Evolution of Complexity from the Statistical Physics Perspective
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Emergence of predation and foodwebs

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Plan

- Repetitive emergence of predation and its significance for diversification and evolution of complexity.

- Phenotype-based models of evolutionary emergence of food webs.

- Predation ability as an independent evolving phenotype

- Conversion efficiency, richness of the environment, and non-linear tradeoffs.

- Future: resource-based environment, empirical functions and allometric, parasitism.

Predation

- The world without predators, “Shangri-La”, phages as the first parasites
- First evidence of predation: decline of stromatolites, hard mineralized exo- and endo-skeletons, holes in shells as a smoking gun,
- Cambrian burst of diversification.
- Metaphoric use of “predation”

Existing Models

- Ecology, A. Lotka and V. Volterra
- Ecology, R. May, random matrices.
- Network-based foodwebs models, e.g. A.J. McKane,
- N. Loeuille and M. Loreau, body mass-structured phenotype-based models.
- Extensive studies of evolving systems with competitive interactions: diversity, evolutionary speed, complexity, unpredictability.

Predation ability as an independent evolving phenotype

In reality, the body size does not define the side in predator-prey interactions: Many largest organisms are herbivores rather than carnivores and smaller predators often feed on larger prey.

So apart from a size difference we propose an independent evolving predation determinant, a continuous "degree of predation" $0 \leq p \leq 1$. Extreme values, $p = 0$ and $p = 1$ correspond to the resource-only consumption and complete predation.

Intermediate values of p still define the fraction of energy that comes from predation, while the complimentary coefficient r defines the resource consumption.

Impossibility to excel both in predation and resource consumption due to various physical and chemical constraints puts p and r under a generally nonlinear tradeoff,

$$p^{\lambda} + r^{\lambda} = 1,$$

which links the individual resource consumption to its predation rate, $r = r(p)$.

Strains and their phenotypes

The system is populated by strains with continuously varying in time population $N(\mathbf{x}, p, t)$, each characterized by its phenotype $\mathbf{x}$ (2-dimensional in our simulation) and a degree of predation p.

Phenotypes $\mathbf{x}$ reflect various characteristics of organisms, such as body size and weight, rates of locomotion in various media, sensory abilities, metabolic characteristics, etc. These characteristics affect their competitive and predatory interactions.

A group of strains with similar phenotypes $\mathbf{x}$ and p forms a species.

The Logistic model accounts for competition

$$\left.\frac{\partial N(\mathbf{x},p,t)}{\partial t}\right|_{comp} = N(\mathbf{x},p,t)\times$$
$$\times\left(r\beta - \delta - r\,\frac{\sum_{x'} r'\alpha(\mathbf{x},\mathbf{x}')N(\mathbf{x}',p',t)}{K(\mathbf{x})}\right).$$

Here

$$\alpha(\mathbf{x},\mathbf{y}) = \frac{1}{\sqrt{2\pi}\sigma_\alpha}\exp\left[-\frac{(\mathbf{x}-\mathbf{y})^2}{2\sigma_\alpha^2}\right]$$

is the competition kernel (symmetric for simplicity) and

$$K(\mathbf{x}) = K_0 \exp\left[-\frac{\sum_j x_j^4}{4}\right]$$

is the carrying capacity, its quartic form guarantees diversification for any σ_α and lack of structural instabilities.

The per capita birth and death rates are β and δ.

The factors r and r' attenuate the birth rate and the competition term by the fraction of resource consumption present in the strains' energy budget.

Predation terms

Predation is taken into account adding gain and loss terms (eating and being eaten) to the population dynamics equation,

$$\frac{\partial N(\mathbf{x},p,t)}{\partial t} = \left.\frac{\partial N(\mathbf{x},p,t)}{\partial t}\right|_{comp} + \\ + \sum_{x'} N(\mathbf{x},p,t)N(\mathbf{x}',p',t)\left(p\chi\gamma(\mathbf{x},\mathbf{x}') - p'\gamma(\mathbf{x}',\mathbf{x})\right).$$

Here

$$\gamma(\mathbf{x},\mathbf{y}) = \frac{1}{\sqrt{2\pi}\sigma_\gamma}\exp\left[-\frac{(\mathbf{x}-\mathbf{y}-\mathbf{m})^2}{2\sigma_\gamma^2}\right]$$

is the attack kernel reflecting the rate of predation of phenotype $\mathbf{x}$ on $\mathbf{x}'$ with the offset $\mathbf{m}$ showing the optimal for the attacker difference between its phenotype and that of the victim. The conversion coefficient χ is a simplified (phenotype-independent) representation of the efficiency of turning prey into predator's offspring. Being a predator does not protect against higher-order predation. Cannibalism is possible, yet is attenuated by γ.

