

Supporting Information

for

Evolution of prudent predation in complex food webs: mechanism and evidence

Orestes Uxio Gutierrez Al-Khudhairy and Axel G. Rossberg

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Appendix S1 Motivation of our algorithm for sampling species

We explain here in detail why Eqs. (3) and (4) are plausible approximations for sampling the interaction strengths of new species entering our model community.

Under quite general conditions it is possible to approximate the dependence of attack rates on the traits of consumers and resources in the form (Rossberg *et al.*, 2010; Nagelkerke & Rossberg, 2014; Rossberg, 2013, Ch. 8):

$$a_{jk} \approx a_0 \exp \left[v_0^{(j)} + f_0^{(k)} - \sum_{k=1}^D \frac{\sigma_k}{2} \left(v_k^{(j)} - f_k^{(k)} \right)^2 \right], \quad (\text{S1})$$

with D denoting the dimensionality of trophic niche space and $v_0^{(j)}, \dots, v_D^{(j)}$ and $f_0^{(k)}, \dots, f_D^{(k)}$ *vulnerability- and foraging traits* of resources and consumers, respectively, which can be computed as functions of observable biological traits (Nagelkerke & Rossberg, 2014). A similar representation has been proposed by Rohr *et al.* (2010). The constant a_0 has dimensions of attack rates and $\sigma_k = \pm 1$. There is some ambiguity in how to choose a_0 , σ_k and the functions mapping observed traits to trophic traits. However, when imposing a condition the mean of $(v_0^{(j)})^2$ over the entire resource pool j is minimised, these ambiguities are resolved up to rigid geometric transformations of the vectors $\mathbf{v}^{(j)} = (v_1^{(j)}, \dots, v_D^{(j)})$ and $\mathbf{f}^{(k)} = (f_1^{(k)}, \dots, f_D^{(k)})$ (Rossberg, 2013, Ch. 8). With the mean of $(v_0^{(j)})^2$ minimised, we shall approximate $v_0^{(j)} = 0$.

For large D and sufficient statistical independence of the components of $\mathbf{v}^{(j)}$ and $\mathbf{f}^{(k)}$ (Rossberg, 2013, Ch. 11), one can approximate the sum in Eq. (S1) for randomly sampled consumer-resource pairs (j, k) by a normal distribution. Denoting the mean of this normal distribution by μ and its variance by σ^2 , and defining $a_k = a_0 \exp(f_0^{(k)} - \mu)$, this leads to Eq. (4).

All traits of consumers and resources can undergo mutations. However, compared to the evolution of foraging traits $f_0^{(k)}, \dots, f_D^{(k)}$, the resulting evolution of vulnerability traits $v_0^{(j)}, \dots, v_D^{(j)}$ is known to be slow (Rossberg *et al.*, 2006; Bersier & Kehrli, 2008; Eklöf & Stouffer, 2016)—a median of 25 times slower in an analysis of Rossberg *et al.* (2006). It shall here be disregarded.

Mutations of any observable biological traits will affect several foraging traits $f_0^{(k)}, \dots, f_D^{(k)}$. The question whether this increases or decreases *short-term fitness* (Goodnight *et al.*, 2008) in a given community depends not only on all traits $f_0^{(k)}, \dots, f_D^{(k)}$ of the focal consumer k but also on the sets of resources and competitors in the community. Even when a mutation leads to an increase in short-term

fitness, the change in $f_0^{(k)}$ associated with this mutation might be positive or negative, provided niche space dimensionality D is not too low, since the associated change in $f_0^{(k)}$ is just one of many random contributions to the change in short-term fitness. As a result, mutants arriving at the focal patch from a source patch may have $f_0^{(k)}$ values that can be higher or lower than the $f_0^{(k)}$ of the propagule that founded the population in the source patch. Because smaller $f_0^{(k)}$ correspond to consumers that, overall, forage less effectively than consumers with larger $f_0^{(k)}$, and low effectiveness is mechanically easier to achieve than high effectiveness, one must plausibly assume that degeneration of traits through mutations (Pomiankowski *et al.*, 1991) leads to a decay of $f_0^{(k)}$ on average unless this is counteracted by selection pressure. Recalling that $a_k = a_0 \exp(f_0^{(k)} - \mu)$, this leads to Eq. (3).

We assume that the relevant species pools are large and diverse, such that different patches have in effect statistically independent, typically non-overlapping species compositions. The random variables ξ_{jk} in Eq. (4) are therefore sampled anew as a propagule arrives at the focal patch, independent of a consumer's interactions with the residents of its source patch. Only the inheritance of a_k must be accounted of.

As a caveat, we note that in reality vulnerability traits do not cover the D -dimensional trophic traits space evenly, e.g. because these traits carry phylogenetic signal (related species have similar consumers, Bersier & Kehrli 2008). Then foraging traits other than $f_0^{(k)}$ might contribute to long-term fitness as well. For simplicity, we disregard this complication in our model.

Appendix S2 Derivation of the sub-models of the deconstructed formulation

We provide the rationale and outline the derivation of the four criteria Eqs. (5-9) driving invasions and extirpations in the deconstructed model formulation.

The *invadability criterion*, Eq. (5), predicts invadability when disregarding the presence of all but the focal consumer in the dimensionless full model, Eq. (2). Formally, it is obtained by computing the equilibrium state of Eq. (2) for $S_C = 1$ and $B_k^C = 0$ (with $k = 1$), which is $B_j^R = 1$ for $1 \leq j \leq S_R$, and then extracting the condition that, by Eq. (2b), this equilibrium is unstable such that the consumer can invade: $\sum_{j=1}^{S_R} H_{jk} B_j^R - 1 = \sum_{j=1}^{S_R} H_{jk} - 1 > 0$.

