



Supplementary Materials for **A general consumer-resource population model**

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Other Supporting Online Material for this manuscript includes the following:
(available at www.sciencemag.org/content/349/6250/854/suppl/DC1)

General_Consumer_Resource_Model (.cdf file)

Materials and Methods

To get a rough estimate of the number of consumer-resource models in the literature, we searched the Web of Science for the topic search string: mathematical population model Not Bayesian NOT "general linear" NOT "model system" NOT "mixed model" NOT "generalized linear" with the addition of either “parasitoid”, “host parasite” or “predator prey”. We counted the results for each search, then selected 100 papers at random and estimated the proportion that were actually on consumer-resource population models. Our efforts could have missed studies that did not have the full complement of search terms. Regardless of the details of our search, there have been thousands of research papers about consumer-resource models.

We limit our modeling to one consumer population and one resource population, a common practice for most consumer-resource models. Most of our examples describe tracking states in the currency of individuals (or their density), but this can be converted to biomass density (e.g., using the approaches of Yodsiz and Innes (10)). Although many consumer-resource interactions happen in discrete time, we describe the general model in continuous time for convenience. Finally, to keep the theory general, we do not define a function’s specific form (5).

When developing the general model, our first consideration was the range of state variables used in past consumer-resource models. Most predator-prey models track a free-living prey and a free-living predator. A few predator-prey models split the prey into vulnerable and invulnerable classes. Microparasite models often consider three host states: susceptible, infected, and resistant (some also include exposed). Macroparasite models track the parasite population separate from the host population and often include a free-living infective state. A highly inclusive starting point for considering potential state variables for a resource, X , is the classic susceptible, exposed, infected, recovered/resistant (SEIR) model for host-pathogen dynamics (2). To generalize the SEIR framework to include other interactions besides pathogens, we use the term *Ingested* for the X_i state and *Resistant* for the X_r state. The SEIR model tracks resource (host) states, but, in doing so, implies that there are two corresponding consumer states: a developing (which we call attacking) state Y_a within the exposed host, and a state Y_c in the infected host (which we recognize as “consuming”). So, while the SEIR model has four resource states, two (X_e & X_i) are synonymous with consumer states (Y_a & Y_c) because the pathogen population is counted in terms of infected hosts. One consumer state often tracked in predator-prey, host-parasitoid, and macroparasite-host models is the free-living stage that seeks out the resource. We call this the *Questing* state, Y_q . Our general model thus has seven states (table 1): a *Questing*, *Attacking*, or *Consuming* consumer and a *Susceptible*, *Exposed*, *Ingested*, or *Resistant* resource. These states encompass the interactive state variables for perhaps all familiar consumer-resource models (with some minor modification in some cases).

We describe the plausible transitions within and among the consumer and resource states using generalized functions (table 1). Generalized functions are placeholders for formulae that must be specified before settling on a final model. In addition to potential transitions from one state to another, each state has background birth and death rates, to which we could also add emigration and immigration (here we ignore this for simplicity). In some cases, a state is produced by another state (e.g., when adults and offspring are

separate states). Some transitions among states result from interactions. For instance, contact between a questing consumer and a susceptible resource leads to a transition to a consuming consumer and an ingested resource. We represent functions with a capital letter with subscripts indicating to and from states. For instance, R_{si} indicates recovery to the susceptible from the infected state. Our generic functions are placeholders for actual functions, which might include one or more state variables, various parameters, and non-linear terms. For instance, deaths could be density-dependent or independent. For this reason, the general model should not be written in matrix form because the state variables associated with each function remain unspecified. In several cases, there are mutually exclusive pathways in the general model. We indicate these using auxiliary parameters that range from 0 to 1 (usually 0 or 1) to specify (as switches) various consumer life-history strategies (table SC1).

To map the general consumer-resource model onto generic consumer life-history strategies, we determined the values for the auxiliary parameters and (some) functions that corresponded to each consumer type. These criteria are taxon-independent for both the consumer and the resource and state-specific. From these rules, we computed a cluster analysis (biplot of principal components 1 and 2, after defining the criteria in table SC1) to show the relationships among consumer types based on their model structures.

We then solved for the basic reproductive number (R_0) of a generalized consumer. R_0 is a familiar metric calculated from demographic models that gives insight into the conditions required for a consumer to persist when encountering an unexploited resource population. Specifically, for $R_0 > 1$, a consumer population is able to increase when rare. By definition, when estimating R_0 , there are assumed to be no other infected/consumed resources in the resource population (and consumer aggregation is not an issue). We assumed no vertical transmission (i.e., parent to offspring transmission), otherwise vertical transmission adds a positive term to R_0 . For multiple consumer states, R_0 is the product of R_0 for each of its states and can be computed as the product of: (i) the expected number of feeding contacts during the time spent in a questing state, (ii) the number of attacking consumers produced during a quest, and (iii) the number of questing states produced during the time spent in a consuming state (Supplementary D). More formally, R_0 can be calculated with the next generation matrix approach (7). In brief, estimating R_0 requires constructing a transmission matrix, T , for contact rates and a transition matrix, S , for losses, conversion and production. The next generation matrix $G = -T.S^{-1}$. The dominant eigenvalue of the next generation matrix is R_0 . After solving for the general R_0 , we used the information in table SC1 to calculate R_0 for the 11 consumer life histories (Supplementary D).

The general model, though seemingly complex, simplifies easily with the following steps.

Specify: To model a generic consumer life history strategy, set the appropriate auxiliary parameters (e.g., table SC1).

Delete: e.g., if there is not a resistant resource state, remove it as well as functions that output to or input from it.

Synonymize: For pathogens or predators, assume a single consumer per ingested resource (i.e., $X_i = Y_c$), and just track one.

Define: Formulate the general functions.

Proportionalize: If the sum of two states is a constant, make one state a proportion of the other (e.g., in many human infectious disease models, the total human population size, X , is assumed to be constant, or in some predator-prey models, the predator population is assumed constant).

Combine: In some cases we don't care to distinguish states and can sum the left and right-hand sides of two or more equations together into a single differential equation, e.g., $dY/dt = dY_q/dt + dY_a/dt + dY_c/dt$. Doing so can leave some state variables remaining and these must then be subsumed (see Supplementary E for an example).

Subsume: If a state reaches equilibrium much faster than other states (e.g., the questing or attacking consumer in a host-parasite model), use separation of time scales to substitute the state for its quasi-equilibrium. If the states have dynamics on similar time scales, one can use the more complicated techniques of matched asymptotics, or combining them.

Simplify: Transform complicated functions with linearization or by setting trivial parameters to 0 or 1, or by defining a time scale that is a function of a parameter, etc. A common way to clear summations from a denominator is to assume that some parameters are much larger than others. Finally, one can identify opportunities to composite parameters for a streamlined presentation.

Track: Traditional population measures should be matched to model output. For predators, field ecologists count questing, attacking and consuming individuals, meaning that the abundance of subsumed states should still be tracked as part of the population. In contrast, for parasites, questing consumer stages are not normally counted in the parasite population.

Supplementary E illustrates the process of building a simple model by applying our framework to an autotroph and its nutrient resource. We also derived several classic consumer-resource models (fig. 1, Supplementary F). For each classic model, we indicate values for each function and auxiliary parameter and rules for keeping, excluding, or collapsing state variables. Often, there was more than one pathway from the general model to a specific model, so we chose the most illustrative option. For classic consumer-resource models in discrete time, we could have either used continuous time versions of these models or written a discrete time version of the general model. A supplementary model builder is available for download at the Science website as a .cdf program file named *General_Consumer_Resource_Model.cdf* (requiring Mathematica or the free Wolfram CDF Player).

Supplementary B. Annotated tables of variables, functions and parameters

Table SB1: State Variables

$X = \sum_j X_j$ total resource population size

$Y = \sum_j Y_j$ total consumer population size

$X_s =$ **Susceptible** (and unattacked) resources.

$X_e =$ **Exposed** resources. These resources have been attacked by a questing consumer, but are not yet being ingested.

$X_i =$ **Ingested** (i.e., infected) resources. These resources are being eaten by a consumer.

$X_r =$ **Resistant** resources. A resistant class is a bridge between some classic predator and pathogen models. Resistant resources cannot be successfully attacked by a consumer. They may have immunity or be hidden from the consumer. In pathogen epidemiology, this state is often not further susceptible, referred to as *Recovered* and the recovered individuals are resistant. However, in many cases, such as concomitant immunity against helminth parasites, resistance is better represented as a continuum of susceptibility than by a state. Both hosts and prey have strategies to defend against or avoid consumers and this has energetic costs for prey (e.g., in terms of reduced feeding) and for hosts (in terms of investment into immune defense). For this reason, it is important to consider if resistance reduces survivorship ($1/D_r$) or births (B_{xr}).

$Y_a =$ **Attacking** consumers. These consumers are engaged in subduing a resource for consumption. This state corresponds to the exposed resource. Examples include attacking predators, “incubating” pathogens, penetrating or migrating parasitic worms.

$Y_c =$ **Consuming** consumers. These consumers are physically ingesting a resource and converting the energy into production shortly after. Examples include feeding predators, parasites established in their hosts, and aphids eating plants.

$Y_q =$ **Questing** consumers. These consumers are not in contact with resources (they are passively or actively seeking resources). Examples include parasite eggs, free virions, hunting predators, flying mosquitoes.

Table SB2: Generalized Functions

$A_i =$ phenomenological description of aggregation of consumers per ingested resource (pertains to macroparasites, micropredators and perhaps to social predators). $A = 1$, indicates a Poisson distribution. Aggregation helps determine how many consumers are lost when a resource dies. Here, we consider the effect of aggregation on resource mortality rates, but note that aggregation can be applied to other vital rates, such as consumer mortality rate.

$B_{cc} =$ vertical transmission of a consumer (pathogen or macroparasite) from parent to offspring. Ignored here unless otherwise specified.

$B_{qc} =$ the production rate of questing individuals from consuming individuals (as per traditional predator models). E.g., Under the typical assumption that consumption increases consumer birth and reduces resource survival, or birth, or both, a general per-capita formulation is $B_{qc} = w[g(B_{xs} - B_{xi}) + K_i]X_i/Y_c$ where w is an index of conversion of consumption to a birth and g is the relative gain of

reducing resource birth rate to killing a resource ($g = 0$ for predators). This and other birth terms could also model somatic growth that contributes to increased biomass density.

B_{xi} = the birth rate of an ingested resource. While not explicitly modeled here, this is an important function to consider prior to modeling dynamics. Under some cases, B_{xi} simplifies to B_{si} . We can expect that B_{xi} is a function of the amount of energy consumed from the resource that results in a decrease in birth rate.

$B_{ex} = (B_{es} + B_{ee} + B_{ei} + B_{er})$. Here, and below, resource births into a state could come from other states, depending on the biology of the system.

$$B_{ix} = (B_{is} + B_{ie} + B_{ii} + B_{ir})$$

$$B_{rx} = (B_{rs} + B_{re} + B_{ri} + B_{rr})$$

$$B_{sx} = (B_{ss} + B_{se} + B_{si} + B_{sr})$$

C_{aq} = the rate of contact (attack to be more specific) between questing consumers and susceptible hosts. Traditionally, this is mass action, but could be ratio dependent, Levy flight, have an aggregation exponent, etc.

D_{-} = the background death rate for each state. The subscript indicates the state. Although this death rate includes predation by consumers not specified in the model, it does not include the effect of a consumer on the death rate of the resource. However, D_a could be a function of the types of resources that questing consumers contact because such states might vary in their sensitivity to consumers that defend themselves. This would be the case for parasites that have infectious states with differential survival in different host states. Note that for most consumers, $Y_c = X_i$, and $Y_a = X_e$, so the complex term $jD_x Y/X$ simplifies to jD_x . The exception is when there is more than one intimate ($j = 1$) consumer per resource (as in a macroparasite). In this case, the loss to the consumer population increases with the number of consumers per resource, requiring us to specify Y/X in that loss term of the general model. Note also that death of a questing parasite state could occur through contact with an ingested or resistant (resource) host, e.g., $D_q = Y_q (d_q + \beta(X_e + X_i + X_r))$.

