



Collective behaviour can stabilize ecosystems

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Collective behaviour is common in bacteria, plants and animals, and therefore occurs across ecosystems, from biofilms to cities. With collective behaviour, social interactions among individuals propagate to affect the behaviour of groups, whereas group-level responses in turn affect individual behaviour. These cross-scale feedback loops between individuals, populations and their environments can provide fitness benefits, such as the efficient exploitation of uncertain resources, as well as costs, such as increased resource competition. Although the social mechanics of collective behaviour are increasingly well-studied, its role in ecosystems remains poorly understood. 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. 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 part in the maintenance of biodiversity.

The mechanisms that underpin ecosystem stability and species coexistence are well-studied, but not yet well-understood^{1–3}. 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^{4–7} and (ii) competition among species for limited resources, which promotes diversity loss via competitive exclusion^{8–10}. The challenges to stability and coexistence can be summarized by two ecological ‘paradoxes’: the paradox of enrichment⁴ addresses the prevalence of conditions that should result in the destabilization of population oscillations, and the paradox of the plankton¹⁰ addresses the longstanding puzzle of how diverse ecological communities can persist although many ecologically similar species are competing for a limited range of resources^{3,9,11}. Stability and coexistence are hypothesized to rely on countervailing processes that attenuate population cycles^{12–14} and that give each species a positive population growth rate whenever their abundance becomes low^{1,3,11}.

Spatial and temporal heterogeneities in species abundance and recruitment play a key part in determining stability and coexistence. When local conditions experienced by individuals differ systematically from their population averages, the ecological impacts of hotspots (for example, 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^{15,16}. In many cases, the spatiotemporal structure promotes stability and coexistence, whereas homogeneous environments tend to be less stable¹⁶.

Although the spatiotemporal structure of the ecosystem is obviously affected by exogenous drivers such as ocean currents, rainfall patterns or habitat fragmentation, collective behaviour generates spatiotemporal patterns that modify the effects of exogenous drivers, as seen in swarms of insects¹⁷, schools of fish¹⁸ or migrating flocks¹⁹ and herds^{20,21}. 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 Serengeti²².

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^{18,23}. For example, locust swarms emerge at critical densities when locust populations transition to collective motion²⁴. The ecosystem state therefore has a key role in the regulation of collective behaviour, and collective behaviour can in turn affect ecosystem states. However, the consequences of feedback between collective behaviour and ecosystem dynamics remain largely unexplored^{25–28}.

Here we demonstrate the ecological potential of this feedback by adding collective behaviour to a simple food-web model^{29,30}, focusing on the particularly common and well-studied case of collective movement¹⁷. Our results show that collective behaviour fundamentally alters the 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 that is inherent to the consumption of resources 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:

$$\begin{aligned}\frac{dP}{dt} &= b f_P(R)P - mP \\ \frac{dQ}{dt} &= b f_Q(R)Q - mQ \\ \frac{dR}{dt} &= rR(1 - \frac{R}{K}) - f_P(R)P - f_Q(R)Q\end{aligned}\quad (1)$$

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, respectively (Table 1). The per capita resource consumption rate of consumer

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Table 1 | Simulation parameters used in the main text

Parameter	Value	Interpretation
$R(0)$	1,000	Initial resource population size
$P(0)$	100	Initial consumer population size for the stability experiments
$P(0)$	10	Initial superior consumer population size for the coexistence experiments
$Q(0)$	10	Initial inferior consumer population size for the coexistence experiments
Δt	0.1	Time step
r	0.03	Maximum per capita rate of increase in the resource population
K	2,000–8,000	Carrying capacity for the stability experiments
K	2,000	Carrying capacity for the coexistence experiments
K^*	3,395.305	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

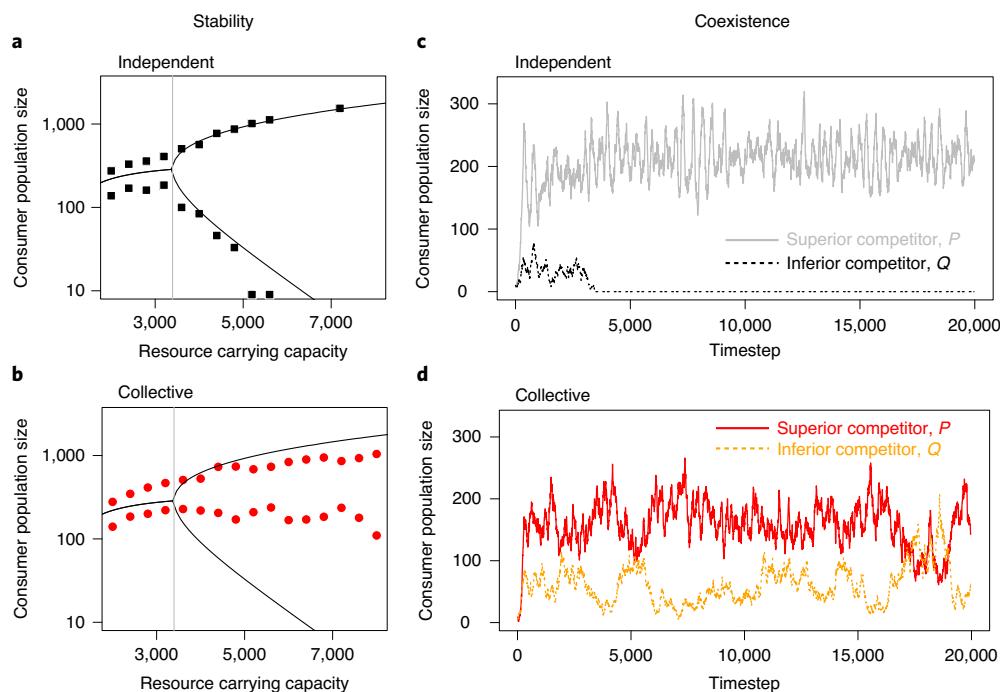


Fig. 1 | Collective behaviour promotes ecosystem stability and species coexistence. **a,b**, Bifurcation diagram showing how minimum and maximum consumer population sizes respond to increasing resource carrying capacity (K) in numerical solutions of equation (1) (lines) and in the agent-based model without collective behaviour (**a**; black squares) compared with 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.

j is given by its functional response $f_j(R) = a_j R / (1 + a_j h R)$, where h is the handling time and $a_j = e c_j$ 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^{3,4}.

