Interactive effects of drought and habitat fragmentation on vital rates of an understory tropical plant

Eric R. Scott1,✉, Maria Uriarte2, and Emilio M. Bruna

04 February, 2021

Text of abstract

1 Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, Florida 32611-0430  
2 Department of Ecology, Evolution and Environmental Biology, Columbia University 1200 Amsterdam Avenue, New York, New York 10027 USA

✉ Correspondence: [Eric R. Scott <[scottericr@gmail.com](mailto:scottericr@gmail.com)>](mailto:scottericr@gmail.com)

Keywords: forest fragmentation; vital rates; *Heliconia acuminata*; drought; ENSO; edge effects

Highlights: These are the highlights

# 1 Introduction

1. Organisms simultanously experience multiple forms of natural and anthropogenic disturbance. While work investigating the demographic effects of individual factors is common, studies investigating how multiple factors interact to influence population dynamics remains poorly understood. They could act in concert to exacerbate or dampen population dynamics. For example, fire and herbivory …(Tye et al. 2016).
   * Cite Pedro F. Quintana-Ascencio in intro—he will likely be a reviewer.
   * Cite Jennifer Williams
   * Emphasize demography. We know about interactions on physiology and other stuff, but we don’t know as much about how demography of plants is shaped by how populations respond to multiple stresses, increasingly anthropogenic.
2. Habitat fragmentation is a major source of environmental stress. **[I’m not sure I’d call it a stress…I think the biotic and abioti changes associated with it are stressful]** Forest fragmentation, in particular, is widespread and has resulted in 70% of the Earth’s remaining forest being within 1km of forest edge (Haddad et al. 2015). Of particular concern are the effects of fragmentation on species-rich tropical ecosystems. In the Brazilian Amazon, for example, over 70,000 km of new forest edges are being created annually (Broadbent et al. 2008) and the proportion of forest >1 km from an forest edge has decreased to from 90% to only 75% (Haddad et al. 2015). Fragmentation can impact plant population dynamics through …
3. In addition to the environmental changes associated with fragmentation, populations persisting in tropical forest remnants experience abiotic stress resulting from climate change. For instance, the northern Amazon has been experiencing a drying trend since the mid-1970s, and ensemble climate models predict substantial decreases in dry season precipitation in southern Amazonia for the 21st century (Malhi et al. 2008). Furthermore, droughts induced by the El Niño Southern Oscillation (ENSO) are predicted to increase in frequency and severity (Cai et al. 2014).
   * Drought is bad because…
   * 1997 ENSO drought (Williamson et al. 2000)
   * 2005 ENSO drought (Marengo et al. 2008, Phillips et al. 2009)
   * 2010 drought (Lewis et al. 2011)
4. It has been hypothesized that drought and fragmentation could act in synergy to further reduce population viability in fragmented landscapes, particularly in the tropics (Didham and Lawton 1999, Laurance et al. 2001). Fragmentation drives several changes in microclimate near forest edges, including increased air temperature, decreased relative humidity, reduced soil moisture, and increased penetration of solar radiation in the forest understory (Didham and Lawton 1999, Ewers and Banks-Leite 2013). This decrease in microclimatic buffering could exacerbate the effects of drought in fragments compared to intact forest. This may be why the drought-induced mortality of trees is higher near forest edges than in forest interiors (Laurance et al. 2001, Schwartz et al. 2019).
5. Alternatively, the populations persisting in fragments may be more resilient to drought if individuals susceptible to desiccation died quickly after fragment isolation.
   * (Betts et al. 2019).

* In addition to variation among vital rates, responses to drought and fragmentation could depend on life history stage or plant size. Large established adults could respond differently than seedlings. This is unknown because there are very few systems where we have data on entire life history in a climate change or fragmentation context.
  + Fragmentation affects plant size (in *Heliconia* (Bruna and Oli 2005) and trees (Schwartz et al. 2019)). Smaller/larger plants might be more susceptible to drought. So differential effects of drought in fragments and continuous forest could be due to an interaction between drought and plant size.

To date, however, this hypothesis remains untested for three primary reasons. First, most studies elucidating how tropical plants respond to fragmentation have studied either juvenile (i.e., seed, seedling) or larger, reproductive plants. . . Additionally, while most studies of tropical plant demography focus on trees, little is known about the understory plants that comprise up to \_\_\_\_% of biomass in tropical forests and are ecologically important .

Second, there is a growing literature on how tropical plants respond to droughts, but few studies have compared the responses of plants in continuous forest with those in forest fragments. Laurance et al. (2001) found that the increase in tree (>10 cm DBH) mortality during a drought were exacerbated in fragments, but the decline in mortality after the drought was also stronger in fragments. However, in a temperate system… (Forner et al. 2020).

