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HOST-ASSOCIATED BACTERIAL ASSEMBLAGES OF LITTORINIDAE GASTROPODS FROM MANGROVE AND BEACH ECOSYSTEMS ON THE BRAZILIAN SEMI-ARID COAST

COMUNIDADES BACTERIANAS ASSOCIADAS A GASTRÓPODES
LITTORINIDAE EM ECOSISTEMAS DE MANGUEZAL E PRAIA NA
COSTA SEMIÁRIDA BRASILEIRA

ENSAMBLAJES BACTERIANOS ASOCIADOS AL HOSPEDADOR EN
GASTERÓPODOS LITTORINIDAE DE ECOSISTEMAS DE MANGLAR
Y PLAYA EN LA COSTA SEMIÁRIDA DE BRASIL

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ABSTRACT

Gastropods of Littorinidae family are ecologically important in coastal ecosystems, but little is known about the microbial communities associated with these molluscs, particularly in semi-arid tropical regions. This study aimed to characterize and compare the bacterial microbiota associated with three Littorinidae species: *Echinolittorina lineolata* (a beach-dwelling species), *Littorina angulifera* (restricted to mangrove habitats), and *Littorina flava* found in two contrasting habitats (beach and mangrove) on the semi-arid coast of northeastern Brazil. Statistical analyses (PERMANOVA and SIMPER) of the culturable microbiota revealed that host species identity was the main factor shaping microbial community composition ($p = 0.001$). Significant differences in microbial assemblages were observed between *L. angulifera* and both *E. lineolata* and beach-associated *L. flava*. Statistical analyses (PERMANOVA and SIMPER) revealed that host species identity was the main factor shaping microbiota composition ($p = 0.001$). Significant differences were found between the microbiota composition of *L. angulifera* and both *E. lineolata* and *L. flava* from beach environment. However, no significant differences were detected between *L. angulifera* and *L. flava* from the mangrove. Dominant taxa contributing to microbial dissimilarities included *Vibrio alginolyticus*, *V. fluvialis*, *Sphingomonas paucimobilis*, and *Streptococcus iniae*, with notable habitat-specific patterns. These findings emphasise the influence of host identity on microbiota structure. Species from the same genus but occurring in different environments presented distinct microbial profiles, while those sharing the same habitat displayed similarities regardless of taxonomic proximity. These results advance our understanding of host-microbe interactions in marine invertebrates and highlight the potential of Littorinidae species as bioindicators of coastal environmental health.

KEYWORDS

Environmental surveillance; biomonitoring; bioindicators

RESUMO

Os gastrópodes da família Littorinidae são ecologicamente importantes em ecossistemas costeiros, mas pouco se sabe sobre as comunidades microbianas associadas a esses moluscos, particularmente em regiões tropicais semiáridas. Este estudo teve como objetivo caracterizar e comparar a microbiota bacteriana associada a três espécies de Littorinidae: *E. lineolata* (espécie característica do ambiente de praia), *L. angulifera* (restrita a habitats de manguezal) e *L. flava*, encontrada em dois ambientes contrastantes (praia e manguezal) ao longo da costa semiárida do Nordeste do Brasil. As análises estatísticas (PERMANOVA e SIMPER) da microbiota cultivável revelaram que a identidade da espécie hospedeira foi o principal fator que moldou a composição da comunidade microbiana ($p = 0,001$). Diferenças significativas nos agrupamentos microbianos foram observadas entre *L. angulifera* e tanto *E. lineolata* quanto *L. flava* associada ao ambiente de praia. No entanto, não foram detectadas diferenças significativas entre *L. angulifera* e *L. flava* do manguezal. Os táxons dominantes que contribuíram para as dissimilaridades microbianas incluíram *Vibrio alginolyticus*, *V. fluvialis*, *Sphingomonas paucimobilis* e *Streptococcus iniae*, com padrões específicos associados ao habitat. Esses achados enfatizam a influência da identidade do hospedeiro na estrutura da microbiota. Espécies do mesmo gênero, mas ocorrendo em ambientes distintos, apresentaram perfis microbianos diferentes, enquanto aquelas que compartilhavam o mesmo habitat exibiram similaridades independentemente da proximidade taxonômica. Esses resultados ampliam a compreensão das interações hospedeiro-microorganismo em invertebrados marinhos e destacam o potencial das espécies de Littorinidae como bioindicadoras da saúde ambiental costeira.

