Alpine Botany

Effect of stand-replacing fires on Mediterranean plant species in their marginal alpine range

--Manuscript Draft--

Manuscript Number:	ALBO-D-13-00015R1
Full Title:	Effect of stand-replacing fires on Mediterranean plant species in their marginal alpine range
Article Type:	Original Article
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Abstract:	In the southern side of the Alps, many relic species with Mediterranean and sub-Mediterranean distribution were described in mild-winter, fire-prone areas. Very few studies have modeled the importance of environmental factors on their distribution. In this paper, we assessed the effect of fire on the occurrence of euri- and steno-Mediterranean (ESM) species in Pinus sylvestris forests of Aosta Valley (Italy), by analyzing vegetation in a chronosequence of six stand-replacing fires (1962-2006). We analyzed species richness along the chronosequence, and modeled it as a function of time since fire, environment, and stand structure. We observed a strong positive association between ESM and total species richness. Temporal vegetation dynamics did not follow the direct succession pattern that is commonly observed in Mediterranean ecosystems. Two distinct maxima of ESM species richness were observed: (i) short lived, ruderal species (32% of all ESM species) in the early post-fire stages, and (ii) dry grassland species (54%) in intermediate stages. The first were facilitated by the consumption of canopy and litter during fire, while the second by delayed tree canopy closure. In multivariate models of ESM species richness, light and elevation were the only significant predictors. Contrary to expectations, time since fire was not significant. Our study suggests that stand-replacing fires play an important role in preserving Mediterranean species in the study area by maintaining an open canopy, and promote local species diversity.
Response to Reviewers:	see attachment (file 'Responce to Reviewers comments_Lonati.pdf')

Ref.: Ms. No. ALBO-D-13-00015
Effect of stand-replacing fires on Mediterranean plant species in their marginal alpine range
Alpine Botany

Dear Jürg Stöcklin,
We reviewed the paper and we provided the revision of your manuscript according to your critical remarks. The reviewers' comments can be found in this document. For each, we added a list of change points.
Sincerely,

Michele Lonati and co-Authors

Answers to Reviewers' comments

Comments of Referee 1

Reviewer #1: General impression
The ms is well written in respect to style and language. I found only few things and I have the impression the ms is already copy-edited. Statistical analyses are simple and results easy to understand. I have two major concerns:
1) Chronosequence: It is well explained why the authors talk of a chronosequence. Most importantly, the burns are in close proximity, which makes the same species pool quite feasible and the idea of a chronosequence obvious. However, the burns cannot be viewed as one study site where species compositions follow a strict succession series like in a monitoring study site. This should be kept in mind if drawing graphs (scatter graphs instead of line graphs) or discussing communities classified into four time classes. Space for time is a too rough approach here; consider that there are only 30 relevés!
2) Essence of the study: In total 28 species Mediterranean plant species (ESM; most of them with a wider distribution, i.e. euri-med) were found in 6 forest burns; the number of these species was smaller on old areas, presumably because of advanced succession. Not surprisingly, the ESM species were more frequent at low elevations and in places with much light.
In summary, I consider the results poor; but given the fact that there is almost no information on vegetation following forest fires (only grey literature in the Valais, but at least recent), the information is new.
Authors' comments: see details, that address all the general impressions

Details
1) Page 2, line 4: according to the following text: euri- and steno-Mediterranean
Authors' comments: we modified the text according to your observation.
Old version:
'In this paper, we assessed the effect of fire on the occurrence of steno- and euri-Mediterranean (ESM) species in *Pinus sylvestris* forests ….'
New version:
'In this paper, we assessed the effect of fire on the occurrence of euri- and steno- Mediterranean (ESM) species in *Pinus sylvestris* forests…'

2) Page 4, line 15: Give a reference for the GIS-software, even if it is open-source.
Authors' comments: we added the reference of the software (Quantum GIS 1.8).
Old version:
'Selected fire perimeters were georeferenced in a GIS.'
New version:
'Selected fire perimeters were georeferenced using Quantum GIS 1.8 (Quantum GIS Development Team, 2012).'
Added in the References:
Quantum Gis Development Team (2012). Quantum GIS Geographic Information System. Open Source Geospatial Foundation Project (http://qgis.osgeo.org)

3) Page 4, line 28: two out of six, not five out of six; the sentence give a fully different picture than what is listed in Table 1. I see three larger burns (22 ha, 47 ha and 168 ha) and three quite small fires (2 ha, 5 ha, 5 ha)
Authors' comments: according with your observation, we used data from the 'Regional plan for forecasting, preventing and countering wildfires' (Bovio et al. 2005; quoted in the text) to define 'small fire' (fires smaller than 8 ha).
Old version:

'Area burned by crown fire was 41 ha on average, and <50 ha in five out of six sites.'
New version:
'Area burned by crown fire was 41 ha on average, and <8 ha in three out of six sites.'

4) Page 5, line 14: What if somebody is not familiar with Pignatti's chorotypes? Explain the meaning of euri- and steno-Mediterranean.
Authors' comments: we added the definition of euri- and steno-Mediterranean in the text.
Added sentence (In yellow):
'The recorded species were classified according to their biogeographic distribution (chorotypes) following Pignatti (1982). For each plot, we computed the total number of euri- and steno-Mediterranean (ESM) species. Steno-Mediterranean species show a distribution range strictly related to the Mediterranean basin, while euri-Mediterranean species show a larger distribution range, extending north and east of Mediterranean coastal areas (Pignatti 1982). The phytosociological optimum was associated to each species according to Aeschimann et al. (2004).'

5) Page 5, line 25: Just a question: why U for 'soil moisture'?
Authors' comments: we agree with your comment. In the original work Landolt codified 'soil moisture' with the letter 'F' (see Landolt, 1977). We replaced 'U' con 'F' in all the paper.

6) Page 7, line 10: This is the earliest stage, i.e. 4th year, or better < 5 years. However, to my impression, there is too little data to make generalisation.
Authors' comments: according to your impression (too little data to make generalisation) we rewrote the results (and the phytosociological description) avoiding generalisation, e.g. we replaced 'stage' with 'site'. We would maintain the phytosociological description, because Figure 3 show a clear separation of the species between the first site (annual early seral species) and the others. We also replaced '5 years' with '4 years' because now we describe the floristic composition of the 'younger site'.
The term 'stage' is still being used in the discussion, because a little generalisation was necessary to respond to the aims of the work.
Old version:
'….. Total shrub cover (including saplings) increased to 30-40% in intermediate successional stages, and decreased from 15 years after fire, when pine saplings exceeded 5 m height as shown by the contemporary increase in tree cover (Table 1). A moderate to high herbaceous cover was registered at all stages, without a clear trend along the chronosequence.
Total species richness (α-diversity) was high in the early post-fire stages, but significantly decreased in the 48 years-old site (24 species) (Fig. 1). Similarly, ESM species richness was significantly higher in the first (4 years-old) and intermediate (15-35 years-old) stages of the chronosequence, while in the oldest site they almost disappeared. Shannon index decreased significantly along the chronosequence, with very low values (less than 3) in the 48 years-old stand, when Scots pine achieved dominance in the tree layer.
A positive and significant correlation was found at the plot scale between ESM and total species richness (Fig. 2a). A similar relationship was found between ESM species richness and the Shannon index (Fig. 2b), although only 25% of the variability of ESM species richness was explained.
DCA ordination evidenced a clear separation between the different stages of the succession (Fig. 3a). The first two axes explained 18.4% of total variance (eigenvalues = 0.480 and 0.230, respectively).
Axis 1 helped discriminate the early (4 years-old), intermediate (5 to 35 years-old) and late (48 years-old) successional stages. Axis 2 helped separate the first intermediate (5 to 7 years-old) from the second intermediate stages (15 to 35-years-old). The species plot evidenced rather clear groups of species (dotted lines in Fig. 3b).
From a phytosociological point of view, the chronosequence can be described by the following:
I – the initial stage (5 years-old) was dominated by therophytic, early-seral species belonging to the classes *Koelerio-Corynephoretea* (e.g., *Minuartia fastigiata*, *Petrorhagia prolifera*), *Thero-Brachypodietea* (e.g., *Linaria simplex*, *Medicago minima*), and *Stellarietea mediae* (e.g., *Ajuga chamaepitys*, *Conyza canadensis*). Also important was the presence of ruderal nitrophilous species from the classes *Agropyretea intermedii-repentis* (e.g., *Convolvulus arvensis*, *Tragopogon dubius*) and *Artemisietea vulgaris* (e.g., *Lactuca serriola*, *Daucus carota*). Only a few of the therophytic species persisted in the intermediate stages (Appendix 1 in the Supplementary Material);
II – in the first intermediate stages (5 to 7 years-old), ruderal species belonging to the class *Artemisietea vulgaris* (e.g., *Carduus nutans*, *Erigeron annuus*, *Senecio inaequidens*) decreased, while species from meso-xerophile shrub and fringe communities (*Crataego-Prunetea* and *Trifolio-Geranietea sanguinei*) and dry grasslands (*Festuco-Brometea*) increased. This last group accounted for a total of 32 species, showing also many characteristic species of the class or related syntaxa;
III- in the second intermediate stages (15 to 35 years-old), species from the *Festuco-Brometea* decreased to 17. We observed an increase of species belonging to the class *Crataego-Prunetea* (e.g., *Prunus spinosa*, *Prunus mahaleb*, *Juniperus communis*), *Querco-Fagetea* s.l. (broadleaved forests: e.g., *Quercus pubescens*, *Prunus aviun*), and *Pyrolo-Pinetea* (Scots pine forests: e.g., *Saponaria ocymoides*, *Arctostaphylos uva-ursi* and *P. sylvestris* itself);

IV – in the final stage (48 years-old) species belonging to the class *Festuco-Brometea* almost disappeared. We observed many species from the class *Querco-Fagetea* s.l. (e.g., *Fraxinus excelsior*, *Sorbus aria*, *Lathyrus montanus*) and some from boreal, acidophilous woody communities (*Vaccinio-Piceetea excelsae*: e.g., *Picea excelsa*, *Melampyrum sylvaticum*, *Vaccinium myrtillus*).

Time since fire was positively correlated to both the first and the second DCA axis (Pearson's R = 0.61, p <0.001, and R = 0.56, p <0.001, respectively). ESM species were abundant in the early and intermediate stages of the succession (Fig. 3b). A significant, negative correlation (R = -0.76) was detected between DCA1 and the number of ESM species (Fig. 4a). DCA2 did not show any significant correlation with ESM species richness (Fig. 4b). ……'

New version:

'….. Total shrub cover (including saplings) increased up to 40% in the first 7 years after fire and decreased from 15 years after fire, when pine saplings exceeded 5 m height as shown by the contemporary increase in tree cover (Table 1). A moderate to high herbaceous cover was registered at all stages, without a clear trend along the chronosequence.

Total species richness (α-diversity) was high in the younger post-fire sites, but significantly decreased in the 48 years-old site (24 species) (Fig. 1). Similarly, ESM species richness was significantly higher in the first (4 years-old) and intermediate (15-35 years-old) stages of the chronosequence, while in the oldest site they almost disappeared. Shannon index decreased significantly along the chronosequence, with very low values (less than 3) in the 48 years-old stand, when Scots pine achieved dominance in the tree layer.

A positive and significant correlation was found at the plot scale between ESM and total species richness (Fig. 2a). A similar relationship was found between ESM species richness and the Shannon index (Fig. 2b), although only 25% of the variability of ESM species richness was explained.

DCA ordination evidenced a clear separation between the different sites of the succession (Fig. 3a). The first two axes explained 18.4% of total variance (eigenvalues = 0.480 and 0.230, respectively).

Axis 1 helped discriminate the youngest (4 years-old), intermediate (5 to 35 years-old) and oldest (48 years-old) sites. Axis 2 helped separate the first intermediate (5 to 7 years-old) from the second intermediate stages (15 to 35-years-old). The species plot evidenced rather clear groups of species (dotted lines in Fig. 3b).

From a phytosociological point of view, a chronosequence can be described by the following:

I – the youngest site (4 years-old) was dominated by therophytic, early-seral species belonging to the classes *Koelerio-Corynephoretea* (e.g., *Minuartia fastigiata*, *Petrorhagia prolifera*), *Thero-Brachypodietea* (e.g., *Linaria simplex*, *Medicago minima*), and *Stellarietea mediae* (e.g., *Ajuga chamaepitys*, *Conyza canadensis*). Also important was the presence of ruderal nitrophilous species from the classes *Agropyretea intermedii-repentis* (e.g., *Convolvulus arvensis*, *Tragopogon dubius*) and *Artemisietea vulgaris* (e.g., *Lactuca serriola*, *Daucus carota*). Only a few of the therophytic species persisted in the intermediate sites (Appendix 1 in the Supplementary Material);

II – in the first intermediate sites (5 to 7 years-old), ruderal species belonging to the class *Artemisietea vulgaris* (e.g., *Carduus nutans*, *Erigeron annuus*, *Senecio inaequidens*) decreased, while species from meso-xerophile shrub and fringe communities (*Crataego-Prunetea* and *Trifolio-Geranietea sanguinei*) and dry grasslands (*Festuco-Brometea*) increased. This last group accounted for a total of 32 species, showing also many characteristic species of the class or related syntaxa;

III- in the second intermediate sites (15 to 35 years-old), species from the *Festuco-Brometea* decreased to 17. We observed an increase of species belonging to the class *Crataego-Prunetea* (e.g., *Prunus spinosa*, *Prunus mahaleb*, *Juniperus communis*), *Querco-Fagetea* s.l. (broadleaved forests: e.g., *Quercus pubescens*, *Prunus aviun*), and *Pyrolo-Pinetea* (Scots pine forests: e.g., *Saponaria ocymoides*, *Arctostaphylos uva-ursi* and *P. sylvestris* itself);

IV – in the oldest site (48 years-old) species belonging to the class *Festuco-Brometea* almost disappeared. We observed many species from the class *Querco-Fagetea* s.l. (e.g., *Fraxinus excelsior*, *Sorbus aria*, *Lathyrus montanus*) and some from boreal, acidophilous woody communities (*Vaccinio-Piceetea excelsae*: e.g., *Picea excelsa*, *Melampyrum sylvaticum*, *Vaccinium myrtillus*).

