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Spontaneous succession in limestone quarries as an effective restoration tool for endangered arthropods and plants

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Summary

1. The view of post-mining sites is rapidly changing among ecologists and conservationists, as sensitive restoration using spontaneous succession may turn such sites into biodiversity refuges in human-exploited regions. However, technical reclamation, consisting of covering the sites by topsoil, sowing fast-growing herb mixtures and planting trees, is still commonly adopted. Until now, no multi-taxa study has compared technically reclaimed sites and sites left with spontaneous succession.

2. We sampled communities of vascular plants and 10 arthropod groups in technically reclaimed and spontaneously restored plots in limestone quarries in the Bohemian Karst, Czech Republic. For comparison, we used paired *t*-tests and multivariate methods, emphasizing red-list status and habitat specialization of individual species.

3. We recorded 692 species of target taxa, with a high proportion of red-listed (10%) and xeric specialist (14%) species, corroborating the great conservation potential of the quarries.

4. Spontaneously restored post-mining sites did not differ in species richness from the technical reclaimed sites but they supported more rare species. The microhabitat cover of leaf litter, herbs and moss, were all directly influenced by the addition of topsoil during reclamation.

5. *Synthesis and applications*. Our results show that the high conservation potential of limestone quarries could be realized by allowing succession to progress spontaneously with minimal intervention. Given the threat to semi-natural sparsely vegetated habitats in many regions, active restoration measures at post-mining sites should be limited to maintenance of early successional stages, instead of acceleration of succession.

Key-words: artificial biotopes, biodiversity conservation, landscape restoration, life-history traits, manipulation of succession, post-industrial habitats, post-mining sites

Introduction

Post-mining sites such as quarries, spoil dumps or mining pits exist as an unavoidable consequence of mineral extraction for industry, and therefore represent an increasing component of many landscapes and regions. The traditionally negative view of such sites among ecologists is rapidly changing, as it is becoming clear that in industrialized and intensively farmed regions, they offer valuable refuges for rare organisms. The conservation potential of quarry sites has been documented for vascular plants (Wheater & Cullen 1997), butterflies (Benes, Kepka & Konvicka 2003), spiders (Tropek & Konvicka 2008) and wild bees (Krauss, Alfert & Steffan-Dewenter 2009). Quarries typically contain periodically disturbed, early

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successional and highly heterogeneous surfaces, with extreme abiotic conditions and minimum productivity (Schulz & Wiegleb 2000; Novak & Prach 2003). Similar conditions have become rare in modern landscapes, because humans increase the productivity of land, promoting middle phases of succession over extremes, so that in many regions those species dependent on early successional, sparsely vegetated habitats are among the most threatened (Thomas, Morris & Hambler 1994; Hoekstra *et al.* 2005; Wenzel *et al.* 2006). Given that quarrying and open-cast mining will remain an important economic activity, restoration should maximize the biodiversity potential of extraction sites, especially in densely populated regions where such sites represent the last localities that have escaped intensive farming, forestry or building development, apart from scattered nature reserves (Pysek *et al.* 2001; Young, Petersen & Clary 2005).

The post-mining restoration method crucially affects the ability of different species to colonize the area, and hence the conservation potential of restored habitats (Ursic, Kenkel & Larson 1997; Prach & Pysek 2001; Hodacova & Prach 2003). In Central Europe, two alternative approaches are used: (1) *technical reclamation*, typically consisting of covering the sites with fertile topsoil then sowing with grass and herb mixtures and/or planting shrubs and trees; and (2) *spontaneous succession*, typically no direct sowing or planting but some suppression of alien and expansive plants (Tischew & Kirmer 2007; Prach & Hobbs 2008). Although the latter method appears more straightforward (Hodacova & Prach 2003; Holec & Frouz 2005), the former method remains preferred because of the perceived need to heal 'scars in the landscape', and to prevent erosion and fertilizer run-off, thus promising benefits for agriculture, forestry or similar activities (Stys & Branis 1999).

Until now, there has been no comprehensive comparison of the effects of the two restoration methods on the conservation potential of the sites. Single-taxon studies exist (vascular plants: Hodacova & Prach 2003; ants: Holec & Frouz 2005) that favour spontaneous succession. These conclusions, however, are open to the critique that different taxa respond to ecosystem manipulation differently and therefore a multi-taxa approach is needed (Niemela & Baur 1998; Ruiz-Jaen & Aide 2005; Tropek, Spitzer & Konvicka 2008). The two previous studies have been restricted to lignite mining sites, whereas other post-mining structures have been neglected (Hobbs 2007). Limestone quarries are thought to be particularly important for restoration, because the base-rich bedrock allows the development of species-rich natural communities, such as calcareous grasslands, which are among the richest and most continentally endangered habitats in Europe (e.g. Jefferson 1984; Poschlod & Wallis DeVries 2002).

In this study, we compare the effects of technical reclamation and spontaneous succession on the communities of vascular plants and 10 arthropod taxa in mined-out limestone quarries. We analysed each group separately, using both univariate and multivariate approaches. The diverse life strategies of the eleven taxa allowed the two restoration methods to be compared and the factors affecting the community composition of the surveyed taxa to be assessed.

