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LETTER

Seed banks alter metacommunity diversity: The interactive effects of competition, dispersal and dormancy

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Abstract

Dispersal and dormancy are two common strategies allowing for species persistence and the maintenance of biodiversity in variable environments. However, theory and empirical tests of spatial diversity patterns tend to examine either mechanism in isolation. Here, we developed a stochastic, spatially explicit metacommunity model incorporating seed banks with varying germination and survival rates. We found that dormancy and dispersal had interactive, nonlinear effects on the maintenance and distribution of metacommunity diversity. Seed banks promoted local diversity when seed survival was high and maintained regional diversity through interactions with dispersal. The benefits of seed banks for regional diversity were largest when dispersal was high or intermediate, depending on whether local competition was equal or stabilising. Our study shows that classic predictions for how dispersal affects metacommunity diversity can be strongly influenced by dormancy. Together, these results emphasise the need to consider both temporal and spatial processes when predicting multi-scale patterns of diversity.

KEYWORDS
competition, dispersal, dormancy, metacommunity, seed bank

INTRODUCTION

The maintenance of biodiversity in ecological communities is shaped by the interplay of local processes including density-independent growth, intraspecific density dependence and interspecific interactions (Andrewartha & Birch, 1954; Mittelbach, 2012; Vellend, 2016). Species coexist locally if niche differences among species (e.g. in their optimal abiotic environments) are large enough to overcome differences in fitness (e.g. competitive abilities), allowing population recovery from rarity (Adler et al., 2007; Chesson, 2000b). Diversity can also be promoted via regional processes, including spatial abiotic heterogeneity, the effect of which is moderated by dispersal (Barabás et al., 2018; Chesson, 2012; Hart et al., 2017). Metacommunity theory has examined how dispersal and spatial heterogeneity interact with local processes to influence diversity (Holyoak et al., 2005; Leibold & Chase, 2018; Leibold et al., 2004; Logue et al., 2011; Thompson et al., 2020). Dispersal may limit arrival in suitable habitats, facilitate coexistence through environmental tracking, or be high enough to erode coexistence in the absence of local stabilising interactions (Mouquet & Loreau, 2003; Thompson et al., 2020). Thus, dispersal modulates the spatial scales at which biodiversity can be maintained by spatial coexistence mechanisms, including by fluctuation-dependent mechanisms (Amarasekare, 2003; Chesson, 2000a; Shoemaker & Melbourne, 2016; Snyder & Chesson, 2003, 2004).

While metacommunity theory tends to emphasise how spatial processes affect diversity over temporal processes (Holyoak et al., 2020), temporal environmental fluctuations also provide opportunities for species coexistence and increased diversity (Bernhardt et al., 2020). Our understanding of species coexistence in temporally variable environments has expanded alongside metacommunity theory over the last few decades (Abrams, 1984; Adler et al., 2006; Chesson, 1994, 2000b, 2018; Chesson & Case, 1986; Levine & Rees, 2004). For example, coexistence in fluctuating environments can be promoted by the temporal storage effect, which arises if species respond differently to fluctuations and have buffered population dynamics, such as can occur through dormant seed banks (Angert et al., 2009; Gremer & Venable, 2014; Pake & Venable, 1996; Warner & Chesson, 1985). Successful 'temporal dispersal' requires surviving in the seed bank long enough to germinate in a reproductively favourable environment (Buoro & Carlson, 2014); unsuccessful germination may be an additional reproductive sink analogous to failed colonisation in a new habitat.

Although spatial and temporal processes interactively shape population and community dynamics, the joint effects of dormancy and dispersal in a spatiotemporally varying environment have rarely been combined in a metacommunity context (Holt et al., 2005; Holyoak et al., 2020; Leibold & Norberg, 2004; Wisnoski et al., 2019). For single species, dispersal and dormancy have previously been shown to exhibit either substitutable or non-substitutable effects on population dynamics depending on the predictability of the environment in space and time (e.g. Buoro & Carlson, 2014; Cohen & Levin, 1987, 1991; Snyder, 2006; Venable & Brown, 1988). However in a community context, the strength of biotic interactions between species increases the complexity of potential metacommunity outcomes. This increased complexity arises because the relative costs and benefits to a species of remaining in a local environment, entering a seed bank or dispersing no longer depend exclusively on intraspecific and abiotic limitation, but instead also reflect interactions with other species. Whether or not species interactions are locally stable likely regulates the scale-dependent effects of dispersal and dormancy on metacommunity diversity.

Extending metacommunity theory to incorporate dormancy has lagged behind growing empirical evidence that dormancy affects metacommunities in numerous ways (Holyoak et al., 2020; Wisnoski et al., 2019). For example, the dormant resting stages of zooplankton that inhabit ephemeral rock pools allow them to contend with extreme hydrological variability and regulate community dynamics during inundation and drying phases (Brendonck et al., 2017). During wet periods, propagule buoyancy can influence inter-pool dispersal along hydrological vectors (e.g. flooding that connects nearby pools), while during dry periods, exposed egg banks of dormant propagules can be dispersed among pools by wind (Vanschoenwinkel et al., 2008). Studies from plant (Plue & Cousins, 2018) and microbial (Wisnoski et al., 2020) metacommunities also suggest that dormancy has non-additive effects on metacommunity diversity, motivating additional theoretical investigations that may inform strategies for restoration ecology or invasive species management (Box 1).

Here, we develop a mathematical model to explore the implications of dormant seed banks for metacommunity diversity (Figure 1). The distribution of biodiversity across spatial scales in metacommunities is an important measure of how diversity within (alpha-diversity) and among (beta-diversity) communities promote diversity at the regional scale (gamma-diversity). We examine the relative importance of dispersal, seed bank survival and germination on spatial diversity along with their interactive effects under two different competitive regimes. We evaluate how the strength of local competition, and thereby stable versus unstable local coexistence, modifies the effects of dormancy on metacommunity diversity. Our model demonstrates that seed bank dynamics can play an especially important role for the maintenance of regional diversity and modify classic predictions for the scaling of diversity (e.g. Leibold & Chase, 2018; Thompson et al., 2020).

