# Extending latent-variable modelling of plant-pollinator interactions

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### The study of floral evolution: Darwin's 'flank movement on the enemy'

- 'no one else has perceived that my chief interest in my orchid book, has been that it was a "flank movement" on the enemy' (Darwin to Asa Gray, July 23<sup>rd</sup> 1862)
- 'If you grant an intelligent designer anywhere in Nature, you may be confident that he has had something to do with the "contrivances" in your Orchids.' (Gray to Darwin, July 2<sup>nd</sup> 1862)





### Measuring Natural Selection

- Positive (or negative) relationship between a trait and a fitness component
- Pollinator-mediated selection arise when pollinators prefer some flowers over others, or when floral traits affect the efficiency of pollen transfer



### Traits are not independent

- To account for (measured) correlated traits, linear selection gradients are estimated as the partial regression coefficients of relative fitness on a set of traits.
- Relative fitness =

individual fitness/population mean fitness

• In plants, we often know or can hypothesize the functions of specific traits in the pollination process



## The Lande-Arnold approach to measuring selection

• Total selection on a trait is the sum of direct selection on the focal trait, and indirect selection on phenotypically correlated traits



Lande & Arnold 1983 Evolution

### Building a fitness function



Visitation (V) = f(Advertisement, Reward) Cross-pollen arrival ( $P_{CROSS}$ ) = f(Advertisement, Reward, Fit) Self-pollen arrival ( $P_{SELF}$ ) = f(Advertisement, Reward, Fit, Herkogamy)

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# Plants do not interact with their pollinators in isolation

### How can we extend single-species

analyses to the community level?





Treating the coflowering community as a unmeasured (latent) variable

- With many coflowering species, it becomes untractable to model the effect of each separately
- Alternative approach is to consider the community as a composite variable representing all coflowering species





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#### Theory: selection analysis with reduced-rank regression

- Reduced-rank regression (Anderson 1951; Izenman 1975) achieves dimension reduction of multivariate problems by projecting an original set of covariates onto a reduced set of composite variables that best explains variance in the response variable. In our case, **the composite scent trait under selection**
- The reduced-rank regression covariates (scent selection axis) are obtained as linear combinations of the original covariates,  $x_{i(n_c+k)} = \sum_{l=1}^{n_c^{O,RRR}} w_{kl} \tilde{x}_{il}$ , where the weights  $w_{kl}$  determine the contribution of the original covariates (volatiles)  $\tilde{x}_{il}$  to the new covariate  $x_{i(n_c+k)}$ .
- The weights  $w_{kl}$  and the regression coefficients  $\beta_{kj}$  are estimated during model fitting (posterior sampling). For the weights, we apply a multiplicative Gamma process shrinkage prior to ensure that the leading axis explains the most variation. Thus, **our approach jointly estimates the structure of the scent selection axis, and selection acting on it**.

## Is the 'scent selection axis' a reasonable approximation?

- Explanatory power always higher for multiple-regression: fully expected
- Predictive power tends to be higher for reduced-rank regression: less overfitting



Reduced-rank regression

Opedal et al. 2022 JEB

### Characterizing the scent selection axis



Opedal et al. 2022 JEB

### Theory: co-flowering community analysis with reducedrank regression

- Reduced-rank regression (Anderson 1951; Izenman 1975) achieves dimension reduction of multivariate problems by projecting an original set of covariates onto a reduced set of composite variables that best explains variance in the response variable. In our case, **the combination of co-flowering species associated with pollination success of a focal plant**
- The co-flowering community variables are obtained as linear combinations of the original covariates,  $x_{i(n_c+k)} = \sum_{l=1}^{n_c^{O,RRR}} w_{kl} \tilde{x}_{il}$ , where the weights  $w_{kl}$  determine the contribution of the original covariates (species)  $\tilde{x}_{il}$  to the new covariate  $x_{i(n_c+k)}$ .
- The weights  $w_{kl}$  and the regression coefficients  $\beta_{kj}$  are estimated during model fitting (posterior sampling). For the weights, we apply a multiplicative Gamma process shrinkage prior to ensure that the leading axis explains the most variation. Thus, **our approach jointly estimates the structure of the community variable, and its effect on a focal species**

#### Still a single focal species, what about multiple?



### Methodological advances towards community-level analyses

- Analysing plant-pollinator interactions and selection at the community level is complex
- Advances in automated pollen identification and joint modelling paves the way forward



RESEARCH ARTICLE

fethods in Ecology and Evolution

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### Methodological advances towards community-level analyses

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#### APPLICATION

#### Joint species distribution modelling with the R-package HMSC

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### Hierarchical joint models

- Hierarchical joint models allows analysing multiple response variables (e.g. pollinator species) while inferring joint responses
- Also allows inferring residual associations after accounting for relevant covariates (e.g phenotype)



### The Rudsviki data

- 20 plots
- 9 bumblebee-pollinated plant species
- 200 censuses, each 10 min
- Number of visits to each species







### Model 1: Latent variables only





### Model 2: Conspecific floral abundances













- Directionality:
- Two-way positive



- Directionality:
- Two-way positive
- One-way positive



- Directionality:
- Two-way positive
- One-way positive
- One-way negative



- Directionality:
- Two-way positive
- One-way positive
- One-way negative
- Two-way positive-negative





### Coflowering Linum species in southern Spain

*Linum suffruticosum* 



Linum suffruticosum



Linum viscosum



Ruiz-Martín et al. 2018 Pérez-Barrales & Armbruster, 2<sup>nd</sup> review



Rocío Pérez-Barrales et al.















