International Conference MPDE'16

Models in Population Dynamics and Ecology

Centre International de Rencontres Mathématiques – Aix-Marseille University

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Effects of host diversity and complex foraging on the dynamics of trophically transmitted parasites

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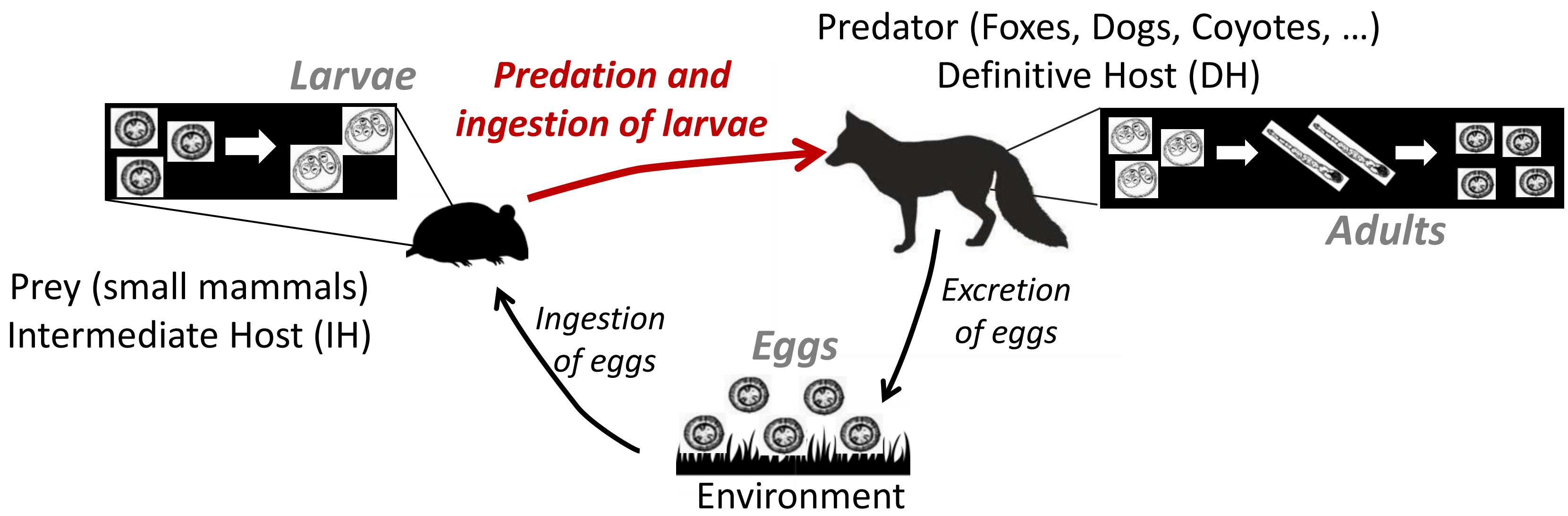
What flow in food webs?

- Matter and energy (Lindeman, 1942; Loreau 2010) → Occurrence and strength of links
- Parasites (Lafferty et al., 2006) → 40 – 75 % of food web links (Dobson et al., 2008)

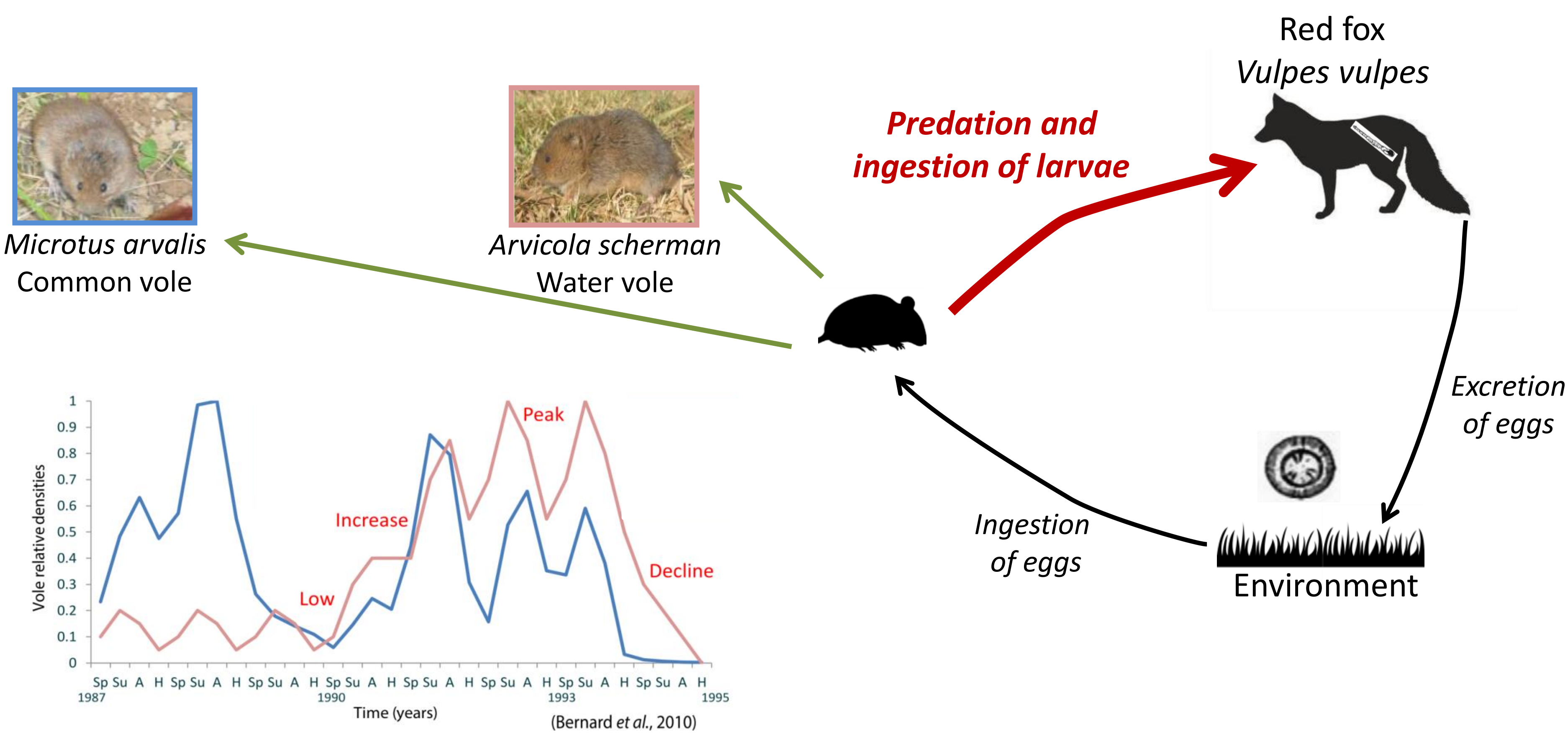
What flow in food webs?

- Matter and energy (Lindeman, 1942; Loreau 2010) ➞ Occurrence and strength of links
- Parasites (Lafferty et al., 2006) ➞ 40 – 75 % of food web links (Dobson et al., 2008)

