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Franck Jabot, Julien Pottier. Macroecology of seed banks: The role of biogeography, environmental stochasticity and sampling. *Global Ecology and Biogeography*, 2017, 26 (11), pp.1247-1257. 10.1111/geb.12631 . hal-01635210

HAL Id: hal-01635210

<https://hal.science/hal-01635210>

Submitted on 14 Nov 2017

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Macroecology of seed banks: The role of biogeography, environmental stochasticity and sampling

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Editor: Brian Enquist

Abstract

Aim: The study of seed banks has been mainly conducted at local scales, thereby hampering our general understanding of the assembly processes of these biodiversity reservoirs. Here, we aim to document worldwide macroecological patterns of seed bank diversity and of their similarity with aboveground vegetation. Our second aim is to investigate the likely drivers of these macroecological patterns and to lay the foundation of a metacommunity theory of seed banks.

Location: Worldwide.

Time period: 1989–2005.

Major taxa studied: Plants.

Methods: We compiled a worldwide dataset of 130 seed banks located in grasslands. We assessed the likely drivers of seed bank diversity and similarity with aboveground vegetation, using structural equation modelling. We then developed a time-averaged neutral model of coupled seed bank–vegetation (S–V) dynamics that includes the effect of environmental stochasticity, and we compared its predictions with empirical findings.

Results: We found evidence for two weak latitudinal gradients in seed bank diversity and S–V similarity, with larger species richness and smaller similarity closer to the tropics. We then showed that seed bank richness and S–V similarity are correlated with the following four distinct drivers: local environmental variability, plant regional diversity, seed bank density and sampling area. Finally, we showed that the predictions of the time-averaged neutral model are remarkably in accord with empirical observations.

Main conclusions: Our results lay the foundations of a metacommunity theory for seed banks. They challenge the standard view that seed banks are principally structured by environmental variability, by highlighting the additional key roles of dispersal and stochastic sampling on seed bank diversity patterns.

KEYWORDS

demographic stochasticity, environmental stochasticity, grassland, latitudinal gradient, metacommunity, regional pool, sampling intensity, time-averaged neutral model

1 | INTRODUCTION

Seed banks have attracted the interest of many vegetation ecologists over the years (Baskin & Baskin, 2001). Numerous studies have documented seed bank diversity, density and their similarity with standing vegetation, in order to understand how seed banks may influence the

regeneration and dynamics of plant communities (Bossuyt & Honnay, 2008; Hopfensperger, 2007), with implications in ecological restoration and conservation (Bakker & Berendse, 1999). In addition, theories on the impacts of seed banks on local community dynamics have been developed and tested (e.g., Bonis, Lepart, & Grillas, 1995; Pake & Venable, 1996; Warner & Chesson, 1985). Seed bank dynamics result

from the balance between seed rain, germination and persistence. Seed bank patterns have therefore been linked to local disturbance regime (Henderson, Petersen, & Redak, 1988), successional ages (Bekker, Verweij, Bakker, & Fresco, 2000), seed longevity (Thompson, Bakker, & Bekker, 1997) and historical factors, such as past land use (Bossuyt & Hermy, 2001), and compared between different types of habitats (Hopfensperger, 2007).

In contrast, the influences of large-scale biogeographical factors and sampling issues have been poorly investigated (Vandvik, Klanderud, Meineri, Måren, & Töpper, 2015). Immigrating propagules from surrounding areas contribute to the seed rain. Quantifying the importance of such immigration events is a long-standing research challenge, but accumulating evidence suggests that long-distance dispersal events do influence local assembly processes (Jones & Muller-Landau 2008; Jordano 2017). Consequently, the diversity of local seed banks should be positively influenced by the diversity of the regional flora. Besides, denser seed banks should tend to harbour larger diversity owing to a sampling effect. Such sampling effects are generally overlooked when comparing different seed bank samples, so that a rigorous framework to assess seed bank diversity patterns is needed (Vandvik et al., 2015). Such a framework would enable the assessment of the respective influences of local, regional and sampling processes on seed bank assembly.

From a more theoretical perspective, there has been no attempt to mobilize existing macroecological theories to shed light on seed bank patterns. Among such theories, neutral theory has received much attention from ecologists over the past 15 years (Hubbell, 2001; Rosindell, Hubbell, & Etienne, 2011). It attempts to understand community assembly, dynamics and evolution based on the combination of stochastic processes and limited dispersal. By providing a clear quantitative framework, neutral theory has reinvigorated many previously loose visions of ecosystems that were based on the unique lens of deterministic processes without rigorous justifications (e.g., Jabot & Chave, 2011; McGill, Etienne, & Gray, 2007; Plotkin et al., 2000). In this vein, neutral predictions have been compared with various community patterns, including species-abundance distributions (Volkov, Banavar, Hubbell, & Maritan, 2003), species spatial turnover (Condit, Pitman, & Leigh, 2002), community phylogenetic structure (Jabot & Chave, 2009) and community dynamics (Kalyuzhny, Kadmon, & Shnerb, 2015).

The neutral-based vision of community assembly and dynamics has not yet penetrated the field of seed bank ecology. This is not surprising, because this field has been structured around the two building ideas of species-specific responses to environmental variations (Facelli, Chesson, & Barnes, 2005; Grubb, 1977; Warner & Chesson, 1985) and of bet-hedging (Slatkin, 1974; Venable, 2007), which may appear at first sight to be fundamentally opposed to neutral assumptions. The recent development of time-averaged neutral models (Jabot & Lohier, 2016; Kalyuzhny et al., 2015) opens a new opportunity to build a neutral-based quantitative assessment of seed ecological patterns. Indeed, time-averaged neutral models relax the strong assumption of constant competitive equivalence among individuals and replace it by a weaker assumption of time-averaged competitive equivalence among individuals (Kalyuzhny et al., 2015). In such models, different individuals

may have different demographic rates at each time step, but their life-time average expectancy in demographic rates is constant. This relaxed form of equivalence among individuals enables the construction of a simple and operational quantitative framework to analyse seed bank community patterns, without ignoring well-established biological evidence surrounding plant regeneration niches (Grubb, 1977).