Materials and methods

STUDY AREA

The study was carried out in the Bohemian Karst Protected Landscape Area, on the outskirts of Prague, Czech Republic (Fig. S1, Supporting information). It is a hilly (208–499 m a.s.l.) karstic region covered by a mosaic of deciduous forests, grasslands at abandoned pastures, arable fields and human settlements. The climate is mildly warm and relatively dry (mean annual temperatures: 8–9 °C, annual precipitation: 480–530 mm). Resulting from its long history of limestone excavation, the area harbours over 100 quarries, mostly abandoned, with several large quarries still in operation (Brunnerova 1974; Lozek, Kubikova & Sprynar 2005).

The main threats to the area include the decline of traditional land use followed by either abandonment or agricultural intensification, causing the flora and fauna of calcareous grasslands to become increasingly rare (Lozek *et al.* 2005). Quarrying itself is not viewed as a major problem, as most of the active quarries are situated on the outskirts of the area. Quarries abandoned in the past were usually left to spontaneous succession, resulting in xeric grasslands and scrubs. At present, there is substantial pressure to restore the quarried landscape using technical reclamation techniques (Lozek *et al.* 2005).

TAXONOMIC GROUPS AND SPECIES CATEGORIZATION

We targeted vascular plants, and 10 arthropod taxa: orthopteroids (Orthoptera, Dermaptera and Blattodea), true bugs (Heteroptera), leafhoppers (Auchenorrhyncha), day-active butterflies and moths (Lepidoptera), spiders (Araneae), ground beetles (Coleoptera: Carabidae), centipedes (Chilopoda), millipedes (Diplopoda), woodlice (Isopoda: Oniscidea) and harvestmen (Opiliones). The arthropods cover diverse feeding modes (mostly herbivores – orthopteroids, true bugs, leafhoppers, butterflies and moths; mostly carnivores – spiders, ground beetles and centipedes; mostly omnivores and detritivores – millipedes, woodlice and harvestmen) and mobility guilds (non-fliers – centipedes, millipedes, woodlice and harvestmen; occasional fliers – orthopteroids, true bugs, leafhoppers, spiders and ground beetles; regular fliers – butterflies and moths).

Besides *species richness*, we analysed the *conservation value* of the communities, based on Czech Republic red-lists (plants: Prochazka 2001; arthropods: Farkac, Kral & Skorpik 2005) with categories *EX* (extinct in the Czech Republic); *CR* (critically endangered); *EN* (endangered); *VU* (vulnerable); *NT* (near threatened); and *LI* (low interest, not threatened). We also classified all species according to their specialization on xeric habitats (herein *xeric specialization*): *ST* (restricted to well-preserved xeric grasslands), *XE* (common xerotermophilous species) and *GE* (widespread generalists and species of non-xeric habitats).

See Table S1 (Supporting information) for nomenclature, species habitat use and species identification references, voucher material storage, and a list of all recorded species with their category memberships.

DATA COLLECTION

We established ten plots (0·2–0·3 ha; Fig. S1 and Table S2, Supporting information), forming five pairs each with one plot technically reclaimed and one left to spontaneous succession. The pairs were situated in the same large quarry (pairs 1, 4 and 5), or in two quarries in close proximity (pairs 2 and 3), and were of comparable age since the termination of quarrying. The maximum distances between plots within each pair were 150 and 100 m (pairs 3 and 5 respectively), the other plots within each pair were contiguous. The relief was always flat (bottoms, wide terraces).

Each plot was characterized by: (i) the relative proportion of the main habitats within a 100 m radius circle around the plot (xeric *grassland*, *ruderal*, *shrubs*, *deciduous* trees, *conifers*; *scree* and *rocks* including quarry walls); (ii) the distance from the nearest seminatural xeric grassland (from Czech habitat mapping; AOPK CR 2008).

In the centre of each plot, a line of five 3 × 3 m quadrats was established, with 2 m between adjoining quadrats. Each quadrat was characterized by the per cent cover of vegetation layers (*E0*: moss; *E1*: herbs; *E2*: shrubs; *E3*: trees), plant *litter* and *bare* substrate.

In each quadrat, the percentage cover (an ordinal scale 1: < 0·01%, 2: < 1%, 3: < 5%, 4: < 10%, 5: < 25%, 6: < 50% and 7: < 100%) of all species of vascular plants was estimated in July 2007. Paired plots were always sampled on the same day.

In the centre of each quadrat, a pitfall trap (diameter 9 cm, depth 15 cm, containing 5% formaldehyde) was exposed from May to August 2007, and emptied four times during the study period (21 May, 4 June, 22 July and 20 August). On the same days, the entire vegetation within the quadrat was swept using a 40 cm diameter net, the catch was killed and preserved in 70% ethanol. The pitfall and sweeping material was sorted to target taxa and identified to species.

