

2<sup>nd</sup>-3<sup>rd</sup> December 2019, Workshop KARATE

LotKA-VolterRA models – when random maTriX theory meets theoretical Ecology

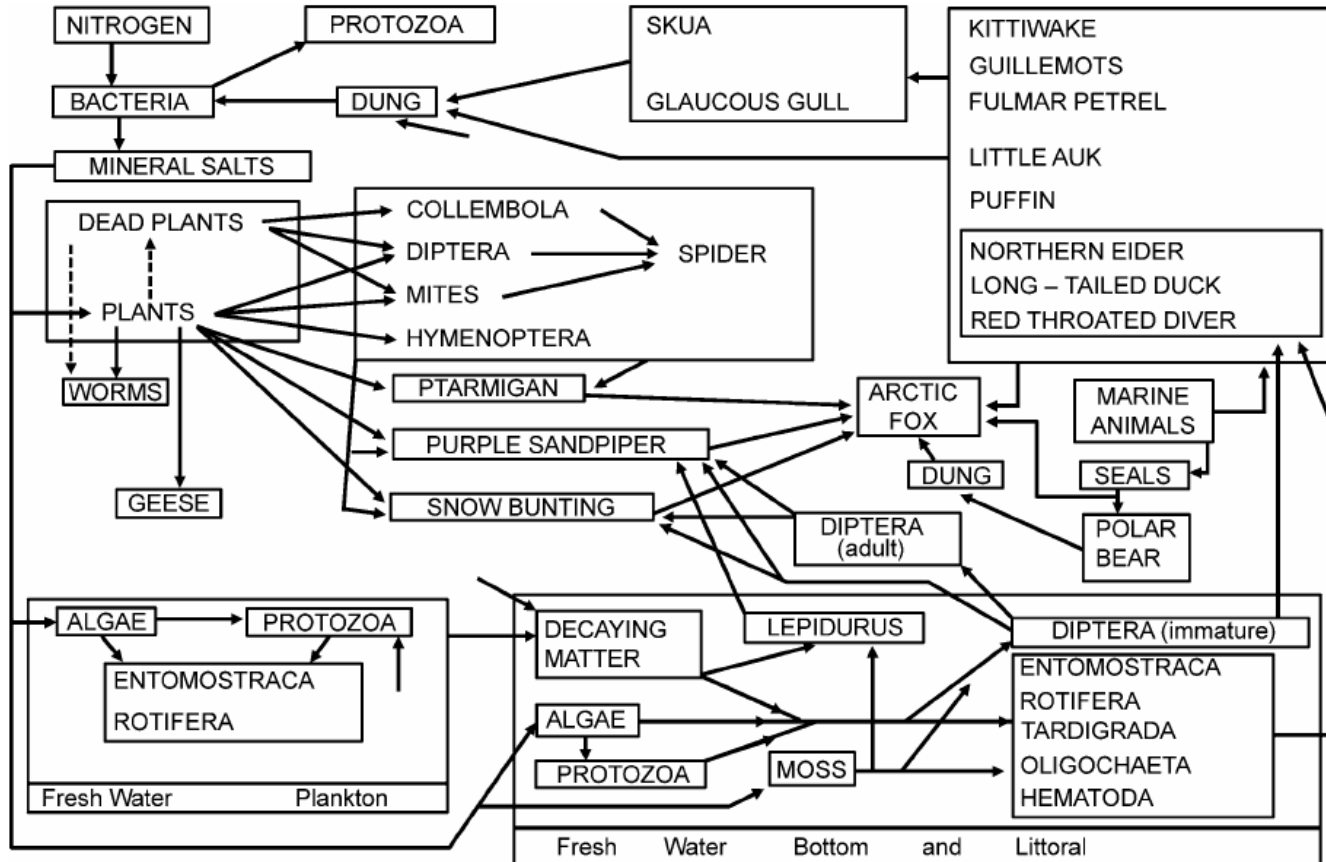


# On parameterising large seasonal food webs

Alix Sauve<sup>1</sup> & Frédéric Barraquand<sup>1,2</sup>

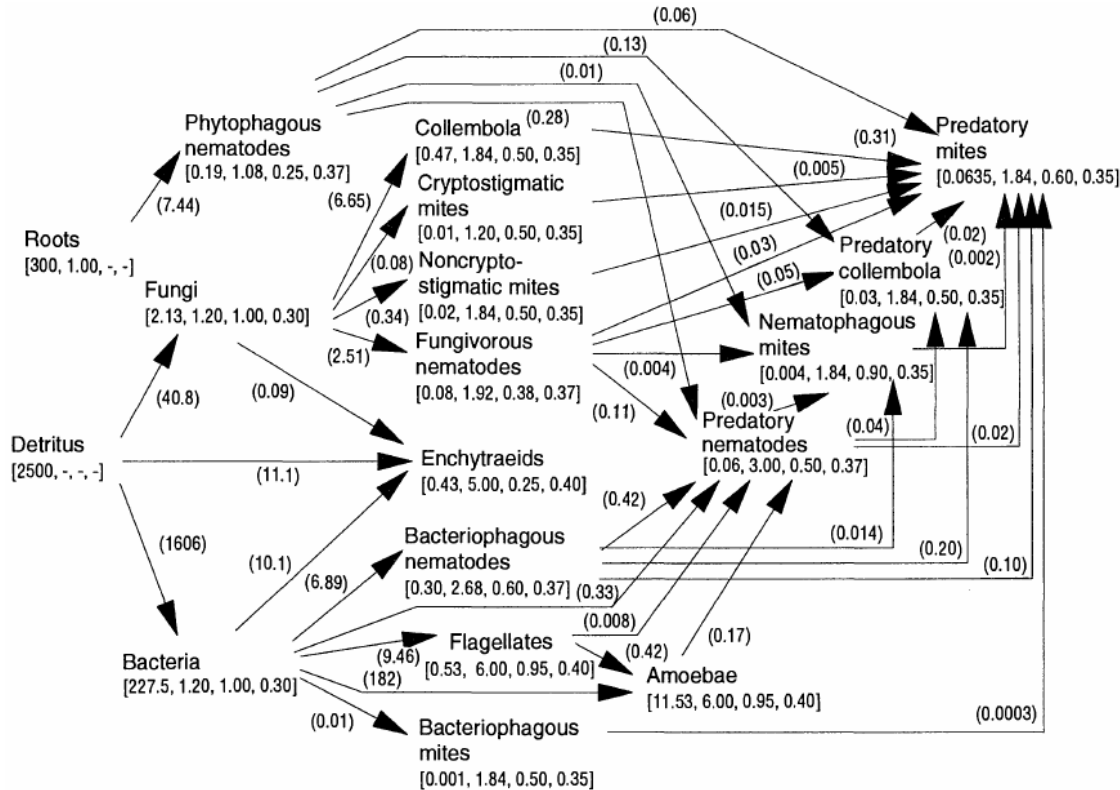
<sup>1</sup>Université de Bordeaux, ETI group, LabEx COTE ; <sup>2</sup>Institut de Mathématiques de Bordeaux

# Food webs historically depict communities with static structures



« Food-cycle among the animals on Bear Island, a barren spot in the arctic zone, South of Spitzbergen. (The dotted lines represent probable food relations not yet proved.) The best way to read the diagram is to start at "marine animals" and follow the arrows. »

# Quantifying trophic links brings on key informations on ecosystems functioning and stability



- Bottom-up and top-down effects act together ;
- No correlation between interaction strength and community stability ;
- The structure of interaction strengths matters to community stability.

# Food web models: « A plague of parameters »

Yodzis & Innes 1992, Am. Nat.

e.g., Rosenzweig-MacArthur model

1 predator  
1 prey

$p$  predators  
 $n$  prey  
 $L$  links



$$\begin{cases} \frac{dP}{dt} = P \left( -m + \frac{e \gamma N}{1 + \gamma h N} \right) \\ \frac{dN}{dt} = N \left( \alpha - \beta N - \frac{\gamma P}{1 + \gamma h N} \right) \end{cases}$$

6 parameters

$$\begin{cases} \frac{dP_i}{dt} = P_i \left( -m_i + \frac{\sum_{k=1}^n e_i \gamma_{ki} N_k}{1 + \sum_{j \in \text{Prey}(i)} \gamma_{ji} h_i N_j} \right) \\ \frac{dN_k}{dt} = N_k \left( \alpha_k - \beta_k N_k - \sum_{i=1}^p \frac{\gamma_{ki} P_i}{1 + \sum_{l \in \text{Prey}(i)} \gamma_{li} h_i N_l} \right) \end{cases}$$

$2 \times p + 2 \times n + 2 \times L$  parameters  
 $L \geq \max(n, p)$

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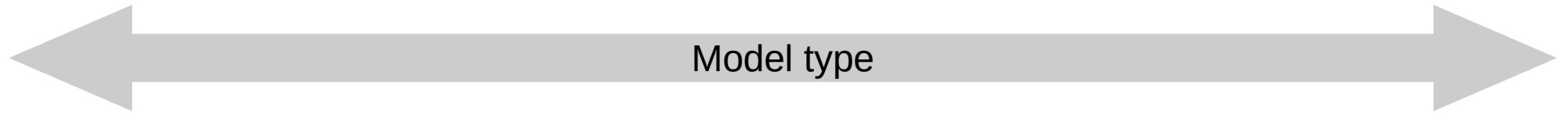
$$\left\{ \begin{array}{l} \frac{dP_i}{dt} = P_i \left( -m_i + \frac{\sum_{k=1}^n e_i \gamma_{ki} N_k}{1 + \sum_{j \in \text{Prey}(i)} \gamma_{ji} h_i N_j} \right) \\ \frac{dN_k}{dt} = N_k \left( \alpha_k - \beta_k N_k - \sum_{i=1}^p \frac{\gamma_{ki} P_i}{1 + \sum_{l \in \text{Prey}(i)} \gamma_{li} h_i N_l} \right) \end{array} \right.$$

Parameterisation matters!  
Non-linearity can create brutal changes of dynamics with small changes of parameter values

# Different parameterisation strategies for different objectives

**'Strategic'**

**'Tactic'**



Models for explanation  
Qualitative predictions

Models for  
quantitative forecasts

# Different parameterisation strategies for different objectives

**'Strategic'**

**'Tactic'**

Model type

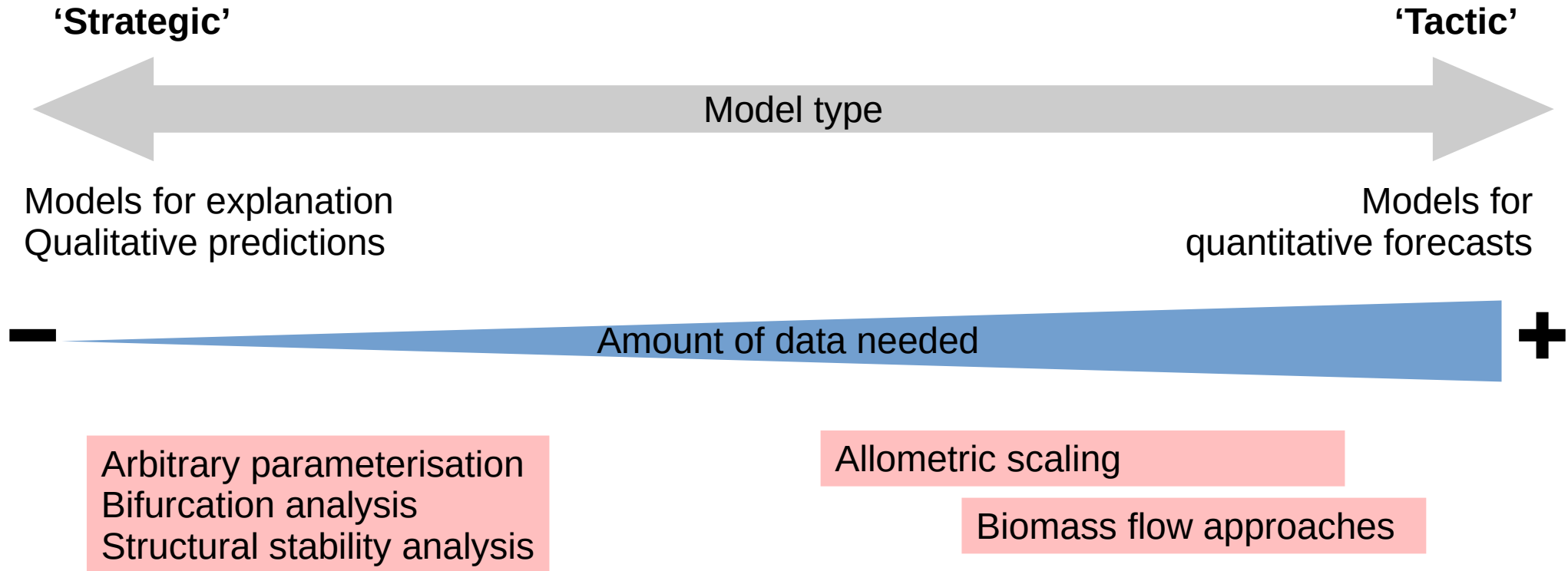
Models for explanation  
Qualitative predictions

Models for  
quantitative forecasts

Amount of data needed



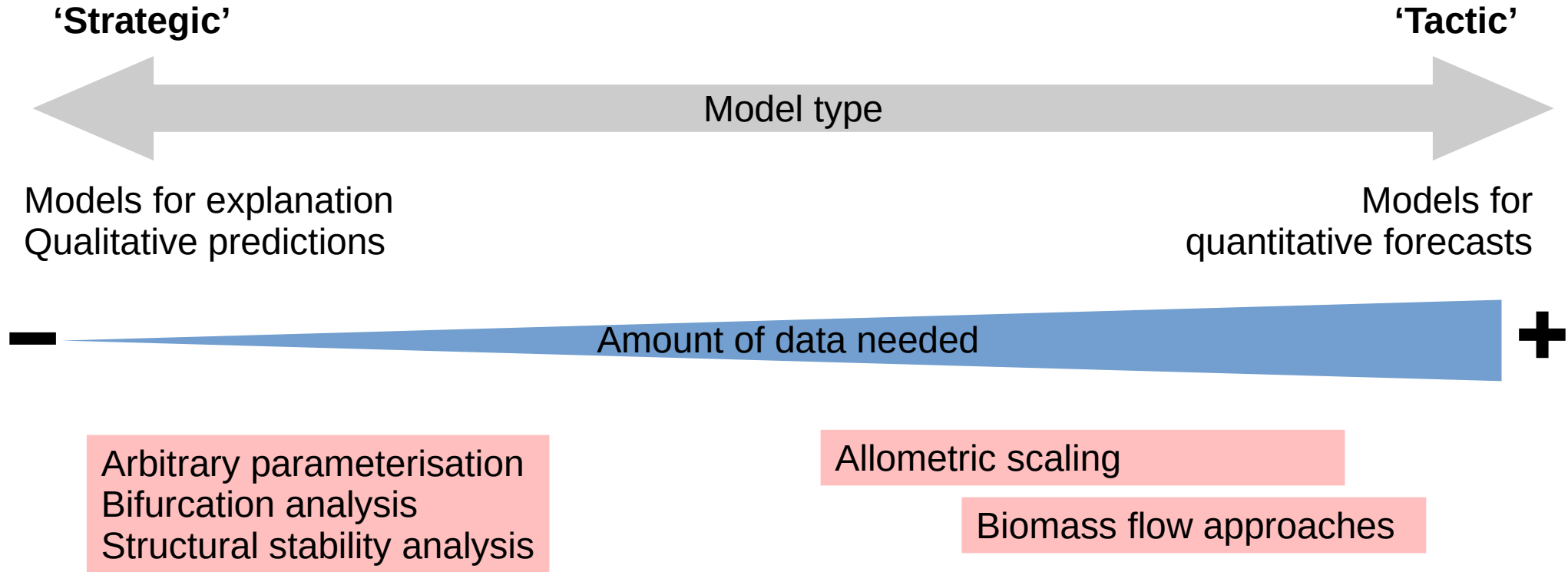
# Different parameterisation strategies for different objectives



McCallum, 2008 « Population parameters (...) »  
Gauzens et al. 2019, Meth. Ecol. Evol.  
Rohr et al. 2014, Science



# Different parameterisation strategies for different objectives

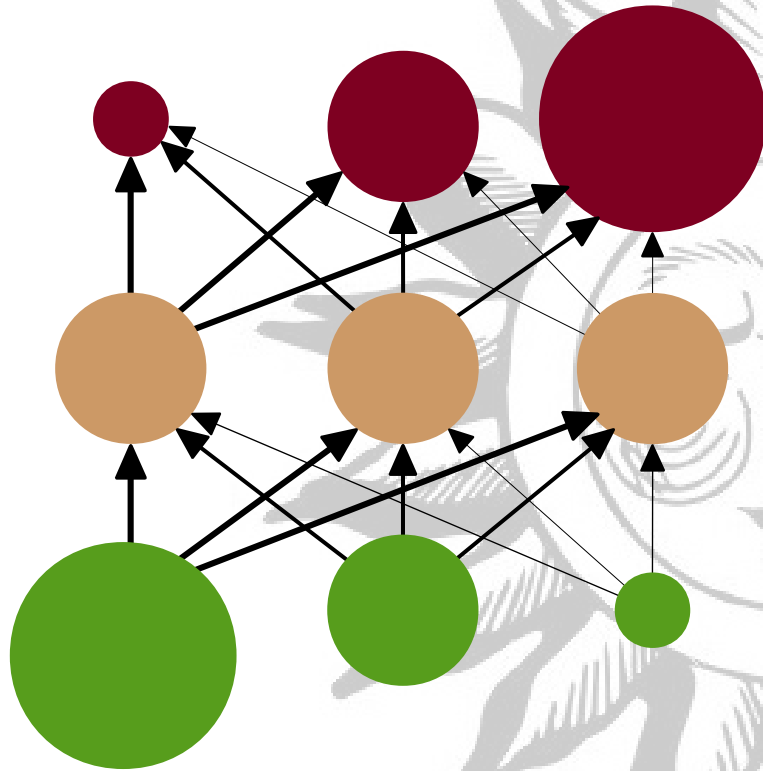


➔ Different strategies which helped to better grasp the dynamics of ecological communities.

