Soil seed bank richness, abundance and density across spatial scales and global biomes

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Abstract

Soil seed banks are an important component of plant population and community dynamics. As a functional strategy that has evolved in response to abiotic disturbance regimes, they are likely to play a key role in determining biodiversity responses to global change. However, like all aspects of biodiversity, patterns in soil seed banks are likely to be scale-dependent. Here, we investigate components of diversity in the soil seed bank across global biomes, accounting for sampled soil area and geographic extent. Species richness increases with spatial scale at a similar rate across terrestrial biomes, but with differences in the slope (beta diversity). At small scales (0.01 m^2), mediterranean systems exhibited the highest seed bank richness, while at larger scales (15 m^2) it was tropical forests. Seed density m^{-2} in the soil was highest in arable systems, followed by tropical and temperate grasslands. Lower densities were found in both high-diversity tropical biomes that are characterised by short-lived seeds, and low-diversity boreal/tundra biomes with more stable established vegetation. Our synthesis shows how a combination of spatial scale and the environmental conditions of different biomes shape global patterns of the multiple components of biodiversity in the soil seed bank.

Keywords

Biodiversity, Dispersal, Ecoregions, Plants, Sampling effort, Seed bank, Seedbank, Species richness

Introduction

In an era of global environmental change, the persistence of populations in newly-unsuitable conditions and the establishment of new populations following disturbance are both key in determining changes in biodiversity over time and in space. For vascular plants, the soil seed bank can play a vital role in both processes. Soil seed banks are the communities of persistent seeds being naturally stored in the soil that contribute to vegetation regeneration after disturbance. Plant species that form seed banks do so as part of a life-history strategy that allows for the buffering of temporal environmental heterogeneity (Chesson 2000; HilleRisLambers *et al.* 2005; Honnay *et al.* 2008), and as such, seed banks are an important component for understanding plant (meta)population and community dynamics (Alexander *et al.* 2012; Wisnoski & Shoemaker 2022). By reflecting previous habitat conditions following land-use change (Auffret & Cousins 2011; Karlík & Poschlod 2014), seed banks are often studied in relation to the potential for ecological restoration of target communities (Bossuyt & Honnay 2008; Török *et al.* 2018). As the climate warms, seed banks are expected to contribute to the maintenance of species richness (Plue *et al.* 2021), although community composition may shift due to the higher seed longevity exhibited by warm-adapted and widespread species (Auffret *et al.* 2023). However, the abundance of seeds in the seed bank is predicted to decline with increasing soil temperatures due to a combination of increased rates of germination and seed degradation (Ooi *et al.* 2009).

Given their importance for biodiversity maintenance and recovery, studying patterns of soil seed bank richness, density and abundance at large spatial scales and across geographic gradients can be useful for understanding patterns of biodiversity (Plue *et al.* 2021; Yang *et al.* 2021). However, biodiversity is known to be scale dependent, and comparisons of seed bank diversity at the global level are therefore likely to be influenced by the scale at which diversity is estimated. Among the most consistent effects of scale on biodiversity is the increase in the

number of species observed given a larger sampling area – the species-area relationship (SAR) – which has been observed across taxa, habitats and biomes (Arrhenius 1921; Drakare *et al.* 2006; MacArthur & Wilson 1963), including in soil seed banks (Plue *et al.* 2021; Vandvik *et al.* 2016). As such, comparisons of local smaller-scale alpha diversity across locations or studies are affected by the sampling effort, because one would expect a higher measured richness in a study that sampled a larger area, within a similar system. When comparing across systems, the shape of a species area relationship can be affected by patterns of beta diversity (community composition in space; Storch 2016), since a system with higher beta diversity across sample points (larger compositional differences), will accumulate more species with increased sampling area than a system with lower beta diversity, even if local-scale alpha diversity is higher in the latter system (Figure 1). This means that depending on the spatial scale chosen, different systems might be predicted to be more or less species-rich than others (Keil & Chase 2019; Sabatini *et al.* 2022). Similar patterns might also emerge in systems where biodiversity is patchily-distributed (which is true of soil seed banks; Plue *et al.* 2010), especially if sampling effort is low.

Soil seed banks, in addition to their importance for the natural maintenance of biodiversity, offer an excellent study system for examining the comparative effects of scale on the prediction of below and aboveground biodiversity. First, they are sampled in a broadly consistent way (extraction of a known amount of soil, with species identified directly from seeds or through germination in the greenhouse). Second, studies have used a relatively wide range of sampling efforts (area of ground covered), including variation in both the size of an individual sample and the number of samples taken. Third, studies of the soil seed bank are common within plant ecology, and the large amounts of data that have been collected could give important insights into how aboveground vegetation regeneration responses to global change (temporal environmental heterogeneity) is spatially scaled.

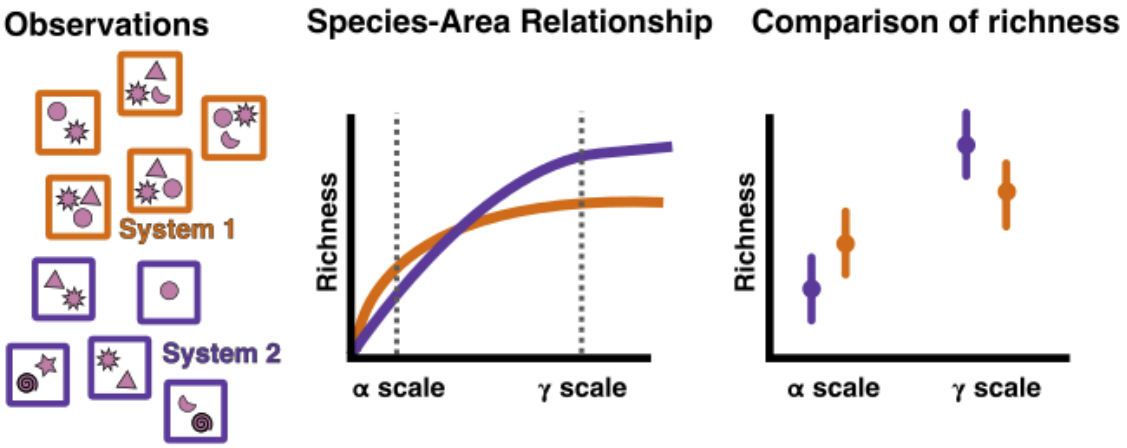

Figure 1. Simplified example showing how differences in alpha and beta diversity across systems (for example biomes) can affect the prediction of richness in space. While individual samples in System 1 contain on average more species than samples in System 2, there is a higher variation in composition (beta diversity, β) between samples in System 2. If this pattern is repeated in space across the different systems, predicted small-scale α (alpha) diversity will be higher in System 1, while predicted richness at the larger ɣ (gamma) scale is higher in System 2. This can then affect interpretations of relative diversity across systems and regions.

