CHAPTER TEN

Host-Symbiont Conflict in Reef-Building Corals and the Risk of Coral Bleaching

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ABSTRACT Tropical coral reef ecosystems depend on the solar-powered symbioses between coral animals and photosynthetic dinoflagellate microalgae, often considered a mutualistic relationship. However, corals can experience conflict with their microalgae, potentially destabilizing their symbiosis compared to more mutualistic partnerships. Corals may parasitize their symbionts, or vice versa. We propose a continuum from mutualistic to parasitic interactions, from cooperation to conflict, among reef-building corals and other photosymbiotic creatures. We outline five axes of quantifiable conflict: (1) reproductive mode, (2) host sex, (3) resource distribution, (4) solar irradiation, and (5) symbiont housing. For each of these five traits we present metrics of conflict and examples from coral and other symbiotic relationships. Host-symbiont conflict in corals may cause coral bleaching, a catastrophic breakdown of symbiosis that can destroy reef ecosystems. We hypothesize that evolutionary host-symbiont conflict makes some coral-symbiont systems unstable—prone to bleaching—in the face of even small temperature fluctuations. The proposed evolutionary conflict perspective opens new avenues for ecological interventions to protect reefs. Additionally, corals and other photosymbiotic animals are a useful case study to illuminate a fundamental question: How do symbioses evolve from conflict to cooperation and vice versa? Finally, coral reefs offer a striking example of how evolutionary conflicts at small scales may have dire consequences for entire ecosystems.

Introduction

Coral Reefs Are Threatened by Paradoxical Bleaching, Perhaps Explainable by Host-Symbiont Conflict. Tropical reefs teem with life. They sustain countless marine species, shore up coastlines against erosion and rising seas, and feed millions of humans. A coral colony is animal, vegetable, and mineral (Figure 10.1). A thin layer of coral animal tissue, punctuated by polyps, spreads over the surface of a calcareous skeleton. Single-celled plants, microalgae often called zooxanthellae (Box 10.1), live inside coral gastrodermal cells where they photosynthesize to provide energy. Diverse

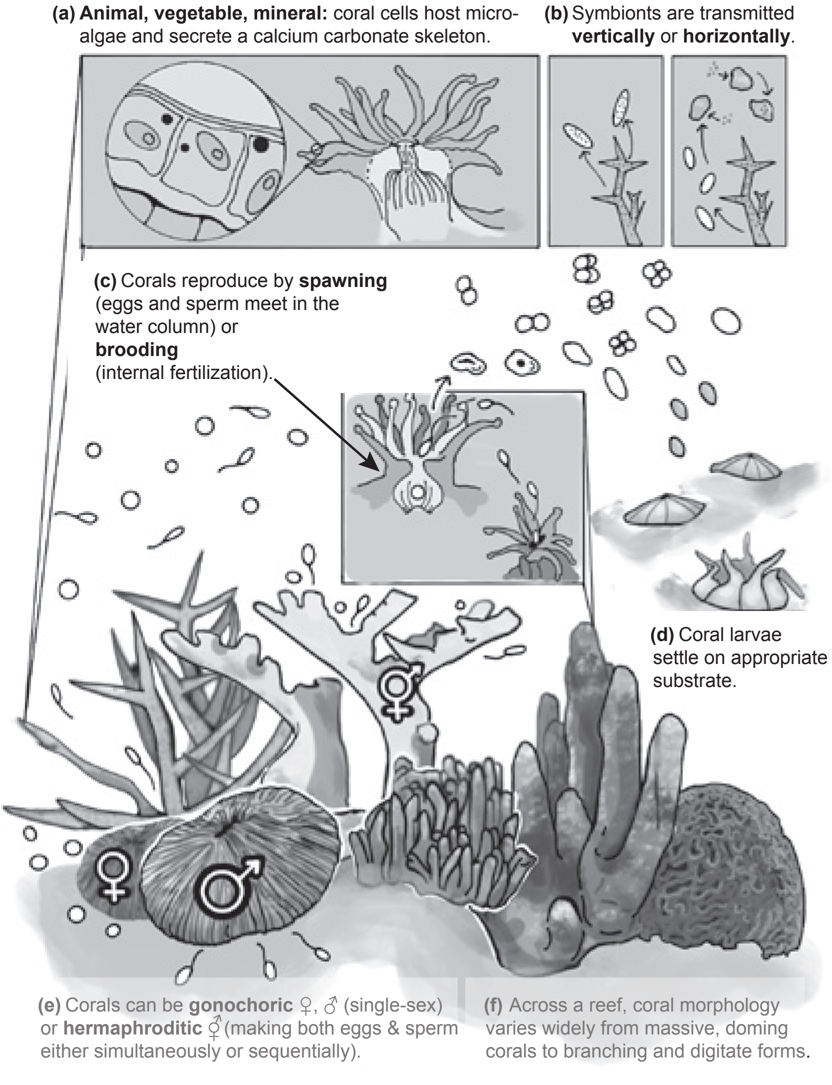

Figure 10.1. Overview of coral life history and reproduction.

bacteria, fungi, and viruses dwell in nooks and crannies to round out the coral holobiont. Many other animals house photosynthetic symbionts, from worms and sponges to clams and sea slugs.

Most tropical corals build their own skeleton through calcification, which forms a habitat for diverse assemblages of fish and marine invertebrates. A single coral polyp grows and divides to become a large colony made up of hundreds or thousands of genetically identical polyps. Coral

BOX 10.1

The Dinoflagellate Microalgae Symbiont

Corals host unicellular microalgae inside their cells. In general, scientists know less about these symbionts than about coral reef ecology and coral biology (Nitschke et al. 2022; Matz 2024). These eukaryotic microalgae in corals, often termed zooxanthellae, are dinoflagellates (order Dinophyceae; family Symbiodiniaceae; formerly, all genus *Symbiodinium*) (LaJeunesse 2020; Nitschke et al. 2022). Symbiodiniaceae originated in the Jurassic Period about 160 million years ago and diversified alongside a major radiation of reef-building corals (LaJeunesse et al. 2018). Across Symbiodiniaceae species, and even within a single species, these microalgae vary tremendously in their growth rate, tolerance to heat stress, photosynthetic efficiency, physiology, and more (Parkinson et al. 2025).

Some Symbiodiniaceae species live exclusively in a free-living form, while the famous symbiotic forms can live either inside the host or freely in the environment. Inside a host, members of Symbiodiniaceae measure 5–13 µm in diameter, are spherical, lack flagella, and have cellulose cell walls (Sheppard et al. 2018; LaJeunesse 2020). In the little-understood free-living state, Symbiodiniaceae seem to alternate between an immobile spherical shape and a mobile “dinomastigote” shape with two round halves and two flagella that allow them to swim (Sheppard et al. 2018). These free-living symbionts live in the water column, on sediments, and on macroalgae surfaces (Fujise et al. 2021). Symbiodiniaceae species can reproduce asexually through mitosis from their spherical form, or sexually, but we know little about their sexual reproduction (Figueroa et al. 2021).

These dinoflagellates photosynthesize to produce and transfer large amounts of glucose, amino acids, and other organic compounds to their host. In turn, the host feeds on particulate matter and provides nutrients to the symbiont. Symbiodiniaceae radiated to specialize within various animal hosts—including corals, sponges, clams, anemones, jellyfish, and flatworms (Thornhill et al. 2014)—and unicellular hosts including ciliates and foraminifera (Parkinson et al. 2025).

Most corals acquire symbionts from the environment, although some vertically transmit them through eggs (see Box 10.2, Figure 10.1, and Figure 10.2). To survive, corals must acquire symbionts during the planula or newly settled polyp stage (Sheppard et al. 2018).

Scientists do not fully understand how corals recruit, select, and acquire symbionts, but it starts when the coral cell envelops the symbiont through phagocytosis (Davy et al. 2012). Corals attract symbionts by emitting nitrogen-containing compounds such as ammonium (Fitt 1985), and through green fluorescence that attracts symbiotic microalgae (Aihara et al. 2019). The microalgae actively swim toward the coral, even against a current (Pasternak et al. 2006). Once acquired, symbionts live in the corals' gastrodermal cells, which border the gastrodermal cavity of the host (Davy et al. 2012). Corals usually host one dominant symbiont species that arises from a single cell dividing mitotically (LaJeunesse 2020; Parkinson et al. 2025).

After a bleaching event, no one knows for sure how the ejected Symbiodinaceae fare. In some cases, they probably die due to broken membranes or destroyed photosystems (Franklin et al. 2004). Further work is needed. Certain Symbiodiniaceae species resist environmental stress, like the heat- and cool-tolerant *Durusdinium trenchii,* which can remain in coral after bleaching events (Nitschke et al. 2022). Conversely, the genus *Cladocopium* dominates coral ecosystems but seems more susceptible to heat. As Parkinson and colleagues (2025) point out, however, these microalgae are so diverse that it is difficult to generalize at the genus level or even the species level.

Does the coral or the dinoflagellate control the symbiosis? It is not clear (LaJeunesse 2020). The coral exerts some control by enclosing the symbiont within not only cytoplasm and host membrane but also a specialized "symbiosome membrane" that cuts it off from outside nutrients. As for who controls bleaching events—do corals expel algae? Do algae flee?—both sides may exert influence, and the term "bleaching" encompasses a wide variety of events (Parkinson et al. 2025) that likely fall under different regulatory controls. However, the coral does seem to control symbiont populations through cellular processes such as autophagy, cell-cycle arrest, and apoptosis (Gorman et al. 2025).

colonies and the reef ecosystem depend on their solar-powered symbioses with the photosynthetic microalgae. The coral–microalgae relationship is classically considered a mutualistic symbiosis that benefits both partners. The symbionts receive nutrients (carbon dioxide, ammonium, and key micronutrients) and shelter; the corals receive energy (in the form of sugars) that is hard to come by in the characteristically nutrient-poor waters where they live.

As waters warm, the symbiosis typically fails. Corals bleach. They lose their symbionts, turn white, and usually die. It is not clear whether the coral or the microalgae controls bleaching or, indeed, what fate befalls the expelled microalgae (LaJeunesse 2020; Parkinson et al. 2025) (see Box 10.1). However, we know that the coral requires symbionts to survive but microalgae can live on their own. Sometimes, a colony can recover from a bleaching event by recruiting new symbionts or allowing remaining symbionts to reproduce and spread within the coral (Nakamura et al. 2003; Rodrigues and Grottoli 2007; Seneca and Palumbi 2015; Thomas and Palumbi 2017; Cornwell et al. 2021; Galindo-Martínez et al. 2022; Walker et al. 2023). Some colonies and reefs are resilient in the face of climate change (Bay and Palumbi 2014; Palumbi et al. 2014; Humanes et al. 2022). But with rapid climate change, corals' natural mechanisms of resilience are inadequate (e.g., Ainsworth et al. 2016; but see Lachs et al. 2023). We have lost over half of the world's coral reefs since 1950 (Eddy et al. 2021). Coral bleaching is an urgent climate catastrophe (Carpenter et al. 2008; Knowlton et al. 2021).

But coral bleaching is also a biological paradox. Why do corals eject the microalgae partners they need to survive? Why does a mere 1°C of warming kill many reef-building coral species but spare other corals and analogous species of photosymbiotic sponges, bivalves, and worms? We hypothesize that the coral symbiosis itself must be subject to countervailing evolutionary pressures that prevent it from becoming more stable. One such evolutionary pressure may be conflicts of interest between the coral host and the symbiotic microalgae.

We propose that host-symbiont conflict drives coral bleaching, which we view as a breakdown of symbiosis. Bleaching-prone reef corals may cooperate less with their symbionts than do hardier corals and other photosymbiotic animals. Less cooperative symbioses are unstable because hosts and parasites rapidly coevolve in an arms race (Woolhouse et al. 2002; Buckingham and Ashby 2022). An arms race is like a tug-of-war; if both sides are evenly matched, the rope is stable. But a small slip of the hands—small mutations or environmental changes—sends the rope flying (Moore and Haig 1991; Haig 1993, 2019; Brandvain and Haig 2018; McCoy and Haig 2020). Alternatively, many scientists consider bleaching to be a maladaptive side-effect of climate change on a fully mutualistic symbiosis. The distinction matters not only to help us understand evolution but also to open new avenues for conserving and rebuilding reefs, for example by engineering "cooperative" microalgae or corals.

To test whether bleaching-prone corals have more parasitic symbioses, we propose strategies to quantify the degree of conflict in photosynthetic symbioses.

Corals and Other Symbiotic Partnerships Vary from Parasitic to Mutualistic. Many seeming mutualisms conceal conflicts. Hosts and symbionts clash over who gets which nutrients and how they are divided; who gets to reproduce and how often; who controls basic biological processes in the symbiotic organism; and more. When plants host nitrogen-fixing bacteria and fungi (Heath and Tiffin 2007), they sanction selfish partners (Kiersi and Denison 2008). When *Wolbachia* bacteria inhabit invertebrates (Werren et al. 2008), they bias their own transmission by feminizing or killing males because they transmit only through the egg (Stouthamer et al. 1999; Werren et al. 2008; Toft and Andersson 2010; Cordaux et al. 2011). Mutualisms benefit the direct fitness of both partners, while parasitisms benefit one partner at a direct fitness cost to the other (West et al. 2007b). As plants and *Wolbachia* have taught us, most symbioses sit somewhere in between. But so far, the coral–microalgae symbiosis—widely considered a mutualism—has largely escaped such scrutiny.

Corals may parasitize their symbiotic microalgae more than other animals. Indeed, there is little evidence that coral–microalgae symbioses are mutualistic at all (Wooldridge 2010; Blackstone and Golladay 2018; Matz 2024). Corals certainly benefit from symbionts, who photosynthesize inside corals and provide energy-rich sugars to their hosts. But do symbionts benefit from corals? Symbionts receive nutrition, and perhaps protection. However, corals restrict symbiont reproduction, trap them in regions of high irradiation, expel symbionts who do not produce and share enough photosynthate, and isolate symbionts singly inside coral cells. Corals even feed on their symbionts (Titlyanov et al. 1996; Wiedenmann et al. 2023) and withhold nitrogen to restrict symbiont growth (Matz 2024). Perhaps symbionts get less out of the supposed mutualism than corals do. In other animals that host photosymbionts, the symbionts are often housed communally, allowed to reproduce, granted a greater portion of photosynthate, and protected from irradiation (Venn et al. 2008).

Corals and other photosymbiotic animals seem to occupy a variety of positions along the parasitism-mutualism spectrum. But to take this idea one step further we must solidify the sometimes nebulous idea of conflict. What does it mean for an animal or endosymbiont to receive a benefit from a symbiotic relationship (Douglas and Smith 1989; Law and Dieckmann 1998)? We can test whether an organism performs better in symbiosis or in isolation, but challenges arise. What does it mean to perform better? For symbionts that can also live freely, we have little information about how successful their life is outside of a host (Box 10.1); for symbionts that cannot live freely, we cannot distinguish between benefit and dependence (Douglas and Smith 1989). Perhaps the free-living ancestors of some symbionts had greater fitness than their dependent, domesticated descendants.

We propose five trait categories to quantify conflict in corals and other photosynthetic animals (Table 10.1). These joint phenotypes are loci of conflict where trait changes help one partner but harm the other (Queller 2014; Queller and Strassmann 2018): (1) reproductive mode, (2) host sex, (3) resource sharing, (4) solar irradiation, and (5) symbiont housing. When the coral or microalgae adopt selfish strategies at the expense of the other, this internal conflict threatens the form and fitness of the whole organism (Schenkel et al. 2024). To borrow Patten and colleagues' (2023) classification of organismal conflicts over transmission versus traits, we offer two categories of transmission distorters—(1) reproductive mode and (2) host sex—and three categories of trait distorters—(3) resource sharing, (4) solar irradiation, and (5) symbiont housing. Each trait varies among coral species and even within individual coral colonies over time.

We predict that coral-microalgae conflict in these domains will correlate with bleaching risk. That is, a changing environment may particularly harm higher-conflict symbioses. Further, by quantifying these traits in animal-microbe photosymbioses, we can ask evolutionary questions such as whether mutualism tends to evolve from parasitism or vice versa.

