DYNAMICS OF STRUCTURED POPULATIONS

31 January 2020
ECOLOGICAL AND EVOLUTIONARY RESPONSES TO CLIMATIC VARIATION

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CONCEPTS

population dynamics

population growth rate

lambda, λ

demography

vital rates

population structure

sensitivity

elasticity

fecundity

stochasticity

stable stage distribution

reproductive value

OUTLINE

- Population dynamics
- Structured populations
- Modelling the dynamics of structured populations
- Case study

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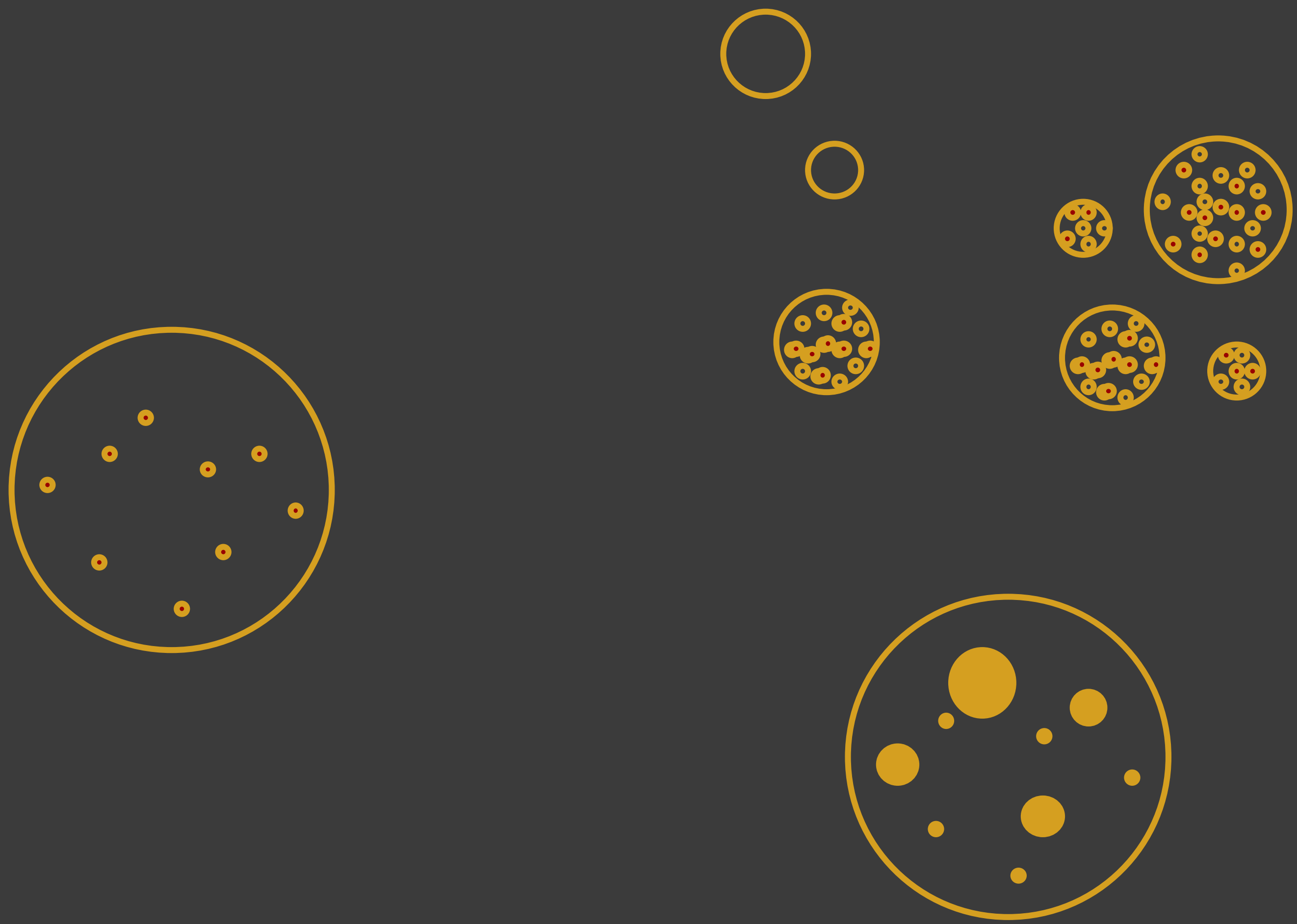
THE POPULATION

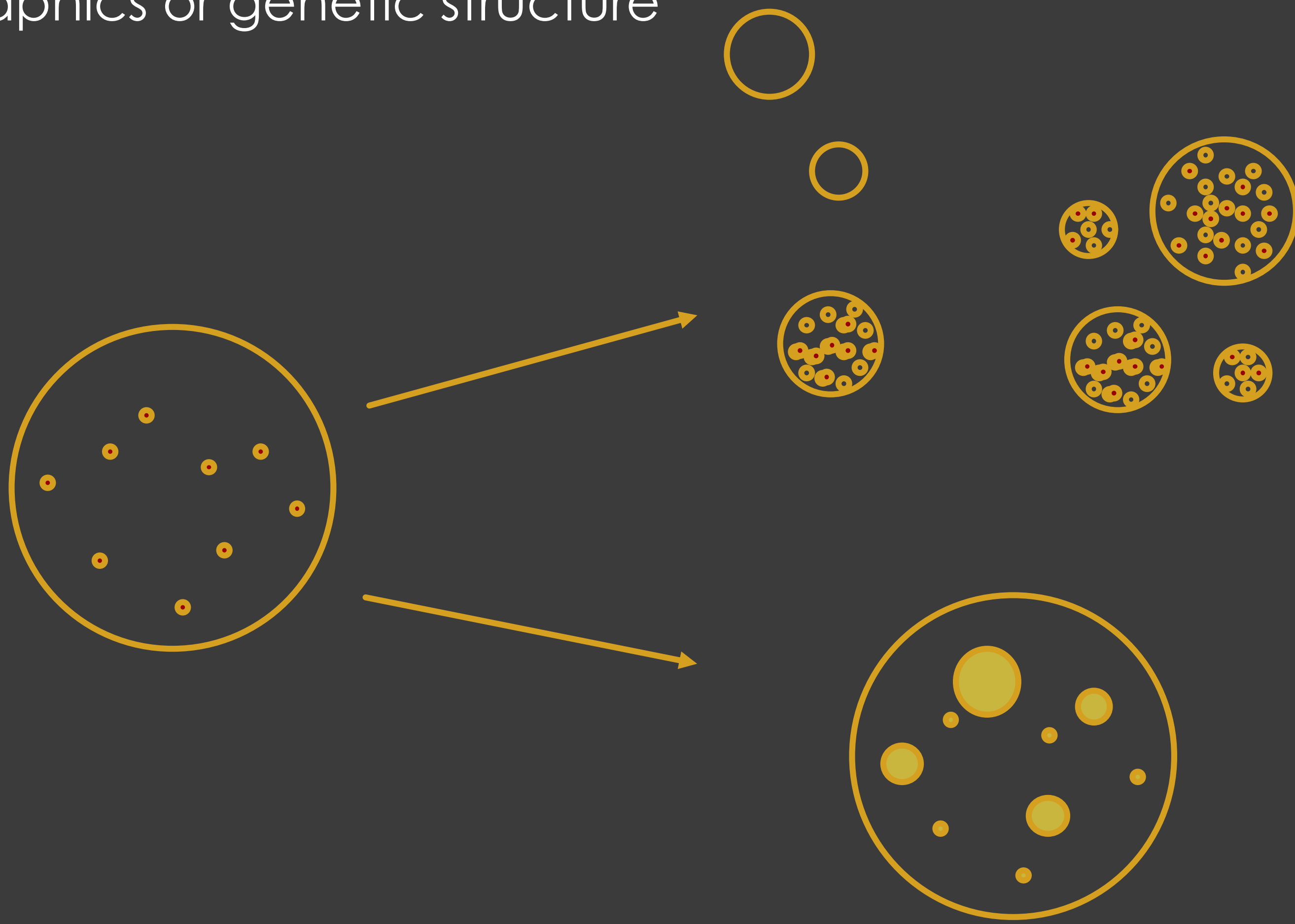
– Spatial disjunction: limited movement between groups
– Genetic: among-group differences in allele frequencies
– Demographic: among-group differences in vital rates



POPULATION DYNAMICS

– Change in population structure through time

- Abundance and spatial distribution
- Demographics or genetic structure



THREE IMPORTANT CONCEPTS

POPULATION DYNAMICS

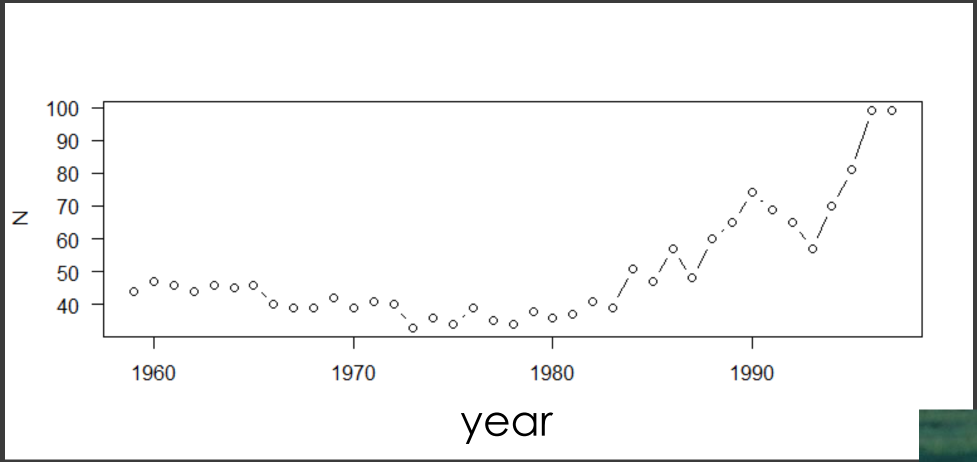
POPULATION GROWTH RATE

DEMOGRAPHY

POPULATION DYNAMICS

Changes in population size and structure through time

$$N_{(t+1)} = N_{(t)} + B - D \ (+ I - E)$$



POPULATION DYNAMICS

Changes in population size and structure through time

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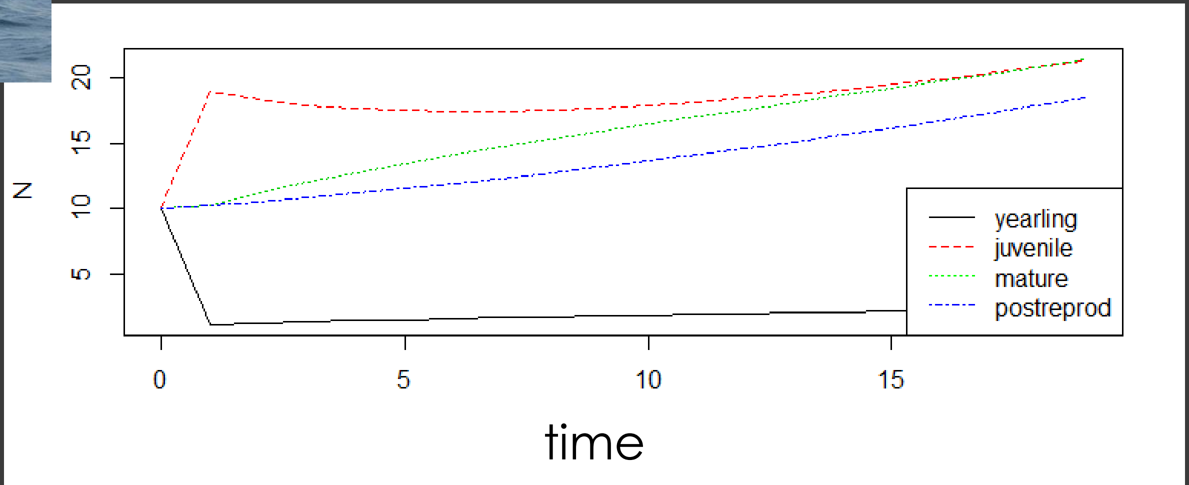


POPULATION GROWTH RATE

λ (lambda)

$$N_{(t+1)} / N_{(t)} = \lambda$$

$$\lambda = e^{r} \quad (r = \ln(\lambda))$$

$\lambda > 1$: Population is increasing

$\lambda < 1$: Population is decreasing

$\lambda = 1$: No change

DEMOGRAPHY

DEMOGRAPHY

Demo = the people; graphy = measurement

Here: study of the processes (vital rates) underlying population dynamics, i.e. reproduction, growth and survival

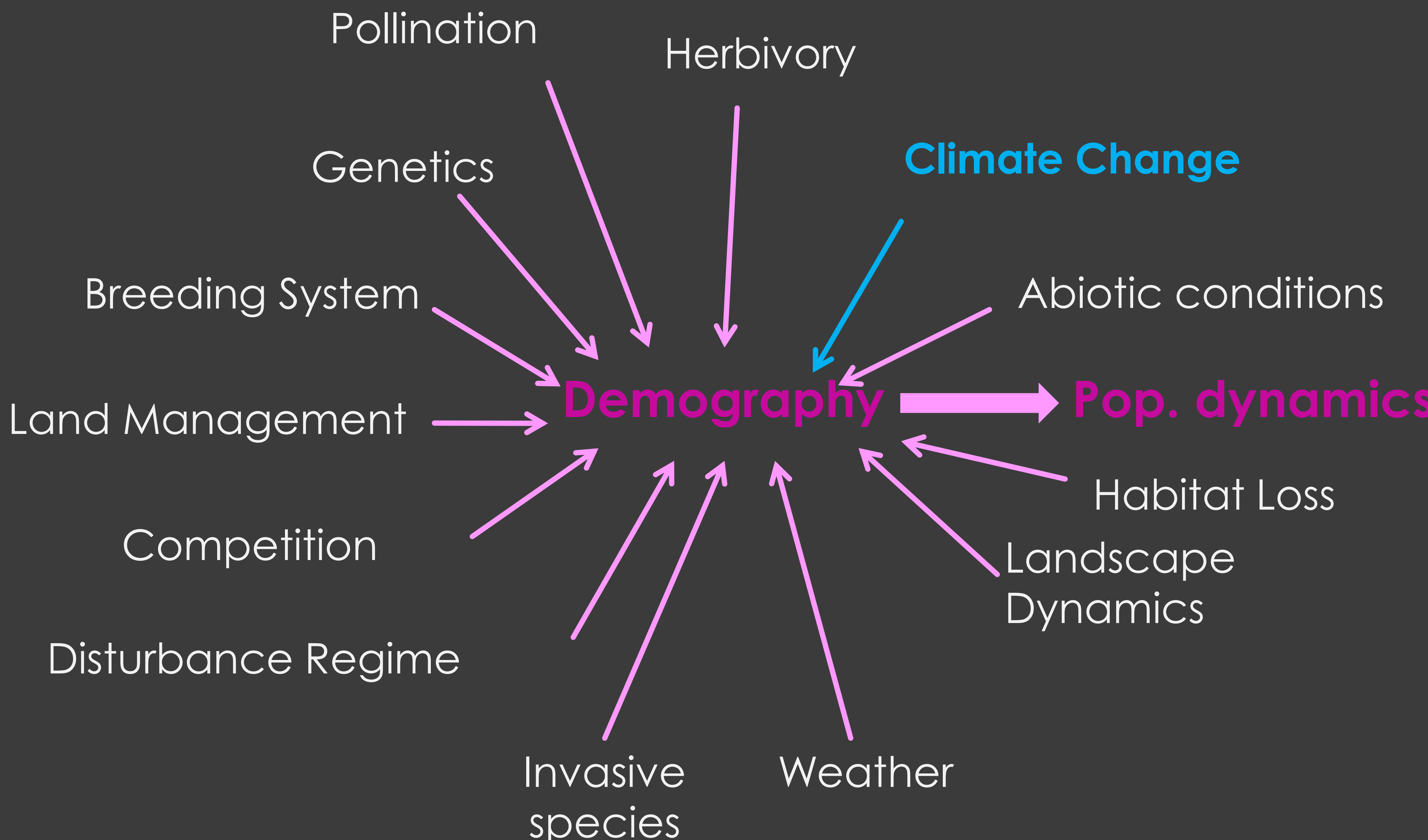
- Answer questions about population dynamics and conservation

- Understanding natural selection and life-history evolution

Important parameters:

- Population viability
- Population growth rate, λ
- Lifetime fitness

CONCEPTUALIZING POPULATION DYNAMICS

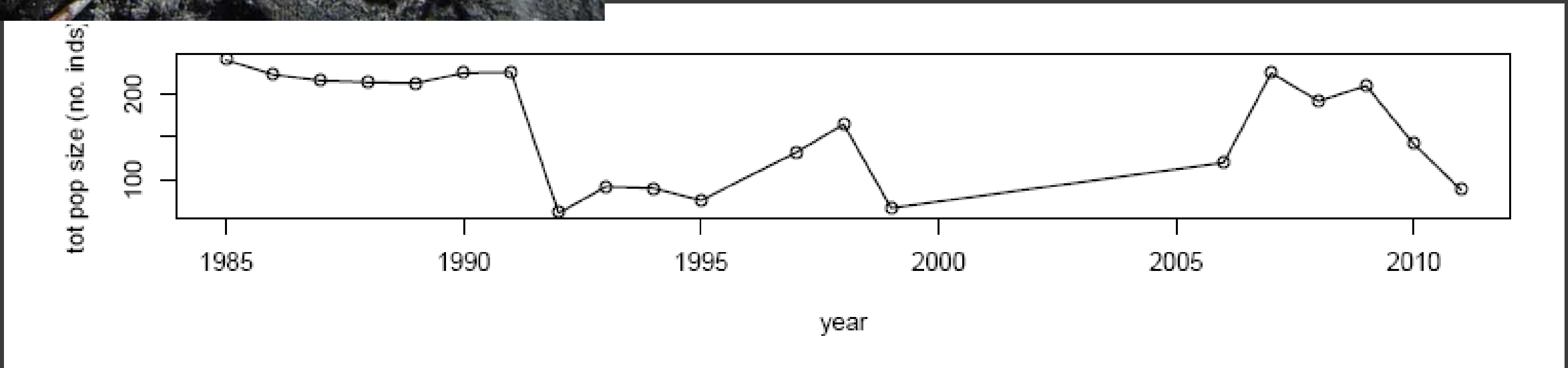


QUESTIONS WITHIN THE FIELD OF POPULATION DYNAMICS

- Is the population increasing or decreasing?
- What is the risk of extinction?
- What are the causes of population decline/increase?
- How are changes in the environment and climate influencing populations?
- How does hunting, fishing and harvesting influence populations?
- What are the best management options for rare and endangered species?

