Review

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Coral evolutionary responses to microbial symbioses

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This review explores how microbial symbioses may have influenced and continue to influence the evolution of reef-building corals (Cnidaria; Scleractinia). The coral holobiont comprises a diverse microbiome including dinoflagellate algae (Dinophyceae; Symbiodiniaceae), bacteria, archaea, fungi and viruses, but here we focus on the Symbiodiniaceae as knowledge of the impact of other microbial symbionts on coral evolution is scant. Symbiosis with Symbiodiniaceae has extended the coral's metabolic capacity through metabolic handoffs and horizontal gene transfer (HGT) and has contributed to the ecological success of these iconic organisms. It necessitated the prior existence or the evolution of a series of adaptations of the host to attract and select the right symbionts, to provide them with a suitable environment and to remove dysfunctional symbionts. Signatures of microbial symbiosis in the coral genome include HGT from Symbiodiniaceae and bacteria, gene family expansions, and a broad repertoire of oxidative stress response and innate immunity genes. Symbiosis with Symbiodiniaceae has permitted corals to occupy oligotrophic waters as the algae provide most corals with the majority of their nutrition. However, the coral–Symbiodiniaceae symbiosis is sensitive to climate warming, which disrupts this intimate relationship, causing coral bleaching, mortality and a worldwide decline of coral reefs.

This article is part of the theme issue 'The role of the microbiome in host evolution'.

1. Reef-building corals: their origin, diversity and microbial associates

Stony corals (Scleractinia) are cnidarian animals that comprise over 1300 extant species in 30 families [1]. They have an evolutionary origin in the deep Palaeozoic (more than 400 Ma) [2]. The fossil record shows that following the Late Permian mass extinction event, metazoan reefs were absent during the first approximately 8–10 Myr of the Early Triassic, with the initial appearance of modern corals dating to the Middle Triassic. Mass extinction occurred again at the end of the Triassic (approx. 200 Ma), resulting in significantly reduced scleractinian diversity. A renewal of coral diversity subsequently ensued during the Middle and Late Jurassic (approx. 176–161 Ma) [3]. Much of this diversity was again lost during the Cretaceous/Palaeogene mass extinction (approx. 66 Ma) [4], but scleractinian corals re-diversified soon after, although it took a long time for reefs to return to their former diversity.

Scleractinians form close associations with a wide taxonomic diversity of microbes, including Symbiodiniaceae and other protists, bacteria, archaea, fungi and viruses. This consortium is called the coral holobiont. The Symbiodiniaceae are estimated to have evolved approximately 160 Ma at the time of the second adaptive radiation of scleractinian corals during the Middle Jurassic Period [5,6]. The bacterial and archaean lineages that form associations with corals are, however, much older than their hosts [7]. These prokaryotes evolved approximately 3 billion years before animals diverged from their protist ancestors 700–800 Ma [8]. Viruses are also ancient and are believed to have evolved

from a common ancestor with the bacteria that lived approximately 3.4 billion years ago [9]. Thus, corals evolved in the presence of a wide diversity of prokaryotes and viruses and these microbes will undoubtedly have affected their evolution. The influence of bacteria on the evolution of eukaryotes is well known. For instance, the mitochondrion arose from the engulfment of a bacterial cell by another cell [10], and bacteria may also have been involved in the evolution of multicellularity [11]. However, apart from a few instances of horizontal gene transfer (HGT), nothing is known about the influence of bacteria on the evolution of the Cnidaria or Scleractinia from more ancestral animals. We therefore focus this review article on the evolution of the coral–Symbiodiniaceae symbiosis. We discuss how selection is believed to operate on the coral animal and Symbiodiniaceae members of the coral holobiont as well as their interactions, the macro- and microevolutionary past and potential future impacts of this symbiosis, and the genomic changes that have occurred owing to microbial symbiosis.

