resilient to environmental variations, are crucial to maintaining the delivery of services associated with forest ecosystems (Kremen et al. 2007; Mäler et al. 2008; Luck et al. 2009).

Fire often acts as a major driver of drastic changing land-use and vegetation dynamics. This situation is especially true in Mediterranean basin areas due to interactions between the historical changes in land uses (such as generalised land abandonment, increasing urbanisation) and recent climate changes involving increases in temperature and the number of future drought events (IPCC 2007; Merlo and Croitoru 2005). These circumstances lead to strong changes in fire regimes and increase the unpredictability of their ecological and social consequences (Rodrigo et al. 2004; Rodrigo 2006; Curt et al. 2009). Species dominating Mediterranean forests have often the capacity to recover rapidly from disturbance impacts such as fire (Merlo and Croitoru 2005). This capability is derived from different strategies varying amongst species including resprouting from unburned tissues or germinating seeds that remained viable in the soil or in the crowns (Broncano et al. 2005; Curt et al. 2009). However, in spite of this capability, Mediterranean forests often do not regenerate after fire or suffer strong transitions to different species composition, threatening the persistence of services associated to an adequate forest cover (Rodrigo et al. 2004; Merlo and Croitoru 2005). Therefore, acquiring information about the resilience or capacity of a forest to recover after fire is becoming a crucial target in making better forest management decisions (González et al. 2005a, b; Rodrigo 2006; Puettmann et al. 2008; Curt et al. 2009).

Our study system consisted of mixed oak-pine-dominated landscapes affected by fire, with seed disperser animal species capable of dispersing seeds before and after fire (Kremen et al. 2007; Castro et al. 2010; Curt et al. 2009). The system offers interesting traits for valuation of resilience as the focal species act both as keystone species and key service providers (Mäler et al. 2008; Luck et al. 2009). The aim of this article is to evaluate the resilience of the forest after fire disturbances, as well as the ecological drivers for this resilience (e.g. biotic seed dispersal and resprouting ability of tree species functions). We define forest resilience as the capacity of quickly recovering appropriate tree cover after a severe fire disturbance. To estimate forest resilience, we explicitly defined adequate minimum post-fire tree overstory in the landscape (i.e. forest resilience) and analysed the management costs needed to mimic, by human actions, such resilience scenarios otherwise obtained though ecological functions.

Three specific questions were addressed. First, to what extend are pine-dominated forests resilient to large fire disturbances? Second is resilience after fire mediated by *Quercus* seed dispersal and resprouting? Third, what is the economic value these ecological functions provide to society in terms of resilience insurance? In other words, we aim at assessing the relative economic value of substituting the ecological functions provided by the ecosystem (e.g. seed dispersal/resprouting) with actions required by anthropogenic management to ensure a similar result (Mäler et al. 2008).

Methods

Study site and species

The study area was located in a north-eastern region of Spain (41°45′–42°6′N; 1°38′–2°1′E, Fig. 1) and included landscape affected by two large fires (>65,000 ha in total) leading to widespread pine mortality and almost complete loss of tree cover occurring in 1994 and 1998 (Rodrigo et al. 2004). The area was dominated by *Pinus halepensis* and *Pinus nigra* forests stands prior to the fires (ICONA 1993; Fig. 1). After an intense disturbance such as a crown fire, *Pinus nigra* forests virtually do not regenerate naturally whilst *Pinus halepensis* forests can recover by germinating seeds from pirophyte cones (Rodrigo et al. 2004; Broncano et al. 2005). Crown fires pose a strong threat to forest associated services in the area by eliminating pine tree cover and promoting vegetation transition to shrublands and grasslands. On the other hand, and due to microclimatic and historical factors, these forests host a variable occurrence rate of *Quercus* spp. in their understory (mainly *Q. ilex* and *Q. faginea,* ICONA 1993; dispersed by jays (*Garrulus glandarius)* in the region, Gómez 2003; Pons and Pausas 2008; authors' personal observations). At any stage of its life, when *Quercus* spp. density is high in this pine forest understory, they have the ability to resprout from unburned tissues contributing to enhance tree persistence after fire (Espelta et al. 2003; Rodrigo et al. 2004; Curt et al. 2009). Therefore, they become an important element for the resilience by ensuring tree cover in these types of systems.

