Species interactions and coevolution

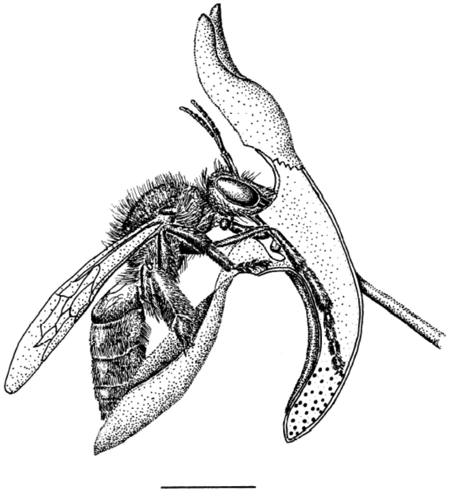
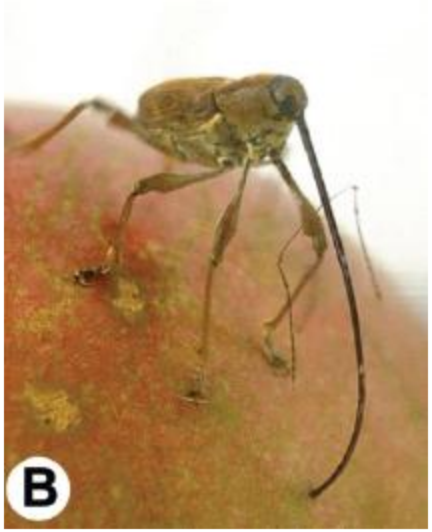


FIG. 1. *Rediviva neliana* visiting flower of *Diascia capsularis*. Scale line = 0.5 cm.



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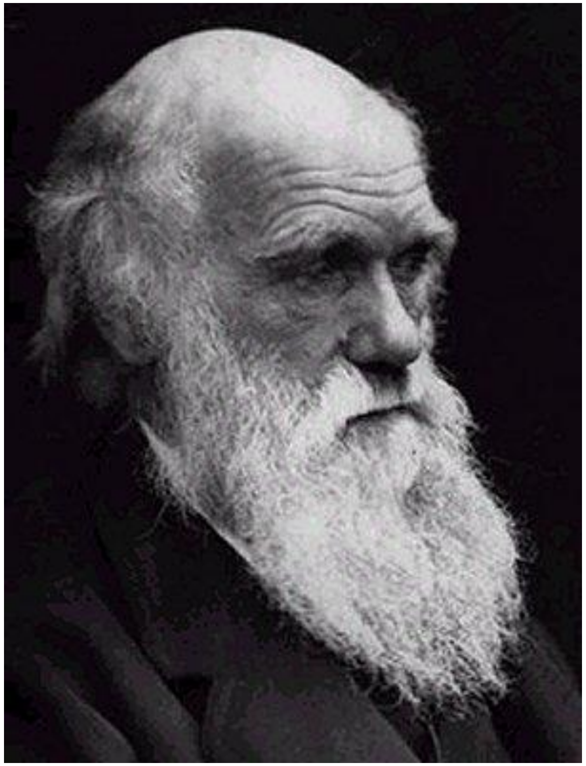
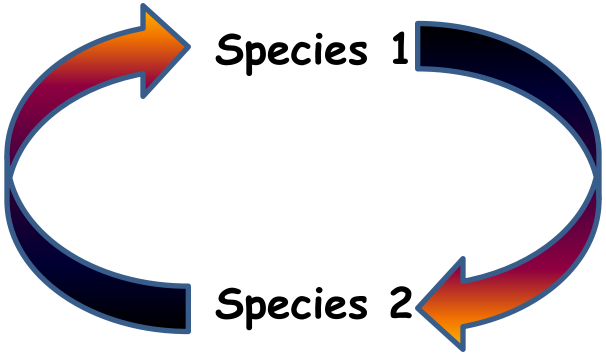
What is coevolution?

