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Review

Ants and heavy metal pollution – A review

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ABSTRACT

Ants due to their nesting habits are ideal for studying temporal fluctuations in trace metal accumulation, changes in morphological traits, as well as for assessing evolutionary processes and monitoring environmental impact of metals derived from human activities. Although metal pollution may affect basic ecological traits such as colony size and survival, ants can be considered relatively resistant to metal pollution at least partly due to relatively high metal regulation efficiency. At both polluted and unpolluted areas the body metal levels in ants vary considerably between species. This observation and other experimental data suggest differences in metal regulation physiology, however the physiological basis of these differences remains unknown. It was shown that metal pollution may suppress the immune defense systems, which in turn could theoretically lead to a higher risk of infections. Biodiversity studies are limited, however the evidence for a clear negative influence of metal pollution on ant species diversity and abundance was not yet provided. Since many aspects of ant ecotoxicology remain unclear, the questions for possible future research are suggested.

1. Introduction

Due to industrial society's reliance on metals heavy metal contamination is a wide-spread problem. Large part of the research on heavy metals has targeted their effects on economically valuable vertebrates and humans. However, various aspects of organism response to metal contamination as tolerance, adaptation or sublethal responses can be successfully explored on invertebrates. Ants occur commonly in virtually all habitats with the exception of Iceland, Greenland and Antarctica. The number of described species totals some 11 000 [1]. Apart from some parasitic species of a reduced or absent worker cast, all ant species are social. This means that at least two adult generations are present in their colonies, the young are cared for, and the task of reproduction is divided among casts.

Ants have certain attributes which make them particularly suitable for studying the impact of heavy metals. Firstly, one can expect that metal exposure of ants living in contaminated areas is relatively high. Apart from some nomadic ants, most species build stationary and perennial colonies, which limit the mobility of colony members. Additionally, because the workers are wingless, colonies use mainly local resources, compared to many other insects. As a consequence, if a colony is established in a contaminated habitat, metals can be easily accumulated in workers, as they cannot avoid the contaminated area. Furthermore, the diet of ants, at least of some genera, is considered to be relatively rich in metals. Many ant species, especially of the genera *Formica* and *Lasius*, supplement their diet with honeydew; an excretion product of aphids that is rich in carbohydrates [2,3]. Honeydew in turn, contains high concentrations of metals, especially cadmium [2].

Due to their nesting habits, ants are ideal for studying temporal changes in metal accumulation, morphological traits or enzyme activity [4], as well as for monitoring environmental changes [5] and for investigating adaptation to long term metal-pollution [6]. They are easy to collect in large numbers, and sampling can be repeated within a given area from independent colonies. Ants are unique organisms allowing one to assess the effects of pollution at different levels: in individuals of the same colony, in colonies of the same species, and among different species. Sampling of workers is cheap and relatively non invasive, and the taxonomic base is fairly good [3,5,7].

Apart from the above reasons to investigate ants in relation to metal pollution, some studies are difficult or impossible to perform on these insects. The most serious problem is the impossibility of obtaining a number of generations in standard laboratory conditions, as in most species nuptial flights are necessarily for reproduction. As a consequence, ants are not adequate organisms on which to study hereditary traits in laboratory conditions. Although cultivation of workers is relatively easy [1], it may be difficult to collect sufficient numbers of queens for laboratory experiments with many replicates. Moreover, in spite of the many taxonomic

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publications and keys, identification of ants is rather difficult and prohibits the incorporating of ants in biodiversity assessment programs. However, identification to genus or morphospecies can be performed by non-specialists after initial instruction and practice [3,8].

2. Physiological basis of metal accumulation and tolerance to metals

Generally, tolerance to metals in invertebrates relies on uptake restriction, metal immobilization and elimination. The variability in the efficiency of these mechanisms among individuals of the same population arises from the phenotypic plasticity and/or from adaptation to polluted environments. This, in turn, influences the differences in tolerance between whole populations and species [9,10] and therefore shapes the composition of communities inhabiting polluted areas.

