Collective behaviour can stabilize ecosystems

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Collective behaviour is common in bacteria[1], plants[2], and animals[3], and thus across ecosystems, from biofilms[4] to cities[5]. With collective behaviour, social interactions among individuals propagate to affect the behaviour of groups, while group-level responses in turn affect individual behaviour. These cross-scale feedbacks between individuals, populations and their environments can provide fitness benefits, such as efficient exploitation of uncertain resources[6], as well as costs, such as increased resource competition[7,8]. While the social mechanics of collective behaviour are increasingly well-studied, its ecological significance remains poorly understood[9]. Here we introduce collective movement into a model of consumer-resource dynamics to demonstrate that collective behaviour can attenuate consumer-resource cycles and promote species coexistence. We focus on collective movement as a particularly well-understood example of collective behaviour[3]. Adding collective movement to canonical unstable ecological scenarios causes emergent social-ecological feedback which mitigates conditions that would otherwise result in extinction. Collective behaviour could play a key role in the maintenance of biodiversity.

Introduction

The mechanisms that underpin ecosystem stability and species coexistence are well studied, but not yet well understood[10–12]. Ecological models that integrate species interaction rates to match abundance data indicate that extant ecosystems must persist despite: (i) population oscillations—driven by environmental fluctuations, and nonlinear effects of abundance on recruitment—which increase the risk of stochastic extinction[13–16] and (ii) competition among species for limited resources, which promotes diversity loss via competitive exclusion[17–19]. The challenges to stability and coexistence can be summarized by two ecological "paradoxes:" the paradox of enrichment[13] addresses the prevalence of conditions that should result in destabilizing population oscillations, and the paradox of the plankton[19] addresses the longstanding puzzle of how diverse ecological communities can persist although many ecologically similar species are competing for a limited range of resources[11,12,20]. Stability and coexistence are hypothesized to rely on countervailing processes which attenuate population cycles[21–23], and which give each species a positive population growth rate whenever their abundance becomes low[10,12,20].

Spatial and temporal heterogeneities in species abundance and recruitment play a key role in determining stability and coexistence. When local conditions experienced by individuals differ systematically from their population averages, the ecological impacts of hotspots (e.g., of recruitment or resource consumption) are not necessarily balanced by the impacts of coldspots. This can result in stability and coexistence outcomes that might not be possible under homogeneous conditions[24,25]. In many cases spatiotemporal structure promotes stability and coexistence, while homogeneous environments tend to be less stable[25].

While spatiotemporal ecosystem structure is obviously impacted by exogenous drivers such as ocean currents, rainfall patterns or habitat fragmentation, collective behaviour generates spatiotemporal patterns that significantly modify the impacts of exogenous drivers, as seen in swarms of insects[3], schools of fish[6] or migrating flocks[26] and herds[27,28]. Spatiotemporal heterogeneities generated by collective behaviour can have ecosystem consequences. For example, group formation has been linked to the stability of predator-prey dynamics for lions and wildebeest in the Serengeti[7]. Ecosystem states can in turn affect collective dynamics, such as through density-dependent transitions from disordered to ordered group behaviour, which are common in taxa that exhibit collective behaviour[6,29]. For example, locust swarms emerge at critical densities when locust populations transition to collective motion[30]. Ecosystem state thus plays a key role in regulating collective behaviour, and collective behaviour can in turn impact ecosystem states. However, the consequences of feedback between collective behaviour and ecosystem dynamics remain largely unexplored[31–33].

Here we demonstrate the ecological potential of this feedback by adding collective behaviour to a simple food web model[34,35], focusing on the particularly common and well-studied case of collective movement[3]. Our results show that collective behaviour fundamentally alters stability and coexistence outcomes in canonical ecosystems, and provides a resolution to both the paradox of enrichment and the paradox of the plankton via a social-ecological feedback loop inherent to resource consumption and recruitment in collective groups. The effects of collective movement on stability and coexistence are distinct from previously-described effects of spatial aggregation on ecosystem processes, and open new avenues for a predictive understanding of stability and biodiversity through the quantitative study of social-ecological dynamics.

