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A Black Queen in a Blue Ocean: How Microbes Evolve to Depend on Each Other

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To our knowledge, all organisms on Earth rely on others in one way or another for their survival. For instance, humans are absolutely dependent on plants for their existence. As a less obvious example, both humans and plants rely on microbes to convert nitrogen gas into forms of nitrogen they can use. And yet all of these organisms -- humans, plants, microbes, and all the rest -- descend from a single common ancestor. How did this state of interdependence arise from that ancient progenitor, apparently reliant only upon itself? Why was it advantageous for the last common ancestor of all life to sacrifice self-sufficiency -- in other words, why is the world no longer the province of a small number of "jack of all trades" species?

These sorts of "deep time" questions were on our minds while studying the curious interaction between marine microbes and what we came to call "helper" bacteria. The open ocean where these little guys live is one of the most inhospitable environments on Earth. Very little nutrition, constant bombardment by deadly solar radiation, nowhere to hide from predators -- one might expect that the organisms that thrive in this vast blue desert would be among Earth's toughest hombres. But that's not the case -- not for the microbes, at any rate.

One marine microbe, *Prochlorococcus*, is a cyanobacterium (a group formerly known as "blue-green algae") and is the most abundant photosynthetic organism in the world. Despite *Prochlorococcus*' obvious success in the perilous marine desert, it is a "90 pound-weakling" when grown by itself in the laboratory. It grows much more slowly than familiar bacteria like E. coli, and it's also very easy to kill with stresses that most living things would barely notice. So how does an organism this vulnerable not only exist in the great blue desert, but dominate?

It turns out that other members of the microbial community "help" them get through the tough spots. *Prochlorococcus*' growth problems only occur when it's in the very unnatural condition of being by itself. When it's co-cultured with a wide variety of other marine bacteria, it grows faster and is much more resistant to damage. The "helper" bacteria protect *Prochlorococcus* from hydrogen peroxide, a toxin that is constantly formed in the presence of oxygen, particularly in the presence of sunlight or when cells are stressed out for any number of reasons.

In order to more efficiently compete for the scarce nutrients in the open ocean, *Prochlorococcus* has undergone "reductive evolution," where it has lost many abilities possessed by its closest ancestors. One of these lost functions is the ability to break down peroxide. Usually, reductive evolution eliminates functions that are no longer necessary for survival -- think blind cave fish or gutless tapeworms. But without defense against peroxide, *Prochlorococcus* couldn't survive in its natural habitat. Fortunately, peroxide freely diffuses in and out of cells, so when the nearby helpers protect themselves by degrading it, they unavoidably also protect *Prochlorococcus* as well. Thus, *Prochlorococcus* gained a reproductive advantage by losing this ability only because its neighbors continued to do all the work.

At first glance, it would appear as if the helpers are charity workers protecting their weak neighbors. But evolutionary theory suggests that altruism is unstable, especially in randomly-mixed habitats like the open ocean. Therefore, to explain how the *Prochlorococcus*-helper interaction arose, we proposed the Black Queen Hypothesis, which describes a process where straightforward, selfish Darwinian evolution results in these sorts of dependencies. Evolutionary biologists love to relate the interactions between organisms to various kinds of games; in our case, the game is Hearts, where the goal is to achieve the lowest score possible. Because the Queen of Spades is worth as many points as all other cards combined, the primary strategy of Hearts is to NOT end up holding her.

In evolution, abilities like peroxide degradation are Black Queens: they are "leaky," meaning that some of the effort an organism spends unavoidably benefits any other organism that happens to be in the environment. If we start with a population where everyone has the ability, then any individual can stop pulling its weight and gain a reproductive advantage. As moochers accumulate, though, the amount of "help" available in the community goes down, ultimately reaching a point where there's no further benefit to ability loss. Eventually, a community will reach a stable equilibrium with the appearance of altruism, but importantly the helpers only help because they can't get away with doing otherwise.

The Black Queen Hypothesis helps explain the prevalence of dependencies in the ocean -- many bacteria require others to provide them with nutrients and vitamins, for instance -- and might also apply to a number of other community interactions in nature, both microbial and otherwise. Essentially, any "leaky" biological function is eligible for Black Queen evolution. The hypothesis also helps us get around the difficult philosophical problem of how natural selection can produce altruism or really any kind of non-antagonistic interaction. And if we stretch it back far enough in time, it helps us understand some of the earliest branchings in evolution, and perhaps why you and I eat plants rather than just being green ourselves.