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Naturally recruited herbaceous vegetation in abandoned Belgian limestone quarries: towards habitats of conservation interest analogues?

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Abstract We examined if naturally recruited herbaceous vegetation in abandoned Belgian limestone quarries tend towards plant communities analogous to semi-natural habitats of conservation interest. We studied taxon-based assemblages (using two-dimensional non-metric multidimensional scaling ordination) and functional patterns (relative to Grime's competitor, stress tolerator and ruderal plant strategies (CSR) classification) of plant communities ($n = 360$ plots) among three different time periods after quarry abandonment (< 3 y, 3–20 y, > 20 y). We compared those successional assemblages with those of habitat of conservation interest plant communities ($n = 53$ plots): lowland hay meadows and rupicolous, xerophilous and mesophilous calcareous grasslands. Our results indicate that naturally recruited herbaceous vegetation compositionally resembled mesophilous grassland, even though initial substrate conditions were more similar to rupicolous or xerophilous grasslands. The specific successional pathway we found in CSR state-space differs from Grime's predictions because there was a functional shift in plant assemblages from dominance by ruderals to dominance by stress-tolerant species. The differences in successional trajectories we found on different types of rock substrate suggest that conservation management should adopt a site-specific approach, recognizing that the highest probabilities of success on hard limestone will be restoration to calcareous grassland analogues.

Keywords Plant community · Conservation · Calcareous grassland · Hay meadow · Passive restoration · Natura 2000

Introduction

In some cases, anthropogenic ecosystems may be considered to be analogous to (semi-)natural habitats and as such may provide opportunities for conserving biodiversity. Lundholm and Richardson (2010) defined habitat analogues as 'anthropogenic ecosystems able to support indigenous biodiversity due to their structural or functional resemblance to natural ecosystems, habitats, or microsites that may be present in the region, but not part of the historic ecosystem on a particular site'. Biodiversity of anthropogenic ecosystems may derive from spontaneous vegetation development after removing or reducing human alteration ('passive restoration'; Prach and del Moral 2015). Therefore, it is necessary to predict

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the potential for anthropogenic ecosystems to maintain species compositions that are analogous to (semi-)natural habitats, particularly vegetation types that are valued enough to receive special protection. This requires one to examine the types of plant communities that spontaneously assemble in anthropogenic habitats and compare those communities to communities in reference (semi-)natural habitats.

Several studies in temperate Europe have demonstrated that herbaceous plant assemblages have developed spontaneously on surface-mined areas after mining activities ceased (Novák and Prach 2003; Prach et al. 2013). Limestone quarries provide large areas of bare bedrock that are dry and nutrient-poor, thus providing opportunities for spontaneous colonization by herbaceous species adapted to xeric and nutrient-poor conditions. Such plants are usually associated with community types that are of particular conservation interest (Tischew and Kirmer 2007; Gilardelli et al. 2015).

Plant assemblages are traditionally compared at the taxonomic level, which allows researchers to reference a target species assemblage directly (Duckworth et al. 2000). However, the composition of a given species assemblage depends on the regional pool of available species and vagaries in local dispersal events, which makes comparisons between regions difficult (Woodward and Cramer 1996). In addition, using predictions based on the taxonomic level alone may not allow one to detect differences in functional ecological patterns (Keddy 1992; Körner 1993). However, a functional-type analysis can also be used to compare plant assemblages and can complement a species-based approach (Walker 1992), still allowing to compare communities that differ in species composition (Hunt et al. 2004). A recognized way to isolate those patterns and to answer other ecological questions is by using predictions based on plant functional groups, such as Grime's competitor, stress tolerator and ruderal plant strategies (CSR) classification scheme (Diaz et al. 1992; Keddy 1992). This CSR classification system has been recognized as being potentially useful for quantifying variation in plant traits along a (primary) successional series and for understanding processes attributed to species assemblages in anthropogenic habitats (Caccianiga et al. 2006). However, the CSR framework has rarely been used in this context (e.g. Simonová and Lososová 2008; Lososová and Láníková 2010). Grime (2001) interpreted data from other authors to suggest that, in general, life strategies of dominant species shift during the course of primary succession from stress-tolerating pioneers to more competitive strategists.

However, several studies have demonstrated that trajectories during succession in abandoned mining sites may vary by site (e.g. Buisson et al. 2006; Alday et al. 2011; Prach et al. 2016). It is obvious that assemblages of plants established in quarries is related to many factors, including the regional pool of available species and the type of rock that was quarried (Horáčková et al. 2016). As a consequence, a multi-site approach is needed to understand the potential for abandoned mining sites to host herbaceous vegetation valued by conservationists and to determine to what extent the mined areas contribute to the preservation of (semi-)natural habitat (Prach et al. 2014). In order to assess the regional pool of available species, reference (semi-)natural habitats are required. In Europe, semi-natural herbaceous vegetation of particular conservation interest covers a wide range of habitat types associated with a wide range of human alterations (WallisDeVries et al. 2002). Hay meadows (Natura 2000 habitat code 6510, 'lowland hay meadows' in the EU Habitats Directive 92/43/EEC – European Community 1992) originated from repeated mowing (Piqueray et al. 2016). Dry calcareous grasslands, including xerophilous to mesophilous assemblages (6110, 'rupicolous calcareous grasslands'; 6210 *pro partim*, 'xerophilous calcareous grasslands' and 6210 *pro partim*, 'mesophilous calcareous grasslands'), emanated from traditional, agro-pastoral practices, primarily sheep herding (Piqueray et al. 2011).

In this study, we address three basic questions related to succession on limestone bedrock. (1) What is the taxon-based direction of spontaneous, primary succession of vegetation on limestone bedrock of abandoned quarries? That is, does succession tend towards a species assemblage analogous to a habitat of that is typical of xeric conditions (a specific Natura 2000 habitat of interest)? (2) Does the functional successional pathway from bare ground follow that predicted by Grime's CSR theory (Grime 2001)? And, (3) from a taxonomic and functional perspective, do the trajectories of species assemblages on different types of limestone rocks and associated with different species pools follow the same trajectory?