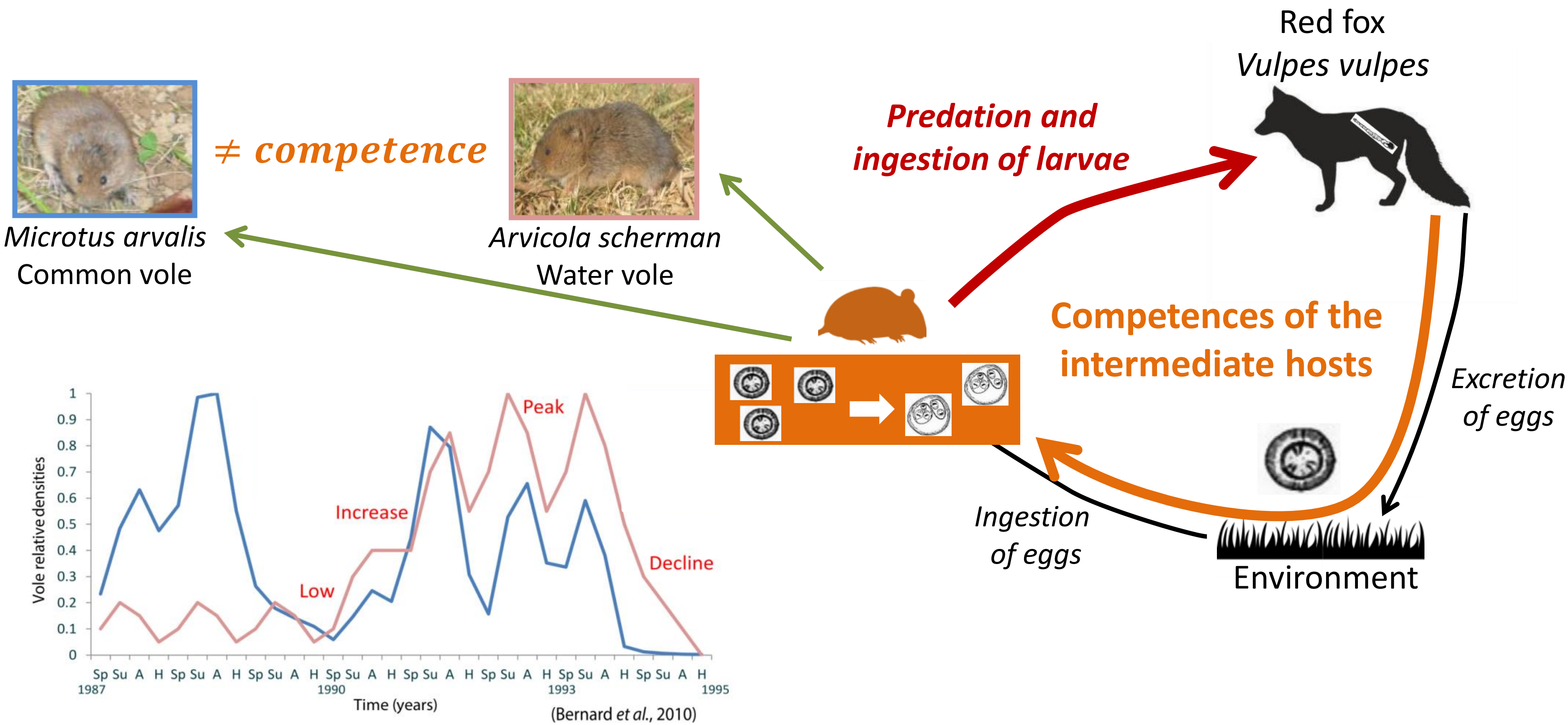
Multi-host parasites: *Echinococcus multilocularis*



Eco-epidemiological system



- Rodents dynamics are commonly fluctuating
  (Kendall, 1998; Schmidt and Ostfeld, 2008; Krebs, 2013)



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  (Kendall, 1998; Schmidt and Ostfeld, 2008; Krebs, 2013)

How prey **biodiversity** influence the **dynamics** of trophically transmitted **parasites**?

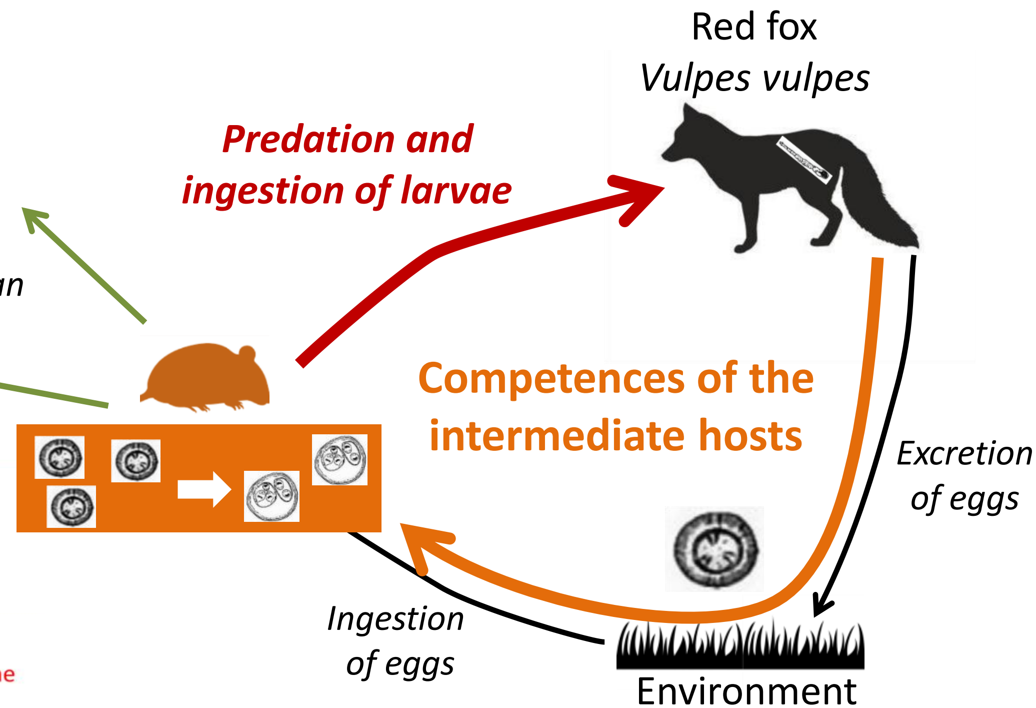
Part 1 - Baudrot et al. (2016), *Ecology*

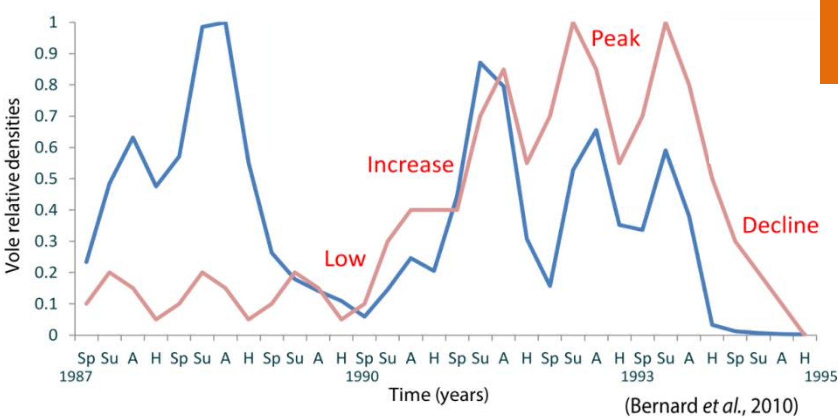
How predators adapt their foraging to changes in the prey community?

Microtus arvalis
Common vole

≠ *competence*

Arvicola scherman
Water vole





- Rodents dynamics are commonly fluctuating
  (Kendall, 1998; Schmidt and Ostfeld, 2008; Krebs, 2013)

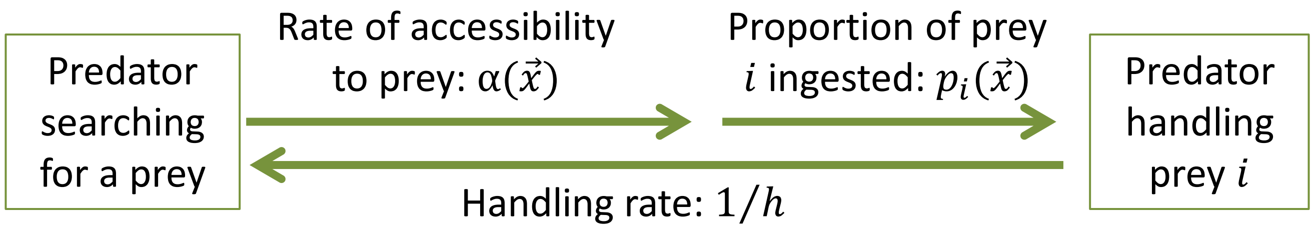
Part 2 – Baudrot et al. (2016), *JTB*

How variability in host competence change the parasite dynamics?

Multi-Species Functional Responses – MSFR: $\Phi_i(\vec{x})$

Rate of ingestion of a prey i depending on the **prey community** (Oaten and Murdoch, 1975; Gentleman et al., 2003)

A general mechanism…



Main previous studies: Poggiale et al. (1998) ; Jeschke (2002); Leeuwen et al. (2007)

Multi-Species Functional Responses – MSFR: $\Phi_i(\vec{x})$

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A general mechanism…

Predator searching for a prey

Rate of accessibility to prey: $\alpha(\vec{x})$

Proportion of prey i ingested: $p_i(\vec{x})$

Predator handling prey i

Handling rate: $1/h$

Main previous studies: Poggiale et al. (1998) ; Jeschke (2002); Leeuwen et al. (2007)

… giving a general formulation…

$$\Phi_i(\vec{x}) = p_i(\vec{x}) \times \frac{\alpha(\vec{x})}{1 + \alpha(\vec{x})h} = p_i(\vec{x}) \times \Theta(\vec{x})$$

p_i: Proportion of prey i ingested
What is the preference?

