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RESEARCH ARTICLE

Unusually high-quality soil seed banks in a Midwestern U.S. oak savanna region: variation with land use history, habitat restoration, and soil properties

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An overarching conclusion in the literature is that soil seed banks rarely contain many restoration-target species and are often liabilities rather than assets to restoration. Our objective was to evaluate composition and spatial variation of seed banks and their potential contributions to restoration, including restoration-target species such as rare species and those characterizing historical habitats. On 64 sites in a Midwestern U.S. oak savanna landscape, we sampled soil seed banks in seven habitat types (restored oak savannas, oak woodlands, and mesic prairies; unmanaged upland oak and mesic forests; and unmanaged and managed pine plantations). The germinable seed bank was exceptionally rich in restoration-target species. In total for the 64 sites, seedlings of 127 species emerged from seed bank samples. Of the 101 native species, 56 were restoration-target species, an unusually high number among seed bank studies. Restoration-target species in seed banks included 13 threatened or endangered species, in addition to 43 other specialist species associated with high-quality native habitats or on a floral list thought to characterize historical ecosystems. When analyzed across the 64-site gradient, seed banks differed among the seven habitat types and varied with historical (1939) land use, recent management activities that restored open-structured habitats, and biophysical gradients of tree density, soil drainage, and soil texture. While not all restoration-target species were detected in the seed bank, the unusually high-quality seed bank is a potential asset to restoration and was partly structured along environmental gradients across the landscape.

Key words: conifer plantation, forest, prairie, propagule supply, rare species, restoration-target species, woodland, woody plant encroachment

Implications for Practice

- Native and restoration-target species dominated seed banks, making seed banks potentially unusually beneficial to restoration.
- Seed banks consisted of 20% nonnative species and only two of these were management-priority species, so seed banks should not be major suppliers of troublesome species at the study sites.
- Restoration practitioners can anticipate usefulness of seed banks to vary among habitat types including across environmental gradients within landscapes.
- A preponderance of evidence exists globally that relying on seed banks for supplying restoration-target species is normally tenuous, but our unusual results and those of a small number of studies with similar findings suggest that seed banks can benefit restoration.

Introduction

To what extent soil seed banks benefit or hinder ecological restoration influences restoration planning, implementation, and effectiveness (Bakker et al. 1996; Bossuyt & Honnay 2008; Haussmann et al. 2019). In terms of potential contributions to plant establishment, five general types of seed banks are likely: (1) depauperate, providing little regeneration potential; (2) those predominately containing ruderals, consisting of generalist species able to colonize a variety of disturbed sites; (3) predominately nonnative species; (4) predominately restoration-target species, consisting of native species desirable for restoration, often specialist species of mature habitats; and (5) relatively balanced mixtures of seed banks (2)–(4). Depauperate seed banks could necessitate introducing propagules to meet restoration goals, although a positive feature of small seed banks is they supply few seeds of nonnative species (Drury et al. 2019). Ruderal-dominated seed banks could assist restoration by fostering rapid establishment of plant cover to stabilize soil and enable

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eventual recovery of restoration-target species, but ruderals could also hinder establishment of target species (Valkó et al. 2011). Suppressing germination may be important for sites containing seed banks dominated by nonnative species (Török et al. 2018). If seed banks store restoration-target species, activities encouraging germination can enable cost-effective restoration without expensive seeding or planting (Metsoja et al. 2014). Seed banks with mixtures of desired and undesired species can be managed by selectively triggering germination when possible for desired species (Davies et al. 2013).

Unfortunately for restoration, persistent seed banks containing restoration-target species would generally not be predicted theoretically and indeed are uncommon among empirical studies (e.g. Thompson et al. 1998; Wang et al. 2010; Zylka et al. 2016; Godefroid et al. 2018). For example, perennial species long-lived in vegetation of mature habitats are often restoration-target species, but these species are not theorized to have been under selective pressure to form large, persistent seed banks (Kiss et al. 2018). Instead, these species are likely to invest in sustaining vegetative growth in relatively stable habitats (e.g. forests rarely severely disturbed) and to produce short-lived seeds, such as large seeds for energizing seedling emergence in shade (Thompson et al. 1998). In contrast, ruderal species are theorized to form large, persistent seed banks for colonizing disturbances unpredictable in space and time (Hyatt & Casper 2000). As a result, species composition of seed banks and mature vegetation typically differs, such that loss of mature plant communities (including those sustained by relatively predictable, low-severity disturbance) is not reversible via recruitment from the seed bank (Jacquemyn et al. 2011).

There are some exceptions, however, where studies have detected abundant restoration-target species in seed banks. These unique studies have spanned a range of habitats such as shrublands in Australia (Davies et al. 2013), perennial grassland in Estonia (Kalamees et al. 2012), coastal sand dunes in the United Kingdom (Plassmann et al. 2009), abandoned agricultural fields in South Africa (Haussmann et al. 2019), and conifer forests in the United States (Abella & Springer 2012). All these studies used the emergence method for assaying seed banks, but perplexingly, other commonalities, such as in land use history, seemingly are lacking among the studies. Additionally, the general habitat types examined in these studies normally have had depauperate or ruderal- and nonnative-dominated seed banks (e.g. Kiss et al. 2018).

Another factor in relationships of seed banks with restoration is how seed banks may vary spatially. This is an uncertainty in the literature, complicating understanding generality of theoretical expectations and hindering tailoring restoration activities to site conditions (Abella et al. 2007; Ma et al. 2017). Within landscapes, seed banks could vary among habitat types (e.g. wetlands c.f. dry forests) or along biophysical gradients such as land use history, soil properties, and tree density (Bekker et al. 1997; Falińska 1998; Abella et al. 2007). Theory and empirical data suggest variable and sometimes opposing expectations for spatial variability in seed banks (Hopfensperger 2007). For example, mesic, productive sites could be theorized to contain large, persistent seed banks via copious seed production stimulated by moisture availability and via organic-rich soil expected to trap seeds (Egawa & Tsuyuzaki 2013). Conversely, xeric sites could harbor large seed banks because of slower seed decomposition, greater fire activity stimulating but not consuming seeds insulated in soil from lethal temperatures, and selecting for seed bank formation by being stressful environments (Anderson et al. 2012). Land use history also has had conflicting influences on seed banks among studies. After intensive anthropogenic land uses, seed banks containing at least some species of less-disturbed habitats have persisted through or quickly replenished after disturbance in some but not other studies (Plue et al. 2010).

Within a biodiversity hotspot of the Midwestern North American oak savanna region, we assessed soil seed banks at two spatial scales: data aggregated for 64 sites undergoing or not undergoing restoration as an estimate of overall seed bank composition, and a finer scale comparing seven habitat types and across land use and biophysical gradients. Our objective was to evaluate abundance and spatial variation of nonnative species in seed banks and the potential contributions of seed banks to native species restoration, especially restoration-target species. Restoration-target species included conservation-priority rare species, specialist species of the region's woodland, savanna, and mesic prairie ecosystems, and major species thought to characterize historical open-structured habitats that are priorities for restoration.

Methods

Study Area

The study area was the 1,692-ha Oak Openings preserve within the 45,000-ha Oak Openings region, an eastern part of the Midwestern oak savanna region (Schetter & Root 2011). The preserve (41°33′N, 83°51′W), managed by Metroparks Toledo, is 40 km southwest of the city of Toledo, in northwestern Ohio, U.S.A. Climate is temperate, averaging 85 cm/year of precipitation, −9/0°C daily low/high temperature for January, and 16/29°C for July (1955 through 2018; Toledo Airport weather station, 5 km from the study area; Midwestern Regional Climate Center, Champaign, Illinois, U.S.A.). On the sandy Oak Openings landscape, distribution of habitat types was and is associated with spatial variation in soil drainage. Pre-Euro-American settlement vegetation was dominated by fire-dependent oak savannas and woodlands on well-drained uplands and nearly treeless mesic prairies on poorly drained lowlands, as recorded by 1817–1832 U.S. government land surveys (Brewer & Vankat 2004). The contemporary Oak Openings region supports the greatest concentration of state-rare species of plants (approximately 160 species) in Ohio and is a regional biodiversity hotspot (Schetter & Root 2011).

