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Evolution: Welcome to Symbiont Prison

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Can egalitarian partnerships exist in nature? A new study demonstrates how protist hosts use and abuse their algal symbionts depending on their needs. While this relationship allows protists to survive in low nutrient conditions, it leaves little room for algal retaliation.

From the deepest sea vents to the mountains with the highest elevation, symbionts allow their hosts to exploit new environments [1]. These partnerships between different species are remarkable not only in their ubiquity, but also in how partners evolve mechanisms to maximize their benefits in varying contexts [2]. Now a new study by Lowe *et al.* [3] in this issue of *Current Biology* adds to this marvel by demonstrating the precision by which hosts can gain benefits from symbionts across a gradient of environments — supporting them when needed and starving them when they are not.

Lowe *et al.* focus on the symbiosis between the protist host *Paramecium bursaria* and the algal symbiont *Chlorella* sp. (Figure 1A), which engage in a facultative photo-symbiosis found in shallow freshwater habitats [3]. In this partnership, endosymbionts provide hosts with maltose and oxygen derived

from photosynthesis, and hosts provide endosymbionts with nitrogen compounds. Although identifying the products of symbiotic exchange has become easier with emerging techniques [4], quantifying the actual costs and benefits of symbiotic trade remains difficult. Lowe *et al.* are able to do this because the fitness of the two partners can be studied both engaged in symbiosis, or not.

The researchers independently manipulated light (affecting symbiont photosynthesis) and bacterial food (affecting host nutrients through heterotrophy), and then grew the partners either in a free-living state or in symbiosis. They found that while the growth rate of free-living hosts did not change with light levels, hosts with endosymbionts suffered net mortality in the dark and achieved the highest growth rates at highest irradiances. Calculating the net benefit of symbiosis across the

manipulated environment, they found the highest payoff for hosts was at high light and low food availability — a potential driver for why hosts with endosymbionts are able to exploit nutrient-limited aquatic habitats [3].

So far, no surprises — this is the power of natural selection, organisms are selected to maximize the resources of their environment, whether it be by using their own mechanisms or exploiting the capacity of others [5,6]. Clearly the protist host has evolved ways to use the symbiont to its advantage under fluctuating nutrient and light environments. But do the symbionts show similar fitness-maximizing strategies? Lowe *et al.* found that while the free-living algal abundance increased at high light, the symbiotic *Chlorella* abundances decreased [3]. Why would a symbiotic, photosynthesizing *Chlorella* experience a fitness cost of symbiosis at high light levels?

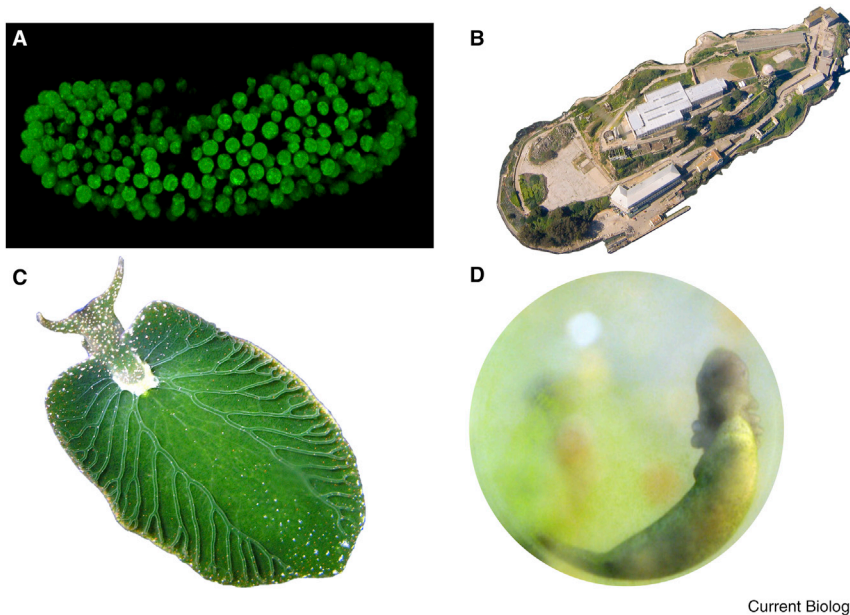


Figure 1. Symbionts imprisoned.

(A) Laser scanning confocal micrograph of chlorophyll fluorescence in *Chlorella* sp. in symbiosis with a single *Paramecium bursaria* host (credit: Ewan Minter and Joanne Marrison, University of York). (B) Aerial photo of Alcatraz Penitentiary, a prison famous for relying on harsh external conditions to dissuade incarcerated individuals from attempting escape (credit: Dylan Ashes, Wikimedia Commons). (C) The ‘solar-powered sea slug’, *Elysia chlorotica*, which utilizes solar energy produced by the algal chloroplasts it has eaten (credit: Sidney Pierce, University of South Florida and Patrick Krug, California State LA). (D) Individual egg from an egg-mass of the spotted salamander (*Ambystoma maculatum*) colonized by the green alga *Oophila amblystomatis* (credit: Roger Hangarter, Indiana University, Bloomington).

