PERSPECTIVE

The endosymbiotic dinoflagellates (*Symbiodinium* sp.) of corals are parasites and mutualists

M. P. Lesser · M. Stat · R. D. Gates

Abstract The evolutionary success and continued survival of reef-building corals under increasing environmental change will, in part, be determined by the composition of their endosymbiotic dinoflagellate communities (*Symbiodinium* sp.). Recent research suggests that differences in the phylotype composition of *Symbiodinium* in the same host can lead to different outcomes for the host when exposed to similar environmental conditions. One explanation for these observations is that symbioses between corals and *Symbiodinium* represent a continuum of interaction states that encompass mutualisms and parasitisms consistent with current evolutionary theory developed for other symbiotic systems. Here, we discuss the evidence supporting the existence of a parasitic to mutualistic continuum in *Symbiodinium* interactions and propose that a consideration of the evolutionary ecology of these associations will advance our understanding of how environmental change will influence the ecological outcomes in these important symbioses. We advocate that a robust taxonomic structure for *Symbiodinium* sp. and empirical studies on sexual reproduction in *Symbiodinium*, the stability of interaction states among *Symbiodinium* symbioses spatially and temporally and how interaction states change as the environment changes will generate data for models that accurately forecast how climate change will influence the persistence of corals and the reefs they structure.

Keywords Corals · Dinoflagellates · Mutualistic · Parasitic · *Symbiodinium* sp

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Why do we need to recontextualize *Symbiodinium* sp. symbioses now?

One of the best-studied marine symbiotic systems is the association between cnidarians (e.g., sea anemones and corals) and photoautotrophic dinoflagellates in the genus *Symbiodinium*, commonly referred to as zooxanthellae. The evolutionary and ecological success of scleractinian corals and coral reefs since the Triassic period has been attributed to the mutualistic endosymbiosis between the coral host and *Symbiodinium*. Modern reef–forming corals and the ecosystems they define are under significant ecological pressure from the negative effects of global climate change and local anthropogenic impacts (Lesser 2004; Hoegh-Guldberg et al. 2007). Given that the integrity of the *Symbiodinium*-coral symbiosis frames the survival of corals; this interaction has been the subject of numerous studies aimed at understanding which *Symbiodinium* phylotypes provide the most, or continuing, benefit to

corals in the face of environmental disturbance, with the goal of better forecasting the impact of climate change on this important symbiosis. This context not only limits our understanding of the stress response of corals but also limits our understanding of the basic biology of *Symbiodinium*-coral symbioses. We believe reframing the context under which we study these symbioses is needed.

Symbioses and the parasitic to mutualistic continuum

The most widely used definition of symbiosis was provided by de Bary (1879) as the "living together of two differently named organisms". While arguments for alternative definitions of symbiosis persisted into the twentieth century (e.g., Lewin 1982), symbiosis today is commonly defined as intimate, enduring associations between individuals of different species (Goff 1982), a description that recognizes that these interactions are dynamic in time and space and that these shifts influence outcomes for one or both partners (Bronstein 1994). Symbioses are ubiquitous in nature and have generated a significant amount of biodiversity on the planet (Moran 2006; Brucker and Bordenstein 2012). It is widely recognized that many ecologically important symbioses are intimate at the cellular level (i.e., endosymbiotic) and have been traditionally represented by the range of symbiotic interactions defined as mutualistic, commensal and parasitic (Leung and Poulin 2008). This framework has expanded to embrace the idea that the fitness outcomes of both partners and the stability of the symbiosis can have significant ecological and evolutionary consequences when considered as a parasitic to mutualistic continuum (Star 1975; Lewis 1985). This is especially true when one or both partners acquire novel capabilities (Herre et al. 1999; Leung and Poulin 2008) that are adaptive in an evolutionary context (Moran 2007), or demonstrate metabolic plasticity in the face of environmental change (Moran 2007). Evolutionary theory frames the mutualistic environment as the coevolution of a host with beneficial symbionts (Moran 2006), where evolutionary stasis occurs as new symbiotic partners are selected against and the evolution of asexuality in the symbiont is favored to reduce genetic recombination and the emergence of novel phenotypes (Sachs et al. 2011a). This mutualistic framework contrasts with the parasitic setting, which is often described as an "antagonistic arms race", favoring rare symbiont genotypes, rapid symbiont evolution to escape host defenses and sexual recombination to produce multiple symbiont phenotypes for selection to act upon (Sachs et al. 2011a) (Fig. 1).

