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Opinion

Facultative lifestyle drives diversity of coral algal symbionts

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The photosynthetic symbionts of corals sustain biodiverse reefs in nutrient-poor, tropical waters. Recent genomic data illuminate the evolution of coral symbionts under genome size constraints and suggest that retention of the facultative lifestyle, widespread among these algae, confers a selective advantage when compared with a strict symbiotic existence. We posit that the coral symbiosis is analogous to a 'bioreactor' that selects winner genotypes and allows them to rise to high numbers in a sheltered habitat prior to release by the coral host. Our observations lead to a novel hypothesis, the 'stepping-stone model', which predicts that local adaptation under both the symbiotic and free-living stages, in a stepwise fashion, accelerates coral alga diversity and the origin of endemic strains and species.

Highlights

The Symbiodiniaceae have been coral symbionts for over 200 million years, yet they retain a facultative lifestyle because both the symbiotic and free-living stages offer unique selective advantages that ensure persistence of the algal lineage.

There exists a dynamic competition and interaction between the coral host and algal symbionts that ensures survival of both under fluctuating environmental conditions.

If algal symbiont-derived redox stress does not explain coral host bleaching, then it is possible that either or both partners generate a chemical cue that precipitates algal expulsion independent of malfunctions in their electron transport chains.

We propose the 'stepping-stone model' as an explanation for the long-term and successful association between coral animals and their facultative algal symbionts, which in a stepwise manner creates novel Symbiodiniaceae lineages worldwide.

Biology and evolutionary history of Symbiodiniaceae

Dinoflagellate microalgae in the family **Symbiodiniaceae** [1] (see Glossary) are best known for their role as symbionts critical to corals and other coral reef organisms such as sea anemones, jellyfish, giant clams, and some foraminifera [2]. Stony corals (Scleractinia) host each algal symbiont in their gastrodermal tissues in a specialized compartment referred to as the **symbiosome**. These microalgae provide photosynthetic energy via carbon fixation that 'powers' coral reefs and supplies essential nutrients to support the most biodiverse ecosystems in tropical and subtropical oceans [3–5]. Environmental stressors, including those caused by anthropogenic activities, increasingly lead to the breakdown of the coral-dinoflagellate symbiosis (i.e., resulting in coral bleaching [6]) and underscore the vulnerability of coral reef health in the face of global climate change. To improve understanding of coral reef resilience to changing environments, it is important to elucidate the longer-term evolution of the coral-dinoflagellate alga symbiosis and the factors that sustain this ecologically important biotic interaction.

The Symbiodiniaceae are members of one of the most complex groups of photosynthetic eukaryotes known (class Dinophyceae), most of which have massive genomes. Symbiodiniaceae genomes, ca. 0.7–2.0 Gbp in size, are smaller compared with other dinoflagellates (ca. 2–200 Gbp) except for parasitic lineages [7] (Box 1). Dinoflagellates also have a unique chromosome structure and gene regulation pathways that are poorly understood [8,9]. Comparative genomic data support the presence of the machinery for sexual reproduction in Symbiodiniaceae [10], which is supported by cytological data targeting *Cladocopium latusorum* symbionts in their *Pocillopora* coral host [11]. Given current understanding, the pairing of a cnidarian host with dinoflagellate symbionts, each of which have large gene inventories (25–50K in the cnidarian, 30–40K in symbionts [12]), provides a fascinating, yet challenging model system for 'omics' and genetics research [13].

Fossil evidence demonstrates a rich stony coral record ca. 245 million years ago (MYA), with dominant reefs having emerged by ca. 225 MYA [14]. Molecular clock analysis suggests that

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Box 1. Footprints of long-term endosymbiosis

Long-term endosymbiosis is predicted to leave 'footprints' on the genomes of captured cells, including reduction in genome size (e.g., gene family contraction) due to a more specialized lifestyle, higher levels of pseudogenization, and enhanced genetic drift due to a reduction in effective population size, N_e [59,60].