Time since fire was positively correlated to both the first and the second DCA axis (Pearson's R = 0.61, p <0.001, and R = 0.56, p <0.001, respectively). ESM species were abundant in the youngest and intermediate sites (Fig. 3b). A significant, negative correlation (R = -0.76) was detected between DCA1 and the number of ESM species (Fig. 4a). DCA2 did not show any significant correlation with ESM species richness (Fig. 4b). ……'

7) Page 9, lines 19-20: This is a rather surprising statement since equilibrium has not been touched in the preceding text. What is in this context equilibrium after fire? A state of unchanged species abundances, i.e. constant plant community? This can only be reached if trees have formed a dark-enough stand or if grass species have formed a stand in which trees are hindered to germinate. But all this is not so easy to derive from 6 different burns. And in addition, there is no deeper consideration of this equilibrium thing.

Authors' comments: we agree with your comment and we decided to remove the second sentence

Old version:

'Total species diversity (Shannon index) was less predictable, probably due to the influence of local environmental variables on species cover. In addition, species abundances following disturbance may not reach equilibrium (Wilson 2012); this could probably affect Shannon diversity index, which is computed on abundance data.'

New version:
'Total species diversity (Shannon index) was less informative, probably due to the influence of local environmental variables on species cover.'

8) Page 9/10: Conclusion: Essentially, 50% of the conclusion is not directly related to the results found, i.e. it seem to me blown up.
Authors' comments: we reduced (of about 50%) the conclusion, limiting comments to the data directly related to the results.
Old version:
'Light conditions and elevation were the most important factors affecting the richness of Mediterranean species in the study area. The late spread of perennial grassland species after fire, probably limited by seed dispersal distance, resulted in a significant but weak dependence of Mediterranean species richness on time since fire.
Soil water limitations in dry, inner-alpine valleys result in a delayed tree canopy closure, and have a positive effect on the maintenance of heliophilous Mediterranean species in the intermediate stages of post-fire succession. Additionally, salvage logging, a management practice commonly applied in Aosta Valley after stand-replacing fires, may significantly delay Scots pine regeneration (Beghin et al. 2010). In unsalvaged areas, deadwood provides safe sites for the establishment of Scots pine regeneration, mitigating insolation and drought (Marzano et al. 2013), but is probably associated to less favorable conditions for Mediterranean species.
Our study suggests that stand-replacing crown fires play an important role in preserving Mediterranean species and promote local species diversity in the study area. Fires create (i) conditions favorable to the development of short-lived Mediterranean species in the first years after disturbance, and (ii) a spatio-temporal mosaic of dry grassland, shrub, and tree patches, characterized by many perennial Mediterranean grassland species. In the light of climate change scenarios, an increase in fire frequency and severity is expected (Zumbrunnen et al. 2009, 2011), along with upward migration of several plant species (Theurillat and Guisan 2001; Fyllas and Troumbis 2009). In dry, inner-alpine valleys, prolonged drought periods and increasing size of stand-replacing fires will aggravate bottlenecks to tree recruitment in Scots pine forests, and induce a shift to non-forest vegetation (Moser et al. 2010; Rigling et al. 2012). These processes are feared to negatively affect plant distribution and diversity (Beaumont et al. 2011). However, in this context, thermophilous Mediterranean species, occurring preferentially on warm and dry sites, should benefit from climate change, conserving their initial habitats and/or expanding to new suitable areas.'

New version:
'Our study suggests that stand-replacing crown fires play an important role in preserving Mediterranean species and promote local species diversity in the study area. Fires create (i) conditions favorable to the development of short-lived Mediterranean species in the first years after disturbance, and (ii) a spatio-temporal mosaic of dry grassland, shrub, and tree patches, characterized by many perennial Mediterranean grassland species.
Light conditions and elevation were the most important factors affecting the richness of Mediterranean species in the study area. Moreover, soil water limitations in dry, inner-alpine valleys result in a delayed tree canopy closure, and have a positive effect on the maintenance of heliophilous Mediterranean species in the intermediate stages of post-fire succession.
In the light of climate change scenarios, an increase in fire frequency and severity is expected (Zumbrunnen et al. 2009, 2011), promoting the conservation of the Mediterranean species across the Alps.'

9) Fig. 1: Since the sequence is not a true chronosequence (look at the bimodal curve, which is counter-intuitive and cannot be explained in a true chronosequence), the time-points must not be related by a line. A fitted curve (regression; linear or quadratic term) is more adequate. In Fig. 3, there is evidence that the 6 burns distinctly differ from each other.
Authors' comments: we removed the line in Figure 1. However, we decided not to draw a fitted curve, because the aim of Figure 1 is the comparison of means (Anova and Post hoc tests) and not the description of a regression line. If you agree, we would like to remove the scale of the 'Years after fire' axis, in order to highlight the differences between means rather than the trend along time.

Original version of Figure1:

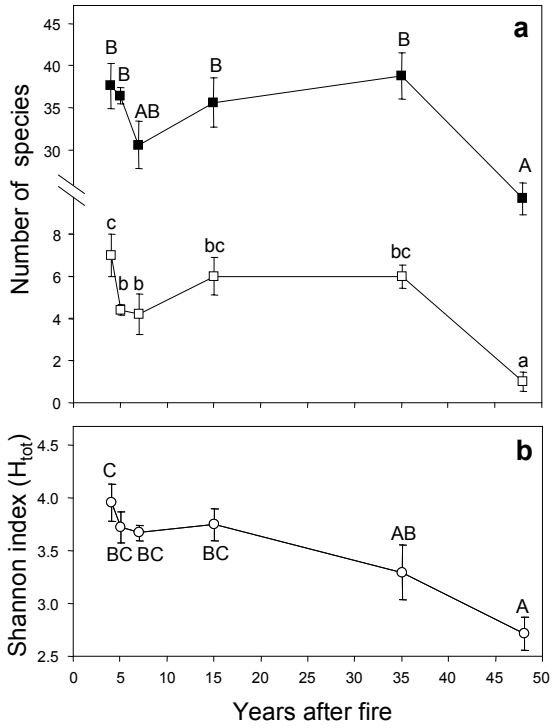
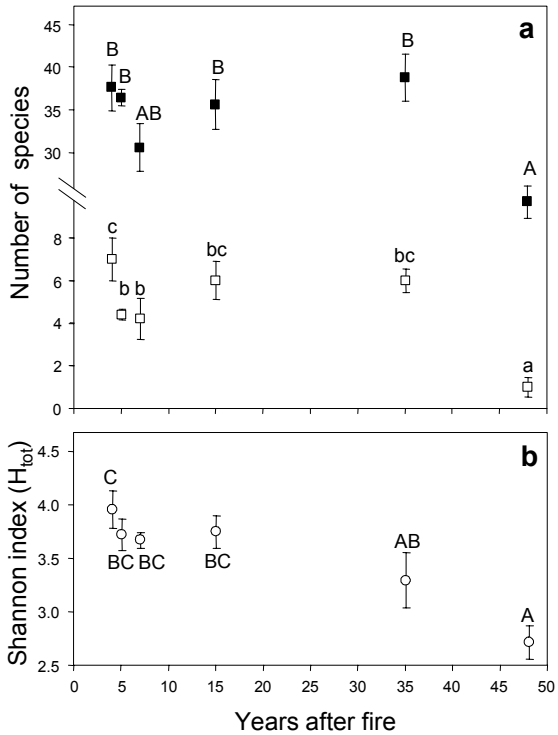
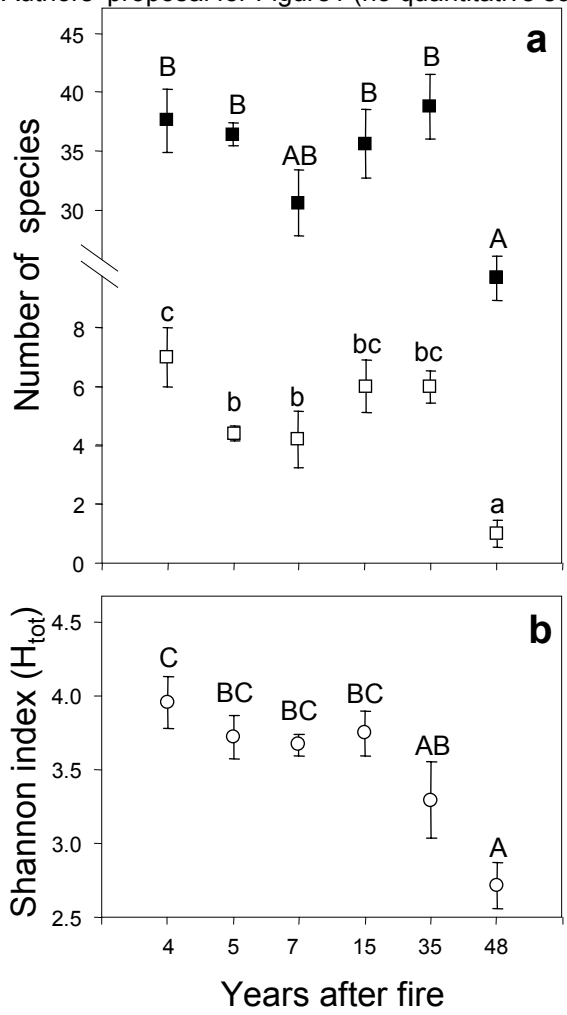


Figure1 without line (as requested by the Referee)



Authors' proposal for Figure1 (no quantitative scale on x axis)



Reviewer #2: The present manuscript is prepared in a very professional manner and provides a good insight in the research activities. The only weak point is related to the low number of plots that have been sampled in the context of this study and the vague description how the location of the plots in the study area was fixed. Some minor comments are given in order to allow the authors to improve their contribution:
Authors' comments: see details, that address all the general impressions

1) P3 L36: The mean values are valid for which altitude? As the study area is larger it is important to know the variation, instead of the man values perhaps.
Authors' comments: we agree with your observation: a range of precipitation and temperature could be more informative. However, we have not modelled climatic variables in the paper. The aim of reporting climatic data in the description of the study area is to outline the climate of the middle valley (dry inner-alpine valley). e detailed in the text the altitude, mean annual precipitation and mean annual temperature of Aosta weather station, that is the nearest to our studied sites (data from over 100 years of observation). These data were sufficient to illustrate the dry inner-alpine conditions of the studied area. Other weather stations close to the study sites have collected data only from a few years.
Old version:
'Mean annual precipitation is approximately 600 mm, and mean annual temperature is 10°C.'
New version:
'In the middle Aosta Valley, 20 km from the study sites, mean annual precipitation is 561.4 mm, and mean annual temperature is 10.6°C (Aosta, 583 m a.s.l.; mean of years 1841-1998) (Mercalli et al. 2003).'
Added in the References:
Mercalli L, Cat Berro D, Montuschi S, Castellano C, Ratti M, Di Napoli G, Mortara G, Guindani N (2003) Atlante climatico della Valle d'Aosta (Climate Atlas of the Aosta Valley). Regione Autonoma Valle d'Aosta, Direzione Protezione Civile, Ufficio Meteorologico, Aosta.

2) P4 L21: Is there some historical information available on the past treatments of the area (records, orthophotos, ..?). This would be important for judge the statement about homogeneity of pre-fire understory communities. Very often a similar management leads to similar structures and species composition. However, it would be important to know, how this past management was done.
Authors' comments: Unfortunately, there are no georeferenced information on past treatments, and old orthophotos (black and white) are of poor quality and not informative to investigate forest structure. However, significant information about past treatments in the area can be found in Camerano at al 2007 (quoted in the text), that confirms our assumption of homogeneity: "The autoecology of Scots pine has favored in the past the application of silvicultural treatments based on clearcut on areas larger than one hectare. These, and the species' ability to rapidly colonize abandoned lands, resulted in the prevalence of even-aged, monolayered stand structures (Camerano at al 2007)" (translated from Italian). We added this sentence to the text.

