# sAPROPOS – Analyses of PROjections of POpulationS

sDiv working group led by Dr Rob Salguero-Gómez

Meetings:

23-25 Nov 2016 6-10 Feb 2017 12-16 Jun 2017

The present is the report of the third and final week in the context of the sAPROPOS working group.

The members of sAPROPOS met at iDiv during 12-16 June 2017 for the third and last event supported by the initial budget conferred by sDiv to Dr Rob Salguero-Gomez. To recapitulate, the goals of sAPROPOS are:

- 1. To produce several high-impact factor publications based on a anovel integration of methodologies to project species viability in the future (detailed below)
- 2. A freeware applications for teaching and general public dissemination purposes
- 3. A scientific symposium
- 4. An associated special feature on demographic viability and climate change
- 5. A general public session to raise awareness on the challenges for biodiversity and ways in which species may cope with them.
- 1. High impact factor papers

The working group spent most of the week developing further frameworks, analyzing data, testing preliminary results against preliminary expectations, and brainstorming on four papers:

- Predictabilit of species' population growth rate and underlying vital rates with moving windows. This approach consists on acquiring temporally well replicated demographic data from COMPADRE (plants), coupling it with monthly records of precipitation and temperature at the locations where the species were studied, and apply moving windows to determine legacy effects. This approach is being written up as a paper for *Methods in Ecology and Evolution*, and it sets the foudnation of a much larger science-driving paper that will capitalize on the methods being described. Thus far, we have found that population growth rate is poorly predicted by this approach, but that we have a stronger signal predicting vital rates. This suggests that species orchestrate demographic responses at the vital-rate level to buffer against environmental stochasticity. We have also found that species are more vulnerable to natural variation in precipitation than in temperature. This important finding is congruent with a recent publication in Science that highlights that, worldwide, selection gradients for changes in temperature are steeper than for changes in temperature.
- Knowledge review of the examination of the effects of climatic variation in the plant kingdom worldwide. During the week of work at iDiv we made major progress developing the searching criteria for further studies to be incorporated in this manuscript, and we agreed on a structure for the paper. Our goals are to review how population ecologists have historically and up to date linked climate effects to plant populations via matrix population models and integral projection models. In the review, we make an explicit link to the

representativity of the handful of studies doing this careful climatic evaluation to the areas where climate change is predicted to be most sever worldwide. A more in-depth summary of this project is found below. This paper will be submitted to *Journal of Ecology* or similar within the next 6 months.

- Knowledge review of the examination of the effects of climatic variation in vertebrates worldwide. This project has had a tremendous momentum in between the second and the third meeting. The leader of the project presented the group with the preliminary results based on what only two members had done since the second meeting. The group worked on finetuning R algorithms to find automatically good candidate papers for the review, and provided critical suggestions for the framework being presented in the paper. Since then, the paper has now incorporated over 10 members who are carefully curating the large sections of the vertebrate demographic literature assigned to each one, taking notes of the main climatic effects found for each vertebrate species' population, their sign (negative/positive) and through what vital rate. The paper is currently in early draft, and we expect to submit it to *Ecology* in four months.
- Inference of demographic rates across birds. This project has become a PhD chapter led by Tamora James, at the University of Sheffield. The project aims at evaluating the extent to which researchers may be able to borrow demographic information from closely related bird species to build full demographic models in species with poor demographic knowledge. If possible, this project will provide integral tools to the evaluation of climate change and poaching in charistmatic, endangered species such as parrots. The project has made major progress during the week in Leipzig, and the months following. The preliminary results, presented at the 2017 BES annual conference in Ghent, Belgium, showcase a greatest strength to phylogenetically impute adult survival than reproduction. See attached poster. The paper is currently in ealry draft, and we expect to submit it to *Conservation Biology* or similar by mid 2018.

#### 2. Freeware application

This part of sAPROPOS is still in early stages of development, and waiting for the main pipeline in the moving-window approach to be optimized.

3. Scientific symposium

We submitted a proposal for the British Ecological Society meeting in 2017, but it was not accepted. We have revisited it and submitted it to the Ecological Society of America meeting in Aug 2018. This has been accepted as a symposium and will highlight the advances made in predictive ecology by members of sAPROPOS and other researchers.

4. Special feature

During this week and in the following months, we discussed and have started to develop a proposal for a special feature that critically evaluates the theory, most recent methods, applications and limitations in predicting species population responses to climate change. Currently this proposal is being written for Journal of Ecology, which has an open call for special features due 28<sup>th</sup> of February.

