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

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

43

44 Introduction

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

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

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

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

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

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

104 **Methods**

105 **Study site**

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

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

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

119 **Focal species**

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

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

135 **Demographic data collection**

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

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

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

156 **Climate data**

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

175 **Statistical Modeling of Vital Rates**

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

$$190 \quad \begin{aligned} g[E(y_i)] &= \alpha_j + s_1(z_i) + s_2(d_{i,t}, \dots, d_{i,t-36}) + \beta x_i \\ \alpha_j &\sim N(\mu_{\alpha_j}, \sigma_{\alpha_j}^2), \text{ for plot } j \end{aligned} \quad (1)$$

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

196
$$s_2(d_{i,t}, \dots, d_{i,t-24}) = \sum_{l=l_0}^L f \cdot w(d_{i,t-l}, l) \quad (2)$$

197 where the crossbasis function, $f \cdot w(d, l)$, is composed of two marginal basis functions: the
198 standard predictor-response function $f(d)$, and the additional lag-response function $w(l)$.
199 These marginal functions are combined as a tensor product smooth such that the shape of
200 one marginal function varies smoothly along the other dimension (see chapter 5 of Wood
201 (2017) and Gasparrini et al. (2017) for more detail). Penalized cubic regression splines
202 were used for both marginal bases of the crossbasis function, with 35 knots for the lag
203 dimension (i.e. number of lagged SPEI values for each observation with 36 months as a
204 maximum lag) and 3 knots for the drought response dimension to restrict the shape of the
205 fitted response to drought to bimodal when most complex. Because of penalization, the
206 number of knots is generally not important as long it is large enough to allow the smooth to
207 represent the ‘true’ relationship (Wood, 2017). Estimated degrees of freedom (edf)
208 represent the ‘true’ complexity of the smooth after penalization with edf = 1 being
209 equivalent to a straight line and larger numbers representing more complex curves.
210 To determine if plot characteristics influenced average vital rates we included a random
211 effect of plot ID on the intercept; this was represented by a_j in eq. 1. We determined the
212 effects of SPEI on plant growth using plant size in year $t+1$ as a response variable. This was
213 modeled with a scaled t family error distribution because residuals were leptokurtic with a
214 Gaussian error structure. Because number of inflorescences was highly zero-inflated, we
215 converted this to a binary response to model reproduction (i.e., 1 for ≥ 1 inflorescence, 0 for
216 no inflorescences). We modeled both reproduction and survival (i.e., from year t to year

217 $t+1$) using a binomial family error distribution with a logit link function. We modeled a
218 potential cost of reproduction by including flowering in the previous year as covariate, x_i ,
219 in eq. 1. Additionally, in models for flowering probability and size, we included plant ID as a
220 random effect to account for variation among individuals. Preliminary analyses showed
221 that this random effect was not significant in the growth models (edf ~ 0 , $p > 0.2$) and as
222 such it was dropped to improve computational efficiency. A random effect of plant ID was
223 not included in survival models since each plant only dies once.

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

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

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

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

241 Results

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

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

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

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

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

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

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

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

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

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

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

305 Figure 4a). In contrast, the most pronounced negative effects of SPEI on the survival of
306 plants in continuous forest were at lag times of 15–20 months and 32–36 months. Drought
307 15–20 months prior to a census (i.e. two dry seasons prior to a census) was significantly
308 associated with reduced survival, while high precipitation (i.e., $\text{SPEI} > 1$) was significantly
309 associated with higher survival. Finally, plants in both habitat types showed an increase in
310 survival probability with very high SPEI values (i.e., extremely high precipitation) at a lag
311 time of 32–36 months. It should be noted, however, that only the first transition year of
312 census data (1998–1999) met these conditions. We compared the effects of SPEI history in
313 continuous forest and fragments by subtracting the fitted values in Figure 4b from Figure
314 4a to produce Figure 4c. This shows that in average conditions ($\text{SPEI} = 0$), there is little
315 difference in survival probability between continuous forest and forest fragments (Figure
316 4c). However, under extreme conditions, survival probability is higher in continuous forest
317 by up to 0.025.

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

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

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

349 Discussion

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

360 Temporal variation in demographic responses to forest fragmentation

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

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

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

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

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

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

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

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

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

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

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

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

454 Third, it may be that the delayed demographic effects we observed are indirectly mediated
455 by the effect of SPEI on other species rather than the direct effects on individual physiology
456 (Evers et al., 2021). For example, tropical trees may not die until three or more years after a
457 drought (Criley & Lekawatana, 1994). When they finally do, the resulting leaf drop (Janssen
458 et al., 2021) and treefalls allow for light penetration to the forest understory (Canham et al.,
459 1990; Leitold et al., 2018), triggering a boom in the growth and flowering of understory

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

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

479 **Conclusions & Future Directions**

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

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

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

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

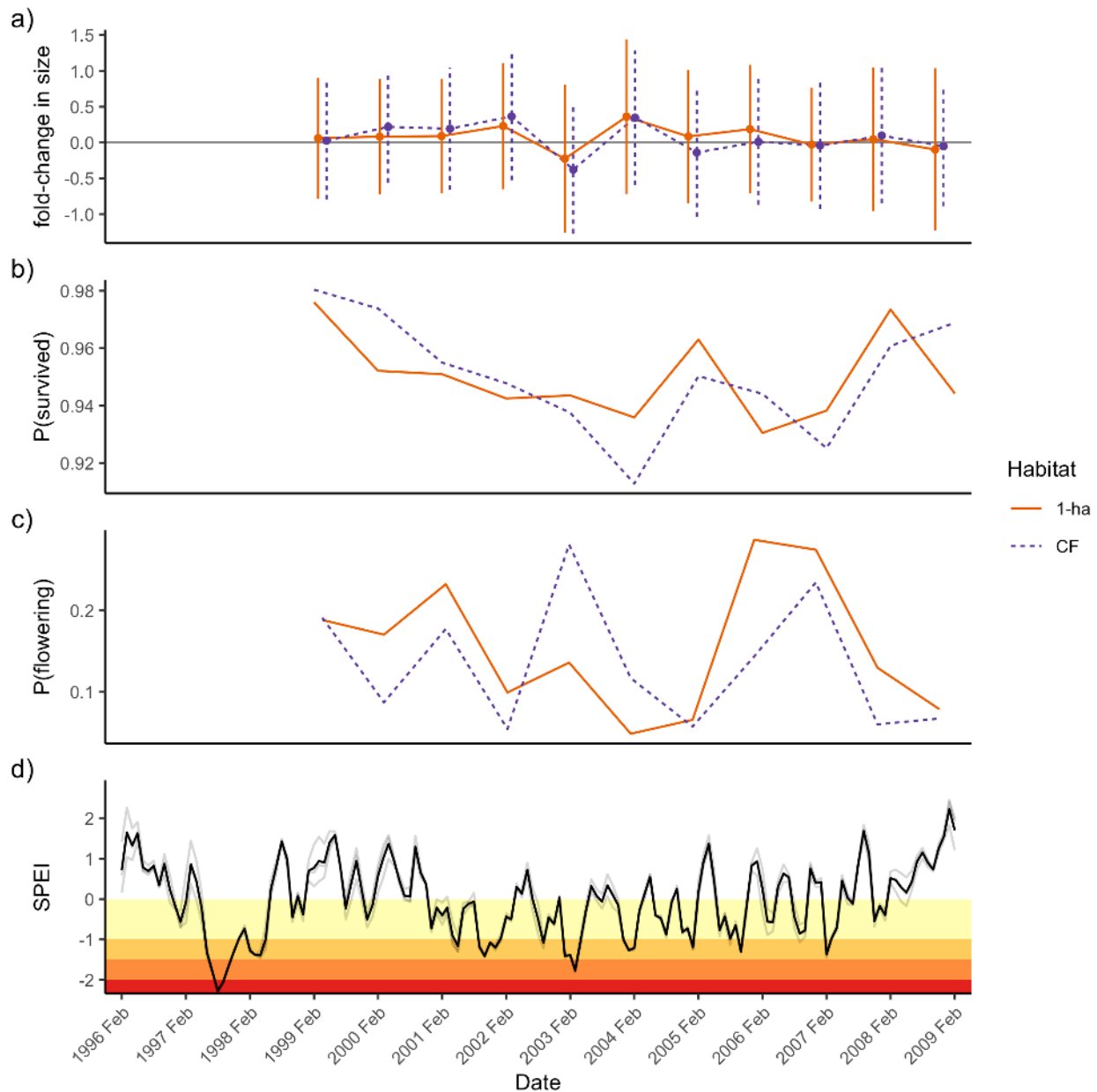
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517 **Data Availability Statement**

