# Shrub-induced understory vegetation changes in reclaimed mine sites

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## Abstract

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

**Highlights:**

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

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

## 1. Introduction

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

In northern Spain, particularly in the provinces of León and Palencia, open-cast coal mining has caused an extensive impact on the landscape, affecting ca. 5,000 ha of land (Alday et al., 2011a). Over the last 20 years, there has been much progress in post-mining restoration and reclamation methods, especially focusing on plant community establishment such as top-soiling, improvement of seed mixtures or tree seedling establishment protocols (Alday et al., 2012; Martínez-Ruiz et al., 2013). However, not all areas subjected to some form of reclamation treatment were always successful in creating self-sustaining ecosystems. Alday et al. (2011b) found that the establishment of plant species over raw coal wastes was very slow even after 40 years, producing unstable communities. Therefore, there are still many questions unresolved in relation to the drivers structuring these plant communities. For example, it has been observed that vegetation development in these reclaimed sites is often accompanied by an increase of shrub density and encroachment (Alday et al., 2011b, 2011c). These processes have been linked to alterations in the spatial pattern of soil resources and ecosystem function (Schlesinger and Pilmanis, 1998). However, the effects of shrub colonization can vary widely from drastic reductions in plant biomass and species richness (Archer, 2010) to just the opposite trends, depending on the species and climate involved (Eldridge et al., 2011). Nevertheless, although this process has been studied in large-scale environments (Pugnaire et al., 2011) or in several degraded ecosystems with secondary succession arrested (Gómez-Aparicio et al., 2004; Stradic et al., 2014), its possible translation and influence on small-scale processes in reclaimed mines are still little explored.

In general, shrubs influence the establishment of associated understorey plants through modifying micro-environmental conditions (Pajunen et al., 2012; Palaniappan et al., 1979). On one hand, shrubs may promote islands of fertility around them (Pugnaire et al., 1996) and facilitate plant establishment and subsequent growth (Schlesinger and Pilmanis, 1998) by accumulating water, soil nutrients and organic matter under their canopies whilst also providing protection from herbivores (Pajunen et al., 2012; Palaniappan et al., 1979). In contrast, established shrubs can also play the opposite role and exclude understorey species either by allelopathy or by reducing the amount of solar radiation or available water (Fargione and Tilman, 2003). This decrease in soil radiation may also influence regeneration processes on seed-dependent species, because dormancy breakage and seed germination is modulated in some species by daily soil temperature fluctuation produced by solar incidence (Santana et al., 2013). Micro-environment modification can also be associated to the proliferation of bryophytes in moist sites (Hettenbergerová et al., 2013), which could also exclude the establishment of new seedling (Lloret, 1994). There has been several studies during the last years addressing (i) the changes in spatial patterns of micro-environmental conditions beneath shrubs (e.g., Pugnaire et al., 1996; Giladi et al., 2013), (ii) the facilitative effects of shrubs on stressful systems (Holzapfel and Mahall, 1999) and (iii) differing response of contrasting functional groups to shrubs (Butterfield and Briggs, 2011). However, there is a lack of similar studies over coal mining reclamation areas, being of fundamental importance for developing future reclamation plans and ecosystem engineering techniques. Further efforts are needed in order to disentangle possible impacts of shrub canopies on diversity and to identify species and functional groups suitable for each specific condition.

In this context, we explored the relationships between shrub canopies and understorey plant species with the objective of designing improved and more effective restoration strategies. Here, we analyzed the shrub canopy impact on reclaimed coal mines in northern Spain. In these mined sites, shrub colonization was produced mainly by two non-thorny, leguminous shrubs with similar vertical structure: *Cytisus scoparius* and *Genista florida* (Alday et al., 2011a). Previous studies on these sites have demonstrated that these shrubs have an important effect on herbaceous richness and biomass accumulation patterns of different functional plant species groups (Pallavicini et al., 2013). However, the individual species responses to shrub interactions and the micro-scale changes produced by shrubs are unexplored, and these are fundamental for gaining knowledge about species performance and restoration of mined land. Here, therefore, we hypothesized that shrub growth, measured as above-ground volume, modified the micro-climate under the canopy and/or the spatial distribution of resources, and hence influenced understorey plant species either by facilitation or competition. Specifically, we asked the following questions: (i) What was the impact of natural leguminous shrub development on ecosystem properties such as organic-matter thickness, bryophyte cover and plant species diversity and cover?, and (ii) How were the understorey plant species and their functional groups associated with shrub canopies? It was expected that this approach would lead to identify shrub-ecosystem effects and plant-shrub interaction patterns that might inform reclamation work in similar areas.