Material and methods

Study sites

This study was conducted in southern Belgium (Fig. 1). The studied abandoned quarries ranged in elevation from 107 to 255 m a.s.l. (Table 1). The distance between the northernmost and the southernmost sites was circa 80 km and the distance between the easternmost and westernmost sites was circa 100 km. Quarry size ranged from 7 to 125 ha. The history of each quarry was reconstructed from records kept by the mining company that had managed the site. Sites were selected for study if they met the following criteria: (1) the time since abandonment could be determined; (2) there existed a sufficiently large, spontaneously herbaceous revegetated area; (3) the site began as barren (lacking soil), stony-calcareous ground created by mining activities, i.e. the mined area was scraped or hard limestone raw materials dumped there, without any evidence of additional human alteration, so that the site was deemed as being entirely revegetated via primary succession; and (4) vegetation was not actively managed or rehabilitated after quarry abandonment.

A total of six sites were surveyed during the 2014 growing season. The six studied sites involved either a sole quarry or a group of quarries located in the same limestone formation and ecological landscape (Table 1). Each of the six study locations was comprised of one of three types of limestone: hard limestone (Middle Carboniferous or Middle Devonian limestone), white chalk (Upper Cretaceous limestone), or dolomite (Upper Devonian limestone) (Dejonghe 2006). Known surfaces of semi-natural herbaceous vegetation of conservation interest (lowland hay meadow and dry calcareous grasslands) within a 5-km radius of the quarries of a site were extracted from the map of Natura 2000 sites in Belgium (Service public de Wallonie 2012) (Table 1).

Field data collection

We used a space-for-time approach to examine a variety of time intervals since quarry abandonment (0–30 years) to investigate the time period needed for primary succession toward grasslands (via natural recruitment) in temperate regions (Prach 2003; Prach et al. 2013). This space-for-time approach enabled us to identify changes in species composition and functional patterns resulting

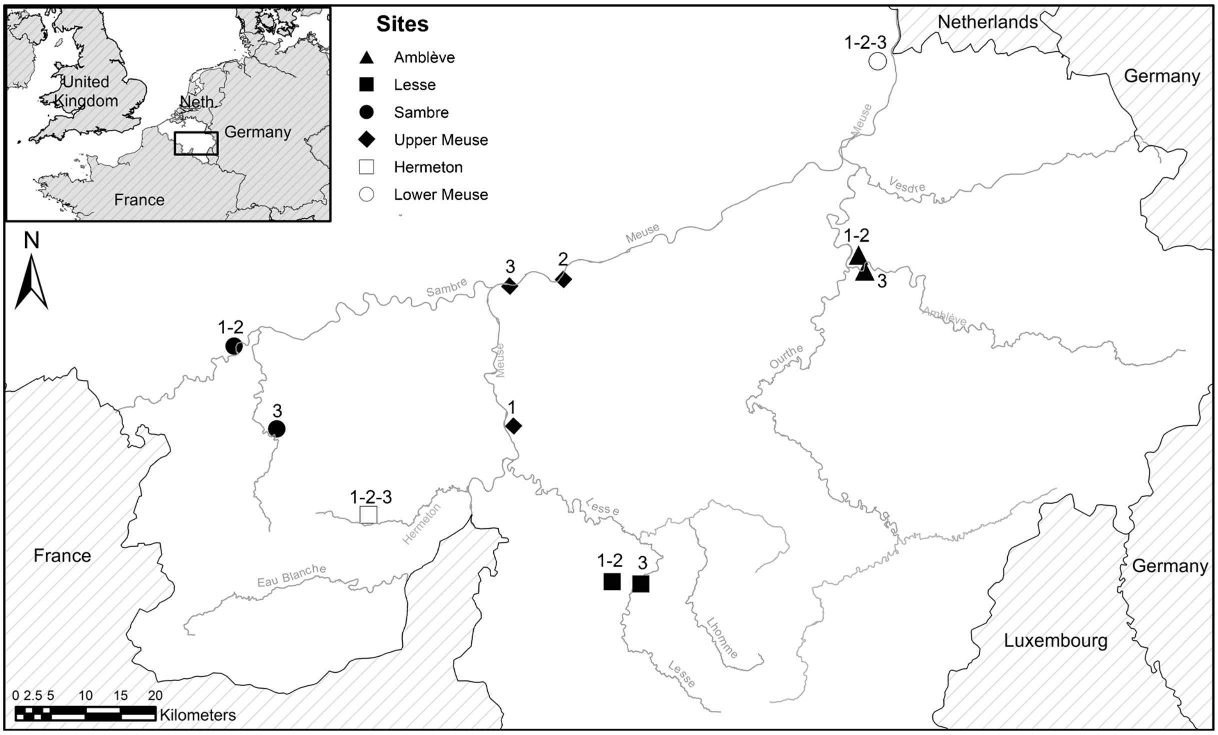

Fig. 1 Location of the 18 subsites sampled in southern Belgium ($n = 360$); time intervals after quarry abandonment (by site): 1, < 3 y (Q1); 2, 3–20 y (Q2); and 3, > 20 y (Q3). Symbols: black – hard limestone, white – chalk and dolomite sites

Table 1 Main characteristics of the 18 subsites studied (six quarry sites, 360 sampled quarry plots) including the surface of dry calcareous grasslands (rupicolous, mesophilous and xerophilous grasslands) and hay meadows habitat-types mapped within a 5-km radius of the subsite