McCallum, 2008 « Population parameters (...) »  
Gauzens et al. 2019, Meth. Ecol. Evol.  
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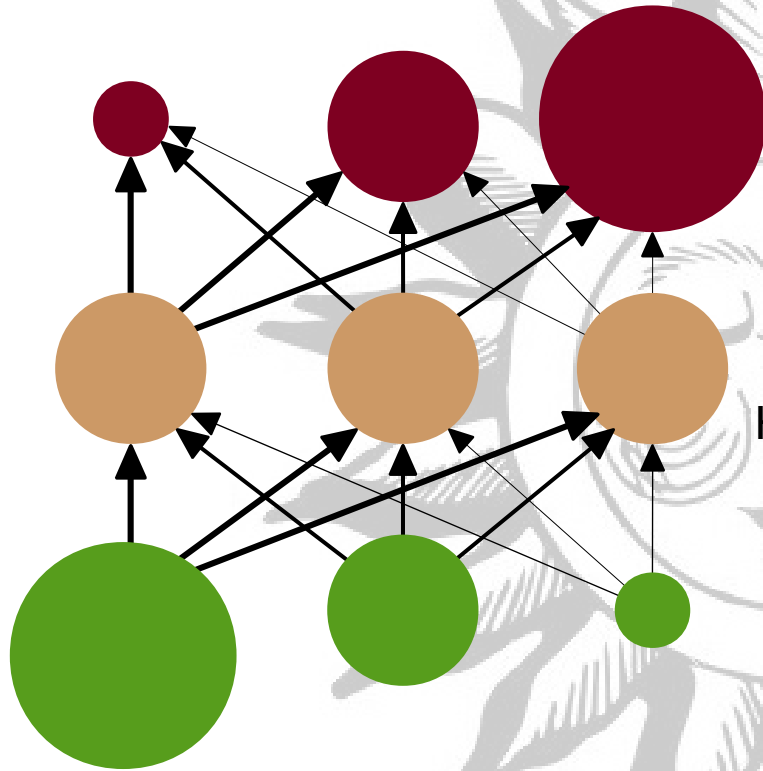
# Moving beyond a frozen picture of food webs: Capturing food web seasonality

Summer

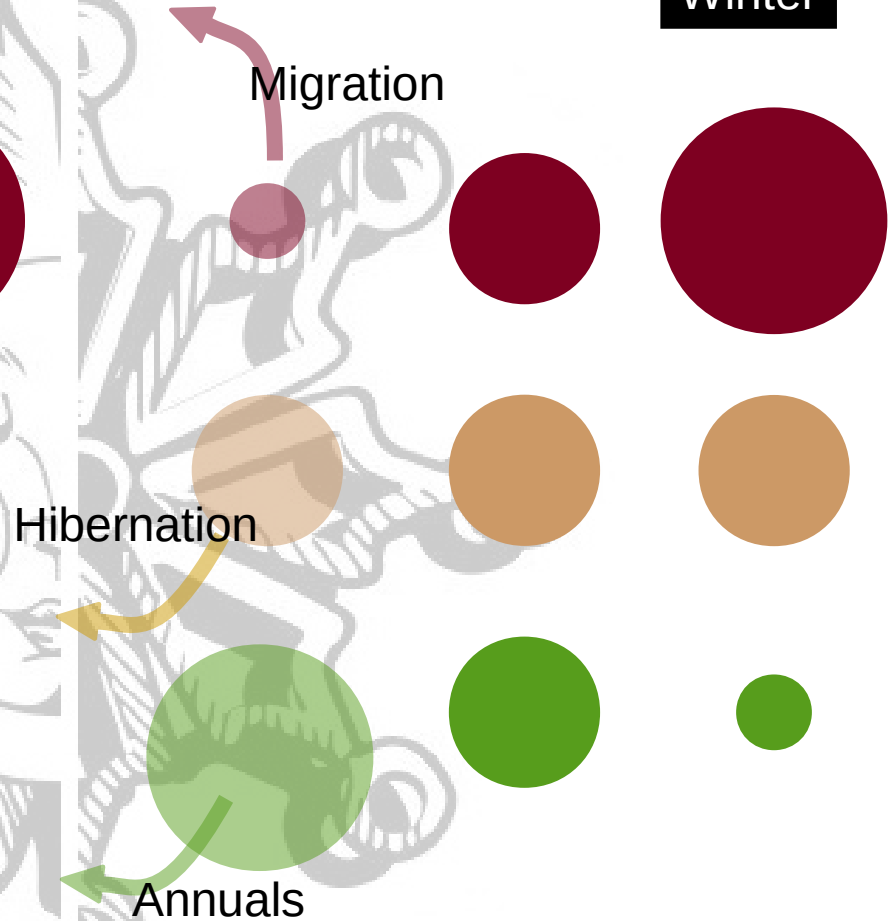


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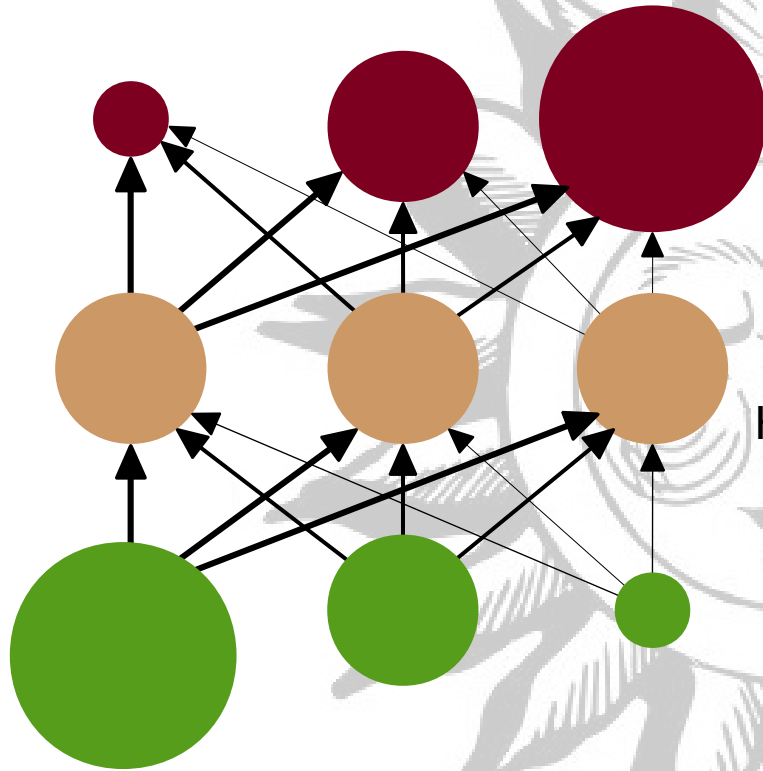


Winter

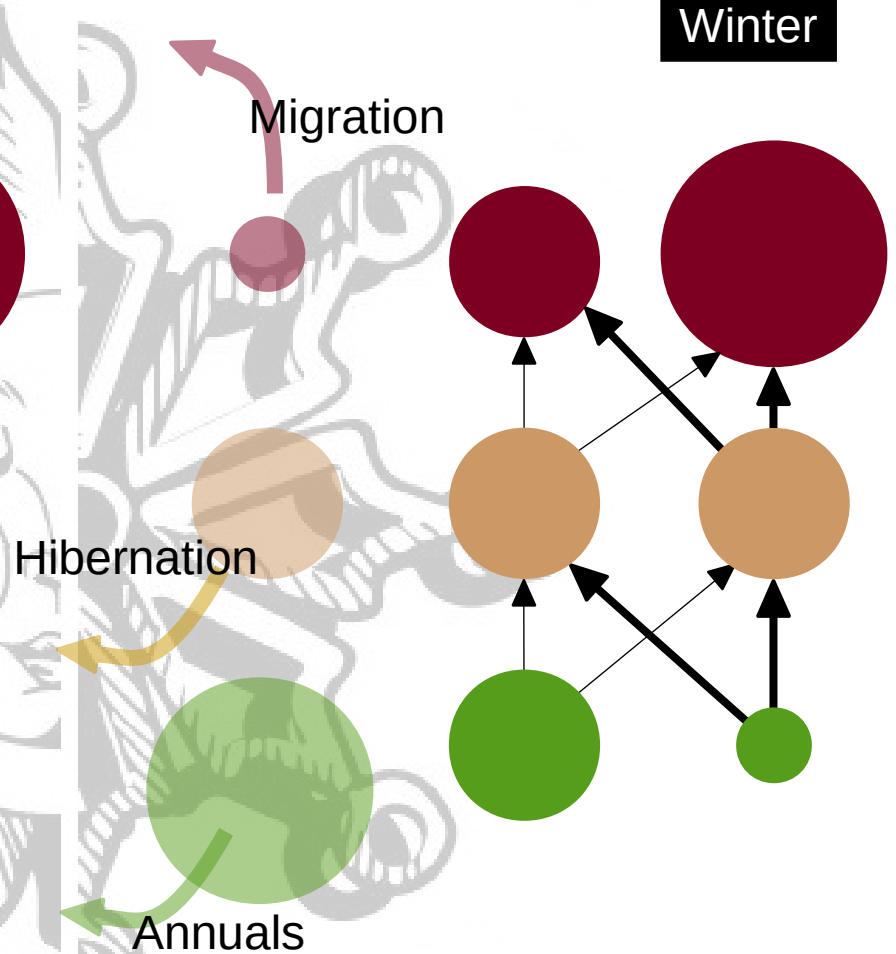


# Moving beyond a frozen picture of food webs: Capturing food web seasonality

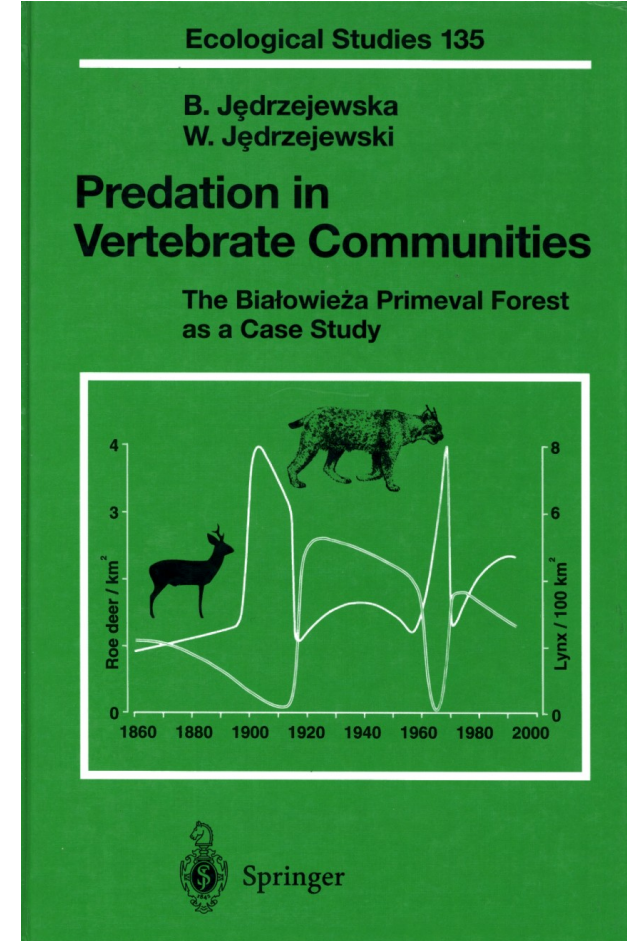
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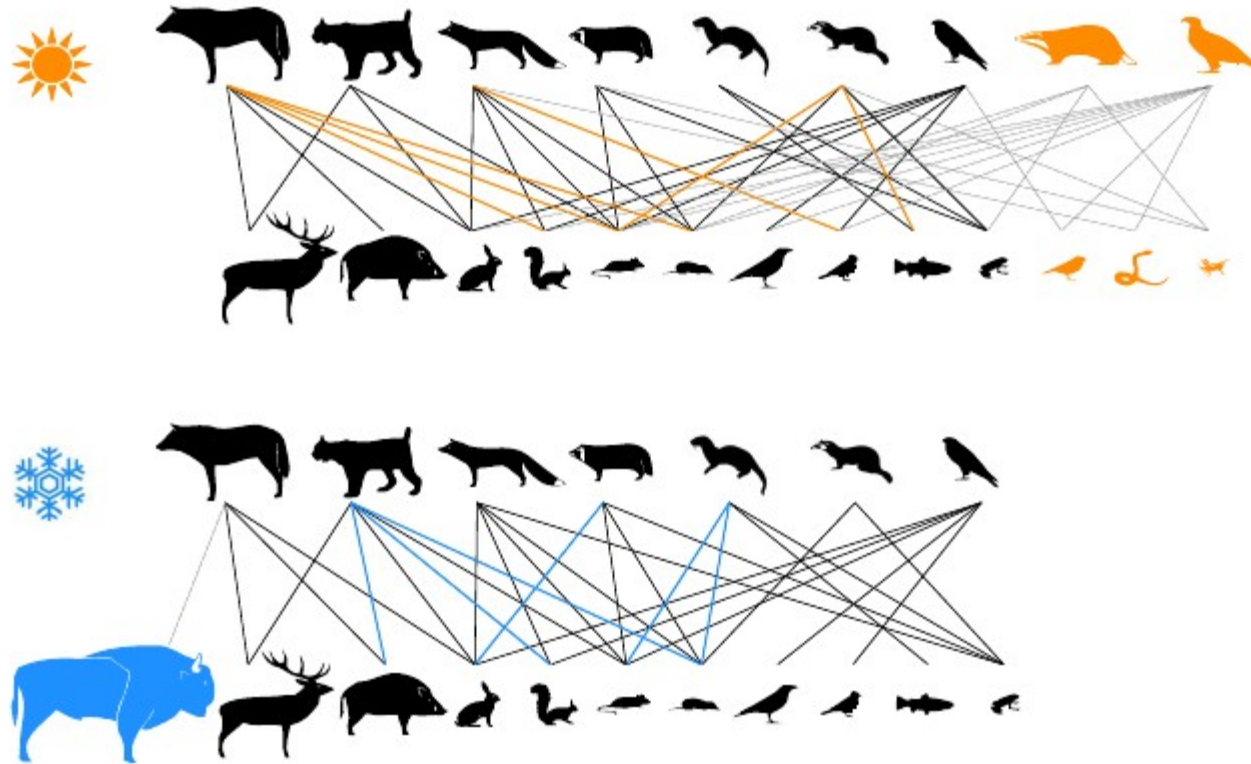
Winter



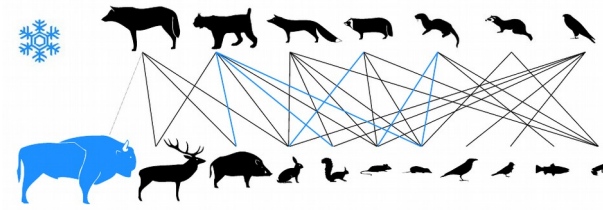
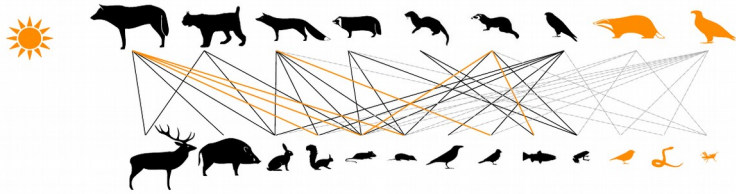
# The food web of the Bialowieza forest: a case study



# The food web of the Bialowieza forest: A topology that changes between seasons



# The food web of the Bialowieza forest: A topology that changes between seasons



Predators' growth rates

$$\frac{dP_i}{dt} = P_i (-m_i + e_i \gamma_{ki} N_k)$$

Preys'

$$\frac{dN_k}{dt} = N_k (\alpha_k - \gamma_{ki} P_i)$$

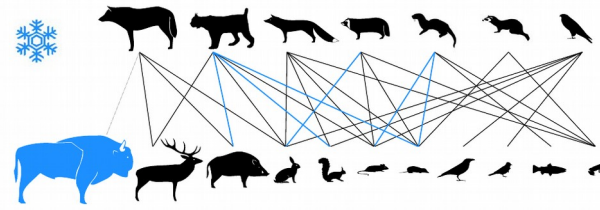
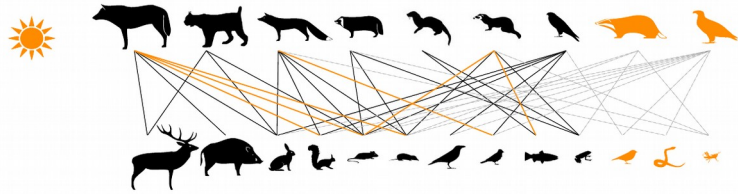
Mortality rate

Conversion efficiency

Intrinsic growth rate

Attack rate

# The food web of the Bialowieza forest: A topology that changes between seasons



Looking for a **feasible** equilibrium

$$\left. \begin{aligned} \frac{dP_i}{dt} &= P_i \left( -m_i + e_i \sum_k \gamma_{ki} N_k \right) \\ \frac{dN_k}{dt} &= N_k \left( \alpha_k - N_k - \sum_i \gamma_{ki} P_i \right) \end{aligned} \right\} \rightarrow \{ \mathbf{P}^*, \mathbf{N}^* \} > 0$$

What are the parameters allowing such equilibrium?

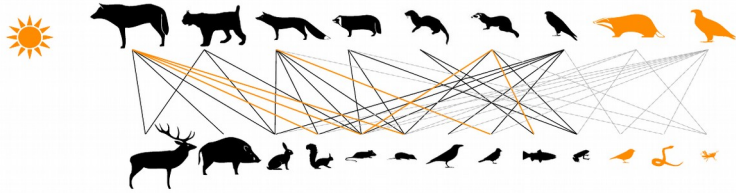
Defining a **feasibility domain**

$$D_F = \{ m_i = e_i \gamma_{1i} N_1 + \dots + e_i \gamma_{S_N i} N_{S_N} \wedge \alpha_i = N_i + \gamma_{i1} P_1 + \dots + \gamma_{iS_p} P_{S_p} \text{ with } N_i > 0 \wedge P_i > 0 \}$$

And its size  $\Omega(\gamma) = \frac{|\det(\mathbf{A})|}{\prod_j (\sum_i A_{ij})}$  with  $\mathbf{A} = \begin{bmatrix} \text{diag}(\mathbf{e} \gamma^t) & \mathbf{I} \\ \mathbf{0} & \gamma \end{bmatrix}$



