Simple rules predict effects of environmental change on coexistence.

Frederik De Laender[1], Camille Carpentier[1], Chuliang Song[2], Géza Meszena[3], György Barabás[4]

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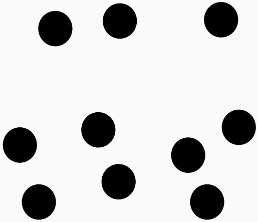
Setting the stage

Effects of environmental change seem hard to predict



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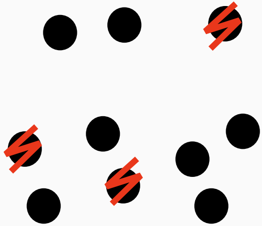

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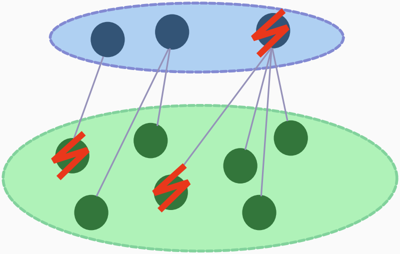

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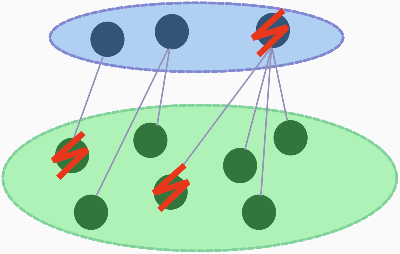

Average responses and **average** ecology predict effects on **coexistence**

We consider cases where feasibility[1] $\equiv$ coexistence

An equilibrium is **feasible** when it is positive for all species.

$$\mathbf{n}^* = -\mathbf{A}^{-1}\mathbf{b} > 0$$

[1] Meszena et al. 2016, TPB, 69. Grilli et al. 2017, Nat. Com. 8; Saavedra et al. 2017, Ecol. Mon. 87; Song et al. 2018, JTB 450.

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For a given $\mathbf{A}$, only certain $\mathbf{b}$ will produce $\mathbf{n}^* > 0$.

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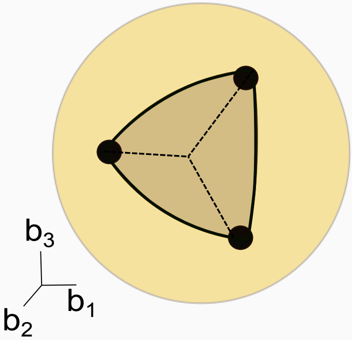
The **feasibility** domain: All $\mathbf{b}$ that make $\mathbf{n}^* > 0$, for a given $\mathbf{A}$.



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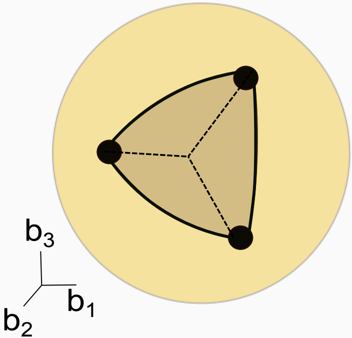
Environmental change affects **A** & **b**.



$$\mathbf{n}^* = -\mathbf{A}^{-1}\mathbf{b} > 0$$
$$\mathbf{n}^*_\varepsilon = -\mathbf{A}_\varepsilon{}^{-1}\mathbf{b}_\varepsilon > 0$$

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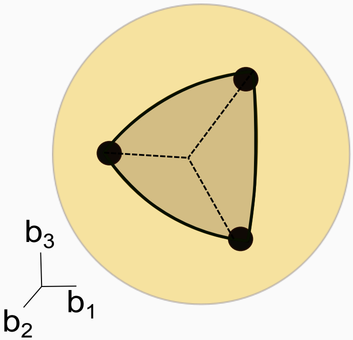
We consider **multiplicative** effects: $b_{\varepsilon,i} = b_i f_i(\varepsilon)$



$$\mathbf{n}^* = -\mathbf{A}^{-1}\mathbf{b} > 0$$
$$\mathbf{n}^*_\varepsilon = -{\mathbf{A}_\varepsilon}^{-1}\mathbf{b}_\varepsilon > 0$$

where $\mathbf{b}_\varepsilon = \mathbf{F}\mathbf{b}$ and
$\mathbf{F} = \mathrm{diag}(f_1(\varepsilon), ..., f_s(\varepsilon))$

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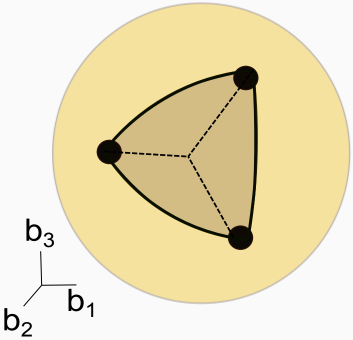
How will **effects** on **A** and **b** affect the feasibility domain?



