

## USEFUL INDICES IN PLANT REPRODUCTIVE ECOLOGY

compiled by Marcos Méndez

### ***Flowering phenology and synchrony***

NOTE: All the indices below can be also applied to fruiting phenology and synchrony.

*Flowering phenology index of Mahoro (2002).*- It measures the rank order of flowering for individual plants within a population, as

$$R_i = \sum_{j=1}^p r_{i,j}$$

where  $i$  are individuals,  $j$  is time during the flowering from beginning to pike of flowering  $p$ , and  $r$  is the rank of each individual according to  $x_{i,j}$  (the ratio of flowers that had already open in the individual by the  $j$ th census day to the total number of flowers opening in the individual during the season). A smaller value of  $R$  indicates earlier blooming. Mahoro (2002) discusses limitations of this and other indices of flowering phenology. This index is not suitable to compare populations (Elzinga et al., 2007).

*Flowering phenology displacement due to competition for pollinators index of Poole & Rathcke (1979).*- It measures in which extent flowering phenologies of a group of coexisting plant species departs from a random distribution in time. The formula given here incorporates improvements made by Williams (1995) and Stone et al. (1998).

$$V = (\text{Sum of squares of the distances}) / (\text{number of species} - 1) \times (\text{range})^2$$

in which  $V$  is the departure of a random distribution, distances referes to the temporal separation of successively blooming species (first to second species, second to third species and so on), and range is the difference between the greatest and lowest values shown by the set of species in question.

*Flowering synchrony index of Augspurger (1983).*- It measures the extent of overlapping in the flowering periods among pairs of individuals in a population, as

$$X_i = \frac{1}{n-1} \frac{1}{f_i} \sum_{j=1}^n e_j \neq 1$$

where  $e_j$  is the number of days that individuals  $i$  and  $j$  are flowering synchronously, with  $j \neq i$ ;  $f_i$  is the number of days individual  $i$  was flowering, and  $n$  is the number of individuals in the population.  $X_i$  varies from 0 (total lack of synchrony) to 1 (perfect synchrony). This index is suitable to compare populations (Elzinga et al., 2007).

*Flowering synchrony index of Marquis (1988).*- It estimates flowering synchrony among individuals of a given species as

$$S = \frac{\sum_{t=0}^n x_t}{\sum_{t=0}^n x_t} \cdot p_t$$

where  $x_t$  is the number of flowers that flowered during time  $t$ ,  $\frac{x_t}{\sum_{t=0}^n x_t}$  is the proportion of

flowers flowering during time  $t$  of the total annual number of flowering flowers,  $n$  is the number of censuses per year, and  $p_t$  is the proportion of the censused individuals in flower during time  $t$ . The proportion of individuals is included here instead of the absolute number because in Marquis (1988) sample size changed over time.

Marquis' measure of flowering phenology has two advantages in relation to the one proposed by Augspurger: (1) it describes the overlap pattern more correctly, and (2) the factor  $p_t$  does include aspects of cross-fertilization (Bolmgren, 1998).

*Flowering synchrony index of Mahoro (2002).*- It estimates flowering synchrony among individuals of a given species as

$$S_i = \frac{1}{2} \left[ 2 - \sum_{j=1}^n |y_{i,j} - \overline{y_{i,j}}| \right]$$

where  $y_{i,j}$  is the ratio of flowers that newly opened since the  $j-1$  census day to the  $j$ th census to the total number of flowers opening during the season in the individual, and mean  $y_{i,j}$  is the mean  $y_{k,j}$  ( $k \neq i$ ), and  $n$  is the last day of census. A larger  $S$  indicates higher synchrony with other individuals.

This index can be applied to estimate flowering synchrony among species of a same community, just by entering the species values for  $y_{i,j}$  and mean  $y_{i,j}$ , instead of the individual values (Osada et al., 2003). This index is not suitable to compare populations (Elzinga et al., 2007).

*Within-individual flowering synchrony index of Bolmgren (1998).*- Flowering synchrony indices above are useful for comparing individuals of a same species, or comparing species of a same community. The within-individual flowering synchrony index estimates within-individual synchronization of flowering as

$$S = \text{average } p / SD_{\text{onset}}$$

where average  $p$  is the mean persistence of individual flowers, and  $SD_{\text{onset}}$  is the standard deviation of the onset of individual flowers.

