Eco-evolutionary consequences of randomly fluctuating environments

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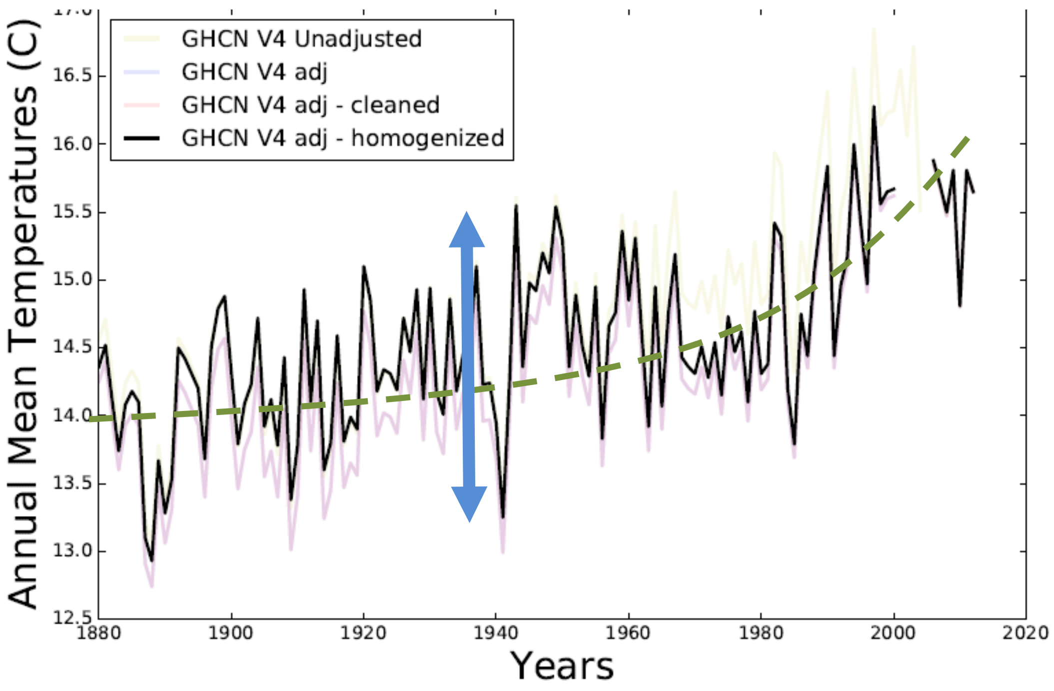
Environments fluctuate randomly

- Virtually all natural environments exhibit **random, stochastic fluctuations**.



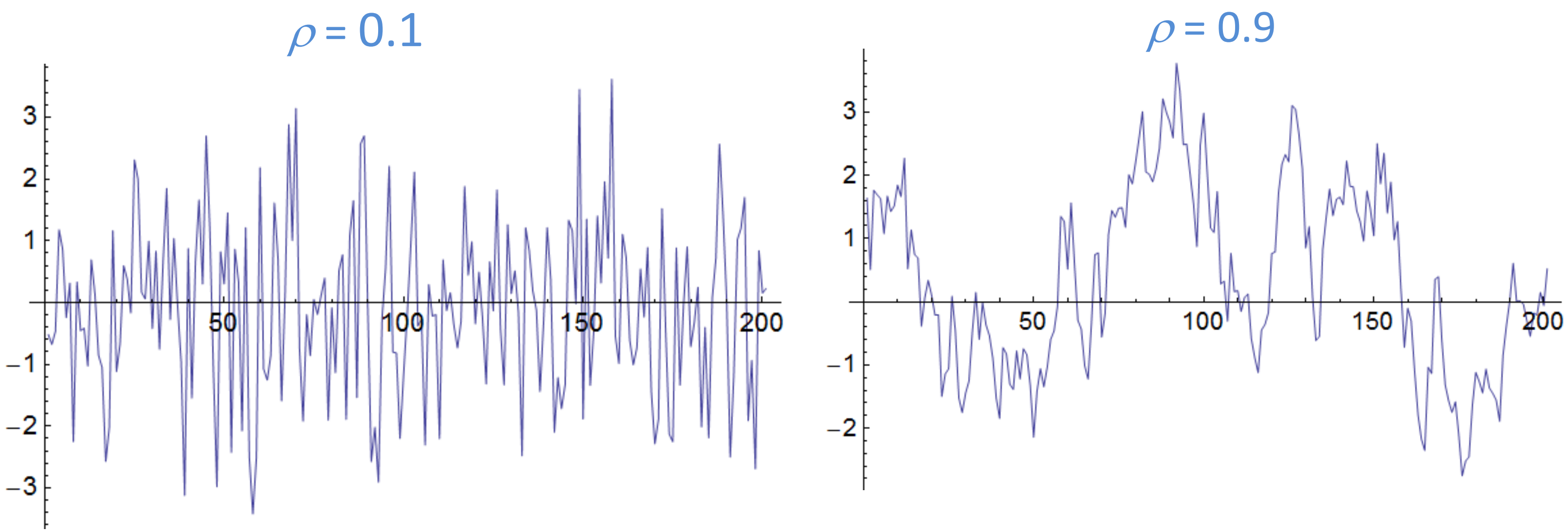
https://data.giss.nasa.gov
Observatoire Palais Longchamp Marseille

- Faster than trends → Major cause of environmental stress for species in the wild
- Global change is also altering the **magnitude and predictability of fluctuations**[1]

1: Boer, G. J. (2009. *J. Clim.*)

Environments fluctuate randomly

- Stochastic fluctuations are **random**, but can be **predicted probabilistically**
- Time scale of predictability depends on their **temporal autocorrelation ρ**

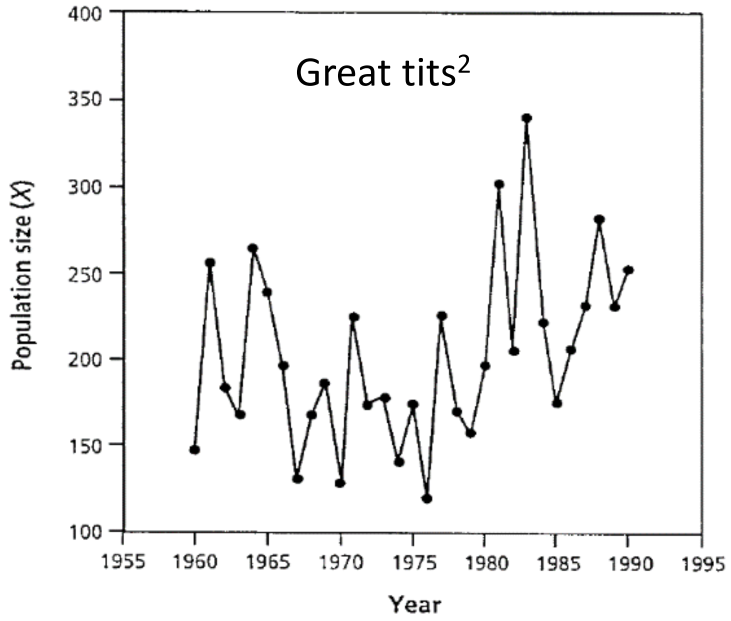


- Also described as the **colour of environmental noise**[1]: from blue (rapid, negatively autocorrelated) to red/brown (slow, positively autocorrelated)

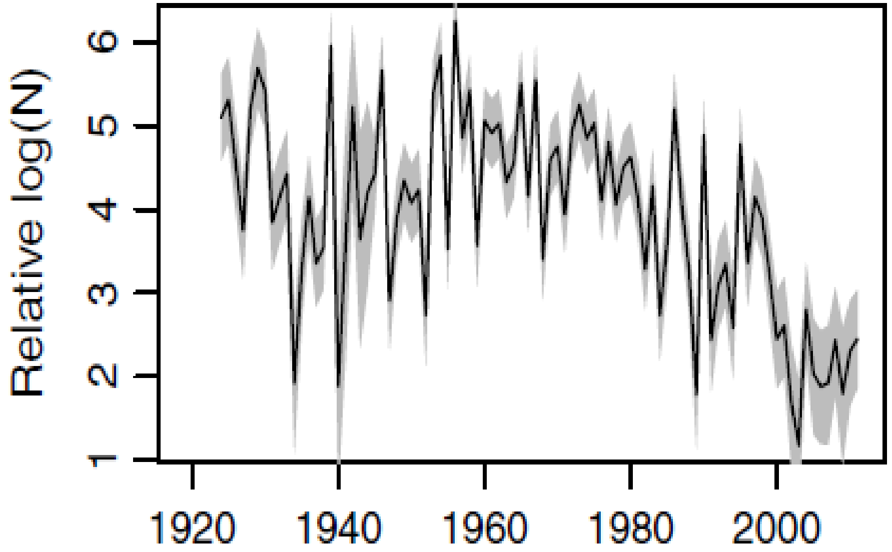
1: Vasseur & Yodzis (2004 Ecology)

Demographic consequences

- Causes fluctuations in demographic vital rates (survival/fecundity)
  → **Fluctuating population size/density**[1]



Cods [3]



- Strong source of stochasticity, acts at all population sizes[1]
  → May put initially large populations at **risk of extinction**.

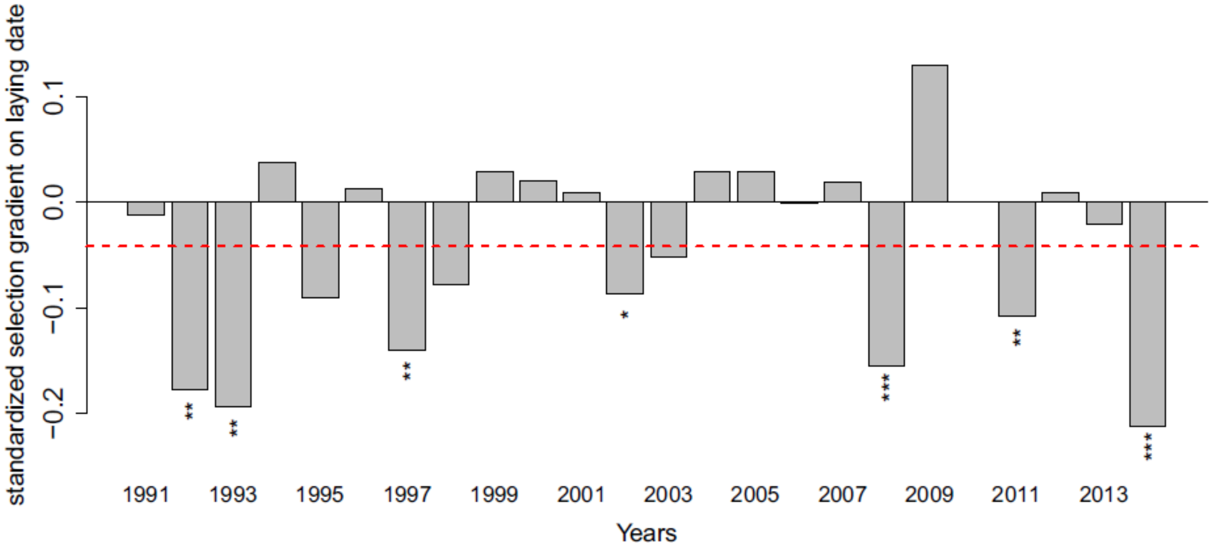
1: reviewed by Lande et al (2003 OUP)
2: Saether et al (1998, Am Nat)
3: Rogers et al (2017 J Anim Ecol)

Evolutionary consequences

- Source of **fluctuating selection**:
  which phenotypes are favored by natural selection depends on the year.

