Last updated: February 17, 2021

Seed banks present a challenge for models of plant population demography. Individual seeds can not be tracked and it is likely that there is greater uncertainty associated with seed bank vital rates. Ecologists have turned to various methods to assess survival and germination from the seed bank, including experimental burials and seed addition experiments.

I've now re-read Rees and Long (1993) and I think that's not the correct approach for the seed bag data. They present an analysis of recruited seedlings, fitting distributions to 5 years of data on emerged seedlings.

Instead, I think it would be useful to look at models for litter decomposition. I read Olson (1963) and Cornwell et al. (2014), which both present logic for analyzing litter decomposition experiments. Cornwell et al. (2014) have a series of functions in Table 1 that could serve as "process models". The approach I'm going to try is to use a sampling model that represents the binomial experiment (seeds in seed bags) and a process model that represents the decay of survival probability.

The base assumption is often that seed mortality proceeds at a constant, absolute rate. Although this assumption has repeatedly been challenged (Lonsdale 1988, Rees and Long 1993) there remain limited assessments for how appropriate it is.

A negative exponential model corresponds to the decay of radioactive isotopes. As described in Cornwell and Weedon (2014), this model has a constant decay parameter k that implies the decaying material be treated as a homogeneous mass with each seed having an equal probability of mortality throughout time. But we know that seeds exhibit phenotypic variation in dormancy-related traits. The negative exponential decay model may be appropriate if seed survival is random in time and largely unrelated to seed characteristics.

The continuous exponential model is one in which seed mortality is described by a continuous quality distribution. For example, if seed survival is a function of a continuous phenotypic trait, we could imagine this model describing the survival process.

The Weibull residence time model represents the seed pool as a distribution of survival times. Parameter alpha controls the shape of the decomposition trajectory and beta the rate of decomposition. This model can reduce to the exponential model when alpha is 1. If alpha is less than 1, the decomposition rate decreases through time. If alpha is greater than 1, the decomposition rate increases through time.

The table below summarizes the models we considered, the parameters, and the number of parameters for each model. The product of the mortality and germination process is a deterministic function that equals the average proportion of seeds that are expected to be intact or germinated. This average proportion is the mean of a beta distribution with process variance that captures variation beyond the effect of seed age on mortality as represented with a mortality process and germination. We might also consider a germination process where germination is randomly distributed and independent for each bag?

Table 1: Seed bag dataset models

Model	Mortality process	Germination process	Parameters	Parameter number
A1	Negative exponential	Constant	k, g	2
A2	Negative exponential	Age-dependent	k, g_{1-3}	4
B1	Compound exponential	Constant	a, b, g	3
B2	Compound exponential	Age-dependent	a, b, g_{1-3}	5
C1	Weibull residence time	Constant	α, β, g	3
C2	Weibull residence time	Age-dependent	α, β, g_{1-3}	5

I also recognize that there are two possible paths

Table 2: Seed bag dataset models

Time	Seeds (S(x))	l(x)	age-specific
Oct_0	100	Ω	l(x+1)/l(x)
$\text{Jan}-\text{pre}_1$	total = intact+germinants	$P(S_1)$	k, g_{1-3}
$\text{Jan}-\text{germ}_1$	germinants	$P(G\|S_1)P(S_1)$	k, g_{1-3}
$\text{Jan}-\text{post}_1$	intact	$[1-P(G\|S_1)]P(S_1)$	k, g_{1-3}
Oct_1	intact	$P(S_2\|S_1, G^c)P(G^c\|S_1)P(S_1)$	a, b, g
$\text{Jan}-\text{pre}_2$	total = intact+germinants	Age-dependent	a, b, g_{1-3}
$\text{Jan}-\text{post}_2$	intact	Age-dependent	a, b, g_{1-3}
Oct_2	intact	Constant	α, β, g
$\text{Jan}-\text{pre}_3$	total = intact+germinant	Age-dependent	α, β, g_{1-3}
$\text{Jan}-\text{post}_3$	intact	Age-dependent	a, b, g_{1-3}
Oct_3	intact	Age-dependent	α, β, g_{1-3}

1 Germination history

Overview: describe fitting model to germination data, describe the survival data, describe joining the two.

