Context-dependent consequences of lagged effects in demographic models

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Abstract

Text of 150 words max summarizing this amazing paper.

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Introduction

Two types of structured population models - matrix models (Leslie 1945; Caswell 2001) and integral projection models (Ellner and Rees 2006) - are fundamental frameworks used to study demography and population dynamics. Their flexibility, in concert with a rapidly growing suite of software, data, and other resources (Salguero-Gómez et al. 2015; Ellner et al. 2016; Levin et al. 2021), have facilitated their use to study a wide range of topics in ecology, evolution, and conservation (Morris and Doak 2002; Crone et al. 2011; Ellner et al. 2016). Mathematical and statistical advances (Williams et al. 2012; e.g., Brooks et al. 2019)have rapidly expand the scope of questions and biological processes that can be investigated with these models (Ellner et al. 2016; e.g., Rees and Ellner 2016). Despite this progress, however, several important biological processes have proven challenging to incorporate in structured population models. In some cases this is because theoretical and analytical methods for doing so remain underdeveloped; in others this is because data with which to parametertize and assess alternative model structures are lacking (Metcalf et al. 2015; Ellner et al. 2016).

One of these biological processes is Delayed Life-history Events (i.e., DLHEs), also known as Lagged Effects (Beckerman et al. 2002).Lagged effects are those in which the demographic vital rates observed in a given year are influenced – or even determined by – past environmental conditions. For instance, environmental conditions during juvenile development can shape the expression of traits (e.g., defensive spikes on Daphnia) that determine adult survival. Alternatively, the physiological mechanisms responsible for a vital rate can take an extended period of time to complete (Evers et al. 2021); for example, flowering bud formation may be initiated several months before flowers appear (Criley and Lekawatana 1994). Vital rates can even be influenced by environmental conditions during the parental life-cycle or historical trade-offs between vital rates (e.g., delayed costs of reproduction, competition-colonization trade-offs). Although these lagged effects could potentially have major consequences for population dynamics (Beckerman et al. 2002), their impacts remain poorly understood for two primary reasons. The first is limited data - parametrizing models requires long-term data on lagged effects and their potential drivers (Metcalf et al. 2015), and these studies can be challenging to design and maintain (Kuss et al. 2008). The second is challenge is technical - incorporating complex biological processes in demographic models can render them less tractable.

Despite these challenges, several recent studies have found there can be large delayed effects of environmental conditions (e.g., climate) on demographic vital rates (Evers et al. 2021; Scott et al. 2022). It remains unclear, however, if including such lagged effects will significantly alter the results of demographic models. Using a decade of survey and climate data, we assessed the effects of precipitation extremes on the demographic vital rates of the Amazonian understory herb Heliconia acuminata (Heliconiaceae). We found that the effects of climate on vital rates could be delayed up to 36 months, with the presence and duration of these effects differing by vital rate and habitat type (i.e., continuous forest, forest fragments). Here we used these data to parameterize three different classes of Intgral Projection Models (IPMs): a deterministic IPM, a stochastic IPM, and a stochastic

IPM with lagged effects of SPEI on vital rates. We then evaluated how model choice influenced projections of population growth rate (i.e., λ) and structure? Based on previous studies (Bruna et al. 2002; Bruna and Kress 2002; Bruna 2003; Bruna and Oli 2005) and demographic theory (Tuljapurkar 1990; Caswell 2001) we predicted that:

(i) λ would be higher in continuous forest forest fragments regardless of model type,
(ii) that projections of λ from deterministic models would be higher than those of stochastic models,
(iii) that λ would be lowest for models including lagged effects, and
(iv) populations would be more skewed towards pre-reproductive size classes in fragments that forest, regadless of wether models included stochaticity or lagged effects.

