Delayed effects of [responses to?] climate lead to demographic divergence in a fragmented Amazonian landscape

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Text of abstract

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Highlights: These are the highlights

# Introduction

Deforestation driven by the expansion of agriculture and other human activities is a primary driver of biodiversity loss worldwide (Haddad et al. 2015). Deforestation also results in landscapes where the remaining forest can be highly fragmented, with remnants of different sizes embedded in a matrix of often highly-contrasting habitat. Although the local extinction of species from individual fragments is common (Haddad et al. 2015), the demographic mechanisms underlying these extinctions are poorly understood (Bruna et al. 2009). However, it is often assumed that that the dramatically altered environmental conditions often observed in fragments can depress rates of reproduction or survivorship (Laurance et al. 1998, Bruna 1999, Zartman et al. 2015), leading to local or regional population declines (Bruna et al. 2009). This is thought to be particularly true in species-rich tropical forests (Didham and Lawton 1999, Laurance et al. 2001), which continue to be cleared and fragmented at unprecedented rates. For example, over 24 million ha of the Brazilian Amazon have been cleared in the last two decades *(CITATION\_4)*, resulting in extensive fragmentation and creation of over 70,000 km of new forest edges annually (Broadbent et al. 2008). Despite this, evidence linking fragmentation-related changes in environmental conditions with population-level demographic responses remains scarce.

Populations in fragmented tropical landscapes are also at risk from climate change (Brodie et al. 2012, Scheffers et al. 2017). These effects may be especially pronounced in Amazonia, parts of which have been experiencing a drying trend since the mid-1970s and where climate models for the 21st century predict substantial decreases in dry season precipitation (Malhi et al. 2008) and increases in both drought frequency and severity (Zeng et al. 2008, Mora et al. 2013, Cai et al. 2014). All of these factors have the potential to exacerbate the microclimatic changes observed in forest fragments that are hypothesized to make populations demographically vulnerable. Plants, unlike animals, are unable to move in response to increased in air temperature, decreased relative humidity, reduced soil moisture, or the increased penetration of solar radiation in the forest understory resulting from fragmentation (Didham and Lawton 1999, Ewers and Banks-Leite 2013, Arroyo-Rodríguez et al. 2017). Alternatively, populations persisting in fragments may be more demographically resilient to drought than those in primary forest if the individuals susceptible to desiccation died quickly after fragment isolation (Betts et al. 2019).

Whether plant populations in tropical forest fragments are particularly susceptible to drought 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. Similarly, there is a growing literature on how tropical plants respond to droughts, but few studies have compared the responses of plants in continuous forest with those 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-Gomez et al. 2015). These data are critical not only because they allow for capturing variation in climatic conditions and the resulting demographic responses (Morris and 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 (Gagnon et al. 2011). Indeed, lagged responses of demographic vital rates to climate may in fact be the rule rather than the exception (Anderegg et al. 2015, Schwalm et al. 2017, Kannenberg et al. 2020, Evers et al. 2021).

We used a decade of demographic and climatic data to assess the effects of climate on populations of a tropical understory herb (*Heliconia acuminata*, Heliconiaceae) in an experimentally fragmented landscape in the Central Amazon. This time series includes “famous” Amazonian droughts in 1997 (McPhaden 1999) and 2005(Marengo et al. 2008, Zeng et al. 2008) that were called “once in a century” climate events. Herbaceous plants represent up to 25% of plant diversity in tropical forests (Gentry and Dodson 1987), are critical food and habitat for myriad species (Snow 1981), and are economically and culturally vital (Ticktin 2003, Nakazono et al. 2004). Nevertheless, the impacts of global change phenomena on their demography remain conspicuously understudied ***(CITATION Bruna, Gaoue)***. We addressed the following questions:  
  
< !–# Gaoue = ? Orou G. Gaoue, Carol C. Horvitz, Ulrich K. Steiner, Shripad Tuljapurkar, Climate, rather than human disturbance, is the main driver of age-specific mortality trajectories in a tropical tree, Ecological Modelling, Volume 400, 2019, Pages 34-40,<https://doi.org/10.1016/j.ecolmodel.2019.03.007>. – >

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 responses, 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 (Figure S\_ ). In subsequent decades the vegetation regenerating around fragments has been periodically cleared to ensure fragment isolation (Bierregaard et al. 2001).

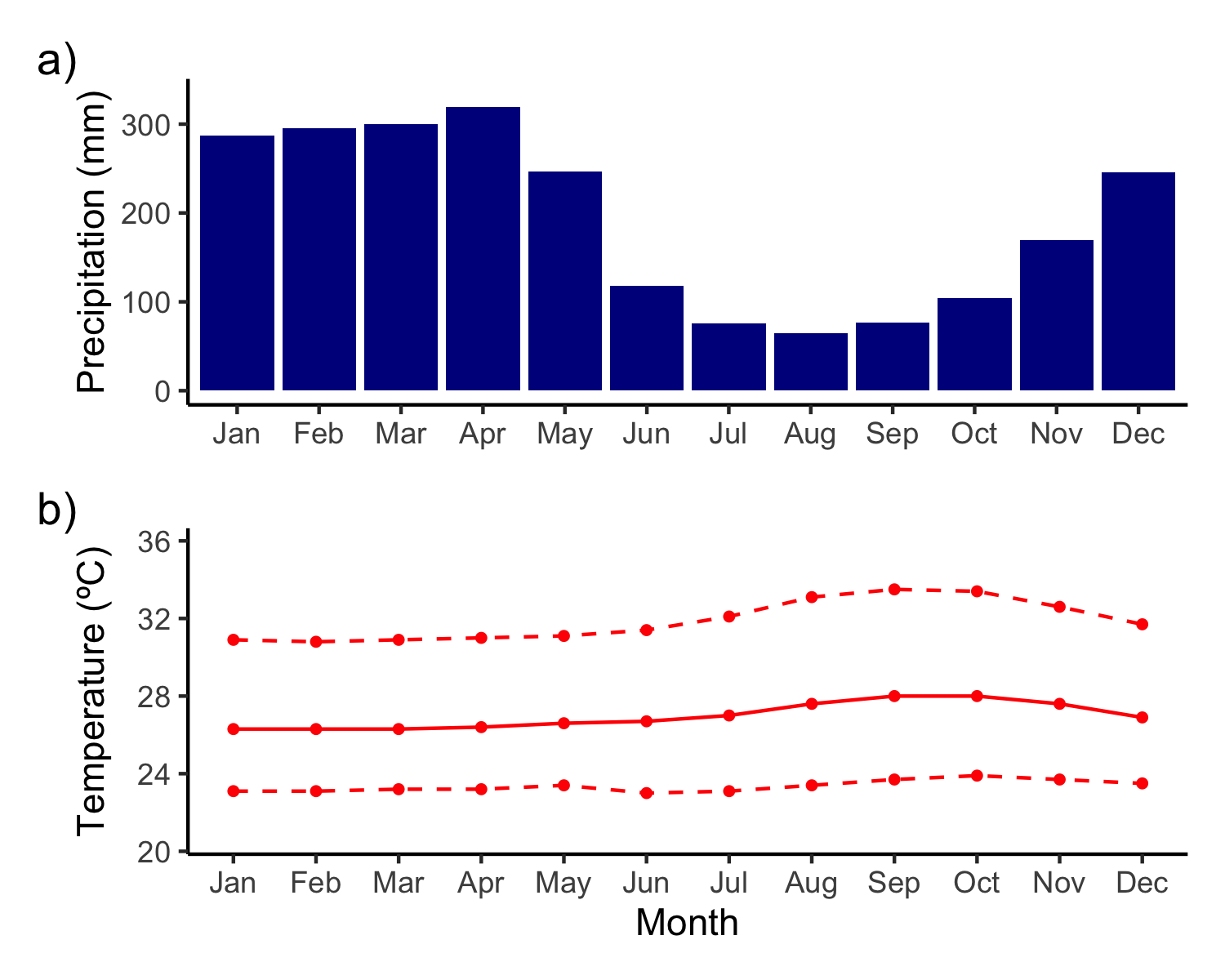


Figure 1: Weather normals for Manaus, Brazil (3º6’S, 60º1’W) for 1981–2010. Precipitation (a) shows a marked dry seasons from June through October. Temperature (b) varies less throughout the year. Mean monthly temperature is shown in the solid red line and monthly minimum and maximum temperatures are shown with the lower and upper dashed lines, respectively. Data from Brazilian National Institute of Meterology (INMET).

