

# Seed banks are biodiversity reservoirs: species–area relationships above versus below ground

Vigdis Vandvik, Kari Klanderud, Eric Meineri, Inger E. Måren and Joachim Töpper

V. Vandvik (*vigdis.vandvik@bio.uib.no*), K. Klanderud, E. Meineri and J. Töpper, Dept of Biology, Univ. of Bergen, Tormøhlensgate 53A, NO-5008 Bergen, Norway. KK also at: Dept of Ecology and Natural Resource Management, Norwegian Univ. of Life Sciences, NO-1432 Ås, Norway. EM also at: Dept of Ecology, Environment and Plant Sciences, Stockholm Univ., Lilla Frescativägen 5, SE-106 91, Stockholm, Sweden. JT also at: Faculty of Engineering and Science, Sogn og Fjordane Univ. College, PO Box 133, NO-6851 Sogndal, Norway. – I. E. Måren, Dept of Geography, Univ. of Bergen, Fosswinckelsgate 6, NO-5007 Bergen, Norway.

Soil seed banks offer plants the possibility to disperse through time. This has implications for population and community dynamics, as recognised by ecological and evolutionary theory. In contrast, the conservation and restoration literature often find seed banks to be depauperate, weedy and without much conservation value or restoration potential. One explanation for these contrasting views might lie in a systematic bias in the sampling of seed banks versus established plant communities. We use the species–area relationship as a tool to assess and compare the per-area species richness and spatial structuring of the diversity of the established plant community versus soil seed banks. To allow this direct comparison we extensively survey the species–area relationship of the vegetation and underlying seed bank of a grassland community across twelve sites spanning regional bioclimatic gradients. We also compile a global dataset of established vegetation and seed banks from published sources. We find that seed banks have consistently higher intercepts and slopes of the relationship, and hence higher diversity at any given spatial scale, than the vegetation both in the field and literature study. This is consistent across habitat types, climate gradients, and biomes. Similarity indices are commonly used to compare vegetation and seed bank, and we find that sampling effort (% of the vegetation area sampled for seed bank) was the strongest predictor of vegetation–seed bank similarity for both the Sørensen ( $R^2 = 0.70$ ) and the Raup–Crick ( $R^2 = 0.25$ ) index. Our study suggests that the perception that seed banks are intrinsically less diverse than established plant communities has been based more on inadequate sampling than on biological reality. Across a range of ecosystems and climatic settings, we find high diversity in seed banks relative to the established community, suggesting potentially important roles of seed banks in population dynamics and diversity maintenance.

Soil seed banks offer plants the opportunity to disperse through time. This has fundamental implications for population and community dynamics, as has been recognised by ecological and evolutionary theory, and documented in numerous empirical studies. On ecological timescales, seed banks represent local ‘biodiversity reservoirs’ that can contribute to local population persistence and biodiversity maintenance through temporal storage effects (Chesson and Huntly 1997, Faist et al. 2013, Plue and Cousins 2013), remnant populations (Eriksson 1996, Plue et al. 2008, Auffret and Cousins 2011) and the maintenance of a functionally diverse below-ground species pool available for germination in response to environmental variability or change (Kalamees and Zobel 2002, Dostal 2005, Clark et al. 2007, Enright et al. 2007, Måren and Vandvik 2009, Anderson et al. 2012, del Cacho and Lloret 2012).

On evolutionary timescales, seed banks increase the mean generation times of populations, thereby affecting the potential rate and even direction of evolutionary change (Brown and Venable 1986, Evans and Cabin 1995, Evans and Dennehy 2005). Seed banks allow evolution of risk-spreading mechanisms such as bet-hedging germination strategies (Cohen 1968, Evans and Dennehy 2005, Ayre et al. 2009, Gremer and Venable 2014) and contribute to the maintenance of genetic and trait diversity within local populations (Cabin et al. 2000, Ayre et al. 2009, Lundemo et al. 2009, Mandak et al. 2012), thus providing a potential source of resilience in the face of disturbance or environmental change. Recently, Alexander et al. (2012) pointed out that disentangling the role of seed banks in community and population dynamics is essential for our general understanding of basic ecological patterns and processes. For example, understanding the relative importance of ‘dispersal through time’ through seed banks versus long-distance dispersal through space is essential for understanding metapopulation dynamics and metacommunity assembly (Vandvik and Goldberg 2006).

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The potential importance of seed banks has also been recognized by applied ecologists, who have been particularly interested in their potential contributions to the conservation and restoration of threatened and declining plant populations (Adams et al. 2005, Eckstein et al. 2009, Ottewell et al. 2011) and communities (Holmes and Cowling 1997, Satterthwaite et al. 2007, Fourie 2008, Kalamees et al. 2012, Faist et al. 2013). However, many empirical case studies of such systems find seed banks to be floristically depauperate and weedy, and many studies conclude that seed banks are mere 'spill-overs' from the extant vegetation of relatively little value for the conservation and/or restoration of natural populations or communities (Bossuyt and Hermy 2003, Bakker et al. 2005, Eycott et al. 2006, Bossuyt and Honnay 2008, Andreu et al. 2009, Dölle and Schmidt 2009, Scott and Morgan 2012). The reactive and weedy nature of seed banks is also suggested as an explanation of the often very low floristic similarity found between seed banks and the standing vegetation (reviewed by Csontos 2007, Hopfensperger 2007, Bossuyt and Honnay 2008).

