Vegetation convergence during early succession on coal wastes: a 6-year permanent plot study
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Abstract

**Question:** Does the course of succession on a coal mine restored by hydroseeding converge with a reference community in terms of species composition and vegetation structure? What is the rate of succession on restored areas? How does the balance between local colonization and extinction rates change during succession? Which species group (native or hydroseeded) determines the successional process?

**Location:** Large reclaimed coal mine in the north of Palencia province, northern Spain (42°50'N, 4°38'W).

**Methods:** Between 2004 and 2009 we monitored annually vascular plant species cover in nine permanent plots (20 m² each) at a restored mine; these plots were structured to account for site aspect (north, south and flat). Three identical permanent plots were established in the surrounding reference community and monitored in 2004 and 2009. We used detrended correspondence analysis to assess successional trends and rates of succession, generalized linear mixed models to derive patterns of vegetation structural changes and turnover through time, and Huisman–Olff–Fresco modelling to illustrate response of individual species through time.

**Results:** The three restored mine areas exhibited a successional trend towards the reference community through time, although speed of convergence differed. However, after 6 years the restored sites had diverged considerably and this was greater than the dissimilarity reduction with respect to the reference community. Richness, diversity and native species cover increased linearly through time, whereas hydroseeded species cover decreased. Success of hydroseeded species initially differed in the three areas, and this was negatively related with native species colonization rates. Response patterns through time of ten hydroseeded and 20 most common native species are described.

**Conclusions:** Vegetation structural parameters rapidly converged with the reference community, whereas compositional convergence needed much longer. At the same time, successional composition trajectories and rates were related to site properties (here aspect).

Introduction

Opencast mining is a major environmental disturbance that often leaves a landscape with no vegetation and very poor soil-forming material on which an ecosystem can develop (Herath et al. 2009). In such damaged systems, the aim of the ecological restoration should be to create a healthy, self-sustaining ecosystem, which is similar to the semi-natural or natural ecosystems that were present before the mining operations. As restoration proceeds, there is an excellent opportunity to study the successional dynamics of vegetation development in these newly
created man-made ecosystems (Brashaw 1997; Alday et al. 2010). The investigation of these early successions in restored mines has both practical and theoretical importance (Grant 2009). Practically, because information on successional development might help guide future ecological restoration treatments in two ways: first by making the restoration process more effective (Walker & del Moral 2009) and second by identifying management intervention points where a successional trajectory can be modified (Grant 2009). Theoretically, because scientific approaches to restoration can provide insights into fundamental ecological theory, including understanding the initial phases of vegetation establishment (Robbins & Matthews 2009), and how the vegetation community structure develops (del Moral & Walker 2007).

When a mine is restored, the success of the initial revegetation treatments provides a starting species pool for the subsequent succession (Alday et al. 2010). Once this pool is established, other processes come into play, including species assembly rules, rates of species colonization and extinction and both positive and negative species interactions; all of which interact to produce species turnover and structural change (Bartha et al. 2003). Therefore, by following the course of succession for the first years of the restoration process, those spatial and temporal changes in vegetation structure and species patterns that determine the initial outcome of succession can be identified and measured; thus providing insights into fundamental community dynamics and restoration success (Walker & del Moral 2009).

A fundamental part of any ecological restoration project must be the identification of a target reference community to serve as a model against which to evaluate the success of the restoration (S.E.R.I. 2004). The most usual way to achieve this is to select an undisturbed reference community from the area surrounding the restored site (e.g. Martínez-Ruiz et al. 2007), or one typical of the local region (Holl 2002). Thereafter, restoration success can be determined in two ways: first, through a comparison of the structure and function of the restored site with the reference community; and second, by calculation of the direction and speed of the trajectory between the restored site and the reference site (Mitchell et al. 2000; Fagan et al. 2008). One common approach to evaluate restoration success is to monitor vegetation change in permanent plots set up in both restored and reference sites (Kirmer & Mahn 2001; Prach & Pyšek 2001). With this approach, change through time provides a test of whether the sites are becoming more similar through time, i.e. convergence (del Moral 2007). In this paper, we investigated whether the community composition that developed on a restored opencast mine in Spain was converging towards reference sites, and progress towards the desired target during the 6 years after the initial restoration work.