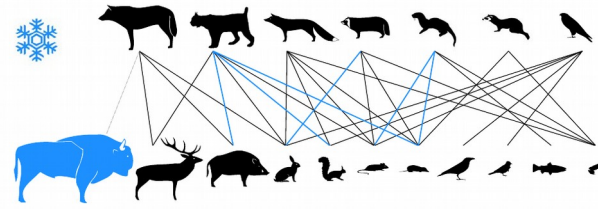
# The food web of the Bialowieza forest: A topology that changes between seasons



$$\frac{dP_i}{dt} = P_i \left( -m_i + e_i \sum_k \gamma_{ki} N_k \right)$$

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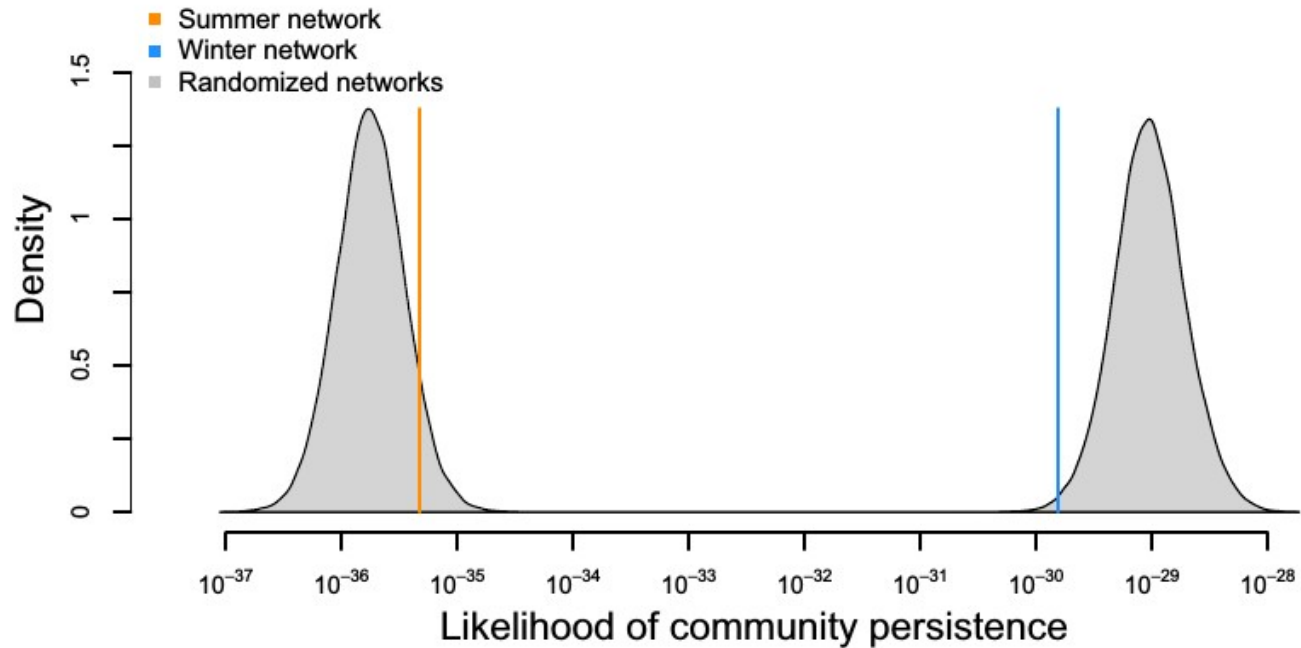
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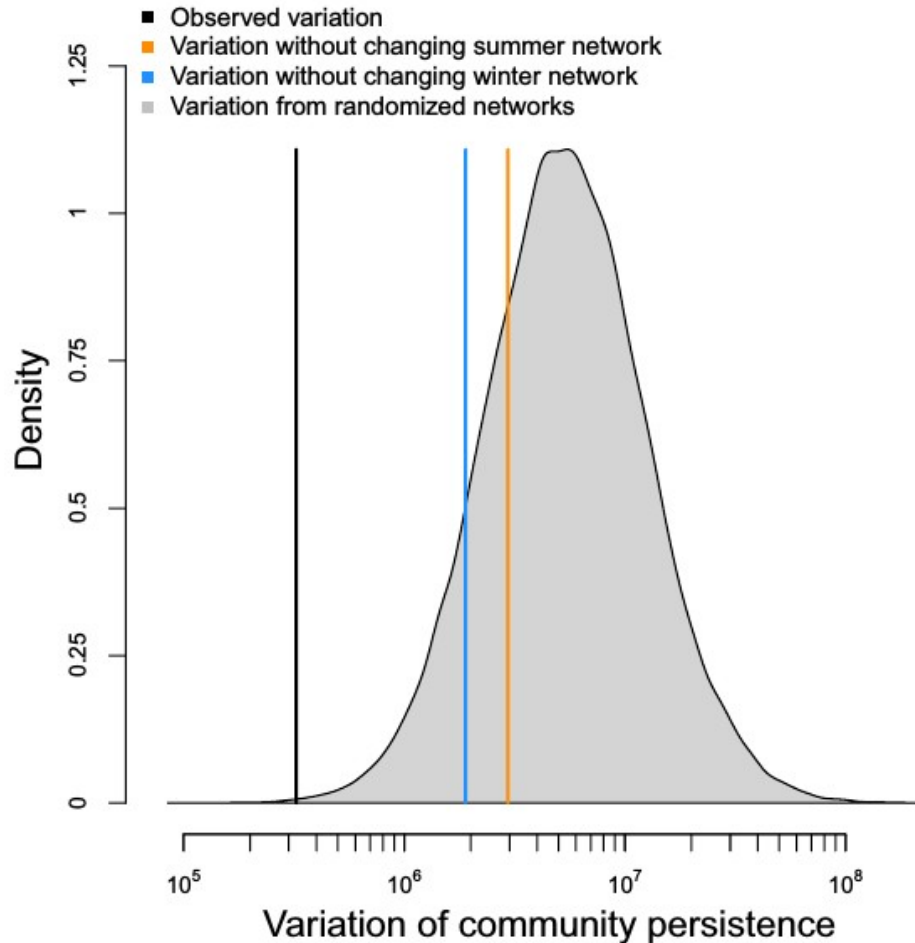
+ their randomisations to test the effect of their interaction distribution

# The food web of the Bialowieza forest: A topology that changes between seasons



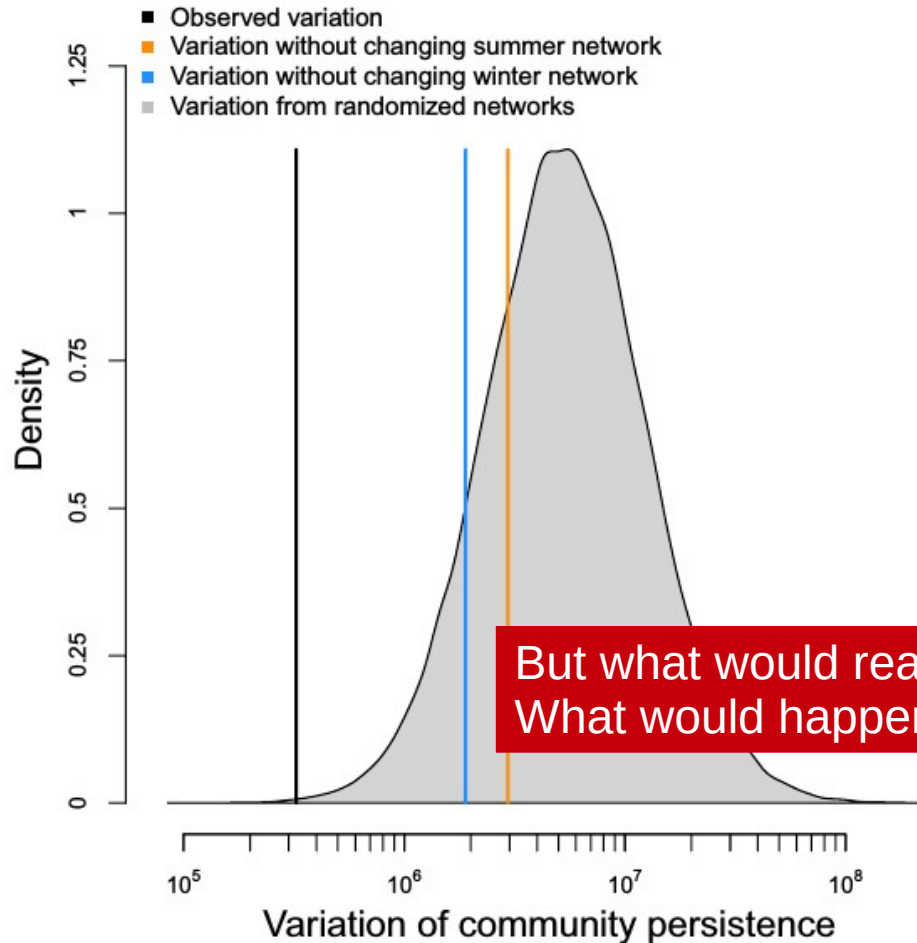
Seasons differ in the probability of the community to persist.

# The food web of the Bialowieza forest: A topology that changes between seasons



The changes in food web structure are such that their minimise the variation of community persistence.

# The food web of the Bialowieza forest: A topology that changes between seasons



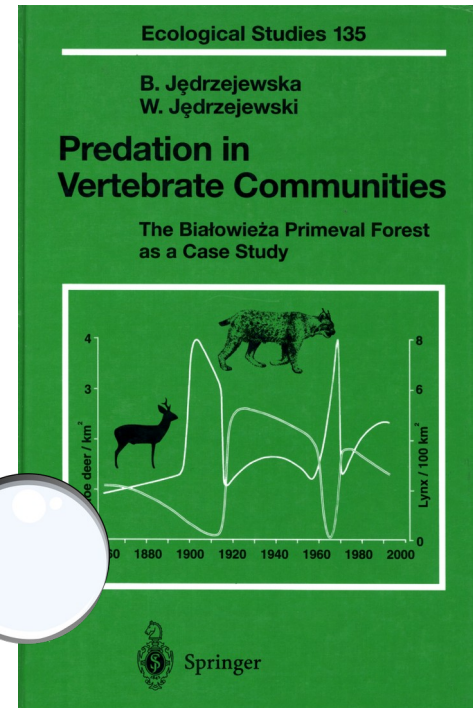
The changes in food web structure are such that their minimise the variation of community persistence.

But what would realistic parameters result in?  
What would happen if we modelled predation seasonality?

# Food web parameterisation: Building on a decade of wildlife surveys

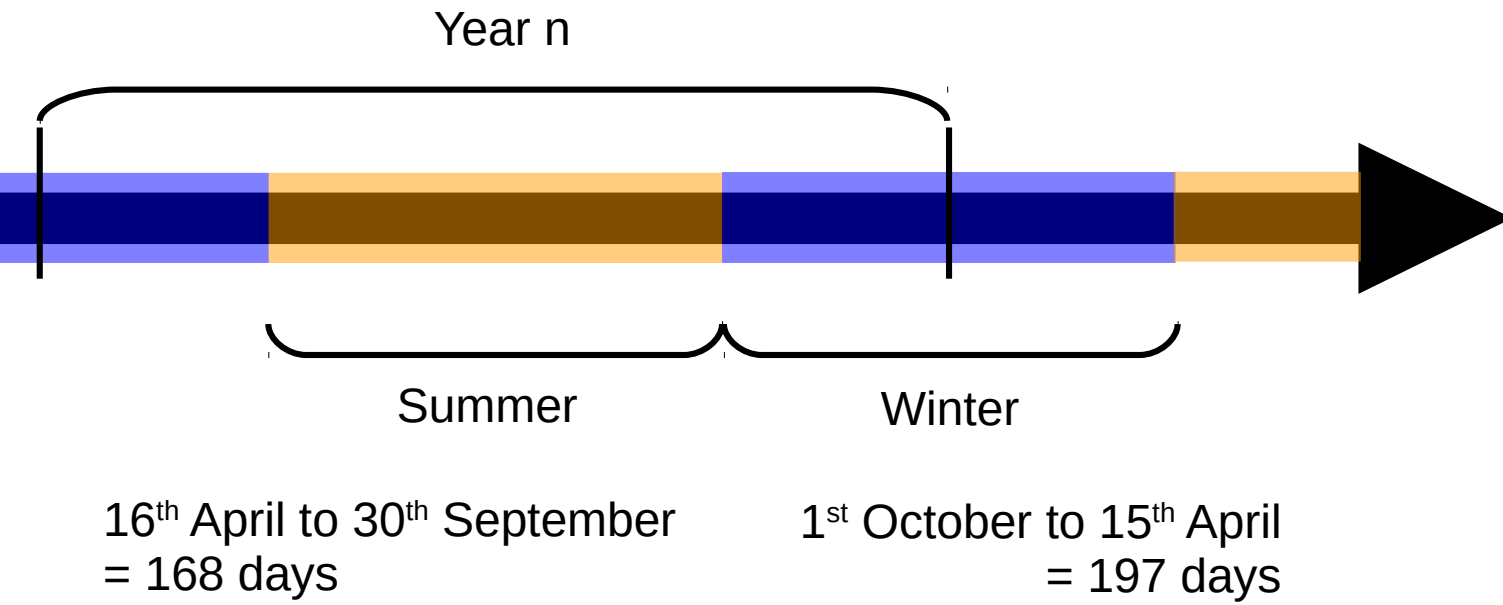
A focus on a given time period 1985±1 → 1995±1,  
and on the Polish part of the Białowieża forest

- Collection of scats and pellets during summer and winter  
→ biomass fractions in predators' diet ↔ dietary preferences  
for each season ( $p_{ki}$ )
- Estimates of daily food intake of predators ( $DFI_i$  for adults and  
juveniles)
- Estimates of seasonal densities of prey ( $R_k$ )
- Body masses ( $M_i, M_k$ )
- Estimates of litter/brood size, birth rates



# Food web parameterisation: Building on a decade of wildlife surveys

A focus on a given time period  $1985 \pm 1 \rightarrow 1995 \pm 1$ ,  
and on the Polish part of the Bialowieza forest



# A basic model for the food web of the Bialowieza forest

General Lotka-Volterra model with predator self-regulation

$$\frac{dP_i}{dt} = P_i \left( -m_i - g_i P_i + \frac{\sum_{k=1}^n e_i f_{ki}(\mathbf{N})}{M_i} \right)$$
$$\frac{dN_k}{dt} = N_k (r_k - \beta_k N_k) - \sum_{i=1}^p \left( \frac{P_i f_{ki}(\mathbf{N})}{M_i} \right)$$

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Linear terms for

- Predator baseline mortality rates
- Prey intrinsic growth rates



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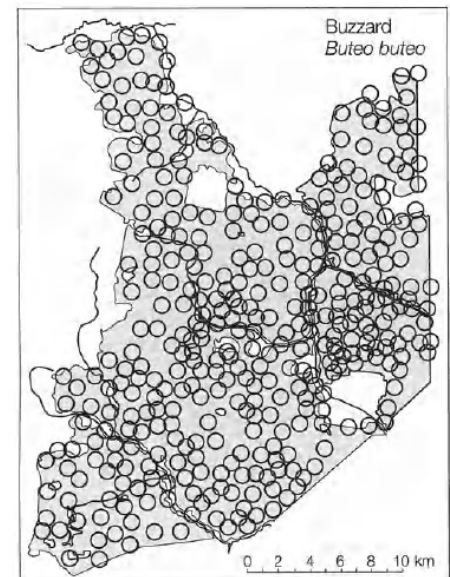
Non-linear self-regulation for both prey and predator species

**For prey**

Feeding resources are not infinite

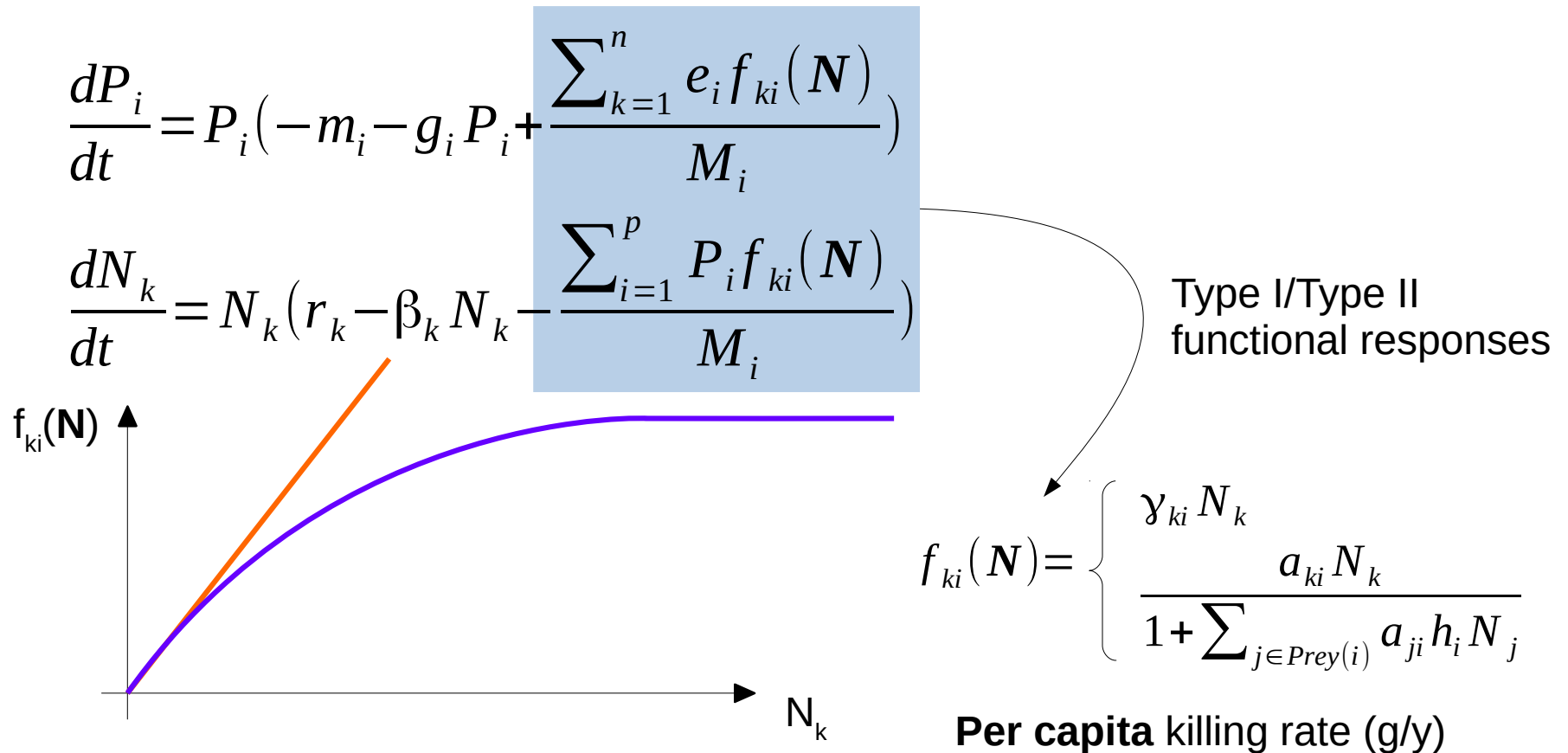
**For predators**

Territoriality constrains predators densities



# A basic model for the food web of the Bialowieza forest

General Lotka-Volterra model with predator self-regulation to describe **biomass** growth



# First step: quantifying per capita predators' intakes

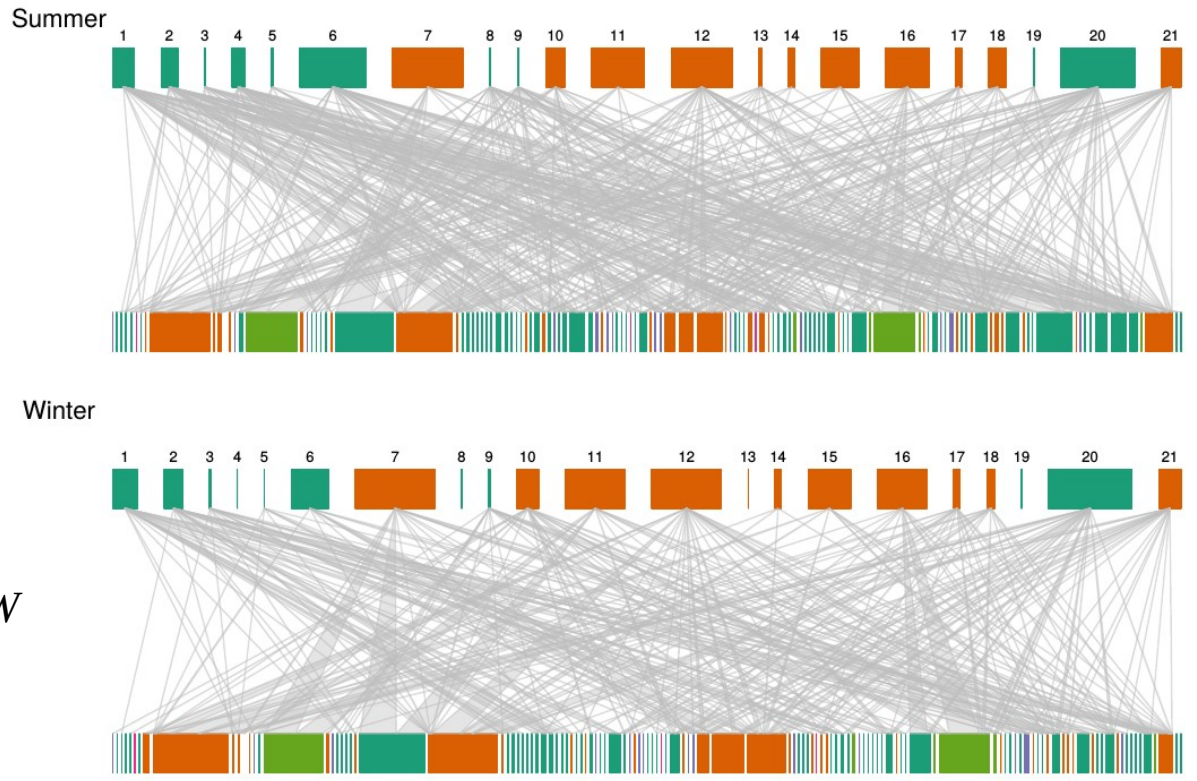
Daily food intake (g/d)

$$\hat{G}_{ki}^S \approx (DFI)_i \times p_{ki}^S \times (n_{days})_i^S$$

Number of days of presence in the forest during Summer (d) for the predator  $i$

$$\hat{G}_{ki}^W \approx (DFI)_i \times p_{ki}^W \times (n_{days})_i^W$$

Preference of predator  $i$  for prey  $k$  during Winter



- Bird
- Mammal
- Fish
- Reptile
- Amphibian

- 1 - Accipiter gentilis
- 2 - Accipiter nisus
- 3 - Aegolius funereus
- 4 - Aquila pomarina
- 5 - Asio otus
- 6 - Buteo buteo
- 7 - Canis lupus

