



SPECIAL FEATURE: ECOLOGICAL RESTORATION

How to develop native plant communities in heavily altered ecosystems: examples from large-scale surface mining in Germany

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Keywords

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Abstract

Questions: Does site alteration caused by mining impede spontaneous colonization of native species assemblies to the advantage of neophytic species at the landscape unit and plant community scale? To what extent can mined site conditions support the establishment of rare plant species assemblies that are locally novel but of regional conservation value? What effects have dispersal limitation and stochasticity on spontaneous succession trajectories and how does community structure and composition differ between actively restored sites and ancient grasslands?

Location: Central German Lignite Mining District.

Methods: We used comprehensive databases to compare floristic composition in mined sites and their surroundings. At the community level, we choose a chronosequence approach to analyse spontaneous colonization of target species into mined sites and the development of calcareous grasslands, compared to ancient as well as actively restored grasslands. Statistical analyses involved Mann–Whitney *U*-test, GNMDS and binary logistic regression.

Results: The proportion of neophytes in spontaneously developing mined sites was low and similar to the unmined surroundings at the landscape unit as well as plant community scale. Mined sites harbour an impressive number of native and even rare species. However, plant communities lacking immigration of target grasses typical for calcareous grasslands lead to divergences regarding species and functional composition compared to ancient calcareous grasslands. In contrast, plots with actively introduced target species at the onset of succession show a generally more rapid trajectory towards ancient grasslands. The probability of establishing in mined sites increases with higher abundance of calcareous dry grassland species in the vicinity, indicating the importance of high propagule pressure in a landscape context, whereas long-distance dispersal traits were significant, but less important.

Conclusions: Spontaneous succession supports the development of native plant communities. However, because of propagule limitation, colonization processes may lead to novel species assemblies. While dispersal stochasticity during spontaneous succession results in a higher γ -diversity, species introduction supports faster trajectories towards desired reference states providing important ecosystem services such as erosion control. The key decision of whether to rely on spontaneous succession or not mainly depends on the surrounding landscape matrix and history, the need for erosion control and/or rapid compensation for lost habitats.

Introduction

Surface mining leads to completely new site conditions, in most cases unique for the affected landscape, e.g. large-scale, nutrient-poor sites surrounded by a eutrophic cultural landscape or large lakes in former floodplain regions. During the mining process, the historical biodiversity of sites is, to a large extent, destroyed. Restoration approaches to mitigate such biodiversity loss and related ecosystem services are quite distinct, ranging from (1) assisted site recovery with native species (active ecological restoration), (2) spontaneous succession without intervention (process conservation), to (3) rapid re-vegetation of the sites with fast-growing, often neophytic species after profound amelioration (traditional or technical rehabilitation). While restoration ecologists mostly oppose the third approach (e.g. SER 2004), the first two are often hotly debated.

Some authors doubt that highly altered anthropogenic ecosystems can be spontaneously colonized by native species assemblies because drastic site alteration, the on-going depletion of regional native species pools and the increasing spread of neophytic species due to the breaching of biogeographic boundaries hamper immigration as well as establishment (Hobbs et al. 2006; Norman et al. 2006; Jackson & Hobbs 2009). Therefore, neophytic species may be used by restoration managers to restore particular functions, such as erosion control, if native species are not available and/or too expensive (Dutta & Agrawal 2003; Ewel & Putz 2004; Eviner et al. 2012). There is a long tradition of introducing neophytic species within mining site restoration schemes (D'Antonio & Meyerson 2002; Holl 2002; Hoelzle et al. 2012) causing an additional propagule pressure within restoration areas, which can in fact subsequently lead to novel ecosystems consisting predominantly of species that have not occurred previously within a given biome, if no counter-actions are performed (Zipper et al. 2011; Fields-Johnson et al. 2012; Evans et al. 2013). However, it is also confirmed that the growth potential of native species has not been fully explored for mined site conditions, and further research is needed in this area (Skeel & Gibson 1996; D'Antonio & Meyerson 2002; Richardson et al. 2010). Above all, invasion of neophytic species seems to be less significant for mined sites in Central Europe compared to North American or Australian mining regions. Although there is evidence for the immigration of neophytic species (e.g. *Robinia pseudoacacia*) from nearby afforestation into spontaneously developing sites, this is not emphasized as a main constraint for the development of native plant communities on most sites (Prach & Pyšek 2001; Hodačová & Prach 2003). In general, the role of the regional species pool in industrially transformed regions for the invasion potential of neophytic species has rarely been studied (but see Řehouňková & Prach 2008). The

occurrence of large-scale, nutrient-poor sites in mined regions even supports the assumption that strongly competitive alien species (= invasive species) will be less dominant than on the often more productive sites in the unmined surroundings (Huston 2004). However, this assumption has rarely been tested at landscape scale.

Contrary to the above-mentioned studies, many authors stress the high value of spontaneously developing sites in former mined land for native biodiversity in general (Hodačová & Prach 2003; Řehouňková & Prach 2008; Lundholm & Richardson 2010) and for special species groups in particular (Beneš et al. 2003; Krauss et al. 2009; Tropek et al. 2010). A high heterogeneity in terms of substrate, hydrology and geomorphology results in a wide variety of niches for establishment of plant and animal species (Řehouňková & Prach 2008; Richardson et al. 2012; Šálek 2013). Therefore, mined sites, such as in the Central German Lignite Mining District, show a high colonization rate with regard to the regional species pool (Kirmer et al. 2008). Above all, nutrient-deficient and competition-poor sites may act as refuges for rare species that are rapidly declining in modern landscapes (Lundholm & Richardson 2010; Tropek et al. 2012).