2. Coral holobionts and hologenomes

The term holobiont means ‘whole unit of life’ [12] and was first used for coral in 2002 by Rohwer *et al.* [13]. It captures the idea that the host and its associated microbes are an integrated unit where both contribute to phenotypic traits of the unit [14]. There is ample and compelling evidence that coral-associated microbes influence trait values of the holobiont, such as upper thermal tolerance limits and growth rates [15,16], and the term has been embraced by the coral community. The sum of the genetic information of host and microbiota is known as the hologenome [17,18]. While the term hologenome is uncontroversial, the hologenome theory as originally proposed [19] received considerable criticism [14,20,21] because it considers the hologenome as the unit of natural selection. It posits that natural selection acts to increase fitness of the holobiont rather than that of its individual members, and that conflict between the evolutionary interest of host and symbionts is suppressed owing to this higher-level selection [14]. A more moderate perspective was subsequently proposed that views host–microbe symbioses as analogues of genetic epistasis, where interactions between host and microbial genotypes are equivalent to interactions among alleles at different genomic loci [20]. Under this model of evolution, selection occurs both at the holobiont level and at the levels of host and individual microbes [20], with the phenotype of an individual holobiont being the product of all the holobiont members’ genomes, the interactions among these genomes, and the environment that the holobiont lives in ($G_{\text{host}} \times G_{\text{microbes}} \times E$) [20]. Thus, the model postulates that colonization of the host by microbes is influenced by both host and microbial genetic factors, that microbial genetic variation affects competition with co-infecting microbes, and that environmental variation substantively influences these dynamics and drives rapid microbial community changes [22].

Observations from coral support this theory. Environmental variation, such as seasonal temperature fluctuations, summer heat waves and light level differences across depth operate on microbial genetic variation to drive changes in the Symbiodiniaceae and bacterial community composition [15,23], and these acquired changes in microbial communities are sometimes heritable [24]. Host genetic variation also has a substantial effect on the establishment of Symbiodiniaceae

communities in both corals with horizontal and those with vertical symbiont transmission (29–62%) [25,26]. Further, fitness of different host–Symbiodiniaceae associations varies with changing environmental conditions. Species in the symbiont genus *Durusdinium* (formerly *Symbiodinium* clade D), for instance, generally increase holobiont thermal tolerance compared with *Cladocopium* (formerly *Symbiodinium* clade C) spp., but a trade-off exists as the former translocate less carbon to their coral host at ambient temperatures [27]. Further, different life stages of the various members composing the coral holobiont can experience divergent selection pressures and some life stages of individual members can be the unit of selection. Most microbial associates are able to live and propagate outside the coral host, and thus the microbial genome alone will be the unit of selection during this ‘free-living’ life phase. Larvae of the majority of coral species lack Symbiodiniaceae [28] and internalized bacteria [29–31], also changing the unit of selection compared with the adult holobiont life stage. Thus, selection operating on both individual and interacting holobiont members needs to be considered when studying and modelling the evolution of corals.

3. Rates of evolution differ among coral holobiont members

Generation times and thus the rate of genetic adaptation differ considerably between Symbiodiniaceae, bacteria and coral. The Symbiodiniaceae symbionts are able to reproduce sexually [32–34] but primarily propagate asexually. Short *in hospite* doubling times (3–74 days [35]) in combination with enormous population sizes (approx. 10^{10} cells in a branching coral approx. 30 cm in diameter [36]) promote the occurrence of random somatic mutations. It is therefore assumed that evolutionary rates are relatively fast in the Symbiodiniaceae compared with their coral hosts, a notion that is supported by the stable increase in thermal tolerance over as little as approximately 40–80 asexual generations of laboratory evolution [37,38]. Division rates are generally even faster in bacteria, HGT is more common in bacteria compared with eukaryotes, and bacteria can undergo adaptive evolution within weeks to months [39]. Coral bacteria have been shown to double in cell numbers within a few hours when grown in seawater spiked with coral mucus [40,41], suggesting coral-associated bacteria are theoretically able to evolve rapidly, but this remains to be demonstrated. For corals, sexual maturity is related to colony size and thus growth rate. The faster-growing branching corals can become sexually mature between 2 and 4 years of age, but some of the slower-growing massive corals may take decades to reach sexual maturity. Thus, the rate of genetic adaptation of the coral host is slow relative to that of its associated microbial symbionts. These different rates of evolution of the various members of the coral holobiont must be considered when studying the response of corals to environmental perturbations, including climate change.

4. Photosymbionts as drivers of coral host evolution

The symbiosis between coral and Symbiodiniaceae is possible owing to a number of traits of the coral animal, which we discuss below. It is, however, unclear whether (some of) these adaptations were already present in corals and facilitated

the evolution of the symbiosis, or whether the symbiosis drove the evolution of these host adaptations.