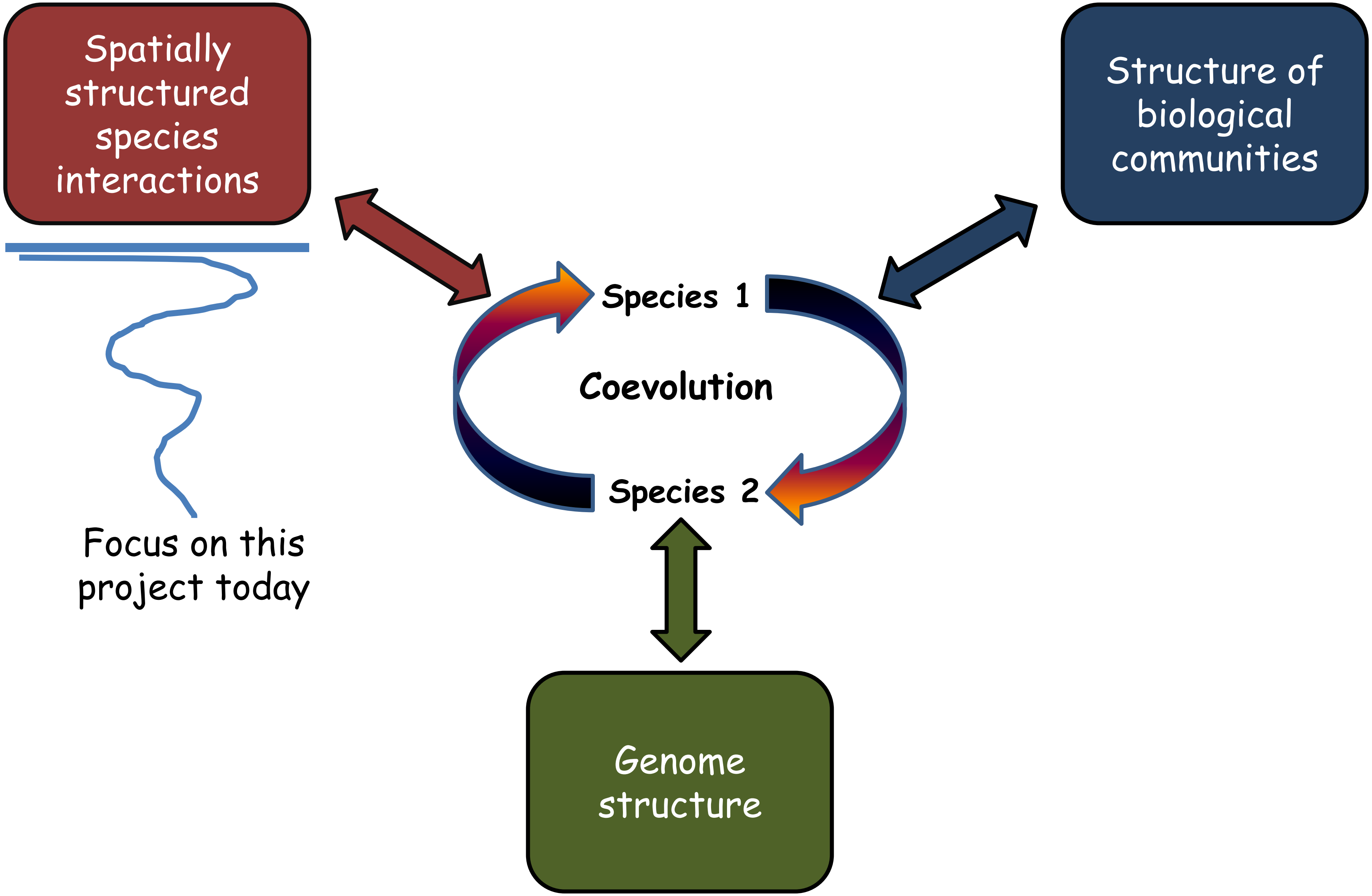




Coevolution: Reciprocal evolutionary change in interacting species (Janzen, 1980)

"Thus I can understand how a flower and a bee might slowly become, either simultaneously or one after the other, modified and adapted to each other in the most perfect manner, by the continued preservation of all the individuals which presented slight deviations of structure mutually favourable to each other."
— Charles Darwin, The Origin of Species

My lab uses mathematical models to study coevolution



Spatially structured species interactions

Focus on this project today

Structure of biological communities

Species 1

Coevolution

Species 2

Genome structure

An example of spatially structured coevolution: toxic newts and resistant snakes

Thamnophis sirtalis

+

Taricha

=

- **Predator-prey interaction**

Butch Brodie

Toxic newts

Taricha granulosa

- Newts contain Tetrodotoxin, a potent neurotoxin
- Some newts contain enough toxin to easily kill a human
- Toxin causes snakes to only “taste” the newts

