Modeling microbial diversity

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KITP
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How can we explain species' diversity?

An astonishing characteristic of life is its great variety:

- In tropical rainforests more than 300 tree species may be found on a single hectare.
- In one gram of soil the number of distinct microbial genomes has been estimated at ~ 2000 -- 18,000.

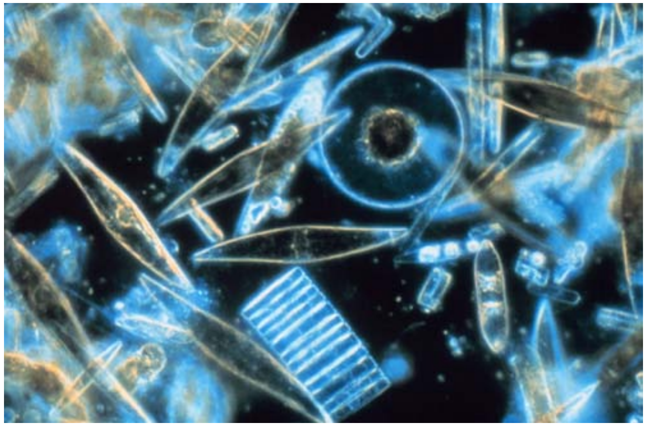
But...the competitive exclusion principle says:

- Two species that compete for the same limiting resource cannot stably coexist.
- In resource competition models, the number of species coexisting in equilibrium cannot exceed the number of resources.

Paradox of the plankton

Originally described by G. E. Hutchinson in 1961:

"…a limited range of resources supports an unexpectedly wide range of plankton species, apparently flouting the competitive exclusion principle…"



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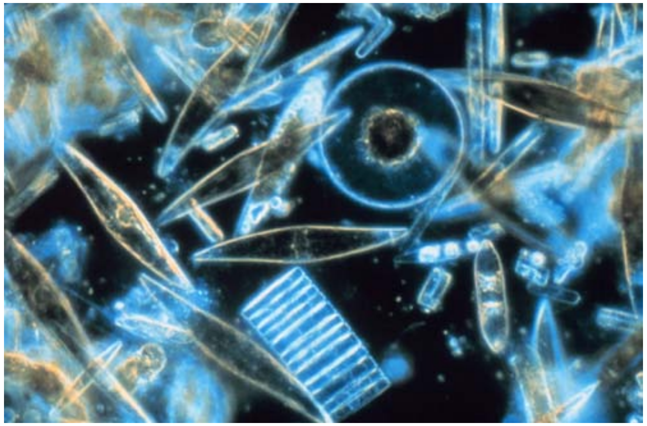


Possible solutions:

- Oscillatory or chaotic population dynamics
- Temporal variation of environment,
  e.g. weather changes, seasonal cycles
- Spatial variation of environment,
  e.g. gradients such as temperature, salinity, exposure to light
- Other limiting factors,
  e.g. predation


EVERYTHING'S A TRADEOFF - NOW THAT I CAN WALK UPRIGHT, I CAN'T WIGGLE MY EARS ANY MORE.
Search: 12261671

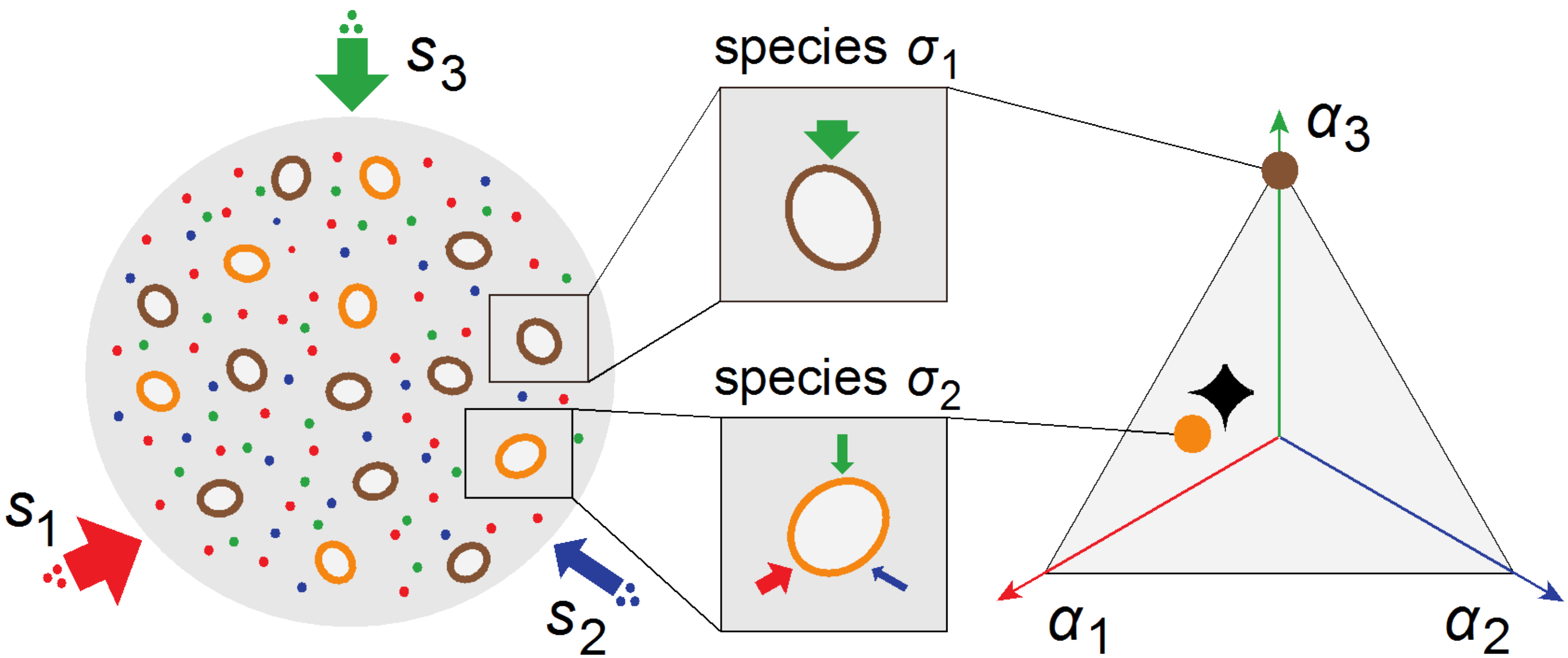
Resource-competition model with trade-offs

p resources

Species: $\vec{\alpha}_\sigma = (\alpha_{\sigma 1}, \ldots, \alpha_{\sigma p})$

Trade-offs in ability to utilize different resources:

$$\sum_{i=1}^{p} w_i \alpha_{\sigma i} = E$$



Resource-competition model with trade-offs

Nutrient concentrations dynamics:

$$\dot{c}_i = s_i - \sum_\sigma n_\sigma \, \alpha_{\sigma i} \frac{c_i}{K_i + c_i} - \mu_i c_i$$

$$= \text{supply} \; - \; \text{consumption} \; - \; \text{loss}$$

Growth rate of species σ:

$$g_\sigma(\vec{c}) = \sum_{i=1}^{p} v_i \, \alpha_{\sigma i} \frac{c_i}{K_i + c_i}$$

Population dynamics:

$$\dot{n}_\sigma = \left(g_\sigma(\vec{c}) - \delta\right) n_\sigma$$

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Simplified parameters:

- no nutrient loss: $\mu_i = 0$
- separation of time scales: $\dot{c}_i = 0$
- “symmetric” nutrients: $w_i = K_i = v_i = 1$

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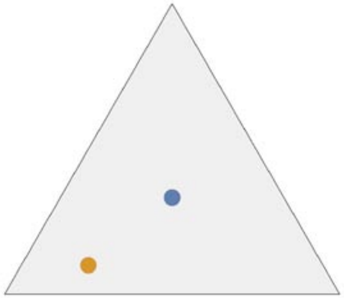
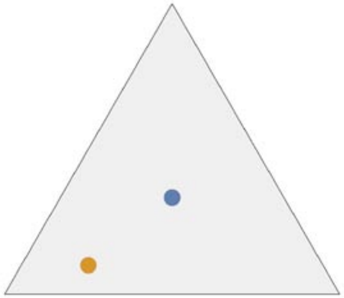
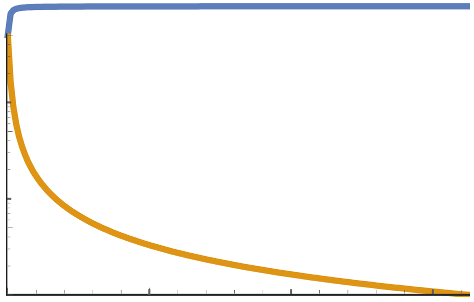
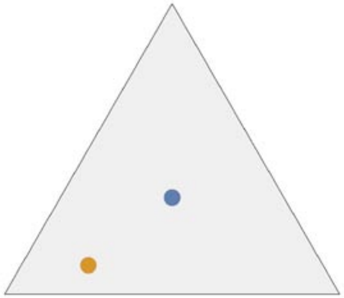
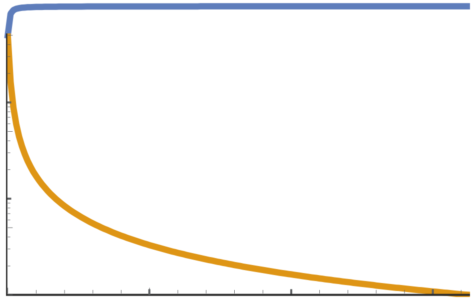
$$\dot{n}_\sigma = \left(\sum_{i=1}^{p} \alpha_{\sigma i} \frac{s_i}{\sum_\kappa \alpha_{\kappa i} n_\kappa} - \delta \right) n_\sigma, \qquad \sum_{i=1}^{p} \alpha_{\sigma i} = E$$

