



## 1 **Abstract**

2 Despite advances in post-mine sites reclamation methods in the recent years, restoration  
3 treatments are not always successful in creating self-sustaining ecosystems. Occasionally,  
4 vegetation remains in a state of arrested succession where conditions are hostile for many late-  
5 successional target species. An in-depth study of the environmental factors that control  
6 vegetation dynamics on reclaimed mined sites may, therefore, improve the methods for late-  
7 successional species introduction, rehabilitating the landscape effectively. In this context, using  
8 12 reclaimed mines in northern Spain colonized mainly by two leguminous shrubs (*Cytisus*  
9 *scoparius* and *Genista florida*) we explored: (i) how organic-matter thickness, bryophyte cover  
10 and plant diversity and cover attributes change across a gradient of dominant shrub  
11 cover/volume, and (ii) how the understorey plant species were associated with these shrub  
12 canopies. We hypothesized that shrub growth modified the micro-climatic conditions and  
13 influenced the understorey plant species either by facilitation or competition. The results reveal  
14 an important positive effect of shrub volume on micro-environmental conditions, such as  
15 organic matter-thickness and bryophyte cover, creating environmental heterogeneity underneath  
16 larger shrub canopies. At the same time, the shrub volume gradient was also associated with  
17 species composition; there was a shift in plant composition from a greater abundance of annual,  
18 light-demanding species and legumes in open conditions towards water-requiring, shade-  
19 adapted, and broad-leaved species under greater shrub volumes. In contrast, there were no shrub  
20 effects in diversity and evenness. The analysis of individual species indicates that 18 out of the  
21 40 most frequent species showed a significant association with shrub volume. Assessment of  
22 the species optima associated with shrub colonization allows the development of new species  
23 mixtures that are tailored to individual site conditions to favour desired plant communities.  
24 Moreover, it seems that shrubs acted as ecosystem engineers in these reclaimed mined sites.  
25 Natural shrub encroachment has been shown in this study as one means through which these

1 ecosystems can be modified to create heterogeneity in micro-environmental conditions and  
2 hence inducing greater overall diversity.

3

4 **Highlights:**

- 5 • Plant species and shrub canopies relationships were assessed in reclaimed mines.
- 6 • Shrub volume impacted on micro-environment and herbaceous species composition.
- 7 • Shrubs create heterogeneity in micro-environment inducing greater overall diversity.
- 8 • Shrubs act as ecosystem engineers enhancing different plant community establishment.

9

10 **Keywords:** shrub volume, under-canopy vegetation, organic matter, bryophytes, grasses and  
11 forbs, restoration.

12

## 1 **1. Introduction**

2 Open-cast mining is a major environmental disturbance that often leaves the landscape with no  
3 vegetation and very poor soil-forming material for subsequent ecosystem development (Herath  
4 et al., 2009). As a consequence, open-cast mining rehabilitation is presented as an ideal model  
5 system for the study of ecosystem development starting from near point zero (Hüttl and Weber,  
6 2001; Marrs and Bradshaw, 1993). In the search for appropriate restoration strategies of these  
7 sites, a key focus has been the identification of mechanisms that both facilitate and prevent  
8 vegetation establishment and development (Pallavicini et al., 2013). Recently, a number of  
9 studies have identified that, after initial reclamation activity, vegetation remains in early-  
10 successional stages or in a state of arrested succession where conditions are hostile for the  
11 colonisation of many late-successional target species (Boyes et al., 2011). An in-depth study of  
12 the mechanisms and environmental factors that control vegetation dynamics of such ecosystems  
13 may, therefore, advance the reclamation methods in order to rehabilitate the landscape quickly  
14 and effectively (Alday et al., 2010; Martínez-Ruiz and Marrs, 2007).

15 In northern Spain, particularly in the provinces of León and Palencia, open-cast coal mining  
16 has caused an extensive impact on the landscape, affecting ca. 5,000 ha of land (Alday et al.,  
17 2011a). Over the last 20 years, there has been much progress in post-mining restoration and  
18 reclamation methods, especially focusing on plant community establishment such as top-  
19 soiling, improvement of seed mixtures or tree seedling establishment protocols (Alday et al.,  
20 2012; Martínez-Ruiz et al., 2013). However, not all areas subjected to some form of reclamation  
21 treatment were always successful in creating self-sustaining ecosystems. Alday et al. (2011b)  
22 found that the establishment of plant species over raw coal wastes was very slow even after 40  
23 years, producing unstable communities. Therefore, there are still many questions unresolved in  
24 relation to the drivers structuring these plant communities. For example, it has been observed  
25 that vegetation development in these reclaimed sites is often accompanied by an increase of  
26 shrub density and encroachment (Alday et al., 2011b, 2011c). These processes have been linked

1 to alterations in the spatial pattern of soil resources and ecosystem function (Schlesinger and  
2 Pilmanis, 1998). However, the effects of shrub colonization can vary widely from drastic  
3 reductions in plant biomass and species richness (Archer, 2010) to just the opposite trends,  
4 depending on the species and climate involved (Eldridge et al., 2011). Nevertheless, although  
5 this process has been studied in large-scale environments (Pugnaire et al., 2011) or in several  
6 degraded ecosystems with secondary succession arrested (Gómez-Aparicio et al., 2004; Stradic  
7 et al., 2014), its possible translation and influence on small-scale processes in reclaimed mines  
8 are still little explored.