Opencast coal mining affects around 5000 ha of land in the León and Palencia regions of northern Spain, where mandatory requirements are in place to ensure vegetation restoration (Alday et al. 2010). During the last 10 years, the most common approach to restore such land has been to reshape the landform, improve the baseline soil-forming materials, and then introduce, through hydroseeding with the application of a homogeneous suspension of water and seeds over the land surface (González-Alday et al. 2008), selected herbaceous species that are adapted to disturbed and early-successional conditions. This approach has been called the ‘passive relay floristic approach’; where practitioners assume that the initial colonizing species will facilitate the later coloniztion of medium- and late-successional native species through time, and the resulting restored community will be similar to surrounding native plant communities (McClain et al. 2011). However, the efficacy of this approach in achieving both the species composition and vegetation structure of reference sites has rarely been tested. There is also little information on the response through time of species introduced within the initial starting vegetation or the native colonizers.

In this paper, we attempt to address these issues. We followed the vegetation dynamics in permanent plots set up on a restored coal mine in northern Spain, during the first 6 years after initial treatment. As this site experiences a Mediterranean climate, and it is known that site aspect is a major factor controlling vegetation development in such situations, specifically plant cover and species composition (Martínez-Ruiz et al. 2007; Alday et al. 2010), we studied the response of vegetation in a structured way to account for site aspect (north- and south-facing slopes and flat area). The results from the restored mine were then compared to the vegetation of a surrounding reference plant community. This case study, therefore, embeds scientific monitoring of vegetation change within an ongoing mined land restoration scheme and provides information of direct relevance to guide restoration practice (Brashaw 1997; Pickett et al. 2001). Specifically, we aimed to answer the following questions: (1) Does the course of succession on a coal mine restored using the standard restoration approach noted above (landform reshaping plus hydroseeding) converge with a reference community in terms of species composition and vegetation structure (richness, diversity and cover)? (2) What is the rate of succession on the restored mine? (3) What is the balance between local colonization and extinction rates on the restored mine? (4) Which native or hydroseeded species determine the successional process? It was hoped that this information would lead to an improved
restoration methodology, thus increasing effectiveness, and would generate knowledge to provide a more predictive understanding of successional dynamics during restoration.

**Methods**

**Site description and restoration treatment**

The study site was located in ‘Pozo Sell’, a 10-ha reclaimed open-pit coal mine near Villanueva de la Peña, Palencia, northern Spain (1.185 m a.s.l.; 42°50’N, 4°38’W). The climate is sub-humid mediterranean with a mean annual temperature of 9°C and average annual precipitation of 980 mm. Rainfall is distributed seasonally, with most rainfall in spring and autumn, and with a pronounced dry season in summer. The vegetation surrounding the site comprises a complex matrix of grasslands (Arenaria montana, Bromus mollis, Plantago alpina, Vulpia myuros), crop fields (Avena sativa, Secale cereale), remnants of natural shrubland (Cistus laurifolius, Erica cinerea, Juniperus communis, Rosa canina) and Quercus pyrenaica woodland (Alday et al. 2010).

After mining stopped, the open pit was filled with coal waste from nearby mines and the surface was covered with 50–100 cm of fine-textured sediments and a layer of cattle manure (30 t ha⁻¹). Thereafter, in October 2003 the entire site was hydroseeded using a slurry containing soluble chemical fertilizer (150 kg ha⁻¹; 8N:15P:15K), and a seed mixture (210 kg ha⁻¹) of grasses and herbaceous legumes (81:19 by weight). The seed mixture included Festuca spp., Avena sativa, Secale cereale, Lolium perenne, Phleum pratense, Poa pratensis, Trifolium pratense, Lotus corniculatus, Medicago sativa and T. repens in 9:3:3:2:2:2:1:1:1:1 proportions.