F_a = the rate at which the attacking consumer fails in its attack. For consumers that can re-quest ($m = 1$), the attacking consumer can return to questing after it fails. For other types of consumers it cannot. For some consumers, failure might depend on the number of consumers attacking, or on whether the attacked resource is resistant. For social predators, failure might decrease with the number of consumers per resource and, for some pathogens, there might be a threshold exposure below which the exposed host is able to defend. Such situations can create an Allee effect for the consumer.

H_{ca} = the rate at which attacking consumers handle the exposed resource prior to converting it for production. For a pathogen, this is when the host is infected, but not infectious. For a macroparasite, it is the time from contact to patency. For a larval parasitoid, it is the time between contact and larval feeding. Note that protelean parasites also return to questing after attacking (so that $H_{qa} = H_{ca}$).

H_{qc} = the rate at which some consuming consumers finish feeding before questing again (especially micropredators).

I_{rs} = the rate that susceptible hosts protect themselves from consumers (thereby becoming resistant).

K_i = the rate that a consumer adds to the mortality/removal rate of an ingested resource. For a predator, the ingested resource is already dead, so K_i is the rate at which the predator consumes the resource and then returns to questing. For consumers of non-living resources, K_i is the rate at which the consumer removes the resource. For parasites, killing is the additional host mortality related to consumption by the parasite. When there is one consumer per resource, $A_i = 1$, and $Y_c = X_i$, so the complex arrangement $A_i K_i Y_c / X_i$ reduces to K_i , which can be expressed either as a per-capita loss term for the consumer (e.g., αY_c) or the resource (αX_i), depending on the state being modeled.

R_- = the rate that ingested resources recover from a consumer. Recovery is related to the death, failure, and handling of consuming consumers. Note that for cases where more than one consumer attacks a resource, recovery implies a simultaneous loss of all consumers. There are various transitions from exposed and ingested resources to consumers, namely: individuals recovering to the resistant/immune class: $R_{rx} = (R_{re} + R_{ri})$; individuals recovering back to the susceptible class: $R_{sx} = (R_{se} + R_{si})$; resources leaving the ingested/infective state: $R_{xi} = (R_{ri} + R_{si})$; resources leaving the exposed state: $R_{xe} = (R_{se} + R_{re})$. A unique aspect of autotrophs is that their resources (nutrients) can be directly recycled after their death and degradation. This can be modeled by establishing a resistant resource state with inputs from resource death, and outputs to the susceptible resource state.

V_{sr} = the rate that resistant resources become susceptible to consumers again. For autotrophs this may relate to nutrient recycling.

Table SB3: Auxiliary parameters

$f = 1$ indicates that the consumer kills the host as a result of feeding (fatal attack).

j = joint death (i.e., intimacy) between consumer and resource, where j_c indicates the consuming consumer and j_a the attacking consumer. This auxiliary parameter is set to 1 if the consumer dies when the resource dies (most parasites), to 0 for a predator and potentially > 0 for a consuming micropredator. We note that killing/consuming the resource in the infected/ingested state is a loss term for the consuming consumer whether or not there is joint death (explaining the lack of a j_c term associated with killing by the consumer). Here, transmission or death is indicated by the presence or absence of an associated gain term in the questing consumer (defined by f , above). We allow separate intimacies for attacking (j_a) and consuming (j_c) consumers. Finally, intimacy is often associated with durability of an interaction. For this reason, intimate associations (parasites) often spend most of their time consuming whereas non-intimate associations (predators) spend most of their time questing.

m = multiple attacks by questing consumer (1 yes, 0 no): $m = 1$ for predator-like consumers; $m = 0$ for parasite-like consumers.

Supplementary C. Consumer strategies and results of a principal components analysis (PCA)

The 11 consumer strategies presented in fig. 2, and below, are operationally defined by biological criteria (table SC1). These biological features are dichotomous, taxonomically independent, are based on the feeding mode for an individual consumer versus a specific resource, and often differ among stages for consumer species with complex life cycles. They sometimes differ for different resources. Asexual multiplication following access to the resource by an individual consumer represents just that single consumer. A few examples across diverse taxa are provided. See Lafferty and Kuris (6) for more rationale.

If the resource is living and the consumer feeds on more than one prey/host, we have:

Predator – prey fitness is reduced to zero, deaths of prey are required to extend consumer life cycle, a single predator kills its prey (thus impact on a prey is density-independent), prey death does not lead to predator death.

Examples: squids, mosquito larvae on algae.

Social predator – like typical predators, but more predators per attacked prey kill prey more effectively. Examples: wolves on moose, army ants.

Micropredator – prey/host fitness is not reduced to zero; death of the host is not required to continue consumer life cycle, impact on host is density-dependent. Examples: adult female mosquitos, cicadas, giraffes.

If the resource is living, death of the host leads to death of the consumer, and the consumer feeds on just a single individual resource (host), we have:

Macroparasite – Host fitness is not reduced to zero; impact on host is density-dependent (impact on the host increases with the number of parasites).

Examples: adult schistosomes, malaria in mosquitos, corn borer grubs.

Pathogen – Host fitness not necessarily reduced to zero, impact on host is density-independent (impact is controlled by extent of effective host defenses, limiting the asexual reproduction of the consumer), Examples: malaria in humans, scale insects.

Castrators – Host fitness reduced to zero; impact on host is density-independent.

Examples: larval trematodes in snail hosts, *Sacculina* on crabs, boll weevil larvae.

Parasitoid – Host fitness reduced to zero, consumer kills host to complete its life cycle; impact on host is intensity-independent. Examples: larval ichneumonid wasps, *Pasteuria* bacteria in *Daphnia*, bruchid beetles in seeds.

If the resource is not living (does not give birth), resources flux into the system, we have:

Detritivore – As for a predator, but feeds on non-living organic particles.

Examples: earthworms, sand dollars.

Scavenger – As for a social predator, but feeds dead organisms. Examples: marabou storks, hagfish, burying beetles.

Decomposer – As for a macroparasite, but feeds on a dead food source.

Examples: termites, blow flies, oyster mushrooms.

Autotroph –Resources (nutrients) either flow through the system or are recycled on the death of consumers, or both. Examples: plants, chemosynthetic bacteria. Plants are often also limited by space (which influences access to light), though space limitation does not define their consumer strategy.

Supplementary E is an example autotroph model.

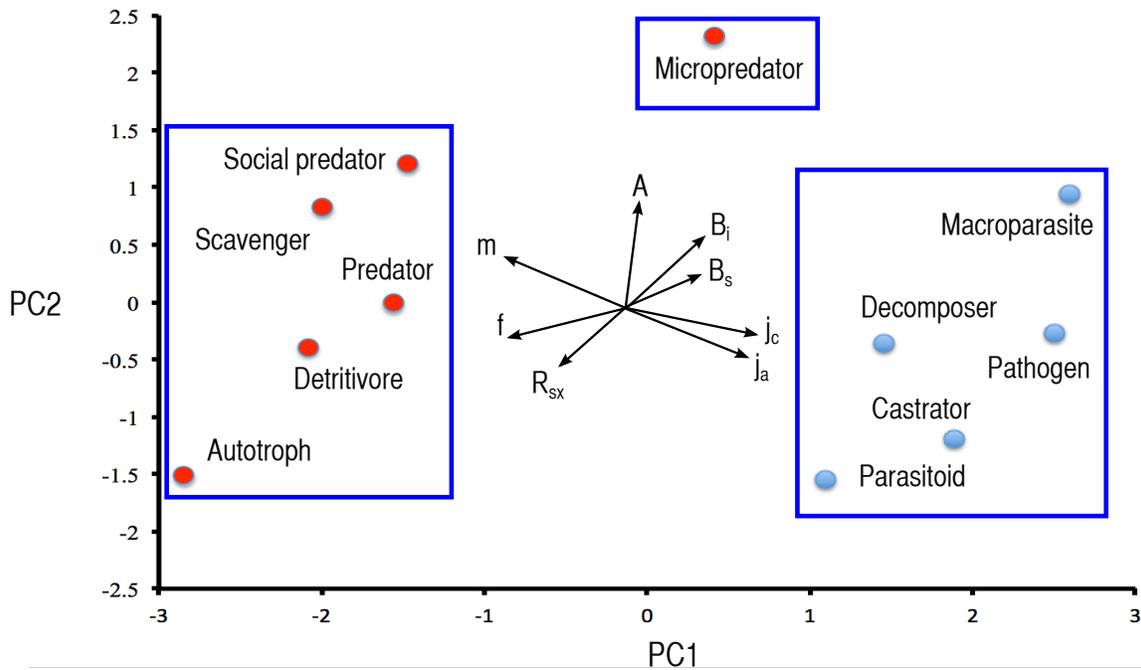


Fig. SC1. Principal components biplot of generic consumer strategies grouped by model structure.

Table SC1 lists all the differences and similarities used for clustering. Tables SC2-4 show the data used for the figure. Arrows indicate how the functions listed in table SC1 affect the PC axes. Blue rectangles indicate groups that have the same general structure for R_0 specified in Supplementary online text D). Red markers are predator-like and blue markers are parasite-like.

To employ the PCA, categorical variables in table SC1 were first converted to either 0 or 1. For a micropredator, j_c was set to 0.5 because it was assumed to be intermediate to a predator or parasite. B_x was set to 1 or 0 to distinguish consumers that feed on live resources (= 1), from dead resources (= 0). One consumer per resource was represented by 0, and multiple consumers per resource represented by 1. The first two principal components separated most consumer strategies and that is what is plotted in fig. SC1, but all data are reported below. The third component mostly distinguishes consumers feeding on living prey from those that consume non-living material, clustering decomposers with detritivores and scavengers.

Table SC2. Eigenvalues.

Strategy	Prin1	Prin2	Prin3	Prin4	Prin5
Autotroph	-2.84	-1.52	-1.08	1.81	0.49
Detritivore	-2.08	-0.39	0.11	-0.43	-1.15
Predator	-1.56	-0.01	1.57	-0.09	-0.12
Social Predator	-1.47	1.21	0.67	-0.66	0.89
Scavenger	-1.99	0.82	-0.79	-0.99	-0.14
Micropredator	0.41	2.31	0.06	0.99	-0.19
Parasitoid	-0.61	-0.35	1.36	-0.15	0.04
Castrator	0.89	2.14	-0.05	0.96	-0.11
Pathogen	-0.25	0.84	-1.53	-0.63	-0.55
Macroparasite	1.10	-1.55	0.96	-0.67	0.54
Decomposer	1.89	-1.19	0.43	-0.25	-0.03

Table SC3. Proportion of the variance explained by each eigenvalue.

Number	Eigenvalue	Cum Percent
1	4.10	51
2	1.48	74
3	0.99	82
4	0.89	93
5	0.33	99

Table SC4. Eigenvectors.

	Prin1	Prin2	Prin3	Prin4	Prin5
m (multiple quests)	-0.45	0.31	0.10	0.14	-0.13
j_a (intimacy)	0.45	-0.31	-0.10	-0.14	0.13
j_c (intimacy)	0.47	-0.17	-0.10	-0.03	0.08
f (fatal ingestion)	-0.41	-0.19	0.28	-0.22	0.30
A_i (aggregation)	0.05	0.64	-0.47	-0.30	0.53
X_s (births, B_s)	0.26	0.19	0.73	0.17	0.52
X_i (births, B_i)	0.29	0.43	0.01	0.58	-0.28
$f(D_y)$ (recycling)	-0.23	-0.34	-0.36	0.67	0.49

Supplementary D. Methods and solutions for a generalized R_0 .

