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**Diversidade genômica do gastrópode *Littoraria flava* (King & Broderip, 1832) e estudo de padrões de fluxo gênico**

Genomic diversity of the gastropod *Littoraria flava* (King & Broderip, 1832) and study of gene flow patterns

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## Resumo

A genética de paisagens marinhas dedica-se a entender como o movimento dos organismos afeta a conectividade das populações. Para espécies com larvas planctotróficas, essa não é uma tarefa trivial, pois as trajetórias e a duração dos estágios larvais são dificilmente previsíveis. Muitos desses grupos frequentemente revelam pouca ou nenhuma diferenciação genética populacional. Entretanto, estudos recentes identificaram algumas espécies que apresentam uma forte estruturação genética em macro e micro escalas espaciais. O presente estudo buscou entender os processos demográficos e fatores ambientais que moldam a dinâmica populacional de um organismo não modelo. Para tanto, foi utilizada a técnica *Genotyping-by-Sequencing* (GBS) para obtenção de polimorfismos de nucleotídeo único (*Single-Nucleotide-Polymorphism*, SNPs), e dois genes mitocondriais (mtDNA) de *Littoraria flava*. As amostras foram coletadas em 11 localidades distribuídas ao longo da costa brasileira, onde em seis foram feitos transectos horizontais. A análise de história demográfica usando mtDNA sugeriu expansão demográfica nas populações Sabiaguaba e Alagoas (Tajima's  $D = -1.665$  e  $-1.174$ , respectivamente,  $p\text{-value} < 0,05$ ). Com base em 6.094 SNPs, foram encontrados três grupos genéticos distintos nas populações amostradas ( $K = 3$ ). Além disso, uma estrutura genética fraca, porém significativa, foi detectada para ambos os marcadores (mtDNA  $F_{ST} = 0,01353$  e SNPs  $F_{ST} = 0,07675$ ,  $p < 0,05$ ). Não foram detectados sinais de subestruturação entre os pontos dos transectos, divergindo dos resultados encontrados com alozimas em trabalhos prévios. A maioria das populações revelou deficiência de heterozigotos com altos valores de  $F_{IS}$ . Apesar desses resultados parecerem refletir um fluxo gênico de acordo com um modelo de metapopulação, outros fenômenos seriam capaz de produzir os mesmos padrões. A análise de genética de paisagens indicou que variáveis relacionadas a temperatura e precipitação são potencialmente capazes de gerar adaptação local. Alguns loci contendo SNPs candidatos parecem ter papéis importantes na locomoção larval, órgãos sensoriais, mobilidade espermática e adesão epitelial ao substrato. Apesar do pouco conhecimento sobre esses mecanismos em *L. flava*, dada a relevância funcional, esses caracteres poderiam estar sob seleção e/ou adaptação ambiental.

**Palavras-chaves:** Fluxo gênico, *Littorinidae*, metapopulação, NGS, *seascape genetics*.

## Abstract

Seascape genetics has been dedicated to understanding how the movement of organisms affects populations connectivity. For species with planktonic larvae, this is not a trivial task, since trajectories and duration of larval stages are hardly predictable. Many of these groups often reveal little or no genetic differentiation among populations. However, recent studies have identified species presenting a strong genetic structure on both large and small spatial scales. This study aimed to understand the demographic processes and environmental factors shaping the population dynamics of a non-model organism. With this purpose, we used Genotyping-by-Sequencing (GBS) to obtain Single-Nucleotide-Polymorphisms (SNPs) markers and two mitochondrial genes (mtDNA) of *Littoraria flava*. The samples were collected from 11 locations distributed along the Brazilian coast, where in six horizontal transects were designed. The demographic history analysis using mtDNA suggested demographic expansion in the Sabiaguaba and Alagoas populations (Tajima's  $D = -1.665$  and  $-1.174$ , respectively,  $p$ -value  $< 0.05$ ). Based on 6,094 SNPs markers, three distinct clusters across the sampled populations ( $K = 3$ ) were found. Additionally, a weak but significant genetic structure was detected for both sets of markers (mtDNA  $F_{ST} = 0.01353$  and SNPs  $F_{ST} = 0.07675$ ,  $p < 0.05$ ). There were no signs of substructure among the sites within transects, diverging from previous results using allozymes. Most populations revealed heterozygote deficiency with high values of  $F_{IS}$ . Despite the results that might reflect a gene flow according to a metapopulation model, other phenomena could produce the same patterns. The seascape genetic analyses indicated that predictors related to temperature and precipitation are potential predictors to cause local adaptation. Some loci containing candidate SNPs appear to be important functions on larval locomotion, sensory organs, sperm mobility and epithelial adhesion to the substrate. Despite the poor knowledge about these mechanisms in *L. flava*, considering their functional relevance, these traits could be under environmental selection and/or adaptation.