Butterflies and moths were recorded on two linear transects (50 m/5 min) per plot, crossing together at right angles in the plots' centre. Each transect was walked five times (3–4 May, 20–21 May, 16–17 July, 2–3 August and 14–15 August). Paired plots were visited consecutively, sequences of the pairs and the plots within the pairs were randomized. *Cloudiness*, *wind* and actual nectar plants abundance (*nectar-abundance*) were recorded on ranked (1–3) scales, and the species of actually flowering plants (*nectar-richness*) were counted.

In all analyses, a *sample* refers to a list of all species with their relative covers for vascular plants (i.e. five samples for each plot), a transect count for butterflies and moths (i.e. two samples for each plot and visit), and a combined pitfall-trapped and swept material for other arthropods (i.e. forming five pairs each with one plot).

UNIVARIATE ANALYSES

To compare *species richness*, *conservation value* and *xeric specialization* between the two restoration methods (*METHOD*: reclamation vs. succession), we used, separately for each of the studied taxa, paired *t*-tests with all samples of each plot pooled. The computing was carried out in Statistica 8.0 (Statsoft, Inc., Tulsa, Ok, USA).

For *species richness*, the response variables were ln-transformed numbers of species per plot. For *conservation value* and *xeric specialization*, we weighted the numbers of records of individual species in a sample by the ranked values denoting constituent species red-list status (*EX* – 5; *CR* – 4; *EN* – 3; *VU* – 2; *NT* – 1; *LI* – 0) and xeric specialization (*ST* – 2; *XE* – 1; *GE* – 0). The resulting per-sample values were again ln-transformed. Four taxa (centipedes, millipedes, woodlice and harvestmen) contained no or few red-listed or xeric specialist species and therefore were excluded from the *conservation value* and *xeric specialization* analyses.

ORDINATIONS

All ordinations were computed in Canoco for Windows 4.5 (ter Braak & Smilauer 2002). To visualize major trends in species composition of differently restored plots, we used an indirect technique, detrended correspondence analysis (DCA), with species data summed across all visits, except for butterflies and moths recorded using a different sampling design.

To investigate how restoration *METHOD* influenced the sampled environments, we used the redundancy analysis (RDA), a linear constrained ordination, with *METHOD* (reclamation vs. succession) as a categorical predictor of *microhabitat structures* (within the 3 × 3 m quadrats – *E0*, *E1*, *E2*, *E3*, *litter*, *bare*); *surrounding habitats* (within the 100 m circle – *grassland*, *ruderal*, *shrubs*, *deciduous*, *conifers*, *scree* and *rocks*); and *distance* from the nearest xeric grassland (*distSt*). The Monte-Carlo permutation tests (999 runs, full model) reflected the sampling design: the quadrats were permuted as linear transects, the pairs of plots as blocks.

The canonical correspondence analysis (CCA) was used to test the effects of restoration *METHOD* on the species compositions of samples. We used square-root transformation and downweighting of rare species options. For all taxa except vascular plants and butterflies and moths, the Monte-Carlo permutation test (999 runs, full model) design reflected both the spatial and temporal arrangements of the samples: quadrats were permuted as line transects, visits as time series, plot pairs as blocks. Because such permutation design does not allow for empty cells, we added a fictional species with abundance = 1 to each cell (cf. Leps & Smilauer 2003).

For vascular plants, only the lines of quadrats and pairs of plots formed the permutation design. For butterflies and moths, the two intersecting transects were permuted as freely exchangeable within each plot visit. Butterfly and moths also probably responded to conditions during the transect walks. We first used the Canoco forward selection procedure to select a minimum covariate CCA model (all variables influencing the ordination at $P < 0{\cdot}05$ level) based on *cloudiness*, *wind*, *nectar-abundance*, *nectar-richness*, and their interactions. The resulting covariate combination (∼*cloudiness* + *nectar-richness* + *nectar-richness* × *nectar-abundances*) was used in all subsequent butterflies and moths models.

A final set of analyses assessed the separate effects of *microhabitat structures*; *surrounding habitats* and the distance *distSt* on the species composition of samples. Under the permutation models outlined above, we used Canoco forward selection to find adequate sets of predictors (all with $P < 0{\cdot}05$), and then tested the significance of whole models. Effects of thus selected predictors on rare species were evaluated visually from ordination diagrams.

Results

We recorded 153 species of vascular plants, 2917 individuals/28 species of orthopteroids, 2347/94 true bugs, 1820/88 leafhoppers, 1290/71 butterflies and moths, 4161/136 spiders, 3182/85 ground beetles, 27/7 centipedes, 3179/13 millipedes, 4624/9 woodlice and 279/8 harvestmen. Out of the 692 species of targeted taxa, 69 (∼10% of the total) are included to the national red-lists (20 NT, 31 VU, 15 EN, 2 CR, 1 EX) and 96 species are considered well-preserved grasslands or forest steppe specialists (Table S1, Supporting information).