9 In general, shrubs influence the establishment of associated understorey plants through  
10 modifying micro-environmental conditions (Pajunen et al., 2012; Palaniappan et al., 1979). On  
11 one hand, shrubs may promote islands of fertility around them (Pugnaire et al., 1996) and  
12 facilitate plant establishment and subsequent growth (Schlesinger and Pilmanis, 1998) by  
13 accumulating water, soil nutrients and organic matter under their canopies whilst also providing  
14 protection from herbivores (Pajunen et al., 2012; Palaniappan et al., 1979). In contrast,  
15 established shrubs can also play the opposite role and exclude understorey species either by  
16 allelopathy or by reducing the amount of solar radiation or available water (Fargione and  
17 Tilman, 2003). This decrease in soil radiation may also influence regeneration processes on  
18 seed-dependent species, because dormancy breakage and seed germination is modulated in  
19 some species by daily soil temperature fluctuation produced by solar incidence (Santana et al.,  
20 2013). Micro-environment modification can also be associated to the proliferation of  
21 bryophytes in moist sites (Hettenbergerová et al., 2013), which could also exclude the  
22 establishment of new seedling (Lloret, 1994). There has been several studies during the last  
23 years addressing (i) the changes in spatial patterns of micro-environmental conditions beneath  
24 shrubs (e.g., Pugnaire et al., 1996; Giladi et al., 2013), (ii) the facilitative effects of shrubs on  
25 stressful systems (Holzapfel and Mahall, 1999) and (iii) differing response of contrasting  
26 functional groups to shrubs (Butterfield and Briggs, 2011). However, there is a lack of similar

1 studies over coal mining reclamation areas, being of fundamental importance for developing  
2 future reclamation plans and ecosystem engineering techniques. Further efforts are needed in  
3 order to disentangle possible impacts of shrub canopies on diversity and to identify species and  
4 functional groups suitable for each specific condition.

5 In this context, we explored the relationships between shrub canopies and understorey plant  
6 species with the objective of designing improved and more effective restoration strategies.

7 Here, we analyzed the shrub canopy impact on reclaimed coal mines in northern Spain. In these  
8 mined sites, shrub colonization was produced mainly by two non-thorny, leguminous shrubs  
9 with similar vertical structure: *Cytisus scoparius* and *Genista florida* (Alday et al., 2011a).

10 Previous studies on these sites have demonstrated that these shrubs have an important effect on  
11 herbaceous richness and biomass accumulation patterns of different functional plant species  
12 groups (Pallavicini et al., 2013). However, the individual species responses to shrub interactions  
13 and the micro-scale changes produced by shrubs are unexplored, and these are fundamental for  
14 gaining knowledge about species performance and restoration of mined land. Here, therefore,  
15 we hypothesized that shrub growth, measured as above-ground volume, modified the micro-  
16 climate under the canopy and/or the spatial distribution of resources, and hence influenced  
17 understorey plant species either by facilitation or competition. Specifically, we asked the  
18 following questions: (i) What was the impact of natural leguminous shrub development on  
19 ecosystem properties such as organic-matter thickness, bryophyte cover and plant species  
20 diversity and cover?, and (ii) How were the understorey plant species and their functional  
21 groups associated with shrub canopies? It was expected that this approach would lead to  
22 identify shrub-ecosystem effects and plant-shrub interaction patterns that might inform  
23 reclamation work in similar areas.

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## 1 **2. Materials and methods**

### 2 *2.1. Site description and selection*

3 The study was conducted into the ‘Guardo-Cervera’ coal basin in the north-west of the  
4 Palencia province, northern Spain (42°48’-42°50’N, 4°44’-4°53’W). Within this basin, 12 mines  
5 relatively close together (within 16 km<sup>2</sup>) were selected for the study, thus minimizing  
6 geographical and climatic variability. All selected mines were reclaimed using the same  
7 methodology and had a similar successional stage; i.e. age since reclamation from 17 to 25  
8 years (8 years span), in order to reduce the possible effect of vegetation age influencing the  
9 results. For more details in age assignment and vegetation change through time see Alday et al.  
10 (2011a). The 12 study sites ranged from 1 to 3 ha, and have been restored using a combination  
11 of topsoil addition, containing a very poor seed bank (González-Alday et al., 2009), followed  
12 by hydroseeding with a grassland species mixture including grasses and legumes (81:19 by  
13 weight; 200 kg ha<sup>-1</sup>), such as *Lolium perenne*, *Lotus corniculatus*, *Medicago sativa*, *Phleum*  
14 *pratense*, *Poa pratensis*, *Trifolium pratense* and *Trifolium repens*. The altitude range was also  
15 relatively small (1165-1419 m a.s.l.). The climate is sub-humid Mediterranean with an annual  
16 mean temperature of 9°C, an average annual precipitation of 980 mm, and with a pronounced  
17 dry season in summer (July-August). The soil covering the reclaimed mines had little edaphic  
18 structure; it had a clay loam texture, a mean pH of 5.8±0.24 and organic matter content of  
19 7.56%±0.50. There were few differences between the mines at the time of sampling in soil  
20 physical-chemical properties or micronutrients concentrations (Alday et al. 2011a). The natural  
21 vegetation surrounding these mines is a mosaic of *Quercus pyrenaica* and *Q. petraea*  
22 woodland, and remnants of natural shrublands, dominated by *Genista florida* and *Cytisus*  
23 *scoparius* (Alday et al., 2011a).

24 The 12 reclaimed mines had a patchy natural colonization of *C. scoparius* and *G. florida*,  
25 producing a shrub abundance gradient that ranged from 36% of mine cover to 80% on 25 years  
26 old mines. Both species have a ballistic type seed-dispersal mechanism (Malo, 2004; Alday et

1 al., 2011b), that favours the seed dispersal on mined sites from the forest border.  
2 Simultaneously, in these areas both species are grazed, in low-intensity, freely by animals (e.g.  
3 deer, cattle and horses); therefore a zoochory seed-dispersal mechanism is also common. At the  
4 same time, both species are non-thorny leguminous shrubs, with similar vertical structure and  
5 capable of actively fix the atmospheric nitrogen (Talavera et al., 1999). They prefer sunny sites  
6 to growth and are good colonizers of degraded areas (Oria de Rueda, 2003). Therefore, both  
7 species are considered into the same functional group sharing common characteristics (i.e.  
8 structure and leaf phenology). As a consequence and based in the methodology carried out in  
9 studies using similar functional group species (Gómez-Aparicio et al., 2004), they were not  
10 differentiated in the study.

