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Evaluating the post-fire natural regeneration of Mediterranean-type scrublands in Central Spain

Rosina Magaña Ugarte[1], María Manuela Redondo García[2] & Daniel Sánchez-Mata[1]

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Abstract. We performed a five-year assessment of the natural vegetation restoration capacity following the 2012 fires in Valdemaqueda (Madrid, Spain) via the characterization of the post-fire and residual vegetation and the analysis of soil physico-chemical characteristics. Six pilot-plots were established in the affected site. Forest species, representative of the potential natural vegetation of the area (*Juniperus oxycedrus* subsp. *lagunae* and *Quercus rotundifolia* woodlands) and broom shrubs (*Cytisus scoparius, Retama sphaerocarpa*) were planted to assess the relationship among the stages of ecological succession, competition, and soil restoration processes following devastating fire events.

The fire-driven alteration of the soil's physico-chemical properties was evident, given the increased pH and reduced C/N ratio in the first years of the study. However, we observed an increased soil enrichment in the last years of study, accompanied by the propagation of herbaceous species, supporting our seed bank findings, showing a clear difference in the sprouting rate between burnt and control plots (80% vs. 20%, respectively). The establishment of robust, pyrophyte shrub species (*Cistus ladanifer, C. laurifolius, Rosmarinus officinalis*) rather than natural succession evidenced the clear conversion of the vegetation in burnt areas. These findings in the pilot-plots allowed evidencing the high vulnerability of the natural vegetation to the settling of pyrophytes, given their low survival rate under the strong competitive pressure of these pyrophytic species. The proliferation of these pyrophytes could translate into changes in soil macro- and microbiota, nutrient dynamics, species diversity, and interaction, added to the alteration of fire regimes in the area. Overall, these results highlight the risk for soil impoverishment and possible erosion of the fire-affected sites. Moreover, they underline the importance of the establishment and regeneration of Genisteae species to outcompete pioneer pyrophytic species, favoring the restoration of the area's potential natural vegetation.

Keywords: wildfire; restoration; Mediterranean scrubland; pioneer species; competition.

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Introduction

In arid and semi-arid areas worldwide, regarded as hotspots of biodiversity, severe vegetation and soil losses are estimated given the significant vulnerability of these habitats to the climate crisis and desertification (Diffenbaugh *et al*., 2007; Salvati *et al*., 2013). In particular, these effects of climate aggravation are exacerbated in the Mediterranean basin, given the predicted increase in temperatures and rainfall scarcity by the end of this century, deriving in prolonged drought periods during summertime (Giorgi & Lionello, 2008). The combination of higher temperatures, elevated solar radiation, and evaporation, together with the low relative humidity and rainfall in Mediterranean-climate zones, could promote an increased susceptibility of desertification in these areas. Furthermore, these adverse climatic conditions could foster fire regime changes, resulting in an increased frequency of more severe fires added to the lengthening of the fire season (Amatulli *et al*., 2013; Pérez-Fernández *et al*., 2016).

Nowadays, fire-prone regions (e.g., Australia, California (USA), Portugal, Spain) face a substantially increased incidence of destructive and wide-ranging wildfires, threatening both biodiversity and human lives. The impact, the level of damage, and the magnitude of these fires have been critically influenced by anthropogenic effects on climate (i.e., climate crisis) and land use (Moreira *et al*., 2020). The latter being of particular importance since it directly translates into the alteration of fire regimes as a consequence of an enhanced buildup of fuel loads, caused by the conversion of natural areas for logging purposes or the expansion of the urban-wildland interface (Kraaij

[1] Department of Pharmacology, Pharmacognosy and Botany, Faculty of Pharmacy, Complutense University. E-28040, Madrid, Spain. Email: rosinamu@ucm.es
[2] Department of Geography, Faculty of Geography and History, Complutense University. E-28040, Madrid, Spain.

et al., 2018; Moreira *et al*., 2020; San Miguel-Ayanz *et al*., 2013). Furthermore, this deliberate conversion of natural vegetation tracts for logging purposes can increase post-fire physical damage and soil erosion, further restricting the restoring capacity of natural environments (Kraaij *et al*., 2018).

Fires of low to moderate severity, as most of those prescribed in forest management are, stimulate the renovation of the dominant vegetation via the removal of undesired species, transient increase of soil pH, and available nutrients (Certini, 2005; Hinojosa *et al*., 2016). However, severe fires, such as wildfires, generally have numerous adverse effects on the soil properties such as the significant removal of organic matter, the deterioration of both structure and porosity, a considerable loss of nutrients through volatilization, ash entrapment in smoke columns, leaching and erosion, and a marked alteration of both quantity and composition of microbial and soil-dwelling invertebrate communities (Certini, 2005). Furthermore, post-fire soil physical damage correlates with the degree of invasion of alien species, thus having a higher disturbance rate in uninvaded or lightly invaded areas than on heavily invaded sites (Kraaij *et al*., 2018; van Wilgen & Scott, 2001). Additionally, the environmental conditions in the affected areas have a significant role in vegetation restoration capacity. The latter is especially crucial in Mediterranean-type climate areas where the disadvantageous conditions (i.e., low rainfall, high temperatures) can significantly challenge the vegetation recovery processes (Pérez-Fernández *et al*., 2016; Vallejo *et al*., 2012).

Short-term responses of soil characteristics and vegetation to fire incidence are well-studied in most biomes across the globe. However, little information is available on the post-fire effects in Mediterranean scrublands from central Spain, despite the higher incidence of wildfires in the latest years and the expected increase in fire severity and frequency outcome of the estimated reduction in rainfall and prolonged annual drought periods, as a consequence of the climate crisis. In turn, this research aims to provide a preliminary overview of early soil and vegetation responses of a fire-affected scrubland characteristic of Central Spain, including post-fire ecological successions and restoration processes of these habitats.

Materials and Methods

Study site

Our study was set in the territory affected by the forest fires of 2004, 2012, and 2013 in the municipality of Valdemaqueda, Madrid. The affected region is delimited by cultivated areas of *Pinus pinaster* s.l., for resin extraction. The area's potential vegetation comprises holm oaks (*Quercus rotundifolia*) with cade junipers (*Juniperus oxycedrus* subsp. *lagunae*), still present in intact natural areas neighboring to those destined for pine-resin extraction. It is worth mentioning the immediate post-fire measurements taken (outsourced, independent from the study) consisted of the extraction of burnt and deadwood present in the affected area, using heavy equipment on repeated occasions, imperiling the soil to erosion processes. The affected area is located along the sloping terrain, with different exposures and aspects (Table 1; Table S2). In turn, six permanent pilot-plots were established through the affected site based on fire incidence, altitude, and vegetation type. We set four permanent plots (25 m^2) on burnt sites at different elevations, encompassing the entire macroclimatic spectrum and the main types of natural vegetation found in the affected areas. Two control plots were also established in unburnt areas adjacent to the burn sectors, following the protocol mentioned above (Table 1).

Soil sampling and analyses of physicochemical characteristics

We took five soil cores from the upper 10 cm of the soil profile, taken at the four corners of each pilot-plot (20 cores per plot), and merged them into one sampling bag per plot. At the laboratory, samples were air-dried at room temperature for two weeks and subsequently sieved. Once all soil samples were dried out, we

Table 1. Location, altitude, and fire incidence details of the permanent pilot-plots established in the present study. Abbreviations in the subscript are as follows: B, burned, NB, not burned.