Within the study area, we sampled soil seed banks in seven habitat types: restored oak savannas and woodlands containing overstory trees of *Quercus velutina* (black oak) and *Q. alba* (white oak); restored treeless mesic prairies; unmanaged oak forests and mesic forests (dominated by *Acer rubrum* [red maple]) on sites that had supported open savanna, woodland, and mesic prairie in the early 1800s; and plantations of *Pinus* *resinosa* (red pine) and *P. strobus* (white pine) that remained either unmanaged or had been managed through restoration tree removal (Fig. 1). The restored oak savannas, woodlands, and mesic prairies had been managed for the last 14–30 years using tree cutting and dormant-season prescribed fire designed to reduce woody plant encroachment and sustain open structure, detailed in Abella et al. (2017). The oak and mesic forest sites that did not receive restoration treatments served as unmanaged comparisons. The pine plantations were established in the 1940s–1950s to revegetate former agricultural lands acquired when the preserve was formed. The pine species are native to the United States, but not to the Oak Openings region. To encourage reestablishment of native open-structured habitats, managers removed some plantations in 2001, detailed in Abella et al. (2018). The soil series of the U.S. soil taxonomy that the habitat types mainly occurred on were the Oakville and Ottokee for the oak habitats, Granby for the mesic prairies and mesic forests, and all three of those soil series for managed and unmanaged pine plantations (Stone et al. 1980).

Seed Bank Sample Collection

To represent a soil seed bank able to at least overwinter to the following growing season, we collected seed bank samples in winter 2018 under snow cover (late January). We collected samples from 64 sites throughout the preserve in seven habitat types based on their availability: 19 sites in restored oak savannas, seven in restored oak woodlands, three in restored mesic prairies, eight in unmanaged oak forests, three in unmanaged mesic forests, 15 in managed pine plantations, and nine in unmanaged pine plantations. There was one centrally located sampling area per site. Sites were 0.5 to 5 ha, received or did not receive restoration treatments, and were associated with typical sizes of soil and vegetation units on the landscape. To sample seed banks, we collected a 360-cm^3 subsample of mineral soil to a depth of 5 cm at 5-m intervals along two parallel 25-m-long transects (25 m apart). The resulting 10 subsamples per site were mixed and combined to make one 3,600-cm^3 sample for each of the 64 sites. Unlike other habitat types, unmanaged pine plantations contained a thick O horizon (surficial organic layer) at least 10 cm deep, which could have trapped appreciable seeds. Therefore, in a subset (four sites) of the unmanaged plantations, we collected 360-cm^3 subsamples (also mixed and combined into one sample per site) of the Oe + a horizon at the same places where mineral soil was collected.

Seed Bank Processing and Taxonomic Identification

We processed seed bank samples by providing treatments and care intended to stimulate germination. From each homogenized sample per site, we extracted three 360-cm^3 volumes of soil. One 360-cm^3 volume per sample received 30 mL of 2000-ppm gibberellic acid, another was heated (placing soil for 30 minutes in an oven set to 100°C), and the last volume was untreated. After treatments, we placed each 360-cm^3 soil volume in a layer 2 cm thick into 4-L, cylindrical plastic pots containing 3 L of a sterilized, water-retaining, peat moss-based mixture (Metro Mix 360, Sun Gro Horticulture Distribution Inc., Agawam, Massachusetts, U.S.A.). The 192 pots were randomly arranged on benches in a greenhouse. During a 16-month emergence period from February 2018 through May 2019, samples were watered daily to soil moisture saturation, kept under natural lighting, and maintained at temperatures about 8°C warmer than outdoors (and always above freezing) in winter and about 8°C cooler than outdoors in summer.

As seedlings matured adequately for taxonomic identification, they were counted, identified to species when possible, and pulled from pots (taxonomy followed Natural Resources Conservation Service 2018). Seedlings not sufficiently developed for identification nor exhibiting much development were periodically transplanted to separate pots to facilitate maturation. Of 2,258 seedlings, 78 (3%) were not identifiable at least as finely as genus because the seedlings died before developing distinctive morphology. These seedlings were deleted from the dataset, leaving 2,180 seedlings (97% of total seedlings) identified at least as finely as genus. Seedlings identifiable only to genus were retained in the dataset and included in statistical analyses if a seedling could be narrowed down to a few possible species sufficient for assigning to categories (e.g. native or nonnative) required for analyses. The acid and heating treatments did not increase the number of emerging seedlings, so seedling counts from the three 360-cm^3 volumes of soil were pooled into a 1,080-cm^3 soil volume for each of the 64 sites.

Data Compilation and Analysis

We first compiled overall seed bank characteristics aggregated for the 64 sites by categorizing species several ways (Table S1). We classified seed bank species by native/nonnative status to the United States, growth form (e.g. forb, graminoid), and longevity (e.g. annual, perennial) following Natural Resources Conservation Service (2018). One exception was that we classified *Pinus resinosa* as nonnative, even though it is native to the United States, because the species was absent historically from the Oak Openings region and was planted in the mid-1900s (Abella et al. 2018). To categorize the degree of habitat specialization of species, we obtained coefficients of conservatism developed for Ohio for each native species detected in seed banks (Andreas et al. 2004). The coefficients describe how specialized native species are in terms of their restriction to high-quality native habitats. The coefficients range from 0 (generalists inhabiting a variety of sites including those severely disturbed by humans) to 10 (specialists usually only inhabiting high-quality natural habitats). Many of the specialist species were inhabitants of open oak savannas, woodlands, and mesic prairies dependent on periodic disturbances (such as fires) curtailing woody plant encroachment (Schetter & Root 2011). We categorized species as state rare (hereafter state-rare species) based on the 2018–2019 rare plant list for the state of Ohio provided by the Ohio Department of Natural Resources (Columbus, Ohio, U.S.A.). We classified species as "historical" species of restoration-target communities based on a list of 100 forb, graminoid, and woody species thought to have characterized pre-Euro-American settlement oak savannas, woodlands,

Oak savanna: 9±1 species, 1087±176 seeds

Oak forest: 4±1 species, 567±128 seeds

Oak woodland: 4±1 species, 370±65 seeds

Mesic forest: 6±2 species, 3873±1061 seeds

Mesic prairie: 9±2 species, 2099±742 seeds

Unmanaged pine: 8±1 species, 1003±269 seeds

Managed pine: 14±1 species, 2938±518 seeds

Oe+a horizon: 8±2 species, 938±470 seeds

Figure 1. Example sites of seven habitat types and the mean ± 1 SEM of species richness (species/1,080 cm^3 of mineral soil) and seed density (seeds/m^2, 0–5 cm mineral soil) in seed banks for each habitat type, plus for Oe + a horizons of unmanaged pine plantations, Oak Openings region, Ohio, U.S.A. Oak savannas, woodlands, mesic prairies, and managed pine plantations had undergone ecological restoration in the past 14–30 years before seed bank sampling in 2018, while oak and mesic forests and unmanaged pine plantations did not receive restoration treatments. Note that the total mean seed densities shown in this figure represent all seedlings identifiable at least as finely as genus and therefore do not exactly match seed densities for seedlings identifiable to species in Fig. 2. Photos by S. R. Abella, 2018.