Fumana procumbens

– a long-lived dwarf shrub in rocky habitats



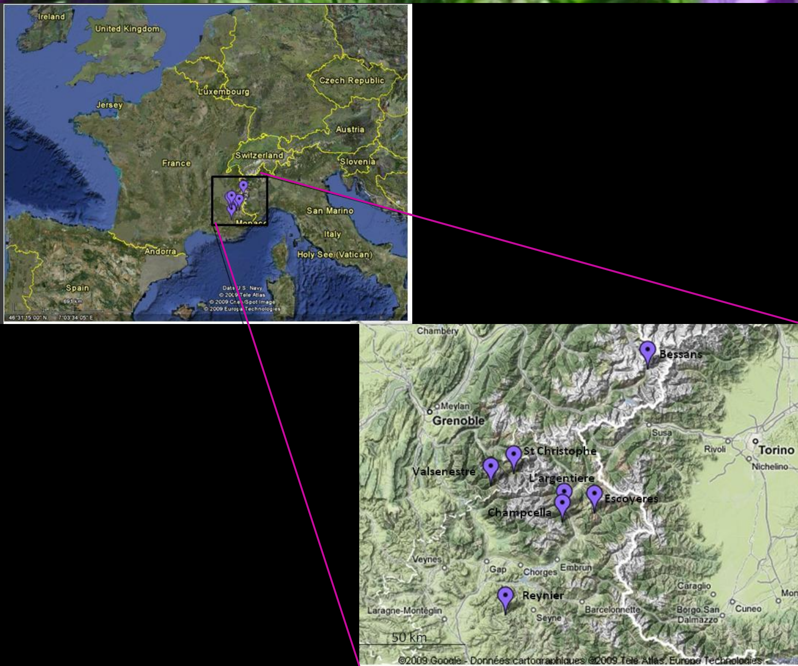
What factors are driving changes in population size among years?

Johan P. Dahlgren, Karin Bengtsson, Johan Ehrlén (2016) Ecology

Dracocephalum austriacum

– an endangered herb growing on exposed cliffs in the Alps

How will population viability be influenced by a warmer climate?



Florence Nicolè, Johan P. Dahlgren, Agnès Vivat,
Irène Till-Bottraud, Johan Ehrlén (2011) Journal of Ecology

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STRUCTURED POPULATIONS

Individuals differ regarding:

- Size
- Age
- Development stage
- Morphological stage
- Etc.

Such differences can be related to differences in:

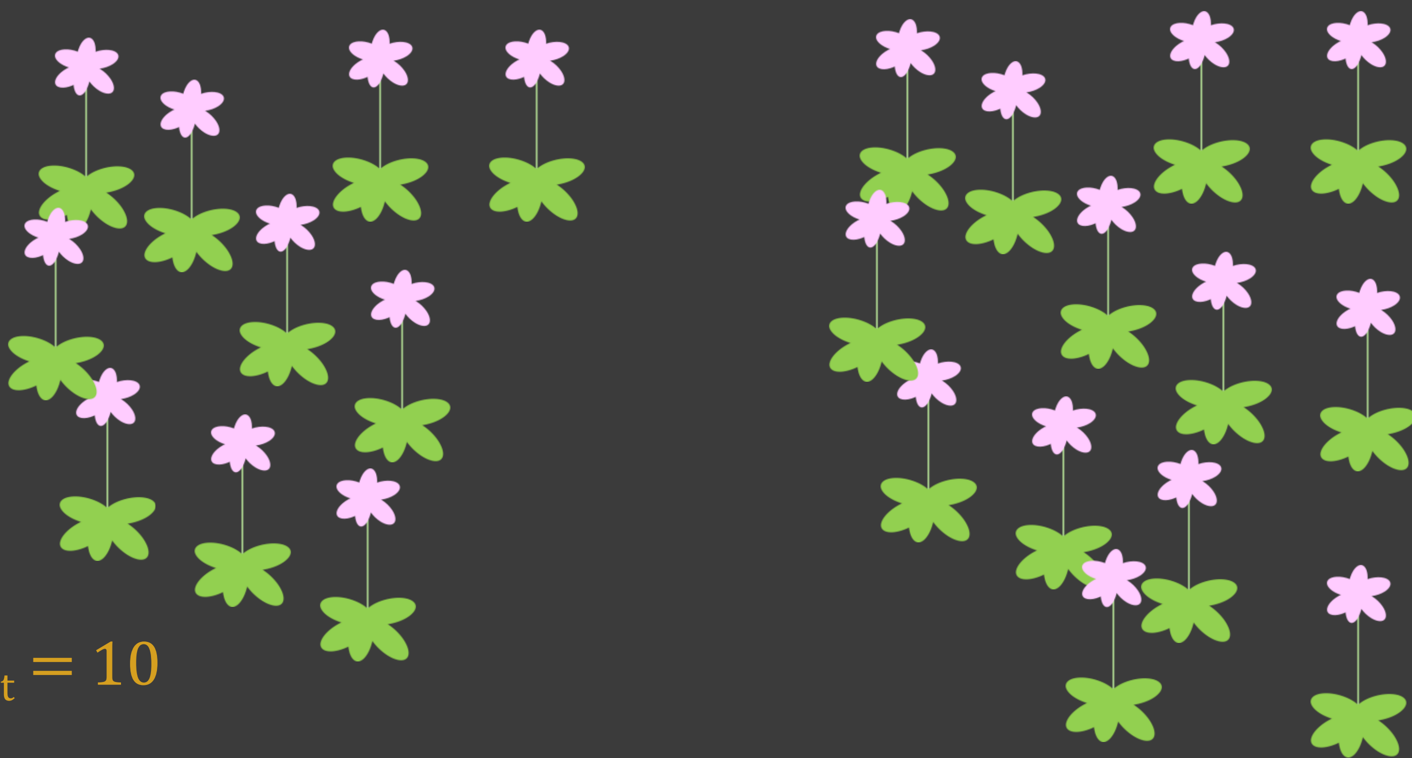
- vital rates (growth, reproduction, mortality)
- impact of stressors

→ differential impact on population growth, and thus more or less important as targets of conservation actions

HOW DOES POPULATION STRUCTURE INFLUENCE POPULATION DYNAMICS ?

UNSTRUCTURED POPULATION:

Year 1 Year 2



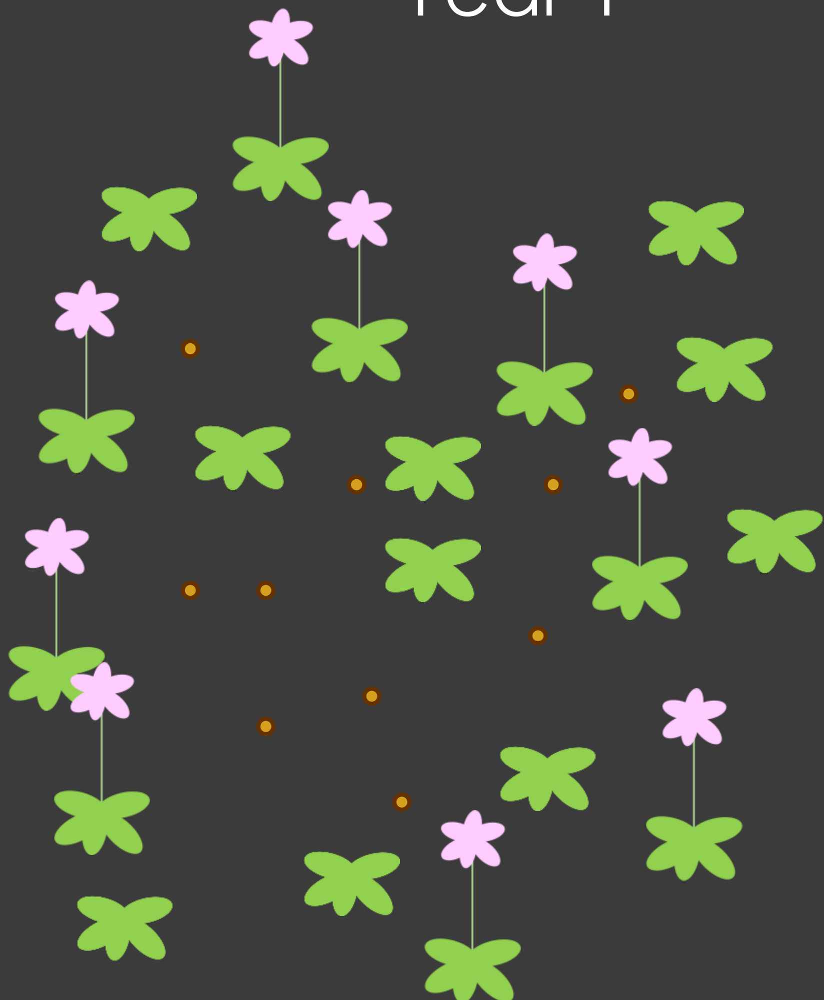
$N_t = 10$

$N_{t+1} = 13$

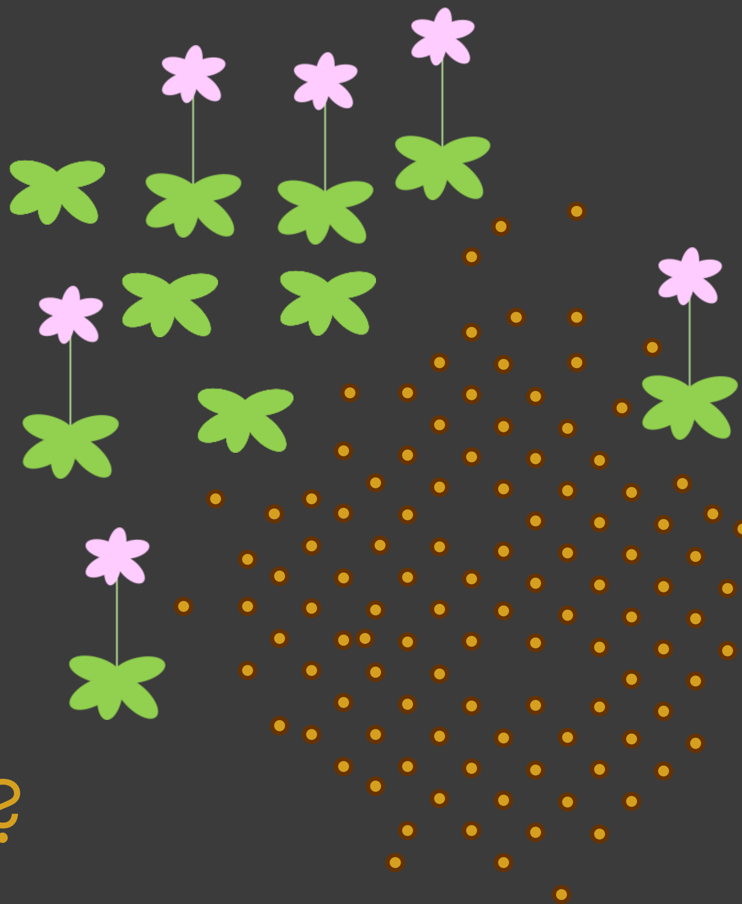
$$\lambda = N_{t+1}/N_t = 13/10 = 1.3$$

STRUCTURED POPULATIONS

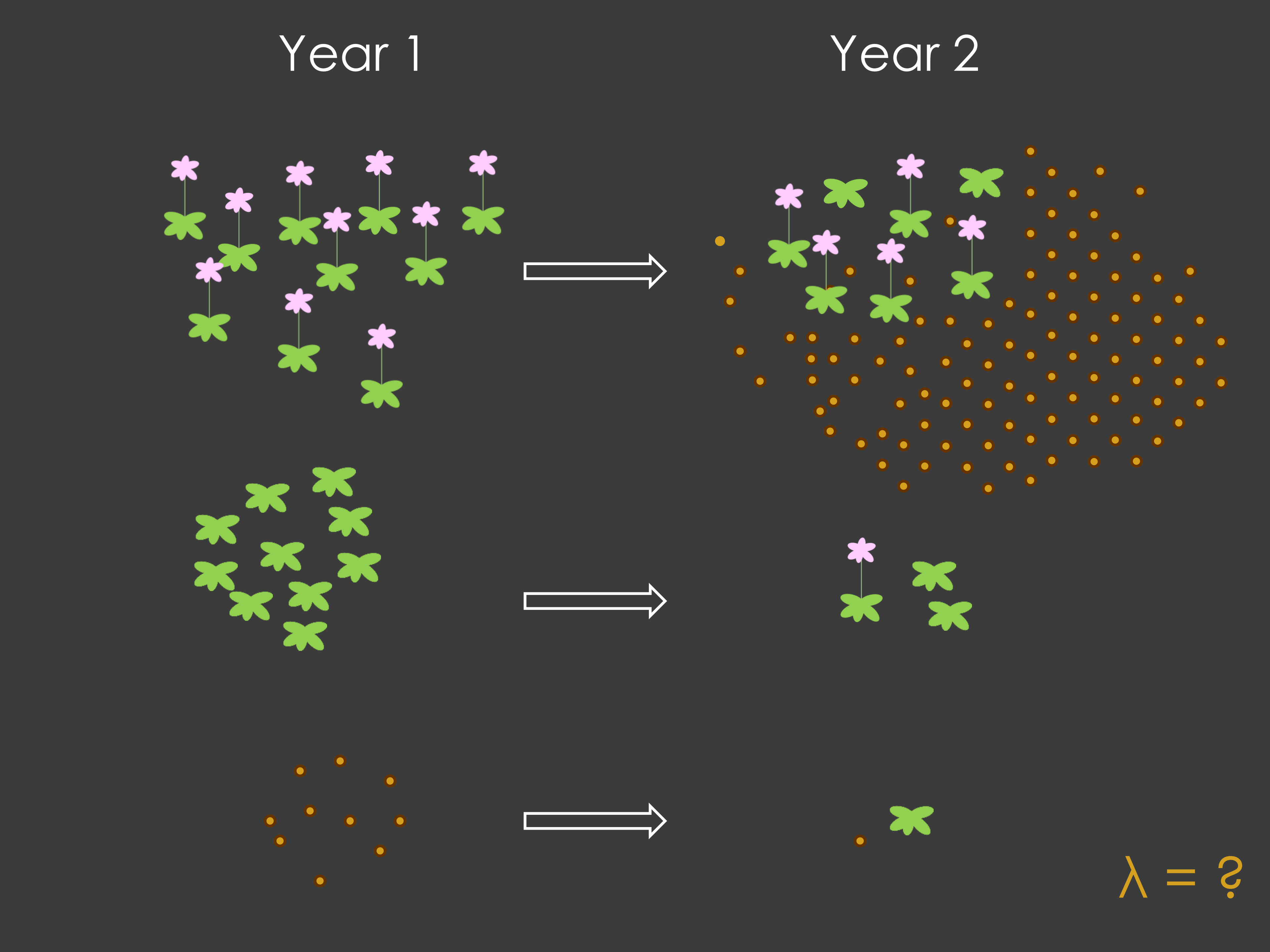
Year 1



Year 2



λ = ?


Year 1
Year 2
λ = ?