For $R_0 > 1$, a consumer population is able to increase when rare. R_0 can be calculated with the next generation matrix approach as per (7). Estimation of R_0 requires constructing a transmission matrix, T , for contact rates and a transition matrix, S , for losses, conversion and production. Here, we also assume an initial condition where population growth rates are substitutable for per-capita rates. The next generation matrix $G = -T.S^{-1}$. The dominant eigenvalue of the next generation matrix is R_0 . Assuming no vertical transmission (i.e., $B_{cc} = 0$), the transmission matrix, T , includes rates that a consumer attacks new resources. For the general model, this matrix has one non-zero element:

	To A	To C	To Q
From A	0	0	0
From C	0	$B_{cc} = 0$	0
From Q	C_{aq}	0	0

The transition matrix, S , for the general model includes loss rates and all the possible transition rates among the three consumer states (to:from). It has six non-zero elements (the diagonal represents loss rates, L , of A, C and Q):

	To A	To C	To Q
From A	$-L_a$	$c:a$	$q:a$
From C	0	$-L_c$	$q:c$
From Q	0	0	$-L_q$

The inverse of S is:

	To A	To C	To Q
From A	$-1/L_a$	$-c:a/L_a L_c$	$-(L_c q:a + c:a q:c)/L_a L_c L_q$
From C	0	$-1/L_c$	$-q:c/L_c L_q$
From Q	0	0	$-1/L_q$

The next generation matrix is the dot product between $-T$ and the inverse of S , or:

	To A	To C	To Q
From A	0	0	0
From C	0	0	0
From Q	C_{aq}/L_a	$c:a C_{aq}/L_a L_c$	$C_{aq}(L_c q:a + c:a q:c)/L_a L_c L_q$

R_0 for the consumer is the dominant eigenvalue of the next generation matrix, namely:

$$(C_{aq}/L_a L_q) \bullet (c:a q:c/L_c + q:a)$$

where, from the general model above:

$$\begin{aligned} L_a &= D_a + F_a + j_a D_e + H_{ca} \\ L_c &= D_c + j_c D_i + K_i + m(1-f) H_{qc} \\ L_q &= D_q + C_{aq} \\ c:a &= H_{ca} \\ q:a &= m F_a \\ q:c &= B_{qc} + m[K_i + (1-f) H_{qc}] \end{aligned}$$

This can be expressed in biological terms. A component of R_0 common to all consumers, R_{01} , includes the success of sequential states. This is the product of three ratios: (1) the proportion of successful quests, (2) The proportion of attacking consumers that proceed to consuming, (3) the number of questing consumers produced per consuming consumer.

Accordingly $R_{01} =$

$$(1) C_{aq}/L_q = C_{aq}/(C_{aq}+D_q) \bullet$$

$$(2) c:a/L_a = H_{ca}/(D_a+F_a+j_a D_e+H_{ca}) \bullet$$

$$(3) q:c/L_c = (B_{qc}+m(1-f)H_{qc}+mK_i)/((D_c+j_c D_i+m(1-f)H_{qc}+K_i))$$

Note that the auxiliary parameters m , f and j_c influence ratio (2), indicating that much of the variation in R_{01} among consumers relates to the number of questing consumers produced per consuming consumer.

Consumers, such as predators and micropredators, for which the questing consumer can quest again after an attack ($m = 1$) have an additional aspect of R_0 , called R_{02} (i.e., for these consumers $R_0 = R_{01} + R_{02}$). R_{02} is the product of the proportion of successful quests (3) and the proportion of failed attacks that return to questing (4). For relevant parameterization, R_{02} is always less than one (it is simply a way to discount the cost of failure for consumers that can quest again after failure). For most of these cases, $j_a = 0$, and $R_{02} =$

$$(3) C_{aq}/L_q = C_{aq}/(C_{aq}+D_q) \bullet$$

$$(4) q:a/L_a = F_a/(D_a+F_a+H_{ca})$$

We note that one could further simplify R_0 by assuming that some rates are faster than others. In particular, if death rates are assumed to be very slow relative to some other rates, many of the ratios that comprise R_0 approach 1 or other simple ratios.

Table SD1. R_0 for the 10 consumer life-history strategies. Equations derive from inputting values from table SC1 into equations for R_0 .

Consumer Life History	R_0
Detritivore, Predator, Social Predator, Scavenger	$\frac{C_{aq}H_{ca}(B_{qc}+K_i)}{[(C_{aq}+D_q)(D_a+F_a+H_{ca})(D_c+K_i)]} + \frac{C_{aq}F_a}{[(C_{aq}+D_q)(D_a+F_a+H_{ca})]}$
Micropredator	$\frac{C_{aq}H_{ca}(B_{qc}+H_{qc}+K_i)}{[(C_{aq}+D_q)(D_a+F_a+H_{ca})(D_c+K_i+j_c D_i+H_{qc})]} + \frac{C_{aq}F_a}{[(C_{aq}+D_q)(D_a+F_a+H_{ca})]}$
Castrator, Pathogen, Macroparasite, Decomposer, non- protelean parasitoid	$C_{aq}H_{ca}B_{qc} / [(C_{aq}+D_q) (D_a+F_a+D_e+H_{ca}) (D_c+D_i+K_i)]$

Of particular interest is the saturation with C_{aq} , because it is common to assume that contact rate increases with the density of resources, X , or $C_{aq} = f(\beta X)$, where β represents a per-capita contact rate (i.e., mass action). Under this common assumption, and plotting

R_0 as a function of X , R_{0I} increases with resource density, and then asymptotes to a maximum set by handling and killing rates (table SD2, fig. 2B). R_{0I} saturates because there is a maximum number of resources that a consumer can handle per unit time. Furthermore, because $R_{0I} > 1$ is the key condition for a consumer being able to persist on a resource, a consumer can never invade a resource species when the maximum value attainable by R_{0I} is smaller than 1, no matter how abundant the resource is, making it harder for the consumer to control the resource (3). In the computation of R_{0I} , or when subsuming the questing state into the other states (through separation of time scales), the ratio, k , of losses from non-contacts (D_q) to losses from contacts (β) defines the resource density at which contact is half the maximum, otherwise known as a half-saturation constant, which corresponds to (but is not identical to) the familiar Michaelis-Menten equation for enzyme kinetics. Although consumption and handling rates increase population growth, they do not affect the half-saturation constant. The smaller the half-saturation constant (the value of X at which R_0 is half its maximum asymptotic value), the quicker R_{0I} saturates with resource density, and the less a consumer is able to persist on a poor-quality resource. Saturation due to limits on the questing consumer is faster for consumers with durable, efficient questing consumers (characteristics more likely to describe a predator than a parasite). The half-saturation constant for consumption also increases the resource threshold density for consumer persistence (table SD2).

Table SD2. R_0 Max:

Predator

$$[H_{ca} B_{qc} + F_a D_c + K_i(F_a + H_{ca})] / [(D_c + K_i)(D_a + F_a + H_{ca})]$$

Micropredator

$$[H_{ca} (B_{qc} + H_{qc} + K_i) + F_a (D_c + j_c D_i + H_{qc} + K_i)] / [(D_c + j_c D_i + H_{qc} + K_i)(D_a + F_a + H_{ca})]$$

Parasite

$$H_{ca} B_{qc} / [(D_c + D_i + K_i)(D_a + D_e + F_a + H_{ca})]$$

R_0 still saturates when a reduced-variable consumer-resource model is derived from the general model, but this is not the same as a saturating functional response. The form of the functional response depends on whether the questing consumer is subsumed (assumed to reach equilibrium fast) (8). If so, the corresponding complication of the remaining equations takes the form of the classic Type II functional response (Michaelis-Menten kinetics, or $gX_s / (X + D_q/\beta)$), where g is a composite of functions and β is a contact parameter representing mass-action. Subsuming the questing state is most likely in pathogen models, which, ironically, rarely consider a saturating functional response (9), though this is often justified with the assumption that infective stages are very short lived. As a consequence of saturation, the proportion of the resource population that can be attacked by a questing consumer declines (reciprocally) with the abundance of the resource, leading to safety in numbers for the resource. Familiar mass-action disease models and frequency-dependent sexually transmitted or vector-transmitted disease models are end points along a continuum of this saturating functional response (9). When the questing consumer is not assumed to rapidly reach equilibrium compared to the other states (i.e., for a predator), R_0 still saturates, but, because the questing consumer is a

dynamic variable, the functional response appears linear in the absence of further assumptions or function specification (see supplementary online text F1 for a worked example of the Lotka-Volterra predator-prey with linear functional response). In other words, a saturating R_0 is universal among consumers. However, when reducing states by subsuming, a saturating functional response (which represents a mortal questing consumer) is imposed only when the questing consumer is subsumed (as one might assume for a parasite). Summing states can also create saturating functional responses, which in some cases can take on complicated forms.

Many species change diet from one life stage to the other. This results in at least five distinct model structures, each of which has, at its core, a basic structure (fig. 3). For instance, protelean life histories add a new transition, specifically the questing state returns to questing after an attack ($H_{qa} = H_{ca}$). Furthermore, some protelean consumers have a free-living consumer stage (others do not). Not surprisingly, this complexity has dynamic consequences. For instance, changes to model structure lead to different structures for R_0 , with examples for the protelean life history given in Table SD3 under the assumption that the free-living stage is non-feeding (compare to table SD1, row 3).

Table SD3. R_0 for ontogenetic diet shifts.

Protelean parasitoid	$\frac{C_{aq}H_{ca}(B_q+K_i)}{[(C_{aq}+D_q)(D_a+F_a+H_{ca})(D_c+D_i+K_i)]} + \frac{C_{aq}(F_a+H_{ca})}{[(C_{aq}+D_q)(D_a+F_a+H_{ca})]}$
Protelean macroparasite, Protelean decomposer	$\frac{C_{aq}H_{ca}(B_q+H_{qc})}{[(C_{aq}+D_q)(D_a+F_a+H_{ca})(D_c+D_i+H_{qc}+K_i)]} + \frac{C_{aq}(F_a+H_{ca})}{[(C_{aq}+D_q)(D_a+F_a+H_{ca})]}$

Supplementary E: How to derive a simple model from the general model

To illustrate how to build simple models from the general model, we consider an autotroph, such as a plant or alga. Autotrophs are the foundation of food webs and they also have some interesting differences from more traditional consumer-resource models. Most importantly, this example shows how going from a large model to a small one retains the legacy of the general model in the form of model structures and the components of composite parameters. The reduction process also clarifies the assumptions used to simplify the model.

Our terminology for the general model states comes from animals, but translates to autotrophs. As for scavengers and detritivores, terms like killing apply only by analogy. The non-living resource fluxes through the system or is recycled within it, or both. Autotrophs require several resources, but most models track only the most limiting resource. If individuals can monopolize the limiting resource (i.e., contest competition for space) the model structure will differ if the resource is diffuse (i.e., scramble competition for nutrients). Here, we model scramble competition because it is most analogous to other consumer-resource interactions.

For scramble competition, the resource can be thought of as occurring in some concentration in the environment. Questing autotrophs make contact with the available resource, reduce its concentration in the attacking state and convert it to production in the consuming state. Unlike most classic models, an individual autotroph can potentially engage in all three consumer states simultaneously. A simple scramble competition model for an autotroph is Tilman's model for plant growth (11). In Tilman's model, nutrients flux into the system from the outside at a particular concentration, are reduced through consumption and flux out of the system at a reduced concentration. Under scramble competition, autotrophs are not intimate with their resources. To this extent, they are most like scavengers (or even filter feeding sessile animals). But unlike scavengers, autotrophs can have recyclable resources (e.g., nutrients released when a plant dies can eventually be added to the nutrient pool).

In this example, we use the approach outlined in the methods for simplifying the general model. Briefly, we first lay out the system of equations and explain how it can be specified to model the autotroph strategy. This leaves several functions that are redundant or irrelevant and can be deleted. We then synonymize the exposed and ingested resource states into the attacking and consuming states by assuming that nutrients are tracked in consumer units. After specifying the functions, we solve for equilibria and simulate dynamics. Because the five-state model is cumbersome, we next use separation of time scales to subsume the resistant resource state and sum the consumer states together, leading to a more traditional two-state consumer-resource model. We then approximate the dynamics of the two-state model with a single-state model and a phenomenological model based on the logistic equation with saturating contact rate. The results show the value of using the general model for building simple models.