PALAVRAS-CHAVE

Vigilância ambiental; biomonitoramento; bioindicadores

RESUMEN

Los gasterópodos de la familia Littorinidae son ecológicamente importantes en los ecosistemas costeros, pero se sabe poco sobre las comunidades microbianas asociadas a estos moluscos, particular-

mente en regiones tropicales semiáridas. Este estudio tuvo como objetivo caracterizar y comparar el microbioma de bacterias asociada a tres especies de Littorinidae: *E. lineolata* (especie característica del ambiente de playa), *L. angulifera* (restringida a hábitats de manglar) y *L. flava*, encontrada en dos ambientes contrastantes (playa y manglar) a lo largo de la costa semiárida del noreste de Brasil. Los análisis estadísticos (PERMANOVA y SIMPER) de la microbiota cultivable revelaron que la identidad de la especie hospedadora fue el principal factor que moldeó la composición de la comunidad microbiana ($p = 0,001$). Se observaron diferencias significativas en las comunidades microbianas entre *L. angulifera* y tanto *E. lineolata* como *L. flava* asociada al ambiente de playa. Sin embargo, no se detectaron diferencias significativas entre *L. angulifera* y *L. flava* del manglar. Los taxones dominantes que contribuyeron a las disimilitudes microbianas incluyeron *Vibrio alginolyticus*, *V. fluvialis*, *Sphingomonas paucimobilis* y *Streptococcus iniae*, con patrones específicos asociados al hábitat. Estos hallazgos enfatizan la influencia de la identidad del hospedador en la estructura de la microbiota. Especies del mismo género, pero que ocurren en ambientes distintos, presentaron perfiles microbianos diferentes, mientras que aquellas que compartían el mismo hábitat mostraron similitudes independientemente de la proximidad taxonómica. Estos resultados amplían la comprensión de las interacciones hospedador-microorganismo en invertebrados marinos y destacan el potencial de las especies de Littorinidae como bioindicadoras de la salud ambiental costera.

PALABRAS CLAVE

Vigilancia ambiental; biomonitoreo; bioindicadores

1 INTRODUCTION

All animals maintain some type of relationship with microorganisms, and these interactions are as diverse as the different existing species (DHAMI; TAYLOR, 2024). Despite the vast diversity of marine invertebrates, particularly molluscs, most studies on host-associated microbiomes have focused on vertebrate hosts, which represent a minimal proportion of animal diversity (HOLT *et al.*, 2022). The microbiota structure of marine organisms is known to be shaped by a complex interaction between host-intrinsic factors, such as diet, developmental stage, and physiology, and extrinsic environmental factors, such as temperature, salinity, nutrient availability, and the presence of environmental impacts (LEMKE; DESALLE, 2023, DHAMI; TAYLOR, 2024).

In estuarine and beachrock reefs, characterized by sharp environmental gradients and often by anthropogenic influence, the microbiota of invertebrates can be particularly dynamic and diverse. However, detailed comparative studies on the microbiota associated with different Littorinidae species that coexist or inhabit distinct niches in the same geographical region, especially on the Brazilian semi-arid coast, are rare. Gastropods of the Littorinidae family are abundant and ecologically

relevant marine organisms, widely distributed in intertidal zones of rocky coasts and estuarine environments worldwide (NG *et al.*, 2011).

Littoraria angulifera inhabits the supralittoral zone of mangroves, living associated with mangrove tree roots and trunks, and is the only Brazilian littorinid species exclusively linked to this ecosystem (MELO *et al.*, 2012). *L. flava* has a broad distribution along the Brazilian coastline, occurring mainly on rocky shores with sandstone reefs, and may also be recorded in mangrove environments (MATTHEWS, 1968; REID; MAK, 1999). *Echinolittorina lineolata*, in turn, occurs along the entire Brazilian coast, occupying both natural and artificial consolidated substrates, such as rocky shores and barnacle-covered structures (RIOS, 1994; MATOS, 2018).

Littorinidae species play roles of great importance in coastal ecosystems, acting as herbivores, detritivores, and prey in complex trophic chains (NG *et al.*, 2011; MALTSEVA *et al.*, 2021). The interaction of these molluscs with the inhabiting microbial communities is a growing field of interest, as the associated microbiota can influence host health, physiology, nutrition, and adaptation to different environmental conditions (LEMKE; DESALLE, 2023).