We propose that this discrepancy between the findings of theoretically-driven and conservation/restoration-motivated seed bank studies can, at least partly, be attributed to the way that seed banks versus the established plant communities are sampled. Methodological developments for seed bank sampling largely focus on determining the minimal area (or volume) and optimal sampling design to capture a 'representative sample' of the seed bank at hand (Bigwood and Inouye 1988, Thompson et al. 1997, Csontos 2007, Plue and Hermy 2012, Baskin and Baskin 2014). The established plant community, on the other hand, is typically sampled more extensively, by total census of species present in (relatively large) plots or other similar methods where the representativeness issue is considered for each sample and not for the amalgamated dataset. This has resulted in a systematic bias in the spatial scale of sampling of seed banks relative to the established plant community; the area sampled for seed banks is up to several orders of magnitude smaller than the areas sampled for the extant vegetation (Thompson et al. 1997 report 20:1 as the average difference in sampling area between vegetation and seed bank in their database). These sampling biases have potentially serious but unknown consequences for vegetation–seed bank similarity estimates and our understanding of the relative biodiversity of the two strata, which are both commonly used in the literature.

The species–area relationship (SAR) is one of the most pervasive ecological patterns that exists. It is found across all organism groups and at all scales, from centimetres to global (Arrhenius 1921, Rosenzweig 1995, Drakare et al. 2006). SARs have previously been implicated as explanations for the systematically lower richness and diversity reported for seed banks relative to vegetation (Forcella 1984) but this has never been systematically tested. We use SAR analysis as a tool to explicitly assess and compare the species richness in the established plant community versus soil seed banks, and how this varies across scales, between study systems and along regional to global climatic gradients. Similarity indices are widely used for vegetation–seed bank comparison (reviewed by Hopfensperger 2007) and we therefore complement the SAR analysis with an assessment of how two different indices, Sørensen (SSI; Sørensen 1948)

and Raup–Crick (RC, Raup and Crick 1979), are affected by the seed bank sampling effort.

To compare SAR and similarity between the seed bank and established plant community, we first conduct an extensive survey of the extant vegetation and the underlying seed banks of a grassland community using the same sampling methods for the two strata. To assess the generality of patterns observed, the study is replicated across twelve field sites along regional-scale climatic gradients. Finally, we complement this field study with a literature survey where we assess the diversity of seed banks versus established plant community across 89 published studies to allow an assessment of SAR relationships and patterns across habitats and along global-scale climatic gradients.

The aims of this study are thus 1) to compare SARs below versus above ground, 2) to explore patterns in the SAR of the vegetation and seed banks along climatic gradients and among habitat types and biomes and 3) to explore how vegetation–seed bank similarity is affected by seed bank sampling effort. The results will be used to evaluate the two alternative views on seed banks emerging from the ecological theory versus conservation literature – as a life-history strategy contributing to population persistence and biodiversity maintenance, or spill-over from the extant communities.

## Material and methods

### Field data

Our field study is conducted in twelve calcareous grassland sites in western Norway. The sites were chosen to fit within a climate grid reflecting the major bioclimatic variation in Norway (following Halvorsen et al. 2009), with three temperature levels (alpine, sub-alpine, boreal; mean growing season temperatures of ca 6.5, 8.5 and 10.5°C, respectively) replicated within each of four levels of humidity (weakly-continental, intermediate, weakly-oceanic and clearly-oceanic; mean annual precipitation of ca 600, 1200, 2000 and 2700 mm, respectively). Site selection was based on temperature and precipitation data obtained from the Norwegian Meteorological Institute (Supplementary material Appendix 1 Table A1). Other factors such as grazing regime and history, bedrock, vegetation type and structure, slope and exposure were kept as constant as possible among the selected sites (Supplementary material Appendix 1 Table A1).

In August 2008, three plots of 64 × 64 cm were randomly placed within each of the grassland sites. Rocky outcrops and areas dominated by shrubs or tussock grasses (> 50% cover) were avoided. The plots were divided into subplots, starting from a 2 × 2 cm plot in a randomly-chosen corner, to obtain nested SAR plots with subplots of 4 cm<sup>2</sup>, 16 cm<sup>2</sup>, 64 cm<sup>2</sup>, 256 cm<sup>2</sup>, 1024 cm<sup>2</sup> and the main plot of 4096 cm<sup>2</sup> (Fig. 1). The vascular plant species composition of each subplot was recorded in the field.

One of the three vegetation survey plots per site was randomly selected for seed bank analyses. The top 3 cm of soil was excavated from each of these seed bank plots, keeping the material from each subplot separate. While additional germinable seeds may occur below the sampled depth, up to 80–98% of seeds in grasslands and heath seed banks can be found in the top 2–5 cm (Pywell et al. 1997, Ma et al. 2010,

2011) Further, several grassland studies have used comparable sample depths (Caballero et al. 2003, Standish et al. 2007, Gonzalez and Ghermandi 2008, Wright and Clarke 2009). Sampling was done in late August (after germination, before dispersal), to avoid sampling transient seed banks as well as the current year's seed rain, and thereby reliably assess the persistent seed bank pools (Thompson et al. 1997, Baskin and Baskin 2014). To further minimize contamination by the current year's seed rain, the established plant community, bryophytes and litter were carefully removed from the samples prior to seed bank excavation.

