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Tree, Sex and Size: Ecological determinants of male versus female fecundity in three *Fagus sylvatica* stands

Sylvie Oddou-Muratorio*, Julie Gauzere*, Aurore Bontemps*, Jean-François Rey # & Etienne K. Klein#

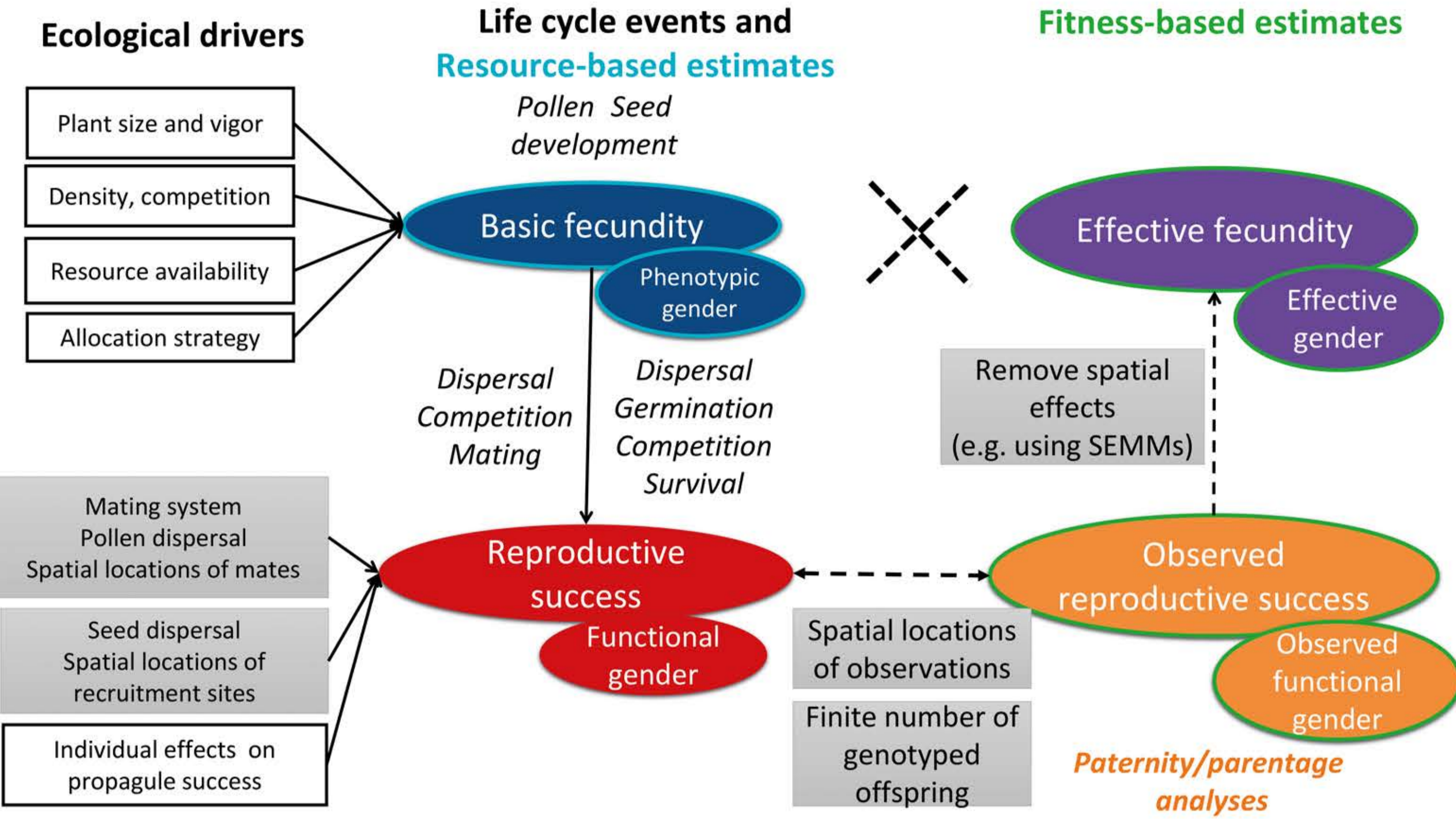
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Inter-individual variations in female (♀) and male (♂) fecundities have major consequences on population evolutionary potential, through genetic drift and selection. In plants, basic fecundities are classically estimated before dispersal through the resource allocated to ♀ (i.e. the biomass/number of ovules, seeds, ovuliferous flowers or fruits) and ♂ (i.e. the biomass/number of pollen grains or staminate flowers) functions. Alternatively, paternity and parentage reconstruction can provide fitness-based estimates of effective fecundity and reproductive success, though the numbers of offspring assigned to a given individual. However, we miss a conceptual framework linking resource-based and fitness-based estimates of fecundity to reproductive success, and tools to obtain comparable estimates of ♀ and ♂ effective fecundities. The present study aims to fill this gap, first by **providing a new method to estimate together ♀ and ♂ effective fecundities accounting for a spatial configuration effect** (implemented in the MEMM program). Then we apply this method to **study the variation in ♀/♂ fecundities and gender in relation to plant size and competition in a major monoecious tree species, the European beech.**

