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Soil seed bank and vegetation in mixed coniferous forest stands with different disturbance regimes

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Abstract

We studied the soil seed bank in mesophyte mixed spruce forest in Koeru, central Estonia, represented by three old stands with low intensity management, and three young regenerating planted stands in areas clear-cut 20–25 years ago. The seed bank consisted of 36-plant species altogether, of which 14 were not represented in the vegetation. There were 42 phanerogam species in the forest understory, which were not represented in the seed bank. There were on average 900 seeds per m^2 in the top 10 cm soil layer, this number was significantly higher in young (1105 seeds) than in old (640 seeds) stands. Differences in the seed bank between the top 0–5 and 5–10 cm layers were negligible. *Rubus idaeus* and *Carex pallescens* were the most abundant species in the seed bank, the first species being abundant in old stand gaps, whereas the second was not represented in the vegetation. CA ordination showed that community composition differed between the vegetation and the seed bank, as well as between young and old stands. Within both young and old stands, there was a poor correspondence between the vegetation and the seed bank.

Keywords: Diversity; Mixed coniferous forest; Seed bank; Forest management; Ordination; Temperate forest; Understory vegetation

1. Introduction

In human-impacted landscapes, forests form a mosaic of different successional stages, representing regeneration stages after agricultural use, fires and logging (Vellend, 2003; Verheyen et al., 2003). Different forest management scenarios may have significant impact on the diversity and composition of plant communities (Decocq et al., 2004; Ramovs and Roberts, 2003; Reich et al., 2001). In the case of severe silvicultural disturbances, there may be a shift from residual and resprouting understory species to species regenerating from seed and spores (Haeussler et al., 2002; Mayer et al., 2004). In particular, regeneration from the soil seed bank may be important. In order to predict the response of vegetation to disturbance, it is necessary to have information about the composition of the soil seed bank in forest ecosystems.

Soil seed banks are reserves of viable ungerminated seeds present in the soil or on the soil surface. The seed bank consists of new seeds shed only recently as well as older seeds that have persisted in the soil for several years. In temperate, boreal and arctic climates, the adaptive significance of seed dormancy is most often the avoidance of low temperatures during seedling establishment (Thompson, 2000).

Poor correspondence between species present in above-ground vegetation and in the soil seed bank is characteristic to European temperate forests in general (Bossuyt and Hermy, 2001). There is evidence that most late-successional tree and shrub species are poorly represented in the persistent soil seed bank. Shade tolerant forest understory species tend to produce relatively short-living seeds in small amounts and those seeds do not accumulate in seed banks. The persistent soil seed banks of temperate forests predominantly contain seeds of early-successional and light-demanding species, some of which are probably preserved in the soil already from previous successional stages of the forest, while others have only recently been dispersed in various ways from adjacent communities. Such seed banks play little or no part in the regeneration of the mature vegetation after a disturbance (Pickett and McDonnell, 1989; Grandin and Rydin, 1998; Bossuyt and Hermy, 2001; Grandin, 2001).

Information about the composition of the viable soil seed bank in differently managed temperate forest ecosystems is still scarce. Some studies report higher number of seeds in the soil seed bank in young secondary forests, compared to old stands (Onaindia and Amezaga, 2000; Sakai et al., 2005), but there is

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little information about the differences in seed species composition between young and old stands.

The seed bank may play a crucial role in determining the composition and spatial structure of understory plant communities in clearcut areas following soil disturbances. At the same time, it may contribute to plant regeneration in old growths as well. Tree fall, which create gaps, is fundamental to the development of natural forest stands (Attiwill, 1994). In such tree-fall gaps, the uprooting of trees often creates favourable conditions for the germination of the seeds in the seed bank (Mayer et al., 2004). According to Bossuyt and Hermy (2001), the effect of former land use on the composition of seed bank decreases after 50 years. Thus, one may assume that the share of ruderal species in the seed bank of old growths is lower in comparison to young regenerating stands.

We were interested in the composition of the soil seed bank and its similarity to understory vegetation in the differentially managed mixed coniferous forest stands. We hypothesised that the seed banks of young planted stands, regenerating after clearcutting about 20–30 years ago, contain more seeds than the seed banks of old forest stands, and more seeds of ruderal species in particular. Also, we hypothesised that, both due to the temporal decrease in the share of ruderal species in the vegetation after clearcutting, and due to the release of part of the seeds in the seed bank as a result of small-scale disturbances (e.g. tree-fall gaps) in old stands, floristic similarity between the seed bank and the understory vegetation will be higher in old stands, compared to young regenerating stands.

