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

There is increasing evidence that an organism's current likelihood of growth, survival, or reproduction can be strongly influenced by previous environmental conditions. These *Lagged Effects*, also known as *Delayed Life-history Events* (i.e., DLHEs) (Beckerman et al. 2002), can simultaneously affect an entire cohort (e.g., juveniles hatching during a period of scarcity will all have delayed maturation and lower lifetime fecundity) or only a subset of the population (e.g., cold temperatures in one year lead to reduced flowering by potentially reproductive individuals in the next). In addition, the temporal delay between an environmental event and changes in demographic vital rates depends on both the intensity of the event and its timing relative to the underlying physiological processes (Criley and Lekawatana 1994; Evers et al. 2021). A drought during the early stages of gestation or floral bud formation, for example, might have a much larger impact on the number of fruits or offspring produced than one several months later whose timing coincides with birth or flowering. The delay or intensity of lagged effects can also depend on local ecological conditions, with individuals in some habitats buffered against – or able to recover more quickly from - the delayed effects of environmental variation.

Because Lagged Effects are often directly linked to reproduction and survival, it is thought they could have major consequences for population dynamics (Beckerman et al. 2002). Although there is emerging evidence that this is indeed the case (Williams et al. 2015; e.g., Molowny-Horas et al. 2017; Tenhumberg et al. 2018), broader efforts to test this hypothesis have been hampered by two primary factors: First, detecting lagged effects requires long-term data on both the putative lagged effect (i.e., probability of flowering) and its potential environmental drivers (Metcalf et al. 2015). These coupled data sets are rare (sensu Evers et al. 2021), in part because studies to disentangle lagged effects can be challenging to design and maintain (Kuss et al. 2008). Second, the methods for identifying lagged effects and modeling their demographic impacts can be challenging to implement. Many of the statistical methods have stringent data requirements (Metcalf et al. 2015) and assumptions, while the including complex biological processes in demographic models can render them less tractable. Addressing these obstacles is a major undertaking; the value of doing so will depend on the effort required vs. the potential consequences of failing to consider lagged effects - consequences that range from overestimating projections of population growth rate (i.e., λ) in a conservation setting to drawing invalid conclusions regarding support for the predictions of ecological or evolutionary theory.

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 Crone et al. (2011). Mathematical and statistical advances (e.g., Williams et al. 2012; Brooks et al. 2019) have rapidly expand the scope of questions and biological processes that can be investigated with these models (e.g., Metcalf et al. 2015; Ellner et al. 2016; Rees and Ellner 2016). Here we investigate how including lagged effects in Integral Projection

Models influences projections of λ and population structure.

We have previously shown that the effects of precipitation extremes on the demographic vital rates of an Amazonian understory herb (*Heliconia acuminata*, Heliconiaceae) can be delayed up to 36 months (Scott et al. 2022), with the presence and duration of these lagged effects varying by vital rate and habitat. We parameterized three classes of Integral Projection Models - a deterministic IPM, a stochastic IPM, and a stochastic IPM with lagged effects of precipitation on vital rates - for populations in two habitat type (i.e., continuous forest vs. forest fragments). 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) projections of λ from deterministic models would be higher than those of stochastic models, and that (ii) for all IPMs the projections of λ forest fragments would be lower than for continuous forest, but that the difference would be proportionately greater for IPM with lagged effects.

Methods

Study System and Demographic Data

Heliconia acuminata (Heliconiaceae) is a perennial, self-incompatible monocot 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 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).

A complete description of the demographic methods, data, and analyses to date can be found in Bruna et al. (2023). Briefly, in 1997–1998 a series of 5000 m^2 plots were established in the BDFFP reserves: N=6 in Continuous Forest and N=4 in 1-ha Forest Fragments. All of the *Heliconia acuminata* in these plots were marked and measured; the plots were censused annually, at which time a team recorded the size of surviving individuals, marked and measured new seedlings, and identified any previously marked plants that died. 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 infloresence (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 olots 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)).