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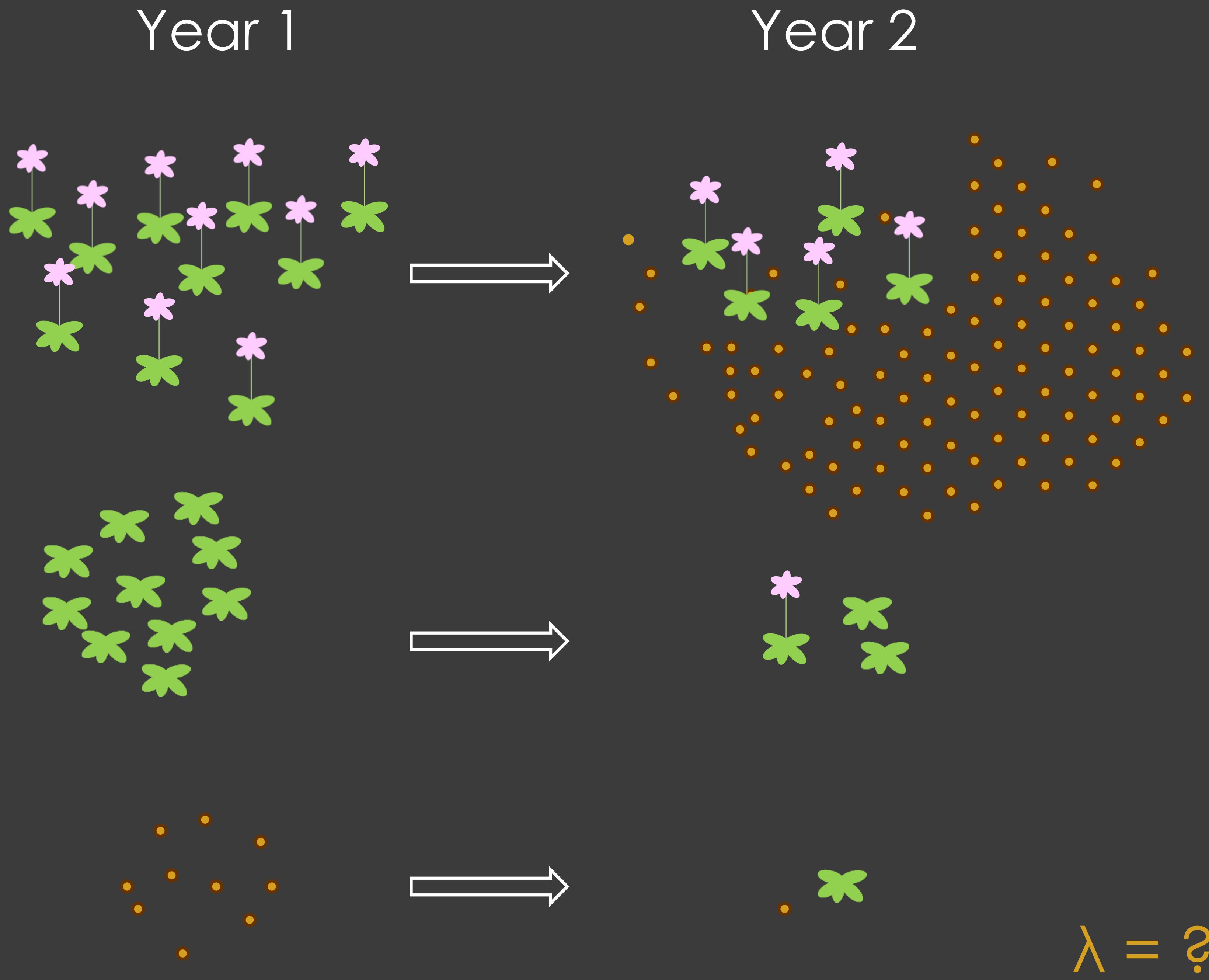
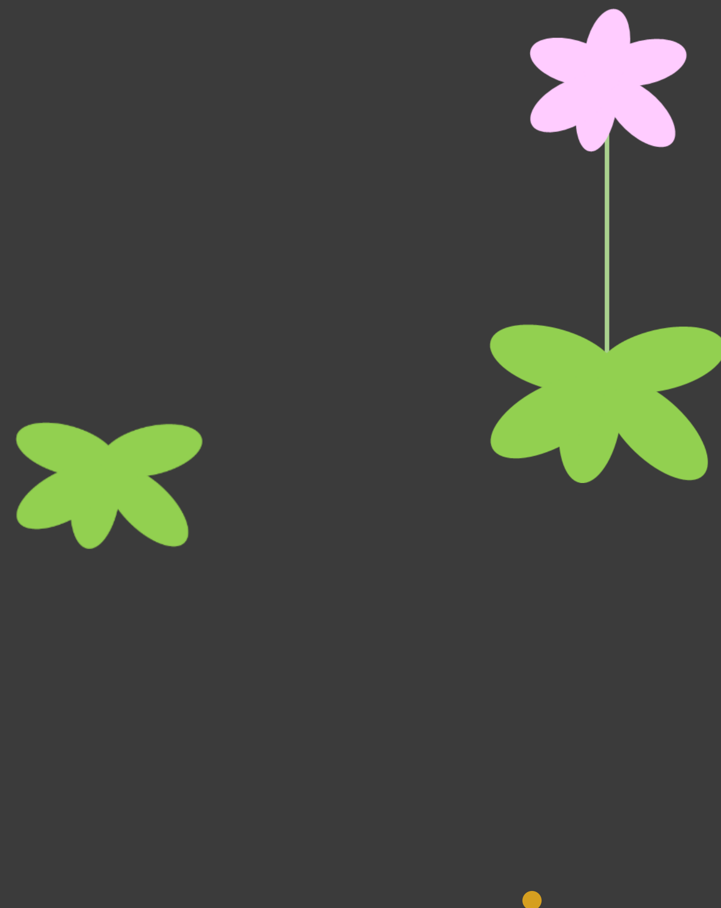
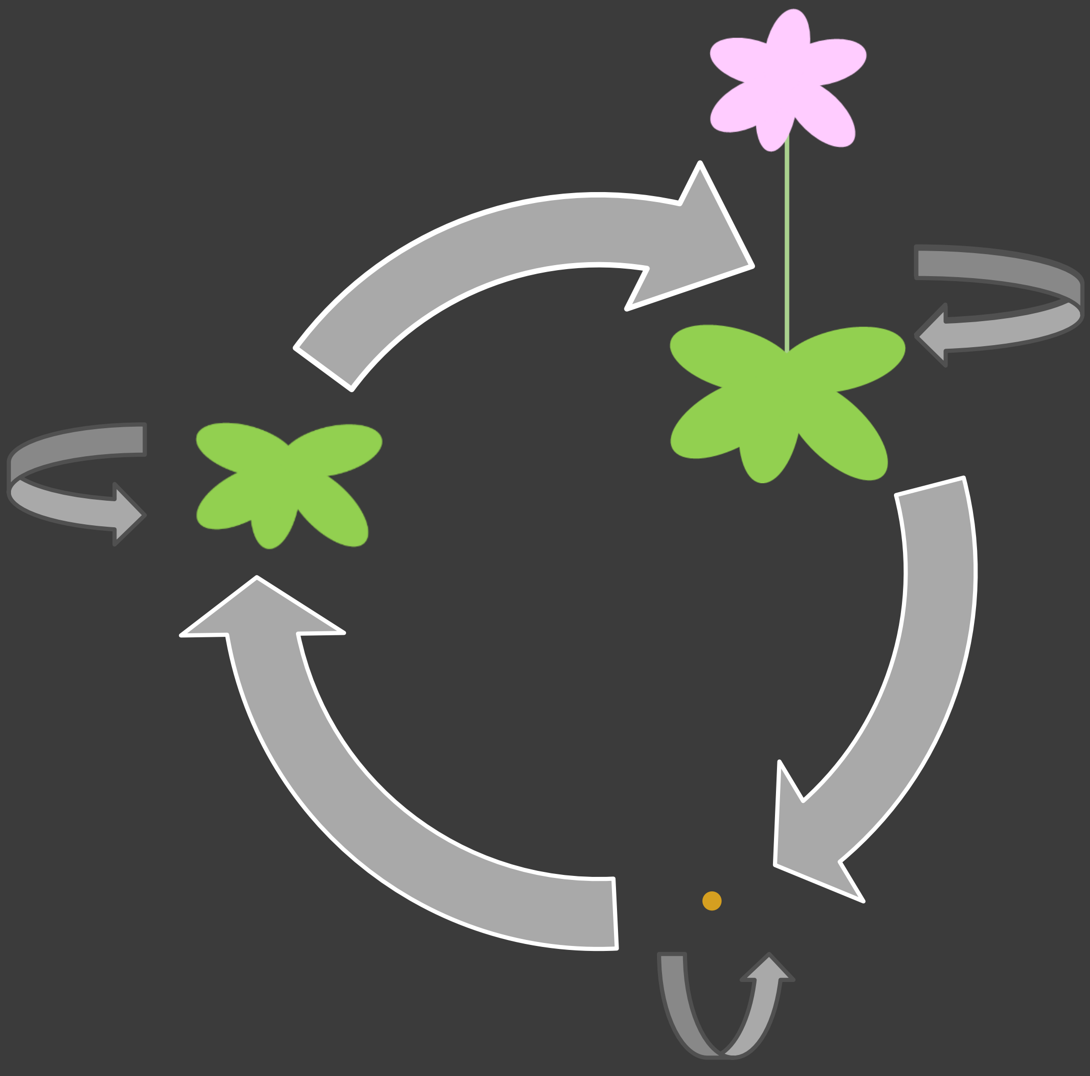
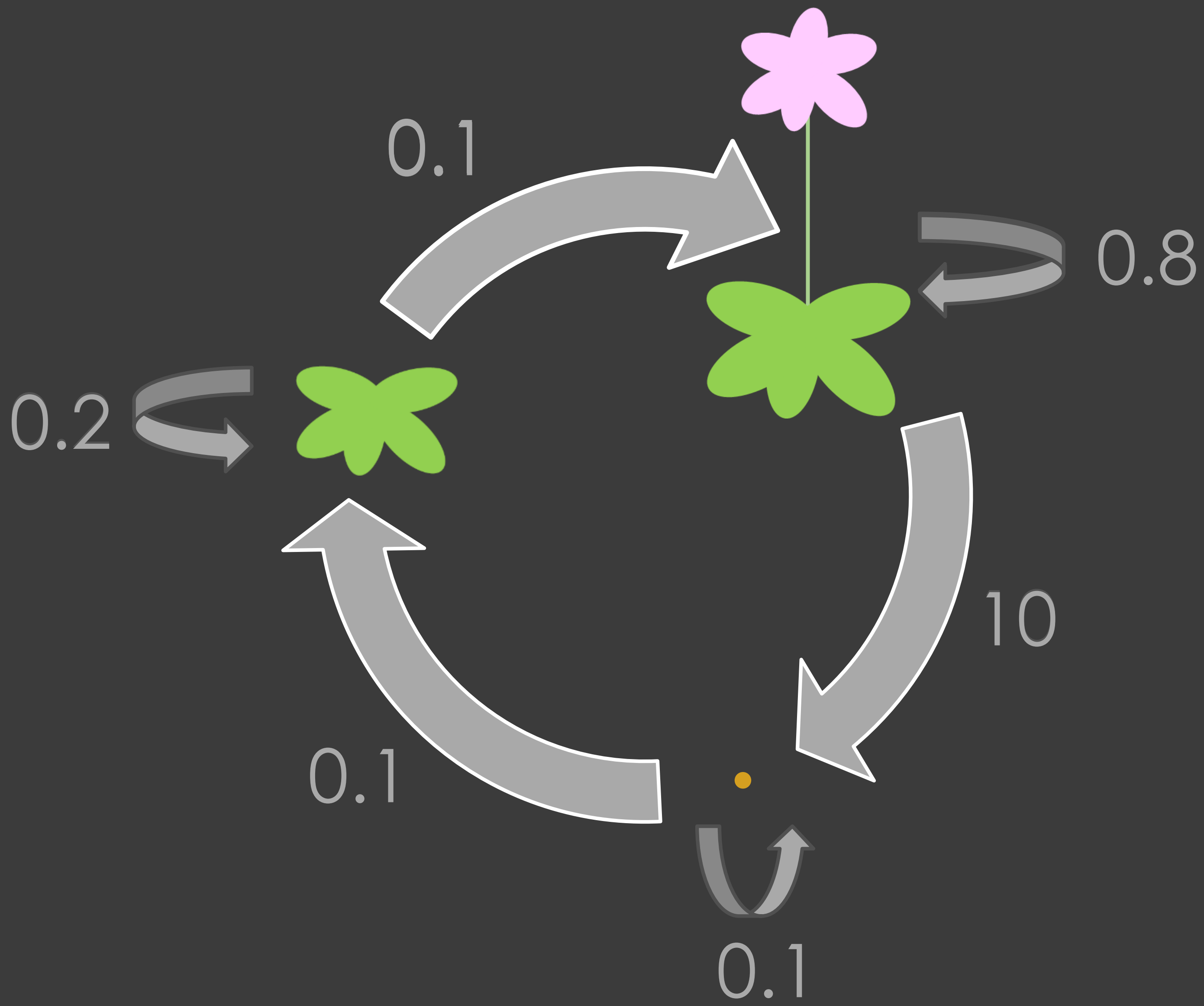
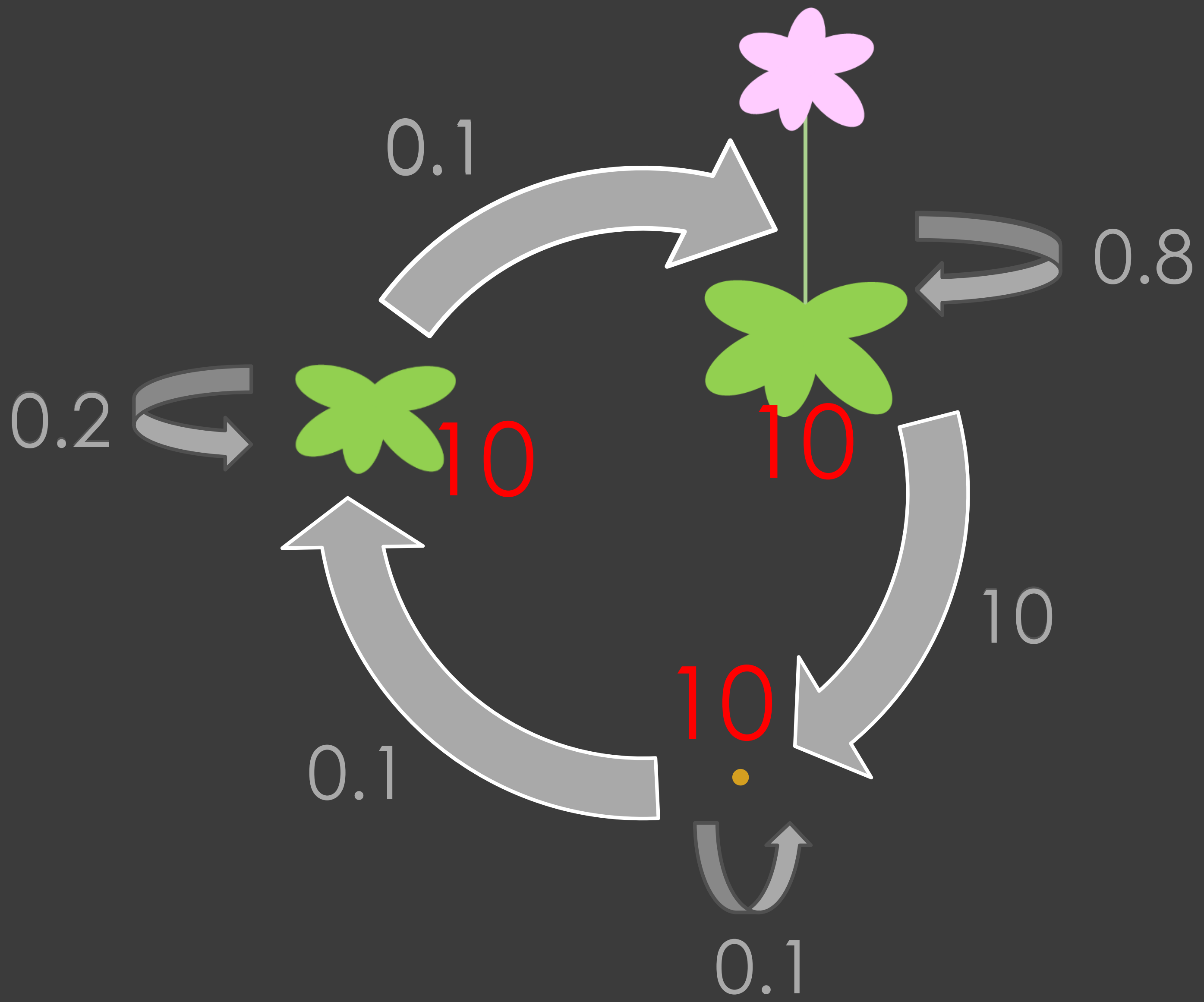
ORGANISMS ARE THEIR LIFE-CYCLES


Year 1
Year 2
λ = ?

