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Soil seed bank and above-ground vegetation changes during grassland succession: Is space-for-time substitution an alternative to re-sampling?

Veränderung von Vegetation und Samenbank während der Sukzession eines Graslands: Kann *space-for-time substitution* eine Wiederholungsaufnahme ersetzen?

Silvia Bittnerová[1, *], Karol Ujházy[2], Katarína Hegedüšová[1], Iveta Škodová[1],
Mariana Ujházyová[3] & Monika Janišová[1]

[1]Institute of Botany, Plant Science and Biodiversity Centre, Slovak Academy of Sciences,
Dúbravská cesta 9, 845 23 Bratislava, Slovakia;
[2]Department of Phytology, Technical University in Zvolen, T. G. Masaryka 24,
960 01 Zvolen, Slovakia;
[3]Deparment of Applied Ecology, Technical University in Zvolen, T. G. Masaryka 24,
960 01 Zvolen, Slovakia
[*]Corresponding author, e-mail: silvia.bittnerova@savba.sk

Abstract

Changes of the above-ground vegetation and soil the seed bank were studied in a secondary oligotrophic montane grassland after abandonment and gradual colonisation by Norway spruce. The main aim was to compare the responses of the above- and below-ground species composition and richness as well as seed density to successional development. Next aim was to study the relationship of above-ground vegetation and soil seed bank along the spruce colonisation gradient. Simultaneously, we asked whether two types of space-for-time substitution approaches give adequate approximation of trends compared to a plots re-sampling approach with a time lag of 11 years. The sample plots were obtained from a 160 m long transect established in the direction of spruce invasion from a linear source (former plantation). The above-ground vegetation was recorded in 2004 and 2015 on 155 circular permanent plots, 21 of which were also sampled for the soil seed bank. For the substitution approach, time was substituted either by the distance (plots differing in position along the spruce colonisation gradient were interpreted as consecutive successional stages) or by soil depth (the deeper soil layer was supposed to represent an earlier successional stage than the upper one). The composition of the soil seed bank was only weekly related to the above-ground vegetation and their dissimilarity increased with succession. Patterns in species composition and species richness of the above-ground vegetation indicated by distance-for-time substitution were similar to those indicated by re-sampling of plots. This implies that the species turnover and the decline along the colonisation gradient in the above-ground vegetation with time can be successfully predicted from studying the initial spatial patterns. Species composition of the soil seed bank differed among the years but not among the soil depth layers. However, differences in species richness were confirmed for both, among the deeper and upper soil depth layers as well as after 11 years. Space-for-time substitution approaches detected differences in seed bank species richness along the succession gradient neither for distance nor for soil depth. The decrease of the seed density with time was confirmed by all approaches used. Due to generally small numbers of species in the soil

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seed bank and the additional a strong temporal decrease of seed densities, the use of the seed bank for grassland restoration is limited. Our results also show that the temporal development of the seed bank species richness during secondary succession cannot be reliably predicted from spatial patterns recorded during a single unrepeated sampling. Taking also in to account the huge variance of succession-induced outcomes, we conclude that the distance-for-time substitution should be used with caution in studies focusing on the seed bank.

Keywords: colonisation gradient, litter accumulation, *Picea abies*, seed density, species richness, semi-natural grassland, Western Carpathians

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

Semi-natural grasslands evolved during extended periods of traditional small-scale farming practices, but have been lost over the last century in most of Europe because of major socio-economic changes and unsustainable land-use policies and practices (CSERGŐ et al. 2013). The greater part of them has been destroyed due to intensification, drainage or conversion to arable land, but also due to abandonment. Especially economically unprofitable remote grasslands are threatened by abandonment or afforestation. Long-term management treatments cessation of grassland generally induces substantial successional changes and shifts in plant species composition due to changing habitat conditions (PRÉVOSTO et al. 2011, VALKÓ et al. 2018).

The success to restore grassland vegetation on abandoned sites strongly depends on the presence of seed sources in the vicinity and the soil seed bank (BOBBINK & WILLEMS 1993). It is well known, that the number of species and seeds in the seed bank decline along the gradient of management history from the original grassland to the closed overgrown community (KALAMEES & ZOBEL 1998). The soil seed bank can provide important information on the species, which may have existed in the above-ground vegetation of the past (HOPFENSPERGER 2007, TÖRÖK et al. 2012, YEHNJONG et al. 2017). Investigating of seed banks also provides information on i) the past management practices and helps to undestand current and future vegetation changes (VALKÓ et al. 2011, TÖRÖK et al. 2012), on ii) former and recent levels of degradation and iii) on the conservation status of the genetic variability of plant populations (HONG et al. 2012). Thus, soil seed banks also play an essential role in the restoration of semi-natural grasslands (BAKKER & BERENDSE 1999, BOSSUYT & HONNAY 2008, JACQUEMYN et al. 2011, KALAMEES et al. 2012, STROH et al. 2012, JANICKA 2016) and contribute to the (dynamic) diversity and many plant communities (LANG & HALPERN 2007). Soil disturbance allows the seed bank to intervene in re-establishing the original community (LÓPEZ-MARIÑO et al. 2000).

Some studies, which focused on grassland vegetation did not find differences in species richness and seed density after abandonment and succession towards forests (MILBERG 1995, MACCHERINI & DOMINICIS 2003). However, POSCHLOD et al. (1998) and BOSSUYT et al. (2006) affirm that the species richness in the soil seed bank is decreasing with time after abandonment. This suggests that the potential to restore grasslands from the seed bank may be limited, particularly if succession has already progressed to the final stage of a dense forest. In this context both the floristic composition and the density of species in the seed bank are important for the restoration success (KLAUS et al. 2017a).

Török et al. (2018) found a marked difference between the above-ground vegetation and the seed bank along the whole chronosequence similar to other studies comparing vegetation and seed banks along temporal gradients (Kalamees & Zobel 1998, Metsoja et al. 2014). It suggests that vegetation changes are most likely driven by spatial dispersal rather than by the recruitment from the seed bank. Furthermore, conifer encroachment has been accompanied by dramatic changes in vegetation composition and structure (Lang & Halpern 2007). It has been suggested that even with tree removal the re-establishment of species of the former vegetation layer is not possible through a fossil seed bank, meaning that a natural recovery would require the dispersal of seeds into the target system (Dutoit & Alard 1995, Poschlod et al. 1998, Bakker & Berendse 1999, Bossuyt & Hermy 2004, Lang & Halpern 2007).

The space-for-time substitution (Pickett 1989) is frequently used in ecology as an alternative of direct long-term studies. This technique extrapolates a temporal trend from a series of different-aged samples from different locations. Although space-for-time substitution was successfully used to detect temporal trends in the development of plant (Pickett 1989, Molnár & Botta-Dukát 1998) as well as animal (Banet & Trexler 2013) communities, its reliability for the prediction of temporal changes of seed banks is still unclear. In our study we focussed on two substitution approaches: time was substituted either by distance (distance-for-time substitution), in that plots differing in position along the Norway spruce colonisation gradient were interpreted as consecutive successional stages, or by soil depth (depth-for-time substitution), in that the deeper soil depth layer was supposed to represent an earlier successional stage compared to the upper one. The validity of these substitutions was evaluated by the comparison of the trends found by the space-for-time approach with the directly (temporally) re-sampled permanent plots.

The aim of our contribution was to detect and compare changes in the above-ground vegetation and the soil seed bank during grassland colonisation by spruce by using several different sampling approaches. We attempted to answer the following specific questions: (1) How did the above-ground vegetation and the soil seed bank change along a spruce colonisation gradient with respect to species composition, species richness and seed density? (2) Are the above-ground vegetation and the soil seed bank related and, if yes, is this relationship affected by succession and depth levels of seed bank sampling? (3) Is space-for-time substitution adequate for both above-ground vegetation and soil seed banks?

2. Methods

2.1 Study site

Our study site is located in central Slovakia at Príslopy in the Poľana Mts. (48°38’10’’N, 19°25’11’’E; 900–920 m a.s.l., northern slope). The region has a cold and moist climate with a mean January temperature -6 to -7 °C and in July between 11.5–13.5 °C, and 1000–1400 mm mean annual precipitation sums. The geological bedrock is formed by andesite lava flows which is now covered by Cambisols.

The grassland area of about 100 ha is surrounded by a large forest complex: predominantly European beech forests with patches of Norway spruce plantations and remnants of original mixed montane fir-beech forests with *Fagus sylvatica*, *Abies alba*, *Acer pseudoplatanus*, *Fraxinus excelsior* and *Picea abies*. Since the deforestation at around 1800 it has been utilized as a hay meadow and later as a pasture (from 1951 until 1990, Ujházy 2003). Since the late 1990s, the studied part of the area has not been under agricultural use any more. In 1890, Norway spruce (*Picea abies*) was planted along with the former forest margin and, after abandonment, started to intensively colonize the grassland sites.

2.2 Field sampling

In 2003 a transect of 20 m × 160 m was established containing all successional stages from the old planted spruce forest margin (based on the historical aerial photos and field research, Fig. 1) to remaining open grassland patches. The transect grid (5 m × 5 m) was marked and geodetically measured (Fig. 2). A detailed study of relationships between vegetation, environmental factors and especially soil biology along the spruce colonisation gradient has been performed during 2003–2005 (HRIVNÁK & UJHÁZY 2005, JANIŠOVÁ et al. 2007, DOVČIAK et al. 2008, GÖMÖRYOVÁ et al. 2009). Among the measured environmental variables there were several characteristics reflecting the successional development of the above-ground vegetation (for more details see JANIŠOVÁ et al. 2007): i) canopy openness (the percentage of open sky seen from beneath a forest canopy) measured by vertical hemispherical photographs using the fish-eye objective; ii) tree index reflecting both density and size of trees in the plot neighborhood; iii) percentage cover of fallen needles forming a separate layer on a soil surface.