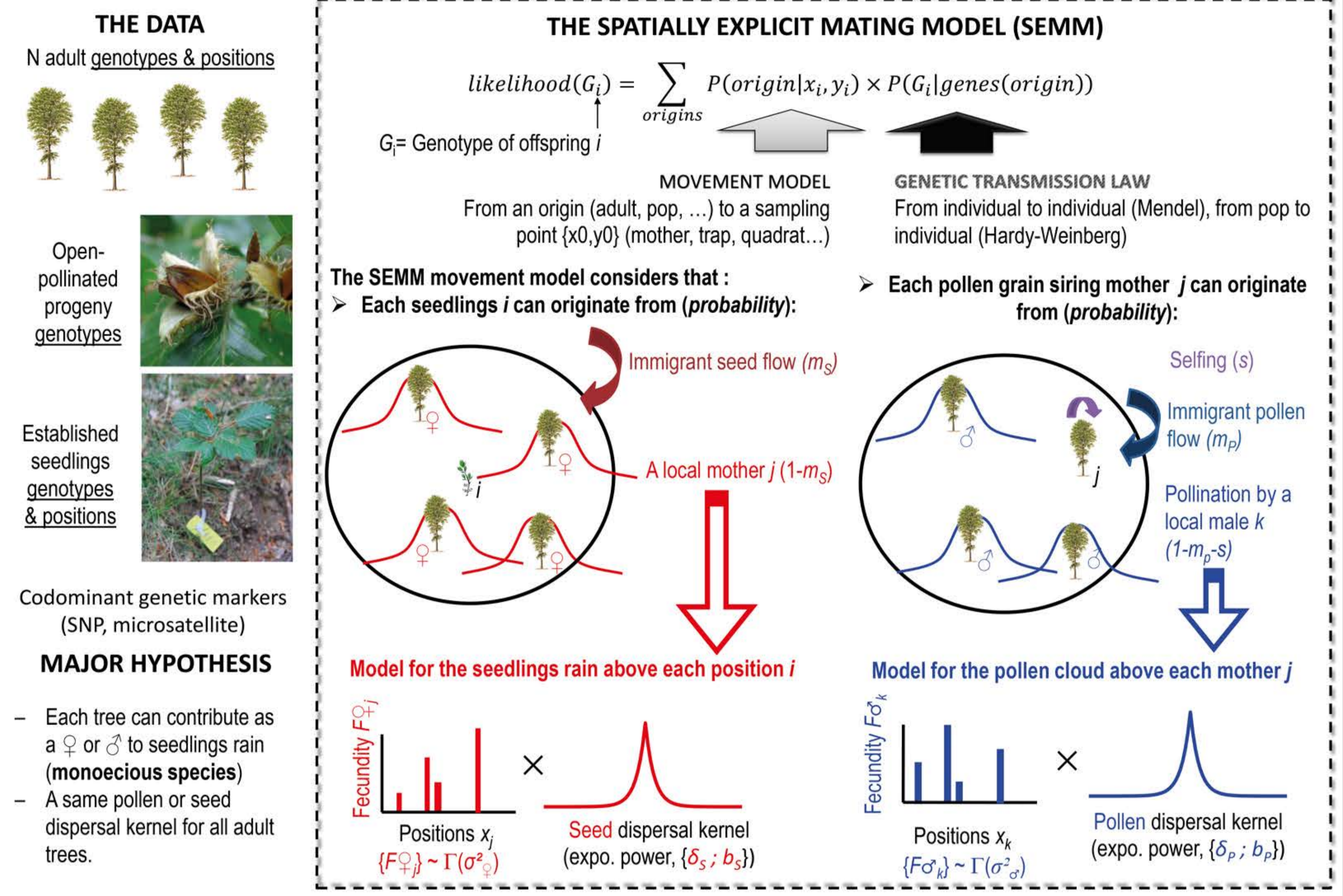
Context and objectives

Bridging the gap between resource-based and fitness-based estimates of fecundity and gender in plants

