The complexity of the commons: Scientists recast social dilemmas

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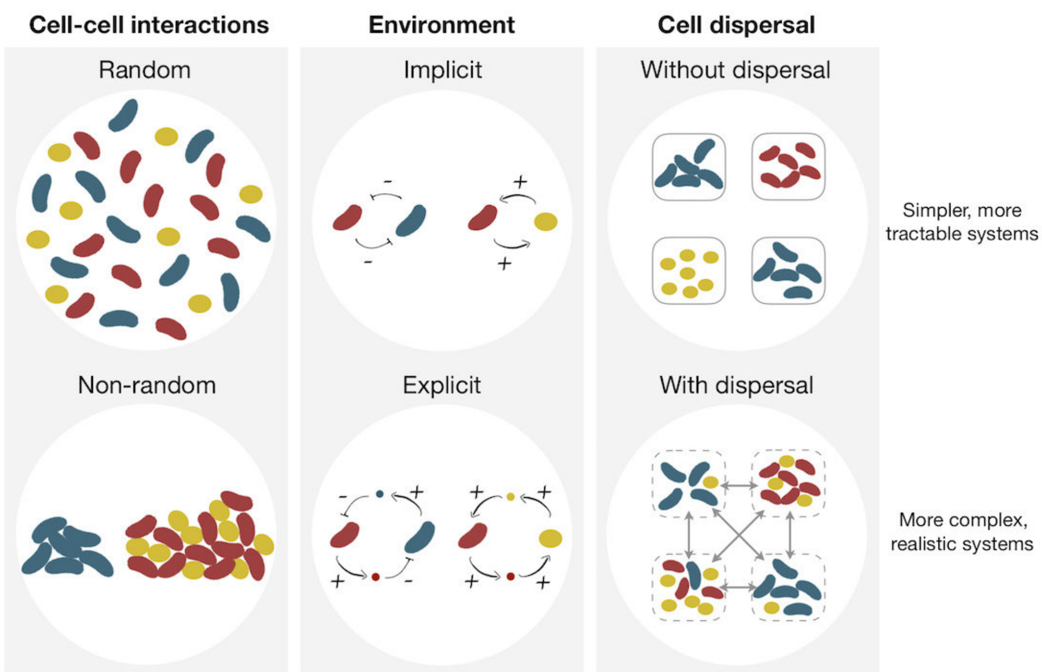

For simplicity, models of social evolution have often assumed that interactions between individuals are random, the physicochemical environment is implicit, and/or individuals cannot move within a patch or disperse between patches (top scenarios). [The authors] focus here on more realistic conditions, where interactions are nonrandom, the environmental dimension is explicit, and individuals can migrate (bottom scenarios), to investigate how these combined effects may influence the ecology and evolution of social behaviors. Credit: Sylvie Estrela et al

Whether it's a pasture open to public grazing or a batch of glucose colonized by microbes, a shared environmental resource is often depicted as a fixed quantity, doomed to depletion if individuals selfishly consume what they can.

This "tragedy of the commons" is a well-known scenario in a broader class of social dilemmas that are used to characterize how individuals choose to cooperate or compete for shared resources.

But these paradigmatic dilemmas may be too simplistic, according to an opinion piece in press at *Trends in Ecology and Evolution*. The article introduces real-world complexity to social dilemmas by accounting for the way individuals modify and adapt to the environments that surround them.

"What we've been doing so far with humans and with microbes and with everything in between is oversimplified," says evolutionary biologist Michael Hochberg, a Santa Fe Institute External Professor based at the University of Montpelier in France. Hochberg and his co-authors decided to investigate social dilemmas during two Santa Fe Institute working groups in 2016 and 2017.

"What our work suggests is that sometimes simple models may fail to capture important features of the ecology of microbial interactions, potentially leading to inaccurate predictions," writes Sylvie Estrela, an evolutionary microbiologist at Yale and the study's lead author.

To account for some of the complexity of real-world social dilemmas, the group created a classification system that goes beyond the basic model of individuals interacting, selfishly or cooperatively, over a fixed resource. Focusing on bacteria as an example, the group studied the dynamics that emerge as bacteria simultaneously help or harm their environment in one of four ways—enriching it with nutrients (helping), detoxifying it (helping), depleting the resources (harming), or polluting it with toxic excretions (harming).

"It's what the interactions are actually producing or consuming or modifying that becomes key," Hochberg says. For instance, bacteria often excrete metabolic waste products that may end up being toxic to themselves and to other neighboring bacteria if the waste persists and accumulates in the environment. But in some cases, such metabolic waste can be food for other bacterial species. Thus, the same behavior can simultaneously harm and help because the same molecule can simultaneously be waste or food, respectively, depending on which microbes are present and how they interact with their environment.

"So rather than having social behaviors that just depend upon interactions between two people or two microbes, the interactions might depend upon the state of the environment as well."

By accounting for the dynamics of the changing environment, the researchers revealed two layers of complexity absent from classic social dilemmas.

The first of these is spatial. Unlike simple social dilemmas that depict what Hochberg calls "perpetual interactions in a given space," the new taxonomy allows bacteria to move from a hostile environment to a more friendly one. So an enriching bacterium surrounded by polluters could relocate, changing the environment it enters and the one it leaves behind.

Such explicit environmental dimensions can have important consequences for the evolution of migration. Estrela gives the example of two organisms that both help themselves and harm the other. "When we abstract away the environment, they both appear to have the same 'social' strategy. Intuitively, one would think that both types should follow the same migration strategy as well—that is move away from each other since they harm each other. But when one takes into account how the two organisms interact with each other and their environment, one finds that the outcome is actually more complex, and the two types may follow different migration strategies."

The second layer is temporal, dealing with niche construction and evolutionary dynamics that play out over time.

"The idea is that when we modify our environments, those modifications can be longer and more durable than our own lifetimes," Hochberg explains. "The ecological inheritance of social behaviors will influence future conditions, but because of the complexity of the system, it is difficult to know just how. This is very relevant to humans because the ways we are modifying our environments will go well beyond our lifetimes, with climate change as one example."

The next challenge, according to Estrela, is "to understand when a simple model is good enough to predict the dynamics and evolution of social interactions, when it is not, and where instead we need more complex and explicit models."

Though the paper doesn't explicitly study social animals or humans, the general framework could be used to study analogous human behaviors such as restorative agriculture on the helping end of the spectrum, or overconsumption of fossil fuels as an example of harming.

More information: Sylvie Estrela et al, Environmentally Mediated Social Dilemmas, *Trends in Ecology & Evolution* (2018). DOI: 10.1016/j.tree.2018.10.004

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