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Genomic Basis of Environmental Adaptation in *Ascidians*

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Abstract *Ascidians* is a type of invertebrate widely distributed in the ocean, adapted to various environmental niches and distributed from intertidal zones to extreme deep-sea environments. Studying the genomic adaptability of sea squirts is of great significance for understanding the survival strategies of marine invertebrates in complex environments. This study explores the genomic basis of adaptive evolution of sea squirts in different environments, including genomic features, molecular mechanisms related to environmental stress, genetic basis of habitat specialization, and the impact of symbiotic relationships on their genome. In addition, attention has been paid to the impact of environmental pressures such as climate change and pollution on the adaptive evolution of sea squirts, providing new insights into the evolution and adaptability research of marine invertebrates.

Keywords Genomic adaptation; *Ascidians*; Environmental stress; Habitat specialization; Symbiotic relationships

1 Introduction

Ascidians, commonly known as sea squirts, are a diverse group of marine invertebrates belonging to the Phylum Chordata, Class *Ascidiacea*. They play a crucial role in the ecology of marine benthic communities, often forming dense populations on submerged surfaces. *Ascidians* are found in a variety of marine environments, from shallow coastal waters to the deep sea, and exhibit a wide range of morphological and ecological adaptations (Nydam et al., 2021). The botryllid *Ascidians*, for instance, include 53 colonial species that thrive in temperate, tropical, and subtropical waters, showcasing their ability to adapt to different environmental conditions.

Understanding the genomic basis of environmental adaptation in *Ascidians* is essential for several reasons. Firstly, *Ascidians* occupy a unique evolutionary position at the boundary between invertebrates and vertebrates, making them valuable models for studying evolutionary processes. Secondly, many *Ascidian* species are invasive, spreading rapidly across the globe and impacting local ecosystems. Investigating the genetic mechanisms underlying their invasive capabilities can provide insights into managing and mitigating their spread (Wei et al., 2020). Additionally, *Ascidians* harbor diverse microbial communities that are species-specific and tissue-specific, which can have significant implications for their health and ecological interactions (Chen et al., 2016). The study of these microbial associations through genomic approaches can reveal new aspects of symbiosis and microbial ecology (Chen et al., 2016).

This study will explore the genetic and molecular mechanisms that enable sea squirts to thrive in diverse and often challenging marine environments. Covers key findings from recent genomic studies, including the identification of gene families involved in stress response, immune function, and metabolic pathways that contribute to environmental adaptation. The study will provide a valuable resource for researchers interested in evolutionary biology, ecology, and genomics at Scian.

2 Genomic Features of *Ascidians*

2.1 General structure of *ascidian* genomes

Ascidians, also known as sea squirts, possess genomes that exhibit unique structural characteristics. The genome of the leathery sea squirt, *Styela clava*, for instance, is approximately twice the size of that of *Ciona intestinalis* type A (*C. robusta*), despite having a comparable number of genes. This expansion is attributed to an increase in transposon number and variation in dominant types (Chen et al., 2020). Additionally, the genomes of *Ascidians* like *Ciona robusta* and *Ciona savignyi* show differences in exon/intron size distributions, which contribute to variations in alternative splicing responses to environmental changes (Huang et al., 2023).

2.2 Unique genomic elements related to adaptation

Ascidians have developed several unique genomic elements that facilitate their adaptation to diverse environments. For example, the genome of *Styela clava* contains an expanded number of genes encoding heat-shock proteins and members of the complement system (Figure 1), which are crucial for stress responses. Additionally, cold-shock protein genes have been horizontally transferred from bacteria, further aiding in environmental adaptation (Wei et al., 2020). In *Ciona robusta*, significant genetic differentiation among populations has been observed, with specific loci showing signatures of directional selection in response to local environmental conditions (Lin et al., 2017). Moreover, DNA methylation patterns driven by local environments have been identified, indicating a strong epigenetic component in adaptation (Hoban et al., 2016).