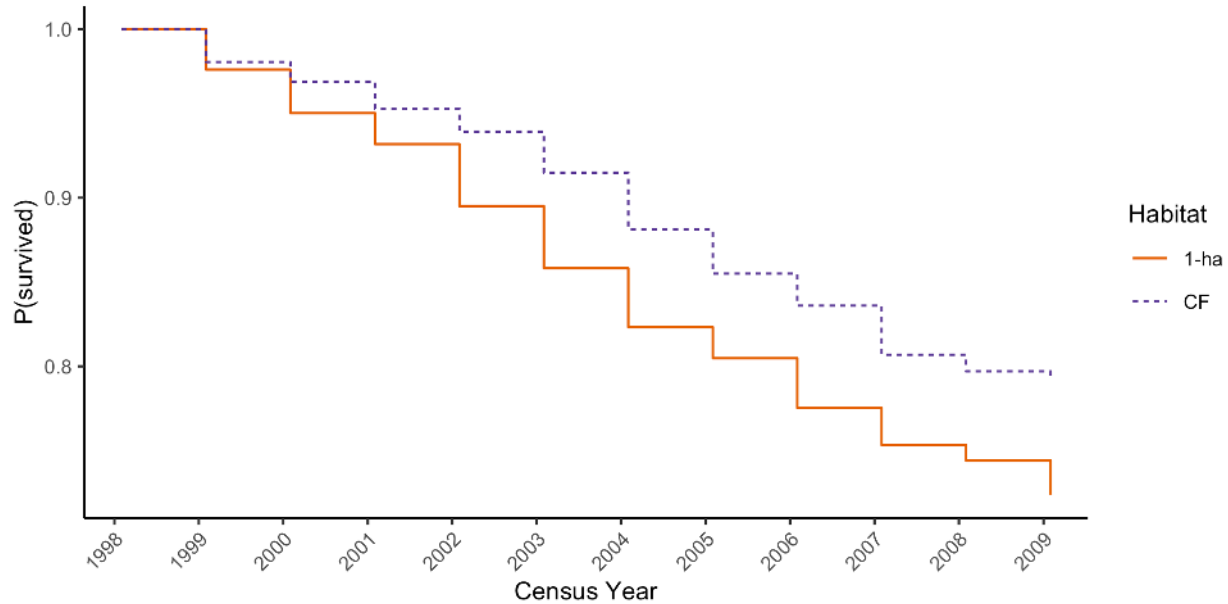
518 Data used in this study are available at the Dryad Digital Repository; R code for analyses
519 and visualizations are archived at Zenodo [links included upon acceptance].

520 **Figures**

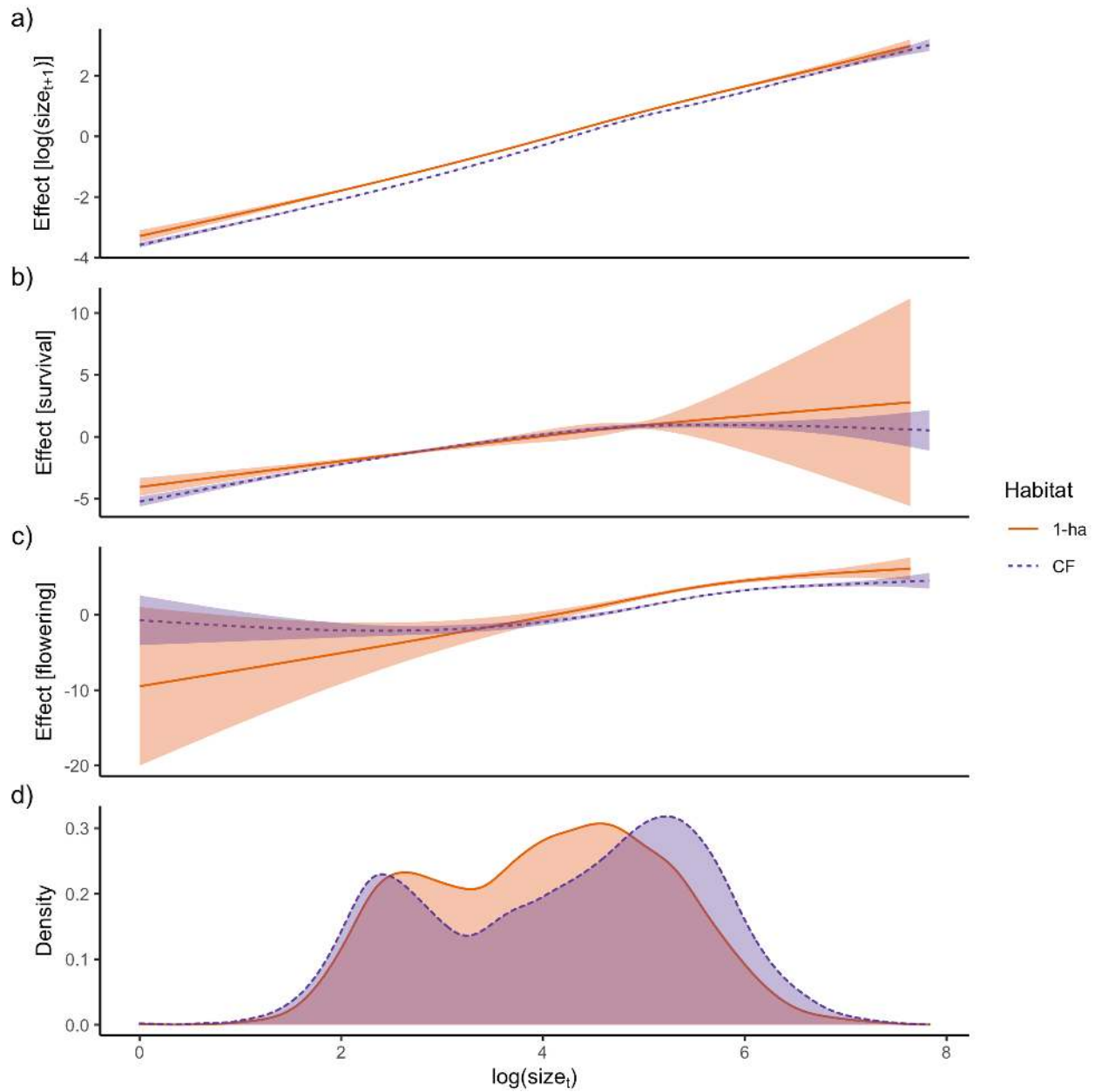


521
522 Figure 1: (a-c) Time series of *H. acuminata* vital rates in 1-ha fragments (solid orange lines) and continuous
523 forest (dashed blue lines) and (d) drought occurrence in the study region. (a) Mean fold-change in plant plant
524 size ($\log_2(\text{size}_{t+1} / \text{size}_t)$) varies by year and habitat. On average, plants grew in most years with the notable
525 exception in 2003, in which on average plants regressed in size in both habitats (i.e., fold-change < 0). Error
526 bars represent the standard deviation. (b) The proportion of plants surviving from one transition year to the
527 next varied from 0.98 (CF in 1998-1999) to 0.91 (CF in 2003-2004). (c) The proportion of *H. acuminata* above

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



533
534 Figure 2: Survivorship curve for plants marked in the 1998 survey year; these plants comprise 49% of those
535 in the complete demographic dataset. The percentage of these plants that were still alive ten years later was
536 79.7% (1629/2055) in continuous forest vs. 72.4% (393/543) in 1-ha fragments.



