Research Article

Three years of vegetation development worth 30 years of secondary succession in urban-industrial grassland restoration

Running head: Urban-industrial grassland restoration

Anna Kövendi-Jakó[1,2], Melinda Halassy[1], Anikó Csecserits[1,3], Karl Hülber[4,5], Katalin Szitár[1,3], Thomas Wrbka[4], Katalin Török[1]

[1] Institute of Ecology and Botany, MTA Centre for Ecological Research, Alkotmány u. 2-4., Vácrátót, 2163 HU

[2] Department Plant Taxonomy, Ecology, and Theoretical Biology, Eötvös Loránd University, Budapest, Pázmány Péter stny. 1/c, Budapest, 1117 HU

[3] GINOP Sustainable Ecosystems Group, MTA Centre for Ecological Research, Klebelsberg Kuno u. 3., Tihany, 8237 HU

[4] Division of Conservation Biology, Vegetation Ecology and Landscape Ecology, Department of Botany and Biodiversity Research, University of Vienna, Rennweg 14., Vienna, 1030 AT

[5] Vienna Institute for Nature Conservation & Analyses, Giessergasse 6/7, Vienna, 1090 AT

Correspondence:

1. Anna Kövendi-Jakó, Institute of Ecology and Botany, MTA Centre for Ecological Research, Alkotmány u. 2-4., Vácrátót, 2163 HU
   Email: kovendi-jako.anna@okologia.mta.hu

Funding:

The study was funded by the LEGO group and by the National Science Foundation of Hungary (NKFI-OTKA FK127996). AKJ was supported by the ÚNKP-18-3 New National Excellence Program of the Ministry of Human Capacities. ACs was funded by the Hungarian Academy of Sciences (MTA PD-036/2015, PD-019/2016, PD009/2017) and by the GINOP-2.3.2-15-2016-00019 grant. KSz was supported by the GINOP-2.3.2-15-2016-00019 grant.

Abstract

Questions:

The restoration of unused urban-industrial areas has largely been neglected despite their great potential for nature conservation purposes. We applied three plant introduction treatments at a highly degraded industrial area to test whether plant material introduced to industrial areas initiate plant assemblages similar to the composition of reference grasslands. We specifically asked (1) Does restoration differ from primary and secondary reference sites in terms of overall species richness and cover three years after plant material introduction? (2) What is the sociability of species of the resulting vegetation at different treatments?

Location:

Restoration and reference grassland sites with acidic sandy soil in the temperate region of EU, NE Hungary, Nyírség.

Methods:

As restoration techniques we (i) directly seeded a single dominant species, (ii) applied a commercial seed mixture, and (iii) transferred hay. We compared species composition, cover, species richness and sociability of species of restoration treatments to reference grasslands. Inventories of vascular plant species were made at five randomly placed 2 m x 2 m sampling units per plot.

Results:

The species composition of seeded restoration plots (by single dominant species and a commercial seed mixture) became similar to reference grasslands. Both type of seeding resulted in similar cover, whereas seeding of commercial seed mixture and hay transfer resulted in similar species richness to reference grasslands. The cover of natural constituents of seeded plots also reached that of reference grasslands, while hay addition resulted in lower cover and higher number of natural constituents than other methods.

Conclusions:

The introduction of propagules in degraded industrial areas can provide after three years similar communities to those of secondary reference grasslands of 30 years of age. We conclude that investing in the restoration of native grasslands at unused urban-industrial sites can be a great opportunity to enhance biodiversity.

Keywords

dry grassland, industrial area, hay transfer, multiple reference sites, old-fields, seed sowing, species richness, sociability of species, urban-industrial restoration, vegetation cover

Introduction

In recent decades semi-natural grasslands have become strongly reduced in area and diversity due to the intensification of agricultural production (Bond, 2016; Török, Janišová, Kuzemko, Rūsiņa, and Stevanović, 2018b) and human land use, including urban, industrial and infrastructure expansion that is foreseen to accelerate (Maes et al. 2015). To compensate for this loss of natural areas, restoration must be up-scaled and extended from agricultural and semi-natural areas to urban and industrial sites (Aronson & Alexander, 2013; Hostetler, Allen, and Meurk, 2011; Klaus, 2013; Standish, Hobbs, and Miller, 2013). Maes et al. (2015) recommends every increase of artificial land to be compensated by a 2.2-fold increase of green infrastructure to maintain ecosystem services. Thus, any kind of unused land or vacant lot should be considered for extending the network of green infrastructure that beside the enhancement of biodiversity (Standish et al. 2013; Deák, Hüse, & Tóthmérész, 2016; Hüse, Szabó, Deák, & Tóthmérész, 2016; Anderson & Minor 2017) could greatly increase human wellbeing (Tzoulas et al. 2007).

Spontaneous secondary succession can be the most cost-effective way of restoration (Prach & Hobbs, 2008; Kiehl, Kirmer, Donath, Rasran, and Hölzel, 2010; Török, Vida, Deák, Lengyel, and Tóthmérész, 2011) but is not appropriate in cases of missing dispersal agents and processes, depletion of soil seed banks and lack of propagule sources (Bakker & Berendse, 1999; Hedberg & Kotowski, 2010). In such cases, artificial introduction of seeds is required (Kiehl et al. 2010; Török et al. 2011). Restoration efforts usually apply seeds of indigenous species aiming to restore (historical) native assemblages as far as it is feasible (Shackelford et al. 2013). Several methods of seed introduction can be used to fit the particular restoration need and abiotic environment. Commercial, low diversity seed mixtures (commonly comprising generalist species) efficiently reduce erosion due to the rapid establishment of a dense vegetation cover compared to hay transfer (Török et al. 2011), but the long-term persistence and ecosystem functioning might be compromised (Kettenring, Mercer, Reinhardt Adams, and Hines, 2014). Collection of local propagules is a viable alternative; however, local seed sourcing is usually difficult in large quantities (Török et al. 2018a) and might lead to poor restoration outcomes due to inbreeding (Broadhurst et al. 2008). The availability of seeds of suitable species in sufficient quantities is a major constraint in restoration (Havens et al. 2015), so the application of a single species can be an option (Piper, Schmidt, and Janzen, 2007; Oliveira, Clemente, Nunes, and Correia, 2014). Alternatively, transferring plant material in the form of hay or raked litter can result in higher species richness than seeding (Hedberg & Kotowski, 2010; Kiehl et al. 2010; Török et al. 2011). Since only few papers report on the greening of industrial areas aside from mining sites (Török et al. 2018a), we need further guidance on how to improve the natural state of urban-industrial areas that can contribute to compensate for land degradation.

The aim of the present study is to test the success of commercial seed mixtures, seeds of a single dominant species and the transfer of hay in restoring a severely disturbed industrial area. We compare the resulting vegetation three years after restoration interventions to those of primary (semi-natural grasslands) and secondary (old-fields) reference grasslands We tested whether plant material introduced to industrial areas initiate plant assemblages similar to the composition of reference grasslands. We specifically asked (1) Does restoration differ from primary and secondary reference sites in terms of overall species richness and cover three years after plant material introduction? (2) What is the sociability of species of the resulting vegetation at different treatments?

Methods

Study area

The study area is located in the Nyírség region (East Hungary, Appendix S1). Annual mean precipitation is 550-600 mm and annual average temperature is 9.8 ºC. The historic landscape was characterised by acidic inland sand dunes (with dune height of 5-10 m) covered with sandy grasslands and dry oak steppe forests on dunes and marshlands in depressions (Boros, 1929; Soó, 1939; Papp & Dudás, 1989). These natural vegetation types have been mostly transformed to arable lands, orchards, vineyards and tree plantations, resulting in the loss of natural habitats and the expansion of invasive species (e.g. *Asclepias syriaca, Robinia pseudo-acacia,* Botta-Dukát, 2008).

Restoration site

The restoration site (9.8 ha) is located around the factory buildings of the LEGO Group at Nyíregyháza, N-E Hungary in the region of Nyírség (lat 47° 57'N; long 21° 39'E). The factory was established at a former orchard and small farmlands, causing the complete loss of vegetation and damage to the original soil surface by flattening the ground. The remaining soil is compacted sand with low humus, calcium, and nutrient content and very low water holding capacity (Appendix S2). No sandy grasslands occur within a three km radius around the factory (Török et al. 2018a).