**Vegetation sampling**

The change in plant species composition following restoration was examined in three separate areas differing in aspect: (1) a north-facing slope, (2) a south-facing slope and (3) a flat area; both sloping areas were approximately 25°. These areas shared the same restoration method, altitude, lack of initial soil seed bank and similar soil properties (González-Alday et al. 2009; Alday et al. 2010). In each of these areas, three permanent plots of 20 m² were randomly located (restored mine; n = 9; Fig. 1). The minimum distance between plots in each area was 50 m and the maximum 120 m. Within each of these nine plots, eight 0.25-m² quadrats were positioned randomly in January 2004 and marked permanently (Alday et al. 2010).

The shrubland community surrounding the restored mine was selected as a reference community because it was in contact with the three selected mine areas. Soil texture was described as sandy loam, with a mean pH of 6.43 ± 0.3, organic matter content of 7 ± 0.8%; and vegetation characterized by shrubs but with an important component of herbaceous species. The species composition of the reference community was analysed in three permanent plots (reference community; n = 3, Fig. 1), which were selected on the basis of proximity to the restored land and topographic similarity. We therefore, selected one reference flat site near the flat mined area and two reference sloping sites, each near their sloping counterpart within the restored area. However, the slope of the reference areas was lower than that of the mine areas (approximately 5° versus 25° of mined aspects), and the aspect of the south reference area was southwest instead south. Within each of these three plots, eight 0.25-m² quadrats were positioned randomly in May 2004 and marked permanently.

The cover (%) of all vascular plant species present in each quadrat was visually estimated by the same observer every spring (May–June) for 6 years (2004–2009) at the restored mine. The vegetation of the reference community was monitored twice: in the spring of 2004 and repeated in 2009. The mean cover of each species in the eight quadrats per plot was used to obtain an estimate of the cover of vascular plant species in each plot at each sampling occasion.

**Data analysis**

All statistical analyses were implemented in the R software environment (version 2.10.1; R Development Core Team, Vienna, Austria, http://www.r-project.org), using the VEGAN package for multivariate analyses (R package version 1.17-0, http://cran.r-project.org/web/packages/vegan), the LME4 package for GLMM (R package version 0.999375-32, http://CRAN.R-project.org/package=lme4) and the GRAVY package for HOF modelling (R package version 0.999914-12, http://CRAN.R-project.org/package=gravy).

**Change in floristic composition through time**

Detrended correspondence analysis (DCA) was used to compare the change in species composition of the restored mine to the reference community. In this analysis, the species data set was down-weighted to reduce the influence of rare species. The VEGAN function ENVI FIT was then used to aid in interpretation of the output. ENVI FIT was used to overlay (1) the centroids for each area (north-facing, south-facing, flat, reference) in each year, and (2) time as a vector onto the species ordination plot. Successional trends for each area were displayed as lines connecting the time series of centroids. The time vector represents a gradient of temporal turnover in species composition; therefore, the rate of succession in the reclaimed areas was estimated as the rate of change in site ordination scores along the time vector (Matthews & Endress 2010).

**Species heterogeneity and turnover**

The Bray-Curtis dissimilarity index was calculated to compare species composition of the restored mine and of the reference community in both 2004 and 2009. This index is a sensitive measure of heterogeneity (Robbins & Matthews 2009) and ranges from zero (complete similarity) to one (no species in common). The significance of the differences in Bray-Curtis average distances between restored mine and reference community were computed using a permutational multivariate analysis of variance (PMAV), with 1000 permutations.

In order to understand the processes of community change, the species turnover for each plot was calculated. Using species presence–absence data from the restored mine (n = 9), the proportional species gain (Gp), loss (Lp) and turnover rates (Tp) were calculated following Matthews & Endress (2010). The slopes of these variables (Gp, Lp, Tp) for each plot were calculated to determine if the rates increased (positive slope) or decreased (negative slope) over time.

