OPINION PIECE

Leveraging new knowledge of *Symbiodinium* community regulation in corals for conservation and reef restoration

Kate M. Quigley[1,2,*], Line K. Bay[2,**], Bette L. Willis[1,**]

[1]ARC Centre of Excellence for Coral Reef Studies, and College of Science and Engineering, James Cook University, Townsville, QLD 4811, Australia
[2]Australian Institute of Marine Science, PMB3, Townsville, QLD 4810, Australia

ABSTRACT: Recent advances in quantifying the heritability of *Symbiodinium* communities associated with corals across a range of reproductive and symbiont transmission modes raise the possibility that corals have more options for responding to a changing environment than previously thought. Here we synthesize recent findings to develop a new perspective on coral–symbiont transmission and explore the relevance of these findings to the development of novel coral reef conservation and management tools. Evidence of diversity in *Symbiodinium* communities among juvenile corals can be attributed to variation in the host genotype acquired. This highlights the importance of inheriting a genetic architecture for regulating *Symbiodinium* community composition that is flexible enough to respond to changing environmental conditions. Emerging evidence from 8 species now exists that the strength and fidelity of coral–*Symbiodinium* associations differ from current paradigms based on host reproductive and symbiont transmission mode. This evidence supports that rapid adaptive responses of the holobiont through variations in *Symbiodinium* community structure are possible. Importantly, evidence of heritable variation in *Symbiodinium* communities indicates that adaptation through natural selection on this community is possible and that the strength of the response will depend on estimates of both heritability and phenotypic variance. We also present a novel analysis applying these results to quantitative genetic theory to model manipulative adaptive shifts. In combination, recent heritability estimates (h^2) reviewed here highlight that inheritance of genes for regulating *Symbiodinium* community structure represents a previously unquantified mechanism by which juvenile corals may adapt to increasing environmental pressures, particularly those due to climate change.

KEY WORDS: *Symbiodinium* · Symbiosis · Coral reef · Adaptation · Coral bleaching

IMPORTANCE OF UNDERSTANDING THE DRIVERS OF *SYMBIODINIUM* COMMUNITY STRUCTURE IN CORALS

The endosymbiont *Symbiodinium* has long been known to be a key partner in maintaining scleractinian and octocoral coral health and enabling the coral holobiont to build reefs (Baker 2003), an insight that began with the foundational work in *Symbiodinium*

taxonomy and morphology (Freudenthal 1962, Schoenberg & Trench 1980, Trench & Blank 1987). Over the last 3 decades, breakdowns in this relationship (termed bleaching) have accounted for wide-scale mortality in the Pacific and Caribbean (Wilkinson & Souter 2008, De'ath et al. 2012). The *Symbiodinium* community hosted is one of the dominant factors that determines bleaching risk, but bleaching variation is also influenced by the host

(Baird et al. 2009a). While bleaching has resulted in large-scale coral mortality over the past 20 yr, there is some evidence of adaptation. Global analyses suggest that the severity of bleaching has decreased in areas that have experienced higher thermal and irradiance stress, which may have prevented corals from declining in even larger numbers in recent decades (Thompson & van Woesik 2009). Other work also points towards increased flexibility and resilience to thermal stress (Glynn et al. 2001, Toller et al. 2001, Brown et al. 2002, Lewis & Coffroth 2004, Berkelmans & van Oppen 2006, Thornhill et al. 2006, LaJeunesse et al. 2009, Coffroth et al. 2010, McGinley et al. 2012, Fabina et al. 2013, Cunning et al. 2015b, Bay et al. 2016, Boulotte et al. 2016, Davies et al. 2018). However, high mortality during isolated or sequential bleaching events and strict patterns in temporal stability in host–symbiont associations suggest limited flexibility (Chen et al. 2003, Goulet & Coffroth 2003, LaJeunesse et al. 2005, Thornhill et al. 2006). Thompson & van Woesik (2009) suggested that the increased resistance to bleaching in recent years may be due to mechanisms such as thermal 'memory', symbiont shuffling, and natural selection for thermally tolerant genotypes. The hereditary mechanisms discussed here may be contextualized in light of these mechanisms. The importance of coral host genetic mechanisms that influence the establishment of *Symbiodinium* communities is only just emerging. Knowledge of these mechanisms is critical to understanding the flexibility of this partnership and underpins assessments of adaptation potential, bleaching risk, and predictions of reef health. The application of new knowledge around *Symbiodinium* community regulation can elucidate the rate and direction of adaptation of this community and identify host and symbiont rescue genotypes for selective breeding.

