UNICAMP. 2017

Day 2. Fitness in clonal plants

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Combining sex and clonality

- Most perennial plants combine sex and asexual reproduction
- Diversity of reproductive strategies

- Measuring life-time fitness in perennial, clonal organisms is complicated

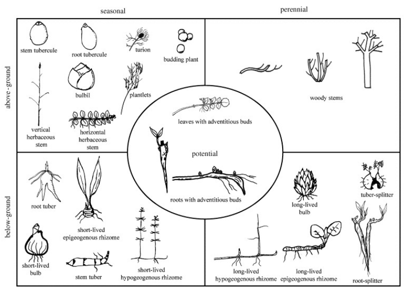
Road Map

- Plant clonality
- Effect of clonality on plant sexual strategies
- What is fitness in clonal plants?
- Units of selection
- Demographic approaches to measure fitness
- Primer of population projection matrixes
- Calculating population growth rate
- Case study using clonal monkeyflowers
- Using R: *popbio* package

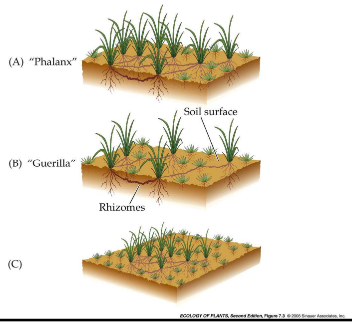
Asexual reproduction

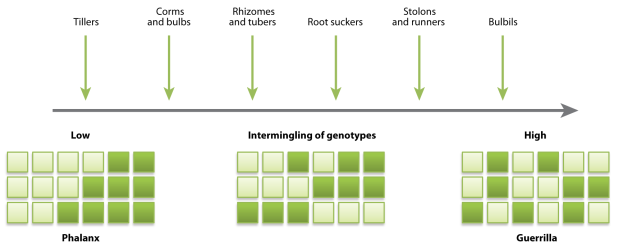
- Clonal (vegetative) growth
- Apomixis (production of seeds without sex)

Clonal propagation involves diverse structures



Clonal architecture





Consequences for Plant Mating

Plant Mating: Who mates with whom and how often?

Barrett (2002)

1. Number of genotypes in the population
2. Spatial distribution of genotypes
3. Persistence of genotypes

Consequences for plant mating:

- Probability of mating with relatives (including itself!).
- Dynamics of deleterious mutations (inbreeding depression), e.g. via accumulation of somatic mutations.
- Benefits of other uniparental modes of reproduction.

Ecological Consequences of Clonality

1. Reduction in Genotypic Diversity:
- Number of plants does not represent the number of unique genotypes

Number of genotypes (G)
Number of plants sampled (N)

G/N = "Proportion Distinguishable" (Ellstrand and Rose, 1987)

Study	Number of taxa	Mean G/N (range)
Ellstrand and Rose (1987)	21	0.17 (0.002-1.0)
Widen et al. (1994)	45	0.27 (0.002-1.0)
Arnaud-Haond et al (2007)	220 studies	0.47 (0-1)
Honnay and Jacquemyn (2008)	77	0.44 (0-1)
Silvertown (2008)	218	0.40 (0-1)

Pollination dynamics in clonal patches

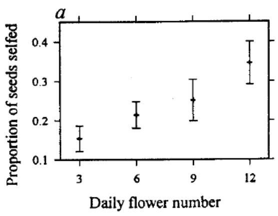
Pollen transfer:

- Between genetic individuals (outcross pollen)
- Within the same genetic individual (self pollen)

Self-pollination can be of three types:

- Within the same flowers
- Between flowers of the same plant (ramet) — geitonogamy
- Between flowers of different ramets of the same genet **

** Exclusive of clonal plants



Eichhornia paniuclata
(Harder and Barrett, 1995)

- Clonality by increasing geitonogamy among ramets increases transfer of self-pollen

Selfing in clonal plants

Decodon verticillatus (Lythraceae)

Total self-fertilization (0.3)

- Within flowers = 18%
- Between flowers = 57%
- Between clones = 25%

Eckert (2000)

Does clonality disfavour the evolution of selfing?

1. Clonality increases self-pollination rates, producing more unfit offspring
2. Clonality provides reproductive assurance
3. Clonality increases inbreeding depression via accumulation of somatic mutations
4. Clonality reduces the genetic advantage of uniparental reproduction gained by selfing

Selection should rarely favour the joint evolution of clonality and selfing

Fryxell's Reproductive Triangle (1957)

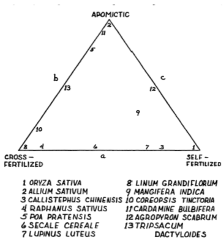


FIG. 1. The "reproductive triangle", a diagrammatic representation of the reproductive method of various species.