Site	Quarry abandonment	Latitude N	Longitude E	Altitude [m]	Chronostratigraphy	Lithological nature	Quarry size [ha]	Grasslands [ha]	Hay meadows [ha]
Sambre	Q1	50°23′38.56″	4°21′26.04″	141	Middle Carboniferous	Hard limestone	50.2	0.0	30.8
Sambre	Q2	50°23′38.66″	4°21′27.37″	137	Middle Carboniferous	Hard limestone	50.2	0.0	30.6
Sambre	Q3	50°16′59.60″	4°27′0.73″	187	Middle Devonian	Hard limestone	21.0	0.0	0.0
Lower Meuse	Q1	50°45′8.72″	5°38′56.49″	107	Upper Cretaceous	White chalk	124.7	14.4	10.3
Lower Meuse	Q2	50°45′16.81″	5°38′58.43″	113	Upper Cretaceous	White chalk	124.7	14.4	10.2
Lower Meuse	Q3	50°45′11.64″	5°39′13.88″	122	Upper Cretaceous	White chalk	124.7	14.3	10.3
Lesse	Q1	50°5′32.83″	5°6′40.55″	238	Middle Devonian	Hard limestone	67.9	49.8	192.5
Lesse	Q2	50°5′33.72″	5°6′47.39″	233	Middle Devonian	Hard limestone	67.9	48.8	190.6
Lesse	Q3	50°5′23.55″	5°10′49.84″	238	Middle Devonian	Hard limestone	7.0	65.4	149.1
Amblève	Q1	50°30′13.42″	5°36′17.20″	171	Middle Carboniferous	Hard limestone	11.4	5.6	6.9
Amblève	Q2	50°30′14.26″	5°36′19.06″	173	Middle Carboniferous	Hard limestone	11.4	5.6	7.1
Amblève	Q3	50°28′53.67″	5°36′48.69″	161	Middle Carboniferous	Hard limestone	19.5	8.4	7.5
Hermeton	Q1	50°10′28.49″	4°38′1.01″	252	Upper Devonian	Dolomite	70.9	33.7	101.7
Hermeton	Q2	50°10′24.33″	4°36′51.01″	255	Upper Devonian	Dolomite	70.9	34.6	99.3
Hermeton	Q3	50°10′35.81″	4°38′41.39″	236	Upper Devonian	Dolomite	70.9	30.5	103.2
Upper Meuse	Q1	50°16′18.92″	4°54′29.65″	204	Middle Carboniferous	Hard limestone	55.5	51.6	0.9
Upper Meuse	Q2	50°28′31.15″	5°1′32.70″	142	Middle Carboniferous	Hard limestone	22.9	3.1	0.5
Upper Meuse	Q3	50°27′48.11″	4°55′57.61″	118	Middle Carboniferous	Hard limestone	10.8	7.0	0.1

Time intervals after quarry abandonment: Q1, < 3 y; Q2, 3–20 y and Q3, > 20 y from primary succession (Pickett 1989). At each site, we selected three subsites, each representing a different time interval since quarry abandonment (total of 18 subsites): < 3 y (hereafter referred to as quarry stage Q1); 3–20 y (Q2); > 20 y (Q3). The main characteristics of the studied subsites are summarized in Table 1. For each of the 18 subsites, 20 square plots (1-m^2) were randomly selected (n = 360 quarry plots). The percent cover of all higher plant species was visually estimated at each plot (sensu Kent and Coker 1992). Taxonomic nomenclature followed Lambinon et al. (2004).

Reference data collection

Reference data (representing plant communities of Natura 2000 herbaceous habitats) were obtained from phytosociological relevés previously analysed for the four target vegetation types with conservation value: (1) rupicolous grassland (habitat code 6110) sampled by Piqueray et al. (2007) in 15 1-m^2 square plots, (2) xerophilous grassland (6210 *pro partim*) sampled by Piqueray et al. (2008) in 15 1-m^2 square plots, (3) mesophilous grassland (6210 *pro partim*) sampled by Piqueray et al. (2007) in 15 1-m^2 square plots (in vegetation cover types 1 and 3), and (4) hay meadow (6510) sampled by Piqueray et al. (2016) in eight 1-m radius circular plots.

Data analysis

Prior to data analysis, cover data for all species were transformed into ordinal coefficients, using the van der Maarel scale to make all the databases comparable (Jongman et al. 1995). Analyses were performed using R statistical software (R Development Core and Team 2010).

An analysis of variance, followed by post hoc pairwise comparisons ('TukeyHSD' in R), were used to test for mean species richness/m^2 differences among stages Q1, Q2, Q3 plots and reference plots. To order the taxonomic variation, a two-dimensional non-metric multidimensional scaling (NMDS) ordination (Shepard 1962; Kruskal 1964; McCune et al. 2002), was run on the Bray-Curtis similarity matrix with all plots (for quarry plots, n = 360 and for reference plots, n = 53), using the 'vegan' package (Oksanen et al. 2017). Joint-plot vectors (hereafter referred to as spiders) and centroids were overlaid onto the ordination using the 'ordispider' command to allow for a better visualization of relationships among plant assemblages. In order to determine the species that correlated most with the axes of NMDS, a Pearson correlation was calculated for each species using the 'cor' command. (We inspected species presenting more than 30% correlation in the ordination.) Statistical differences between plant assemblages were tested using a pairwise analysis of similarities (ANOSIM), using the 'anosim' command (Clarke 1993). Between-group distance was compared by evaluating the centroid distances of each plant assemblages in the ordination (NMDS inter-group distance). Within-group variation (scattered in the NMDS spider plot) was evaluated by comparing the mean of maximum plot dispersion along axes 1 and 2 of the ordination, i.e. NMDS intra-group distances.

Information on CSR values of sampled species was extracted from a CSR electronic spreadsheet that identified CSR types for 1,000 European species (Hodgson et al. 1999). If the species was not present in that spreadsheet, the BiolFlor database (Klotz et al. 2002) was used. All 413 CSR positions for vegetation plots (quarry plots, n = 360 and reference plots, n = 53) were calculated from percent cover data for all the species in each plot, using the spreadsheet-based tools from Hunt et al. (2004). In order to compare those 413 CSR signatures, they were plotted in a CSR triangle by using the 'compositions' package of van den Boogaart et al. (2013). In this triangle, spiders and centroids were overlaid using the 'ordispider' command to allow for a better visualisation of functional relationships between all assemblages.