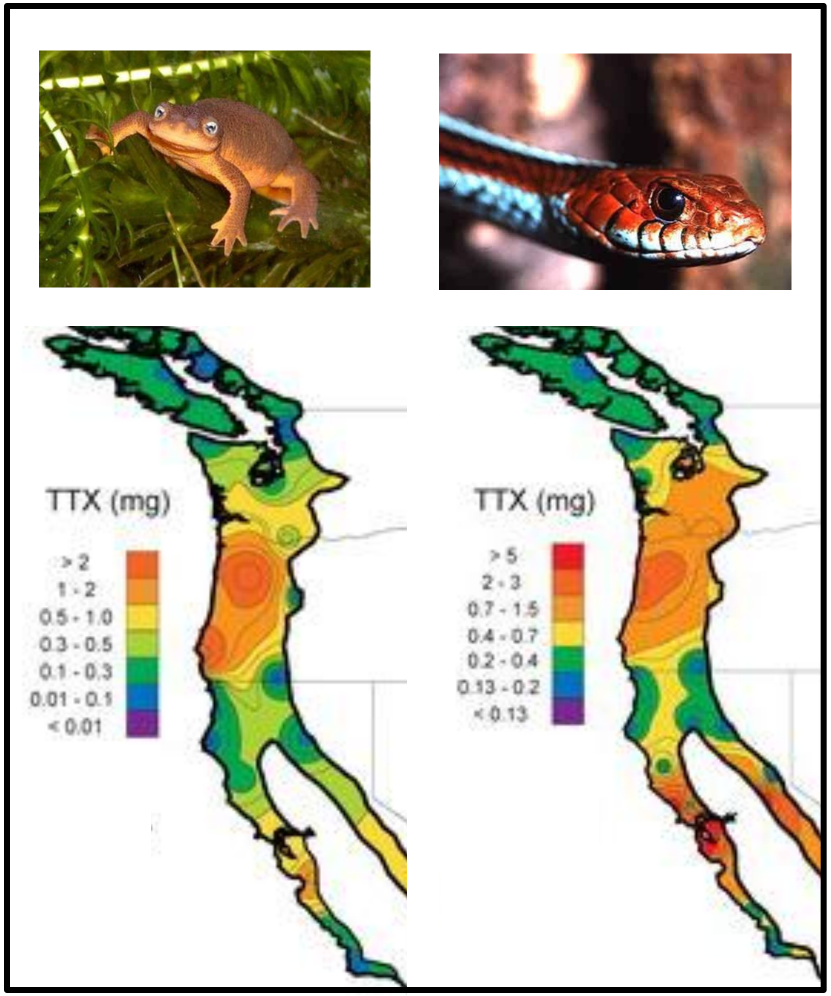
Resistant snakes

Thamnophis sirtalis

- Some snakes have evolved modified sodium channels
- These snakes are more resistant to tetrodotoxin
- Consequently, resistant snakes can eat toxic newts

Toxic newts and resistant garter snakes

(Hanifin et al. 2008, PLoS Biology)

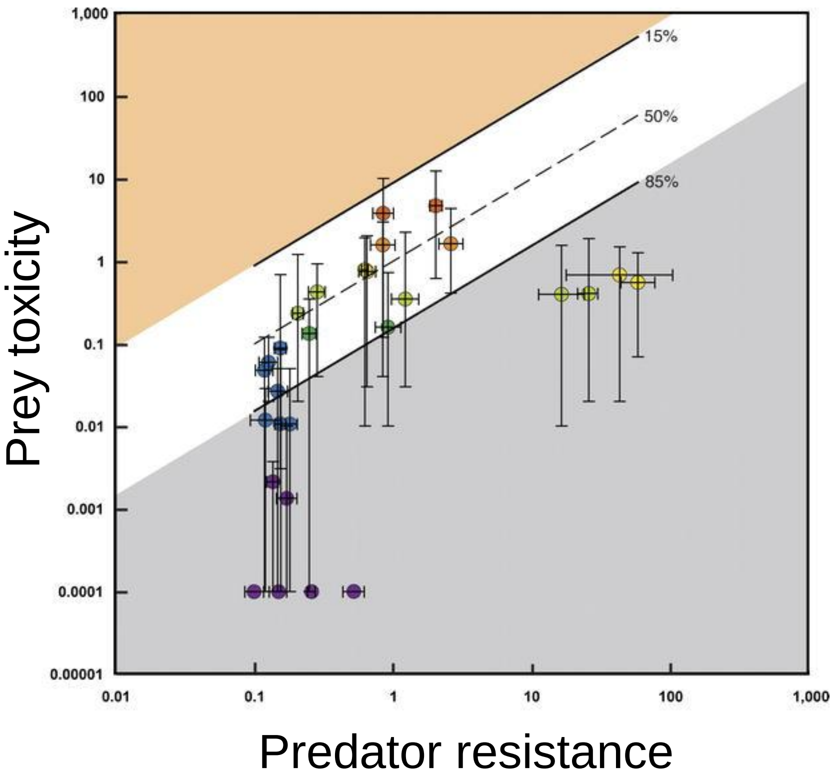


Observation #1:

Newt toxicity and snake resistance
Are spatially variable

Toxic newts and resistant garter snakes

(Hanifin et al. 2008, PLoS Biology)



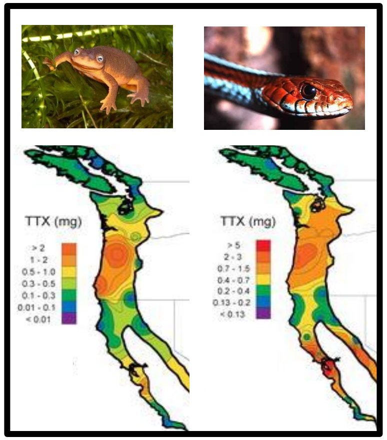
Observation #2:

Newt toxicity and snake resistance are positively correlated

Summarizing the Data

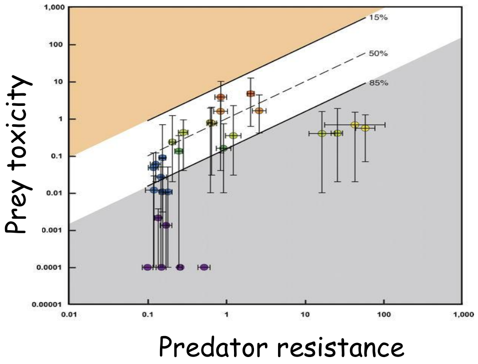
(Hanifin et al. 2008, PLoS Biology)

- Newt toxicity varies across space



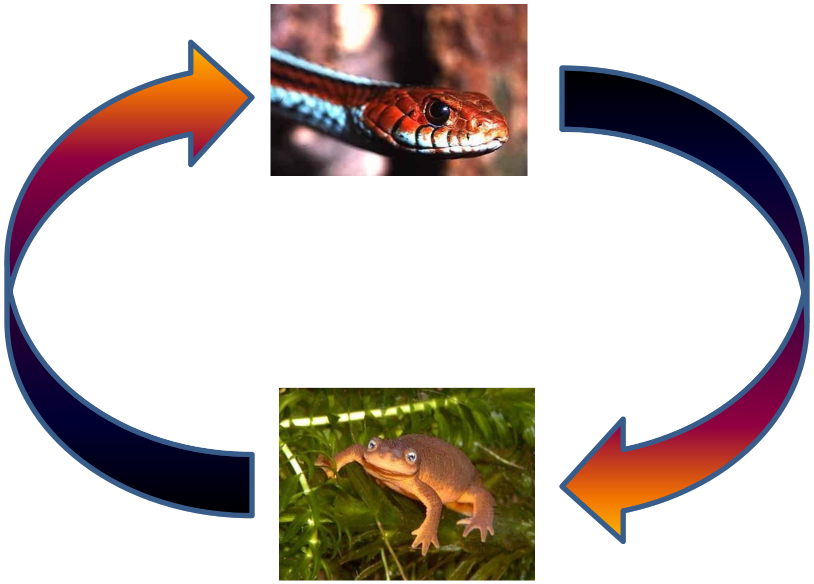
- Snake resistance varies across space

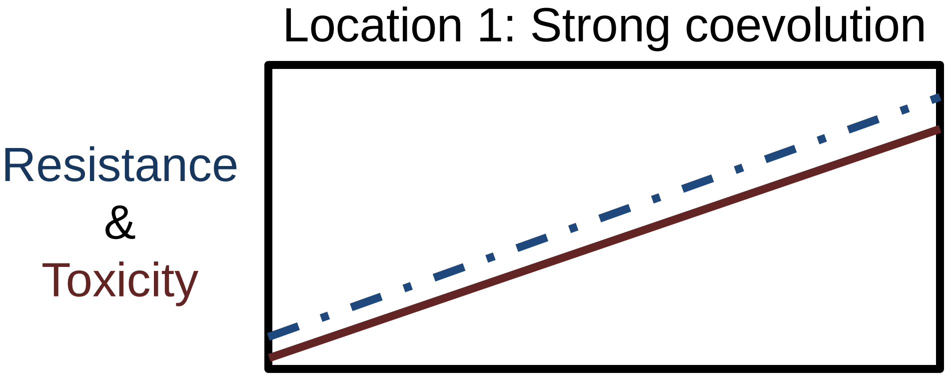
- Toxicity and resistance are positively correlated

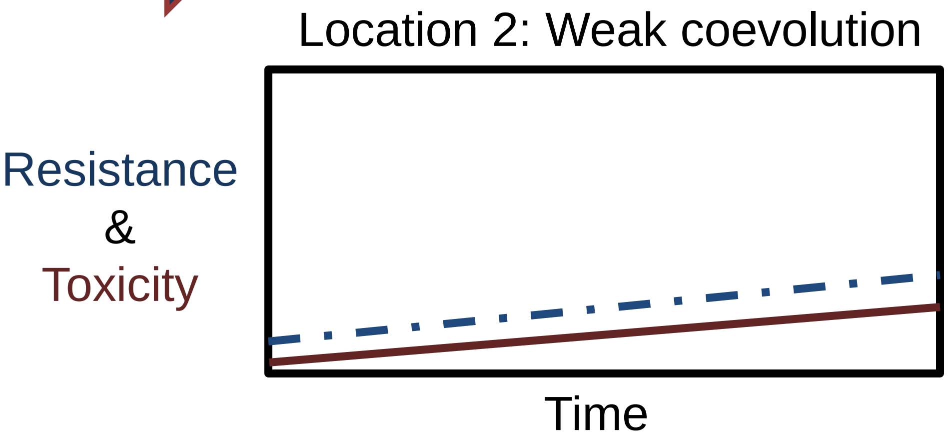


These observations have led to the development of a <u>coevolutionary hypothesis</u>