Results

Consumer-resource model We consider a simple ecosystem with two consumer species, P and Q, feeding on a resource species R in a homogeneous environment:

$$\begin{aligned} \frac{dP}{dt} &= bf_P(R)P - mP \\ \frac{dQ}{dt} &= bf_Q(R)Q - mQ \\ \frac{dR}{dt} &= rR\left(1 - \frac{R}{K}\right) - f_P(R)P - f_Q(R)Q \end{aligned} \tag{1}$$

where b is the resource conversion efficiency, m is the consumer mortality rate, and r and K are the maximum per-capita recruitment rate and carrying capacity of the resource population. The per-capita resource consumption rate of consumer j is given by its functional response $f_j(R) = a_jR/(1 + a_jhR)$, where h is the handling time and $a_j = ec_j$ is the hazard of encounter (e) and subsequent capture (c_j). We assume the two consumer species differ only with respect to their capture efficiencies c_j. This model is commonly used to study the paradox of enrichment and the paradox of the plankton[12, 13] .

To add collective behaviour we represent equation (1) using an individual-based simulation in which consumer and resource individuals occupy a square landscape with side length L and periodic boundary conditions (Methods). We use a landscape that is large relative to an individual's powers of movement and in which behavioural dynamics are fast relative to trophic dynamics. Absent collective behaviour, individuals move independently and exhibit diffusive mixing at the population level. All trophic and behavioural interactions occur within an individual's interaction radius ρ, yielding a constant expected encounter hazard of $e_0 = \pi\rho^2/L^2$ for ensembles of independent individuals (note we use several flavours of e to represent different views of the encounter rate, including e_0 and, below, an effective encounter rate $\bar{e}$ that is estimated from data; see Methods for details). New individuals arise at a random location within a distance ρ of their parent. Following a consumption event the consumer involved reproduces with probability b. The consumer then waits an average handling time of h before being eligible for consumption again. With collective behaviour, each individual avoids collisions, moves towards, and aligns with its conspecific neighbours (within a distance ρ) according to a well-studied model of collective movement[36,37].

We first consider the impact of collective behaviour on the paradox of enrichment, considering the model with only one consumer species, P. In ecosystems composed of independent individuals, increasing resource carrying capacity (K) causes consumer and resource populations to oscillate with increasing amplitude (Fig. 1a). In contrast, these limit cycles are attenuated with collective behaviour in the consumer (Fig. 1b), or in both the consumer and the resource (SI), leading to long-term persistence under levels of enrichment that would cause ensembles of independent individuals to go extinct.

We next examined how collective behaviour alters species coexistence by simulating exploitative competition between a superior consumer (P) and an inferior one (Q) that has a lower