Results

Taxonomic variation

A total of 156 plant species were recorded in the 360 quarry plots. A similar number of species was identified from each of the three quarry successional stages (n = 120 plots/successional stage; stage Q1: 101 species, Q2: 107 species, Q3: 105 species). Mean species richness/m^2 was significantly lower in stage Q1 (< 3 y), but similar among stages Q2 (3–20 y) and Q3 (> 20 y; F = 20.2, $P < 0.001$; Table 2). The mean species richness/m^2 in Q1 was similar to that of xerophilous and rupicolous grassland reference habitats, while, the mean species richness/m^2 in Q2 and Q3 were similar to rupicolous and mesophilous grasslands reference habitats, respectively (F = 16.51, $P < 0.001$; Table 2). Species richness/

Table 2 Mean species richness/m^2 of plant assemblage in quarry plots (n = 360) and reference plots (n = 53) with standard error terms, percentage of shared species between groups and NMDS inter- and intra-group distance

Group	Species richness/m²	NMDS intra-group distance
Q1	11.4 ± 0.5	6.05
Q2	14.0 ± 0.3	1.75
Q3	15.1 ± 0.5	2.40
Hm	23.4 ± 2.0	1.33
Mg	18.5 ± 1.3	1.92
Rg	13.2 ± 0.8	1.25
Xg	11.3 ± 0.5	1.01
Groups comparisons	**Shared species [%]**	**NMDS inter-group distance**
Q1 - Q2	37	0.80
Q1 - Q3	34	0.86
Q2 - Q3	34	0.34
Mg - Rg	16	0.38
Mg - Xg	19	0.65
Rg - Xg	21	0.36
Hm - Mg	21	1.13
Hm - Rg	5	1.51
Hm - Xg	9	1.71
Q1 - Hm	14	1.25
Q2 - Hm	20	0.54
Q3 - Hm	19	0.82
Q1 - Mg	17	1.60
Q2 - Mg	19	0.96
Q3 - Mg	22	0.74
Q1 - Rg	15	1.89
Q2 - Rg	16	1.32
Q3 - Rg	16	1.06
Q1 - Xg	11	2.23
Q2 - Xg	12	1.61
Q3 - Xg	14	1.39

Time intervals after quarry abandonment: Q1, < 3 y; Q2, 3–20 y and Q3, > 20 y. Abbreviations for reference plots (n = 53): Hm – hay meadow, Mg – mesophilous grassland, Rg – rupicolous grassland and Xg – xerophilous grassland)

m^2 in hay meadow reference habitat could not be considered in the analysis as their sampled area was not comparable. Stages Q1, Q2 and Q3 had 12% of their species in common, but the highest percentage of shared species occurred between stages Q1 and Q2 (37%; Table 2). Overall, the percentage of shared species between quarry stages and reference habitats remained lower than among quarry stages (Table 2). Quarry stage Q2 shared the most species with the hay meadows reference habitat, and quarry stage Q3 shared the most species with the mesophilous grasslands (Table 2).

All quarry stages and reference habitat species assemblages differed significantly from one another (pairwise ANOSIM tests, all $P < 0.001$). NMDS analysis found that the hay meadow reference assemblage was more differentiated from other reference species assemblages (Fig. 2, Table 2). The species assemblage in quarry stage Q1 was more heterogeneous than any of the other quarry stages and reference habitats, as demonstrated by the longer extension of the spider plot (Fig. 2a) and the higher NMDS intra-group distance for this stage class (Table 2). Quarry stage Q1 also separated from

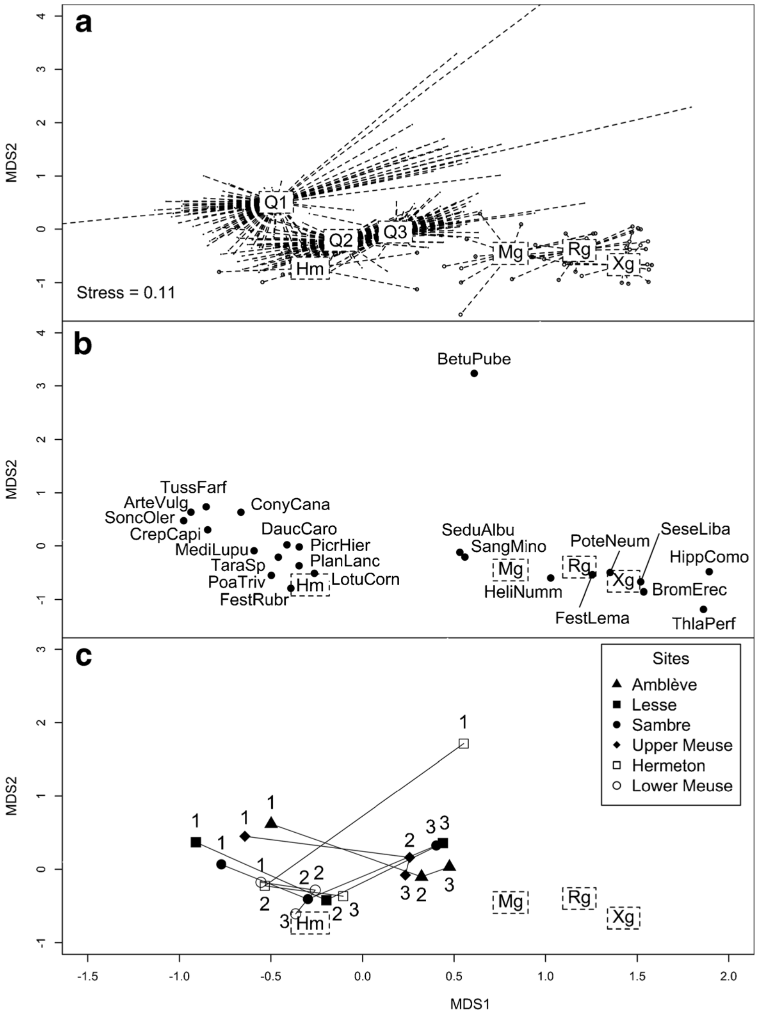

Fig. 2 NMDS ordination diagram of plant assemblages in quarry plots ($n = 360$) and reference plots ($n = 53$; Hm, hay meadows; Mg, mesophilous grasslands; Rg, rupicolous grasslands; and Xg, xerophilous grasslands). Squares represent centroids of quarry stages and reference habitats. **a** Time intervals after quarry abandonment: Q1, < 3 y; Q2, 3–20 y; and Q3, > 20 y. The end of the lines represents the ordination position of vegetation plots. **b** Species with greater than 30% correlation with the axes of the NMDS are pointed. Abbreviations of species names are denoted by the first four letters of the generic name and the first four of the specific epithet (for complete names, see the Appendix). **c** Lines indicate trajectories, by site. Sites are indicated by different symbols (black – hard limestone sites, white – white chalk and dolomite sites). Numbers indicate the time intervals after quarry abandonment (by site): 1, < 3 y (Q1); 2, 3–20 y (Q2); and 3, > 20 y (Q3)