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$$\mathbf{F} = \mathrm{diag}(f_1(\varepsilon), ..., f_s(\varepsilon))$$

$$\Leftrightarrow -(\underbrace{\mathbf{F}^{-1}\mathbf{A}_\varepsilon}_{\text{new } \mathbf{A}})^{-1}\mathbf{b} > 0$$

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From environmental change ε to effects on feasibility

$$b_{\varepsilon,i} = b_i f_i(\varepsilon)$$
$$\alpha_{\varepsilon,ij} = \alpha_{ij} g_j(\varepsilon)$$

Assumptions:

- multiplicative effects

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From environmental change ε to effects on feasibility

$$b_{\varepsilon,i} = b_i(1 + r_i\varepsilon)$$
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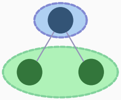
How do species responses r cause effects of ε on feasibility?

Simple communities

Approach

$$\mathbf{A} = \begin{pmatrix} -1 & 0 & -\alpha \\ 0 & -1 & -\alpha \\ \alpha & \alpha & 0 \end{pmatrix}$$



$$\mathbf{A} = \begin{pmatrix} -1 & -\alpha_2 & 0 \\ \alpha_2 & 0 & -\alpha_3 \\ 0 & \alpha_3 & 0 \end{pmatrix}$$

- incorporate responses r

[2] Gourion and Seeger, 2010, Comp.Appl.Math., 29.

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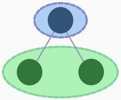

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- express[2] feasibility (Ξ)

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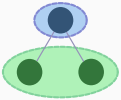

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- incorporate responses r
- express[2] feasibility (Ξ)
- derive $\frac{\partial \Xi}{\partial \varepsilon}$ and examine relationship with r's.

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Summary stats predict effects on feasibility (Ξ): bitrophic community

- $\frac{\partial \Xi}{\partial \varepsilon} = \underbrace{h(\alpha)}_{\text{ecology}} \underbrace{\delta}_{\substack{\text{species}\\\text{responses}}}$

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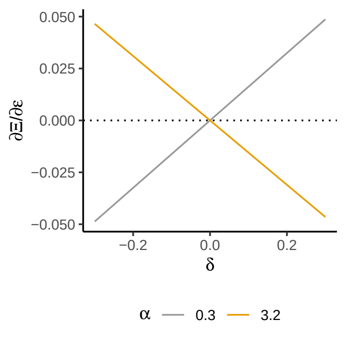

- $\underbrace{\frac{\partial \Xi}{\partial \varepsilon} = h(\alpha)}_{\text{ecology}} \; \underbrace{\delta}_{\text{species responses}}$
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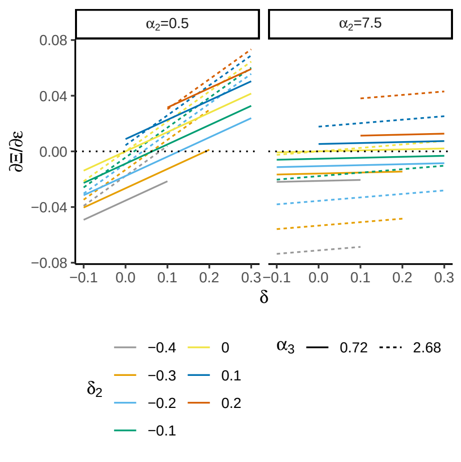
- $h(\alpha) > 0$ when consumption α is weak (and vice-versa)

Summary stats predict effects on feasibility (Ξ): tritrophic community



- $\frac{\partial \Xi}{\partial \varepsilon} = h_2(\alpha_2, \alpha_3)\delta + h_3(\alpha_2, \alpha_3)\delta_2$
- $\delta = r_1 - r_2 + r_{2g}$
- $\delta_2 = r_1 - r_{2g} - r_3 + r_{3g}$