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 at the BDFFP reserves ranges from 1900-2300 mm. There is a pronounced dry season from June to October (Figure 1).

## 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 along forest edges or in treefall gaps, others—such as *H. acuminata*—are found at lower densities in the darker and cooler forest understory. These species produce fewer infloresences and are pollinated by traplining rather than territorial hummingbirds (Berry and Kress 1991). While some *Heliconia* species are at least partially self-compatible (Kress 1983), pollen transfer experiments indicate self-fertilization in *Heliconia acuminata* is extremely rare *[darrigo unpubl. data]*.

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 = **1.1** flowering shoots (range = 1-7), each of which has an inflorescence with 20–25 flowers (Bruna and Kress 2002). Fruits mature April-May, have 1–3 seeds per fruit (=2), and are eaten by a thrush and several species of manakin (Uriarte et al. 2011). Dispersed seeds germinate ~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).

## Demographic data collection

In 1997–1998 we established a series of 5000 plots (m) in the BDFFP reserves in which we marked and measured all *Heliconia acuminata*. The plots are located in continuous forest (n=6), 10-ha fragments (n=3), and 1-ha fragments (n=4), with distance between plots ranging from 500 m–41 km. Plots in 1-ha fragments were on one randomly selected half of the fragment, plots in 10-ha fragments were in the fragment center, and plots in continuous forest were placed in locations 500-4000 m from the borders of secondary and mature forest (**Supplemental\_\_** ). This study uses data from 1-ha fragments and Continuous Forest sites.

Each plot is subdivided into 50 quadrats (m) to simplify the annual surveys, during which we recorded the number of vegetative shoots each plant had, the height of each plant to the tallest leaf, and the identity of any flowering plants. We also surveyed plots regularly during the rainy season to identify any that flowered after the survey. Height and shoot number are correlated with leaf area, the probability of flowering, and rates of survivorship (Bruna 2002, Bruna and Kress 2002). Plants that were not found for three consecutive surveys were considered dead. There is a seven-fold range in *H. acuminata* density in the forest plots, with density in several of the plots comparable to that in low-density fragments (Bruna and Kress 2002).

## Weather data

Data on precipitation and potential evapotranspiration in our sites were obtained from a published gridded dataset (0.25º x 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). SPEI calculations were done using the SPEI package in R version 4.0.2 (2020-06-22) (Beguería and Vicente-Serrano 2017, R Core Team 2020). The timing of drought events based on these SPEI calculations is consistent with that resulting from SPEI calculated with other data sources (e.g., nearby weather stations, the global SPEI database (Beguería 2017), TRMM ((TRMM) 2011)), though the magnitude of drought can sometimes differ (**Supplemental \_\_**).

## Statistical Modeling of Vital Rates

We assessed the effects of drought history on plant vital rates using 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. Crossbasis functions were created using the *dlnm* package with possible lags from 0–36 months (Gasparrini 2011, R Core Team 2020). We chose 36 months as a maximum lag because prior *H. acuminata* individuals transplanted to forest fragments typically recovered from transplant shock within 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) using the *mgcv* package with restricted maximum likelihood (Wood 2017). The general form of the vital rate models was as follows:

where is a smooth function of plant size (natural log of height shoot number), fit using a penalized cubic regression spline, is the crossbasis function in which is the SPEI value during the census month of an observation (February) and is the SPEI months prior (see Gasparrini et al. 2017 for details). The crossbasis function, can also be written:

where the crossbasis function, , is composed of two marginal basis functions: the standard predictor-response function , and the additional lag-response function . 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 Wood (n.d.) 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 months) and 3 knots for the drought response dimension to restrict 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 great enough to allow the smooth to represent the ‘true’ relationship (Wood 2017). A random effect of plot ID on the intercept is represented by , allowing for plot characteristics to influence average vital rates. For plant growth the response was plant size (natural log of height shoot number) in year t+1 modeled with a scaled t family error distribution. A scaled t family was chosen because residuals were leptokurtic with a Gaussian error structure. The data on number of infloresences was converted to binary (1 for ≥1 inflorescence, 0 for no inflorescences). When survival and flowering were the response variables we used a binomial family error distribution with a logit link function.

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 and Wood (2011).

Because the dlnm package does not currently allow modeling of factor by smooth interactions, we fit separate models for plants in fragments and in continuous forest to allow the shape of the crossbasis function to differ between habitats.