1.1 Germination

Germination

$$
\begin{aligned}
[\boldsymbol{\mu}_{\mathrm{g}}, \boldsymbol{\sigma}_{\mathrm{g}}, \boldsymbol{\mu}_{\mathrm{g}}^{\mathrm{pop}}, \boldsymbol{\sigma}_{\mathrm{g}}^{\mathrm{pop}} | \mathbf{y}] \propto & \prod_{i=1}^{I}\prod_{j=1}^{J}\prod_{k=1}^{K}\prod_{l=1}^{L} \mathrm{binomial}(y_{ijkl}|n_{ijkl}, \mathrm{logit}^{-1}(\alpha_{\mathrm{g},ijkl})) \\
& \times \mathrm{normal}(\alpha_{\mathrm{g},ijkl}|\mu_{\mathrm{g},jkl}, \sigma_{\mathrm{g},jkl}) \\
& \times \mathrm{normal}(\mu_{\mathrm{g},jkl}|\mu_{\mathrm{g},jl}^{\mathrm{pop}}, \sigma_{\mathrm{g},jl}^{\mathrm{pop}}) \\
& \times \text{half-normal}(\sigma_{\mathrm{g},jkl}|0,1) \\
& \times \mathrm{normal}(\mu_{\mathrm{g},jl}^{\mathrm{pop}}|0,1)\text{half-normal}(\sigma_{\mathrm{g},jl}^{\mathrm{pop}}|0,1).
\end{aligned} \tag{1}
$$

To represent the germination history of seeds in the experiment, I constructed probability functions. The distribution γ_{ya} represents the probability that a seed has germinated. The subscript corresponds to seeds of age $a = \ldots$ and experimental year $y = \ldots$.

The experiment was initiated in three consecutive years (2006, 2007, 2008). Seed bags from the first year were collected at ages 1, 2, and 3. Seed bags from the second year were collected at ages 1 and 2. Seed bags from the third year were collected at age 3. We thus have the following probability distributions:

$$
\begin{aligned}
\gamma_{1a} &= (\gamma_{11}, \gamma_{12}, \gamma_{13}) \\
\gamma_{2a} &= (\gamma_{21}, \gamma_{22}) \\
\gamma_{3a} &= (\gamma_{31})
\end{aligned}
\tag{2}
$$

Seeds from each experimental year and age were collected twice. First, the seed bags were unearthed in the January as seeds were germinating. At this point, we counted intact seeds and emerging seedlings and summed these to get a count of total seeds just before germination. The seed bags were then returned to the ground from January to October. At this point, the seed bags were unearthed again and removed from the field to get counts of intact seeds.

1.2 Joint

We used these probability distributions to summarize the event histories leading up to each count. In total, we defined twelve probabilities, one for each seed count. These probabilities are defined by age-specific germination rates and the experimental design, specifically the timing of when seeds were unearthed. Event histories 1-6 correspond to seed bags from experimental year 1; event histories 7-10 correspond to seed bags from experimental year 2; event histories 11-12 correspond to seed bags from experimental year 3. The probabilities are composed of germination probabilities for seeds of age 1 ($\gamma_{\cdot\cdot 1}$), age 2 ($\gamma_{\cdot\cdot 2}$), and age 3 ($\gamma_{\cdot\cdot 3}$). The germination probabilities are indexed by site j, experimental year k, and age l;

for example, germination of 1-year old seeds at site j from the experimental year k is given by γ_{jkl}. The compound event histories are defined by:

$$
\begin{aligned}
\theta_{j1,1} &= 1 \\
\theta_{j1,2} &= (1-\gamma_{j1,1}) \\
\theta_{j1,3} &= (1-\gamma_{j1,1}) \\
\theta_{j1,4} &= (1-\gamma_{j1,1}) \times (1-\gamma_{j1,2}) \\
\theta_{j1,5} &= (1-\gamma_{j1,1}) \times (1-\gamma_{j1,2}) \\
\theta_{j1,6} &= (1-\gamma_{j1,1}) \times (1-\gamma_{j1,2}) \times (1-\gamma_{j1,3}) \\
\theta_{j2,1} &= 1 \\
\theta_{j2,2} &= (1-\gamma_{j2,1}) \\
\theta_{j2,3} &= (1-\gamma_{j2,1}) \\
\theta_{j2,4} &= (1-\gamma_{j2,1}) \times (1-\gamma_{j2,2}) \\
\theta_{j3,1} &= 1 \\
\theta_{j3,2} &= (1-\gamma_{j3,1})
\end{aligned}
\tag{3}
$$