After three months storage at ambient moisture and 2–4°C, the samples were sieved dry through a 0.4 cm meshed sieve to remove roots, twigs and stones, and mixed with water to a slush before they were transferred to germination trays (following ter Heerdt et al. 1996, as modified by Mären and Vandvik 2009). This was done to achieve bulk reduction and optimize seed bank recovery (see evaluation by Baskin and Baskin 2014). Additional data points on fine spatial scales (2 × 2 cm – 32 × 32 cm) were created post hoc, when possible, by sampling these finer-scale plots as described above from other parts of the 64 × 64 cm turfs during the greenhouse work. This was done to increase sampling effort on the finest spatial scales within each plot. We thus sampled a total of 28 plots at the smallest scale, or an average of 2.3 replicates per SAR plot. Each individual sample was thoroughly mixed and spread out in a ca. 0.1 cm deep layer, so that most seeds were exposed to light and suitable germination conditions, on trays (30 × 60 cm) filled with 5 cm of sterile subsoil, consisting of equal amounts of sterile peat, perlite and growth soil. Trays were arranged at random in a heated greenhouse and kept at diurnal temperatures of 15/25°C under artificial growth light provided by high pressure sodium lamps of 400 watts with a light regime of 8 h darkness and 16 h light. This regime was maintained for two four-month germination periods, interrupted by six months of cold-stratification at 4°C in darkness. The positions of the trays were randomized bimonthly. Six control trays of sterile peat, perlite and growth soil were randomly placed among the seed bank samples to monitor any airborne contaminants. Emerging seedlings were counted every two weeks and removed as soon as they could be identified; difficult taxa (mainly Juncaceae, Cyperaceae and Poaceae) were potted and grown to maturity under greenhouse conditions for identification. Treatment with gibberellic acid (GA<sup>3</sup>) has proven highly effective in dormancy-breaking in alpine species (Hoyle et al. 2013), the trays were therefore watered once with 400 ml 0.33 mM GA<sup>3</sup>, after the second germination period to stimulate further germination. This did not yield a detectable additional seedling emergence and the experiment was hence terminated. Following Thompson et al. (1997) we expect these methods to reveal all or nearly all viable individuals and species in the persistent soil seed banks. Nomenclature follows Lid and Lid (2005).

Under this protocol, a total of 188 taxa of higher plants were recorded in the seed bank and vegetation, 147 in the standing vegetation and 133 in the seed banks. A total of 39 475 seedlings germinated from the seed bank samples. We removed from this dataset three taxa of spore plants, one greenhouse contaminant (*Cardamine hirsuta*) and merged seven pairs of taxa which were difficult to determine when

sterile, resulting in 167 taxa (123 in the vegetation, 134 in the seed bank) and 38 237 seedlings that were included in the statistical analyses (Supplementary material Appendix 1 Table A2).

## Literature survey

We searched the ISI Web of Knowledge (1987–2014), using the search strings (seed bank\* OR seedbank\*) AND (species richness\* OR composition\* OR diversity\*), refining the search by language (English), document type (Article), and Web of Science categories/journals that enabled us to exclude the non-ecological literature. This search yielded 1312 articles which were searched for data on seed bank species richness and area sampled. Only terrestrial systems were included in the survey. The bulk of the articles were discarded because these studies dealt with specific species and not the whole soil seed bank or were conducted in aquatic environments. Studies for which the methods descriptions were not sufficiently detailed to allow calculation of the area sampled, and/or total number of species recovered from the seed bank were excluded. This yielded 89 studies, of which 21 also provided data on the species richness and total area sampled for the extant vegetation and 83 provided data on the depth of soil sampling, allowing us to calculate soil volume. Some of these 89 studies could contribute several data points (e.g. when area and species richness was reported separately for different sites), yielding a total of 250 data points for seed banks and 74 data points for the extant vegetation. Vegetation data points with area sampled ≥ 100 m<sup>2</sup> (23) were not included in these analyses as these generally had very low seed bank sampling effort (<< 1%), thus compromising the statistical comparison (non-overlapping data ranges). The data were categorised by their broad habitat types; forest (seed bank: 93, vegetation: 0), grassland (112, 30) and heathland (45, 19) and by their biogeographic region; tropical (16, 0), Mediterranean-type (44, 1), temperate (118, 3), boreal (35, 17), arctic-alpine (37, 28). The geographic range of the dataset is global, including 26 countries and five continents (Supplementary material Appendix 1 Table A3).

## Statistical analyses

The most commonly used mathematical formulation of the SAR is the power-law,

$$S = cA^z$$

describing a linear increase of log species richness ( $S$ ) with log area ( $A$ ) with an intercept of  $c$  and a slope of  $z$  (Arrhenius 1921, Rosenzweig 1995, Hubbell 2001). The field study was analysed using linear mixed models and we included, in addition to area, the effect of stratum (vegetation or seed bank), mean summer temperature (°C), mean annual precipitation (in 1000 mm) and their interactions as fixed effects, and the 12 sites as random factors in mixed effects models.

For the literature study, we ran similar models including area, soil volume, habitat type (forest, grassland or heathland) and biogeographic region (arctic-alpine, boreal, temperate, Mediterranean or tropical) and their interactions with area as fixed effects. For the subset of the literature datasets where



Figure 1. One of the species–area relationship plots being sampled for seed banks. The  $64 \times 64$  cm,  $32 \times 32$  cm,  $16 \times 16$  cm,  $8 \times 8$  cm and  $4 \times 4$  cm plots are delineated by white lines on the photo (the  $2 \times 2$  cm plot was too small to be clearly visible). Photo: Eric Meineri.

data on sampling area and species richness was also reported for the vegetation, we ran separate SAR analyses testing the effects of area, stratum (vegetation or seed bank), habitat type and their interactions. We started these analyses from the full models with interaction terms and performed backward selection based on the Akaike's information criterion (AIC) and likelihood ratio tests to select the best model for the data. To facilitate comparisons of SARs within our data and with other studies, we report summary statistics from separate SAR analyses for each stratum (vegetation or seed bank), climate (bioclimatic zones, sections or regions) or habitat (forest, heathland, grassland) in all cases where these parameters are retained in the final models. Models and error structures for these analyses were as described above, but we also ran additional standard linear models to obtain approximate adjusted  $R^2$  for each of these relationships.