537

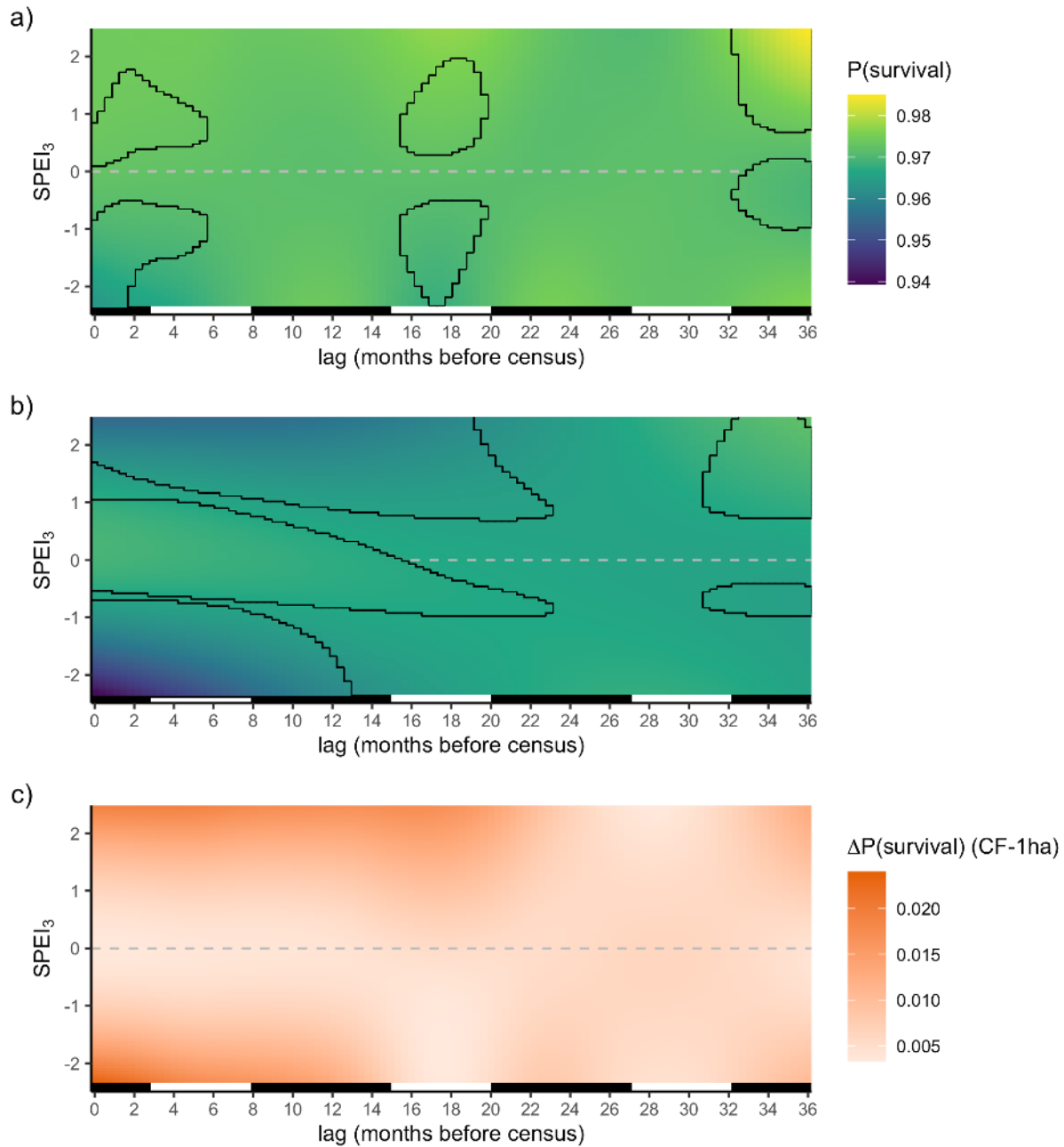
538 Figure 3: Smooth effect from models of plant size in the previous census on (a) survival, (b) log(size), and (c)

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

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

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

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



543

544 Figure 4: Smooth effect of lagged SPEI on *H. acuminata* survival in (a) continuous forest, (b) 1-ha fragments,

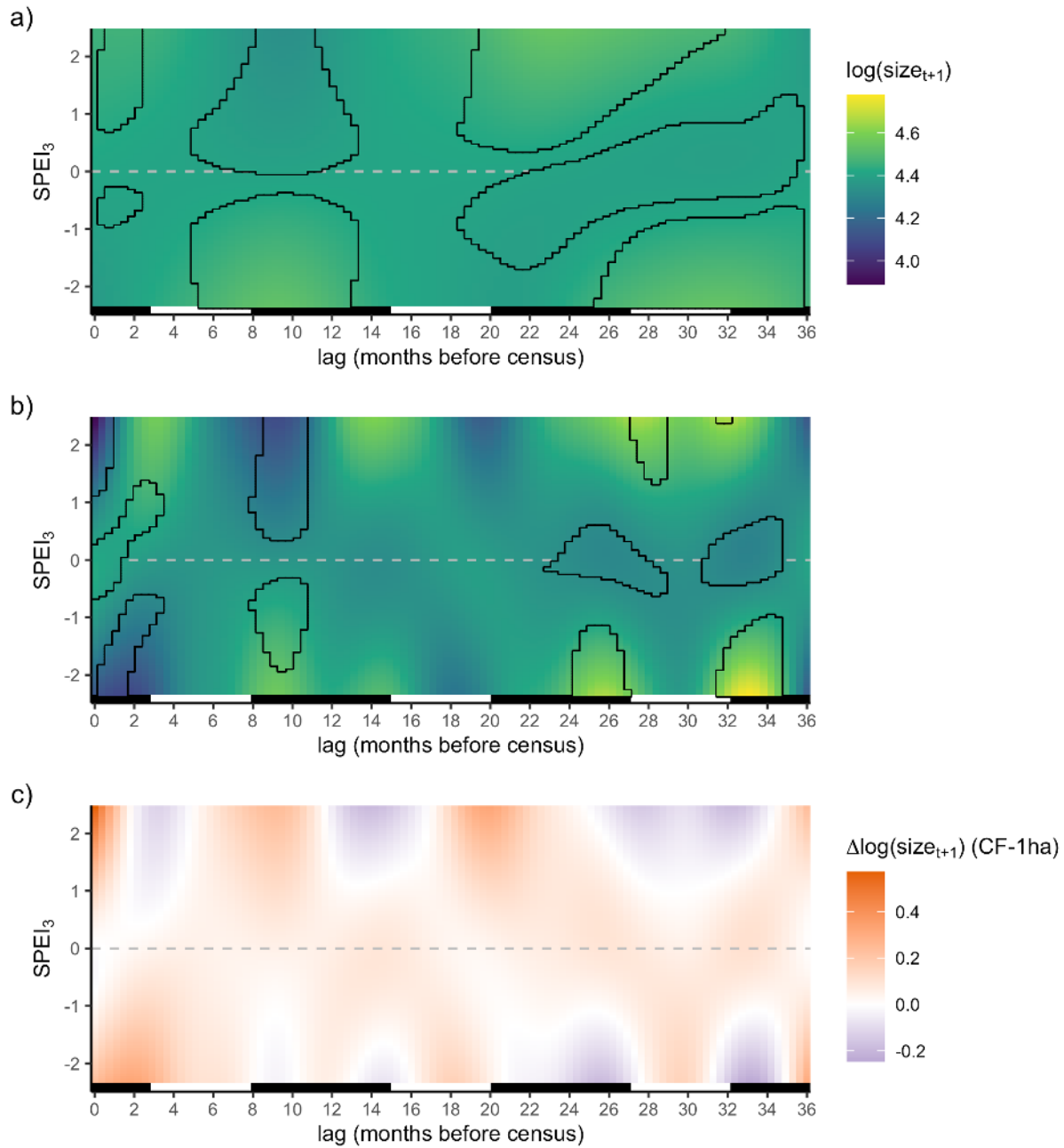
545 (c) and the difference between the two. Outlines show regions where the effect of SPEI is significant, defined

546 as those where the 95% confidence interval around the response does not overlap the intercept. The bar on