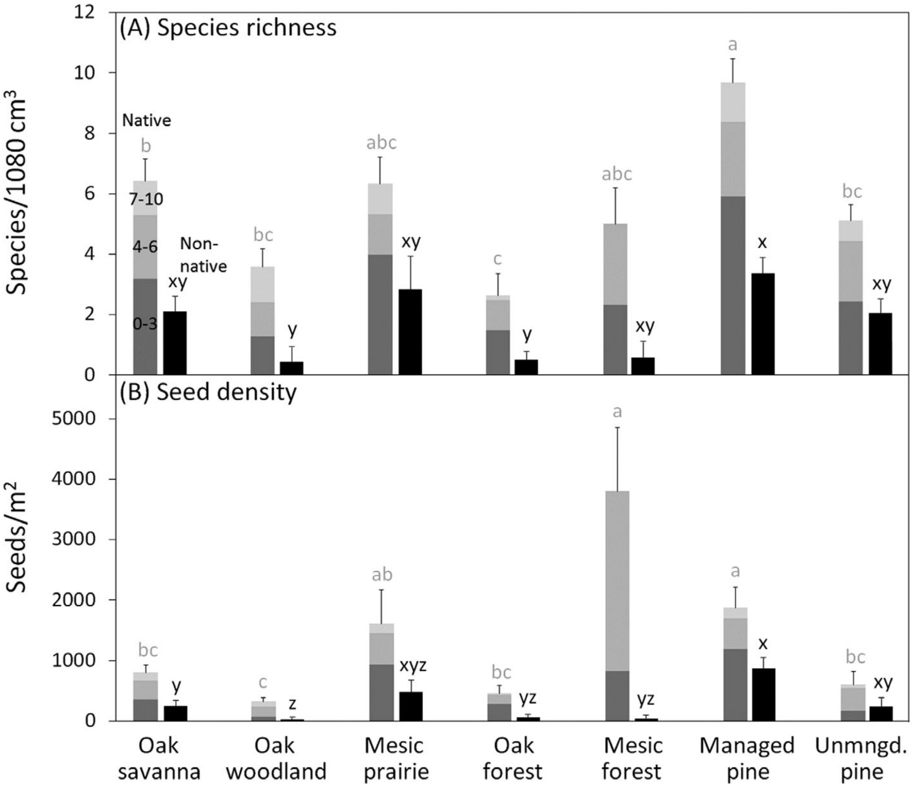

Figure 2. Mean (A) species richness and (B) seed density in seed banks (0–5 cm mineral soil) compared across seven habitat types in the Oak Openings region, Ohio, U.S.A. Error bars stand for +1 SEM for mean total species richness and seed density for native (left bars) and nonnative species (right-side solid black bars). Native species are subdivided based on a coefficient of conservatism representing the degree that species are restricted to high-quality natural habitats. Coefficients 0–3 represent generalist species, 4–6 moderately specialized species, and 7–10 conservative, specialist species usually restricted to natural habitats. One-way ANOVA statistics comparing habitat types for each seed bank measure are as follows: (A) native richness: $F_{[6,57]} = 9.5$, $p < 0.001$; nonnative richness: $F_{[6,57]} = 5.2$, $p < 0.001$; (B) native seed density: $F_{[6,57]} = 9.7$, $p < 0.001$; nonnative seed density: $F_{[6,57]} = 7.2$, $p < 0.001$. Separately for native and nonnative species, means without shared letters differ at $p < 0.05$ (Tukey tests).

and mesic prairies in the Oak Openings region. This list was based on 1817–1832 land surveyor notes and species inhabiting remnant communities with partly open tree canopies in the 1980s (Brewer & Vankat 2004). The specialist, state-rare, and historical species formed three categories of restoration-target species desirable for seed banks to contain. The three categories of restoration-target species were not mutually exclusive, as some species could be in multiple categories. To assess a possibility of undetected restoration-target species not actually forming persistent soil seed banks and therefore unable to be detected, we totaled how many of the 100 species on the Oak Openings historical list were detected in our study and in 29 previous seed bank studies in eastern North American savannas, woodlands, forests, and wetlands (Table S2). To identify the nonnative species of highest management priority, we categorized nonnative species based on their legal classification in 2018 as invasive or noxious weeds in Ohio (Ohio Department of Agriculture, Columbus, Ohio, U.S.A.).

In addition to compiling overall seed bank characteristics aggregated for all 64 sites, we examined seed banks among habitat types and along land use and biophysical gradients. We compared mean species richness (per 1,080 cm^3 of soil) and density (seeds/m^2 calculated from sample volume and corresponding to a 0–5 cm depth) of mineral soil seed banks across the seven habitat types using one-way analysis of variance (ANOVA). For ANOVA $p < 0.05$, we separated means with Tukey's test in PAST 3.22. We minimized possible influence of the different numbers of sites (replicates) among habitat types by statistically analyzing only site means (i.e. not cumulative measures like total species richness of a habitat type contingent on numbers of sample sites), performing ANOVA using Box-Cox-transformed data meeting assumptions of normality and equality of variance, and calculating species-accumulation curves as a function of increasing numbers of sites. Shapes of the curves did not confirm, but suggested, that differences among habitat types in seed bank species richness averaged at the site level (species/1,080 cm^3 of soil) would be maintained if cumulatively extrapolating species richness to a standardized larger number of sites was desired (Fig. S1).

We used regression trees to model variation in seed bank density (seeds/m^2 in 0–5 cm mineral soil) separately for nonnative, all native, and specialist (coefficient of conservatism 4–10) species along land use and biophysical gradients. Regression trees hierarchically partition data for a response variable into increasingly homogeneous subsets and accept continuous or categorical explanatory variables screened for inclusion in final models based on optimizing fit (Breiman et al. 1984). For each of the 64 sites, we obtained 16 potential explanatory variables: 0–5 cm mineral soil properties (soil samples collected at the same time as seed bank samples and analyzed for texture, pH as 1:1 soil: water, and loss-on-ignition as heating to 550°C for 4 hours as a surrogate for organic matter), soil series and series broadly classified as xeric or mesic based on soil drainage (Stone et al. 1980), tree basal area and density for all stems ≥1 cm in diameter at 1.4 m (separately for *Quercus* spp., *Acer rubrum*, and *Pinus* spp. and in total for all trees, with data obtained from 0.05-ha plots on the seed bank sampling sites), and land use history (1939 land use from aerial photos, year a site was acquired by Metroparks Toledo for incorporation into the preserve, and whether a site was under recent restoration management through tree cutting or prescribed fire initiated and ongoing within the last 14–30 years). We computed regression trees using the RandomTree algorithm in Weka 3.8, pruned them based on maximizing the correlation coefficient with the fewest number of splits, and used 5-fold cross-validation to assess models.

Results

Overall Seed Bank Characteristics

In total, we detected 127 species in seed banks (Table 1, Table S1). Most of the species were native (80%), with 20% nonnative. Of 26 nonnative species, only two were classified as invasive (*Alliaria petiolata*, garlic mustard) or noxious (*Cirsium arvense*, Canada thistle) in Ohio. Constituting 71% of species, perennial species dominated seed banks: 61% of total seed bank species were long-lived perennials and another 10% were short-lived perennials. The remainder consisted of 21% annual and 8% biennial species. Seed banks mostly contained herbaceous species (90%), with 55% being forb and 35% graminoid species. Woody plants including shrubs, trees, and vines constituted the remaining 10% of species. Long-lived perennial graminoids were the most abundant group with 36 species (28% of total species), followed by perennial forbs with 30 (24%) and annual forbs with 19 species (15%).

Restoration-target species were common in seed banks (Tables 1 & 2). In total, seed banks contained 56 native species (44% of all seed bank species and 55% of all native species) with coefficients of conservatism of at least 4 or that were on the historical species list. Thirteen species, or 10% of total species in seed banks, were state-rare species. Examples included the threatened *Dichanthelium meridionale* (matting rosette grass), *Helianthemum canadense* (Canada frostweed), *Krigia virginica* (dwarf dandelion), *Lipocarpha micrantha* (dwarf bulrush), *Polygala polygama* (racemed milkwort), *Pycnanthemum verticillatum* var. *pilosum* (whorled mountainmint), and the endangered *D. spretum* (Eaton's rosette grass). Most of the state-rare species in seed banks were specialists typically found in open prairie-savanna or wetland habitats. Including many of the state-rare species, seed banks contained 17 species (13% of all detected species) with coefficients of conservatism above 7, representing highly specialized, restoration-priority species. Of 100 species on the diagnostic list for historical Oak Openings communities, we detected 19 in seed banks (Table S2). Forty-one additional species on the historical list were recorded by at least one of 29 previous seed bank studies using the emergence method in eastern North America (Table S2). This equates to a capability for forming persistent seed banks documented for at least 60% of species on the historical list.

Variation Among Habitat Types and Along Land Use and Biophysical Gradients

On average, native seed bank species richness in mineral soil varied by a factor of four and seed density by a factor of

Table 1. Summary of 127 species detected in soil seed banks on 64 sites in the Oak Openings region, Ohio, U.S.A. These species include 126 species detected in 0–5 cm mineral soil and one species detected only in the Oe + a horizon. The 101 native species are subdivided into nonmutually exclusive categories of specialist (species with coefficients of conservatism from 4 to 10 typifying high-quality natural habitats), rare (state-rare species in Ohio), and historical species (based on species characterizing pre-Euro-American-settlement ecosystems in the region).

	Number of Species				
		Native			
	Nonnative	*All*	*Specialist*	*Rare*	*Historical*
Graminoid					
Annual	4	3	3	1	0
Short-lived perennial	0	2	1	0	0
Perennial	1	35	20	3	5
Forb					
Annual	5	14	4	2	0
Biennial	3	7	2	1	1
Short-lived perennial	5	6	1	0	2
Perennial	7	23	10	6	7
Vine	0	2	0	0	0
Shrub	0	6	2	0	2
Tree	1	3	1	0	2
Total	26	101	44	13	19

Table 2. Distribution among habitat types of 43 native specialist species (coefficient of conservatism 4–10) in 0–5 cm mineral soil seed banks in the Oak Openings region, Ohio, U.S.A. The status column lists the coefficient of conservatism with state-rare species in parentheses. Percent frequency is the percent of sites in which a species was detected in mineral soil seed banks.

