Divergent patterns of richness and density in the global soil seed bank

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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 patterns across the world's biomes and habitats. At the same time, patterns in soil seed banks are likely to reflect scale-dependent patterns observed in above-ground vegetation. Here, we investigate components of diversity in the soil seed bank across global biomes and ecosystems, accounting for sampled soil area and geographic extent. We found that patterns of species richness in the soil seed bank diverged from patterns of density, although there were high levels of uncertainty in the results, especially at smaller spatial scales. Importantly, habitat degradation consistently led to lower richness, potentially limiting future ecosystem recovery. Among ecosystems, Mediterranean and tropical regions were broadly found to have high species richness, but seed density m^{-2} in the soil was highest in wetlands and arable systems. Lower densities were found generally in both high-diversity tropical biomes that are characterised by short-lived seeds, and low-diversity boreal and tundra biomes with more stable established vegetation. We show how different components of the soil seed bank depend on the interplay between local environmental conditions and global biomes, with implications for understanding biodiversity at the global scale.

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 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 (Grubb 1977; Thompson 1987). 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 in the above-ground vegetation (Plue *et al.* 2021). 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).

Despite the potential advantage of producing seeds that persist in the soil, not all species contribute to soil seed banks. Instead, the ability to form seed banks is a functional strategy for plants to (re)establish and maintain populations, which has evolved in response to both predictable and unpredictable disturbance regimes (Saatkamp *et al.* 2014). Such disturbances are not randomly distributed in space, and as such plant communities in different bioclimatic environments can be expected to rely on seed banking to different extents. 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). A similar pattern exists in temperate Europe, where 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, where climatic conditions are broadly stable and exposure to freezing temperatures and drought conditions is historically rare, relatively few species produce seeds that are able to

survive dessication – a trait associated with long-term persistence – which may affect the size and composition of soil seed banks (Tweddle *et al.* 2003; Wyse & Dickie 2017).

While it can be interesting to broadly compare plant communities from different world regions, ecological assemblages can differ considerably among habitats within the same biome. The frequency of disturbance within a habitat is generally mirrored by the strategies of the resulting plant communities (Grime 1977). For example, in temperate and boreal regions, forests are dominated by long-lived trees, with the understorey often covered by species that largely rely on vegetative reproduction (Klimešová & Herben 2015; Nilsson & Wardle 2005). Species-rich grazed grasslands in the same regions are characterised by regular, low-intensity and spatially-heterogeneous disturbances, and as such harbour plants with a wide range of regeneration strategies (Eriksson & Jakobsson 1998; Ladouceur *et al.* 2019). Intensively-used arable lands on the other hand are well-known to support abundant communities of ruderal species with annual life-histories and high seed production (Gaba *et al.* 2017; Kuester *et al.* 2014). As such, habitat is an important component in understanding how different functional traits are represented in different regions, while differences between broad habitat types can differ in different world regions (Kambach *et al.* 2023). Moreover, communities in the same broad habitat categories can differ in their responses to environmental degradation in different biomes (Newbold *et al.* 2020). Therefore, when studying plant communities at global scales, it is important to consider the potential roles of different habitats and environmental degradation driving any variation within or between biomes. This could be especially relevant in the case of soil seed banks, which exist partially as a strategy to respond to disturbance.

Studying patterns of soil seed bank diversity across large spatial scales and geographic gradients can be useful for understanding the biogeography and macroecology of their role in biodiversity maintenance and recovery (Plue *et al.* 2021; Vandvik *et al.* 2016; Yang *et al.* 2021). However, biodiversity is known to be scale-dependent, and comparisons of soil seed

banks across biomes and habitats are therefore likely to be influenced by the scale at which diversity is estimated. It has been established that the number of species in soil seed banks increases with area (Plue *et al.* 2021; Vandvik *et al.* 2016), but while it is well-known that this accumulation of species varies according to habitat and biome in the established vegetation as well as in other taxa (Arrhenius 1921; Drakare *et al.* 2006; Keil & Chase 2019; Sabatini *et al.* 2022), such patterns are still largely unknown in the soil seed bank, at least not at spatial scales that span multiple biomes. Integrating a scale-explicit approach to understanding diversity in the soil seed bank across habitats, within and between biomes and in response to habitat degradation is an important step for plant community and macroecology, allowing critical insights for both broad scale patterns of biodiversity and the context-dependent interpretations of local dynamics.

In this paper, we use a global database to examine spatial patterns of soil seed banks in terms of species richness and seed density. Seed bank studies are usually (through necessity) small-scale comparisons across environmental gradients or investigations into the effects of environmental degradation. Here, we harness 1442 studies from all seven of the world's continents, with the large number of studies and variation in study grain allowing us to address questions not usually possible within the same global synthesis. Specifically, we analyse seed bank biodiversity at two spatial resolutions, comparing diversity within and between broad habitat categories and biomes, and also analysing the effects of habitat degradation. Our study contributes to a broader understanding of seed bank ecology, in terms of responses to environmental change, habitat restoration, and future investigations of the soil seed bank.