## 2. Materials and methods

### *2.1. Site description and selection*

The study was conducted into the ‘Guardo-Cervera’ coal basin in the north-west of the Palencia province, northern Spain (42º48’-42º50’N, 4º44’-4º53’W). Within this basin, 12 mines relatively close together (within 16 km$^2$) were selected for the study, thus minimizing geographical and climatic variability. All selected mines were reclaimed using the same methodology and had a similar successional stage; i.e. age since reclamation from 17 to 25 years (8 years span), in order to reduce the possible effect of vegetation age influencing the results. For more details in age assignment and vegetation change through time see Alday et al. (2011a). The 12 study sites ranged from 1 to 3 ha, and have been restored using a combination of topsoil addition, containing a very poor seed bank (González-Alday et al., 2009), followed by hydroseeding with a grassland species mixture including grasses and legumes (81:19 by weight; 200 kg ha$^{-1}$), such as *Lolium perenne*, *Lotus corniculatus*, *Medicago sativa*, *Phleum pratense*, *Poa pratensis*, *Trifolium pratense* and *Trifolium repens*. The altitude range was also relatively small (1165-1419 m a.s.l.). The climate is sub-humid Mediterranean with an annual mean temperature of 9ºC, an average annual precipitation of 980 mm, and with a pronounced dry season in summer (July-August). The soil covering the reclaimed mines had little edaphic structure; it had a clay loam texture, a mean pH of 5.8±0.24 and organic matter content of 7.56%±0.50. There were few differences between the mines at the time of sampling in soil physical-chemical properties or micronutrients concentrations (Alday et al. 2011a). The natural vegetation surrounding these mines is a mosaic of *Quercus pyrenaica* and *Q. petraea* woodland, and remnants of natural shrublands, dominated by *Genista florida* and *Cytisus scoparius* (Alday et al., 2011a).

The 12 reclaimed mines had a patchy natural colonization of *C. scoparius* and *G. florida,* producing a shrub abundance gradient that ranged from 36% of mine cover to 80% on 25 years old mines. Both species have a ballistic type seed-dispersal mechanism (Malo, 2004; Alday et al., 2011b), that favours the seed dispersal on mined sites from the forest border. Simultaneously, in these areas both species are grazed, in low-intensity, freely by animals (e.g. deer, cattle and horses); therefore a zoochory seed-dispersal mechanism is also common. At the same time, both species are non-thorny leguminous shrubs, with similar vertical structure and capable of actively fix the atmospheric nitrogen (Talavera et al., 1999). They prefer sunny sites to growth and are good colonizers of degraded areas (Oria de Rueda, 2003). Therefore, both species are considered into the same functional group sharing common characteristics (i.e. structure and leaf phenology). As a consequence and based in the methodology carried out in studies using similar functional group species (Gómez-Aparicio et al., 2004), they were not differentiated in the study.

