Identifying conversion efficiency as a key mechanism underlying foodwebs adaptive evolution : A step forward, or backward ?

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work in collaboration with

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IECL & Inria Nancy

Mathematical Models in Evolutionary Biology
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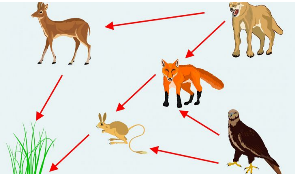
Our context and objectives



- Modelling by PDMP (Piecewise Deterministic Markov Processes) :
  - random mutations occur at dicreet times
  - deterministic dynamics between mutations

- Our goal :
  - understanding the emergence of foodweb structures
  - identifying the fondamental mechanisms
  - remove the artificial contraints of the extand models (for example forcing the individuals to feed on smaller individuals)

The general model

Between 2 mutation times, the populations dynamics are given by

$$\frac{\dot{N}_i}{N_i} = \underbrace{\sum_{j=0}^{n} \lambda_{ij}\,\gamma_{ij}\,N_j}_{\text{reprodution}} - \underbrace{\sum_{j=1}^{n} \alpha_{ij}\,N_j - \sum_{j=1}^{n} \gamma_{ji}\,N_j - m_i}_{\text{competition, predation and natural death}} \quad , \qquad i = 1, \ldots, n$$

with

- γ_{ij} : **consumption rate** of prey j by predator i
- λ_{ij} : **production efficiency** of individuals of species i by consumption of one individual of species j (biomass conversion + reproduction) ;
- m_i : **mortality rate** of species i.
- α_{ij} : direct **competition rate** between species i and j

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The resource dynamics is given by a **logistic equation**

$$\frac{\dot{N}_0}{N_0} = r_g - k_0\,N_0 - \sum_{i=1}^{n} \gamma_{i0}\,N_i$$

or a chemostat equation

$$\dot{N}_0 = I - e\,N_0 - \sum_{i=1}^{n} \gamma_{i0}\,N_i\,N_0 + \nu \sum_{i=0}^{n} N_i \left(m_i + \sum_{j=1}^{n} \alpha_{ij}\,N_j + \sum_{j=1}^{i-1} (1 - \lambda_{ij})\,\gamma_{ij}\,N_j \right) .$$

Traits submitted to mutations

Models can be structure in :

- the linear scale : species are characterized by
  r : individual mass

- the log-scale : species are characterized by
  $z = log(r/r_0)$: log-mass

Traits submitted to mutations

Models can be structure in :

- the linear scale : species are characterized by
  r : individual mass
  d : predation distance (the mass of the favourite prey is $r - d$)
  s : specialization
- the log-scale : species are characterized by
  $z = log(r/r_0)$: log-mass
  μ : predation proportion (the mass of the favourite prey is $e^{-\mu}\, r$)
  σ : specialization

where one or several traits are submitted to rare mutations

Models of the literature

	Evolving phenotypes	Boundaries	Ordered predation	Cannibalism	Mutations size
LL05	r	$0 < r$	yes	no	large
BLLD11	z	$z \in \mathbb{R}$	no	yes	small
AD13	r d s	$0 < r$ $0 < d$ $0 < s$	yes	no	large
ARRDG15, AD16 & BDA17	z μ σ	$z \in \mathbb{R}$ $\mu \in [0.5, 3]$ $\sigma \in [0.5, 1.5]$	no	yes	large
RBB16	z, abstract trait	$z \in \mathbb{R}$	no	no	large

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BLLD11	Brännström, Loeuille, Loreau, Dieckmann 2011
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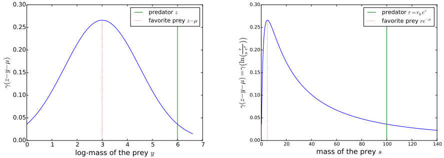
Model by Brännström, Loeuille, Loreau, Dieckmann with evolution of μ

Species i is characterized by its log-mass $z_i = \ln(\frac{r_i}{r_0})$ and its predation proportion μ_i.

- predation rate of z_i on z_j

$$\gamma_{ij} = \gamma(z_i - z_j - \mu_i) = \frac{M_\gamma}{\sqrt{2\pi}\,\sigma_\gamma}\, e^{-\frac{(z_i - z_j - \mu_i)^2}{2\,\sigma_\gamma^2}}$$



with the production efficiency

$$\lambda_{ij} = \lambda(z_i, z_j) = \lambda_0\, e^{z_j - z_i} = \lambda_0\, \frac{r_j}{r_i}$$

- resource consumption : predation + conversion of individual with log-mass 0.
- competition rate between z_i and z_j

$$\alpha_{ij} = \alpha(z_i - z_j) = \frac{M_c}{\sqrt{2\pi}\,\sigma_c}\, e^{-\frac{(z_i - z_j)^2}{2\,\sigma_c^2}}$$

- death rate of z_i at rate $m_i = m(z_i) = d_0\, e^{-q\,z_i}$ $(q = 0.25)$

+ logistic equation for the resource dynamics.