# Results

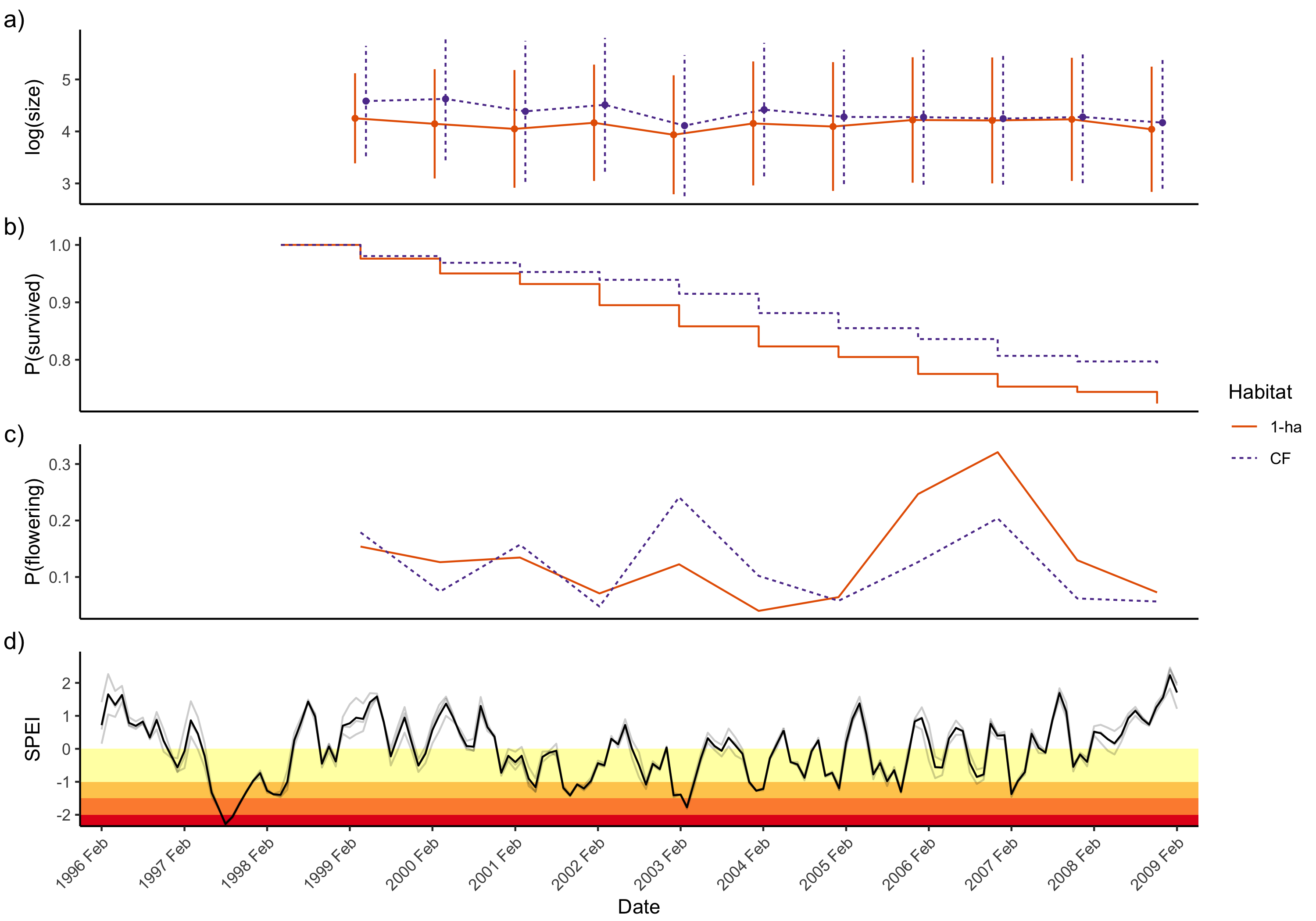


Figure 2: Timeseries of demographic parameters and drought ocurrence. Mean plant size ± standard deviation (a) shows that plants were smaller in fragments (red) than continuous forest (blue). (b) shows the survival curve for the 1998 cohort of plants in both fragments and continuous forest. c) shows the proportion of plants with 4 or more shoots flowering each census. In d), monthly 3-month SPEI is plotted. Light grey lines represent values from different grid cells encompassing BDFFP and the dark line is the site mean. Yellow, orange, dark orange, and red stripes show mild, moderate, severe, and extreme drought, respectively.

The meteorological drought occurrences indicated by SPEI mostly agree with drought events in the Amazon reported in the literature. 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 2d).  
The 2005 dry season (June–October) was also reported as an exceptionally dry year, although this drought mostly affected the south western 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).

Mean plant size dropped dramatically in 2003 in both habitat types, corresponding with a severe drought (-1.5 > SPEI > -2) during the February census (SPEI = -1.39) (Figure 2d). Two noticeable peaks in the proportion of flowering mature plants occur in severe drought years (2003 and 2007) (Figure 2c).

## Survival

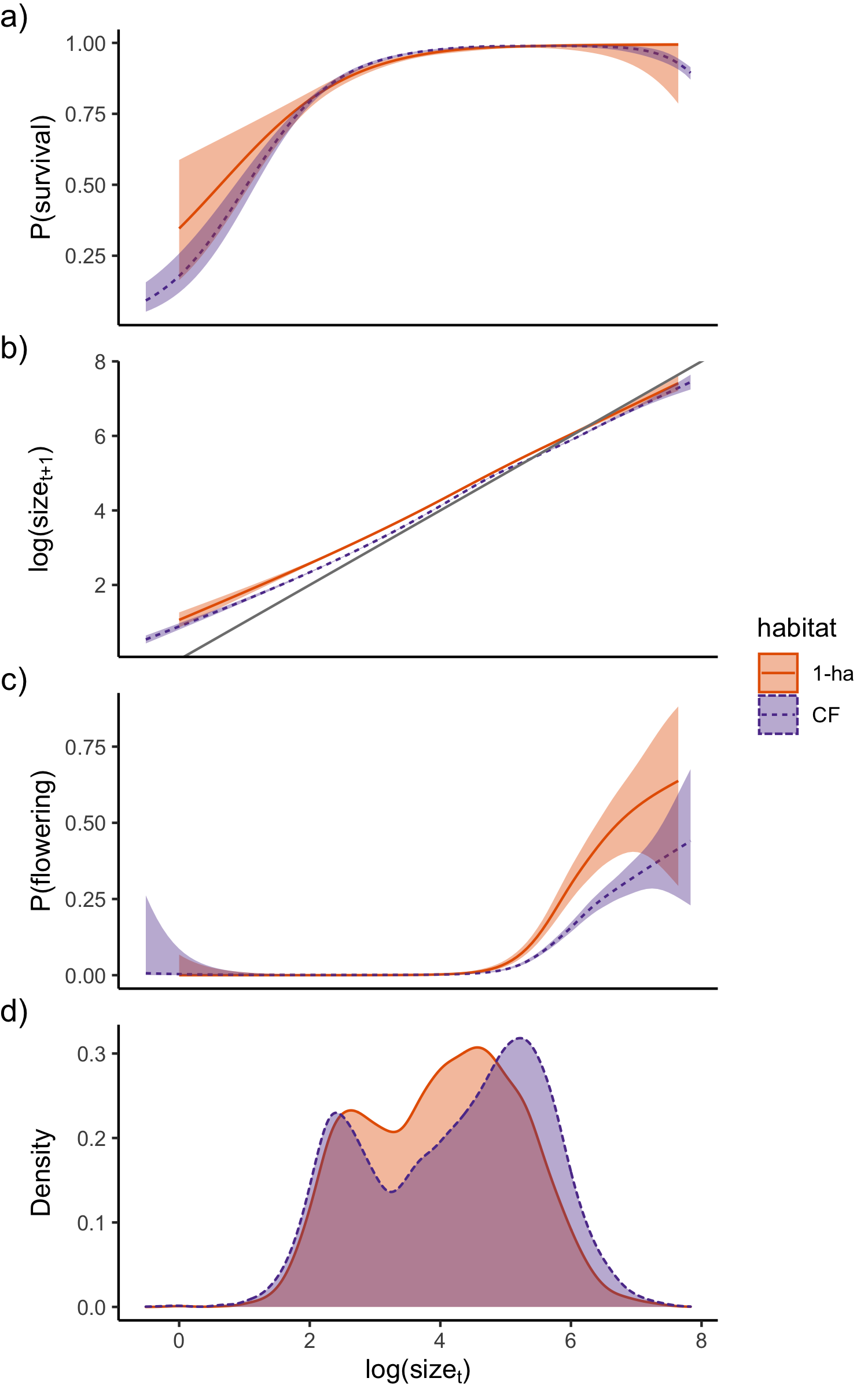


Figure 3: Smooth effect of plant size in the previous census on a) survival, b) log(size), and c) flowering probabiility, modeled by a cubic regression splines. Panel d) shows the smoothed density of different plant sizes in the two habitat types. 95% confidence intervals are shown and include uncertainty in the model intercept and uncertainty due to smoothness selection. The smooths for 1-ha fragments and continuous forest are fit in separate models. The model intercepts were added to the fitted values of the smooth and values are back-transformed to the response scale. In b), a 1:1 line is shown in dashed red to indicate the line of no growth.

Overall survival rate across the entire dataset was the same (0.95) in both CF and 1-ha. The proportion of surviving plants across both habitat types was lowest in 2004 (0.92) which coincided with a moderate drought in Jan 2004 / Feb 2005 and a severe drought in Jan–Mar of 2004 (Figure 2b,d). The lowest survival for 1-ha fragment plots (0.93) was in the 2006 census corresponding to wetter than average conditions (SPEI > 0.5), but with a moderate drought the preceding October.

Log transformed plant size had a significant effect on survival in both continuous forest and 1-ha fragments (both p < 0.001). Survival probability of large plants approached 1 in both habitat types (Figure 3a). Survival of the smallest plants was higher in 1-ha fragments, but the 95% confidence intervals for 1-ha fragments and continuous forest overlapped for all sizes.