11

## 12 *2.2. Vegetation sampling*

13 The vegetation and soil were sampled in June of 2008. At each mine (n=12), 10 1×1m quadrats  
14 were located randomly to provide a statistically-rigorous sample of both vegetation and the  
15 prevailing environment. Since the shrubs abundance ranged from 36 to 80% in the mines we  
16 were able to have three quadrats types: (i) no shrub cover (n=20), (ii) low shrub cover (<50%,  
17 n=40) and (iii) high shrub cover (>50%, n=60). Although, our design has limitations to  
18 disentangle effectively the shrubs effects, the reduce number of restored mined with similar age  
19 force us to use it. At each quadrat (n=120), the cover of every vascular plant species was  
20 estimated visually. Information on a range of environmental variables was also collected, these  
21 were: shrub cover (%), shrub height (m), and cover of bryophytes (%), bare soil and rocks  
22 cover (%). In addition, a soil sample was collected from each quadrat using a soil auger  
23 (diameter=8cm, depth=10cm; Pallavicini et al., 2013) and organic-matter layer thickness  
24 (OMT, cm, i.e. the organic litter layer accumulated over the soil A horizon) was measured.  
25 Bryophyte cover was used as a surrogate measure of moisture availability (Hettenbergerová et  
26 al., 2013; Lloret, 1994,).



1        Thereafter, the cover of a range of functional groups was calculated using individual species  
2 cover values; these were based on life-forms, i.e. annuals or biennial and perennials (Alday et  
3 al., 2011b) and taxonomic groups; i.e. *Asteraceae*, *Fabaceae* and *Poaceae*. These three  
4 taxonomic groups were the most frequent and abundant within the plant communities on these  
5 restored coal-mining areas (González-Alday and Martínez-Ruiz, 2007). Thus, we analysed six  
6 functional groups based on life-form and taxonomy: i.e. annual and perennial *Asteraceae*,  
7 annual and perennial *Fabaceae*, annual and perennial *Poaceae*.

8        In order to calculate the shrub volume ( $S_v$ ,  $m^3$ ) we multiplied the shrub cover of a  
9 quadrat ( $m^2$ ) by the shrub height (m) following Pujanen et al. (2011). Since the mine sites were  
10 colonized mainly by two shrubby legume species, *Genista florida* and *Cytisus scoparius* (Alday  
11 et al., 2011a), which share similar development and vertical structure, we did not differentiate  
12 between them to get the shrub volume.

13

#### 14 2.4. Data analysis

15 All statistical analyses were implemented in the R software environment (version 2.15.3; R  
16 Development Core Team, 2013) using the NLME (Pinheiro et al., 2013) and vegan (Oksanen et  
17 al., 2013) packages.

18 We used linear and non-linear mixed effects models (“nlme” and “lme” functions within the  
19 NLME package; Pinheiro and Bates 2000) to analyze the relationships between shrub volume  
20 ( $S_v$ ,  $m^3$ ) and (i) organic matter thickness (OMT; cm), (ii) bryophytes cover and herbaceous  
21 plant cover (%) and (iii) diversity (plant species richness and evenness) at quadrat level. In all  
22 cases, linear and nonlinear models were fitted (null, linear and asymptotic) and the model that  
23 reduced the Akaike Information Criterion (AIC) most, relative to the null model, was selected.  
24 The asymptotic regression model (function “SSasymp”) was selected to explain the  
25 relationships between OMT and shrub volume; the full equation is  $y = a + (b - a) \times \exp(\exp(c) \times S_v)$ ,  
26 where  $y$  is OMT,  $a$  is the asymptote of OMT,  $b$  is the  $y$ - intercept and  $c$  determines the rate at

1 which the OMT asymptote is reached. In all these analyses, quadrats nested within mine nested  
2 within mine age were included as random factors, because quadrats within a given mine were  
3 expected to be more similar to each other than to quadrats from other mines, and mines of the  
4 same age were expected to be more similar than random mines from the successional sequence.  
5 The OMT and bryophyte cover were square-root transformed and richness log-transformed to  
6 obtain satisfactory residual distributions. The heteroscedasticity was modelled using the  
7 “varIdent” structure function that allows different variances for each level of a mine (Pineiro  
8 and Bates 2000). All values are reported as the mean±standard error of the fixed factors.

9       Vegetation community data were first analyzed by Detrended Correspondence Analysis  
10 (DCA) to determine the relationships between most common species (occurrence greater than  
11 10% of the sampled quadrats, 40 species in total) and shrub volume, bare soil and rock cover  
12 entered as passive variables onto species ordination space (passive fit: function “envfit”;  
13 Oksanen et al., 2013). Second, we computed the weighted average scores of the most common  
14 species for the shrub volume (“wascores” function; Oksanen et al., 2013). The function  
15 computes the average value of shrub volume for all plots in which a species occurred, weighted  
16 by species abundance (Oksanen et al., 2013). This helped to test the species-specific  
17 associations between understorey species and shrub volume, identifying if the species  
18 abundance optima has a negative or positive association with shrub canopy volume. The tests of  
19 significance between species and shrub volume were done using permutation tests; comparing  
20 if the real “wascore” value was greater or lower (positive or negative association) than the null-  
21 population distribution obtained by permuting all plots freely (n=120, 999 unrestricted  
22 permutations). Finally, new randomizations (999 permutations stratified by mine) were done  
23 only for those species with positive or negative significant relationships in order to describe the  
24 species-specific distributions related to shrub volume.