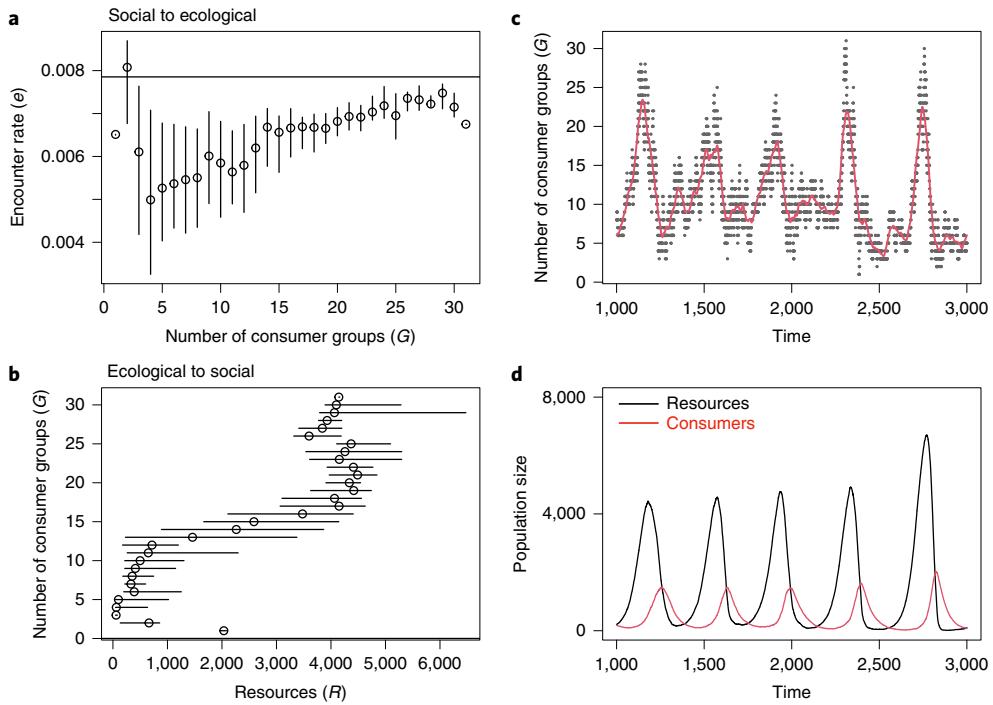


Fig. 2 | A social-ecological feedback loop stabilizes ecosystems with collective consumers. The system is enriched to $K=12,000$, which would result in the extinction of populations of independent individuals (Fig. 1). **a**, The social to ecological component of the feedback loop: with collective consumers, the per capita encounter rate varies with the number of consumer groups, rather than remaining stationary around e_0 , denoted by the horizontal line (Extended Data Fig. 1). **b**, The ecological to social component of the feedback loop: the number of consumer groups varies in turn with the abundance of resources, creating a feedback loop between resource abundance and consumption beyond what would occur through resource limitation alone. Lines span interquartile ranges. **c**, Cycles in the number of consumer groups over time. **d**, Concordant cycles in resource abundance. The 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 Fig. 4).

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 that 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, and moves towards and aligns with its conspecific neighbours (within a distance ρ) according to a well-studied model of collective movement^{31,32}.

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 the resource carrying capacity (K) causes consumer and resource populations to oscillate with increasing amplitude (Fig. 1a). By contrast, these limit cycles are attenuated with collective behaviour in the consumer (Fig. 1b), or in both the consumer and the resource (Supplementary Information), 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 the coexistence of species by simulating exploitative competition between a superior consumer (P) and an inferior one (Q) that has a lower 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 plankton¹⁰ and also at the core of ecological³³ and evolutionary⁸ theory. The presence of collective behaviour fundamentally changes this outcome, enabling the long-term persistence of both consumer species using 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 that involves the resource encounter rate as well as the number and size of the collective consumer groups.

In populations of independent consumers, the per capita resource encounter rate e is stationary over time and identically distributed across subsets of the population (that is $e \sim e_0$ for independents) (Extended Data Fig. 1). However, when consumers form social groups, systematic differences emerge in the access to resources, indicated by the fact that resource densities are lower in the vicinities of non-feeding consumers (Extended Data Fig. 2). This disparity causes a decrease in the 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

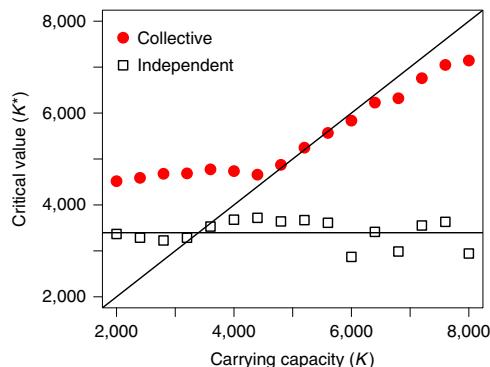


Fig. 3 | With collective consumers, enriching the system increases the critical value of enrichment at which population cycles begin (K^*), following approximately $K^* \approx K$. By contrast, the critical point is fixed for independent consumers (black squares). The diagonal line is the 1:1 line; red dots show $K^* \approx K$. The horizontal line shows the theoretical value for K^* derived from equation (1). At each value of K , an agent-based simulation was run, an effective \bar{e} was calculated from the output, and the squares and circles are the resulting critical $K^*(\bar{e})$ when all other parameter values remain unchanged (equation (5) in the Methods).

when the population is composed of many small groups (Fig. 1a and Extended Data Figs. 2 and 3). In collective consumers, ecological dynamics (per capita resource encounter rate and, therefore, 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 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 and Extended Data Figs. 2 and 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 the number and size of groups by shifting the balance between rates of group fission and extinction to favour more smaller groups when resources are abundant (Supplementary Information). 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 Fig. 5).

To summarize the social–ecological feedback loop, the number and size of collective consumer groups affects 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 through resource limitation alone³⁴ (Extended Data Fig. 6). 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 (Fig. 1c,d and Extended Data Fig. 1).

An unanticipated result is obtained by fitting a constant effective encounter rate \bar{e} to match the ecosystem model (equation (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 popula-

tion 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 the resource enrichment (K). By contrast, in collective consumers, the effective encounter rate \bar{e} is tuned to the level of resource enrichment (that is $\bar{e} \neq e_0$) 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 describe the 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 groups³⁵. These processes are distinct from the stabilizing effects of aggregation that have previously been described¹⁶ in that they involve the emergence of dynamic aggregation patterns that are tuned to population dynamics through social–ecological feedback (Fig. 2). These feedback loops respond through collective cognition to changing ecological conditions at other trophic levels (Figs. 2 and 3 and Extended Data Figs. 7–9).

