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Effects of different site preparation treatments on species diversity, composition and plant traits in *Pinus halepensis* woodlands.

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Abstract

Biodiversity maintenance is a key component of Mediterranean forest management, yet studies on the effects of silvicultural treatments on plant diversity are scarce. Our experiment assessed the impact of five different site preparation treatments on the composition, diversity, ecological traits (life form, pollination mode, leaf morphology, seed dispersal mode), indicator values (shade tolerance, nutrients demand) of the understory vegetation in a mature thinned *Pinus halepensis* stand in southern France. The treatments — chopping, chopping followed by scarification in one or two directions, prescribed burning, control — were replicated four times and applied on a total of 40 plots. Vegetation relevés were performed on each plot the first, second and fourth year following treatment applications. Plant diversity, measured by the species richness or Shannon's index, increased in the non-control treatment plots in the first year but then decreased through time. Vegetation composition differed between treatments, with the chopping treatment exhibiting composition and ecological trait values more comparable to those of control plots than the other treatments. The burning and scarification treatments led to higher abundance of therophytes, plants with malacophyllous leaves and insect-pollinated plants, and shade-intolerant and nutrient- demanding species.
However, these changes were transient in time, the shade-intolerant species remained abundant but the ruderal species decreased while the ligneous species increased indicating a gradual return to a forest vegetation composition. For the Mediterranean area, most of the findings were similar to those in temperate forests subjected to the same site preparation treatments.

Key words: sustainable management, functional traits, plant diversity, Mediterranean forest, *Pinus halepensis*,

Introduction

Mediterranean areas are biodiversity hotspots due to the wide range of climatic and edaphic conditions and anthropogenic disturbances (Pons and Quézel 1985; Médail and Quézel 1999). Natural woodlands represent a large part of the biodiversity reservoir, and forest management can be used to assure compatibility between timber production, biodiversity maintenance and recreational value (Kint 2005).

Aleppo pine (*Pinus halepensis* Mill) woodlands are very extensive and this exclusively Mediterranean conifer covers 250.000 ha in Southern France and 2.5 million ha across the Mediterranean Basin (Quézel 2000). The extensive cover of this species is due to its ability to withstand drought, its edaphic plasticity, and its ability to colonize land after agricultural abandonment and to reproduce in post-fire conditions (Ne'eman et al. 2004). Despite their extension, Aleppo pine woodlands are seldom managed, mainly for economic reasons, and there have been few relevant studies on the effects of silvicultural and site preparation treatments on biodiversity (but see De Las Heras et al. 2004; Torras and Saura 2008; Moya et al. 2009). However, more active forest management is needed to mitigate the impact of climate change. Possible management activities could include thinning to reduce competition among trees for water, diversifying and regenerating the stands and site preparation methods for stand regeneration (Lindner et al. 2008; Resco de Dios et al. 2007). The compatibility of such management operations with biodiversity conservation is therefore a critical challenge in order to maintain timber production and other aspects of the ecological value of the woodlands (Eriksson and Hammer 2006). In fact, while some studies have reported that forest management may have a detrimental effect on plant diversity (Roberts and Gilliam 1995), others have reported zero or even positive effects (e.g. Battles et al. 2001; Ramovs and Roberts 2005, Newmaster et al. 2007; Wang and Chen 2010). The contrasting influences of the disturbances caused by forestry operations on species diversity can be explained by the frequency, intensity and nature of these disturbances. On one hand, disturbances can increase species diversity by lowering the abundance of some widespread species, thus enabling other successional species to be established, and by encouraging environmental heterogeneity which in turn enhances specialization and resource partitioning (Grubb 1977; Tilman and Pacala 1993). On the other hand, disturbances can favor some expanding species to the detriment of other non-disturbance-adapted species, thus leading to an overall decrease in plant diversity (Freedman et al. 1994). According to the intermediate-disturbance hypothesis (Huston 1994), diversity is expected to peak at intermediate disturbance levels and then decline (Roberts and Gilliam 1995). This theory has been extensively studied in temperate and boreal forest ecosystems (e.g. Battles et al. 2001; Widenfalk and Weslien 2009), but not in managed Mediterranean forests.

In this context, our study was designed to assess the effects of different site preparation treatments applied in a mature thinned Aleppo pine stand (to enhance regeneration) on vegetation composition and diversity. We measured the vegetation response over four years following the treatments in order to establish the influence of the treatments on vegetation over time. To gain deeper insight into vegetation response, we also analyzed the changes in functional traits such as life form, type of pollination, leaf morphology, mode of dispersal, and in indicator values for light and nutrient regime. More specifically, the study addresses two main questions:

1- How does species composition and diversity vary between treatments and over time?
2- How do the functional traits and indicator values characterizing light and nutrient availability change between the treatments and over time?

Materials and methods

Study site

The study was set up in Southern France (43°54'01"- 4°44'55"), 80 km north-west of Marseille, on mature Aleppo pine natural woodland (altitude 105 m). The climate is meso-Mediterranean, with annual mean temperature of 14°C and annual mean rainfall of 689 mm. Soils are weakly developed lime soils, composed of an organic first layer (5-10 cm), an alteritic second layer of variable depth (10-40 cm) and calcareous bedrock. The general topography is a north-facing gentle slope. The combined effects of slope and soil depth variation lead to fluctuating soil fertility at the local scale (1m).

Before treatments, the stand comprised a dominant *Pinus halepensis* tree layer with scattered *Quercus ilex* trees in the subcanopy layer, a well-developed shrub layer dominated by *Buxus sempervirens*, *Quercus coccifera* and *Viburnum tinus*, and a sparse ground layer dominated by *Brachypodium retusum*. The stand was heavily thinned (regeneration cut) during winter 2004, leaving a basal area of 12 m^2/ha (initial basal area 20 m^2/ha) and a density of 210 trees/ha (initial density 410 trees/ha).

Treatments and experimental design

Soil and vegetation treatments were applied in winter and spring 2005. They were originally designed to enhance pine seedling establishment as soil or vegetation treatments were usually not used in the Mediterranean area to promote stand regeneration (Prévosto and Ripert, 2008). A randomized block design was set up inside the thinned stand using 5 soil and vegetation treatments consisting of:

i) Mechanical chopping of ground vegetation (CHOP): this treatment was performed using a bulldozer with a horizontal power-driven shaft equipped with hammers.

ii) Mechanical chopping followed by scarification in one direction (SCA1): scarification consisted in loosening forest floor and top soil to an approximate depth of 20 cm. It was performed with a set of heavy tines mounted at the rear of a forest tractor.

iii) Mechanical chopping followed by scarification in two perpendicular directions (SCA2).

iv) Prescribed fire (FIRE): after cutting the shrub vegetation burning was carried out by a specialized team from the French National Forestry Office. A backfire was lit with a drip torch in the upper part of the slope leaving fire to spread downward. A strip of 0.5m of bare soil was previously established along the plot perimeter for fire control.

v) Control (CONT): the control consisted of the thinned stand without any soil or vegetation treatments.

Each of these treatments was applied either with slash present or with slash removed and carried out between February and May 2005. Previous analyses (not shown) showed that slash presence or absence influenced vegetation cover in the fire treatment only, but had no influence on vegetation composition and species diversity regardless of treatments. Therefore, the rest of the study analyzes vegetation response to soil and vegetation treatments at plot level after combining subplots with and without slash. The treatments were replicated four times in four 34 m × 82 m blocks and applied on a total of forty 14 m × 14 m plots (8 plots/ treatment).

In this experiment, conducted in a single forest, we assumed that the main sources of variation were linked to the treatments and to the local site factors (mainly changes in soil and vegetation conditions) but not to the stand characteristics. Such an assumption can of course limit the generalization of the results beyond our study site and calls for additional experiments in other Mediterranean Aleppo pine forests.

Vegetation analysis

Vegetation relevés were completed in spring 2006, 2007 and 2009, i.e. 1, 2 and 4 years after treatment application, respectively. All vascular species were recorded for each plot and each species was assigned an abundance-dominance value according to an ordinal scale derived from Braun-Blanquet's procedure (1932):

1 = very few individuals (cover<1%), 2 = cover<5%, 3 = cover [5-25%[, 4 = cover [25-50%[, 5 = cover [50-75%[, 6 = cover [75-100%[.

In addition, herb cover, shrub cover and bare soil were visually evaluated on fifteen 1.0 m^2 subplots per plot at regular intervals along 5 transects.

Plant diversity was evaluated by computing three classical indices: Species richness, the Shannon-Wiener index, and the Evenness index.

The Shannon-Wiener index was calculated as:

$H' = -\sum p_i \ln p_i$

where p_i is the proportion of total cover of the *i* th species, for the computation the centers of the above classes were used (respectively: 0.5, 2.5, 15, 37.5, 62.5, 87.5)

Evenness was calculated as:

$E = H'/\ln S$,

where H' is the Shannon-Wiener index and S is the total number of species

H', E and S were calculated at plot level and averaged for each treatment.

Plant traits and plant indicator values were computed using presence/absence data as previous studies showed that abundance-weighted analyses of plant traits or indicator values showed little difference compared to studies using simple presence-absence data (Schaffers and Sýkora 2000; Dzwonko 2001, but see Cingolani et al. 2007). The traits are the Raunkiaer life-forms, pollination mode (entomogamy, anemogamy, autogamy), leaf morphology (graminoid type, malacophyllous = soft leaves with delicate tissue, microphyllous, sclerophyllous = firm stiff leaves with thickened epidermis and cuticula, miscellaneous), seed dispersal mode (anemochory, zoochory, barochory). We also established plant indicator values related to the light demand (shade-intolerant, shade-tolerant) and nutrients demand (oligotrophic, mesotrophic, eutrophic). All values were extracted from the Mediterranean BASECO database (Gachet et al. 2005). Each species of each plot was assigned to one category of the trait or indicator value. Frequency of each trait or indicator value category was then computed per plot across species. In a second step, the mean of the frequencies of all the plots included in the given treatments was calculated.

Statistical analysis

Vegetation composition variation between treatments was analyzed using correspondence analysis (CA) performed on a data matrix composed of the coefficients of abundance-dominance of the species - after discarding species whose occurrence was ≤ 3 - and all the plots of the first and the last year (2006,2009). Then, plots and the species were projected onto the CA factorial map using the two first axes. Calculations were run on ADE-4 software (Thioulouse et al. 1997).

Comparisons between treatments and between years for plant diversity indicators and ecological trait values were evaluated using ANOVA followed by a multiple range test (Tukey test). Variance normality and homogeneity were checked before each analysis, and when these conditions were not met, transformations were applied in order to approach the ANOVA assumptions.