Construction of Integral Projection Models

We projected the growth rate and structure of *Heliconia acuminata* populations in Continuous Forest and Forest Fragments with three classes of IPMs - Deterministic, Stochastic, and Stochastic with Lagged Environmental Effects. Each of these IPMs required different functional forms of the underlying vital rate functions used to describe the *H. acuminata* life cycle (Figure 1). All models were density-independent, with the deterministic model serving as the foundation for the more complex models.

(1) Deterministic IPM: In this model the size and structure of a population in year $t+1$ is determined by the survival and growth of plants alive in year t (Equation 1) plus the number of new seedlings that entered the population (Equation 2).

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

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

Equation 1 has two components. The first is the sub-kernel $P(z', z)$, which describes the size-dependent survival and growth/regression of mature plants (Equation 3):

$$P(z', z) = s(z)G(z', z) \tag{3}$$

The second is sub-kernel $R(z')$, which describes the survival of seedlings established in year t and their size when entering the mature plant population in year $t+1$ (Equation 4):

$$R(z') = s_s G_s(z') \tag{4}$$

Note that in Equation 4 both the probability that new seedlings survive their first year, s_s, and their size at the end of this year, $G(z', z)$, are size-independent. IPMs can include transitions between individuals from a discrete state to a continuous one (i.e., from 'seedling' to 'mature plant of size z',' Ellner et al. 2016); we treat seedlings as a distinct and discrete category because they have lower survival and growth in their first year than comparably sized plants (Bruna 2003; Scott et al. 2022).

The number of new seedlings entering the population in year $t+1$ is a function of the number of mature plants in year t and a sub-kernel describing the size-dependent fecundity of these individuals (Equation 5):

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

Both the probability that a mature plant will flower, $p_f(z)$, and the number of seeds a flowering plant will produce, $f(z)$, are size-dependent. All seeds germinate and establish as seedlings with probability g.

We used the annual census data (Bruna 2003) to fit the deterministic vital rate functions for growth, survival, and flowering in each habitat type (i.e., Fragments, Continuous Forest; the data from all plots within a habitat class were pooled to create a single 'summary population' (Bruna 2003). For established plants these were modeled as a smooth function of size in the previous census with generalized additive models (GAMs) fit with the `mgcv` library (Wood 2011) for the R statistical programming language (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 a scaled t family distribution provided a better fit to the data than a Gaussian fit, as the residuals with a simple Gaussian model were Leptokurtic. To model size-specific fecundity we used data on the number of fruits per flowering plant (Bruna 2021) and seeds per fruit (Bruna 2014) that were collected outside of the demographic plots (to avoid altering within-plot recruitment) and experimentally-derived estimates of seed germination and seedling establishment (Bruna 1999, 2002) .

(2) Stochastic IPMs: To include temporal stochasticity in our IPMs we included a random effect of year. This was done using a factor–smooth interaction that allowed the functional form of the relationship between plant size and vital rates to vary among transition years (Figure 1). We generated kernels for every transition year using the long-term survey data (Bruna et al. 2023) and random smooths for year. We then randomly selected one of these sets of kernels to use in each iteration of the IPM. This procedure is equivalent to *'kernel resampling'* (*sensu* Metcalf et al. 2015) or matrix selection for matrix population models (Caswell 2001).

(3) Stochastic IPMs with lagged effects of precipitation on vital rates: We explicit modeled the lagged effects of precipitation extremes on vital rates using the procedure described in Scott et al. (2022). Briefly, we first calculated the Standardized Precipitation Evapotranspiraton Index (i.e., SPEI) for our study site using a published gridded dataset based on ground measurements (Xavier et al. 2016). After we fit vital rate models using the long-term survey data (Figure 1), we modeled delayed effects of SPEI with Distributed Lag Non-linear Models (i.e., DLNMs) with a maximum lag of 36 months (Scott et al. 2022). To iterate these parameter-resampled IPMs (*sensu* Metcalf et al. 2015) we first created a random sequence of SPEI values by sampling years of the observed (monthly) SPEI data. For every year we then calculated a lag of 36 months from the month in which that year's census was completed. These values were then used to predict the fitted values from vital rate models, which generated different kernels for each iteration of the IPM. The kernels of successive iterations are not entirely independent – the SPEI values used to calculate vital rates include values used in the previous two iterations – they are ergodic.

