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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# 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 species in forest fragments can have depressed rates of reproduction or survivorship (Bruna, 1999; Laurance et al., 1998; Zartman et al., 2015), leading to local or regional population declines, the demographic mechanisms underlying these extinctions are poorly understood (Bruna et al., 2009). However, it is often assumed that these detrimental effects are caused by dramatically altered environmental conditions often observed in fragments—e.g., increased air temperature, decreased relative humidity, reduced soil moisture, increased solar radiation (Arroyo-Rodríguez et al., 2017; Didham & Lawton, 1999; Ewers & Banks-Leite, 2013). The demographic consequences of habitat fragmentation are thought to be particularly important in species-rich tropical forests (Didham & 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 (Silva Junior et al., 2021), resulting in their extensive fragmentation and the creation of over 70,000 km of new forest edges annually (Broadbent et al., 2008). Despite this, evidence linking changes in population-level demographic responses with changes in environmental conditions remains scarce.

Climate change has been shown to alter the demography of species in temperate zones (Doak & Morris, 2010; Selwood et al., 2015; Sletvold, 2005; Williams et al., 2015), and these effects can be exacerbated in fragmented landscapes (Holyoak & Heath, 2016; Oliver et al., 2015). While the demographic consequences for tropical species are expected to be similarly severe (Brodie et al., 2012; Scheffers et al., 2017), surprisingly little is known about the consequences of changing climates for taxa in tropical biomes, including Amazonia (Paniw et al., 2021). Climate models for the next 50-100 years predict that some parts of the Amazon basin will experience more frequent and severe droughts as well as more frequent periods of high precipitation (Cai et al., 2014; Duffy et al., 2015; Mora et al., 2013; Zeng et al., 2008). These changes could exacerbate the altered environmental conditions in fragments thought to make populations demographically vulnerable. Plant populations may be particularly sensitive as an increase in the frequency and severity of extreme precipitation events can have detrimental consequences for survival and reproduction (Esteban et al., 2021; Gaoue et al., 2019). These results, coupled with evidence that growth and survivorship are already lower in fragments (Bruna et al., 2002; Laurance et al., 1998; Zartman et al., 2015), has led to speculation that plants in forest fragments are particularly at risk from drought and other climatic extremes (Laurance et al., 2001; Opdam & Wascher, 2004; Selwood et al., 2015).

Whether plant populations in tropical forest fragments are more 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-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 (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; 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 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 in disturbed areas or 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 & Kress, 1991). While some *Heliconia* species are at least partially self-compatible (Kress, 1983), pollen transfer experiments indicate self-fertilization in *Heliconia acuminata* is rare *[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 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 (), 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 & Kress, 2002).

## Demographic data collection

In 1997–1998 we established a series of 5000 m2 plots (m) in the BDFFP reserves in which we marked and measured all *Heliconia acuminata*. The plots are located in continuous forest (), 10 ha fragments (), and 1-ha fragments (), 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 whether each plant was flowering. 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 & 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 continuous forest plots comparable to that in low-density fragments (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 evapotranspirtaion of the previous three months. SPEI calculations were made using the SPEI package in R version 4.0.2 (2020-06-22) (Beguería & 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, though the magnitude of drought can sometimes differ (**Supplemental \_\_**).

## 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 recovered 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 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 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) 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). 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 . 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 and the natural log of height shoot number as our proxy for plant size . A scaled t family was chosen because residuals were leptokurtic with a Gaussian error structure. For reproduction in year t our response variable was whether or not a plant had any inflorescences (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, .

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 modeling of factor by smooth interactions. This means we could not include habitat as an interaction term. 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.

# Results

Meteorological droughts in our focal region, as indicated by SPEI, are generally consistent with those 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).

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

Our dataset comprised 27,388 plants in continuous forest and 6,893 plants in forest fragments, with plots in CF having on average 2.6-fold more plants than plots in 1-ha fragments (CF = 4565 ± 3473 SD; 1-ha = 1723 ± 179 SD). When summarizing across years and plots, the proportion of *Heliconia acuminata* that survived in CF and 1-ha was similarly high (P(surv) = 0.95). The proportion of surviving plants was lowest in the 2003–2004 transition year (), which coincided with droughts in both the 2003 and 2004 rainy seasons (Figure 2b,d). The lowest survival for 1-ha fragment plots () 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. Survival was size dependent in both continuous forest and 1-ha fragments ( for the effect of log-transformed plant size in year t on suvival in year t+1 in both habitats). While the survival probability of large plants approached 1 in both habitat types (Figure 3a), the survival of the smallest plants was higher in 1-ha fragments. However, the 95% confidence intervals for 1-ha fragments and continuous forest overlapped for all sizes.

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 the proxy for plant size used in our models was the product of these two metrics, plants in fragments were consequently substantially larger than those in forest fragments (150 ± 175 SD vs. 112 ± 141 SD, respectively). This disparity in plant size was most pronounced in the initial years of our surveys and then diminished over time (Figure 2a), likely due to a combination of greater seedling recruitment in CF and plant mortality or shrinkage. Mean plant size dropped dramatically in 2003 in both habitat types, corresponding with a severe drought during the February census (SPEI = -1.39) (Figure 2d). As with survival, size in year t was a significant predictor of size in year t+1 ( 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 3b).

While the overall proportion of plants flowering was very low, it was nevertheless almost 40% higher in continuous forest than 1-ha fragments (0.05 ± 0.21 vs. 0.04 ± 0.19, respectively). This disparity was largely due to the fact that flowering is size-dependent ( in both habitats), with the probability of flowering increasing dramatically once plants reached the threshold size of about 148 [log(size) > 5] (Figure 3c), which corresponds roughly to \_\_\_\_ shoots . Even though flowering probability of large plants [log(size) > 5] was greater in 1-ha fragments compared to continuous forest, there were proportionally far fewer plants above the reproductive threshold size in forest fragments (Figure 3d). Indeed, the most striking difference between habitat types coincided with a severe drought in 2003, when the percentage of flowering plants with four or more shoots was 24.1% in continuous forest vs. only 12% in 1-ha fragments (Figure 2c).

## Delayed effects of drought on demographic vital rates

Drought history had a significant effect on survival in both habitats (), 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 < -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. 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.