The interpretation of broad patterns of biodiversity can also be complicated by species' functional traits, which vary across gradients of ecosystem and climate (Kambach *et al.* 2023). The ability to form seed banks is a functional strategy that has evolved in response to both predictable and unpredictable disturbance regimes (Saatkamp *et al.* 2014), that are not randomly distributed in space. For example, in arid systems dominated by drought, it is advantageous to have an annual life history and form persistent seed banks to buffer annual changes in water availability (DeMalach *et al.* 2021; Friedman 2020). Even in temperate Europe, species with warmer distributions have been found to have a higher seed bank persistence than more northerly species (Auffret *et al.* 2023). In tropical systems, high seed loss due to pathogens and seed predation means that long-term seed banks are often depleted (Dalling *et al.* 1998; Skoglund 1992). As such, biomes that can differ markedly in terms of established plant diversity (Sabatini *et al.* 2022) might show divergent patterns in terms of soil seed bank richness and density. We already know that patterns of species diversity can be

complicated due to broad differences in beta-diversity (Keil & Chase 2019; Wilson *et al.* 2012), but these relationships have not yet been established for soil seed banks.

In this synthesis, we use a global database to examine spatial patterns of soil seed banks in terms of diversity, density and abundance. Specifically, we investigate the relationship of species richness with increasing area sampled, and whether this differs across the world's biomes. We expect that dominant seed-banking strategies in different biomes combine with patterns of diversity in the established vegetation to result in scale-dependent patterns in the soil seed bank across the world. For example, tropical rainforests may have relatively low small-scale alpha diversity compared to temperate grasslands, but much higher larger-scale gamma diversity (as in the established vegetation; Wilson *et al.* 2012), driven by high beta diversity. Potentially low seed abundance in high-richness tropical seed banks will result in relatively few sampled seeds per species, while biomes characterised by extreme drought conditions might be expected to have higher abundance. Our study contributes to a broader understanding of global patterns of biodiversity, as well as for seed bank ecology, in terms of responses to environmental change, habitat restoration, and future seed bank studies.

Material and Methods

The global seed bank database

To study the effects of spatial scale on soil seed banks, we compiled a global database of seed bank richness, abundance and density (Auffret et al., submitted). Briefly, we searched the Web of Science using the search term "seed bank*" OR seedbank*, including papers included in the Web of Science until the end of 2019 (a few papers returned by the search were subsequently published in journals in 2020). All resulting papers were checked for being both community seed bank studies (i.e., taking soil samples and counting and identifying all seeds, rather than

focussing on one or more specific species), and containing information about species richness (number of species), seed abundance (number of seeds), and/or seed density (number of seeds per unit area or volume) in the seed bank. Most of the papers were in English, but data were also extracted from papers published in, for example, Spanish and Portuguese (often South American studies), as well as French and German. Due to a large data gap, the database was supplemented by an additional database and literature search featuring studies published in Russian and carried out in a number of former Soviet states. In total, this resulted in 7224 unique studies to be checked, and 1442 studies from which records could be extracted or obtained. A record refers to a row in the database, and represents a known number of soil samples with specified geographical coordinates. Depending on how results were reported in a specific study, a record can represent one or more locations or environments. Each record can also provide one or more commonly recorded seed bank metrics (mainly total species, total number of seeds, seeds m^{-2} density), which we term observations. A study can provide multiple observations by reporting more than one metric, and/or by (for example) reporting metrics across several distinct records (i.e. different locations or environments). In total, the 1442 studies provided 8087 observations across 3096 records (Figure 2, Table S1). The database includes soil seed bank data from 94 countries and all seven continents. Full details regarding which data were extracted and how are available in Auffret et al. (submitted). Below, we describe only the variables in the database that were used for this synthesis.

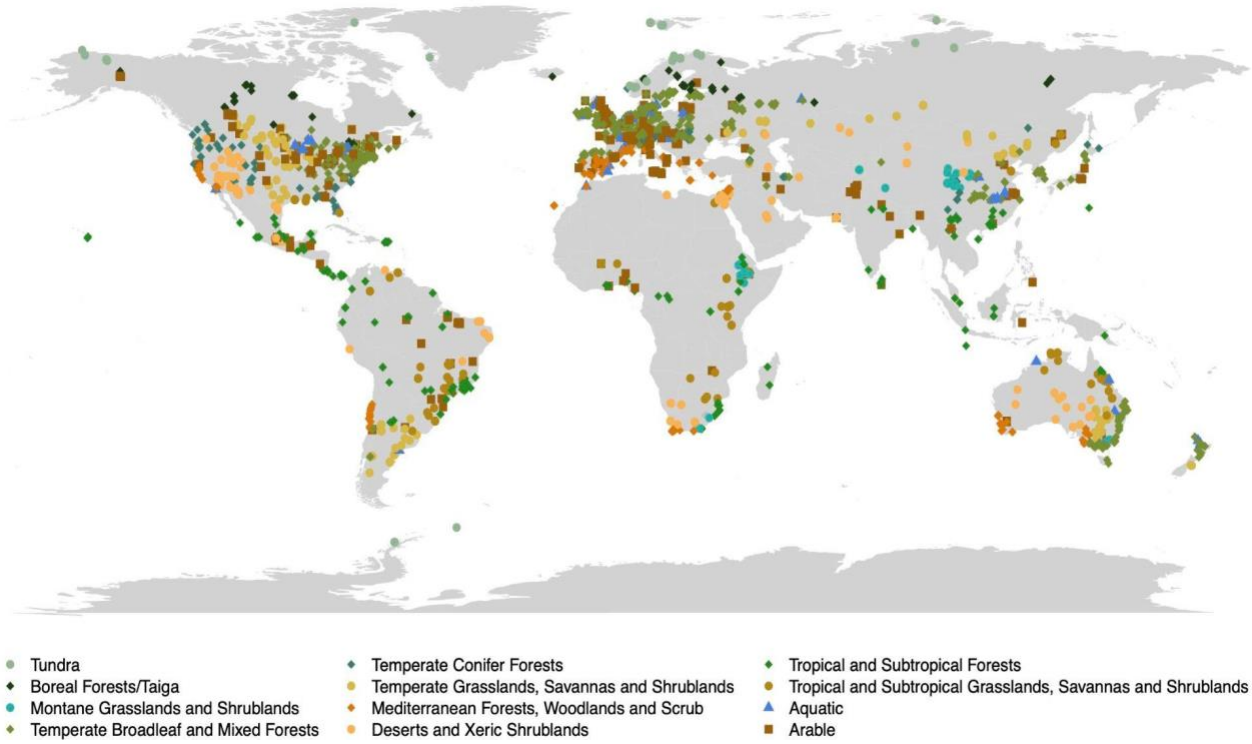

Figure 2. The global record of the soil seed bank. Points indicate the location of each record collected from the literature (n=3096; some records have the same location). Colours indicate WWF Biomes, plus aquatic and arable systems. Shapes to aid in point differentiation indicate that forests are diamonds, aquatic are triangles, arable are squares, and all other systems are circles.