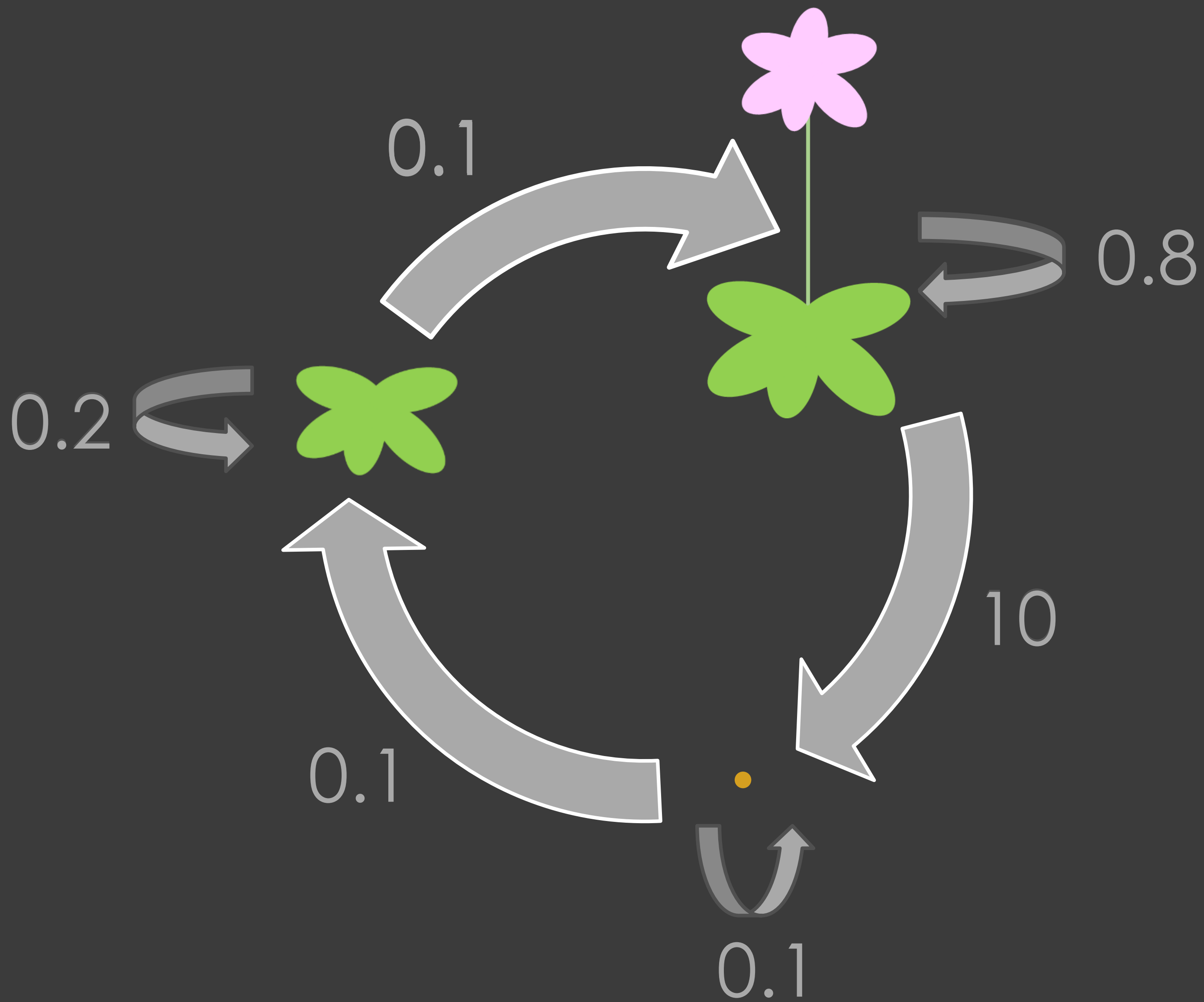





0.1
0.8
0.2
10
0.1
0.1


0.1
0.8
0.2
10
10
10
10
0.1
0.1

$$N = \begin{bmatrix} 10 \\ 10 \\ 10 \end{bmatrix} \times$$



POPULATION SIMULATION

Year	1	2	3	4	5	6	7	8	9	10	11	12
Seeds	10.0	101.0	100.1	85.0	79.2	76.6	73.6	70.2	67.0	63.9	61.1	58.3
Vegetative	10.0	3.0	10.7	12.2	10.9	10.1	9.7	9.3	8.9	8.5	8.1	7.7
Flowering	10.0	9.0	7.5	7.1	6.9	6.6	6.3	6.0	5.7	5.5	5.2	5.0
	30.0	113.0	118.3	104.2	97.0	93.3	89.5	85.5	81.6	77.9	74.4	71.0
Lambda		3.767	1.047	0.881	0.931	0.962	0.959	0.955	0.954	0.955	0.955	0.955
Stage distribution	0.33	0.89	0.85	0.82	0.82	0.82	0.82	0.82	0.82	0.82	0.82	0.82
	0.33	0.03	0.09	0.12	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.11
	0.33	0.08	0.06	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.07

Stable stage distribution

STABLE STAGE DISTRIBUTION

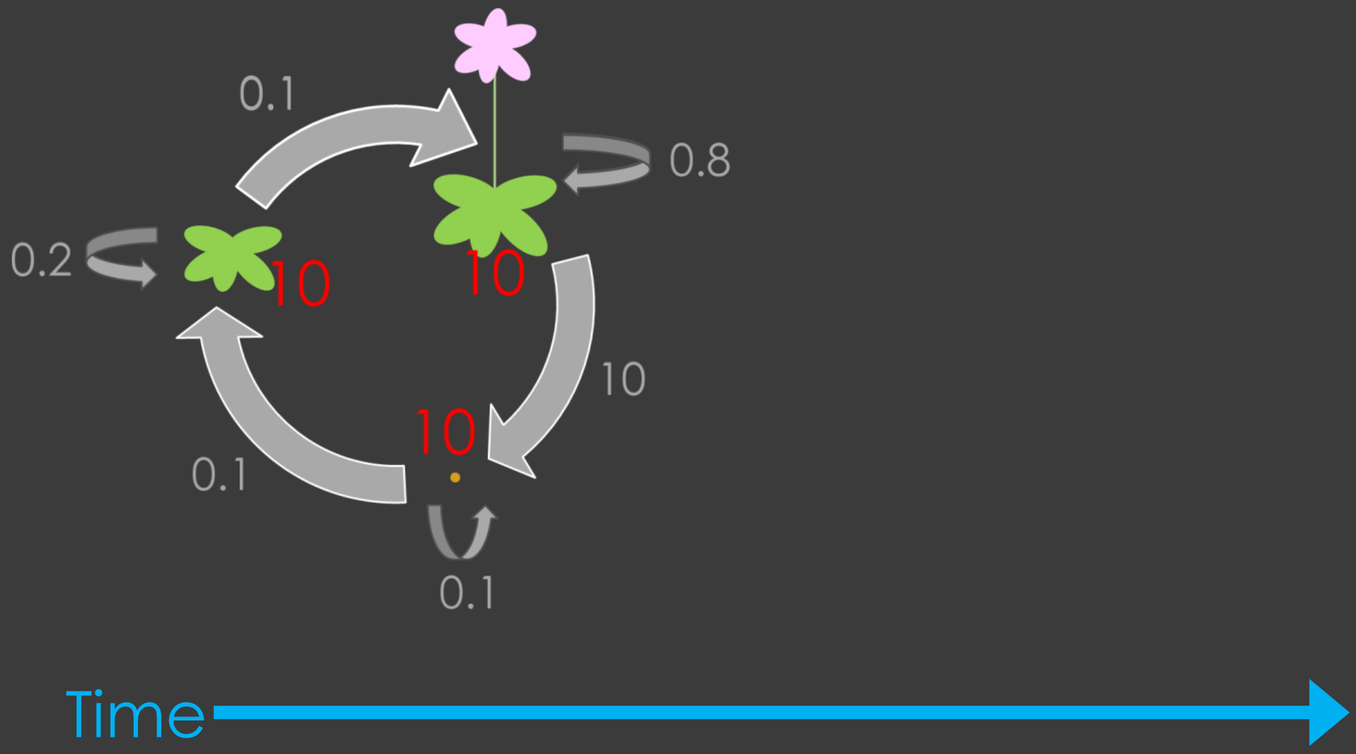
Constant proportion of individuals in each stage. Lambda is stable

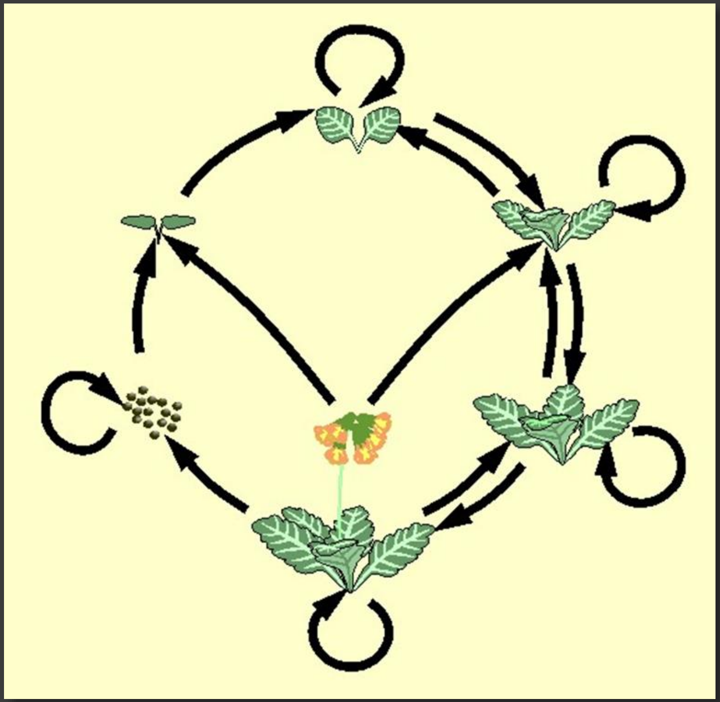
Useful for comparison among populations: individuals from different classes do not contribute equally to population growth rate.

REPRODUCTIVE VALUE

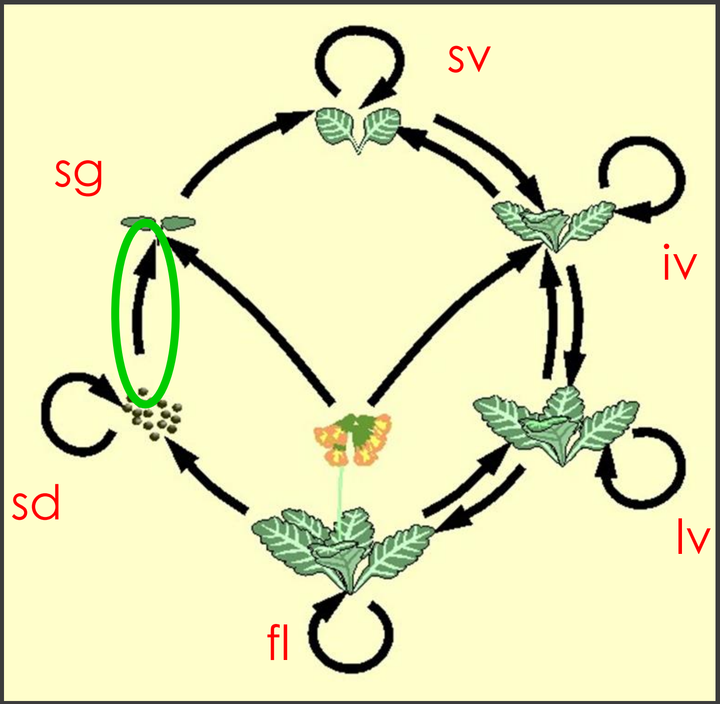
The contribution of individuals from each stage to future population sizes

POPULATION MODELS ARE PROJECTIONS



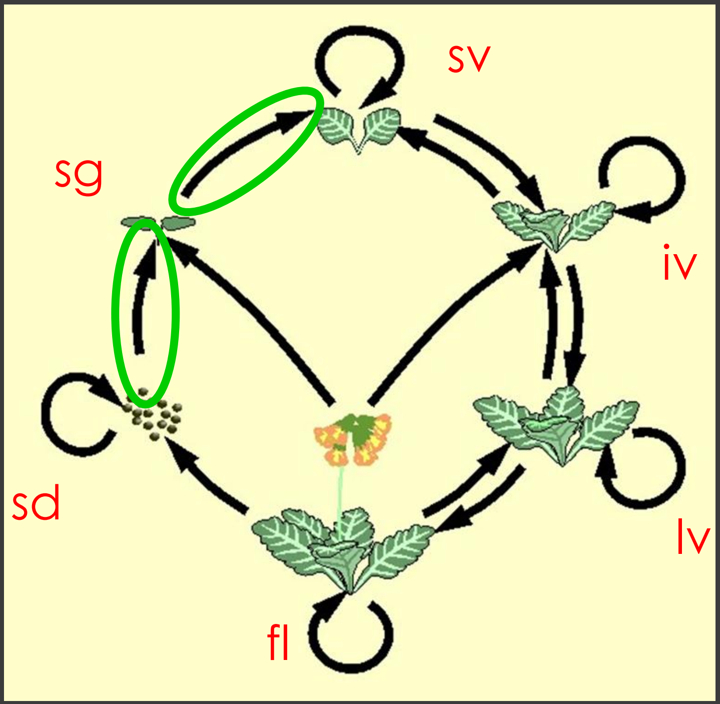


THE LIFE-CYCLE OF *PRIMULA VERIS*



THE LIFE CYCLE IS ISOMORPHIC TO A TRANSITION MATRIX

	Seed	Seedling	Small veg	Interm veg	Large veg	Flowering
Seed	a_{sdsd}					a_{sdfl}
Seedling	a_{sgsd}					a_{sgfl}
Small veg		a_{svsg}	a_{svsv}	a_{sviv}		
Interm veg			a_{ivsv}	a_{iviv}	a_{ivlv}	a_{ivfl}
Large veg				a_{lviv}	a_{lvlv}	a_{lvfl}
Flowering					a_{fllv}	a_{flfl}



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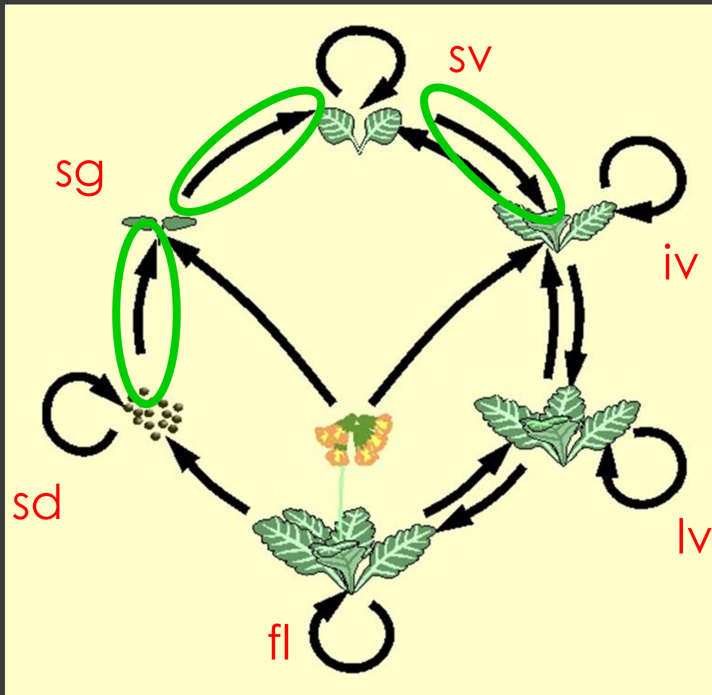

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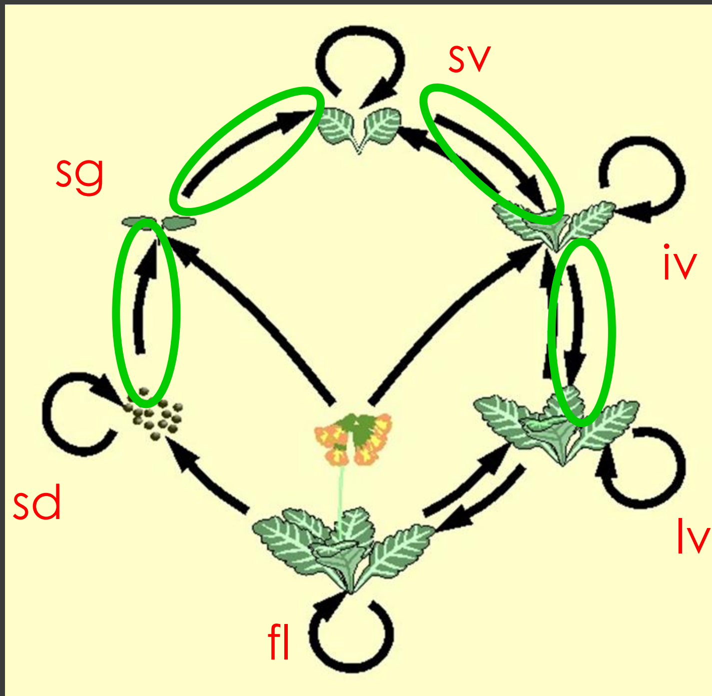

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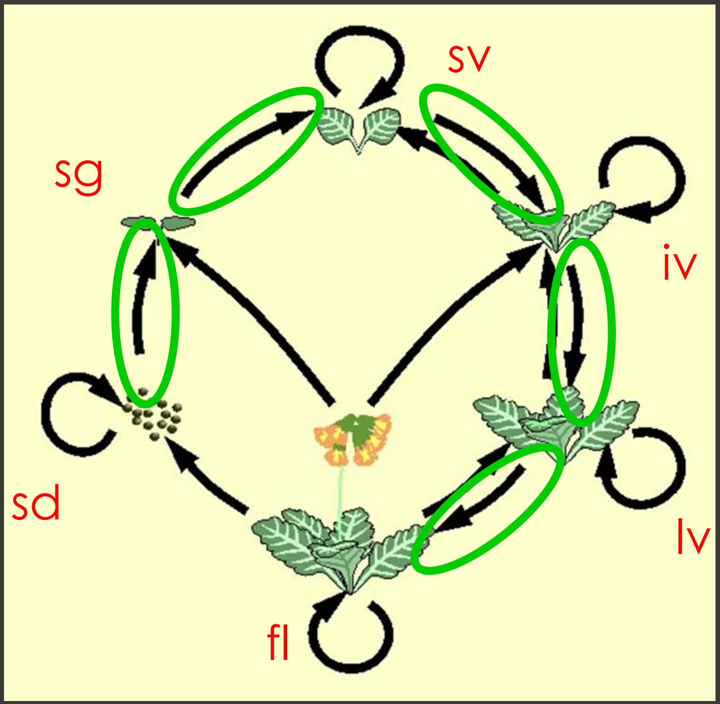

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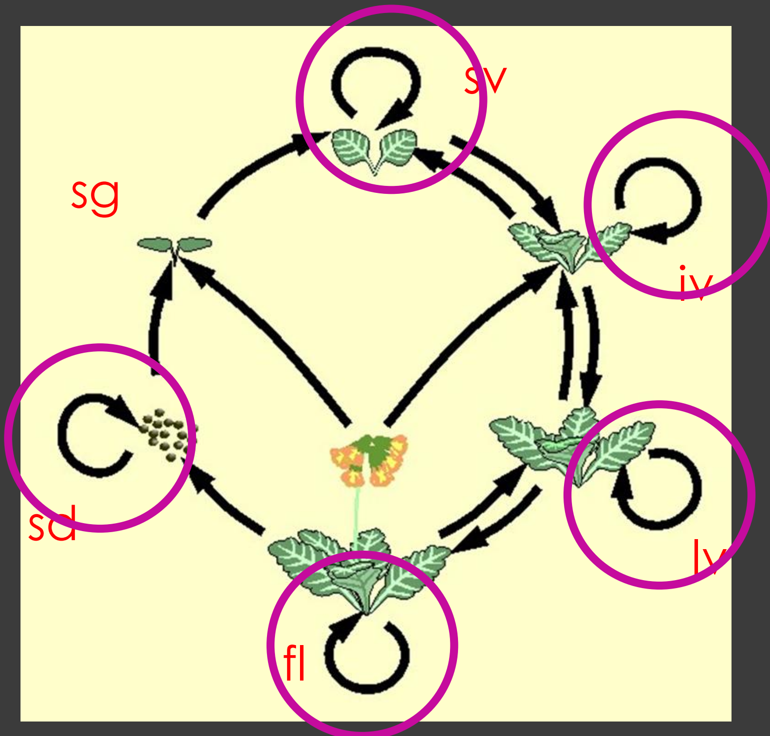