Individuals in our model interact spatially to modulate intra- and interspecific competition, a feature that is shared with other cross-scale ecosystem models, such as the perfect plasticity approximation³⁶ of forest ecosystem dynamics, which assumes that trees place their canopies to minimize competitive overlap with neighbouring crowns. However, whereas the modulation of intra- and interspecific competition is a hardwired assumption of the perfect plasticity approximation, in our model competition modulation is an emergent property of collective behaviour through the 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 have 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 diseases³⁷, managing fisheries^{28,38}, forecasting coupled biogeochemical cycles^{39,40} and predicting the formation, growth and dissolution of human social groups including firms⁴¹ and societies⁴². 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

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

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

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

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

where $\langle \mathbf{v} \rangle_i$ represents the 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 neighbours. 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, and moves towards and aligns with its conspecific neighbours according to the Couzin model^{31,32}. 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^{31,43}.

Because species capable of conspecific behavioural responses will probably 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 $\langle \mathbf{v} \rangle_i$. In these simulations, consumers turn toward resource individuals in their local

neighbourhood, whereas resource individuals orient away from consumers (Supplementary Information).

At each time step of length Δt , each resource individual reproduces with probability $r(1 - \frac{\bar{R}}{K})\Delta t$, 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 $h^{-1}\Delta t$.

Importantly, the landscape is large and behaviour is fast, relative to the 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 six 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, which suggests that these results do not depend on the ratio of timescales between behavioural and ecological processes (Extended Data Fig. 3). Table 1 shows the simulation parameters used in the main text. A sensitivity analysis, the full computer code and simulation output are provided in the Supplementary Information.

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 equation (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 in which the collective behaviour is active, representing the best constant encounter rate to capture the dynamics of the ecosystem model with collective behaviour using the 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

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

Analysis of agent-based simulations. The encounter rate is estimated from the agent-based simulation as

$$e_j = \frac{1}{RC_j} \sum_i n_{ij} \quad (5)$$

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

We estimated the 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 the effective encounter rate under collective behaviour, \bar{e} , by fitting the analytical model to the 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

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

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 equation (1) using \bar{e} instead of e , and μ and σ represent the mean and s.d. over time. We used the `optimize()` function in R to search for the value of \bar{e} that minimized h in the interval $(0.25e_0, 1.5e_0)$.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

Output from the agent-based simulations can be found on GitHub (<https://github.com/BenjaminDalziel/collectives-ecosystems>) and Zenodo (<https://zenodo.org/record/4925028>).

Code availability

Simulation code and scripts for statistical analysis can be found on GitHub (<https://www.github.com/BenjaminDalziel/collectives-ecosystems>) and Zenodo (<https://zenodo.org/record/4925028>).

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Author contributions

B.D.D. conceived the work, analysed the data and drafted the manuscript. B.D.D., M.N., J.R.W. and S.P.E. interpreted the data and revised the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

Extended data is available for this paper at <https://doi.org/10.1038/s41559-021-01517-w>.

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1038/s41559-021-01517-w>.