Laying date of blue tits in Mediterranean forests
(near Montpellier and Corsica)

Charmantier et al (2015 Evol Appl)



Marrot et al (2018)

Evolutionary consequences

- Source of **fluctuating selection**
- Can cause the evolution of specific response mechanisms such as **phenotypic plasticity** = phenotypic change in response to environment of expression

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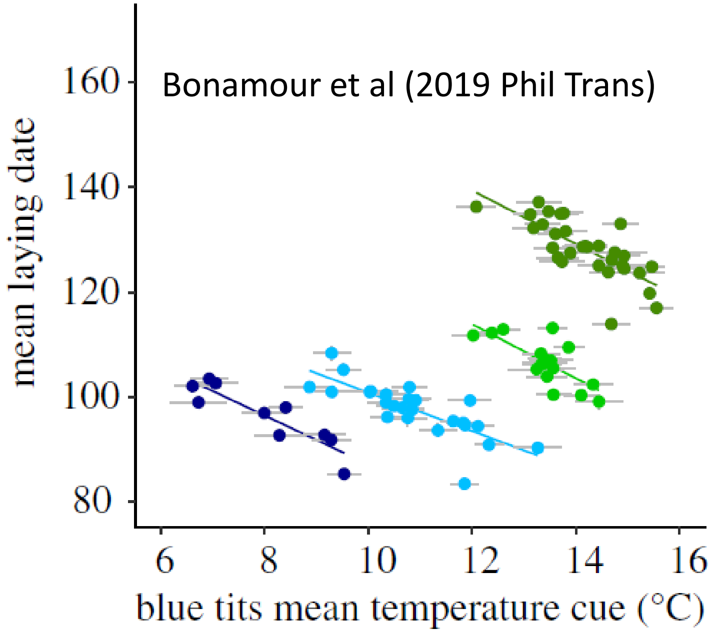
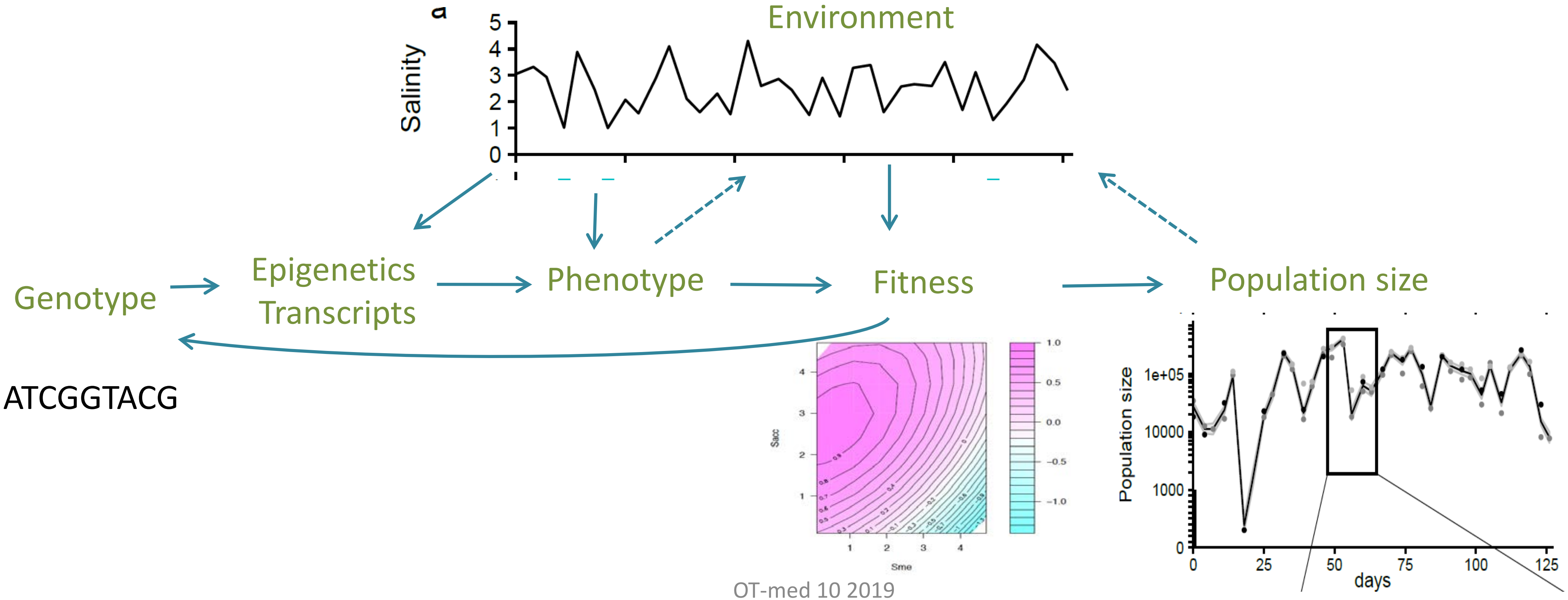


Predictability of population responses

StG FluctEvol

- How do random environmental fluctuations translate into **fluctuations at all levels of population biology**?
- What determines the **predictability of responses** at each level?



Predictability of population responses

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- How do random environmental fluctuations translate into **fluctuations at all levels of population biology**?
- What determines the **predictability of responses** at each level?

Investigated by a combination of approaches:

→**Field studies over time/space**: observe change in wild populations *in natura*

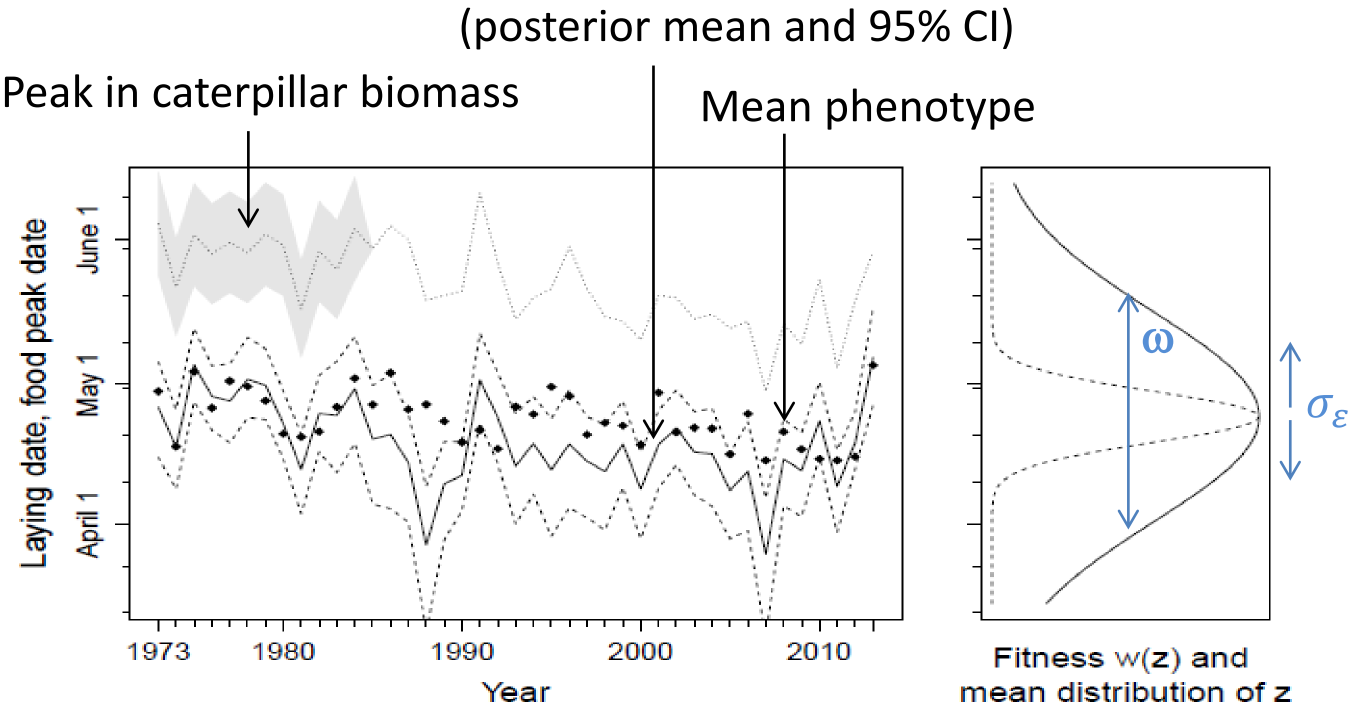
→**Theoretical modeling**: understanding general principles, predicting core processes

→ **Multigenerational laboratory experiments**: manipulate drivers of population biology

I – Natural populations

How much does selection fluctuate in the wild?

- Adaptation to changing environment often conceptualized as tracking of a moving optimum phenotype[1], but little direct empirical demonstration.
- Movements of a fitness peak can be estimated from time series of traits and fitness, using random regression[2].
  Example in great tits:



Parameter	Posterior mean ± S.E.
ω (days)	20.55 ± 1.7
σ_ϵ (days)	6.75 ± 1.66
Autocorrelation α	0.3029 ± 0.2419
Intercept *A* (April day)	19.43 ± 1.95
Slope *B* (days/°C)	−5.01 ± 1.09

1: Kopp & Matuszewski (2014 Evol Appl)
2: Chevin et al (2015 Evolution)

Meta-analysis across long-term studies

- Apply to compiled long-term datasets of reproductive phenology, major phenotypic response to climate change

Superb fairywren
(*Malurus cyaneus*)

Eurasian oystercatcher
(*Haematopus ostralegus*)

Sheep
(*Ovis aries*)

Eastern grey kangaroo
(*Macropus giganteus*)

Savannah sparrow
(*Passerculus sandwichensis*)

Hi hi
(*Notiomystis cincta*)

Great tits
(*Parus major*)

Mountain goats
(*Oreamnos americanus*)

Reindeer
(*Rangifer tarandus*)

Northern wheatear
(*Oenanthe oenanthe*)

Collared flycatcher
(*Ficedula albicollis*)

Red squirrel
(*Tamiasciurus hudsonicus*)

Red deer
(*Cervus elaphus*)

Alpine swift
(*Tachymarptis melba*)

Bighorn sheep
(*Ovis canadensis*)

Blue tits
(*Cyanistes caeruleus*)

Red-winged Fairy-wren
(*Malurus elegans*)

Pied flycatcher
(*Ficedula hypoleuca*)