Resident genome syndrome

These traits characterize 'resident genome syndrome' and was hypothesized to explain genome evolution in Symbiodiniaceae [61]. However, more recent analysis of over a dozen Symbiodiniaceae genomes has not turned up the classic markers associated with an obligate symbiotic lifestyle among presumably symbiotic lineages: for example, gene family and genome reduction when compared with facultative or free-living lineages. In fact, there is no clear pattern of genome evolution found when comparing different Symbiodiniaceae genomes that can be easily explained by lifestyle [62].

Effrenium genome data

The genomes of three putatively obligate free-living Symbiodiniaceae in the genus *Effrenium* are also 1.2–1.9 Gbp in size and differ only in subtle ways (longer introns, more extensive mRNA editing) from the symbiotic lineages [62]. The genomes of these putative, ancestrally free-living Symbiodiniaceae are of similar size and complexity as those that form symbioses, suggesting that massive genome reduction occurred prior to the origin of the coral alga symbiosis and was not an outcome of this interaction.

Long-term Symbiodiniaceae genome evolution

The <2 Gbp size of all Symbiodiniaceae nuclear genomes characterized thus far is likely better explained by the existence of an extremophilic, free-living ancestor that underwent genome streamlining. This idea argues against the resident genome syndrome and is supported by analysis of the free-living, psychrophilic (polar dwelling) sister group of Symbiodiniaceae, *Polarella glacialis*, that has a comparable haploid genome size of 1.4 Gbp. This is far smaller than the genome size of free-living dinoflagellates outside the order Suessiales in which the family Symbiodiniaceae are classified (Figure I) [62,63].

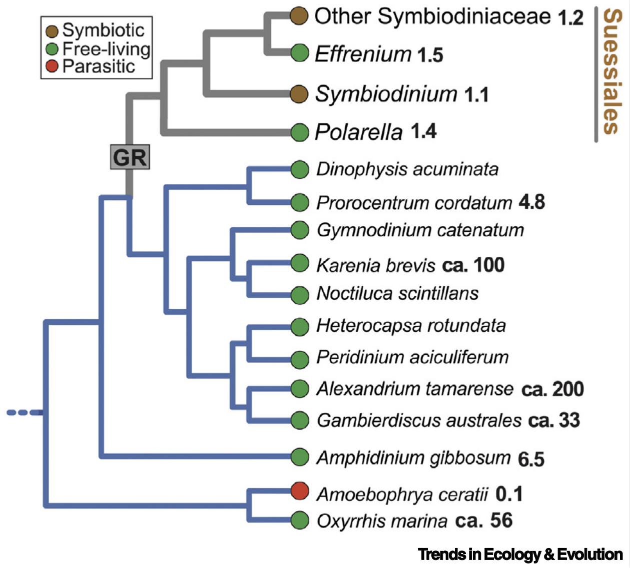

Figure I. Phylogeny of Symbiodiniaceae and other dinoflagellates. This image is adapted from Shah *et al.* [62], with the tree built using genome-wide data from 33 dinoflagellates. The Suessiales is indicated with the vertical line and the distribution of lifestyles is marked with different colors (see key within the figure). Approximate nuclear haploid genome size is shown, when available, in bold font after the species names. The putative branch on which massive genome reduction occurred in the Suessiales ancestor is marked with GR (for details, see [62]).

the Symbiodiniaceae radiation occurred ca. 140–200 MYA and likely supported the coral radiation [1]. This idea is buttressed by analysis of nitrogen isotopes in coral fossils that suggest photosymbionts (presumably, ancestral Symbiodiniaceae) were present during early coral diversification in shallow waters [15]. Therefore, it is surprising that despite this long-term symbiosis, many Symbiodiniaceae are **facultative**, that is, they still retain a free-living stage [8,16,17]. These algae can persist as coccoid cells maintained in symbiosomes [18] in the cnidarian animal

Glossary

Environmental DNA (eDNA): nuclear or organellar DNA released to the environment, which can be detected and analyzed to study species distribution and diversity without the need for isolating nucleic acids from organisms.

Facultative: an organism that can live both as a symbiont (or parasite) and as free-living. Many Symbiodiniaceae taxa have facultative lifestyles.