Methods

There are a number of reasons why soil seed banks lend themselves to the study of global patterns and scale-dependence of biodiversity. First, the global distribution of seed bank ecologists means that empirical studies of the soil seed bank are common and far-reaching. Second, they are sampled in a broadly consistent way, through the extraction of a known amount of soil, with species identified directly from seeds or through germination in the greenhouse. Third, studies have used a relatively wide range of sampling efforts or sampling grains (area of ground covered), including variation in both the size of an individual sample and the number of samples taken. Taken together, these advantages show real potential for giving important insights into how biodiversity is distributed in space, and how vegetation regeneration responses to global change are spatially scaled.

The global seed bank database

To study the effects of spatial scale, habitat type and quality on soil seed banks, we used a global database of seed bank richness, abundance and density (Auffret *et al.* 2024). Briefly, the database is based on a Web of Science search 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 (by the study authors) geographical coordinates. Depending on the detail in which study location and design, and seed bank 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 1, Table 1, 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*. (2024). Below, we describe only the variables in the database that were used for this analysis.

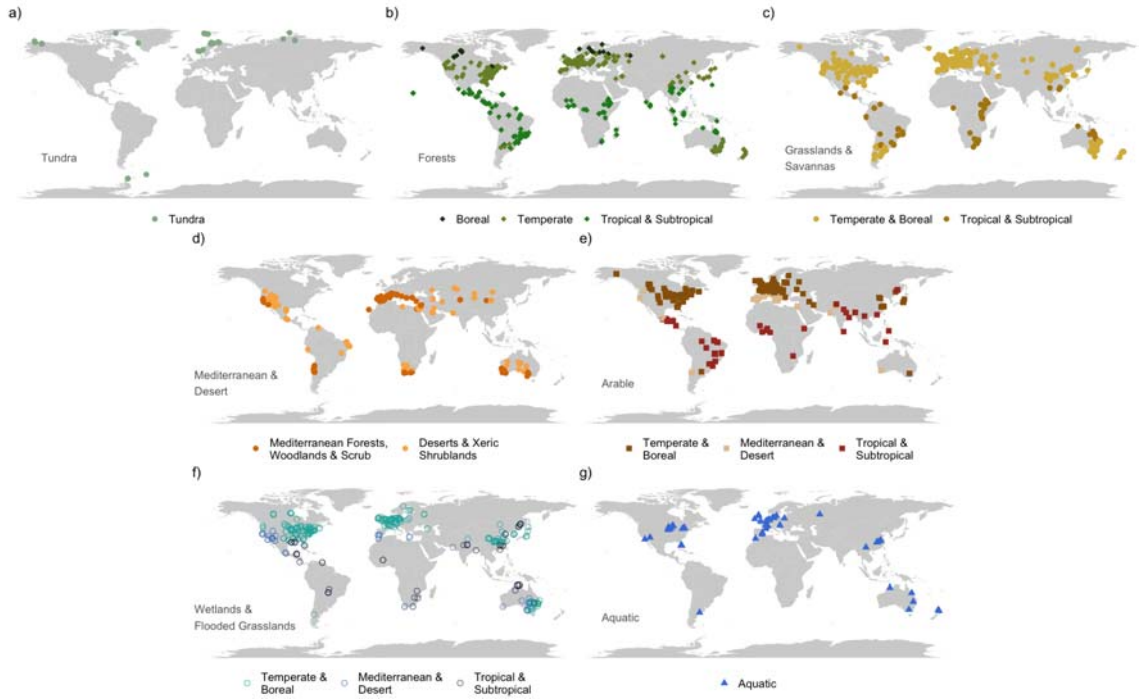

Figure 1: The global record of the soil seed bank. Points indicate the location of each record collected from the literature (n=3096; some records have the same location). Colours indicate unique ecosystem realm, biome, and biome functional subtype categories for each record. Biomes Include: a) Tundra, b) Forests, c) Grasslands & Savannas, d) Mediterranean & Desert (a-d - Natural Terrestrial Realm), e) Arable (e - Terrestrial Intensive Land Use Realm), f) Wetlands & Flooded Grasslands (f - Marine-Terrestrial-Freshwater Transitional Realms), g) Aquatic (g - Marine & Freshwater Realms). Each Biome is divided into biome subtypes ranging from boreal-tropical depending on context. Shapes to aid in point differentiation indicate that forests are diamonds, arable are squares, wetland are open circles, aquatic are triangles, and all other systems are filled circles.

Modelled variables

From the global seed bank database, we extracted the two most common metrics from the soil seed bank literature as response variables: [1] the total number of species recorded in a reported area soil seed bank sampled; [2] the density of seeds m^{-2} in the soil. 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).

Samples can also be collected (and pooled) at several sites in order to capture variation across different locations representing the same habitat or treatment category, often described as 'replicates' within a study. We assume that authors of component papers chose a combination of soil samples and sites that they expected would characterise the soil seed bank in their study system. In our analysis, we used the total sampled area in m^2 or the sample grain 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. We also included the number of sites contributing to each observation as a measure of geographical extent. While this is an imperfect measure, 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).