Sampling information

Soil seed bank studies often involve the collection of multiple samples of soil with a soil corer. These samples are then usually pooled, in order to account for the spatial patchiness of species and seeds in the soil (Matlack & Good 1990; Plue & Hermy 2012; Thompson 1986). Therefore, different numbers of cores of different sizes can contribute towards reported metrics of richness, density and abundance coming from soil seed bank studies. Our database therefore also contains detailed sampling information, including soil sample sizes, the number of samples taken, and the number of sites sampled for each observation. This allowed us to quantify

different aspects of sampling effort across studies with standardised metrics, including the total sampled area and volume, the total number of samples, and the total number of sites that went into each observation. A site is a distinct location from which soil samples have been taken, usually as a form of replicate in study authors' data collection, but within one record (with one set of geographical coordinates). Where coordinates were not provided by a study's authors, we estimated them from the description of the study location(s).

We used total sampled area in m^2 as our measure of sampling scale, calculated as the size of the individual soil samples multiplied by the total number of samples taken for a particular observation. This metric accounts for differences in soil core sizes across studies, and we expect seed bank abundance and species richness to accumulate across sampled areas for plant communities (Plue *et al.* 2021; Vandvik *et al.* 2016). Despite variation among studies, we do not consider sample depth nor volume. The majority of viable seeds are found in the very top layer of the soil (McDonald *et al.* 1996; Sanou *et al.* 2019), and as such sample depth is of negligible importance in determining reported seed bank metrics (Vandvik *et al.* 2016; Yang *et al.* 2021). Sampling depth is also roughly constant across all studies, with the mode, median and mean depth all being 100 mm.

Number of sites was used as a measure of geographical extent. This could be important because among-site heterogeneity means that a given area sampled from one site would contain seeds of fewer species than if the same sampled area (equal sampling grain) came from many sites across a wider spatial extent. Measured seed abundance could also be affected by the number of sites from which samples were taken, although not necessarily in any particular direction. While admittedly an imperfect measure of an observation's geographical extent, we found it to be a parsimonious covariate, as well as the only such metric that was

available in all records. More than half of our observations represent samples collected within a single site (n = 4763).

Following soil collection and eventual pooling, seeds in the soil seed bank are typically assessed in different ways that can affect estimations of richness and density (Price *et al.* 2010). Therefore, we also extracted this information for the database. The different methods are 'Emergence': the most common, by which the soil is planted in a greenhouse and emerging seedlings identified; 'Field': similar to emergence, but soil samples are planted in natural field conditions; 'Extraction': where soil samples are examined under a microscope and individual seeds identified and counted. Some observations involved a combination of two of the above.

Response variables

Our database contains three main metrics from the soil seed bank literature that we use as response variables: [1] the total number of species recorded in a reported area soil seed bank sampled (hereafter species richness) ; [2] the total number of seeds recorded in the area sampled (hereafter abundance), and [3] seed density m^{-2} in the soil (hereafter density). Typically, seed density is back-calculated by a study's authors as the number of seeds in the samples divided by the area of ground covered by the sampling regime. Where only one of either total seeds or seed density were provided by the authors, we calculated the other variable. In addition to these three variables, we calculated (where possible according to available information): [4] the number of seeds per species, as a measure of the soil seed bank richness-abundance relationship. This metric tells us how evenly species are distributed among individual seeds for a given sample. Higher values indicate a greater number of seeds per species generally. Like any ratio, differences can arise from changes to either or both of the considered variables Here, it reflects differing abundance between two observations, and

shared richness, consistent abundance between two observations and differing richness, or of course something in between. On average, the abundance:species ratio can be an informative, quantitative measure of the relationship between soil seed bank abundance and richness. We used the absolute values of observations from every record, so that this measure does not depend on the size of the sampled soil area at which observations were observed.

Biomes

We overlaid each record's geographical coordinates with the WWF terrestrial ecoregion map (Olson *et al.* 2001) to assign each observation to an ecoregion (hereafter 'biome'). The 14 biomes that included a soil seed bank observation were merged into 10 'broad' categories (Table S2), to reduce the number of categories with very few observations (Figure 2, S3, see below). Because the biome map contains categories of *terrestrial* ecoregions, and because arable systems are very different to natural and semi-natural systems, we also used the seed bank database's habitat classification (five broad categories interpreted from study descriptions) to create two further 'biomes' for aquatic and arable habitats. That is, all observations classified as aquatic (including soil and sediment from both fresh and saltwater water bodies and courses, but not wetlands) and arable habitats (including croplands, orchards and vineyards, but not meadow, pasture or forest plantations) were put into these categories, regardless of their geographical location. Each observation was assigned to one of the following categories: Tundra, Boreal Forests/Taiga, Montane Grasslands and Shrublands, Temperate Broadleaf and Mixed Forests, Temperate Conifer Forests, Temperate Grasslands, Savannas and Shrublands, Mediterranean Forests, Woodlands and Scrub, Deserts and Xeric Shrublands, Tropical and Subtropical Forests, Tropical and Subtropical Grasslands, Savannas and Shrublands, Aquatic or Arable (for number of observations within each see Table S2 & S3).

Statistical Models

We used our four response variables together with sampling information and biome membership to fit five models to examine global patterns of soil seed bank communities, and how these are related to spatial scale. Each model contains a different number of observations, based on the different metrics that are present in each record (Table S1).

To quantify species richness as a function of sampling area across the different biomes (**richness-area model**), we fit a univariate hierarchical linear model. Total sampled area (m^2) was a continuous predictor, biome was an interacting categorical predictor and number of sites was a continuous covariate. We assumed a Poisson distribution with a log-link function and we log-transformed and centred the total sampling area and centred the number of sites. This model contained 2792 observations (Table S1, S3). Relating to how results are later presented regarding the effect of number of sites (as a proxy of geographic extent) in determining patterns of seed bank richness, 1632 observations were quantified within one site, 1036 from between two and twenty sites, 110 from between twenty and one hundred sites, and 14 observations between one hundred and 2591 sites.