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

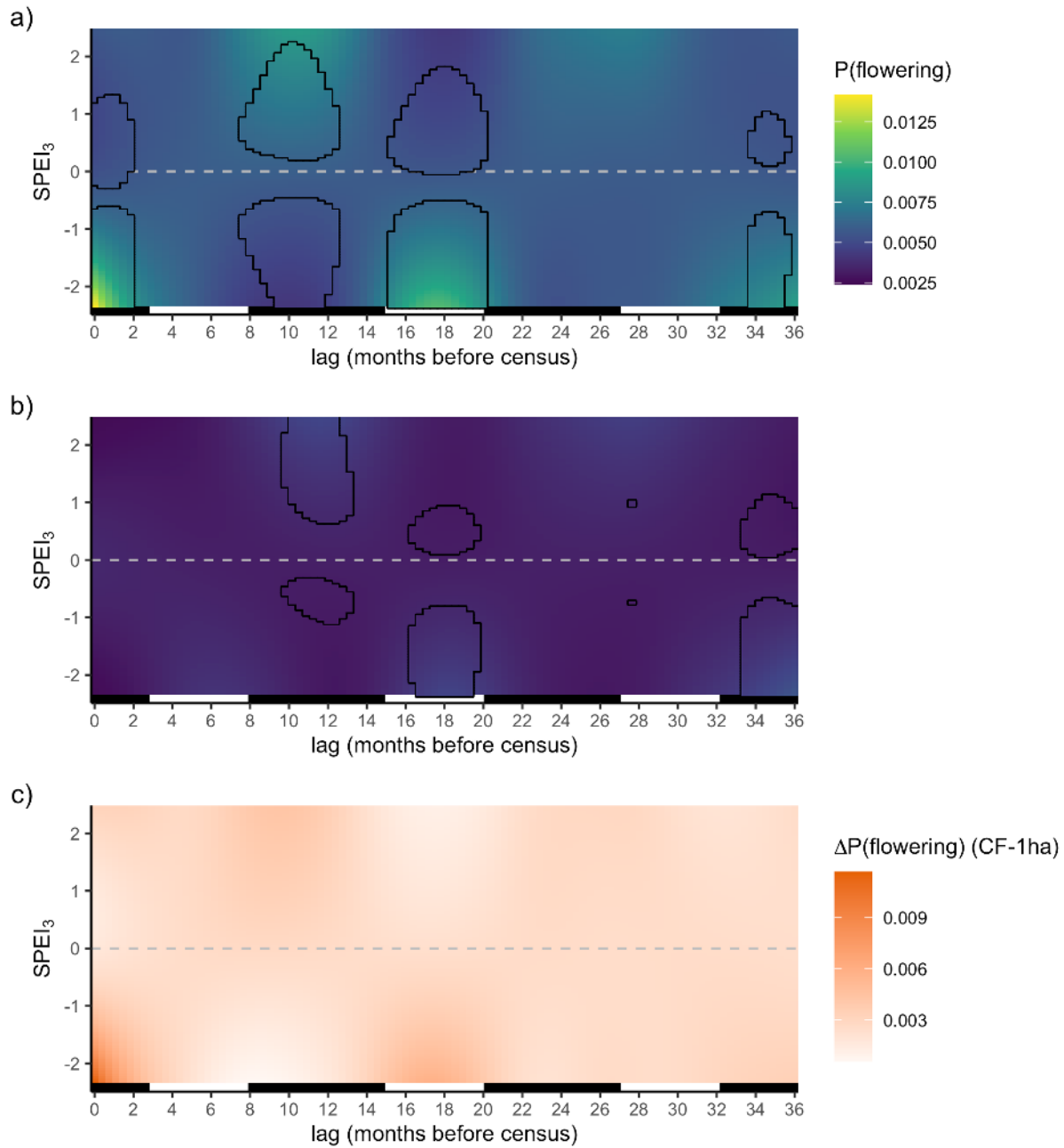
548 October). Surface is modeled as a crossbasis function with cubic regression splines for each marginal basis.

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



551
552 Figure 5: Smooth effect of lagged SPEI on *H. acuminata* growth in (a) continuous forest, (b) 1-ha fragments,
553 (c) and the difference between the two. Outlines show regions where the effect of SPEI is significant, defined
554 as those where the 95% confidence interval around the response does not overlap the intercept. The bar on

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



557
558 Figure 6: Smooth effect of lagged SPEI on *H. acuminata* flowering probability in (a) continuous forest, (b) 1-ha
559 fragments, (c) and the difference between the two. Outlines show regions where the effect of SPEI is
560 significant, defined as those where the 95% confidence interval around the response does not overlap the
561 intercept. The bar on the bottom of each panel indicates the wet seasons (black, November–May) and dry

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

565 **References**

- 566 Aguirre, B. A., Hsieh, B., Watson, S. J., & Wright, A. J. (2021). The experimental manipulation
567 of atmospheric drought: Teasing out the role of microclimate in biodiversity experiments.
568 *Journal of Ecology*, *109*(5), 1986–1999. [https://doi.org/https://doi.org/10.1111/1365-](https://doi.org/10.1111/1365-2745.13595)
569 [2745.13595](https://doi.org/10.1111/1365-2745.13595)
- 570 Alfaro-Sánchez, R., Muller-Landau, H. C., Wright, S. J., & Camarero, J. J. (2017). Growth and
571 reproduction respond differently to climate in three Neotropical tree species. *Oecologia*,
572 *184*(2), 531–541. <https://doi.org/10.1007/s00442-017-3879-3>
- 573 Alroy, J. (2017). Effects of habitat disturbance on tropical forest biodiversity. *Proceedings of*
574 *the National Academy of Sciences*, *114*(23), 6056–6061.
575 <https://doi.org/10.1073/pnas.1611855114>
- 576 Anderegg, W. R. L., Schwalm, C., Biondi, F., Camarero, J. J., Koch, G., Litvak, M., Ogle, K., Shaw,
577 J. D., Shevliakova, E., Williams, A. P., Wolf, A., Ziaco, E., & Pacala, S. (2015). Pervasive
578 drought legacies in forest ecosystems and their implications for carbon cycle models.
579 *Science*, *349*(6247), 528–532. <https://doi.org/10.1126/science.aab1833>
- 580 Arroyo-Rodríguez, V., Saldaña-Vázquez, R. A., Fahrig, L., & Santos, B. A. (2017). Does forest
581 fragmentation cause an increase in forest temperature? *Ecological Research*, *32*(1), 81–88.
582 <https://doi.org/10.1007/s11284-016-1411-6>
- 583 Beguería, S., & Vicente-Serrano, S. M. (2017). *SPEI: Calculation of the standardised*
584 *precipitation-evapotranspiration index*. <https://CRAN.R-project.org/package=SPEI>
- 585 Betts, M. G., Wolf, C., Pfeifer, M., Banks-Leite, C., Arroyo-Rodríguez, V., Ribeiro, D. B., Barlow,
586 J., Eigenbrod, F., Faria, D., Fletcher, R. J., Hadley, A. S., Hawes, J. E., Holt, R. D., Klingbeil, B.,
587 Kormann, U., Lens, L., Levi, T., Medina-Rangel, G. F., Melles, S. L., ... Ewers, R. M. (2019).
588 Extinction filters mediate the global effects of habitat fragmentation on animals. *Science*,
589 *366*(6470), 1236–1239. <https://doi.org/10.1126/science.aax9387>
- 590 Bianchi, C. A., & Haig, S. M. (2013). Deforestation trends of tropical dry forests in Central
591 Brazil. *Biotropica*, *45*(3), 395–400. [https://doi.org/https://doi.org/10.1111/btp.12010](https://doi.org/10.1111/btp.12010)
- 592 Bierregaard, R. O., Gascon, C., Lovejoy, T. E., & Mesquita, R. (Eds.). (2001). *Lessons from*
593 *Amazonia: The ecology and conservation of a fragmented forest*. Yale University Press.
- 594 Bierregaard, R. O., Lovejoy, T. E., Kapos, V., & Hutchings, R. W. (1992). The biological
595 dynamics of tropical rainforest fragments. *BioScience*, *42*(11), 859–866.
596 <https://doi.org/10.2307/1312085>