In order to categorise the global seed bank observations to an ecosystem in a systematic way (McGill & Miller, 2022), we used a combination of authors self-declared habitat descriptions coming from the global seed bank database (aquatic, open grassy systems, forest, arable, or wetland; Auffret et al. 2024), the WWF terrestrial ecoregions or biomes based on an observation's geographic coordinates (Olson *et al.* 2001), as well as realms in the fashion of the function-based typology for the Earth's ecosystems (Keith et al. 2022). Observations with habitat defined as arable or aquatic were placed in an arable and aquatic 'biome', respectively. Habitat and biome were used to categorise all observations into one of 15 biome subtypes (Table 1), with the aim to maintain ecologically-relevant distinctions of ecosystems (the combination of biome and biome subtype) while also including a reasonable number of observations within each group. Each ecosystem was then assigned into either the aquatic, terrestrial or transitional realm. Within the terrestrial realm, we assigned biomes as tundra, forests, grasslands, mediterranean and desert, and arable systems, while we included all aquatic observations within an aquatic biome within the aquatic realm. The transitional realm included wetlands in the mediterranean and desert, temperate and boreal, and tropical biomes (Table 1). Finally, the database labelled non-

arable observations as coming from undisturbed or degraded habitats, based on descriptions from the individual studies. Examples of degraded habitats include drained wetlands, early-mid successional secondary forests, abandoned semi-natural grassland or any habitat under restoration. This was included as a binary classification within each ecosystem.

Table 1: Realm, Biome and Biome subtype categories assigned to each observation. The combination of biome and biome subtype is what we refer to as an ecosystem. 'Degraded' indicates whether the area samples were taken from was considered to be degraded by authors of the original study. The number of observations collected for each Biome subtype, and degraded status listed for species richness, and seed density m^{-2}.

Realm	Biome	Biome subtype	Degraded	N species	N seeds	N density
Terrestrial	Tundra	Tundra	0	43	42	40
Terrestrial	Tundra	Tundra	1	3	3	3
Terrestrial	Forest	Boreal	0	26	22	22
Terrestrial	Forest	Boreal	1	11	11	11
Terrestrial	Forest	Temperate	0	266	268	285
Terrestrial	Forest	Temperate	1	160	139	144
Terrestrial	Forest	Tropical	0	155	151	152
Terrestrial	Forest	Tropical	1	136	136	135
Terrestrial	Grassland	Temperate and Boreal	0	475	451	456
Terrestrial	Grassland	Temperate and Boreal	1	340	263	265
Terrestrial	Grassland	Tropical	0	51	45	45
Terrestrial	Grassland	Tropical	1	33	32	31
Terrestrial	Mediterranean and Desert	Deserts and Xeric Shrublands	0	107	82	83
Terrestrial	Mediterranean and Desert	Deserts and Xeric Shrublands	1	33	29	35
Terrestrial	Mediterranean and Desert	Mediterranean Forests, Woodlands and Scrub	0	129	123	121
Terrestrial	Mediterranean and Desert	Mediterranean Forests, Woodlands and Scrub	1	69	61	61
Terrestrial	Arable	Mediterranean and Desert	0	48	43	43

Terrestrial	Arable	Temperate and Boreal	0	159	140	154
Terrestrial	Arable	Tropical	0	65	58	59
Transitional	Wetland	Mediterranean and Desert	0	40	23	23
Transitional	Wetland	Mediterranean and Desert	1	9	7	7
Transitional	Wetland	Temperate and Boreal	0	276	250	249
Transitional	Wetland	Temperate and Boreal	1	103	89	90
Transitional	Wetland	Tropical	0	50	42	42
Transitional	Wetland	Tropical	1	11	10	10
Aquatic	Aquatic	Aquatic	0	74	65	64
Total number of observations				2872	2585	2630

Statistical Models

For each response (i.e. species richness and seed density) and biome (e.g. terrestrial grasslands and transitional wetlands) we fit a univariate mixed effects linear model. This amounted to 14 models in total (two responses × seven biomes; Table S2). In general, if there were different biome subtypes within a biome then these were treated as categorical fixed effects that interacted with habitat degradation. If not (e.g. tundra), then degradation was the only categorical fixed effect. In the arable biome, there was no fixed effect for degradation, because we consider arable to already represent a degraded system. For each model, intercepts were allowed to vary for every record, nested within study identity as random effects.

In the species richness models, we quantified richness as a function of sampling area across the different biomes by fitting total sampled area (m^2) (sample grain) as a continuous predictor, biome subtype as an interacting categorical predictor (where relevant), degradation as an interacting categorical predictor (a three-way interaction where relevant), and the number of sites as a continuous covariate as a proxy for study extent. This approach, allowing drivers of diversity to vary with sampling grain within a single model, has been found to effectively unify disparate results from previous studies, enabling efficient integration of heterogeneous biodiversity data (Keil & Chase 2019). We assumed a Poisson distribution with a log-link function and we log-transformed and centred the total sampling area and the number of sites. We set the lower bound of slopes to be zero as informative prior information. This prevented uncertainty estimates for shallow slopes (aquatic realm) from overlapping with negative values, which does not logically hold. Seed density models included only degradation interacting with biome subtype as fixed effects, and assume a lognormal distribution. For all model specifications and details see Table S2.