**Key-words:** Gene flow, *Littorinidae*, metapopulation, NGS, seascape genetics.

## Introduction

### Seascape genetics

Understanding how populations' connectivity is influenced by the marine environment and other abiotic characteristics is one of the major goals of seascape genetics (SELKOE *et al.*, 2016). The assumptions underlying the seascape genetics presume an association between genetic, spatial and temporal patterns. Comprehending how this association works is fundamental to untangle the evolution of natural populations (LIGGINS *et al.*, 2019). However, because direct observations are essentially unlikely for many species, marine populations connectivity is often indirectly inferred (HELLBERG, 2009; SELKOE *et al.*, 2016). An indirect method uses spatial distributions of alleles or/and phenotypic traits to evaluate the level or pattern of gene flow in a population. Evolutionary studies usually take two main approaches: (1) assessing the variation in genomic regions that determine phenotypic traits and thereby influence fitness using adaptive markers; (2) evaluating the variation in DNA sequences presumed neutral, which may not affect fitness. These markers provide very different answers: while the adaptive markers can be used to understand the interaction between phenotype *versus* genotype and elucidate adaptation processes, neutral markers tell us about the genetic structure and connectivity of populations (CONOVER *et al.*, 2006; PALUMBI, 2003).

Most marine species have traditionally been assumed to have open populations that are interconnected by gene flow. This assumption comes from the apparent lack of dispersal barriers in marine systems and the fact that most marine invertebrates have planktonic larvae (BOHONAK, 1999; GROSBURG & CUNNINGHAM, 2001; PALUMBI, 1994). However, this paradigm has changed considerably since several studies revealed highly dispersal species presenting strong genetic structure on both large and small spatial scale (COWEN *et al.*, 2000; e.g. BEAUMONT, 1982; BUCKLIN, 2000; CARINI & HUGHES, 2006; HEIPEL *et al.*, 1999; KRAMARENKO & SNEGIN, 2015; LAUNEY, 2002; RYNEARSON & ARMBRUST, 2004; TAYLOR, 2003). These findings clearly suggest that genetic differentiation depends not only on the dispersal capacity, but also on other mechanisms such as behavior, hydrographical barriers to dispersal, oceanic environment, local adaptation and life-history traits (e.g. high fecundity, population sizes and life cycle) (PALUMBI, 2003; WAPLES, 1998).