The condition for the *overexploitation* of resource j during the expansion phase of an invading consumer k , Eq. (7), is obtained by analysing the dimensionless full model, Eq. (2), for the case of only one consumer and one resource: $S_C = 1$, $S_R = 1$ (with $j = k = 1$). We consider again the situation where the consumer is initially absent $B_k^C = 0$ and the resource at equilibrium $B_j^R = 1$, $dB_j^R/dt = 0$. Then the consumer invades at low abundance. To estimate the minimum of B_j^R attained during the consumer invasion, i.e. during the transient before a new equilibrium is reached, we approximate dynamics by disregarding the density dependence of resource production expressed by the term $-B_j^R$ in Eq. (2a). This approximation is justified because we are interested in situations where B_j^R falls below $M_{\min} \ll 1$. It reduces the model to the classical Lotka-Volterra predator-prey equations

$$\frac{dB_j^R}{dt} = s \left[1 - H_{jk} B_k^C \right] B_j^R, \quad (S2a)$$

$$\frac{dB_k^C}{dt} = \rho_k \left[H_{jk} B_j^R - 1 \right] B_k^C. \quad (S2b)$$

Evaluating the conservation law known for this system (Lotka, 1920) for the initial conditions $B_j^R = 1$, $dB_j^R/dt = 0$, one finds that at its minimum B_j^R satisfies $\ln(B_j^R) = -H_{jk}(1 - B_j^R)$ (Rossberg, 2013, Sec. 20.3.3). Since we are interested in situations where the minimum is deep ($B_j^R < M_{\min} \ll 1$), this condition can be approximated as $\ln(B_j^R) = -H_{jk}$. It follows that B_j^R falls below M_{\min} during consumer k 's invasion if $\ln(M_{\min}) > -H_{jk}$, which is equivalent to Eq. (7).

The conditions for *consumer-mediated competitive exclusion*, for *exploitative competitive exclusion* and for *Pyrrhic competition* all derive directly from exact equilibrium solutions of the dynamic model. The general multispecies model, Eq. (2), is well studied (MacArthur, 1970, 1972; Case & Casten, 1979; Chesson, 1990). To write down its equilibrium solution, let \mathbf{H} be the matrix with entries H_{jk} and define the competition matrix as the matrix with entries

$$C_{kl} = \sum_{j=1}^{S_R} H_{jk} H_{jl}, \quad \text{that is} \quad \mathbf{C} = \mathbf{H}^T \mathbf{H}. \quad (S3)$$

Denote by \mathbf{s} the vector of intrinsic consumer growth rates

$$s_k = R_k - 1, \quad (S4)$$

with $R_k = \sum_{j=1}^{S_R} H_{jk}$ defined as in the main text. The vector \mathbf{b}^C of consumer population biomasses B_j^C at equilibrium is then given by

$$\mathbf{b}^C = \mathbf{C}^{-1} \mathbf{s}. \quad (S5)$$

83 and that of resource population biomasses B_j^R by

$$\mathbf{b}^R = \mathbf{1} - \mathbf{H}\mathbf{B}^C. \quad (\text{S6})$$

84 In the case of only one consumer ($S_C = 1$, $k = 1$), the biomass of the resource j is therefore $B_j^R =$
 85 $1 - H_{jk}(C_{kk})^{-1}s_k$. The resource with the lowest biomass is that with the largest H_{jk} , i.e., the main
 86 resource of k . Its biomass is negative, implying resource extinction (Holt, 1977), if

$$C_{kk} < H_{jk}s_k. \quad (\text{S7})$$

87 The criterion for consumer-mediated competitive exclusion, Eq. (8), spells out this condition.

88 For the two-consumer ($S_C = 2$) problem, we have, with $k = 1$ and $l = 2$,

$$\mathbf{C}^{-1} = \frac{1}{C_{kk}C_{ll} - C_{kl}^2} \begin{pmatrix} C_{ll} & -C_{kl} \\ -C_{kl} & C_{kk} \end{pmatrix}. \quad (\text{S8})$$

89 Combining Eqs. (S5) and (S8), we find that (for $S_C = 2$) $B_k^C < 0$ if

$$C_{ll}s_k - C_{kl}s_l < 0 \quad (\text{S9})$$

90 or equivalently

$$s_k < \frac{C_{kl}s_l}{C_{ll}}. \quad (\text{S10})$$

91 Our criterion of exploitative competitive exclusion, Eq. (6) spells out this condition.

92 Now, assume that Eq. (S10) and the corresponding condition with l 's and k 's role reversed both fail
 93 to be satisfied. This alone does not guarantee coexistence of all species. Combining Eqs. (S5), (S6)
 94 and (S8), one can see that the equilibrium abundance of resource B_i^R is predicted to be negative if

$$1 < H_{ik} \frac{C_{ll}s_k - C_{kl}s_l}{C_{kk}C_{ll} - C_{kl}^2} + H_{il} \frac{C_{kk}s_l - C_{kl}s_k}{C_{kk}C_{ll} - C_{kl}^2}. \quad (\text{S11})$$

95 This can be re-arranged to

$$C_{kk}C_{ll} - C_{kl}^2 < s_k (H_{ik}C_{ll} - H_{il}C_{kl}) + s_l (H_{il}C_{kk} - H_{ik}C_{kl}), \quad (\text{S12})$$

96 and our condition for Pyrrhic competition, Eq. (9), spells out this inequality.