2. Material and methods

2.1. Koeru site

The study site was located in Koeru, central Estonia (58°97′N; 26°05′E). It is a flat area where the landscape is a mosaic of cultivated areas and forests. Study site is a forested patch of 130 ha, representing the *Hepatica nobilis* site type (Lõhmus, 2004). The soil is calcaric cambisol. Norway spruce (*Picea abies*) is the predominating tree species; *Corylus avellana* prevails in the shrub layer. Altogether 69 herbaceous vascular plant species were recorded in the field layer, *Oxalis acetosella*, *Fragaria vesca*, *Viola mirabilis* and *H. nobilis* were the most abundant species. *Dicranum scoparium* and *Cirriphyllum piliferum* were the most common bryophytes.

According to the available information, Koeru forest area has not been tilled in earlier times. On the oldest map available (from 1828) the area is indicated as a forest. The forest has been managed and clearcutting has taken place in patches of approximately 1–2 ha. At the same time, part of the forest can still be classified as old growth, where different age classes are represented and the oldest spruces are 130–140 years old. In those areas, selective felling has been practiced, but there is still coarse woody debris on the ground (cf. Moora et al., 2007).

Our study sites were located within a uniform forest area with an approximate size of 0.8 km^2. We sampled two successional stages, representing forest ecosystems under low (old stands) and high intensity (young stands) management. Old stands (sites X, Y, Z) were represented by mature spruce forests with uneven age distribution In these stands the intensity of forest management has been low and they represent ecosystems that are close to their natural state. The overstory is predominated by *P. abies*, while middle-aged *Acer platanoides* and *Fraxinus excelsior* can be found in the regrowth. Early-successional stages (sites R, S, T) were represented by young dense stands in areas that were clearcut 20–25 years ago and then planted with Norway spruce. Single trees of *Betula pendula* and *Tilia cordata* occurred in the tree layer as well. In recent years, planted stands have been thinned repeatedly.

In order to characterise soil conditions, five topsoil (0–5 cm) and subsoil (6–10 cm) samples were collected from each stand. Samples were sieved to remove roots and then analysed. Soil pH_{KCl}, N, K, P, Mg and Ca contents, as well as content of organic matter (loss of ignition) were determined according to Moore and Chapman (1986). Mixed model GLM (StatSoft, 2001), where random factor site (three levels) was nested within the fixed factor disturbance regime (low and high intensity management) was used to characterise soil conditions in different depth (topsoil 0–5 cm, subsoil 6–10 cm) in study area.

2.2. Methods

The soil seed bank was sampled at the end of June 2004. At that time, seeds released in the previous summer had had a possibility to germinate during the autumn and spring, while seeds from the current season would not yet have been released. Thus, the collected soil seed bank samples comprised mainly of persistent seeds.

In each stand, six randomly located 1 m × 1 m plots were used for soil seed bank sampling. In each 1 m × 1 m plot, 10 soil cores (4 cm diameter) of 10 cm depth were collected at regular intervals. After removal of the litter, the samples were divided into subsamples of 0–5 and 5–10 cm depth. The 10 cores at each depth per plot were pooled. As suggested by ter Heerdt et al. (1996), the pooled samples were washed on a fine sieve (mesh width 0.2 mm), which resulted in a considerable decrease in bulk. The remaining material was spread in a thin layer over a 4 cm thick layer of sterilized potting soil in plastic trays (15 cm × 25 cm). A control tray filled with sterilized potting soil monitored any airborne seed contaminants. All trays were randomly arranged in an unheated greenhouse and were watered regularly with tap water. The emerged seedlings were identified as soon as possible, counted and removed during the whole growing period. Unidentifiable seedlings were transplanted and grown, where necessary, until flowering. No attempt was made to assess the number of ungerminated seeds possibly remaining in the samples.

Vegetation sampling was carried out on five randomly located 5 m × 5 m plots in each study site, where the percent coverage of vascular plant species was recorded. All species growing outside vegetation plots were listed as well. For other characteristics of the vegetation (cf. Moora et al., 2007).