Simulation procedure

- System is initiated with a single strain with phenotype close to the maximum of carrying capacity and predation coefficient $p = 0$.

- Population dynamics is integrated in time, strains with very small population (below 10^{-7}) are purged.

- Once every ~ 1 time units a new mutant (small-population strain) is added, the ancestor is chosen with probability proportional to its population, mutations Δ both in $\mathbf{x}$ and p are small, $\Delta \sim 10^{-2}$.

- To make it run faster, every $\sim 10^3$ time units the strains that are within 2Δ are clustered, preserving total population and phenotypic center of mass.

Parameters

σ_a =0.5

σ_γ =0.5, 0.25 − 1

m =0.5, 0 − 1

β =3, 2 − 4

δ =2, 1 − 3

λ =1, 0.9 − 1.1

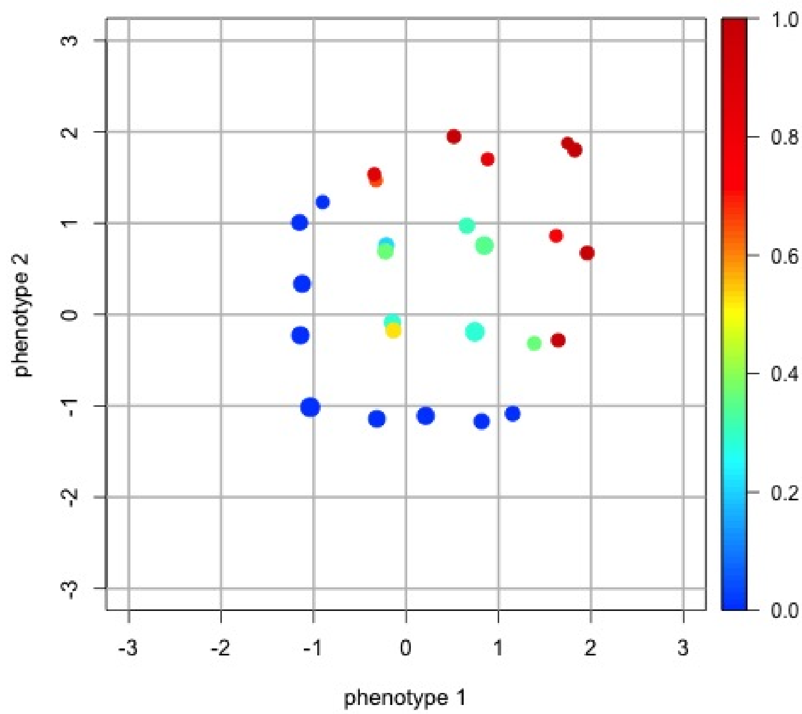
χ =0.4, 0.006 − 0.75