		Average seeds/m^2 (% frequency)						
Species	*Status*	*Oak savanna*	*Oak woodland*	*Mesic prairie*	*Oak forest*	*Mesic forest*	*Managed pine*	*Unmanaged pine*
Annual forb								
Hedeoma hispida	(7)						3 (7)	
Hypericum majus	6					15 (33)	61 (13)	5 (11)
Krigia virginica	(8)	66 (37)					22 (20)	5 (11)
Polygonum tenue	4	5 (5)						
Annual graminoid								
Fimbristylis autumnalis	5						19 (13)	
Lipocarpha micrantha	(8)						3 (7)	
Vulpia octoflora var. *octoflora*	4	2 (5)						
Biennial forb								
Nuttallanthus canadensis	4						77 (20)	5 (11)
Polygala polygama	(10)	12 (16)	26 (29)				3 (7)	10 (11)
Short-lived perennial forb								
Verbena hastata	4	49 (11)					15 (13)	5 (11)
Short-lived perennial graminoid								
Cyperus odoratus	4						3 (7)	
Perennial forb								
Baptisia tinctoria	(6)	2 (5)						
Boehmeria cylindrica	4				6 (13)	15 (33)		5 (11)
Galium triflorum	4							5 (11)
Helianthemum bicknellii	(9)	2 (5)	7 (14)					
Helianthemum canadense	(9)		13 (29)					
Liatris squarrosa	(8)	2 (5)		108 (33)			28 (27)	
Pycnanthemum verticillatum var. *pilosum*	(5)	5 (5)					3 (7)	
Viola lanceolata	(8)						19 (7)	
Viola sagittata	4							10 (11)
Perennial graminoid								
Agrostis perennans	4						3 (7)	
Andropogon gerardii	5						3 (7)	
Aristida purpurascens	(7)	15 (11)		15 (33)				
Carex muehlenbergii	7	15 (16)						
Carex swanii	4	5 (11)	7 (14)	494 (67)	127 (63)	2,886 (100)	90 (40)	98 (22)
Carex tonsa var. *rugosperma*	8	10 (16)	7 (14)				3 (7)	15 (33)
Cyperus lupulinus	4	166 (79)	86 (43)	15 (33)	17 (13)		185 (73)	221 (89)
Dichanthelium acuminatum var. *lindheimeri*	9	2 (5)		15 (33)			74 (33)	
Dichanthelium boreale	6				6 (13)			
Dichanthelium depauperatum	8						3 (7)	
Dichanthelium meridionale	(9)		7 (14)					5 (11)
Dichanthelium sabulorum var. *thinium*	6	27 (26)	40 (43)				3 (7)	10 (11)
Dichanthelium spretum	(9)						3 (7)	
Digitaria cognata	4	29 (26)					3 (7)	
Juncus marginatus	4					15 (33)	12 (7)	
Leersia virginica	4	5 (11)	26 (14)					
Muhlenbergia mexicana	4						9 (7)	
Rhynchospora capitellata	7		26 (14)					
Schizachyrium scoparium	5	7 (11)		15 (33)			3 (7)	
Sporobolus cryptandrus	6	2 (5)						
Shrub								
Rhus copallinum	4	5 (11)				31 (67)	3 (7)	
Rubus idaeus	6						15 (7)	10 (11)
Tree								
Quercus velutina	7				6 (13)			

12 among the seven habitat types (Fig. 2). In general, oak forests contained the fewest native species, significantly fewer than in managed pine plantation and restored oak savanna habitats which were among the most species-rich. While they were not the most species-rich, seed banks in mesic forests contained among the highest native seed densities, significantly higher than all but managed pine and restored mesic prairies. Native specialist species with coefficients of conservatism of at least four were distributed across all habitat types, although the most specialized species (coefficients 7–10) were least abundant in forests.

Nonnative species did not dominate seed banks in any habitat type, but the species richness and seed density of nonnatives did vary among habitat types (Fig. 2). Managed pine plantations, for example, contained more species and seeds of nonnatives than did oak forests and restored oak woodlands. In general, restored oak woodlands and oak and mesic forests contained the fewest nonnative seeds, followed by restored oak savannas which had fewer seeds than managed pine plantations.

Unmanaged pine plantations, which had thick litter layers, displayed seed banks in the Oe + a horizon similar to those in their mineral soil. Oe + a horizons averaged eight species/1,083 cm^3 (identical to in mineral soil) and 938 seeds/m^2 (similar to the 1,003 seeds/m^2 in mineral soil). The native perennial forb *Viola cucullata* (marsh blue violet), a moderately specialized wetland species (coefficient of conservatism = 6), was the only species unique to the Oe + a horizon.

Seed bank densities in mineral soil among the 64 sites were correlated with variation in tree basal area and density, soil properties, and land use history including 1939 land use, year a site was acquired for incorporation into the preserve, and whether a site was under recent restoration through tree cutting or prescribed fire (Fig. 3). Seed density of nonnative species was maximized on open sites (<3 m^2/ha tree basal area) and on sites acquired before 1947 which were generally abandoned agricultural fields. Total average native seed density was maximized in mesic soil, particularly in unmanaged sites representing mesic forests and mesic sites of unmanaged pine plantations. Seed density of specialist native species (coefficient of conservatism 4–10) was maximized if the 1939 land use had been agriculture.

Discussion

Why Were Seed Banks Unusually High Quality?

The preponderance of restoration-target species—especially long-lived perennials—in seed banks was unusual, and reasons for this unique finding seem difficult to pinpoint. A potential hypothesis is that by being maintained by periodic fires and disturbances that remove trees, savanna-prairie landscapes inherently contain seed banks of restoration-target species because they are disturbance-dependent, favoring formation of seed banks (Thompson et al. 1998; Kiss et al. 2018). However, other studies in savannas-prairies in eastern North America (e.g. Laughlin 2003; Leicht-Young et al. 2009; Ralston & Cook 2013; Zylka et al. 2016) and in open habitats globally (e.g. Jacquemyn et al. 2011; Godefroid et al. 2018; Török et al. 2018) have concluded that seed banks have minimal utility for restoration and therefore do not support the hypothesis.

Another hypothesis could be that, in recent decades, the restoration activities of tree cutting to reduce woody plant encroachment and prescribed fire increased quality of seed banks in restored as well as in some unrestored habitats. This hypothesis might be at least partly supported. Neff et al. (2009) found that seed banks accumulated rapidly during restoration, increasing in size by an order of magnitude within 3 years of restoring a tidal wetland. In our study, restored oak savannas and managed plantations had seed banks at least twice as large as their unmanaged counterparts. Low-severity prescribed fires, such as those applied to savannas in our study, do not appear to deplete mineral soil seed banks based on collecting samples before and immediately after fires are extinguished (Schuler & Liechty 2008; Keyser et al. 2012). Tree cutting that produced low-density overstories was associated with large seed banks in our study, as restored oak woodlands with minimal cutting and appreciable tree canopy cover contained small seed banks similar to oak forests. Restoration activities creating open conditions could have increased seed banks through processes such as stimulating seed production or filtering species composition toward seed bank-forming species (Schelling & McCarthy 2007). It is possible that these restoration activities augmented seed banks even where restoration did not occur, such as in unmanaged pine plantations, by increasing seed availability at the landscape scale. The study area is fragmented with interspersed patches of habitat types (Schetter & Root 2011), and seed from restoration sites or remnant native habitats could have dispersed into plantations. In a fragmented landscape in Ontario, Canada, most seed of deciduous tree species dispersed <25 m into pine plantations from nearby deciduous forest fragments, but seed of some species (including *Quercus* spp.) dispersed 150 m (Hewitt & Kellman 2002). Further research on seed dispersal patterns and inputs and residence time in seed banks could provide insight for whether accumulation of restoration-target species resulted from long-ago or more recent inputs.