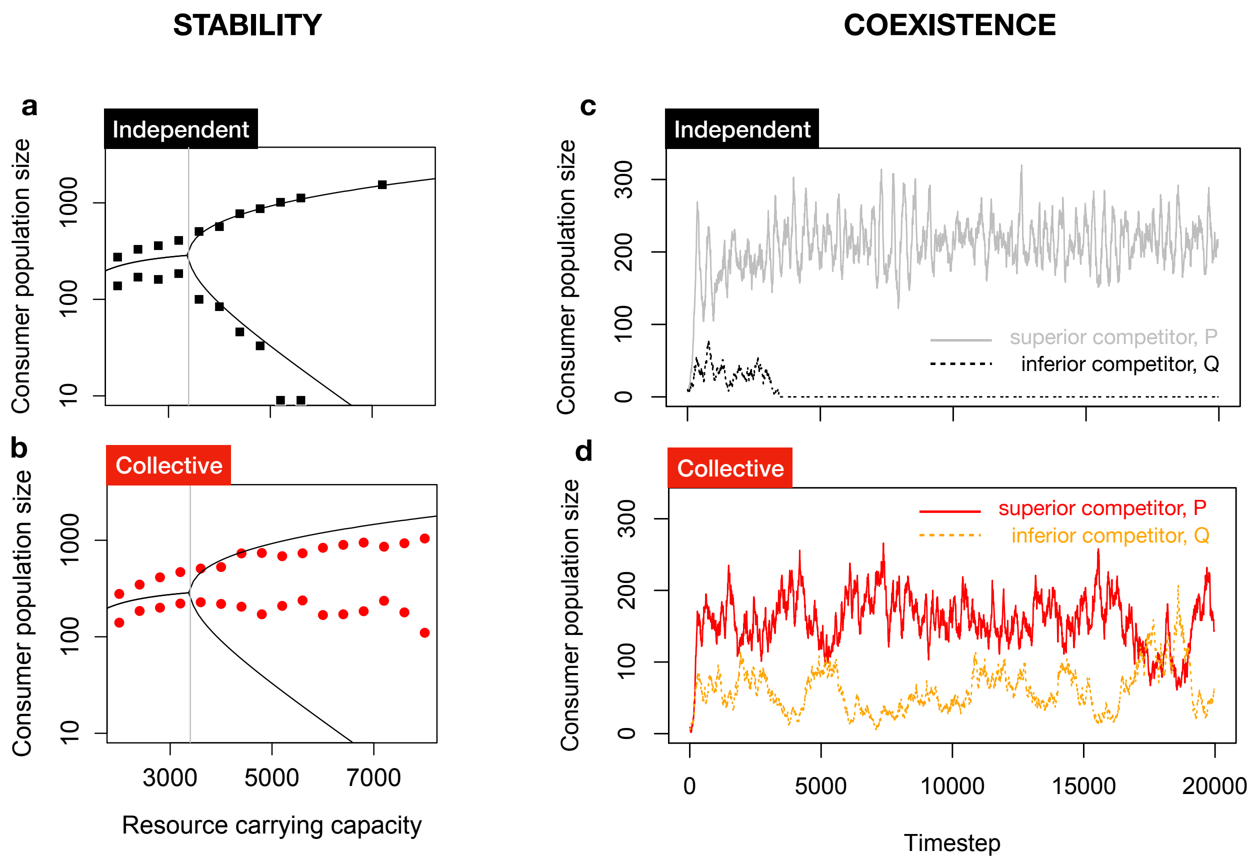

Figure 1: Collective behaviour promotes ecosystem stability and species coexistence. **a,b.** Bifurcation diagram showing how minimum and maximum consumer population sizes respond to increasing resource carrying capacity (K) in numerical solutions of eqn 1 (lines) and in the agent-based model without collective behaviour (a, black squares) versus when collective behaviour is present in the consumer (b, red points). The carrying capacity at which limit cycles are analytically expected (K^*) is shown as a vertical line. Variations in population sizes for $K < K^*$ are due to demographic stochasticity in the agent-based model. **c**. With two consumers, the competitively superior consumer P excludes the inferior consumer Q in the absence of collective behaviour. **d**. With collective behaviour in the consumer, both consumer species persist indefinitely. See Table 1 for simulation parameters.

capture efficiency, $c_Q/c_P < 1$, but is otherwise identical. In the absence of collective behaviour, this results in the exclusion of the inferior competitor—a key feature of the paradox of the plankton[19] and also at the core of ecological[38] and evolutionary[17] theory. The presence of collective behaviour fundamentally changes this outcome, allowing long-term persistence of both consumer species on a single resource (Fig. 1c,d).

Social-ecological feedback The impacts of collective behaviour on ecosystem stability and species coexistence share a common mechanism—an emergent social-ecological feedback loop involving resource encounter rate and the number and size of collective consumer groups.

In populations of independent consumers, per-capita resource encounter rate e is stationary over time and identically distributed across subsets of the population (i.e. $e \sim e_0$ for independents; Extended Data figure 1). However, when consumers form social groups, systematic differences emerge in access to resources, indicated by the fact that resource densities are significantly lower in the vicinities of non-feeding consumers (Extended Data figure 2). This disparity causes a decrease in per-capita resource encounter rate averaged over the consumer population that scales with the number and size of collective groups, attaining the lowest values when the population forms into fewer, larger groups, and the highest values when the population is composed of many small groups (Fig. 2a, Extended Data figure 2, Extended Data figure 3). In collective consumers, ecological dynamics (per-capita resource encounter rate, and thus consumer recruitment) are therefore affected by social conditions (the number and size of social groups).