The understorey vegetation of 155 plots of 0.5 m^2 was recorded in 2004 and 2015. Percentage cover of vascular plant and bryophyte species was estimated for each plot and species frequencies in the four circle quadrants were recorded. Soil samples for soil seed bank analyses were collected from 21 plots distributed along the transect covering all successional stages (Fig. 2). Standardized soil sample ring kits (four soil samples, one sample per quadrant, were taken from each plot – in total 0.4 dm^3 of soil per 0.5 m^2 plot) were used. In September 2004, soil samples from two soil depth layers (0–4 cm and 4–8 cm) and in September 2015 from one soil depth (0–4 cm, within a formerly not disturbed part of the quadrant) were collected. Samples were stored in moist conditions at 3–4 °C for six months. In March of the year following soil collection, each soil sample of 0.1 dm^3 was spread out over a 5 cm thick layer of commercial sterilized potting soil in an 18 × 13 × 5 cm plastic container, forming an approximately 1 cm thick layer. Containers were placed in an unheated glasshouse. Four control containers containing potting soil only were included in the experiment to test for contamination by seeds from the air, glasshouse environment or those present in the potting soil and no seedlings were found in these control containers during the experiment. Containers were continuously watered with automatic water system to keep the soil moist. To avoid differences in light intensity among the containers, we randomized their position regularly once a week. Germinating seedlings were recorded for nine months. During the first six months every two weeks, later with monthly frequency. Seedlings of all emerging species were counted and removed after identification. Unidentifiable seedlings were transplanted and grown in pots until species identification was possible. Some seedlings were identified only to genus level and have been merged within higher taxonomical units *Carex* spp. (*C. pilulifera*, *C. hirta*, *C. caryophyllea*, *C. pallescens*), *Luzula* spp. (*L. luzuloides*, *L. campestris*), *Polypodiales* (*Dryopteris filix-mas*, *Athyrium filix-femina*), *Trifolium* spp. (*T. repens*, *T. campestre*), *Viola* spp. (*V. canina*, *V. reichenbachiana*, *V. riviniana*). Likewise, some bryophytes were merged for the purpose of statistical analses of the above-ground vegetation: *Brachythecium* spp. (*B. rutabulum*, *B. salebrosum*), *Dicranum* spp. (*D. scoparium*, *D. polysetum*), *Marchantiophyta* (*Blepharostoma trichophyllum*, *Lophocolea heterophylla*), *Plagiomnium* spp. (*P. affine*, *P. cuspidatum*, *P. rostratum*, *P. undulatum*), *Rhytidiadelphus* spp. (*R. squarosus*, *R. triquetrus*). The nomenclature of vascular plants follows (EURO+MED 2006) and bryophytes (MARHOLD & HINDÁK 1998).

Based on the identified seedlings, number of species and absolute number of seedlings were counted for each circle and circle quadrant in the respective soil depth layers. These data were used to calculate species richness of the seed bank and density of viable seeds (seed density in the further text).

Seed longevity was classified either according to seed ability to remain viable and germinable in soil (GRIME et al. 1988) or based on soil depth where viable seeds were recorded with regard to species' occurrence in the above-ground vegetation (BAKKER et al. 1996). Using the later mentioned approach, we classified species found during our experiment to three groups: transient (species present in the vegetation and absent from soil seed bank or only present in the top soil), short-term persistent (species absent or present in the vegetation but always present in soil seed bank, and more frequent in the upper soil layer than in lower one) and long-term persistent (species absent or present in the above-ground vegetation but always present in soil seed bank, and seeds with similar frequency in lower and upper soil layers).

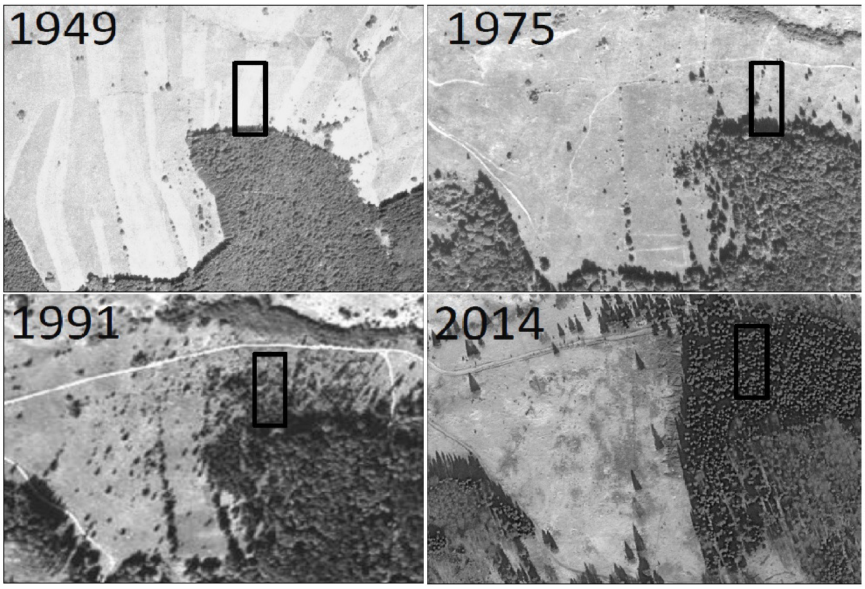

Fig. 1. Historical aerial photos of the studied area with obvious advance of tree colonisation in the former grassland area.

Abb. 1. Luftbilder des Untersuchungsgebiets aus verschiedenen Zeiten. Deutlich erkennbar ist die zunehmende Besiedlung der Untersuchungsfläche (Rechteck) durch Fichten.

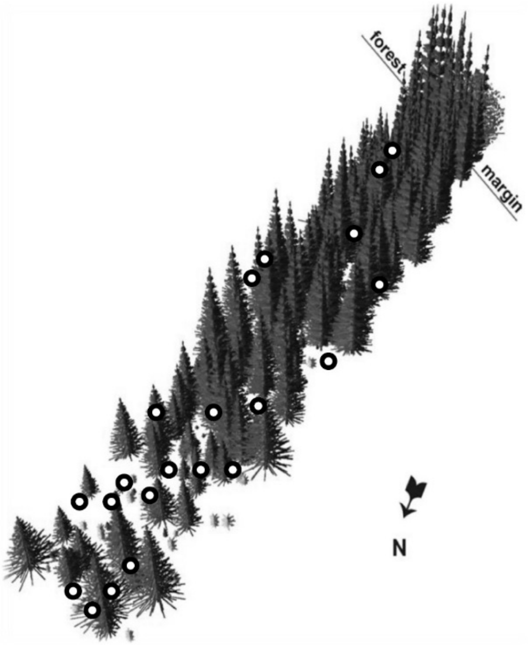

Fig. 2 Perspective view of the transect area (according HRIVNÁK & UJHÁZY 2005). Circles show the position of the 21 plots from which the soil samples were taken.

Abb. 2. Perspektivische Ansicht des Transekts (nach HRIVNÁK & UJHÁZY 2005). Die Kreise zeigen die Lage derjenigen 21 Aufnahmeflächen, in denen Bodenproben genommen wurden.

2.3 Data analysis

Log-transformed percentage cover of vascular plant and bryophyte species in the above-ground vegetation was used in the detrended correspondence analysis (DCA). Thick layer of needles and intensive shade under the closed canopy caused that no species were found on several plots below spruce trees. Therefore, a hypothetical non-existing species with a constant cover value of 0.1% was added to each above-ground vegetation sample including the empty ones to keep them in the analyses. Recent (recorded in 2015) and historical (recorded in 2004) samples of above-ground vegetation (155 samples from each year) were used to estimate the progress of the successional development. The ordination scores of the 2004-samples along the first axis in the detrended correspondence analysis (DCA) was then used as an approximation of the successional development for each of the 21 plots investigated for relationships between seed banks and above-ground vegetation. We considered several available alternatives among the measured variables (canopy openness, tree index and % cover of needles) but finally, we decided to use the complex environmental gradient reflected by the first axis of the DCA analysis. The advantage is that it reflects complex changes induced by the successional development of individual plots (not only decreasing light availability and accumulation of needles on the soil surface, but both of them, including also other accompanying processes, which were not directly measured). The correlations between the first DCA axis scores and individual single environmental variables were significant (Pearson correlation coefficient 0.79, -0.81 and 0.63 for tree index, canopy openness and cover of needles, respectively).

Principal correspondence analysis (PCA) based on the species composition was used to plot the above-ground vegetation and seed bank data in a multidimensional space (gradient length calculated by the DCA on the 1st axis was 2.99). Species frequencies (number of circle quadrants in which the particular species was present, i.e., values 0, 1, 2, 3 or 4) were used as input data. PCA was also used to visualize the relation of seed banks in the two different soil depth layers.