Results

Vegetation composition

Results of the correspondence analysis (Fig.1) showed that the control plots gathered on the positive part of axe 1 and negative part of axe 2 were characterized by ligneous species and shade tolerant species such as *Juniperus oxycedrus, Staehelina dubia, Viburnum tinus, Teucrium polium* commonly found in clear Aleppo pine forests in this area. Plots subjected to the other treatments, in particular the fire treatment, were more widely spread across the ordination diagram and showed greater differences in species composition (see also Online Resources 1 and 2). They exhibited shade-intolerant and ruderal species more frequently encountered in fallow lands (e.g. *Sonchus tenerimus, Picris echioides, Senecio vulgaris, Crepis sancta)* on the negative part of axis 1. Projecting the 2009 plots on the 2006 factorial map (Fig.1B) indicated a general shift in plot vegetation with all treatments (although more limited for the control plots) from a vegetation typical of open and disturbed conditions (negative part of axis 1) towards a vegetation typical of clear forests (positive part of axis 1) but with shade-intolerant species (positive part of axis 2). In 2009, plots from the chopping treatment were closer to the control plots while plots subjected to the other treatments showed more variable trajectories.

Plant cover

Bare soil cover (Fig. 2) was lowest in control and chopping treatment and highest for fire treatment. Soil cover decreases sharply over time, from 13% in 2006 for all treatments pooled to 2% the last year ($P<0.001$). In contrast, shrub cover was highest with control treatment and lowest in the intense scarification treatment plots, whatever the year, increasing significantly from 2006 (17%) to 2009 (28%, $P<0.001$). Herb cover was at its minimum with control treatment, although except for the CHOP treatment, differences with other treatments were not always significant, depending on the year. Like shrub cover, herb cover increased strongly over the years, even with the control treatment, from 12% in 2006 to 32% in 2009 ($P<0.001$). It was noted that herb layer came to be dominated by *Brachypodium retusum*, which developed from 18% of total herb cover in 2006 to 60% in 2009 ($P<0.001$).

Plant diversity

Plant diversity indicators are shown in Fig. 3. Species richness was significantly lower in control plots than with the other treatments the first year. This tendency persisted in the following years, although differences were less marked between chopping treatment and controls in 2007 and 2009. The number of species decreased over time, from 35.9 species/plot in 2006 (all treatments pooled) to 32.1 species/plot in 2009 ($P=0.03$).

Results for Shannon and Evenness indices exhibited the same patterns of change as total number of species. These indices showed an even more marked reduction of differences among treatments in the last year, as only the fire treatment showed a significantly higher value than the control treatment. The general decrease over time was also more marked, from 4.03 in 2006 to 3.41 in 2009 ($P<0.001$) for the Shannon index and from 1.29 to 0.99 ($P<0.001$) for the Evenness index.

Plant traits

- Life form

We found no or only minor between-treatment differences in Chamaephytes and Hemicrophytes (Fig. 4), and only the Chamaephytes significantly increased from 2006 (15.5%) to 2009 (19.8%; $P<0.001$). Geophytes (not shown) were of low abundance (<3%) and decreased over years (1.8% in 2006 to 0.3% in 2009,

P<0.001). Phanerophytes were more abundant in controls and then with the chopping treatment than with the other treatments, whereas therophytes showed the reverse trend. Phanerophytes slightly increased over years (28% in 2006 to 31% in 2009, P=0.01) whereas therophytes sharply decreased (22% in 2006 to 13% in 2009).

- Pollination mode (see Online Resource 3)

Type of pollination is dominated by entomogames, although their abundance decreased with time (61% in 2006 to 52% in 2009, P<0.001). Entomogames were most abundant in the fire treatment and least abundant in the control treatment. In contrast, the anemogames showed a higher abundance in control treatment plot than with fire or scarification treatments - the chopping treatment being intermediate - but differences were only significant in 2009. Contrary to the entomogames, their abundance increased with time (22% in 2006 to 26% in 2009, P<0.001). Lastly, the autogames did not vary among treatments whatever the year, although their abundance increased with time (17% in 2006 to 22% in 2009, P<0.001).

- Leaf morphology (Online Resource 4)

Changes in leaf morphology types showed that abundance of graminoid form was only significantly different between the control and the fire treatments, and tended to increase with time (18% in 2006 to 20% in 2009, P=0.002).
Species with malacophyllous leaves were less abundant in control treatment plots compared to the fire and scarification treatments, the chopping treatment being intermediate, at least for the last year. The abundance of the malacophyllous species decreased with time (27% in 2006 to 22% in 2009, P<0.001).
Sclerophyllous–leaved species were more abundant in controls than with the other treatments, but the differences tended to decrease between treatments, as in the last year, only the control treatment significantly differed from the scarification treatments. Frequency of sclerophylls did not vary significantly over time (P=0.10).
Species with microphyllous leaves did not vary significantly between treatments, except in 2007, and their abundance remained stable over the different years.

<u>Indicator values</u>

- Shade tolerance

Shade-intolerant species were far more abundant than shade-tolerant species (Fig. 5), with mean percentages of 75% vs 25% for all treatments combined, and these proportions remained stable over the years (P=0.45). Variations in the frequencies of these species were more pronounced the year following treatment applications, whereas in 2007 and in 2009 the differences were only significant between the control treatment and the fire and scarification treatments.

- Nutrients

Oligotrophic species were much more abundant than eutrophic species, and significant differences between treatments were only found in 2006 between the control and the other treatments. However, for all treatments combined, oligotrophic species increased significantly from 66% in 2006 to 76% in 2009 (P<0.001). Eutrophic species showed similar patterns: significant differences only in 2006 between the control treatment -showing fewer eutrophic species - and the other treatments, and abundance decreasing sharply over the years (28% in 2006 to 18% in 2009, P<0.001).
Mesotrophic species were not abundant (<8% whatever the year or treatment) and did not vary between treatments or over the years (data not shown).

Discussion

Species diversity

Plant diversity, measured by species richness or Shannon index, increased in the treated plots but decreased over time. The disruption of the vegetation cover generated by the treatments had created favorable conditions for species to become established, increasing light resources for small herbs due to the shrub clearing, creating more safe sites for seeds to germinate and grow due to increased bare soil and lower competition, and probably also higher nutrient availability (Schumann et al. 2003; Decocq et al. 2004). However, the increase in diversity was only transient in time, as it decreased from the second year after treatment application. This pattern is classically observed in forests (Peltzer et al. 2000) and in different Mediterranean plant communities after disturbances. Studying the vegetation recovery of shrublands and Aleppo pine forests after fire, Trabaud and Lepart (1980) and Trabaud (1987) reported that floristic richness peaked between the 10th and 40th month post-disturbance, then declined and stabilized. Similarly, Kazanis and Arianoutsou (1996) noted on burned Aleppo pine stands in Greece that herbaceous taxa dominated the flora during the first four years post-fire, with species richness peaking the second year before decreasing thereafter. Pérez-Ramos et al. (2008), studying the impact of shrub clearing on species diversity in the understorey of cork oak forest in southern Spain, also noted that species richness in their open woodland site peaked one year after the treatment before substantially decreasing. Consistently with these studies, the increase in species richness reported here was largely due to therophytes, mainly the rapidly-spreading ruderals (e.g. *Sonchus sp., Picris echioides, Senecio vulgaris*) taking advantage of the favorable conditions produced by the treatments. With time, as resources become less abundant and competition with pre-existent species more severe, the opportunities for these plants to establish decreased, resulting in lower species richness. The treatments therefore produced fluctuations in resource availability, which is a key factor controlling a community's susceptibility to colonization (Davis et al. 2000), and offered a temporal 'window' (Gross 1980) for plant establishment, primarily benefiting small herbs.

Vegetation composition

Vegetation composition differed strongly between treatments, although the chopping treatment showed composition and plant traits values that were with time more comparable to the control than to the other treatments. Chopping, by only removing the aerial parts of pre-existing vegetation, was characterized by less profound disturbances than those induced by the fire and scarification treatments, which led to a much greater proportion of bare soil offering ruderal species favorable conditions to successfully establish either from the seed bank or from propagules brought from the outside. These changes in vegetation and soil cover also explain why pine recruitment was found to be higher with the fire and scarification treatments than with the control and chopping treatment in a previous study within the same experiment (Prévosto and Ripert, 2008).

We detected major fluctuations in vegetation composition with time in all treatments even if changes were more limited in the control. Changes in the control treatment could be explained by the high light availability due to the regeneration cut allowing shade intolerant species to establish as in the other treatments. The wide variations in vegetation composition that partially overrode the treatment effects were likely to have been induced by fluctuations in soil depth, soil stoniness, micro-topography and differences in initial floristic composition at plot level (Puerto and Rico 1997). The high fine-grain heterogeneity of the environment, commonly encountered in Mediterranean areas, has regularly been put forward to partly explain the

vegetation's response unrelated to treatments (e.g. Gómez-Aparicio et al. 2005; Pérez-Ramos et al. 2008). Despite this variability, the vegetation composition of the treatments generally converged over time to mirror the control treatment. This result illustrates the resilience of the Mediterranean vegetation, i.e. its capacity to return, in a relatively short time period, to the composition that was prevalent before the disturbances occurred (Perez-Ramos et al. 2008). This resilience can be explained by the high resprouting ability of shrubs, typical for most Mediterranean woody species (Canadell and López-Soria 1998). Some herbaceous plants are also highly resilient to fire (Vila-Cabrera et al. 2008) and other disturbances due to their efficient propagation strategies and their capacity to develop in stressful environments, particularly high irradiance and low water resources. This is the case for *Brachypodium retusum,* the dominant species of the herb layer in our study, for which cover increased rapidly with all treatments. *Brachypodium retusum* is known to play an important role in the recovery of Mediterranean ecosystems due to its rhizomatous below-ground system and its ability to compete with other species (De Luis et al. 2004; Clary et al. 2004).

Plant traits

The analysis of the changes in plant life-forms showed a greater abundance of therophytes in the fire and scarification treatment plots compared to the chopping or control treatment, whereas phanerophytes showed the reverse trend. As explained above, the more pronounced disturbances with the fire and scarification treatments favored the development of the many annual and ruderal species, as also recorded in other studies in the Mediterranean woodlands (De Las Heras et al. 2004; Gondard et al. 2007; Pérez-Ramos et al., 2008). This development was only transient in time, and the decline in therophytes was associated with an increase in phanerophytes and chamaephytes, many of which were resprouting plants.