For Bayesian inference and estimates of uncertainty, we fit models using the Hamiltonian Monte Carlo (HMC) sampler Stan (Carpenter *et al.* 2017) in brms (Burkner 2018), R Project for Statistical Computing version 4.4.0 (R Project) (see more detail below). We fit all models with four chains, differing iterations and differing assumed distributions (Supplementary Information, Model Details Table S2). 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 S2, Figure S1a-g). We selected model structure and distributions based on this and on model performance (Rhats, sample sizes) (Supplementary Information, Table S2 Figure S1a-g).

Quantifying scale-dependent richness

Relative differences in local species richness (alpha diversity) between habitats or biomes do not always match patterns of richness when larger areas are considered (gamma diversity). This indicates spatial variation in beta diversity (Whittaker's beta = gamma / alpha) (Whittaker 1972). To investigate this divergence between scales, we first predicted the overall average species richness at two spatial scales for every biome using the species richness models to keep richness estimates for every biome consistent. We predicted richness at 0.01 m^2 (alpha diversity), and at a larger scale, gamma diversity at 15 m^2, keeping modelling parameters constant. These are arbitrary values, but we consider 0.01 m^2 to be a commonly sampled size in soil seed bank studies, that falls within the interquartile range of seed bank sampling in the database (Auffret et al. 2024). Additionally, this is a common soil sample size in soil seed bank studies, that has been previously used for pattern 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. In the main results we report diversity at both alpha and

gamma scales assuming each observation was carried out at one site, as this represents the majority of our values, and acts as our baseline estimates for diversity.

We estimated the average number of seeds m^{-2} globally for observations within non-disturbed natural terrestrial, arable, wetland and aquatic realms. To do so, we combined estimates of the fixed effect (i.e. fitted values) values across all models (i.e. biomes) from each realm, and predicted the mean seed density m^{-2} across all fitted values from all models within each broad group. Finally, to look at the joint-relationship between the density of seed in the soil seed bank and species richness, we predicted species richness at the 1 m^2 scale used for seed density, following the same methods for this prediction at $1m^2$, as for our alpha and gamma diversity. For all data cleaning, management, wrangling and analyses, we used the R Project for Statistical Computing version 4.4.0 (R Project). To handle data, quantify metrics, summarise results, and visualise data and estimates we used the brms, tidyverse, bayesplot, and ggplot2 packages (Bürkner 2018; Gabry *et al.* 2019; Wickham 2009; Wickham *et al.* 2019).

Results

Soil seed banks of the world

The total number of seeds counted across the 1185 studies and 2585 observations of seed density 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 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 tropical forest in South Africa (Boyes *et al.* 2011), with the maximum being 501 119 seeds m^{-2} observed in a study from temperate 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 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 595 sites (total sampled area of 59.5 m^2) in arable fields across Finland (Salonen *et al.* 2011).

Local and global patterns in the soil seed bank

We found that patterns of species richness in the soil seed bank diverged from patterns of density. That is, high relative abundance of seeds in the soil seed bank does not necessarily translate to a large number of species. We also find that habitat degradation appears to have

impacted the seed bank across the world.In such a large and heterogeneous dataset, there was generally a large variation in seed bank richness and density within and between ecosystems. Here, we describe noteworthy results in terms of overlap in 50% and 90% credible intervals (hereafter CIs) and consistency in the relative values of model estimates that are rounded to whole numbers (i.e. whole species or whole seeds m^{-2}). All model results and further supplementary information can be found in Tables S1-S4, and Figures S2a-g.

Richness and density across ecosystems and biomes

Using the species richness models to predict average soil seed bank diversity for each ecosystem, we found that species richness generally increased from the $0.01m^2$ alpha scale to the 15 m^2 gamma scale, with model estimates always higher at the gamma scale and 50% credible intervals not overlapping in all undisturbed and 80% of degraded (including arable) systems. Relative values of predicted richness varied according to scale, with one example being that boreal and temperate grasslands had a higher predicted richness than tropical forests at the alpha scale (but with overlapping CIs), while tropical forests had higher richness at the gamma scale (no overlap of 50% CIs). Generally, differences in estimated richness across ecosystems were more clear at the gamma scale, so we place most focus there. In undisturbed systems, mediterranean forests and shrublands were predicted to have the highest richness compared to all eleven other undisturbed ecosystems (no overlap of 50% CIs, overlap with six undisturbed ecosystems at 90% CIs; Figure 2, Table S4). Tundra and aquatic systems generally had the lowest species richness, each having a lower estimate than the other ten undisturbed ecosystems, and lower than eight of the other ecosystems (50% CIs). Undisturbed tropical ecosystems were estimated to be broadly more species-rich than their equivalent temperate and boreal ecosystems. Estimated values were higher for tropical forests than both boreal and temperate forests, for tropical grasslands compared to temperate and boreal grasslands and tropical arable compared to temperate and boreal arable, while tropical wetlands had similar estimated richness as temperate and boreal wetlands. Despite this consistency, estimates were only clearly different in forest

ecosystems (50% CIs), although tropical wetlands were more species-rich than mediterranean and desert wetlands.