Multispecies responses of above-ground vegetation and seed bank species abundances and proportions relative to sampling time and soil depth (for seed bank only) were analyzed by the redundancy analysis (RDA). Log-transformed percentage cover of species of above-ground vegetation and absolute numbers of seedlings per plot were used as input data. To test for differences in species proportions, standardization of samples was applied in CANOCO software using the ‘norm’ function. Sampling year (or soil depth layers) were used as the only constraining variables while plot numbers and position along the transect (distance from the colonisation starting line) were used as covariables to define blocks in the Monte Carlo permutation tests. DCA first axis score was also set as a covariable. Restricted permutations for line transect (to compare soil depth layers) or time series (to compare the years 2004 vs. 2015) were used. The same parameters were set to identify whether the successional development can modify the effects of sampling time or soil depth. For this purpose, DCA first axis score was not used as a covariable but as a constraining variable in interaction with sampling time or soil depth, respectively. Multivariate analyses were provided in CANOCO 4.5 software (TER BRAAK & ŠMILAUER 2002).

To analyze relationships between seed bank and above-ground vegetation species, frequencies in each of the 21 samples were used and the Sørensens dissimilarity index (SDI) (SØRENSEN 1948) was calculated in JUICE 7.0 software (TICHÝ 2002). Simple regression models for SDI as dependent variable and succession gradient (expressed as the DCA 1st axis score) as predictor were run, while linear and quadratic relationships were compared and the model with the lowest Akaike information criterion (AIC) was selected.

Non-parametric Wilcoxon pair tests were used to search for differences in species composition in both above-ground vegetation and seed banks in different soil depth layers in 2004. Simple linear regression models were used to analyze overall and species-specific seed densities and the species richness along the succession gradient. Regression analyses were performed in R (R CORE TEAM 2015).

3. Results

3.1 Changes of the above-ground vegetation

During the 11 years (2004–2015) profound changes of the above-ground vegetation were observed including shifts in both species composition and species frequencies/cover values (Table 1). Within the 21 plots in which the soil seed bank was sampled, 50 taxa of vascular plants and 9 taxa of bryophytes were recorded in the above-ground vegetation. Compared to 2004, the number of vascular plant taxa decreased by 59% in 2015 (49 and 20 vascular plant taxa in 2004 and 2015, respectively), while the number of bryophytes did not change (nine identical taxa in both years). Among the taxa not any longer recorded in 2015 there were typical grassland species (such as *Cardamine pratensis*, *Rumex acetosa*, *Thymus pulegioides*), as well as typical forest species including shrubs and trees (*Abies alba*, *Acer pseudoplatanus*, *Oxalis acetosella*, *Senecio ovatus*). Only two new species were recorded in 2015, *Campanula patula* and *Plagiothecium platyphyllum*. The average cover of vascular plants decreased by 74% from 38.9% in 2004 compared to 10.1% in 2015 (Wilcoxon test: $p < 0.001$), while the average cover of bryophytes did not change (39.9% in 2004 compared to 40.1% in 2015, Wilcoxon test: $p = 0.232$).

Plots used for seed bank sampling were classified in four successional stages: i) species-rich grasslands typical for an initial stage of spruce colonisation and dominated by typical species of oligotrophic grasslands (*Agrostis capillaris*, *Carex pilulifera*, *Festuca rubra*, *Potentilla erecta*, *Veronica officinalis*); ii) overshadowed grasslands dominated by less light-demanding species (*Ajuga repens*) and/or some acidophilous species (*Avenella flexuosa*, *Vaccinium myrtillus*) reflecting acidification of the upper soil layer by spruce needles; iii) bryophyte-dominated stands (mainly dominated by *Plagiomnium affine* agg. and *Hylocomium splendens*) without substantial representation of vascular plants; iv) spruce litter (needles) as the final stage when spruce outcompeted the understorey vegetation (maximum cover of plants 5% of the soil surface).

From the 2004 to the 2015 sampling, most plots experienced a shift in the same direction, which was strongly correlated with the first DCA axis representing the complex succession gradient. However, the cover of spruce needles was slightly increasing. Species-rich grassland plots (stage i) developed towards overshadowed acidophilous grasslands (stage ii). The other plots with well-developed herb layer developed towards the bryophyte-dominated stands (stage iii), in some cases even towards the bare stage (stage iv) covered by spruce needles (Fig. 3). This changes were induced by decreasing light availability in the plots and by the increase of the needles cover along the transect, both factors were positively correlated with the first ordination axis.

The above-ground vegetation differed significantly in species abundances and proportions between the two sampling years (2004 and 2015), and its species composition was significantly shifted along the successional gradient during the 11 years (Table 2).

3.2 Changes in the seed bank

A total of 3804 seeds of 34 vascular plant taxa germinated during our experiment from the 21 sample taken. In 2004, 956 seedlings of 25 taxa germinated from the deeper (4–8 cm) soil depth layer and 2089 seedlings of 26 taxa from the upper (0–4 cm) soil depth layer. In 2015, 759 seedlings of 15 taxa germinated from the upper (0–4 cm) soil layer. Thus, seed density per 1 m^2 in 2004 amounted to 9948 seeds in the upper and 4555 seeds in the deeper

Table 1. Occurrences of plant species in the established vegetation and in the seed bank; % presence = percentage of the 0.5 m^2 plots in which the species was present; Mean cover % = average of percentage cover of species in the plots; Seed density = seed bank density in plots ± standard deviation; Seed bank type = T – transient, ST – short-term persistent, LT – long-term persistent (seed bank type in this study according Bakker et al. (1996), calculated only by species with seed density ≥ 3/0.4 m^2; seed bank type according database: LEDA (Kleyer et al. 2008). **Carex pilulifera* – Long-term seed bank type.

Tabelle 1. Vorkommen von Pflanzenarten in der aktuellen Vegetation und in der Samenbankbank. Die Prozentsätze und Deckungswerte beziehen sich auf 0,5 m²-Flächen. Die Samenbanktypen (nach Bakker et al. 1996) sind: T – unbeständig, ST – kurzfristig beständig, LT – dauerhaft beständig. Es wurden lediglich Arten mit ≥ 3 Samen pro 0,4 m² berücksichtigt; Samenbanktypen nach der LEDA-*Traitbase* (Kleyer et al. 2008).

	2004				2015			Seed bank type	
	Above-ground		Seed density		Above-ground		Seed density		
	% presence	Mean cover %	0-4 cm	4-8 cm	% presence	Mean cover %	0-4 cm	in this study	database
Vacular plants									
Abies alba	10	0.1	0	0	0	-	0	T	-
Acer pseudoplatanus	5	1	0	0	0	-	0	T	-
Agrostis capilaris	57	5.32	81 ± 4.7	38 ± 1.8	24	4.3	42 ± 2.48	ST	T
Achillea millefolium	24	1.2	1	0	5	0.1	1	T	T
Ajuga reptans	43	3.44	22 ± 14.14	3 ± 0	33	1.68	0	T/ST	T
Alchemilla spp.	5	2	0	1	0	-	0	T	T
Avenella flexuosa	71	7.08	0	0	33	5.57	0	T	T
Betula pendula	5	1.5	0	1	0	-	0	T	ST
Brachypodium pinnatum	5	45	0	1	0	-	0	T	T
Briza media	14	2.67	1	0	0	-	0	T	T
Calamagrostis arundinacea	5	4	0	0	0	-	0	T	-
Campanula patula	0	-	432 ± 11.13	285 ± 9.66	10	0.1	149 ± 6.36	ST	T
Cardamine pratensis	5	0.1	0	0	0	-	0	T	T
Carex spp. *	43	2.07	389 ± 17.48	228 ± 13.74	24	4.02	349 ± 14.93	ST	T
Carlina acaulis	29	2.18	0	0	0	-	0	T	T
Corylus avellana	5	0.5	0	0	0	-	0	T	T
Cruciata glabra	43	0.92	0	0	14	2.03	0	T	-
Cirsium arvense	0	-	0	0	0	-	1	-	T
Dactylis glomerata	0	-	1	1	0	-	0	-	-
Danthonia decumbens	24	1.7	11 ± 0.98	1	0	-	1	T/ST	T
Deschampsia cespitosa	5	2	0	0	0	-	0	T	T
Festuca rubra	19	0.9	0	0	19	2.75	0	T	T
Fragaria vesca	29	5.93	28 ± 1.81	8 ± 0.82	10	4.5	0	ST	T
Galeopsis bifida	0	-	1	0	0	-	0	-	-
Galium verum	10	0.55	0	0	0	-	0	T	T
Hieracium murorum	5	5	0	0	5	1	0	T	-
Helictochloa praeusta	52	16.59	0	0	14	11.33	0	T	-
Hypericum maculatum	57	4.72	872 ± 46.04	277 ± 14.6	29	1.6	145 ± 6.76	ST	T
Chenopodium album	0	-	0	1	0	-	0	-	ST
Juncus articulatus	0	-	3 ± 0	2 ± 0	0	-	0	ST	ST
Juncus conglomeratus	0	-	12 ± 0.71	6 ± 0.58	0	-	0	ST	T
Juniperus communis	5	5	0	0	0	-	0	T	T