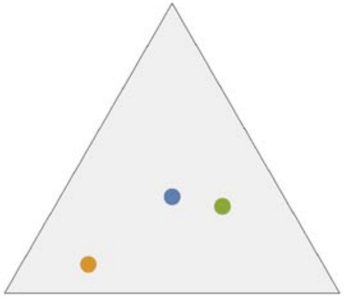


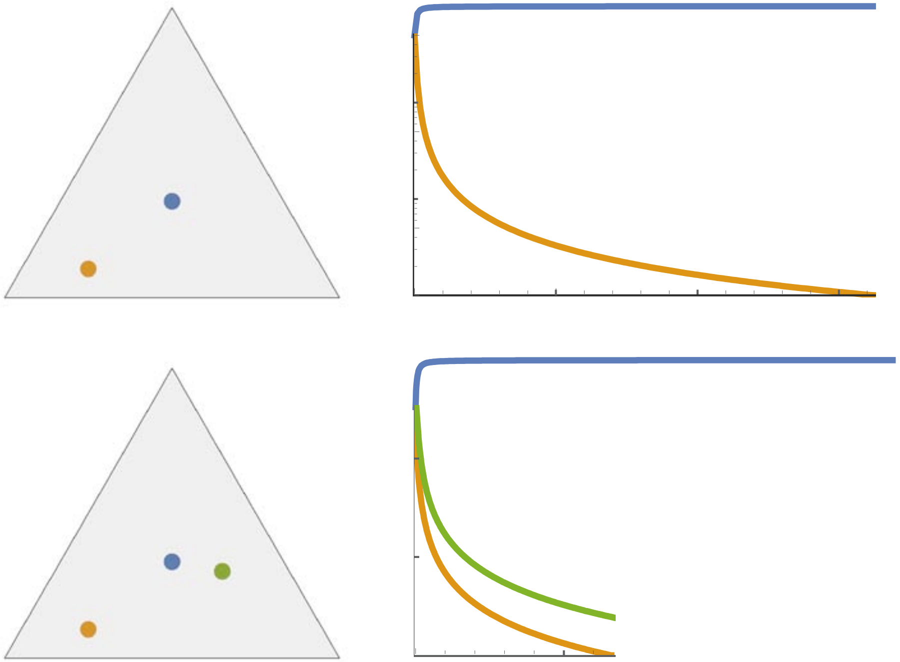


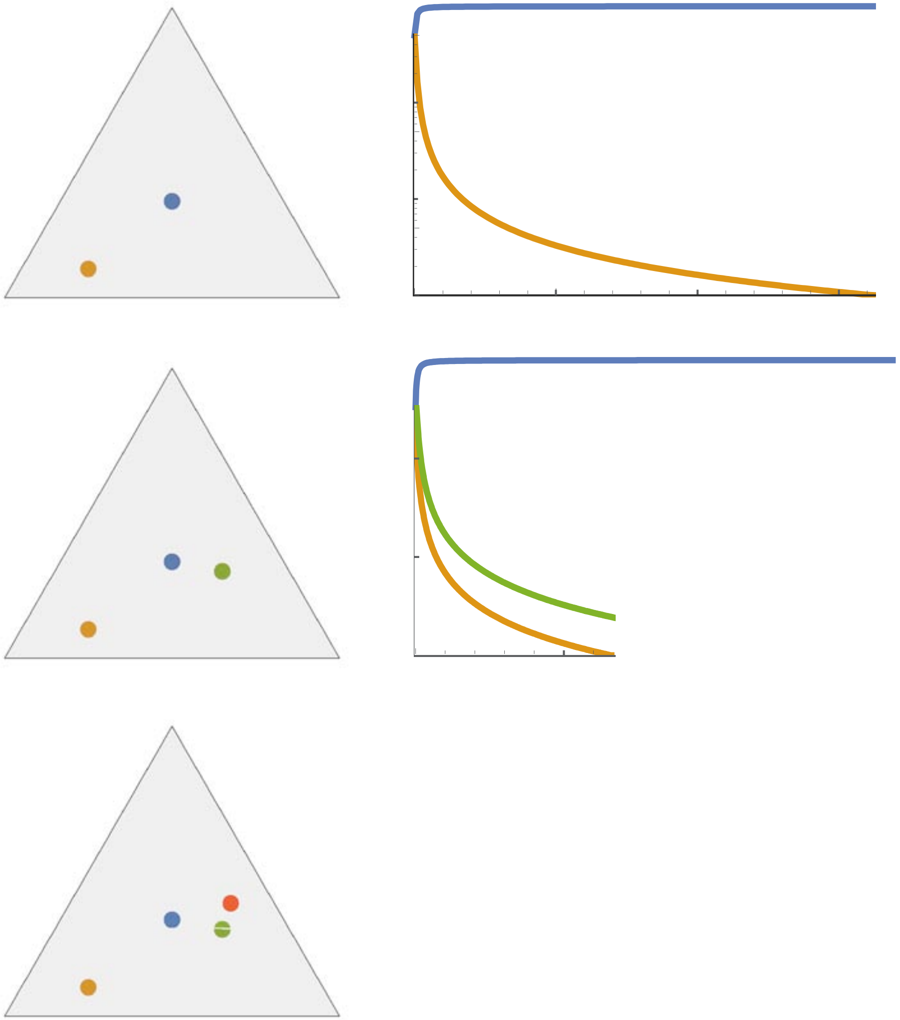


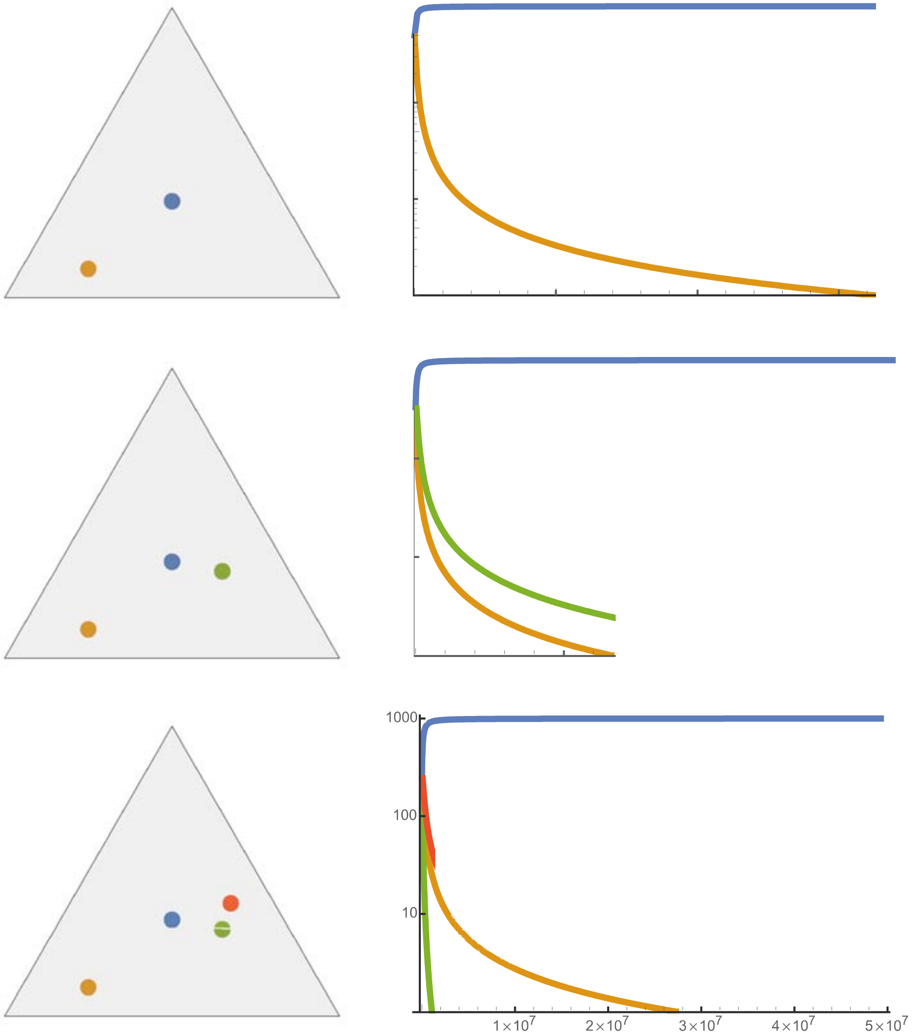












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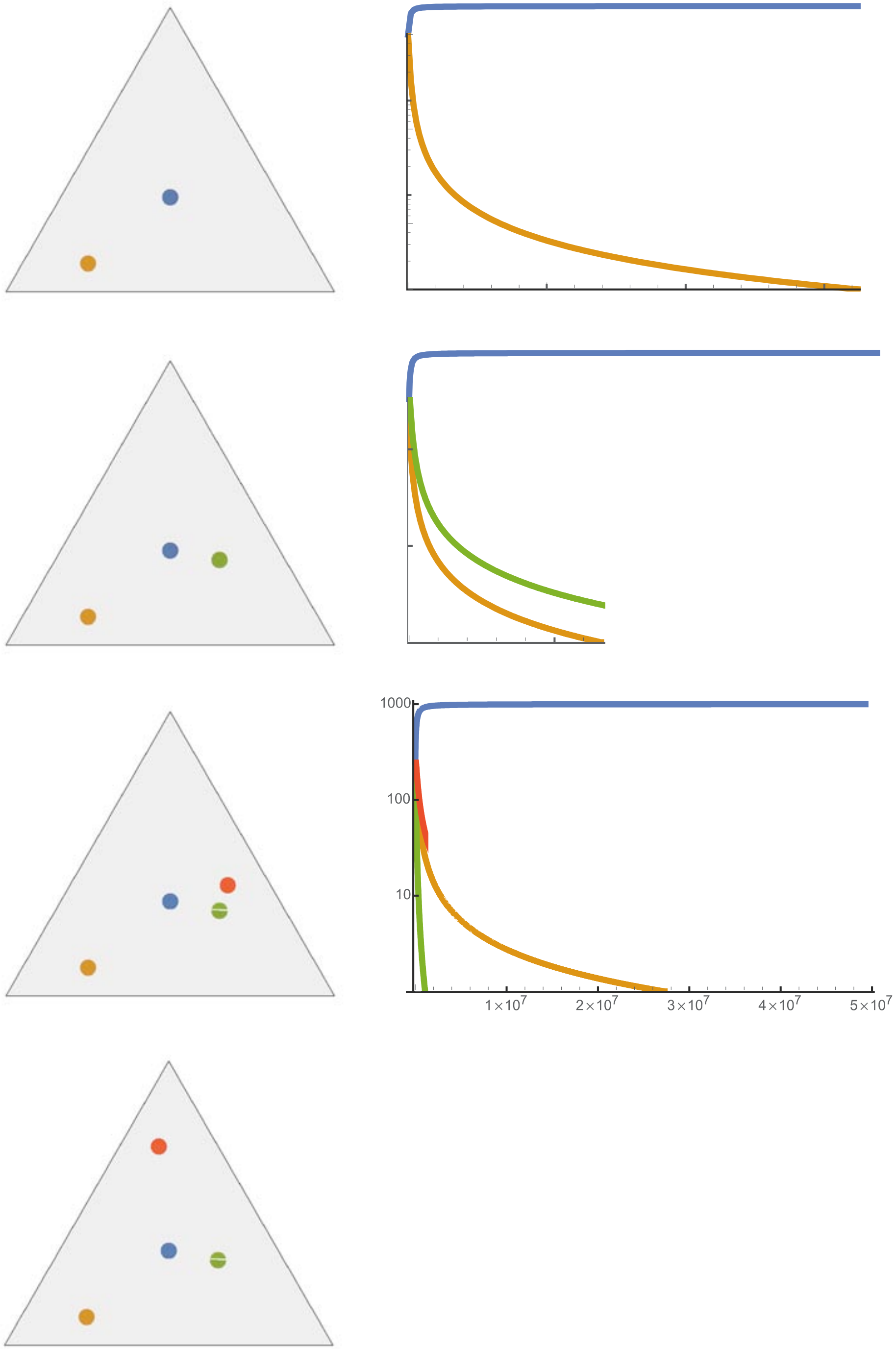
