



The role of genetic diversity and past-history selection pressures in the susceptibility of *Chironomus riparius* populations to environmental stress



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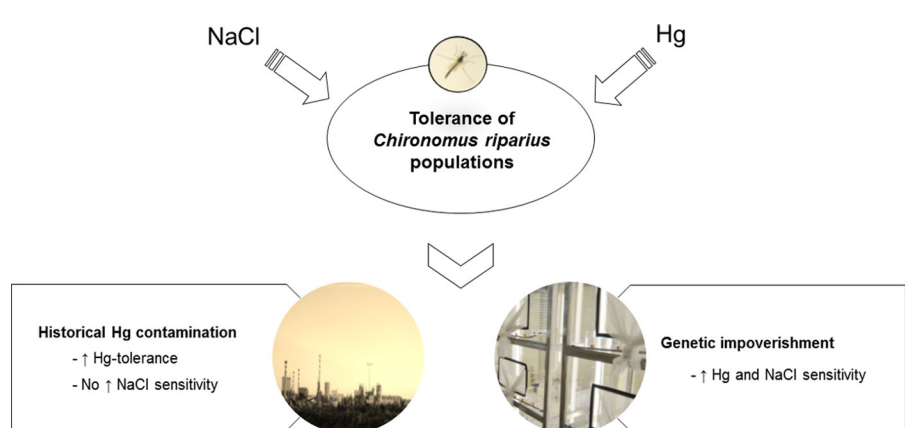
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HIGHLIGHTS

- We explored the role of genetic background and genetic diversity in mercury and salinity tolerance of *C. riparius* populations.
- We found high tolerance to mercury and no increased sensitivity to salinity in a population from a mercury-impacted site.
- We found increased susceptibility to mercury and salinity in genetically impoverished populations.
- Our findings are discussed in terms of the suitability of *C. riparius* as a model species in evolutionary toxicology.
- The validity of ecotoxicological tests using genetically eroded populations is also discussed.

GRAPHICAL ABSTRACT



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ABSTRACT

Natural populations experiencing intense selection and genetic drift may exhibit limited potential to adapt to environmental change. The present study addresses the following aspects of the “genetic erosion” hypothesis in the midge *Chironomus riparius*: does long-term mercury (Hg) contamination affect the Hg tolerance of midge populations inhabiting such impacted areas? If so, is there any fitness cost under changing environmental conditions? And does genetic impoverishment influence the susceptibility of *C. riparius* to cope with environmental stressful conditions? For this end, we tested the acute and chronic tolerance to Hg and salinity in four *C. riparius* populations differing in their levels of genetic diversity (assessed through microsatellite markers) and past-histories of Hg exposure.

Results showed that the midge population collected from a heavily Hg-contaminated site had higher Hg tolerance compared to the population collected from a closely-located reference site suggesting directional selection for Hg-tolerant traits in its native environment despite no genetic erosion in the field. No increased susceptibility under changing environmental conditions of salinity stress was observed. Moreover, results also showed that populations with higher genetic diversity performed better in the partial life-cycle assays providing evidence on the key role that genetic diversity plays as mediator of populations' susceptibility to environmental stress. Our findings are discussed in terms of the suitability of *C. riparius* as a model organism in evolutionary toxicology studies as well as the validity of ecotoxicological assessments using genetically eroded laboratory populations.

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1. Introduction

Evolutionary toxicology is a rapidly growing discipline whose purpose is to elucidate the long-term detrimental effects imposed by pollutants in natural populations over timescales that exceed the lifespan of the organisms (Bickham, 2011; Coutellec and Barata, 2011). Research in this field has mostly focused on disentangling the trans-generational and heritable effects of pollutants, how they shape the gene pool of populations and which negative effects they produce in the fitness and evolutionary potential of populations (Bickham, 2011; Ribeiro and Lopes, 2013).

Recently, mounting evidence on the long-term consequences of environmental pollutants has accumulated in the non-biting midge *Chironomus riparius* Meigen (Marinković et al., 2012; Müller et al., 2012; Nowak et al., 2009; Stefani et al., 2014; Vogt et al., 2007a). *Chironomus riparius* has great ecological relevance as it is an abundant and ubiquitous benthic species, that can occupy virtually all freshwater habitats within the Holarctic, where it constitutes a major food resource for the diet of many predators, and plays also an important role in detritus processing and nutrient recycling (Armitage et al., 2012). Furthermore, *C. riparius* is easy to culture under laboratory conditions, it has a short life-cycle, high reproductive output and is sensitive to different pollutants (Armitage et al., 2012; Campos et al., 2014; Rodrigues et al., 2015), which makes it a potential model organism for evolutionary toxicology studies. To date, however, little work has been carried out on natural populations of the species (Postma et al., 1995) and, thus, most of the empirical evidence has arisen from studies using laboratory populations (Marinković et al., 2012; Müller et al., 2012; Nowak et al., 2012; Stefani et al., 2014).