	2004				2015			Seed bank type	
	Above-ground		Seed density		Above-ground		Seed density		
	% presence	Mean cover %	0-4 cm	4-8 cm	% presence	Mean cover %	0-4 cm	in this study	database
Leucanthemum vulgare	0	-	1	1	0	-	0	-	T
Lipandra polysperma	0	-	2	0	0	-	0	-	LT
Lonicera xylosteum	5	1	0	0	0	-	0	T	T
Lotus corniculatus	10	1.55	3 ± 0	2 ± 0	0	-	1	T/ST	T
Luzula spp.	52	1.7	43 ± 3.94	20 ± 1.33	14	0.7	11 ± 1.06	T/ST	T
Nardus stricta	33	7.86	0	0	10	-	0	T	T
Oxalis acetosella	5	0.1	12 ± 1.55	11 ± 0.84	0	3	0	ST/LT	T
Phyteuma spicatum	10	1.25	0	0	5	1	0	T	T
Picea abies	67	0.76	0	0	5	10	0	T	T
Pilosella officinarum	14	2	0	0	0	-	0	T	T
Pimpinella saxifraga	10	0.75	0	0	0	-	0	T	T
Platanthera bifolia	5	3	0	0	5	0.5	0	T	-
Polypodiales	0	-	0	0	0	-	32 ± 4.16	ST	-
Potentilla aurea	10	0.1	0	2 ± 0	0	-	0	T	T
Potentilla erecta	62	7.04	46 ± 3.19	16 ± 0.49	24	6.4	22 ± 1.75	T/ST	T
Prunella vulgaris	10	0.1	0	0	0	-	0	T	T
Prunus cerasifera	5	0.1	0	0	0	-	0	T	T
Ranunculus auricomus agg.	5	0.1	0	0	0	-	0	T	T
Ranunculus polyanthemos	5	0.1	0	0	0	-	0	T	T
Rosa canina agg.	5	1	0	0	5	3	0	T	T
Rumex acetosa	24	0.64	0	0	0	-	0	T	T
Scrophularia nodosa	0	-	8 ± 0	5 ± 2.12	0	-	0	ST	LT
Solanum nigrum	0	-	1	0	0	-	0	-	ST
Senecio ovatus	5	0.5	0	0	0	-	0	T	T
Taraxacum officinalis	0	-	6 ± 1	0	0	-	0	ST	T
Thymus pulegioides	5	0.5	0	0	0	-	0	T	T
Trifolium spp.	0	-	0	0	0	-	2 ± 0	-	T
Urtica dioica	0	-	3 ± 0	1	0	-	1	ST	ST
Vaccinium myrtillus	5	50	0	0	0	-	0	T	T
Veronica chamaedris	19	0.43	6 ± 1.73	5 ± 0.5	0	-	1	T/ST	T
Veronica officinalis	33	0.8	821 ± 5.41	34 ± 1.55	14	1.17	27 ± 1.29	ST	ST
Viola spp.	10	0.75	22 ± 2.38	6 ± 0	0	-	10 ± 0.79	ST	T
Non-vascular plants									
Aulacomnium palustre	24	11.4	0	0	14	7.03	0	-	-
Brachythecium spp.	29	3.85	0	0	10	9	0	-	-
Cirriphyllum piliferum	5	0.1	0	0	0	-	0	-	-
Dicranum spp.	48	1.16	0	0	14	1.4	0	-	-
Hylocomium splendens	90	22.48	0	0	76	20.85	0	-	-
Marchantiophyta	10	7.5	0	0	10	0.3	0	-	-
Plagiomnium spp.	95	7.51	0	0	81	20.3	0	-	-
Plagiothecium platyphyllum	0	-	0	0	5	-	0	-	-
Pleurozium schreberi	62	7.19	0	0	29	3.18	0	-	-
Rhytidiadelphus squarrosus	62	21.32	0	0	19	24	0	-	-

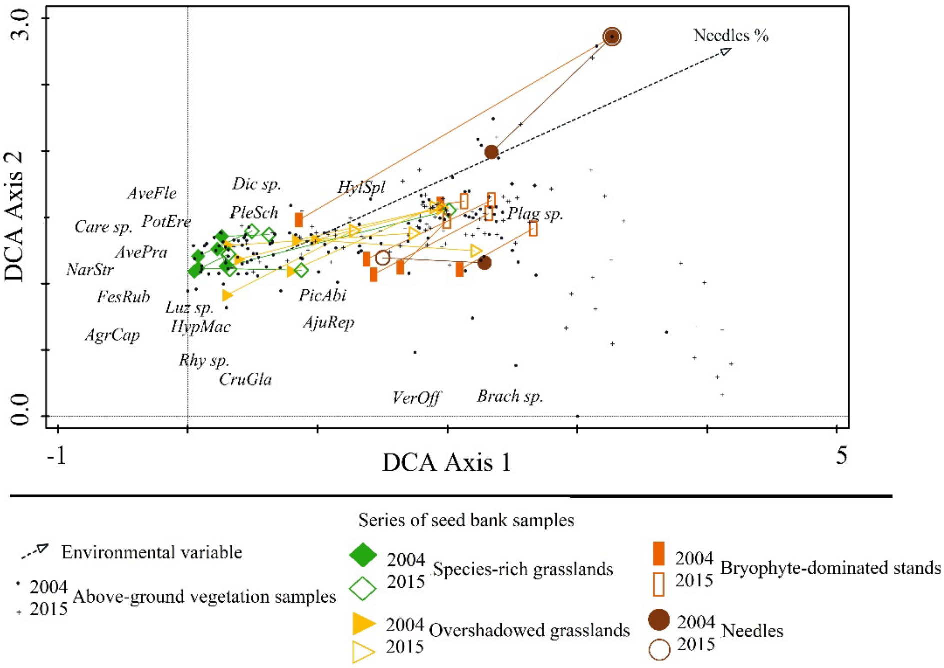

Fig 3. DCA ordination of 155 transect plots in both sampling dates (2004: black circles; 2015: black crosses). The temporal shift in species composition of the above-ground vegetation follows the first ordination axis, which was interpreted as the succession gradient. Seed-bank samples are classified according to the four successional stages i) to iv) (green diamond: i); yellow triangle: ii); orange box: iii); brown circle: iv); see the text for details) and sampling year (2004: full-colored symbols, 2015: empty symbols. The percentage cover of needles represents an environmental factor which is strongly positively related to the colonisation progress of Norway spruce. In the DCA, species cover values (%) were logarithmically transformed; eigenvalues of the 1st axis = 0.392 and the 2nd axis = 0.161; gradient length of the 1st axis was 4.18; total inertia was 2.323, adjusted explained variation was 9.1%.

Abb. 3. DCA-Ordination von 155 Transekt-Aufnahmeflächen aus den Jahren 2004 (Punkte) und 2015 (Kreuze). Die erste DCA-Achse spiegelt die zeitliche Veränderung der Artenzusammensetzung der Vegetation wieder und wird daher als Sukzessionsgradient interpretiert. Die Samenbankproben wurden nach vier Sukzessionsstadien unterteilt: i) grüne Rauten, ii) gelbe Dreiecke, iii) orangene Schachteln, iv) braune Kreise; für Details s. Text) Gefüllte Symbole stehen für das Untersuchungsjahr 2004, leere Symbole für 2015. Eingeblendet ist die Prozentdeckung der Nadeln; sie repräsentiert den Prozess der Besiedlung mit Fichten. Die %-Deckungswerte der Arten wurden in der DCA log-transformiert; Eigenvalues Achse 1 = 0,392 und Achse 2 = 0,161; Länge Achse 1: 4,18; *total inertia*: 2,323; die angepasste erklärte Varianz betrug 9,1 %.

oil depth layers, respectively. In 2015, 3614 seeds were recorded in the upper soil depth layer. Overall, the seed bank was dominated by *Hypericum maculatum* (33.7%), *Carex* spp. (25.2%) and *Campanula patula* (22.6%), which together accounted for 81.5% of all emerging seedlings. In addition, *Agrostis capillaris* (4.2%), and *Veronica officinalis* (3.7%) had rather high proportions of emerging seedlings, while other vascular plant taxa germinated only sporadically (Table 1).

Table 2. Summary of the results. The upper part of the table shows the results of the multivariate analyses (Wilcoxon test and single regression models). For Wilcoxon tests with detected significant differences the treatments with larger mean values are in bold. The results of the univariate analyses are shown in the lower part of the table. Where appropriate the explained variation is shown in brackets.
upper – the upper soil layer 0–4 cm below the soil surface; lower – the lower soil layer 4–8 cm below the soil surface. ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$; n.s. - non significance.

Tabelle 2. Zusammenfassung der Ergebnisse. Im oberen Teil der Tabelle werden die Ergebnisse der multivariaten Analysen (Wilcoxon-Test und Einzelregressionen) gezeigt. Signifikante Unterschiede nach den Wilcoxon-Tests zwischen den Behandlungen in fett. Die Ergebnisse der univariaten Analy-sen finden sich im unteren Teil der Tabelle.
upper – Oberboden von 0–4 cm Tiefe; lower – Unterbo-den von 4–8 cm Tiefe. ***$p < 0{,}001$; **$p < 0{,}01$; *$p < 0{,}05$; n.s. – nicht signifikant.