Reproductive Mode: Symbionts Are Passed Down or Acquired from the Environment

> ***Hypothesis:*** Animal hosts that reproduce together with their symbionts through vertical transmission have more mutualistic symbioses because host and symbiont fates are tied.
>
> ***Synopsis:*** Many reef-building corals reproduce independently of their symbionts, a predictor of evolutionary conflict. When larvae

Table 10.1. Five Domains of Quantifiable Conflict in Coral-Microalgae Symbiosis

	Theoretical predictions	
Trait	*High-conflict state*	*Low-conflict state*
Reproductive mode *Corals pass down microalgae through eggs or get them from the environment (vertical or horizontal transmission).*	Coral reproduces without symbionts (horizontal transmission), so symbionts meet an evolutionary dead end and have little incentive to improve host fitness.	Coral and symbiont reproduce together (vertical transmission), so their evolutionary interests are aligned. Symbionts are incentivized to improve host fitness.
Host sex *Male coral polyps are an evolutionary dead end for microalgae, who only transmit through the egg in female vertical transmitters.*	Symbionts would rather be in a female. Symbionts can bias their own transmission at the cost of host fitness by feminizing hosts, killing males, and more (selfish strategies are not yet known in coral but widespread in other creatures).	Symbionts reproduce with the host and do not need to alter sex determination in hosts (e.g., in hermaphroditic corals, at least some of the symbionts can reproduce through the female line).
Resource sharing *Coral hosts extract more or less photosynthate from microalgae.*	Photosynthate is inequitably shared (e.g., some corals extract 95% of the photosynthate from microalgae).	Photosynthate is more equitably shared; microalgae retain a substantial portion for their own cellular and reproductive needs.
Solar irradiation *Corals irradiate symbionts to increase productivity or screen light and protect microalgae from stress.*	Corals expose symbionts to irradiation to maximize photosynthetic production but therefore hold symbionts under high stress levels.	Symbionts are protected from harmful UV radiation and intense light; they are maintained at lower, safer levels of productivity.
Symbiont housing *Symbionts may be housed in large groups or isolated within individual membranes inside coral cells.*	Corals isolate approximately one symbiont per host cell to restrict nutrients, restrict reproduction, and detect cheaters.	Symbionts are housed communally and/or flexibly, with freedom to move, reproduce, and interact with environmental nutrients.

BOX 10.2

Coral Reproduction and Life Cycles

Corals are diverse. Like many marine invertebrates, corals have biphasic life histories that can vary in (a)sexual reproduction, parental investment in offspring, pelagic larval durations, and timing of sexual reproduction, among many other factors (Sheppard et al. 2018). Here we present a brief overview of these traits and outline how they affect their partnership with members of the Symbiodiniaceae.

Most corals can reproduce asexually and sexually (Richmond 1997). Most corals are also colonial, meaning that they are composed of many genetically identical polyps. Colonies grow when new polyps bud off from older polyps, and polyps across the colony can communicate with one another and share resources. However, polyps do not need to be physically connected to survive, which means that if the colony is broken into pieces, each piece can continue growing. Therefore, among corals growing on a reef, many individuals could be genetically identical. Corals can also undergo sexual reproduction where individuals produce either eggs, sperm, or both (Figure 10.2).

Coral reproduce sexually through brooding or, as is more common (Baird et al. 2009; Hartmann et al. 2017), through broadcast spawning (Figures 10.1 and 10.2). Spawning colonies release gametes into the water column, often coordinating with exquisite precision so that all colonies of a species across a region spawn at the same hour on a single night each year. After fertilization, the embryo will develop into a planula larva that will reside in the water column for hours or weeks before it tries to settle on suitable substrate (Figure 10.1). Planula larvae do not feed, but vertical transmitters' larvae have symbionts who provision them with photosynthate.

Alternatively, corals can brood their larvae: After fertilization the planula develop inside the parent colony, typically spend a limited time in the plankton (if any), and are therefore less likely to travel long distances before settling on a hard substrate.

Finally, symbionts can either be maternally provisioned or environmentally acquired (i.e., vertically or horizontally transmitted; see Figure 10.2) (Baird et al. 2009; Hartmann et al. 2017).

These two categories describe how symbionts are passed down from generation to generation of coral hosts (Figure 10.1). Maternal (vertical) transmission typically involves the parent preloading eggs with symbionts that will then give rise to the next generation of corals with those same symbionts. Environmental (horizontal) acquisition tends to occur near the end of the larval stage around settlement. In this case, the planula develops in the plankton without symbiont partners and then acquires symbionts from its environment (likely from symbiont populations in the benthos, although much less is known about this stage of the symbiont life cycle). Hosts and symbionts are significantly more likely to coevolve in vertical transmitters (Swain et al. 2018). In these cases, the symbiont's fitness partially relies on the reproductive success of their coral host, which propagates the symbiont to offspring. Consequently, vertical transmitters are expected to exhibit less conflict, as the fitness of both partners aligns with the host's reproductive success (Swain et al. 2018; Drew et al. 2021).

pick up symbionts from their environment ("horizontal transmission"), the symbiont has little evolutionary incentive to improve the reproductive fitness of the host. In contrast, "vertical transmitters," who transmit their symbionts from parent to egg, have more tightly aligned evolutionary interests. What is good for the goose is good for the gosling—and for all the gosling's vertically inherited symbionts. Generally, vertical transmission selects for cooperation while horizontal transmission selects for conflict (Drew et al. 2021). We hypothesize that vertically transmitting corals have a more mutualistic, stable symbiosis with, e.g., equitable resource sharing.

In Corals: Most Reef-Building Corals Horizontally Acquire Symbionts, a Seeming Paradox

Most scleractinian coral species are horizontal transmitters who reproduce independently of their symbionts. Estimates vary from approximately 71% (Fadlallah 1983), to as many as 85% (Harrison and Wallace 1990). Transmission mode is tightly tied to reproductive strategy (Figure 10.2). Corals either spawn (males and females broadcast eggs and

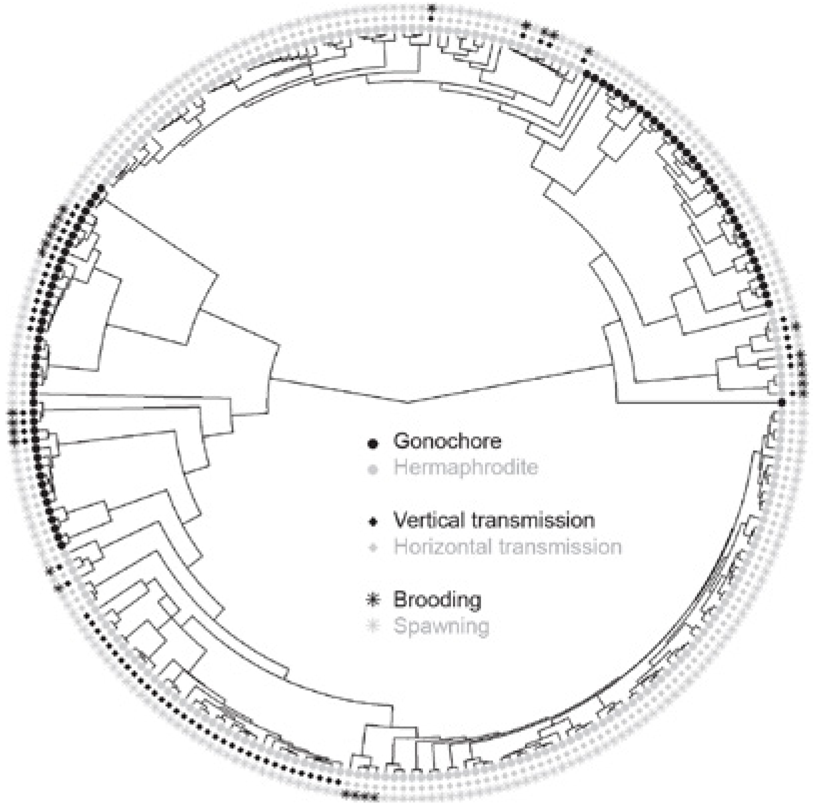

Figure 10.2. Scleractinian corals vary in sexual system, symbiont transmission mode, and reproductive strategy. Data sources: Gault, J. et al. (2021a). Lineage-specific variation in the evolutionary stability of coral photosymbiosis. [Dataset]. Dryad; Gault, J. et al. (2021b). Lineage-specific variation in the evolutionary stability of coral photosymbiosis. *Science Advances*, 7(39); Hartmann, A. C., et al. (2017). The paradox of environmental symbiont acquisition in obligate mutualisms. *Current Biology*, 27(23), 3711–3716; Madin, J. S., et al. (2016). The Coral Trait Database, a curated database of trait information for coral species from the global oceans. *Scientific Data*, 3(1), 160017.

sperm) or brood (eggs are internally fertilized by sperm, develop in the polyp, then disperse as motile larva) (Baird et al. 2009). The majority of spawners horizontally acquire symbiotic microalgae (75%), while the majority of brooders vertically transmit their symbionts (~90%) (Baird et al. 2009) (Figure 10.2). Corals that must acquire microalgae after fertilization pick up symbionts in the planula stage or as a recently settled polyp (Box 10.2) (Sheppard et al. 2018). Interestingly, corals have convergently evolved vertical transmission at least four times, and horizontal and vertical transmitters may even coexist within a genus (Baird et al.

2009; Hartmann et al. 2017). Likewise, brooding, which is most often found in vertical transmitters, has arisen multiple independent times among both gonochoric and hermaphroditic lineages; brooding is much more common in the Atlantic (48%) than in the Indo-Pacific (10%) (Kerr et al. 2010). Some corals categorized as "vertical transmitters" also recruit symbionts from the environment through horizontal transmission. For example, scientists have shown that larvae of the brooding and horizontally transmitting coral *Seriatopora hystrix* only inherited 33% of the symbiont genetic variability from parents, indicating substantial horizontal transmission as well (Quigley et al. 2018).

Vertically Transmitting Corals May Be More Robust to Environmental Perturbation and Have Stabler Symbiotic Associations. Scientists predict that vertical transmitters will have stabler symbioses than horizontal transmitters (Swain et al. 2018; Drew et al. 2021). Some vertically transmitting coral are more resistant to environmental change (van Woesik et al. 2011; Putnam et al. 2012) and have more consistent symbiont populations over time compared to horizontal transmitters. For example, vertically transmitting *Porites* corals may be more stable than horizontally transmitting acroporids.

During bleaching events, some vertical transmitters seem more resilient and stable (Thornhill et al. 2006). For example, three brooding Atlantic corals (*Agaricia agaricites, Porites astreoides,* and *Siderastrea radians*) did not change their symbiont communities during environmental fluctuations and a moderate bleaching event (Thornhill et al. 2006). In other studies, researchers directly compared brooders, typically vertical transmitters, with spawners, which are typically horizontal transmitters. Brooders outperformed spawners in Caribbean reefs after overfishing, heat waves, and outbreaks of disease in the 1980s and 1990s (Hughes 1994; Knowlton 2001). After a mass bleaching in Belize, brooders outnumbered spawners among new coral recruits (McField 1999). Brooders survived at higher levels (73%) than spawners (29%) through the Oligocene-Miocene extinction, a time of great global cooling during which about half of all Caribbean corals went extinct (Edinger and Risk 1995). However, after the 1998 mass bleaching event on the Great Barrier Reef, brooders recovered more slowly than spawners (Emslie et al. 2008).

Kenkel and Bay (2018) tested how thermal stress affected cooperativity in three vertically transmitting coral species and their closest horizontally transmitting relatives. They quantified cooperation as the percent of photosynthetically fixed carbon produced by the symbiont and translocated to the host; parasitism was defined as the difference in that value between heat-exposed and control fragments. They found no clear link between parasitism and vertical transmission, but parasitism correlated with symbiont diversity during bleaching—suggesting, as some theory predicts, that genetic homogeneity of symbionts (rather than vertical transmission per se) drives mutualism (Kenkel and Bay 2018; see also Thornhill et al. 2006 and "Theory Predicts that Mutualism Is Tied to Vertical Transmission"). Perhaps genetically homogenous coral-symbiont-holobionts operate more effectively, like a superorganism, with less intrinsic conflict.

Corals May Horizontally Transmit Symbionts to Protect Sea-Surface-Going Larvae or Cope with Environmental Change. Why do so many corals horizontally transmit their symbionts, if theory predicts that selection should favor reproducing together? A recent phylogenetic study proposes an answer: Spawning helps dispersal, but the hot, bright sea-surface conditions necessarily encountered by dispersing coral larvae and gametes are too harmful for symbionts (Hartmann et al. 2017). High levels of light and ultraviolet (UV) radiation harm the microalgae's photosystem and cause them to release toxic factors into the coral larvae (Hartmann et al. 2017). In the rare spawning corals that also vertically transmit symbionts, eggs are smaller and have less wax ester (possibly adaptations to allow the eggs to sink away from the surface more quickly), as well as higher amounts of antioxidants and photoprotective compounds (independent of the parental light environment) compared to eggs of symbiont-free relatives. In a separate study, *Acropora intermedia* coral larvae with symbionts indeed face greater stress and mortality in simulated ocean surface conditions (Yakovleva et al. 2009).

Other factors favor horizontal transmission in corals. In the short term, corals that can acquire symbionts from the environment may be more flexible in the face of environmental change (Lesser et al. 2013; Bennett and Moran 2015), and capable of swapping out weaker for tougher symbionts (Herre et al. 1999). After mass bleaching, symbiont communities often change dramatically toward heat-tolerant clades (Quigley et al. 2022; Palacio-Castro et al. 2023). In horizontally transmitting species, host and symbiont independently adapt to local conditions based on gene flow rates, effective population size, and selection strength. Coral may have limited local adaptation because larvae are planktonic, so gene flow is high between distant locations with different environments (Cornwell 2020; Fuller et al. 2020). Conversely, symbiont populations tend to be highly genetically structured (Santos et al. 2003; Andras et al. 2013; Cornwell and Hernández 2021), suggesting that microalgae can adapt to local conditions. Therefore, coral hosts who horizontally acquire symbionts can enjoy the benefits of a locally adapted symbiont. Finally, coral transmission mode correlates with life history (e.g., competitive, weedy, stress-tolerant, or generalist) (Darling et al. 2012).

In sum, many factors favor horizontal symbiont transmission in most reef-building corals. But as a consequence, the evolutionary fates of many coral species are less tied to those of their symbionts. Therefore, we predict higher levels of host-symbiont conflict in horizontally transmitting corals.

Beyond Corals: Theory, Experiment, and Observation Show That Vertical Transmission Is Tied to Cooperativity

Theory Predicts That Mutualism Is Tied to Vertical Transmission. When hosts vertically transmit their symbionts from parent to offspring, symbionts who help their host are also helping themselves. Horizontally transmitted symbionts benefit less from improving their host's fitness (Ewald 1987). Theory predicts that in mutualistic symbioses, hosts should vertically transmit their symbionts (Anderson and May 1982; Frank 1996; Sachs et al. 2004; Lesser et al. 2013; Hartmann et al. 2017). Indeed, along the evolutionary spectrum from parasitism to mutualism, many scholars identify the origin of vertical transmission as a key step—perhaps even an essential one—in the origin of mutualism (Ewald 1987; Toft and Andersson 2010). Four arguments support this view (Wilkinson and Sherratt 2001): (1) shared reproduction reduces the incentive to exploit a host (Sachs et al. 2004); (2) offspring need not spend energy finding and recruiting symbionts; (3) genetically uniform symbionts are cheaper (Douglas 1994), less prone to cheating (Maynard Smith 1998), and less competitive with one another (Frank 1996); and (4) hosts can inherit communities of coadapted symbionts, experimentally engineering a better internal ecosystem (Wilkinson and Sherratt 2001). However, horizontally transmitting symbioses are common and can be stable and mutualistic, particularly if symbionts are genetically homogenous, cheaters can be punished, or there are few alternatives to symbiosis (Herre et al. 1999).

Experiments Show That Horizontal Transmission Increases Parasitism in Non-Coral Symbioses. In the laboratory, symbionts forced to transmit horizontally tend to become more parasitic (Bull et al. 1991; Sachs and Wilcox 2005; Stewart et al. 2005; Dusi et al. 2015). In one study of bacteria and symbiotic filamentous bacteriophages, selection favored benevolent symbionts when transmission was limited to vertical but not when horizontal transmission was allowed (Bull et al. 1991). The newly vertically transmitting bacteriophages lost the ability to transmit horizontally; that is, they became dependent on the symbiosis.

Scientists have experimentally evolved jellyfish *Cassiopea xamachana* and their symbiont *Symbiodinium microadriaticum* to enforce either vertical or horizontal transmission. Horizontally transmitted symbionts became more parasitic; they reproduced and dispersed more per host body mass and they decreased host fitness and growth (Sachs and Wilcox 2005). However, the smaller hosts also restricted symbiont fitness (Sachs and Wilcox 2005). Parasitism may lead to pyrrhic victories!

In experimentally evolved barley stripe mosaic virus and its barley host *Hordeum vulgare,* vertical transmission is associated with mutualism. Over four generations of horizontal transmission, virulence tripled, as measured by lifelong viable seed output; after three subsequent generations of vertical transmission, virulence decreased by 40% (Stewart et al. 2005).

Researchers experimentally evolved the protozoan *Paramecium caudatum* and its parasite *Holospora undulata* to show that a parasite with both vertical and horizontal transmission can evolve into a less-harmful symbiont with vertical transmission (Dusi et al. 2015).

While comparable studies of transmission mode and parasitism are rarer in wild populations (Kenkel and Bay 2018), Herre (1993) examined eleven species of fig wasp (*Pegocapsus* or *Tetrapus* spp.) and their corresponding nematode parasites (*Parasitodiplogaster* spp.). Sometimes one wasp infects a fig, allowing only vertical transmission; other times multiple wasps swap nematodes inside the same fig. In these wasps, vertical transmission is negatively correlated with virulence.