Sampling design and data analysis

To analyse forest resilience patterns in the area, we estimated tree cover densities from burned sites before and after fires and estimated the minimum pre-fire tree densities needed to ensure adequate post-fire tree cover due to posterior resprouting. In this study, an area with a minimum of 127 trees/ha after a fire was considered as being forested according to the criteria used by the National Forest Inventory (IFN in Spanish, ICONA 1993–2000) and its definition of minimum sapling cover necessary to becoming a proper forest (a minimum of 1 regenerated sapling between 2.5 and 7.5 cm diameter (ø) identified within the 5-m radius sub-plot) (DGCN 2005). Therefore, values below 127 trees/ha were considered as shrublands or grasslands, whilst values equal or above 127 saplings/ha were assumed to become forest, independently of environmental or topographic conditions.

We used field data obtained from plots of the Spanish IFN. The IFN consists of permanent plots distributed on a 1-km^2 grid, with a re-measurement interval of about 10 years. The plots have a mobile radius where the trees are recorded within different distances from the centre depending on their diameter. Within the minimum radius sub-plot (5 m), the densities of seedlings and saplings of every tree species were measured. In the study area, the second inventory (IFN2, ICONA 1993) took place during 1989–1990, whilst the third inventory (IFN3, DGCN 2005) was completed in 2000–2001. Because fires in the study area occurred in 1994 and 1998, the data from the plots included samples before and after the fires occurred. From all available inventory plots, we selected those including *Pinus halepensis* and *P. nigra* as predominant overstory

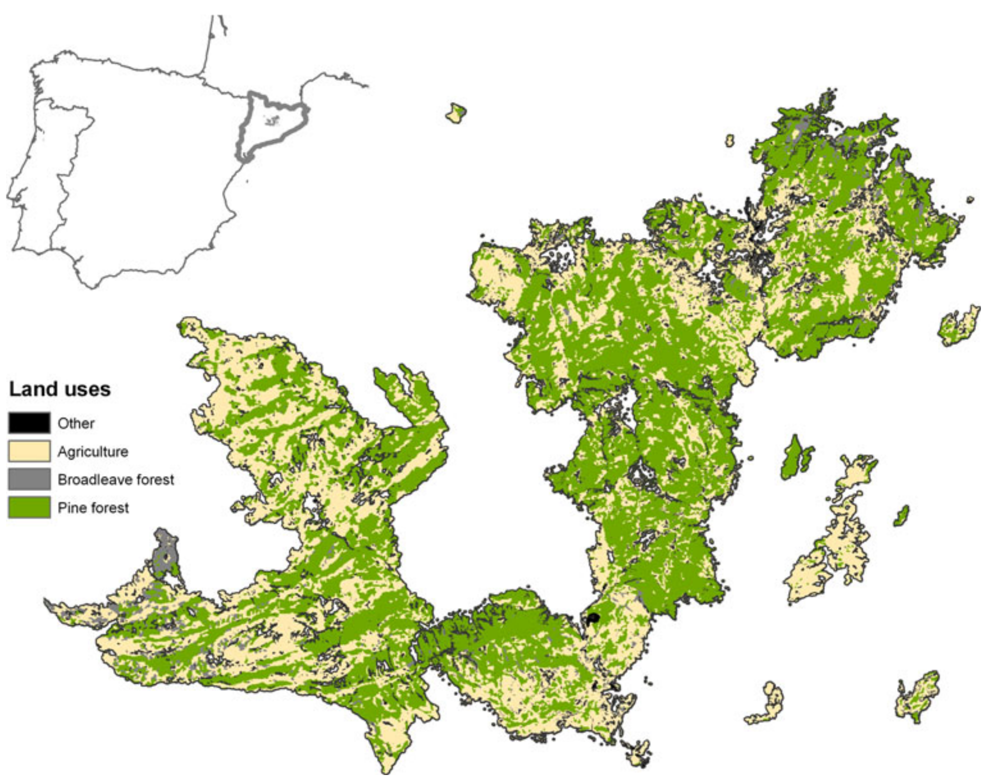

Fig. 1 Study sites. Geographical location of the study sites showing the main land uses before fire

