An Analysis of Synchrony Indices

End-semester Project Report

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A. Introduction

Plants can flower under a wide range of conditions. Along with abiotic factors (temperature and moisture), biotic factors such as pollinator availability, seed disperser availability and seed predator avoidance are hypothesised to play a major role in determining the temporal pattern of flowering, also known as flowering phenology. Reproductive synchrony is defined as a phenomenon caused by biological interactions to produce a tighter clustering of reproductive events than would have been imposed by environmental seasonality alone (Ims 1990).

Flowering synchrony can have many consequences – increased synchrony in flowering can increase pollinator visitation rates, increase outcrossing opportunities, decrease seed predation rates and even lead to assortative mating at the population level (Elzinga et al., 2007). We observe great variation in flowering synchrony. In this project, I aim to analyse various synchrony indices that are used to quantify flowering overlap and check how they correlate with mating opportunities.

B. Synchrony Indices

Synchrony indices measure flowering synchrony by taking in flowering intensity and duration of individuals in a population and producing a number between 0 and 1. Essentially, all indices' numerator is a measure of flowering overlap, and the denominator is a normalisation factor. Some popular indices are – Augspurger's index (Augspurger 1983), Marquis' index (Marquis 1988), Mahoro's index (Mahoro 2002) and Freitas' Index (Freitas and Bolmgren 2008). In my project, I focus on Augspurger's index, Freitas' index and three new indices developed by Dr Souparna Chakrabarty (Chakrabarty 2020) and Dr Deepak Barua. The heuristic behind the calculation of the indices is shown in Fig 1.

The formulae for various indices are given by –

1. Augspurger's index: $s_i = \frac{1}{N-1}\frac{1}{d_i}\sum_{j=1}^{N} t_j\,,\ \ i \neq j$
2. Freitas index: $s_i = \frac{1}{T}\frac{1}{N-1}\sum_{t=1}^{T}\sum_{j=1}^{N}\sqrt{f_{i,t} * f_{j,t}}\,,\ \ i \neq j$
3. SC Index: $s_i = \frac{\sum_{j=1}^{N}\sum_{t=1}^{T} f_{i,t} * f_{j,t}}{\sum_{j=1}^{N}(\sum_{t=1}^{T} f_{i,t} * \sum_{t=1}^{T} f_{j,t})},\ \ i \neq j$
4. New Index: $s_i = \frac{1}{N-1}\frac{\sum_{j=1}^{N}\sum_{t=1}^{T} f_{i,t} * f_{j,t}}{\sum_{j=1}^{N}\max_{start=1,\ t+1}(\sum_{t=1}^{T} f_{i,t} * f_{j,t})},\ \ i \neq j$
5. April Index: $s_i = f_{max,\,i}\,\frac{\sum_{j=1}^{N}\sum_{t=1}^{T} f_{i,t} * f_{j,t}}{\sum_{j=1}^{N}\max_{start\ ,\ t+1}(\sum_{t=1}^{T} f_{i,t} * f_{j,t})},\ \ i \neq j$

s_i – synchrony index of the individual
N – Total number of individuals
T – Flowering duration
f_i – Flowering intensity of individual i
t_j – number of days during which i was flowering with j

The formula for calculation of population synchrony (for all synchrony indices) is given by –