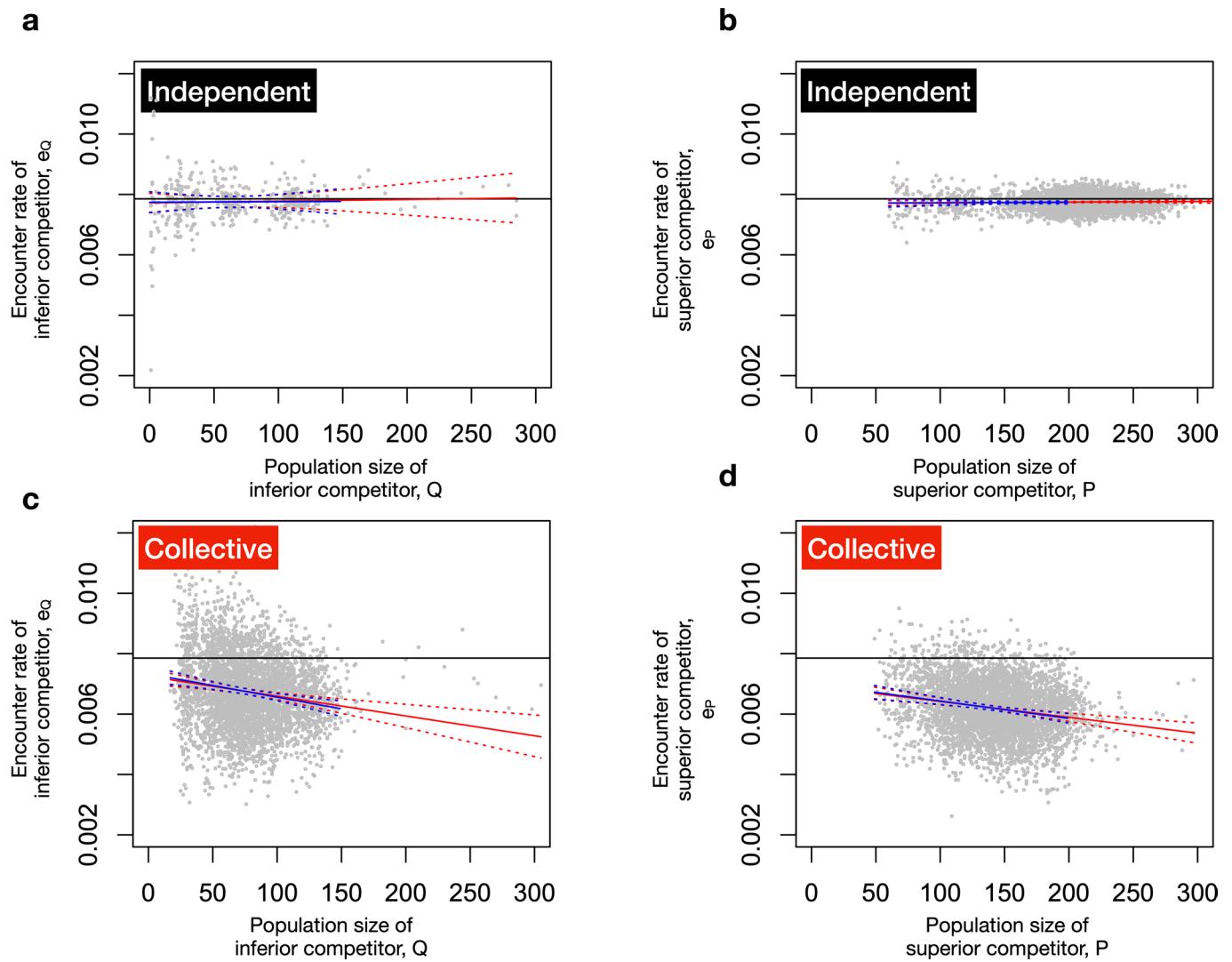
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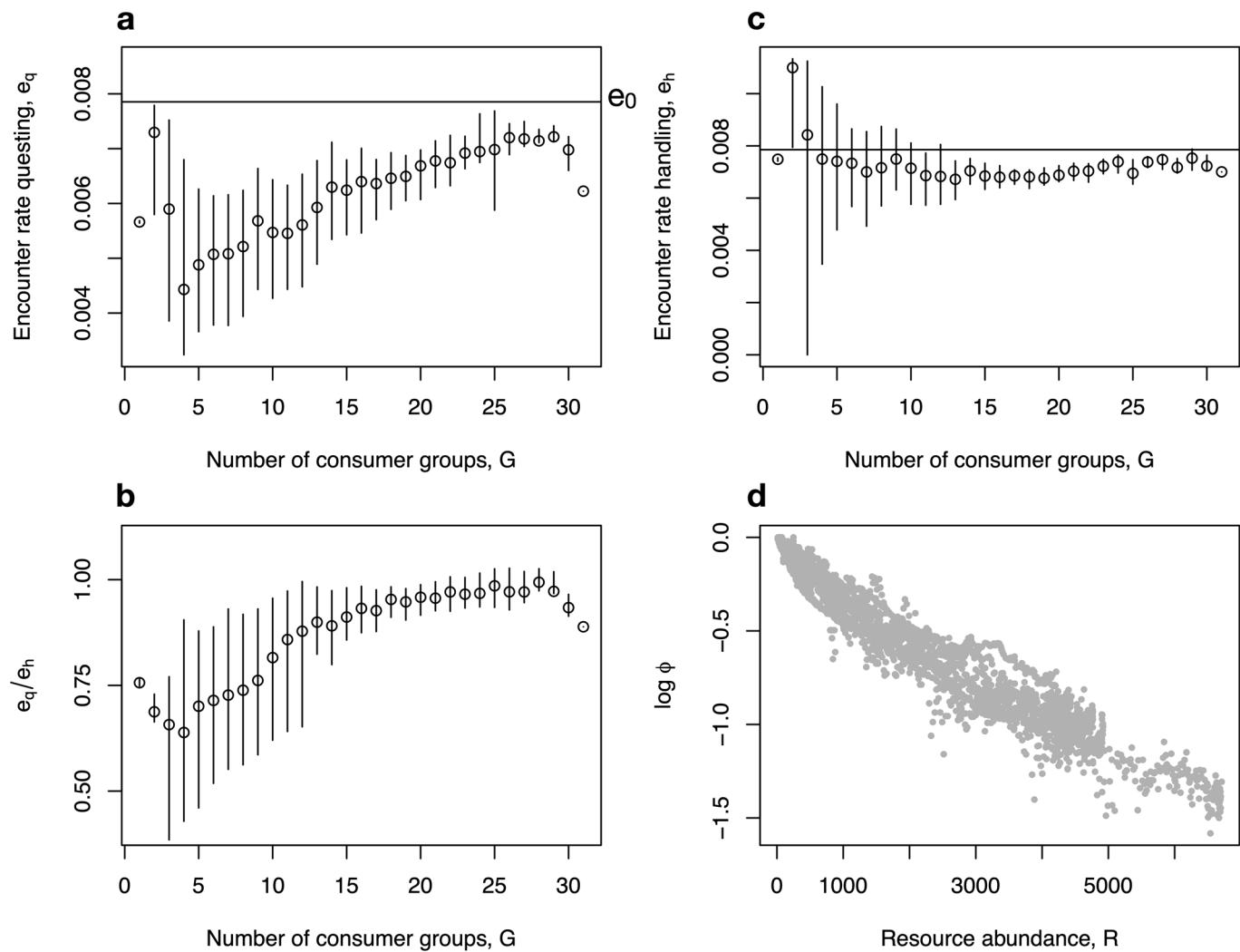
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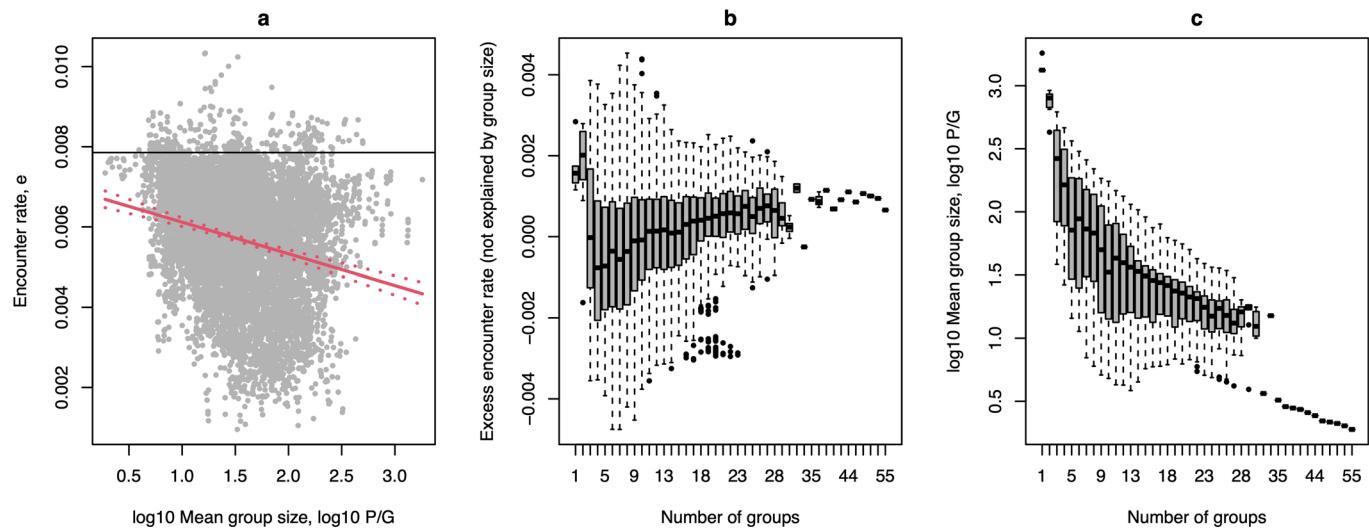
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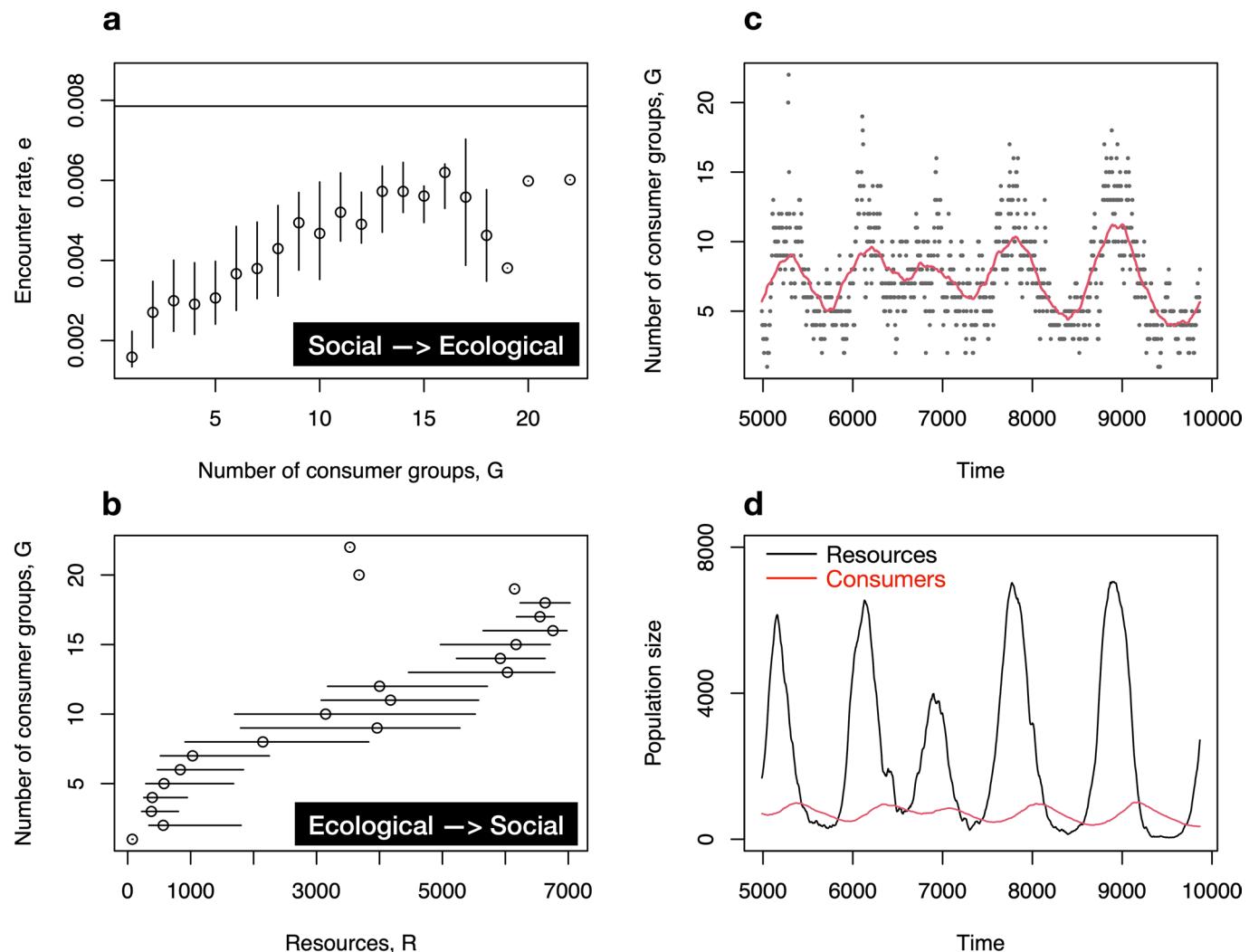
Extended Data Fig. 1 | Negative density dependence in resource encounter rates promotes coexistence in collective consumers, reversing canonical competitive exclusion. Solid lines show linear fits. Blue lines show fits that omit outlying abundances driven by initial conditions. Dashed lines enclose 5 standard errors on either side of lines of best fit. For independent consumers (top row), encounter rates remain near the expected value of e_0 (black horizontal line). For collective consumers, mean encounter rate is lower and decreases with increasing abundance. Simulation parameters are given in Table 1.