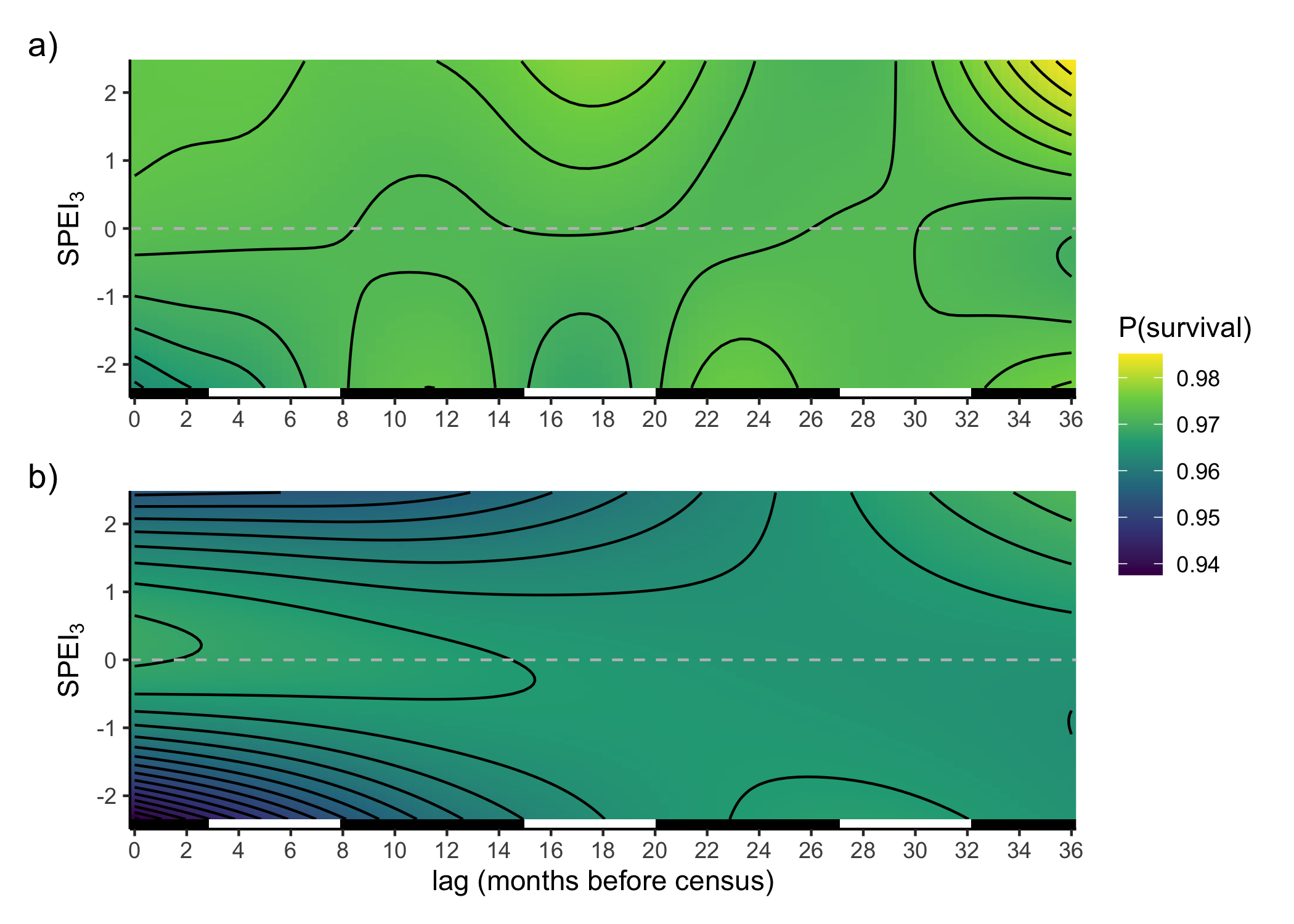


Figure 4: Smooth effect of lagged SPEI on survival in a) continuous forest and b) 1-ha fragments. Surface is modeled as a crossbasis function with cubic regression splines for each marginal basis. Model intercepts were added to fitted values of the crossbasis function and back-transformed to the response scale. Contour lines correspond to a change of 0.002. The bar on the bottom of each panel indicates wet seasons (black, November–May) and dry seasons (white, June–October).

Drought history had a significant effect on survival in both habitats (P < 0.001), but the shape of the crossbasis surface differed. For 1-ha fragments, recent SPEI values (i.e. within the past 0–12 months) had the strongest effect on survival, with the highest survival near SPEI of 0 and decreasing survival when plants were exposed to either drier or wetter conditions over the prior 0–12 months (Figure 4a). In continuous forest, recent SPEI had a weaker effect with only SPEI values less than -1 leading to slightly reduced survival probabilities (Figure 4b). However, SPEI at a lag time of 15–20 months, corresponding to June–October of the previous year (i.e. not the most recent dry season, but the one before that), also affected survival probabilities in continuous forest. Lower SPEI (drought) 15–20 months prior to census was associated with reduced survival and higher SPEI at these lag times was associated with higher survival. Plants in both continuous forest and 1-ha fragments showed an increase in survival probability with very high (wet) SPEI values at a lag time of 36 months. However, it should be noted that only the first year of census data (1999) had an SPEI value greater than 2 within 36 months in the past.

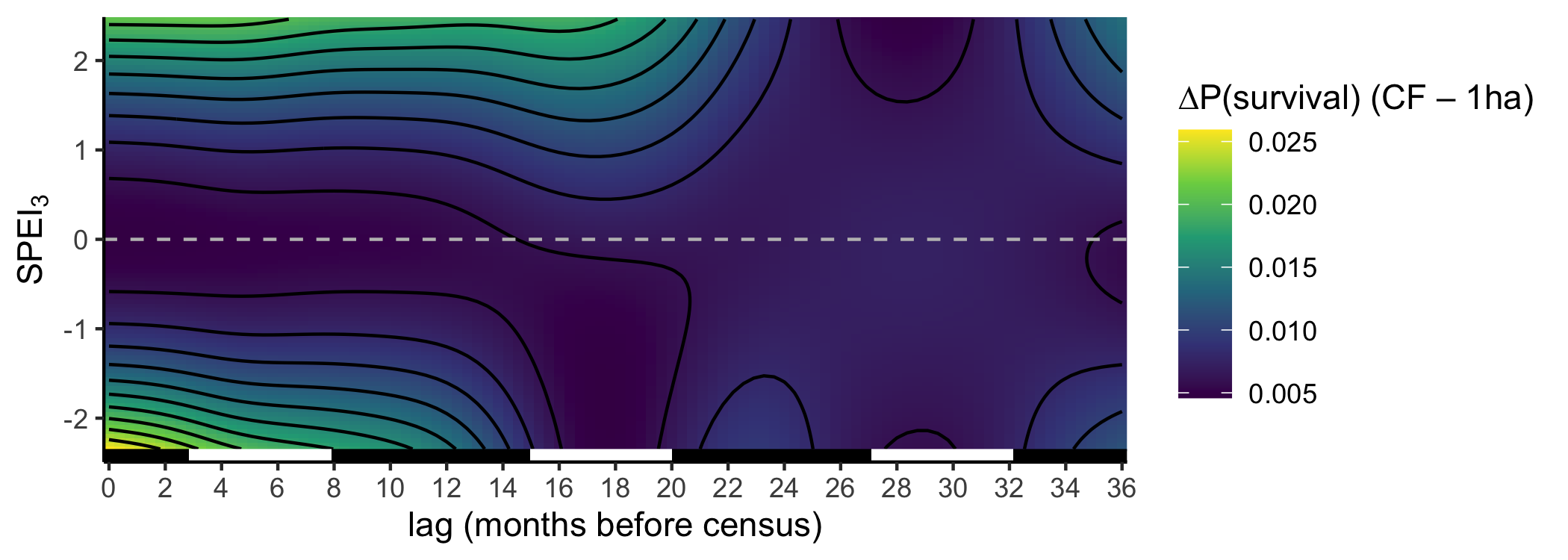


Figure 5: The difference between predicted effects of SPEI history on survival in continuous forest and 1-ha fragments.

Subtracting the estimated contribution of SPEI history to survival in fragments from that in continuous forest shows that in average conditions (SPEI = 0), there is little difference in survival probability between continuous forest and fragments (Figure 5). However, under extreme conditions, survival probability is higher in continuous forest by up to 0.02.

The random effect of plot was significant for continuous forest ( p < 0.001), but not for 1-ha fragments (p = 0.257).

## Growth

Plants were on average larger in continuous forest compared to 1-ha fragments. In continuous forest, plants had an average of 2.9 ± 1.8 shoots (mean ± standard deviation) and were on average 40.6 ± 26.5 cm tall with an average size (shoots height) of 150 ± 175. In 1-ha fragments, plants had 2.5 ± 1.5 shoots on average and a mean height of 36.2 ± 24.1 cm and a mean size of 112 ± 141. The size difference between plants in continuous forest and 1-ha fragments was more dramatic early on in the timeseries with mean sizes becoming more similar over time (Figure 2a).