SPECIES RICHNESS AND CONSERVATION CONCERN

For *species richness* (Fig. 1a), spontaneous succession plots hosted more species of butterflies and moths only; all the other taxa showed no differences. For *conservation value* (Fig. 1b), spontaneous succession was preferred by five taxa (vascular plants, orthopteroids, true bugs, butterflies and moths, and

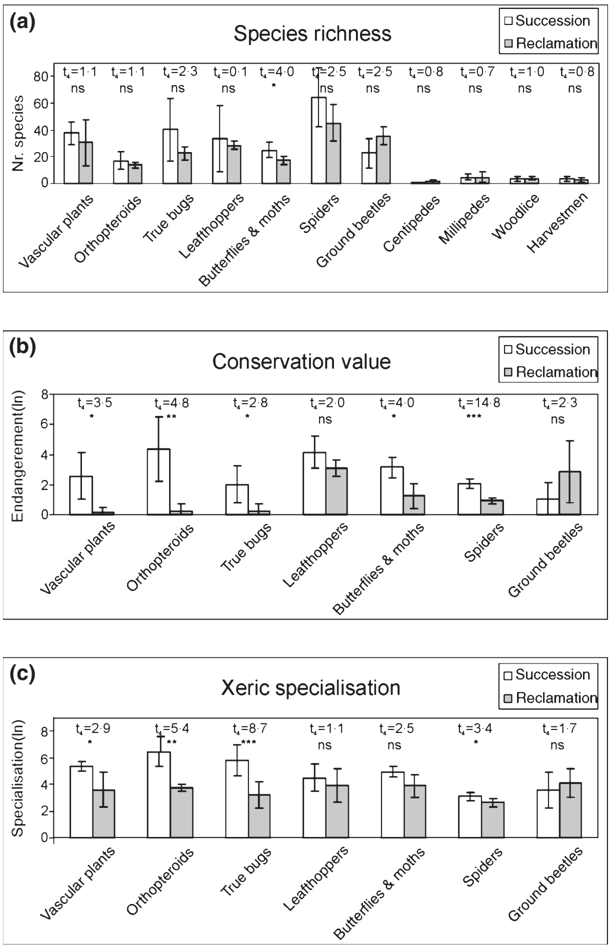

Fig. 1. Results of paired *t*-tests comparing differently restored quarried plots. (a) *species richness* (number of species per plot); (b) *conservation value* (individuals in plot weighted by their red-list status); and (c) *xeric specialization* (individuals in plot weighted by their habitat requirements). Ln-transformed means per plot with associated 0·95 confidence intervals are shown in (b) and (c). *t*- and *P*-values (**P* < 0·05; ***P* < 0·01; ****P* < 0·001) refer to separate effect of *METHOD* in individual analyses.

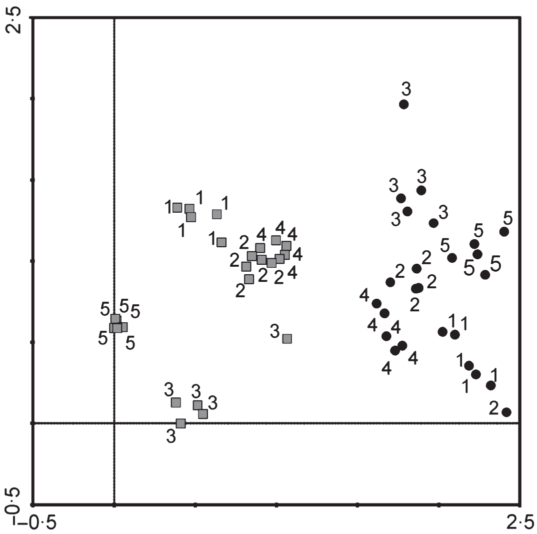

Fig. 2. Indirect ordination diagram (detrended correspondence analysis) of individual samples within the quarries according to restoration *METHOD*: grey squares – spontaneous succession, black circles – technical reclamation. The numbers denote samples from identical pair of plots (see Table S2, Supporting information). First axis eigenvalue = 0·384, 11·9%; second axis eigenvalue = 0·193, 6%.

spiders); the remaining two taxa did not differ by restoration method (leafhoppers, ground beetles). For *xeric specialization* (Fig. 1c), spontaneous succession hosted more specialized communities of four taxa (vascular plants, orthopteroids, true bugs, butterflies and moths, and spiders); the remaining three taxa showed no differences (leafhoppers, butterflies and moths, and ground beetles). Therefore, none of the analyses revealed a negative impact of spontaneous succession comparing with technical reclamation on *species richness*, *conservation value* or *xeric specialization*.

SPECIES COMPOSITION

The DCA revealed a major difference between communities of the reclamation and succession plots (Fig. 2). Despite the paired design, plots restored by the two methods formed two clearly separated clusters along the first ordination axis (eigenvalue = 0·384, 11·9%; second axis eigenvalue = 0·193, 6%), revealing the restoration *METHOD* as the major factor structuring the biotic communities.

The RDA analysis (1st axis eigenvalue: 0·013, 30·3%, F = 19·160, P = 0·001; Fig. 3) showed that technically reclaimed plots contained a high cover of *E1* (herbs) and *litter*, and tended to have *ruderal* in proximity. Spontaneous succession plots contained more *bare* substrate, while *grassland*, *scree* and *rocks* prevailed in proximity. The plots did not differ in *distSt*.