The uptake of a metal may be restricted by limited metal assimilation through the gut wall or by avoiding contaminated food or habitats. The efficiency of metal assimilation varies greatly between species, which is related to different feeding physiologies and trace metal requirements [11–13]. The ability to discriminate between polluted and unpolluted food was documented mainly for isopods [14,15] and snails [16], but this phenomenon has been also described for other invertebrates, such as earthworms, collembolans, or enchytraeids [17–20]. Recently, it was suggested that avoidance of polluted habitats may be an important factor shaping the community's structure [21,22]. In turn, elimination and immobilization are the mechanisms, by which the internal metal concentration is regulated after crossing the gut barrier. Firstly, metals can be deactivated by binding them to metallothioneins, water soluble and heat stable proteins that are found in all animals. Thanks to their high cysteine content, metallothioneins are able to selectively bind metal ions even at low concentrations [23]. Their prime function is the storage of essential metals, such as Zn or Cu, which function as enzyme components. However, apart from the regulatory function, metallothioneins also play a key role in metal detoxification. Secondly, metals can be deactivated by depositing them in insoluble granules. In this way, metals are isolated from the metabolic processes and can be stored for a long time in the organism or can be excreted with faeces. According to Hopkin [24], different types of granules can be distinguished depending on their chemical composition and affinity to metals. The internal sequestration of metals can be studied with methods based on different centrifiguration steps, which help to separate the total metal content in the body into fractions bound with metallothioneins, granules, enzymes and microsomes/lysosomes [25,26].

In invertebrates metals are usually accumulated in certain tissues or organs more efficiently than in others. In insects this is the midgut ephitelium [24]. The internal distribution of metals in the body may differ, between populations living in polluted and uncontaminated areas, and the storage capacity of these special tissues and organs can be increased in polluted habitats [27,28].

3. Accumulation of metals in ants

Ants accumulate high concentrations of metals both in polluted and unpolluted areas [2,4,29]. Metal body concentrations in ants originating from polluted areas are higher than in ants from unpolluted areas, but the values of between-site differences are species-dependent. Metal accumulation in ants was studied in relation to differences between casts, interspecific variation, tissue specific accumulation and time-related effects [29–31].

A variation in the metal body burden between casts (males, females, workers) and life stages (larvae, pupae, adults) is well-known. The workers of ants can be divided into functional groups such as reserve workers, nurses, inside workers and outside workers (foraging workers). Maavara [30] showed that in uncontaminated areas, the highest metal concentrations were found in foraging workers, while the lowest were detected in queens and pupae. High metal concentrations in workers and low in larvae/pupae and/or sexuals (males and females), were found also in ants from polluted habitats [30,32]. The repeatability of this pattern, suggests the existence of some general mechanism of progeny protection, against metal transfer in the ant colonies, in which workers serve as a metal "barrier"[30]. This should be treated rather as a hypothesis as it reminds unclear whether workers are really able to inhibit the transfer of metals to the larvae [30]. Furthermore, the difference in metal body concentrations between larvae/pupae and workers may be the result of differences in feeding (prey/honeydew) or be a result of metal accumulation with increasing age. The differences in BAF values (Bioaccumulation Factor, calculated as: metal concentration in the body/metal concentration in the nest material) between *Formica polyctena* pupae, workers inside the nest and workers foraging outside modified from Migula and Głowacka (1996) [32] are presented in Fig. 1.

The most extensive study on differences between species in metal accumulation abilities between species was performed by Rabitsch [29] who assessed differences in accumulation abilities of Zn, Cd, Pb and Cd between 8 ant species in a lead/zinc smelter area. The Zn and Cd body levels provided by this and other similar studies are presented in Table 1. Noticeable difference in the metal body burden between subfamilies Myrmicinae and Formicinae, was attributed to different feeding preferences. Formicinae are well known consumers of honeydew, which contains, as mentioned above, high concentrations of metals [2]. However, it should be noted that the body metal levels vary considerably between even closely related species, which cannot always be attributed to the variable percentage of honeydew in the diet. Cluster analysis on the data presented in Table 1 revealed that Formicinae ants originating form unpolluted sites form two different clusters according to their Cd body concentrations (Fig. 2). No clear genus-dependent pattern