All IPMs were constructed and iterated using the `ipmr` package (Levin et al. 2021) for the

R statistical programming language (R Core Team 2020). 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, but discarded 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 then back-transformed to allow for direct comparison with projections of λ from deterministic models. The initial starting vector primarily influences a population's transient dynamics; we therefore used the distribution of established plant sizes and proportion of seedlings in the full demographic data set as the initial population vector for all models. Finally, we estimated the 95% confidence intervals for each IPMs projections of λ. To do so we first created 500 populations for each habitat type by sampling individual plants with replacement (i.e., bootstrapping) until the population size of each matched that of the initial population vector. We then re-fit the vital rate models for growth, survival, and flowering for each of these bootstrapped population and constructed new IPMs for each population as above (the models for germination and establishment rate, fruits per flowering plant, and seeds per fruit were not refit because these were estimated using different data sets). The projections of λ for the new populations were then used to estimate the upper and lower 95% bias-corrected percentile intervals (Caswell 2001; Manly 2018). This workflow was managed using the `targets` R package (Landau 2021), which also allowed us to track computational time spent processing and analyzing each class of IPM.

Statistical analyses

Comparison of CF vs FF

- For det need to bootstrap
- for within stoch and lag: glm/t-test.
- Comparison of pop structure in figure (test for increasing variance with variance / F or permutation test). Villase nor, J. A., & González-Estrada, E. (2024). A non-parametric test for homogeneity of variances. Communications in Statistics - Theory and Methods, 54(2), 646–654. https://doi.org/10.1080/03610926.2024.2316274 OR https://www.datanovia.com/en/lessons/homogeneity-of-variance-test-in-r/#google_vignette

Results & Discussion

Lambda Comparison

1. We found that including Delayed Life-History Events in Intergral Projection Models led to significantly lower projections of λ
2. It is reassuring that all IPM models projected higher values of λ in continuous forest than forest fragments (Table 2); this is consistent with the results of previous studies comparing the relative rankings of projections from stochastic and deterministic models (e.g., Kaye and Pyke 2003.)
3. However, the underestimating λ by 2-3% difference in λ resulting projections from the different IPMs could have major implications for many of the contexts in which IPMs

are brought to bear.
4. If you are doing conservation and management, a growth rate lower by 5-6 % would really rock your world.
5. For instance, underestimating λ by failing to include lagged effects could be especially severe in studies of climate change, given many DLHE are climate driven.

Pop Structure Comparison

1. Including lagged effects in IPMs also resulted in more variable projections of future population structure (Figure 2 a), especially in forest fragments where we have previously shown lagged effects have very large impacts on growth and survival (Scott et al. 2022).
2. Consequently, projections of population structure were also far less less consistent across habitats (Figure 2 b).
3. Finally, the choice of IPM also resulted in some subtle but notable differences in projected population structure.
4. For example, the deterministic IPM projected the population in Continuous Forest had slightly more of the smallest and largest plants than the population in Forest Fragments.
5. In other words, populations in forest fragments had proportionatly less recruitment and fewer individuals growing into the larger and reproductivce size classes (Bruna and Oli 2005).
6. The shift towards intermediately sized, pre-reproductive plants in forest fragments is even more dramatic when using the parameter-resampled stochastic IPM (Figure 2 b).

So...should we care?