3) P4 L36: It would be good to know, how the authors avoided the trampling effect during field sampling, as the regeneration sample was investigated in the center of the plot (which is unusual, generally satellite plots are taken from a distance of the center, to avoid that effect...)
Authors' comments: herbaceous vegetation and tree saplings were sparse (see Table 2), so during field work it was quite easy to avoid trampling. During field work only 2 people were simultaneously on any plot, further reducing trampling effects. Other works used a similar sampling design (here after some examples):
Klanderud K. et al. 2010. Recovery of plant species richness and composition after slash-and-burn agriculture in a tropical rainforest in Madagascar. Biodiv Conserv 19:187-204. Each plot consisted of six 5x5 m sub-plots and each sub-plot had a 1x1m quadrat in its centre.
Lundqvist L., Fridman E., 1996. Influence of local stand basal area on density and growth of regeneration in uneven-aged *Picea abies* stands. Scand J For Res 11 (1-4): 364-369. Basal area of trees of at least 2 m height within three different radii from the subplot centres was measured.
Belden A.C., Pallardy S. G. (2009) Successional trends and apparent *Acer saccharum* regeneration failure in an oak-hickory forest in central Missouri, USA. Plant Ecol 204:305-322. "Saplings were sampled in a 0.04 ha nested concentric plot."

4) P7 L37: It is unclear if there are now 5 plots per site or less then that available for the analysis? From Figure 3 it seems, that the number is balanced, however this should be explained.
Authors' comments: the Referee probably meant P4 L37. The number of plot is balanced (5 plot per site). The sentence was rewriter for better clarity.
Old version:
'A total of 30 plots were established and located on the ground with a GPS unit. In each plot …'
New version:

'A total of 30 plots (5 per site) were established and located on the ground with a GPS unit. In each plot …'

5) P7 L35: The "basal area" and the "time since fire" is indirectly related. The larger the trees get, the more time since the last fire has passed. Therefore it might be important to check the significance of the criteria by removing the criteria time since fire or basal area from the GLM analysis.
Authors' comments: at P7 L33-35 we described the univariate models (see 'Methods-Data analysis' and Table 3a). We rewrote the text to explain more clearly that this part relates to Table 3a.
Old version:
'Of all variables entered in univariate GLM of ESM species richness, six were significant (Table 3). Light accounted for the highest D^2 (52%). The number of ESM species was also significantly explained by elevation (37%), moisture (31%) and tree basal area (26%). Time since fire and percent tree cover were less informative (D^2 < 20%).'
New version:
'Of all univariate GLM of ESM species richness, only six were significant (Table 3a). The model using light as a predictor accounted for the highest D^2 (52%). The number of ESM species was also significantly predicted by models based on elevation (37%), moisture (31%) or tree basal area (26%). Time since fire and percent tree cover models were less informative (D^2 < 20%).'

Using the stepwise GLM procedure (multivariate models, Table 3b) 'a correlation analysis was previously performed to exclude highly collinear predictors (R>0.80).' (See 'Methods-Data analysis'). The two variables 'time since fire' and 'basal area' were highly correlated (R=0.91) and 'basal area' was removed from the predictors. However the stepwise procedure selected only two variables (Light and Elevation), as reported in Table 3b.

6) P8 L14: Please provide an explanation for "direct succession".
Authors' comments: In the 'Introduction' the process of 'direct succession', or 'autosuccession', was already defined as: 'The high fire resilience of Mediterranean species results in the process of direct succession (or 'autosuccession' *sensu* Hanes 1971), in which the species present in the pre-fire vegetation regenerate directly after the disturbance, and successively self-thin due to competition as the stand matures (Hanes 1971; Whittaker and Levin 1977, Buhk et al. 2006).'

7) P9 L32: The distance from the unburned edge is also related to the location of the plots within the study area. It would be important to know, how the location of the plots was fixed, and what impact this might have on the results (e.g. centering the plots in the middle....). Especially when checking Table 1 it is not clear how the decision regarding the location was done. The elevation range is sometimes more then 500 m ....
Authors' comments: we agree with your observation and improved our description of sampling design in the text. What we did was superimposing on each site (crown fire area) a 25x25m grid and randomly extracting 5 grid nodes. Therefore, difference of elevation between plots and distance from the unburned edge were randomly distributed within each site.
Old version:
'Within each fire perimeter, we randomly established 5 circular plots (radius = 12 m), providing a minimum distance of 25 m between plots to avoid spatial autocorrelation. Distance from the unburned edge ranged from …'
New version:
'Within each fire area, we superimposed a 25x25 m grid and randomly selected 5 grid points, providing a minimum distance of 25 m between plots to avoid spatial autocorrelation. Distance from the unburned edge ranged from …'

8) Figure 2: the symbols should be labeled in a similar way as in figure 3 in order to support the identification of the different sites.
Authors' comments: according to your observation we changed the symbols in Figure 2. We also changed the captions of Figure 2.

Old version:

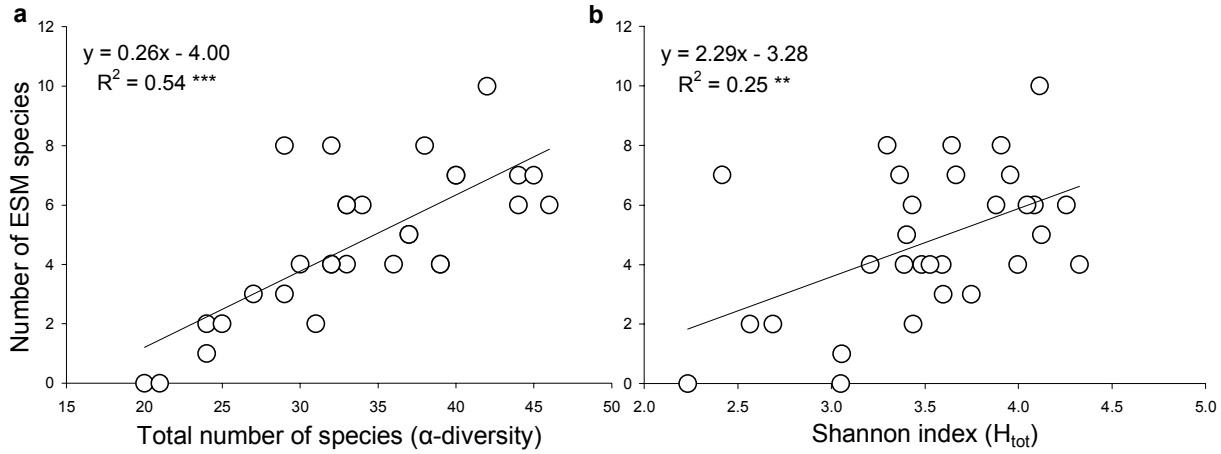


Fig. 2 Linear regression between ESM species richness and **a** total number of species and **b** Shannon index (n = 30; ** $p \leq 0.01$, *** $p \leq 0.001$)

New version:

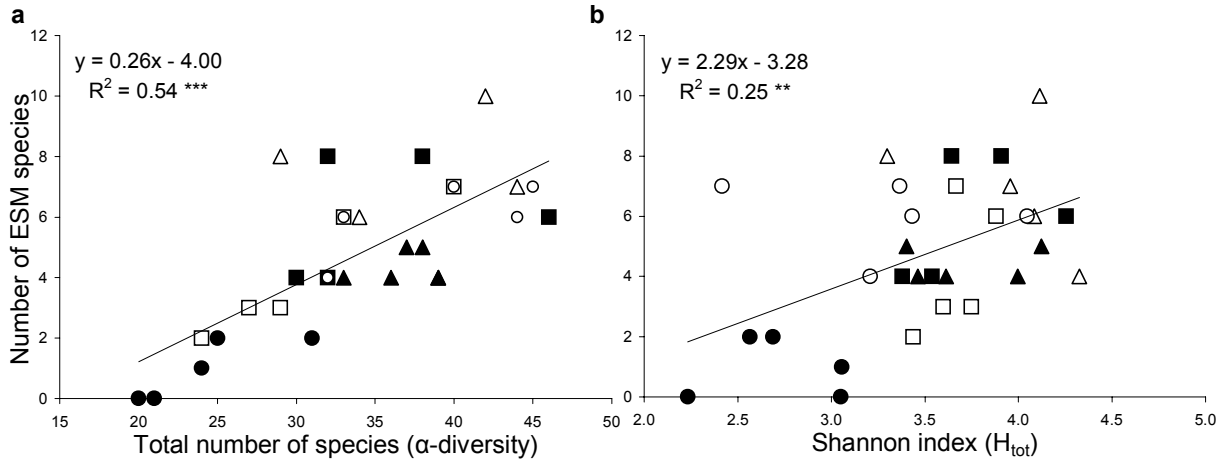


Fig. 2 Linear regression between ESM species richness and **a** total number of species and **b** Shannon index (n = 30; ** $p \leq 0.01$, *** $p \leq 0.001$). The different symbols are related to time since fire: (△) 4 years-old plots, (▲) 5 years-old plots, (□) 7 years-old plots, (■) 15 years-old plots, (○) 35 years-old plots, (●) 48 years-old plots.

Effect of stand-replacing fires on Mediterranean plant species in their marginal alpine range

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Abstract

In the southern side of the Alps, many relic species with Mediterranean and sub-Mediterranean distribution were described in mild-winter, fire-prone areas. Very few studies have modeled the importance of environmental factors on their distribution. In this paper, we assessed the effect of fire on the occurrence of euri- and steno-Mediterranean (ESM) species in *Pinus sylvestris* forests of Aosta Valley (Italy), by analyzing vegetation in a chronosequence of six stand-replacing fires (1962-2006). We analyzed species richness along the chronosequence, and modeled it as a function of time since fire, environment, and stand structure. We observed a strong positive association between ESM and total species richness. Temporal vegetation dynamics did not follow the direct succession pattern that is commonly observed in Mediterranean ecosystems. Two distinct maxima of ESM species richness were observed: (i) short lived, ruderal species (32% of all ESM species) in the early post-fire stages, and (ii) dry grassland species (54%) in intermediate stages. The first were facilitated by the consumption of canopy and litter during fire, while the second by delayed tree canopy closure. In multivariate models of ESM species richness, light and elevation were the only significant predictors. Contrary to expectations, time since fire was not significant. Our study suggests that stand-replacing fires play an important role in preserving Mediterranean species in the study area by maintaining an open canopy, and promote local species diversity.

Keywords

Chronosequence • Conservation • Forest fire • Inner-alpine valleys • *Pinus sylvestris* L. • Plant diversity

Introduction

The southern side of the Alps is characterized by a relatively high plant biodiversity (Aeschimann et al. 2011b), as a results of glacial and postglacial history (Habel et al. 2010). Many mild-winter areas in the southern Alps host xerothermic vegetation complexes, and are characterized by the presence of relic species with Mediterranean or sub-Mediterranean distribution (Braun-Blanquet 1961; Aeschimannet al. 2004; Schwabe and Kratochwil 2004). Many of these species reach here their northern range limits and, although globally common, they are locally rare, so as to be included in Red Lists as species with high conservation priority (Conti et al. 1997; Moser et al. 2002). At the regional scale (γ-diversity), a strong positive correlation was observed between the richness of Mediterranean species and the total species richness (Aeschimann et al. 2011a, 2011b).

Many Mediterranean species have evolved strategies to survive periodic fires (Naveh 1975; Pausas 1999). The high fire resilience of Mediterranean species results in the process of direct succession (or 'autosuccession' *sensu* Hanes 1971), in which the species present in the pre-fire vegetation regenerate directly after the disturbance, and successively self-thin due to competition as the stand matures (Hanes 1971; Whittaker and Levin 1977, Buhk et al. 2006). This quick regeneration after fire is considered an evolutionary adaptation to the long-lasting influence of fire in the Mediterranean basin (Naveh 1975).

In many parts of the southern Alps, fire has shaped the vegetation since the Neolithic Age (Tinner et al. 1999). In these fire-prone areas, pyrophytic Mediterranean species often occur, and fire plays an important role in their maintenance. For example, in southern Switzerland the Mediterranean sageleaf rockrose (*Cistus salviifolius*) usually occurs on warm rocky outcrops that are permanently treeless, but the species was observed to temporarily extend its occurrence in burnt, tree-free spots (Moretti et al. 2006).

There has been very little work on modelling the distribution of Mediterranean species in their relict alpine range, (Moretti et al. 2006). Most studies were merely descriptive of individual species' ecology or sinecology (e.g., Rey 1989 on *Thymus vulgaris* in Aosta Valley; Vagge and Biondi 2008 on *Juniperus phoenicea* and *J. thurifera* in the Western Alps). To our knowledge, no research to date has modelled the occurrence of the whole Mediterranean biogeographic species group in post-fire vegetation dynamics of the Alps.

The present work aims to assess the role of fire in maintaining Mediterranean species in a dry, inner-alpine valley of the southwestern Alps (Aosta Valley, Italy). We measured the richness of Mediterranean species in a chronosequence of stand-replacing fires affecting Scots pine (*Pinus sylvestris*) forests. The study addresses the following questions: (1) how did Mediterranean species richness change along the chronosequence? (2) how did Mediterranean species richness relate to total species richness? (3) which ecological factors affected Mediterranean species occurrence?

Methods

1) Study area

The research was carried out in Aosta Valley, northwestern Italy. The regional topography is strongly influenced by late glacial dynamics (Burga 1988). Orographic seclusion, East-West direction, and foëhn winds contribute to a climate with relative low precipitation, typical of inner-alpine regions (Schwabe and Kratochwil 2004). In the middle Aosta Valley, 20 km from the study sites, mean annual precipitation is 561.4 mm, and mean annual temperature is 10.6°C (Aosta, 583 m a.s.l.; mean of years 1841-1998) (Mercalli et al. 2003). The area is characterized by a complex geology, with dominant

calcareous schists and subordinate silicate rocks with base-rich or calcium carbonate-rich patches, and rare serpentine bedrocks (Guyot 1935).