On the other hand, there is evidence that dispersal limitations can mask the potential fit between abiotic characteristics and biota from analogous habitats in the surroundings (Richardson et al. 2010; Fischer et al. 2013). If seed sources in the immediate surroundings of the mined sites are depleted and plant species have to rely on long-distance dispersal, immigration of species is mostly driven by chance (Whisenant et al. 1995; Ozinga et al. 2005; Kirmer et al. 2008). Although species tend to accumulate in mined sites over time (Kirmer et al. 2008), the colonization of species groups without adaptations to long-distance dispersal, such as calcareous dry grassland species can be seriously delayed (Jefferson & Usher 1986; Ash et al. 1994). However, surface mining in rainfall-limited landscapes with boulder clay or loess layers, such as the southern part of the Central German Lignite Mining District, creates numerous slopes with site conditions obviously suitable for the development of calcareous dry grasslands, which are considered the most diverse but seriously endangered habitat in Europe (Poschold & WallisDeVries 2002; Pullin et al. 2009). Consequently, restoration of dry grassland on suitable mined sites appears desirable to counteract, at least to some degree, the losses due to intensification or cessation of traditional management practices, as well as on-going mining activities (Novák & Prach 2010). Beside the intrinsic high conservation value of those species-rich habitats, they offer essential ecosystem services, such as erosion control and recreational options (Kirmer et al. 2012). Mined slopes near settlements, in particular, require immediate re-vegetation to prevent

erosion and dust storms, thus necessitating the active introduction of suitable plant species. To replace the common restoration practise of sowing commercial seed mixtures containing only a few cultivars and neophytic species, site-specific seed mixtures of wild plants or methods for applying green hay from natural communities in the unmined surrounding landscape have been successfully developed (e.g. Rydgren et al. 2010; Baasch et al. 2012; Kirmer et al. 2012). Baasch et al. (2012) stated that dry grassland species were not only able to establish after species transfer on mined site but also to migrate into adjacent spontaneously developing sites within 9 yrs. However, detailed information about the time frame necessary for the successful spontaneous colonization of calcareous dry grassland species into mined sites, which show suitable site conditions but are not in the vicinity of donor populations, is missing. Previous studies of grassland restoration have focused on restoration efforts in agricultural settings (e.g. Walker et al. 2004; Kiehl et al. 2006; Fagan et al. 2008; Török et al. 2010; Prach et al. 2013). Little is known about the effects of site alteration caused by mining activities on the spontaneous recovery and resilience of native calcareous grasslands on the mined sites (but see Ash et al. 1994; Novák & Prach 2003). Recent studies suggest that a gradual convergence between restored and ancient grasslands is only achievable by assisted site recovery (Vickers et al. 2012).

Based on analyses at different space and time scales, in our model region we aim at recommendations for a restoration approach that combines the advantages of spontaneous as well as assisted site recovery with species introduction.

At the landscape unit scale we address the following hypotheses: A similar proportion of neophytic plants (H1a) and a lower proportion of invasive plant species will be found in spontaneously developing mined sites than in the surrounding areas (H1b), and a similar proportion of rare (Red List) species will be found in spontaneously developed mined sites compared to the surrounding areas (H2), thus showing the high significance of restoration aimed at process conservation. Hypothesis 3 and 4 address processes at the plant community scale: compositional and functional differences expressed by species number and coverage of phytosociological and functional groups between mined sites and ancient dry grasslands are caused by dispersal limitation and stochasticity. Overcoming such barriers via human-assisted seed introduction will reduce the extent of these differences (H3). Furthermore we want to explore if hypothesis 1a can be supported with our data at the plant community scale. We hypothesize that the number and coverage of neophytic species in mined sites and ancient dry grasslands is similar (H4).

Our analyses will contribute to the contemporary discussion on realistic restoration goals and reference states for highly degraded ecosystems.

Methods

Study area

Investigations were carried out in the southern part of the Central German Lignite Mining District (51°14'36" N, 11°54'18" E), which is situated in the Central German region, with a relatively low yearly precipitation between 450–550 mm and a mean annual temperature between 8.4 and 9.9 °C. The region has a long mining tradition, resulting in the extraction of about six billion tons of lignite with ca. 15 km³ overburden until 1997 (Berkner 1998). The mined sites of the southern part mostly consist of loamy substrates (e.g. loess, boulder clay) with predominantly moderate to neutral pH values and smaller areas of inhospitable tertiary silt and sand with high lignite content and low pH. Because no topsoil was reused in the dumping process, all sites exhibited the features of primary succession (no soil development, no soil seed bank).

Plant species composition at the landscape unit scale

To study general plant species composition at the landscape unit scale (H1a, H1b and H2), we used cumulative species lists from five mined sites that developed spontaneously (see Kirmer et al. 2008) and encompassed an area of 1.0 km² to 2.6 km². These data were sampled in several research projects on spontaneous recovery beginning in 1994 (Tischew & Kirmer 2007) and were compiled in the comprehensive Post-Mining Vegetation Database Eastern Germany (Jünger et al. 2012). The current analysis encompassed species that were found between 1994 and 2002. All mined sites were mapped with a comparable level of effort, covering all vegetation types of the whole area.

Each selected mined site is located within a different grid cell of the floristic mapping in Saxony-Anhalt and Saxony (Higher Plants of Saxony-Anhalt Database, Landesamt für Umweltschutz Saxony-Anhalt Halle, working status 1998; Flora of Saxony Database, Sächsisches Landesamt für Umwelt und Geologie Dresden, working status 1999). In both federal states, floristic mappings began in 1949 and provide an inventory of all higher plant species based on grid cells with a mesh size of 5.5 km. Mapping of grid cells did not include surface mines because they were forbidden zones with limited access.

We compared the proportion of native, archaeophytic, neophytic and invasive species (for definitions see La Sorte et al. 2007; Essl et al. 2011) as well as Red List species (Red List Saxony-Anhalt and Germany) between each mined

site and its surrounding grid cell. Differences between mined sites and their surrounding grid cell were tested using the Whitney–Mann *U*-test (SPSS 19.0, IBM, Armonk, NY, USA) because of not normally distributed data.

