



Symbiotic Life of Echinoderm Larvae

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Echinoderm larvae have served as a fundamental system for understanding development and life history evolution over much of the last century. In the last few decades, our understanding of echinoderm larvae has expanded to the microbiota that they associate with. These symbionts and the communities that they form in relation to echinoderm larval host are the focus of this review. Our synthesis of the literature suggests three primary themes. First, larval echinoderms associate with “subcuticle bacteria” that appear to colonize select tissue types. Second, the bacterial communities associated with larval echinoderms exhibit compositional shifts that are correlated with several fundamental properties of larval biology (e.g., development and morphological plasticity) and ecology (e.g., feeding environment). Third, echinoderm larvae exhibit specific responses to pathogenic bacteria that may aid in maintaining the symbiont community and avoid dysbiosis. To our knowledge, no studies have focused on whether climate-related stressors impact the composition of these symbiont communities or how changes in bacteria may modulate response by larvae to these environmental stressors. Lastly, we conclude by outlining techniques that need to be established in echinoderm larvae to transition from correlations between larvae and their associated microbiota to the function of these symbionts.

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ECHINODERMS AND THEIR LARVAE

The phylum Echinodermata is characterized by their pentaradial symmetry and global distribution in marine ecosystems. This group first appeared in the Cambrian and is composed of ~7,000 extant species (Appeltans et al., 2012) that are grouped into five classes: Crinoidea (feather stars and sea lilies), Holothuroidea (sea cucumbers), Asteroidea (sea stars), Ophiuroidea (brittle stars), and Echinoidea (sea urchins). Echinoderm life cycles are primarily bi-phasic, where the adults reside on the sea floor and the embryonic stages are suspended in the water column (Thorson, 1950; Mileikovsky, 1971; Young and Chia, 1987). This phylum is, perhaps, most recognized for its remarkable diversity of larval forms that have fascinated biologists for more than a century (Levin and Bridges, 1995).

Echinoderm development, in general, follows either a lecithotrophic (non-feeding) or planktotrophic (feeding) trajectory (Thorson, 1950; Mileikovsky, 1971; Strathmann, 1985). Lecithotrophs develop from relatively large and energy-rich eggs (~300 μm to 1 mm in diameter, or where $s \geq 1$; Vance, 1973; McEdward and Miner, 2006) with sufficient maternal investment to complete development and undergo metamorphosis. The developmental period for lecithotrophs typically lasts a few days and, due to a shorter pelagic larval duration, can result in marginal dispersal between populations (Thorson, 1950; Mileikovsky, 1971; Strathmann, 1985). Planktotrophs, on the other hand, develop from more energy-poor eggs (~100 to ~300 μm in diameter, or where $s < 1$; Vance, 1973; McEdward and Miner, 2006) with sufficient maternal input

to complete embryogenesis and develop into larvae with initial feeding structures. The remaining energetic supply required for larval development and metamorphosis is acquired from exogenous resources (e.g., phytoplankton, detritus, and other particles) that are concentrated by a cilia-lined feeding apparatus (Strathmann, 1987; Feehan et al., 2018). These particulates are often dilute, leading to a pelagic larval duration lasting weeks to months and, in some cases, years (Thorson, 1950; Mileikovsky, 1971; Strathmann, 1985; Olson and Olson, 1989).

Nearly four decades ago, Rivkin et al. (1986) recognized that the planktotrophic larvae of the asteroid *Porania antarctica* selectively interacts with the environmental microbiota through bacterivory. It has since been observed that additional planktotrophic echinoderms exhibit bacterivory and that this feeding mode is hypothesized to be important, but not essential, to the metabolic requirements of the larva (Pearse et al., 1991; Douillet, 1993; Ayukai, 1994; Moal et al., 1996; Gosselin and Qian, 1997). Based on maximum clearance rates and particle abundance, it is estimated that echinoderm larvae interact with ~20 million bacteria each day by feeding alone (Carrier et al., 2018a). It is, however, unknown which bacterial (or other microbial) groups that echinoderm larvae may target and whether these microbes are selected strictly for bacterivory or as a symbiont that may be acquired by horizontal transmission.