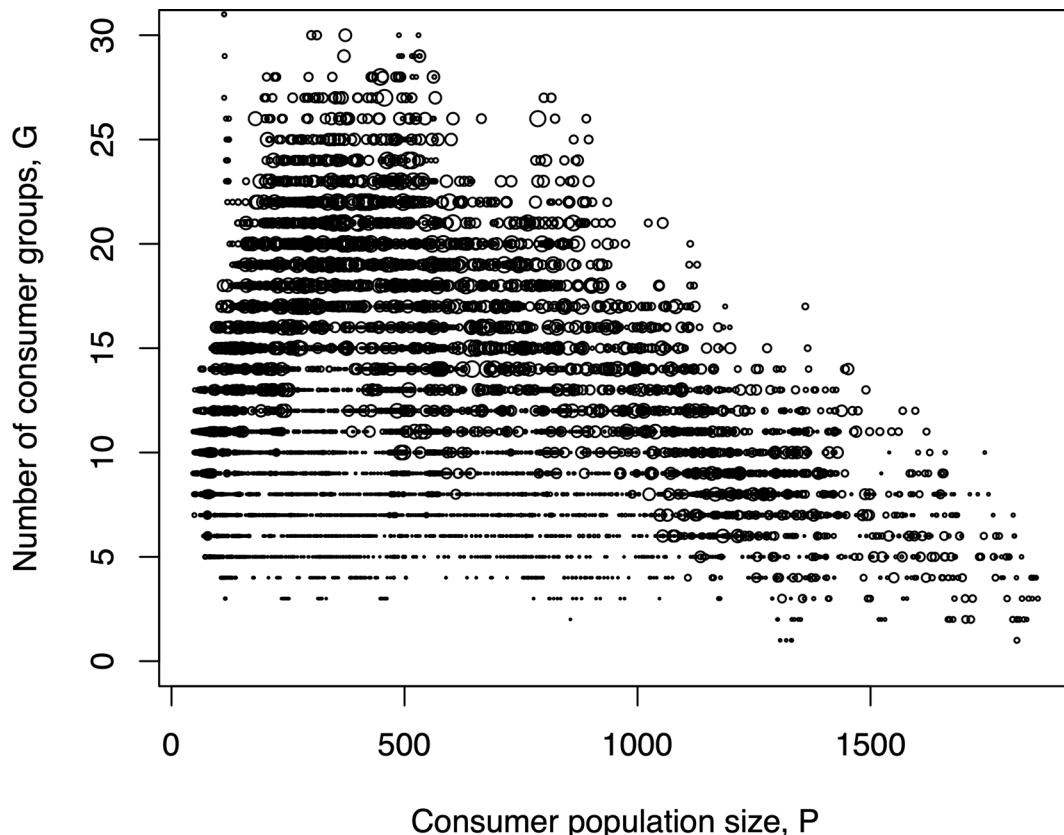
Extended Data Fig. 2 | Systematic differences in access to resources in collective consumers dependent on group structure and resource abundance. **a** The per-capita encounter rate of questing consumers is positively correlated with the number of consumer groups. **b-c** The per-capita encounter rate of handling consumers is less strongly correlated with the number of groups, so questing consumers are more strongly disadvantaged when the consumer population forms into fewer groups. **d** The fraction of the consumer population questing varies with resource abundance as $\phi \sim e^{-\kappa R}$ where κ is a scaling parameter.