$$S = \frac{1}{N}\sum_{i=1}^{N} s_i$$

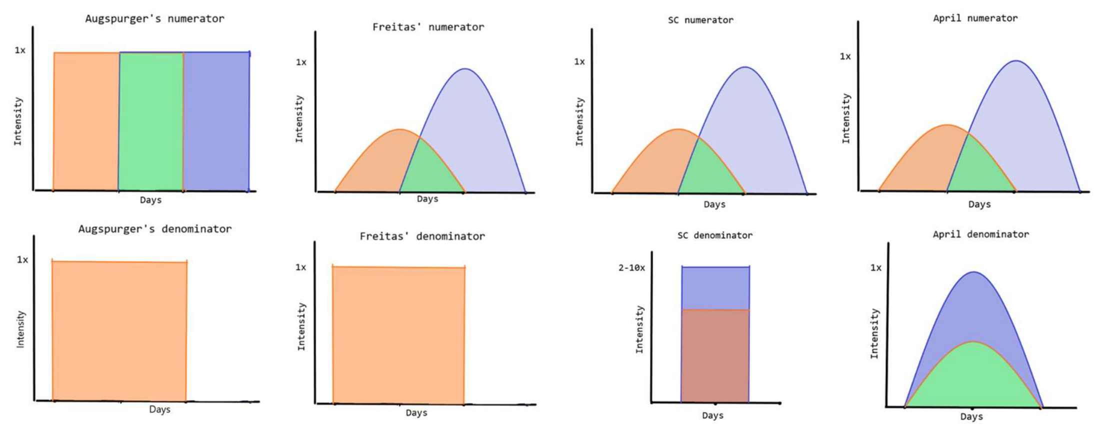

Figure 1. Illustration of the logic behind synchrony indices

Augspurger's index measures the duration of overlap and divides it by the flowering duration of the individual. It doesn't account for the potential differences in flowering intensity within a population. Freitas' index numerator captures the overlap in flowering duration and intensity, but Freitas and Bolmgren 2008 don't provide an explanation for their choice of the denominator, which is the same as Augspurger's index and essentially a measure of flowering duration. It is not the most appropriate normalisation factor.

SC index, developed by Dr Souparna Chakravarty in his PhD thesis, captures the flowering intensity overlap as well, but its denominator is the maximum overlap possible when both individuals put out all their flowers on a single day. While it makes sense to have maximum flowering overlap in the denominator, the SC index denominator becomes too large for populations with long flowering duration, and in turn, the value of the SC index remains quite low.

In order to make the denominator more biologically realistic, the denominator of the New index is defined as the maximum overlap possible between two individuals while keeping their flowering duration constant. But, the $1/N-1$ term makes the New SI decrease rapidly with an increase in population size. Even if the term is removed (and it is, in my calculations of New index), the value of the SI remains quite high. Moreover, the calculation becomes entirely relative to the population, and the index can't differentiate two populations that have maximum possible overlap but have different flowering intensities.

To overcome this, I introduced another modification in the formula – multiplying the value by f_{max}, which means the synchrony of an individual plant is weighted by its maximum intensity. I have named this the April index.

C. Methods

Literature study

I started the project by reading about phenology, flowering synchrony and the biotic factors that shape flowering synchrony (Schaik et al., 1993, Elzinga et al., 2007). The notes from these readings and my discussions with Dr Barua can be found here.

Understanding synchrony indices

In order to understand various synchrony indices, I first simulated toy populations with 2-5 individuals flowering over 5-10 days using Python and R. Flowering intensity of an individual is calculated using the formula - $f_{i,t} = \frac{n_{i,t}}{\max\limits_{N,\,T}(n)}$, the number of flowers produced by an individual on a day is divided by the maximum number of flowers produced in the population on any given day. I analysed the results of synchrony indices of these small populations. A detailed analysis of that can be found in my mid-semester report and notes. The code for simulating populations, the .csv files with toy flowering data and the code to calculate synchrony indices can be found at this Github link.

Analysing the variation of synchrony indices

I coded the formulae of synchrony indices in R and ran them on large populations (300 individuals flowering over the course of a year) obtained from Aparna Sundaresan (Sundaresan 2021). The populations are created using two parameters, as shown in Fig. 2 – Fsd (the flowering duration) and Tsd (intrapopulation variance in the mean flowering day). The number of flowers produced (100) remains constant throughout. The obtained results are presented in the next section.