Sørensen (SSI; Sørensen 1948) and Raup–Crick (RC, Raup and Crick 1979) indexes of similarity were calculated for each site in the field study between the vegetation and the seed bank for six seed bank sampling effort levels. SSI is commonly used in studies comparing similarities between standing vegetation and seedbank although this index does not account for different sampling size and design between compared vegetation and seedbank communities. In contrast, RC is designed to handle comparison of similarity between communities with different sampling design. SSI index reports the proportion similarity between the compared communities while RC reports a probability that the compared communities are more similar to each other than to a random community drawn from the regional species pool. For each site, SSI and RC were calculated between the full vegetation data (three  $64 \times 64$  cm plots; sampling area:  $12\,288\text{ cm}^2$ ) and six seed bank species composition datasets constructed from the nested SAR plot (plot sizes  $2 \times 2$  cm –  $64 \times 64$  cm) to represent sampling areas of  $4$ – $4096\text{ cm}^2$  and hence sampling efforts

relative to the extant vegetation of 0.3–33.3%. We analysed the effect of increasing log [sampling effort] on SSI and RC using mixed effect linear model nested on site. Similar linear models were used to extract approximate adjusted  $R^2$ -values. We also assessed whether the effect of log[sampling effort] differed between SSI and RC in term of average and slope using mixed effect linear models including SSI and RC indices pulled together as response variable and log[sampling effort], index type and their interactions as explanatory variables.

All analyses were performed in the R software ver. 2.15.3 (< [www.r-project.org](http://www.r-project.org) >) using the nlme package (Pinheiro et al. 2007) for mixed effects models.

Data available from the Dryad Digital Repository: < <http://dx.doi.org/10.5061/dryad.q401b> > (Vandvik et al. 2015).

## Results

The three-way interaction between area, stratum and temperature is retained in the final SAR model for the field study, indicating that vegetation and seed bank have different SARs and that this relationship also varies with site temperature (Supplementary material Appendix 1 Table A4). The model selection revealed particularly strong support for retaining stratum (vegetation versus seed bank) in the model ( $\Delta\text{AIC} = 105.8$ ;  $p < 0.001$ ), but temperature effects were also strongly supported ( $\Delta\text{AIC} = 44.4$ ;  $p < 0.001$ ). There is no indication that precipitation, or its interactions, affects the vegetation or seed bank SARs (AIC decreases by at least 36.9 when precipitation is dropped from the models). Given these strong indications of variation, the SARs of grassland vegetation and seed banks appear remarkably similar (Fig. 2). However, there is a consistent pattern of lower intercepts but higher slopes in the seed bank SARs, that is,

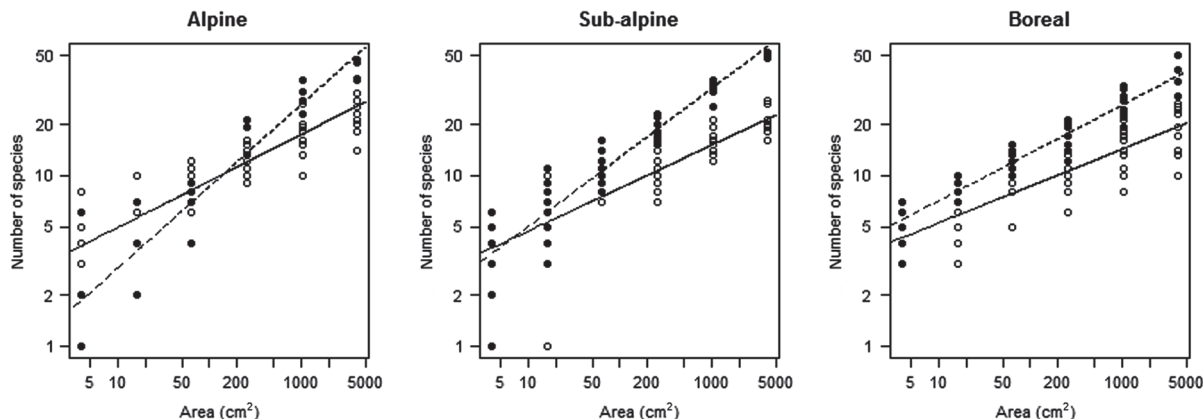


Figure 2. Species–area relationships (SAR) in seed banks (black symbols, dotted lines) and extant vegetation (open symbols, solid lines) of calcareous grasslands in Norway.

fine-scale species richness is lower but rises more rapidly with increasing area in the seed banks (Fig. 2, Table 1). The slopes of all SARs become shallower towards warmer climates but the difference between the vegetation and seed banks increases, so that seed banks supersede vegetation in species richness at all scales in boreal sites but only at scales  $> 100$  cm<sup>2</sup> in alpine sites (Fig. 2, Table 1). Seed bank density varied between the study sites (mean  $\pm$  SD:  $7\,776 \pm 3872$  seeds m<sup>-2</sup>), but there was no relationship between climate and seed bank density, or between seed bank density and species richness (analyses not shown).

In the analyses of species–area relationships based on data from published seed bank studies, the interaction between area and habitat is retained in the final model ( $\Delta$ AIC = 9.9,  $p = 0.001$ , final model adjusted  $R^2 = 0.54$ ), whereas soil depth and biogeographic regions are not (AIC increases by

at least 1.3 in models retaining regions). The SAR slopes become progressively shallower, and the explained variances decrease, from forests to grasslands and heathlands indicating that a higher proportion of the total seed bank diversity is recovered at relatively finer spatial scales in the heathlands and grasslands as compared to the forests (Supplementary material Appendix 1 Table A5, Fig. 3, Table 1).