In this opinion piece, we focus on heritable, adaptive variation in symbiont selection and synthesize recent results that explore the role of the host in regulating this important community, both during the early phases of recognition and establishment in juveniles, and during bleaching and recovery in adults. We also present a novel analysis to model manipulative adaptive shifts and argue that consideration of host constraints on symbiont establishment, maintenance, and stability will be especially important for restoration initiatives that focus on active manipulation of *Symbiodinium* communities.

NEW INSIGHTS INTO REGULATION OF THE CORAL–SYMBIONT RELATIONSHIP

Coral host genetic underpinnings of the *Symbiodinium* community

Until recently, it was unknown how mechanisms regulating the structure of *Symbiodinium* communities were balanced during coral juvenile ontology, i.e. between environmental availability or by genetic factors inherited from their parents. It is now clear that *Symbiodinium* communities in scleractinians and octocorals are regulated to some extent by heritable genetic mechanisms (*Acropora tenuis*, *Montipora digitata*, *Seriatopora hystrix*, *Orbicella faveolata*, and the octocoral *Briareum asbestinum*), regardless of whether the coral host is a broadcast spawner or brooder, and whether the symbiont community is transmitted vertically or horizontally (McIlroy & Coffroth 2017, Poland & Coffroth 2017, Quigley et al. 2017a, 2018; Fig. 1). This aligns with previous transcriptomic results showing the influence of cnidarian host selection/regulation of *Symbiodinium* (Rodriguez-Lanetty et al. 2006, Schwarz 2008, Voolstra et al.
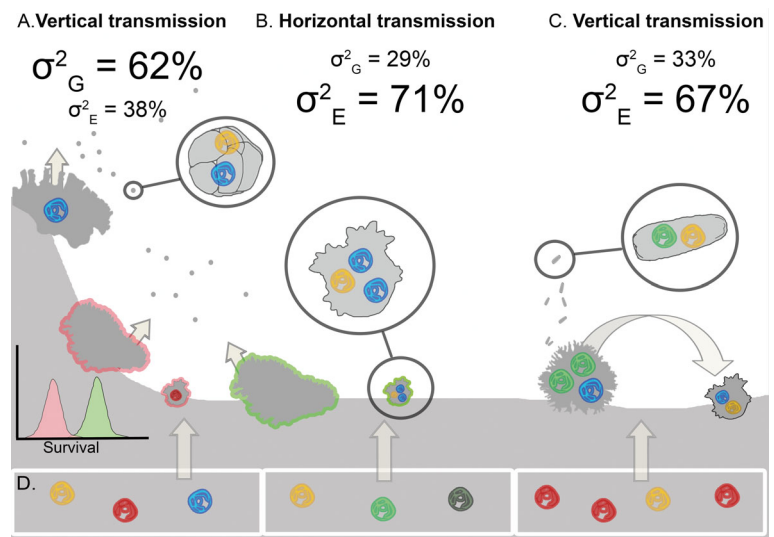

A. **Vertical transmission** $\sigma^2_G = 62\%$ $\sigma^2_E = 38\%$

B. **Horizontal transmission** $\sigma^2_G = 29\%$ $\sigma^2_E = 71\%$

C. **Vertical transmission** $\sigma^2_G = 33\%$ $\sigma^2_E = 67\%$

Survival

D.