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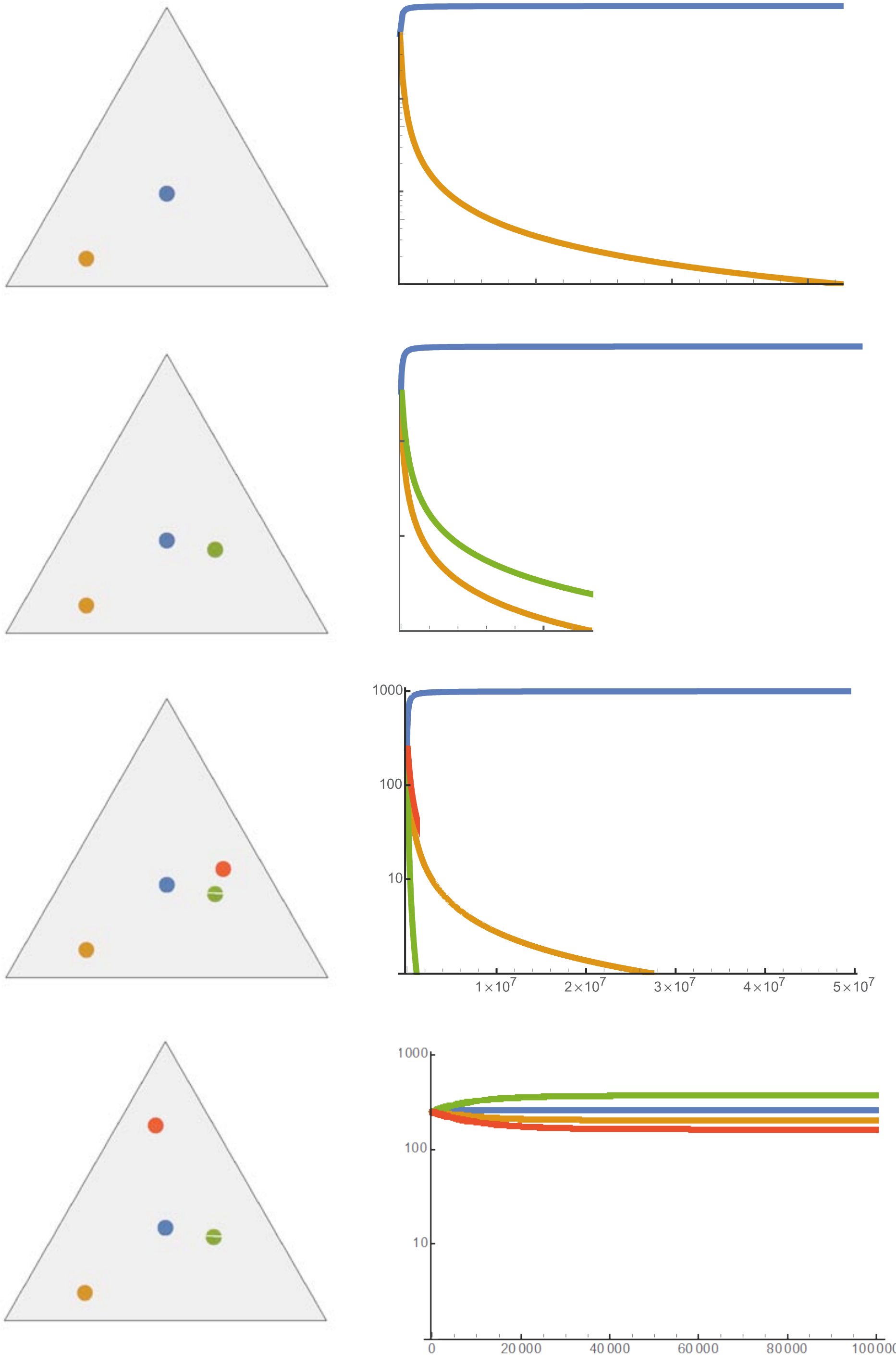
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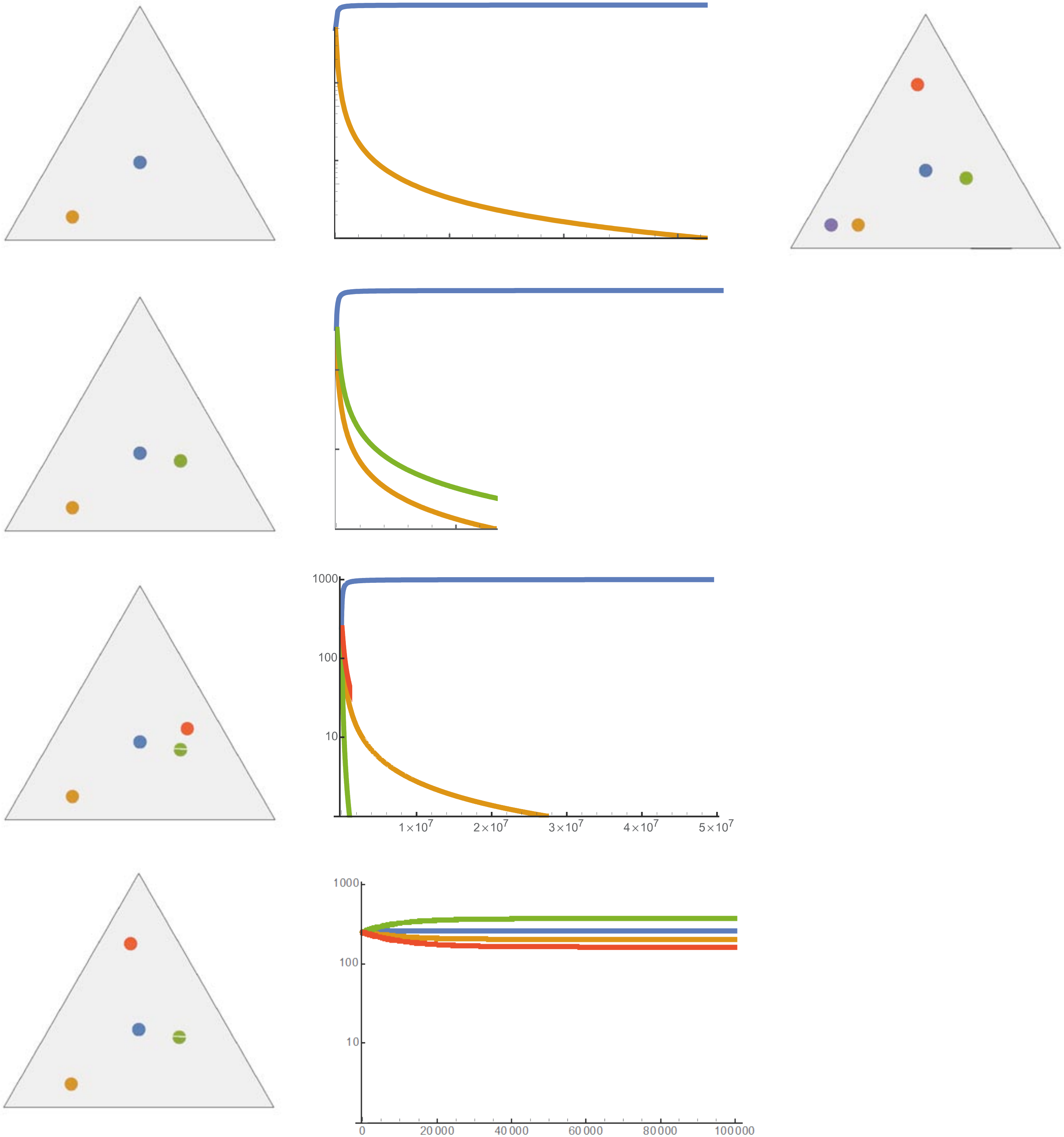
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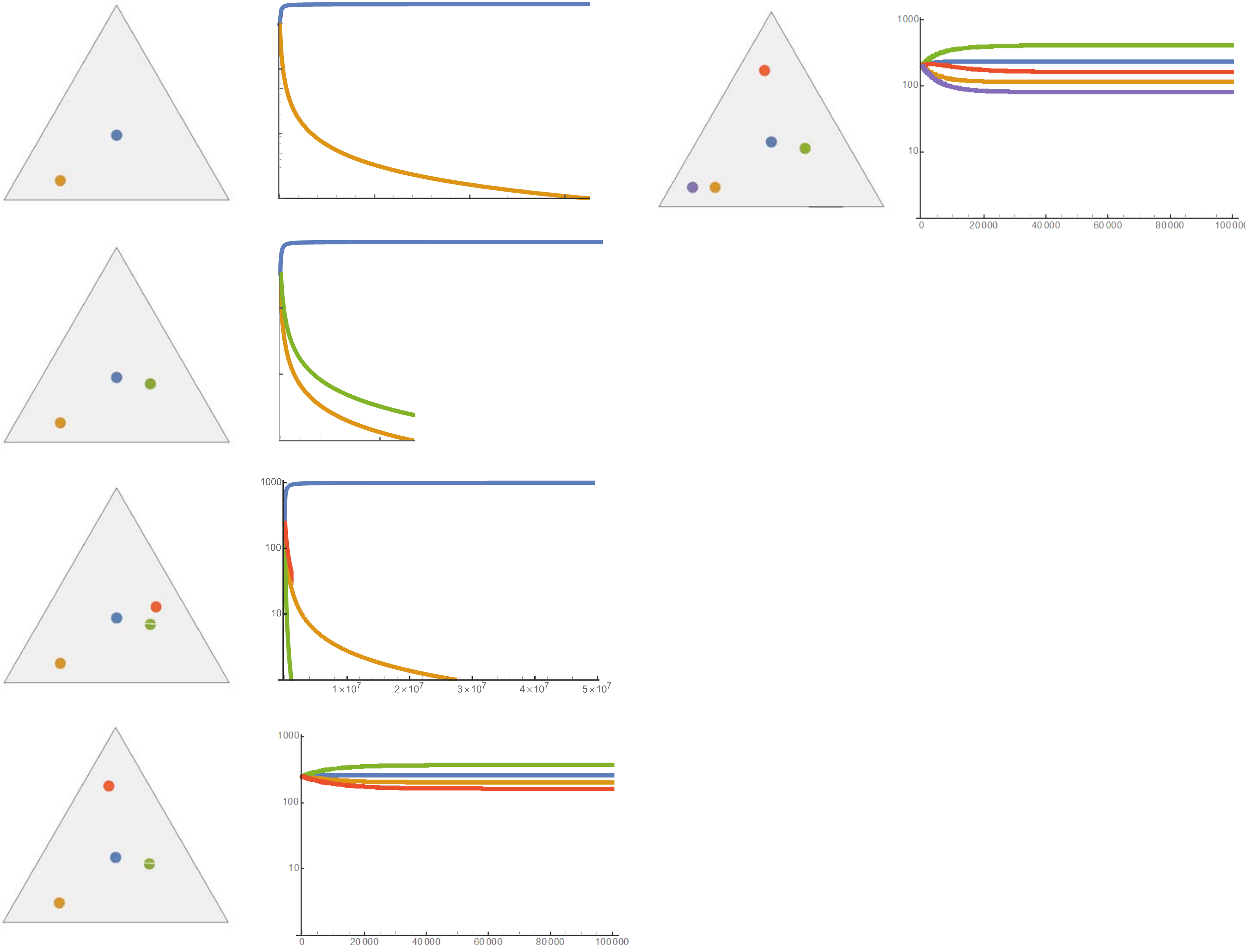