Dynamics

Between 2 mutations times, the density N_i of the species (z_i, μ_i) is given by

$$\frac{\dot{N}_i}{N_i} = \underbrace{\sum_{j=0}^{n} \lambda_{ij}\, \gamma_{ij}\, N_j}_{\text{reproduction}} - \underbrace{\sum_{j=1}^{n} \alpha_{ij}\, N_j}_{\text{competition}} - \underbrace{\sum_{j=1}^{n} \gamma_{ij}\, N_j}_{\text{pred. death}} - \underbrace{m_i}_{\text{death}}$$

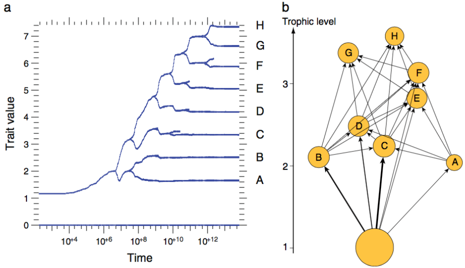
At a mutation time : a species (z_i, μ_i) give birth to a new species (y, η) with

$$y \sim \mathcal{N}(z_i, \sigma_z^2)\,, \qquad \eta \sim \mathcal{N}(\mu_i, \sigma_\mu^2)$$

Adaptive dynamics context :

- rare mutations : the foodweb reaches its stationnary state before a mutation occurence
- small mutations : σ_z and σ_μ are small

- **Model of Brännström (without evolution of μ, i.e. $\sigma_\mu = 0$) with $\sigma_z = 0.01$**



Branching events under good assumptions (the range of predation is sufficiently large,...)

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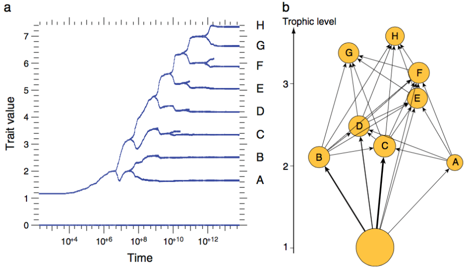
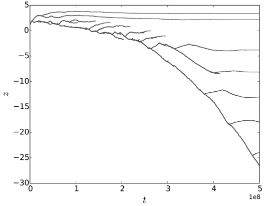


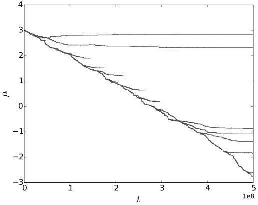
Branching events under good assumptions (the range of predation is sufficiently large,...)

- **Model of Brännström with evolution of μ with $\sigma_z = 0.01$ and $\sigma_\mu = 0.001$**

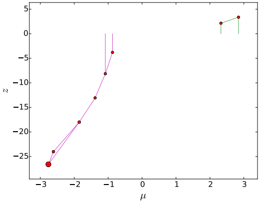
Evolution of z



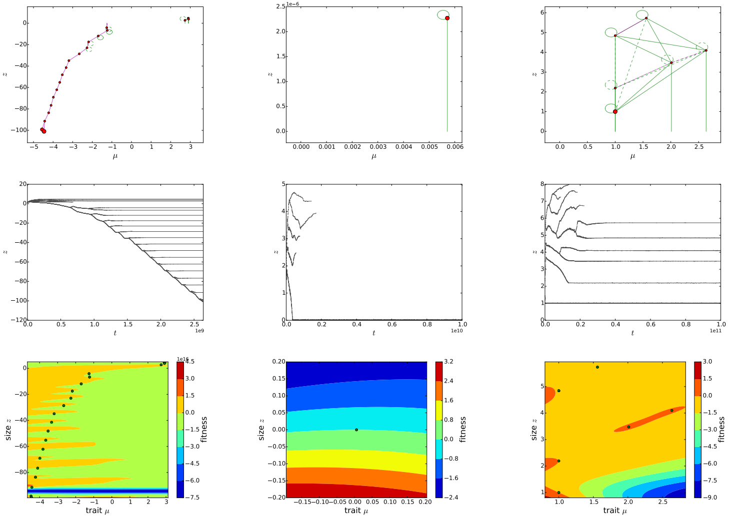
Evolution of μ



Food web



Model of Brännström with evolution of μ and different constraints



without positivity constaints

with positivity constaints

with constraints ≥ 1

Back to the model of BLLD with evolution of μ

Species i is characterized by its log-mass $z_i = \ln(\frac{r_i}{r_0})$ and its predation proportion μ_i.

