Delayed effects of climate on vital rates lead to demographic divergence in Amazonian forest fragments

Eric R. Scott[1,✉], María Uriarte[2], and Emilio M. Bruna[1,3,4]

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[1] Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, Florida 32611-0430

[2] Department of Ecology, Evolution and Environmental Biology, Columbia University 1200 Amsterdam Avenue, New York, New York 10027 USA

[3] Center for Latin American Studies, University of Florida, Gainesville, Florida 32611-5530

[4] Biological Dynamics of Forest Fragments Project, INPA-PDBFF, CP 478, Manaus, Amazonas 69011-970 Brazil

✉ Correspondence: Eric R. Scott <scottericr@gmail.com>

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Abstract

Deforestation often results in landscapes where remaining forest habitat is highly fragmented, with remnants of different sizes embedded in an often highly contrasting matrix. Local extinction of species from individual fragments is common, but the demographic mechanisms underlying these extinctions are poorly understood. It is often hypothesized that altered environmental conditions in fragments drive declines in reproduction, recruitment, or survivorship. The Amazon basin, in addition to experiencing continuing fragmentation, is warming and experiencing changes in precipitation leading to altered frequency and intensity of droughts and unusually wet periods. Whether plant populations in tropical forest fragments are particularly susceptible to extremes in precipitation remains unclear. Most studies of plants in fragments are relatively short (1–6 years), focus on a single life-history stage, and often do not compare to populations in continuous forest. Even fewer studies consider delayed effects of climate on demographic vital rates despite the importance of delayed effects in studies that consider them. Using a decade of demographic and climate data from an experimentally fragmented landscape in the Central Amazon, we assess the effects of climate on populations of an understory herb (*Heliconia acuminata*, Heliconiaceae). We used distributed lag non-linear models to understand the delayed effects of temperature and precipitation on survival, growth, and flowering. We detected delayed effects of climate up to 36 months. Drought two dry seasons prior to the February census decreased survival and increased flowering probability while drought in the wet season a year prior to the census decreased flowering probability and increased growth. The effects of extremes in precipitation on survival and growth were more pronounced in forest fragments compared to continuous forest. The

complex delayed effects of climate and habitat fragmentation in our study point to the importance of long-term demography experiments in understanding the effects of anthropogenic change on plant populations.

Introduction

The expansion of agriculture and other human activities is a primary driver of deforestation in the tropics (Alroy, 2017; Haddad et al., 2015). It also results in landscapes where the remaining forest can be highly fragmented, with patches of different sizes embedded in a matrix of often contrasting habitat (Bianchi & Haig, 2013; Taubert et al., 2018). This fragmentation is associated with myriad ecological changes, including the local and regional extinction of plant species (da Silva & Tabarelli, 2000; Laurance et al., 2006). Although the demographic mechanisms responsible these extinctions are poorly understood (Bruna et al., 2009), it is often hypothesized that the dramatically altered environmental conditions in tropical forest fragments (Arroyo-Rodríguez et al., 2017; Didham & Lawton, 1999; Ewers & Banks-Leite, 2013) drive declines in plant reproduction, recruitment, or survivorship (Bruna, 1999; Laurance et al., 1998; Zartman et al., 2015). Despite the prevalence of this hypothesis (Betts et al., 2019; Didham & Lawton, 1999; Laurance et al., 2001), efforts to link population-level demographic responses with altered environmental conditions in fragments remains scarce.

Studies in temperate systems have shown that the demography of species can also be altered by climate change (Doak & Morris, 2010; Selwood et al., 2015; Sletvold, 2005; Williams et al., 2015), and that the effects of climate change could be more pronounced when habitat is fragmented (Holyoak & Heath, 2016; Oliver et al., 2015). While the demographic consequences of climate change for tropical species are expected to be similarly severe (Brodie et al., 2012; Scheffers et al., 2017), surprisingly little is known about the responses of these species to climatic variability (Paniw et al., 2021). Tropical plants may be particularly sensitive to climate change—they typically have narrow ranges

of climatic tolerance (Feeley et al., 2012), and recent results suggest increases in the frequency and severity of extreme precipitation events reduce survival and reproduction (Esteban et al., 2021; Gaoue et al., 2019). This sensitivity to climatic fluctuations, coupled with evidence that plant growth and survivorship are lower in fragments (Bruna et al., 2002; Laurance et al., 1998; Zartman et al., 2015), has led to speculation that plants in forest fragments will be especially susceptible to climate change (Laurance et al., 2001; Opdam & Wascher, 2004; Selwood et al., 2015).

Whether the demography of plant populations in tropical forest fragments is more susceptible to climatic extremes remains unclear for three primary reasons. First, most studies of plants in fragments have focused on a single life-history stage or process (Bruna et al., 2009; Ehrlen et al., 2016), making it challenging to draw broader demographic conclusions. Second, there is a growing literature on how tropical plants respond to droughts (Esquivel-Muelbert et al., 2019; González-M et al., 2020; Uriarte et al., 2016), but few studies have compared the responses of plants in continuous forest with those of plants in forest fragments (Laurance et al., 2001). Finally, the multi-year data needed to test population-level hypotheses about climate change and fragmentation are scant, especially for tropical systems (Crone et al., 2011; Salguero-Gómez et al., 2015). These data are critical not simply because they allow for capturing variation in climatic conditions and the resulting demographic responses (Morris & Doak, 2002; Teller et al., 2016). They are also essential because while some demographic effects of fragmentation or drought can be detected immediately, others may take years to manifest (*e.g.,* Gagnon et al., 2011). Indeed, lagged responses of demographic vital rates to climate may be the rule rather than the

exception (Anderegg et al., 2015; Evers et al., 2021; Kannenberg et al., 2020; Schwalm et al., 2017).

Herbaceous plants represent up to 25% of plant diversity in tropical forests (Gentry & Dodson, 1987), are critical food and habitat for myriad species (Snow, 1981), and are economically and culturally vital (Nakazono et al., 2004; Ticktin, 2003). Nevertheless, the impacts of global change phenomena on their demography remain conspicuously understudied (Bruna et al., 2009). We used a decade of demographic and climatic data from an experimentally fragmented landscape in the Central Amazon to assess the effects of climate on populations of a tropical understory herb (*Heliconia acuminata*, Heliconiaceae). This time series, which included the severe droughts of 1997 (McPhaden, 1999) and 2005 (Marengo et al., 2008; Zeng et al., 2008), allowed us to address the following questions: (1) Does drought increase or decrease the growth, survival, and fertility of plant populations in continuous forest? (2) Are there delayed effects of drought on demographic vital rates, and if so what lag times are most critical? (3) Are the effects of drought on the vital rates of populations in fragments similar in direction and magnitude to those in continuous forest?

Methods

Study site

The Biological Dynamics of Forest Fragments Project (BDFFP) is located ~70 km north of Manaus, Brazil (2º30' S, 60ºW). In addition to large areas of continuous forest, the BDFFP has forest fragment reserves isolated from 1980–1984 by felling the trees surrounding the area chosen for isolation and, in most cases, burning the downed trees once they dried (Bierregaard et al., 1992). In subsequent decades the vegetation regenerating around

fragments has been periodically cleared to ensure fragment isolation (Bierregaard et al., 2001).

The BDFFP reserves are located in nonflooded (i.e., *terra firme*) tropical lowland forest with a 30–37m tall canopy (Rankin-de-Mérona et al., 1992) and an understory dominated by stemless palms (Scariot, 1999). The soils in the reserves are nutrient-poor xanthic ferrosols; their water retention capacity is poor despite having a high clay content. Mean annual temperature in the region is 26º C (range=19–39º C), and annual rainfall ranges from 1900–2300 mm. There is a pronounced dry season from June to October (Figure S1).