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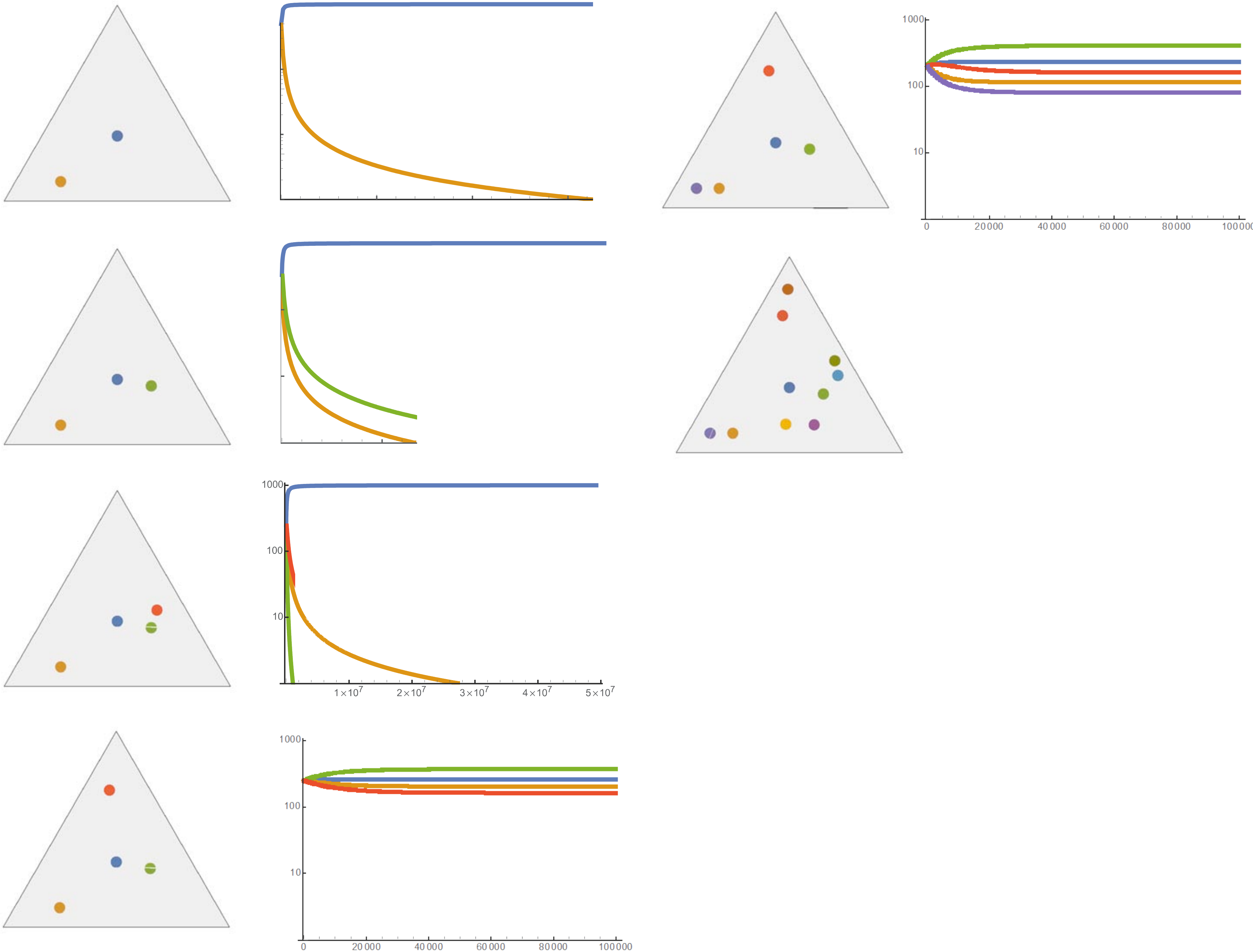
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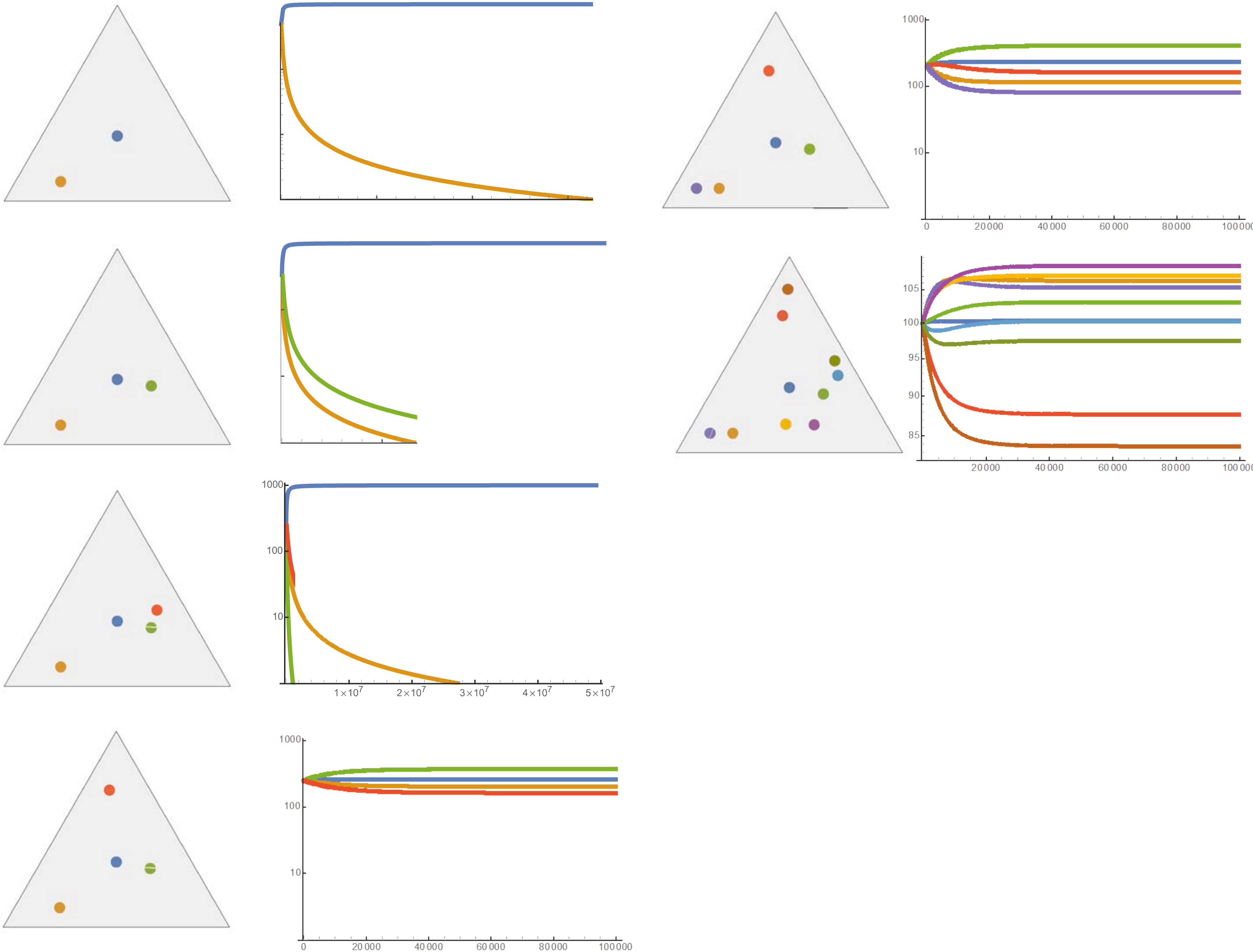