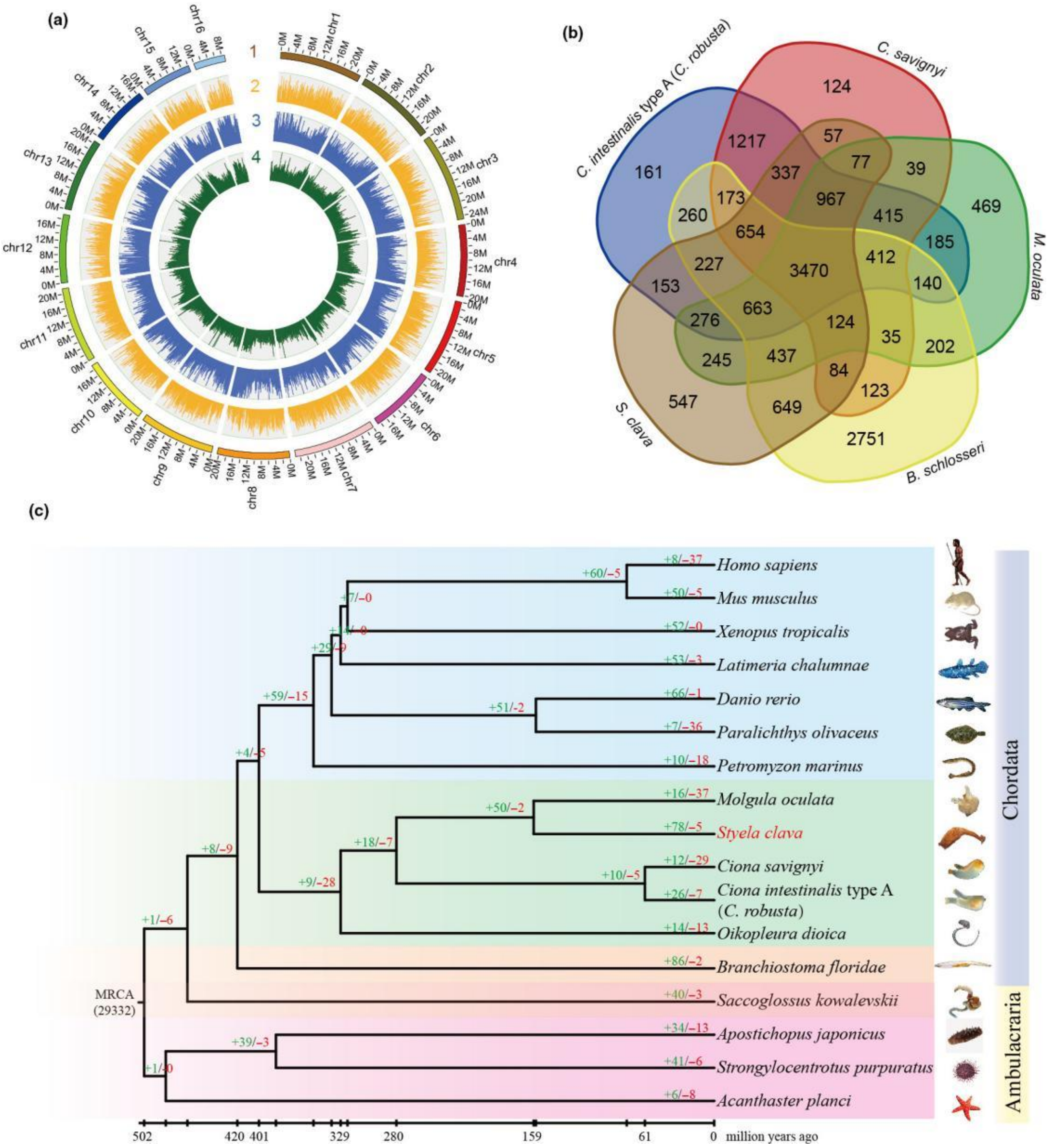

Figure 1 Genome map, gene family and phylogenetic position of *Styela clava* (Adopted from Wei et al., 2020)

Image caption: a, Chromosome-level genome map of *S. clava*; b, Venn diagram of common and unique gene families among five *ascidian* species; c, The phylogenetic position, divergence time estimation and gene family analysis of *S. clava* (Adopted from Wei et al., 2020)

2.3 Comparative genomics: *Ascidians* and other marine invertebrates

Comparative genomic studies between *Ascidians* and other marine invertebrates reveal both shared and unique adaptive strategies. For instance, the genetic basis of adaptation in *Ascidians* shows parallels with other marine organisms, such as the presence of genes under positive selection related to stress responses and environmental tolerance (Valero et al., 2021). However, *Ascidians* also exhibit distinct features, such as the specific expansion of gene families related to their unique tunic structure and the presence of horizontally transferred genes. Additionally, the genomic landscape of adaptation in *Ascidians* is shaped by both genetic and epigenetic variations, a feature that is increasingly recognized in other marine invertebrates as well (Guo et al., 2022).