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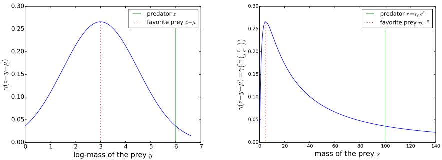

with the production efficiency

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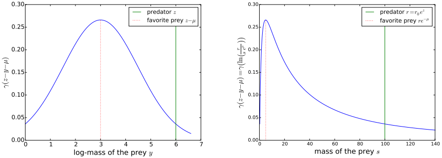

with the production efficiency

$$\lambda_{ij} = \lambda(z_i, z_j) = \xi(z_i - z_j)\, e^{z_j - z_i}$$

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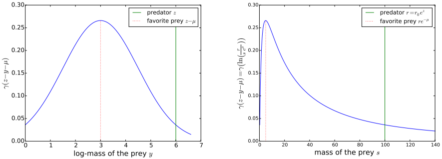

with the production efficiency

$$\lambda_{ij} = \lambda(z_i, z_j) = \frac{e^{z_j}\, \xi(z - y)}{e^{z_i}} = \frac{\text{units of biomass created by predation of } z_j}{\text{biomass of the predator } z_i}$$

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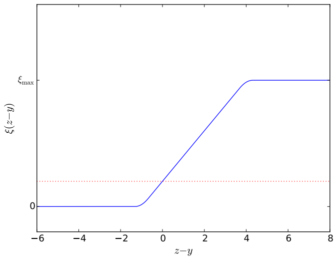
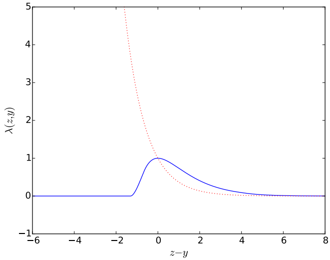
One choice of ξ for the study in 0

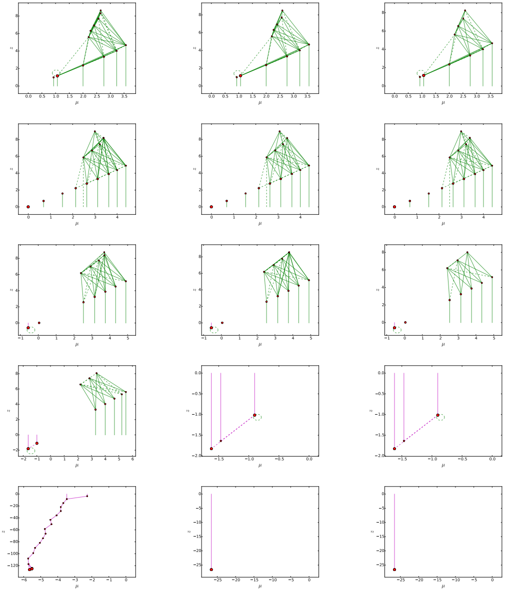
production efficiency

$$\lambda_{ij} = \lambda(z_i, z_j) = \frac{e^y\, \xi(z-y)}{e^z} = \frac{\text{units of biomass created by predation of } z_j}{\text{biomasse of the predator } z_i}$$





	$\sigma_z > \sigma_\mu$	$\sigma_z = \sigma_\mu$	$\sigma_z < \sigma_\mu$
$\xi'(0)/\xi(0) = 3$			
$\xi'(0)/\xi(0) = 1.2$			
$\xi'(0)/\xi(0) = 1$			
$\xi'(0)/\xi(0) = 0.8$			
$\xi'(0)/\xi(0) = 0.1$			



Invasion fitness

The invasion fitness of a mutant population (y, η) is

$$f(y,\eta) = \underbrace{\sum_{i=0}^{n} \lambda(y,z_i)\,\gamma(y - z_i - \eta)\,N_i^*}_{\text{reproduction by predation}} - \underbrace{\sum_{i=1}^{n} \gamma(z_i - y - \mu_i)\,N_i^*}_{\text{death by predation}}$$

$$- \underbrace{\sum_{i=1}^{n} \alpha(z_i - y)\,N_i^*}_{\text{competition}} - \underbrace{m(y)}_{\text{natural death}}$$

The mutant population can invade if and only if $f(y, \eta) > 0$.
(Remark : for all i, $f(z_i, \mu_i) = 0$).