The social structure of the collective consumer population varies in turn with the abundance

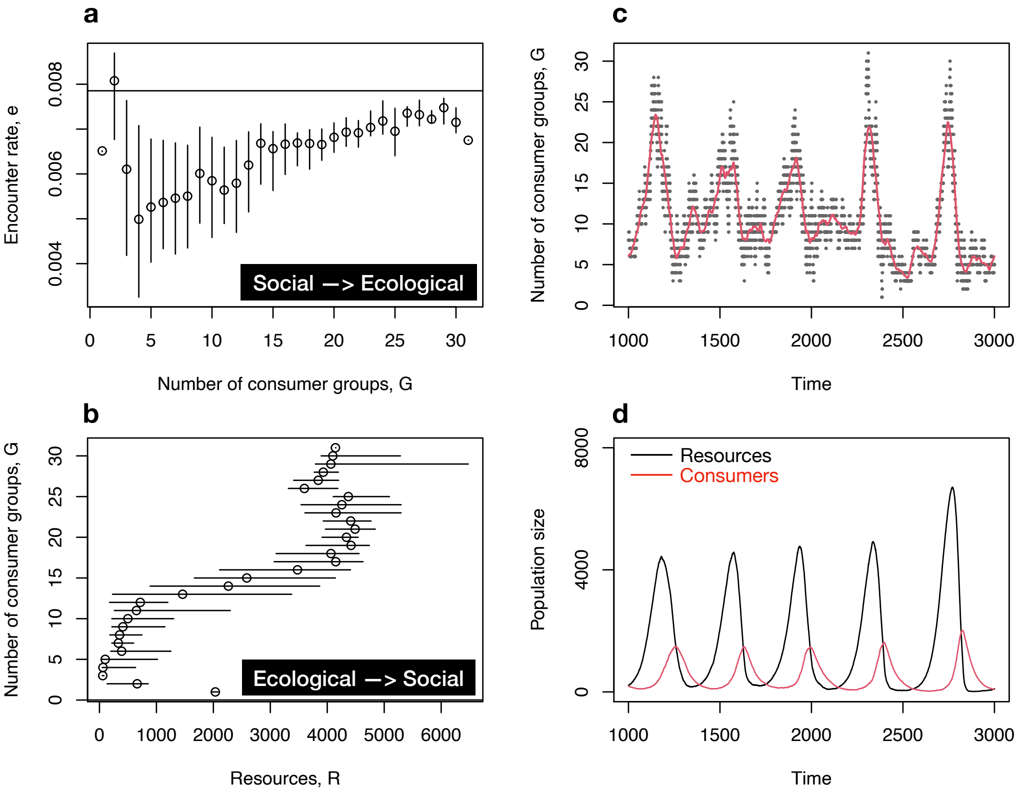

Figure 2: A social-ecological feedback loop stabilizes ecosystems with collective consumers. The system is enriched to $K = 12000$, which would result in extinction for populations of independent individuals (Fig. 1). **a.** With collective consumers, the per-capita encounter rate varies with the number of consumer groups, rather than remaining stationary around e_0 (Extended Data figure 1). **b.** The number of consumer groups varies in turn with the abundance of resources, creating a feedback between resource abundance and consumption beyond what would occur through resource limitation alone. Lines span interquartile ranges. **c.,d.** Concordant cycles in resource abundance and the number of consumer groups. Red line in c shows a rolling average over 10 time units. Similar results are obtained when the timescale for behavioural decisions Δt, the consumer's mortality rate m and its conversion efficiency b are all decreased by a factor of 10, speeding up behaviour and slowing consumer demography by an order of magnitude (Extended Data figure 4).

of resources, indicating that social dynamics are reciprocally affected by ecological conditions. Both the size and number of consumer groups varies with the abundance of resources (fig 2b-d, Extended Data figure 2, Extended Data figure 3). The number and size of groups is determined by the rates of group fusion (when two groups combine to form one), group fission (when one group splits into two) and extinction (when a group of size one goes extinct). We hypothesize that resource abundance affects groups number and size by shifting the balance between rates of group fission and extinction to favor more, smaller groups when resources are abundant (SI). In resource-rich environments, singleton groups are more likely to grow via reproduction before they go extinct, and fast-growing groups are more likely to undergo fission. Consistent with our hypothesis, there are more consumer groups for the same number of consumers when more resources are present (Extended Data figure 5).