The higher abundance of annual and ruderal plants can also be put forward to explain the differences in leaf morphology, with a greater abundance of plants with malacophyllous leaves and a lower abundance of plants with scleromorphic leaves in the fire and scarification treatments immediately after the disturbances.

The lower proportion of insect-pollinated plants in the control plots than with the other treatments is consistent with the lower floral richness also detected in the control (Potts et al. 2006), and can be explained in part by the higher abundance of wind-pollinated graminoid species (Daehler 1998).

The scarification and fire treatments produced a higher abundance of shade intolerant and eutrophic species, although the differences in eutrophic species were only significant in the year following treatment. The removal of the shrub layer with the chopping treatments or all the pre-existing vegetation layers with the other treatments led to greater light availability, favoring the establishment of new light-demanding species (Heinrichs and Schmidt 2009). The controlled fire was likely to induce greater nutrient availability, particularly nitrogen, but this effect is usually restricted to a relatively short period (< 1-2 years) following the fire event (see Carter and Foster, 2004 for a review). The scarification treatments may also have induced greater transient nutrient availability due to better decomposition and mineralization of the organic matter, as reported in previous studies (Smolander et al. 2000; Piirainen et al. 2007).

Conclusion

This study showed that different types of disturbances led to different vegetation composition patterns and a significant but transient increase in species richness and Shannon index, thus supporting the intermediate disturbance hypothesis. Changes were more pronounced in the fire and scarification treatment plots, which induced a

higher percentage of bare soil, than with the chopping treatment where vegetation composition remained closer to the control plots. Fire and scarification treatments were also shown to be the most effective treatments to promote pine recruitment (Prévosto and Ripert, 2008). Indeed, by freeing resources and reducing the importance of some monopolistic species, these treatments favored the emergence and the survival of pine seedlings and enabled at the same time the rapid establishment of shade-intolerant, more nutrient-demanding and ruderal species (Gilliam and Roberts, 1995; Battles et al. 2001). The resulting increase in species richness was however both transient and linked to opportunistic species and did not result in an improvement of the biodiversity of the forest. The decrease in ruderal species and the increase in ligneous species with time indicated a gradual return to the pre-treatment conditions although shade-intolerant species remained abundant. This resilience was largely due to the efficient vegetative reproduction system of most species (e.g. the resprouting capacity of most ligneous species) and their capacity to resist the severe environmental conditions prevailing in Mediterranean habitats.

In the absence of clear biodiversity conservation objectives, this study shows that various forestry treatments can be applied. In particular, prescribed fire and scarification treatments can be recommended to enhance pine recruitment as the changes they induce in vegetation composition and diversity are only transient. Our results on the impact of silvicultural treatments on vegetation changes are in line with those usually found in temperate areas. However, further studies are needed to know to what extent these findings can be applied to Allepo pine forests located in other sites and climatic conditions.

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References

Battles JJ, Shlisky AJ, Barrett RH, Heald RC, Allen-Diaz BH (2001) The effects of forest management on plant diversity in a Sierran conifer forest. For Ecol Manage 146:211-222

Braun-Blanquet J (1932) Plant sociology. The study of plant communities. McGraw Hill, New York, USA (reprint 1983, Koeltz, Koenigstein).

Canadell J, Lopez-Soria L (1998) Lignotuber reserves support regrowth following clipping of two Mediterranean shrubs. Funct Ecol 12:31-38

Carter MC, Foster CD (2004) Prescribed burning and productivity in southern pine forests: a review. For Ecol Manage 191: 93-109

Cingolani AM, Cabido M, Gurvich DE, Renison D, Díaz S (2007) Filtering processes in the assembly of plant communities: Are species presence and abundance driven by the same traits? J Veg Sci 18:911-920

Clary J, Savé R, Biel C, De Herralde F (2004) Water relations in competitive interactions of Mediterranean grasses and shrubs. Ann Appl Biol 144:149-155

Daehler CC (1998) The taxonomic distribution of invasive angiosperm plants: ecological insights and comparison to agricultural weeds. Biol Conserv 84:167-180

Davis A, Grime P, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invisibility. J Ecol 88:528-534

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

De Las Heras J, González-Ochoa A, López-Serrano F, Simarro ME (2004) Effects of silviculture treatments on vegetation after fire in *Pinus halepensis* Mill. woodlands (SE Spain). Ann For Sci 61:661-667

De Luis M, Raventós J, Cortina J, Gonzalez-Hidalgo JC, Sánchez JR (2004) Fire and torrential rainfall: effects on the perennial grass *Brachypodium retusum*. Plant Ecol 173: 225-232

Dzwonko Z (2001) Assessment of light and soil conditions in ancient and recent woodlands by Ellenberg indicator values. J Appl Ecol 38:942-951

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. For Ecol Manage 237:208-217

Freedman B, Woodley S, Loo J (1994) Forestry practices and biodiversity, with particular reference to the Maritime Province of eastern Canada. Environ Rev 2:33-77

Gachet S, Vela E, Tatoni T (2005) BASECO: a floristic and ecological database of Mediterranean French flora. Biodiv Conserv 14:1023-1034

Gómez-Aparicio L, Valladares F, Zamora R, Quero JL (2005) Response of tree seedlings to the abiotic heterogeneity generated by nurse shrubs: an experimental approach at different scales. Ecography 28:757-768

Gondard H, Santa Regina I, Salazar S, Peix A, Romane F (2007) Effect of forest management on plant species diversity in *Castanea sativa* stands in Salamanca (Spain) and the Cévennes (France). Sci Res Essays 2:62-70

Gross KL (1980) Colonization by *Verbascum Thapsus* (Mullein) of an old field in Michigan: experiments of the effects of vegetation. J Ecol 68:919-927

Grubb PJ (1977) The maintenance of species richness in plant communities: the importance of the regeneration niche. Biol Rev 52:107-145

Gilliam FS, Roberts MR (1995) Impacts of forest management on plant diversity. Ecol Appl 5:911-912

Heinrichs S, Schmidt W (2009) Short-term effects of selection and clear cutting on the shrub and herb layer vegetation during the conversion of even-aged Norway spruce stands into mixed stands. For Ecol Manage 258:667-678

Huston M (1994) Biological diversity: the coexistence of species on changing landscape. Cambridge University Press, New York.

Kazanis D, Arianoutsou M (1996) Vegetation composition in a post-fire succession gradient of *Pinus halepensis* forests in Attica, Greece. Int J Wildland Fire 6:83-91

Kint V (2005) Structural development in ageing temperate Scots pine stands. For Ecol Manage 214:237-250

Lindner M, Garcia-Gonzalo J, Kolström M, Green T, Reguera R, Maroschek M, Seidl R, Lexer MJ, Netherer S, Schopf A, Kremer A, Delzon S, Barbati A, Marchetti M, Corona P (2008) Impacts of climate change on European forests and options for adaptation. European Commission, Luxembourg, Belgium

Médail F, Quézel P (1999) Biodiversity hotspots in the Mediterranean Basin: setting global conservation priorities. Conserv Biol 13:1510-1513

Moya D, De Las Heras J, López-Serrano FR, Condes Q, Alberdi I (2009) Structural patterns and biodiversity in burned and managed Aleppo pine stands. Plant Ecol 200:217-228

Ne'eman G, Goubitz S, Nathan R (2004) Reproductive traits of *Pinus halepensis* in the light of fire- a critical review. Plant Ecol 171:69-79

Newmaster SG, Parker WC, Wayne Bell F, Paterson JM (2007) Effects of forest floor disturbances by mechanical site preparation on floristic diversity in a central Ontario clearcut. For Ecol Manage 246:196-207

Peltzer DA, Bast ML, Wilson SD, Gerry AK (2000) Plant diversity and tree responses following contrasting disturbances in boreal forest. For Ecol Manage 127:191-203

Puerto A, Rico M (1997) Soil depth as determinant of structural trends in Mediterranean grasslands with abundant slaty outcrops. Ekol Bratisl 16:3-16

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. For Ecol Manage 255:3242-3253

Piirainen S, Finér L, Mannerkoski H, Starr M (2007) Carbon, nitrogen and phosphorus leaching after site preparation at a boreal forest clear-cut area. For Ecol Manage 243: 10-18

Pons A, Quézel P (1985) The history of the flora and vegetation and past and present human disturbance in the Mediterranean region. In: Gómez-Campo C (ed) Plant Conservation in the Mediterranean Area, The Hague, Netherlands, pp. 25-43

Potts SG, Petanidou T, Roberts S, O'Toole C, Hulbert A, Willmer P (2006). Plant-pollinator biodiversity and pollination services in a complex Mediterranean landscape. Biol Conserv 129:519-529

Prévosto B, Ripert C (2008) Regeneration of *Pinus halepensis* stands after partial cutting in southern France: Impacts of different ground vegetation, soil and logging slash treatments. For Ecol Manage 256:2058-2064

Quézel P. (2000) Taxonomy and biogeography of Mediterranean pines (*Pinus halepensis* and *Pinus brutia*). In: Néeman G, Trabauds L (eds). Ecology, Biogeography and Management of *Pinus halepensis* and *P Brutia* Forest Ecosystems in the Mediterranean Basin. Backhuys Publishers, Leiden, pp 1-12

Ramovs BV, Roberts MR (2005) Response of plant functional groups within plantations and naturally regenerated forests in southern Brunswick, Canada. Can J For Res 35:1261-1276

Resco de Dios V, Fischer C, Colinas C (2007) Climate change effects on Mediterranean forests and preventive measures. New Forests 33:29-40

Roberts MR, Gilliam FS (1995) Patterns and mechanisms of plant diversity in forested ecosystems: implications for forest management. Ecol Appl 5:969-977

Schaffers AP, Sýkora K (2000) Reliability of Ellenberg indicator values for moisture, nitrogen and soil reaction: a comparison with field measurements. J Veg Sci 11:225-244

Schumann ME, White AS, Witham JW (2003) The effects of harvest-created gaps on plant species diversity, composition, and abundance in a Maine oak-pine forest. For Ecol Manage 176:543–561

Smolander A, Paavolainen L, Mälkönen E (2000) C and N transformation in forest soil after mounding for regeneration. For Ecol Manage 134: 17–28

Thioulouse J, Chessel D, Dolédec S, Olivier JM (1997) ADE-4: A multivariate analysis and graphical display software. Stat Computing 7: 75-83

Tilman D, Pacala S (1993) The maintenance of species richness in plant communities. In: Ricklefs RE, Schluter D (eds) Species diversity in ecological communities: historical and geographical perspectives. University of Chicago Press, Chicago, pp 13-25

Trabaud L (1987) Dynamics after fire of sclerophyllous plant communities in the Mediterranean basin. Ecol Medit 13: 25-37

Trabaud L, Lepart J (1980) Diversity and stability in garrigue ecosystems after fire. Vegetatio 43:49-57

Torras O, Saura S (2008) Effects of silvicultural treatments on forest biodiversity indicators in the Mediterranean. For Ecol Manage 255:3322-3330

Vila-Cabrera A, Saura-Mas S, Lloret F (2008) Effects of fire frequency on species composition in a Mediterranean shrubland. Ecoscience 15:519-528

Wang S, Chen HYH (2010) Diversity of northern plantations peaks at intermediate management intensity. For Ecol Manage 259:360-366

Widenfalk O, Weslien J (2009) Plant species richness in managed boreal forests — Effects of stand succession and thinning. For Ecol Manage 257:1386-1394

Figure captions

Fig. 1. Factorial maps of the correspondence analysis (inertia of the first horizontal factorial axis: 11.43%, inertia of the second vertical axis: 7.51%) A) Projection of the plant species (names of the main species indicated) B) Projection of the plots. Arrows indicate the trajectories from the 2006 plots to the 2009 plots. Symbols are as follows: (●) Control, (○) Chopping, (△) Chopping + scarification in one direction, (▲) Chopping + scarification in two directions, (◆) Controlled fire.