(a) Solar power permits colonization of oligotrophic environments

The three-dimensional framework of coral reefs can be primarily attributed to the formation of exoskeletons by scleractinian corals. While all scleractinians deposit calcium carbonate skeletons, only those that harbour Symbiodiniaceae symbionts have sufficiently high calcification rates to contribute to tropical coral reef building [42]. The Symbiodiniaceae provide corals with a large portion of their nutrition through the translocation of photosynthate to the host tissues [43]. This solar energy source is believed to be partly responsible for the high calcification rates. The absence of reef building in scleractinian fossils from the Mid-Triassic suggests they lacked Symbiodiniaceae symbionts, but it is possible they may have formed symbioses with less efficient photosymbionts [3]. Thus, symbiosis with Symbiodiniaceae has allowed corals to thrive and radiate, but at the same time necessitated the prior existence or the evolution of a number of host adaptations [44].

(b) Symbiodiniaceae recognition and maintenance mechanisms

Most coral species acquire their Symbiodiniaceae symbionts from the environment each generation, with maternal or mixed-mode transmission occurring in only about 15% of the scleractinian species [28]. The diversity of Symbiodiniaceae species in the environment is considerably larger than that found in individual coral species or colonies, and coral specificity for one or a small number of algal species and strains is the norm (reviewed in [15]). This points to the existence of recognition mechanisms that permit the host to distinguish between symbionts and non-symbionts [45,46], a notion that is supported by the fact that colonies of the same coral species in a population tend to harbour the same algal symbiont communities, and by the observation that aposymbiotic coral larvae and young recruits can only be infected by a subset of Symbiodiniaceae species in the laboratory. Little is known about this recognition mechanism, other than that it involves host pattern recognition receptors (such as lectins) and symbiont microbe-associated molecular patterns (MAMPs, such as glycans) [47–49]. Additional host adaptations allowing symbionts to colonize the host cells, for the host to control symbiont growth rates and to remove symbionts when population sizes are too large or symbionts are dysfunctional, were likely also driven by the origin of the coral–Symbiodiniaceae symbiosis [44,50]. Selection at the level of the Symbiodiniaceae symbiont favours selfish replication, which is controlled by the host by limiting the amount of nitrogen available to the symbiont [51]. The process of removal of dysfunctional Symbiodiniaceae symbionts by the host is initiated by an increase in Symbiodiniaceae-produced reactive oxygen species (ROS) that leak into the host tissues, triggering a cellular cascade in the host resulting in apoptosis and other symbiont removal processes [52].

The Symbiodiniaceae are located within a series of membranes of host and Symbiodiniaceae origin (the symbiosome) inside the coral's gastrodermal cells. Corals thus need to ensure that their intracellular conditions are suitable for symbiont photosynthesis. This includes the provisioning of these endosymbiotic algae with inorganic carbon through

carbon-concentrating mechanisms (carbonic anhydrase [53]), provisioning of nitrogen via ammonium carriers [54] and phosphorus via sodium/phosphate symporters for the uptake of phosphate across host membranes [55]. Corals also have transporters to translocate fixed carbon from the symbiont to their own tissues [56]. The coral-derived outer membrane of the symbiosome expresses vacuolar-type H^+ -ATPase (VHA) to acidify the symbiosome space for proper symbiont photosynthetic activity [57]. Further, light conditions within the coral tissues need to be favourable for photosynthesis. Symbiodiniaceae self-shading is common in healthy corals, which have Symbiodiniaceae cell densities of around 1–2 million per cm^2 of coral surface area. Light-scattering characteristics of the coral skeleton [58] and tissue [59,60] maximize light delivery to the Symbiodiniaceae cells, and these traits may have facilitated the evolution of the symbiosis and/or evolved as a consequence of symbiosis. Corals also produce sunscreens in the form of mycosporine-like amino acids (MAAs) [61] and photoprotective fluorescent proteins (FPs) [62] to prevent themselves and their endosymbiotic Symbiodiniaceae from being harmed by excessive sunlight and UV radiation. Symbiodiniaceae photosynthesis causes large diel fluctuations in intracellular oxygen levels [63] and pH [64,65]. Hyperoxia leads to oxidative stress, in response to which corals have evolved an extensive ROS scavenging repertoire via several enzymatic and non-enzymatic antioxidants, such as superoxide dismutases, glutathione peroxidases, glutathiones [66] and certain FPs [67].