More recent theory suggests that mutualisms and parasitisms represent differences in the balance between reciprocal exploitation and conflict avoidance between
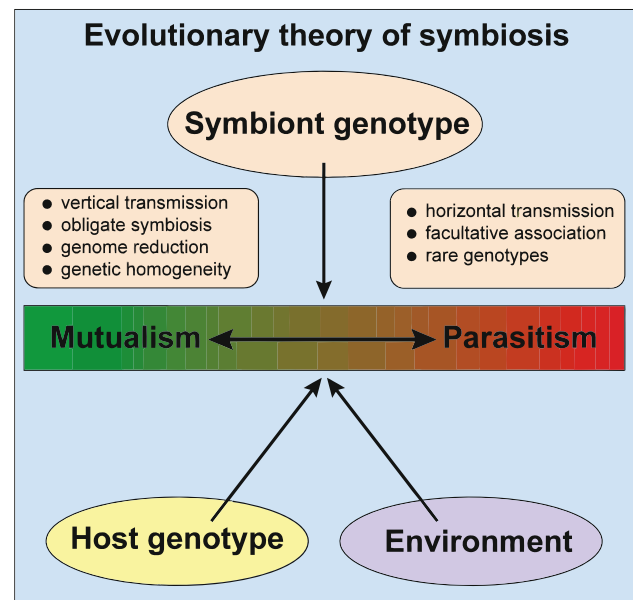

Fig. 1 Illustration of the mutualistic to parasitic continuum with the host and symbiont phylotype and the environment as primary drivers of the continuum and the life-history characteristics commonly identified as state characters (i.e., phenotypes) under upon which selection acts

symbiotic partners (Sachs et al. 2011a). Here, mutualisms are maintained under a scenario of reciprocal exploitative interactions (Herre et al. 1999; Sachs et al. 2011a), simultaneously keeping the contribution of each partner to a minimum while selfishly maximizing their own fitness. In contrast, parasites gain benefits with little or no reciprocation and are described as cheaters or exploiters (Herre et al. 1999; Sachs and Simms 2006; Sachs et al. 2011a). Three factors are considered important in conflict avoidance in symbioses: (i) vertical transmission of symbionts, which favors increased metabolic integration that leads to symbiont genome reduction and obligate dependency for a specific host; (ii) genetic uniformity of symbionts, which reduces the number of competitive phenotypes that a host has to contend with; and (iii) little or no dependency of symbionts on a free-living state (Herre et al. 1999; Sachs et al. 2011a).

The balance between interaction states can be upset by conflicts over resource exchange between symbiotic partners, symbiont transmission strategy and mode of symbiont reproduction (i.e., sexual versus asexual) (Douglas and Smith 1983; Herre et al. 1999; Douglas 2010; Sachs et al. 2011a). Additionally, the effects of abiotic and biotic factors can influence the dynamics between partners during reciprocal exploitation and affect the trajectory of any symbiotic partnership (Herre et al. 1999). Changing conditions, either external or internal, can create strong selection for symbionts that maximize their own fitness at

the expense of their host, with the transition from mutualism to parasitism over both ecological and evolutionary timescales (Toft and Andersson 2010; Sachs et al. 2011a). While these transitions appear to be rare, they can occur if the symbiont is facultative and able to persist outside the host in a free-living state (Sachs and Simms 2006).

Evolutionary theories of symbiosis also propose that the horizontal transfer of taxonomically diverse symbionts uncouples symbiont effectiveness from host fitness despite selective pressures to maximize symbiont integration with its host (Herre et al. 1999; Moran 2007; Leung and Poulin 2008). In contrast, the vertical transmission of symbionts between parent and offspring leads to phylogenetic homogeneity of symbionts and increases symbiont effectiveness for the host (Herre et al. 1999). A recent analysis of the available genomic data on bacterial symbionts of eukaryotic hosts tested several of these hypotheses and showed that most bacterial mutualisms evolved from free-living lineages expressing novel traits (e.g., nitrogen fixation) that could be exploited by the host, or by horizontal transfer of beneficial symbiont genes to hosts (Toft and Andersson 2010; Sachs et al. 2011b). The analysis also showed that bacterial mutualisms could evolve from parasitic lineages when vertical transmission of symbionts evolves in the host (Toft and Andersson 2010; Sachs et al. 2011b). Transitions to vertically transmitting symbionts are driven by selection on the host who has the most to gain from establishing a long-term beneficial symbiosis with a specialized partner (Frank 1996; Toft and Andersson 2010; Sachs et al. 2011b).

