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Influence of harvesting intensity on the floristic composition of natural Mediterranean maritime pine forest

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ABSTRACT

Understorey plant species composition is an important part of forest ecosystems and its conservation is becoming an increasingly frequent objective in forest management plans. However, there is a lack of knowledge of the effect of timber harvesting on the characteristic understorey species in the Mediterranean region. We investigated the effects of three different harvest intensities on the short-term dynamics of understorey vegetation in a natural Maritime pine forest in Spain, and compared the results with uncut controls. Clear-cutting induced both qualitative and quantitative differences with respect to the controls, but intermediate levels of harvesting (25% and 50% removal) induced only quantitative differences. Harvesting reduced the frequency and cover of 56% of characteristic forest species, but only 22% showed an increase. Of the most abundant plant families only the Fabaceae showed a significant response with respect to harvesting intensity. Our findings suggest that Light- and Medium-harvest regimes are better management options than clear-cutting if the aim is to conserve the understorey vegetation.

1. Introduction[1]

Disturbance plays an important role in structuring natural communities, as it is likely to influence both community composition and population persistence (Vandvik et al., 2005). Forest management treatments, especially harvesting, are examples of a large-scale disturbance that could be expected to impact on species composition and forest structure (Bengtsson et al., 2000). As there is now increasing societal demand to obtain multiple outputs from silvicultural systems, where timber production and the conservation of woodland understorey species are integrated (Kimmins, 2004), there is a need for developing harvesting protocols that maintain woodland species composition (Burke et al., 2008).

The changes in environmental conditions and habitat loss provided by silvicultural treatments (as clear-cutting or shelterwood; Cavallin and Vasseur, 2009) influence the distribution of forest herbaceous species leading to differences in species composition, especially in pine forests of Mediterranean region (Torras and Saura, 2008). Disturbance-sensitive species may be unable to recover after harvest, and they may decline, or even become locally extinct; this decline has been demonstrated in both deciduous and conifer harvested forests in Canada (de Graaf and Roberts, 2009). Knowledge of the response of the understorey layer to different harvest disturbances is, therefore, an important requirement for developing sustainable forest management practices, which are integrated with conservation programs (Kimmins, 2004; Uytvanck and Hoffmann, 2009).

Pinus pinaster Ait. (Maritime pine) is a natural forest species in the western Mediterranean basin, distributed mainly through the Iberian Peninsula, France and Italy (Alía et al., 1996). In central Spain, this natural forest has been traditionally managed mainly for resin production, with timber extraction as a secondary objective (González-Alday et al., 2009). Currently, resin extraction is low and, coupled with the low economic value of the timber; the management policy has been re-focussed towards the development of multi-functional forests, where there is an increased emphasis on preserving the structural and functional attributes of the ecosystem for nature conservation purposes (Leone and Lovreglio, 2004). Management strategies are, therefore, being developed to consider

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[1] Nomenclature follows Aizpuru et al. (1999) and Castroviejo et al. (1986–2009).

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commercial activity (resin and timber) in conjunction with maintaining landscape and ecological protection functions. These new functions included carbon stocks (Bravo et al., 2009), mushroom production and the conservation of understorey species (Pérez-Ramos et al., 2008), which must also include the conservation of endemic species, and the singular genetic diversity of *P. pinaster* (de Lucas et al., 2009). With the need to regenerate the forest naturally, foresters recognize the necessity for an improved knowledge of the ecology of the understorey vegetation and how it responds to forest harvesting. The use of different tree harvesting intensities as a means of enhancing natural regeneration is one of the management alternatives being considered for implementation.

The inclusion of forest conservation objectives in management strategies requires information about the understorey vegetation performance (D'Amato et al., 2009). However, the response of forest understorey species to forest management practices, and tree harvesting in particular, has not been well-studied (Burke et al., 2008; Torras and Saura, 2008). This is especially true for the Mediterranean region, which is a biodiversity hotspot (Blondel and Aronson, 1999). The objective of this study was to assess the initial impact (first three years) of tree harvesting intensity on the understorey species composition of a natural Maritime pine forest in semi-arid Mediterranean conditions in Spain. We hypothesized that: (1) the harvest treatments would induce quantitative and qualitative changes in species composition in relation to uncut control areas; (2) the treatments would affect characteristic forest species more than other species, reducing both their cover and frequency; and (3) the treatments would influence the cover of the most abundant families (Asteraceae, Fabaceae, Poaceae, etc). A further aim was to identify indicator species that would be typical of the different harvesting treatments. Ultimately, we want to better understand the forest dynamics and to be able to assess the importance of tree harvesting on understorey component.