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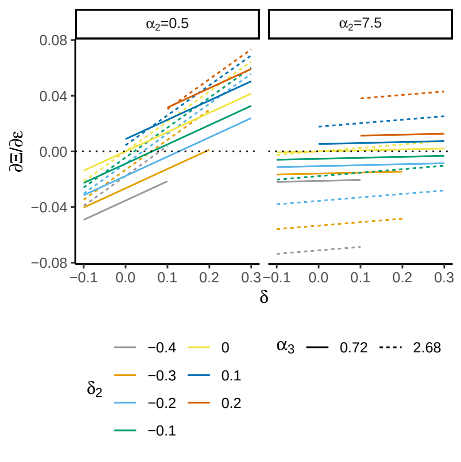

- $\frac{\partial \Xi}{\partial \varepsilon} = h_2(\alpha_2, \alpha_3)\delta + h_3(\alpha_2, \alpha_3)\delta_2$
- $\delta = r_1 - r_2 + r_{2g}$
- $\delta_2 = r_1 - r_{2g} - r_3 + r_{3g}$
- Effects of δ and δ_2 depend on consumption & predation, but **always positive**.

Do these predictions scale up to more complex communities? Simulation results

Yes in bitrophic communities

Simple communities:

- responses: $\delta = \frac{r_1 + r_2}{2} - r_3 + r_{3g}$
- ecology: α

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$$\delta = \underbrace{\overline{r_r}}_{\text{avg. across resources}} - \underbrace{\overline{r_c}}_{\text{avg. across consumers (mortality)}} + \underbrace{\overline{r_{cg}}}_{\text{avg. across consumers (consumption)}}$$

- ecology: $\overline{\alpha}$

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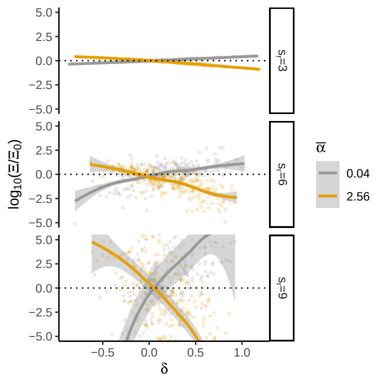

s_r =nr of resources

$s_c = s_r/3$

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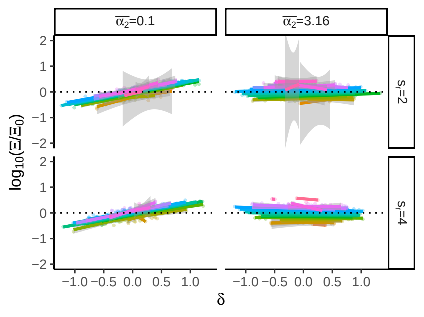
Effect of δ is positive (negative) when consumption $\overline{\alpha}$ is weak (strong)

Probably not in tritrophic communities



$s_c = s_p = 1$
colours = different δ_2

- Effect of δ stops being positive when consumer-resource interactions are strong.

What is δ in real life?

Example 1: δ depends on temperature optima

$$\varepsilon = \Delta T$$

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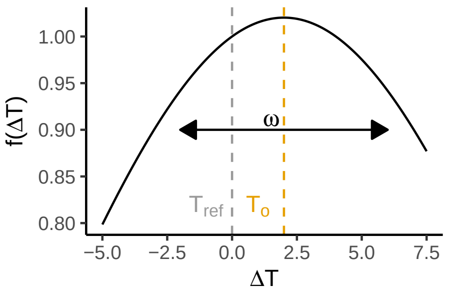

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$$\delta = \underbrace{\left(\overline{\omega_r^{-2}(T_{o,r} - T_{ref})}\right)}_{\text{resources}} + \underbrace{\left(\overline{\omega_c^{-2}(T_{o,c} - T_{ref})}\right)}_{\text{consumers}}$$

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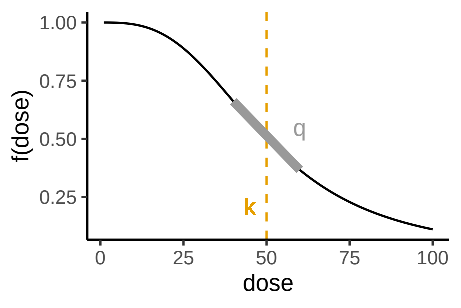
Example 2: δ depends on pollutant thresholds k

$$\delta \approx -\underbrace{\overline{k_r^{-q_r} q_r}}_{\text{resources}} - \underbrace{\overline{k_c^{-q_c} q_c}}_{\text{consumers}}$$