3 Molecular Mechanisms of Environmental Adaptation

3.1 Gene families associated with stress response

Gene families such as heat shock proteins (*HSP*s) play a crucial role in the stress response of *Ascidians*. *HSP*s are highly conserved proteins that assist in protein folding, repair, and protection against stress-induced damage. In the invasive *ascidian Ciona savignyi*, a comprehensive study identified 32 *HSP*-related genes, including *HSP20, HSP40, HSP60, HSP70, HSP90*, and *HSP*100, which are differentially expressed in response to temperature and salinity challenges (Huang et al., 2018). These proteins help maintain cellular homeostasis under stress conditions by preventing protein misfolding and aggregation. The expansion of *HSP* gene families, such as *HSP*70, has also been observed in other *Ascidians* like *Styela clava*, suggesting a genomic basis for their broad environmental adaptability (Wei et al., 2020).

3.2 Epigenetic modifications and adaptation

Epigenetic modifications, particularly DNA methylation, are pivotal in the rapid adaptation of *Ascidians* to environmental changes. In *Ciona robusta*, significant DNA methylation variations were observed in genes associated with temperature and salinity, such as heat shock protein 90 and Na+-K+-2Cl− cotransporter (Pu and Zhan, 2017). These modifications occur mainly in gene bodies and are correlated with environmental factors, indicating that epigenetic regulation plays a role in local adaptation during biological invasions. Such epigenetic changes can lead to phenotypic plasticity, allowing *Ascidians* to thrive in diverse and changing environments (Cheaib et al., 2015).

3.3 Transcriptional regulation of adaptation to salinity and temperature

3.3.1 Heat shock proteins and thermal tolerance

Heat shock proteins (*HSP*s) are central to the thermal tolerance of *Ascidians*. The transcriptional response of *HSP* genes to heat stress is well-documented, with *HSP*70 being one of the most responsive genes. In *Ciona savignyi*, *HSP*70-4 showed the highest induction after 1 hour of high-temperature treatment, highlighting its role in thermal adaptation (Huang et al., 2018). The regulation of *HSP*s involves heat shock transcription factors (HSFs), which bind to heat shock elements (HSEs) in the promoters of *HSP* genes, initiating their transcription in response to heat stress (Rossoni and Weber, 2019).

3.3.2 Ion Transporters in osmoregulation

Ion transporters are essential for osmoregulation in *Ascidians*, enabling them to maintain cellular ion balance under varying salinity conditions. The Na+-K+-2Cl− cotransporter, for instance, is crucial for adapting to salinity changes. In *Ciona robusta*, DNA methylation of this transporter gene was significantly correlated with salinity levels, suggesting that both transcriptional and epigenetic mechanisms regulate its expression. Additionally, in the fish *Cynoglossus semilaevis*, *HSP*70 genes were upregulated under low salinity stress, indicating a potential cross-talk between heat shock proteins and ion transporters in osmoregulation (Deng et al., 2021).

4 Genetic Basis of Habitat Specialization

4.1 Adaptation to intertidal and subtidal zones

Ascidians, like many marine organisms, exhibit remarkable adaptations to various environmental conditions, including intertidal and subtidal zones. The leathery sea squirt, *Styela clava*, provides a compelling example of genomic adaptations that facilitate survival in diverse habitats. The expansion of gene families related to heat-shock proteins and the complement system, as well as the horizontal transfer of cold-shock protein genes, underscores the genetic mechanisms that enable *S. clava* to thrive in fluctuating thermal environments (Wei et al., 2020). Similarly, the *ascidian Pyura chilensis* demonstrates significant genetic differentiation across environmental gradients, particularly around the 30 °S transition zone of the Humboldt Current System. This differentiation is driven by adaptive loci correlated with sea surface temperature and other environmental variables, highlighting the role of local adaptation in maintaining genetic structure despite potential gene flow (Segovia et al., 2020).