Reference sites

The target sandy grasslands have a high natural value and are protected by the Habitat Directive of the European Union (priority habitat code 6260; Romão, 1996). We selected both open (*Festuco vaginatae – Corynephoretum* Aszód 1935) and closed sandy grasslands (*Potentillo arenariae – Festucetum pseudovinae* Soó 1940, *Pulsatillo hungaricae - Festucetum rupicolae* Borhidi 1996). Open sand grasslands develop on low humus content, loose sandy soils at dune tops with a maximum cover of 75% (Bölöni, Botta-Dukát, Illyés, and Molnár, 2011). Closed sand grasslands develop on humus-rich sandy soils mostly at the foothills of surrounding mountains or at the lowland. The minimum plant cover is 50 % (Bölöni et al. 2011). The two types have originally formed a mosaic in the landscape, depending on relief, exposure and soil quality. However, both types have very fragmented occurrences in the study area presently. We further refer to grasslands selected at permanent grassland sites as primary reference.

Secondary grasslands developed on old-fields by spontaneous succession over more than 30 years were used as secondary reference sites (hereafter referred to as secondary reference). These sites created by land abandonment have the potential for the recovery of native temperate grasslands by old-field succession (Cramer, Hobbs, and Standish, 2008). In Central-Eastern Europe, spontaneous succession follows the pathway towards natural vegetation with a rapid development of low diversity, but weedy grasslands in the first ten years (Molnár & Botta-Dukát, 1998, Csecserits & Rédei, 2001; Halassy, 2001; Ruprecht, 2006; Csecserits et al. 2011; Albert et al. 2014).

Five sites representing the target vegetation were selected as reference for comparison with the restoration site. Primary reference sites representing extensively used, ancient grasslands were selected at three locations (Bátorliget 23 ha, Magy 6.5 ha, Martinka 185 ha). Two of them (Bátorligeti legelő nature conservation area, Martinkai legelő at Hajdúsámson) are in protected areas. The soil of these sites is slightly acidic or neutral sandy soil with low humus, calcium, and nutrient content, and higher nitrogen content (Appendix S2). Secondary reference sites were selected at two locations and included vineyards abandoned in the 1960s (Geszteréd) and in the end of 1980s (Ófehértó). Their soil is slightly acidic adobe sandy with low humus, calcium and nutrient content, and very low water holding capacity (Appendix S2). All reference sites are grazed with sheep or cattle. Both open and closed grasslands were studied at each of the five locations, referred to as primary open (POR), primary closed (PCR) and secondary open (SOR) and secondary closed (SCR) reference grasslands.

Restoration treatments

Around the factory we have seven restoration plots with different plant material introduction methods according to the availability of species at the time of release from construction (Török et al. 2018a). We present here in detail the results of the plant material introduction of 2014 at four restoration plots ranging from 1 to 4.5 ha in size (Fig. 1). Since plots of land became available too late in 2013 for applying the plant material introduction, lucerne (*Medicago sativa*) and rye *(Secale cereale)* were seeded (20 kg/ha) to reduce erosion by wind and to avoid a vegetation dominated by weeds and invasive species (mainly ragweed, *Ambrosia artemisiifolia*). All restoration plots were treated by deep soil loosening, ploughing, and seedbed preparation before applying one of the following restoration treatments: 1) introduction of commercial seeds (abbreviation: COM) of *Festuca pseudovina* as matrix grass species (30 kg/ha) and 26 native generalist forb species (15 kg/ha) produced in the Hungarian Lowland (Sep 2014). 2) Seeding of *Festuca rupicola* (60 kg/ha) as a single dominant generalist (abbreviation: DOM) harvested by reaping machine in the Hortobágy National Park (Sep 2014). Mulching by cut autumn biomass was applied on seeded plots (COM, DOM) shortly after seeding to control erosion by wind and for weed suppression (9 - 10 bales/ha). 3) Transfer of dried hay (two plots; abbreviation: HAY) obtained from donor sites within a 60 km distance from the factory. Early summer hay with a high content of *Festuca spp.* seeds (23.5 - 26 bales/ha; one bale weighted about 250 kg) was collected in two sites in Jun and in early Jul 2014, which was manually distributed to cover the whole plots by about 5 cm (Jul 2014). Bales from a late harvest (from Aug 2014) containing mainly forb seeds (3.5 - 5 bales/ha) were collected from a third site, this hay was distributed on top at a 3 cm thickness (Aug 2014). Seed content of hay and mulch was estimated by germination experiment of hay and mulch samples (data not shown). The restoration plots were mown twice yearly since seeding. For more details on the applied restoration treatments see Table 1.

Data recording and analyses

The success of restoration treatments was assessed by comparing the species composition at restoration plots to those of primary and secondary reference sites. Cover (in percentage) of each vascular plant species was visually estimated in five randomly placed sampling units (2 m x 2 m) at each restoration plots (yearly), at the three primary reference sites (in June either in 2015 or in 2016), and at the two secondary reference sites (in June 2017). In this paper we use cover data of restoration plots only from June 2017, i.e. three years after applying the restoration treatments, resulting in n=20 restoration and n=50 reference sampling units altogether. Due to uncertainties in the identification of young vegetative plants, *Festuca rupicola*, *F. pseudovina,* and *F. valesiaca* were merged as *Festuca spp.* for all analyses. Total cover (i.e. sum of individual species´ cover) and species richness (i.e. number of species) were calculated for each of the 70 sampling units. Nomenclature follows Király (2009).

We examined the sociability of species in the restoration plots compared to reference grasslands by merging the social behaviour types defined by Borhidi (1995), based on Grime (1979), in three major categories:1) natural constituents (NC - comprising specialists, competitors, generalists and natural pioneers); 2) disturbance tolerant species (DT, as in Borhidi, 1995); and 3) weeds (W - including introduced cultivated plants, ruderal competitors and adventive competitors). The number of species and cover values belonging to each category of sociability per sampling unit was used for analyses. For more details on the categories of studied species see Appendix S3.

Composition of sampling units was compared using non-metric multidimensional scaling (NMDS) and Analysis of Similarity (ANOSIM, Clarke, 1993) based on Bray-Curtis dissimilarity and Sørensen index. Number of dimensions (k) was set to two. For data processing the package “vegan” (Oksanen et al. 2017) of the R 3.3.1 statistical environment (R Core Team, 2016) was applied.

We used (generalized) linear mixed effects models (GLMM) implemented in the package “afex” (Singmann, Bolker, Westfall, and Aust, 2018) to compare total cover and species richness among restoration plots (COM, DOM, HAY) and reference sites (PCR, POR, SCR, SOR), used as seven levels of study sites factors in all models. Models were fit to data comprising species richness and total cover of all species of a sampling unit and separately to the three species groups based on sociability types. To consider potential independence of the data of the five sampling units at a site we allowed for a random intercept for each site in each model. For total cover and species richness a Gaussian and Poisson distribution were assumed. For the social behaviour type DT total cover data was transformed by square roots to fulfil the assumptions of normality and homoscedasticity. In case of total cover of the social behaviour type W the model residuals showed heterogeneity of variance for cover data even after square root transformation and, therefore linear mixed-effects (LME) models (Zuur et al. 2009) were applied by using the *“nlme”* package (Pinheiro et al. 2017) with varIdent variance structure which allowed for different residual spread for each level of the sites variable. For post hoc pairwise comparisons Tukey HSD tests were applied by using “*multcomp*“ package (Hothorn, Bretz, and Westfall, 2008), with p values adjusted by the method of Benjamini and Hochberg (1995).

Results

Composition based on multivariate analyses

According to the results of NMDS and ANOSIM analysis of cover data, the four reference grassland types proved to have significantly different composition from each other. As for the restoration treatments, the composition of sown restoration plots (COM, DOM) was similar to three reference sites, except for POR (Fig. 2; Table 2). HAY differed significantly from the seeding treatments (COM, DOM) and from all reference sites. Referring to the species composition all study sites differed significantly from each other (except the two secondary reference grasslands (SCR-SOR) based on the results of NMDS and ANOSIM analysis for presence/absence data (Appendix S4; S5).