Correspondence Analysis (CA), using PC-Ord ver. 4.36 (McCune and Grace, 2002), was performed for detection of compositional differences in 5 m × 5 m vegetation plots and

pooled seed bank samples, using relative frequency data indicating either relative cover of a species in relation to a total cover, or relative frequency of species in seed bank subsamples. The pattern diversity—spatial turnover of a community in a homogeneous environment (Pielou, 1966) was calculated as one minus the Jaccard coefficient of similarity (Colwell and Coddington, 1994). Jaccard coefficient of similarity was calculated using EstimateS (Colwell, 2005). Mixed model GLM (StatSoft, 2001), where random factor site (three levels) was nested in to the fixed factor disturbance regime (low and high intensity managements) was used to analyse the number of species and the number of seeds in topsoil and subsoil (depth, two levels) seed bank.

3. Results

Altogether 394 seeds belonging to 36 plant species were recorded in seed bank samples. Soil samples from old stands hold 144 seeds from 24 species and samples from young stands, 250 seeds belonging to 28 species (Table 1). The most abundant species in the soil seed bank where *Rubus idaeus*, *Carex pallescens*, *Veronica chamaedrys*, *Hypericum perforatum* and *Agrostis capillaris*. These five species made up to 65% of seeds recorded in soil seed bank samples. The average number of seeds per m^2 ranged from 480 (old forest stand W) to 1207 (young forest stand T). The average seed density over all study sites was 900 m^{-2}.

Table 1
The relative abundance (% occurrence in six pooled samples within each site) of plant species in the seed bank (SB, 0–5 and 5–10 cm layers of the soil) and vegetation V (% occurrence in 24 pooled samples within each site), number of species and number of seeds in old (Z, W, Y) and in young (R, S, T) study sites

Species	SB[a]		V^a	SB[b]		V^b	SB[c]		V^c	SB[d]		V^d	SB[e]		V^e	SB[f]		V^f
	0–5	5–10		0–5	5–10		0–5	5–10		0–5	5–10		0–5	5–10		0–5	5–10	
Adoxa moschatellina	0	0	0	0	0	0	0	0	0	0	0	0	17	0	0	0	0	0
Agrostis capillaris	0	0	0	0	17	4	0	0	0	50	33	8	17	0	8	17	17	12
Arenaria serpyllifolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17	0
Campanula persicifolia	0	33	0	17	0	0	0	33	0	0	17	8	0	0	32	17	0	8
Carex pallescens	50	33	0	17	33	0	33	33	0	50	50	0	17	0	0	0	33	0
Cerastium fontanum	0	33	0	17	0	0	17	0	0	0	0	0	0	17	0	17	33	0
Dactylis glomerata	0	0	4	0	0	12	0	17	8	0	0	28	0	0	20	0	17	40
Deschampsia caespitosa	0	0	8	0	17	24	17	0	8	0	0	32	0	17	32	17	17	36
Epilobium adenocaulon	0	0	0	0	0	0	0	0	0	17	0	0	17	33	0	0	0	0
Festuca rubra	0	0	0	0	0	4	0	0	0	0	17	0	0	17	0	0	17	8
Fragaria vesca	0	17	56	0	0	84	50	50	96	17	33	44	0	0	32	17	0	48
Galium album	0	0	0	0	0	0	17	0	0	0	0	16	17	0	20	0	0	8
Geum rivale	0	17	68	0	0	52	0	33	72	0	0	36	0	0	52	0	0	68
Glechoma hederacea	0	0	0	0	0	0	0	0	0	0	17	0	0	0	0	0	0	0
Hypericum perforatum	17	0	16	0	17	40	17	33	8	17	0	24	50	33	24	50	33	32
Juncus sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17	0
Luzula pilosa	0	0	48	0	17	60	0	0	64	0	0	52	0	0	76	0	0	88
Medicago lupulina	0	0	0	0	0	0	17	0	0	0	0	0	0	0	0	0	0	0
Melica nutans	0	0	0	0	0	4	0	0	8	0	0	8	0	0	40	17	0	16
Moehringia trinervia	0	17	0	0	17	0	50	50	0	0	0	0	0	0	0	17	33	0
Mycelis muralis	17	33	28	0	17	32	0	0	12	0	0	4	0	0	0	0	0	4
Oxalis acetosella	0	0	100	17	0	100	0	0	100	0	0	68	0	0	88	0	0	92
Poa pratensis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17	50	0
Potentilla erecta	0	0	0	0	0	0	0	17	0	0	0	0	0	0	0	0	0	0
Ranunculus acris	0	0	0	0	0	0	0	0	0	17	0	12	0	0	8	0	0	4
Rubus idaeus	17	33	24	17	17	52	17	50	32	17	50	0	33	33	4	33	67	12
Rumex acetosa	0	0	0	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sagina nodosa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17	0	0
Stellaria graminea	0	0	0	0	0	0	17	0	0	0	0	0	33	0	0	17	0	4
Stellaria media	17	0	0	0	0	0	17	0	0	0	17	0	33	17	0	0	33	4
Taraxacum sp.	0	0	4	0	0	0	0	0	4	0	17	8	0	0	8	0	0	16
Veronica chamaedrys	33	33	64	17	50	52	67	17	48	17	50	56	33	50	60	50	67	68
Veronica officinalis	17	0	0	0	17	24	0	0	8	0	0	0	0	17	0	17	0	4
Veronica serpyllifolia	17	17	0	0	0	0	17	0	0	0	17	0	0	33	0	0	0	0
Viola riviniana	0	0	32	0	0	48	0	0	36	0	0	76	0	0	76	17	0	84
Number of species	8	10	35	7	10	43	13	10	41	8	11	46	10	10	43	15	14	51
Number of seeds	23	18		9	27		29	38		41	47		33	38		42	49	