Finally, the long-term data needed to test population-level hypotheses about climate change-fragmentation synergies are scant, especially for tropical systems (Crone et al. 2011, Salguero-Gomez et al. 2015). However, without multi-decadal sampling one cannot capture enough droughts to quantify their ecological impact, nor the variation in vital rates needed to parameterize demographic models of long-lived species in changing climates (Morris and Doak 2002, Teller et al. 2016). Long-term data are also needed because while some demographic effects of fragmentation or drought on can be detected immediately, others may take years to manifest.

We investigated the effects of drought on the growth, survival, reproduction, and recruitment of a understory herb in an experimentally fragmented landscape in the Central Amazon. Specifically, we asked 1) Does drought increase or decrease the growth, survival, and fertility rates of plant populations in continuous forest? 2) Are the effects of drought on the vital rates of populations in fragments similar in direction and magnitude to those in continuous forest? 3) Are the effects of drought and fragmentation on vital rates consistent across life-history stages?

# 2 Methods

## 2.1 Study site

The Biological Dynamics of Forest Fragments Project (BDFFP) is located ~70 km north of Manaus, Brazil (2º30’ S, 60ºW). In addition to large areas of continuous forest, the BDFFP has forest fragment reserves that range in size from 1-100 ha (Fig. – ). These fragments were isolated from 1980–1984 by felling the trees surrounding the area chosen for isolation and - in most cases - burning the downed trees once they dried. In subsequent decades the vegetation regenerating around fragments has been periodically cleared to ensure fragment isolation (Bierregaard et al. 2001).

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

## 2.2 Focal species

*Heliconia acuminata* (LC Rich.) (Heliconiaceae) is a perennial monocot distributed throughout Central Amazonia (Kress 1990); it is the most abundant understory herb at the BDFFP (Ribeiro et al. 2010). While many *Heliconia* species grow in large patches along forest edges or in disturbed areas, others—including as *H. acuminata*—are usually found at lower densities and in the more shaded forest understory. These species produce fewer infloresences and are pollinated by traplining rather than territorial hummingbirds (Berry and Kress 1991). In our sites *H. acuminata* is pollinated by *Phaeothornis superciliosus* and *P. bourcieri* (Bruna et al. 2004); reproductive plants have = **X.X** flowering shoots (range = 1-7), each of which has an inflorescence with 20–25 flowers (Bruna and Kress 2002). Fruits mature April-May and are consumed by a thrush and several species of manakin (Uriarte et al. 2011). Dispersed seeds (1–3 seeds per fruit, =2 ) germinate ~6 months after dispersal at the beginning of the rainy season, and have higher rates of germination and seedling establishment in continuous forest than forest fragments (Bruna 1999, Bruna and Kress 2002). *Heliconia acuminata* is self-incompatible and does not reproduce vegetatively.

## 2.3 Demographic data collection

In 1997–1998 we established a series of 5000 plots (m) in the BDFFP reserves in which we marked and measured all *Heliconia acuminata*. The plots are located in continuous forest (n=6), 10-ha fragments (n=3), and 1-ha fragments (n=4), with distance between plots ranging from 500 m–41 km. Plots in 1-ha fragments were on one randomly selected half of the fragment, plots in 10-ha fragments were in the fragment center, and plots in continuous forest were placed in locations 500-4000 m from the borders of secondary and mature forest (Fig or Table ). Each plot is subdivided into 50 quadrats (m) to simplify the annual surveys, during which we recorded the number of vegetative shoots each plant had, the height of each plant to the tallest leaf, and the identity of any flowering plants. We also surveyed plots regularly during the rainy season to identify any that flowered after the survey. Height and shoot number are correlated with leaf area, the probability of flowering, and rates of survivorship (Bruna 2002, Bruna and Kress 2002). Plants that were not found for three consecutive surveys were considered dead. In 2008 we mapped the location of all established plants to the nearest 10 cm; in subsequent years we did the same with all new seedlings. There is a seven-fold range in H. acuminata density in the forest plots, with density in several of the plots comparable to that in low-density fragments (Bruna and Kress 2002).