Overall, vertical transmission seems to increase mutualism. But nature has many exceptions. For example, in humans, some vertically transmitted human pathogens may be less virulent to the mother but devastating to the child, like rubella, syphilis, Zika, and more. Broadly, infectious disease research can help us understand the parasitism-mutualism continuum of symbiosis.

Predictions: Vertically Transmitting Corals Will Be More Mutualistic and Stable

We predict that vertically transmitting corals have a more mutualistic, stable symbiosis. That is, we predict that they will bleach less easily, share more nutrients with their symbionts, subject their symbionts to less extreme radiation, and more. We expect more beneficial clades of Symbiodiniaceae to be associated with vertically transmitting corals (Lesser et al. 2013). Vertical transmitters that do not brood and horizontal transmitters that do not spawn deserve further study to determine the significance of the transmission mode itself. Corals could be compared to the well-studied system of bioluminescent *Vibrio* bacteria in bobtail squid and other fauna (McFall-Ngai 1999, 2008; Nyholm and McFall-Ngai 2004, 2021; McFall-Ngai and Ruby 2021).

Are mutualisms more likely to evolve from parasitisms, and vertical transmission from horizontal transmission, or vice versa? In bacteria, most mutualists evolved from parasitic rather than free-living ancestors, and mutualists have low diversification rates—suggesting that mutualism most often arises from parasitism (Sachs et al. 2014). Vertical transmission can evolve from horizontal even in an exploitative symbiosis (Moran 2007), which some authors describe as making the best of a bad situation (Law and Dieckmann 1998; Wilkinson and Sherratt 2001). Drew et al. (2021) reported many cases where symbionts evolved to be more mutualistic but nearly as many cases show the reverse. It is not easy to determine which transition is more common. One cannot always detect when symbioses dissolve (Sachs and Simms 2006), or when species go extinct. Mutualism and parasitism are themselves fluid and changing categories.

Host Sex: A Symbiont Would Rather Find Itself in a Female

> ***Hypothesis:*** Symbiotic microalgae inside vertically transmitting corals will evolve strategies to feminize their host or feminize the sex ratio of subsequent generations.

Synopsis: Symbionts who find themselves inside a male have met an evolutionary dead end; they will not be transmitted to future generations. For symbiotic microalgae offered the opportunity to reproduce together with their coral host, they are transmitted through the egg. The sperm, which is produced by the father, typically does not contribute any cytoplasmic ingredients to animal offspring (for some fascinating exceptions, including freshwater mussels, see Bright and Bulgheresi 2010). Therefore, strong selective pressure favors a symbiont that can feminize its host or feminize the sex ratio of its host's offspring. In turn, the host is selected to evolve new, resistant means of sex determination and new techniques to separate symbionts from offspring sex determination. We predict that coral and symbiotic microalgae will show genetic or phenotypic signatures of symbiont attempts to feminize the host through parthenogenesis, male killing, phenotypic feminization of genetic males, or cytoplasmic incompatibility. Further, we predict that conflict over host sex will lead corals to rapidly change systems of sex determination and reproductive strategies.

In Corals: Very Little Is Known About Sex Determination or Any Feminizing Influence of Symbionts

To our knowledge, little is known about coral sex determination. Likewise, researchers have not documented any feminizing influence of Symbiodiniaceae. Below, we describe some interesting features of coral life history that hint at future research into host-symbiont conflict, sex determination, and reproductive strategies.

Corals Vary Between Gonochorism and Hermaphroditism, Within Species and Across the Phylogeny. Hermaphroditism can arise from genetic conflicts within animals (e.g., in scale insects; Gardner and Ross 2011). A selfish, feminizing endosymbiont could be predicted to favor the evolution of hermaphroditism in the host.

Some corals are hermaphrodites and some are gonochores; even closely related species can have opposite reproductive strategies (Figure 10.2; see Baird et al. 2009). Across the coral phylogeny, corals tend to transition from gonochorism to hermaphroditism; conversely, gaining a gonochoric life history is difficult and limited to brooders (Kerr et al. 2010). Hermaphroditism has evolved independently at least three times in primarily reef-building clades (Kerr et al. 2010). In addition, gonochorism is highly favored to be lost, and yet it is the predicted ancestral state of the common ancestor to scleractinian corals.

Further, certain coral species considered to be gonochoric can also be hermaphroditic. After eutrophication in Barbados, 2.7% of colonies (n = 10) of the mounding coral *Porites porites* showed hermaphroditism (Tomascik and Sander 1987). Nine of these colonies were mostly male with one to three ovaries while one was mostly female with one testis and three spermaries. At that reef, the male-to-female sex ratio among the otherwise gonochoric colonies was 2:1. In another surprising example, the supposedly gonochoric Indo-Pacific *Diploastrea heliopora* had both male and female polyps within a single colony, and even some hermaphroditic polyps with co-occurring mature ovaries and immature spermaries (Guest et al. 2012). Its polyps seemed to change sexes over time.

Might these examples of hermaphroditism represent evolutionary responses to a feminizing symbiont? If a host coral evolves to be hermaphroditic, symbionts found within that genetic individual are in luck: they can be passed to the next generation through female gametes. Therefore, symbionts would face lower selective pressure to exert a feminizing influence. Hermaphroditism may therefore be a strategy to limit the evolutionary incentives on symbionts to manipulate host sex. For now, this is just speculation. Many other selective forces favor hermaphroditism (Jarvis et al. 2022).

Parthenogenesis Can Occur in Multiple Species of Coral. Parthenogenesis, by which females produce offspring with no contribution from a male, is one host trait often induced by selfish endosymbionts. Parthenogenesis may be more widespread in corals than we currently suspect.

Parthenogenesis (and/or asexual planulae production) has been frequently described in *Pocillopora damicornis* (Ayre and Miller 2004). In one study, 94% of larvae were produced parthenogenetically, but ten of thirteen colonies also produced some sexual larvae (Combosch and Vollmer 2013). Likewise, twenty-four experimental colonies of the Florida coral *Porites astreoides* produced larvae exclusively through parthenogenesis (Vollmer 2018). The gonochoristic coral *Porites divaricata* reproduced asexually across a mangrove population, almost certainly due to parthenogenesis (Lord et al. 2023).

We raise two further comments of interest. First, the strange reproductive strategies of sea anemones, a close relative to corals, deserve further comparative study (Schlesinger et al. 2010; Armoza-Zvuloni et al. 2014). And second, in marine invertebrates, including cnidarians, parthenogenesis significantly coincides with brooding (Lively and Johnson 1997).

Corals Who Can Switch Symbiont Lineages May Be Able to Resist Any Feminizing Influence. Many coral species can switch symbiont lineages later in life, perhaps when they encounter environmental change or a better symbiont (Byler et al. 2013). Indeed, all reef-building corals may have this capacity. In one survey of fifty-four coral species and 106 symbiont types, no instances were found of a single host species interacting exclusively with a single symbiont lineage (Fabina et al. 2012). A dynamic, heterogenous coral holobiont might spare the host from the negative effects of a strictly vertically transmitted symbiont.

Beyond Corals: Endosymbionts and Parasites Manipulate Host Sex to Bias Their Own Transmission, Complicate the Evolution of Sex Determination in Hosts, and Reduce Host Fitness

Across the tree of life, many symbionts and parasites adopt nefarious strategies to maximize their own transmission at the cost of host fitness. Scientists have learned much from the model system of *Wolbachia,* a bacterial associate of insects, arthropods, worms, and more. *Wolbachia* ranges from parasitic to mutualistic (Werren et al. 2008). It is transmitted only through female eggs, and it has evolved a bewildering array of selfish strategies to help itself reproduce (Stouthamer et al. 1999; Werren et al. 2008; Toft and Andersson 2010). Four main strategies help selfish symbionts like *Wolbachia* bias their own transmission (Toft and Andersson 2010; Cordaux et al. 2011): parthenogenesis, killing males, feminizing males, and causing cytoplasmic incompatibility. As a result, hosts rapidly evolve new systems of sex determination and may face fitness costs or even extinction risk. Below, we give a brief overview of *Wolbachia* and other parasites/symbionts. We hope these biological stories will help scientists investigate similar, as-yet-unknown phenomena in corals and their microalgae.

Symbionts and Parasites Adopt Selfish Strategies to Increase Their Transmission: Parthenogenesis, Male Killing, Feminization, and Cytoplasmic Incompatibilities. Scientists describe four main strategies by which symbionts or parasites increase their transmission.

First, symbionts induce parthenogenesis, where mothers produce offspring with no male involvement. Symbionts will then occur in all descendants. *Wolbachia* disrupts early cell divisions in some mites, hymenopterans, and thrips—clades where males typically develop from unfertilized eggs. For example, in the wasp *Leptopilina clavipes, Wolbachia* disrupts anaphase of asexual embryonic development to produce one diploid female rather than two haploid males (Pannebakker et al. 2004).

Second, symbionts can simply kill any male offspring. Males are a dead end, while females carry symbionts that they can then transmit through the egg. Scientists do not fully understand how *Wolbachia* kills males. In the WZ/WW corn borer moths *Ostrinia* spp., *Wolbachia* apparently causes dosage compensation to fail in male embryos due to a downregulated zinc finger protein gene *Masc* (Fukui et al. 2015).

Third, symbionts can turn genetic males into functional females who produce symbiont-containing eggs. *Wolbachia* feminizes some isopod and insect males (Werren et al. 2008; Wedell 2020), which is surprising because sex determination occurs in a totally different manner in isopods (circulating hormones) and insects (typically heterogamy) (Cordaux et al. 2011). *Wolbachia* feminizes common pillbugs, *Armadillidium vulgare* (Leclercq et al. 2016; Cormier et al. 2021); the common grass yellow butterfly, *Eurema hecabe* (Hiroki et al. 2002); and—by disrupting male imprinting—leafhoppers, *Zyginidia pullula* (Negri et al. 2006, 2009). Far across the tree of life, eukaryotic microsporidia feminize isopod hosts such as *Gammarus roeselii* (Cormier et al. 2021) and *G. duebeni* (Dunn et al. 2020).

Fourth, through cytoplasmic incompatibility, symbionts can turn infected sperm into a weapon that poisons eggs devoid of symbionts, or even eggs devoid of the *right* symbionts (Verspoor et al. 2020). *Wolbachia* causes cytoplasmic incompatibility in several arachnids, isopods, and insects (Werren et al. 2008): if sperm from *Wolbachia*-infected males encounters uninfected eggs, development fails. For example, *Wolbachia* infects the tiny parasitoid wasp *Nasonia vitripennis,* desynchronizing development of paternal relative to maternal pronuclei to abort uninfected embryos (Tram and Sullivan 2002).

Selfish Parasites/Symbionts May Complicate Host Sex Determination, Disrupt Sexual Reproduction, and Harm Host Fitness. Hosts rapidly evolve countermeasures to selfish symbionts. This arms race leaves signatures in a clade's phylogeny and life history.

First, selfish symbionts can cause the host to have varied and young sex-determining chromosomes (Rigaud et al. 1997; Cordaux et al. 2011;

Becking et al. 2017). Isopods are stolid bearers of reproductive parasites across many species and over many generations (Rigaud et al. 1997; Cordaux et al. 2011; Becking et al. 2017). Their sex chromosomes are unusual for three reasons: (1) sex chromosomes look morphologically similar to other chromosomes; (2) closely related species vary in male or female heterogamety, having transitioned between XX/XY and ZZ/ZW three to thirteen times since the late Cretaceous (Becking et al. 2017); and (3) WW females and YY males can be healthy and fertile (Cordaux et al. 2011).

Second, hosts can evolve parthenogenesis, lose sexual reproduction, or both (Stouthamer et al. 2010; but see Birky and Gilbert 1971). This has occurred in more than twenty-five species of arthropods (Kageyama et al. 2012). It is possible that haplodiploidy, where males are haploid (have one set of chromosomes) and females are diploid (have two sets of chromosomes), evolved to "rescue" haploids as viable males from endosymbionts that killed males by destroying paternal chromosomes (Normark, 2004; Cordaux et al., 2011). Similarly, a host with male-killing symbionts could "rescue" its males through hermaphroditism.

Third, selfish symbionts harm host fitness in the short and long term. With cytoplasmic incompatibility (Verspoor et al. 2020), infected males often produce fewer gametes (Price and Wedell 2008; Zanders and Unckless 2019) and have less competitive sperm (Champion de Crespigny and Wedell 2006). Over evolutionary time, as the host genome evolves to counteract the selfish endosymbiont, populations can become reproductively incompatible (Verspoor et al. 2020). Crossbreeding worsens these effects as selfish elements invade a susceptible genome. Further, scientists predict that spermatogenesis will become more complex to oppose the effects of the endosymbiont (Verspoor et al. 2020).

Finally, sex-ratio distortions with too few males can lead to extinction (Wedell 2020). Such extinctions are difficult to detect in the fossil record. However, males are an evolutionary waste if they do not successfully mate, as is the case for many males of many species. From this perspective, a species with a 60:40 female-to-male sex ratio may be less extinction-prone than one with a 50:50 ratio.

Predictions: Coral's Microalgae May Exert a Feminizing Influence on Corals, Causing Complex and Labile Sex Determination and Contributing to Extinction Risk

How can we detect feminizing effects of symbionts in corals, if indeed such effects are present? We predict that some symbiotic microalgae will have evolved techniques to alter host sex through parthenogenesis, male killing, feminization, or cytoplasmic incompatibility—all effects that have been described widely in other endosymbionts, primarily in arthropods.

Further, we predict that any efforts by symbionts to alter host sex will have cascading effects on the phylogeny and evolution of corals, as has been shown in so many arthropods and other clades (Kageyama et al. 2012, 2017; Leclercq et al. 2016; Cordaux and Gilbert 2017; Wedell 2020). Specifically, these effects may (1) drive rapid evolution of sex determination systems, (2) eliminate or alter sexual reproduction, and (3) harm male fitness or burden males with costly counteradaptations, and more. We predict that if microalgae feminize corals, then coral sex-determination systems will be labile, polymorphic, and complex (Cordaux et al. 2011). When host sex determination evolves quickly, we predict further downstream consequences that could harm the ecosystem. Gynandromorphs may become more common or species may split into reproductively incompatible species (Wedell 2020).

Currently, almost nothing is known about such effects in corals or other photosymbiotic animals. We hope this section may inspire some to study the selfish effects of symbiotic microalgae further.

Resources: Coral Hosts Take More or Less Photosynthate from Their Symbionts

> ***Hypothesis:*** Animal hosts which compel their symbionts to give more photosynthate experience higher levels of conflict and are more susceptible to bleaching.
>
> ***Synopsis:*** The same species of microalgae symbionts that live inside coral also live freely in the ocean (Box 10.1). Indeed, many photosymbiotic animals must acquire their symbionts from the environment as they develop. But the lives of these symbiotic microalgae look very different outside of an animal host. Free-living microalgae use the products of photosynthesis for their own purposes, such as building cellular components or reproducing. They only leak about 5% of the energy-rich sugars (i.e., photosynthate). However, inside corals and other animals, symbiotic microalgae transfer 20%–95% of the photosynthate to their host, apparently because the host causes them to do so, though we do not yet fully

understand how. Indeed, symbionts leak more energy-rich sugars when their animal host is starving or otherwise stressed, at the expense of their own energy budget. We argue that the amount of photosynthate given to a host is one metric of host-symbiont conflict. Early experiments show that hosts vary significantly in the amount of photosynthate they receive from their symbiont, and we predict that this quantity varies alongside other metrics of conflict. Further, we predict that some symbionts may have coevolved resistance to "greedy" hosts that cause high amounts of photosynthate to leak from the symbionts.

In Corals and Symbiodiniaceae: Animal Hosts Cause Symbionts to Leak 20%–95% of Their Photosynthate and More Under Stressful Conditions

From the symbiont's evolutionary perspective, selection favors adaptations to use photosynthate for its own reproduction and health (Blackstone and Golladay 2018). Corals, and other animal hosts, cause their symbionts to leak substantial amounts of photosynthate for use by the animal host. Further, hosts regulate symbionts by controlling how much nitrogen they share with them (Xiang et al. 2020), and how much carbon they concentrate and deliver to them (Wooldridge 2010). We consider corals that cause symbionts to leak more photosynthate to be more selfish and less mutualistic. Conversely, we consider symbiont clades that fix more carbon, share more photosynthate, and promote more growth in the coral host to be more mutualistic and less selfish. Resource sharing is one useful metric of the degree of conflict in a symbiosis.