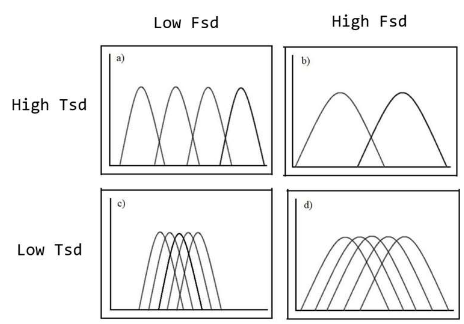

Figure 2. Depiction of Fsd and Tsd

Examine whether synchrony indices are a good measure of mating opportunities

One of the major consequences of flowering synchrony is increased pollinator visitation and outcrossing/mating opportunities. So, I wanted to check whether synchrony indices correlate with mating opportunities. For this, I first defined mating opportunity (MO) as –

$$MO_i = \sum_{t=1}^{T} (n_{i,t} * N_t)$$

Where $n_{i,t}$ is the number of flowers produced by i^{th} individual on day t and N_t is the total number of flowers on day t. The MO of the population is calculated as the mean of the MOs of the individuals. Then, I plotted the synchrony indices of the populations against their mating opportunities.

D. Results

<u>Prediction</u> (from Ganguly et al., 2021): When Tsd is high, i.e., individuals are flowering far apart, as Fsd increases, synchrony indices should increase and then decrease, as illustrated in Fig. 3.