The comparison of vegetation and seed bank SARs in the literature survey dataset was restricted to grasslands and heathlands, as there was not sufficient vegetation data available for forests. The final model includes the area–habitat interaction that also featured in the full dataset, in addition to an additive term for stratum (Supplementary material Appendix 1 Table A5–A6). The model selection ( $\Delta$ AIC = 45.8  $p < 0.001$ ; for the area–habitat interaction,  $\Delta$ AIC = 56.3  $p < 0.001$ ; for stratum, final model adjusted  $R^2 = 0.81$ ). In both grasslands and heathlands, the vegetation SARs have similar slopes but lower intercepts than the seed bank SARs indicating that seed bank species richness is generally higher than vegetation species richness at all sampling scales (Fig. 3, Table 1).

Sørensen and Raup–Crick similarity values are highly dependent on sampling effort. The SSI values based on the nested-plot analyses range from 0 to 75% (mean<sub>SSI</sub>  $\pm$  SD =  $38 \pm 20\%$ ; Fig. 4) with a strong and positive relationship between seed bank sampling effort and vegetation–seed bank similarity (SSI =  $0.381 + 0.069 \ln[\text{effort}]$ ;  $p < 0.001$ ;  $R^2 = 0.70$ ). The RC values based on the nested-plot analyses were more variable (0 to 99%), higher (mean<sub>RC</sub>  $\pm$  SD =  $0.85 \pm 22\%$ ;  $p < 0.001$ ; Fig. 4) and less affected by the seed bank sampling effort (interaction coefficient =  $-0.022$ ;  $p = 0.012$ ). Still, RC remains significantly affected by increasing sampling effort (RC =  $0.0846 \ln[\text{effort}] + 0.047$ ;  $p < 0.001$ ;  $R^2 = 0.25$ ). According to these models, the expected SSI and RC values at a sampling effort of 1:20 is 49% and 92% respectively.

## Discussion

Our analyses revealed systematic differences between the established plant community and the seed banks in terms of species–area relationships and species composition. However, in contrast to the often-stated concerns

Table 1. Species–area relationships (SAR) in the seed bank and the extant vegetation of different climates or habitats, based on data from the field study and the literature survey. Number of observations (n), parameter estimates for the intercept (c) and slope (z) along with adjusted  $R^2$ -values are given. Note that because of differences in scale, different area values (cm<sup>2</sup> vs m<sup>2</sup>) are used in the calculations for the two types of data and the intercepts are therefore not directly comparable.

Climate/habitat	Stratum	n	Intercept	Slope	Adjusted $R^2$
Field study <sup>†</sup>					
Alpine	seed bank	24	-0.05	0.48	0.87
Sub-alpine	seed bank	65	0.67	0.41	0.89
Boreal	seed bank	54	1.30	0.28	0.92
Alpine	vegetation	72	0.97	0.27	0.79
Sub-alpine	vegetation	71	0.97	0.25	0.76
Boreal	vegetation	72	1.16	0.22	0.79
Literature study <sup>‡</sup>					
Forest	seed bank	93	3.93	0.42	0.64
Grassland	seed bank	111	3.95	0.32	0.51
Heathland	seed bank	45	3.64	0.19	0.20
Grassland*	seed bank	30	4.34	0.44	0.84
Heathland*	seed bank	19	3.52	0.13	0.21
Grassland*	vegetation	30	3.42	0.36	0.84
Heathland*	vegetation	19	3.05	0.19	0.47

<sup>†</sup>based on the subset of retrieved studies that includes both seed bank and vegetation data

<sup>‡</sup>area in cm<sup>2</sup> in SAR calculations from the field study

\*area in m<sup>2</sup> in SAR calculations from the literature study

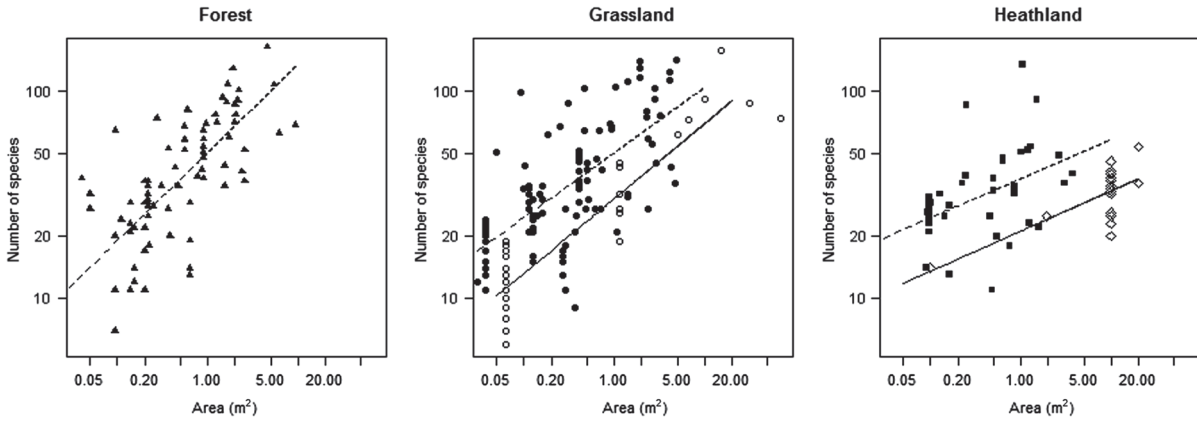


Figure 3. Species–area relationships (SAR) derived from published seed bank studies (seed banks: solid symbols, dotted lines), and, where available, extant vegetation data from the same studies (open symbols, solid lines) from forests ( $n = 93$  for seed banks, 0 for vegetation), grasslands ( $n = 112, 30$ ) and heathlands ( $n = 45, 19$ ).