## 2.4 Weather data

Precipitation and potential evapotranspiration data were obtained from a gridded dataset (0.25º x 0.25º resolution) built using data from 3,625 ground-based weather stations across Brazil (Xavier et al. 2016). The estimates of potential evapotranspiration were calculated using the Pennman-Monteith method, and then along with monthly precipitation were used to calculate the standardized precipitation evapotranspiration index (SPEI) (Vicente-Serrano et al. 2010). SPEI is a proxy for meteorological drought that integrates precipitation and evapotranspiration anomalies over a specified time scale. Positive SPEI values for a given month indicate conditions wetter than the historical average for that month, while negative values of SPEI indicate droughts with intensity categorized as mild (0 to -1), moderate (-1 to -1.5), severe (-1.5 to -2), or extreme (< -2) (McKee et al. 1993). Because *H. acuminata* lacks deep taproots to access groundwater, it probably relies primarily on soil moisture rather than deeper water sources that can persist for longer timescales. We therefore quantified periods of drought with the 3-month SPEI, which we calculated using the SPEI package in R version 4.0.2 (2020-06-22) (Beguería 2017a, R Core Team 2020). The timing of drought events based on these SPEI calculations is consistent with that resulting from SPEI calculated with other data sources (e.g., nearby weather stations, the global SPEI database (Beguería 2017b), TRMM (“TRMM (TMPA/3B43) rainfall estimate L3 1 month 0.25 degree x 0.25 degree V7” 2011)), though the magnitude of drought can sometimes differ (Appendix 1).

## 2.5 Statistical Modeling

We assessed the effects of drought history on plant vital rates using distributed lag non-linear models (DLNMs) (Gasparrini et al. 2017). DLNMs model potentially delayed effects of predictor variables by fitting a bi-dimensional predictor-lag-response association spline, referred to as a crossbasis function. This function allows the effect of a predictor to vary non-linearly through lag time and across predictor intensity. Crossbasis functions were created using the *dlnm* package with possible lags from 0–36 months (Gasparrini 2011, R Core Team 2020). We chose 36 months as a maximum lag because *H. acuminata* individuals transplanted to forest fragments typically recovered from transplant shock within 36 months (Bruna et al. 2002). The crossbasis function was fit to the data in the context of a generalized additive model (GAM) using the *mgcv* package with restricted maximum likelihood (Wood 2017). The general form of the vital rate models was as follows:

$$
g[\textrm{E}(y\_{i})] = \alpha\_j + s\_1(x\_i) + s\_2(d\_{i,t}, ..., d\_{i,t-24}) \\
\alpha\_j \sim N(\mu\_{\alpha\_j}, \sigma^2\_{\alpha\_j}), \textrm{for plot }j
$$

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

Where the crossbasis function, , is composed of two marginal basis functions: the standard predictor-response function , and the additional lag-response function . These marginal functions are combined as a tensor product smooth such that the shape of one marginal function varies smoothly along the other dimension (see Wood (n.d.) and Gasparrini et al. (2017) for more detail). Penalized cubic regression splines were used for both marginal bases of the crossbasis function, with 35 knots for the lag dimension and 3 knots for the drought response dimension to restrict the fitted response to drought to bimodal at most complex. A random effect of plot ID on the intercept is represented by . For plant growth the response was plant size (height shoot number) in year t+1 modeled with a scaled t family error distribution and a log link function (). A scaled t family was chosen because residuals were leptokurtic with a Gaussian error structure. The data on number of infloresences was converted to binary (1 for ≥1 inflorescence, 0 for no inflorescences). When survival and flowering were the response variables we used a binomial family error distribution with a logit link function.

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

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

# 3 Results

Start with descriptive results of drought events—how many droughts, how severe, timing of droughts, etc.

## 3.1 Survival

Overall survival rate across the entire dataset is 0.95 in both CF and 1-ha. Survival was lowest in 2004 which coincided with a moderate drought in Jan 2004 / Feb 2005 and a severe drought in Jan–Mar of 2004. Survival was lower in continuous forest compared to 1-ha fragments in this year (~0.91 compared to ~0.94, will get exact numbers from data). The lowest survival for 1-ha fragment plots (about 0.93) was actually in the 2006 census corresponding to unusually wet weather (SPEI >0.5), but with a moderate drought the preceding October.

### 3.1.1 Continuous Forest

size: p < 0.001 (figure = surv\_cf\_size.png)

plot: p < 0.001

SPEI: p < 0.001 (figure = surv\_cf\_spei.png)

Lags 6-0 (Aug–Feb) and 20-15 (Jun–Nov) show reduced survival with drought. Lags 14-7 (Dec - Jul) and 26-21 (Dec-May) show increased survival with drought. Lag 36-33 (Feb - May) shows quadratic relationship with increased survival in dry and wet conditions (this seems like it’s gotta be spurious).

### 3.1.2 1-ha fragment

size: p <0.001 (figure = surv\_1ha\_size.png)

plot: p = 0.258

SPEI: p < 0.001 (figure = surv\_1ha\_spei.png)

Crossbasis is very flat with essentially no effect of SPEI beyond 6 months lag. Recent SPEI has bimodal effect with both low and high values reducing survival.