Extended Data Fig. 3 | Encounter rate depends on both the average size and number of collective groups. **a** Solid line shows best fit via linear regression, dashed lines enclose ± 5 standard errors. **b** Residual variation in encounter rate as a function of the number of groups. **c** The average size of groups is inversely correlated with the number of groups.



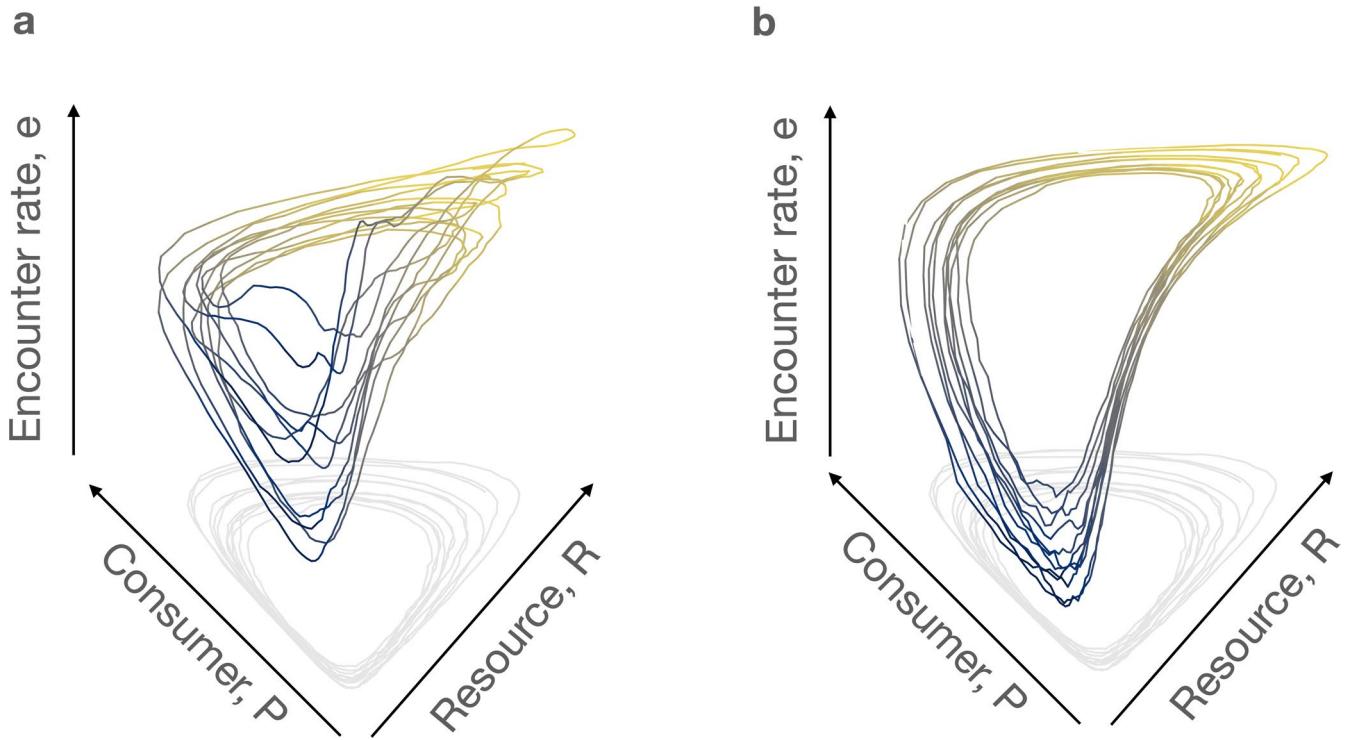
Extended Data Fig. 4 | A social-ecological feedback loop stabilizes ecosystems with collective consumers. Results analogous to those shown in Fig. 2 but with the timescale for behavioural decisions δ , consumer mortality rate m and conversion efficiency b all decreased by a factor of 10, relative to their values shown in Table 1.