the other quarry stages and reference habitats in the ordination diagram (Fig. 2a) and displayed higher NMDS inter-group distances with Q2 and Q3 (Table 2) whereas the species assemblages of quarry stages Q2 and Q3 displayed considerable overlap (Fig. 2a) and lower NMDS inter-group distance (Table 2). Quarry stage Q2 and Q3 were more similar to reference habitats than Q1, as indicated by the positions of the centroid of spider plots in Fig. 2a and the lower NMDS intra-group distance (Fig. 2a) when compared to references habitats (Table 2). Stage Q2 was very similar compositionally to the hay meadow type, whereas the stage Q3 species assemblage was intermediate in species composition between hay meadow and the mesophilous grassland reference types (Fig. 2a, Table 2).

Functional variation

The CSR analysis clearly distinguished the hay meadow type from the other reference plant communities (mesophilous, xerophilous or rupicolous grasslands), particularly relative to the more stress-tolerant species assemblage (Fig. 3). Plant assemblages naturally established in abandoned quarries (quarry plots, $n = 360$) were more similar to hay meadows than to other reference habitats, regardless of the life stage considered (stages Q1, Q2 or Q3; Fig. 3a). Plant assemblages initially established on bare ground of abandoned quarries (stage Q1) were comprised of species between R/CSR and CR/CSR in CSR life strategies (Table 3), with a large variability among assemblages (Fig. 3a). Overall, the C and S components of plant communities

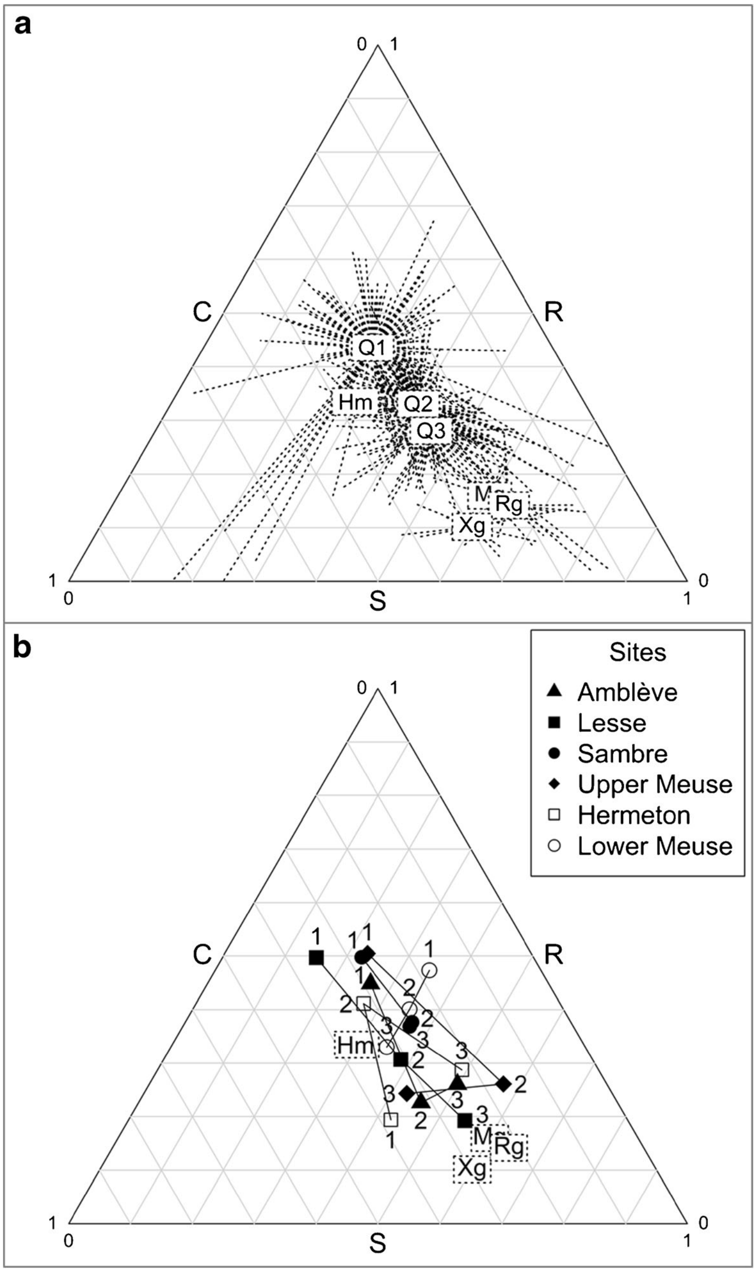

Fig. 3 CSR signatures of plant assemblages quarry plots (*n* = 360) and reference plots (*n* = 53; Hm, hay meadows; Mg, mesophilous grasslands; Rg, rupicolous grasslands; and Xg, xerophilous grasslands). Squares represent centroids of quarry stages and reference habitats. **a** Time intervals after quarry abandonment: Q1, < 3 y; Q2, 3–20 y; and Q3, > 20 y. The end of the lines represents the position of vegetation plots. **b** Lines indicate trajectories, by site. Sites are indicated by different symbols (black = hard limestone sites, white = white chalk and dolomite sites). Numbers indicate the time intervals after quarry abandonment (by site): 1, < 3 y (Q1); 2, 3–20 y (Q2); and 3, > 20 y (Q3)

tended to increase in abundance from quarry stage Q1 to stage Q3 (Fig. 3a), but strict S strategists displayed the highest increase in abundance (Table 3). In contrast, the increase in species with the C strategy was mainly due to increases in intermediate strategies with S strategists (SC, CSR, S/CSR, SC/CSR; Table 3). This means that over time species assemblages became functionally more similar to stress-tolerant, calcareous grasslands (xerophilous, rupicolous or mesophilous grasslands). In addition, quarry stage Q1 displayed a higher heterogeneity in functional strategies of its species assemblages than quarry stages Q2 or Q3 (Fig. 3a).