- 597 Broadbent, E. N., Asner, G. P., Keller, M., Knapp, D. E., Oliveira, P. J. C., & Silva, J. N. (2008).
598 Forest fragmentation and edge effects from deforestation and selective logging in the
599 Brazilian Amazon. *Biological Conservation*, 141, 1745–1757.
600 <https://doi.org/10.1016/j.biocon.2008.04.024>
- 601 Brodie, J., Post, E., & Laurance, W. F. (2012). Climate change and tropical biodiversity: A
602 new focus. *Trends in Ecology & Evolution*, 27(3), 145–150.
603 <https://doi.org/10.1016/j.tree.2011.09.008>
- 604 Brooks, M. E., Kristensen, K., Darrigo, M. R., Rubim, P., Uriarte, M., Bruna, E. M., & Bolker, B.
605 M. (2019). Statistical modeling of patterns in annual reproductive rates. *Ecology*, 100(7).
606 <https://doi.org/10.1002/ecy.2706>
- 607 Bruna, E. M. (1999). Seed germination in rainforest fragments. *Nature*, 402(6758), 139.
608 <https://doi.org/10.1038/45963>
- 609 Bruna, E. M. (2002). Effects of forest fragmentation on *Heliconia acuminata* seedling
610 recruitment in central Amazonia. *Oecologia*, 132(2), 235–243.
611 <https://doi.org/10.1007/s00442-002-0956-y>
- 612 Bruna, E. M. (2003). Are plant populations in fragmented habitats recruitment limited?
613 Tests with an Amazonian herb. *Ecology*, 84(4), 932–947. [https://doi.org/10.1890/0012-9658\(2003\)084\[0932:APPIFH\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[0932:APPIFH]2.0.CO;2)
- 615 Bruna, E. M., Fiske, I. J., & Trager, M. D. (2009). Habitat fragmentation and plant
616 populations: Is what we know demographically irrelevant? *Journal of Vegetation Science*,
617 20(3), 569–576. <https://doi.org/10.1111/j.1654-1103.2009.01060.x>
- 618 Bruna, E. M., & Kress, W. J. (2002). Habitat fragmentation and the demographic structure of
619 an Amazonian understory herb (*Heliconia acuminata*). *Conservation Biology*, 16(5), 1256–
620 1266. <https://doi.org/10.1046/j.1523-1739.2002.99494.x>
- 621 Bruna, E. M., Kress, W. J., Marques, F., & Silva, O. F. da. (2004). *Heliconia acuminata*
622 reproductive success is independent of local floral density. *Acta Amazonica*, 34(3), 467–
623 471. <https://doi.org/10.1590/S0044-59672004000300012>
- 624 Bruna, E. M., Nardy, O., Strauss, S. Y., & Harrison, S. (2002). Experimental assessment of
625 *Heliconia acuminata* growth in a fragmented Amazonian landscape. *Journal of Ecology*,
626 90(4), 639–649. <https://doi.org/10.1046/j.1365-2745.2002.00707.x>
- 627 Bruna, E. M., & Oli, M. K. (2005). Demographic effects of habitat fragmentation on a tropical
628 herb: Life-table response experiments. *Ecology*, 86(7), 1816–1824.
629 <https://doi.org/10.1890/04-1716>
- 630 Bruna, E. M., & Ribeiro, M. B. N. (2005). The compensatory responses of an understory herb
631 to experimental damage are habitat-dependent. *American Journal of Botany*, 92(12), 2101–
632 2210. <https://doi.org/10.3732/ajb.92.12.2101>

- 633 Canham, C. D., Denslow, J. S., Platt, W. J., Runkle, J. R., Spies, T. A., & White, P. S. (1990). Light
634 regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests.
635 *Canadian Journal of Forest Research*, 20(5), 620–631. <https://doi.org/10.1139/x90-084>
- 636 Condit, R., Aguilar, S., Hernandez, A., Perez, R., Lao, S., Angehr, G., Hubbell, S. P., & Foster, R.
637 B. (2004). Tropical forest dynamics across a rainfall gradient and the impact of an El Niño
638 dry season. *Journal of Tropical Ecology*, 20(01), 51–72.
639 <https://doi.org/10.1017/S0266467403001081>
- 640 Connell, J. H., & Green, P. T. (2000). Seedling dynamics over thirty-two years in a tropical
641 rain forest tree. *Ecology*, 81(2), 568–584.
- 642 Côrtes, M. C., Uriarte, M., Lemes, M. R., Gribel, R., Kress, W. J., Smouse, P. E., & Bruna, E. M.
643 (2013). Low plant density enhances gene dispersal in the Amazonian understory herb
644 *Heliconia Acuminata*. *Molecular Ecology*, 22(22), 5716–5729.
645 <https://doi.org/10.1111/mec.12495>
- 646 Criley, R., & Lekawatana, S. (1994). Year around production with high yields may be a
647 possibility for *Heliconia chartacea*. *Acta Horticulturae*, 397, 95–102.
648 <https://doi.org/10.17660/ActaHortic.1995.397.7>
- 649 Crone, E. E., Menges, E. S., Ellis, M. M., Bell, T., Bierzychudek, P., Ehrlen, J., Kaye, T. N., Knight,
650 T. M., Lesica, P., Morris, W. F., Oostermeijer, G., Quintana-Ascencio, P. F., Stanley, A., Ticktin,
651 T., Valverde, T., & Williams, J. L. (2011). How do plant ecologists use matrix population
652 models? *Ecology Letters*, 14(1), 1–8.
- 653 da Silva, J. M. C., & Tabarelli, M. (2000). Tree species impoverishment and the future flora of
654 the Atlantic forest of northeast Brazil. *Nature*, 404(6773), 72–74.
655 <https://doi.org/10.1038/35003563>
- 656 Didham, R. K., Kapos, V., & Ewers, R. M. (2012). Rethinking the conceptual foundations of
657 habitat fragmentation research. *Oikos*, 121(2), 161–170. <https://doi.org/10.1111/j.1600-0706.2011.20273.x>
- 659 Didham, R. K., & Lawton, J. H. (1999). Edge structure determines the magnitude of changes
660 in microclimate and vegetation structure in tropical forest fragments. *Biotropica*, 31(1), 17–
661 30. <https://doi.org/10.1111/j.1744-7429.1999.tb00113.x>
- 662 Doak, D. F., & Morris, W. F. (2010). Demographic compensation and tipping points in
663 climate-induced range shifts. *Nature*, 467(7318), 959–962.
- 664 Driscoll, D. A., Banks, S. C., Barton, P. S., Lindenmayer, D. B., & Smith, A. L. (2013).
665 Conceptual domain of the matrix in fragmented landscapes. *Trends in Ecology & Evolution*,
666 28(10), 605–613. <https://doi.org/10.1016/j.tree.2013.06.010>
- 667 Duffy, P. B., Brando, P., Asner, G. P., & Field, C. B. (2015). Projections of future
668 meteorological drought and wet periods in the Amazon. *Proceedings of the National*
669 *Academy of Sciences*, 112(43), 13172–13177. <https://doi.org/10.1073/pnas.1421010112>