Comparisons with the few other studies globally that have recorded abundant restoration-target species in seed banks further suggest a perplexing lack of commonalities among studies. For instance, Davies et al. (2013) found that seed banks were rich in restoration-target species in fire-dependent but long unburned (20–70 years) *Eucalyptus* woodlands on an Australian island. In that study, areas with recent livestock grazing contained fewer restoration-target species in seed banks that responded to fire-related cues than did ungrazed areas (Davies et al. 2013). In contrast, in Estonia alvar grasslands and wet meadows dependent on large herbivores to curtail woody plant encroachment, sites with recent grazing contained seed banks richer in mature grassland species than those ungrazed for 50 years (Kalamees et al. 2012; Metsoja et al. 2014). The Estonia alvars were not intensively cleared for agriculture due to their thin soil, a situation differing from our study where much of the landscape had been cleared. In another example, Plassmann et al. (2009) reported that seed banks in the United Kingdom in coastal dunes, degraded by artificial stabilization of natural sand movement, contained numerous restoration-target

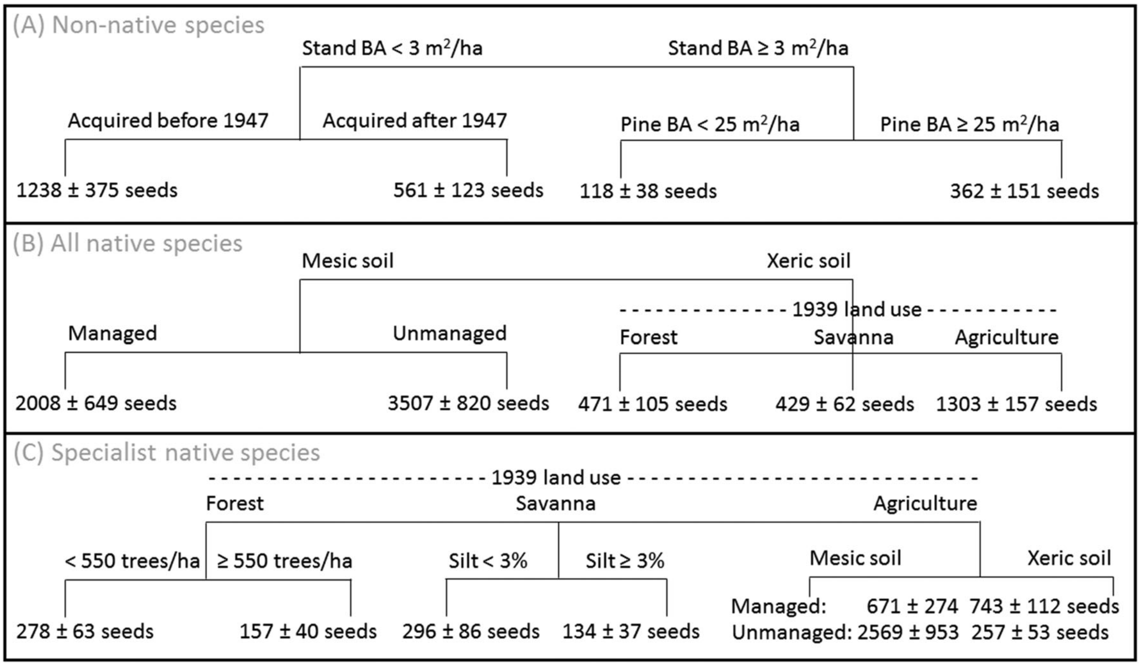

Figure 3. Regression tree models estimating seed bank density (mean ± 1 SEM for number of seeds in 0–5 cm mineral soil) as a function of land use, soil, and tree variables in the Oak Openings region, Ohio, U.S.A. Managed and unmanaged refers to whether sites received restoration treatments (prescribed burning and tree thinning to reduce woody plant encroachment), including pine plantation removal intended to reestablish native ecosystems. Acquisition date is when a site was acquired by Metroparks Toledo for inclusion in Oak Openings Preserve. BA stands for basal area. Tree density is for all stems ≥1 cm in diameter at 1.4 m. Cross-validated correlation coefficients for each model: (A) 0.33, (B) 0.52, and (C) 0.45.

species of former dune ecosystems. Fire was not a noted part of the development of the natural dune ecosystems, differing from the Davies et al. (2013) study in Australia and our study. Further research may help identify circumstances fostering seed banks capable of benefitting restoration and therefore exceptions to the generalization of limited seed bank utility to restoration.

Correlations With Land Use History

Severe anthropogenic disturbances, such as clearing and farming, normally reduce seed bank quality (Bekker et al. 1997). While pinpointing cause and effect (if any) between historical land use and seed bank composition was beyond the scope of our study, we can conclude that intensive agricultural activities and the establishment of plantations did not predispose contemporary seed banks to lack restoration-target species. In fact, many sites cultivated in 1939 had high-quality seed banks in 2018. There may be three possible explanations.

First, it is possible that agricultural activities did not negatively affect seed banks as much as it seems they could. Restoration-target species in our study were generally species of open-structured habitats and may have even benefitted from clearing, in comparison to continued forest maturation during fire exclusion through the 1900s (Haney et al. 2008). Savanna-prairie species could have maintained small populations on the edges of agricultural clearings. That situation would be similar to how contemporary railroad corridors and edges of cemeteries contain some of the only residual populations of savanna-prairie species in much of Midwestern North America where forest now comprises nearly all semi-natural habitat (Chapman & Brewer 2008). It is also possible that agricultural practices were of relatively low intensity on the sand farms in our study area and left uncultivated areas (e.g. sand dunes, low areas; Moseley 1928).

Second, historical land uses might only have indirectly related to contemporary seed banks by triggering a sequence of other events associated with later land uses and vegetation development which did affect seed banks (Falińska 1998). For example, all 24 pine plantation sites had been used for agricultural activities in 1939, and the agricultural use and concern for eroding soil on abandoned fields were precisely what partly influenced decisions to establish plantations to revegetate the fields. While contemporary plantation seed banks contained restoration-target species, they also contained among the most seeds of nonnative species. The sequence of land use events on plantation sites from historical agriculture, to tree planting, through tree cutting activities likely represented the most severe sequence of disturbances and the most opportunities for nonnative plant introduction among habitat types (Artigas & Boerner 1989). In another example, sites that were oak forest (which had small current seed banks) in 1939 had likely been forest for at least several decades prior and would remain so to the present day as these sites were acquired and protected in the preserve. The oak forests, along with plantation sites, could exemplify why year of land protection entered into seed bank models. Sites acquired early, by the late 1940s, were primarily old fields associated with abandonment of farms. In contrast, many sites acquired later were oak forests, which may have had small seed banks at that time or seed banks that became depleted over time. As the 1900s progressed, forests became less open and matured, a process expected to reduce seed banks (Falińska 1998).

A third possibility is that historical land use had little residual influence on contemporary seed banks, which instead were driven by recent conditions. The few available studies of seed bank accumulation after disturbance provide some support for this idea. After an agricultural field was abandoned in New Jersey, for example, seed banks accumulated rapidly, with species richness quadrupling within 6 years (Leck & Leck 1998). This suggests that even if past land uses had eliminated the seed bank, appreciable seed banks could have accumulated recently.

Variation in Potential Seed Bank Contributions Among Habitat Types

While seed banks overall were of high quality, potential contributions of seed banks to restoration varied among habitat types. Restored oak savannas had high-quality seed banks containing restoration-target species of predominately perennial graminoids, the annual and biennial forbs *Krigia virginica* and *Polygala polygama*, and at least low densities of perennial forbs. This diversity of restoration-target species is encouraging for the storage of savanna species during periods of woody plant encroachment unfavorable for savanna species aboveground (Matlack & Good 1990). Dense layers of tree saplings can develop within 4 years without fire in savannas followed quickly by contraction of savanna plant populations (Haney et al. 2008). Cycles of increasing and decreasing woody plant encroachment may have characterized historical savannas under variable fire regimes and commonly occurs in contemporary savanna restoration due to challenges with implementing frequent or high-severity burning (Ralston & Cook 2013). Restoration practices that sustain or increase existing high-quality seed banks might promote savanna resiliency, aided by further research on seed bank longevity to identify maximum fire-free periods savanna plants can reliably recover from via seed banks.

Seed banks in restored oak woodlands were small and further contained some wetland species unlikely capable of inhabiting vegetation in dry woodland sites. However, the woodland seed banks did contain some restoration-target species and had few nonnative species. The small size of oak woodland seed banks was most similar to that of oak forests, but seed banks in woodlands contained four state-rare species compared to none in oak forests.

Seed banks in restored mesic prairies contained some restoration-target species, such as the obligate wetland grass *Dichanthelium acuminatum* var. *lindheimeri* (Lindheimer panicgrass), and facultative wetland, moderately specialized native species, including *Carex swanii* (Swan's sedge), *Bulbostylis capillaris* (densetuft hairsedge), and *Dichanthelium clandestinum* (deertongue). Species largely restricted to wetlands were less frequent in our study than previously in seed banks of sandy wetlands in New Jersey (Vivian-Smith & Handel 1996). Mesic prairies in our study were on moist soil but without standing water, therefore intermediate between upland and aquatic habitats. This may account for the facultative status of most species.