2. Methods

2.1. Study area

This study was conducted in a natural, maritime pine forest in Segovia province in Central Spain (41°22′N, 4°29′W). The site is at an elevation of 760 m asl, and experiences a semi-arid Mediterranean climate with a mean annual temperature of 11.2 °C, a mean annual rainfall of 461 mm, and a dry period between mid-June to mid-September (M.A.P.A., 1987). The soils have a sandy-siliceous texture and are of Quaternary age (Junta de Castilla y León, 1988). The vegetation of the area is dominated by *P. pinaster* with some isolated trees of *Pinus pinea* (Stone pine), and a few crop fields (González-Alday et al., 2009). The baseline tree density was 140 stems/ha, and tree age ranged from 80 to 100 years; the current site silvicultural practice is to allow natural regeneration following a shelter-wood system adapted for resin production (González-Alday et al., 2009).

2.2. Harvest treatments

Sixteen continuous hectares of natural maritime pine forest with similar abiotic conditions, forest structure and vegetation composition (González-Alday et al., 2009) were selected for study within a 20,000 ha forest. Twelve 70 m × 70 m treatment plots were delimited. To these plots three replicates of four harvesting treatments were applied randomly in autumn 2003. The four treatments were: (1) no harvesting, the experimental control (coded H0); (2) light harvesting (25% of basal area removed, coded H25); (3) moderate harvesting (50% of basal area removed, coded H50); and (4) complete harvesting (100% of basal area removed as a clear-cut treatment, coded H100). A three-step harvesting procedure was adopted: (1) all trees that needed to be felled to achieve the basal area reduction criteria were marked; (2) the selected trees were felled by chainsaw; (3) all harvested timber was removed from the plot. The use of chainsaws to harvest the timber followed by low-intensity removal is common practice in European conservation forestry management, where the aim is to minimise site disturbance. This is the usual practice in the Mediterranean region (Serrada et al., 2008). Accordingly, the disturbance induced in this study will be much less than that produced by clear-cutting operations in intensively-managed forests, where mechanical treatment through the use of harvesters and skidders is practiced.

2.3. Sampling the understorey vegetation

The central 50 m × 50 m area within each treatment plot ($n = 12$) was delimited as the sampling area to avoid edge effects. In each sampling area, 20 quadrats (1 m × 1 m) were located randomly and the cover (%) of all vascular plant species was estimated visually by the same observer in May 2006, three years after treatment. Only vascular plants were assessed because the understorey vegetation of these dry xeric woodlands does not have a large bryophyte or macro-lichen component (Oria de Rueda, 2003).

2.4. Data analysis

All statistical analyses were implemented in the R software environment (version 2.7.2; R Development Core Team, 2008), using the VEGAN package for multivariate analyses (Oksanen et al., 2008) and the LABDSV package for indicator species analysis (Roberts, 2007). Attribution of plant species as characteristic *P. pinaster* forest species was based on Ruiz de la Torre (1996).

Multivariate analysis was used to test and quantify the effects of the harvest treatments on the floristic composition of the field layer plant community in the short-term. Hypothesis 1 was tested using Permutational Multivariate Analysis of Variance (PMAV); here distance matrices were used to examine and quantify the differences in floristic composition between treatments (Oksanen et al., 2008). Bray and Curtis and Jaccard distance measures were used to test quantitative and qualitative differences, respectively. The overall differences between harvest treatments ($\alpha = 0.05$) and all pair-wise comparisons were tested with respect to the control (H0). Bonferroni correction was used to adjust for the significance level of each contrast (Sokal and Rohlf, 1995); here the critical probability level for detecting significance between contrasts was $\alpha = 0.017$.

Detrended Correspondence Analysis (DCA) was then performed to describe the plant community using the cover data for each plant species that were present in more than four sampled quadrats. To aid interpretation the harvest treatments were fitted onto the DCA ordination plot using the VEGAN ENFIT function and 1000 permutations (Oksanen et al., 2008). Standard deviational ellipses of each treatment were then used to illustrate the position of each harvest treatment on the biplots (Oksanen et al., 2008). In order to describe more clearly the response of forest characteristic species to harvest treatments and to help in their classification, response surface models of each species cover values were fitted over DCA ordination results by GAM models using the VEGAN ORDISURF function (Oksanen et al., 2008).

Univariate analysis was also performed with ANOVA and generalized linear models (GLM) to evaluate the significance of harvest treatments relative to controls, on the cover and frequency of characteristic species and most abundant families (Hypothesis 2 and 3). Cover data (%) were transformed ($\arcsin(\sqrt{x}/100)$) before ANOVA to meet normality and variance assumptions (Crawley, 2007). ANOVA's were only calculated if the characteristic species was present in more than 50% of the plots. Tukey's HSD tests were used to enable pair-wise comparisons of means ($\alpha = 0.05$). The effect of harvest treatments on frequency (the number of quadrats occupied by each species) was modelled using GLM with a Poisson error distribution and a logarithmic link function (Crawley, 2007). The model simplification guidelines for count data with categorical explanatory variables of Crawley (2007) were used.

