

1 **Model and methods**

2 **Model description**

3 We use the food web approach for size-structured populations proposed by Hartvig et al. 2011.
4 In this framework, size at maturation characterises each consumer species. All model parameters
5 are made species independent through scaling with individual body size and size at maturation.
6 Parameter values are determined from cross-species analysis of fish communities Hartvig et al.
7 2011.

8 We assume that there are F food sources available, with densities R_j ($j = 1, \dots, F$) and N
9 consumer species with density N_i each ($i = 1, \dots, N$). The consumer species are characterised by
10 their feeding niche trait x_i . Consumer individuals are born with a body mass of $m = m_b$ and mature
11 with a body mass of $m = m_{\text{mat}}$. Growth and reproduction of the consumers dependent on size-
12 dependent food intake, $I_i(m, \mathbf{R}, x_i)$, where $\mathbf{R} = (R_1, \dots, R_F)$ denotes the food source vector.

13 **Food ingestion**

14 The food consumption of an individual of species i depends on its size, its feeding niche trait value
15 x_i , and on the densities of the food sources \mathbf{R} . We assume that for each food source, there exist
16 an optimal trait value θ_j , which maximises the attack rate on this food source. When the feeding
17 niche trait x_i of an individual equals θ_j , the attack rate constant $\gamma_{i,j}(x_i)$ on resource j equals the
18 maximum, size-independent, attack rate A , and decreases in a Gaussian manner as x_i moves away
19 from the optimal trait value θ_j following

$$\gamma_{i,j}(x_i) = A \exp[-(x_i - \theta_j)^2 / (2\tau^2)]. \quad (1)$$

In this equation parameter τ determines the width of the Gaussian function and parameter A the maximum height. See figure 1 for some examples (*Just for myself, not necessary in ms*).

With this function, a species that has a value of $x_i = 1$, is highly specialized on a food source with $\theta_j = 1$, and will also be able to feed on food sources with values of θ_j close to one, but not very well on food sources with a θ_j far away from one.

