

Incipient local adaptation in a fungus: heavy metal tolerance through allele and copy-number variation

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Introduction

Human-altered environments can shape the evolution of organisms. Fungi are no exception, though little is known about how they adapt to heavy metal polluted soils.

Here, we document local adaptation to heavy metals in *Suillus luteus*, a symbiotic fungus associated with pine trees. We scanned 38 whole genomes of *S. luteus* individuals from recently severely polluted and unpolluted soil (Fig. 1). Polluted sites were enriched with Zn and Cd.

We detected evidence of incipient polygenic metal adaptation, with a single population showing allelic and gene copy number differences in genes involved in metal homeostasis.

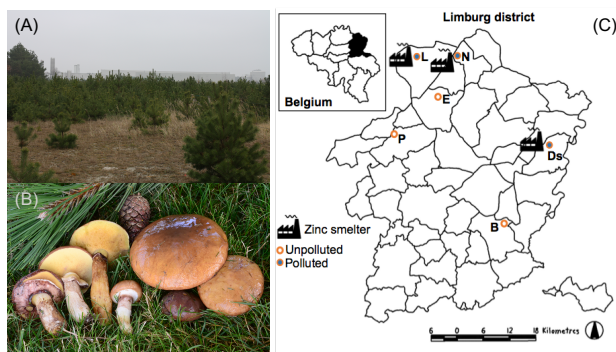


Figure 1 – Sampling sites and *Suillus luteus*. (A) Lommel, one of the sampled polluted sites (photo by Joske Ruytinx). (B) *Suillus luteus* fruitbodies (photo by Noah Siegel). (C) Sampled localities in Belgium (Limburg district). *Suillus luteus* specimens were collected from three heavy metal polluted sites (full circles) and three unpolluted localities (empty circles). Initials indicate names of sampling localities: B=Bilzen, D=Dilsen-Stokkem, E=Eksel, L=Lommel, N=Neerpelt, P=Paal. (Smelter icon <http://chittagongit.com/icon/factory-icon-transparent-6.html>).

Pre-print
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Results

- We found no evidence of population structure based on site of origin or metal pollution, indicating shared genetic variation likely maintained by ongoing gene flow.
- Despite overall low genetic differentiation, we identified regions of allelic and gene copy number divergence enriched in transporter proteins (Fig. 2).
- Among the differentiated regions we identified 47 metal tolerance candidate genes, encoding for metal exclusion, storage, immobilization, and detoxification (Fig. 3)

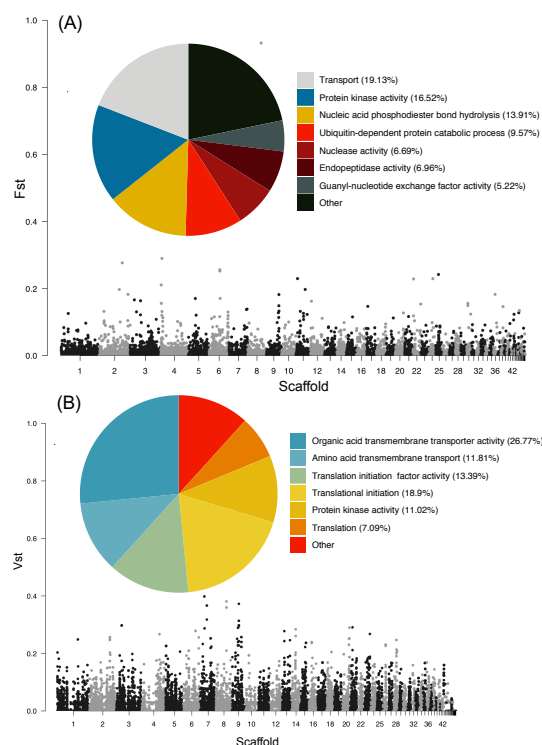


Figure 2 – Genomic differentiation in *S. luteus*. (A) F_{st} values in 5kb windows; (B) gene copy number variants in 250bp windows. Pie charts show proportions of top 5% gene ontology (GO) enrichment analyses.

Discussion

We found evidence of incipient local adaptation in *S. luteus*, with absence of population structure but signatures of selection between soil types. We detected allelic divergence and gene copy number variation in genes involved with metal homeostasis. These included metal exclusion, storage, immobilization, and detoxification that most likely play an important role in metal homeostasis and assist in persisting under heavy metal stress.

Our results suggest multiple alleles of small effects contribute to heavy metal tolerance, reflecting different strategies to withstand contamination. Variants were shared across the whole population but under selection in isolates exposed to pollution.

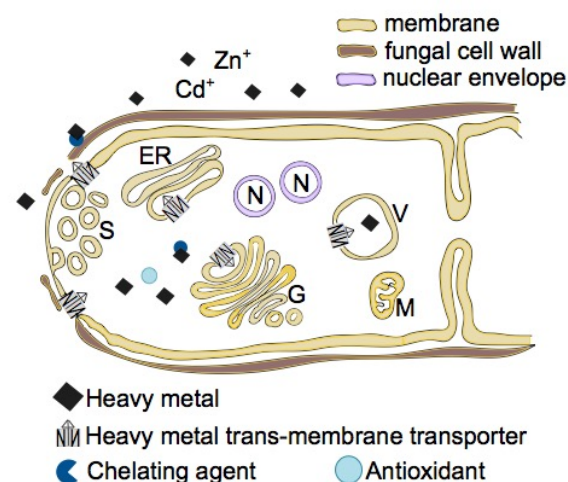


Figure 3 – Heavy metal tolerance in *S. luteus* includes metal exclusion, storage, immobilization, and detoxification. Trans-membrane transporters and chelating agents regulate metal influx and immobilization within the cell; antioxidants ameliorate oxidative stress caused by reactive oxygen species. S=Spitzenkörper; ER=endoplasmic reticulum; G=Golgi apparatus; V=vesicle/fungal vacuole; N=nucleus; M=mitochondrion. See pre-print for details on the candidate genes.