Much work has been done to determine the degree of mutualism in various clades of microalgae symbionts (Table 10.2) (Lesser et al. 2013). In the alphabet soup of Symbiodiniaceae clades, some seem generous but weak, while others are selfish but tough. Photosynthetic rate can inversely vary with heat tolerance (Cunning et al. 2015), as can the amount of photosynthate a symbiont shares and coral growth rates (see Matsuda et al. 2023). For example, clade-C1 symbionts share more photosynthate and promote more calcification in corals, while rarer thermally tolerant clade-D symbionts seem to be less generous partners who are more resilient to stress. The more parasitic clade-A symbionts associate with sicker coral, fix less carbon, and share less photosynthate with their host (Stat et al. 2008). However, these microalgae are so diverse within and across

Table 10.2. Broadly, Symbiodiniaceae Vary from Selfish and Hardy to Mutualistic and Less Hardy (Clade D vs. Clade C1)

Symbiont type	*Animal host*	*Study findings*
Mutualistic clade C1 versus selfish clade D	Juvenile branching corals *Acropora millepora*	Mutualistic clade C1 symbionts translocated photosynthate to the host at 121% the rate of the more selfish clade D symbionts and had 87% greater rates of electron transport through photosystem II (Cantin et al. 2009).
Selfish clade D	Caribbean corals	An opportunistic, thermally tolerant, and genetically homogenous clade D endosymbiont lineage *Durusdinium trenchii* from the Indo-Pacific invaded the Caribbean after mass bleaching in 2005 (LaJeunesse et al. 2014).
Selfish clade D	*Orbicella* spp. corals	*Durusdinium trenchii* photosynthesizes at normal rates compared to other symbionts but promotes up to 50% less coral calcification (Pettay et al. 2015).
Mutualistic clade C1 versus selfish clade D	Coral *Acropora tenuis* experimentally inoculated	Thermally tolerant clade D acquired less nitrogen than clade C1 at normal temperatures but fixed 35% more carbon than clade C1 at higher temperatures. Clade C1 outcompetes clade D at nitrogen acquisition under normal temperatures, which may explain why the less thermally tolerant clade C1 dominates globally (Baker et al. 2013).

Note: Symbiodiniaceae vary tremendously both within and across clades, complicating attempts to generalize.

species that it is difficult to generalize (Parkinson et al. 2025). In Table 10.2 we report a selection of studies on symbiont mutualism (Cantin et al. 2009; Baker et al. 2013; LaJeunesse et al. 2014; Pettay et al. 2015).

Corals presumably also vary along a parasitic-to-mutualistic continuum, but comparatively little is known. One metric of parasitism in corals is how much photosynthate they force their microalgae to leak. Up to 95% of carbon fixed by symbionts is leaked to the coral hosts (Muscatine et al. 1983, 1997). Scientists can trace the fate of carbon to determine translocation rate. Less directly, scientists can expose different strains of microalgae to tissue homogenate from different animal hosts, then measure how much photosynthate the microalgae leak in the presence of that tissue. That leakage rate can be interpreted as a metric of host greediness; the more leakage, the greedier the host. Additionally, symbionts may have coevolved resistance to the particular greedy strategies of their typical host; if this is true, we might expect giant clam symbionts to be ill-prepared to handle coral tissue homogenate and leak photosynthate profusely. Studies of photosynthate leakage offer tantalizing hints at host-symbiont coevolution and variable greediness across hosts. For example, reef-building corals seem greedier than other animals (Table 10.3) (Muscatine 1967; Sutton and Hoegh-Guldberg 1990; Masuda et al. 1994). It is important to note that symbionts inside a coral

Table 10.3. Microalgae Symbionts Leak Different Amounts of Photosynthate in the Presence of Tissue from Different Animal Hosts, a Metric of Animal Greediness

Animal host(s)	*Results*
Scleractinian coral *Plesiastrea versipora,* zoanthid *Zoanthus robustus,* nudibranch *Pteraeolidia ianthina,* and soft coral *Capnella gaboensis*	Tissue from the scleractinian coral caused microalgae to leak up to 42% of the photosynthate, but tissue from the zoanthid and nudibranch caused very little photosynthate leakage. Tissue from the soft coral lysed microalgae, a somewhat hard-to-interpret result (Sutton and Hoegh-Guldberg 1990).
Giant clam *Tridacna crocea* and scleractinian coral *Pocillopora damicornis*	Symbionts isolated from a giant clam and a scleractinian coral were exposed to tissue homogenate from their own, and each other's, hosts. With their own hosts, each leaked ~37% and 38%, respectively. With each other's hosts in two exposures, the clam's symbionts leaked 22% and 23% and the coral's symbionts leaked 29% and 5% (Muscatine 1967).
Giant clams *Tridacnidae* (*T. derasa, T. crocea, T. maxima, T. squamosa, Hippopus hippopus*) cockles *Cardiidae* (*Fragum fragum, F. mundum, F. unedo*), non-photosymbiotic bivalves (*Mytilus edulis, Meretrix lusoria, Ruditapes philippinarum*), and gastropods (*Umbonium giganteum, Turbo argyrostoma*)	When symbionts from giant clams *T. derasa* were tested, giant clam (*Tridacninae*) tissue homogenate promoted more translocation of photosynthate than did tissue from *Cardiidae* cockles or non-photosymbiotic bivalves and gastropods (Masuda et al. 1994). The researchers also showed that *T. derasa* tissue homogenate caused photosynthate leakage in certain free-living algae within Dinophyceae but not in other clades.

do seem to produce more photosynthate overall compared to in free-living forms; for further discussion, see "Solar Irradiation: Corals Can Screen and Protect Symbionts or Expose Symbionts to Irradiation to Grow Quickly."

Further, animal hosts seem to take more photosynthate from their symbionts when they are stressed or starved. Microalgae from healthy anemone host *Exaiptasia pallida* released 14% of photosynthate, while those from starved anemones released 25%, despite lower photosynthesis rates in the starved condition (Davy and Cook 2001). The authors saw similar results for the same microalgae incubated with tissue homogenate from the coral *Montastrea annularis*. For the coral *Stylophora pistillata,* translocation was significantly higher for corals living in lower-pH waters (80% translocation at pH 7.2; 60% at pH 8.1), allowing the coral to receive the same amount of translocated carbon (5.5–6.1 µg C $cm^{-2}h^{-1}$) in both scenarios even though it represented a greater portion of the symbiont's available carbon (Tremblay et al. 2013).

Beyond Corals: In Plant-Rhizobium Symbioses, Resource Sharing Varies with the Degree of Conflict

In many other symbioses, scientists use resource sharing between host and symbiont as a metric of cooperation or conflict. Phenotypes can be considered more- or less-cooperative strategies to maximize payoffs in resource markets (Noë and Hammerstein 1994, 1995; Kiersi and Denison 2008; Werner et al. 2014). In the famous plant-rhizobium system, plants create root nodules to house bacterial partners in the right conditions to convert atmospheric nitrogen into ammonia (van Rhijn and Vanderleyden 1995). The plants invest energy by giving photosynthate and phosphorus to their bacterial partners (Ma and Chen 2021). Plants can also house mycorrhizal fungi in their roots, which uptake phosphorus and mitigate drought stress (Smith and Smith 2012). These plant symbioses determine success across local (Porter and Rice 2013) and global (Afkhami et al. 2014) habitats amid environmental change.

Both plants and fungi adjust the amount of resources they give their partner depending on how generous their partner is. As Kiers et al. (2011) demonstrated, this bidirectional system of control prevents the fungal symbionts from being exploited, and therefore stabilizes the symbiosis. They found that plant *Medicago truncatula* transfers more carbon resources to a more cooperative fungal partner, *Glomus intraradices,* compared to the less-cooperative close relatives *G. custos* and *G. aggregatum*. Next, they manipulated how much phosphorus and carbon the fungi and plants could give, respectively, ultimately finding that plants gave more carbon to generous fungi that provided more phosphorus. Likewise, fungi gave more phosphorus to generous plants.

Theoretical models show that plants should sanction rhizobia that fix less nitrogen, which is predicted to stabilize symbiotic interactions (West et al. 2002). Yet these sanctions cannot fully purge the population of poor performers, which persist at low frequencies (Frederickson 2013). Heath and Tiffin (2009) found that plants appear to select for the most beneficial partners, which increase in frequency across generations, leading to increased fitness for both hosts and symbionts. In the same study, the optimal symbiont changed depending on the host's genotype. In short, there is no universal best symbiont. Furthermore, the order in which symbionts colonize a plant matters: a less beneficial symbiont may not be actively sanctioned if it arrives after a well-performing symbiont partner in the nodule. Perhaps these priority effects prevent poorly performing genotypes from being selected out of the population (Boyle et al. 2021).

The plant-mycorrhizal fungi symbiosis is a biological market in which each partner regulates its provision of nutrients in response to the other (Kiers et al. 2016). Fungal partners can even control the market value of the phosphorus they provide by compensating with alternate sources during shortages and storing surpluses, as van't Padje et al. (2021) showed in their study of the fungus *Rhizophagus irregularis* living in carrot root *Daucus carota*. More broadly, biological market theory clarifies the evolution of symbioses. For example, Werner et al. (2014) identified six strategies microbes may pursue to improve their performance in biological resource markets: "(i) avoid bad trading partners; (ii) build local business ties; (iii) diversify or specialize; (iv) become indispensable; (v) save for a rainy day; and (vi) eliminate the competition."

These experimental and theoretical studies show how we can use resource sharing to quantify cooperation and conflict.

Predictions: Corals and Symbionts Will Co-Evolve in an Arms Race over Resource Sharing, and Faster-Growing Corals Will Extract Greater Amounts of Photosynthate from Their Symbionts

We predict that as coral hosts evolve to be more demanding, symbionts will evolve resistance. Perhaps symbionts from very demanding host species would share far less if exposed to tissue from an undemanding host. Resource sharing can be seen as a tug-of-war, where both sides are pulling hard but, if equally matched, the rope does not move.

Additionally, we predict that corals with a fast-growing lifestyle will extract a greater proportion of photosynthate from their symbionts. Further, we propose that corals generally extract greater amounts of photosynthate than other animal hosts—such as sponges, bivalves, and acoels—and that the rate of photosynthate seizure will correlate with other metrics of conflict. Hosts that require, and receive, higher amounts of photosynthate will be more susceptible to changing environmental conditions that impact the symbiont photosystem.

Solar Irradiation: Corals Can Screen and Protect Symbionts or Expose Symbionts to Irradiation to Grow Quickly

> ***Hypothesis:*** Animal hosts that irradiate their symbionts will experience higher levels of conflict than hosts with photoprotective adaptations; the irradiators will be more susceptible to bleaching.
>
> ***Synopsis***: Animal hosts face a photonic tradeoff between efficiency and protection. They can concentrate light to enhance photosynthesis, or they can screen light to protect their symbionts. In particular, they can specifically screen out UV wavelengths that tend to be the most harmful to host and symbiont, though this depends strongly on depth. We propose that one metric of host-symbiont conflict is the degree to which hosts irradiate their symbionts. Corals expertly irradiate their symbionts to "farm" microalgae with efficient light-concentrating adaptations (Hoogenboom et al. 2008; Barott et al. 2015; Kramer et al. 2022). Corals can build gigantic reefs and support entire ecosystems because they invented intensive agriculture. But intensive agriculture has downsides. In corals that irradiate their symbionts with more and higher-energy photons, symbionts must contend with constant levels of light stress. And when global warming adds heat stress to the mix, they bleach. Shallow corals, and corals at the reef crest, expose their microalgae to higher heat stress and light stress than deeper corals. We hypothesize that corals run microalgae's photosynthetic machinery at a rate that is beneficial to them as hosts but stressful for the symbi-

onts. Thus even a small amount of heat stress can destabilize this light-stressed system and cause catastrophic bleaching. Across corals and other photosymbiotic animals, we predict that highly irradiating animal hosts will bleach more easily and severely.

In Corals: Corals Are Ultraefficient Farmers of Photosynthetic Symbionts

Reef-building corals farm their microalgae symbionts (Wooldridge 2010; Matz 2024). Corals house their symbionts singly, each within an animal cell, where the microalgae cannot move to escape irradiation. Indeed, being housed singly places many restrictions on microalgae (see “Symbiont Housing: Symbionts May Be Housed in Large Groups or Isolated”). In addition, from the nanoscale to the macroscale, corals manipulate incident light with their highly scattering tissue and skeleton to irradiate their symbionts and maximize photosynthetic output. Together, the coral approaches theoretical limits for photosynthetic efficiency (approaching eight photons to fix one CO_2 molecule; see Brodersen et al. 2014). Coral reefs are among the most productive and diverse ecosystems on earth despite occurring in nutrient-poor waters (Sheppard et al. 2018).

Symbionts living inside a coral experience a manyfold increase in irradiation compared to free-living forms. In the outer layers of coral tissue, corals concentrate light to irradiate their symbionts (Wangpraseurt et al. 2012). In the coral *Porites branneri,* symbionts living within coral absorb two to five times more light than those living outside (Enríquez et al. 2005). In general, symbionts living within corals have a higher photosynthetic efficiency (Wangpraseurt et al. 2016). Free-living Symbiodiniaceae are motile and can move away from regions where irradiation is too high (Box 10.1). Generally, heat stress and light stress act through separate but related pathways to damage the photosystem of microalgae and often kill them (Downs et al. 2013).

Corals have many adaptations to irradiate their symbiont, but these adaptations can backfire, causing or amplifying bleaching. Corals are highly efficient light collectors (Stambler and Dubinsky 2005). Their skeletons scatter light efficiently, further irradiating their symbionts (Enríquez et al. 2005; Kaniewska et al. 2011). Coral tissue itself is highly scattering and works in concert with the skeleton to propagate and homogenize the light field across symbiont-bearing areas (Wangpraseurt et al. 2016). Skeletons vary in their scattering efficiency between species, a variation that correlates with bleaching risk (Marcelino et al. 2013; Swain et al. 2016; see also Enríquez et al. 2017). Simulations show that irradiance experienced by coral photosymbionts increases exponentially as a coral bleaches (Terán et al. 2010). In general, these photonic adaptations explain why light stress drives photoinhibition and causes or amplifies coral bleaching (see Brown et al. 1994, 1999; Lesser and Farrell 2004; Anthony and Kerswell 2007; Castro-Sanguino et al. 2024).

Corals have some apparently photoprotective adaptations, including fluorescent pigments (Salih et al. 2000; Dove et al. 2001; Bollati et al. 2020) and an additional algal symbiont called *Ostreobium* (Rodríguez-Román et al. 2006; Yamazaki et al., 2008; del Campo et al. 2017; Galindo-Martínez et al. 2022). These photoprotective adaptations may benefit the host, the symbiont, or both. The green fluorescent proteins of corals are upregulated during bleaching events (Bollati et al. 2020) and may dissipate harmful energy from ultraviolet radiation to reduce light stress (Salih et al. 2000; Dove et al. 2001). In an experimental study of *Acropora palifera,* non-fluorescent color morphs were significantly more photo-inhibited by full sunlight than their fluorescent morph peers (Salih et al. 2000). Similarly, the endolithic algal symbiont of many corals (*Ostreobium* spp.) seems to protect some bleaching corals by screening sunlight. For example, in several bleaching-resistant individuals of *Orbicella faveolata,* the algal symbiont *Ostreobium* bloomed near the skeletal surface during bleaching events, absorbing a substantial proportion of incident light and therefore relieving the coral of light stress (Galindo-Martínez et al. 2022). Their bleaching-prone peers had no such algal bloom.

Coral fluorescence may itself hint at underlying host-symbiont conflict. Fascinatingly, a genetic analysis suggests that a coevolutionary arms race between corals and their symbiotic dinoflagellates caused fluorescent colors to diverge in corals. Specifically, Field et al. (2006) showed that adaptive evolution caused cyan and red fluorescence to evolve from the ancestral green color in the great star coral *Montastrea cavernosa*. Surprisingly, they showed that an intermolecular binding interface that is not related to color production was also subjected to positive natural selection. They performed reverse mutagenesis to experimentally test which mutations affected color phenotype, resurrecting ancestral versions of the proteins inferred from statistical genetic analysis. Through this work, they confirmed positive selection at sites that do not seem to impact the color phenotype. Further, these sites appeared to have a binding function and showed signatures of continuous readjustment—a well-known hallmark of a coevolutionary chase, where "one of the interacting partners benefits from maximizing the interaction and the other from avoiding or restricting it" (Field et al. 2006). Field et al. noted that such signatures are seen in systems such as sperm-egg and host-parasite recognition. They proposed that the fluorescent proteins therefore somehow regulate the symbiotic dinoflagellates, acting as regulatory photosensors analogous to phytochromes in plants. Further work is needed to follow up on these results.

Beyond Corals: Many Photosymbiotic Creatures Protect Symbionts from Light Stress

Bivalves, acoels, foraminifera, and other hosts have evolved photonic adaptations to protect their symbionts from light stress.