Θ: Total of prey ingested
$\approx$ **energy available/time**

Multi-Species Functional Responses – MSFR: $\Phi_i(\vec{x})$

Rate of ingestion of a prey i depending on the **prey community** (Oaten and Murdoch, 1975; Gentleman et al., 2003)

A general mechanism…

Predator searching for a prey → Rate of accessibility to prey: $\alpha(\vec{x})$ → Proportion of prey i ingested: $p_i(\vec{x})$ → Predator handling prey i

Predator handling prey i → Handling rate: $1/h$ → Predator searching for a prey

Main previous studies: Poggiale et al. (1998) ; Jeschke (2002); Leeuwen et al. (2007)

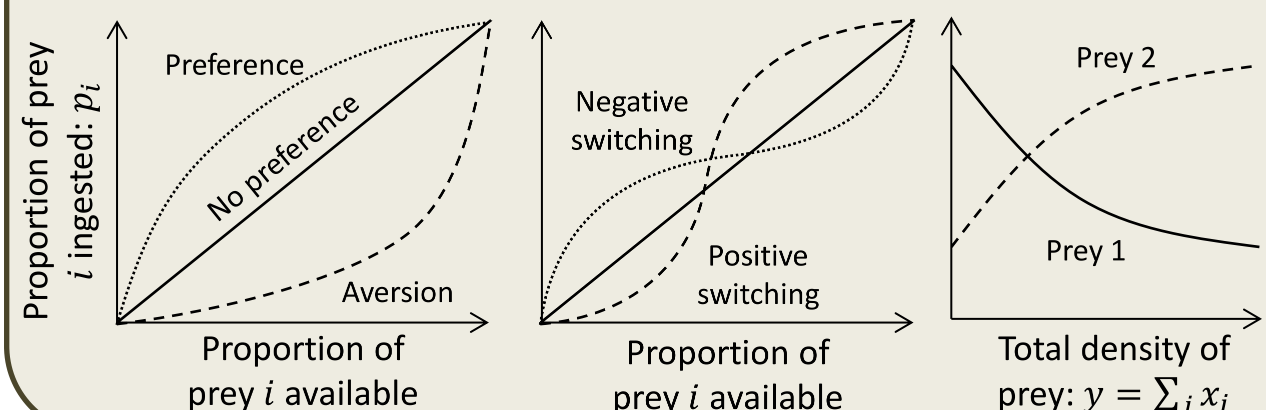
… giving a general formulation…

$$\Phi_i(\vec{x}) = \boxed{p_i(\vec{x})} \times \boxed{\Theta(\vec{x})}$$

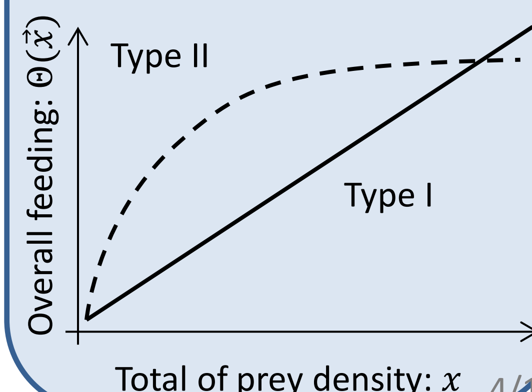
… several phenomenological properties…

(Holling 1959; Murdoch, 1972; Oaten and Murdoch, 1975; Tilman 1980, Holt 1983; Chesson, 1984; Gentleman et al., 2003; Van Leeuwen et al., 2007; Morozov and Petrovskii, 2013; Vallina et al., 2014)

Preference | Switching | Rank switching

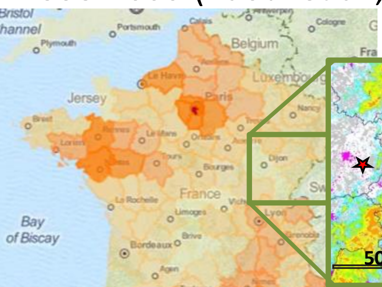


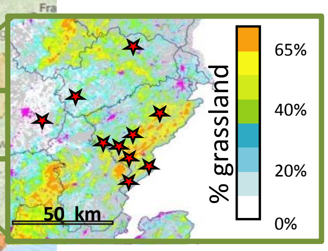
Shape of the total of prey ingested



10 study sites (aver. 85.6 km²)

1995-2000 (Raoul et al., 2010)





Identification of teeth and bones in faeces

Model	$p_i(\vec{x})$	Switching	Rank switching	$\theta(\vec{x})$	Overall feeding	*Vulpes vulpes* n.p.	*Vulpes vulpes* $WAIC$	*Vulpes vulpes* $\Delta WAIC$ (rank)
H2.1	$\frac{a_i x_i}{\sum_j a_j x_j}$	NO	NO	$\frac{\sum_j a_j x_j}{1+\mathrm{h}\sum_j a_j x_j}$	NO	3	666.25	221.57 (9)
H2.2	$\frac{a_i \lambda_i y^{r_i}}{\sum_j a_j \lambda_j y^{r_j}}$	NO	YES	$\frac{\sum_j a_j x_j}{1+\mathrm{h}\sum_j a_j x_j}$	NO	5	501.12	56.44 (8)
H2.3	$\frac{a_i \lambda_i y^{r_i}}{\sum_j a_j \lambda_j y^{r_j}}$	NO	YES[a]	$\frac{\sum_j a_j {x_j}^{n_j}}{1+\mathrm{h}\sum_j a_j x_j^{n_j}}$	YES[b]	7	494.22	49.54 (6)
KTW.1	$\frac{a_i x_i^m}{\sum_j a_j x_j^m}$	YES	NO	$\frac{\sum_j a_j x_j}{1+\mathrm{h}\sum_j a_j x_j}$	NO	4	500.86	56.18 (7)
KTW.2	$\frac{a_i x_i^{m_i}}{\sum_j a_j x_j^{m_j}}$	YES[a]	YES[a]	$\frac{\sum_j a_j x_j}{1+\mathrm{h}\sum_j a_j x_j}$	NO	5	462.19	17.51 (5)
KTW.3	$\frac{a_i \lambda_i^{m_i} y^{r_i}}{\sum_j a_j \lambda_j^{m_j} y^{r_j}}$	YES[a]	YES[b]	$\frac{\sum_j a_j x_j}{1+\mathrm{h}\sum_j a_j x_j}$	NO	7	458.99	14.31 (3)
H3.1	$\frac{a_i x_i^{m_i}}{\sum_j a_j x_j^{m_j}}$	YES[a]	YES[a]	$\frac{\sum_j a_j x_j^{m_j}}{1+\mathrm{h}\sum_j a_j x_j^{m_j}}$	YES[a]	5	444.68	0.00 (1)
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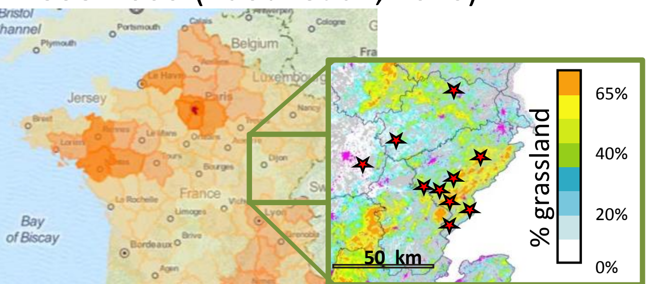