Methods

Study System and Demographic Data

Overview of the Heliconia project

Construction of Integral Projection Models

In preliminary investigation, we found that the survival and growth of plants was better explained by treating seedlings and mature plants separately. Seedlings are physiologically different from small plants because they necessarily lack the underground reserves (of carbohydrates and meristems) that a small, mature plant may have. Therefore, we used general IPMs to model population dynamics with seedlings treated as a separate discreet class not structured by size. General IPMs allow for combinations of continuous and discrete states and transitions between them (Ellner et al. 2016).

We built three classes of IPMs for comparison which each required different functional forms of their underlying vital rates models. The simplest IPM was a general, density-independent, deterministic IPM with four sub-kernels: growth and survival (P, Equation 4), fecundity (F, i.e. production of new seedlings, Equation 5), probability of staying a seedling (always 0), and recruitment (R, i.e. seedling survival and establishment, Equation 3) (Equation 1, Equation 2, Figure 1). The probability of staying a seedling, was always equal to zero, since our definition of seedlings was first year plants only.

$$n(z', t+1) = R(z')n_s(t) + \int_L^U P(z', z)n(z, t)\, dz \tag{1}$$

$$n_s(t+1) = \int_L^U F(z)n(z, t)\, dz \tag{2}$$

$$R(z') = s_s G_s(z') \tag{3}$$

$$P(z', z) = s(z)G(z', z) \tag{4}$$

$$F(z) = p_f(z)f(z)g \tag{5}$$

The number and size of mature plants in the next census is determined by seedlings entering the mature plant population (i.e. recruitment) and survival and growth (or regression) of mature plants (Equation 1). Seedlings survive (s_s) and grow into mature plants of a particular size ($G_s(z')$) (Equation 3).

Mature plants survive as a function of size ($s(z)$), and grow (or regress) to a new size as a function of their previous size ($G(z', z)$) (Equation 4). Mature plants flower with a probability that is a function of size ($p_f(z)$) and produce a number of seeds as a function of size ($f(z)$), which germinate and establish as seedlings with probability g (Equation 5).

Vital rate models for growth ($G_s(z'$) and $G(z', z)$) , survival (s_s and $s(z)$), and flowering ($p_f(z)$) were fit using the long term demographic dataset. For established plants, these three vital rates were modeled as a smooth function of size in the previous census using generalized additive models (GAMs) fit with the `mgcv` package(Wood 2011) in R version 4.4.1 (2024-06-14) (R Core Team 2020) . For consistency, seedling survival and growth were also modeled using GAMs, but without size in the previous census as a predictor (i.e. intercept only models). For growth models ($G_s(z'$) and $G(z', z)$) a scaled t family distribution provided a better fit to the data than a gaussian fit as the residuals were leptokurtic with a simple Gaussian model.

To estimate reproduction we drew on additional data sources to estimate the number of fruits per flowering plant as a function of plant size and the number of seeds per fruit (together $f(z)$). Germination and establishment rates in continuous forest and forest fragments were estimated using data from …. .

To build the general, density-independent, stochastic, kernel-resampled IPMs, we included environmental stochasticity in all vital rate models built using the long term demographic datset by adding a random effect of year (Figure 1). The random effect of year was included using a factor–smooth interaction which allowed the relationship between plant size and vital rates to vary in functional form among transition years. The kernel-resampling approach is to generate kernels corresponding to each transition year in the demographic dataset using the random smooths for year, and to iterate the IPM by drawing from these randomly. This is equivalent to the matrix selection approach for matrix population models described by Caswell (2001).

For the third method, we modeled the impacts of drought on vital rates explicitly and created general, density-independent, stochastic, parameter-resampled IPMs (sensu Metcalf et al. (2015)). We calculated the standardized precipitation evapotranspiraton index (SPEI) for our site using a published gridded dataset based on ground measurements (Xavier et al.

