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 jth 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.

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).

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

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

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

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

where $y_{i,j}$ is the ratio of flowers that newly opened since the j-1 census day to the jth 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).

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 = average p / SD_{onset}

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

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

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

where V_i is the visitation index for plant i, M_j is the number of pollinators in the population at the j^{th} census, F_{ij} is the number of open flowers on plant i at the j^{th} census and $d_{j-1, j}$ is the number of days between the j^{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 x 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

$$\text{PE}i = \frac{Pi - Z}{U - Z}$$

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.

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

$$\text{PRE}i = \frac{Ri - N}{V - N}$$

where R*i* 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

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

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 taked 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.

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 is 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.

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 = $1 - \frac{1}{2}\sum_{I=1}^{n}\left|P_{ai} - P_{bi}\right|$

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:

PERS = (nº fruits / nº flowers) x (mean nº seeds per fruit / mean nº ovules per flower)

Breeding system

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

ISI = (self fruit set) / (cross fruit set).

where self fruit set and cross fruit set are data obtained from controlled pollination experiments. Values ≥ 1 indicate self-compatibility; values 0.2 > ISI < 1 indicate partial self-compatibility. ISI < 0.2 indicates mostly self-incompatibility and 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.

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

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

where δ_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 = $1-\frac{w_s}{w_0}$ if $w_s \leq w_0$

and

RP = $\frac{w_0}{w_s}-1$ 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.

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

$IGS = \sum G / t$

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

References

Augspurger, C. K. (1983). Phenology, flowering synchrony and fruit set of six neotropical shrubs. *Biotropica* 15: 257-267.

Ågren, J.; Schemske, D. W. (1993). Outcrossing rate and inbreeding depression in two annual monoecious herbs, *Begonia hirsuta* and *B. semiovata*. *Evolution* 47: 125-135.

Charlesworth, D.; Charlesworth, B. (1987). Inbreeding depression and its evolutionary consequences. *Annu. Rev. Ecol. Syst.* 18: 237-268.

Fox, C. W. (2005). Problems in measuring among-family variation in inbreeding depression. *Amer. J. Bot.* 92: 1929-1932.

Freitas, B. M.; Paxton, R. J. (1998). A comparison of two pollinators: the introduced honey bee *Apis mellifera* and an indigenous bee *Centris tarsata* on cashew *Anacardium occidentale* in its native range of NE Brazil. *J. Appl. Ecol.* 35: 109-121.

Johnston, M. O.; Schoen, D. J. (1994). On the measurement of inbreeding depression. *Evolution* 48: 1735-1741.

Jules, E. S.; Rathcke, B. J. (1999). Mechanisms of reduced *Trillium* recruitment along edges of old-growth forest fragments. *Conserv. Biol.* 13: 784-793.

Kay, K. M.; Schemske, D. W. (2003). Pollinator assemblages and visitation rates for 11 species of neotropical *Costus* (Costaceae). *Biotropica* 35: 198-207.

Mahoro, S. (2002). Individual flowering schedule, fruit set, and flower and seed predation in *Vaccinium hirtum* Thunb. (Ericaceae). *Can. J. Bot.* 80: 82-92.

Marquis, R. J. (1988). Phenological variation in the neotropical understory shrub *Piper* *arieianum*: causes and consequences. *Ecology* 69: 1552-1565.

Osada, N.; Sugiura, S.; Kawamura, K.; Cho, M.; Takeda, H. (2003). Community-level flowering phenology and fruit set: comparative study of 25 woody species in a secondary forest in Japan. *Ecol. Res.* 18: 711-723.

Poole, R. W.; Rathcke, B. J. (1979). Regularity, randomness and aggregation in flowering phenologies. *Science* 203: 470-471.

Ramírez, N. (1993). Reproductive biology in a tropical shrubland of Venezuelan Guayana. *J. Veg. Sci.* 4: 5-12.

Ramírez, N. (2004). Ecology of pollination in a tropical Venezuelan savanna. *Plant Ecol.* 173: 171-189.

Schemske, D. W.; Browak, N. (1981). Treefalls and the distribution of understory birds in a tropical forest. *Ecology* 62: 938-945.

Spears, E. E. Jr (1983). A direct measure of pollinator effectiveness. *Oecologia* 57: 196-199.

Stone, G. N.; Willmer, P.; Rowe, J. A. (1998). Partitioning of pollinators during flowering in an African *Acacia* community. *Ecology* 79: 2808-2827.

Talavera, S.; Bastida, F.; Ortiz, P. L.; Arista, M. (1999). Pollinator attendance and reproductive success in *Cistus libanotis* L. (Cistaceae). *Int. J. Plant Sci.* 162: 343-352.

Udovic, D. (1981). Determinants of fruit set in *Yucca whipplei*: reproductive expenditure vs. pollinator availability. *Oecologia* 48: 389-399.

Wiens, D.; Calvin, C. L.; Wilson, C. A.; Davern, C. I.; Frank, C.; Seavey, S. R. (1987). Reproductive success, spontaneous embryo abortion, and genetic load in flowering plants. *Oecologia* 71: 501-509.

Williams, M. R. (1995). Critical values of a statistic to detect competitive displacement. *Ecology* 76: 646-647.

Yang, J.; Lovett-Doust, J.; Lovett-Doust, L. (1999). Seed germination patterns in green dragon (*Arisaema dracontium*, Araceae). *Amer. J. Bot.* 86: 1160-1167.

Zapata, T. R.; Arroyo, M. T. K. (1978). Plant reproductive ecology of a secondary deciduous tropical forest in Venezuela. *Biotropica* 10: 221-230.