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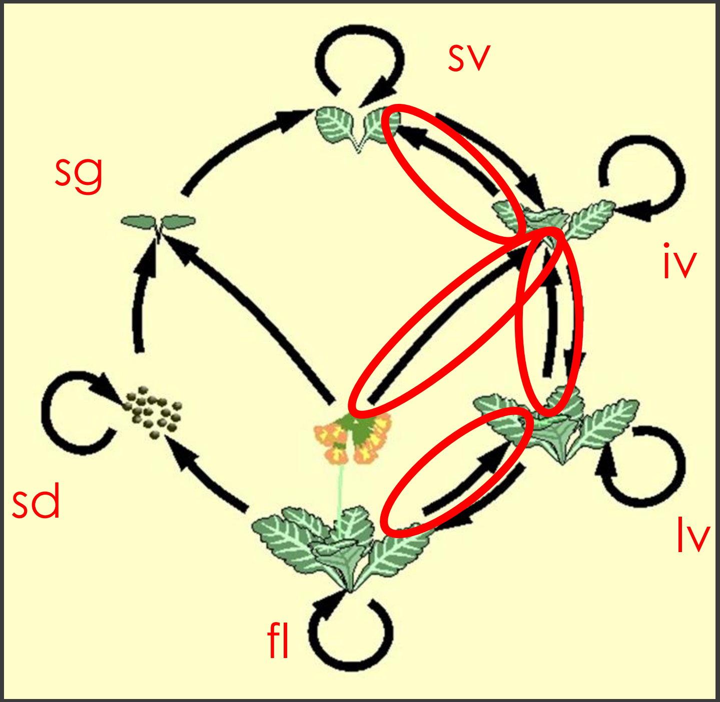

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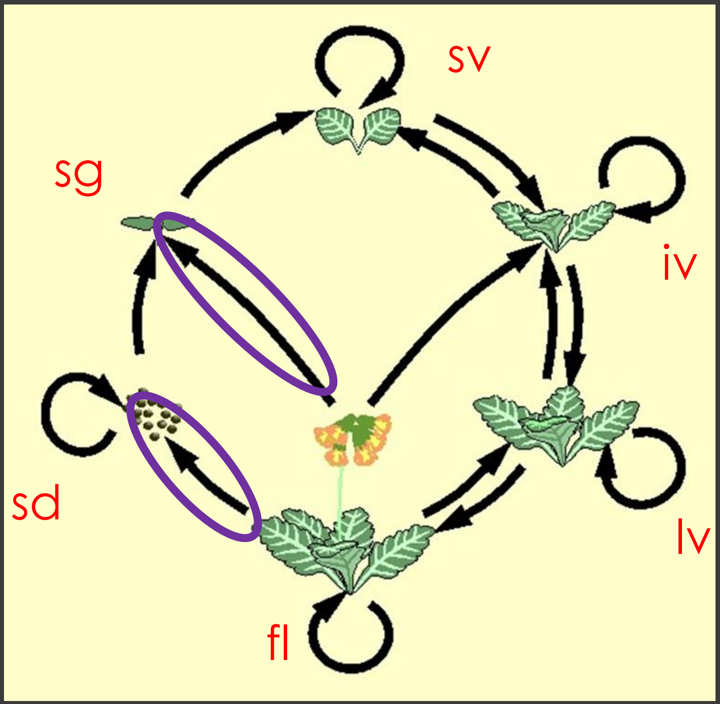

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MATRIX ALGEBRA

- Right multiplying a vector with a matrix

$$\mathbf{n}_{(t+1)} = \mathbf{A}\mathbf{n}_{(t)}$$

MATRIX ALGEBRA
- Right multiplying a vector with a matrix

$$\begin{pmatrix} n_{(t+1)}1 \\ n_{(t+1)}2 \\ n_{(t+1)}3 \\ n_{(t+1)}4 \\ n_{(t+1)}5 \\ n_{(t+1)}6 \end{pmatrix} = \begin{pmatrix} a_{11} & a_{12} & a_{13} & a_{14} & a_{15} & a_{16} \\ \dots & \dots & \dots & \dots & \dots & \dots \\ \dots & \dots & \dots & \dots & \dots & \dots \\ a_{41} & a_{42} & a_{43} & a_{44} & a_{45} & a_{46} \\ \dots & \dots & \dots & \dots & \dots & \dots \\ \dots & \dots & \dots & \dots & \dots & \dots \end{pmatrix} \times \begin{pmatrix} n_{(t)}1 \\ n_{(t)}2 \\ n_{(t)}3 \\ n_{(t)}4 \\ n_{(t)}5 \\ n_{(t)}6 \end{pmatrix}$$

$$\mathbf{n}_{(t+1)} \qquad \mathbf{A} \qquad \mathbf{n}_{(t)}$$

MATRIX ALGEBRA
- Right multiplying a vector with a matrix

Entries referred to as matrix elements (a) with subscripted numbers for the row and column.
a_{41} is the matrix element on row 4, column 1

$$\begin{bmatrix} n_{(t+1)}1 \\ n_{(t+1)}2 \\ n_{(t+1)}3 \\ n_{(t+1)}4 \\ n_{(t+1)}5 \\ n_{(t+1)}6 \end{bmatrix} = \begin{pmatrix} a_{11} & a_{12} & a_{13} & a_{14} & a_{15} & a_{16} \\ \dots & \dots & \dots & \dots & \dots & \dots \\ \dots & \dots & \dots & \dots & \dots & \dots \\ a_{41} & a_{42} & a_{43} & a_{44} & a_{45} & a_{46} \\ \dots & \dots & \dots & \dots & \dots & \dots \\ \dots & \dots & \dots & \dots & \dots & \dots \end{pmatrix} \times \begin{bmatrix} n_{(t)}1 \\ n_{(t)}2 \\ n_{(t)}3 \\ n_{(t)}4 \\ n_{(t)}5 \\ n_{(t)}6 \end{bmatrix}$$

$$\mathbf{n}_{(t+1)} \qquad \mathbf{A} \qquad \mathbf{n}_{(t)}$$

MATRIX ALGEBRA

- Right multiplying a vector with a matrix

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$$\times$$

$$\begin{pmatrix} n_{(t+1)}1 \\ n_{(t+1)}2 \\ n_{(t+1)}3 \\ n_{(t+1)}4 \\ n_{(t+1)}5 \\ n_{(t+1)}6 \end{pmatrix} = \begin{pmatrix} a_{11} & a_{12} & a_{13} & a_{14} & a_{15} & a_{16} \\ \dots & \dots & \dots & \dots & \dots & \dots \\ \dots & \dots & \dots & \dots & \dots & \dots \\ a_{41} & a_{42} & a_{43} & a_{44} & a_{45} & a_{46} \\ \dots & \dots & \dots & \dots & \dots & \dots \\ \dots & \dots & \dots & \dots & \dots & \dots \end{pmatrix} \times \begin{pmatrix} n_{(t)}1 \\ n_{(t)}2 \\ n_{(t)}3 \\ n_{(t)}4 \\ n_{(t)}5 \\ n_{(t)}6 \end{pmatrix}$$

$$\mathbf{n}_{(t+1)} \qquad \mathbf{A} \qquad \mathbf{n}_{(t)}$$

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- Right multiplying a vector with a matrix

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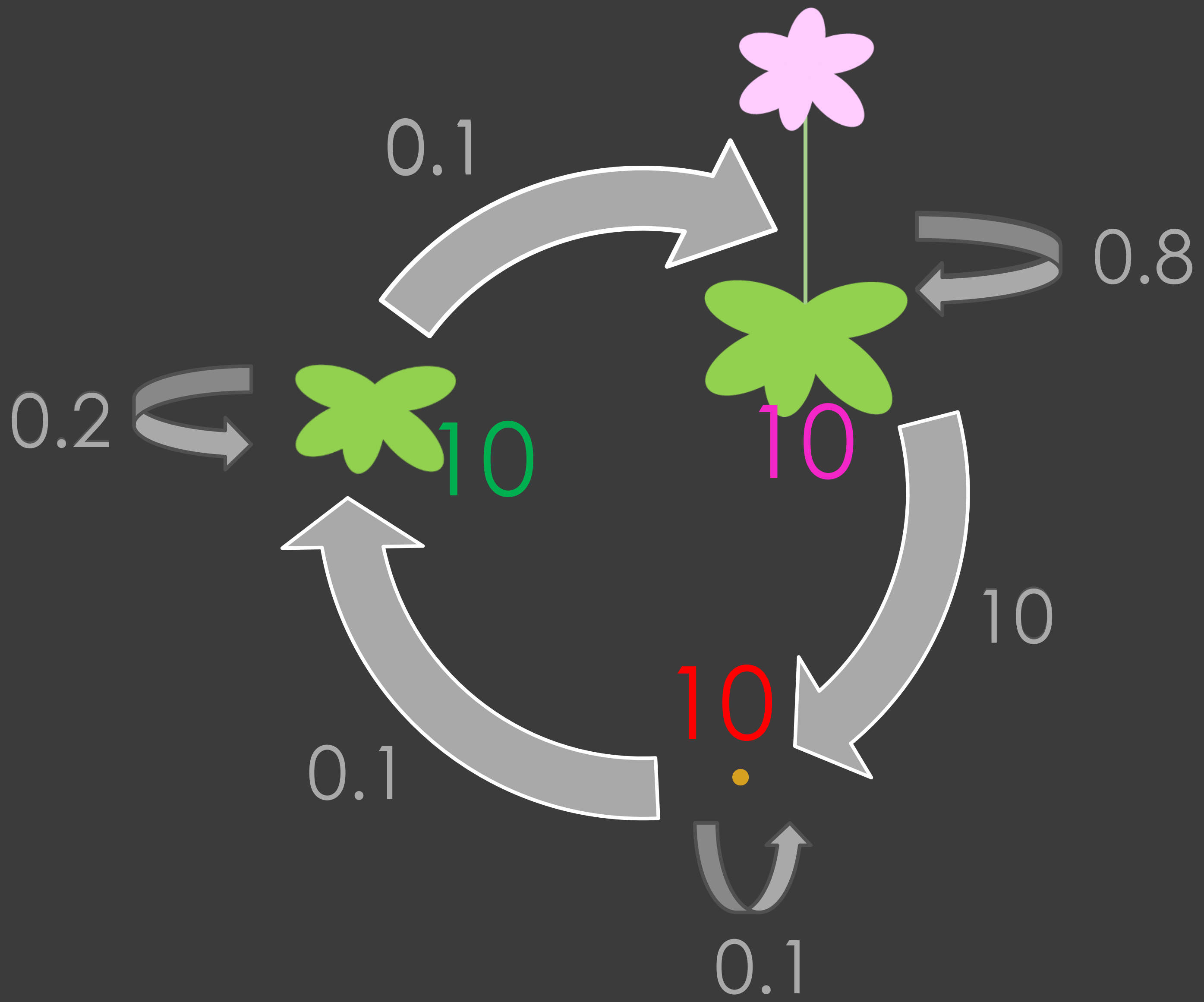
PROJECT THE POPULATION TO THE NEXT TIMESTEP



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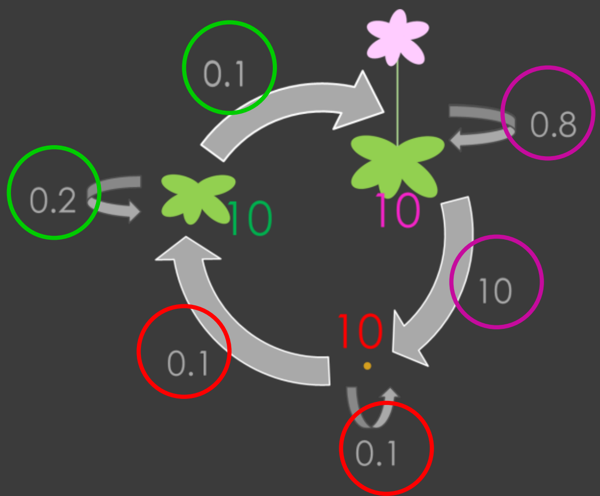


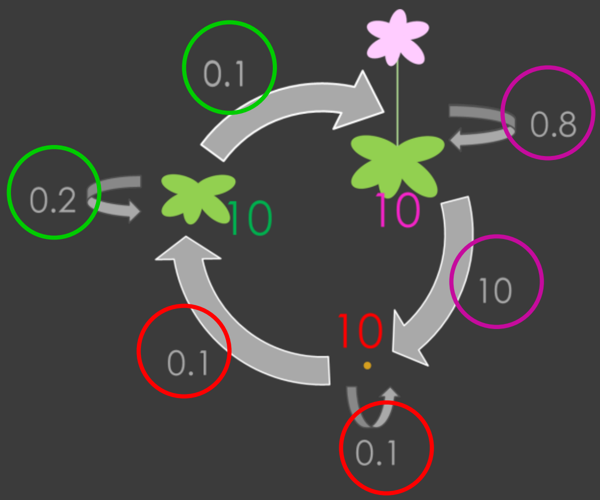
How many individuals will be in each size class in the next timestep?

n_{t+1}			Seeds	Vegetative	Flowering		n_t
101.0	=	Seeds	(10×0.1)	$+ 0$	$+ (10 \times 10)$	×	10
3.0		Vegetative	(10×0.1)	$+ (10 \times 0.2)$	$+ 0$		10
9.0		Flowering	0	$+ (10 \times 0.1)$	$+ (10 \times 0.8)$		10

Transition matrix with vital rates

Population vector

PROJECT THE POPULATION TO THE NEXT TIMESTEP



What is the population growth rate (λ)?

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

n_{t+1}			Seeds	Vegetative	Flowering		n_t
101.0	=	Seeds	(10×0.1)	$+ 0$	$+ (10 \times 10)$	×	10
3.0		Vegetative	(10×0.1)	$+ (10 \times 0.2)$	$+ 0$		10
9.0		Flowering	0	$+ (10 \times 0.1)$	$+ (10 \times 0.8)$		10

Transition matrix with vital rates

Population vector

MATRIX PROPERTIES

- The dominant right eigenvalue of the matrix, λ_1, corresponds to the deterministic population growth rate
- The right eigenvector corresponds to the stable-stage distribution
- The left eigenvector corresponds to the reproductive values

Population projection

Rana temporaria, the common frog

Conservation status: Least concern

Main threat: Habitat loss (wetlands)

IUCN Redlist (www-iucnredlist.org/species/58734/86470817)

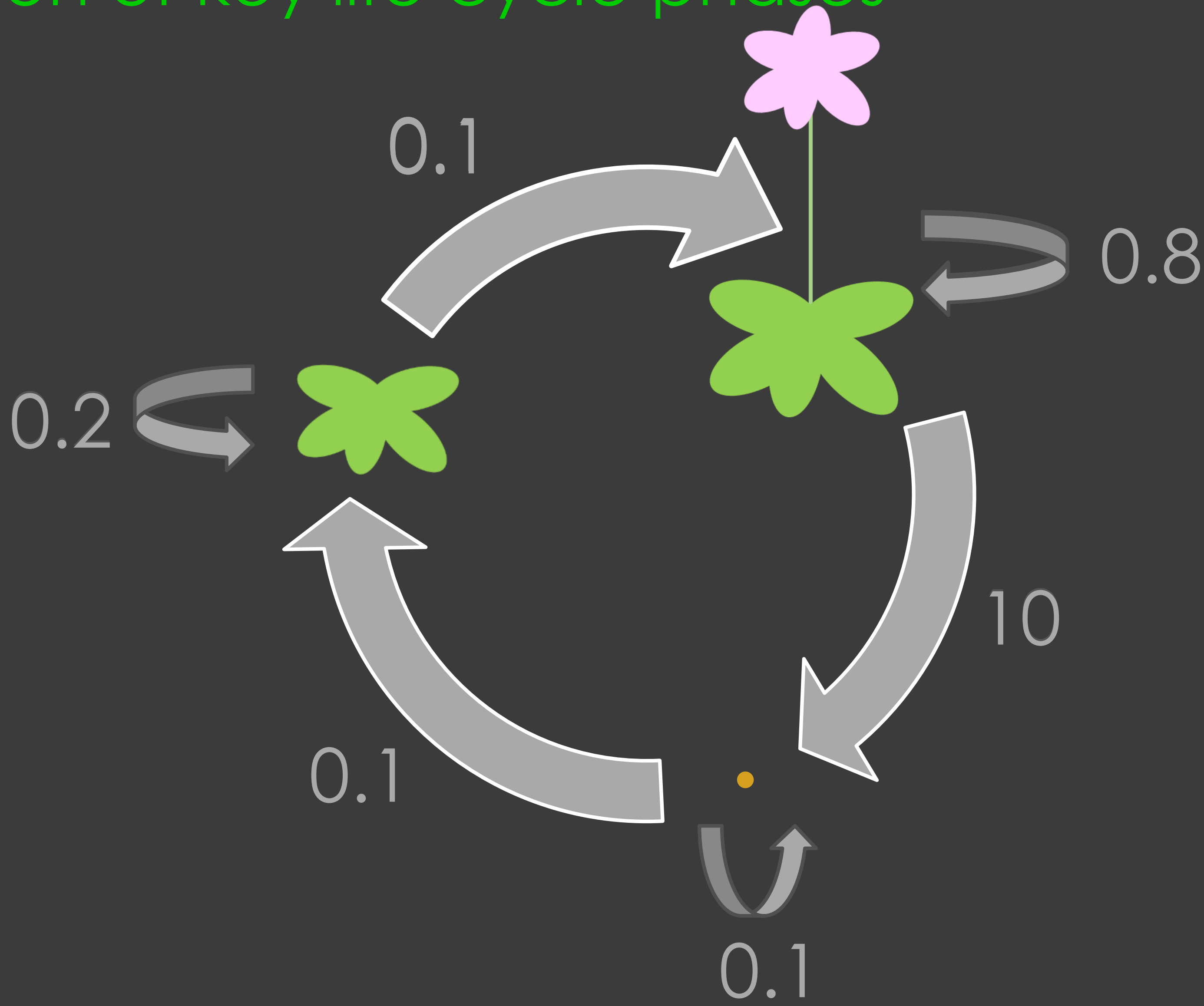
Population projection

Your task: Predict future population sizes and the (long term) growth rate (λ) for a population of the common frog.

