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Assessing the Influence of Temporal Autocorrelations on the Population Dynamics of a Disturbance Specialist Plant Population in a Random Environment

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ABSTRACT: Biological populations are strongly influenced by random variations in their environment, which are often autocorrelated in time. For disturbance specialist plant populations, the frequency and intensity of environmental stochasticity (via disturbances) can drive the qualitative nature of their population dynamics. In this article, we extended our earlier model to explore the effect of temporally autocorrelated disturbances on population persistence. In our earlier work, we only assumed disturbances were independent and identically distributed in time. We proved that the plant seed bank population converges in distribution, and we showed that the mean and variance in seed bank population size were both increasing functions of the autocorrelation coefficient for all parameter values considered, but the interplay between increasing population size and increasing variability caused interesting relationships between quasi-extinction probability and autocorrelation. For example, for populations with low seed survival, fecundity, and disturbance frequency, increasingly positive autocorrelated disturbances decreased quasi-extinction probability. Higher disturbance frequency coupled with low seed survival and fecundity caused a nonmontone relationship between autocorrelation and quasi-extinction, where increasingly positive autocorrelations eventually caused an increase in quasi-extinction probability. For higher seed survival, fecundity, and/ or disturbance frequency, quasi-extinction probability was generally a monotonically increasing function of the autocorrelation coefficient.

Keywords: disturbance specialist, stochastic autocorrelations, seed bank, stochastic integral projection model, density dependence, Monte Carlo simulation.

Introduction

Natural environments are variable in space and time, and understanding how environmental stochasticity affects popula-

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tion dynamics is an important task for population ecologists from both a theoretical and an empirical point of view (Chesson and Warner 1981; Chesson 1982; Ellner 1984; Chesson and Ellner 1989; Doak et al. 2005; Schwager et al. 2006; Benaïm and Schreiber 2009; Alexander et al. 2012; Ellner and Schreiber 2012; Schreiber 2012; Mustin et al. 2013; Nieddu et al. 2014; Sharma et al. 2015; Roth and Schreiber 2014; Haridas et al. 2015). One aspect of environmental stochasticity that has been a focus for theoretical population ecologists of late has been temporal autocorrelation (Johst and Wissel 1997; Petchey et al. 1997; Heino 1998; Palmqvist and Lundberg 1998; Ripa and Heino 1999; Heino et al. 2000; Greenman and Benton 2003, 2005; Vassuer and Yodzis 2004; Schwager et al. 2006; Lögdberg and Wennergren 2012; Mustin et al. 2013). Theoretical and empirical work has shown that population processes are strongly affected by the "color" of environmental stochasticity where, generally, reddened noise is positively autocorrelated, blue noise is negatively autocorrelated, and white noise—or noise that is independent and identically distributed (IID) in space and/or time—is uncorrelated.

Natural disturbances acting on disturbance specialist plants are an example where the qualitative dynamics of a population are affected mostly by the characteristics of environmental stochasticity rather than by an underlying deterministic skeleton (Alexander and Schrag 2003; Claessen et al. 2005a, 2005b; Eager et al. 2013, 2014b). Disturbance specialist plants use seed banks to combat environmental variability, which is a widespread phenomenon in nature (see, e.g., MacDonald and Watkinson 1981; Roberts 1981; Doyle et al. 1986; McGraw 1986; Alexander and Schrag 2003; Fenner and Thompson 2005; Moody-Weis and Alexander 2007; Colbach et al. 2008; Alexander et al. 2009, 2012). By dispersing through time and space, these seed banks buffer the effects of environmental variation on population size and persistence ability, which is particularly important for annual

species, as deleterious perturbations can leave a population void of remaining aboveground biomass. For example, in the case of the disturbance specialist *Helianthus annuus*, seeds generally germinate only in freshly disturbed soil (Alexander and Schrag 2003; Moody-Weis and Alexander 2007; Alexander et al. 2009; Snow et al. 2009). Therefore, these populations are also able to capitalize on environmental stochasticity that comes in the form of disturbance, since disturbances not only create a more favorable environment for germination and recruitment by removing more competitive species but also enhance the chance of population persistence and/or permanence by helping seed bank formation (Moody-Weis and Alexander 2007; Alexander et al. 2009). The frequency, intensity, timing, and spatial extent of natural disturbances can greatly influence the probability of germination and survival of seeds in a seed bank (Froud-Williams et al. 1984; Claessen et al. 2005*a*; Moody-Weis and Alexander 2007; Miller et al. 2012; Jauni et al. 2015), meaning any mathematical modeling of disturbance specialist plants needs to incorporate these factors into its model structure.

Autocorrelated disturbances in real ecosystems are largely thought to originate from autocorrelations in purely environmental variables as well as autocorrelations in the dynamics of constituent populations. Caswell and Cohen (1995) stated that most of the purely environmental factors in ecology elicit positively autocorrelated noise in life-history parameters, but resulting population dynamics of various species are often negatively autocorrelated in response (Greenman and Benton 2005). Since natural disturbances can come about via purely environmental processes (e.g., wind storms, flooding, landslides, and fires) and/or through the constituent agents that ultimately cause disturbances (e.g., general predation and foraging; earthworm cast and mole burial; caching activities of birds, rodents, ants, and so on; digging activities of mammals; and road construction by humans; Johst and Wissel 1997; Petchey et al. 1997; Eager et al. 2013), we explored both negatively and positively autocorrelated disturbances in this article, as our model is for a general disturbance specialist plant population. For wild sunflower specifically, reanalyzing the data from Alexander et al. (2009) and using the presence/absence of aboveground sunflowers as a proxy for disturbance/nondisturbance, we found autocorrelation coefficients ranging between 0.09 and 0.44 for the presence/absence of disturbance each year, meaning that it is likely that populations in these specific systems are subject to positively autocorrelated disturbances. All data are available from the Dryad Digital Repository, http://dx.doi.org/10.5061/dryad.bq340 (Eager et al. 2017).

In this article, we sought to determine how autocorrelated disturbances affected the population dynamics of a disturbance specialist plant population and its seed bank. To do so, we altered our model from Eager et al. (2013) and Eager et al. (2014*b*), a nonlinear integral projection model, to char-

acterize disturbances using a Markov chain. Our earlier work demonstrated that increasing disturbance frequency increased population viability for all parameter values considered, while disturbance intensity was not monotonically related to population viability when disturbance frequency was low. For low disturbance frequency, increasing disturbance intensity actually decreased long-term population sizes and increased quasi-extinction probability, which was a fairly surprising result. All of this work assumed that disturbances were IID in time, however, limiting its applicability to populations of many disturbance specialist plants in nature.

Various authors (e.g., Lawton 1988; Caswell and Cohen 1995; Johst and Wissel 1997; Heino 1998; Lögdberg and Wennergren 2012; Mustin et al. 2013) have shown that increasingly positive autocorrelated environments lead to an increase in extinction risk, while others (Ripa and Lundberg 1996) have concluded that increasingly positively autocorrelated environmental variables decrease extinction risk. Whether autocorrelation causes an increase in extinction risk has often been traced to other ecological factors, such as the presence of over- or undercompensatory density dependence, with the former causing a decrease in extinction risk with increasingly positive autocorrelation and the latter causing an increase in extinction risk under increasingly positive autocorrelation (Petchey et al. 1997; Ripa and Heino 1999; Greenman and Benton 2005; Schwager et al. 2006; Ruokolainen and Fowler 2009). When age or stage structure is introduced into the modeling framework, extinction risk becomes dependent on the mechanistic ways in which individuals go through various life-history stages to produce new members of the population (Ruokolainen et al. 2009). Disturbance specialist plant populations have relatively unique life history, involving a trade-off in seed survival and germination that is further complicated by the fact that seedling recruitment cannot occur without a disturbance and is subject to undercompensatory density dependence. Given that our environmental variable that was subject to autocorrelations (the presence of a disturbance) took drastically different values, increasing autocorrelation in this variable should have increased the variability in population dynamics, which led us to conjecture that increasingly positive autocorrelations would yield an increase in the likelihood of population extinction that largely coincided with previous results from the literature. However, the amount of time a disturbance specialist plant population spends away from its carrying capacity, due to prolonged streaks of nondisturbance years, might work to reduce the effects of undercompensatory density dependence and alter how the likelihood of extinction varies with respect to increasingly positive autocorrelations.

Using our integral projection model, we proved that the plant seed bank population converges in distribution as $t \to \infty$, and we employed numerical experiments to determine how autocorrelations affected properties of this sta-

tionary distribution. Specifically, we explored how autocorrelations affected the population's long-term population size, variance, and quasi-extinction probability as well as how it affected the aforementioned relationship between population viability and intensity of disturbance found in both Eager et al. (2013) and Eager et al. (2014b). We found that the mean, variance, and rare intrinsic growth rate of the seed bank's total population size were all increasing functions of the autocorrelation coefficient for all parameter values considered, but the interplay between increasing population sizes and increasing variability caused different relationships between quasi-extinction probability and autocorrelation, which ran counter to some of the results of previous research discussed above. For example, quasi-extinction probability decreased with increasingly positive autocorrelation if disturbances were infrequent and seed survival and fecundity were low, while more frequent disturbances caused a nonmontone relationship between autocorrelation and extinction; increasingly positive autocorrelations eventually caused an increase in quasi-extinction probability. For higher seed survival probability and/or fecundity, quasi-extinction probability was generally an increasing function of the autocorrelation coefficient. Finally, we showed that the nonmonotone relationship between population size and disturbance intensity (defined by mean depth of disturbance) found in Eager et al. (2013) and Eager et al. (2014b) persisted for low disturbance frequency and that populations near extinction levels fared better with lower disturbance intensities, a relationship that changed if disturbance frequency or seed survival increased.

Model

In this article, we used a nonlinear stochastic integral projection model (IPM; Easterling 2000; Ellner 2006; Ellner and Rees 2007; Coulson 2012; Rees et al. 2014; Merow et al. 2014) that is closely related to the one we used in Eager et al. (2013). This model was a discrete-time model where the continuous stage variable described a seed's depth x in the seed bank. We modeled the following sequence of events: disturbance, redistribution of seeds, seed survival, plant recruitment, and production of new seeds. We considered only disturbances that occurred after seeds had been dispersed, because for plants such as wild sunflowers, disturbances before dispersal have had a negligible effect on the seed bank (Moody-Weis and Alexander 2007). Disturbances were modeled as a single event each time step, thought of as the average of the postdispersal disturbances to the population in a given year.

Disturbance and Redistribution of Seeds

We modeled disturbances using a stochastic process $\{\theta(t)\}_{t=0}^{\infty}$. At each time step t, we broke $\theta(t)$ into two random vari-

ables, $\theta_1(t)$ and $\theta_2(t)$. The term $\theta_1(t)$ took the values 0 (no disturbance) or 1 (disturbance) according to a Markov chain (Doob 1953) with the following transition matrix:

$$M = \begin{pmatrix} p & 1-p \\ 1-q & q \end{pmatrix},$$

where p was the probability of transitioning from a disturbance year to a disturbance year and q was the probability of transitioning from a nondisturbance year to a nondisturbance year. This Markov chain admitted an autocorrelation coefficient $r = p + q - 1$, with values in the interval $[-1, 1]$. In the case where disturbance years were likely followed by disturbance years and nondisturbance years were followed by nondisturbance years ($p \approx q \approx 1$), the value of r was near 1. In the case where disturbance years were likely followed by nondisturbance years and vice versa ($p \approx q \approx 0$), the value of r was near -1. The IID case was recovered when $p + q = 1$. The long-term proportion of years with a disturbance was given by the invariant distribution of the Markov matrix M. This long-term proportion of disturbance years was

$$h = \frac{1-q}{1-r}.$$

Given p and q, we could solve for h and r, and vice versa. To keep a close comparison with the results in Eager et al. (2013) and Eager et al. (2014b), we characterized $\theta_1(t)$ by prescribing a probability of disturbance h (which ranged from 0.42 to 0.69 in our four wild sunflower sites) and autocorrelation coefficient r and solved for p and q to run our simulations.

The random variable $\theta_2(t)$ will be the same as in Eager et al. (2013) and Eager et al. (2014b)—an exponential distribution truncated by the maximum depth in the seed bank D. Formally,

$$\Pr(\theta_2(t) \le x) = \begin{cases} 1 - e^{-x/p} & x < D \\ 1 & x = D, \end{cases} \tag{1}$$

where ρ is the parameter we will refer to as the mean depth of disturbance. Each time step, the depth of disturbance $\theta_2(t)$ is drawn independently of previous years, always using equation (1) above, making the sequence of disturbance depths (conditioned on the existence of a disturbance) an IID sequence of random variables.