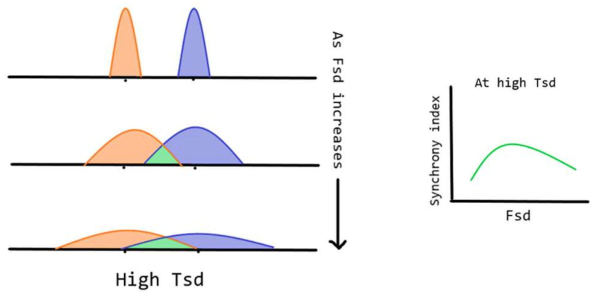

Figure 3. Illustration of how SI should vary with Fsd at high Tsd

<u>Variation of Indices with Fsd and Tsd</u>

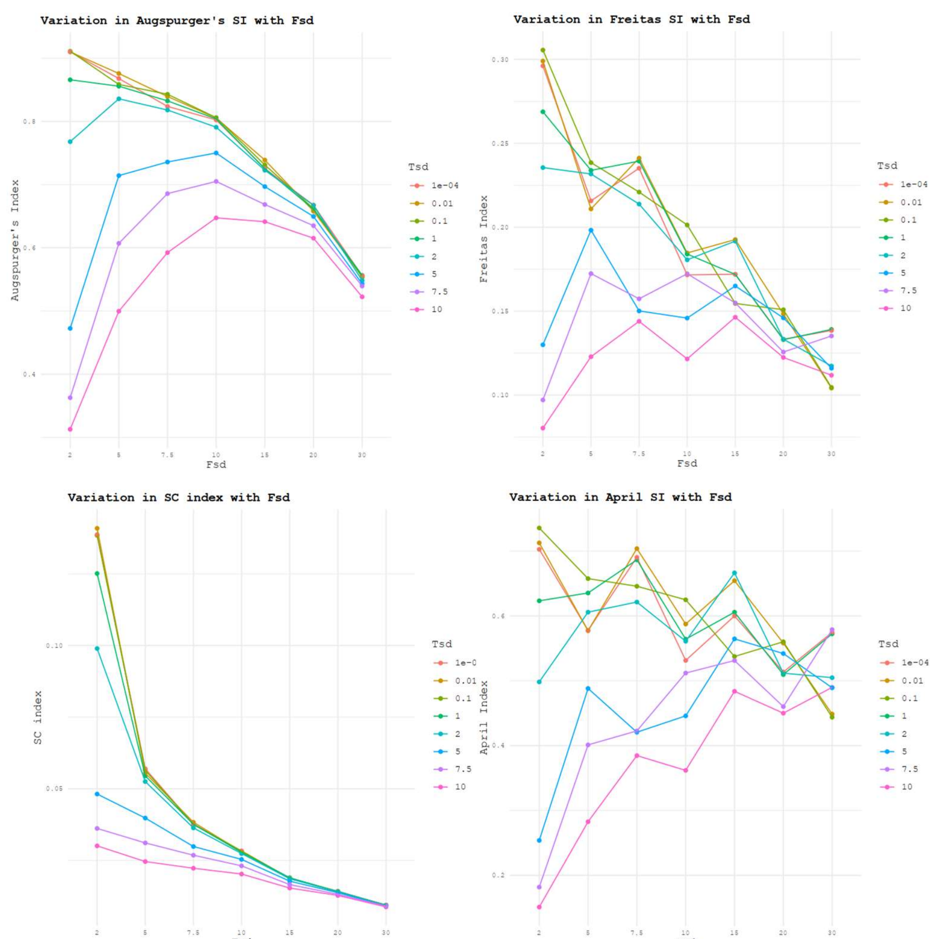

Figure 4. Variation of synchrony indices with Flowering duration (Fsd)

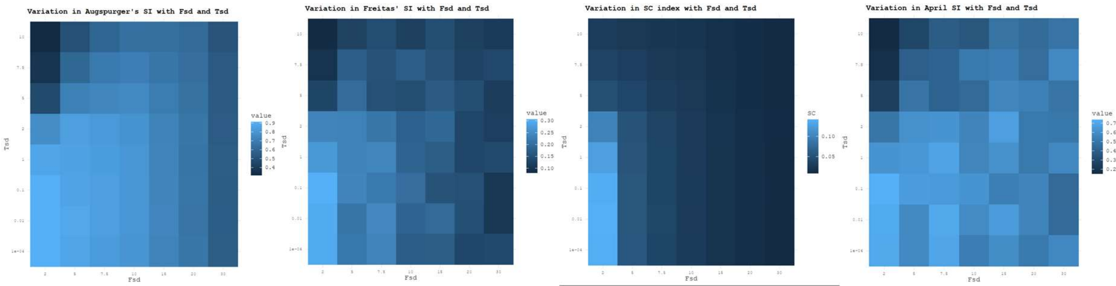

Figure 5. Heatmap representation of variation in Synchrony indices with Fsd and Tsd