4.2 Role of horizontal gene transfer in habitat specialization

Horizontal gene transfer (HGT) plays a crucial role in the genomic adaptation of *Ascidians* to their environments. In *Styela clava*, the acquisition of cold-shock protein genes from bacteria exemplifies how HGT can introduce novel genetic material that enhances environmental resilience. This genetic exchange allows *S. clava* to better cope with cold stress, which is particularly advantageous in temperate and polar regions (Valero et al., 2021). The integration of these horizontally transferred genes into the host genome and their subsequent functional assimilation illustrate the dynamic nature of *ascidian* genomes in response to environmental pressures (Li, 2024).

4.3 Case study: genomic insights from polar and tropical *Ascidians*

The study of *Ascidians* from polar and tropical regions provides valuable insights into the genomic basis of environmental adaptation. For instance, the genomic analysis of *Styela clava* reveals significant expansions in gene families associated with stress responses, which are critical for survival in both cold polar waters and warmer temperate zones (Feng et al., 2021). Additionally, the research on *Pyura chilensis* along the southeast Pacific coast demonstrates how local environmental factors, such as temperature and productivity, drive adaptive genetic differentiation (Figure 2). This differentiation is crucial for the species' ability to inhabit diverse ecological niches within the Humboldt Current System (Segovia et al., 2020).

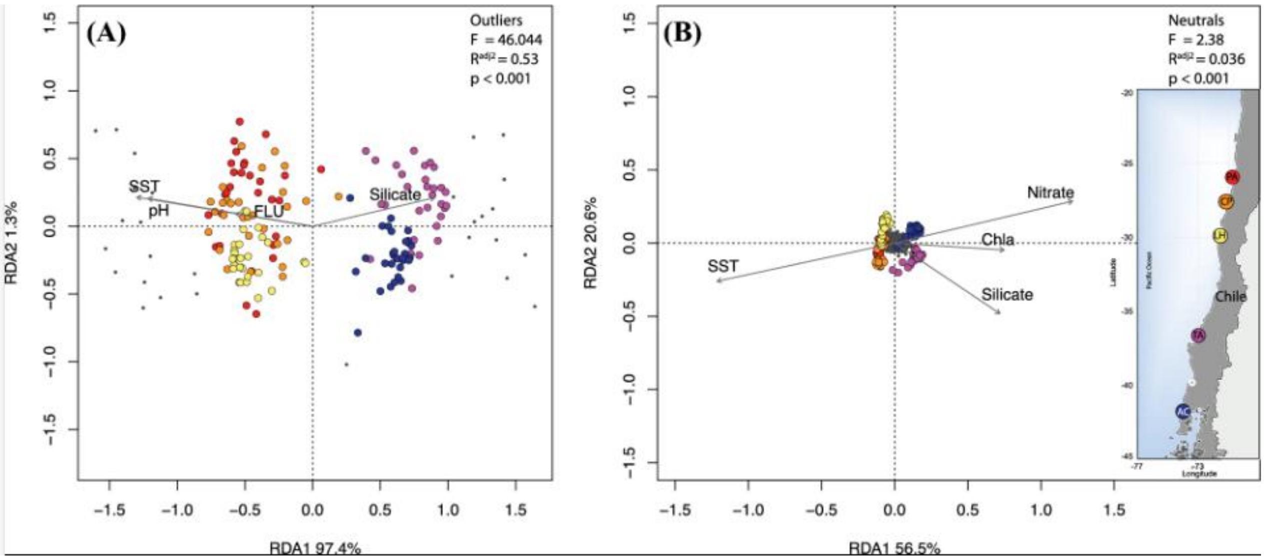

Figure 2 Redundancy analysis (RDA) showing the relative contributions of oceanographic variables to the genetic structure of outlier and neutral genotypes. SNP genotypes in gray; individuals are represented by different colors according to their location according to the map in the right panel. Plot shows the most relevant variables obtained with *ordistep* and *ordiR2step* functions (Adopted from Segovia et al., 2020)