Giant clams engage in "photonic cooperation" with their symbionts: Layered iridocytes enhance photosynthetic capabilities while screening damaging UV light (Rossbach et al. 2020). Specifically, the clams' mantles forward-scatter photosynthetically active radiation, back-reflect nonproductive wavelengths, and absorb and fluoresce ultraviolet light (Holt et al. 2014; Ghoshal et al. 2016; Rossbach et al. 2020; Holt 2024). Similarly, heart cockles (*Corculum cardissa* and spp.) transmit greater than 30% of visible sunlight but screen ultraviolet radiation (McCoy et al. 2024), through transparent windows in their otherwise opaque shell (Kawaguti 1950; Carter and Schneider 1997; Farmer et al. 2001). The heart cockle's windows are composed of aragonite fiber-optic cable bundles, proposed to be an adaptation to transmit photosynthetically active radiation while scattering and absorbing ultraviolet light (McCoy et al. 2024).

The photosymbiotic acoelomorph flatworm *Convolutriloba longifissura* has two types of pigment cell that seem to protect algal symbionts from light stress (Hirose and Hirose 2007).

Remarkably, the photosymbiotic foraminifera *Marginopora vertebralis* protects its photosynthetic symbionts by shuttling them away from the bright sun, deeper into the cavities of the foram's body. Apparently, stress response by the symbiont is interpreted as a signal by the host, who actively responds and contracts actin filaments to move symbionts deeper into the calcium carbonate structure (Petrou et al. 2017).

Fascinatingly, sunlight plays a role in the only example of a photosymbiosis that transitions from mutualistic to parasitic as the animal host grows up (Melo Clavijo et al. 2018): the queen conch *Strombus gigas* (Banaszak et al. 2013). In their larval stage, the conch have what seems to be a mutualistic relationship with their *Symbiodinium* symbionts, which photosynthesize because sunlight can penetrate the larval gastropod. But in adults, which have a thick shell that blocks all but 0.1%–20% of sunlight, photosynthesis is less effective and it seems that the adult snail must provide nutrition to their symbionts without receiving much, if anything, in return (Banaszak et al. 2013).

A large body of research investigates how plants protect their photosystems against light stress (Schwenkert et al. 2022; Shi et al. 2022), another fruitful source of comparison to corals. Red and brown algae produce mycosporine-like amino acids that protect tissue from UV irradiation (Frohnmeyer and Staiger 2003; Rui et al. 2019).

Predictions: Photonic Adaptations to Irradiate Symbionts Correlate with Bleaching Risk and Other Metrics of Conflict

We predict that corals will consistently irradiate their symbionts at higher levels than non-coral photosymbiotic animals, and that across species, irradiation will correlate with bleaching risk. Further, we anticipate that levels of irradiation align with metrics of nutrient sharing and transmission mode. Because the available downwelling irradiance varies dramatically with depth, scientists could take advantage of this natural experiment to compare levels of conflict in shallow versus mesophotic coral reefs. We predict that shallow-sea corals, which have the opportunity for intensive agriculture with greater downwelling irradiance, will experience higher levels of conflict than the deeper, mesophotic corals. Irradiation generally represents a farm-and-discard strategy rather than a protect-and-coexist strategy. We suspect that reef building corals so dramatically irradiate their symbionts because they are in direct competition with seaweeds and other corals for space in the narrow band of seas with appropriate temperature and sunlight. Global real estate for reefs is limited, and these creatures largely cannot move; they can only grow. Therefore, they face intense competition for growth. In contrast, the deep-sea houses scleractinian corals with no seaweed competition. Scleractinian corals likely arose in the deep sea at depths of 200–2,300 m, without sunlight and photosymbionts (Campoy et al. 2023). To better understand the evolutionary history of host-symbiont conflict over irradiation, scientists could compare the ecology of deep-sea to shallow-sea corals as well comparing symbiotic to aposymbiotic species.

Symbiont Housing: Symbionts May Be Housed in Large Groups or Isolated

> ***Hypothesis:*** Symbionts living communally in animal hosts have more power and less conflict with their host compared to those isolated in individual coral cells, which can be controlled and coerced.
>
> ***Synopsis:*** Corals typically isolate each symbiont inside a membrane inside a coral cell. Unlike corals, other animals house their symbiotic microalgae in communal spaces extracellularly, such as those found in heart cockles (*Corculum* spp.) and giant clams Tridacninae, or in higher numbers intracellularly, such as in sponges (*Cliona* spp.). Symbionts housed communally have more power because hosts cannot detect cheaters in a shared physiological space. The host detects only total photosynthate produced, allowing individual symbionts to contribute less and potentially even reproduce unnoticed. Corals seem to have solved this problem by housing symbionts within single cells, individually monitoring their photosynthetic performance and individually providing them with the carbon needed to survive and photosynthesize (or withholding carbon to punish cheaters). We predict that photosymbionts vary from singly-housed-intracellular to multiply-housed-intracellular to communally-housed-extracellular; along that spectrum, we predict symbionts to reproduce more and provide less photosynthate when they are more communally housed.

In Corals: Intracellular Symbionts May Be Restricted from Reproduction and Monitored for Defection

Corals Generally Have One Symbiont Per Cell, Enabling Close and Specific Monitoring. In most animals that host photosymbionts, including corals, symbionts are intracellular and surrounded by a host-derived membrane called the symbiosomal membrane (Venn et al. 2008). The animal host provides carbon dioxide, water, and other important materials to the symbiont and therefore controls most aspects of the metabolic partnership (Venn et al. 2008; Wooldridge 2010; Blackstone and Golladay 2018). Animal hosts seem to restrict symbiont reproduction, just as we restrict cells within our own body from dividing freely and developing into cancer (see Okasha 2021).

Corals host one or only a few symbionts per host cell (Blackstone and Golladay 2018). Across thirty-three species of anthozoan, including twenty scleractinian corals, most animals host only one symbiont per cell (average symbionts per cell = 1.54 ± 0.30; range 1.11–2.19; see Muscatine et al. 1998). High nutrient levels seem to prompt symbionts to reproduce. When eleven species were flooded with nutrients, the number of symbionts per cell increased from an average of 1.46 ± 0.21 to 1.77 ± 0.28 (Muscatine et al. 1998). In other species, symbionts are often housed in more communal situations (see "Beyond Corals: Housing Varies Dramatically Across Photosymbioses, and Plant Hosts Monitor the Specific Cooperativity of Rhizobium Symbionts").

Because corals house symbionts singly, they can detect cheaters. Evolutionary theorists predict the evolution of defector symbionts that will divide more quickly and share less photosynthate than the host prefers (Blackstone and Golladay 2018). These defectors could hide from host oversight if they lived in communal pools, but singly housed symbionts cannot hide. For example, in a coral relative, the sea anemone *Aiptasia pulchella,* the host preferentially expels rapidly dividing symbionts (Baghdasarian and Muscatine 2000).

Perhaps one-on-one cellular symbioses could also create a stronger mutualism, in which policing enables both parties to exchange more materials without the looming threat of cheating (by either party). This idea deserves further consideration.

Environmental Stress Causes Bleaching by Disrupting Corals' Innate Mechanisms for Detecting and Expelling Cheater Symbionts. Corals' cheater-detection mechanisms may malfunction under environmental stress, causing them to eject both defecting and healthy symbionts (Blackstone and Golladay 2018). Defectors that fail to export photosynthate cause product inhibition and collapse carbon concentration mechanisms, resulting in electron backup in photosystems I and II. Then, reactive oxygen species form, potentially causing damage and programmed cell death. High heat and light levels also trigger these processes, not because the symbionts are defecting per se, but because environmental stress reduces the rate of photosynthesis (Blackstone and Golladay 2018). Under heat stress, cooperators look an awful lot like defectors, causing corals' cheater-detection systems to overreact and drive massive coral bleaching.

Host carbon supply to symbionts depends on their photosynthesis, which serves as a checkpoint against cheaters. Host enzymes concentrate carbon to provide $CO_{2(aq)}$ to microalgae. However, corals need to receive photosynthate from symbionts to activate carbon concentration. Heat or light stress disrupts symbiont photosynthesis and causes a vicious cycle: Less CO_2 is provided to the symbionts, they photosynthesize less, and so on (Wooldridge 2010).

Indeed, in six scleractinian coral species—*Acropora selago, Acropora muricata, Heliofungia actiniformis, Ctenactis echinata, Oxypora lacera,* and *Pocillopora eydouxi*—corals expelled mostly degraded symbiont cells under normal conditions but released many healthy symbiont cells during heat stress (Fujise et al. 2013). One thermally tolerant species *P. eydouxi* did not change the number of symbionts expelled between the two conditions.

Symbionts Reproduce Less Inside Corals Compared to in Culture; Little Is Known About Free-Living Symbiodiniaceae. Because corals host symbionts singly within cells, they can restrict symbiont reproduction. Generally, we expect that symbionts will be allowed to reproduce less inside a host than in their free-living state, particularly in the case of non-cooperative symbioses. While little is known, studies have shown that symbionts double in number far more quickly outside of a coral host than within one (Wooldridge 2010). In a host, Symbiodiniaceae typically double every 70–100 days (Wilkerson et al. 1988); in culture, symbionts double approximately every three days (Fitt and Trench 1983).

Symbiont reproduction rates vary across coral hosts, potentially representing degrees of host-symbiont conflict. Across nine different coral species (*Madracis mirabilis, Acropora cervicornis, Agaricia agaricites, Acropora palmata, Porites astreoides, Montastraea annularis, Montastraea cavernosa, Eusmilia fastigiata,* and *Dendrogyra cylindrus*), the symbiont mitotic index—a metric of reproduction—varied from 1.1% to 14.1%. Certain corals had far greater rates of microalgae reproduction (specifically, *Eusmilia fastigiata* and *Dendrogyra cylindrus*). Within the coral *Acropora cervicornis,* the mitotic index was higher at branch tips than branch base, suggesting that the coral allows or facilitates reproduction when it must populate growing tissue with symbionts. Finally, the mitotic index was greater in deeper habitats (Wilkerson et al. 1988).

The counterpoint to reproduction is, of course, predation. Free-living microalgae get to reproduce more, but is that offset by greater predation risk? Many authors hypothesize that corals protect their symbionts from predators, but to our knowledge no study has shown this. Generally, more research is needed on Symbiodiniaceae reproduction and predation inside and outside of a host (Box 10.1).

Beyond Corals: Housing Varies Dramatically Across Photosymbioses, and Plant Hosts Monitor the Specific Cooperativity of Rhizobium Symbionts

Symbionts Are Singly Intracellular, Multiply Intracellular, Extracellular, and Everything in Between. Symbionts occupy every imaginable position on the spectrum from extracellular to intracellular. Smith et al. (1997) illustrated this diversity, from the mostly extracellular algal symbiont in lichens with only 20% cell surface contact, to acoelomorph worm symbionts confusingly described as either intra- or extracellular, to fully intracellular *Chlorella* symbionts in green hydra. How a host organizes and houses symbionts is a key nexus of coevolution through cooperation and conflict (Fronk and Sachs 2022).

In photosymbiotic animals, most symbionts are either intracellular or localized within specific regions of the host (Venn et al. 2008; Rumpho et al. 2011; Melo Clavijo et al. 2018). We will mention a few interesting cases described by Melo Clavijo et al. (2018) that hint at variable rates of cheating and conflict within photosymbiotic clades.

Most colonial ascidians (family Didemnidae) have extracellular symbioses with cyanobacteria *Prochloron* or *Synechocystis trididemni,* but at least one species, *Lissoclinum punctatum,* has an intracellular *Procholon* symbiont (Hirose et al. 2009; Hirose 2015). In the salamander *Ambystoma maculatum,* eggs can bear *Oophila* algae intracellularly, extracellularly in the egg capsule, or not at all (Burns et al. 2017). Giant clams (Norton et al. 1992; Lucas 2014; Fatherree 2023) and heart cockles (Kawaguti 1950; Farmer et al. 2001; Li et al. 2020) are an interesting exception to the intracellular symbiosis rule (Venn et al. 2008): In these bivalves, *Symbiodinium* live extracellularly in specialized tubes that connect to the stomach and wind through the soft tissue to sun-exposed upper mantle.

Sponges can have either intracellular or extracellular photosymbionts (Trautman and Hinde 2001). For example, the bioeroding sponge *Cliona orientalis* (part of the *Cliona viridis* species complex) houses *Gerakladium* dinoflagellates (Symbiodiniaceae) at varying densities within its cells (Achlatis et al. 2019). The sponge *Haliclona cymaeformis* has an extracellular symbiosis with the red macroalga *Ceratodictyon spongiosum* (Pile et al. 2003).

Too little is known about the number of symbionts per cell in intracellular associations. Usually, symbiont density is calculated in ways that do not control for the number of host cells. But Muscatine et al. (1998) reported the number of symbionts per cell in a sample of marine organisms, such as the hydroid *Myrionema amboinense* (ten to twelve symbionts in the cytoplasm) (Fitt and Cook 1990), and green hydra (fifteen to twenty symbiont cells per vacuole) (Muscatine and Pool 1979; McAuley 1982, 1984). Muscatine et al. further cite research showing that supplementing hydra with extra nutrition increases the symbiont count in the vacuoles to fifty to sixty symbionts and causes the symbiosis to break down (Muscatine and Neckelmann 1981; Neckelmann and Muscatine 1983; Blank and Muscatine 1987).

Taken together, these examples suggest that symbiont housing relates tightly to the equity of nutrient sharing.

Plant-Rhizobium Symbioses: Theoretical and Experimental Evidence Shows That Nutrients Are Not Public Goods but Are Allocated Based on Specific Partner Generosity. Theoretical work suggests that persistent, stable symbioses are more likely to evolve when nutrients are not public goods; that is, when partners can discriminate and adjust resource availability (West et al. 2007a; Frank 2010; Ghoul et al. 2014; Kiers et al. 2016). In biology, hosts often harbor multiple different strains of symbiont mixed together at fine spatial scales. Theory predicts that the hosts should monitor each partner to provide more resources to the generous. Indeed, in plant-rhizobia symbioses, plants penalize partners that are artificially manipulated to not fix nitrogen; indeed, such "cheating" rhizobia are 50% less reproductively successful (Kiers et al. 2003). Using soybean *Glycine max* with *Bradyrhizobium japonicum,* Kiers et al. (2003) showed that the plants detected and punished cheaters across three spatial scales: whole plant, half root, and individual nodules.

Plants appear to selectively favor generous symbionts over cheaters even within the same nodule. Researchers studied the pea plant *Mimosa pudica* and two variants of bacterial symbiont *Cupriavidus taiwanensis,* one that can fix nitrogen, and one that cannot (Daubech et al. 2017). After the symbionts invaded root nodules, they initially reproduced at the same rates, but then the fixers began outcompeting the non-fixers even within the same nodule. Within twenty days, nodules containing non-fixers degenerated (Daubech et al. 2017).

Predictions: Singly Housed Symbionts Receive Fewer Nutrients, Share More Nutrients, and Reproduce Less

We predict that the number of symbionts housed per cell represents the freedom afforded the symbiont by the host and will therefore correlate with other metrics of conflict: reproductive rate of the symbiont, nutrients received by the symbiont, and more. Across photosymbiotic animals, corals, with their singly housed intracellular symbionts, seem to sit at the high-conflict, high-control end of the spectrum. Symbionts housed in groups will be freer to reproduce more and share less. Further, we predict that evolutionary transitions will tend to proceed from extracellular symbionts housed communally along the spectrum to intracellular symbionts housed singly.

Conclusion

Coral reef ecosystems depend on the dynamic interplay between corals and photosynthetic microalgae. While traditionally viewed as mutualistic, we suggest that animal hosts and their symbiotic microalgae experience a spectrum of interactions ranging from parasitic to mutualistic. Parasitic relationships may destabilize the symbiotic equilibrium, driving coral bleaching. Our proposed framework offers five avenues for quantifying conflict within these symbioses: reproductive mode, host sex determination, resource allocation, solar irradiation, and detecting cheaters. By quantifying these conflicts, we aim to deepen our understanding of how cooperative symbioses evolve and shed light on the mechanisms underlying coral bleaching. By doing so, perhaps we can design new ecological interventions to help vulnerable reef ecosystems. Taken together, we emphasize the role of evolutionary conflict in shaping entire ecosystems, as exemplified by the dance of conflict and cooperation within coral reefs.

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References

Achlatis, M., Schönberg, C. H. L., van der Zande, R. M., LaJeunesse, T. C., Hoegh-Guldberg, O., and Dove, S. (2019). Photosynthesis by symbiotic sponges enhances their ability to erode calcium carbonate. *Journal of Experimental Marine Biology and Ecology, 516,* 140–149.

Afkhami, M. E., McIntyre, P. J., and Strauss, S. Y. (2014). Mutualist-mediated effects on species' range limits across large geographic scales. *Ecology Letters, 17*(10), 1265–1273.

Aihara, Y., Maruyama, S., Baird, A. H., Iguchi, A., Takahashi, S., and Minagawa, J. (2019). Green fluorescence from cnidarian hosts attracts symbiotic algae. *Proceedings of the National Academy of Sciences of the United States of America, 116*(6), 2118–2123.

