Hierarchical models for hard-to-see stages

Estimating survivorship and germination in soil seed banks

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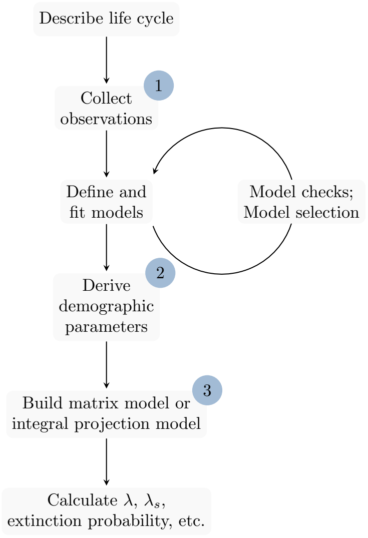
Seed banks are important to model plant populations

- Soil seed banks are critical for plant life history strategies that rely on bet hedging and predictive germination to persist in variable environments
- Plant ecologists who seek to incorporate seed banks into population models run into challenges – seeds are far more difficult to follow than aboveground plants
- We present a model to estimate seed mortality and germination using observations from experiments with the seed bank

Seed banks in the demographic modeling workflow

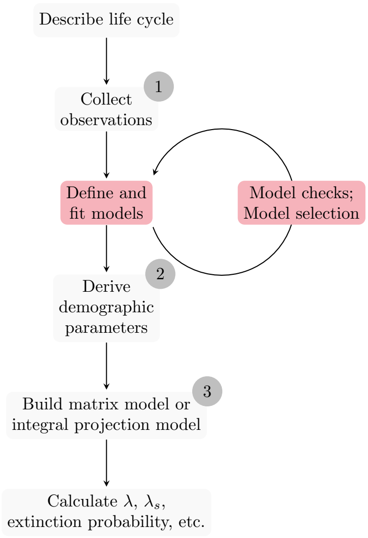


Previous work demonstrates how to do the following:

1. Use experimental seed banks to infer seed fates [1]
2. Propagate uncertainty from seed rates to population growth[2]
3. Modify parameters and age structure of matrix, and use simulations to explore consequences[3]

[1]Kalisz 1991,[2]Paniw et al. 2017,[3]Doak et al. 2002; Nguyen et al. 2019

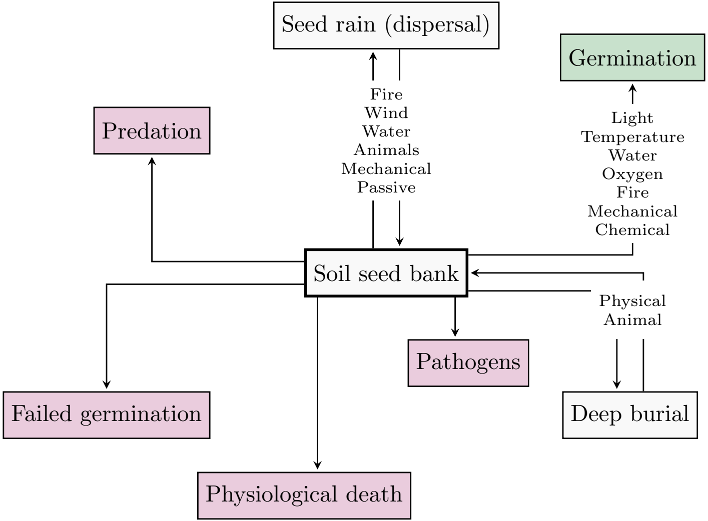
Seed banks in the demographic modeling workflow



Our goals in this talk are to:

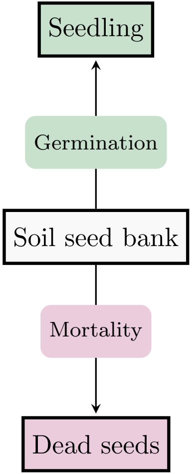
1. Describe models for inference about seed fates
2. Use Bayesian framework to fit models
3. Integrate model checking and selection