**Change in vegetation structure**

Generalized linear mixed models (GLMMs) were then used to determine the relationship between area (north-, south-facing, flat) and time on community composition variables (species richness, Shannon–Wiener diversity index, cover of hydroseeded and native species and species turnover). In these analyses, areas (north-, south-facing, flat) were treated as categorical fixed factors, time nested within plot was included as random factor to account for temporal and spatial autocorrelation (Pinheiro & Bates 2000). Model simplification data followed Crawley (2007) using the Akaike information criterion (AIC, Pinheiro & Bates 2000). Models were fitted using the GLMER function, the REML method and turnover data (%) were arcsine-transformed (sin−1√(x/100)), whereas the Laplace method, the log-link function and a Poisson error distribution were used for count data (Crawley 2007). All values are reported as the mean ± standard error of the fixed factors, and the magnitude of the effects was calculated as the estimated difference from the flat area. Fitting mixed effects models allow inferences to be made about the fixed effects, which represent average characteristics of the population presented by area, and the variability between plots.

**Response of individual species through time**

In order to illustrate the response pattern of individual species through time, the cover of (a) the ten hydroseeded species and (b) the 20 most common native species were fitted using Huisman–Olff–Fresco (HOF) models (Huisman et al. 1993). HOF models allow testing of alternative responses to ecological gradients using a hierarchical set of five response models, ranked by their increasing complexity (Model I, no species trend; Model II, increasing or decreasing trend to a maximum; Model III, increasing or decreasing trend below the maximum attainable response; Model IV, symmetrical response curve; Model V, skewed response curve; Huisman et al. 1993). The species cover data were transformed (sin−1(√(x/100)) and a Gaussian error structure was used (Huisman et al. 1993). The AIC statistic was used to select the most parsimonious model for each species; smaller values of AIC indicate better fit of the model.

**Results**

Eighty-seven vascular plant species were recorded in the restored mine during the 6-year period. All of the ten hydroseeded species were found, especially during the first 3 years. The remaining 77 species included some uncommon species (Cnipodium vulgare, Crocus nudiflorus, Crucianella angustifolia, Medicago arabica), early colonizers and ruderals (Brassica nigra, Capsella bursa-pastoris, Lactuca spp., Malva sylvestris) and species characteristic of the reference community (Avenula sulata, Helianthemum hirtum, Hieracium pilosella, Trifolium campestre). In contrast, 68 vascular plant species were recorded in the reference community over the two sampling dates. The most abundant herbaceous species in the reference community were: Airea caryophyllea, Astragalus sempervirens, Bromus mollis, Ononis repens and Plantago alpina and most abundant shrubs
were: *Crataegus monogyna*, *Erica vagans*, *Rosa canina*, *Thymus mastigophorus* and *Thymus zygis*.

**Change in floristic composition through time**

The DCA of species composition produced eigenvalues (λ) of 0.49, 0.12, 0.09 and 0.07, and gradient lengths (GL) of 3.90, 1.62, 1.30 and 1.01 for the first four axes, respectively. The species–time bi-plot showed that the passive fit of time was significant (*P* = 0.006; Fig. 2a), and increased towards the positive end of the first axis. Hydroseeded species, such as *Avena sativa*, *Secale cereale*, *Festuca* spp., *Lotus corniculatus*, *Trifolium pratense* and *T. repens* were found at the negative end of axis 1, being negatively correlated with time. Early-successional species and ruderals such as *Capsella bursa-pastoris*, *Erodium cicutarium*, *Anthemis arvensis* and *Lactuca* spp. occupied an intermediate position on the ordination, and species that tended to be more common on the reference community, including *Arenaria montana*, *Avenula sulcata*, *Bromus mollis* and *Helianthemum hirtum* were found at the positive end of axis 1 and correlated positively with time.

The positions of the centroids of the four areas (north-facing, south-facing, flat, reference) for each year revealed several interesting patterns of species compositional dynamics (Fig. 2b). Two different results are apparent. The first is the move of centroids on axis 1, where all three restored mine areas are moving through time towards the reference community (moving from left to right on axis 1). The speed of convergence of the three restored mine areas towards the reference community differed (*F*₁,₁₀ = 12.68; *P* < 0.01); i.e. between 2004 and 2009 the flat area moved 1.48 units along the time vector (0.30 units yr⁻¹), compared to 1.23 (0.24 units yr⁻¹) and 1.00 (0.20 units yr⁻¹) on the south- and north-facing areas, respectively. The second is the move of centroids on axis 2; in 2004 at the start of restoration all mine areas were relatively similar to each other (especially the two sloping areas), but there was increasing divergence through time. The flat area is close to the reference community on this axis, but the other areas lag behind.