Size in year t was a significant predictor of size in year t+1 (p < 0.001). The 95% confidence intervals for the effect of size in year t in fragments and continuous forest overlapped for most sizes, but was slightly higher in continuous forest for mid-sized plants (Figure 3b).

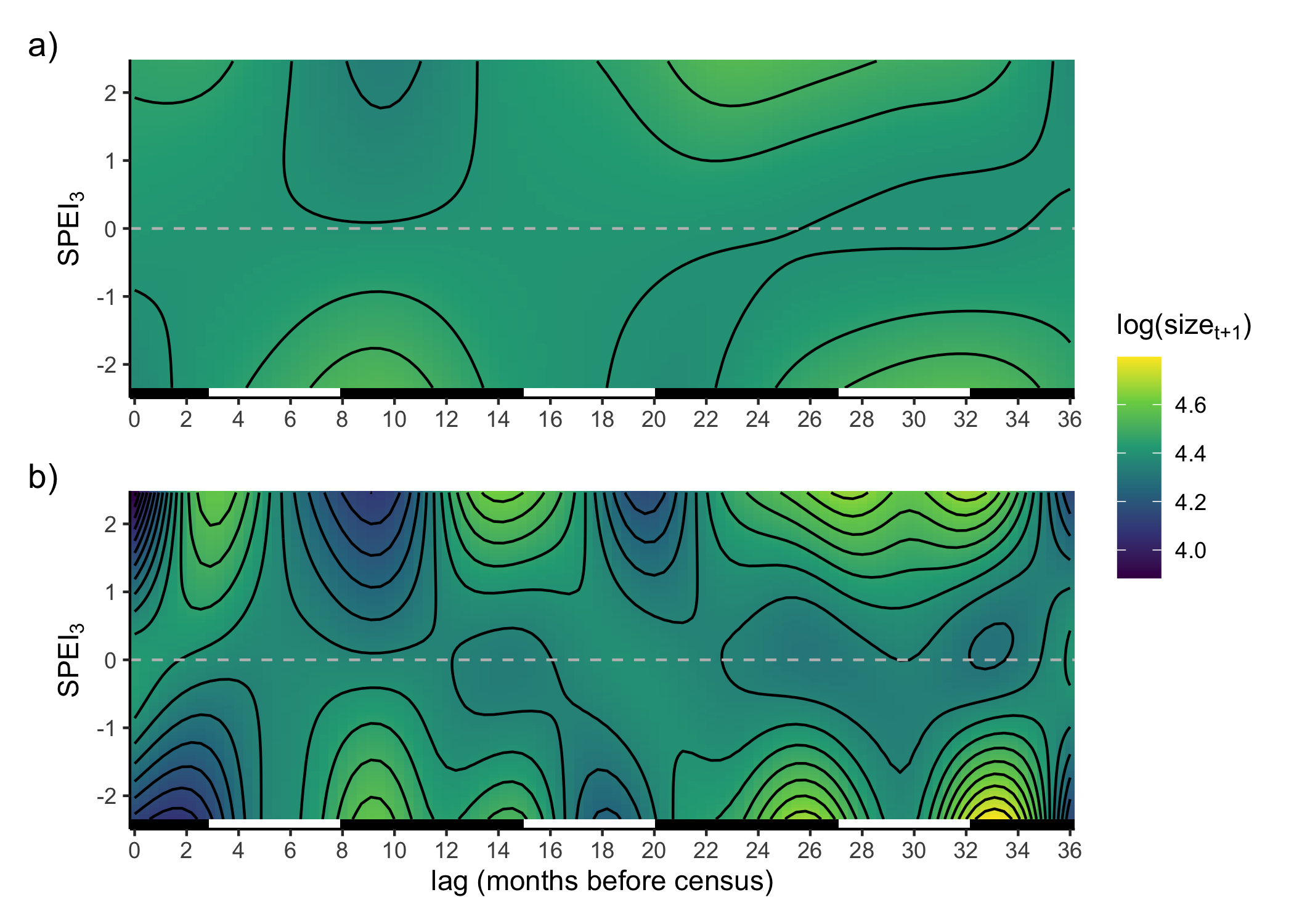


Figure 6: Smooth effect of lagged SPEI on plant growth for a) continuous forest and b) 1-ha fragments. Surface is modeled as a crossbasis function with cubic regression splines for each marginal basis. Model intercepts were added to fitted values of the crossbasis function. Contour lines correspond to a change of 0.05. The bar on the bottom of each panel indicates wet seasons (black, November–May) and dry seasons (white, June–October).

Drought history also had a significant effect on plant size in both habitats (p < 0.001). The fitted crossbasis functions for fragments and continuous forest showed somewhat similar patterns, although the surface for 1-ha fragments was much more complex (edf = 17.9 for 1-ha fragments; edf = 5.9 for continuous forest; see also Figure 6). Drought at lags 8–11 (March - June, the end of the wet season) increase growth in both habitats, but more strongly in 1-ha fragments.

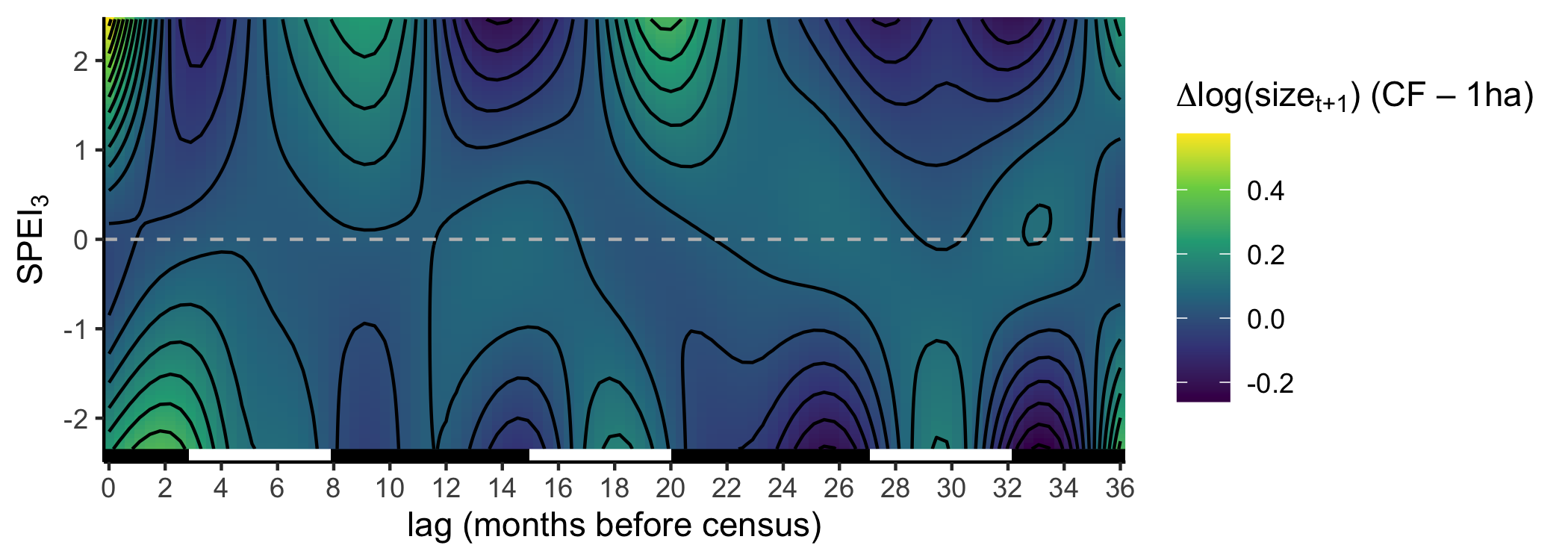


Figure 7: The difference between predicted effects of SPEI history on plant size in continuous forest and 1-ha fragments.