*Flowering synchrony index for genders of sexually dimorphic species at the population level of Dainou et al. (2012).*- For dioecious or other sexually dimorphic species, a within-year synchrony index  $S$  is defined as the average proportion of individuals of the two sexes (or groups) that flower together at a given time, regardless of the intensity or abundance of flowers:

$$S = \sum \frac{d_j}{N_m} \text{ and } d_j = \frac{1}{T_j} \sum_{t=1}^{T_j} f_{i(t)}$$

where  $i$  is a female and  $j$  is a male,  $d_j$  is the mean synchrony index for a male  $j$  with all females  $i$  in the population,  $f_{i(t)}$  is the proportion of females flowering with male  $j$  at time  $t$ ,  $t$  is the flower census number order,  $T_j$  is the total number of censuses when male  $j$  is flowering and  $N_m$  is the total number of males.

### **Pollination Ecology**

*Visitation Index of Udovic (1981).*- It estimates the number of visits by pollinators to individual plants over the blooming period, when the sampling is not extensive or frequent enough to get a direct measure. It is calculated as

$$V_i = \sum_{j=1}^n M_j \cdot \left[ \frac{(F_{i,j} \cdot d_{j-1,j})}{\sum_{k=1}^m F_{k,j}} \right]$$

where  $V_i$  is the visitation index for plant  $i$ ,  $M_j$  is the number of pollinators in the population at the  $j^{\text{th}}$  census,  $F_{ij}$  is the number of open flowers on plant  $i$  at the  $j^{\text{th}}$  census and  $d_{j-1,j}$  is the number of days between the  $j^{\text{th}}$  census and the previous one. This index assumes that for a given number of pollinators, the number of visits to a given plant in an interval will be proportional to the fraction of open flowers in the population which belong to that plant.

This index was developed to study the interaction between *Yucca* and its specialised pollinator. Before one applies it, it would be wise to think if the assumptions are met for the particular system studied.

*Visitation rate index of Talavera et al. (1999).*- It measures visitation rate in a relative way, by taking into account both frequency of visits and activity rate, as

$$I_{VR} = F \times AR$$

where  $F$  is the number of individuals of an insect species relative to the total number of insects included in the census, and  $AR$  is the activity rate, i.e. number of flowers that an individual insect visited per minute.

*Pollinator Efficiency Index of Spears (1983).*- It measures the relative efficiency of a species or individual as pollinator as

$$PE_i = \frac{P_i - Z}{U - Z}$$

where  $P_i$  is the mean number of seeds set per flower by a plant population receiving a single visit from species  $i$ ;  $Z$  is the mean number of seeds set per flower by a plant population receiving no visitation; and  $U$  is the mean number of seeds set per flower by a plant population exposed to unrestricted visitation.

*Pollinator Effectiveness Index of Junker et al. (2010).*- It measures the pollinator effectiveness as

$$E = f \times (t \times c)^p \times d$$

where E is the effectiveness index (pollen h<sup>-1</sup>), f is the visitation frequency (visits h<sup>-1</sup>), t is the visitation time (h visit<sup>-1</sup>), c are the stigma contacts (contacts h<sup>-1</sup>), and d is the pollen deposition (pollen contact<sup>-1</sup>). p is introduced to take into account the likely saturation effect in pollen deposition in several visits by a pollinator within a given inflorescence.

*Pollen deposition effectiveness (single visit scale) of Ne'eman et al. (2010).*- It is equal to the number of pollen grains delivered *d* by a given pollinator to the stigma of a given flower in a single visit. This requires an experimental design using bagged virgin flowers which are presented to a single visit by a pollinator.

$$D_v = d.$$

*Pollen deposition effectiveness (per time scale) of Ne'eman et al. (2010).*- It is the pollen deposition effectiveness per single visit multiplied by the visit frequency *f*.

$$D_t = D_v f r$$

where *r* is the proportion of flowers in the observed patch that actually have receptive stigmas.

NOTE: read Ne'eman et al. (2010) for further consideration of the fuzzy concepts of pollinator effectiveness and pollinator efficiency.