Free-living: an organism that does not rely on an association with another (e.g., through parasitism or symbiosis) for survival.

Holobiont: the meta-organism that includes a host and all associated organisms that live in, on, or around it, as a functional ecological unit. The coral holobiont includes the cnidarian animal host, Symbiodiniaceae photosymbionts, other eukaryotes (e.g., fungi and protists), the prokaryote microbiome, and viruses.

Horizontal transmission: symbiont transmission to progeny independent of the parent. In corals, this refers to the acquisition of algal symbionts each generation from the surrounding waters.

Ohnologs: gene duplicates that have arisen from whole-genome duplication event(s), named after Susumu Ohno, a pioneer in the field.

Symbiodiniaceae: this family in the order Suessiales comprises marine dinoflagellates that often form symbioses with corals, sea anemones, and other marine invertebrates although they also have free-living stages. These cells were once referred to as Zooxanthellae, but this term is no longer in common usage. Symbiodiniaceae is divided into at least 15 clades with 11 named genera thus far, although their taxonomy and diversity are still poorly understood.

Symbiosome: an intracellular, membrane-enclosed compartment in the coral gastrodermis that contains a Symbiodiniaceae cell.

Vertical transmission: symbiont transmission directly from the parent to progeny. In corals, this refers to the transmission of algal symbionts in the egg each generation.

Whole-genome duplication (WGD): the process whereby the entire genome of an organism is duplicated once or several times, often referred to as polyploidy. WGD may be evolutionarily beneficial by generating multiple gene copies (ohnologs) that create more host, or as a biflagellate free-living cell like other planktonic dinoflagellates [5]. Symbiont proliferation is controlled by the host (i.e., reflecting the division rate of gastrodermal cells), which is higher in symbiotic than aposymbiotic cells [19,20]. It is estimated that free-living Symbiodiniaceae are needed by 80–85% of coral species that recruit symbionts each generation, through a process known as **horizontal transmission** [21,22]. And, except some species (e.g., *Galaxea acrhelia*, *Porites lobata*, *Montipora* spp.) that inherit their symbionts through the egg via **vertical transmission**, and some facultative hosts (which can acquire their symbionts via horizontal transmission, or in some cases, vertical transmission that can live without Symbiodiniaceae [23]), most corals recruit algal symbionts from the local environment each generation. These two strategies may have different outcomes for the host, with horizontal transmission potentially conferring fitness advantages to the symbionts, and vertical transmission, the coral animal within the **holobiont** [24]. Recent work suggests, however, that vertical transmission may place a burden on coral larvae due to redox stress derived from photosynthesis [25]. These results point to the need for additional research on the role of algal genotype in coral health and resilience, an interaction that likely differs among coral species. Nonetheless, consistent with horizontal transmission, analysis of diversity using **environmental DNA (eDNA)** shows that members of different Symbiodiniaceae genera (e.g., *Cladocopium*, *Durusdinium*, and *Fugacium*) are present in the water, sediments, and/or associated with macrophytes in reef habitats [17]. These recent developments lead us to pose two major hypotheses that we explore in this Opinion article: (i) given the long-term interaction between Symbiodiniaceae and corals, these algae are under selection to retain a facultative lifestyle, with the corollary that symbiosis offers unique advantages not available in the free-living phase; and (ii) the facultative lifestyle is a major evolutionary driver of Symbiodiniaceae diversity.

protein products or give rise to diverged genes with novel functions favored by selection.

Why retain a facultative lifestyle?