2016) as described in Scott et al. (2022). For all vital rate models fit using the long term demographic dataset, we modeled delayed effects of SPEI using distributed lag non-linear models with a maximum lag of 36 months (Scott et al. 2022) (Figure 1). To iterate these parameter-resampled IPMs, a random sequence of SPEI values was created by sampling years of the observed monthly SPEI data. Then, 36 month lags are calculated for each year starting in February (the month of the demographic census). These values are then used to predict fitted values from the vital rates models, generating different kernels at each iteration of the IPM. With this method, the kernels of successive iterations are not entirely independent because the SPEI values used in calculating vital rates include values used in the previous two iterations, but they are ergodic.

All IPMs were constructed and iterated using the `ipmr` package in R (Levin et al. 2021). The IPMs used 100 meshpoints and the midpoint rule for calculating kernels . For each type of IPM we iterated the model for 1000 time steps, discarding the first 100 time steps to omit transient effects. Stochastic growth rates (λ_s) were calculated as the average $ln(\lambda)$ from each time step (Caswell 2001) and back-transformed to be on the same scale as deterministic lambdas for comparison. We used the distribution of established plant sizes and proportion of seedlings from the full dataset as a starting population vector. While other starting population vectors were possible, the choice is of little importance as it will only impact transient dynamics, which we aren't interested in for this study.

To estimate uncertainty around the per-capita growth rates (lambdas), we created 500 bootstraps of the demographic dataset by sampling individual plants with replacement within each habitat. For each bootstrap, we then re-fit vital rates models (all except germination and establishment rate, fruits per flowering plant, and seeds per fruit, which were estimated using different datasets), constructed IPMs, and calculated a value for lambda as described above. We then used these bootstraped estimates of lambda to calculate bias corrected 95% confidence intervals (Ellner et al. 2016).

This workflow was managed using the `targets` R package (Landau 2021) which also allowed us to track computational time spent on each IPM for comparison.

Statistical analyses

All about the stats.

Results & Discussion

1. For all vital rates estimated using the long term demographic dataset, the DLNM model fit the best (dAIC = 0) followed by the model with a random effect of year, followed by the deterministic model (Table 1).

2. Population growth rates were consistently higher in continuous forest compared to forest fragments across IPM types (Table 3).

3. We found that the the choice of Integral Projection Model didn't change the relative ranking of lambda in Continous Forest and Fragments.

4. The time to iterate the DLNM models is much higher than than deterministic and kernel-resampled.

5. The greater use of computational resources is likely a result of `predict()` being much slower for GAMs with 2D smooths because the number of knots is much higher compared to the GAMs used for the vital rates models in the determinsitic and kernel-resampled IPMs.

6. Figure 2 has some interesting things in it:
   - For the deterministic IPM (and the kernel-resampled IPM?) there are slightly more of the smallest plants and the largest plants in CF compared to FF (i.e. more medium sized plants in FF).
   - For the kernel-resampled IPM (random effect of year), the fluctuations are extremely similar between CF and FF
   - For the parameter-resampled IPM (DLNM) the size structure of the population is a LOT more variable in FF. This makes sense as we know lagged effects are more important in fragments.
   - Also, the fluctuations in size structure in CF do not match the fluctuations in FF as well (can see this by the increased spread of points in Figure 2 (B)
   - Also, in the parameter-resampled IPM (and only in this one), we see a shift toward smaller plants in FF compared to CF
   - These results are consistent with those of Kaye and Pyke (2003), who found who found that the method effected stochastic lambda but relative ranking of populations was consistent.

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CRediT Statement

ERS contributed to the conceptualization, methodology, formal analysis, and led the writing of the original draft. EMB contributed to the conceptualization, methodology, and writing and also acquired funding.

Data Availability Statement

Data and R code used in this study are archived with Zenodo at .

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Table 1: Comparison of vital rate models used to build IPM. The 'Effect of Environment' column describes how environmental effects were included in models. Those with 'none' were used to build deterministic IPMs; those with a random effect of year were used to build stochastic, kernel-resampled IPMs; and those with a distributed lag non-linear model (DLNM) were used to build stochastic, parameter-resampled IPMs. 'edf' is the estimated degrees of freedom of the penalized GAM. ΔAIC is calculated within each habitat and vital rate combination. ΔAIC within 2 indicates models are equivalent.