Just prior to recognizing that echinoderm larvae were bacterivorous, Cameron and Holland (1983) observed that bacteria were living inside the tissues of healthy larvae. In this review we synthesize the properties of these bacteria and how they relate to the biology and ecology of the echinoderm larval host. In the first section, we provide an overview of our understanding of echinoderm larvae and their bacterial symbionts through the lens of microscopy and next-generation sequencing. In the second section, we summarize how larval-associated microbiota may be relevant in coping with anthropogenic stressors and outline the techniques needed to transition toward understanding the function of these symbionts.

BACTERIAL SYMBIONTS OF ECHINODERM LARVAE

Over the last few decades our understanding of echinoderm larvae and their microbes has gone through two primary phases. The first phase uses microscopy and focuses on “subcuticle bacteria” (or, due to their location within larval tissues, could be also be characterized as endosymbionts but this has not been explicitly tested). The second phase has developed in recent years and uses next-generation sequencing and other molecular tools to characterize larval-associated bacterial communities. This phase may be further divided into two focal points: the dynamics of these bacterial communities under different ecological conditions and the immune responses of the larval host when faced with pathogenic bacteria.

Subcuticle Bacteria

While determining how to preserve the thin cuticle overlying the epidermis for transmission and scanning electron microscopy,

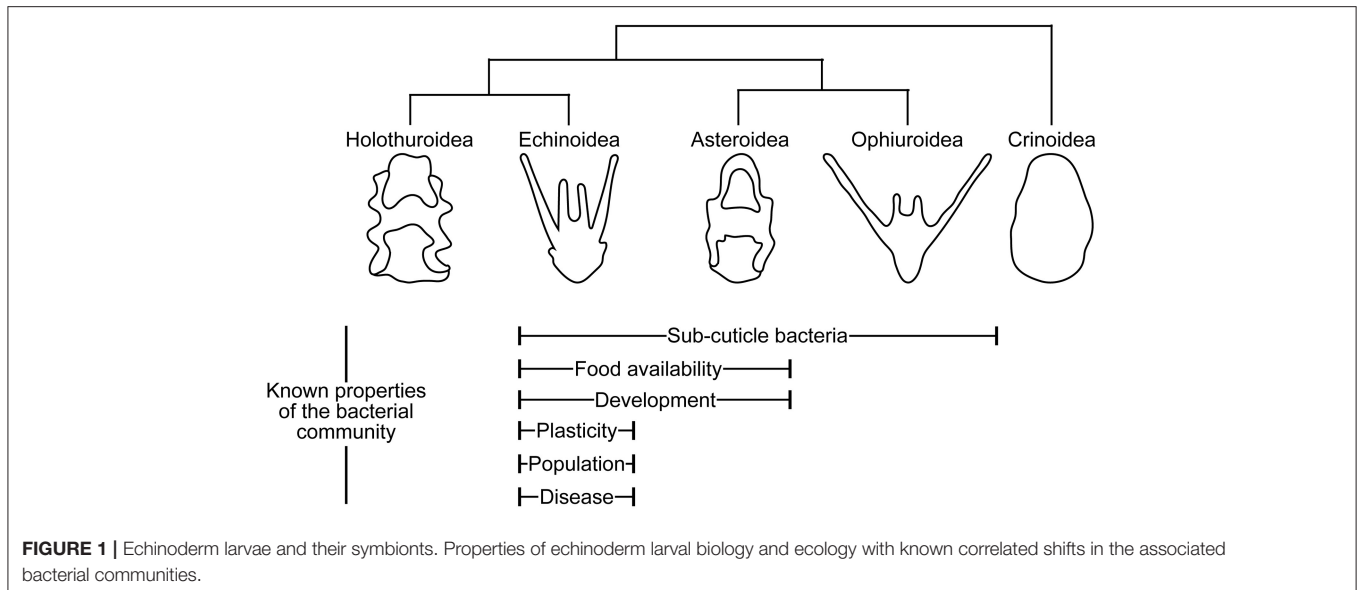
Holland and Neelson (1978) observed that adults for each of the five echinoderm classes had a high abundance of what they called ‘subcuticle bacteria.’ Holland and Neelson (1978) did not test whether embryonic or larval stages also contained subcuticle bacteria. They did, however, speculate on the nature of transmission for echinoderms, stating that because the eggs are “unattached to any follicle cells, and no bacteria have ever been observed on or in echinoderm eggs” that “it is probable that each new generation of such echinoderms acquires its subcuticular bacteria from the surrounding sea water.” Moreover, Holland and Neelson (1978) suggested that, if acquired during the embryonic or larval stages, the echinoderm must select for these symbiotic bacteria from a diverse community of environmental microbiota.