The random variable $\theta(t)$ used to characterize the disturbance at each time t could thus be written as $\theta(t) = \theta_1(t)\theta_2(t)$ for every $t = 0, 1, 2, \ldots$. Using this definition, $\theta(t)$ determined both the occurrence and depth of disturbance for each time step t. We defined the disturbance ker-

nel K at time t for the disturbance $\theta(t)$, acting on the seed bank population u, as

$$
\int_0^D K(x, y, \theta(t)) u(y) dy = \begin{cases} (\theta(t))^{-1} \int_0^{\theta(t)} u(y) dy & 0 \le x \le \theta(t) \\ u(x) & \theta(t) \le x \le D, \end{cases}
$$

$$(2)$$

with the convention that the top term on the right-hand side of equation (2) was equal to zero when $\theta(t) = 0$. The top term in the right-hand side of equation (2) modeled the seed bank population u being uniformly redistributed within the interval $[0, \theta(t)]$ of depths that were disturbed, and the bottom term was the population u being left alone within the interval $[\theta(t), D]$ of depths that were not disturbed.

Survival

We assumed that the fraction of seeds that survived from one time step to the next depended only on the seed's depth x in the seed bank, that seeds survived at their lowest rates near the surface of the soil, and that seed survival increased with seed depth. We used the function from Mohler (1993) below:

$$
s(x) = s_0(1 - e^{-bx}),
$$

where $s_0 \in (0, 1)$ was the maximum survival probability of a seed and $b > 0$ modeled the gain in survival probability that occurred through an incremental increase in seed depth.

Plant Recruitment

We assumed that germination could occur only in a time step when a disturbance occurs; that is,

$$
g(x, \theta(t)) = \begin{cases} g_p(x) & \theta(t) \ne 0 \\ 0 & \theta(t) = 0, \end{cases}
$$

where $g_p(x)$ was the probability of a seed of depth x germinating in a given time step, given a disturbance. We assumed that a seed germinated at its highest rate near the surface of the soil and that the probability of germination decreased as depth increased (Chancellor 1964; Sester et al. 2007). We used the function from Mohler (1993):

$$
g_p(x) = g_0 e^{-ax},
$$

where $g_0 \in (0, 1)$ was the maximum germination probability of a seed (which occurred near the surface of the soil) and $a > 0$ modeled the loss in germination probability through an incremental gain in seed depth.

It has been shown empirically that even disturbance specialist plants experience density dependence in some years (see, e.g., fig 3 in Alexander and Schrag 2003), and we explicitly included density dependence in our model by assuming that seedling recruitment probability decreases with seedling density. We assumed that total seedling recruitment followed a Holling type II functional response (Holling 1959), with the density of plants $f(y)$ that result from y seedlings per unit area given by

$$
f(y) = \frac{\alpha y}{\beta + y},
$$

where α was the maximum number of adult plants that can grow in a given area and β was the half-saturation constant.

Seed Production

We assumed that seed production is not affected by plant density, although there is some evidence in the literature that density dependence can occur during the seed production process (Mercer et al. 2014). However, we show in Eager et al. (2014*a*) that this would have a small effect on equilibrium population dynamics, since our model already assumed density-dependent recruitment. We assumed an annual disturbance specialist plant and 1 year as the time step, and thus we modeled the plant population with a scalar—essentially characterizing the plant population by its average mature plant. This assumption ignored the size structure of plants, which was reasonable because we were envisioning an annual plant and our time step was 1 year. Each plant was assumed to produce an average of c seeds, which were distributed in the seed bank with depth distribution $J(x)$. We assumed that J was a truncated exponential distribution with mean $\mu \ll \rho < D$. Since $\mu \ll \rho < D$, most of the newly created seeds died if there was no disturbance following reproduction, because seed survival at shallow depths was relatively low. Additionally, most of the newly created seeds were set near the surface of the soil, and thus the average disturbance affected the majority of these new seeds.

Full Integral Projection Model

Let $n(x, t)$ be the density of seeds in the seed bank between the depths x and $x + \delta x$ and $p(t)$ the total density of plants in the population at time t, for $t = 0, 1, 2, \dots$. The seed bank population $n(x, t)$ is an integrable function on the interval $[0, D]$, while the plant population $p(t)$ is a scalar value for each time t. The model can be written as

$$
n(x, t+1) = s(x)(1 - g(x, \theta(t)) \int_0^D K(x, y, \theta(t))(n(y, t) + cJ(y)p(t))dy,
$$

$$
p(t+1) = f\left(\int_0^D g(x, \theta(t)) \int_0^D K(x, y, \theta(t))(n(y, t) + cJ(y)p(t))dydx\right),
$$

$$(3)$$

for $t = 0, 1, 2, \ldots$ and the initial seed bank population $n(x, 0) > 0$. The first line in the model (3) can be read right to left and states that the seed bank population at time $t + 1$ in the interval $[x, x + \delta x]$ results from three processes: the redistribution of the existing seeds at time t via the disturbance kernel $K(x, y, \theta(t))$, followed by dormancy and survival. The second line states that the density of plants at time $t + 1$ results from redistribution of the existing seeds at time t, followed by germination and seedling recruitment.

In part A of the appendix, we showed that the population $\{[n(x, t), p(t)]^T\}_{t=0}^{\infty}$ converged to a stationary random population, $[n(x)^*, p^*]^T$. Thus, as $t \to \infty$, the population modeled with (3) had a convergent long-term mean and variance. The stationary random population $[n(x)^*, p^*]$ was completely concentrated on the extinction state $[0, 0]^T$ if the value of

$$\lambda := \lim_{t \to \infty} \|A(\theta(t)) \circ A(\theta(t-1)) \circ \ldots \circ A(\theta(0))1\|_{\infty}^{1/t},$$

was less than one, where $A(\theta(t))$ is the model (3) linearized about the extinction state $[0, 0]^T$, and 1 is the function that is the constant 1 on the interval $[0, D]$. Since λ, a constant with probability one (Hardin et al. 1988; Ellner and Rees 2007; Benaïm and Schreiber 2009), gives the population's tendency to grow or decrease when rare (near extinction), we called λ the rare intrinsic growth rate of the population (Eager et al. 2014b). Here, $\circ$ denotes operator composition, and since each $A(\cdot)$ is a linear integral operator, we used the methods of Ellner and Rees (2007) for approximating λ.

It is important to note that other studies have treated seed depth as a discrete variable and constructed Markov chain–like matrix models to model seed movement (see, e.g., Doyle et al. 1986; McGraw 1986; Jordan et al. 1995; Gonzalez-Andujar 1997; Claessen et al. 2005a, 2005b; Pekrun et al. 2005; Mohler et al. 2006; Colbach et al. 2008). However, the predictions of these models can change as matrix dimension increases (Easterling et al. 2000; Ellner and Guckenheimer 2006; Tenhumberg et al. 2009) and cannot capture even the mean field dynamics of associated stochastic models for the disturbance-driven dynamics of populations subject to natural, variable disturbances. By using a nonlinear stochastic IPM, we did not have to explore the effects of matrix dimension (i.e., the number of seed layers) or worry about the error introduced by Jensen's inequality when one uses a mean field model (Eager et al. 2013).

Model Analysis

All simulations were done in R (R Core Development Team 2014) and used the same numerical integration techniques as in Eager et al. (2013; sample computer programs are available in a zip file online). The nonautocorrelation parameter values that we considered are in table 1 in Eager et al. (2013)

and are displayed in each figure legend. We used $D = 1$ as our maximum depth so that our depth values could be considered as proportions of maximum depth.

For each run, we simulated the population dynamics from an initial population density of 5,000 seeds per area, uniformly distributed throughout the seed bank depth interval $[0, D]$, and 15 plants per area. We simulated the population out to 10,000 time steps to eliminate transient dynamics from our analysis and recorded the total seed bank density

$$\|n(x, 10{,}000)\|_1 = \int_0^D n(x, 10{,}000)dx$$

for 500 different runs. We took the mean, median, and variance of these 500 runs as a proxy for the stationary random population distribution. These mean, median, and variance values are mean, median, and variance values across simulations (i.e., different sample paths) and not across time, although as $t \to \infty$ these values became equivalent. We also approximated the value of the rare intrinsic growth rate λ of the population by simulating the population out 150 time steps and computing the average value of

$$\lambda_{150} := \|A(\theta(150)) \circ A(\theta(149)) \circ \cdots \circ A(\theta(0))\mathbf{1}\|_{\infty}^{1/150}$$

for 500 different runs as a proxy for the rare intrinsic growth rate λ alluded to in the previous section.

We performed this simulation study for 30 h values spaced evenly between 0 and 1; the ρ values 0.14, 0.31, 0.48, 0.66, and 0.83 displayed in Eager et al. (2013); and the r values -0.75, -0.45, -0.15, 0.00, 0.15, 0.45, and 0.75. Notice that the $r = 0.00$ value (the IDD case) is what was explored in Eager et al. (2013).

As in Eager et al. (2013), we also computed the probability of quasi-extinction by recording the number of trajectories that were below 50 seeds per area when $t = 1{,}000$ for these scenarios. Since continuous (as opposed to individual-based) models never actually reach the zero state in finite time if they are initially positive, we had to create a threshold (in this case, one-hundredth of the initial population) under which we viewed the population as extinct. As expected, quasi-extinction probability increased when this threshold increased, but the qualitative results regarding how they were affected by model parameters were largely unaffected.

In this article, we also explored the effect of r by calculating the mean and variance of the survival probability, the mean and variance of the germination probability, and the mean and variance of total seed production (on a per capita basis) of the entire seed bank population for 20 evenly spaced r values between -0.85 and 0.85 (extended from above by 0.1 in both directions for more sample points) and how these calculations affected the quasi-extinction probability and total size of the seed bank population.

Results

To illustrate the effects of autocorrelations on the total seed bank population $\|n(x, t)\|_1$, we projected example population dynamics for various values of the autocorrelation coefficient r in the case where maximum seed survival in the seed bank was low ($s_0 = 0.5$) and high ($s_0 = 0.95$), including the IID case where $r = 0$. In cases of both low and high seed survival, the number of time steps where the population size was large increased as r increased (see figs. 1 and 2, respectively). Disturbances generally play two positive roles for disturbance specialist plants; they redistribute seeds to more advantageous depths in the seed bank and serve as a catalyst for germination. Thus, a string of consecutive disturbances that is more likely with higher r will have a positive effect on population sizes, while the more oscillatory nature of population dynamics subject to more negative r will keep population sizes relatively low. Strings of consecutive years without a disturbance are also more likely for increasing r, but it appears that a year without a disturbance did not have the negative effect on populations commensurate with the positive effect of a disturbance year. In the $s_0 = 0.5$ case, it appears that there were multiple time steps where the population was dangerously close to extinction for all r values considered, but as r became less negative and then more positive, the average size of the population increased due to the increased frequency of consecutive years of dis-

turbance working to offset consecutive years without a disturbance.

In the maximum seed survival $s_0 = 0.95$ case, the increase in population size as r becomes less negative, and subsequently more positive, was a bit more profound than in the $s_0 = 0.5$ case, although all populations were a safe distance away from extinction. In the negative r case, the population never achieved very high or low population values, since disturbance years were most often followed by nondisturbance years, and vice versa, which prevented any substantial population growth or decrease from happening. On the other hand, when the autocorrelation coefficient r was positive, disturbance years were most often followed by disturbance years, which further increased population sizes before any long streaks of nondisturbance years. Positive r values also increased variability in population size, as a string of disturbance years elicited population sizes that were substantially different from that of a string of disturbance-free years. For reference, example sequences of the disturbance variable $\theta_1(t)$ for different h and r values are displayed in figure A1 (figs. A1–A9 available online).