### *2.2. Vegetation sampling*

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

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

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

### *2.4. Data analysis*

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

We used linear and non-linear mixed effects models (“nlme” and “lme” functions within the NLME package; Pinheiro and Bates 2000) to analyze the relationships between shrub volume (Sv, $m^3$) and (i) organic matter thickness (OMT; cm), (ii) bryophytes cover and herbaceous plant cover (%) and (iii) diversity (plant species richness and evenness) at quadrat level. In all cases, linear and nonlinear models were fitted (null, linear and asymptotic) and the model that reduced the Akaike Information Criterion (AIC) most, relative to the null model, was selected. The asymptotic regression model (function “SSasymp”) was selected to explain the relationships between OMT and shrub volume; the full equation is $y=a+(b-a)\times\exp(\exp(c)\times Sv)$, where $y$ is OMT, $a$ is the asymptote of OMT, $b$ is the $y$- intercept and $c$ determines the rate at which the OMT asymptote is reached. In all these analyses, quadrats nested within mine nested within mine age were included as random factors, because quadrats within a given mine were expected to be more similar to each other than to quadrats from other mines, and mines of the same age were expected to be more similar than random mines from the successional sequence. The OMT and bryophyte cover were square-root transformed and richness log-transformed to obtain satisfactory residual distributions. The heteroscedasticity was modelled using the “varIdent” structure function that allows different variances for each level of a mine (Pinheiro and Bates 2000). All values are reported as the mean±standard error of the fixed factors.

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

## 3. Results

### 3.1. Shrub volume influence on ecosystem properties

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

### 3.2. Plant species association with shrub volume

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

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

## 4. Discussion

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

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

The improvement of soil conditions beneath the canopy of shrubs, such as nutrients and particularly the accumulation of organic matter, has been described in many systems throughout the world (Moro et al., 1997; Palaniappan et al., 1979; Puignaire et al., 2011). Here, similar results were found; OMT was related significantly to shrub volume in a non-linear asymptotic relationship, indicating that there is a threshold shrub volume beyond which OMT accumulation underneath slows. Similar studies on different forest areas across Europe have showed that litter layer increased positively with shrub cover (Pujanen et al., 2012). This relationship may arise from the greater amount of litter produced by shrubs in comparison with herbaceous species (Barth and Klemmedson, 1978), but it is also possible that as shrub volume increases the litter produced is not only collected underneath the shrubs, but some might be dispersed to a wider area by wind (Puignaire et al., 2011).

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

Perhaps the most interesting result was the positive relationship of bryophyte cover and shrub volume. Conflicting results have been found in similar studies elsewhere. In temperate and arctic areas negative relationships between bryophytes and shrub volume have been reported (Cavard et al., 2011; Pujanen et al., 2011). In contrast, studies on arid and semi-arid environments positive relationships have been reported (Smith and Stark, 2014). Our results for a Mediterranean climate are in line with those for arid/semi-arid regions. This phenomenon is best explained by the biotic mechanisms produced by shrub growth. In these mined sites under Mediterranean climate, where soil structure is lacking (Alday et al., 2012) and soil moisture is a limiting factor for vegetation development (González-Alday et al., 2008), the effect of increasing shrub volume will produce an increase in both OMT and shade. These two processes will increase moisture availability, OMT through an increase of water holding capacity and shade by reducing soil temperature, and hence subsequent soil moisture evaporation (Maestre et al., 2009; Moro et al., 1997). As a consequence the development of bryophytes under shrub canopies is favoured compared to open areas. However, there must take in consideration that some rainfall interception and consumption by shrubs is also produced (Pugnaire et al., 2011). Regardless, the positive effect of shrub volume on both OMT and bryophytes will produce an increase in environmental heterogeneity on mined areas, producing different niche availabilities for species establishment (Pugnaire et al., 2011).

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

Previous research on the effect of shrubs on vascular plant species diversity in Mediterranean environments (Maestre and Cortina, 2005; Maestre et al., 2009) or semi-natural grasslands in temperate regions (Rejmanek and Rosén, 1988) have shown that shrub cover can lead to either increases or decreases in species richness. Here, we failed to detect any effect on understory vascular plant species richness and evenness along the shrub volume gradient. The plant species richness and evenness remained constant across the shrub volume gradient with values of 18±0.65 and 0.76±0.01, respectively, although there was a decrease in herbaceous plant cover. This lack of a relationship between vascular plant diversity and shrub volume on these mine sites can be explained by the significant effect of shrub volume on species composition. Here, the shift in plant composition from a greater abundance of annual, light-demanding species and legumes in open conditions towards water-requiring, shade-adapted, and broad-leaves species as shrub volume increased can keep species richness and evenness constant (Alday et al., 2010). This process is likely to have resulted from suppression by shrubs via competition with light-demanding species, but at the same time, producing conditions that favoured water-demanding and shade-tolerant species by means of enlarging niche availability (Pugnaire et al., 2011). Nevertheless, herbaceous cover declined along an increasing shrub volume gradient in these mine sites; this is a common effect under shrubs produced by the competition under shrubs for space (Pugnaire et al., 2004).