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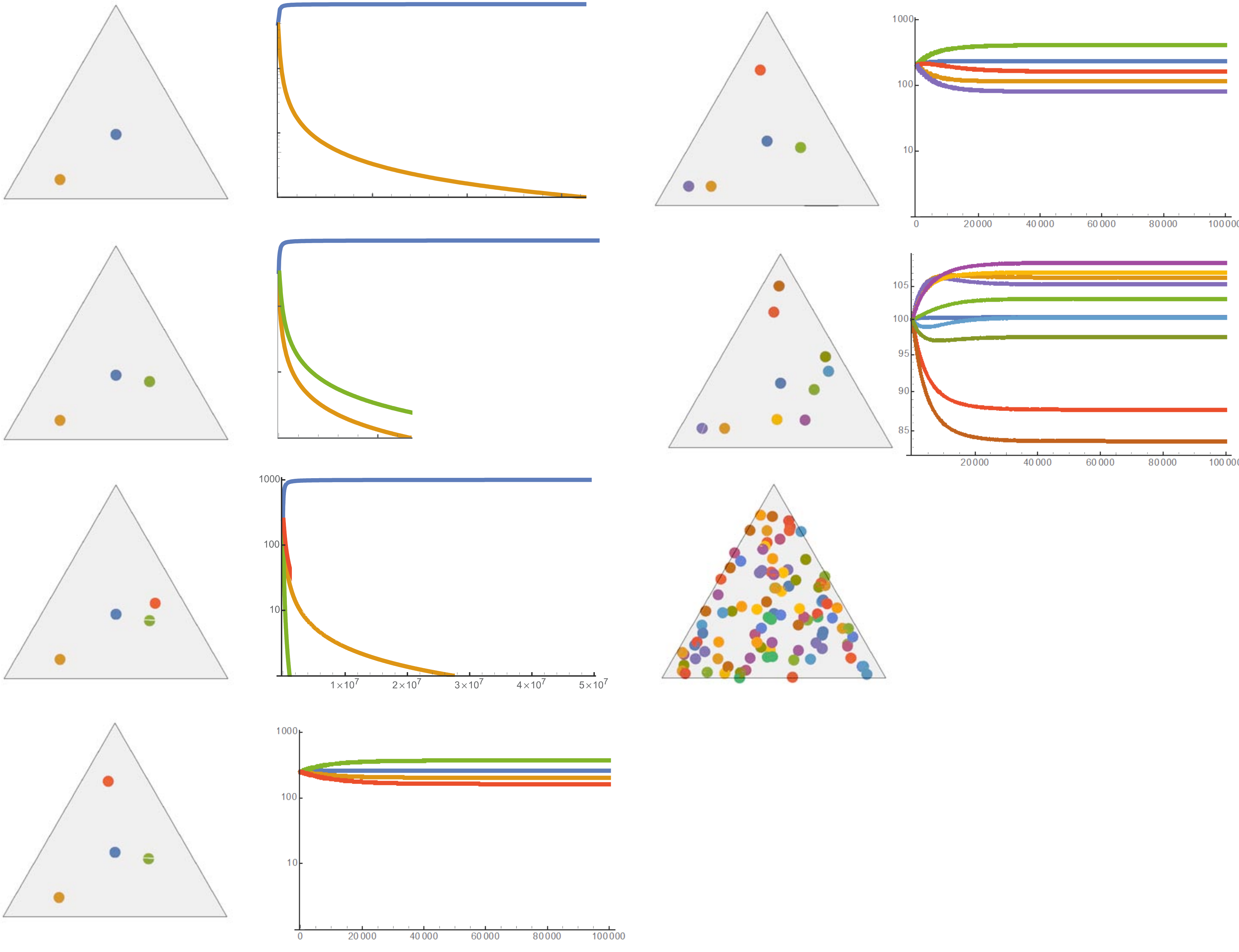

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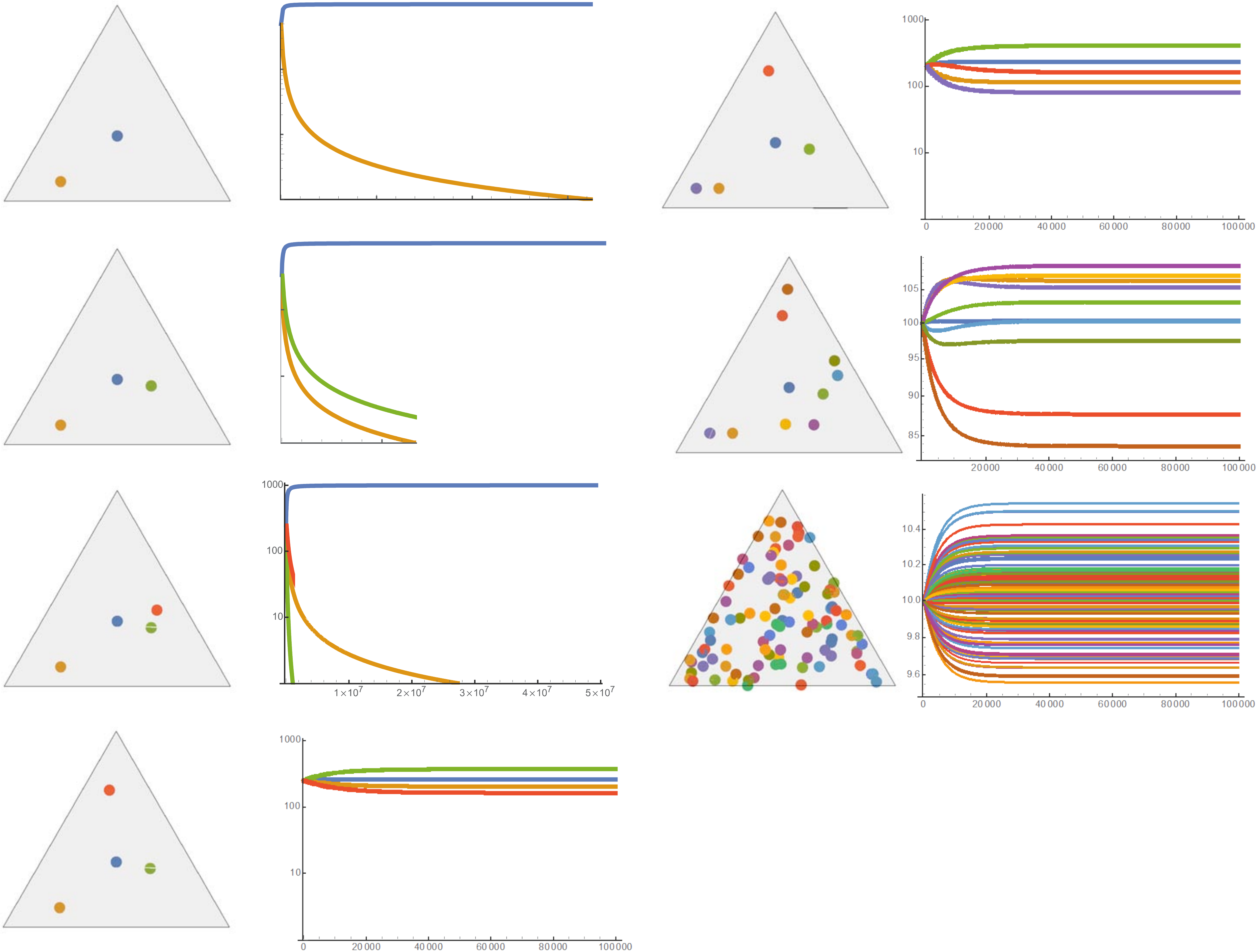
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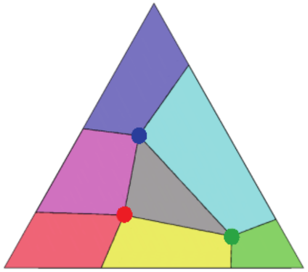
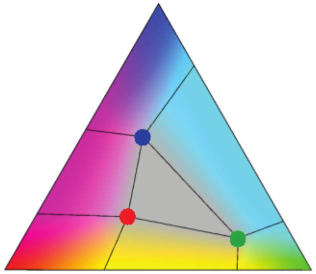
species = # resources:



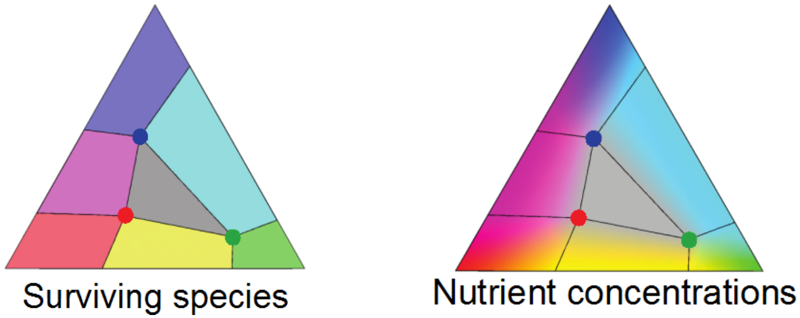
Surviving species



Nutrient concentrations

$$g_\sigma(\vec{c}) = \sum_i \alpha_{\sigma i} \frac{c_i}{1 + c_i}$$

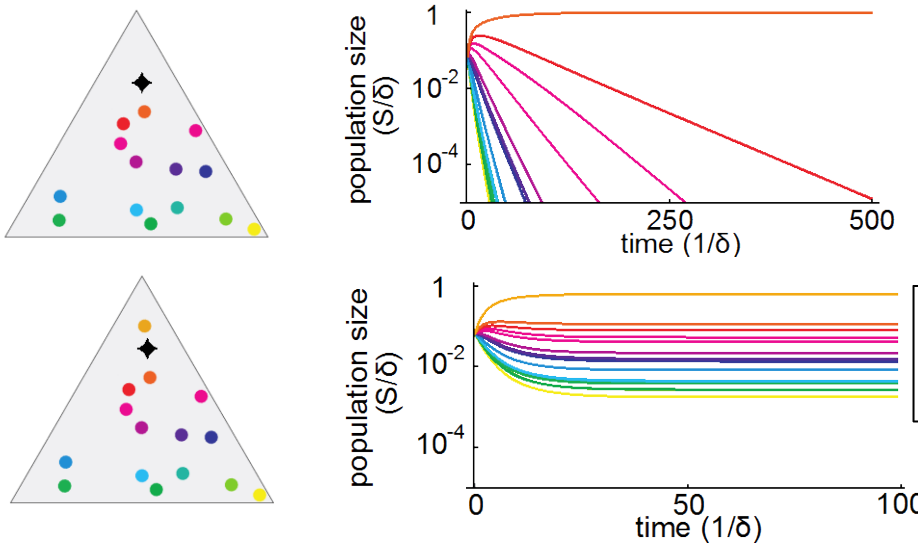
species = # resources:



$$g_\sigma(\vec{c}) = \sum_i \alpha_{\sigma i} \frac{c_i}{1 + c_i}$$

species ≥ # resources:

A collection of $\{\vec{\alpha}_\sigma\}$ species coexist in steady state $\Leftrightarrow$ the supply $\vec{s}$ lies within the convex hull of the species $\{\vec{\alpha}_\sigma\}$.

