

Recolonisation and changes in bryophyte and lichen biodiversity in burned areas from the Serra da Estrela (Portugal)

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Abstract – The bryophyte and lichen vegetation was monitored over a period of three years in both a control plot and a burned plot in seven different areas of the Serra da Estrela Natural Park. During the post-fire succession, the changes in the floristic composition and the macroclimatic and environmental factors that influence them were analysed using Redundancy Analysis. The highest diversity was attained 3-8 years after fire, when colonists and fugitive elements were replaced by species with longer lifespans and more demanding life strategies. Eighty-nine bryophytes (17 hepatics and 72 mosses) and 63 lichen species were identified, including some bryophyte species that are rare in Portugal and some lichen species considered to be rare in Europe.

Bryophytes / Lichens / post-fire / recolonisation / Natural Park of Serra da Estrela / Portugal / Iberian Peninsula

Résumé – Dans sept secteurs brûlés du Parc Naturel de la Serra da Estrela, les bryophytes et les lichens ont été surveillés pendant une période de trois ans, dans une parcelle de contrôle et une parcelle de terrain brûlé. Les changements de la composition floristique pendant la succession de l'après-feu et les facteurs macroclimatiques et d'environnement qui les influencent ont été analysés en employant l'analyse de redondance. La plus haute diversité a été atteinte 3-8 ans après le feu quand les colonistes et fugitives ont été remplacées par des espèces de longue durée ou de stratégie plus exigeante. Quarante-neuf bryophytes (17 hépatiques et 72 mousses) et 63 espèces de lichens ont été identifiées, parmi lesquelles on trouve des bryophytes rares au Portugal et des lichens considérés rares en Europe.

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INTRODUCTION

Bryophytes and lichens are important elements in the re-colonisation processes after fire, and in the establishment of appropriate ecological conditions for the development of communities of vascular plants (Arianoutsou-Faragitaki & Margaritis, 1982; During & Tooren, 1990). They live in micro-habitats usually produced by the vascular plant vegetation that, generally, strongly determines the ecological factors directly affecting the bryophytes (During & Tooren, 1990). Brasell *et al.* (1986) were the first to highlight the importance of coloniser bryophytes (*Funaria hygrometrica* and *Marchantia polymorpha*) in the fixation of nitrogen in burned soils. Clément & Touffet (1988, 1990) and Glouaguen (1990) observed high covers of *Polytrichum* species during the first stages of re-colonisation of pastures after fire in Brittany. In SE Spain, Heras-Ibáñez *et al.* (1990, 1991, 1992, 1994) carried out similar studies in burned areas.

From the point of view of biodiversity management, firing when properly used can be important in maintaining biodiversity and also in preserving semi-natural habitats (Rego, *pers. com.*). Over recent years, the traditional use of fire to improve pasture regeneration in several zones of Portugal has been decreasing, as well as bush clearing in mountain areas such as Serra da Estrela. The main cause of this phenomenon is rural depopulation and the abandoning of marginal lands.

Serra da Estrela is one of the areas in Portugal with the greatest bryophyte and lichen diversity and as such, it has been subject to many studies (Aptroot *et al.*, 1992; Boom & Giralt, 1996, 1999; Jansen, 1993; Jones, 1999; Sérgio *et al.*, 2000; Tavares, 1945). The high floristic diversity can be found in the sheltered valleys, which became refuge sites for some rare species after the Quaternary glaciations (Jansen *et al.*, 1997; Rego, 2001).

The present study has as its primary objectives an evaluation of the changes in floristic composition during the post-fire succession, as well as the recolonisation process exhibited by bryophytes and lichens, in burned and unburned (control) contiguous plots, in selected areas of the Serra da Estrela. The main macroclimatic and environmental factors that influence them were also considered. The period of time elapsed during this study was not enough to evaluate and recognize the establishment of the most sensitive and rare species, but it is, however, an important contribution to the understanding of bryophyte and lichen recolonization after fire.

MATERIAL AND METHODS

Site description

The Serra da Estrela Natural Park (Parque Natural da Serra da Estrela, PNSE) was created in 1976 and is located in the western part of the Central System, in eastern centre Portugal, between 40°15' and 40°17' N, and 7°15' and 7°50' W, consists of the Serra da Estrela massif and some surrounding areas (Fig. 1). According to Rivas-Martinez (1987), it has the mesomediterranean, supramediterranean and oromediterranean bioclimatic belts, with cold winters and cool summers. Average monthly temperatures vary between 1.2°C in February and 18.8°C in July (INMG 1991). Average annual rainfall has a maximum of

2965 mm at Penhas da Saúde, and a minimum of 935.5 mm at Guarda (INMG 1991). Geologically, Serra da Estrela consists mainly of Carboniferous granitic layers with Cambrian and Precambrian schist outcrops, which have been heavily influenced by glacial activity. Minimum altitude at PNSE is 800 m and the highest peak is at 1993 m, within an area of about 10 Km². The altitude range results in a zonation of the plant communities. These have been described by Costa *et al.* (1998) and Pinto da Silva & Teles (1999) as the superior, median and basal zones. Thus, the highest areas are dominated by scrub vegetation of *Juniperus communis* L. subsp. *alpina*; mat-grass lawns of *Nardus stricta* L.; pastures; saxicolous and lake communities. In the median zone the plant communities include oak forest, chestnut groves and extensive shrublands (*Cytisus multiflorus* (L'Hérit.) Sweet), heathlands of *Erica australis* L. subsp. *aragonensis* (Wk.) P. Cout., riverine-broom scrub of *Genista florida* L. subsp. *polygaliphylla* (Brot.) P. Cout. and vegetation of rivulets and small lakes. The basal zone is made of complex mediterranean plant formations.

The Atlantic influence is evident in most of the sites studied above 1300 m (Fig. 1). Biogeographically these sites belong to the Estrelense sector (Costa *et al.*, 1998). However, site number 7 is located at a lower altitude (*ca* 1200 m), and shows a strong Mediterranean influence. According to Costa *et al.* (1998), it is included in the Lusitano-Duriense sector.