Building the Reproductive Triangle

Total Reproduction = Outcrossing + Selfing + Clonal

- **Clonal Reproduction:**
  Approximated as the proportion of adults produced via clonality

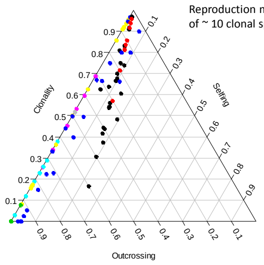
  Clonal Fraction = 1 - Genets / Ramets = 1 - G/N

- **Reproduction via Outcrossing:**
  Adults produced sexually * Outcrossing rate (estimated via genetic markers)
  = (G/N) * t

- **Reproduction via Selfing:**
  Adults produced sexually * (1-Outcrossing rate)

Collected estimates of both clonal fraction and outcrossing rates from the literature

Reproductive Triangle



Reproduction mode in ~ 50 populations of ~ 10 clonal species

Vallejo-Marin, unpublished

What is fitness in clonal organisms?

Fitness

- *The success of an entity in reproducing; hence the average contribution of an allele or genotype to the next generation or succeeding generations.* Futuyma (2013)
- *The fitness of a trait or allele is… the expected reproductive success of an individual who has that trait or allele relative to other members in the populations.* Bergstrom and Dugatkin (2016)

Fitness in sexual organisms

Individual (=genotype) fitness

- Number of offspring contributed to the next generation
- E.g., in a dioecious plant, the fitness of a female individual is the expected number of offspring produced * offspring quality
- Male plant, number of offspring sired * quality

Allele fitness

- Average number of offspring produced by individuals carrying a **particular allele**

Fitness: Survival (viability) and Fertility

Genotype	Viability	Fertility	Fitness
AA	v_{11}	f_{11}	W_{11}
Aa	v_{12}	f_{12}	W_{12}
aa	v_{22}	f_{22}	W_{22}

Viability: Survival to reproductive age
Fertility: Offspring produced

Relative fitness

$$w_{11} = W_{11} / W_{11}$$
$$w_{12} = W_{12} / W_{11}$$
$$w_{22} = W_{22} / W_{11}$$

W = Absolute fitness
w = relative fitness

Genotype	Viability	Fertility	Absolute Fitness	Relative Fitness
AA	0.90	3.00	2.70	1.0
Aa	0.90	2.00	1.80	0.67
aa	0.45	2.00	0.90	0.33

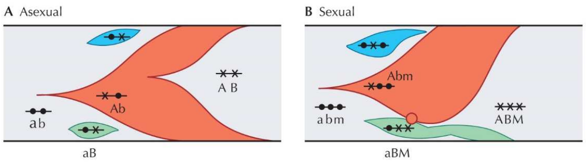
Two *levels* of individuals: genets and ramets

- Genet: Genetically unique individual
- Ramet: Physiologically independent unit

- Which *individuals* should we count to measure fitness in clonal organisms?

Asexuality results in linkage disequilibrium

- Recombination breaks associations between loci
- In asexuals, loci are not statistically independent but are transmitted together with other loci



Fitness in asexuals: Number of individuals in genotypic classes

Operational definitions

- Number of individuals per lineage (e.g., yeast cells in sexual vs. asexual lineages)
- Clonal plants: seeds + clones

How to weight seeds vs. clones?

- Seeds and vegetative propagules often make different contributions to the next generation
- E.g., plants may produce many seeds, but the probability of establishment may be low
- In contrast, clonal propagules may be less numerous but have a higher competitive advantage


A demographic approach

- Measure plant fitness in groups of individuals (populations)

$$n_{t+1} = \lambda * n_t$$

n = number of individuals
λ = population growth rate

If $\lambda_1 > \lambda_2$, then species 1 has higher fitness than species 2 (higher rate of population growth)

Primer in population demography

Modelling population demography: Structured populations

- A structured population is simply a population in which there are different classes of individuals

- Age structure: Individuals classified by age
- Stage structure: Individuals classified by stage

- Individuals from different classes make different contributions to population growth

Modelling population growth

- How does survival and fertility affect population growth?
- Which stages have the strongest effects on population growth?

Modelling population growth:

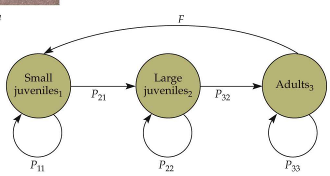
- Short- and long term growth
- Population structure
- Reproductive value
- Sensitivity of growth at specific changes in survival and reproduction

Life cycle graphs

Coryphantha robbinsorum

F (=effective fertility)= average number of fruits * average seeds per fruit * seed survival and germination * survival to first census

seeds



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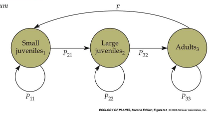
Coryphantha robbinsorum