- 8 - Falco subbuteo
- 9 - Glaucidium passerinum
- 10 - Lutra lutra
- 11 - Lynx lynx
- 12 - Martes martes
- 13 - Meles meles
- 14 - Mustela erminea

- 15 - Mustela nivalis
- 16 - Mustela putorius
- 17 - Mustela vison
- 18 - Nyctereutes procyonoides
- 19 - Pernis apivorus
- 20 - Strix aluco
- 21 - Vulpes vulpes

# Quantifying discovery rates for the type I functional response

$$G_{ki} = \int_y^{y+1} f_{ki}(\mathbf{N}) dt = \underbrace{\int_y^{y+1/2} f_{ki}(\mathbf{N}) dt}_{G_{ki}^S \approx \eta^S \times f_{ki}(\bar{N}^S)} + \underbrace{\int_{y+1/2}^{y+1} f_{ki}(\mathbf{N}) dt}_{G_{ki}^W \approx \eta^W \times f_{ki}(\bar{N}^W)}$$

$$f_{ki}(\mathbf{N}) = \gamma_{ki} N_k$$

Discovery rate (ha/y)

= the area **annually** explored by the predator  $i$  to find prey  $k$

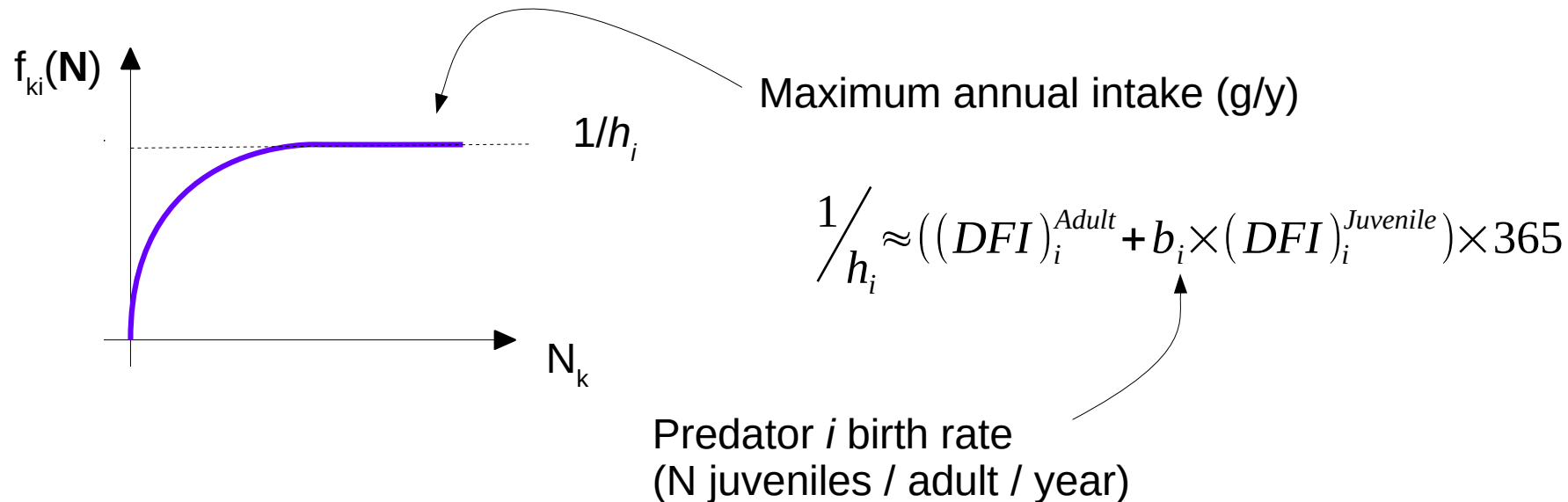
$$\begin{aligned} G_{ki}^S &\approx \eta^S \times \gamma_{ki}^S \times \bar{N}_k^S \\ G_{ki}^W &\approx \eta^W \times \gamma_{ki}^W \times \bar{N}_k^W \end{aligned} \Rightarrow \begin{aligned} \gamma_{ki}^S &\approx \frac{G_{ki}^S}{\eta^S \times \bar{N}_k^S} \\ \gamma_{ki}^W &\approx \frac{G_{ki}^W}{\eta^W \times \bar{N}_k^W} \end{aligned}$$

# Quantifying discovery rates and handling times for the type II functional response

$$f_{ki}(\mathbf{N}) = \frac{a_{ki} N_k}{1 + \sum_{j \in \text{Prey}(i)} a_{ji} h_i N_j}$$

Discovery rate (ha/y)  
= the area **annually** explored by the predator  $i$  to find prey  $k$

Handling time (y/g)



# Quantifying discovery rates and handling times for the type II functional response

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**Following Baudrot et al. (2016 in Ecology):**

$$\alpha_i(\mathbf{N}) = \sum_k a_{ki} N_k \leftarrow \text{The total biomass of prey discovered by one predator } i \text{ (g/y)}$$

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← The total biomass of prey discovered by one predator  $i$  (g/y)

$$p_{ki}(\mathbf{N}) = \frac{a_{ki} N_k}{\sum_k a_{ki} N_k} = \frac{a_{ki} N_k}{\alpha_i(\mathbf{N})}$$

← The preference of predator  $i$  for the prey  $k$  depends on prey relative densities

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$$C_i = (C_i)^{\text{Searching}} + \sum_k (C_i)_k$$

← Predators either search or « handle » their prey



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$$f_{ki}(\mathbf{N}) = \frac{p_{ki}(\mathbf{N}) \times \alpha_i(\mathbf{N}) \times (C_i)^{\text{Searching}}}{C_i}$$

← The proportion of searching individuals

# Quantifying discovery rates and handling times for the type II functional response

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$$C_i = (C_i)^{\text{Searching}} \left( 1 + h_i \times \sum_k p_{ki}(\mathbf{N}) \times \alpha_i(\mathbf{N}) \right)$$

$$f_{ki}(\mathbf{N}) = \frac{p_{ki}(\mathbf{N}) \times \alpha_i(\mathbf{N})}{1 + h_i \times \sum_k p_{ki} \alpha_i(\mathbf{N})}$$

# Quantifying discovery rates and handling times for the type II functional response

$$f_{ki}(\mathbf{N}) = \frac{a_{ki} N_k}{1 + \sum_{j \in \text{Prey}(i)} a_{ji} h_i N_j}$$

Discovery rate (ha/y)  
= the area **annually** explored by the predator  $i$  to find prey  $k$

For a given time  $t$ ,

$$f_{ki}(\mathbf{N}) = \frac{p_{ki}(\mathbf{N}) \times \alpha_i(\mathbf{N})}{1 + h_i \times \alpha_i(\mathbf{N})}$$

$$G_{ki} = \int_y^{y+1} f_{ki}(\mathbf{N}) dt = \underbrace{\int_y^{y+1/2} f_{ki}(\mathbf{N}) dt}_{\text{Summer}} + \underbrace{\int_{y+1/2}^{y+1} f_{ki}(\mathbf{N}) dt}_{\text{Winter}}$$

$$G_{ki}^S \approx \frac{\eta^S \times p_{ki}^S(\mathbf{N}^S) \times \alpha_i^S(\mathbf{N}^S)}{1 + h_i \times \alpha_i^S(\mathbf{N}^S)}$$

$$G_{ki}^W \approx \frac{\eta^W \times p_{ki}^W(\mathbf{N}^W) \times \alpha_i^W(\mathbf{N}^W)}{1 + h_i \times \alpha_i^W(\mathbf{N}^W)}$$

# Quantifying discovery rates and handling times for the type II functional response

$$G_{ki} = \int_y^{y+1} f_{ki}(N) dt = \underbrace{\int_y^{y+1/2} f_{ki}(N) dt}_S + \underbrace{\int_{y+1/2}^{y+1} f_{ki}(N) dt}_W$$

$$G_{ki}^S \approx \frac{\eta^S \times p_{ki}^S(N^S) \times \alpha_i^S(N^S)}{1 + h_i \times \alpha_i^S(N^S)}$$

$$\hat{\alpha}_i^S = \frac{1/\eta_S \times \sum_k G_{ki}^S}{1 - h_i/\eta_S \times \sum_k G_{ki}^S}$$

$$\hat{a}_{ki}^S = \frac{\hat{p}_{ki}^S \times \hat{\alpha}_i^S}{\bar{N}^S}$$

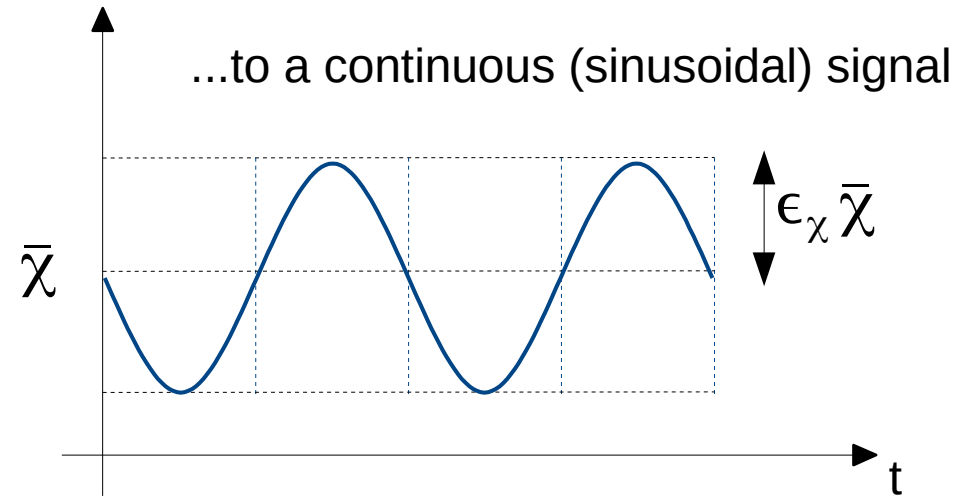
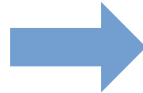
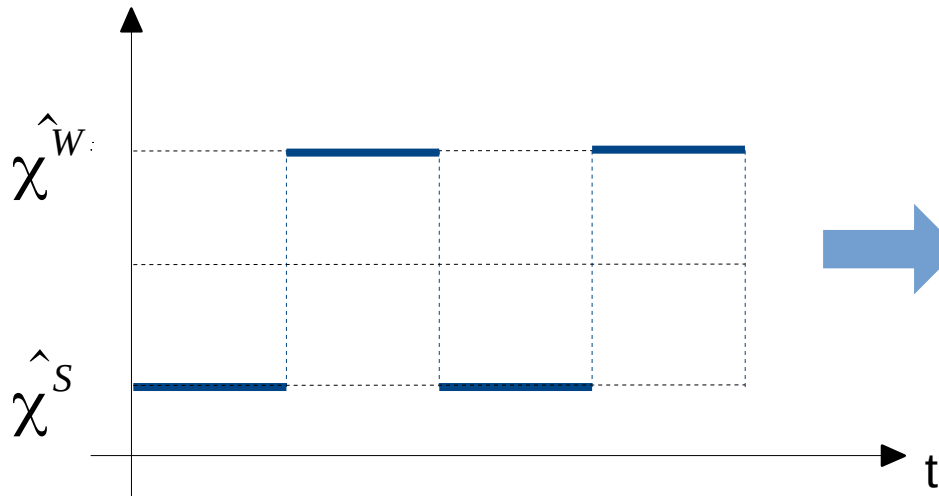
$$G_{ki}^W \approx \frac{\eta^W \times p_{ki}^W(N^W) \times \alpha_i^W(N^W)}{1 + h_i \times \alpha_i^W(N^W)}$$

$$\hat{\alpha}_i^W = \frac{1/\eta_W \times \sum_k G_{ki}^W}{1 - h_i/\eta_W \times \sum_k G_{ki}^W}$$

$$\hat{a}_{ki}^W = \frac{\hat{p}_{ki}^W \times \hat{\alpha}_i^W}{\bar{N}^W}$$

# Modelling a seasonal food web: One model to simulate all seasons

From an estimated rectangular signal...



$$\chi(t) = \bar{\chi}(1 + \epsilon_\chi \sin(2\pi t)) \quad \text{if } \chi^s > \chi^w$$

$$\chi(t) = \bar{\chi}(1 + \epsilon_\chi \sin(2\pi t + \frac{\pi}{2})) \quad \text{otherwise}$$

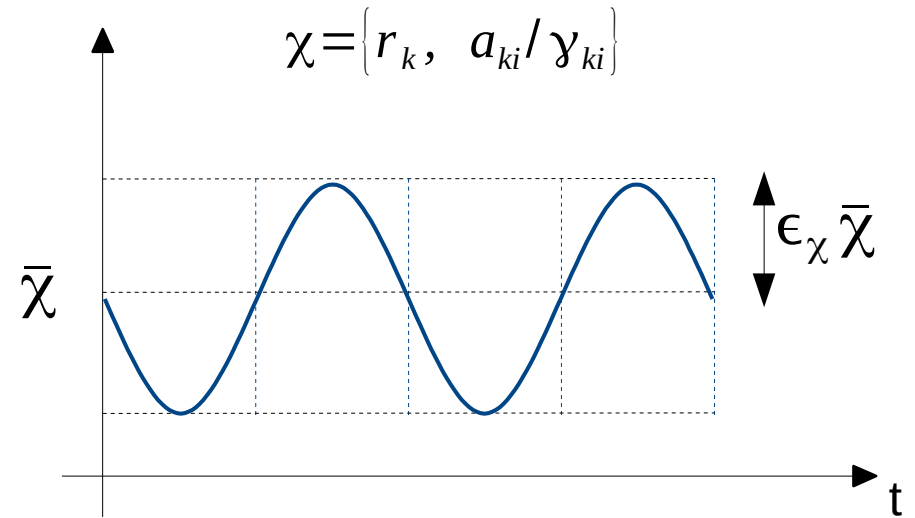
# Modelling a seasonal food web: One model to simulate all seasons

$$\frac{dP_i}{dt} = P_i \left( -m_i - g_i P_i + \frac{\sum_{k=1}^n e_i f_{ki}(N, t)}{M_i} \right)$$

$$\frac{dN_k}{dt} = N_k \left( r_k(t) - \beta_k N_k - \frac{\sum_{i=1}^p P_i f_{ki}(N, t)}{M_i} \right)$$

$$f_{ki}(N, t) = \begin{cases} \gamma_{ki}(t) N_k \\ \frac{a_{ki}(t) N_k}{1 + \sum_{j \in \text{Prey}(i)} a_{ji}(t) h_i N_j} \end{cases}$$

= A non-autonomous ODE system



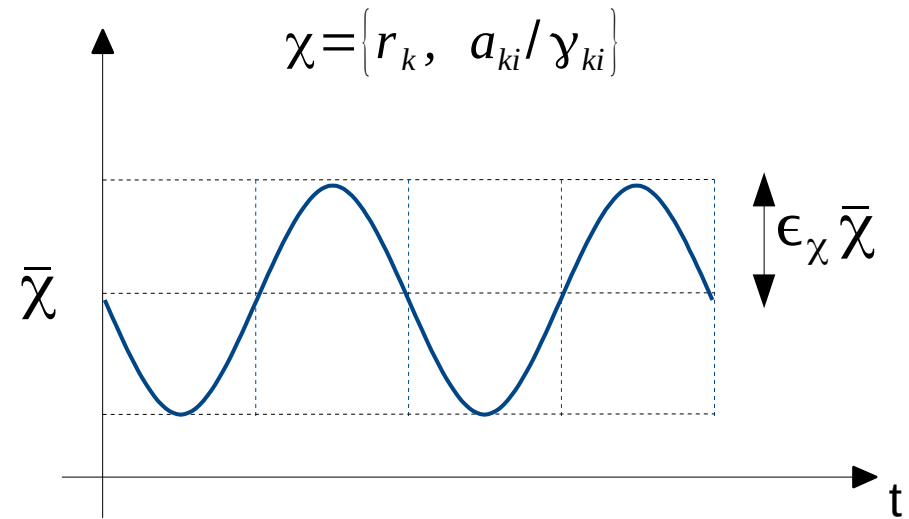
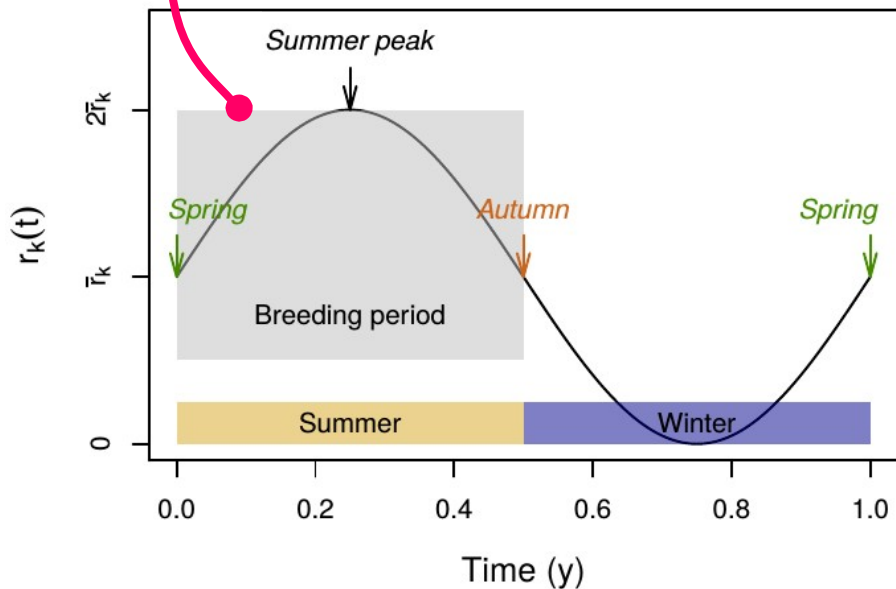
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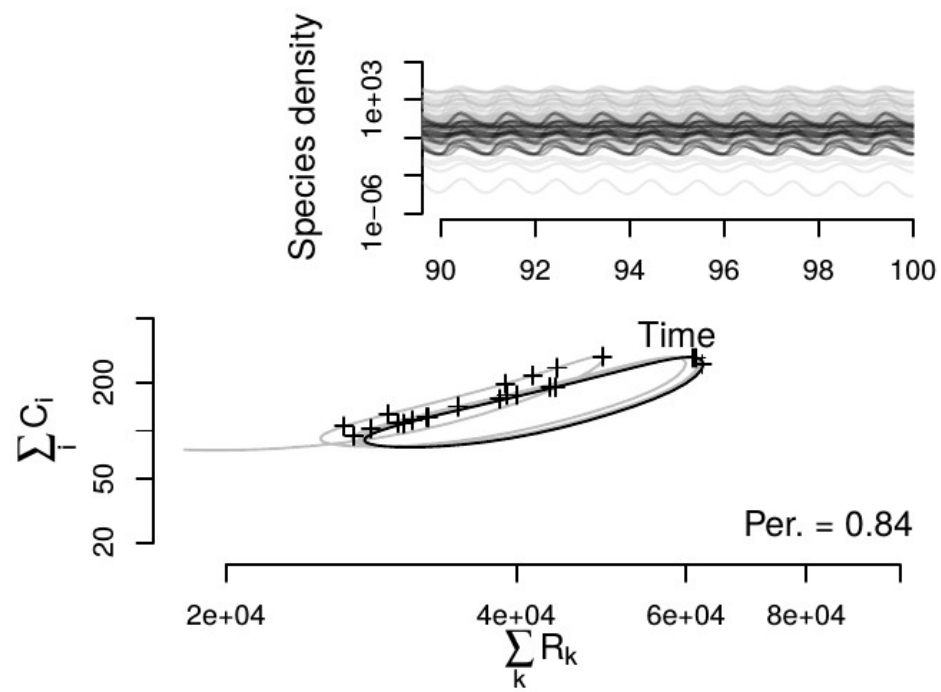