5. General public session

During this week, we hosted a series of mini-lectures by 6 (1:1 sex ratio) members of sAPROPOS for researchers at iDiv. This has provided us with a unique opportunity to engage better with iDiv beyond the scope of sAPROPOS, including on-going collaborations with Nadja Rudgers Tiffany Knight, and Stan Harpole. However, we have not yet hosted the general public session. We will probably do this some time at the end of 2018 or early 2019, once the main papers from sAPROPOS have been at least submitted.

## LIFE HISTORY DETERMINANTS OF CLIMATE SENSITIVITY

How do plants respond to climate variability, and do their life history modulate this response?

- 1. We are the first to extensively use a "moving window" regression approach first pioneered by van de Pol and Cockburn (2011) to comparatively estimate the effect of climate on plant demography. To do so, we used survival, growth, and reproduction data from the COMPADRE plant matrix database (Salguero-Gomez et al. 2015), and monthly weather data obtained from fetchClimate.
- 2. We then use estimates of climate effects to test the relationship between the sensitivity of  $\lambda$  to vital rates (henceforth "vital rate sensitivity"), and the climate sensitivity of each vital rate (henceforth "climate sensitivity"). Our hypothesis posits that climate sensitivity should correlate negatively with vital rate sensitivity. This hypothesis is justified by the "buffering hypothesis", which posits that the vital rates with highest sensitivity should also have the lowest temporal variability (Pfister 1998). Assuming that temporal variability is at least in part caused by climate variability, climate sensitivity should correlate negatively with vital rate sensitivity should correlate negatively with vital rate sensitivity.

## **Preliminary results**

## 1. Moving windows to estimate the effects of climate on demographic rates

We addressed the performance of "moving window" models using 35 data sets from the COMPADRE plant matrix database. We selected data sets with at least 6 transition matrices (demographic censuses from at least 7 years), and fit models on survival, growth, and fecundity data. We then fit three types of models on this data: a null model without climate effect, an "average climate model" using the climate of the previous 24 months as predictor, and a "moving window" model, which weights the importance of the 24 monthly anomalies preceding each demographic observation. We fit these models in STAN (Stan Development Team 2017) and compared them using a leave-one-year-out cross-validation. Our models had limited ability to predict climate effects. The model that did not include a climate effect (the "null" model) was most frequently selected as best model, and the "average climate model" was the runner up (Table 1). Therefore, we decided to use estimates from the average climate model in our subsequent analyses linking climate sensitivity to vital rate sensitivity.

The poor performance of our climate models has two origins. First, our model selection is extremely conservative compared to the common practice in ecology. We used a cross-validation and scored models based on log posterior predictive density. Both of these choices are more conservative than the standard for model selection in ecological studies, which is based on AIC. Second, the moving window models we founded our initial analyses upon might be too inflexible. New analyses based upon more flexible moving window models provided encouraging results and are currently ongoing.

#### 2. Life history determinants of climate sensitivity

We found support for our expectation that climate sensitivity decreases with vital rate sensitivity (Fig. 1). Moreover, we found that the sensitivity to precipitation was roughly ten times larger than the sensitivity to air temperature (Fig. 2). This unexpected result agrees with what Siepelski et al. (2017) found in their synthesis study on the effect of climate variability on natural selection.

**Table 1**. Model selection table showing the number of selected models based on vital rate, and climate predictor (precipitation and air temperature). Each vital rate refers to up to 35 separate plant populations.

Model	Vital rate	Best models (precipitation)	Best models (Air temp.)
	Survival	22	22
	Growth	23	15
NULL	Fecundity	25	29
	Survival	5	5
Average	Growth	2	8
Climate	Fecundity	3	2
	Survival	1	0
Moving	Growth	0	2
window	Fecundity	4	1





Figure 2. Sensitivity of vital rates to air temperature and precipitation.



## **PLANT REVIEW**

We reviewed how population ecologists link climate effects to plant populations via structured population models (henceforth SPM). We assess the state of our knowledge on three main areas:

- (1) How good is the coverage of SPM studies that explicitly model climate drivers across the range of plant life histories, locations, and biomes on Earth?
- (2) How good is the coverage, within each study that parameterized a SPM, across the range of weather conditions that plants experience?
- (3) How close are we to a standard methodology for considering the effects of climate drivers on plant demography in a comparative setting?

We also provide suggestions on best practices to adopt when assessing the effects of climate on plant populations in the context of historical data analysis or experiments. We have carried out preliminary analyses on the above three points, and we have produced a manuscript draft with Introduction, Methods, and Results. Below we present our preliminary results.