Drought history also had a significant effect on plant size in both habitats (). 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 = 12.9 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. 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.

Drought history had a significant effect on flowering probability in both habitat types (). 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 = 8.1, continuous forest edf = 10.3). 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 substantially 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. 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.

FInally, with the exception of survival in 1-ha fragments (), the delayed effects of SPEI on all three vital rates varied significantly among plots ( for the random effect of plot). We did not see evidence for a cost of reproduction. Flowering in the previous year was a significant predictor of growth ( for continuous forest, for fragments) and flowering ( in both continuous forest and fragments), but the coefficients were positive, indicating that flowering in the previous year was positively related to both size and flowering probability in the current year.

# Discussion

Understanding how landscape structure and environmental conditions act to influence population dynamics is fundamental to many of the conceptual frameworks for studying and conserving fragmented landscapes (Didham et al., 2012; Driscoll et al., 2013). Despite this, surprisingly few studies have compared the structure and demography of populations in habitat fragments and continuous habitat; those that have are typically short term (i.e., <4 years). Using a decadal dataset of plant demography, we show that some—but not all—results from short-term studies can be extrapolated to longer times scales. Our results also add to the emerging body of work showing delayed effects of climate drivers on demographic vital rates (Evers et al., 2021; Teller et al., 2016; Tenhumberg et al., 2018). Finally, we show for the first time that the magnitude, direction, and temporal lag in demographic responses to drought differs between forest fragments and continuous forest.

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## Temporal variation in demographic responses to forest fragmentation

Decadal comparisons of *Heliconia acuminata* growth and survival largely mirrored those of prior experiments and surveys (Bruna & Kress, 2002). In contrast, conclusions regarding the effect of fragmentation on flowering differed substantially from those based on short-term surveys (Bruna & Kress, 2002). While in some years the probability a plant flowered was far lower in fragments than in continuous forest, in others it was comparable or even higher. The probability that individual plants flowered continued to be size-dependent, with a similar size threshold below which plants were unlikely to produce inflorescences. However, while in our initial three-year survey the relationship between plant size and probability of flowering was similar in both habitat types (Bruna & Kress, 2002), when using the decadal dataset were found that flowering probability for the largest plants is actually higher in forest fragments (i.e., average fitted probability of flowering for plants in upper size quartile = 0.125 in CF vs. 0.094 in FF).

These size-dependent differences in flowering probability had only a modest effect on the previously observed disparities in flowering plant abundance—populations in fragments are smaller, and they have proportionately fewer of these large plants (Bruna & Kress, 2002). However, they could potentially lead to major habitat-specific differences in lifetime reproductive effort for these long-lived plants, as they translate into flowering once every 7.97 years in fragments vs. every 10.63 years in continuous forest (assuming stasis in size and average SPEI). Our results underscore why caution is needed when using short-term studies to draw conclusions regarding the effects of fragmentation on long-lived organisms: seemingly small (i.e., non-significant) differences in vital rates, when compounded over multiple years, can lead to demographic divergence among populations (Gagnon et al., 2011).

## Delayed effects of climate on demographic vital rates

Precipitation extremes and other climatic factors are known to have immediate effects on the growth, survival, or reproduction of plants (Esteban et al., 2021; S. J. Wright & Calderon, 2006), including *Heliconia* (Stiles, 1975; Westerband et al., 2017) and other tropical herbs (S. Joseph Wright, 1992). These effects can be complex or even contradictory—mild droughts can increase the growth rates of tropical trees, perhaps due to reductions in cloud cover (Condit et al., 2004), 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” (S. J. Wright et al., 1999; Pau et al., 2013).

Despite this, models of population dynamics have rarely included the effects of environmental drivers. 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 this emerging literature—that the effects of precipitation extremes on the demography of *Heliconia acuminata* could be delayed for up to 3 growing seasons.

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

There are several, non-mutually-exclusive explanations for delayed effects of SPEI on demography. The first is that the physiological processes underlying vital rates might be initiated long before they are demographically apparent (Evers et al., 2021), and hence be shaped by climatic events at any point in that physiological window. For example, the flowering shoots of *Heliconia chartacea* begin to develop 6-10 months prior to the appearance of infloresences. Adverse conditions during the 6 months following initiation, rather than the months when infloresences are starting expand, leads to the aborted production of flowering shoots (Criley & Lekawatana, 1994). 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 below-ground rhizomes (*sensu* Pumisutapon et al., 2012). The carbohydrates stored in rhizomes allow *Heliconia* to regenerate above-ground 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, while droughts can kill some tropical trees immediately (Laurance et al., 2001), others take three years or more (Criley & Lekawatana, 1994). This will potentially lead to a boom in growth and flowering years after the drought, when the canopy gaps resulting from delayed leaf drop (Janssen et al., 2021) and treefalls allow for light penetration to the forest understory (Canham et al., 1990). Similar delayed changes in the local environment could also influence the foraging behavior of *H. acuminata*’s pollinators (Bruna et al., 2004; Stouffer & Bierregaard, 1996) and seed dispersers (Uriarte et al., 2011). While more work is needed to explain why the delayed effects of SPEI on survival and growth are greater in forest fragments than interiors, it may be due to the proportionately greater amount of litterfall on edges (Vasconcelos & Luizão, 2004) altering the abundance of pathogens or mycorrhizae.

Finally, demographic delays could be an artefact 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 is 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.

***THIS INFO PROB NEEDS TO BE WORKED IN SOMEWHERE ABOVE***

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).

## Conclusions & Future Directions

Climate models for the Amazon predict a future of extremes—increases in the frequency and geographic extent of droughts, but also increases in the frequency and area affected by periods of unusual wetness (Duffy et al., 2015). Our results support the hypothesis that populations in fragments could be more susceptible to the effects of changing climate than those in continuous forest (Laurance et al., 2014). However, they also indicate that the demographic responses to climate change of populations in fragmented landscapes may be far more complex than previously appreciated. Multi-factorial, multi-season experiments are needed to determine if habitat-specific differences in environmental conditions and local ecological neighborhood interact to delay the demographic responses of plants to climatic variability and the mechanisms underlying these responses (*sensu* Bruna & Ribeiro, 2005; Markewitz et al., 2010; Westerband et al., 2017; Westerband & Horvitz, 2015)

Also needed are statistical tools that can test for synergistic effects of fragmentation and climate in vital rates, as those currently available do not allow for including interaction terms. This also limits the ability to include size by climate interactions in a DLNM; although plant responses to both fragmentation and climatic extremes can be size-specific (Bruna & Oli, 2005; Schwartz et al., 2019). The ability to identify size-specific lagged responses may be especially complicated given size and growth are rarely measured at the same time scale as SPEI and other putative climatic drivers.