Total cover and species richness

Study sites significantly differed (*chisq*= 51.33, *df*= 6, *p*< 0.001) based on the GLMM analysis of total cover. Tukey tests proved significant differences between closed and open types of reference sites (PCR-POR: *z*= -4.938, *p*< 0.001; PCR-SOR: *z*= -5.654, *p*< 0.001; SCR-POR: *z*= 3.554, *p*= 0.007; SCR-SOR: *z*= -4.374, *p*< 0.001, Fig. 3a). Concerning restoration treatments, gradually lower cover from the commercial seeding, dominant species seeding, and hay addition was detected, however, not significant. The total vegetation cover of restoration sampling units was similar to that of reference sites, except for significant differences found between COM and SOR (*z*= -3.624, *p*= 0.005) and between HAY and PCR (*z* = -3.930, *p*= 0.002). Species richness differed significantly among study sites (*chisq*= 14.777, *df*= 6, *p*= 0.022) based on the GLMM analysis. According to Tukey test, all restoration treatments resulted in similar species richness to one another, and to the reference sites, except DOM with the lowest species richness per sampling unit, which was significantly different from both closed reference sites (PCR-DOM: *z*= -3.139, *p*= 0.027; SCR-DOM: *z*= 2.951, *p*= 0.047) (Fig. 3b).

Sociability of species

According to the results of GLMM the total cover of NC species was significantly different among the study sites (*chisq*= 44.282, *df*= 6, *p*< 0.001). Based on Tukey HSD tests, there was a significant difference between closed and open types of reference sites in case of primary grasslands (PCR-POR: *z*= -3.780, *p*= 0.003; PCR-SOR: *z*= -3.243, *p*= 0.019). Restoration treatments resulted in similar cover of NC compared to reference sites, except for HAY that had significantly lower total cover of NC than closed reference sites (HAY-PCR: $z= -6.153$, $p< 0.001$; HAY-SCR: $z= -4.394$, $p< 0.001$). HAY and COM ($z= -3.602$, $p= 0.006$) as well as HAY and DOM ($z= -3.038$, $p= 0.037$) resulted in significant difference in total cover of NC (Fig. 4a). Study sites had significant effect on the species richness of NC species ($chisq= 28.351$, df= 6, $p< 0.001$). Based on Tukey HSD test the reference sites were similar to each other. HAY resulted in a similar species richness to reference sites, whereas COM and DOM resulted in significantly lower number of NC compared to primary open grasslands (COM-POR: $z= -3.513$, $p= 0.008$; DOM-POR: $z= -4.104$, $p< 0.001$), primary closed (DOM-PCR: $z= -3.416$, $p= 0.01$), and secondary closed grasslands (DOM-SCR: $z= -3.096$, $p= 0.029$, Fig. 4b).

Study sites had significant effect on the cover of DT species ($chisq= 23.152$, $df= 6$, $p< 0.001$) based on GLMM. The reference sites were not significantly different from each other based on cover of DT species according to the Tukey HSD test. Restoration treatments resulted in similar cover of DT compared to reference sites, except for HAY that resulted in significantly higher total cover than open reference sites (POR-HAY: $z= 3.653$, $p= 0.005$; SOR-HAY: $z= 3.746$, $p= 0.003$, Fig. 4c). Study sites had significant effect on the species richness of DT ($chisq= 22.327$, $df= 6$, $p= 0.001$) based on GLMM. According to Tukey HSD test, significantly higher richness of DT was found for PCR, than POR (POR-PCR: $z= -4.129$, $p< 0.001$). Restoration treatments resulted in similar species richness of DT compared to reference sites, except for HAY that had significantly higher species richness of this group than POR ($z= 3.343$, $p= 0.014$, Fig. 4d).

Although W species had higher mean total cover in the restored than in the reference grasslands, these differences were not significant based on the LME analyses ($chisq= 6.766$, $df= 6$, $p= 0.343$, Fig. 4e). Concerning species richness of W, the study sites had significant effect ($chisq= 28.484$, $df= 6$, $p< 0.001$). Significant difference of species richness of W was not detected among reference sites and among restoration sites. HAY and COM addition had significantly higher species richness of W than primary reference sites (COM-PCR: $z= 3.861$, $p= 0.002$; COM-POR: $z= 3.375$, $p= 0.013$; HAY-PCR: $z= 3.975$, $p= 0.001$; HAY-POR: $z= 3.446$ $p= 0.01$, Fig. 4f).

Discussion

Overall cover and species richness

Our study proved the difference in total cover of closed versus open grasslands, both in primary and secondary references. Treated samples have intermediate total cover, while only hay additions resulted in lower cover values than primary closed reference. The seeding of commercial seed mixture allowed for a rapid establishment of the seeded species resulting in the highest vegetation cover (85 %) similar as found by Török et al. (2011). Sowing of the dominant grass species resulted more than 70 % average cover by the third growing season, which is in the range reported by other studies applying low-diversity seed mixtures (Török et al. 2010; Vida et al. 2010). This method is more cost-effective than sowing commercial seed mixtures (Török et al. 2011), but at the expense of having less species rich assemblages. Hay transfer, which is often used to start secondary succession (Rasran, Vogt, and Jensen, 2006; Kiehl, Thormann, and Pfadenhauer, 2006), resulted in a slightly lower species cover. Important factors affecting the restoration success when transferring hay are the species composition of donor sites, the timing of the hay collection and hay storage (Rasran et al. 2006; Kiehl et al. 2010; Török et al. 2011). In our study, the application of dry, stored hay can be an explanation for lower plant cover, as dry hay usually contains lower amount of viable seeds than that of fresh plant material without storage (Kiehl et al. 2010).

Contradicting several studies, the primary and secondary reference grasslands are very similar in species richness (Molnár & Botta-Dukát, 1998; Prach et al. 2016). The colonization of specialist species can take hundreds of years based on these studies, so primary reference grasslands should have higher richness. Fragmented cultivation might have led to specialist species survival at field margins (Hackett & Lawrence 2014) that could contribute to similar species richness at secondary reference sites. Besides, we assume that dispersal by moderate grazing also helps to increase species richness at secondary sites. In the restoration plots species introduction resulted in similar richness to reference grasslands, hay transfer resulting in slightly higher values, however, not significant. The early success of grass species can be contradictory in the long run decreasing the efficiency of further species establishment. Sown grass species (either applied alone or in seed mixtures) can become dominant very fast on the cost of sown or naturally introduced forb species and decrease overall species richness in the long run in restoration sites (Török et al. 2011). The dense cover of dominant species as perennial grasses entails spontaneous colonization of rare species to be very slow even in case of propagule availability in the surroundings (Török et al. 2010; Vida et al. 2010). This limitation for species establishment justifies further interventions including the diversification of the grasslands, like the application of establishment gaps with high-diversity sowing (Valkó et al. 2016). Contrary to several studies (Kiehl et al. 2006; Kiehl et al. 2010; Török et al. 2011), hay transfer resulted in similar species richness to other restoration treatments, which can be explained by the application of dry, stored hay with lower viable seed content. For further restoration projects we suggest using seed-containing hay in combination with single species or seed mixture seeding, preferably from late harvest to increase the number of forbs in the vegetation (Török et al. 2012).

Sociability of species

The goal in this experiment was to introduce the natural constituents of the target community. Reference sites had higher cover and species richness of natural constituent species. Both types of seedings (dominant species and commercial seed mixture) introduced very few natural constituent species, but these reached a total cover similar to that of the reference grasslands. At the same time, the hay transfer performed slightly higher richness in natural constituents with lower total cover, which supports the idea of using this technique as a complementary treatment to seeding (Török et al. 2012). Despite restoration sites being at an early stage of succession (3rd year), the expected higher cover of disturbance tolerant species and weeds compared to references was not confirmed. The number of weed species was higher with hay transfer and commercial seed mixture than that of primary reference sites. Hay transfer resulted in more open vegetation with gaps, which provide physical space for germination and establishment of weedy species from the soil seed bank. This problem can be detected especially in former agricultural areas, where the original seed bank was replaced by weedy species in the soil seed bank (Bakker & Berendse, 1999). This is less expected in industrial areas, where the seed bank is destroyed, rather than replaced by weedy species. The cover of natural constituents of the restoration plots should be further increased by regular mowing to decrease the total cover and richness of weeds as in other studies (Kiehl et al. 2010; Török et al. 2011).