*Pollen Removal Efficiency Index of Freitas and Paxton (1998).*- It is a modification of the the PE<sub>*i*</sub> index of Spears (1983). It measures the relative efficiency of a species or individual as pollinator as

$$PRE_i = \frac{R_i - N}{V - N}$$

where *R<sub>i</sub>* is the mean number of pollen grains removed per flower by a plant population receiving a single visit from species *i*; *N* is the mean number of pollen grains removed per flower by a plant population receiving no visitation; and *V* is the mean number of pollen

grains removed per flower by a plant population exposed to unrestricted visitation.

*Pollinator Specificity Index of Ramírez (1993).*- It estimates the specificity of particular pollinator species as

$$PSI = \frac{1}{N}$$

where N is the number of plant species visited by the pollinator. This index does not consider the presence of pollen loads. If pollen loads are taken into account, a *Visitor Specificity Index* results.

*Pollen Transportation Specificity Index of Ramírez (1993).*- It is calculated as

$$PTS = \frac{1}{L}$$

where L is the number of different pollen loads placed on the same site of the pollinator.

*Floral constancy of de Jager et al. (2011).*- It is a modification of the constancy index of Gegear & Lavery (2005):

$$CI = (O-E)/(O+E-2OE)$$

where O is the observed probability of transition between species and E is the expected probability of transition. CI ranges from -1 (complete discrimination between species) through 0 (random visitation) to 1 (continuous switching between species).

O is calculated by direct observation of pollinator foraging behaviour as:

$$P(T_{A \rightarrow B}) = \frac{n_{AB} + n_{BA}}{n_{AA} + n_{AB} + n_{BA} + n_{BB}}$$

where  $n_{AA}$  and  $n_{BB}$  are transitions within species and  $n_{AB}$  and  $n_{BA}$  are transitions between species.

*Visitor activity index of Ramírez (2004).*- It estimates the status as pollinator of each floral

visitor species using the formula:

$$VA = \frac{(A \cdot B \cdot C) + (A \cdot B \cdot D \cdot E)}{2}$$

where A-E are five qualitative criteria utilised to distinguish floral visitors from pollinators.

A - Presence and abundance of pollen from the visited plant, coded as 1 for abundant, 0.5 for scarce, and 0 for no pollen.

B - Part of the body where pollen was located and its relationship with the position or orientation of the sexual organs in the blossom during the pollination process, coded as 1 if the criterium is fulfilled and 0 otherwise.

C - Pollen load on the body of the vector can make contact with the stigma during a visit, coded as 1 if the criterium is fulfilled and 0 otherwise.

D - Relationship between the blossom size and floral visitor size, coded as 1 if fulfilled and 0 otherwise.

E - Relative abundance of each visiting species (number of visits per unit time).

The first part of the expression (A \* B \* C) indicates pollen transference, while the second one (A \* B \* D \* E) indicates flower-visitor adaptation, attractiveness and constancy. A and B act as compensatory factors dropping to zero the value of VA when D and E are one and there is no pollen transference.

VA varies from 0 to 1; visitor species are considered as pollinators when the values of VA are significantly different from zero.

*Pollinator importance index of Gibson et al. (2006).*- It estimates the importance of a given pollinator P for a focal plant species X as

$$PI = (\text{relative abundance of pollinator}) \times (\text{pollen fidelity})$$

where relative abundance of pollinator is the proportion of all insects carrying pollen from X that are of the species P, and pollen fidelity is the mean proportion of individual pollen loads of P which correspond to plant X.

*Proportional similarity in pollinator assembly of Kay and Schemske (2003).*- It estimates the proportional similarity (PS) in pollinator assembly for pairs of sympatric species, using the formula

$$PS = 1 - \frac{1}{2} \sum_{i=1}^n |P_{ai} - P_{bi}|$$

where  $P_{ai}$  and  $P_{bi}$  are the proportion of the total visitation rate made up by taxon  $i$  for plant species  $a$  and  $b$  respectively. This index ranges from 0 to 1 and takes into account both the identity of pollinators and their relative visitation rates.

This index is taken from Schemske & Browak (1981), who applied it to the comparison of bird communities and it seems to be in origin a measure of similarity utilised in multivariate statistics. In fact, under some circumstances similarity of pollinator assemblies can also be assessed by using multivariate techniques.