Pilot-plot ID	Pilot-plot	Altitude (m asl)	Exposure	Treatment	Year of wildfire
Sta. Cat_B	Santa Catalina-Risco Grande	1386	NE	Burned	2012
Sta. Cat_{NB}	Santa Catalina-Umbria	1380	NW	Control (Not burned)	-
Er_{NB}	Ermita	1000	W	Control (Not burned)	-
Q_B	Solana de los Quejigos	1000	W	Burned	2013
CC_B	Camino de los Corrales	800	E	Burned	2004, 2012
A_B	Atalaya	800	E	Burned	2004

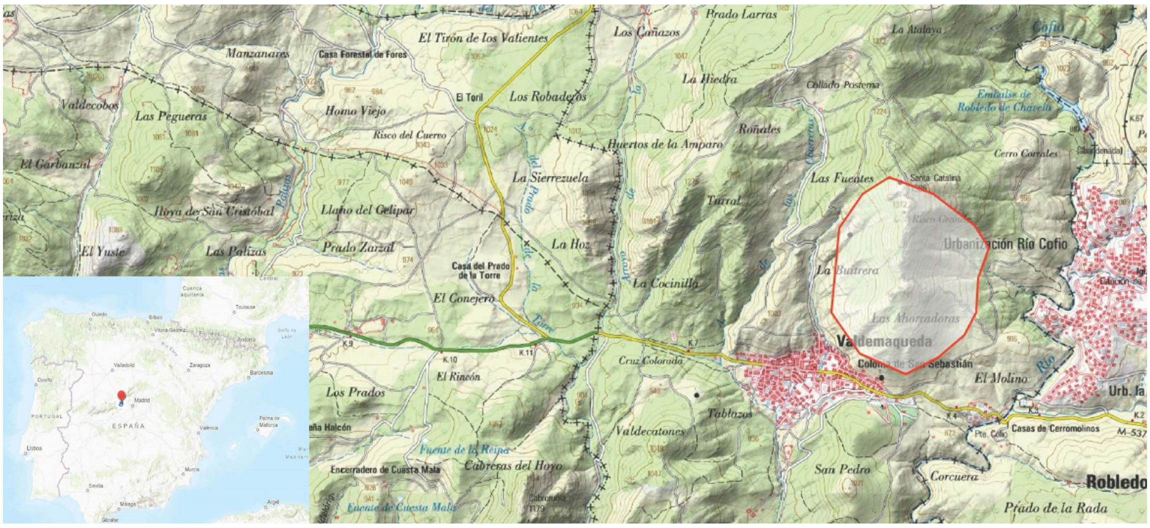

Figure 1. The geographical location of the Valdemaqueda municipality, within the Madrid Autonomous Community. The study area is circled in red.

proceeded to perform all the analyses of physicochemical characteristics (Anon., 2006; Soil Survey staff, 1999).

Particle size and classification of soils

The previously dried soil samples were used to assess the granulometric parameters. The following soil fractions were estimated and expressed in percentage: fine soil fraction for total natural soil (<2 mm), fine gravel (2-20 mm), and gravels (>20 mm).

We determined the proportion of the various size fractions for the mineral part of the soil and expressed them in percentages. The sand (50-2000 µm), silt (20-50 µm), and clay (<2 µm) fractions of each soil sample were separated and determined following the protocol by van Reeuwijk (2002). The textures in the sand fraction (only coarse sand and fine sand) were further identified following the limits established in the Soil Survey Staff (1999). The proportions of sand, clay, and slit of the soil samples were plotted on the International Soil Society texture triangle to obtain the soil sample texture (Table S1). The pH was also measured in H2O, with a suspension of soil-DIO water (1:2.5 by volume), using a glass electrode.

Micro-element analysis of soil samples

Total soil organic carbon (C_{Soil}, %), total soil nitrogen (N_{Soil}, %), soil organic matter content (SOM, %) of the fine earth fraction, and sulfur (S, %) content were determined using the “Flash Combustion Method” using a FLASH 2000 analyzer (Thermo Scientific).

Determination of the Cation-exchange capacity of soil samples

The cation-exchange capacity (CEC) of soil samples was used as an indicator of soil fertility. The measurements of the potassium (K) and sodium (Na) adsorbed to colloid (cmol/kg soil) were measured following the protocol by Burt (2004). While calcium (Ca) and magnesium (Mg) were measured using a gas chromatographer with a FID detector (Agilent Technologies, Santa Clara, CA, USA).

Evaluation of the aboveground vegetation

The characterization of the vegetation types and the estimation of fire’s influence on potential changes in the taxonomic diversity of the study site were assessed in the surrounding perimeter and inside each pilot-plot. Visual estimation of cover and identification of the species encompassed in these plant communities was performed following the established by Mucina and van der Maarel (1989) in 20 subplots (100x100 cm) inside and in the surroundings of the pilot-plots during the spring-summer periods 2014-2018.

Throughout the study, we assessed the survival and growth rates of woody individuals planted inside the pilot-plots in spring 2014 (mainly shrub species representative of the potential vegetation). The growth of these planted individuals was assessed from autumn 2014 and on. We also registered the establishment of new individuals growing in these plots (recruitment) and the new species colonizing within the pilot-plots, the outcome of the natural regeneration of the area. The growth and survival rate of these recruited individuals were registered as they established in the pilot-plots (i.e., after 2014).

The taxonomy usually follows the proposals of Euro+Med PlantBase (2006), except for the cade juniper on the territory, *Juniperus oxycedrus* subsp. *lagunae* (Pau) Rivas Mart. Higher syntaxonomical units are accepted from Mucina *et al*. (2016), while species pools are structured following the proposals of Rivas-Martínez *et al.* (2002; 2011).

Soil seed bank

Soil samples were taken to assess the fires' effects on the temporal seed bank and, consequently, obtain a good indication of the regeneration of vegetation of the fire-affected area. Thirty soil samples were taken from the topsoil (5 cm), since this is the area where most seeds accumulate in the soil (Vilà & Gimeno, 2007), in the perimeter outside each pilot-plots (control and treated) in 2015 and 2017 using a metallic core (diam: 5 cm, height: 5 cm). After collection, all samples were kept at 4 °C for two months. Afterward, all individual soil samples were sieved through a 0.5 cm mesh to retain the coarse fraction, with one additional sieving through a 0.2 cm mesh to reduce the volume of fine material and favor the scarification of seeds to promote germination (Thompson *et al.*, 1997).

Next, each soil sample was placed in a small tray (14x11x5 cm, one core sample per tray) and thoroughly mixed with a sterile substrate of vermiculite and peat (1:1:0.5) to improve the water-retention capacity of the soil. Afterward, all trays were transferred to the greenhouse to monitor seedling emergence. Greenhouse conditions were set to maintain a mean 25 °C day/night temperature, with individual tray irrigation every three days. Seedlings were identified as soon as they emerged in the trays and subsequently removed. When the identification was not feasible at the species level at this early stage, the seedlings were kept in their respective trays until they attained a sufficient development that allowed their proper identification.

When growing under favorable conditions, seed germination should occur in its majority within two months (Graber & Thompson, 1978; Thompson *et al.*, 1997). In our case, we maintained and followed-up the seed bank for three months in both years to allow the germination and identification of all potentially viable seeds present in the soil samples. After the third month, we added a solution of gibberellic acid (1000 ppm) to stimulate seed emergence in those with endogenous dormancy (Hartman & Kester, 1991). Emergence was monitored for another month in the gibberellic acid-treated trays.

Results

Effects of fire on soil physico-chemical characteristics

Minor differences in the soil pH were observed between 2015 and 2017 (Table 2), maintaining a moderately acidic soil in the measurements closer to the fire events. Nevertheless, in the latest samples (2017), a slight increase in the pH was observed in most of the burned sites, and the increase in the lime fraction and reduction of the clay fraction in all sites (Table S1).