To summarize the social-ecological feedback loop, the number and size of collective consumer groups impacts resource uptake (with more efficient uptake when there are many small groups), and resource abundance in turn affects the number and size of collective groups (with more and smaller groups favoured when resources are more abundant). This attenuates population cycles by reducing resource consumption when resources are scarce to a greater degree than would occur with independent consumers via resource limitation alone[39]. By causing systematically higher encounter rates when consumer population sizes become small, this social-ecological feedback also allows the coexistence of collective consumer species where competitive exclusion would otherwise prohibit it (Extended Data figure 1, Fig. 1cd).

An unanticipated result is obtained by fitting a constant effective encounter rate $\bar{e}$ to match the ecosystem model (eqn. 1) to the simulation data, and examining the critical value of resource enrichment at which limit cycles are predicted to begin, K^*. The critical value K^* is inversely proportional to e, so changing the encounter rate changes the level of enrichment at which population cycles are predicted. Without collective behaviour, the effective encounter rate $\bar{e}$ recovers the expected value $\bar{e} \approx e_0$, as required. In this case K^* is invariant to changes in resource enrichment (K). By contrast, in collective consumers the effective encounter rate $\bar{e}$ is tuned to the level of resource enrichment (i.e. $\bar{e} \not\approx e_0$) and K^* thus varies with K. Remarkably, increasing levels of enrichment cause emergent decreases in the effective encounter rate of collective consumers that keep the system at or just below the value of K^* at which destabilizing limit cycles would otherwise begin (Fig 3).

Discussion

We have described ecosystem impacts of collective behaviour driven by emergent hierarchies in access to resources and reproductive opportunities, and thus by general processes associated with complex social groups[40]. These processes are distinct from the stabilizing effects of aggregation which have been previously described[25] in that they involve the emergence of dynamic aggregation patterns tuned to population dynamics via social-ecological feedback (Fig. 2). These respond via collective cognition to changing ecological conditions at other trophic levels (Fig 2,3).

Individuals in our model interact spatially to modulate intra- and inter- specific competition,

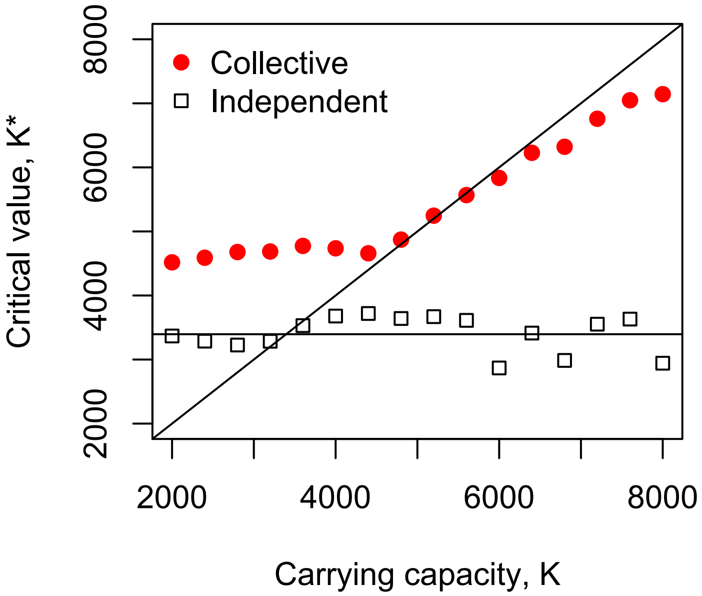

Figure 3: With collective consumers, enrichment is itself associated with an increase in the critical value of enrichment at which population cycles begin (K^*), following approximately $K^* \approx K$ (red dots). In contrast, the bifurcation point is fixed for independent consumers (black squares). The diagonal line is the 1:1 line. The horizontal line shows the theoretical value for K^* derived from eqn 1. At each value of K, an agent-based simulation was run, an effective $\bar{e}$ was calculated from the output, and the squares/circles are the resulting critical $K^*(e)$ when all other parameter values unchanged (eqn. 5 in Methods).

a feature shared in common with other cross-scale ecosystem models, such as the perfect plasticity approximation (PPA[41]) of forest ecosystem dynamics which assumes trees place their canopies to minimize competitive overlap with neighbouring crowns. However, whereas modulation of intra- and inter- specific competition is a hardwired assumption of the PPA, in our model competition modulation is an emergent property of collective behaviour via dynamic adjustments in the size and structure of social groups.