5 Case Study: *Ascidians* in Extreme Environments

5.1 Adaptation mechanisms in deep-sea *Ascidians*

Deep-sea environments present unique challenges such as high hydrostatic pressure, low temperatures, and limited light. While specific studies on deep-sea *Ascidians* are limited, insights can be drawn from related marine organisms. For instance, the genomic basis of adaptation in Arctic Charr (*Salvelinus alpinus*) to deep-water habitats has been explored, revealing significant genetic divergence between deep and shallow water morphs (Wang et al., 2024). Genes involved in processes such as gene expression, DNA repair, cardiac function, and membrane transport were identified as crucial for adaptation to deep-water conditions (Kess et al., 2021). These findings suggest that similar genomic mechanisms may be at play in deep-sea *Ascidians*, enabling them to thrive in such extreme environments.

5.2 Genomic responses to hypoxia in polar *Ascidians*

Polar regions are characterized by extreme cold and often hypoxic conditions. The leathery sea squirt, *Styela clava*, has shown significant genomic adaptations to cold environments, including the expansion of gene families related to heat-shock proteins and the horizontal transfer of cold-shock protein genes from bacteria (Wei et al., 2020). These adaptations likely play a crucial role in enabling *Ascidians* to survive in hypoxic polar waters. Additionally, studies on *Ciona robusta* and *Ciona savignyi* have demonstrated species-specific alternative splicing responses to environmental stresses, including temperature variations, which may also contribute to their ability to cope with hypoxic conditions (Figure 3) (Huang et al., 2023).