K_0 =4, 1 − 16

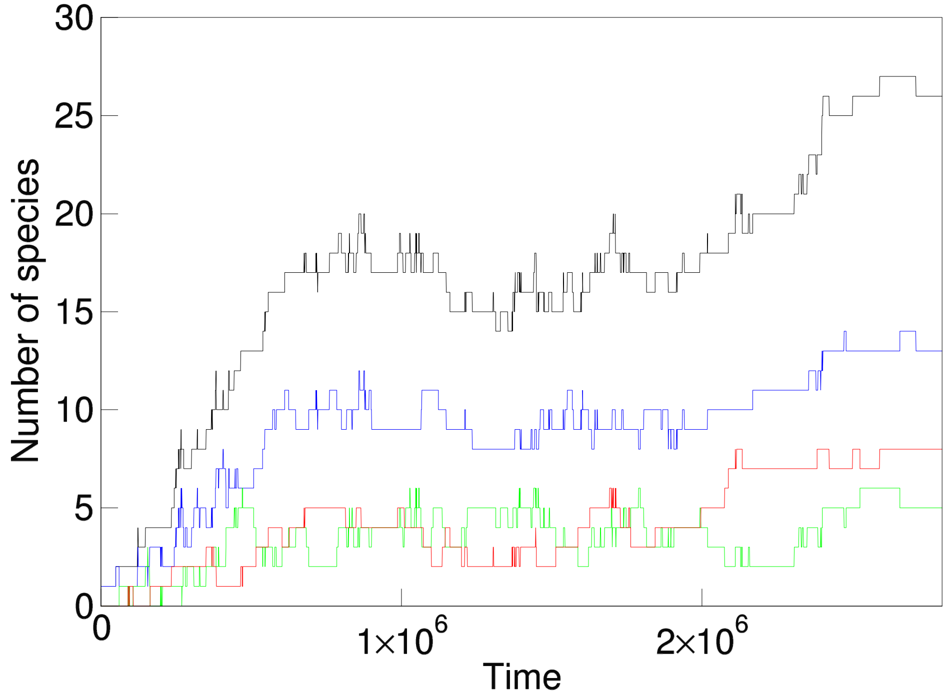
$T_{final} = 1.4 \times 10^6$

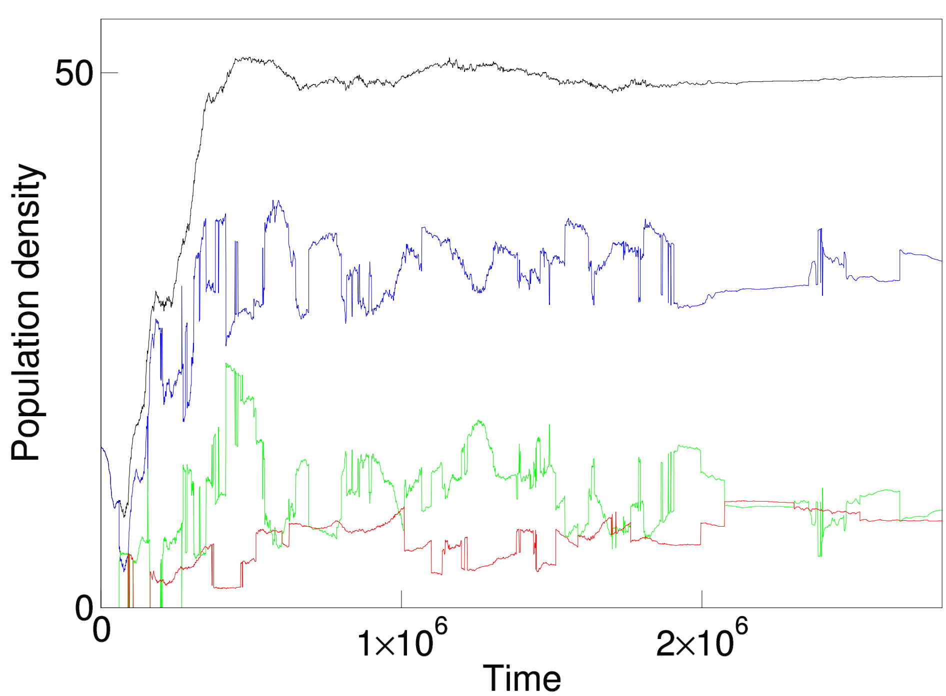
A "3d" view

"Standard" scenario

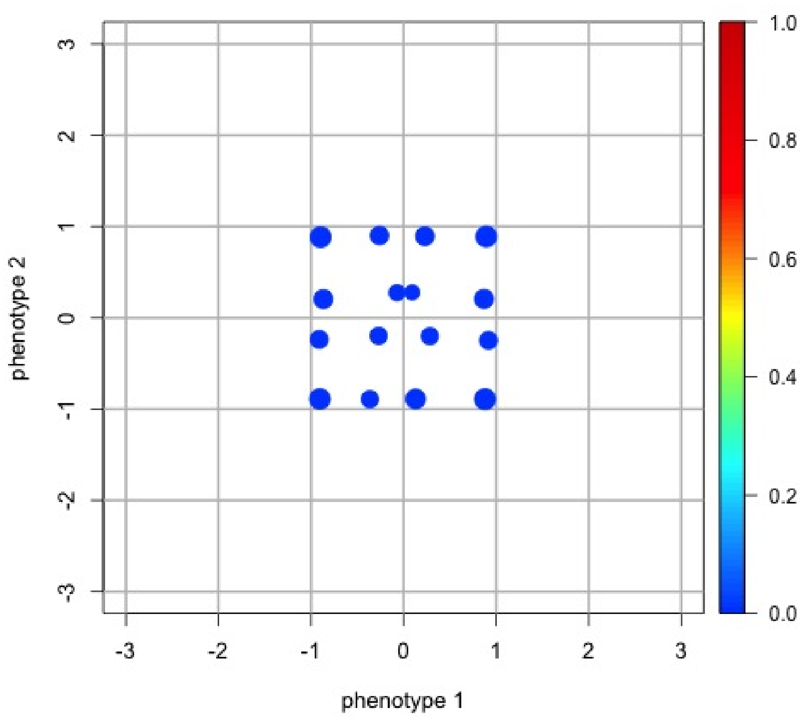


Diversification and population dynamics

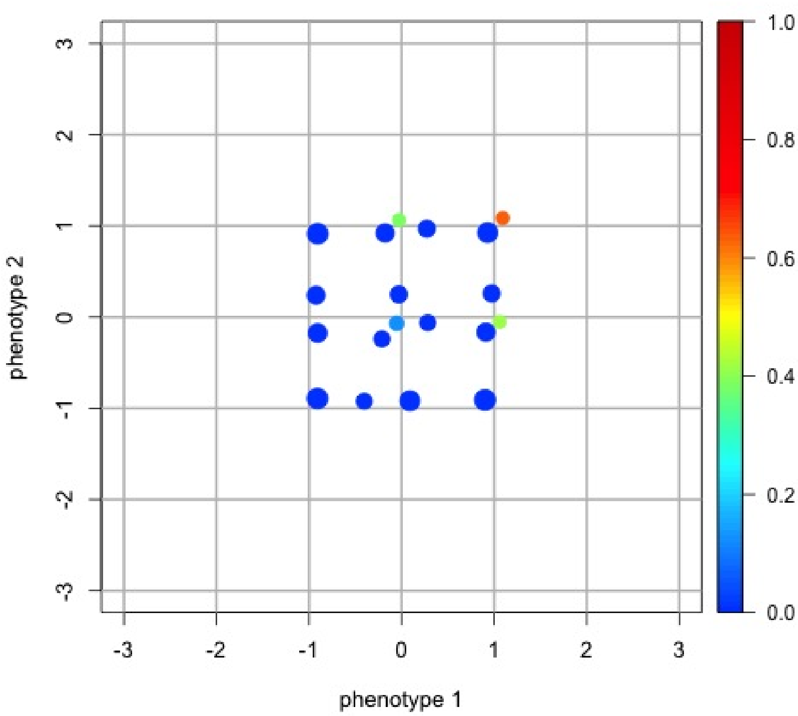




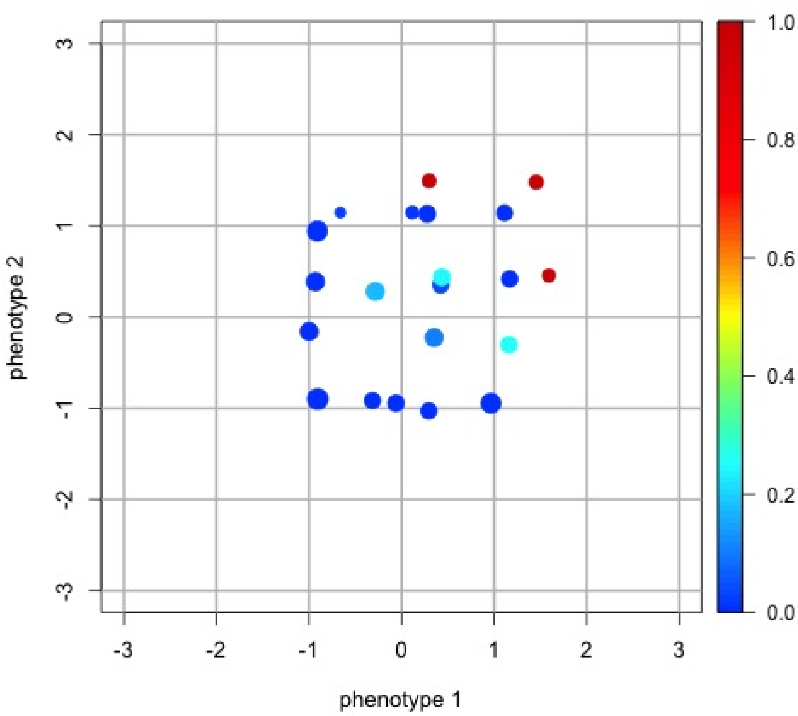
Very inefficient conversion, $\chi = 0.063$, only consumers evolve