**Species heterogeneity and turnover**

The mean Bray-Curtis dissimilarity index between the three restored mine areas was 0.26 ± 0.01 in 2004, and the mean distance between reclaimed areas and reference community was three times greater (0.95 ± 0.01; PMAV with 1000 permutations; *P* < 0.001, *r*² = 0.77). However, by 2009, the dissimilarity between the restored mine areas and the reference community was reduced to 0.82 ± 0.01 (13% reduction), although they were still significantly dissimilar (PMAV with 1000 permutations; *P* < 0.001, *r*² = 0.44). Moreover, the dissimilarity among
restored mine areas increased through time, reaching 0.53 ± 0.02 in 2009 (27% increase).

The GLMMs showed that on the restored mine, both the inter-annual species gains ($G_p$) and losses ($L_p$) declined between 2004 and 2009, independently of the area considered (Fig. 3). However, the decrease was sharper for gains ($G_p$) slope = $-0.10 ± 0.01$; $t$-value = 6.45, $P < 0.01$ versus $L_p$ slope = $-0.05 ± 0.01$; $t$-value = 4.76, $P < 0.01$). This indicates that the number of colonizers per year was reducing faster than species losses. Overall species turnover ($T_p$) declined with time from 0.46 ± 0.03 between 2004 and 2005 to 0.25 ± 0.02 5 years later (slope = $-0.07 ± 0.01$; $t$-value = $-7.37$, $P < 0.01$) as a consequence of these decreasing rates of species gains and losses.

**Change in vegetation structure**

Richness at the restored mine increased from 21 ± 0.9 to 36 ± 0.8 species per plot between 2004 and 2009, almost reaching the value of the reference community (41 ± 0.6 in 2009). GLMMs showed that species richness increased log-linearly over time, with a common positive slope for all areas (slope = 0.10 ± 0.015; $z$-value = 6.66, $P < 0.01$), but with different intercepts for each area in 2004 (north-facing = $-0.16 ± 0.06$, $z$-value = $-2.68$, $P < 0.05$; south-facing = $-0.10 ± 0.06$, $z$-value = $-1.63$, $P = 0.10$; flat = $3.10 ± 0.01$, $z$-value = 44.35, $P < 0.001$). The different intercepts suggest different colonization rates for areas and plots in 2004 (Fig. 4a). A similar result was found for diversity, which also increased linearly over time with the same slope for all areas (slope = 0.012 ± 0.01, $t$-value = 8.01, $P < 0.01$; Fig. 4b) and different intercepts.

Here, in 2009, the mean diversity index per plot was 3.00 ± 0.07 compared to the reference community value of 3.26 ± 0.04.

The cover of hydroseeded species per plot decreased progressively over the 6 years from 60 ± 5.30% to 24 ± 4.23%, with a corresponding increase in cover of native species from 13 ± 1.4% to 55 ± 2.9% (Fig. 4c, d). The response was linear in both cases, although the slope is steeper for the increase in native species cover (slope = 8.60 ± 1.00; $t$-value = 8.66, $P < 0.001$) than for the reduction in hydroseeded species cover (slope = $-6.92 ± 0.56$; $t$-value = $-12.29$, $P < 0.001$). The different intercepts found for the three areas in 2004 with respect to the hydroseeded species cover reflected differential hydroseeding success in the different areas of the restored mine (north-facing = 28.30 ± 5.71, $t$-value = 4.95, $P < 0.01$; south-facing = 0.16 ± 5.71, $t$-value = 2.83, $P < 0.05$; flat = 50.18 ± 4.49, $t$-value = 11.17, $P < 0.001$). Particularly noteworthy is that there is a negative correlation between hydroseeded species cover and native species richness during 2004–2005 ($r = -0.82, P < 0.001$).

