

Context-dependent consequences of lagged effects in demographic models

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Abstract

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14 Text of 150 words max summarizing this amazing paper.

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Introduction

Integral Projection Models (i.e., IPMs) are an important and widely used tool for studying demography and population dynamics (Ellner and Rees 2006; Rees and Ellner 2009; Rees et al. 2014). 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 expanded 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 parameterize 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 such lagged effects could potentially have major consequences for population dynamics (Beckerman et al. 2002), their demographic impacts remain poorly understood (Williams et al. 2015; but see Molowny-Horas et al. 2017; Tenhumberg et al. 2018). There are two primary reasons for this limited understanding. The first is a lack of empirical data (sensu Evers et al. 2021). Detecting lagged effects requires long-term data on both the putative lagged effects and their potential drivers (Metcalf et al. 2015), and studies to detect them can be challenging to design and maintain (Kuss et al. 2008). The second challenge is technical - incorporating complex biological processes such as lagged effects in demographic models can render the models less tractable.

We used a decade of survey and climate data to assess the effects of precipitation extremes on the demographic vital rates of the Amazonian understory herb *Heliconia acuminata* (Scott et al. 2022). Our analyses revealed that the effects of climate on vital rates could be delayed up to 36 months, and that the presence and duration of these effects could differ by vital rate and habitat type (i.e., continuous forest vs. forest fragments). Here we investigate how including lagged effects in Integral Projection Models influences projections of population growth rate (i.e., λ) and structure. To do so we parameterized and compared

three different classes of Integral Projection Models: a deterministic IPM, a stochastic IPM, and a stochastic IPM with lagged effects of SPEI on vital rates. 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 forest than 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, regardless of whether models included stochasticity or lagged effects.

Methods

Study System and Demographic Data

Heliconia acuminata (Heliconiaceae) is a perennial, self-incompatible monocot (Kress 1990) that is distributed throughout much of the Amazon basin (Kress 1990). While some *Heliconia* species grow in large aggregations on roadsides, gaps, and in other disturbed habitats, others - including *H. acuminata* - grow primarily in the forest understory (Kress 1983; Ribeiro et al. 2010). Understory *Heliconia* species typically produce fewer flowers and are pollinated by traplining hummingbirds (Stouffer and Bierregaard 1996; Bruna et al. 2004).

The models and analyses here are based on 11 years (1998-2009) of demographic data collected on >8500 *H. acuminata* found at Brazil's Biological Dynamics of Forest Fragments Project (BDFFP), located ~70 km north of Manaus, Brazil. The BDFFP reserves include both continuous forest and forest fragments that range in size from 1-100 ha. These fragment reserves were originally isolated in the early 1980's by the creation of cattle pastures, with the secondary growth surrounding them periodically cleared to ensure their continued isolation. The habitat in all sites is non-flooded lowland rain forest with rugged topography. A complete summary of the BDFFP and its history can be found in Bierregaard et al. (2001).

In 1997-1998 a series of 5000 m² plots were established in the BDFFP's Continuous Forest Reserves (N=6 plots) and 1-ha Fragments (N=4 plots) in which all of the *Heliconia acuminata* were marked and measured. The plots were censused annually, at which time a team marked and measured new seedlings, identified any previously marked plants that died, and recorded the size of surviving individuals. Each plot was also surveyed 4-5 times during the flowering season to identify reproductive plants; in our site *H. acuminata* begin flowering early in the rainy season (e.g., January) and most reproductive plants produce a single inflorescence (range = 1-7) with 20-25 flowers (Bruna and Kress 2002). Fruits mature April-May and have 1-3 seeds per fruit ($\bar{x} = 2$) that are dispersed by a thrush and several species of manakin (Uriarte et al. 2011). Dispersed seeds germinate approximately 6 months after dispersal at the onset of the subsequent rainy season, with rates of germination and seedling establishment higher in continuous

forest than forest fragments (Bruna 1999; Bruna and Kress 2002). On average plots in CF also had more than twice as many plants as the plots in 1-ha fragments (CF median = 788, range = [201, 1549]; 1-ha median = 339, range = [297, 400]). A complete description of the demographic methods, data, and analyses to date can be found in (Bruna et al. 2023).

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 discrete 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.

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

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

$$R(z') = s_s G_s(z') \quad (3)$$

$$P(z', z) = s(z)G(z', z) \quad (4)$$

$$F(z) = p_f(z)f(z)g \quad (5)$$

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 dataset 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 evapotranspiration 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 bootstrapped 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 2).
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. DLNM models take much, much longer to iterate: while the Deterministic and Kernel-resampled stochastic models took ~0.02 and ~0.07 min to iterate (respectively), the Parameter-resampled stochastic models with lagged effects took ~87.12 min.
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.