MATERIALS AND METHODS

Metacommunity model with a seed bank

To address how dormancy and dispersal jointly affect spatial diversity patterns, we use a discrete time, spatially explicit model of species abundances in a metacommunity with local seed banks (Figure 1). The total population size of species i in patch x at time $t + 1$ is given by:

$$N_{ix}(t+1) = \underbrace{S_{ix}(t)}_{\text{Seed survival}} + \underbrace{P_{ix}(t)}_{\text{Seed production}} - \underbrace{E_{ix}(t)}_{\text{Emigration}} + \underbrace{I_{ix}(t)}_{\text{Immigration}}. \tag{1}$$

Seed production, $P_{ix}(t)$, is regulated by both density-independent abiotic constraints and density-dependent biotic interactions that determine realised growth, $R_{ix}(t)$, and depend on the number of germinated individuals of the population, $G_{ix}(t)$. Seed production in a given year and patch are generally modelled as follows:

$$P_{ix}(t) = \underbrace{G_{ix}(t)}_{\text{Germination}} \times \underbrace{R_{ix}(t).}_{\text{Aboveground growth}} \tag{2}$$

Furthermore, a proportion of seeds that undergo delayed germination may survive in the seed bank, $S_{ix}(t)$; the seeds generated by the aboveground community exhibit spatially explicit emigration, $E_{ix}(t)$ and immigration, $I_{ix}(t)$. Thus, for each species $S_{ix}(t)$ encompasses processes occurring in the ungerminated portion of the population, while $P_{ix}(t)$, $E_{ix}(t)$ and $I_{ix}(t)$ occur in the germinated portion of the population.

Local seed bank dynamics

Within a local metacommunity patch, each species' total seed population, $N_{ix}(t)$, is separated into a germinating fraction, $G_{ix}(t)$, and a non-germinating fraction,

Box 1 Empirical applications of metacommunities with seed banks

Beyond strengthening our theoretical understanding of the processes that maintain biodiversity across spatial scales, integrating seed banks into metacommunity ecology has wide-ranging empirical applications. Applied ecology has been at the forefront in considering seed bank effects on diversity and community composition. In turn, seed bank theory has contributed to recent advances in biological control (Rees & Hill, 2001; Strydom et al., 2017), restoration ecology (Bakker et al., 1996; Kiss et al., 2018; Ma et al., 2019), agriculture (Buhler et al., 1997; Menalled et al., 2001; Ryan et al., 2010) and invasive species management (Gioria & Pyšek, 2016, 2017; Strydom et al., 2017). Despite the importance of seed germination and survival in applied contexts, theory for the joint effects of dormancy and dispersal on cross-scale diversity patterns is less developed, but presents numerous exciting opportunities for future empirical research.

Empirical research on spatially structured seed banks has uncovered a range of patterns and insights. First, seed banks provide ‘ecological memory’ that moderates the effectiveness of biological control strategies and restoration at the landscape scale. This occurs because germination of viable seeds can re-establish populations, especially when coupled with high dispersal at large spatial scales (Bakker et al., 1996). For example, in the Tibetan Plateau, subalpine meadows that had been used for farming for 30 years were left abandoned, allowing up to 20 years of natural regeneration (Ma et al., 2019). Even with 30 years of farming, the persistent seed bank remained nearly unchanged, preserving the composition of the pre-disturbance subalpine community. As a result of the long-term persistence of the pre-disturbance community in the seed bank, the aboveground community exhibited high resilience, allowing for the natural recovery of the community to the pre-disturbance state after agriculture was abandoned (Ma et al., 2019). However, the seed bank can also preserve a memory of spatial dynamics, such as dispersal limitation or priority effects due to different colonisation histories among restoration sites. This may classically manifest as unexplained variation in restoration success, similar to spatial differences in seed bank dynamics observed in other agricultural systems (e.g. Mahaut et al., 2018). The long-term ‘ecological memory’ in persistent seed banks, combined with the capacity for rapid spatial spread via dispersal, suggests that the spatial configuration of aboveground and belowground diversity may be important for promoting successful restorations, either via natural regeneration or through the addition of seed mixtures.

Second, it is common to find differences in diversity or species composition between the seed bank and the aboveground community (Hopfensperger, 2007; Vandvik et al., 2016), which suggests the potential for historical belowground contingencies (depending on disturbance history, order of germination, or seed bank composition) that could lead to spatial variation in restoration success or control efficacy. For example, a review of experimental and field studies of seed banks found that, in ecosystems such as wetlands, with a disturbance regime shaped by frequent disturbance-recolonisation dynamics, persistent seed banks may be able to promote natural recovery of the aboveground community (Kiss et al., 2018). However, ecosystems that lack a frequent history of disturbance, or in communities that contain species with transient seed banks, active measures may be needed for successful restoration, such as direct seed addition (Kiss et al., 2018). In locations that suffer from a lack of diversity, alternative strategies may focus on spatial processes for restoration success. For example, restored sites may benefit from diversity spillover effects of wind-dispersed species from nearby remnant patches that maintain high diversity (Sperry et al., 2019). Sufficiently high rates of spatial dispersal may also be necessary to supplement temporal seed bank dynamics for the maintenance of some specialist species (Plue & Cousins, 2018). Thus, restoration planners should carefully consider the combined effects of spatial dispersal and germination from the seed bank, helping to ensure that restored populations are capable of establishing in intended habitats and tracking favourable environments through both time and space.

Third, efforts to curb the spatial spread of invasive species may also need to combat large seed banks dominated by the invasive. For example, in the South African fynbos biome, a biodiversity hotspot, invasion by several Australian *Acacia* species has threatened the rich native biodiversity and efforts to combat their spread have been costly. *Acacia*'s ability to form large seed banks is a major contributing factor to their successful spread (Richardson & Kluge, 2008). Metacommunity models that examine the species traits common to invaders may be crucial for predicting how species spread in a spatial community context and which measures might be effective for controlling their spread. Empirical investigations into the joint spatial and temporal processes that promote or hinder invasive spread may be especially important to reduce the social and economic burdens of invasive species.