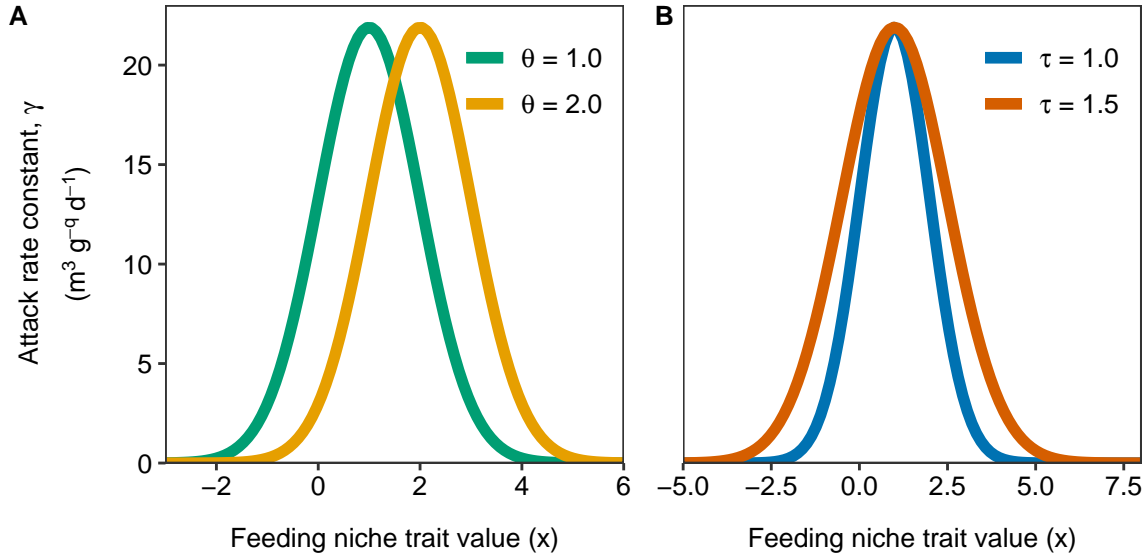


Figure 1: The attack rate constant $\gamma_{i,j}(x_i)$ (equation 1) as a function of the feeding niche trait value x . The constant reaches its maximum value $A = 21.9$ when the feeding niche trait value x equals the optimal trait value of the food source θ_j . Parameter τ , which determines the width of the curves, equals 1 in panel A and is variable in panel B. Parameter θ , determining for which niche trait value $a_{i,j}(x_i)$ reaches its maximum, varies in panel A and equals 1 in panel B.

Scenario 1: A shared juvenile food source

We assume that the attack rates of species i on resource j increases with consumer size following $a_{i,j}(x_i, m) = \gamma_{i,j}(x_i)m^q$, where parameter q is a positive exponent signifying that larger individuals search a larger volume per unit time. In addition, we assume that all individuals start their lives feeding on a shared juvenile food source R_{Juv} . The larger individuals get, the less time they spend feeding upon the juvenile food source, and the more time they spend feeding on the adult resources.

31 The fraction of time, $\phi(m)$, individuals feed upon the juvenile resource therefore decreases with
 32 body size following

$$\phi(m) = 1 - \frac{1}{1 + \exp(-(m - m_{\text{shift}}))}, \quad (2)$$

33 where parameter m_{shift} indicates the body mass where individuals spend half of their time feeding
 34 on the juvenile resource.

35 We assume a Holling type 2 functional response for the consumers, with hm^n indicating the
 36 maximum size-specific food intake. The total rate of food intake than equals

$$I_i(m, \mathbf{R}, x_i) = hm^n \frac{(1 - \phi(m)) \sum_j a_{i,j}(x_i, m) R_j + \phi(m) a_{i,\text{juv}}(x_i, m) R_{\text{juv}}}{(1 - \phi(m)) \sum_j a_{i,j}(x_i, m) R_j + \phi(m) a_{i,\text{juv}}(x_i, m) R_{\text{juv}} + hm^n} \quad (3)$$

37 **Maintenance costs**

38 Ingested food is assimilated with an efficiency of α and first used to cover maintenance costs.
 39 Maintenance costs are proportional to body mass and equal km^p . The difference between the
 40 mass-specific assimilation rate and the maintenance costs determines the net biomass production
 41 of individuals which equals

$$E_i(m, \mathbf{R}, x_i) = \alpha I(m, \mathbf{R}, x_i) - km^p. \quad (4)$$

42 **Reproduction**

43 A fraction $\psi(m)$ of the net biomass production is used for reproduction, the remaining energy is
 44 used for somatic growth. We use a smooth step function for energy allocation to reproduction
 45 switching from zero to one around the size at maturation m_{mat}

$$\psi_i(m) = \left[1 + \frac{m}{m_{\text{mat}}}^{-u}\right]^{-1} \left(\frac{\eta_{\text{mat}} m}{m_{\text{mat}}}\right)^{1-n}, \quad (5)$$

where parameter u determines the steepness of the curve.

The reproduction rate of individuals is then given by

$$b_i(m, \mathbf{R}, x_i) = \begin{cases} \psi_i(m) E_i(m, \mathbf{R}) \frac{\varepsilon}{2m_b} & E_i(m, \mathbf{R}, x_i) > 0 \\ 0 & \text{otherwise,} \end{cases} \quad (6)$$

where ε is the efficiency of offspring production, and the factor 2 in the denominator takes into account that only females spawn. The total rate of offspring production of species i can be calculated by integrating equation 6 over all individuals

$$R_i(\mathbf{R}, x_i) = \int_{m_b}^{\infty} b_i(m, \mathbf{R}, x_i) N_i(m, t) dm \quad (7)$$