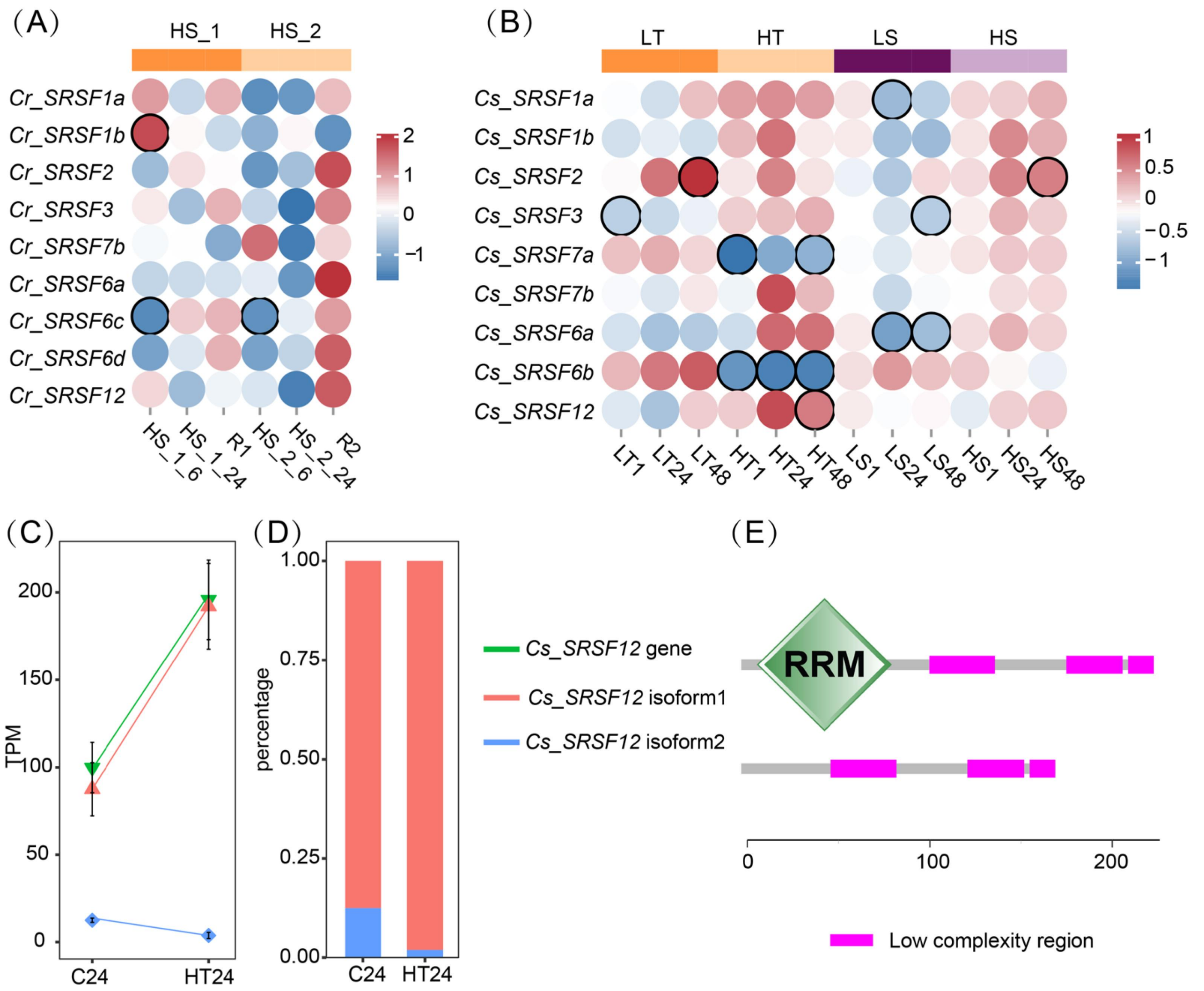

Figure 3 Gene expression and alternative splicing response of serine/arginine-rich splicing factor (*SRSF*) genes to environmental changes (Adopted from Huang et al., 2023)

Image caption: (A) *SRSF* gene expression changes under recurrent high salinity stresses in C. *robusta*, of which *Cr_SRSF7a* and *Cr_SRSF6b* genes were excluded from differential expression analysis due to their low expression level. The Log2 foldchange values between treatment and control groups were used to draw the heatmap, and the color circles with black borders indicate significantly changed genes (adjusted p value < 0.05). (B) *SRSF* gene expression changes under low (LT) and high temperature (HT), and low (LS) and high salinity (HS) stresses in C. *savignyi*. (C) Transcript expression level of two isoforms of alternatively spliced gene (*Cs_SRSF12*) after 24 h of control and HT stress groups. (D) Percentage of two isoforms of *Cs_SRSF12* gene. (E) Conserved domains of isoform1 (upper) and isoform2 (lower) (Adopted from Huang et al., 2023)

5.3 Lessons from *Ascidians* in anthropogenic impacted areas (e.g., pollution)

Ascidians in areas impacted by human activities, such as pollution, exhibit notable genomic adaptations. For example, the *Ascidian Pyura chilensis* shows significant genetic differentiation across environmentally heterogeneous regions, driven by local adaptation to factors such as sea surface temperature and upwelling-associated variables (Segovia et al., 2020). Similarly, the marine invasive *Ascidian Molgula manhattensis* has demonstrated genomic signatures of local adaptation to salinity-related variables, highlighting the role of environmental selection in driving adaptive divergence (Chen et al., 2021). These studies underscore the importance of understanding the genomic basis of adaptation in *Ascidians* to predict their responses to anthropogenic changes and to develop effective conservation strategies.

6 Symbiotic Relationships and Their Genomic Impacts

6.1 Symbiosis with microorganisms in *Ascidians*

Ascidians, or sea squirts, are known to harbor diverse and host-specific microbial communities. These symbiotic relationships are crucial for the *Ascidians*' adaptation to various environments. For instance, studies have shown that *Ascidians* host a wide range of microbial symbionts, including bacteria and archaea, which are distinct from the surrounding seawater bacterioplankton. These microbial communities are involved in essential functions such as ammonia-oxidization, denitrification, and heavy-metal processing, which can enhance the host's tolerance to different environmental conditions (Evans et al., 2017). Additionally, the microbiomes of *Ascidians* have been found to include bacteria from phyla such as Cyanobacteria, *Proteobacteria, Bacteroidetes, Actinobacteria*, and *Planctomycetes*, which contribute to various ecological roles, including UV protection and defense against predators (Matos and Antunes, 2021).