Dufrene–Legendre indicator species analysis (ISA) was then used to determine which, if any, understorey species were representative of a particular harvest treatment (Dufrene and Legendre, 1997). This procedure combines information about frequency and abundance of species among treatments and assigns an indicator value (IV), which indicates the affinity of each species to each treatment (0 no affinity and 1 perfect affinity; Roberts, 2007). For each species, the significance of indicator value (IV) was tested using a Monte Carlo simulation procedure with 1000 permutations. Only species with an indicator value >0.10, and $P < 0.05$ are discussed.

3. Results

One hundred and seven understorey vascular plant species were encountered in the study. Eighteen species characteristic of the sandy *P. pinaster* community (Ruiz de la Torre, 1996), including *Lavandula pedunculata*, *Helichrysum italicum*, *Corynephorus canescens* and *Sedum amplexicaule* were found in uncut controls (H0). The most frequent understorey species (i.e. occurring in more than 80% of the total sampled quadrats) were *Hypochoeris maculata*, *Micropyrum tenellum* and *Vulpia myuros*. Thirteen species, including *Medicago polymorpha, Leontodon taraxacoides*, *Rumex crispus* and *Thymus mastichina* were found only once, and most of these species were in the clear-cut plots (H100).

3.1. *Effects of harvesting on species composition (Hypothesis 1)*

All harvesting treatments influenced species composition significantly relative to the uncut controls (PMAV quantitative data: all contrasts with 1000 permutations; $P < 0.012$; Table 1), and accounted for 45% of the variance in the species data. Re-analysis using the qualitative data set showed overall differences between treatments ($F = 2.02$, $P < 0.001$; Table 1), and accounted for 43% of the variance in the data. However, here only the clear-cut plots showed significant differences from controls.

The DCA produced eigenvalues (λ) of 0.52, 0.40, 0.27 and 0.28, and gradient lengths (GL) of 3.95, 4.21, 3.41 and 3.31 for the first four axes respectively. The fit of harvest treatments to this ordination was significant ($P < 0.001$). The species plot (Fig. 1a) showed that the overall distribution of species reflected the harvest treatments applied. The biplot coupled with SD-ellipses (Fig. 1b) indicated that the four harvesting treatments occupied different regions of the ordination space. The uncut controls (H0) were located on the upper left hand quadrant and contained *P. pinaster* and *S. amplexicaule*; the clear-cut treatment (H100) occupied the lower right hand quadrant and contained a great number of species including grassland weeds *Cynodon dactylon*, *Geranium molle* and

Table 1
Comparison of tree harvesting intensity on the understorey floristic composition of natural maritime pine communities under semi-arid Mediterranean conditions in Spain using Permutational Multivariate Analysis of Variance with 1000 permutations. Quantitative and qualitative analyses are presented based on different Indices. Pair-wise contrasts with respect to the uncut controls are also shown; significance was assessed (*) after Bonferroni correction with $\alpha < 0.017$.

Type of analysis	Index	Harvest treatment/contrasts	*F*-value	*P*-value
Quantitative	Bray & Curtis	All treatments	2.16	0.003*
		Control (H0) vs Light harvesting (H25)	1.88	<0.001*
		Control (H0) vs Medium harvesting (H50)	3.02	0.012*
		Control (H0) vs Complete harvesting (H100)	4.05	<0.001*
Qualitative	Jaccard	All treatments	2.02	0.001*
		Control (H0) vs Light harvesting (H25)	1.25	0.308
		Control (H0) vs Medium harvesting (H50)	1.94	0.169
		Control (H0) vs Complete harvesting (H100)	6.35	0.016*