The CEC analyses from burned plots (i.e., Sta. Cat_B, Q_B, CC_B) show a high content of alkaline cations Ca^{2+} and Mg^{2+} in years closer to the fire events, contrasting their lower values in the 2018 samples (Table 3). In each plot, minor variations were observed in the CEC throughout the study period while showing considerable differences among sites, independent of fire incidence. Furthermore, the C/N ratio decreased between 2015 and 2017 in all plots (Table 2), regardless of fire incidence. However, we observed a broader range on the C/N decrease (58.07–72.75%) in burned plots than in the unburnt sites (64.94–63.39%). The slope could have influenced the latter since the burned plots are located on steeper slopes than those unaffected by the fire.

Soil seed bank

Results from the 2015 soil seed bank reported the germination of 48 species from 20 different families (Table 4). In this round, the highest-incidence families were the Asteraceae (10 species), Fabaceae (6 spe-

Table 2. Comparison of the general characteristics of topsoil (0-10 cm) in pilot-plots between the year after the last fire event (2015) and the three following years (2017). Values of the total soil carbon content (C), nitrogen (N), sulfur (S), carbon/nitrogen ratio (C/N), and soil organic matter content (SOM) are given in percentage. EC, Electric Conductivity.

Pilot-plot	Sta. Cat_B		Sta. Cat_{NB}		Er_{NB}		Q_B		CC_B		A_B	
Year sample	2015	2017	2015	2017	2015	2017	2015	2017	2015	2017	2015	2017
pH, (H_2O)	5.7	5.7	5.8	5.9	6.3	6.0	6.8	6.9	5.9	6.1	6.0	6.7
EC (µS)	76.9	74.3	68.9	68.4	40.5	40.0	64.1	65.0	63.7	64.2	71.3	70.9
C (%)	3.53	4.64	3.82	3.17	5.29	4.27	3.10	3.16	1.76	1.85	1.56	1.31
N (%)	0.19	0.43	0.18	0.23	0.21	0.26	0.17	0.26	0.14	0.24	0.13	0.15
S (%)	0.03	0.03	0.04	0.02	0.04	0.03	0.04	0.04	0.05	0.03	0.04	0.01
C/N	18.58	10.79	21.22	13.78	25.19	16.42	18.24	12.15	12.57	7.71	12.00	8.73
SOM (%)	6.07	7.98	6.57	5.45	9.10	7.34	5.33	5.44	3.03	3.18	2.68	2.25

Table 3. Cation exchange capacity (CEC) and exchangeable cations in topsoil (0–10 cm) of soils outside pilot-plots. Units for Na, K, Ca, Mg and CEC are in $cmol/kg_{soil}$

Pilot-plot	Year	Exchangeable bases				
		Na^+	K^+	Ca^{2+}	Mg^{2+}	CEC
Sta. Cat_B	2015	0.76	0.8	11.69	3.09	16.05
	2017	0.38	0.58	9.08	1.71	14.55
Sta. Cat_{NB}	2015	0.76	0.65	12.01	3.50	16.92
	2017	0.72	0.50	12.24	2.61	16.21
Q_B	2015	0.65	0.81	11.09	3.09	15.39
	2017	0.89	0.44	12.53	1.98	15.84
Er_{NB}	2015	0.81	0.80	15.09	4.03	20.40
	2017	0.52	0.42	12.37	2.53	19.04
CC_B	2015	0.78	0.57	7.03	1.05	9.38
	2017	0.53	0.25	8.46	0.82	10.06
A_B	2015	0.73	0.56	8.02	1.16	11.40
	2017	0.57	0.24	7.48	0.82	9.12

Table 4. Number of seedlings and species identified per pilot-plot in the greenhouse experiment. Data correspond to the seed bank samples from 2017 (see Appendix 1 for identified species).

Pilot-plot	No. Identified seedlings	No. species	Species density (N/m^2)
Sta. Cat_B	53	25	2.12
Sta. Cat_{NB}	18	9	0.72
Er_{NB}	75	21	3
Q_B	84	25	3.36
CC_B	238	26	9.52
A_B	34	15	1.36

cies), and Caryophyllaceae (6 species). In contrast, we observed a substantial increase in species richness in the 2017 soil seed bank, with a highly similar number of families (22). Nonetheless, we included two more families among those with the highest incidence of germination in our seed bank, with the most abundant being the following: Caryophyllaceae (6 species), Scrophulariaceae (7 species), Fabaceae (8 species), Poaceae (7 species) y Asteraceae (6 species).

Compared to prior seed bank results (i.e., 2015), we observed substantial differences in the germination rate between treatments in the 2017 samples. Our results indicated that 80% of the total sprouted seedlings corresponded to samples from burned plots, while only 20% of the seedlings emerged in control plots (not burned).

Post-fire stages of ecological succession, competition, and soil restoration processes

During four years (2014-2018), we assessed the rates of persistence, recruitment, and growth rates of the four main shrub species present within the pilot-plots to determine the fire effects on post-fire ecological successions and restoration processes. Persistence and growth rates were recorded for the individuals of each species planted since the establishment of the pilot-plots (i.e., 2014), while persistence, recruitment, and growth were recorded for species and new individuals establishing inside the pilot-plots after 2014. Our results revealed a substantial and steady increase in plant density and height for *Cistus ladanifer* at all elevations (Figure 2, Figure S2a), with the highest individuals found at the lowest elevationss (pilot-plots CC_B, A_B). Similarly, *Cytisus scoparius* and *Rosmarinus officinalis* showed a steady increase in plant height (Figures S1a, S1b, respectively) at mid- and low-altitude plots.

Compared to unburnt plots, those affected by wildfire registered a higher density of individuals was registered in plots affected by wildfire (Sta. $Cat._B$, Q_B, CC_B, A_B), particularly in those located at mid- and low-elevations (Figure 2). Densities of pioneer pyrophyte species, mainly *Cistus ladanifer* (Figure 2d), were considerably higher than the density of the potential natural vegetation and Genisteae (*Cytisus scoparius*, *Retama sphaerocarpa*; Figure 2a, b) in burned sites. Conversely, unburnt plots (Sta. $Cat._{NB}$, Er_{NB}) showed minor variations in the density of individuals. Furthermore, we observed a greater density of individuals and species diversity in the mid- and low-elevation plots burned in recent years (i.e., Q_B, CC_B), compared to those that suffered the incidence of wildfires in earlier years (Sta. $Cat._B$).