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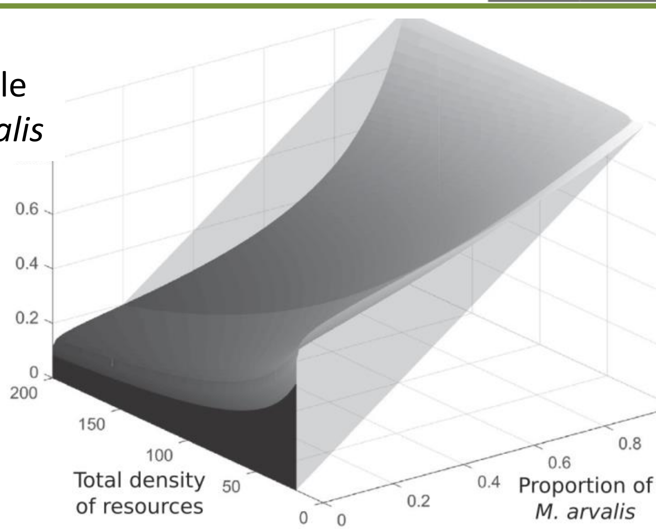
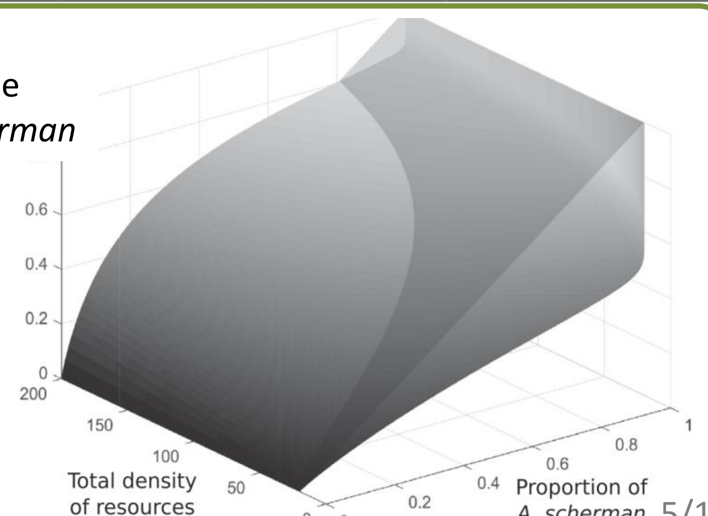
Common vole

Microtus arvalis



Water vole

Arvicola scherman



Frequency-dependent and **density-dependent** switching are critical properties
→ **inclusion in the epidemiological model…**

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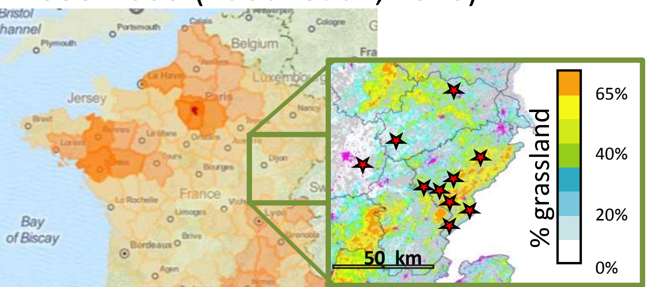

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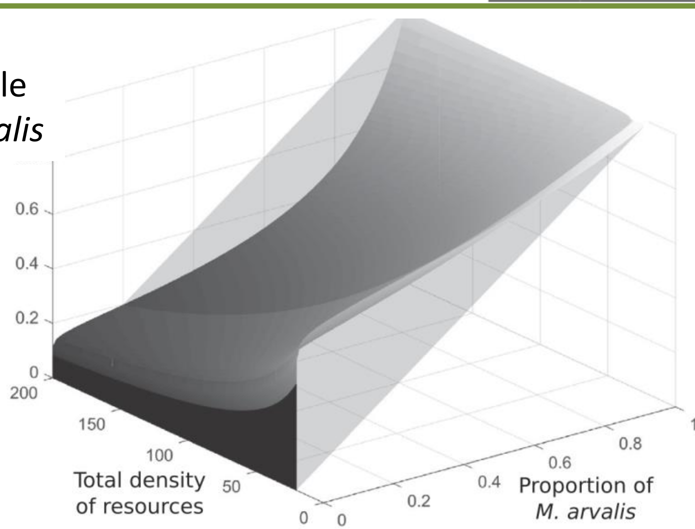
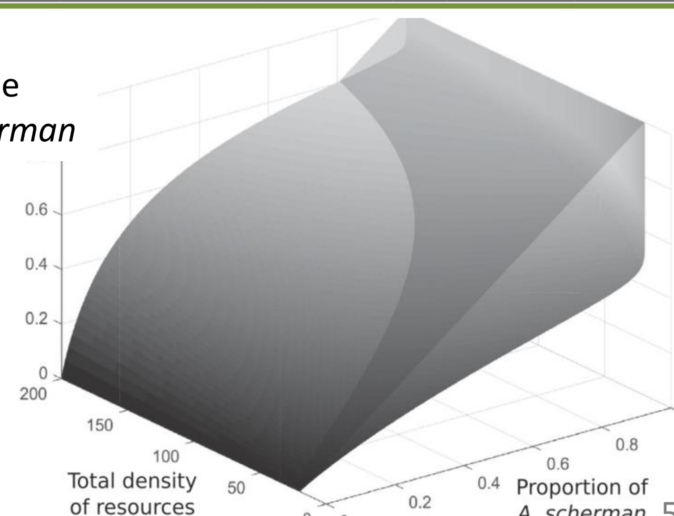
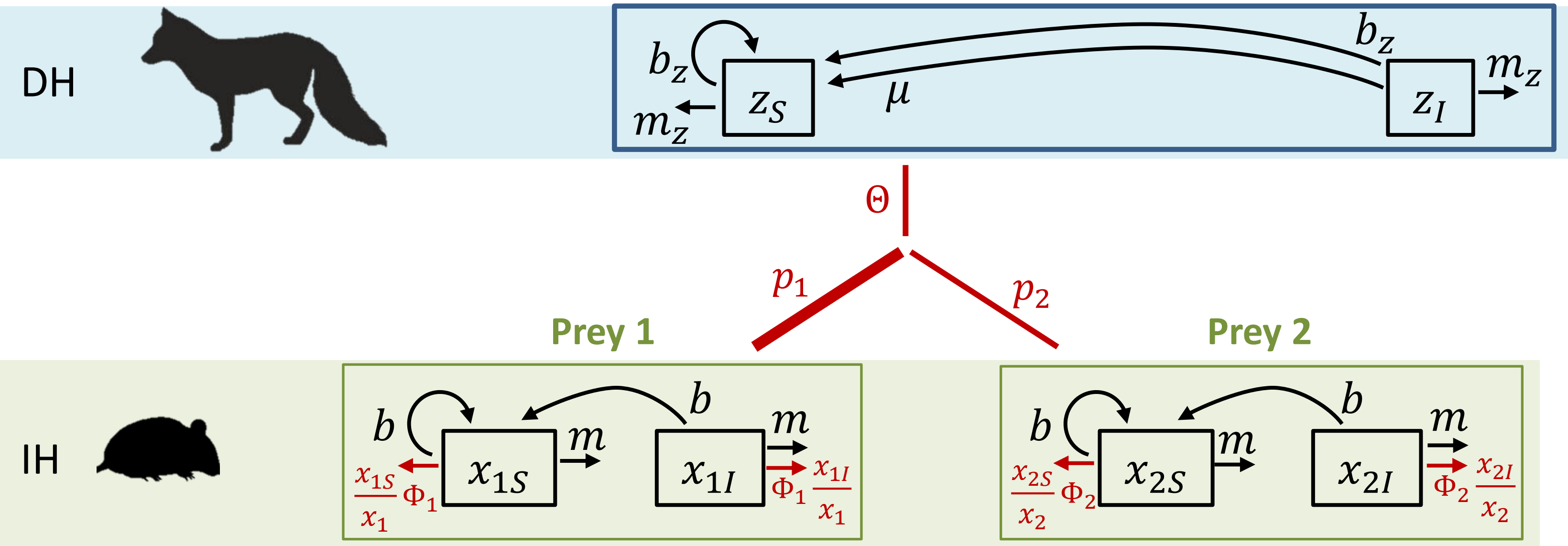
Common vole
Microtus arvalis