Seed banks in oak forests were depauperate compared to other habitat types, but contained some species on the historical savanna and woodland list, and should not be liabilities to restoration because nonnatives were sparse (only 7% of total seeds). Our results of relatively small seed banks in oak forests were consistent with previous studies, such as in the central Appalachian Mountains in Virginia (Schiffman & Johnson 1992), the Arkansas Ozarks (Schuler & Liechty 2008), and the southern Appalachians in North Carolina (Keyser et al. 2012). Reasons for sparse oak forest seed banks are uncertain but may include few seed bank-forming species in extant vegetation, minimal disturbance in recent decades precluding replenishment of seed banks by disturbance-promoted species, low rates of seed production by understory plants under shaded conditions, or lack of viable seed retention in prevailing soil conditions. The most frequent native species we detected in oak forest seed banks included *Carex swanii*, *Rubus* spp., and *Phytolacca americana* (American pokeweed). *Carex swanii* and another seed bank sedge, *Carex pensylvanica* (Pennsylvania sedge), are two of the most abundant sedges in oak forest vegetation and likely were common in historical savannas and woodlands formerly occupying oak forest sites (Brewer & Vankat 2004). *Rubus* spp. and *P. americana* may form seed banks persisting for decades and, along with dispersal of their fruits by animals, could contribute to colonization in post-disturbance canopy gaps (Whitney 1986; Hyatt & Casper 2000).

Mesic forests contained large seed banks, seven times larger than oak forests, possibly because of copious seed production and soil high in organic matter retaining seed (Ma et al. 2017). Graminoids constituted at least 52% of seeds in all habitat types but were especially abundant (90% of seeds) in mesic forest seed banks. Major graminoids were the facultative wetland species *Carex swanii* and *Juncus tenuis* (poverty rush). Mesic forest seed banks also contained some moderately specialized, facultative wetland native forbs, including the annual *Hypericum majus* (large St. Johnswort) and the perennials *Boehmeria cylindrica* (smallspike false nettle) and *Ludwigia alternifolia* (seedbox). Seed densities of trees were also highest in this habitat, primarily of *Acer rubrum*, which can form seed banks persisting over 2 years (Hille Ris Lambers et al. 2005). Nonnative species did not dominate seed banks of any habitat type, but with only 0.7% of seeds, nonnatives were notably minimal in mesic forest seed banks. Current mesic forests were likely historically prairies before their structure was altered by cessation of fires and construction of drainage ditches. If restoration to prairies is desired, mesic forest seed banks are likely to supply primarily native graminoids (including those with affinities for wetlands), moderately specialized native forbs, the shrub *Rhus copallinum* (winged sumac), and canopy-gap generalists such as the annual forb *Erechtites hieraciifolius* (American burnweed) and the shrubs *Rubus* spp.

Managed pine plantation sites contained seed banks with a diverse mixture of restoration-target, ruderal native, and nonnative species. It is not clear whether the species dispersed in after plantations were removed or persisted in the soil through agricultural activities preceding plantation establishment, approximately 50 years of plantation occupancy, and tree cutting activities to remove the plantations. Nevertheless, the presence in seed banks of eight state-rare species along with additional restoration-target species suggests that propagules helpful for restoration can exist on sites of former intensive land use.

Although seed banks in unmanaged plantations were smaller than those in managed plantations, they did contain three state-rare species (*Krigia virginica*, *Polygala polygama*, and *Dichanthelium meridionale*) plus other specialized natives such as *Verbena hastata* (swamp verbena), *Viola sagittata* (arrowleaf violet), *Cyperus lupulinus* (slender nutsedge), *Carex swanii*, and *Carex tonsa* var. *rugosperma* (parachute sedge). As a result, plantation seed banks appear more useful to restoration in our study than previously in 40-year-old pine plantations in southern Ohio where seed banks contained few conservation-priority species (Artigas & Boerner 1989). If converting plantations to native habitats is desired, seed banks in existing plantations can likely supply a mixture of ruderal native (e.g. *Erechtites hieraciifolius* and *Rubus* spp.) and restoration-target species, with proportions of nonnative species similar to extant seed banks in restored oak savannas and mesic prairies. Disturbance of the O-horizon should not influence seed bank composition much because seed banks in O-horizons and mineral soil were similar.

Undetected Restoration-Target Species

While seed banks were unusually rich in restoration-target species, not all restoration-target species were detected in seed banks. Restoration-target species undetected in samples of the persistent seed bank could result from the species (1) not forming persistent seed banks, (2) being capable of forming persistent seed banks but being absent from a site, (3) being too infrequent for detection, or (4) having seed germination requirements unmet by the emergence method.

Compiling species detected in seed banks assayed using the emergence method in 29 previous studies in eastern North America helped evaluate the first and second possibilities. For the 40 species among the 100 on the Oak Openings historical list not detected in seed banks in our study or in the 29 previous studies, there is variable evidence for seed bank-forming capability. For example, *Ceanothus americanus* (New Jersey tea), undetected in seed banks in our study and the 29 previous studies, had 28% germination for freshly collected seed subjected to 10 weeks of cold stratification, simulating overwintering, and seed also germinated when exposed to gibberellic acid (Schramm & Johnson 1981). Our seed bank collections followed overwintering and also included applying gibberellic acid. In another example, *Tephrosia virginiana* (goat's-rue) was not detected in seed banks in our study or in the 29 earlier studies. A seed-burial experiment in *Pinus palustris* (longleaf pine) savannas in southern Georgia reported that *T. virginiana* seeds buried for 8 years retained 87% viability, suggesting potential for formation of long-lived seed banks (Kaeser & Kirkman 2012). *Lupinus perennis* (wild lupine) was another species not detected in seed banks but that comprised savanna vegetation (Abella et al. 2018). Freshly collected *L. perennis* seeds can become permeable and germinate via acid scarification, heating, or fire (Grigore & Tramer 1996). However, the species' large seeds (typically 20–30 mg) would not necessarily be predicted to be long-lived in soil (Halpern 2005).

Although the species-accumulation curves that we calculated for each habitat type began leveling off at our available sample size, they suggested that sampling additional sites (and probably more soil at sites) within the study area would result in accumulating more species. This would likely be especially true for the most infrequent species, supporting the third possibility that we failed to detect some restoration-target species that do form persistent but low-density seed banks. While collecting more soil would likely detect more species, sampling and assaying large soil volumes is a recognized challenge in seed bank research due to the soil disturbance, transport, and greenhouse space required (Vandvik et al. 2016).

We sought to partly overcome the fourth possibility—unmet germination requirements—by providing additional germination stimulants within the emergence method. Although in place of emergence using the seed extraction method can also fail to detect certain seeds, has challenges for determining viability and germinability similar to the emergence method (Chiquoine & Abella 2018), and previously detected fewer seeds than did emergence for a Midwestern prairie (Johnson & Anderson 1986), applying extraction to samples may help determine whether viable seeds of some species occurred in seed banks but failed to germinate.

Based on containing readily germinable seed of a diversity of restoration-target species, soil seed banks in our study represent a potentially unusually beneficial resource to restoration. Further research seeking to pinpoint reasons for the existence of these unusually high-quality seed banks may help identify the types of circumstances in which restorationists can consider employing soil seed banks to reestablish restoration-target species.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Composition of mineral soil (0–5 cm) seed banks in the Oak Openings region, northwestern Ohio, U.S.A.

Table S2. List of 100 species thought to be major species characterizing historical oak savannas, woodlands, and prairies of the Oak Openings region, northwestern Ohio, U.S.A.

Figure S1. Species-accumulation curves in seed banks (0–5 cm mineral soil) as a function of number of sites sampled (1,083 cm^3 of soil assayed per site) in the Oak Openings region, Ohio, U.S.A.

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Table S1. Composition of mineral soil (0-5 cm) seed banks in the Oak Openings region, northwestern Ohio, U.S.A. Seed banks are shown for four habitat types undergoing restoration (oak savanna, woodland, mesic prairie, and managed pine plantations) and three unmanaged habitat types (oak and mesic forests and unmanaged pine plantations). Seed bank measures include frequency (F, % of sites inhabited) and average seed bank density (S, seeds/m^2). Species status describes nativity and for native species, coefficients of conservatism (ranging from generalists at 0 to specialists at 10) with values in parentheses noting a state-rare species. One additional species, the native perennial forb *Viola cucullata* , not on this list was detected only in Oe+a horizon samples from unmanaged pine plantations.