House sparrow
(*Passer domesticus*)

Dipper
(*Cinclus cinclus*)

Columbian ground squirrel
(*Urocitellus columbianus*)

De Villemereuil et al (in prep)

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- Apply to compiled long-term datasets of reproductive phenology, major phenotypic response to climate change

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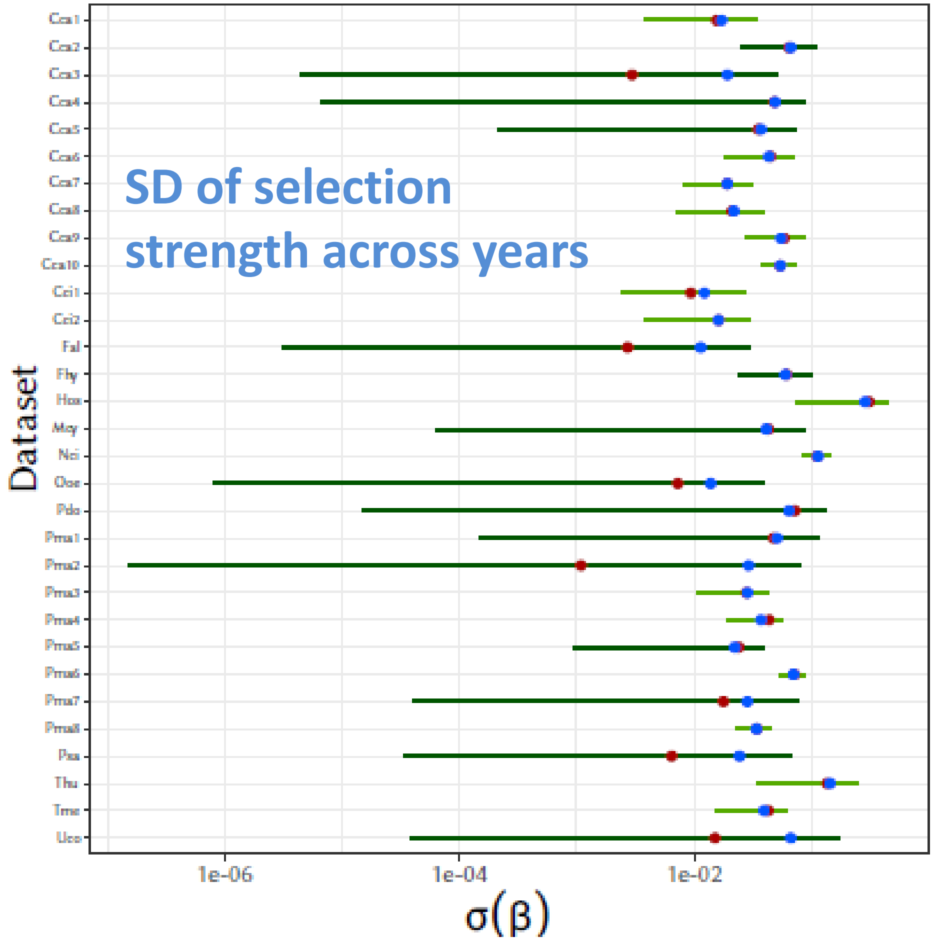
- What is the **prevalence and evolutionary significance of fluctuating selection**?

De Villemereuil et al (in prep)

Meta-analysis across long-term studies

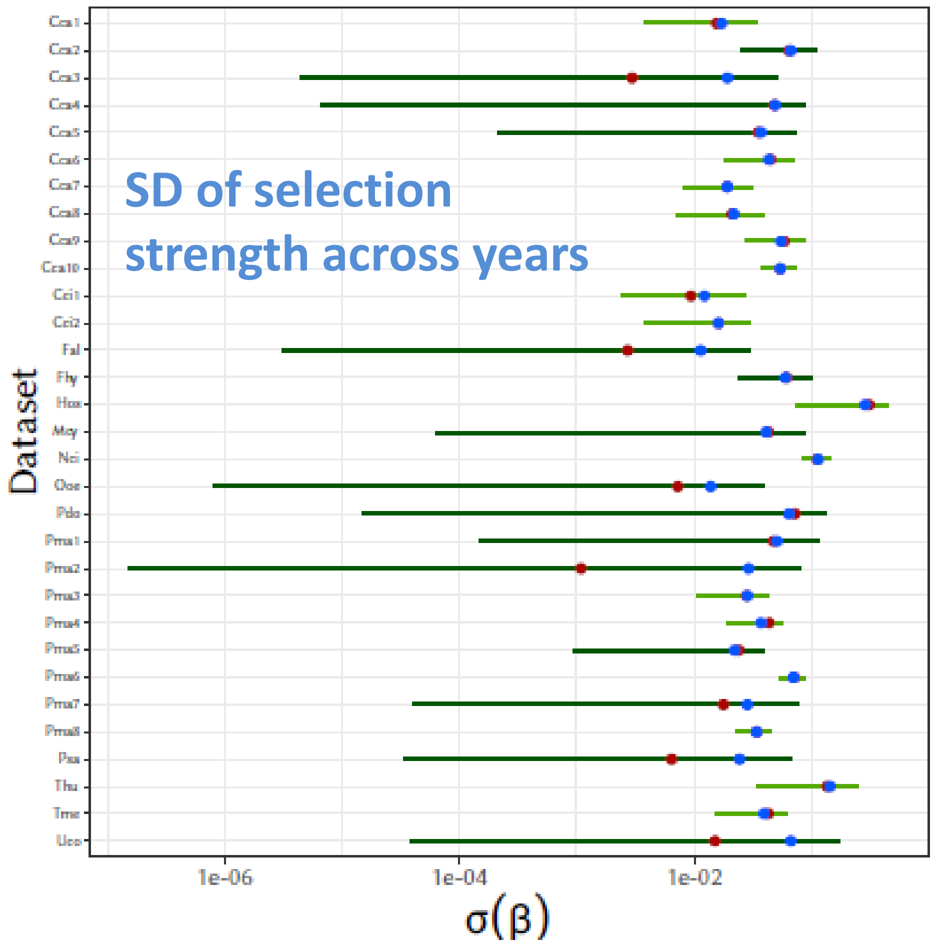
- Evidence for **fluctuating selection**



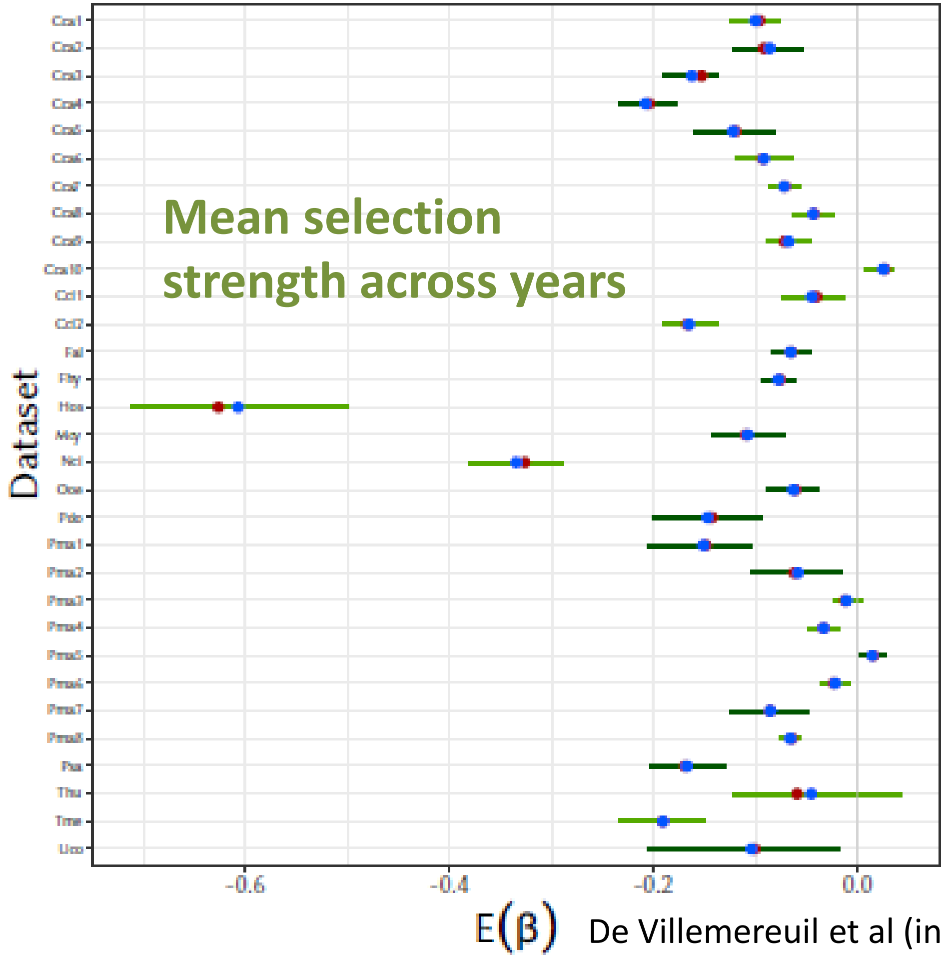
De Villemereuil et al (in prep)

Meta-analysis across long-term studies

- Evidence for **fluctuating selection**, but also **directional selection for earlier breeding**



Model | EXP. | OPT.



De Villemereuil et al (in prep)

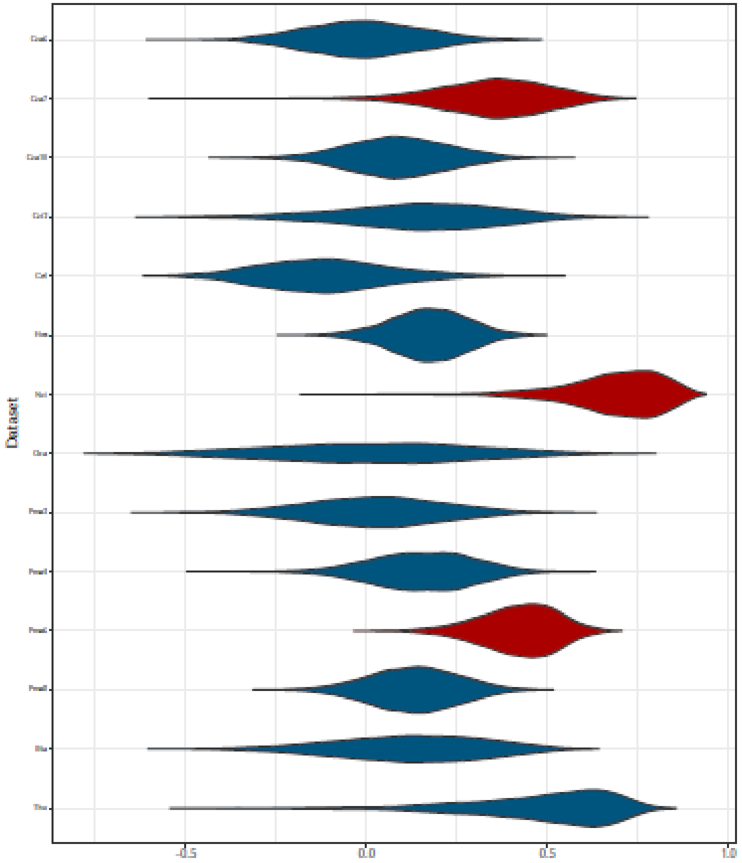
Meta-analysis across long-term studies

- Evidence for **fluctuating selection**, but also **directional selection for earlier breeding**

- What's the **evolutionary significance** of selection that fluctuates in **magnitude but not direction**?