Scots pine stands belong to the *Ononido-Pinion* alliance (Braun-Blanquet 1961; Filipello et al. 1985), that is described as a xerothermic woodland of colline and montane altitudes on alkaline soils, geographically centered on the dry valleys of the inner Alps (Mucina et al. 1993). Scots pine contribute 6% of forest cover in Aosta Valley (Camerano et al. 2007), but represented 29% of total burned area in the period 1961-2010 (source: Corpo Forestale Regione Autonoma Valle d'Aosta, Nucleo Antincendi Boschivi). The regional fire regime is characterized by a winter-early spring fire season, with prevailing low-severity, surface fires (average burned size: 7.6 ha). An increase in size and intensity of fires has been observed in the last decades (Bovio et al. 2005).

2) Site selection

Vegetation dynamics were assessed along a chronosequence of sites with known fire dates. Although longitudinal observations of permanent plots allow for a better description of vegetation dynamics, chronosequences are considered a valid alternative (e.g. Foster and Tilman 2000; Prévosto et al. 2011), as long as sources of variation other than time are controlled for (Delarze et al. 1992; Capitanio and Carcaillet 2008; Gonzàlez-Tagle et al. 2008).

We selected from a regional database of wildfires in Aosta Valley (source: Corpo Forestale Regione Autonoma Valle d'Aosta, Nucleo Antincendi Boschivi) all crown fires which occurred in Scots pine forests between 1961 and 2010. Selected fire perimeters were georeferenced using Quantum GIS 1.8 (Quantum GIS Development Team, 2012).

In order to minimize sources of variation other than time, we selected six fires according to a space-for-time substitution (Yanai et al. 2003). Fire perimeters were located in the same bioclimatic belt according to Blasi (2010), and were clipped to homogenous elevation (1100 to 1600 m a.s.l.), slope, aspect (southerly), and relative slope position. Topographic information was obtained from a 10-m resolution Digital Terrain Model. Selected sites were located in the neighbouring municipalities of Verrayes and Saint-Denis (45°46' N, 7°32' E), with a maximum distance between any two sites of about 5 km (Table 1). We also assumed homogeneity of pre-fire understory community based on the fact that mature, closed-canopy stands of Scots pine (conducive to crown fire) in ecologically similar sites should be associated to homogenous edaphic conditions. The autoecology of Scots pine has favored in the past the application of silvicultural treatments based on clearcut on areas larger than one hectare. These, and the species' ability to rapidly colonize abandoned lands, resulted in the prevalence of even-aged, monolayered stand structures (Camerano at al 2007).

We used individual fires as treatments, similarly to previous research in post-fire regeneration dynamics (Capitanio and Carcaillet 2008; González-Tagle et al. 2008). Lack of true replication is common in wildfire studies (van Mangtem et al. 2001). Pseudoreplication (i.e., subsampling within the same fire area) could not be entirely avoided, due to the limited number of wildfire events satisfying the conditions for site selection.

Area burned by crown fire was 41 ha on average, and <8 ha in three out of six sites. Following regional post-disturbance management policies, all sites had been salvage logged, i.e., all dead trees were harvested after fire (Lindenmayer at al. 2004). Salvage logging in Aosta Valley is ordinarily carried out 1-4 years after fire (Beghin et al. 2010).

At all sites, browsing of the terminal shoots, fraying, and bark stripping on forest regeneration by wild ungulates were very negligible.

3) Data collection

Sampling was carried out in summer 2011. Within each fire area, we superimposed a 25x25 m grid and randomly selected 5 grid points, providing a minimum distance of 25 m between plots to avoid spatial autocorrelation. Distance from the unburned edge ranged from 2 to 169 m. A circular subplot (radius = 5 m) was established at the center of each plot for tree regeneration and vegetation analysis. A total of 30 plots (5 per site) were established and located on the ground with a GPS unit. In each plot we measured the following variables:

(a) Stand structure and regeneration: we recorded the species, frequency, and diameter at 1.3 m height (DBH) of all individuals with DBH ≥ 7.5 cm (adult trees). Individuals with height > 1.3 m and DBH < 7.5 cm (saplings) and individuals with height ≤ 1.3 m (seedlings) were measured in each subplot, by recording their DBH and root collar diameter (RCD) respectively;

(b) Ground cover: percent cover of bare soil, rocks, herb, lower shrub (height ≤ 1.3 m), upper shrub (height between 1.3 and 5.0 m) and tree (height >5.0 m) layers was visually estimated in each subplot;

(c) Vegetation: we visually assessed presence/absence and percent cover of each species in the herbaceous, lower shrub (height ≤ 1.3 m), upper shrub (height between 1.3 and 5.0 m), and tree layers (height > 5.0 m) in each subplot. Species with very low cover (<1%) were registered as sporadic ('+'), according to Braun-Blanquet (1932), and subsequently weighted using a 0.3% conversion value (Tasser and Tappeiner 2005). Floristic nomenclature followed Pignatti (1982).

4) Vegetation and environmental parameters

The recorded species were classified according to their biogeographic distribution (chorotypes) following Pignatti (1982). For each plot, we computed the total number of euri- and steno-Mediterranean (ESM) species. Steno-Mediterranean species show a distribution range strictly related to the Mediterranean basin, while euri-Mediterranean species show a larger distribution range, extending north and east of Mediterranean coastal areas (Pignatti 1982). The phytosociological optimum was associated to each species according to Aeschimann et al. (2004). Characteristic species of each class (or related syntaxa) were defined according to Theurilliat et al. (1994).

For each plot, topographic variables (elevation, slope and aspect) were derived from a 10-m resolution Digital Terrain Model. Aspect was transformed into southness (southness = 180 - |aspect - 180|), to provide an interpretable, non circular variable (Chang et al. 2004). Distance to nearest forest edge was calculated in a GIS using crown fire perimeter and GPS position of each plot.

At the plot scale, the following vegetation descriptors were computed: (i) total species richness, i.e., the total number of plant species; (ii) Shannon diversity index (H_{tot}), based on the percent cover of each species; (iii) woody species basal area (BA, m^2 ha^{-1}), computed using the DBH of adult trees and saplings and the RCD of seedlings; (iv) woody species density (individuals ha^{-1}), computed using seedlings, saplings and adult trees; (v) mean Landolt (1977) indicator values for light (L), soil moisture (F) and nutrient content (N), based on species presence/absence (unweighted indices). Previous research suggested that unweighted indices are more responsive to environmental variation than indices weighted on species abundance, because they assign a greater importance to sporadic species with high indicator power (Smartt et al. 1976; Wilson 2012). Mean Landolt indicator values were computed excluding ESM species, in order to ensure total independence between the predictors and the response variable (i.e., ESM species richness).

5) Data analysis

We assessed between-site differences in woody species density (BA and individuals per hectare), ground cover (percent cover of bare soil, herb, total shrub and tree layers), and biodiversity variables (ESM and total richness, Shannon index) by univariate ANOVA with a Ryan-Einot-Gabriel-Welsch (REGWQ) post-hoc test ($p \leq 0.05$). Prior to the analysis, data were tested for normality and homoscedasticity, and transformed as appropriate.

The relationship between ESM species richness and overall biodiversity indices was tested by Pearson's correlation ($p \leq 0.05$). All variable were tested for normality to meet assumptions of the analysis.

A non-canonical Detrended Correspondence Analysis (DCA) was performed on by-segment basis on presence/absence data in order to detect indirect floristic gradient along the chronosequence. The use of DCA on a by-segment basis ensures that distances in the ordination plot approximate ecological distances in terms of species turnover, which is a desirable property in vegetation succession studies (Buhk at al. 2006). Correlation statistics (Pearson's R, $p \leq 0.05$) were used to assess relationship of each DCA axis with ESM species richness and time since fire.

Finally, we assessed the relative effect of time since fire, environmental and stand structural variables on ESM species richness by Generalized Linear Models (GLM). Because of the nature of the dependent variable (count), a Poisson error distribution was assumed and a logarithmic link function was used (McCullagh and Nelder 1983). Predictors were standardized (Z-scores) to allow for analysis of effect size by scrutinizing model parameters (B coefficients). In a first step, a GLM was fitted using one predictor at a time. Subsequently, a multivariate GLM was built using a forward stepwise optimization, i.e., predictors were retained only if their addition resulted in a significant parameter estimate. A correlation analysis was previously performed to exclude highly collinear predictors ($R>0.80$). Akaike Information Criterion with small-sample correction (AICC) and percent deviance explained (D^2) were used as measures of goodness-of-fit. D^2 was calculated as (Null deviance−Residual deviance)/Null deviance, where Null deviance is the deviance of an intercept-only GLM, and Residual deviance is the deviance that remains unexplained after model fit.

All the statistical analysis were performed using SPSS 19 (SPSS Inc, Chicago). DCA was performed using CANOCO 4.5 (ter Braak and Šmilauer 1998).

Results

A total of 165 plant species were found at the sites, among which 28 ESM species (17.0%) (Appendix 1 in the Supplementary Material). Over a half of ESM species found at the sites (57%) have their phytosociological optimum in dry, nitrogen-poor grasslands of the class *Festuco-Brometea*, with many characteristic species belonging to the continental, steppic swards of the order *Festucetalia valesiaceae* (e.g., *Euphorbia seguierana*, *Ononis pusilla*, *Koeleria vallesiana*). Five ESM species belong to pioneer communities with therophytes (*Koelerio-Corynephoretea*), and four to nitrophilous, pioneer therophytic communities (*Thero-Brachypodietea* and *Stellarietea mediae*). Only three ESM species are associated to forest mantles and mature woody stands (*Cratego-Prunetea*, *Quercetea pubescentis* and *Pyrolo-Pinetea*).

Stand structural variables differed significantly along the chronosequence (Table 2). Regeneration density was initially high (on average about 2240 trees ha^{-1} in the first 7 years after fire) due to sprouter species (mainly *Quercus pubescens* and *Populus tremula*), and increased 15-35 years after fire, in concomitance with Scots pine establishment. Scots pine showed very scarce regeneration in the first 7 years after fire, but its contribution gradually increased, until it became the dominant species in the mature stand (48 years after fire). Total shrub cover (including saplings) increased up to 40% in the first 7 years after fire and decreased from 15 years after fire, when pine saplings exceeded 5 m height as shown by the

contemporary increase in tree cover (Table 1). A moderate to high herbaceous cover was registered at all stages, without a clear trend along the chronosequence.

Total species richness (α-diversity) was high in the younger post-fire sites, but significantly decreased in the 48 years-old site (24 species) (Fig. 1). Similarly, ESM species richness was significantly higher in the first (4 years-old) and intermediate (15-35 years-old) stages of the chronosequence, while in the oldest site they almost disappeared. Shannon index decreased significantly along the chronosequence, with very low values (less than 3) in the 48 years-old stand, when Scots pine achieved dominance in the tree layer.

A positive and significant correlation was found at the plot scale between ESM and total species richness (Fig. 2a). A similar relationship was found between ESM species richness and the Shannon index (Fig. 2b), although only 25% of the variability of ESM species richness was explained.

DCA ordination evidenced a clear separation between the different sites of the succession (Fig. 3a). The first two axes explained 18.4% of total variance (eigenvalues = 0.480 and 0.230, respectively).

Axis 1 helped discriminate the youngest (4 years-old), intermediate (5 to 35 years-old) and oldest (48 years-old) sites. Axis 2 helped separate the first intermediate (5 to 7 years-old) from the second intermediate stages (15 to 35-years-old). The species plot evidenced rather clear groups of species (dotted lines in Fig. 3b).

From a phytosociological point of view, a chronosequence can be described by the following:

I – the youngest site (4 years-old) was dominated by therophytic, early-seral species belonging to the classes *Koelerio-Corynephoretea* (e.g., *Minuartia fastigiata*, *Petrorhagia prolifera*), *Thero-Brachypodietea* (e.g., *Linaria simplex*, *Medicago minima*), and *Stellarietea mediae* (e.g., *Ajuga chamaepitys*, *Conyza canadensis*). Also important was the presence of ruderal nitrophilous species from the classes *Agropyretea intermedii-repentis* (e.g., *Convolvulus arvensis*, *Tragopogon dubius*) and *Artemisietea vulgaris* (e.g., *Lactuca serriola*, *Daucus carota*). Only a few of the therophytic species persisted in the intermediate sites (Appendix 1 in the Supplementary Material);

II – in the first intermediate sites (5 to 7 years-old), ruderal species belonging to the class *Artemisietea vulgaris* (e.g., *Carduus nutans*, *Erigeron annuus*, *Senecio inaequidens*) decreased, while species from meso-xerophile shrub and fringe communities (*Crataego-Prunetea* and *Trifolio-Geranietea sanguinei*) and dry grasslands (*Festuco-Brometea*) increased. This last group accounted for a total of 32 species, showing also many characteristic species of the class or related syntaxa;

III- in the second intermediate sites (15 to 35 years-old), species from the *Festuco-Brometea* decreased to 17. We observed an increase of species belonging to the class *Crataego-Prunetea* (e.g., *Prunus spinosa*, *Prunus mahaleb*, *Juniperus communis*), *Querco-Fagetea* s.l. (broadleaved forests: e.g., *Quercus pubescens*, *Prunus aviun*), and *Pyrolo-Pinetea* (Scots pine forests: e.g., *Saponaria ocymoides*, *Arctostaphylos uva-ursi* and *P. sylvestris* itself);

IV – in the oldest site (48 years-old) species belonging to the class *Festuco-Brometea* almost disappeared. We observed many species from the class *Querco-Fagetea* s.l. (e.g., *Fraxinus excelsior*, *Sorbus aria*, *Lathyrus montanus*) and some from boreal, acidophilous woody communities (*Vaccinio-Piceetea excelsae*: e.g., *Picea excelsa*, *Melampyrum sylvaticum*, *Vaccinium myrtillus*).