**Question**: Currently the figures are expected values for the average plant across both plots. This makes it look like survival is a lot higher in 1-ha fragments when in reality survival is exactly the same (0.95) because plants are smaller in 1-ha fragments. Should these plots instead be for an average sized plant within the habitat type?

## 3.2 Growth

Plants were on average larger in continuous forest compared to 1-ha fragments. In continuous forest, plants had an average of 2.91 shoots and were on average 40.6 cm tall with an average size (shoots height) of 150. In 1-ha fragments, plants had 2.53 shoots on average and a mean height of 36.2 cm and a mean size of 115.

The size difference between plants in continuous forest and 1-ha fragments was more dramatic early on in the dataset with mean sizes becoming more similar over time.

**NOTE**: I considered adding a covariate of year to account for yearly trends in growth, but since there is also a trend in SPEI over the time of this experiment, they were concurve (wiggly collinearity), and shouldn’t both be included in model.

### 3.2.1 Continuous Forest

size: p < 0.001

plot: p < 0.001

SPEI: p < 0.001

Predicted results show only lagged effects of SPEI on growth (f(x) at lags 0 and 1 is flat). Wet conditions in preceding winter months improve growth (lags 4-2, Oct - Dec). Positive effect of drought on growth at lags 11-8 (Mar - Jun) and 34-24 (nearly the entirety of year t-2).

### 3.2.2 1-ha fragment

size: p < 0.001

plot: p < 0.001

SPEI: p < 0.001

Crossbasis looks very similar to continuous forest but more extreme. SPEI has a stronger effect on growth in fragments. Wet conditions at lag 0 predict the greatest shrinkage of plants in fragments (∆size = -75 at SPEI >2), but at lags 5-2 (Sept-Dec) high SPEI has a less negative effect on plant size. We only expect plant growth (∆size > 0) in years when SPEI was low at lags 34-32

The size of plants significantly predicted their size in the following year in continuous forest (edf = 7.8, P < 0.001 ) and forest fragments (edf = 7.4, P < 0.001). In continuous forest, plants under a size of 259 were predicted to grow from year t-1 to year t, and the fit line was below 1:1 for larger plants, indicating that larger plants tended to shrink, on average. In 1 ha fragments, the fit line followed a 1:1 line more closely, indicating that plants tended to stay the same size on average from year to year over the course of this study. Drought history also had a significant effect on plant size in both continuous forest (edf = 14.7, p < 0.001) and fragments (edf = 17.8, p < 0.001).

## 3.3 Flowering

Probability of flowering increased with size and was generally higher in continuous forest compared to 1-ha fragments. The exceptions to this are in 2006 and 2008 when the proportion of flowering plants was lower in continuous forest. The most striking difference between habitat types in flowering proportion was in 2003 when 9.7% of plants flowered in the continuous forest plots and only 2.7% flowered in fragment plots.

### 3.3.1 Continuous forest

size: p < 0.001

plot: p<0.001

SPEI: p < 0.001

Flowering probability was increased by recent drought (at lag = 0 with SPEI < 1) and drought at lags 20-15 (Jun - Nov). Drought at lags 13-7 reduced flowering probability

## 3.4 Size by year interaction

In continuous forest plots there was support for size by year interactions for growth (95% LRnull = 4.54, LRobs = 45.69) and survival (95% LRnull = 3.91, LRobs = 29.18) , but not for flowering (95% LRnull = 4.44, LRobs = 1.77). However, in 1 ha fragments, we saw no evidence of size by year interaction. For growth 95% LRnull = 4.45, LRobs = 4.35, for survival 95% LRnull = 4.47, LRobs = 0.62, and for flowering probability 95% LRnull = 3.86, LRobs = 2.82. This is consistent with the DLNMs in that the crossbasis functions for \_\_\_ and \_\_\_ were much flatter in fragments compared to continuous forest.

# 4 Discussion

Caveats:

One limitation of the DLNM approach is that it does not currently allow for modeling of interactions with a crossbasis function. This limitation meant that we were unable to model a potential size by environment (i.e. drought history) interaction, which may occur with many plant species (Tredennick et al. 2018). To check for a size by environment interaction, we followed the methods of Tredennick et al. (2018) and fit a pair of generalized linear mixed effects models (GLMMs) for each vital rate using the *lme4* package (Bates et al. 2015). Rather than explicitly modeling the effects of drought history, we modeled environmental stochasticity with random effects of year. For each vital rate, we essentially replaced the crossbasis function in Eq 1. with a random effect of year on either the intercept or both the intercept and relationship with plant size. We assessed the significance of the year-by-size interaction by testing the likelihood ratio of models with and without the interaction against an expected likelihood ratio distribution under the null hypothesis of no interaction (Tredennick et al. 2018).