In general, the effect of autocorrelation on population dynamics depended on the parameter scenario, and for most of the parameter scenarios considered, the long-term median of survival probability, germination probability, seed production, and the total seed bank population never varied substantially from the mean. Thus, we focused on the mean as the
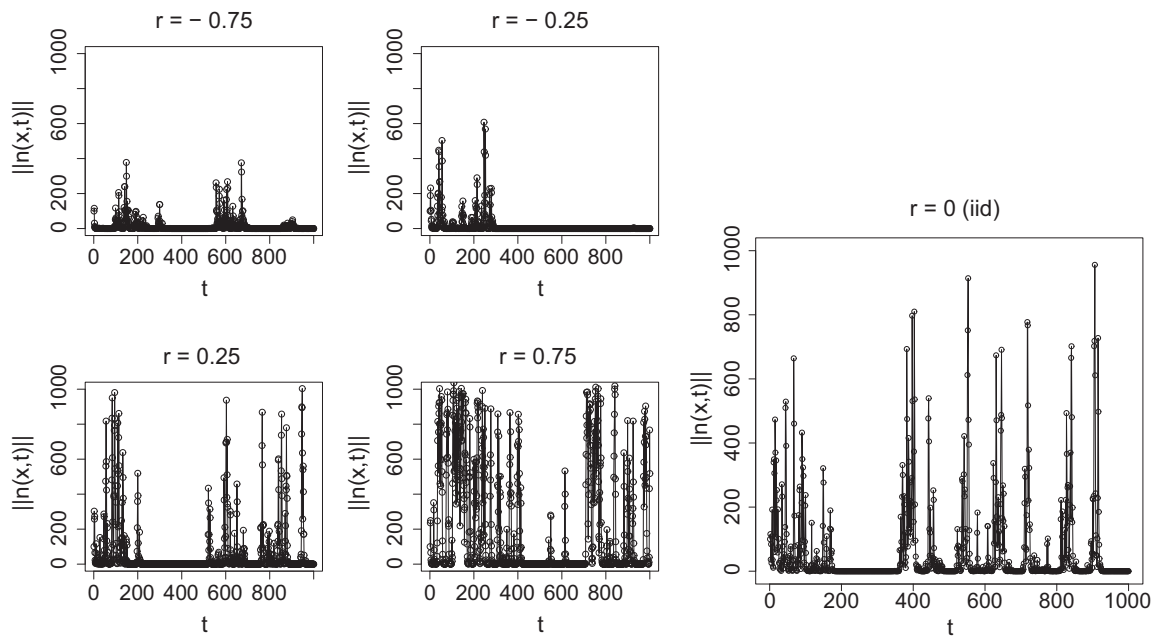

Figure 1: Example simulations of the total seed bank population $\|n(x, t)\|_1$ for four different scenarios for the correlation coefficient r (*left*), compared with the independent and identically distributed case (*right*), for low seed bank survival $s_0 = 0.5$. Parameter values used for this simulation are $h = 0.5$, $\rho = 0.5$, $c = 50$, $\alpha = 40$, $\beta = 50$, $a = 10$, $b = 10$, $g_0 = 0.95$, and $\mu = 0.02$. The initial seed bank population density was 100 seeds per area, distributed uniformly in the seed bank. The initial density of the plants was 15 plants per area.
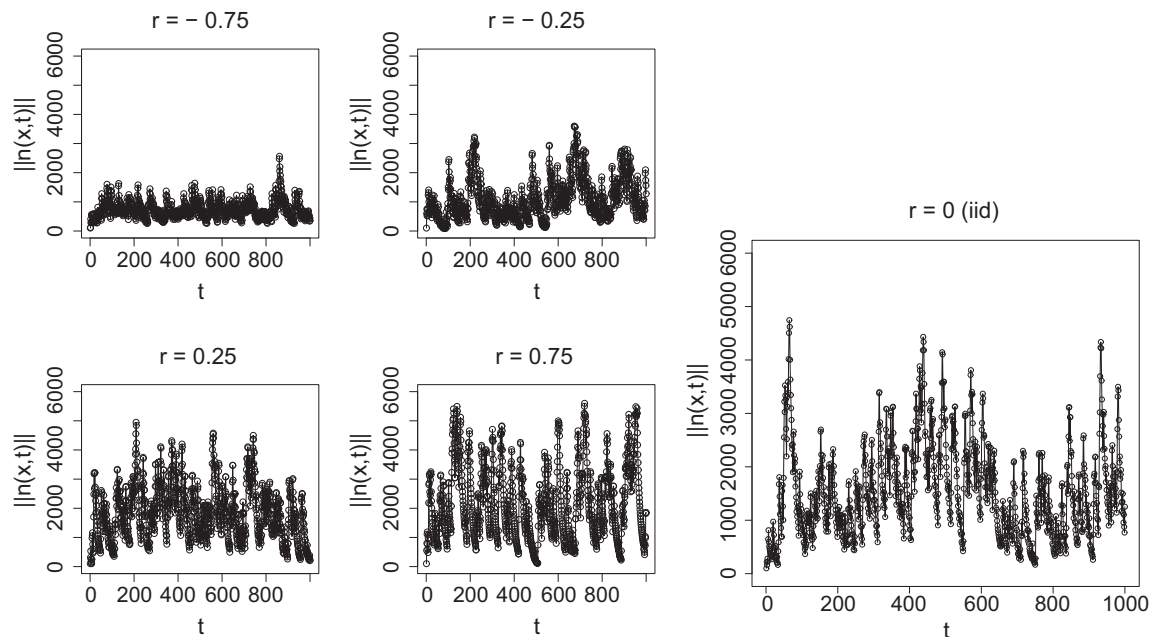
Figure 2: Example simulations of the total seed bank population $\|n(x, t)\|_1$ for four different scenarios for the correlation coefficient r (*left*), compared with the independent and identically distributed case (*right*), for high seed bank survival $s_0 = 0.95$. Parameter values were otherwise the same as in figure 1.

long-term centrality measurement of these metrics. Both per capita mean germination and survival probabilities increased with increasing autocorrelation coefficient r (figs. 3c, 3e, 4c, 4e, A2d, A2f, A3d, A3f), while variance in both of these values decreased with increasing r for all parameter combinations considered (figs. 3d, 3f, 4d, 4f, A2e, A2g, A3e, A3g). For larger fecundity values ($c = 150$), the differences in these values were exacerbated with differing probability of disturbance h (figs. 4e, 4f, A3d, A3f), where both mean seed survival and germination probabilities were increasing functions of h for negative r and decreasing functions of h for positive r. Mean and variance in seed production were mostly constant in r, with the former increasing in h and the latter decreasing in h (figs. A2h, A2i, A3h, A3i).

We found that, for all parameter combinations considered, the mean and variance of the total seed bank population increased with increasing autocorrelation coefficient r (figs. 3a, 3b, 4a, 4b, A2b, A2c, A3b, A3c). The long-term mean of the total seed bank population increased roughly linearly with h (figs. A4, A7), while the variance in the long-term population size was a unimodal function of the disturbance frequency h (figs. A6, A9). The variance changed more substantially as a function of the autocorrelation coefficient r for smaller h (h values lower than 0.55, although this threshold depends on the other parameters in the model) than for larger h (above 0.55) due to the presence of a carrying capacity limiting upward variability for populations with larger

h (and hence larger mean population sizes). Populations with larger h can largely only vary downwardly, whereas populations with lower h can vary in both directions, leading to higher variability.

For small probability of disturbance h, maximum seed survival s_0, and fecundity c, increasing the autocorrelation coefficient r decreased quasi-extinction probability, while for larger h and small s_0 and c, the relationship was nonmonotone: quasi-extinction probability decreased initially before increasing for larger r (fig. 5a). These dynamics can be partially explained by how the mean and variance of the total seed bank population responded to changes in r. An increase in the variance of the total seed bank population (fig. 3b) as r increased was eventually enough to increase the quasi-extinction probability for large h and small s_0 and c, even as the mean total seed bank population was simultaneously increasing (fig. 3a). For higher s_0 values, the quasi-extinction probability was generally small, but as r became large enough, the quasi-extinction probability eventually increased, especially for small h (fig. 5b, 5d), due to the aforementioned increase in the population size's variance. For higher c values, quasi-extinction probability was generally increasing with r (fig. 5c, 5d). However, for some parameter values (high s_0 and/or high c), small h values corresponded to quasi-extinction probabilities that initially increased for increasing (but negative) r before decreasing for intermediate r and then increasing as r became large. The initial increases in extinction
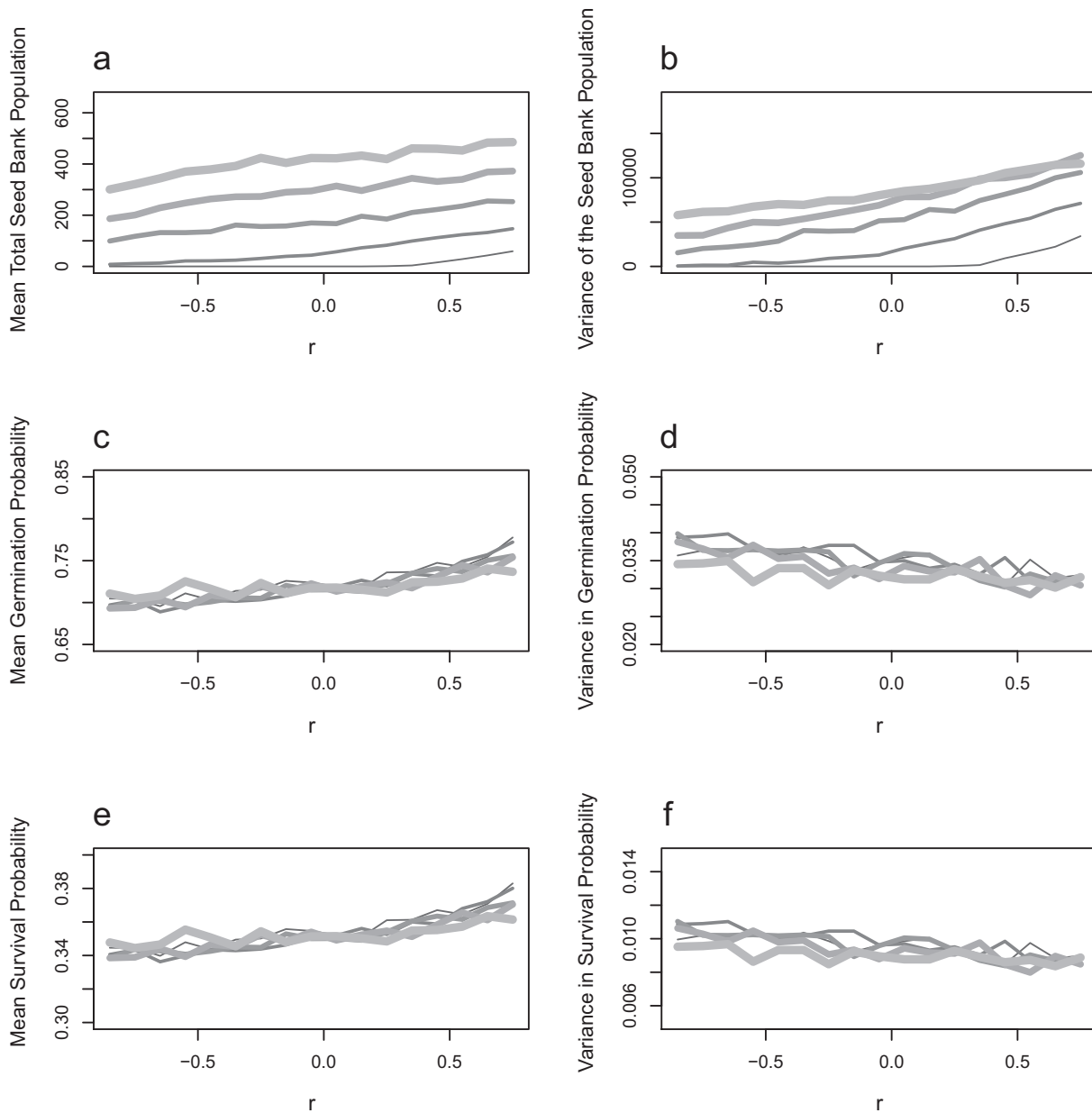
Figure 3: The mean (*a*) and variance (*b*) of the total seed bank population, mean (*c*) and variance (*d*) of the germination probability of seeds in the seed bank, and mean (*e*) and variance (*f*) of the survival probability of seeds in the seed bank. These simulations were performed with low seed survival $s_0 = 0.5$ and low fecundity $c = 50$, with $\rho = 0.5$; $\alpha = 40$; $\beta = 50$; $g_0 = 0.95$; $a = 10$; $b = 10$; $\mu = 0.02$; and h equal to 0.4, 0.5, 0.6, 0.7, and 0.8, shown with increasing line thickness and decreasing line darkness.

probabilities in fig. 5*b* and 5*c* are due to the small population sizes elicited by low h and negative r, coupled with the increased variability associated with negative r values greater than −1 (see fig. A2*b*, A2*c*).