Finally, no analytical approach assessing the potential for demographic lags can compensate for a lack of long-term data (Evers et al., 2021; Tenhumberg et al., 2018). Unfortunately, long-term data monitoring the entire life-cycle of tropical taxa are rare, and 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.

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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.”< !–# this can go in supplemental – >

# Figures

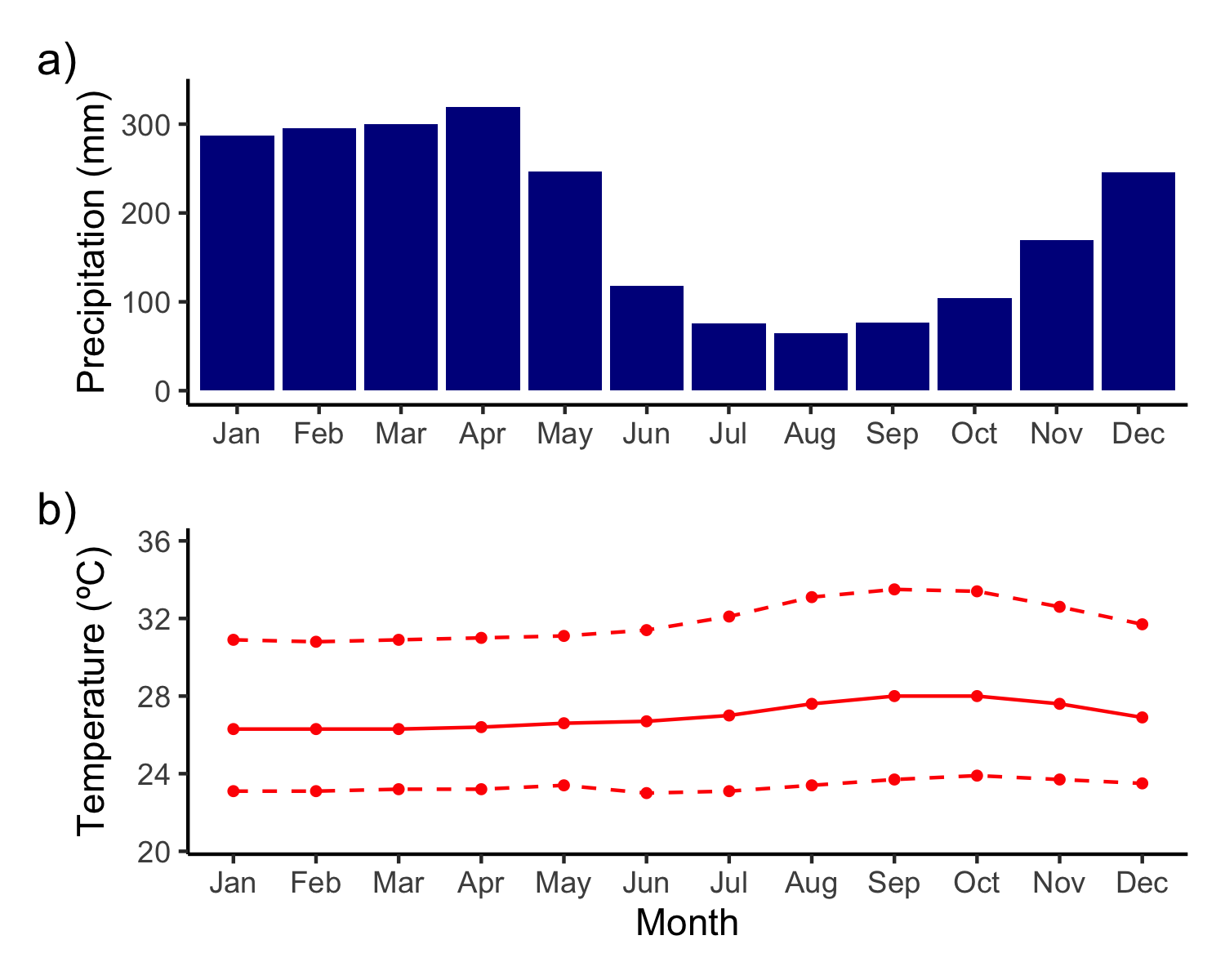


Figure 1: Weather normals for Manaus, Brazil (3º6’S, 60º1’W) for 1981–2010. Precipitation (a) shows a marked dry seasons from June through October. Temperature (b) varies less throughout the year. Mean monthly temperature is shown in the solid red line and monthly minimum and maximum temperatures are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