Vegetation development at the plant community scale using the example of calcareous dry grasslands

To test hypotheses 3 and 4 we used relevés from the Post-Mining Vegetation Database Eastern Germany (Jünger et al. 2012) with estimation of percentage coverage of plant species. To ensure a good representation of all vegetation types, the plots for the relevés were randomly sampled after stratification of the mined sites into the general types (1) pioneer vegetation, (2) grasslands and (3) pioneer woodlands (see also Økland 2007). From the data set for the southern part of the Central German Lignite Mining District (915 plots with loess and boulder clay substrates), we first selected 118 plots with the potential to develop spontaneously into calcareous dry grasslands fulfilling the following requirements: (1) sites with spontaneous succession, (2) pH value ≥ 6 , (3) fewer than three species with Ellenberg indicator value for moisture ≥ 7 and species of moist vegetation types with $\leq 5\%$ coverage, (4) species characteristic for mesophile grasslands with $\leq 40\%$ cumulative coverage, (5) coverage of woody species $\leq 40\%$, and (6) plot size between 5×5 m and 10×10 m. We found no significant correlation between species richness and plot size in the selected plots of different size. Out of those 118 plots, we randomly selected nine plots for each of six age classes (0–5, 6–10, 11–20, 21–30, 31–40, >40 yrs) if more than nine plots per class were available. However, in the younger age classes (0–5, 6–10) only nine plots fulfilled the above-mentioned requirements. The used chronosequence approach proved to be a very useful tool for this study due to the length of time necessary for grassland development and the lack of studies covering this time scale (see also Bakker et al. 1996; Fagan et al. 2008).

In addition, we selected nine 5×5 -m plots within different ancient calcareous grasslands as reference sites in the area surrounding each mined site within a radius of 25 km. These represented *Bromion erecti* W. Koch 1926 communities on dry loess or boulder clay sites and were managed with low-intensity grazing regimes.

The data set for analysing the colonization success after species introduction was based on a complete block trial managed by occasional mowing in the Roßbach mined site that was implemented in early September 2000 (see Baasch et al. 2012). The substrate consisted of dumped loess with a pH (CaCl₂) of 7.5. Species introduction was accomplished by two methods: transfer of seed-rich green hay (H) and sowing of a regional seed mixture covered with seed-poor hay mulch (M). We compared percentage cover

by each species group occupying the nine ancient grassland as well as the nine plots with spontaneous succession in each age class to that of nine 5×5 -m plots with actively restored grasslands created 1, 6 and 11 yrs prior to the sampling.

In order to analyse community composition, we divided all plant species into the following phytosociological groups: (1) calcareous dry grassland species, consisting of species typically occurring in the classes Festuco-Brometea BR.-BL. & TX ex BR.-BL. 1949 and their fringe communities (Trifolio-*Geranietea sanguinei* T. MÜLLER 1962) representing our target species group; (2) dry mesophile grassland species, consisting of species related to \pm dry and less nutrient-rich sites within the class *Arrhenatherion elatioris* W. Koch 1926 and frequently found with lower coverage in calcareous dry grasslands on loess or boulder clay; (3) other herbaceous species; and (4) woody species. In addition, we distinguished functional groups (grasses, legumes and other herbs) and the origin of species (native, archaeophytic, neophytic and invasive neophytic species; see La Sorte et al. 2007). Because only neophytic species are listed on the black list of invasive species in Germany (Essl et al. 2011), we pooled native and archaeophytic species for selected analyses. For differences between species number and coverage in functional groups, phytosociological groups, and provenance groups for different site groups, we used Mann–Whitney *U*-test (SPSS 19.0) because the data were not normally distributed (Levene test ≤ 0.05). Significance levels were indicated in the following way: [***] $P \leq 0.001$, [**] $0.01 \geq P > 0.001$, [*] $0.05 \geq P > 0.01$.

To analyse the colonization probability of calcareous dry grassland species into mined sites, we studied the 54 chronosequence plots, which were dispersed across 11 different grid cells on the floristic maps. Each occurrence of the 43 calcareous grassland species successfully established in mined site plots was paired with its occurrence in the corresponding surrounding grid cell of the floristic mapping (5.5×5.5 km, mesh size = 30.25 km surrounding area) as well as their abundance in the southern part of the Central Lignite mining district (altogether 48 grid cells with a total area of 1452 km²). As other independent parameters we selected seed weight class (ranging from 1 = light to 8 = heavy seeds) and terminal velocity, mostly derived from LEDA (<http://www.leda-traitbase.org>), in the case of missing data from ENSCOBASE (<http://enscobase.maich.gr/>), or the Ecological Database of the British Isles (<http://www.ecoflora.co.uk>). Data were analysed in SPSS 19.0 using binary logistic regression with forward selection. The criterion for inclusion of variables in the forward selection was a probability of 0.05. The Wald statistic was used as a measure of the relative effect size of the variable in the full model. Nagelkerke's R^2 gives the cumulative proportion of

explained variance after entrance of the variable into the model. The regression coefficient indicates a positive or negative effect of the independent variables: occurrence and abundance in surrounding grid cells, affiliation to age classes, seed weight classes and terminal velocity.