We posit that retention of a facultative lifestyle by Symbiodiniaceae must be due to a selective benefit, whereby both free-living and symbiotic stages offer distinct advantages that neither does by itself. The putative drivers of coral algal evolution and diversification are shown in Figure 1. Under this model, the coral symbiosis offers a safe haven, that despite the relative rarity of sexual reproduction (1.5% of symbiotic cells [10]), and the restriction of symbionts to primarily vegetative growth, enables increase in algal population size within host symbiosomes. Earlier studies revealed 1–3 million Symbiodiniaceae cells/cm^2 coral surface area in *Acropora valida* and *Pocillopora damicornis* [26,27]. These abundances are orders of magnitude greater than for free-living Symbiodiniaceae that are subject to predation, infection by parasites, and other stresses in the environment. For example, free-living *Cladocopium* cells near Heron Island, Australia, range from about four to 1000 cells/cm^3 in different habitats (i.e., water, sediments, macroalgal surfaces), with these values being 1–175 cells/cm^3 for *Durusdinium* [17]. These values do not differ significantly between spawning and nonspawning times of the year [17]. Although the in-host and free-living cell abundance numbers are difficult to compare directly, data from these studies clearly demonstrate the high density of algae in coral tissues. This observation leads us to speculate that beyond providing refuge in a nutrient-rich, stable environment, the high concentrations of algae within host tissues comprise a pool of the fittest [e.g., most thermally (or other stress) tolerant] genotypes that, once they are released by the coral to the environment, may then be favored by other corals under horizontal transmission [28,29] because they confer local selective advantages to different host population members or to other species (Figure 1). In addition, the higher concentrations of these fit genotypes make them statistically more likely to be retained by surrounding corals. This virtuous cycle could be a driver of Symbiodiniaceae biodiversity, as shown in Figure 1, with both horizontal and vertical transmission favored under different circumstances for different coral species. As such, algal strains and species that are highly adaptive in specific habitats or under specific stressors may be advantageous under vertical transmission, ensuring their transmission to subsequent generations, whereas rapidly changing

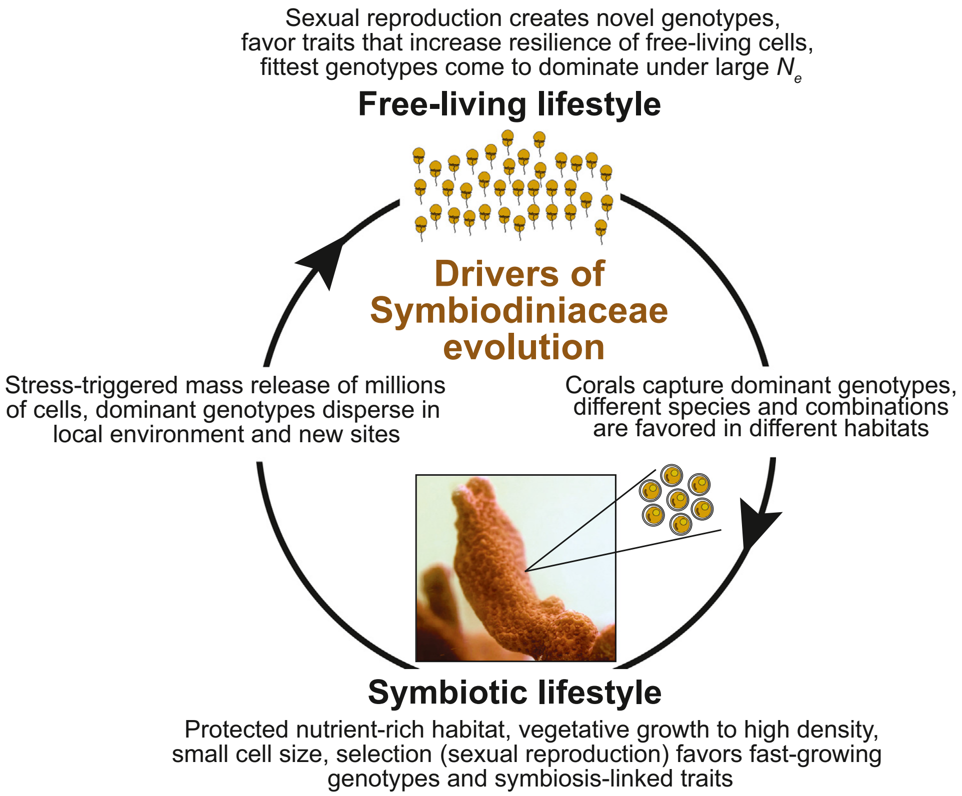

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Figure 1. The stepping-stone model of Symbiodiniaceae evolution. The putative virtuous cycle formed by the symbiotic and free-living stages of coral algal symbionts that drives local adaptation and rise of the fittest genotypes. We postulate that this cycle explains the long-term retention of the facultative lifestyle in Symbiodiniaceae.

environments may favor horizontal transmission to ensure the capture of physiologically beneficial genotypes [25,30].