Number of **Juveniles** at time *t + 1:*

$n_1(t+1) = P_{11}\, n_1(t) + Fn_3(t)$

Number of **Large Juveniles** at time *t + 1:*

$n_2(t+1) = P_{21}\, n_1(t) + P_{22}n_2(t)$

Number of **Adults** at time *t + 1:*

$n_3(t+1) = P_{32}\, n_2(t) + P_{33}n_3(t)$

Matrix Model

Transition Matrix   Population Vector

$$\begin{bmatrix} n_1(t+1) \\ n_2(t+1) \\ n_3(t+1) \end{bmatrix} = \begin{bmatrix} P_{11} & 0 & F \\ P_{21} & P_{22} & 0 \\ 0 & P_{32} & P_{33} \end{bmatrix} \times \begin{bmatrix} n_1(t) \\ n_2(t) \\ n_3(t) \end{bmatrix}$$

$$\mathbf{n}_{\mathbf{t+1}} = \mathbf{M}\mathbf{n}_{\mathbf{t}}$$

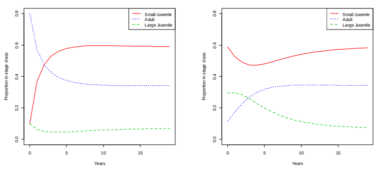
- Multiplying a vector times a matrix

Row $\times$ column

How to build a matrix:
Describes the transition probabilities from "column" number stage to "row" number stage.

Analysing matrix models

- Repeated multiplication of the vector and matrix reaches a stable structure:
  That is, the population size keeps changing, but the proportion of individuals in each class remains constant



Analysing matrix models

- Repeated multiplication of the vector and matrix reaches a stable structure:
  That is, the population keeps growing, but the proportion of individuals in each class remains constant

- The transition matrix can be replace by a single number:
  λ (eigenvalue)

- Eigenvalues and Eigenvectors

  M = transition matrix
  x = vector

$$\mathbf{Mx} = \underbrace{\lambda}_{\text{eigenvalue}} \underbrace{\mathbf{x}}_{\text{eigenvector}}$$

Eigenvalues and eigenvectors

- The eigenvalues tell us about population changes in numbers

$\lambda = 1$ Population is stable

$\lambda > 1$ Population is growing

$\lambda < 1$ Population is declining

- The eigenvectors tell us how many at each stage

Eigenvalues and eigenvectors

- Each matrix has a number of eigenvalues and eigenvectors
- A matrix with *N* rows and columns (stages) has *N* eigenvalues and eigenvectors
- A 3x3 matrix: $\lambda_1, \lambda_2, \lambda_3$
- One eigenvalue is always larger than the rest: Dominant or **leading eigenvalue**
- Overtime, the population growth rate approaches the **leading eigenvalue**, and the structure its associated eigenvector
- Population growth and structure can be predicted using eigenvalues and eigenvectors

Demography of *Coryphanta*

Site A (northeastern exposure)	Site B (southwestern exposure)	Site C (hilltop) A_{max}
$A_{\text{site A}} = \begin{bmatrix} 0.672 & 0 & 0.561 \\ 0.018 & 0.849 & 0 \\ 0 & 0.138 & 0.969 \end{bmatrix}$	$A_{\text{site B}} = \begin{bmatrix} 0.493 & 0 & 0.561 \\ 0.013 & 0.731 & 0 \\ 0 & 0.234 & 0.985 \end{bmatrix}$	$A_{\text{site C}} = \begin{bmatrix} 0.434 & 0 & 0.560 \\ 0.333 & 0.610 & 0 \\ 0 & 0.304 & 0.956 \end{bmatrix}$

$\lambda = 0.9978$ $\lambda = 0.9977$ $\lambda = 1.1187$

- Long-term prediction of population growth

Sensitivity and Elasticity

- How does *lambda* change as the individual elements of a transition matrix change?
- Sensitivity: Rate at which lambda changes when all other elements in the matrix are held constant

$$\begin{bmatrix} P_{11} & 0 & F \\ P_{21} & P_{22} & 0 \\ 0 & P_{32} & P_{33} \end{bmatrix} \quad a_{ij}$$

$$\text{Sensitivity} = \frac{\partial \lambda}{\partial a_{ij}}$$

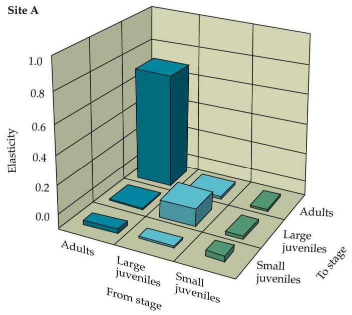
- Partial derivative with respect to a_{ij}

Sensitivity and Elasticity

- Sensitivities: How to compare among scales and account for matrix elements that are defined as zero?
- Elasticity (e_{ij}): The <u>proportional</u> sensitivity of lambda with respect to change in an element of the matrix

$$e_{ij} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}}$$

- Elasticities are comparable across the matrix
- Elasticities add up to one
- Comparable across matrices based on the same life cycle graph



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A case study using monkeyflowers

- Handouts for this practical exercise are provided separately