Including autocorrelation in disturbance frequency did not change the qualitative effect of the original disturbance parameters h (probability of disturbance) and ρ (mean depth of disturbance) on the long-term mean and variance of the total seed bank population or the rare intrinsic growth rate λ, seen in Eager et al. (2013) and Eager et al. (2014*b*). When maximum seed survival s_0 was low, the effect of the mean depth of disturbance ρ on the long-term mean of the total seed bank population depended on probability of disturbance h: when disturbances were infrequent, the mean of the total seed bank population was a decreasing function of ρ, while when disturbances were more frequent, the relationship switched
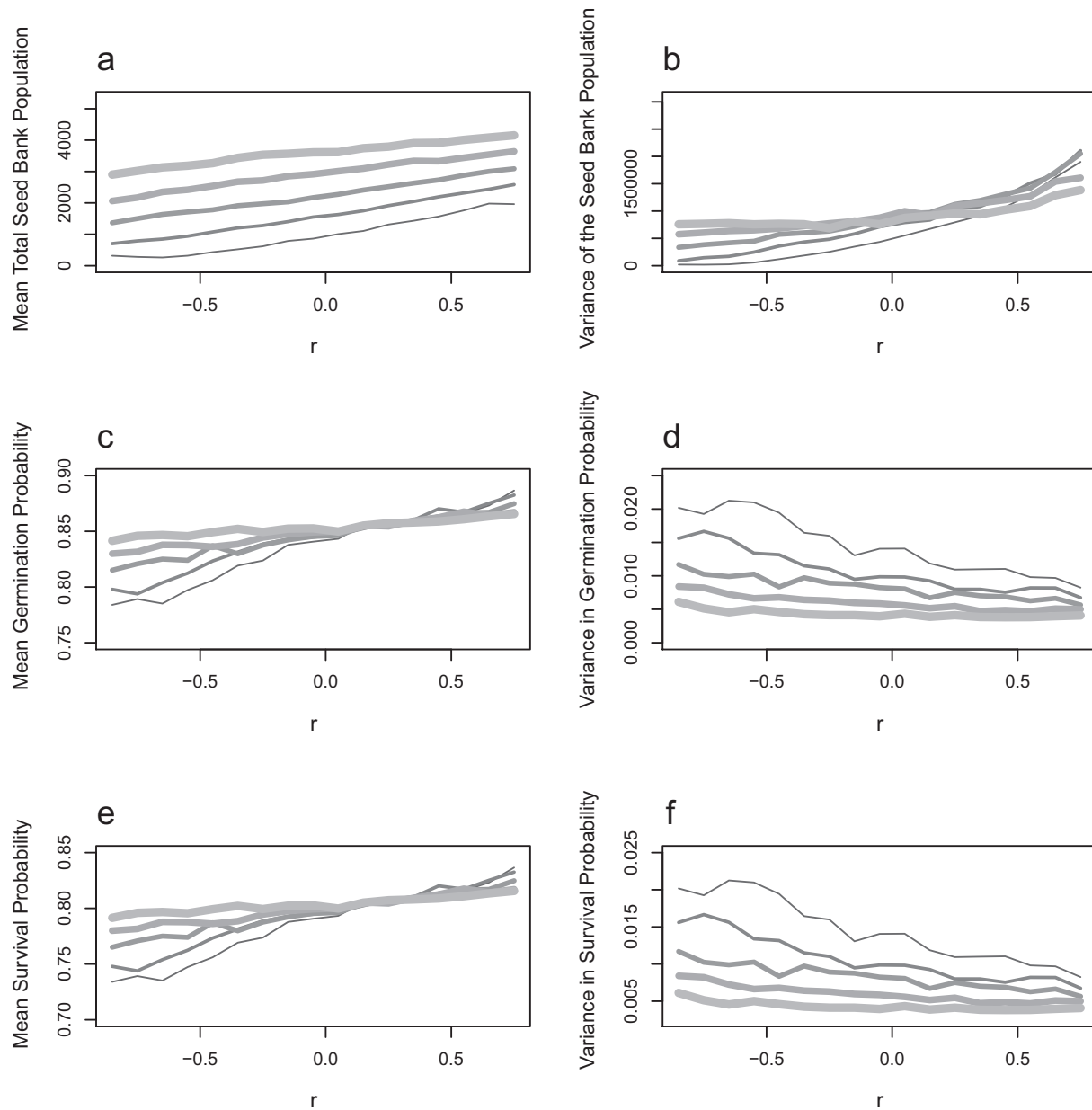
Figure 4: The mean (*a*) and variance (*b*) of the total seed bank population, mean (*c*) and variance (*d*) of the germination probability of seeds in the seed bank, and mean (*e*) and variance (*f*) of the survival probability of seeds in the seed bank. These simulations were performed with low seed survival $s_0 = 0.5$ and high fecundity $c = 150$, with $\rho = 0.5$; $\alpha = 40$; $\beta = 50$; $g_0 = 0.95$; $a = 10$; $b = 10$; $\mu = 0.02$; and h equal to 0.4, 0.5, 0.6, 0.7, and 0.8, shown with increasing line thickness and decreasing line darkness.

(fig. A4). However, as the autocorrelation coefficient r increased, this pattern appeared to become less pronounced. For all r values, the high-survival ($s_0 = 0.95$) case did not elicit a nonmonotone relationship between the long-term mean of the total seed bank population and ρ (fig. A6). The rare intrinsic growth rate value λ was an increasing function of the disturbance frequency h and a decreasing function of

the mean depth of disturbance ρ for all parameter combinations considered (figs. A5, A8).

Discussion

How populations respond to environmental variability and to temporal autocorrelations specifically is an important ques-
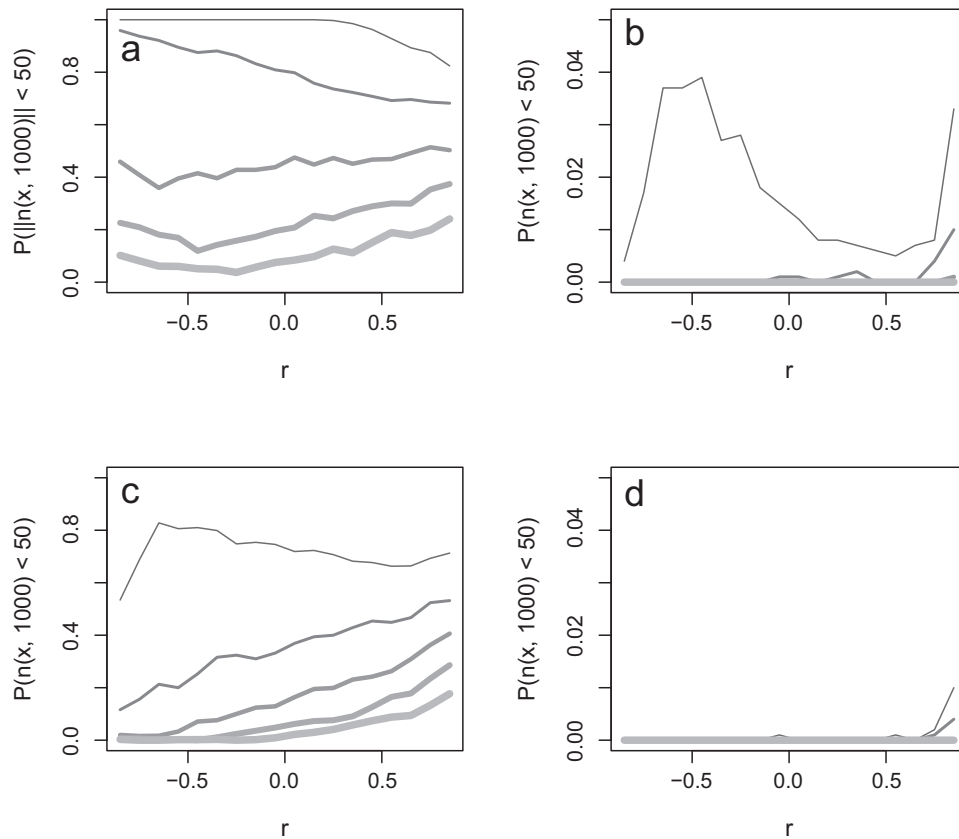
Figure 5: The quasi-extinction probability of the plant seed bank population as a function of the autocorrelation coefficient when $s_0 = 0.5$ (*a*); $c = 50$, $s_0 = 0.95$, $c = 50$ (*b*); $s_0 = 0.5$, $c = 150$ (*c*); and $s_0 = 0.95$, $c = 150$ (*d*). These simulations were performed with $\rho = 0.5$; $\alpha = 40$; $\beta = 50$; $g_0 = 0.95$; $a = 10$; $b = 10$; $\mu = 0.02$; and h equal to 0.4, 0.5, 0.6, 0.7, and 0.8, shown with increasing line thickness and decreasing line darkness.

tion in population ecology (Johst and Wissel 1997; Petchey et al. 1997; Heino 1998; Palmqvist and Lundberg 1998; Ripa and Heino 1999; Heino et al. 2000; Greenman and Benton 2003, 2005; Vassuer 2004; Schwager et al. 2006; Logdberg and Wennergren 2012; Mustin et al. 2013). Using an IPM to model a general disturbance specialist, we found that, for all parameter scenarios considered, the long-term mean and variance of the total seed bank population increased with increasing autocorrelation coefficient r. The increased possibility of a string of disturbance years allowed for population sizes to accumulate more rapidly than if disturbances are IID or negatively correlated, and the positive impact of consecutive disturbance years was higher than the negative impact of consecutive nondisturbance years (on average), since fecundity generally generates more recruits than mortality takes away in a stable, density-dependent population. The increased possibility of a string of nondisturbance years to go along with the strings of disturbance years yielded the corresponding higher variability for larger r, however. This interaction between the mean and variance of the total seed bank

population caused a complicated picture with regard to quasi-extinction probability: for low maximum seed survival s_0, fecundity c, and disturbance frequency h ("low viability" scenarios), more positively autocorrelated disturbances yielded lower quasi-extinction probabilities (by allowing otherwise weaker populations to build on the higher likelihood of consecutive disturbance years), while higher h in these cases yielded more nonmonotone effects. For example, in the case where s_0 and c were low and h was high, quasi-extinction probabilities were the lowest for $r \approx -0.35$ and increased for increasing r values (by weakening otherwise-strong populations through the higher likelihood of consecutive nondisturbance years). For high s_0 and/or high c ("high viability" scenarios), the highest extinction probability generally occurred for the highest r, although, for low h, there was still some nonmonotonicity; that is, quasi-extinction probability peaked when $r \approx -0.5$ before decreasing for larger r (fig. 5*b*, 5*c*) due to low population sizes coupled with increasing variability (fig. A2*b*, A2*c*). These results coincide roughly with the general results in the review article by Ruo-

kolainen et al. (2009), because when (undercompensatory) density-dependent effects are more drastic (when average population sizes are higher), extinction risk increases with increasingly positive autocorrelation as a result of enhanced population fluctuations.

Increasing the autocorrelation coefficient r had the effect of increasing both the average seed survival and the average germination probability of a given seed in the seed bank as well as decreasing the variances in both of these values. Higher mean seed survival and germination rates, along with decreasing variability in both of these rates, would seem to imply more viable populations in response to increasingly positive autocorrelations. However, this was generally not the case for these high-viability scenarios, where quasi-extinction probability increased with increasing r. This was likely due to density dependence in conjunction with variance in the total seed bank population size, the impact of both of which substantially increased as r increased. When seed bank population sizes were high, there were generally many aboveground plants in the event of a string of disturbance years and, subsequently, many newly created seeds present to take advantage of an increase in germination probability. However, there is a maximum number of seeds that can eventually become plants in any given year, and the density dependence in seedling establishment causes a diminishing benefit of repeated disturbances with increasing r. Meanwhile, with the risk of repeated nondisturbance years increasing with increasing r, extinction risk increased in these scenarios despite higher (per capita) mean seed survival and germination probabilities. In low-viability scenarios, disturbances were infrequent enough that populations experiencing additional germination probability for increasing r from an otherwise smaller total seed bank population would generally not be as limited by density-dependent establishment. This, coupled with the higher seed survival (particularly for lower h values), yielded lower extinction probabilities and substantially higher mean population sizes for increasing r values in these scenarios.

We found that a nonmontone relationship between total seed bank population size and mean depth of disturbance ρ found in Eager et al. (2013) was preserved for low maximum seed survival s_0, that populations near extinction had increasing mean population sizes when mean depth of disturbance ρ was smaller. We reasoned in Eager et al. (2013) and Eager et al. (2014b) that disturbance specialist plants that are near extinction levels actually do better when less of the population is disturbed each time step, since burying seeds deeper in the seed bank (where survival is relatively low) was less preferable than leaving them near the surface of the soil (where the germination rate is higher). This relationship also manifests itself when looking at the rare intrinsic growth rate λ, which gave insight into how well a population grows, on average, when rare. We found that, for every parameter and autocorrelation scenario, λ was a decreasing function of ρ. However, it appeared that λ grew with increasing r for the parameter combinations that we considered, which would seem to imply that increasing r decreases extinction probability. This highlights the limitations with continuous-space models like IPMs: populations that take arbitrarily small population sizes habitually at or before increasing to a stochastic equilibrium, or populations that persist at very small population sizes, were considered nonextinct ($\lambda > 1$) from a mathematical point of view but quasi-extinct by the standards we have set in this article. Creating a quasi-extinction threshold is preferable to insisting that long-term populations are mathematically or computationally zero, since small populations are especially prone to demographic stochasticity, which, especially when coupled with environmental stochasticity, increased extinction risk (Lande 1993).

Previous work (e.g., Lawton 1988; Caswell and Cohen 1995; Johst and Wissel 1997; Heino 1998; Logdberg and Wennergren 2012; Mustin et al. 2013) all concluded, for various model structures and complexities, that increasingly positively autocorrelated environments lead to an increase in extinction risk, while Ripa and Lundberg (1996) concluded the opposite—that increasingly positively autocorrelated environments decreased extinction risk. Our results suggest that the effect of r depends on population viability. If populations have a high risk of going extinct (caused by low-viability scenarios), increasingly autocorrelated disturbances are beneficial, but if population viability is high (caused by high-viability scenarios), increasingly positive autocorrelated disturbances decrease population persistence. Petchey et al. (1997), Ripa and Heino (1999), Greenman and Benton (2005), Schwager et al. (2006), Ruokolainen and Fowler (2009), and Ruokolainen et al. (2009) alluded to other ecological factors, such as over- versus undercompensatory density dependence, as influencing whether increasingly positive autocorrelated environments caused extinction risks to increase or decrease. Generally, overcompensatory density dependence (caused by scramble competition) coupled with positively autocorrelated environmental fluctuations was found to decrease extinction risk, while the opposite was true for undercompensatory density dependence (caused by contest competition, as in our model). Our results mostly coincide with previous work; that more-viable populations—populations experiencing the effects of undercompensatory density dependence—had higher extinction risks as a result of increasingly positive autocorrelations. Populations that were less viable did not experience density dependence as heavily and thus were less likely to have increasing extinction risk as r increased.