6.2 Genomic modifications influenced by symbiotic interactions

Symbiotic interactions can lead to significant genomic modifications in both the host and the symbionts. For example, the genome of the *Ascidian Styela clava* has undergone expansion due to an increase in transposon numbers and variations in dominant types. This genomic expansion includes the horizontal transfer of cold-shock protein genes from bacteria, which likely aids in the adaptation to cold environments (Wei et al., 2020). Similarly, the genome of the sponge symbiont "*Candidatus Synechococcus spongiarum*" has undergone streamlining, losing genes related to environmental toxin resistance and polysaccharide biosynthesis, which suggests adaptation to the stable environment within the sponge host (Gao et al., 2014). These genomic changes highlight the dynamic nature of symbiotic relationships and their impact on the genetic architecture of the involved organisms.

6.3 Role of symbiosis in *Ascidians*' adaptation to extreme environments

Symbiotic relationships play a crucial role in the adaptation of *Ascidians* to extreme environments. The presence of specific microbial communities can enhance the host's ability to withstand harsh conditions. For instance, the microbial symbionts in *Ascidians* have been linked to functions such as heavy-metal processing and bioaccumulation, which can be vital for survival in polluted environments (Knobloch et al., 2019). Moreover, the integration of microbial genes into the host genome, such as the cold-shock protein genes in *Styela clava*, provides additional mechanisms for coping with extreme temperatures (Rúav et al., 2016). These symbiotic interactions not only facilitate the immediate survival of *Ascidians* in challenging environments but also drive long-term evolutionary adaptations through genomic modifications.

7 Environmental Stress and Adaptive Evolution in *Ascidians*

7.1 Impact of climate change on *Ascidians*

Climate change poses significant challenges to marine organisms, including *Ascidians*, by altering temperature and salinity levels in their habitats. The leathery sea squirt (*Styela clava*) has shown remarkable genomic adaptations to these changes, including the expansion of heat-shock protein genes and the horizontal transfer of cold-shock protein genes from bacteria, which help it survive in varied environmental conditions (Wei et al., 2020). Additionally, the estuarine oyster study highlights the role of gene expansion in solute carrier families, which are crucial for temperature and salinity stress responses, suggesting similar mechanisms might be at play in *Ascidians* (Li et al., 2021).

7.2 Evolutionary genomic responses to pollution and ocean acidification

Ascidians, like other marine organisms, face significant threats from pollution and ocean acidification. The study on the marine copepod *Acartia tonsa* provides insights into how marine species can adapt to multiple stressors, including warming and acidification, through polygenic responses targeting cellular homeostasis and stress response mechanisms (Brennan et al., 2021). Similarly, the rapid adaptation of killifish to polluted environments through introgression of toxicant-resistant genes from a related species underscores the potential for genetic variability to facilitate evolutionary rescue in *Ascidians* facing pollution (Oziolor et al., 2019). The genomic analysis of the invasive *Ascidian Molgula manhattensis* revealed significant genetic differentiation driven by local environmental factors, particularly salinity, indicating that pollution and other environmental stressors can drive adaptive divergence in *Ascidian* populations (Chen et al., 2021).

7.3 Molecular mechanisms underpinning resistance to environmental stressors

The molecular mechanisms that enable *Ascidians* to resist environmental stressors are diverse and complex. Proteomic studies on the stolon of *Ciona robusta* have identified key pathways involved in stress response, including cytoskeleton stability, signal transduction, and posttranslational modifications, which are crucial for maintaining structural integrity and activating stress responses under temperature and salinity stress (Li et al., 2021). Additionally, alternative splicing (AS) mechanisms play a significant role in the phenotypic plasticity of *Ascidians*, with species-specific and environmental context-dependent AS responses observed in *Ciona robusta* and *Ciona savignyi*, highlighting the importance of AS in rapid adaptation to environmental changes (Huang et al., 2023). The interplay between genetic and epigenetic variations also contributes to local adaptation, as seen in *Ciona intestinalis* populations, where DNA methylation patterns driven by local environments complement genetic adaptations, enhancing the rapid adaptive capacity of *Ascidians* (Chen et al., 2022).

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Conflict of Interest Disclosure

The author affirms that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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