that were located within the perimeters of forest fires that took place between the two inventories ($N = 412$ plots). To avoid confusion with resprouting roots and ensure that *Quercus* spp. in the plot where biotic dispersed, plots containing adults *Quercus* spp. were excluded. Thus, because the spatial location and distance to other adult *Quercus*, we are confident that the majority were established there naturally, due to biotic seed dispersal at anytime before the IFNs (Gómez 2003; Hougner et al. 2006). Within these plots, the number of small established trees with resprout ability in the 5-m radius subplots was measured (*Quercus* spp. of >2.5 and <7.5 cm of diameter, hereafter called saplings), and a semi-quantitative account of densities for four categories (0–3) for smaller resprouters (<2.5 cm ø, hereafter called seedlings) was also assessed: 0 = no seedlings/plot; 1 = 1–4 seedlings/plot; 2 = 5–15 seedlings/plot; and 3 ≥ 15 seedlings/plot). As the data comprises two periodical censuses of forests, we could further compare tree species composition and densities before and after the fire occurred.

To analyse the studied forest resilience after fire, we calculated the probabilities to find individual resprouters (either saplings or seedlings) before and after the fire occurred. Plot data were split following (1) the dominance of *P. halepensis* and *P. nigra* pine species and (2) the presence and absence of saplings (2.5–7.5 cm ø as described above) and presence and absence of seedlings (<2.5 cm ø) resprouters. The variable used to describe fire damage at the plot level was the proportion of dead trees after fire. All dead trees corresponded to the pre-fire dominant species in the plots (*P. halepensis* or *P. nigra*). This information was then used to estimate the restoration need (N_{Rest}) after fire for each plot. A post-fire restoration would be needed to ensure resilience ($N_{\mathrm{Rest}} = 1$) if minimum densities for a forest were not reached (127 trees/ha), and fire damage was equal or higher than 0.8 (as the threshold of intense fire damage in González et al. 2007); otherwise the plot would not require post-fire restoration and $N_{\mathrm{Rest}} = 0$.

Statistical models were then built using N_{Rest} as the dependent variable and pre-fire densities of saplings (D_{resp}) and presence of seedlings (PS_{resp}) as explanatory variables. We used a generalised linear model (GLZ) using a binomial distribution and logit link function (Eq. 1), as:

$$N_{\mathrm{Rest}} \sim D_{\mathrm{resp}} + PS_{\mathrm{resp}} + D_{\mathrm{resp}} * PS_{\mathrm{resp}}. \tag{1}$$

Potential resilience scenarios

Economic valuations, derived from activities carried out to ensure appropriate post-fire tree cover, were assessed through three different scenarios of human forest management: (1) a pre-fire management scenario (Sc. 1) in which we assumed no pre-fire seed dispersal; (2) a pre-fire management scenario in which enrichment of plantations with oaks was carried out increasing the densities of natural established oak saplings to further ensure complete recovering after fire (Sc. 2, Puettmann et al. 2008); and (3) a post-fire management scenario (Sc. 3), assuming no resprouting ability, in which the restoration of the tree cover is done after fire through planting the previous tree species (*P. nigra*) within the burned area (Espelta et al. 2003; Rodrigo et al. 2004). In Sc. 1 and Sc. 2, we estimated the costs of planting oak seedlings in the understory of the *Pinus nigra* stands, mimicking the dispersal function (Gómez 2003), at densities that would further ensure post-fire resprouting and recovering. All economic valuations were computed only for plots without proper tree cover (i.e. needing restoration) after fire, and excluding the areas previously populated by *P. halepensis*. For each scenario, we conservatively used the less expensive method without including potential replacement of seedlings due to post-planting losses.

Pre-fire management scenarios

To ensure post-fire resilience in the absence of natural seed dispersal, the pre-fire artificial management should include the costs of manually planting seedlings or saplings at densities that ensure post-fire tree recovering. Costs were computed relying on the assumption of full tree recovering after fire ($N_{\mathrm{Rest}} = 0$). These were based on nominal logistic inverse models to compute the mean, lower and upper limit of saplings/ha values at $\alpha = 0.05$ needed to ensure recovering after fire, considering the presence or absence of seedlings.