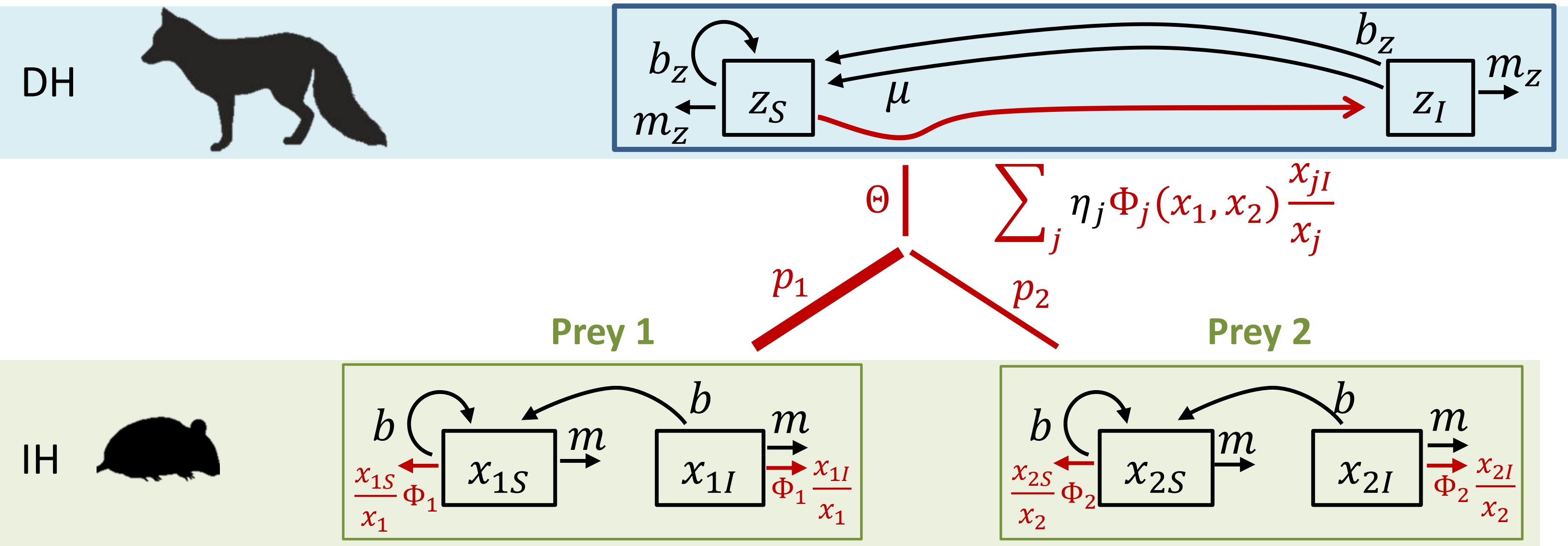
Water vole
Arvicola scherman



Trophically Transmitted Parasite



		Population growth	**Predation**	**Epidemic**
$\frac{dz_S}{dt}$	$=$	$b_z z - \left(m_z + (b_z - m_z)\frac{z_S + z_I}{k_z}\right) z_S$		$+\mu z_I$
$\frac{dx_{iS}}{dt}$	$=$	$b x_i - \left(m + (b - m)\frac{\sum_j x_{jS} + x_{jI}}{k}\right) x_{iS}$	$-\mathrm{p}_i(x_1, x_2)\Theta(x_1, x_2)\frac{x_{iS}}{x_i} z$	
$\frac{dz_I}{dt}$	$=$	$-\left(m_z + (b_z - m_z)\frac{z_S + z_I}{k_z}\right) z_I$		$-\mu z_I$
$\frac{dx_{iI}}{dt}$	$=$	$-\left(m + (b - m)\frac{\sum_j x_{jS} + x_{jI}}{k}\right) x_{iI}$	$-\mathrm{p}_i(x_1, x_2)\Theta(x_1, x_2)\frac{x_{iI}}{x_i} z$	



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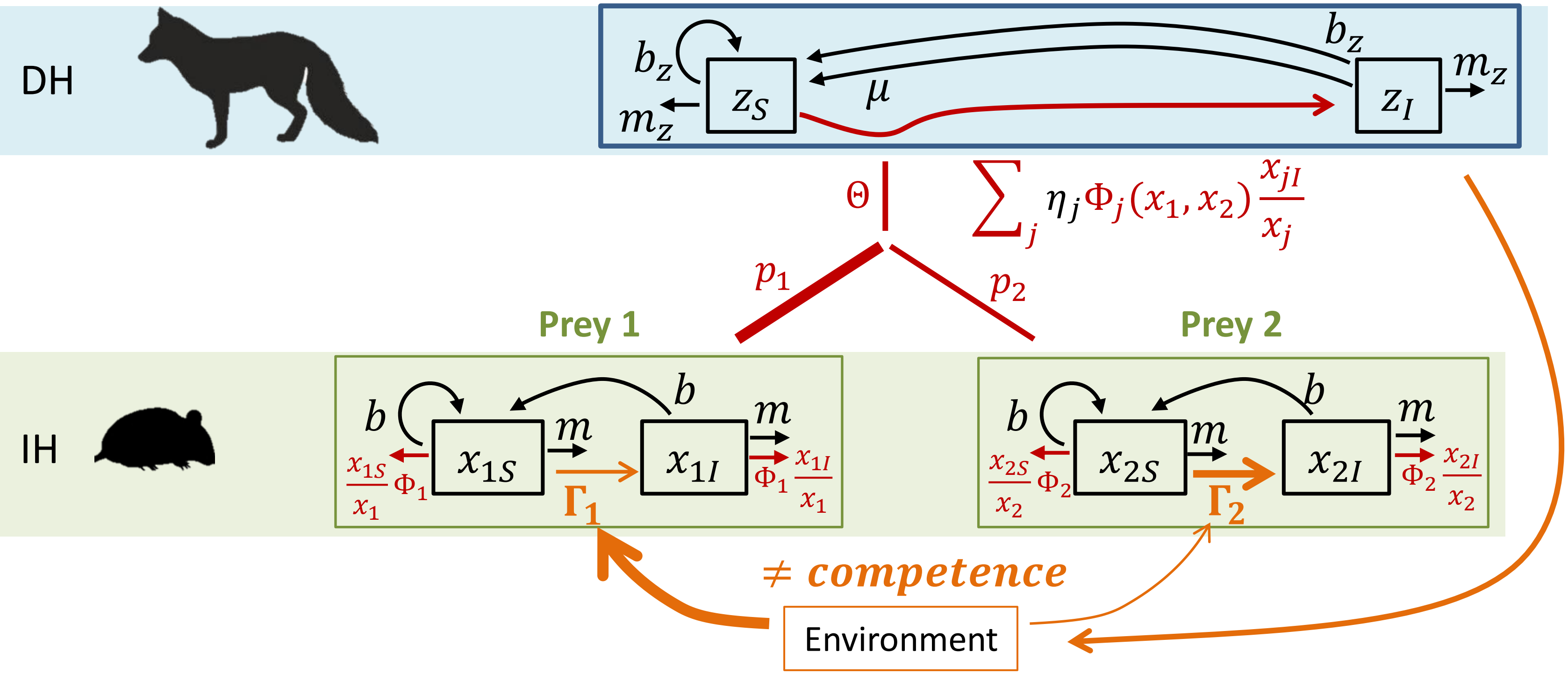
$\frac{dz_S}{dt}$	$=$	$b_z z - \left(m_z + (b_z - m_z)\frac{z_S + z_I}{k_z}\right) z_S$		$-z_S \sum_i \eta_i \Phi_i(x_1, x_2) \frac{x_{iI}}{x_i} + \mu z_I$
$\frac{dx_{iS}}{dt}$	$=$	$b x_i - \left(m + (b - m)\frac{\sum_j x_{jS} + x_{jI}}{k}\right) x_{iS}$	$-\mathrm{p}_i(x_1, x_2)\Theta(x_1, x_2)\frac{x_{iS}}{x_i} z$	
$\frac{dz_I}{dt}$	$=$	$-\left(m_z + (b_z - m_z)\frac{z_S + z_I}{k_z}\right) z_I$		$+z_S \sum_i \eta_i \Phi_i(x_1, x_2) \frac{x_{iI}}{x_i} - \mu z_I$
$\frac{dx_{iI}}{dt}$	$=$	$-\left(m + (b - m)\frac{\sum_j x_{jS} + x_{jI}}{k}\right) x_{iI}$	$-\mathrm{p}_i(x_1, x_2)\Theta(x_1, x_2)\frac{x_{iI}}{x_i} z$	