25

### 1 **3. Results**

#### 2 *3.1. Shrub volume influence on ecosystem properties*

3 The ranges of the environmental and diversity variables detected across all sampled quadrats  
4 were: OMT 0-3.8 cm, bryophyte cover 0-100%, shrub volume 0-4.25 m<sup>3</sup>, plant species richness  
5 3-33 and evenness from 0.30 to 0.91. Non-linear mixed-effects analysis showed that OMT had  
6 a positive significant asymptotic association with shrub volume (Table 1, Fig. 1a). OMT  
7 increased as shrub volume increased at a rate of 0.80±0.07 (i.e. 0.64 cm of OMT per shrub  
8 volume unit); however, this increase stabilized when OMT reaches an asymptote at 1.76±0.18  
9 (i.e. 3.10 cm of OMT). At the same time, bryophyte cover showed a linear positive relationship  
10 with shrub volume with a significant slope of 0.44±0.20 (Table 1, Fig. 1b), increasing from  
11 3.5% at 0 m<sup>3</sup> to 13% at 4 m<sup>3</sup>. Total herbaceous plant cover was associated negatively with  
12 shrub volume, showing a decreasing trend from 121% at 0 m<sup>3</sup> to 64% at 4 m<sup>3</sup> (Table 1, Fig. 1c).  
13 In contrast, there were no significant relationships between plant richness and evenness with  
14 shrub volume (*p*-values>0.05), therefore, they had constant values of 18±0.65 and 0.76±0.01  
15 respectively, across the shrub volume gradient.

16

#### 17 *3.2. Plant species association with shrub volume*

18 A total of 187 species were recorded in the 12 studied mines as a whole, but only 40 species  
19 had a frequency greater than 10%; i.e. present in more than 12 quadrats. The vegetation  
20 ordination using DCA produced eigenvalues ( $\lambda$ ) of 0.29, 0.27, 0.17 and 0.17 and gradient  
21 lengths (GL) of 3.56, 2.62, 3.59 and 3.23 for the first four axes (Fig. 2a). The fit of  
22 environmental variables onto species ordination space identified two main gradients. The first  
23 axis was significantly related with bare soil and rock cover ( $R^2=20\%$ , *p*-value<0.001); both  
24 increasing towards the positive end of axis 1 where quadrats with low vegetation cover were  
25 located. In addition, the fit of shrub volume onto species ordination space was significant (*p*-  
26 value<0.001; Fig. 2a, b), explaining 17.5% of the variance and showed an increase in shrub

1 volume towards the positive end of the axis 2 (Fig. 2a). The quadrats with a low shrub volume  
2 appeared on the negative side of axis 2 (Fig. 2a), associated with species such as *Achillea*  
3 *millefolium*, *Lotus corniculatus* or *Hieracium pilosella*, whereas quadrats with a greater shrub  
4 volume appeared at the positive end of axis 2, associated with species as *Lactuca* spp. and  
5 *Stellaria media*.

6 The analysis of association between the six functional-taxonomic groups against shrub  
7 canopy volume revealed that only the perennial *Fabaceae* species group had a significant  
8 negative association, showing a *Fabaceae* abundance optimum slightly lower than the average  
9 shrub volume ( $p$ -value=0.05;  $0.72\pm 0.09$  vs.  $1.17\pm 0.10$ ). At the same time, 18 out of the 40  
10 species analysed (45%) showed a significant association with shrub volume (Fig. 3). Eight  
11 species had plant cover optimum lower (0.26 to 0.72) than mean shrub volume ( $1.17\pm 0.10$ ),  
12 these were *Dianthus* spp. and *Hieracium pilosella*, three legumes *Trifolium striatum*, *T.*  
13 *campestre* and *Medicago lupulina*, two early-colonizers *Cerastium glomeratum* and *Anthemis*  
14 *arvensis*, and a grass *Festuca* spp. These species have their maximum abundance on quadrats  
15 with a shrub volume lower than  $1.17\text{ m}^3$ . In contrast, 10 species showed a significant positive  
16 association with shrub volume with plant cover optimum ranging from 1.54 (*Agrostis*  
17 *castellana*) to 3.23 (*Lactuca* spp.). This group is composed by four grasses (*Dactylis glomerata*,  
18 *Agrostis castellana*, *Poa pratensis* and *Vulpia myuros*), four *Asteraceae* (*Lactuca* spp.,  
19 *Hypochoeris radicata*, *Achillea millefolium* and *Senecio jacobea*) and *Stellaria media* and  
20 *Rumex acetosella*. These species had their maximum abundance at quadrats with shrub volumes  
21 greater than  $1.17\text{ m}^3$ . Particularly interesting are *Medicago lupulina* and *Dactylis glomerata*  
22 which showed tolerance to a wide range of shrub volumes (*Medicago*  $0.40$  to  $1.90\text{ m}^3$ ; *Dactylis*  
23  $0.65$  to  $1.80\text{ m}^3$ ).

24

## 1 **4. Discussion**

2 Knowledge on the natural dynamics of shrub encroachment and their interaction with other  
3 community components in newly-created ecosystems is rather weak. Therefore, developing an  
4 understanding of these processes on reclaimed mine sites can both help to discern micro-  
5 environmental and vegetation changes, and hence inform reclamation works in similar areas.  
6 The results presented here clearly show an important effect of shrub volume on both the micro-  
7 environmental conditions, such as OMT and bryophyte cover, and herbaceous species  
8 composition. Although the main compositional changes in these mined sites were generated by  
9 a gradient from bare soil/rock cover through to plots with a high plant cover (Pallavicini et al.,  
10 2013), our analysis here demonstrated a secondary gradient related to shrub volume that  
11 conditioned species composition and reclamation. Shrub colonization changed the micro-  
12 environment under their canopies modifying the spatial- and temporal-heterogeneity of  
13 conditions within these reclaimed mine sites, and this might favour the establishment of late-  
14 successional target species (e.g., *Q. pyrenaica* and *Q. petraea*).