Methods: Matrix multiplication (manual perturbations) & analytical methods (eigen-analysis)

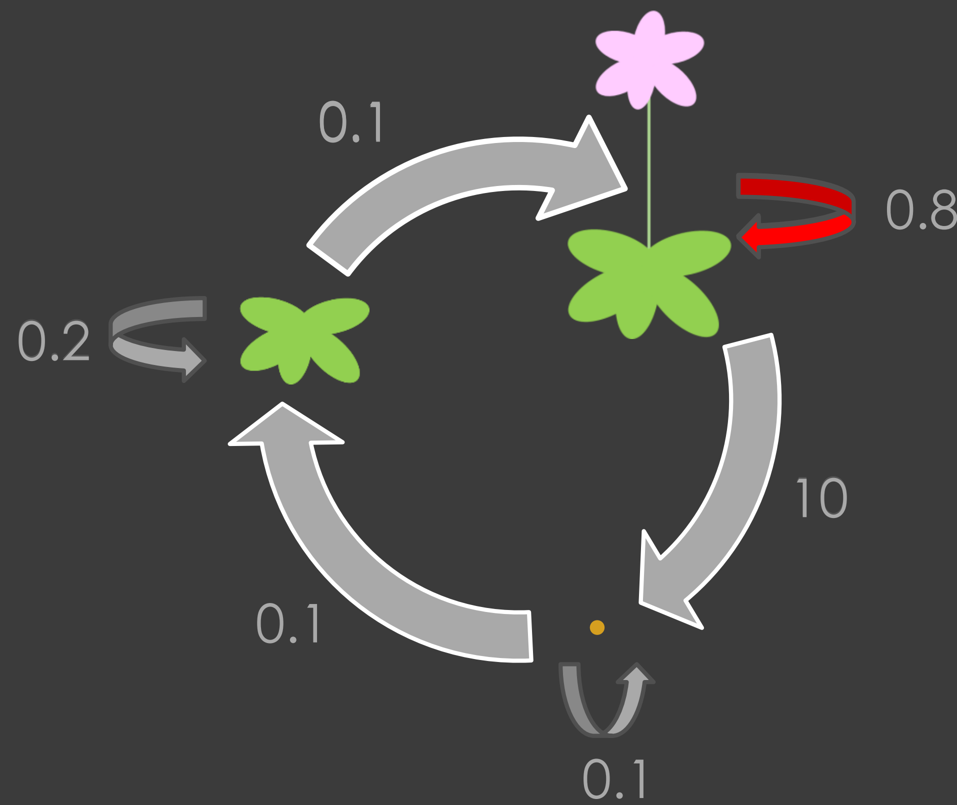
Questions for assignment
(Temporary) link:
https://fogelstrom.github.io/popDynamicsEERCV/

THE IMPORTANCE OF THE PARTS TO THE WHOLE
- Identification of key life cycle phases



THE IMPORTANCE OF THE PARTS TO THE WHOLE
- Identification of key life cycle phases

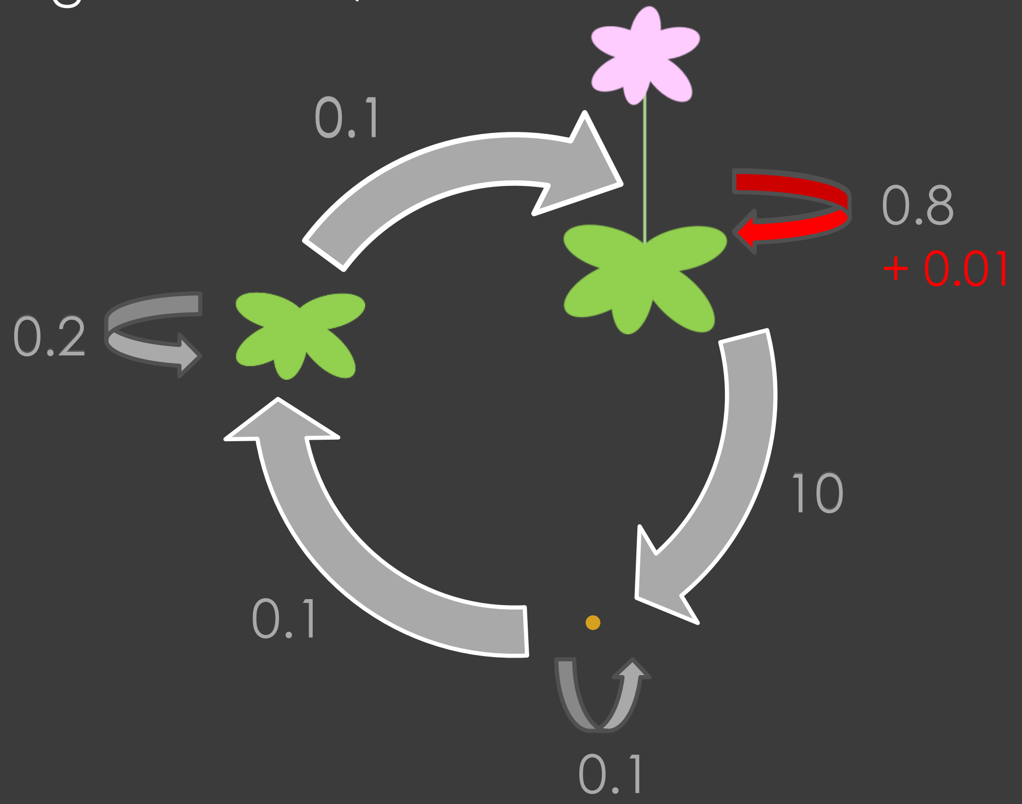
Sensitivity and Elasticity estimate how "important" a particular transition is to population growth by examining the effects of small changes in different parts of the life cycle



SENSITIVITY, s_{ij}

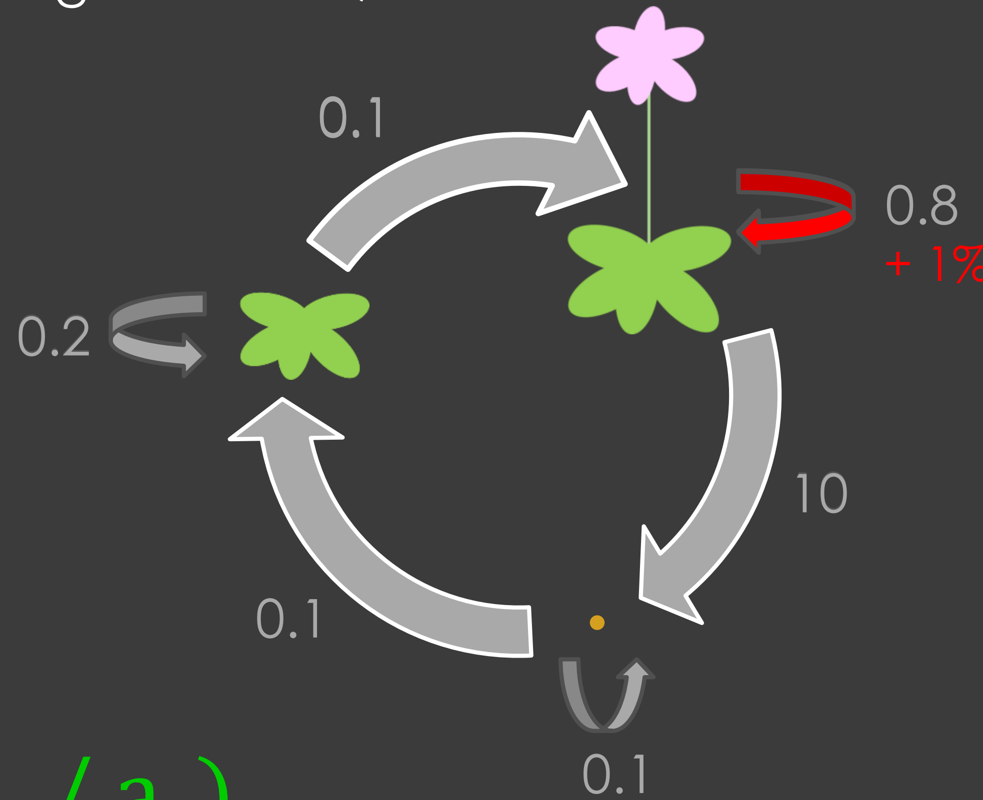
estimates the effects of small absolute changes in a matrix element, a_{ij}, on population growth rate, λ

$$s_{ij} = d\lambda \,/\, da_{ij}$$



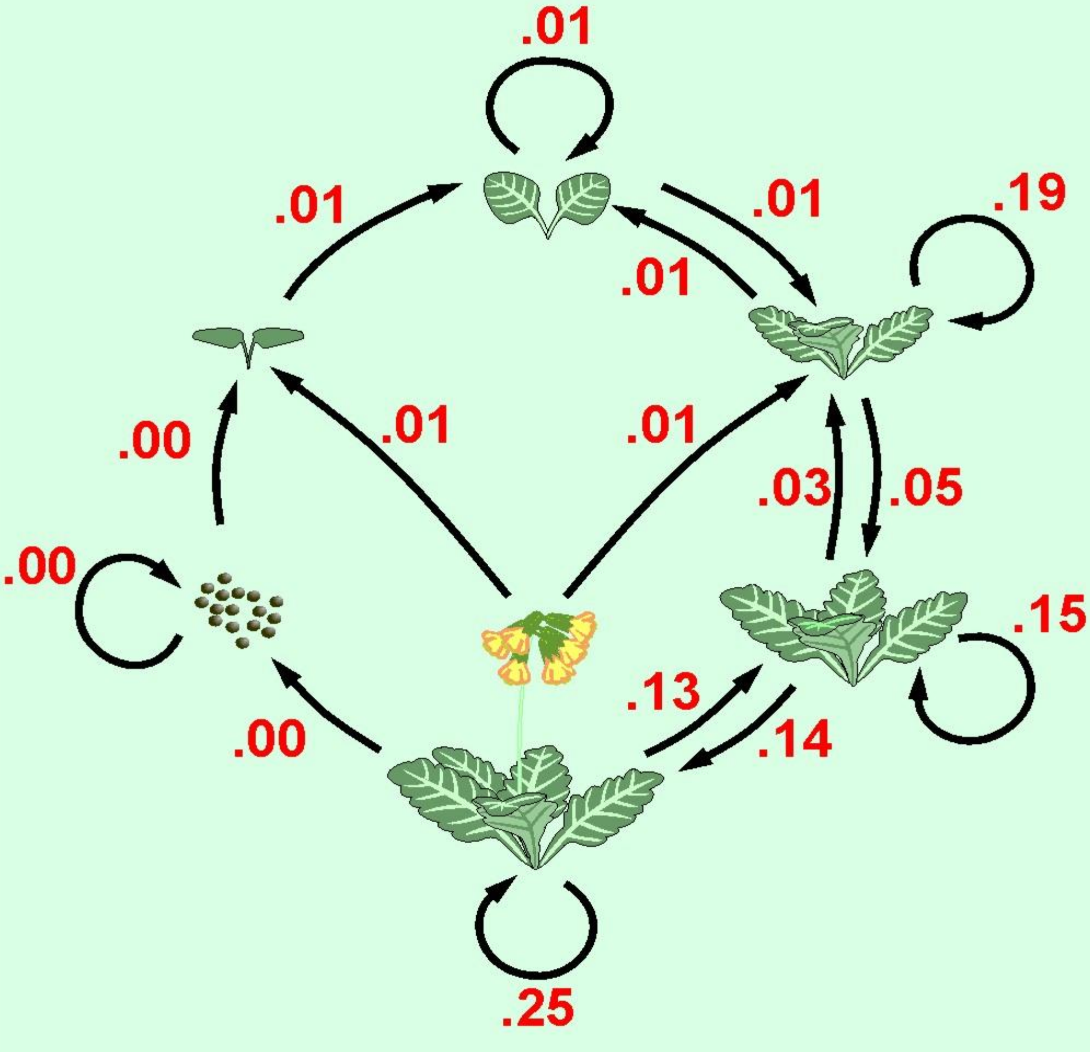
ELASTICITY, e_{ij}

estimates the effects of small relative changes in a matrix element, a_{ij}, on population growth rate, λ



$$e_{ij} = (d\lambda / \lambda) / (da_{ij} / a_{ij})$$

Primula veris – elasticites



Estimate sensitivities and elasticities

Hudsonia montana The mountain golden heather
endemic to North Carolina, USA
fragmented populations on mountain slopes.
only seven populations are known

Conservation status: threatened

Main threats:
disturbance from hikers and mountain climbers.
Altered fire regimes

Estimate sensitivities and elasticities

Your task: find out which vital rates have the strongest influence on population growth rate.

Use your results to choose a management regime that
1) increases seed survival in the seed bank, or
2) increases seed production in the smallest size class (tiny)

Methods: Sensitivity and elasticity analysis (manual and analytical)

Questions for assignment

(Temporary) link:
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STOCHASTICITY

Environmental: Random climate fluctuations

Demographic: Random fluctuations in vital rates, or in population age or size structure

STOCHASTICITY

The stochastic growth rate (λ_S) is the geometric mean of λ

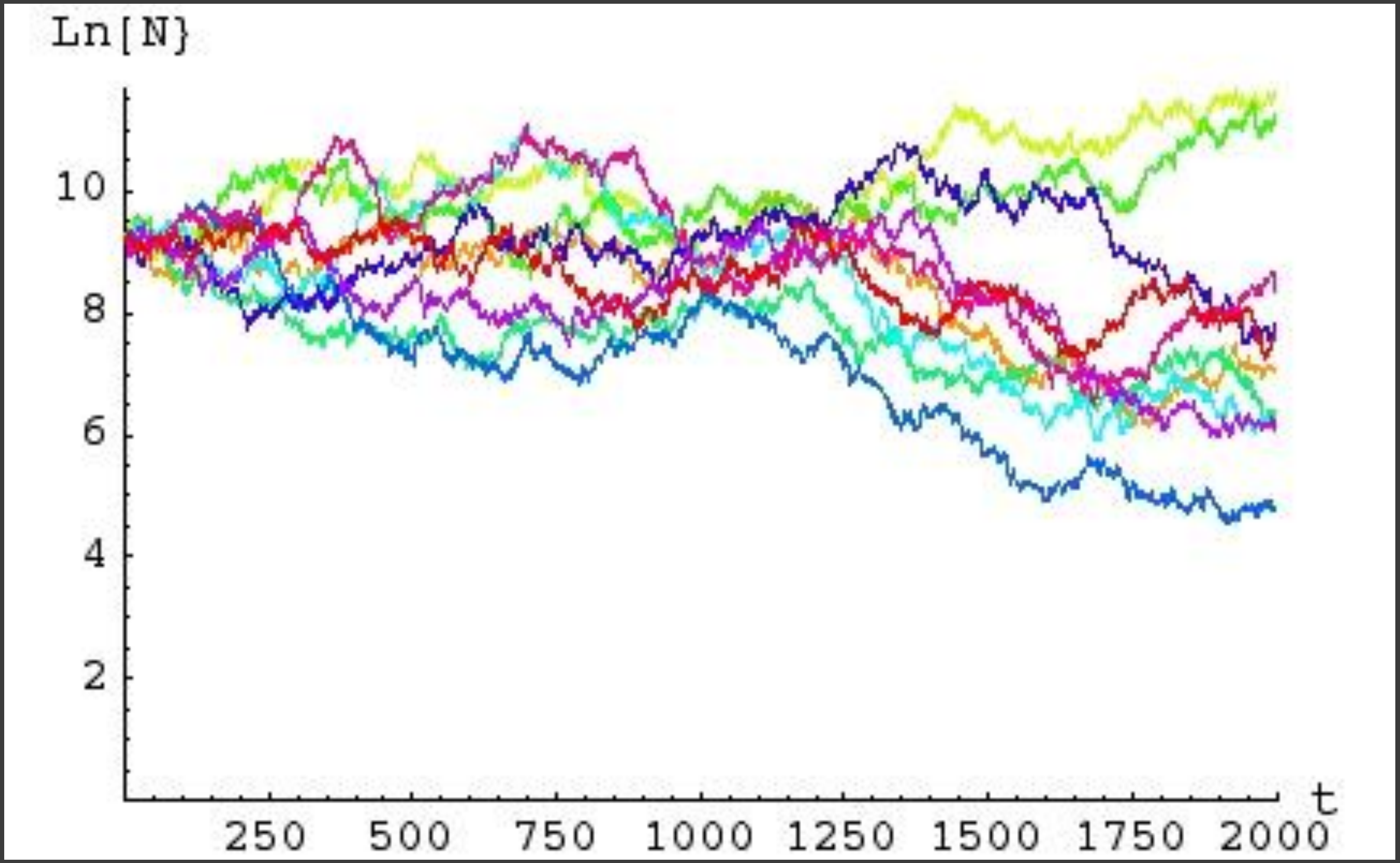
$$\lambda_S = e^{\bar{r}}$$

STOCHASTICITY

Stochasticity can be taken into account by

- Incorporating environmental stochasticity into demographic models: Among-year variation
- Incorporating demographic stochasticity into demogrphic models

STOCHASTIC MATRIX SIMULATIONS



LINKING VARIATION IN POPULATION DYNAMICS TO ENVIRONMENTAL VARIATION

Effects of the environment or climate on individual organisms

- Direct effects – organisms experience changes in vital rates due to changed environmental conditions, e.g. in terms of altered light availability, temperature, humidity etc.