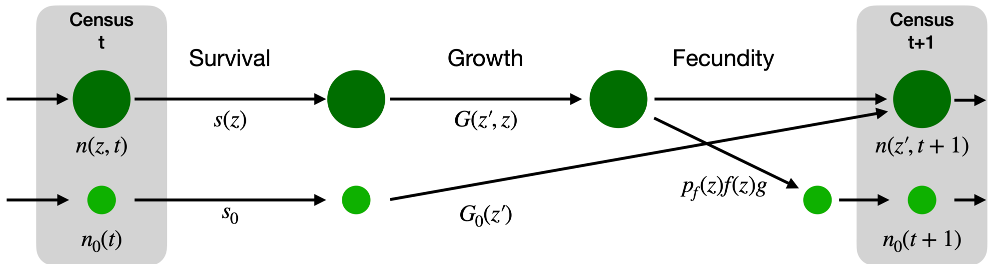
Habitat	Vital Rate	Effect of Environment	edf	ΔAIC
CF	Survival	Random effect of year	43.26	0
CF	Survival	DLNM	19.72	78.92
CF	Survival	None	4.976	260
CF	Growth	Random effect of year	78.43	0
CF	Growth	DLNM	23.87	158.5
CF	Growth	None	7.81	1896
CF	Flowering	DLNM	19.59	0
CF	Flowering	Random effect of year	17.19	1.627
CF	Flowering	None	7.468	381.9
CF	Seedling survival	None	1	0
CF	Seedling survival	Random effect of year	1.817	1.386
CF	Seedling survival	DLNM	4.008	1.528
CF	Seedling growth	Random effect of year	9.475	0
CF	Seedling growth	DLNM	8.952	2.902
CF	Seedling growth	None	1	172.3
FF	Survival	DLNM	14.95	0
FF	Survival	Random effect of year	19.21	35.68
FF	Survival	None	4.333	51.25
FF	Growth	DLNM	25.18	0
FF	Growth	Random effect of year	37.84	200
FF	Growth	None	5.599	382.8
FF	Flowering	DLNM	20.61	0
FF	Flowering	Random effect of year	13.81	27.4
FF	Flowering	None	5.007	101.7
FF	Seedling survival	DLNM	5.574	0
FF	Seedling survival	Random effect of year	5.088	5.721
FF	Seedling survival	None	1	6.491
FF	Seedling growth	Random effect of year	6.25	0
FF	Seedling growth	DLNM	8.182	2.29
FF	Seedling growth	None	1	5.745

Table 2: Figure caption to be written

IPM Type	mean time (min.)
Deterministic	0.02
Stochastic, kernel-resampled	0.07
Stochastic, parameter-resampled	87.12

Table 3: Population growth rates for continuous forest (CF) and forest fragments (FF) under different kinds of IPMs with bootstrapped, bias-corrected, 95% confidence intervals.

IPM	Habitat	λ
Deterministic	FF	0.9778 (0.9736, 0.9823)
Deterministic	CF	0.9897 (0.9877, 0.9920)
Stochastic, kernel-resampled	FF	0.9787 (0.9735, 0.9835)
Stochastic, kernel-resampled	CF	0.9913 (0.9892, 0.9939)
dlnm	FF	0.9595 (0.9459, 0.9689)
dlnm	CF	0.9795 (0.9752, 0.9867)



Description	Deterministic	Stochastic, kernel-resampled	Stochastic, parameter-resampled
Survival	$s(z)$	$s_y(z)$	$s(z;\theta_{0-36})$
Growth	$G(z';z)$	$G_y(z';z)$	$G(z',z;\theta_{0-36})$
Flowering	$p_f(z)$	$p_{f_y}(z)$	$p_f(z;\theta_{0-36})$
Size-specific fecundity	$f(z)$	$f(z)$	$f(z)$
Germination & establishment	g	g	g
Seedling survival	s_0	s_{0_y}	$s_0(\theta_{0-36})$
Seedling growth	$G_0(z')$	$G_{0_y}(z')$	$G_0(z';\theta_{0-36})$

Figure 1: Lifecycle diagram of Heliconia acuminata. Each transition is associated with an equation for a vital rate function. The functions shown on the diagram correspond to those used to construct a general, density-independent, deterministic IPM. The table below shows the equivalent equations for stochastic, kernel-resampled IPMs and stochastic, parameter-resampled IPMs.