The average estimated number of seeds m^{-2} in the soil seed bank was 5 737 m^{-2} (median 6 129) for natural terrestrial and wetland ecosystems, 9 434 m^{-2} (median 11 001) for arable systems, 8 124 m^{-2} (median 9 562) for aquatic systems (Figure 3, Table S5). Wetlands exhibited high seed densities, often higher than other ecosystems within their equivalent biome subtype (90% CIs). For example, tropical wetlands had higher seed densities than tropical forests, and temperate and boreal wetlands had higher seed densities than forests and grasslands in the same regions. Within the terrestrial realm, undisturbed temperate and boreal grasslands had the highest predicted seed density, higher than boreal forests and temperate forests (90% CIs).

The effects of habitat degradation

In all ecosystems, habitat degradation always resulted in a lower estimated species richness at the 15 m^2 scale in terms of predicted values, but again, despite this consistency, the difference was only clear in mediterranean forests, woodlands and scrub according to the 50% credible intervals. At the 0.01 m^2 scale, the predicted values were often the same in undisturbed and degraded ecosystems. Compared to species richness, habitat degradation had much more variable effects on seed density m^{-2} (Figure 3, Figure 4). Broadly speaking, degradation was more likely to result in lower predicted seed densities compared to undisturbed habitats in open ecosystems, with clear differences (50% CIs) for tropical grasslands, mediterranean and desert wetlands and aquatic ecosystems. On the other hand, seed density estimates were generally higher with degradation in forest ecosystems, with clear differences in both temperate and tropical forests (50% CIs). No ecosystems exhibited clear differences in richness or density with degradation according to the 90% CIs.

Divergent patterns of richness and density

Despite relatively high species richness, seed bank density was generally low in tropical systems. Tropical forests had the lowest density across undisturbed ecosystems, being lower than all eleven other undisturbed ecosystems (no overlap of 50% CIs, of which eight had no overlap of 90% CIs). Undisturbed tropical wetlands, forests and grasslands had a lower density than their equivalent ecosystems in temperate and boreal regions (50% CI). Disturbed tropical grasslands were similarly low in seed density, while arable ecosystems in tropical regions were lower than the equivalent systems in other regions (90% CI). Otherwise, arable systems combined relatively low richness with high seed density. Mediterranean and desert, and temperate and boreal arable ecosystems were predicted to have more seeds in the soil than all other ecosystems in the terrestrial realm (50% CIs), while arable ecosystems often had lower richness at the gamma scale than other degraded ecosystems within similar biome subtypes (for example, temperate and boreal arable ecosystems had lower richness than temperate forests and temperate and boreal wetlands; 50% CIs). On the other hand, mediterranean forests, woodlands and scrub combined high species richness with relatively high seed density (higher than all other forest ecosystems, 90% CI), while tundra combined its low species richness with low density, especially when degraded, where density was lower than all other degraded ecosystems (50% CI).