(c) Impact of photosymbiont genotypic diversity on coral responses and evolution

The Symbiodiniaceae family comprises many species in seven genera and five additional evolutionary lineages that currently lack formal nomenclature [5]. Some coral species harbour taxonomically distinct Symbiodiniaceae symbionts in different habitats or geographical locations, and even individual coral colonies are often able to form a stable symbiosis with more than one Symbiodiniaceae species or strain simultaneously; sometimes different symbiont species dominate different parts of the colony (reviewed in [15]). While there is a lack of cophylogeny between coral and Symbiodiniaceae symbionts, there is evidence for some level of specificity. This is prevalent in recent divergences in the Caribbean, such as the case of the recently evolved *Cladocopium* C3 radiation only found in *Orbicella* corals [68] and *Symbiodinium fitti* in *Acropora* [69], but also in deeper divergences where distinct *Breviolum* spp. associate with different coral species in the subfamily Faviinae (*B. faviinorum*), the family Meandrinidae (*B. meandrinum*) and the threatened coral *Dendrogyra cylindrus* (*B. dendrogyrum*) [70]. *Orbicella* spp. are the only Caribbean coral taxa that can harbour both *B. faviinorum* and *B. meandrinum* [70]. An example of specificity from the Indo-Pacific is the predominant association of *Cladocopium* C15 with the coral genera *Montipora* and *Porites* [71]. However, despite the existence of some level of host–Symbiodiniaceae specificity, symbiont flexibility is high, with the environment playing an additional and sometimes substantial role in Symbiodiniaceae symbiont community composition. This flexibility provides corals with the ability to rapidly acclimatize to environmental change and to survive in a broader range of environments through shifts/differences in the relative abundance or presence/absence of certain Symbiodiniaceae species.

An example of how Symbiodiniaceae symbiont species can enable the colonization of new niches comes from *Cladocopium*-containing corals in the Caribbean (C3 radiation), which are more prevalent in deeper waters, where light penetration is lower [68]. Further, the burgeoning amount of transcriptome data coupled with the physiology of coral bleaching across diverse coral holobionts [72–76] are beginning to define the thermal boundaries of different coral–Symbiodiniaceae combinations [77–79]. Thermal tolerance is a trait critical for coral survival, especially under the threats of climate change [80]. While the Symbiodiniaceae community harboured by a particular coral colony plays a large role in holobiont thermal tolerance [15], it is becoming apparent that there is some level of phylogenetic constraint to the ability of Symbiodiniaceae lineages to respond to different thermal regimes, which in turn impacts coral homeostasis, and there are also many host-driven responses to thermal stress independent of the Symbiodiniaceae symbiont [79]. There is likely as much phenotypic variation in terms of thermal tolerance within coral species as there is across Symbiodiniaceae species [81–83].

Widely divergent Symbiodiniaceae species (i.e. belonging to different Symbiodiniaceae genera) have been shown to elicit distinct transcriptomic responses in conspecific host colonies [82,83] and in the same host genotype [84]. Perhaps more surprising, even extremely closely related Symbiodiniaceae strains of the same species (e.g. with an evolutionary divergence of only approx. 8 years) can have a major impact on the genes expressed by genotypically similar coral hosts [85]. Thus, the Symbiodiniaceae endosymbionts directly influence coral gene expression patterns and the holobiont phenotype even if the host genotype is the same. This means that the same host genome can be exposed to different selective forces depending on the Symbiodiniaceae genotype it harbours. By extension, the level of specificity of the coral–Symbiodiniaceae symbiosis thus influences the strength and direction of selection, and this may result in inflated selective forces operating on the host genomes than would be expected based on host genome diversity alone. In the Caribbean elkhorn coral, *Acropora palmata*, different host genotypes associate with distinct *S. fitti* strains [26], and this may increase selection operating on these host populations. In addition, individual colonies can harbour multiple Symbiodiniaceae species from different genera, providing a gamut of photosymbionts with different physiological traits [15]. For instance, intra-colony Symbiodiniaceae diversity in Caribbean *Orbicella* spp. [68,70] includes species from different genera with distinct light affinities [84,86]. This photosymbiont diversity could have enabled colonization of shallow waters by *O. annularis* and *O. faveolata* after the extinction of the shallow *O. nancyi* in the Pleiocene [87]. These heterogeneous genotype by genotype interactions illustrate the different evolutionary trajectories that can drive both host and Symbiodiniaceae diversification. Such evolutionary forces can operate over long evolutionary times scales, such as the colonization of deeper water by corals associating with *Cladocopium* C3 species in the Caribbean, or they can occur relatively rapidly, as in the example discussed next.