97 We now outline how these conditions can efficiently be evaluated for large S_R and S_C . The most time
 98 consuming step is the computation of \mathbf{C} in Eq. (S3), as (for practical purposes) the number of operations
 99 this requires increases as $\mathcal{O}(S_C^2 S_R)$ with system size. All remaining calculations can be done using just
 100 $\mathcal{O}(S_C^2)$ or $\mathcal{O}(S_C S_R)$ operations.

101 Denote, for any square matrix A , by $\mathbf{diag}(A)$ the vector formed by its diagonal elements, and by
 102 $\mathbf{Diag}(\mathbf{v})$, for any vector \mathbf{v} , the diagonal matrix with \mathbf{v} on the diagonal. We can evaluate the $S_C \times S_C$
 103 matrix Φ with entries Φ_{kl} given by the left hand side of Eq. (S9) as

$$\Phi = \mathbf{s} \mathbf{diag}(\mathbf{C})^T - \mathbf{C} \mathbf{Diag}(\mathbf{s}). \quad (\text{S13})$$

104 To test for extirpations, set the diagonal of Φ to exactly zero to remove small numerical errors. Extirpation
 105 of consumer k by our (simplified) criterion follows if row k of Φ constrains negative elements.

106 The $S_C \times S_C$ matrix \mathbf{D} with entries $D_{kl} = C_{kk}C_{ll} - C_{kl}^2$, containing the determinants of all two-consumer
 107 competition problems (the denominators in Eqs. (S8), (S11)), can be computed as

$$\mathbf{D} = \mathbf{diag}(\mathbf{C}) \mathbf{diag}(\mathbf{C})^T - \mathbf{C} \circ \mathbf{C}, \quad (\text{S14})$$

108 with \circ denoting elementwise multiplication. After finding for each consumer k the index $m(k)$ of its
 109 main resource, one can constructed the $S_C \times S_C$ matrix \mathbf{M} with entries

$$M_{kl} = H_{m(k)l}. \quad (\text{S15})$$

110 Using this, we obtain the $S_C \times S_C$ matrix $\mathbf{\Delta}$ with entries given by the difference between left and right
 111 hand side of Eq. (S12) for the main resource of each consumer k as

$$\mathbf{\Delta} = \mathbf{D} - \mathbf{Diag}(\mathbf{diag}(\mathbf{M}))\mathbf{\Phi} - \mathbf{M} \circ \mathbf{\Phi}^T. \quad (\text{S16})$$

112 To test for extirpations, set the diagonal of $\mathbf{\Delta}$ to exactly zero to remove small numerical errors.
 113 Extirpation of the main resource of consumer k by our (simplified) criterion follows if row k of $\mathbf{\Delta}$
 114 contains negative elements.

115 By striking a new balance between code complexity, speed, and accuracy in the multi-objective
 116 optimisation problem of finding fast, simple and accurate models, our deconstructed formulation carves
 117 out emergent properties (*sensu* Rossberg, 2007) of the full model, Eq. (2), e.g., those shown in Figs. 2
 118 and 3.

Appendix S3 The evolutionary steady-state condition including mutation bias

We derive the evolutionary steady state condition for base attack rate, Eq. (11).

To understand the effect of mutation bias, we invoke the Price equation (Price, 1972). It predicts that the expected rate of evolutionary change of the a trait q is given by

$$d\mathbb{E}q/dt = \text{cov}[f(q), q] + \mathbb{E}\dot{q}, \quad (\text{S17})$$

with $f(q)$ denoting the invasion fitness (for a given environment) of lineages of type q , and the last term representing the mutation bias (the mean inherent rate of change of traits). For trait values q^* corresponding to evolutionary steady states, both sides of Eq. (S17) must evaluate to zero. Following Page & Nowak (2002), we expand $f(q)$ to first order at $q = q^*$. Combined with the population-dynamical equilibrium condition $f(q^*) = 0$, this leads to $0 = f'(q^*) \text{var } q + \mathbb{E}\dot{q}$, or equivalently

$$f'(q^*) = -\frac{\mathbb{E}\dot{q}}{\text{var } q}. \quad (\text{S18})$$

This condition generalises the conventional criterion for evolutionary singular strategies, $f'(q^*) = 0$, to situations with mutation bias.

To apply Eq. (S18) to our models, we set $q = \ln a$ and

$$\mathbb{E}\dot{q} = \frac{\ln \gamma_0}{L^*}, \quad (\text{S19})$$

where L^* is the mean lifetime of populations in the community. With time measured in units of consumer additions and considering that consumer richness remains approximately constant in the steady state, $L^* = S_C^{-1}$. The standing mutational variance $\text{var } q = \text{var}(\ln a)$ is obtained from the distribution of a over the simulation steady state.

We approximate steady-state invasion fitness, i.e. the mean inherent rate of increase ($f(q) > 0$) or decrease ($f(q) < 0$) of the number of populations of type q in the simulation steady state, as $f(q) \approx \ln[R(a)]/L(a)$, where $R(a)$ is the mean number of populations that inherit their base attack rate *via* Eq. (3) from a population with base attack rate a (the “mean lifetime reproductive success”), and $L(a)$ is the mean lifetime of populations with base attack rate a . With a^* representing the geometric mean of a over the simulation steady state, such that $\ln a^*$ is the arithmetic mean of $\ln a$, we expect that $R(a^*) = 1$. This leads to

$$f'(q^*) \approx \left. \frac{d\{\ln[R(a)]/L(a)\}}{d \ln a} \right|_{a=a^*} = \frac{1}{L(a)} \left. \frac{d \ln[R(a)]}{d \ln a} \right|_{a=a^*} \approx \frac{1}{L^*} \left. \frac{d \ln[R(a)]}{d \ln a} \right|_{a=a^*}. \quad (\text{S20})$$

Putting Eqs. (S19) and (S20) into Eq. (S18) and multiplying both sides with L^* yields Eq. (11).