Studies over the intertidal zone often emphasize the ability of the high degree of heterogeneity environmental features to generate the afore-mentioned micro spatial scale variation. This heterogeneity can be measured by predictors such as available nutrients, temperature of sea surface, pH, wave exposure, average salinity, dissolved oxygen, substrate extension, presence/absence of competition and predation, among others (MENGE, 2000; NAVARRETE *et al.*, 2005). These complex mosaics of environmental conditions of many coastlines have considerable potential to create local adaptation by natural selection on small scales (FUNK *et al.*, 2012). Local adaptation can occur when some individuals with determined genotype frequencies have higher relative fitness than others from different habitats despite the random genetic drift and gene flow effects (KAWECKI & EBERT, 2004). Therefore, it is expected that the potential for local adaptation decrease in species with high levels of gene flow (CONOVER *et al.*, 2006; HEREFORD, 2009; PALUMBI, 1994; YAMADA, 1989). Local selective pressure may be substantial when considering the great environmental heterogeneity experienced by marine species, and local adaptation may be far more common in marine systems than assumed previously (COWEN, 2006; HEREFORD, 2009; YEAMAN & WHITLOCK, 2011; e.g. BURFORD *et al.*, 2014; SANDOVAL-CASTILLO *et al.*, 2018). It is expected that genomic regions under selection present higher variation when compared to selectively 'neutral' gene regions (CONOVER *et al.*, 2006). Nonetheless, the task of identifying signatures of selection and local adaptation in marine species is not trivial, and usually requires the combination of knowledge about gene function, landscape effects and species' biology to provide concrete evidence of outlier loci adaptive roles (MANEL *et al.*, 2003).

In South America, the Brazilian coast extends over 8,000 km under the influence of an extensive set of oceanographic and ecological conditions. Many Brazilian population genetic studies test the presence of intrinsic biogeographical barriers, as well as the effects of environmental factors on dispersal along the coast range. These studies include many taxonomic groups, such as ascidian (DIAS *et al.*, 2006; NÓBREGA *et al.*, 2004; ROCHA *et al.*, 2012); bryozoa (MIRANDA *et al.*, 2018; VIEIRA *et al.*, 2012); mollusca (ANDRADE *et al.*, 2005; ANDRADE & SOLFERINI, 2007; JOSÉ & SOLFERINI, 2007; MOREIRA *et al.*, 2011); nemertea (ANDRADE *et al.*, 2011); polychaeta (PAIVA *et*

*al.*, 2019; SEIXAS *et al.*, 2018); porifera: (LAZOSKI *et al.*, 2001), and reef fishes (JOYEUX *et al.*, 2008; ROCHA, 2003; ROCHA *et al.*, 2002) across continental and island lands under different hypotheses. With the advance of bioinformatics tools in incorporating ecological and biotic factors into computational modeling, testing hypotheses about connectivity in the marine system has become increasingly accurate (CHAN *et al.*, 2011; KNOWLES, 2009). These approaches have improved the quality of genetic diversity inferences in Brazilian marine populations.

