Synchrony is more than overlap: measuring phenological synchronization considering time length and intensity

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ABSTRACT – (Synchrony is more than overlap: measuring phenological synchronization considering time length and intensity). The degree of flowering and fruiting synchronization is believed to have ecological and evolutionary relevance at several scales. Here we discuss some measures that have been used to estimate synchrony and propose an index that incorporates both the entire length of an individual phenophase and variation in the number of flowers or fruits over that time period. This new index describes more accurately the phenological synchrony among individuals and populations.

Key words - fitness, phenology, pollination, population ecology, seed dispersal

RESUMO – (Sincronia é mais que sobreposição: medindo sincronia fenológica considerando a duração e a intensidade). O grau de sincronização de floração e frutificação é considerado de relevância ecológica e evolutiva em várias escalas. Neste trabalho são discutidas algumas medidas utilizadas para estimar sincronia e é proposto um novo índice, o qual inclui a duração total da fenofase de certo indivíduo e a variação na quantidade de flores e frutos neste intervalo de tempo. Esse índice estima com maior acurácia a sincronia fenológica entre indivíduos e populações.

Palavras-chave - dispersão de sementes, ecologia de populações, fenologia, polinização, sucesso reprodutivo

"*Also lacking is a rigorous measure of population overlap incorporating both the entire length of an individual's reproductive phase and variation in number of available reproductive units – flowers/fruits – over that time period*" (Augspurger 1985).

The gregarious flowering for a few days in the year, especially that of certain tropical tree species whose individuals are scattered throughout the forest, is one of the most remarkable phenomena in nature, and such events of high synchronization have been noted for a long time (see Augspurger 1985 for early citations). The degree of flowering, and also fruiting, synchronization is believed to have ecological and evolutionary relevance at several scales, from intra-individual sequence of flower opening to community- and landscape-wide interspecific patterns (*e.g.*, Frankie *et al.* 1974, Augspurger 1983, Ollerton & Lack 1992, 1998, Bronstein 1995, Borchert *et al.* 2005). For example, asynchronous ripening of fruits among certain species in the community has been interpreted as reflecting adaptations to reduce competition for seed dispersers and consequently to maximize plant reproduction (Wheelwright 1985). On other scale, flowering synchrony of individuals in a certain population can affect both the quantity and genetic quality of their offspring, because it influences the number of potential mates of each individual and also affects foraging efficiency of pollinators (Schemske 1977). To test adequately hypotheses that focus on such mechanisms (*e.g.*, higher synchrony results in higher outbreeding), it is necessary to associate any measure of plant fitness – such as pollen loads on stigmata, seed set or genetic variability – to the synchronization degree of flowering.

From the early descriptive methods that categorized tropical tree species as either synchronous or asynchronous (Janzen 1967, Frankie *et al.* 1974), several quantitative methods have been proposed to measure phenological synchronization (*e.g.*, Primack 1980, Augspurger 1983, Marquis 1988, Gorchov 1990, Gómez 1993, Bolmgren 1998, Mahoro 2002). Flowering synchrony may simply be quantified as the standard deviation or variance of the day of onset of flowering (Rathcke & Lacey 1985, Gorchov 1990). However, variance and standard deviation does not capture the important aspect of overlap among individuals in the population. Augspurger (1983), based on Primack (1980), developed a method of quantifying overlap throughout the flowering time, from the perspective of both the individual and the population.

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The Augspurger index of synchrony for a certain individual i (X_i) is a composite measure of the amount of overlap of a given individual's flowering days (or weeks, months) with those of all individuals in the sampled population; perfect synchrony and no synchrony occur, respectively, when $X = 1$ and $X = 0$ (Augspurger 1983). The amount of overlap of all individuals with each other in the population defines the population synchrony (Z), which equals the mean of the values of individual synchrony (Augspurger 1983). This index includes the entire flowering time, and also considers the temporal overlap between each set of two individuals in the population from the perspective of both individuals, which advances Primack's (1980) method that summarizes overlap from the perspective of only one of two individuals. These qualities are reflected on the large application of Augspurger's (1983) method in phenological studies, including those addressing tropical tree species (*e.g.*, Ollerton & Lack 1998, Lepsch-Cunha & Mori 1999, Buide *et al.* 2002, McIntosh 2002, SanMartin-Gajardo & Morellato 2003). However, as Augspurger (1983) herself had noted, neither Augspurger's nor Primack's measures of synchronization take into account differences in the intensity of the phenophase. Thus, in a strict sense, these methods measure the *overlap* among individuals or populations rather than the *synchrony* among them.