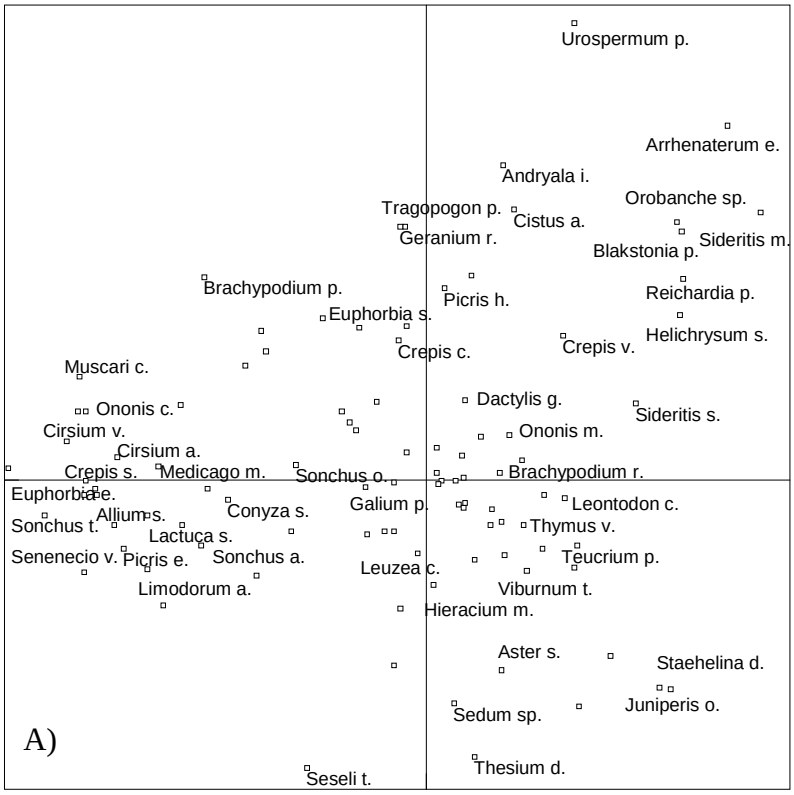
Fig. 2. Changes between treatments in soil, shrub and herb covers for the different years. Letters indicate statistical differences between treatments for a given year (P<0.05, Tukey test). Treatments are as follows: CONT (control), CHOP (chopping), FIRE (controlled fire), SCA1 (chopping+scarification in one direction), SCA2 (chopping + scarification in two directions).

Fig. 3. Changes between treatments in species richness (total number of species/plot), Shannon index and Evenness index (mean frequency ± SE) for the different years. Letters indicate statistical differences between treatments (P<0.05, Tukey test). CONT (control), CHOP (chopping), FIRE (controlled fire), SCA1 (chopping+scarification in one direction), SCA2 (chopping + scarification in two directions).

Fig. 4. Changes between treatments in life-form (mean frequency ± SE in %) for the different years. Letters indicate statistical differences between treatments (P<0.05, NS: not significant). CONT (control), CHOP (chopping), FIRE (controlled fire), SCA1 (chopping+scarification in one direction), SCA2 (chopping + scarification in two directions).

Fig. 5. Changes between treatments in light and nutrient requirement types (mean frequency ± SE in %) for the different years. Letters indicate statistical differences between treatments (P<0.05, NS: not significant). See Fig. 2 for significations of the treatment tags.

Fig. 1


Urospermum p.
Arrhenaterum e.
Andryala i.
Orobanche sp.
Tragopogon p.
Cistus a.
Geranium r.
Sideritis m.
Blakstonia p.
Brachypodium p.
Picris h.
Reichardia p.
Euphorbia s.
Helichrysum s.
Crepis c.
Crepis v.
Muscari c.
Dactylis g.
Ononis c.
Sideritis s.
Cirsium v.
Ononis m.
Cirsium a.
Crepis s.
Medicago m.
Sonchus o.
Brachypodium r.
Euphorbia e.
Galium p.
Leontodon c.
Allium s.
Conyza s.
Sonchus t.
Thymus v.
Lactuca s.
Senenecio v.
Picris e.
Sonchus a.
Teucrium p.
Leuzea c.
Limodorum a.
Viburnum t.
Hieracium m.
Aster s.
Staehelina d.
Juniperis o.
Sedum sp.
A)
Thesium d.
Seseli t.

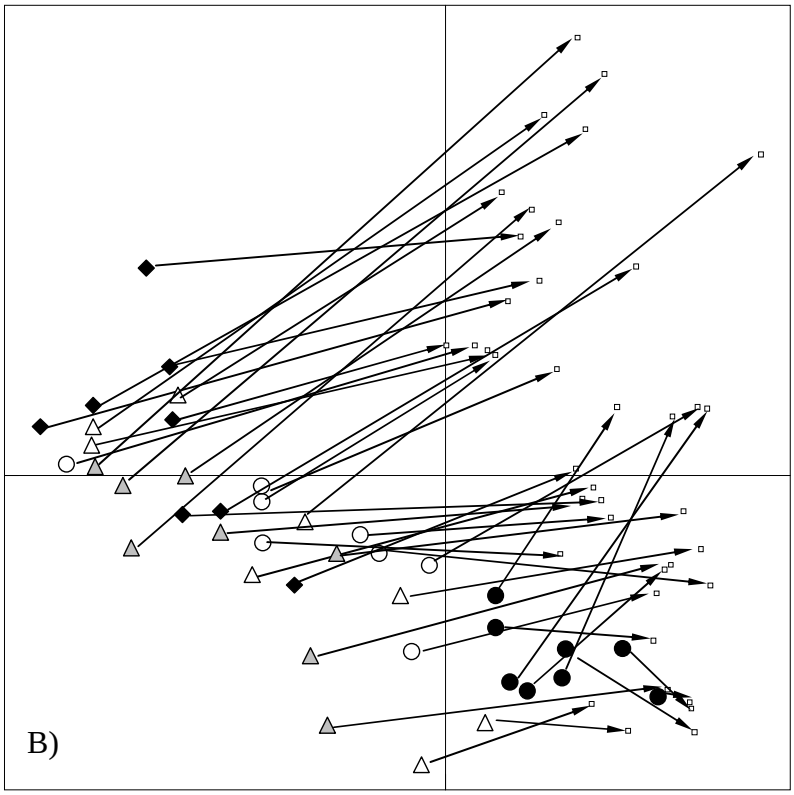

B)

Fig. 2

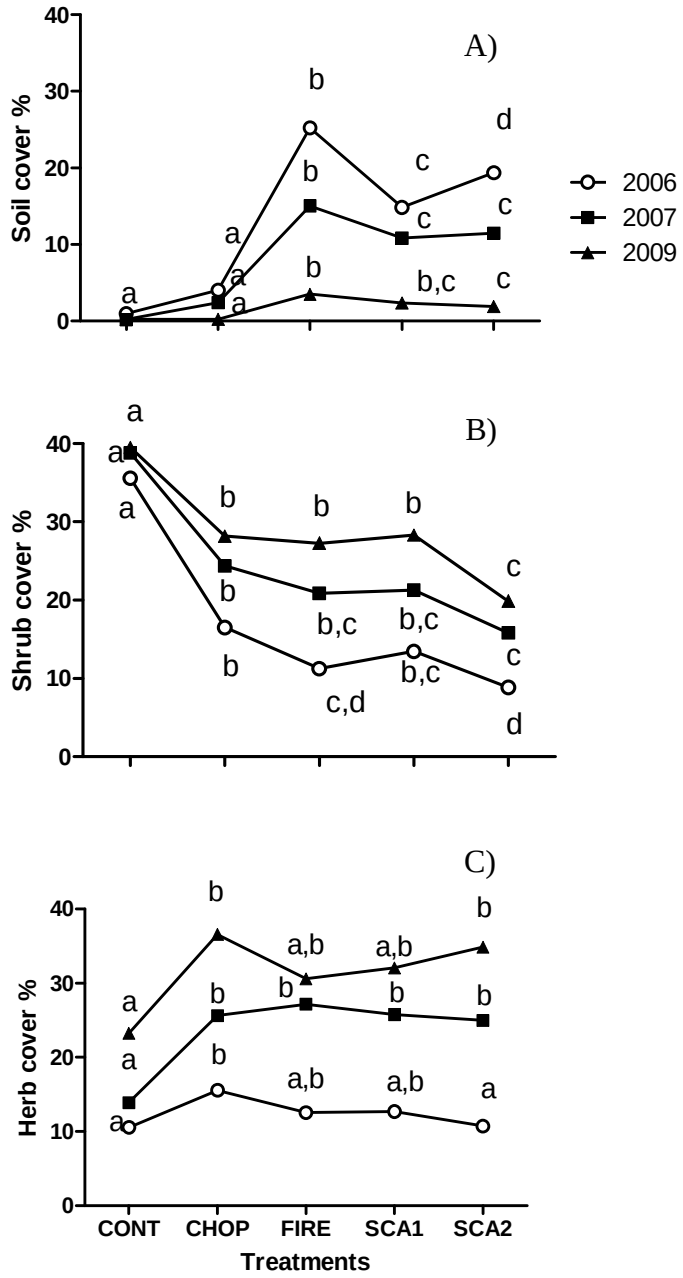

A)
Soil cover %
40
30
20
10
0
2006
2007
2009
B)
Shrub cover %
C)
Herb cover %
CONT
CHOP
FIRE
SCA1
SCA2
Treatments