A more realistic probability of restoration was calculated for each individual plot using the probability for tree recovering after fire obtained from the N_{Rest} GLM formula. Thus, we considered the probabilities of restoration obtained from the previously adjusted model, fitting the following Eq. 2 to each individual plot:

$$P(N_{\mathrm{Rest}}) = \frac{1}{1 + \mathrm{Exp}\left\{-\left(0.85 + 0.01 \times D_{\mathrm{resp}} + PS_{\mathrm{resp}}\left\{\begin{smallmatrix} 0 \Rightarrow -1.30 \\ 1 \Rightarrow 1.30 \end{smallmatrix}\right\} + PS_{\mathrm{resp}}\left\{\begin{smallmatrix} 0 \Rightarrow (D_{\mathrm{resp}} - 219.72) \times (-0.002) \\ 1 \Rightarrow (D_{\mathrm{resp}} - 219.72) \times (0.002) \end{smallmatrix}\right.\right)\right.} \tag{2}$$

where $PS_{resp} = 1$ when there are seedlings present in the plot, and 0 otherwise. Individual probabilities were considered for each plot to compute the full valuation of planting before the fire to ensure proper tree cover after the fire. For this valuation, we used the value of $P(N_{Rest})$ at each plot multiplied by average cost/ha in euros of manually planting seedlings in the understory of *Pinus* forests to ensure adequate post-fire tree cover of 1,043 individuals/ha, as the mean density to ensure post-fire tree cover (see further results in Table 1). We conservatively[1] estimated the cost of planting seedlings of *Quercus* spp. in the understory of *Pinus* stands at 1,326 €/ha (Forestal Catalana 2007). Savings costs accrued by seed disperser's activity were computed for each plot using the replacement cost method (as in Hougner et al. 2006). This entails subtracting the restoration needs costs (R_{Costs}) from the potential costs of pre-fire managing by planting seedlings in the whole area (W_{Costs}). For the whole area valuation (Eq. 3), we assumed that each plot represented an area of 100 ha (ICONA 1993–2000).

$$\mathrm{Total}_{\mathrm{Saved\ costs}} = \sum_{i:j} W_{i\mathrm{Costs}}(/ha) - R_{i\mathrm{Costs}}(/ha) \qquad (3)$$

where W represent the total costs for the whole area (using the estimate of 1,326 €/ha) and R_i corresponds to the real costs considering restoration at each stand (computed using 1,326 €/ha* $P(N_{Rest})$.

Post-fire management scenario

First, we calculated the costs of reforesting the area burned that did not show adequate post-fire tree cover using a medium cost of 1,020 €/ha (Espelta et al. 2003; Forestal Catalana 2007). To calculate the costs saved on post-fire reforestation because of the resprouters' effect, we subtracted this value from the potential costs of restoring the whole study area.

Results

Ranges of resilience

The average pre-fire sapling density value (D_{resp}) needed to ensure proper recovering after fire when oak seedlings were present in the pine forest understory before fire was 820.9 individuals/ha (ind./ha), (99% confidence interval, 595.3–1,351.1 ind./ha) (See specific ranges of *Quercus* densities after fire for each plot in Fig. 2). Alternatively, in cases in which no seedlings were present in the understory before fire, the mean value of D_{resp} needed to ensure resilience was higher at 1,042.9 ind./ha, (99% confidence interval, 758.7–1,709.2 ind./ha).

Table 1 Results of the GLZ analysing the necessity of post-fire restoration in relation to density of saplings (D_{resp}) and presence (or absence) of seedlings (PS_{resp})

	χ^2	*P*-value
D_{resp}	69.83	0.04
PS_{resp}	4.22	<0.0001
$D*PS$	0.22	0.64

Resilience of the forest after fire

Before the fire, 335 plots (81.31% of the total) presented already established *Quercus* spp. individuals (saplings and seedlings in, respectively, 48.66 and 51.34% of the plots) (Fig. 3).