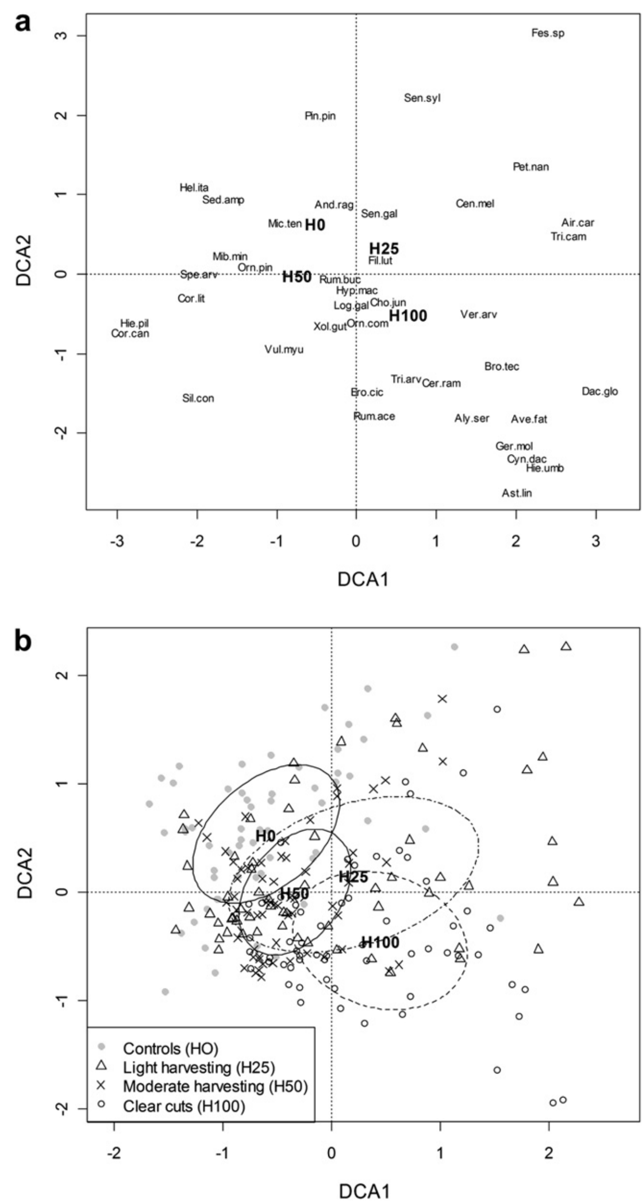

Fig. 1. DCA ordination for the first two axes of understorey plant species in natural maritime pine stands under semi-arid Mediterranean conditions in Spain subject to four harvesting intensity treatments. (a) Species in relation to harvest intensity; and (b) plot positions within each harvest treatment with their SD ellipses. Harvest treatment codes: H0 = Control; H25 = Light harvesting; H50 = Medium harvesting; H100 = Clear-cut. Species codes are shown in Table 3.

Avena fatua; and the two intermediate harvesting treatments (H25 and H50) were located between these two extremes with considerable overlap. The H25 treatment ellipse contained *Aira caryophyllea* and *Festuca* spp. as distinctive species, whereas H50 contained *Mibora minima*, *Corrigiola litoralis* and *Ornithopus pinnatus*.

3.2. Effects of harvesting on characteristic forest species (Hypothesis 2)

Fourteen species characteristic of *P. pinaster* forest showed significant treatment effects on either their frequency or cover. From these results, three types of response to harvest treatments were observed (Table 2) and one example of each type is illustrated in Fig. 2 using plant cover isolines. The three responses types were: (1) Species with a reduced cover or frequency as a result of harvesting. This group contained nine species including both shrub and herbs, e.g. *H. italicum*, *L. pedunculata, C. canescens* and *Senecio sylvaticus* (Fig. 2a). (2) Species that maintained their cover and frequency overall the treatments. This group contained four species, but only one showed a significant response (*Andryala ragusina,* Fig. 2b). (3) Species that showed a significant increase in cover or frequency as a result of harvesting. This group contained four herb species, *H. maculata*, *V. myuros*, *Xolantha guttata* and *Ornithopus compressus* (Fig. 2c).

3.3. Effects of harvesting on the most abundant plant families (Hypothesis 3)

The harvest treatments only showed a significant effect relative to the control on the Fabaceae ($F_{[3,8]} = 5.34$, $P = 0.026$), where legume cover was greatest in the clear-cut treatment (H100, 18.1 $\pm$ 3.2%), intermediate in the H25 and H50 treatments (H25 = 16.5 $\pm$ 4.3%; H50 = 8.8 $\pm$ 1.0%), and lowest in the controls (*H*0 = 4.6 $\pm$ 0.9). Effects on harvesting on the Poaceae, Asteraceae and other families (Caryophyllaceae, Geraniaceae, Crassulaceae) were not significant.

3.4. Determination of the understorey species associated with the different harvest treatments

The ISA identified six indicator species for the control and intermediate harvesting treatments (H0, H25, H50) and 21 indicators for the clear-cut treatment (Table 3). Therefore, 20% of the total understorey species sampled ($n = 107$) were indicators of the clear-cut treatment, and if the 12 indicator species detected in the H25 and H50 harvest treatments are included, 31% were indicative of a harvest effect.

Species indicative of the control treatment included species which reduced their cover and frequency with harvest intensity, e.g. *P. pinaster* seedlings, *S. amplexicaule* and *S. sylvaticus*. Likewise, both intermediate harvest treatments were identified by two *P. pinaster* community species (H25 = *A. ragusina* and *X. guttata*; H50 = *M. tenellum* and *M. minima*). The indicator species of the clear-cut treatment (H100) included a large number of generalists and ruderals (e.g. *Rumex acetosella*, *Erodium cicutarium*, *A. fatua*, *Cerastium ramossisimum, G. molle*), with just three *P. pinaster* characteristic species (*H. maculata*, *O. compressus*, *V. myuros*).

4. Discussion

Harvesting trees had a significant impact on the short-term vegetation dynamics in the natural maritime pine forests in Spain. Harvesting produced clear changes in the composition of understorey species, and especially on the characteristic species of these forest communities including members of the Fabaceae. Disturbance caused by the increasing severity of harvest treatment provide new opportunities for early-successional species to colonise and hence for sites to develop differences in species composition and distribution (Burke et al., 2008; Torras and Saura, 2008).