To quantify the average seed density per m^2 for every biome (**seed density model**), and the ratio of seeds per species for every biome (**abundance:species ratio model**), we fit two univariate hierarchical linear models, both with. biome as a categorical predictor variable. Note that the response variable density m^{-2} is already corrected for soil sample size. The ratio is a scale-agnostic response. As a result, spatial scale predictors were left out of these models. Both models assumed a lognormal distribution. The density model contained 2626 observations, and the ratio model contained 2373 observations. In both cases we removed four observations (0.2 %) with zero seeds (i.e. samples were taken but no seeds were counted or seedlings emerged), as the log of zero is unknown.

In order to test for the effect of soil sampled area on the number of seeds sampled (abundance) and the effect of number of seeds sampled on the number of species observed, we fit two hierarchical linear models (Table S4, S5). To quantify the abundance of seeds as a function of soil area sampled m^2 (**abundance-area model**), we used total sampled area as a continuous predictor, biome as an interacting categorical predictor and number of sites as a continuous covariate. We assumed a gamma distribution with a log-link function, we log-transformed and centred the total sampled area and centred the number of sites (m^2). The abundance-area model contained 2565 observations, with 1515 observations quantified within one site, and 945 from two to twenty sites, 98 from twenty to one hundred sites, and 11 observations from one hundred to 2591 sites. To quantify the accumulation of species richness per seed sampled from the soil seed bank we built a **richness-abundance model**, which used species richness as the response variable, the total number of seeds as a continuous predictor, biome as an interacting categorical predictor, and number of sites as a continuous covariate. We assumed a Poisson distribution with a log function. We log-transformed and centred the total number of seeds and number of sites. The richness-abunance model contained 2357 observations.

Across all statistical models, random intercepts were allowed to vary, with unique study (i.e. publication, some of which provided multiple records/distinct locations), nested within detection method (emergence, extraction, field), included as random effects. We visualised all model estimates on a linear scale. For Bayesian inference and estimates of uncertainty, we fit models using the Hamiltonian Monte Carlo (HMC) sampler Stan (Carpenter *et al.* 2017) and interfaced through the brms package in R version 4.3.1 (Bürkner 2018). We fit all models with four chains, differing iterations and differing assumed distributions (Supplementary Information, Model Details Table S4). We used weakly regularising priors, visually inspected HMC chains for convergence, and conducted posterior predictive checks to ensure the model represented the

distribution of the data for each (Supplementary Information, Table S4 Figure S1). We selected model structure and distributions based on this and on model performance (Rhats, sample sizes) (Supplementary Information, Table S4 Figure S1). We set the lower bound of slopes in our species area model to be zero. This prevented uncertainty estimates for shallow slopes (aquatic systems) from overlapping zero, which does not logically hold for our richness-area model.

Predicting global patterns of soil seed banks

Geographic patterns of species richness in small areas (alpha diversity) can comparatively differ across habitats or global change drivers from patterns in large areas (gamma diversity). This indicates spatial variation in beta diversity (since beta = gamma / alpha). To investigate this divergence between scales, we predicted the overall average species richness at two spatial scales for every biome using the richness-area model to keep estimates for every biome consistent. We predicted richness at 0.01 m^2 (alpha diversity), and larger scale, gamma diversity at 15 m^2, assuming the same sampling depth. These are arbitrary values, but we consider 0.01 m^2 to be a straightforward value that people can visualise, that falls within the interquartile range of seed bank sampling in our database. Additionally, this is a common soil sample size in soil seed bank studies, that has been previously used for prediction of soil seed bank richness and density (Yang *et al.* 2021). Gamma diversity at 15 m^2 was chosen as the largest scale that we felt confident predicting across biomes, given the input data and model outputs. We predicted diversity at our alpha scale and gamma scale assuming sampling for each observation was carried out at one site, twenty sites and 100 sites. In the main results we report diversity at both alpha and gamma scales for one site, as this represents the majority of our values, and acts as our baseline estimates for diversity. We then estimate beta diversity from these predicted values at our fixed scales to complement slope estimates within our richness-area model. Finally, we predicted average seeds m^{-2} from the abundance-area model,

and compared the seeds m^{-2} (density) predictions of this model to our seed density model directly.

Results

Abundance and richness in the soil seed bank

The total number of seeds counted across the 1185 studies and 2585 observations of seed abundance was 35 932 626. Five studies (or 0.2% of all observations) found no seeds within samples. This included an investigation of aquatic systems in Canada (Westcott *et al.* 1997), deserts and xeric shrublands in Egypt (Zaghloul 2008), temperate broadleaf and mixed forests in Germany and the Netherlands (Kirmer & Mahn 2001; Sarneel *et al.* 2014), and tundra in Antarctica (Malfasi *et al.* 2020). Ten studies observed only one species in their seed bank samples, while the maximum was 246 species in 88 m^2 of soil across 156 arable sites in the midwest of the United States (Gibson *et al.* 2016). The minimum (non-zero) observed density of seeds in the seed bank was 3 seeds m^{-2} in a coastal dune forest in the tropical and subtropical forest biome in South Africa (Boyes *et al.* 2011), with the maximum being 501 119 seeds m^{-2} observed in a study from temperate broadleaf and mixed forests in Germany (Burmeier *et al.* 2010). The minimum number of seeds greater than zero recorded in a soil seed bank observation was two seeds in two studies in temperate broadleaf and mixed forests in the United States, and tropical and subtropical forests in Indonesia with 0.67 seeds m^{-2} and 0.16 m^{-2} of soil sampled, respectively (Baptista & Shumway 1998; Graham & Page 2018), with the maximum being 5 907 132 seeds in samples taken in arable systems in 462 m^2 soil from 924 samples across 22 sites in the United Kingdom (Hawes *et al.* 2010).

Naturally, such raw maximum and minimum values are at least partly an outcome of each investigation's scientific focus and study design. Indeed, there was a large variation in sampling

effort across records. The minimum total number of samples was one sample, used in 19 studies, with the maximum being 114 000 samples taken in arable systems representing 224 m^2 of soil sampled across 228 sites in China (He *et al.* 2019). The minimum total sampled area was 0.0015 m^2 (5 sites, 15 total samples) in temperate broadleaf and mixed forests from the United States (Hausman *et al.* 2007), with the maximum being 816 m^2 (20 sites, 20 400 samples) in another large arable study in the UK (Holland *et al.* 2008). The minimum number of sites was one, representing the majority of our samples (1832 observations from 692 studies), with the maximum being 2591 sites (total sampled area of 12.95 m^2) in UK arable fields in a study of wood mouse (*Apodemus sylvaticus*) habitat (Tew *et al.* 2000).