Fig. 3

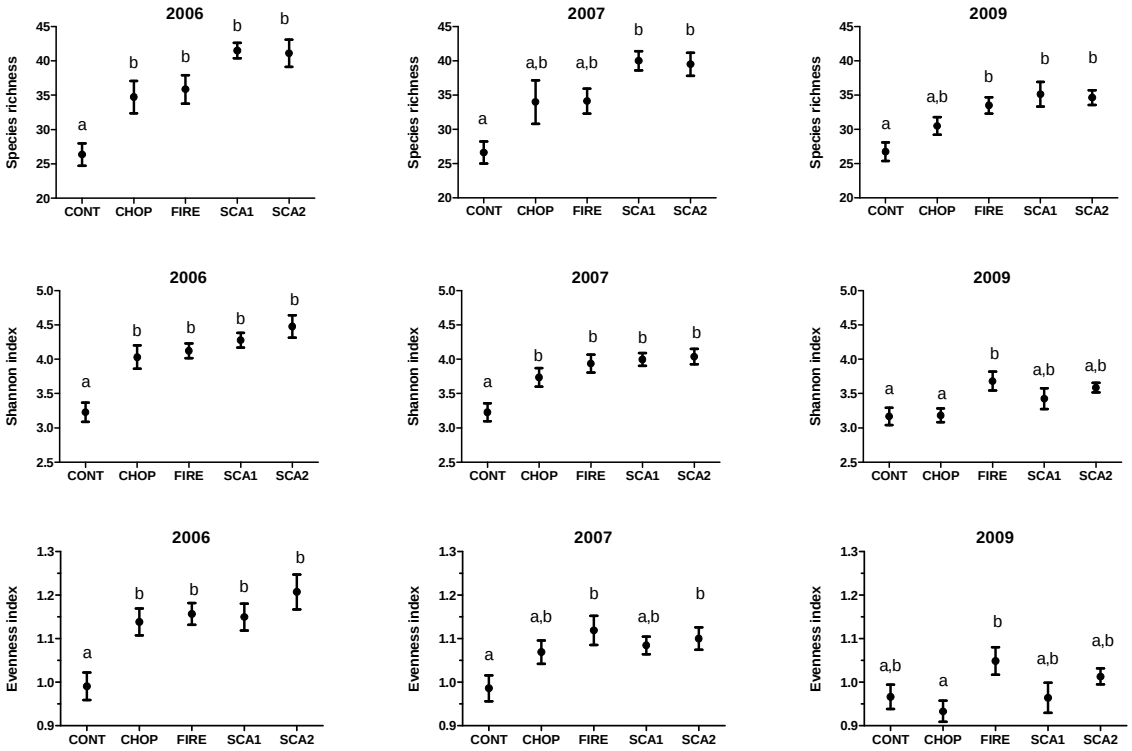

2006
2007
2009
Species richness
Shannon index
Evenness index
CONT
CHOP
FIRE
SCA1
SCA2
a
b
a,b

Fig. 4

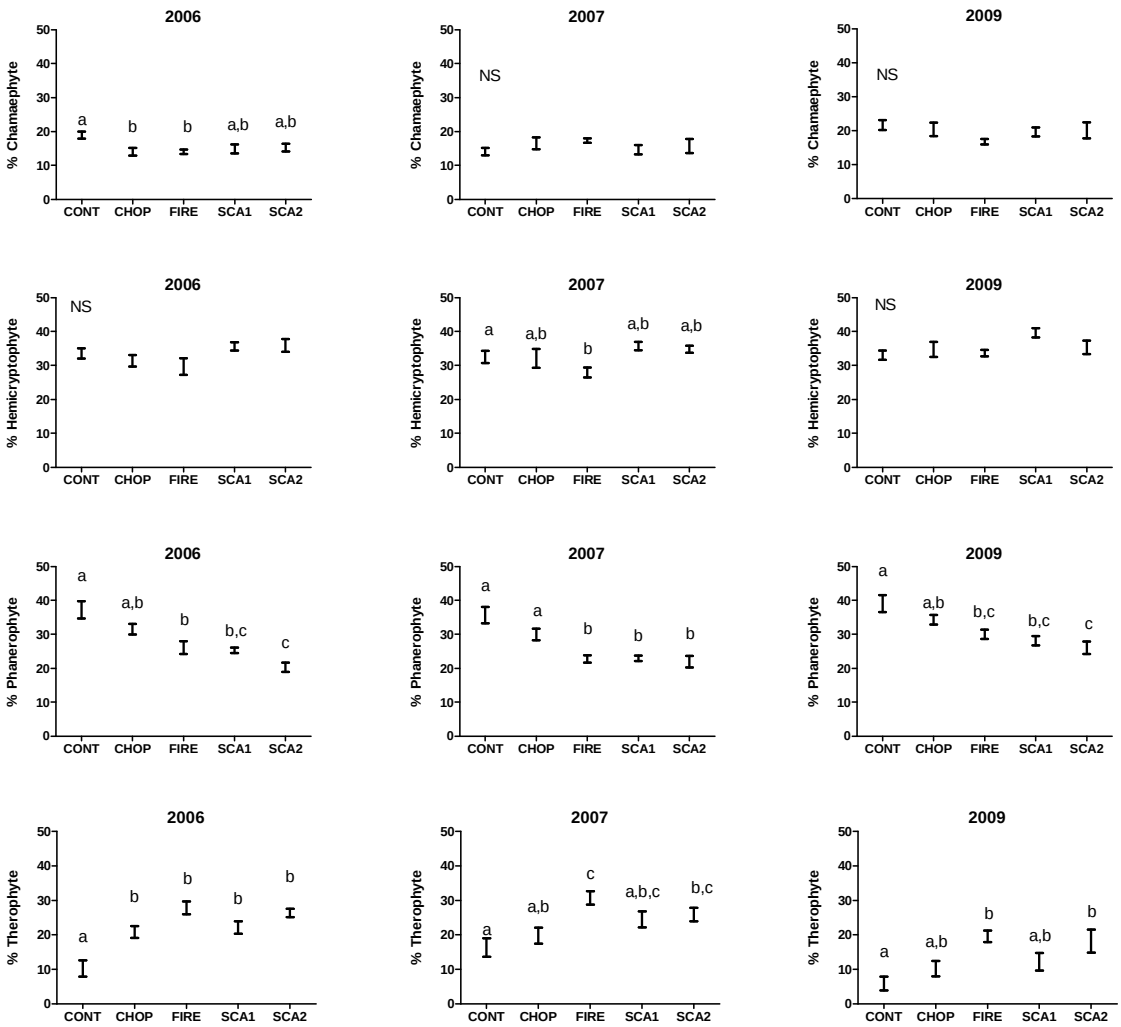
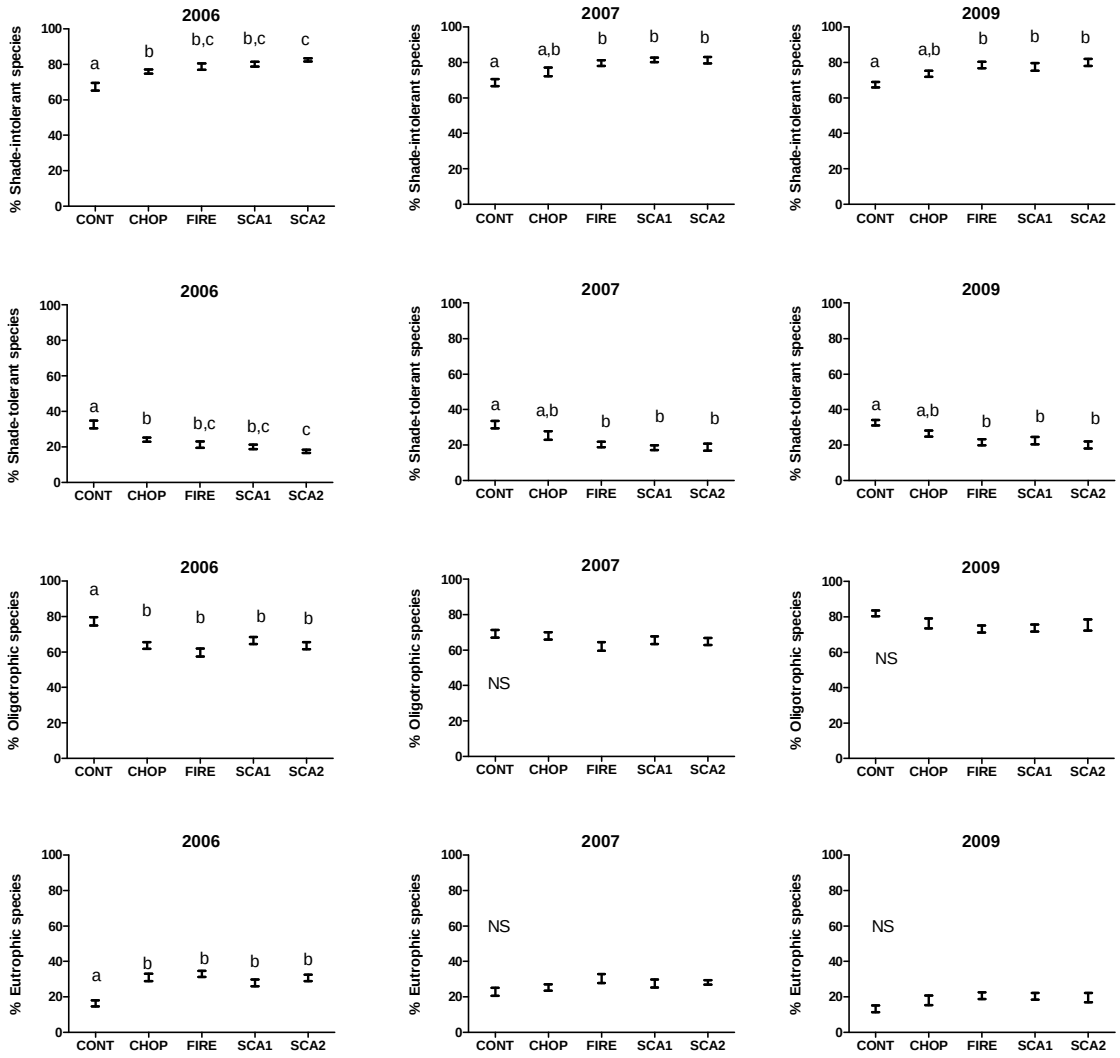