Ainsworth, T. D., Heron, S. F., Ortiz, J. C., et al. (2016). Climate change disables coral bleaching protection on the Great Barrier Reef. *Science, 352*(6283), 338–342.

Anderson, R. M., and May, R. M. (1982). Coevolution of hosts and parasites. *Parasitology, 85*(2), 411–426.

Andras, J. P., Rypien, K. L., and Harvell, C. D. (2013). Range-wide population genetic structure of the Caribbean sea fan coral, *Gorgonia ventalina*. *Molecular Ecology, 22*(1), 56–73.

Anthony, K., and Kerswell, A. (2007). Coral mortality following extreme low tides and high solar radiation. *Marine Biology, 151,* 1623–1631.

Armoza-Zvuloni, R., Kramarsky-Winter, E., Loya, Y., Schlesinger, A., and Rosenfeld, H. (2014). Trioecy, a unique breeding strategy in the sea anemone *Aiptasia diaphana* and its association with sex steroids. *Biology of Reproduction, 90*(6), 122, 1–8.

Ayre, D., and Miller, K. (2004). Where do clonal coral larvae go? Adult genotypic diversity conflicts with reproductive effort in the brooding coral *Pocillopora damicornis*. *Marine Ecology Progress Series, 277,* 95–105.

Baghdasarian, G., and Muscatine, L. (2000). Preferential expulsion of dividing algal cells as a mechanism for regulating algal-cnidarian symbiosis. *The Biological Bulletin, 199*(3), 278–286.

Baird, A. H., Guest, J. R., and Willis, B. L. (2009). Systematic and biogeographical patterns in the reproductive biology of scleractinian corals. *Annual Review of Ecology, Evolution, and Systematics, 40*(1), 551–571.

Baker, D. M., Andras, J. P., Jordán-Garza, A. G., and Fogel, M. L. (2013). Nitrate competition in a coral symbiosis varies with temperature among *Symbiodinium* clades. *The ISME Journal, 7,* 1248–1251.

Banaszak, A. T., García Ramos, M., and Goulet, T. L. (2013). The symbiosis between the gastropod *Strombus gigas* and the dinoflagellate *Symbiodinium*: An ontogenic journey from mutualism to parasitism. *Journal of Experimental Marine Biology and Ecology, 449,* 358–365.

Barott, K. L., Venn, A. A., Perez, S. O., Tambutté, S., and Tresguerres, M. (2015). Coral host cells acidify symbiotic algal microenvironment to promote photosynthesis. *Proceedings of the National Academy of Sciences of the United States of America, 112*(2), 607–612.

Bay, R. A., and Palumbi, S. R. (2014). Multilocus adaptation associated with heat resistance in reef-building corals. *Current Biology, 24*(24), 2952–2956.

Becking, T., Giraud, I., Raimond, M. et al. (2017). Diversity and evolution of sex determination systems in terrestrial isopods. *Scientific Reports, 7*(1).

Bennett, G. M., and Moran, N. A. (2015). Heritable symbiosis: The advantages and perils of an evolutionary rabbit hole. *Proceedings of the National Academy of Sciences of the United States of America, 112*(33), 10169–10176.

Birky, C. W., Jr., and Gilbert, J. J. (1971). Parthenogenesis in rotifers: The control of sexual and asexual reproduction. *American Zoologist, 11*(2), 245–266.

Blackstone, N. W., and Golladay, J. M. (2018). Why do corals bleach? Conflict and conflict mediation in a host/symbiont community. *BioEssays, 40*(8), e1800021.

Blank, R., and Muscatine, L. (1987). How do combinations of nutrients cause symbiotic chlorella to overgrow hydra? *Symbiosis, 3,* 123–134.

Bollati, E., D'Angelo, C., Alderdice, R., Pratchett, M., Ziegler, M., and Wiedenmann, J. (2020). Optical feedback loop involving dinoflagellate symbiont and scleractinian host drives colorful coral bleaching. *Current Biology, 30*(13), P2433–P2445.

Boyle, J. A., Simonsen, A. K., Frederickson, M. E., and Stinchcombe, J. R. (2021). Priority effects alter interaction outcomes in a legume–rhizobium mutualism. *Proceedings of the Royal Society B, 288*(1946), 20202753.

Brandvain, Y., and Haig, D. (2018). Outbreeders pull harder in a parental tug-of-war. *Proceedings of the National Academy of Sciences of the United States of America, 115*(45), 11354–11356.

Bright, M., and Bulgheresi, S. (2010). A complex journey: Transmission of microbial symbionts. *Nature Reviews Microbiology, 8*(3), 218–230.

Brodersen, K. E., Lichtenberg, M., Ralph, P. J., Kühl, M., and Wangpraseurt, D. (2014). Radiative energy budget reveals high photosynthetic efficiency in symbiont-bearing corals. *Journal of the Royal Society Interface, 11*(93), 20130997.

Brown, B., Dunne, R., Scoffin, T., and Le Tissier, M. (1994). Solar damage in intertidal corals. *Marine Ecology Progress Series, 105,* 219–230.

Brown, B. E., Ambarsari, I., Warner, M. E., et al. (1999). Diurnal changes in photochemical efficiency and xanthophyll concentrations in shallow water reef corals: Evidence for photoinhibition and photoprotection. *Coral Reefs, 18*(2), 99–105.

Buckingham, L. J., and Ashby, B. (2022). Coevolutionary theory of hosts and parasites. *Journal of Evolutionary Biology, 35*(2), 205–224.

Bull, J. J., Molineux, I. J., and Rice, W. R. (1991). Selection of benevolence in a host-parasite system. *Evolution, 45*(4), 875–882.

Byler, K. A., Carmi-Veal, M., Fine, M., and Goulet, T. L. (2013). Multiple symbiont acquisition strategies as an adaptive mechanism in the coral *Stylophora pistillata*. *PLoS One, 8*(3), e59596.

Campoy, A. N., Rivadeneira, M. M., Hernández, C. E., Meade, A., and Venditti, C. (2023). Deep-sea origin and depth colonization associated with phenotypic innovations in scleractinian corals. *Nature Communications, 14*(1), 7458.

Cantin, N. E., van Oppen, M. J. H., Willis, B. L., Mieog, J. C., and Negri, A. P. (2009). Juvenile corals can acquire more carbon from high-performance algal symbionts. *Coral Reefs, 28*(2), 405–414.

Carpenter, K. E., Abrar, M., Aeby, G., et al. (2008). One-third of reef-building corals face elevated extinction risk from climate change and local impacts. *Science, 321*(5888), 560–563.

Carter, J. G., and Schneider, J. A. (1997). Condensing lenses and shell microstructure in *Corculum* (Mollusca: Bivalvia). *Journal of Paleontology, 71*(1), 56–61.

Castro-Sanguino, C., Stick, D., Duffy, S., Grimaldi, C., Gilmour, J., and Thomas, L. (2024). Differential impacts of light on coral phenotypic responses to acute heat stress. *Journal of Experimental Marine Biology and Ecology, 581,* 152057.

Champion de Crespigny, F. E., and Wedell, N. (2006). *Wolbachia* infection reduces sperm competitive ability in an insect. *Proceedings of the Royal Society B, 273*(1593), 1455–1458.

Combosch, D. J., and Vollmer, S. V. (2013). Mixed asexual and sexual reproduction in the Indo-Pacific reef coral *Ocillopora damicornis*. *Ecology and Evolution, 3*(10), 3379–3387.

Cordaux, R., Bouchon, D., and Grève, P. (2011). The impact of endosymbionts on the evolution of host sex-determination mechanisms. *Trends in Genetics, 27*(8), 332–341.

Cordaux, R., and Gilbert, C. (2017). Evolutionary significance of *Wolbachia*-to-animal horizontal gene transfer: Female sex determination and the *f* element in the isopod *Armadillidium vulgare*. *Genes, 8*(7), 186.

Cormier, A., Chebbi, M. A., Giraud, I., et al. (2021). Comparative genomics of strictly vertically transmitted, feminizing microsporidia endosymbionts of amphipod crustaceans. *Genome Biology and Evolution, 13*(1), evaa245.

Cornwell, B. H. (2020). Gene flow in the anemone *Anthopleura elegantissima* limits signatures of local adaptation across an extensive geographic range. *Molecular Ecology, 29*(14), 2550–2566.

Cornwell, B. H., Armstrong, K., Walker, N. S., et al. (2021). Widespread variation in heat tolerance and symbiont load are associated with growth tradeoffs in the coral *Acropora hyacinthus* in Palau. *eLife, 10,* e64790.

Cornwell, B. H., and Hernández, L. (2021). Genetic structure in the endosymbiont Breviolum "muscatinei" is correlated with geographical location, environment and host species. *Proceedings of the Royal Society B, 288*(1946), 20202896.

Cunning, R., Silverstein, R. N., and Baker, A. C. (2015). Investigating the causes and consequences of symbiont shuffling in a multi-partner reef coral symbiosis under environmental change. *Proceedings of the Royal Society B, 282*(1809), 20141725.

Darling, E. S., Alvarez-Filip, L., Oliver, T. A., McClanahan, T. R., and Côté, I. M. (2012). Evaluating life-history strategies of reef corals from species traits. *Ecology Letters, 15*(12), 1378–1386.

Daubech, B., Remigi, P., Doin de Moura, G., et al. (2017). Spatio-temporal control of mutualism in legumes helps spread symbiotic nitrogen fixation. *eLife, 6,* e28683.

Davy, S. K., Allemand, D., and Weis, V. M. (2012). Cell biology of cnidarian-dinoflagellate symbiosis. *Microbiology and Molecular Biology Reviews, 76*(2), 229–261.

Davy, S. K., and B. Cook, C. (2001). The influence of "host release factor" on carbon release by zooxanthellae isolated from fed and starved *Aiptasia pallida* (Verrill). *Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology, 129*(2), 487–494.

del Campo, J., Pombert, J.-F., Šlapeta, J., Larkum, A., and Keeling, P. J. (2017). The "other" coral symbiont: Ostreobium diversity and distribution. *The ISME Journal, 11*(1), 296–299.

Douglas, A. E. (1994). *Symbiotic Interactions.* Oxford University Press.

Douglas, A. E., and Smith, D. C. (1989). Are endosymbioses mutualistic? *Trends in Ecology and Evolution,* 4(11), 350–352.

Dove, S. G., Hoegh-Guldberg, O., and Ranganathan, S. (2001). Major colour patterns of reef-building corals are due to a family of GFP-like proteins: *Coral Reefs, 19*(3), 197–204.

Downs, C. A., McDougall, K. E., Woodley, C. M., et al. (2013). Heat-stress and light-stress induce different cellular pathologies in the symbiotic dinoflagellate during coral bleaching. *PLoS One, 8*(12), e77173.

Drew, G. C., Stevens, E. J., and King, K. C. (2021). Microbial evolution and transitions along the parasite–mutualist continuum. *Nature Reviews Microbiology, 19*(10), 623–638.

Dunn, A. M., Rigaud, T., Ford, A. T., Cothran, R., and Thiel, M. (2020). Environmental influences on crustacean sex determination and reproduction: Environmental sex determination, parasitism and pollution. *The Natural History of the Crustacea: Reproductive Biology, 6,* 394–428.

Dusi, E., Gougat-Barbera, C., Berendonk, T. U., and Kaltz, O. (2015). Long-term selection experiment produces breakdown of horizontal transmissibility in parasite with mixed transmission mode. *Evolution, 69*(4), 1069–1076.

Eddy, T. D., Lam, V. W. Y., Reygondeau, G., et al. (2021). Global decline in capacity of coral reefs to provide ecosystem services. *One Earth, 4*(9), 1278–1285.

Edinger, E. N., and Risk, M. J. (1995). Preferential survivorship of brooding corals in a regional extinction. *Paleobiology, 21*(2), 200–219.

Emslie, M., Cheal, A., Sweatman, H., and Delean, S. (2008). Recovery from disturbance of coral and reef fish communities on the Great Barrier Reef, Australia. *Marine Ecology Progress Series, 371,* 177–190.

Enríquez, S., Méndez, E. R., Hoegh-Guldberg, O., and Iglesias-Prieto, R. (2017). Key functional role of the optical properties of coral skeletons in coral ecology and evolution. *Proceedings of the Royal Society B, 284*(1853), 20161667.

Enríquez, S., Méndez, E. R., and Prieto, R. I. (2005). Multiple scattering on coral skeletons enhances light absorption by symbiotic algae. *Limnology and Oceanography, 50*(4), 1025–1032.

Ewald, P. W. (1987). Transmission modes and evolution of the parasitism-mutualism continuum. *Annals of the New York Academy of Sciences, 503*(1), 295–306.

Fabina, N. S., Putnam, H. M., Franklin, E. C., Stat, M., and Gates, R. D. (2012). Transmission mode predicts specificity and interaction patterns in coral-symbiodinium networks. *PLoS One, 7*(9), e44970.

Fadlallah, Y. H. (1983). Sexual reproduction, development and larval biology in scleractinian corals: A review. *Coral Reefs,* 2(3), 129–150.

Farmer, M. A., Fitt, W. K., and Trench, R. K. (2001). Morphology of the symbiosis between *Corculum cardissa* (Mollusca: Bivalvia) and *Symbiodinium corculorum* (Dinophyceae). *The Biological Bulletin, 200*(3), 336–343.

Fatherree, J. W. (2023). *The Giant Clams: All About These Beautiful, Unique, and Fascinating Reef Animals*. Bowker.

Field, S. F., Bulina, M. Y., Kelmanson, I. V., Bielawski, J. P., and Matz, M. V. (2006). Adaptive evolution of multicolored fluorescent proteins in reef-building corals. *Journal of Molecular Evolution, 62*(3), 332–339.

Figueroa, R. I., Howe-Kerr, L. I., and Correa, A. M. S. (2021). Direct evidence of sex and a hypothesis about meiosis in Symbiodiniaceae. *Scientific Reports, 11*(1), 18838.

Fitt, W., and Cook, C. (1990). Some effect of host feeding on growth of zooxanthellae in the marine hydroid *Myrionema amblonense* in the laboratory and in nature. In *Endocytobiology IV: Proceedings of the Fourth International Colloquium on Endocytobiology and Symbiosis, Lyon, July 4–8, 1989,* edited by P. Nardon, V. Gianinazzi-Pearson, Grenier, L. Margulis, and D. C. Smith, 281–284. INRA.

Fitt, W. K. (1985). Chemosensory responses of the symbiotic dinoflagellate *Symbiodinium microadriaticum* (dinophyceae). *Journal of Phycology, 21*(1), 62–67.

Fitt, W. K., and Trench, R. K. (1983). The relation of diel patterns of cell division to diel patterns of motility in the symbiotic dinoflagellate *Symbiodinium microadria ticum* Freudenthal in culture. *New Phytologist, 94*(3), 421–432.

Frank, S. A. (1996). Models of parasite virulence. *Quarterly Review of Biology, 71*(1), 37–78.

Frank, S. A. (2010). A general model of the public goods dilemma. *Journal of Evolutionary Biology, 23*(6), 1245–1250.

Franklin, D. J., Hoegh-Guldberg, O., Jones, R. J., and Berges, J. A. (2004). Cell death and degeneration in the symbiotic dinoflagellates of the coral *Stylophora pistillata* during bleaching. *Marine Ecology Progress Series, 272,* 117–130.

Frederickson, M. E. (2013). Rethinking mutualism stability: Cheaters and the evolution of sanctions. *Quarterly Review of Biology, 88*(4), 269–295.

Frohnmeyer, H., and Staiger, D. (2003). Ultraviolet-B radiation-mediated responses in plants. Balancing damage and protection. *Plant Physiology, 133*(4), 1420–1428.

Fronk, D. C., and Sachs, J. L. (2022). Symbiotic organs: The nexus of host–microbe evolution. *Trends in Ecology and Evolution, 37*(7), 599–610.

Fujise, L., Suggett, D. J., Stat, M., et al. (2021). Unlocking the phylogenetic diversity, primary habitats, and abundances of free-living Symbiodiniaceae on a coral reef. *Molecular Ecology, 30*(1), 343–360.

Fujise, L., Yamashita, H., Suzuki, G., and Koike, K. (2013). Expulsion of zooxanthellae (*Symbiodinium*) from several species of scleractinian corals: Comparison under non-stress conditions and thermal stress conditions. *Galaxea, Journal of Coral Reef Studies, 15*(2), 29–36.

Fukui, T., Kawamoto, M., Shoji, K., et al. (2015). The endosymbiotic bacterium *Wolbachia* selectively kills male hosts by targeting the masculinizing gene. *PLoS Pathogens, 11*(7), e1005048.

Fuller, Z. L., Mocellin, V. J. L., Morris, L. A., et al. (2020). Population genetics of the coral *Acropora millepora*: Toward genomic prediction of bleaching. *Science, 369*(6501), eaba4674.

Galindo-Martínez, C. T., Weber, M., Avila-Magaña, V., et al. (2022). The role of the endolithic alga *Ostreobium* spp. during coral bleaching recovery. *Scientific Reports, 12*(1).