A common occurrence of plants from Mediterranean

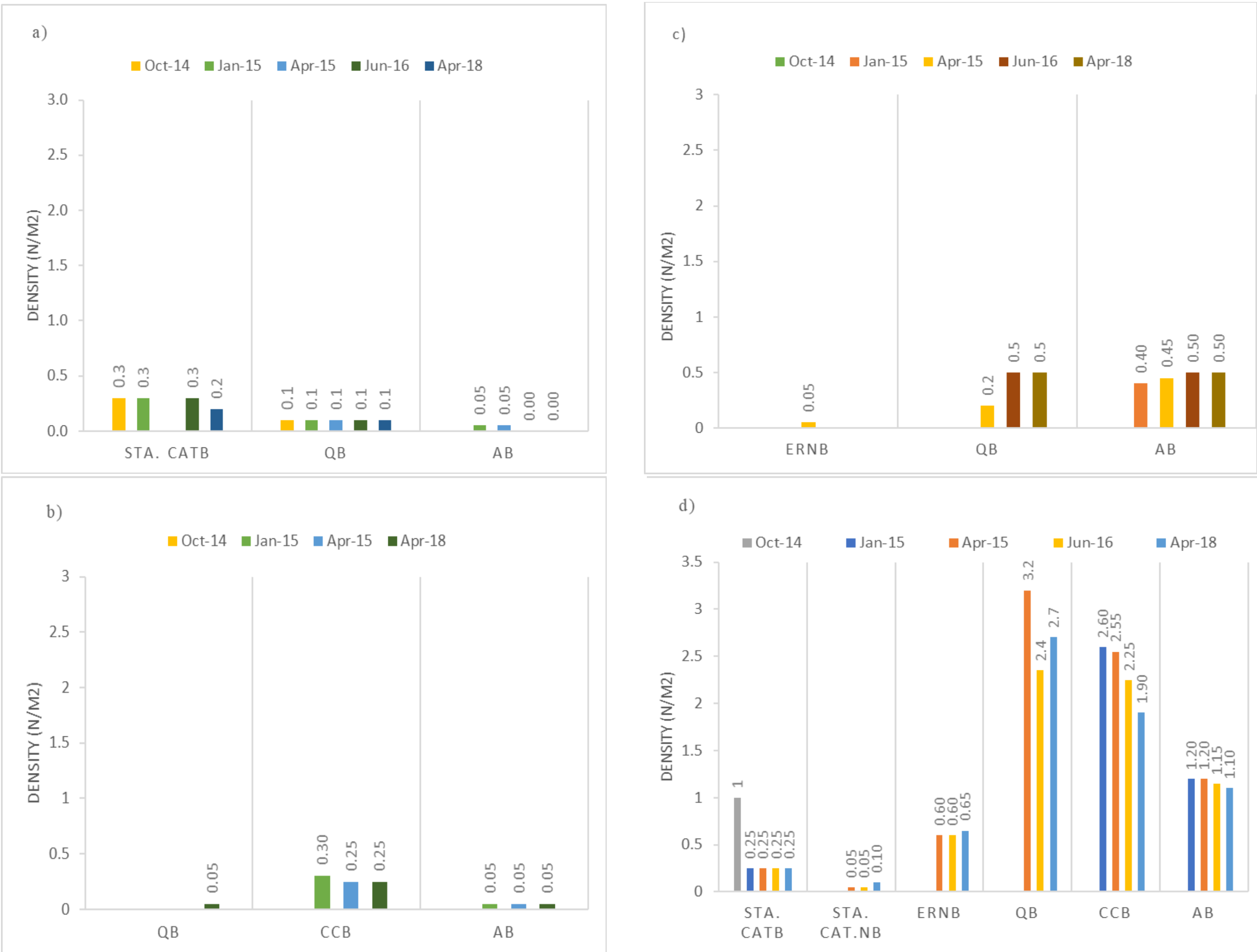

Figure 2. Density of individuals (no. individuals per m²) of a) *Cytisus scoparius*, b) *Retama sphaerocarpa*, c) *Rosmarinus officinalis*, and d) *Cistus ladanifer* through four years of assessment (2014-2018). The pilot-plot abbreviation is as follows: Sta. Cat. $_B$, Sta. Catalina – Risco Grande (Burned); Sta. Cat. $_{NB}$, Sta. Catalina – Umbria (Not burned); ER_{NB}, Ermita (Not burned); Q_B, Solana de los Quejigos (Burned); CC_B, Camino de los Corrales (Burned); A_B, Atalaya (Burned).

annual grasslands of *Helianthemion guttati* (and higher syntaxa) was found in the vegetation plots of 2017 throughout the entire study area. These species were found together withan assortment of ruderal and segetal species (framed in several anthropogenic phytosociological vegetation classes) in the foothills (pilot-plots CC_B and A_B; Tables 5, 6) and mid-altitudes (Er_{NB} and Q_B; Tables 7, 8), emerging among individuals of *Cistus ladanifer*, *Cytisus scoparius*, *Retama sphaerocarpa* or *Rosmarinus officinalis* shrublands. The richest plot with a higher incidence of species from *Helianthemetea guttati* was found in the fire-affected Q_B. In contrast, the unburnt plot located at the same altitude, Er_{NB}, denoted the poorest species richness from Heliantemetea guttate and instead bore xerophilous silicicolous grasslands (*Hieracio castellani-Plantaginion radicatae*) and ruderals, among others. As for the high-altitude burned areas (i.e., Sta. Cat.$_B$), we registered the occurrence of perennial xerophilous siliceous grasslands of *Hieracio castellani-Plantaginion radicatae* (*Jasiono sessiliflorae-Koelerietalia crassipedis*, *Festucetea indegestae*; Table 9), together with several perennial species distinctive of dry grasslands (*Stipo giganteae-Agrostietea castellanae*) and, similar to the observed at mid- and low-altitudes, a vast set of annuals from *Helianthemetea guttati*.

Discussion

In fire-affected areas, recovery of SOM initiates with the natural or artificial re-establishment of vegetation, a commonly fast process owing to the high net primary productivity of secondary ecological successions (Certini, 2005). Nevertheless, despite the positive, short-term effects of leaf matter burning (e.g., higher soil N available for plants, nitrate availability), its long-term effects have a more pondering effect. The latter fosters an enhanced direct exposure of the topsoil to environmental factors, making it more prone to erosion. Moreover, the burning of the vegetal cover and roots prompts the loss of mechanical support in the soil, leading to the decapitation of the soil profile and, ultimately, resulting in the loss of the soil's ecological utility, hindering the natural recovery of the burned area.

Rapid plant recolonization is crucial for safeguarding soil N in fire-affected areas (Weston & Atwill, 1996). Expressly, the recovery of the organic N pool can occur at a relatively fast rate if N-fixer species are within the recolonizing flora, a regular instance in burnt areas (Johnson & Curtis, 2001; Certini, 2005). The increased total soil N found in all burned sites allows inferring a positive effect of establishing N-fixing species, *Cytisus scoparius* and *Retama sphaerocarpa* (Adams & Atwill, 1984; Spehn *et al*., 2002; Temperton *et al*., 2007; Fornara & Tilman, 2009). The lower N_{TOTAL} measured in years closer to the burning (i.e., 2015) compared to the higher values in later years (i.e., 2017) implies the increase in N_{TOTAL} is not related to the enhanced release of N from burning residues (Alcañiz *et al*., 2018; Pellegrini *et al*., 2018). Thus, the observed increase in N_{TOTAL} could suggest the N-fixers' potential contribution in our pilot-plots to the soil N pools (Johnson & Curtis, 2001; Fornara & Tilman, 2009). Moreover, the minor changes in the soil C of burned pilot-plots (Table 2) could be suggested as an additional prospective benefit of establishing N-fixing species since their enhanced N input has been linked to facilitating C sequestration (Johnson & Curtis, 2001). Nevertheless, further studies assessing the organic N fraction are still required.

Fire intensity is strongly associated with the alterations in the amount and availability of soil nutrients due to the severe influence of fire on the biological, chemical, and physical properties of soils (James *et al*., 2018). Resembling the findings by Tomkins *et al*. (1991) and Santín *et al*. (2018), our results show a high availability of nutrients in years closer to the fire events (i.e., 2015; Table 3) than in later years, as an outcome of the combustion of residues and organic matter (Certini, 2005). The similar Ca^{2+}, Mg^{2+}, K^{+}, and Na^{+} levels in control and more-recently burned plots (i.e., Sta. Cat_B, Q_B, CC_B) allows suggesting a persistent fire-induced availability of these nutrients up to 3 years after fire (Simard *et al*., 2001; Certini 2005). However, this persistence effect shows to decline >3 years after the fire, as seen in plots burned more than ten years ago (i.e., A_B), possibly due to processes such as leaching or soil erosion. In line with the latter, the increase in the soil pH could be related to the increase in SOM observed in 2017 samples, enhancing the buffering capacity of the soils in the affected area, which is linked to the CEC.

