

The mutualistic trade-off

Mini proposal 2

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Abstract (mock)

It is generally believed that there is a trade-off between the number of mutualistic partners a plant species has, and the strength of its interactions (mutualistic benefit). The trade-off arises from the premise that an increase on the number of mutualistic partners might increase facilitation, but might also increase competition for pollinators because it can lead to a reduction of the proportion of conspecific pollen deposited on the stigmas. Species properties and the environmental context seem to influence whether sharing pollinators leads to facilitation or competition (Tur *et al.* 2016), however the specific mechanisms behind these observations are poorly understood. Furthermore, recent theoretical advances that explicitly include the mutualistic trade-off in pollination models have highlighted its importance. Indeed, it has been shown that the trade-off is related to the feasibility and stability of mutualistic communities (Rohr *et al.* 2014), the species' response to change (Saavedra *et al.* 2013), the onset of critical transitions (Dakos & Bascompte 2014), and the spread of perturbations (Suweis *et al.* 2015). However, The extent to which the trade-off operates in nature and its relationship with facilitation-competition dynamics has not been empirically evaluated. Here, we used data on the quality and quantity of pollination in six pollination communities to quantify the empirical support for the mutualistic trade-off concept and identify the mechanisms that structure it. Contrasting to our initial expectation, we found that the mutualistic benefit is only weakly related to the number of pollination partners. We found that this relationship is weak because plants with a large number of shared partners are able to reduce the cost of sharing by increasing the niche partitioning. Importantly, the niche partitioning strategies are modulated by plant abundance and are not homogeneously employed by all plant species.

Questions & hypotheses

1. Is the trade-off between mutualistic benefit and the number of mutualistic partners observed in nature?
 - *H1-null*: There is no relationship between the proportion of conspecific pollen deposited and the number of mutualistic partners. *H1-alternative 1*: The trade-off δ can be characterized at a community scale using the relationship

$$\sum_j \gamma_{ij} = \sum_j \gamma_0 y_{ij} / d_i^\delta = \gamma_0 d_i^{1-\delta},$$

where $\sum_j \gamma_{ij}$ is the proportion of conspecific pollen, γ_0 represents the community level of mutualistic strength and d_i is the number of mutualistic partners of species i . *H1-alternative 2*: the trade-off is species specific:

$$\sum_j \gamma_{ij} = \gamma_0 d_i^{1-\delta_i}$$

- *Methods:* We will use stigmatic pollen deposition data to fit a non linear regression for each of the hypothesis alternatives. We will then use AIC to determine the support for each of them.
2. What is the relationship between the mutualistic trade-off and facilitation-competition dynamics?
 - If support is found for H1-alternative 1. *H2-null:* there is no relationship between δ and the proportion of species that experience facilitation in the community. *H2-alternative:* there is a positive relationship.
 - If support is found for H1-alternative 2. *H2-null:* there is no relationship between δ_i and the species specific slope of facilitation β_i . *H2-alternative:* there is a relationship.
 - *Methods:* β_i will be calculated following Tur *et al.* (2016) - model 1. Which uses a poisson GLMM with number of conspecific pollen grains per stigma as response variable, total number of heterospecific pollen grains as predictor with plant receptor species as random slope and intercept. We will then use a simple linear regression to identify the relationship between δ_i and β_i or δ and β_f (which correspond to the proportion of plant species for which $\beta_i \pm 2SE > 0$).
 3. What is the relative importance of the strategies that plant can use to achieve high mutualistic strength while minimizing competition?
 - *H3-null:* there is no relationship between abundance + niche partitioning due to shared pollinator species + niche partitioning due to individual pollinator variation + niche partitioning due to temporal overlap and the proportion of conspecific pollen. *H3-alternative 1:* there is a positive relationship between all these strategies and proportion of conspecific pollen, they operate at the community level (no important variation among plant species). *H3-alternative 2:* there is a positive relationship but plants are specific on their strategy (e.g. abundant species do not need to partition niche, less abundant species do need to do that but they either focus on avoiding phenological overlap or pollinator overlap).
 - *Methods:* overall abundance will be calculated by adding the independent abundances obtained at different sample occasions; species level pollinator niche overlap will be calculated constructing an animal-individual/plant-species matrix and using normal β -diversity approaches, the overlap will be then partitioned between individual and species level by removing the overlap found in a animal-species/plant-species matrix, following the overlap will be partitioned between a nested and modular component; temporal overlap will be calculated using a similar approach but constructing abundance plant-species/month matrices. Because it is likely that there are large interactions between all these predictors, we will use random regression forests or boosted regression trees to quantify the relative importance of variables. To determine the extent to which plants employ different strategies we will use a PCA or similar to reduce the dimensionality and calculate the overlap in the hypervolume of strategies.

Dataset

The dataset is spatially structured in three sites. Each site has four fragments (two restored and one agricultural). In total there is 11 fragments because one of the restored sites was too small to accommodate two fragments. In each fragment two transects were performed. For the season 2010-2011 there is data on:

- Individual level pollen transfer networks (sampled one per month between November and March).

- Stigmatic pollen deposition for 3-9 of the most abundant species in each fragment. This subset includes both generalist (~75%) and specialist (~25%) species. In total there are 26 species and 49 species-fragment estimations. Heterospecific pollen deposition was not further identified. Stigmas were collected only on December and February and the date was not recorded.
- Visitation networks (sampled one per month between November and March).
- Independent plant and insect abundance estimates in 50x2m random transects (abundance is therefore not available for species present in the interaction networks but not in the abundance transects; sampled one per month between November and March).

In addition to this, there is also abundance and visitation data for the 2008-2009 season, and abundance, visitation, and pollen transfer data for the 2009-2010 season.

Different components of this data set have been published by Marrero *et al.* (2014), Marrero *et al.* (2016), and Marrero *et al.* (2017). Marrero *et al.* (2014) used visitation data and determined that there were differences on the degree of specialization between land uses (agricultural vs. restored) as well as the richness of plants and pollinators. Marrero *et al.* (2016) used pollen deposition data and determined that the pollination service (both the absolute number and the proportion of conspecific pollen deposited on stigmas) is reduced in agricultural communities when compared to restored communities. Finally, Marrero *et al.* (2017) used pollen transfer networks and found that pollen diversity and pollination niche overlap (at the species level) is greater in agricultural communities. The increase on niche overlap was in turn positively associated with an increased abundance of exotic plants.

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