Trophically Transmitted Parasite



	Population growth	Predation	Epidemic
$\frac{dz_S}{dt} =$	$b_z z - \left(m_z + (b_z - m_z)\frac{z_S + z_I}{k_z}\right) z_S$		$-z_S \sum_i \eta_i \Phi_i(x_1, x_2) \frac{x_{iI}}{x_i} + \mu z_I$
$\frac{dx_{iS}}{dt} =$	$b x_i - \left(m + (b - m)\frac{\sum_j x_{jS} + x_{jI}}{k}\right) x_{iS}$	$-p_i(x_1, x_2)\Theta(x_1, x_2)\frac{x_{iS}}{x_i} z$	$-z_I \Gamma_i x_{iS}$
$\frac{dz_I}{dt} =$	$-\left(m_z + (b_z - m_z)\frac{z_S + z_I}{k_z}\right) z_I$		$+z_S \sum_i \eta_i \Phi_i(x_1, x_2) \frac{x_{iI}}{x_i} - \mu z_I$
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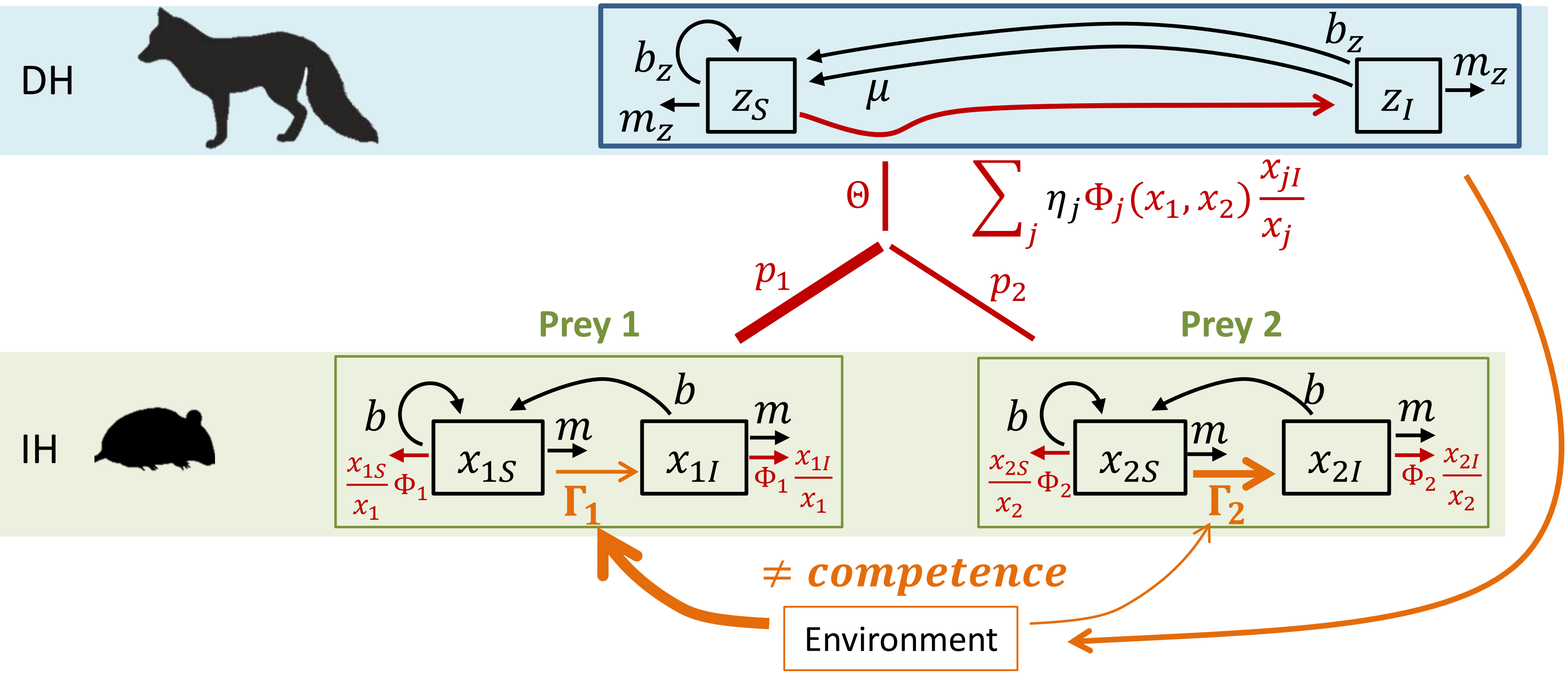
How biodiversity of IH may influence the dynamic of the parasite?



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Measure of disease risk : Basic reproductive number = $\mathcal{R}_0$

Expected number of secondary cases per primary case in a **disease-free population**

Disease Free Equilibrium - DFE

Total pop. $=\sum$ *clinical state* ➡ $\mathrm{DFE}=(z_S=z^*, x_{iS}=x_i^*, z_I=0, x_{iI}=0)$

- Math: *DFE is stable (LAS) if* $0<\mathcal{R}_0<1$ *and unstable if* $\mathcal{R}_0>1$
- Bio: *If* $\mathcal{R}_0>1 \Rightarrow$ *Epidemic, if* $0<\mathcal{R}_0<1 \Rightarrow$ *No epidemic*

Measure of disease risk : Basic reproductive number = $\mathcal{R}_0$

Expected number of secondary cases per primary case in a **disease-free population**

Disease Free Equilibrium - DFE

Total pop. $= \sum$ *clinical state* $\Rightarrow$ $\text{DFE} = (z_S = z^*, x_{iS} = x_i^*, z_I = 0, x_{iI} = 0)$

- Math: *DFE is stable (LAS) if* $0 < \mathcal{R}_0 < 1$ *and unstable if* $\mathcal{R}_0 > 1$
- Bio: *If* $\mathcal{R}_0 > 1 \Rightarrow$ *Epidemic, if* $0 < \mathcal{R}_0 < 1 \Rightarrow$ *No epidemic*

Explicit formulation of the DFE

Change of variables:

- Total prey density: $y = x_1 + x_2$
- Proportion of prey 1: $\lambda_1 = x_1/(x_1 + x_2)$

Assumptions:

- Consistency of MSFR: $p_i = p_{iS} + p_{iI}$
  (Morozov and Petrovskii, 2013)
- Overall feeding: $\Theta(x_1, x_2) = \theta(y)$
- Preference: $p_1(x_1, x_2) = \rho_1(\lambda_1, y)$

Measure of disease risk : Basic reproductive number = $\mathcal{R}_0$

Expected number of secondary cases per primary case in a **disease-free population**

Disease Free Equilibrium - DFE

Total pop. $=\sum$ *clinical state* ➡ $\mathrm{DFE}=(z_S=z^*, x_{iS}=x_i^*, z_I=0, x_{iI}=0)$

- Math: *DFE is stable (LAS) if* $0<\mathcal{R}_0<1$ *and unstable if* $\mathcal{R}_0>1$
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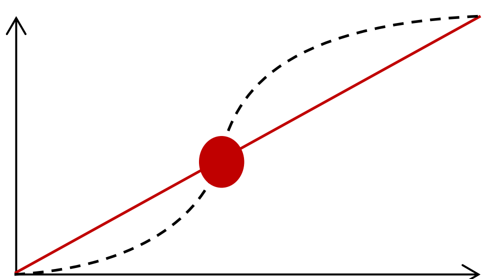
Conditions for the DFE

$\boldsymbol{\lambda_1^*=\rho_1(\lambda_1^*,y^*)}$ ➡ Switching (or no preference)

$$z^*=k_z$$

$$ry^*\left(1-\frac{y^*}{k}\right)=\theta(y^*)z^*$$



Measure of disease risk : Basic reproductive number = $\mathcal{R}_0$

Next Generation Matrix (Diekmann et al., 1990 and 2009, Driessche and Watmough, 2002)

Foraging behavior (MSFR)

$$\mathcal{R}_0 = \sqrt{\frac{\eta z^*}{b(b_z+\mu)} \times \left(\Gamma_1 \Phi_1(x_1^*, x_2^*) + \Gamma_2 \Phi_2(x_1^*, x_2^*)\right)}$$