The CCA analyses revealed that restoration *METHOD* imposed significant effects on community compositions in all taxa but harvestmen (Table 1). Among the taxa with significant responses, rare species (red-listed and xeric specialists combined) preferred spontaneous succession to technical reclamation; the only exception was ground beetles (Fig. 4).

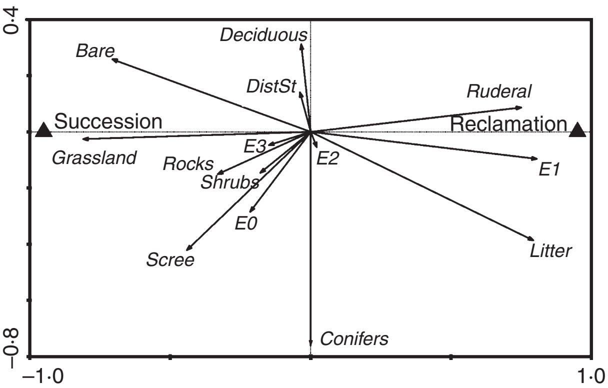

Fig. 3. Redundancy analysis diagram (RDA) revealing the *microhabitat structures* and *surroundings habitats* responsible for differences between plots restored via spontaneous succession and technical reclamation. First axis eigenvalue: 0·013, 30·3%, F = 19·160, P = 0·001.

Table 1. Results of the canonical correspondence analyses (CCA) of the impact of restoration *METHOD* on the community composition of studied taxa

	1st Axis F, P^1	1st Axis eigenvalue	Explained variation^2 (%)
Vascular plants	6·7***	0·52	13·2
Orthopteroids	21·5***	0·22	10·0
True bugs	9·6***	0·18	4·7
Leafhoppers	7·8***	0·16	3·9
Butterflies and moths	2·2***	0·06	2·4
Spiders	11·0***	0·23	5·4
Ground beetles	6·2***	0·10	3·1
Centipedes	4·7*	0·01	2·4
Millipedes	17·5***	0·05	8·3
Woodlice	7·2***	0·02	3·6
Harvestmen	1·3	–	–

^{1}P-values: *P < 0·05; **P < 0·01; ***P < 0·001.
^{2}The variation in species data explained by the first ordination axes.

Table S1 (Supporting information) presents individual species responses as 1st axis scores.

Cover of *litter* was the most frequently selected *microhabitat structure* (Table 2). It displayed negative effects on rare species in vascular plants, orthopteroids, true bugs, leafhoppers, spiders and ground beetles; and a positive effect on ground-dwelling detritivores (millipedes and woodlice). Other important factors were moss (*E0*) cover, affecting rare species of true bugs, leafhoppers and ground beetles positively, and vascular plants negatively. Herb layer (*E1*) negatively affected rare leafhoppers, spiders and ground beetles.

The crucial *surrounding habitats* (Table 2) were *grassland* (all taxa except leafhoppers and woodlice) and *ruderal* (all except ground beetles, centipedes and woodlice). Increasing *grassland* representation had generally positive effects on rare species (except for centipedes and harvestmen), whereas that of *ruderal* had mainly negative effects (all taxa but ground beetles, centipedes and woodlice). The distance from the nearest semi-natural xeric grassland had significant effect on communities of all taxa, but mostly no effect on rare species.

Discussion and conclusions

The high conservation potential of limestone quarries is illustrated by a high proportion of red-listed species (10%) and xeric specialists (14%) in our samples. We showed that this potential depends on the restoration method used. Although the quarried sites restored via technical reclamation and spontaneous succession did not differ in species richness in most of the studied taxa, spontaneously restored sites surpassed the technically reclaimed ones in the representation of threatened species and xeric habitats specialists. These differences were corroborated by ordination analyses, which revealed the restoration method as a major factor structuring biotic communities of the quarried sites, and documented the preference of rare species for spontaneous succession. In situations when species richness does not differ between sites or treatments, rarity or decline represents the only objective criteria for conservation prioritization (Thomas *et al.* 1994). The colonization of spontaneously developed habitats within the quarries by high numbers of threatened and habitat-specialized species indicates that spontaneous succession is an effective tool for biodiversity conservation. These patterns were consistent in vascular plants and many arthropod taxa, with a few exceptions such as in case of leafhoppers or ground beetles. In none of the studied taxa, however, did rare species exhibit an affinity to technical reclamation.

Contrary to the spontaneously restored sites, the technically reclaimed ones contained less bare ground and more continuous vegetation cover, with accumulation of litter. The vegetation development is slower under spontaneous succession than under reclamation, as succession involves 'successionally blocked' habitats of open rocks, sparse grasslands and scrub. Spontaneous processes can restore these habitats for plants (as shown earlier by Wheater & Cullen 1997; Schulz & Wiegleb 2000) and for numerous arthropods from detritivores to predators, and from good to poor dispersers.