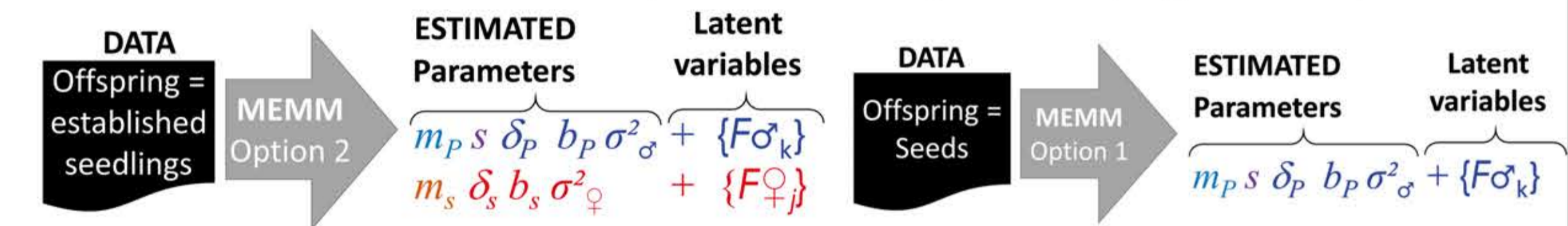


- **Basic fecundity and phenotypic gender** encompass only the production of pollen and seed and are estimated before dispersal by the number/biomass of seed/pollen (**resource-based estimates**).
- **Reproductive success** is driven by basic fecundity together with additional factors, including spatial processes and individual effects on propagule success.
- **Reproductive success and functional gender** are **observed after dispersal** using **parentage/paternity analyses**, which are potentially biased by spatial and sampling effects.
- **Spatially Explicit Mating Models (SEMM)** get rid of these confounding effects to retrieve the **effective fecundity and gender**, which accounts for individual effects on propagule success.