Vegetation sampling and data analysis

Fieldwork was carried out between January 1997 and November 1999, in seven burnt areas on the Serra da Estrela (Fig. 1). Fourteen 2500 m² permanent plots were chosen in such a way as to represent the main shrub vegetation types of the Natural Park, as well as areas where wildfires occurred at different times. In each area, two plots were selected: a burned plot and an adjacent control one, where the vegetation did not show any evidence of recent fire. In general, the sites and environmental conditions of the control and burned plots were similar. To understand the dynamics of plant recolonisation, the vegetation composition was monitored in the permanent plot of each burnt area, once a year over a period of three years (4 plots) and two years (3 plots). The monitoring technique involved the selection of two representative quadrats (1 m²) in each plot (2500 m²). In these quadrats, quantitative occurrence was estimated in absolute value (%) for each bryophyte and lichen species. For each quadrat, time elapsed after fire, altitude, N-S aspect, E-W aspect, percentage cover of cryptogams, shrub vegetation and percent cover of free soil were recorded in semi-quantitative ordinal or quantitative scales.

One inventory was made for each quadrat, except for site number 7 where only one quadrat was selected, due to the homogeneous composition of the cryptogamic vegetation. The species present outside the quadrats and situated in a vicinity of 10 cm, were also considered as data for biodiversity analysis (f in the Annex).

Changes in the floristic composition and cover of each bryophyte and lichen species during the post fire-succession, together with the variables mentioned above, were analysed using Redundancy Analysis (RDA) carried out by means of CANOCO (Ter Braak, 1991). The results of the RDA analyses are given in the form of biplots and the abbreviations of each taxon are those used in the Annex. RDA calculates axes with a maximum of correspondence to environmental variables (represented by arrows) assuming a linear response of the species.



Fig. 1. A. Location of the studied area in Portugal, showing the provinces. B. Studied sites in the Serra da Estrela Natural Park (the grid refers to the UTM co-ordinates 10×10 km).

The distances between the arrows, representing the variables and the species position in the ordination diagram, permit an approximate determination of the importance of these variables in influencing the distribution of individual species (Jongman *et al.*, 1987).

Nomenclature follows Sérgio *et al.* (1994), Corley *et al.* (1981) and Corley & Crundwell (1991) for mosses, and Grolle & Long (2000) for hepatics. For lichens, nomenclature is generally from Nimis (1993), and from Clauzade & Roux (1985) for species not considered in the aforementioned work. Indication of species as rare or endangered follows Sérgio *et al.* (1994) for bryophytes and Burgaz *et al.* (1999), Martínez (1999) and Sérusiaux (1989) for lichens.

Table 1. Characteristics of the studied sites: locality including the province (BB: Beira Baixa and BA: Beira Alta), plot number (N: unburned = control and F: burned), UTM co-ordinates 1x1 Km, altitude, aspect, dominant vascular species of each community, sampling date and time elapsed after fire (years).

Studied site	Unburned and burned plot number	UTM, altitude and aspect	Dominant vascular species	Sampling dates and years after fire
1 - BB: Lagoa do Viriato	N1 F1	29TP2163, 1550 m, NE	<i>Erica arborea</i> L., <i>E. cinerea</i> L., <i>E. umbellata</i> L.	21/01/1997 - 8 years 08/07/1998 - 9 years 05/11/1999 - 10 years
2 - BA: Canal da Central do Sabugueiro	N2 F2	29TPE1571, 1400 m, N	<i>Genista florida</i> L., <i>Cytisus striatus</i> (Hill) Rothm.	22/07/1997 - 1 year 09/07/1998 - 2 years 04/11/1999 - 3 years
3 - BA: Fraga da Varanda	N3 F3	29TPE1875, 1350 m, W	<i>Genista florida</i> L., <i>Cytisus striatus</i> (Hill) Rothm.	22/01/1997 - 3 years 09/07/1998 - 4 years 04/11/1999 - 5 years 04/11/1999 - 1 year (new burned area)
4 - BA: near Lagoa Seca	N4 F4	29TPE2367, 1410 m, W	<i>Genista florida</i> L., <i>Cytisus striatus</i> (Hill) Rothm.	23/01/1997 - 3 years 09/07/1998 - 4 years 03/11/1999 - 5 years
5 - BA: Barragem do Lagoacho	N5 F5	29TPE1770, 1590m, N	<i>Genista florida</i> L., <i>Cytisus striatus</i> (Hill) Rothm.	19/11/1998 - 0,5 year 03/11/1999 - 1,5 year
6 - BA: Lagoa Comprida	N6 F6	29TPE1468, 1580 m, NW	<i>Erica arborea</i> L., <i>E. australis</i> L.	20/11/1998 - 0,5 year 20/11/1998 - 0,5 year
7 - BA: between Quinta da Maceira and Cerro do Gato	N7 F7	29TPE3180, 1190 m, W	<i>Chamaespartium tridentatum</i> (L.) P. Gibbs	19/11/1998 - 1 year 05/11/1999 - 2 years

RESULTS AND DISCUSSION

A synthesis of the floristic composition (lichens and bryophytes) of each studied plot (the total of 2 quadrats in burned and 2 in unburned plots) is presented in the Annex. Although the present study was carried out in a limited number of sites, corresponding to specific habitats, relatively high cryptogams diversity was recorded. Eighty-seven bryophytes (17 hepatics and 70 mosses) and 63 lichen species were identified. Despite the evident heterogeneity of environmental conditions among plots, as deduced from the diversity of recorded species, the biodiversity was higher in the control plots than in the burned plots. This difference decreases with the number of years after fire. In area 1 (N1 and F1), where the fire occurred 8-10 years ago, values were 32 (control) and 25 (burned), (see Annex). It is worth noticing that biodiversity in area 6, with the most recent fires, changed from 77 to 10 one and a half year after fire. In the studied areas where fires occurred between 0-2 years and 3-5 years ago (areas 2, 3, 4, 5 and 7), the differences between the total biodiversity, in burned and control plots, are less significant as show in the Annex.

Another result presented in the Annex concerns the occurrence of individual or species groups in both burned and control plots, although other ones can be observed only in control plots or in areas where fire occurred more than 9-11 years ago. This is particularly evident for the lichen species.

Considering the differences for each organism group studied (lichens, hepatics and mosses), the total species number between control and burned plots are represented in Figure 2. In general, after fire all the studied groups show a significant decrease on their species number. In sites 2, 4, 5 and 6, the decrease in the total number of lichen species is particularly evident. For hepatics, the decrease in species number is significant in sites 2, 5 and 6 and for mosses in sites 2, 4 and 6.

