

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

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16

17 Abstract

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

40 fragments compared to continuous forest. The complex delayed effects of climate and
41 habitat fragmentation on *H. acuminata* vital rates points to the importance of long-term
42 demography experiments in understanding the effects of anthropogenic change on plant
43 populations.

44

45 Introduction

46 The expansion of agriculture and other human activities is a primary driver of
47 deforestation in the tropics (Alroy, 2017; Haddad et al., 2015). It also results in landscapes
48 where the remaining forest can be highly fragmented, with patches of different sizes
49 embedded in a matrix of often contrasting habitat (Bianchi & Haig, 2013; Taubert et al.,
50 2018). This fragmentation is associated with myriad ecological changes, including the local
51 and regional extinction of plant species (da Silva & Tabarelli, 2000; Laurance et al., 2006).
52 Although the demographic mechanisms responsible these extinctions are poorly
53 understood (Bruna et al., 2009), it is often hypothesized that the dramatically altered
54 environmental conditions in tropical forest fragments (Arroyo-Rodríguez et al., 2017;
55 Didham & Lawton, 1999; Ewers & Banks-Leite, 2013) drive declines in plant reproduction,
56 recruitment, or survivorship (Bruna, 1999; Laurance et al., 1998; Zartman et al., 2015).
57 Despite the prevalence of this hypothesis (Betts et al., 2019; Didham & Lawton, 1999;
58 Laurance et al., 2001), efforts to link population-level demographic responses with altered
59 environmental conditions in fragments remains scarce.

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

68 of climatic tolerance (Feeley et al., 2012), and recent results suggest increases in the
69 frequency and severity of extreme precipitation events reduce survival and reproduction
70 (Esteban et al., 2021; Gaoue et al., 2019). This sensitivity to climatic fluctuations, coupled
71 with evidence that plant growth and survivorship are lower in fragments (Bruna et al.,
72 2002; Laurance et al., 1998; Zartman et al., 2015), has led to speculation that plants in
73 forest fragments will be especially susceptible to climate change (Laurance et al., 2001;
74 Opdam & Wascher, 2004; Selwood et al., 2015).

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

90 exception (Anderegg et al., 2015; Evers et al., 2021; Kannenberg et al., 2020; Schwalm et al.,
91 2017).

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

105 **Methods**

106 **Study site**

107 The Biological Dynamics of Forest Fragments Project (BDFFP) is located ~70 km north of
108 Manaus, Brazil (2°30' S, 60°W). In addition to large areas of continuous forest, the BDFFP
109 has forest fragment reserves isolated from 1980–1984 by felling the trees surrounding the
110 area chosen for isolation and, in most cases, burning the downed trees once they dried
111 (Bierregaard et al., 1992). In subsequent decades the vegetation regenerating around

112 fragments has been periodically cleared to ensure fragment isolation (Bierregaard et al.,
113 2001).

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

120 **Focal species**

121 *Heliconia acuminata* (LC Rich.) (Heliconiaceae) is a perennial monocot distributed
122 throughout Central Amazonia (Kress, 1990) and is the most abundant understory herb at
123 the BDFFP (Ribeiro et al., 2010). While many *Heliconia* species grow in large patches in
124 treefall gaps and other disturbed areas, others, such as *H. acuminata*, are found at lower
125 densities in the darker and cooler forest understory (Rundel et al., 2020). These species
126 produce fewer inflorescences and are pollinated by traplining rather than territorial
127 hummingbirds (Bruna et al., 2004; Stouffer & Bierregaard, 1996). In our sites *H. acuminata*
128 is pollinated by *Phaeothornis superciliosus* and *P. bourcierii* (Bruna et al., 2004). Plants begin
129 flowering at the start of the rainy season; reproductive plants have $\bar{x} = 1.1$ flowering
130 shoots (range = 1–7), each of which has an inflorescence with 20–25 flowers (Bruna &
131 Kress, 2002). Fruits mature April-May, have 1–3 seeds per fruit ($\bar{x} = 2$), and are eaten by a
132 thrush and several species of manakin (Uriarte et al., 2011). Dispersed seeds germinate
133 approximately 6 months after dispersal at the onset of the subsequent rainy season, with

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

136 **Demographic data collection**

137 This study uses data collected in four 1-ha fragment reserves and six continuous forest
138 sites. In 1997–1998 we established a 5000 m² plots (50 × 100m) in each of these sites in
139 which we marked and measured all *Heliconia acuminata*; plots in 1-ha fragments were on
140 one randomly selected half of the fragment, while plots in continuous forest were located
141 500–4000 m from the borders of secondary and mature forest. The distance between plots
142 ranged from 500 m–41 km. Our dataset comprised 4,083 plants in continuous forest and
143 1,010 plants in forest fragments. Plots in CF had on average 2.7-fold more plants than plots
144 in 1-ha fragments (CF = 681 ± 493 SD; 1-ha = 253 ± 30 SD).

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

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

157 **Climate data**

158 Data on precipitation and potential evapotranspiration in our sites were obtained from a
159 published gridded dataset ($0.25^{\circ} \times 0.25^{\circ}$ resolution) built using data from 3,625 ground-
160 based weather stations across Brazil (Xavier et al., 2016). We used these data to calculate
161 the standardized precipitation evapotranspiration index (SPEI) (Vicente-Serrano et al.,
162 2010). SPEI is a proxy for meteorological drought that integrates precipitation and
163 evapotranspiration anomalies over a specified time scale. Positive SPEI values for a given
164 month indicate conditions wetter than the historical average for that month, while negative
165 values of SPEI indicate droughts with intensity categorized as mild (0 to -1), moderate (-1
166 to -1.5), severe (-1.5 to -2), or extreme (< -2) (McKee et al., 1993). SPEI can be calculated to
167 represent different temporal scales of drought; we used 3-month SPEI because—given its
168 shallow roots and rhizome—*H. acuminata* relies primarily on soil moisture rather than
169 deeper water sources that can persist for longer timescales (Vicente-Serrano et al., 2010).
170 Note that 3-month SPEI is still monthly data—each month’s SPEI value simply takes into
171 account precipitation and evapotranspiration of the previous three months. SPEI
172 calculations were made using the SPEI package (Beguería & Vicente-Serrano, 2017). The
173 timing of drought events based on these SPEI calculations is consistent with that resulting
174 from SPEI calculated with other data sources, though the magnitude of drought sometimes
175 differed (Figure S2; Table S1).

176 **Statistical Modeling of Vital Rates**

177 To assess the effects of drought history on plant vital rates we used Distributed Lag Non-
178 linear Models (DLNMs, Gasparrini et al., 2017). DLNMs capture how potentially delayed
179 effects of predictor variables (e.g. SPEI) affect an outcome (e.g. growth) well beyond the
180 event period. They do so by fitting a bi-dimensional predictor-lag-response association
181 spline, referred to as a crossbasis function. This models a non-linear relationship between
182 predictor and response (e.g. between SPEI and vital rates) and allows the shape of that
183 relationship to vary smoothly over lag time. Using the `dlnm` package (Gasparrini, 2011; R
184 Core Team, 2020), we created crossbasis functions with possible lags from 0–36 months.
185 We chose 36 months as a maximum lag because prior transplant experiments with *H.*
186 *acuminata* showed they typically recover from transplant shock in less than 36 months
187 (Bruna et al., 2002) so this is a reasonable upper bound for lagged effects of drought.
188 The crossbasis function was fit to the data in the context of a generalized additive model
189 (GAM) with restricted maximum likelihood using the `mgcv` package (Wood, 2017). The
190 general form of the vital rate (y) models was as follows:

$$191 \quad \begin{aligned} g[E(y_i)] &= \alpha_j + s_1(z_i) + s_2(d_{i,t}, \dots, d_{i,t-36}) + \beta x_i \\ \alpha_j &\sim N(\mu_{\alpha_j}, \sigma_{\alpha_j}^2), \text{ for plot } j \end{aligned} \quad (1)$$

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

197
$$s_2(d_{i,t}, \dots, d_{i,t-24}) = \sum_{l=l_0}^L f \cdot w(d_{i,t-l}, l) \quad (2)$$

198 where the crossbasis function, $f \cdot w(d, l)$, is composed of two marginal basis functions: the
199 standard predictor-response function $f(d)$, and the additional lag-response function $w(l)$.
200 These marginal functions are combined as a tensor product smooth such that the shape of
201 one marginal function varies smoothly along the other dimension (see chapter 5 of Wood
202 (2017) and Gasparrini et al. (2017) for more detail). Penalized cubic regression splines
203 were used for both marginal bases of the crossbasis function, with 35 knots for the lag
204 dimension (i.e. number of lagged SPEI values for each observation with 36 months as a
205 maximum lag) and 3 knots for the drought response dimension to restrict the shape of the
206 fitted response to drought to bimodal when most complex. Because of penalization, the
207 number of knots is generally not important as long it is large enough to allow the smooth to
208 represent the 'true' relationship (Wood, 2017). Estimated degrees of freedom (edf)
209 represent the 'true' complexity of the smooth after penalization with edf = 1 being
210 equivalent to a straight line and larger numbers representing more complex curves.

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

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

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

231 The `d1nm` package does not currently allow the modeling of interaction terms, which means
232 we could not assess the interaction of habitat type and lagged effects. We therefore fit
233 separate models for plants in fragments and in continuous forest to allow the shape of the
234 crossbasis function to differ between habitats. Significant main effects of habitat type were
235 assessed by looking for overlap in the 84% confidence intervals of model intercepts; the
236 84% CIs of two samples drawn from the same population overlap about 95% of the time
237 (Payton et al., 2003).

238 All analyses were conducted in R version 4.0.2 (2020-06-22) (R Core Team, 2020).

239 Results

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

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

249 *Survival*: Across all plots, the proportion of plants surviving was lowest in the 2003–2004
250 transition year ($P_{\text{surv}} = 0.92$). This coincided with droughts in both the 2003 and 2004
251 rainy seasons (Figure 1b,d) and was preceded by a drop in average plant size in the 2002–
252 2003 transition year (Figure 1a). The lowest survival for 1-ha fragment plots ($P_{\text{surv}} = 0.93$)
253 was for the 2005–2006 transition year, which encompassed a moderate drought in October
254 2005 and and wetter than average conditions ($\text{SPEI} > 0.5$) in December 2005 and January
255 2006 (Figure 1b,d). The lowest survival for continuous forest was in 2004 ($P_{\text{surv}} = 0.91$).
256 When summarizing across years, plots, and plant sizes, the survival probability of *Heliconia*
257 *acuminata* was similarly high in both continuous forest and fragments ($P_{\text{surv}} = 0.95$; Figure
258 1b; the overlapping 85% CI of model intercepts indicate no significant difference).
259 However, survival in both habitats was size dependent ($p < 0.001$ for the effect of log-
260 transformed plant size in year t on survival in year $t+1$ in both habitats). The survival

261 probability of large plants approached 1 in both habitat types (Figure 3b), but the smallest
262 plants had higher survival in 1-ha fragments.

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

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

277 *Flowering:* The overall proportion of plants that flowered was very low. While it was almost
278 40% higher in continuous forest than 1-ha fragments (0.05 ± 0.21 vs. 0.04 ± 0.19 ,
279 respectively), this difference was not statistically significant (84% CIs of model intercepts
280 overlapped). The observed disparity was largely due to the fact that flowering is also size-
281 dependent ($p < 0.001$ in both habitats), with the probability of flowering increasing
282 dramatically once plants reached the threshold size of about 148 (i.e., $\log(\text{size}) > 5$ in

283 Figure 3c). Despite the flowering probability of large plants being greater in fragments than
284 continuous forest, populations in fragments had proportionately fewer plants above the
285 reproductive size threshold (Figure 3d). The most striking difference between habitat
286 types coincided with a severe drought in 2003, when the percentage of flowering
287 reproductive-sized plants was 28% in continuous forest vs. only 13.6% in 1-ha fragments
288 (Figure 1c).