Individual growth

Since we assume that individuals do not shrink in body mass in case their biomass production is negative, somatic growth equals

$$g_i(m, \mathbf{R}, x_i) = \begin{cases} (1 - \psi(m))(\alpha I(m, \mathbf{R}, x_i) - km^p) & E_i(m, \mathbf{R}, x_i) > 0 \\ 0 & \text{otherwise.} \end{cases} \quad (8)$$

Mortality

All individuals experience a background mortality of μ_b . Background mortality does not depend on size and equals m_b . In addition, we assume that individuals experience starvation mortality in case food intake is not sufficient to cover maintenance costs (when $E_i(m, \mathbf{R}, x_i) < 0$). We assume that starvation mortality is proportional to the energy deficiency, and inversely proportional to body

59 mass (since bigger individuals have more reserves).

$$\mu_s(m, \mathbf{R}, x_i) = \begin{cases} 0 & E_i(m, \mathbf{R}, x_i) > 0 \\ \frac{E_i(m, \mathbf{R}, x_i)}{\xi m} & \text{otherwise} \end{cases} \quad (9)$$

60 The total mortality rate experienced by an individual is than given by $\mu(m, \mathbf{R}, x_i) = \mu_b +$
 61 $\mu_s(m, \mathbf{R}, x_i)$

62 Population dynamics

63 The population dynamics of species i depends on individual growth $g_i(m)$ and mortality $\mu_i(m)$ and
 64 is given by

$$\begin{aligned} \frac{\partial N_i(m, t)}{\partial t} + \frac{\partial g_i(m, \mathbf{R}, x_i) N_i(m, t)}{\partial m} &= -\mu_i(m, \mathbf{R}, x_i) N_i(m, t), \\ g_i(m_b, \mathbf{R}, x_i) N_i(m_b, t) &= R_i(\mathbf{R}, x_i). \end{aligned} \quad (10)$$

65 Food dynamics

66 All food sources grow following semi-chemostat dynamics with turnover rate δ , and will, in the
 67 absence of consumers, reach a density of $R_{i, \max}$. The dynamics of an adult food source j are given
 68 by

$$\frac{dR_j}{dt} = \delta(R_{j, \max} - R_j) - \sum_i \int_{m_b}^{\infty} h m^n \frac{(1 - \phi(m)) a_{i,j}(x) R_j}{(1 - \phi(m)) \sum_k a_{i,k}(x_i, m) R_k + \phi(m) a_{i, \text{juv}}(x_i, m) R_{\text{juv}} + h m^n} N_i(m) dm. \quad (11)$$

69 The dynamics of the juvenile food source R_{juv} is given by

$$\frac{dR_{\text{juv}}}{dt} = \delta(R_{\text{juv},\text{max}} - R_{\text{juv}}) - \sum_i \int_{m_b}^{\infty} h m^n \frac{\phi(m) a_{i,\text{juv}}(x) R_{\text{juv}}}{(1 - \phi(m)) \sum_j a_{i,j}(x_i, m) R_j + \phi(m) a_{i,\text{juv}}(x_i, m) R_{\text{juv}} + h m^n} N_i(m) dm. \quad (12)$$

The total productivity of the system is the sum of the maximum densities of each of the food source,

$$\phi = \sum_j R_{j,\text{max}}$$

. We assume that all adult food sources have a productivity of $R_{\text{Adlt},\text{max}}$, the maximum density of the juvenile resource equals $R_{\text{juv},\text{max}}$

Parameterization

Following Hartvig et al. 2011, but all rates are per day instead of per year, see table 1.

Adaptive dynamics approach

Invasion fitness, separation of time-scales, and, most importantly, clonal reproduction. etc.

Model analysis

All analyses were performed using the PSPManalysis software package (de Roos 2016). This software package allows for the equilibrium and evolutionary analysis of physiologically structured population models (see Diekmann et al. 2003; Kirkilionis et al. 2001; de Roos 2008 for more details). The model-specific files needed for PSPManalysis together with an R script that executes all the calculations made in this manuscript will be made available.