This perspective makes the coral symbiosis less of a period of captivity for the alga, but rather, a time for beneficial genotypes to multiply and dominate coral tissues and potentially spread to other colonies on the reef. Of course, the proportion of different species and strains will vary from colony to colony and under different stressors and seasons. Nonetheless, if the Symbiodiniaceae are seen as units of photosynthetic cells, then we speculate that symbiosis may be the 'bioreactor' that selects winner genotypes and allows them to rise to high numbers in a sheltered habitat, analogous to a true algal bioreactor. In this way, micronutrients and inorganic carbon are provisioned, under normal conditions, by the coral host to enhance photosynthetic performance [3]. And, as would be expected in an experimental evolution approach that selects for growth rate (or some other attribute, possibly to support corals that feed on their symbionts [31]), algal cells become smaller in size to increase nutrient absorption [32], lose flagella-based motility (due to confinement in symbiosomes), and potentially undergo rare sexual reproduction to create novel, potentially beneficial allelic combinations. All these traits are present in symbiotic Symbiodiniaceae (Figure 1). However, the symbiotic lifestyle has drawbacks, which would be apparent under thermal anomalies or other stress conditions. Under heat stress, in-host algae are provisioned less by the host, that attempts to conserve precious resources such as nitrogen, phosphorus, and amino acids to ensure its own survival [33–36].

The inability to manage redox stress due to malfunctions in electron transport in stressed algal symbionts is often cited as the major reason for coral bleaching, but little direct evidence exists to support this hypothesis [37]. Furthermore, algae have efficient mechanisms in place (e.g., nonphotochemical quenching) for dealing with excess excitation energy to protect photosystems from damage [38]. Therefore, given the apparent energy deficit experienced by the host under thermal or other forms of stress, it is counterintuitive that, from the host perspective, algal symbionts are expelled into the environment instead of being consumed and used directly for energy and other resources within the symbiosomes. These compartments are relatives of lysosomes, that once modified, may be able to readily carry out this function [39]. Furthermore, evidence suggests that corals actively 'farm and feed' on symbiotic algae, demonstrating their capacity to consume symbionts under normal conditions [31]. In support of this idea, a recent study of corals infected with stony coral tissue loss disease (SCTLD) reported increased expression by the host of Ras-related protein 7 (*rab7*). This gene is a marker of algal symbiont degradation under SCTLD and likely transforms the symbiosomes into a digestive organelle [40]. From the symbiont perspective, the algae may drive their expulsion under unfavorable host conditions through the secretion of a chemical signal, but this idea is yet to be tested. In any case, we posit that the dissociation of Symbiodiniaceae from the host (either due to bleaching or via normal shedding) favors the algae more than it does the coral by allowing the fittest algal genotypes to return to a free-living lifestyle or associate with other hosts, be they corals or other marine taxa.

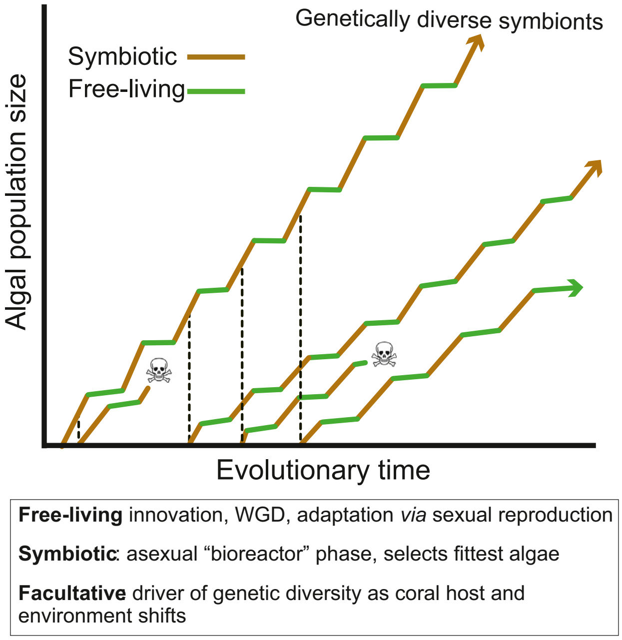
Why retain a free-living lifestyle?