Time since fire was positively correlated to both the first and the second DCA axis (Pearson's $R = 0.61$, $p < 0.001$, and $R = 0.56$, $p < 0.001$, respectively). ESM species were abundant in the youngest and intermediate sites (Fig. 3b). A significant,

negative correlation (R = -0.76) was detected between DCA1 and the number of ESM species (Fig. 4a). DCA2 did not show any significant correlation with ESM species richness (Fig. 4b).

Of all univariate GLM of ESM species richness, only six were significant (Table 3a). The model using light as a predictor accounted for the highest D2 (52%). The number of ESM species was also significantly predicted by models based on elevation (37%), moisture (31%) or tree basal area (26%). Time since fire and percent tree cover models were less informative (D2 < 20%). The total number of ESM species increased with light and decreased with increasing time since fire, tree cover, basal area, moisture and, elevation.

Using the stepwise GLM procedure, ESM species richness was best predicted by a combination of light and elevation, which resulted in the lowest AICC (Table 3b).

Discussion

In the Alpine flora, the proportion of ESM species on the total number of species is 16.1% on average, ranging from 24% in the southwestern regions (Maritime Alps, Alpes-de-Haute-Provence and Drôme), to 4% in Oberbayern (Aeschimann et al. 2011b). In Aosta Valley, the reported proportion of ESM to total number of species is 11.8%; therefore, the studied chronosequence appeared rich in Mediterranean species (17%), a likely consequence of the submediterranean, mild-winter climate of the study area.

Post-fire vegetation dynamic was typical of secondary succession in temperate regions (Grime 2002; Prévosto et al. 2011), i.e., a transition from annual/ruderal species (belonging to the classes *Thero-Brachypodietea*, *Stellarietea mediae*, *Agropyretea intermedii-repentis* and *Artemisietea vulgaris*) to perennial herbaceous species characteristic of dry grassland and fringe communities (*Festuco-Brometea* and *Trifolio-Geranietea*), to woody shrub species (*Crataego-Prunetea*), and finally woodland species (*Pyrolo-Pinetea* and *Vaccinio-Picetea*).

Despite Scots pine achieved dominance 48 years after fire, pine regeneration was initially delayed (up to 15 years), similarly to observations in other dry areas, both in Mediterranean and Alpine regions (Rodrigo et al. 2004; Moser et al. 2010; Vilà-Cabrera et al. 2012). This behavior is in disagreement with direct succession, which is commonly observed in Mediterranean ecosystems (Trabaud and Lepart 1981; Buhk et al. 2006; Arnan et al. 2007). In autosuccesion, pre-fire species regenerate directly after fire. Pioneer, short-lived species do not prepare the site for the subsequent settlement of later successional species, but they grow side by side in the first post-fire stages (Buhk at al. 2006). In the observed chronosequence, however, ESM species were the components of a replacement process characterized by the gradual substitution of distinct successional stages.

Our results are consistent with observations of ESM species richness in steppic, herbaceous complexes of the order *Festucetalia valesiaceae* in dry, inner-alpine regions of the central and western Alps (Royer 1991; Schwabe and Kratochwil 2004). In fact, the most important group of ESM species recorded in our work has its phytosociological optimum in dry grasslands of *Festuco-Brometea* and related syntaxa, including *Festucetalia valesiaceae*. According to Braun-Blanquet (1961), the association between dry grassland species and forest communities of the *Ononido-Pinion* alliance in Aosta Valley is a consequence of high light penetration through the low-growing, open tree canopy (see also Mucina et al. 1993; Kelly and Connolly 2000). In the study area, moisture limitations resulted in a sparse canopy cover and a high total species richness up to the intermediate stages of the chronosequence (35 years since fire). By contrast, in the moister Insubric region, species richness was observed to decline already 15 years after disturbance (Delarze et al. 1992), due to the rapid recovery of herbaceous and woody species.

Along the chronosequence, two distinct maxima of ESM species richness were observed, corresponding to two groups of species differing in post-fire germination strategy:

(a) Annual/ruderal species (32% of total ESM species recorded) were more abundant in the early successional stages. These species, belonging to the classes *Koelerio-Corynephoretea, Thero-Brachypodietea*, and *Stellarietea mediae*, germinate soon after fire, and are facilitated by the combustion of canopy and litter (Schütz 2000). The presence of these species in pre-fire, closed-canopy forest may be explained as a legacy of previous disturbances, or as a result of dispersal from surrounding areas (Halpern et al. 1999; Latzel et al. 2011). Annual ESM species disappeared quickly (5 years after fire), and only few therophytic species persisted in the intermediate post-fire stages. However, their small seeds can persist in the buried soil seed bank, and may cyclically spread after new fires. Therefore, the soil seed bank plays a crucial role to the survival of many ESM species in the studied area, as observed for other rare species (Keddy and Reznicek 1982; Rowell et al. 1982; McCue and Holtsford 1998).

(b) Dry grassland species (57% of total ESM species recorded), belonging to the class *Festuco-Brometea* (mainly perennial), were more abundant in intermediate successional stages (15 to 35 years since fire). Calcareous grassland species form a transient seed bank (Willems 1996; Davies and Waite 1998; Kalamees and Zobel 2002), usually confined to the upper soil (Akinola et al. 1998) and consequently susceptible to fire damage (Cespedes at al. 2012). Only a few ESM legume species (e.g., *Ononis natrix, O. pusilla*: Buhk and Hensen 2005) may be stimulated by fire, which is able to break the physical barriers of their hard-coated seeds (Martin et al. 1975; Auld and O'Connell 1991). Since seed dispersal distance of these species is limited to a few meters or less (Verkaar et al. 1983; Kalamees and Zobel 2002; Becker 2010), their re-colonization by seed is slow. Open canopies, however, allow grassland species to persist for many years in sub-optimal forest habitat, as observed by Heubes et al. (2001) in central Europe. In the study area, it is likely that dry, grassland species were well represented in pre-fire, mature stands, as demonstrated by the moderate to high herbaceous cover observed in the older sites. After a fire, these herbs were therefore able to resprout, and replenish the soil seed bank.

In the Alps, at the regional scale (γ-diversity), a strong positive association was observed between the richness of Mediterranean species and total species richness (Aeschimann et al. 2011a, 2011b). In our work, the strong correlation between total species richness and the number of ESM species at the plot scale (α-diversity) confirmed the role of Mediterranean species as indicator species (*sensu* Spellerberg 1994) at the community-ecosystem level (*sensu* Noss 1990). Total species diversity (Shannon index) was less informative, probably due to the influence of local environmental variables on species cover.

ESM species richness was weakly related to time since fire: the variable was significant in the univariate GLM, but was not selected by the stepwise algorithm. Significant differences in ESM species richness emerged only between the first and last successional stages. This was probably due to the slow re-colonization of dry grassland species.

The number of ESM species was significantly higher under high light conditions and at low elevations, due to their heliophilous and thermophilous character (Thompson 2005). The negative relationship between ESM species richness and stand structural variables, e.g., tree basal area and canopy cover, and ecological variables that favor Scots pine establishment and growth, e.g., moisture (Castro et al. 2004; Moser at al. 2010), was consistent with the light preferences of ESM species.

Other topographic variables did not affect ESM species richness, conforming to expectations of homogeneity under the adopted site selection criteria. On a larger scale, we expect Mediterranean species to abound at competition-free sites, like rocky outcrops or steep slopes, as described e.g. for *Cistus salviifolius* in the southern Alps (Moretti et al. 2006).

Finally, distance from the unburned edge was not significant in models of ESM species richness. This indicates the absence of edge effects suggesting that even small crown fires may be important for ESM establishment and persistence.

Conclusion

Our study suggests that stand-replacing crown fires play an important role in preserving Mediterranean species and promote local species diversity in the study area. Fires create (i) conditions favorable to the development of short-lived Mediterranean species in the first years after disturbance, and (ii) a spatio-temporal mosaic of dry grassland, shrub, and tree patches, characterized by many perennial Mediterranean grassland species.

Light conditions and elevation were the most important factors affecting the richness of Mediterranean species in the study area. Moreover, soil water limitations in dry, inner-alpine valleys result in a delayed tree canopy closure, and have a positive effect on the maintenance of heliophilous Mediterranean species in the intermediate stages of post-fire succession.

In the light of climate change scenarios, an increase in fire frequency and severity is expected (Zumbrunnen et al. 2009, 2011), promoting the conservation of the Mediterranean species across the Alps.

Acknowledgment This research was partially supported by the Alcotra project 2007/2013 ‘‘Foreste di protezione: tecniche gestionali e innovazione nelle Alpi occidentali – Forêts de protection: techniques de gestion et innovation dans les Alpes occidentales’’, with the co-sponsorship of Piedmont Region and Aosta Valley Autonomous Region. We thank James N. Long and Diego Trucchi for field sampling, Giancarlo Cesti and Corpo Forestale Regione Autonoma Valle d’Aosta, Nucleo Antincendi Boschivi for data provision.

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Figure captions

Fig. 1 Mean (±SE) of **a** total species richness (■), ESM species richness (□), and **b** Shannon index (○) at different times since fire. Sites with no letters in common were significantly different (REGWQ post-hoc test, $p \leq 0.05$)

Fig. 2 Linear regression between ESM species richness and **a** total number of species and **b** Shannon index (n = 30; ** $p \leq 0.01$, *** $p \leq 0.001$). The different symbols are related to time since fire: (B) 4 years-old plots, (▲) 5 years-old plots, (□) 7 years-old plots, (■) 15 years-old plots, (○) 35 years-old plots, (●) 48 years-old plots.