Gardner, A., and Ross, L. (2011). The evolution of hermaphroditism by an infectious male-derived cell lineage: An inclusive-fitness analysis. *The American Naturalist, 178*(2), 191–201.

Gault, J., Bentlage, B., Huang, D., and Kerr, A. (2021a). Lineage-specific variation in the evolutionary stability of coral photosymbiosis. [Dataset]. *Dryad,* July 29. https://doi.org/10.5061/dryad.tdz08kq0p.

Gault, J., Bentlage, B., Huang, D., and Kerr, A. M. (2021b). Lineage-specific variation in the evolutionary stability of coral photosymbiosis. *Science Advances, 7*(39), eabh4243.

Ghoshal, A., Eck, E., Gordon, M., and Morse, D. E. (2016). Wavelength-specific forward scattering of light by Bragg-reflective iridocytes in giant clams. *Journal of the Royal Society Interface, 13*(120), 20160285.

Ghoul, M., Griffin, A. S., and West, S. A. (2014). Toward an evolutionary definition of cheating. *Evolution, 68*(2), 318–331.

Gorman, L. M., Tivey, T. R., Raymond, E. H., et al. 2025. Stability of the cnidarian–dinoflagellate symbiosis is primarily determined by symbiont cell-cycle arrest. *Proceedings of the National Academy of Sciences of the United States of America, 122*(14), e2412396122.

Guest, J. R., Baird, A. H., Goh, B. P. L., and Chou, L. M. (2012). Sexual systems in scleractinian corals: An unusual pattern in the reef-building species *Diploastrea heliopora*. *Coral Reefs, 31*(3), 705–713.

Haig, D. (1993). Genetic conflicts in human pregnancy. *Quarterly Review of Biology, 68*(4), 495–532.

Haig, D. (2019). Cooperation and conflict in human pregnancy. *Current Biology, 29*(11), R455–R458.

Harrison, P. L., and Wallace, C. C. (1990). Reproduction, dispersal and recruitment of scleractinian corals. In *Coral Reefs,* edited by Z. Dubinsky, 133–207. Elsevier Science Publishers.

Hartmann, A. C., Baird, A. H., Knowlton, N., and Huang, D. (2017). The paradox of environmental symbiont acquisition in obligate mutualisms. *Current Biology, 27*(23), 3711–3716.

Heath, K. D., and Tiffin, P. (2007). Context dependence in the coevolution of plant and rhizobial mutualists. *Proceedings of the Royal Society B, 274*(1620), 1905–1912.

Heath, K. D., and Tiffin, P. (2009). Stabilizing mechanisms in a legume-rhizobium mutualism. *Evolution, 63*(3), 652–662.

Herre, E. A. (1993). Population structure and the evolution of virulence in nematode parasites of fig wasps. *Science, 259*(5100), 1442–1445.

Herre, E. A., Knowlton, N., Mueller, U. G., and Rehner, S. A. (1999). The evolution of mutualisms: Exploring the paths between conflict and cooperation. *Trends in Ecology and Evolution, 14*(2), 49–53.

Hiroki, M., Kato, Y., Kamito, T., and Miura, K. (2002). Feminization of genetic males by a symbiotic bacterium in a butterfly, *Eurema hecabe* (Lepidoptera: Pieridae). *Naturwissenschaften, 89*(4), 167–170.

Hirose, E. (2015). Ascidian photosymbiosis: Diversity of cyanobacterial transmission during embryogenesis. *Genesis, 53*(1), 121–131.

Hirose, E., and Hirose, M. (2007). Body colors and algal distribution in the acoel flatworm *Convolutriloba longifissura:* Histology and ultrastructure. *Zoological Science, 24*(12), 1241–1246.

Hirose, E., Neilan, B. A., Schmidt, E. W., and Murakami, A. (2009). Enigmatic life and evolution of prochloron and related cyanobacteria inhabiting colonial ascidians. In *Handbook on Cyanobacteria,* edited by P. Gault, 161–189. Nova Science Publishers.

Holt, A. L. (2024). Simple mechanism for optimal light-use efficiency of photosynthesis inspired by giant clams. *PRX Energy, 3*(2).

Holt, A. L., Vahidinia, S., Gagnon, Y. L., Morse, D. E., and Sweeney, A. M. (2014). Photosymbiotic giant clams are transformers of solar flux. *Journal of the Royal Society Interface, 11*(101), 20140678.

Hoogenboom, M. O., Connolly, S. R., and Anthony, K. R. N. (2008). Interactions between morphological and physiological plasticity optimize energy acquisition in corals. *Ecology, 89*(4), 1144–1154.

Hughes, T. P. (1994). Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science, 265*(5178), 1547–1551.

Humanes, A., Lachs, L., Beauchamp, E. A., et al. (2022). Within-population variability in coral heat tolerance indicates climate adaptation potential. *Proceedings of the Royal Society B, 289*(1981), 20220872.

Jarvis, G. C., White, C. R., and Marshall, D. J. (2022). Macroevolutionary patterns in marine hermaphroditism. *Evolution, 76*(12), 3014–3025.

Kageyama, D., Narita, S., and Watanabe, M. (2012). Insect sex determination manipulated by their endosymbionts: Incidences, mechanisms and implications. *Insects, 3*(1).

Kageyama, D., Ohno, M., Sasaki, T., et al. (2017). Feminizing *Wolbachia* endosymbiont disrupts maternal sex chromosome inheritance in a butterfly species. *Evolution Letters, 1*(5), 232–244.

Kaniewska, P., Magnusson, S. H., Anthony, K. R. N., Reef, R., Kühl, M., and Hoegh-Guldberg, O. (2011). Importance of macro- versus microstructure in modulating light levels inside coral colonies. *Journal of Phycology, 47*(4), 846–860.

Kawaguti, S. (1950). Observations on the heart shell, *Corculum. cardissa* (L.), and its associated zooxanthellae. *Pacific Science, 4*(1), 43–49.

Kenkel, C. D., and Bay, L. K. (2018). Exploring mechanisms that affect coral cooperation: Symbiont transmission mode, cell density and community composition. *PeerJ, 6,* e6047.

Kerr, A. M., Baird, A. H., and Hughes, T. P. (2010). Correlated evolution of sex and reproductive mode in corals (Anthozoa: Scleractinia). *Proceedings of the Royal Society B, 278*(1702), 75–81.

Kiers, E. T., Duhamel, M., Beesetty, Y., et al. (2011). Reciprocal rewards stabilize cooperation in the mycorrhizal symbiosis. *Science, 333*(6044), 880–882.

Kiers, E. T., Rousseau, R. A., West, S. A., and Denison, R. F. (2003). Host sanctions and the legume–rhizobium mutualism. *Nature, 425*(6953), 78–81.

Kiers, E. T., West, S. A., Wyatt, G. A. K., Gardner, A., Bücking, H., and Werner, G. D. A. (2016). Misconceptions on the application of biological market theory to the mycorrhizal symbiosis. *Nature Plants, 2*(5), 1–2.

Kiersi, E. T., and Denison, R. F. (2008). Sanctions, cooperation, and the stability of plant-rhizosphere mutualisms. *Annual Review of Ecology, Evolution, and Systematics, 39,* 215–236.

Knowlton, N. (2001). The future of coral reefs. *Proceedings of the National Academy of Sciences of the United States of America, 98*(10), 5419–5425.

Knowlton, N., Corcoran, E., Felis, T., et al. (2021). *Rebuilding Coral Reefs: A Decadal Grand Challenge.* International Coral Reef Society and Future Earth Coasts. https://doi.org/10.53642/NRKY9386.

Kramer, N., Guan, J., Chen, S., Wangpraseurt, D., and Loya, Y. (2022). Morpho-functional traits of the coral *Stylophora pistillata* enhance light capture for photosynthesis at mesophotic depths. *Communications Biology, 5*(1), 1–11.

Lachs, L., Donner, S. D., Mumby, P. J., et al. (2023). Emergent increase in coral thermal tolerance reduces mass bleaching under climate change. *Nature Communications, 14*(1), 4939.

LaJeunesse, T. C. (2020). Zooxanthellae. *Current Biology, 30*(19), R1110–R1113.

LaJeunesse, T. C., Parkinson, J. E., Gabrielson, P. W., et al. (2018). Systematic revision of Symbiodiniaceae highlights the antiquity and diversity of coral endosymbionts. *Current Biology, 28*(16), 2570–2580.

LaJeunesse, T. C., Wham, D. C., Pettay, D. T., Parkinson, J. E., Keshavmurthy, S., and Chen, C. A. (2014). Ecologically differentiated stress-tolerant endosymbionts in the dinoflagellate genus *Symbiodinium* (Dinophyceae) Clade D are different species. *Phycologia, 53*(4), 305–319.

Law, R., and Dieckmann, U. (1998). Symbiosis through exploitation and the merger of lineages in evolution. *Proceedings of the Royal Society B, 265*(1402), 1245–1253.

Leclercq, S., Thézé, J., Chebbi, M. A., et al. (2016). Birth of a W sex chromosome by horizontal transfer of *Wolbachia* bacterial symbiont genome. *Proceedings of the National Academy of Sciences of the United States of America, 113*(52), 15036–15041.

Lesser, M. P., and Farrell, J. H. (2004). Exposure to solar radiation increases damage to both host tissues and algal symbionts of corals during thermal stress. *Coral Reefs, 23*(3), 367–377.

Lesser, M. P., Stat, M., and Gates, R. D. (2013). The endosymbiotic dinoflagellates (*Symbiodinium* sp.) of corals are parasites and mutualists. *Coral Reefs, 32*(3), 603–611.

Li, J., Lemer, S., Kirkendale, L., Bieler, R., Cavanaugh, C., and Giribet, G. (2020). Shedding light: A phylotranscriptomic perspective illuminates the origin of photosymbiosis in marine bivalves. *BMC Evolutionary Biology, 20*(50).

Lively, C. M., and Johnson, S. G. (1997). Brooding and the evolution of parthenogenesis: Strategy models and evidence from aquatic invertebrates. *Proceedings of the Royal Society B, 256*(1345), 89–95.

Lord, K. S., Lesneski, K. C., Buston, P. M., Davies, S. W., D'Aloia, C. C., and Finnerty, J. R. (2023). Rampant asexual reproduction and limited dispersal in a mangrove population of the coral *Porites divaricata*. *Proceedings of the Royal Society B, 290*(2002), 20231070.

Lucas, J. S. (2014). Giant clams. *Current Biology, 24*(5), R183–R184.

Ma, Y., and Chen, R. (2021). Nitrogen and phosphorus signaling and transport during legume–rhizobium symbiosis. *Frontiers in Plant Science, 12*, 683601.

Madin, J. S., Anderson, K. D., Andreasen, M. H., et al. (2016). The Coral Trait Database, a curated database of trait information for coral species from the global oceans. *Scientific Data, 3*(1), 160017.

Marcelino, L. A., Westneat, M. W., Stoyneva, V., et al. (2013). Modulation of light-enhancement to symbiotic algae by light-scattering in corals and evolutionary trends in bleaching. *PLoS One, 8*(4), e61492.

Masuda, K., Miyachi, S., and Maruyama, T. (1994). Sensitivity of zooxanthellae and non-symbiotic microalgae to stimulation of photosynthate excretion by giant clam tissue homogenate. *Marine Biology, 118*(4), 687–693.

Matsuda, S. B., Opalek, M. L., Ritson-Williams, R., Gates, R. D., and Cunning, R. (2023). Symbiont-mediated tradeoffs between growth and heat tolerance are modulated by light and temperature in the coral *Montipora capitata*. *Coral Reefs, 42*(6), 1385–1394.

Matz, M. V. (2024). Not-so-mutually beneficial coral symbiosis. *Current Biology, 34*(17), R798–R801.

Maynard Smith, J. (1998). *Evolutionary Genetics*. 2nd ed. Oxford University Press.

McAuley, P. (1984). Variation in green hydra. A description of three cloned strains of *Hydra viridissima* Pallas 1766 (Cnidaria: Hydrozoa) isolated from a single site. *Biological Journal of the Linnean Society, 23*(1), 1–13.

McAuley, P. J. (1982). Temporal relationships of host cell and algal mitosis in the green hydra symbiosis. *Journal of Cell Science, 58*, 423–431.

McCoy, D. E., Burns, D. H., Klopfer, E., et al. (2024). Heart cockle shells transmit sunlight for photosynthesis using bundled fiber optic cables and condensing lenses. *Nature Communications, 15*, 9445.

McCoy, D. E., and Haig, D. (2020). Embryo selection and mate choice: Can "honest signals" be trusted? *Trends in Ecology and Evolution, 35*(4), 308–318.

McFall-Ngai, M. (2008). Hawaiian bobtail squid. *Current Biology, 18*(22), R1043–R1044.

McFall-Ngai, M. J. (1999). Consequences of evolving with bacterial symbionts: Insights from the squid-vibrio associations. *Annual Review of Ecology, Evolution, and Systematics, 30*(30), 235–256.

McFall-Ngai, M., and Ruby, E. (2021). Getting the message out: The many modes of host–symbiont communication during early-stage establishment of the squid-vibrio partnership. *mSystems, 6*(5).

McField, M. D. (1999). Coral response during and after mass bleaching in Belize. *Bulletin of Marine Science, 64*(1), 155–172.

Melo Clavijo, J., Donath, A., Serôdio, J., and Christa, G. (2018). Polymorphic adaptations in metazoans to establish and maintain photosymbioses. *Biological Reviews, 93*(4), 2006–2020.

Moore, T., and Haig, D. (1991). Genomic imprinting in mammalian development: A parental tug-of-war. *Trends in Genetics, 7*(2), 45–49.

Moran, N. A. (2007). Symbiosis as an adaptive process and source of phenotypic complexity. *Proceedings of the National Academy of Sciences of the United States of America, 104*(S1), 8627–8633.

Muscatine, L. (1967). Glycerol excretion by symbiotic algae from corals and tridacna and its control by the host. *Science, 156*(3774), 516–519.

Muscatine, L., Falkowski, P., and Dubinsky, Z. (1983). Carbon budgets in symbiotic associations. In *Intracellular Space as Oligogenetic Ecosystem: Proceedings,* edited by H. E. A. Schenk and W. Schwemmler, 649–658. De Gruyter.

Muscatine, L., Falkowski, P. G., Porter, J. W., Dubinsky, Z., and Smith, D. C. (1997). Fate of photosynthetic fixed carbon in light- and shade-adapted colonies of the symbiotic coral *Stylophora pistillata. Proceedings of the Royal Society B, 222*(1227), 181–202.

Muscatine, L., Ferrier-Pagès, C., Blackburn, A., Gates, R. D., Baghdasarian, G., and Allemand, D. (1998). Cell-specific density of symbiotic dinoflagellates in tropical anthozoans. *Coral Reefs, 17*(4), 329–337.

Muscatine, L., and Neckelmann, N. (1981). Regulation of numbers of algae in the hydra-chlorella symbiosis. *Berichte der Deutschen Botanischen Gesellschaft, 94*(1), 571–582.

Muscatine, L., and Pool, R. R. (1979). Regulation of numbers of intracellular algae. *Proceedings of the Royal Society B, 204*(1155), 131–139.

Nakamura, T., Yamasaki, H., and Woesik, R. van. (2003). Water flow facilitates recovery from bleaching in the coral *Stylophora pistillata. Marine Ecology Progress Series, 256,* 287–291.

Neckelmann, N., and Muscatine, L. (1983). Regulatory mechanisms maintaining the hydra-chlorella symbiosis. *Proceedings of the Royal Society B, 219*(1215), 193–210.

Negri, I., Franchini, A., Gonella, E., et al. (2009). Unravelling the *Wolbachia* evolutionary role: The reprogramming of the host genomic imprinting. *Proceedings of the Royal Society B, 276*(1666), 2485–2491.

Negri, I., Pellecchia, M., Mazzoglio, P. J., Patetta, A., and Alma, A. (2006). Feminizing *Wolbachia* in *Zyginidia pullula* (Insecta, Hemiptera), a leafhopper with an XX/X0 sex-determination system. *Proceedings of the Royal Society B, 273*(1599), 2409–2416.

Nitschke, M. R., Rosset, S. L., Oakley, C. A., et al. (2022). The diversity and ecology of *Symbiodiniaceae:* A traits-based review. In *Advances in Marine Biology,* edited by C. Sheppard, 55–127. Academic Press.

Noë, R., and Hammerstein, P. (1994). Biological markets: Supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behavioral Ecology and Sociobiology, 35*(1), 1–11.

Noë, R., and Hammerstein, P. (1995). Biological markets. *Trends in Ecology and Evolution, 10*(8), 336–339.

Normark, B. B. (2004). Haplodiploidy as an outcome of coevolution between male-killing cytoplasmic elements and their hosts. *Evolution, 58*(4), 790–798.

Norton, J. H., Shepherd, M. A., Long, H. M., and Fitt, W. K. (1992). The zooxanthellal tubular system in the giant clam. *The Biological Bulletin, 183*(3), 503–506.