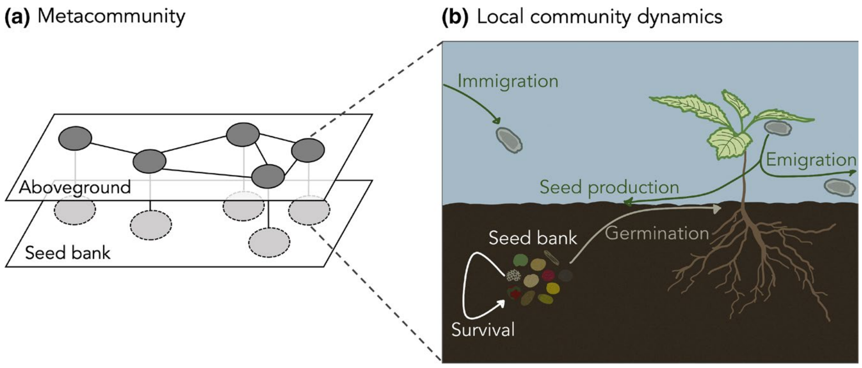

FIGURE 1 Overview of the metacommunity model. (a) Local aboveground communities (dark grey) are uniformly distributed at random across the landscape. In the model, we simulated 100 patches (shown here as grey ovals). For simplicity, lines connecting local communities indicate strong routes of dispersal within the metacommunity (all patches are potentially connected in the model, but nearby patches are more likely to exchange individuals via dispersal). Patches are also connected to their local seed banks (light grey) through the processes of seed survival and germination. (b) Local community dynamics are governed by aboveground seed production, seed bank survival and seed germination, and immigration and emigration with other patches in the metacommunity

$N_{ix}(t) - G_{ix}(t)$, such as occurs in an annual plant community (Levine & HilleRisLambers, 2009). To reflect the stochastic nature of germination and survival in natural systems, we model these processes as arising from a binomial distribution. The aboveground, germinating fraction of the community is described as:

$$G_{ix}(t) \sim \text{Binomial}(n = N_{ix}(t), p = g) \tag{3}$$

where $N_{ix}(t)$ is the total population size of species i in patch x at time t, and g is the probability of germination. Because we model an annual plant community, we then compute the non-germinating fraction, $N_{ix}(t) - G_{ix}(t)$, which survives with probability s in the seed bank and is modelled as follows:

$$S_{ix}(t) \sim \text{Binomial}(n = N_{ix}(t) - G_{ix}(t), p = s). \tag{4}$$

Aboveground growth

We determine realised aboveground growth ($R_{ix}(t)$, that is, the per capita production of new seeds) for species i in patch x, taking into account density-dependent and density-independent limits on population growth of the germinated fraction of the population. We use the classic Beverton-Holt model (Beverton & Holt, 1957) due to its parallel use in both spatial and temporal community ecology theory (Hallett et al., 2019; Levine & HilleRisLambers, 2009; Shoemaker & Melbourne, 2016; Thompson et al., 2020):

$$R_{ix}(t) = \frac{\overbrace{r_{ix}(t)}^{\text{Density-independent growth}}}{1 + \underbrace{\sum_{j=1}^{S} \alpha_{ij} G_{jx}(t)}_{\text{Density-dependent effects}}}, \tag{5}$$

where α_{ij} is the competition coefficient describing the density-dependent effects of species j on species i. Note that this summation includes the density-dependent effects of both interspecific ($i \neq j$) and intraspecific ($i = j$) competition. We further incorporate density-independent abiotic conditions that affect population growth, r_{ix}, through a Gaussian function describing species i's niche optimum (z_i) and niche breath (σ_i) in relation to the environmental conditions in patch x

$$r_{ix}(t) = r_{i,\max} \exp^{-\left(\frac{z_i - \text{env}_x(t)}{2\sigma_i}\right)^2}, \tag{6}$$

such that species i's density-independent growth rate r_{ix} in patch x is reduced from the maximum, $r_{i,\max}$.

To incorporate demographic stochasticity in seed production (Eq. 2), we model population size using a Poisson distribution ($\text{Poisson}\left(\max\left\{G_{ix}(t)R_{ix}(t), 0\right\}\right)$), providing integer values for each population or zero if the change in population size leads to local extinction. We incorporate stochasticity throughout our model due to its importance on both population and community dynamics, especially for small population sizes (Lande, 1993; Shoemaker, Sullivan, et al., 2020).

Dispersal

We model the number of emigrants leaving patch x, $E_{ix}(t)$, with a binomial distribution

$$E_{ix}(t) \sim \text{Binomial}(n = G_{ix}(t), p = d), \tag{7}$$

where d is the probability of dispersal. We assume dispersal occurs from the germinated portion of the community, $G_{ix}(t)$. The emigrating fraction of species i in a metacommunity with M patches is given by $\sum_{x=1}^{M} E_{ix}(t)$. From this pool of emigrants, immigration success in each patch is proportionally determined following a negative exponential dispersal kernel with geographic distance between patches

$$I_{ix}(t) = \frac{\sum_{y\neq x}^{M} E_{iy}(t)^{-L_i\delta_x}}{\sum_{x=1}^{M} E_{ix}(t)}, \tag{8}$$

where L_i determines the steepness at which dispersal success decays with geographic distance (δ_x) between patches x and y. The number of immigrants of species i to patch x is proportional to the fraction of the emigrant pool that did not originate in patch x, $\sum_{y\neq x}^{M} E_{iy}(t)$, weighted by distance from the focal patch ($-L_i\delta_x$), relative to the total size of the emigrant pool for species i, $\sum_{x=1}^{M} E_{ix}(t)$.

Simulations

To investigate (1) the relative importance of germination versus survival on diversity dynamics, (2) how dispersal regulates the effects of germination vs. survival, and (3) how local competition modifies metacommunity dynamics with a seed bank, we ran 20,000 total simulations of our metacommunity model across a wide range of parameter space, as described below.

Abiotic conditions

To ensure our results are not contingent upon a given landscape and environmental structure, for each metacommunity simulation, we generated a different landscape structure (i.e. patch connectivity) and environmental conditions. Each metacommunity consisted of 100 patches randomly distributed across a 100×100 spatial grid, drawn from a uniform distribution and rounded to the nearest integer. Spatio-temporal environmental variation was generated anew for each simulation with the 'env_generate()' function in the R code provided by Thompson et al. (2020) to accompany the revised metacommunity framework that our work extends. To briefly overview, we generated stochastic environmental conditions for each patch in the metacommunity and only scenarios with sufficient spatial heterogeneity (i.e. initial environmental differences in the environmental variable greater than 0.6) were kept for simulating metacommunity dynamics. This step ensured that temporal environmental trajectories were spatially autocorrelated, yet sufficiently spatially decoupled across the landscape to support metacommunity dynamics.

Density-independent abiotic response

To incorporate density-independent growth rates that depend on the environment, species were assigned niche optima (z_i) evenly distributed in the range [0,1], with equal niche breadth ($\sigma_i = 0.5$) among species. Species growth rates under the given environmental conditions in each patch decreased following the Gaussian function defined in Eq. 6, such that greater mismatches between species traits and environmental conditions resulted in lower realised density-independent growth rates, $r_{ix}(t)$.