219
220 6. Figure 2 has some interesting things in it:

- 221 • For the deterministic IPM (and the kernel-resampled IPM?) there are
222 slightly more of the smallest plants and the largest plants in CF compared
223 to FF (i.e. more medium sized plants in FF).
- 224 • For the kernel-resampled IPM (random effect of year), the fluctuations are
225 extremely similar between CF and FF
- 226 • For the parameter-resampled IPM (DLNM) the size structure of the popu-
227 lation is a LOT more variable in FF. This makes sense as we know lagged
228 effects are more important in fragments.
- 229 • Also, the fluctuations in size structure in CF do not match the fluctuations
230 in FF as well (can see this by the increased spread of points in Figure 2 (B))
- 231 • Also, in the parameter-resampled IPM (and only in this one), we see a shift
232 toward smaller plants in FF compared to CF
- 233 • These results are consistent with those of Kaye and Pyke (2003), who found
234 who found that the method effected stochastic lambda but relative ranking
235 of populations was consistent.

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242 CRediT Statement

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

246 Data Availability Statement

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

248 Literature Cited

249 Beckerman, A., T. G. Benton, E. Ranta, V. Kaitala, and P. Lundberg. 2002. [Population](#)
250 [dynamic consequences of delayed life-history effects](#). Trends in Ecology & Evolution 17:263–
251 269.

252 Bierregaard, R. O., C. Gascon, T. E. Lovejoy, and R. Mesquita, eds. 2001. Lessons from
253 Amazonia: The ecology and conservation of a fragmented forest. Yale University Press, New
254 Haven.

- Brooks, M. E., K. Kristensen, M. R. Darrigo, P. Rubim, M. Uriarte, E. Bruna, and B. M. Bolker. 2019. [Statistical modeling of patterns in annual reproductive rates](#). *Ecology* 100.
- Bruna, E. M. 1999. [Seed germination in rainforest fragments](#). *Nature* 402:139.
- Bruna, E. M. 2003. [Are plant populations in fragmented habitats recruitment limited? Tests with an Amazonian herb](#). *Ecology* 84:932–947.
- Bruna, E. M., and W. J. Kress. 2002. [Habitat fragmentation and the demographic structure of an Amazonian understory herb \(*Heliconia acuminata*\)](#). *Conservation Biology* 16:1256–1266.
- Bruna, E. M., W. J. Kress, F. Marques, and O. F. da Silva. 2004. [Heliconia acuminata reproductive success is independent of local floral density](#). *Acta Amazonica* 34:467–471.
- Bruna, E. M., O. Nardy, S. Y. Strauss, and S. Harrison. 2002. [Experimental assessment of Heliconia acuminata growth in a fragmented Amazonian landscape](#). *Journal of Ecology* 90:639–649.
- Bruna, E. M., and M. K. Oli. 2005. [Demographic Effects of Habitat Fragmentation on a Tropical Herb: Life-Table Response Experiments](#). *Ecology* 86:1816–1824.
- Bruna, E. M., M. Uriarte, M. R. Darrigo, P. Rubim, C. F. Jurinitz, E. R. Scott, O. Ferreira da Silva, et al. 2023. [Demography of the understory herb Heliconia acuminata \(Heliconiaceae\) in an experimentally fragmented tropical landscape](#). *Ecology* 104:e4174.
- Caswell, H. 2001. *Matrix population models: Construction, analysis, and interpretation*. Sinauer Associates, Sunderland.
- Criley, R., and S. Lekawatana. 1994. [Year around production with high yields may be a possibility for Heliconia chartacea](#). *Acta Horticulturae*, New ornamental crops and the market for floricultural products 397:95–102.
- Crone, E. E., E. S. Menges, M. M. Ellis, T. Bell, P. Bierzychudek, J. Ehrlén, T. N. Kaye, et al. 2011. [How do plant ecologists use matrix population models?](#) *Ecology Letters* 14:1–8.
- Ellner, S. P., D. Z. Childs, and M. Rees. 2016. *Data-driven modelling of structured populations: A practical guide to the integral projection model*. Springer Science+Business Media, New York, NY.
- Ellner, S. P., and M. Rees. 2006. [Integral projection models for species with complex demography](#). *American Naturalist* 167:410–428.
- Evers, S. M., T. M. Knight, D. W. Inouye, T. E. X. Miller, R. Salguero-Gómez, A. M. Iler, and A. Compagnoni. 2021. [Lagged and dormant season climate better predict plant vital](#)

287 rates than climate during the growing season. *Global Change Biology* 27:1927–1941.