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

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

294 *Survival:* For 1-ha fragments, there was a significant effect on survival of SPEI in the
295 preceding 13 months. The highest survival was near SPEI of 0, with mortality increasing as
296 conditions became either drier or wetter (i.e., as SPEI values became increasingly negative
297 or positive, respectively; Figure 4b). Wet conditions in the preceding 23 months (i.e., SPEI >
298 1) also had a significant negative effect on survival in fragments (Figure 4b). In contrast,
299 the effect of recent SPEI in continuous forest was weaker, with only the 6 months preceding
300 a census having a significant effect on survival (Figure 4a). These short-term effects of SPEI
301 on survival were also unidirectional—the probability of survival declined, albeit only
302 slightly, with increasingly negative values of SPEI (i.e., as droughts became more severe;
303 Figure 4a). In contrast, the most pronounced negative effects of SPEI on the survival of
304 plants in continuous forest were at lag times of 15–20 months and 32–36 months. Drought

305 15–20 months prior to a census (i.e. two dry seasons prior to a census) was significantly
306 associated with reduced survival, while high precipitation (i.e., SPEI > 1) was significantly
307 associated with higher survival. Finally, plants in both habitat types showed an increase in
308 survival probability with very high SPEI values (i.e., extremely high precipitation) at a lag
309 time of 32–36 months. It should be noted, however, that only the first year of census data
310 (1999) met these conditions. We compared the effects of SPEI history in continuous forest
311 and fragments by subtracting the fitted values in Figure 4b from Figure 4a to produce
312 Figure 4c. This shows that in average conditions (SPEI = 0), there is little difference in
313 survival probability between continuous forest and forest fragments (Figure 4c). However,
314 under extreme conditions, survival probability is higher in continuous forest by up to
315 0.025.

316 *Growth:* The effects of drought history on trends in plant size were generally similar for
317 continuous forest and fragments. However, the crossbasis function for 1-ha fragments
318 indicated more complex responses in some situations (edf = 17.8 for 1-ha fragments; edf =
319 13.0 for continuous forest; see also Figure 5). For example, under average conditions (i.e.,
320 SPEI = 0), growth is similar or slightly higher in continuous forest over all lag periods
321 (Figure 5c). However, the growth of plants in fragments is reduced when the current wet
322 season is unusually wet (i.e., SPEI > 2), and as a result the plants in continuous forests will
323 be larger by up to $\log(\text{size}) = 0.57$. In contrast, drought at lags of 8–11 months (i.e., the end
324 of the preceding year's wet season) led to increased growth in both habitats, with a more
325 pronounced response in 1-ha fragments.

326 *Flowering:* Overall, the the probability of flowering was higher in continuous forest than in
327 1-ha fragments for all values of SPEI (Figure 6), although this difference was not significant
328 (84% CIs of intercepts overlap). The responses in 1-ha fragments were also more muted as
329 indicated by the shape of the crossbasis function (1-ha edf = 8.3, continuous forest edf =
330 10.6) (Figure 6). This led to some important inter-habitat differences in plant responses to
331 prior droughts. In continuous forests, recent drought (i.e., at lag = 0–2 with SPEI < -1),
332 drought two dry seasons prior (lags 15–20) and in the wet season 34–36 months prior all
333 increased the probability of flowering. However, drought at the end of the rainy season one
334 year prior (lags 7–13) significantly reduced flowering probability (Figure 6a). In fragments,
335 recent drought had no significant effect on flowering probability and only drought at two
336 dry seasons prior (lags 16–20) and in the wet season 33–36 months prior increased
337 flowering probability (Figure 6b). The effects of drought on flowering probability were
338 strong in continuous forest compared to 1 ha fragments (Figure 6c). We found no evidence
339 for a cost of reproduction: in both forest and fragments, plants that had flowered in the
340 previous year were on average more likely to be larger (CF: $p = 0.048$; 1-ha: $p = 0.030$)
341 and flower again (CF: $p < 0.001$; 1-ha: $p = 0.004$). The random effect of plant ID on
342 flowering probability was also significant (CF: $p < 0.001$; 1-ha: $p = 0.003$), indicating
343 significant individual-level variation in flowering probability.

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

347 **Discussion**

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

358 **Temporal variation in demographic responses to forest fragmentation**

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

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

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

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

391 **Delayed effects of climate on demographic vital rates**

392 Climate anomalies are known to have immediate effects on the growth, survival, or
393 reproduction of plants (Esteban et al., 2021; Wright & Calderon, 2006), including *Heliconia*
394 (Stiles, 1975; Westerband et al., 2017) and other tropical herbs (Wright, 1992). These
395 effects can be complex or even contradictory—mild droughts can increase the growth rates
396 of tropical trees and seedling survival, perhaps due to reductions in cloud cover and
397 concomitant increases in solar radiation (Alfaro-Sánchez et al., 2017; Condit et al., 2004;
398 Huete et al., 2006; Jones et al., 2014; Uriarte et al., 2018), but in severe drought years
399 growth can be extremely low and mortality can be sharply elevated (Connell & Green,
400 2000; Edwards & Krockenberger, 2006; Engelbrecht et al., 2002). There is also evidence
401 that the effects can persist for multiple years (Phillips et al., 2010), such as a boom in
402 drought-year fruit production followed by severe post-drought “famine” (Pau et al., 2013;
403 Wright et al., 1999).

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

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

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

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

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

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

452 Third, it may be that the delayed demographic effects we observed are indirectly mediated
453 by the effect of SPEI on other species rather than the direct effects on individual physiology
454 (Evers et al., 2021). For example, tropical trees may not die until three or more years after a
455 drought (Criley & Lekawatana, 1994). When they finally do, the resulting leaf drop (Janssen
456 et al., 2021) and treefalls allow for light penetration to the forest understory (Canham et al.,
457 1990; Leitold et al., 2018), triggering a boom in the growth and flowering of understory

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

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

477 **Conclusions & Future Directions**

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

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

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

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

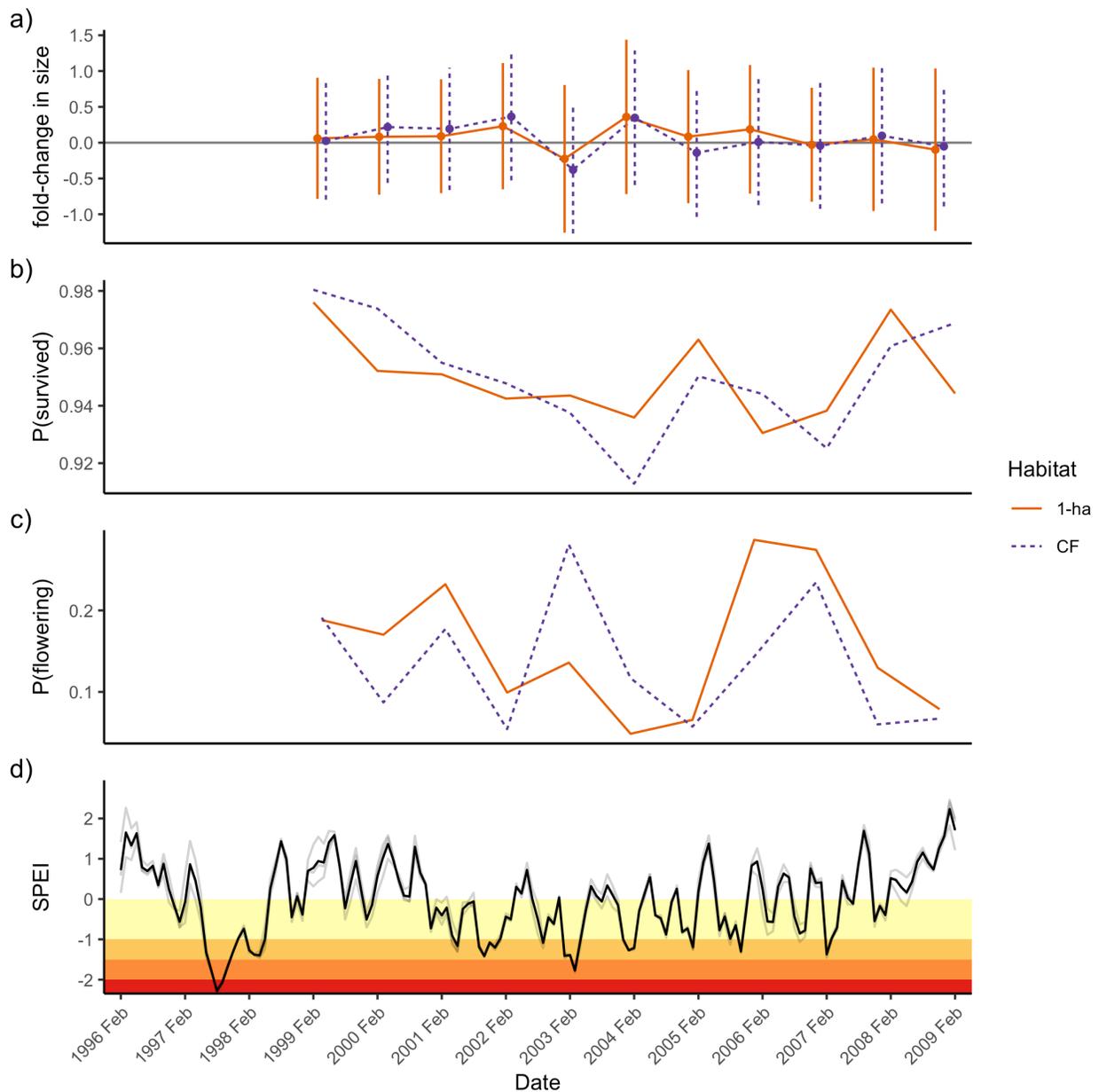
508 **Acknowledgments**

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514 Technical Series.