1. Including delayed life-history events in demographic models has important implications both projections of population growth rate and population structure.
2. These projections may be more accurrate - the underlying vital rate models for IPMS with Lagged effects all had the best fit to the survey data (dAIC = 0, Table 1).
3. While this may not be critical in situations where relative differences allow for hypothesis testing, it may be especially important in conservation or manaagement settings.
4. Including lagged effects comes at a cost, however.
5. While Deterministic and Kernel-resampled Stochastic IPMs took only ~0.02 and ~0.07 min to iterate (respectively), the Stochastic IPMs with using parameter-resampled kernels and lagged effects took ~87.12 min.
6. This is largely due to the required computational resources and algorithms (i.e., `predict()`), which are much slower forGeneral Additive Models (i.e., GAMs) with 2D smooths because of the much higher number of knots than for the GAMs used in Determinsitic and Kernel-resampled IPMs.
7. Advances in computational power and access to high-performance computing resources

could lower this cost.

8. However, computational power cannot compensate for limited data.
9. Detecting lagged effects and evaluating their consequences requires long-term demographic data - data that are only available for a relatively small number of species, few of which are in the tropics.
10. The increasing evidence that lagged effects are ubiquitous, and that they can have major demographic impacts, underscores the need to support the collection of such long-term data, the complementary development of experimental and statistical approaches to disentangling lagged effects, and community driven efforts to identify priority or model systems for in-depth investigation.

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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, writing, and, acquired funding.

Data Availability Statement

Data and R code used in this study are archived with Zenodo at *(doi and url to be added on acceptance)*.

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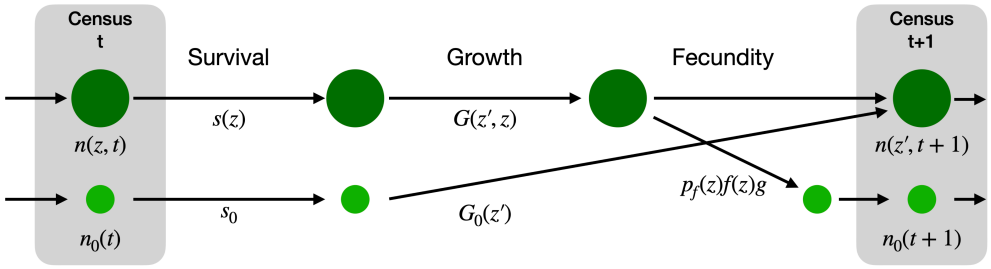

Description	Deterministic	Stochastic, kernel-resampled	Stochastic, parameter-resampled
Survival	$s(z)$	$s_y(z)$	$s(z;\theta_{0-36})$
Growth	$G(z';z)$	$G_y(z';z)$	$G(z',z;\theta_{0-36})$
Flowering	$p_f(z)$	$p_{f_y}(z)$	$p_f(z;\theta_{0-36})$
Size-specific fecundity	$f(z)$	$f(z)$	$f(z)$
Germination & establishment	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: Life cycle 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.