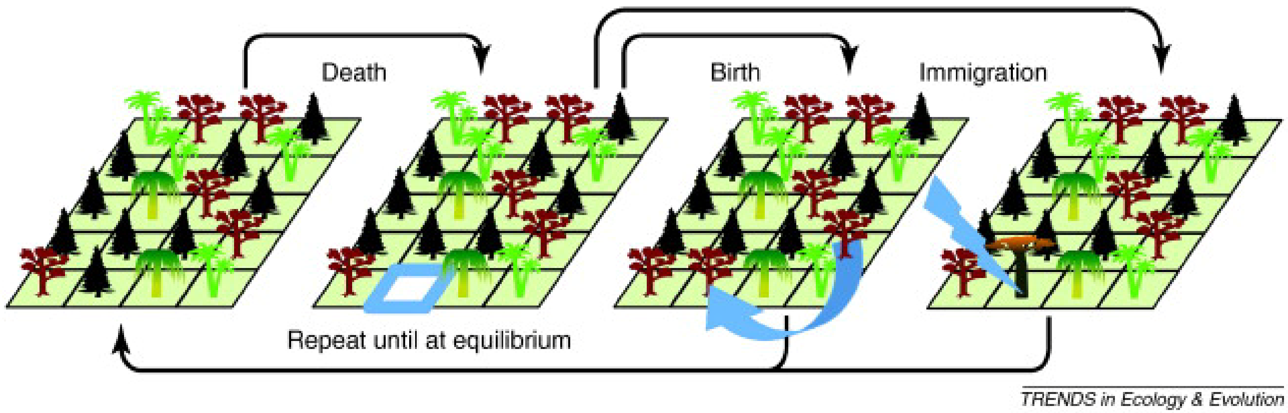


Gold species acts as "keystone species".

Competition → nutrient concentrations become too low for certain species to survive → at most #resources - 1 species survive.
Cooperation → balanced nutrient concentrations → all species are equally fit → all species survive!

The neutral theory of biodiversity

Neutral theory: species are ecologically equivalent, and diversity emerges from ecological drift.



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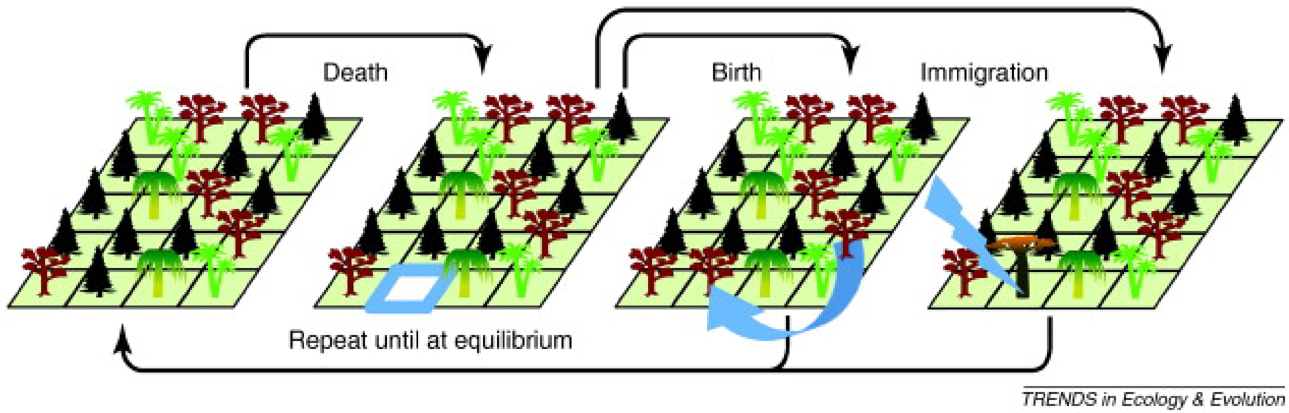
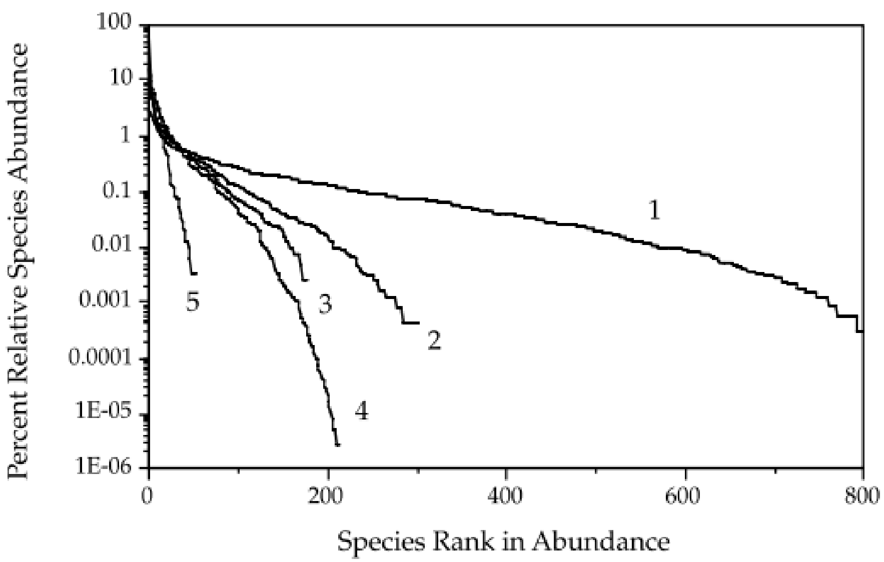




1. Tropical wet forest in Amazonia
2. Tropical dry deciduous forest in Costa Rica
3. Marine planktonic copepod community from the North Pacific gyre
4. Terrestrial breeding birds of Britain
5. Tropical bat community from Panama

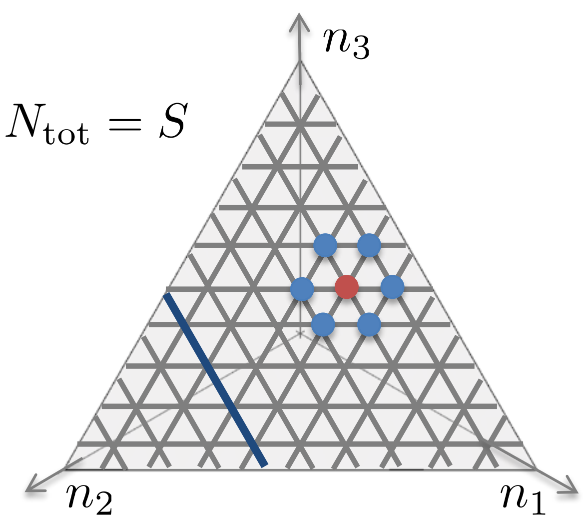
S. Hubbell: The Unified Neutral Theory of Biodiversity and Biogeography

Discrete, stochastic version of the model

Birth-death-immigration process $\vec{N}(T)$:

1. At $T = 0$, $\vec{N}(T)$ starts from a fixed initial population $\vec{N}(0)$.
2. At each time step
   (i) a random individual dies:
   P(individual from species σ dies) = $\frac{N_\sigma}{N_{\text{tot}}}$

   (ii) it is replaced by a random new individual:
   P(new individual is an immigrant) = ν
   P(new individual is from species σ) = $(1-\nu)\frac{g_\sigma(\vec{N},\vec{S}\,)N_\sigma}{N_{\text{tot}}}$



In deterministic model:

$$\dot{n}_\sigma = (g_\sigma(\vec{n},\vec{s}) - \delta)\, n_\sigma , \quad n_{\text{tot}} = s/\delta$$

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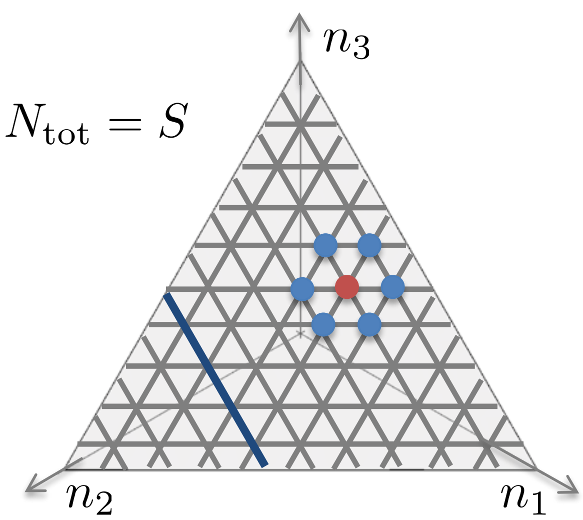

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Connection between deterministic and stochastic models:

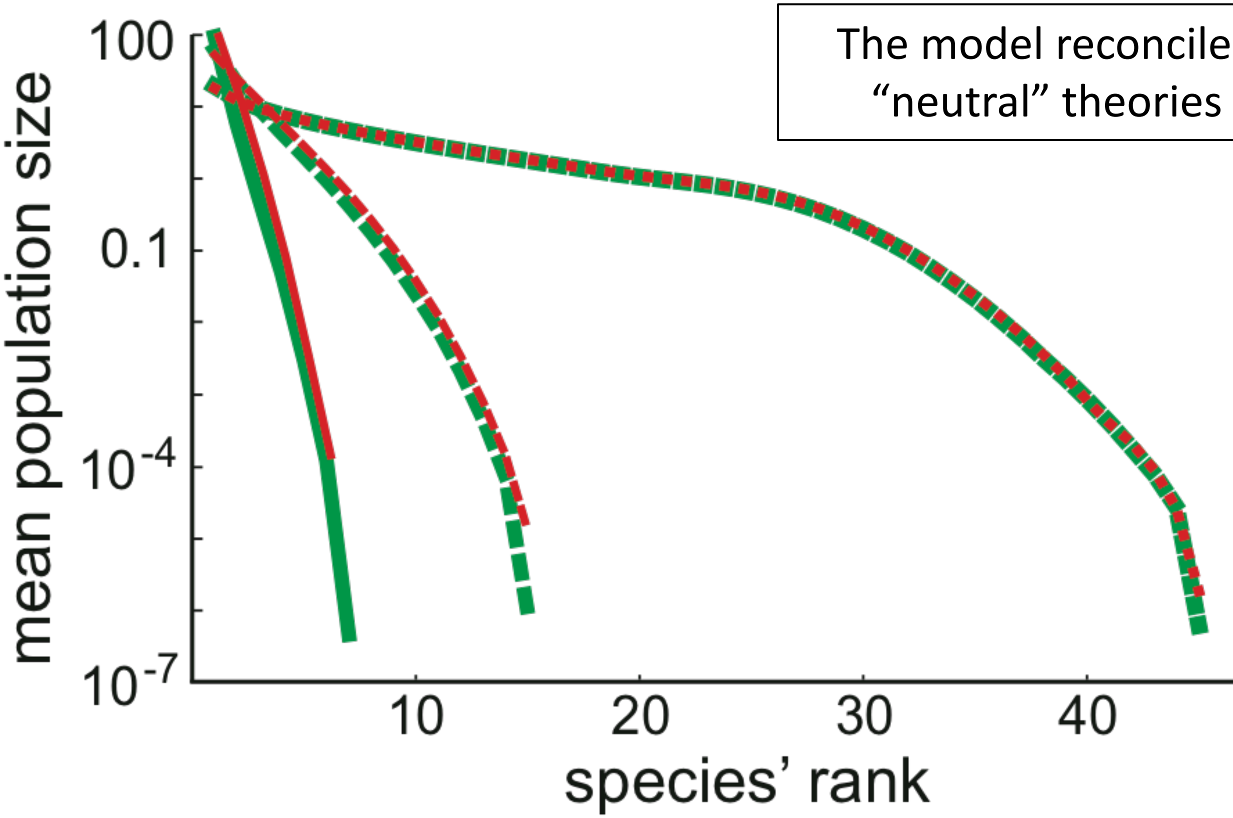
If there are many organisms per each non-extinct species, i.e. S and N_σ are large, and $T = O(S)$ then

$$N_\sigma(T) \approx \frac{\delta S}{s}\, n_\sigma\!\left(\frac{s}{\delta^2 S}T\right).$$

Connection to the neutral theory of biodiversity

Rank-abundance curves

red – resource-competition model
green – neutral model
total population: $N_{\text{tot}} = 100$
immigration probabilities: $\nu = 0.001, 0.01, 0.1$



The model reconciles "niche" and "neutral" theories of diversity.

Robustness of coexistence

I. Against population disturbances
II. Against fluctuations in nutrient availability
III. Against variability in species' budgets and death rates

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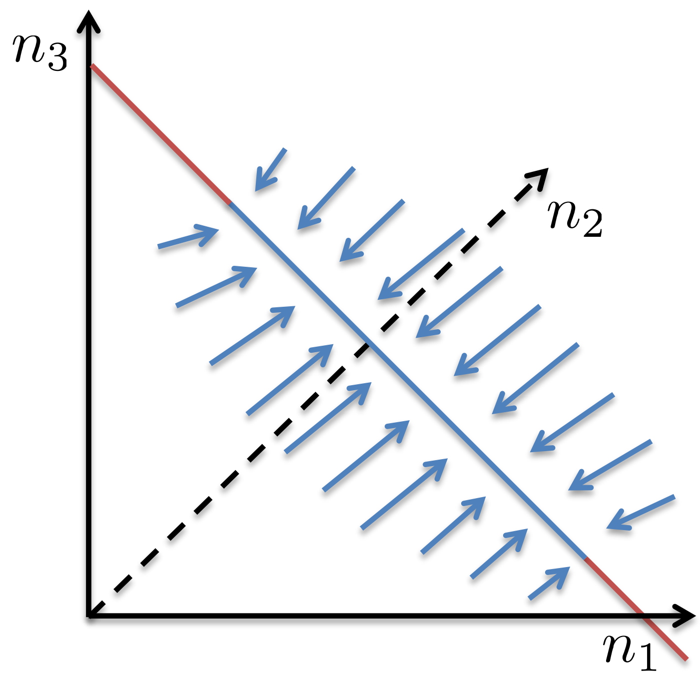
I. Against population disturbances:

The population fixed points are the solutions to the system of linear equations with #resources equations and #species variables:

$$n_1\vec{\alpha}_1 + \ldots + n_m\vec{\alpha}_m = \frac{E}{\delta}\vec{s}$$

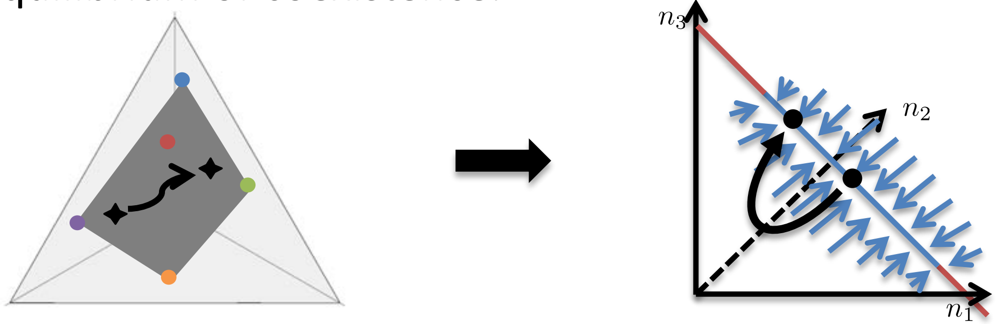
The population fixed points form the non-negative subset of a #species-#resources dimensional plane, and this set is an attractor of the dynamical system.



Robustness of coexistence

II. Against fluctuations in nutrient availability:

If nutrient supply changes, but remains in the convex hull of the species, the populations find a new equilibrium of coexistence.



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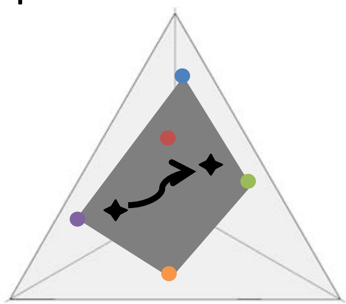
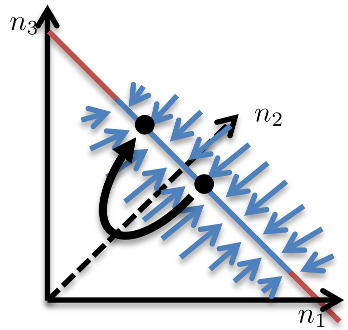
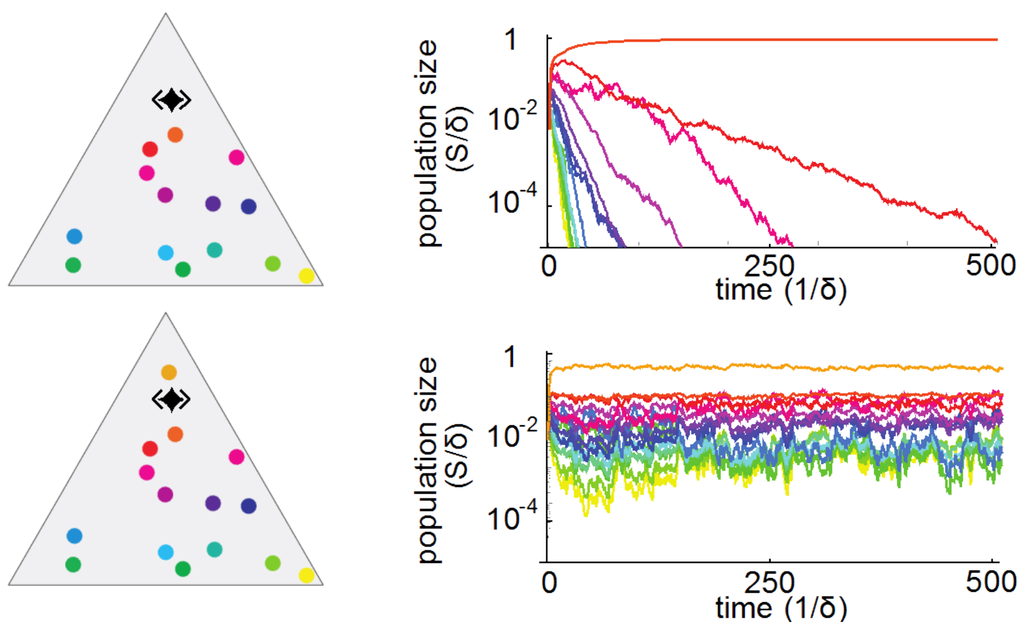




Time-dependent nutrient supply: The supply regularly changes, at a fixed time interval T, to a new randomly selected supply, while the total supply is fixed:



Mean supply hypothesis:
A collection of species $\{\vec{\alpha}_\sigma\}$ coexist.

⇕

The mean supply $\langle\vec{s}\rangle$ lies within the convex hull of the species $\{\vec{\alpha}_\sigma\}$.