The free-living lifestyle likely offers three major benefits to Symbiodiniaceae. The first, supported by their widespread distribution in the open oceans, is the opportunity to disperse to new locations and potentially, new hosts [41]. The second is to undergo more frequent sexual recombination to generate higher genetic variation, compared with the predominantly clonal propagation under symbiosis [28]. This idea is supported by the high genomic divergence observed among isolates of the same Symbiodiniaceae species [9,42]. The third benefit is to access nutrients (e.g., nitrogen sources) that, under environmental stress, are no longer adequately supplied by the coral host to support the high-density symbiotic cell population [34,36]. We posit that these three features accelerate Symbiodiniaceae evolution and create large numbers of locally adapted genotypes that can interact in a myriad of ways with coral hosts (Figure 1). The **whole-genome duplication (WGD)** observed in two strains of *Durusdinium trenchii* provides a compelling example of how the free-living lifestyle can create wholesale genetic change that results in more stable and thermally resistant symbionts that come to dominate local reefs under climate change [43]. Given that genome growth is the opposite of what is expected to occur in obligate symbionts, the *D. trenchii* example shows that selection to improve fitness, putatively during the free-living stage (i.e., via WGD), can lead to significant positive outcomes for the algae during symbiosis. Specifically, the free-living stage of *D. trenchii* is under selection to maximize nutrient acquisition, evade predators and parasites, and tolerate fluctuating environmental conditions (e.g., incident light, nutrients, or warming oceans). These traits may be significantly enhanced by WGD that expands gene family size via **ohnologs** to enable functional specialization of duplicated genes and potentially allow 'escape from extinction' [44]. By contrast, the symbiotic lifestyle should favor adaptations that enhance the host-symbiont relationship and integrate better nutrient and metabolite cycling between the two partners [43]. The *D. trenchii* work suggests that the switch between these two lifestyles impacts the genome of this algal symbiont and may explain the retention of this species within corals facing thermal stress [45]. By contrast, *Cladocopium* species often confer a faster growth rate to corals [46]; therefore, these algae, or a mixture of both species, may be favored in different environments with negligible physiological trade-offs for the host [47,48].

We postulate that the facultative lifestyle, widespread among Symbiodiniaceae, rather than being an inexplicable peculiarity, is in fact a major driver of their evolution that has been maintained by natural selection for the >200-million-year span that corals have existed. During symbiosis, the microalgae exploit host animal resources to facilitate population growth under favorable conditions. By contrast, the free-living stage serves to aid dispersal, increase genetic variation, and escape limitations posed by a malfunctioning symbiosis (i.e., under stress), driving adaptation to changing environmental conditions [28,49]. This combination of lifestyles has allowed Symbiodiniaceae to become a highly successful and globally dispersed group of dinoflagellate algae [41]. In unvarnished terms, corals in many regions of the world are regrettably destined for loss under climate change [50], but their algal symbionts will likely thrive due to their facultative lifestyle and massive genetic potential that allows host shifts and the ability to gain energy through mixotrophy [51,52]. This observation may explain why the dual lifestyle is key to Symbiodiniaceae evolution and should be integrated into experiments and interpretation of data that address algal or coral fitness.