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- Direct effects – organisms experience changes in vital rates due to changed environmental conditions, e.g. in terms of altered light availability, temperature, humidity etc.

- Indirect effects – organisms use the environment as a cue

- Effects mediated by species interactions – changes in the environment affect interactions among species

Responses of vital rates of individuals to the environment translates into effects on:

- Population growth rate and extinction risk
- Abundance
- Distribution

Linking variation in vital rates and population growth rates to environmental variation

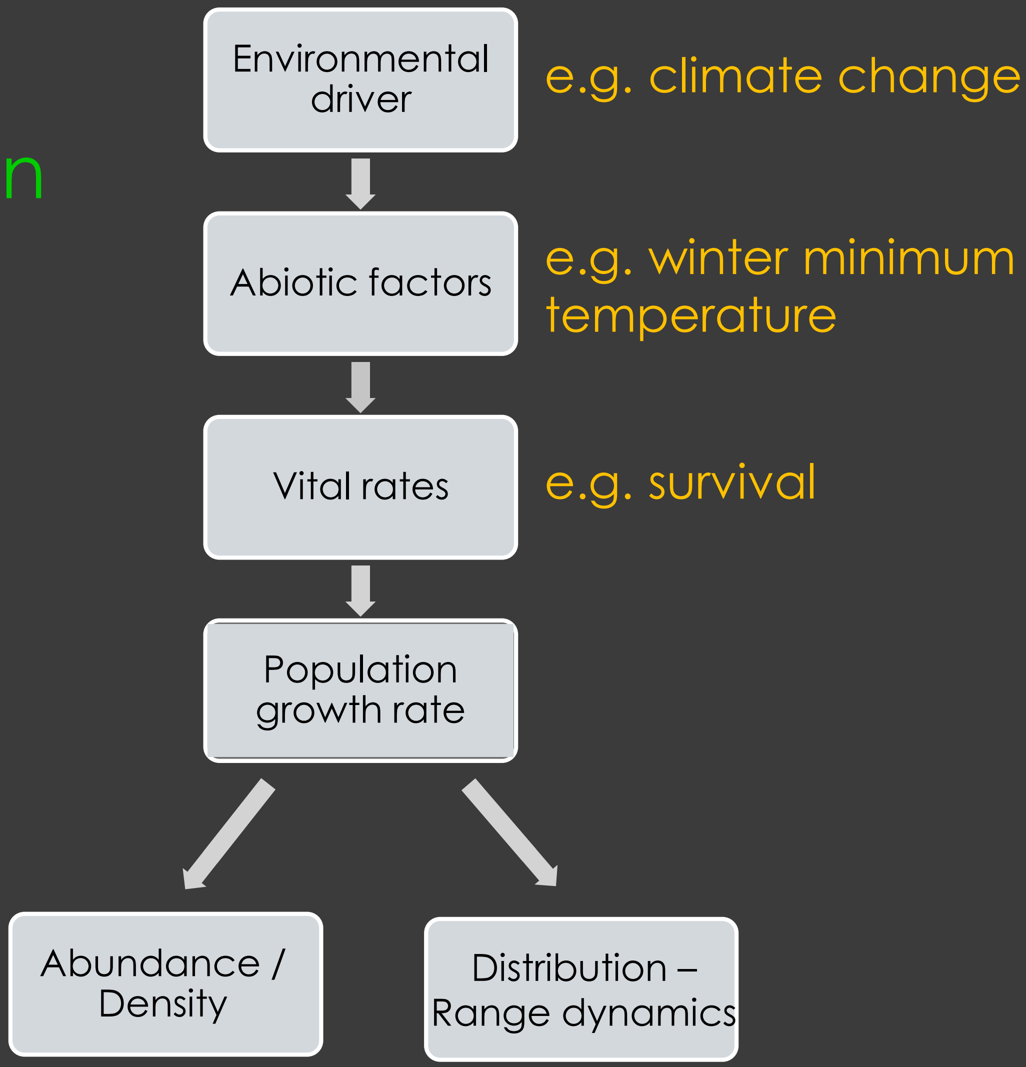
Necessary to …

… Identify the drivers of temporal and spatial variation in population dynamics – to understand the causes of population decline and increase

… Predict population dynamics if the environment changes

… Frame populations dynamics in terms of factors that are manageable, and provide tools for efficient management actions

Linking variation in vital rates and population growth rates to environmental variation



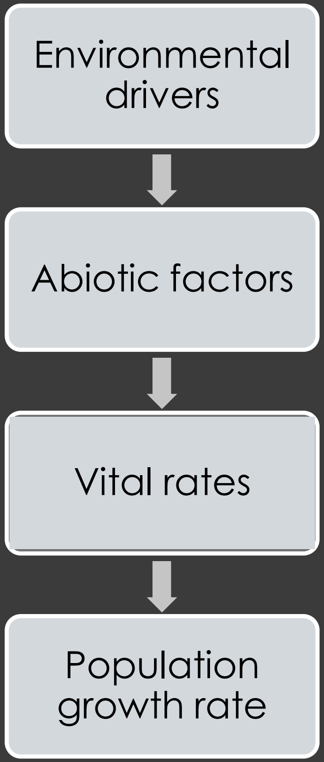
What tools do we need to do to link population dynamics to environmental variation?

Predict future changes in drivers

Link environmental factors to drivers

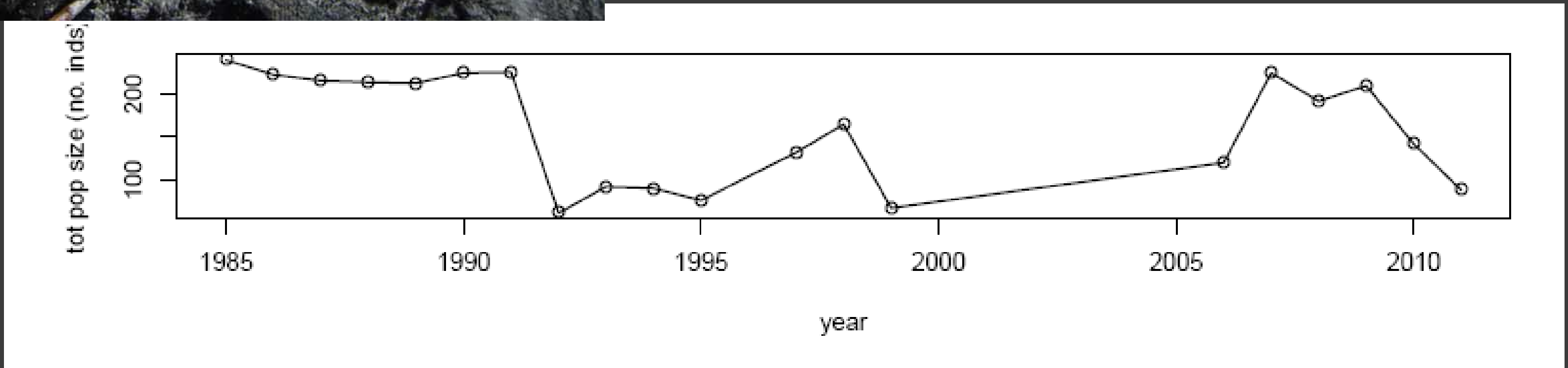
Link vital rates to environmental factors

Link population dynamics to vital rates



Fumana procumbens

– a long-lived dwarf shrub in rocky habitats



What factors are driving changes in population size among years?

Johan P. Dahlgren, Karin Bengtsson, Johan Ehrlén 2016, Ecology

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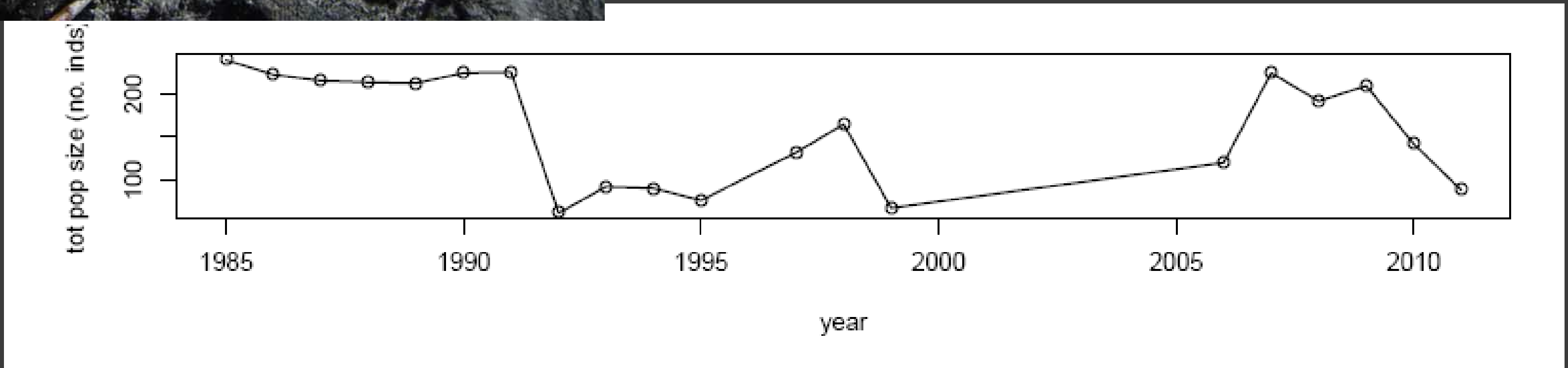

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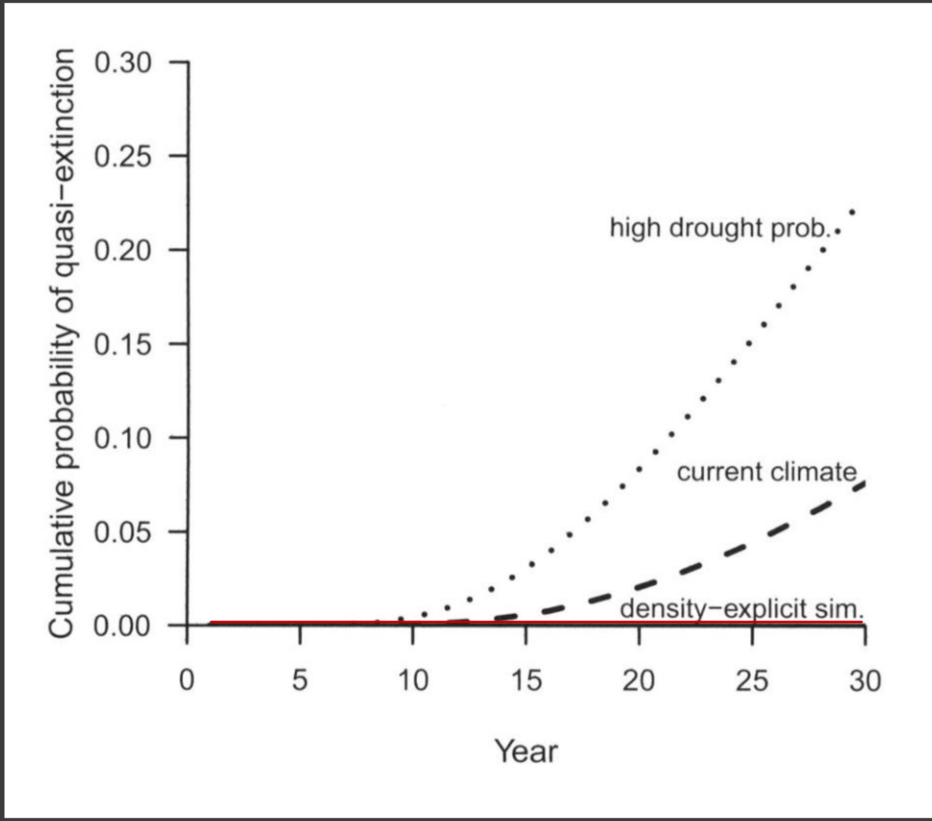
Linking population dynamics to environmental variation – and population density



Bad year (climate) -> reduction in pop.size
-> reduced density -> release -> increased growth rate

Johan P. Dahlgren, Karin Bengtsson, Johan Ehrlén 2016, Ecology

POPULATION VIABILITY ANALYSIS

Hudsonia montana The mountain golden heather

Your task:

1. Calculate stochastic growth rate (λ_S)

2. Evaluate potential effects of increased disturbance

3. Estimate probability of quasi-extinction

(Temporary) link:
https://fogelstrom.github.io/popDynamics19/

OUTLINE

- Population dynamics
- Structured populations
- Modelling the dynamics of structured populations
- Case study

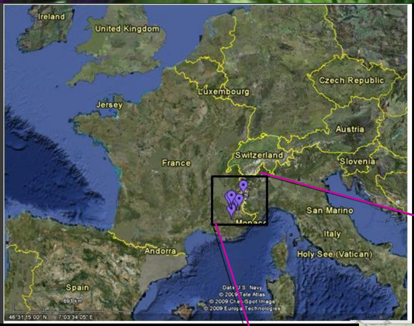
Dracocephalum austriacum

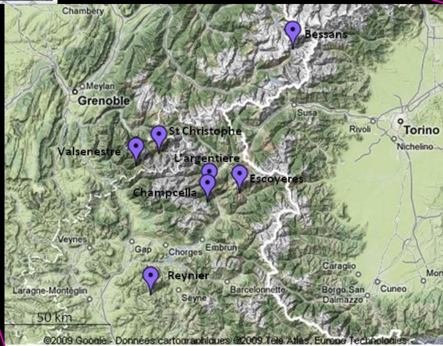
– an endangered herb growing on exposed cliffs in the Alps

Questions:

Will the population viability of this species be influenced by a warmer climate?

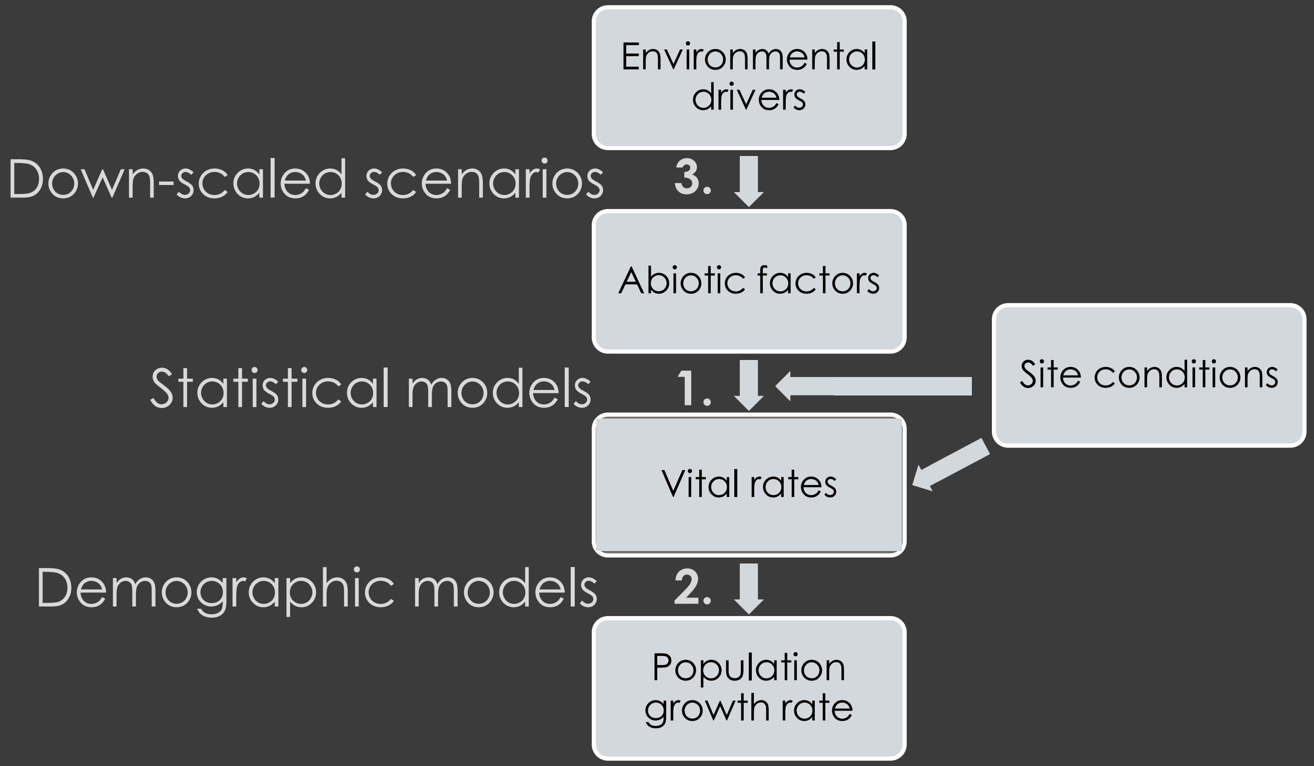
Will climate effects depend on local habitat conditions?