Focal species

Heliconia acuminata (LC Rich.) (Heliconiaceae) is a perennial monocot distributed throughout Central Amazonia (Kress, 1990) and is the most abundant understory herb at the BDFFP (Ribeiro et al., 2010). While many *Heliconia* species grow in large patches in treefall gaps and other disturbed areas, others, such as *H. acuminata,* are found at lower densities in the darker and cooler forest understory (Rundel et al., 2020). These species produce fewer inflorescences and are pollinated by traplining rather than territorial hummingbirds (Bruna et al., 2004; Stouffer & Bierregaard, 1996). In our sites *H. acuminata* is pollinated by *Phaeothornis superciliosus* and *P. bourcieri* (Bruna et al., 2004). Plants begin flowering at the start of the rainy season; reproductive plants have $\bar{x} = 1.1$ flowering shoots (range = 1–7), each of which has an inflorescence with 20–25 flowers (Bruna & Kress, 2002). Fruits mature April-May, have 1–3 seeds per fruit ($\bar{x} = 2$), and are eaten 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

133 rates of germination and seedling establishment higher in continuous forest than forest
134 fragments (Bruna, 1999; Bruna & Kress, 2002).

135 Demographic data collection

136 This study uses data collected in four 1-ha fragment reserves and six continuous forest
137 sites. In 1997–1998 we established a 5000 m^2 plots (50 × 100m) in each of these sites in
138 which we marked and measured all *Heliconia acuminata*; plots in 1-ha fragments were on
139 one randomly selected half of the fragment, while plots in continuous forest were located
140 500–4000 m from the borders of secondary and mature forest. The distance between plots
141 ranged from 500 m–41 km. Our dataset comprised 4,083 plants in continuous forest and
142 1,010 plants in forest fragments. Plots in CF had on average 2.7-fold more plants than plots
143 in 1-ha fragments (CF = 681 ± 493 SD; 1-ha = 253 ± 30 SD).

144 Each plot was subdivided into 50 quadrats (10 × 10m) to simplify annual surveys, during
145 which we recorded the number of vegetative shoots each plant had, the height of each plant
146 to the tallest leaf, and whether each plant was flowering (height and shoot number are
147 correlated with leaf area, the probability of flowering, and rates of survivorship (Bruna,
148 2002; Bruna & Kress, 2002). In this study, we used the product of shoot number and plant
149 height as our measure of plant size. Preliminary analysis showed that the product of shoot
150 number and height was a better predictor of total leaf area (which in turn is assumed to be
151 a strong predictor of aboveground biomass) than either shoot number or height alone
152 (Table S2). Plants that were not found for three consecutive surveys were considered
153 dead. We also surveyed plots regularly during the rainy season to identify any that

flowered after the survey. For additional details on the location of plots, survey methods, and *H. acuminata* population structure see Bruna & Kress (2002).

Climate data

Data on precipitation and potential evapotranspiration in our sites were obtained from a published gridded dataset (0.25º × 0.25º resolution) built using data from 3,625 ground-based weather stations across Brazil (Xavier et al., 2016). We used these data to calculate the standardized precipitation evapotranspiration index (SPEI) (Vicente-Serrano et al., 2010). SPEI is a proxy for meteorological drought that integrates precipitation and evapotranspiration anomalies over a specified time scale. Positive SPEI values for a given month indicate conditions wetter than the historical average for that month, while negative values of SPEI indicate droughts with intensity categorized as mild (0 to -1), moderate (-1 to -1.5), severe (-1.5 to -2), or extreme (< -2) (McKee et al., 1993). SPEI can be calculated to represent different temporal scales of drought; we used 3-month SPEI because—given its shallow roots and rhizome—*H. acuminata* relies primarily on soil moisture rather than deeper water sources that can persist for longer timescales (Vicente-Serrano et al., 2010). Note that 3-month SPEI is still monthly data—each month's SPEI value simply takes into account precipitation and evapotranspiration of the previous three months. SPEI calculations were made using the `SPEI` package (Beguería & Vicente-Serrano, 2017). The timing of drought events based on these SPEI calculations is consistent with that resulting from SPEI calculated with other data sources, though the magnitude of drought sometimes differed (Figure S2; Table S1).

Statistical Modeling of Vital Rates

To assess the effects of drought history on plant vital rates we used Distributed Lag Non-linear Models (DLNMs, Gasparrini et al., 2017). DLNMs capture how potentially delayed effects of predictor variables (e.g. SPEI) affect an outcome (e.g. growth) well beyond the event period. They do so by fitting a bi-dimensional predictor-lag-response association spline, referred to as a crossbasis function. This models a non-linear relationship between predictor and response (e.g. between SPEI and vital rates) and allows the shape of that relationship to vary smoothly over lag time. Using the `dlnm` package (Gasparrini, 2011; R Core Team, 2020), we created crossbasis functions with possible lags from 0–36 months. We chose 36 months as a maximum lag because prior transplant experiments with *H. acuminata* showed they typically recover from transplant shock in less than 36 months (Bruna et al., 2002) so this is a reasonable upper bound for lagged effects of drought.

The crossbasis function was fit to the data in the context of a generalized additive model (GAM) with restricted maximum likelihood using the `mgcv` package (Wood, 2017). The general form of the vital rate (y) models was as follows:

$$\begin{aligned} &g[\mathrm{E}(y_i)] = \alpha_j + s_1(z_i) + s_2\left(d_{i,t}, \ldots, d_{i,t-36}\right) + \beta x_i \\ &\alpha_j \sim N\left(\mu_{\alpha_j}, \sigma^2_{\alpha_j}\right), \text{ for plot j} \end{aligned} \tag{1}$$

where $s_1(z_i)$ is a smooth function of plant size (natural log of height × shoot number), fit using a penalized cubic regression spline, $s_2(\cdot)$ is the crossbasis function in which $d_{i,t}$ is the SPEI value during the census month of an observation (February) and $d_{i,t-l}$ is the SPEI l months prior (see Gasparrini et al. 2017 for details). The crossbasis function, $s_2(\cdot)$ can also be written:

$$s_2(d_{i,t}, \ldots, d_{i,t-24}) = \sum_{l=l_0}^{L} f \cdot w(d_{i,t-l}, l) \qquad (2)$$

where the crossbasis function, $f \cdot w(d, l)$, is composed of two marginal basis functions: the standard predictor-response function $f(d)$, and the additional lag-response function $w(l)$. These marginal functions are combined as a tensor product smooth such that the shape of one marginal function varies smoothly along the other dimension (see chapter 5 of Wood (2017) and Gasparrini et al. (2017) for more detail). Penalized cubic regression splines were used for both marginal bases of the crossbasis function, with 35 knots for the lag dimension (i.e. number of lagged SPEI values for each observation with 36 months as a maximum lag) and 3 knots for the drought response dimension to restrict the shape of the fitted response to drought to bimodal when most complex. Because of penalization, the number of knots is generally not important as long it is large enough to allow the smooth to represent the 'true' relationship (Wood, 2017). Estimated degrees of freedom (edf) represent the 'true' complexity of the smooth after penalization with edf = 1 being equivalent to a straight line and larger numbers representing more complex curves.

To determine if plot characteristics influenced average vital rates we included a random effect of plot ID on the intercept; this was represented by a_j in eq. 1. We determined the effects of SPEI on plant growth using plant size in year t+1 as a response variable. This was modeled with a scaled t family error distribution because residuals were leptokurtic with a Gaussian error structure. Because number of inflorescences was highly zero-inflated, we converted this to a binary response to model reproduction (i.e., 1 for ≥1 inflorescence, 0 for no inflorescences). We modeled both reproduction and survival (i.e., from year t to year

t+1) using a binomial family error distribution with a logit link function. We modeled a potential cost of reproduction by including flowering in the previous year as covariate, x_i, in eq. 1. Additionally, in models for flowering probability and size, we included plant ID as a random effect to account for variation among individuals. Preliminary analyses showed that this random effect was not significant in the growth models (edf ~ 0, $p > 0.2$) and as such it was dropped to improve computational efficiency. A random effect of plant ID was not included in survival models since each plant only dies once.