Density-dependence and local coexistence

Density-dependence was incorporated via intra- (α_{ii}) and interspecific (α_{ij}) competition coefficients in the Beverton-Holt growth component of the model (Eq. 5). Intraspecific competition was always set to $\alpha_{ii} = 1$. We explored two different scenarios to evaluate the implications of local competitive dynamics versus dispersal and dormancy. In *equal intra- and inter-specific competition* ($\alpha_{ii} = \alpha_{ij}$), species coexistence arises from differential responses to abiotic conditions along with dispersal and/or dormancy, as the lack of differences in intra- versus interspecific competition cannot promote coexistence. Alternatively, for *stable competition* ($\alpha_{ii} > \alpha_{ij}$), species can coexist locally in communities due to competitive differences; these processes operate in unison with spatial and temporal coexistence mechanisms arising from dispersal and dormancy. To generate the species interaction matrices, values in the off-diagonal (α_{ij}) were set to 1 for the 'equal intra- and interspecific competition' scenario, and were drawn from a uniform distribution in the range $[0, 1]$ for the 'stable competition' scenario. The interaction matrix was rescaled by a factor of 0.05 to allow for larger population sizes (Thompson et al., 2020).

Dispersal and dormancy

We simulated our above metacommunity model across a range of parameter values to examine the effect of seed bank germination, survival and dispersal rates on diversity dynamics. We simulated 10 germination rates, evenly spaced from 10% germination to 100% germination (i.e. no seed bank) per year (i.e. $g = [0.1, \cdots, 1]$). We also simulated across two survival rates in the seed bank: high survival per year ($s = 0.99$), and an intermediate/risky strategy with approximately half the survival rate ($s = 0.5$). Last, we simulated across 50 dispersal rates, evenly distributed in logarithmic space ($d = [10^{-5}, \cdots, 1]$), ranging from extremely low dispersal (i.e. no metacommunity connectivity; dynamics depend on local processes only) to a well-mixed system with no dispersal limitation between patches (i.e. every individual leaves the patch every year when $d = 1$).

We ran 10,000 simulations each for equal and stabilising competition coefficients, yielding 10 replicate simulations for each combination of dispersal, germination and survival rates. We generated a new landscape configuration and new species interaction matrix for each of the 10 replicate simulations.

Initialisation

Each simulation was initialised with 40 species present above ground in each metacommunity patch ($N_{ix} = 1$). Ten additional colonisation events, each consisting of 400 (40 species × 100 patches) independent draws from a Poisson distribution ($\lambda = 0.5$), occurred during the first 100 time steps ($t = 10, 20, \cdots, 100$) to combat stochastic extinction during the early, low-abundance phases of the transitory 'burn-in' period (Thompson et al., 2020). We analysed extant diversity at the end of 2800 time steps (years).

Analysis

To quantify changes in aboveground biodiversity across spatial scales, we calculated local (alpha), among-patch (beta) and metacommunity (gamma) diversity for each simulation following a multiplicative partitioning framework:

$$\text{gamma} = \text{mean(alpha)} \times \text{beta} \tag{9}$$

Differences in alpha-, beta- and gamma-diversity from replicate simulations illustrate expected variation for a set of dispersal, seed bank survival and germination rates given demographic and environmental stochasticity as well as variation in landscape configuration and competition interactions. To assess the overall relationship between dispersal and diversity at different scales, we visualised trends with generalised additive models computed across all simulations for each parameter set using the ggplot2 R package (Wickham, 2016).

To quantify the additive, nonlinear, and interactive effects of dispersal and dormancy on diversity across scales, we performed a sensitivity analysis. We randomly sampled parameter space for species' germination, survival and dispersal rates. Germination and survival were sampled from a uniform distribution in the range $[0, 1]$. Dispersal rates were computed as 10^w, where $w \sim \text{Uniform}(min = -5, max = 0)$. We simulated 20 different landscape configurations and environmental trajectories for metacommunities of 40 species and 100 patches, as above. To quantify the effects of different parameters on diversity, we simulated 250 different parameter combinations for a given landscape/environmental context for both equal and stabilising competition scenarios. Then, we quantified the sensitivity of alpha-, beta- and gamma-diversity to changes in germination, survival, and dispersal, by performing multiple regression analysis across 10,000 simulations. Predictors were re-scaled with a mean of zero and standard deviation of 1 so that regression coefficients corresponded to effect sizes. Dispersal was normalised on a logarithmic, rather than linear, scale due to the wide variation of dispersal rates across orders of magnitude. We included quadratic terms in the regression to quantify the nonlinear responses of diversity to changes in parameter values, and we included interactions among dispersal, germination, and survival to quantify the non-independence of these processes. Code to reproduce all analyses is available at https://doi.org/10.5281/zenodo.5207007.

RESULTS

Seed banks strongly influenced classic patterns for how local, regional and beta diversity scales with increasing dispersal rate. The diversity-dispersal relationships arising from combined dispersal and seed bank dynamics often deviated widely from patterns for communities without seed banks under both equal (Figure 2) and stabilising competition (Figure 3). A sensitivity analysis revealed strong nonlinear effects of dispersal, germination and seed survival on diversity across spatial scales, emphasising that seed bank dynamics can have effects comparable to dispersal on metacommunity diversity dynamics (Figure 4). Furthermore, interactive effects between spatial and temporal processes strongly impacted diversity, especially patterns in alpha and gamma diversity.

Diversity under equal intra- and inter-specific competition

To understand how seed bank dynamics can modify patterns of diversity in the absence of local stabilising mechanisms, we first analysed the scenario where intra- and interspecific competition were equal. In the absence of dormancy, equal competition classically results in a unimodal relationship between dispersal and alpha-diversity, and declining relationships with beta- and gamma-diversity (yellow curves in the first column, $g = 1$, in Figure 2). However, reduced rates of seed germination dramatically altered this classic dispersal-diversity relationship. Deviations from the classic relationship were strongest for alpha and gamma diversity when seed bank survival was high but germination rates were low. With high seed survival (right column, Figure 2), reduced germination shifted the traditional hump-shaped relationship, such that increased dormancy increased alpha-diversity at higher dispersal rates ($d > 10^{-2}$). For example, at high dispersal rates, when the probability of germination was 0.10, local communities had roughly 4 times higher diversity than scenarios without a seed bank.