- Significant evidence for **plastic tracking of optimum** across studies (+in some individual studies).

  → Plasticity has probably evolved to reduce the phenotypic mismatch in a fluctuating environment



Plasticity – optimum correlation
De Villemereuil et al (in prep)

II - Theory

Evolutionary demography

- **Evolution and demography are connected through the fitness landscape**[1] relating population mean fitness $\bar{W}$ to the mean phenotype $\bar{z}$:

Demography: $N_{t+1} = \bar{W}_t N_t$

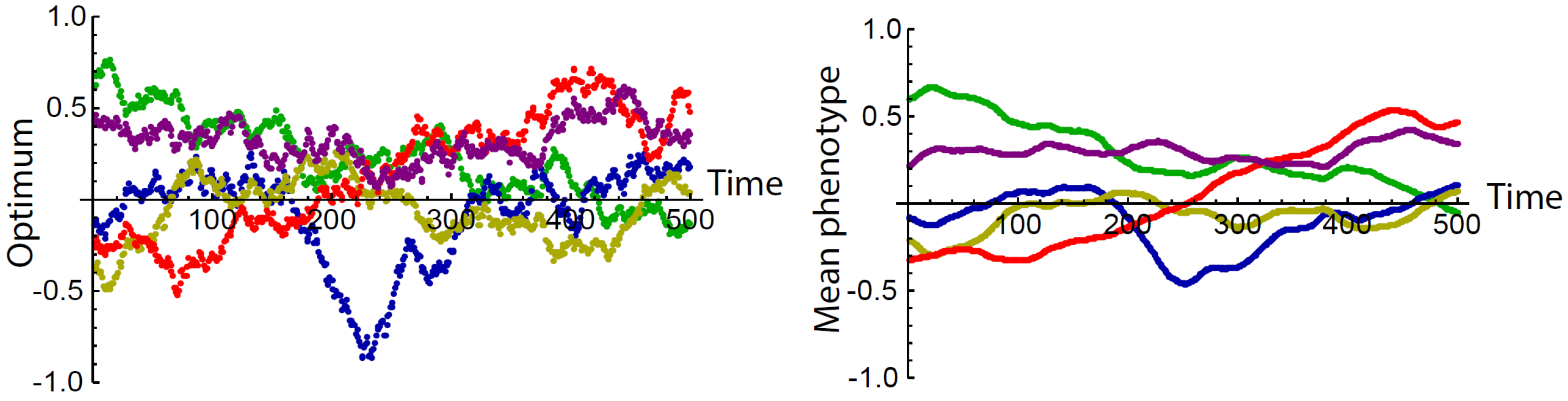
Evolution: $\Delta\bar{z} = G\,\dfrac{\partial ln\bar{W}}{\partial\bar{z}}$ (G : additive genetic variance of z)

- **Plastic and evolutionary responses** to the changing environment can be **plugged into demography** to project the **population dynamics and extinction risk**

1 : Wright (1937 PNAS)
Lande (1976 Evolution, 1982 Ecology)
Crow & Kimura (1970)

Evolutionary responses to fluctuating optimum

- In a changing environment, the mean phenotype in the long run is a weighted average of past optima[1], with more weight on more recent optima.



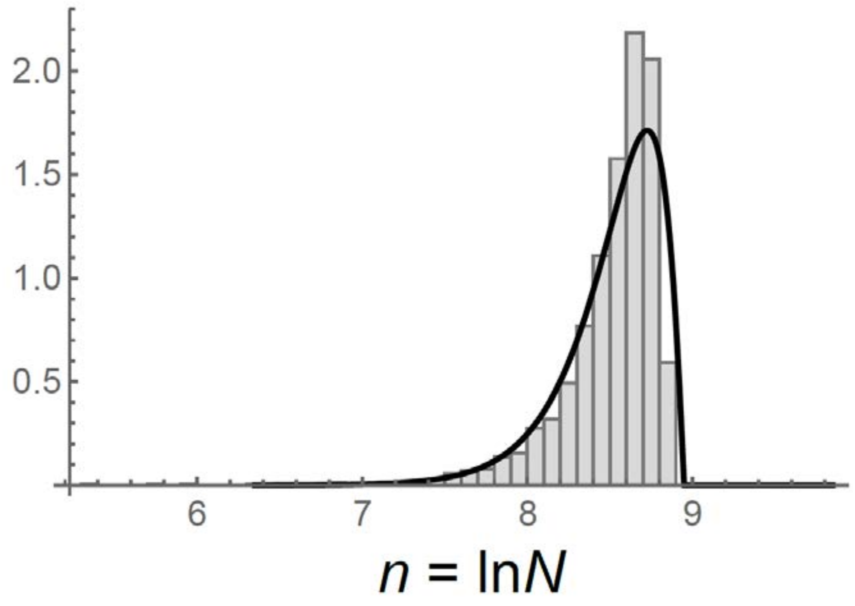
- The stationary phenotypic mismatch with optimum determines the effect of environmental fluctuations on population dynamics

1 : Charlesworth et al (1993 Genet Res);
Figure from Chevin (2013 Evolution)

Population dynamics in stochastic environment

Combined with population dynamics:

- The **expected population growth** rate and (log) population size[1,2] are:
  - **Reduced by the phenotypic mismatch variance**
  - **Increased by mismatch autocorrelation** (allow better evolutionary tracking)
- **Variance of population size** (among independent lineages) increases with **mismatch autocorrelation**[2].
- The distribution of log(*N*) is **skewed, with excess of low population sizes** at high extinction risk



1: Lande & Shannon (1996 Evoution)
2: Chevin et al (2017 Am Nat)

Phenotypic plasticity and stochastic fluctuations

- **Plasticity buffers population fluctuations** if environment is **highly predictable**, but may **amplify them** and increases extinction risk if **predictability is low**.

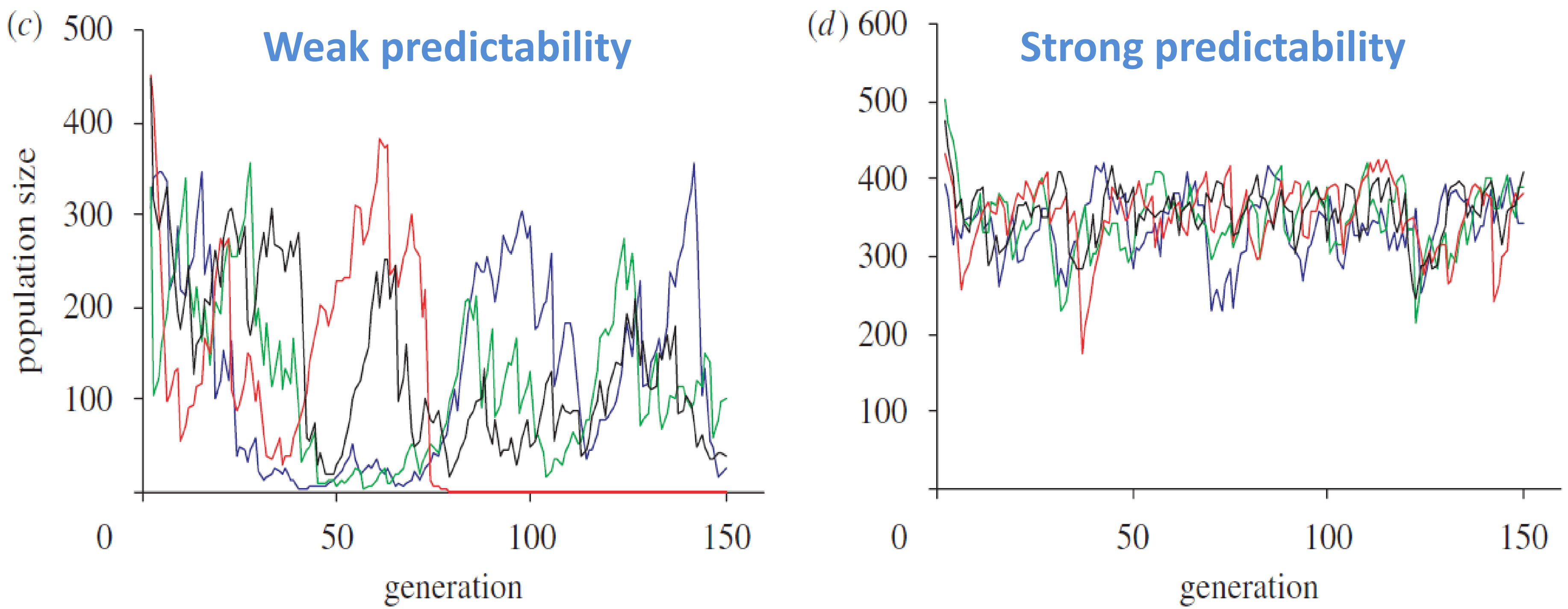


Figure: Reed et al (2010, Proc B)

Also Chevin et al (2013 Phil Trans)

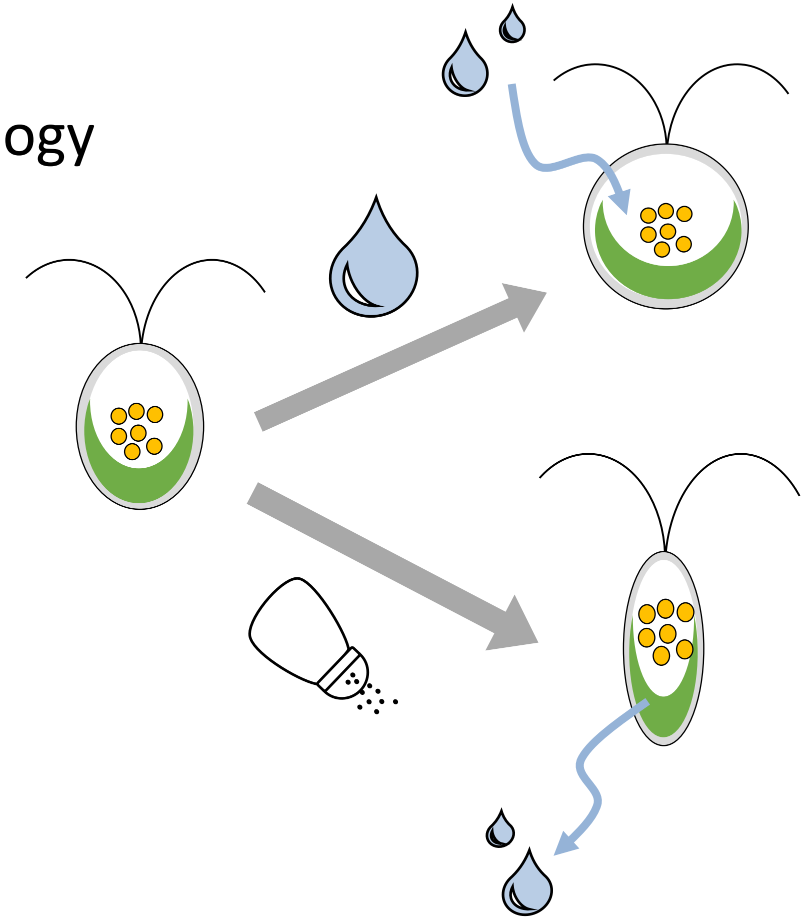
III – Laboratory Experiments

Dunaliella salina:
A model organism for salinity tolerance

- **Halotolerant micro-algae** (freshwater to NaCl saturation).
- Common in coastal mediterranean lagoons & salterns.
  → Shallow water where **salinity fluctuates** with precipitation, wind, sunlight…
- **Extremophile**: few ecological interactions
  → Niche easily mimicked in the lab
- **Short generation time** ~ 1 day
  → multigenerational experiments