In the process of fitting the models, the penalty on the crossbasis smooth (and other smoothed terms) is optimized such that more linear shapes are favored unless the data supports non-linearity (Wood, 2017). We applied an additional penalty to shrink linear portions toward zero with the `select=TRUE` option to the `gam()` function, and inferred statistical significance of model terms with p-values from the `summary.gam()` function as recommended in Marra & Wood (2011).

The `dlnm` package does not currently allow the modeling of interaction terms, which means we could not asses the interaction of habitat type and lagged effects. We therefore fit separate models for plants in fragments and in continuous forest to allow the shape of the crossbasis function to differ between habitats. Significant main effects of habitat type were assessed by looking for overlap in the 84% confidence intervals of model intercepts; the 84% CIs of two samples drawn from the same population overlap about 95% of the time (Payton et al., 2003).

All analyses were conducted in R version 4.0.2 (2020-06-22) (R Core Team, 2020) using the `targets` package for workflow management (Landau, 2021). Figures were created with

the aid of the `gratia`, `ggplot2`, and `patchwork` packages (Pedersen, 2020; Simpson, 2021; Wickham, 2016).

Results

The meteorological droughts in our focal region indicated by SPEI are generally consistent with those reported in the literature (Table S1). For example, the drought associated with the 1997 El Niño Southern Oscillation (ENSO) event was one of the most severe on record for the Amazon (Williamson et al., 2000); correspondingly, 1997 has the lowest SPEI values in our timeseries (Figure 1d). The 2005 dry season (June–October) was also reported as an exceptionally dry year, although this drought mostly affected the southwestern Amazon (Marengo et al., 2008; Zeng et al., 2008). Our SPEI data show the 2005 dry season to be a moderate drought (-1 > SPEI > -1.5).

Survival, growth, and flowering in continuous forest vs. fragments

Survival: Across all plots, the proportion of plants surviving was lowest in the 2003–2004 transition year ($P_{surv} = 0.92$). This coincided with droughts in both the 2003 and 2004 rainy seasons (Figure 1b,d) and was preceded by a drop in average plant size in the 2002–2003 transition year (Figure 1a). The lowest survival for 1-ha fragment plots ($P_{surv} = 0.93$) was for the 2005–2006 transition year, which encompassed a moderate drought in October 2005 and and wetter than average conditions (SPEI > 0.5) in December 2005 and January 2006 (Figure 1b,d). The lowest survival for continuous forest was in 2004 ($P_{surv} = 0.91$). When summarizing across years, plots, and plant sizes, the survival probability of *Heliconia acuminata* was similarly high in both continuous forest and fragments ($P_{surv} = 0.95$; Figure 1b; the overlapping 85% CI of model intercepts indicate no significant difference).

However, survival in both habitats was size dependent ($p < 0.001$ for the effect of log-transformed plant size in year *t* on survival in year *t+1* in both habitats). The survival probability of large plants approached 1 in both habitat types (Figure 3b), but the smallest plants had higher survival in 1-ha fragments.

Growth: Plants in continuous forest had an average of 2.9 shoots (± 1.8 SD) and were on average 40.6 cm tall (± 26.5 SD). Plants in 1-ha fragments had on average 13.8% fewer shoots (2.5 ± 1.5 SD) and were 10.8% shorter (36.3 cm ± 24.1 SD). Because our proxy for plant size was the product of these two metrics, plants in continuous forest were on average 34% larger than those in forest fragments (150 ± 175 SD vs. 112 ± 141 SD, respectively), with fragments having proportionately fewer large plants (Figure 3d). This difference was not significant, however (overlap in 84% CI of model intercepts), and the disparity in plant size—which was most pronounced in the initial years of our surveys—diminished over time (Figure 1a).

Mean plant size dropped dramatically in 2003 in both habitat types, corresponding with a severe drought during the February census (SPEI = -1.39) (Figure 1d). As with survival, size in year t was a significant predictor of size in year t+1 ($p < 0.001$ in both habitats). While the effect was generally similar across size classes and habitat types, the impact of plant size on growth was greatest for mid-sized plants in continuous forest (Figure 3a).

Flowering: The overall proportion of plants that flowered was very low. While it was 27% higher in continuous forest than 1-ha fragments (0.048 ± 0.213 vs. 0.038 ± 0.19, respectively), this difference was not statistically significant (84% CIs of model intercepts overlapped). The observed disparity was largely due to the fact that flowering is also size-

283 dependent ($p < 0.001$ in both habitats), with the probability of flowering increasing
284 dramatically once plants reached the threshold size of about 148 (i.e., log(size) > 5 in
285 Figure 3c). Despite the flowering probability of large plants being greater in fragments than
286 continuous forest, populations in fragments had proportionately fewer plants above the
287 reproductive size threshold (Figure 3d). The most striking difference between habitat
288 types coincided with a severe drought in 2003, when the percentage of flowering
289 reproductive-sized plants was 28% in continuous forest vs. only 13.6% in 1-ha fragments
290 (Figure 1c).

291 **Delayed effects of drought on demographic vital rates**

292 Drought history had a significant ($p < 0.001$) effect on the survival, growth, and flowering
293 of plants in both habitats. Comparing the respective crossbasis surfaces, however, reveals
294 that the specific climatic drivers, their timing, and their impact on individual vital rates all
295 differed among habitats.

296 *Survival:* For 1-ha fragments, there was a significant effect on survival of SPEI in the
297 preceding 13 months. The highest survival was near SPEI of 0, with mortality increasing as
298 conditions became either drier or wetter (i.e., as SPEI values became increasingly negative
299 or positive, respectively; Figure 4b). Wet conditions in the preceding 23 months (i.e., SPEI >
300 1) also had a significant negative effect on survival in fragments (Figure 4b). In contrast,
301 the effect of recent SPEI in continuous forest was weaker, with only the 6 months preceding
302 a census having a significant effect on survival (Figure 4a). These short-term effects of SPEI
303 on survival were also unidirectional—the probability of survival declined, albeit only
304 slightly, with increasingly negative values of SPEI (i.e., as droughts became more severe;

Figure 4a). In contrast, the most pronounced negative effects of SPEI on the survival of plants in continuous forest were at lag times of 15–20 months and 32–36 months. Drought 15–20 months prior to a census (i.e. two dry seasons prior to a census) was significantly associated with reduced survival, while high precipitation (i.e., SPEI > 1) was significantly associated with higher survival. Finally, plants in both habitat types showed an increase in survival probability with very high SPEI values (i.e., extremely high precipitation) at a lag time of 32–36 months. It should be noted, however, that only the first transition year of census data (1998–1999) met these conditions. We compared the effects of SPEI history in continuous forest and fragments by subtracting the fitted values in Figure 4b from Figure 4a to produce Figure 4c. This shows that in average conditions (SPEI = 0), there is little difference in survival probability between continuous forest and forest fragments (Figure 4c). However, under extreme conditions, survival probability is higher in continuous forest by up to 0.025.

Growth: The effects of drought history on trends in plant size were generally similar for continuous forest and fragments. However, the crossbasis function for 1-ha fragments indicated more complex responses in some situations (edf = 17.8 for 1-ha fragments; edf = 13.0 for continuous forest; see also Figure 5). For example, under average conditions (i.e., SPEI = 0), growth is similar or slightly higher in continuous forest over all lag periods (Figure 5c). However, the growth of plants in fragments is reduced when the current wet season is unusually wet (i.e., SPEI>2), and as a result the plants in continuous forests will be larger by up to log(size) = 0.57. In contrast, drought at lags of 8–11 months (i.e., the end of the preceding year's wet season) led to increased growth in both habitats, with a more pronounced response in 1-ha fragments.