The general model system of equations

$$\begin{aligned} dY_q/dt &= B_{qc} - D_q + m(1-f)H_{qc} + fmA_iK_i Y_c/X_i + mF_a - C_{aq} \\ dY_a/dt &= C_{aq} - D_a - H_{ca} - j_a D_e Y_a/X_e - F_a \\ dY_c/dt &= B_{cc} - D_c + H_{ca} - j_c D_i Y_c/X_i - A_i K_i Y_c/X_i - m(1-f)H_{qc} \\ dX_s/dt &= B_{sx} - D_s + R_{sx} + V_{sr} - I_{rs} - C_{aq} \\ dX_e/dt &= B_{ex} - D_e - R_{xe} - H_{ca} + C_{aq} \\ dX_i/dt &= B_{ix} - D_i - R_{xi} + H_{ca} - K_i \\ dX_r/dt &= B_{rx} - D_r + R_{rx} - V_{sr} + I_{rs} \end{aligned}$$

Specify an autotroph:

$$m \rightarrow 1, f \rightarrow 1, j_a \rightarrow 0, j_c \rightarrow 0, B_{sx} \rightarrow \rho X_0, B_{ix} \rightarrow 0, Y_c/X_i \rightarrow 1, Y_a/X_e \rightarrow 1, A_i \rightarrow 1, V_{sr}, B_{rx} \rightarrow f(D_y)$$

Delete the irrelevant functions:

$$B_{cc}, B_{ex}, D_r, F_a, I_{rs}, R_{sx}, R_{rx}, R_{xe}, R_{xi}$$

Synonymize the redundant state variables. With a single consumer per ingested resource (i.e., $X_i \cong Y_c$), $dX_e/dt \cong dY_a/dt$, this leaves an initial system of five equations:

$$\begin{aligned} dY_q/dt &= B_{qc} - D_q + K_i - C_{aq} \\ dY_a/dt &= C_{aq} - D_a - H_{ca} \\ dY_c/dt &= -D_c + H_{ca} - K_i \\ dX_s/dt &= B_{sx} - D_s + V_{sr} - C_{aq} \\ dX_r/dt &= f(D_y) - V_{sr} \end{aligned}$$

Define functions. Contact is mass action ($C_{aq} = \beta Y_q X_s$). Per-capita death rates (d_y) do not differ among consumer states. A “killing” rate (α) of nutrients is associated with a proportional production rate (e) of additional questing states. Resources are expressed in plant units to simplify the terms. Resources flux through the system at rate ρ , entering at a concentration X_0 , and leaving at a concentration X_s after being depleted by consumers. A proportion (λ) of the resources from a dead consumer are recycled back into the system after being temporarily unavailable while decomposing (v) in the resistant state.

$$\begin{aligned} dY_q/dt &= e\alpha Y_c - d_y Y_q + \alpha Y_c - \beta Y_q X_s \\ dY_a/dt &= \beta Y_q X_s - d_y Y_a - h Y_a \\ dY_c/dt &= -d_y Y_c + h Y_a - \alpha Y_c \\ dX_s/dt &= \rho X_0 - \rho X_s + v X_r - \beta Y_q X_s \\ dX_r/dt &= \lambda d_y (Y_a + Y_c + Y_q) - v X_r \end{aligned}$$

This system has a finite equilibrium that can be solved analytically or simulated numerically. The joint solution to this system of equations can be plotted to show an autotroph population over time as it invades an unexploited resource with slow, but exponential growth, then settles at a carrying capacity set by depletion of finite resources (solid lines, fig. SE1).

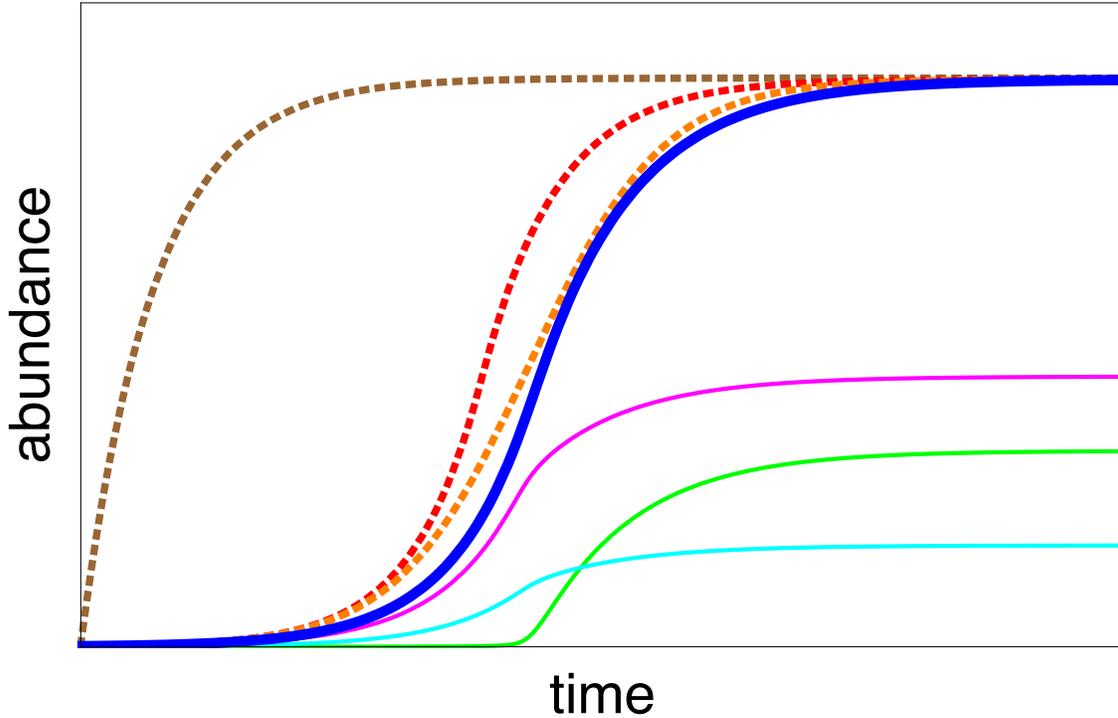


Fig. SE1. Simulations of the autotroph models over time (from invasion to equilibrium). Time is on the X-axis. Autotroph abundance of different states (or all states combined) is on the Y-axis. One autotroph is added to a system with nutrients and its population slowly expands until a ceiling of 881 set by declining nutrient concentrations. The solid lines are from the five-state model (resource states not shown): green = Questing (Y_q), magenta = Attacking (Y_a), cyan = Consuming (Y_c), thick blue line = All autotrophs ($Y_q + Y_a + Y_c = Y$). The red-dotted line is the simple two-state autotroph-nutrient approximation. The brown-dotted line is the one-state autotroph approximation assuming no saturating contact. The orange-dotted line is the single-state (autotroph) approximation with saturating contact and a logistic carrying capacity. Parameters: $e \rightarrow .8, \beta \rightarrow .8, X_0 \rightarrow 20, h \rightarrow .03, \rho \rightarrow .4, \alpha \rightarrow 0.07, \beta \rightarrow .8, d_y \rightarrow .01, v \rightarrow .1, \lambda \rightarrow 1$. Time from 0 to 3000. Equilibril values: $\hat{X}_s = 0.07, \hat{Y}_q = 304, \hat{Y}_a = 420, \hat{Y}_c = 157,$

$$\sum \hat{Y} = 881.$$

Combine the consumer stages by summing all the consumer equations and only track their total Y .

$$dY/dt = aeY_c - d_y Y$$

$$dX_s/dt = \rho X_0 - \rho X_s + v X_r - \beta Y_q X_s$$

$$dX_r/dt = \lambda d_y Y - v X_r$$

Subsume state variables using separation of time scales, with a preference for subsuming states likely to equilibrate faster than others. We are least interested in tracking the inaccessible nutrient pool, and we will assume that it equilibrates quickly enough that it can be subsumed into the dynamics of the susceptible resources. For a dynamic consuming state and susceptible state, assume dX_r/dt equilibrates fast as does the relative proportions of consuming states:

$$\hat{X}_r \rightarrow \frac{\lambda d_y Y}{v}, \hat{Y}_q \rightarrow \frac{\alpha(e+1)Y_c}{d+\beta X_s}, \hat{Y}_c \rightarrow \frac{\beta h Y X_s}{(\alpha+d_y)(d_y+h)+\beta X_s(\alpha+d_y+h)}, \text{ and substitute into } dY/dt, \\ dX/dt:$$

$$dY/dt = \frac{\alpha \beta e h Y X_s}{(d_y + h)(d_y + \alpha) + (d_y + h + \alpha)\beta X_s} - d_y Y$$

$$dX/dt = \rho(X_0 - X_s) + \lambda d_y Y - \frac{(d_y + h)(d_y + \alpha)\beta Y X_s}{(d_y + h)(d_y + \alpha) + (d_y + h + \alpha)\beta X_s}$$

which, after collecting parameter sets into composites $w = (d_y + h)(d_y + \alpha)$, $z = (d_y + h + \alpha)$, $g = \alpha e h$ and $k = w/\beta$, the two-state system of equations can be written as:

$$dY/dt = \frac{g Y X_s}{k + z X_s} - d_y Y$$

$$dX/dt = \rho(X_0 - X_s) + \lambda d_y Y - \frac{w Y X_s}{k + z X_s}$$

Continuing with the assumption that space is not limiting, the joint equilibria are:

$$\hat{Y} = \frac{\rho(X_0 - \hat{X})(k + z\hat{X})}{w\hat{X} - \lambda d_y(k + z\hat{X})}, \hat{X} = \frac{d_y k}{g - d_y z}$$

These joint equilibria show how the final nutrient concentration, sometimes called R-star (11), is independent of the initial nutrient concentration, flux, or nutrient recycling. In contrast, an autotroph's final abundance increases with initial nutrient concentration, flux and recycling. The simple model (red-dotted line, fig. SE1) has the same asymptote as the five-state model (thick-blue line, fig. SE1), but it equilibrates faster due to the assumption of separation of time scales.

Simplify using approximations. One could write a single model for Y assuming that X equilibrates quickly. Unfortunately, the solution for X at equilibrium as a function of Y has two complicated roots. A simpler approach would be to assume that z is very small (no saturating contact function) and then solve for X_s at equilibrium so that a one-state model is:

$$\hat{X} \rightarrow \frac{(\rho X_0 + \lambda d_y Y)}{w Y / k + \rho}, \text{ and substitute into } dY/dt,$$

$$dY/dt = \frac{g Y (\rho X_0 + \lambda d_y Y)}{w Y + \rho k} - d_y Y$$

which is analogous to Schoener's (12) single-level competition model but with nutrient recycling. This model (brown-dotted line, fig. SE1) has the same equilibrium as the five-state model (thick-blue line, fig. SE1), but equilibrates very fast because, in addition to separation of time scales, contact rate does not saturate at the initially high nutrient concentration.

Alternatively, we can use the solution for the carrying capacity and the exponential growth rate above, combined with density dependence from the logistic growth curve.

$$d\mathbf{Y}/dt = \left(\frac{gYX_0}{k + zX_0} - d_y Y \right) \left(1 - \frac{Y}{\hat{Y}} \right)$$

This approximation (orange-dotted line, fig. SE1) fits the dynamics even better than the two-state model (red-dotted line fig. SE1), with the disadvantage of having a phenomenological structure.

Track the autotroph population as $Y = Y_q + Y_a + Y_c$ (fig. SE1). Whereas, for the resource concentration, we might choose to track only the X_s component or ignore resources entirely.

Ideally, simple models will capture important aspects of the general model such as equilibria and R_0 , and hopefully, the simple model will also approximate the dynamics. Simulations of the four models over time show that they differ in the rate at which they approach the equilibrium. The two-state model, for instance, approaches faster than expected because several elements are assumed to reach equilibrium quickly. In particular, the two-state model does not account for the delay in nutrient recycling that occurs when nutrients in dead consumers are temporarily unavailable. The single-state model has these limitation plus the lack of the five-state model's saturating contact rate, leading to the poorest match to the five-state model. For the logistic approximation, self-limitation is purely phenomenological, so, while it fits well, we should not be surprised that it differs a bit from the depletion of nutrients.