According to the observed post-fire responses in our study area, only 60 of the measured plots (representing 14.56% of the total number of plots) would require restoration operations because the availability of oaks to persist in the understory of pine forest after fire impact (showed in Fig. 3 as the sum of $*N_{Rest} = 0$ and $N_{Rest} = 1$). Furthermore, considering that areas previously stocked with pine species (*P. halepensis,* on the left of Fig. 3, $*N_{ref} = 0$), usually regenerates after fire (see Rodrigo et al. 2004), the number of plots needing restoration after fire to ensure proper tree cover decreases to 29 out of 243 (shown in black in Fig. 2 and right side of Fig. 3), corresponding to 11.93% of total plots previously dominated by *P. nigra*.

Variability in post-fire tree cover

Restoration need after fire (N_{Rest}) depended on pre-fire sapling density (D_{resp}) and the presence of seedlings (PS_{resp}) before fire but not on the interaction of the sapling density and the presence of seedlings ($D_{resp}*PS_{resp}$) (Table 1). Thus, plots with higher sapling densities or the presence of seedlings in the pine understory recovered their tree cover better after fire (see Fig. 2 for visually see which areas recover after fire and which ones need restoration). The full model explained 34% ($P < 0.0001$) of the total variance.

[1] Using the cheapest techniques available and without considering extra potential costs of seedlings replacement following post-planting failures caused by environmental factors from Catalonian public forest enterprise fares.

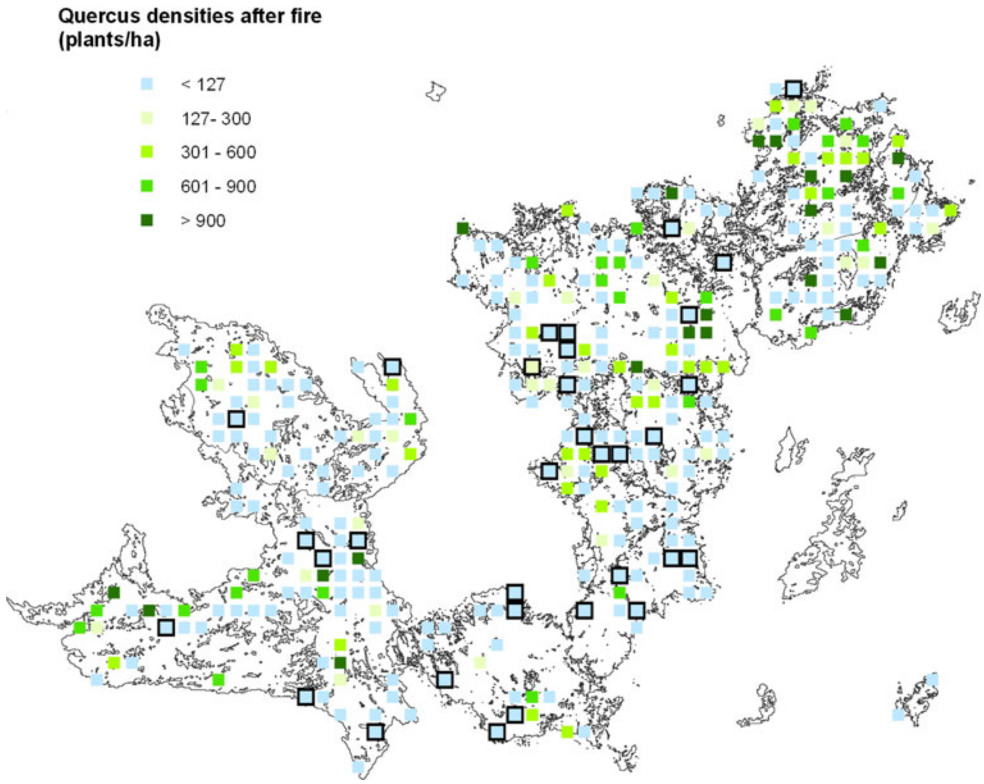

Fig. 2 Post-fire resprouters densities. Picture shows the ranges of post-fire densities of *Quercus* spp. *Squares* with a *black border* correspond to areas with ≥80% of the trees damaged after the fire and present low post-fire *Quercus* densities. Therefore, correspond to areas that would need post-fire restoration ($N_{\mathrm{Rest}} = 1$, see methods)

Economic valuation of resilience management scenarios

Scenario 1: Pre-fire management assuming no seed dispersal before fire

Planting oak seedlings before fire to ensure post-fire tree recovery was considered necessary in 243 plots (an equivalent of $2.43 * 10^4$ ha of total area). The management costs to obtain a minimum planting density to ensure post-fire resprouting and further tree cover was estimated at 1,326 €/ha (i.e. planting all the seedlings to ensure posterior recovering, See Methods, Forestal Catalana 2007). Carrying out those management practices to compensate for the absence of the seed dispersal function could thus, add up to 32.22 millions of € for the whole study area (Tables 2 and 3).