Flowering: Overall, the the probability of flowering was higher in continuous forest than in 1-ha fragments for all values of SPEI (Figure 6), although this difference was not significant (84% CIs of intercepts overlap). The responses in 1-ha fragments were also more muted as indicated by the shape of the crossbasis function (1-ha edf = 8.3, continuous forest edf = 10.6) (Figure 6). This led to some important inter-habitat differences in plant responses to prior droughts. In continuous forests, recent drought (i.e., at lag = 0–2 with SPEI < -1), drought two dry seasons prior (lags 15–20) and in the wet season 34–36 months prior all increased the probability of flowering. However, drought at the end of the rainy season one year prior (lags 7–13) significantly reduced flowering probability (Figure 6a). In fragments, recent drought had no significant effect on flowering probability and only drought at two dry seasons prior (lags 16–20) and in the wet season 33–36 months prior increased flowering probability (Figure 6b). The effects of drought on flowering probability were strong in continuous forest compared to 1 ha fragments (Figure 6c). We found no evidence for a cost of reproduction: in both forest and fragments, plants that had flowered in the previous year were on average more likely to be larger (CF: $p = 0.048$; 1-ha: $p = 0.030$) and flower again (CF: $p < 0.001$; 1-ha: $p = 0.004$). The random effect of plant ID on flowering probability was also significant (CF: $p < 0.001$; 1-ha: $p = 0.003$), indicating significant individual-level variation in flowering probability.

Finally, with the exception of survival in 1-ha fragments ($p = 0.253$), the delayed effects of SPEI on all three vital rates varied significantly among plots ($p < 0.01$ for the random effect of plot).

349 ## Discussion

350 Understanding how landscape structure and abiotic conditions act to influence population
351 dynamics is central to many conceptual frameworks for studying and conserving
352 fragmented landscapes (Didham et al., 2012; Driscoll et al., 2013). Our results support the
353 emerging consensus that the effects of climatic extremes on demographic vital rates can be
354 delayed for months or even years (Evers et al., 2021; Teller et al., 2016; Tenhumberg et al.,
355 2018). We also found that the delayed responses of populations in fragments can differ
356 significantly in magnitude, direction, and lag time from those of populations in continuous
357 forest. This suggests that the hypothesized synergies between climate and fragmentation
358 on population dynamics (Laurance & Williamson, 2001; Opdam & Wascher, 2004; Selwood
359 et al., 2015) are likely to be pervasive, but also far more complex than previously thought.

360 ### Temporal variation in demographic responses to forest fragmentation

361 Many studies investigating the biological consequences of habitat fragmentation on plant
362 growth, survival, and reproduction comprise short-term (≤3 year) experiments and
363 observations. Our results underscore the difficulty in extrapolating long-term trends from
364 such short-term studies, particularly when studying long-lived organisms or when the
365 responses of interest can vary with size or age. For instance, one would have reached a very
366 different conclusion regarding the effect of fragmentation on annual survival if the study
367 windows were 1999–2002 (i.e., higher survival in continuous forest), 2002–2005 (i.e.,
368 higher survival in fragments), or 2004–2007 (i.e, no clear effect of fragmentation) (Figure
369 1b). It is only when evaluating over longer time windows that it becomes apparent
370 mortality is elevated in fragments relative to continuous forest (Figure 2), and that the
371 observed interannual variation is largely driven by dynamic patterns of recruitment

372 (Bruna, 2002) coupled with low mortality for plants beyond the smallest size classes
373 (Bruna, 2003).

374 Similarly, conclusions regarding the effects of fragmentation on flowering—which is also
375 both rare and size-dependent (Brooks et al., 2019)—would also differ based on the year in
376 which they were investigated. This could lead to erroneous extrapolations regarding the
377 effects of fragmentation on reproductive mutualists or population genetic structure (Côrtes
378 et al., 2013; Uriarte et al., 2010; Uriarte et al., 2011). Conclusions based on short-term
379 observations of temporally variable vital rates could lead to conservation and management
380 practices that are ineffective or even counterproductive, especially when when failing to
381 consider how the consequences of this variation might be modulated by organismal life
382 history (Morris et al., 2008).

383 It is important to emphasize, however, that the overall effects of SPEI on survival and
384 growth are more severe in fragments than continuous forest (Figures 4, 5). Furthermore,
385 the magnitude of plant responses to climatic extremes is also greater in habitat
386 fragments—extreme drought in dry seasons and extreme precipitation in during rainy
387 seasons are most detrimental to growth and survival in fragments. While intact forest and
388 its canopy buffer populations from climatic extremes, populations in fragments—especially
389 near edges with high contrast matrix—likely lack this protection (Didham & Lawton, 1999;
390 Ewers & Banks-Leite, 2013). We suggest it is these climate extremes, rather than trends in
391 average temperature, precipitation, or SPEI (Laurance et al., 2014), that that are the causal
392 mechanism underlying reduced plant growth and survival in forest fragments.

Delayed effects of climate on demographic vital rates

Climate anomalies are known to have immediate effects on the growth, survival, or reproduction of plants (Esteban et al., 2021; Wright & Calderon, 2006), including *Heliconia* (Stiles, 1975; Westerband et al., 2017) and other tropical herbs (Wright, 1992). These effects can be complex or even contradictory—mild droughts can increase the growth rates of tropical trees and seedling survival, perhaps due to reductions in cloud cover and concomitant increases in solar radiation (Alfaro-Sánchez et al., 2017; Condit et al., 2004; Huete et al., 2006; Jones et al., 2014; Uriarte et al., 2018), but in severe drought years growth can be extremely low and mortality can be sharply elevated (Connell & Green, 2000; Edwards & Krockenberger, 2006; Engelbrecht et al., 2002). There is also evidence that the effects can persist for multiple years (Phillips et al., 2010), such as a boom in drought-year fruit production followed by severe post-drought "famine" (Pau et al., 2013; Wright et al., 1999).

Despite these insights, models of plant population dynamics rarely include the effects of environmental drivers [but see Williams et al. (2015); Tenhumberg et al. (2018); Molowny-Horas et al. (2017)). This has largely been due to the challenge (both ecologically and statistically) of detecting any demographic responses to climatic extremes that are delayed for multiple growing seasons. To address this, researchers have begun to use a number of statistical methods that test for time lags in demographic responses without *a priori* assumptions about the influence of any particular climate window (Evers et al., 2021; Teller et al., 2016; Tenhumberg et al., 2018). Our expansion of this approach, which offers an unbiased way of identifying these delayed effects without overfitting (but see Pierre et al. (2020) and Ogle et al. (2015) for alternative methods) yielded results consistent with

416 this emerging literature—that the effects of precipitation extremes on the demography of
417 *Heliconia acuminata* could be delayed for up to 3 growing seasons.

418 While it appears that delayed effects of climate on demographic vital rates may be
419 ubiquitous (Evers et al., 2021), the extent to which they vary spatially or with habitat
420 remains an open question. Our results clearly indicate that they can, with habitat-specific
421 differences in how environmental conditions influenced future vital rates. For example,
422 extreme values of SPEI—both positive (unusually high precipitation) and negative
423 (drought conditions)—led to declines in the probability of individual survival in both
424 habitat types. However, the magnitude of these declines was far greater in forest
425 fragments. Similarly, the detrimental effects of extremes in SPEI on growth rates were also
426 more pronounced in fragments. In contrast, variation in SPEI had far stronger effects on the
427 probability of flowering in continuous forest than fragments. These results should be
428 interpreted with some caution, however, as the relatively low number of plants in
429 fragments that are above the threshold-size for flowering could limit the power to detect
430 delayed effects.