The recovery of the natural balance is associated with species diversity. The latter relating to the observed increase in species diversity in the latest seed bank (i.e., 2017; Table 4, Table S1) compared to the lower species richness found in samples from the year following the last fire event (i.e., 2015). The high species diversity observed in plots burned in recent years (Table 4) could be related to the reduced soil acidity, higher SOM, and lower C/N (Table 3). In recent years, the increase in N_{TOTAL} could have facilitated the abundant sprouting of herbaceous species, with inclinations for nitrophylous taxa. Additionally, vegetation plots recorded in 2017 indicate a higher incidence of plants from Mediterranean ephemeral grasslands than the rate of purely ruderal, indicating the preference of the former type of plants for such nutrients. The observed increase in species richness might be associated with the observed soil enrichment, and the decrease in soil acidity, the outcome of the spread of N-fixing species in the study plots (Fornara & Tilman, 2009). In Mediterranean-type bioclimates, the vegetation type-conversion is mostly shaped by combining two plant stress factors: fire regimes and the summer drought period characteristic of these habitats (Jacobsen & Pratt, 2018). Resembling the findings by Dickens and Allen (2014), our results evidence the harmful effects of forest fires on maintaining the natural vegetation-types. The latter is supported by the enhanced establishment and rapid growth of pyrophytic pioneer species favored by the fire-removal of the vegetation cover and not due to the natural succession stages of vegetation (Supplementary Figure 2). Additionally, the enhanced species richness found in the seed bank samples from burned plots, compared to those untouched by fire, suggests fire and summer drought as stress factors that act as strong drivers of species richness in this area (Jacobsen & Pratt, 2018). Furthermore, studies in chaparral habitats have demonstrated that the vegetation-types' conversion always leads to functional-type conversions (Jacobsen & Pratt, 2018). The observed vegetation-type conversion could lead to changes in ecosystem services, such as alterations in nutrient-cycles, species interactions, and even influence the fire regimes (Schoennagel *et al*., 2004; Dickens & Allen, 2014). For instance, our results from the soil seed bank confirmed the observations from the vegetation plots, indicating that, albeit being adjacent zones, the plots located in the "Camino de los Corrales" area (CC_B) denoted a slightly higher species richness than that of the "Atalaya" area (AB). The latter could be attributed to the "Atalaya" ranch establishment, which altered the zone for intensive hunting purposes, thus, fostering a vegetation-poor area in the forest layer before it burned. Consequently, the "Atalaya" site required a longer time to be colonized by the diaspora of surrounding areas, e.g., CC_B, to regain species diversity. These alterations in species richness and vegetation-type conversions can be further associated with the enhanced vulnerability of Mediterranean-type ecosystems to the effects of climate change.

The forecasted lengthening of the drought period and increase in temperature regimes could escalate the risk of fires, particularly in areas with higher fuel loads (San Miguel-Ayanz *et al*., 2013). Additional fuel resulting from the invasion of pyrophyte species can increase the intensity and severity of fires in the area, intensifying the extent of fire destruction and the difficulty of controlling them (Keeley, 2009; San Miguel-Ayanz *et al*., 2013). The latter is particularly threatening for areas where non-endemic species have been introduced for primary activity purposes. Similar to the occurred in the study area, the substitution of natural Fynbos shrublands in South Africa by plantations of *Pinus pinaster* s.l. and E*ucalyptus globulus* enhanced the fuel loads and, consequently, the fire risk and intensity of wildfires (Kraaij *et al*., 2018).

Final remarks and future perspectives

• The introduction of species with forestry exploitation purposes produces changes in the composition of the natural species. This leads to a higher fire-prone biomass content, which heightens these areas' vulnerability to forest fires.

• Identification and establishment of fire-risk zones are indispensable, combined with creating efficient fire-prevention policies that incorporate the paradigm shift proposed by Moreira et al. (2020): rating policy effectiveness as a function of prevented socio-ecological damage and loss rather than as a function of area burned.

• Use the present study results regarding the alteration of edaphic properties to create a suitable strategy and protocols to restore the fire-affected scrublands in Central Spain.

• Highlight the importance of studying the post-fire evolution of the soil microbial communities, given their fundamental role in biological processes, which directly influences soil quality. The latter being particularly vital in areas significantly affected by the fire since improving soil quality will allow the rooting and, subsequently, the restoration of the aboveground vegetal cover.

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Supplementary Material

Figure S1. Plant height of Genisteae species a) *Cytisus scoparius* and b) *Retama sphaerocarpa* planted in pilot-plots, assessed through 4 years following the wildfires.
Figure S2. Variations in plant height of woody pioneer pyrophytes: a) *Cistus ladanifer* and b) *Rosmarinus officinalis*, and potential vegetation species c) Q*uercus rotundifolia* in the pilot-plots through 4 years following the wildfires.

Table S1. Comparison of the proportion of the size fractions (%) of soil samples collected in the pilot-plots' surroundings 5 and 7 years after wildfires (2015 and 2017).
Table S2. Geographic coordinates and details of the permanent pilot-plots established in the study.

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Table 5. Plots recorded in the "Camino de los Corrales" area (CCB, burned). For all plots, the altitude is 800 m asl. Indexes correspond to those of Br.-Bl. 1964. See text for more explanations on plant communities and syntaxa.