A coevolutionary hypothesis



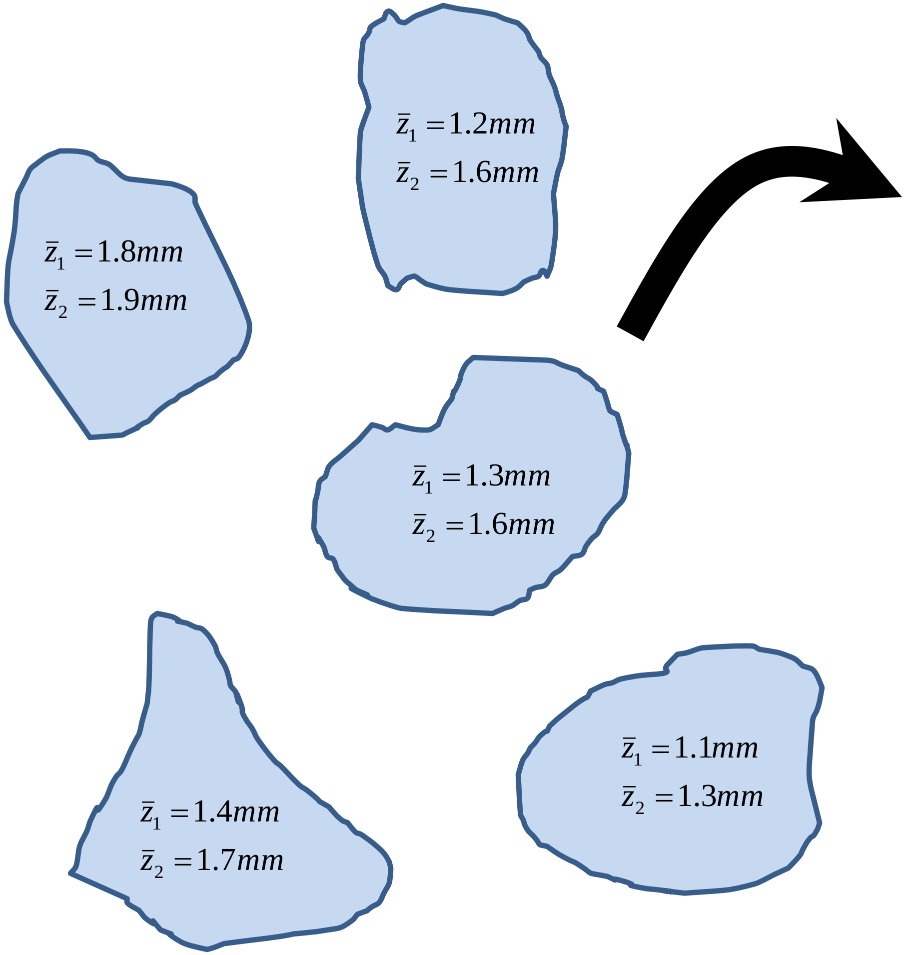

Location 1: Strong coevolution


Location 2: Weak coevolution

*** We can test this coevolutionary hypothesis using mathematical models ***

Developing an appropriate model

- The data consists of toxicity and resistance measured in <u>many populations</u>