431 There are several, non-mutually-exclusive explanations for delayed effects of SPEI on
432 demography. The first is that the physiological processes underlying vital rates might be
433 initiated long before they are demographically apparent (Evers et al., 2021), and hence be
434 shaped by climatic events at any point in that physiological window. For example, the
435 flowering shoots of *Heliconia chartacea* begin to develop 6–10 months prior to the
436 appearance of inflorescences (Criley & Lekawatana, 1994). Adverse conditions during the 6
437 months following initiation, rather than the months when inflorescences are starting

expand, leads to the aborted production of flowering shoots. Interestingly, we observed the opposite effect—drought conditions increased the probability of flowering two years later. While this could reflect bet-hedging in response to stress (Nihad et al., 2018), this does not appear to be the case, as growth or survival do not appear to decrease following reproduction (see also (Horvitz & Schemske, 1988). In fact, flowering in one year is associated with increased reproduction and growth in the next .

Demographic responses will also be delayed if abiotic stress causes plants to invest in belowground rhizomes (*sensu* Pumisutapon et al., 2012). The carbohydrates stored in rhizomes allow *Heliconia* to regenerate aboveground biomass following damage (Rundel et al., 1998) and protect the buds that give rise to new shoots from stressful conditions (Klimešová et al., 2018). This may be why drought led to delayed increases in growth—by shedding shoots and leaves (Bruna et al., 2002) and investing in rhizomes, plants are generating proportionately more buds with which to regenerate when conditions improve. This would also be consistent with the results of prior experiments, in which the growth rates of *H. acuminata* 8 months after they were mechanically damaged far exceeded those of control plants (Bruna & Ribeiro, 2005).

Third, it may be that the delayed demographic effects we observed are indirectly mediated by the effect of SPEI on other species rather than the direct effects on individual physiology (Evers et al., 2021). For example, topical trees may not die until three or more years after a drought (Criley & Lekawatana, 1994). When they finally do, the resulting leaf drop (Janssen et al., 2021) and treefalls allow for light penetration to the forest understory (Canham et al., 1990; Leitold et al., 2018), triggering a boom in the growth and flowering of understory

plants (Bruna & Oli, 2005). Similar delayed changes in the local environment could also influence the foraging behavior of a plant's pollinators (Bruna et al., 2004; Stouffer & Bierregaard, 1996), seed dispersers (Uriarte et al., 2011), or herbivores (Scott et al., 2021). While more work is needed to explain why the (delayed) effects of SPEI on *H. acuminata* survival and growth are greater in fragments than forest interiors, one hypothesis, motivated by recent intriguing results from other systems (Sapsford et al., 2017), is that the greater litterfall on edges (Vasconcelos & Luizão, 2004) may be altering the abundance of pathogens or mycorrhizae.

Finally, demographic delays could be an artifact of the timing of responses in relation to the census date. If extreme drought in the dry season before the census increased plant mortality during that season, for example, this would nevertheless appear in models as a delayed effect (e.g. in Figure 4b). In our case, this potential explanation for delayed effects applies only to plant size and survival, as plots were surveyed regularly throughout the reproductive season to identify flowering plants. This possibility is not unique to our study, rather it is a consequence of conducting demographic censuses on an annual scale while the climate is quantified monthly or seasonally. While the very slow growth and extremely low mortality rates of *H. acuminata* mean this effect is unlikely to be acting in our system, it may be that for some species it will be important to conduct demographic surveys at the same temporal scale at which climate is aggregated.

Conclusions & Future Directions

Over 24 million ha of the Brazilian Amazon have been cleared in the last two decades (Silva Junior et al., 2021), resulting in their extensive fragmentation (Broadbent et al., 2008).

482 Climate models predict a future of extremes for these forests—increases in the frequency
483 and geographic extent of droughts, but also increases in the frequency and area affected by
484 periods of unusual wetness (Duffy et al., 2015). Our results support the hypothesis that
485 populations in Amazonian forest fragments could be more susceptible to the effects of
486 changing climate than those in continuous forest (Laurance et al., 2014). However, they
487 also indicate that the demographic responses to climate change of populations in
488 fragmented landscapes may be far more complex than previously appreciated. Multi-
489 factorial, multi-season experiments (*sensu* Aguirre et al., 2021; Bruna & Ribeiro, 2005;
490 Markewitz et al., 2010; Westerband et al., 2017), ideally manipulating multiple
491 combinations of climatic variables (Mundim & Bruna, 2016), are needed to determine how
492 and why habitat-specific differences in environmental conditions interact to delay the
493 demographic responses of plants to climatic variability. Also needed are statistical tools
494 that can test for synergistic effects of fragmentation and climate in vital rates, as those
495 currently available do not allow for including interaction terms. This also limits the ability
496 to include size by climate interactions in a DLNM; although plant responses to both
497 fragmentation and climatic extremes can be size-specific (Bruna & Oli, 2005; Schwartz et
498 al., 2019). The ability to identify size-specific lagged responses may be especially
499 complicated given size and growth are rarely measured at the same time scale as SPEI and
500 other putative climatic drivers.

501 Finally, no analytical approach assessing the potential for demographic lags can
502 compensate for a lack of long-term data (Evers et al., 2021; Tenhumberg et al., 2018).
503 Unfortunately, long-term data monitoring the entire life-cycle of tropical taxa are rare, and
504 those doing so in fragmented landscapes are virtually nonexistent (Bruna & Ribeiro, 2005).

Without investing in collecting such data, generalizations regarding the demographic consequences of climate change in these species rich and increasingly fragmented habitats will continue to prove elusive. More generally, however, researchers need to consider how delayed responses to climate could influence the interpretation of data in studies where the organisms lifespan exceeds the study's duration.

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Data Availability Statement

Data used in this study are available at the Dryad Digital Repository; R code for analyses and visualizations are archived at Zenodo [links included upon acceptance].