Variation of Indices with Mating Opportunities

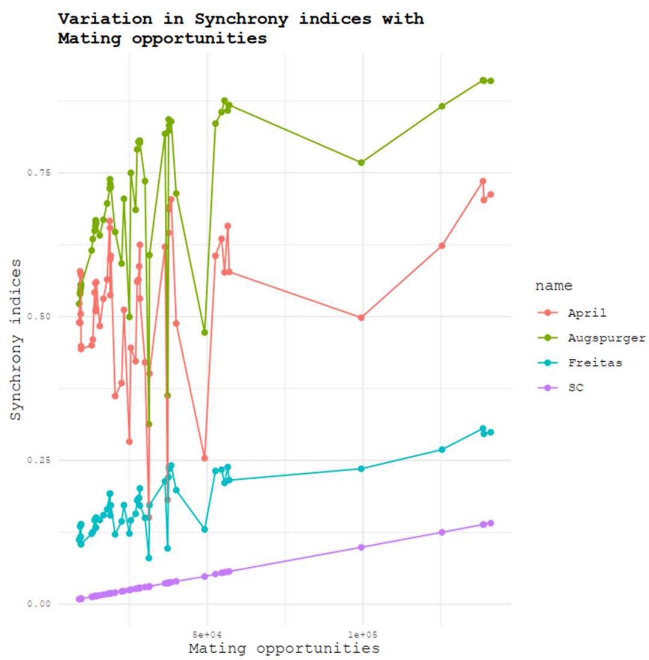

Figure 6. Variation in synchrony indices with mating opportunities

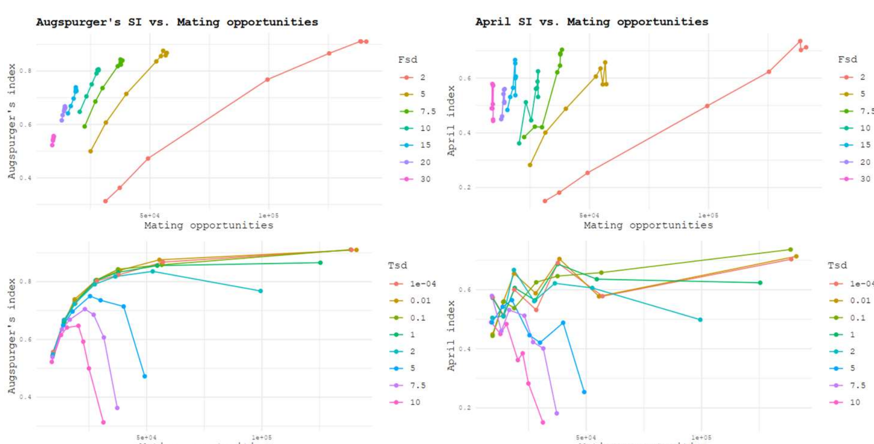

Figure 7. Variation of Augspurger's and April Index with mating opportunities grouped by Fsd and Tsd

E. Discussion

Flowering synchrony can be described by several quantities. For instance, the standard deviation of the intrapopulation mean day of flowering (Tsd) can be a measure of synchrony. Synchrony indices quantify the flowering overlap. We have seen how Augspurger's, Freitas', SC and April indices quantify flowering duration and intensity.

Augspurger's shows a clear trend with flowering duration and an increase in SI with increasing flowering duration at Tsd, as expected (Fig. 4a). SC index decreases monotonically with increasing flowering duration, but it has a very small range of [0 – 0.15] and shows a bimodal distribution of values for a range of Fsd and Tsd (Fig. 5c). Freitas' and April indices show some oscillations in the trend of SI with an increase in flowering duration, but as with all indices, the value of Sis seems to converge to a point at very high Fsd, irrespective of the Tsd (Fig. 4).

One of the major inferences that we can draw from the synchrony index of a population is the mating opportunities available to the individuals because of synchronous flowering. I wanted to check how well various synchrony indices capture mating opportunities of various populations. Among the four SIs, the SC index correlates perfectly with mating opportunities. Other indices show very large oscillations, as seen in Fig. 6. That is, with increasing mating opportunities, the Freitas', April and Augspurger's synchrony indices don't correlate well but instead vary quite a bit.

When these points are grouped by Tsd and Fsd, we can see why they show this trend – the slope of increase in synchrony index varies with the flowering duration of the population, which in turn modulates the flowering intensity. This means that the same SI value may represent vastly different mating opportunities for different populations with different flowering durations.

If we had the flowering duration and intensity data of several populations, then we could modify the calculation of flowering intensity to the following – $f_{i,t} = \frac{n_{i,t}}{\max_{N,\ T,Fsd}(n)}$ where the denominator is the maximum number of flowers produced by an individual across all populations. When the calculation of the intensity is modified, the variation of synchrony indices with mating opportunities changes to the plot shown in Fig. 8b. The variation in Freitas' and April indices decreases significantly, and it correlates better with mating opportunities. In comparison, the variation in Augspurger's index remains the same because it doesn't take into effect the flowering intensity of individuals.

The 'oscillations' in April and Freitas' index are dampened because of this modification, as seen in Fig. 9. By introducing the maximum number of flowers produced in the calculation of intensity, the denominator of these synchrony indices is set to a constant, while the numerator represents overlap in flowering, which captures mating opportunities better.

So, in the lack of complete data from multiple populations, comparing synchrony indices from isolated populations might be misleading because these indices don't capture mating opportunities very well, and we must be cautious of this bias.