Robustness of coexistence

III. Against variability in species' budgets and death rates:

Definition of species σ :

enzyme distribution: $(\max(\alpha_{\sigma 1}+\xi_{\sigma 1}),\ldots,\max(\alpha_{\sigma p}+\xi_{\sigma p}))$ with $\sum_{i=1}^{p}\alpha_{\sigma i}=E$

death rate: $\delta_\sigma=\delta+\xi_\sigma,$

where $\xi_{\sigma i}$ and ξ_σ are iid random variables with Gaussian distribution $\mathcal{N}(0,\Sigma^2)$

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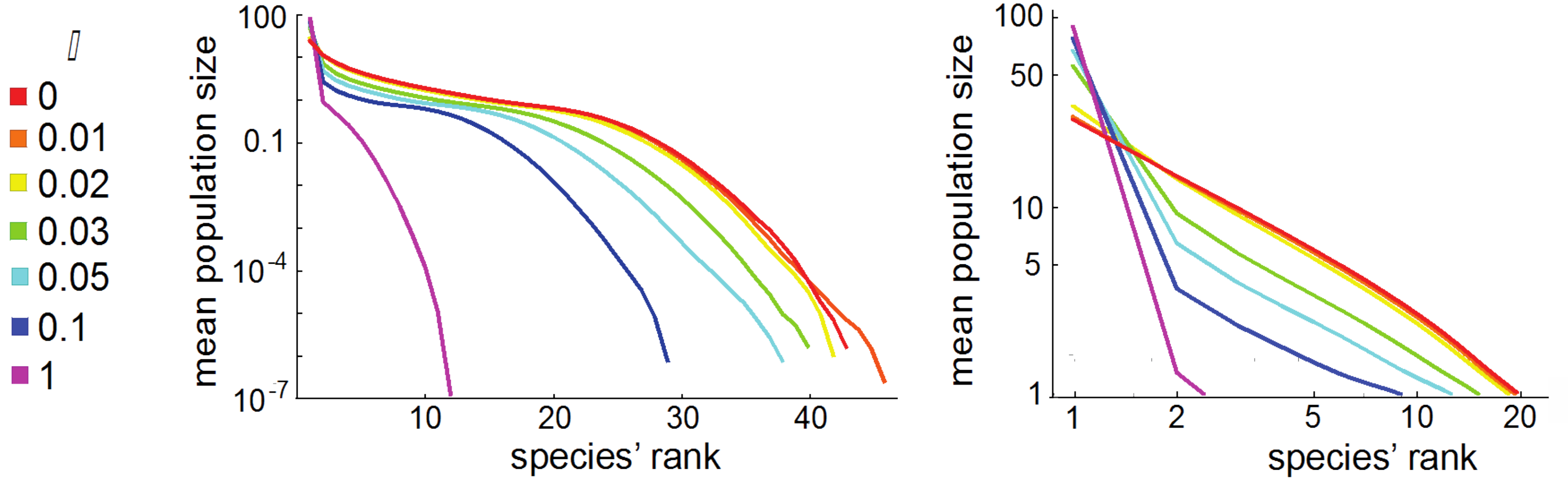
In the deterministic version of the model, diversity is lost. However, in the stochastic version, diversity can be maintained:



$\Sigma\leq 0.02$ ⇨ High diversity

$\Sigma\geq 0.03$ ⇨ Low diversity

Robustness of coexistence

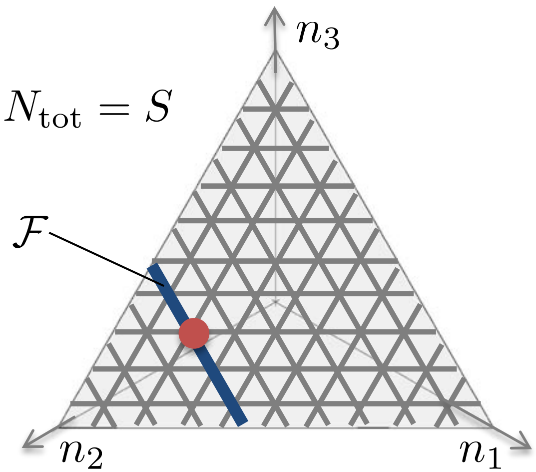
There is a critical standard deviation Σ^* that separates the high and low diversity regimes:

Estimate a species' lifetime T_0 when $\Sigma = 0$:

Assume $P(\#\text{ species present} \gg \#\text{ resources}) \approx 1.$

$\vec{N}(T)$ converges to $\mathcal{F}$, and on $\mathcal{F}$ the process is governed by neutral birth and death probabilities.

$$T_0 \propto S^2$$



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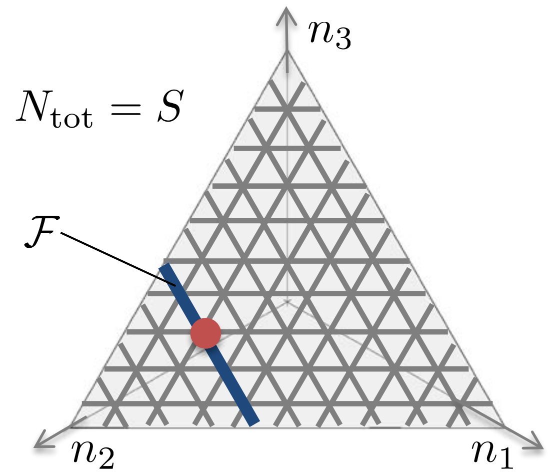

Estimate a species' lifetime T_Σ when $\Sigma > 0$:

$$\frac{dn_\sigma}{dt} = \left(\left(\sum_{i=1}^{p}(\alpha_{\sigma i} + \xi_{\sigma i})c_i\right) - \delta\right) n_\sigma \propto -\Sigma\, n_\sigma$$

$$T_\Sigma \propto \frac{S\log(S)}{\Sigma}$$

Robustness of coexistence

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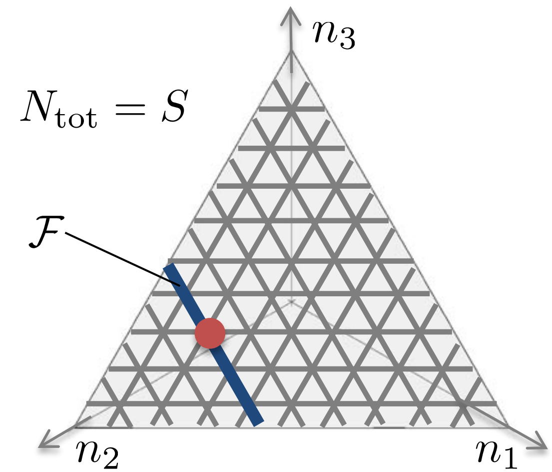

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$$T_0 \propto S^2$$

Estimate a species' lifetime T_Σ when $\Sigma > 0$:

$$\frac{dn_\sigma}{dt} = \left(\left(\sum_{i=1}^{p}(\alpha_{\sigma i} + \xi_{\sigma i})c_i\right) - \delta\right) n_\sigma \propto -\Sigma\, n_\sigma$$

$$T_\Sigma \propto \frac{S\log(S)}{\Sigma}$$

$$T_0 = T_\Sigma \quad \Rightarrow \quad \boxed{\Sigma^* \propto \log(S)/S}$$

Conclusions

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Thank you!

Posfai, Taillefumier, & NSW, Phys Rev Lett (2017)

Proof of convex hull condition

What are the steady-state concentrations of nutrients required for coexistence?

$$\text{growth rate} = \text{death rate}$$

$$\sum_{i=1}^{p} \alpha_{\sigma i} \frac{c_i}{1+c_i} = \delta$$

$$\Downarrow \text{ at least \#resources equations}$$

$$\frac{c_1^*}{1+c_1^*} = \ldots = \frac{c_p^*}{1+c_p^*} = \frac{\delta}{E}$$

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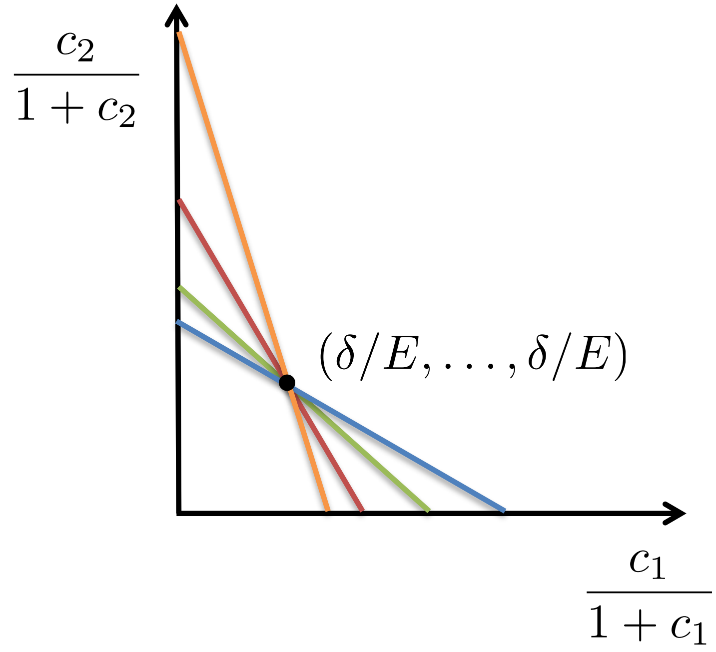

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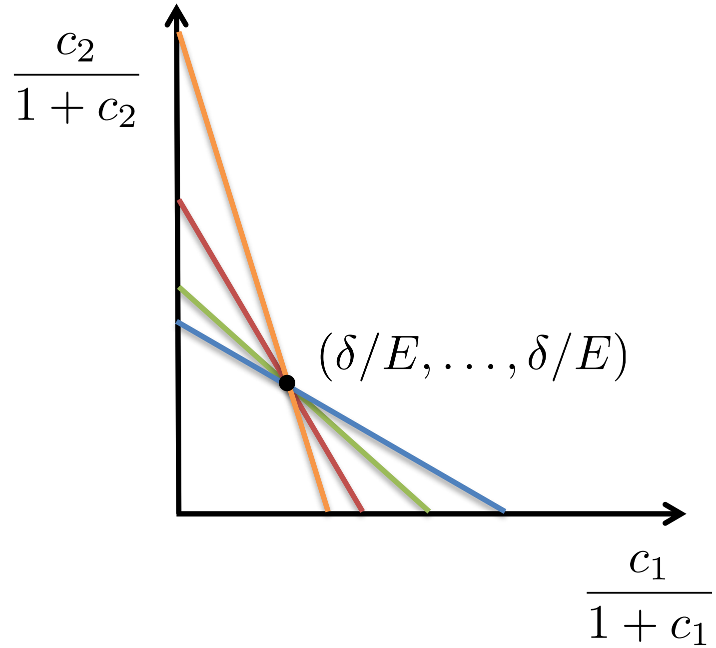

What strategies can adjust their populations to achieve these steady-state nutrient concentrations?

$$\frac{\delta}{E} = \frac{c_i^*}{1+c_i^*} = \frac{s_i}{\sum_\sigma n_\sigma \alpha_{\sigma i}}$$

$$n_1 \vec{\alpha}_1 + \ldots + n_m \vec{\alpha}_m = \frac{E}{\delta} \vec{s}$$

The solutions $\vec{n}$ form a #species − #resources dimensional plane in the space of population sizes.

$\exists$ solution $\vec{n} > 0$ if the supply $\vec{s}$ is in the convex hull of the strategies $\vec{\alpha}_\sigma$.