Technical reclamation invariably involves inputs of topsoil, which diminishes microtopographic heterogeneity and imports nutrients and plant diaspores. These conditions favour first, fast-growing ruderal vegetation from buried seeds, and ultimately the establishment of competitive species (*sensu* Grime 1977). The sown plant mixtures also contain well-establishing competitive species. The resulting vegetation prevents colonization of the sites by more sensitive plants from the surrounding environments, disfavouring stress-tolerant, slowly growing species, including rare xerotermophilous specialists (Prach, Pysek & Smilauer 1999; Chytry, Tichy & Rolecek 2003).

Increasing vegetation diversity is expected to increase the diversity of herbivores (i.e. orthopteroids, true bugs, leafhoppers, and butterflies and moths) (Huston 1979), but the link is more likely to be mediated through microhabitat heterogeneity (Haddad *et al.* 2001; Hawkins & Porter 2003), which is much higher at spontaneous succession sites. The succession begins at rugged bare rocks with boulders, holes, crevices, etc., and proceeds patchily, as colonizing plants establish themselves and modify their own environments. In addition, endangered herbivores often depend on rare stress-tolerant plants (Nickel & Hildebrandt 2003; Dennis *et al.* 2004).

Even soil-dwelling groups (millipedes, woodlice and centipedes), poorly adapted to xeric environments because of lack of water-saving mechanisms (Lewis 1981; Hopkin & Read 1992; Warburg 1993), did not differ between succession and reclamation plots. The single red-listed and the few xerophilous species preferred spontaneous succession (Fig. 4).

Among predators, the results for spiders are attributable to the high numbers of endangered xerothermophilous species in Central Europe (Niemela & Baur 1998; Rezac, Rezacova & Pekar 2007). Many spiders depend on richly structured environments, with rocks, crevices and open ground for ground-dwellers, or vegetation with diverse three-dimensional architecture for plant-dwellers and web-builders (Marshall 1997; Rezac *et al.* 2007; Tropek & Konvicka 2008). Technical

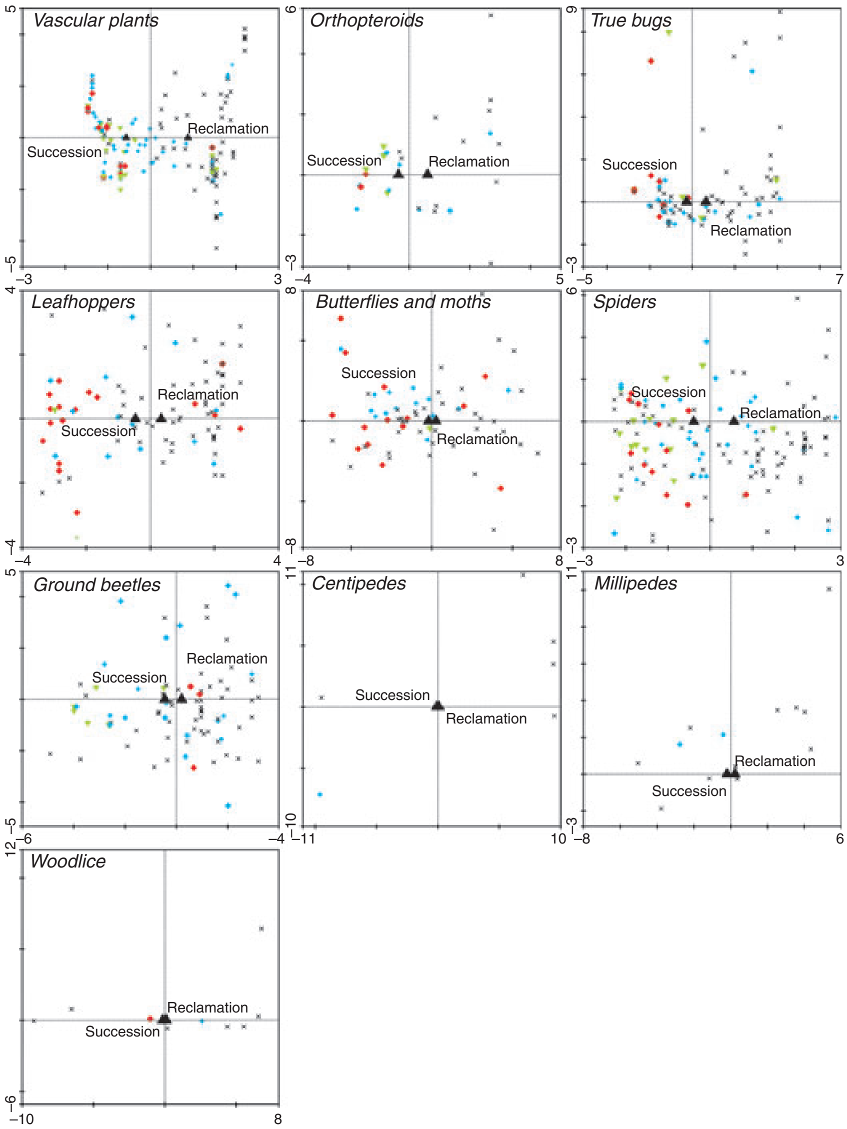

Fig. 4. Canonical correspondence analyses diagrams of relationships of vascular plants and ten arthropod taxa in studied limestone quarries to the restoration *METHOD*. The symbols distinguish red-listed species (red diamonds), non red-listed species restricted to well-preserved xeric grasslands (green triangles), common xerotermophilous species (blue stars) and generalists plus species of non-xeric habitats (black crosses). See Table 1 for associated statistics and Table S1 (Supporting information) for individual species' 1st axis ordination scores.

reclamation replaces the high structural diversity of successional patches by uniformity.