Appendix S4 Mechanisms determining “birth rate”

To derive an analytic representation of the dependence of birth rate $b(a)$ of a resident consumer on base attack rate a , we must account for three elements common to both model formulations:

1. The mutation step, Eq. (3), determining the new consumer’s based attack rate from that of the resident.
2. The sampling of the new consumer’s attack rates according to Eq. (4), and the test whether it can invade.
3. The fact that time is measured in numbers of successful consumer invasions.

Crucial is the probability of successful invasion in 2. We begin with an analysis of this element, adding subsequently considerations of 1 and 3.

Competitive exclusion by a resident consumer according to Eq. (6) always implies an inability to invade according to Eq. (5), so that (for $S_C > 0$) only Eq. (6) needs to be considered. However, Eq. (5) can be understood as a correction of the invadability criterion, Eq. (5). To see this, re-arrange Eq. (6) as

$$\sum_{j=1}^{S_R} H_{jk} \left[1 - H_{jl} \frac{\sum_{i=1}^{S_R} H_{il} - 1}{\sum_{i=1}^{S_R} H_{il}^2} \right] - 1 < 0. \quad (\text{S21})$$

The term in square brackets represents the population biomass (in units of K) that resource j would have if l was the only extant consumer. The deconstructed formulation ensures that, at the end of a model iteration, no extant resource satisfies the criterion for consumer-mediated competitive exclusion, Eq. (8) and all extant consumers satisfy the simple invadability criterion, Eq. (5). These loop invariants guarantees that the value of the expression in brackets in Eq. (S21) lies between 0 and 1 for all k and l . Satisfaction of Eq. (S21) therefore implies violation of Eq. (5).

Because there is no mechanism active in the model that would favours values of the expression in square brackets that are particularly close to zero (see also Fig. S1), most of the variation in the terms of the sum over j is due to the log-normal distribution of the invader’s attack rates H_{jk} . The presence of competitors merely moderates the effect of this variation. It can be represented by substituting the square bracket by a suitable constant $0 < \beta < 1$: the fitting parameter introduced in the main text.

The sum over j in Eq. (S21) can then be written as $\alpha_0 a_k \beta \sum_{j=1}^{S_R} e^{\sigma \xi_{jk}}$. The distribution of the sum in this last expression is, for a given number of resources S_R , often well approximated by a single log-normal distribution with suitable choices for mean $\mu_{S_R} \approx \sigma \sqrt{2 \ln S_R}$ and standard deviation $\sigma_{S_R} \approx \sigma / \sqrt{1 + 2 \ln S_R}$ of the logarithm (Rossberg *et al.*, 2011). (We estimated μ_{S_R} and σ_{S_R} numerically from 10,000 samples of log-normal sums, which is more accurate.)

From this log-normal approximation, the invasion probability for species with given base attack rate a_k is obtained as

$$P_{\text{inv}}(a_k) = \Phi \left(\frac{\ln(\alpha_0 \beta a_k) + \mu_{S_R}}{\sigma_{S_R}} \right), \quad (\text{S22})$$

with $\Phi(x)$ denoting the cumulative standard normal distribution function. For the full model, the same functional form as in Eq. (S22) can be chosen based on the same rationale: compared to the variation in of link strengths, the variation in resource biomasses is small.

Denote by $P_{\text{inv}}^*(a_r)$ the probability for the “offspring” of resident species r to invade successfully. The log-normal approximation for the sum in $\alpha_0 a_k \beta \sum_{j=1}^{S_R} e^{\sigma \xi_{jk}}$ used above combines seamlessly with the log-normal distribution of a_k resulting from the mutation of base attack rate a_r of the resident “parent”

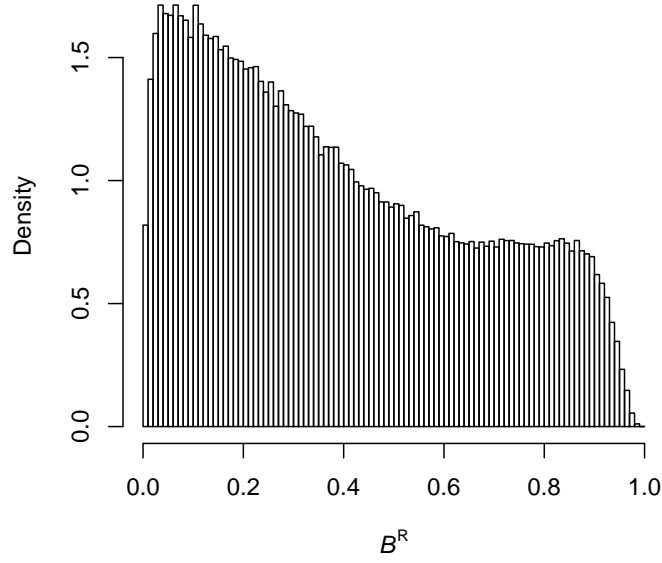


Figure S1: Histogram of resource biomasses B^R in the steady state of the full model, sampled from community snapshots after every 200 consumer additions. Neither values close to zero nor values close to one are very frequent.