The stepping-stone model of Symbiodiniaceae evolution

The ideas presented here suggest that the high known diversity of Symbiodiniaceae taxa [2] will likely be overshadowed by their unknown diversity as more coral holobionts are studied in detail. This notion is captured by our stepping-stone model of Symbiodiniaceae evolution shown in Figure 2, which predicts that population growth under symbiosis, local adaptation, combined with the facultative lifestyle will accelerate algal diversity and lead to novel endemic strains and species worldwide. To test this idea, we summarized the phylogeny of the broadly applied Symbiodiniaceae taxonomic marker ITS2 using SymPortal [53]. We focused on symbionts from two coral species that inhabit the isolated Hawaiian Archipelago, a region that hosts many marine and terrestrial endemics [54]. Use of standard alignment [55] and phylogenetic tools [56] produced a tree, albeit with limited resolution due to the short sequences used for the analysis (ca. 256 bp), that has some useful attributes. Focusing on sequences from Hawai'i, USA (outer



Free-living innovation, WGD, adaptation *via* sexual reproduction

Symbiotic: asexual "bioreactor" phase, selects fittest algae

Facultative driver of genetic diversity as coral host and environment shifts

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Figure 2. Hypothesized evolutionary trajectory of a locally adapted Symbiodiniaceae lineage in a coral colony that gives rise to novel algal lineages through time. The population size of some strains and species is posited to increase during the 'bioreactor' symbiotic stage (see legend) primarily due to enhanced vegetative growth, with selection (e.g., based on photosynthetic performance and/or stress tolerance) choosing the winners, which also increases coral health and resilience. This leads to the origin of novel genotypes that start at small population size (see broken lines), with some rising to prominence or being lost (marked with skull-and-crossbones). Release from corals leads to spread of the fittest symbionts. Algae in the free-living stage undergo sexual reproduction and local adaptation to the nonsymbiotic condition (e.g., WGD in *Durusdinium trenchii*), prior to the next cycle of symbiosis. Over time, we postulate that the facultative lifestyle, paired with different coral or other hosts, and changing environmental conditions, recruitment of novel genotypes accelerates overall Symbiodiniaceae diversity.

blue lines, Figure 3), the paraphyletic *Durusdinium* clade in Kāne ohe Bay with the highest abundance is spread primarily among strains from the Red Sea and the Persian-Arabian Gulf, suggesting these latter regions may be a source of the Hawaiian populations (or vice versa). Therefore, *Durusdinium* strains in Kāne ohe Bay are, on first principles, not endemics, insofar as a single genetic marker can address this complex trait [i.e., other genome regions may (and will likely) provide evidence of local adaptation]. The opposite appears to hold for the *Cladocopium* clade, whereby some abundant Hawaiian strains form a monophyletic group, and others have an affiliation with sequences from the Great Barrier Reef or are dispersed throughout the tree. These latter results suggest that the stepping-stone model may apply to some *Cladocopium* strains from Kāne ohe Bay. A Hawaiian *Breviolum* strain appears to also share affinity with cells from the Red Sea and the Israeli Mediterranean Sea (Figure 3). Admittedly, these data are preliminary and need to be expanded to many more sites worldwide using both ITS2 and genome data (including other islands in Hawai'i) to test the ideas presented here.

Concluding remarks

We conclude by returning to the two major hypotheses presented in this article: (i) coral algae are under selection to retain a facultative lifestyle (i.e., a solely obligate symbiotic lifestyle is less