Supplementary F. Reduction of the general model into classic consumer-resource models

Below, we use the approach in the Methods to derive the following classic consumer resource models from the general model:

- 1) Lotka-Volterra (predator-prey)
- 2) Saturated predator (spruce budworm)
- 3) Invulnerable Prey (prey with refuge)
- 4) Chemostat (bacteria in culture)
- 5) SI (non-lethal disease)
- 6) SIR (Kermack-McKendrick non-lethal disease)
- 7) SEIR (measles)
- 8) SEI (rabies)
- 9) QSI (insect pathogen)
- 10) Macroparasite

Deriving classic models from a general framework shows the relationships among these models, specifies simplifying assumptions, and reveals composite parameters (table SF1). As in Supplementary E, we first list the seven equations describing the general model. We used bold font to report components of the general model that correspond to a particular classic model. Most classic models don't consider a resistant consumer state and ignore at least one state variable when tracking the consumer population (and sometimes ignore a resource state variable as well). Unspecified state variables refer to sums across states (e.g., $X = X_s + X_e + X_i + X_r$). We also indicate equilibria with an accent (e.g., \hat{X}). In the derivations, we specify the generalized functions using several parameters that represent per-capita rates: birth rate = b , death rate = d , flux rate = ρ , contact rate = β , conversion rate = e , killing rate = α , handling rate = h , density dependence = μ , loss of resistance = ν , gain of resistance = ι , recovery from ingestion = r , and parasite aggregation = κ . All except the macroparasite model reduce state variables by equating exposed resources to attacking consumers and ingested resources to consuming consumers. All classic models further reduce state variables through separation of time scales. Most models reduce the complexity of the functional response by assuming that some rates (e.g., handling or questing, or both) happen fast. For instance, we often assume that the dynamics of some states are fast relative to others, such that they rapidly reach their quasi-equilibria relative to Y_q . However, the Lotka-Volterra model reduces the complexity of the functional response by ignoring the attacking and consuming states of the consumer. Most general functions are linear products of state variables, but several models use one or more non-linear functions (e.g., for density dependence or when assuming constant population sizes). Finally, several simple-looking parameters are actually composites of many parameters (the reduction allows us to define these explicitly), including the half-saturation constant k .

Table SF1. Summary of the derivation of 10 classic models.

Each classic model follows one of the consumer strategies, might exclude from consideration resistant resources, equates a 1:1 relationship between attacking consumers and exposed resources as well as consuming consumers and ingested resources, can have non-linear functions, subsumes at least one state variable to reduce complexity, can composite parameters to simplify presentation, can assume some processes happen fast or are constant to simplify model structure, and ignores some state variables when tracking the consumer or resource population.

Classic Model	Type	Exclude	Synonymize	Nonlinear	Subsume	Composite	Assume	Ignore	Track
Lotka-Volterra	Predator	X_r	$Y_a = X_e$ $Y_c = X_i$		Y_a, Y_c	birth, growth		Y_a, Y_c	Y_q, X_s
Saturated predator	Predator	X_r	$Y_a = X_e$ $Y_c = X_i$	C_{aq}	Y_q, Y_a	birth, \hat{X}	Y_c const.	Y_q, Y_a	X_s
Invulnerable Prey	Predator		$Y_a = X_e$ $Y_c = X_i$	D_r	Y_q, Y_a	birth, death	H_{ca} fast	Y_q, Y_a	Y_{cs}, X_s, X_r
Chemostat	Predator	X_r	$Y_a = X_e$ $Y_c = X_i$	B_x	Y_q, Y_a	contact	H_{ca} fast B_x fast	Y_q, Y_a	Y_{cs}, X_s
SI	Pathogen		$Y_a = X_e$ $Y_c = X_i$	B_x	Y_q, X_e	contact	H_{ca} fast D_q fast	Y_q, X_r, X_e	X_{ss}, X_i
SIR	Pathogen		$Y_a = X_e$ $Y_c = X_i$	B_x	Y_q, X_e	contact	D_q fast	Y_q, X_e	X_{ss}, X_i, X_r
SEIR (rabies)	Pathogen		$Y_a = X_e$ $Y_c = X_i$	B_x	Y_q	(contact)	H_{ca} fast D_q slow (D_q fast)	Y_q	X_s, X_e, X_i, X_r
SEI	Pathogen	X_r	$Y_a = X_e$ $Y_c = X_i$	D_x	Y_q	contact	D_q fast	Y_q	X_{ss}, X_e, X_i
Q-SI	Pathogen	X_r	$Y_a = X_e$ $Y_c = X_i$		X_e		H_{ca} fast	X_e	X_{ss}, X_i, Y_q
Macroparasite	Macroparasite	X_r		K_{jv}	X_e		H_{ca} fast	Y_a	X, Y_q, Y_c

1) Lotka-Volterra predator-prey model (13), with further reduction to the logistic
 The Lotka–Volterra prey–predator model is perhaps the most widely used consumer–resource model in Ecology. It is simple but has unusual features that are not often specified, including complicated composite parameters and tracking only questing consumers. Here, the prey has Malthusian growth in the absence of the predator and contact with the predator is mass action.

The general model

$$\begin{aligned} dY_q/dt &= B_{qc} - D_q + m(1-f)H_{qc} + fmA_iK_i Y_c/X_i + mF_a - C_{aq} \\ dY_a/dt &= C_{aq} - D_a - H_{ca} - j_a D_e Y_a/X_e - F_a \\ dY_c/dt &= B_{cc} - D_c + H_{ca} - j_c D_i Y_c/X_i - A_i K_i Y_c/X_i - m(1-f)H_{qc} \\ dX_s/dt &= B_{sx} - D_s + R_{sx} + V_{sr} - I_{rs} - C_{aq} \\ dX_e/dt &= B_{ex} - D_e - R_{xe} - H_{ca} + C_{aq} \\ dX_i/dt &= B_{ix} - D_i - R_{xi} + H_{ca} - K_i \\ dX_r/dt &= B_{rx} - D_r + R_{rx} - V_{sr} + I_{rs} \end{aligned}$$

Specify a predator:

$$m \rightarrow 1, f \rightarrow 1, j_a \rightarrow 0, j_c \rightarrow 0, B_{ix} \rightarrow 0, Y_c/X_i \rightarrow 1, Y_a/X_e \rightarrow 1, A_i \rightarrow 1$$

Delete unused functions: $B_{cc}, B_{ex}, B_{rx}, H_{qc}, I_{rs}, V_{sr}, R_{rx}, R_{xe}, R_{xi}, R_{sx}, D_e, D_i, D_r, F_a$

Synonymize. With a single consumer per ingested resource (i.e., $X_i = Y_c$), $dX_c/dt = dY_a/dt$, $dX_i/dt = dY_c/dt$, leaving a system of four equations:

$$\begin{aligned} dY_q/dt &= B_{qc} - D_q + K_i - C_{aq} \\ dY_a/dt &= C_{aq} - D_a - H_{ca} \\ dY_c/dt &= -D_c + H_{ca} - K_i \\ dX_s/dt &= B_{sx} - D_s - C_{aq} \end{aligned}$$

Define functions. Contact is mass action between questing and susceptible states, birth, death and handling are linear, consumer births are expressed as a linear conversion, e , of prey to predator.

$$\begin{aligned} dY_q/dt &= e\alpha Y_c - d_q Y_q + \alpha Y_c - \beta Y_q X_s \\ dY_a/dt &= \beta Y_q X_s - d_a Y_a - h Y_a \\ dY_c/dt &= -d_c Y_c + h Y_a - \alpha Y_c \\ dX_s/dt &= b_s X_s - d_s X_s - \beta Y_q X_s \end{aligned}$$

Subsume Y_a and Y_c using separation of time scales.

$$\hat{Y}_a \rightarrow \frac{\beta Y_q X_s}{d_a + h}, \quad \hat{Y}_c \rightarrow \frac{h Y_a}{\alpha + d_c}, \text{ and substitute into } dY_q/dt:$$

$$\begin{aligned} dY_q/dt &= \frac{e\alpha h \beta Y_q X_s}{(d_a + h)(\alpha + d_c)} - d_q Y_q + \frac{\alpha h \beta Y_q X_s}{(d_a + h)(\alpha + d_c)} - \beta Y_q X_s \\ dX_s/dt &= b_s X_s - d_s X_s - \beta Y_q X_s \end{aligned}$$

Simplify by setting $b_s - d_s$ as the composite parameter a and redefining “conversion”, as the composite parameter $\theta = \frac{(1+e)ah}{(d_a+h)(a+d_c)} - 1$.

Track: Assume that attacking and consuming consumers as well as exposed and ingested resources are too rare to bother counting. This leaves the classic Lotka Volterra (1925) prey–predator equations predator-prey model for questing predators.

$$\begin{aligned} dY_q/dt &= \theta\beta Y_q X_s - d_q Y_q \\ dX_s/dt &= aX_s - \beta Y_q X_s \end{aligned}$$

This solution will reduce to the logistic equation if the prey resource is limited by density dependence. Here, we start with the solution for the Lotka-Volterra predator-prey model (above), but we make d_s non linear by adding a density dependent term μ .

$$\begin{aligned} dY_q/dt &= \theta\beta Y_q X_s - d_q Y_q \\ dX_s/dt &= b_s X_s - (d_s + \mu X_s) X_s - \beta Y_q X_s \end{aligned}$$

Subsume X_s using separation of time scales.

$\hat{X}_s \rightarrow \frac{a - \beta Y_q}{\mu}$, and substitute into dY_q/dt :

$$dY_q/dt = \frac{\theta\beta Y_q (a - \beta Y_q)}{\mu} - d_q Y_q$$

Simplify by setting $\frac{\theta\beta a - \mu d_q}{\mu}$ as the composite parameter φ and $\frac{\theta\beta a - \mu d_q}{\theta\beta^2}$ as the composite carrying capacity \hat{Y}_q .

Track: Again, assume that attacking and consuming consumers as well as exposed and ingested resources are too rare to bother counting. This leaves the logistic equation for a consumer feeding on a logistic resource.

$$dY_q/dt = \varphi Y_q \left(1 - \frac{Y_q}{\hat{Y}_q}\right)$$

2) Saturated predators (Spruce Budworm) (14)

The Spruce budworm is a predator-prey model with *a*) a Holling type III functional response, *b*) logistic dynamics of the resource and *c*) a constant number of "predatory" birds. This version tracks only the consuming state of the predator, Y_c .

The general model

$$\begin{aligned} dY_q/dt &= B_{qc} - D_q + m(1-f)H_{qc} + f mA_i K_i Y_c/X_i + mF_a - C_{aq} \\ dY_a/dt &= C_{aq} - D_a - H_{ca} - j_a D_e Y_a/X_e - F_a \\ dY_c/dt &= B_{cc} - D_c + H_{ca} - j_c D_i Y_c/X_i - A_i K_i Y_c/X_i - m(1-f)H_{qc} \\ dX_s/dt &= B_{sx} - D_s + R_{sx} + V_{sr} - I_{rs} - C_{aq} \\ dX_e/dt &= B_{ex} - D_e - R_{xe} - H_{ca} + C_{aq} \\ dX_i/dt &= B_{ix} - D_i - R_{xi} + H_{ca} - K_i \\ dX_r/dt &= B_{rx} - D_r + R_{rx} - V_{sr} + I_{rs} \end{aligned}$$

Specify a predator:

$$m \rightarrow 1, f \rightarrow 1, j_a \rightarrow 0, j_c \rightarrow 0, B_{ix} \rightarrow 0, Y_c/X_i \rightarrow 1, Y_a/X_e \rightarrow 1, A_i \rightarrow 1$$

Delete unused functions: $B_{cc}, B_{ex}, B_{rx}, D_r, I_{rs}, H_{qc}, F_a, R_{rx}, R_{xe}, R_{xi}, R_{sx}, V_{sr}$

Synonymize. With a single consumer per ingested resource (i.e., $X_i = Y_c$), $dX_c/dt = dY_a/dt$, $dX_i/dt = dY_c/dt$, leaving a system of four equations:

$$\begin{aligned} dY_q/dt &= B_{qc} - D_q + K_i - C_{aq} \\ dY_a/dt &= C_{aq} - D_a - H_{ca} \\ dY_c/dt &= -D_c + H_{ca} - K_i \\ dX_s/dt &= B_{sx} - D_s - C_{aq} \end{aligned}$$

Define functions. Contact is attractive (birds switch to susceptible insects when insects are abundant), birth, and handling are linear, consumer births are expressed as a linear conversion, e , of prey to predator, and the resource has density-dependent growth.

$$\begin{aligned} dY_q/dt &= e\alpha Y_c - d_q Y_q + \alpha Y_c - \beta Y_q X_s^2 \\ dY_a/dt &= \beta Y_q X_s^2 - d_a Y_a - h Y_a \\ dY_c/dt &= -d_c Y_c + h Y_a - \alpha Y_c \\ dX_s/dt &= b_s X_s - X_s(d_s + \mu X_s) - \beta Y_q X_s^2 \end{aligned}$$

Subsume Y_q and Y_a using separation of time scales:

$$\hat{Y}_q \rightarrow \frac{\alpha(e+1)Y_c}{d_q + \beta X_s^2}, \hat{Y}_a \rightarrow \frac{\beta Y_q X_s^2}{d_a + h} \text{ and substitute into } dY_c/dt \text{ and } dX_s/dt:$$

$$\begin{aligned} dY_c/dt &= -d_c Y_c + \frac{\alpha\beta(e+1)hY_c X_s^2}{(d_a + h)(d_q + \beta X_s^2)} - \alpha Y_c \\ dX_s/dt &= b_s X_s - X_s(d_s + \mu X_s) - \frac{\alpha\beta(e+1)Y_c X_s^2}{d_q + \beta X_s^2} \end{aligned}$$

Simplify by assuming the predator population, and particularly, Y_c is a constant, set the composite resource growth parameter $a = b_s - d_s$, defining the composite resource

carrying capacity parameter as $\hat{X} = a/\mu$, and set the composite prey “conversion” parameter $\phi = \alpha(e + 1)$.