Seed banks are complex and challenging to observe



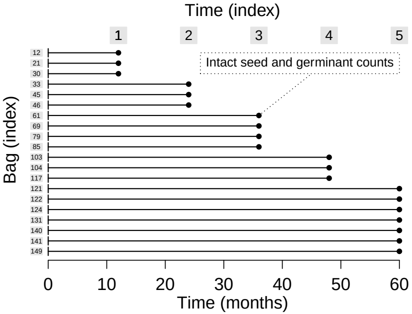
After Figure 1 in Simpson et al. 1989

Mortality and germination are the key processes



Seeds effectively leave the seed bank by two routes. They **germinate** and become seedlings, or they **die** and become dead seeds. Seeds that do not germinate or experience mortality persist – they remain in the seed bank.

Seed bag burial experiment and sample observations



Indices		Variable	Data (counts)			Calculated (counts)	
Bag	Time	Time (months)	Starting seeds	Intact seeds	Germinants	Survivors	Surviving seeds
i	j	t_{ij}	n_{ij}	—	$y_{g,i}$	y_{ij}	$n_{g,i}$
12	1	12	100	27	27	54	54
21	1	12	100	25	29	54	54
30	1	12	100	21	22	43	43
33	2	24	100	2	4	6	6
45	2	24	100	8	9	17	17
46	2	24	100	1	4	5	5
61	3	36	100	0	1	1	1
69	3	36	100	1	2	3	3
79	3	36	100	2	2	4	4
85	3	36	100	0	1	1	1
103	4	48	100	1	0	1	1
104	4	48	100	0	0	0	0
117	4	48	100	0	0	0	0
121	5	60	100	0	0	0	0
122	5	60	100	0	0	0	0
124	5	60	100	0	0	0	0
131	5	60	100	0	0	0	0
140	5	60	100	0	1	1	1
141	5	60	100	0	1	1	1
149	5	60	100	1	0	1	1

Seed bag burials are commonly used to estimate seed mortality and germination. Seeds are buried in bags and dug up after some time to count intact seeds, to count germinated seeds, and to conduct additional assays (e.g. for seed viability).

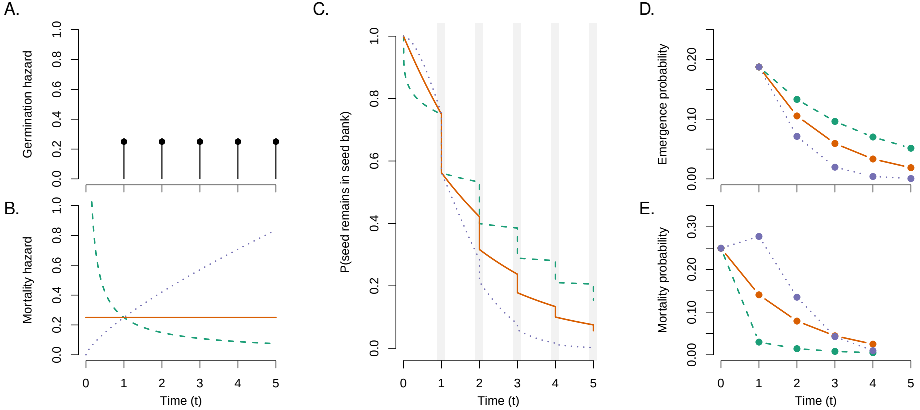
A deterministic model to describe seed fates

Persistence in the seed bank after $j = 1, 2, \ldots$ years is the product of a seed's germination history (whether or not it germinated each year) and mortality history (whether it died). For discrete germination and continuous, constant mortality risk, a possible model is

$$f(p_{\mathrm{g}}, \lambda, t_{ij}) = \overbrace{(1 - p_{\mathrm{g}})^{(j-1)}}^{\text{germination history}} \times \overbrace{\exp(-\lambda t_{ij})}^{\text{survival function for mortality}} \tag{1a}$$

A deterministic model to describe seed fates

The age structure of the seed bank depends on how the risk of germination or mortality – hazards, in the language of event history analysis[1] – changes with seed age.