2006
2007
2009
% Chamaephyte
% Hemicryptophyte
% Phanerophyte
% Therophyte
CONT
CHOP
FIRE
SCA1
SCA2
NS
a
b
b
a,b
a,b
a
a,b
b
a,b
a,b
a
a,b
b
b,c
c
a
a
b
b
b
a
b
b
b
b
a
a,b
c
a,b,c
b,c
a
a,b
b
a,b
b

Fig. 5


2006
2007
2009
% Shade-intolerant species
% Shade-tolerant species
% Oligotrophic species
% Eutrophic species
CONT
CHOP
FIRE
SCA1
SCA2
a
b
b,c
c
a,b
NS

Online Resource 1. List of the plants in the treatments over years. The number indicates the occurrence of the species in the treatment (0 to 8) for the given year. Treatment abbreviations: CO (control), CH (chopping), FI (controlled fire), S1 (chopping + scarification in one direction), S2 (chopping + scarification in two directions)

	2009					2007					2006				
Species	**CO**	**CH**	**FI**	**S1**	**S2**	**CO**	**CH**	**FI**	**S1**	**S2**	**CO**	**CH**	**FI**	**S1**	**S2**
Aetheorhiza bulbosa	0	0	0	1	1	0	2	1	2	2	0	0	0	0	0
Allium sphaerocephalon	1	0	0	1	1	3	3	3	4	5	0	3	6	5	6
Amelanchier ovalis	1	1	1	0	0	2	0	0	0	0	1	1	0	0	0
Anagallis arvensis arv.	0	0	1	0	0	0	0	1	0	0	0	1	1	1	1
Andryala integrifolia	0	1	6	2	2	2	0	6	1	5	0	0	3	0	0
Anthyllis vulneraria pra.	0	0	0	0	1	0	0	0	0	2	0	0	0	0	2
Aphyllanthes monspeliensis	8	8	8	8	7	8	7	8	7	5	8	8	8	8	7
Argyrolobium zanonii	7	8	8	8	8	2	7	8	8	8	5	6	8	8	8
Asparagus acutifolius	6	6	6	5	6	8	7	6	7	7	8	8	8	8	7
Aster sedifolius	1	1	2	2	1	2	2	1	3	1	4	1	2	3	2
Aster salignus	0	0	0	0	0	0	0	0	1	0	0	1	0	0	2
Aster squamatus	0	0	0	0	0	0	0	0	0	0	0	2	0	2	1
Asterolinon linum-stellatum	5	3	7	4	8	4	5	8	8	7	4	4	6	8	8
Avenula bromoides	0	1	2	2	3	3	2	3	5	3	2	3	1	5	4
Biscutella coronopifolia lae.	0	0	1	4	1	0	0	0	3	1	1	2	1	3	3
Brachypodium phoenicoides	0	1	1	1	0	0	1	1	0	0	0	1	1	0	0
Brachypodium retusum	8	8	7	8	8	8	7	7	7	8	8	8	8	8	8
Bromus erectus	7	7	8	8	7	0	2	1	5	3	4	5	2	6	5
Bupleurum baldense	0	0	0	0	2	1	1	0	1	2	0	0	0	0	1
Buxus sempervirens	8	8	7	8	8	8	8	8	7	8	8	7	7	8	8
Carduus nigrescens	0	0	0	2	0	0	2	2	2	4	1	1	1	2	2
Carduus pycnocephalus	0	0	0	1	0	0	1	2	2	1	0	0	0	0	0
Carex halleriana	8	8	7	8	8	8	8	4	7	8	7	6	7	8	8
Celtis australis	0	1	0	0	1	0	1	0	1	1	0	2	0	2	0
Centaurea paniculata	0	1	0	0	0	0	2	0	0	0	0	2	0	0	0
Cerastium semidecandrum	0	0	1	0	0	0	0	2	0	4	0	0	1	2	4
Cirsium arvense	0	2	4	1	1	0	4	5	5	5	0	6	8	5	7
Cirsium vulgare	0	0	1	2	0	1	5	4	4	6	0	4	4	4	4
Cistus albidus	1	2	3	5	4	1	1	1	4	3	0	0	1	2	1
Clematis flammula	1	0	2	0	0	0	0	1	0	0	1	0	3	0	0
Conyza sumatrensis	1	2	4	3	2	0	3	8	6	8	1	8	8	7	8
Crataegus monogyna	1	0	0	0	1	0	0	1	0	0	0	1	1	0	1
Crepis capillaris	2	2	7	4	5	0	4	8	5	6	1	3	5	3	2
Crepis foetida	2	5	8	5	6	4	5	6	8	7	3	6	6	7	8
Crepis sancta nem.	0	0	0	0	1	2	3	0	2	1	1	3	1	5	5
Crepis vesicaria tar.	3	7	8	5	7	3	5	3	5	6	0	1	3	4	2
Dactylis glomerata his.	5	5	4	3	5	3	3	4	3	3	4	4	2	3	3
Dittrichia vicosa	0	0	1	2	0	0	1	6	1	2	0	1	1	1	0
Euphorbia exigua	0	0	0	0	0	0	0	0	0	0	0	0	2	3	1
Euphorbia serrata	1	3	6	3	3	1	2	5	3	3	1	2	4	4	3
Festuca sp.	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8
Filago sp.	0	1	4	0	2	0	3	8	4	3	0	3	6	3	5
Fumana ericoides	6	6	7	8	8	2	5	7	6	7	4	5	7	7	7
Galium corrudifolium	2	3	4	6	5	4	1	1	5	5	4	3	4	5	4
Galium parisiense	1	0	0	0	2	3	4	3	4	0	0	0	2	0	2
Genista scorpius	6	8	8	7	7	3	7	5	5	5	4	7	7	6	4
Geranium robertianum pur.	0	2	2	1	2	1	1	1	2	0	0	0	2	1	0
Helianthemum hirtum	2	3	3	2	4	0	0	3	1	3	0	0	2	0	1
Hieracium murorum	3	5	3	3	5	3	5	4	3	6	3	4	4	4	6
Hippocrepis ciliata	0	0	0	0	0	0	1	0	0	2	0	1	0	1	1
Hippocrepis scorpioides	3	2	3	2	2	1	1	2	1	2	1	1	2	1	1
Hyperichum perforatum	0	2	0	1	0	1	2	0	2	0	0	1	0	0	0
Juniperus oxycedrus	5	1	0	4	0	3	1	0	3	0	3	1	0	3	0
Juniperus phoenicea	0	0	0	0	0	0	0	0	0	0	2	1	1	0	0
Koeleria vallesiana	4	2	2	7	3	4	2	1	6	5	1	1	1	5	4
Lactuca perennis	1	3	2	6	6	1	1	1	3	6	0	1	1	5	5
Lactuca serriola	0	1	1	3	0	5	5	8	8	8	2	6	7	8	8
Leontodon crispus	3	2	4	6	5	3	4	1	4	3	4	1	1	3	2
Leuzea conifera	4	3	4	7	4	4	4	4	6	3	4	2	5	7	6
Limodorum abortivum	0	0	0	0	0	0	1	0	1	0	0	3	0	0	1
Linum strictum	0	2	0	0	3	0	2	0	2	3	0	1	0	1	2
Lonicera implexa	6	5	2	2	2	2	3	1	2	2	4	3	1	2	1
Medicago lupulina	0	0	0	1	0	0	0	2	1	0	0	1	0	0	1
Medicago minima	0	0	3	1	1	0	0	2	3	3	3	3	5	3	4
Muscari comosa	0	1	0	0	0	0	2	1	2	1	0	1	1	2	0
Olea europaea sil.	1	1	3	0	0	2	1	2	0	1	2	0	2	1	2
Ononis columnae	0	0	0	1	1	0	1	1	1	1	0	2	6	4	5
Ononis minutisima	4	7	8	7	7	1	6	7	8	6	3	4	4	5	4
Papaver rhoeas	0	0	0	1	1	0	0	6	2	4	0	1	5	2	2
Petrorhagia dubia	2	0	0	0	1	0	0	2	3	0	0	0	0	0	0
Phillyrea angustifolia	0	1	0	1	1	0	0	0	1	2	0	1	0	2	1