# 5 Conclusion

# 6 Acknowledgments

We thank —-, —-, —-, and — anonymous reviewers for helpful discussions and comments on the manuscript. We also thank the technicians and students who helped conduct the *Heliconia* censuses and the BDFFP and INPA for logistical support. Financial support was provided by the U.S. National Science Foundation (awards DEB-0614339, DEB-0614149, INT 98-06351, and DEB-1948607). This is publication No. —- in the BDFFP Technical Series.

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

# 7 References

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Beguería, S. 2017a. Sbegueria/SPEIbase: Version 2.5.1. Zenodo.

Beguería, S. 2017b, July. Sbegueria/SPEIbase: Version 2.5.1. Zenodo.

Berry, F., and W. J. Kress. 1991. Heliconia: An identification guide. Smithsonian Institution Press, Washington D.C., USA.

Betts, M. G., C. Wolf, M. Pfeifer, C. Banks-Leite, V. Arroyo-Rodríguez, D. B. Ribeiro, J. Barlow, F. Eigenbrod, D. Faria, R. J. Fletcher, A. S. Hadley, J. E. Hawes, R. D. Holt, B. Klingbeil, U. Kormann, L. Lens, T. Levi, G. F. Medina-Rangel, S. L. Melles, D. Mezger, J. C. Morante-Filho, C. D. L. Orme, C. A. Peres, B. T. Phalan, A. Pidgeon, H. Possingham, W. J. Ripple, E. M. Slade, E. Somarriba, J. A. Tobias, J. M. Tylianakis, J. N. Urbina-Cardona, J. J. Valente, J. I. Watling, K. Wells, O. R. Wearn, E. Wood, R. Young, and R. M. Ewers. 2019. Extinction filters mediate the global effects of habitat fragmentation on animals. Science 366:1236–1239.

Bierregaard, R. O., C. Gascon, T. E. Lovejoy, and R. Mesquita, editors. 2001. Lessons from Amazonia: The ecology and conservation of a fragmented forest. Yale University Press, New Haven.

Bierregaard, R. O., C. Gascon, T. E. Lovejoy, and R. Mesquita, editors. 2001. Lessons from Amazonia: The ecology and conservation of a fragmented forest. Yale University Press, New Haven.

Broadbent, E. N., G. P. Asner, M. Keller, D. E. Knapp, P. J. C. Oliveira, and J. N. Silva. 2008. Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon. Biological Conservation 141:1745–1757.

Bruna, E. M. 1999. Seed germination in rainforest fragments. Nature 402:139.

Bruna, E. M. 2002. Effects of forest fragmentation on Heliconia acuminata seedling recruitment in central Amazonia. Oecologia 132:235–243.

Bruna, E. M., and W. J. Kress. 2002. Habitat Fragmentation and the Demographic Structure of an Amazonian Understory Herb (Heliconia acuminata). Conservation Biology 16:1256–1266.

Bruna, E. M., W. J. Kress, F. Marques, and O. F. da Silva. 2004. Heliconia acuminata reproductive success is independent of local floral density. Acta Amazonica 34:467–471.

Bruna, E. M., O. Nardy, S. Y. Strauss, and S. Harrison. 2002. Experimental assessment of Heliconia acuminata growth in a fragmented Amazonian landscape. Journal of Ecology:11.

Bruna, E. M., and M. K. Oli. 2005. Demographic effects of habitat fragmentation on a tropical herb: life-table response experiments. Ecology 86:1816–1824.

Cai, W., S. Borlace, M. Lengaigne, P. van Rensch, M. Collins, G. Vecchi, A. Timmermann, A. Santoso, M. J. McPhaden, L. Wu, M. H. England, G. Wang, E. Guilyardi, and F.-F. Jin. 2014. Increasing frequency of extreme El Niño events due to greenhouse warming. Nature Climate Change 4:111–116.

Crone, E. E., E. S. Menges, M. M. Ellis, T. Bell, P. Bierzychudek, J. Ehrlen, T. N. Kaye, T. M. Knight, P. Lesica, W. F. Morris, G. Oostermeijer, P. F. Quintana-Ascencio, A. Stanley, T. Ticktin, T. Valverde, and J. L. Williams. 2011. How do plant ecologists use matrix population models? Ecology Letters 14:1–8.

Didham, R. K., and J. H. Lawton. 1999. Edge Structure Determines the Magnitude of Changes in Microclimate and Vegetation Structure in Tropical Forest Fragments. Biotropica 31:17–30.

Didham, R. K., and J. H. Lawton. 1999. Edge Structure Determines the Magnitude of Changes in Microclimate and Vegetation Structure in Tropical Forest Fragments. Biotropica 31:17–30.