	Re-sampling	Depth-for-time substitution 4–8 cm vs. 0–4 cm	Space-for-time substitution Successional gradient
Type of multivariate analysis	*RDA* *Monte-Carlo permutation test*	*RDA* *Monte-Carlo permutation test*	*RDA* *Monte-Carlo permutation test* *(1st DCA score as constraining variable)*
Species abundances (above-ground vegetation)	2004 vs. 2015 *** [7.5%]	-	2004 vs. 2015 ** [5.5%]
Species proportion (above-ground vegetation)	2004 vs. 2015 ** [7.1%]	-	2004 vs. 2015 * [5.9%]
Species abundances (seed bank)	upper (2004) vs. upper (2015) *** [16.3 %]	lower (2004) vs. upper (2004) ** [7.9%]	lower (2004) vs. upper (2004) n.s. 2004 vs. 2015 *** [10.9 %]
Species proportion (seed bank)	upper (2004) vs. upper (2015) *** [8.7 %]	lower (2004) vs. upper (2004) n.s.	lower (2004) vs. upper (2004) n.s. 2004 vs. 2015 *** [6.6 %]
Type of univariate analysis	*Wilcoxon test*	*Wilcoxon test*	*Regression model* *(trend along the successional gradient)*
Species richness (above-ground vegetation)	**2004** > 2015 ***	-	2004 *** (decreasing) [42.7 %] 2015 *** (decreasing) [91.0 %]
Species richness (seed bank)	**upper (2004)** > upper (2015) **	lower (2004)< **upper (2004)***	lower (2004) n.s. upper (2004) n.s. upper (2015) n.s.
Seed density (seed bank)	**upper (2004)** > upper (2015) **	lower (2004) < **upper (2004)***	upper (2004) *** (decreasing) [58.9 %] lower (2004) n.s. upper (2015) *** (decreasing) [54.2 %]

The results from the upper soil depth differed in species abundances as well as in species proportions in the soil seed bank when the two sampling years (2004 vs. 2015) were compared. The successional status of individual plots in 2004 (the DCA 1st axis coordinates set as a covariable) significantly affected the changes performed during the 11 years in both species abundances and proportions (Table 2). Number of seedlings of grassland species in 2015 decreased if compared to 2004 (e.g., *Potentilla erecta* by 52.2%, *Campanula patula* by 67.1%, *Veronica officinalis* by 67.1%, *Luzula* spp. by 74.4%). On the other hand, ferns, representing forest species, were recorded only in eight of the re-sampled plots.

The soil seed bank of the two depth layers sampled in 2004 showed significant differences in the abundances of species (number of seedlings from the deeper soil layer was lower by 54.4%) but not in the relative proportions of the species. The successional status of the individual plots was not related to temporal changes in neither species abundances nor species proportions (Table 2).

3.3 Species richness of above-ground vegetation

Species richness of above-ground vegetation decreased along the spatially sampled succession gradient (DCA 1st-axis ordination scores) in both years (Fig. 4a, b). The significant decrease in species richness (by 60.3%) in 2015 compared to 2004 was also confirmed by re-sampling of plots (Table 2).

3.4 Species richness of soil seed banks

Species richness of the seed bank did not change along the spatially sampled succession gradient (DCA 1st-axis ordination scores) for any of the years and soil depth layers. However, in 2015 re-sampled plots exhibited significantly lower species richness than the initial plots in 2004, indicating decreasing species richness in the soil seed banks. According to the depth-for-time substitution approach, the deeper soil layer exhibited lower species richness than the upper soil layer (Table 2).

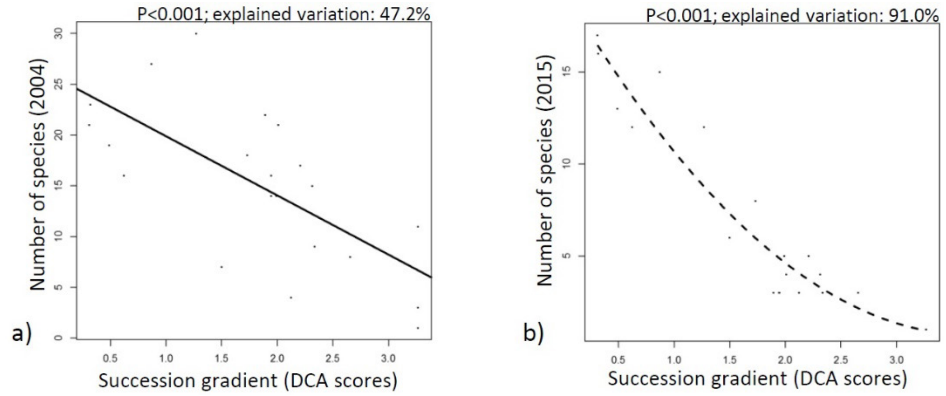

Fig. 4. Changes of the species richness of above-ground vegetation along the successional gradient expressed by the DCA first ordination axis scores of the respective plots. **a)** significant decreasing linear trend from 2004, **b)** significant decreasing quadratic trend of the re-sampled data from 2015.

Abb. 4. Zusammenhang zwischen Artenreichtum der Vegetation und der ersten DCA-Achse, die einem Sukzessionsgradienten entspricht. **a)** Signifikant lineare Abnahme im Jahr 2004; **b)** signifikant quadratische Abnahme im Jahr 2015.

3.5 Seed density

A decrease of seed density with time was confirmed by all three approaches used (temporal re-sampling, distance-for-time and depth-for-time substitutions). Based on re-sampling, the density of viable seeds in the upper soil layer decreased by 2.75 times from 2004 to 2015 (Table 2, Fig. 5a, b).

Only four individual species showed significant trends in seed density development during the spatial sampling along the spruce colonisation gradient (Fig. 6): *Hypericum maculatum* had a decreasing quadratic trend in the upper soil layer in 2004 and an increasing linear trend in the lower soil layer in 2004; *Carex* spp. had a decreasing quadratic trend in the upper soil layer in both, 2004 and 2015; *Potentilla erecta* had a decreasing quadratic trend in the upper soil layer in 2004; and *Veronica officinalis* had a decreasing quadratic trend in the upper soil layer in 2015.

3.6 Relation between soil seed bank and above-ground vegetation

The species composition of the above-ground vegetation and the soil seed bank differed considerably and only 31.3% of species (20 out of 75 vascular plant taxa found in the sampling plots - e.g., *Agrostis capilaris*, *Hypericum maculatum*, *Potentilla erecta*) were found in both, the above-ground vegetation and soil seed bank. Fourteen taxa (21.9%, e.g., *Dactylis glomerata*, *Juncus conglomeratus*, *Urtica dioica*), were represented only in the soil seed bank while 30 taxa (46.9%, e.g., *Cruciata glabra*, *Festuca rubra*, *Nardus stricta*) were represented only in the above-ground vegetation.

The species composition of soil seed bank in individual plots had low similarity with species composition of above-ground vegetation. In the PCA ordination graph (Fig. 7a), the above-ground vegetation samples are clearly separated from the soil seed bank samples independently of sampling year and soil depth layer. The variability of the vegetation composition of the seed bank samples was lower than that of the above-ground vegetation. Furthermore, the overlap of seed bank samples from different years and soil depth layers was larger than the overlap with re-sampled above-ground vegetation records.

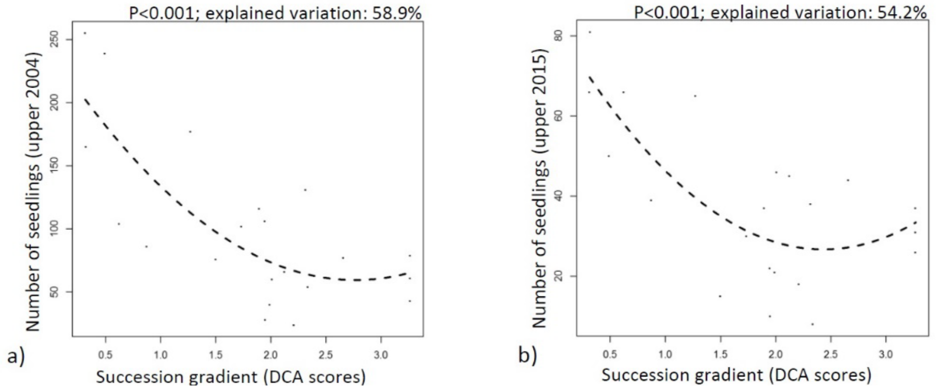

Fig. 5 Seed density of all species in the upper soil layer as a response variable showed a significant decreasing quadratic trend along the succession gradient expressed by the DCA first ordination axis scores of the respective plots. **a)** data from 2004, **b)** re-sampled data from 2015.

Abb. 5. Signifikant quadratische Abnahme der Gesamtsamendichte im Oberboden mit der ersten DCA-Achse, die einem Sukzessionsgradienten entspricht. Zusammenhang in **a)** 2004 und **b)** 2015.