Counts of seeds were indexed by sites j, rounds of observation starting in a series of years k, and event histories m.

$$
\begin{aligned}
\lambda_{ijk} &= \exp(\eta_{ijk}) \\
g(\eta_{ijk}, t_{ijkm}, \theta_{jkm}) &= \theta_{jkm} \times \exp(-\lambda_{ijk} \times t_{ijkm}) = \theta_{jkm} \times \exp(-(\exp \eta_{ijk}) \times t_{ijkm}) \\
[\boldsymbol{\eta}, \boldsymbol{\mu}, \boldsymbol{\sigma}, \boldsymbol{\mu}^{\text{pop}}, \boldsymbol{\sigma}^{\text{pop}} | \mathbf{y}] &\propto \prod_{i=1}^{I} \prod_{j=1}^{J} \prod_{k=1}^{K} \prod_{m=1}^{M} \text{binomial}(y_{ijkm} | n_{ijkm}, g(\eta_{ijk}, t_{ijkm}, \theta_{jkm})) \\
&\quad \times \text{normal}(\eta_{ijk} | \mu_{jk}, \sigma_{jk}) \\
&\quad \times \text{normal}(\mu_{jk} | \mu_j^{\text{pop}}, \sigma_j^{\text{pop}}) \\
&\quad \times \text{half-normal}(\sigma_{jk} | 0, 1) \\
&\quad \times \text{normal}(\mu_j^{\text{pop}} | 0, 1) \text{half-normal}(\sigma_j^{\text{pop}} | 0, 1).
\end{aligned}
\tag{4}
$$

In constructing our survival function, we have two types of data for each experimental year and age. Counts from January represent totals from prior to the germination of seeds of that age. The survival function of seeds at time T, $S^1_{ya}(T)$, for these counts in each experimental year y is described by

$$S_a^{\text{jan}} = \prod_{j=1}^{a} (1 - \gamma_{yj})^{I(j=j-1)} \tag{5}$$

Counts from October represent totals from after the germination of seeds of that age. The survival function of seeds at time T, $S^2_{ya}(T)$, for these counts in each experimental year y is described by

$$S_a^{\text{oct}} = \prod_{j=1}^{a} (1 - \gamma_{yj}) \tag{6}$$

The functions S^{jan} and S^{oct} describe the probability that a seed with a particular event (germination) history survives to January and October, respectively.

To include both types of data in the seed bag experiment model, I combined the two functions and introduced an additional index for the type of data the function describes. The index $d = 1, 2$ now represents whether the data are counts from January ($d = 1$) or October ($d = 2$)

$$S_{da} = \prod_{j=1}^{a} \prod_{i=1}^{d} (1 - \gamma_{yj})^{I(d=2)} \tag{7}$$

The probability described below could probably be expressed compactly with indicator functions but I'm running into blocks on getting this to work. Below, $I(\cdot)$ is an indicator function that takes on the value of 1 when the statement in parentheses is true and the value of 0 when the statement in parentheses is false.