We used global non-metric multidimensional scaling (GNMDS) to analyse successional trajectories towards ancient calcareous grasslands (reference state). GNMDS ordination was run with the Bray–Curtis distance measure comparing the similarity in species composition of sample sets and also taking into account the abundances of species. GNMDS was calculated using the ‘vegan’ package in R (R Foundation for Statistical Computing, Vienna, AT). We used 600 maximum initial configurations and 600 maximum iterations and subjected the best GNMDS solution to varimax rotation with PCA (R Development Core Team). The resulting axes were re-scaled to half-change units. In order to interpret the results and reveal gradients that are reflected by NMDS axes, we ran non-parametric correlation analyses (Spearman-Rho) to test for relationships between axes scores and the age of sites. The two-dimensional solution showed only a weak correlation of 0.35 between age of the sites and the second axis. Already the three-dimensional solution showed a clear correlation (Spearman-Rho correlation coefficient = 0.60; $P \leq 0.001$) to the second axis. Higher dimensional solutions only marginally improved the correlation. Thus, we used the three-dimensional model with a stress value of 0.17. ‘Stress’ indicates the goodness of fit, with values less than 0.2 corresponding to an acceptable indication of similarities between samples (Clarke 1993). We also calculated the value of similarity (1 minus Bray–Curtis distance) between the different sites and age groups with respect to reference sites, i.e. all plots within a certain age group were compared with all reference site plots.

Results

Plant species composition at the landscape unit scale

In comparison with the surrounding cultural landscape, colonization by vascular plants was exceptionally high in mined sites (Table 1). Although the extension of mined sites reached only 5% of the area of a grid cell, the number of species was quite similar to the surroundings. In the southern part of the Central German Mining District, the cultural landscape was dominated by arable land, and many mining site species had their next occurrences at a distance of more than 3 km. The proportion of neophytic and invasive neophytic species as well as Red List species in mined sites was quite similar to the surrounding area not disturbed by mining. Differences were only significant for archaeophytic species (Table 1).

Table 1. Average proportion of native, archaeophytic and neophytic species in five mined sites in the southern part of the Central German Lignite Mining District and their surroundings within a distance of max. 3 km. Invasive and Red List species are presented as percentage of the total species number. Significant differences (U -test) are indicated.

	Mined Sites	Surroundings	P
Total species number	259.8	311.2	
SD	19.9	35.1	
Native species (%)	79.1	72.3	0.095
SD	3.5	6.8	
Archaeophytes (%)	13.2	19.0	0.008**
SD	1.6	5.0	
Neophytes (%)	7.8	8.6	0.690
SD	2.2	2.0	
Invasive neophytes (%)	0.9	1.1	1.000
SD	0.5	0.2	
Red list species (%)	7.1	7.3	1.000
SD	1.4	2.2	

Comparing each mined site with its surroundings, we found 9.6 ± 4.7 (\pm SD) neophytes and 13.4 ± 5.9 Red List species in mined sites that were not present in the surrounding grid cell. In total, 11.0 ± 4.7 neophytes and 5.4 ± 2.3 Red List species occurred in mined site and the surrounding area, and 14.8 ± 4.4 neophytes, as well as 17.0 ± 11.6 Red List species occurred only in the surroundings. A total of 65% of the neophytic species only found in mined sites escaped from afforestations: e.g. *Elaeagnus angustifolia*, *Populus balsamifera*, *Robinia pseudoacacia*, *Populus x canadensis* and *Quercus rubra*, the last three of which are listed as invasive species.

Vegetation development at the plant community scale using the example of calcareous dry grasslands

Vegetation composition, functional and provenance groups

In comparison to reference sites, spontaneous succession plots in all age classes exhibited significantly lower average species numbers ($P \leq 0.001$) as well as a lower average coverage ($P = 0.003$) of calcareous dry grassland species (Fig. 1). Although the total number of target species in mined sites was extraordinarily high, including orchids like *Ophrys apifera*, *Gymnadenia conopsea* and *Epipactis atrorubens* (see Appendix S1), the average number was lower and stagnated in the older stages of spontaneously developing sites, indicating a very scattered colonization in the different age classes.

Target grasses in particular (e.g. *Brachypodium pinnatum*, *Bromus erectus*, *Briza media*, *Helictotrichon pubescens*, *Koeleria macrantha*) were not able to immigrate spontaneously into mined sites. When introduced via green hay or seed mixture, coverage of target grasses increased with time (Figs 1, 2). However, compared to reference sites, number and coverage of calcareous dry grassland grasses remained