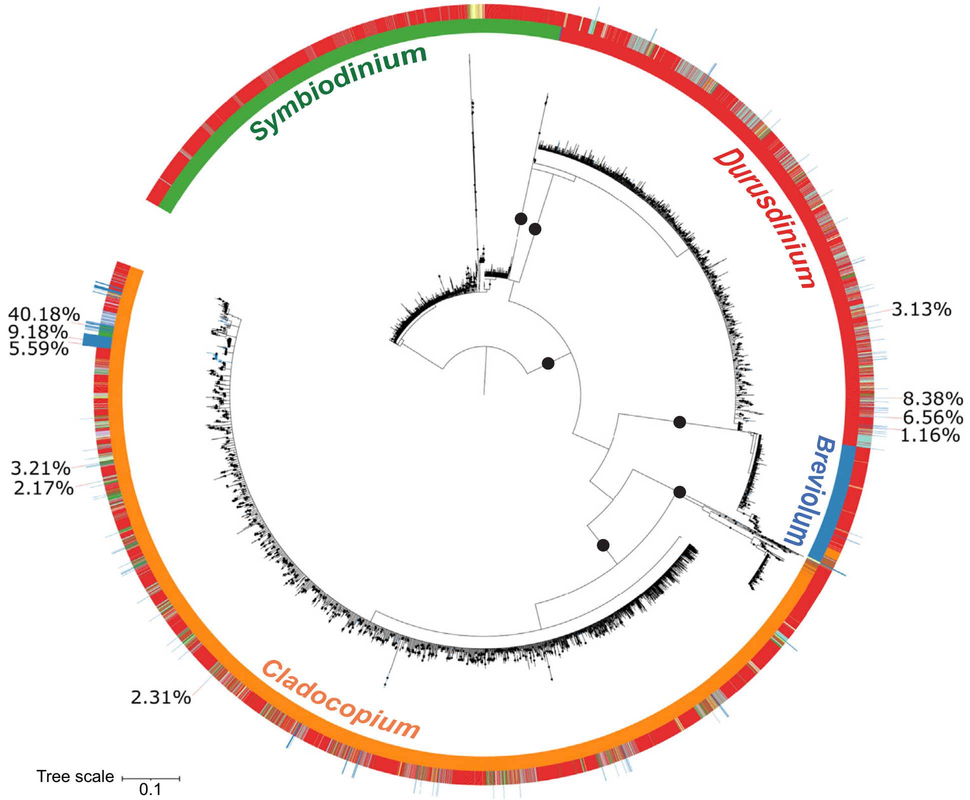

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Figure 3. Unrooted tree of ITS2 sequences from Hawaii and other global locations. The data for 119 *Pocillopora acuta* and 132 *Montipora capitata* individuals are from colonies collected in Kāne ohe Bay, Hawai'i (BioProject: PRJNA761780). Ultrafast bootstrap node support [58], when ≥95%, is shown using black-filled circles on each node. The unit of branch length is in number of substitutions per site. The data come from the SymPortal predicted genera *Durusdinium*, *Cladocopium*, *Breviolum*, and *Symbiodinium*. Sequences of the 251 Hawaii samples are shown as blue lines (for other locations, see Figure S1 in the supplemental information online). The relative abundance of these Hawaiian ITS2 sequences (when >1%) is also shown.

Outstanding questions

Given the stepping-stone model holds, what is the true diversity of Symbiodiniaceae worldwide, and how do these algae disperse across the long distances that often separate coral reefs?

Is the stepping-stone model specific to the coral alga symbiosis, or would it also apply to other facultative algal symbionts?

How has local adaptation to resident coral species and abiotic conditions impacted the genome evolution and rich gene inventory of Symbiodiniaceae?

How widespread is whole-genome duplication among Symbiodiniaceae and how does selection shape these genomes, post-duplication?

What is the trigger for the release of algae from coral host tissues, if not driven by the production of reactive oxygen species (ROS) by either partner in the symbiosis?

favored) and (ii) the facultative lifestyle drives Symbiodiniaceae biodiversity. Our distillation of the existing data, focusing on recent genomic information, provides insights that are consistent with both these hypotheses and forms a testable framework for future research (see Outstanding questions). The coral symbiosis, in our opinion, is robust on a worldwide scale. The long-term survival of this symbiosis, despite undergoing several past mass extinction events, is testament to its success [57]. This attribute is explained by the dynamic and competitive interaction that exists between the cnidarian host and Symbiodiniaceae, ensuring survival of both, with their associated microbiomes. The stepping-stone model attempts to provide the algal side of the story and should prove useful in the unfolding drama precipitated by climate change. Our hope is that a more nuanced understanding of how algae contribute to coral resilience in changing environments and the rules that govern this ecologically vital symbiotic relationship will follow.

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Declaration of interests

The authors declare no conflicts of interest.

Supplemental information

Supplemental information associated with this article can be found at https://github.com/povalis/TREE-supplemental-information https://doi.org/10.1016/j.tree.2023.10.005.

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