The microbiomes can play a fundamental role in the acclimation of marine organisms, with their flexibility being considered a promising strategy for adapting to future ocean scenarios, contributing to the preservation of biodiversity and ecosystem functioning. Additionally, associated microorganisms can be very important for survival in extreme environments, acting as mediators of acclimation and adaptation to environmental changes (PINNOW *et al.*, 2023). Although hosts may also respond to environmental stressors through phenotypic plasticity, microbe-mediated acclimation has gained prominence as a particularly relevant resilience mechanism in the face of rapid climate change.

Considering the ecological relevance of gastropods of the Littorinidae family and their microbiota structure, and the complexity of the coastal ecosystems of northeastern Brazil, this study aimed to characterize and compare the composition of bacterial microbiota associated with three Littorinidae species: *Echinolittorina lineolata* (d'Orbigny, 1840), *Littoraria angulifera* (Lamarck, 1822), and *L. flava* (King, 1832), collected in different habitats of the Brazilian semi-arid coast. Thus, the present work seeks to elucidate the influence of host identity and environment on structuring of these microbial communities, contributing to the understanding of host-microbe interactions and the potential of these molluscs as bioindicators of environmental health.

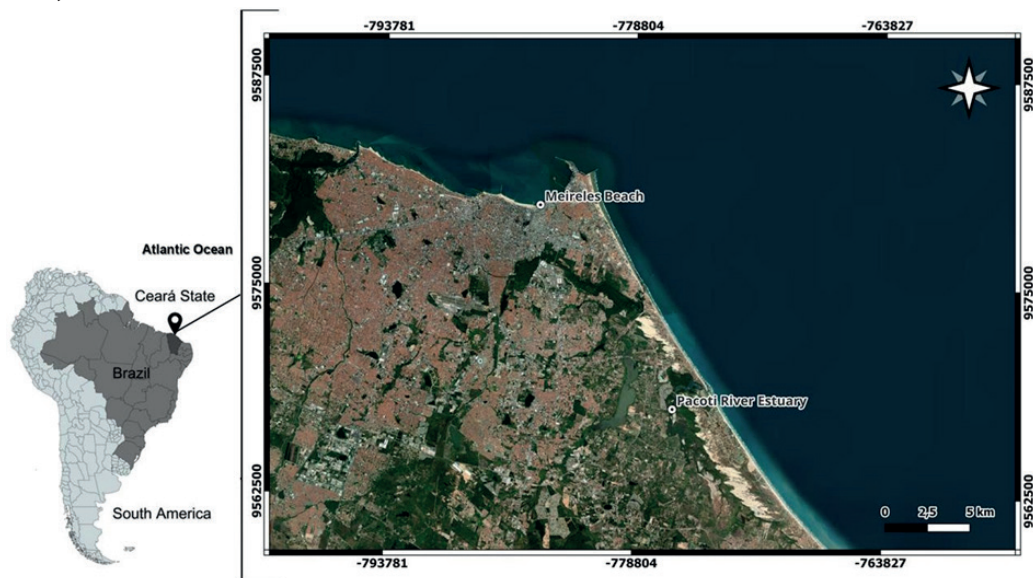
2. METHODS

2.1 STUDY AREA

The study area is found in the eastern region of Ceará state, in Brazil's semiarid northeastern coast, a region characterized by frequent dry periods. The region is characterized by a tropical semi-arid climate with an average annual precipitation of approximately 1,200 mm, concentrated between January and June (rainy season), followed by a dry season from July to December (MAIA *et al.*, 2018). Nevertheless, annual climatic variability can lead to shifts in the pluviometric regime (LIMA; LIRA, 2021). Mean annual temperatures range from 26 to 29°C (FUNCEME, 2025).

Field sampling took place in two contrasting ecosystems within this Brazilian semi-arid coastal state: a beachrock reef located at Meireles Beach in Fortaleza, Ceará, Brazil, and a mangrove forest situated in the Pacoti River estuary in Eusébio, Ceará, Brazil (Figure 1).

Figure 1 - Study areas located in Meireles Beach, Fortaleza, and in Pacoti River Estuary, Eusébio, both in Ceará, Brazil.



2.2 FIELD AND LABORATORY METHODS

A total of 40 adult individuals were manually collected using sterile gloves. Three distinct species of littorinids were sampled in two coastal ecosystems. The species collected and their respective environments were: *E. lineolata* (10 individuals) and *L. flava* (10 individuals) on a beachrock reef at Meireles Beach, in Fortaleza (beach environment); and *L. angulifera* (10 individuals) and *L. flava* (10 individuals) in the mangrove of the Pacoti River estuary, in Eusébio. After field sampling, the individuals were anesthetized in a 10% magnesium chloride ($MgCl_2$) solution. Subsequently, individuals were stored individually in sterile tubes containing Brain Heart Infusion (BHI) broth for bacterial enrichment and transported to the laboratory in light-protected isothermal boxes using ice packs, ensuring the stability of the samples until processing.