Fig. 1. (A–C) Contributions of heritable genetic variation (σ^2_G) and environmental influence (σ^2_E) on the establishment of *Symbiodinium* communities in corals with both major modes of reproduction (spawning and brooding) and symbiont transmission (horizontal and vertical transmission). Adult colonies of *Acropora tenuis* may produce high (green) or low (red) surviving cohorts of juveniles, as influenced by genetic constraints and uptake of (D) a diversity of free-living *Symbiodinium* that are biogeographically distinct and locally adapted (white boxes)

2009, Schnitzler & Weis 2010). However, transcriptomic results demonstrating regulation in which the host is able to exclude symbiont types (sensu Rodriguez-Lanetty et al. 2006, Voolstra et al. 2009) are distinct from variation among hosts for choosing alternative symbiont communities in that only the latter leads to natural selection. Therefore, evidence of host genetic influence confirms that there is substantial raw genetic material for adaptation (cf. Falconer & Mackay 1995) and hence substantial potential for evolution of the symbiont community in these cnidarians. Therefore, under rapid environmental change, corals (with or without assistance) may be able to leverage this variation for rapid evolution in tolerance.

Counter-intuitively, host genetic influence in juveniles of spawning, horizontally transmitting corals was much greater than expected, and on par with host processes regulating communities in juveniles of brooding, vertically transmitting corals. Selectivity demonstrated by juvenile *A. tenuis* and *A. millepora* corals when acquiring *Symbiodinium* from the environment further corroborates our conclusion that host genetics contribute significantly to regulation of the symbiont community (Quigley et al. 2017b; Fig. 1D). In combination, high environmental influence (σ^2_E), low transfer fidelity (i.e. not all maternal types represented), and mixed-mode transmission (novel types in juveniles that are not found in the maternal line) point to much higher flexibility in *Symbiodinium* community regulation than previously thought in the species examined, but may vary by genera/species, geographic location, and thermal stress history. Such flexibility may especially positively impact the resilience of brooding species.

Mixed-mode *Symbiodinium* transmission in vertically transmitting corals

Until recently, the accepted paradigm from studies of over 400 coral species was that the early life history stages of corals acquire *Symbiodinium* either solely from the environment through horizontal transmission or solely from the maternal parent through vertical transmission (Baird et al. 2009b). The assumptions underlying this dichotomy in *Symbiodinium* acquisition are intuitive; high fidelity of transfer was assumed in vertical transmitters, whereas non-specific and completely open environmental acquisition was assumed in horizontal transmitters (Cumbo et al. 2013). A form of mixed-mode transmission that included both vertical and horizontal trans-

mission was suspected but lacked evidence in scleractinian corals (*Montipora capitata* and *Stylophora pistillata*; Padilla-Gamiño et al. 2012, Byler et al. 2013), and was hypothesized to occur in adult octocorals (Lewis & Coffroth 2004, Coffroth et al. 2010). However, there is now evidence for mixed-mode transmission of the *Symbiodinium* community in corals that release either zooxanthellate eggs or larvae (Quigley et al. 2017a, 2018, Reich et al. 2017). For example, in at least 3 vertically transmitting corals (*Montipora digitata*, *Seriatopora hystrix*, *Porites astreoides*), transmission of *Symbiodinium* communities lacked fidelity and hence not all types were transferred from the maternal line to offspring (either eggs, planulae, or juveniles) (Quigley et al. 2017a, 2018, Reich et al. 2017). Moreover, a number of unique *Symbiodinium* strains were found in eggs and planulae that were not detected in the maternal line, suggesting secondary uptake from environmental sources in early life history stages of these species following primary maternal provisioning. In bacterial–invertebrate symbioses, host fitness benefits that occur when vertical symbiont acquisition is followed by secondary horizontal acquisition (Mushegian et al. 2018) attest to the value of this mixed-mode strategy. Although it is likely that not all environmentally acquired or low-abundance *Symbiodinium* form stable (Coffroth et al. 2010) or functional symbioses (Lee et al. 2016, but see Ziegler et al. 2018), this new research signifies greater potential for adaptation than initially detected. Mixed-mode transmission of *Symbiodinium* in corals previously assumed to be solely vertical transmitters has important implications for the acclimatization and adaptation potential of hosts, as it suggests that uptake of novel, stress-resistant *Symbiodinium* types is possible. This will require an understanding of drivers of *Symbiodinium* communities post-uptake (including symbiosis establishment and maintenance), and further work assessing the long-term trajectories of novel and stress-resistant types is needed (Little et al. 2004, Abrego et al. 2009, Poland et al. 2013, Yorifuji et al. 2017).