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

Surprisingly, only the “perennial *Fabaceae*” species group out of six functional-taxonomic groups tested, showed a significant negative association with shrub volume. Moreover, two of the main herbaceous plant species producing negative associations with shrub volume were legumes; i.e. *T. striatum* and *M. lupulina*. These results are in accordance to the concept that closer the species are related the more likely it is that they will share important ecological traits, and more compete with each other (Webb et al., 2002). The rest of the species impacted by shrub volume were either light-demanding species or early-colonizers, such as *Lotus corniculatus* and *Hieracium pilosella* (Alday et al., 2011a). These negative associations may result from either competition for light or by means of a reduction in seed germination by shading (Seifan et al., 2010; Soliveres et al., 2010). Recent studies in Mediterranean climates have demonstrated that a decrease in soil radiation influences the regeneration of seed-dependent species, because dormancy breakage and seed germination is modulated in some species by daily soil temperature fluctuation produced by solar incidence (Santana et al., 2013). In addition, light incidence also promotes the germination of these species directly (Baeza and Roy, 2008). Fernández-Santos et al. (2004) reported similar results under *Cistus multiflorus,* and suggested a positive effect of leguminous shrubs on the micro-environment for bryophytes, although some herbaceous species (e.g. *Achillea millefolium, Dactylis glomerata*) were lost through competition. Here, however, 10 species (four grasses and six forbs) showed a positive association with shrub volume. These positive associations may result from either the micro-environmental improvement, i.e. shade, water retention, nitrogen fixation by legume shrubs (Palaniappan et al., 1979; Puignaire et al., 2011; Vetaas, 1992), or escape from herbivory (Pujanen et al., 2011). Facilitation by micro-site improvement is clear in the cases of *A. millefolium* and *S. jacobea*; two species that require a relatively high soil nutrient status (Grime, 1977). However, escape from herbivory might be the reason for the increase in *Lactuca* spp. and *H. radicata*, two ruderal species with large leaves and rapid growth (Grime, 1977), which showed greater cover values under greater shrub volumes, reducing the grazing damage underneath by physical shelter (Baraza et al., 2006).

## 5. Conclusions

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

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

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

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

| | Shrub volume | *t*-value | *p*-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 |