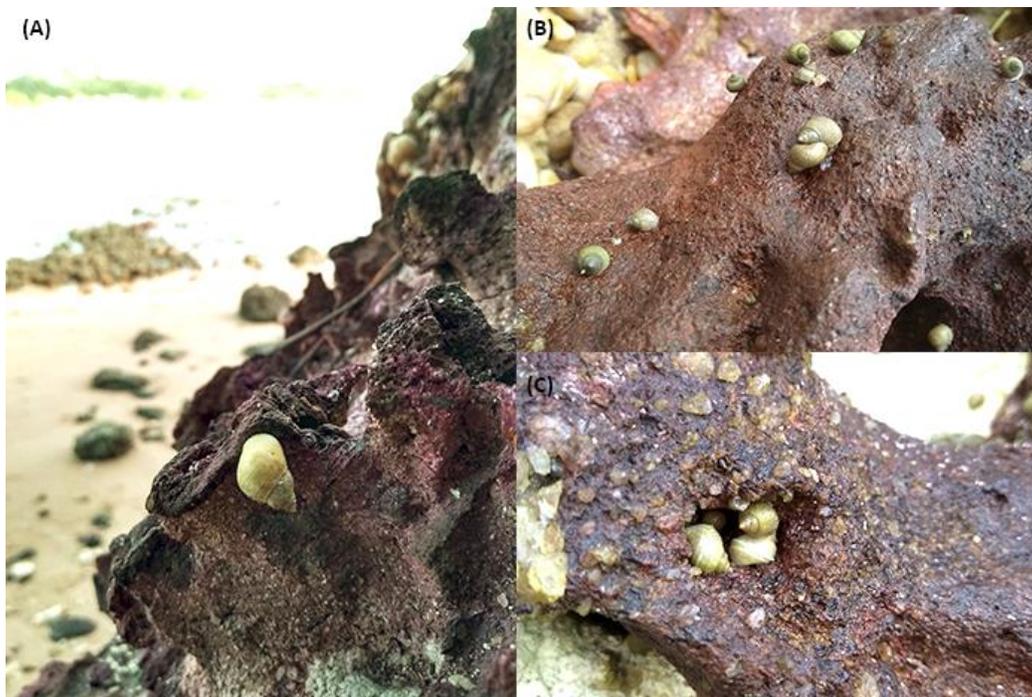
### ***Littorinidae***

The littorinids are a group of small gastropods that occurs on rocky shores and mangroves around the world, with shell lengths ranging from 0.5 to 4 cm. The group lives on intertidal zones and can feed on algae or lichens (REID, 1989, 1996). In the majority of the species, spawning releases hundreds of eggs, followed by a planktonic larval stage (RIOS *et al.*, 1994). The larvae can remain in the water column for weeks (REID, 1999; SCHELTEMA, 1971). From the littorinids, only the genus *Echinolittorina* Habe, 1956 and *Littoraria* Griffith & Pidgeon, 1834 occur on the Brazilian coast (REID, 1986). *Littoraria* is a group of 39 molluscs closely associated with mangroves, distributed in tropical or subtropical regions, mainly occupying mangrove trees, salt marshes, driftwood, and a minority in rocky shores (REID, 1999). The species *Littoraria flava* (KING & BRODERIP, 1832) and *Littoraria angulifera* are found in Brazil, being restricted to tropical zones and usually associated with mangroves or rocky shores near rivers (REID, 1986).

*Littoraria flava* (Fig. 1) shows a continuous distribution in the supratidal area of rocky shores and estuarine environment along the Western Atlantic (REID *et al.*, 2010). The species is oviparous and dioecious. Its spawning happens only when the animals are completely submerged, when hundreds of single egg capsules with approximately 30 µm of diameter are released. Each capsule keeps a single embryo, which will develop until the veliger phase (personal observation, unpublished data). Under laboratory conditions, this process takes approximately three days. Although its adult phase is relatively sedentary, the larvae disperse widely. The length of the larval phase is still unknown, but estimated between 3 and 10 weeks (REID, 1999; REID, 1986; RIOS *et al.*, 1994). The consequences of a planktonic stage to gene flow dynamics in *L. flava* were studied using allozymes (ANDRADE *et al.*, 2005; ANDRADE & SOLFERINI, 2007). The authors found

moderate structure on the macrogeographic scale, but even stronger variation across few meters, i.e. subpopulations in a single rocky shore. These results could be explained due to asynchronous spawning associated with recurrent colonization or to a possibility that allozymes may undergo natural selection (JANSON, 1987; JOHANNESSON & TATARENKOV, 1997; TATARENKOV & JOHANNESSON, 1999).

**Fig. 1.** *Littoraria flava* in its natural habitat. Praia de Gamboa rocky shore, Espírito Santo, Brazil. The specimens can be (A) solitary (B) close to each other or (C) in aggregations within rocky shore fissures.



### Phylogeography in marine systems

Phylogeographic studies goals include assessing the influence of geographic events and environmental factors over species ecology and evolutionary history, considering a wide range of spatial and temporal scales. In broad terms, one of the most important contributions of phylogeography is to emphasize non-equilibrium aspects of population structure and microevolution (AVISE, 2012). These methods can be applied in a comparative context, revealing patterns in entire communities or shared responses from different species due to a common demographic history (AVISE, 2012; KNOWLES,