N. Species	13	20	20	19	20	16	15	16	21	17	17	20	17	22	22	20	22	24	24	24
Plot N.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Characteristics of *Helianthemion guttati* (*Helianthemetalia guttati, Helianthemetea guttati*)																				
Tuberaria guttata	2	1	2	2	1	1	1	1	1	2	1	1	4	1	2	1	2	1	1	2
Trifolium cherleri	2	1	1	2	1	+	+	2	2	2	1	2	1	+	2	1	3	1	2	1
Hypochaeris glabra	+	+	1	1	1	1	1	1	1	1	1	1	1	1	3	1	1	1	1	1
Ornithopus compressus	+	1	1	1	1	1	1	1	1	1	+	1	1	+	1	1	1	1	1	1
Tolpis umbellata	1	1	1	2	1	1	1	2	1	.	.	1	1	1	1	1	1	1	1	1
Vulpia myuros	1	1	1	2	1	1	1	1	1	2	1	1	2	2	1	1	3	2	1	.
Leontodon saxatilis subsp. *rothii*	.	.	.	1	1	1	1	1	1	.	1	1	1	1	1	1	1	1	1	1
Asterolinon linum-stellatum	.	.	+	.	+	.	1	1	.	.	+	+	+	1	1	1	1	+	+	+
Trifolium arvense	.	.	.	.	.	.	.	.	+	+	1	1	1	1	1	1	1	1	1	1
Anthyllis cornicina	+	+	+	+	.	+	+	+	1	.	.	.	.	.	.	.	.	.	.	
Silene scabriflora	.	.	.	.	.	.	.	.	1	+	.	+	+	+	+	+	+	.	.	
Coronilla repanda subsp. *dura*	.	+	1	+	.	+	.	+	+	.	.	.	.	.	.	.	.	.	.	.
Anthyllis lotoides	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+	.	1	+	1	.
Filago minima	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	+	+	+	.	.
Sedum arenarium	.	.	1	+	.	.	.	.	.	+	.	.	+	.	.	.	.	.	.	.
Vulpia ciliata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	3
Corynephorus divaricatus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	+
Holcus gayanus	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Helianthemum ledifolium	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.
Linaria spartea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.
Transgressives from different anthropogenic vegetation classes																				
Avena barbata	2	3	1	2	2	2	2	2	3	2	3	2	1	3	1	3	2	3	3	2
Anisantha tectorum	1	2	3	1	3	3	3	3	2	1	2	1	1	1	+	+	+	1	+	+
Anthemis arvensis	1	2	2	2	1	1	2	2	2	1	2	1	1	2	+	2	1	1	+	1
Vicia sativa subsp. *nigra*	+	1	+	+	+	+	.	.	.	+	+	+	.	+	.	+	1	+	+	+
Andryala arenaria	.	+	+	+	+	.	.	1	+	+	+	.	.	1	+	+	+	+	.	+
Bellardia trixago	.	1	+	.	+	+	+	.	.	+	+	1	.	.	+	.	.	+	1	+
Vicia disperma	.	.	.	.	.	.	.	.	.	.	1	1	.	+	+	1	1	1	1	1
Echium vulgare	1	1	3	.	.	.	.	1	.	1	.	1	.	.	.	.	.	.	.	
Calendula arvensis	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	1	+	1	+
Anisantha madritensis	.	.	.	.	.	.	.	.	.	.	.	.	+	1	+	.	.	+	+	.
Vicia lutea	.	+	.	.	+	+	.	.	+	.	.	.	.	.	.	.	.	.	.	.
Geranium molle	.	.	.	.	+	.	.	.	.	.	.	+	.	.	.	+	+	.	.	.
Coincya monensis subsp. *orophila*	.	+	+	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.
Eryngium campestre	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
Corrigiola telephiifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1	.	.	.	.	.
Torilis nodosa	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	1
Silene gallica	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+
Spergularia purpurea	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Brassica barrelieri	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Erodium cicutarium	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.
Anisantha diandra	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
Other species																				
Poa bulbosa	.	.	1	1	+	+	+	+	+	1	+	+	1	+	+	1	1	+	.	+
Leopoldia comosa	.	+	.	.	+	.	.	.	+	.	.	.	.	.	.	+	.	.	.	+

Paronychia argentea	.	.	.	.	.	.	1	.	.	.	.	.	.	.	+	.	+	.	.	.
Trifolium glomeratum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1	+
Thapsia villosa	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sanguisorba verrucosa	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cistus ladanifer (pl.)	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Dactylis glomerata	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Parentucellia latifolia	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.
Asphodelus cerasiferus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
Trifolium scabrum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+

Table 6. Plots recorded in the "Atalaya" area (AB, burned). For all plots, the altitude is 800 m asl. Indexes correspond to those of Br.-Bl. 1964. See text for more explanations on plant communities and syntaxa.

N. Species	14	15	16	15	17	18	16	18	15	13	13	13	13	15	15	14	16	15	12	15
Plot N.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Characteristics of Helianthemion guttati (*Helianthemetalia guttate*, *Helianthemetea guttati*)																				
Tuberaria guttata	3	1	1	1	1	1	+	+	1	1	+	+	1	1	1	2	+	1	1	1
Ornithopus compressus	3	2	4	3	4	2	3	3	3	1	3	2	3	3	4	3	4	2	3	3
Asterolinon linum-stellatum	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	+	+
Hypochaeris glabra	1	1	1	2	1	1	1	1	2	1	1	1	1	2	1	1	2	1	3	2
Vulpia myuros	2	2	1	1	1	1	2	1	3	2	3	3	2	2	2	2	3	2	1	1
Anthyllis lotoides	+	+	+	+	1	+	+	+	1	1	+	+	1	+	+	2	+	1	+	+
Leontodon saxatilis subsp. *rothii*	2	1	+	1	+	.	1	+	1	+	1	+	+	+	+	+	.	1	+	.
Scleranthus polycarpos	1	+	+	+	1	4	+	+	1	1	.	1	1	1	1	1	+	+	1	1
Coronilla repanda subsp. *dura*	1	+	+	1	1	+	+	1	+	1	+	+	+	.	+	+	1	1	+	1
Trifolium cherleri	1	3	2	1	+	+	.	.	.	1	+	2	1	1	+	1	1	1	+	+
Andryala integrifolia	.	+	+	.	+	+	+	.	+	+	+	+	.	+	.	.	+	+	.	.
Linaria spartea	+	+	+	.	.	+	+	+	+	.	.	.	.	.	+	.	.	.	.	.
Trifolium arvense	+	+	.	+	+	.	.	.	.	.	.	.	.	.	.	1	1	+	+	+
Trifolium hirtum	.	.	+	.	+	.	.	+	.	.	.	.	.	.	1	+	+	.	.	.
Anthyllis cornicina	.	.	.	.	.	.	.	+	.	.	.	.	.	+	.	.	.	.	.	.
Micropyrum tenellum	.	.	+	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.
Transgressives from diverse anthropogenic vegetation classes																				
Avena barbata	1	2	+	+	1	2	2	2	1	+	+	1	1	1	1	1	3	1	2	2
Vicia sativa subsp. *nigra*	.	.	+	.	+	+	+	+	+	.	+	.	1	+	+	+	+	.	.	.
Anisantha madritensis	1	+	.	+	1	4	+	+	.	.	.	.	+	.	.	.	.	.	.	1
Vicia disperma	.	.	.	.	+	+	1	1	+	.	.	+	.	+	1	.	+	.	.	.
Vicia lathyroides	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.
Geranium molle	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Anisantha tectorum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	+
Leopoldia comosa	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Bellardia trixago	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
Lactuca serriola	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.
Anisantha rigida	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Other species																				
Thapsia villosa	.	.	.	.	.	.	.	.	+	1	.	.	.	.	.	.	.	+	.	.
Reseda lutea	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.
Sanguisorba verrucosa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Narcissus cernuus	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hypochaeris radicata	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Table 7. Plots recorded in the “Solana de los Quejigos” area (QB, burned). For all plots, the altitude is 1000 m asl. Indexes correspond to those of Br.-Bl. 1964. See text for more explanations on plant communities and syntaxa.