288 Kaye, T. N., and D. A. Pyke. 2003. The effect of stochastic technique on estimates of
289 population viability from transition matrix models. *Ecology* 84:1464–1476.

290 Kress, J. 1990. The diversity and distribution of heliconia (Heliconiaceae) in Brazil. *Acta*
291 *Botanica Brasileira* 4:159–167.

292 Kress, W. J. 1983. Self-incompatibility systems in Central American heliconia. *Evolution*
293 37:735–744.

294 Kuss, P., M. Rees, H. H. Ægisdóttir, S. P. Ellner, and J. Stöcklin. 2008. Evolutionary
295 demography of long-lived monocarpic perennials: A time-lagged integral projection model.
296 *Journal of Ecology* 96:821–832.

297 Landau, W. M. 2021. The targets R package: A dynamic Make-like function-oriented
298 pipeline toolkit for reproducibility and high-performance computing 6:2959.

299 Levin, S. C., D. Z. Childs, A. Compagnoni, S. Evers, T. M. Knight, and R. Salguero-Gómez.
300 2021. *Ipmr: Flexible implementation of Integral Projection Models in R*. *Methods in Ecology*
301 *and Evolution* 12:1826–1834.

302 Metcalf, C. J. E., S. P. Ellner, D. Z. Childs, R. Salguero-Gómez, C. Merow, S. M. McMahon,
303 E. Jongejans, et al. 2015. Statistical modelling of annual variation for inference on stochastic
304 population dynamics using Integral Projection Models. *Methods in Ecology and Evolution*
305 6:1007–1017.

306 Molowny-Horas, R., M. L. Suarez, and F. Lloret. 2017. Changes in the natural dynamics
307 of *Nothofagus dombeyi* forests: Population modeling with increasing drought frequencies.
308 *Ecosphere* 8:1–17.

309 Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology: Theory and
310 practice of population viability analysis. Sinauer, Sunderland, MA.

311 R Core Team. 2020. R: A language and environment for statistical computing. Vienna,
312 Austria.

313 Rees, M., D. Z. Childs, and S. P. Ellner. 2014. Building integral projection models: A user's
314 guide. *Journal of Animal Ecology* 83:528–545.

315 Rees, M., and S. P. Ellner. 2009. Integral projection models for populations in temporally
316 varying environments. *Ecological Monographs* 79:575–594.

317 ———. 2016. Evolving integral projection models: Evolutionary demography meets eco-
318 evolutionary dynamics. *Methods in Ecology and Evolution* 7:157–170.

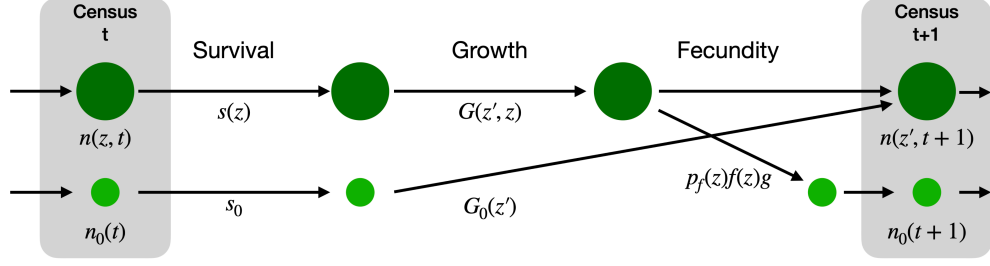
- 319 Ribeiro, M. B. N., E. M. Bruna, and W. Mantovani. 2010. [Influence of post-clearing](#)
320 [treatment on the recovery of herbaceous plant communities in Amazonian secondary forests.](#)
321 *Restoration Ecology* 18:50–58.
- 322 Salguero-Gómez, R., O. R. Jones, C. R. Archer, Y. M. Buckley, J. Che-Castaldo, H. Caswell,
323 D. Hodgson, et al. 2015. [The COMPADRE Plant Matrix Database: An open online reposi-](#)
324 [tory for plant demography.](#) (M. Rees, ed.) *Journal of Ecology* 103:202–218.
- 325 Scott, E. R., M. Uriarte, and E. M. Bruna. 2022. [Delayed effects of climate on vital rates](#)
326 [lead to demographic divergence in Amazonian forest fragments.](#) *Global Change Biology*
327 28:463–479.
- 328 Stouffer, P. C., and R. O. Bierregaard. 1996. Forest fragmentation and seasonal patterns of
329 hummingbird abundance in Amazonian Brazil. *Ararajuba* 4:9–14.
- 330 Tenhumberg, B., E. E. Crone, S. Ramula, and A. J. Tyre. 2018. [Time-lagged effects of](#)
331 [weather on plant demography: Drought and *Astragalus scaphoides*.](#) *Ecology* 99:915–925.
- 332 Tuljapurkar, S. 1990. [Population Dynamics in Variable Environments.](#) (S. Levin, ed.) *Lecture*
333 *Notes in Biomathematics* (Vol. 85). Springer, Berlin, Heidelberg.
- 334 Uriarte, M., M. Anciães, M. T. B. da Silva, R. Rubim, E. Johnson, and E. M. Bruna. 2011.
335 [Disentangling the drivers of reduced long-distance seed dispersal by birds in an experimen-](#)
336 [tally fragmented landscape.](#) *Ecology* 92:924–937.
- 337 Williams, J. L., H. Jacquemyn, B. M. Ochocki, R. Brys, T. E. X. Miller, and R. Sheffer-
338 son. 2015. [Life history evolution under climate change and its influence on the population](#)
339 [dynamics of a long-lived plant.](#) *Journal of Ecology* 103:798–808.
- 340 Williams, J. L., T. E. Miller, and S. P. Ellner. 2012. Avoiding unintentional eviction from
341 integral projection models. *Ecology* 93:2008–2014.
- 342 Wood, S. N. 2011. Fast stable restricted maximum likelihood and marginal likelihood esti-
343 mation of semiparametric generalized linear models 73:3–36.
- 344 Xavier, A. C., C. W. King, and B. R. Scanlon. 2016. [Daily gridded meteorological variables](#)
345 [in Brazil \(1980–2013\).](#) *International Journal of Climatology* 36:2644–2659.

