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

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Text of abstract

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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 particualar 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). 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 indicate wetter than average months, while negative values of SPEI indicate droughts with intensity categorized as mild (0 - -1), moderate (-1 - -1.5), severe (-1.5 - -2), or extreme (< -2) (McKee et al. 1993). A 3 month time scale for SPEI was deemed as most relevant for *H. acuminata* as it relies primarily on soil moisture and not water sources buffered over longer timescales (e.g. it lacks deep taproots to access groundwater). We calculated 3-month SPEI using the SPEI package in R version 4.0.2 (2020-06-22) (Beguería 2017a, R Core Team 2020). We compared the SPEI values calculated using this data source to several others including near by weather stations, the global SPEI database (Beguería 2017b) and TRMM (“TRMM (TMPA/3B43) rainfall estimate L3 1 month 0.25 degree x 0.25 degree V7” 2011) and the timing of drought events is consistent among these datasets although the exact magnitude of drought differs among datasets (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 dose-lag-response association spline, called a crossbasis function. This crossbasis 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 in R with a maximum lag of 36 months (Gasparrini 2011, R Core Team 2020). This particular maximum lag time was chosen because previous experiments showed that *H. acuminata* individuals recovered from transplant shock after 36 months, so we expected at most 36 months lag time in the response to drought (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 in R with restricted maximum likelihood (Wood 2017). In the process of fitting the model, 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.

The general form of the vital rate models was as follows:

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

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). Penalized cubic regression splines were used for both dimensions 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 inflorescence). For survival and flowering as a response, we used a binomial family error distribution with a logit link.

NOTE FOR EMILIO: In Gasparrini et al. 2017, the crossbasis function is defined like so:

Where “the bi-dimensional dose-lag-response function is composed of two marginal functions: the standard dose-response function , and the additional lag-response function that models the lag structure….” I like this summation notation because it clarifies that the function is two-dimensional, but I’m not sure it’s mathematically appropriate to drop into the model equation.  
The crossbasis function could also be represented by something a lot more abstract like where is the SPEI history and is a vector (0, …, 36) describing the lag structure of . This is closer to how the model is written in R. Let’s talk about the clearest way to write and describe these models.

Because DLNMs do 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.

Statistical significance of crossbasis functions and covariates was determined by ….

# 3 Results

## 3.1 DLNMs

## 3.2 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

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

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### 7.0.1 Colophon

This report was generated on 2021-01-28 20:15:01 using the following computational environment and dependencies:

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#> version R version 4.0.2 (2020-06-22)  
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#> ctype en\_US.UTF-8   
#> tz America/New\_York   
#> date 2021-01-28   
#>   
#> ─ Packages ───────────────────────────────────────────────────────────────────  
#> ! package \* version date lib source   
#> P assertthat 0.2.1 2019-03-21 [?] CRAN (R 4.0.2)  
#> P backports 1.2.0 2020-11-02 [?] CRAN (R 4.0.2)  
#> P bookdown 0.21 2020-10-13 [?] CRAN (R 4.0.2)  
#> P callr 3.5.1 2020-10-13 [?] CRAN (R 4.0.2)  
#> P cli 2.1.0 2020-10-12 [?] CRAN (R 4.0.2)  
#> P crayon 1.3.4 2017-09-16 [?] CRAN (R 4.0.2)  
#> P desc 1.2.0 2018-05-01 [?] CRAN (R 4.0.2)  
#> P devtools 2.3.2 2020-09-18 [?] CRAN (R 4.0.2)  
#> P digest 0.6.27 2020-10-24 [?] CRAN (R 4.0.2)  
#> P ellipsis 0.3.1 2020-05-15 [?] CRAN (R 4.0.2)  
#> P evaluate 0.14 2019-05-28 [?] CRAN (R 4.0.1)  
#> P fansi 0.4.1 2020-01-08 [?] CRAN (R 4.0.2)  
#> 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 4.0.2)  
#> P knitr 1.30 2020-09-22 [?] CRAN (R 4.0.2)  
#> P magrittr 1.5 2014-11-22 [?] CRAN (R 4.0.2)  
#> P memoise 1.1.0 2017-04-21 [?] CRAN (R 4.0.2)  
#> P pkgbuild 1.1.0 2020-07-13 [?] CRAN (R 4.0.2)  
#> P pkgload 1.1.0 2020-05-29 [?] CRAN (R 4.0.2)  
#> P prettyunits 1.1.1 2020-01-24 [?] CRAN (R 4.0.2)  
#> P processx 3.4.4 2020-09-03 [?] CRAN (R 4.0.2)  
#> P ps 1.4.0 2020-10-07 [?] CRAN (R 4.0.2)  
#> P R6 2.5.0 2020-10-28 [?] CRAN (R 4.0.2)  
#> P remotes 2.2.0 2020-07-21 [?] CRAN (R 4.0.2)  
#> renv 0.12.0 2020-08-28 [1] CRAN (R 4.0.2)  
#> P rlang 0.4.8 2020-10-08 [?] CRAN (R 4.0.2)  
#> P rmarkdown 2.5 2020-10-21 [?] CRAN (R 4.0.2)  
#> P rprojroot 1.3-2 2018-01-03 [?] 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 4.0.2)  
#> P testthat 3.0.0 2020-10-31 [?] CRAN (R 4.0.2)  
#> P usethis 1.6.3 2020-09-17 [?] CRAN (R 4.0.2)  
#> P withr 2.3.0 2020-09-22 [?] CRAN (R 4.0.2)  
#> P xfun 0.19 2020-10-30 [?] CRAN (R 4.0.2)  
#> P yaml 2.2.1 2020-02-01 [?] CRAN (R 4.0.2)  
#>   
#> [1] /Users/emiliobruna/Dropbox (UFL)/Research/Heliconia/HeliconiaDemography/renv/library/R-4.0/x86\_64-apple-darwin17.0  
#> [2] /private/var/folders/\_g/qm39nv914lvc1bn8\_d99t4sw0000gn/T/RtmpzxLStK/renv-system-library  
#>   
#> P ── Loaded and on-disk path mismatch.

The current Git commit details are:

#> Local: master /Users/emiliobruna/Dropbox (UFL)/Research/Heliconia/HeliconiaDemography  
#> Remote: master @ origin (https://github.com/BrunaLab/HeliconiaDemography)  
#> Head: [7510709] 2021-01-28: EB Edits to Intro