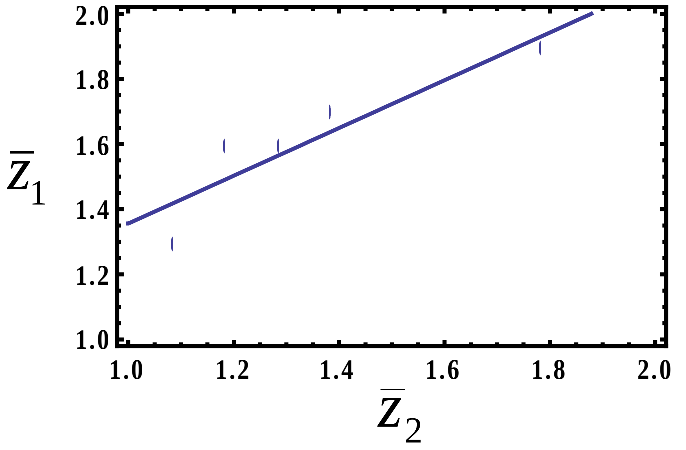
$\bar{z}_1 = 1.2mm$
$\bar{z}_2 = 1.6mm$

$\bar{z}_1 = 1.8mm$
$\bar{z}_2 = 1.9mm$

$\bar{z}_1 = 1.3mm$
$\bar{z}_2 = 1.6mm$

$\bar{z}_1 = 1.4mm$
$\bar{z}_2 = 1.7mm$

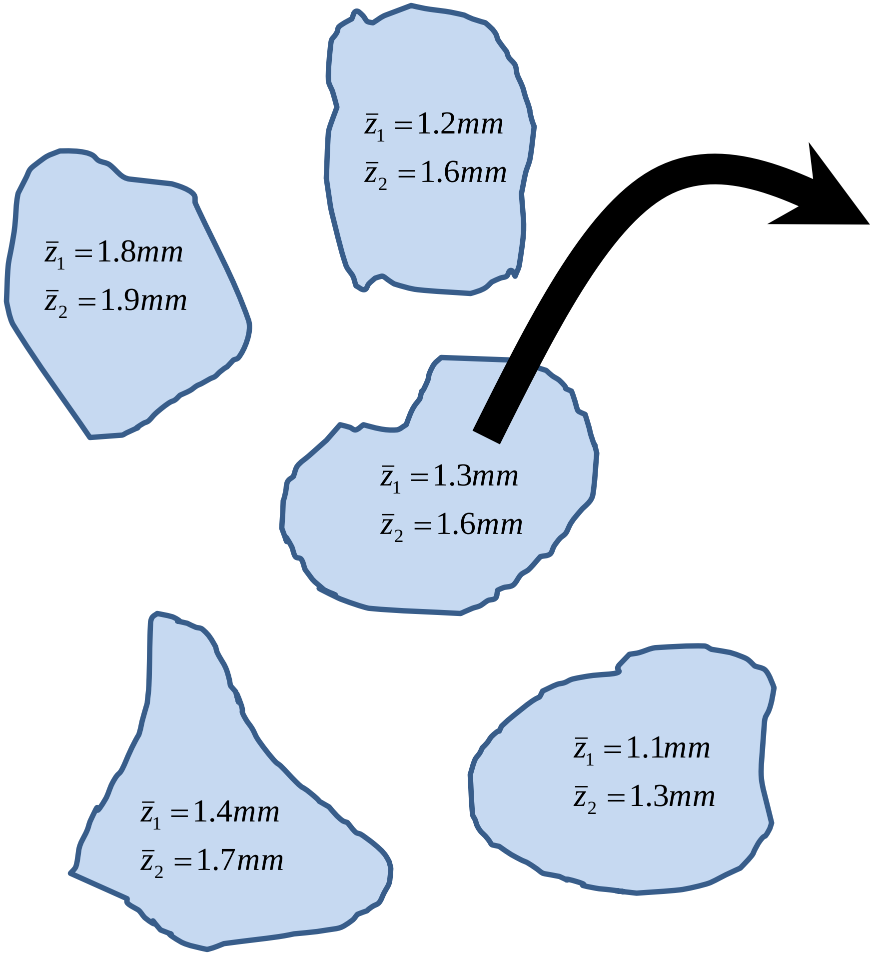
$\bar{z}_1 = 1.1mm$
$\bar{z}_2 = 1.3mm$



➔ Our model must predict mean trait values in replicate populations

Let's start by modeling one of these populations

If we assume that additive genetic variance is constant:



$$\Delta\bar{z}_1 = G_1\left(\frac{1}{\overline{W}_1}\frac{\partial\overline{W}_1}{\partial\bar{z}_1}\right)$$

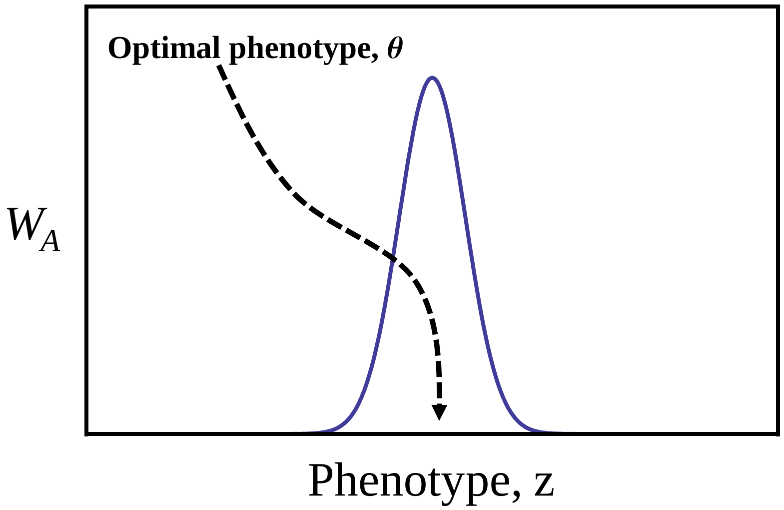
$$\Delta\bar{z}_2 = G_2\left(\frac{1}{\overline{W}_2}\frac{\partial\overline{W}_2}{\partial\bar{z}_2}\right)$$