In the laboratory, each individual was processed by maceration, using sterile mortar and pestle, and the samples were homogenized with 0.9% saline solution. The macerated samples were then inoculated onto Blood agar and MacConkey agar plates, which were incubated at 37°C for 48 hours for bacterial colony growth. Isolated colonies were subjected to identification using the automated VITEK® 2 Compact system (BioMérieux). This system allowed for species-level bacterial identification.

2.3 STATISTICAL ANALYSIS

Microbial composition data were analysed using the software PRIMER (Plymouth Routines in Multivariate Ecological Research) version 6.0 with the PERMANOVA+ add-on (ANDERSON *et al.*, 2008). A species-by-sample matrix containing the occurrence of each identified bacterial taxon per host individual was constructed for the analyses. Prior to statistical testing, a presence-absence data matrix of bacterial taxa was constructed and standardised, and a Euclidean distance similarity matrix was subsequently calculated to evaluate differences in bacterial community composition among host groups.

To test whether microbial assemblages differed according to host species and habitat, a Permutational Multivariate Analysis of Variance (PERMANOVA) was performed using 999 permutations under a reduced model. The factor Littorinidae species was considered fixed and included the following groups: *Echinolittorina lineolata*, *Littoraria angulifera*, *L. flava* (mangrove), and *L. flava* (beachrocks). The pseudo-F statistic and permutation-based p-values were used to assess statistical significance ($\alpha = 0.05$). When significant differences were detected, pairwise PERMANOVA tests were conducted to identify which host groups differed in their associated microbiota composition. To determine which bacterial taxa contributed most to the observed similarities within groups and dissimilarities among groups, a Similarity Percentage analysis (SIMPER) was applied.

3. RESULTS

A total of 38 bacterial isolates belonging to 10 taxa were identified across the analysed Littorinidae species. The microbial community was dominated by *Vibrio alginolyticus* (20.93%) and *V. fluvialis* (18.60%), together representing approximately 40% of all isolates. *Streptococcus iniae* was exclusively detected in *Littoraria angulifera*, accounting for 26.32% of the isolates within this host group. Other taxa showed more restricted distributions, such as *Sphingomonas paucimobilis* in beach-associated *L. flava* and *Kocuria kristinae* in mangrove-associated *L. flava*, while *Enterobacter cloacae* were more frequent in mangrove-dwelling snails. These taxonomic differences underscore the distinct microbial signatures observed between host species and their respective habitats.

Analysis of the microbiota structure associated with Littorinidae species revealed a significant influence of host species identity on microbiota structure. PERMANOVA analysis indicated that the Littorinidae identity had a significant effect on microbial composition (Pseudo-F = 3.6821; $p=0.001$; Table 1). Subsequent pairwise tests were performed to investigate specific differences between mollusc species. It was observed that the microbiota of *L. angulifera* (mangrove), differed significantly from that of *L. flava* (beachrocks) ($t = 1.449$; $p = 0.032$). Similarly, *L. angulifera* showed a distinct microbiota from *E. lineolata*, also collected in the beach environment ($t = 2.6199$; $p=0.001$). However, no significant differences were found in microbiota structure between *L. angulifera* and *L. flava* collected in the mangrove environment ($t = 0.95015$; $p=0.408$).

Table 1 - Permutational Multivariate Analysis of Variance (PERMANOVA) of the microbiota structure associated with Littorinidae species. The data in red represents a significant result ($p < 0.05$).

Factors	Degrees of freedom	SS	MS	Pseudo-F	P(perm)
Littorinidae species	2	27311	13656	3.6821	0.001
Residual	31	1.1497E5	3708.6		
Total	33	1.4228E5			

Source: Research data

Likewise, *L. flava* (beachrocks) not differ significantly from *E. lineolata* ($t = 1.4499$; $p=0.492$) nor from *L. flava* (mangrove) ($t = 1$; $p=0.495$) in terms of its microbiota. However, the microbiota of *E. lineolata* was significantly distinct from that of *L. flava* collected in the mangrove ($t = 2.1331$; $p=0.009$).