In strictly neutral models, although all individuals of a community have the same probability of realizing demographic events such as birth, death, reproduction and dispersal, there is some level of inter-individual variability in the effective realizations of these demographic events, owing to chance. This inter-individual variability is generally called demographic stochasticity, and it can lead to some level of unevenness in species abundances by ecological drift (Hubbell, 2001). Chance variability may also occur during the random sampling of a community, an idea already present in the literature on rarefaction (Heck, van Belle, & Simberloff, 1975) and null models (Gotelli & Graves, 1996). Its consequences on seed bank patterns have recently been stressed (Vandvik et al., 2015). On top of demographic and sampling variabilities, time-averaged neutral models consider that there is some level of inter-individual variability in their probability of realizing demographic events at each time step, although they all have the same time-averaged demographic probabilities. This last source of inter-individual variability is generally called environmental stochasticity in the literature (Ives, Dennis, Cottingham, & Carpenter, 2003; Lande, Engen, & Saether, 2003). It is an operational way to model the temporal environmental variability encountered by plant individuals and seed banks without explicitly modelling environmental variables (Chesson, 2000). Consequently, standard and time-averaged neutral models should enable the assessment of whether empirically observed seed bank macroecological patterns may be explained by the combined action of demographic and sampling stochasticity (strict neutrality), whether the inclusion of environmental stochasticity is necessary (time-averaged neutrality) or whether additional deterministic processes need to be invoked to explain seed ecological patterns.

In this study, we aim at (a) assessing the respective roles of local, regional and sampling processes in the assembly of seed banks and at (b) comparing observed seed bank patterns with predictions of strictly neutral and time-averaged neutral models. We focus on two macroecological patterns of (a) seed bank diversity and (b) seed bank-vegetation (S-V) similarity. These two seed bank characteristics are among the most commonly studied and are therefore amenable to generalization. We first compile empirical evidence for seed bank macroecological patterns from published studies and assess, using structural equation modelling, the influence of the following four drivers: local environmental variability, plant regional diversity, seed bank density and sampling area. The first driver relates to the standard vision of a seed bank assembly controlled by environmental variability; the second driver relates to a metacommunity view of seed bank assembly; and the last two drivers relate to stochastic and sampling processes. Sampling area can be seen here as a nuisance variable rather than a genuine ecological driver. It was included to control for the influence of variable sampling protocols among empirical studies. We then develop a

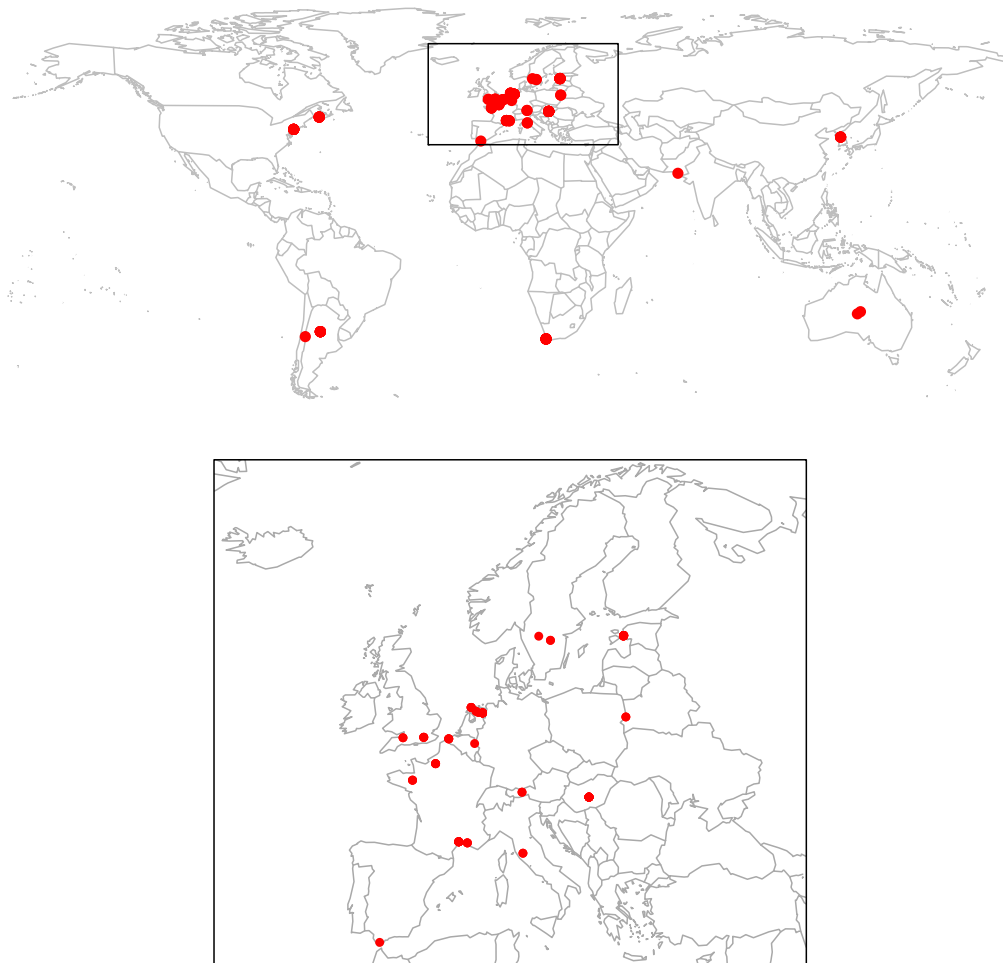


FIGURE 1 Location of field studies documenting seed bank–vegetation similarities in grasslands

time-averaged neutral model with a seed bank to establish neutral predictions regarding these patterns. Comparing neutral predictions with empirical evidence enables us to assess the likely drivers of seed bank macroecological patterns.