The difference between the effects of SPEI history in continuous forest and 1-ha fragments shows that growth is equal or slightly higher in continuous forest for average conditions (SPEI = 0) over all lag periods (Figure 7. However, growth in continuous forests is higher by up to log(size) = 0.57 when the current wet season is unusually wet (SPEI>2). This is due to reduced growth in fragments under wet conditions.

The random effect of plot is significant in both habitat models (p < 0.001).

## Flowering

There was a pronounced threshold in flowering probability corresponding with a log size of about 5 (Figure 3c). The mean proportion of flowering plants across all census years was generally higher in continuous forest (0.050 ± 0.021) compared to 1-ha fragments (0.036 ± 0.027). In fact, the proportion of flowering plants was higher in continuous forest in all survey years except 2006 and 2008 (Figure 2c). The most striking difference between habitat types in flowering proportion coincided with a severe drought in 2003 when the percentage of flowering plants with four or more shoots was 24.1% in continuous forest and 12% in 1-ha fragments (Figure 2c). The back-transformed model intercepts, representing the flowering probability of averaged sized plants in each habitat given average SPEI, showed a similar pattern with 0.008 for continuous forest and 0.004 for 1-ha fragments.

Plant size had a significant effect on flowering probability in both habitats (p < 0.001). Flowering probability increased rapidly with log-transformed plant size greater than 5 in both habitats (Figure 3c). Flowering probability of large plants (log(size) > 5) was greater in 1-ha fragments compared to continuous forest. However, because mean plant size is larger in continuous forest (Figure 3d), overall flowering probability was greater.

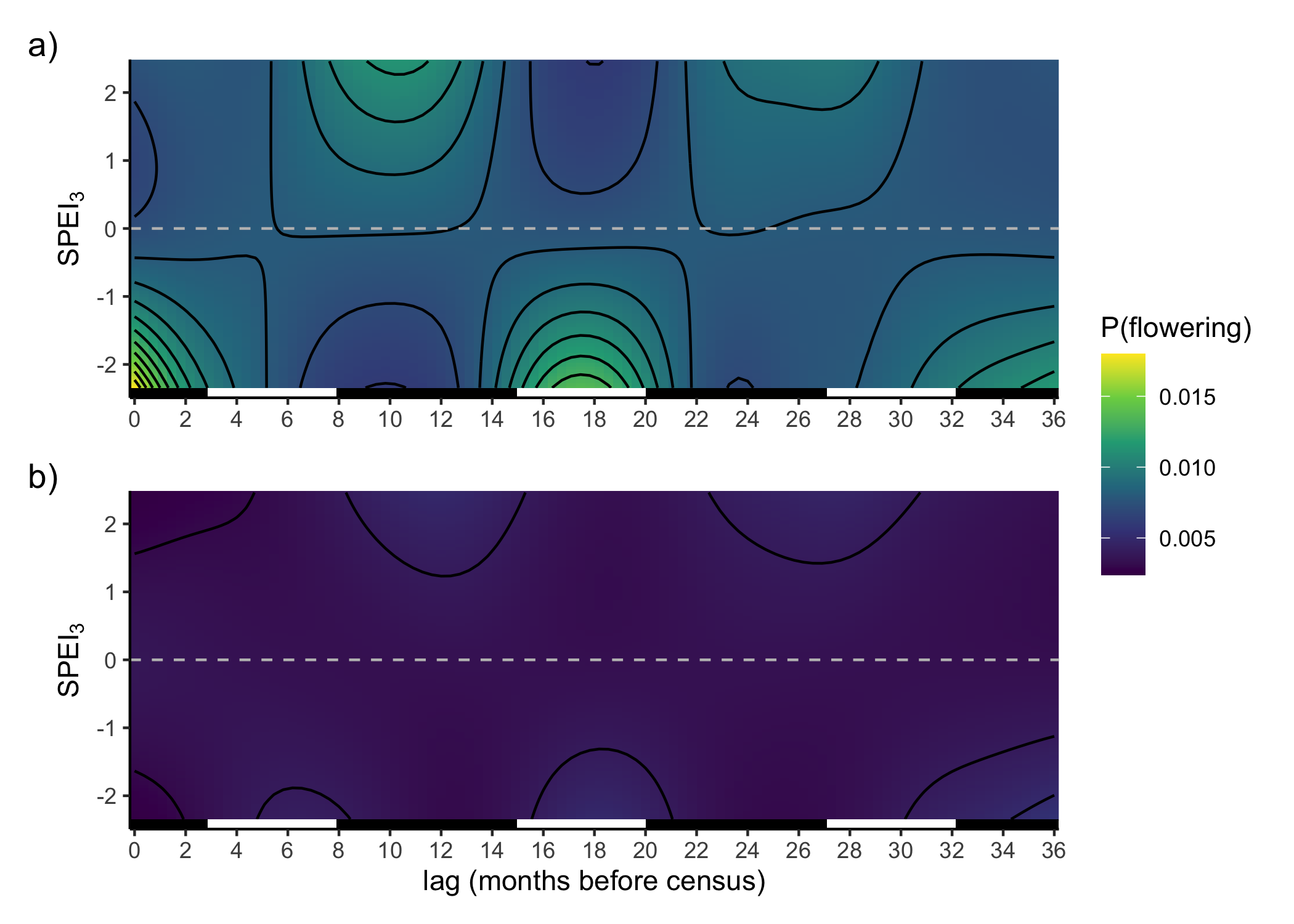


Figure 8: Smooth effect of lagged SPEI on flowering probability. Surface is modeled as a crossbasis function with cubic regression splines for each marginal basis. Model intercepts were added to fitted values of the crossbasis function and back-transformed to the response scale. Contour lines correspond to a change of 0.001. The bar on the bottom of each panel indicates wet seasons (black, November–May) and dry seasons (white, June–October).

Drought history had a significant effect on flowering probability in both habitat types (p < 0.001). Flowering probability was overall higher at all values of SPEI in continuous forest compared to 1-ha fragments (Figure 8). The effects of SPEI on flowering probability were also stronger and more complex in continuous forest compared to fragments (1-ha edf = 8.5, continuous forest edf = 10.5). In continuous forest, flowering probability was increased by recent drought (at lag = 0 with SPEI < -1) and drought at lags 15–20 (Jun-Nov, two dry seasons ago). Drought at lags 7–13 reduced flowering probability. The shape of the crossbasis function was similar in 1-ha fragments, but significantly muted (Figure 8a). That is, the variation in fitted values along the SPEI dimension was much lower at all values of the lag dimension in fragments.