**Response of individual species through time**

The cover of eight of the ten hydroseeded species decreased with time since restoration, whereas most of the native species showed an increasing response (Figs 5, 6). For the hydroseeded species, three groups were identified based on the type of significant response. Group 1 contained six species (Avena sativa, Lolium perenne, Lotus corniculatus, Trifolium repens, T. pratense, Secale cereale) for which cover declined through time (HOF models II, IV); Group 2 comprised three species (Festuca spp., Medicago sativa, Poa pratensis), which either maintained a stable cover for 4–5 years and declined steeply (HOF model III) or showed a skewed response with an optimum at 4 years and a subsequent decline (HOF Model V). Finally, Group 3 contained just Phleum pratense; this species showed no response to time and had a stable cover of 8% (HOF model I).

Although the cover of the most common native species increased through time, they could also be separated into three response groups (Fig. 6). Group 1, with species that showed a continual increase through time (HOF model II) and included two herbs (Capsella bursa-pastoris, Medicago polymorpha) and one woody species (Helianthemum hirtum). Group 2 comprised ten species (Arenaria montana, Arenaria spp., Bromus mollis, Cerastium fontanum, C. glomeratum, Geranium molle, Hypochoeris radicata, Trifolium scabrum, T. striatum, Vulpia myuros); the cover of these species increased and reached a maximum between 3 and 4 years after restoration (HOF model III). Finally, Group 3 contained seven species with unimodal/skewed response
This group showed a turnover of species: *Erodium cicutarium*, *Erophila verna* and *Minuartia mediterranea* peaked at 3 years; *Anthemis arvensis* and *T. campestre* peaked at 4 years; and both *Filago pyramidata* and *Veronica* spp. peaked at 5 years after restoration.

**Discussion**

**Vegetation convergence (composition and structure)**

An important result was that the vegetation structure (richness, diversity and cover) and the species compositional trajectories in the three restored mine areas (north-facing, south-facing and flat) were becoming increasingly similar (converging) to the reference community over time, albeit at different speeds. These successional trends are driven by a reduction in hydroseeded species cover and an increase of native richness and cover, which is consistent with the theory of relay floristics. However, most of the native species that had colonized within the 6-year period were classified as widespread species with long-distance dispersal mechanisms (anemochorous and zoochorous species; e.g. González-Alday & Martínez-Ruiz 2007). As a consequence, reliance on the passive relay floristic restoration approach may be adequate for species with good dispersal mechanisms, but may be inappropriate for less common species or those with limited dispersal ability. These conclusions mirror those from other studies of vegetation restoration using a relay floristic approach in mined sites (Parrotta & Knowles 2001; Holl 2002).

The second noteworthy result was that in 2004, the species composition in the three restored mine areas was more similar than it was in 2009, essentially showing
some divergence along the trajectory towards the reference community, greatest between the flat area and the two sloping areas. These divergent trajectories may be caused by a combination of (1) differential success of establishment of the hydroseeded species (greatest in north-facing followed by south-facing and flat areas, i.e. an effect of topography; Alday et al. 2010), and (2) the establishment of autochthonous species in the flat area, which might be favoured by the higher topographic similarity between the flat restored area and reference areas, since reference slopes are 5°. In any case, it seems that environmental (topographic) differences among the three different aspects are related to these initial compositional differences (Alday et al. 2010). Furthermore, it is well known that successful early establishment of a founder population, here hydroseeded species, can have important implications for successional trajectories (del Moral & Lacher 2005). Thus, the environmental differences connected with compositional differences are producing diverse trajectories even in close locations. These results are in agreement with other studies that demonstrate the frequency of multiple trajectories in early successions (del Moral 2007; del Moral et al. 2010).

In the three restored areas, the reduction in cover of hydroseeded species over the analysed period was accompanied by a significant increase in species richness, diversity and native species cover. These general patterns of richness, diversity and native cover changes over the first 6 years after restoration are consistent with other successional studies on different surfaces, including glacier forelands (Robbins & Matthews 2009), mine sites (Martínez-Ruiz et al. 2007) and lava flows (Cutler 2010). The richness and diversity \( H' \) increase was produced by the arrival of early successional species, including annuals, ruderals and some species present in the reference community. These new arrivals increased in cover and collectively had a greater cover than the hydroseeded species after 6 years. The cover of native species appeared to increase sharply between 2005 and 2006, which was almost certainly produced by the impact of an exceptionally dry year (Alday et al. 2010). It is likely that these new colonizers were better adapted to disturbance produced by the severe droughts prevalent in the Mediterranean region than the hydroseeded species (Alday et al. 2010).