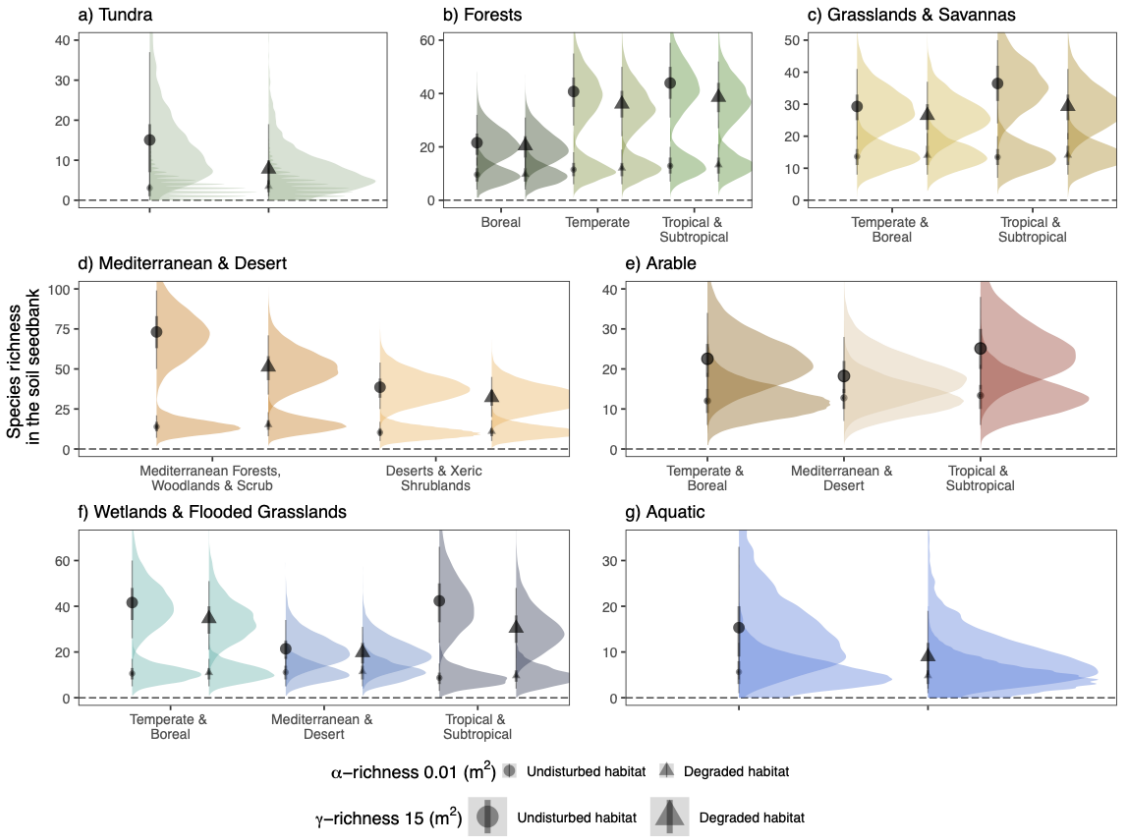

Figure 2: Scale-dependent diversity in the soil seed banks of the world. Panels represent ecosystem realm and biomes. Colours represent ecosystem type and groups. Points represent average predicted species richness at two spatial scales of soil sampled across realm/biomes. Large points represent the gamma (15 m^2) scale, small points represent the alpha (0.01 m^2) scale. Densities represent 24 000 predictive draws of the posterior distributions of overall richness at each scale, within each Biome subtype and degradation group. The black points show the mean, bar represents 50 (thick) and 90% (thin) credible intervals. Colours indicate unique ecosystem Biome subtypes. Shapes indicate undisturbed habitat (circle) and disturbed/degraded habitat (triangle). Y axes vary for clarity.