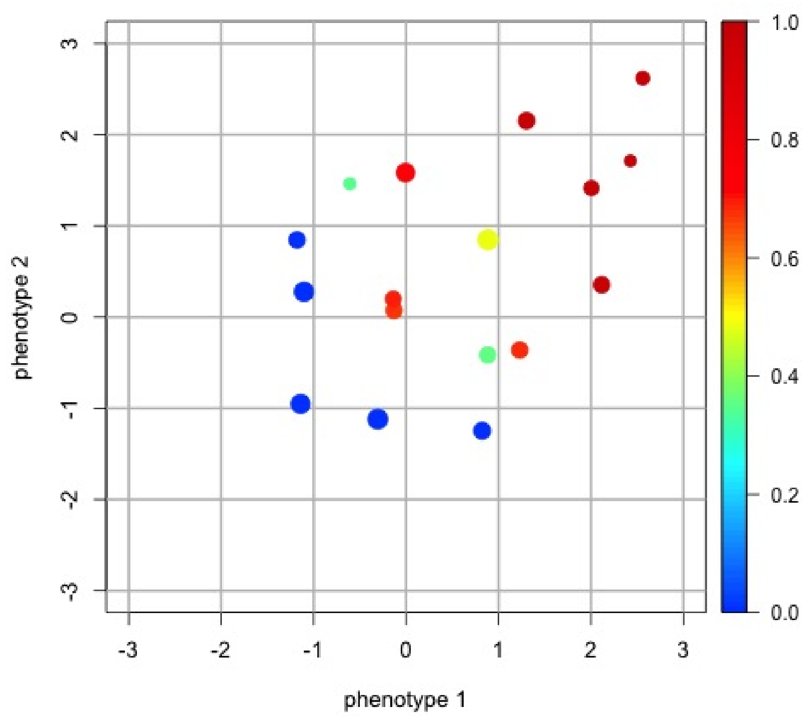
A bit better conversion, $\chi = 0.125$, first predator appears



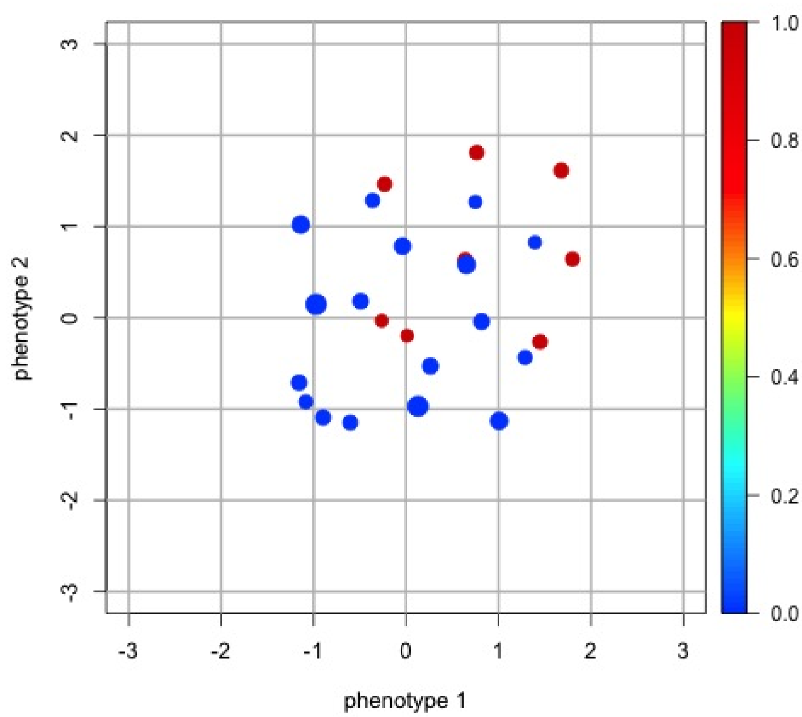
Even better conversion, $\chi = 0.25$, more predators predator appears