Seed banks minimised the erosion of gamma-diversity classically observed with increased dispersal,

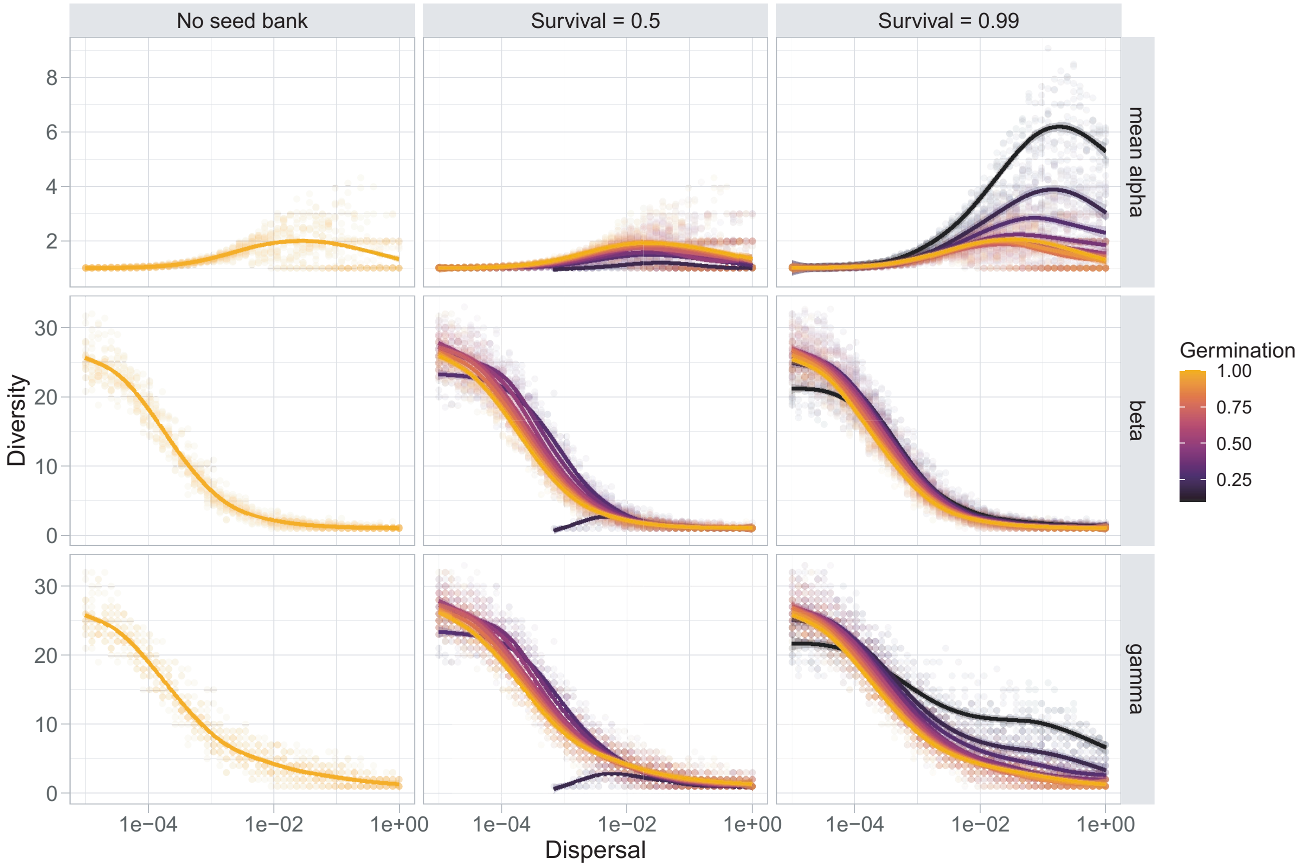

FIGURE 2 Dispersal-diversity relationships across a range of germination (colours) and survival rates (columns) with equal competition. In these scenarios, germination plays a key role in shifting the relationships between diversity at different scales and dispersal rates, while survival rate influences the scale-dependent effects of germination and places constraints on the feasible combinations of dispersal and germination that maintain metacommunity diversity. When survival is lower, higher germination rates and higher dispersal rates are necessary to overcome the losses due to reduced survival rates. When survival is high, low germination can reduce gamma-diversity at low dispersal rates, but maintain higher gamma-diversity at higher dispersal rates. Germination is 100% in the left column and ranges from 10% (black) to 100% (orange), increasing by 10% increments, in the middle and right columns

maintaining nearly 10 times higher gamma diversity at high dispersal rates and low germination rates (right column, Figure 2). However, at low rates of dispersal ($d < 10^{-4}$), reduced germination decreased gamma-diversity relative to scenarios without a seed bank. This effect arose as reduced germination had a slightly negative effect on beta-diversity with low dispersal rates (e.g. $d < 10^{-4}$, Figure 2). With high survival ($s = 0.99$), alpha- and gamma-diversity were more sensitive to small changes in germination rates at the low end of the germination gradient (e.g. from $g = 0.1$ to $g = 0.2$) than in the intermediate-to-high range (e.g. from $g = 0.7$ to $g = 0.8$) (Figure 2).

Lower survival ($s = 0.5$) exhibited patterns more similar to classic results, especially for moderate to high germination rates. Specifically, reduced survival in the seed bank increased the germination rates necessary for maintaining metacommunity diversity (middle column, Figure 2). At the lowest germination rates, lower seed bank survival also introduced a minimum dispersal threshold ($d \approx 10^{-3}$) necessary for any species to persist ($g < 0.4$; Figure S1). When germination was higher than the minimum threshold for species persistence, yet lower than complete germination, seed banks maintained higher beta- and gamma-diversity across much of the dispersal gradient ($d < 10^{-2}$). Thus, low germination rates were no longer as beneficial for the maintenance of diversity, regardless of spatial scale, as they were when seed bank survival was high.

Nonlinear responses of diversity to germination, survival, and dispersal were also seen in the sensitivity analysis (Figure 4). Increased germination initially had positive effects on alpha-, beta-, and gamma-diversity (because some germination was necessary for species to persist). However, as germination became too high, the seed bank was eroded and diversity was lost at local and regional scales. Similarly, we found a positive quadratic effect of the survival rate on alpha and gamma diversity, suggesting that as survival increased, higher diversity was maintained in local communities and at the metacommunity scale. Dispersal had a hump-shaped effect on alpha-diversity and an erosive effect on beta- and gamma-diversity (Figures 2 and 4). Interactive effects between dispersal and seed bank dynamics were evident