Scenario 2: Pre-fire management enrichment complementing the natural density of oaks

Considering the existence of natural established saplings and seedlings, the costs of carrying out enrichment practices to ensure enough pre-fire sapling densities for an adequate tree recovery after the fire (i.e., $N_{\mathrm{Rest}} = 0$) ranged between 0 and 699.42 €/ha (calculated for each individual plot using $P(N_{\mathrm{Rest}}) * 1{,}326$ €/ha, Table 2). The total costs of adding supplementary seedlings for ensuring adequate post-fire tree recovery for the whole area, only for stands with previous P. *nigra*, ($N = 243$ plots $\sim 2.43 * 10^4$ ha of total area) would be 41,485.19 €. In other words, the ecological functions of seed dispersal and resprouting ability could save between 626.58 and 1,326.00 €/ha, depending on the plot, compared to the artificial pre-fire management cost, (1,326 €/ha, Scenario 1). The total savings for the whole study area could reach 280,732.81 €, a considerable reduction in comparison with scenario 1 in which already existing, naturally dispersed *Quercus* individuals were not included (Table 3).

Scenario 3: Post-fire management assuming no resprouting

This will imply a potential post-fire management action by substituting the resprouting ability. In this valuation, those plots showing no tree cover after fire for lack of resprouting were excluded ($n = 41$). Thus, including the costs of planting the previous vegetation (*Pinus nigra*) after fire (1,020 €/ha, Forestal Catalana 2007) for the whole area (202 plots $\sim 2.02 * 10^4$ ha of total area) could reach up to 20.60 millions of € (Table 3).

Discussion

Mediterranean tree species are often adapted to harsh environmental conditions and are historically resilient to