Symbiosis between corals and *Symbiodinium*

Originally described as one panmictic species, *Symbiodinium microadriaticum* (Freudenthal 1962), subsequent studies have shown that separate species exist within the genus *Symbiodinium* (Blank and Trench 1985; Trench and Blank 1987). Using multiple markers and molecular genetic approaches, we now know that this genus is much more diverse than originally appreciated (Rowan and Powers 1991a, b; Baker 2003; Takabayashi et al. 2004) and to date, nine divergent lineages of *Symbiodinium* (Fig. 2) known as clades A-I (Pochon et al. 2006; Stat et al. 2006; Pochon and Gates 2010) have been described. There is also evidence that some of this genetic diversity is reflected in functional diversity such as thermal tolerance (Kinzie et al. 2001; Jones and Berkelmans 2011). For example, phylotypes of clade D *Symbiodinium* appear to become dominant during and after bleaching in corals; bleaching is a stress response that manifests as a paling in coral coloration associated with a breakdown of the

symbiosis, often driven by anomalously high ocean temperatures (Baker 2003; Stat et al. 2006; Berkelmans and van Oppen 2006; LaJeunesse et al. 2009; Mieog et al. 2009). The functional diversity in *Symbiodinium* also results in ecological niche partitioning among clades along gradients of abiotic factors such as underwater irradiance (Rowan and Knowlton 1995; Baker 2003; Pochon and Gates 2010). Corals can harbor one or more clades, and more than one within clade phylotype (Takabayashi et al. 2004; Pochon et al. 2006; Stat et al. 2006; Pochon and Gates 2010). This diversity of symbionts within individual corals theoretically creates the potential for physiological plasticity through "shuffling" *Symbiodinium* types or "switching" from one dominant *Symbiodinium* type that is more physiologically suited to the prevailing environmental conditions (Trench and Blank 1987; Baker 2003; Stat et al. 2006).
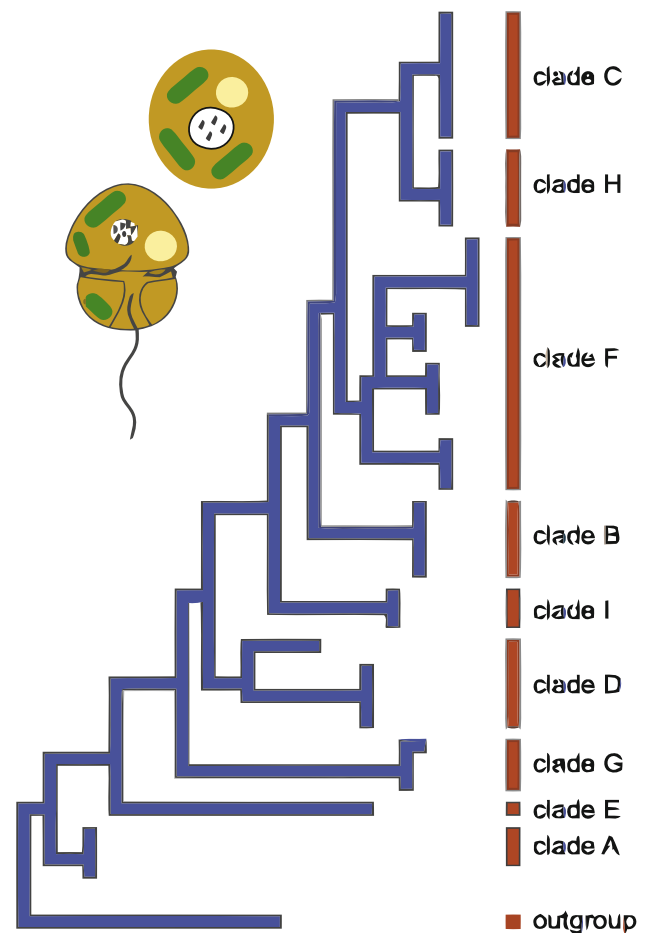

Fig. 2 Illustration of maximum likelihood clade phylogeny for the genus *Symbiodinium* sp. (showing illustrations of both cyst and zoospore stages) based on the 28S rDNA marker (adapted from Pochon and Gates (2010)). The out-group is represented by the dinoflagellate, *Gymnodinium simplex*