The rare intrinsic growth rate λ increased with increasing autocorrelation coefficient r for all parameter values considered (figs. A5, A8). In earlier work, the intrinsic growth rate of the population has been found to change the way in which populations respond to autocorrelation, with higher intrinsic growth rates contributing to more variable population dy-

namics, which lead to increasing extinction risk in response to increasingly positive autocorrelated environments (Roughgarden 1975; Heino 1998; Schwager et al. 2006). Since quasi-extinction increased with r only when population viability was high, our results appear to coincide with the literature in only those scenarios.

Our environmental variable (disturbances), rather than being simply a weak additive noise term on a population with a strong deterministic signature (which is often how stochastic population models are constructed), was really driving the population dynamics simulated by these models. Whether a disturbance occurred, and how deeply disturbances affected the seed bank if they occurred, fundamentally altered how populations in one year contributed to populations in the next year. Attempts to capture the "average" dynamics with a deterministic model in systems like these are generally futile (Eager et al. 2013*a*) because of the drastic differences between a disturbance year and a nondisturbance year as well as nonlinearities in the model caused by density dependence. However, allowing disturbances to be the specific mechanism causing stochasticity and autocorrelation in our model added to our ability to understand how autocorrelation affects population dynamics. Without disturbance, a disturbance specialist plant cannot reproduce, meaning that environmental noise was necessary for these populations to persist. However, under certain parameter combinations, positively autocorrelated noise could cause the population to go extinct anyway, because sustained time periods with frequent disturbance cannot allow the population sizes to increase as much under undercompensatory density dependence, because a similarly long streak of nondisturbance years can deplete population sizes. Since many aspects of the plant seed bank dynamics for disturbance specialist plants may exhibit overcompensatory density dependence (e.g., seed production or seed survival and germination; Moody-Weis and Alexander 2007; Pico and Retana 2008; Jauni et al. 2015), future models may need to include overcompensatory density dependence to better understand how different density dependence assumptions affect model predictions. Since models with overcompensatory density dependence often predict decreases in population size when population sizes in previous years are large, overcompensatory density dependence will likely decrease mean seed bank population size in our model. In our current model, undercompensatory density dependence simply imposes a "cap" on large populations instead of suppressing them. Counterintuitively, it may be the case that adding overcompensatory density dependence would decrease a population's extinction risk as autocorrelation increases, since a prolonged streak of nondisturbance years may drive a population to low enough levels that the relief from density dependence is higher than the losses incurred by a decrease in disturbance frequency.

For wild sunflower, we found that disturbance frequency was positively autocorrelated with values ranging from 0.09 to 0.44 (Alexander et al. 2009). Thus, at least as they relate to wild sunflower, our most important results center around what happens when the autocorrelation coefficient r is greater than 0. These results can be summarized in the following way: for populations with favorable conditions, increasingly positive autocorrelated disturbances will increase extinction risk (even as they increase the population's mean total population size, survival probability, and germination probability). Populations with unfavorable conditions, while having extinction probabilities generally higher than those from populations with more favorable conditions, will see relief in extinction risk from increasingly autocorrelated disturbances. The former result stems from density dependence limiting the positive effects of a string of disturbance years, leaving them more vulnerable when a prolonged streak of nondisturbance years hits. The latter stems from frequently low population sizes limiting the effects of density dependence, so in these cases, these populations can take advantage of prolonged streaks of disturbance to counterbalance the negative effects of prolonged streaks without disturbance. Future work will explore autocorrelations in other demographic variables, such as seed survival and germination, and how these autocorrelations influence autocorrelations in disturbances and subsequently affect population dynamics and extinction risk.

Acknowledgments

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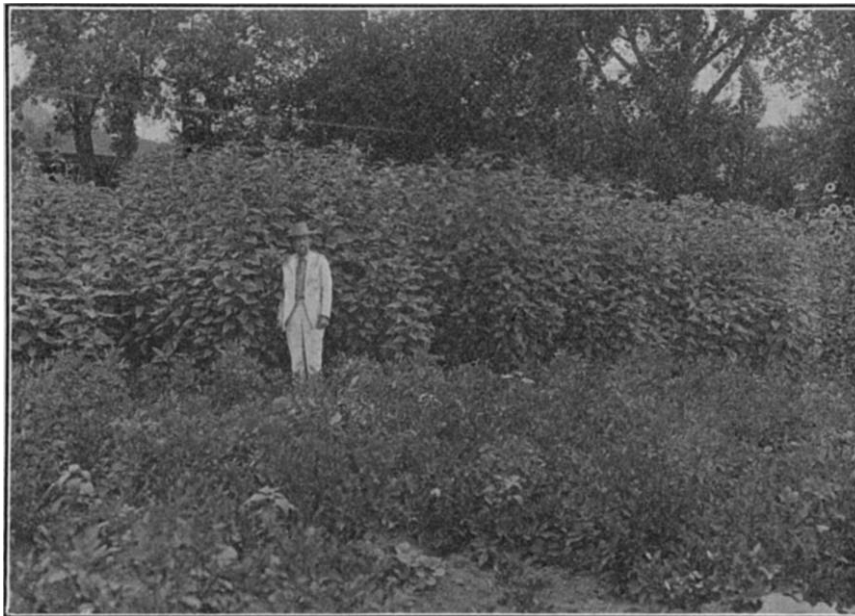
"*Helianthus tuberosus* var. *albus* (var. *fusiformis* at extreme left). The flowers are *Helianthus annuus*." From "The Varieties of *Helianthus tuberosus*" by T. D. A. Cockerell (*The American Naturalist*, 1919, 53:188–192).

Appendix from E. A. Eager et al., "Assessing the Influence of Temporal Autocorrelations on the Population Dynamics of a Disturbance Specialist Plant Population in a Random Environment" (Am. Nat., vol. 190, no. 4, p. 570)

Part A.

To prove the convergence of the stationary distribution μ^* for $\{[n(x,t),\ p(t)]^T\}_{t=0}^{\infty}$, we need to work in the space $C^+[0,D]$ of positive continuous functions over the interval $[0,D]$. To do so, we need to use the kernel approximation as in Eager et al. (2014b) to make $K(x,y,\theta)$, a continuous function of the spatial variables x and y and disturbance depth θ. Please see Eager et al. (2014b, pp. 1815–1816) for how this is done. With this kernel construction, the population

$$x(\cdot)_t := n(\cdot,t) + cJ(\cdot)p(t),$$

with $n(x,t)$ and $p(t)$ from equation (3), solves the stochastic difference equation (with the dependence on space omitted)

$$x_{t+1} := H(\theta_t, x_t) := A_0(\theta_t)x_t + bf(c(\theta_t)^T x_t), \tag{A1}$$

where the stochastic process modeling the disturbances $\{\theta_t\}_{t=0}^{\infty} \subset \Omega$, the probability space of all possible disturbance scenarios. Here, $b \in C^+[0,D]$ is the function $cJ(\cdot)$, $A_0(\omega)$ are the linear operators from $C^+[0,D]$ to itself defined by

$$A_0(\theta)u := \int_0^D s(\cdot)(1 - g(\cdot,\theta))K(\cdot,y,\theta)u(y)dy,$$

and $cT(\theta)$ are the functionals from $C^+[0,D]$ into $\mathbb{R}^+$ defined by

$$c(\theta)^T u := \int_0^D \int_0^D g(x,\theta)K(x,y,\theta)u(y)dydx,$$

for $u \in C^+[0,D]$.

To best handle the years without disturbance, we create $\mathcal{J} = \{t \in N | \theta_t > 0\}$, the subset of all time steps for which there is a disturbance, which can be ordered to create a subsequence $\{\hat{t}\}_{t=0}^{\infty} \in \mathbb{N} \cup \{0\}$, as in Eager et al. (2014b). We create this subsequence in the following way: if $\theta_0 > 0$ (there is a disturbance at $t = 0$), define $\hat{t} \in \mathcal{J}$ to be the time step of the $(t + 1)$st disturbance. If $\theta_0 = 0$ (there is no disturbance at $t = 0$), let $\hat{0} = 0$ and define $\hat{t} \in \mathcal{J}$ to be the time step of the tth disturbance. To allow us to use the results in Hardin et al. (1988), we study the population on the sequence of time steps $\{\hat{t}\}_{i \in \mathcal{J}}$. We note that, when $\theta_t = 0$, in addition to being linear, the model (A1) is also completely deterministic. To see this, note that, when $\theta_t = 0$, the model (A1) becomes

$$
\begin{aligned}
x(z)_{t+1} &= \int_0^D s(z)(1 - g(z,0))K(z,y,0)x(y)_t dy \\
&\quad + \kappa J(z)f\left(\int_0^D \int_0^D g(z,0)K(z,y,0)x(y)_t dydz\right) \\
&= s(z)x(z)_t dy + \kappa J(z)f(0) \\
&= s(z)x_t(z)
\end{aligned}
$$

by the definition of $K(\cdot,\cdot,0)$ and the fact that $g(z,0) = 0$ for all $z \in [0,D]$. Therefore, if we let τ_t be the number of time steps between (disturbance) time steps $\hat{t}$ and $\widehat{t+1}$ and only track x_t for those time steps $\hat{t}$ where there are disturbances (i.e., gather together all nondisturbance time steps into one $\hat{t}$ time step), then the model (A1) becomes

$$x_{\widehat{t+1}} := \hat{H}(\theta_{\hat{t}}, x_{\hat{t}}) := \hat{A}_0(\theta_{\hat{t}})x_{\hat{t}} + bf(\hat{c}(\theta_{\hat{t}})^T x_{\hat{t}}), \tag{A2}$$

1

with

$$\hat{A}_0(\theta)u := \int_0^D s(\cdot)(1 - g(\cdot))K(\cdot, y, \theta_2)s(y)^\tau u(y)dy,$$

and

$$\hat{c}(\theta)^T u := \int_0^D \int_0^d g(z)K(z, y, \theta_2)s(y)^\tau u(y)dydz.$$

With this reformulation, our stochastic process is now the sequence $\{(\theta_2)_i, \tau_i\}_{i \in J}$, where $(\theta_2)_i$ is just the depth of disturbance at the time step $\hat{t}$, and the random variable $\hat{t}$ is the number of time steps between the disturbance at time $\hat{t}$ and $t + 1$.

It also follows that $(\theta_2)_i$ and τ_i are probabilistically independent for each $\hat{t}$. With this, we will define the stochastic process $\{\hat{\theta}_i\}_{i \in J} = \{(\theta_2)_i, \tau_i\}_{i \in J}$, where $\{\hat{\theta}_i\}_{i \in J}$ is now a sequence of IID random variables coming from the space Ω of all possible environmental states defining the stochastic process. Note that the probability spaces $\hat{\Omega}$ and Ω contain the same relevant probabilistic information, because the values of when $\theta = 0$ do not influence the population. Also notice that, since $\theta_i \neq 0$ for all $\hat{t}$, it follows that $g(z, \theta_i)$ is simply $g(z)$ for all $\hat{t}$. We need to assume, for analytical tractibility, that the number of consecutive years without a disturbance is bounded above by $T \gg 1$ and that the depth of disturbance θ_2 is bounded below by the positive number $\underline{\theta_2} \ll 1$.

If we can prove that the probability measures $\{\mu_i\}_{i \in J}$ associated with the sequence $\{x_i\}_{i \in J}$ converge weakly to the measure $\hat{\mu}^*$, independent of initial population, we will have that the probability measures $\{\mu_t\}_{t=0}^\infty$ associated with the sequence $\{x_t\}_{t=0}^\infty$ (that explicitly includes nondisturbance time steps) converge weakly as well. This argument follows exactly from pages 1817–1820 in Eager et al. (2014b), with the vector of probabilities $[p_0, p_{1,\ldots}, p_T]^T$ representing the stationary distribution of the "age" of the seed bank, or the number of time steps since the last disturbance, being the leading right eigenvector of the following $T \times T$ transition matrix

$$\begin{pmatrix} p & 1-q & 1-q & \cdots & 1-q & 1 \\ 1-p & 0 & 0 & \cdots & 0 & 0 \\ 0 & q & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \ddots & \cdots & \vdots & \vdots \\ 0 & 0 & 0 & q & 0 & 0 \\ 0 & 0 & 0 & \cdots & q & 0 \end{pmatrix}.$$

It is not difficult to show that

$$p_0 = \frac{1-q}{(1-q) + (1-p)(1-q)^T}$$

and that $p_i = (1-p)q^{T-1}p_0$ for $i = 1, 2, 3, \ldots, T$. This stationary distribution is different than that in Eager et al. (2014b) because of the change from IID disturbances to autocorrelated ones.