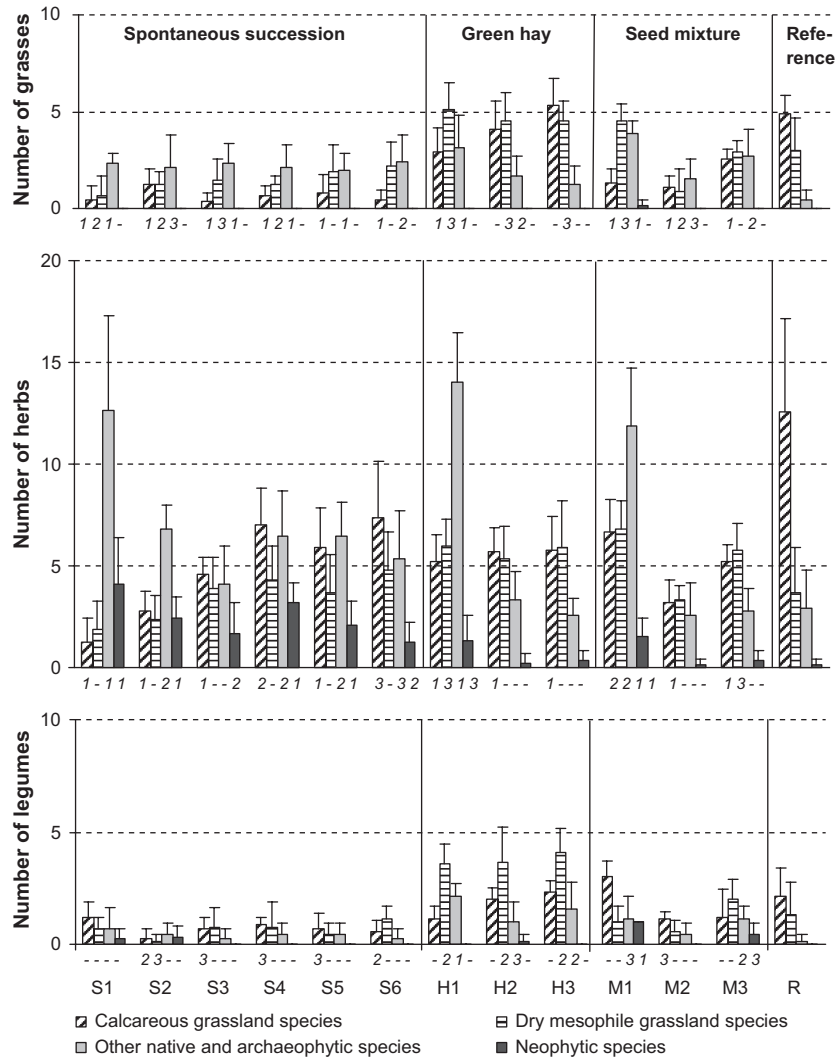


Fig. 1. Average number of species in functional groups (grasses, herbs without legumes, legumes) in different age classes of spontaneous succession and assisted site recovery in mined sites, as well as in reference sites with calcareous grasslands ($n = 9$, \pm SD). S1 = 0–5 yrs, S2 = 6–10 yrs, S3 = 11–20 yrs, S4 = 21–30 yrs, S5 = 31–40 yrs, S6 = >40 yrs, H1/M1 = 1 yr, H2/M2 = 6 yrs, H3/M3 = 11 yrs, R = >90 yrs. Significant differences to reference sites (U -test) are indicated: 1 = ***, 2 = **, 3 = *, -: not significant.

significantly lower, except on green hay plots after 11 yrs of development.

Target herbs also increased in number and coverage during succession (Figs 1, 2), but compared to reference sites, both number and coverage remained significantly lower. Plots in mined sites with and without species introduction showed similar values after 11 yrs of development.

With regard to number and coverage of target legumes, results were very heterogeneous. On species introduction plots, coverage of legumes was highest after 6 yrs, declining rapidly in the following years, and eventually reaching a level more or less similar to the reference sites. On spontaneously developing sites, the average number and

coverage of target legumes fluctuated at a very low level and in most cases, while differences from reference sites remained significant.

Typical grasses for dry mesophile grasslands (e.g. *Agrostis capillaris*, *Arrhenatherum elatius*, *Dactylis glomerata*, *Festuca rubra*, *Poa pratensis*), as well as many herbs and legumes, were successful in colonization of mined sites, increasing their average coverage to the level of the reference site in the course of succession (Fig. 2). Average and total species numbers were almost the same for older age classes of spontaneous as well as species introduction and reference sites, but species introduction sites showed the highest total number of established dry mesophile grassland species (Fig. 2, Table 2).

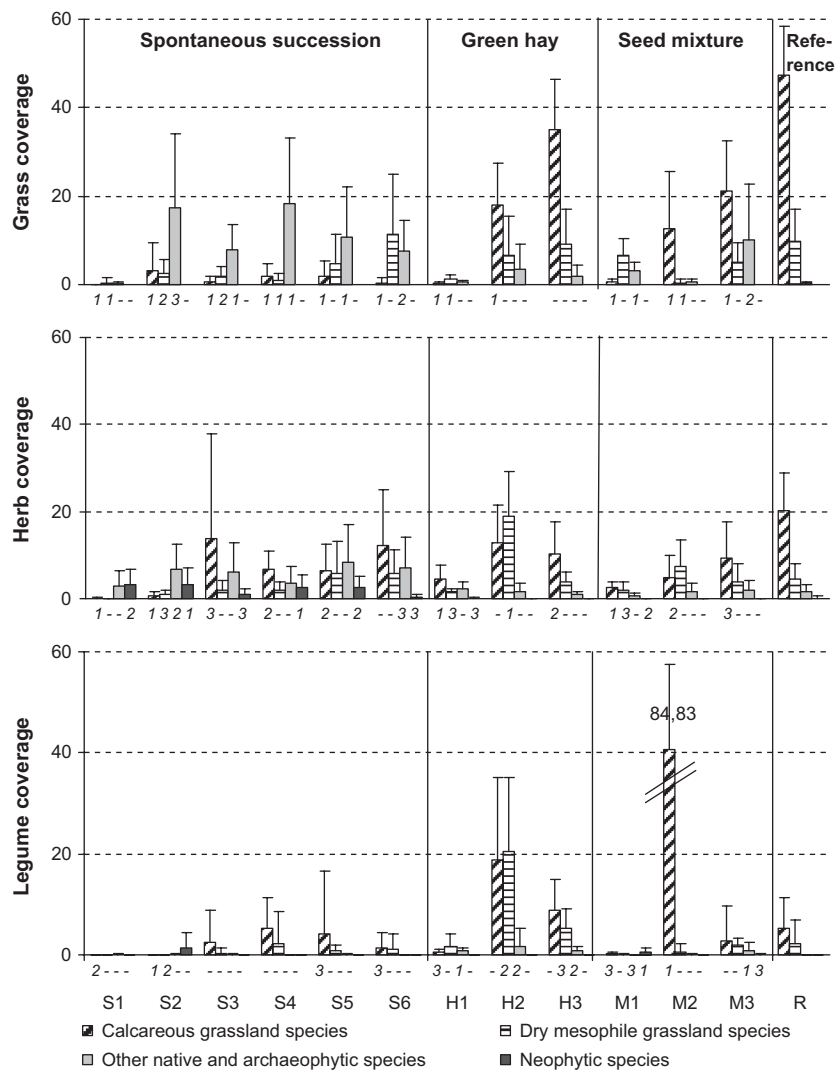


Fig. 2. Average cumulative coverage of species in functional groups (grasses, herbs without legumes, legumes) in different age classes of spontaneous succession and assisted site in mined sites, as well as in reference sites with calcareous grasslands ($n = 9$, — SD). S1 = 0–5 yrs, S2 = 6–10 yrs, S3 = 11–20 yrs, S4 = 21–30 yrs, S5 = 31–40 yrs, S6 = >40 yrs, H1/M1 = 1 yr, H2/M2 = 6 yrs, H3/M3 = 11 yrs, R = >90 yrs. Significant differences to reference sites (U -test) are indicated: 1 = ***, 2 = **, 3 = *, -: not significant.