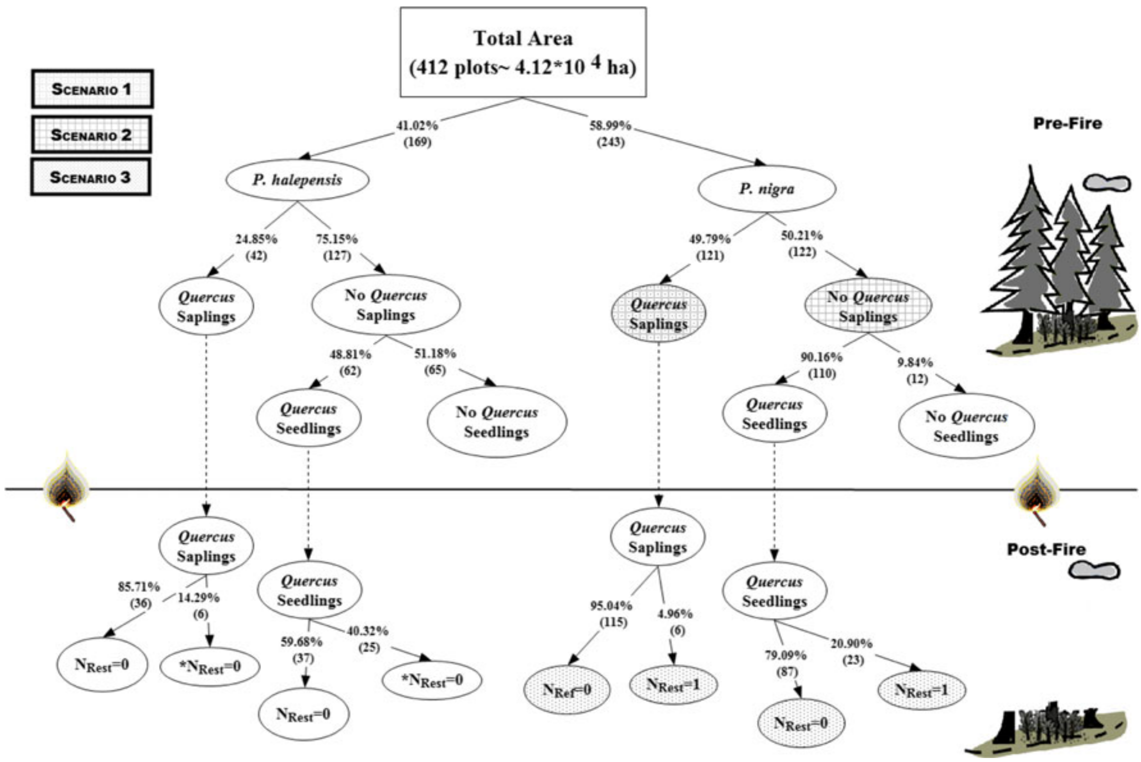

Fig. 3 Forest resilience after fire. Diagram showing the transitions before and after fire of pre-fire pine forested plots. Plots are split into presence or absence of resprouters (*Quercus* spp.) sapling and seedling in their understory. Percentage between levels indicates the per cent of the previous step that correspond to the next level. Numbers in brackets correspond to the number of plots with the target final value. The post-fire restoration need ($N_{Rest} = 1$) is defined a posteriori for those plots having <127 trees/ha (see methods) and fire damage ≥80% of the pre-fire trees in the plot. $*N_{Rest}$ corresponds to post-fire plots where no *Quercus* but *Pinus halepensis* saplings/seedlings were established

Table 2 Economic estimates based on the probabilities of restoration need

$P(N_{Rest} = 0)$	$P(N_{Rest} = 1)$	N plots[a]	Σ R_{Cost}/ha	Σ Saving/ha
0.47	0.53	12	8,393.04	7,518.90
0.60	0.40	5	2,634.74	3,995.25
0.61	0.39	1	522.93	803.07
0.72	0.28	5	1,851.78	4,778.22
0.81	0.19	6	1,486.12	6,469.88
0.82	0.18	2	485.18	2,166.82
0.86	0.14	110	20,687.70	125,172.30
0.88	0.12	7	1,109.51	8,172.49
0.92	0.08	2	201.56	2,450.44
0.93	0.07	3	292.43	3,685.57
0.94	0.06	35	2,828.44	43,581.58
0.95	0.05	1	66.966	1,259.03
0.96	0.04	3	178.057	3,799.94
0.97	0.03	10	341.65	12,918.37
0.98	0.02	8	236.13	10,371.85
0.99	0.01	10	121.82	13,138.19
1.00	0.00	23	47.35	30,450.65

Columns indicate the probabilities of not needing and needing restoration, and the sum of the costs and savings compared to the estimate of 1,326 €/ha and based on individual probabilities at each plot

[a] Each plot represent an area of 100 ha as the IFN points out in its sampling design (see Methods)

disturbances (Rodrigo et al. 2004; Thompson et al. 2009). Our results support this view. Most burned forests recovered their tree cover after a major fire impact but in some cases that resulted in a change in dominant tree species. The observed changes in species dominance after the disturbance agreed with those previously described in other

Table 3 Economic global evaluation of each hypothetical human-management scenario

Scenario	Cost/Ha (€/ha)	Plots[a]	Costs to ensure resilience (millions €)
Pre-fire oak plantation (Sc. 1)	1,326	243	32.22
Pre-fire oak enrichment (Sc. 2)	0–699	243	0.04
Post-Fire pine reforestation (Sc. 3)	1,020	202	20.60

[a] Each plot represent an area of 100 ha as the IFN points out in its sampling design (see Methods)

studies (see references in Espelta et al. 2003; Rodrigo et al. 2004; Broncano et al. 2005). Therefore, changes in climate and/or land uses could significantly affect not only the species composition but also the biological functions of this forests type. The final outcomes under expected future scenarios will depend on, amongst other things, changes in fire regimes and forest management activities (see references in Thompson et al. 2009; Merlo and Croitoru 2005). For example, shorter fire occurrence intervals will be particularly harsh on pines because it would not allow them to reach their reproductive stage (Rodrigo et al. 2004).