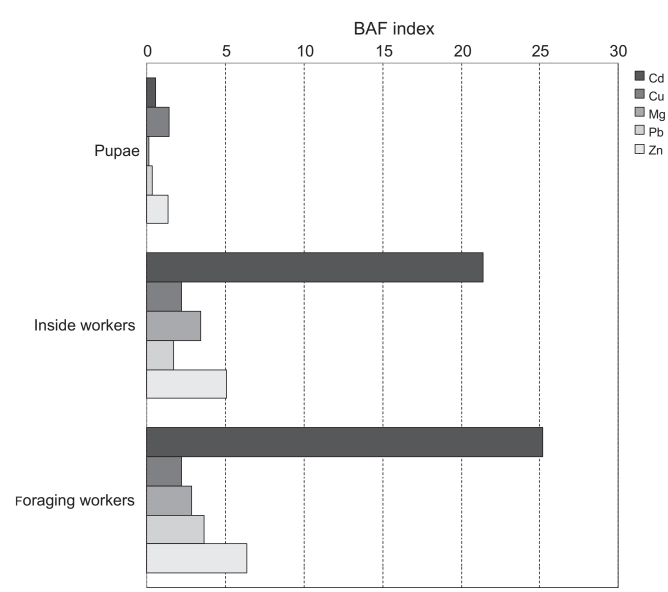

Fig. 1. Comparison of BAF values (metal concentration in the body/metal concentration in the nest material) showing differences between pupae and two worker groups of *Formica polyctena* originating from metal-polluted area Pazurek, Poland. Data are modified from Migula and Głowacka (1996) [32].

Table 1
Zn and Cd (mg kg^{-1}) body concentrations in different species of ants in different stages and groups of workers according to various authors. Stages: w- workers (unspecified), fw- foraging workers, iw- inside workers, sw-surface workers, pu-pupae.

Species	Stage	Site polluted /unpolluted	Zn	Cd	Locality	Source
Formicinae						
Formica fusca	w	Polluted	545	14.9	Austria, Arnoldstein	[29]
Formica lugubris	w	Unpolluted	662	15.1	Czech Republic, Spalenec	[2]
Formica aquilonia	sw	Unpolluted	–	5.9	Estonia, Valgesoo Forest	[30]
Formica aquilonia	iw	Unpolluted	–	4.3	Estonia, Valgesoo Forest	[30]
Formica aquilonia	pu	Unpolluted	–	0.09	Estonia, Valgesoo Forest	[30]
Formica aquilonia	w	Polluted	550	10.1	Finland, Harjavalta	[4]
Formica polyctena	iw	Polluted	842	38.5	Poland, Pazurek	[32]
Formica polyctena	iw	Unpolluted	291	10.7	Poland, Knurów	[32]
Formica polyctena	fw	Unpolluted	395	11.8	Poland, Knurów	[32]
Formica polyctena	pu	Unpolluted	90	0.35	Poland, Knurów	[32]
Formica polyctena	fw	Unpolluted	1055	45.3	Poland, Knurów	[32]
Formica polyctena	pu	Unpolluted	220	0.95	Poland, Knurów	[32]
Formica pratensis	w	Unpolluted	1392	90.1	Czech Republic, Kvetna	[2]
Formica pratensis	pu	Polluted	277	1.0	Austria, Arnoldstein	[29]
Formica rufa	iw	Polluted	–	29.8	Czech Republic, Kvetna	[2]
Formica rufa	sw	Polluted	–	27.6	Czech Republic, Kvetna	[30]
Formica sanguinea	w	Unpolluted	600	6.9	Finland, Espoo	[47]
Formica truncorum	w	Unpolluted	590	9.0	Finland, Espoo	[47]
Formica cunicularia	sw	Polluted	907	29.5	Poland, Sierbowice	[33]
Formica cunicularia	sw	Unpolluted	335	19.5	Poland, Sierbowice	[33]
Lasius flavus	w	Unpolluted	190	5.9	Finland, Bromarv	[47]
Lasius platyhtorax	w	Polluted	276	28.6	Austria, Arnoldstein	[29]
Lasius platyhtorax	pu	Unpolluted	128	2.0	Austria, Arnoldstein	[29]
Lasius platyhtorax	pu	Polluted	233	4.8	Austria, Arnoldstein	[29]
Lasius niger	sw	Polluted	187	60.7	Poland, Olkusz	[35]
Lasius niger	sw	Unpolluted	61	4.91	Poland, Sierbowice	[35]
Camponotus ligniperda	w	Unpolluted	964	90.6	Austria, Arnoldstein	[29]
Camponotus vagus	w	Unpolluted	1286	58.7	Austria, Arnoldstein	[29]
Myrmicinae						
Myrmica rubra	w	Unpolluted	128	0.3	Finland, Perniö	[47]
Myrmica ruginodis	w	Unpolluted	128	0.6	Finland, Perniö	[47]
Myrmica sabuleti	w	Polluted	435	7.2	Austria, Arnoldstein	[29]
Leptothorax acervorum	w	Polluted	5.7	232	Austria, Arnoldstein	[29]
Tetramorium caespitum	w	Polluted	211	3.7	Austria, Arnoldstein	[29]