Figures

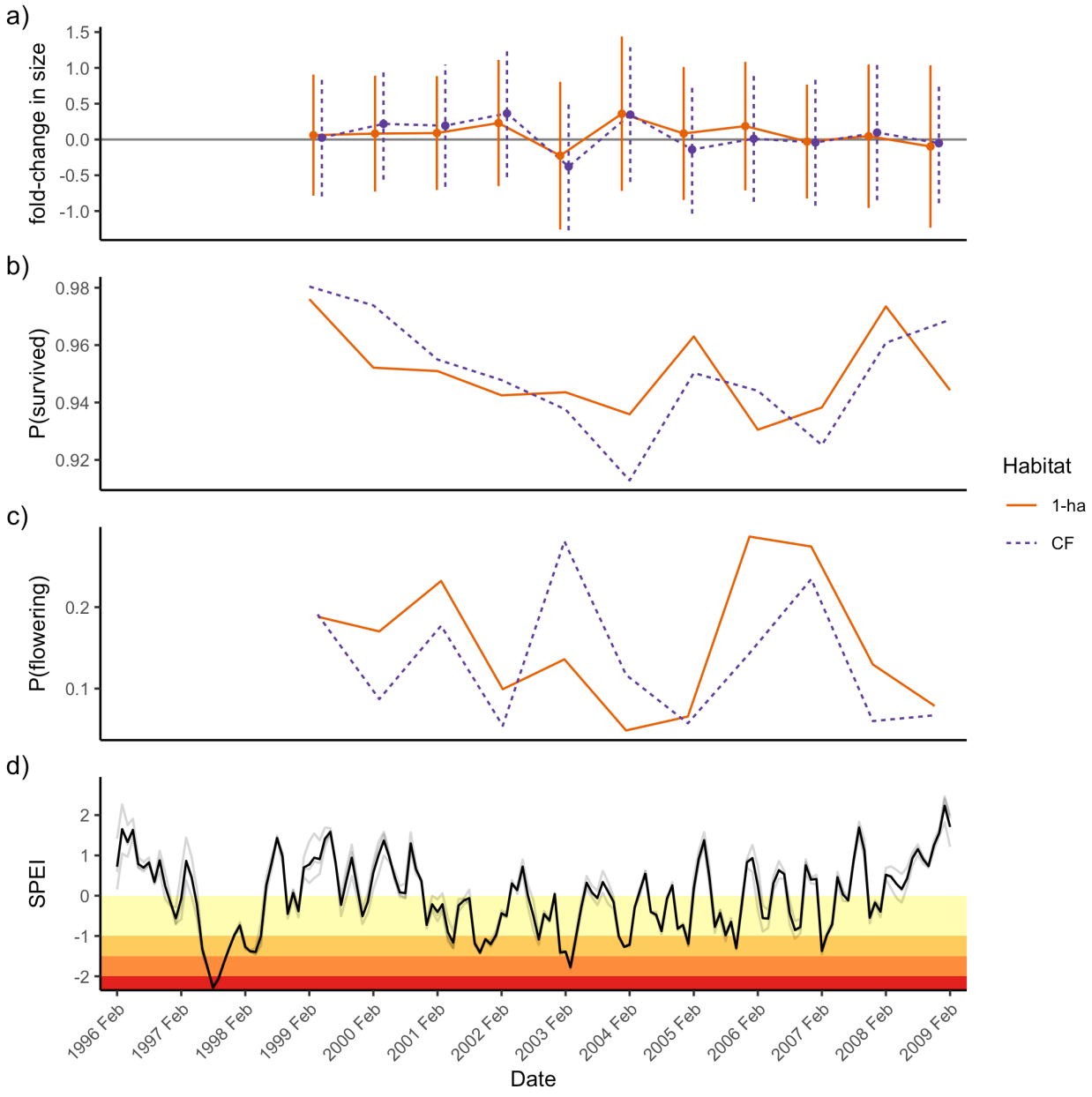


Figure 1: (a-c) Time series of *H. acuminata* vital rates in 1-ha fragments (solid orange lines) and continuous forest (dashed blue lines) and (d) drought occurrence in the study region. (a) Mean fold-change in plant plant size ($\log2(size_{t+1} / size_t)$) varies by year and habitat. On average, plants grew in most years with the notable exception in 2003, in which on average plants regressed in size in both habitats (i.e., fold-change < 0). Error bars represent the standard deviation. (b) The proportion of plants surviving from one transition year to the next varied from 0.98 (CF in 1998-1999) to 0.91 (CF in 2003-2004). (c) The proportion of *H. acuminata* above

the size threshold for reproduction that flowered each year is on average low but variable. The size threshold is determined by the upper 90th percentile size of flowering plants across all years. (d) Monthly 3-month SPEI for our study region. Gray lines represent values from different grid cells encompassing BDFFP; the dark line represents the site mean. Colored stripes represent drought intensity: yellow = mild, orange = moderate, dark orange = severe, red = extreme.

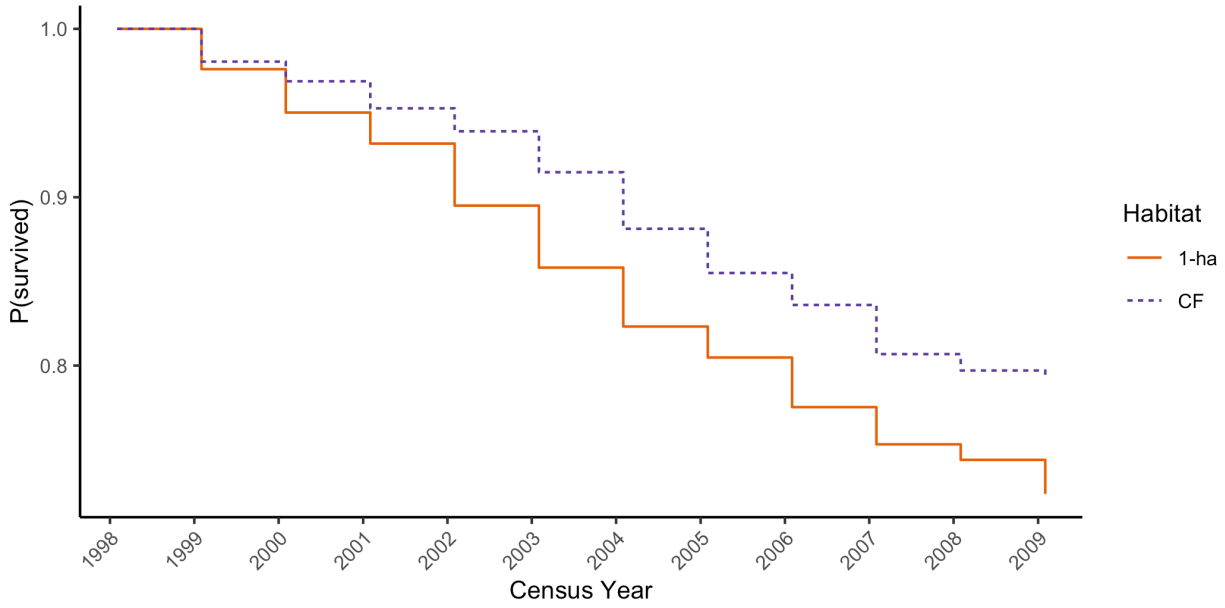
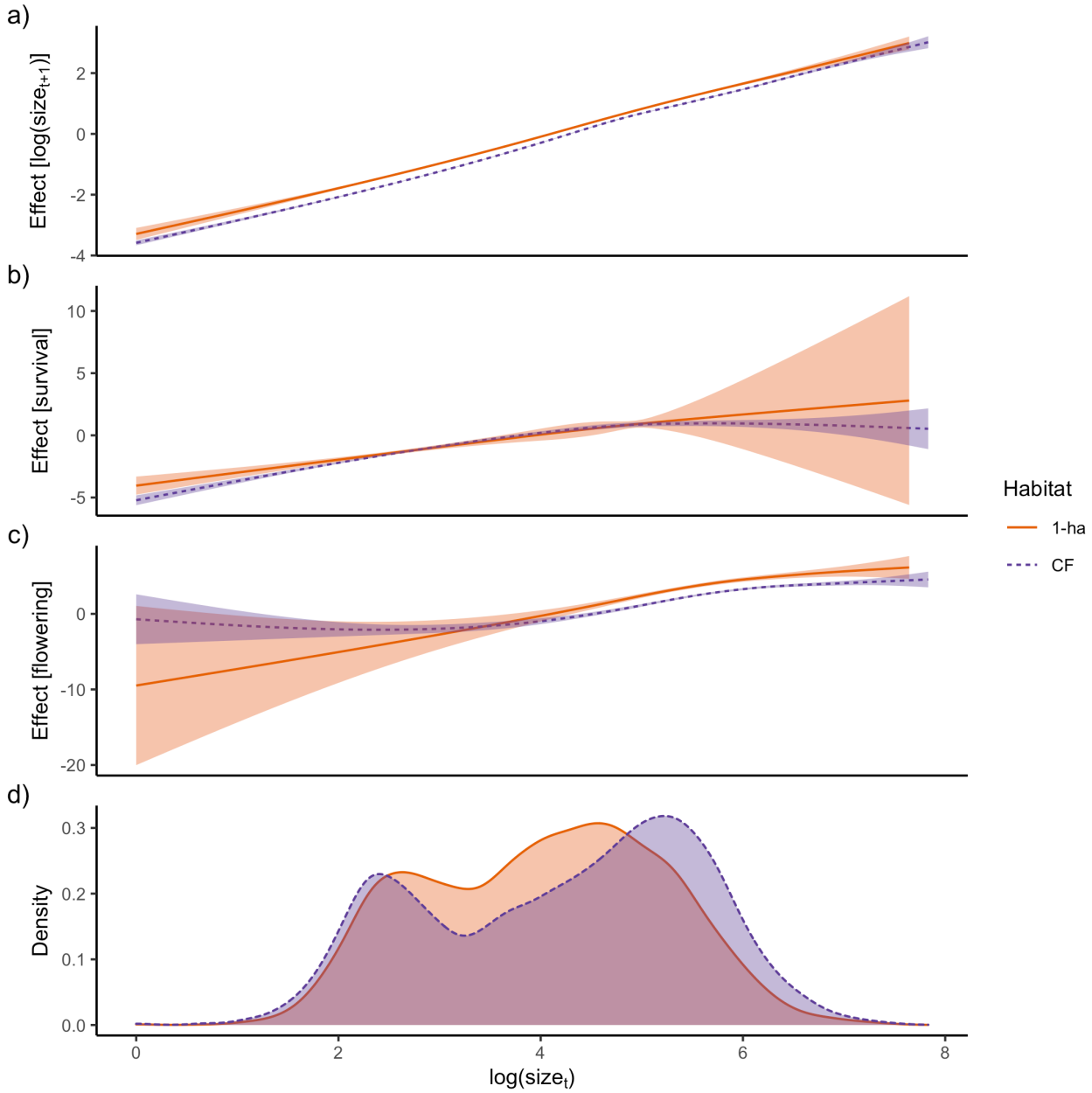