In the early stages of succession, the total and average number of other native and archaeophytic, and to a lesser extent, neophytic species was highest (Table 2, Fig. 1), but for all groups, species numbers decreased considerably during succession. In the neophytic species group, only *Solidago canadensis* is considered as invasive. Altogether, the average coverage of neophytes was extremely low in all age classes, ranging from 1.2% to 5.0%. In the native and archaeophytic species group, we found a high variety of many common species but also some rare arable weeds (e.g. *Thymelaea passerina*, *Filago arvensis*) and other non-competitive species with low N indicator values (e.g. *Dianthus deltooides*, *Erucastrum nasturtiifolium*, *Helichrysum arenarium*). *Calamagrostis epigejos* tended to develop higher

coverage on plots with spontaneous succession compared to species introduction plots of the same age (Table 2). However, this difference was only significant for seed mixture plots ($P = 0.044$). Native woody plants continuously increased their number and coverage on spontaneously developing sites (Table 2), but differences with reference sites were not significant. Neophytic woody species remained at a very low level in all age stages and types of sites (Table 2).

Dispersal limitations and stochasticity

In the full model, four variables were significant in determining the spontaneous occurrence of species in mined

Table 2. Total number (No) and average coverage (Co) of phytosociological and provenance groups on different restoration sites in mined areas, as well as calcareous grassland reference sites in the unmined surroundings (H = green hay, M = seed mixture; after 1, 6, 11 yrs; all sites groups $n = 9$).

	Spontaneous succession mined sites							Species introduction mined sites							Reference
	0-5	6-10	11-20	21-30	31-40	>40	All sites	H1	M1	H6	M6	H11	M11	All sites	
Calcareous grassland (target) species															
No	9	12	21	21	23	29	43	15	19	23	11	23	20	37	57
Co	0.2	3.9	17.2	15.0	12.5	14.1		5.1	3.5	49.3	101.7	54.2	33.3	72.8	
Dry mesophile grassland species															
No	12	13	19	18	21	20	29	27	24	26	13	27	23	39	26
Co	0.5	3.5	6.2	5.3	11.8	19.9		4.4	8.9	46.5	8.5	18.4	11.2	18.3	
<i>Calamagrostis epigejos</i>															
Co	0.2	16.3	5.5	16.2	10.3	4.8		0	0	2.8	0.2	1.9	1.4	0	
Other Native & Archaeophytic herbaceous species															
No	46	32	23	31	30	28	82	47	43	17	16	13	15	61	18
Co	3.3	24.4	14.0	21.9	19.4	14.9		3.4	3.8	6.6	2.2	3.5	12.8	2.0	
Neophytic herbaceous species															
No	9	9	8	8	4	5	13	5	8	2	1	2	2	6	1
Co	3.1	4.6	0.8	2.6	2.6	0.4		0.1	0.7	0.02	0.01	0.04	0.1	0.1	
Native woody species															
No	5	3	3	9	13	14	22	3	2	2	1	3	2	6	11
Co	0.5	3.2	1.5	3.8	12.3	17.3		0.1	0.1	0.6	0.5	1.5	1.9	4.9	
Neophytic woody species															
No	2	1	3	3	2	3	6	0	2	0	0	0	0	2	0
Co	0.1	0.4	0.3	1.3	0.6	0.2		0	0	0	0	0	0	0	

Table 3. Results of binary logistic regression (full model) with calcareous dry grassland species occurring in spontaneously developing mined sites as dependent variable ($P =$ significance level).

Variable	Regression coefficient	Wald	df	P	Nagelkerke R^2
Occurrence in surrounding grid Cell	1.087	53.887	1	≤ 0.0005	0.071
Age class Mined sites	0.234	36.561	1	≤ 0.0005	0.120
Seed weight class	0.403	55.586	1	≤ 0.0005	0.161
Terminal Velocity	-0.923	112.205	1	≤ 0.0005	0.188
Constant	-2.582	155.922	1	≤ 0.0005	

sites (Table 3). The variable with the highest effect in the full model was occurrence in the surrounding grid cell. Both seed weight class and terminal velocity were significant dispersal traits. Age of the study sites proved also to be of significant influence. Abundance in the regional species pools of the entire mining region was not significant ($P = 0.197$).

Successional trajectories towards ancient calcareous grasslands

Global non-metric multidimensional scaling (GNMDS) revealed different patterns of vegetation development for sites with spontaneous succession compared to those

receiving species introductions (Fig. 3). NMDS ordination clearly separated sites with spontaneously developing vegetation from all sites with species introduction through axis 1, indicating parallel trajectories from distinct starting points to distinct end points. The change in species composition over time was mainly reflected in axis 2, which is significantly correlated with the age of sites (Spearman-Rho correlation coefficient = 0.60, $P \leq 0.001$). Many sites of lower age were scaled across the lower part of the NMDS plot, whereas older sites were mainly scattered in the upper part.

Similarity between sites with spontaneous succession and reference sites increased slightly with time. Despite this trend, similarity (1 minus Bray-Curtis distance) in species composition remained very low even for sites older than 40 yrs, (0.10 ± 0.07). Sites with species introduction generally reached higher similarity values to reference sites within a shorter time period. Vegetation trajectories toward a species composition similar to those of reference sites were most distinct for the development of sites restored using hay transfer (0.41 ± 0.11).

