Response to Reviews

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8/9/2021

Cascading effects of increasing k:

* Changed shape of crossbasis functions (edf changes, now not always more complex in fragments)
* Changes in which lags are significant
* Individual-level random effects impossible to fit due to computational limitations. Using a sub-sample, checked with and without invididual-level random effects. Changes r2, but very minimal changes to shape of smooths, edfs, and significance of smooths. Dropped from flowering model.

# 1 Reviewer 1

**General comments**

Scott and colleagues present the results of an interesting series of analyses designed to disentangle the lagged effects of climate and forest fragmentation on the demographic performance of a tropical understory plant. As ecologists seek to understand not just how changes in mean climate, but also changes in extremes, will influence population persistence, studies such as this that capitalize on long time series are critical to making progress. The authors find that the effects of swings in precipitation (both drought and particularly wet years) affect survival, growth and flowering, but that these effects are both lagged and differ by whether plants were in continuous forest or the smallest fragment size (1 ha). Overall, it’s a well written paper, and an application of a relatively new modeling approach to address the questions. The results highlight both the challenges with understanding the complex factors driving population persistence and also how critical it will be to grapple with them. Below I provide suggestions for improvement, particularly aimed to make the new modeling approach more accessible.

## 1.1

By the end of the introduction, I expected that the paper would focus on drought, and was then puzzled by the choice of the words ‘extreme precipitation’ – this of course makes sense later that the results are focused both on the effects of drought and extreme wet. The introduction could set up the reader better to understand both. Since drought is well covered, adding background and hypotheses for why extreme wet would have a negative effect on vital rates would help.

We edited a sentence in the introduction that cites Esteban et al. (2021) to clarify that both extreme dry and wet conditions reduce growth and survival of trees in the Amazon. *“…recent results suggest increases in the frequency and severity of extreme precipitation events* ***(both drought and extreme wet)*** *reduce survival and reproduction….”* Additionally, we added a sentence describing forecasted changes in precipitation in the Amazon.

## 1.2

In the intro and discussion, I think it would also be helpful to describe a little bit more about mechanisms for why extreme precipitation matters more in fragments compared to continuous forest. I wondered if the authors thought this was too obvious (edge effects, etc), but I think it’d be helpful to spell this out more clearly. L466 – 467 offer a new hypothesis, but briefly revisiting the ‘old’ evidence/hypotheses also seems important.

## 1.3

One challenge of using a new modeling approach is making the methods of the paper understandable and to stand alone. As written in the methods and results, I found the implementation very difficult to follow. A slightly longer summary of the methods would help.

We have added an additional paragraph to the methods describing how the crossbasis smooth was fit using the mgcv and dlnm packages. We are not entirely sure if this is the type of description the reviewer was looking for. If the reviewer(s) or editor see this as too detailed for the main text, we are happy to remove it, move it to a supplement, or simply replace it with a reference to the (now available) archived code for the analysis. See also our response to 3.3.

In the results, I was surprised to see only a few p-values and not much else about the models in terms of how they were assessed for goodness of fit. While I am not at all suggesting that p-values are the solution, I would have liked a little more sense of how well the models fit. One way to do that might be to show the raw data plotted with the model fits so the reader can see, for example, what kind of functions were drawn. Another might be to present something in table format (the comparable version of a table of AICs or of the results of frequentist tests).

Because model selection was performed automatically by shrinkage using the select = TRUE option in the gam() function, we cannot show relative model fits (i.e., we did not perform model selection and can’t show dAIC). However, we have now included a table with R2 values for each model indicating fit as well as estimated degrees of freedom and p-values for each term. We have replaced many of the parenthetical p-values reported in the results section with references to this table.

## 1.4

Related to above, I think it’s important to see more of the raw data than are presented in Fig. 1. (I’m thinking of a version of Fig 3 that shows size in t+1, survival, and flowering rather than effect size on the y-axis, with the data and lines showing the shape of the GAMs). This could be an appendix, but it would help with interpreting Figures 3 – 6.