Parental colony genetics can shape juvenile abundances on reefs

Quantitative genetic breeding designs that produce larval families of known pedigree have demonstrated that parental identity impacts a number of key traits, including larval weight, larval survival and settlement success, and juvenile survivorship (Meyer et al. 2009, Kenkel et al. 2011, Baums et al. 2013,

Dixon et al. 2015, Quigley et al. 2016). Breeding colony identity can therefore directly impact the demography of coral populations through its impact on pre- and post-settlement larval ecology, and in particular, through the significant impact of maternal parental identity on juvenile survival. A recent study found that the maternal line differed in the levels of density-dependent and density-independent mortality of their offspring, potentially due to differences in transmitted symbiont recognition mechanisms given differences in these communities (Quigley et al. 2016). Although the exact mechanisms (recognition or otherwise) remain to be described, these results demonstrate clear links between parental identity and juvenile survival, as have been described in other taxa (reviewed by Badyaev & Uller 2009), including tropical pomacentrid fish (Green & McCormick 2005) and many insect species (Mousseau & Dingle 1991). Knowledge of genetic effects has direct implications for predicting the maintenance and recovery of reefs (i.e. growth and survivorship), given that larval availability, settlement success, and juvenile survival are all key processes that underpin recovery potential (Ritson-Williams et al. 2009).

Tracking variation in juvenile survivorship among families of known genetic background has elucidated links between post-settlement success and the *Symbiodinium* community established. Results suggest that the maternal line transmits a genetic architecture that influences the symbiont community acquired, with potential flow-on effects for juvenile survival (Suzuki et al. 2013, Quigley et al. 2016, Yorifuji et al. 2017). The highly conserved *Symbiodinium* community found in families with high juvenile survival may represent a locally adapted symbiont community (cf. Howells et al. 2012) or the presence of an 'optimal', keystone symbiont community typified by a specific and conserved assemblage, i.e. potentially a core symbiosome for the juvenile life stage (cf. Ainsworth et al. 2015). The imbalance or deregulation of this locally adapted or keystone community may manifest as a form of dysbiosis, a condition where symbiosis disruption leads to low survival. Dysbiosis may take a variety of forms (Vangay et al. 2015, Egan & Gardiner 2016), including: (1) loss/ reduced abundances of keystone *Symbiodinium* types (e.g. A3, C1, D1, D1a in *A. tenuis* on the central Great Barrier Reef; Quigley et al. 2016); (2) increased diversity associated with unstructured communities that are highly variable within and among coral families; (3) changes in metabolic function; and (4) increased abundances of pathobionts (potentially *Symbiodinium* from clades E and F) (Starzak et al.

2014). Pathobionts are symbionts that become pathogens when environmental conditions select against symbiotic behaviour, recently demonstrated in *Symbiodinium* A3 and C7 (Baker et al. 2018). Regardless of the causative agent of dysbiosis, these results demonstrate clear links between *Symbiodinium* community composition and juvenile survival (Abrego et al. 2008, McIlroy et al. 2016), with direct implications for coral reef resilience.

APPLICATION OF NEW KNOWLEDGE OF *SYMBIODINIUM* COMMUNITY REGULATION FOR SELECTIVE BREEDING

Ample opportunity for adaptation

Recent findings confirming that host genetics underpin regulation of the *Symbiodinium* community in corals, in combination with emerging evidence of the mixed-mode nature of symbiont transmission and of the influence of parental colonies on juvenile survival, highlight that there are a number of routes by which the coral host can acclimatize and/or adapt relatively rapidly, at least in the species examined. Although these combined results indicate that naturally induced directional selection is possible, engineered interventions may be needed on shorter time scales to keep pace with rapid climate change (Gonzalez et al. 2013). Artificial directional selection or selective breeding (Visscher et al. 2008) has been shown to improve the health and fitness of a range of organisms (reviewed by Mueller & Sachs 2015) and may be possible for corals. Accordingly, selective breeding of coral hosts and their symbiotic communities has been proposed as a promising approach to help restore degraded reefs (van Oppen et al. 2015, Theis et al. 2016). Although assisted *Symbiodinium* evolution is particularly promising given rapid generation times of the symbionts, trade-offs and limitations exist when manipulating symbioses. For example, transfer of thermal tolerance to the host *in hospite* may be limited (Chakravarti et al. 2017). The limited genomic resources across *Symbiodinium* taxa and the genome structure are also challenging (Levin et al. 2016, 2017), and trade-offs amongst different traits may result during selection (i.e. growth versus genetic diversity; Cunning et al. 2015a, van Oppen et al. 2015). Moderate to high heritability estimates and evidence for additive genetic variance (Quigley et al. 2017a, 2018) suggest that, at least for efforts directed at selecting symbiont populations in the coral host, assisted evolution even on non-assisted communities