Species richness-area relationship in the soil seed bank

For all terrestrial biomes examined, the species richness of seeds in the soil seed bank increased with area sampled (Figure 3, Table S5). Richness-area slopes were broadly similar across biomes, as evidenced by the largely overlapping credible intervals (hereafter CI; Fig. 3b). These slopes indicate beta diversity, or in other words the ratio between soil seed bank richness at large scales and richness at small scales. The overall mean slope was steepest in the desert and xeric shrubland biome, while slopes were relatively shallow in temperate, montane and mediterranean biomes (Figure 3, Figure S2). Sampling across larger geographical extents (larger number of sites) resulted in a stronger accumulation of richness with sampling area across biomes (Figure 3, S2) .

Predicted average diversity across biomes and scales

Alpha, beta and gamma diversity

Using the richness-area model to predict average soil seed bank diversity for each biome, we found that both alpha diversity at the 0.01m^2 scale and gamma diversity at the 15 m^2 scale were

broadly similar across biomes, as shown by the largely overlapping credible intervals. However, we consider the slight differences observed in these values to still be worth discussing. When values of mean predicted richness per biome (excluding arable and aquatic) are plotted onto the world biome map (Figure 4), it shows that soil seed banks in tropical biomes appear to be relatively species-rich at the larger gamma spatial scale, whereas temperate biomes appear more species-rich at the smaller alpha scale. Mediterranean forests, woodland and scrub showed the highest predicted alpha diversity, as well as the third highest gamma diversity (Figure 4), but inferred beta diversity was low (Table S5, Figure S2). Beta diversity was relatively high in tropical biomes, which exhibited the highest gamma diversity, as well as relatively high levels of alpha diversity. High beta diversity can also occur in biomes where both alpha and gamma diversity are low relative to other systems, if the difference between these measures of richness are large enough within biomes, as evidenced by tundra, and deserts and xeric shrublands. The effect of beta diversity on broad comparisons of species richness at different scales is clear. Comparing model estimates across all two-way combinations of biomes shows that the relative richness (i.e. which biome has a higher estimated richness than the other) changes in 30% of all cases when comparing the alpha and the gamma scale (Figure 4a-b, S3, S4). This reduces to 27% when including arable and aquatic biomes, probably because of the consistently low richness of aquatic soil seed banks.

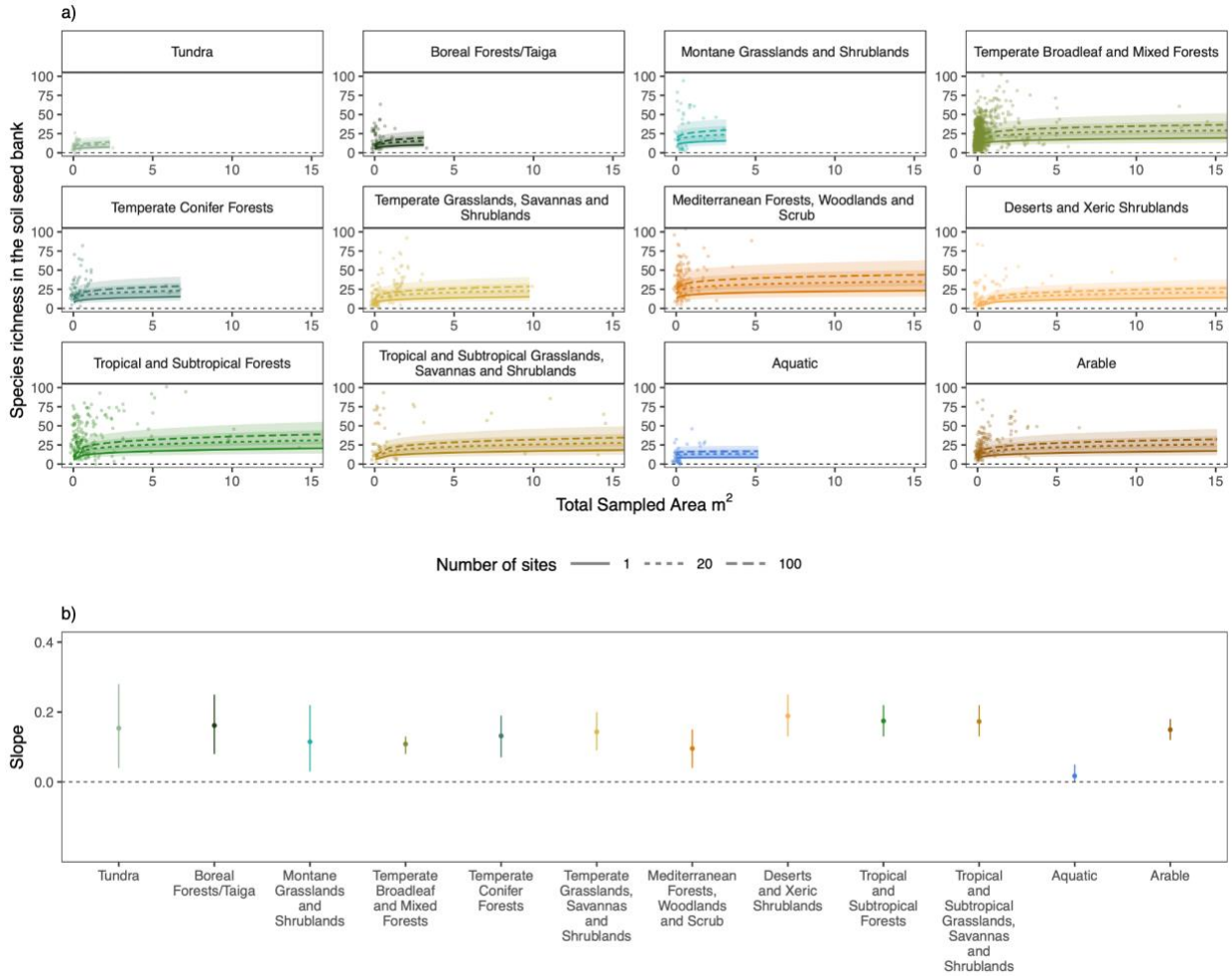

Figure 3. Species richness in the soil seedbank predicted by area of total soil samples (m^2). In a) each point is the species richness reported for a given total area of soil sampled in the literature, each colour is a realm or biome, and each line is the estimated relationship between the number of species and sampled area within each biome, the line types represent predicted estimates for differing numbers of sites (1, 20, 100), and the shaded area around lines are the 95% credible intervals. In b), the points represent the overall effect (i.e. slope) of area on species richness for every biome estimated for one site. Error bars represent the 95% credible intervals, and the dashed reference line at 0 represents a slope of 0. Plotted on a linear scale, see Figure S2 for log-scale.