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$$\partial_y f(y,\eta) = \sum_{i=0}^{n} \left[\frac{\xi'(y-z_i)}{\xi(y-z_i)} - 1 - \frac{y-z_i-\eta}{\sigma_\gamma^2} \right] \lambda(y,z_i)\,\gamma(y-z_i-\eta)\,N_i^*$$

$$- \sum_{i=1}^{n} \frac{z_i-y-\mu_i}{\sigma_\gamma^2}\,\gamma(z_i-y-\mu_i)\,N_i^* - \sum_{i=1}^{n} \alpha'(z_i-y)\,N_i^* - m'(y)$$

and

$$\partial_\eta f(y,\eta) = \sum_{i=0}^{n} \frac{y-z_i-\eta}{\sigma_\gamma^2}\,\lambda(y,z_i)\,\gamma(y-z_i-\eta)\,N_i^* \,.$$

Study for the 'resource-like species' $(0,0)$

We assume that the 'resource-like species' is associated to the index $i = 1$.

$$\partial_y f(0,0) = \sum_{i=0}^{n} \left[\frac{\xi'(-z_i)}{\xi(-z_i)} - 1 + \frac{z_i}{\sigma_\gamma^2} \right] \lambda(0, z_i)\, \gamma(-z_i)\, N_i^*$$

$$- \sum_{i=1}^{n} \frac{z_i - \mu_i}{\sigma_\gamma^2}\, \gamma(z_i - \mu_i)\, N_i^* - \sum_{i=1}^{n} \alpha'(z_i)\, N_i^* - m'(0)$$

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- the 'resource-like species' is far from the rest of the foodweb : for $i \geq 2$, $\gamma(-z_i)$ and $\alpha'(-z_i)$ are small
- $\alpha'(0) = 0$

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- the 'resource-like species' is far from the rest of the foodweb :
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  Or species preferentially consume others species and $\gamma(z_i - \mu_i)$ is small

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- Either species preferentially consume the resource and $z_i - \mu_i \approx 0$
  Or species preferentially consume others species and $\gamma(z_i - \mu_i)$ is small

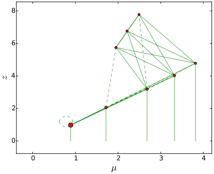
$$\partial_y f(0,0) \approx \left[\frac{\xi'(0)}{\xi(0)} - 1 \right] \lambda(0,0) \gamma(0) (N_0^* + N_1^*) - m'(0)$$

(In our simulations : $m'(0) = -0.025$ and $\lambda(0,0)\gamma(0)(N_0^* + N_1^*) > 25$)

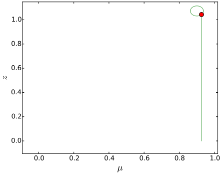
Importance of the relative speed of evolution : Ito Dieckmann theory

For $\xi'(0)/\xi(0) = 4$:

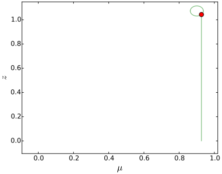
$0.01 = \sigma_z > \sigma_\mu = 0.001$
faster evolution in z than μ