The model (3) in the main body of this article (with the modified kernel) satisfies assumptions (A1)–(A5) and thus properties (H1)–(H7) in Eager et al. (2014b). Thus, the proof of the following theorem establishing the stationary distribution of $\{[n(x,t), p(t)]^T\}_{t=0}^\infty$ follows directly from pages 1823–1827 in that article:

Theorem 1.   *Suppose (A1), (A2), (A3), (A4), and (A5) in Eager et al. (2014b) for the model (A2) are satisfied and $x_0 \neq 0 \in C[0, D]^+$ with probability 1. Then x_t converges in distribution to a stationary distribution μ^*, independent of x_0, such that either $\mu^*(\{0\}) = 0$ or $\mu^*(\{0\}) = 1$. If $\lambda > 1$, then $\mu^*(\{0\}) = 0$, and if $\lambda < 1$, then $\mu^*(\{0\}) = 1$.*

Additionally, $n(\cdot, t)$ and $p(t)$ converge in distribution to unique stationary distributions μ_1^* and μ_2^*, respectively, independent of $n(\cdot, 0)$ and $p(0)$.
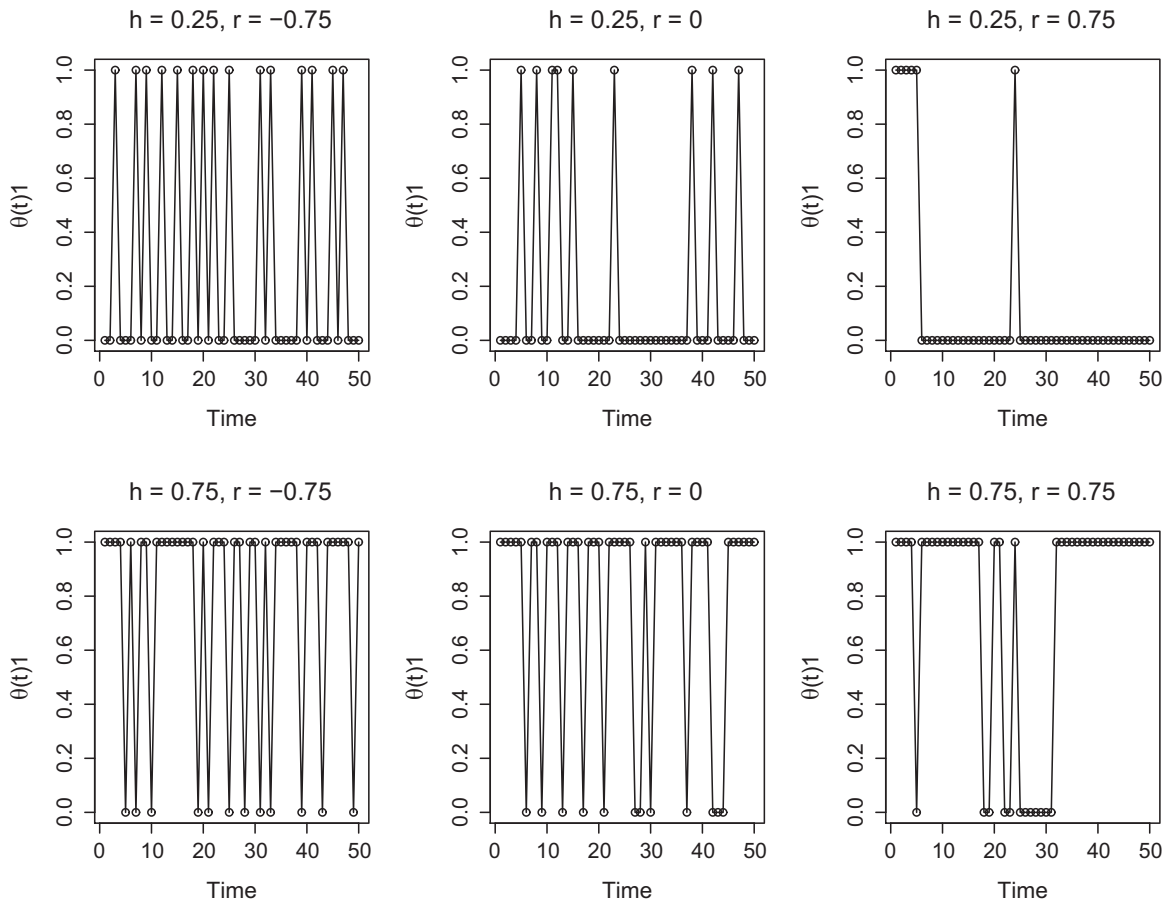
Part B.   Supplementary Figures

Figure A1: Example sequences of $\theta_1(t)$ values for probability of disturbance values $h = 0.25$ and 0.75 and autocorrelation coefficients $r = -0.75$, 0, and 0.75 for 50 time steps each.
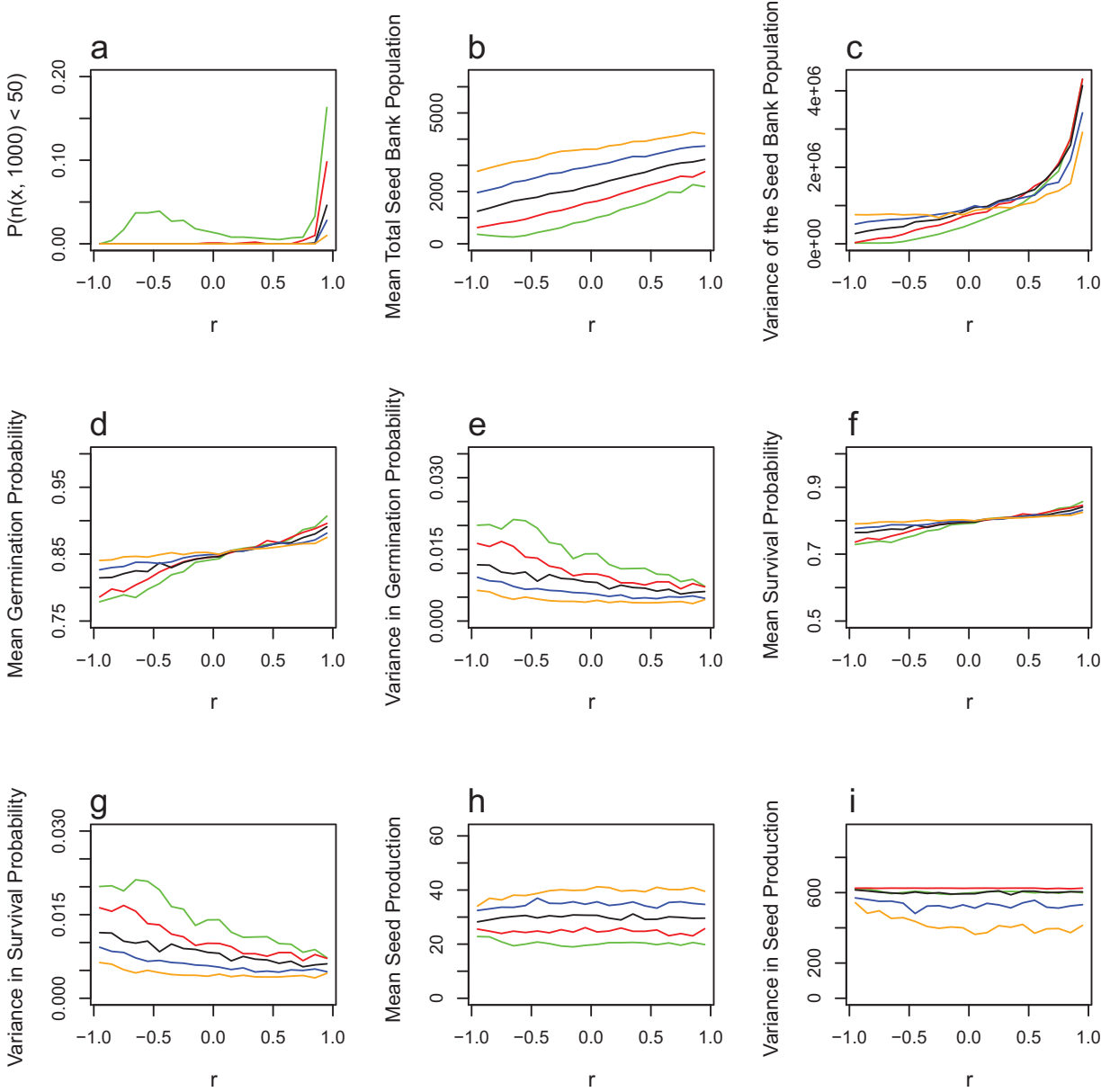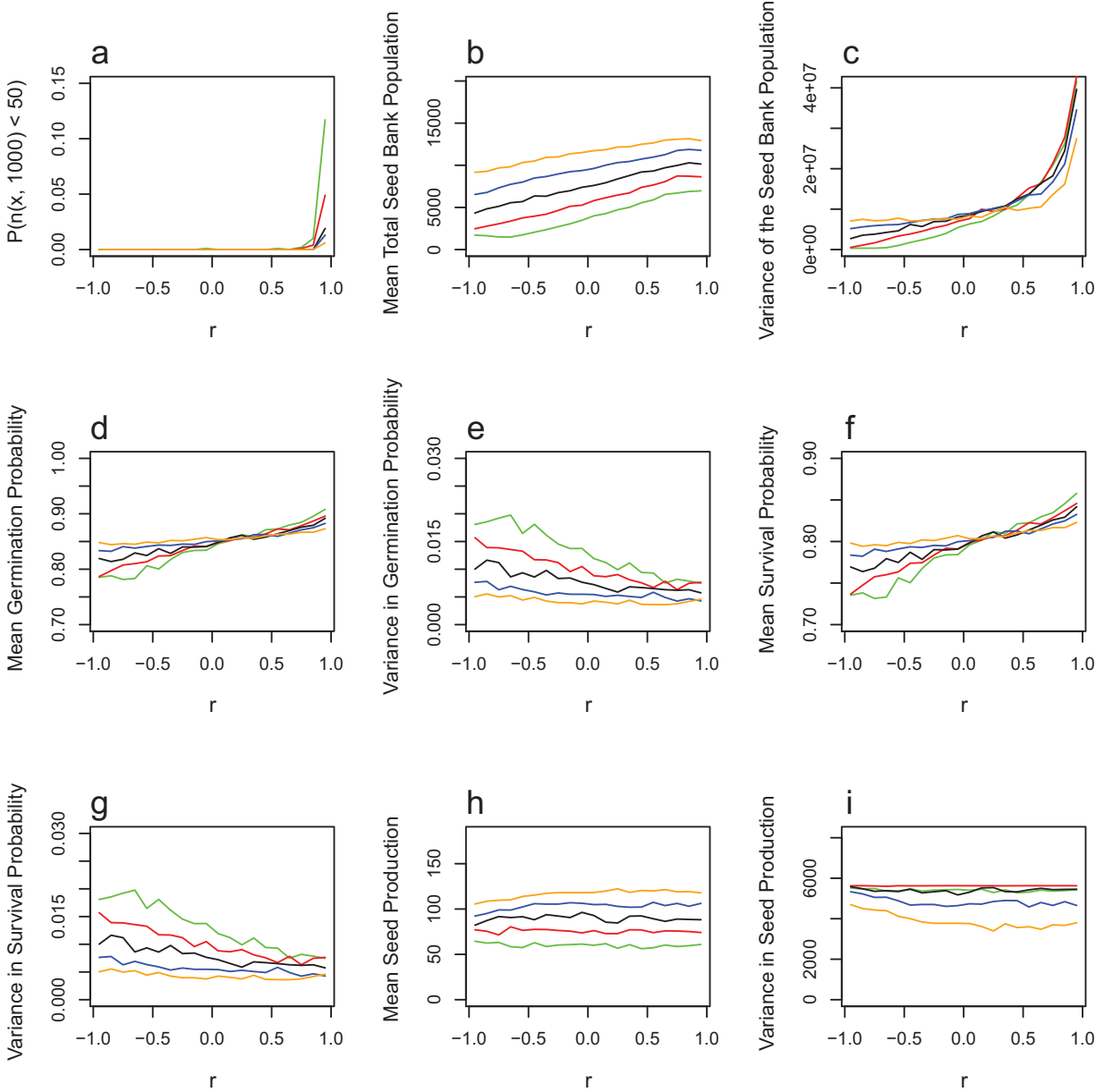
Figure A2: The quasi-extinction probability (*a*), mean (*b*), and variance (*c*) of the total seed bank population, mean (*d*) and variance (*e*) of the germination probability of seeds in the seed bank, mean (*f*) and variance (*e*) of the survival probability of seeds in the seed bank, and the mean (*g*) and variance (*i*) of the seed production of seeds in the seed bank. These simulations were performed with high seed survival $s_0 = 0.95$ and low fecundity $c = 50$, with $\rho = 0.5$; $\alpha = 40$; $\beta = 50$; $g_0 = 0.95$; $a = 10$; $b = 10$; $\mu = 0.02$; and *h* equal to 0.4 (green), 0.5 (red), 0.6 (black), 0.7 (blue), and 0.8 (orange).