Fig. 3 DCA ordination of **a** sample plots (different symbols in relation to time since fire) and **b** species. Species labels are centred on scores, with minor adjustments to avoid text overlap. Gray circles and bold labels identify ESM species. Dotted lines evidence separations between species groups. Species codes: Aab: *Artemisia absinthium.* Aag: *Alyssum argenteum.* Aal: *Ailanthus altissima.* **AAR**: *Acinos arvensis.* **AAY**: *Alyssum alyssoides.* Aca: *Achnatherum calamagrostis.* **ACH**: *Ajuga chamaepitys.* Acm: *Artemisia campestris.* Aco: *Achillea collina.* Adi: *Antennaria dioica.* Agl: *Arabis glabra.* Ahi: *Arabis hirsuta.* Ali: *Anthericum liliago.* **AMO**: *Astragalus monspessulanus.* Ano: *Achillea nobilis.* Aon: *Astragalus onobrychis.* Aov: *Amelanchier ovalis.* Apy: *Ajuga pyramidalis.* Aru: *Asplenium ruta-muraria.* Auv: *Arctostaphylos uva-ursi.* Avl: *Artemisia vulgaris.* **AVU**: *Anthyllis vulneraria* subsp. *polyphylla*. Ber: *Bromus erectus.* Bla: *Biscutella laevigata.* Bpe: *Betula pendula.* Bra: *Bupleurum ranunculoides*. Bru: *Brachypodium rupestre.* Bvu: *Berberis vulgaris.* **CAB**: *Colutea arborescens.* Cal: *Chenopodium album.* Cap: *Clematis alpina.* Car: *Cirsium arvense.* Cav: *Convolvulus arvensis.* Cca: *Conyza canadensis.* Cer: *Cirsium eriophorum.* Cgr: *Chrysopogon gryllus.* Chu: *Carex humilis.* **CMI**: *Chaenorhinum minus.* Cnu: *Carduus nutans.* Cro: *Campanula rotundifolia.* Csc: *Centaurea scabiosa.* Ctr: *Centaurea triumfetti*. Cut: *Carlina utzka.* Cva: *Calamagrostis varia*. Cvi: *Clematis vitalba.* Cvl: *Crupina vulgaris.* Cvr: *Coronilla varia*. Cvu: *Carlina vulgaris.* Dca: *Daucus carota.* Dte: *Diplotaxis tenuifolia.* Eac: *Erigeron acer.* Ean: *Epilobium angustifolium.* Eat: *Epipactis atropurpurea.* Eau: *Erigeron annuus.* **ECA**: *Eryngium campestre.* Ecy: *Euphorbia cyparissias.* Ena: *Erucastrum nasturtiifolium.* Erh: *Erysimum rhaeticum.* **ESE**: *Euphorbia seguierana.* Evu: *Echium vulgare.* Far: *Festuca arundinacea.* **FCI**: *Festuca cinerea*. Fex: *Fraxinus excelsior*. Fpr: *Fumana procumbens.* Fva: *Festuca valesiaca.* Fve: *Fragaria vesca.* Gap: *Galium aparine.* Gcn: *Gymnadenia conopsea.* **GCO**: *Galium corrudifolium.* Gve: *Galium verum.* Hco: *Hippocrepis comosa.* Hfo: *Helleborus foetidus.* Hnu: *Helianthemum nummularium* subsp. *obscurum.* Hpe: *Hieracium peletieranum.* Hpi: *Hieracium piloselloides.* Hpr: *Hypericum perforatum.* Hsy: *Hieracium sylvaticum.* Hto: *Hieracium tomentosum.* Ico: *Inula conyza.* Jco: *Juniperus communis.* Kpy: *Koeleria pyramidata.* Ksa: *Kernera saxatilis.* **KVA**: *Koeleria vallesiana.* **LCO**: *Leopoldia comosa.* Lcr: *Lotus corniculatus.* Lde: *Larix decidua.* Lhi: *Leontodon hispidus.* Lmo: *Lathyrus montanus.* **LPE**: *Lactuca perennis.* Lse: *Lactuca serriola.* Lsi: *Laserpitium siler*. **LSM**: *Linaria simplex*. Lvu: *Ligustrum vulgare.* **MCI**: *Melica ciliata*. Mfa: *Medicago sativa* subsp. *falcata*. **MFS**: *Minuartia fastigiata.* Mlu: *Medicago lupulina*. **MMI**: *Medicago minima.* Mof: *Melilotus officinalis.* Msa: *Medicago sativa* subsp. *sativa.* Msy: *Melampyrum sylvaticum.* Oca: *Orobanche caryophyllacea.* Oha: *Oxytropis halleri.* Ola: *Odontites lanceolata.* **OLU**: *Odontites lutea.* **ONA**: *Ononis natrix.* Opi: *Oxytropis pilosa*. **OPU**: *Ononis pusilla.* Ore: *Ononis repens.* Oro: *Ononis rotundifolia.* Ovi: *Onobrychis viciifolia.* Pav: *Prunus avium.* Pch: *Polygala chamaebuxus.* Pex: *Picea excelsa.* Pgr: *Prunella grandiflora.* Phi: *Picris hieracioides.* Pma: *Prunus mahaleb*. Pni: *Populus nigra.* Por: *Peucedanum oreoselinum.* Ppa: *Poa pratensis.* Pph: *Phleum phleoides.* **PPR**: *Petrorhagia prolifera*. **PSA**: *Petrorhagia saxifraga.* Psp: *Prunus spinosa*. Psx: *Pimpinella saxifraga*. Psy: *Pinus sylvestris.* Pta: *Potentilla tabernaemontani.* Ptr: *Populus tremula*. Pun: *Pinus uncinata.* Qpu: *Quercus pubescens.* Rca: *Rosa canina.* Rid: *Rubus idaeus.* Rul: *Rubus spp.* Sar: *Sorbus aria.* Sca: *Salix caprea.* Sgr: *Scabiosa gramuntia.* Sin: *Senecio inaequidens.* **SIT**: *Silene italica.* Smi: *Sanguisorba minor.* Smo: *Sedum montanum.* Snu: *Silene nutans.* Soc: *Saponaria ocymoides.* Sot: *Silene otites.* Spe: *Stipa pennata.* **SPR**: *Salvia pratensis.* Sre: *Stachys recta.* Ste: *Sempervivum tectorum.* **TCH**: *Teucrium chamaedrys.* **TCR**: *Tragopogon crocifolius.* Tdu: *Tragopogon dubius.* Thu: *Thymus humifusus.* Tla: *Taraxacum laevigatum.* Tli: *Thesium linophyllon.* Tme: *Trifolium medium.* Tmo: *Teucrium montanum.* Tof: *Taraxacum officinale*. **TVU**: *Thymus vulgaris.* Var: *Viola arvensis.* Vly: *Verbascum lychnitis.* Vmy: *Vaccinium myrtillus.* Vof: *Veronica officinalis.* Vri: *Viola riviniana.* Vru: *Viola rupestris.* Vsa: *Vicia sativa.* Vth: *Verbascum thapsus*.

Fig. 4 Correlation between the number of ESM species and DCA scores on **a** axis1 and **b** axis 2 (Pearson correlation; ns = not significant)

Elettronic supplemental material (ESM1.xls):

Appendix 1 Code, life form, phytosociological optimum, occurrence, and abundance of each species recorded at the study sites. Nomenclature follows Pignatti (1982). Species were divided in two groups: euri/steno-Mediterranean (ESM), and other biogeographic groups. T = therophyte, B = biennial, G = geophyte , H = hemicryptophyte, CH = chamaephyte, P = phanerophyte.

Figure1_Word picture

FIG. 1 (original file PowerPoint MSOffice2003)

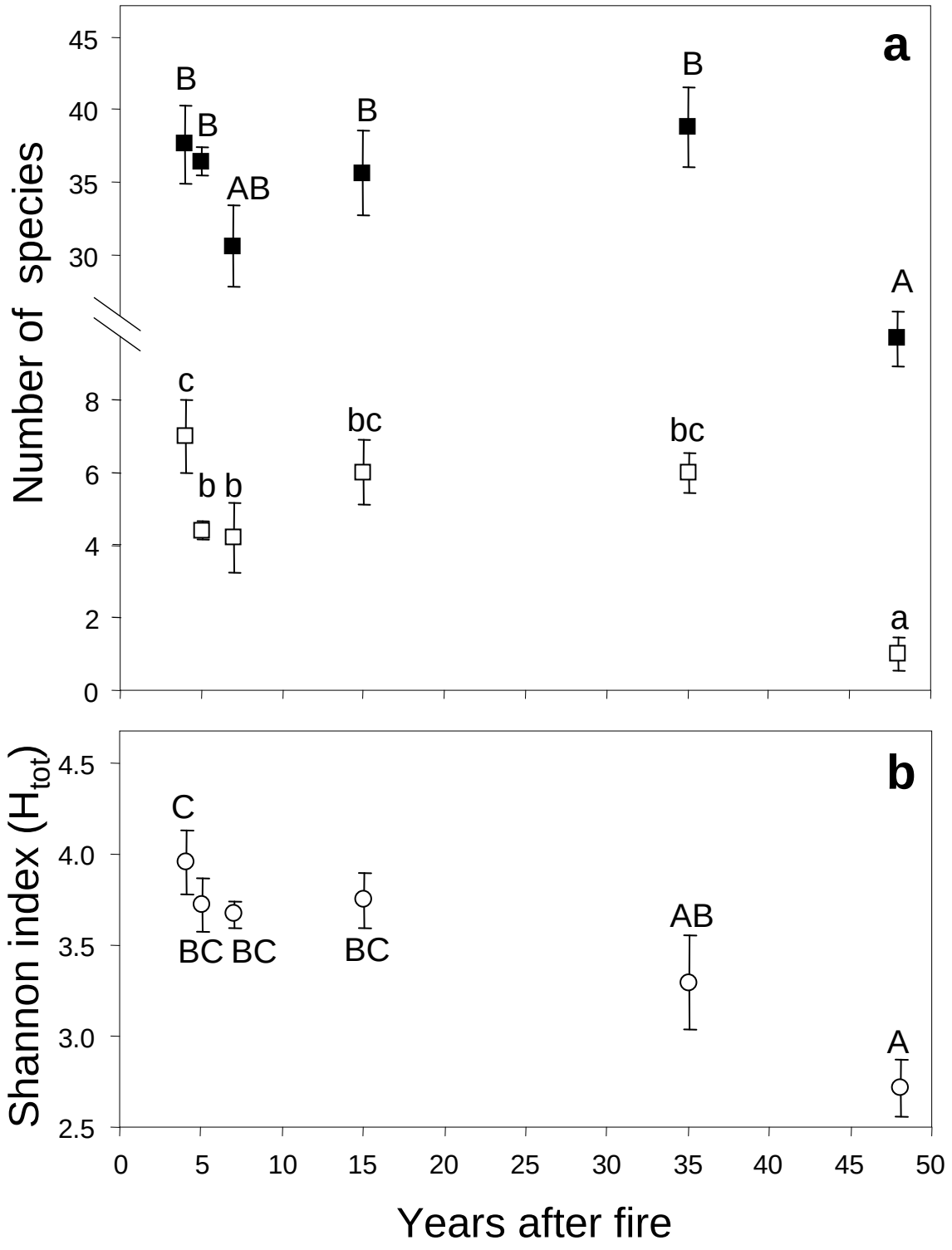

Figure1_original file

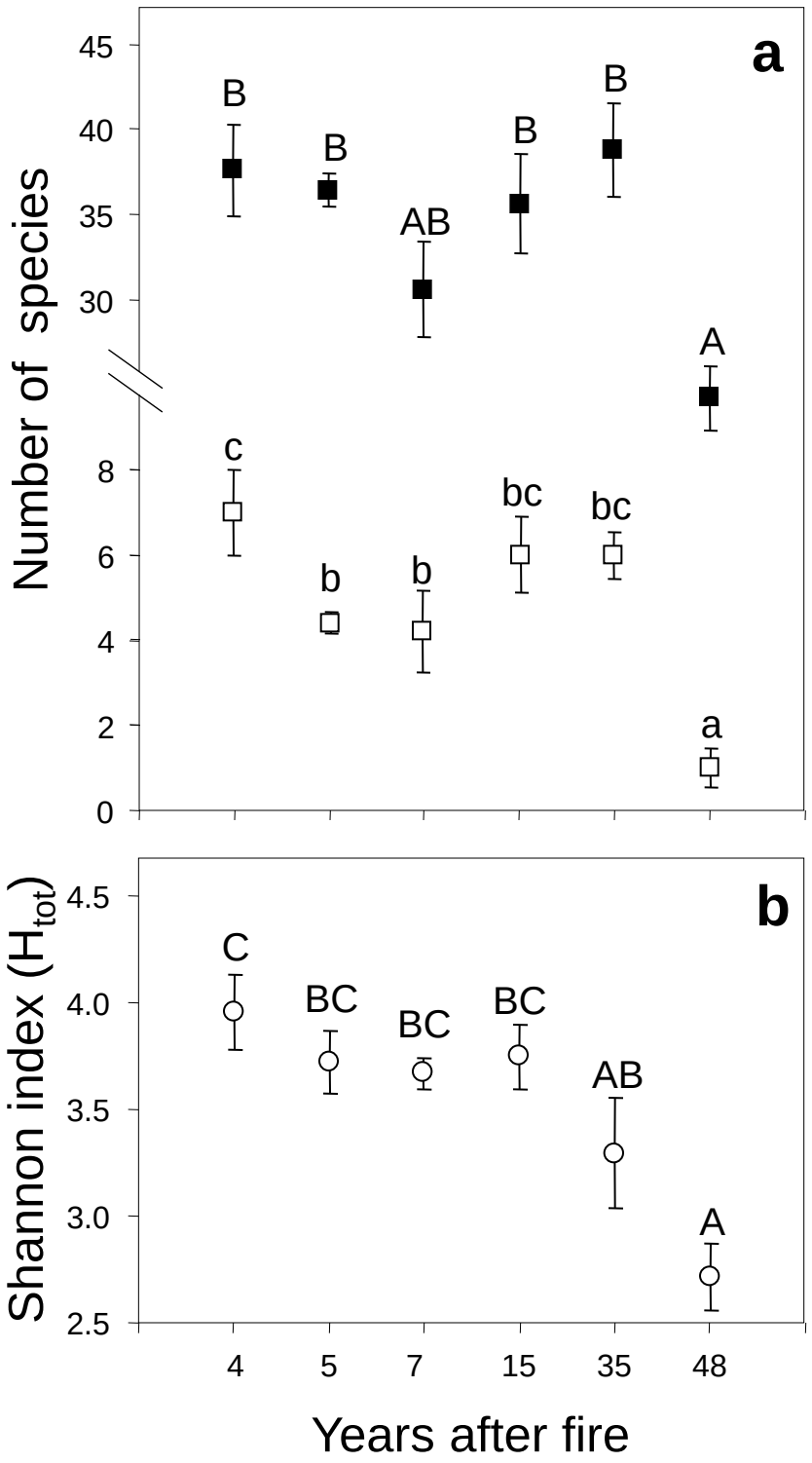

Figure2_Word picture

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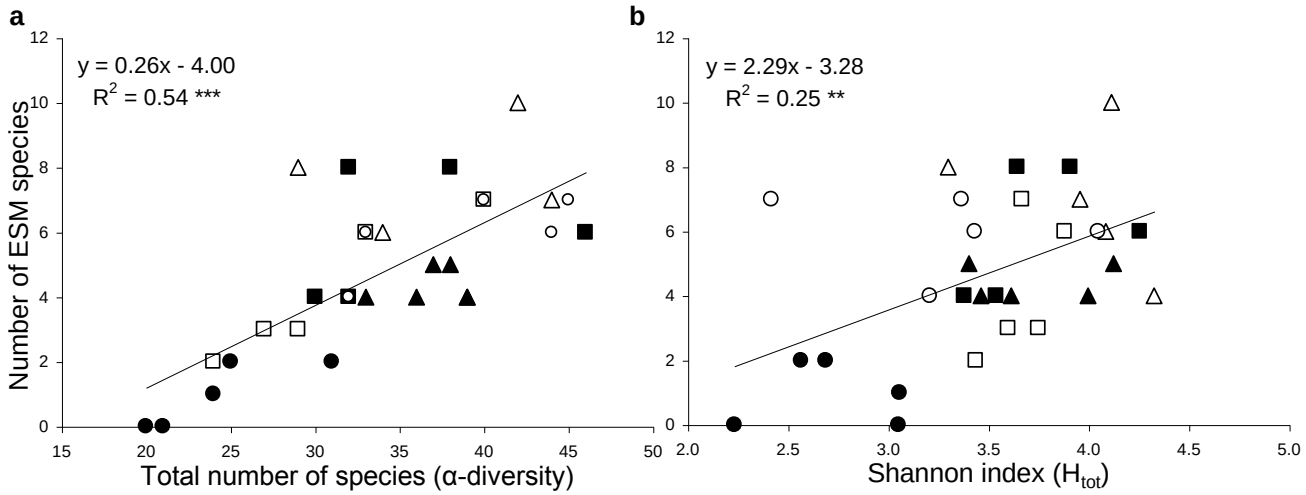