Success of restoration

We found that the vegetation composition of seeded plots (dominant species and commercial seed mixture) became similar to that of the reference sites based on cover data, except the primary open grassland that also differed from the other reference sites. In contrast, the vegetation composition of the plot with hay addition remained significantly different from all other samples. These results suggest that seeding successfully accelerated succession towards secondary grasslands and primary closed grasslands in three years, compared to secondary reference grasslands developed in more than 30 years. Several investigations (Molnár & Botta-Dukát, 1998; Csecserits & Rédei, 2001; Halassy, 2001; Ruprecht, 2006; Csecserits et al. 2011; Albert et al. 2014) found that spontaneous succession at old-fields in the Pannonian region can develop to semi-natural grasslands on disturbed areas within 10-20 years, however the cover of specialist species remains low (Molnár & Botta-Dukát, 1998; Prach et al. 2016), and the cover of alien species is much higher than in natural grasslands (Csecserits et al. 2011; Csecserits et al. 2016). Mitchley, Jongepierova and Fajmon (2012) consider 10-60 years insufficient to restore species rich grasslands. Overall, our study supports that this time-consuming succession can be accelerated by seeding.

We provide a summary of the advantages and disadvantages of seed introduction methods based on six criteria (Table 3) to help selecting the most appropriate technique in future restoration projects at unused industrial areas or vacant lots. The study demonstrated that there is no single “best method” for restoration; the selection should be based on the particular demand and circumstances (Shackelford et al. 2013; Adams, Hodge, Macgregor, and Sandbrook, 2016). Multiple constraints exist in all restoration projects, but in case of intensively modified landscapes, like urban-industrial sites, efforts needed to handle the constraints can be higher (Arenas, Escudero, Mola, and Casado, 2017). This guidance helps to select appropriate method in future projects, linked to the green infrastructure policy of the European Union (European Commission, 2013). For example, in case of limited seed availability, hay addition can be a good alternative; or if rapid green surface is a priority, commercial seed mixtures are appropriate; low budget can be the reason for single species seeding and still reaching similar target species cover to reference grasslands. It is important however, that the aim to enhance biodiversity should not be compromised (Standish et al. 2013). In our case the applied restoration methods significantly contributed to increase species richness, cover and similarity towards reference grasslands, but little significant difference was detected among the restoration treatments.

Conclusions

The potential of unused urban-industrial areas for enhancing biodiversity is widely ignored in the world, although their restoration has advantages for conservation (Klaus, 2013; Deák et al. 2016; Hüse et al. 2016) and green infrastructure development (Hostetler et al. 2011; Deák et al. 2016; Hüse et al. 2016). Instead of creating intensively managed, species poor green areas, these non-built-up lands could be used to restore more self-sustainable, native biodiversity refuges (Török et al. 2018a) that provide additional ecosystem services, like pollination (Kovács-Hostyánszki et al. 2017) or amenity value (Martens, Gutscher, and Bauer, 2011). We tested the role of restoration treatments in enhancing the species cover, richness, naturalness in terms of sociability of species and similarity to reference grassland composition and provide guidance on how to choose best method for a given situation. The success of our grassland restoration project is encouraging regarding the difficulties of urban-industrial area restoration, like dispersal (limitation of available propagule and dispersal agents), biotic (competition) and abiotic (soil, microclimate) constraints (Klaus, 2013). In three years the restored vegetation reached a state similar to that of old-fields by spontaneous succession of more than 30 years. We conclude that the re-creation of native grasslands by assisted introduction of species at industrial areas provides a great opportunity to enhance biodiversity in a relatively short period of time and thus contribute to the development of green infrastructure in Europe (Standish et al. 2013; Liquete et al. 2015).

Acknowledgments

The authors thank the LEGO group for providing the infrastructure and the Hortobágy National Park Directorate for providing plant material for restoration. We thank Csaba Szigetvári, who helped to find appropriate reference sites Gardening work has been carried out by the Deep Forest Ltd. We thank students and Barbara Lhotsky for help in field work.

Author contributions

ACs, AKJ, KT, MH conceived and designed the study; ACs, AKJ, MH, KT did collections and other field work; AKJ, KSz, KH made statistical analyses; AKJ, MH, KH, KSz, KT, TW wrote and edited the paper. All authors contributed critically to the drafts and gave final approval for publication.

Data accessibility

Data are available from ZENODO: https://zenodo.org/record/1227269 (Kövendi-Jakó, 2018)

References

Adams, W. M., Hodge, I. D., Macgregor, N.A., & Sandbrook, L. (2016). Creating restoration landscapes: partnerships in large-scale conservation in the UK. *Ecology and Society, 21,* 1. https://doi.org/10.5751/ES-08498-210301

Albert, Á. J., Kelemen, A., Valkó, O., Miglécz, T., Csecserits, A., Rédei, T., … Török, P. (2014). Secondary succession in sandy old-fields: a promising example of spontaneous grassland recovery. *Applied Vegetation Science, 17,* 214-224.https://doi.org/10.1111/avsc.12068

Anderson, E.C., & Minor, E.S. (2017). Vacant lots: An underexplored resource for ecological and social benefits in cities. *Urban Forestry & Urban Greening, 21,* 146-152. https://doi.org/10.1016/j.ufug.2016.11.015

Arenas, J. M., Escudero, A., Mola, I., & Casado, M. A. (2017). Roadsides: an opportunity for biodiversity conservation. *Applied Vegetation Science, 20,* 527–537. https://doi.org/10.1111/avsc.12328

Aronson, J., & Alexander, S. (2013). Ecosystem restoration is now a global priority: time to roll up our sleeves. *Restoration Ecology, 21*, 293–296. https://doi.org/10.1111/rec.12011

Aszód, L. (1935). Adatok a nyírségi vegetáció ökológiájához és szociológiájához [Data on the vegetation ecology and sociology of Nyírség]. *Tiscia, 1,* 75–107 (in Hungarian).

Bakker, J. P., & Berendse, F. (1999). Constraints in the restoration of ecological diversity in grassland and heathland communities. *Trends in Ecology & Evolution, 14,* 63–68. https://doi.org/10.1016/S0169-5347(98)01544-4

Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society, Series B (Methodological),* 289–300.

Bond, W. J. (2016). Ancient grasslands at risk. *Science, 351,* 120–122. doi: 10.1126/science.aad5132

Borhidi, A. (1995). Social behaviour types, the naturalness and relative ecological indicator values of the higher plants in the Hungarian flora. *Acta Botanica Hungarica, 39,* 97–181.

Borhidi, A. (1996). *Critical revision of the Hungarian plant communities.* Janus Pannonius University, Pécs, HU.

Boros, Á. (1929). Die Flora und die Planzengeographen verhältnisse des Nyírség [in German]. - Mathematischer und Naturwissenschaftlicher Anzeiger der Ungarischen Akademie der Wissenschaften *XLVI. Sonderabdruck,* 48–59.