Symbiodinium as mutualists and parasites

The dinoflagellate symbionts of corals, and many other invertebrate taxa, are alveolate protists that form a monophyletic group closely related to ciliates with apicomplexan parasites as a sister group within the Gymnodiniales–Peridiniales–Prorocentrales dinoflagellate complex (Leander and Keeling 2004; Stat et al. 2006; Wisecaver and Hackett 2011; Stat et al. 2012). To reconcile the functional and taxonomic diversity of *Symbiodinium* and understand the full range of effects on holobiont fitness, the taxonomy and evolutionary history of *Symbiodinium*, as well as evolutionary theories on symbioses (see above), must be considered. Currently, the marker most commonly used to identify different phylotypes of *Symbiodinium* is the nuclear gene for the ribosomal internal transcribed spacer 2 (ITS2). Despite the apparent shortcomings of this marker (Stat et al. 2012), the majority of the studies on *Symbiodinium* cited here use the ITS2 marker, and the data are congruent with several other molecular markers. For *Symbiodinium*, the cladal phylogeny (Fig. 2) identifies clade A as the most ancestral, having originated 65–50 MYA, with the other clades diverging later during the Eocene to Miocene (Pochon et al. 2006). Clade C and F show significantly greater amounts of within-clade diversity compared to clade A and are the most derived lineages in *Symbiodinium* evolution and the dominant symbiont lineages in corals and foraminiferans, respectively (Pochon et al. 2006; Stat et al. 2006; Pochon and Gates 2010). Geographically, clade A and B *Symbiodinium* are more common in corals in the Caribbean than in the Pacific (Baker 2003; LaJeunesse 2004), as well as in sea anemones and soft corals (LaJeunesse 2002), while clade C is the dominant symbiont in the Pacific and Indian Ocean. Given the diversity within *Symbiodinium* clades, the range of host species and the range of environments experienced by corals and other marine invertebrates in symbiosis with *Symbiodinium* (i.e., temperate to tropical ecosystems), we expect a range of interaction states from mutualistic to parasitic will likely be present in all cladal lineages (e.g., Sachs et al. 2011a, b). This could be a reflection of the different ages of each *Symbiodinium* clade, but note that clade A, the oldest clade, is arguably more parasitic (see below). Numerous transitions between mutualism and parasitism resulting in closely related taxa (i.e., *Symbiodinium* phylotypes) with both mutualistic and parasitic attributes in related hosts (Moran and Werneberg 2000) is also a likely scenario.

In assessing the interaction states of corals, the importance of photobiology is one of the most common phenotypic characteristics used to describe functional differences among *Symbiodinium* phylotypes and is central to the importance of the association between *Symbiodinium* and its many hosts. A comprehensive laboratory study on the photobiology (i.e., bio-physical and bio-optical approaches) of several *Symbiodinium* phylotypes has revealed that many phylotypes have a broad strategy to photoacclimate to varying irradiances by modifying the number of photosystem II (PSII) reaction centers while others photoacclimate by changing their absorption cross section (Hennige et al. 2009). In another study, the relationship between photosynthesis and irradiance of freshly isolated *Symbiodinium* from five species of scleractinian corals, four species of sea anemones and one species of jellyfish that spanned three clades (i.e., clades A, B and C) revealed significant within clade functional variability but little to no difference in critical parameters of the photosynthesis–irradiance relationship among clades. In this case, the authors concluded that the differences in photosynthetic performance that were detected did not map to *Symbiodinium* identity at the cladal level (Savage et al. 2002). Tchernov et al. (2004) examined the effects of thermal stress on different *Symbiodinium* phylotypes. They showed significant functional variability in *Symbiodinium* phylotypes and identified both heat resistant and tolerant phylotypes within clades A, B, C using active chlorophyll fluorescent measurements to assess the number of functional PSII units (Tchernov et al. 2004). Similarly, Brading et al. (2011) demonstrate *Symbiodinium* phylotype variability in their response to ocean acidification and suggest that ocean acidification would disproportionately affect free-living *Symbiodinium;* the source population of symbionts for most corals which are dependent on horizontal transmission.