Discussion

Colonization processes at the landscape unit and plant community scale

Mined ecosystems are largely divergent in structure and function from historic ecosystems because of alterations regarding resource availability, stress intensity and changes

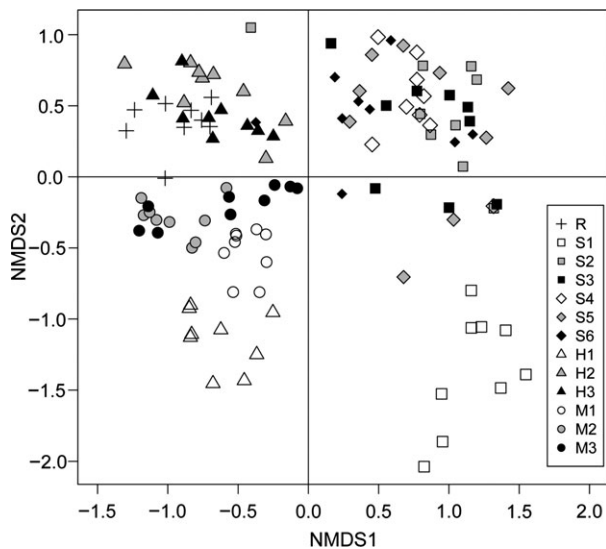


Fig. 3. Global non-metric multidimensional scaling of calcareous dry grassland plots using Bray–Curtis distance measure (3D solution, stress value = 0.17). R = reference sites >90 yrs; S = spontaneous succession sites with S1 = 0–5 yrs, S2 = 6–10 yrs, S3 = 11–20 yrs, S4 = 21–30 yrs, S5 = 31–40 yrs, S6 = >40 yrs; H = green hay sites with H1 = 1 yr, H2 = 6 yrs, H3 = 11 yrs; M = seed mixture sites with M1 = 1 yr, M2 = 6 yrs, M3 = 11 yrs.

in the spatial arrangement of ecosystem components (Kozlov & Zvereva 2007). Our study sites in surface-mined land represent, in many ways, the kind of highly altered ecosystem described by Hobbs et al. (2006) as ‘novel ecosystems’, but for the fact that these areas are not predominantly governed by neophytes. Although the disturbance history of mined sites is supposed to support neophytic species in natural succession (Ross et al. 2004; Fields-Johnson et al. 2012), we found a similar proportion of neophytes in spontaneously developing mined sites compared to the unmined surroundings (see also Řehouňková & Prach 2008 for sand pits in the Czech Republic). This finding confirms H1a. However, results are not in line with several studies from North American or Australian mining regions (Norman et al. 2006; Bowles 2011; Hoelzle et al. 2012), and can be related either to a generally lower abundance of neophytes in the surrounding areas and/or a better long-distance dispersal potential of native species, as well as to a less extensive introduction of neophytic species via active restoration measures in the Central German Lignite Mining District.

In addition, in North American and Australian mining regions, topsoil transfer approaches are often implemented, which may lead to more nutrient-rich sites favoured by many invasive neophytic species (Huston 2004). However, we have to note that we also observed an on-going invasion of a few strongly competitive neo-

phytes commonly used in technical mine rehabilitation from the 1970s through the 1990s (e.g. *Elaeagnus angustifolia*, *Robinia pseudoacacia*) from nearby plantings into two of the spontaneously developing sites. Therefore, we have to reject H1b because we did not find a (significant) lower proportion of invasive neophytes in the spontaneously developing sites compared to the unmined surroundings. But overall, the proportion of invasive neophytes in both site groups was surprisingly low (0.9% and 1.1%). Lockwood et al. (2005) and Pyšek et al. (2009) found that the number of species introduced, and in particular their propagule pressure, appear to be the most important determinants of the number of established neophytic species in any given region. Therefore, a future invasion of a limited number of strongly competitive neophytes into the spontaneously developing sites cannot be excluded (see also Řehouňková & Prach 2008). Many studies showed that former restoration approaches favoured active seeding and planting of fast-growing neophytic species, which impedes natural succession due to increased propagule pressure and aggressive growth characteristics (Holl 2002; Grant 2006; Zipper et al. 2011). Other approaches, such as fertilization, also increase neophytic species richness and coverage compared to unfertilized sites (Norman et al. 2006). Technical reclamation approaches including surface grading, which destroys small- and large-scale substrate heterogeneity, and planting of mono-specific forest stands have proven to be highly unsuitable for enhancing native biodiversity (Hodačová & Prach 2003; Norman et al. 2006; Mudrak et al. 2010; Angel et al. 2012; Tropek et al. 2012). In contrast, on spontaneously developing sites we found an impressive number of native and even rare species adapted to these nutrient-poor and/or highly dynamic sites (Ash et al. 1994; Kirmer et al. 2008; Tomlinson et al. 2008; Tropek et al. 2010), confirming our second hypothesis. We therefore agree with Lundholm & Richardson (2010) and Fischer et al. (2013) that habitats strongly influenced by on-going or historical human activities can be ecologically analogous to natural habitats supporting native biodiversity. In particular, the low soil fertility of mining substrates supports stress-tolerant but poorly competitive species, which are usually rare in the surroundings and thus of high nature conservation value (Marrs 1993).

Lastly, comparing mined sites and unmined surroundings, we found an unexpected and significantly higher number of archaeophytes in the latter, highlighting their divergence in landscape history due to the prolonged agricultural land use in the surroundings (La Sorte et al. 2007).

At the plant community level, the lack of immigrating target species, especially grasses typical for calcareous dry

grasslands, impedes successional trajectories towards ancient calcareous grasslands. This leads to distinct divergence regarding species and functional composition, thus supporting our third hypotheses. However, the total number of 43 target species that spontaneously colonized the mined sites indicates the high potential of those large-scale, nutrient-poor sites for the development of otherwise declining calcareous grasslands (see also Novák & Prach 2003). The relatively low frequency of most target species indicates that long-distance dispersal events are not regular (del Moral et al. 2005; Kirmer et al. 2008), and species saturation at the community level will take longer time periods, as has been shown for other sites where calcareous grasslands were restored (Ash et al. 1994; Fagan et al. 2008). The probability of establishment on restoration sites increases with a higher abundance in the nearby surroundings, indicating the importance of high propagule pressure in a landscape context (Hubbell 2001; Novák & Prach 2003; Walker et al. 2004; Alday et al. 2011). Although less important than the 'recruitment lottery' driven by species abundance in the surrounding landscape (Kirmer et al. 2008), specific traits of the propagules including seed weight and terminal velocity also proved significant to the success of long-distance dispersal events (Nathan et al. 2002; Tackenberg et al. 2003; Kirmer et al. 2008).