Figure2_original file

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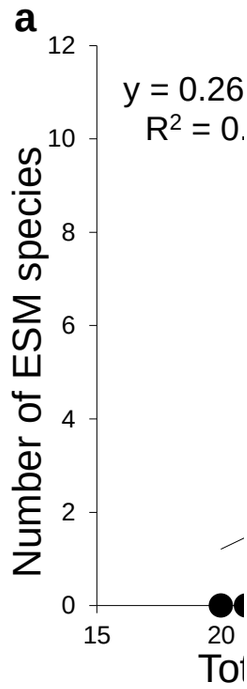
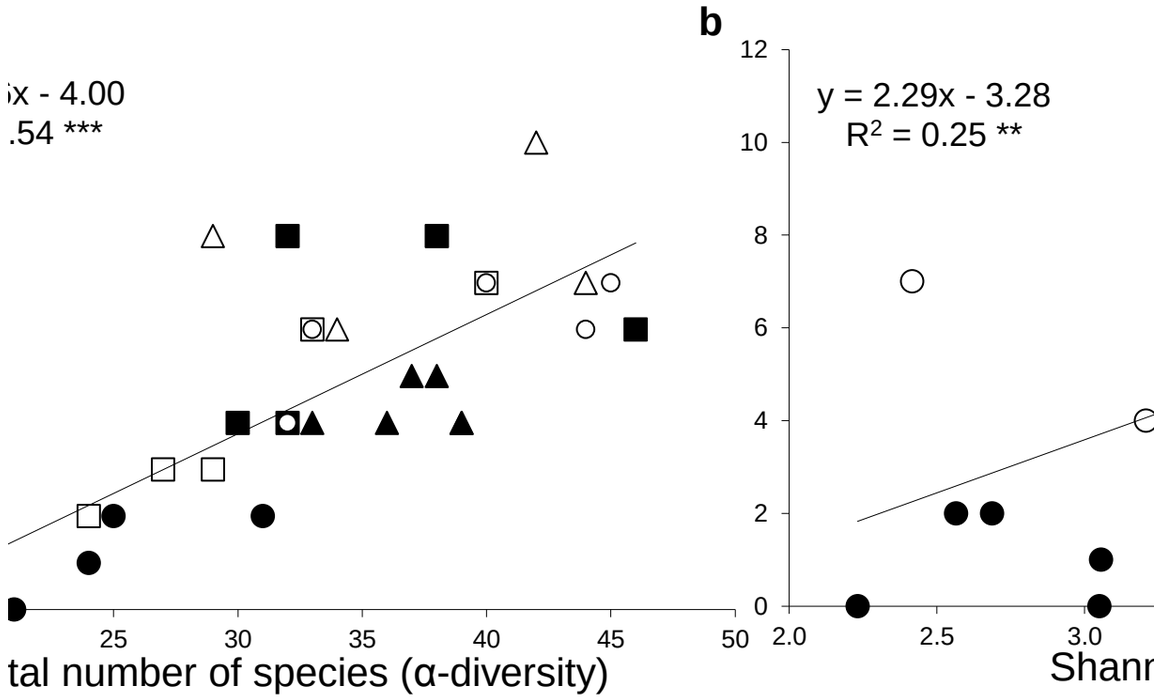
plot02	0.3201	1.4994	7	44	3.956168
plot03	0	1.4294	10	42	4.113935
plot04	0.2586	0.8664	6	34	4.085528
plot05	0.1912	0	4	39	4.326149
plot06	2.0877	0.5367	4	36	3.995833
plot07	1.7981	0.3625	4	33	3.462399
plot08	1.7765	0.2528	4	39	3.61213
plot09	1.7685	0.2915	5	37	3.401677
plot10	1.7195	0.6033	5	38	4.123186
plot11	2.3025	0.7698	6	33	3.881335
plot12	2.2996	0.7381	7	40	3.666051
plot13	2.3361	0.7144	3	27	3.598292
plot14	2.4764	0.9113	2	24	3.437279
plot15	2.6488	0.5549	3	29	3.748663
plot16	1.5161	1.0003	4	32	3.378288
plot17	1.1455	0.9256	8	38	3.906621
plot18	1.6838	1.1842	8	32	3.64303
plot19	1.4661	0.8383	6	46	4.255176
plot20	1.8635	1.1024	4	30	3.538155
plot21	1.4445	2.0297	4	32	3.208002
plot22	1.6925	2.2013	7	40	3.364782
plot23	1.3491	1.8184	6	33	3.432826
plot24	1.6856	1.9611	6	44	4.045512
plot25	1.8999	1.8768	7	45	2.416108
plot26	2.8416	1.5048	2	25	2.565162
plot27	3.6269	0.8911	1	24	3.056024
plot28	3.7626	1.1018	0	20	2.231995
plot29	3.2878	0.5856	0	21	3.050584
plot30	3.2231	1.4562	2	31	2.68737

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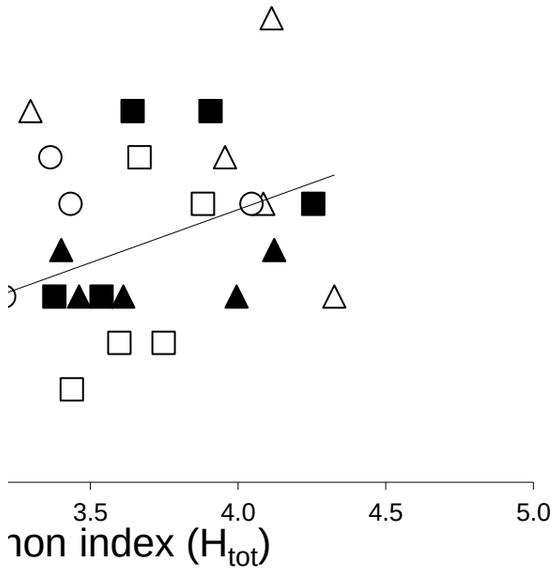
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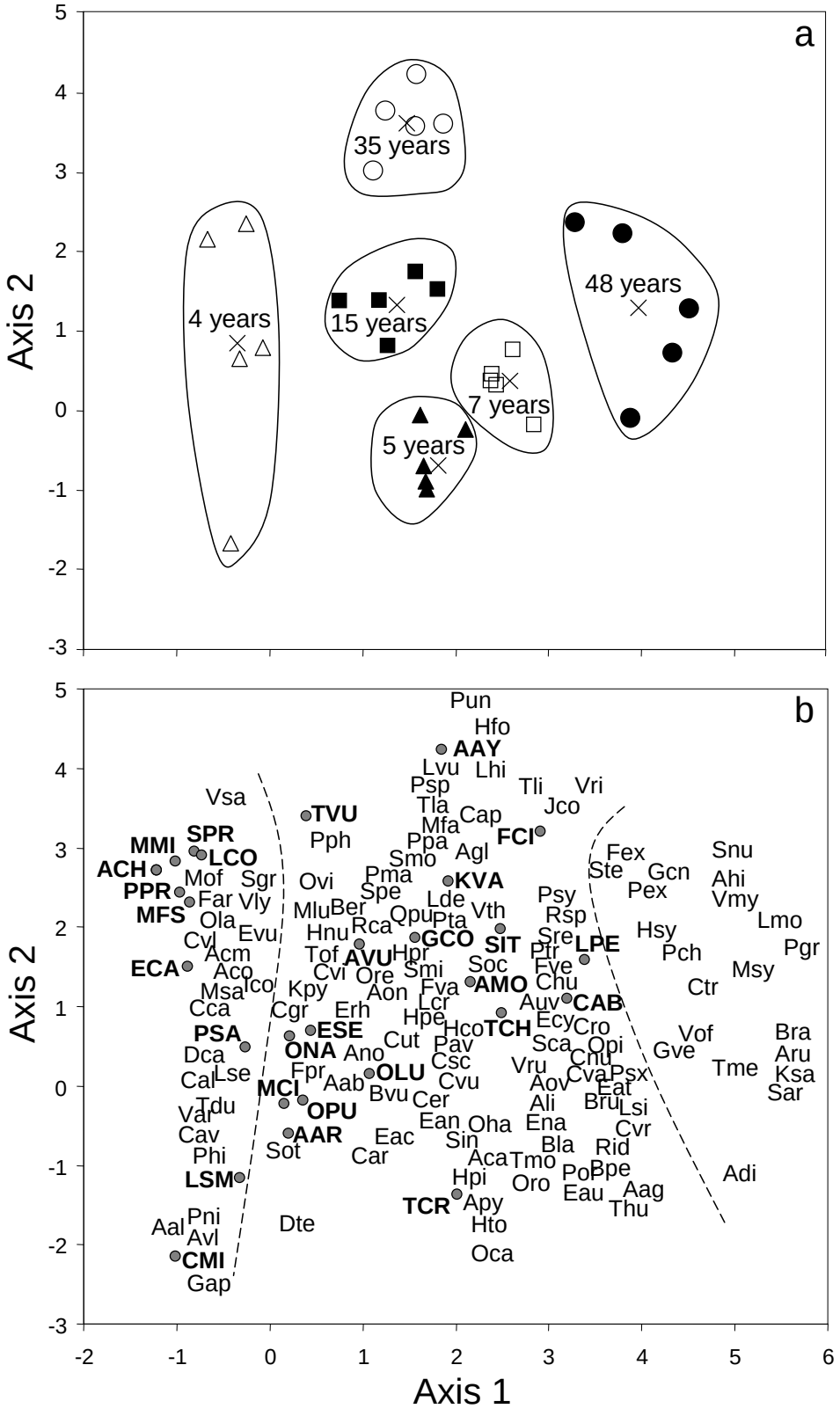
FIG. 3 (original file PowerPoint MSOfice2003)



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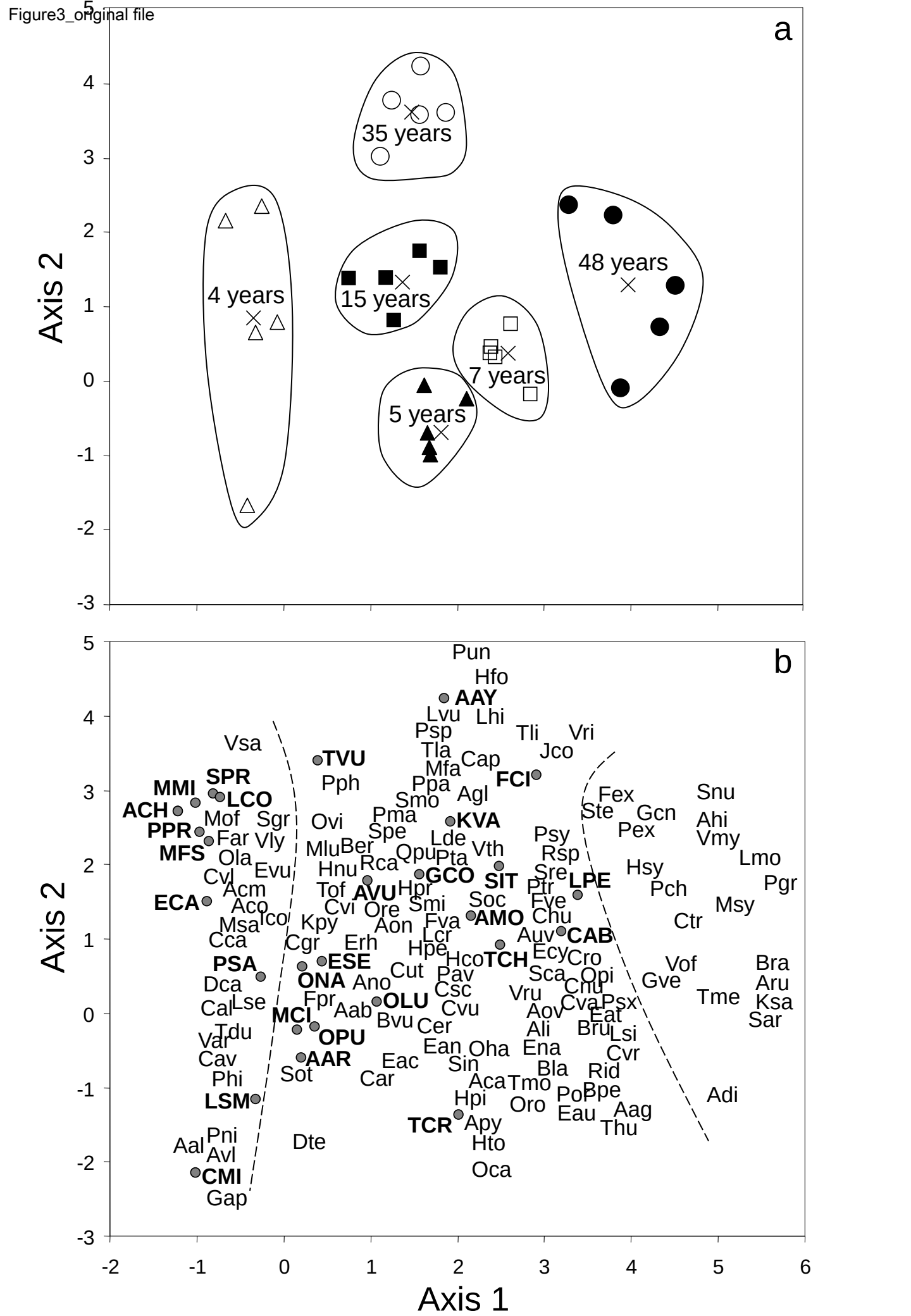