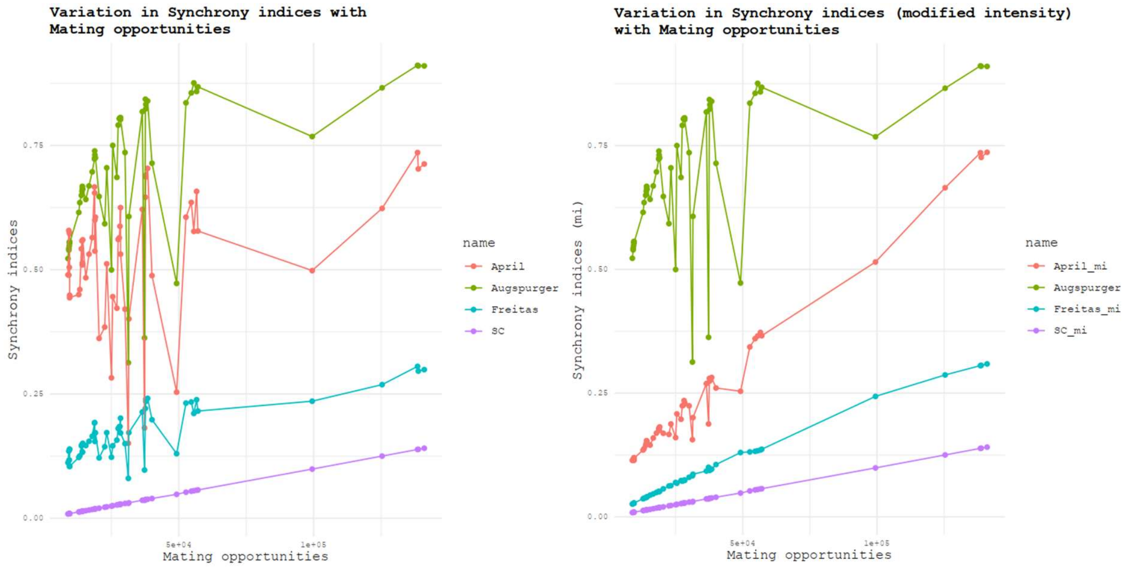

Figure 8. Variation of Synchrony indices with and without modified intensity

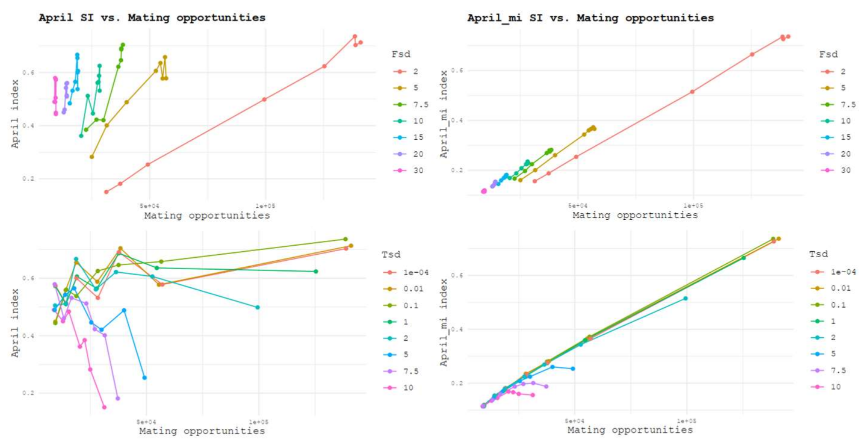

Figure 9. Variation of April index (without and with modified intensity) with Mating opportunities grouped by Fsd and Tsd

F. Future directions

1. Examine why Freitas and April indices don't vary smoothly in the initial plots.
   - Perhaps we can do this by calculating indices for larger Tsd and Fsd values at higher resolution.
2. Normalise Augspurger's index such that it correlates linearly with mating opportunities.
   - Modify the denominator of flowering duration in the denominator of Augspurger's index.
3. Simulate more realistic populations with a range of flowering intensity, and compare the synchrony index of this population with uniform populations, where all individuals have the same flowering duration and flowering intensity.
4. Explore the interaction between synchrony and pollinator visitation
   - At low Fsd (many flowers on a day), there is competition for pollinators. But this is also modulated by mating opportunities.

G. Acknowledgements

I would like to thank Dr Deepak Barua for giving me this opportunity to work with him, for being a supportive mentor and the insightful discussions on flowering synchrony. I would like to thank DB Lab members for taking me under their wing and engaging in interesting conversations. I learned a lot more about ecology, thermotolerance and invasive species through my discussions with them about their work, and by attending various lab talks by researchers around the world. I'm grateful to Dr Souparna Chakravarty and Aparna Sundaresan for sharing their code and data, upon which I have built my semester work. I would also like to thank Divyansh, my batchmate and friend, for his help with working out the pseudocode.

H. References

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