N. Species	25	20	23	19	18	24	17	17	25	22	15	17	19	20	21	26	24	21	25	16
Plot N.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Characteristics of Helianthemion guttati (*Helianthemetalia guttati*, *Helianthemetea guttati*)																				
Tuberaria guttata	2	1	1	1	2	1	1	3	2	2	4	4	4	3	3	2	2	3	1	1
Hypochaeris glabra	2	2	3	3	2	3	3	3	2	2	4	2	2	4	2	1	3	3	2	1
Jasione montana	1	2	2	2	1	2	3	3	2	2	1	1	1	1	+	1	1	1	1	+
Coronilla repanda subsp. *dura*	+	+	1	+	1	+	+	1	+	+	2	1	1	1	1	1	1	1	1	+
Vulpia myuros	1	2	1	+	+	+	+	2	1	1	1	.	1	1	1	1	1	2	1	+
Asterolinon linum-stellatum	1	1	1	1	1	1	1	1	1	1	.	.	1	1	1	1	+	1	1	+
Anthyllis lotoides	+	.	+	1	1	1	+	+	+	+	.	+	1	1	+	+	1	+	+	+
Trifolium cherleri	+	+	.	1	1	+	.	+	.	.	.	2	2	1	3	2	1	1	1	.
Trifolium arvense	.	.	+	.	.	+	+	.	.	.	+	1	2	1	1	1	1	1	+	1
Filago minima	+	+	1	.	+	+	+	.	+	+	.	.	.	.	.	+	+	+	+	+
Linaria spartea	+	+	+	.	+	+	.	.	+	+	.	.	.	+	.	.	+	.	+	1
Andryala integrifolia	1	+	1	+	1	1	+	+	+	1	.	.	.	.	.	.	.	.	.	.
Scleranthus polycarpos	1	+	.	+	+	+	.	1	+	+	.	.	.	.	.	.	.	.	.	.
Leontodon saxatilis subsp. *rothii*	.	.	.	.	.	.	.	.	.	.	1	+	1	1	1	1	1	1	2	+
Tolpis umbellata	.	.	.	.	.	.	.	.	.	.	1	1	1	1	1	+	+	2	1	1
Andryala arenaria	.	.	.	.	.	.	.	.	.	.	+	+	+	.	.	+	+	+	1	3
Ornithopus compressus	.	.	.	.	.	.	.	.	.	.	.	.	1	1	1	1	1	1	1	+
Anthyllis cornicina	.	.	.	.	.	.	.	.	.	.	.	+	+	+	.	+	+	+	+	.
Lathyrus angulatus	+	+	+	.	.	+	.	.	+	+	.	.	.	.	.	.	.	.	.	.
Anisantha madritensis	.	.	+	.	.	+	.	.	+	+	.	.	+	.	.	.	.	.	.	.
Trifolium hirtum	.	.	.	.	.	.	.	.	.	+	+	+	.	.	+	+	.	.	.	.
Lactuca serriola	.	1	.	+	.	.	.	.	.	1	.	+	.	.	.	.	.	.	.	.
Teesdalia nudicaulis	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.
Vicia lathyroides	.	.	.	+	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.
Astragalus pelecinus	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Alyssum granatense	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Veronica verna	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.
Petrorhagia nanteuillii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.
Silene scabriflora	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.
Transgressives from diverse anthropogenic vegetation classes																				
Avena barbata	+	1	1	1	1	1	.	.	1	1	1	+	1	1	1	2	2	2	+	.
Vicia sativa subsp. *nigra*	+	+	1	+	+	+	+	+	+	+	+	.	.	+	+	.	+	1	1	1
Anisantha tectorum	3	1	4	1	+	1	+	+	3	1	.	1	.	.	+	+	1	.	+	.
Bellardia trixago	1	+	1	.	.	+	1	1	1	+	+	.	+	+	1	.	.	+	1	.
Vicia disperma	+	+	1	+	+	2	+	+	+	+	.	.	.	.	.	.	.	.	.	.
Anthemis arvensis	+	1	.	1	.	.	.	.	+	1	.	.	.	.	+	1	+	+	.	.
Geranium molle	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Spergularia purpurea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.
Other species																				
Poa bulbosa	2	2	1	1	.	2	2	1	2	2	.	.	1	+	1	1	1	1	1	.
Dactylis glomerata	+	.	+	.	.	.	.	.	+	.	+	+	+	+	+	1	.	.	1	.
Cistus ladanifer	+	.	+	.	1	.	.	+	.	.	.	.	.	+	+	+	+	.	1	1
Helichrysum stoechas	+	.	.	.	.	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.
Rosmarinus officinalis	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	+	.
Paronychia argentea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	1	.	.
Polytrichum piliferum	1	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.
Anthoxanthum ristatum	.	.	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.

Arrhenatherum elatius subsp. *bulbosum*	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	+	.
Thapsia villosa	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hypochaeris radicata	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.
Polytrichum juniperinum	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Table 8. Plots recorded in the "Ermita" area (Er_{NB}, not burned). For all plots, the altitude is 1000 m asl. Indexes correspond to those of Br.-Bl. 1964. See text for more explanations on plant communities and syntaxa.

N. Species	12	11	7	14	11	9	7	8	11	10	5	10	9	7	5	5	8	2	4	8
Plot N.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Characteristics of Helianthemion guttati (*Helianthemetalia guttate, Helianthemetea guttati*)																				
Vicia lathyroides	1	1	1	1	1	2	2	3	+	1	2	1	3	1	1	1	2	1	1	2
Lathyrus angulatus	.	2	1	1	1	1	2	2	1	1	1	1	2	1	+	.	2	+	1	1
Ornithopus compressus	1	1	.	+	+	+	+	1	+	2	.	.	.	.	.	.	1	.	.	+
Trifolium hirtum	.	4	4	3	1	1	+	2	1	1	.	.	.	.	.	.	.	.	.	2
Jasione montana	1	1	+	+	.	1	.	.	3	.	.	.	1	2	.	.	2	.	.	.
Crucianella angustifolia	1	.	.	+	+	.	+	.	.	+	.	.	.	.	.	.	.	.	.	.
Alyssum minus	1	.	.	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cerastium semidecandrum	1	.	.	+	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.
Hypochaeris glabra	.	.	.	.	.	.	.	.	.	+	1	.	.	.	.	.	.	.	.	.
Trifolium glomeratum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Aphanes microcarpa	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.
Transgressives from diverse anthropogenic vegetation classes																				
Vicia disperma	1	+	.	1	1	1	+	1	1	.	.	+	2	+	+	.	.	.	+	.
Cardamine hirsuta	1	.	.	+	+	+	.	.	.	+	.	+	+	.	.	2	.	.	.	.
Myosotis ramosissima subsp. *gracillima*	+	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	+	.	.	.
Anisantha tectorum	.	.	.	.	4	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.
Arabidopsis thaliana	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Other species																				
Polytrichum piliferum	.	2	.	1	1	2	1	1	3	.	.	4	3	4	1	2	2	.	1	+
Lotus corniculatus	+	.	3	+	.	2	.	.	1	3	.	+	+	2	.	.	.	.	.	.
Pinus pinaster (pl.)	+	+	+	.	.	.	.	+	.	.	+	.	+	.	1	1	.	.	.	+
Poa bulbosa	.	.	1	+	3	.	.	.	+	.	.	+	1	.	.	.	+	.	.	.
Hypochaeris radicata	.	+	.	.	.	.	.	.	1	.	.	.	.	1	.	+	+	.	.	.
Dactylis glomerata	.	.	.	+	.	.	.	.	.	+	+	.	.	.	.	.	.	.	.	.
Pilosella officinarum	.	.	.	.	.	.	.	1	.	.	.	+	.	.	.	.	.	.	.	+
Thymus mastichina	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Thapsia villosa	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

Table 9. Plots recorded in the "Santa Catalina-Risco Grande" (Sta. $Cat._B$, burned). For all plots, the altitude is 1386 m asl. Indexes correspond to those of Br.-Bl. 1964. See text for more explanations on plant communities and syntaxa.

N. Species	19	20	20	20	13	17	18	17	20	21	14	18	18	19	19	22	18	19	17	16
Plot N.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Characteristics of Hieracio castellani-Plantaginion radicatae (*Jasiono sessiliflorae-Koeleretalia crassipedis, Festucetea indigestae*)																				
Plantago holosteum	4	2	2	2	2	4	4	3	4	3	3	2	3	3	4	3	3	2	2	4
Thymus zygis	1	3	3	3	3	1	2	1	2	2	+	+	+	+	+	+	3	+	1	+
Koeleria crassipes	.	+	2	1	.	1	1	.	+	.	.	.	.	1	+	+	+	+	.	.
Bufonia macropetala	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+
Dianthus legionensis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Transgressives from Stipo giganteae-Agrostietea castellanae (*Agrostietalia castellanae, Stipo giganteae-Agrostietea castellanae*)																				
Centaurea ornata	+	1	.	+	.	.	.	.	+	.	.	.	.	.	.	+	.	.	.	.
Agrostis castellana	.	.	.	.	.	+	.	+	+	+	.	.	.	.	.	.	.	.	.	.
Thapsia villosa	.	.	.	+	+	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.