15

### 16 *4.1. Shrub volume relations with OMT and bryophyte cover*

17 The improvement of soil conditions beneath the canopy of shrubs, such as nutrients and  
18 particularly the accumulation of organic matter, has been described in many systems throughout  
19 the world (Moro et al., 1997; Palaniappan et al., 1979; Puignaire et al., 2011). Here, similar  
20 results were found; OMT was related significantly to shrub volume in a non-linear asymptotic  
21 relationship, indicating that there is a threshold shrub volume beyond which OMT  
22 accumulation underneath slows. Similar studies on different forest areas across Europe have  
23 showed that litter layer increased positively with shrub cover (Pujanen et al., 2012). This  
24 relationship may arise from the greater amount of litter produced by shrubs in comparison with  
25 herbaceous species (Barth and Klemmedson, 1978), but it is also possible that as shrub volume

1 increases the litter produced is not only collected underneath the shrubs, but some might be  
2 dispersed to a wider area by wind (Puignaire et al., 2011).

3 Irrespective, OMT accumulation beneath the shrub canopy is usually greater than in  
4 surrounding open spaces without shrubs (Palaniappan et al., 1979; Moro et al., 1997, Santana et  
5 al., 2012). Organic matter build up changes in the soil physical properties, nitrogen  
6 concentrations and nutrient cycling, improving soil water retention and moisture in comparison  
7 with open spaces (Palaniappan et al., 1979; Puignaire et al., 2004). This is an important result  
8 from an ecosystem engineering and mining sites restoration perspective, because the shrubs  
9 introduce small-scale conditions (heterogeneity) thus favouring the creation of new niches for  
10 species establishment; in particular those species that require either shade or moist conditions  
11 (Maestre et al., 2009). This is especially true for many target species constrained by suitable  
12 habitats that are not adapted to the harsh open conditions in these newly-created ecosystems.  
13 For example, in this study all *Q. pyrenaica* or *Q. petraea* seedlings, the most important species  
14 of the surrounding reference communities, were found under shrubs volumes greater than 0.65  
15 m<sup>3</sup>.

16 Perhaps the most interesting result was the positive relationship of bryophyte cover and  
17 shrub volume. Conflicting results have been found in similar studies elsewhere. In temperate  
18 and arctic areas negative relationships between bryophytes and shrub volume have been  
19 reported (Cavard et al., 2011; Pujanen et al., 2011). In contrast, studies on arid and semi-arid  
20 environments positive relationships have been reported (Smith and Stark, 2014). Our results for  
21 a Mediterranean climate are in line with those for arid/semi-arid regions. This phenomenon is  
22 best explained by the biotic mechanisms produced by shrub growth. In these mined sites under  
23 Mediterranean climate, where soil structure is lacking (Alday et al., 2012) and soil moisture is a  
24 limiting factor for vegetation development (González-Alday et al., 2008), the effect of  
25 increasing shrub volume will produce an increase in both OMT and shade. These two processes  
26 will increase moisture availability, OMT through an increase of water holding capacity and

1 shade by reducing soil temperature, and hence subsequent soil moisture evaporation (Maestre et  
2 al., 2009; Moro et al., 1997). As a consequence the development of bryophytes under shrub  
3 canopies is favoured compared to open areas. However, there must take in consideration that  
4 some rainfall interception and consumption by shrubs is also produced (Pugnaire et al., 2011).  
5 Regardless, the positive effect of shrub volume on both OMT and bryophytes will produce an  
6 increase in environmental heterogeneity on mined areas, producing different niche availabilities  
7 for species establishment (Pugnaire et al., 2011).

8

#### 9 *4.2. Plant species association with shrub volume, diversity and herbaceous cover*

10 Previous research on the effect of shrubs on vascular plant species diversity in Mediterranean  
11 environments (Maestre and Cortina, 2005; Maestre et al., 2009) or semi-natural grasslands in  
12 temperate regions (Rejmanek and Rosén, 1988) have shown that shrub cover can lead to either  
13 increases or decreases in species richness. Here, we failed to detect any effect on understory  
14 vascular plant species richness and evenness along the shrub volume gradient. The plant species  
15 richness and evenness remained constant across the shrub volume gradient with values of  
16  $18 \pm 0.65$  and  $0.76 \pm 0.01$ , respectively, although there was a decrease in herbaceous plant cover.  
17 This lack of a relationship between vascular plant diversity and shrub volume on these mine  
18 sites can be explained by the significant effect of shrub volume on species composition. Here,  
19 the shift in plant composition from a greater abundance of annual, light-demanding species and  
20 legumes in open conditions towards water-requiring, shade-adapted, and broad-leaves species  
21 as shrub volume increased can keep species richness and evenness constant (Alday et al., 2010).  
22 This process is likely to have resulted from suppression by shrubs via competition with light-  
23 demanding species, but at the same time, producing conditions that favoured water-demanding  
24 and shade-tolerant species by means of enlarging niche availability (Pugnaire et al., 2011).  
25 Nevertheless, herbaceous cover declined along an increasing shrub volume gradient in these

1 mine sites; this is a common effect under shrubs produced by the competition under shrubs for  
2 space (Pugnaire et al., 2004).

3 Although, the shrub volume gradient had a significant effect on the species composition in  
4 these mined sites, explaining 17.5% of the compositional variation, this gradient was of slightly  
5 lesser importance that the primary correlated with soil coarseness (20% of the compositional  
6 variation). It is well known that an increase of bare soil and rocks will produce difficult  
7 conditions for plant establishment in terms of structure and niche-space (Felinks and Wiegand,  
8 2008; Pallavicini et al., 2013), which will control vegetation establishment, its subsequent  
9 composition and hence the restoration potential on these mined sites.