The first indicator function indicates whether we are observing the total number of seedlings in January (before germination).

$$\gamma_{jkl} = (1-\gamma_{1_{kl}})^{(1-I(j=1\wedge l=1))} \times (1-\gamma_{2_{kl}})^{(1-I(j=1\wedge l=2))} \times (1-\gamma_{3_{kl}})^{(1-I(j=1\wedge l=3))}$$

The models below represent the joint likelihood for data from the seed bag experiments. All data from seed bags and viability trials is in the form of binomial trials: we have counts of seeds at the start and end of an experimental window of time. All models for the parameters $\gamma_1, \gamma_2, \gamma_3, \gamma_4, \gamma_5$ have the same structure for seeds in bag i in year j in population k. If the number of seeds starting the trial (trials) is n_{ijk} and the number of seeds at the end of the trial (successes) is y_{ijk}, we write a model that has a population-level mean and year-level means drawn from the population-level distribution. The probability of success for each bag is drawn from this year- and population-level distribution:

I compared convergence diagnostics (R-hat, effective sample size) for centered and non-centered parameterizations of the model. Here, I use the centered parameterization because this led to improved convergence. In each model, we obtain the population-level posterior distribution probability of success (the γs) by marginalizing across years and taking the inverse logit.

The seed bank experiments might used to obtain age-specific survival and recruitment terms. So the terms could be survival to month 3 (equal to age-specific survival at midpoint), germination at month 3, survival from month 3 to month 12 (equal to age-specific survival at midpoint), germination at month 15, survival from month 15 to 24, germination at month 27, survival from month 27 to 36. There are some errors in the data still, need to look at those. For germination there is no clear pattern to germination, either for individual sites or across sites. There are monotonic increases, monotonic decreases, and nonmonotonic patterns. Might also help to look at viability across age.

The seed pot experiments seem like they would be amenable to the kind of functions fit in the paper by Rees and Long. In those cases there are only 3 time points which would limit the application of the empirical seedling recruitment curves. But perhaps overlaying them per population would allow us to figure out whether there is consistency across years or whether particular cohorts follow different curves, and how this varies in space?

I will estimate survival/mortality rates at 4 time points (0-3 months, 3-12 months, 15-24 months, 27-36 months), and germination at 3 time points (3 months, 15 months, 27 months). This will allow me to figure out what kind of model (cf Rees and Long) might be most appropriate for the data, especially for the emergence data from the seed pot trials.

Table 3: Summary of models in Rees and Long (1993).

Model	Description
Exponential	...
Compound exponential	...
Weibull	...
Log logistic	...

We start with

$$\begin{aligned} y_{it} &\sim \text{binomial}(n_i, \gamma) \\ \gamma &\sim \text{beta}(1, 1) \end{aligned} \tag{8}$$

to say that the observations of the number of seeds counted in bag i at time t are represented as y_{it} drawn from a binomial distribution. In this case, n_i is the number of trials, the number of seeds starting the experiment; y_{it} is the number of successes, the number of seeds remaining. The γ is the probability of success on a single trial.

$$[\gamma|\boldsymbol{y}, \boldsymbol{n}] \propto \text{binomial}(y_{it}|n_i, \gamma)\text{beta}(\gamma|1, 1) \tag{9}$$

We then have sampling variability that is implicit in the binomial. There are thus two sources of uncertainty. Uncertainty arising from sampling and uncertainty arising because of . . . .

The case where each bag has its own mean survival at each time, acknowledging variation among bags:

$$
\begin{aligned}
y_{it} &\sim \text{binomial}(n_i, \gamma_{it}) \\
\gamma_{it} &\sim \text{beta}(\alpha, \beta)
\end{aligned}
\tag{10}
$$

Giving the following :

$$
\begin{aligned}
[\boldsymbol{\gamma}, \alpha, \beta | \boldsymbol{y}, \boldsymbol{n}] \propto\ & \text{binomial}(y_{it}|n_i, \gamma_{it})\text{beta}(\gamma_{it}|\alpha, \beta) \\
& \text{gamma}(\alpha|0.001, 0.001)\text{gamma}(\beta|0.001, 0.001)
\end{aligned}
\tag{11}
$$

We now want to model the process "change in being intact with time" as

$$
g(k, t_i) = \exp(-kt_i) \tag{12}
$$

This deterministic model represents the average proportion of seeds that are expected to be intact as a function of time under a negative exponential process. The function $g(k, t_i)$ is the overall mean probability of being intact at time t_i. This is the mean of the beta distribution; the variance is the variation in probability of being intact at time t_i that arises from differences among time. The uncertainty that arises from sampling - which we can estimate because of replication - is distinct from this process variance. I think the process variance is all effects that create variation beyond the seed age, as represented with a negative exponential function.