Figure4_Word picture

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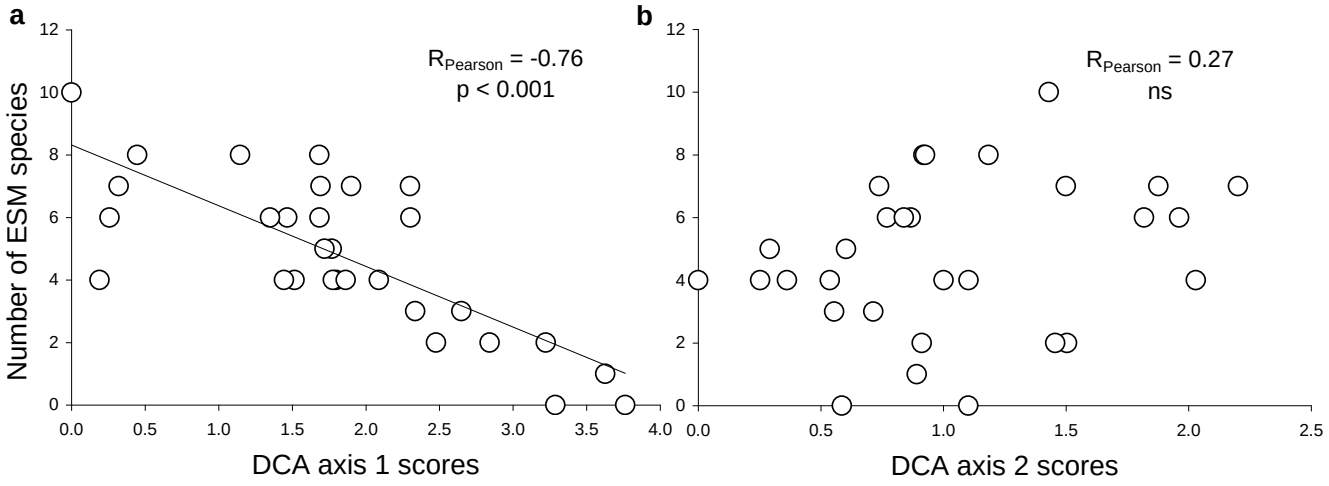

Figure4_original file

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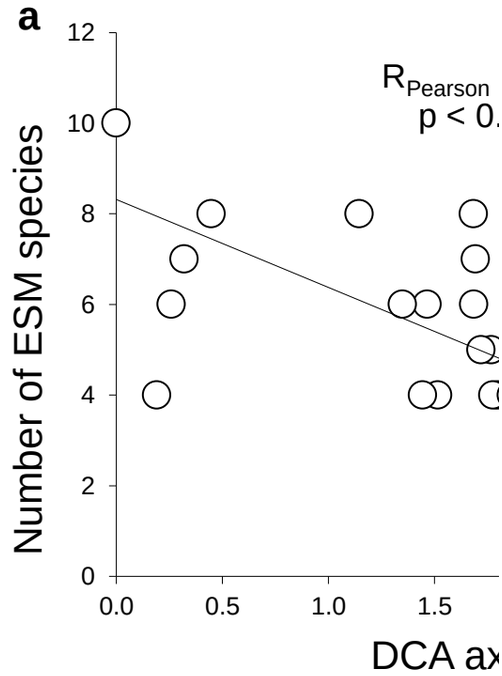
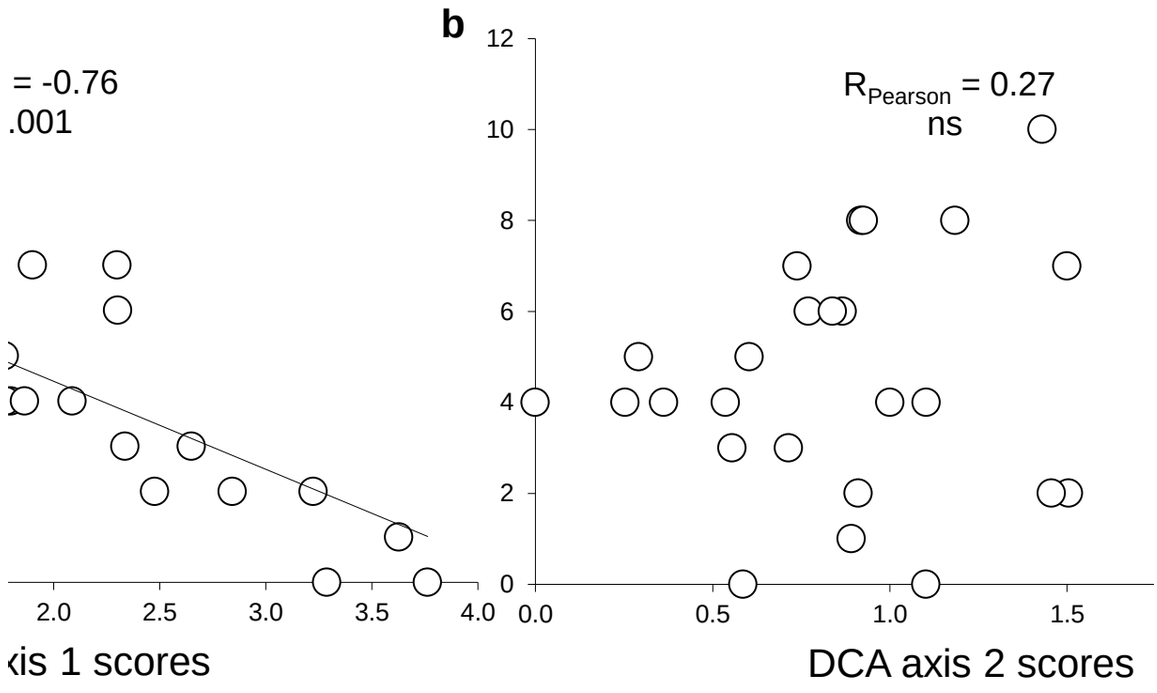
plot01	0.4471	0.9187	8
plot02	0.3201	1.4994	7
plot03	0	1.4294	10
plot04	0.2586	0.8664	6
plot05	0.1912	0	4
plot06	2.0877	0.5367	4
plot07	1.7981	0.3625	4
plot08	1.7765	0.2528	4
plot09	1.7685	0.2915	5
plot10	1.7195	0.6033	5
plot11	2.3025	0.7698	6
plot12	2.2996	0.7381	7
plot13	2.3361	0.7144	3
plot14	2.4764	0.9113	2
plot15	2.6488	0.5549	3
plot16	1.5161	1.0003	4
plot17	1.1455	0.9256	8
plot18	1.6838	1.1842	8
plot19	1.4661	0.8383	6
plot20	1.8635	1.1024	4
plot21	1.4445	2.0297	4
plot22	1.6925	2.2013	7
plot23	1.3491	1.8184	6
plot24	1.6856	1.9611	6
plot25	1.8999	1.8768	7
plot26	2.8416	1.5048	2
plot27	3.6269	0.8911	1
plot28	3.7626	1.1018	0
plot29	3.2878	0.5856	0
plot30	3.2231	1.4562	2




b
= -0.76
.001
$R_{Pearson}$ = 0.27
ns
12
10
8
6
4
2
0
2.0
2.5
3.0
3.5
4.0
0.0
0.5
1.0
1.5
xis 1 scores
DCA axis 2 scores

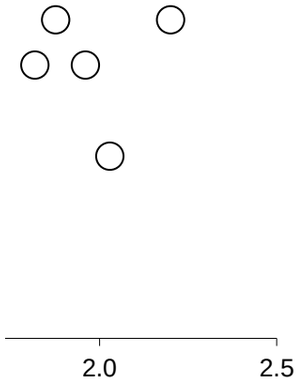

2.0
2.5

Table 1 Characteristics of the six selected fires in Scots pine forests

Year	Municipality	Site	Years since fire	Latitude Longitude (WGS84)	Area burned by crown fire [ha]	Elevation range of crown fire [m a.s.l.]	Aspect
2006	Verrayes	Menfrey	4	45°46'00"N 7°30'50"E	4.6	1020-1340	SE
2005	Verrayes	Hers	5	45°46'10"N 7°29'54"E	167.9	1305-1890	S
2003	St. Denis	Vorpeillere	7	45°45'40"N 7°35'06"E	46.4	970-1525	SE
1995	Verrayes	Del	15	45°46'19"N 7°33'15"E	22	1160-1460	S
1975	Verrayes	Chialey	35	45°46'16"N 7°32'36"E	2.1	1245-1335	S
1962	St.Denis	Lavasè	48	45°45'54"N 7°34'57"E	5.4	1490-1550	SW

Table 2 Differences in stand structural variables (mean, SE= standard error) among fire treatments (ANOVA F-test). Sites with no letters in common were significantly different (REGWQ post-hoc test, $p \leq 0.05$)

Structural variables	Site		Menfrey	Bourra	Vorpeillere	Del	Chialey	Lavasè	
	Years since fire		4	5	7	15	35	48	
	F	Sig.	mean	mean	mean	mean	mean	mean	SE
Woody species regeneration									
Total density (n. individuals ha^{-1})	5.2	0.002	2420 ab	1095 a	3215 ab	5509 b	7214 b	5764 b	615.8
Total basal area (m^2 ha^{-1})	51.0	< 0.001	1.3 ab	0.1 a	3.1 b	14 c	20.6 c	45.6 d	3.10
Scots pine regeneration									
Pine density (n. individuals ha^{-1})	21.6	< 0.001	0 a	26 a	331 a	3135 b	963 ab	4386 b	346.4
Pine basal area (m^2 ha^{-1})	48.0	< 0.001	0.0 a	0.0 a	0.3 a	4.9 a	15.5 b	40.7 c	2.90
Ground cover									
Tree % cover (height > 5 m)	102.5	< 0.001	0 a	0 a	4 a	2 a	57 b	68 c	5.5
Shrub % cover (height < 5 m)	15.3	< 0.001	12 ab	7 ab	41 d	29 cd	21 bc	4 a	2.8
Herbaceous % cover	4.8	0.004	65 bc	55 ab	64 bc	76 c	39 a	65 bc	3.0

Table 3 Summary of univariate **a** and multivariate GLM **b** of ESM species richness (best model after stepwise selection). Significant predictors ($p \leq 0.05$) in bold; df: degrees of freedom; D^2: percent deviance explained; AICC: Akaike's Information Criterion with small sample correction

Models/variables	Parameters	B	sig.	df	Residual deviance	D^2 %	AICC
a) Univariate models							
Time since fire (years)	**time**	**-0.28**	**0.009**	**28**	**38.0**	**19**	**137.6**
	intercept	1.53	0.000				
Elevation (m)	**elevation**	**-0.38**	**0.000**	**28**	**29.7**	**37**	**129.2**
	intercept	1.50	0.000				
Slope (°)	slope	0.16	0.097	28	43.4	8	143.0
	(intercept)	1.55	0.000				
Southness (°)	southness	0.09	0.355	28	45.9	2	145.4
	(intercept)	1.56	0.000				
Edge distance (m)	distance	0.04	0.664	28	46.8	1	146.4
	(intercept)	1.56	0.000				
Tree density (trees ha^{-1})	density	-0.09	0.406	28	46.1	2	145.7
	(intercept)	1.56	0.000				
Tree basal area (m^2 ha^{-1})	**basal area**	**-0.34**	**0.002**	**28**	**35.0**	**26**	**134.6**
	(intercept)	1.51	0.000				
Tree cover (%)	**tree**	**-0.24**	**0.027**	**28**	**40.3**	**14**	**139.4**
	(intercept)	1.54	0.000				
Shrub cover (%)	shrub	0.10	0.294	28	45.6	3	145.2
	(intercept)	1.56	0.000				
Herbaceous cover (%)	herbaceous	0.04	0.693	28	46.8	0	146.4
	(intercept)	1.56	0.000				
Bare soil (%)	bare soil	-0.03	0.803	28	46.9	0	146.5
	(intercept)	1.56	0.000				
Rocks (%)	rocks	-0.03	0.784	28	46.9	0	146.5
	(intercept)	1.56	0.000				
Light (L)	**L**	**0.50**	**0.000**	**28**	**22.7**	**52**	**122.2**
	(intercept)	1.46	0.000				
Nitrogen (N)	N	0.07	0.786	28	46.9	0	146.5
	(intercept)	259.08	0.000				
Moisture (F)	**F**	**-0.32**	**0.000**	**28**	**32.3**	**31**	**131.9**
	(intercept)	1.51	0.000				
b) Multivariate model							
All variables included	**L**	**0.39**	**0.000**	**27**	**20.0**	**58**	**122.1**
	Elevation	**-0.18**	**0.042**				
	(intercept)	1.45	0.000				

Appendix 1

Click here to download Supplementary Material: ESM_1.xls