515 **Data Availability Statement**

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

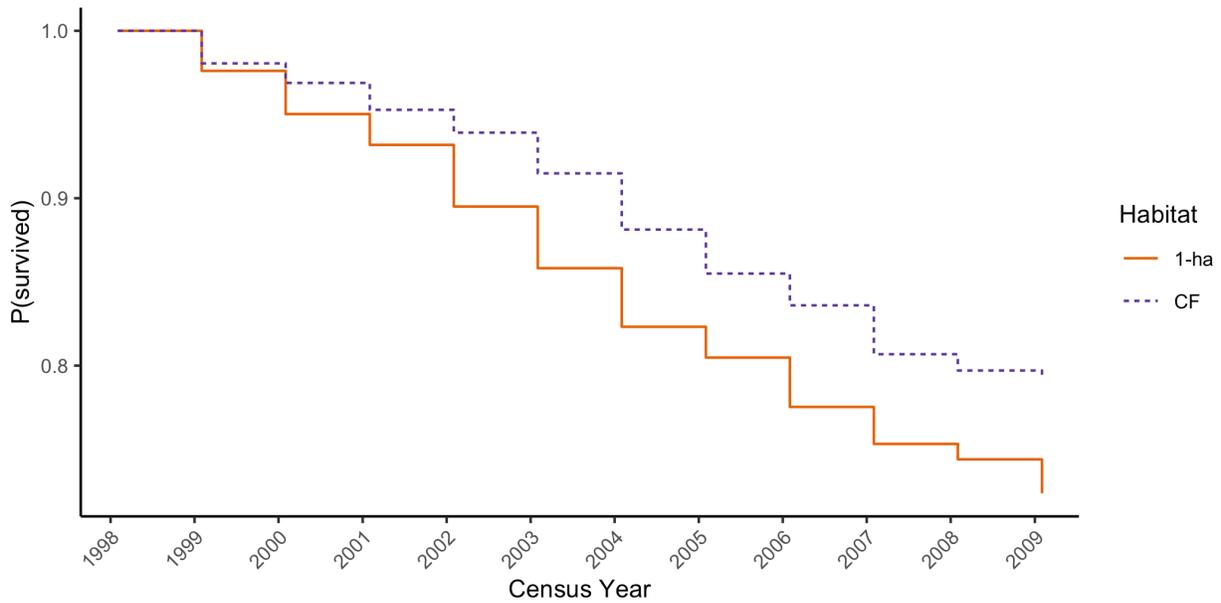
518 **Figures**



519

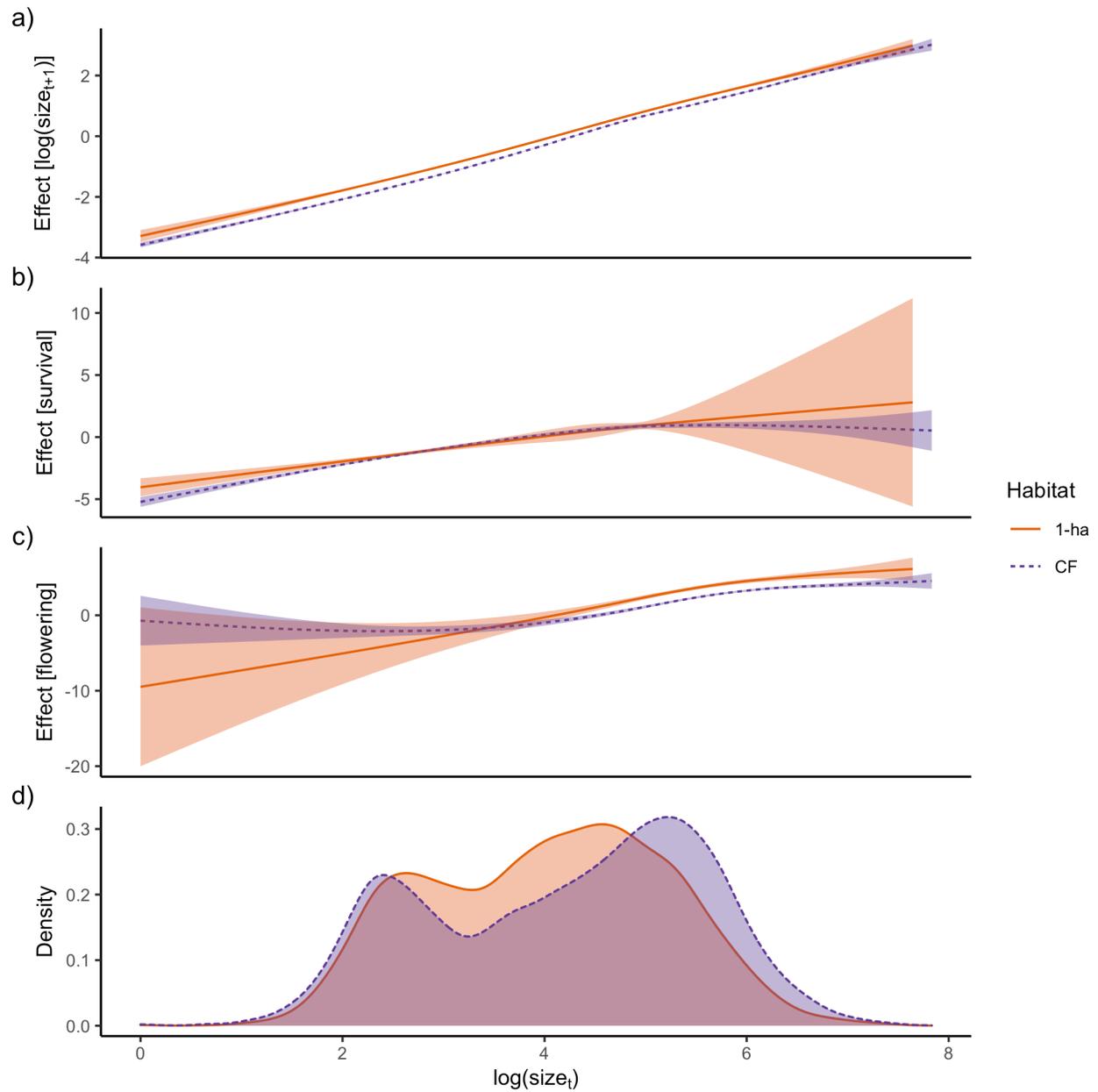
520 *Figure 1: (a-c) Time series of H. acuminata vital rates in 1-ha fragments (solid orange lines)*
 521 *and continuous forest (dashed blue lines) and (d) drought occurrence in the study region. (a)*
 522 *Mean fold-change in plant plant size ($\log_2(\text{size}_{t+1} / \text{size}_t)$) varies by year and habitat. On*
 523 *average, plants grew in most years with the notable exception in 2003, in which on average*
 524 *plants regressed in size in both habitats (i.e., fold-change < 0). Error bars represent the*
 525 *standard deviation. (b) The proportion of plants surviving from one transition year to the next*
 526 *varied from 0.98 (CF in 1998-1999) to 0.91 (CF in 2003-2004). (c) The proportion of H.*
 527 *acuminata above the size threshold for reproduction that flowered each year is on average*
 528 *low but variable. The size threshold is determined by the upper 90th percentile size of*
 529 *flowering plants across all years. (d) Monthly 3-month SPEI for our study region. Gray lines*

530 represent values from different grid cells encompassing BDFFP; the dark line represents the
531 site mean. Colored stripes represent drought intensity: yellow = mild, orange = moderate, dark
532 orange = severe, red = extreme.



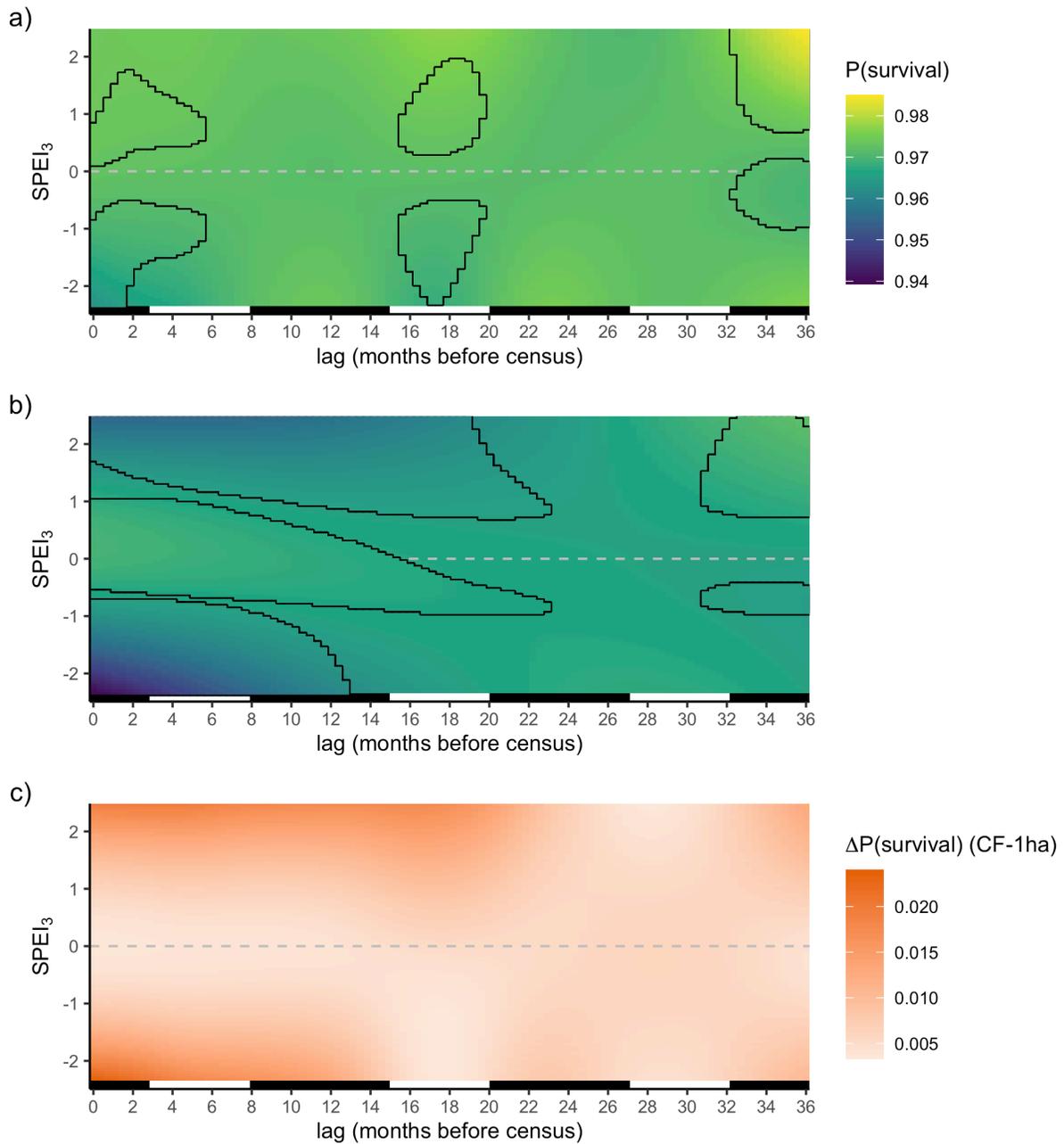
533

534 *Figure 2: Survivorship curve for plants marked in the 1998 survey year; these plants comprise*
535 *49% of those in the complete demographic dataset. The percentage of these plants that were*
536 *still alive ten years later was 79.7% (1629/2055) in continuous forest vs. 72.4% (393/543) in*
537 *1-ha fragments.*