Botta-Dukát, Z. (2008). Invasion of alien species to Hungarian (semi-)natural habitats. *Acta Botanica Hungarica, 50,* 219–227. https://doi.org/10.1556/ABot.50.2008.Suppl.11

Bölöni, J., Botta-Dukát, Z., Illyés, E., & Molnár, Z. (2011). Hungarian landscape types: classification of landscapes based on the relative cover of (semi-) natural habitats. *Applied Vegetation Science, 14,* 537-546. https://doi.org/10.1111/j.1654-109X.2011.01139.x

Broadhurst, L. M., Lowe, A., Coates, D. J., Cunningham, S. A., McDonald, M., Vesk, P. A., & Yates, C. (2008). Seed supply for broadscale restoration: maximizing evolutionary potential. *Evolutionary Applications, 1,* 587–597. https://doi.org/10.1111/j.1752-4571.2008.00045.x

Clarke, K. R. (1993). Non-parametric multivariate analysis of changes in community structure. *Australian Journal of Ecolo*gy, *18,* 117–143. https://doi.org/10.1111/j.1442-9993.1993.tb00438.x

Cramer, V., Hobbs, R., & Standish, R. (2008). What's new about old fields? Land abandonment and ecosystem assembly. *Trends in Ecology & Evolution, 23,* 104–112. https://doi.org/10.1016/j.tree.2007.10.005

Csecserits, A., & Rédei, T. (2001). Secondary succession on sandy old-fields in Hungary. *Applied Vegetation Science, 4,* 63–74. https://doi.org/10.1111/j.1654-109X.2001.tb00235.x

Csecserits, A., Czúcz, B., Halassy, M., Kröel-Dulay, G., Rédei, T., Szabó, R., ... Török, K. (2011). Regeneration of sandy old-fields in the forest steppe region of Hungary. *Plant Biosystems, 145,* 715-729. https://doi.org/10.1080/11263504.2011.601340

Csecserits, A., Botta-Dukát, Z., Kröel-Dulay, G., Lhotsky, B., Ónodi, G., Rédei, T., ... Halassy, M. (2016). Tree plantations are hot-spots of plant invasion in a landscape with heterogeneous land-use. *Agriculture, Ecosystems & Environment, 226,* 88-98. https://doi.org/10.1016/j.agee.2016.03.024

Deák, B., Hüse, B., & Tóthmérész, B. (2016). Grassland vegetation in urban habitats–testing ecological theories. *Tuexenia, 36,* 379-393. doi: 10.14471/2016.36.017

European Commission (2013). *Building a Green Infrastructure for Europe*. European Union.

Grime, J. P. (1979). *Plant strategies and vegetation processes.* Chichester, UK: J. Wiley and Sons.

Hackett, M., & Lawrence, A. (2014). *Multifunctional role of field margins in arable farming*. CEA report. Cambridge Environmental Assessments.

Halassy, M. (2001). Possible role of the seed bank in the restoration of open sand grassland in old fields. *Community Ecology, 2,* 101–108. https://doi.org/10.1556/ComEc.2.2001.1.11

Havens, K., Vitt, P., Still, S., Kramer, A.T., Fant, J. B., & Schatz, K. (2015). Seed sourcing for restoration in an era of climate change. *Natural Areas Journal, 35,* 122–133. https://doi.org/10.3375/043.035.0116

Hedberg, P., & Kotowski, W. (2010). New nature by sowing? The current state of species introduction in grassland restoration, and the road ahead. *Journal for Nature Conservation, 18,* 304–308. https://doi.org/10.1016/j.jnc.2010.01.003

Hostetler, M., Allen, W., & Meurk, C. (2011). Conserving urban biodiversity? Creating green infrastructure is only the first step. *Landscape and Urban Planning, 100,* 369–371. https://doi.org/10.1016/j.landurbplan.2011.01.011

Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal, 50,* 346–363. https://doi.org/10.1002/bimj.200810425

Hüse, B., Szabó, S., Deák, B., & Tóthmérész, B. (2016). Mapping an ecological network of green habitat patches and their role in maintaining urban biodiversity in and around Debrecen city (Eastern Hungary). *Land Use Policy, 57*, 574-581. doi:10.1016/j.landusepol.2016.06.026

Kettenring, K. M., Mercer, K. L., Reinhardt Adams, C., & Hines, J. (2014). Editor’s choice: Application of genetic diversity–ecosystem function research to ecological restoration. *Journal of Applied Ecology, 51,* 339–348. https://doi.org/10.1111/1365-2664.12202

Kiehl, K., Thormann, A., & Pfadenhauer, J. (2006). Evaluation of initial restoration measures during the restoration of calcareous grasslands on former arable fields. *Restoration Ecology, 14,* 148–156. https://doi.org/10.1111/j.1526-100X.2006.00115.x

Kiehl, K., Kirmer, A., Donath, T. W., Rasran, L., & Hölzel, N. (2010). Species introduction in restoration projects–Evaluation of different techniques for the establishment of semi-natural grasslands in Central and Northwestern Europe. *Basic and Applied Ecology, 11,* 285–299. https://doi.org/10.1016/j.baae.2009.12.004

Király, G. (Eds.) (2009). *Új magyar füvészkönyv. Magyarország hajtásos növényei. Határozókulcs. Ábrák* [New Hungarian herbal. Vascular plants of Hungary. Identification keys]. Jósvafő, HU: Aggteleki Nemzeti Park Igazgatóság.

Klaus, V. H. (2013). Urban grassland restoration: A neglected opportunity for biodiversity conservation. *Restoration Ecology, 21,* 665–669. https://doi.org/10.1111/rec.12051

Kovács-Hostyánszki, A., Espíndola, A., Vanbergen, A. J., Settele, J., Kremen, C., & Dicks, L. V. (2017). Ecological intensification to mitigate impacts of conventional intensive land use on pollinators and pollination. *Ecology Letters, 20,* 673-689. https://doi.org/10.1111/ele.12762

Liquete, C., Kleeschulte, S., Dige, G., Maes, J., Grizzetti, B., Olah, B., & Zulian, G. (2015). Mapping green infrastructure based on ecosystem services and ecological networks: A Pan-European case study. *Environmental Science & Policy, 54,* 268–280. https://doi.org/10.1016/j.envsci.2015.07.009

Maes, J., Barbosa, A., Baranzelli, C., Zulian, G., e Silva, F. B., Vandecasteele, I., … Lavalle, C. (2015). More green infrastructure is required to maintain ecosystem services under current trends in land-use change in Europe. *Landscape Ecology, 30,* 517–534. https://doi.org/10.1007/s10980-014-0083-2

Martens, D., Gutscher, H., & Bauer, N. (2011). Walking in ‘wild’ and ‘tended’ urban forests: the impact on psychological well-being. *Journal of Environmental Psychology, 31,* 36–44. https://doi.org/10.1016/j.jenvp.2010.11.001

Mitchley, J., Jongepierová, I., & Fajmon, K. (2012). Regional seed mixtures for the re-creation of species-rich meadows in the White Carpathian Mountains: results of a 10-yr experiment. *Applied Vegetation Science, 15,* 253-263. https://doi.org/10.1111/j.1654-109X.2012.01183.x

Molnár, Z., & Botta-Dukát, Z. (1998). Improved space-for-time substitution for hypothesis generation: secondary grasslands with documented site history in SE-Hungary. *Phytocoenologia, 28,* 1–29.

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., … Wagner, H. H. (2017, August 24). Vegan: Community Ecology Package. R package version 2.4-4. Retrieved from https://CRAN.R-project.org/package=vegan

Oliveira, G., Clemente, A., Nunes, A., & Correia, O. (2014). Suitability and limitations of native species for seed mixtures to revegetate degraded areas. *Applied Vegetation Science, 17,* 726–736. https://doi.org/10.1111/avsc.12099

Papp, L., & Dudás, M. (1989). Adatok a Közép-, a Dél-Nyírség és környékének botanikai értékeiről [Data of botanical values of Middle-, South-Nyírség and surroundings] [in Hungarian]. *Calandrella* II/2.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Heisterkamp, S., Van Willigen, B., & Maintainer, R. (2017, January 22). Package ‘nlme’. *Linear and nonlinear mixed effects models,* 3-1. R package version 3.1-128. Retrieved from https://cran.r-project.org/web/packages/nlme/index.html

Piper, J. K., Schmidt, E. S., & Janzen, A. J. (2007). Effects of species richness on resident and target species components in a prairie restoration. *Restoration Ecology, 15,* 189–198. https://doi.org/10.1111/j.1526-100X.2007.00203.x

Prach, K., & Hobbs, R. J. (2008). Spontaneous succession versus technical reclamation in the restoration of disturbed sites. *Restoration Ecology, 16,* 363–366. https://doi.org/10.1111/j.1526-100X.2008.00412.x

Prach, K., Tichý, L., Lencová, K., Adámek, M., Koutecký, T., Sádlo, J., … Řehounková, K. (2016). Does succession run towards potential natural vegetation? An analysis across seres. *Journal of Vegetation Science, 27,* 515–523. https://doi.org/10.1111/jvs.12383

R Core Team (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from https://www.R-project.org/.