Shortly thereafter and on multiple occasions since these original observations, studies have identified subcuticle bacteria in the developmental stages of echinoderms. These symbionts, thus far, have been found in three asteroids (Cameron and Holland, 1983; Bosch, 1992; Cerra et al., 1997), one ophiuroid (Walker and Lesser, 1989), and one echinoid (Heyland et al., 2018; Schuh et al., 2019) (**Figure 1; Table 1**). In these five species, subcuticle bacteria have been observed within the mouth and gut lumen, out-pockets of the extracellular matrix that surrounds the larval body, embedded in the inner layer of the secondary cuticle of the rudiment epidermis, and are engulfed and, in some cases, digested by epidermal cells (Cameron and Holland, 1983; Walker and Lesser, 1989; Bosch, 1992; Cerra et al., 1997; Heyland et al., 2018; Schuh et al., 2019).

The function of these subcuticle bacteria remains essentially unknown. Two cases, however, may suggest that these symbionts interact with and functionally benefit the larval host. First, the brittle star *Amphipholis squamata* has a “vestigial” pluteus (i.e., greatly reduced larval arms and lacking a ciliated mouth) that is brooded within their central plate. Using transmission and scanning electron microscopy, Walker and Lesser (1989) found that a rod-shaped *Octadecabacter* was abundant and actively dividing within the tissues of this “vestigial” pluteus (Morrow et al., 2018). This *Octadecabacter*, which strictly associates with these larvae and is not found in the environment, can uptake dissolved free amino acids that are then incorporated into bacterial proteins and increase the total amino acid uptake for *A. squamata* (Walker and Lesser, 1989; Lesser and Blakemore, 1990; Lesser and Walker, 1992). Second, clonal larvae of the sea star *Luidia* collected from the Gulf Stream had one to three rod-shaped morphotypes of subcuticle bacteria (Bosch, 1992). For *Luidia* as well as *Acanthaster*, some symbionts were located in the gut and auto-fluoresced (Bosch, 1992; Galac et al., 2016; Carrier et al., 2018b), suggesting the potential ability to be phototrophic. Collectively, these examples suggest, but do not show explicitly, that bacterial symbionts may have metabolic functions that could potentially benefit the larval host.

Bacterial Communities

The subcuticle bacteria discussed above are a portion of the collection of bacteria associated with echinoderm larvae. Using next-generation sequencing, larval-associated bacterial communities have been reported for six species of echinoderm



larvae: two asteroids (Galac et al., 2016; Carrier et al., 2018b) and four echinoids (Carrier and Reitzel, 2018, 2019a,b; Carrier et al., 2019) (**Figure 1**; **Table 1**). In general, these bacterial communities are composed of a couple hundred bacterial species (i.e., Operational Taxonomic Units or OTUs, as defined by $\geq 99\%$ similarity of the phylogenetically-conserved 16S rRNA gene) (Galac et al., 2016; Carrier and Reitzel, 2018, 2019b; Carrier et al., 2018b, 2019). The predominant bacterial families encompassing these diverse communities are the α - and γ -Proteobacteria (Proteobacteria) and the Flavobacteriaceae (Bacteroidetes) (Galac et al., 2016; Carrier et al., 2018b, 2019; Carrier and Reitzel, 2019a,b).

Like many other studies of animal and plant microbes, the bacterial communities associated with echinoderm larvae are species-specific and taxonomically distinct from the environmental microbiota (Galac et al., 2016; Carrier and Reitzel, 2018; Carrier et al., 2018b), suggesting that these communities are, at least in part, selected by the host. This host-specificity, however, appears to be lost when larvae are cultured under traditional laboratory settings for rearing the developmental stages of marine invertebrates (i.e., fine-filtered or artificial saltwater) (Schuh et al., 2019). Specifically, *Strongylocentrotus purpuratus* larvae cultured under traditional laboratory settings associate with bacterial communities that are less diverse in total taxa and the phylogenetic breadth of those taxa, and retain $\sim 40\%$ of the OTUs harbored by “wild-type” counterparts (Schuh et al., 2019). This implies that studying larval-associated bacterial communities is most accurately performed at near-natural conditions, such as by filtering ambient seawater to 5- μm to remove most debris and planktonic predators while retaining the environmental microbiota (Carrier and Reitzel, 2018; Hodin et al., 2019).