We changed Fig 3 to be on the response scale as suggested (see our response to 1.9, but showing the raw data made the plots visually cluttered, in our opinion. Another way we approached this comment is by excluding areas of the heatmaps in figures 4-6 that are far from observed data, equivalent to not drawing regression lines beyond the range of data. We implemented this with the exclude.too.far() function in the mgcv package. Displaying raw data on the heatmaps was too messy and not informative in a 2d plot.

## 1.5

I suggest that a little more about the limitations of this modeling approach in the discussion would help set the context for interpreting the results and make the paper more robust.

(Something I’m considering adding to the discussion):

“The main limitation for detecting lagged effects with any method is data, and the specifics of data limitations have not yet been systematically explored. Teller et al. (2016) used simulations to show that 20–25 years of data were required to detect lagged effects using their method, but this cutoff depends on the effect size and the number of climate extremes in the dataset. Additionally, there is some evidence that appropriate spatial replication could drastically reduce the number of years of data required (Aldo Compagnoni’s ESA talk).”

In some ways it seems like the analysis is adding more precision (by using monthly climate data) than the plants perceive and that would be measured in a yearly census.

On the contrary, averaging weather conditions over an entire year likely obscures ways plants perceive environmental variation. For example, a drought in the wet season may have a different effect than a drought in the dry season. This differential response to season- or month-level climate data is observable in yearly plant census. Collapsing finer temporal scale environmental drivers to yearly averages (or a few means of arbitrarily chosen climate windows) is exactly what we avoid with this method.

While the authors mention this, what about adding something short about when using this type of analysis is critical and when it might not be (should all demographers adopt this approach? Why or why not?)

We have added additional detail to the conclusions recommending that all demographers consider lagged effects when possible in light of recent research (including this study).

## 1.6

I was curious about why the paper did not include analyses of recruitment. Perhaps it is beyond the scope of this paper, but I wondered how new recruits responded to drought and wet also, both in number, as well as how big they were in the first year.

The reviewer is correct that recruitment is an important aspect of demography that could be effected by SPEI and fragmentation. However, we believed the analyses in this paper were complicated enough to not include additional analyses. We intend to follow up this paper with analyses of recruitment and integrating all vital rate models with an integral projection model. We simply felt doing all of this (describing and interpreting DLNMs, modeling recruitment, and integrating all into an IPM) would be too much for a single paper.

## 1.7

I had a hard time linking these statements in the results to the figures.

L272–273—How do you see disparities in plant size here? I thought this was about growth?

Models which predict size in year t+1 as a function of size in year t, such as ours, are often described as growth functions because they can be used to project change in size (i.e. growth). However, we agree that it would be more clear for this section heading to be “size” rather than “growth”

L277–278—How does this show the effect of size on growth is greatest for mid-size plants? More generally, I got a little confused with the flipping back and forth between growth & plant size in the results and discussion. More precise language would help.

We have edited the text to omit “growth,” and hopefully clarify: “…the impact of plant size on size in the following year was greatest for mid-sized plants in continuous forest.”

L331–332—How can you see in this figure that the response is ‘more muted as indicated by the shape of the crossbasis function?’

Our point was actually that SPEI had less of an impact on flowering probability in fragments. We edited this sentence to read: “SPEI had less of an effect on flowering probability in 1-ha fragments as indicated by the narrower range of the evaluated smooth (Figure 6b).”

## 1.8

L442-443 – What is a mechanism for why plants might flower more after drought? (the discussion talks about the opposite) The next paragraph kind of goes there, but the link could be tighter.

## 1.9 Figures:

Fig 2 – This was only cited in the discussion as far as I can tell. Bring it back into the results?

… see also response to 3.8.

Fig 3A – The results mention something about survival approaching 1 – I wasn’t sure if that was supposed to be visible here.

This was referring to a previous iteration of the figure where the y-axis was on the response scale. We have reverted the figure to this version (see response below) and this should be obvious now.