The emergence of new stable adult host–symbiont combinations is likely a rare event, but when it occurs it may result in rapid adaptations. A key example is the recent (i.e. several decades ago) introduction of the Indo-Pacific algal symbiont *Durussdinium trenchii* into the Caribbean [88]. This symbiont species has rapidly spread across the Greater Caribbean and is currently found in symbiosis with many coral species, possibly

owing to its ability to increase thermal tolerance of corals it inhabits by 1–2°C [88,89]. After multiple bleaching events in the Florida Keys, *O. faveolata* colonies with a greater proportion of *D. trenchii* show the highest bleaching resistance [90]. However, trade-offs between thermal tolerance and other traits exist, for instance, calcification rates are lower in *O. faveolata* colonies that associate with *D. trenchii* compared with colonies with native homologous Symbiodiniaceae, suggesting this new association is suboptimal. The arrival of this immigrant has altered selective forces operating in *O. faveolata*, while the evolutionary consequences of this introduction still remain to be shown for other Caribbean corals.

5. Symbiosis secrets hidden within coral genomes

Owing to their symbiotic lifestyle, corals have highly conserved genes involved in oxidative stress, DNA repair from UV radiation, cell cycle and apoptosis [61,91–93], but photosymbiosis has also influenced coral genome evolution via gene duplications and gene family expansions for cellular functions involved with the establishment and maintenance of endosymbiosis [93,94]. Despite the still relatively low number of coral genomes available, a core set of orthologous symbiosis-related genes has been uncovered [92–94]. Overall, the genomic evidence has unveiled a more sophisticated innate immunity repertoire in symbiotic cnidarians when compared with non-symbiotic anthozoan relatives, likely reflecting the nature of the complex lifestyle of permanently communicating with the endosymbiotic algae [61,92–94]. In some cases, subfunctionalization of duplicated genes (e.g. *Sym32*, *NPC2*) has been revealed as important for proper symbiosome function [45]. There have also been several cases of lineage-specific gene family expansions of innate immunity genes such as NOD-like receptors in *Stylophora pistillata* and *Acropora digitifera* [94] and caspase-like and JNK signalling genes in *Pocillopora damicornis* and *O. faveolata* [92]. It is less clear if other gene expansions such as the Scleractinian Coral-specific Repeat families (SCORs), which are repeats located in intragenic regions, have a role in symbiosis [93].

It is important to highlight how symbiosis may have led to parallel gene family evolution by co-option for a photosymbiotic lifestyle, demonstrated by outgroup comparisons with a symbiotic (*Exaiptasia diaphana*—formerly *Aiptasia pallida*) and an asymbiotic anemone (*Nematostella vectensis*). A cnidarian-specific gene family (CniFLs) has undergone an expansion independently in both *E. diaphana* and coral genomes but not in *N. vectensis* [95]. CniFLs have been assigned a putative function in innate immunity in the lectin-complement pathway hinting again at a role linked to the establishment of symbiosis by exaptation of this pathway [95]. Several transposable element (TE) families have undergone parallel expansions in *E. diaphana* and the coral *A. digitifera* while this was not observed in the genome of *N. vectensis*. Whether the TE gene family expansions are linked to symbiosis remains to be tested.