- 670 Edwards, W., & Krockenberger, A. (2006). Seedling mortality due to drought and fire
671 associated with the 2002 El Niño event in a tropical rain forest in north-east Queensland,
672 Australia. *Biotropica*, 38(1), 16–26. <https://doi.org/10.1111/j.1744-7429.2006.00098.x>
- 673 Ehrlén, J., Morris, W. F., von Euler, T., & Dahlgren, J. P. (2016). Advancing environmentally
674 explicit structured population models of plants. *Journal of Ecology*, 104(2), 292–305.
675 <https://doi.org/10.1111/1365-2745.12523>
- 676 Engelbrecht, B. M. J., Wright, S. J., & De Steven, D. (2002). Survival and ecophysiology of tree
677 seedlings during El Niño drought in a tropical moist forest in Panama. *Journal of Tropical
678 Ecology*, 18, 569–579.
- 679 Esquivel-Muelbert, A., Baker, T. R., Dexter, K. G., Lewis, S. L., Brienen, R. J. W., Feldpausch, T.
680 R., Lloyd, J., Monteagudo-Mendoza, A., Arroyo, L., Álvarez-Dávila, E., Higuchi, N., Marimon, B.
681 S., Marimon-Junior, B. H., Silveira, M., Vilanova, E., Gloor, E., Malhi, Y., Chave, J., Barlow, J., ...
682 Phillips, O. L. (2019). Compositional response of Amazon forests to climate change. *Global
683 Change Biology*, 25(1), 39–56. <https://doi.org/10.1111/gcb.14413>
- 684 Esteban, E. J. L., Castilho, C. V., Melgaço, K. L., & Costa, F. R. C. (2021). The other side of
685 droughts: Wet extremes and topography as buffers of negative drought effects in an
686 Amazonian forest. *New Phytologist*, 229(4), 1995–2006.
687 <https://doi.org/10.1111/nph.17005>
- 688 Evers, S. M., Knight, T. M., Inouye, D. W., Miller, T. E. X., Salguero-Gómez, R., Iler, A. M., &
689 Compagnoni, A. (2021). Lagged and dormant season climate better predict plant vital rates
690 than climate during the growing season. *Global Change Biology*, 27(9), 1927–1941.
691 <https://doi.org/10.1111/gcb.15519>
- 692 Ewers, R. M., & Banks-Leite, C. (2013). Fragmentation impairs the microclimate buffering
693 effect of tropical forests. *PLoS ONE*, 8(3), e58093.
694 <https://doi.org/10.1371/journal.pone.0058093>
- 695 Feeley, K. J., Malhi, Y., Zelazowski, P., & Silman, M. R. (2012). The relative importance of
696 deforestation, precipitation change, and temperature sensitivity in determining the future
697 distributions and diversity of Amazonian plant species. *Global Change Biology*, 18(8), 2636–
698 2647. <https://doi.org/10.1111/j.1365-2486.2012.02719.x>
- 699 Gagnon, P. R., Bruna, E. M., Rubim, P., Darrigo, M. R., Littell, R. C., Uriarte, M., & Kress, W. J.
700 (2011). Growth of an understory herb is chronically reduced in Amazonian forest
701 fragments. *Biological Conservation*, 144(2), 830–835.
702 <https://doi.org/10.1016/j.biocon.2010.11.015>
- 703 Gaoue, O. G., Horvitz, C. C., Steiner, U. K., & Tuljapurkar, S. (2019). Climate, rather than
704 human disturbance, is the main driver of age-specific mortality trajectories in a tropical
705 tree. *Ecological Modelling*, 400, 34–40. <https://doi.org/10.1016/j.ecolmodel.2019.03.007>
- 706 Gasparrini, A. (2011). Distributed lag linear and non-linear models in R: The package dlnm.
707 *Journal of Statistical Software*, 43(8), 1–20. <https://doi.org/10.18637/jss.v043.i08>

- 708 Gasparrini, A., Scheipl, F., Armstrong, B., & Kenward, M. G. (2017). A penalized framework
709 for distributed lag non-linear models: Penalized DLNMs. *Biometrics*, 73(3), 938–948.
710 <https://doi.org/10.1111/biom.12645>
- 711 Gentry, A. H., & Dodson, C. (1987). Contribution of nontrees to species richness of a tropical
712 rain forest. *Biotropica*, 19(2), 149–156. <https://doi.org/10.2307/2388737>
- 713 González-M, R., Posada, J. M., Carmona, C. P., Garzón, F., Salinas, V., Idárraga-Piedrahita, Á.,
714 Pizano, C., Avella, A., López-Camacho, R., Norden, N., Nieto, J., Medina, S. P., Rodríguez-M, G.
715 M., Franke-Ante, R., Torres, A. M., Jurado, R., Cuadros, H., Castaño-Naranjo, A., García, H., &
716 Salgado-Negret, B. (2020). Diverging functional strategies but high sensitivity to an
717 extreme drought in tropical dry forests. *Ecology Letters*, n/a(n/a).
718 <https://doi.org/10.1111/ele.13659>
- 719 Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., Lovejoy, T. E.,
720 Sexton, J. O., Austin, M. P., Collins, C. D., Cook, W. M., Damschen, E. I., Ewers, R. M., Foster, B.
721 L., Jenkins, C. N., King, A. J., Laurance, W. F., Levey, D. J., Margules, C. R., ... Townshend, J. R.
722 (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science*
723 *Advances*, 1(2), e1500052. <https://doi.org/10.1126/sciadv.1500052>
- 724 Holyoak, M., & Heath, S. K. (2016). The integration of climate change, spatial dynamics, and
725 habitat fragmentation: A conceptual overview. *Integrative Zoology*, 11(1), 40–59.
726 <https://doi.org/10.1111/1749-4877.12167>
- 727 Horvitz, C. C., & Schemske, D. W. (1988). Demographic cost of reproduction in a Neotropical
728 herb: An experimental field study. *Ecology*, 69(6), 1741–1745.
729 <https://doi.org/10.2307/1941152>
- 730 Huete, A. R., Didan, K., Shimabukuro, Y. E., Ratana, P., Saleska, S. R., Hutyrá, L. R., Yang, W.,
731 Nemani, R. R., & Myneni, R. (2006). Amazon rainforests green-up with sunlight in dry
732 season. *Geophysical Research Letters*, 33(6). <https://doi.org/10.1029/2005GL025583>
- 733 Janssen, T., van der Velde, Y., Hofhansl, F., Luyssaert, S., Naudts, K., Driessen, B., Fleischer,
734 K., & Dolman, H. (2021). Drought effects on leaf fall, leaf flushing and stem growth in
735 Neotropical forest; reconciling remote sensing data and field observations. *Biogeosciences*
736 *Discussions*, 1–41. <https://doi.org/10.5194/bg-2021-30>
- 737 Jones, M. O., Kimball, J. S., & Nemani, R. R. (2014). Asynchronous Amazon forest canopy
738 phenology indicates adaptation to both water and light availability. *Environmental Research*
739 *Letters*, 9(12), 124021. <https://doi.org/10.1088/1748-9326/9/12/124021>
- 740 Kannenberg, S. A., Schwalm, C. R., & Anderegg, W. R. L. (2020). Ghosts of the past: How
741 drought legacy effects shape forest functioning and carbon cycling. *Ecology Letters*, 23(5),
742 891–901. <https://doi.org/10.1111/ele.13485>
- 743 Klimešová, J., Martínková, J., & Ottaviani, G. (2018). Belowground plant functional ecology:
744 Towards an integrated perspective. *Functional Ecology*, 32(9), 2115–2126.
745 <https://doi.org/10.1111/1365-2435.13145>