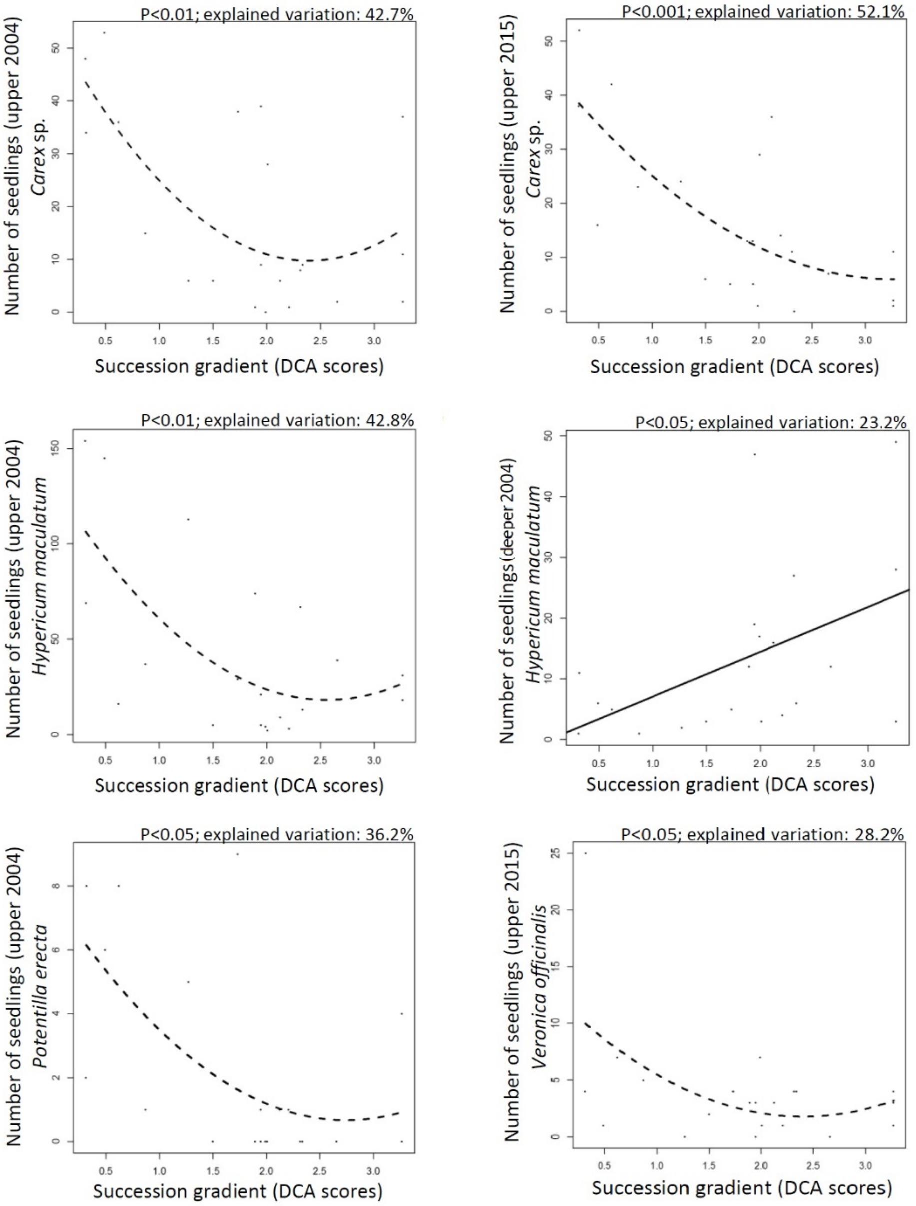

Fig 6. Vascular plant species with significant trends of seed density along the succession gradient.

Abb. 6. Gefäßpflanzen mit signifikant ab- oder zunehmender Samendichte entlang des Sukzessionsgradienten der 1. DCA-Achse.

While the successional development of the above-ground vegetation follows approximately the first PCA ordination axis and is well reflected in historical plots (2004) as well as their recently re-sampled counterparts (2015), the temporal shift of the soil seed bank samples follows rather the second PCA ordination axis with no clear pattern (Fig. 7b).

The successional development of the above-ground vegetation corresponds roughly to the first PCA ordination axis with a significant shift of the 2015 samples opposite the axis direction. The temporal shift of the soil seed bank samples follows rather the second PCA ordination axis, where seed-bank samples from 2015 are more similar to the late-successional stages of vegetation.

In 2004, the seed bank of the upper soil depth layer was not more similar to the above-ground vegetation than the seed bank of the deeper soil depth layer (Wilcoxon test, $Z = 0.5$, $p = 0.099$).

Sørensen dissimilarity of species composition in the above-ground vegetation and the soil seed bank of the upper soil depth layer increased during succession (expressed by the first DCA ordination axis scores) in both study years (Fig. 8a, b).

4. Discussion

Our experiment was carried out in an abandoned grassland where regular management was last applied about 10–20 years prior to transect establishment. Cessation of grazing and gradual spruce colonisation of the abandoned grassland resulted in profound changes in plant communities, microclimate and soil microbial community (GÖMÖRY et al. 2006, GÖMÖRYOVÁ et al. 2009) detectable already in 2004 at the beginning of our investigations. The next decade, after the transect establishment, was characterized by a gradual increase of spruce cover and a decrease of grassland species proportion and richness. In accordance with numerous studies on successional development of the above-ground vegetation along a succession gradient (SLUIS 2002, HRIVNÁK & UJHÁZY 2005) or studies based on re-sampling (DULLINGER et al. 2003) we indicated the spread of expansive grasses (*Brachypodium pinnatum*, *Calamagrostis arundinacea*, *Helictochloa praeusta*) and woody species following the abandonment and gradual decrease of species richness. The above-ground vegetation performed changes in species abundances and relative species proportions. We expected that succession-induced changes obvious in the above-ground vegetation will also be reflected in a species composition and richness of the soil seed bank. This was confirmed for all studied parameters – species abundances, proportions, richness as well as seed densities. Similarly to the decreasing cover of the herb layer, seed abundances of individual species decreased significantly in the soil seed bank. However, the direction of the seed bank changes did not correspond to the direction of the above-ground vegetation development as they were obviously driven by different ecological mechanisms.

Species composition of the soil seed bank did not change markedly during the 11 years, but seed density decreased strongly. Similar results were reported from another temperate mesic grassland (BAKKER et al. 1996, JACQUEMYN et al. 2011) with high proportions of seeds representing meadow species in later successional stages. Contrastingly, studies focusing on riparian grasslands of wetland vegetation reported rather an enhancement of species richness and density during succession, although here moisture (LOONEY & GIBSON 1995, AMIAUD & TOUZARD 2004) and salinity (EGAN & UNGAR 2000) gradients played important roles along with the succession. However, such comparisons can be made only with regard to the stage of succession. We suppose that rapid decline of seed density is char-

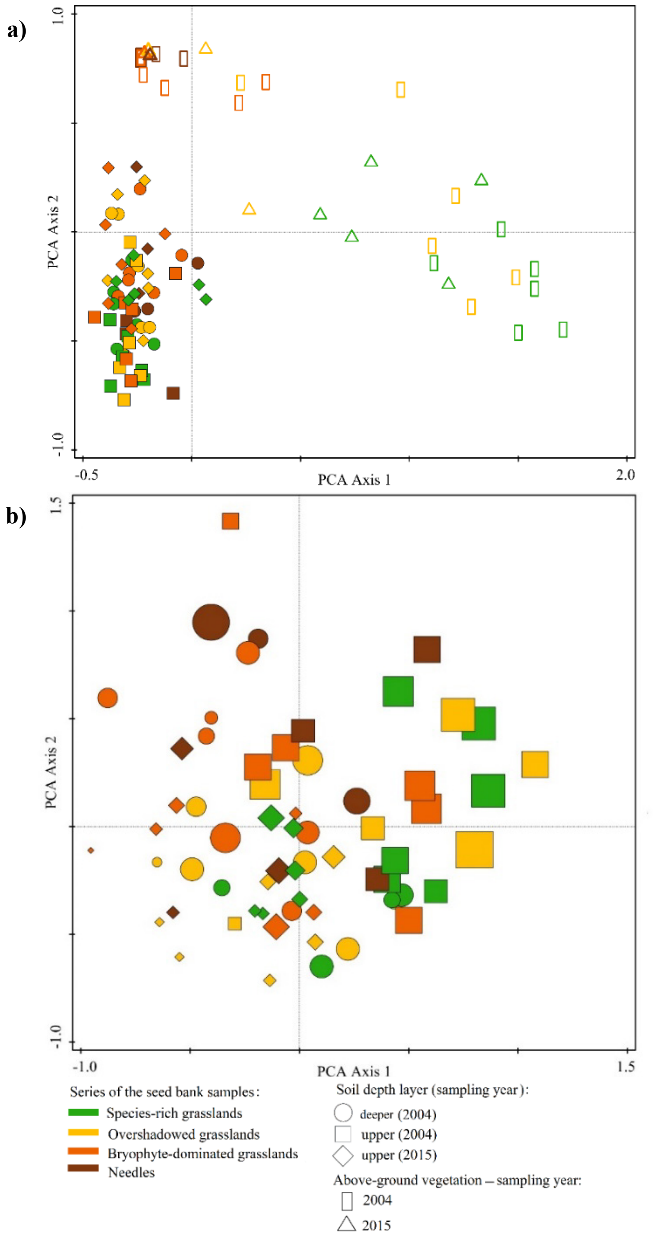

Fig. 7. PCA graphs based on species frequencies. **a)** Joint graph of soil seed bank and above-ground vegetation samples (total inertia = 2792.49, eigenvalues of the 1st axis = 0.303 and the 2nd axis = 0.250; variation explained by the 1st and 2nd axes = 55.3%). **b)** Soil seed bank samples, (total inertia = 682.16; eigenvalues of the 1st axis = 0.203 and the 2nd axis = 0.192; variation explained by the 1st and 2nd axes = 39.5%). Symbol size reflects number of seedlings in the individual plots. In both graphs, plots are colored according to the four successional stages of their above-ground vegetation in 2004 ascending from species-rich grasslands (green) through overshadowed grasslands (yellow) to bryophyte-dominated (orange) and bare stages (brown). Full-colored symbols representing seed bank samples, empty symbols are for the above-ground vegetation samples. Bryophyte species were omitted from the analyses.

acteristic to the latest phase of the grassland transition to the forest community, and the situation would be different in the previous less shaded stages (cf. FALIŃSKA 1999). There were no new vascular plant species able to form abundant populations in the transect area. Therefore, new seed sources were not available and seed production of present species was limited by intensive spruce shading. However, a declining seed density can also be associated with environmental conditions. Wetlands often have extensive seed banks, while seed banks of rather dry habitats are often quite depleted (HÖLZEL & OTTE 2001, KLAUS et al. 2017a). Differences between the dry and wet habitats are well documented from the tropical areas (e.g., KUNZ & MARTINS 2016, MADAWALA et al 2016), where the wet and dry seasons are changing and the species composition in seed bank is markedly affected by the changes of the above-ground vegetation during the year. Differences between the wetlands and dry grasslands of the soil seed banks in temperate climate zones are studied mainly using the successional gradient (LOONEY & GIBSON 1995, WOLTERS & BAKKER 2002, AMIAUD & TOUZARD 2004). The soil properties and its development are important factors to understand relation between the soil seed bank composition, density and species richness. Therefore the broad view is important for study seed banks processes. Many studies deals about the relationships between the soil-nutrient-content or vegetation type and seed viability and species richness (e.g., MÜZNBERGOVÁ 2012, HE et al. 2016) but the soil development in relation to the seed density is not clear. This opens new research field for studying influence of soil changes with different water-regime in the time in connection to soil seed bank.