4.1. Effects of harvesting on species composition (Hypothesis 1)

The understorey species composition was influenced both quantitatively and qualitatively by harvest treatment; therefore,

Table 2
The effects of four harvesting intensity treatments on the frequency and mean cover values ($\pm$SE) of representative species found in a natural maritime pine communities under semi-arid Mediterranean conditions in Spain. Harvesting treatments codes: H0 = Control; H25 = Light harvesting; H50 = Medium harvesting; H100 = Clear-cut. Frequency data were analyzed using GLM and cover data were analyzed using ANOVA. Significant differences are indicated by asterisks; letter "a" letter after cover values indicate significant differences vs. control plots ($P < 0.05$) determined using the Tukey HSD test.

	Frequency					Cover				
	H0	H25	H50	H100	χ^2	H0	H25	H50	H100	$F_{[3,8]}$
Reduced										
Corynephorus canescens	10	4	4		15.01*	0.50 ± 0.18	0.10 ± 0.08	0.12 ± 0.07	–	–
Halimium umbellatum	12	6			28.81*	0.30 ± 0.12	0.07 ± 0.05	–	–	–
Helichrysum italicum	21	10	11	3	18.89*	5.30 ± 1.10	2.20 ± 0.78	2.20 ± 0.70	0.35 ± 0.26a	5.38*
Lavandula pedunculata	1	1	1		1.33	0.42 ± 0.42	0.03 ± 0.03	0.16 ± 0.16	–	–
Malcomia triloba	9	6			22.48*	0.26 ± 0.12	0.33 ± 0.17	–	–	–
Mibora minima	15	2	12		31.85*	0.66 ± 0.22	0.10 ± 0.08	1.05 ± 0.39	–	–
Pinus pinaster	47	19	21	4	73.83*	2.85 ± 0.57	0.65 ± 0.20a	0.29 ± 0.09a	0.26 ± 0.25a	12.38*
Sedum amplexicaule	51	40	40	18	41.76*	8.18 ± 0.84	2.91 ± 0.53a	2.36 ± 0.43a	0.31 ± 0.11a	13.06*
Senecio sylvaticus	22	16	3		50.25*	2.12 ± 0.46	1.06 ± 0.40	0.02 ± 0.17	–	–
Spergularia arvensis	25	10	18	6	19.82*	1.06 ± 0.27	0.31 ± 0.13a	0.50 ± 0.14	0.12 ± 0.07a	7.00*
Maintained										
Andryala ragusina	24	50	45	26	37.08*	1.24 ± 0.33	1.95 ± 0.31	2.03 ± 0.54	0.21 ± 0.05	1.60
Jasione montana	9	9	14	16	3.96	0.87 ± 0.42	0.27 ± 0.17	0.27 ± 0.13	0.12 ± 0.06	2.73
Lupinus angustifolius	14	13	16	25	7.12	0.92 ± 0.33	1.07 ± 0.35	0.60 ± 0.18	1.30 ± 0.30	0.18
Micropyrum tenellum	37	40	48	36	7.05	3.60 ± 0.80	7.20 ± 1.25	10.12 ± 1.07	3.10 ± 0.72	3.40
Increased										
Hypochoeris maculata	44	43	49	53	6.76	3.32 ± 0.53	1.73 ± 0.32	2.85 ± 0.54	10 ± 1.50a	4.12*
Ornithopus compressus	24	47	44	49	29.44*	1.06 ± 0.27	5.24 ± 0.69	3.22 ± 0.54	5.75 ± 1.03a	10.94*
Vulpia myuros	36	40	49	55	21.19*	6.87 ± 1.28	10.19 ± 1.53	15.40 ± 1.67a	15.30 ± 1.75a	4.36*
Xolantha guttata	13	38	26	25	22.10*	0.36 ± 0.18	2.18 ± 0.47	0.80 ± 0.30	1.80 ± 0.47a	5.59*