The main results concerning bryophyte and lichen diversity as well as the soil recolonisation by these cryptogams and the factors affecting this process are followingly exposed and commented.

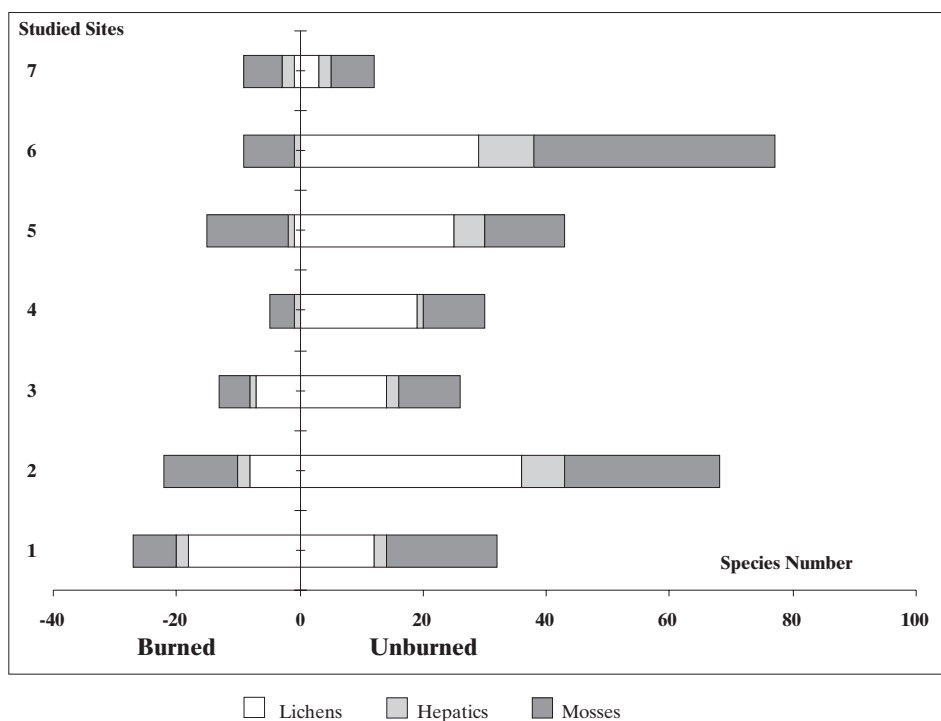


Fig. 2. Variation in species number (lichens, hepatics and mosses) observed between the different unburned and burned plots.

Biodiversity

Some bryophyte taxa were found only in unburned plots (Annex). Examples of these are *Diplophyllum albicans*, all *Marsupella* species, the majority of *Scapania* species, all *Andreaea* species, *Bartramia pomiformis*, *Hedwigia stellata*, *Hypnum imponens*, *H. mamillatum*, all *Rhynchostegium* species and *Scleropodium*

purum. For lichens, it can be seen that a significant species number were observed only in control plots. Examples being: *Bryoria fuscescens*, *Cetraria islandica*, many *Cladonia* species, *Evernia prunastri*, *Lasallia hispanica* and *Leptogium corniculatum*. We can also point out that the major part of foliose lichen species (some *Parmelia* and *Peltigera* species) were generally recorded in control plots, a result that may be explained by the slow growth of these organisms. In contrast to these species, some taxa are well represented both in control and in all burned plots. Some examples among the most frequent ones are *Ceratodon purpureus* and *Polytrichum piliferum* for bryophytes, and some *Cladonia* species for lichens. On the other hand, other species were found only in burned plots, as is the case of *Funaria hygrometrica*. This is a species characteristic of burned areas where significant soil mobilisation has occurred (Southorn, 1976).

In Figure 2, we can compare the species number for each organism group studied, between burned and control plots as well as between the different burned plots. Analysing the different groups, and the lichens in particular, the highest diversity for unburned plots was found in sites 2 and 6. However, considering a proportion of the total biodiversity per site, sites 4 and 5 (about 55-65%) have the highest percentage. In contrast, it is in the burned plots of these sites, burned one and a half years before, that lichen biodiversity is lower (0-5%). On the other hand, lichens attain the maximum diversity, 18 species (about 67%), in site 1, ten years after the fire. For bryophytes, it can be seen that hepatics are the least frequent group. For unburned plots the highest diversity value corresponds to site 6 with 9 species (about 10%). We can also observe that hepatics are better represented proportionally on plots burned about one and a half years ago (sites 6 and 7). Finally, the mosses are the best group represented in burned and control plots. Their diversity varies from 10 to 39 species (about 50-70%) in unburned plots. They are also frequent in all burned plots, with a variation between 4 and 13 species (80-85%) in sites 4 and 5 respectively.

The results of this study suggest that the recolonization processes are dependent on the heterogeneity of microenvironmental conditions among the studied plots. So, in plots number 1 and 6, both close to dikes, several differences in the microrelief and water availability of the substrate in each plot were observed. In fact, the highest diversity of lichens and bryophytes in plot number 6, is related to a higher edaphic humidity and to the presence of small niches in the substrate. Plots number 2 and 5, both facing northwards and close to important natural water resources, show a similar pattern in biodiversity composition. Plots number 3 and 4, both facing W and with similar microenvironmental conditions, have a similar floristic composition. The different conditions mentioned above also contributed to the recolonization processes, as well as to the total biodiversity of the burned plots. Plots 3 and 4, which are subject to drier conditions, present a slower recovery in biodiversity as compared to plots where water availability of the substrate is higher. The floristic richness of these plots five years after fire is considerably lower than that of plot 5, which was burned only one and a half years before.

The lowest bryophyte and lichen number was observed in site number 7 (lowest altitude), where the soil is thin and derived from schists, experiencing a considerable mediterranean influence that favours particular environmental conditions of drieress and where scrub communities with *Chamaespartium tridentatum* (L.) P. Gibbs dominate.