Dunaliella salina:
A model organism for salinity tolerance

- Plastic responses to salinity are well understood:
  - Cell shape and size:
    No cell wall → flexible morphology



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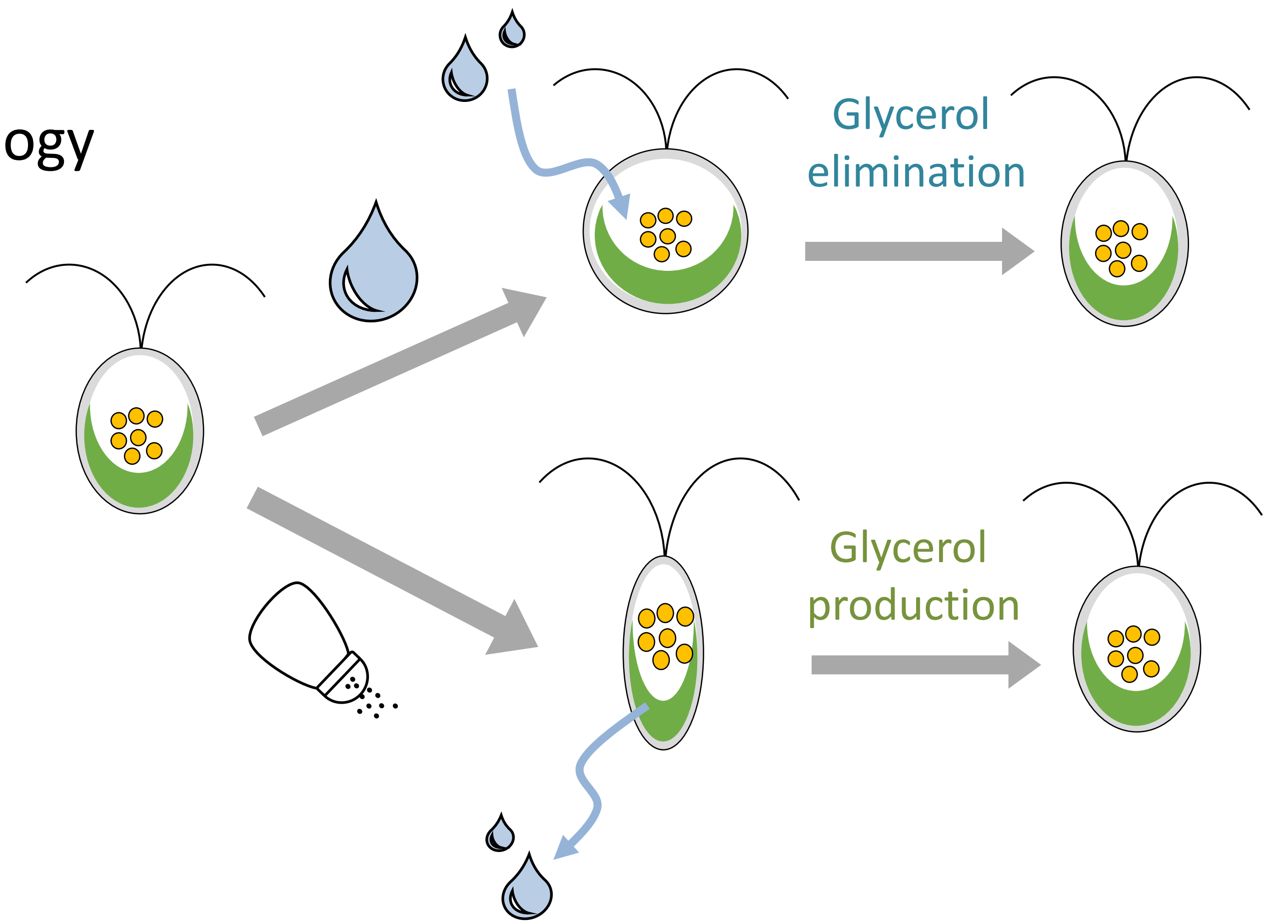
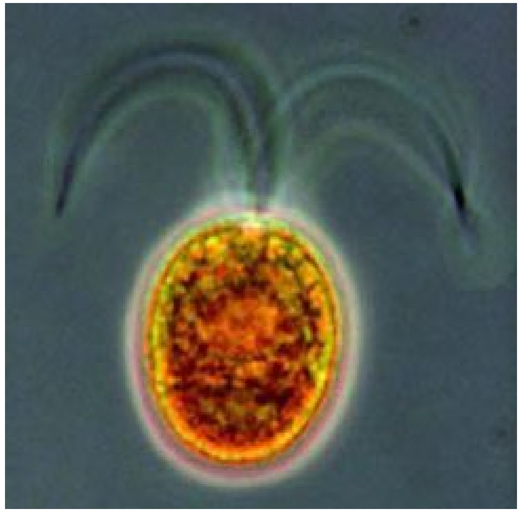
    Glycerol → osmotic stress



Dunaliella salina:
A model organism for salinity tolerance

- Plastic responses to salinity are well understood:
  - Cell shape and size:
    No cell wall → flexible morphology
  - Metabolites:
    Glycerol → osmotic stress
    Carotene: Protection against light, oxidative stress.
  - Ion transport, iron acquisition…



High carotene cell

Long-term experiment under fluctuating salinity

- Salinity changed at each transfer (twice a week) using a pipetting robot

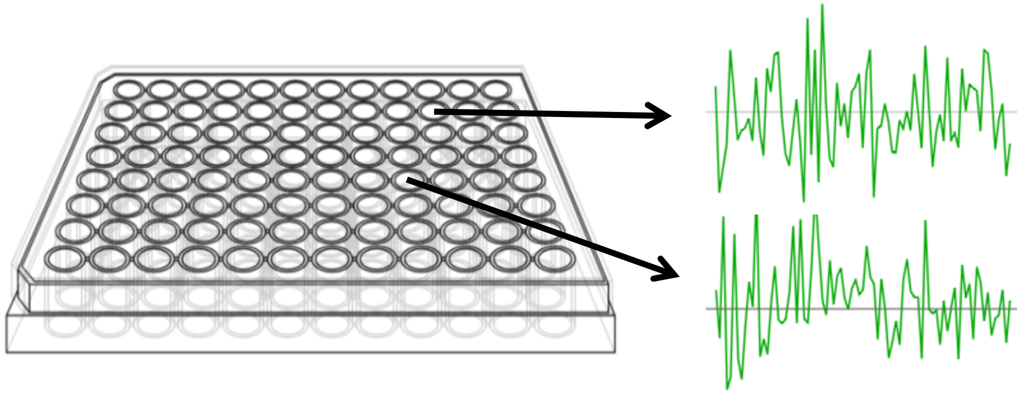
  - ➢ High replication
  - ➢ Complex fluctuation pattern

- Exposed during several months
  → hundreds of generations.

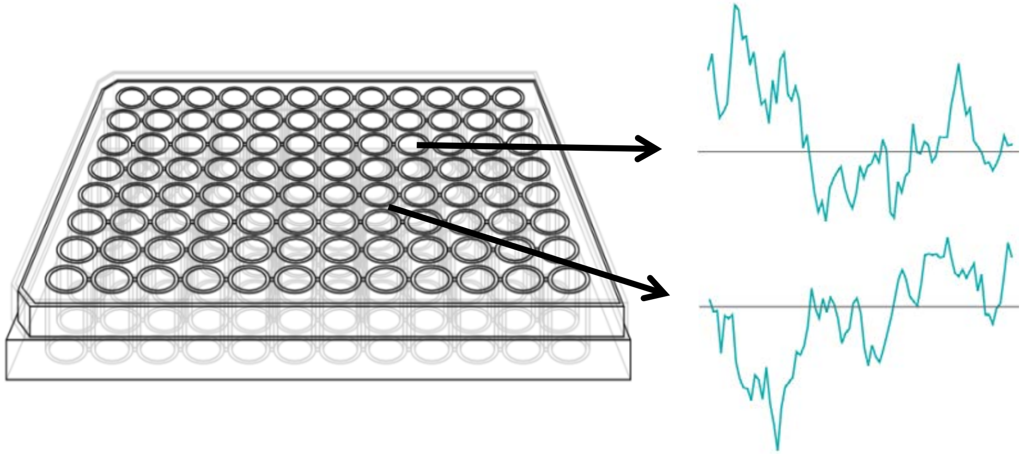
Long-term experiment under fluctuating salinity