Whether these variations in photosynthetic capabilities are related to differences in interaction states are largely unknown. There is evidence that it can be very important (Stat et al. 2008), and for corals, understanding the result of these differences in photobiology (i.e., differences in photosynthesis, translocation of photosynthate or production of reactive oxygen species) could serve as an important phenotypic character under which the dynamics of the parasitic to mutualistic continuum evolve.

In an example of potential parasitic phylotypes, members of clade A were shown to have enhanced photoprotective capabilities resulting in significant tolerances for high solar irradiances and thermal stress (Robison and Warner 2006; Reynolds et al. 2008; Suggett et al. 2008; Ragni et al. 2010). Members of clade A, however, also show lower rates of carbon fixation as well as a decrease in the release of fixed carbon products (Stat et al. 2008), and hosts that associate with clade A often exhibit lower overall fitness (Stat et al. 2008; Mieog et al. 2009). However, in the sea anemone *Condylactis gigantea,* more photosynthetically fixed carbon is translocated to the host from its clade A symbiont than anemones with clade B symbionts, and

clade B symbionts are also more sensitive to thermal stress (Loram et al. 2007), highlighting the potential contribution to host phylogeny in determining the interaction state of the symbiosis. Finally, in the thermally resistant coral *Porites astreoides*, the photorepair of the D1 protein of PSII is significantly greater in their clade A symbionts than in *Montastraea faveolata* with symbionts of clade B and C (Hennige et al. 2011).

In addition to observed differences in phylotype performance between clades of *Symbiodinium* within clade differences (e.g., Hennige et al. 2009; Ragni et al. 2010) could be important. Current data suggest that most clade A symbionts are less beneficial to corals, and their cladal phylogeny suggests that they were the first *Symbiodinium* to infect a suitable host (Stat et al. 2008). If this is true, then clade C *Symbiodinium* could be broadly interpreted as the "best" symbionts for corals; they generally have higher rates of carbon fixation (Stat et al. 2008) and provide a greater fitness benefit, at least in the Pacific, and translocate higher amounts of carbon to the host and positively influence host growth rate compared to members of clades A and D (Stat et al. 2008; Cantin et al. 2009; Mieog et al. 2009; Jones and Berkelmans 2010). The greater diversity of clade C symbionts compared to other *Symbiodinium* lineages is potentially related to increases in phenotypic variation and adaptation to different environmental conditions resulting in the adaptive radiation of this lineage. Furthermore, there is also evidence of phenotypic variability within a specific ITS2 phylotype. Different populations of a single phylotype (*Symbiodinium* ITS2 phylotype C1) that can be harbored by multiple hosts (i.e., generalist) and are associated with the coral *Acropora millepora* located at two sites from the Great Barrier Reef. These sites represent a warmer and colder environment and show variation in thermal tolerance that is consistent with local selection and adaptation (Howells et al. 2011). The results described above are likely to be affected, and the interpretation of their meaning confounded by, whether studies are conducted on cultures or on the intact holobiont, host type (i.e., sea anemone versus coral), mode of symbiont transmission or geographic origin of the host (Fig. 1).

For corals harboring a broad suite of different *Symbiodinium* phylotypes, there is increasing evidence that most corals do harbor multiple different *Symbiodinium* phylotypes (Fay and Weber 2012; Silverstein et al. 2012); theory predicts a net decrease in holobiont fitness due to conflict among symbionts (Frank 1996). During stressful environmental conditions, however, corals harboring a diverse assemblage of symbionts could have an immediate, but not necessarily long-term, advantage if one of the symbionts can maintain some benefit to the host when other phylotypes of *Symbiodinium* cannot. Corals that associate with phylotypes of *Symbiodinium* clade D (i.e., specifically ITS2