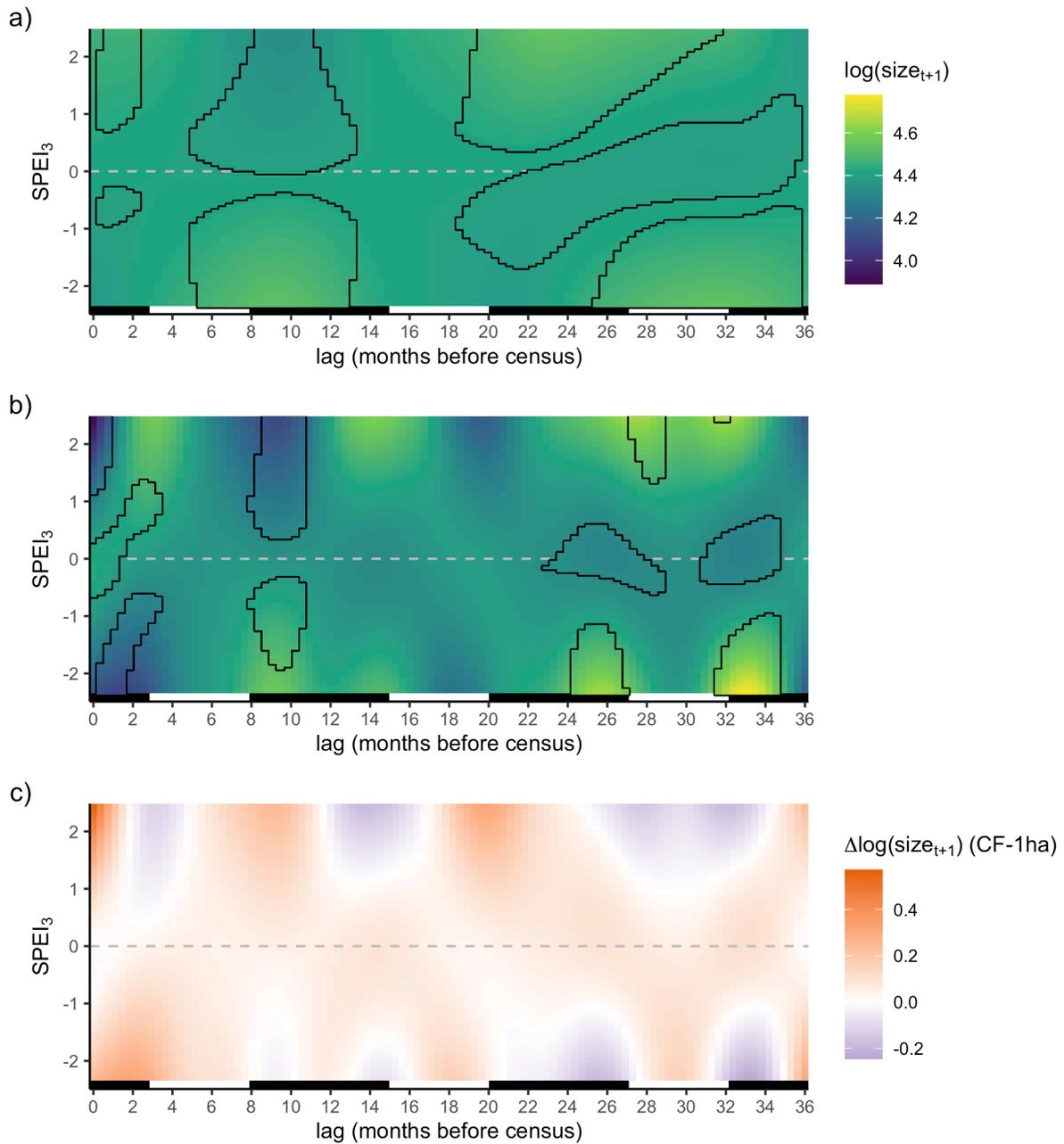
538

539 *Figure 3: Smooth effect from models of plant size in the previous census on (a) survival, (b)*
 540 *log(size), and (c) flowering probability; these values correspond to the additive term $s_1(z_i)$ in*
 541 *eq. 1. The bands depicting the 95% confidence interval include uncertainty in the intercept*
 542 *and uncertainty due to smoothness selection; the smooths for 1-ha fragments and continuous*
 543 *forest are fit in separate models. (d) Plant size distribution by habitat type (solid line = 1-ha*
 544 *fragments, dashed line = Continuous Forest).*



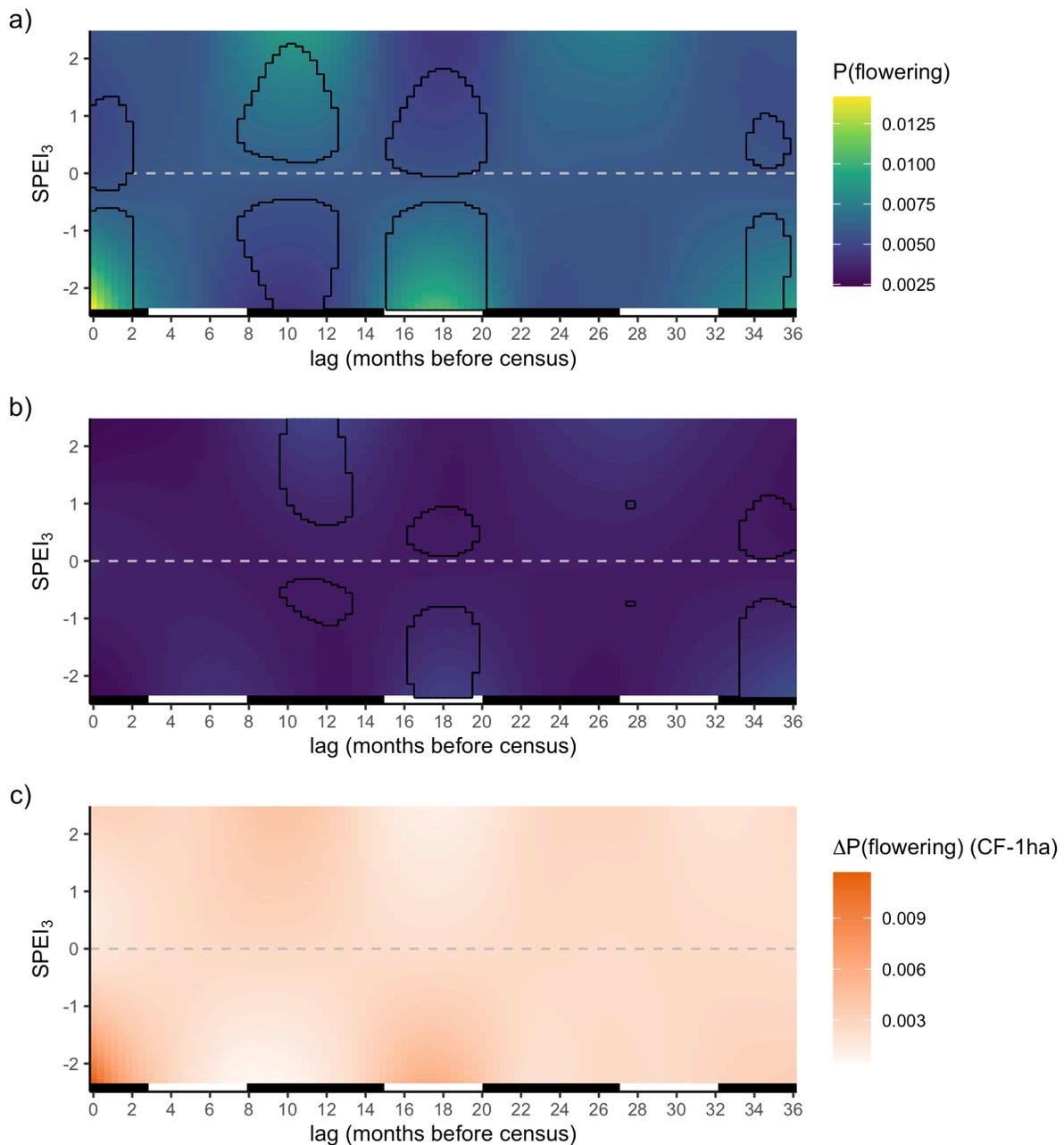
545

546 *Figure 4: Smooth effect of lagged SPEI on $H. acuminata$ survival in (a) continuous forest, (b)*
 547 *1-ha fragments, (c) and the difference between the two. Outlines show regions where the*
 548 *effect of SPEI is significant, defined as those where the 95% confidence interval around the*
 549 *response does not overlap the intercept. The bar on the bottom of each panel indicates the wet*
 550 *seasons (black, November–May) and dry seasons (white, June–October). Surface is modeled as*
 551 *a crossbasis function with cubic regression splines for each marginal basis. Model intercepts*
 552 *were added to fitted values of the crossbasis function and back-transformed to the response*
 553 *scale.*



554

555 *Figure 5: Smooth effect of lagged SPEI on $H. acuminata$ growth in (a) continuous forest, (b) 1-*
 556 *ha fragments, (c) and the difference between the two. Outlines show regions where the effect*
 557 *of SPEI is significant, defined as those where the 95% confidence interval around the response*
 558 *does not overlap the intercept. The bar on the bottom of each panel indicates the wet seasons*
 559 *(black, November–May) and dry seasons (white, June–October).*



560

561 *Figure 6: Smooth effect of lagged SPEI on $H. acuminata$ flowering probability in (a)*
 562 *continuous forest, (b) 1-ha fragments, (c) and the difference between the two. Outlines show*
 563 *regions where the effect of SPEI is significant, defined as those where the 95% confidence*
 564 *interval around the response does not overlap the intercept. The bar on the bottom of each*
 565 *panel indicates the wet seasons (black, November–May) and dry seasons (white, June–*
 566 *October). Surface is modeled as a crossbasis function with cubic regression splines for each*
 567 *marginal basis. Model intercepts were added to fitted values of the crossbasis function and*
 568 *back-transformed to the response scale.*

569 **References**

- 570 Aguirre, B. A., Hsieh, B., Watson, S. J., & Wright, A. J. (2021). The experimental manipulation
571 of atmospheric drought: Teasing out the role of microclimate in biodiversity experiments.
572 *Journal of Ecology*, 109(5), 1986–1999. [https://doi.org/https://doi.org/10.1111/1365-](https://doi.org/10.1111/1365-2745.13595)
573 [2745.13595](https://doi.org/10.1111/1365-2745.13595)
- 574 Alfaro-Sánchez, R., Muller-Landau, H. C., Wright, S. J., & Camarero, J. J. (2017). Growth and
575 reproduction respond differently to climate in three Neotropical tree species. *Oecologia*,
576 184(2), 531–541. <https://doi.org/10.1007/s00442-017-3879-3>
- 577 Alroy, J. (2017). Effects of habitat disturbance on tropical forest biodiversity. *Proceedings of*
578 *the National Academy of Sciences*, 114(23), 6056–6061.
579 <https://doi.org/10.1073/pnas.1611855114>
- 580 Anderegg, W. R. L., Schwalm, C., Biondi, F., Camarero, J. J., Koch, G., Litvak, M., Ogle, K., Shaw,
581 J. D., Shevliakova, E., Williams, A. P., Wolf, A., Ziaco, E., & Pacala, S. (2015). Pervasive
582 drought legacies in forest ecosystems and their implications for carbon cycle models.
583 *Science*, 349(6247), 528–532. <https://doi.org/10.1126/science.aab1833>
- 584 Arroyo-Rodríguez, V., Saldaña-Vázquez, R. A., Fahrig, L., & Santos, B. A. (2017). Does forest
585 fragmentation cause an increase in forest temperature? *Ecological Research*, 32(1), 81–88.
586 <https://doi.org/10.1007/s11284-016-1411-6>
- 587 Beguería, S., & Vicente-Serrano, S. M. (2017). *SPEI: Calculation of the standardised*
588 *precipitation-evapotranspiration index* [Manual].
- 589 Betts, M. G., Wolf, C., Pfeifer, M., Banks-Leite, C., Arroyo-Rodríguez, V., Ribeiro, D. B., Barlow,
590 J., Eigenbrod, F., Faria, D., Fletcher, R. J., Hadley, A. S., Hawes, J. E., Holt, R. D., Klingbeil, B.,
591 Kormann, U., Lens, L., Levi, T., Medina-Rangel, G. F., Melles, S. L., ... Ewers, R. M. (2019).
592 Extinction filters mediate the global effects of habitat fragmentation on animals. *Science*,
593 366(6470), 1236–1239. <https://doi.org/10.1126/science.aax9387>
- 594 Bianchi, C. A., & Haig, S. M. (2013). Deforestation Trends of Tropical Dry Forests in Central
595 Brazil. *Biotropica*, 45(3), 395–400. [https://doi.org/https://doi.org/10.1111/btp.12010](https://doi.org/10.1111/btp.12010)
- 596 Bierregaard, R. O., Gascon, C., Lovejoy, T. E., & Mesquita, R. (Eds.). (2001). *Lessons from*
597 *Amazonia: The ecology and conservation of a fragmented forest*. Yale University Press.
- 598 Bierregaard, R. O., Lovejoy, T. E., Kapos, V., & Hutchings, R. W. (1992). The biological
599 dynamics of tropical rainforest fragments. *BioScience*, 42(11), 859–866.
600 <https://doi.org/10.2307/1312085>
- 601 Broadbent, E. N., Asner, G. P., Keller, M., Knapp, D. E., Oliveira, P. J. C., & Silva, J. N. (2008).
602 Forest fragmentation and edge effects from deforestation and selective logging in the
603 Brazilian Amazon. *Biological Conservation*, 141, 1745–1757.
604 <https://doi.org/10.1016/j.biocon.2008.04.024>