2 | METHODS

2.1 | Data compilation

We compiled the grassland studies mentioned in the meta-analysis of Hopfensperger (2007) and retained those that had information on seed bank density. We restricted our compilation to grassland studies, because forests and wetlands present additional complexities, such as mast seeding and flooding events. This led to a number of 29 studies, altogether reporting 130 values of seed bank diversity, density and similarity with standing vegetation, and sampling a wide array of grassland types (Figure 1). In these empirical studies, plants and seeds were sampled locally at spatial scales ranging from 0.4 to 7,500 m² for plants and from 0.02 to 1.41 m² for seeds (Supporting Information Appendix S1). Seed bank–vegetation similarity was calculated following the Sorensen formulation for presence–absence data as in most empirical studies, and sampling area was estimated as the total area sampled for

seed bank assessment. Two types of covariables were further compiled: (a) the regional pool richness retrieved from the global map of vascular plants (Ellis, Antill, & Kreft, 2012; Kreft & Jetz, 2007), and (b) climatic variability calculated as the coefficient of variation of the annual number of wet days in the period 1901–2009 that was retrieved from the CRU v3.10 database (Harris, Jones, Osborn, & Lister, 2014). Preliminary analyses indeed revealed that this environmental predictor was the most correlated with seed bank patterns, among other climatic parameters available from this database. The full dataset, including seed bank patterns and covariables, is provided in Supporting Information Appendix S2.

2.2 | Structural equation modelling

We used structural equation modelling to assess the correlations between seed bank patterns (richness and S-V similarity) and the four drivers: seed bank density, sampling area, plant regional pool richness and climatic variability (coefficient of variation of the number of wet days). In the structural equation model, the indirect effects of the drivers on S-V similarity through their effect on seed bank richness were included, because seed bank richness enters into the computation of S-V similarity. Model fit was performed with the R package lavaan (Rosseel, 2012).

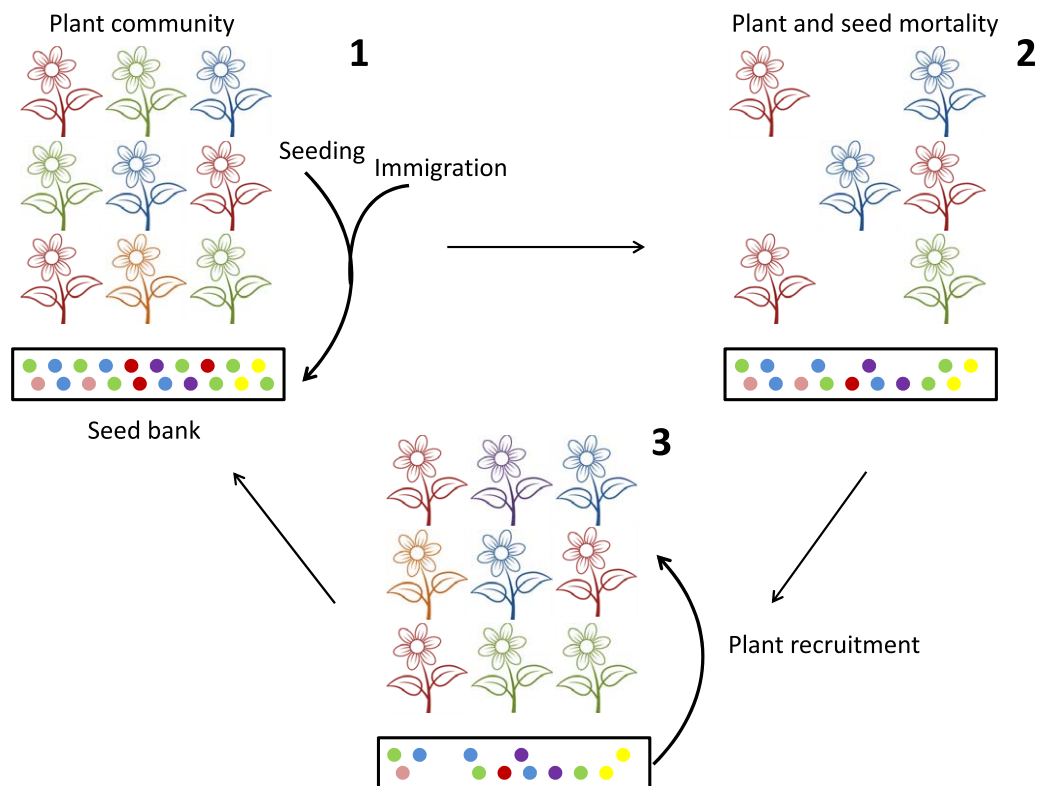


FIGURE 2 Model description

2.3 | A time-averaged neutral model with a seed bank

We modelled the dynamics of a plant community of J individuals and of its associated seed bank (Figure 2). At each annual time step t , each plant individual of species i produces a number $p \times f_i(t)$ of seeds, where p is the community-average seed production per individual and $f_i(t)$ represents the fertility of species i at time step t relative to this community average. Values of $f_i(t)$ are independently drawn from a lognormal distribution with mean 1 and variance V . When this variance V is null, the model is neutral in the sense that all plant individuals are exchangeable at each time step, irrespective of the species to which they belong. When the variance V is strictly positive, plant individuals are no longer exchangeable at a given time step, although they have the same temporally averaged fertility p . This is why this type of model is called a time-averaged neutral model (Kalyuzhny et al., 2015). The seeds produced by the plant community contribute to the seed bank, and i additional seeds are also added by immigration from the surrounding regional pool containing S_{pool} species. The species-abundance distribution in this regional pool is modelled with a log-series distribution with parameter θ (Hubbell, 2001). This parameter controls the evenness of species abundances in the regional pool. A constant proportion d_{seed} of the seeds dies between two successive time steps, irrespective of the species to which they belong. Likewise, each plant individual has a fixed probability d_{plant} of dying at each time step, after having produced its seeds. At the following time step, the $J_{\text{dead}}(t)$ dead plant individuals are replaced by the same number of new individuals randomly recruited from the surviving seeds of the seed bank. Individuals of the different species are drawn with a multinomial distribution, with

species-specific probabilities proportional to $s_i(t)$, where $s_i(t)$ is the number of seeds of species i in the seed bank at time step t .