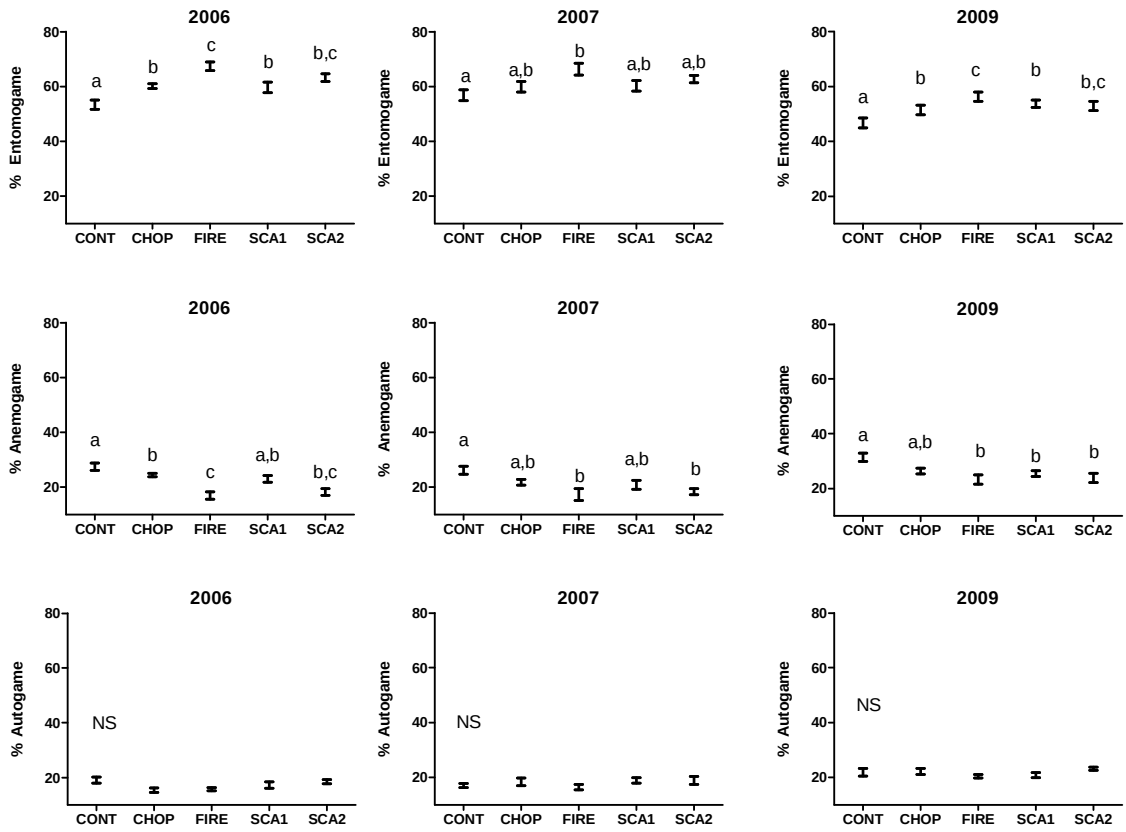
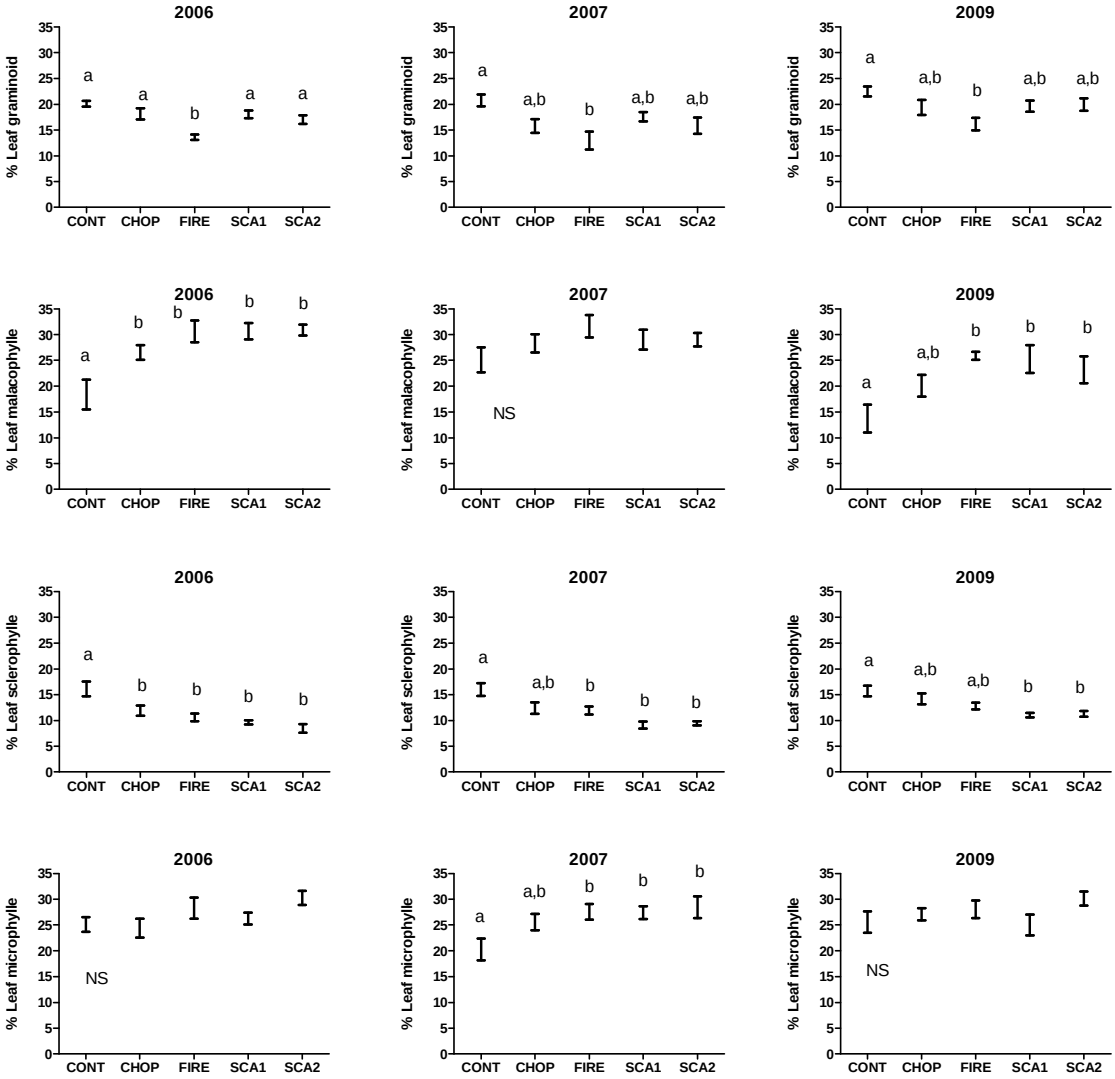
Species	2009					2007					2006				
	CO	CH	FI	S1	S2	CO	CH	FI	S1	S2	CO	CH	FI	S1	S2
Picris echioides	0	0	0	0	0	0	4	1	4	2	0	5	3	5	6
Picris hieracioides	1	2	4	4	4	0	5	2	3	3	0	3	3	2	2
Pinus halepensis	6	7	8	8	8	5	8	5	8	7	5	8	8	8	8
Pistacia therebinthus	1	1	3	1	0	1	2	3	1	1	1	2	3	1	1
Populus alba	0	0	0	0	0	0	1	0	0	0	0	3	0	3	0
Populus nigra	0	0	0	0	0	0	0	0	0	0	0	0	0	2	3
Quercus coccifera	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8
Quercus ilex	8	8	8	7	8	7	7	8	7	6	8	8	8	6	5
Reseda phyteuma	0	0	1	0	1	0	0	2	2	2	1	0	1	5	6
Rhamnus alaternus	8	8	8	8	8	7	7	7	8	7	8	8	7	8	8
Rosmarinus officinalis	8	8	8	7	6	8	8	6	6	5	7	8	5	7	4
Rubia peregrina	7	8	8	8	7	8	7	3	8	6	7	8	7	8	7
Rubus sp.	0	1	0	0	0	0	1	0	0	1	1	1	0	1	0
Sedum sp.	0	1	0	1	2	0	1	0	1	3	1	0	0	1	3
Senecio vulgaris	0	0	0	0	0	0	0	0	0	0	1	1	7	2	6
Seseli tortuosum	0	0	0	0	0	0	0	0	0	0	0	0	0	2	3
Silybum Marianum	0	0	0	0	0	0	0	1	0	1	0	0	2	0	1
Sonchus asper	0	3	0	4	1	7	4	3	6	4	5	8	8	8	8
Sonchus oleraceus	2	6	8	5	7	8	7	8	7	8	6	8	8	8	8
Sonchus tenerrimus	0	0	0	1	0	3	3	3	4	4	0	1	1	2	1
Staehelina dubia	6	3	0	3	3	5	2	1	1	2	5	2	0	1	0
Teucrium polium	6	5	5	6	6	4	5	3	5	6	6	2	2	4	7
Thesium divaricatum	0	0	0	1	1	0	0	0	0	0	0	1	0	2	1
Thymus vulgaris	8	8	5	8	8	8	8	3	7	6	8	8	2	8	7
Tragopogon porrifolius	0	0	0	2	4	1	1	0	2	2	0	1	0	1	2
Trigonella monspeliaca	0	0	0	0	0	0	0	1	0	1	1	0	1	0	0
Urospermum picroides	0	0	0	2	2	2	2	1	4	2	0	0	0	0	0
Viburnum tinus	8	8	5	7	5	8	8	4	5	6	7	8	4	6	6

Online Resource 2. Mean cover (in %) according to treatments. Covers were calculated using the center of the Braun-Blanquet classes (respectively: 0.5%, 2.5%, 15%, 37.5%, 62.5%, 87.5%). Treatment abbreviations: CO (control), CH (chopping), FI (controlled fire), S1 (chopping + scarification in one direction), S2 (chopping + scarification in two directions)