		Oak savanna		Oak woodland		Mesic prairie		Oak forest		Mesic forest		Managed pine		Unmanaged pine	
Species	Status	F	S	F	S	F	S	F	S	F	S	F	S	F	S
Annual forb															
Ambrosia artemisiifolia	0											7	3		
Arabidopsis thaliana	Non-native											20	102		
Bidens frondosa	2											7	3		
Cardamine hirsuta	Non-native	5	5									33	133		
Chamaesyce maculata	0	32	19	14	7			13	12			20	22		
Erechtites hieraciifolius	2			14	7					33	46	7	3	44	36
Erigeron annuus	0	5	2												
Hedeoma hispida	(7)											7	3		
Hypericum gentianoides	3	5	2									7	3		
Hypericum majus	6									33	15	13	62	11	5
Krigia virginica	(8)	37	66									20	22	11	5
Mollugo verticillata	0	11	7									27	15	33	36
Polygonum hydropiper	Non-native							13	6						
Polygonum tenue	4	5	5												
Silene antirrhina	1	5	7			33	15					7	3		
Solanum ptycanthum	1	5	5									27	19		
Sonchus asper	Non-native	11	5					25	23			20	9	44	21
Triodanis perfoliata	2	5	29												
Veronica arvensis	Non-native	5	2			67	231					20	46	11	46
Annual graminoid															
Digitaria ischaemum	Non-native	21	37											22	10
Digitaria sanguinalis	Non-native	16	10												
Fimbristylis autumnalis	5											13	19		
Lipocarpha micrantha	(8)											7	3		
Setaria faberi	Non-native											7	3		
Setaria viridis	Non-native	16	10									7	3	11	5
Vulpia octoflora var. *octoflora*	4	5	2												
Biennial forb															
Alliaria petiolata	Non-native			14	7							20	25	11	15
Conyza canadensis	0	16	10	14	7	33	46					47	136		
Geranium carolinianum	3											13	6		
Lindernia dubia	2	5	2												
Nuttallanthus canadensis	4											20	77	11	5
Oenothera biennis	1											7	12		
Polygala polygama	(10)	16	12	29	26							7	3	11	10
Pseudognaphalium obtusifolium	2	37	41									73	167		
Senecio vulgaris	Non-native	16	10							33	15	13	9	11	5

Verbascum thapsus	Non-native	26	46			67	170					73	164	11	5
Short-lived perennial forb															
Cerastium fontanum ssp. *vulgare*	Non-native					33	15								
Hackelia virginiana	2	11	7	14	7									11	5
Lepidium virginicum	1	11	10									13	31		
Melilotus spp.	Non-native					33	15								
Oxalis corniculata	Non-native	16	22			67	62					53	52	22	10
Polygonum virginianum	3	5	2												
Rudbeckia hirta	1											7	3		
Stellaria media	Non-native											13	164	11	118
Stellaria media ssp. *pallida*	Non-native											7	9		
Verbena hastata	4	11	49									13	15	11	5
Viola sororia	1											7	9	11	21
Short-lived perennial graminoid															
Bulbostylis capillaris	3	5	5			33	231			33	15	33	151	11	5
Cyperus odoratus L	4											7	3		
Perennial forb															
Achillea millefolium	1	5	17			67	93					20	80		
Baptisia tinctoria	(6)	5	2												
Boehmeria cylindrica	4							13	6	33	15			11	5
Cirsium arvense	Non-native			14	7										
Circaea lutetiana	3			14	13										
Epilobium coloratum	1	5	2												
Euthamia graminifolia	2											7	3		
Fragaria virginiana	1							13	6			20	28	22	15
Galium triflorum	4													11	5
Helianthemum bicknellii	(9)	5	2	14	7										
Helianthemum canadense	(9)			29	13										
Liatris squarrosa	(8)	5	2			33	108					27	28		
Ludwigia alternifolia	3									33	93	7	19		
Monarda fistulosa	3											7	3		
Oxalis dillenii	0	5	7									13	12	11	5
Oxalis stricta	0					33	62					7	3	22	10
Phytolacca americana	1	5	2	14	7			25	46			13	12		
Pycnanthemum verticillatum var. *pilosum*	(5)	5	5									7	3		
Rorippa sylvestris	Non-native	5	2												
Rumex acetosella	Non-native	21	107									33	148		
Rumex obtusifolius	Non-native											7	3		
Solanum carolinense	0			14	13										
Solidago rugosa	2	16	17												
Taraxacum officinale	Non-native	26	15	14	7			25	12	33	15	7	3	33	36
Trifolium repens	Non-native											13	15		
Urtica dioica	Non-native	5	2												
Verbena urticifolia	3											13	9		
Viola lanceolata	(8)											7	19		
Viola sagittata	4													11	10

Perennial graminoid															
Agrostis hyemalis	3	11	63									7	9		
Agrostis perennans	4											7	3		
Agrostis scabra	3	16	17			33	15					20	19		
Andropogon gerardii	5											7	3		
Andropogon virginicus	3	5	5												
Aristida purpurascens	(7)	11	15			33	15								
Carex blanda	1							13	6						
Carex spp.		11	5	29	26			25	23			13	111		
Carex muehlenbergii	7	16	15												
Carex pensylvanica	3	5	2					13	6					11	10
Carex swanii	4	11	5	14	7	67	494	63	127	100	2886	40	90	22	98
Carex tonsa var. *rugosperma*	8	16	10	14	7							7	3	33	15
Cyperus esculentus	0	5	2												
Cyperus lupulinus	4	79	166	43	86	33	15	13	17			73	185	89	221
Cyperus strigosus L.	1											7	6		
Dichanthelium acuminatum var. *fasciculatum*	2	5	2			33	15			33	31	33	102	22	10
Dichanthelium acuminatum var. *lindheimeri*	9	5	2			33	15					33	74		
Dichanthelium boreale	6							13	6						
Dichanthelium clandestinum	2					67	108					27	154	11	5
Dichanthelium depauperatum	8											7	3		
Dichanthelium meridionale	(9)			14	7									11	5
Dichanthelium sabulorum var. *thinium*	6	26	27	43	40							7	3	11	10
Dichanthelium spretum	(9)											7	3		
Digitaria cognata	4	26	29									7	3		
Eragrostis spectabilis	2											7	3		
Festuca brevipila	Non-native	11	5												
Juncus spp.												13	6	11	98
Juncus marginatus	4									33	15	7	12		
Juncus tenuis	1	53	58	29	20	67	355	50	185	33	540	47	123	11	5
Leersia virginica	4	11	5	14	26										
Muhlenbergia mexicana	4											7	9		
Muhlenbergia schreberi	0	5	2									13	9		
Rhynchospora capitellata	7			14	26										
Schizachyrium scoparium	5	11	7			33	15					7	3		
Sporobolus cryptandrus	6	5	2												
Tridens flavus	1	5	5									7	6		
Vine															
Parthenocissus quinquefolia	2	5	2												
Vitis spp.												7	6		
Shrub															
Rhus copallinum	4	11	5							67	31	7	3		
Rhus glabra	2							13	6						
Rhus typhina	2							13	23						
Rubus idaeus	6											7	15	11	10
Rubus occidentalis	1	5	2												

Rubus spp.		11	7					63	52	33	46	47	56	33	36
Tree															
Acer rubrum	2									33	77			11	5
Cercis canadensis	3	5	2							33	31	13	9	11	10
Pinus resinosa	Non-native											7	3	11	5
Quercus velutina	7							13	6						

Table S2. List of 100 species thought to be major species characterizing historical oak savannas, woodlands, and prairies of the Oak Openings region, northwestern Ohio, U.S.A. The list was compiled from Brewer & Vankat (2004). The left seed bank column notes species detected in seed banks in our study (×). The right-side seed bank column describes whether species have formed persistent seed banks in any study, including ours and 29 previous seed bank studies in eastern North American savannas, woodlands, forests, and wetlands. The example reference column is by definition not intended to exhuastively enumerate all references for a species but rather to provide an example reference for each species.