A pseudocode of the model is presented in Supporting Information Appendix S1, and a commented R code to simulate this model of community dynamics was archived on Github at the following address: https://github.com/franckjabot/TNTB_seedbank/tree/v1.

2.4 | Simulation protocol

We simulated communities of $J_p = 100$ plant individuals. The plant community was initialized by a random draw of J_p individuals from the regional pool, and the community dynamics was launched for 3,000 time steps, so that a dynamic equilibrium had been reached. Simulations were continued during 2,000 additional time steps, and we recorded various community statistics every 10 time steps, leading to 200 sets of community statistics for each parameter combination. These 200 sets of community statistics were then summarized using averaged values. Community statistics examined were the total species richness S_{seed} and S_{plant} of the seed bank and of the plant community, respectively, the seed bank size N_{seed} , the sampled species richness of the seed bank by simulating a sampling of 0.01% (S_1), 0.1% (S_2) and 1% (S_3) of the seed bank, respectively, and the associated Sorensen similarity (Sor_1 , Sor_2 and Sor_3) between the sampled seed bank and the plant community. Sorensen similarity was computed as $Sor_{1,2,3} = 2 \times C_{1,2,3} / (S_{1,2,3} + S_{\text{plant}})$, where $C_{1,2,3}$ is the number of species in common between the sampled seed bank and the plant community. Given that Sorensen similarity uses total species numbers, it is very sensitive to the sampling intensity of the seed bank; therefore, we computed three

different Sorensen similarity values, S_{or_1} , S_{or_2} and S_{or_3} , using the three simulated sampling intensities.

We used a full factorial design to explore the model predictions. We varied each parameter widely, so as to ensure that we scanned most biologically reasonable cases. Parameter p of seed production was varied in {10; 50; 250; 1,250}, which is in line with empirical ranges (e.g., Aarssen & Taylor, 1992). Note that we did not explore the upper end of this seed production range because of computing time limitations (N_{seed} already reached 2,500,000 in some simulations with p equal to 1,250). Parameter d_{seed} of seed mortality was varied in {0.05; 0.1; 0.2; 0.4}, leading to an average seed life span in the soil between 2.5 and 20 years, which encompasses seed longevities commonly reported (Bekker et al., 1998). Parameter d_{plant} of plant mortality was varied in {0.03; 0.1; 0.3; 1}, which encompasses the cases of annual plants and of long-lived (c. 30 years) perennial ones (Hara & Herben, 1997). Parameter i of the annual number of immigrating seeds was varied in {10; 50; 250; 1,250}, which leads to a range of cases from very strongly dispersal-limited communities (i small and p large) to almost dispersal-unlimited communities (i large and p small). Parameter S_{pool} of regional pool richness was varied in {10; 25; 50; 100}. This range is below the empirically observed values reported in Supporting Information Appendix S2, but it was chosen for computing time limitations. As we are interested in qualitative model behaviour, this underestimated range should not be problematic. Parameter θ of regional diversity was varied in {1; 5; 25; 125}. These values are in line with previous studies on neutral models (e.g., Jabot & Chave, 2009). We further checked that this range of θ values lead to widely variable evenness values in the pool, from c. 0.3 to 0.9, whatever the richness of the pool (Supporting Information Table S1). Finally, we varied parameter V of environmental variance in {0; 0.1; 0.3; 1}, which is in line with previous studies on time-averaged neutral models (Jabot & Lohier, 2016; Kalyuzhny et al., 2015). Note that the case $V = 0$ refers to a strictly neutral model without environmental stochasticity. This full factorial design leads to a total of $4^7 = 16,384$ simulations, among which 4,096 were strictly neutral, and 12,288 were time-averaged neutral. Model simulation results are provided in Supporting Information Appendix S3.

We finally assessed whether empirical findings were consistent with the predictions of the strictly neutral and time-averaged neutral models of plant community dynamics with a seed bank. In these comparisons, seed bank density was \log_{10} -transformed in both empirical and simulation analyses. The effect of the \log_{10} -transformed sampling area in empirical studies was compared with the effect of sampling intensity in simulation studies. Strictly speaking, these two quantities are comparable only under the assumption that the seed bank is well mixed. However, most empirical studies pool several seed bank samples, thereby minimizing the potential bias linked to seed bank spatial structuring. \log_{10} -transformed regional pool richness was used in both empirical and simulation analyses. The effect of the \log_{10} -transformed coefficient of variation in the number of wet days in empirical analyses was compared with the effect of the \log_{10} -transformed environmental variance A in the time-averaged neutral model.

3 | RESULTS

3.1 | Empirical macroecological patterns

Based on our analysis of published studies, we first found evidence for a latitudinal gradient in both seed bank richness (Figure 3a; $R^2 = 0.10$, $p < .001$, $n = 121$) and S-V similarity (Figure 3b; $R^2 = 0.07$, $p = .003$, $n = 130$). We then assessed whether these latitudinal gradients may be explained by among-site variations in environmental variability, regional pool richness, seed bank density and sampling area. Among these four putative drivers, environmental variability was the most strongly correlated with latitude ($Cor = -0.63$; Supporting Information Table S2), whereas the three other tested drivers were less correlated with latitude ($|Cor| < 0.2$; Supporting Information Table S2). We found that the four tested covariables were indeed significantly linked to variations in seed bank richness and S-V similarity (Figure 4; Supporting Information Table S4). All four tested drivers had similar magnitudes of effects on both seed bank richness and S-V similarity, highlighting that seed bank macroecological patterns are driven not only by environmental variability, but also by the density of the seed bank, the intensity of seed bank sampling, and biogeographical effects linked to the size of the regional species pool.