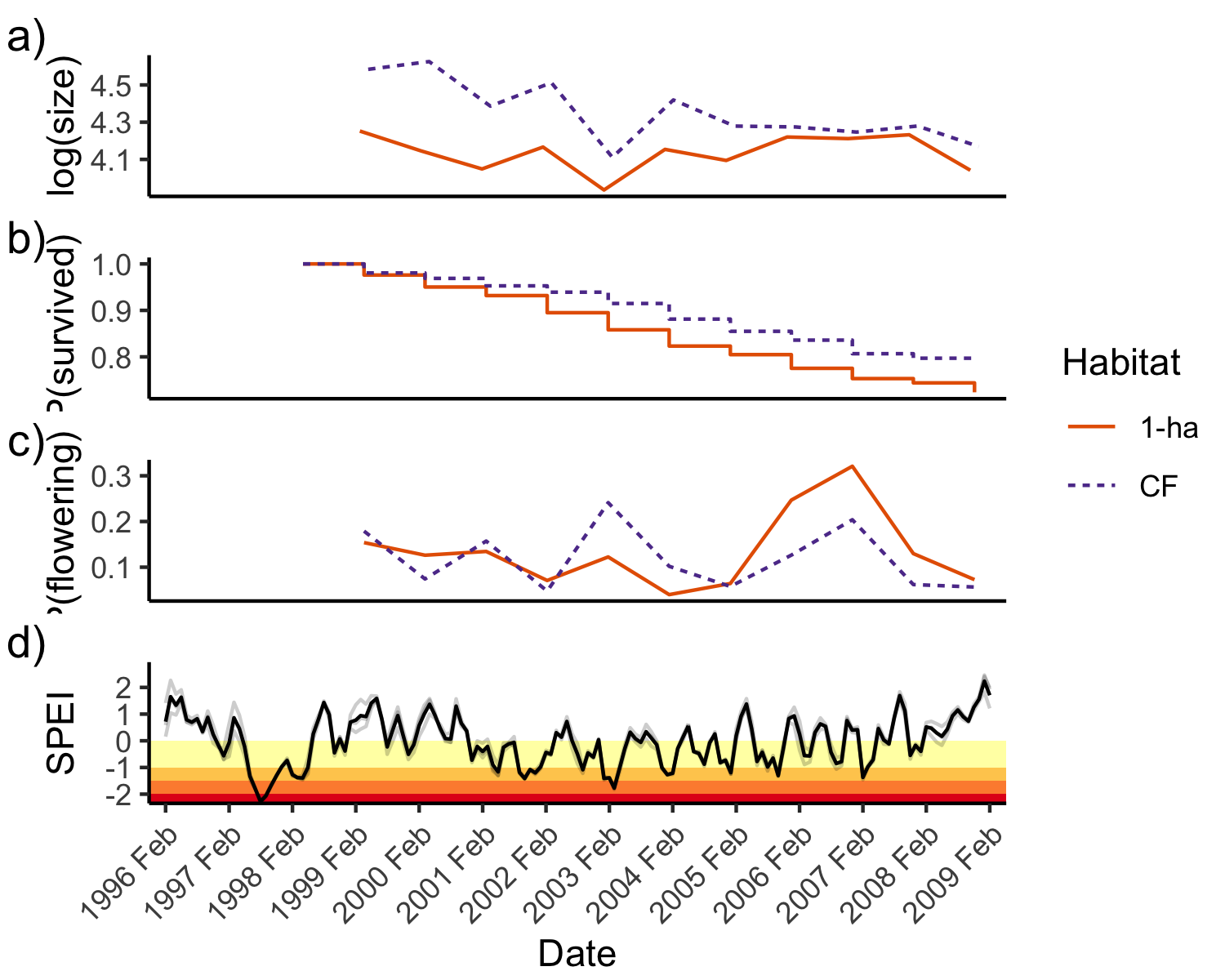


Figure 2: Timeseries of demographic parameters and drought ocurrence. Mean plant size ± standard deviation (a) shows that plants were smaller in fragments (red) than continuous forest (blue). (b) shows the survival curve for the 1998 cohort of plants in fragments and continuous forest. c) shows the proportion 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.