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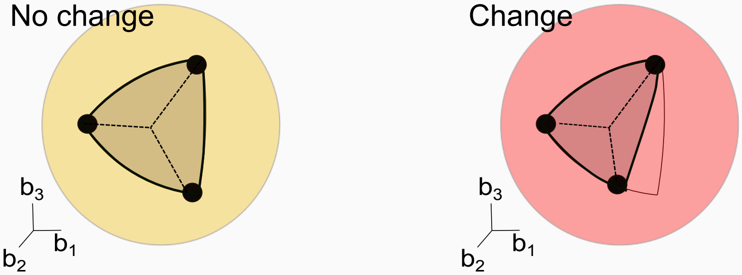
What are “effects on feasibility” in real life?

What does it mean when feasibility shrinks?



Communities persist over a narrower range of b_i

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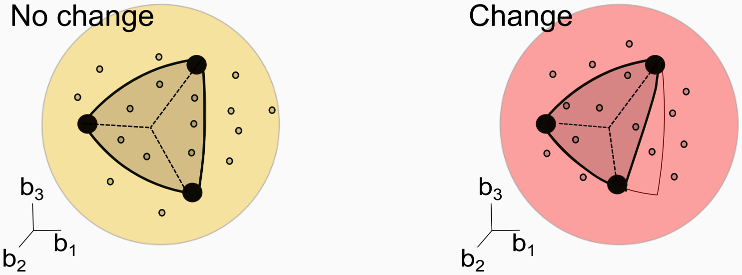

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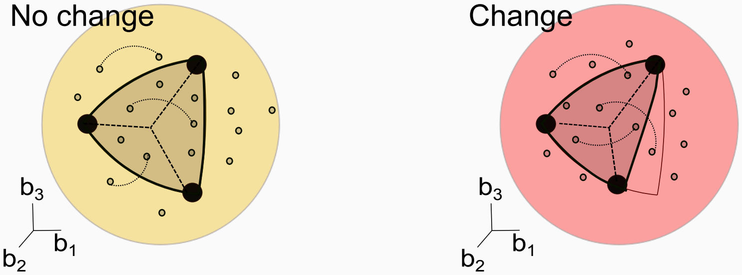

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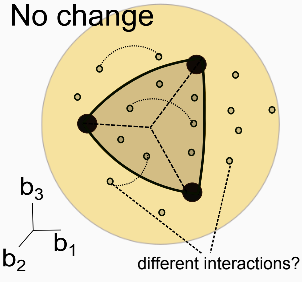

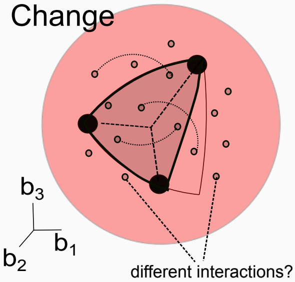

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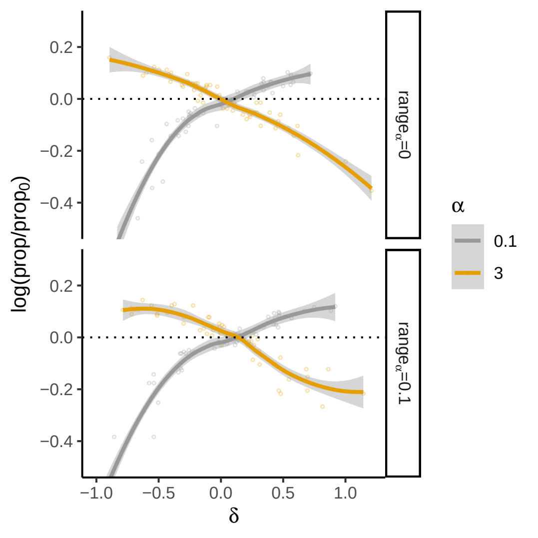
However: communities organise into metacommunities...

However: environmental conditions can also change interactions.

Does δ predict effects on site occupancy?

Yes in bitrophic communities ($s = 3$)



- Theoretical results still stand;
- No influence of dispersal or within-region differences of α (range).

