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Supplementary information

Collective behaviour can stabilize ecosystems

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Social-ecological dynamics Resource encounter rate can be decomposed by the status of consumers—either questing for resources or handling a resource item—as

$$e = (1 - \phi)e_q + \phi e_h \tag{7}$$

where ϕ is the proportion of the consumer population that is currently handling and e_q and e_h are the mean encounter rates among questing and handling consumers. Under random mixing, encounter rate does not vary systematically between the questing and handling subsets of the consumer population. However, when the consumer population forms social groups, systematic differences in access to resources emerge, evidenced by the questing consumer population having a systematically lower encounter rate than the handling subset, i.e., $e_q < e_h$ (Extended Data figure 2). This systematic disparity in access to resources is minimized when the population is composed of many small groups. In addition, encounter rate e is more strongly affected by the systematic disparity in access to resources as they become scarce (and thus ϕ approaches 0).

The number of groups at a particular time reflects a balance between the propensities of three processes: fission (one group splits into two); fusion (two groups combine to form one); and extinction (a singleton group goes extinct). We hypothesize that in resource-rich environments, fast-growing groups are more likely to undergo fission and that the likelihood that singleton groups will go extinct before they grow via reproduction is reduced. The net result is an increase in the equilibrium number of consumer groups when resources are abundant. Consistent with this hypothesis, our simulations show more consumer groups for the same number of consumers when more resources are present (Extended Data figure 5). We focus more on the number of groups G rather than mean group size P/G as a measure of fluctuating social structure because the former is less directly tied to the abundance of consumers. (Mean group size (P/G) is inversely proportional to the number of groups (S3).)

The feedback between resource abundance and per-capita encounter rate mediated by the number and size of consumer groups can be viewed through a phase portrait in state space, considering encounter rate as a third state variable, along with consumer and resource population sizes (Extended Data figure 6, left panel). When viewed this way, a Monod function provides a phenomenological model of the relationship between resources and encounter rate that approximates the emergent pattern in the simulations

$$e(R) = e_0 \frac{R}{R + g} \tag{8}$$

where g captures the net impact of consumer collective behavior on encounter rate (Extended Data figure 6, right panel). Adding this expression for $e(R)$ to model (1) has recently been shown to be stabilizing under enrichment[39]. To the extent that this phenomenological model is an accurate approximation for the net impacts of consumer collective behaviour on resource uptake, the ecosystem impacts of collective behaviour we describe will hold under a different timescale separations for behavioral and ecological interactions, and are robust to variations in the details of the underlying behavioural rulesets.

Sensitivity analysis We confirmed that the stability and coexistence results described in the main text continue to hold under the following modifications: including collective behaviour in the resource species as well as the consumer; including predators moving in pursuit of prey, and prey moving to avoid predators (see Methods); using an alternative, simpler, model of collective movement[29] featuring alignment only (i.e. individuals do not attempt to move toward each other or avoid collisions); and under varying levels of random noise in individual movement decisions (using high turn rate to allow more influence of noise). With pursuit behaviours, predators turn to move toward prey within the radius of interaction, demonstrating the same aggregation behaviour as if the prey were conspecific predators in the Couzin model. Similarly, with avoidance behaviour, prey turn away from predators in the same manner as the conspecific avoidance behaviours in the Couzin model. For low noise simulations $\eta = 0$, for high noise simulations $\eta = 10$, the high maximum turn rate value was $\Delta\theta_{max} = 4$. Results of these simulations are shown in Figures S7 and S8. While there are many possible modifications of the behavioral rules that could change the results, our results indicate that complex behavioural models are not required to generate the social-ecological feedback we describe; simple models, which have been widely applied to understand collective behaviour in natural populations, predict significant impacts of collective behaviour on ecosystem stability. However, more realistic behavioral rules, such as individuals reducing their sociality when starving, may reduce the feedbacks described here.

Our results have shown that collective behavior may drive coexistence, but the processes that drive the evolution and maintenance of collective behaviour remain an area of open research[32]. With this in mind we performed the coexistence experiments where one of the competing consumers behaved independently and the other exhibited collective behaviour. In our model, collective behaviour was required in both consumers in order to achieve coexistence (Figure S9). When the superior competitor behaved independently, the inferior competitor could not persist, regardless of whether or not the inferior competitor displayed collective behaviour. Independent inferior competitors dominated superior competitors who behaved collectively.