In vegetation, only species, which occurred in the seed bank, are mentioned in the table.
[a] Study site Z.
[b] Study site W.
[c] Study site Y.
[d] Study site R.
[e] Study site S.
[f] Study site T.

We recorded 42 phanerogam plant species in the vegetation which were not represented in the seed bank, including species characteristic for old forest stands, like *Actaea spicata*, *Circea alpina* and *Galeobdolon luteum*. The seed bank contained 14 species that were not present in the vegetation. Among them, three species (*Adoxa moschatellina*, *Moehringia trinerva* and *Potentilla erecta*) occur sparsely in Koeru forest outside vegetation sample plots, while others are characteristic, rather, to disturbed sites in forests (clearcuts, road verges).

The CA ordination diagram, based on relative frequencies of species in the vegetation and in the soil seed bank, is presented in Fig. 1. The first axis explained 75.5% and the second axis 6% of the total variation. The first ordination axis separated vegetation plots and soil seed bank samples. Old forest stands and young forest stands were separated along the second axis. The similarity of seed bank species composition and abundance among stands was little bit higher than the similarity of vegetation among stands. The seeds of *A. capillaris*, *Epilobium adenocaulon* and *Festuca rubra* occurred frequently in young stands seed bank. In two old stands, *Mycelis muralis*, a species represented more abundantly in the vegetation of old forest, was also abundantly represented in the seed bank. At the same time, the similarity between the species composition of seed bank and vegetation did not differ when young and old stands were compared to each other.

The average pattern diversity of the seed bank (0.18 in both cases) did not differ among young and old stands.

The mean number of species in the soil seed bank did not differ significantly between old and young forest stands ($F = 1.331$; d.f. = 1, 30; $P = 0.257$). The highest number of species per site was recorded in young forest site S (21), while the lowest number was found in old forest site W (14).

The mean number of seeds in the soil seed bank differed significantly between old and young forest stands ($F = 312.111$; d.f. = 1, 30; $P = 0.013$). The seed bank samples from young forest contained on average five seeds more than old forest seed bank samples. There were on average 1105 seeds per m^2 in young stands and 640 seeds per m^2 in old stands.

The seed number ($F = 0.914$; d.f. = 1, 64; $P = 342$) and the seed species number ($F = 1.970$; d.f. = 1, 64; $P = 0.165$) in upper and lower soil layers did not differ significantly. The seeds of half of the species were present both in upper and lower soil layers. *Veronica serpyllifolia* was the only species that was found only in the lower soil layer in young forest.