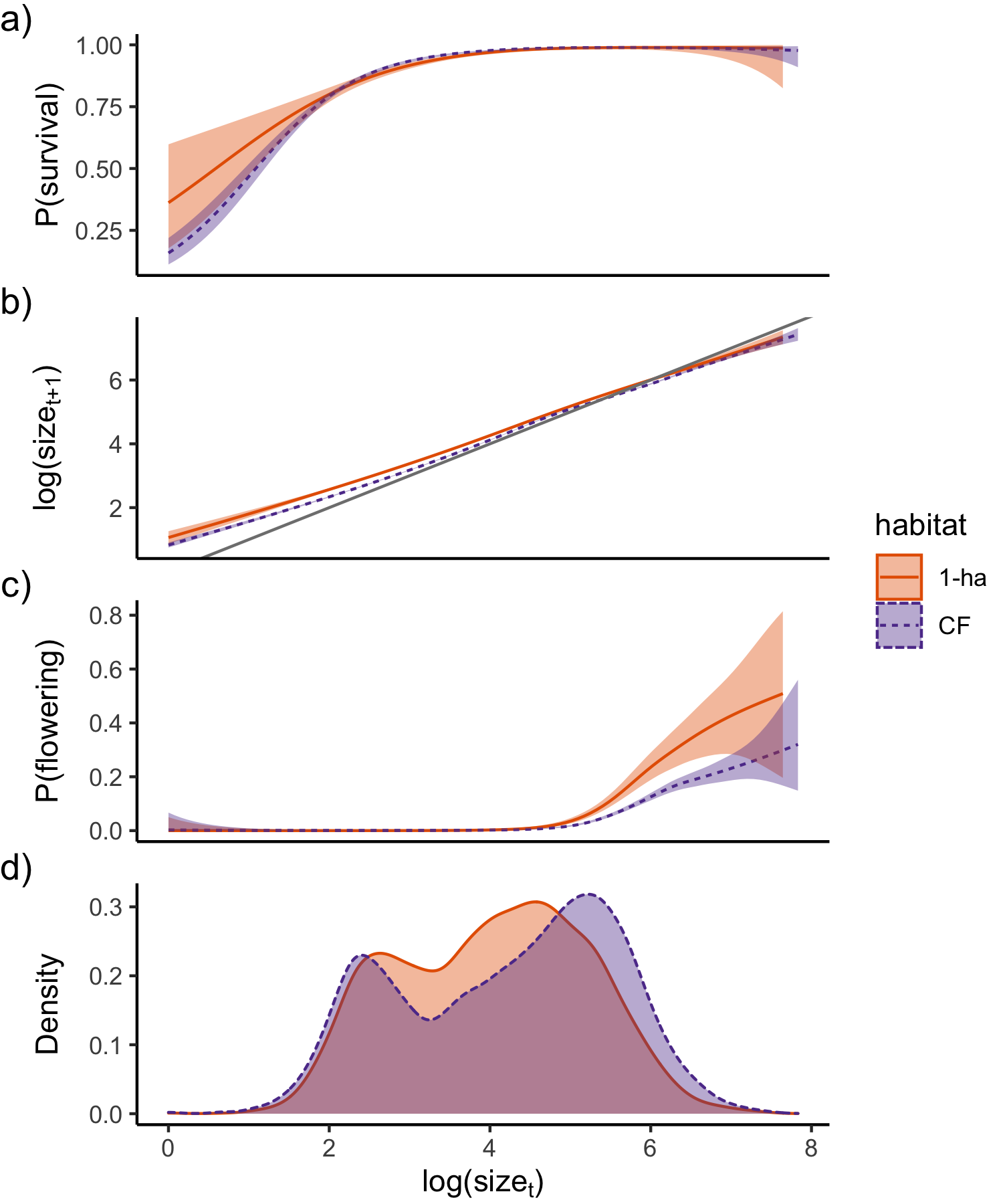


Figure 3: Smooth effect of plant size in the previous census on a) survival, b) log(size), and c) flowering probabiility, modeled by cubic regression splines. Panel d) shows the smoothed density of different plant sizes in the two habitat types. 95% confidence intervals are shown and include uncertainty 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.

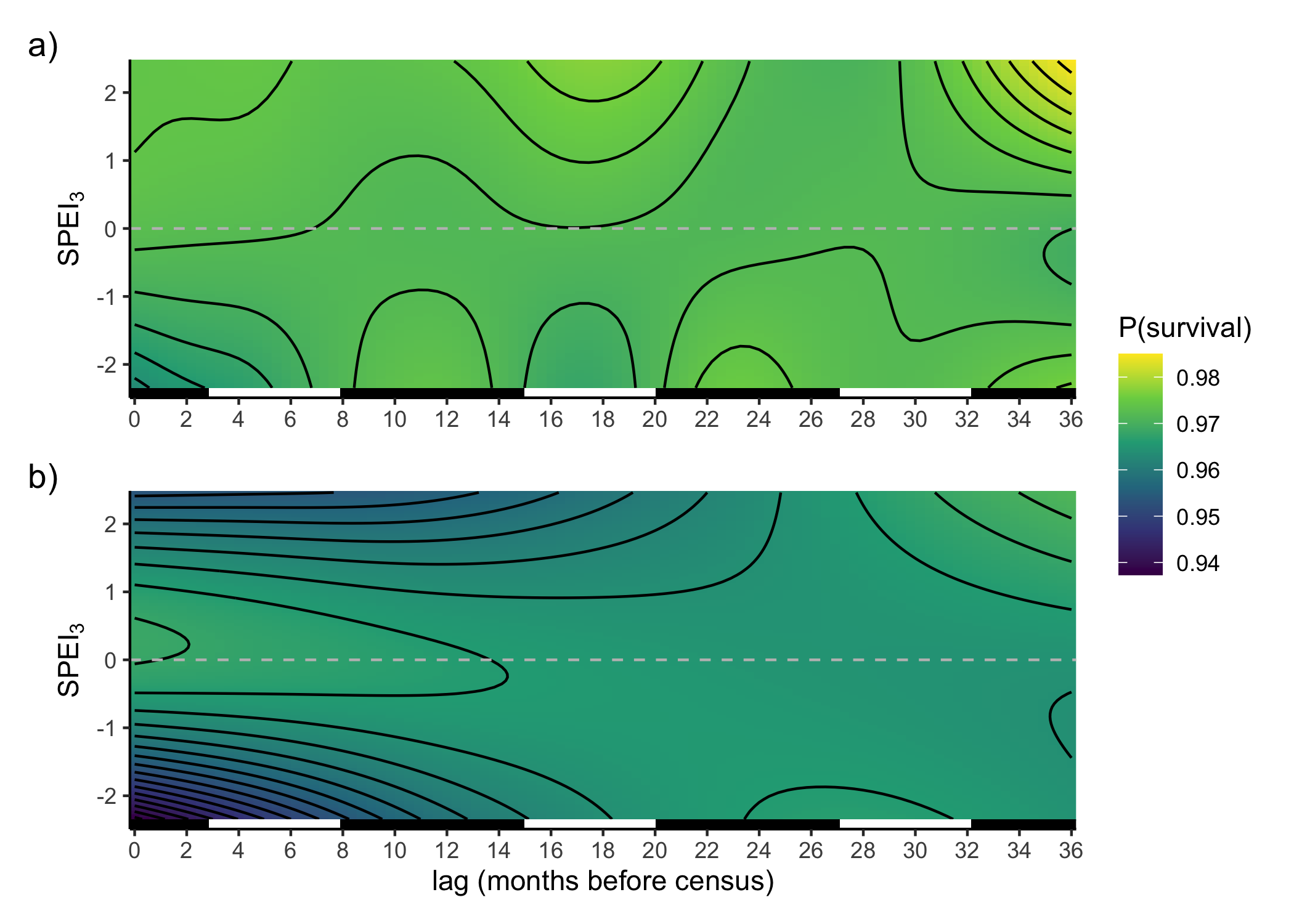


Figure 4: Smooth effect of lagged SPEI on survival in a) continuous forest and b) 1-ha fragments. Surface is modeled as a crossbasis function with cubic regression splines for each marginal basis. Model intercepts were added to fitted values of the crossbasis function and back-transformed to the response 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).