Track: Tracking only the susceptible component of the budworm population leaves:

$$d\mathbf{X}_s/d\mathbf{t} = aX_s(1 - \frac{X_s}{\hat{X}}) - \frac{\phi Y_c X_s^2}{k + X_s^2}$$

3) The Invulnerable prey-predator model (15)

This is a Lotka–Volterra predator-prey model where prey can take refuge, here represented by the resistant prey state. All three versions of Abrams and Walters’s (1996) models can be replicated by the general model; here we have considered the second one, where only invulnerable prey are reproductive and density dependence is a function of a weighted sum of the two prey categories. The model also includes a Type II functional response for the predator, which emerges naturally during model simplification. This version only tracks the consuming consumers Y_c .

The general model

$$\begin{aligned} dY_q/dt &= B_{qc} - D_q + m(1-f)H_{qc} + fmA_iK_i Y_c/X_i + mF_a - C_{aq} \\ dY_a/dt &= C_{aq} - D_a - H_{ca} - j_a D_e Y_a/X_e - F_a \\ dY_c/dt &= B_{cc} - D_c + H_{ca} - j_c D_i Y_c/X_i - A_i K_i Y_c/X_i - m(1-f)H_{qc} \\ dX_s/dt &= B_{sx} - D_s + R_{sx} + V_{sr} - I_{rs} - C_{aq} \\ dX_e/dt &= B_{ex} - D_e - R_{xe} - H_{ca} + C_{aq} \\ dX_i/dt &= B_{ix} - D_i - R_{xi} + H_{ca} - K_i \\ dX_r/dt &= B_{rx} - D_r + R_{rx} - V_{sr} + I_{rs} \end{aligned}$$

Specify a predator:

$$m \rightarrow 1, f \rightarrow 1, j_a \rightarrow 0, j_c \rightarrow 0, B_{ix} \rightarrow 0, Y_c/X_i \rightarrow 1, Y_a/X_e \rightarrow 1, A_i \rightarrow 1$$

Delete unused functions: $B_{cc}, B_{ex}, B_{sx}, F_a, H_{qc}, R_{rx}, R_{sx}, R_{xe}, R_{xi}$

Synonymize. With a single consumer per ingested resource (i.e., $X_i = Y_c$), $dX_c/dt = dY_a/dt$, $dX_i/dt = dY_c/dt$, leaving a system of five equations:

$$\begin{aligned} dY_q/dt &= B_{qc} - D_q + K_i - C_{aq} \\ dY_a/dt &= C_{aq} - D_a - H_{ca} \\ dY_c/dt &= -D_c + H_{ca} - K_i \\ dX_s/dt &= -D_s + V_{sr} - I_{rs} - C_{aq} \\ dX_r/dt &= B_{rx} - D_r - V_{sr} + I_{rs} \end{aligned}$$

Define functions. Contact is mass action between questing and susceptible states, birth, death and handling are linear, consumer births are expressed as a linear conversion, e , of prey to predator, and the death of resistant resources is density dependent and proportional to birth rate so that $D_r \rightarrow b_r X_r (\mu_r X_r + \mu_s X_s)$.

$$\begin{aligned} dY_q/dt &= e\alpha Y_c - d_q Y_q + \alpha Y_c - \beta Y_q X_s \\ dY_a/dt &= \beta Y_q X_s - d_a Y_a - h Y_a \\ dY_c/dt &= -d_c Y_c + h Y_a - \alpha Y_c \\ dX_s/dt &= -d_s X_s + v X_r - \iota X_s - \beta Y_q X_s \\ dX_r/dt &= b_r X_r - b_r X_r (\mu_r X_r + \mu_s X_s) - v X_r + \iota X_s \end{aligned}$$

Subsume Y_a and Y_q using separation of time scales.

$$\hat{Y}_a \rightarrow \frac{\beta Y_q X_s}{d_a + h} \quad \hat{Y}_q \rightarrow \frac{\alpha(e+1)Y_c}{d_q + \beta X_s} \text{ and substitute into } dY_c/dt, dX_s/dt \text{ assuming } d_a = d_c:$$

$$dY_c/dt = -d_c Y_c + \frac{\alpha\beta(e+1)hY_c X_s}{(d_c+h)(d_q+\beta X_s)} - \alpha Y_c$$

$$d\mathbf{X}_s/dt = -d_s X_s + v X_r - \iota X_s - \frac{\alpha\beta(e+1)Y_c X_s}{d_q + \beta X_s}$$

$$d\mathbf{X}_r/dt = b_r X_r - b_r X_r (\mu_r X_r + \mu_s X_s) - v X_r + \iota X_s$$

Simplify by assuming $h \gg d_c$, setting composite parameters $\phi = \alpha(e + 1)$, $\Omega = (d_c + \alpha)$, and half saturation constant $k = d_q/\beta$.

Track: Assume that attacking and questing consumers are too rare to bother counting. This leaves the of Abrams and Walters's predator model with prey born into a resistant state and density-dependent deaths.

$$d\mathbf{Y}_c/dt = -\Omega Y_c + \frac{\phi Y_c X_s}{X_s + k}$$

$$d\mathbf{X}_s/dt = -d_s X_s + v X_r - \iota X_s - \frac{\phi Y_c X_s}{k + X_s}$$

$$d\mathbf{X}_r/dt = b_r X_r - b_r X_r (\mu_r X_r + \mu_s X_s) - v X_r + \iota X_s$$

4) Chemostat (16):

The Monod model is similar to a Lotka–Volterra model for a microbe growing in a chemostat apparatus. Nutrients are fluxed through a tank with bacteria that deplete the resource before the medium fluxes out of the tank along with unlucky microbes. There are several ways to reduce this model provided the questing state is subsumed.

The general model

$$dY_q/dt = B_{qc} - D_q + m(1-f)H_{qc} + f mA_i K_i Y_c/X_i + mF_a - C_{aq}$$

$$dY_a/dt = C_{aq} - D_a - H_{ca} - j_a(D_e + R_{xe}) Y_a/X_e - F_a$$

$$dY_c/dt = B_{cc} - D_c + H_{ca} - j_c(D_i + R_{xi}) Y_c/X_i - A_i K_i Y_c/X_i - m(1-f)H_{qc}$$

$$dX_s/dt = B_{sx} - D_s + R_{sx} + V_{sr} - I_{rs} - C_{aq}$$

$$dX_e/dt = B_{ex} - D_e - R_{xe} - H_{ca} + C_{aq}$$

$$dX_i/dt = B_{ix} - D_i - R_{xi} + H_{ca} - K_i$$

$$dX_r/dt = B_{rx} - D_r + R_{rx} - V_{sr} + I_{rs}$$

Specify a predator on a resource without births:

$$m \rightarrow 1, f \rightarrow 1, j_a \rightarrow 0, j_c \rightarrow 0, B_{ix} \rightarrow 0, Y_c/X_i \rightarrow 1, Y_a/X_e \rightarrow 1, A_i \rightarrow 1$$

Delete unused functions: $B_{cc}, B_{ex}, B_{ix}, B_{rx}, D_r, F_a, H_{qc}, I_{rs}, R_{rx}, R_{sx}, R_{xe}, R_{xi}, V_{sr}$

Synonymize. Define resources in consumer units so there is a single consumer per ingested resource (i.e., $X_i = Y_c$), $dX_e/dt = dY_a/dt$, $dX_i/dt = dY_c/dt$, leaving a system of four equations:

$$dY_q/dt = B_{qc} - D_q + K_i - C_{aq}$$

$$dY_a/dt = C_{aq} - D_a - H_{ca}$$

$$dY_c/dt = -D_c + H_{ca} - K_i$$

$$dX_s/dt = B_{sx} - D_s - C_{aq}$$

Define functions. Contact is mass action between questing and susceptible states. Death and handling are linear. Resources flux into the system at rate ρ , entering at a concentration X_0 . Depleted resources, X_s , and consumers flux out of the system at rate ρ .

$$dY_q/dt = e\alpha Y_c - (d_q + \rho)Y_q + \alpha Y_c - \beta Y_q X_s$$

$$dY_a/dt = \beta Y_q X_s - (d_a + \rho)Y_a - hY_a$$

$$dY_c/dt = -(d_c + \rho)Y_c + hY_a - \alpha Y_c$$

$$dX_s/dt = \rho X_0 - \rho X_s - \beta Y_q X_s$$

Subsume Y_q and Y_a using separation of time scales:

$$\hat{Y}_q \rightarrow \frac{\alpha(e+1)Y_c}{(d_q + \rho + \beta X_s)}, \hat{Y}_a \rightarrow \frac{\beta X_s}{(h + d_a + \rho)} \frac{\alpha(e+1)Y_c}{(d_q + \rho + \beta X_s)}$$

$$dY_c/dt = -(d_c + \rho)Y_c + \frac{\alpha\beta(e+1)hY_c X_s}{(d_a + h + \rho)(d_q + \rho + \beta X_s)} - \alpha Y_c$$

$$dX_s/dt = \rho(X_0 - X_s) - \frac{\alpha\beta(e+1)Y_c X_s}{d_q + \rho + \beta X_s}$$

Simplify by assuming $h \gg (d_a + \rho)$, then defining the composite parameters $\phi = \alpha(e+1)$,

$\psi = (d_c + \rho + \alpha)$, and half-saturation constant for contacts as $k = (d_q + \rho)/\beta$.

Track just the consuming part of the population:

$$dY_c/dt = -\psi Y_c + \frac{\phi X_s Y_c}{k + X_s}$$

$$dX_s/dt = \rho(X_0 - X_s) - \frac{\phi X_s Y_c}{k + X_s}$$

5) SI, with simplification to the logistic (17)

This is a model for a non-lethal disease, where the resource population size is assumed to be constant in time, but the model explicitly accounts for host mortality and thus births are set so as to balance natural mortality. Diseased individuals may recover and become immune, but these are not tracked. As the total host population, X , is constant, the number of individual in the resistant class was computed by Hethcote (1976) as $X_r = X - X_s - X_e - X_i$.