182 species as per Eq. (3). We can therefore obtained $P_{\text{inv}}^*(a_r)$ from Eq. (S22) by correcting $\mu_{S_R}^* = \mu_{S_R} + \ln \gamma_0$
 183 and $\sigma_{S_R}^* = [\sigma_{S_R}^2 + (\ln \gamma_1)^2]^{1/2}$ to account for mutational variance and bias. Hence

$$P_{\text{inv}}^*(a_r) = \Phi \left(\frac{\ln(\alpha_0 \beta a_r) + \mu_{S_R}^*}{\sigma_{S_R}^*} \right). \quad (\text{S23})$$

184 Because we measure time in units of consumer invasions, and both variants of our model attempt
 185 consumer invasions from random resident species until one succeeds, the probability for offspring of
 186 resident consumer r to invade in a given time step is $P_{\text{inv}}^*(a_r) / \sum_{k=1}^{S_C} P_{\text{inv}}^*(a_k)$ (guaranteeing that the
 187 probability for offspring of some consumer k to invade evaluates to 1). Since species richness and the
 188 distribution of a_r fluctuate somewhat through time, we calculated the “birth” rate in Fig. 3c,g as the
 189 average of this probability for a given base attack rate a over the model steady states:

$$b(a) = \text{Average through time of } \frac{P_{\text{inv}}^*(a)}{\sum_{k=1}^{S_C} P_{\text{inv}}^*(a_k)}. \quad (\text{S24})$$

Appendix S5 Serial extinction

We derive Eq. (15) for the consumer's intrinsic growth rate after serial extinction

Note first that, because resources are successively removed in decreasing order of the consumer's attack rate in the deconstructed model formulation (and also in the simplified model, Box 2), the distribution of attack rates after serial extinction is the same as before, except for being truncated from above at the point where Eq. (8) becomes violated. In situations where the sums in Eq. (8) are not dominated by just a few resources, the central limit theorem can be invoked and the sums approximated by their expectation values, which then permits analytic computation of the truncation threshold H_* and other properties of the end state.

The calculations simplify by first approximating the relevant section of the upper tail of the log-normal attack-rate distribution, Eq. (4), by a Pareto distribution, which can be derived in the limit of high resource richness S_R (Rossberg *et al.*, 2011; Rossberg, 2013). By this approximation, the consumer has on average Z resources with H_{jk} larger than some "observation threshold" H_0 , and for these

$$P[H_{jk} \leq x] \approx 1 - \left(\frac{H_0}{x}\right)^\nu, \quad (\text{S25})$$

with $\nu = \sigma^{-1}\sqrt{2\ln S_R}$. Empirically, typical values for ν are in the range 0.5 to 0.6 (Rossberg *et al.*, 2011; Rossberg, 2013). Values $\nu \geq 1$ would correspond to extreme omnivory where the proportional contribution of each resource species to a consumer's diet scales as $1/S_R$, i.e. no resource makes a sizeable contribution to the diet. We are unaware of such a situation occurring in nature, and therefore assume $0 < \nu < 1$ in this study. The value of the link density Z is chosen to control the typical strengths H_{\max} of the strongest attack rate before serial extinction, specifically the $\exp(-1)$ -quantile of the distribution of $\max_j H_{jk}$. In the limit of large Z , this leads to the condition

$$\exp(-1) = (P[H_{jk} \leq H_{\max}])^Z = \left[1 - \left(\frac{H_0}{H_{\max}}\right)^\nu\right]^Z \approx \exp\left[-\left(\frac{H_0}{H_{\max}}\right)^\nu Z\right] \quad (\text{S26})$$

and so

$$Z \approx \left(\frac{H_{\max}}{H_0}\right)^\nu. \quad (\text{S27})$$

It goes without saying that H_{\max} is proportional to base attack rate a_k and can therefore be use as a proxy for the latter.

With this preparation, we can now take expectation values on both sides of Eq. (8) for the case of truncation at H_* , the largest threshold where it is not violated, to approximate

$$\mathbb{E}\left[\sum_j^{H_{jk} \leq H_*} H_{jk} - 1\right] = H_*^{-1} \mathbb{E}\left[\sum_j^{H_{jk} \leq H_*} H_{jk}^2\right] \quad (\text{S28})$$

as

$$\left[Z \int_{H_0}^{H_*} p(x) x dx - 1\right] = H_*^{-1} Z \int_{H_0}^{H_*} p(x) x^2 dx, \quad (\text{S29})$$

where $p(x) = -(d/dx)P[H_{jk} \leq x]$ is the probability density of the untruncated attack rate distribution. Evaluation of the integrals after inserting Eq. (S25) leads to

$$\frac{Z\nu H_*^{-\nu} (H_* H_0^\nu - H_*^\nu H_0)}{1 - \nu} - 1 = H_*^{-1} \frac{Z\nu H_*^{-\nu} (H_*^2 H_0^\nu - H_*^\nu H_0^2)}{2 - \nu} \quad (\text{S30})$$