Ground beetles did not prefer any of the reclamation methods, although successional stages with sparse vegetation represent important habitats for them (e.g. Ljungberg 2002). We found only a low proportion of red-listed ground beetles in the sampled communities, in contrast to the other taxa (cf. Table S1, Supporting information). However, our observation that xeric specialists among ground beetles tend to avoid large patches of bare substrate are consistent with other studies (Clark, Gage & Spence 1997; Tyler 2008; Kagawa & Maeto 2009), which explain this pattern by lower food supply, lack of compact tufts for shelter, and the need of deep soil for overwintering.

Harvestmen did not differ between the restoration methods. This taxon contains only a few warm grassland specialists in Central Europe (Silhavy 1956) and the majority of recorded species in the study were common generalists (cf. Table S1, Supporting information).

As in many studies (Benes *et al.* 2003; Novak & Konvicka 2006; Kirmer *et al.* 2008), the surrounding habitats influenced the composition of the recorded communities: rare species responded positively to grasslands and negatively to ruderals. On the other hand, the distance to the nearest seminatural xeric grassland, as a crude measure of site connectivity, did not affect the distribution of rare species. This was inconsistent with some previous studies (Novak & Konvicka 2006; Kirmer *et al.* 2008) and the inconsistency may perhaps be attributed to a high overall connectivity of xeric grasslands in the Bohemian Karst, especially so a few decades ago, when the quarries were being abandoned (Lozek *et al.* 2005; Kadlec *et al.* 2008).

CONSERVATION POLICY IMPLICATIONS

Our finding that technical reclamation in limestone quarries, in contrast to using spontaneous succession, does not contribute to conserving specialized and/or endangered species, agrees with the results of single-taxon studies in lignite spoil dumps (Hodacova & Prach 2003; Holec & Frouz 2005), and with numerous reports dealing with other post-mining habitats (e.g. Benkewitz, Tischew & Lebender 2002; Rehounkova & Prach

Table 2. Results of the canonical correspondence analyses (CCA) of the impact of environmental predictors on community composition of studied taxa

Model[1]	Patterns for rare species[2]	*F*-, *P*[3]-values	Eig[4]	Per cent[5]
Vascular plants				
3 m (*E1* + *E0* + litter)	Negative: *E0*, litter	3·5***	0·78	20·0
100 m (grassland + shrubs + deciduous + ruderal)	Positive: grassland; negative: ruderal	5·6***	1·39	35·5
distSt	No general pattern	3·7***	0·31	7·8
Orthopteroids				
3 m (litter + *E0* + *E3* + bare)	Positive: bare; negative: litter	7·9***	0·32	14·0
100 m (grassland + ruderal + deciduous + shrubs)	Positive: grassland, deciduous, shrubs; negative: ruderal	10·0***	0·39	17·0
distSt	Positive effect	14·1***	0·15	6·8
True bugs				
3 m (litter + *E0*)	Positive: *E0*; negative: litter	5·4***	0·21	5·2
100 m (grassland + shrubs + ruderal + deciduous)	Positive: grassland, shrubs; negative: ruderal. deciduous	5·4***	0·40	10·2
distSt	Negative effect	3·1*	0·06	1·6
Leafhoppers				
3 m (litter + *E0* + *E1*)	Positive: *E0*; negative: litter, *E1*	4·5***	0·27	6·6
100 m (ruderal + rocks + scree + shrubs)	Positive: rocks, scree, shrubs; negative: ruderal	5·9***	0·46	11·0
distSt	No general pattern	6·0***	0·13	3·0
Butterflies and moths				
100 m (grassland + ruderal)	Positive: grassland; negative: ruderal	2·2***	0·12	4·6
distSt	No general pattern	2·1***	0·06	2·3
Spiders				
3 m (litter + *E0* + *E1* + *E2*)	Negative: litter, *E1*	4·6***	0·37	8·7
100 m (grassland + ruderal + conifers + rocks)	Positive: grassland, rocks; negative: ruderal. conifers	6·1***	0·47	11·3
distSt	No general pattern	8·2***	0·17	4·1
Ground beetles				
3 m (*E1* + *E3* + *E0* + litter)	Positive: *E0*; negative: *E1*, *E3*, litter	3·1***	0·20	6·0
100 m (scree + grassland + shrubs + rocks)	Positive: grassland	4·1***	0·27	7·9
distSt	No general pattern	5·1***	0·09	2·5
Centipedes				
3 m (litter + *E2* + *E1*)	No general pattern	7·0***	0·05	9·8
100 m (deciduous + grassland + conifers + rocks)	No general pattern	5·8***	0·05	10·0
distSt	No general pattern	16·8***	0·04	7·9
Millipedes				
3 m (litter + *E0*)	Positive: litter	15·5***	0·08	14·0
100 m (deciduous + ruderal + grassland + rocks)	Positive: grassland. rocks	16·3***	0·16	26·0
distSt	No general pattern	29·1***	0·08	13·0
Woodlice				
3 m (litter)	Positive: litter	8·9***	0·02	4·5
100 m (deciduous + shrubs + rocks)	Positive: shrubs; negative: deciduous	9·1***	0·06	13·0
distSt	Negative effect	9·0***	0·02	4·4
Harvestmen				
3 m (*E0* + litter + bare + *E1*)	No general pattern	3·5***	0·09	6·8
100 m (deciduous + shrubs + grassland + ruderal)	No general pattern	4·1***	0·11	7·8
distSt	Negative effect	7·5***	0·05	3·8