Fig 3 – I mentioned this earlier, but I wasn’t really clear on how to interpret effect size. I see the explanation in L 539 in the legend, but I don’t really know what that means. Since this is such an important result of the paper, it would help the reader if they were walked through this idea. What is a negative vs. positive effect size in relation to plant size (does this compare to the median size)? I am likely missing something here. (I think the challenge for me is that I kept wanting the figures to fit into a more standard demographic paper – like the probability of survival based on size, but then I realized something different was being shown here.)

These plots were the evaluated smooths on the link scale. We agree that they were difficult to interpret in that form, so we have added the model intercept and back-transformed them to be on their respective response scales (e.g. probability for flowering and survival). This is equivalent to the marginal effect of log(size\_t)—that is, without considering the additive effect of lagged SPEI or the random intercepts for different plots and for plants that had not flowered in the previous year (the reference level for the flwr\_prev factor we included as a parametric covariate). We have not clarified that in the figure caption.

Figs 4 – 6 – Where the isocline circles are large, does that mean it’s a very large time span? I was a bit confused when describing the results of Fig 4b (L296-297), for example, the lag is described as the preceding 13 months in the 1 ha fragment, rather than 0 – 13 months (although now I see maybe the word preceding was meant to indicate this whole range). A little bit more explanation in the legends would help these figures be more intuitive.

We’ve revised the figure captions to clarify: *“Outlines show combinations of SPEI and lag time that have a significant effect on survival, defined as areas where the 95% confidence interval around the response does not overlap the intercept.”*

# 2 Reviewer 2

**General comments**

The manuscript by Scott et al analyzed an eleven year long demographic data set on the herb, Heliconia acuminata in the Central Amazon to evaluate the effect of drought and fragmentation on survival growth and fecundity. The authors also employ distributed lag non-linear models to explore delayed effects of drought. This work is an important contribution adding to the sparce literature documenting the role of weather variables on plant vital rates. The manuscript is generally well written. I hope the authors will find my comments helpful in improving this already very good manuscript.

## 2.1

The results are all about the effect of SPEI on plant vital rates, but the abstract implies that the manuscript presents the effect of temperature and precipitation on vital rates separately.

We have edited the abstract. Now the sentence to which the reviewer refers reads: *“We used distributed lag non-linear models to understand the delayed effects of standardized precipitation evapotranspiration index (SPEI) on survival, growth, and flowering.”*

## 2.2

Line 51-52. I find this sentence confusing. What specific demographic mechanisms are you referring to? Do you mean that high mortality rate lead to extinction and we don’t know what causes high mortality rates?

Bruna, Fiske, and Trager (2009) discusses the lack of knowledge of what demographic vital rates (e.g. survival, reproduction, recruitment) contribute most to population declines in fragments. We have edited this line to clarify: "

## 2.3

Line 146. Can you explain what you mean with “the height of each plant to the tallest leaf?” If the tallest leaf is growing more horizontally the height of the plant would be shorter than the length of the largest leaf?

This is just the height of the plant from the ground to the tallest leaf leaf tip, not the tip of the youngest leaf. The reviewer is correct that the height of a plant growing more horizontally (for example if it was knocked over by a branchfall) could be shorter than the length from the base to the end of the tallest leaf. We edited the description to read: “…the height of each plant (i.e. distance from the ground to the tallest leaf tip)”

## 2.4

Lines 251ff: I don’t see a reference of Fig 2 in the result section.

## 2.5

Line 277-278: I don’t see in Figure 3a that the impact of size on growth was greatest for mid-sized plants in continuous forest. It looks to me that the 1-ha and CF lines are extremely close together and not statistically different. Perhaps you can say that there is a tendency of small plants having a larger growth in fragments while large plants grow slightly more in CF.

We thank the reviewer for pointing out this mistake. We have edited this line to read “Although plants were significantly larger in continuous forest compared to fragments, the effect of size in year t on size in year t+1 is nearly identical in the two habitats.” See also our response to 1.9.