Supporting hypothesis 3, the spontaneously developing sites show a higher number and coverage of native species, not typical for grasslands (mostly ruderals) over a long period of time, indicating the novelty of the species assemblies on anthropogenically altered sites (Fischer et al. 2013). However, the decreasing number and remarkable low coverage of neophytic species, including the only occurring invasive species *Solidago canadensis*, shows that those sites do not support the development of neophytes, thus confirming hypothesis 4 (Richardson et al. 2010; Holl & Aide 2011). This is also true for the species introduction sites.

The spontaneously developing sites show an increase of the commonly distributed native grass *Calamagrostis epigejos*, which is able to develop dense swards, arresting succession for longer periods (Prach 2003; Mudrak et al. 2010). However, on dry and nutrient-poor mined sites its competitive power is less pronounced (Baasch et al. 2010), and further immigration processes of additional calcareous herbs are hampered, but not restricted. *C. epigejos* partly replaces the functionally similar target grasses, and once successfully established, it could hamper successful establishment of target grasses because of similar resource requirements and resource-use patterns (Petermann et al. 2010). Otherwise, active introduction of target grasses at the onset of succession leads to dry grassland communities highly resistant to *C. epigejos* (Baasch et al. 2012), i.e. manipulation of plant community composition can help in

reducing the establishment potential of invading species, enhancing resilience within the developing ecosystems (Walker & del Moral 2009; Young et al. 2009; Prach et al. 2013). This also indicates the importance of colonization and establishment history (e.g. Chase 2003). Confirming hypothesis 3, compared to spontaneously developing sites, species introduction sites show a generally more rapid trajectory towards a similar species and functional composition as that found on reference sites. This particularly applies to the hay transfer sites, as species and functional composition was more balanced in the hay than in the artificially composed seed mixture, where the share of legumes was obviously too high.

Because the establishment window for grassland communities within the successional series is limited to a maximum of 60 yrs before woody plants dominate the mined sites (Tischew & Lorenz 2005; Tischew & Kirmer 2007), it is unlikely that the reference state will be reached without managing the sites through grazing or mowing. Meanwhile, in one of our sites (Kayna-Süd) a low-intensity, year-round grazing regime with wild horses and Heck cattle has promisingly controlled woody plant development and *Calamagrostis epigejos* spread in test plots (unpubl. data). The implementation of a low-intensity grazing regime is highly recommended because grazing is also presumed to support zoochorous diaspore transfer from adjacent grasslands (Poschlod et al. 1998) or between grassland patches within large-scale surface-mined land.

The slow initial vegetation development and the lack of typical target grasses can lead to severe erosional processes, particularly if appropriate seed sources are missing in the immediate surroundings, as in our spontaneously developing plots. In contrast, both species introduction methods provide effective immediate as well as long-term erosion control as an important ecosystem service of dry grasslands on slopes (Baasch et al. 2012). Therefore, a combination of species introduction methods and spontaneous succession is recommended. A faster and denser vegetation development may also support future land-use options, such as grazing with robust animal breeds. The presence of typical dry grassland species such as *Bromus erectus* increases the nutritional value compared to *C. epigejos*-dominated grasslands (Briemle et al. 2002). On the other hand, if supporting native biodiversity is a priority goal, dispersal stochasticity leads to a higher γ -diversity. In addition, more open, spontaneously developing grasslands support many competition-poor grassland species such as orchids, which were not yet observed on species introduction sites, and rare ruderal species frequently found on younger successional sites. The latter indicates the conservation value of early successional stages (Troppek et al. 2012), which will be shortened by transferring later successional species.

Realistic goals for restoration practice and use of reference states

The current discussion regarding the new EU Strategy on restoring green infrastructure offers an opportunity to implement ecological restoration principles in environmental politics. However, discussions of realistic goals for restoration practice and the use of reference states are contradictory (e.g. Hobbs & Norton 1996; Grant 2006; Prach & Hobbs 2008; Tropek et al. 2010, 2012; Holl & Aide 2011). Based on our experiences in restoration research and practice, we recommend high-quality restoration aiming at integration of mined sites into the landscape matrix, and thereby promoting connectivity with the surroundings. In justifying the often incompletely recognized potentials of mined sites, alternative reference states should be acknowledged (e.g. found in older successional stages), and realistic targets must be formulated. They should include a high diversity at the landscape unit scale by intentional utilization of topography and substrate heterogeneity caused by mining activities. Nutrient-poor and dynamic ecosystems should be accepted, because they favour a high diversity of site-adapted native plants and animals typical for the respective successional stage, including rare species.

The key decision of whether to rely on spontaneous succession or not depends on (1) the propagule pressure of invasive neophytic as well as site-adapted native species, which is related to the surrounding landscape matrix and history; (2) site conditions appropriate for plant establishment due to non-toxic conditions; (3) the need for erosion control; and/or (4) the necessity for rapid or immediate compensation for lost habitats and the public demand for fast development of recreational possibilities. In any case, establishment of native plants and animals using modern restoration approaches is a realistic goal, as is acceptance of novel assemblies and community structures. Nonetheless, natural ecosystems in the surroundings are valuable reference systems to evaluate general successional trajectories, particularly if analogous ecosystem features emerge.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Frequency of species within studied age classes and reference sites ($n = 9$).