Seed density in the soil seed bank

According to the density model, the average number of seeds found in a 1 m^2 area of soil across all of our global samples is 4458 (CI: 857-11066). There was a large variation in seed density across studies and within biomes (Figure 6). Nonetheless, deserts and xeric shrublands, tropical and subtropical forests and tundra soil seed banks generally contained fewer seeds than the global average . Only arable seed banks and temperate broadleaf and mixed forests had a mean soil seed bank density larger than the global average. The average predicted seeds m^{-2} from the abundance-area model is 3079 (CI: 159-11884; Figure S7). This is around 600 seeds fewer than the density model estimates for seed density (3693; CI: 677-9719). These estimates complement one another and overlap, but for simplicity we report values from the density model in the main text because uncertainty was lower.

Abundance:Species ratio

Across all observations, we found that the average overall global ratio of seeds/species in the soil seed bank was 102 (CI: 43-222; Figure 7). Arable systems had the highest value at 181 seeds per species (CI: 120-320), while tropical and subtropical forests (56; CI: 37-99) and tundra (46; CI: 23-99) had values lower than the global average.

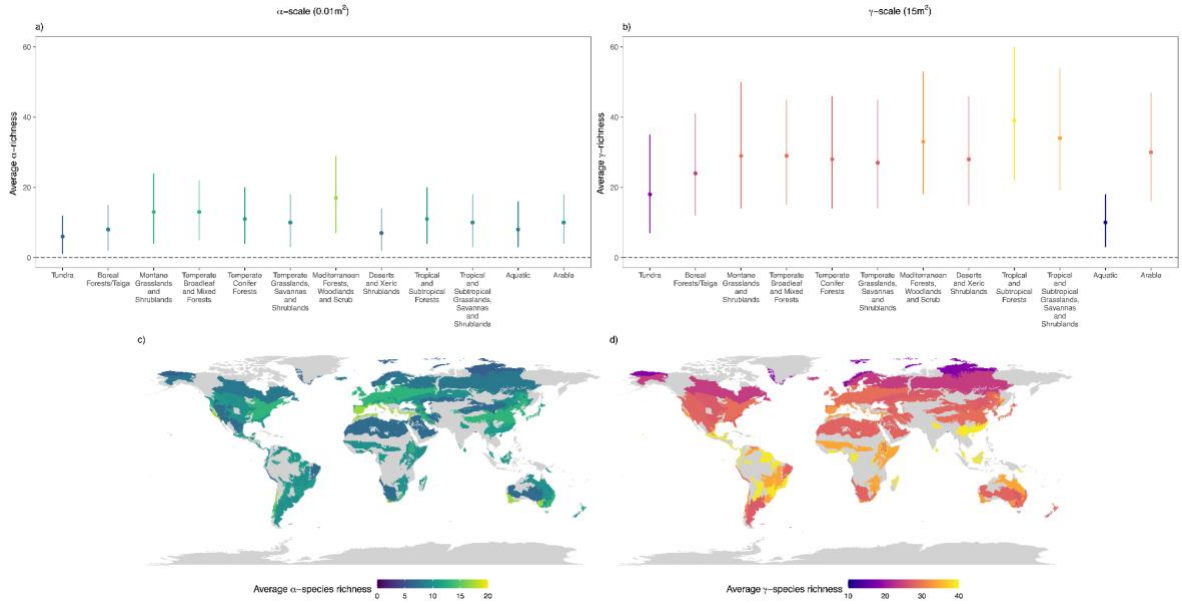

Figure 4. Predicted diversity at two spatial scales of soil sampled across realm/biomes, for one site. In **a)**, a-scale is the mean species richness predicted at 0.01 m^2, and in **b)** g-scale mean species richness predicted at $15m^2$. Each point represents the average predicted value, and lines represent the 95% credible interval. Each colour represents a continuous gradient of species richness. Y-axes are varied for clarity. Responses presented in the ascending value of y-axis responses. For **c)** and **d)**, mean values for one site are predicted across biome areas that have observations within them. Colours represent a continuous richness gradient for each. Aquatic and arable predictions are present in **a)** and **b)** but removed for **c)** and **d)**. Expanded predictions for 20 and 100 sites in Figure S3 and S4 and in Table S6.