SIMPER analysis identified the bacterial taxa contributing most to within-group similarity and between-group dissimilarity (Table 2). Within-group similarity varied among host groups. *Littoraria angulifera* (ASD = 0.97) was primarily characterised by *Streptococcus iniae* (26.32%), *Vibrio fluvialis* (23.68%), and *Enterobacter cloacae* (19.74%), with additional contribution from *Streptococcus thoralensis* (14.47%). In *L. flava* from beachrock (ASD = 1.03), the highest similarity was mainly driven by *Vibrio alginolyticus* (25.81%) and *Sphingomonas paucimobilis* (25.81%), followed by *V. fluvialis*, *Kocuria kristinae*, and *Acinetobacter haemolyticus* (each contributing 16.13%). In contrast, *Echinolittorina lineolata* showed the lowest similarity (ASD = 0.42), largely dominated by *V. alginolyticus* (46.67%), with additional contributions from *A. haemolyticus* and *V. fluvialis* (26.67% each). For *L. flava* from the mangrove (ASD = 0.93), similarity was mainly explained by *V. fluvialis* (28.57%), *Enterobacter cloacae*, *Proteus* spp., *Aerococcus viridans*, and *K. kristinae* (each 17.86%).

Between-group dissimilarities were also driven by a limited number of taxa. The highest dissimilarity was observed between *L. angulifera* and beach-associated *L. flava* (2.29), followed by comparisons between *L. angulifera* and *E. lineolata* (2.16) and between *E. lineolata* and mangrove-associated *L. flava* (1.93). These differences were mainly associated with variations in the contribution of *Vibrio* spp., particularly *V. alginolyticus* and *V. fluvialis*, as well as the presence of *Streptococcus iniae* and *Sphingomonas paucimobilis* in specific host groups.

Table 2 - Results of similarity analysis (SIMPER) identifying the bacterial species with the highest contribution to the similarities observed within and between groups, calculated using Euclidean distance. (ASD=average similarity)

Species	<i>Littoraria angulifera</i>		<i>L. flava</i> (mangrove)		<i>L. flava</i> (beachrocks)		<i>Echinolittorina lineolata</i>	
	Av. Value	Contrib%	Av. Value	Contrib%	Av. Value	Contrib%	Av. Value	Contrib%
	ASD = 0.97		ASD = 0.93		ASD = 1.03		ASD = 0.42	
<i>S. iniae</i>	0.385	26.32						
<i>Streptococcus thoralensis</i>	0.154	14.47						
<i>Vibrio fluvialis</i>	0.308	23.68	0.333	28.57	0.167	16.13	0.111	26.67
<i>Enterobacter cloacae</i>	0.231	19.74	0.167	17.86				
<i>Proteus</i> spp			0.167	17.86				
<i>Aerococcus viridans</i>			0.167	17.86				
<i>Kokuria kristinae</i>			0.167	17.86	0.167	16.13		
<i>Sphingomonas paucimobilis</i>					0.333	25.81		
<i>Acinetobacter haemolyticus</i>					0.167	16.13	0.111	26.67
<i>V. alginolyticus</i>					0.333	25.81	0.778	46.67
Average dissimilarity								
<i>L. angulifera</i> x <i>L. flava</i> (beachrocks)								
2.29								
<i>L. angulifera</i> x <i>L. flava</i> (mangrove)								
1.9								
<i>L. angulifera</i> x <i>E. lineolata</i>								
2.16								
<i>E. lineolata</i> x <i>L. flava</i> (mangrove)								
1.93								

Source: Research data

4 DISCUSSION

The present study demonstrates that the composition of the culturable bacterial microbiota associated with Littorinidae gastropods is primarily structured by host species identity. This finding is consistent with previous studies showing that microbial assemblages in marine invertebrates are strongly influenced by host-related factors such as physiology, diet, and behaviour (DHAMI; TAYLOR, 2024; LI *et al.*, 2024; CHIU *et al.*, 2025).

Significant differences in microbiota composition were observed between *Littoraria angulifera* and both *Echinolittorina lineolata* and beach-associated *L. flava*, whereas no significant differences were detected between species sharing the same mangrove habitat. These results suggest that host identity is a major driver of microbiota structure, but that environmental conditions may modulate this effect, particularly when species occupy similar ecological niches. The lack of significant differences between *L. angulifera* and mangrove-associated *L. flava* supports the idea that shared habitat conditions can partially override host-specific influences, as also suggested for other invertebrate systems (LEMKE; DESALLE, 2023; BIJNENS *et al.*, 2025).