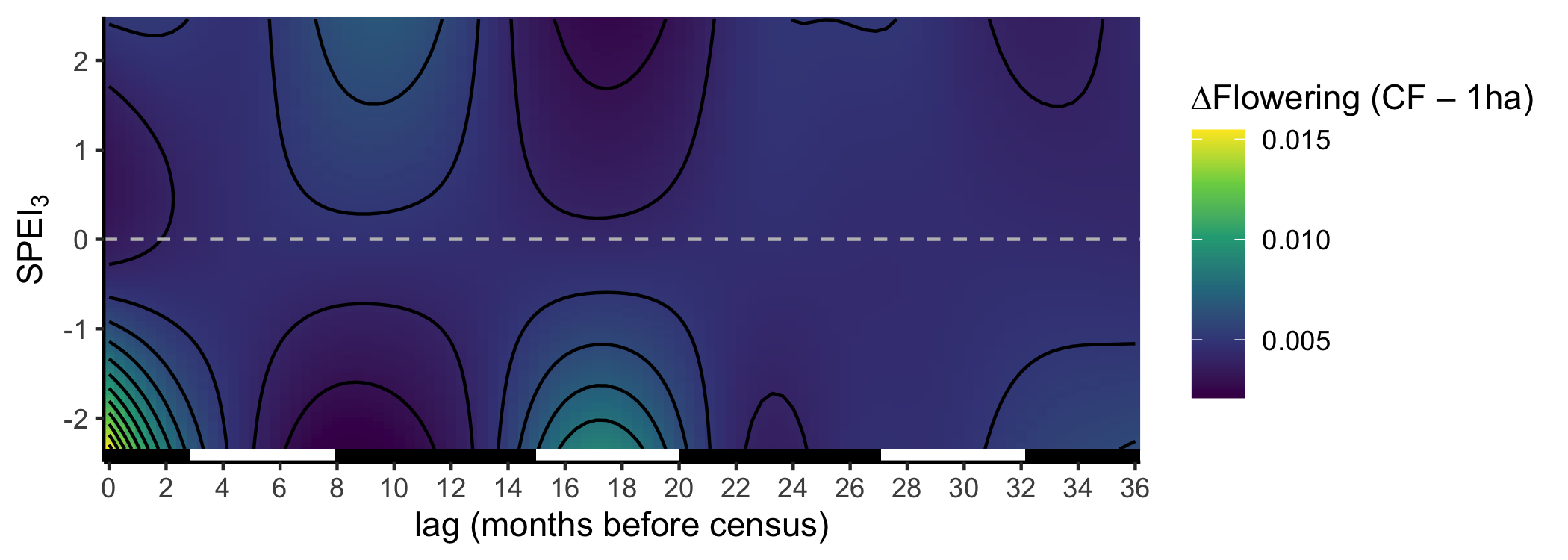


Figure 9: The difference between predicted effects of SPEI history on flowering probability in continuous forest and 1-ha fragments.

Plotting the difference between the crossbasis smooths for continuous forest and 1-ha fragments revealed that flowering probability is higher in continuous forest compared to 1-ha fragments and is increased by recent drought and drought during the dry season 15–20 months prior to the census (Figure 9). The least difference between habitat types occurs when there is strong drought at about 8–12 months lag or very wet conditions at 15–20 months lag.

The random effect of plot also had a significant effect in both habitats (p < 0.001).

# Discussion

#### Citations / information to allocate to appropriate paragraphs

* Criley and Lekawatana (1994) : under hort conditions, shoots that flower in spring emerge in June/July the previous year. ~6 months after shoot emergence that the developing infloresence is susceptible to adverse effects.
* Dowd (2020) (unpublished thesis, could write MB and ask for update): precipitation and fragmentations influenced fruit/seed production (conditional on flowering) by *Heliconia* (one step past flowering, so might be worth citing to say that there are other ways reprod. can be affected
* Lots of great stuff about the importance of rhizomes, including for drought resistance, in Klimešová et al. (2018). Rhizome resistance to variability in environmental conditions also a conclusion in this study on invasion by another zingiberales ( Pinheiro et al. (2021)
* Westerband et al. (2017): *Heliconia* grew more at low than high precipitation. Leaf life span and biomass allocation did not differ among treatments. The effect of environmental variability was dependent on early life conditions as well as precipitation, suggesting that generalist species may experience high fitness as forest environments become more variable by maintaining high growth at the expense of survival.
* the observed effects on reproduction can have effects beyond demography, eg. gene flow and genetic structure among and between plots already shaped by fragmentation ( Cortes et al. (2013), there can also be drought effects eg Sifres et al. (2007))
* There can be cascading effects on other species (hispine beetles that depend on Heliconia flowers/fruits, hummingbirds and seed dispersers ( Stiles (1975)
* Wright (1992): seasonal drought. experimental irrigation influences survival and growth of tropical herbs
* Effects of precip extremes on understory plants can be also be indirect:
  + high precip = lots of clouds, less photosynthesis, less or slower growth
  + low precip = trees lose leaves or die, more light gets through or gaps open. This can be positive (more light = more growth) but not always ( Westerband and Horvitz (2015)) there is a threshold that can lead to photoinhibition ( He et al. (1996), Mulkey et al. (1991)). Drought and herbivory effects can be additive, at least in seedlings ( Barton and Shiels (2020))
* Horvitz and Schemske (1988): no evidence for short term (next season) cost of reproduction in another understory monocot (Calathea) BUT
* Horvitz and Schemske (2002) (*Calathea ovandensis*) Survival of juveniles was positively affected by plant size, but not by herbivory, local competition, or fruit production. Survival of large stages was not generally affected by any of the factors. Relative growth rates of all stages were negatively affected by plant size; larger plants grew more slowly than smaller plants. Additionally, growth rate of juveniles was negatively affected by local competition, whereas growth rate of reproductives was positively affected by reproduction. Next year’s inflorescence production was positively affected by plant size for both pre-reproductive and reproductive stages. For reproductives, it was additionally positively affected by current fruit production.
* Rundel et al. (1998) Heliconia appear to allocate much of their above-ground biomass to leaf tissues and have a relatively low investment in support tissues. Investment in leaf form vs structure interpreted as a trade-off between economy and protection against tissue loss from falling branches; presence of below-ground rhizomes in Heliconia may be key. See also Rundel et al. (2020)
* Stiles (1975)?: drought resulted in less flowering in Heliconia
* Mulkey and Wright (1996) and Bonal et al. (2016) will have goods stuff; haven’t looked them over yet
* Wright and Calderon (2006): Increase in flower and seed production after El Niño events for trees and lianas. Might be due to increases solar irradiance. Maybe evidence of lagged effects? Table 2 is inconsistent with text, so not sure…
* Many humid tropical forest species time reproduction to coincide with dry season peak to avoid low irradiance in wet season. (refs within Wright and Calderon (2006). van Shaik et al. 1993; Wright and vanSchaik 1994). But *Heliconia* times reproduction so seeds only germinate at start of rainy season.
* (Esteban et al. 2021) negative effects of large positive SPEI
* In Manaus, the canopy is as green or greener in the dry season compared to the wet season (Guan et al. 2015), so dry season drought may result in relatively large increases in light penetration to the understory.
* refs in Leitold et al. (2018) peak in tree mortality can happen up to 3 years after drought event in experimental studies. Observational studies show mortality happening in same year as 2007 and 2010 droughts.

Understanding how landscape structure and environmental conditions act to influence population dynamics is fundamental to many of the emerging conceptual frameworks for studying and conserving fragmented landscapes (Didham et al. 2012, Driscoll et al. 2013).

This study adds to the growing body of work that finds delayed effects of climate drivers on vital rates without *a priori* assumptions about the influence of particular climate windows (Teller et al. 2016, Tenhumberg et al. 2018, Evers et al. 2021). We found evidence for delayed effects of drought which are sometimes stronger predictors of vital rates than more recent conditions. The approach we took 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), yet few demographic studies have the data required for modeling lagged effects (Crone et al. 2011, Teller et al. 2016). This demonstrates the importance of long term demographic experiments in determining the effects of changing habitats on populations.

*Heliconia acuminata* individuals were smaller in forest fragments, although they grew slightly faster than plants in continuous forest, closing the size gap over the decade of demographic data. Size regression became more likely as plants increased in size, which is typical of long-lived forest understory plants . Our results confirm those of Bruna and Kress (2002), showing that probability of flowering increases with plant size and plant growth decreases with plant size . Flowering probability for the largest plants is actually higher in forest fragments; however, because there are fewer large plants in fragments overall flowering probability is much lower. The average fitted probability of flowering for plants in the upper quartile for size is 0.125 in continuous forest and 0.094 in forest fragments, equivalent to flowering once every 7.97 years and 10.63 years, respectively. Seemingly small differences in vital rates such as these can be extremely important as they compound over many years, especially in long-lived organisms(Gagnon et al. 2011).

