

Evolutionary dynamics of resource–consumer population: Nonlocal PDEs approach

Jimmy GARNIER

with E. Faou¹, S. Ibanez² and L. Ledru²

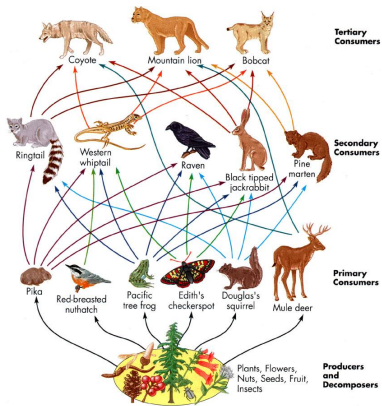
¹INRIA Bretagne Atlantique, IRMAR, France

²Université Savoie Mont-Blanc, LECA, France



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Food web and resource–consumer interactions



Food web describes the feeding connections (who eats whom) in an ecological community.

Hypothesis: The food web results in the **interaction** of species which are submitted to **foraging** and **Drawinian evolution**.

Objective: Understand the effect of **adaptive foraging** on evolution of resource–consumer system.

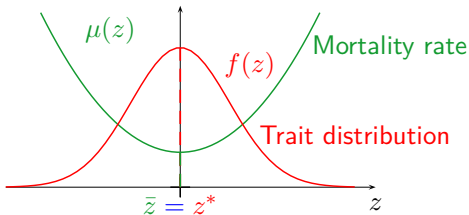
Adaptation and trait distribution

Adaptation: evolutionary process whereby an organism becomes better able to live in its habitat.

Hyp: Adaptation is driven by **mutation** and **selection**.

Adaptive trait z quantify the adaptedness of an organism to its environment: mortality rate $\mu(z)$, interaction forces $\Delta(z, y)$ between consumers z and resources y , carrying capacity of resources $K(y)$.

Population density $f(t, z)$ describes the frequency of adaptive trait z inside the population with **mean trait** z^* .

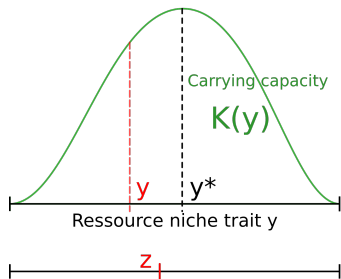


Adaptation occurs when **mean trait** equal **optimal trait**:
 $z^* = \bar{z} = \operatorname{argmin}_{z \in \mathbb{R}} \mu(z)$

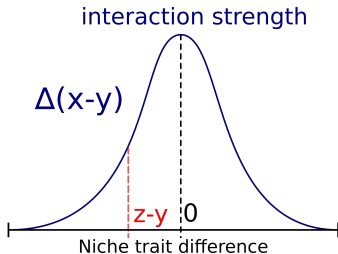
Selection at a community scale

Niche position and interaction strength

Species scale



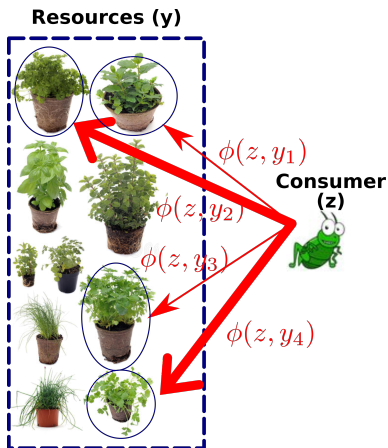
Community scale



- ▶ Adaptation acts at a species scale characterized by its trait.
- ▶ Interactions between species create evolution trade off at the community scale.

⇒ **Selection at the community scale.**

Adaptive foraging



Foraging: Consumers spread their foraging efforts $\phi(z, y)$ over the resources.

Effective interaction between consumer and resource
 = interaction strength * foraging effort
 = $\Delta(z, y)\phi(z, y)$

Adaptive foraging: Consumers adapt their foraging effort on the abundance of resources.