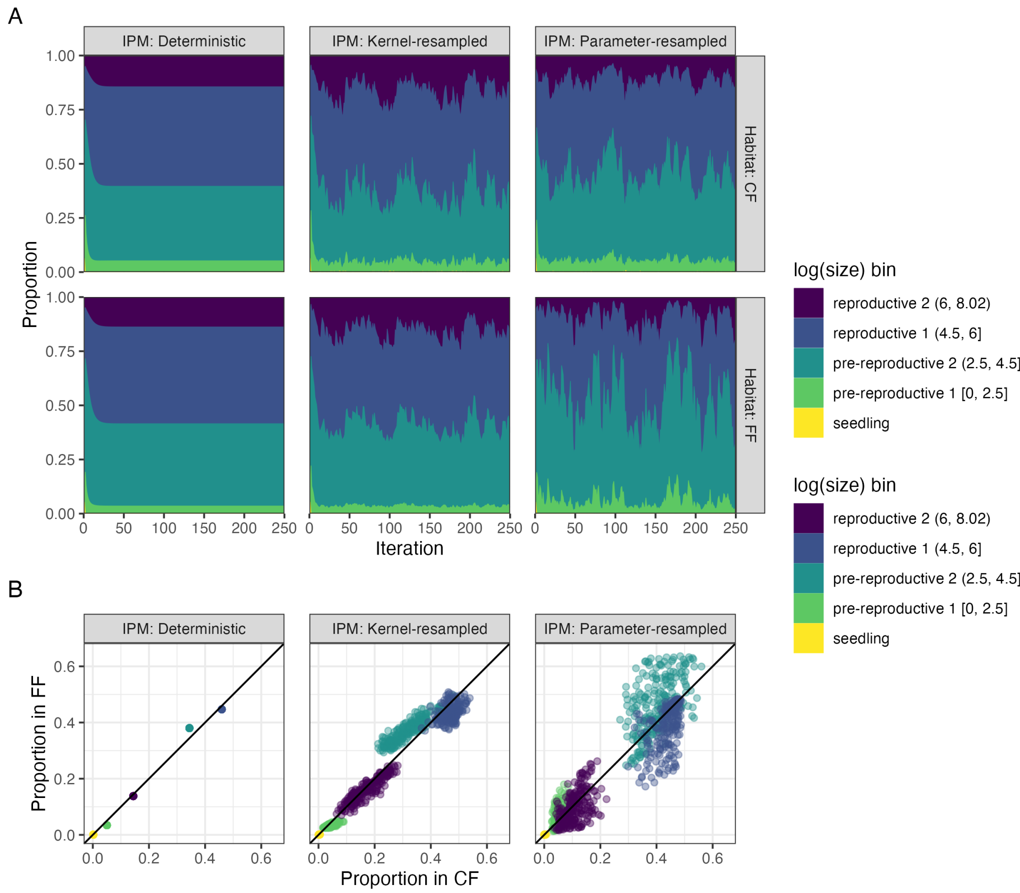

A
IPM: Deterministic
IPM: Kernel-resampled
IPM: Parameter-resampled
Habitat: CF
Habitat: FF
Proportion
Iteration
log(size) bin
reproductive 2 (6, 8.02)
reproductive 1 (4.5, 6]
pre-reproductive 2 (2.5, 4.5]
pre-reproductive 1 [0, 2.5]
seedling
B
Proportion in FF
Proportion in CF

Figure 2