has potential. Even without the creation of new host genotypes through natural or artificial mutation, at least 2 sources of holobiont variation are available, i.e. the influence of host genetics on the *Symbiodinium* community acquired and on juvenile survival, further highlighting the potential for evolutionary rescue of corals. High diversity of *Symbiodinium* types in sediments (Quigley et al. 2017b) may also increase the probability of establishing stress-resilient *Symbiodinium*–host partnerships (within the constraints of host genetics), thereby facilitating evolutionary and genetic rescue.

Identification of rescue genotypes that produce juveniles with high survival

The success of selective breeding is dependent on the availability of appropriate rescue genotypes (i.e. individuals in the population that are resilient to stress) (Gonzalez et al. 2013). Indirect evidence of natural selection can potentially be seen across locations where different coral genera/species have bleached in initial versus subsequent events (Glynn et al. 2001, Maynard et al. 2008, Thompson & van Woesik 2009, Guest et al. 2012, but see Hughes et al. 2017). In one scenario, maternal-line genotypes could act as rescue genotypes if they provision offspring with a genetic architecture that is correlated with high juvenile survival, as shown by Quigley et al. (2016) (Fig. 1). Although improving adult survival is also critical in the face of increasing coral bleaching, a focus on juvenile survival may promote population replenishment to build reef resilience. Once such maternal-line genotypes are identified, they could be used in targeted selection programmes to produce high-quality brood stock for restoring degraded reefs (Drury et al. 2017). Further work should focus on identifying host genotypes that correlate with stress-tolerant host phenotypes and identify the mechanisms driving high survival of particular coral cohorts.

Identification of rescue genotypes that produce juveniles with locally adapted *Symbiodinium* communities

An important focus for selective breeding efforts would be the identification of corals with high abundances of keystone *Symbiodinium* communities or types for particular species and habitats (Fig. 2). In this approach, maternal-line genotypes would act as
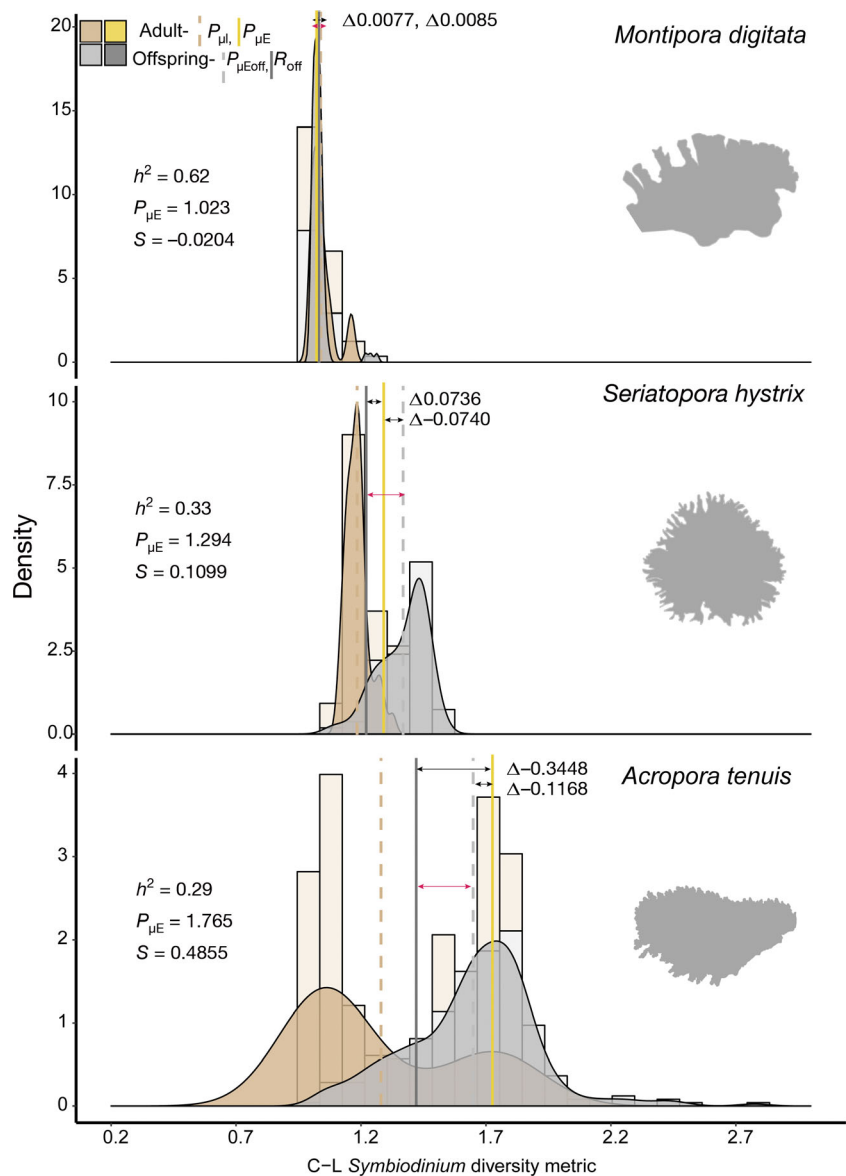