A well-known strong decrease in seed density along a succession gradient in mesic grassland (BAKKER et al. 1996, JACQUEMYN et al. 2011) was confirmed only in the upper soil depth layer. The seed density in the lower soil layer was generally low, probably due to limited seed persistence of most represented species, thus the difference among the successional stages were not significant. The differences in seed longevity is probably the main reason why the depth-for-time substitution cannot be recommended as an adequate approach for studying soil seed bank composition along the successional gradient. Seed persistence affects species composition, species richness as well as the density of viable seeds, so that the lower soil layer assumed to represent an earlier successional stage is much more seed-depleted than the upper soil layer only due to the on average higher age of the seeds therein. However, certain assumptions on seed bank persistence based on species presence in the deeper soil layers (BAKKER et al. 1996) are justifiable.

Although it is clear that the soil layer is disturbed and mixed frequently predominantly due to human and animal activities, some of our findings and findings of other authors emphasize the importance to distinguish between several depth layers in soil seed bank studies.

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Abb. 7. PCA auf Grundlage der Artfrequenzen. **a)** Gemeinsamer Graph für die Samenbank und Vegetation; *total inertia* = 2792,5, Eigenvalues Achse 1 = 0,303 und Achse 2 = 0,250. Die ersten beiden Achsen erklären 55,3 % der Gesamtvariation. **b)** Samenbankproben; *total inertia* = 682,16; Eigenvalues Achse 1 = 0,203 und Achse 2 = 0,192; Die ersten beiden Achsen erklären 39,5 % der Gesamtvariation; die Größe der Symbole zeigt den Artenreichtum der Gefäßpflanzen an; die Farben der Symbole zeigen das Sukzessionsstadium der Vegetation (im Jahr 2004) an (vgl. Abb. 3 und Methodenkapitel): Artenreiches Grasland, beschattetes Grasland, Moos-dominiertes Grasland, vegetationsfreier Boden. Moose wurden in der Analyse nicht berücksichtigt.

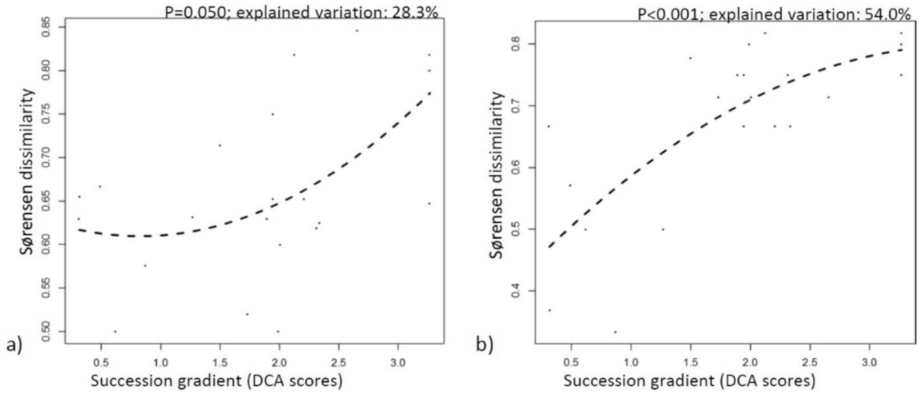

Fig. 8. Sørensen dissimilarity of soil seed bank composition in the upper soil layer and above-ground vegetation in **a)** 2004 and **b)** 2015 as a response variable predicted by the successional status of individual plots expressed by their first DCA ordination axis scores.

Abb. 8. Sørensen-Unähnlichkeit der Samenbank des Oberbodens und der Vegetation für die Jahre **a)** 2004 und **b)** 2015.

According to our observations, *Hypericum maculatum* was the only species with an increasing seed density in the lower soil layer along the spruce colonisation gradient. In the upper soil layer its seed density was highest in the earliest successional stages. As *H. maculatum* is a typical indicator of grassland abandonment, its maximal seed density in different successional stages in the two soil depth layers may indicate shifts in the successional development of the above-ground vegetation. Also findings of MILBERG (1995) suggest that the depth distribution of seeds may reflect well the above-ground development. He refers seed concentration of species lost from the above-ground vegetation in the deeper soil layer, although newly appearing, colonising species were evenly distributed among the layers.

The absence of ruderal species in the soil seed bank is common for mesic grasslands that have never been used as a cropland (TÖRÖK et al. 2012). In our study, the seed density of ruderal species (*Galeopsis bifida*, *Chenopodium album*, *Lipandra polysperma*) was negligible and they were also absent from the above-ground vegetation. It suggests that the studied grasslands were used exclusively as meadows or pastures without being ploughed after the deforestation. The presence of *Juncus* species (*J. conglomeratus* and *J. articulatus*) in the soil seed bank (while none of them was detected above-ground) confirms their known extraordinarily long persistence in the soil (c.f. MILBERG 1995 and works cited by him). In the case of *Juncus* spp., also the seed dispersal (likely by deer or another forest ungulate species) from the wet grasslands in the proximity of the area can be the explanation of their presence in the seed bank of a mesic site (cf. LEDA database [KLEYER et al. 2008]).

After the 11 years, the soil seed bank in the re-sampled plots consisted of 16 species, 13 of them being also present in the soil seed bank sampled in 2004 (at least in one of the layers). As no management was performed in the study area between the sampling and the re-sampling, we suppose that all these species have long-term persistent seed banks. This is inconsistent with several other studies (e.g., BAKKER et al. 1996 , KALAMEES & ZOBEL 1997, BISTEAU and MAHY 2005), classifying *Agrostis capillaris*, *Campanula patula*, *Carex caryophyllea*, *C. pilulifera*, *Hypericum maculatum*, *Luzula campestris*, *L. luzuloides*, *Veronica officinalis* and *Viola canina*, as taxa with short-persistent seed banks. To support our opinion, we have to argue, that most of these species are constant members of the former oligotrophic pasture of the *Violion caninae* phytosociological alliance, which was occurring in the study area in its typical form several decades ago (KLIMENT & UJHÁZY 2014, phytosociological relevés from the area dated from 1995–1996). This suggests that the seed bank composition reflects the former vegetation quite strongly and the above-mentioned species are in many plots better represented in the soil seed bank samples than in the above-ground vegetation (e.g., *Campanula patula* with high abundance in the seed bank samples but absent from the transect above-ground vegetation in 2004 and in 2015 only with two individuals above-ground). Another group of species includes frequent species of the herb layer missing in the soil seed bank irrespective from soil depth or above-ground successional development, e.g., *Cruciata glabra*, *Festuca rubra*, *Nardus stricta*. These species probably have transient seed banks and did not produce new seeds in the shaded sites during the last decade.

5. Conclusions

Although the space-for-time substitution approaches give satisfactory results in most cases (PICKETT 1989, KALAMEES et al. 2012, KŮROVÁ 2016), studies based on re-sampling such as monitoring programs or longer experiments with replicated treatments (e.g., WILLIAMS 1984, 1985, VIRAGH & GERENCSER 1988, MILBERG & HANSSON 1994, MILBERG 1995) still remain the only reliable trials to capture succession processes, both below- and above-ground. As emphasized by several authors (e.g., MILBERG 1995), conclusions from studies based on chronosequences may be misleading because of the implicit assumptions of predictable vegetation development and similarities in soil conditions, microclimate, history, availability of propagules, etc.

Although the soil seed bank can under certain circumstances play an essential role for the restoration of semi-natural grasslands, the seed bank itself is in most cases not sufficient for a successful habitat restoration. Many factors such as vegetation history, management, grassland type and site conditions influence the process of succession. Moreover, continuous management is necessary for a successful restoration (KISS et al. 2016, KLAUS et al. 2017a, b, 2018). The restoration success also depends also on the current successional stage of the respective plant community and presence of seed sources in the surroundings (LANG & HALPERN 2007). When agricultural management is absent for several decades and the majority of species is already missing in the seed bank, a potential to restore a species-rich grassland from seed bank is low. Our results show that only few target grassland species have a high chance to be supported by restoration activities after spruce removal in the studied site (*Agrostis capillaris*, *Campanula patula*, *Carex pilulifera*, *Potentilla aurea*, *P. erecta*, *Veronica officinalis* and *Viola canina*), as their representation in the soil seed bank was reasonable and persisting. The next components of the original grasslands should be reintroduced from still existing neighboring communities still containing species with the short-term or transient seed bank (HÖLZEL & OTTE 2003, JACQUEMYN et al. 2011).

In conclusion, restoration of similar habitats would be successful only in sites where a major part of the original species pool survived in near-by areas, and where the species propagules can be distributed by grazing animals within the period of restoration.