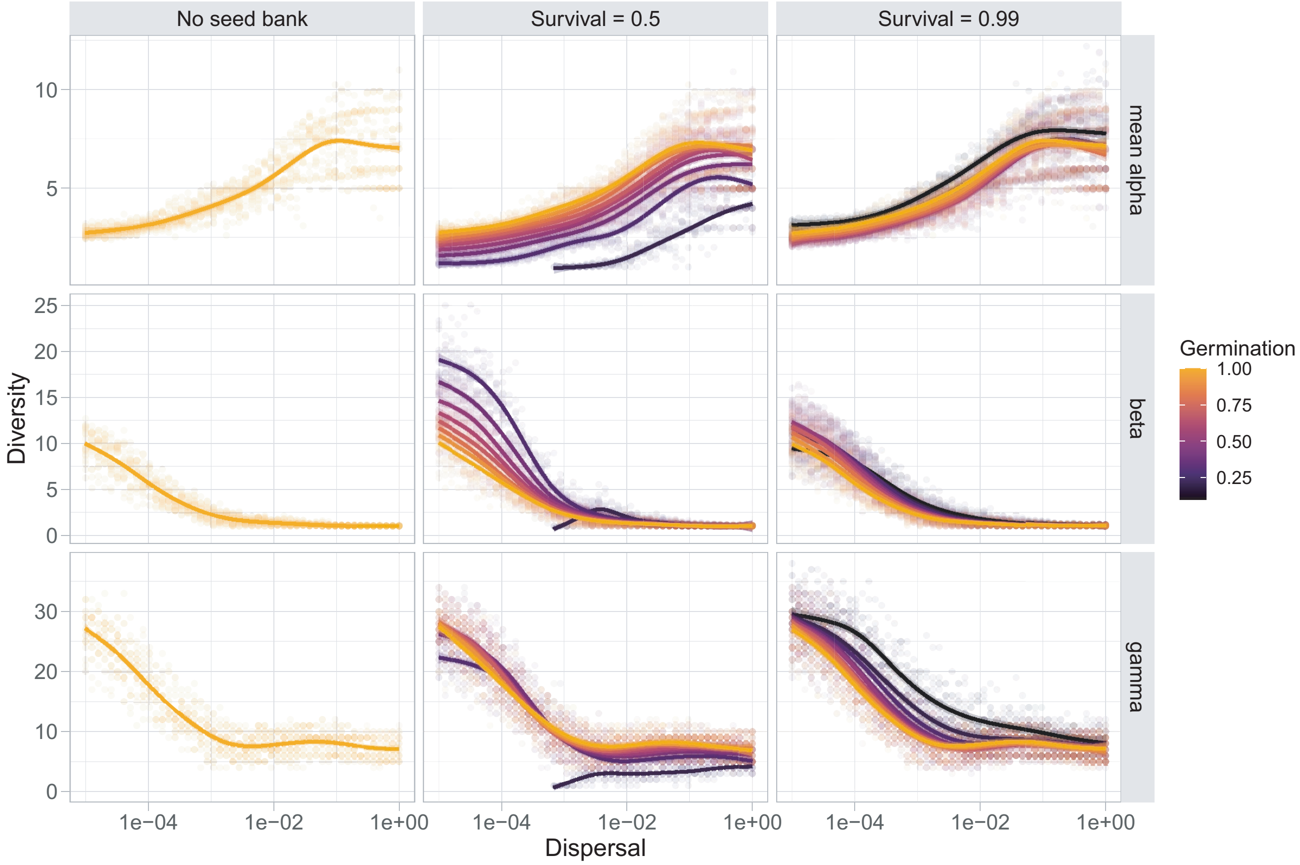

FIGURE 3 Dispersal-diversity relationships across a range of germination (colours) and survival rates (columns) with stabilising competition. In this scenario, survival in the seed bank is again a key mechanism that regulates the effects of germination at different scales. When survival is low, reduced germination has a negative effect on local diversity by limiting the growth of potentially coexisting species across all dispersal rates. However, intermediate germination rates maintain high beta-diversity when dispersal is lower. When survival is high, low germination rates maintain alpha-diversity at all dispersal rates and promote beta-diversity at intermediate dispersal. Consequently, low germination rates maintain high gamma-diversity at all dispersal rates, but especially at low-to-intermediate rates of dispersal. Germination is 100% in the left column and ranges from 10% (black) to 100% (orange), increasing by 10% increments, in the middle and right columns

(Figure 4). When dispersal was high, increased germination reduced gamma-diversity (dispersal:germination term) while increased survival promoted alpha-diversity (dispersal:survival term). Additionally, germination also had negative effects on alpha-diversity at high dispersal via interactions with both seed survival and dispersal (dispersal:germination:survival term).

Diversity with stabilising local competition

Natural communities often exhibit niche differentiation that stabilises coexistence (Adler et al., 2018). Local stable competitive interactions created stronger seed bank effects for moderate survival rates—especially for beta diversity—than under equal competition (Figure 3, Figure S2). In contrast to simulations without seed banks, dormancy promoted gamma-diversity at all dispersal levels when seed survival was high, and had strikingly large positive effects on beta-diversity when survival was lower and dispersal was limiting (Figure 3).

When seed bank survival was high ($s = 0.99$, right column of Figure 3), mean alpha-diversity was a generally increasing function of dispersal. This positive dispersal-diversity relationship arose because all species could potentially coexist locally due to stronger intraspecific than interspecific competition. Thus, increasing dispersal allowed species to reach all patches where positive growth was possible given abiotic conditions. This trend is evident in the sensitivity analysis, where the linear and nonlinear effects of dispersal were positive when coexistence was stabilising (compared to the opposing effects in the equal competition scenario; Figure 4). Across all dispersal rates, germination had relatively minimal effects on beta-diversity compared to dynamics without a seed bank. The consequence of reduced germination for diversity maintenance was strong at the regional scale (Figure 3, bottom-right panel), where low germination maintained higher gamma-diversity in the metacommunity across the entire dispersal gradient. The increase in diversity relative to conditions lacking a seed bank was largest at low-to-intermediate dispersal rates.