The soil conditions were relatively homogeneous. The average content of organic matter, total N, Ca, P, K, Mg and pH_{KCl} in study sites is given in Table 2. Study sites within young and old stands did not differ significantly from each other. pH_{KCl} and Ca content did not differ between top- and subsoil, while the content of organic matter ($F = 23.0$; d.f. = 1, 52; $P < 0.0001$), nitrogen ($F = 17.0$; d.f. = 1, 52; $P < 0.0001$), phosphorus ($F = 4.41$; d.f. = 1, 52; $P < 0.04$), potassium ($F = 14.04$; d.f. = 1, 52; $P < 0.0001$) was higher; and magnesium ($F = 3.7$; d.f. = 1, 52; $P < 0.062$) marginally nonsignificantly higher in the topsoil. The disturbance regime did not influence significantly soil characteristics, except there was a significant interaction between disturbance regime and soil layer in the case of the content of organic matter ($F = 4.8$; d.f. = 1, 52; $P < 0.032$). There were no differences in the

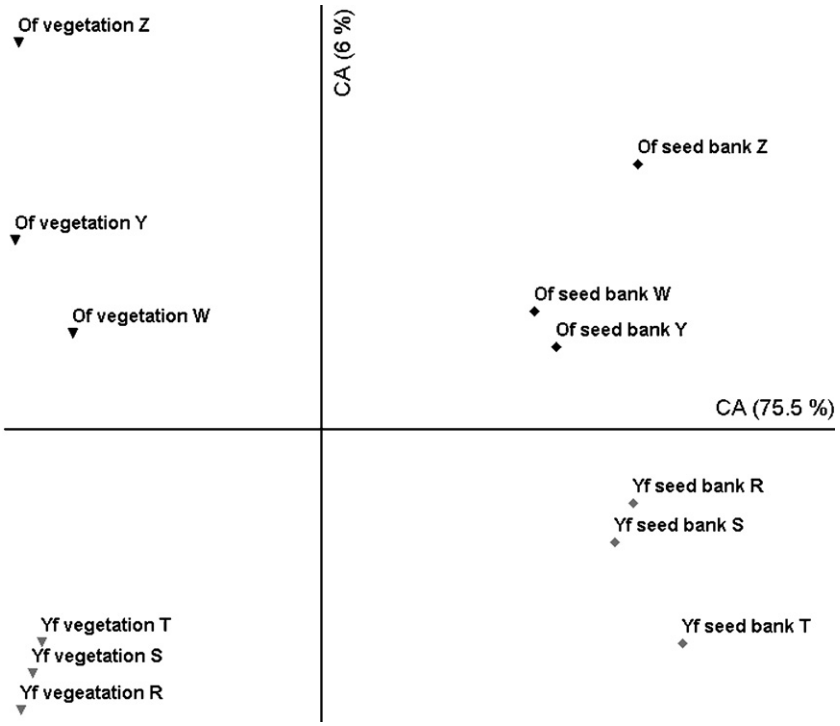

Fig. 1. The CA ordination diagram, based on relative frequencies of plant species in the vegetation and in the soil seed bank. Black triangles and black squares mark old forest (OF) study sites (Z, W, Y). Empty triangles and empty squares mark young forest (YF) study sites (R, S, T). Triangles mark the vegetation and squares mark the soil seed bank.

Table 2
The mean content and standard deviation of pH_{KCl}, total N, Ca, P, K, Mg and organic matter (OM) of the topsoil (0–5 cm) (1) and subsoil (5–10 cm) (2) of the study sites averaged over five soil samples in each site

Study site	Z		W		Y		R		S		T	
	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
pH_{KCl} (1)	5.2	0.7	5.6	0.5	5.7	0.8	5.6	0.6	5.6	0.9	5.3	0.8
pH_{KCl} (2)	5.1	0.6	5.6	0.7	5.8	0.9	5.4	0.7	5.5	1.0	5.4	0.9
N (%) (1)	0.276	0.024	0.284	0.041	0.236	0.082	0.202	0.054	0.256	0.128	0.245	0.044
N (%) (2)	0.168	0.030	0.167	0.048	0.183	0.057	0.175	0.011	0.195	0.104	0.208	0.049
Ca (mg/kg) (1)	1661.4	457.6	1743.4	497.4	1806.4	688.2	1219.8	297.1	1604.4	989.4	1693.0	657.3
Ca (mg/kg) (2)	1201.2	378.9	1274.0	467.9	1616.4	565.1	1078.0	417.2	1430.2	955.0	1657.2	729.1
P (mg/kg) (1)	7.2	2.8	7.1	4.2	10.6	7.8	6.6	3.6	11.7	8.4	4.4	1.9
P (mg/kg) (2)	2.3	0.7	3.3	2.3	9.5	2.5	4.2	1.1	6.2	5.4	4.2	2.9
K (mg/kg) (1)	68.0	22.0	43.1	5.4	49.2	28.8	72.2	55.8	91.1	62.5	29.7	7.8
K (mg/kg) (2)	21.8	2.7	18.9	6.5	32.8	5.7	42.0	24.6	43.1	29.0	25.7	12.3
Mg (mg/kg) (1)	218.5	74.8	241.5	39.6	284.2	158.2	243.0	40.5	193.7	82.2	212.0	68.2
Mg (mg/kg) (2)	169.5	71.5	186.6	74.4	231.4	65.8	230.5	21.5	167.4	67.4	189.0	75.1
OM (%) (1)	8.2	1.0	9.1	2.3	6.7	2.5	6.7	1.9	6.9	2.9	6.8	1.1
OM (%) (2)	4.5	0.7	4.9	1.2	5.2	1.6	5.5	0.4	5.2	2.0	6.2	1.4