Florence Nicolè, Johan P. Dahlgren, Agnès Vivat, Irène Till-Bottraud, Johan Ehrlén (2011) Journal of Ecology

Model of effects of climate change on population dynamics, and of how such effects vary with site conditions



DESIGN

- ~1500 individuals in 7 populations followed 7 years
- Measurements of 5 vital rates
- Measurement of 12 environmental factors
- Data on temperature and precipitation from local weather stations
- Climate change scenarios – Down-scaled

BUILDING A DEMOGRAPHIC MODEL – FIELD DATA

- Recordings over several years
- Permanently marked individuals
- All life cycle stages
- Measuring and recording vegetative and reproductive traits
- Time of year

BUILDING AN INTEGRAL PROJECTION MODEL

- Continuous, fine-grained matrix model
- Models vital rates as functions of variables.
- Parameterized using relationships from statistical models
- Possible to include multiple state variables, including environmental parameters

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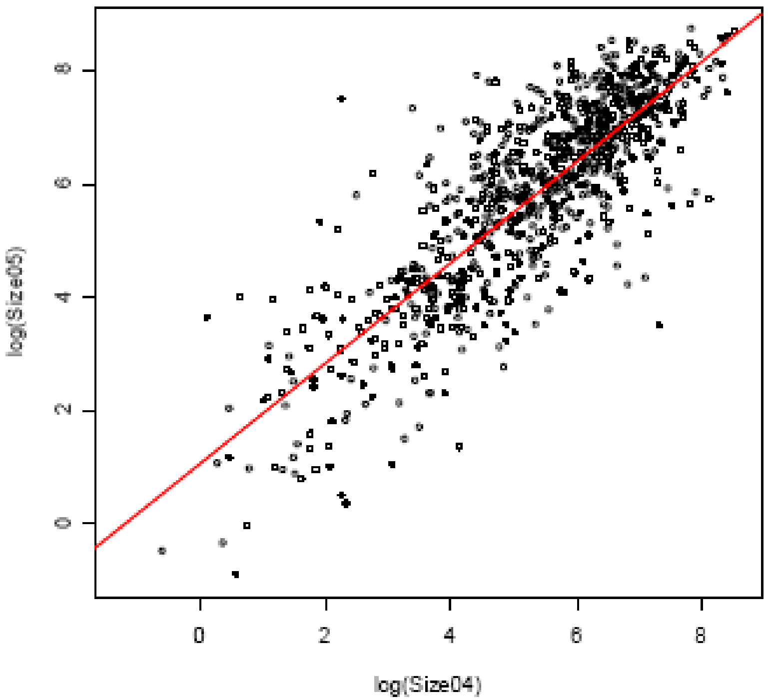
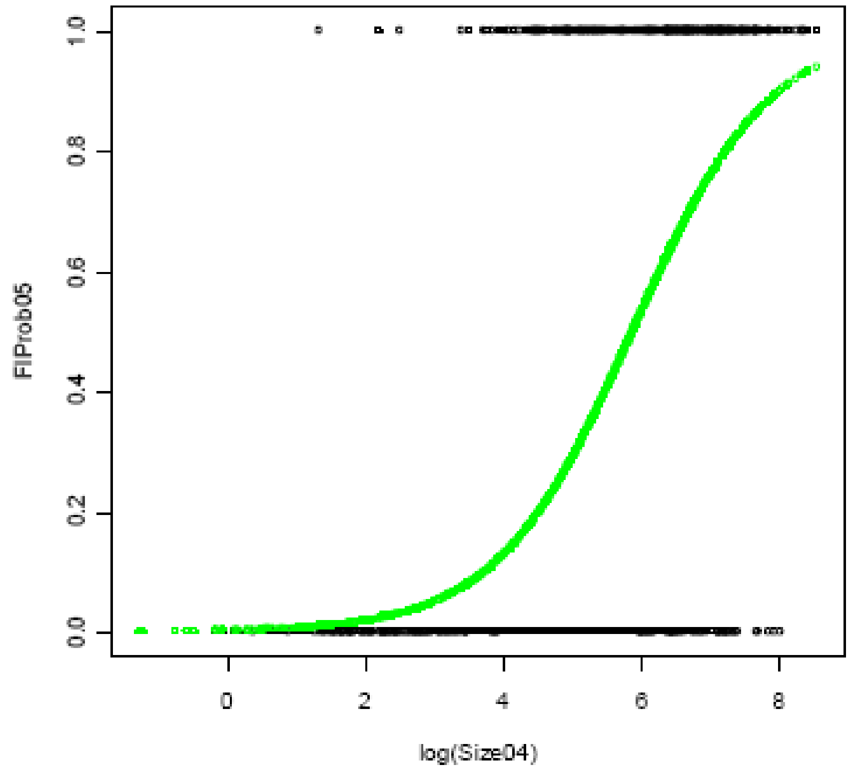
```
> summary(mod1<-lm(log(Size05)~log(Size04)))

Call:
lm(formula = log(Size05) ~ log(Size04))

Residuals:
     Min       1Q   Median       3Q      Max
-4.09389 -0.51484  0.03605  0.54020  4.36272

Coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)   1.0711     0.1108   9.667   <2e-16 ***
log(Size04)   0.8865     0.0199  44.540   <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' '
1

Residual standard error: 0.9554 on 890 degrees of freedom
  (110 observations deleted due to missingness)
Multiple R-Squared: 0.6903,     Adjusted R-squared:  0.69
F-statistic:  1984 on 1 and 890 DF,  p-value: < 2.2e-16

> abline(mod1,col="red",lwd=2)
```



```
> summary(mod2<-glm(FlProb05~log(Size04+0.1),binomial))

Call:
glm(formula = FlProb05 ~ log(Size04 + 0.1), family =
binomial)

Deviance Residuals:
    Min        1Q    Median        3Q       Max
-2.1420   -0.8220  -0.2534   0.8465   3.0473

Coefficients:
                  Estimate Std. Error z value Pr(>|z|)
(Intercept)       -6.02128    0.41847  -14.39   <2e-16 ***
log(Size04 + 0.1)  1.02360    0.07179   14.26   <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' '
1

(Dispersion parameter for binomial family taken to be 1)

    Null deviance: 1348.06  on 1001  degrees of freedom
Residual deviance:  984.72  on 1000  degrees of freedom
AIC: 988.72

Number of Fisher Scoring iterations: 5

> plot(log(Size04),FlProb05)
> points(log(Size04),predict(mod2,type="response")
+ ,col="green")
```



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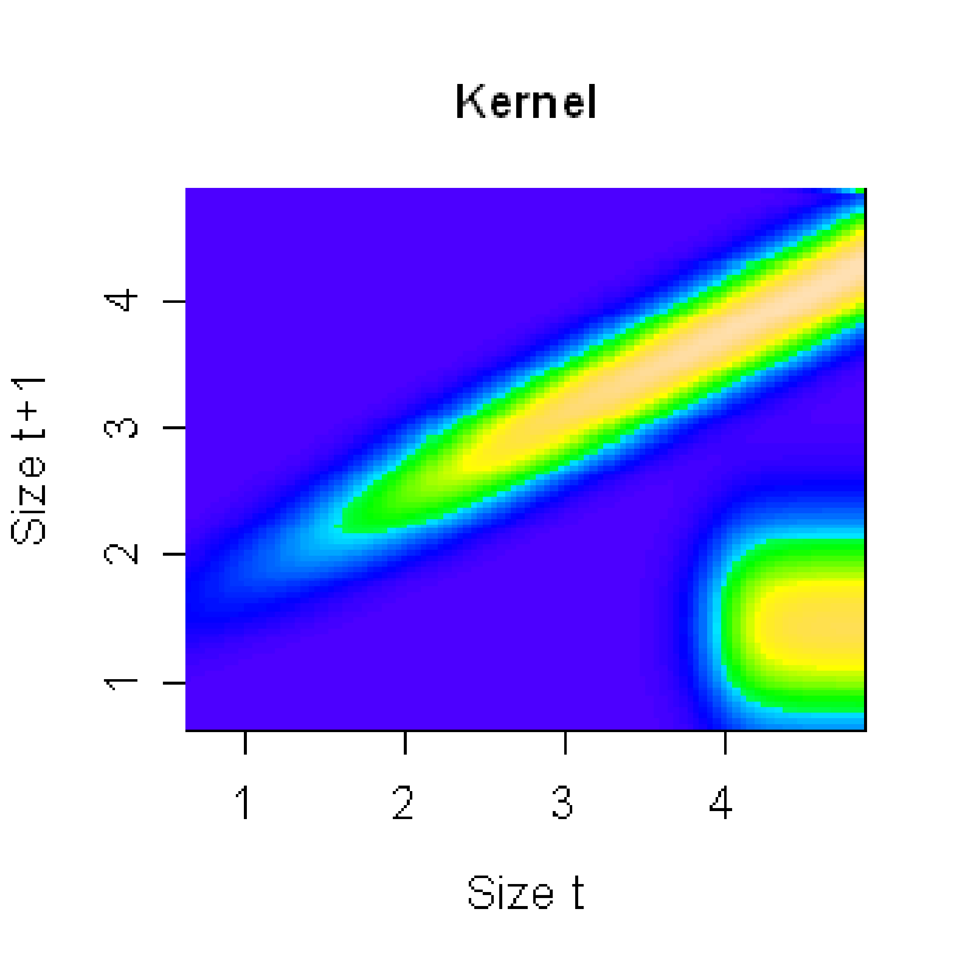
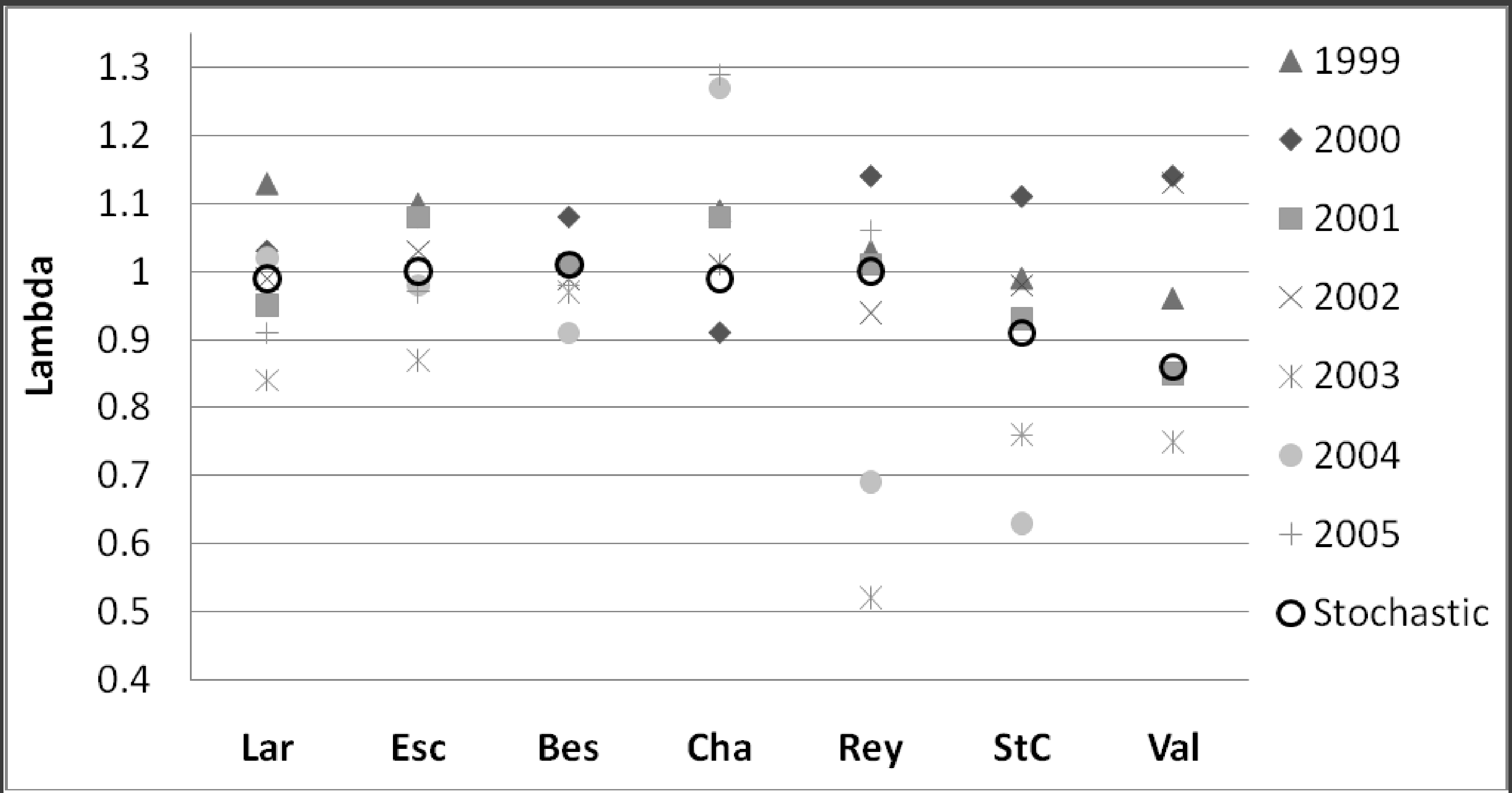
INTEGRAL PROJECTION MODELS



Stochastic and yearly deterministic growth rate for each population of *Dracocephalum austriacum* over the census period (1999-2006).



1 & 2 Relationship between climatic and environmental factors and population growth rates

Among populations:

$\lambda_S = 1.13$

$- (0.085 \times \text{Slope inclination})$

Among years:

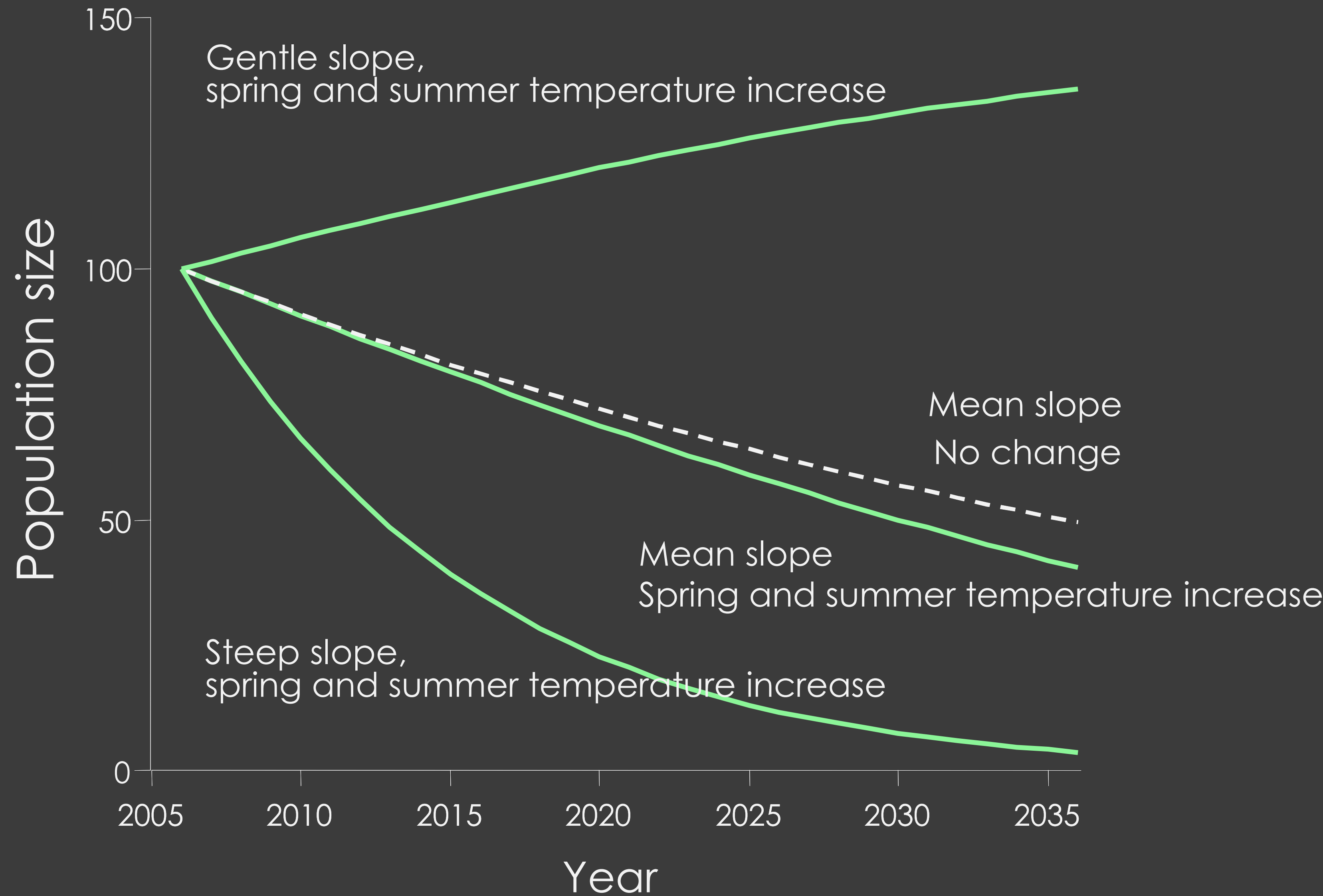
$\lambda_D = 1.21$

$- (0.014 \times \text{Summer temp})$

$+ (0.016 \times \text{Spring temp})$

$- (0.007 \times \text{Summer temp} \times \text{Slope})$

3. Effects of climate change scenario A1B (IPCC) on population size of *Dracocephalum*



CONCLUSIONS

- Different aspects of a warmer climate may have opposing effects on population viability
- Climatic effects may depend on local habitat quality.
- Such interactive effects should be accounted for when down-scaling effects of large-scale environmental changes on viability of local populations

OVERALL CONCLUSIONS

- Demography is fundamental to understand variation in population growth rates, abundances and distributions of species, to link this variation to environmental variation, and to identify and halt decline in threatened species

- For organisms with structured populations, life cycle approaches and demographic models, such as matrix models, are important and useful tools to examine these questions