	2009					2007					2006				
Species	**CO**	**CH**	**FI**	**S1**	**S2**	**CO**	**CH**	**FI**	**S1**	**S2**	**CO**	**CH**	**FI**	**S1**	**S2**
Aetheorhiza bulbosa				0.3	0.3		0.1	0.1	0.4	0.6					
Allium sphaerocephalon	0.1			0.1	0.1	0.2	0.4	0.2	0.3	0.6		0.4	0.4	0.8	0.4
Amelanchier ovalis	0.1	0.1	0.1			0.4					0.1	0.1			
Anagallis arvensis arv.			0.3					0.3				0.1	0.1	0.1	0.1
Andryala integrifolia		0.1	0.9	0.4	0.6	0.1		0.6	0.3	0.8			0.2		
Anthyllis vulneraria pra.					0.3					0.1					0.6
Aphyllanthes monspeliensis	1.8	2.0	2.5	1.8	1.7	1.5	1.9	1.3	1.7	1.1	3.3	2.0	1.8	2.0	1.4
Argyrolobium zanonii	1.7	2.3	8.8	2.3	2.5	0.6	2.2	2.5	2.5	2.5	1.3	1.6	2.5	2.3	2.5
Asparagus acutifolius	1.4	1.9	1.6	1.3	1.6	2.5	2.2	1.9	1.9	2.2	2.0	2.5	2.5	2.3	1.9
Aster sedifolius	0.3	0.3	0.1	0.1	0.3	0.1	0.4	0.3	0.4	0.3	0.3	0.3	0.1	0.4	0.4
Aster salignus									0.1			0.1			0.1
Aster squamatus												0.1		0.1	0.1
Asterolinon linum-stellatum	1.1	0.9	1.7	0.8	2.3	1.0	1.6	5.4	7.2	10.0	0.8	1.0	2.9	2.0	2.3
Avenula bromoides		0.1	0.1	0.1	0.2	0.4	0.4	0.2	0.8	0.4	0.4	0.2	0.1	0.6	0.5
Biscutella coronopifolia lae.			0.1	0.5	0.3				0.7	0.3	0.1	0.6	0.1	0.4	0.2
Brachypodium phoenicoides		0.3	0.3	0.3			0.3	0.1				4.7	0.3		
Brachypodium retusum	56.3	65.6	36.6	71.9	62.5	53.1	39.4	21.6	39.1	37.8	26.6	23.4	10.3	14.7	14.7
Bromus erectus	0.9	1.4	2.0	2.3	1.9		0.1	0.1	0.3	0.2	0.8	0.8	0.1	1.1	0.8
Bupleurum baldense					0.1	0.1	0.1		0.1	0.4					0.1
Buxus sempervirens	26.3	15.0	14.4	15.0	11.6	32.2	17.8	13.1	13.1	13.1	38.1	15.9	11.6	15.0	8.8
Carduus nigrescens				0.1			0.4	0.1	0.1	0.3	0.1	0.1	0.1	0.1	0.4
Carduus pycnocephalus				0.1			0.3	0.1	0.4	0.1					
Carex halleriana	2.5	2.5	2.2	4.1	2.5	4.1	4.1	2.8	3.8	2.3	3.8	1.9	1.4	2.5	2.3
Celtis australis		0.1			0.1		0.1		0.1	0.1		0.1		0.1	
Centaurea paniculata		0.3					0.1					0.4			
Cerastium semidecandrum			0.1					0.4		1.0			0.1	0.1	0.5
Cirsium arvense		0.4	0.3	0.1	0.1		1.3	1.6	3.1	3.1		1.4	3.8	3.1	3.3
Cirsium vulgare			0.1	0.1		0.1	0.3	0.8	0.8	1.4		0.5	0.8	0.8	0.5
Cistus albidus	0.3	0.1	4.8	2.9	2.3	0.1	0.1	1.9	0.8	0.7			0.3	0.4	0.1
Clematis flammula	0.1		0.4					0.3			0.1		0.2		
Conyza sumatrensis	0.3	0.1	0.8	0.2	0.1		0.9	2.5	1.6	2.5	0.3	2.3	2.0	1.4	2.3
Crataegus monogyna	0.1				0.1			0.1				0.1	0.1		0.1
Crepis capillaris	0.1	0.6	1.7	0.5	0.8		1.3	2.3	1.3	1.6	0.1	0.7	1.1	0.2	0.4
Crepis foetida	0.1	1.3	2.0	0.6	0.9	0.8	1.3	1.9	3.6	2.2	0.2	1.4	1.1	1.2	2.3
Crepis sancta nem.					0.1	0.1	0.4		0.1	0.3	0.1	0.4	0.1	0.8	1.1
Crepis vesicaria tar.	0.4	1.2	1.8	1.1	1.4	0.4	1.3	0.7	1.3	1.1		0.1	0.2	0.3	0.1
Dactylis glomerata his.	0.8	1.1	0.8	0.9	1.6	0.4	0.7	0.3	0.7	0.7	0.5	0.8	0.1	0.7	0.4
Dittrichia vicosa			0.1	0.1			0.3	1.4	0.1	0.4		0.1	0.1	0.1	
Euphorbia exigua													0.1	0.2	0.1
Euphorbia serrata	0.3	0.4	0.6	0.7	0.7	0.1	0.6	0.3	0.4	0.4	0.1	0.1	0.5	0.8	0.4
Festuca sp.	1.9	1.4	1.1	1.9	3.6	0.9	0.9	0.4	1.4	1.4	4.9	3.3	0.4	1.7	1.7
Filago sp.		0.1	0.8		0.4		0.2	1.0	0.3	0.4		0.2	0.4	0.2	0.3
Fumana ericoides	1.4	1.6	2.2	2.3	2.5	0.4	1.1	1.9	1.6	1.9	1.0	1.6	1.7	1.7	1.9
Galium corrudifolium	0.1	0.4	0.5	1.4	1.1	0.5	0.1	0.1	1.1	1.3	0.3	0.4	0.5	0.8	1.0
Galium parisiense	0.1				0.1	0.7	0.3	0.7	1.3				0.1		0.4
Genista scorpius	0.6	1.0	1.3	1.4	1.4	0.9	1.2	0.6	0.8	0.8	0.5	0.9	0.7	0.6	0.5
Geranium robertianum pur.		0.1	0.1	0.1	0.1	0.1	0.1	0.3	0.6				0.1	0.1	
Helianthemum hirtum	0.1	0.2	0.9	0.4	1.0			0.4	0.3	0.7			0.1		0.1
Hieracium murorum	2.0	0.8	0.2	0.7	1.1	2.3	1.6	1.0	0.7	1.1	2.3	1.0	0.5	1.0	1.1
Hippocrepis ciliata							0.1			0.1		0.1		0.1	0.1
Hippocrepis scorpioides	0.7	0.4	0.9	0.1	0.4	0.3	0.1	0.4	0.1	0.4	0.1	0.3	0.1	0.3	0.1
Hyperichum perforatum		0.4		0.3		0.1	0.4		0.4			0.1			
Juniperus oxycedrus	2.1	0.1		0.3		2.5	0.1		0.2		0.4	0.1		0.2	
Juniperus phoenicea											0.1	0.1	0.1		
Koeleria vallesiana	0.3	0.1	0.1	0.9	0.4	0.5	0.1	0.1	0.9	0.8	0.1	0.3	0.1	0.8	0.5
Lactuca perennis	0.1	0.2	0.1	0.4	0.6	0.1	0.1	0.1	0.2	0.6		0.1	0.1	0.6	0.6
Lactuca serriola		0.1	0.1	0.2		0.8	1.6	2.3	4.9	3.8	0.4	1.6	2.2	1.8	1.5
Leontodon crispus	0.7	0.1	0.8	0.6	0.8	0.7	0.3	0.1	0.8	0.4	0.8	0.1	0.3	0.7	0.6
Leuzea conifera	0.8	0.4	0.3	1.2	0.3	0.5	0.5	0.3	1.1	0.4	1.0	0.4	0.8	1.7	1.4
Limodorum abortivum							0.1		0.1			0.2			0.1
Linum strictum		0.1			0.4		0.4		0.1	0.2		0.1		0.1	0.1
Lonicera implexa	0.4	0.6	0.4	0.1	0.1	0.1	0.4	0.3	0.1	0.1	0.3	0.2	0.1	0.1	0.1
Medicago lupulina				0.1				0.4	0.1			0.1			0.1
Medicago minima			0.2	0.1	0.1			0.4	0.4	0.4	0.2	0.2	0.8	0.4	1.0
Muscari comosa		0.1					0.1	0.1	0.4	0.1		0.1	0.1	0.6	
Olea europaea sil.	0.1	0.1	0.2			0.1	0.1	0.1		0.1	0.1		0.1	0.1	0.1
Ononis columnae				0.3	0.3		0.1	0.1	0.1	0.1		0.6	1.1	1.0	0.6
Ononis minutisima	1.3	1.9	8.8	2.2	3.8	0.1	1.6	2.2	2.3	1.9	0.4	1.0	1.0	1.3	1.3
Papaver rhoeas				0.1	0.1			0.6	0.4	0.3		0.1	0.3	0.1	0.1
Petrorhagia dubia	0.4				0.1			0.6	0.2						
Phillyrea angustifolia		0.1		0.1	0.3				0.1	0.4		0.1		0.1	0.1

Species	2009					2007					2006				
	CO	CH	FI	S1	S2	CO	CH	FI	S1	S2	CO	CH	FI	S1	S2
Picris echioides							0.5	0.3	0.8	0.1		0.6	0.7	0.3	0.6
Picris hieracioides	0.1	0.4	0.8	0.8	0.8		0.6	0.4	0.4	0.4		0.2	0.2	0.1	0.1
Pinus halepensis	0.4	1.9	5.6	5.4	5.6	1.3	2.5	1.6	2.5	2.2	0.8	2.0	2.5	2.3	2.5
Pistacia therebinthus	0.1	0.1	0.2	0.1		0.1	0.1	0.2	0.1	0.1	0.1	0.1	0.2	0.1	0.1
Populus alba							0.1					0.2		0.2	
Populus nigra														0.1	0.2
Quercus coccifera	23.4	27.5	24.7	11.9	13.4	23.4	17.8	20.3	18.8	13.1	14.7	14.7	19.1	20.3	14.4
Quercus ilex	7.2	6.9	8.8	8.2	11.3	5.1	6.9	4.1	8.4	9.7	3.6	2.3	3.8	4.8	4.7
Reseda phyteuma			0.1		0.1			0.1	0.4	0.1	0.1		0.1	0.3	0.6
Rhamnus alaternus	2.5	2.5	5.6	8.8	8.8	8.4	3.8	6.9	4.1	3.8	2.3	2.3	1.9	2.5	2.3
Rosmarinus officinalis	5.4	4.1	2.0	1.9	1.6	8.8	2.0	1.1	1.4	0.8	5.3	2.3	0.8	1.7	0.8
Rubia peregrina	2.2	2.5	2.5	2.3	2.2	4.1	2.2	0.9	2.5	1.9	2.2	5.6	1.9	4.1	1.9
Rubus sp.		0.1					0.1			0.3	0.3	0.1		0.1	
Sedum sp.		0.1		0.1	0.1		0.1		0.1	0.2	0.1			0.1	0.2
Senecio vulgaris											0.1	0.1	1.4	0.1	0.6
Seseli tortuosum														0.4	0.4
Silybum Marianum								0.1		0.1			0.1		0.1
Sonchus asper		0.2		0.3	0.1	0.9	1.0	0.4	1.4	0.5	0.6	2.0	5.6	2.0	2.5
Sonchus oleraceus	0.1	0.4	1.5	0.6	1.4	1.8	1.9	2.0	3.3	3.6	0.9	2.5	8.8	3.6	5.6
Sonchus tenerrimus				0.1		0.7	0.4	0.7	0.8	0.5		0.1	0.1	0.1	0.3
Staehelina dubia	0.9	0.2		0.7	0.2	0.6	0.1	0.1	0.3	0.4	0.8	0.1		0.3	
Teucrium polium	1.4	0.6	0.8	1.4	1.4	0.8	0.6	0.2	0.6	1.1	0.4	0.1	0.1	0.5	0.9
Thesium divaricatum				0.3	0.1							0.1		0.1	0.1
Thymus vulgaris	8.8	2.0	1.3	6.9	3.8	6.9	2.3	0.4	1.7	3.2	5.6	2.3	0.1	3.6	1.7
Tragopogon porrifolius				0.1	0.5	0.1	0.1		0.1	0.1		0.1		0.1	0.1
Trigonella monspeliaca								0.1		0.1	0.1		0.1		
Urospermum picroides				0.4	0.4	0.1	0.1	0.1	0.5	0.6					
Viburnum tinus	8.5	8.3	2.4	3.0	3.1	10.0	6.7	2.3	2.4	2.9	5.3	3.8	0.8	1.4	1.9

Online Resource 3. Changes between treatments in pollination mode (mean frequency ± SE in %) for the different years. Letters indicate statistical differences among treatments (P<0.05, NS: not significant). See Fig. 2 for significations of the treatment tags.



Online Resource 4. Changes between treatments in leaf anatomy types (mean frequency ± SE in %) for the different years. Letters indicate statistical differences between treatments (P<0.05, NS: not significant). See Fig. 2 for significations of the treatment tags.