Site trajectories

While altogether the pattern of samples in the ordination followed a temporal (successional) sequence towards mesophilous grasslands, our more

Table 3 Relative importance of CSR strategies of plant assemblage in quarry plots (n = 360), according to successional stage after quarry abandonment

	Q1	Q2	Q3
N of plots	120	120	120
N of species	101	107	105
CSR plant strategy			
C	5.2	3	4.1
S	1.3	5.4	11
R	4.9	2.1	1.3
CR	10.5	5.7	1.8
SR	11.2	6.2	9.9
SC	1.2	2	4
CSR	9.2	13.4	15.1
C/CR	2.6	0.4	0
C/SC	1.9	1.3	1
R/CR	7.8	2.5	0.8
R/SR	7.8	6.5	3.2
S/SR	1.6	2.8	2.1
S/SC	0	0	0
S/CSR	8.1	16.1	13
R/CSR	11.9	7.9	9.5
C/CSR	1	5.3	2.8
SC/CSR	1.6	4.2	5.2
SR/CSR	6.4	5.8	4.5
CR/CSR	5.9	9.3	10.7

Time intervals after quarry abandonment: Q1, < 3 y; Q2, 3–20 y and Q3, > 20 y. Values are percent frequencies

detailed, site-by-site examination indicated a more compositionally and functionally complex pattern (Figs. 2c, 3b). High compositional heterogeneity in quarry stage Q1 arose mainly from a single site (Hermeton) where barren ground was colonized by *Betula pubescens* seedlings. By contrast, other sites were much more similar in their colonizing species assemblages, mostly characterized by pioneering ruderal species, i.e. *Tussilago farfara*, *Artemisia vulgaris*, *Sonchus oleraceus* and *Conyza canadensis* (Fig. 2b,c). On a site-basis, quarry stage Q2 and/or stage Q3 were more compositionally similar to hay meadow or mesophilous grassland habitats, with two groups of sites separating on the ordination. (1) In the Hermeton and Lower Meuse sites, plant assemblages were more similar to hay meadow types by stages Q2 and Q3; these two sites were composed of soils formed from white chalk and dolomite. (2) In the other sites, species compositions of stage Q3 sites tended to be more similar to mesophilous grassland, while stage Q2 sites were more heterogeneous (Fig. 2c); the soils of those latter sites were formed from hard limestone.

The functional trajectories of individual sites differed slightly in their compositional patterns relative to reference sites (Fig. 3b). However, the contrast between white chalk and dolomite sites with hard limestone was less pronounced in the CSR space. In the white chalk and dolomite sites, functional plant assemblages were more similar to hay meadow sites in quarry stages Q2 and Q3 (except for quarry stage Q3 in Hermeton). In hard limestone sites, quarry stage Q3 tended to be more functionally similar to mesophilous grassland, while quarry stage Q2 was more heterogeneous across sites (Fig. 3b), except for quarry stage Q3 in Sambre.

Discussion

Examining changes over time between taxon-based assemblages and diverse functional patterns allows researchers to answer general theoretical questions about successional development in limestone quarries after mining activities cease (Walker and del Moral 2003). Comparing developmental trajectories of plant communities relative to natural reference communities provides a practical framework for examining natural recovery of plant communities in abandoned mines (Walker et al. 2007). Our study suggests that herbaceous plant assemblages that develop spontaneously on bare ground in abandoned limestone quarries in southern Belgium tend to succeed toward analogues to semi-natural plant communities that are recognized as having high conservation value. Several studies in temperate Europe have established that in abandoned surface quarries a period of 20 years is usually long enough for plant assemblages to develop a composition that is similar to natural or semi-natural herbaceous plant communities (Novák and Prach 2003; Prach et al. 2013). Results of our study support the general observation that woody species do not usually re-establish on dry and rocky substrate of abandoned quarry sites (Prach 1987; Novák and Prach 2003; Prach et al. 2013). However, one of the subsites studied (stage Q1 of Hermeton site) was colonized by *Betula pubescens* seedlings.

Both taxon-based and functional analyses showed changes in plant assemblages over time (since quarry abandonment), particularly between the youngest colonizing stage (Q1, < 3 y old) and more mature stages. However, the similarity between the two mature stages (Q2, 3–20 y and Q3, > 20 y) was even more pronounced. In addition, species assemblages tended also to be more homogeneous in the older stages (Q2, Q3) both from a compositional and functional perspective, which is in agreement with findings of Saar et al. (2017).

Based on CSR theory and the initial substrate conditions we encountered at our sites, we did not expect to observe the changes we observed in species assemblages over time. Based on a literature review, Grime (2001) suggested that, in the simplest cases, plant life strategies shift during primary succession from stress-tolerant pioneer species to more competitive species. This hypothesis has been disputed by those who have found a different pattern of primary succession at glacier retreat fronts (Caccianiga et al. 2006) and on land along uplift coasts (Ecke and Rydin 2000). We also observed a succession pattern in abandoned limestone quarries that differed from Grime’s predictions in that we found that initial plant assemblages were comprised of species adapted to life strategies between R/CSR and CR/CSR, with more stress tolerant strategists dominating later successional stages. The initial successional stage was also compositionally dominated by species typically considered to be ruderal species. In this developmental sequence, a large number of species initially colonized the limestone bedrock, among which ruderal plants were relatively more important, but then the ruderal species tended to be replaced by stress-tolerant species as the sites matured. This successional sequence mimics that observed during primary succession along glacial fronts, wherein pioneer plant assemblages are comprised of species with strong ruderal characteristics, which then are replaced by more stress-tolerant species later in the successional process (Caccianiga et al. 2006).

Surprisingly, although the initial substrate conditions in our study sites were more similar to those of rupicolous and xerophilous grasslands (Piqueray et al. 2007), natural recruitment tended toward plant assemblages that were compositionally more similar to hay meadow or mesophilous grassland habitat that occur on deeper soils. Two explanations are possible for these observations. For one, environmental conditions on abandoned limestone sites may be more favourable for colonization by mesophilous species than predicted by the apparent xeric and harsh conditions of the bedrock. The effect of environmental factors is indirectly supported by the differences in species assemblages we found on different geologic substrates, i.e. plant assemblages developing on white chalk and dolomite were similar to natural hay meadows in latter successional stages. Likewise, an increase over time in S-strategy species on hard limestone suggests that successional plant assemblages on limestone are becoming more similar to stress-tolerant grasslands.