10 Surprisingly, only the “perennial *Fabaceae*” species group out of six functional-taxonomic  
11 groups tested, showed a significant negative association with shrub volume. Moreover, two of  
12 the main herbaceous plant species producing negative associations with shrub volume were  
13 legumes; i.e. *T. striatum* and *M. lupulina*. These results are in accordance to the concept that  
14 closer the species are related the more likely it is that they will share important ecological traits,  
15 and more compete with each other (Webb et al., 2002). The rest of the species impacted by  
16 shrub volume were either light-demanding species or early-colonizers, such as *Lotus*  
17 *corniculatus* and *Hieracium pilosella* (Alday et al., 2011a). These negative associations may  
18 result from either competition for light or by means of a reduction in seed germination by  
19 shading (Seifan et al., 2010; Soliveres et al., 2010). Recent studies in Mediterranean climates  
20 have demonstrated that a decrease in soil radiation influences the regeneration of seed-  
21 dependent species, because dormancy breakage and seed germination is modulated in some  
22 species by daily soil temperature fluctuation produced by solar incidence (Santana et al., 2013).  
23 In addition, light incidence also promotes the germination of these species directly (Baeza and  
24 Roy, 2008). Fernández-Santos et al. (2004) reported similar results under *Cistus multiflorus*,  
25 and suggested a positive effect of leguminous shrubs on the micro-environment for bryophytes,  
26 although some herbaceous species (e.g. *Achillea millefolium*, *Dactylis glomerata*) were lost



1 through competition. Here, however, 10 species (four grasses and six forbs) showed a positive  
2 association with shrub volume. These positive associations may result from either the micro-  
3 environmental improvement, i.e. shade, water retention, nitrogen fixation by legume shrubs  
4 (Palaniappan et al., 1979; Puignaire et al., 2011; Vetaas, 1992), or escape from herbivory  
5 (Pujanen et al., 2011). Facilitation by micro-site improvement is clear in the cases of *A.*  
6 *millefolium* and *S. jacobea*; two species that require a relatively high soil nutrient status (Grime,  
7 1977). However, escape from herbivory might be the reason for the increase in *Lactuca* spp.  
8 and *H. radicata*, two ruderal species with large leaves and rapid growth (Grime, 1977), which  
9 showed greater cover values under greater shrub volumes, reducing the grazing damage  
10 underneath by physical shelter (Baraza et al., 2006).

11

## 12 **5. Conclusions**

13 Restoration of open-cast coal mines in north Spain often results in an arrested succession  
14 (Alday et al., 2011a). Nevertheless, natural shrub encroachment has been shown in this study as  
15 one means through which these ecosystems can be modified to create heterogeneity in micro-  
16 environmental conditions, and hence inducing greater overall diversity. As shrubs increased  
17 there was an increase in OMT and moisture (evidenced by the increase in bryophytes), together  
18 with a reduction in light received at ground level, and changes in herbaceous species  
19 composition were produced. These result also suggest that shrubs can be used as ecosystem  
20 engineers, either by encouraging natural regeneration or by deliberate introduction, to enhance  
21 overall environmental heterogeneity and different plant communities. Indeed, they may be  
22 considered nurse plants in the future to facilitate the introduction of late-successional species  
23 such as *Q. pyrenaica* and *Q. petraea*. The use of shrubs for such purposes has been  
24 demonstrated in both land restoration schemes elsewhere (Marrs et al., 1982) and in  
25 Mediterranean areas (Gómez-Aparicio et al., 2004).

1 Simultaneously, assessment of the species optimum associated with shrub colonization  
2 allows the development of new species mixtures that are tailored to individual site conditions to  
3 favour desired plant communities. Particularly interesting is the potential use in restoration  
4 programmes of those species which showed a wide tolerance to shrubs and open spaces, e.g.  
5 *Medicago lupulina* and *Dactylis glomerata*. At the same time, this work also allows to sort  
6 herbaceous species that can be optimal for the initial colonisation of open spaces in the early  
7 stages of succession (e.g., *Trifolium campestre*, *T. striatum*, *Plantago lanceolata*, *Festuca* spp.  
8 or *Anthemis arvensis*).

9 These suggestions have been derived from observations within ongoing coal mine  
10 restoration schemes. Clearly, the use of shrubs as ecosystem engineers/nurse plants to enhance  
11 the introduction of late-successional species of interest (e.g. *Q. pyrenaica* and *Q. petraea*) in  
12 order to accelerate mine sites restoration and the effectiveness of these suggested species  
13 mixtures need to be tested in future experiments.

14  
15

## 16 **Acknowledgments**

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21

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- 20

1 **Table 1.** The model parameters derived from non-linear and linear mixed-effects models  
 2 relating organic-matter thickness (OMT), bryophyte cover and total herbaceous cover to shrub  
 3 volume in reclaimed open-cast coal mines in north Spain.

4

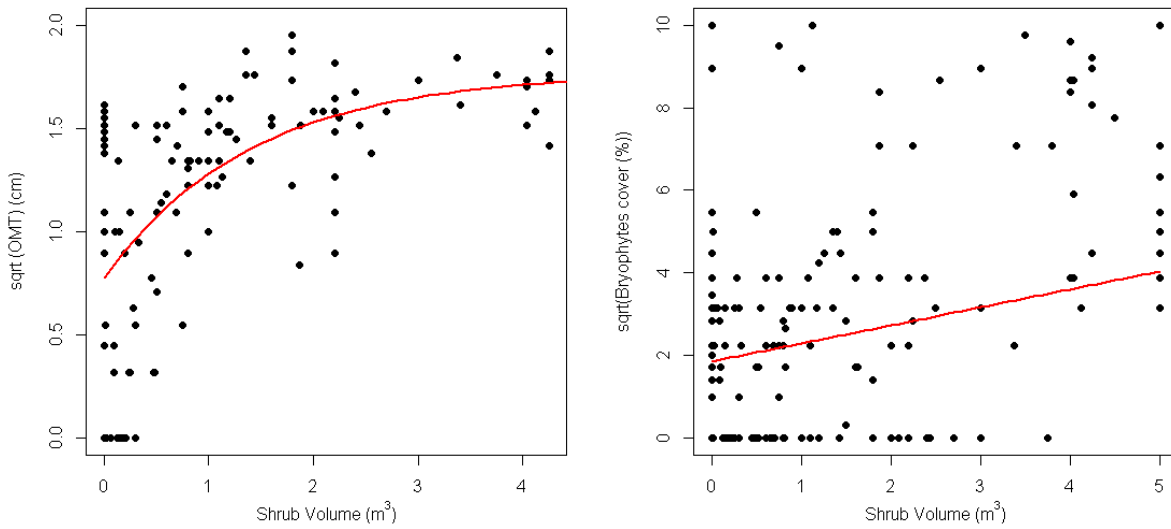
	Shrub volume	<i>t</i> -value	<i>p</i> -value
OMT (cm)			
Intercept	-0.35±0.43	-0.81	0.417
Asymptote	1.76±0.18	9.95	<0.001
Rate of increase	0.80±0.07	10.87	<0.001
Bryophytes (%)			
Intercept	1.91±0.40	4.79	<0.001
slope	0.44±0.20	2.22	0.029
Total herbaceous cover (%)			
Intercept	121.61±19.24	6.32	<0.001
slope	-11.51±3.41	-3.38	0.010