Evolutionary consequences of adaptative foraging

(Heckmann et al., 2012) Adaptive foraging tends to stabilize community.

(May,1973) Comunity stability is closely linked to Diversity.

Objectives:

In the context of evolution, what is the effect of different foraging strategies on the evolution of community and their emergence.

Q? What is the effect of those strategies on community diversity?

Q? What is the effect of those strategies on community stability and productivity?

A simple evolution model of consumer with trait constant resources : stochastic approach



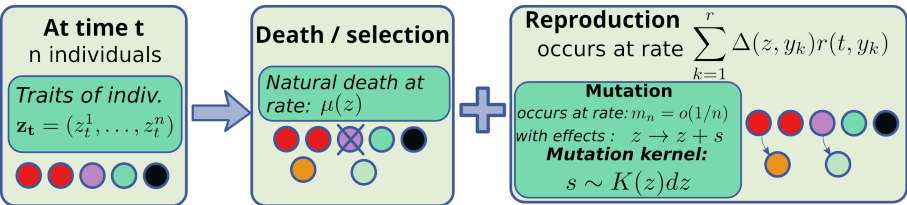
An Individual Based Model of consumers

The model describes interaction between consumers (z_i) that evolve under mutation and selection and resources with fixed trait (y_k) (Champagnat et al. , 2013).

- ▶ **At time $t = 0$:** initial distribution
- ▶ **Resources** with traits (y_1, \dots, y_r) and distribution $r(t, y_k)$:

$$\partial_t r^n(t, y_k) = r^n(t, y_k) (g - r^n(t, y_k)) - r^n(t, y_k) \left(\frac{1}{n} \sum_{i=1}^{N(t)} \Delta(z_t^i, y_k) \right)$$

- ▶ Each **consumer** has **2 independent exponential clocks**;



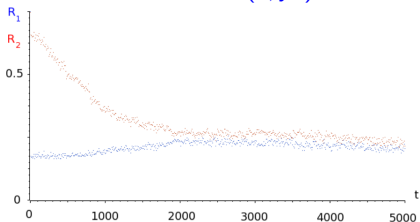
Goal: Describe the trait distribution of consumer $\nu_t^n = \frac{1}{n} \sum_{i=1}^{N(t)} \delta_{z_i}$.

An asexual Individual Based Model

Numerical simulation with $n = 300$ individuals (*Champagnat et al. , 2013*)

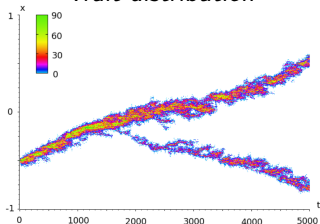
2 Resources

Concentration $r^n(t, y_k)$



Consumers

Trait distribution



Observation: The trait distribution of consumers and the concentrations of resources converge to an equilibrium.

Main objective: Describe the equilibrium of trait distribution and concentrations.

From stochastic to deterministic model

(Champagnat et al. , 2013) Under the assumption $m_n = o(1/n)$ then for any $N > 0$ and (z_1, \dots, z_N) , the sequence of processes $(\langle \nu_t^n, \sum_{i=1}^N \delta_{z_i} \rangle, r^n(t, y_k))$ converges in probability to a deterministic continuous couple $(c(t, z_i), r(t, y_k))$ solution of the following system of ordinary differential equations

$$\begin{aligned} \partial_t c(t, z_i) &= c(t, z_i) \left(-\mu(z_i) + \sum_{k=1}^r \Delta(z_i, y_k) r(t, y_k) \right) \\ \partial_t r(t, y_k) &= r(t, y_k) \left(g - r(t, y_k) - \sum_{j=1}^N \Delta(z_j, y_k) u(t, z_j) \right) \end{aligned}$$

Goal: Describe the equilibrium of the deterministic model.