"Introduction" of susceptibles

Competence of hosts

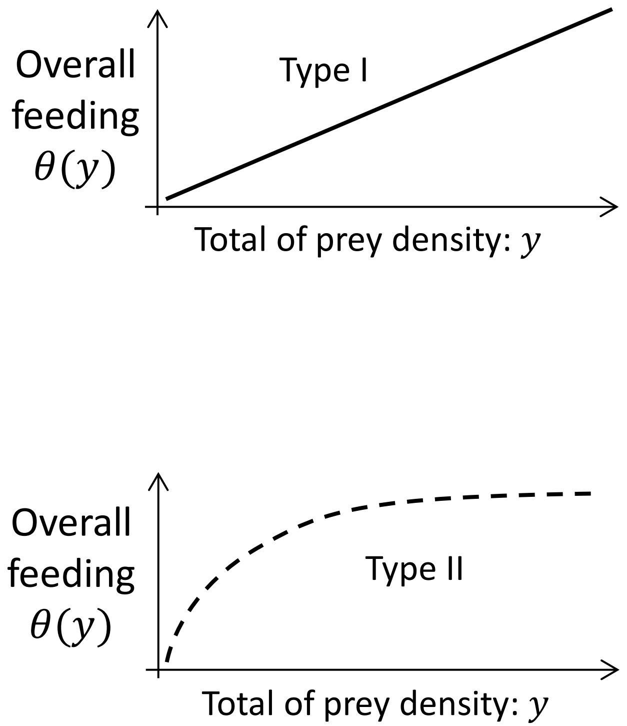
With the change of variables + condition at DFE

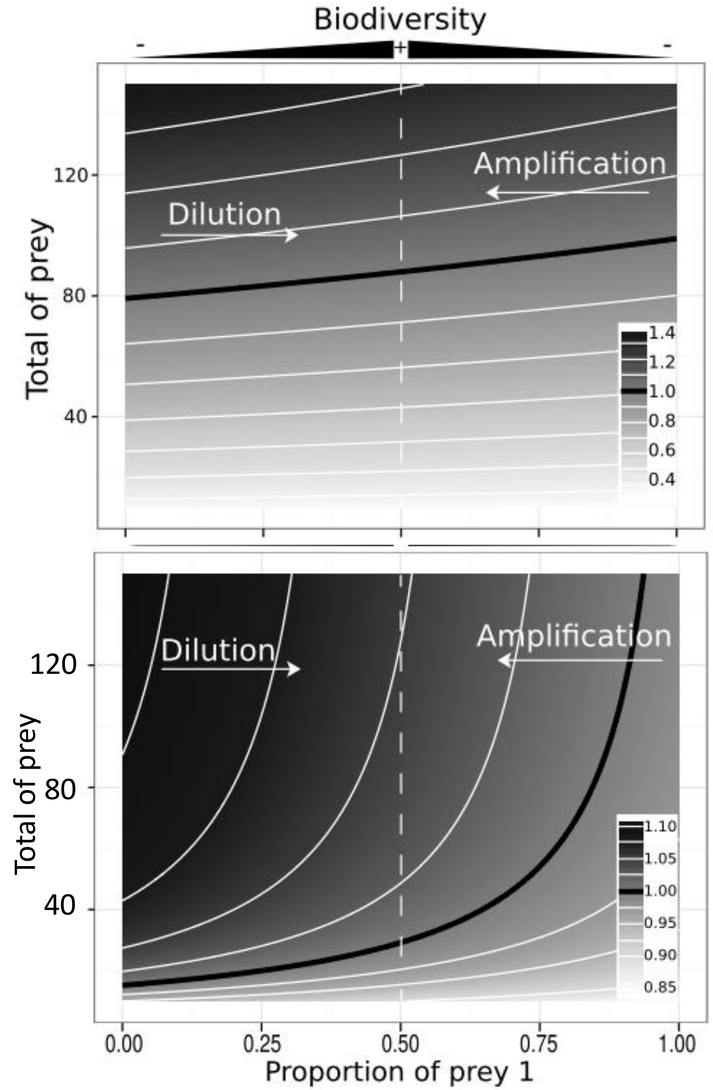
$$\mathcal{R}_0 = \sqrt{\frac{\eta z^* \theta(y^*)}{b(b_z+\mu)} \times \left(\Gamma_2 + \boxed{\lambda_1^* \times (\Gamma_1 - \Gamma_2)}\right)}$$

- Diversity of IH
- $\neq$ competences

Overall feeding + Different competences

$\Gamma_1 = 1.2 \times 10^{-4} < \Gamma_2 = 1.5 \times 10^{-1}$





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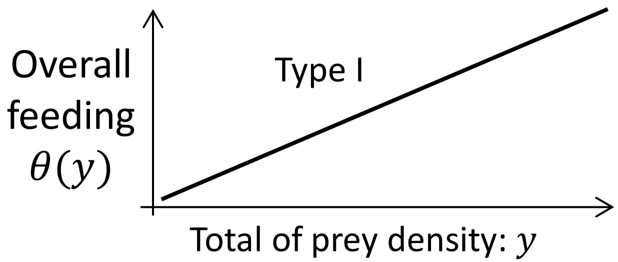
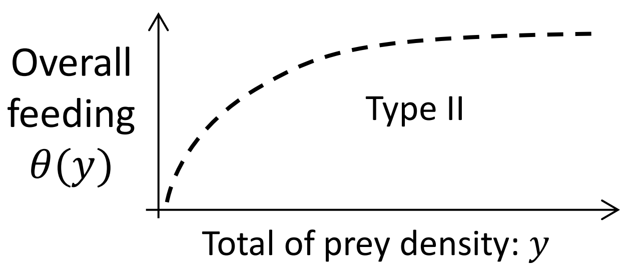
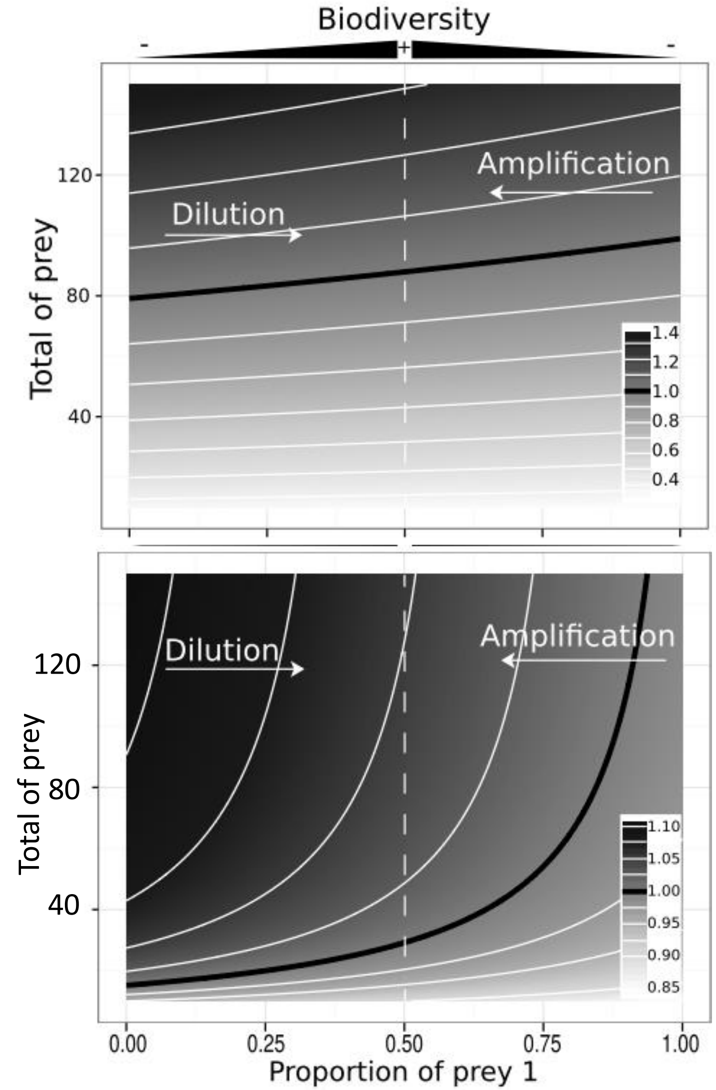