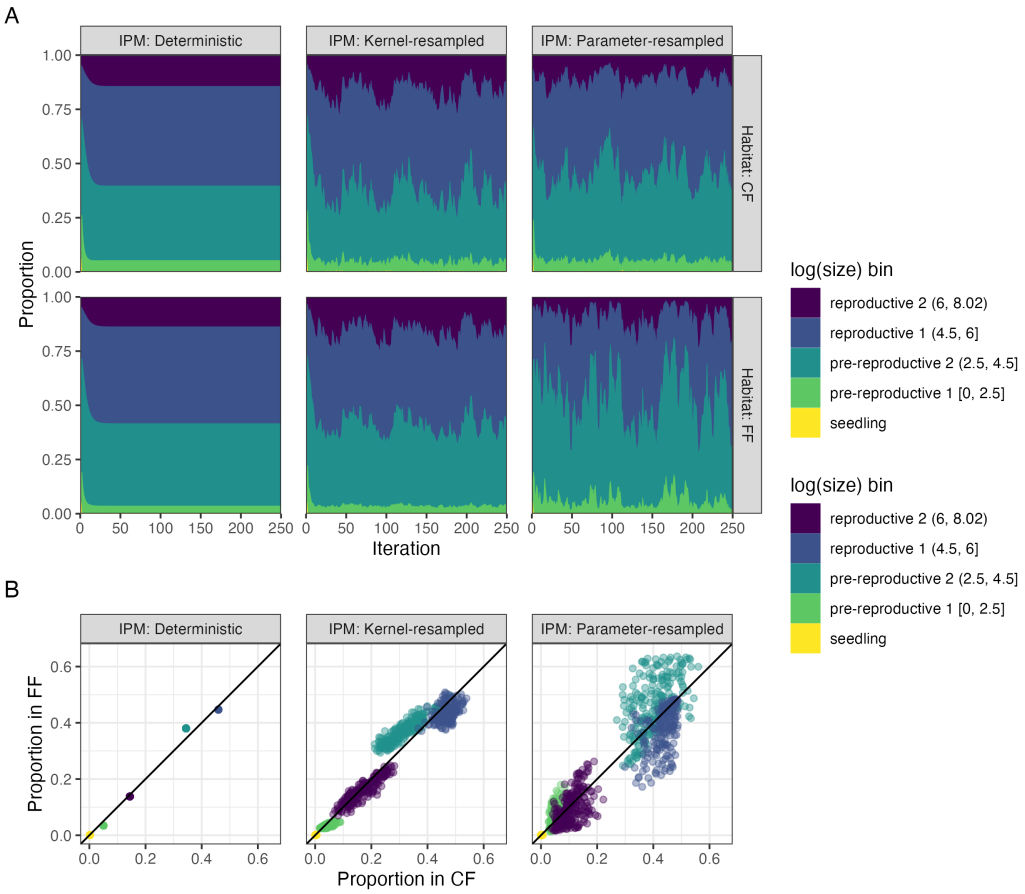

Figure 2: **(A)** The proportion of *Heliconia acuminata* populations in different size/stage classes when simulating population dyammics with three different Integral Projection Models. Results are shown for the first 250 iterations of populations in both in Continuous Forest (CF) and Forest Fragments (FF); for the criteria used to define the size categories see Table 3. **(B)** For each interation, the relative proportion of the population in each size class (FF vs CF). Note that this excludes transient dynamics (iterations 1-30). Values on the 1-1 line indicate an iteration where CF and FF have the same proportion of the population in a given size class.