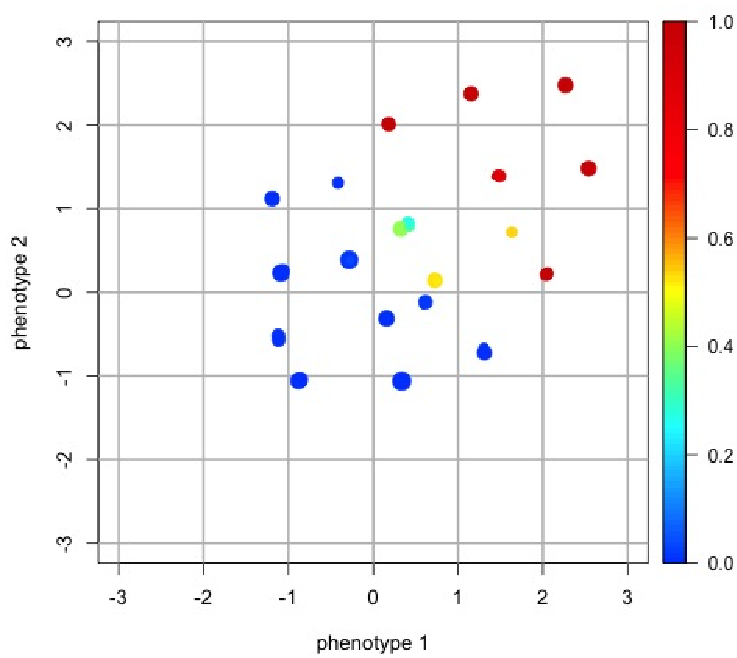
Very efficient conversion, $\chi = 0.75$ lower diversity and non-stationarity



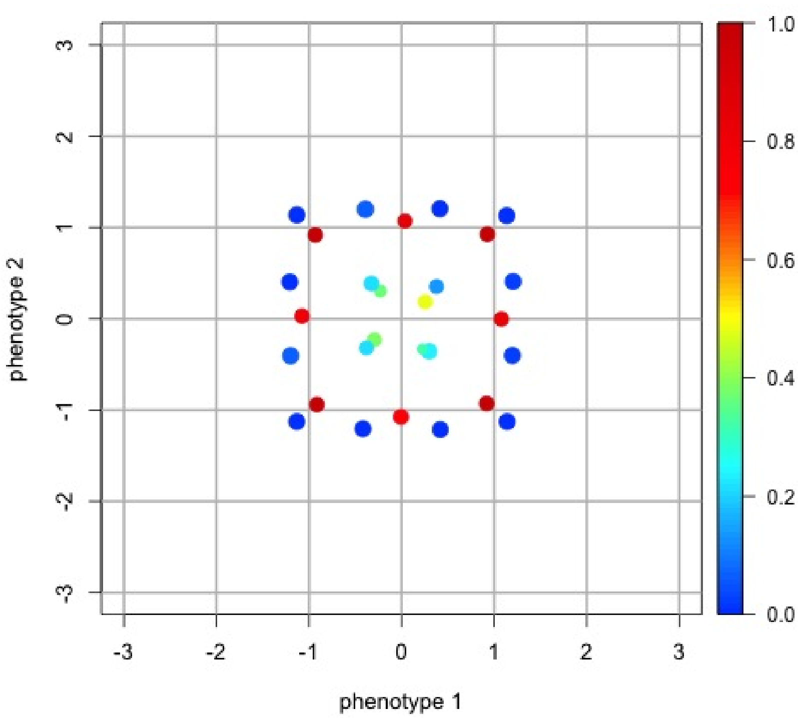
"Concave" tradeoff, $\lambda = 0.9$, no omnivores