3.2 | Consistency with the predictions of the neutral models with a seed bank

We then assessed whether these empirical findings were consistent with the predictions of the strictly neutral and time-averaged neutral models of plant community dynamics with a seed bank. We found a striking agreement between theoretical predictions and empirical observations for six of the eight correlations of Figure 4 with both the strictly neutral and the time-averaged neutral models (Figure 5). Below, we detail the model results for seed bank richness and S-V similarity in turn.

First, we recovered in model simulations that seed bank density was positively correlated with sampled seed bank richness S_2 at intermediate sampling intensity (Figure 5a; $R^2 = 0.03$). This result was also recovered at low ($R^2 = 0.20$) and high ($R^2 = 0.003$) sampling intensities, and was similar when looking separately at strictly neutral and time-averaged neutral simulations. The effect size of these relationships decreases with sampling intensity. Second, sampling intensity was found to have a positive impact on seed bank richness, for both strictly neutral and time-averaged neutral simulations (Figure 5b; average increases in seed bank richness of 2.5 and 6.6 species when sampling intensity increases from 0.01 to 0.1 and 1%, respectively, in the strictly neutral model, and of 2.4 and 6.5 species in the time-averaged neutral model; all paired Wilcoxon tests p -value $< 10^{-15}$). Third, regional pool richness S_{pool} was found to have a weak positive impact on sampled seed bank richness S_2 in most simulations of both strictly neutral and time-averaged neutral models (Figure 5c; average increases in seed bank richness of 1.1, 1.5 and 1.7 species when S_{pool} increases from 10 to 25, 50 and 100, respectively, in the strictly neutral model, and of 1, 1.4 and 1.5 species in the time-averaged neutral model; all paired Wilcoxon tests p -value $< 10^{-5}$). Similar results were obtained when considering sampled

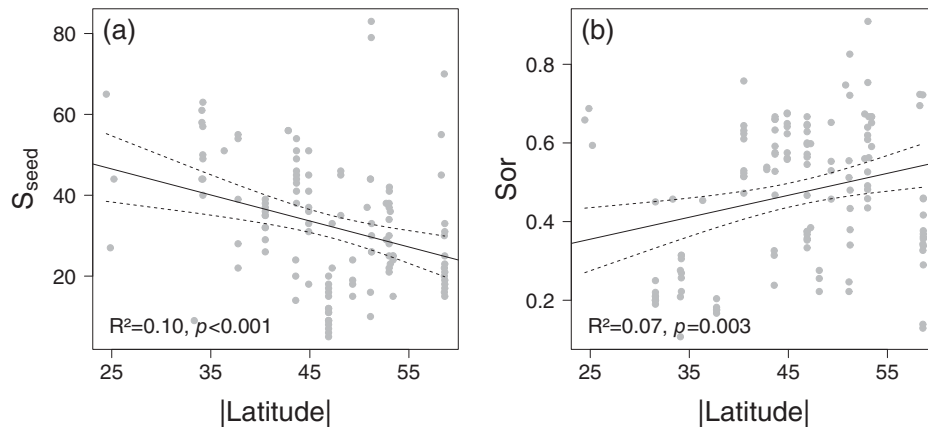


FIGURE 3 Latitudinal gradients of seed bank richness and seed bank–vegetation similarity. (a) Seed bank richness (S_{seed}). (b) Sorensen index (Sor) of similarity between seed bank and aboveground vegetation. Full regression results are provided in Supporting Information Table S3. Regression lines (continuous) and their confidence intervals (dashed) are depicted

seed bank richness at low and large sampling intensities (Supporting Information Figures S12 and S13).

First, seed bank–vegetation similarity was found to have a unimodal relationship with seed bank density (Figure 5d). More precisely, this relationship was strictly positive at low sampling intensities (Supporting Information Figure S12e) and progressively turned to unimodal at increasing sampling intensities (Figure 5d; Supporting Information Figure S13e). Second, sampling intensity was found to have a positive but saturating effect on S-V similarity for both the strictly neutral and the time-averaged neutral models (Figure 5e; average increases in Sor_2 of 0.14 when sampling intensity increases from 0.01 to 0.1 or 1% in both the strictly neutral model and the time-averaged neutral model; all paired Wilcoxon tests p -value $< 10^{-15}$). These results can be

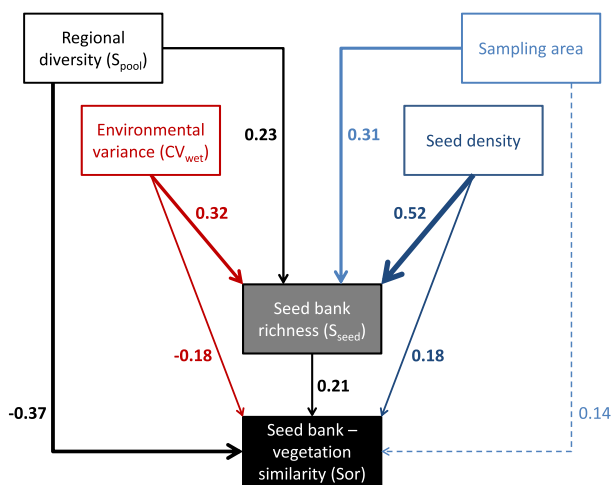


FIGURE 4 Structural equation modelling of seed bank richness and seed bank–vegetation similarity. All the plain arrows correspond to significant ($p < .05$) relationships, whereas the dashed arrow corresponds to a non-significant trend ($p = .09$). Arrow widths represent the magnitude of standardized regression coefficients that are also mentioned next to the arrows. All p -values and summary of direct, indirect and total effects of the four drivers are reported in Supporting Information Table S4