*Average Specificity Value of Ramírez (1993).*- It is calculated for the plant species  $a$  as

$$ASV_a = \sum_{i=1}^n \frac{PSI_i}{N_a}$$

where  $PSI$  is the pollination specificity index of each pollinator species  $i$ , and  $N_a$  is the number of pollinator species recorded on plant species  $a$ .

*Community Pollination Index of Ramírez (1993).*- It estimates the proportion of pollinator sharing as

$$CPI = \frac{N_a}{\sum_{i=1}^n x_i}$$

where  $N_a$  is the number of pollinator species recorded on plant species  $a$ , and  $x_i$  is the number of plant species visited by the pollinator species  $i$ .

### **Reproductive success**

*Percent Pollination Limitation Index of Jules and Rathcke (1999).*- It measures the extent in which reproductive success is limited by an insufficient pollen delivery, as compared to resources, as

$$PPL = \frac{100(PS - C)}{PS}$$

where PS is the seed set of pollen-supplemented plants and C is the seed set of control plants.

*Preemergent Reproductive Success of Wiens et al. (1987).*- It measures the number of ovules that complete development and survive to enter the environment as:

$$\text{PERS} = (\text{n}^\circ \text{ fruits} / \text{n}^\circ \text{ flowers}) \times (\text{mean n}^\circ \text{ seeds per fruit} / \text{mean n}^\circ \text{ ovules per flower})$$

### **Breeding system**

*Self-incompatibility Rate of Zapata and Arroyo (1978).*- It measures the self-incompatibility of a plant species as:

$$\text{ISI} = (\text{self fruit set}) / (\text{cross fruit set}).$$

where self fruit set and cross fruit set are data obtained from controlled pollination experiments. Values  $\geq 1$  indicate self-compatibility; values  $0.2 > \text{ISI} < 1$  indicate partial self-compatibility.  $\text{ISI} < 0.2$  indicates mostly self-incompatibility and  $\text{ISI} = 0$  indicates total self-incompatibility.

*Selfing Rate of Charlesworth and Charlesworth (1987).*- It estimates the frequency of self-pollination as

$$S = \frac{P_x - P_o}{P_x - P_s}$$

where  $P_x$  are seeds resulting from cross-pollination,  $P_o$  are seeds resulting from open pollination and  $P_s$  are seeds resulting from self-pollination.

*Contribution of autogamy and geitonogamy to selfing of Eckert (2000).*- It estimates the contribution of autogamy and three components of geitonogamy (within-branch, between-branch, between-ramets) to self-fertilization from the differences in the selfing between intact and emasculated flowers. Subscripts refer to: intact flowers = 0; single-flower emasculation = 1; whole-branch emasculation = 2. Seeds are produced through selfing (s) or outcrossing (t). The selfed fraction includes two components: autogamy (a) and geitonogamy (g). Thus  $(a + g) + t = 1$ . The geitonogamous component includes within-

branch (w), between-branch (b) and between-ramet (r) components. Thus  $(a + [w + b + r]) + t = 1$ .

For single flower emasculations,  $s_0 = a + g$ , and  $s_1 = g$ .  $a$  cannot be estimated as  $s_0 - s_1$  because  $s_1$  overestimates geitonogamous selfing in intact flowers ( $g_0$ ) because the absolute siring success of both outcross and geitonogamous pollen on emasculated flower will be higher without competition from autogamous pollen. Because  $a_0 + g_0 + t_0 = 1$  and  $g_1 + t_1 = 1$ , it follows that

$$\frac{g_0}{1 - s_0} = \frac{g_1}{1 - s_1} = \frac{s_1}{1 - s_1}$$

so that

$$g_0 = \frac{s_1(1 - s_0)}{1 - s_1}$$

and

$$a_0 = s_0 - g_0.$$

Components w, b and r of geitonogamous selfing can be calculated in a similar fashion. Using selfing rates for intact flowers ( $s_0 = a_0 + w_0 + b_0 + r_0$ ) and flowers from whole-branch emasculations ( $s_2 = b_2 + r_2$ ), it follows that