2009). Since there is not a precise model of how genetic lineages are spatially configured, comparative assessments of many species have revealed a good deal about the nature of intraspecific evolution (AVISE, 2009). Several molecular markers have similarly been employed in phylogeographic investigations, such as microsatellites and mitochondrial sequences. Nonetheless, these markers have very different forms of hereditary transmission and dynamics (KARL *et al.*, 2012). The mitochondrial DNA (mtDNA) presents relatively rapid evolution and therefore a high level of polymorphism, which has led to its widespread use as a genetic marker for demographic history analyses (e.g. UTHICKE & BENZIE, 2003; LEE & BOULDING, 2007; CRANDALL *et al.*, 2007; BAKER *et al.*, 2008; LIU *et al.*, 2012). Because it is haploid and most likely uniparentally transmitted, the mtDNA has a smaller effective size and for this reason it is expected to be more strongly affected by genetic drift than nuclear loci (AVISE, 2012; KARL *et al.*, 2012). Thus, the mtDNA has shown to be a useful tool for investigation of demographic events, population structure and dynamics over time (AVISE, 2009, 2012).

Although genetic approaches are particularly useful to understand both demographic processes and gene flow dynamics in marine systems, they still present many challenges: difficulties in collecting, markers development and the fact that most of the theoretical models hardly explain the data (SELKOE *et al.*, 2008). In this scenario, methods that generate genome-wide datasets via Next-Generation-Sequencing (NGS) have become a helpful tool by providing a large number of loci with high levels of polymorphism, the Single-Nucleotide-Polymorphisms (SNPs). These methods enable great accuracy to quantify genomic variation for both neutral and non-neutral signatures (NOSIL *et al.*, 2009; RELLSTAB *et al.*, 2015; STAPLEY *et al.*, 2010), facilitating population genetic studies of non-model organisms (BENESTAN *et al.*, 2015; LIGGINS *et al.*, 2019; LUIKART *et al.*, 2003). Besides, it does not require any development or genetic information *a priori*. Even though NGS techniques have been increasingly applied, the combination of neutral and adaptive markers for non-model organisms is yet far to be common (EKBLUM & GALINDO, 2011; HELYAR *et al.*, 2011; SEEB *et al.*, 2011), being used more frequently in studies of economically important organisms such as bivalves (LAL *et al.*, 2016; VAN WYNGAARDEN *et al.*, 2017), lobsters (BENESTAN *et al.*, 2015) and fishes (DIBATTISTA *et al.*, 2017; LIMBORG *et al.*, 2012).

## Conclusions

In this study, we applied two molecular markers to uncover the genetic diversity patterns in a widespread marine gastropod, *Littoraria flava*. By employing NGS sequencing, we were able to genotype thousands of genetic markers to clarify the processes and environmental factors underlying the population structure and diversity of a non-model marine organism. This approach seems to open new research opportunities to better understand marine molecular evolution in rocky shore organisms.

The demographic history investigation showed signs of range expansion for only two sampled locations. There was no evidence of subpopulations according to the established sites within transects. Because of the low amount of significant  $F_{ST}$ , significant heterozygote deficiency and high positive  $F_{IS}$  estimates in several localities, the findings might reflect a gene flow dynamics according to the metapopulation model. However, other phenomena, such as natural selection, Wahlund effects and small sample size, could produce similar patterns.

According to the environmental association analyses, environmental predictors related to temperature and precipitation explained almost the entire variation across the study area. Because of its relevance in intertidal zones, both predictors would be able to generate local adaptation on rocky shores. A set of putative adaptive genes associated with the cilia and flagella movement were found, which might have great biological relevance for the survival and performance on the marine environment. In gastropods, these structures can play several important functions for both adults and larvae, such as adhesion and mobility to the substrate, capture of food in suspension during the larval phase and the locomotion across the water column. Although these mechanisms are not well-known in *L. flava*, it is possible that these features have been experiencing environmental adaptation and/or natural selection, given their biological importance for the gastropod growth and survival.

This is the first Brazilian study with a seascape genetic approach in a littorinid. This methodology provided results that can be useful for several types of comparative investigations, including population genetics, demographic histories and local adaptation, for non-model or economically important organisms. Furthermore, by incorporating other biological and abiotic features into posterior analyses, the data obtained here can serve

as a basis for deeper studies about the connectivity of marine species, which should increase the understanding of the mechanisms underlying the population dynamics in marine systems.

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