It is worth remarking the occurrence of species that are relatively rare in Portugal. Among these, *Plagiothecium cavifolium* is a moss only recorded in the Serra do Bussaco, and *Pogonatum urnigerum*, an endangered species in Portugal

has been only reported from the Minho region. Rare and endangered bryophytes were exclusively found in unburned plots. *Lophozia ventricosa*, *Cynodontium jeneri* and *Rhizomnium magnifolium* (Annex) are the most representative ones. Lichens restricted to the Serra da Estrela flora and considered to be vulnerable at the national level, were also found in unburned plots – e.g., *Peltigera britannica*. Rare species at the European level were also found in plots 6-10 years after fire occurrence or in unburned plots – e.g., *Cetraria sepincola*, *Cladonia portentosa*, *Lasallia hispanica*, *Saccomorpha icmalea* as well as some others *Peltigera* species.

Soil recolonisation

Some species are as well represented in the first years after fire, as in the later stages and in the control plots, as seen in the biodiversity analysis (Annex). Among them, some of the most important ones are *Cephaloziella divaricata*, *Polytrichum piliferum* and *Ceratodon purpureus*. This later species is considered a “fire moss”, capable of colonising burned areas through dispersal of a high number of small spores (Auclair, 1983; Crane *et al.*, 1983). The taxa mentioned are able to attain high cover rapidly, favouring the accumulation of organic matter and the further development of a more diversified flora. *Saccomorpha icmalea* was found only in one burned plot, although it is considered to be a pioneer species after fire (Purvis *et al.*, 1992). According to Rego (*pers. com.*) the high thermic amplitude at the soil surface is an important factor limiting the post fire development of some species.

It is evident that some taxa appear only in the control quadrats, or in fire plots with more than three years elapsed after the fire (Annex). This is the case of *Bryum alpinum* (plots number 1 and 3), a moss frequently found at the intermediate stages of colonisation (Espósito *et al.*, 1998).

Funaria hygrometrica is a fugitive species that was found in plots number 2, 3, 5 and 6, which were recently burned (0-2 years). It was also observed that its cover decreases with the recovery of the terricolous communities. *F. hygrometrica* is a typical pyrophile element, which may be associated with *Polytrichum juniperinum*, a taxon that is an indicator of an increase of the light availability and a reduction of substrate moisture after fire (Urdíroz Ariz & Ederra Indurain, 1996).

Pleurozium schreberi, a perennial species found only once (unburned plot number 6) is, on the contrary, a moss that recovers very slowly after fire (Annex). According to Viereck & Dyrness (1979), the cover of this moss increases only when soil and shrub layer conditions become favourable. Since it is a relatively rare species in Portugal, and has a boreal range, it risks being extremely vulnerable in Serra da Estrela due to fire. Other perennial such as *Hypnum cupressiforme*, a frequent species in unburned areas, was only recorded in plots with more than three years elapsed after fire (plot number 2) (Annex).

Lichens recolonised burned areas to a much lesser extent than mosses, at least during the first stages (Annex). Foliose species such as those of the genera *Peltigera* and *Parmelia* appeared only in places where fire had occurred more than nine years ago (plot number 1). As mentioned before, this fact is related to the generally low growth rate of lichens, as well as to the intensity and type of fire to which they have been exposed. A rapid and light fire may allow the survival of some thalli that allow an accelerated soil recolonisation. However, the effects of a strong fire lead to a long recovery time; studies carried out in Alaska with *Cladonia* species led to the conclusion that the time needed for the community to attain the initial stage of recolonisation after an intense fire is about 200 years (Thomson, 1968).

Although an evaluation of the life strategy sequences (sensu During, 1979; 1992) along recolonization processes was not made in this study, some considerations can be made. The annual shuttle plants, such as *Pleuridium acuminatum*, are not frequent in burned and unburned plots. The colonist (s. lat.) bryophytes (*Cephaloziella divaricata*, *Ceratodon purpureus*, *Polytrichum piliferum*) are generally well represented in the majority of the studied unburned plots, being the dominant life strategy in all burned plots. As for the short-lived shuttle taxa, such as *Andreaea* spp. and *Bartramia pomiformis*, a decrease in their frequency was observed in all burned plots.

Another interesting consideration concerns the regenerative capacity of some mosses. Species such as *Dicranum scoparium*, *Polytrichum commune*, *P. formosum*, and even *Sphagnum* plants may regenerate from underground parts that remained more or less protected during fire. According to Balagurova *et al.* (1996), some *Sphagnum* species are capable of surviving under temperatures close to 60°C for several days. In most of the burned areas, soil cover by bryophytes and lichens may be partly due to the regeneration of fragments present before the fire that were able to develop within a short period of time. It was observed that some bryophytes, such as species of *Racomitrium* (*R. elongatum* in plot F6), regenerated from gametophyte remains that were brought by wind or water from unburned zones, and that were able to settle and grow in the burned areas.

Another point to be noted concerns the substrate affinity. Although the studied plots were dominated exclusively by terricolous taxa, some moss or lichen species that are common on rock appeared: *Andreaea*, *Grimmia*, *Orthotrichum*, *Racomitrium*, *Lasallia*, a few *Parmelia* species, *Platismatia* and *Umbilicaria*. These organisms represent an interface between the saxicolous and terricolous communities that, due to the lack of soil or organic matter by the degradation and moving of material after successive fires, develop on small pebbles.

Influence of environmental factors on bryophyte and lichen recovery

The ordination obtained by the Redundancy analysis (RDA) shows that, in a given place, the changes in vegetation composition are correlated with the environmental factors considered in the analysis. The proportion of cumulative variance between species and environmental factors is of 60.8% in the two first axes (calculated from the factor centroids) and 22.1% of total variance is explained by the species. The RDA biplots of axes 1 and 2 (Figs 3 and 4) can be used to assess the influence of environmental factors on the distribution of individual species. The tips of the arrows indicate the position of each environmental factor, the length and proximity to the axis of the arrow show the relative weight of each factor in determining the axes (Ter Braak, 1991).

The observation of Figure 4 suggests that the variable “years after fire” has a strong influence on species distribution. Sites affected by recent fires are plotted as opposed to those burned more than 19 years ago. The variable “north-south aspect” has also a strong influence on the vegetation composition, especially on the unburned plots (unburned for more than 19 years).