Didham, R. K., and J. H. Lawton. 1999. Edge Structure Determines the Magnitude of Changes in Microclimate and Vegetation Structure in Tropical Forest Fragments. Biotropica 31:17–30.

Ewers, R. M., and C. Banks-Leite. 2013. Fragmentation Impairs the Microclimate Buffering Effect of Tropical Forests. PLoS ONE 8:e58093.

Forner, A., T. Morán-López, D. Flores-Rentería, I. Aranda, and F. Valladares. 2020. Fragmentation reduces severe drought impacts on tree functioning in holm oak forests. Environmental and Experimental Botany 173:104001.

Gasparrini, A. 2011. Distributed Lag Linear and Non-Linear Models in *R* : The Package **dlnm**. Journal of Statistical Software 43.

Gasparrini, A., F. Scheipl, B. Armstrong, and M. G. Kenward. 2017. A penalized framework for distributed lag non-linear models: Penalized DLNMs. Biometrics 73:938–948.

Haddad, N. M., L. A. Brudvig, J. Clobert, K. F. Davies, A. Gonzalez, R. D. Holt, T. E. Lovejoy, J. O. Sexton, M. P. Austin, C. D. Collins, W. M. Cook, E. I. Damschen, R. M. Ewers, B. L. Foster, C. N. Jenkins, A. J. King, W. F. Laurance, D. J. Levey, C. R. Margules, B. A. Melbourne, A. O. Nicholls, J. L. Orrock, D.-X. Song, and J. R. Townshend. 2015. Habitat fragmentation and its lasting impact on Earth’s ecosystems. Science Advances 1:e1500052.

Kress, J. 1990. The diversity and distribution of Heliconia (Heliconiaceae) in Brazil. Acta Botanica Brasileira 4:159–167.

Laurance, W. F., G. B. Williamson, P. Delamônica, A. Oliveira, T. E. Lovejoy, C. Gascon, and L. Pohl. 2001. Effects of a Strong Drought on Amazonian Forest Fragments and Edges. Journal of Tropical Ecology 17:771–785.

Laurance, W. F., G. B. Williamson, P. Delamônica, A. Oliveira, T. E. Lovejoy, C. Gascon, and L. Pohl. 2001. Effects of a Strong Drought on Amazonian Forest Fragments and Edges. Journal of Tropical Ecology 17:771–785.

Laurance, W. F., G. B. Williamson, P. Delamônica, A. Oliveira, T. E. Lovejoy, C. Gascon, and L. Pohl. 2001. Effects of a Strong Drought on Amazonian Forest Fragments and Edges. Journal of Tropical Ecology 17:771–785.

Lewis, S. L., P. M. Brando, O. L. Phillips, G. M. F. van der Heijden, and D. Nepstad. 2011. The 2010 Amazon Drought. Science 331:554–554.

Malhi, Y., J. T. Roberts, R. A. Betts, T. J. Killeen, W. Li, and C. A. Nobre. 2008. Climate Change, Deforestation, and the Fate of the Amazon. Science 319:169–172.

Marengo, J. A., C. A. Nobre, J. Tomasella, M. D. Oyama, G. Sampaio de Oliveira, R. de Oliveira, H. Camargo, L. M. Alves, and I. F. Brown. 2008. The Drought of Amazonia in 2005. Journal of Climate 21:495–516.

Marra, G., and S. N. Wood. 2011. Practical variable selection for generalized additive models. Computational Statistics & Data Analysis 55:2372–2387.

McKee, T. B., N. J. Doesken, and J. Kleist. 1993. The Relationship of Drought Frequency and Duration to Time Scales.

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology: Theory and practice of population viability analysis. Sinauer, Sunderland, MA.

Phillips, O. L., L. E. O. C. Aragao, S. L. Lewis, J. B. Fisher, J. Lloyd, G. Lopez-Gonzalez, Y. Malhi, A. Monteagudo, J. Peacock, C. A. Quesada, G. van der Heijden, S. Almeida, I. Amaral, L. Arroyo, G. Aymard, T. R. Baker, O. Banki, L. Blanc, D. Bonal, P. Brando, J. Chave, A. C. A. de Oliveira, N. D. Cardozo, C. I. Czimczik, T. R. Feldpausch, M. A. Freitas, E. Gloor, N. Higuchi, E. Jimenez, G. Lloyd, P. Meir, C. Mendoza, A. Morel, D. A. Neill, D. Nepstad, S. Patino, M. C. Penuela, A. Prieto, F. Ramirez, M. Schwarz, J. Silva, M. Silveira, A. S. Thomas, H. t. Steege, J. Stropp, R. Vasquez, P. Zelazowski, E. A. Davila, S. Andelman, A. Andrade, K.-J. Chao, T. Erwin, A. Di Fiore, E. H. C., H. Keeling, T. J. Killeen, W. F. Laurance, A. P. Cruz, N. C. A. Pitman, P. N. Vargas, H. Ramirez-Angulo, A. Rudas, R. Salamao, N. Silva, J. Terborgh, and A. Torres-Lezama. 2009. Drought Sensitivity of the Amazon Rainforest. Science 323:1344–1347.