D1a but potentially other phylotypes as well) under elevated ocean temperatures often show this immediate advantage (Jones et al. 2008; LaJeunesse et al. 2009), but not always (see Abrego et al. 2008 for a counter example). Clade D *Symbiodinium* generally exhibits low diversity, which is widely distributed, represents less than 10 % of the symbiont population in multi-phylotype assemblages and exhibits a generalist lifestyle (Stat and Gates 2011) consistent with an opportunistic phenotype. While reef corals exposed to chronically higher ocean temperatures can be dominated by clade D *Symbiodinium*, increased abundances of clade D are most often, but not always, observed just after coral bleaching caused by thermal stress (Stat and Gates 2011). Corals dominated by clade D *Symbiodinium* show significantly reduced rates of growth and reproduction (Jones and Berkelmans 2010, 2011), indicating lower long-term holobiont fitness, but their dominance in bleached corals can result in an acquired thermal tolerance of 1.0–1.5 °C in elevated ocean temperatures (Berkelmans and van Oppen 2006), which has short-term holobiont fitness benefits (Donner et al. 2005, 2007; Donner 2009). In general, the ephemeral dominance of clade D *Symbiodinium* after coral bleaching results in lowered fitness for corals over ecological timescales (Stat and Gates 2011), a feature consistent with a cheater strategy exhibited by many parasites (Herre et al. 1999; Sachs and Simms 2006; Sachs et al. 2011a). Taken together, these observations suggest that the lowering of holobiont fitness occurs when corals are in symbiosis with a less beneficial symbiont (e.g., many members of clade A) or when multiple symbionts are present and a less beneficial symbiont (e.g., clade D) can flourish under the right conditions (e.g., thermal stress) consistent with features of parasitism.

What features of the *symbiodinium*-host lifestyle correlate with the parasitic to mutualistic continuum?

Dinoflagellates, including *Symbiodinium,* are the sister group to the apicomplexans, a well-known group of parasites (Hackett et al. 2004) and a priori share the cellular machinery and numerous genes associated with a parasitic lifestyle (Schwarz 2008; Hill and Hill 2012). In particular, the mechanisms of *Symbiodinium* interaction with host cells during the invasion and the establishment of a successful symbiosis are deeply rooted in the biology and evolution of parasites and their hosts (Schwarz 2008; Davy et al. 2012).

One characteristic that may influence the interaction state of *Symbiodinium* symbioses is transmission mode. Vertically transmitted symbionts (i.e., most brooders and some broadcast spawners) are generally represented by a greater number of obligate associations which are

mutualistic, while most horizontally transmitted symbionts (i.e., most broadcast spawners) are facultative and parasitic in nature in that they are found both in symbiosis and free-living in the environment (Bright and Bulgheresi 2010). These distinctions are consistent with evolutionary theory on the role of transmission mode in symbiont integration (Bright and Bulgheresi 2010) and can have significant consequences for the degree of metabolic integration between the host and symbiont and any corresponding differences in the benefits to the host and symbionts (Leung and Poulin 2008; Stat et al. 2008; Mieog et al. 2009; Bright and Bulgheresi 2010).

As in bacterial symbioses, there is evidence supporting the hypothesis that vertical transmission of *Symbiodinium* can lead to a more beneficial association. In the jellyfish *Cassiopea*, estimates of holobiont fitness with clade A phylotypes acquired by horizontal transmission showed a shift to parasitism and a reduction in host fitness (Sachs and Wilcox 2006). The same clade A phylotype acquired by vertical transmission, however, produced a stable, higher fitness association (Sachs and Wilcox 2006). Contrary evidence on Pacific acroporids showed no differences in phylotype diversity between host species with vertical and horizontal symbiont transmission (van Oppen 2004). But a recent meta-analysis of *Symbiodinium* interactions from the Indo-Pacific and Atlantic oceans clearly shows that symbiont specificity to a host is associated with transmission mode, and there is significant fidelity of symbiont phylotypes to either a vertical or horizontal transmission lifestyle and only a few generalist phylotypes associated with both of these transmission strategies (Fabina et al. 2012).

Symbiodinium often exhibits a facultative life cycle that includes a free-living motile stage outside of its host, and this stage is important for the transmission of symbionts because the majority of corals acquire new *Symbiodinium* symbionts each generation from the environment (Stat et al. 2006). For obligate *Symbiodinium* the apparent absence of a free-living stage of the symbiont could be interpreted as a step toward successful mutualism. Clade A *Symbiodinium* exhibit facultative lifestyles by maintaining members that are both free-living and symbiotic with lower overall genetic diversity and a propensity for parasitism (Stat et al. 2008). In contrast, other clades of *Symbiodinium* (e.g., phylotypes of clade C) appear to have become more dependent on their hosts for specific metabolic needs but in corals most of these associations result from horizontally transmitted symbionts (Fabina et al. 2012; Putnam et al. 2012). One interpretation is that these symbioses may eventually evolve into vertically transmitted, and increasingly obligate, mutualistic associations that maintain high levels of holobiont fitness (Moran 2007). Another largely unknown feature of *Symbiodinium* sp. is the presence of sexual reproduction and how this might contribute to the evolution of multiple interaction states. Lastly, it has been suggested that both coral hosts and their *Symbiodinium* symbionts have the potential to obtain novel genetic diversity via selection on somatic mutations (van Oppen et al. 2011).