The next problem is that the process is not simply one of decay, decomposition, or mortality. Instead, there are annual events interspersed into this, namely germination. In this way I think the situation resembles the complement of case 2 in Olson (1963). Modeling germination and survival jointly would account for the full data. Here's one idea:

$$
\begin{aligned}
h_1(k, t_1) &= \exp(-kt_1) \\
h_2(k, t_1) &= g_1 \exp(-kt_1) \\
h_3(k, t_2) &= (1 - g_1) \exp(-kt_2) \\
h_4(k, t_3) &= (1 - g_1) \exp(-kt_3) \\
h_5(k, t_3) &= (1 - g_1)(g_2) \exp(-kt_3) \\
h_6(k, t_4) &= (1 - g_1)(1 - g_2) \exp(-kt_4) \\
h_7(k, t_5) &= (1 - g_1)(1 - g_2) \exp(-kt_5) \\
h_8(k, t_5) &= (1 - g_1)(1 - g_2)g_3 \exp(-kt_5) \\
h_9(k, t_6) &= (1 - g_1)(1 - g_2)(1 - g_3) \exp(-kt_6)
\end{aligned}
\tag{13}
$$

Perhaps it would be productive to break the probability into two processes, one accounting for mortality and another accounting for decay. The one accounting for mortality would follow one of the following processes. First, we consider a negative exponential mortality trajectory.

$$g(k, t_i) = \exp(-kt_i) \tag{14}$$

Then, we consider a continuous exponential mortality trajectory:

$$g(a, b, t_i) = \frac{1}{(1 + bt_i)^a} \tag{15}$$

Then, we consider a mortality trajectory for Weibull residence times:

$$g(\alpha, \beta, t_i) = \exp -(\frac{t_i}{\beta})^\alpha \tag{16}$$

The mortality process would be multiplied with the process "change in removal from population with age due to germination", represented as

$$
\begin{aligned}
h_1(\boldsymbol{g}) &= 1 \\
h_2(\boldsymbol{g}) &= g_1 \\
h_3(\boldsymbol{g}) &= (1 - g_1) \\
h_4(\boldsymbol{g}) &= (1 - g_1) \\
h_5(\boldsymbol{g}) &= (1 - g_1)g_2 \\
h_6(\boldsymbol{g}) &= (1 - g_1)(1 - g_2) \\
h_7(\boldsymbol{g}) &= (1 - g_1)(1 - g_2) \\
h_8(\boldsymbol{g}) &= (1 - g_1)(1 - g_2)g_3 \\
h_9(\boldsymbol{g}) &= (1 - g_1)(1 - g_2)(1 - g_3)
\end{aligned}
\tag{17}
$$

In turn we would consider models that combine age-dependent and -independent germination functions and mortality functions.

The following equations correspond to the full conditional distributions for models at the first time point. Subsequent models incorporate germination in the function $m(\dots, \sigma^2)$. Specifically, the mean is the product of the mortality up to time t_i, represented by $g(\dots)$, germination up to time t_i, represented by $h(\dots)$. We will use the information from the seed bag experiments to determine whether there is an appropriate mortality process with which to model the recruitment data from the seed pots. What I would like to do with this is get a mortality and germination process that's appropriate for these sites and use the posterior for the parameters in that process as informed priors to model the seed recruitment from the seed pots.

Finally, we also consider the model proposed in Gremer and Venable (2014), namely one in which seed mortality is seasonal and age-dependent.

$$
\begin{aligned}
g(k, t_i) &= \exp(-kt_i) \\
[k, \alpha, \beta | \boldsymbol{y}, \boldsymbol{n}] &\propto \text{binomial}(y_{it} | n_i, \gamma_{it}) \text{beta}(\gamma_{it} | m(g(k, t_i), \sigma^2)) \\
&\times \text{gamma}(k | 0.001, 0.001) \\
&\times \text{inverse gamma}(\sigma^2 | 0.001, 0.001)
\end{aligned}
\tag{18}
$$