understood as follows: large seed banks are storing species that are not present in the established community. As a larger number of seeds are sampled, either because of a larger seed bank density (Figure 5d) or because of a larger percentage of the seed bank that is sampled (Figure 5e), S-V similarity first increases because the species present in the established community are progressively sampled in the seed bank (Supporting Information Figure S14a). But as the number of seeds sampled continues to increase, new species that are not present in the adult community are progressively recovered in the seed bank, thereby decreasing S-V similarity (Supporting Information Figure S14b,c). The median sampling intensity in empirical studies, which we define as the ratio of the seed bank sampling area on the plant sampling area, was equal to 0.95%, which is close to the high-intensity case modelled (i.e. 1%). This is likely to explain the milder effect of seed density on S-V similarity found in empirical studies, compared with its effect on seed bank richness and why sampling area was found to have a positive but non-significant effect on S-V similarity in empirical studies (Figure 4). Third, regional pool richness S_{pool} was found to have a weak negative impact on S-V similarity in most simulations of both strictly neutral and time-averaged neutral models (Figure 5f; average decreases in Sor_2 of 0.048, 0.065 and 0.069 when S_{pool} increases from 10 to 25, 50 and 100, respectively, in the strictly neutral model, and of 0.044, 0.059 and 0.066 in the time-averaged neutral model; all paired Wilcoxon tests p -value $< .0003$). Similar results were obtained when considering sampled seed bank richness at low and large sampling intensities (Supporting Information Figures S12 and S13).

3.3 | Additional predictions of the time-averaged neutral model

The strictly neutral model did not make any prediction regarding the effect of environmental variance that is not taken into account in this model. The predictions of the time-averaged neutral model regarding the effect of environmental variance were partly in line with empirical observations. More precisely, environmental variance V was found to have variable effects on seed bank richness S_2 , depending on model

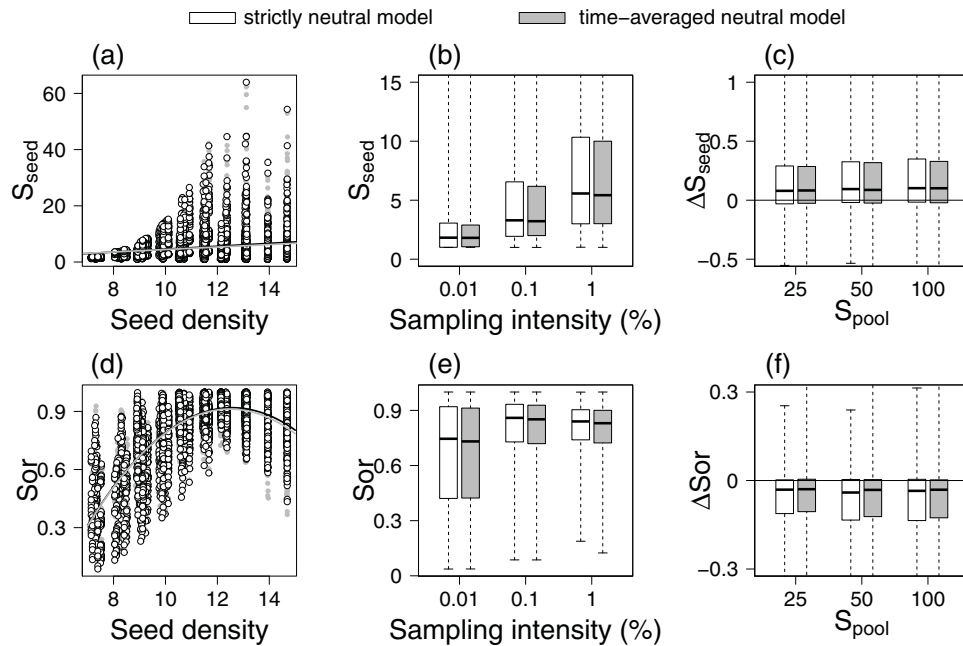


FIGURE 5 Predictions of the strictly neutral and time-averaged neutral models. (a–c) Effects of (a) seed density, (b) sampling intensity and (c) regional pool richness on seed bank richness (S_{seed}) in model simulations. (d–f) Effects of the same parameters on seed bank–vegetation (S–V) similarity (S_{or}). S_{seed} and S_{or} are based on a sampling of 0.1% of the seed bank in (a, c, d, f). Seed density is measured by $\ln(N_{seed})$. ΔS_{seed} is the relative variation in sampled seed bank richness S_{seed} caused by an increase in the S_{pool} parameter from its minimal value (10) to a larger value (25, 50 or 100), all the other model parameters being fixed. ΔS_{or} is defined in a similar manner for the S_{or} index. Box plots are partly truncated for clarity in (b, c, f). Full box plot ranges are depicted in Supporting Information Figure S11

parameter combinations (Figure 6a). Positive effects were recovered for simulations with low plant mortality d_{plant} and large seed mortality d_{seed} (Figure 6a; Supporting Information Table S5). These parameter values correspond to scenarios for grasslands dominated by perennial plants (low d_{plant}) with modest seed longevity (Stöcklin & Fischer, 1999). In contrast, the positive effect of V on S was not recovered when d_{plant} was high and d_{seed} low (Supporting Information Table S5). This latter combination of parameter values corresponds to scenarios for grasslands dominated by annual plants. Other model parameters had lower impacts on this relationship (Supporting Information Tables S7 and S9).