The general model

$$dY_q/dt = B_{qc} - D_q + m(1-f)H_{qc} + fmA_iK_iY_c/X_i + mF_a - C_{aq}$$

$$dY_a/dt = C_{aq} - D_a - H_{ca} - j_aD_eY_a/X_e - F_a$$

$$dY_c/dt = B_{cc} - D_c + H_{ca} - j_cD_iY_c/X_i - A_iK_iY_c/X_i - m(1-f)H_{qc}$$

$$dX_s/dt = B_{sx} - D_s + R_{sx} + V_{sr} - I_{rs} - C_{aq}$$

$$dX_e/dt = B_{ex} - D_e - R_{xe} - H_{ca} + C_{aq}$$

$$dX_i/dt = B_{ix} - D_i - R_{xi} + H_{ca} - K_i$$

$$dX_r/dt = B_{rx} - D_r + R_{rx} - V_{sr} + I_{rs}$$

Specify a pathogen:

$$m \rightarrow 0, f \rightarrow 0, j_a \rightarrow 1, j_c \rightarrow 1, B_{ix} \rightarrow B_{ix}, Y_c/X_i \rightarrow 1, Y_a/X_e \rightarrow 1, A_i \rightarrow 1$$

Delete unused functions: $B_{cc}, B_{ex}, B_{ix}, B_{rx}, F_a, H_{qc}, I_{rs}, K_i, R_{sx}, R_{xe}, V_{sr}$

Synonymize. With a single consumer per ingested resource (i.e., $X_i = Y_c$), $dX_c/dt = dY_a/dt$, $dX_i/dt = dY_c/dt$, leaving a system of five equations:

$$dY_q/dt = B_{qc} - D_q - C_{aq}$$

$$dX_s/dt = B_{sx} - D_s - C_{aq}$$

$$dX_e/dt = -D_e - H_{ca} + C_{aq}$$

$$dX_i/dt = -D_i - R_{xi} + H_{ca}$$

$$dX_r/dt = -D_r + R_{rx}$$

Define functions. As for other pathogen models, questing stages are indiscriminant and die if they contact non-susceptible hosts, or $D_q = Y_q(d_q + \beta(X_e + X_i + X_r))$. Recovery and handling are linear, all resource states have the same death rate d_x . Birth rate into the susceptible class is d_xX .

$$dY_q/dt = b_cX_i - d_qY_q - \beta Y_qX$$

$$dX_s/dt = d_xX - d_xX_s - \beta Y_qX_s$$

$$dX_e/dt = -d_xX_e - hX_e + \beta Y_qX_s$$

$$dX_i/dt = -d_xX_i - rX_i + hX_e$$

$$dX_r/dt = -d_xX_r + rX_i$$

Subsume Y_q and X_e using separation of time scales:

$$\hat{Y}_q \rightarrow \frac{b_cX_i}{d_q + \beta X}, \hat{X}_e \rightarrow \frac{\beta Y_qX_s}{d_x + h} \text{ and substitute into } dX_s/dt \text{ and } dX_i/dt:$$

$$dX_s/dt = d_xX - d_xX_s - \frac{\beta b_cX_iX_s}{d_q + \beta X}$$

$$d\mathbf{X}_i/dt = -d_x X_i - r X_i + \frac{h\beta Y_q X_s}{(d_x + h)(d_q + \beta X)}$$

$$d\mathbf{X}_r/dt = -d_x X_r + r X_i$$

Simplify by assuming $b_c = 1$, $h \gg d_x$ and $d_q \gg \beta X$, then defining the composite parameter $c = \beta/d_q$.

Track: Ignoring the exposed and resistant component of the host population leaves:

$$d\mathbf{X}_s/dt = d_x - d_x X_s - c X_i X_s$$

$$d\mathbf{X}_i/dt = -d_x X_i - r X_i + c X_i X_s$$

An additional reduction to the logistic is possible by simplifying more and tracking only X_i . Renaming X as K , and defining $X_s = K - X_i$, and setting d_x and $r = 0$, leads to the familiar logistic equation, which indicates how a consumer of a fixed resource saturates to a carrying capacity.

$$d\mathbf{X}_i/dt = c X_i \left(1 - \frac{X_i}{K}\right)$$

6) SIR (18)

This is the Kermack-McKendrick model for a non-lethal disease with fast dynamics over a short time scale, and no “background” mortality for the susceptible population. The total host population size is assumed to be constant. The model is:

The general model

$$dY_q/dt = B_{qc} - D_q + m(1-f)H_{qc} + f mA_i K_i Y_c/X_i + mF_a - C_{aq}$$

$$dY_a/dt = C_{aq} - D_a - H_{ca} - j_a D_e Y_a/X_e - F_a$$

$$dY_c/dt = B_{cc} - D_c + H_{ca} - j_c D_i Y_c/X_i - A_i K_i Y_c/X_i - m(1-f)H_{qc}$$

$$dX_s/dt = B_{sx} - D_s + R_{sx} + V_{sr} - I_{rs} - C_{aq}$$

$$dX_e/dt = B_{ex} - D_e - R_{xe} - H_{ca} + C_{aq}$$

$$dX_i/dt = B_{ix} - D_i - R_{xi} + H_{ca} - K_i$$

$$dX_r/dt = B_{rx} - D_r + R_{rx} - V_{sr} + I_{rs}$$

Specify a pathogen:

$$m \rightarrow 0, f \rightarrow 0, j_a \rightarrow 1, j_c \rightarrow 1, B_{ix} \rightarrow B_{ix}, Y_c/X_i \rightarrow 1, Y_a/X_e \rightarrow 1, A_i \rightarrow 1$$

Delete unused functions:

$$B_{sx}, B_{cc}, B_{ex}, B_{ix}, B_{rx}, D_s, D_e, D_i, D_r, D_a, D_c, F_a, H_{qc}, I_{rs}, K_i, R_{sx}, R_{xe}, V_{sr}$$

Synonymize. With a single consumer per ingested resource (i.e., $X_i = Y_c$), $dX_e/dt = dY_a/dt$, $dX_i/dt = dY_c/dt$, leaving a system of five equations:

$$dY_q/dt = B_{qc} - D_q - C_{aq}$$

$$dX_s/dt = -C_{aq}$$

$$dX_e/dt = -H_{ca} + C_{aq}$$

$$dX_i/dt = -R_{xi} + H_{ca}$$

$$dX_r/dt = R_{rx}$$

Define functions. Contact is mass action, recovery and handling are linear, births ignored.

$$dY_q/dt = b_c X_i - d_q Y_q - \beta Y_q X$$

$$dX_s/dt = -\beta Y_q X_s$$

$$dX_e/dt = -h X_e + \beta Y_q X_s$$

$$dX_i/dt = -r X_i + h X_e$$

$$dX_r/dt = r X_i$$

Subsume Y_q and X_e using separation of time scales:

$$\hat{Y}_q \rightarrow \frac{b_c X_i}{d_q + \beta X}, \hat{X}_e \rightarrow \frac{\beta Y_q X_s}{h}, \text{ and substitute into } dX_i/dt \text{ and } dX_s/dt:$$

$$dX_s/dt = -\frac{\beta b_c X_i X_s}{d_q + \beta X}$$

$$dX_i/dt = -r X_i + \frac{\beta b_c X_i X_s}{d_q + \beta X}$$

$$dX_r/dt = r X_i$$

Simplify by assuming $d_q \gg \beta X$, then defining the composite parameter $c = \beta b_c / d_q$.

Track: Ignoring the exposed component of the host population leaves the model formulated in the original Kermack and McKendrick form, namely:

$$d\mathbf{X}_s/d\mathbf{t} = -cX_iX_s$$

$$d\mathbf{X}_i/d\mathbf{t} = -rX_i + cX_iX_s$$

$$d\mathbf{X}_r/d\mathbf{t} = rX_i$$

7) SEIR with further reduction for measles (2)

This model describes the dynamics of a lethal disease. It assumes that births balance deaths in the disease-free population, but population size is not constant because of disease-induced mortality. Transmission is assumed to be frequency dependent.

The general model

$$dY_q/dt = B_{qc} - D_q + m(1-f)H_{qc} + f mA_i K_i Y_c/X_i + mF_a - C_{aq}$$

$$dY_a/dt = C_{aq} - D_a - H_{ca} - j_a D_e Y_a/X_e - F_a$$

$$dY_c/dt = B_{cc} - D_c + H_{ca} - j_c D_i Y_c/X_i - A_i K_i Y_c/X_i - m(1-f)H_{qc}$$

$$dX_s/dt = B_{sx} - D_s + R_{sx} + V_{sr} - I_{rs} - C_{aq}$$

$$dX_e/dt = B_{ex} - D_e - R_{xe} - H_{ca} + C_{aq}$$

$$dX_i/dt = B_{ix} - D_i - R_{xi} + H_{ca} - K_i$$

$$dX_r/dt = B_{rx} - D_r + R_{rx} - V_{sr} + I_{rs}$$

Specify a pathogen:

$$m \rightarrow 0, f \rightarrow 0, j_a \rightarrow 1, j_c \rightarrow 1, B_{ix} \rightarrow B_{ix}, Y_c/X_i \rightarrow 1, Y_a/X_e \rightarrow 1, A_i \rightarrow 1$$

Delete unused functions: $B_{cc}, B_{ex}, B_{ix}, B_{rx}, F_a, H_{qc}, I_{rs}, R_{xe}$

Synonymize. With a single consumer per ingested resource (i.e., $X_i = Y_c$), $dX_c/dt = dY_a/dt$, $dX_i/dt = dY_c/dt$, leaving a system of five equations:

$$dY_q/dt = B_{qc} - D_q - C_{aq}$$

$$dX_s/dt = B_{sx} - D_s + V_{sr} - C_{aq}$$

$$dX_e/dt = -D_e - H_{ca} + C_{aq}$$

$$dX_i/dt = -D_i - R_{xi} + H_{ca} - K_i$$

$$dX_r/dt = -D_r + R_{rx} - V_{sr}$$

Define functions. Contact, recovery and handling are linear, and all resource states have the same death rate, d_x .

$$dY_q/dt = b_c X_i - d_q Y_q - \beta Y_q X$$

$$dX_s/dt = d_x X - d_x X_s + v X_r - \beta Y_q X_s$$

$$dX_e/dt = -d_x X_e - h X_e + \beta Y_q X_s$$

$$dX_i/dt = -d_x X_i - r X_i + h X_e - \alpha X_i$$

$$dX_r/dt = -d_x X_r + r X_i - v X_r$$

Subsume Y_q and X_e using separation of time scales:

$$\hat{Y}_q \rightarrow \frac{b_c X_i}{d_q + \beta X}, \hat{X}_e \rightarrow \frac{\beta Y_q X_s}{d_x + h}, \text{ and substitute into } dX_s/dt \text{ and } dX_i/dt:$$

$$dX_s/dt = d_x X - d_x X_s + v X_r - \frac{\beta b_c X_i X_s}{d_q + \beta X}$$

$$dX_i/dt = -d_x X_i - r X_i + \frac{h \beta Y_q X_s}{(d_x + h)((d_q + \beta X))} - \alpha X_i$$

$$dX_r/dt = -d_x X_r + r X_i - v X_r$$

Simplify by assuming $h \gg d_x, d_q \ll \beta X$

Track: Ignoring the exposed component of the host population leaves:

$$\begin{aligned} d\mathbf{X}_s/dt &= d_x X - d_x X_s + v X_r - \frac{b_c X_i X_s}{X} \\ d\mathbf{X}_i/dt &= -d_x X_i - r X_i + \frac{b_c X_i X_s}{X} - \alpha X_i \\ d\mathbf{X}_r/dt &= -d_x X_r + r X_i - v X_r \end{aligned}$$

To model measles, Anderson and May use a slightly different version of the SEIR model above to emphasize the time course of the infection and the tendency to permanent immunity.

Subsume Y_q using separation of time scales:

$\hat{Y}_q \rightarrow \frac{b_c X_i}{d_q + \beta X}$, and substitute into dX_e/dt :

$$\begin{aligned} d\mathbf{X}_e/dt &= -d_x X_e - h X_e + \frac{\beta b_c X_i X_s}{d_q + \beta X} \\ d\mathbf{X}_i/dt &= -d_x X_i - r X_i + h X_e - \alpha X_i \\ d\mathbf{X}_r/dt &= -d_x X_r + r X_i - v X_r \end{aligned}$$

Simplify by making immunity permanent ($v = 0$), additional mortality in the infected state negligible ($\alpha = 0$), assuming $d_q \gg \beta X$, then defining the composite parameter $c = \beta b_c / d_q$.