Larval-associated bacterial communities are variable in community membership and composition but exhibit non-random shifts that correlate with multiple components of larval biology and ecology. These communities, for example,

are established on unfertilized eggs but not the sperm of sea urchins (Carrier and Reitzel, 2019b; Schuh et al., 2019). When cultured using coarsely (5- μm) filtered seawater, echinoderm larvae exhibit a development-based succession in symbiont composition and, using fluorescent *in situ* hybridization, these bacteria localize in the mouth and gut lumen (Carrier and Reitzel, 2019b; Schuh et al., 2019). Following fertilization, the diversity of these communities increases by $\sim 20\%$ during the early embryonic stages and decreased by nearly $\sim 85\%$ following hatching and through metamorphosis (Carrier and Reitzel, 2019b). From egg to hatching, the early embryonic stages appear to converge taxonomically with the environmental microbiota but then exhibit a host-mediated selection by diverging from this community following the onset of feeding (Carrier and Reitzel, 2019b). In cases where embryonic development includes asexual reproduction (e.g., cloning), the larval clones deviate little from the parent larva by maintaining a high proportion of particular bacteria, including phototropic species (Galac et al., 2016; Carrier et al., 2018b).

The six species of echinoderm larvae with profiled bacterial communities are planktotrophs, and by definition, are required to feed. Five of these species (echinoids: *Strongylocentrotus purpuratus*, *S. droebachiensis*, *Mesocentrotus franciscanus*, and *Lytechinus variegatus*; asteroid: *Acanthaster* sp.) have been differentially fed to test whether community composition varies with food quantity. In each case, bacterial communities are diet-specific with well-fed larvae distinguished from diet-restricted treatments (Carrier and Reitzel, 2018, 2019a; Carrier et al., 2018b). When diet-restriction is prolonged, larval sea urchins compensate by elongating their feeding arms to increase water filtration capacity (Hart and Strathmann, 1994; Miner, 2004; McAlister and Miner, 2018). This change in morphology is correlated with a shift in the composition of the bacterial symbionts, such that larval urchins associate with phenotype-specific microbiota (Carrier and Reitzel, 2018, 2019a; Carrier et al., 2018b).

TABLE 1 | List of echinoderm species noted to associate with bacterial symbionts.

	Species	Type	References
Asteroids	<i>Acanthaster</i> sp.	Bacterial community by 16S rRNA profiling	Carrier et al., 2018b
	<i>Luidia</i> sp.	Subcuticle bacteria by electron microscopy	Bosch, 1992
	<i>Patiria miniata</i>	Subcuticle bacteria by electron microscopy	Cameron and Holland, 1983
	<i>Patiriella calcar</i>	Subcuticle bacteria by electron microscopy	Cerra et al., 1997
Crinoidea	N/A	N/A	N/A
Echinoids	<i>Lytechinus variegatus</i>	Bacterial community by 16S rRNA profiling	Carrier and Reitzel, 2019a
	<i>Mesocentrotus franciscanus</i>	Bacterial community by 16S rRNA profiling	Carrier and Reitzel, 2018, 2019b
	<i>Strongylocentrotus purpuratus</i>	Bacterial community by 16S rRNA profiling	Carrier and Reitzel, 2018, 2019b
		Subcuticle bacteria by <i>in situ</i> hybridization	Schuh et al., 2019
	<i>Strongylocentrotus droebachiensis</i>	Bacterial community by 16S rRNA profiling	Carrier and Reitzel, 2018, 2019b; Carrier et al., 2019
Holothuroidea	N/A	N/A	N/A
Ophiuroidea	<i>Amphipholis squamata</i>	Subcuticle bacteria by electron microscopy	Walker and Lesser, 1989

Establishment of a phenotype-specific bacterial community for larvae of the sea urchin *L. variegatus* follows a four-stage succession (Carrier and Reitzel, 2019a). First, larvae across degrees of food availability associated with bacterial communities similar in both composition and structure. Second, different food environments (i.e., algal concentrations) induced diet-specific bacterial communities in both membership and composition. Third, the bacterial communities of diet-restricted larvae associated with similar bacterial communities that are also distinct from that of well-fed larvae, with the latter coinciding with a reduction in community diversity. Lastly, composition and structure are maintained from the prior successional stage and now correlate with the short- and long-arm phenotypes (Carrier and Reitzel, 2019a). This suggests that changes in the larval-associated bacterial community shifts prior to the expression of the environmentally elicited morphological phenotypes and that microbial communities may respond to environmental variation more quickly than morphological changes.