Here is the unjust side of symbioses — in most cases, one partner remains in control [7]. While it is still an open question as to exactly how the protists control the density of the *Chlorella*, Lowe *et al.* argue that the hosts ‘adjust’ their symbiont load according to the light environment. This is backed up by work from a different lab, which has shown that hosts likely digest their symbiont populations in low light [8]. Now Lowe *et al.* add to the story by suggesting hosts actively reduce symbiont load in high light, potentially by restricting nitrogen supply to symbiotic *Chlorella* [3]. This is because at high light, host energetic requirements are met by fewer symbionts. As a result, hosts that shed unnecessary symbionts may be more fit.

As an ‘unnecessary’ symbiont, this leaves few options for *Chlorella*. Like in any exploitative partnership, individuals may attempt liberation. While the mechanics of escape are not known, the researchers noted that free-living populations of algal cells that had successfully escaped from symbiosis

could be observed [3]. How these deserters fare after escape is unknown. The researchers found that their density peaked at low light (where hosts gained no benefit of symbiosis) rather than high light (where free-living algae gain most benefit), again leading to the conclusion that the host is somehow in control. For the algal symbionts, the best chance of escape was when outside conditions were not good for them anyway — a situation that has discouraged escape attempts from the most notorious penitentiaries of the world (Figure 1B).

Some animals, such as *Socoglossa* sea slugs (Figure 1C) and spotted salamanders (Figure 1D) have likewise capitalized on photosynthesizing organisms to exploit novel niches, sequestering live chloroplasts in their own cells to enhance development [9–11]. These nutritional animal symbioses — and those in other taxonomic groups, such as dinoflagellates, ciliates, foraminiferans and metazoans — depend on functional chloroplasts (i.e. kleptoplasts) housed within their non-

photosynthetic host tissues [12]. What differs among these symbioses is the degree to which the photosynthesizing cells benefit, or not, from the relationship. Recent attempts at quantification found that, despite costs of a potentially shortened lifespan, sequestered kleptoplasts may actually photosynthetically outperform comparable chloroplasts from algal cells [12,13]. This begs the question of why captivity is necessary for the realization of photosynthetic potential?

When dependence on a photosynthetic partner becomes entrenched, dynamics may change. The flatworm *Symsagittifera roscoffensis* lives in symbiosis with the green algae *Tetraselmis convolutae* [14]. However, unlike *P. bursaria*, the host is obligately dependent on the algae, which it must acquire from the environment following hatching [14]. Despite the strong dependency of the host on the symbiont, new behavioral work has revealed that the flatworm hosts do not adjust light stimuli to their symbionts’ needs. Instead, the hosts favor high light conditions that are not optimal, and may even be harmful to the symbiotic cells [14]. While this may be maladaptive, and simply linked to an inability of the host eyes to sense certain light wavelengths, it also may allow flatworm hosts — similar to protest hosts — the ability to purge symbionts under high light conditions. In any case, the symbionts remain incarcerated by the host, with no option for retribution. Apparently egalitarian partnerships are as rare in nature as they are in politics.

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Plant Biology: Seedling Emergence through Soil

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The resistance encountered by a seedling as it pushes through the soil causes inhibition of stem elongation and stimulates stem thickening, facilitating soil penetration. A new study demonstrates that two proteolytic pathways work in double-negative fashion — one targeting the other — to protect transcription factors central to this response.

A germinating seed buried under the soil or under leaf litter faces two problems — first, there is little or no light to drive its life-sustaining photosynthesis; and, second, it must generate sufficient mechanical force to push aside whatever is covering it. Until the seedling reaches the light, it must rely on stored energy reserves to sustain it. Only when it perceives a light signal does it initiate the rapid changes in developmental pattern from one that emphasizes shoot vertical growth (skotomorphogenesis) to one that trades vertical growth for rapid development of cotyledons and leaves — with simultaneous elaboration of the complex machinery for photosynthesis that will make the seedling photoautotrophic (photomorphogenesis). Two environmental signals impact seedling emergence directly: light and mechanical disturbance. As a seedling penetrates

upward through soil, it encounters decreased mechanical resistance, but increased light. The steepness of the gradient of light through the soil to the surface is determined by the optical properties of the soil. There are separate literatures dealing with signal-transduction pathways activated by both signals, but to date, only little effort at integration of these pathways. In this issue of *Current Biology*, Shi *et al.* [1] present evidence that CONSTITUTIVE PHOTOMORPHOGENESIS 1 (COP1), a RING E3-ubiquitin ligase, already very well known for its major involvement in photomorphogenesis and other plant signal-transduction pathways [2], is also intimately involved in the response to mechanical disturbance encountered by penetration of the growing shoot through the soil. The study elucidates an ingenious mechanism by which COP1 coordinates two major pathways

essential for seedling emergence and survival.

It has been known for decades that a physical barrier to plant growth leads to the production of ethylene. Although growing pea shoots normally produce low levels of ethylene, the level increases dramatically when they encounter a physical barrier [3]. Likewise, bean roots encountering a physical barrier increase their production of ethylene as much as six-fold [4]. A recent study [5] demonstrated that a thin soil overlay was sufficient to stimulate ethylene production strongly. The quantities produced were sufficient to activate the ethylene-activated signal-transduction cascade and produce the well-known triple response — inhibition of hypocotyl elongation, stimulation of hypocotyl lateral expansion, and excessive curling of the apical hook that protects the growing