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[1] Also called survival analysis or failure time analysis.

A statistical model for seed and seedling counts

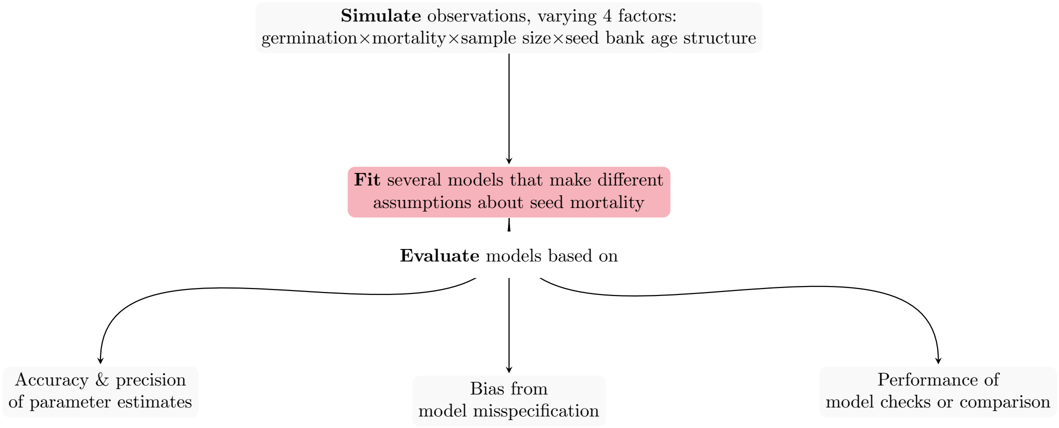
We define a Bayesian statistical model by nesting the process model in a likelihood function and placing priors on the parameters. The probability of germination, p_{g}, is shared by the model for seedling observations (1b) and for seed counts (1c) via the germination history (1a).

$$f(p_{\mathrm{g}}, \lambda, t_{ij}) = \overbrace{(1 - p_{\mathrm{g}})^{(j-1)}}^{\text{germination history}} \times \overbrace{\exp(-\lambda t_{ij})}^{\text{survival function for mortality}} \tag{1a}$$

$$[p_{\mathrm{g}}, \lambda | \mathbf{y}_{\mathrm{g}}, \mathbf{y}] \propto \prod_{i=1}^{I} \Bigg[\Big[\mathrm{binomial}(y_{\mathrm{g},i} | n_{\mathrm{g},i}, p_{\mathrm{g}}) \mathrm{beta}(p_{\mathrm{g}} | 1, 1) \Big] \tag{1b}$$

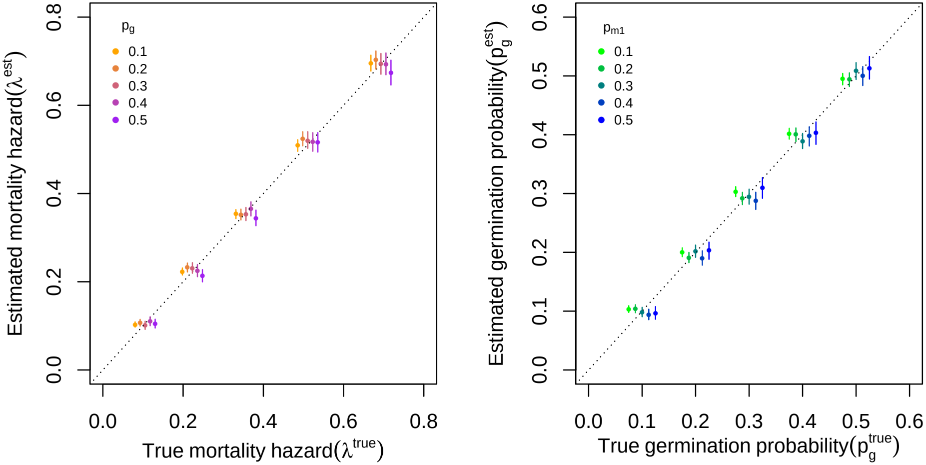
$$\times \Big[\prod_{j=1}^{J} \mathrm{binomial}(y_{ij} | n_{ij}, f(p_{\mathrm{g}}, \lambda, t_{ij})) \mathrm{gamma}(\lambda | 0.001, 0.001) \Big] \Bigg] \tag{1c}$$