content of organic matter between top- and subsoil in young stands, while the in the old stands, higher content of organic matter was observed in the topsoil.

4. Discussion

The seed bank in the soil of Koeru mesophyte mixed coniferous forest was relatively poor in seeds and species. Both the average seed density and species richness fell well within the range reported from temperate coniferous forests (Bossuyt and Hermy, 2001), while higher numbers of both species and seeds have been recorded from deciduous old growths (Jankowska-Błaszczuk et al., 1998; Leckie et al., 2000). As reported elsewhere in temperate forests in Europe (Mayer et al., 2004), *R. idaeus* and *Carex* spp. (*C. pallescens* in our case) were the most common species in the seed bank (Table 1).

Some authors report relatively good representation of late-successional forest species in the seed bank, which shows the potential significance of the seed bank in community regeneration (Leckie et al., 2000; Mayer et al., 2004), while other authors argue that due to the scarcity of typical forest species in the bank, its significance as the source of seeds is negligible for understory regeneration (Warr et al., 1994; Eriksson, 1995; Onaindia and Amezaga, 2000; Wienk et al., 2004). Our data rather confirm a poor correspondence between species present in the flora and in the seed bank—58% of the forest understory species were not represented in the bank. Among those species that were rather abundant on the forest floor, only three (*F. vesca*, *Geum rivale* and *V. chamaedrys*) were relatively frequent also in the seed bank. Among phanerogam species specifically characteristic to old stands in Koeru study area (*A. spicata*, *C. alpina*, *G. luteum*, *M. muralis*), only the last one had a considerable seed bank in the soil.

We hypothesised that the seed bank in young regenerating stands contains more seeds per unit than in old stands. This hypothesis was confirmed by field data. Similar pattern has been observed by Onaindia and Amezaga (2000), who compared native stands and plantations and Sakai et al. (2005), who focused on the comparison of a middle-aged stand and a former clearcut. At the same time, seed species richness did not differ between old and young stands. Similar result has been received by Landenberger and McGraw (2004), while Sakai et al. (2005) even recorded less species in the seed bank of clearcut areas. We also recorded more ruderal species in the seed bank than in the vegetation. At the same time, one representative of ruderal strategy, *R. idaeus*, was more abundant in the vegetation of old than of young stands. Its occurrence is connected with canopy gaps in old stands (Moora et al., 2007). Besides efficient bird dispersal and the ability to regenerate vegetative, the abundant seed bank of *R. ideaus* is evidently a key to its rapid regeneration in tree-fall gaps.

Our second hypothesis was about the possible successional convergence of the species composition of understory vegetation and the seed bank—we assumed higher similarity between the vegetation and the seed bank in old stands. This hypothesis was not confirmed, since most of the typical forest species were not represented in the bank and the seed bank in old stands still consisted of several generalist and ruderal species. The species turnover among the seed bank samples within stand remained equally high in young and old stands, while the pattern diversity of the vegetation was lower in old stands (Moora et al., 2007). Similarly, Sakai et al. (2005) report clumped distribution of buried viable seeds in the soil.

The seed bank of herb-rich mixed coniferous forest did not correspond well to the vegetation in both management regimes. However, there were more seeds in the seed bank of young forest than in the seed bank of old forest. The increased seed number in young forest seed bank was mostly due to the ruderal species but the seed bank of old forest consisted ruderal species as well. It is concluded, that due to the scarcity of typical forest species in the seed bank, its significance as the source of seeds is relatively negligible for understory regeneration after the disturbance.

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