5

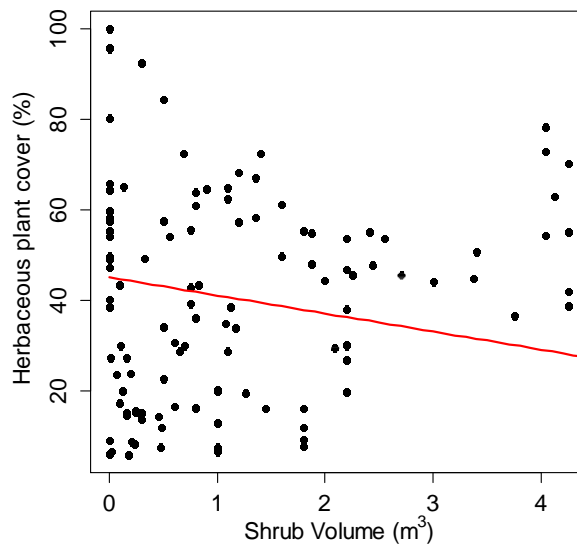
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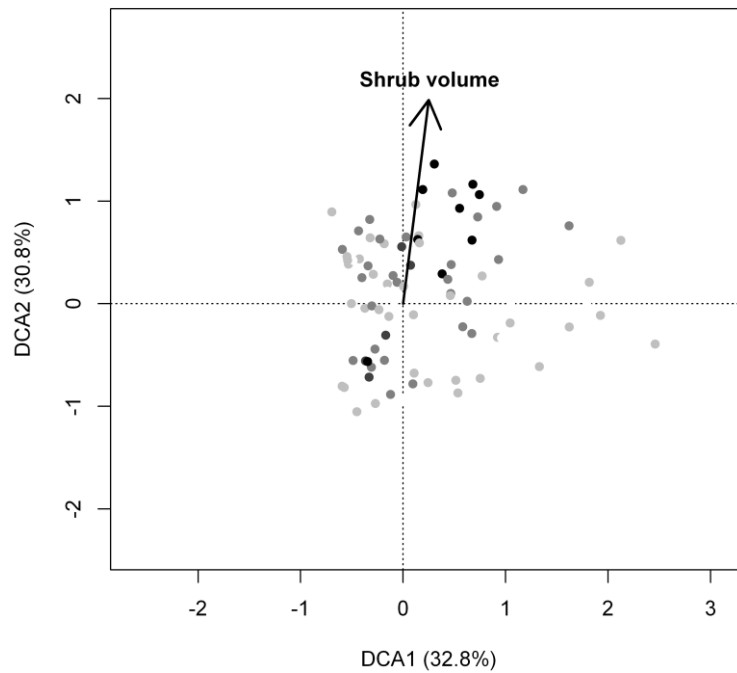
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4 **Fig. 1.** The relationship between (a) organic-matter thickness (OMT), (b) bryophyte cover (%),  
5 (c) herbaceous plant cover (%) and shrub volume (m<sup>3</sup>) in reclaimed open-cast coal mines in  
6 north Spain. The line represents the best model predictions (n=120 quadrats); see Table 1 for  
7 equation details.

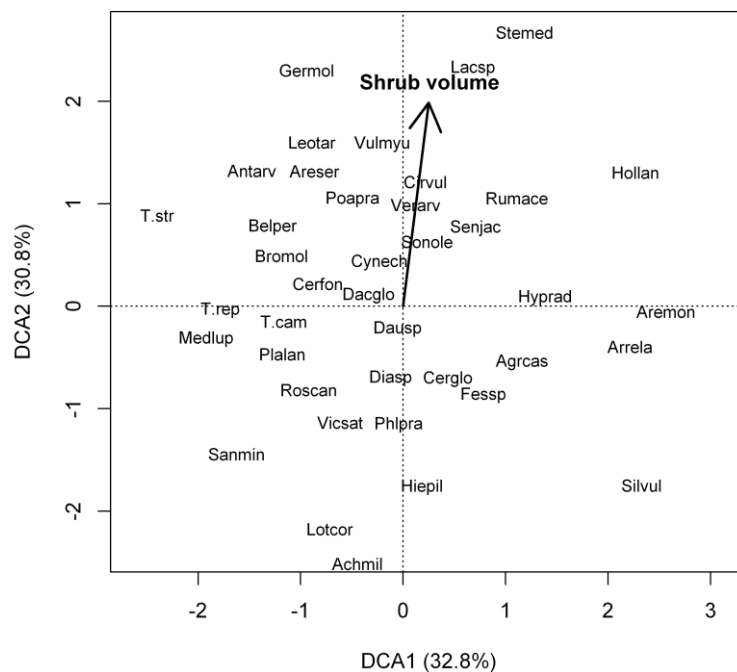
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1 a)