Erweitere deutsche Zusammenfassung

Einleitung – Halbnatürliches Grasland hat sich über lange Zeiträume traditionell-kleinbäuerlicher Bewirtschaftung entwickelt; im Europa des 20. Jahrhunderts ist es jedoch durch starke sozioökonomische Veränderungen sowie nicht-nachhaltige Landwirtschaftspolitik in erheblichem Ausmaß verloren gegangen (Csergő et al. 2013). Der Erfolg einer Wiederherstellung eines brachgefallenen Graslands hängt von verfügbaren Samenquellen in der Umgebung sowie vom Vorhandensein einer Samenbank im Boden ab (Bobbink & Willems 1993). Allerdings nimmt die Anzahl der Arten und Samen in der Samenbank mit der Dauer der Nutzungsaufgabe ab (Kalamees & Zobel 1998). Grundsätzlich kann die Samenbank wichtige Informationen darüber liefern, welche Arten in einem Grasland in der Vergangenheit existierten. Wir untersuchten Veränderungen der (oberirdischen) Vegetation und (unterirdischen) Samenbank eines brachgefallenen, anthropogenen, oligotroph-montanen Graslands, in das Fichten eingewandert waren. Das Hauptziel war der Vergleich der Veränderung der Artenzusammensetzung der Vegetation und Samenbank sowie des Artenreichtums und der Samendichte während der Wiederbewaldung. Außerdem wollten wir wissen, inwieweit sich die Ergebnisse von zwei *space-for-time substitution*-Ansätzen mit den Ergebnissen einer tatsächlich Wiederholungsaufnahme nach 11 Jahren deckten.

Methoden – Das Untersuchungsgebiet liegt in den Poľana-Bergen im Zentrum der Slowakei. Seit seiner Entwaldung um 1800 wurde in dem Gebiet zunächst eine Nutzung als Heuwiese und später als Weide praktiziert. Ab den späten 1990er Jahren wurde die Nutzung teilweise eingestellt und es kam – von um 1890 angelegten Aufforstungsflächen aus – zu einer spontanen Ansiedlung von Fichten (*Picea abies*). Dies gilt auch für unsere Untersuchungsfläche. In dieser Fläche wurden die Vegetation und Samenbank entlang eines 160 m langen Linientransekts aufgenommen, der vom Rand der Aufforstungsfläche in das ehemalige Grasland hinein reichte. So wurde in den Jahren 2004 und 2015 auf 155 Rundflächen mit je 0,5 m² Größe die Vegetation und in 21 Flächen davon die Samenbank in zwei Bodentiefen aufgenommen. In diesem *substitution*-Ansatz diente die Entfernung der Aufnahmeflächen zur Aufforstungsfläche als Ersatz für den Zeitpunkt der Wiederbewaldung bzw. das Ausmaß der Sukzession. Zusätzlich wurde angenommen, dass die Samenbank in den beiden Bodentiefen diesem Gradienten entsprach, indem die untere Bodenschicht ein älteres und die obere Bodenschicht ein jüngeres Sukzessionsstadium repräsentierte. Zur Einschätzung des Ausmaßes der Sukzession wurden aktuelle und historische Vegetationsdaten genutzt, und die Ergebnisse einer DCA-Ordination der Vegetation beider Jahre wurden als Annährung an die Sukzession der 21 Samenbankproben betrachtet. Eine PCA wurde zur Abbildung der Daten der oberirdischen Vegetation und der Samenbankdaten genutzt. *Multispecies responses* der Häufigkeiten und Anteile der Arten in der Vegetation und der Samenbank auf die Aufnahmezeit (2004 vs. 2011) und Bodentiefe (nur für die Samenbank) wurden mit Hilfe von RDA analysiert. Zum Vergleich der Ähnlichkeit der Artenzusammensetzung zwischen Samenbank und Vegetation diente der Sørensen-Index. Einfache Regressionsmodelle dienten zur Analyse der Beziehungen zwischen der Gesamtsamensichte und artspezifischen Samendichten des Bodens sowie des Artenreichtums der Vegetation entlang des Sukzessionsgradienten.

Ergebnisse – der Vegetationsuntersuchungen: Die Flächen der Samenbankuntersuchungen wurden nach ihrer Vegetation in vier Sukzessionsstadien klassifiziert: i) Artenreiches Grasland mit dominantem Auftreten typischer Arten oligotropher Weiden wurde als Initialstadium der Fichtenbesiedlung betrachtet; ii) beschattetes Grasland mit dominantem Auftreten von schattenverträglichen Arten und/oder dem Auftreten von azidophilen Arten infolge der Versauerung des Oberbodens durch Fichtenadeln wurde als erstes Folgestadium betrachtet; iii) moosdominierte Vegetation ohne nennenswerte Präsenz von Gefäßpflanzen als zweites Folgestadium; iv) mehr oder weniger vegetationsfreie Nadeldecken mit maximal 5 % Unterwuchsdeckung als Endstadium der Konkurrenz durch die Fichten als drittes Folgestadium. Während der 11 Jahre zwischen Erst- und Wiederholungsaufnahme der Vegetation zeigten die meisten Flächen eine eng mit der ersten DCA-Achse (die den Sukzessionsgradienten repräsentierte) korrelierte einseitig-gerichtete Veränderung – die jedoch von der Richtung der zunehmenden Deckung der Fichtennadeln (als weiteres Maß der Bewaldung) etwas abwich (Abb. 3). Die Vegetation der Jahre 2004 und

2015 unterschied sich signifikant in den Häufigkeiten und Anteilen der einzelnen Arten, und die Gesamtartenkombination hatte sich über die 11 Jahre entlang des Sukzessionsgradienten signifikant verändert (Tab. 2).

Samenbankuntersuchungen: Die Samenbank des Oberbodens unterschied sich zwischen den Jahren 2004 und 2015 sowohl in den Häufigkeiten als auch in den Anteilen der Arten. In 2004 war der Sukzessionsstatus der einzelnen Aufnahmeflächen mit den Veränderungen der Häufigkeiten und Anteilen der Arten während der 11 Jahre signifikant korreliert (Tab. 2). Im Jahr 2004 unterschieden sich die beiden Bodenhorizonte in ihren Artenhäufigkeiten, aber nicht in ihren Artanteilen. Die Sukzession der Vegetation spiegelte nicht die Häufigkeiten und Anteile der Arten wieder (Tab. 2). In beiden Jahren nahm der Artenreichtum der Vegetation entlang des Sukzessionsgradienten ab. Tatsächlich hatte auch der Artenreichtum der Flächen zwischen 2004 und 2015 signifikant abgenommen. Der Artenreichtum in den beiden Bodentiefen unterschied sich dagegen entlang des Sukzessionsgradienten nicht signifikant. Im Vergleich zum Oberboden in 2004 hatten sowohl der Unterboden in 2014 als auch der Oberboden in 2015 signifikant niedrigere Artenzahlen (Tab. 2). Die Abnahme der Samendichte mit der Zeit bestätigte sich in allen verfolgten Untersuchungsansätzen: Wiederaufnahme der Samenbank, *distance-for-time substitution* und *depth-for-time substitution* (Tab. 2, Abb. 5a, b). Die Artenzusammensetzung der Samenbank korrespondierte in einzelnen Flächen nur wenig mit der Artenzusammensetzung der Vegetation (Abb. 7a). Die Sørensen-Unähnlichkeit der Artenzusammensetzung der Vegetation und der Samenbank des Oberbodens nahm in beiden Jahren mit zunehmender Sukzession zu (Abb. 8a, b). Unsere Ergebnisse zeigen, dass die Entwicklung des Artenreichtums der Samenbank während einer Sekundärsukzession eines Graslands nicht auf der Grundlage räumlicher Muster belastbar vorhergesagt werden kann, zumindest nicht, wenn nur eine einzige, nichtwiederholte Aufnahme durchgeführt wird. Vor dem Hintergrund der starken Variation der Ergebnisse mit einen Sukzessionshintergrund schlussfolgern wir, dass bei Samenbankuntersuchungen ein *distance-for-time substitution*-Ansatz nur mit erheblicher Vorsicht genutzt werden sollte.

Diskussion – Die Analyse der Artenzusammensetzung der Vegetation zeigte verschiedene Veränderungen der Häufigkeiten und Anteile der Arten. Wir hatten erwartetet, dass sich sukzessionsinduzierte Veränderungen der Vegetation auch in der Samenbank widerspiegeln. Tatsächlich hatten parallel zu der Krautschicht auch in der Samenbank verschiedene Arten signifikant abgenommen. Allerdings korrespondierten Samenbank und Vegetation nicht in der Richtung ihrer Gesamtveränderung – offenbar wirken hier unterschiedliche ökologische Mechanismen. Während sich die Artenzusammensetzung der Samenbank während der 11 Jahre nicht substanziell änderte, nahm die Samendichte um ein Mehrfaches ab. Dabei war die Samendichte im Unterboden generell gering – dies lag wahrscheinlich an der begrenzten Lebensdauer der Samen der meisten Arten, und wohl daher unterschieden sich die Sukzessionsstadien auch nicht signifikant. Die unterschiedliche Lebensdauer der Samen war wahrscheinlich auch der Hauptgrund dafür, dass die *depth-for-time substitution* nicht funktionierte und diese Methode daher nicht ohne Weiteres zur Untersuchung von Samenbanken entlang von Sukzessionsgradienten zu empfehlen ist. Grundsätzlich spielt die Samenbank bei der Wiederherstellung von halbnatürlichem Grasland eine wichtige Rolle, aber oftmals reicht sie nicht dafür aus. Unsere Ergebnisse zeigen, dass nur einige Grasland-Zielarten ein Wiederherstellungspotential besitzen, indem diese Arten eine persistente Samenbank ausbilden und auch in nennenswerter Menge in der Samenbank vorkommen. Bei uns waren dies *Agrostis capillaris*, *Campanula patula*, *Carex pilulifera*, *Potentilla aurea*, *P. erecta*, *Veronica officinalis* und *Viola canina.*

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