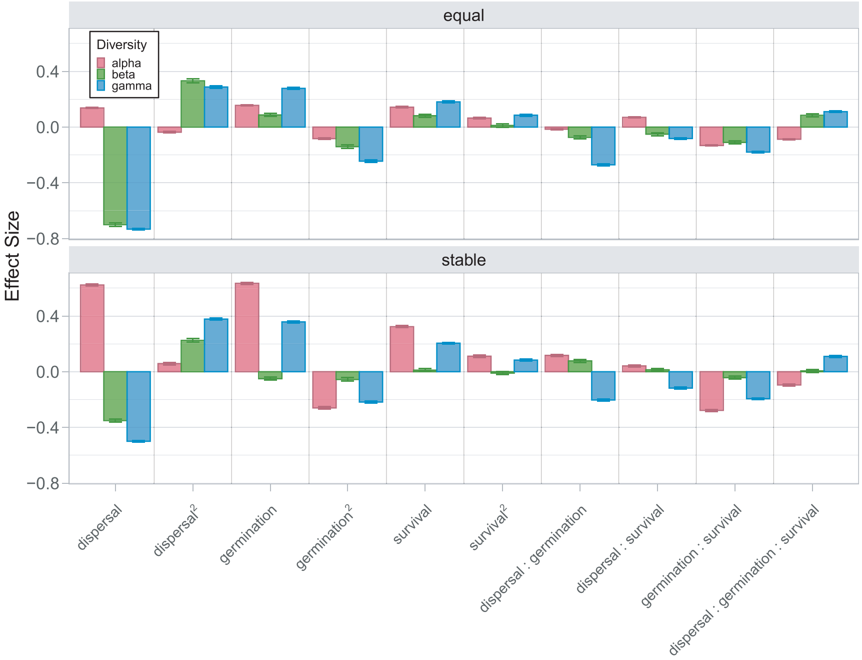

FIGURE 4 Sensitivity analysis quantifying the effects of dispersal, germination, survival, and their interactions on biodiversity across scales (alpha, beta and gamma). Note dispersal effects are quantified on a log scale, matching the previous figures. We detect strong linear, nonlinear (quadratic) and interactive effects on diversity. We observed strong hump-shaped effects of germination on alpha- and gamma-diversity (positive linear and negative quadratic effects), and positive effects of survival on diversity. In addition to these nonlinear effects, we also detected important interactions between dispersal and seed bank processes that have scale-dependent effects on diversity

When seed bank survival was lower, we observed qualitatively different effects of seed banks on metacommunity diversity (middle column, Figure 3). Reduced germination had consistently negative effects on mean alpha-diversity across the entire dispersal gradient. The lower the germination rate, the higher the rate of dispersal necessary to maintain diversity (Figure S2). Germination had an opposite effect on beta-diversity, where lower germination rates ($g = 0.3$) maximised beta diversity for low to moderate dispersal. This created relatively stable effects on gamma-diversity across germination rates, as long as germination was above a minimum threshold ($g \geq 0.2$).

The sensitivity analysis revealed that germination and survival tended to have stronger linear and nonlinear effects on alpha-diversity when competition was stabilising than when it was equal (Figure 4). The positive effects of germination on alpha- and gamma-diversity in this case occurred because reduced germination decreased alpha-diversity when species could stably coexist and survival in the seed bank was not guaranteed (Figure 3). Because stable coexistence was possible, there was a strong positive effect of survival on alpha- and gamma-diversity. The analysis again revealed scale-dependent interactions between seed bank processes and dispersal. For example, as dispersal increased, higher germination (dispersal:germination term) and survival (dispersal:survival term) rates reduced gamma-diversity, but gamma-diversity benefited from a positive interaction between dispersal, germination, and survival (Figure 4).

DISCUSSION

While seed banks are common across ecosystems and taxonomic groups from plants to microbes, they are rarely considered in a spatially explicit, metacommunity context. Here we show that dormant seed banks affect classic patterns of diversity in metacommunities via interactions among germination, survival, and dispersal. Seed banks are important drivers of community diversity patterns, regardless of local competitive dynamics. Under equal competition, high survival in the seed bank dramatically enhances alpha- and gamma-diversity and fundamentally changes dispersal-diversity expectations, especially at high dispersal rates. Under stabilising competition, seed banks promote gamma-diversity when survival is high, and beta-diversity when seed survival and dispersal are lower. Diversity in the metacommunity is driven by the interplay of seed bank and dispersal dynamics, with strong nonlinear interactive effects.

When do seed banks matter for metacommunity dynamics?

While our simulations spanned a broad range of parameter space, specific combinations of seed bank and dispersal processes generated larger biodiversity responses than others (Figures 2 and 3). Our results, therefore, can inform when and under what scenarios it is important to jointly consider seed bank and dispersal dynamics for metacommunity diversity.

For example, under equal competition, seed banks promoted alpha- and gamma-diversity when survival and dispersal were high. This region of parameter space may be well aligned with microbial systems, where dormancy is often common and dispersal rates are relatively high (Hanson et al., 2012; Lennon et al., 2021; Lennon & Jones, 2011; Louca, 2021). Many microorganisms have evolved traits that substantially enhance their longevity (e.g. spores) well beyond the typical generation time of an actively growing cell (Lever et al., 2015; Moger-Reischer & Lennon, 2019; Shoemaker et al., 2021). Their small body size combined with improved survival rates when dormant can jointly contribute to the high dispersal capabilities inferred for microorganisms in nature (Mestre & Höfer, 2021). Consistent with our models, dormant seed banks could help explain the maintenance of extraordinarily high microbial biodiversity at local and regional scales, but low spatial beta-diversity often detected in microbial communities (Lennon et al., 2021; Locey et al., 2020; Nemergut et al., 2013; Wisnoski et al., 2019).

In modelled communities with local stabilising competition, seed banks enhanced beta-diversity, especially when dispersal and survival were low (Figure 3). Stabilising competition is often detected in plant communities (Adler et al., 2018), suggesting our local stabilisation model may provide insight into the roles of seed banks for spatial diversity patterns. For example, terrestrial plant communities tend to exhibit high beta-diversity relative to other systems (Graco-Roza et al., 2021), matching model predictions for low to moderate dispersal and moderate survival in the seed bank. Plant systems have been shown to experience dispersal limitation (Myers & Harms, 2009; Tilman, 1997), and separately beta-diversity has been shown to be high for organisms with seed dispersal (Soininen et al., 2007). In plant systems, burial (Bonis & Lepart, 1994), damage (Long et al., 2015), and consumption (Horst & Venable, 2018; Janzen, 1971), likely yield low to moderate seed survival (Saatkamp et al., 2009). With lower survival in the seed bank, our model highlights that germination must be high enough to overcome loss from the seed bank, but that seed banks may play an important role in maintaining the high metacommunity beta-diversity that is often observed empirically.

Seed banks alter the spatial scaling of biodiversity

Theoretical and empirical research has demonstrated the benefits of seed banks for local diversity maintenance under temporally varying environments, such as through temporal buffering and the storage effect (Chesson, 2000b; Saatkamp et al., 2014; Sears & Chesson, 2007). However, our work indicates that local processes alone may provide an incomplete picture of how seed bank dynamics influence aboveground diversity. Rather, dispersal plays a critical role in regulating the ability of seed banks to maintain locally diverse communities. In parallel, local seed banks modify the impact of dispersal for regional diversity patterns.