## **Preliminary results**

1. How good is the coverage of MPM studies that explicitly model climate drivers across the range of plant life histories, locations, and biomes on Earth?

We assessed coverage of SPM with respect to study locations (Fig. 3) and biomes (Fig. 4). Studies linking SPM to climate drivers have been carried out in all continents. However, there is a strong bias to conducting studies in North America and Europe, and, accordingly, in cold and dry biomes (Fig. 4).

2. How good is the coverage, within each study that parameterized a SPM, across the range of weather conditions that plants experience?

We assessed how previous SPM studies covered the range of mean annual temperature and precipitation, with respect to the range observed during the 30 years preceding each study (Fig. 5). Based on our analysis, the coverage of observed climatic conditions asymptotes for studies with 10 years of data. In other words, adequately sampling inter-annual variability in temperature requires at least 10 years of data collection.

3. How close are we to a standard methodology for considering the effects of climate drivers on plant demography in a comparative setting?

In studies using long-term data sets, we advocate the use of "moving window" models (e.g. van de Pol and Cockburn 2011) in order to assess the effect of inter-annual climatic variability on demography. We carried out a qualitative comparison between the climate effects obtained through our moving window approach, and the climate effects reported in 7 of the studies we considered in this review. We found almost perfect qualitative correspondence between what authors found and moving windows results (Table 2). Finally, we provide recommendations to authors who plan to study the effect of climate on demographic rates via field experiments.

**Figure 3**. Locations of SPM in the COMPADRE database (grey dots) and the subset of these studies that consider climate drivers (green dots).



**Figure 4**. Whittaker biome plot, and dots showing the average temperature and precipitation of the locations where a SPM was linked to inter-annual climate variability.



**Figure 5**. Annual temperature and annual precipitation for a subset of focal plant species across all of their study populations, the years in which the SPM were considered (yellow points), and 30 additional years for each study population (blue points).



**Table 2**. Qualitative comparison between climate effects sizes found in the literature, and climate effect size found by "moving window" climate models.

Species	Effect sign in the literature	Effect size estimated by moving window
Astragalus cremnophylax var. cremnophylax	-	+
Brassica insularis	-	-
Cryptantha flava	+	+
Daphne rodriguezii	+	+
Helianthemum juliae	+	+
Opuntia imbricata	+	+
Purshia subintegra	+	+

#### REFERENCES

- Pfister, C. A. 1998. Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications. Proceedings of the National Academy of Sciences 95:213–218.
- van de Pol, M., and A. Cockburn. 2011. Identifying the Critical Climatic Time Window That Affects Trait Expression. The American Naturalist 177:698–707.

Stan Development Team. 2017. RStan: the R interface to Stan. R package version 2.17.2.

- Salguero-Gómez, 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. Römer, 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. Vélez-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.
- Siepielski, A. M., M. B. Morrissey, M. Buoro, S. M. Carlson, C. M. Caruso, S. M. Clegg, T. Coulson, J. DiBattista, K. M. Gotanda, C. D. Francis, J. Hereford, J. G. Kingsolver, K. E. Augustine, L. E. B. Kruuk, R. A. Martin, B. C. Sheldon, N. Sletvold, E. I. Svensson, M. J. Wade, and A. D. C. MacColl. 2017. Precipitation drives global variation in natural selection. Science 355:959–962.

#### **Review of animal demography**

The two main goals of this project is to assess (a) the current state of knowledge regarding how animal populations will respond demographically to climate; (b) how well demographic studies represent the biomes and species predicted to be most vulnerable to climate change.

To address these two goals, the working group designed and began to implement a largescale literature review during the three meetings of sAPROPOS in 2016. In this review, we have been collecting available information on how climatic variables differentially affect key life-cycle processes in all tetrapod groups (mammals, birds, reptiles, and amphibians). At least 10 members of the working group are currently actively involved in completing the review. We plan to have all mammal species assessed by the end of February 2018 and publish the first results of this comprehensive work in 2018. Thus far, we have extracted demographic responses to climate for 112 species (see Figure 1). Our results thus far indicate that the most vulnerable taxa and habitats (according to the IUCN Report 2016) are little assessed in demographic studies (Figure 2). For taxa where detailed demographic responses to climate have been quantified, such responses are complex and highly contextdependent.



Figure 1 Distribution across biomes of 100 species which have been reviewed thus far by members of this project



*Figure 2 Number of studies reviewed per biome. Exclamation marks indicate biomes containing the largest proportion of endangered species (IUCN)*