Rasran, L., Vogt, K., & Jensen, K. (2006). Seed content and conservation evaluation of hay material of fen grasslands. *Journal for Nature Conservation, 14,* 34–45. https://doi.org/10.1016/j.jnc.2005.08.002

Romão, C. (1996). *Interpretation manual of European Union habitats*. European Commision.

Ruprecht, E. (2006). Successfully recovered grassland: a promising example from Romanian old-fields. *Restoration Ecology, 14,* 473–480. https://doi.org/10.1111/j.1526-100X.2006.00155.x

Shackelford, N., Hobbs, R., Burgar, J. M., Erickson, T. E., Fontaine, J. B., Laliberte, E., … Standish, R. (2013). Primed for change: Developing ecological restoration for the 21st century. *Restoration Ecology, 21,* 297–304. https://doi.org/10.1111/rec.12012

Singmann, H., Bolker, B., Westfall, J., & Aust, F. (2018, April 4). Afex: Analysis of Factorial Experiments. R package version 0.20-1. Retrieved from https://CRAN.R-project.org/package=afex

Soó, R. (1939). *A Nyírség természeti kincsei* [Nyírség natural assets] [in Hungarian]. Budapest, HU: Merkantil-nyomda.

Soó, R. (1940). Vergangenheit und Gegenwart der pannonischen Flora und Vegetation. *Nova Acta Leopold, 9,* 1–49.

Standish, R., Hobbs, R., & Miller, J. R. (2013). Improving city life: options for ecological restoration in urban landscapes and how these might influence interactions between people and nature. *Landscape Ecology, 28,* 1213–1221. https://doi.org/10.1007/s10980-012-9752-1

Török, K., Csecserits, A., Somodi, I., Kövendi-Jakó, A., Halász, K., Rédei, T., & Halassy, M. (2018a). Restoration prioritization for industrial area applying multiple potential natural vegetation modeling. *Restoration Ecology, 26*, 476-488. https://doi.org/10.1111/rec.12584

Török, P., Deák, B., Vida, E., Valkó, O., Lengyel, S., & Tóthmérész, B. (2010). Restoring grassland biodiversity: Sowing low-diversity seed mixtures can lead to rapid favourable changes. *Biological Conservation, 143,* 806–812. https://doi.org/10.1016/j.biocon.2009.12.024

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. *Biodiversity and Conservation, 20,* 2311–2332. https://doi.org/10.1007/s10531-011-9992-4

Török, P., Miglécz, T., Valkó, O., Kelemen, A., Tóth, K., Lengyel, S. & Tóthmérész, B. (2012). Fast restoration of grassland vegetation by a combination of seed mixture sowing and low-diversity hay transfer. *Ecological Engineering 44,* 133–138. https://doi.org/10.1016/j.ecoleng.2012.03.010

Török, P., Janišová, M., Kuzemko, A., Rūsiņa, S., & Stevanović, Z. D. (2018b). Grasslands, their threats and management in Eastern Europe. In: Squires, V.R., Dengler, J., Feng, H., Hua, L. (Eds.) *Grasslands of the world: diversity, management and conservation.* Boca Raton, US: CRC Press.

Tzoulas, K., Korpela, K., Venn, S., Yli-Pelkonen, V., Kaz´mierczak, A., Niemela, J., & James, P. (2007). Promoting ecosystem and human health in urban areas using Green Infrastructure: a literature review. *Landscape and urban planning*, *81,* 167–178. https://doi.org/10.1016/j.landurbplan.2007.02.001

Valkó, O., Deák, B., Török, P., Kirmer, A., Tischew, S., Kelemen, A., … Tóthmérész, B. (2016). High-diversity sowing in establishment windows: a promising new tool for enhancing grassland biodiversity. *Tuexenia, 36,* 359–378. http://dx.doi.org/10.14471/2016.36.020

Vida, E., Valkó, O., Kelemen, A., Török, P., Deák, B., Miglécz, T., … Tóthmérész, B. (2010). Early vegetation development after grassland restoration by sowing low-diversity seed mixtures in former sunflower and cereal fields. *Acta Biologica Hungarica*, *61*, 226–235. https://doi.org/10.1556/ABiol.61.2010.Suppl.22

Zuur, A. F. (Ed.) 2009. *Mixed effects models and extensions in ecology with R, Statistics for biology and health.* New York, US: Springer.

Table 1. Summary of restoration treatments applied. For details on seeding rates per species see Török et al. (2018a). Quantity of grass and forb species by hay transfer are derived from germination experiment (data not shown). One-third of the bales used for hay transfer or mulch were sampled before distribution in 2014. Roughly cleaned samples of hay and mulch were measured and germinated under controlled conditions (temperature: 16±0.3°C; dew point:12±0.2g/m3; humidity: 84±0.7%) on clean construction sand in trays at the experimental area of the National Botanical Garden, Vácrátót. Germinated adult species were identified at species level. Germination data (number of specimen and species) from hay or mulch samples were used to determine the seed content of species of hay and mulch; and to estimate introduced seed quantity (kg/ha) to restoration plots (* seeds added by hay transfer or mulch), by using thousand seed weight data.

Restoration plot	COM	DOM	HAY1	HAY2
area (ha)	4.5	2.6	1	1.7
Preparatory plant				
Timing	2013 autumn	2014 spring	2013 autumn	2013 autumn
Preparatory plant (kg/ha)	20	20	20	20
Hay transfer				
Timing			2014 summer	2014 summer
Grass (bale)			26	40
Forb (bale)			5	6
Seeding				
Timing	2014 autumn	2014 autumn		
Dominant grass	*Festuca pseudovina*	*Festuca rupicola*		
grass (kg/ha)	30	60	1.769*	0.717*
forb (kg/ha)	15		0.093*	0.08*
Mulching				
Timing	2014 autumn	2014 autumn		
Mulch (bale)	42	26		
grass (kg/ha)	0.022*	0.007*		
forb (kg/ha)	0.005*	0.132*		

Table 2. Results of ANOSIM analyses. Composition of reference sites and restoration plots compared using ANOSIM analyses based on cover data. Significant differences are given in bold. Abbreviations: primary closed reference (PCR), primary open reference (POR), secondary closed reference (SCR), secondary open reference (SOR), commercial seed mixture (COM), seeds of a single dominant species (DOM), hay transfer (HAY).

	HAY	COM	DOM	POR	PCR	SOR
	R/p value	*R/p* value	*R/p* value	*R/p* value	*R/p* value	*R/p* value
COM	**0.31/0.021**	.	.	.	.	.
DOM	**0.27/0.033**	0.25/0.068	.	.	.	.
POR	**0.64/0.001**	**0.61/0.001**	**0.57/0.001**	.	.	.
PCR	**0.53/0.001**	0.05/0.316	0.01/0.428	**0.47/0.001**	.	.
SOR	**0.41/0.001**	0.15/0.14	0.03/0.296	**0.29/0.006**	**0.15/0.045**	.
SCR	**0.45/0.001**	0.16/0.097	0.08/0.219	**0.51/0.001**	**0.16/0.04**	**0.16/0.015**

Table 3. Guidance helping to select the most appropriate restoration treatment regarding six priorities (naturalness = appropriate ratio of sociability of species, total cover, species richness) or constraints (treatment effort, cost effectiveness, shortage of local propagules). Treatments are assessed as highly appropriate/effective (+++), moderately appropriate/effective (++) or less appropriate/effective (+) concerning six selection criteria. Assessment was based on results of this study (see Fig. 3 and 4) supplemented by expert knowledge. (* Lower treatment effort is considered more effective; mulching after seeding increases efforts in commercial seed mixture and sowing of dominant species.)

Treatment	Naturalness	Total cover	Species richness	Treatment effort*	Cost effectiveness	Shortage of local propagules
Commercial seed mixture	++	+++	++	++	+++	+++
Sowing of dominant species	++	++	+	++	+	++
Hay transfer	+	+	+++	+++	++	+

Figures

Figure 1. Map of three applied plant introduction treatments at an unused urban-industrial area in Nyírség, NE Hungary. Restoration treatments were the following: commercial seed mixture (COM); seeds of a single dominant species (DOM), hay transfer (HAY). Species is listed in Appendix S3.