- 605 Brodie, J., Post, E., & Laurance, W. F. (2012). Climate change and tropical biodiversity: A
606 new focus. *Trends in Ecology & Evolution*, 27(3), 145–150.
607 <https://doi.org/10.1016/j.tree.2011.09.008>
- 608 Brooks, M. E., Kristensen, K., Darrigo, M. R., Rubim, P., Uriarte, M., Bruna, E. M., & Bolker, B.
609 M. (2019). Statistical modeling of patterns in annual reproductive rates. *Ecology*, 100(7).
610 <https://doi.org/10.1002/ecy.2706>
- 611 Bruna, E. M. (1999). Seed germination in rainforest fragments. *Nature*, 402(6758), 139.
612 <https://doi.org/10.1038/45963>
- 613 Bruna, E. M. (2002). Effects of forest fragmentation on *Heliconia acuminata* seedling
614 recruitment in central Amazonia. *Oecologia*, 132(2), 235–243.
615 <https://doi.org/10.1007/s00442-002-0956-y>
- 616 Bruna, E. M. (2003). Are plant populations in fragmented habitats recruitment limited?
617 Tests with an Amazonian herb. *Ecology*, 84(4), 932–947. [https://doi.org/10.1890/0012-9658\(2003\)084\[0932:APIFJH\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[0932:APIFJH]2.0.CO;2)
- 618
- 619 Bruna, E. M., Fiske, I. J., & Trager, M. D. (2009). Habitat fragmentation and plant
620 populations: Is what we know demographically irrelevant? *Journal of Vegetation Science*,
621 20(3), 569–576. <https://doi.org/10.1111/j.1654-1103.2009.01060.x>
- 622 Bruna, E. M., & Kress, W. J. (2002). Habitat fragmentation and the demographic structure of
623 an Amazonian understory herb (*Heliconia acuminata*). *Conservation Biology*, 16(5), 1256–
624 1266. <https://doi.org/10.1046/j.1523-1739.2002.99494.x>
- 625 Bruna, E. M., Kress, W. J., Marques, F., & Silva, O. F. da. (2004). *Heliconia acuminata*
626 reproductive success is independent of local floral density. *Acta Amazonica*, 34(3), 467–
627 471. <https://doi.org/10.1590/S0044-59672004000300012>
- 628 Bruna, E. M., Nardy, O., Strauss, S. Y., & Harrison, S. (2002). Experimental assessment of
629 *Heliconia acuminata* growth in a fragmented Amazonian landscape. *Journal of Ecology*,
630 90(4), 639–649. <https://doi.org/10.1046/j.1365-2745.2002.00707.x>
- 631 Bruna, E. M., & Oli, M. K. (2005). Demographic Effects of Habitat Fragmentation on a
632 Tropical Herb: Life-Table Response Experiments. *Ecology*, 86(7), 1816–1824.
633 <https://doi.org/10.1890/04-1716>
- 634 Bruna, E. M., & Ribeiro, M. B. N. (2005). The compensatory responses of an understory herb
635 to experimental damage are habitat-dependent. *American Journal of Botany*, 92(12), 2101–
636 2210. <https://doi.org/10.3732/ajb.92.12.2101>
- 637 Canham, C. D., Denslow, J. S., Platt, W. J., Runkle, J. R., Spies, T. A., & White, P. S. (1990). Light
638 regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests.
639 *Canadian Journal of Forest Research*, 20(5), 620–631. <https://doi.org/10.1139/x90-084>
- 640 Condit, R., Aguilar, S., Hernandez, A., Perez, R., Lao, S., Angehr, G., Hubbell, S. P., & Foster, R.
641 B. (2004). Tropical forest dynamics across a rainfall gradient and the impact of an El Niño

- 642 dry season. *Journal of Tropical Ecology*, 20(01), 51–72.
643 <https://doi.org/10.1017/S0266467403001081>
- 644 Connell, J. H., & Green, P. T. (2000). Seedling dynamics over thirty-two years in a tropical
645 rain forest tree. *Ecology*, 81(2), 568–584.
- 646 Côrtes, M. C., Uriarte, M., Lemes, M. R., Gribel, R., Kress, W. J., Smouse, P. E., & Bruna, E. M.
647 (2013). Low plant density enhances gene dispersal in the Amazonian understory herb
648 *Heliconia Acuminata*. *Molecular Ecology*, 22(22), 5716–5729.
649 <https://doi.org/10.1111/mec.12495>
- 650 Criley, R., & Lekawatana, S. (1994). Year around production with high yields may be a
651 possibility for *Heliconia chartacea*. *Acta Horticulturae*, 397, 95–102.
652 <https://doi.org/10.17660/ActaHortic.1995.397.7>
- 653 Crone, E. E., Menges, E. S., Ellis, M. M., Bell, T., Bierzychudek, P., Ehrlen, J., Kaye, T. N., Knight,
654 T. M., Lesica, P., Morris, W. F., Oostermeijer, G., Quintana-Ascencio, P. F., Stanley, A., Ticktin,
655 T., Valverde, T., & Williams, J. L. (2011). How do plant ecologists use matrix population
656 models? *Ecology Letters*, 14(1), 1–8.
- 657 da Silva, J. M. C., & Tabarelli, M. (2000). Tree species impoverishment and the future flora of
658 the Atlantic forest of northeast Brazil. *Nature*, 404(6773), 72–74.
659 <https://doi.org/10.1038/35003563>
- 660 Didham, R. K., Kapos, V., & Ewers, R. M. (2012). Rethinking the conceptual foundations of
661 habitat fragmentation research. *Oikos*, 121(2), 161–170. <https://doi.org/10.1111/j.1600-0706.2011.20273.x>
- 662
- 663 Didham, R. K., & Lawton, J. H. (1999). Edge structure determines the magnitude of changes
664 in microclimate and vegetation structure in tropical forest fragments. *Biotropica*, 31(1), 17–
665 30. <https://doi.org/10.1111/j.1744-7429.1999.tb00113.x>
- 666 Doak, D. F., & Morris, W. F. (2010). Demographic compensation and tipping points in
667 climate-induced range shifts. *Nature*, 467(7318), 959–962.
- 668 Driscoll, D. A., Banks, S. C., Barton, P. S., Lindenmayer, D. B., & Smith, A. L. (2013).
669 Conceptual domain of the matrix in fragmented landscapes. *Trends in Ecology & Evolution*,
670 28(10), 605–613. <https://doi.org/10.1016/j.tree.2013.06.010>
- 671 Duffy, P. B., Brando, P., Asner, G. P., & Field, C. B. (2015). Projections of future
672 meteorological drought and wet periods in the Amazon. *Proceedings of the National
673 Academy of Sciences*, 112(43), 13172–13177. <https://doi.org/10.1073/pnas.1421010112>
- 674 Edwards, W., & Krockenberger, A. (2006). Seedling mortality due to drought and fire
675 associated with the 2002 El Niño event in a tropical rain forest in north-east Queensland,
676 Australia. *Biotropica*, 38(1), 16–26. <https://doi.org/10.1111/j.1744-7429.2006.00098.x>

677 Ehrlén, J., Morris, W. F., von Euler, T., & Dahlgren, J. P. (2016). Advancing environmentally
678 explicit structured population models of plants. *Journal of Ecology*, *104*(2), 292–305.
679 <https://doi.org/10.1111/1365-2745.12523>

680 Engelbrecht, B. M. J., Wright, S. J., & De Steven, D. (2002). Survival and ecophysiology of tree
681 seedlings during El Niño drought in a tropical moist forest in Panama. *Journal of Tropical
682 Ecology*, *18*, 569–579.

683 Esquivel-Muelbert, A., Baker, T. R., Dexter, K. G., Lewis, S. L., Brienen, R. J. W., Feldpausch, T.
684 R., Lloyd, J., Monteagudo-Mendoza, A., Arroyo, L., Álvarez-Dávila, E., Higuchi, N., Marimon, B.
685 S., Marimon-Junior, B. H., Silveira, M., Vilanova, E., Gloor, E., Malhi, Y., Chave, J., Barlow, J., ...
686 Phillips, O. L. (2019). Compositional response of Amazon forests to climate change. *Global
687 Change Biology*, *25*(1), 39–56. <https://doi.org/10.1111/gcb.14413>

688 Esteban, E. J. L., Castilho, C. V., Melgaço, K. L., & Costa, F. R. C. (2021). The other side of
689 droughts: Wet extremes and topography as buffers of negative drought effects in an
690 Amazonian forest. *New Phytologist*, *229*(4), 1995–2006.
691 <https://doi.org/10.1111/nph.17005>

692 Evers, S. M., Knight, T. M., Inouye, D. W., Miller, T. E. X., Salguero-Gómez, R., Iler, A. M., &
693 Compagnoni, A. (2021). Lagged and dormant season climate better predict plant vital rates
694 than climate during the growing season. *Global Change Biology*, *n/a*(n/a).
695 <https://doi.org/10.1111/gcb.15519>

696 Ewers, R. M., & Banks-Leite, C. (2013). Fragmentation impairs the microclimate buffering
697 effect of tropical forests. *PLoS ONE*, *8*(3), e58093.
698 <https://doi.org/10.1371/journal.pone.0058093>

699 Feeley, K. J., Malhi, Y., Zelazowski, P., & Silman, M. R. (2012). The relative importance of
700 deforestation, precipitation change, and temperature sensitivity in determining the future
701 distributions and diversity of Amazonian plant species. *Global Change Biology*, *18*(8), 2636–
702 2647. <https://doi.org/10.1111/j.1365-2486.2012.02719.x>

703 Gagnon, P. R., Bruna, E. M., Rubim, P., Darrigo, M. R., Littell, R. C., Uriarte, M., & Kress, W. J.
704 (2011). Growth of an understory herb is chronically reduced in Amazonian forest
705 fragments. *Biological Conservation*, *144*(2), 830–835.
706 <https://doi.org/10.1016/j.biocon.2010.11.015>

707 Gaoue, O. G., Horvitz, C. C., Steiner, U. K., & Tuljapurkar, S. (2019). Climate, rather than
708 human disturbance, is the main driver of age-specific mortality trajectories in a tropical
709 tree. *Ecological Modelling*, *400*, 34–40. <https://doi.org/10.1016/j.ecolmodel.2019.03.007>

710 Gasparrini, A. (2011). Distributed lag linear and non-linear models in R: The package dlnm.
711 *Journal of Statistical Software*, *43*(8), 1–20. <https://doi.org/10.18637/jss.v043.i08>

712 Gasparrini, A., Scheipl, F., Armstrong, B., & Kenward, M. G. (2017). A penalized framework
713 for distributed lag non-linear models: Penalized DLNMs. *Biometrics*, *73*(3), 938–948.
714 <https://doi.org/10.1111/biom.12645>