R Core Team. 2020. R: A language and environment for statistical computing. Vienna, Austria.

Rankin-de-Mérona, J. M., G. T. Prance, R. W. Hutchings, M. F. da Silva, W. A. Rodrigues, and M. E. Uehling. 1992. Preliminary results of a large-scale tree inventory of upland rain forest in the central Amazon. Acta Amazonica 22:493–534.

Ribeiro, M. B. N., E. M. Bruna, and W. Mantovani. 2010. Influence of post-clearing treatment on the recovery of herbaceous plant communities in amazonian secondary forests. Restoration Ecology 18:50–58.

Salguero-Gomez, R., O. R. Jones, C. R. Archer, Y. M. Buckley, J. Che-Castaldo, H. Caswell, D. Hodgson, A. Scheuerlein, D. A. Conde, E. Brinks, H. de Buhr, C. Farack, F. Gottschalk, A. Hartmann, A. Henning, G. Hoppe, G. Roemer, J. Runge, T. Ruoff, J. Wille, S. Zeh, R. Davison, D. Vieregg, A. Baudisch, R. Altwegg, F. Colchero, M. Dong, H. de Kroon, J. D. Lebreton, C. J. E. Metcalf, M. M. Neel, I. M. Parker, T. Takada, T. Valverde, L. A. Velez-Espino, G. M. Wardle, M. Franco, and J. W. Vaupel. 2015. The COMPADRE Plant Matrix Database: An open online repository for plant demography. Journal of Ecology 103:202–218.

Scariot, A. 1999. Forest fragmentation effects on palm diversity in central Amazonia. Journal of Ecology 87:66–76.

Schwartz, N. B., A. M. Budsock, and M. Uriarte. 2019. Fragmentation, forest structure, and topography modulate impacts of drought in a tropical forest landscape. Ecology 100:e02677.

Teller, B. J., P. B. Adler, C. B. Edwards, G. Hooker, and S. P. Ellner. 2016. Linking demography with drivers: climate and competition. Methods in Ecology and Evolution 7:171–183.

Tredennick, A. T., Brittany J. Teller, P. B. Adler, G. Hooker, and S. P. Ellner. 2018. Size-by-environment interactions: a neglected dimension of species’ responses to environmental variation. Ecology Letters 21:1757–1770.

TRMM (TMPA/3B43) rainfall estimate L3 1 month 0.25 degree x 0.25 degree V7. 2011. Goddard Earth Sciences Data; Information Services Center (GES DISC), Greenbelt, MD.

Tye, M. R., E. S. Menges, C. Weekley, P. F. Quintana-Ascencio, and R. Salguero-Gómez. 2016. A demographic ménage à trois: interactions between disturbances both amplify and dampen population dynamics of an endemic plant. Journal of Ecology 104:1778–1788.

Uriarte, M., M. Anciães, M. T. B. da Silva, P. Rubim, E. Johnson, and E. M. Bruna. 2011. Disentangling the drivers of reduced long-distance seed dispersal by birds in an experimentally fragmented landscape. Ecology 92:924–937.

Vicente-Serrano, S. M., S. Beguería, and J. I. López-Moreno. 2010. A Multiscalar Drought Index Sensitive to Global Warming: The Standardized Precipitation Evapotranspiration Index. Journal of Climate 23:1696–1718.

Williamson, G. B., W. F. Laurance, A. A. Oliveira, P. Delamônica, C. Gascon, T. E. Lovejoy, and L. Pohl. 2000. Amazonian Tree Mortality during the 1997 El Niño Drought. Conservation Biology 14:1538–1542.

Wood, S. N. 2017. Generalized additive models: An introduction with r. Second edition. CRC Press/Taylor & Francis Group, Boca Raton.

Wood, S. N. (n.d.). Chapter 5: Smoothers. Pages 195–247 Generalized additive models: An introduction with R.

Xavier, A. C., C. W. King, and B. R. Scanlon. 2016. Daily gridded meteorological variables in Brazil (19802013). International Journal of Climatology 36:2644–2659.