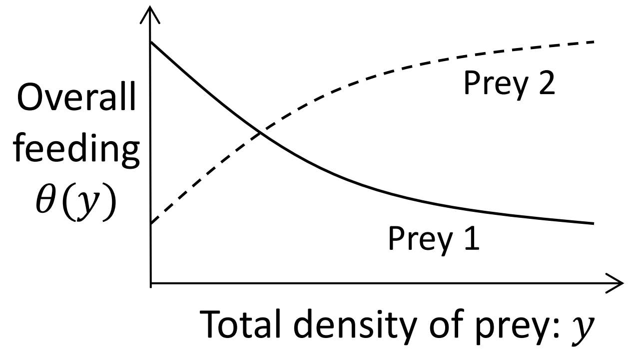


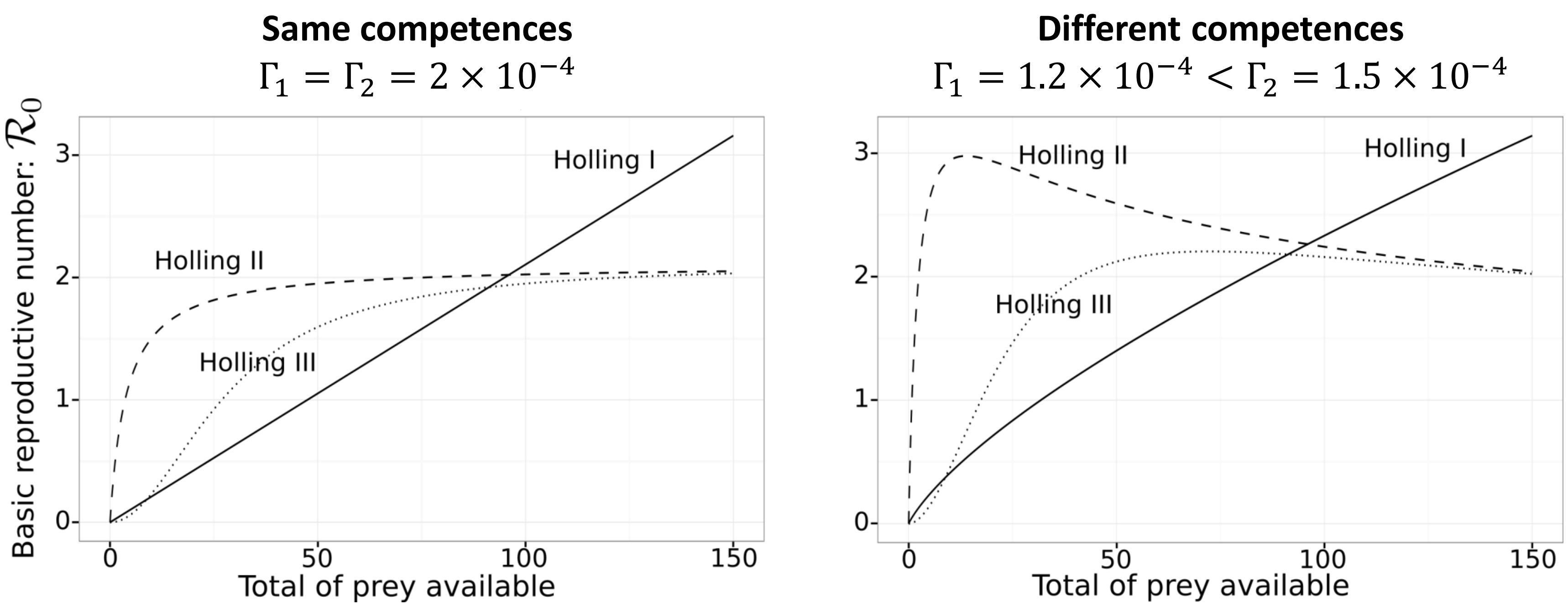
Level plot of $\mathcal{R}_0$



- The ingestion rate influences the speed of dilution/amplification of the disease
- A limited overall feeding emphasizes the dilution/amplification effect

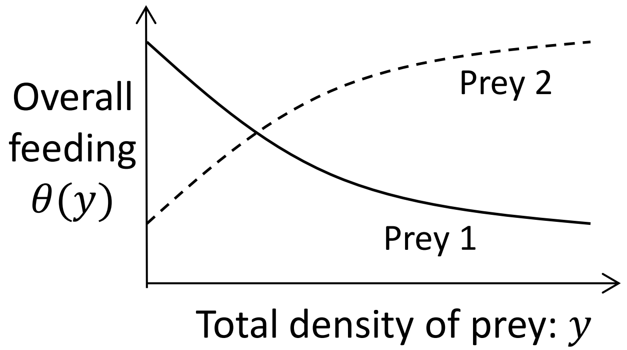
Different competences + Limited ingestion + **Rank switching**



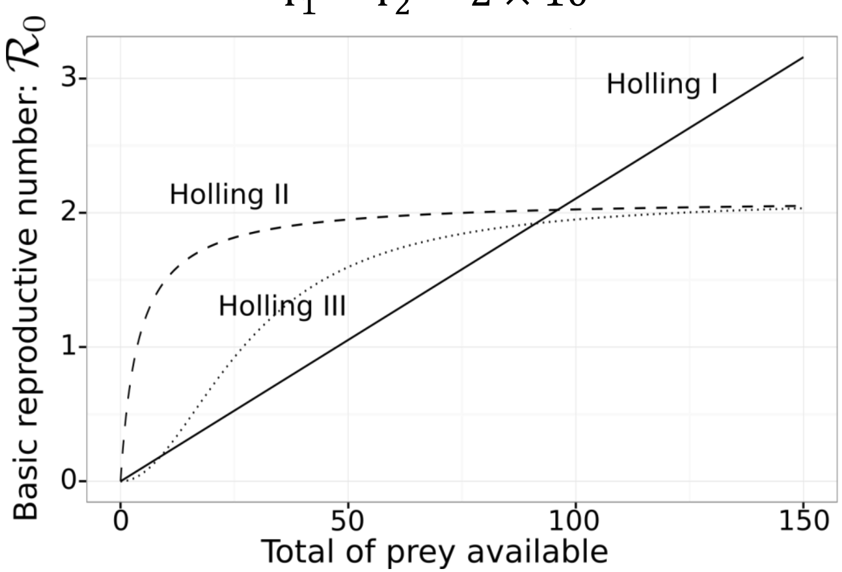


Different competences + Limited ingestion + **Rank switching**

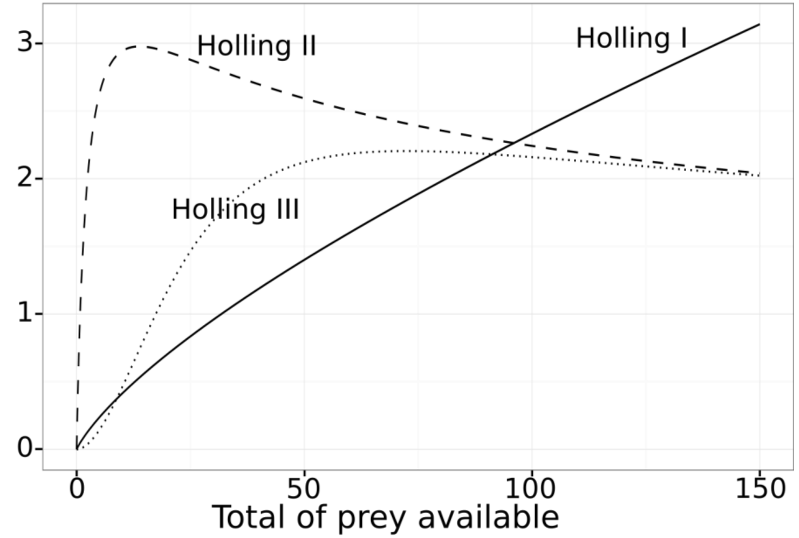
➡ **density-dependent dilution** of disease



Same competences
$\Gamma_1 = \Gamma_2 = 2 \times 10^{-4}$



Different competences
$\Gamma_1 = 1.2 \times 10^{-4} < \Gamma_2 = 1.5 \times 10^{-4}$



- Develop MSFR ➡ Apply on multi-host parasite ➡ Assess the disease risk
- **Frequency-dependent** and **total-density dependent switching** in red foxes - voles
- Foraging × Competence ➡ **New tools/ideas on dilution/amplification of disease risk**

Perspectives

- Increase food web complexity (more species, competition, mutualism, migration)
- Integration of variability (Random Matrix Theory)

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Perspectives

- Increase food web complexity (more species, competition, mutualism, migration)
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➡ **Why not for a post-doctoral proposal? ☺**

Thank you

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