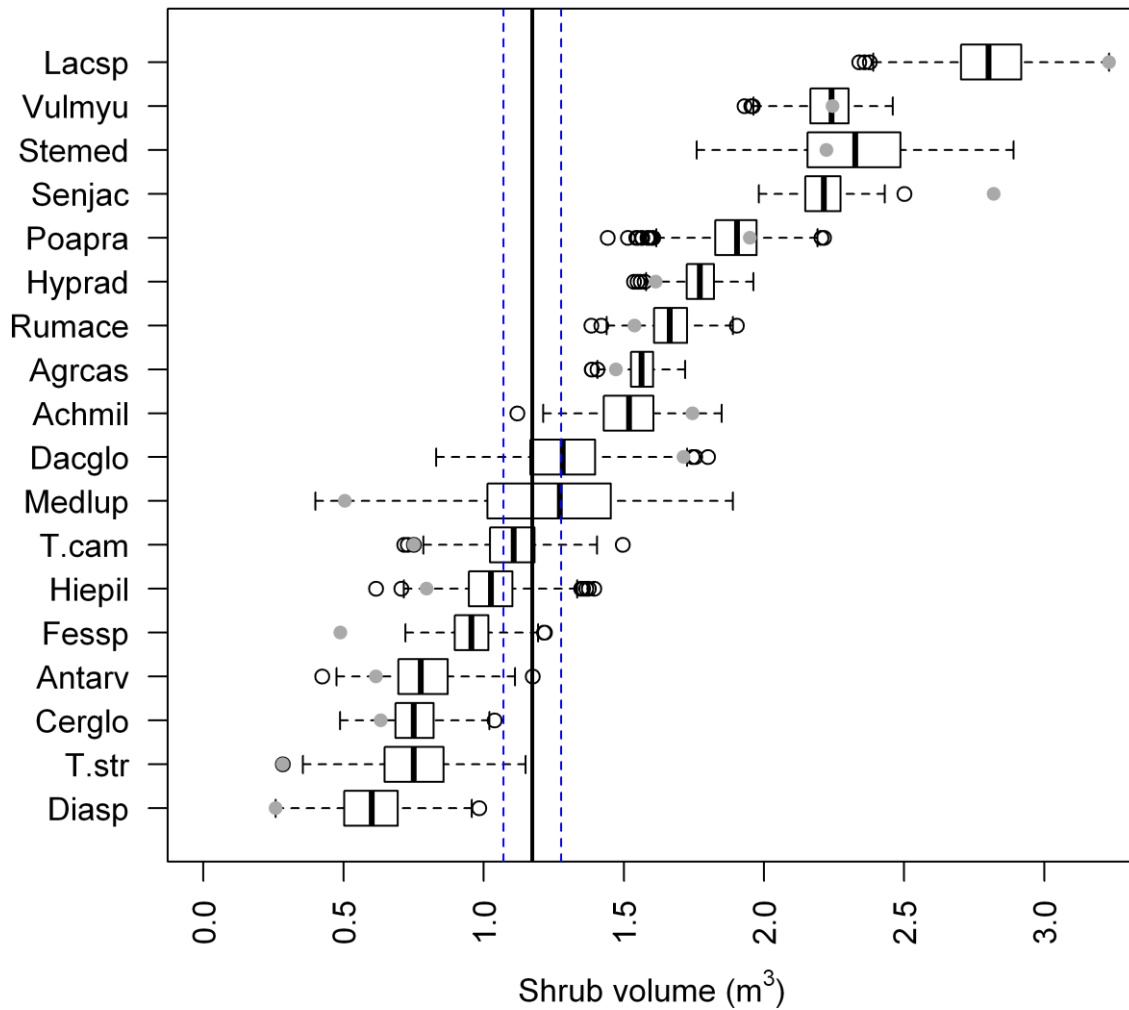


2  
3 b)



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6 **Fig. 2.** DCA biplots for the first two axes of floristic compositional data (120 quadrats grey  
7 circles) sampled in the 12 reclaimed coal mines in north Spain. Shrub volume was fitted as  
8 passive variable. The grey scale indicate the shrub volume in each quadrats; i.e greater shrub  
9 volumens in darker quadrats. The variance explained by each axis is in parentheses. Species  
10 codes: Achmil=*Achillea millefolium*; Agrcas=*Agrostis castellana*; Antarv=*Anthemis arvensis*;

1 Aremon=*Arenaria montana*; Areser=*Arenaria serphyllifolia*; Arrela=*Arrenatherum elatius*;  
2 Belper=*Bellis perennis*; Bromol=*Bromus mollis*; Cerfon=*Cerastium fontanum*;  
3 Cerglo=*Cerastium glomeratum*; Cirvul=*Cirsium vulgare*; Cynech=*Cynosurus echinatus*;  
4 Dacglo=*Dactylis glomerata*; Dausp=*Daucus* sp.; Diasp=*Dianthus* sp.; Fessp=*Festuca* spp.;  
5 Germol=*Geranium molle*; Hiepil=*Hieracium pilosella*; Hollan=*Holcus lanatus*;  
6 Hyprad=*Hypochoeris radicata*; Lacsp=*Lactuca* spp.; Leotar=*leontodon taraxacoides*;  
7 Lotcor=*Lotus corniculatus*; Medlup=*Medicago lupulina*; Phlpra=*Phleum pratense*;  
8 Plalan=*Plantago lanceolata*; Poapra=*Poa pratensis*; Roscan=*Rosa canina*; Rumace=*Rumex*  
9 *acetosella*; Sanmin=*Sanguisorba minor*; Senjac=*Senecio jacobea*; Silvul=*Silene vulgaris*;  
10 Sonole=*Sonchus oleraceus*; Stemed=*Stellaria media*; T.cam=*Trifolium campestre*;  
11 T.rep=*Trifolium repens*; T.str=*Trifolium striatum*; Verarv=*Veronica arvensis*; Vicsat=*Vicia*  
12 *sativa*; Vulmyu=*Vulpia myuros*.  
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**Fig. 3.** Plant species that had a significant relationship with shrub volume in vegetation developed on reclaimed open-case coal mines in north Spain ( $p$ -value $<0.05$ ). The boxplots represents the species-specific distributions related to shrub volume, whereas grey points indicate the true weighted averages measured for each species. The vertical lines represented the mean shrub volume $\pm$ se and the boxplots are arranged by medians. Species codes as in Figure 2.