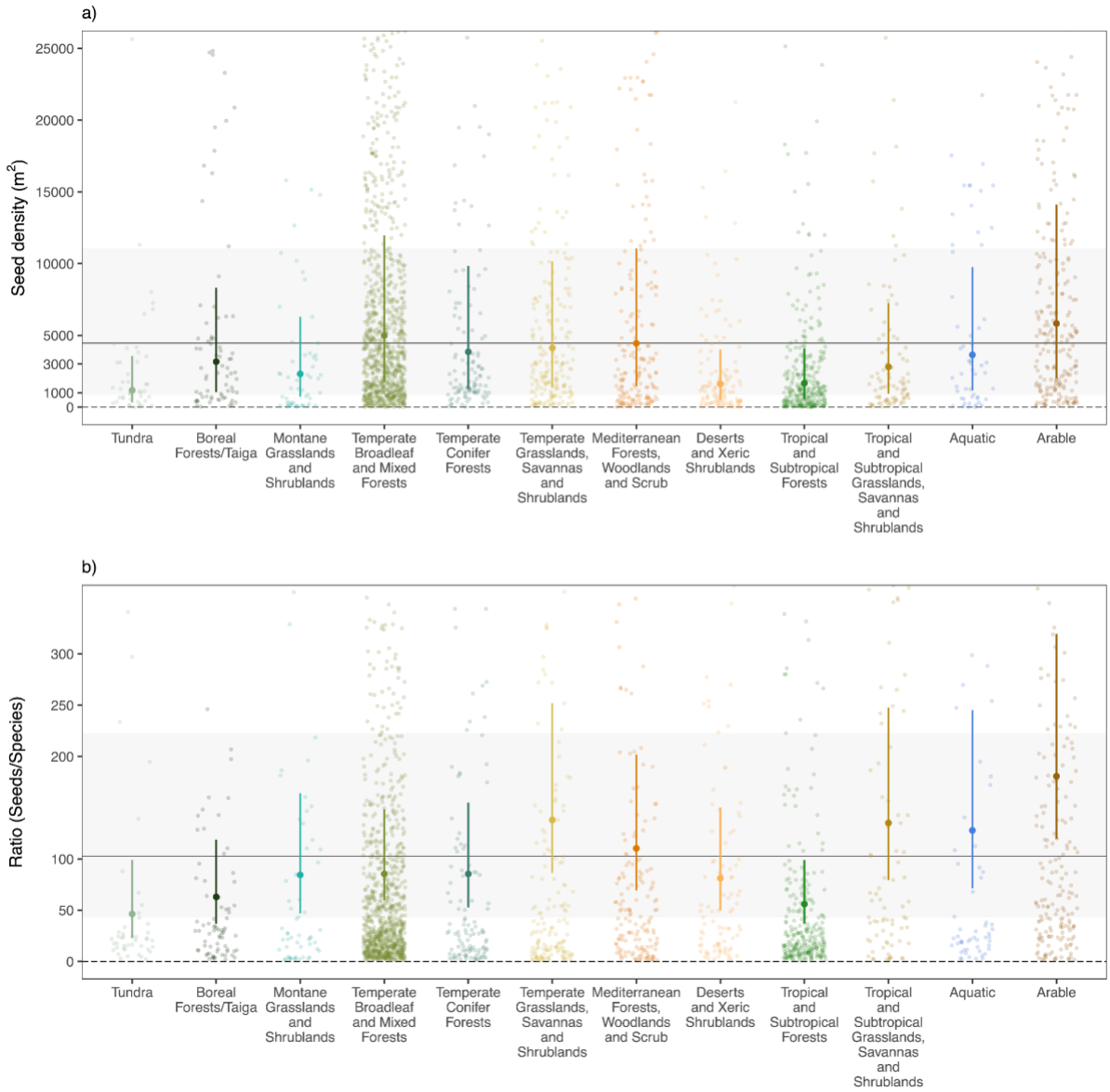

Figure 5. a) Density of seeds m^{-2} in the soil seed bank. b) Ratio of seed abundance/species richness The black line represents the overall predicted overall average density across every sample **a)** 4458 seeds m^{-2}, **b)** 102 seeds per species, shaded area around the black line represents the 95% credible interval of the predicted overall average **a)** 857-11066, **b)** 42.8-222). The points represent the overall mean conditional effect estimate for each biome, colours represent biomes, error bars represent the 95% credible intervals, and the dashed reference line at 0 represents a value of 0. See also Figure S7.

Discussion

We have used a global database of published soil seed bank studies to estimate richness-area relationships and average seed density across the world's biomes. Unsurprisingly, we found that with the exception of aquatic systems, species richness in the seed bank accumulates with spatial scale, both in terms of sampled area and geographic extent (number of sites sampled). Despite large variation within biomes, differences in the slopes of richness-area relationships result in diverging patterns of estimated richness and seed abundance between biomes at different spatial scales, which has consequences for how we compare biodiversity across regions.

Species richness in soil seed banks across scales

We found that the species richness sampled in soil seed banks increases with increasing area of ground sampled, at least in terrestrial systems (Figure 3). This has previously been shown in a review of grassland seed bank studies (Vandvik *et al.* 2016), and is now confirmed across biomes. Surprisingly, aquatic systems did not exhibit a significant positive richness-area relationship in the seed bank. This is probably due to their generally low levels of plant species richness, at least on the spatial scales often used in plant surveys and soil seed bank studies. In systems such as these that are relatively species poor and sparsely populated (Cui *et al.* 2013; Rodrigo *et al.* 2013), increasing the sampled area – at least within the constraints of a soil seed bank study – will not necessarily or consistently result in an increase in the number of species identified.

Across terrestrial biomes, richness-area slopes were generally similar (to the degree of precision of our estimates). However, the broad pattern of tropical biomes having steeper slopes compared to temperate biomes demonstrated how spatial scaling of species richness can affect syntheses of biodiversity. At the 0.1 m^2 scale, highest values of mean richness in the soil seed

bank were concentrated in mid-latitude temperate and mediterranean regions, while at the 15 m^2 scale, richness was more concentrated in the tropics (Fig 4). The latter pattern is in line with other findings of relatively high tropical vs. temperate and boreal diversity, also documented in global studies of mammals (Marsh *et al.* 2022), soil fungi (Tedersoo *et al.* 2014) and trees (Liang *et al.* 2022). For vascular plants, Sabatini *et al.* (2022) also identified a clearer gradient in species richness at large spatial grains, while Keil & Chase (2019) found that areas of relatively high beta diversity in trees – where richness was relatively low at smaller scales and relatively high at larger scales – to be concentrated in low latitudes. Our modelled patterns of soil seed bank richness at the 0.1 m^2 spatial scale were broadly similar to those found by Yang *et al.* (2021), but findings of low richness in the tropics and (predicted) higher richness in northern latitudes were not supported at the larger 15 m^2 scale. Although the disturbances that are likely to allow establishment from soil seed banks (for example by grazing animals) are probably in the magnitude of a few square centimetres, seed banks are largely analysed in relation to community and ecosystem-level responses to environmental changes. Therefore, it is informative to consider patterns of species richness at different spatial scales, a caveat being that our measure of gamma diversity at 15 m^2 is still rather small compared to other studies.

Biogeographical patterns of seed bank density

Our estimated global average of 4458 seeds m^{-2} means that in the broadest sense, if you put your finger to the earth, you are likely to be pointing at a seed. The high density of seeds in the soil is a testament to the formation of soil seed banks as an important component of plant population and community dynamics, and a valuable strategy for many plant species to facilitate establishment following disturbance (Alexander *et al.* 2012; Chesson 2000; Plue *et al.* 2017). Perhaps unsurprisingly, arable soils contained the highest number of seeds per square metre (Figure 6). These highly and regularly-disturbed systems accumulate the persistent seeds of opportunistic ruderal “weed” species that can be problematic for agricultural production. Indeed,

many of the 202 studies contributing to the 769 arable observations in the global seed bank database were investigations of the effects of agricultural management on the weed seed bank (e.g. Ikeda *et al.* 2007; Rotchés-Ribalta *et al.* 2017; Schwartz *et al.* 2015).

In non-arable systems, only the temperate broadleaf and mixed forest biome had a mean predicted seed density higher than the global average, with other temperate biomes and the mediterranean biome slightly below. In the European flora, it has been shown that species with relatively warm, southerly distributions are more likely to have persistent seeds than cool-adapted species (Auffret *et al.* 2023). In warmer regions, where the extreme climatic events may be more frequent, the soil seed bank can play an important role in vegetation recovery and stability (DeMalach *et al.* 2023; Lloret *et al.* 2012). On the other hand, both natural and semi-natural habitats in more northerly boreal zones can be considered more stable and dominated by long-lived perennial species, for which regeneration via the soil seed bank is a less important strategy than for example clonality (Økland 1995). In alpine and tundra environments, low seed bank abundance and a high proportion of clonal species could be expected due to a low diversity and density of adult individuals, combined with the risks of seed production during short growing seasons (Gough 2006; Körner 2021). Therefore, seed densities may be relatively low in these systems, even if richness can be relatively high (Figure 3; Bossuyt & Honnay 2008). In tropical biomes, warm temperatures are generally combined with high levels of precipitation. This leads to a high risk of seed degradation in the soil, resulting in a low soil seed bank density as a consequence of the majority of species having short-lived seeds, with the production of a high annual seed rain being a more common strategy (Baskin & Baskin 2014; Dalling *et al.* 1998; Skoglund 1992).