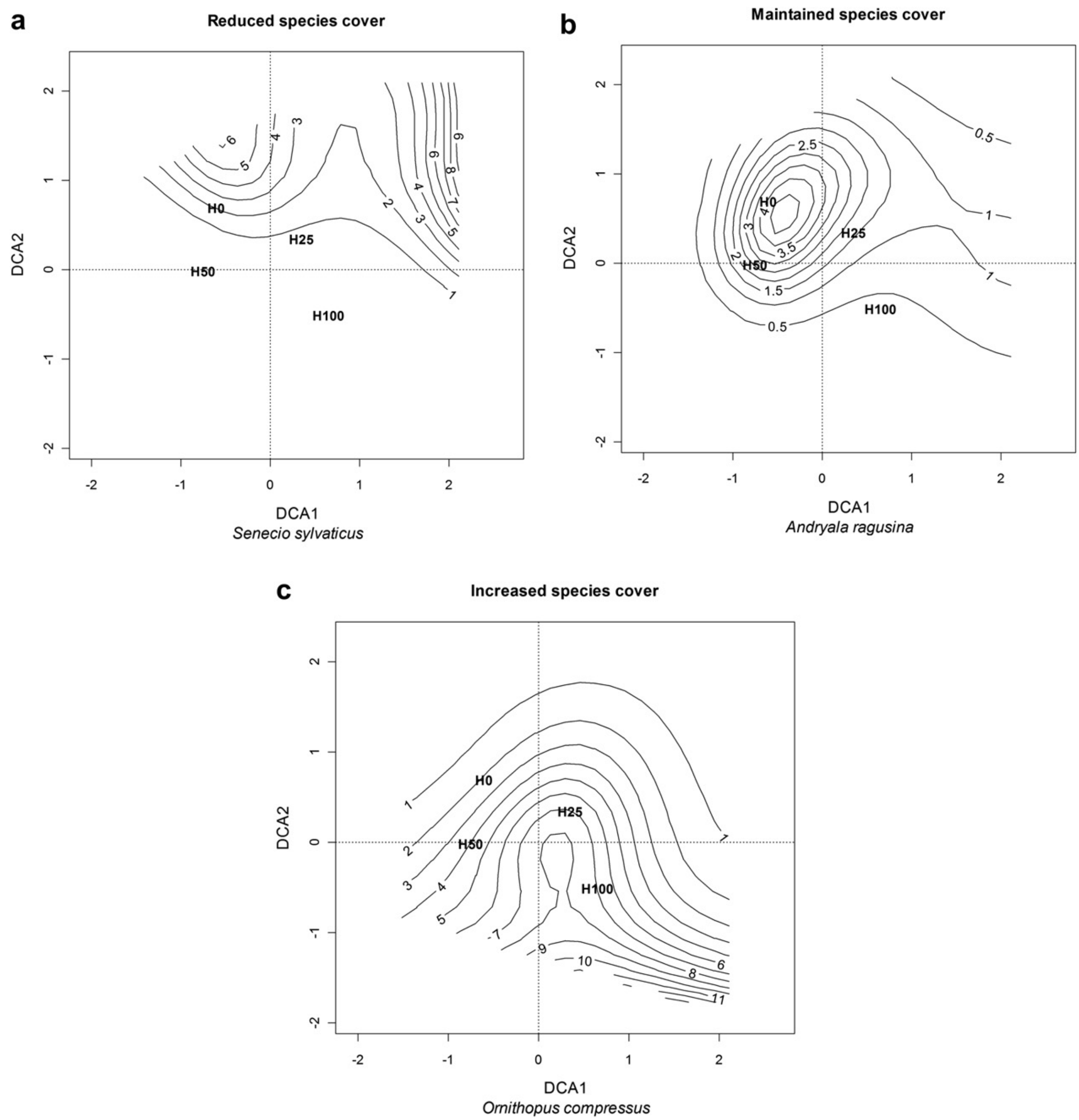

Fig. 2. Examples of the three identified responses (Table 2) to harvest intensity treatments in natural maritime pine stands under semi-arid Mediterranean conditions in Spain. The isolines values represent the predicted plant cover of each species fitted by GAM on the DCA ordination of understorey species compositions (Fig. 1). The three responses with respect to harvesting are: (a) Reduction: plant cover isolines values decreased moving away from H0 (*Senecio sylvaticus*), (b) Maintenance: similar values over the treatments (*Andryala ragusina*), and (c) Increased: plant cover isolines values increased as they approached to H50 and H100 (*Ornithopus compressus*). Harvest treatment codes: H0 = Control; H25 = Light harvesting; H50 = Medium harvesting; H100 = Clear-cut.

Hypothesis 1 is accepted. The greatest differences in species composition from the controls (H0) were found in the clear-cut treatment (H100). The clear-cut treatment had a much reduced cover and frequency of species characteristic of these woodland communities (Pérez-Ramos et al., 2008), and a much greater abundance of early-successional species such as *A. fatua*, *E. cicutarium*, *G. molle* and *R. acetosella*. The drastic effects of clear-cutting on environmental conditions produced new homogeneous open areas that promoted the colonization of common herbaceous species characteristic of disturbed sites (Torras and Saura, 2008; Zang and Ding, 2009), with increased light and substrate availability (Burke et al., 2008). Not surprisingly, similar patterns have been documented under different forest types and indeed other ecosystems. For example, in temperate deciduous forest in France selective cutting systems had a deleterious negative impact on true forest species, and increased the dominance of early-successional species (Decocq et al., 2004). A similar short-term increase in ruderal species has been described after (a) clearing cork oak forest in the Iberian Peninsula (Pérez-Ramos et al., 2008), and (b) in clear-cut treatments in conifer and deciduous forest in Canada (de Graaf and Roberts, 2009). Therefore, whilst this may be a general effect after forest management, it is an important result for the implementation of conservation management in the natural Maritime pine forests in Spain. Clear-cutting, even when implemented

Table 3
Indicator species in the understorey natural maritime pine communities under semi-arid Mediterranean conditions in Spain for each of the four harvesting intensity treatments. Only species with significant indicator values >0.10 are presented. Late-successional species characteristic of *Pinus pinaster* communities were denoted as (✓), whereas early-successional species as (E) and medium-successional species as (M).