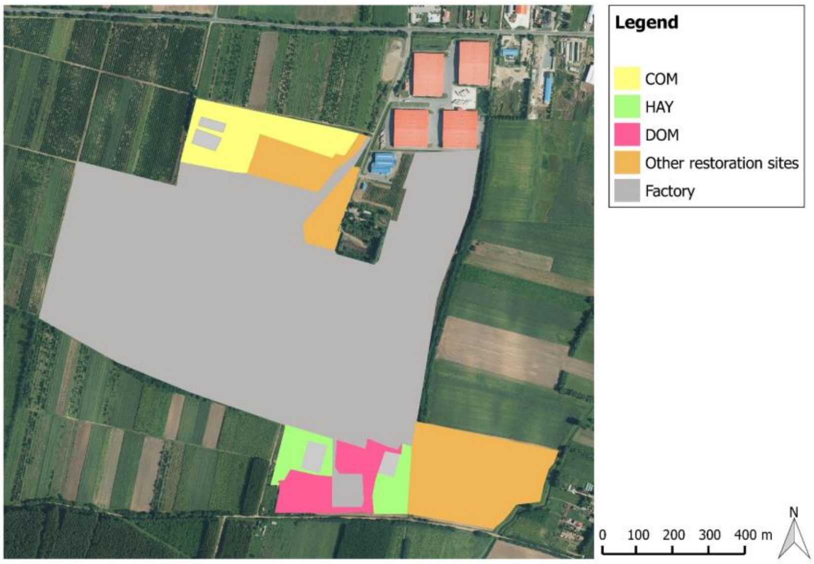


Figure 2. Non-Metric Multidimensional Scaling (NMDS) of the composition of three restoration treatments (COM, DOM, HAY) and four reference types (PCR, POR, SCR, SOR) based on cover data by using of Bray-Curtis dissimilarity. Abbreviations: primary closed reference (PCR), primary open reference (POR), secondary closed reference (SCR), secondary open reference (SOR), commercial seed mixture (COM), seeds of a single dominant species (DOM), hay transfer (HAY).

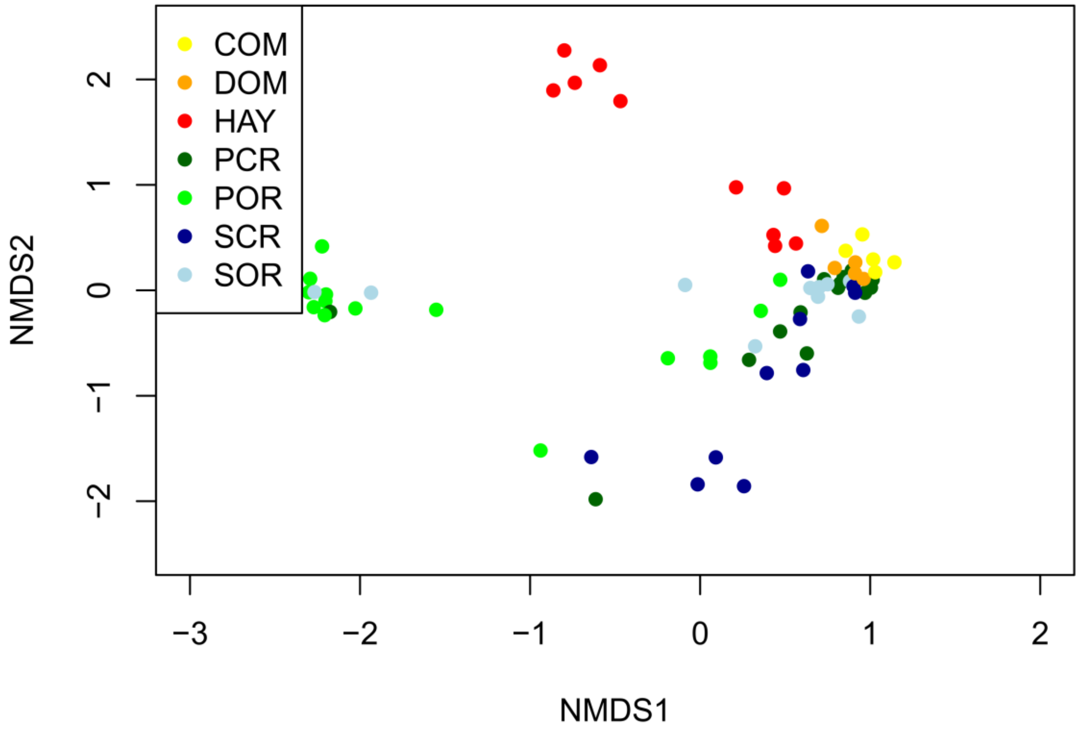
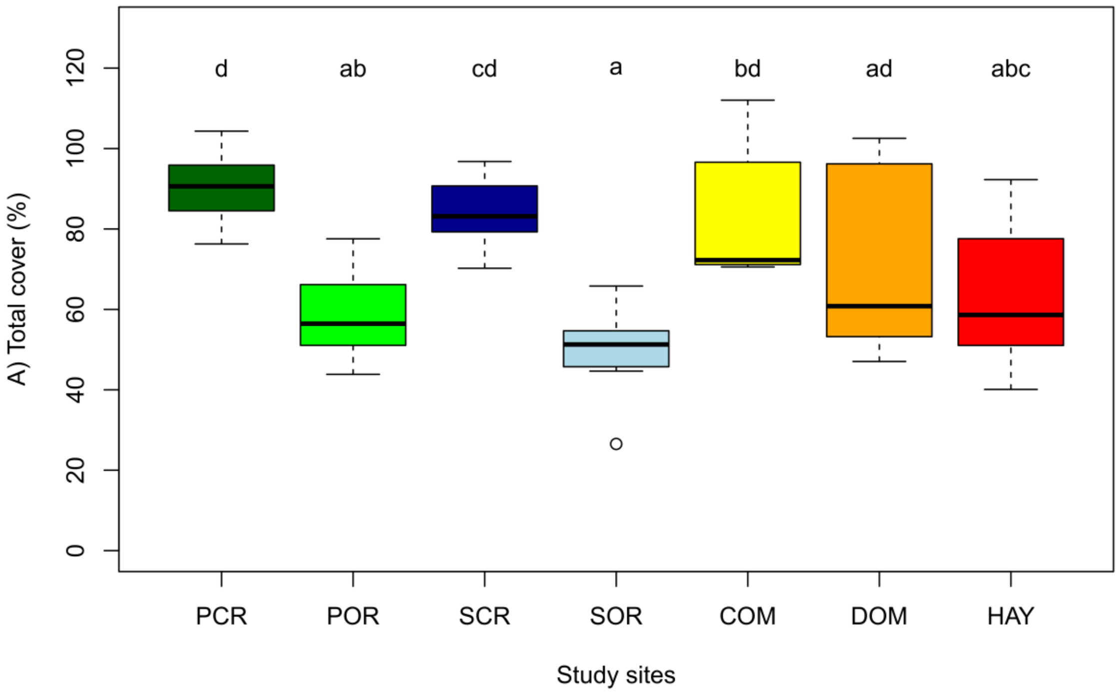


Figure 3. Total cover (A) and species richness (B) of restoration plots and reference sites. Figures represent the distribution of total cover/species richness data based on the minimum, first quartile, median, third quartile, and maximum. Total cover (i.e. sum of individual species´ cover) and species richness (i.e. number of species) were calculated for each of the 70 sampling units. Significant differences among study sites are indicated by lower case letters. Abbreviations: primary closed reference (PCR), primary open reference (POR), secondary closed reference (SCR), secondary open reference (SOR), commercial seed mixture (COM), seeds of a single dominant species (DOM), hay transfer (HAY).