Species projection on axis 1 (Fig. 3- abbreviations on the Annex) reveals a gradient that represents the natural succession of the different communities over time, the initial point being the year when fire occurred. The communities burned less than two years ago (Fig. 4- F297, F298, F399, F598, F599, F699) are dominated by bryophytes such as *Ceratodon purpureus*, a moss with a colonist life strategy, and *Funaria hygrometrica*, a species with a fugitive life strategy and a great abil-

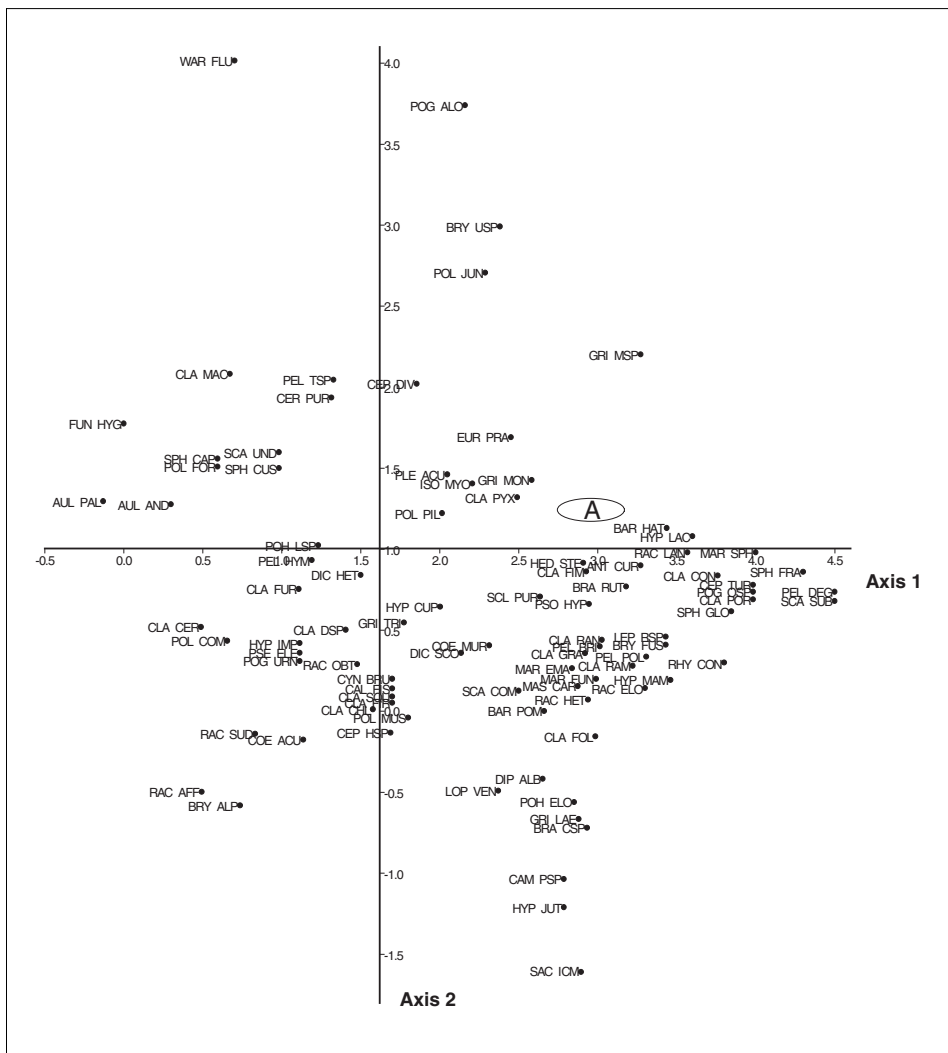


Fig. 3. Ordination diagram of species scores on axes 1 and 2 based on RDA analysis. (A = CEP STE, CLA RAG, CYN JEN, FON ANT, LOP BIC, NAR SCA, PEL MAL, PLE SCH, PLG CAV, PTE FIL, RAC ACI, RAC AQU, RAC LAM, RHI MAG, RHY ALO, RHY RIP, RHY TRI, SCA SCA, SPH AUR, SPH COM, SPH PAP, SQU CAR).

ity to occupy burned soils. In some sites near ponds or streams and in Mat-grass communities, *Sphagnum* species can occur. As mentioned before, although this genus includes hygrophilous plants, we observed post-fire regeneration of almost completely burned gametophytes. Although some fires were very intense, species linked to hygrophytic communities remained, and besides *Sphagnum* spp., *Aulacomnium palustre*, *Scapania undulata* and *Warnstorfia fluitans* were found (F698).