Harvest treatment	Species codes	Species	Species characteristic	Indicator value	*p*-value
Uncut controls (H0)	Pin.pin	*Pinus pinaster*	✓	0.55	0.001
	Sed.amp	*Sedum amplexicaule*	✓	0.51	0.001
	Sen.syl	*Senecio sylvaticus*	✓	0.24	0.001
	Spe.arv	*Spergularia arvensis*	✓	0.22	0.001
	Hel.ita	*Helichrysum italicum*	✓	0.19	0.001
	Cor.can	*Corynephorus canescens*	✓	0.10	0.015
Light harvesting (H25)	And.rag	*Andryala ragusina*	✓	0.30	0.009
	Xol.gut	*Xolantha guttata*	✓	0.27	0.003
	Hie.pil	*Hieracium pilosella*	M	0.25	0.001
	Air.car	*Aira caryophyllea*	M	0.17	0.001
	Fes.sp	*Festuca* sp.	E-M	0.10	0.024
	Dac.glo	*Dactylis glomerata*	E	0.10	0.001
Intermediate harvesting (H50)	Mic.ten	*Micropyrum tenellum*	✓	0.34	0.001
	Rum.buc	*Rumex bucephalophorus*	M	0.26	0.019
	Orn.pin	*Ornithopus pinnatus*	M	0.19	0.005
	Cor.lit	*Corrigiola litoralis*	M	0.12	0.001
	Mib.min	*Mibora minima*	✓	0.12	0.017
	Log.gal	*Logfia gallica*	M	0.11	0.044
Clear-cut (H100)	Hyp.mac	*Hypochoeris maculata*	✓	0.49	0.001
	Rum.ace	*Rumex acetosella*	E	0.41	0.001
	Sen.gal	*Senecio gallicus*	E	0.36	0.001
	Ero.cic	*Erodium cicutarium*	E	0.33	0.001
	Orn.com	*Ornithopus compressus*	✓	0.31	0.002
	Vul.myu	*Vulpia myuros*	✓	0.29	0.001
	Tri.arv	*Trifolium arvense*	E	0.27	0.001
	Bro.tec	*Bromus tectorum*	E	0.26	0.001
	Cer.ram	*Cerastium ramossisimum*	E	0.24	0.019
	Cho.jun	*Chondrilla juncea*	E	0.20	0.015
	Pet.nan	*Petrorhagia nanteuilii*	E	0.20	0.001
	Cyn.dac	*Cynodon dactylon*	E	0.19	0.001
	Hie.umb	*Hieracium umbellatum*	E	0.15	0.001
	Tri.cam	*Trifolium campestre*	E	0.14	0.007
	Sil.con	*Silene continhoi*	M	0.13	0.017
	Ver.arv	*Veronica arvensis*	E	0.12	0.010
	Aly.ser	*Alyssum serpyllifolium*	E	0.12	0.001
	Ger.mol	*Geranium molle*	E	0.11	0.001
	Ast.lin	*Asterolinon linum-stellatum*	E-M	0.10	0.002
	Ave.fat	*Avena fatua*	E	0.10	0.001
	Cen.mel	*Centaurea melitensis*	E	0.10	0.004
	Fil.lut	*Filago lutescens*	E-M	0.10	0.001

sensitively, will produce an undesirable ecological outcome for the conservation of the characteristic understorey species of these ecosystems.

A particularly noteworthy result was that the compositional differences between the control treatment (H0) and the intermediate levels of harvesting (H25, H50) were only quantitative. Two types of change were detected. Firstly, a group of species had a reduced cover after harvesting, these included characteristic species such as *H. italicum, S. amplexicaule*, *S. sylvaticus*, *Spergularia arvensis*. Secondly, a group that increased as a result of harvesting, this group included characteristic species such as *A. ragusina*, *M. tenellum, X. guttata*, and *A. caryophyllea* and *Hieracium pilosella*. Collectively, these results suggest that the light and medium harvesting intensities (H25, H50) are adequate to maintain the species complement in this ecosystem at least for the three years after harvest. Similar results have been found in oak-pine forest in Maine (Schumann et al., 2003). Moreover, as harvest intensity increases there appears to be an increased impact on understorey species composition. Low levels of harvesting (<50%), did not affect the qualitative component of species composition; essentially the forest appears resilient to these partial harvesting intensities. These conclusions mirror those from woodlands in south-western Ontario Canada, after a partial harvest (Burke et al., 2008). However, when the forest was completely cleared there was substantive damage to the species composition with both quantitative and qualitative components affected (Cayuela et al., 2008). Presumably, somewhere between a 50–100% harvest there is a shift towards damaging the ecosystem qualitatively, but we do not know this threshold level yet. Further research is needed to quantify this threshold in more detail.