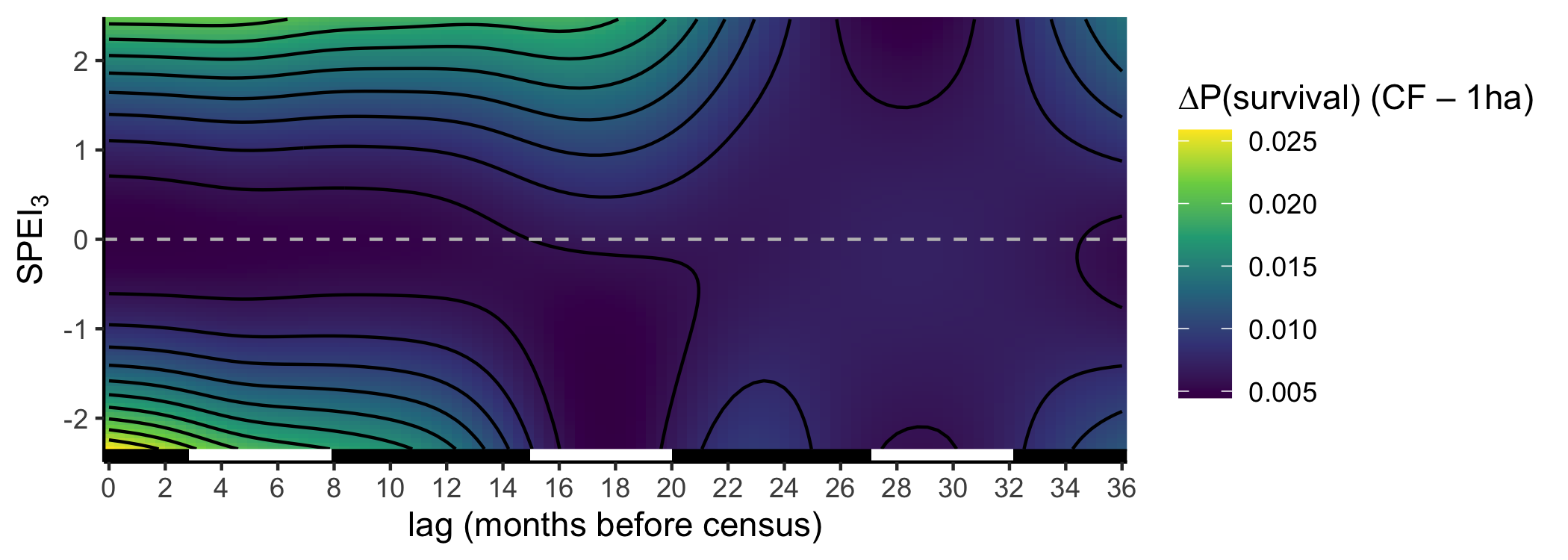


Figure 5: The difference between predicted effects of SPEI history on survival in continuous forest and 1-ha fragments.

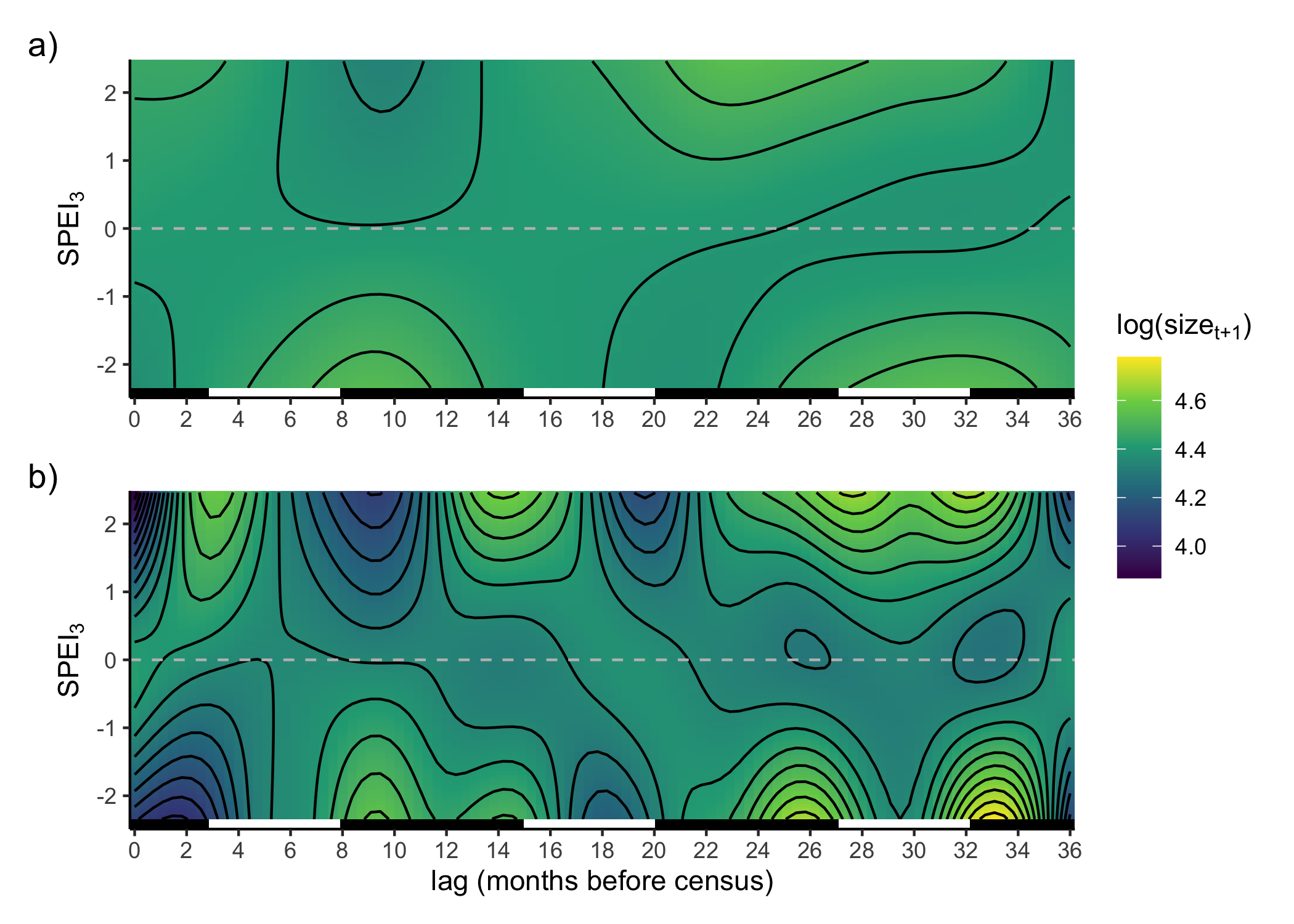


Figure 6: Smooth effect of lagged SPEI on plant growth for a) continuous forest and b) 1-ha fragments. Surface is modeled as a crossbasis function with cubic regression splines for each marginal basis. Model intercepts were added to fitted values of the crossbasis function. Contour lines correspond to 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).