Estimating ♀ and ♂ individual fecundities with MEMM

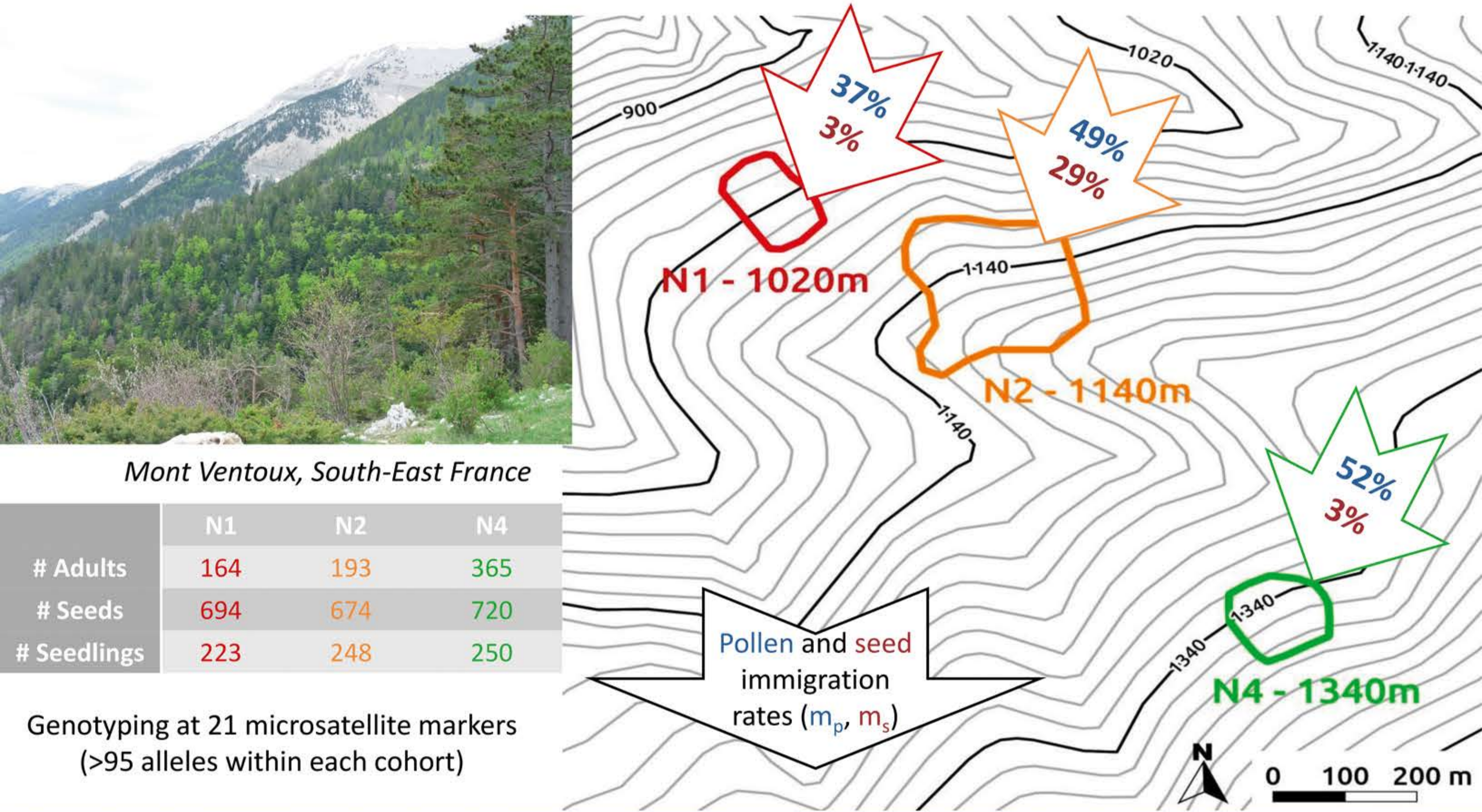


IMPLEMENTATION : All parameters and latent variables were estimated in a Bayesian framework using the **MEMM program** with 2 options :



The MEMM program (Mixed Effect Mating Model) can be downloaded at : <https://gitlab.paca.inra.fr/frey/MEMMseedlings.git>