Notably, germination, survival, and dispersal interactively shape alpha-diversity (Figures 2–4). Previous models lacking dormancy have shown that high rates of dispersal in the absence of local coexistence can reduce alpha-diversity by favouring regional rather than local competitors (Mouquet & Loreau, 2003). Our results indicate that temporal mechanisms associated with seed banks can counteract diversity losses under high rates of dispersal, specifically when competition is equal and seed bank survival is high (Figure 2). High seed bank survival provides more opportunities for successful germination. The lower the germination rate, the more slowly the stockpile of dormant diversity in the seed bank is depleted (Thompson, 1987; Thompson & Grime, 1979). Consistent with the temporal storage effect (Chesson, 2000a), losses due to poorly timed germination (e.g. during unfavourable environments) are minimised at lower germination rates, while recruitment benefits gained from successful germination replenish the population in the seed bank. Low germination may also reduce aboveground competition and the number of dispersers, further buffering against dispersal-induced diversity loss.

Regional diversity depends strongly on the interplay of dispersal and germination, with germination thresholds for local and regional persistence appearing at low dispersal rates. However, once dispersal is high enough to facilitate environmental tracking across space and time, lower germination rates may be able to maintain gamma-diversity (Figures 2 and 4). Because dormant seeds do not disperse in our model, low germination rates may also be key for preserving reproductive gains in favourable environments, by potentially contributing to fitness-density covariance that promotes regional coexistence (Snyder & Chesson, 2003, 2004). For example, a simplified model with dispersal of dormant propagules found that, while dormancy increased maximum alpha-diversity, it also made alpha-, beta- and gamma-diversity more sensitive to the homogenising effects of dispersal (Wisnoski et al., 2019), consistent with the view that spatial structure of the seed bank contributes to regional-scale coexistence.

When remaining in the seed bank is risky (i.e. survival = 0.5), our model suggests reduced germination decreases aboveground alpha-diversity but increases beta-diversity. While dispersal had negative effects on beta-diversity both with and without a seed bank (Figure 4), the presence of a seed bank led to an approximately 1.5- (Figure 2) to 2-fold (Figure 3) increase in beta-diversity when dispersal was in the intermediate range. The preservation of beta-diversity has important implications for the regional maintenance of biodiversity and ecosystem multi-functionality by combating spatial homogenisation in community structure (Hautier et al., 2018; Socolar et al., 2016; Wang et al., 2021). This aligns with previous models that suggest dormancy may promote metapopulation persistence when dispersal is limiting and local environments vary through time (Cohen & Levin, 1991; Snyder, 2006; Venable & Brown, 1988). Our work extends these ideas into a metacommunity context to show that seed banks can increase beta-diversity at the cost of mean local richness, especially for low to moderate dispersal rates with local stabilisation (Figures 2 and 3). However, at higher rates of dispersal, homogenisation sets in regardless of seed bank dynamics. As a result, gamma-diversity can be lower with a seed bank than without one because of the negative interaction between spatial homogenisation and ‘temporal dispersal’ limitation. In the extreme case, with low survival, low germination and low dispersal, the metacommunity cannot persist.

Future directions

Our aim in this study was to develop an understanding of how seed bank dynamics interact with local scale processes (e.g. competition) and regional processes (e.g. dispersal) to affect patterns of diversity. Building on previous reviews and syntheses (Buoro & Carlson, 2014; Holyoak et al., 2020; Wisnoski et al., 2019), our model demonstrates a range of intuitive yet novel predictions regarding the implications of temporal coexistence mechanisms in a spatial, metacommunity context. While here we focus on the implications of seed banks and dispersal for biodiversity, our results identify a need to characterise the spatiotemporal coexistence mechanisms that emerge from the interactions between seed dormancy and dispersal. While temporal and spatial fluctuation-dependent mechanisms of coexistence have been examined independently (e.g. Ellner et al., 2019; Hallett et al., 2019; Shoemaker, Barner, et al., 2020), their interactive effects are rarely considered. However, the nonlinear interactive effects of dispersal and seed bank processes on diversity in our model (Figure 4) suggest that spatiotemporal variability can further generate stabilising mechanisms of species coexistence and presents an exciting direction for future research integrating metacommunity and coexistence theory.

Future studies could also examine the possible effects of trait covariation when incorporating species interactions—thereby extending the competition-colonisation trade-off to include seed banks. We performed a preliminary investigation to address this question, which ultimately demonstrated that interspecific trait covariation can either promote or erode diversity depending on the specific trait combinations present in the metacommunity (see Supplemental Materials, Figures S4–S6). The effects of trait covariation on coexistence are likely to depend closely on how species traits align with environmental variation in space and time. A finer scale examination of these traits may reveal favourable strategies or trait syndromes that allow species to coexist in spatiotemporally variable landscapes (Buoro & Carlson, 2014; Rubio de Casas et al., 2015; Wisnoski et al., 2019). In addition, we encourage experimental manipulations testing the theoretical results we present here. For example, researchers could manipulate rates of dispersal in plant communities by physically moving seeds among plots, and seed survival by collecting, marking, and removing seeds from seed banks. Similar experiments could also be done in other systems where germination cues may be directly manipulated, such as in zooplankton communities where light cycles associated with seasonality can trigger germination (Stross, 1966).

CONCLUSIONS

Seed bank dormancy has played a key role in empirical studies of diversity and community turnover, including in restoration settings (Box 1; Saatkamp et al., 2014). Simultaneously, dormancy is classically invoked as a key mechanism that promotes coexistence through the temporal storage effect (Adler et al., 2006; Angert et al., 2009; Warner & Chesson, 1985). Yet, despite this history, its incorporation into metacommunity models has lagged, making it difficult to predict how dispersal and dormancy will alter diversity at local and regional scales. Here, we demonstrate that seed survival and germination interact with dispersal to affect diversity across spatial scales. For example, the combination of high dispersal and low germination can overcome the classic hump-shaped relationship between dispersal and alpha-diversity predicted in many metacommunity models, but only when seed bank survival is high and competitive interactions are equal. The implications of dormant seed banks scale nonlinearly with space to influence regional patterns of biodiversity. Integrating empirical and theoretical insights is a key step towards understanding the spatial scales at which dormant seed banks promote or erode diversity in nature.

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AUTHORSHIP

NIW and LGS conceived the study, developed the approach, and wrote the paper. NIW wrote the first draft of the manuscript, implemented the model and analysis, and made the figures.

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DATA AVAILABILITY STATEMENT

All code and data are archived on Zenodo and the DOI is included in the manuscript (DOI: https://doi.org/10.5281/zenodo.5207007).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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