- Random change, with environmental autocorrelation as the treatment

Low predictability



High predictability



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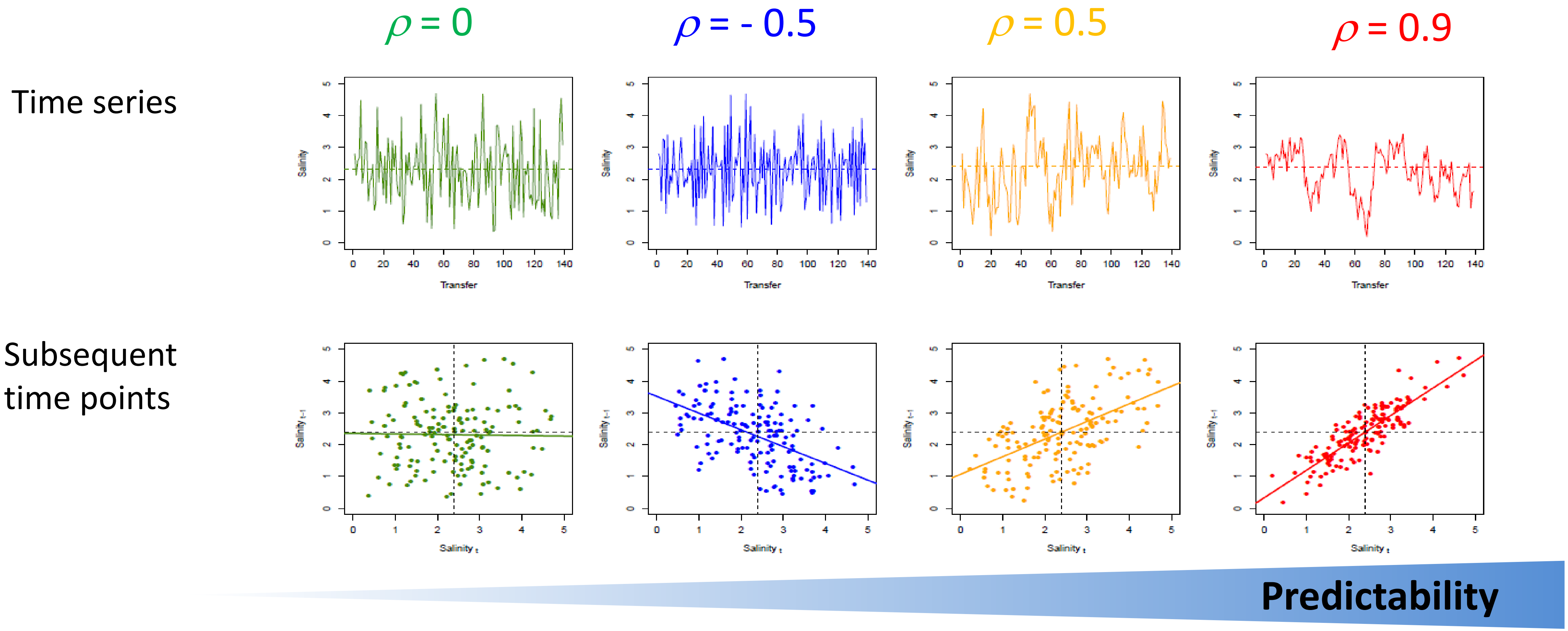
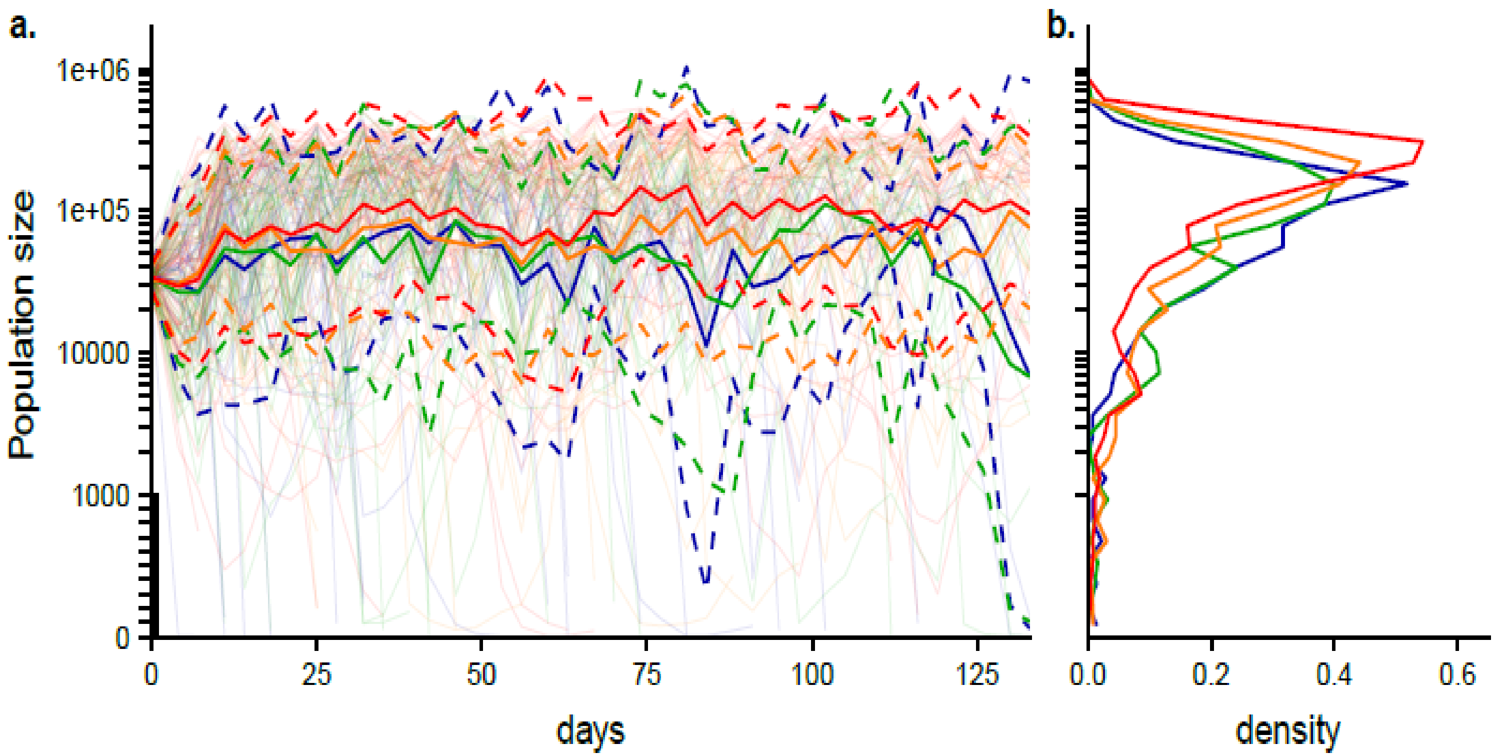


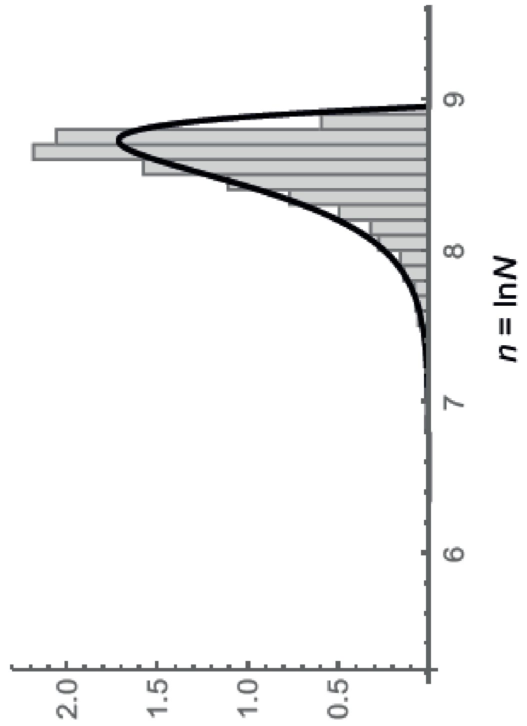
Population dynamics consistent with optimum

- Tracking population size through time (flow cytometry + OD + fluorescence)
- Populations fluctuations reach stationary distribution similar to those predicted under theory with moving optimum[1]

Experiment: Rescan et al (under review)

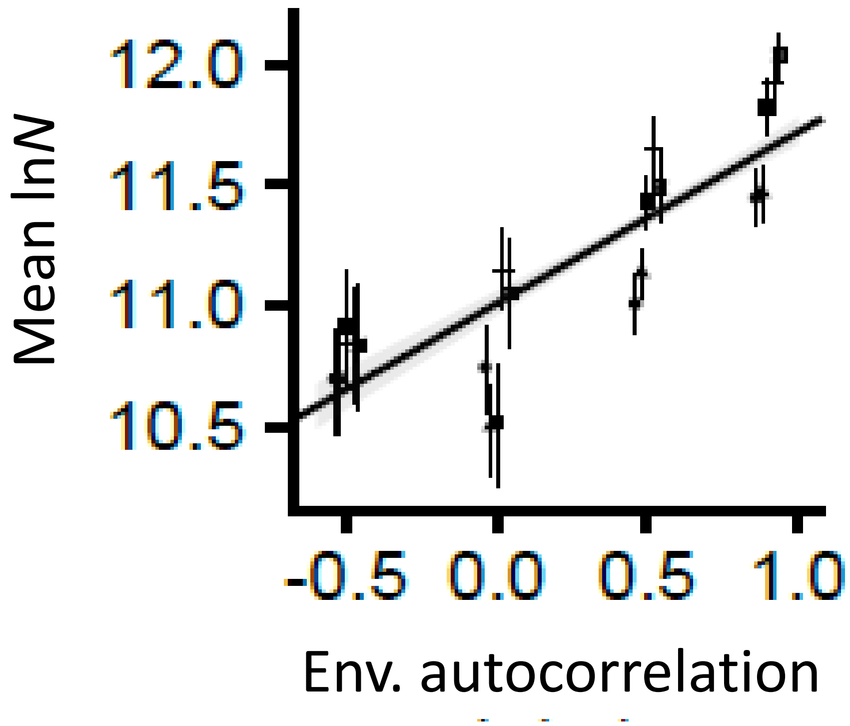
Theory: Chevin et al (2017 Am Nat)

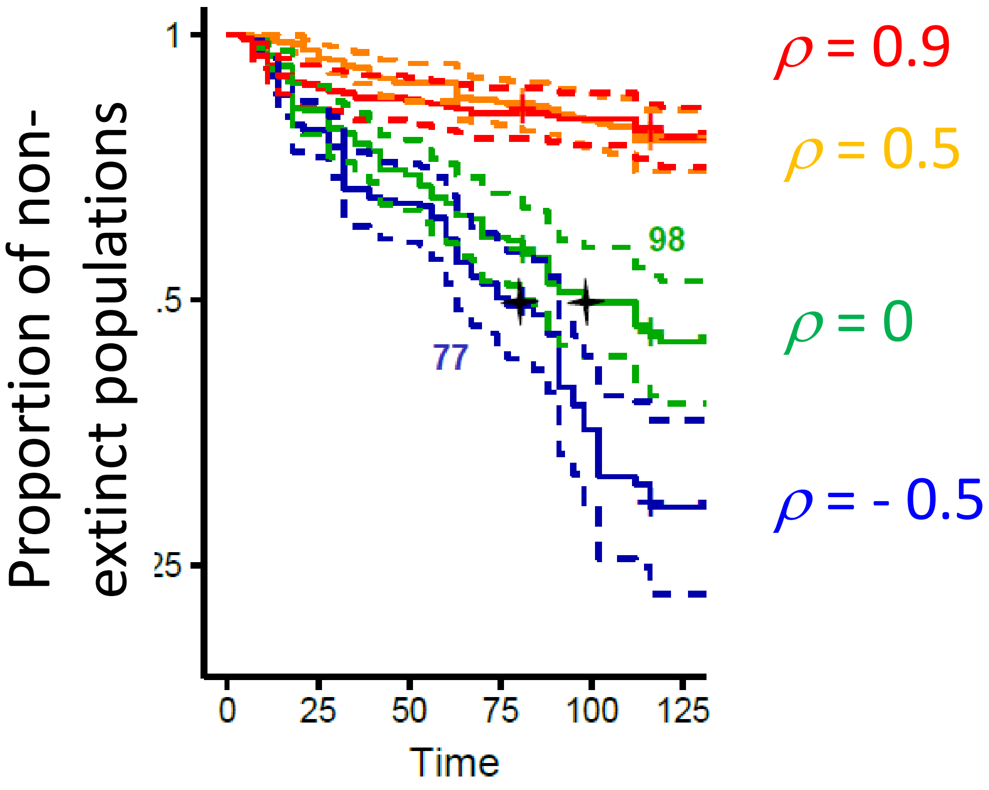




Autocorrelation strongly affects population dynamics

- **Higher mean population size** and **fewer extinctions** at higher autocorrelation