Figure 2: Survivorship curve for plants marked in the 1998 survey year; these plants comprise 49% of those in the complete demographic dataset. The percentage of these plants that were still alive ten years later was 79.7% (1629/2055) in continuous forest vs. 72.4% (393/543) in 1-ha fragments.



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538 Figure 3: Smooth effect from models of plant size in the previous census on (a) survival, (b) log(size), and (c)

539 flowering probability; these values correspond to the additive term $s_1(z_i)$ in eq. 1. The bands depicting the

540 95% confidence interval include uncertainty in the intercept and uncertainty due to smoothness selection;

541 the smooths for 1-ha fragments and continuous forest are fit in separate models. (d) Plant size distribution by

542 habitat type (solid line = 1-ha fragments, dashed line = Continuous Forest).

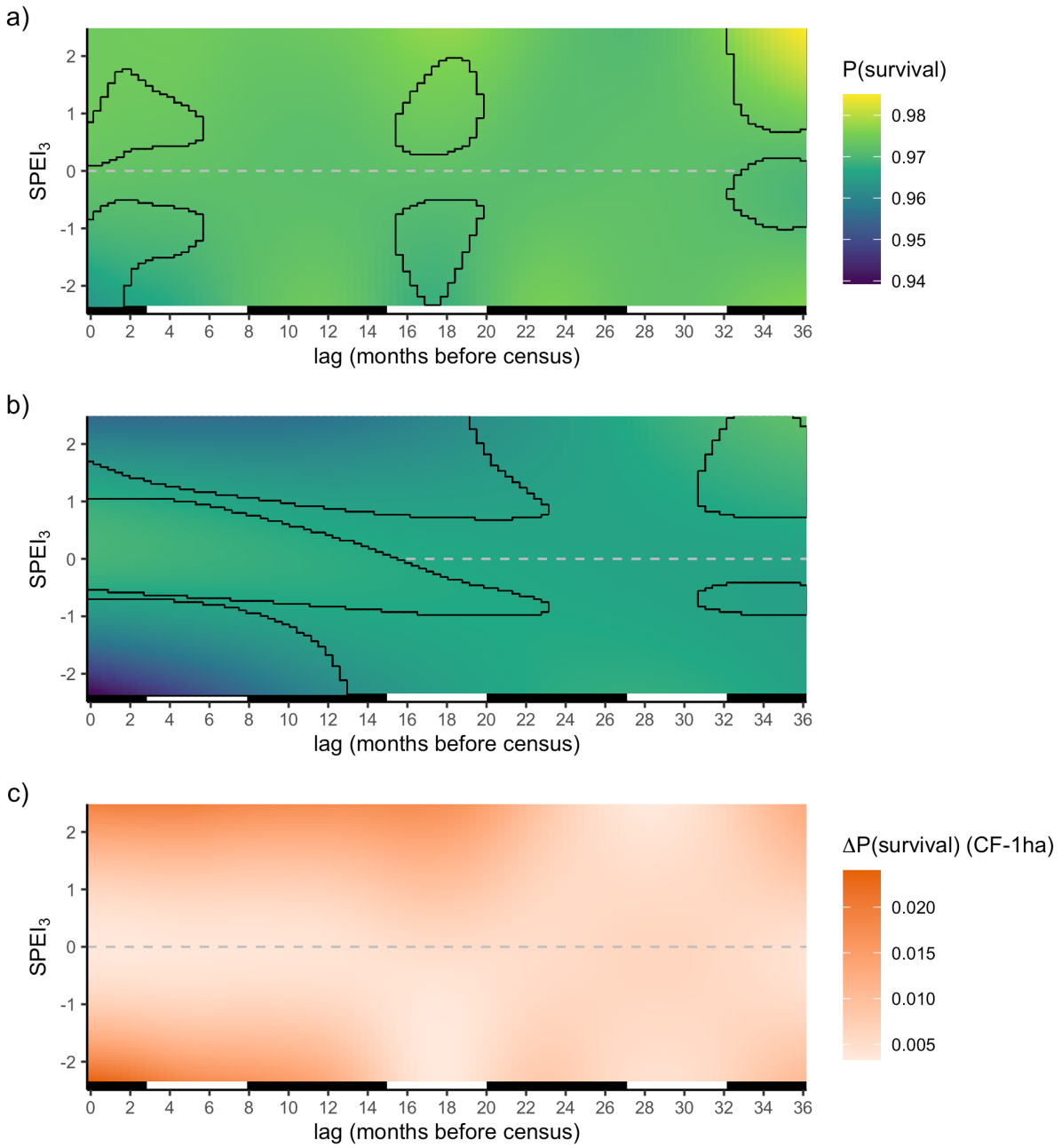

Figure 4: Smooth effect of lagged SPEI on *H. acuminata* survival in (a) continuous forest, (b) 1-ha fragments, (c) and the difference between the two. Outlines show regions where the effect of SPEI is significant, defined as those where the 95% confidence interval around the response does not overlap the intercept. The bar on the bottom of each panel indicates the wet seasons (black, November–May) and dry seasons (white, June–October). Surface is modeled as a crossbasis function with cubic regression splines for each marginal basis.

Model intercepts were added to fitted values of the crossbasis function and back-transformed to the response scale.