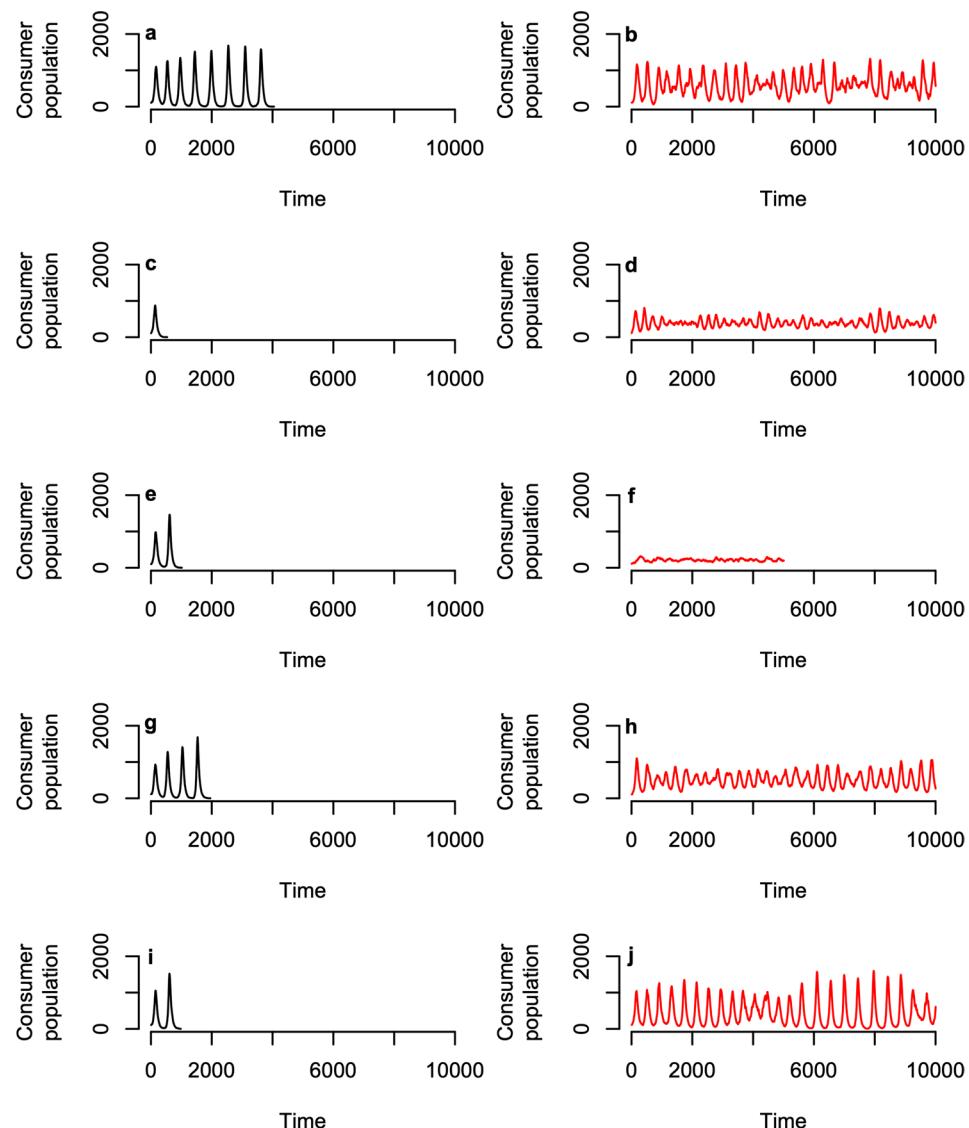
Extended Data Fig. 5 | Resource abundance affects the relationship between consumer population size and the number of consumer groups. There are more consumer groups for the same number of consumers when more resources are present. Point size is proportional to resource abundance.