Taken together, our results indicate that the widespread existence of collective behaviour in ecosystems could play a key role in their stability and diversity. Quantifying the mechanisms of interaction between social and trophic dynamics has applications to controlling the spread of infectious diseases[42], managing fisheries[33,43], forecasting coupled biogeochemical cycles[44,45], and predicting the formation, growth and dissolution of human social groups including firms[46] and societies[47]. In its ubiquity, its fundamental impacts on biological systems, and its potential to enhance forecasting, collective behaviour may be an important element of the rules of life.

Methods

Data availability Output from the agent-based simulations are located at www.github.com/BenjaminDalziel/colle ecosystems

Code availability Simulation code and scripts for statistical analysis are located at www.github.com/BenjaminDal ecosystems

Agent-based simulation The position $\mathbf{x}_i$ of individual i changes over time according to

$$\mathbf{x}_i(t + \Delta t) = \mathbf{x}_i + s\mathbf{v}_i(t) \tag{2}$$

where s represents scalar speed and $\mathbf{v}_i$ velocity (direction of movement), scaled each time step to have unit magnitude. Velocity evolves according to

$$\mathbf{v}_i(t + \Delta t) = \langle \mathbf{v} \rangle_i(t) + \eta \mathbf{z}(t) \tag{3}$$

where $\langle \mathbf{v} \rangle_i$ represents expected resultant velocity (described below), η is a scalar noise parameter and $\mathbf{z}(t)$ is a random variable drawn from a standard bivariate normal distribution (zero mean, unit variance in each coordinate).

An individual's expected resultant velocity $\langle \mathbf{v} \rangle_i$ is affected by its current velocity and possibly by the positions and velocities of its conspecific neighbors. When collective behaviour is absent, $\langle \mathbf{v} \rangle_i(t) = \mathbf{v}_i(t)$ and so $\mathbf{v}_i(t + \Delta t) = \mathbf{v}_i(t) + \eta \mathbf{z}(t)$. When collective behaviour occurs, $\langle \mathbf{v} \rangle_i(t)$ is influenced by social interactions as each individual avoids collisions, move towards, and aligns with its conspecific neighbors according to the Couzin model[36,37]. We tracked the resulting collective groups by assigning conspecific individuals to the same group if and only if they interacted behaviourally during a given time step, with individuals assigned to their own group by definition. To track groups computationally we used an adaption of methods for equivalence classes[36,48].

Because species capable of conspecific behavioural responses will likely also respond to nearby resources or predation risk, we also investigated behavioural responses between consumer and resource individuals (regardless of whether collective behaviour is active) by including pursuit and avoidance terms in $\langle v \rangle_i$. In these simulations, consumers turn toward resource individuals in their local neighborhood, while resource individuals orient away from consumers (SI).

At each time step of length Δt, each resource individual reproduces with probability $r\left(1-\frac{R}{K}\right)\Delta t$, and each consumer individual dies with probability $m\Delta t$. If a resource individual is within a distance ρ of a consumer who is not in the handling state from a previous consumption event, the resource is captured with probability $c_j\Delta t$. Handling consumers become eligible for consumption with probability $h^{-1}\Delta t$.

Crucially, the landscape is large and behaviour is fast, relative to lifespan of a consumer (50 time units; Table 1): moving in a straight line, it would take a consumer approximately their entire lifespan to cross the arena diagonally and the periodicity of consumer-resource cycles is approximately 6 consumer lifetimes. Similar results to those shown in Fig 2 are obtained when the timescale for behavioural decisions Δt, consumer mortality rate m and conversion efficiency b are all decreased by a factor of 10, thus speeding up behaviour and slowing consumer demography by an order of magnitude, suggesting these results do not depend on the ratio of timescales between behavioural and ecological processes (Extended Data figure 3). Table 1 shows simulation parameters used in the main text. Sensitivity analysis, full computer code and simulation output is provided in the SI.