## 2.6

Lines 287-289. While this statement is true, there are also years where flowering is lower in CF (e.g., 2002 similar values as following the drought in 2003 in fragments). I feel that the reporting of the results is a bit biased towards concluding that plants do worse in fragments compared to CF, especially since none of the result reported so far are significant.

The difference in flowering probability between cointinuous forests and fragments is in fact significant. We have added Table 1 that shows the model intercepts ± 84% confidence intervals, which is comparable to testing a main effect of habitat if we were able to include both habitats in the same model.

## 2.7

Delayed effects: Since the authors fit separate models for plants in fragments and in continuous forest to allow for the crossbasis function to differ between habitats we don’t know if any of the small differences reported in Fig 4c, 5c and 6c are statistically significant. Hence, I would recommend interpreting the results concerning the difference between fragments and CF with caution. I would like to see at least a justification for why representing the difference figures are meaningful.

## 2.8

Line 301-301: This is somewhat misleading because as you describe later SPEI at time lags 15-20 and 32-36 are significant also. I wonder if it might be better to describe the entire Fig 4b and then the entire Fig 4a. What springs to my mind is that the area that is significant is much larger in in fragments compared to CF. It seems that in CF only a few months are significant. Surprisingly they fall not consistently in the dry or wet season.

## 2.9

Line 323-325: I don’t know why the growth of plants in fragments would affect the size of plant in CF.

## 2.10

Lines 355-359: The analysis did not consider testing a statistical difference between habitat type (see comment 7), so I think this sentence is misleading (overinterpreting the results).

While we could not test for an interaction between habitat and lagged SPEI (i.e. whether the shape of the crossbasis smooth was *significantly* different between habitats), we did test for a main effect of habitat by looking for overlap in 84% confidence intervals of model intercepts (see also response to 2.6). However, to reduce confusion here, we have changed “significantly” to “substantially” so as not to imply statistical significance for all of “magnitude, direction and lag time.” See also our response to 2.7.

## 2.11

Line 370: There are no confidence intervals in Fig 2, so we don’t know if the difference is significant.

Figure 2 shows the survivorship curve of plants tagged in 1998. These are exact counts and therefore do not have confidence intervals. They do not require statistics to interpret if they are different. We think the confusion may have come from the axis scale and label (“P(survived)”) which we intended to be interpreted as “proportion of plants surviving” but may have been interpreted as “probability of survival.” We have changed the scale to a percentage and the axis label to “% surviving.”

## 2.12

Lines 383 ff: see comment 7

## 2.13

Line 412: I think it would be very informative if you were to expand on this and explain how exactly your method differs from what others have used to detect delayed effects.

…see also our response to 1.5.

## 2.14

424-427: I think this is exaggerating since the differences between habitat types is not significant.

…see also our response to 2.10

## 2.15

You may also consider arguing that an 11-year long time series is not sufficient to detect delayed effects (see Tenhumberg et al. 2018)

…see also our response to 1.5 and 2.13.

## 2.16

Lines 437-438 change “starting expand” with “starting to expand”

We have made this correction.

## 2.17

Line 440: Can you explain a bit more in detail why drought increasing flowering probability two years in the future would be a bet hedging response?

see our response to 1.8.

## 2.18

Line 448: Alternatively, drought may reduce nutrient availability such that after covering maintenance costs there is nothing left to allocate.

## 2.19

Lines 451-453: I think herbivory is this is very different from drought. Drought reduced nutrient availability while herbivory removes some plant biomass triggering compensatory growth.

## 2.20

Lines 468 ff: I suggest deleting this paragraph. It doesn’t really matter when exactly a plant dies during a growing season, all that matters for population dynamics is how many plants die from one growing season to the next. Distributed Lag Non-Linear Models account for the exact timing of the weather events.

## 2.21

The discussion includes reasons for why we expect delayed effect in plants in general, but it does not relate the specifics of the significant delays to the life history of H. acuminata. For instance, why does too much rain reduce survival? Why is there an effect of SPEI during the dry season (18-20 months in the past but during the wet season 32-36 months in the past? Why do plants in fragments have a decrease survival when precipitation is high during dry and wet periods (1-18 months time lag)? Etc.