Sampling three *F. sylvatica* plots along an altitudinal gradient



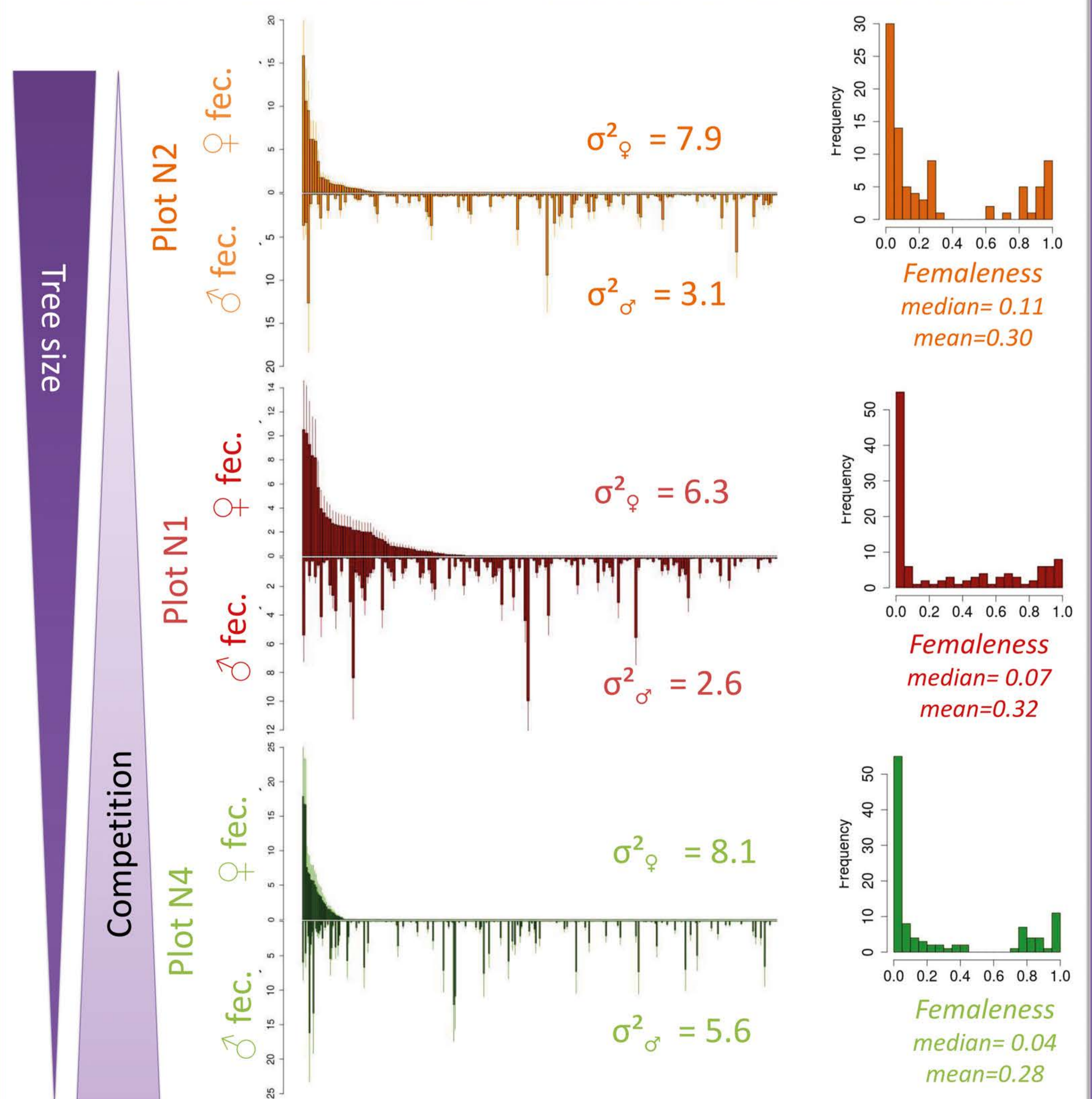
Previous result : Pollen immigration increased with altitude: protogyny combined with temperature variation may result in oriented pollen flow from bottom to top (Gauzere et al. Mol Ecol. 2013)

Result: ecological drivers of fecundity and gender

| | Ecological driver | ♀ fecundity | ♂ fecundity | Femaleness |
|-----------------|------------------------------------|-------------|-------------|------------|
| Individual size | Maximum stem diameter | ↗ | | |
| | Sum of stems' diameter | | ↗ | |
| | Tree stature (dominated, dominant) | | ↗ | |
| Competition | Conspecific competition | ↘ | ↘ | ↘ |
| | Total competition | ↘ | | ↘ |

- The effects of size and competition were consistent across the three plots.
- Both ♀ and ♂ effective fecundities were resource-limited in the studied species.
- Size effects were sex-specific and consistent with the higher unit cost of ♀ as compared to ♂ reproduction, and with the limitation of ♂ fecundity by mating opportunities.
- Effective gender was independent of size, but femaleness decreased under limited resources (i.e. with increasing competition and density), consistent with the higher unit cost of ♀ reproduction

Result: ♀ and ♂ effective fecundities and femaleness



- Both ♂ and ♀ fecundities distribution were L-shaped (Y-scale is relative, and vary among plots)
- The variance in ♀ fecundities ($\sigma^2_{\text{♀}}$) tended to be higher than the variance in ♂ fecundity ($\sigma^2_{\text{♂}}$)
- The variance in fecundities tended to be higher at high elevation (significant for $\sigma^2_{\text{♀}}$)
- The three plots were male-biased, without significant correlation between ♂ and ♀ fecundity

Conclusions

- SEMM- and resources-based estimates of fecundity are complementary: the latter estimate the resources allocated to reproduction while the former can only estimate a relative amount of pollen or seed produced. Moreover, SEMM-estimates account for individual effects that act independently on location to modify the success of mating.
- In the monoecious tree *Fagus sylvatica*, both ♂ and ♀ fecundities increased with tree size and decreased with competition in the neighborhood (with sex-specific strategies to deal with limited resources).
- This study suggests that the evolutionary potential of *Fagus sylvatica* population is enhanced by low variance in fecundity at low elevation, and high pollen flow at high elevation.