about their depauperate and weedy nature (Hopfensperger 2007, Bossuyt and Honnay 2008), we find that when the two strata are sampled with the same sampling effort (i.e. at the same spatial scale), the seed banks predictably contain higher species richness than what is found in the established plant community. This holds true both for our field study where seed banks and vegetation of boreal and alpine grasslands were systematically sampled using the same species–area plots (across scales from  $4 \text{ cm}^2$  up to  $0.41 \text{ m}^2$  within sites, total sample area of  $4.9 \text{ m}^2$ ), and for our global literature study of published datasets from forests, grasslands and heathlands (seed bank sampling at scales from  $100 \text{ cm}^2$  –  $9.5 \text{ m}^2$  and vegetation sampling at scales from  $625 \text{ cm}^2$  –  $100 \text{ m}^2$ ). The only exception was our alpine field study sites, where fine-scale species richness was higher in the vegetation than in the seed bank, but even here, seed bank species richness surpassed that of the established plant community at

spatial scales  $> 100 \text{ cm}^2$ . Further, the seed banks of the field study were not generally ‘weedy’ of nature, as the majority of species found exclusively in the seed bank were characteristic alpine and grassland species (only seven out of 40 species exclusive to the seed banks can be characterized as weeds or ruderals, as compared to three out of 26 for the species exclusive to the vegetation and three out of 79 species common to both; Supplementary material Appendix 1 Table A2). These findings contrast many reports of species-poor and weedy seed banks in the published literature (Bossuyt et al. 2002, Eycott et al. 2006, Frieswyk and Zedler 2006, Andreu et al. 2009).

### Seed bank sampling

A major difference between our study and a majority of other published studies relates to sampling design, as ours

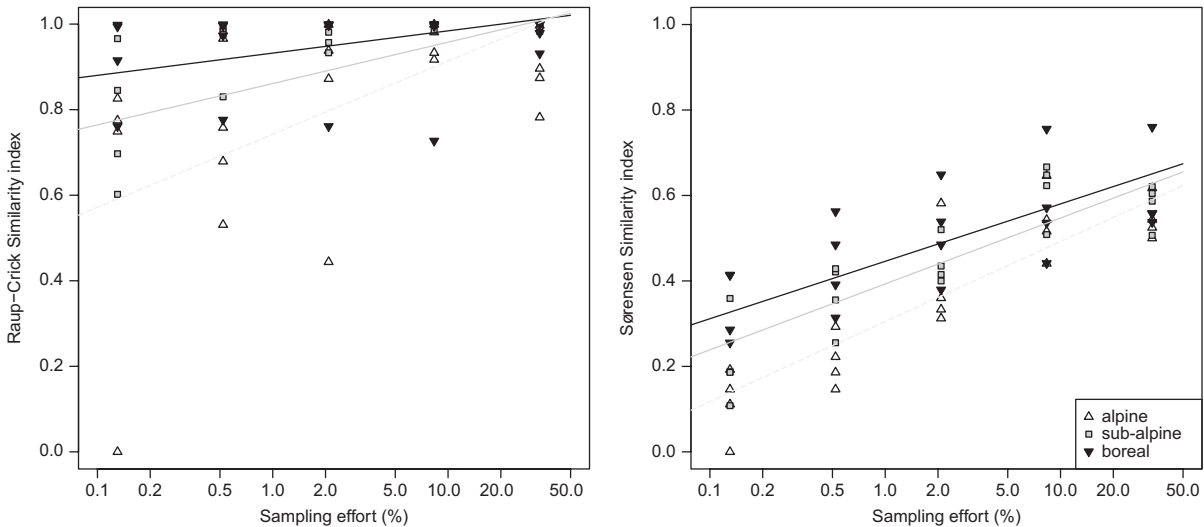


Figure 4. Change in Raup–Crick similarity index and Sørensen similarity index between the extant vegetation and seed bank with increasing seed bank sampling effort. The similarity indices are calculated for each of 12 sites for sampling efforts from 0.3–33.3% by sampling vegetation as species recorded in three  $64 \times 64 \text{ cm}$  plots per site (sampling area:  $12\,288 \text{ cm}^2$ ) and the seed bank at six sampling effort levels by means of a nested species–area plot (area from  $4$ – $4096 \text{ cm}^2$ ).

is the only study that we are aware of that has compared seed bank and vegetation sampled at the same spatial resolution (i.e. 100% sampling effort; the SAR plots in Fig. 1 and 2). In fact, standard seed bank sampling procedures yield sampling efforts of around 5% (Thompson et al. 1997) and the 21 studies in our literature survey that also reported vegetation data had a median seed bank sampling effort of only 1.4% (interquartile range 0.3–6.1%, Supplementary material Appendix 1 Table A3) relative to the vegetation sampling. This is problematic for vegetation–seed bank comparisons, as our analysis shows that sampling effort had a major impact on the similarity between the vegetation and seed bank (explaining 70% of the variance in Sørensen similarity and 25% in Raup–Crick, surpassing climate as a predictor in both). One could argue that this is partly driven by an unrealistically wide range of sampling efforts explored in our analysis (0.03–33%). However, the range of sampling efforts in the published literature is also very wide (the studies included in our literature review range from 0.02–100%). Further, the predicted similarity at 5% sampling effort from our analyses (49%) is remarkably similar to the average % Sørensen similarity reported from 55 grassland studies (54%) in Hopfensperger's (2007) review of vegetation–seed bank similarity. Few studies unequivocally report the total richness and areas sampled for both vegetation and seed bank. It is therefore not possible to re-examine this and other previous reviews (Bossuyt and Hermy 2003, Csontos 2007, Bossuyt and Honnay 2008) to determine to what extent sampling effort issues influence the vegetation–seed bank relationships reported in these studies.