The other explanation for our assemblages succeeding toward hay meadow and mesophilous grassland is that colonization by species typical for dry calcareous grassland habitats (rupicolous, xerophilous and partially mesophilous species) may be limited by the occurrence of species in the landscape and their specific dispersal capacities. Generalist mesophilous species (typical of hay meadows) are likely to be more common in the human influenced landscape of the studied region. In parallel, with the exception of a few anemochorous species, most species of dry calcareous grasslands have low dispersal abilities and are mainly dispersed by sheep in pasture systems (Piqueray et al. 2011), while none of our study sites had been grazed. Kirmer et al. (2008) demonstrated that dispersal was a major limitation to colonization of restored sites.

In answer to our main three questions, our study results support three conclusions related to primary succession in limestone quarries: (1) Naturally recruited herbaceous vegetation compositionally resembles mesophilous communities, although substrate conditions are more similar to rupicolous or xerophilous grasslands, probably as a consequence of dispersal limitations. (2) The specific successional pathway found in the CSR state-space differs from Grime's predictions in that there was a functional shift in plant assemblages from dominance by ruderals to dominance by stress-tolerant species. (3) Different successional pathways develop on different types of rocks in abandoned quarries.

Implication for conservation

It is widely accepted that one major determinant of the success of any restoration programme is the choice of an appropriate reference ecosystem (Holl and Cairns 2002). Our results indicate that, depending on specific, initial site conditions, species compositions of successional trajectories on abandoned limestone quarries vary between mesophilous calcareous grasslands and hay meadows. On abandoned sites where plant assemblages tend to naturally succeed toward mesophilous calcareous grassland, active intervention could be directed to promote species assemblages analogous to species-rich temperate grasslands, which have a particular high conservation value (WallisDeVries et al. 2002). Restorations will need to overcome dispersal limitations (i) by integrating the restoration sites into local grazing systems, including semi-natural references habitats (Pykälä 2005), (ii) by directly planting (sowing seeds) species of interest at restoration sites (Hedberg and Kotowski 2010), (iii) or by transferring grassland hay (with intact seeds) to the restoration sites (Török et al. 2011).

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Appendix 1

List of full species names used in Fig. 2b: *Betula pubescens* Ehrh., *Lotus corniculatus* L., *Bromus erectus* Huds., *Tussilago farfara* L., *Daucus carota* L., *Festuca lemanii* Bast., *Potentilla neumanniana* Reichenb., *Medicago lupulina* L., *Plantago lanceolata* L., *Taraxacum* sp., *Sanguisorba minor* Scop., *Conyza canadensis* (L.) Cronq., *Poa trivialis* L., *Picris hieracioides* L., *Hippocrepis comosa* L., *Sonchus oleraceus* L., *Sedum album* L., *Thlaspi perfoliatum* L., *Artemisia vulgaris* L., *Helianthemum nummularium* (L.) Mill., *Festuca rubra* L., *Crepis capillaris* (L.) Wallr., *Seseli libanotis* (L.) Koch.

References

Alday JG, Marrs RH, Martinez-Ruiz C (2011) Vegetation convergence during early succession on coal wastes: a 6-year permanent plot study. *J Veg Sci* 22:1–12

Buisson E, Dutoit T, Torre F, Römermann C, Poschlod P (2006) The implications of seed rain and seed bank patterns for plant succession at the edges of abandoned fields in Mediterranean landscapes. *Agric Eco-Syst Environm* 115:6–14

Caccianiga M, Luzzaro A, Pierce S, Ceriani RM, Cerabolini B (2006) The functional basis of a primary succession resolved by CSR classification. *Oikos* 112:10–20

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. *Austral J Ecol* 18:117–143

Dejonghe L (2006) Current status of chronostratigraphic units named from Belgium and adjacent areas. *Geol Belgica* 9:1–224

R Development Core Team P (2010) *R: a language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria

Diaz S, Acosta A, Cabido M (1992) Morphological analysis of herbaceous communities under different grazing regimes. *J Veg Sci* 3:689–696

Duckworth JC, Kent M, Ramsay PM (2000) Plant functional types: an alternative to taxonomic plant community description in biogeography? *Progr Phys Geogr* 24:515–542

Ecke F, Rydin H (2000) Succession on a land uplift coast in relation to plant strategy theory. *Ann Bot Fenn* 37:163–171

European Community (ed) (1992) *Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora*. European Union Official Journal. European Community, Brussels

Gilardelli F, Sgorbati S, Armiraglio S, Citterio S, Gentili R (2015) Ecological filtering and plant traits variation across quarry geomorphological surfaces: implication for restoration. *Environm Managem* 55:1147–1159

Grime JP (2001) *Plant strategies, vegetation processes, and ecosystem properties* (2nd edition). John Wiley & Sons, Chichester

Hedberg P, Kotowski W (2010) New nature by sowing? The current state of species introduction in grassland restoration, and the road ahead. *J Nat Conservation* 18:304–308

Hodgson JG, Wilson PJ, Hunt R, Grime JP, Thompson K (1999) Allocating C-S-R plant functional types: a soft approach to a hard problem. *Oikos* 85:282–294

Holl KD, Cairns JR (2002) Monitoring and appraisal. In Perrow MR, Davy AJ (eds) *Handbook of ecological restoration.* Cambridge University Press, Cambridge, pp 409–432

Horáčková M, Řehounková K, Prach K (2016) Are seed and dispersal characteristics of plants capable of predicting colonization of post-mining sites? *Environm Sci Pollut Res Int* 23: 13617–13625

Hunt R, Hodgson JG, Thompson K, Bungener P, Dunnett NP, Askew AP (2004) A new practical tool for deriving a functional signature for herbaceous vegetation. *Appl Veg Sci* 7: 163–170

Jongman RHG, ter Braak CJF, van Tongeren OFR (eds) (1995) *Data analysis in community and landscape ecology.* Cambridge University Press, Cambridge