Recent research also suggests that microbial communities differ not only between species but also between populations (e.g., ascidians: Dishaw et al., 2014; seaweed: Marzinelli et al., 2015; fish: Llewellyn et al., 2016; sponges: Marino et al., 2017). Differential feeding of larvae of the echinoid *S. droebachiensis* from three populations in different ocean basins showed parallel responses that resulted in diet-specific bacterial communities (Carrier et al., 2019). Despite each population associating with a diet-specific bacterial community, variation in membership and community composition correlated more strongly with geographic location (Carrier et al., 2019). Moreover, when comparing the taxonomic membership between populations, 20–30% of bacterial taxa were specific to a single location while ~10% were shared between all three locations (Carrier et al., 2019). Collectively, these data suggest that larvae for a given species associates with a population-specific bacterial community. It is, however, worth noting that this comparison was not performed using common garden culturing, and that it would be expected that these communities are more taxonomically similar but still population-specific, when cultured using identical seawater.

Pathogenic Bacteria

Biological responses to foreign “particles” by echinoderm larvae were first recognized in the late nineteenth century (Metchnikoff, 1891; Tauber, 2003). More recently, echinoderm larvae have been used as a comparative system to define the cellular and molecular mechanisms of immunity when combating pathogenic bacteria. Due to the availability of a genome (Sodergren et al., 2006), the majority of this work has used the echinoid *Strongylocentrotus purpuratus*. The immune response by *S. purpuratus* to pathogenic bacteria was recently reviewed by Buckley and Rast (2017) and Heyland et al. (2018). We refer the reader to these in-depth reviews for the molecular underpinnings of larval immunity, as this section will focus on the ecological components.

From the amoebic disease (*Paramoeba invadens*) of *S. droebachiensis* in Nova Scotia (Scheibling and Stephenson, 1984; Feehan et al., 2013) to the major epizootic that decimated *Diadema antillarum* throughout the Caribbean (Lessios et al., 1984; Lessios, 2016) or, more recently, the densovirus-associated wasting disease of asteroids (Hewson et al., 2014; Harvell et al., 2019), the ecological impacts of disease on echinoderms have been well-documented over the last few decades (Feehan and Scheibling, 2014). Less of this work, however, has focused on embryonic and larval echinoderms. Echinoderm larvae potentially interact with ~20 million bacteria each day by feeding alone (Carrier et al., 2018a), and a portion of these bacteria may be consumed through bacterivory, be symbionts acquired by horizontal transmission, or pathogenic bacteria that require an immune response.

When faced with variation in food quantity, larval echinoids exhibit a trade-off in the expression of immune and metabolic genes (Carrier et al., 2015, 2018a), such that well-fed larvae upregulate metabolism and suppress immunity. High food availability is also suitable environmental conditions for bacteria to express pathogenic characteristics. If faced with a pathogen in these feeding conditions, food-induced suppression of the immune system may result in a suboptimal physiological response, and larvae may be less able to regulate the associated microbiota. Echinoid larvae may then be at risk of

pathogen-induced disease or exhibiting dysbiosis, both of which are hypothesized to be precursors to larval mortality (Carrier et al., 2018a).