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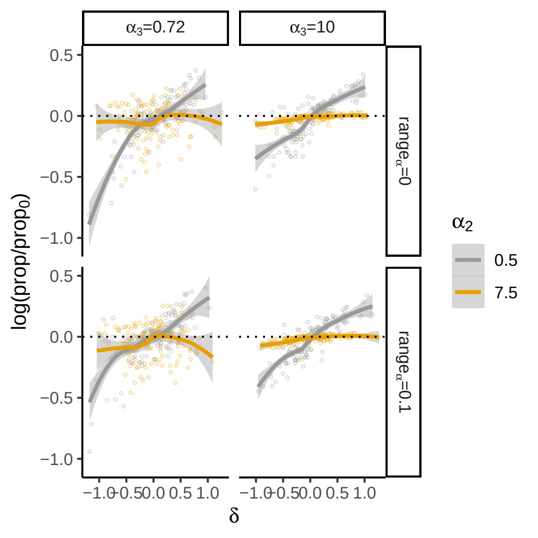

- Theoretical results still stand;
- No influence of dispersal or within-region differences of α_2 or α_3 (range).

Wrap-up

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- Applicable to predict site occupancy;
- But: what about more complex models?
- But: what about testing this empirically?
- But: what about other definitions of coexistence?

Time for questions

Supplements

How do species responses change α in bitrophic communities?

W/o environmental change: $\begin{pmatrix} -\frac{1}{\sqrt{\alpha_1^2+1}} & 0 & -\frac{\alpha_1}{\sqrt{\alpha_1^2+\alpha_2^2}} \\ 0 & -\frac{1}{\sqrt{\alpha_2^2+1}} & -\frac{\alpha_1}{\sqrt{\alpha_1^2+\alpha_2^2}} \\ \frac{\alpha_1}{\sqrt{\alpha_1^2+1}} & \frac{\alpha_2}{\sqrt{\alpha_2^2+1}} & 0 \end{pmatrix}$

W environmental change:

$$\begin{pmatrix} -\frac{1}{\sqrt{\alpha_1^2 f_1^2 f_3^{-2} g_3^2+1}} & 0 & -\frac{\alpha_1 f_2}{\sqrt{\alpha^2(f_1^2+f_2^2)}} \\ 0 & -\frac{1}{\sqrt{\alpha^2 f_2^2 f_3^{-2} g_3^2+1}} & -\frac{\alpha f_1}{\sqrt{\alpha^2(f_1^2+f_2^2)}} \\ \frac{\alpha f_1 f_3^{-1} g_3}{\sqrt{\alpha^2 f_1^2 f_3^{-2} g_3^2+1}} & \frac{\alpha f_2 f_3^{-1} g_3}{\sqrt{\alpha^2 f_2^2 f_3^{-2} g_3^2+1}} & 0 \end{pmatrix}$$

Remember:

$f_i = f_i(\varepsilon) = 1 + r_i\varepsilon$

$g_j = g_j(\varepsilon) = 1 + r_j\varepsilon$

How do species responses change α in tritrophic communities?

(make other assumption!)

W/o environmental change: $$\begin{pmatrix} \frac{1}{\sqrt{\alpha_2^2+1}} & \frac{\alpha_2}{\sqrt{\alpha_2^2+\alpha_3^2}} & 1 \\ -\frac{\alpha_2}{\sqrt{\alpha_2^2+1}} & 0 & 0 \\ 0 & -\frac{\alpha_3}{\sqrt{\alpha_2^2+\alpha_3^2}} & 0 \end{pmatrix}$$

W environmental change: $$\begin{pmatrix} \frac{1}{\sqrt{\alpha_2^2 f_1^2 f_2^{-2} g_2^2+1}} & \frac{\alpha_2 g_2}{\sqrt{\alpha_2^2 g_2^2+\alpha_3^2 f_1^2 f_3^{-2} g_3^2}} & 1 \\ -\frac{\alpha_2 f_1 f_2^{-1} g_2}{\sqrt{\alpha_2^2 f_1^2 f_2^{-2} g_2^2+1}} & 0 & 0 \\ 0 & -\frac{\alpha_3 g_3}{\sqrt{\alpha_2^2 f_1^{-2} f_3^2 g_2^2+\alpha_3^2 g_3^2}} & 0 \end{pmatrix}$$

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