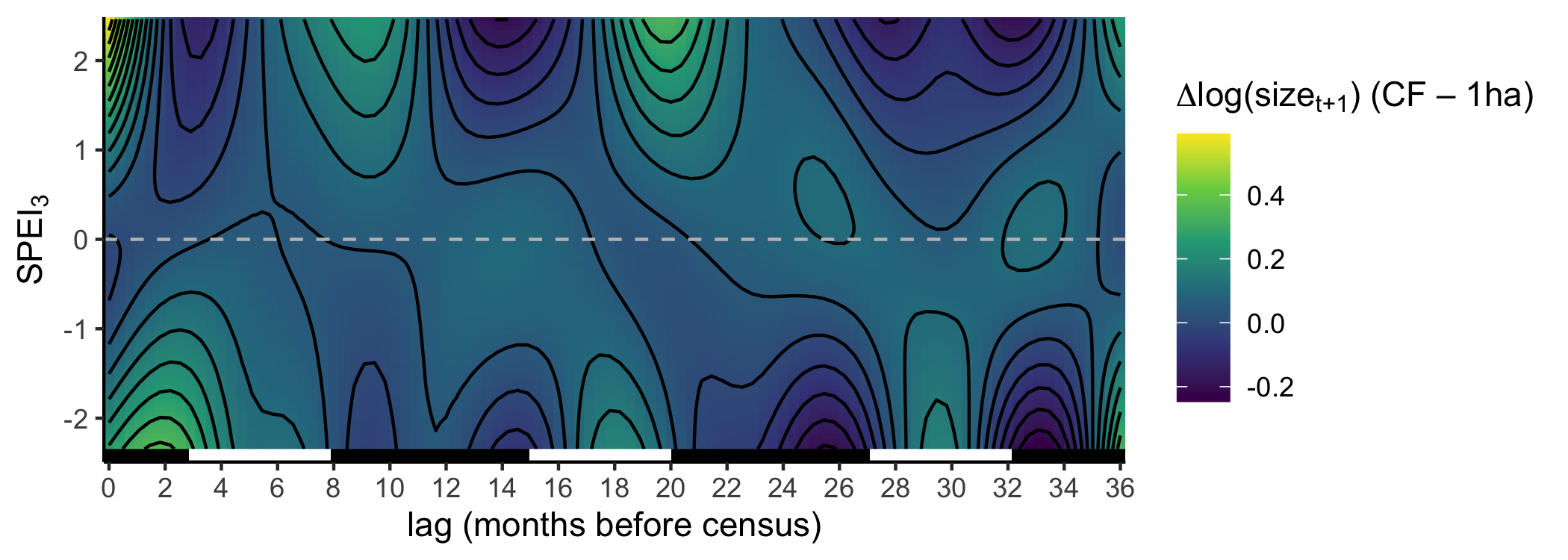


Figure 7: The difference between predicted effects of SPEI history on plant size in continuous forest and 1-ha fragments.

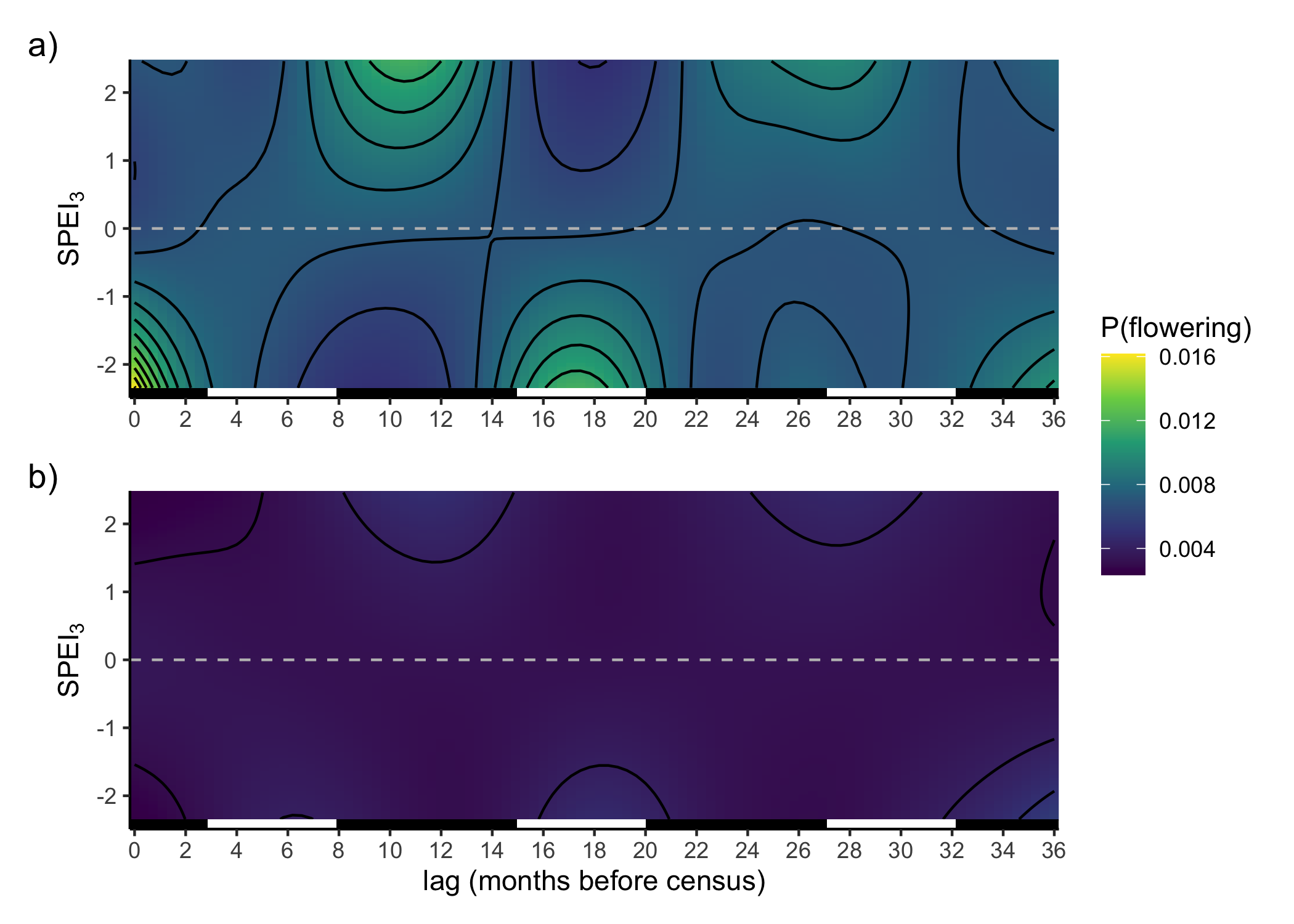


Figure 8: Smooth effect of lagged SPEI on flowering probability. Surface is modeled as a crossbasis function with cubic regression splines for each marginal basis. Model intercepts were added to fitted values of the crossbasis function and back-transformed to the response scale. Contour lines correspond 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).