Simulation study to validate modeling approach



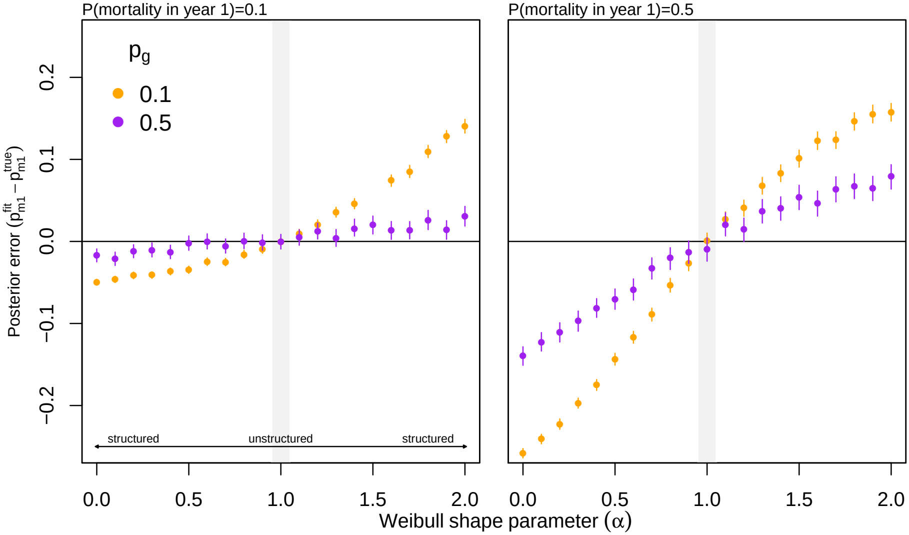
Accuracy and precision of parameter estimates

We recover all combinations of germination and mortality when we fit the ‘correct model’; when we use the same model to simulate and fit observations.

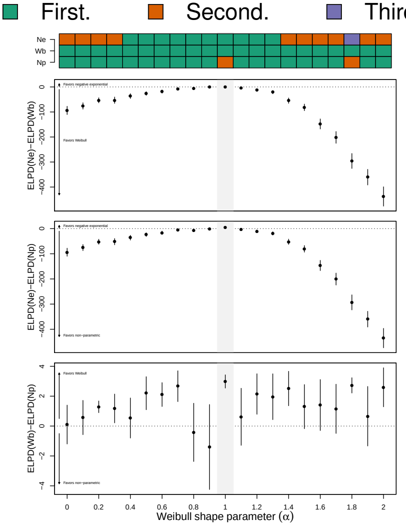


Bias from model misspecification

Estimates are biased when we fit a model that assumes an unstructured seed bank to observations from an age-structured seed bank.



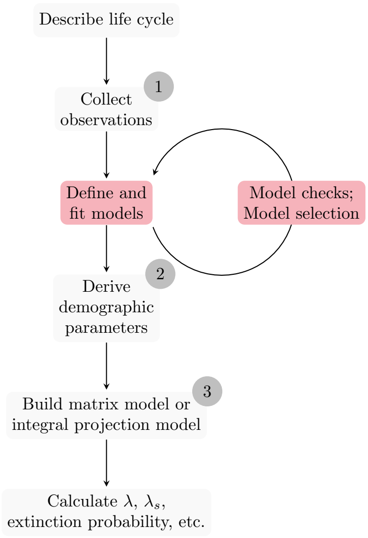
Performance of model comparison[1]



When fit to observations simulated from an age-structured seed bank, models with constant mortality (Ne) show low predictive accuracy.

[1] We used leave-one-out cross-validation. The top panel summarizes model rank (cutoff of 4 SEs) and the bottom panels show pairwise model comparisons.

Seed banks in the demographic modeling workflow



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Acknowledgments

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