Track: Ignoring the susceptible component of the host population leaves:

$$\begin{aligned} d\mathbf{X}_e/dt &= -d_x X_e - h X_e + c X_i X_s \\ d\mathbf{X}_i/dt &= -d_x X_i - r X_i + h X_e \\ d\mathbf{X}_r/dt &= -d_x X_r + r X_i \end{aligned}$$

8) SEI for rabies in wildlife (19)

This is a model for a lethal disease for a wildlife host with logistic dynamics. It tracks susceptible, exposed and infected individuals; transmission is assumed to be density dependent and there is no resistant class. The wildlife population is regulated by density dependence.

The general model

$$dY_q/dt = B_{qc} - D_q + m(1-f)H_{qc} + f mA_i K_i Y_c/X_i + mF_a - C_{aq}$$

$$dY_a/dt = C_{aq} - D_a - H_{ca} - j_a D_e Y_a/X_e - F_a$$

$$dY_c/dt = B_{cc} - D_c + H_{ca} - j_c D_i Y_c/X_i - A_i K_i Y_c/X_i - m(1-f)H_{qc}$$

$$dX_s/dt = B_{sx} - D_s + R_{sx} + V_{sr} - I_{rs} - C_{aq}$$

$$dX_e/dt = B_{ex} - D_e - R_{xe} - H_{ca} + C_{aq}$$

$$dX_i/dt = B_{ix} - D_i - R_{xi} + H_{ca} - K_i$$

$$dX_r/dt = B_{rx} - D_r + R_{rx} - V_{sr} + I_{rs}$$

Specify a pathogen:

$$m \rightarrow 0, f \rightarrow 0, j_a \rightarrow 1, j_c \rightarrow 1, Y_c/X_i \rightarrow 1, Y_a/X_e \rightarrow 1, A_i \rightarrow 1$$

Delete unused functions: $B_{cc}, B_{ex}, B_{ix}, B_{rx}, D_r, F_a, H_{qc}, I_{rs}, R_{xe}, R_{xi}, R_{rx}, R_{sx}, V_{sr}$

Synonymize. With a single consumer per ingested resource (i.e., $X_i = Y_c$), $dX_c/dt = dY_c/dt$, $dX_i/dt = dY_c/dt$, leaving a system of four equations:

$$dY_q/dt = B_{qc} - D_q - C_{aq}$$

$$dX_s/dt = B_{sx} - D_s - C_{aq}$$

$$dX_e/dt = -D_e - H_{ca} + C_{aq}$$

$$dX_i/dt = -D_i + H_{ca} - K_i$$

Define functions. Contact is linear, resource has density-dependent growth, recovery and handling are linear, and all resource states have the same death rate, d_x .

$$dY_q/dt = b_c X_i - d_q Y_q - \beta Y_q X$$

$$dX_s/dt = b X_s - (d_x + \mu X) X_s - \beta Y_q X_s$$

$$dX_e/dt = -(d_x + \mu X) X_e - h X_e + \beta Y_q X_s$$

$$dX_i/dt = -d_x X_i - \mu X X_i + h X_e - \alpha X_i$$

Subsume Y_q using separation of time scales:

$$Y_q \rightarrow \frac{b_c X_i}{d_q + \beta X_s} \text{ and substitute into } dX_s/dt \text{ and } dX_e/dt:$$

$$dX_s/dt = b X_s - (d_x + \mu X) X_s - \frac{\beta b_c X_i X_s}{d_q + \beta X}$$

$$dX_e/dt = -(d_x + \mu X) X_e - h X_e + \frac{\beta b_c X_i X_s}{d_q + \beta X}$$

$$dX_i/dt = -(d_x + \mu X) X_i + h X_e - \alpha X_i$$

Simplify by assuming $d_q \gg \beta X$, then defining the composite parameter $c = \beta b_c / d_q$.

Track: Ignoring the questing state of the pathogen leaves:

$$d\mathbf{X}_s/dt = bX_s - (d_x + \mu X)X_s - cX_iX_s$$

$$d\mathbf{X}_e/dt = -(d_x + \mu X)X_e - hX_e + cX_iX_s$$

$$d\mathbf{X}_i/dt = -(d_x + \mu X)X_i + hX_e - \alpha X_i$$

9) Q-SI insect/pathogen model with free-living infective stages (20)

Here we provide the reduction of the general model to “Model G” described in section 11 by Anderson and May. This model describes the dynamics of a lethal disease and its Malthusian host. It tracks the dynamics of susceptible and infected individuals assuming density-dependent transmission, the potential for recovery from the infected back to the susceptible class and free living infective consumers. Different from many other pathogen models is the ability of the infected class to reproduce.

The general model

$$dY_q/dt = B_{qc} - D_q + m(1-f)H_{qc} + fmA_iK_i Y_c/X_i + mF_a - C_{aq}$$

$$dY_a/dt = C_{aq} - D_a - H_{ca} - j_a D_e Y_a/X_e - F_a$$

$$dY_c/dt = B_{cc} - D_c + H_{ca} - j_c D_i Y_c/X_i - A_i K_i Y_c/X_i - m(1-f)H_{qc}$$

$$dX_s/dt = B_{sx} - D_s + R_{sx} + V_{sr} - I_{rs} - C_{aq}$$

$$dX_e/dt = B_{ex} - D_e - R_{xe} - H_{ca} + C_{aq}$$

$$dX_i/dt = B_{ix} - D_i - R_{xi} + H_{ca} - K_i$$

$$dX_r/dt = B_{rx} - D_r + R_{rx} - V_{sr} + I_{rs}$$

Specify a pathogen:

$$m \rightarrow 0, f \rightarrow 0, j_a \rightarrow 1, j_c \rightarrow 1, Y_c/X_i \rightarrow 1, Y_a/X_e \rightarrow 1, A_i \rightarrow 1$$

Delete unused functions: $B_{cc}, B_{ex}, B_{ix}, B_{rx}, D_r, F_a, H_{qc}, I_{rs}, R_{xe}, R_{rx}, V_{sr}$

Synonymize. With a single consumer per ingested resource (i.e., $X_i = Y_c$), $dX_e/dt = dY_a/dt$, $dX_i/dt = dY_c/dt$, leaving a system of four equations:

$$dY_q/dt = B_{qc} - D_q - C_{aq}$$

$$dX_s/dt = B_{sx} - D_s + R_{sx} - C_{aq}$$

$$dX_e/dt = -D_e - H_{ca} + C_{aq}$$

$$dX_i/dt = -D_i - R_{xi} + H_{ca} - K_i$$

Define functions. Contact, recovery and handling are linear. Questing states are lost whenever they contact a host in any state, and all resource states have the same death rate, d_x .

$$dY_q/dt = b_c X_i - d_q Y_q - \beta Y_q X$$

$$dX_s/dt = b_s X - d_x X_s + r X_i - \beta Y_q X_s$$

$$dX_e/dt = -d_x X_e - h X_e + \beta Y_q X_s$$

$$dX_i/dt = -d_x X_i - r X_i + h X_e - \alpha X_i$$

Subsume X_e using separation of time scales:

$$\hat{X}_e \rightarrow \frac{\beta Y_q X_s}{d_x + h} \text{ and substitute into } dX_i/dt:$$

$$dY_q/dt = b_c X_i - d_q Y_q - \beta Y_q X$$

$$dX_s/dt = b_s X - d_x X_s + r X_i - \frac{\beta h Y_q X_s}{d_x + h}$$

$$dX_i/dt = -d_x X_i - r X_i + \frac{\beta h Y_q X_s}{d_x + h} - \alpha X_i$$

Simplify by assuming $h \gg d_x$

Track: Ignoring the exposed component of the host population leaves the SIW model described by eqs (59)–(62) in Anderson and May 1981:

$$\mathbf{dY}_q/\mathbf{dt} = b_c X_i - d_q Y_q - \beta Y_q X$$

$$\mathbf{dX}_s/\mathbf{dt} = b_s X - d_x X_s + r X_i - \beta Y_q X_s$$

$$\mathbf{dX}_i/\mathbf{dt} = -d_x X_i - r X_i + \beta Y_q X_s - \alpha X_i$$

10) Macroparasite (21)

The macroparasite model was a major development that recognized that host mortality increased with parasite intensity and the aggregated distribution of parasites in their hosts meant that the parasite population was not uniformly distributed in the host population. The family of macroparasite models tracks the host population (combined infected and uninfected) and the parasite population. The host population is often assumed not to be constant. In some versions, two states of the parasite population are tracked, consuming (worms) and questing (eggs). In others, the egg is assumed to equilibrate fast relative to other processes.

The general model

$$dY_q/dt = B_{qc} - D_q + m(1-f)H_{qc} + fmA_iK_iY_c/X_i + mF_a - C_{aq}$$

$$dY_a/dt = C_{aq} - D_a - H_{ca} - j_aD_eY_a/X_e - F_a$$

$$dY_c/dt = B_{cc} - D_c + H_{ca} - j_cD_iY_c/X_i - A_iK_iY_c/X_i - m(1-f)H_{qc}$$

$$dX_s/dt = B_{sx} - D_s + R_{sx} + V_{sr} - I_{rs} - C_{aq}$$

$$dX_e/dt = B_{ex} - D_e - R_{xe} - H_{ca} + C_{aq}$$

$$dX_i/dt = B_{ix} - D_i - R_{xi} + H_{ca} - K_i$$

$$dX_r/dt = B_{rx} - D_r + R_{rx} - V_{sr} + I_{rs}$$

Specify a macroparasite (where κ represents aggregation):

$$m \rightarrow 0, f \rightarrow 0, j_a \rightarrow 1, j_c \rightarrow 1$$

Delete unused functions: $B_{cc}, B_{ex}, B_{ix}, B_{rx}, D_r, F_a, H_{qc}, I_{rs}, R_{xe}, R_{xi}, R_{rx}, R_{sx}, V_{sr}$

Combine the resource (host) state variables by summing their right and left-hand sides:

$$dY_q/dt = B_{qc} - D_q - C_{aq}$$

$$dY_a/dt = C_{aq} - D_a - H_{ca} - \frac{D_eY_a}{X_e}$$

$$dY_c/dt = -D_c + H_{ca} - \frac{D_iY_c}{X_i} - \frac{A_iY_cK_i}{X_i}$$

$$dX/dt = B_{sx} - D_e - D_i - D_s - K_i$$

Define functions. Contact is mass action for all hosts, recovery and handling are linear, parasite distribution within the host population is a negative binomial with clumping parameter κ :

$$dY_q/dt = b_cY_c - d_qY_q - \beta Y_qX$$

$$dY_a/dt = \beta XY_q - d_aY_a - hY_a - d_eY_a$$

$$dY_c/dt = -d_cY_c + hY_a - \frac{Y_c d_i X_i}{X_i} - \alpha Y_c \left(1 + \left(\frac{\frac{1}{\kappa} + 1}{X}\right)^{Y_c}\right)$$

$$dX/dt = b_xX - d_eX_e - d_iX_i - d_sX_s - \alpha Y_c$$

Subsume Y_a using separation of time scales:

$$\hat{Y}_a \rightarrow \frac{\beta XY_q}{d_a + d_e + h}, \text{ and substitute into } dY_c/dt:$$

$$dY_q/dt = b_cY_c - d_qY_q - \beta XY_q$$

$$dY_c/dt = -d_c Y_c + \frac{\beta h X Y_q}{d_a + d_e + h} - d_i Y_c - \alpha Y_c \left(1 + \left(\frac{1}{k} + 1\right) \frac{Y_c}{X}\right)$$

$$dX/dt = b_x X - d_e X_e - d_i X_i - d_s X_s - \alpha Y_c$$

Simplify by assuming $h \gg (d_a + d_e)$, and $d_x = d_s = d_e = d_i$

Track: Ignoring the attacking component of the consumer population leaves:

$$dY_q/dt = b_c Y_c - d_q Y_q - \beta X Y_q$$

$$dY_c/dt = -d_c Y_c + \beta X Y_q - d_i Y_c - \alpha Y_c \left(1 + \left(\frac{1}{k} + 1\right) \frac{Y_c}{X}\right)$$

$$dX/dt = (b_x - d_x) X - \alpha Y_c$$

References and Notes

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