Encounter rate In model (1) the encounter rate e in the functional responses f represents the instantaneous per-capita hazard that a random consumer individual and a random resource individual will be separated by a distance of less than ρ. The encounter rate is a constant in the canonical ecosystem model represented by eqn 1, which assumes random mixing, implying that conspecifics behave independently from one another. In this case the value of e is constant, given by $e_0 = \pi\rho^2/L^2$. With collective behaviour, we demonstrate that e varies predictably with the number of collective groups. Finally, we fit a constant effective encounter rate $\bar{e}$ to simulation data with collective behaviour active, representing the best constant encounter rate to capture the dynamics of the ecosystem model with collective behaviour using methods described below.

The critical level of enrichment K^* at which limit cycles arise in model (1) through a Hopf bifurcation depends on the value of e. From the standard analysis of the Rosenzweig-MacArthur model we know that as enrichment is varied, the bifurcation occurs when the predator nullcline intersects the peak of the prey nullcline. This happens at the K^* that satisfies

$$eK^* = \frac{1}{c}\left(\frac{1}{h} + \frac{2m}{b - hm}\right) \tag{4}$$

Analysis of agent-based simulations Encounter rate is estimated from the agent-based simulation as

$$e_j = \frac{1}{RC_j}\sum_i n_{ij} \tag{5}$$

where n_{ij} is number of resource individuals in range of the ith consumer individual of type j, C_j is the abundance of that type, and R is the abundance of the resource.

We estimated per-capita recruitment rate $\frac{1}{C_j}\frac{dC_j}{dt}$ from the (discrete-time) abundances in the agent-based simulation using $\frac{1}{C_j}\frac{dC_j}{dt} = \frac{d}{dt}\log C_j \approx \frac{\Delta y}{\Delta t}$ where $y = \log C_j$ observed from the agent-based simulation.

We estimate effective encounter rate under collective behaviour, $\bar{e}$, by fitting the analytical model to abundance time series from the agent-based simulation, with all parameters fixed to their true values except for e. Specifically, we choose $\bar{e}$ to minimize the loss function

$$h^2(\bar{e}) = (\mu_x - \mu_{\hat{x}})^2 + (\mu_y - \mu_{\hat{y}})^2 + (\sigma_x - \sigma_{\hat{x}})^2 + (\sigma_y - \sigma_{\hat{y}})^2 \tag{6}$$

where the observed values $x = \log(R)$ and $y = \log(C_j) = \log(P)$ are from the simulation, $\hat{x}$ and $\hat{y}$ refer to the corresponding values predicted by eqn 1 using $\bar{e}$ instead of e, and μ and σ represent means and standard deviation over time. We used the *optimize()* function in R to search for the value of $\bar{e}$ that minimized h on the interval $(0.25e_0, 1.5e_0)$.

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Table 1: Simulation parameters used in main text

Parameter	Value	Interpretation
R(0)	1000	Initial resource population size
P(0)	100	Initial consumer population size - stability experiments
P(0)	10	Initial superior consumer population size - coexistence experiments
Q(0)	10	Initial inferior consumer population size - coexistence experiments
Δt	0.1	Time step
r	0.03	Maximum per-capita rate of increase in resource population
K	2000-8000	Carrying capacity - stability experiments
K	2000	Carrying capacity - coexistence experiments
K^*	3395.305	Value of K where limit cycles begin given c_P, h, b, m, ρ and L
ρ	5	Radius of attraction, alignment and resource encounter
ρ_0	1	Radius at which collision avoidance is triggered
$\Delta\theta_{max}$	1	Maximum turn rate in radians
c_P	0.015	Probability per unit time of capture given encounter for the superior consumer
c_Q	0.0135	Probability per unit time of capture given encounter for the inferior consumer
c_Q/c_P	0.9	Relative capture efficiency of the inferior consumer
b	0.3	Probability that a resource consumption event will produce a new consumer
m	0.02	Consumer mortality rate. Mean consumer lifespan $= 1/m$
h	5	Consumer handling time
s_C	3	Speed of consumer individuals
s_R	1	Speed of resource individuals
η	1	Noise in consumer and resource velocities
L	100	Arena length