- 715 Gentry, A. H., & Dodson, C. (1987). Contribution of nontrees to species richness of a tropical
716 rain forest. *Biotropica*, 19(2), 149–156. <https://doi.org/10.2307/2388737>
- 717 González-M, R., Posada, J. M., Carmona, C. P., Garzón, F., Salinas, V., Idárraga-Piedrahita, Á.,
718 Pizano, C., Avella, A., López-Camacho, R., Norden, N., Nieto, J., Medina, S. P., Rodríguez-M, G.
719 M., Franke-Ante, R., Torres, A. M., Jurado, R., Cuadros, H., Castaño-Naranjo, A., García, H., &
720 Salgado-Negret, B. (2020). Diverging functional strategies but high sensitivity to an
721 extreme drought in tropical dry forests. *Ecology Letters*, n/a(n/a).
722 <https://doi.org/10.1111/ele.13659>
- 723 Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., Lovejoy, T. E.,
724 Sexton, J. O., Austin, M. P., Collins, C. D., Cook, W. M., Damschen, E. I., Ewers, R. M., Foster, B.
725 L., Jenkins, C. N., King, A. J., Laurance, W. F., Levey, D. J., Margules, C. R., ... Townshend, J. R.
726 (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science*
727 *Advances*, 1(2), e1500052. <https://doi.org/10.1126/sciadv.1500052>
- 728 Holyoak, M., & Heath, S. K. (2016). The integration of climate change, spatial dynamics, and
729 habitat fragmentation: A conceptual overview. *Integrative Zoology*, 11(1), 40–59.
730 <https://doi.org/https://doi.org/10.1111/1749-4877.12167>
- 731 Horvitz, C. C., & Schemske, D. W. (1988). Demographic cost of reproduction in a Neotropical
732 herb: An experimental field study. *Ecology*, 69(6), 1741–1745.
733 <https://doi.org/10.2307/1941152>
- 734 Huete, A. R., Didan, K., Shimabukuro, Y. E., Ratana, P., Saleska, S. R., Hutyrá, L. R., Yang, W.,
735 Nemani, R. R., & Myneni, R. (2006). Amazon rainforests green-up with sunlight in dry
736 season. *Geophysical Research Letters*, 33(6). <https://doi.org/10.1029/2005GL025583>
- 737 Janssen, T., van der Velde, Y., Hofhansl, F., Luyssaert, S., Naudts, K., Driessen, B., Fleischer,
738 K., & Dolman, H. (2021). Drought effects on leaf fall, leaf flushing and stem growth in
739 Neotropical forest; reconciling remote sensing data and field observations. *Biogeosciences*
740 *Discussions*, 1–41. <https://doi.org/https://doi.org/10.5194/bg-2021-30>
- 741 Jones, M. O., Kimball, J. S., & Nemani, R. R. (2014). Asynchronous Amazon forest canopy
742 phenology indicates adaptation to both water and light availability. *Environmental Research*
743 *Letters*, 9(12), 124021. <https://doi.org/10.1088/1748-9326/9/12/124021>
- 744 Kannenberg, S. A., Schwalm, C. R., & Anderegg, W. R. L. (2020). Ghosts of the past: How
745 drought legacy effects shape forest functioning and carbon cycling. *Ecology Letters*, 23(5),
746 891–901. <https://doi.org/10.1111/ele.13485>
- 747 Klimešová, J., Martínková, J., & Ottaviani, G. (2018). Belowground plant functional ecology:
748 Towards an integrated perspective. *Functional Ecology*, 32(9), 2115–2126.
749 <https://doi.org/10.1111/1365-2435.13145>
- 750 Kress, W. J. (1990). The diversity and distribution of *Heliconia* (Heliconiaceae) in Brazil.
751 *Acta Botanica Brasiliense*, 4(1), 159–167.

- 752 Laurance, W. F., Andrade, A. S., Magrath, A., Camargo, J. L. C., Campbell, M., Fearnside, P. M.,
753 Edwards, W., Valsko, J. J., Lovejoy, T. E., & Laurance, S. G. (2014). Apparent environmental
754 synergism drives the dynamics of Amazonian forest fragments. *Ecology*, 95(11), 3018–
755 3026. <https://doi.org/10.1890/14-0330.1>
- 756 Laurance, W. F., Ferreira, L. V., Rankin de Merona, J. M., & Laurance, S. G. (1998). Rain forest
757 fragmentation and the dynamics of Amazonian tree communities. *Ecology*, 79(6), 2032–
758 2040.
- 759 Laurance, W. F., Nascimento, H. E. M., Laurance, S. G., Andrade, A., Ribeiro, J. E. L. S., Giraldo,
760 J. P., Lovejoy, T. E., Condit, R., Chave, J., Harms, K. E., & D'Angelo, S. (2006). Rapid decay of
761 tree-community composition in Amazonian forest fragments. *Proceedings of the National
762 Academy of Sciences*, 103(50), 19010–19014. <https://doi.org/10.1073/pnas.0609048103>
- 763 Laurance, W. F., & Williamson, G. B. (2001). Positive feedbacks among forest fragmentation,
764 drought, and climate change in the Amazon. *Conservation Biology*, 15(6), 1529–1535.
765 <https://doi.org/10.1046/j.1523-1739.2001.01093.x>
- 766 Laurance, W. F., Williamson, G. B., Delamônica, P., Oliveira, A., Lovejoy, T. E., Gascon, C., &
767 Pohl, L. (2001). Effects of a strong drought on Amazonian forest fragments and edges.
768 *Journal of Tropical Ecology*, 17(6), 771–785.
- 769 Leitold, V., Morton, D. C., Longo, M., dos-Santos, M. N., Keller, M., & Scaranello, M. (2018). El
770 Niño drought increased canopy turnover in Amazon forests. *New Phytologist*, 219(3), 959–
771 971. <https://doi.org/10.1111/nph.15110>
- 772 Marengo, J. A., Nobre, C. A., Tomasella, J., Oyama, M. D., Sampaio de Oliveira, G., de Oliveira,
773 R., Camargo, H., Alves, L. M., & Brown, I. F. (2008). The drought of Amazonia in 2005.
774 *Journal of Climate*, 21(3), 495–516. <https://doi.org/10.1175/2007JCLI1600.1>
- 775 Markewitz, D., Devine, S., Davidson, E. A., Brando, P., & Nepstad, D. C. (2010). Soil moisture
776 depletion under simulated drought in the Amazon: impacts on deep root uptake. *New
777 Phytologist*, 187(3), 592–607. <https://doi.org/10.1111/j.1469-8137.2010.03391.x>
- 778 Marra, G., & Wood, S. N. (2011). Practical variable selection for generalized additive models.
779 *Computational Statistics & Data Analysis*, 55(7), 2372–2387.
780 <https://doi.org/10.1016/j.csda.2011.02.004>
- 781 McKee, T. B., Doesken, N. J., & Kleist, J. (1993, January). The relationship of drought
782 frequency and duration to time scales. *Eighth Conference on Applied Climatology*.
- 783 McPhaden, M. J. (1999). The child prodigy of 1997-98. *Nature*, 398(6728), 559–561.
784 <https://doi.org/10.1038/19193>
- 785 Molowny-Horas, R., Suarez, M. L., & Lloret, F. (2017). Changes in the natural dynamics of
786 *Nothofagus Dombeyi* forests: Population modeling with increasing drought frequencies.
787 *Ecosphere*, 8(3), e01708. <https://doi.org/10.1002/ecs2.1708>

- 788 Morris, W. F., & Doak, D. F. (2002). *Quantitative conservation biology: Theory and practice of*
789 *population viability analysis*. Sinauer.
- 790 Morris, W. F., Pfister, C. A., Tuljapurkar, S., Haridas, C. V., Boggs, C. L., Boyce, M. S., Bruna, E.
791 M., Church, D. R., Coulson, T., Doak, D. F., Forsyth, S., Gaillard, J.-M., Horvitz, C. C., Kalisz, S.,
792 Kendall, B. E., Knight, T. M., Lee, C. T., & Menges, E. S. (2008). Longevity can buffer plant and
793 animal populations against changing climatic variability. *Ecology*, *89*(1), 19–25.
794 <https://doi.org/10.1890/07-0774.1>
- 795 Mundim, F. M., & Bruna, E. M. (2016). Is there a temperate bias in our understanding of how
796 climate change will alter plant–herbivore interactions? A meta- analysis of experimental
797 studies. *American Naturalist*, *188*, S74–S89.
- 798 Nakazono, E. M., Bruna, E. M., & Mesquita, R. C. G. (2004). Experimental harvesting of the
799 non-timber forest product *Ischnosiphon polyphyllus* in central Amazonia. *Forest Ecology and*
800 *Management*, *190*(2-3), 219–225. <https://doi.org/10.1016/j.foreco.2003.10.013>
- 801 Nihad, K., Krishnakumar, V., & Sheela, V. L. (2018). Relationship between stress and
802 flowering in *Heliconia* (*Heliconia stricta*). *International Journal of Agriculture Sciences(IJAS)*,
803 *10*(3), 5137. <https://doi.org/10.9735/0975-3710.10.3.5137-5139>
- 804 Ogle, K., Barber, J. J., Barron-Gafford, G. A., Bentley, L. P., Young, J. M., Huxman, T. E., Loik, M.
805 E., & Tissue, D. T. (2015). Quantifying ecological memory in plant and ecosystem processes.
806 *Ecology Letters*, *18*(3), 221–235. <https://doi.org/10.1111/ele.12399>
- 807 Oliver, T. H., Marshall, H. H., Morecroft, M. D., Brereton, T., Prudhomme, C., & Huntingford, C.
808 (2015). Interacting effects of climate change and habitat fragmentation on drought-
809 sensitive butterflies. *Nature Climate Change*, *5*(10), 941–945.
810 <https://doi.org/10.1038/nclimate2746>
- 811 Opdam, P., & Wascher, D. (2004). Climate change meets habitat fragmentation: Linking
812 landscape and biogeographical scale levels in research and conservation. *Biological*
813 *Conservation*, *117*(3), 285–297.
- 814 Paniw, M., James, T. D., Ruth Archer, C., Römer, G., Levin, S., Compagnoni, A., Che-Castaldo, J.,
815 Bennett, J. M., Mooney, A., Childs, D. Z., Ozgul, A., Jones, O. R., Burns, J. H., Beckerman, A. P.,
816 Patwary, A., Sanchez-Gassen, N., Knight, T. M., & Salguero-Gómez, R. (2021). The myriad of
817 complex demographic responses of terrestrial mammals to climate change and gaps of
818 knowledge: A global analysis. *Journal of Animal Ecology*. [https://doi.org/10.1111/1365-](https://doi.org/10.1111/1365-2656.13467)
819 [2656.13467](https://doi.org/10.1111/1365-2656.13467)
- 820 Pau, S., Wolkovich, E. M., Cook, B. I., Nyctch, C. J., Regetz, J., Zimmerman, J. K., & Wright, S. J.
821 (2013). Clouds and temperature drive dynamic changes in tropical flower production.
822 *Nature Climate Change*, *3*(9), 838–842.
- 823 Payton, M. E., Greenstone, M. H., & Schenker, N. (2003). *Overlapping confidence intervals or*
824 *standard error intervals: What do they mean in terms of statistical significance?* *3*(34), 1–6.
825 <https://doi.org/10.1673/031.003.3401>