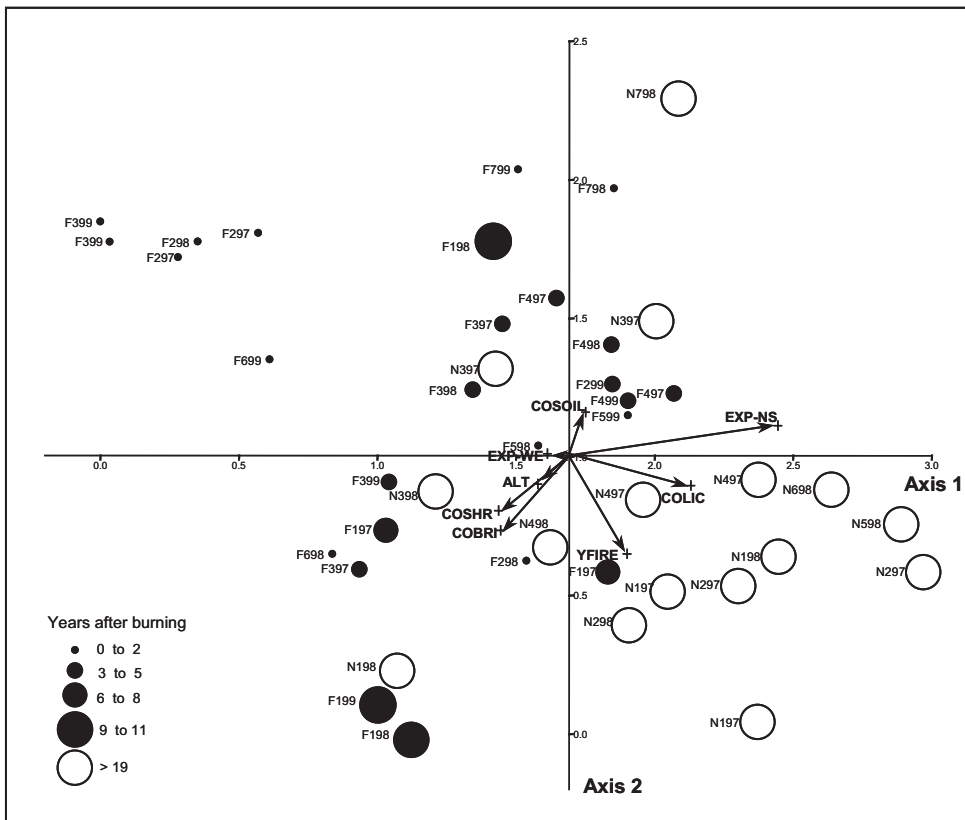


Fig. 4. RDA biplot of the environmental variables (arrows) on axes 1 and 2. Sample numbers are referred to in Material and Methods. Abbreviations: YFIRE = years after burning; COBRI = percentage cover of bryophytes; COLIC = percentage cover of lichens; COSHR = percentage cover of shrubs; COSOIL = percentage of free soil; EXP-NS = North-South aspect; EXP-WE = West-East aspect; ALT = altitude.

In burned zones (Fig. 4- F299, F397, F398, F497, F498, F499) especially in shrub communities of the *Genista florida* and *Cytisus striatus* type, or heathlands, the highest diversity was attained 3-8 years after fire, when cover by bryophyte species was also high and favoured by a well-developed shrub layer. In this situation *Bryum alpinum* dominated, together with species of *Polytrichum* and *Racomitrium*.

In communities not influenced by fire and north to northwest facing (Fig. 3 and Fig. 4- N497, N598, N698) diversity was clearly higher, but cover was lower, and pleurocarpic and perennial mosses, such as *Antitrichia curtipendula*, *Brachythecium rutabulum*, *Hypnum jutlandicum* and *H. mamillatum* dominated. In such places, foliose hepatics were also present, e.g. *Cephaloziella turneri*, *Diplophyllum albicans*, *Lophozia ventricosa*, *Marsupella emarginata* and *Scapania compacta*, favoured by soil stability and, in some cases, higher humidity. Here, the shrub cover was not the highest since the tree layer dominated in many communities, which had remained unburned for more than 19 years.

Lichen cover was also positively related with plots not affected by fire. Places recently burned virtually lacked lichen cover, with only a few primary thalli of *Cladonia* that is characteristic of pioneer stages (Fig. 3 and Fig. 4- F298, F598). Intermediate values of floristic richness appeared 3-8 years after fire, with predominance of the *Cladonia* species (F398, F499). The highest values, both for diversity and cover, were recorded in unburned communities, with *Bryoria fuscescens*, *Coelocaulon muricatum*, *Massalongia carnosa*, several *Peltigera* species and *Psoroma hypnorum*, as characteristic elements (N198, N298, N698).

Altitude was not an important factor for the interpretation of the community dynamics, with an inverse gradient along axis 2 (Fig. 4). As mentioned in biodiversity analysis, site number 7 presents a particular position on the biplot, since it represents the lowest altitude studied, experiencing a considerable mediterranean influence.

CONCLUSIONS

Colonisation dynamics after fire depends on the type of vegetation that has been burned, which in turn affects fire intensity and type and, consequently, the whole colonisation process. In later stages of this succession, the organic matter accumulated on the soil and the hydric conditions, together with other environmental factors, are the primary factors determining the development and regeneration of cryptogamic communities.

Concerning the composition of cryptogamic communities over time, it is possible to observe an increase of biodiversity, which results from the successional dynamics of these populations. The cryptogamic communities that develop in the first years after fire are mainly composed by colonist and fugitive bryophyte species (e.g. *Ceratodon purpureus* and *Funaria hygrometrica*). These taxa tend to be progressively replaced by species with longer life spans and more demanding life strategies, concerning substrate, nutrient and water availabilities. This is the case of the lichens *Cladonia* spp. and *Peltigera* spp., and the pleurocarpic bryophytes, which may form more or less extended carpets and alternate with small clumps of foliose hepatics, developing close to areas of running water, such as *Lophozia ventricosa*, *Nardia scalaris* and species of *Marsupella* and *Scapania*.

An important aim of nature management is to preserve the existing biodiversity. In some cases, and if carefully used, burning seems to contribute to expand this diversity. In specific habitats of the Serra da Estrela, the traditional use of burning by the shepherds (to create grasslands or migratory ways), can contribute to the diversification of the vegetation mosaic and the enlargement of biodiversity.

Regarding the prospect of fire occurrence, it seems that the appropriate management of the Serra da Estrela area should include a mosaic of vegetation with different age classes in order to provide adequate habitat for both fire adapted and fire sensitive cryptogamic species.

The result of this study represents the first study of recolonisation after fire in Serra da Estrela by lichens and bryophytes, and provides a basis for future analysis of the influence of natural fire on the diversity of the terricolous cryptogams.

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ANNEX

List of taxa (bryophytes and lichens) recorded in the studied sites. The species present outside the plot area are marked with (f). N-unburned (plot number) and F-burned (plot number).

Species abbreviations are given for taxa considered in statistical analysis. Conservation status indicated for species being in a special situation: R = rare; V = vulnerable; E = endangered.

○ Presence in unburned plot. First occurrence in burned plot • 0-2 ; ● 3-5; ● 6-8; ● 9-11 years after fire.