When faced with pathogenic bacteria, echinoid larvae exhibit immune responses, for example, by expressing genes in the interleukin 17 (IL17) complex (Ho et al., 2016; Buckley and Rast, 2017; Buckley et al., 2017). IL17s are known to both serve as a primary barrier to foreign bodies and to regulate the composition of larval-associated microbiota (Buckley and Rast, 2017). For *S. purpuratus*, exposure to the pathogen *V. diazotrophicus* coincides with successive expression of gut epithelial-specific IL17 subtypes to prevent progression of *V. diazotrophicus* and maintain the gut microbiota (Buckley and Rast, 2017; Buckley et al., 2017). When *S. purpuratus* larvae are made nearly germ-free, they become more susceptible to *Vibrio*-induced infections and mortality than counterparts with their native bacteria (Schuh et al., 2019). Pathogens that elicit a response appear to be lineage-specific, as not all *Vibrio* species or strains induce the expression of the IL17s (Buckley and Rast, 2017; Buckley et al., 2017). Such responses by the larval host may contribute to maintaining homeostatic symbioses (e.g., Mortzfeld and Bosch, 2017), but the functional underpinnings for larval echinoderms have yet to be determined (but see Ho et al., 2016; Buckley and Rast, 2017; Buckley et al., 2017).

LARVAL ECHINODERMS IN A CHANGING ENVIRONMENT

Our understanding of echinoderm larvae and their relationship with microbial symbionts has been studied at ambient conditions. Marine invertebrates and their life history stages are, however, encountering a suite of anthropogenic stressors (Byrne et al., 2018) that may disrupt homeostatic symbioses (e.g., Rosenberg et al., 2007). To our knowledge, no studies have focused on how climate-related stressors (e.g., temperature and pH) affect the associated microbiota of echinoderm larvae. Similar to the cnidarian planula (Mortzfeld et al., 2015) and sponge amphiblastula (Webster et al., 2011), we hypothesize that an acclimation response to abiotic or biotic stressors would include shifts in symbiont composition. This, in particular, provides larvae with an opportunity to acquire bacterial symbionts with genes that are novel to the larval hologenome and that may aid in ameliorating physiological stress. Whether at ambient conditions or facing climate-related stressors, the function of larval-associated symbionts as well as if the host benefits from these partnerships remains uncertain.

Determining if and how microbial symbionts contribute to the larval holobiont requires a transition from 16S rRNA profiling to functional studies (Williams and Carrier, 2018). The functional potential and expression profiles of microbial symbionts may be assessed using metagenomics (e.g., Slaby et al., 2017) and metatranscriptomics (e.g., Moitinho-Silva et al., 2014). The impact that particular taxa or the symbiont community have on the larval host may then be assessed by generating microbe-free larvae through an antibiotic treatment or gnotobiotic chambers (Rawls et al., 2004; Bates et al., 2006; Smith et al., 2007;

Gloeckner et al., 2013; Leigh et al., 2016; Schuh et al., 2019) and adding back single or a mix of culturable taxa (e.g., Domin et al., 2018). Such techniques can be coupled with established visualization approaches (electron microscopy: Cerra et al., 1997; fluorescent *in situ* hybridization: Schuh et al., 2019) to define the spatial distribution of these symbiont and which tissues they colonize. Lastly, viruses, archaea, and fungi are also functionally important members of host-associated microbial communities (e.g., Webster and Thomas, 2016). Similar molecular and sequencing approaches can and should be used to characterize if and how they interact with the larval host as well as other microbial groups within the microbiome.

CONCLUSION

Our understanding of symbioses between larval echinoderms and microbes has primarily developed in the last few years; yet, in this time we suggest that three primary themes have materialized. First, larval echinoderms associate with subcuticle bacteria that appear to colonize select tissues. Second, the bacterial communities associated with larval echinoderms exhibit compositional shifts that are correlated with several fundamental properties of larval biology and ecology. Third, the echinoderm larval host exhibits strict responses to pathogenic microbiota that may aid in maintaining the symbiont community to avoid dysbiosis.

As echinoderms larvae continue to serve as a fundamental system for understanding development and life history evolution (Love and Strathmann, 2018), this diversity in form and function may act as a strong foundation to understand how and to what extent bacteria and other microbes influence the many dimensions of larval biology (Hammer et al., 2019). In particular, these diverse developmental approaches enable the fields of animal-microbe symbiosis and larval biology to test for unique functional links between host and symbiont during, for example, morphological plasticity and life history transitions. And in a time where it is becoming clear that the bacterial flora cannot be ignored, we must remember that echinoderm larvae have always and will continue to live and evolve in a sea of microbes (Walne, 1956; Zilber-Rosenberg and Rosenberg, 2008; McFall-Ngai et al., 2013; Bordenstein and Theis, 2015).

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication. Specifically, TC drafted and edited the manuscript and AR edited the manuscript.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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