- 746 Kress, W. J. (1990). The diversity and distribution of *Heliconia* (Heliconiaceae) in Brazil.
747 *Acta Botanica Brasileira*, 4(1), 159–167.
- 748 Landau, W. M. (2021). The targets R package: A dynamic Make-like function-oriented
749 pipeline toolkit for reproducibility and high-performance computing. *Journal of Open*
750 *Source Software*, 6(57), 2959. <https://doi.org/ghwrqs>
- 751 Laurance, W. F., Andrade, A. S., Magrath, A., Camargo, J. L. C., Campbell, M., Fearnside, P. M.,
752 Edwards, W., Valsko, J. J., Lovejoy, T. E., & Laurance, S. G. (2014). Apparent environmental
753 synergism drives the dynamics of Amazonian forest fragments. *Ecology*, 95(11), 3018–
754 3026. <https://doi.org/10.1890/14-0330.1>
- 755 Laurance, W. F., Ferreira, L. V., Rankin de Merona, J. M., & Laurance, S. G. (1998). Rain forest
756 fragmentation and the dynamics of Amazonian tree communities. *Ecology*, 79(6), 2032–
757 2040.
- 758 Laurance, W. F., Nascimento, H. E. M., Laurance, S. G., Andrade, A., Ribeiro, J. E. L. S., Giraldo,
759 J. P., Lovejoy, T. E., Condit, R., Chave, J., Harms, K. E., & D'Angelo, S. (2006). Rapid decay of
760 tree-community composition in Amazonian forest fragments. *Proceedings of the National*
761 *Academy of Sciences*, 103(50), 19010–19014. <https://doi.org/10.1073/pnas.0609048103>
- 762 Laurance, W. F., & Williamson, G. B. (2001). Positive feedbacks among forest fragmentation,
763 drought, and climate change in the Amazon. *Conservation Biology*, 15(6), 1529–1535.
764 <https://doi.org/10.1046/j.1523-1739.2001.01093.x>
- 765 Laurance, W. F., Williamson, G. B., Delamônica, P., Oliveira, A., Lovejoy, T. E., Gascon, C., &
766 Pohl, L. (2001). Effects of a strong drought on Amazonian forest fragments and edges.
767 *Journal of Tropical Ecology*, 17(6), 771–785.
- 768 Leitold, V., Morton, D. C., Longo, M., dos-Santos, M. N., Keller, M., & Scaranello, M. (2018). El
769 Niño drought increased canopy turnover in Amazon forests. *New Phytologist*, 219(3), 959–
770 971. <https://doi.org/10.1111/nph.15110>
- 771 Marengo, J. A., Nobre, C. A., Tomasella, J., Oyama, M. D., Sampaio de Oliveira, G., de Oliveira,
772 R., Camargo, H., Alves, L. M., & Brown, I. F. (2008). The drought of Amazonia in 2005.
773 *Journal of Climate*, 21(3), 495–516. <https://doi.org/10.1175/2007JCLI1600.1>
- 774 Markewitz, D., Devine, S., Davidson, E. A., Brando, P., & Nepstad, D. C. (2010). Soil moisture
775 depletion under simulated drought in the Amazon: impacts on deep root uptake. *New*
776 *Phytologist*, 187(3), 592–607. <https://doi.org/10.1111/j.1469-8137.2010.03391.x>
- 777 Marra, G., & Wood, S. N. (2011). Practical variable selection for generalized additive models.
778 *Computational Statistics & Data Analysis*, 55(7), 2372–2387.
779 <https://doi.org/10.1016/j.csda.2011.02.004>
- 780 McKee, T. B., Doesken, N. J., Kleist, J., & others. (1993). The relationship of drought
781 frequency and duration to time scales. *Proceedings of the 8th Conference on Applied*
782 *Climatology*, 17, 179–183.

- 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., Nytch, 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? *Journal of*
825 *Insect Science*, 3(34), 1–6. <https://doi.org/10.1673/031.003.3401>
- 826 Pedersen, T. L. (2020). *Patchwork: The composer of plots* [Manual].
- 827 Phillips, O. L., van der Heijden, G., Lewis, S. L., López-González, G., Aragão, L. E. O. C., Lloyd, J.,
828 Malhi, Y., Monteagudo, A., Almeida, S., Dávila, E. A., Amaral, I., Andelman, S., Andrade, A.,
829 Arroyo, L., Aymard, G., Baker, T. R., Blanc, L., Bonal, D., de Oliveira, Á. C. A., ... Vilanova, E.
830 (2010). Drought–mortality relationships for tropical forests. *New Phytologist*, 187(3), 631–
831 646. <https://doi.org/10.1111/j.1469-8137.2010.03359.x>
- 832 Pierre, J.-S., Hullé, M., Gauthier, J.-P., & Rispe, C. (2020). Critical windows: A method for
833 detecting lagged variables in ecological time series. *Ecological Informatics*, 61, 101178.
834 <https://doi.org/10.1016/j.ecoinf.2020.101178>
- 835 Pumisitapon, P., Visser, R. G. F., & de Klerk, G.-J. (2012). Moderate abiotic stresses increase
836 rhizome growth and outgrowth of axillary buds in *Alstroemeria* cultured in vitro. *Plant Cell,*
837 *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)
838 [0160-7](https://doi.org/10.1007/s11240-012-0160-7)
- 839 R Core Team. (2020). *R: A language and environment for statistical computing*.
- 840 Rankin-de-Mérona, J. M., Prance, G. T., Hutchings, R. W., da Silva, M. F., Rodrigues, W. A., &
841 Uehling, M. E. (1992). Preliminary results of a large-scale tree inventory of upland rain
842 forest in the central Amazon. *Acta Amazonica*, 22(4), 493–534.
843 <https://doi.org/10.1590/1809-43921992224534>
- 844 Ribeiro, M. B. N., Bruna, E. M., & Mantovani, W. (2010). Influence of post-clearing treatment
845 on the recovery of herbaceous plant communities in Amazonian secondary forests.
846 *Restoration Ecology*, 18, 50–58.
- 847 Rundel, P. W., Cooley, A. M., Gerst, K. L., Riordan, E. C., Sharifi, M. R., Sun, J. W., & Tower, J. A.
848 (2020). Functional traits of broad-leaved monocot herbs in the understory and forest edges
849 of a Costa Rican rainforest. *PeerJ*, 8, e9958. <https://doi.org/10.7717/peerj.9958>
- 850 Rundel, P. W., Sharifi, M. R., Gibson, A. C., & Esler, K. J. (1998). Structural and physiological
851 adaptation to light environments in Neotropical *Heliconia* (Heliconiaceae). *Journal of*
852 *Tropical Ecology*, 14(6), 789–801. <https://doi.org/10.1017/S0266467498000571>
- 853 Salguero-Gómez, R., Jones, O. R., Archer, C. R., Buckley, Y. M., Che-Castaldo, J., Caswell, H.,
854 Hodgson, D., Scheuerlein, A., Conde, D. A., Brinks, E., Buhr, H., Farack, C., Gottschalk, F.,
855 Hartmann, A., Henning, A., Hoppe, G., Römer, G., Runge, J., Ruoff, T., ... Vaupel, J. W. (2015).
856 The COMPADRE Plant Matrix Database: An open online repository for plant demography.
857 *Journal of Ecology*, 103(1), 202–218. <https://doi.org/10.1111/1365-2745.12334>

- 858 Sapsford, S. J., Paap, T., Hardy, G. E. St. J., & Burgess, T. I. (2017). The 'chicken or the egg':
859 Which comes first, forest tree decline or loss of mycorrhizae? *Plant Ecology*, 218(9), 1093–
860 1106. <https://doi.org/10.1007/s11258-017-0754-6>
- 861 Scariot, A. (1999). Forest fragmentation effects on palm diversity in central Amazonia.
862 *Journal of Ecology*, 87(1), 66–76. <https://doi.org/10.1046/j.1365-2745.1999.00332.x>
- 863 Scheffers, B. R., Edwards, D. P., Macdonald, S. L., Senior, R. A., Andriamahohatra, L. R.,
864 Roslan, N., Rogers, A. M., Haugaasen, T., Wright, P., & Williams, S. E. (2017). Extreme
865 thermal heterogeneity in structurally complex tropical rain forests. *Biotropica*, 49(1), 35–
866 44. <https://doi.org/10.1111/btp.12355>
- 867 Schwalm, C. R., Anderegg, W. R. L., Michalak, A. M., Fisher, J. B., Biondi, F., Koch, G., Litvak,
868 M., Ogle, K., Shaw, J. D., Wolf, A., Huntzinger, D. N., Schaefer, K., Cook, R., Wei, Y., Fang, Y.,
869 Hayes, D., Huang, M., Jain, A., & Tian, H. (2017). Global patterns of drought recovery. *Nature*,
870 548(7666), 202–205. <https://doi.org/10.1038/nature23021>
- 871 Schwartz, N. B., Budsock, A. M., & Uriarte, M. (2019). Fragmentation, forest structure, and
872 topography modulate impacts of drought in a tropical forest landscape. *Ecology*, 100(6),
873 e02677. <https://doi.org/10.1002/ecy.2677>
- 874 Scott, E. R., Wei, J.-P., Li, X., Han, W.-Y., & Orians, C. M. (2021). Differing non-linear, lagged
875 effects of temperature and precipitation on an insect herbivore and its host plant.
876 *Ecological Entomology*, early view. <https://doi.org/10.1111/een.13023>
- 877 Selwood, K. E., McGeoch, M. A., & Nally, R. M. (2015). The effects of climate change and land-
878 use change on demographic rates and population viability. *Biological Reviews*, 90(3), 837–
879 853. <https://doi.org/10.1111/brv.12136>
- 880 Silva Junior, C. H. L., Pessôa, A. C. M., Carvalho, N. S., Reis, J. B. C., Anderson, L. O., & Aragão,
881 L. E. O. C. (2021). The Brazilian Amazon deforestation rate in 2020 is the greatest of the
882 decade. *Nature Ecology & Evolution*, 5(2), 144–145. <https://doi.org/10.1038/s41559-020-01368-x>
- 884 Simpson, G. L. (2021). *Gratia: Graceful 'ggplot'-Based graphics and other functions for GAMs*
885 *fitted using 'mgcv'* [Manual].
- 886 Sletvold, N. (2005). Density-dependent growth and survival in a natural population of the
887 facultative biennial *Digitalis purpurea*. *Journal of Ecology*, 93(4), 727–736.
888 <https://doi.org/10.1111/j.1365-2745.2005.01008.x>
- 889 Snow, D. W. (1981). Tropical frugivorous birds and their food plants - a world survey.
890 *Biotropica*, 13(1), 1–14. <https://doi.org/10.2307/2387865>
- 891 Stiles, F. G. (1975). Ecology, flowering phenology, and hummingbird pollination of some
892 Costa Rican *Heliconia* species. *Ecology*, 56(2), 285–301. <https://doi.org/10.2307/1934961>
- 893 Stouffer, P. C., & Bierregaard, R. O. (1996). Forest fragmentation and seasonal patterns of
894 hummingbird abundance in Amazonian Brazil. *Ararajuba*, 4(1), 9–14.