Individual based model

For the individual based model, we use an additive diploid multilocus approach. Each individual is assigned a genotype that in turn determines its phenotype. All individuals have up to three diploid genotypes, with N loci each. One set of loci determines the ecological character x , the second set codes for the mating character which determines the degree of assortative mating a , and the third determines the neutral marker trait n . The mating character a is determined by the additive effect of N diallelic loci. The difference between the number of $+$ and $-$ alleles divided by the total number of alleles determines the mating character a which therefore has a value between -1 and 1. The ecological and neutral traits are both determined by the sum of the corresponding alleles. The alleles determining these traits can have every possible value.

The IBM is based on the same life history as the deterministic model described above. In the deterministic model, the dynamics of the system involve densities (biomass per litre). In the IBM, however, individual consumers are discrete entities, such that birth and death events can only occur as discrete, stochastic, events. We therefore also have to specify the size of the system.

The change in food source density R_j in a time step Δt equals

$$\Delta R_j = [\delta(R_{j,\max} - R_j) - \sum (I_{i,j}(m, \mathbf{R}, x_i)) / s] \Delta t, \quad (13)$$

where s is the size of the system in litres and $\sum (I_{i,j}(m, \mathbf{R}, x_i))$ is the sum of the intake of food source j over all individual consumers.

The increase in body mass of an individual is determined by its current size m , its trait value x , and total food availability \mathbf{R} following

$$\Delta m = g(m, \mathbf{R}, x) \Delta t, \quad (14)$$

101 where $g(m, \mathbf{R}, x)$ is determined by equation 8.

102 We assume that all individuals (both males and females) have a reproductive buffer B , which
 103 first increases following $\Delta B = b_i(m, \mathbf{R}, x) \Delta t$. Mature individuals with enough energy to produce
 104 offspring (i.e., $B \geq 1$) can reproduce (see below). After reproduction, the number of produced off-
 105 spring is subtracted from the reproductive buffer B . At each timestep, individuals have a probability
 106 to die of $\mu(m, \mathbf{R}, x) \Delta t$.

107 In the IBM, mating can either be clonal or sexual. With clonal reproduction (traits a and n
 108 become obsolete in this case), there is no difference between males and females, and all individuals
 109 reproduce as many discrete offspring as they have energy for. Newborn individuals inherit the
 110 genotype of their parent, but each inherited allele has a probability of μ to mutate. In case of a
 111 mutation, the offspring allele equals the allele of the parent $+p$, with p normally distributed with a
 112 mean of zero and standard deviation σ .

113 In case of sexual reproduction we assume for simplicity that both males and females invest
 114 equal amounts of energy in offspring production. While biologically unrealistic (sperm is cheaper
 115 to produce than eggs), this assumption ensures that the IBM is comparable to the deterministic
 116 model with clonal reproduction. We assume that only females express their assortability, in keeping
 117 with female-limited mating. The probability that a female with assortative mating phenotype a and
 118 trait w_f (either ecological trait x or neutral trait n) will mate with a male with trait w_m is described

119 by the following mate-choice function (following Bolnick and Doebeli 2003):

$$P(a, w_f, w_m) = \begin{cases} \exp(-0.5(\frac{a^2}{s_a})^2(|w_f - w_m|)^2) & a > 0 \\ 1 & a = 0 \\ \exp(-0.5(\frac{a^2}{s_a})^2(2 - |w_f - w_m|)^2) & a < 0. \end{cases} \quad (15)$$

120 In this equation parameter s_a is a scaling parameter determining the slope of the mate-choice func-
 121 tion. To avoid a bias against marginal phenotypes in the population, mating probabilities are nor-
 122 malized, so that the sum of mating probabilities over all potential partners is 1 for all phenotypes.
 123 This implies that all females reproduce and that there is no cost to a female for assortative mating.