A) Total cover (%)
0
20
40
60
80
100
120
d
ab
cd
a
bd
ad
abc
PCR
POR
SCR
SOR
COM
DOM
HAY
Study sites

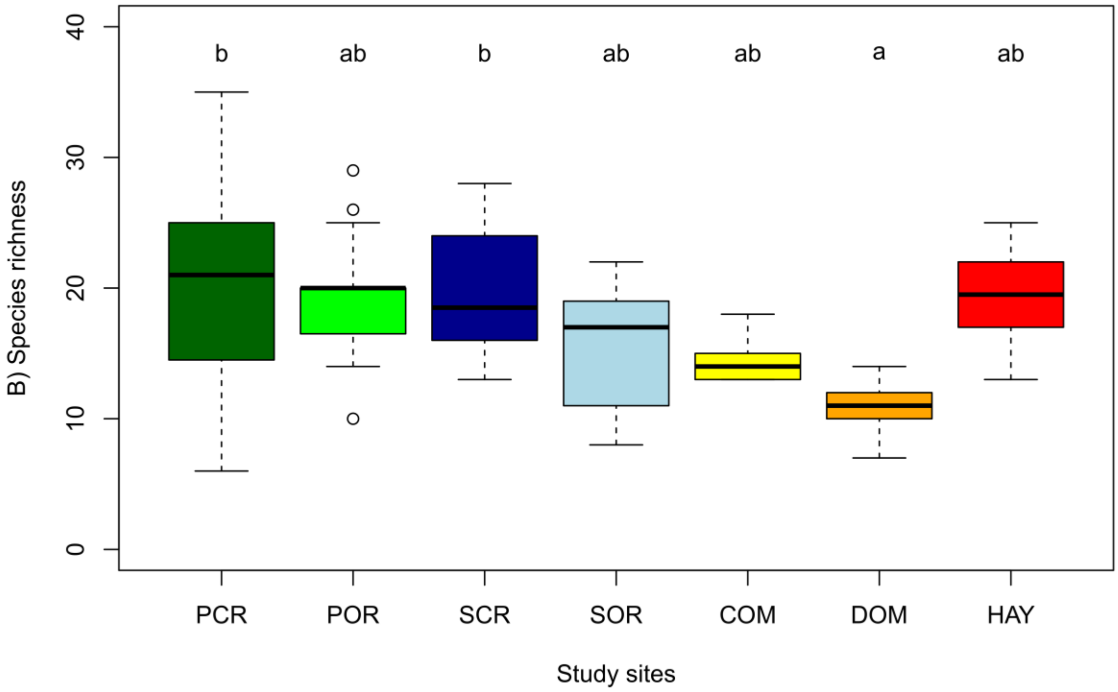
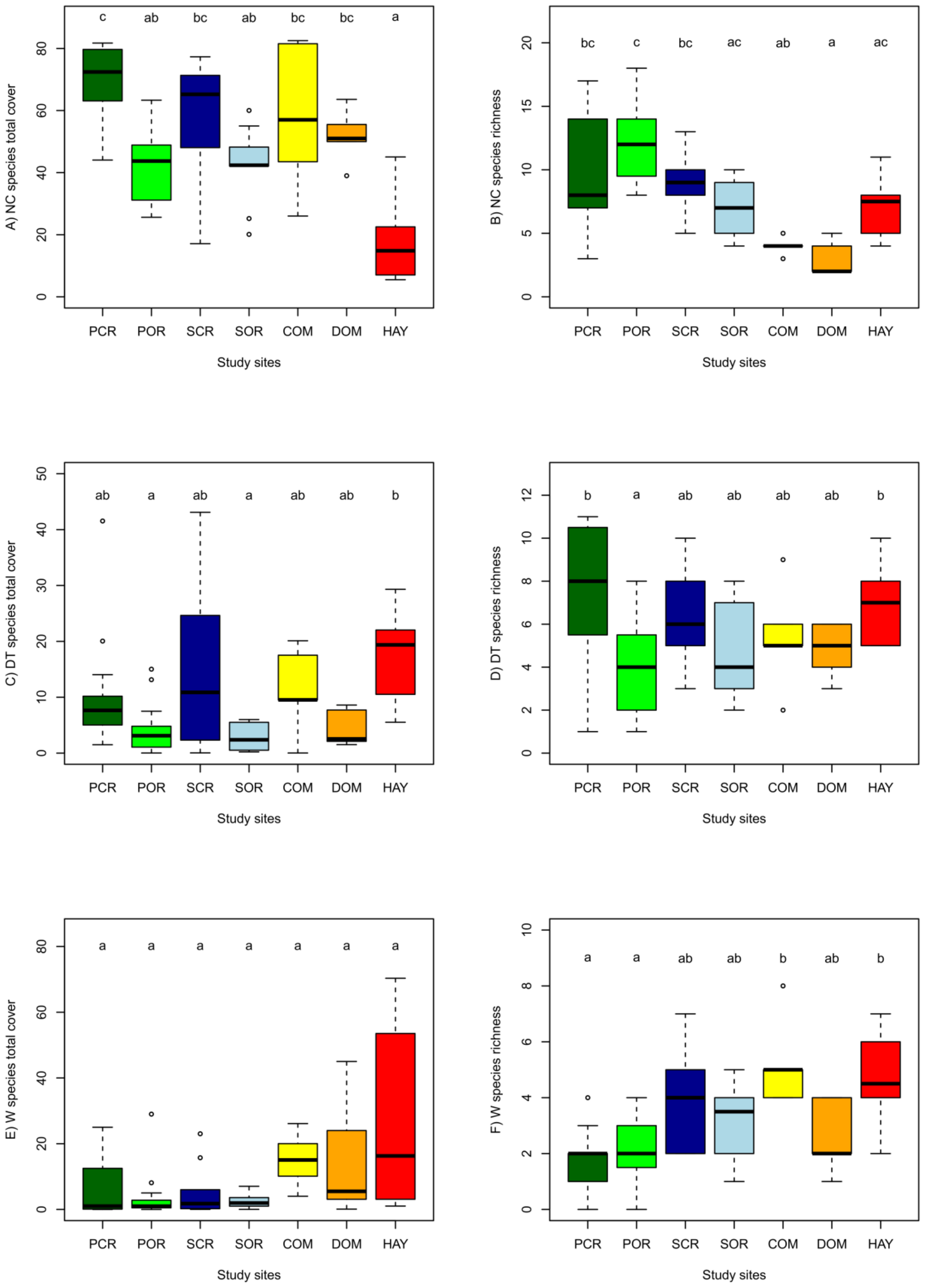

B) Species richness
0
10
20
30
40
b
ab
b
ab
ab
a
ab
PCR
POR
SCR
SOR
COM
DOM
HAY
Study sites

Figure 4. Total cover (A,C,E) and species richness (B,D,F) of sociability of species in restoration plots and reference sites. Figures represent the distribution of total cover/species richness data based on the minimum, first quartile, median, third quartile, and maximum. Total cover (i.e. sum of individual species´ cover) and species richness (i.e. number of species) were calculated for each of the 70 sampling units. Merged Borhidi (1995) categories: 1) natural constituents (NC); 2) disturbance tolerant species (DT); and 3) weeds (W). Significant differences among study sites are indicated by lower case letters. Abbreviations: primary closed reference (PCR), primary open reference (POR), secondary closed reference (SCR), secondary open reference (SOR), commercial seed mixture (COM), seeds of a single dominant species (DOM), hay transfer (HAY).


A) NC species total cover
c ab bc ab bc bc a
0 20 40 60 80
B) NC species richness
bc c bc ac ab a ac
0 5 10 15 20
C) DT species total cover
ab a ab a ab ab b
0 10 20 30 40 50
D) DT species richness
b a ab ab ab ab b
0 2 4 6 8 10 12
E) W species total cover
a a a a a a a
0 20 40 60 80
F) W species richness
a a ab ab b ab b
0 2 4 6 8 10
PCR POR SCR SOR COM DOM HAY
Study sites

Supporting information

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

Appendix S1. Map of study sites.

Appendix S2. Basic soil properties of the restoration and reference sites.

Appendix S3. List of plant species, their life form and sociability of species.

Appendix S4. Results of NMDS analysis based on presence/absence data.

Appendix S5. Results of ANOSIM analysis with species richness.