### 7.0.1 Colophon

This report was generated on 2021-02-04 10:24:55 using the following computational environment and dependencies:

#> ─ Session info ───────────────────────────────────────────────────────────────  
#> setting value   
#> version R version 4.0.2 (2020-06-22)  
#> os macOS Catalina 10.15.7   
#> system x86\_64, darwin17.0   
#> ui X11   
#> language (EN)   
#> collate en\_US.UTF-8   
#> ctype en\_US.UTF-8   
#> tz America/New\_York   
#> date 2021-02-04   
#>   
#> ─ Packages ───────────────────────────────────────────────────────────────────  
#> ! package \* version date lib source   
#> P assertthat 0.2.1 2019-03-21 [?] CRAN (R 4.0.0)  
#> P bookdown 0.21 2020-10-13 [?] CRAN (R 4.0.2)  
#> callr 3.5.1 2020-10-13 [1] CRAN (R 4.0.2)  
#> P cli 2.2.0 2020-11-20 [?] CRAN (R 4.0.2)  
#> P crayon 1.3.4 2017-09-16 [?] CRAN (R 4.0.0)  
#> P desc 1.2.0 2018-05-01 [?] CRAN (R 4.0.0)  
#> P devtools 2.3.2 2020-09-18 [?] CRAN (R 4.0.2)  
#> digest 0.6.27 2020-10-24 [1] CRAN (R 4.0.2)  
#> P ellipsis 0.3.1 2020-05-15 [?] CRAN (R 4.0.0)  
#> P evaluate 0.14 2019-05-28 [?] CRAN (R 4.0.0)  
#> P fansi 0.4.1 2020-01-08 [?] CRAN (R 4.0.0)  
#> P fs 1.5.0 2020-07-31 [?] CRAN (R 4.0.2)  
#> P glue 1.4.2 2020-08-27 [?] CRAN (R 4.0.2)  
#> P htmltools 0.5.0 2020-06-16 [?] CRAN (R 4.0.0)  
#> P knitr 1.30 2020-09-22 [?] CRAN (R 4.0.2)  
#> P lifecycle 0.2.0 2020-03-06 [?] CRAN (R 4.0.0)  
#> P magrittr 2.0.1 2020-11-17 [?] CRAN (R 4.0.2)  
#> P memoise 1.1.0 2017-04-21 [?] CRAN (R 4.0.0)  
#> P pkgbuild 1.2.0 2020-12-15 [?] CRAN (R 4.0.2)  
#> P pkgload 1.1.0 2020-05-29 [?] CRAN (R 4.0.0)  
#> P prettyunits 1.1.1 2020-01-24 [?] CRAN (R 4.0.0)  
#> P processx 3.4.5 2020-11-30 [?] CRAN (R 4.0.2)  
#> P ps 1.5.0 2020-12-05 [?] CRAN (R 4.0.2)  
#> P purrr 0.3.4 2020-04-17 [?] CRAN (R 4.0.0)  
#> R6 2.5.0 2020-10-28 [1] CRAN (R 4.0.2)  
#> P remotes 2.2.0 2020-07-21 [?] CRAN (R 4.0.2)  
#> P rlang 0.4.10 2020-12-30 [?] CRAN (R 4.0.2)  
#> P rmarkdown 2.6 2020-12-14 [?] CRAN (R 4.0.2)  
#> P rprojroot 2.0.2 2020-11-15 [?] CRAN (R 4.0.2)  
#> P sessioninfo 1.1.1 2018-11-05 [?] CRAN (R 4.0.2)  
#> P stringi 1.5.3 2020-09-09 [?] CRAN (R 4.0.2)  
#> P stringr 1.4.0 2019-02-10 [?] CRAN (R 4.0.0)  
#> P testthat 3.0.1 2020-12-17 [?] CRAN (R 4.0.2)  
#> P usethis 2.0.0 2020-12-10 [?] CRAN (R 4.0.2)  
#> withr 2.3.0 2020-09-22 [1] CRAN (R 4.0.2)  
#> P xfun 0.20 2021-01-06 [?] CRAN (R 4.0.2)  
#> P yaml 2.2.1 2020-02-01 [?] CRAN (R 4.0.0)  
#>   
#> [1] /Users/scottericr/Documents/HeliconiaDemography/renv/library/R-4.0/x86\_64-apple-darwin17.0  
#> [2] /private/var/folders/b\_/2vfnxxls5vs401tmhhb3wqdh0000gp/T/RtmpGhTlOY/renv-system-library  
#> [3] /Library/Frameworks/R.framework/Versions/4.0/Resources/library  
#>   
#> P ── Loaded and on-disk path mismatch.

The current Git commit details are:

#> Local: master /Users/scottericr/Documents/HeliconiaDemography  
#> Remote: master @ origin (https://github.com/BrunaLab/HeliconiaDemography.git)  
#> Head: [4ce1de5] 2021-02-04: work on results