Fig. 2. Density plots of coral host phenotypic values of their respective *Symbiodinium* communities. Pale bars in the background represent data. Dashed lines represent mean initial parental phenotypic values ($P_{\mu I}$) and mean offspring experimentally derived values ($P_{\mu Eoff}$). Solid lines represent mean desired parental ($P_{\mu E}$) and expected mean offspring phenotypic values (R_{off}). Red arrows highlight the difference between $P_{\mu Eoff}$ and R_{off}; grey arrows highlight the difference between $P_{\mu E}$ and R_{off} or $P_{\mu Eoff}$. S: selective potential

rescue genotypes by contributing to high juvenile survival through the provisioning of offspring with genes for establishing and regulating these communities, as has recently been proposed for both *Symbiodinium* and bacterial communities in corals (van Oppen et al. 2015). The importance of host genetic architecture is highlighted during times of stress or disease, when regulation breaks down, leading to pathogenic (or non-beneficial) communities of greater diversity and random structure (Quigley et al. 2016, McDevitt-Irwin et al. 2017). Therefore, selection on genotypes of corals that exhibit beneficial consortia may result in hosts that are more resilient to stress and may open up other possibilities for symbiont community manipulations to further improve coral health and survival. One potential optimal phenotype has been identified in *Acropora tenuis* (Fig. 1, Quigley et al. 2016), and the high diversity of *Symbiodinium* types in sediments (Coffroth et al. 2006, Manning & Gates 2008, Adams et al. 2009, Cunning et al. 2017, Quigley et al. 2017b) provides ample opportunities for the discovery of a range of other optimal host–symbiont phenotypes. Further work is needed to determine the rescue phenotypes to be targeted and to identify the underlying genotypic determinants.

USING ESTIMATES OF HERITABLE VARIATION TO DEVELOP MODELS OF HOLOBIONT ACCLIMATION AND ADAPTATION POTENTIAL

Adaptive selection on heritable variation associated with the coral host and the *Symbiodinium* community is a significant, but hitherto unquantified, mechanism by which the coral holobiont may be able to respond to environmental stressors. Recent verification of a genetic basis for host regulation of this community suggests that symbiont communities will evolve in response to a changing climate to enable longer-term persistence of their hosts. Accordingly, the potential for the coral holobiont to respond through selection on its symbiont community should be incorporated into coral reef conservation and restoration intervention strategies. The presence of substantial host genetic regulation, however, may preclude the use of some intervention methods (see McIlroy & Coffroth 2017), for example by preventing the uptake of naturally thermally tolerant or artificially selected strains of *Symbiodinium*, thereby potentially limiting the effectiveness of some 'probiotic-like' interventions (cf. Peixoto et al. 2017). The breeder's equation (Falconer & Mackay 1995) can be