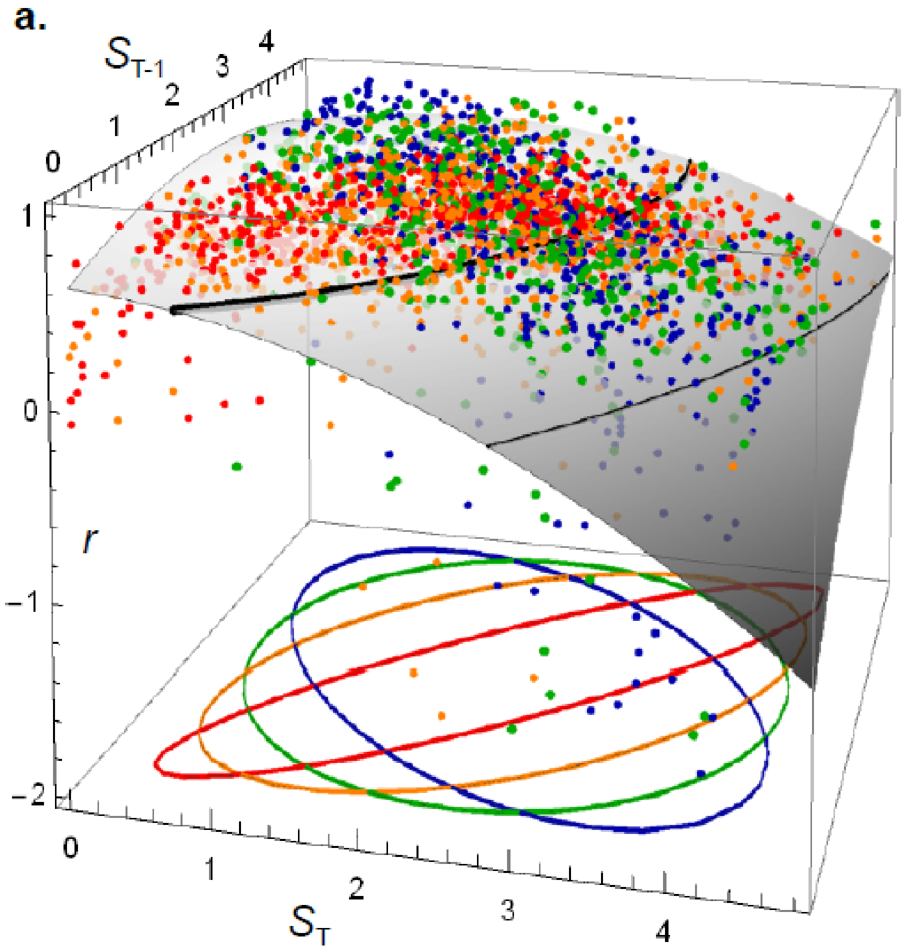




Rescan et al, under review

Optimum with environmental memory

- Well-explained by a **tolerance curve with optimum**, as function of both **current and previous salinity** → **Phenotypic memory**, mediated by plasticity

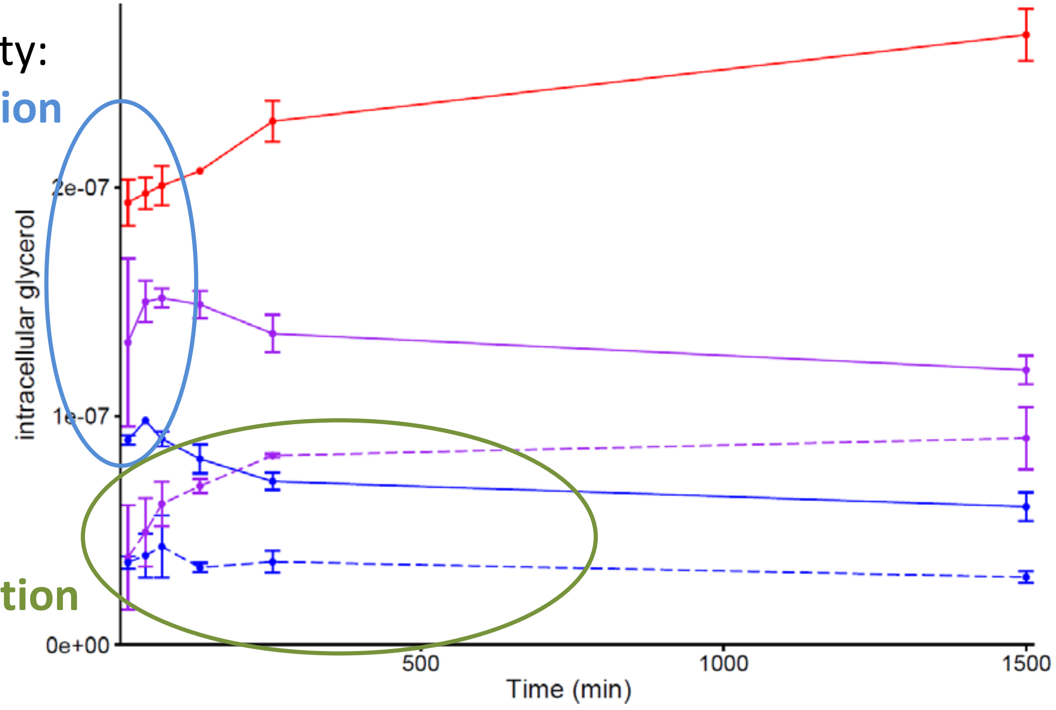


Rescan et al, under review

Mechanism of environmental memory

- Likely contribution from dynamics of glycerol across salinity transitions.

Coming from high salinity:
Rapid change via **excretion**



Moving to high salinity

Moving to medium salinity

Moving to low salinity

Coming from low salinity:
Slower change requiring **production**

Rescan et al, under review

Conclusions

- Combination of **theoretical modeling**
  analysis of wild populations
  multigenerational experiments
  is fruitful for understanding eco-evolutionary responses to changing environments.

- A substantial part of population responses to environmental variation may be captured by adressing effects of plasticity and evolution under a fluctuating optimum

- Environmental autocorrelation is an important driver of population processes at different scales.

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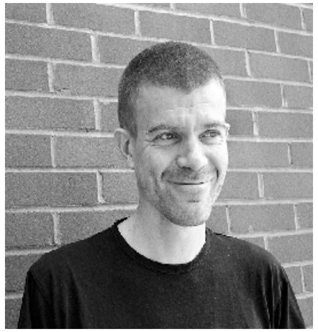
UCLA



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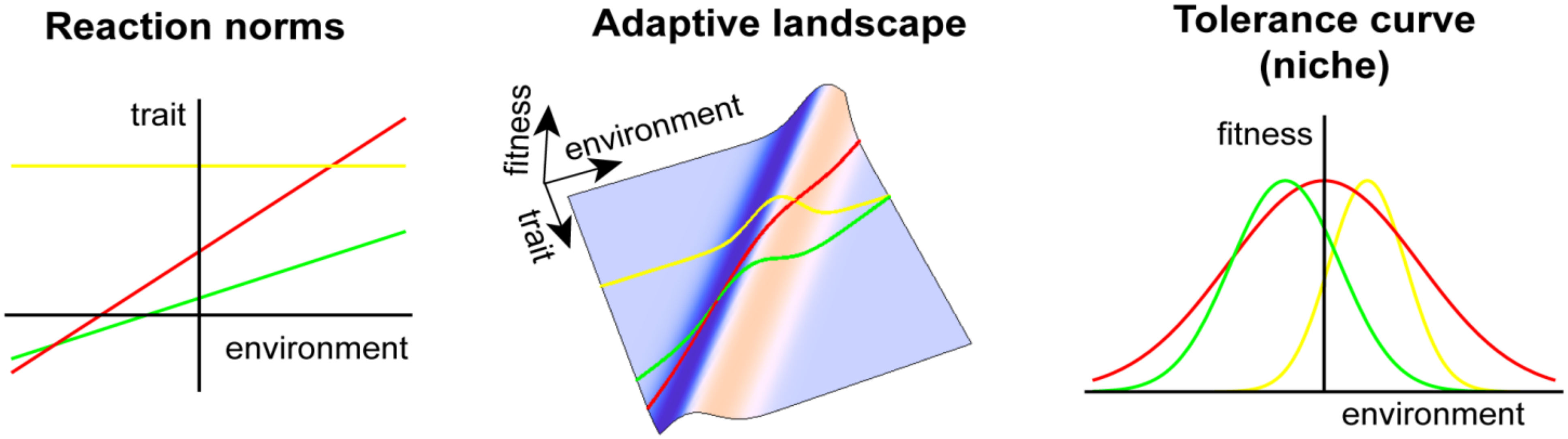
Plasticity, evolution and demography interact

- Phenotypic plasticity of traits under selection underlies environmental tolerance[1]



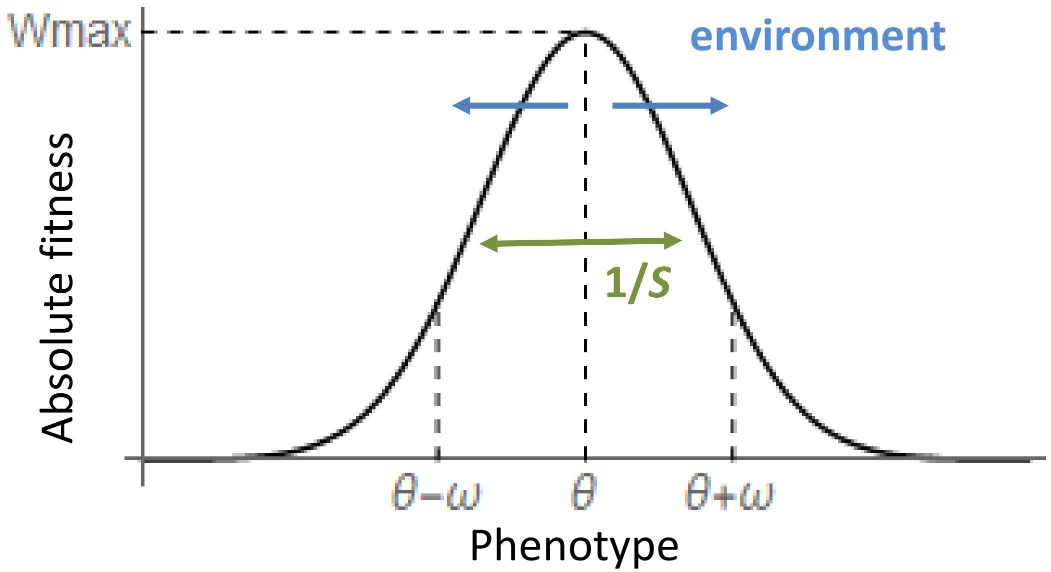
- **Populations dynamics and extinction risk** are largely driven by plastic and evolutionary responses to fluctuating environments

1: Chevin, Lande & Mace (2010 PLoS Biol)

Conceptual framework: Moving optimum models

- Fitness peak with optimum for ecologically important trait. Strength of stabilizing selection = *S* inversely proportional to width of fitness peak.