How does environmental change modulate the parasitic to mutualistic continuum?

While horizontal transmission is the primary mechanism of symbiont acquisition in most coral-*Symbiodinium* symbioses, there is evidence that corals with vertically acquired symbionts, such as members of the genus *Porites*, are more resistant to a range of environmental conditions (van Woesik et al. 2011; Putnam et al. 2012), and maintain successful mutualisms with a greater number of functional attributes (e.g., growth) that may contribute to overall fitness (Barshis et al. 2010). There are also exceptions to this. Corals in the genera *Pocillopora*, *Stylophora*, *Seriatopora* and some species of *Porites* are vertical transmitters and are sensitive to environmental stress (van Woesik et al. 2011). These taxa are branching, fast growing, weedy species that harbor *Symbiodinium* phylotypes in Clade C. Clade C phylotypes are extremely diverse in the Pacific, and are associated with a wide variety of hosts. If *Symbiodinium* diversity reflects the potential for multiple interaction states then a range of metabolic integration and fidelity of symbionts is likely to exist. In fact, Putnam et al. (2012) found that as expected massive poritids harbor a single symbiont phylotype (i.e., specialists), are highly resistant to environmental stress and are known to be successful long-term mutualists. But pocilloporids and acroporids with generalist symbionts and variable routes of symbiont transmission are sensitive to thermal stress and destabilization of the symbioses (van Woesik et al. 2011; Putnam et al. 2012). These results suggest that coral morphology is another interacting axis upon which the parasitic to mutualistic continuum should be interpreted especially under stressful environmental conditions.

Concluding remarks and future directions

When one examines the range of phenotypes in the different phylotypes of *Symbiodinium,* it appears that many *Symbiodinium* associations, and their resulting interaction states, do not follow all of the tenets outlined above to avoid conflict and maintain a mutualistic lifestyle (Herre et al. 1999). Nevertheless, using the parasitic to mutualism continuum as an evolutionary ecology framework to understand the functional diversity of *Symbiodinium* could have important ramifications for understanding the

ecological outcomes observed during exposure of corals to environmental changes such as thermal stress or ocean acidification or combinations thereof.

We have argued that *Symbiodinium* symbioses represent a range of interaction states that encompass mutualistic to parasitic symbioses. If true, this could provide novel insights into the potential fitness consequences of different *Symbiodinium* symbioses generally, and specifically when these associations are exposed to a range of environmental stressors. The literature clearly shows that some *Symbiodinium* are not as beneficial to corals as others; thus, it is critical to consider the taxonomic composition, functional limits and interactions states that affect ecological fitness (i.e., survival and fecundity) to the holobiont when studying changes in *Symbiodinium*-coral associations. Theoretical models could still provide, in the absence of any consensus on taxonomic affinities, a framework from which important questions are generated and tested with empirical studies (e.g., Johnstone and Bshary 2002; Golubski and Klausmeier 2010). Currently, the amount of data available on the photobiology of *Symbiodinium,* whether from cultures or *in hospite* studies, would be the best character state to assess immediately regarding interaction states. Additionally, a recent model of interaction states between *Symbiodinium* sp. and their hosts that emphasizes the role of the host as a modulator of a "controlled parasitism" (Wooldridge 2010) over its symbionts can be combined with the concepts presented here. In particular, a comprehensive and widely accepted system of *Symbiodinium* nomenclature will provide the much-needed framework to assess whether the parasitic to mutualistic continuum is widely applicable to *Symbiodinium* symbioses. In this context, here we have used the current nomenclature only to identify phylotypes with what we interpret as parasitic or mutualistic characteristics except as it relates to clade A and D phylotypes which appear to us to have more parasitic attributes. More functional data are needed from representatives of all clades before any association with evolutionary history can be drawn. We propose that the evolutionary ecology context of interaction states along a parasitic to mutualistic continuum could advance our understanding of all possible outcomes in *Symbiodinium* symbioses (i.e., mutualistic to parasitic), including other partners in the coral holobiont but especially the host (Abrego et al. 2008; Fitt et al. 2009; Barshis et al. 2010), and that this will be important in assessing who will be the winners and losers in the future of increasing environmental change effecting coral reefs.

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