was detected. It is worth noticing that although *Formica cunicularia* and *Formica lugubris* differ considerable in the percentage of honeydew in their diet [3], they were clustered together. These observations indicate the possibility of significant differences in metal regulation between species. Grześ [33] confirmed the considerable differences in metal regulation physiology between three ants species: *Myrmica rubra*, *Lasius flavus* and *Formica cunicularia*. However, the physiological basis of these differences, for instance related to the involvement of granules and metallothioneins remains unknown.

Some authors criticized the idea of metal biomagnification in trophic chains and postulated that species physiology is the factor which is much more important in determining the body metal level, than the metal concentration in the diet [34]. In the light of this argument, it is probable that the differences in metal concentrations between the subfamilies Formicinae and Myrmicinae, result from their respective, distinctive metal regulation physiologies. Some authors indicate the need for further studies, to explain the variability in trace metal levels between ant species on the grounds of physiology [4,29]. Such studies would help to find out how ants are generally able to maintain high body concentrations of metals, without major deleterious effects. Rabitsch [31] suggested that the high metal accumulation capacity of ants, is accomplished through active metal excretion. Recent studies confirmed the ability of *Lasius niger* to regulate body cadmium concentration once it reaches a certain threshold [35].

The nesting and social habits of ants provide a unique chance to study time-related accumulation patterns. Rabitsch [36] studied the temporal fluctuations of Cd, Pb, Cu, Fe, Zn and Mg in the workers of *Formica pratensis*, originating from five contaminated and reference sites in southern Austria in the vicinity of lead/zinc smelter in the period from April to November. Sites were placed on heterogeneous soils formed on limey material and showed elevated concentrations of Pb, Zn, Cu and Cd. He found that temporal fluctuations in the body metal concentrations were comparable between the sites and that the metal concentrations, apart from Fe, were the lowest concentrations in spring and autumn. For most metals and sites, this pattern was correlated with changes in body dry weight, with the highest weights recorded for spring and autumn. The author suggested therefore, that next to ant activity and nutrition, changes in body weight must contribute to the metal dynamic in ants through the dilution effect (any weight increase causes a decrease in the body concentration). Time-dependent metal fluctuations were found also in the study by Migula and Głowacka [32]. Changes in Pb, Cd, Zn, Mg and Cu in inside-colony and foraging workers of *Formica polyctena*, originating from five localities polluted with different metals, were investigated. The accumulation patterns varied between metals and colonies, showing some similarities between investigated worker groups, but no general pattern, common for all metals, was identified. The authors explained a decrease in the Pb content as a "dilution effect", resulting from the elevated proportion of newly emerged progeny. The observed decreases in metal concentration may be also explained by the elimination of the most poisoned workers from the colony, after they started feeding on contaminated food.