The resilience of forests after fire was mediated by a combination of concatenated ecological functions of biotic seed dispersal and posterior resprouting ability of seed-dispersed tree species. In our system, the European jay, *Garrulus glandarius,* naturally disperses the *Quercus* spp. acorns into *Pinus* spp. forests stands (Gómez 2003; Hougner et al. 2006). Jays move and cache a huge amount of acorns during the fall for consumption during the winter (Gómez 2003). Interestingly, they tend to cache the acorns in specific areas that are especially good for the survival and growth of the *Quercus* seedlings (Gómez et al. 2004; Puerta-Piñero et al. 2007). This situation leads to a well-established seedling and sapling bank under pines overstory, which creates a forest with large number of tree species (Thompson et al. 2009). This higher number of species before the fire contributes itself to a significant role by enhanced biodiversity and number of ecological functions within these mixed stands (Hooper et al. 2005). Therefore, when fire occurs, oaks are able to resprout, thus conferring to the forest the ability of rapidly recover the tree overstory and ground cover (Rodrigo et al. 2004; Broncano et al. 2005).

In addition, enhanced ecosystem resilience ensures the provision of goods and services to society. The costs for assuring resilience because the presence of resprouting species was considerably lower than those reported for other species of trees (Espelta et al. 2003). The densities of saplings before fire to ensure post-fire recovering went from one-third (595–1,042 ind./ha) to three quarters (1,100–1,600 ind./ha) of the plant densities commonly used for reforestation purposes after disturbances (Pemán and a Navarro-Cerrillo 1998). Under these conditions, the values of both seed dispersal and resprouting ability are of great importance to society in terms of economic savings. The total estimated costs for a human-assisted seed dispersal scenario (Sc. 1) were more than 775 times (costs Sc. 1/costs Sc. 2) the estimated costs associated with a natural scenario sustained by ecological functions (Sc. 2). By contrast, without the capacity of the tree species to resprout after fire, the costs borne by society could be more than 495 times higher than under the natural situation (costs Sc. 3/costs Sc. 2). Taking into account both ecological functions (seed dispersal and resprouting) simultaneously, the savings from maintaining these mixed *Pinus-Quercus* forests could be between half and the total costs of before fire managing actions to ensure forest cover resilience. Obviously, our economic valuation was rather conservative as it only takes into account the economic implications of restoring a predefined vegetation cover and, for example, do not consider management implications associated to dominant species shifts. The main take home message derived from our results for decision makers is that ensuring key ecological processes within forests increase forest resilience and recovery after a disturbance like fire leading to a generally significant saving of economic resources. In a perspective of increased future impacts of disturbances and decrease availability of economic resources for forest management, the implications of the present study can be far reaching and extended to other forest planning exercises.

In the present context of rapid environmental change, protection and restoration of biodiversity elements contribute to maintenance of the mixed *Pinus-Quercus* Mediterranean-type forests and their ongoing capacity to quickly recover from disturbances (SCBD 2001; González et al. 2005a; Hooper et al. 2005; Thompson et al. 2009). Although our study includes a Mediterranean system containing a few key species, we believe that our results are straightforward and easily transfer to other systems incorporating different species and disturbances. However, it is clear that forest resilience can be overcome and that not all forest types or tree species recover equally well to all forms and combinations of stressors (Luck et al. 2009). Important elements of the system, for example, the case of jays dispersing acorns in our study, should be incorporated into silvicultural plans. In the Mediterranean Basin, important changes in fire regimes are expected in many areas in response to climate warming (Thomson et al., 2009). In these systems, particular care must be taken to maintain those ecological functions that strengthen the resilience of forests: dispersion and development of resprouting species. Management actions aiming at improving the growth conditions of *Quercus* species developing in the understory (e.g. creating a diverse range of irradiance (Gómez-Aparicio et al. 2009; González-Moreno et al. 2011)) or still promoting enrichment plantations of conifer stands with resprouting species (Prévosto et al. 2011) could be envisaged.

Overall, as stated by Puettmann et al. (2008), new silvicultural tools are needed to reinforce the maintenance of the heterogeneity in ecosystem structure, composition and function (SCBD 2001). Modelling the impact of future land-use scenarios on service provision and the economic value of forests under different alternatives to optimise the allocation of economic resources is the forthcoming challenge (Thompson et al. 2009).

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