[1]Model obtained via a forward selection from *microhabitat structures* (3 m), *surrounding habitats* (100 m) and distance from the nearest xeric grassland (*distSt*). See 'Materials and methods' for description of individual predictors.
[2]Effects on red-listed species and xeric specialists (combined), evaluated visually from the ordination diagrams. Only predictors with clearly positive or negative effects are mentioned.
[3]*F*-values and significances of all canonical axes assessed via Monte-Carlo permutation (999 runs per analysis): $*P < 0{\cdot}05$; $**P < 0{\cdot}01$; $***P < 0{\cdot}001$.
[4]Eigenvalues of all canonical axes.
[5]The per cent variation in species data explained by all canonical axes.

2008). In addition to these biodiversity benefits, spontaneous succession is considerably cheaper – the target state, structured surfaces open for spontaneous succession, is achieved immediately after the end of mineral extraction (e.g. Prach & Hobbs 2008).

Despite the evidence for the biodiversity benefits of spontaneous succession, it is rarely implemented at present. For example, the huge lignite quarries in the Czech Republic are reclaimed using technical approaches, and no area is legislatively reserved for natural processes (Stys & Branis 1999); only 15% of each post-mining area is reserved for spontaneous succession in Germany (Schulz & Wiegleb 2000); and similar situations apply across Europe and probably elsewhere (cf. Ursic *et al.* 1997; Nicolau 2003; Holl 2002; Carrick & Kruger 2007). Given the rapid losses of temperate biodiversity (e.g. Hoekstra *et al.* 2005; Wenzel *et al.* 2006), and given that nutrient-poor and disturbance-dependent biotopes such as grasslands, heaths and rocks are among those most seriously affected, the prevalence of technical reclamation schemes over spontaneous succession is puzzling. The scale of the problem is also important: mining areas represent almost 1% of the world's land (Walker 1992), an area that could make a major contribution to biodiversity if its potential was realized.

We offer two explanations for the low popularity of spontaneous succession among practitioners. The first is the prevalence of the utilitarian view of landscape use among restoration practitioners, resulting in a preference for 'productive' goals (agriculture, forestry and occasionally recreation) over conservation. The second reason stems from the ingrained equilibrium view of natural communities (the 'equilibrium paradigm' *sensu* Wallington, Hobbs & Moore 2005), emphasizing such environmental policy goals as soil formation, prevention of erosion, nutrient cycling and water management. This equilibrium view still appears to prevail among restoration practitioners (Wallington *et al.* 2005; Prach & Hobbs 2008), despite the evidence that disturbances are common in natural communities, representing a crucial mechanism of species' coexistence (e.g. Sousa 1984; Hobbs & Huenneke 1992; Wu & Loucks 1995), and that successionally advanced communities do not necessarily harbour more specialized and/or threatened species compared with less advanced ones (Thomas *et al.* 1994).

As a result of its biodiversity conservation potential, spontaneous succession should be the preferred restoration method if no other public concerns (e.g. risks of uncontrolled erosion, toxin leaks, recreational use or public safety issues) require the application of technical approaches. It appears especially suitable for sites within protected areas and/or adjoining valuable natural communities, as these sites have strong potential for the development of rare habitats (Novak & Konvicka 2006). For such sites, active interventions should be limited to channelling successional developments, such as control of invasive species, or local blocking of succession to support endangered specialists of early successional formations. Even in cases where other public demands favour the technical approaches, restoration schemes should apply suitable near-natural methods, such as mulching with diaspore-rich plant material, covering the surfaces with hay containing plant propagules, or direct sowing of targeted species (Kirmer & Mahn 2001; Tischew & Kirmer 2007; Prach & Hobbs 2008). Restoration techniques such as levelling off sites, importing topsoil and sowing/planting fast-growing vegetation should be kept at an absolute minimum.

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Supporting Information

Additional Supporting information may be found in the online version of this article.

Fig. S1. Position of the Bohemian Karst and the pairs of studied plots.

Table S1. Categorisation and the restoration methods affinities of all recorded species, nomenclature, determination literature and voucher material storage

Table S2. Characterisation of individual study plots

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