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Goal: Describe the equilibrium of the deterministic model.

For any $N > 0$ and traits $(z_1, \dots, z_N), (y_1, \dots, y_r)$, there exists a unique weakly stable equilibrium of the system.

From stochastic to deterministic model

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Main issue: At this scale no mutation occurs : $\mathbb{P}(T_{mut}^n < T) \rightarrow 0$ as $n \rightarrow \infty$ for all $T > 0$ -> **NO EVOLUTION**

Evolution of consumer and resources : Nonlocal PDE approach



A quantitative model of evolution

Resources dynamics model: resources density $r(t, y)$ described at time (t) with trait (y) by

$$\partial_t r = r \left(\left(g - \frac{\rho(t)}{K(y)} \right) - \int C(t, z, y) c(t, z) dz \right) + D_r \partial_y^2 r(t, y)$$

Mutations: describes by the diffusion operator with D_r corresponds to the mean effects of mutations.

Selection at resource scale: Trait y affects carrying capacity K ,

$$K(y) := \frac{e^{-\frac{y^2}{2\sigma_K^2}}}{\sqrt{2\pi\sigma_K^2}} \quad \text{with} \quad \sigma_K^2 \quad \text{mean size of the resource niche.}$$

Density-dependence: Mortality increases with the total quantity of resources

$$\rho(t) = \int r(t, y) dy$$

A quantitative model of evolution

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Selection at system scale: $C(t, z, y)$ potential consumption of resource y by a consumer of trait z .

A quantitative model of evolution

Consumer dynamics model: consumer density $c(t, z)$ described at time (t) with trait (z) by

$$\partial_t c = c \left(-\mu(z) + \int C(t, z, y) r(t, y) dy \right) + D_c \partial_y^2 r(t, y)$$

Mutations: describes by the diffusion operator with D_c corresponds to the mean effects of mutations.

Selection at consumer scale: Trait z affects mortality μ ,

$$\mu(z) := d + m(z) \text{ with } m \text{ increasing with } |z| \text{ and } \alpha = m''(0) > 0.$$

Selection at system scale: $C(t, z, y)$ potential consumption of resource y by a consumer $c(t, z)$ of trait z .

Consumption and foraging strategies

Consumption of resource $r(t, y)$ by the consumer z depends on the effective interaction between consumers and resources $\Delta(z, y)\phi(t, z, y)$ and the searching time h .

$$C(t, z, y) = \frac{\Delta(z, y)\phi(t, z, y)}{1 + h \int \Delta(z, y)\phi(t, z, y)r(t, y)dy}$$

Foraging strategies:



Mower consumers: random foraging, $\phi_{RF}(t, z, y) = \frac{r(t, y)}{\int r(t, y)dy}$.

Consumption and foraging strategies

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Smart consumers: adaptive foraging. Efforts ϕ_{AF} evolves in time depending on consumer trait z .

$$\begin{aligned} \partial_t \phi_{AF}(t, z, y) = & v_\phi C(t, z) \left(\int_{\mathbb{R}} r(t, y) \phi_{AF}(t, z, y') [u(t, z, y) - u(t, z, y')]_+ dy' \right. \\ & \left. - \int_{\mathbb{R}} r(t, y') \phi_{AF}(t, z, y) [u(t, z, y') - u(t, z, y)]_+ dy' \right) \end{aligned}$$

where $u(t, z, y)$ is the intake of consumer z when spending all its effort on resource y : $u(t, x, y) = \frac{\Delta(z, y)r(t, y)}{1 + hb \int_{\mathbb{R}} \phi_{AF}(t, z, y)\Delta(z, y)r(t, y)dy}$

Consumption and foraging strategies

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Mixed consumers: sum of the two strategies weighted by a trait $x \in (0, 1)$, $\phi_{MF}(t, z, y) = (1 - x)\phi_{RF}(t, y) + x\phi_{AF}(t, z, y)$.