Of course, the reason why some hydroseeded species were included during the restoration was because of the

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**Fig. 5.** Significant response curves of the ten hydroseeded species with respect to age since reclamation, at the ‘Pozo Sell’ reclaimed open-pit coal mine. Species codes: Avsa = A. sativa; Fesp = Festuca spp.; Loco = Lotus corniculatus; Lope = Lolium perenne; Mesa = Medicago sativa; Phpr = Phleum pratense; Popr = Poa pratensis; Trpr = Trifolium pratense; Trre = T. repens; Sece = Secale cereale.
very poor soil seed bank available before treatment (González-Alday et al. 2009). The rapid cover produced by hydroseeded species can reduce soil erosion (Albadalejo et al. 2000) and start to ameliorate the extreme habitat conditions found on mineral wastes (Bradshaw & Chadwick 1979). In particular, the accumulations of both organic matter and nutrients (Bossuyt et al. 2003) and the establishment of a functional nutrient cycle (Marrs & Bradshaw 1993) should help to facilitate the establishment of new individuals. However, it is well known that species already present at a site have a competitive advantage over invaders as long as no further disturbance occurs (Wiegleb & Felinks 2001). Therefore, the competitive interactions between hydroseeded and native species might limit further site colonization (Matesanz et al. 2006). Our results support the second explanation; in the first 3 years, particularly on the north- and south-facing plots, the density of hydroseeded species cover reduced the colonization of native species. This was evidenced by the inverse relationship between hydroseeded species cover and species richness resulting in less diverse assemblages.

In 6 years, despite the fact that richness and diversity on the restored mine sites reached similar levels to those of the reference community, native cover and especially species composition still differed considerably from the reference area, with a Bray-Curtis dissimilarity index of 0.82. Therefore, a much longer time frame is needed for the restored sites to achieve a similar community composition and structure to the reference community. Similar conclusions were reached by McClain et al. (2011) for a riparian forest restored using a passive relay floristic approach.

Fig. 6. Significant response curves of the most abundant native species with respect to age since reclamation, at the ‘Pozo Sell’ reclaimed open-pit coal mine. For species codes, refer to Fig. 2.
Rate of succession, local colonization and extinction rates on the restored mine sites

The rate of succession towards the reference community was different across the three studied areas. The DCA scores of the flat area moved closer to the reference community than either the north- or south-facing slopes. This is due to differences in the establishment of hydroseeded and native species discussed above. Variability in early successional composition rates among areas or plots has been demonstrated in other studies of ecological restoration (Prach et al. 1993), and in successional studies on lava flows (Cutler et al. 2008), volcanic ash substrates (del Moral 2007) and glacial plains (Marteinsdóttir et al. 2010) in which mosaic patterns of vegetation often result.

The existence of differences in the early successional rates based on species composition suggests that within-area constraints and stochastic factors (e.g. extreme drought) play an important role in influencing species assembly and succession (Pickett et al. 2001; Marteinsdóttir et al. 2010).