Likewise, environmental variance was found to have variable effects on S–V similarity (Figure 6b; Supporting Information Table S6), depending on the subdomains of the parameter space considered. The negative effects highlighted from empirical studies were recovered for simulations with high plant mortality d_{plant} and low seed mortality d_{seed} , which corresponds to grasslands dominated by annuals. In contrast, in the case of grasslands dominated by perennials (low d_{plant} and high d_{seed}), simulations did not recover the empirical patterns (Supporting Information Table S6). Other model parameters had lower impacts on this relationship (Supporting Information Tables S8 and S10).

4 | DISCUSSION

Our study found evidence, for the first time to our knowledge, of a weak latitudinal gradient in seed bank richness and seed bank–vegetation similarity, with a smaller richness and a larger S–V similarity

at higher latitudes (Figure 3). This finding adds to the already numerous latitudinal gradients evidenced for biodiversity patterns in general (Willig, Kaufman, & Stevens, 2003). For terrestrial plants, a number of latitudinal gradients have been demonstrated concerning aboveground species richness (Gentry, 1988; Silvertown, 1985), beta diversity (Qian & Ricklefs, 2007), biotic interactions (Schemske, Mittelbach, Cornell, Sobel, & Roy, 2009), assembly rules (Qiao, Jabot, Tang, Jiang, & Fang, 2015), evolutionary rates (Davies, Savolainen, Chase, Moat, & Barraclough, 2004) and phylogenetic diversity (Kerkhoff, Moriarty, & Weiser, 2014). A latitudinal gradient in seed size has also been evidenced, with plants having larger seeds in the tropics (Moles, Ackerly, & Tweddle, 2007). The new macroecological patterns evidenced here are particularly interesting in that they stress the importance of metacommunity processes to understand seed bank patterns. Besides, the large remaining variability around these latitudinal gradients calls for an integrated explanation of seed bank diversity patterns mobilizing both regional and local processes.

Indeed, the field of seed bank ecology has been mainly focused on the impacts of environmental variability on the recruitment of plants from the seed banks (Facelli et al., 2005; Grubb, 1977; Warner & Chesson, 1985). From this research tradition follows the view of seed banks as biodiversity reservoirs whose patterns may be crucially impacted by environmental variability (Faist, Ferrenberg, & Collinge, 2013; Thompson & Grime, 1979; Vandvik et al., 2015). Our results recover this view, but they also point out that major macroecological seed bank patterns are partly attributable to processes acting at the metacommunity scale, with both the diversity of the regional pool and the

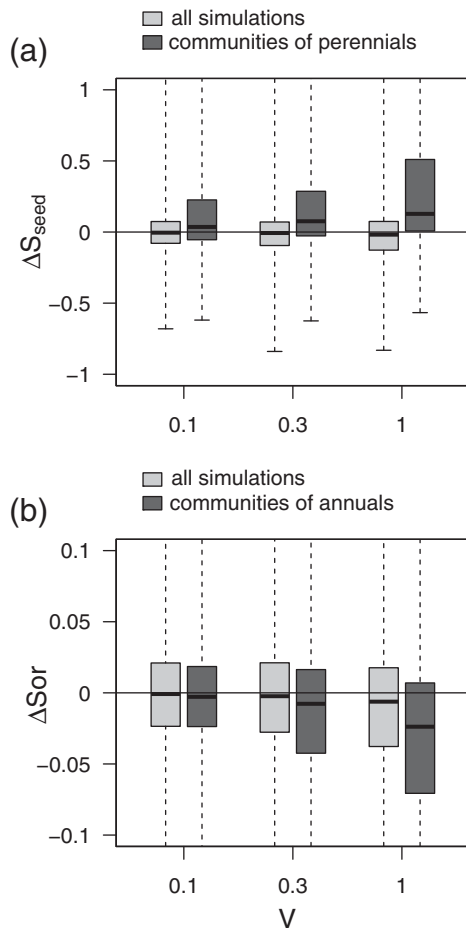


FIGURE 6 Effect of environmental variance in the time-averaged neutral model. Effects of the environmental variance parameter (V) on (a) seed bank richness and (b) seed bank–vegetation (S–V) similarity. ΔS_{seed} and ΔSor are defined as in Figure 5. Dark grey boxes of (a) correspond to a subset of model simulations for which parameters $d_{\text{seed}} = 0.4$ and $d_{\text{plant}} = 0.03$ (communities of perennials). They correspond in (b) to simulations with $d_{\text{seed}} = 0.05$ and $d_{\text{plant}} = 1$ (communities of annuals). Box plots are partly truncated for clarity. Full box plot ranges are depicted in Supporting Information Figure S11

immigration rate from this pool having impacts on the similarity between seed banks and aboveground vegetation (Figure 4).

Another important result of our study is that, on top of metacommunity processes, seed bank density and sampling area are likely to have significant impacts on seed bank patterns by being positively correlated with sampled species richness and S–V similarity (Figures 4 and 5a,b,d,e). This is consistent with the recent conclusions of Vandvik et al. (2015) based on their study of species–area relationships of seed banks. Both the strictly neutral and the time-averaged neutral models further predicted that the positive relationship between seed bank density and S–V similarity turned to unimodal for very large seed densities and at medium and high sampling intensities (Figure 5e; Supporting Information Figure S13e). This phenomenon is attributable to a progressive sampling in the seed bank of species not present in the established plant community (Supporting Information Figure S14).

It may explain the somewhat milder effects of seed density and sampling area on S–V similarity found in empirical studies (Figure 4). These results stress the need to standardize empirical findings cautiously when performing comparisons of seed bank patterns across studies, because sampling and density effects are at least as important as environmental and regional processes in shaping seed bank patterns (Figure 4). Interestingly, such sampling effects provide a potential explanation for the general pattern of larger S–V similarity in grasslands compared with forests (Bossuyt & Honnay, 2008). Indeed, these authors compiled published seed bank studies and found evidence of this pattern, but also that grasslands tended to have a larger seed density and diversity. The larger S–V similarity of grasslands compared with forests could thus be solely attributable to a sampling effect.