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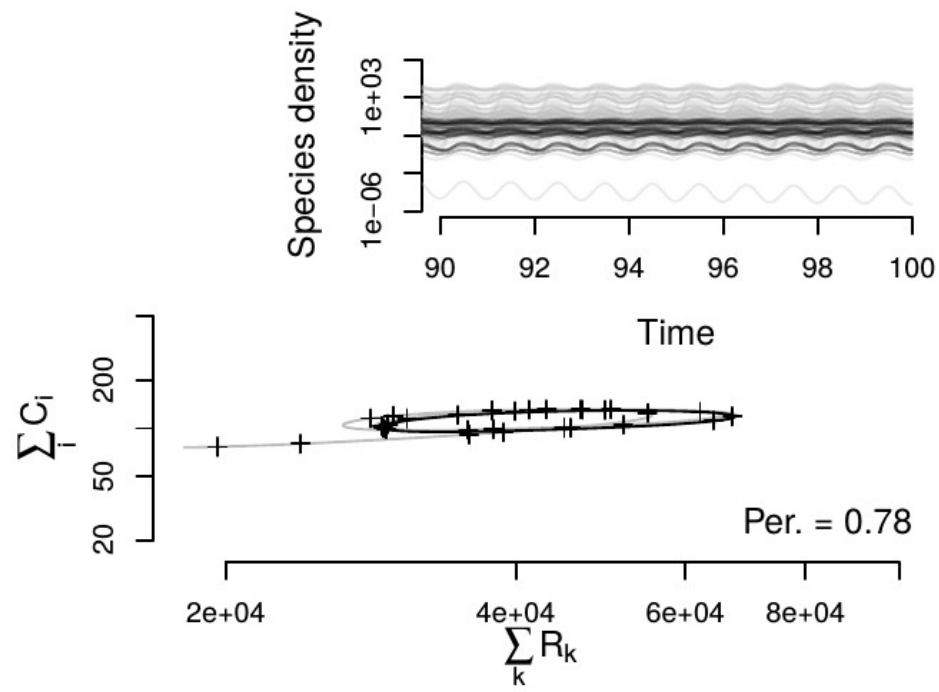
$$\chi(t) = \bar{\chi} (1 + \epsilon_{\chi} \sin(2\pi t + \frac{\pi}{2})) \quad \text{otherwise}$$

# Resulting dynamics: Annual cycles

## Type I



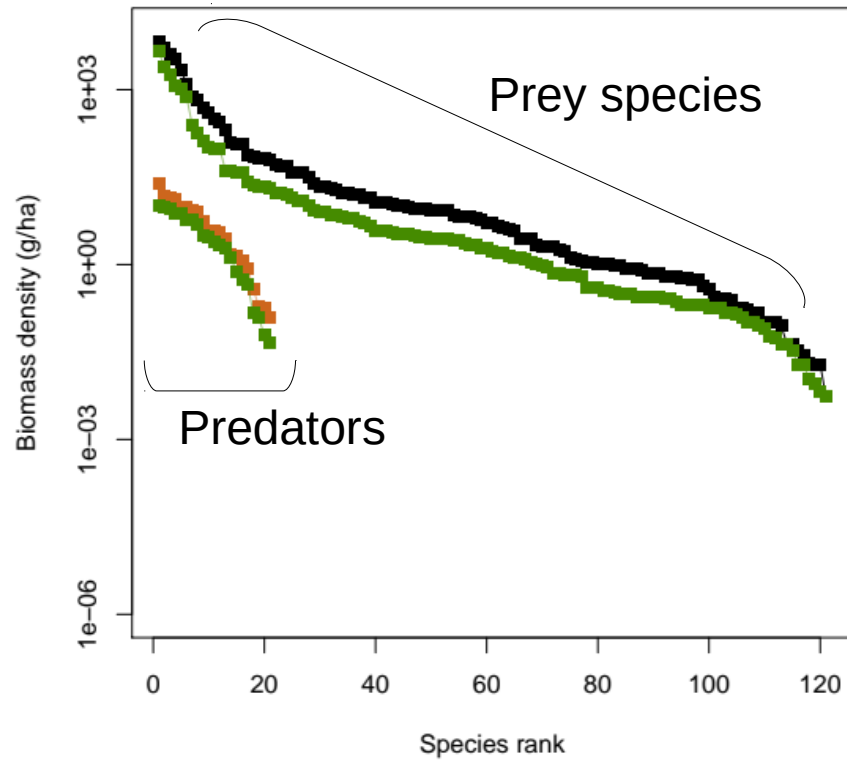
## Type II



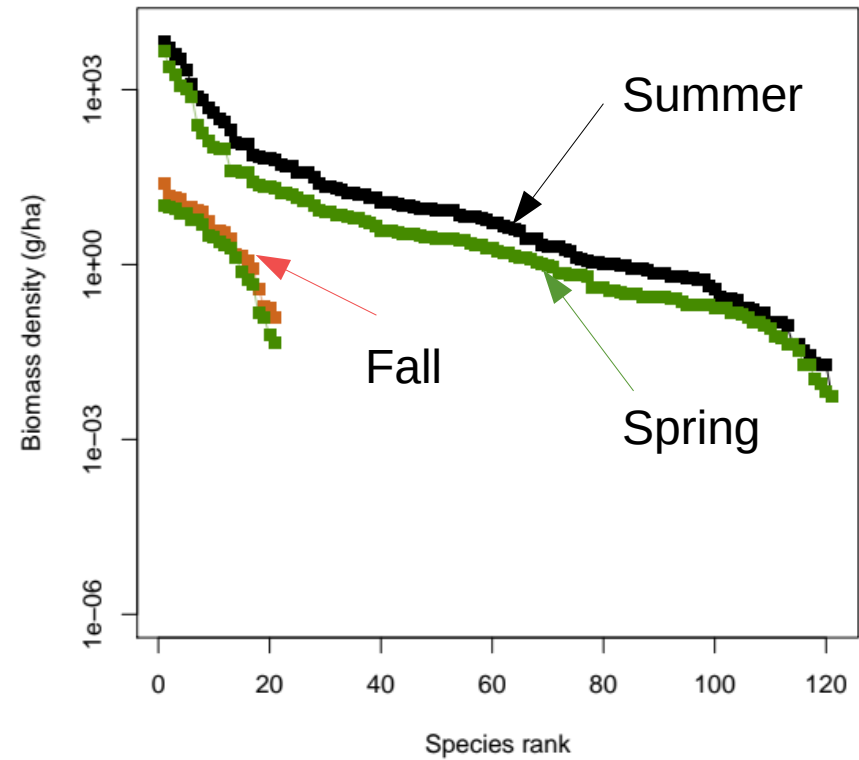


# Persistence is high but sensitive to estimates of predator regulation

## Type I

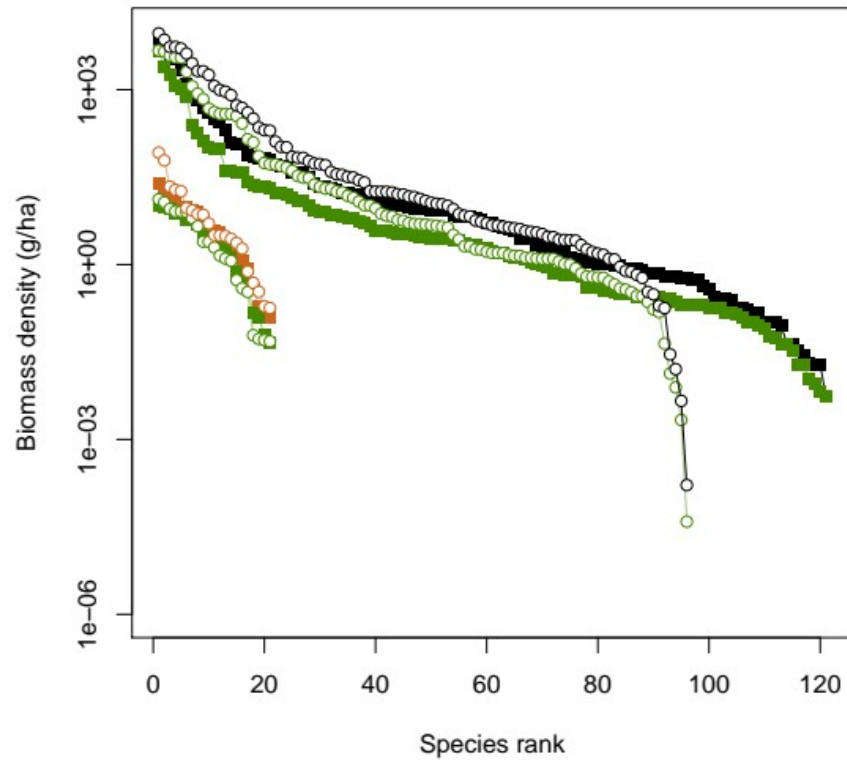


## Type II

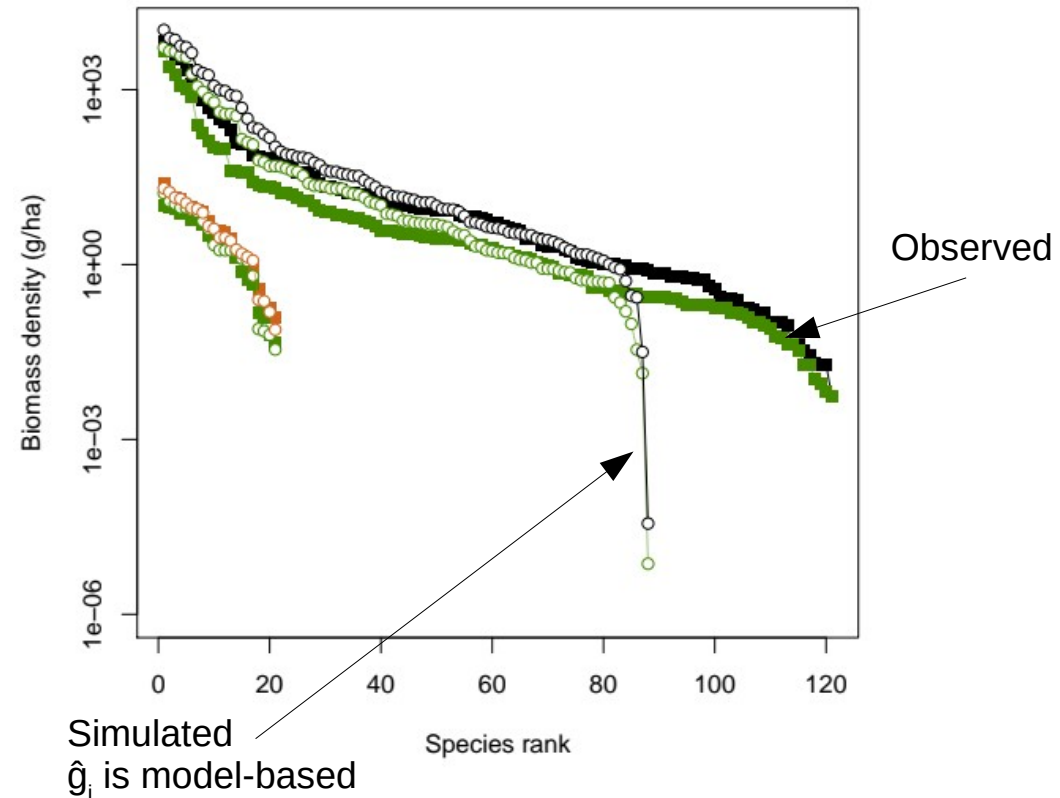


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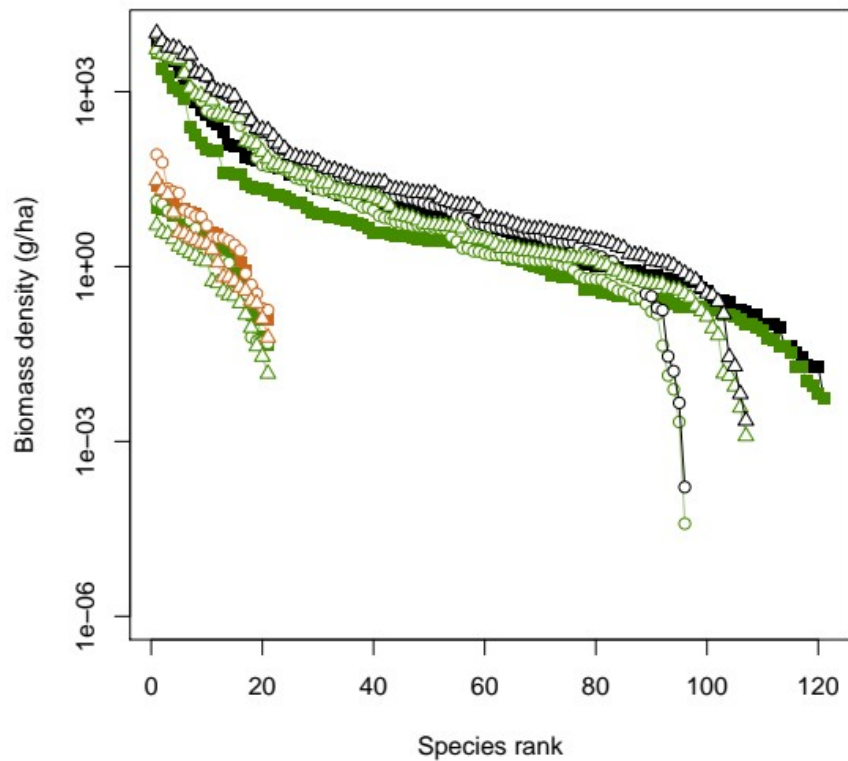


## Type II

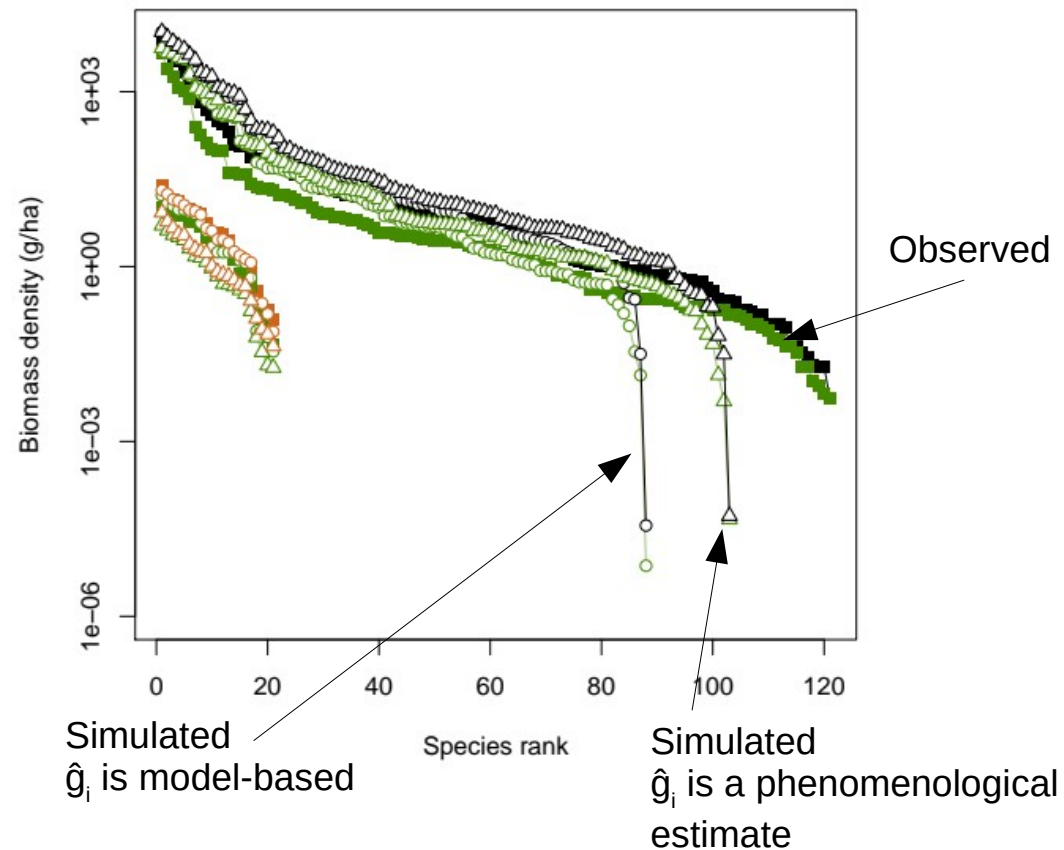


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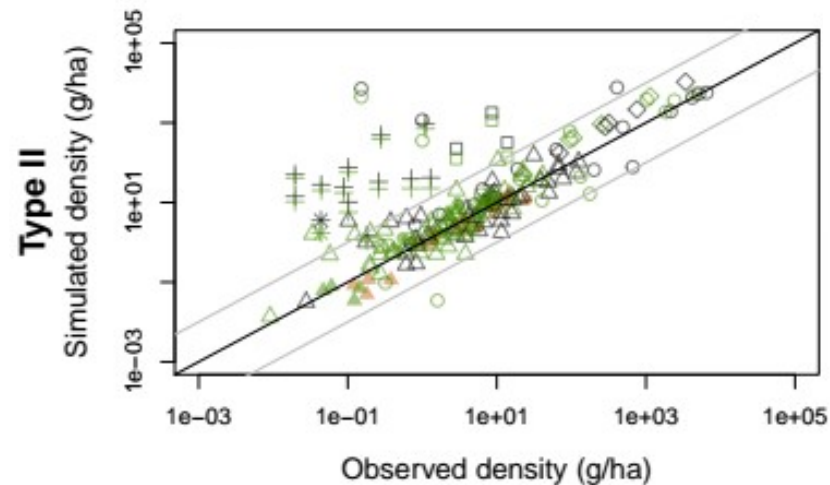
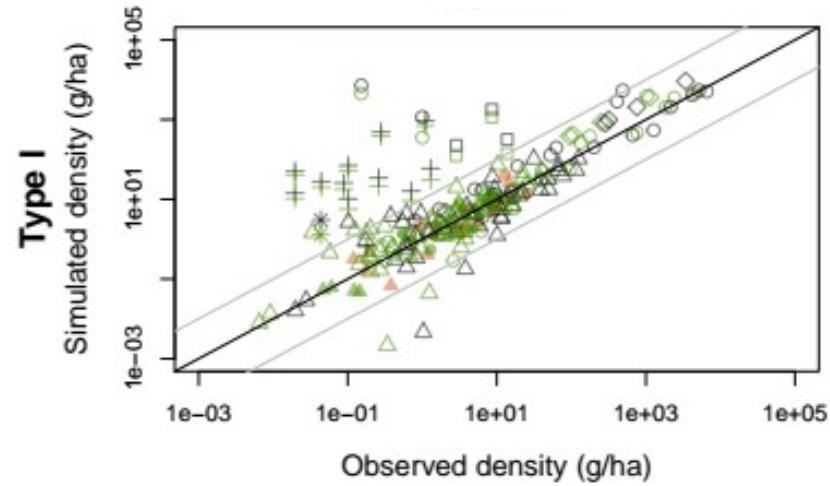
## Type I