4. Metabolic balance and adaptation

The metabolic state of pollution-exposed organisms may be assessed by measuring the pool of phosphoadenine nucleotids

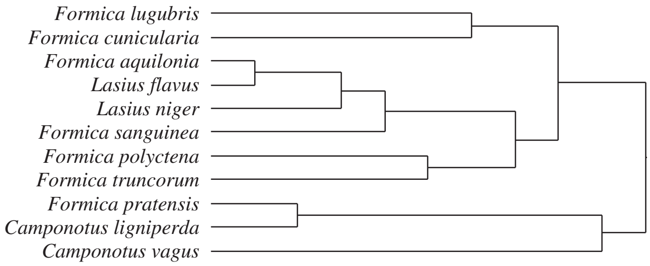

Fig. 2. Hierarchical cluster analysis (Ward's method) of Formicinae ants from unpolluted areas showing similarities in their Cd body concentrations. For data sources see Table 1. The obtained pattern does not follow the feeding preferences of *Formica* ants.

(ATP, ADP, AMP) and by the adenylate energy charge (AEC) calculated from the equation: $AEC = (ATP + 1/2ADP)/(ATP + ADP + AMP)$ [37,38]. Experiments performed on wild colonies of *Formica aquilonia* in Finland and *Formica polyctena* in Poland, fed with Cd and Hg-contaminated honey, showed an inhibition of ATPase in workers of *F. polyctena* and in all developmental stages of *F. aquilonia* [37], thereby indicating the pollution-induced changes in the energy budget. Simultaneously, and compared to *F. aquilonia*, *F. polyctena* was found to be less sensitive to Hg and Cd contamination, as its energetic processes were maintained at normal levels ($AEC > 0.8$, [32]).

The immunobalance is another trait potentially affected by metal pollution. It was shown that metal pollution may suppress the immune defence systems, which in turn could theoretically lead to a higher risk of infections [39]. Sorvari et al. [6] compared encapsulation response (the immunodefense reaction against a novel "passive" antigen) between wild and non-wild colonies of *Formica aquilonia*, transferred from a clean to polluted site along a metal-pollution gradient. The immune response reached its highest values at moderate levels of body metal concentrations, with the minima at the lowest and highest concentrations, thereby suggesting immuno-stimulation at medium levels of pollution and immuno-suppression at the sites with the highest pollution. No differences were found between local and translocated colonies, proving that ants in the polluted area had not adapted to the long-term pollution levels. The pattern could not result from changes in fat content or body mass along the pollution gradient, since none of these traits exhibited any trend along the gradient. However, there is no empirical evidence to support the view that the decreased immunoresponse may increase the susceptibility of *F. aquilonia* to infections and parasites. Nevertheless, it was previously documented at the same study area, that different *Formica* species had smaller colonies in the polluted than in the control sites [4]. If that particular decrease in colony size resulted from the higher mortality of workers, the explanation should be sought either in decreased immunoresponse or/and the lack of adaptation to high metal concentrations [6].

Grześ [40] indicated the difference in Zn tolerance between workers and larvae of the ant *Myrmica rubra*. Workers fed with Zn-contaminated food survived better than larvae and their mortality was negatively correlated with the pollution of the site of their origin, indicating enhanced metal tolerance. Larvae were more sensitive to Zn than the adults, and had higher body mass at the most polluted sites comparing with the control sites. The higher body mass of larvae may have enhanced tolerance to metal pollution, however this hypothesis needs yet to be evaluated.

5. Effects of metal pollution on other aspects of ants ecology

Literature records summarizing the influence of metal pollution on ants ecology are presented in Table 2. The pollution-mediated changes at the community level, is the least intensively investigated aspect of ants ecotoxicology. Apart from the already mentioned decrease in colony sizes in the polluted area, Eeva et al. [4] showed that the abundance ant colonies are species-dependent. Two *Formica* species from among the five tested, showed differences in relative abundance between the polluted and unpolluted areas: *F. lugubris* was less abundant while *F. rufa* was more abundant in the polluted area. The occurrence of the other species (*F. aquilonia*, *F. polyctena* and *F. pratensis*) was determined more by site characteristics than by the distance from the pollution source.

Grześ [41] investigated changes in ants biodiversity in meadows and forests along the metal pollution gradient. Regardless of species composition differences between these two ecosystems,

Table 2
Summary of literature records on the influence of environmental metal pollution on ecological aspects of ants.