- 826 Phillips, O. L., van der Heijden, G., Lewis, S. L., López-González, G., Aragão, L. E. O. C., Lloyd, J.,
827 Malhi, Y., Monteagudo, A., Almeida, S., Dávila, E. A., Amaral, I., Andelman, S., Andrade, A.,
828 Arroyo, L., Aymard, G., Baker, T. R., Blanc, L., Bonal, D., de Oliveira, Á. C. A., ... Vilanova, E.
829 (2010). Drought–mortality relationships for tropical forests. *New Phytologist*, *187*(3), 631–
830 646. <https://doi.org/10.1111/j.1469-8137.2010.03359.x>
- 831 Pierre, J.-S., Hullé, M., Gauthier, J.-P., & Rispe, C. (2020). Critical windows: A method for
832 detecting lagged variables in ecological time series. *Ecological Informatics*, *61*, 101178.
833 <https://doi.org/10.1016/j.ecoinf.2020.101178>
- 834 Pumisitapon, P., Visser, R. G. F., & de Klerk, G.-J. (2012). Moderate abiotic stresses increase
835 rhizome growth and outgrowth of axillary buds in *Alstroemeria* cultured in vitro. *Plant Cell*,
836 *Tissue and Organ Culture (PCTOC)*, *110*(3), 395–400. [https://doi.org/10.1007/s11240-012-](https://doi.org/10.1007/s11240-012-0160-7)
837 [0160-7](https://doi.org/10.1007/s11240-012-0160-7)
- 838 R Core Team. (2020). *R: A language and environment for statistical computing*.
- 839 Rankin-de-Mérona, J. M., Prance, G. T., Hutchings, R. W., da Silva, M. F., Rodrigues, W. A., &
840 Uehling, M. E. (1992). Preliminary results of a large-scale tree inventory of upland rain
841 forest in the central Amazon. *Acta Amazonica*, *22*(4), 493–534.
842 <https://doi.org/10.1590/1809-43921992224534>
- 843 Ribeiro, M. B. N., Bruna, E. M., & Mantovani, W. (2010). Influence of post-clearing treatment
844 on the recovery of herbaceous plant communities in Amazonian secondary forests.
845 *Restoration Ecology*, *18*, 50–58.
- 846 Rundel, P. W., Cooley, A. M., Gerst, K. L., Riordan, E. C., Sharifi, M. R., Sun, J. W., & Tower, J. A.
847 (2020). Functional traits of broad-leaved monocot herbs in the understory and forest edges
848 of a Costa Rican rainforest. *PeerJ*, *8*, e9958. <https://doi.org/10.7717/peerj.9958>
- 849 Rundel, P. W., Sharifi, M. R., Gibson, A. C., & Esler, K. J. (1998). Structural and physiological
850 adaptation to light environments in Neotropical *Heliconia* (Heliconiaceae). *Journal of*
851 *Tropical Ecology*, *14*(6), 789–801. <https://doi.org/10.1017/S0266467498000571>
- 852 Salguero-Gómez, R., Jones, O. R., Archer, C. R., Buckley, Y. M., Che-Castaldo, J., Caswell, H.,
853 Hodgson, D., Scheuerlein, A., Conde, D. A., Brinks, E., Buhr, H., Farack, C., Gottschalk, F.,
854 Hartmann, A., Henning, A., Hoppe, G., Römer, G., Runge, J., Ruoff, T., ... Vaupel, J. W. (2015).
855 The COMPADRE Plant Matrix Database: An open online repository for plant demography.
856 *Journal of Ecology*, *103*(1), 202–218. <https://doi.org/10.1111/1365-2745.12334>
- 857 Sapsford, S. J., Paap, T., Hardy, G. E. St. J., & Burgess, T. I. (2017). The ‘chicken or the egg’:
858 Which comes first, forest tree decline or loss of mycorrhizae? *Plant Ecology*, *218*(9), 1093–
859 1106. <https://doi.org/10.1007/s11258-017-0754-6>
- 860 Scariot, A. (1999). Forest fragmentation effects on palm diversity in central Amazonia.
861 *Journal of Ecology*, *87*(1), 66–76. <https://doi.org/10.1046/j.1365-2745.1999.00332.x>
- 862 Scheffers, B. R., Edwards, D. P., Macdonald, S. L., Senior, R. A., Andriamahohatra, L. R.,
863 Roslan, N., Rogers, A. M., Haugaasen, T., Wright, P., & Williams, S. E. (2017). Extreme

- 864 thermal heterogeneity in structurally complex tropical rain forests. *Biotropica*, 49(1), 35–
865 44. <https://doi.org/10.1111/btp.12355>
- 866 Schwalm, C. R., Anderegg, W. R. L., Michalak, A. M., Fisher, J. B., Biondi, F., Koch, G., Litvak,
867 M., Ogle, K., Shaw, J. D., Wolf, A., Huntzinger, D. N., Schaefer, K., Cook, R., Wei, Y., Fang, Y.,
868 Hayes, D., Huang, M., Jain, A., & Tian, H. (2017). Global patterns of drought recovery. *Nature*,
869 548(7666), 202–205. <https://doi.org/10.1038/nature23021>
- 870 Schwartz, N. B., Budsock, A. M., & Uriarte, M. (2019). Fragmentation, forest structure, and
871 topography modulate impacts of drought in a tropical forest landscape. *Ecology*, 100(6),
872 e02677. <https://doi.org/10.1002/ecy.2677>
- 873 Scott, E. R., Wei, J.-P., Li, X., Han, W.-Y., & Orians, C. M. (2021). Differing non-linear, lagged
874 effects of temperature and precipitation on an insect herbivore and its host plant.
875 *Ecological Entomology*, n/a(n/a). <https://doi.org/10.1111/een.13023>
- 876 Selwood, K. E., McGeoch, M. A., & Nally, R. M. (2015). The effects of climate change and land-
877 use change on demographic rates and population viability. *Biological Reviews*, 90(3), 837–
878 853. <https://doi.org/10.1111/brv.12136>
- 879 Silva Junior, C. H. L., Pessôa, A. C. M., Carvalho, N. S., Reis, J. B. C., Anderson, L. O., & Aragão,
880 L. E. O. C. (2021). The Brazilian Amazon deforestation rate in 2020 is the greatest of the
881 decade. *Nature Ecology & Evolution*, 5(2), 144–145. <https://doi.org/10.1038/s41559-020-01368-x>
- 883 Sletvold, N. (2005). Density-dependent growth and survival in a natural population of the
884 facultative biennial *Digitalis purpurea*. *Journal of Ecology*, 93(4), 727–736.
885 <https://doi.org/10.1111/j.1365-2745.2005.01008.x>
- 886 Snow, D. W. (1981). Tropical frugivorous birds and their food plants - a world survey.
887 *Biotropica*, 13(1), 1–14. <https://doi.org/10.2307/2387865>
- 888 Stiles, F. G. (1975). Ecology, flowering phenology, and hummingbird pollination of some
889 Costa Rican *Heliconia* species. *Ecology*, 56(2), 285–301. <https://doi.org/10.2307/1934961>
- 890 Stouffer, P. C., & Bierregaard, R. O. (1996). Forest fragmentation and seasonal patterns of
891 hummingbird abundance in Amazonian Brazil. *Ararajuba*, 4(1), 9–14.
- 892 Taubert, F., Fischer, R., Groeneveld, J., Lehmann, S., Müller, M. S., Rödiger, E., Wiegand, T., &
893 Huth, A. (2018). Global patterns of tropical forest fragmentation. *Nature*, 554(7693), 519–
894 522. <https://doi.org/10.1038/nature25508>
- 895 Teller, B. J., Adler, P. B., Edwards, C. B., Hooker, G., & Ellner, S. P. (2016). Linking
896 demography with drivers: Climate and competition. *Methods in Ecology and Evolution*, 7(2),
897 171–183. <https://doi.org/10.1111/2041-210X.12486>
- 898 Tenhumberg, B., Crone, E. E., Ramula, S., & Tyre, A. J. (2018). Time-lagged effects of weather
899 on plant demography: Drought and *Astragalus scaphoides*. *Ecology*, 99(4), 915–925.
900 <https://doi.org/10.1002/ecy.2163>

- 901 Ticktin, T. (2003). Relationships between El Niño Southern Oscillation and demographic
902 patterns in a substitute food for collared peccaries in Panama. *Biotropica*, 35(2), 189–197.
903 <https://doi.org/10.1111/j.1744-7429.2003.tb00278.x>
- 904 Uriarte, M., Anciães, M., da Silva, M. T. B., Rubim, R., Johnson, E., & Bruna, E. M. (2011).
905 Disentangling the drivers of reduced long-distance seed dispersal by birds in an
906 experimentally fragmented landscape. *Ecology*, 92(4), 924–937.
907 <https://doi.org/10.1890/10-0709.1>
- 908 Uriarte, M., Bruna, E. M., Rubim, P., Anciães, M., & Jonckheere, I. (2010). Effects of forest
909 fragmentation on the seedling recruitment of a tropical herb: assessing seed vs. safe-site
910 limitation. *Ecology*, 91(5), 1317–1328. <https://doi.org/10.1890/09-0785.1>
- 911 Uriarte, M., Muscarella, R., & Zimmerman, J. K. (2018). Environmental heterogeneity and
912 biotic interactions mediate climate impacts on tropical forest regeneration. *Glob Chang Biol*,
913 24(2), e692–e704. <https://doi.org/10.1111/gcb.14000>
- 914 Uriarte, M., Schwartz, N., Powers, J. S., Marín-Spiotta, E., Liao, W., & Werden, L. K. (2016).
915 Impacts of climate variability on tree demography in second growth tropical forests: The
916 importance of regional context for predicting successional trajectories. *Biotropica*, 48(6),
917 780–797. <https://doi.org/10.1111/btp.12380>
- 918 Vasconcelos, H. L., & Luizão, F. J. (2004). Litter production and litter nutrient
919 concentrations in a fragmented Amazonian landscape. *Ecological Applications*, 14(3), 884–
920 892. <https://doi.org/10.1890/03-5093>
- 921 Vicente-Serrano, S. M., Beguería, S., & López-Moreno, J. I. (2010). A multiscalar drought
922 index sensitive to global warming: The standardized precipitation evapotranspiration
923 index. *Journal of Climate*, 23(7), 1696–1718. <https://doi.org/10.1175/2009JCLI2909.1>
- 924 Westerband, A. C., Horvitz, C. C., & Gilliam, F. (2017). Early life conditions and precipitation
925 influence the performance of widespread understory herbs in variable light
926 environments. *Journal of Ecology*, 105(5), 1298–1308. [https://doi.org/10.1111/1365-
927 2745.12757](https://doi.org/10.1111/1365-2745.12757)
- 928 Williams, J. L., Jacquemyn, H., Ochocki, B. M., Brys, R., Miller, T. E. X., & Shefferson, R. (2015).
929 Life history evolution under climate change and its influence on the population dynamics of
930 a long-lived plant. *Journal of Ecology*, 103(4), 798–808. [https://doi.org/10.1111/1365-
931 2745.12369](https://doi.org/10.1111/1365-2745.12369)
- 932 Williamson, G. B., Laurance, W. F., Oliveira, A. A., Delamônica, P., Gascon, C., Lovejoy, T. E., &
933 Pohl, L. (2000). Amazonian tree mortality during the 1997 El Niño drought. *Conservation
934 Biology*, 14(5), 1538–1542. <https://doi.org/10.1046/j.1523-1739.2000.99298.x>
- 935 Wood, S. N. (2017). *Generalized additive models: An introduction with R* (Second edition).
936 CRC Press/Taylor & Francis Group.