## Type II

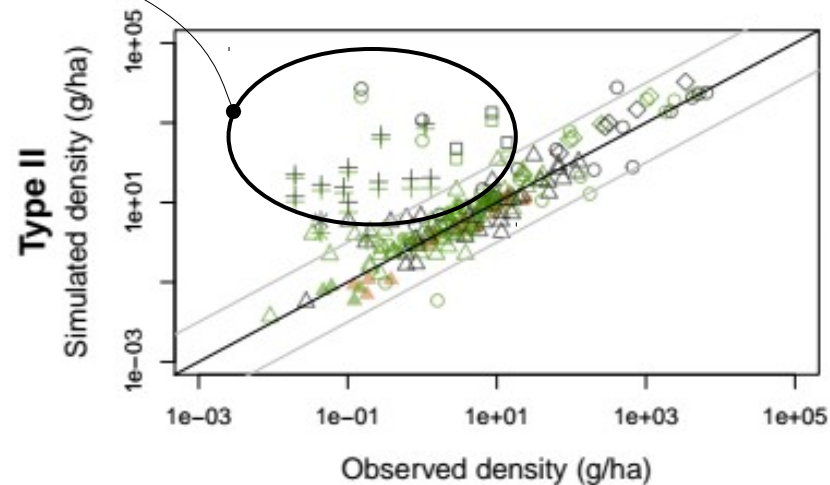
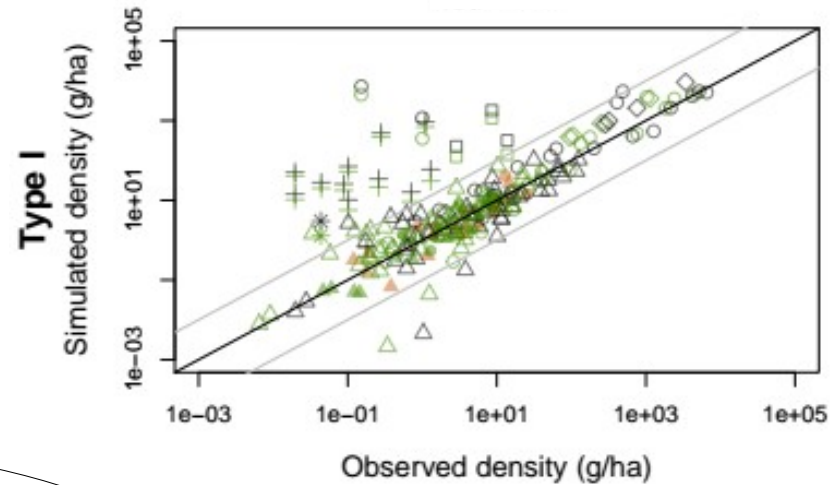


# Seasonal densities are reproduced



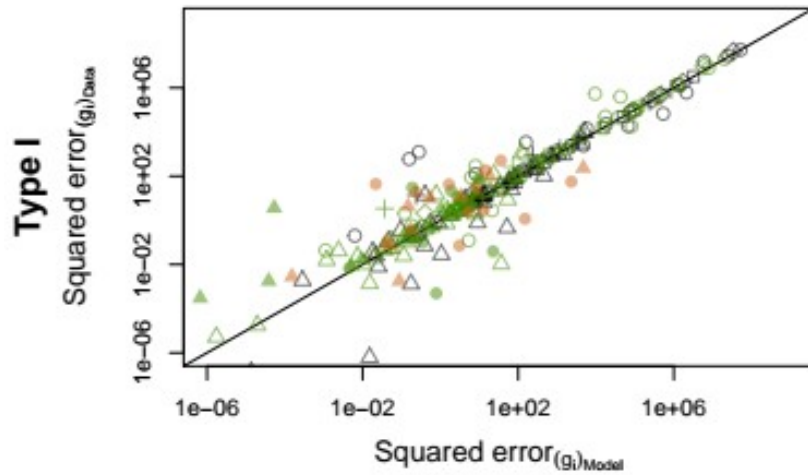
# Seasonal densities are reproduced

Mostly species for which we have little information about their densities



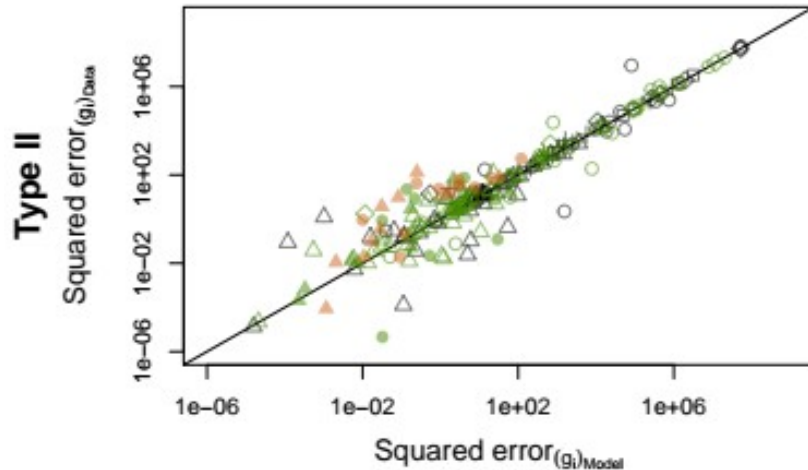
- Species type**
- ◇ Amphibian
  - △ Bird
  - + Fish
  - Mammal
  - \* Other
  - Reptile

# Where are the errors?



**Season**

- Spring
- Summer
- Autumn



**Species type**

- ◇ Amphibian
- △ Bird
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# Summary of the parameterisation of the seasonal food web of the Bialowieza Forest

This parameterisation is site-specific.

i.e.,  $\hat{a}_{ki} = f(\mathbf{R}^{obs})$

This facilitates comparison between sites.

But, it requires a lot of data.

There is a general trade-off between food web resolution and temporal resolution.

e.g., Boit et al. 2012, Ecol. Lett. ; Curtsdotter et al. 2019 J. Anim. Ecol.  
vs. e.g., Hudson et al. 2013, Proc. R. Soc. B.

# Summary of the parameterisation of the seasonal food web of the Bialowieza Forest

- This parameterisation is site-specific.

**Simulations produce life-like patterns of densities.**

- A prerequisite to numerical experiments.
- Model accuracy could be improved by collecting missing data (mostly densities...).
- Trade-off between persistence and accuracy.



# Summary of the parameterisation of the seasonal food web of the Bialowieza Forest

- This parameterisation is site-specific.
- Simulations produce life-like patterns of densities.

**Simulated dynamics are annual, but observations suggest a different story.**

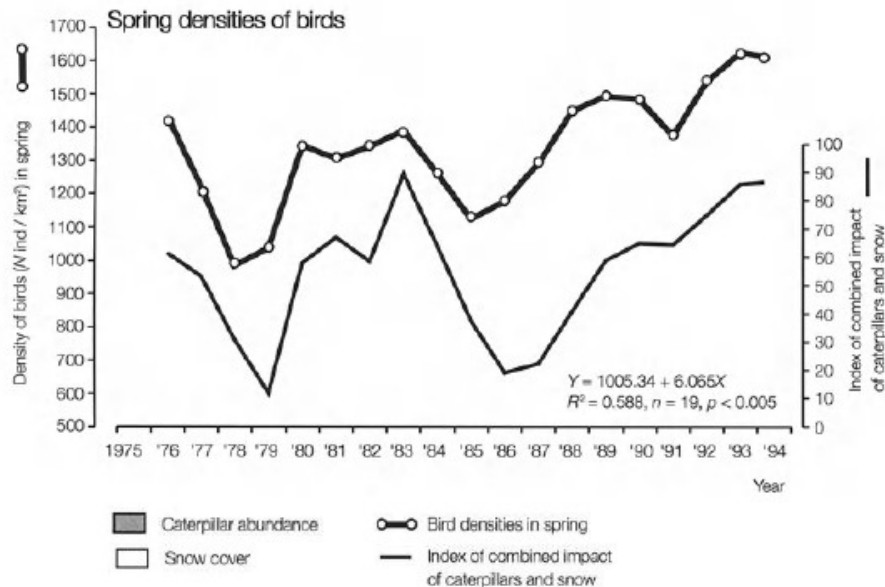


Fig. from Jedrzejewska & Jedrzejewski, 1998

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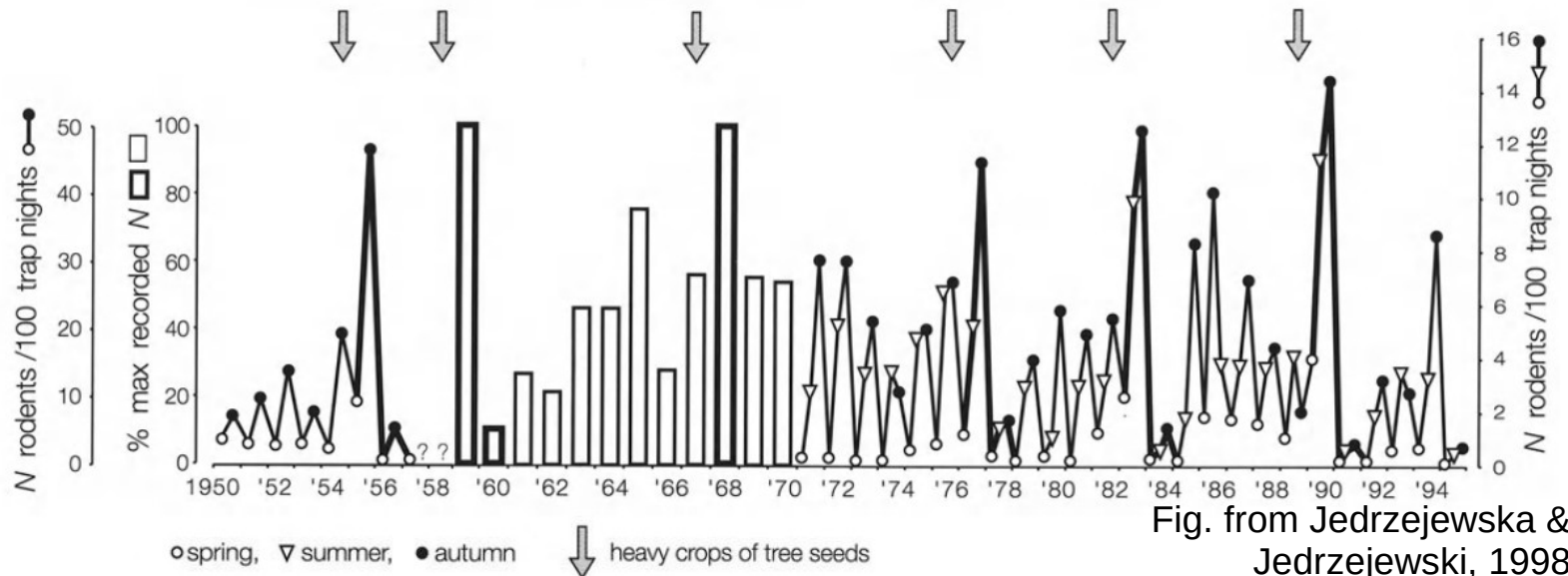


Fig. from Jedrzejewska & Jedrzejewski, 1998

# The case of cycling rodent dynamics

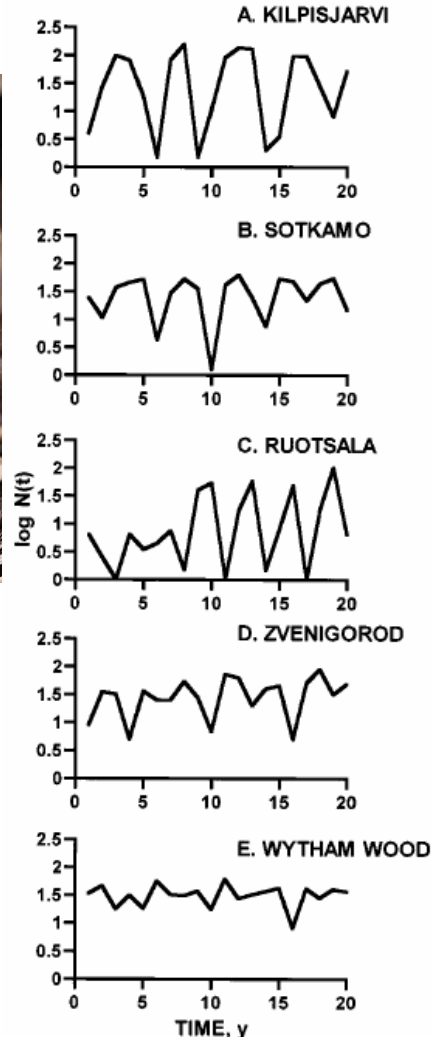


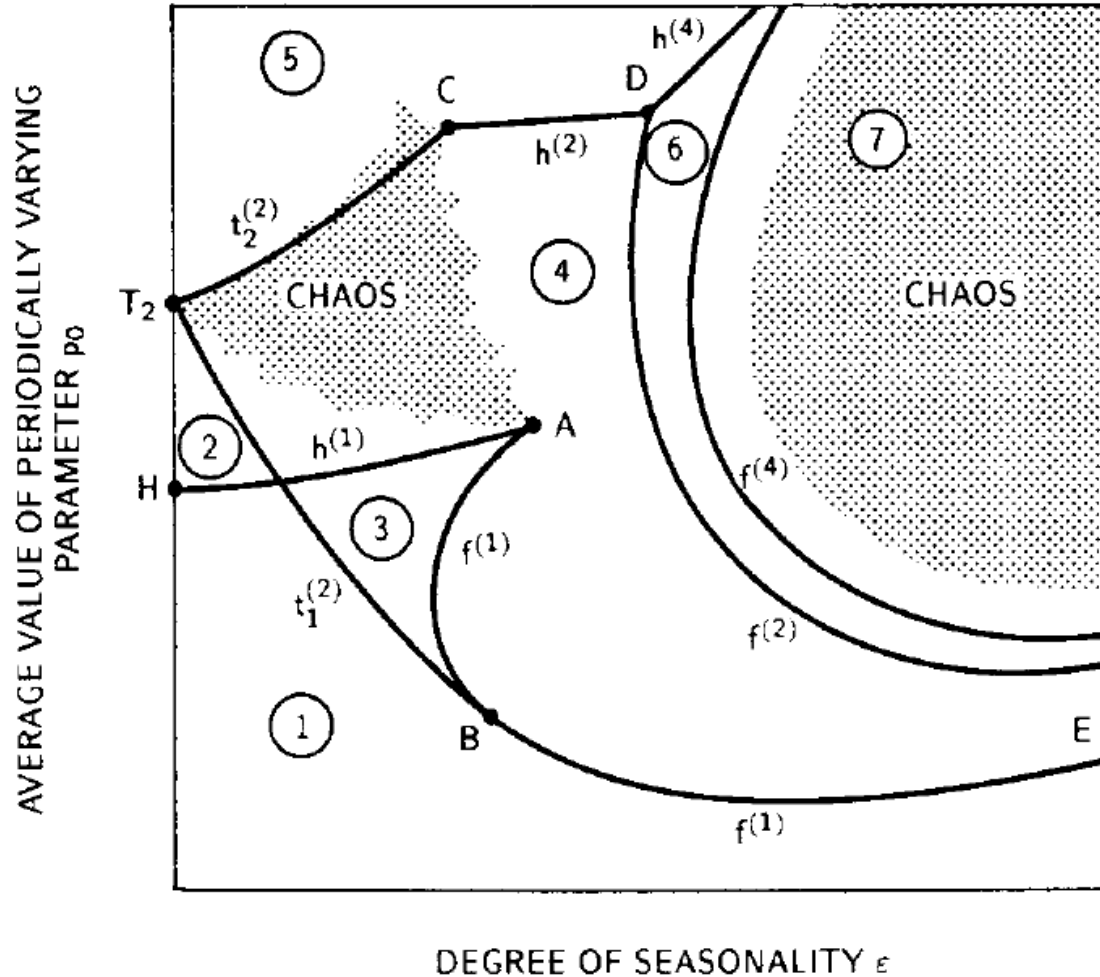
Fig. from Turchin & Hanski, 1997, *Am. Nat.*

- Widespread multiannual population fluctuations for many small rodents, especially at higher latitudes.
- Hypotheses are many !

Barraquand et al. 2017, *Ecol. Lett.*, Myers, 2018, *Proc. R. Soc. B*

- Models of population dynamics usually focus on the interplay between predation and seasonality.
- **BUT**, it is often necessary to explore parameter space to find the parameterisation that mimic observed time series.