$$
\begin{aligned}
g(a, b, t_i) &= \frac{1}{(1 + bt_i)^a} \\
[k, \alpha, \beta | \boldsymbol{y}, \boldsymbol{n}] &\propto \text{binomial}(y_{it} | n_i, \gamma_{it}) \text{beta}(\gamma_{it} | m(g(a, b, t_i), \sigma^2)) \\
&\times \text{gamma}(a | 0.001, 0.001) \text{gamma}(b | 0.001, 0.001) \\
&\times \text{inverse gamma}(\sigma^2 | 0.001, 0.001)
\end{aligned}
\tag{19}
$$

$$
\begin{aligned}
g(\alpha, \beta, t_i) &= \exp -(\frac{t_i}{\beta})^\alpha \\
[k, \alpha, \beta | \boldsymbol{y}, \boldsymbol{n}] &\propto \text{binomial}(y_{it} | n_i, \gamma_{it}) \text{beta}(\gamma_{it} | m(g(\alpha, \beta, t_i), \sigma^2)) \\
&\times \text{gamma}(\alpha | 0.001, 0.001) \times \text{gamma}(\beta | 0.001, 0.001) \\
&\times \text{inverse gamma}(\sigma^2 | 0.001, 0.001)
\end{aligned}
\tag{20}
$$

Modeling seed survival

We chose to work with a Weibull residence time model, which represents the seed pool as a distribution of survival times. For background on this see Pinder et al. (1978); Cornwell and Weedon (2014); Dahlgren et al. 2016. Parameter alpha controls the shape of the decomposition trajectory and beta the rate of decomposition. This model can reduce to the exponential model when alpha is 1. If alpha is less than 1, the decomposition rate decreases through time. If alpha is greater than 1, the decomposition rate increases through time. (see Pinder et al. 1978 for another description).

Consider a survivorship trajectory for Weibull residence times:

$$g(\alpha, \beta, t_i) = \exp -(\frac{t_i}{\beta})^{\alpha} \tag{21}$$

The mortality process would be multiplied with the process "change in removal from population with age due to germination", represented as

$$\begin{aligned}
h_1(\boldsymbol{g}) &= 1 \\
h_3(\boldsymbol{g}) &= (1 - g_1) \\
h_4(\boldsymbol{g}) &= (1 - g_1) \\
h_6(\boldsymbol{g}) &= (1 - g_1)(1 - g_2) \\
h_7(\boldsymbol{g}) &= (1 - g_1)(1 - g_2) \\
h_9(\boldsymbol{g}) &= (1 - g_1)(1 - g_2)(1 - g_3)
\end{aligned} \tag{22}$$

I compactly represent this history as the product of germination history and survivorship. I describe germination history as the product of a matrix of binary values and a vector of corresponding probabilities of not germinating. In the matrix of binary values, each row corresponds to a sampling instance in the seed bag experiment. Columns 1-3 correspond to whether the seeds of age 1-3 had germinated at the respective sampling event. The vector describes the probability that seeds of age 1-3 did not germinate. The vector is in turn multiplied with the survival time function. These terms combine the loss of seeds from germination and the loss of seeds from decay/mortality.

$$h(\alpha, \beta, t_i) = \begin{bmatrix} 0 & 0 & 0 \\ 1 & 0 & 0 \\ 1 & 0 & 0 \\ 1 & 1 & 0 \\ 1 & 1 & 0 \\ 1 & 1 & 1 \end{bmatrix} \begin{bmatrix} 1 - g_1 & 1 - g_2 & 1 - g_3 \end{bmatrix}^\top \exp -(\frac{t_i}{\beta})^\alpha \tag{23}$$

Because we model germination as conditionally dependent on the number of intact seeds at the time of germination, we estimate the germination rate independently. We combine that information with the information from the survival time model. We use the survival function associated with a Weibull distribution as the deterministic function for how seed survivorship changes over time. The Weibull has a shape and scale parameter; we estimate a shape parameter for each population. See Smits 2015 for logic from survival analysis. This is equivalent to saying that we are assuming the change in survivorship is a population-level property but that the scale varies from year to year within each population.