$$(b_0 + r_0) = \frac{s_2(1 - s_0)}{(1 - s_2)}.$$

$$w_0 = s_0 - a_0 - (b_0 + r_0).$$

Between-ramet geitonogamous selfing (r) is calculated from the selfing rate of emasculated flowers on plants with a single flowering branch ( $s'_0 = a'_0 + w'_0 + r'_0$ ) and  $s'_2 = r'_2$ , where prime (') denotes single-branch plant. The component  $r'_0$  could be calculated as described, but it underestimates r for the population as a whole, because  $a'_0$ ,  $w'_0$ ,  $r'_0$  and  $t'_0$  all increase in the absence of b. Thus, r must be estimated as  $r_0 = s'_2 (1 - s_0) / (1 - s'_2)$ . The between-branch component is then:

$$b_0 = \frac{s_2(1 - s_0)}{(1 - s_2)} - \frac{s'_2(1 - s_0)}{(1 - s'_2)}$$

Standard errors for each component can be derived by performing the same calculations for each of the 1000 sets of bootstrap values for the estimates of  $s$  and calculating the standard deviation of the resulting distribution.

*Inbreeding depression.*- It estimates inbreeding depression of a *population* as

$$\delta_p = 1 - \frac{w_s}{w_x}$$

where  $\delta_p$  is the population inbreeding depression,  $w_s$  is the *average* fitness of the self progeny and  $w_x$  is the *average* fitness of the outcross progeny. Positive values indicate inbreeding depression, while negative values indicate outbreeding depression. Fitness is calculated by means of controlled pollination experiments. Note that these average values can be calculated for the whole population, regardless of family origin, or for each family tested and then averaged across families to obtain the population inbreeding depression. When family-structured inbreeding depression is in focus, follow the advice provided by Johnston & Schoen (1994) and Fox (2005). Accurate estimation of inbreeding depression can require more complicate experimental designs than usually utilised (Fox, 2005).

*Inbreeding depression index of Ågren & Schemske (1993).*- It estimates inbreeding depression as the relative performance of crosstypes (RP) following the formula:

$$RP = 1 - \frac{w_s}{w_0} \text{ if } w_s \leq w_0$$

and

$$RP = \frac{w_0}{w_s} - 1 \text{ if } w_s > w_0$$

where  $w_s$  is the fitness of selfed progeny, and  $w_0$  is the fitness of outcrossed progeny. This index varies from -1 to 1. Positive values indicate that outcrossed progeny outperform

selfed progeny, negative values that selfed progeny outperform outcrossed. This measure has an advantage over the traditional expression for inbreeding depression ( $\delta_p = 1 - \frac{w_s}{w_x}$ ) in that it gives equal weight to "inbreeding" and "outbreeding depression", when averaged over several lines or maternal parents. Caveats described by Fox (2005) apply also to this index.

*Reciprocity Index for tristylous species of Eckert & Barrett (1994).* -

$$RI = \frac{1}{3} \left[ \left| 1 - \frac{lS - sL}{L - S} \right| + \left| 1 - \frac{lM - mL}{L - M} \right| + \left| 1 - \frac{mS - sM}{M - S} \right| \right]$$

where small letters in the numerator refer to the length of the stamen level of a given morph type (capital letters: L- long styled, M- middle styled, S- short styled) and capital letters refer to the style length of the morph that corresponds with the letter.

*Precision Index for tristylous species of Eckert & Barrett (1994).* - It is calculated as a measure for variation within the organ levels

$$PI = \frac{(CV_S + CV_M + CV_L)}{3}$$

where CV is the coefficient of variation at a given level.

### **Seed ecology**

*Germinability* (Yang et al. 1999).- It measures the germination of the seeds produced by a plant as

(number of germinating seeds x 100) / number of seeds initiated

*Relative germinability* (Yang et al. 1999).- It measures the germination of the seeds produced by a plant as

G = (number of germinating seeds x 100) / number of viable seeds initiated

*Index of germination rate* (Yang et al. 1999).- It measures the germination rate of the seeds

produced by a plant as

$$\text{IGS} = \sum G / t$$

where  $G$  is the relative germinability, at 5-d intervals, and  $t$  is total germination period.

*Dormancy* (Yang et al. 1999).- It measures the extent of seed dormancy of the seeds produced by a plant as

(number of ungerminated but viable seeds x 100) / number of seeds initiated

*Relative dormancy* (Yang et al. 1999).- It measures the extent of seed dormancy of the seeds produced by a plant as

(number of ungerminated but viable seeds x 100) / number of viable seeds initiated

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