## 2.22

Lines 484-486: I don’t think this study strongly support that plants do worse in fragments than CF.

## 2.23

Line 499: This is confusing. If you measure size every year than you calculate growth as the change in size from one year to the next, don’t you?

That’s correct. This line meant to point out that size is usually measured in yearly censuses while weather data can be more easily collected at monthly or daily timescales. We’ve edited this sentence to read: “The ability to identify size-specific lagged responses may be especially complicated given size is rarely measured at the same time scale (e.g. monthly) as climate drivers.”

# 3 Reviewer 3

**General comments**

This is a really nice addition to the growing literature on lagged climate effects on plant demography, and also expands the tool kit for these studies. The combination of experimentally generated fragmentation with long term demographic data is also unique and very valuable. The paper is very clear and concise, with a few minor exceptions discussed in detail below. The one surprising omission was that the authors didn’t use an Integral Projection Model to put the vital rates together into a metric of population growth potential. I enjoyed reading this.

We thought it would be too much to describe and interpret DLNMs for the vital rates, model recruitment, *and* integrate all those models into an integral projection model. We though the description and interpretation of the DLNMs for survival, size, and flowering were complex and interesting enough to stand on their own. We do intend to follow up with an IPM in a future publication. See also our response to 1.6.

## 3.1

Line 152 – “Plants not found for 3 consecutive seasons …” when were they considered to have died? first year they were missed or last? How many plants were not found in an average survey, and why? Does Heliconia show whole plant dormancy?

We have edited to clarify: *“After the initial census year, between 80% and 97% of marked plants were found. Of plants that had missing values for some years, but were found again in a subsequent year, 95% had 2 or fewer years of missing values. Therefore, plants that were not found for three consecutive surveys, and no subsequent survey, were considered to have died in the transition year after their last observation.”*

Some of the missing values in the data do represent *Heliconia* plants that lost all above-ground tissue but re-sprouted in successive years, but other missing values may simply be imperfect “recapture.”

## 3.2

Line 166 - given the shallow roots, why not use 1 month SPEI and let the model do the smoothing over longer time frames? You describe why not using longer smooths, but not shorter.

## 3.3

Line 191 - 194 (equation and description) for clarity you should describe what the index variables i and j are indexing, and I think clearer to have y\_ij for ith plant in jth plot. Indexes on the random effect description suggest there is a separate variance estimated for each plot? d\_it suggests that each plant has a separate SPEI estimate? I think it is probably aggregated at a higher level than individual?

We thank the reviewer for the very helpful comments on our model equation. We have changed to and added an explanation of the indexing as suggested. We have also corrected the error in the random effect equation so that only one variance is estimated. is intended to indicate that each plant observation is associated with a measure of SPEI for the past 36 months. The SPEI history varies among plants spatially (there are three grid cells in the weather data within BDFFP, so different plots experience different climate) and temporally (observations from all years are pooled).

I would reorganize the following paragraph so that all the descriptive text for the components of (1) occurs before the digression on the details of the crossbasis function.

We moved the explanation of covariates and random effects earlier as suggested.

## 3.4

Line 205 - I’m not sure “bimodal” is correct here – a cubic function can have 2 local extrema, is that what you mean?

## 3.5

Line 205-207 – “number of knots not important …” yes, but package mgcv includes tools for checking those assumptions, would be helpful to include residual analysis and the results of gam.check() in an appendix.

This comment was especially helpful and made us re-think limiting the number of “knots” to 3 in the SPEI dimension. The term *k* is probably more accurately described as the “maximum basis complexity” or “maximum basis dimension.” We had thought that by limiting k to 3, we were simply limiting the complexity of the smooth in the SPEI dimension. However, after taking the reviewer’s suggestions we realized that there were other unexpected consequences. We increased *k* for the SPEI dimension for all models and for other smooths for some models. This resulted in some changes in the the shape of the crossbasis smooth and which areas of it were statistically significant. We have updated the methods and results sections accordingly.   
  