$\sigma_z = \sigma_\mu = 0.01$
equivalent speed



$0.001 = \sigma_z < \sigma_\mu = 0.01$
faster evolution in μ than z



Importance of the relative speed of evolution : Ito Dieckmann theory

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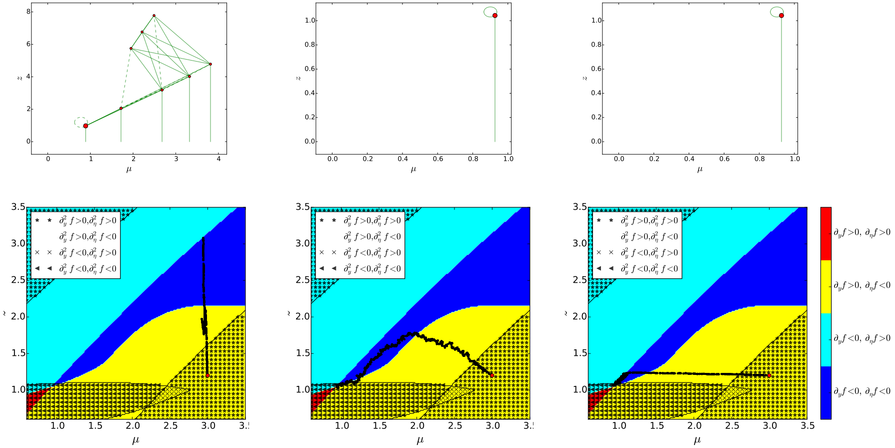
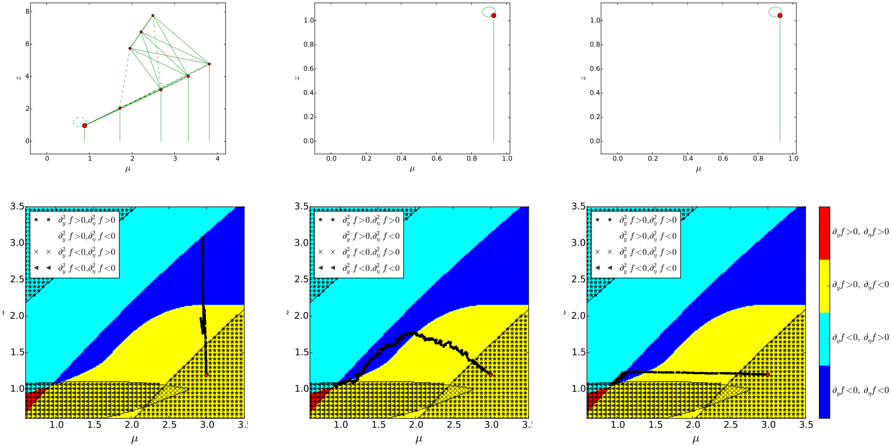
$0.01 = \sigma_z > \sigma_\mu = 0.001$ faster evolution in z than μ	$\sigma_z = \sigma_\mu = 0.01$ equivalent speed	$0.001 = \sigma_z < \sigma_\mu = 0.01$ faster evolution in μ than z



Importance of the relative speed of evolution : Ito Dieckmann theory

For $\xi'(0)/\xi(0) = 4$:

$0.01 = \sigma_z > \sigma_\mu = 0.001$	$\sigma_z = \sigma_\mu = 0.01$	$0.001 = \sigma_z < \sigma_\mu = 0.01$
faster evolution in z than μ	equivalent speed	faster evolution in μ than z

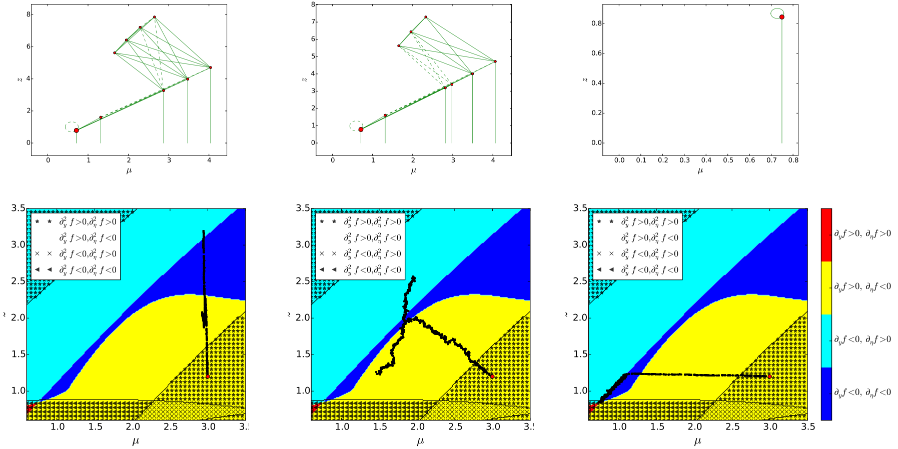


 $= \{\partial_z f = 0\}$  $= \{\partial_\mu f = 0\}$

Importance of the relative speed of evolution : Ito Dieckmann theory

For $\xi'(0)/\xi(0) = 5.5$:

$0.01 = \sigma_z > \sigma_\mu = 0.001$ faster evolution in z than μ	$\sigma_z = \sigma_\mu = 0.01$ equivalent speed	$0.001 = \sigma_z < \sigma_\mu = 0.01$ faster evolution in μ than z



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Conclusion

- we obtained satisfactory foodweb structures without artificial constraint
- the shape of our tradeoff (biomass conversion efficiency) given satisfying structures is consistent with the biological litterature

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- foodwebs structures are very sensitive to assumptions

Conclusion

- we obtained satisfactory foodweb structures without artificial constraint
- the shape of our tradeoff (biomass conversion efficiency) given satisfying structures is consistent with the biological litterature

- foodwebs structures are very sensitive to assumptions

- What can we learn from these models ?