Abbrev.	Species	N1	N2	N3	N4	N5	N6	N7	F1	F2	F3	F4	F5	F6	F7
Liverworts															
BARHAT	R Barbilophozia hatcheri (Evans) Loeske						○			●					
CALFIS	Calypogeia fissa (L.) Raddi		○												
CEPDIV	Cephaloziella divaricata (Sm.) Schiffn.	○		○	○	○	○	○	●	●		●			●
CEPSP	Cephaloziella sp.	○	○						●		●				
CEPSTE	Cephaloziella stellulifera (Spruce) Schiffn.						○	○							●
CEPTUR	Cephaloziella turneri (Hook.) K. Muell.		of			of									
DIPALB	Diplophyllum albicans (L.) Dum.		of			of									
LOPBIC	Lophozia bicrenata (Schmid. ex Hoffm.) Dum.					of									
LOPVEN	R Lophozia ventricosa (Dicks.) Dum.		○												
MAREMA	Marsupella emarginata (Ehrh.) Dum.		○			of									
MARFUN	Marsupella funcikii (Web. & Mohr) Dum.		of												
MARSPH	Marsupella sphacelata (Gieseke ex Lindenb.) Dum.					of	of								
NARSCA	Nardia scalaris S. Gray						of								
SCACOM	Scapania compacta (A. Roth) Dum.		○												
SCASCA	Scapania scandica (Arnelt et H. Buch) Macvicar						of								
SCASUB	Scapania subalpina (Nees ex Lindenb.) Dum.					○	of								
SCAUND	Scapania undulata (L.) Dum.														*f
Mosses															
	Andreaea heinemannii Hampe & C. Muell.					of									
	Andreaea rothii var. falcata (Schimp.) Lindb.						of								
	R Andreaea rupestris Hedw. var. rupestris						of								
ANTCUR	Antitrichia curtipendula (Hedw.) Brid.					○	of			*f					
AULAND	Aulacomnium androgynum (Hedw.) Schwaegr.	○												*f	●
AULPAL	Aulacomnium palustre (Hedw.) Schwaegr.									*f					
BARPOM	Bartramia pomiformis Hedw.	○	○			of									
BRARUT	Brachythecium rutabulum (Hedw.) B., S. & G.		of							●					
BRACSP	Brachythecium sp.	○													
BRYALP	Bryum alpinum With.	○	○	○	○	of	of		●	*f	●				
BRYSP	Bryum sp.						○			●					●
CAMSP	Campylopus sp.	of													
CERPUR	Ceratodon purpureus (Hedw.) Brid.	○	○	○	○	of	○	○	●	●	●	●	●	●	●
CYNBRU	Cynodontium bruntonii (Sm.) B., S. & G.		○												
CYNJEN	V Cynodontium jenneri (Schimp.) Stirt.						of								
DICHET	Dicranella heteromalla (Hedw.) Schimp.		of	○											
DICSCO	Dicranum scoparium Hedw.	○	○		○	○	○			●			●	*f	
EURPRA	Eurhynchium praelongum (Hedw.) B., S. et G.			○											
EURPUM	Eurhynchium pumilum (Wils.) Schimp.						○								
FONANT	Fontinalis antipyretica Hedw.						○								
FUNHYG	Funaria hygrometrica Hedw.									●	●		●	●	
GRILAE	Grimmia laevigata (Brid.) Brid.						of								
GRIMON	Grimmia montana B. & S.						○								*f
GRISP	Grimmia sp.				○										
GRITRI	Grimmia trichophylla Grev.						of					●			
HEDSTE	Hedwigia stellata Hedenäs		of			of	of								
HYPUP	Hypnum cupressiforme Hedw. s. lat.	○	○	○		○	○			●					
HYPIMP	R Hypnum imponens Hedw.		of												
HYPJUT	Hypnum jutlandicum Holmen & Warncke	○													
HYPMAM	Hypnum mamillatum (Brid.) Loeske	of	○			○									
ISOMYO	Isoetecium myosuroides Brid.						of								
	Orthotrichum rupestre Schleich. & Schwaegr.						of								

Abbrev.	Species	N1	N2	N3	N4	N5	N6	N7	F1	F2	F3	F4	F5	F6	F7
	<i>Orthotrichum striatum</i> Hedw.		○												•
PLACAV	E <i>Plagiothecium cavifolium</i> (Brid.) Iwats.						○f								•
PLEACU	<i>Pleuridium acuminatum</i> Lindb.				○			○				•			•
PLESCH	<i>Pleurozium schreberi</i> (Brid.) Mitt.						○f								
POGALO	<i>Pogonatum aloides</i> (Hedw.) P. Beauv.			○				○							
POGNAN	<i>Pogonatum nanum</i> (Hedw.) P. Beauv.							○f							•
POGSP	<i>Pogonatum</i> sp.						○f								
POGURN	E <i>Pogonatum urnigerum</i> (Hedw.) P. Beauv.			○f											
POHELON	<i>Pohlia elongata</i> Hedw.		○	○f											
POHSP	<i>Pohlia</i> sp.			○f	○f								•		
POLCOM	<i>Polytrichum commune</i> Hedw.		○	○f	○		○f		•		•		•	•	
POLFOR	<i>Polytrichum formosum</i> Hedw.														•
POLJUN	<i>Polytrichum juniperinum</i> Hedw.		○	○f	○	○	○	○		•					•
POLPIL	<i>Polytrichum piliferum</i> Hedw.		○	○	○	○	○	○	•	•	•	•	•		•
PSEELE	<i>Pseudotaxiphyllum elegans</i> (Brid.) Iwats.		○f												
PTEFIL	<i>Pterigynandrum filiforme</i> Hedw.						○f								
RACACI	<i>Racomitrium aciculare</i> (Hedw.) Brid.						○f								
RACAFF	<i>Racomitrium affine</i> (Web. & Mohr) Lindb.		○							•f					
RACAQU	<i>Racomitrium aquaticum</i> (Schrad.) Brid.						○f								
RACELO	<i>Racomitrium elongatum</i> (Ehrh.) Frisvoll		○	○	○	○	○						•		
RACHET	<i>Racomitrium heterostichum</i> (Hedw.) Brid.		○	○	○	○	○		•	•					
RACLAM	<i>Racomitrium lamprocarpum</i> (C. Muell.) Jaeg.						○f								
RACLAN	<i>Racomitrium lanuginosum</i> (Hedw.) Brid.					○	○								
RACOB	<i>Racomitrium obtusum</i> (Brid.) Brid.			○											
RACSUD	R <i>Racomitrium sudeticum</i> (Funck) B., S. & G.		○f	○f											
RHIMAG	V <i>Rhizomnium magnifolium</i> (Horik.) T. Kop.						○f								
RHYALO	<i>Rhynchostegium alopecuroides</i> (Brid.) A.J. Smith						○f								
RHYCON	<i>Rhynchostegium confertum</i> (Dicks.) B., S. & G.			○											
RHYRIP	<i>Rhynchostegium riparioides</i> (Hedw.) C. Jens.						○f								
RHYTRI	<i>Rhytidiadelphus triquetrus</i> (Hedw.) Warnst.						○f								
SCLPUR	<i>Scleropodium purum</i> (Hedw.) Limpr.			○f			○f								
SPHAUR	<i>Sphagnum auriculatum</i> Schimp.						○f								
SPHCAP	<i>Sphagnum capillifolium</i> (Ehrh.) Hedw.						○					•f	•		
SPHCOM	<i>Sphagnum compactum</i> Dc. ex Lam. & Dc.						○f								
SPHCUS	<i>Sphagnum cuspidatum</i> Ehrh. ex Hoffm.						○f								
SPHPAP	R <i>Sphagnum papillosum</i> Lindb.						○f							•	
	<i>Tortula ruralis</i> (Hedw.) Gaertn., Meyer & Scherb.						○f								
WARFLU	R <i>Warnstorfia fluitans</i> (Hedw.) Loeske						○f								
Lichens															
BRYFUS	<i>Bryoria fuscescens</i> (Gyelnik) Brodo & D.Hawksw.			○f											
	<i>Cetraria chlorophylla</i> (Wild.) Vainio			○f		○f					•f				
	<i>Cetraria islandica</i> (L.) Ach.						○								
R	<i>Cetraria sepincola</i> (Ehrh.) Ach.			○f		○f			•f						
	<i>Cetraria</i> sp.			○f											
CLACER	<i>Cladonia cervicornis</i> (Ach.) Flotow			○	○						•				
CLACHL	<i>Cladonia chlorophaea</i> (Flörke) Sprengel		○	○											
CLACOC	<i>Cladonia coccifera</i> (L.) Willd.			○f	○	○	○	○	○	•f	•	•f			
CLACON	<i>Cladonia coniocraea</i> (Flörke) Sprengel				○	○	○								
CLAFIM	<i>Cladonia fimbriata</i> (L.) Fr.		○	○	○f	○					•				
CLAFIR	<i>Cladonia firma</i> (Nyl.) Nyl.			○f											
CLAFOL	<i>Cladonia foliacea</i> (Huds.) Willd.		○		○				•						
CLAFUR	<i>Cladonia furcata</i> (Hudson) Schrader		○	○	○	○f	○				•				
CLAGRA	<i>Cladonia gracilis</i> (L.) Willd.			○	○	○				•f					
CLAMAC	<i>Cladonia macilenta</i> Hoffm.				○										
CLAPOR	R <i>Cladonia portentosa</i> (Dufour) Coem.					○									
CLAPYX	<i>Cladonia pyxidata</i> (L.) Hoffm.		○	○		○f	○	○							
CLARAM	<i>Cladonia ramulosa</i> (With.) Laundon		○			○f	○								
CLARAN	R <i>Cladonia rangiferina</i> (L.) F. H. Wigg.				○										
CLARAG	<i>Cladonia rangiformis</i> Hoffm.						○								
CLASQUA	<i>Cladonia squamosa</i> Hoffm.			○f											
	<i>Cladonia</i> sp.		○	○	○		○	○	•			•	•		•