The seed bank's role in vegetation recovery following disturbance is not only about seed density, but also the identity of the species in the seed bank. Although the global seed bank

database does not contain community information, we can use two commonly-reported seed bank metrics: species abundance and species richness, whose ratio can tell us something about seed bank community structure. The high ratio in arable systems indicates that although agricultural fields have been shown here to have a higher seed density than most natural and semi-natural systems, soil seed bank communities are usually dominated by relatively few common species. Interestingly, the two biomes with seed/species ratios consistently lower than the global average were the biomes with the highest predicted gamma richness (tropical and subtropical forests) and tundra, which had the lowest predicted richness of all terrestrial biomes at both spatial scales. This shows how low densities of seeds in the soil can develop for different reasons (described in the previous paragraph) in both high and low diversity biogeographic regions, resulting in the same pattern of apparent community evenness in the seed bank.

Global insights into seed bank sampling

The large number of soil seed bank studies that have been carried out across the world has allowed our synthesis to be more ‘global’ than many large reviews of biodiversity, which often suffer from biases relating to the absence or restricted availability of data from some regions (Boakes *et al.* 2010; Hughes *et al.* 2021; Nuñez & Amano 2021). However, our study may still suffer from other biases, originating from the fact that seed banks have not been sampled randomly across the world, but in places where scientists have been interested in finding and identifying seeds in the seed bank (Boyd *et al.* 2023). Within the biomes studied here, there are a range of different habitat types, not all of which are likely to have been sampled equally. Nonetheless, the global seed bank database contains samples from many different environments across the world’s biomes. Combined with variation in sampling effort, this wealth of soil seed bank data has still allowed us to gain interesting insights into the spatial scaling and biogeographic patterns of seed bank diversity. It has also shed some light on sampling issues

that could and potentially should be improved in seed bank ecology. It is well-known that sampling multiple sites per treatment gives improved confidence in ecological findings (sample replication; Filazzola & Cahill Jr 2021). As expected, our results show that sampling a larger number of sites results in a higher reported species richness (Figure 3). However, around half of our observations represented a single site. Reporting soil seed bank data at the smallest scale possible within the supplementary information of individual studies (eg. replicate, pooled replicates or site level), or at least making it possible to estimate the geographic spread of sites included in an observation, would better aid the inclusion of studies in meta-analyses and in global syntheses (Gerstner *et al.* 2017).

Our results also indicate that many seed bank studies may not be sampling an adequately large, or at least representative area of soil. Although the sampling effort required to compare seed bank richness at global scales is beyond the scope of most individual studies (which can affect our results and interpretations, see previous paragraph), our analysis of the effect of area on seed abundance (area-abundance model) revealed slopes consistently lower than one across all biomes (Supplementary Figure S5). In other words, a doubling of sampling effort (across studies) does not result in a doubling of seed abundance. This indicates that common levels of sampling effort are not adequately capturing the small-scale heterogeneity of seed abundance in the soil (Matlack & Good 1990; Plue *et al.* 2010). Although – save a fully-representative random sampling effort within biomes (Boyd et al. 2023) – one would not necessarily expect a slope of one, these consistently shallow slopes are concerning. We suspect that this pattern arises because as spatial scale increases, the effects of heterogeneity of seed accumulation in the soil would be replaced by the effects of small-scale habitat heterogeneity supporting different species with different levels of seed production and seed bank persistence. Therefore, we add our voices to the recurring pleas for more comprehensive

and structured sampling of soil seed banks (Plue & Hermy 2012; Thompson 1986; Vandvik *et al.* 2016).

The growth of soil seed bank synthesis

What can we learn from studying the soil seed bank? In addition to the continual publication of studies investigating soil seed banks at local scales, there has been an upswing in the synthesis of large datasets to understand broad spatial or ecological patterns relating to soil seed banks. This includes the macro-environmental determinants of small-scale richness and density (Yang *et al.* 2021), and the evolutionary history of seed bank persistence (Gioria *et al.* 2020). Here, we complement such findings with an understanding of the spatial scaling of species richness in the soil seed bank, and broad biogeographical patterns in seed bank richness and density. Other large-scale work considers the important role that soil seed banks may play in species and community responses to global changes, related to the trade-off related to seeds being able to persist or disperse in space (Chen *et al.* 2020), or the role of soil seed banks in facilitating biological invasions (Gioria *et al.* 2021). We believe that the future of soil seed bank synthesis lies beyond simple measures of community richness and density, or categorisation of species as having or not having persistent seeds. Collating a large number of datasets including community data from the soil seed bank and established vegetation across biomes and systems (see Plue *et al.* 2021 for a less-than-comprehensive European study) would allow us to delve deeper into a mechanistic understanding of the role of soil seed banks, biodiversity, restoration and responses to global change.

Acknowledgements

Many thanks to all the researchers, students and assistants who have spent their time in the field, lab and greenhouse carrying out investigations of the soil seed bank. Thanks also to those

who clearly state their study design and summary results in their publications, as well as those who responded to our requests for further information. AGA is supported by the Swedish Research Council (2020-04276). EL is supported by the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, funded by the German Research Foundation (DFG–FZT 118, 202548816). VO thanks RSF (# 19-14-00038p). We thank Christian Krause and the UFZ administrative and support staff of the High-Performance Computing Cluster EVE, a joint effort of the Helmholtz Centre for Environmental Research (UFZ) and iDiv, for access to, and support associated with, EVE. EL Thanks the Biodiversity Synthesis and Physiological Diversity groups at iDiv for helpful comments on analysis and interpretation.

Statement of authorship

AGA, EL, JP and NSH developed the project and coordinated data collection. AGA, JP, EL, NSH, ED, TGE, IK, JK, DK, ML, VO, MP and DR - collected data. EL and AGA verified and analysed data, assisted by JK, PK and ML. EL and AGA created figures. AGA and EL wrote the manuscript, assisted by NSH, PL, ED, IK, JK, DK, ML, MP, DR, PK and JP.

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