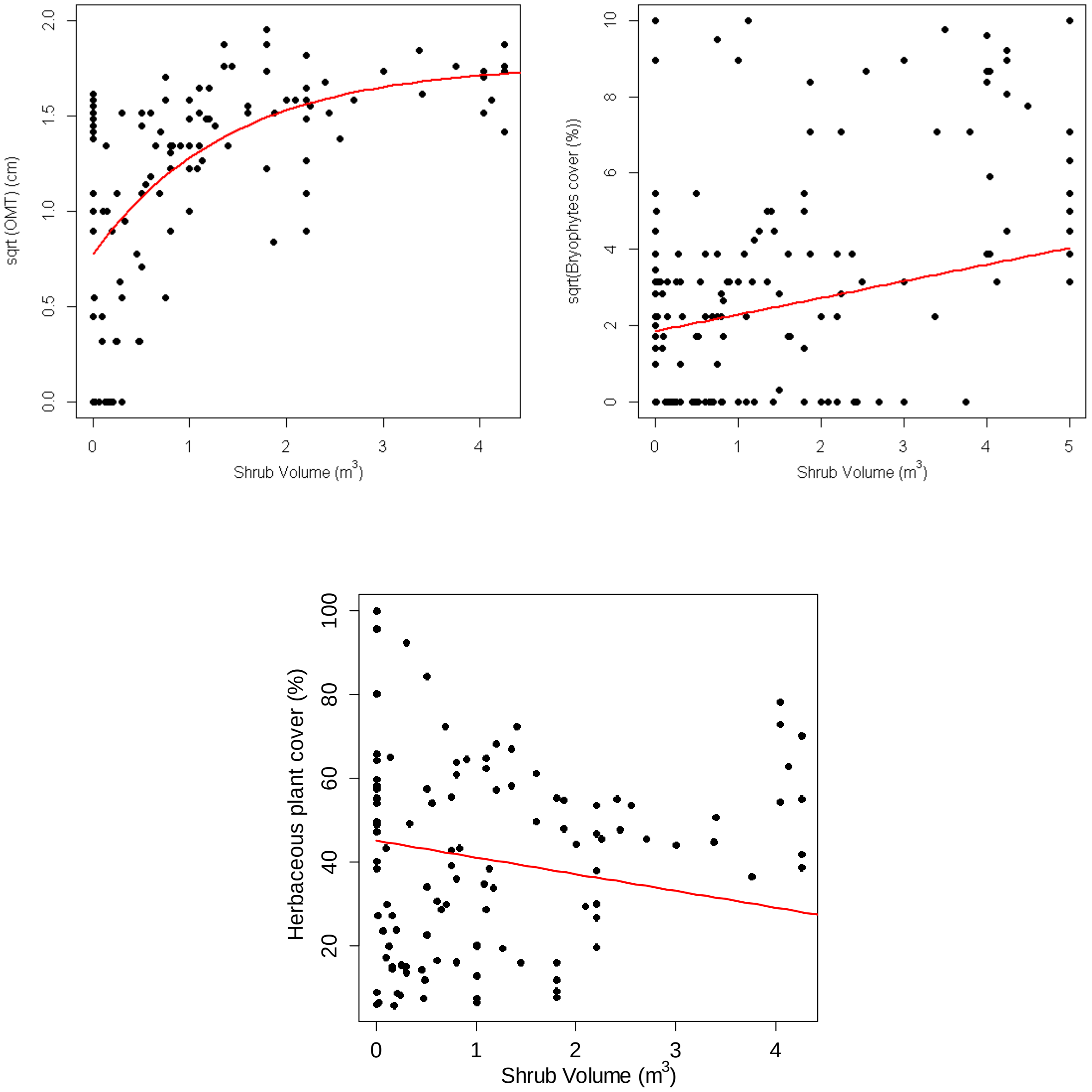
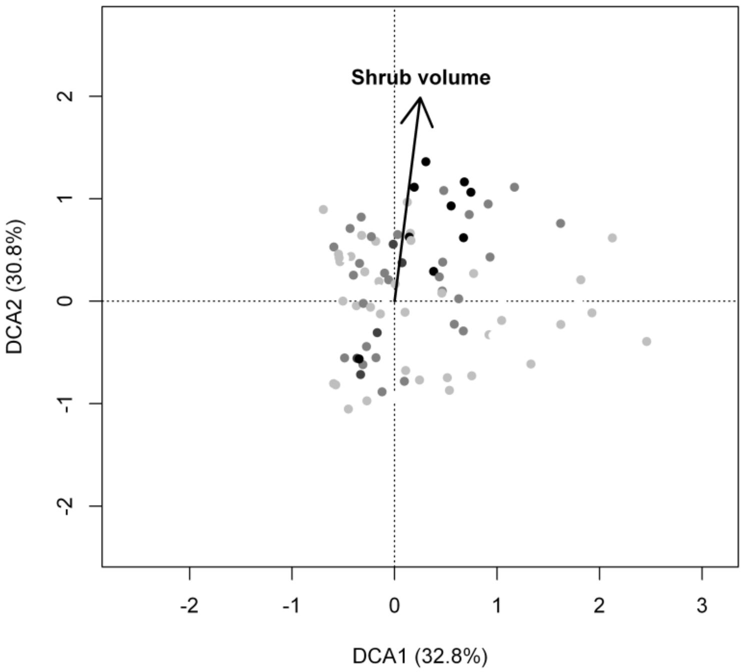