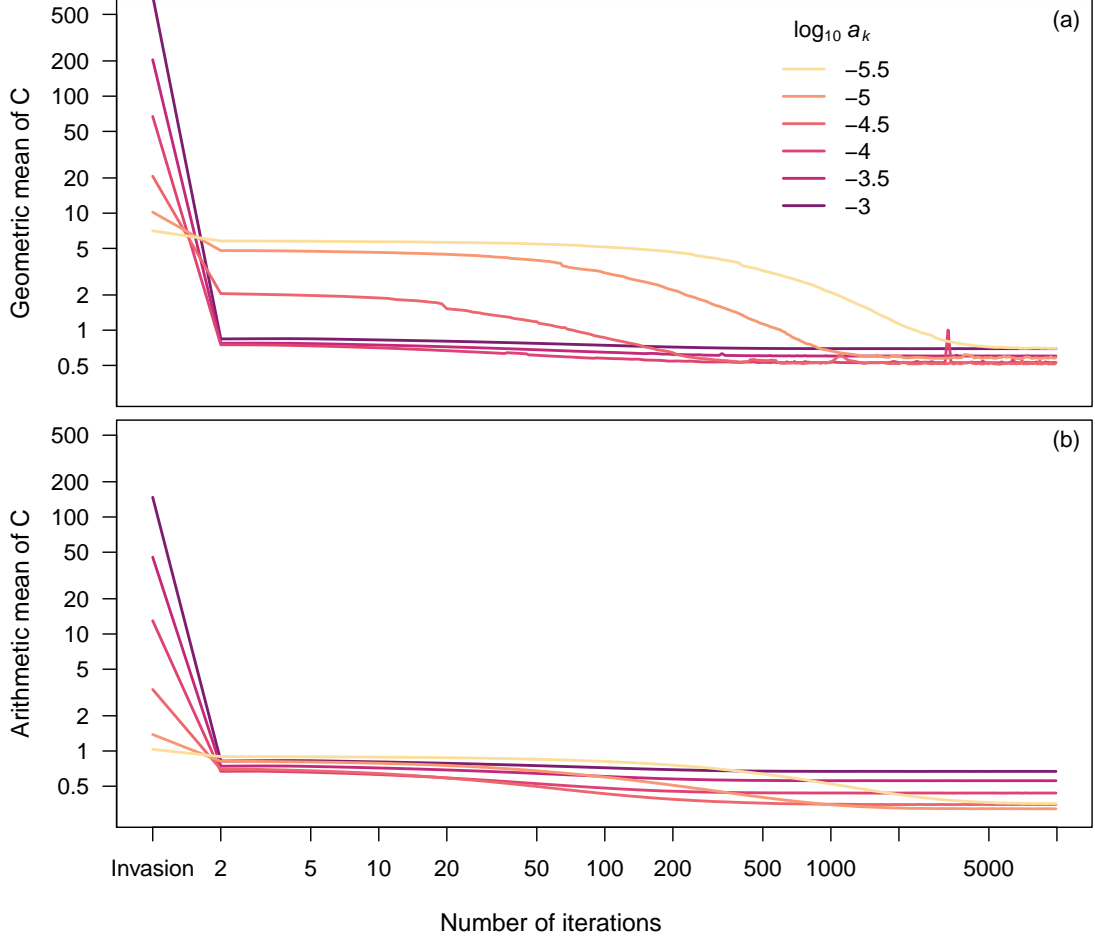


Figure S2: **Dependence of intrinsic growth rate $C = 1 - \sum_j H_{jk}$ on base attack rate in the course of repeated serial extinction and resource turnover.** Panel (a) shows geometric means of C over 10^6 replicated runs of the model of Box 2 over 10^4 iterations, panel (b) arithmetic means. For high base attack rates a_k (dark lines), both geometric and arithmetic means approach the same value ≈ 0.86 (indicating a near-deterministic outcome) after the first iteration of consumer-mediated competitive exclusion, largely independent of base attack rate, as predicted by the analytic theory. The value is different from the analytic prediction $1 - \sigma^{-1} \sqrt{2 \log S_R} \approx 0.14$ valid for large S_R , because $S_R = 224$ is not sufficiently large.

and, after inserting Eq. (S27) and taking the limit of low observation threshold ($H_0 \rightarrow 0$),

$$\frac{H_*^{-\nu} [\nu H_* H_{\max}^{\nu} - H_*^{\nu} (1 - \nu)]}{1 - \nu} = \frac{\nu H_*^{1-\nu} H_{\max}^{\nu}}{2 - \nu}. \quad (\text{S31})$$

217 This equation can be solved for H_* , yielding

$$H_* = \left[\frac{(1 - \nu)(2 - \nu)}{\nu H_{\max}^{\nu}} \right]^{1/(1-\nu)}. \quad (\text{S32})$$

218 The expected intrinsic growth rate of the consumer after serial extinction equals the left hand sides of
 219 Eqs. (S28)-(S31). When putting Eq. (S32) into the left hand side of Eq. (S31) it simplifies considerably,
 220 leading to the final result

$$\mathbb{E} \left[\sum_k^{H_{ki} \leq H_*} H_{ki} - 1 \right] = 1 - \nu. \quad (\text{S33})$$

221 With $0 < \nu < 1$, this result implies that $\mathbb{E} \sum_j^{H_{jk} \leq H_*} H_{jk}$ attains values between 1 and 2. On the other
 222 hand, the upper cutoff H_* declines with increasing H_{\max} (or base attack rates a_i) as $H_{\max}^{-\nu/(1-\nu)}$ by
 223 Eq. (S32). For large base attack rates the sum $\sum_j^{H_{jk} \leq H_*} H_{jk}$ therefore has contributions from many
 224 small terms, justifying our application of the central limit theorem to approximate of the sums entering
 225 Eq. (8) by their expectation values. Figure S2b qualitatively confirms this result.