➔ To predict (co)evolution we need to calculate mean fitness

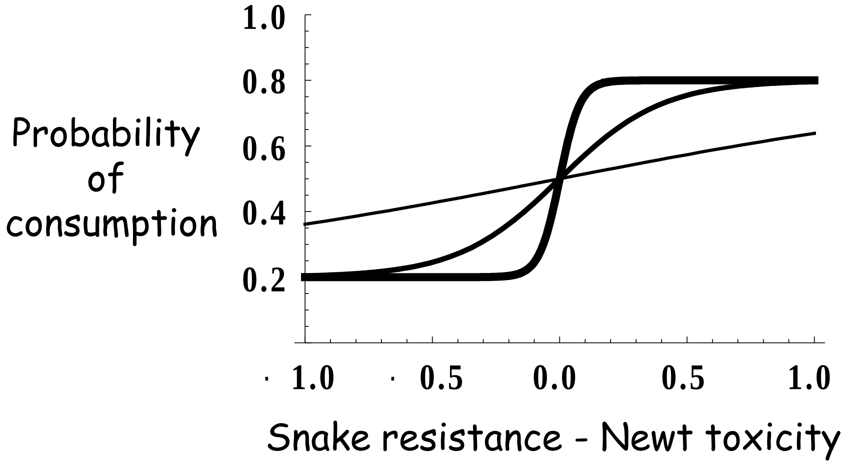
Defining individual fitness

$$W_T(z_i) = W_A(z_i)W_B(z_i, z_j)$$

Abiotic environment:



Species interactions:



Developing recursions for trait means

$$\overline{W}_1 = \int\int W_A(z_1)W_B(z_1,z_2)\phi(z_1)\phi(z_2)\}dz_1dz_2 \qquad \overline{W}_2 = \int\int W_A(z_2)W_B(z_2,z_1)\phi(z_1)\phi(z_2)\}dz_1dz_2$$

Assume weak selection

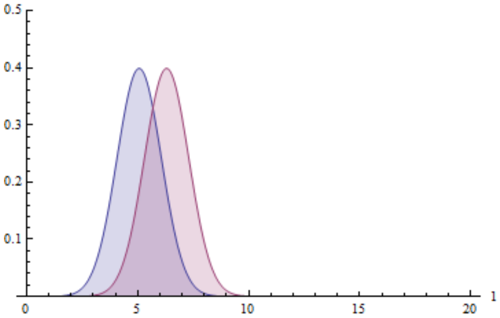
$$\Delta\bar{z}_i = G_i\left(\frac{1}{\overline{W}_i}\frac{\partial\overline{W}_i}{\partial\bar{z}_i}\right)$$

Incorporate genetic drift

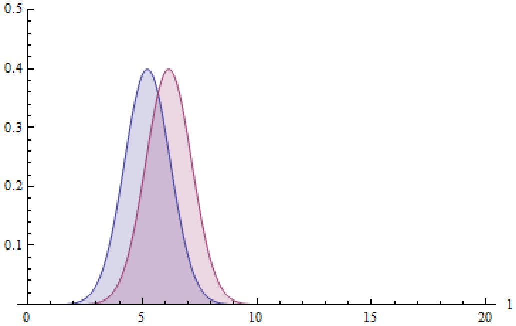
$$\Delta\bar{z}_i \approx G_i\left[\underbrace{2\gamma_i(\theta_i-\bar{z}_i)}_{\text{Abiotic selection}}+\underbrace{s_{\mathrm{D}i}}_{\text{Biotic selection}}\right]+\underbrace{\zeta_i}_{\text{Drift}}+O\left(\varepsilon^2\right)$$

Model predictictions for local coevolution

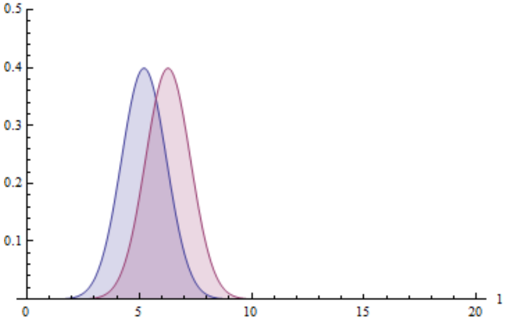
Weak selection on newts
Strong selection on snakes