**Fig. 1.** The relationship between (a) organic-matter thickness (OMT), (b) bryophyte cover (%), (c) herbaceous plant cover (%) and shrub volume (m$^3$) in reclaimed open-cast coal mines in north Spain. The line represents the best model predictions (n=120 quadrats); see Table 1 for equation details.

a)



b)

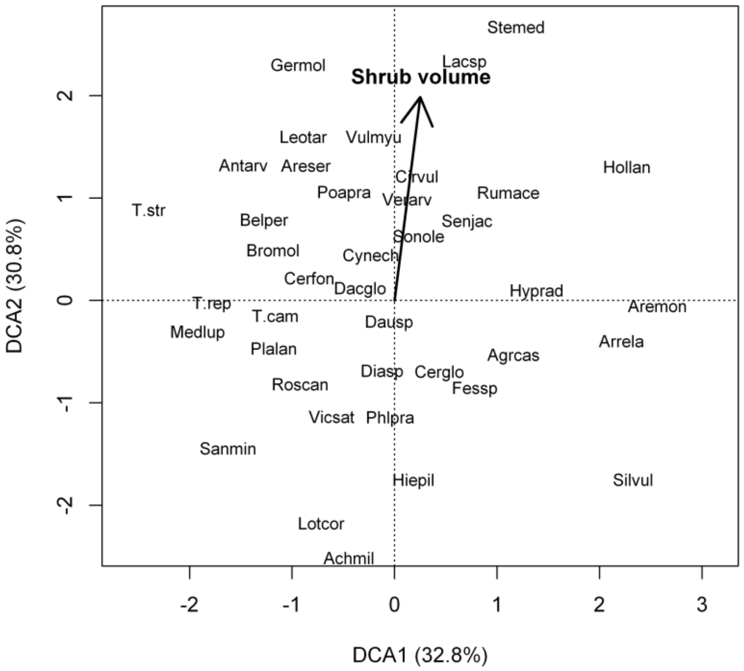


**Fig. 2.** DCA biplots for the first two axes of floristic compositional data (120 quadrats grey circles) sampled in the 12 reclaimed coal mines in north Spain. Shrub volume was fitted as passive variable. The grey scale indicate the shrub volume in each quadrats; i.e greater shrub volumens in darker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

Aremon=*Arenaria montana*; Areser=*Arenaria serphyllifolia*; Arrela=*Arrenatherum elatius*; Belper=*Bellis perennis*; Bromol=*Bromus mollis*; Cerfon=*Cerastium fontanum*; Cerglo=*Cerastium glomeratum*; Cirvul=*Cirsium vulgare*; Cynech=*Cynosurus echinatus*; Dacglo=*Dactylis glomerata*; Dausp=*Daucus* sp.; Diasp=*Dianthus* sp.; Fessp=*Festuca* spp.; Germol=*Geranium molle*; Hiepil=*Hieracium pilosella*; Hollan=*Holcus lanatus*; Hyprad=*Hypochoeris radicata*; Lacsp= *Lactuca* spp.; Leotar=*leontodon taraxacoides*; Lotcor=*Lotus corniculatus*; Medlup=*Medicago lupulina*; Phlpra=*Phleum pratense*; Plalan=*Plantago lanceolata*; Poapra=*Poa pratensis*; Roscan=*Rosa canina*; Rumace=*Rumex acetosella*; Sanmin=*Sanguisorba minor*; Senjac=*Senecio jacobea*; Silvul=*Silene vulgaris*; Sonole=*Sonchus oleraceous*; Stemed=*Stellaria media*; T.cam=*Trifolium campestre*; T.rep=*Trifolium repens*; T.str=*Trifolium striatum*; Verarv=*Veronica arvense*; Vicsat=Vicea sativa; Vulmyu=*Vulpia myuros*.