Therefore, a more accurate synchronization measure should consider at least the following two factors: the overlap of the phenophase occurrence and the similarity of the phenophase intensity among overlapping individuals. Marquis' (1988) estimate of flowering synchrony accounts for these two factors, as the synchronization level of individual i is a function of the proportion of opened inflorescences (or proportion of flowers or flowering intensity) at time t of the total annual number of inflorescences of this individual, multiplied by the proportion of the censured individuals in flower at time t (p_t). This means that maximum synchrony for an individual is reached when its within-individual resource display pattern coincides with the peak number of flowering individuals in the population (Bolmgren 1998). The factor p_t means that it is important to a certain individual to flower at the same time as a lot of other individuals in population. For this, Marquis' measure is more appropriated when studying phenological synchrony in relation to, for instance, pollinator foraging, plant fitness or cross-fertilization rates. However, p_t inclusion does not assure that the individual detected as the most synchronous in the population is flowering at the same time as most flowers are present, because it does not consider the flowering intensity of the other individuals

in the population, *i.e.*, similarly to the Primack's method, Marquis' index does not consider the overlap between each set of two individuals in the population from the perspective of both individuals. This fact limits in some extension the quantitative component of this estimate and also does not permit to measure accurately the relationship between any plant fitness parameter of a certain individual in relation to each other individual in the population.

To fulfill the desirable characteristics of both Augspurger's and Marquis' estimates, that is, to merge the overlap between two individuals from the perspective of both individuals and the intensity component of synchronization, we suggest the following definitions of d_i and S:

$$d_i = \frac{1}{T_i} \frac{1}{N-1} \sum_{j=1}^{N} \sum_{t=1}^{T} \sqrt{f_{i,t}\ f_{j,t}}\ ,\ j \neq i$$

d_i = level of synchronization for individual i in relation to the population of censured individuals j
f = relative value of the phenophase intensity, ranging from 0 to 1
T_i = total number of censuses where $f_i > 0$
N = total number of individuals in studied population
j = individual in population
t = census order number
T = total number of censuses over time for studied population (in reality when $f_j > 0$)

$$S = \sum \frac{d_i}{N}$$

S = synchrony index of the population

As Augspurger's index, d_i and S range from 0 to 1 value, which mean, respectively, no synchrony and perfect synchrony. The intensity of a phenophase may be calculated by different means, for example, counting directly the number of flowers or inflorescences in the individual at each census or by the Fournier (1974) semi-quantitative method – with its five categories of intensity (0 to 4) divided by 25% intervals – in which the intensity level 4 equals $f = 1$. Fournier method is the most used non-qualitative method to register phenology in tropical trees (*e.g.*, Morellato *et al.* 2000, Bencke & Morellato 2002), obviously because in most cases direct counts of flower production are practically impossible for trees. Thus, the measure of synchrony presented here could be applied for many of the data sets of tropical phenological studies already carried out, in addition to those studies

of phenotypic selection of characters in relation to phenological parameters. To exemplify the using of such an index, we calculated the values of flowering synchrony among individuals of two Rubiaceae understory species from southeastern Brazil (original data from SanMartin-Gajardo & Morellato 2003) by means of both Augspurger's and our index. The values of the Augspurger index of synchrony for each individual (X_i) were from 1.2 to 3.2-fold higher than the equivalent d_i values in *Psychotria birotula*, and from 0.5 to 4.5-fold higher in *P. nuda*. Considering the population synchrony (*Z vs. S*) the values were 2.2 and 3.0-fold higher for, respectively, *P. birotula* and *P. nuda*. Thus, the index proposed here corrects overestimation of synchronization when its measurement does not take into account differences in the intensity of the phenophase. Otherwise, values calculated by both indices were significantly correlated (figure 1), although similar values of overlapping (X_i) can result in markedly distinct values of synchrony (d_i).