Strong selection on newts
Weak selection on snakes



Strong selection on newts
Strong selection on snakes

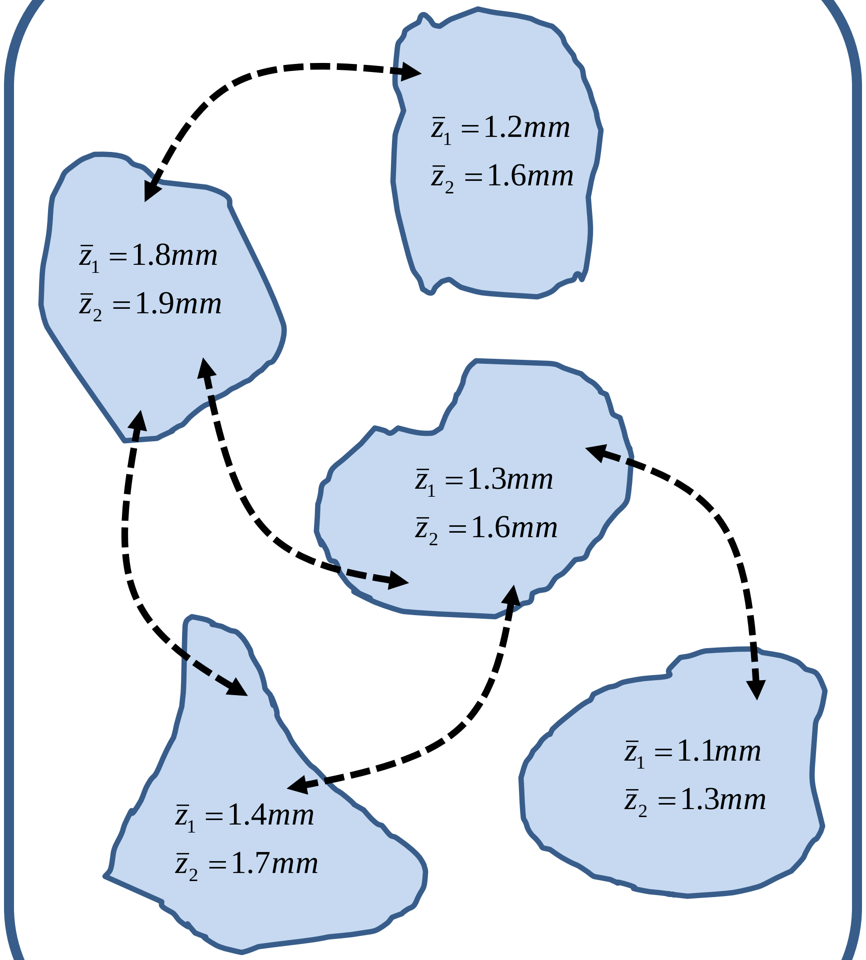


Toxicity and Resistance

→ Equilibrium trait values depend on the strength of biotic selection

But we need a model of MANY populations!

Empirical Data



Minimal model

- Multiple populations
- Gene flow (island model)

➔ Requires more equations

Adding multiple populations and gene flow

$$\Delta\bar{z}_{i,1} \approx G_i\left[2\gamma_i\left(\theta_{i,1}-\bar{z}_{i,1}\right)+2s_{\mathrm{M}i}\left(\bar{z}_{j,1}-\bar{z}_{i,1}\right)+s_{\mathrm{D}i}\right]+(1-m_i)\bar{z}_{i,1}+m_i\bar{Z}_i+\zeta_i+O\left(\varepsilon^2\right)$$

$$\Delta\bar{z}_{i,2} \approx G_i\left[2\gamma_i\left(\theta_{i,2}-\bar{z}_{i,2}\right)+2s_{\mathrm{M}i}\left(\bar{z}_{j,2}-\bar{z}_{i,2}\right)+s_{\mathrm{D}i}\right]+(1-m_i)\bar{z}_{i,2}+m_i\bar{Z}_i+\zeta_i+O\left(\varepsilon^2\right)$$

$$\vdots$$

$$\Delta\bar{z}_{i,n} \approx G_i\left[2\gamma_i\left(\theta_{i,n}-\bar{z}_{i,n}\right)+2s_{\mathrm{M}i}\left(\bar{z}_{j,n}-\bar{z}_{i,n}\right)+s_{\mathrm{D}i}\right]+(1-m_i)\bar{z}_{i,n}+m_i\bar{Z}_i+\zeta_i+O\left(\varepsilon^2\right)$$

- **In principle, we could then just solve this system of 2n equations**

- **In practice, this is impossible**

➔ This difficulty can be overcome by making a change of variables that reveals a tractable approximation

What does our final approximation predict?

At equilibrium and assuming weak selection:

The spatial variability in toxicity or resistance is:

$$\boxed{\hat{\sigma}^2_{\bar{z}_i} = \frac{G_i}{2N_i\left(m_i + 2\gamma_i G_i\right)}}$$

The correlation between toxicity and resistance is:

$$\boxed{\hat{\rho} \approx 0 + O(\varepsilon^2)}$$

What is missing from these equations?

What does this tell us?

Does this provide support for the coevolutionary hypothesis?