The reclaimed areas studied here followed the general temporal patterns in rates of plant species change during early succession as defined by Anderson (2007). Initially, colonization rates (species gains) started high and then declined through time. Here, this was complicated by an initial increase (2005–2006), which probably occurred because species began to colonize from the surrounding landscape, leading to an initial increase in species richness. Second, when the richness approached the number of species in the available reference community (here in 2007), the probability that a colonizing species is a new one declines (Bartha et al. 2003). At the same time, any new propagules face a reduced number of available microsites for germination, and an increased competitive pressure from the stabilized vegetation composed of both hydroseeded and native species (Matthews & Endress 2010), hence the rate of species colonization declines with time. Third, extinction rates (loss rate) were always lower than colonization rates and had a shallower slope, suggesting that nearly half of colonizing species disappeared because they were not well adapted to the prevailing abiotic conditions or were displaced by competition. The remaining half of the colonizing species established for more than 1 year, thus colonization dominated early successional change (Anderson 2007). Fourth, species turnover declined as it is the sum of the species gained and lost, and is driven by the same mechanisms that drive turnover (colonization, reduction of available microsites and competition; Anderson 2007). Therefore, if the restoration were based on a passive relay floristic approach, it would require low turnover rates during each stage, interspersed with spikes at each stage transition (Anderson 2007). Our results are consistent with this, since after the hydroseeded stage (2004–2005) important changes in species composition occurred; there was an influx of widespread native species (2006) followed by a decline in turnover with time, thus increasing the community stability (e.g. Odum 1969). However, this suggests that a much longer time frame will be needed to achieve our ecological restoration objective.

Native or hydroseeded species determine the successional process

The success of the initial restoration treatments provides the starting species pool for succession (Lepš et al. 2007). As a consequence, during the first 2 years after restoration (2004–2005) succession was mostly determined by performance of the hydroseeded species, either through competitive interactions or adaptation to environmental conditions (Alday et al. 2010). The hydroseeded species provided most of the initial vegetation cover in the three mine areas, mainly through the high cover of Trifolium repens, T. pratense, Festuca spp. and Lolium perenne, which formed dense communities, leaving little chance for native species establishment (Ninot et al. 2001). In later years, the cover of hydroseeded species decreased, although only three species disappeared (Avena sativa, Secale cereale and Lotus corniculatus), and four species maintained a cover above 10% (Poa pratensis, T. repens, Festuca spp. and Lolium perenne). Although these results were in agreement with the hypothesis that commercial seed mixtures act as facilitating species, growing rapidly for the first few years after hydroseeding and gradually vanishing as more competitive or better adapted species colonize (Mitchley et al. 1996; Merlin et al. 1999), the persistence of four species with cover values above 10% after 6 years, suggests that this theoretical view should be taken with some caution. The period studied here was clearly too short to demonstrate complete elimination and there are examples of hydroseeded species dominating vegetation for up to 8 years (Muller et al. 1998). A longer observational period is needed to determine when and if all hydroseeded species will disappear.

The lack of a seed bank on this mine (González-Alday et al. 2009) meant that native seeds had to arrive via dispersal from outside the mine area (neighbouring vegetation). As a consequence, most of the native species that colonized were either animal- or wind-dispersed, e.g. Arenaria montana, Bromus mollis, Cerastium fontanum, Medicago mediterranea, Trifolium campestre, T. striatum or Vulpia myuros. These species were the first colonizers, and their cover peaked 3 years after restoration started (peaked in 2006) but they maintained stable cover values thereafter. From 2006 onwards, the increasing cover of these native species was responsible for movement of the
vegetation composition towards the reference community, conditioning the successional process (e.g. Lanta & Lepš 2009). On the other hand, some native species, mainly ruderal species (Erodium cicutarium, Erophila verna, Anthemis arvensis, Veronica spp.), peaked in cover, with a rapid increase to their optimum and then a subsequent decline, possibly as a result of competition from the hydroseded and from other native species.

Conclusions

After 6 years of mine restoration, vegetation structure (richness, diversity and plant cover) approached that of the reference community. In contrast, species composition, although becoming similar to the reference community, still differed from it considerably after 6 years, suggesting that a much longer time frame is needed to achieve our ecological restoration objective. At the same time, the increasing differences in species composition between the three mine sampling areas and their different successional rates indicate that within-area constraints appear and play an important role in determining species assembly and succession, producing diverse trajectories even in close locations.

The present work shows that reliance on the relay floristic approach may not be adequate for less common or dispersal-limited species, therefore much longer time frames are needed with this method to achieve a species composition similar to that of the reference community. Finally, these results identified the main species involved in the short-term succession of former coal mines in the Pozo Sell region and will help to guide future restoration strategies.

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References


Vegetation convergence during early succession