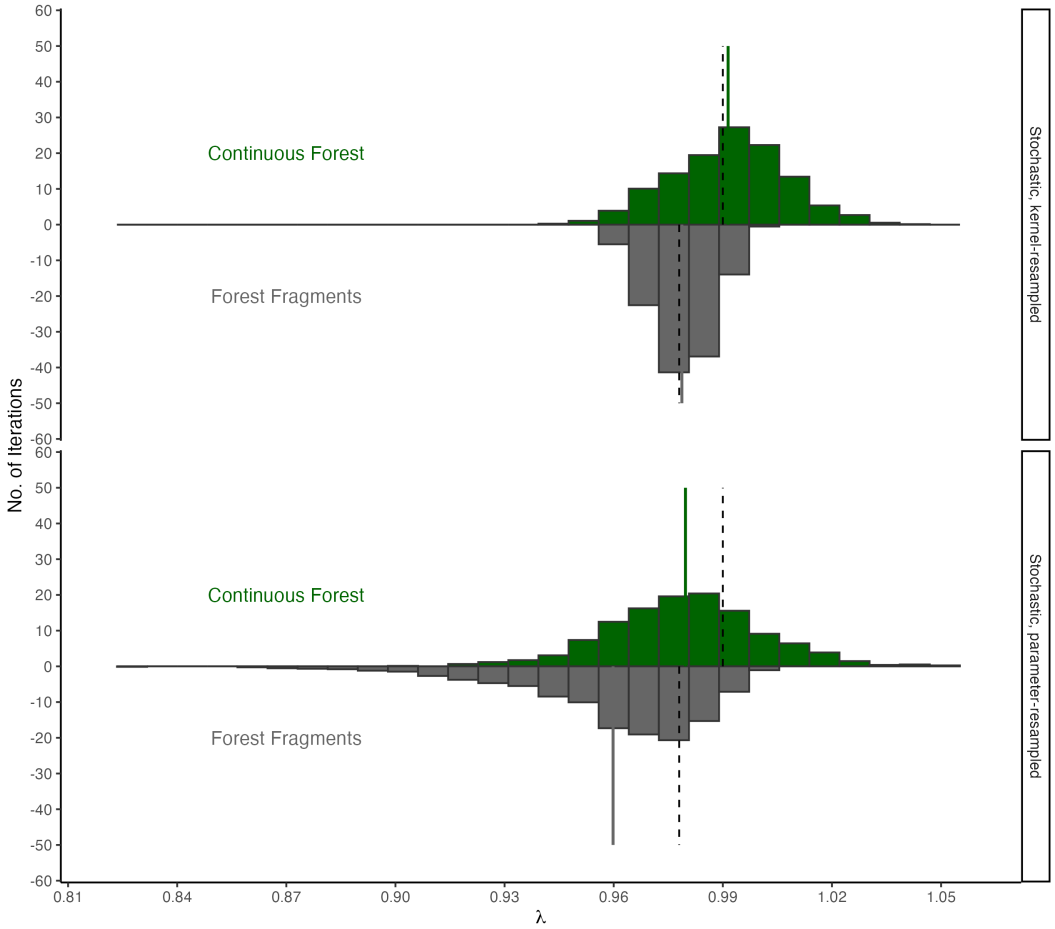

Figure 3: Distribution of 900 values of projected with (A) Stochastic, kernel-resampled IPMs and (B) Stochastic, paramenter-resampled IPMs. IPMs were used to project for both Continuous Forest (green) and Forest Fragments (gray). The solid line indicates the mean value, the dashed line indicates the value of λ in that habitat projected with Deterministic IPMs.

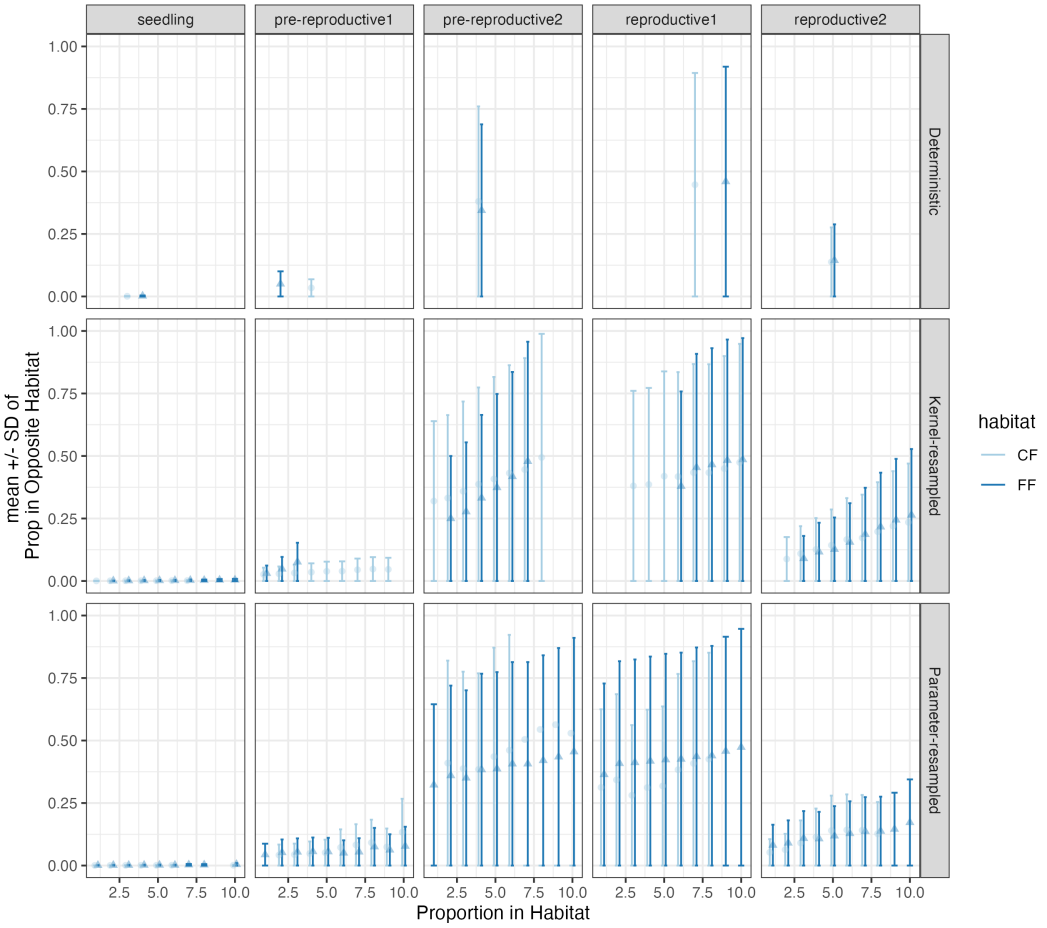
seedling
pre-reproductive1
pre-reproductive2
reproductive1
reproductive2
Deterministic
Kernel-resampled
Parameter-resampled
mean +/- SD of
Prop in Opposite Habitat
Proportion in Habitat
habitat
CF
FF
0.00
0.25
0.50
0.75
1.00
2.5
5.0
7.5
10.0