Nyholm, S. V., and McFall-Ngai, M. (2004). The winnowing: Establishing the squid–vibrio symbiosis. *Nature Reviews Microbiology, 2*(8), 632–642.

Nyholm, S. V., and McFall-Ngai, M. J. (2021). A lasting symbiosis: How the Hawaiian bobtail squid finds and keeps its bioluminescent bacterial partner. *Nature Reviews Microbiology, 19*(10), 666–679.

Okasha, S. (2021). Cancer and the levels of selection. *British Journal for the Philosophy of Science, 75*(3), 537–560.

Palacio-Castro, A. M., Smith, T. B., Brandtneris, V., et al. (2023). Increased dominance of heat-tolerant symbionts creates resilient coral reefs in near-term ocean warming. *Proceedings of the National Academy of Sciences of the United States of America, 120*(8), e2202388120.

Palumbi, S. R., Barshis, D. J., Traylor-Knowles, N., and Bay, R. A. (2014). Mechanisms of reef coral resistance to future climate change. *Science, 344*(6186), 895–898.

Pannebakker, B. A., Pijnacker, L. P., Zwaan, B. J., and Beukeboom, L. W. (2004). Cytology of *Wolbachia*-induced parthenogenesis in *Leptopilina clavipes* (Hymenoptera: Figitidae). *Genome,* 47(2), 299–303.

Parkinson, J. E., Peixoto, R. S., and Voolstra, C. R. (2025). Symbiodiniaceae. In *Coral Reef Microbiome,* edited by Raquel S. Peixoto and Christian R. Voolstra, 9–23. Springer Nature Switzerland.

Pasternak, Z., Blasius, B., Abelson, A., and Achituv, Y. (2006). Host-finding behaviour and navigation capabilities of symbiotic zooxanthellae. *Coral Reefs, 25*(2), 201–207.

Patten, M. M., Schenkel, M. A., and Ågren, J. A. (2023). Adaptation in the face of internal conflict: The paradox of the organism revisited. *Biological Reviews, 98*(5), 1796–1811.

Petrou, K., Ralph, P. J., and Nielsen, D. A. (2017). A novel mechanism for host-mediated photoprotection in endosymbiotic foraminifera. *The ISME Journal, 11*(2).

Pettay, D. T., Wham, D. C., Smith, R. T., Iglesias-Prieto, R., and LaJeunesse, T. C. (2015). Microbial invasion of the Caribbean by an Indo-Pacific coral zooxanthella. *Proceedings of the National Academy of Sciences of the United States of America, 112*(24), 7513–7518.

Pile, A. J., Grant, A., Hinde, R., and Borowitzka, M. A. (2003). Heterotrophy on ultraplankton communities is an important source of nitrogen for a sponge–rhodophyte symbiosis. *Journal of Experimental Biology, 206*(24), 4533–4538.

Porter, S. S., and Rice, K. J. (2013). Trade-offs, spatial heterogeneity, and the maintenance of microbial diversity. *Evolution, 67*(2), 599–608.

Price, T. A. R., and Wedell, N. (2008). Selfish genetic elements and sexual selection: Their impact on male fertility. *Genetica, 134*(1), 99–111.

Queller, D. C. (2014). Joint phenotypes, evolutionary conflict and the fundamental theorem of natural selection. *Philosophical Transactions of the Royal Society B, 369*(1642), 20130423.

Queller, D. C., and Strassmann, J. E. (2018). Evolutionary conflict. *Annual Review of Ecology, Evolution, and Systematics, 49,* 73–93.

Quigley, K. M., Ramsby, B., Laffy, P., Harris, J., Mocellin, V. J. L., and Bay, L. K. (2022). Symbioses are restructured by repeated mass coral bleaching. *Science Advances, 8*(49), eabq8349.

Quigley, K. M., Warner, P. A., Bay, L. K., and Willis, B. L. (2018). Unexpected mixed-mode transmission and moderate genetic regulation of *Symbiodinium* communities in a brooding coral. *Heredity, 121*(6), 524–536.

Richmond, R. H. (1997). Reproduction and recruitment in corals: Critical links in the persistence of reefs. In *Life and Death of Coral Reefs,* edited by C. Birkeland, 175–197. Chapman & Hall.

Rigaud, T., Juchault, P., and Mocquard, J.-P. (1997). The evolution of sex determination in isopod crustaceans. *BioEssays, 19*(5), 409–416.

Rodrigues, L. J., and Grottoli, A. G. (2007). Energy reserves and metabolism as indicators of coral recovery from bleaching. *Limnology and Oceanography, 52*(5), 1874–1882.

Rodríguez-Román, A., Hernández-Pech, X., E. Thome, P., Enríquez, S., and Iglesias-Prieto, R. (2006). Photosynthesis and light utilization in the Caribbean coral *Montastraea faveolata* recovering from a bleaching event. *Limnology and Oceanography, 51*(6), 2702–2710.

Rossbach, S., Subedi, R. C., Ng, T. K., Ooi, B. S., and Duarte, C. M. (2020). Iridocytes mediate photonic cooperation between giant clams (Tridacninae) and their photosynthetic symbionts. *Frontiers in Marin Science, 7,* 465.

Rui, Y., Zhaohui, Z., Wenshan, S., Bafang, L., and Hu, H. (2019). Protective effect of MAAs extracted from *Porphyra tenera* against UV irradiation-induced photoaging in mouse skin. *Journal of Photochemistry and Photobiology B: Biology, 192,* 26–33.

Rumpho, M. E., Pelletreau, K. N., Moustafa, A., and Bhattacharya, D. (2011). The making of a photosynthetic animal. *Journal of Experimental Biology, 214*(2), 303–311.

Sachs, J. L., Mueller, U. G., Wilcox, T. P., and Bull, J. J. (2004). The evolution of cooperation. *Quarterly Review of Biology, 79*(2), 135–160.

Sachs, J. L., and Simms, E. L. (2006). Pathways to mutualism breakdown. *Trends in Ecology and Evolution, 21*(10), 585–592.

Sachs, J. L., Skophammer, R. G., Bansal, N., and Stajich, J. E. (2014). Evolutionary origins and diversification of proteobacterial mutualists. *Proceedings of the Royal Society B, 281*(1775), 20132146.

Sachs, J. L., and Wilcox, T. P. (2005). A shift to parasitism in the jellyfish symbiont *Symbiodinium microadriaticum*. *Proceedings of the Royal Society B, 273*(1585), 425–429.

Salih, A., Larkum, A., Cox, G., Kühl, M., and Hoegh-Guldberg, O. (2000). Fluorescent pigments in corals are photoprotective. *Nature, 408*(6814).

Santos, S. R., Gutiérrez-Rodríguez, C., Lasker, H. R., and Coffroth, M. A. (2003). *Symbiodinium* sp. associations in the gorgonian *Pseudopterogorgia elisabethae* in the Bahamas: High levels of genetic variability and population structure in symbiotic dinoflagellates. *Marine Biology, 143*(1), 111–120.

Schenkel, M. A., Patten, M. M., and Agren, J. A. (2024). Quantifying internal conflicts and their threats to organismal form and fitness. *bioRxiv.* https://doi.org/10.1101/2024.02.05.578856.

Schlesinger, A., Kramarsky-Winter, E., Rosenfeld, H., Armoza-Zvoloni, R., and Loya, Y. (2010). Sexual plasticity and self-fertilization in the sea anemone *Aiptasia diaphana*. *PLoS One, 5*(7), e11874.

Schwenkert, S., Fernie, A. R., and Geigenberger, P. (2022). Chloroplasts are key players to cope with light and temperature stress. *Trends in Plant Science, 27*(6), 577–587.

Seneca, F. O., and Palumbi, S. R. (2015). The role of transcriptome resilience in resistance of corals to bleaching. *Molecular Ecology, 24*(7), 1467–1484.

Sheppard, C., Davy, S., Pilling, G., and Graham, N. (2018). *The Biology of Coral Reefs*. 2nd ed. Oxford University Press.

Shi, Y., Ke, X., Yang, X., Liu, Y., and Hou, X. (2022). Plants response to light stress. *Journal of Genetics and Genomics, 49*(8), 735–747.

Smith, D. C., Richmond, M. H., and Smith, D. C. (1997). From extracellular to intracellular: The establishment of a symbiosis. *Proceedings of the Royal Society B, 204*(1155), 115–130.

Smith, S. E., and Smith, F. A. (2012). Fresh perspectives on the roles of arbuscular mycorrhizal fungi in plant nutrition and growth. *Mycologia, 104*(1), 1–13.

Stambler, N., and Dubinsky, Z. (2005). Corals as light collectors: An integrating sphere approach. *Coral Reefs, 24*(1), 1–9.

Stat, M., Morris, E., and Gates, R. D. (2008). Functional diversity in coral–dinoflagellate symbiosis. *Proceedings of the National Academy of Sciences of the United States of America, 105*(27), 9256–9261.

Stewart, A. D., Logsdon, J. M., and Kelley, S. E. (2005). An empirical study of the evolution of virulence under both horizontal and vertical transmission. *Evolution, 59*(4), 730–739.

Stouthamer, R., Breeuwer, J. A., and Hurst, G. D. (1999). *Wolbachia* pipientis: Microbial manipulator of arthropod reproduction. *Annual Review of Microbiology, 53,* 71–102.

Stouthamer, R., Russell, J. E., Vavre, F., and Nunney, L. (2010). Intragenomic conflict in populations infected by parthenogenesis inducing *Wolbachia* ends with irreversible loss of sexual reproduction. *BMC Evolutionary Biology, 10*(1), 229.

Sutton, D. C., and Hoegh-Guldberg, O. (1990). Host–zooxanthella interactions in four temperate marine invertebrate symbioses: Assessment of effect of host extracts on symbionts. *The Biological Bulletin, 178*(2), 175–186.

Swain, T. D., DuBois, E., Gomes, A., et al. (2016). Skeletal light-scattering accelerates bleaching response in reef-building corals. *BMC Ecology, 16*(1), 1–18.

Swain, T. D., Westneat, M. W., Backman, V., and Marcelino, L. A. (2018). Phylogenetic analysis of symbiont transmission mechanisms reveal evolutionary patterns in thermotolerance and host specificity that enhance bleaching resistance among vertically transmitted *Symbiodinium*. *European Journal of Phycology, 53*(4), 443–459.

Terán, E., Méndez, E., Enríquez, S., and Iglesias-Prieto, R. (2010). Multiple light scattering and absorption in reef-building corals. *Applied Optics, 49,* 5032–5042.

Thomas, L., and Palumbi, S. R. (2017). The genomics of recovery from coral bleaching. *Proceedings of the Royal Society B, 284*(1865), 20171790.

Thornhill, D. J., Fitt, W. K., and Schmidt, G. W. (2006). Highly stable symbioses among western Atlantic brooding corals. *Coral Reefs, 25*(4), 515–519.

Thornhill, D. J., Lewis, A. M., Wham, D. C., and LaJeunesse, T. C. (2014). Host-specialist lineages dominate the adaptive radiation of reef coral endosymbionts. *Evolution, 68*(2), 352–367.

Titlyanov, E. A., Titlyanova, T. V., Leletkin, V. A., Tsukahara, J., van Woesik, R., and Yamazato, K. (1996). Degradation of zooxanthellae and regulation of their density in hermatypic corals. *Marine Ecology Progress Series, 139,* 167–178.

Toft, C., and Andersson, S. G. E. (2010). Evolutionary microbial genomics: Insights into bacterial host adaptation. *Nature Reviews Genetics, 11*(7).

Tomascik, T., and Sander, F. (1987). Effects of eutrophication on reef-building corals. *Marine Biology, 94*(1), 77–94.

Tram, U., and Sullivan, W. (2002). Role of delayed nuclear envelope breakdown and mitosis in *Wolbachia*-induced cytoplasmic incompatibility. *Science, 296*(5570), 1124–1126.

Trautman, D. A., and Hinde, R. (2001). Sponge/algal symbioses: A diversity of associations. In *Symbiosis: Mechanisms and model systems,* 521–537. Springer.

Tremblay, P., Fine, M., Maguer, J. F., Grover, R., and Ferrier-Pagès, C. (2013). Photosynthate translocation increases in response to low seawater pH in a coral–dinoflagellate symbiosis. *Biogeosciences, 10*(6), 3997–4007.

van Rhijn, P., and Vanderleyden, J. (1995). The rhizobium-plant symbiosis. *Microbiological Reviews, 59*(1), 124–142.

van't Padje, A., Werner, G. D. A., and Kiers, E. T. (2021). Mycorrhizal fungi control phosphorus value in trade symbiosis with host roots when exposed to abrupt "crashes" and "booms" of resource availability. *New Phytologist, 229*(5), 2933–2944.

Venn, A. A., Loram, J. E., and Douglas, A. E. (2008). Photosynthetic symbioses in animals. *Journal of Experimental Botany, 59*(5), 1069–1080.

Verspoor, R. L., Price, T. A. R., and Wedell, N. (2020). Selfish genetic elements and male fertility. *Philosophical Transactions of the Royal Society B, 375*(1813), 20200067.

Vollmer, A. (2018). Rare parthenogenic reproduction in a common reef coral, *Porites astreoides. HCNSO Student Theses and Dissertations.* https://nsuworks.nova.edu/occ_stuetd/464.

Walker, N. S., Nestor, V., Golbuu, Y., and Palumbi, S. R. (2023). Coral bleaching resistance variation is linked to differential mortality and skeletal growth during recovery. *Evolutionary Applications, 16*(2), 504–517.

Wangpraseurt, D., Jacques, S. L., Petrie, T., and Kühl, M. (2016). Monte Carlo modeling of photon propagation reveals highly scattering coral tissue. *Frontiers in Plant Science, 7,* 1404.

Wangpraseurt, D., Larkum, A. W., Ralph, P. J., and Kühl, M. (2012). Light gradients and optical microniches in coral tissues. *Frontiers in Microbiology, 3,* 316.

Wedell, N. (2020). Selfish genes and sexual selection: The impact of genomic parasites on host reproduction. *Journal of Zoology, 311*(1), 1–12.

Werner, G. D. A., Strassmann, J. E., Ivens, A. B. F., et al. (2014). Evolution of microbial markets. *Proceedings of the National Academy of Sciences of the United States of America, 111*(4), 1237–1244.

Werren, J. H., Baldo, L., and Clark, M. E. (2008). *Wolbachia:* Master manipulators of invertebrate biology. *Nature Reviews Microbiology, 6*(10).

West, S. A., Griffin, A. S., and Gardner, A. (2007a). Evolutionary explanations for cooperation. *Current Biology, 17*(16), R661–R672.

West, S. A., Griffin, A. S., and Gardner, A. (2007b). Social semantics: Altruism, cooperation, mutualism, strong reciprocity and group selection. *Journal of Evolutionary Biology, 20*(2), 415–432.

West, S. A., Kiers, E. T., Pen, I., and Denison, R. F. (2002). Sanctions and mutualism stability: When should less beneficial mutualists be tolerated? *Journal of Evolutionary Biology, 15*(5), 830–837.

Wiedenmann, J., D'Angelo, C., Mardones, M. L., et al. (2023). Reef-building corals farm and feed on their photosynthetic symbionts. *Nature, 620*(7976), 1018–1024.

Wilkerson, F. P., Kobayashi, D., and Muscatine, L. (1988). Mitotic index and size of symbiotic algae in Caribbean reef corals. *Coral Reefs, 7*(1), 29–36.

Wilkinson, D. M., and Sherratt, T. N. (2001). Horizontally acquired mutualisms, an unsolved problem in ecology? *Oikos, 92*(2), 377–384.

Wooldridge, S. (2010). Is the coral-algae symbiosis really "mutually beneficial" for the partners? *BioEssays, 32,* 615–625.

Woolhouse, M. E. J., Webster, J. P., Domingo, E., Charlesworth, B., and Levin, B. R. (2002). Biological and biomedical implications of the co-evolution of pathogens and their hosts. *Nature Genetics, 32*(4), 569–577.

Xiang, T., Lehnert, E., Jinkerson, R. E., et al. (2020). Symbiont population control by host-symbiont metabolic interaction in *Symbiodiniaceae-cnidarian* associations. *Nature Communications, 11*(1).

Yakovleva, I., Baird, A., Yamamoto, H., Bhagooli, R., Nonaka, M., and Hidaka, M. (2009). Algal symbionts increase oxidative damage and death in coral larvae at high temperatures. *Marine Ecology Progress Series, 378,* 105–112.

Yamazaki, S. S., Nakamura, T., and Yamasaki, H. (2008). Photoprotective role of endolithic algae colonized in coral skeleton for the host photosynthesis. In *Photosynthesis: Energy from the Sun,* edited by J. F. Allen, E. Gantt, J. H. Golbeck, and B. Osmond, 1391–1395. Springer Netherlands.

Zanders, S. E., and Unckless, R. L. (2019). Fertility costs of meiotic drivers. *Current Biology, 29*(11), R512–R520.