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Genome-wide genetic diversity of rove beetle populations along a metal pollution gradient



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ABSTRACT

To what extent chemical contamination affects genetic diversity of wild populations remains an open question in ecotoxicology. Here we used a genome-wide approach (615 nuclear RADseq loci containing 3017 SNPs) and a mtDNA fragment (ATP6) to analyze the effect of long-term exposure to elevated concentrations of metals (Cd, Pb, Zn) on genetic diversity in rove beetle (*Staphylinus erythropterus*) populations living along a pollution gradient in Poland. In total, 96 individuals collected from six sites at increasing distance from the source of pollution were analyzed. We found weak differentiation between populations suggesting extensive gene flow. The highest genetic diversity was observed in a population inhabiting the polluted site with the highest metal availability. This may suggest increased mutation rates, possibly in relation to elevated oxidative stress levels. The polluted site could also act as an ecological sink receiving numerous migrants from neighboring populations. Despite higher genetic diversity at the most polluted site, there was no correlation between the genetic diversity and metal pollution or other soil properties. We did not find a clear genomic signature of local adaptation to metal pollution. Like in some other cases of metal tolerance in soil invertebrates, high mobility may counteract possible effects of local selective forces associated with soil pollution.

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1. Introduction

Anthropogenic activities lead to a range of negative changes in the environment, including chemical contamination. This constitutes a challenge for populations to survive unfavorable conditions. Large healthy populations with high levels of genetic diversity can effectively cope with novel selection pressures (Frankham et al., 2010). However, chronic exposure to pollution may decrease genetic diversity of populations diminishing their evolutionary potential (Van Straalen, 2002; Dallinger and Höckner, 2013).

Population-level effects start, however, in individual organisms exposed to pollution. Toxic chemicals cause damage to their body cells and disturb their physiology. It has been suggested that organisms exposed to toxicants face a trade-off associated with energy allocation to competing metabolic processes, including detoxification (Sibly and Calow, 1989; Posthuma and Van Straalen, 1993). Therefore, life history traits such as growth, reproduction and survival are often affected due to increased metabolic

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http://dx.doi.org/10.1016/j.ecoenv.2015.04.048 0147-6513/© 2015 Elsevier Inc. All rights reserved. expenditure to detoxification (Jones and Hopkin, 1998; Spurgeon et al., 2000). This may result in reduced individual fitness and decreased size of wild populations. In addition, when populations have become small, genetic drift may remove variation faster (Gillespie, 1998). Eventually a population may enter the "extinction-vortex" (Frankham et al., 2010).

The population genetic responses to pollution were recently grouped into four categories called "the four cornerstones of Evolutionary Toxicology" (Bickham, 2011). These include: genomewide changes of genetic diversity, changes in allele frequency distribution due to selection, changes in population differentiation due to altered dispersal patterns, and changes in allele frequency due to increased mutation rate. Clearly, the key feature in all these categories is genetic diversity. Pollution impacts population genetic diversity by affecting four major evolutionary processes: genetic drift, selection, migration, and mutation.

Results of the existing studies aiming at assessing effects of metal pollution on genetic diversity of populations are inconclusive and contradictory. For example, reduction of genetic diversity was reported in populations of the marsh frog (*Rana ridibunda*) from contaminated wetlands of Sumgayit, Azerbaijan (Matson et al., 2006) and in sandhoppers (*Talitrus saltator*) living at the metal-polluted Tyrrhenian coast in central Italy (Ungherese

et al., 2010). Based on gene flow estimations, Matson et al. (2006) concluded that the polluted Sumgayit region acted as an ecological sink characterized by a high frequency of immigrant frogs from surrounding areas. On the other hand, Eeva et al. (2006), studying two bird species exposed to metals and nuclear radiation in Finland and Russia, reported decreased genetic diversity in populations of the pied flycatcher (Ficedula hypoleuca), but increased genetic diversity in the great tit (Parus major) living at polluted sites. The difference in species response was explained by different dispersal patterns and detoxification abilities. The genetic erosion hypothesis of Van Straalen and Timmermans (2002) was supported by the study of Andre et al. (2010). They investigated highly differentiated populations of the earthworm Lumbricus rubellus from a Pb-polluted habitat near Cwmystwyth, Wales, UK, and hypothesized a reduction of genetic diversity through the loss of distinct mtDNA genetic lineages. At the same time, a number of authors reported no influence of metal pollution on population genetic diversity in different animal species, for example the wood mouse Apodemus sylvaticus (Berckmoes et al., 2005), the earthworm Dendrobaena octaedra (Simonsen et al., 2008) or the ground beetle Pterostichus oblongopunctatus (Lagisz et al., 2010). Therefore, the question to what extent long-term exposure to chemical pollutants affects genetic diversity of wild populations remains open.