It has been suggested that spatial patterns in the seed bank and standing vegetation may not be functionally comparable, as the seeds are distributed in a three-dimensional space, whereas the vegetation is limited to a two-dimensional plane (all plants are rooted; Thompson et al. 1997). However, this argument ignores the three-dimensional structure of vegetation, which is multi-layered both above- and below ground, as well as the relatively shallow nature of most seed banks, where the vast majority of seeds is found within a few cm from the soil surface (Pywell et al. 1997, Ma et al. 2010, 2011).

We found that the slopes of seed bank species–area relationships were consistently steeper than those of the corresponding vegetation. This indicates that the species are more patchily distributed in the seed banks than in the established plant community, corroborating previous reports of high spatial heterogeneity in soil seed banks (reviewed by Baskin and Baskin 2014 pp. 199–207, Bigwood and Inouye 1988, Plue et al. 2010, Thompson 1986). Several of these sources propose sampling designs involving many small and randomly or systematically distributed samples to recover the spatial pattern and structure of seed banks. The suggested sampling efforts are typically relatively low, for example Plue and Hermy (2012) recommends a sampling effort of 3%, which is even lower than the 5% reported as a typical difference in sampling effort between vegetation and seed bank sampling by Thompson et al. (1997). Such sampling designs may be cost-effective and capture a representative sample of the seed bank community for minimal sampling effort, and thus be optimal for seed bank assessment,

conservation monitoring, and related research questions (Plue et al. 2013).

However, our study demonstrates the limitations of such low sampling effort data, which cannot be used for direct comparisons of the diversity, connectivity, or other functional aspects of the two strata. For example, a study of vegetation development after fire in central Spain reports weaker spatial patterning in the seed bank relative to the corresponding standing vegetation. As this study is based on a traditional low-effort seed bank sampling (seed bank sampling effort of 1.02%, relative to the vegetation sampling, calculated from Torres et al. 2013), our findings raise the question of if and to what extent these results may be driven simply by differences in power between the sampling methods employed above- versus below-ground.

Many published studies are based on surprisingly low sampling efforts (Supplementary material Appendix 1 Table A3), which is worrying as area sampled was a remarkably strong predictor of seed bank richness in our literature review. Optimising lab techniques so that larger soil volumes and hence areas can be processed is a cost-effective and practical approach to improving quality in seed bank data (e.g. use of bulk reduction, Måren and Vandvik 2009, ter Heerdt et al. 1996).

In contrast, little was gained by including information on sampling depth or volume (this variable were not retained in the final model). This seemingly counterintuitive finding relates to the strong vertical stratification in seed banks; seed densities and diversities typically decrease rapidly with depth (Ma et al. 2010) – a practical implication of this is that seed bank studies should consider maximising sampling area at the expense of depth (see also Plue et al. 2012). An exception would be cases where depth is explicitly in focus, such as in successional systems where deeper seedbanks may reflect 'memories of communities past' (Milberg 1995, Pywell et al. 2011, Ma et al. 2013).

### Assessing similarity

Given the pervasiveness of species–area relationships in nature (Arrhenius 1921, Rosenzweig 1995, Drakare et al. 2006), including soil seed banks (Forcella 1984, this study), and the strong impacts of seed bank sampling area (i.e. effort) on estimates of species richness and similarity (this study), there is little reason to doubt that scale and sampling issues have consequences for seed bank–vegetation similarity estimates. Our results therefore question the usefulness of similarity measures as a means of quantifying the vegetation–seed bank relationship, especially when sampling efforts are unknown or vary between strata or data points (e.g. across studies in meta-analyses). Both similarity measures tested were affected by sampling effort, but Raup–Crick was more robust than Sørensen, suggesting that the former index should be preferred in cases where quantification of the similarity between the two strata are of interest (see also Plue and Hermy 2012). Studies that explicitly aim to compare or assess the roles of and relationship between the established plant and seed bank communities should strive for comparability in sampling the two strata – this could be achieved either through increasing sampling area in the seed bank or through decreasing sampling area for the vegetation. Nested vegetation plots, where

direct comparability with the seedbank is ensured at the subplot level, may be a workable compromise.

### **SAR above and below ground**

Relative to what we expected based on the published literature, the seed bank species–area relationships were, arguably, surprisingly similar to those of the established plant community. This suggests either that the two strata impact each other, or that they are driven by the same underlying external factors. A majority of seeds disperse relatively short distances, for example, in alpine vegetation median seed dispersal distances are generally less than 50 cm (Silvertown and Lovett Doust 1993, Körner 1999), and hence spatial patterns in above- and below-ground will tend to reinforce each other. Fine-scale environmental heterogeneity (Lenoir et al. 2013) may contribute to the spatial structure of the aboveground community, which may be transferred to the below-ground seed bank community through local dispersal. The grasslands used in our field study are grazed by domestic herbivores. Ungulate grazers create small-scale disturbances which give opportunities for recruitment of new species and individuals from the seed bank (Kalamees and Zobel 2002, Vandvik and Goldberg 2006, Auffret and Cousins 2011) and for seed rain incorporation into the seed bank (Thompson et al. 1997), thereby potentially contributing to the reinforcement between the two strata. However, grazing has also been shown to decrease both vegetation–seed bank similarity and seed bank beta-diversity (Chaidefrou et al. 2009), which could operate through promoting dispersal (Vandvik and Goldberg 2006) and/or negatively impacting local seed production. There are thus strong functional and causal links between the seed bank and vegetation, suggesting that seed banks may play important roles in diversity maintenance and function as important biodiversity ‘reservoirs’ across a range of systems and ecological settings.