Abbrev.	Species	N1	N2	N3	N4	N5	N6	N7	F1	F2	F3	F4	F5	F6	F7
COEACU	Coelocaulon aculeatum (Schreber) Link	○	○		○	Of	○		●	•		•			
COEMUR	Coelocaulon muricatum (Ach.) Laudon	Of	Of		○	Of	○		•	•					
	Cornicularia normoerica (Gunn.) Du Rietz					Of	Of								
	Evernia prunastri (L.) Ach.		Of		Of										
	Hypogymnia physodes (L.) Ach.	Of	Of	Of		Of	Of		•f						
	Hypogymnia tubulosa (Schaer.) Hav.	Of	Of		Of	Of	Of		•f			•f			
R	Lasallia hispanica (Frey) Sancho & Crespo		Of		Of										
	Lasallia pustulata (L.) M érat		Of		Of	Of			•f						
	Leptogium corniculatum (Hoffm.) Minks					Of									
MASCAR	Massalongia carnosa (Dickson) Korber	○	Of		○	Of	○		●						
	Ochrolechia tartarea (L.) Massal.		Of												
	Parmelia caperata (L.) Ach.			○.f								•f			
	Parmelia conspersa (Ehrh. ex Ach.) Ach.						Of		•						
	Parmelia omphalodes (L.) Ach.		○			○	Of		•						
	Parmelia protomatrae Gyelnik				○				•						
	Parmelia pulla Ach. s. lat.				○				•						
	Parmelia saxatilis (L.) Ach.		Of			○	Of								
	Parmelia stygia (L.) Ach.				○										
	Parmelia subaurifera Nyl.		Of	Of											
	Parmelia sulcata Taylor				Of										
	Parmelia taractica Krempelh.				○				●						
PELBRI	R Peltigera britannica (Gyelnik) Hartw. & Tonsb.		○				Of				•f				
PELDEG	R Peltigera degenii Gyelnik						Of								
PELHYM	R Peltigera hymenina (Ach.) Delise ex Duby		○									•			
PELMAL	R Peltigera malacea (Ach.) Funck							○							
PELPOL	Peltigera polydactyla (Neck.) Hoffm.		○			○									
PELSP	Peltigera sp.			○											
	Platismatia glauca (L.) W. Culb. & C. Culb.		○				Of	Of							
POLMUS	Polychidium muscicola (Swartz) Gray		○						●						
	Pseudoevernia furfuracea (L.) Zopf.		Of	Of	Of	Of	Of		●						
PSOHYP	Psoroma hypnorum (Vahl.) S. Gray		Of				○								
	Rhizocarpon geographicum (L.) DC						Of		•						
SACICM	R Saccomorpha icmalea (Axx.) Clauz. & Roux								•						
SPHFRA	Sphaerophorus fragilis (L.) Pers.					Of									
SPHGLO	Sphaerophorus globosus (Huds.) Vain.		Of			○									
SQUCAR	Squamarina cartilaginea (With.) P. James							Of							
	Umbilicaria crustulosa (Ach.) Frey						Of	Of							
	Umbilicaria cylindrica (L.) Duby		Of												
	Umbilicaria grisea Hoffm.							Of							
	Umbilicaria polyphylla (L.) Hoffm.		Of												
	Usnea esperantiana Clerc		Of												
Total number		32	67	25	29	44	77	12	25	22	12	8	11	10	9