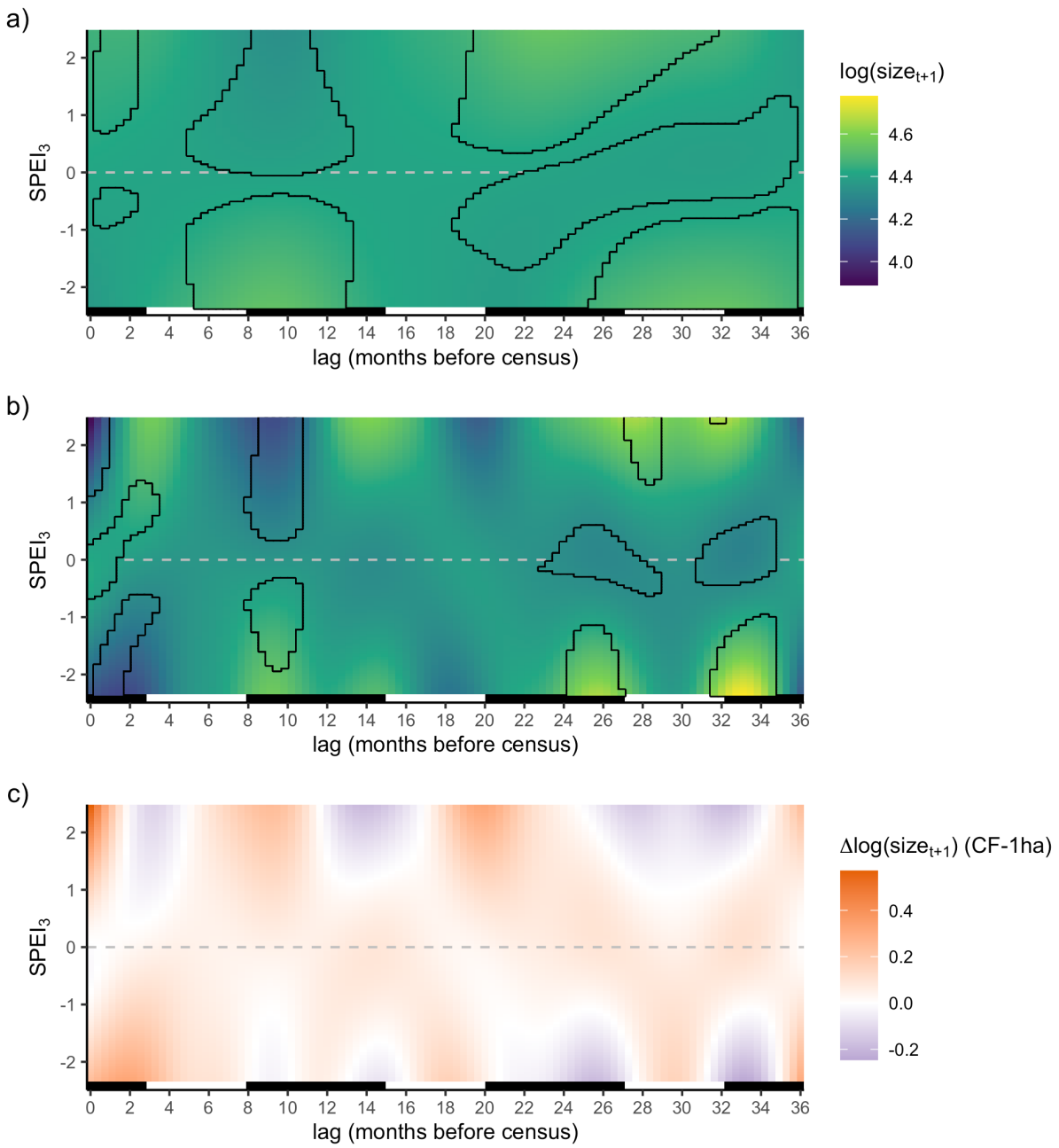

Figure 5: Smooth effect of lagged SPEI on *H. acuminata* growth in (a) continuous forest, (b) 1-ha fragments, (c) and the difference between the two. Outlines show regions where the effect of SPEI is significant, defined as those where the 95% confidence interval around the response does not overlap the intercept. The bar on

the bottom of each panel indicates the wet seasons (black, November–May) and dry seasons (white, June–October).

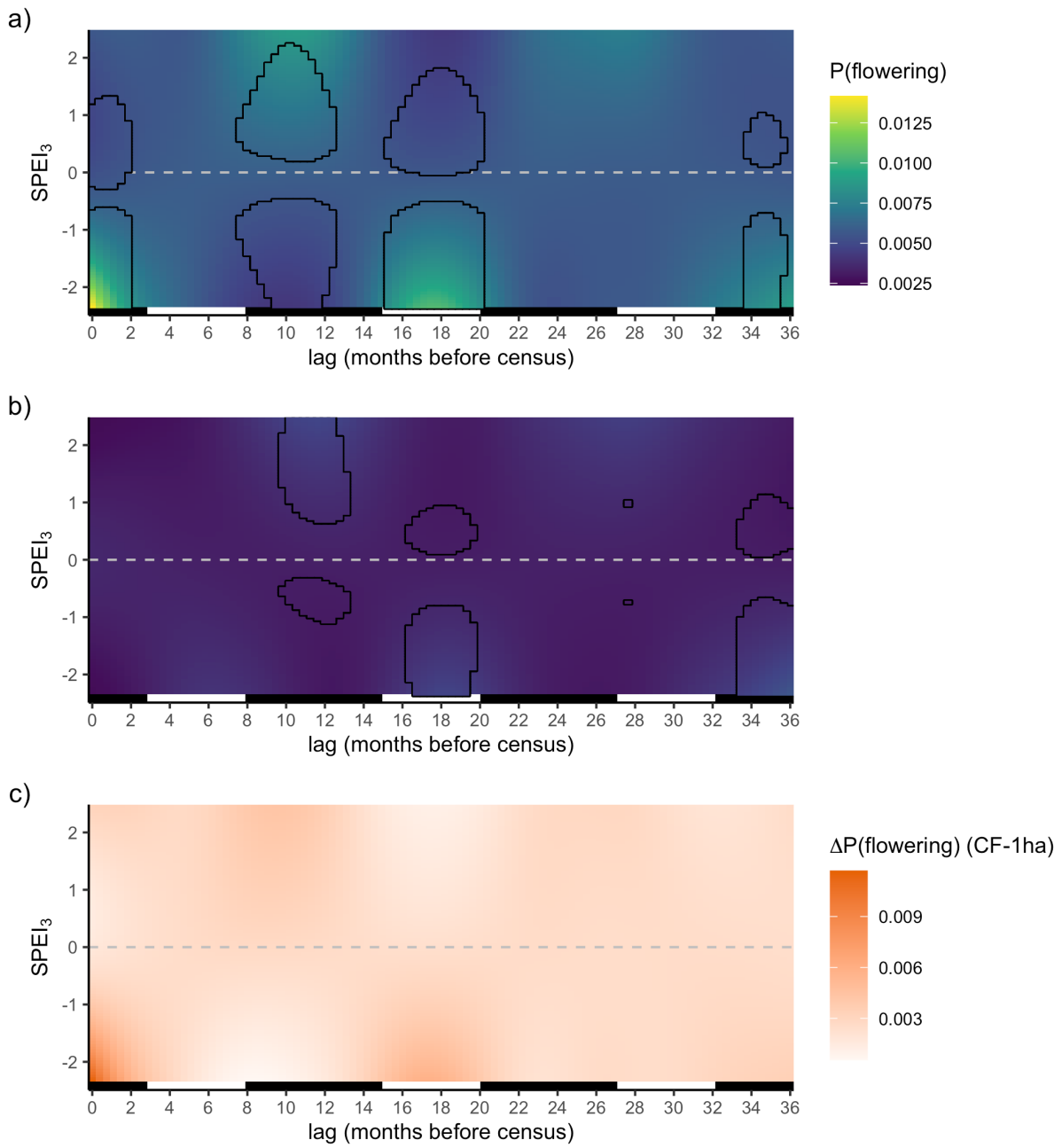

Figure 6: Smooth effect of lagged SPEI on *H. acuminata* flowering probability in (a) continuous forest, (b) 1-ha fragments, (c) and the difference between the two. Outlines show regions where the effect of SPEI is significant, defined as those where the 95% confidence interval around the response does not overlap the intercept. The bar on the bottom of each panel indicates the wet seasons (black, November–May) and dry

seasons (white, June–October). Surface is modeled as a crossbasis function with cubic regression splines for each marginal basis. Model intercepts were added to fitted values of the crossbasis function and back-transformed to the response scale.

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