As part of a comprehensive case-study on the evolutionary responses of natural populations of *C. riparius* to historical metal contamination in Portuguese freshwaters, here we investigated the influence of both genetic background and levels of genetic diversity in the susceptibility of midge populations to environmental stress. Previous research performed in our laboratory showed that *C. riparius* populations collected from metal impacted sites had an overall higher tolerance to acute cadmium (Cd) stress in comparison to populations from reference sites. Since all populations had been maintained under clean laboratory conditions for several generations prior of performing the ecotoxicological tests, differences in Cd-tolerance were suggested to have a genetic basis, i.e., tolerance traits were conferred to midges via differences in their genetic background (Pedrosa et al., submitted for publication). Furthermore, we also found evidences for higher constitutive levels of the cellular thiols metallothionein and glutathione in populations collected from metal contaminated sites suggesting, therefore, improved defence mechanisms that likely allow these populations to better cope with metal toxicity (Pedrosa et al., submitted for publication).

Among the experimental populations of our case-study, one *C. riparius* population was collected from S. Filipe ditch, a coastal man-made stream that received mercury-rich effluents from a chlor-alkali plant for decades. Although the discharges were interrupted in 1975, the ditch is still considered a hotspot of mercury (Hg) contamination (Costa and Jesus-Rydyń, 2001; Reis et al., 2009) and the local surface sediments can reach concentrations of up to $17.40 \mu\text{g} \cdot \text{g}^{-1}$ Hg (Pedrosa et al., submitted for publication). Therefore, we hypothesized that the *C. riparius* population collected from this site genetically adapted to Hg as a result of intense and continuous selection for Hg-tolerant traits. However, and although genetic adaptation to Hg may have increased the short-term survival of the population under such adverse environmental conditions, theory on micro-evolutionary responses predicts that pollutant-adapted populations may carry substantial fitness costs that cause them to become more vulnerable under changing environmental conditions (Kliot and Ghanim, 2012; Posthuma and Van Straalen, 1993; Ribeiro and Lopes, 2013). Therefore, studying evolutionary processes of pollution-tolerant populations gains increasing relevance at the light of the ongoing and future climate changes that are

likely to alter the aquatic ecosystems and introduce a suite of new selective pressures (Hoffmann and Sgro, 2011; Pauls et al., 2013). In this sense, the projections of rising sea level associated with coastal erosion make saline intrusion a potential important perturbation for aquatic populations inhabiting coastal freshwater ecosystems (IPCC, 2014). Salinity has the potential to significantly affect the survival, growth and reproduction of freshwater organisms (Loureiro et al., 2013) and, hence, it is critical to better understand and anticipate how aquatic biota already impacted by chemical pollution will cope with such additional pressure.

Moreover, and besides the role played by the intrinsic genetic background of populations, also the amount of genetic diversity harbored by populations has the potential to influence the susceptibility to environmental stress (Frankham et al., 2002). High levels of genetic diversity are, in general, seen as indicators of population's health that potentially increase the responsiveness to environmental stress. Conversely, low levels of genetic diversity are suggestive of increased vulnerability to environmental stress (Nowak et al., 2012; Vogt et al., 2007b). As such, while the levels of genetic diversity of our experimental populations were found to be similarly high in the field (Pedrosa et al., submitted for publication), maintenance of midge populations in the laboratory for relatively long periods of time may result in the loss of considerable amounts of genetic variation (Nowak et al., 2007b). Laboratory populations are established from a limited number of organisms, they are reproductively isolated and have comparatively much smaller population sizes which make them particularly prone to losses of genetic variation caused by chance events (i.e. random genetic drift) and, so, these effects need also to be considered when investigating the sensitivity of midge populations to environmental stress (Nowak et al., 2007b).

Against this background, the present study was undertaken to address the following questions:

i) Does long-term historical Hg contamination influence the Hg-tolerance of *C. riparius* populations inhabiting such impacted areas? If so, are there fitness cost under changing environmental conditions?

ii) And, also, do levels of genetic diversity affect the susceptibility of *C. riparius* populations to cope with environmental stressful conditions?

For that, we assessed the acute and chronic tolerance to Hg and salinity in four *C. riparius* populations varying in their past-history selection pressures and levels of genetic diversity: two natural populations collected one from the Hg-contaminated site S. Filipe ditch and one from a closely located reference site, one laboratory population and a "Gen⁺ population" generated from the cross-breeding of several *C. riparius* populations. In addition, we also monitored the levels of genetic diversity of the two natural populations under common-garden laboratory conditions in order to assess the degree of genetic impoverishment over time in the laboratory. We used microsatellite markers to characterize the levels of genetic diversity and the genetic divergence among the experimental populations.

2. Material and methods

2.1. Experimental *C. riparius* populations

Four pure *C. riparius* populations were chosen for the present work: populations CONT, GEN⁺, LAB and REF.

Population CONT was collected from the heavily Hg-contaminated site S. Filipe ditch (40°45'01"N, 8°34'37.48"W) and population REF was collected from a nearby reference site located in the Jardim river (40°44'29"N, 8°31'41"W). In order to establish pure *C. riparius* populations in the laboratory, each field-collected *Chironomus* sp. larva was morphologically checked with a stereo microscope and only *Chironomus thummi* type larvae (which include *C. riparius* and its sibling sister species *Chironomus piger*) were grown in breeding chambers, allowed to mate and lay the egg ropes. Each egg rope was afterwards collected, cultivated individually and genotyped according to mtDNA barcoding methodology (Pfenninger et al., 2007). A total of 10C. *riparius* egg ropes was used to establish populations CONT and

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