Figure 4: ——

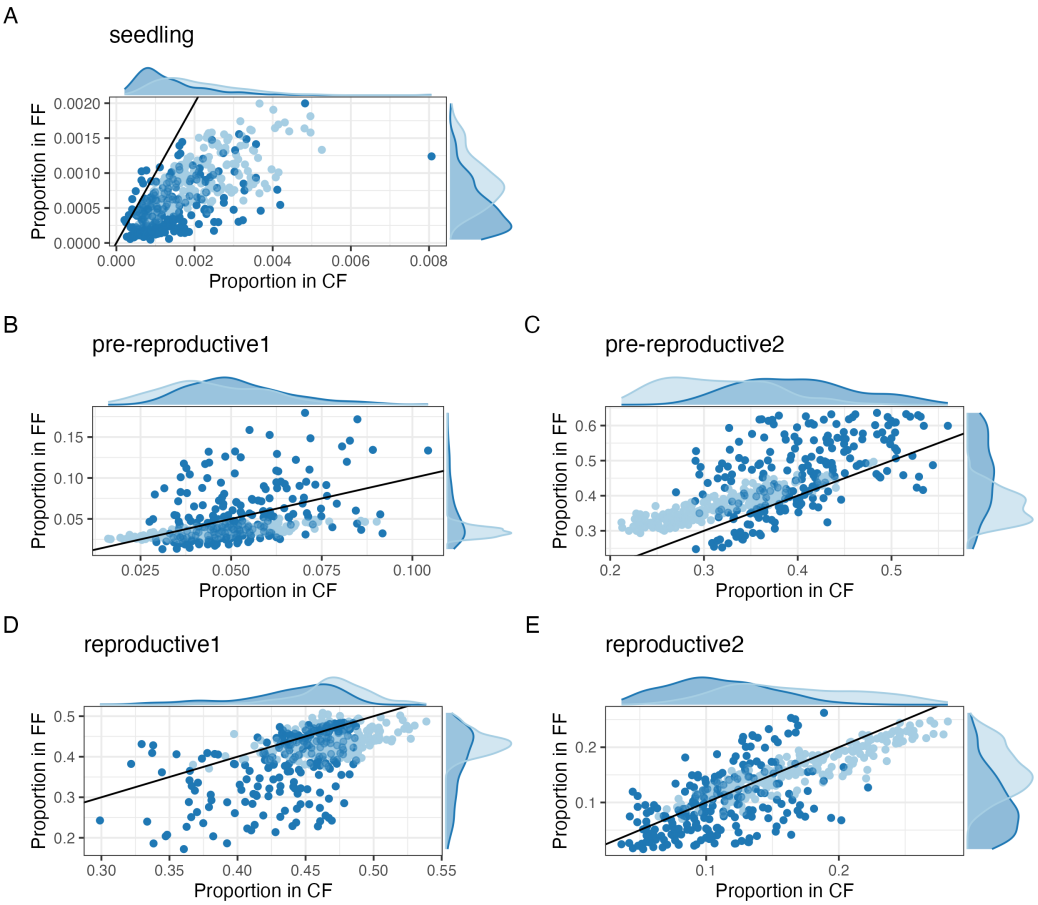
A
seedling
Proportion in FF
0.0020
0.0015
0.0010
0.0005
0.0000
0.000
0.002
0.004
0.006
0.008
Proportion in CF
B
pre-reproductive1
Proportion in FF
0.15
0.10
0.05
0.025
0.050
0.075
0.100
Proportion in CF
C
pre-reproductive2
Proportion in FF
0.6
0.5
0.4
0.3
0.2
0.3
0.4
0.5
Proportion in CF
D
reproductive1
Proportion in FF
0.5
0.4
0.3
0.2
0.30
0.35
0.40
0.45
0.50
0.55
Proportion in CF
E
reproductive2
Proportion in FF
0.2
0.1
0.1
0.2
Proportion in CF