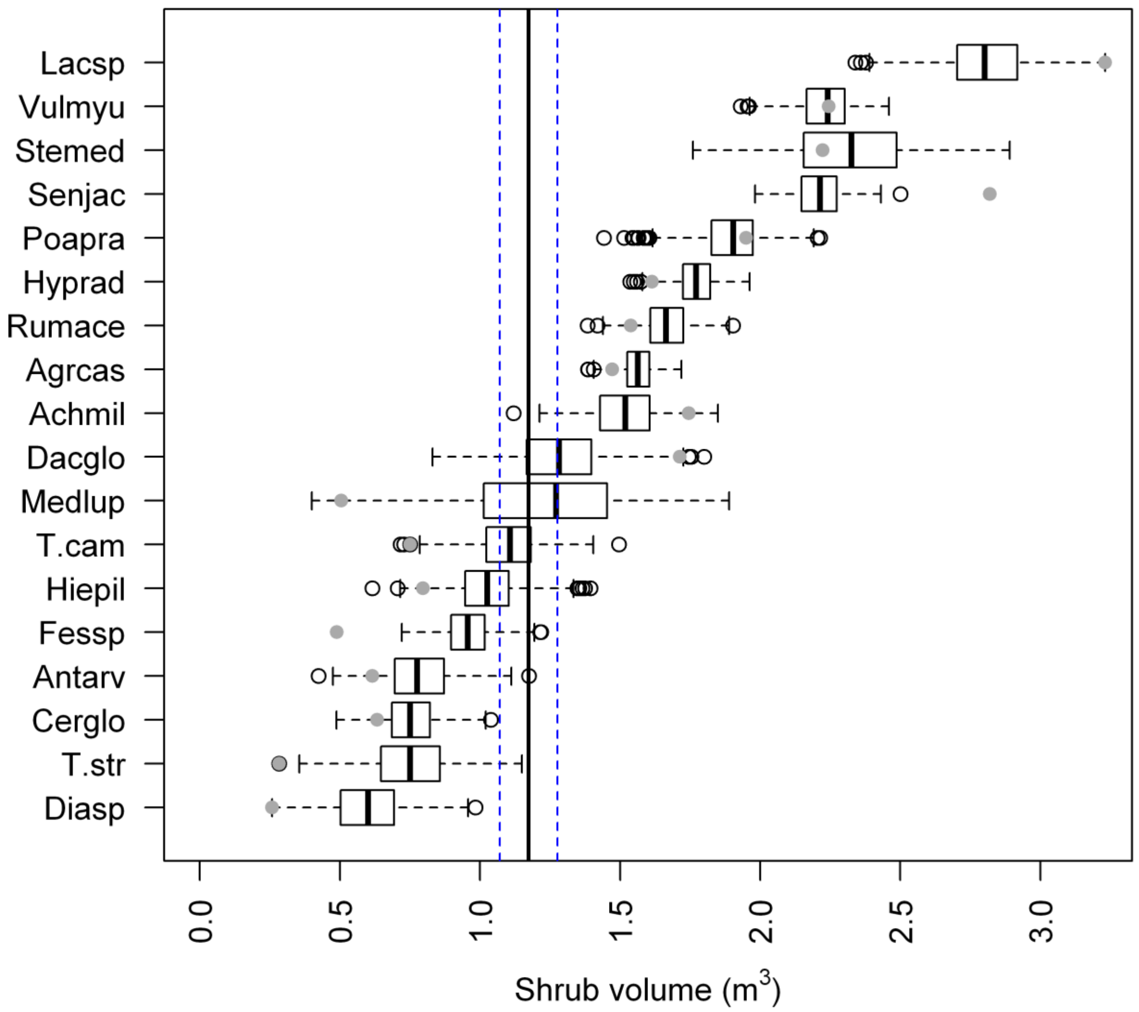


**Fig. 3.** Plant species that had a significant relationship with shrub volume in vegetation developed on reclaimed open-case coal mines in north Spain (*p*-value<0.05). The boxplots represents the species-specific distributions related to shrub volume, whereas grey points indicate the true weighted averages measured for each species. The vertical lines represented the mean shrub volume±se and the boxplots are arranged by medians. Species codes as in Figure 2.