Evidence for HGT from Symbiodiniaceae symbionts has been reported for symbiotic anemones and corals [91,95]. A phylogenomic analysis revealed approximately a dozen non-redundant HGT genes in corals, half of them from diverse photosynthetic eukaryotes and the rest of bacterial origin [91]. Examples include the MAA pathway, which confers UVR photoprotection and a polynucleotide kinase

3-phosphatase (PNK3P). Recent data from Symbiodiniaceae suggest that the MAA pathway may be particularly intertwined with coral–algal genome coevolution. Despite MAA enzymes having been acquired through multiple HGT events from bacteria in ancestral eukaryotic lineages, they have been reported as encoded in the genome of symbiotic cnidarians [61,95] and in the genus *Symbiodinium* (the most basal Symbiodiniaceae lineage), but not in more derived genera (i.e. *Breviolum*, *Fugacium*, *Cladocopium*) [96,97]. While it remains to be further tested with additional genome data, the loss of this pathway in the crown Symbiodiniaceae so far surveyed has been suggested as linked to the host's lifestyle (i.e. irradiance preference) and its endogenous UV-absorbing capacity [97].

6. Microbial genomes and symbiosis

Metabolic complementarity by both the Symbiodiniaceae and bacterial genomes has become apparent, suggesting coevolutionary adaptation [98]. In particular, bacterial associates seem to act as metabolic mediators to generate a successful coral–Symbiodiniaceae–bacterial symbiosis. Corals have been reported to lack pathways for synthesis of essential amino acids as well as B-vitamins; they must therefore acquire them from either their Symbiodiniaceae symbionts or other microbial associates [61,98,99]. Corals lack the ability to fix nitrogen, and new metagenomic evidence supports microbial metabolic complementarity via N-fixing bacteria [98]. Genome sequencing of putative coral microbial symbionts (e.g. *Endozoicomonas*, *Halomonas*) has also shown enrichment for nutrient transport processes, which are required for maintenance of homeostasis [99,100].

As mentioned above, HGT has been reported to occur from bacterial lineages into the anthozoan ancestor (10 phylogenetically confirmed genes with strong support) and in several more instances (six genes confirmed with strong support) into the coral ancestor [91]. Cases of lineage-specific HGT are also starting to emerge, such as the case of a four-gene cluster of unknown function but of apparent proteobacterial origin in the coral *Montipora capitata* [93]. The *M. capitata* genomic evidence supports a gene transfer agent (GTA) as the putative HGT mechanism for this gene cluster. GTAs are phage-like genetic elements that can drive random gene transfer between genomes and have shown higher frequency of transfer in natural microbial communities from reef environments [101]. Given this high frequency, it will be important to screen for other GTA-mediated events into the genomes of other coral hosts.

The vast microbial diversity found in different holobionts hints at rather dynamic coevolutionary processes that will be context dependent. For instance, Symbiodiniaceae photosymbionts are likely bringing a subset of associated microbial taxa into the holobiont that are independent from the coral host's own microbiome. Different levels of metabolic

complementarity are therefore at play depending on the Symbiodiniaceae symbiont species a particular coral associates with.

7. Conclusion

As detailed in this review, different coral–Symbiodiniaceae associations can have distinct phenotypes and environmental tolerances, and microbial associates can influence the evolutionary trajectory of scleractinian corals. Other coral-associated microbes are almost certainly also important, but little information exists on their functional roles and their influence on coral evolution. Models predicting the evolutionary responses of corals to environmental change need to consider coral-associated microbes in addition to the coral animal. The Symbiodiniaceae provide corals with new metabolic capabilities, but this comes at a cost of losing independence, and a large majority of corals cannot survive without these algae. The photosymbionts are a liability during climate change-driven summer heat waves, causing them to overproduce ROS as a consequence of heat-damage to their photosystems and/or owing to the energetic disruption of the host carbon-concentrating mechanisms [102], as the Symbiodiniaceae symbionts become more parasitic at higher temperatures [103]. The ROS trigger a host response resulting in removal of the Symbiodiniaceae from the coral tissues (i.e. coral bleaching) [52]. Coral bleaching has resulted in dramatic coral mortality and global coral reef decline [104]. While there is some evidence suggesting corals are adapting to climate warming [105], the extreme mortality rates during summer heat waves indicate adaptation is occurring too slowly to keep up with the rate of climate change. Even the relatively fast evolutionary rates of coral-associated microbes are apparently too slow to prevent heat-related coral death. Microbial manipulation and/or host selective breeding may provide options for assisted evolution of corals aimed at enhancing thermal tolerance [106–108]. Given the influence of microbial symbionts on the evolutionary trajectories of their coral host, as highlighted in this review, host–symbiont interactions must not be ignored in such interventions, and combining microbial manipulations with host breeding may result in the best outcomes [109].

Data accessibility. This article has no additional data.

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