Figure 5: ——

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
Continuous Forest				
	Survival	Random effect of year	43.26	0.00
		DLNM	19.72	78.92
		None	4.98	260.01
	Growth	Random effect of year	78.43	0.00
		DLNM	23.87	158.46
		None	7.81	1896.03
	Flowering	DLNM	19.59	0.00
		Random effect of year	17.19	1.63
		None	7.47	381.86
	Seedling survival	None	1.00	0.00
		Random effect of year	1.82	1.39
		DLNM	4.01	1.53
	Seedling growth	Random effect of year	9.47	0.00
		DLNM	8.95	2.90
		None	1.00	172.33
Forest Fragments				
	Survival	DLNM	14.95	0.00
		Random effect of year	19.21	35.68
		None	4.33	51.25
	Growth	DLNM	25.18	0.00
		Random effect of year	37.84	199.98
		None	5.60	382.76
	Flowering	DLNM	20.61	0.00
		Random effect of year	13.81	27.40
		None	5.01	101.70
	Seedling survival	DLNM	5.57	0.00
		Random effect of year	5.09	5.72
		None	1.00	6.49
	Seedling growth	Random effect of year	6.25	0.00
		DLNM	8.18	2.29
		None	1.00	5.74

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)
	CF	0.9897 (0.9877, 0.9920)
Stochastic, kernel resampled		
	FF	0.9787 (0.9735, 0.9835)
	CF	0.9913 (0.9892, 0.9939)
Stochastic, parameter-resampled		
	FF	0.9595 (0.9459, 0.9689)
	CF	0.9795 (0.9752, 0.9867)

Table 3: Size and stage categories used for comparing *Heliconia acuminata* population structure. Note that seedlings are a discrete size class not based on size (see *Methods* for additional details).

category	log(size)	avg. prob. survival	prob. flowering
seedlings	-	-	-
pre-reproductive 1	0–2.5	≤ 0.9	≈ 0
pre-reproductive 2	2.5-4.5	≥ 0.8	≈ 0
reproductive 1	4.5-6	≥ 0.95	≤ 0.25
reproductive 2	≥ 6	≥ 0.95	≥ 0.2