Many explanations for how flowering and fruiting patterns could evolve in response to natural selection – *i.e.*, the adaptive meaning of those patterns – have been proposed in literature. Moreover, distinct adaptive explanations are given for similar phenological patterns. For example, flowering asynchrony is interpreted either as a bet-hedging strategy due to intraspecific competition for pollinators, for avoiding of seed predators, or as a mechanism to increase out-breeding by promoting inter-plant pollinator movement and mate opportunities (see Ollerton & Lack 1998 for quotations). Besides other adaptive ideas, within population asynchrony on flowering was also interpreted as a result of relaxed selection on natural genetic variability or environmental heterogeneity (Ollerton & Lack 1992, but see Fox & Kelly 1993), and phylogenetic inertia has been taking into account for explanations of interspecific synchrony (Kochmer & Handel 1986). The profusion of ideas in the literature about the adaptive nature of flowering synchrony has generated, in the last three decades, several experimental studies addressing the relationship between this phenological parameter and plant fitness (Primack 1980, Augspurger 1981, Taylor & Inouye 1985, Bishop & Schemske 1998, Kudo & Suzuki 2004, Parra-Tabla & Vargas 2004). In this sense, the use of a measure that describes more accurately the synchronization among individuals, populations and species, as proposed here (see also Malo 2002 for an alternative way to quantify phenological curves), is appropriate for the investigation of consequences of the phenological patterns. This approach could even include the analysis of data from those studies that had found that phenological synchronization was not a significant predictor of reproductive success (*e.g.*, Gómez 1993, Buide *et al.* 2002, Fuchs *et al.* 2002, McIntosh 2002), since it is expected that some kind of effect is a fine-scale acting.
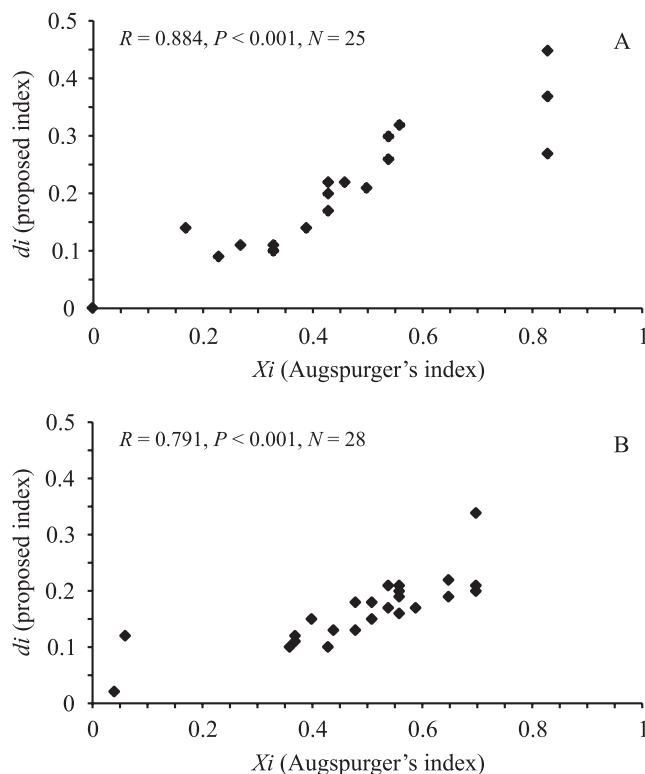
Figure 1. Spearman correlation of the index of flowering synchrony for each individual of *Psychotria birotula* (A) and *Psychotria nuda* (B), calculated by two distinct indices.

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