- 895 Taubert, F., Fischer, R., Groeneveld, J., Lehmann, S., Müller, M. S., Rödig, E., Wiegand, T., &
896 Huth, A. (2018). Global patterns of tropical forest fragmentation. *Nature*, 554(7693), 519–
897 522. <https://doi.org/10.1038/nature25508>
- 898 Teller, B. J., Adler, P. B., Edwards, C. B., Hooker, G., & Ellner, S. P. (2016). Linking
899 demography with drivers: Climate and competition. *Methods in Ecology and Evolution*, 7(2),
900 171–183. <https://doi.org/10.1111/2041-210X.12486>
- 901 Tenhumberg, B., Crone, E. E., Ramula, S., & Tyre, A. J. (2018). Time-lagged effects of weather
902 on plant demography: Drought and *Astragalus scaphoides*. *Ecology*, 99(4), 915–925.
903 <https://doi.org/10.1002/ecy.2163>
- 904 Ticktin, T. (2003). Relationships between El Niño Southern Oscillation and demographic
905 patterns in a substitute food for collared peccaries in Panama. *Biotropica*, 35(2), 189–197.
906 <https://doi.org/10.1111/j.1744-7429.2003.tb00278.x>
- 907 Uriarte, M., Anciães, M., da Silva, M. T. B., Rubim, R., Johnson, E., & Bruna, E. M. (2011).
908 Disentangling the drivers of reduced long-distance seed dispersal by birds in an
909 experimentally fragmented landscape. *Ecology*, 92(4), 924–937.
910 <https://doi.org/10.1890/10-0709.1>
- 911 Uriarte, M., Bruna, E. M., Rubim, P., Anciães, M., & Jonckheere, I. (2010). Effects of forest
912 fragmentation on the seedling recruitment of a tropical herb: assessing seed vs. safe-site
913 limitation. *Ecology*, 91(5), 1317–1328. <https://doi.org/10.1890/09-0785.1>
- 914 Uriarte, M., Muscarella, R., & Zimmerman, J. K. (2018). Environmental heterogeneity and
915 biotic interactions mediate climate impacts on tropical forest regeneration. *Global Change*
916 *Biology*, 24(2), e692–e704. <https://doi.org/10.1111/gcb.14000>
- 917 Uriarte, M., Schwartz, N., Powers, J. S., Marín-Spiotta, E., Liao, W., & Werden, L. K. (2016).
918 Impacts of climate variability on tree demography in second growth tropical forests: The
919 importance of regional context for predicting successional trajectories. *Biotropica*, 48(6),
920 780–797. <https://doi.org/10.1111/btp.12380>
- 921 Vasconcelos, H. L., & Luizão, F. J. (2004). Litter production and litter nutrient
922 concentrations in a fragmented Amazonian landscape. *Ecological Applications*, 14(3), 884–
923 892. <https://doi.org/10.1890/03-5093>
- 924 Vicente-Serrano, S. M., Beguería, S., & López-Moreno, J. I. (2010). A multiscalar drought
925 index sensitive to global warming: The standardized precipitation evapotranspiration
926 index. *Journal of Climate*, 23(7), 1696–1718. <https://doi.org/10.1175/2009JCLI2909.1>
- 927 Westerband, A. C., Horvitz, C. C., & Gilliam, F. (2017). Early life conditions and precipitation
928 influence the performance of widespread understory herbs in variable light
929 environments. *Journal of Ecology*, 105(5), 1298–1308. <https://doi.org/10.1111/1365-2745.12757>
- 931 Wickham, H. (2016). *Ggplot2: Elegant graphics for data analysis*. Springer-Verlag New York.

- 932 Williams, J. L., Jacquemyn, H., Ochocki, B. M., Brys, R., Miller, T. E. X., & Shefferson, R. (2015).
933 Life history evolution under climate change and its influence on the population dynamics of
934 a long-lived plant. *Journal of Ecology*, *103*(4), 798–808. [https://doi.org/10.1111/1365-](https://doi.org/10.1111/1365-2745.12369)
935 [2745.12369](https://doi.org/10.1111/1365-2745.12369)
- 936 Williamson, G. B., Laurance, W. F., Oliveira, A. A., Delamônica, P., Gascon, C., Lovejoy, T. E., &
937 Pohl, L. (2000). Amazonian tree mortality during the 1997 El Niño drought. *Conservation*
938 *Biology*, *14*(5), 1538–1542. <https://doi.org/10.1046/j.1523-1739.2000.99298.x>
- 939 Wood, S. N. (2017). *Generalized additive models: An introduction with R* (Second edition).
940 CRC Press/Taylor & Francis Group.
- 941 Wright, S. J. (1992). Seasonal drought, soil fertility and the species density of tropical forest
942 plant communities. *Trends in Ecology & Evolution*, *7*(8), 260–263.
943 [https://doi.org/10.1016/0169-5347\(92\)90171-7](https://doi.org/10.1016/0169-5347(92)90171-7)
- 944 Wright, S. J., & Calderon, O. (2006). Seasonal, El Niño and longer term changes in flower and
945 seed production in a moist tropical forest. *Ecology Letters*, *9*(1), 35–44.
946 <https://doi.org/10.1111/j.1461-0248.2005.00851.x>
- 947 Wright, S. J., Carrasco, C., Calderon, O., & Paton, S. (1999). The El Niño Southern Oscillation
948 variable fruit production, and famine in a tropical forest. *Ecology*, *80*(5), 1632–1647.
- 949 Xavier, A. C., King, C. W., & Scanlon, B. R. (2016). Daily gridded meteorological variables in
950 Brazil (1980). *International Journal of Climatology*, *36*(6), 2644–2659.
951 <https://doi.org/10.1002/joc.4518>
- 952 Zartman, C. E., Amaral, J. A., Figueiredo, J. N., & Dambros, C. D. (2015). Drought impacts
953 survivorship and reproductive strategies of an epiphyllous leafy liverwort in central
954 Amazonia. *Biotropica*, *47*(2), 172–178.
- 955 Zeng, N., Yoon, J. H., Marengo, J. A., Subramaniam, A., Nobre, C. A., Mariotti, A., & Neelin, J. D.
956 (2008). Causes and impacts of the 2005 Amazon drought. *Environmental Research Letters*,
957 *3*(1), 1–9. <https://doi.org/10.1088/1748-9326/3/1/014002>