- 937 Wright, S. J. (1992). Seasonal drought, soil fertility and the species density of tropical forest
938 plant communities. *Trends in Ecology & Evolution*, 7(8), 260–263.
939 [https://doi.org/10.1016/0169-5347\(92\)90171-7](https://doi.org/10.1016/0169-5347(92)90171-7)
- 940 Wright, S. J., & Calderon, O. (2006). Seasonal, El Niño and longer term changes in flower and
941 seed production in a moist tropical forest. *Ecology Letters*, 9(1), 35–44.
942 <https://doi.org/10.1111/j.1461-0248.2005.00851.x>
- 943 Wright, S. J., Carrasco, C., Calderon, O., & Paton, S. (1999). The El Niño Southern Oscillation
944 variable fruit production, and famine in a tropical forest. *Ecology*, 80(5), 1632–1647.
- 945 Xavier, A. C., King, C. W., & Scanlon, B. R. (2016). Daily gridded meteorological variables in
946 Brazil (1980). *International Journal of Climatology*, 36(6), 2644–2659.
947 <https://doi.org/10.1002/joc.4518>
- 948 Zartman, C. E., Amaral, J. A., Figueiredo, J. N., & Dambros, C. D. (2015). Drought impacts
949 survivorship and reproductive strategies of an epiphyllous leafy liverwort in central
950 Amazonia. *Biotropica*, 47(2), 172–178.
- 951 Zeng, N., Yoon, J. H., Marengo, J. A., Subramaniam, A., Nobre, C. A., Mariotti, A., & Neelin, J. D.
952 (2008). Causes and impacts of the 2005 Amazon drought. *Environmental Research Letters*,
953 3(1), 1–9. <https://doi.org/10.1088/1748-9326/3/1/014002>
- 954

955 **Colophon**

956 This report was generated on 2021-06-22 18:37:48 using the following computational
957 environment and dependencies:

```
958 #> - Session info
959 -----
960 #> setting value
961 #> version R version 4.0.2 (2020-06-22)
962 #> os      macOS 10.16
963 #> system x86_64, darwin17.0
964 #> ui      X11
965 #> language (EN)
966 #> collate en_US.UTF-8
967 #> ctype   en_US.UTF-8
968 #> tz      America/New_York
969 #> date    2021-06-22
970 #>
971 #> - Packages
972 -----
973 #> ! package      * version      date      lib
974 #> P Amelia        * 1.7.6        2019-11-25 [?]
975 #> P anytime       0.3.9        2020-08-27 [?]
976 #> P assertthat    0.2.1        2019-03-21 [?]
977 #> P backports     1.2.1        2020-12-09 [?]
978 #> P base64enc     0.1-3        2015-07-28 [?]
979 #> P bbmle         * 1.0.23.1    2020-02-03 [?]
980 #> P bdsmatrix     1.3-4        2020-01-13 [?]
981 #> P bookdown      0.22         2021-04-22 [?]
982 #> P broom         * 0.7.6        2021-04-05 [?]
983 #> P cachem        1.0.4        2021-02-13 [?]
984 #> P callr         3.7.0        2021-04-20 [?]
985 #> P cellranger    1.1.0        2016-07-27 [?]
986 #> P checkmate     2.0.0        2020-02-06 [?]
987 #> P cli           2.5.0        2021-04-26 [?]
988 #> P cluster       2.1.2        2021-04-17 [?]
989 #> P codetools     0.2-18      2020-11-04 [?]
990 #> P colorspace    * 2.0-1        2021-05-04 [?]
991 #> P conflicted    * 1.0.4        2019-06-21 [?]
992 #> P crayon        1.4.1        2021-02-08 [?]
993 #> P data.table    1.14.0       2021-02-21 [?]
994 #> P DBI           1.1.1        2021-01-15 [?]
995 #> P dbplyr        2.1.1        2021-04-06 [?]
996 #> P DEoptimR     1.0-8        2016-11-19 [?]
997 #> P desc          1.3.0        2021-03-05 [?]
998 #> P devtools      2.4.0        2021-04-07 [?]
999 #> P digest        0.6.27      2020-10-24 [?]
1000 #> P dlnm         * 2.4.5        2021-03-21 [?]
```

1001	#>	P dotenv	* 1.0.3	2021-04-22	[?]
1002	#>	P dplyr	* 1.0.5	2021-03-05	[?]
1003	#>	P ellipsis	0.3.2	2021-04-29	[?]
1004	#>	P evaluate	0.14	2019-05-28	[?]
1005	#>	P fansi	0.4.2	2021-01-15	[?]
1006	#>	P farver	2.1.0	2021-02-28	[?]
1007	#>	P fastmap	1.1.0	2021-01-25	[?]
1008	#>	P forcats	* 0.5.1	2021-01-27	[?]
1009	#>	P foreign	0.8-81	2020-12-22	[?]
1010	#>	P Formula	* 1.2-4	2020-10-16	[?]
1011	#>	P fs	1.5.0	2020-07-31	[?]
1012	#>	P generics	0.1.0	2020-10-31	[?]
1013	#>	P ggplot2	* 3.3.3	2020-12-30	[?]
1014	#>	P glue	* 1.4.2	2020-08-27	[?]
1015	#>	P goftest	1.2-2	2019-12-02	[?]
1016	#>	P gratia	* 0.6.0.9112	2021-06-11	[?]
1017	#>	P gridExtra	2.3	2017-09-09	[?]
1018	#>	P gtable	0.3.0	2019-03-25	[?]
1019	#>	P haven	2.4.1	2021-04-23	[?]
1020	#>	P here	* 1.0.1	2020-12-13	[?]
1021	#>	P highr	0.9	2021-04-16	[?]
1022	#>	P Hmisc	* 4.5-0	2021-02-28	[?]
1023	#>	P hms	1.0.0	2021-01-13	[?]
1024	#>	P htmlTable	2.1.0	2020-09-16	[?]
1025	#>	P htmltools	0.5.1.1	2021-01-22	[?]
1026	#>	P htmlwidgets	1.5.3	2020-12-10	[?]
1027	#>	P httr	1.4.2	2020-07-20	[?]
1028	#>	P igraph	1.2.6	2020-10-06	[?]
1029	#>	P janitor	* 2.1.0	2021-01-05	[?]
1030	#>	P jpeg	0.1-8.1	2019-10-24	[?]
1031	#>	P jsonlite	1.7.2	2020-12-09	[?]
1032	#>	P knitr	* 1.33	2021-04-24	[?]
1033	#>	P labeling	0.4.2	2020-10-20	[?]
1034	#>	P latex2exp	* 0.5.0	2021-03-18	[?]
1035	#>	P lattice	* 0.20-44	2021-05-02	[?]
1036	#>	P latticeExtra	0.6-29	2019-12-19	[?]
1037	#>	P lifecycle	1.0.0	2021-02-15	[?]
1038	#>	P lmomco	* 2.3.6	2020-03-14	[?]
1039	#>	P Lmoments	1.3-1	2019-03-15	[?]
1040	#>	P lubridate	* 1.7.10	2021-02-26	[?]
1041	#>	P magrittr	2.0.1	2020-11-17	[?]
1042	#>	P MASS	7.3-54	2021-05-03	[?]
1043	#>	P Matrix	1.3-3	2021-05-04	[?]
1044	#>	P memoise	2.0.0	2021-01-26	[?]
1045	#>	P mgcv	* 1.8-35	2021-04-18	[?]
1046	#>	P modelr	0.1.8	2020-05-19	[?]
1047	#>	P munsell	0.5.0	2018-06-12	[?]
1048	#>	P mvnfast	0.2.5.1	2020-10-14	[?]
1049	#>	P mvtnorm	1.1-1	2020-06-09	[?]
1050	#>	P nlme	* 3.1-152	2021-02-04	[?]

1051	#>	P nnet	7.3-16	2021-05-03	[?]
1052	#>	P numDeriv	2016.8-1.1	2019-06-06	[?]
1053	#>	P patchwork	* 1.1.1	2020-12-17	[?]
1054	#>	P pillar	1.6.0	2021-04-13	[?]
1055	#>	P pkgbuild	1.2.0	2020-12-15	[?]
1056	#>	P pkgconfig	2.0.3	2019-09-22	[?]
1057	#>	P pkgload	1.2.1	2021-04-06	[?]
1058	#>	P png	0.1-7	2013-12-03	[?]
1059	#>	P prettyunits	1.1.1	2020-01-24	[?]
1060	#>	P processx	3.5.2	2021-04-30	[?]
1061	#>	P ps	1.6.0	2021-02-28	[?]
1062	#>	P purrr	* 0.3.4	2020-04-17	[?]
1063	#>	P qqplotr	* 0.0.5	2021-04-23	[?]
1064	#>	P R6	2.5.0	2020-10-28	[?]
1065	#>	P RColorBrewer	1.1-2	2014-12-07	[?]
1066	#>	P Rcpp	* 1.0.6	2021-01-15	[?]
1067	#>	P readr	* 1.4.0	2020-10-05	[?]
1068	#>	P readxl	* 1.3.1	2019-03-13	[?]
1069	#>	P remotes	2.3.0	2021-04-01	[?]
1070	#>	P renv	0.13.2	2021-03-30	[?]
1071	#>	P reprex	2.0.0	2021-04-02	[?]
1072	#>	P rlang	0.4.11	2021-04-30	[?]
1073	#>	P rmarkdown	* 2.7	2021-02-19	[?]
1074	#>	P robustbase	0.93-7	2021-01-04	[?]
1075	#>	P rpart	4.1-15	2019-04-12	[?]
1076	#>	P rprojroot	2.0.2	2020-11-15	[?]
1077	#>	P rstudioapi	0.13	2020-11-12	[?]
1078	#>	P rvest	1.0.0	2021-03-09	[?]
1079	#>	P scales	1.1.1	2020-05-11	[?]
1080	#>	P sessioninfo	1.1.1	2018-11-05	[?]
1081	#>	P snakecase	0.11.0	2019-05-25	[?]
1082	#>	P SPEI	* 1.7	2017-06-07	[?]
1083	#>	P statmod	* 1.4.35	2020-10-19	[?]
1084	#>	P stringi	1.5.3	2020-09-09	[?]
1085	#>	P stringr	* 1.4.0	2019-02-10	[?]
1086	#>	P survival	* 3.2-11	2021-04-26	[?]
1087	#>	P tarchetypes	* 0.2.0	2021-05-11	[?]
1088	#>	P targets	* 0.4.2	2021-04-30	[?]
1089	#>	P testthat	3.0.2	2021-02-14	[?]
1090	#>	P tibble	* 3.1.1	2021-04-18	[?]
1091	#>	P tidyr	* 1.1.3	2021-03-03	[?]
1092	#>	P tidyselect	1.1.1	2021-04-30	[?]
1093	#>	P tidyverse	* 1.3.1	2021-04-15	[?]
1094	#>	P tsibble	* 1.0.1	2021-04-12	[?]
1095	#>	P tsModel	* 0.6	2013-06-24	[?]
1096	#>	P usethis	2.0.1	2021-02-10	[?]
1097	#>	P utf8	1.2.1	2021-03-12	[?]
1098	#>	P vctrs	0.3.8	2021-04-29	[?]
1099	#>	P withr	2.4.2	2021-04-18	[?]
1100	#>	P xfun	0.22	2021-03-11	[?]

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1101 #> P xml2          1.3.2      2020-04-23 [?]
1102 #> P yaml         2.2.1      2020-02-01 [?]
1103 #> source
1104 #> CRAN (R 4.0.2)
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1233 #>
1234 #> [1] /Users/scottericr/Documents/HeliconiaDemography/renv/library/R-
1235 4.0/x86_64-apple-darwin17.0
1236 #> [2]
1237 /private/var/folders/b_/2vfnxxls5vs401tmhbb3wqdh0000gp/T/RtmpKX4NCE/renv-
1238 system-library
1239 #> [3]
1240 /private/var/folders/b_/2vfnxxls5vs401tmhbb3wqdh0000gp/T/RtmpxFg51N/renv-
1241 system-library
1242 #>
1243 #> P — Loaded and on-disk path mismatch.
```

1244 The current Git commit details are:

```
1245 #> Local:      emilio /Users/scottericr/Documents/HeliconiaDemography
1246 #> Remote:     emilio @ origin
```

```
1247 (https://github.com/BrunaLab/HeliconiaDemography.git)
1248 #> Head: [5e4dd7c] 2021-06-22: minor edits to results and discussion
```