Centaurea paniculata	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	.	.	.	.
Characteristics of *Helianthemetalia*																				
Leontodon saxatilis subsp. *rothii*	2	1	+	+	.	1	+	1	1	1	1	2	1	1	1	1	1	1	+	1
Trifolium arvense	1	1	1	1	.	+	1	.	1	1	+	1	1	1	2	2	1	1	+	1
Vulpia myuros	1	1	1	1	.	+	+	+	+	1	+	+	1	+	.	+	+	+	.	+
Trifolium cherleri	1	+	.	+	.	+	.	+	.	+	1	+	+	+	+	+	+	.	1	+
Asterolinon linum-stellatum	1	+	.	.	.	.	+	.	.	+	+	1	1	1	1	1	1	.	+	+
Ornithopus compressus	1	+	.	+	.	.	+	.	.	+	.	+	+	+	.	+	+	1	.	.
Plantago lagopus	.	+	1	1	.	.	.	.	.	+	.	.	.	.	+	+	.	.	+	.
Crucianella angustifolia	+	1	+	.	.	.	.	.	+	.	.	+	+	.	.	.	.	.	.	.
Andryala integrifolia	.	.	.	.	+	.	.	.	+	1	.	+	.	.	.	.	.	.	.	.
Trifolium glomeratum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1	.	+	.	.
Hypochaeris glabra	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+
Helianthemum licifolium	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.
Anthyllis lotoides	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
Transgressives from diverse anthropogenic vegetation classes																				
Anthemis arvensis	1	+	1	1	+	1	+	+	+	+	1	+	+	+	+	.	+	+	+	+
Avena barbata	1	1	1	1	1	1	1	1	.	1	1	.	1	+	1	+	+	1	+	.
Tragopogon porrifolius	+	+	.	.	.	.	.	+	+	+	.	.	.	.	.	.	.	.	.	.
Anisantha tectorum	+	.	.	.	.	.	1	+	.	.	.	.	.	.	+	.	.	.	.	.
Cichorium intybus	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.
Lupinus angustifolius	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.
Vicia sativa subsp. *nigra*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.
Other species																				
Poa bulbosa	2	2	3	3	2	2	2	2	2	2	2	2	1	2	2	1	2	2	3	3
Festuca ampla	.	.	1	1	+	+	+	+	.	+	+	+	+	+	1	+	+	+	+	1
Stipa lagascae	2	1	1	1	1	1	1	+	+	+	1	1	+	.	.	+	.	+	.	.
Parentucellia latifolia	.	.	+	1	1	1	1	+	+	1	1	1	1	.	.	+	.	1	1	.
Lotus corniculatus	.	.	.	.	1	+	1	1	+	+	.	+	1	.	+	+	+	1	.	+
Helianthemum cinereum subsp. *rotundifolium*	1	+	+	+	1	+	.	.	+	+	+	+	+	+	.	.	+	.	.	.
Paronychia argentea	+	.	+	.	+	+	+	1	+	+	.	.	+	.	+	.	+	.	.	.
Trifolium scabrum	1	+	+	.	.	.	+	.	.	.	.	+	.	+	+	+	.	1	.	+
Dactylis glomerata	.	1	+	+	.	.	.	+	1	.	.	.	.	.	.	.	.	.	.	.
Herniaria glabra	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	+	.	.	.
Rumex acetosella subsp. *angiocarpus*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	+	.	1	.
Sanguisorba verrucosa	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.
Hypericum perforatum	.	.	+	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Biscutella laevigata	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Paronychia polygonifolia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.

Appendix 1. List of species identified in the seed bank in 2017 collected from the pilot-plots. Names of sampled areas correspond to those of Table 1.

Species	Sta. Cat_B	Sta. Cat_{NB}	Er_{NB}	Q_B	CC_B	A_B
Andryala arenaria	-	-	-	x	x	-
Anthemis arvensis	-	-	-	-	x	-
Anthoxantum aristatum	-	-	-	x	-	-
Antirrhinum graniticum	x	-	-	-	x	x
Aphanes arvensis	-	-	-	-	x	-
Avena barbata	-	-	-	x	-	-
Cardamine hirsuta	-	x	x	-	-	-
Cerasium diffusum	-	-	-	x	-	-
Cerastium pumilum	x	-	x	-	x	-
Coincya monensis subsp. *orophila*	-	-	-	-	x	-
Coronilla repanda subsp. *dura*	x	-	-	x	-	-
Corynephorus divaricatus	x	-	-	-	-	-
Corynephorus fasciculatus	-	-	-	-	x	-
Crassula tillaea	-	-	-	-	x	x
Crepis capillaris	x	-	-	-	-	-
Cyperus sp.	-	x	-	-	-	-
Digitalis thapsi	x	-	x	-	x	x
Erodium cicutarium	-	-	-	-	x	-
Euphorbia sp.	-	x	-	-	-	-
Filago minima	x	-	-	-	-	-
Fumaria officinalis	-	-	-	-	x	-
Fumaria parviflora	-	-	-	-	x	-
Helianthemum aegyptiacum	-	-	x	-	x	x
Helianthemum salicifolium	-	-	-	x	x	x
Heliotropium europaeum	-	-	x	-	x	-
Herniaria cinerea	x	-	-	-	-	-
Hypochaeris glabra	-	-	-	x	-	x
Jasione montana	-	-	x	x	x	-
Lamium amplexicaule	-	-	-	-	x	-
Lathyrus sp.	-	x	x	x	-	x
Linaria spartea	x	-	-	x	x	x
Lotus corniculatus	x	x	x	x	-	x
Mibora minima	-	-	x	x	-	-
Misopates orontium	-	-	-	x	-	x
Myosotis ramosissima subsp. *gracillima*	-	x	x	-	x	x
Myosotis persoonii	-	-	x	-	-	-
Plantago lanceolata	x	-	-	-	-	-
Poa bulbosa	-	-	-	x	-	-
Reseda lutea	x	-	-	-	-	x
Rubus sp.	-	-	x	-	-	-
Rumex acetosella subsp. *angiocarpus*	x	-	-	-	x	-
Rumex sp.	-	-	x	-	-	-
Scleranthus polycarpos	x	-	-	-	-	-
Sedum caespitosum	x	-	-	-	-	-
Senecio vulgaris	-	-	-	x	-	-
Spergula pentandra	-	-	-	x	-	-
Teesdalia nudicaulis	-	-	-	x	-	-
Thymus zygis	x	-	-	-	-	-
Tolpis umbellata	-	-	-	-	x	-
Trifolium arvense	x	-	x	x	-	x
Trifolium cherleri	-	-	-	x	-	-
Trifolium glomeratum	-	-	x	-	-	x

Trifolium campestre	-	-	-	x	-	-
Trifolium sp.	-	-	x	x	-	x
Tuberaria macrosepala	-	-	-	-	x	-
Tuberaria guttata	x	-	x	x	x	-
Urtica sp.	x	-	-	-	-	x
Verbascum thapsus	-	x	x	-	-	-
Veronica hederifolia	x	-	-	-	-	-
Veronica verna	x	-	x	-	x	-
Vicia angustifolia	-	x	-	-	-	-
Vicia lathyroides	x	-	x	-	x	-
Vulpia myuros	x	-	x	x	x	x