Figure A3: The quasi-extinction probability (*a*), mean (*b*), and variance (*c*) of the total seed bank population, mean (*d*) and variance (*e*) of the germination probability of seeds in the seed bank, mean (*f*) and variance (*e*) of the survival probability of seeds in the seed bank, and the mean (*g*) and variance (*i*) of the seed production of seeds in the seed bank. These simulations were performed with high seed survival $s_0 = 0.95$ and high fecundity $c = 150$, with $\rho = 0.5$; $\alpha = 40$; $\beta = 50$; $g_0 = 0.95$; $a = 10$; $b = 10$; $\mu = 0.02$; and h equal to 0.4 (green), 0.5 (red), 0.6 (black), 0.7 (blue), and 0.8 (orange).
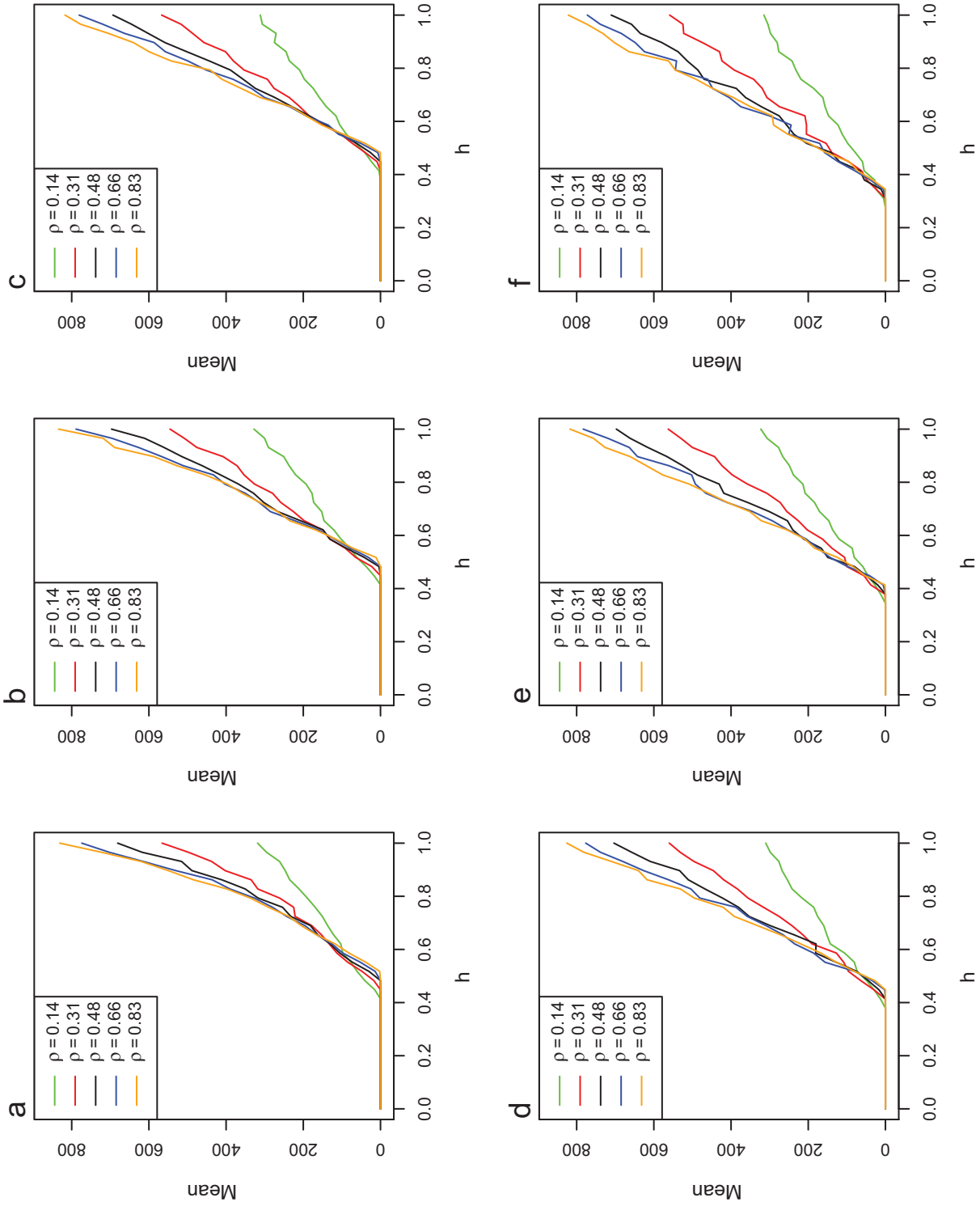
Figure A4: The mean of the total seed bank population $\|n(x, t)\|_1$ as a function of the disturbance frequency h, with varying mean depth of disturbance values ρ and r values given by $r = -0.75$ (a), $r = -0.45$ (b), $r = -0.15$ (c), $r = 0.15$ (d), $r = 0.45$ (e), and $r = 0.75$ (f). In all plots, $c = 50$, $\alpha = 40$, $\beta = 50$, $g_0 = 0.95$, $a = 10$, $b = 10$, and $\mu = 0.02$, with low seed bank survival $s_0 = 0.5$.
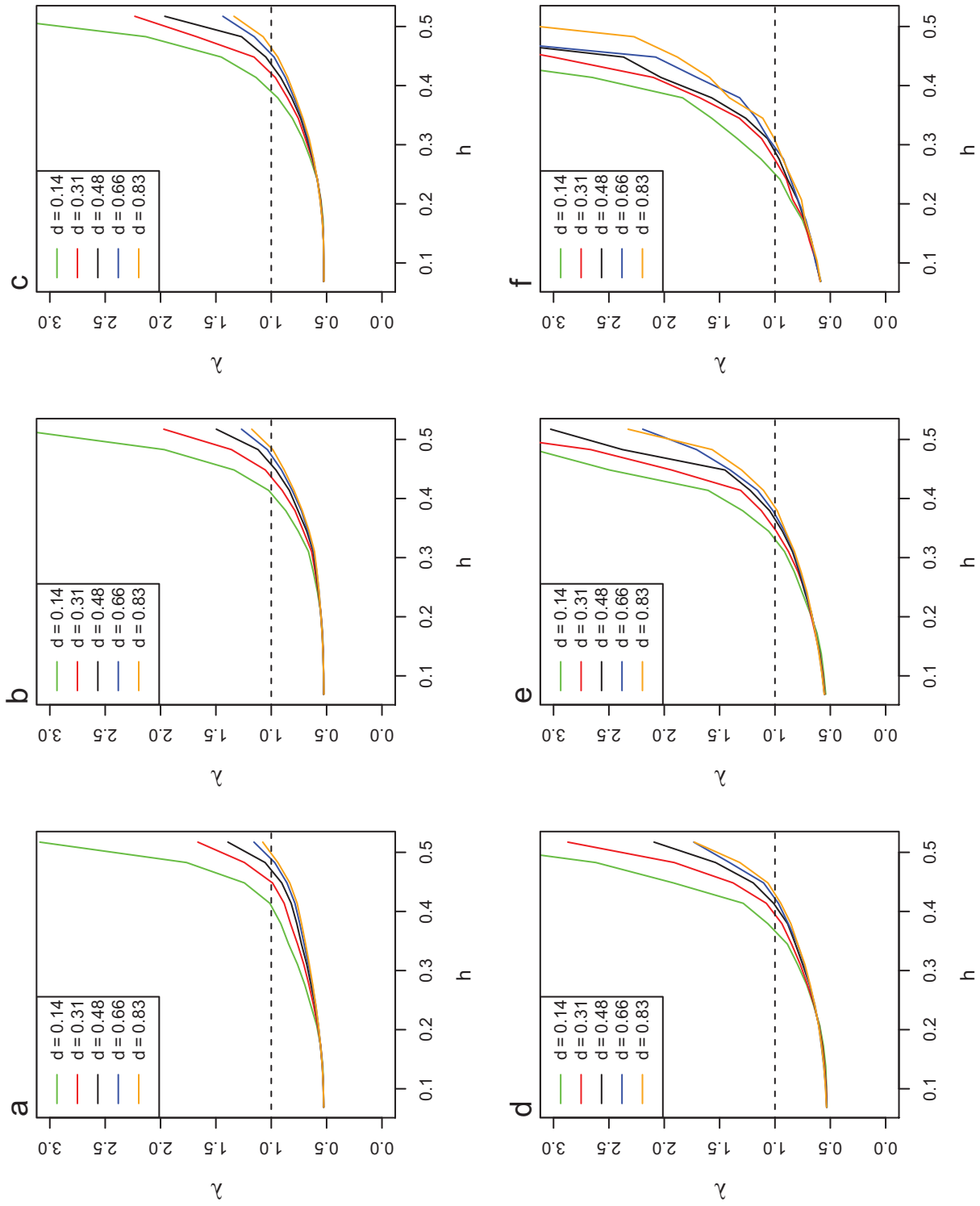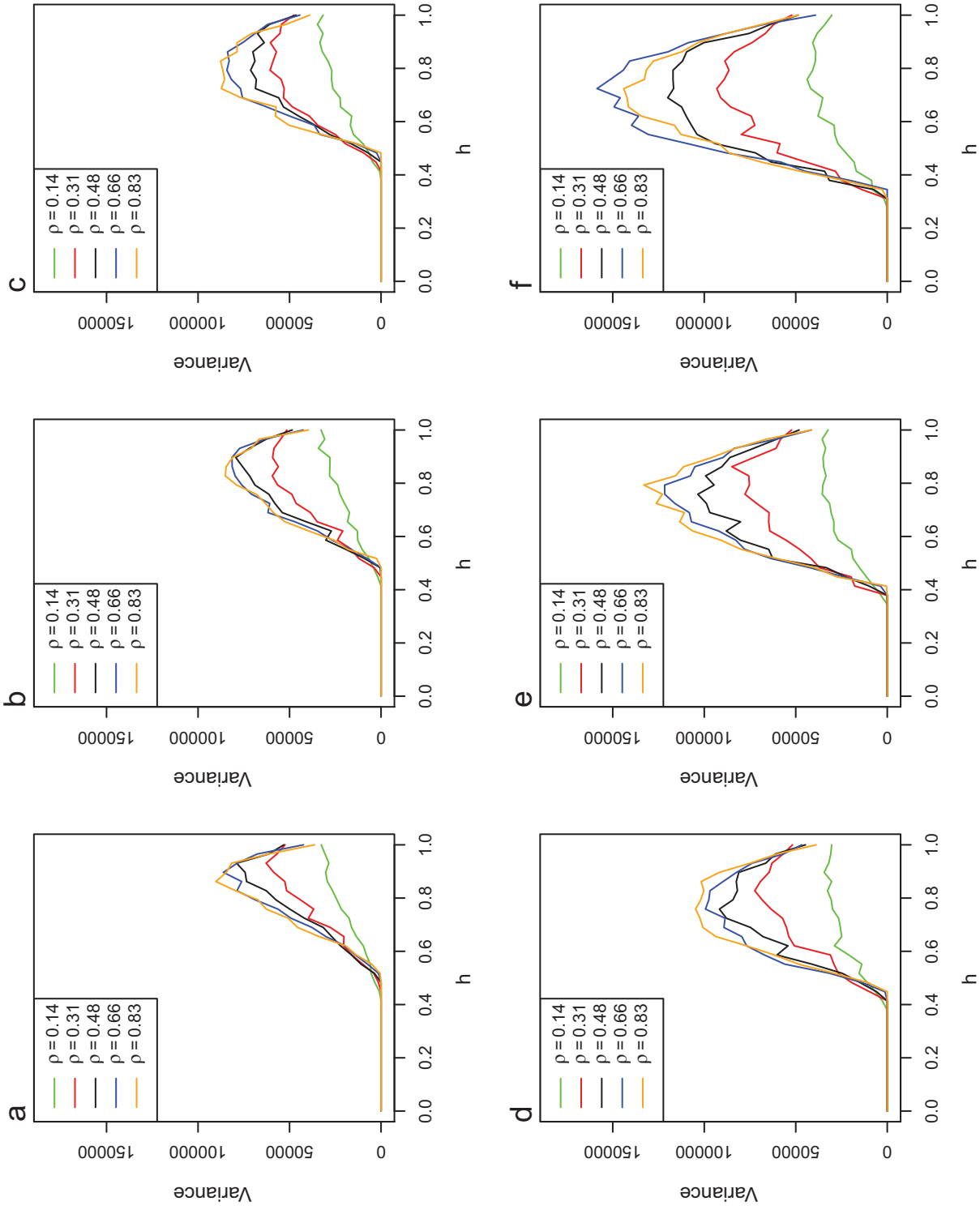
Figure A5: The rare intrinsic growth rate λ as a function of the disturbance frequency h, with varying mean depth of disturbance values ρ and r values given by $r = -0.75$ (*a*), $r = -0.45$ (*b*), $r = -0.15$ (*c*), $r = 0.15$ (*d*), $r = 0.45$ (*e*), and $r = 0.75$ (*f*). In all plots $c = 50$, $\alpha = 40$, $\beta = 50$, $g_0 = 0.95$, $a = 10$, $b = 10$, and $\mu = 0.02$, with low seed bank survival $s_0 = 0.5$.