In contrast, no statistically significant differences were detected between *L. flava* populations from beach and mangrove environments, indicating that the microbiota of this species may exhibit a degree of stability across habitats. This pattern suggests potential ecological plasticity, allowing *L. flava* to maintain a relatively consistent microbial assemblage despite environmental variation, a feature that has been associated with microbial-mediated acclimation in marine organisms (PINNOW *et al.*, 2023).

Differences in microbiota composition among host groups were largely driven by a small subset of bacterial taxa, particularly *Vibrio alginolyticus*, *V. fluvialis*, *Streptococcus iniae*, and *Sphingomonas paucimobilis*. The predominance of *Vibrio* species is expected in marine environments, as these bacteria are widely distributed in seawater and frequently associated with marine invertebrates (SAKIB *et al.*, 2018). However, their differential contribution among host species suggests that host-specific conditions influence their relative abundance, reinforcing the role of intrinsic biological factors in structuring microbial communities.

The exclusive occurrence of *Streptococcus iniae* in *L. angulifera* is particularly noteworthy, given its relevance as a zoonotic pathogen associated with fish and human infections (WANG *et al.*, 2020). This finding suggests that mangrove-associated gastropods may act as reservoirs of potentially pathogenic bacteria, highlighting their potential role in environmental monitoring and public health surveillance.

Habitat-related patterns were also evident in the distribution of specific taxa. The higher contribution of *Sphingomonas paucimobilis* and *V. alginolyticus* in beach-associated individuals may be associated with environmental conditions such as higher salinity, hydrodynamic exposure, and anthropogenic inputs. *S. paucimobilis* is widely distributed in aquatic environments and has been reported in contaminated water systems, being considered an opportunistic bacterium with bioindicator potential (GULATI; GHOSH, 2017). Additionally, increased occurrence of *Vibrio* spp. has been associated with anthropogenic influence and environmental disturbance in coastal systems (HASAN; SHAKIR, 2025).

In contrast, the presence of *Proteus* spp. and *Aerococcus viridans* in mangrove-associated samples likely reflects the organic-rich and more stable environmental conditions typical of these ecosystems. Members of the genus *Proteus* are commonly found in soil and water and have been reported in association with various animal hosts, although their ecological role remains poorly understood (DRZEWIECKA, 2016).

Despite these habitat-related patterns, the overall results indicate that host species identity exerts a stronger influence than habitat on microbiota structure, although both factors interact in shaping microbial assemblages. This interaction reflects the complex balance between intrinsic and extrinsic drivers of microbiota composition in marine invertebrates (LEMKE; DESALLE, 2023; DHAMI; TAYLOR, 2024).

From an ecological perspective, the presence of bacterial genera with diverse functional roles, including *Vibrio*, *Acinetobacter*, *Sphingomonas*, and *Enterobacter*, suggests that Littorinidae gastropods harbour microbiota potentially involved in nutrient cycling and organic matter degradation. Members of the genus *Acinetobacter*, for instance, are widely distributed in marine and terrestrial environments and play important roles in environmental processes (JUNG; PARK, 2015).

Finally, these findings reinforce the potential use of Littorinidae gastropods as bioindicators of environmental conditions in coastal ecosystems. Because these organisms are directly exposed to environmental fluctuations, their associated microbiota may reflect local anthropogenic impacts, environmental disturbances, and shifts in microbial dynamics. In this context, understanding host-microbe interactions becomes increasingly important, particularly under scenarios of environmental change affecting marine ecosystems (BOWLER *et al.*, 2009).

5 CONCLUSION

This study demonstrates that host species identity is the primary factor structuring the culturable bacterial microbiota associated with Littorinidae gastropods on the Brazilian semi-arid coast. Significant differences observed among host species indicate that intrinsic biological traits play a key role in shaping host-associated microbial assemblages.

At the same time, the absence of significant differences between some groups sharing similar habitats suggests that environmental conditions may modulate microbiota composition, particularly when species occupy overlapping ecological niches. These findings highlight the combined influence of host-related and environmental factors, with a predominant effect of host identity.

The identification of key bacterial taxa associated with specific host groups contributes to a better understanding of host-microbe interactions in marine invertebrates. Furthermore, the results support the potential use of Littorinidae gastropods as bioindicators of environmental conditions, as their associated microbiota reflects both host characteristics and habitat-related influences.

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