Aspect	Investigated trait	Metal-pollution influence	Species	Main pollutants of the site	Source
Colony size	Nest mound volumes	Nests 34% smaller in the polluted area than in the unpolluted area; the between-site difference significant	*Formica aquilonia, F. polyctena , F. lugubris , F. rufa , F. pratensis*	Cu, Zn, Ni, Pb, As	[4]
Relative abundance	Relative abundance of nests	*Formica lugubris* and *F. rufa* significantly influenced by pollution	*Formica aquilonia, F. polyctena , F. lugubris, F. rufa , F. pratensis*	Cu, Zn, Ni, Pb, As	[4]
Body size	Head width, body mass	Unrelated to the site pollution	*Formica aquilonia*	Cu, Zn, Ni, Pb, As	[4]
Biodiversity	Species richness	Increased along the pollution gradient most probably due to reduced predation and competition pressure	community	Zn, Cd, Pb, Cu	[41]
Immunobalance	Encapsulation rate	Reached the highest values detected at moderate levels of body metal concentrations	*Formica aquilonia*	Cu, Zn, Ni, Pb, As	[6]
Workers survival	Mortality under laboratory dietary Zn-exposure	Uncorrelated with dietary Zn-dose but negatively correlated with metal pollution of the site of ants origin	*Myrmica rubra*	Zn, Cd, Pb,Cu	[40]
Larvae survival	Mortality under laboratory dietary Zn-exposure	Correlated with dietary Zn-dose but uncorrelated with metal pollution of the site of ants origin	*Myrmica rubra*	Zn, Cd, Pb, Cu	[40]
Developmental instability	Right-minus-left differences in bilateral morphological traits	Independent on ants body metal level but higher in young colonies	*Formica pratensis*	Zn, Pb	[45]

the increase in species diversity with increasing metal pollution was very clear in both ecosystems. In the light of the other previous research [42,43] this result can be explained by indirect effects of metal pollution, that is, changes in species interactions rather than by metal pollution level of the study sites.

The other aspect studied by Eeva et al. [4] was the difference in body size between populations of *Formica aquilonia* originating from polluted and unpolluted sites. Significant differences among body mass, head width and residual mass were detected between the nests but the variance was unrelated with the pollution of the site. Regarding other possible changes in morphology of ants, no relationship between right-minus-left differences in bilateral morphological traits and site metal pollution were found [45].

6. Research questions

Considering the effect of metals on ants many important aspects remain still unclear. Therefore the following research questions are suggested.

1. How ants may prevent soil degradation in polluted environments?

The role of ants in soil modification is well known (reviewed in [8]). Metal pollution may decrease the functional diversity of bacteria [44], which may lead to a decrease in the litter decomposition rate. Since fungi and ammonifying bacteria are very active and better represented in ant nests than in the surrounding soil [8,46], the activity of the ants could contribute to maintaining the nutrient balance in polluted areas, preventing soil degradation and accelerate the recovery of metal-polluted areas.

2. How ants may benefit from their social structure in polluted environments?

Ants may deal with the effects of pollution, not only by individual-based tolerance mechanisms as metal regulation, but also as changes in life histories corresponding to whole colony functioning such as queen longevity or larvae developmental rate.

3. How metal pollution may change the interactions between ants and symbiotic and parasitic organisms?

Many species of insects and other arthropods have developed complex interactions with ants. Some have specialized on ant predation or are obligatory ant parasites, depending on the ant society during part or all of their life cycle [1]. Because of the tied relationship of some species with ants, the impact of pollution on the ants- myrmecohiles interaction would influence functioning of the colony.

7. Conclusions

The body concentrations of metals may differ considerably between species, casts and life stages. Although some works showed the ability of ants to regulate Cd actively, the physiological basis of metal regulation efficiency is still to be evaluated. More studies are needed to assess how pollution shapes the community structure of ants. It should be emphasized that since ant species may vary in their impact on the ecosystem, the loss of some particular species (keystone species) may be particularly harmful for the functioning of an ecosystem. As ants are social organisms and are associated with many other insects, further investigations on how metal pollution alters the ant-insect relationship and how ants can benefit from their social structure in polluted environments, seem to be particularly desirable.

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