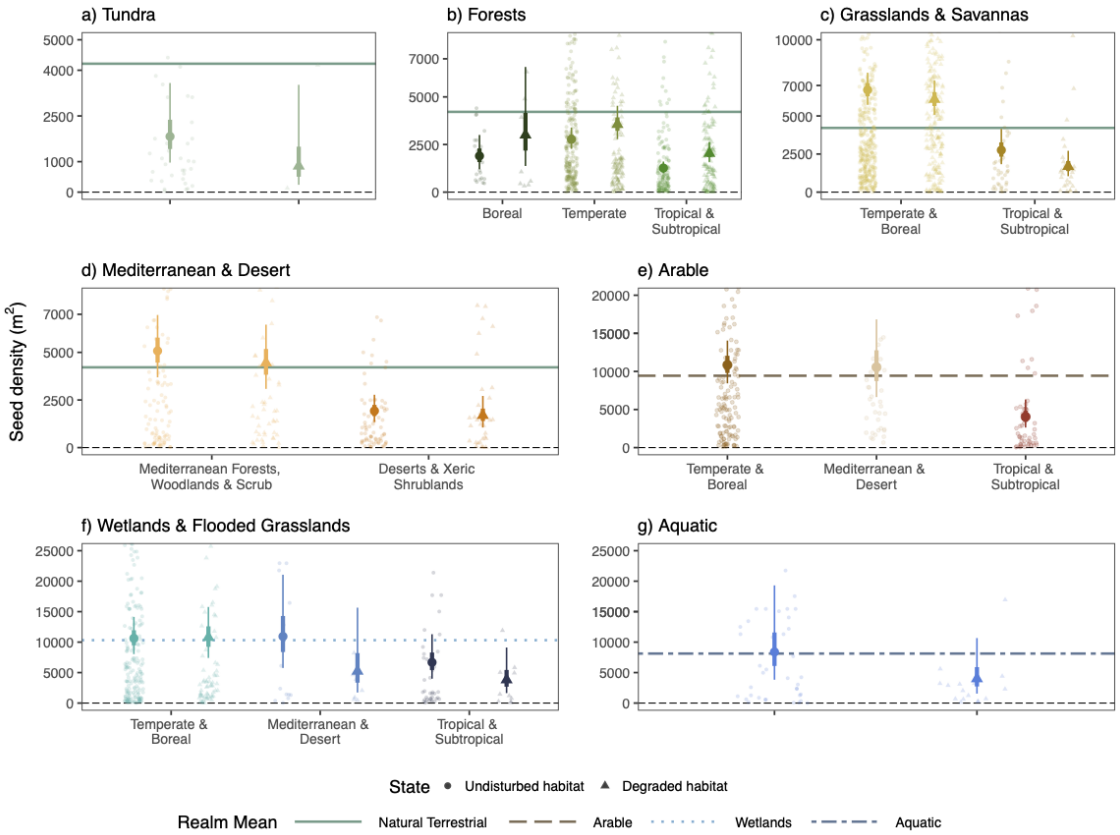

Figure 3: Density of seeds m^{-2} in the soil seed bank. Panels represent ecosystem realms and biomes. Background jittered points represent empirical estimates of seeds m^{-2} within sampled soil banks. The large points show the mean, bar represents 50 (thick) and 90% (thin) credible intervals. Colours represent ecosystem types and groups, and the dashed reference line at 0 represents a value of 0. Shapes indicate undisturbed habitat (circle) and disturbed/degraded habitat (triangle). Thick colored lines represent the mean fixed effect value across broad realms (Natural Terrestrial, Arable, Wetlands, Aquatic). Y-axes vary for clarity.

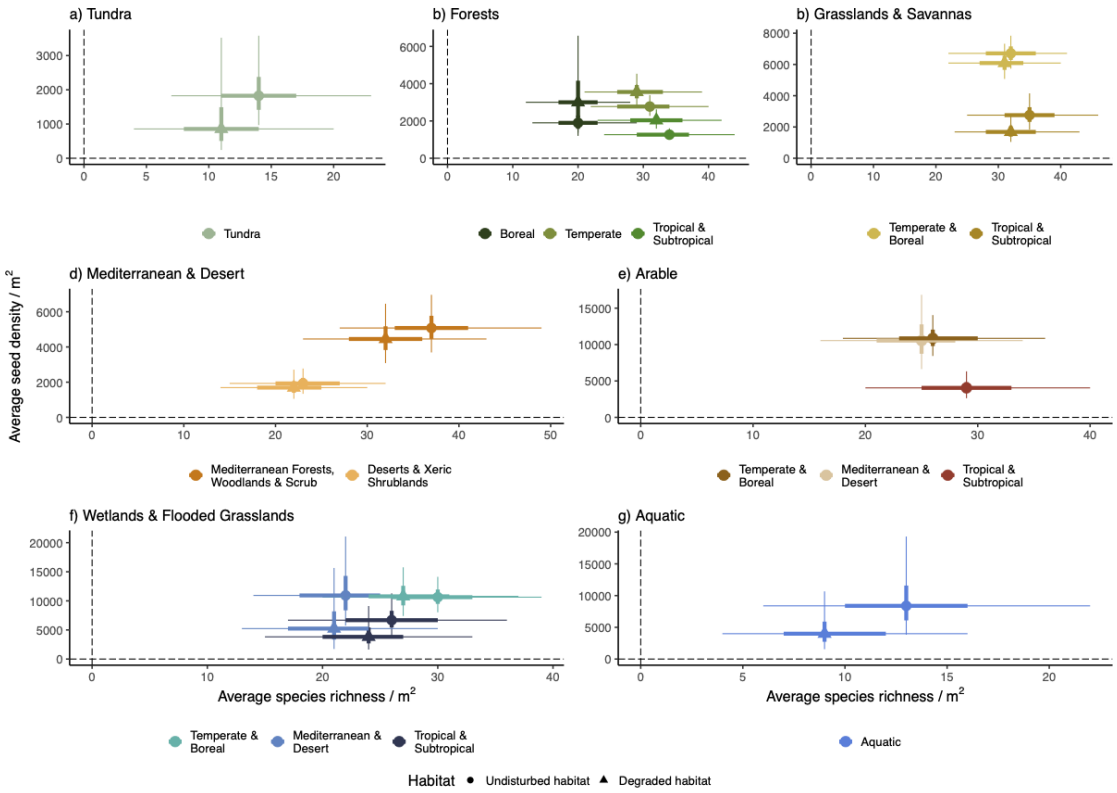

Figure 4: The joint relationship between predicted species richness m^{-2} and seed density m^{-2} in the soil seed banks of the world. Panels represent ecosystem realms and biomes. The large points show the mean, bar represents 50 (thick) and 90% (thin) credible intervals. Colours represent ecosystem groups and habitat state, and the dashed reference line at 0 represents a value of 0. Shapes indicate undisturbed habitat (circle) and disturbed/degraded habitat (triangle). X and Y axes vary for clarity.

Discussion

We have used a global database of published soil seed bank studies to explore patterns of biodiversity in the soil seed bank worldwide. Although there was a high uncertainty in our results, we found that across the world's biomes and ecosystems, patterns in species richness in the seed bank often diverged from patterns of seed density. Strikingly, we also found that the richness of soil seed banks appeared higher in undisturbed compared to degraded habitat, suggesting how across the world's ecosystems, soil seed banks also reflect the ongoing depletion of biodiversity as a result of anthropogenic activities

(Eichenberg *et al.* 2021; Newbold *et al.* 2020). This indicates that the potential for seed banks to contribute to the recovery and restoration of degraded ecosystems might be limited. Seed density, on the other hand, was not always lower in disturbed habitats, showing how different aspects of biodiversity can show diverging patterns in response to global change pressures (Blowes *et al.* 2022). Our estimated global average of more than 5000 seeds m^{-2} also 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).