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: 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.

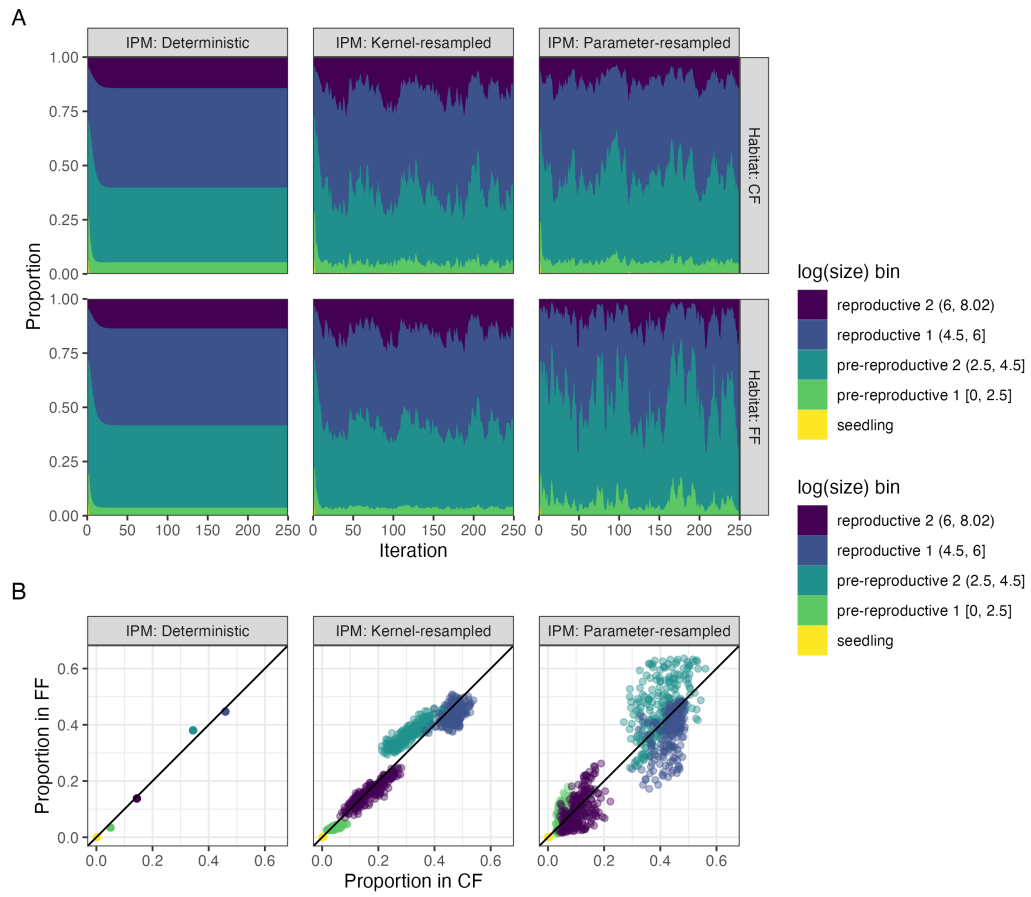


Figure 2