4.2. Effects of harvesting on characteristic forest species (Hypothesis 2)

The harvesting treatments reduced the cover and frequency relative to the control treatment of 56% of the characteristic species, whereas 22% of species either maintained or increased their cover and frequency. Thus, Hypothesis 2 is partially accepted.

The species that were affected negatively by harvesting treatments were mainly the indicator species of control plots (H0), which have an affinity for shade (Aizpuru et al., 1999; Castroviejo et al., 1986–2009). It is reasonable, therefore, to hypothesise that their reduction after harvesting can be attributed to the sensitivity of these species to microclimate change, such as increased light (Suding, 2001), a reduction in suitable microhabitats (D'Amato et al., 2008) and competitive displacement by early-successional colonizers (Roberts and Gilliam, 2003; D'Amato et al., 2009). It is also possible that the two shrubs *H. italicum* and *L. pedunculata* were damaged physically during the harvesting operations (González-Alday et al., 2009). These results were in agreement with Decocq et al. (2004) who found a negative impact of silvicultural practices on characteristic forest species in temperate deciduous woodland in France.

In contrast, *A. ragusina*, *Jasione montana*, *Lupinus angustifolius* and *M. tenellum* were not affected by harvesting, possibly because they are better adapted to high light intensities (*L*-values = 7, Ellenberg et al., 1991). However, most of these species had greater frequency and cover in the Light- and Medium-harvest treatment (H25, H50). These results suggest that some form of intermediate disturbance generates suitable canopy conditions and its associated microhabitats for the maintenance of these species (Kimmins, 2004). Indeed *A. ragusina* and *M. tenellum* were indicator species of Light harvesting (H25) and Medium harvesting (H50) respectively.

The species that were affected positively by harvesting were *H. maculata*, *V. myuros*, *X. guttata* and *O. compressus*, most likely through a combination of factors. These species tend to require light conditions (*L*-values >8, Ellenberg et al., 1991) and they appear to thrive in newly-created, dry microhabitats (Ruiz de la Torre, 1996; D'Amato et al., 2009). It is also likely that these species are able to disperse over long distances, as they have appropriate dispersal mechanisms such as anemochory and zoochory. It is, therefore, important to consider the life-history strategy of each species involved and any interactions between species and between species and their environment (Cavallin and Vasseur, 2009), because impacts on individual species may go unnoticed in community-level analyses (Loya and Jules, 2008).

4.3. Effects of harvesting on the most abundant plant families (Hypothesis 3)

The harvest treatments, in comparison with controls, only influenced the plant cover of the Fabaceae; thus Hypothesis 3 is partially accepted. Many studies on understorey species have shown an increased plant cover after tree removal, as Moore et al. (2006) over Ponderosa pine forest in USA, and especially of Fabaceae and Poaceae after forestry management in *P. pinaster* woodlands in Spain (Pérez and Moreno, 1998). Our results for the Fabaceae are consistent with this general pattern since legumes cover increased with harvest intensity. The lack of response to harvest treatments of other families (Poaceae, Asteraceae, Caryophyllaceae, Geraniaceae) may be attributable to the short-term period since harvest, which restricted species recruitment (Cadenasso and Pickett, 2001), and the response of these other families, which were composed mainly of opportunistic species (Pérez and Moreno, 1998), will increase in the longer-term.

4.4. Conclusions

For conservation management, the Light- and Medium-harvest treatments (H25 and H50) were better conservation options than the clear-cut treatment, even though all had a significant impact on understorey community composition. In the partial harvest treatments (H25 and H50) most of the characteristic species survive, at least in the short-term. The species that are least able to tolerate disturbance were reduced and this affects the conservation value and regeneration potential of the developing vegetation. If management of these forests includes a conservation objective, it is essential to consider the different responses of understorey vegetation to harvesting in the management planning phase, and the selection of harvesting intensities. Otherwise substantive and expensive restoration action may be needed to return the understorey vegetation to its original state (Duffy and Meier, 1992). Clearly, further investigations are needed to assess the longer-term effect of these harvest treatments on understorey vegetation, because of the well-know resilience of Mediterranean ecosystems (Pérez-Ramos et al., 2008). At the same time, will be interesting to analyze the exact causes of the different species' responses (plant traits), and the potential value of alternative silvicultural practices, such as single tree selection. Our results point the way for the development of better multi-use forest management strategies, where conservation of biodiversity can be integrated with maintaining the landscape and ecological protection functions of these woodland ecosystems, whilst still producing a sustainable supply of resin and timber.

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