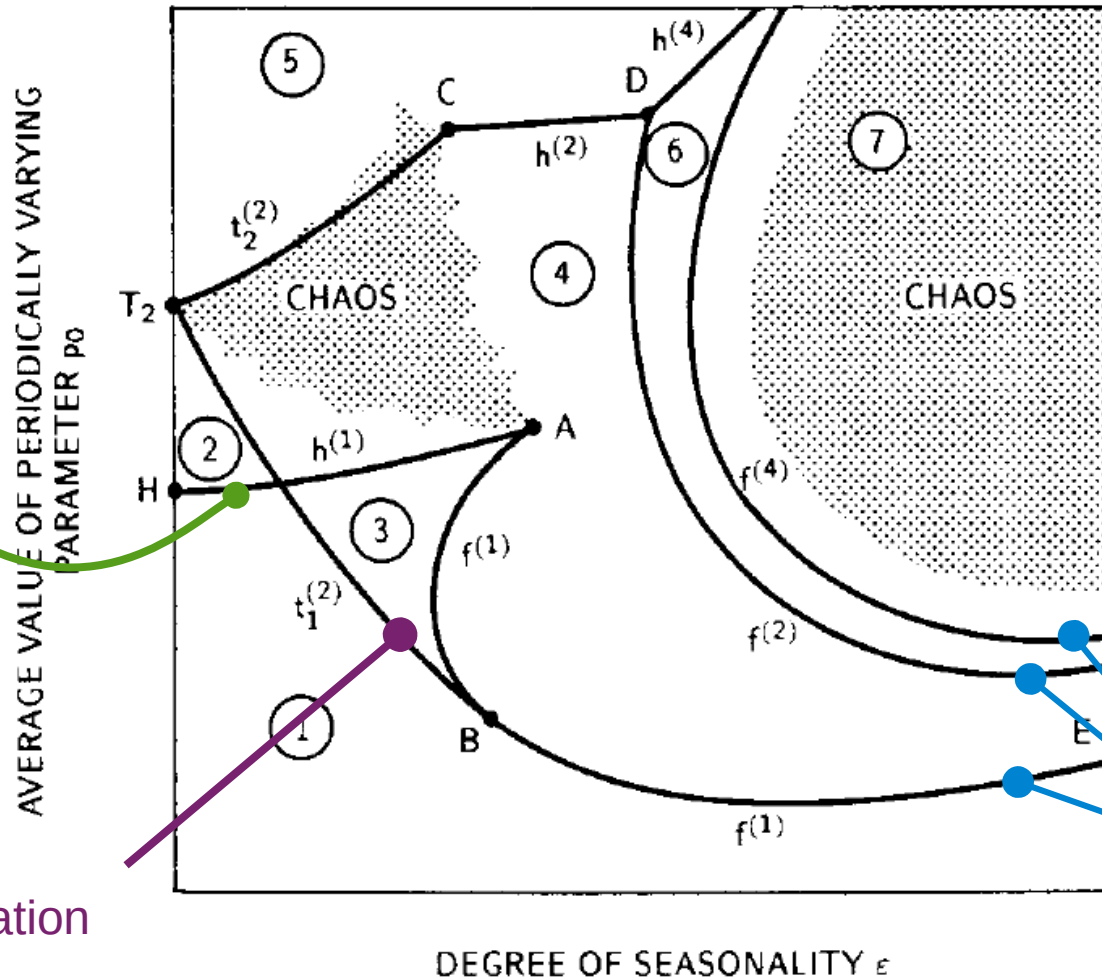
# Seasonal models of population dynamics often predict complex dynamics



Rinaldi et al. 1993,  
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e.g., Rosenzweig-  
MacArthur model

# Seasonal models of population dynamics often predict complex dynamics



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Neimark-Sacker  
bifurcation

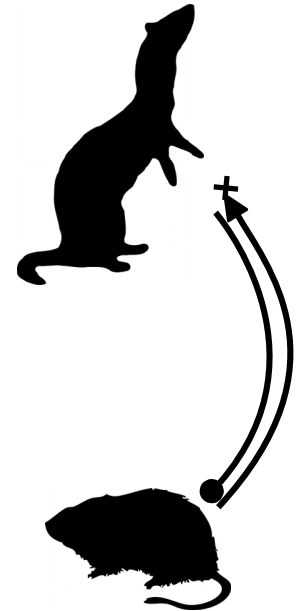
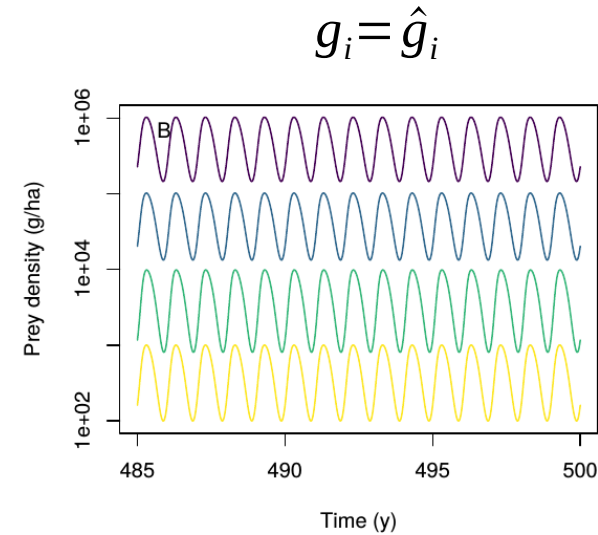
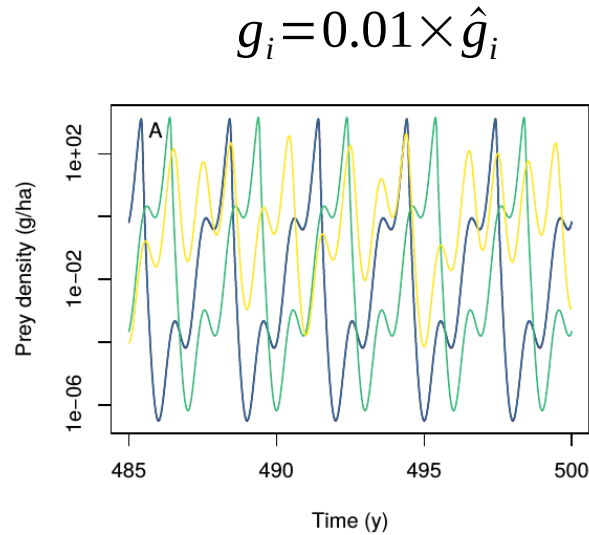
Fold bifurcation

Period-doubling  
bifurcations

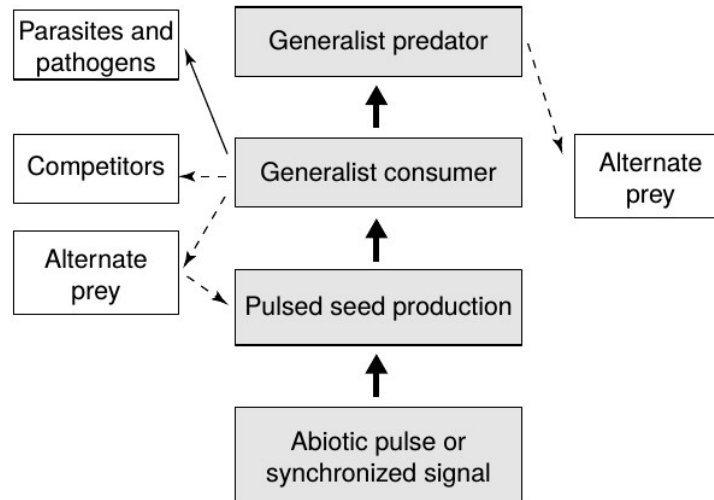
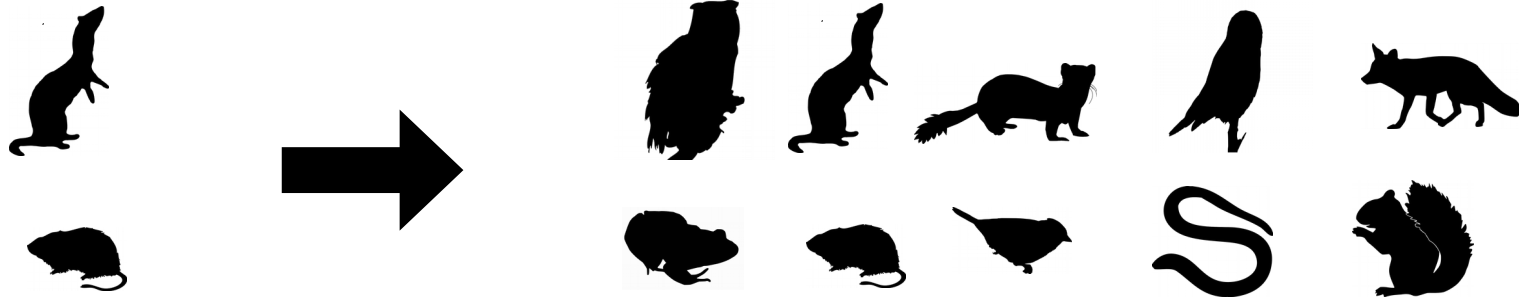
# From 2D-models to nD-models : implications of scaling up or down food web models?

Ingredients for more complex dynamics are gathered...

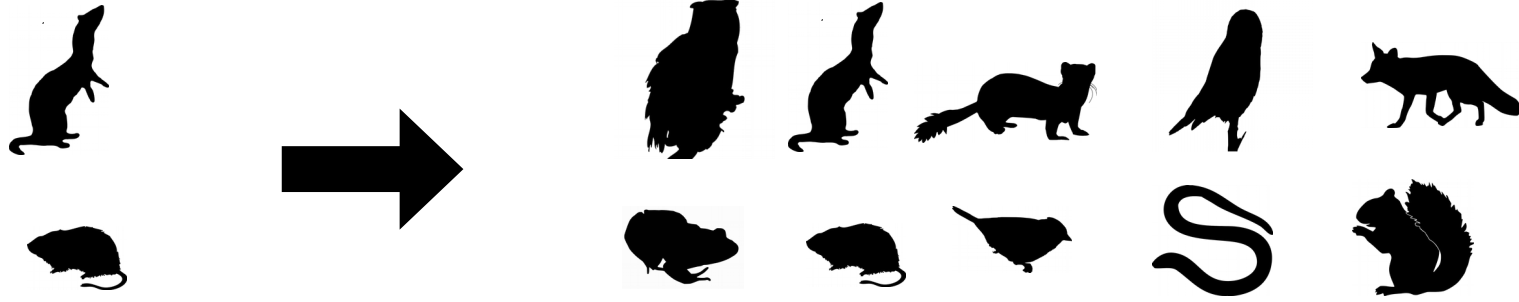
...provided predator's regulation is low enough!



# From 2D-models to nD-models : implications of scaling up or down food web models?



# From 2D-models to nD-models : implications of scaling up or down food web models?



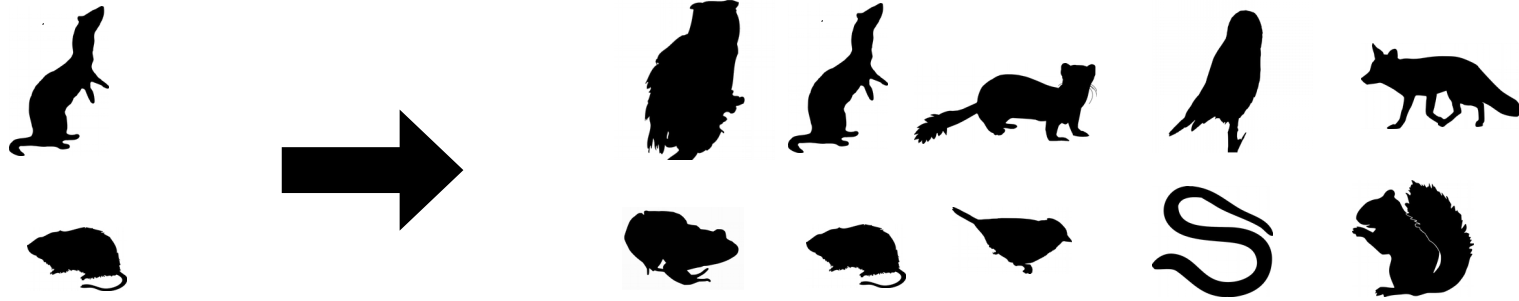
- Each species competes with itself.
- The predator has only one food source.

- Intra- and inter-specific competition.
- Multiple sources of food for predators.

If generalist, the predator can hunt other prey :  $a_{ki} \downarrow$   
Competition for territory should be harsher:  $g_i \uparrow$   
Competition on basal species should be higher:  $K_k \downarrow$



# From 2D-models to nD-models : implications of scaling up or down food web models?



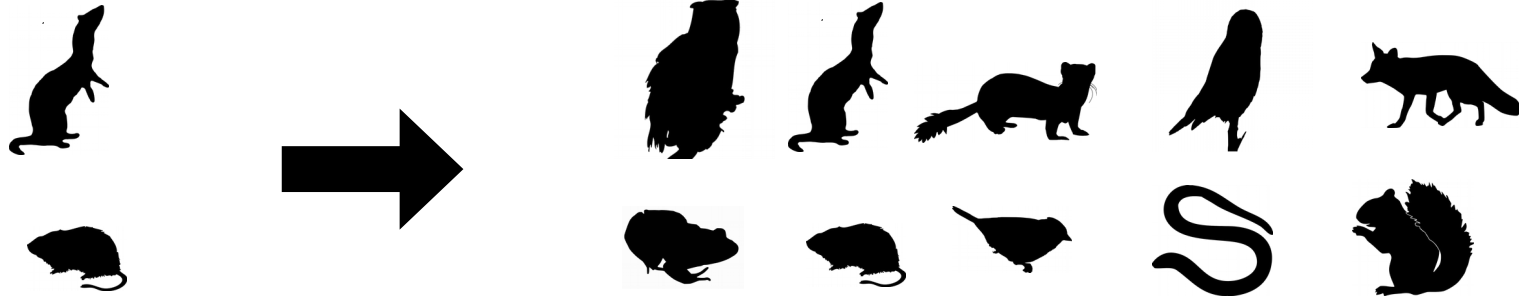
- Each species competes with itself.
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Community-level competition processes in food webs strongly constrain parameter space relative to modelled predator-prey pairs.

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# From 2D-models to nD-models : implications of scaling up or down food web models?



- Each species competes with itself.
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- Intra- and inter-specific competition.
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Community-level competition processes in food webs strongly constrain parameter space relative to modelled predator-prey pairs.

Prey oscillations may be due to processes that are not usually modelled in food web models.

# Thank you for your attention

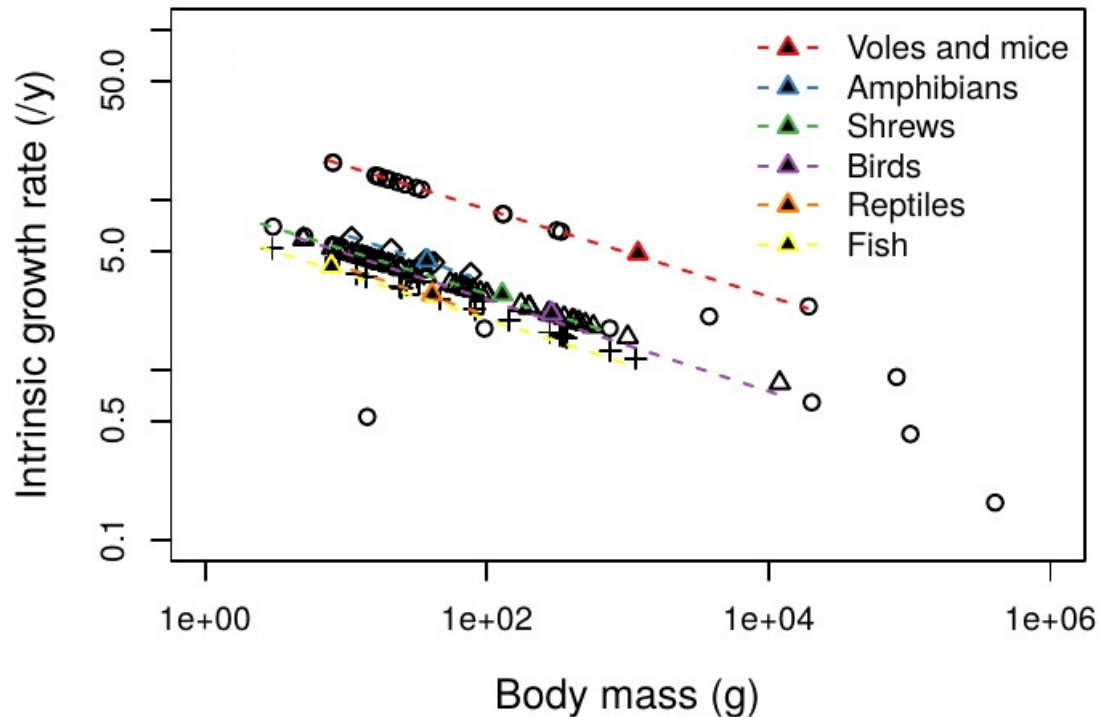
- Barraquand et al. (2017). Moving forward in circles: challenges and opportunities in modelling population cycles. *Ecol. Lett.*, 20(8), 1074-1092.
- Baudrot et al. (2016). The adaptation of generalist predators' diet in a multi-prey context: insights from new functional responses. *Ecology*, 97(7), 1832-1841.
- Boit, et al. (2012). Mechanistic theory and modelling of complex food-web dynamics in Lake Constance. *Ecol. Lett.*, 15(6), 594-602.
- Curtisdotter et al. (2019). Ecosystem function in predator-prey food webs: confronting dynamic models with empirical data. *J. Anim. Ecol.*, 88(2), 196-210.
- de Ruiter et al. (1995). Energetics, patterns of interaction strengths, and stability in real ecosystems. *Science*, 269(5228), 1257-1260.
- Dunne (2009). Food webs. *Encyclopedia of complexity and systems science*, 3661-3682.
- Gauzens et al. (2019). fluxweb: An R package to easily estimate energy fluxes in food webs. *MEE*, 10(2), 270-279.
- Hudson & Reuman (2013). A cure for the plague of parameters: constraining models of complex population dynamics with allometries. *Proc. R. Soc. B*, 280(1770), 20131901.
- Humphries et al. (2017). To everything there is a season: summer-to-winter food webs and the functional traits of keystone species. *ICB*, 57(5), 961-976.
- Jedrzejewska & Jedrzejewski (1998). Predation in vertebrate communities: the Bialowieza Primeval Forest as a case study (Vol. 135). Springer Science & Business Media.
- McCallum (2008). Population parameters: estimation for ecological models (Vol. 3). John Wiley & Sons.
- Ostfeld & Keesing (2000). Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *TREE*, 15(6), 232-237.
- Myers (2018). Population cycles: generalities, exceptions and remaining mysteries. *Proc. R. Soc. B*, 285(1875), 20172841.
- Rinaldi et al. (1993). Multiple attractors, catastrophes and chaos in seasonally perturbed predator-prey communities. *Bull. Math. Biol.*, 55(1), 15-35.
- Rohr et al. (2014). On the structural stability of mutualistic systems. *Science*, 345(6195), 1253497.
- Saavedra et al. (2016). Seasonal species interactions minimize the impact of species turnover on the likelihood of community persistence. *Ecology*.
- Turchin & Hanski (1997). An empirically based model for latitudinal gradient in vole population dynamics. *Am. Nat.*, 149(5), 842-874.
- Yodzis & Innes (1992). Body size and consumer-resource dynamics. *Am. Nat.*, 139(6), 1151-1175.