Numerical results: emergence of community

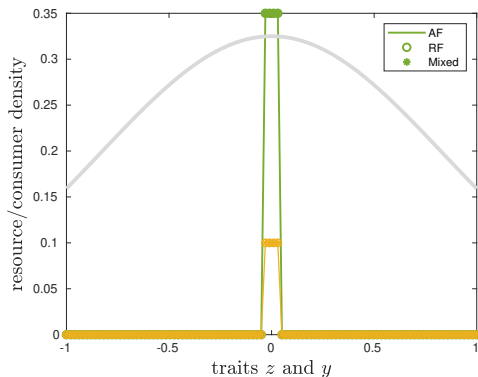
Diffusion rate $D_r = D_c = 10^{-2}$,

Resources distribution $r(t, y)$

Consumers distribution $c(t, z)$

Carrying capacity distribution

$$K(y) \frac{e^{-\frac{y^2}{2\sigma_K^2}}}{\sqrt{2\pi\sigma_K^2}} \text{ with } \sigma_K^2 = 0.75$$



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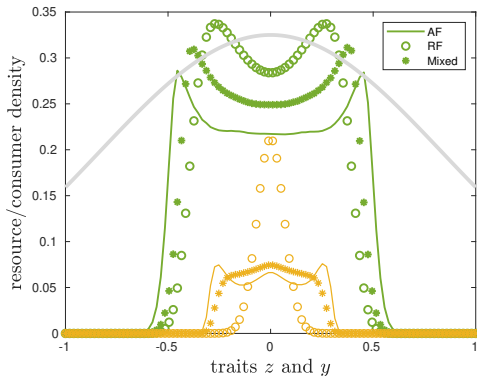
○ **Random foraging:** consumer concentrate around optimal trait of resource.

— — — **Adaptive foraging:**

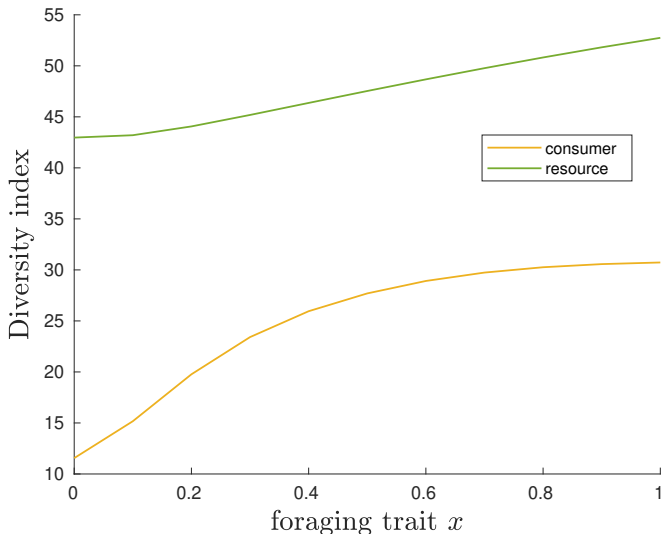
Resource are pushed toward niche borders and consumer distribution have 3 peaks;

★ **Mixed foraging ($x = 0.5$):**

Resource spreads over the niche as well as consumers.



Effect of foraging on diversity



Adaptive foraging promotes diversity among resource-consumer system.

Conclusions

- ★ General model to describe the evolution of community of interacting species.
- ★ Deterministic model that allows multiple traits to dominate in population.

Future work

- **Description** and **quantification** of the equilibrium distribution;
- **Link** with a stochastic model;

Thank you for your attention

References

N. Champagnat, P.E. Jabin, S Méléard, *Adaptation in a stochastic multi-resources chemostat model*, J Math Pures Appl, 101(6), 755-788, 2014.

E. Faou, **J Garnier**, S Ibanez and L Ledru, **Eco-evolution of adaptative foraging**, ongoing work;