Keddy PA (1992) A pragmatic approach to functional ecology. *Funct Ecol* 6:621–626

Kent M, Coker P (1992) *Vegetations descriptions and analysis: a practical approach.* British Library, London

Kirmer A, Tischew S, Ozinga WA, von Lampe M, Baasch A, van Groenendael JM (2008) Importance of regional species pools and functional traits in colonization processes: predicting recolonization after large-scale destruction of ecosystems. *J Appl Ecol* 45:1523–1530

Klotz S, Kühn I, Durka W (2002) BIOLFLOR - Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. *Schriftenreihe Vegetationsk* 38:1–334

Körner C (1993) Scaling from species to vegetation: the usefulness of functional groups. In *Schulze ED, Mooney HA (eds) Biodiversity and ecosystem function. Ecological studies. Springer-Verlag*, Berlin, pp 116–140

Kruskal JB (1964) Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika* 29:1–27

Lambinon J, Delvosalle L, Duvigneaud J (2004) *Nouvelle flore de la Belgique, du Grand-Duché de Luxembourg, du nord de la France et des régions voisines (ptéridophytes et spermatophytes). Jardin Botanique National de Belgique*, Meise, Belgium

Lososová Z, Láníková D (2010) Differences in trait compositions between rocky natural and artificial habitats. *J Veg Sci* 21: 520–530

Lundholm JT, Richardson PJ (2010) Habitat analogues for reconciliation ecology in urban and industrial environments. *J Appl Ecol* 47:966–975

McCune B, Grace JB, Urban DL (2002) *Analysis of ecological communities*. MjM Software Design, Gleneden Beach, CA

Novák J, Prach K (2003) Vegetation succession in basalt quarries: Pattern on a landscape scale. *Appl Veg Sci* 6:111–116

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D et al. (2017) *Vegan: community ecology package. R package, version* 2.4-3

Pickett STA (1989) Space-for-time substitution as an alternative to long-term studies. In Likens EG (ed) *Long-term studies in ecology: approaches and alternatives. Springer*, Berlin, pp 110–135

Piqueray J, Bisteau E, Bottin G, Mahy G (2007) Plant communities and the species richness of calcareous communities in southeast Belgium. *Belg J Bot* 140:157–173

Piqueray J, Mahy G, Vanderhoeven S (2008) Naturalization and impact of a horticultural species, Cotoneaster horizontalis (Rosaceae) in biodiversity hotspots in Belgium. *Belg J Bot* 141:113–124

Piqueray J, Bisteau E, Cristofoli S, Palm R, Poschlod P, Mahy G (2011) Plant species extinction debt in a temperate biodiversity hotspot: community, species and functional traits approaches. *Biol Conservation* 144:1619–1629

Piqueray J, Rouxhet S, Hendrickx S, Mahy G (2016) Changes in the vegetation of hay meadows under an agri-environment scheme in South Belgium. *Conservation Evidence* 13:47–50

Prach K (1987) Succession of vegetation on dumps from strip coal mining, N.W. Bohemia, Czechoslovakia. *Folia Geobot Phytotax* 22:339–354

Prach K (2003) Spontaneous succession in Central-European man-made habitats: what information can be used in restoration practice? *Appl Veg Sci* 6:125–129

Prach K, del Moral R (2015) Passive restoration is often quite effective: response to Zahawi et al. (2014). *Restorat Ecol* 23: 344–346

Prach K, Lencová K, Řehounková K, Dvořáková H, Jírová A, Konvalinková P et al. (2013) Spontaneous vegetation succession at different central European mining sites: a comparison across seres. *Environm Sci Pollut Res* 20:7680–7685

Prach K, Řehounková K, Lencová K, Jírová A, Konvalinková P, Mudrák O et al. (2014) Vegetation succession in restoration of disturbed sites in Central Europe: the direction of succession and species richness across 19 seres. *Appl Veg Sci* 17: 193–200

Prach K, Tichý L, Lencová K, Adámek M, Koutecký T, Sádlo J et al. (2016) Does succession run towards potential natural vegetation? *An analysis across seres. J Veg Sci* 1–9

Pykälä J (2005) Plant species responses to cattle grazing in mesic semi-natural grassland. *Agric Eco-Syst Environm* 108:109–117

Saar L, de Bello F, Pärtel M, Helm A (2017) Trait assembly in grasslands depends on habitat history and spatial scale. *Oecologia* 184:1–12

Service public de Wallonie (2012) *Projet d'arrêté de désignation des sites Natura2000, enquêtes publiques 2012* [http://geoportail.wallonie.be/walonmap/, accessed November 2017]. *WalOnMap*, Brussels, Belgium

Shepard RN (1962) The analysis of proximities: multidimensional scaling with an unknown distance function II. *Psychometrika* 27:219–246

Simonová D, Lososová Z (2008) Which factors determine plant invasions in man-made habitats in the Czech Republic? *Perspect Pl Ecol Evol Syst* 10:89–100

Tischew S, Kirmer A (2007) Implementation of basic studies in the ecological restoration of surface-mined land. *Restorat Ecol* 15:321–325

Török P, Vida E, Deák B, Lengyel S, Tóthmérész B (2011) Grassland restoration on former croplands in Europe: an assessment of applicability of techniques and costs. *Biodivers & Conservation* 20:2311–2332

van den Boogaart KG, Tolosana R, Bren M (2013) *The composition package: compositional data analysis*. R package, version 0.9-11

Walker BH (1992) Biodiversity and ecological redundancy. *Conservation Biol* 6:18–23

Walker LR, del Moral R (eds) (2003) *Primary succession and ecosystem rehabilitation*. Cambridge University Press, Cambridge

Walker LR, Walker J, Hobbs RJ (eds) (2007) *Linking restoration and ecological succession*. Springer, New York

WallisDeVries MF, Poschlod P, Willems JH (2002) Challenges for the conservation of calcareous grasslands in northwestern Europe: integrating the requirements of flora and fauna. *Biol Conservation* 104:265–273

Woodward FI, Cramer W (1996) Plant functional types and climatic change: introduction. *J Veg Sci* 7:306–308