# Estimates of prey intrinsic growth rates

Intrinsic growth rates of the prey scale with species body mass following the quarter power law (Savage et al., 2004).

$$r_k \propto M_k^{-1/4}$$
$$r_{k,g} = E_g \times M_{k,g}^{-1/4}$$

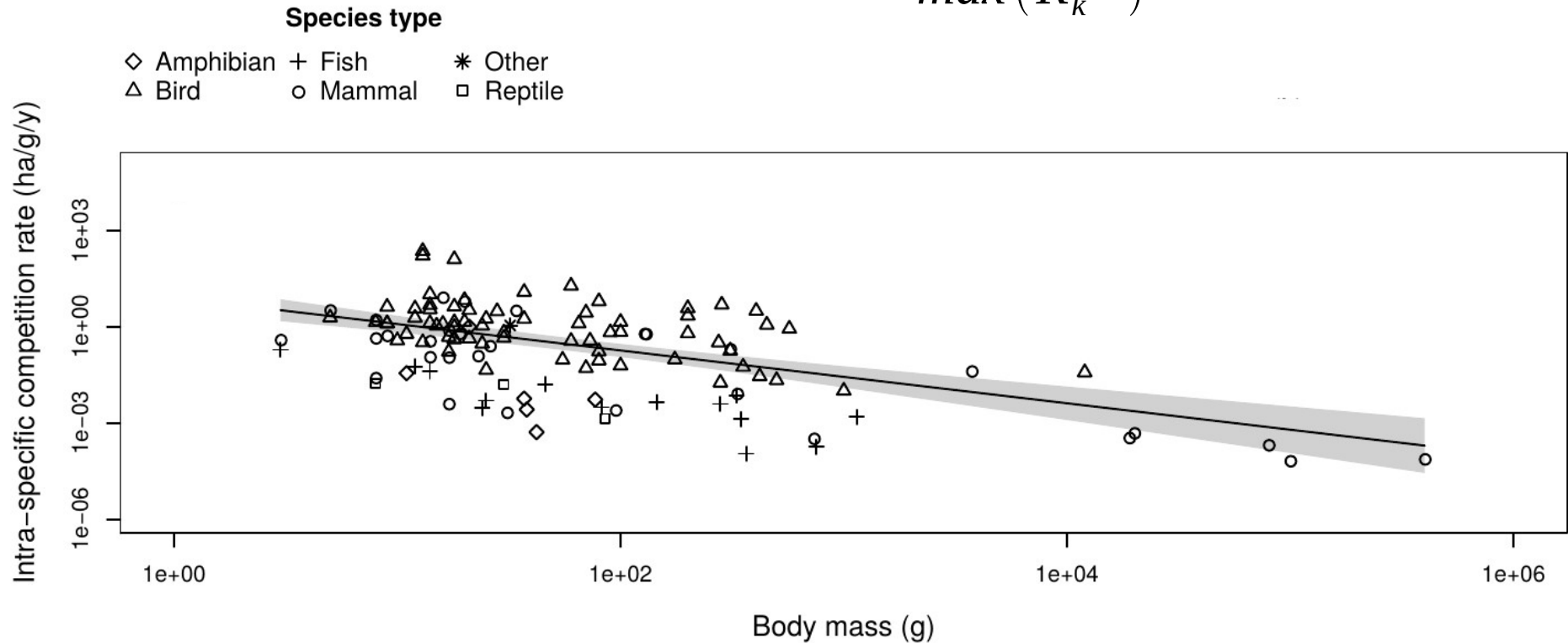


## Species type

- ◇ Amphibian
- △ Bird
- + Fish
- Mammal
- \* Other
- Reptile

# Estimates of prey intraspecific competition rates

$$\hat{\beta}_k = \frac{\hat{r}_k}{\max(R_k^{Obs})}$$

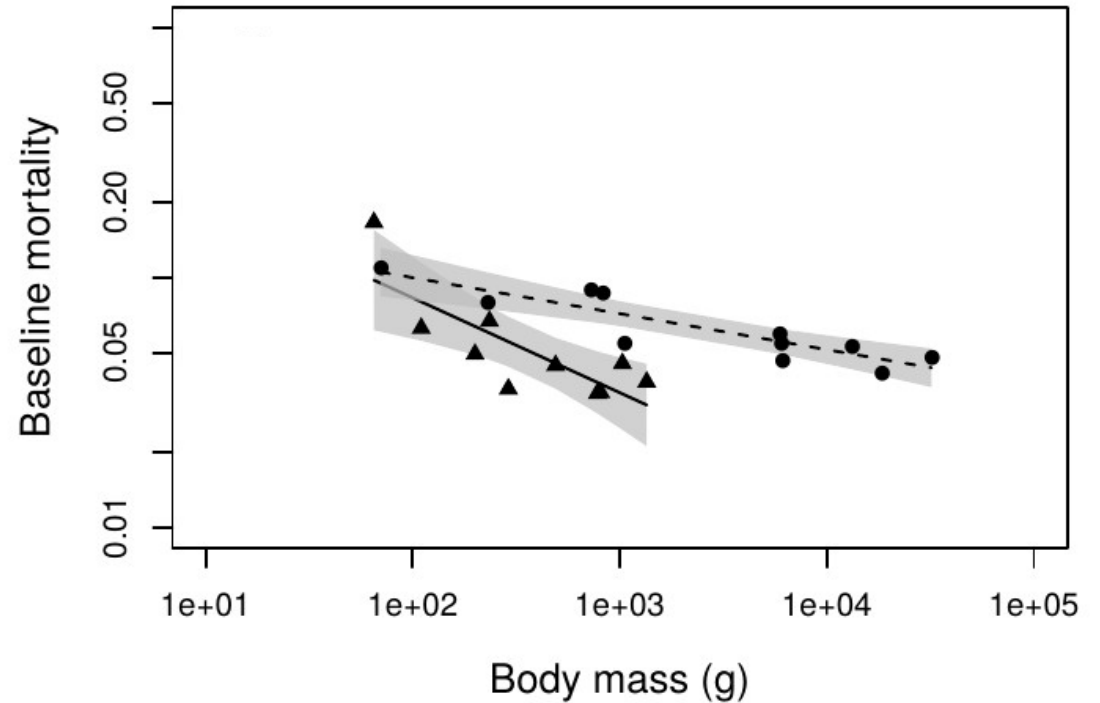


# Estimates of predator baseline mortality rates

$$\hat{m}_i = 1 / \Lambda_i$$

Max. longevity  
(e.g., in captivity)

Database *AnAge*  
(De Magalhães et al., 2005)



# Estimates of predator density-dependent mortality rates

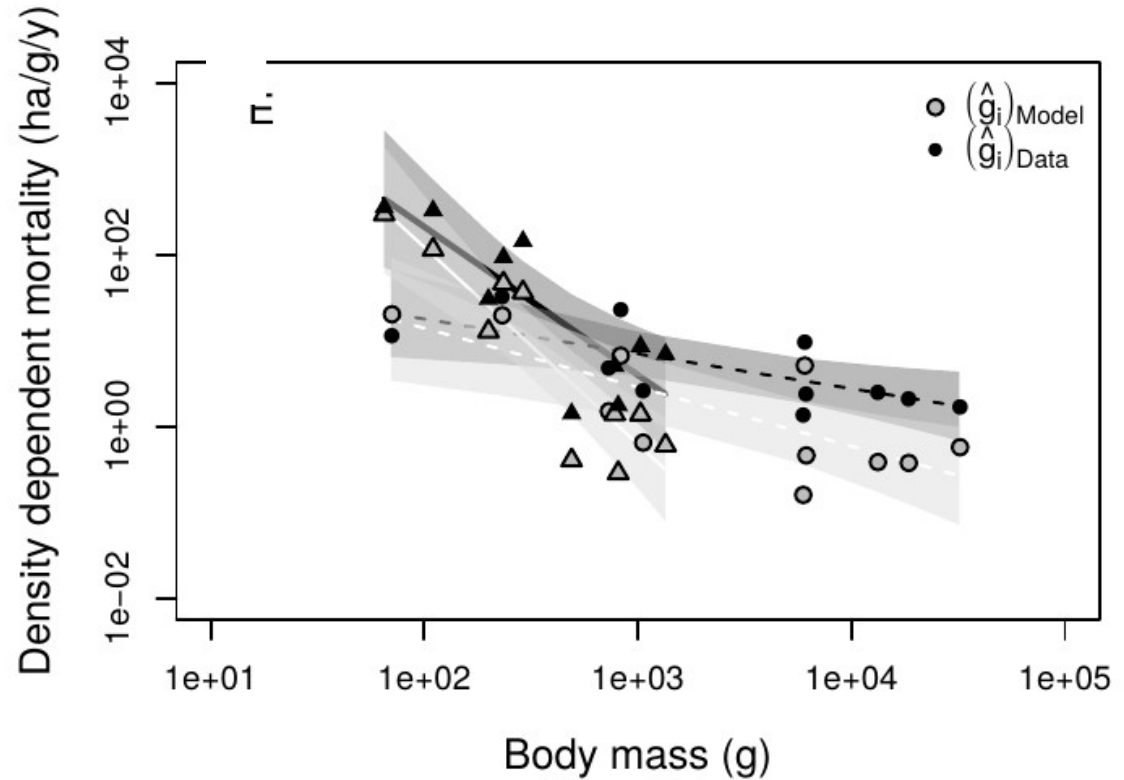
The phenomenological estimate  $(\hat{g}_i)_{Data}$

H: Year-round average values of predator biomass densities are constant.

$$r_i = e \frac{\sum_k f_{ki}(\mathbf{R})}{M_i}$$

$$r_i - g_i \bar{C}_i = 0 \Rightarrow (\hat{g}_i)_{Data} = \frac{(\hat{r}_i)_{Obs}}{\bar{C}_i}$$

$$(\hat{r}_i)_{Obs} = \frac{365}{198} \times \log\left(\frac{C_i^{Autumn}}{C_i^{Spring}}\right)$$





# Estimates of predator density-dependent mortality rates

The phenomenological estimate  $(\hat{g}_i)_{\text{Data}}$

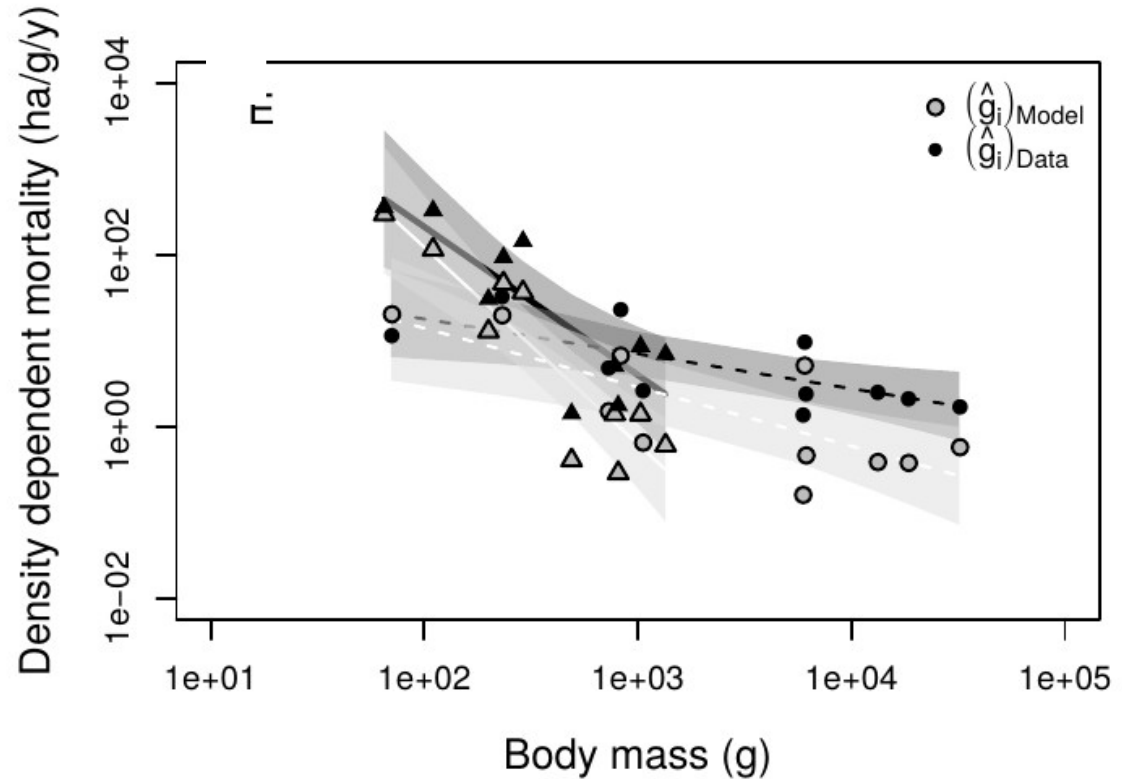
H1: Year-round average values of predator biomass densities are constant.

The model-based estimate  $(\hat{g}_i)_{\text{Model}}$

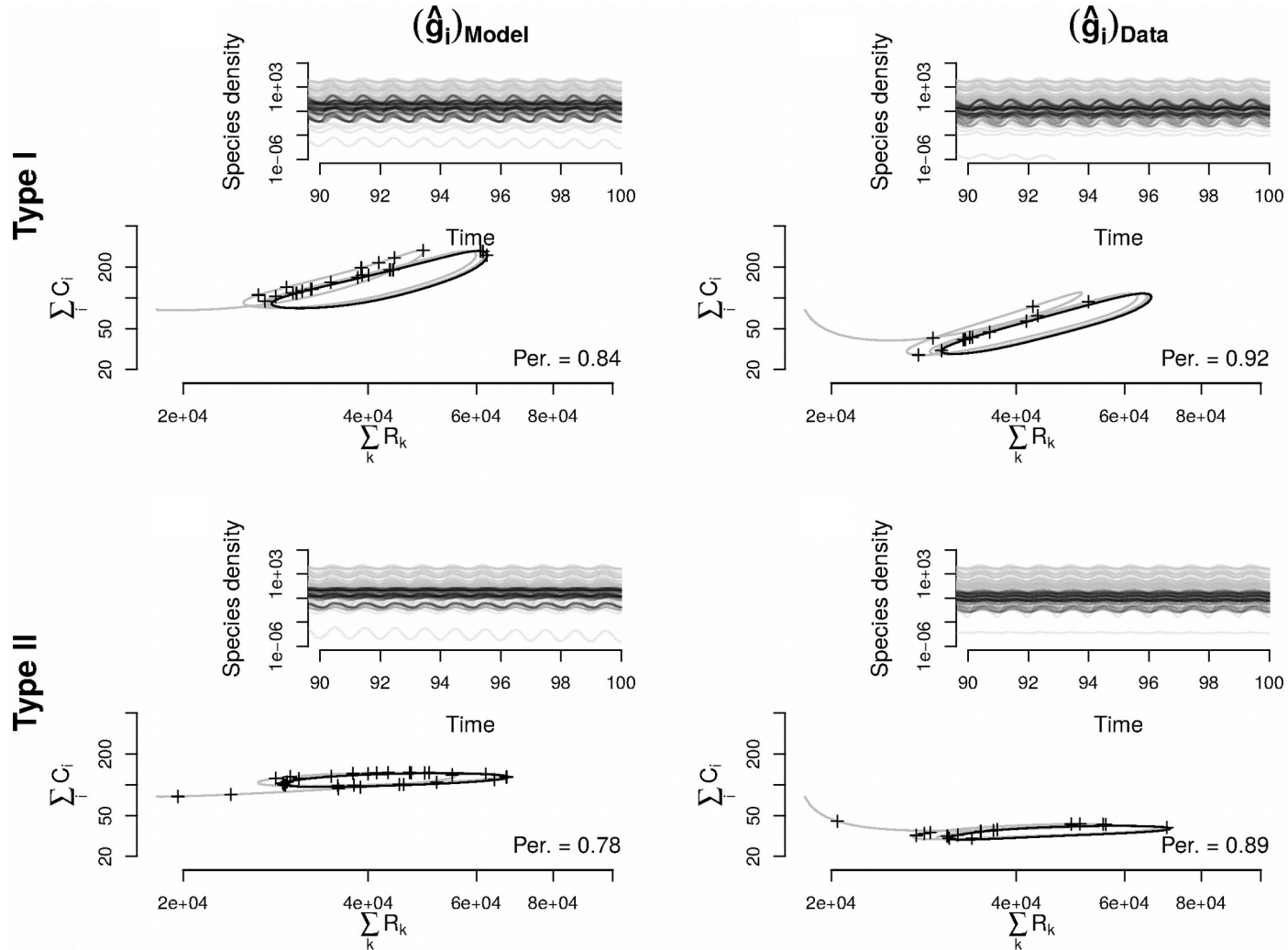
H1 + H2

H2:  $g_i$  limits the predator density to a given threshold when the population kill a maximum biomass of prey.

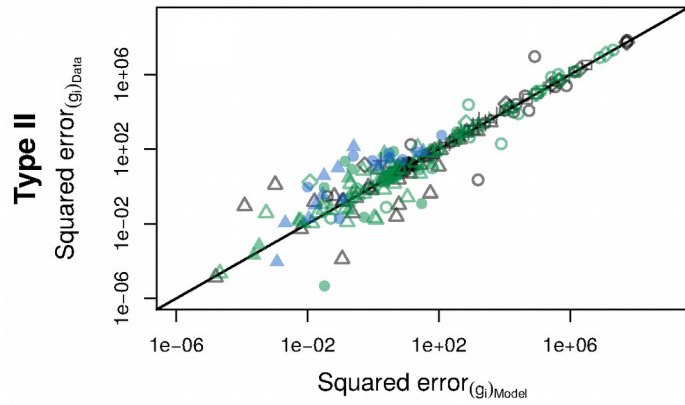
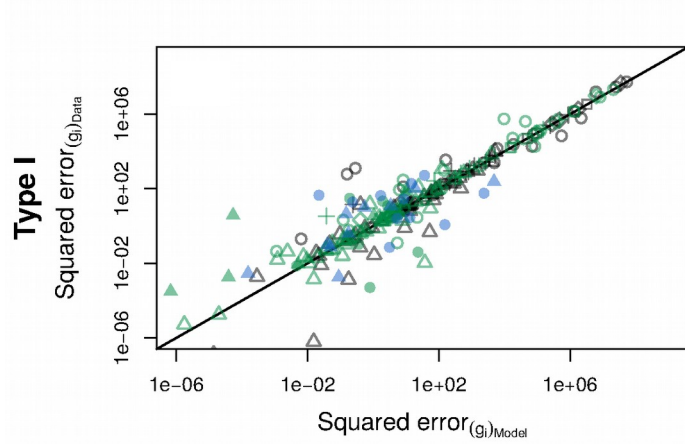
$$(\hat{g}_i)_{\text{Model}} = \frac{\left(\frac{e}{h_i \times M_i}\right)^{-m_i}}{C_i^{\text{Autumn}} \times 1.5}$$



# Dynamics for different functional responses and estimates of density-dependent mortality rates



# SADs for different functional responses and estimates of density-dependent mortality rates

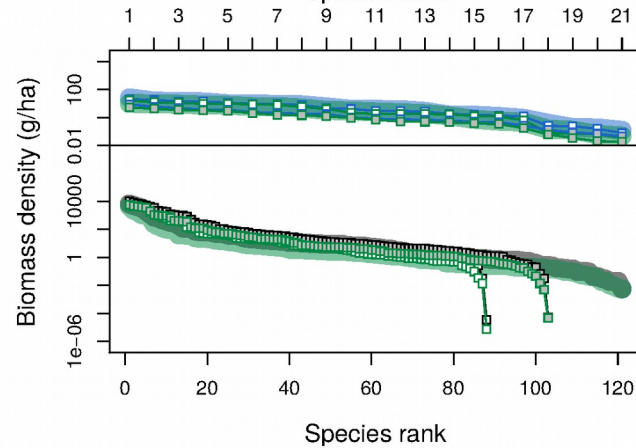
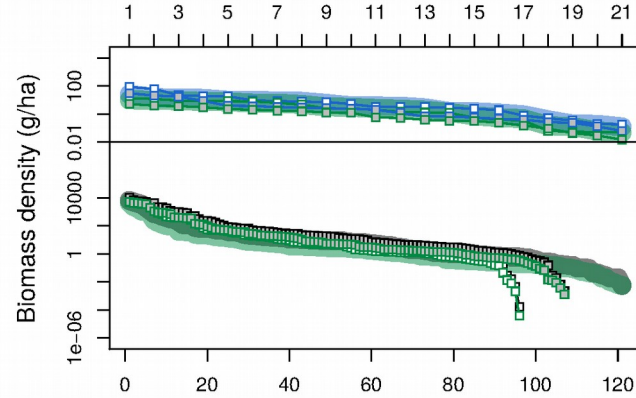


**Season**

- Spring
- Summer
- Autumn

**Species type**

- ◇ Amphibian
- △ Bird
- + Fish
- Mammal
- \* Other
- Reptile



- Observed
- $(g_i)_{Model}$
- $(g_i)_{Data}$
- Spring
- Summer
- Autumn