Scale-dependence of species richness in soil seed banks worldwide

We found that the species richness in terrestrial soil seed banks generally increases with increasing area of ground sampled, but that the strength of this relationship varies across biomes, ecosystems and between undisturbed and degraded habitats (Figure 2). Our findings support those of Vandvik et al. (2016), who found that species accumulate more rapidly in alpine and subalpine grasslands than in boreal zones (empirical), and in forests compared to grassland and heathland (literature), and we extend the results to include other global biomes. We found that richness estimates across small and large scales (in our case 0.01 m^2 and 15m^2) appeared to show relatively large differences in mediterranean and tropical biomes compared to temperate biomes, demonstrating how species' spatial distributions affect how we interpret relative differences in biodiversity across regions (Table S3). Overall, our broad patterns of richness distribution in the global soil seed bank are 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 (Keil & Chase 2019; Liang *et al.* 2022). However, like others, we also found some differences depending on the spatial scale of our predictions. For vascular plants,

Sabatini *et al.* (2022) 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 0.01 m^2 scale were broadly similar to those found by Yang *et al.* (2021), although their findings of low richness in the tropics and (predicted) higher richness in northern biomes were not supported when considering larger spatial scales. Our results were characterised by high levels of uncertainty. However, global maps of biodiversity do not generally map uncertainty and only plot according to mean predicted values. Our findings highlight the need to be cautious when drawing conclusions from such maps, with different aspects of biodiversity varying across space and scale, and with a large degree of uncertainty.

Patterns and determinants of seed bank richness and density

Our analyses revealed substantial variation in the diversity of the soil seed bank among the world's ecosystems. Importantly, we often found divergent patterns between species richness and seed density. While mediterranean and tropical ecosystems were broadly predicted to have higher richness than temperate and boreal ecosystems and tundra, seed density was generally characterised by high variation within biomes. However, mediterranean forests and shrublands systems exhibited both high richness and density (Figures 2-4, Table S3). In regions that are characterised by a warm climate and frequent extreme climatic events, the soil seed bank can play an important role in vegetation recovery and stability of biodiversity (DeMalach *et al.* 2023; Lloret *et al.* 2012), and it follows that many plant species will form persistent seed banks. Previous work from Europe has shown that species with relatively warm, southerly distributions are more likely to have persistent seeds than cool-adapted species (Auffret *et al.* 2023), and we also found lower richness in temperate and boreal grasslands and forests, and lower density in the majority of temperate and boreal habitats compared to their Mediterranean counterparts. The vegetation in the

temperate and 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 density 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). In tropical ecosystems, relatively few species produce persistent seeds (Tweddle *et al.* 2003; Wyse & Dickie 2017), while the warm and often moist conditions combined with high diversity of other taxa mean that seeds are subject to degradation, predation and attacks from pathogens (Baskin & Baskin 2014; Dalling *et al.* 1998; Skoglund 1992). This can result in low soil seed bank density, but the high overall diversity in the vegetation means that species richness is still high relative to other biomes.

Our results show an imprint of anthropogenic activity on soil seed banks worldwide. Perhaps unsurprisingly, arable soils contained among the highest number of seeds per square metre (Figure 3,4). Highly and regularly-disturbed arable systems accumulate the persistent seeds of comparatively few 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 (Ikeda *et al.* 2007; Rotchés-Ribalta *et al.* 2017; Schwartz *et al.* 2015). However, in non-arable open ecosystems, seed density was often lower with habitat degradation, while the opposite was true for forested ecosystems. Many degraded forests are those that are recovering from previous agricultural or silvicultural management, and therefore their seed banks can still reflect those of highly-disturbed conditions (Daïnou *et al.* 2011; Dupuy & Chazdon 1998; Plue *et al.* 2010). In other habitats, degradation generally appeared to result in both reduced richness and density in the soil seed bank, in line with reports of reduced biodiversity in the established vegetation over time (Daru *et al.* 2021; Jandt *et al.* 2022; but see Vellend *et al.* 2013), with

consequences for the potential of passive restoration in reversing biodiversity losses (Atkinson *et al.* 2022; Ladouceur *et al.* 2023).

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 cover a greater global extent 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). 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. However, some ecosystems were better-represented than others, which may affect our predictions of richness at different spatial scales. It is also well-known that sampling multiple sites per treatment gives improved confidence in ecological findings (sample replication; Filazzola & Cahill Jr 2021), but around half of all observations in the database represented a single site. There have previously been calls to improve the seed bank sampling to improve representativeness (Bigwood & Inouye 1988; Plue & Hermy 2012), and we add to this a request to report soil seed bank data at the smallest scale possible (e.g. replicate, pooled replicates or site level), or at least making it possible to estimate the geographic spread of sites included in an observation. This would help to create an even better understanding of seed bank diversity and its spatial scaling.

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 – not forgetting to standardise according to spatial scale – 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.

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