We found that the effects of variation in SPEI differed between forest fragments and continuous forest habitat. At mean SPEI, overall survival of plants was similar in fragments and continuous forest, but extremes in SPEI, both positive (wet) and negative (dry) had much greater detrimental effects on survival in habitat fragments. Similarly variation in SPEI had a greater impact on plant size in fragments compared to continuous forest with a general trend of unusually wet wet seasons and unusually dry dry seasons having a greater negative impact in fragments. Flowering probability showed a different pattern with a greater effect of variation in SPEI in continuous forests. However, with few plants large enough to flower, it is likely we simply did not detect the full effects of variation in SPEI on flowering probability in forest fragments with our models. Both variation in precipitation and extreme conditions are predicted to increase as climate change progresses ( ) and our results demonstrate that this may have a greater negative impact on understory plants in forest fragments compared to continuous forests.

Reduced microclimate buffering could possibly explain the greater effects of variation in SPEI in fragments compared to continuous forest. A major consequence of forest fragmentation is reported alteration in microclimate near forest edges (Didham and Lawton 1999, Ewers and Banks-Leite 2013). It is possible that increases in temperature, evaporative drying, wind speed, and solar radiation commonly found near forest edges exacerbated the effects of extremes in SPEI on *H. acuminata* growth and survival in fragments compared to continuous forest. It is also possible that the microclimate experienced by plants in continuous forest plots was simply more stable compared to that of 1 ha fragments. Bruna et al. (2002) found that the growth of transplanted *H. accuminata* plants transplanted near edges was reduced relative to continuous forest. A greater understanding of the microclimatic changes in fragments during extreme climate events and their effects on understory plants is needed, but we believe differences in microclimate buffering are a likely explanation for the observed differences between fragments and continuous forest.

Past climate conditions were important for survival, size, and flowering probability. Extremes in SPEI in the 15 months prior to the census reduced survival in forest fragments (Figure 4). Extremes in SPEI in the past 36 months affected plant size, although the direction of the effects was seasonally dependent (Figure 6). Generally, unusually dry dry seasons and unusually wet wet seasons had negative impacts on plant size, and this pattern was more extreme in fragments compared to continuous forest. For flowering, the SPEI of the current wet season and the dry season two dry seasons ago (lag of 15–20 months) had the strongest influence on flowering probability with dry weather corresponding to an increase in flowering (Figure 8).

There are several possible non-mutually-exclusive explanations for delayed effects of SPEI on vital rates. First, delayed effects may represent a demographic delay since we do not know precisely when since the previous survey the plant died or changed size. For example, if extreme drought in the dry season before the census increases plant mortality in that season, this would show up as a delayed effect in our models (e.g. in Figure 4b) despite the impact of drought potentially being immediate. This explanation for delayed effects applies only to plant size and survival, as flowering occurs very close to the yearly demographic census (Jan–Apr).

Second, these delayed effects may represent a physiological delayed effect of environmental conditions. Under horticultural conditions, flowering shoots of *Heliconia chartacea* that flower in Spring begin to emerge in June or July of the previous year, and the developing inflorescence may be aborted in response to adverse conditions up to 6 months after initiation (Criley and Lekawatana 1994). Although flowering occurs in late January through April in *H. acuminata*, the initiation of a primordial flowering shoot likely happens many months earlier. The increase in flowering rate of plants following a drought could also be a bet-hedging strategy in response to stress (Nihad et al. 2018) . We also considered that some delayed effects could be a result of a cost of reproduction leading to reduced growth, survival, and/or flowering probability in the following season. However, when flowering in the previous season is included as a covariate, it predicts higher growth and flowering probability—likely a reflection of size being a good predictor of these vital rates (Supplemental\_\_\_). Our models show that drought two dry seasons prior to the census increase flowering probability. A greater understanding of the effects of light, drought, season, and their interactions on flowering in *H. acuminata* is needed to provide a probable mechanism for this pattern.

Finally, delayed effects could be mediated by indirect effects and ecological interactions. Drought in tropical forests can increase tree mortality and leaf drop, resulting in decreased canopy cover and increased light penetration to the understory (). This increase in light could then result in increased growth or flowering for understory plants ( ). Janssen et al. (Janssen et al. 2021) showed that increase in litterfall due to drought was delayed. Here, the delayed effect of drought on *H. acuminata* could be partly explained by a delay of the response of canopy trees to drought and the response of *H. acuminata* to increased insolation. Furthermore, literfall in response to drought has shown to be greater at forest edges compared to interiors, which could explain the increased delayed effects of SPEI on survival and growth in forest fragments. Drought is also associated with increased insolation, so negative SPEI could also be a proxy for increased insolation, which would be exacerbated at forest edges potentially.

* (Janssen et al. 2021) Used machine learning to combine remote sensing and ground surveys of literfall from published datasets. Estimates green-up, literfall, growth, etc. for central and southern america including the Amazon. Drought results in anomolously high leaf flushing at start of drought followed by increased litterfall durring the drought. Dry season droughts result in green-up, but not wet season droughts. During drought, old leaves are shed and new leaves are maintained. 2-5 months for newly flushed leaves to fully expand.
* Ecological Consequences of these patterns: an eye towards a drier/wetter future

# Conclusions & Future Directions

* There could be size-specific effects: Fragmentation affects plant size (in *Heliconia* (Bruna and Oli 2005) and trees (Schwartz et al. 2019)). Smaller/larger plants might be more susceptible to drought. So differential effects of drought in fragments and continuous forest could be due to an interaction between drought and plant size. The dlnm package does not currently allow for modeling of interactions, and we lacked data on plant size at the same time scale as SPEI (monthly), so interactions with size were not included in this analysis.
* Synergistic effects of fragmentation and climate (need the stats to catch up with us) “Organisms simultaneously experience multiple forms of disturbance. While work investigating the demographic effects of individual factors is common, studies investigating how multiple factors interact to influence population dynamics remains poorly understood. They could act in concert to exacerbate or dampen population dynamics.”
* Very few demographic studies have the data required to fit models that include delayed effects.
* Loop back to: need whole-life-cycle approach to ID these effects, why fragmentologists don’t do this is killing Emilio.

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If TRMM data is used, they suggest: “The TMPA data were provided by the  
NASA/Goddard Space Flight Center’s Mesoscale Atmospheric Processes Laboratory and  
PPS, which develop and compute the TMPA as a contribution to TRMM.”

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### Colophon

This report was generated on 2021-04-09 16:31:54 using the following computational environment and dependencies:

#> ─ Session info ───────────────────────────────────────────────────────────────  
#> setting value   
#> version R version 4.0.2 (2020-06-22)  
#> os macOS Catalina 10.15.7   
#> system x86\_64, darwin17.0   
#> ui X11   
#> language (EN)   
#> collate en\_US.UTF-8   
#> ctype en\_US.UTF-8   
#> tz America/New\_York   
#> date 2021-04-09   
#>   
#> ─ Packages ───────────────────────────────────────────────────────────────────  
#> ! package \* version date lib  
#> P Amelia \* 1.7.6 2019-11-25 [?]  
#> P anytime 0.3.9 2020-08-27 [?]  
#> P assertthat 0.2.1 2019-03-21 [?]  
#> P backports 1.2.1 2020-12-09 [?]  
#> P base64enc 0.1-3 2015-07-28 [?]  
#> P bbmle \* 1.0.23.1 2020-02-03 [?]  
#> P bdsmatrix 1.3-4 2020-01-13 [?]  
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#>   
#> [1] /Users/scottericr/Documents/HeliconiaDemography/renv/library/R-4.0/x86\_64-apple-darwin17.0  
#> [2] /private/var/folders/b\_/2vfnxxls5vs401tmhhb3wqdh0000gp/T/RtmpM0rcKi/renv-system-library  
#> [3] /private/var/folders/b\_/2vfnxxls5vs401tmhhb3wqdh0000gp/T/RtmpTATyvb/renv-system-library  
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#> P ── Loaded and on-disk path mismatch.

The current Git commit details are:

#> Local: master /Users/scottericr/Documents/HeliconiaDemography  
#> Remote: master @ origin (https://github.com/BrunaLab/HeliconiaDemography.git)  
#> Head: [81f299b] 2021-04-09: switched color palette to be distinguishable in grayscale and added linetype as aesthetic mapping for habitat. Closes #34