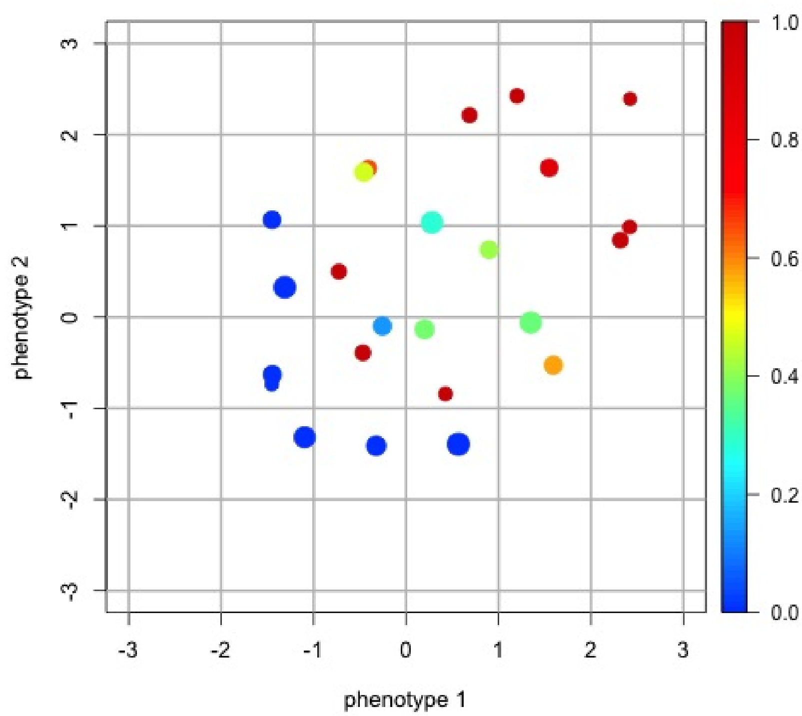
Larger optimal predation size offset. $m = 1$, fewer omnivores and a cascade of pure predators



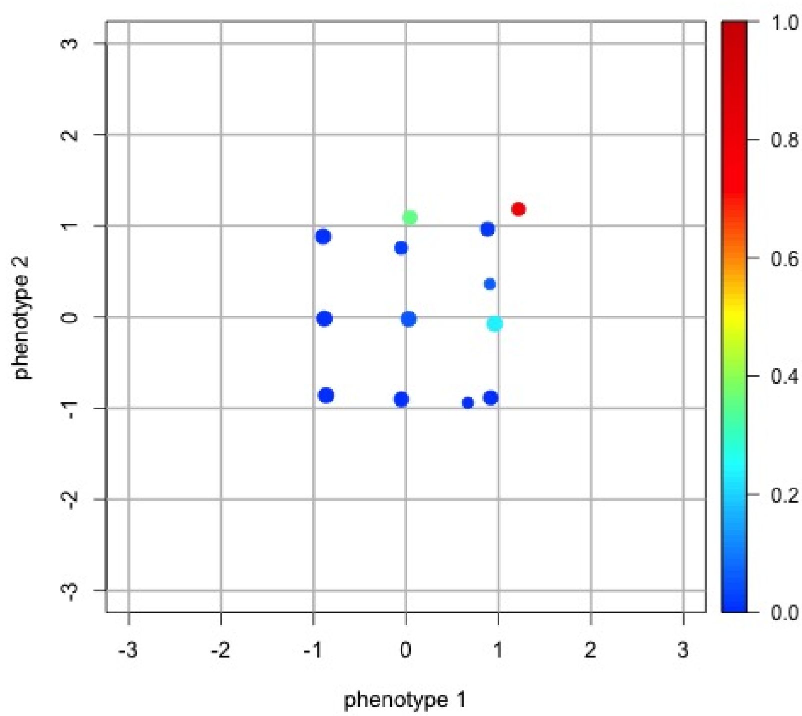
Zero optimal predation size offset. $m = 0$



Large carrying capacity, $K_0 = 16$, fewer consumers and more predators



Small carrying capacity $K_0 = 1$, more consumers, but not as many as for small χ



Conclusion

- The model predicts realistic-looking foodwebs for a wide range of parameters

- Inefficient predators only appear when the prey is sufficiently diverse, which was probably the case with the first predators in each ecological scenario

- Largest diversity develops for intermediate values of conversion efficiency and carrying capacity

- Very high conversion efficiency produces non-stationary ecology and evolution, most probably due to multilevel foodwebs of pure predators

- Adding allometry and phenotype-dependent conversion efficiency

- Replacing logistic growth by explicit resources, first attempts resulted in essentially non-stationary ecology and evolution

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