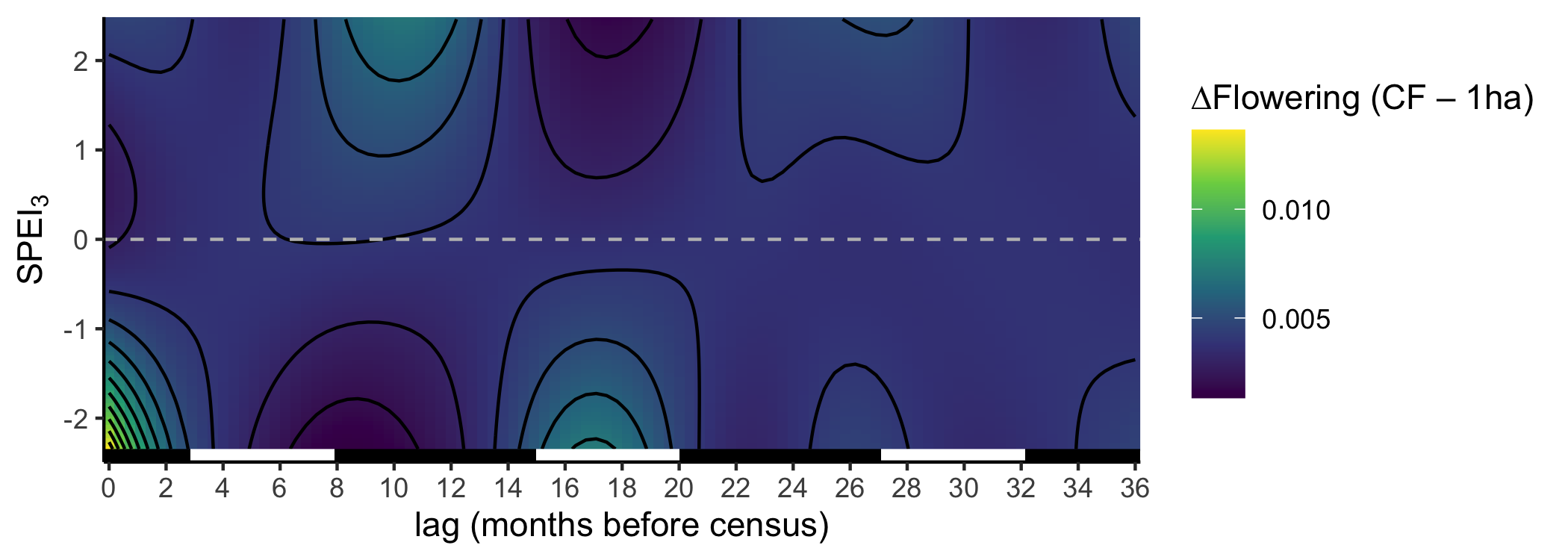


Figure 9: The difference between predicted effects of SPEI history on flowering probability in continuous forest and 1-ha fragments.

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* 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).
* While the alteration of microclimate near forest edges is one of the fundamental results to have emerged from the study of fragmented landscapes (Didham & Lawton, 1999; Ewers & Banks-Leite, 2013), little is known regarding how variable it is. It We hypothesize that the microclimate in continuous forest plots is more stable than that in 1 ha fragments, and that this stability will demographically buffers populations in forest interiors (Bruna et al., 2002).
* There can be cascading effects on other species (hispine beetles that depend on Heliconia flowers/fruits, hummingbirds and seed dispersers ( Stiles (1975)
* eg. gene flow and genetic structure among and between plots already shaped by fragmentation ( Côrtes et al. (2013), there can also be drought effects eg Sifres et al. (2007))
* (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

# Citations / information could allocate to appropriate paragraphs

* 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
* 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 & 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 & Shiels (2020)
* Mulkey & Wright (1996) and Bonal et al. (2016) will have goods stuff; haven’t looked them over yet
* S. J. Wright & 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…
* (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.
* Leitold et al. (2018) increased canopy turnover during drought. Similar increase in continuous and (large) fragments. Increase in turnover more variable in fragments. Coarse woody debris increased 62% during drought.

### Colophon

This report was generated on 2021-05-06 10:19:03 using the following computational environment and dependencies:

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#> P vctrs 0.3.8 2021-04-29 [?] CRAN (R 4.0.2)   
#> P withr 2.4.2 2021-04-18 [?] CRAN (R 4.0.2)   
#> P xfun 0.22 2021-03-11 [?] CRAN (R 4.0.2)   
#> P xml2 1.3.2 2020-04-23 [?] CRAN (R 4.0.2)   
#> P yaml 2.2.1 2020-02-01 [?] CRAN (R 4.0.2)   
#>   
#> [1] /Users/scottericr/Documents/HeliconiaDemography/renv/library/R-4.0/x86\_64-apple-darwin17.0  
#> [2] /private/var/folders/b\_/2vfnxxls5vs401tmhhb3wqdh0000gp/T/RtmpZPHSJj/renv-system-library  
#> [3] /private/var/folders/b\_/2vfnxxls5vs401tmhhb3wqdh0000gp/T/Rtmpl8Ippa/renv-system-library  
#>   
#> P ── Loaded and on-disk path mismatch.

The current Git commit details are:

#> Local: eric-edits /Users/scottericr/Documents/HeliconiaDemography  
#> Remote: eric-edits @ origin (https://github.com/BrunaLab/HeliconiaDemography.git)  
#> Head: [f15879c] 2021-05-06: add "sensu" back