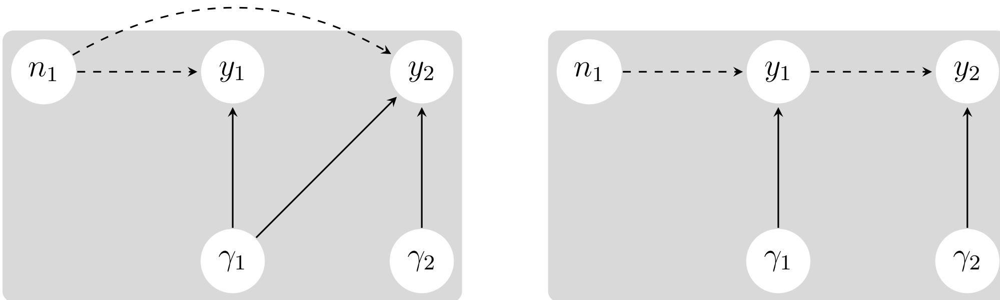
Because germination terms are present in both the survival and germination models, data on both seed survivorship and germination inform estimates of germination. Including the germination terms in the survivorship model means that the expected number of seeds surviving to a given time is the product of a survival function and germination. With low germination proportions, the dominant process is mortality. As germination increases, the

Pinder et al. (1978) also give the mean longevity calculated from a Weibull:

$$\text{scale} \times \Gamma(1 + (\frac{1}{\text{shape}})) \tag{24}$$

Which seems like an interesting extension of the data on hand. If we don't assume an exponential decay model of seed survival then the value of both the shape and scale parameters are relevant. So populations with an, on average, higher longevity would correspond to being a safer seed bank.

Identifiability within years

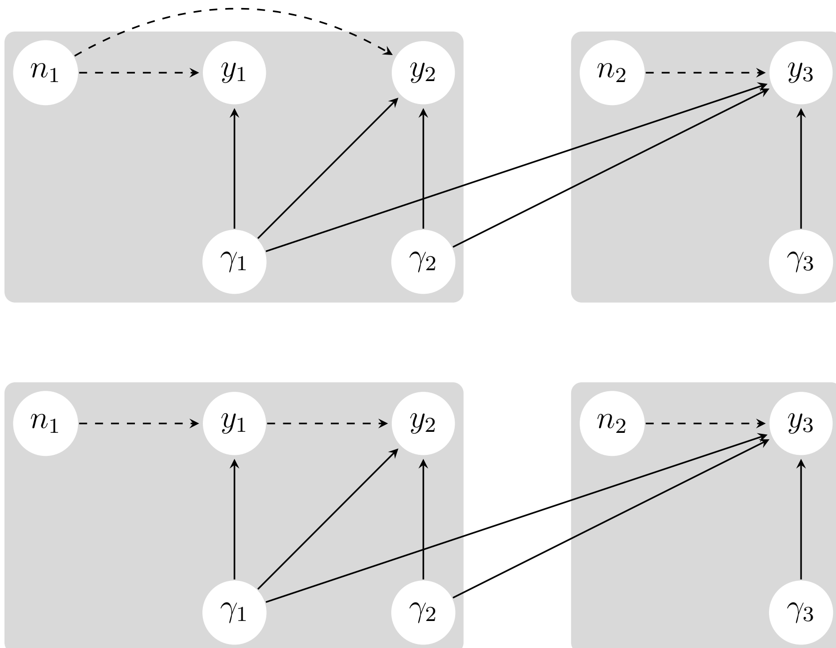


(a) Directed acyclic graphs for the hierarchical models for seed bag rates. Solid arrows depict the relationships among random variables, and dashed arrows depict the deterministic relationships.