- Changing environment causes **moving optimum phenotype**[1].



1 : Reviewed by Kopp & Matuszewski (2014 Evol Appl)

Sustained environmental change (warming)

No plasticity

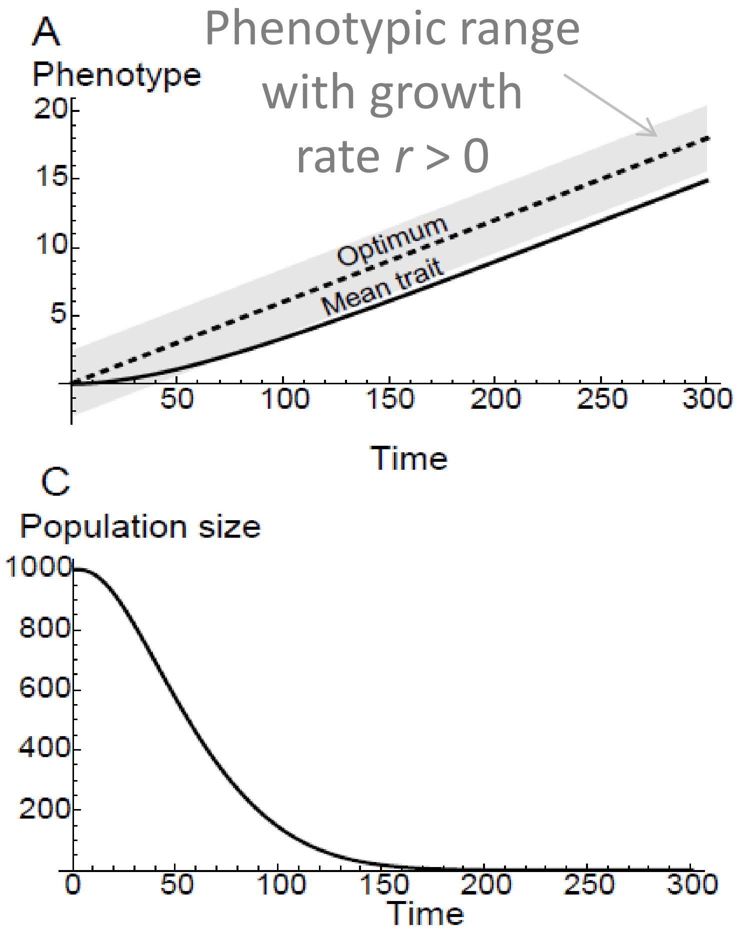


Fig from Chevin, Collins & Lefèvre, 2013 Funct. Ecol

Sustained environmental change (warming)

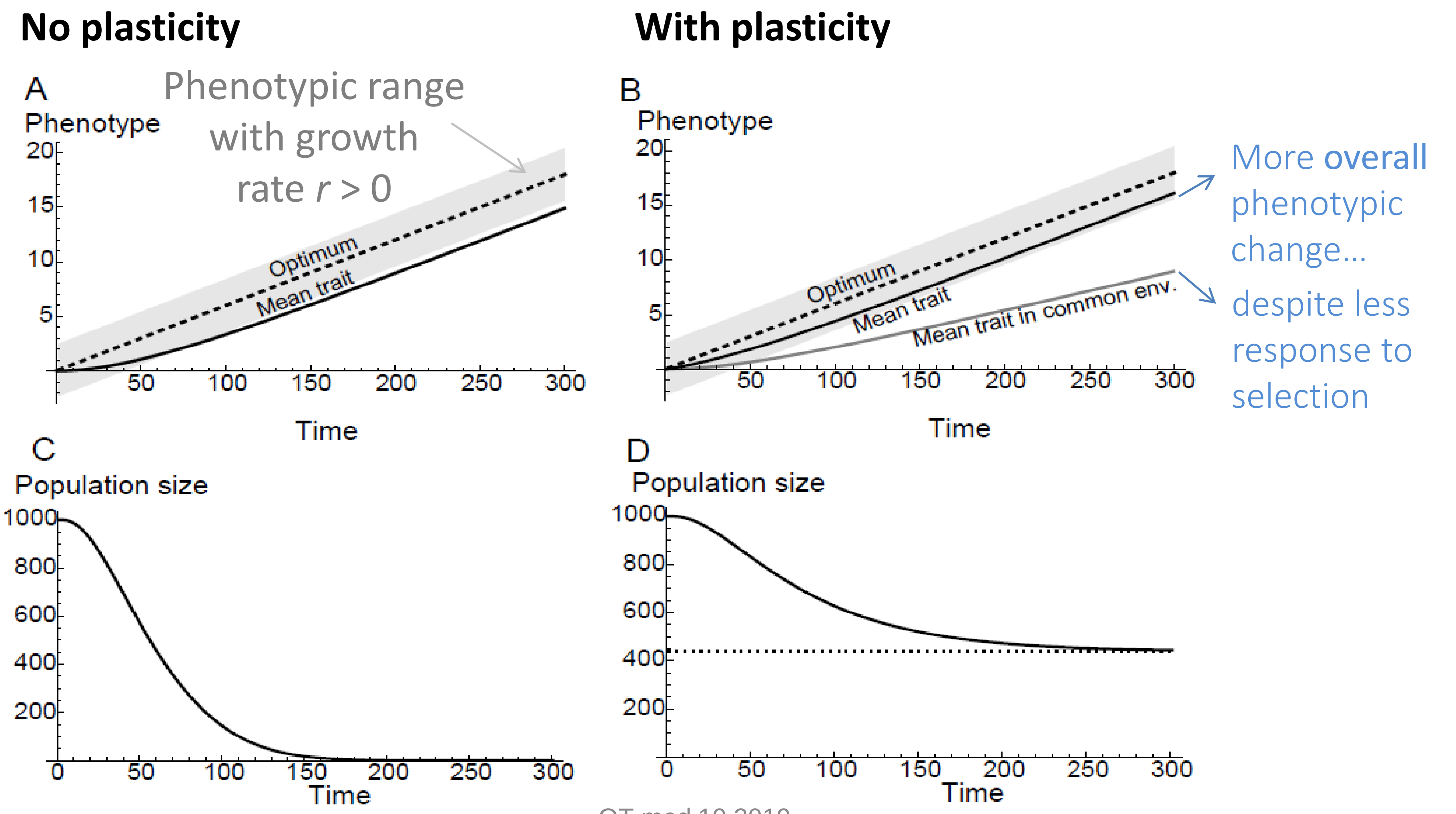


Fig from Chevin, Collins & Lefèvre, 2013 Funct. Ecol

Condition for persistence

- **Critical rate of environmental change** beyond which $r < 0$:

$$\eta_c = \sqrt{\frac{2r_{max}\gamma}{T}}\frac{V_a}{|B-b|}$$

Demography
- r_{max} intrinsic rate of increase of well-adapted population
- T generation time

Evolution
- γ strength of stabilizing selection
- V_a additive genetic variance
- B Environmental sensitivity of selection (rate of change in the optimum)

Plasticity
- b phenotypic plasticity

Lynch & Lande 1993
Chevin, Lande and Mace 2010, PLoS Biol

Meta-analysis across long-term studies

- Relative support for models with and without an optimum, fluctuating selection, …

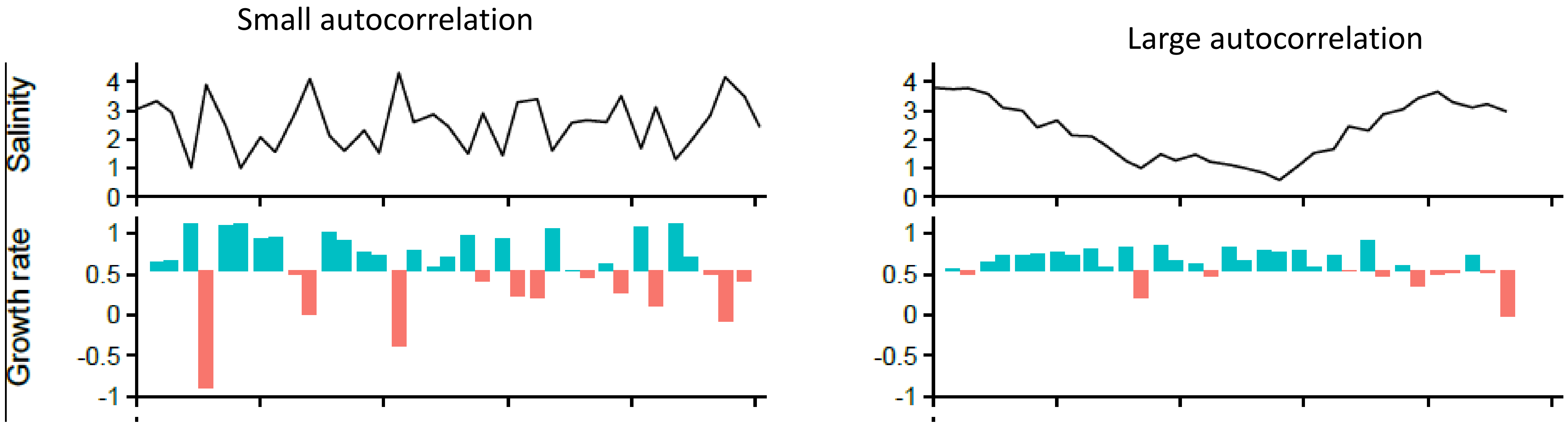
Taxon	NOSEL	EXPFIX	EXPIID	EXPAR1	OPTFIX	OPTIID	OPTAR1
Bird	0.027	0.024	0.229	0.191	0.055	0.202	0.272
Mammal	0.123	0	0.192	0.115	0.031	0.262	0.277
Total	0.047	0.019	0.221	0.175	0.05	0.215	0.273

Total support for fluctuating selection
89.3% for birds
84.6% for mammals

De Villemereuil et al (in prep)
1: Vehtari et al. 2017

Population dynamics consistent with optimum

- The influence of salinity on population growth can be estimated from times series of population size and salinity



Rescan et al, under review