The large influence of biogeographical factors and of sampling processes on seed bank diversity patterns is further confirmed by the agreement between six of the eight empirical correlations found in our analyses of published data (Figure 4) and the predictions from both a strictly neutral model and a time-averaged neutral model (Figure 5). The positive correlation between environmental variability and seed bank richness was further recovered with the time-averaged neutral model, in the subdomain of the parameter space corresponding to long-lived perennial plants with modest seed longevity in the seed bank (Figure 6a; Supporting Information Table S5). The last negative correlation between environmental variability and seed bank–vegetation similarity was recovered in model simulations only in the subdomain of the parameter space corresponding to annual plants (Figure 6b). It is worth noting that this negative effect was not strong in our data analysis, possibly because the set of empirical studies mixes both sites dominated by perennials, such as temperate and mountainous grasslands, and sites dominated by annuals, such as Mediterranean fields. In addition, the observed relationship between S–V similarity and environmental variance was partly annealed by the positive indirect effect of seed bank richness (Figure 4). We therefore contend that more empirical comparisons with better controlled protocols should be conducted before a definitive assessment of the time-averaged neutral model can be made on this particular pattern. Besides, it is worth noting that the studied responses of seed bank richness and of its similarity with aboveground vegetation are not mutually independent, as evidenced by the structural equation model (Figure 4). Therefore, the cumulative evidence brought by the eight investigated relationships should somehow be tempered. Nonetheless, our results support a clear influence of strictly neutral processes on the structuring of seed bank diversity patterns, although environmental variability does contribute positively to seed bank diversity.

Given the large variability among studies in sampling protocols, biogeographical and ecological contexts, our comparison between model predictions and empirical patterns was restricted to qualitative analyses. In this perspective, we explored the predictions of the two models on a large range of parameter values, so as to obtain broad and qualitatively robust predictions. The downside of this simulation approach is that we typically obtained modest correlations when analysing the univariate influence of the four tested drivers on model outputs (Figure 5).

Importantly, these modest effect sizes should not be interpreted as meaning that the various drivers have a modest influence on seed bank patterns, but rather that these influences are interacting and nonlinear. In line with this interpretation, the structural equation modelling analysis reached relatively large R^2 (0.35 and 0.32; see Supporting Information Table S4). Nonetheless, an interesting perspective would be to focus on more standardized empirical data in order to infer the parameters of the time-averaged neutral model quantitatively. This would allow a finer quantification of the respective influences of dispersal, drift and environmental variability on seed bank and plant diversity patterns. Such analyses have been performed recently with a time-averaged neutral model without a seed bank (Jabot & Lohier, 2016) using approximate Bayesian techniques (Beaumont, 2010; Lagarrigues, Jabot, Lafond, & Courbaud, 2015). These same techniques could easily be extended to the present model with a seed bank. Such quantitative inferences would be of great interest for conservation purposes, because the diversity of seed banks and their similarity with above-ground vegetation are crucial properties to stabilize local communities through rescue effects (Piessens, Honnay, Nackaerts, & Hermy, 2004).

From a more theoretical perspective, our study offers an extension of strictly neutral and time-averaged neutral models by explicitly modelling the coupled dynamics of the seed bank. It therefore offers a theoretical framework to study seed bank diversity patterns and the impact of seed banks on plant community dynamics in a metacommunity context. Our simple approach to modelling coupled metacommunities of seed banks and plants is especially timely, because recent evidence suggests that anthropogenic impacts on plant communities may also occur indirectly through seed banks (Basto et al., 2015). It is thus important to develop integrated spatial theory to understand this coupled dynamics of seed banks and vegetation in a metacommunity context (Vandvik & Goldberg, 2006). Time-averaged neutral models are particularly appealing, because they enable the effect of environmental variability on plant dynamics to be taken into account (Pake & Venable, 1996) within an economical modelling framework. This approach extends previous work on lottery competitive systems (Chesson & Warner, 1981; Fagerström, 1988) by considering the effect of dispersal limitation on top of environmental variability, thereby connecting seed bank and metacommunity ecology.

We have documented two latitudinal gradients in seed bank richness and seed bank-vegetation similarity, and we have provided an explanation for these patterns, rooted in metacommunity ecology (Holyoak, Leibold, & Holt, 2005). But many other seed bank macroecological patterns still need general explanations that may need further elaborations beyond this neutral framework. For instance, the impact of disturbances on seed bank dynamics has been recurrently studied with directional trends in seed bank composition following disturbance (Falińska, 1999; Helsen, Hermy, & Honnay, 2015; Royo & Ristau, 2013) and different similarity trends in grasslands and forests (Hopfensperger, 2007). To study such other general patterns, it may be necessary to include additional ingredients to this time-averaged neutral framework, such as multiple guilds, as has been done for strictly neutral models (Janzen, Haegeman, & Etienne, 2015; Scheffer & Van

Nes, 2006), but also bud banks (Klimešová & Klimeš, 2007; Vesik & Westoby, 2004) or seed trade-offs (Muller-Landau, 2010). Such elaborations on this neutral framework may enable the study of the dynamical consequences of these various ecological ingredients and deepen our understanding of seed bank metacommunities.

ACKNOWLEDGMENTS

We thank Brian Enquist, Allen Hurlbert and an anonymous referee for their constructive comments that considerably improved the manuscript.

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SUPPORTING INFORMATION

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How to cite this article: Jabot F, Pottier J. Macroecology of seed banks: The role of biogeography, environmental stochasticity and sampling. *Global Ecol Biogeogr*. 2017;26:1247–1257. <https://doi.org/10.1111/geb.12631>