226 Interestingly, above considerations imply that, despite having the same niche width in terms of the
 227 spread σ of the log-normal attack-rate distribution, invaders with higher base attack rate will have more
 228 diverse diets post Impact than those with lower attack rates. This might explain why invasive alien
 229 consumers are often found to be 'generalists'.

Box 1 Algorithm of the evolutionary metapopulation model.

The model state is given by N patches which are either empty of occupied by a population with base attack rate a_i ($1 \leq i \leq N$). The model is simulated as follows:

1. Occupy a proportion p of patches with populations with identical initial base attack rates a_i .
2. Select an occupied source patch r for dispersal. Sample the base attack rate a_k of a propagule according to Eq. (3).
3. Sample a target patch l .
4. If patch l is occupied:
 - (a) If $a_l < a_k$, replace the new population of patch l with one that has base attack rate a_k , otherwise do nothing.
5. If patch l is not occupied:
 - (a) With invasion probability $P_{inv}(a_k)$, establish in patch l a new population with base attack rates a_k and then remove the population from another occupied patch m , sampled at

random from all occupied patches with probability proportional to $1/L(a_m)$. $P_{inv}(a)$ is our approximation of invasion probability for the deconstructed community model, Eq. (S22) with $\beta = 0.45$ and $S_R = 224$ (corresponding to the mean equilibrium richness in Fig. 2), and $L(a)$ the polynomial fit to mean population life time in Fig. 3h ($\log_{10} L = -0.04105026(\log_{10} a)^2 - 0.78404937 \log_{10} a - 0.77341520$).

6. Continue from Step 2 for a predetermined number of interactions.

The values of γ_0 , γ_1 , and σ are as in Tab. 1.

The algorithm can be reformulated in such a way that only the list of a_i value of occupied patches i is kept in memory. In each iteration, Step 3a is then executed with probability p and otherwise Step 4a. When invasion is successful in Step 4a, the new a_k value is stored in the memory location where a_m was previously stored. This formulation permits us to take the limit $p \rightarrow 0$ while keeping the number of occupied patches pN fixed.

Appendix S6 The limited impact of cheaters

Cheaters exploit benefits offered by more altruistic conspecifics to their advantage, thus potentially counteracting the evolution of altruism. To obtain a bound on the impact of cheaters on prudent predation, we devised a simple evolutionary metapopulation model. The model describes a landscape of N patches that are either occupied by the focal species or not. The population occupying patch i has an associated base attack rate a_i .

In our metapopulation model we assume that cheating occurs if a population of the focal species disperses to a patch that is already occupied, and the propagule's base attack rate is larger than that of the resident in that patch. The propagule then replaces the resident population. This model disregards that conspecific propagules will not only differ in their base attack rates from residents, but also in other foraging traits (Appendix Appendix S1), and therefore have, on average, a reduced likelihood of establishment success. Our metapopulation model is therefore biased to overestimates the likelihood of cheating. We shall see that the predicted impact of cheating remains limited despite this.

Contrasting conventional stochastic patch occupancy models in the tradition of Levins (1969), patch occupancy p , i.e., the proportion of occupied patches, is a parameter in our model. The reason is evidence that species richness both at patch level (α) and at landscape level (γ) is regulated through ecological structural stability limits (O'Sullivan *et al.*, 2019), which our metapopulation model cannot explicitly represent. Mean occupancy is uniquely determined by α and γ as $p = \alpha/\gamma$. By fixing p we represent these limits implicitly.

The model is detailed in Box 1. We chose $pN = 1000$ over a range of p values, evaluated the algorithm over $4 \cdot 10^7$ iterations, and sampled base attack rates from the last 3/4 of each run to characterise the steady state (which was reached after less than a 10^{th} of iterations).

In the limit $p \rightarrow 0$, where cheating does not occur, the model attained a steady state with mean logarithmic base attack rate $\overline{\log_{10} a} = -5.14$, close to the value obtained with the deconstructed model, and an approximately normal distribution of $\log_{10} a$ in the steady state similar to that in Fig. 3e. These results further confirm our reconstruction of the fitness landscape in Fig. 3.

As shown in Fig. S3, $\overline{\log_{10} a}$ increases linearly with p for low p . An occupancy of $p = 0.3$, for example, leads to an approximate 3-fold increase in geometric mean base attack rates. Hence, cheating makes consumers somewhat less prudent, but does not fundamentally undermine the evolution of prudent predation.

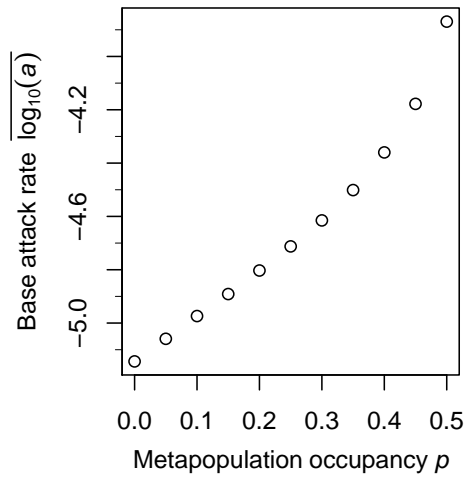


Figure S3: **The impact of cheaters on evolutionary stable base attack rate a .** Simulation results from the meta-population model described in Box 1. The higher the occupancy p of patches by the metapopulation, the larger the probability that occupied patches are overtaken by invading cheaters with higher base attack rates. This effect increases steady state base attack rates, but does not prevent a steady state from being reached.