Species	Seed bank in our study	Seed bank documented in any study	Example reference
Savanna			
Agalinis tenuifolia			
Apocynum cannabinum			
Asclepias tuberosa			
Baptisia tinctoria	×	Yes	Present study
Comandra umbellata		Yes	Leicht-Young et al. 2009
Comptonia peregrina		Yes	Dow & Schwintzer 1999
Conyza canadensis	×	Yes	Present study
Danthonia spicata		Yes	Laughlin 2003
Dichanthelium acuminatum var. *fasciculatum*	×	Yes	Present study
Dichanthelium scabriusculum		Yes	Artigas & Boerner 1989
Euphorbia corollata		Yes	Johnson & Anderson 1986
Koelaria macrantha		Yes	McNicoll & Augspurger 2010
Lechea leggettii		Yes	Matlack & Good 1990
Lespedeza capitata		Yes	Matthews et al. 2017
Lespedeza hirta		Yes	Schelling & McCarthy 2007
Liatris aspera			
Lithospermum canescens			
Lithospermum caroliniense			
Lupinus perennis			
Monarda fistulosa	×	Yes	Present study
Phlox pilosa		Yes	Johnson & Anderson 1986
Prunus pumila			
Rhus copallinum	×	Yes	Present study
Salix humilis		Yes*	Whittle et al. 1998
Schizachyrium scoparium	×	Yes	Present study
Smilax glauca			
Solidago nemoralis		Yes	Leck & Leck 1998
Tephrosia virginiana			
Viola pedata		Yes	Leicht-Young et al. 2009
Savanna, woodland			
Carex pensylvanica	×	Yes	Present study
Fragaria virginiana	×	Yes	Present study
Gaylussacia baccata		Yes	Matlack & Good 1990
Potentilla simplex			
Prunus serotina		Yes	Landenberger & McGraw 2004
Quercus coccinea			
Quercus ellipsoidalis			
Quercus velutina	×	Yes	Present study
Rosa carolina			
Rubus flagellaris	×	Yes	Present study
Symphyotrichum oolentangiense			
Vaccinium angustifolium		Yes	Hill & Vander Kloet 2005
Vaccinium pallidum		Yes	Hill & Vander Kloet 2005
Woodland			
Acer rubrum	×	Yes	Present study
Amelanchier arborea		Yes	Hanlon et al. 1998
Anemone quinquefolia			
Aralia nudicaulis			
Gaultheria procumbens			
Geranium maculatum		Yes	Schiffman & Johnson 1992
Hamamelis virginiana			
Helianthus divaricatus		Yes	Leicht-Young et al. 2009
Lysimachia quadrifolia		Yes	Keyser et al. 2012
Maianthemum racemosum			
Malus coronaria			

Polygonatum biflorum			
Prunus virginiana			
Quercus macrocarpa			
Sassafras albidum		Yes	Artigas & Boerner 1989
Viola sororia	×	Yes	Present study
Savanna, woodland, mesic prairie			
Quercus alba		Yes	Schuler & Liechty 2008
Quercus palustris			
Savanna, mesic prairie			
Andropogon gerardii	×	Yes	Present study
Ceanothus americanus			
Corylus americana			
Populus tremuloides			
Sorghastrum nutans		Yes	Johnson & Anderson 1986
Woodland, mesic prairie			
Aronia prunifolia			
Quercus bicolor			
Solidago rugosa	×	Yes	Present study
Mesic prairie			
Asclepias incarnata			
Calamagrostis canadensis		Yes	Keddy & Reznicek 1982
Calamagrostis inexpansa			
Carex scoparia		Yes	Leck & Leck 2005
Cephalanthus occidentalis		Yes	Middleton 2000
Cladium mariscoides		Yes	Stark et al. 2003
Cornus sericaea			
Epilobium coloratum	×	Yes	Present study
Equisetum arvense		Yes	LaDeau & Ellison 1999
Eupatorium perfoliatum		Yes	LaDeau & Ellison 1999
Eupatorium purpureum		Yes	Keyser et al. 2012
Euthamia graminifolia	×	Yes	Present study
Gentiana procera			
Hypericum kalmianum		Yes	Lundholm & Stark 2007
Iris versicolor			
Juncus canadensis		Yes	Keddy & Reznicek 1982
Juncus tenuis	×	Yes	Present study
Nyssa sylvatica		Yes	Hille Ris Lambers et al. 2005
Oxypolis rigidior			
Polygonum pensylvanicum		Yes	Neff et al. 2009
Populus deltoides		Yes	Siegley et al. 1988
Pycnanthemum virginianum			
Rubus hispidus		Yes	McGraw 1987
Salix discolor			
Sambucus canadensis		Yes	Landenberger & McGraw 2004
Scirpus validus		Yes	van der Valk & Davis 1978
Solidago ulmifolia			
Spiranthes cernua			
Thalictrum pubescens		Yes	Blood et al. 2010
Typha latifolia		Yes	Schelling & McCarthy 2007
Verbena hastata	×	Yes	Present study
Viola sagittata	×	Yes	Present study

*Difficult to distinguish to species as seedlings so kept at genus level.

Table S2 References

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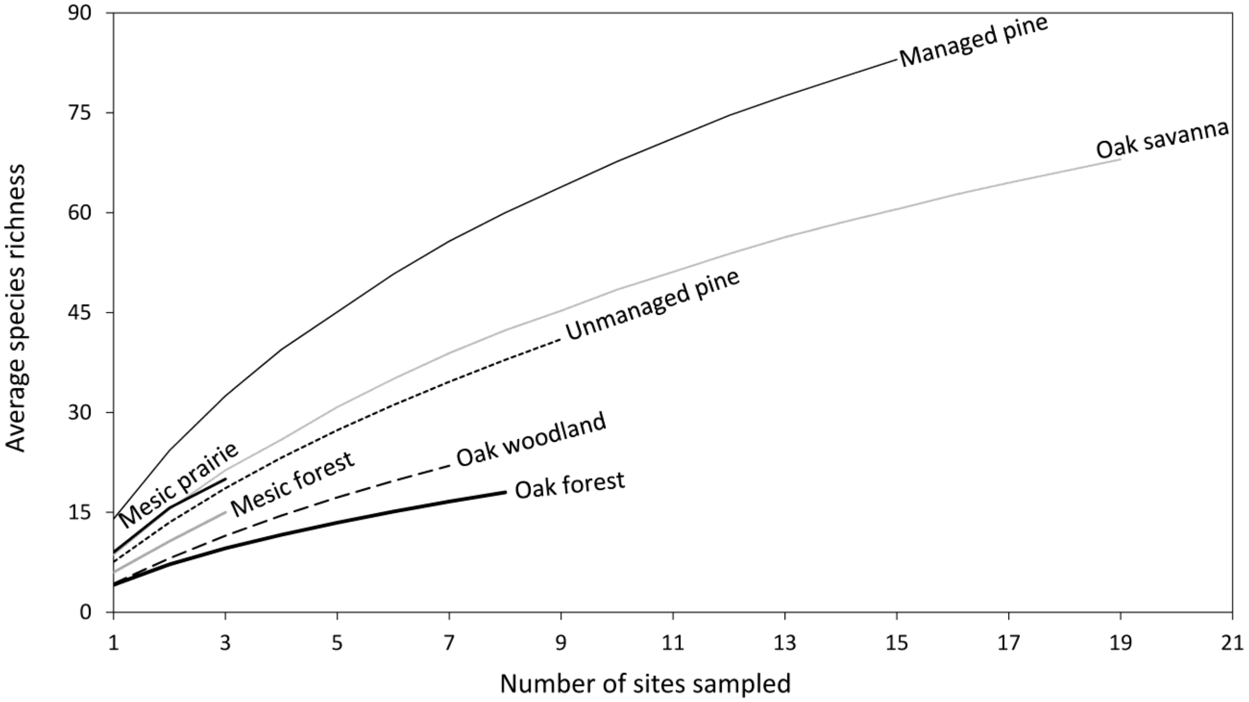

Figure S1. Species-accumulation curves in seed banks (0-5 cm mineral soil) as a function of number of sites sampled (1083 cm^3 of soil assayed per site) in the Oak Openings region, Ohio, U.S.A. Curves are shown for four habitat types undergoing restoration (oak savanna, woodland, mesic prairie, and managed pine plantations) and three unmanaged habitat types (oak and mesic forests and unmanaged pine plantations). Curves were computed in PC-ORD 7.07 by averaging species richness for unique combinations of sites for each subsample size (number of sites) using sampling without replacement. Curves end at the number of sites sampled within each habitat type, with the species richness value at that end point representing the observed number of species detected in a habitat type. Standard deviations as a measure of variability for species richness estimates at the starting point of one site sampled and near the end point of curves at the total number of sites sampled minus one (there is no variability around the richness estimate under sampling without replacement when all sites have been included in curves within each habitat type) are as follows:

Habitat type	1 site	Total minus 1 site
	Standard deviation	
Oak savanna	3.7	1.6
Oak woodland	1.7	1.8
Mesic prairie	3.0	1.2
Oak forest	2.2	1.7
Mesic forest	3.0	2.5
Managed pine	3.8	1.7
Unmanaged pine	2.5	2.0