### **SAR, habitat and climate**

In this study, seed bank species–area relationships differed between habitat types and varied along regional climatic gradients. The progressively shallower SAR slopes from forests to grasslands and heathlands may relate both to the smaller stature and smaller-scaled spatial variability in the vegetation in these habitats (c.f. the reinforcement between vegetation and seed bank patterns discussed above), to the higher seed bank densities and generally higher functional importance of seed banks in the latter ecosystems (Baskin and Baskin 2014, Hopfensperger 2007), and to the role of grazers in dispersing seeds away from the parent plants. Within our grassland field-study system, we found consistent patterns of decreasing seed bank SAR slopes towards warmer climates, but no effect of precipitation. Lower total seed production in alpine climates and hence lower seed bank densities and higher stochastic variability is one potential explanation for this pattern (Billings and Mooney 1968, Molau and Larsson 2000, Cummins and Miller 2002). Alternatively, the pattern could be driven by lower seed mortality in colder soils. However, we found no climate-related variation in seed bank density and no relationship between seed bank density and species richness, suggesting the climate-related variation

in seed bank SAR reflects variation in community structure and functional role of seed banks rather than a simple density effect. It might seem surprising that a climatic signal was detected along a ca 4°C temperature gradient within western Norway, but not among the bioclimatic ones in our global literature survey (tropical – arctic-alpine), especially as a previous global review of SARs revealed that they are strongly affected by latitude and climate (Drakare et al. 2006). High noise in our literature data due to variability among communities (e.g. our forest dataset contains both tropical, deciduous and coniferous forests), relatively low sample size for a global-scale study ( $n = 250$ ) and methodological inconsistencies between the studies (e.g. different detection probabilities in seedling emergence versus seed identification methods; reviewed by Baskin and Baskin 2014) are some potential explanations.

### **The role of seed banks in conservation and restoration**

Given the strong similarity in spatial structure, it might seem surprising that the species composition in the vegetation and seed bank is relatively dissimilar; both in terms of floristics and perhaps especially in terms of relative abundance (Supplementary material Appendix 1 Table A2). Low similarity between vegetation and seed banks are often taken as evidence of low conservation value and / or restoration potential of seed banks (Bakker et al. 2005, Bossuyt and Honnay 2008, Andreu et al. 2009, Scott and Morgan 2012). The same has been concluded from low seed densities, few target species (Bossuyt and Honnay 2008), and low diversity (Mitlacher et al. 2002, Jacquemyn et al. 2011) However, these interpretations ignore the differences in life-history strategies between species that dominate the two strata (cf. Alexander et al. 2012). Persistent seed banks or persistent established plants represent alternative routes by which plants can buffer temporal environmental or demographic stochasticity or change through temporal storage effects (Chesson and Huntly 1997, Faist et al. 2013, Plue and Cousins 2013) or remnant populations (Eriksson 1996, Plue et al. 2008, Auffret and Cousins 2011). This may explain why seed banks can buffer populations against local extinctions following habitat area loss (Piessens and Hermy 2006) and also why seed banks can reflect ‘memories of communities past’ during secondary succession in e.g. forests, grasslands, heaths and dunes (Plue et al. 2008, Plassmann et al. 2009, Auffret and Cousins 2011, Metsoja et al. 2014). It follows that evoking these ‘memories’ can be a powerful restoration tool in restoring these earlier-successional communities, but also that situations where seed banks are dominated by invasives or other undesirable species can be a considerable challenge for restoration (Honnay et al. 2002, Fisher et al. 2009).

### **Conclusion**

In conclusion, we have combined a detailed field survey with analyses of data extracted from the published literature to document that grassland, heathland and forest seed banks generally harbour high species richness relative to the established plant community and are similarly structured in terms



of species–area relationships. This implies that they are not mere spill-overs from the extant vegetation but represent important biodiversity reservoirs, and this pattern holds true for forest, grassland and heath ecosystems on a global scale. This vegetation–seed bank relationship varies with climate and habitat, however, reflecting the variation in the functional role of seed banks across study systems.

Our study demonstrates how similarity indices, which have been much-used to compare established vegetation and seed banks, are strongly affected by sampling effort (which was a stronger predictor than climate for both Sørensen and Raup–Crick similarity) and should be used and interpreted with great care.

Studies aiming to uncover the relative diversity and/or species composition of seed banks versus the established plant community should employ comparable sampling designs and efforts for the two strata. This can be obtained by (sub)-sampling smaller areas for the extant vegetation, e.g. by the use of nested plots, and/or by increasing sampling effort for the seed bank. Many published studies have surprisingly low seed bank sampling efforts, and future studies should employ effective lab methods that use bulk-reduction to allow handling of larger volumes. In many cases, sampling area can be increased at the expense of depth. Seed banks are wonderfully diverse, as is seed bank research, and a variety of carefully chosen sampling designs and approaches will be needed.

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Supplementary material (available online as Appendix oik-02022 at <[www.oikosjournal.org/appendix/oik-02022](http://www.oikosjournal.org/appendix/oik-02022)>). Appendix 1: Table A1. Additional information about the field study sites. Table A2. Summary of the field vegetation and greenhouse seed bank emergence data. Table A3. Summary of the data retrieved from the published seed bank studies, with references. Table A4. Fixed factor parameter estimates and statistics for the final field seed bank model. Table A5. Fixed factor parameter estimates and statistics for the final literature study model. Table A6. Fixed factor parameter estimates and statistics for the final vegetation and seed bank model.