Appendix S7 Steepness and basic reproduction number

We derive the relation between basic reproduction number and the steepness of stock recruitment relations given in Eq. (17).

Consider first the following caricature model of a fish stock feeding on a single resource:

$$\frac{dB^R}{dt} = \left[s \left(1 - \frac{B^R}{K} \right) - a \text{SSB} \right] B^R, \quad (\text{S34a})$$

$$\frac{d\text{SSB}}{dt} = \epsilon a B^R \text{SSB} - \rho \text{SSB} - F \text{SSB}. \quad (\text{S34b})$$

The parameter F denotes the fishing mortality rate, otherwise model structure and parameterization are as in Eq. (1). If one assumes, for simplicity, that (i) all mature individuals have the same body mass m , (ii) recruits are produced instantaneously, and (iii) the parameter ρ is dominated by natural mortality rather than respiration, then recruitment is given by the first term on the right-hand side of Eq. (S34b):

$$m \text{Rec} = \epsilon a B^R \text{SSB} = \epsilon a K \text{SSB} - \frac{\epsilon a^2 K}{s} \text{SSB}^2. \quad (\text{S35})$$

In the second step we eliminated B^R by solving Eq. (S34a) with $dB^R/dt = 0$ for $B^R > 0$. Stock-recruitment relations of this quadratic form are frequently used in fisheries science and named after Schaefer (1954). Virgin ($F = 0$) equilibrium SSB evaluates to

$$\text{SSB}_0 = s \frac{\epsilon a K - \rho}{\epsilon a^2 K}. \quad (\text{S36})$$

From Eqs. (16), (S35) and (S36) one obtains the steepness

$$h = \frac{1}{25} \left(1 + \frac{4\epsilon a K}{\rho} \right). \quad (\text{S37})$$

The basic reproduction number R is defined as recruitment per mature individual (of which there are SSB/m) in units of ρ , in the limit $\text{SSB} \rightarrow 0$, which evaluates to

$$R = \lim_{\text{SSB} \rightarrow 0} \frac{m \text{Rec}}{\text{SSB} \rho} = \frac{\epsilon a K}{\rho}. \quad (\text{S38})$$

Hence Eq. (S37) implies Eq. (17).

We now verify that Eq. (17) remains valid if one generalises Eq. (S34) to a situation with multiple resources. We assume that the fish stock is initially fully established at SSB_0 , such that resources that would not withstand its consumption have been extirpated. By Eq. (S6), the biomass of each resource is then a linear function of consumer biomass, here SSB. With the linear functional response of Lotka-Volterra models, this implies

$$m \text{Rec} = (c_1 - c_2 \text{SSB}) \text{SSB} \quad (\text{S39})$$

with some positive constants c_1 and c_2 . As above, we can evaluate

$$R = \lim_{\text{SSB} \rightarrow 0} \frac{m \text{Rec}}{\text{SSB} \rho} = \frac{c_1}{\rho}, \quad (\text{S40})$$

yielding $c_1 = \rho R$. Furthermore, recruitment balances mortality for the unfish stocks with $\text{SSB} = \text{SSB}_0$. So $m \text{Rec}(\text{SSB}_0) = \rho \text{SSB}_0$, which implies

$$c_2 = \rho \frac{R-1}{\text{SSB}_0}. \quad (\text{S41})$$

283 With these values for c_1 , c_2 , plugging Eq. (S39) into the definition of steepness, Eq. (16), yields again
284 Eq. (17).

Supporting figures

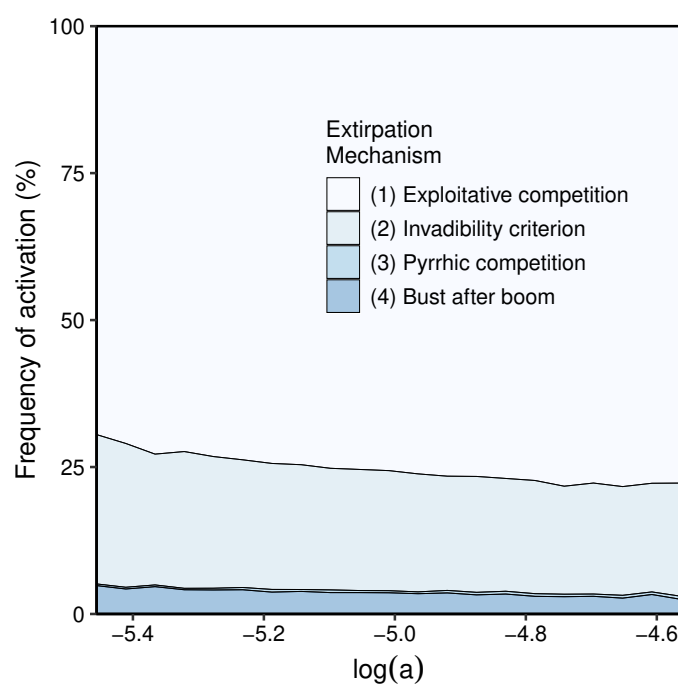


Figure S4: **Activation frequency of consumer extirpation mechanisms** The classification relates to different steps in the deconstructed model formulation (Box 1). *Exploitative competition* refers to Step 5; *Pyrrhic competition* to failure to meet the invadability condition by a consumer losing its main resource, or by the competitor causing this, in Steps 6, 7; *Bust after boom* refers to Step 3d; and *Invadability criterion* to failure to satisfy Eq. (5) at any other point in the algorithm. Extirpations through Pyrrhic competition are very rare, and those through bust after boom contribute just a few percent of cases.

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