Detecting genetic responses to environmental change is not straightforward in the absence of a priori candidate loci with a large effect on the phenotype of interest (Hoffmann and Willi, 2008). In the above mentioned studies, researchers usually used small numbers of molecular markers. These were mainly single mtDNA genes, microsatellites, RAPD or AFLP. What seems to be lacking is a genome-wide approach which could allow for better insight into population genetic processes occurring across a whole genome. This was highlighted by Bickham et al. (2000) in their review of genetic effects of pollution in natural populations with the statement: "The challenge for the future lies in gaining an integrated perspective of the genomic response to contaminant exposure and to the forces that promote population divergence". Recent developments of next-generation sequencing (NGS) technologies (Mardis, 2013), applicable also for non-model species (Baird et al., 2008; Catchen et al., 2011; Peterson et al., 2012; Zieliński et al., 2014), and their decreasing costs, increase the potential for detailed population genomics research.

Here, we aimed at testing the association between population genetic diversity and soil contamination. We took advantage of next-generation sequencing methods to assess the impact of multigenerational exposure to elevated concentrations of metals (Cd, Pb, Zn) on rove beetle (Staphylinus erythropterus) populations living along a metal pollution gradient in Southern Poland. Genetic diversity, gene flow and population structure were estimated for both the mitochondrial and the nuclear genome using restrictionsite associated DNA sequencing (RADSeq). Estimated population genetics parameters were related to metal concentrations in soil. Our prediction was that *S. erythropterus* populations would show a reduction of genetic diversity with increasing pollution due to toxicity, population size decline (bottleneck), and directional selection. We expected this effect to be dispersal dependent as higher dispersal potential results in more intensive gene flow which may overcome the selection and bottleneck impact. Here we report results concerning just the most dispersive species, however, in the whole project we test several species with different dispersal capabilities.

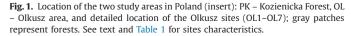
2. Materials and methods

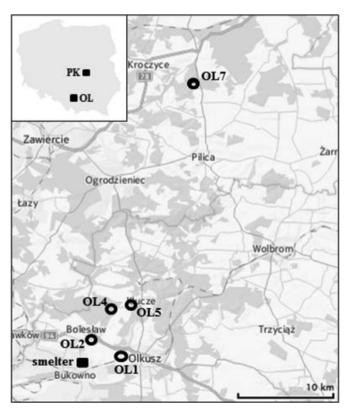
2.1. Staphylinus erythropterus

The rove beetle Staphylinus erythropterus Linné, 1758, belongs to the family Staphylinidae - one of the largest families of beetles (Coleoptera) (Herman, 2001). It is a common and widespread species, distributed in nearly all zoogeographical regions. It can be found throughout Poland, living mainly on the soil surface and in the litter layer in forests. As a holometabolous insect, it has a four-stage life cycle, including egg, larva, pupa and imago. There is only one generation of S. erythropterus during a year (Szujecki, 1980). Eggs are laid in May and June, usually on the soil surface. To develop they must absorb water from the environment. The predatory larva lives in deeper soil layers. Metamorphosis of pupa takes place in August, in soil chambers dug by the larva (Szujecki, 1980). Adults, also predators, feed on soft-bodied invertebrates (e.g. nematodes, mites, springtails, slugs, earthworms) and other insect larvae or pupae. They are able to fly actively and dispersal is most intensive in Spring during the reproduction season. As all life stages of S. erythropterus live in the topsoil litter layer, where most emitted metals end-up, they are exposed to pollution, especially considering the fact they absorb soil porewater and feed on animals recognized as macroconcentrators of metals. According to the review of Bohac (1999) Staphylinid larvae are considered more sensitive to pesticide and radionuclide pollution than imagos. However, Zvereva et al. (2003) concluded that beetle larvae are less sensitive to metal pollution than adults because they are able to get rid of accumulated metals during molting.

2.2. Sampling

The study was conducted at six sites located in two distinct areas in Poland, approximately 180 km apart (Fig. 1). Five sites





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