We have also now included a supplemental document with model validation, including checks that *k* is adequately large .

## 3.6

Line 211 - random effect – how did you deal with this in the predictions? set to zero in design matrix, Choose a particular value, sample from the posterior? The code would tell me but not available.

What we show in the figures are not predictions (i.e. results of predict() in R), but partial effects plots generated with the gratia package (equivalent to mgcv::plot.gam()). For figures 4, 5, and 6 we have added the model intercepts to evaluated smooths and back-transformed (when applicable) the estimates. These plots, therefore, do not include the additive effects of other smooths, parametric covariates, or random effects. We think that this is an intuitive way to display the results. We added a paragraph to the methods explaining our strategy for visualizing the GAM results.

We apologize for not including a link to the code for the project. All analysis code can be found here: [<https://github.com/BrunaLab/HeliconiaDemography>](https://github.com/BrunaLab/HeliconiaDemography). It is so rare for a reviewer to make suggestions based on analysis code, and we are very grateful for these comments!

## 3.7

Line 253 - fig 1a shows mean change in size, not mean size?

We clarified the reference to the figure: “…was preceded by a drop in average plant size in the 2002-2003 transition year (i.e. negative growth in Figure 1a).” Also see our response to 1.7.

## 3.8

Figure 2 isn’t referenced in this section, not used until discussion. Maybe move to supplement or add a sentence in results?

…see also our response to 1.9

## 3.9

Line 260 – you mention the CI of the model estimated coefficients, but these aren’t provided anywhere that I could find. I think a table based on the summary of the two fitted models discussed here (and elsewhere too) should be added. And report the variance of the random effect.

…see also our response to 1.3

## 3.10

Figure 4 and 5 – very nice way to display the confidence limit. I did have to spend a while looking at them and doing a bit of head scratching to figure out which side the significant values were on, especially for the ones that are along the middle where the difference in color is not large. I wonder if a diverging color scheme with values close to the mean set to white would make this easier to see? Or if you could add some hatching or change the alpha transparency on one side to highlight those regions more clearly.

In the updated version of figure 4 (see response to 3.5), a smaller area of the plot is significantly different from the intercept, and heatmap area far from observed data is grayed out. We believe these two things make it easier to see the outlines around significant values, but we are open to trying other modifications of the plot if the reviewers think it is still difficult to interpret in this way.

## 3.11

Line 413 – “our expansion of this approach …” I’m not sure that the expansion is the penalty that prevents over fitting – both Teller et al and Tenhumberg et al used the penalized spline function in mgcv. What IS an expansion is the non-linear cross basis function. Both Teller et al and Tenhumberg et al used (essentially) linear cross basis functions, so using dlnm is super-cool and interesting.

## 3.12

Line 471 – this demographic delay left me a bit confused for a while until I stopped looking at figure 4b and started looking at 4a. Then it made a lot of sense. However, wouldn’t it be that the demographic effect takes place AFTER the census for an echo to appear at previous lags?

Bruna, Emilio M., Ian J. Fiske, and Matthew D. Trager. 2009. “Habitat Fragmentation and Plant Populations: Is What We Know Demographically Irrelevant?” *Journal of Vegetation Science* 20 (3): 569–76. <https://doi.org/10.1111/j.1654-1103.2009.01060.x>.

Esteban, Erick J. L., Carolina V. Castilho, Karina L. Melgaço, and Flávia R. C. Costa. 2021. “The Other Side of Droughts: Wet Extremes and Topography as Buffers of Negative Drought Effects in an Amazonian Forest.” *New Phytologist* 229 (4): 1995–2006. <https://doi.org/10.1111/nph.17005>.

Teller, Brittany J., Peter B. Adler, Collin B. Edwards, Giles Hooker, and Stephen P. Ellner. 2016. “Linking Demography with Drivers: Climate and Competition.” Edited by Jessica Metcalf. *Methods in Ecology and Evolution* 7 (2): 171–83. <https://doi.org/10.1111/2041-210X.12486>.