124 The total number of offspring equals the sum of the female and male reproductive investment.
 125 We assume a 50:50 sex ratio at birth. At each locus, one offspring allele is chosen randomly from
 126 the two maternal alleles and the other from the two paternal alleles at this locus. With a probability
 127 μ a mutation occurs in the inherited alleles. In the diallelic alleles (determining mating trait a) a
 128 mutation will reverse the value of the allele. For the remaining alleles, the offspring allele equals
 129 the allele of the parent $+p$, with p normally distributed with a mean of zero and standard deviation
 130 σ .

131 For each time step Δt , we first calculate the changes in state variables and update them. Next,
 132 we remove consumers that have died (due to starvation or background mortality) from the popu-
 133 lation. Lastly, adult individuals reproduce new offspring, which are added to the population. To
 134 determine which individual dies in a certain time step Δt , we draw for each individual a random
 135 number from a uniform distribution on the interval $[0, 1)$. If this number is smaller than the mortal-
 136 ity probability for this individual, it dies. We use a similar approach to determine which offspring
 137 mutates in which allele.

138 For all simulations, we used a value of $\Delta t = 0.1$. We implemented the model in C++, code will

139 be made available.

Table 1: Parameters

Variable	Description	Value	Unit	Reference
Feeding on resource				
q	Exponent for search volume	0.8	-	Hartvig et al.
n	Exponent for maximum food intake	0.75	-	Hartvig et al.
h	Maximum food intake	0.233	$\text{g}^{1-n} \text{day}^{-1}$	Hartvig et al.
A	Maximum size-specific attack rate	21.9	$m^3 \text{g}^{-q} \text{day}^{-1}$	Hartvig et al.
τ	Width of the function describing the attack rate as a function of the feeding niche trait value	1	-	-
σ	Width of the size-specific attack rate function	variable	-	-
Growth and Reproduction				
m_b	Body mass at birth	0.5	milligram	Hartvig et al.
m_{mat}	Body mass at maturation	100?	gram	-
η_{mat}	Body mass at maturation relative to asymptotic mass	0.25	Hartvig et al. 2011	
u	Width of maturation transition	10	-	Hartvig et al.
ε	Efficiency of offspring production	0.1	-	Hartvig et al.
α	Assimilation efficiency	0.6	-	Hartvig et al.
k	Standard metabolism	0.0274	$\text{g}^{1-p} \text{day}^{-1}$	Hartvig et al.
p	Exponent of standard metabolism	0.75	-	Hartvig et al.
Mortality				
ξ	Fraction of energy reserves	0.1	-	Hartvig et al.
μ_b	Background mortality rate	0.01	day^{-1}	
Resource dynamics				
δ	Resource turnover rate	0.1	day^{-1}	-
ϕ	Total productivity of the system	gram L^{-1}	-	-
F	Number of available food sources	7 (of which 1 juvenile food source)	-	-

References

- Bolnick, D. I. and M. Doebeli, 2003. Sexual dimorphism and adaptive speciation: Two sides of the same ecological coin. *Evolution* 57:2433–2449.
- Diekmann, O., M. Gyllenberg, and J. A. J. Metz, 2003. Steady-state analysis of structured population models. *Theoretical population biology* 63:309–338.
- Hartvig, M., K. H. Andersen, and J. E. Beyer, 2011. Food web framework for size-structured populations. *Journal of Theoretical Biology* 272:113–122.
- Kirkilionis, M. A., O. Diekmann, B. Lissner, M. Nool, B. Sommeiller, and A. M. de Roos, 2001. Numerical continuation of equilibria of physiologically structured population models I: theory. *Mathematical Models and Methods in Applied Sciences* 11:1101–1127.
- de Roos, A., 2008. Demographic analysis of continuous-time life-history models. *Ecology Letters* 11:1–15.
- , 2016. PSPManalysis: A package for numerical analysis of physiologically structured population models. <https://staff.fnwi.uva.nl/a.m.deroos/pspmanalysis/index.html>.