Figure A6: The variance of the total seed bank population $\|n(x,t)\|_1$ as a function of the disturbance frequency h, with varying mean depth of disturbance values ρ and r values given by $r = -0.75$ (a), $r = -0.45$ (b), $r = -0.15$ (c), $r = 0.15$ (d), $r = 0.45$ (e), and $r = 0.75$ (f). In all plots, $c = 50$, $\alpha = 40$, $\beta = 50$, $g_0 = 0.95$, $a = 10$, $b = 10$, and $\mu = 0.02$, with high seed bank survival $s_0 = 0.5$.
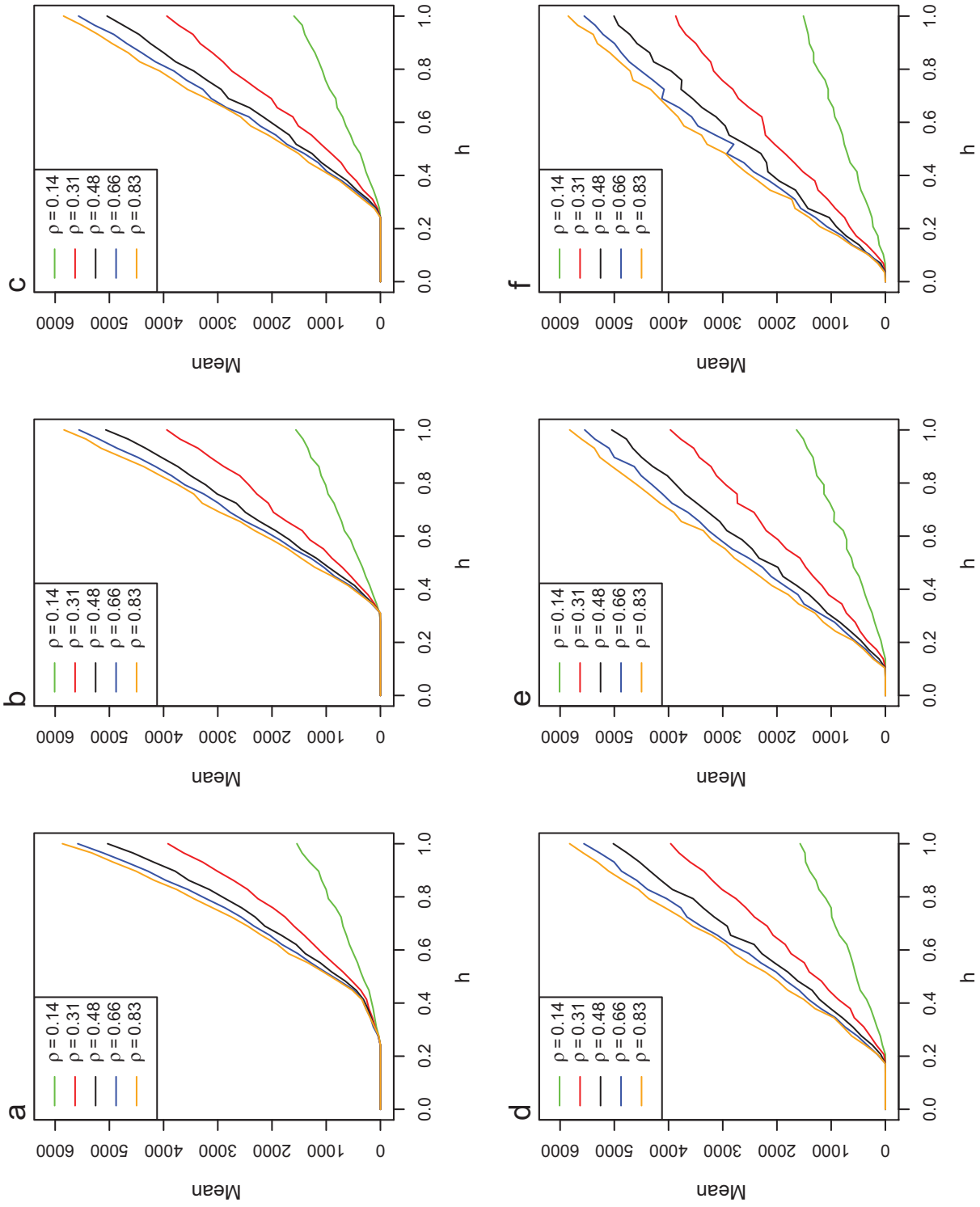
Figure A7: The mean of the total seed bank population $\|n(x,t)\|_1$ as a function of the disturbance frequency h, with varying mean depth of disturbance values ρ and r values given by $r = -0.75$ (a), $r = -0.45$ (b), $r = -0.15$ (c), $r = 0.15$ (d), $r = 0.45$ (e), and $r = 0.75$ (f). In all plots, $c = 50$, $\alpha = 40$, $\beta = 50$, $g_0 = 0.95$, $a = 10$, $b = 10$, and $\mu = 0.02$, with high seed bank survival $s_0 = 0.95$.
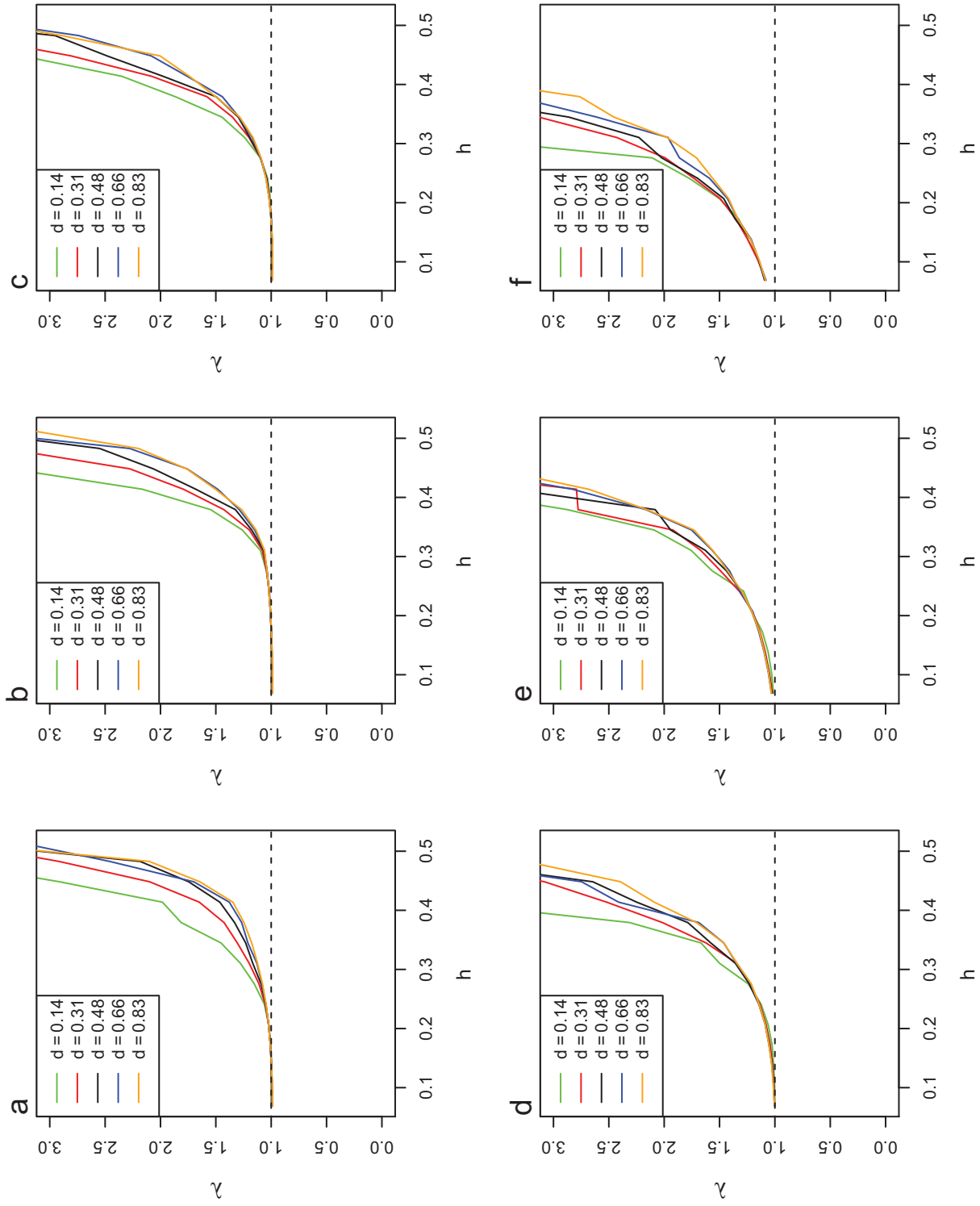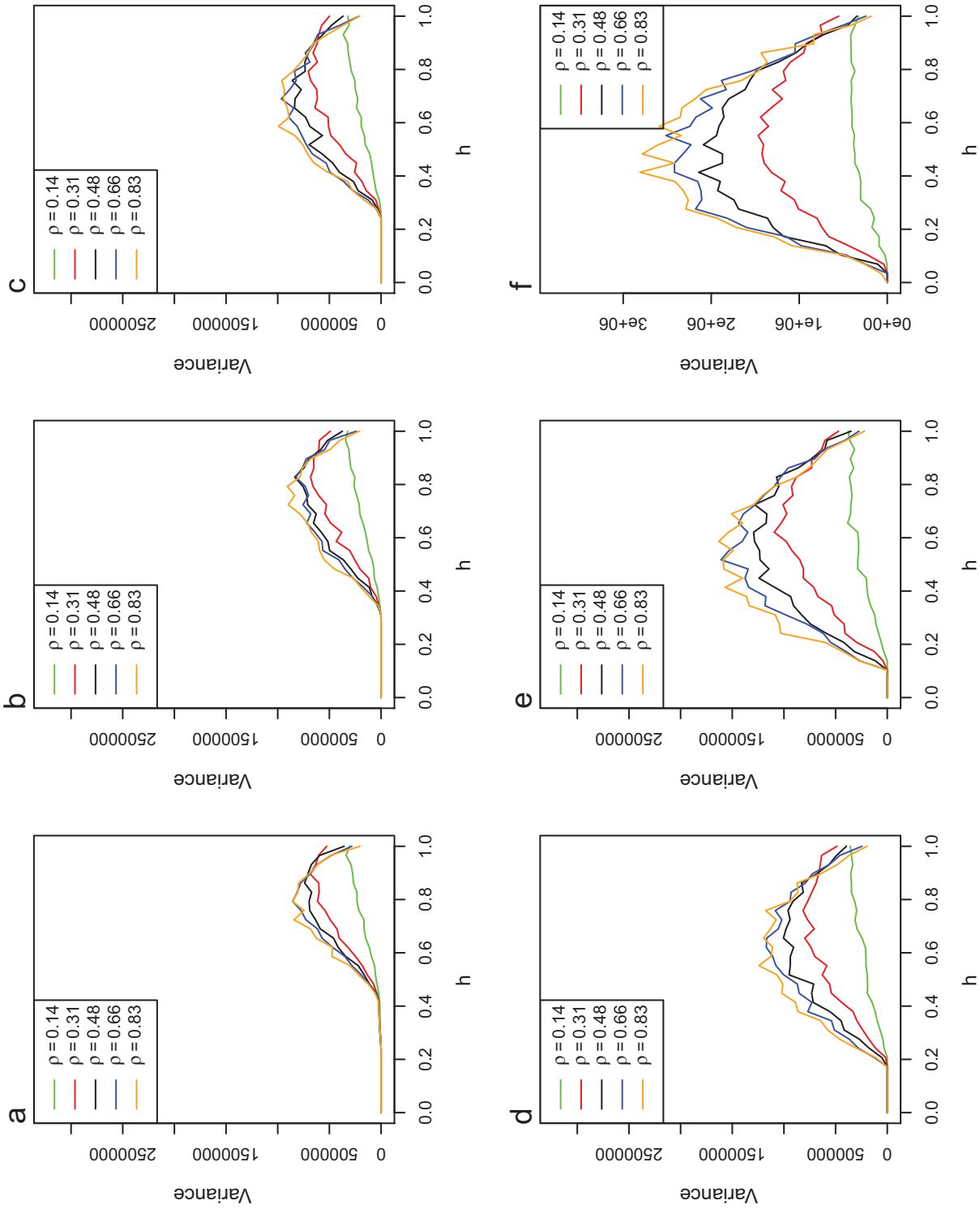
Figure A8: The rare growth rate λ as a function of the disturbance frequency h, with varying mean depth of disturbance values ρ and r values given by $r = -0.75$ (*a*), $r = -0.45$ (*b*), $r = -0.15$ (*c*), $r = 0.15$ (*d*), $r = 0.45$ (*e*), and $r = 0.75$ (*f*). In all plots, $c = 50$, $\alpha = 40$, $\beta = 50$, $\alpha = 10$, $b = 10$, and $\mu = 0.02$, with high seed bank survival $s_0 = 0.95$.

Figure A9: The variance of the total seed bank population $\|n(x,t)\|_1$ as a function of the disturbance frequency h, with varying mean depth of disturbance values ρ and r values given by $r = -0.75$ (a), $r = -0.45$ (b), $r = -0.15$ (c), $r = 0.15$ (d), $r = 0.45$ (e), and $r = 0.75$ (f). In all plots, $c = 50$, $\alpha = 40$, $\beta = 50$, $g_0 = 0.95$, $a = 10$, $b = 10$, and $\mu = 0.02$, with high seed bank survival $s_0 = 0.95$.