SIMULATION DATA

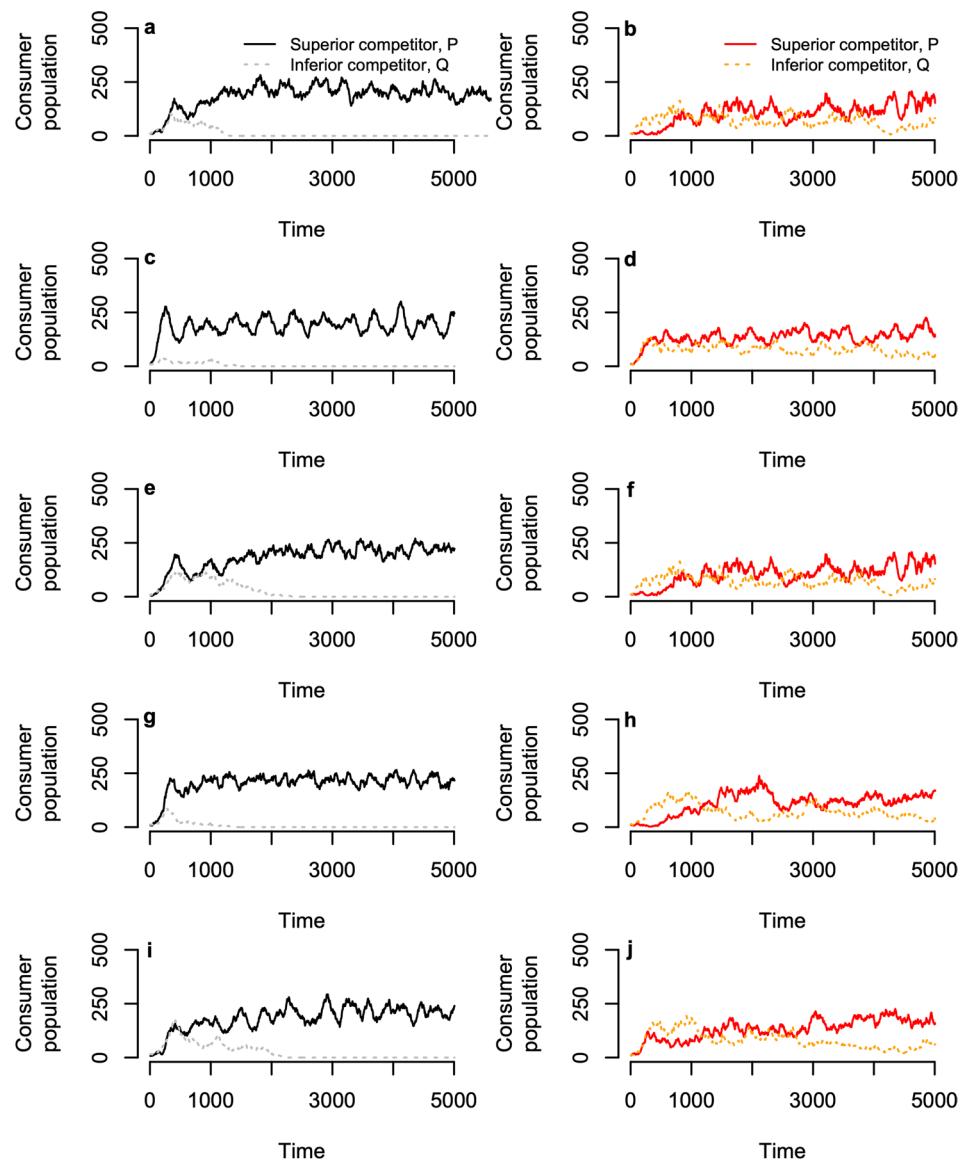
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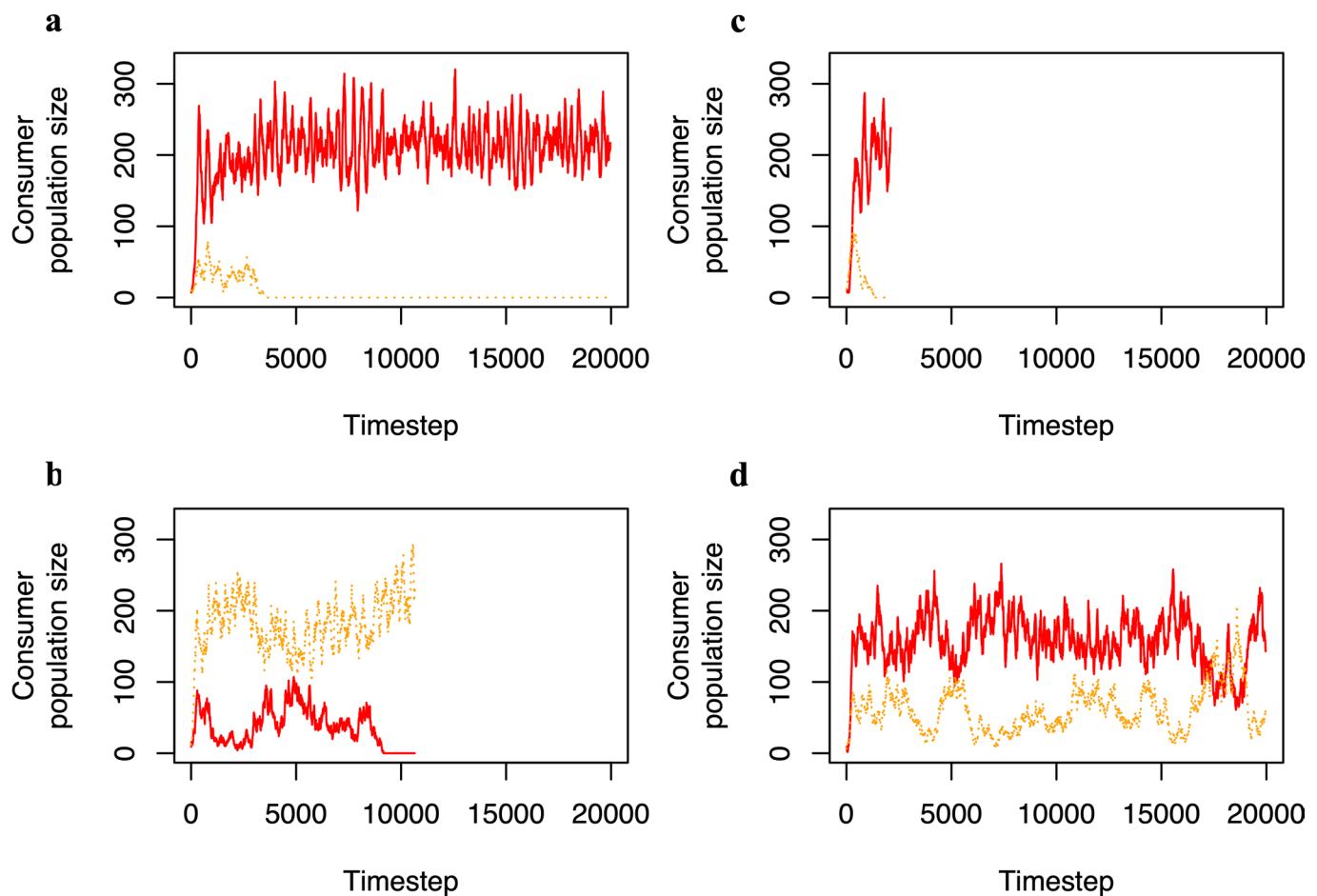
Extended Data Fig. 6 | Phase portraits of the one-consumer resource system with per-capita encounter rate viewed as a state variable. **a** Data from the individual-based simulation with $K = 8000$ and the rest of the parameters at the values specified in Table 1, with encounter rate calculated using eqn. (5). **b** The same data, but replacing observed encounter rate with a Monod function $e(R) = e_0 R / (R + g)$ where R is taken from the simulation data and the parameter $g = 250$ expresses the strength of the net impact of collective behaviour on encounter rate, as the resource abundance at which encounter rate is half its maximum value. Encounter rates shown are smoothed with a moving average with a bandwidth of 5 time units.



Extended Data Fig. 7 | Collective behaviour promotes ecosystem stability in a range of contexts. Stability results analogous to Fig. 1a,b with independent consumers in black and collective consumers in red for **a,b** collective resource, **c,d** pursuit and avoidance behaviours, **e,f**, alignment only, **g,h** low noise, and **i,j**, high noise. See Sensitivity Analysis in Supplementary Information.



Extended Data Fig. 8 | Collective behaviour promotes ecosystem species coexistence in a range of contexts. Coexistence results analogous to Fig. 1c,d with independent consumers in black and collective consumers in red for **a,b** collective resource, **c,d** pursuit and avoidance behaviours, **e,f**, alignment only, **g,h** low noise, and **i,j**, high noise. See Sensitivity Analysis in Supplementary Information.



Extended Data Fig. 9 | Coexistence results when one of the competing consumers may behave independently while the other exhibits collective behaviour. **a** both consumers independent; **b** superior consumer behaves collectively, inferior consumer independent; **c** superior consumer independent, inferior consumer behaves collectively; **d** both collective. The relative capture efficiency of the inferior consumer is 0.9 (Table 1).

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Data collection Agent based simulations were done in the Unity development environment version 2019.4.15f1 (unity.com).

Data analysis Data analysis was done in R version 4.0.4 (r-project.org)

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

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Data exclusions	No data were excluded from analysis
Reproducibility	Code that reproduces the simulations and analyses are available at www.github.com/BenjaminDalziel/collectives-ecosystems .
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