used to better understand constraints associated with host regulation and predict symbiont community responses. This method has long been used in agriculture to select for traits of commercial interest, and is defined simply as:

$$R = h^2 S \qquad (1)$$

where h^2 is the narrow-sense heritability, S is the selective potential, and R is the response to selection. It can be decomposed further as:

$$(R_{off} - P_{\mu I}) = h^2 (P_{\mu E} - P_{\mu I}) \qquad (2)$$

where the mean initial parental phenotypic value ($P_{\mu I}$) and the desired parental value ($P_{\mu E}$) are known. Along with the narrow-sense heritability of the trait, it is possible to estimate the expected mean phenotypic value of the offspring (R_{off}). Given this, we simulated mean phenotypic shifts expected in the offspring of 3 coral species with varying levels of heritability of the *Symbiodinium* community, based on selective breeding for communities with high abundances of the stress-tolerant *Symbiodinium* type D1 (Fig. 2). To this end, parental colonies of *Montipora digitata*, *Seriatopora hystrix*, and *Acropora tenuis* with the highest proportions of D1 *Symbiodinium* relative to other adults were selected (Leinster and Cobbold diversity metric [C-L], Quigley et al. 2017a), and the mean phenotypic diversity value for the community was calculated to represent the desired phenotype for selection ($P_{\mu E}$: *M. digitata* = 1.02, *S. hystrix* = 1.29, *A. tenuis* = 1.76) (Quigley et al. 2017a, 2018).

Given differences in the calculated heritability of the *Symbiodinium* community for each of the 3 species and Eq. (1), the selection coefficient S varied substantially across species, with *A. tenuis* having the largest and *S. hystrix* and *M. digitata* the smallest coefficients, most likely due to the increased phenotypic variance of *A. tenuis*. The predicted shift in *Symbiodinium* communities in offspring (R_{off}) also varied across species. Following one round of simulated selective breeding, R_{off} in *M. digitata* eggs shifted 3.6% closer to targeted breeding values than in the scenario where selective breeding was not used. Rapid selection in this species was a consequence of the high heritability and small desired phenotypic deviance needed to reach targeted phenotypic values. Experimental offspring values for *S. hystrix* also shifted closer to targeted parental values ($P_{\mu E}$) with intervention (R_{off}) compared to without intervention ($P_{\mu Eoff}$).

These simulations demonstrate that processes by which *Symbiodinium* communities are winnowed during ontogeny may need to be considered during

selective breeding programmes. For example, experimental values for *A. tenuis* offspring without intervention ($P_{\mu Eoff}$) were closer to targeted parental values ($P_{\mu E}$) than projected offspring values with intervention (R_{off}). Consequently, multiple generations of selective breeding may be necessary for this species. Alternatively, the use of $P_{\mu I}$ during selective breeding may not be advisable for *A. tenuis* given the disparity between adult and juvenile communities in this species. To facilitate phenotypic change, it is best to select $P_{\mu I}$ that are very close to the targeted values. The use of sibling variances could therefore potentially replace the use of $P_{\mu I}$. Interestingly, experimentally derived values for phenotypic shifts were greater than expected in *A. tenuis* and may be linked to a natural propensity to host higher abundances of D1 in juveniles, thereby increasing the efficacy of positive selection. In conclusion, we must also stress that the application of this new knowledge of *Symbiodinium* community regulation for selective breeding may also carry some risks. For example, these strategies may risk introducing non-native symbiont strains, allow for the potential colonization of parasitic strains, or result in significant growth–survival trade-offs that are associated with higher stress tolerance. Before any intervention is undertaken, these risks must be weighed against any potential benefits.

In summary, we highlight substantial flexibility in symbiont transmission modes and, importantly, substantial adaptive potential of the *Symbiodinium* community across multiple coral reproductive modes in a handful of coral species. In a broader research context, these results contribute to understanding how symbiosis is established and maintained, and can be used directly in evolutionary rescue models to help scientists, conservationists and managers predict and ameliorate pressures from environmental changes faced by coral reefs worldwide.

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