$$
\begin{aligned}
[\gamma_1, \gamma_2 | \boldsymbol{y_1}, \boldsymbol{y_2}] \propto\ & \text{binomial}(y_1 | n_1, \text{logit}^{-1}(\alpha_1)) \\
& \times \text{binomial}(y_2 | n_1, \text{logit}^{-1}(\alpha_1) \times \text{logit}^{-1}(\alpha_2)) \\
& \times \text{normal}(\alpha_1 | \mu_1, \sigma_1) \text{normal}(\alpha_2 | \mu_2, \sigma_2) \\
& \times \text{normal}(\mu_1 | 0, 1000) \text{half-normal}(\sigma_1 | 0, 1) \\
& \times \text{normal}(\mu_2 | 0, 1000) \text{half-normal}(\sigma_2 | 0, 1).
\end{aligned}
\tag{25}
$$

$$
\begin{aligned}
[\gamma_1, \gamma_2 | \boldsymbol{y_1}, \boldsymbol{y_2}] \propto\ & \text{binomial}(y_1 | n_1, \text{logit}^{-1}(\alpha_1)) \\
& \times \text{binomial}(y_2 | y_1, \text{logit}^{-1}(\alpha_2)) \\
& \times \text{normal}(\alpha_1 | \mu_1, \sigma_1) \text{normal}(\alpha_2 | \mu_2, \sigma_2) \\
& \times \text{normal}(\mu_1 | 0, 1000) \text{half-normal}(\sigma_1 | 0, 1) \\
& \times \text{normal}(\mu_2 | 0, 1000) \text{half-normal}(\sigma_2 | 0, 1).
\end{aligned}
\tag{26}
$$

Identifiability across years

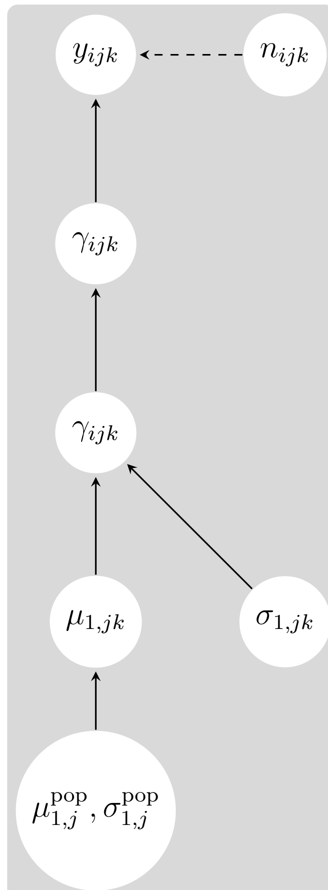


(a) Directed acyclic graphs for the hierarchical models for seed bag rates. Solid arrows depict the relationships among random variables, and dashed arrows depict the deterministic relationships.

$$
\begin{aligned}
[\gamma_1, \gamma_2 | \boldsymbol{y_1}, \boldsymbol{y_2}] \propto\, & \text{binomial}(y_1 | n_1, \text{logit}^{-1}(\alpha_1)) \\
& \times \text{binomial}(y_2 | n_1, \text{logit}^{-1}(\alpha_1) \times \text{logit}^{-1}(\alpha_2)) \\
& \times \text{normal}(\alpha_1 | \mu_1, \sigma_1)\text{normal}(\alpha_2 | \mu_2, \sigma_2) \\
& \times \text{normal}(\mu_1 | 0, 1000)\text{half-normal}(\sigma_1 | 0, 1) \\
& \times \text{normal}(\mu_2 | 0, 1000)\text{half-normal}(\sigma_2 | 0, 1).
\end{aligned} \tag{27}
$$

$$
\begin{aligned}
[\gamma_1, \gamma_2 | \boldsymbol{y_1}, \boldsymbol{y_2}] \propto\ & \text{binomial}(y_1 | n_1, \text{logit}^{-1}(\alpha_1)) \\
& \times \text{binomial}(y_2 | y_1, \text{logit}^{-1}(\alpha_2)) \\
& \times \text{normal}(\alpha_1 | \mu_1, \sigma_1)\text{normal}(\alpha_2 | \mu_2, \sigma_2) \\
& \times \text{normal}(\mu_1 | 0, 1000)\text{half-normal}(\sigma_1 | 0, 1) \\
& \times \text{normal}(\mu_2 | 0, 1000)\text{half-normal}(\sigma_2 | 0, 1).
\end{aligned} \tag{28}
$$

Exponential decay



(a) Directed acyclic graphs for the hierarchical models for seed bag rates. Solid arrows depict the relationships among random variables, and dashed arrows depict the deterministic relationships.