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Focus

Unintentional effects of neonicotinoids in ants (Hymenoptera: Formicidae)

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The world is facing precipitous declines in abundance and diversity of the global entomofauna (CARDOSO & al. 2020). There is consensus that anthropogenic pollution by agrochemicals is one of the most important drivers of recent declines (SÁNCHEZ-BAYO & WYCKHUYS 2019). Agrochemicals such as fungicides, herbicides, and pesticides are used in vast amounts to cope with the increasing global food demand (TILMAN & al. 2002). However, pervasive contaminations of the environment with pesticides pose unacceptable risks to non-target organisms because of their non-selective toxicity, and may thus jeopardise ecosystem services provided by beneficial arthropods, including social insects (ants, termites, some wasps and bees; DESNEUX & al. 2007, NEUMANN & al. 2015, PISA & al. 2015). There are multiple classes of pesticides, many of which are potentially harmful to non-target organisms, but neonicotinoid insecticides have recently become the most important group of pesticides (JESCHKE & al. 2011). This brief review will therefore focus on neonicotinoids due to their global importance and incredible turnover rates (JESCHKE & al. 2011).

Although environmental neonicotinoid concentrations are often low, they may still induce adverse sublethal effects, including negative impacts on foraging behaviour, cognitive abilities, immune functions, colony development, fertility, and social interactions (e.g., STRAUB & al. 2016, GOÑALONS & FARINA 2018; reviewed in BLACQUIERE & al. 2012, PISA & al. 2015, WOOD & GOULSON 2017). Hitherto, a plethora of research has focused on social pollinators (honey bees and bumblebees), whereas ecotoxicological studies on the impact of neonicotinoids on ants remain scarce. Ants are of immeasurable economic and ecological importance as they play indispensable roles in terrestrial environments and provide essential ecosystem services such as biological control (HÖLLDOBLER & WILSON 1990, DEL TORO & al. 2012, MORRIS & al. 2018). In light of the current biodiversity crisis, it seems of paramount importance to understand how neonicotinoids might affect these social insects.

Multiple ant species are considered among the world's worst invasive species with tremendous ecological and economic impacts (LOWE & al. 2000, HOLWAY & al. 2002). Consequently, research efforts have been dedicated to combating pest ants using neonicotinoids or new neonicotinoid analogues (e.g., TOLLERUP & al. 2004, BLIGHT & al. 2011, BUCZKOWSKI & al. 2014a, b, NONDILLO & al. 2014, MOTHAPO & WOSSLER 2016, COOPER & al. 2019, LI & al. 2019, WANG & al. 2020). Due to dose- and time-dependent toxicity, efficient transmission by trophallaxis and solubility in aqueous solutions, neonicotinoids have become common ingredients in bait formulations for domestic use and the management of invasive ants (RUST & al. 2004). While neonicotinoid baits help to manage invasive ants effectively (intentional exposure), exposure of some non-target ant species or other non-target organisms (unintentional exposure) has been reported (BELIZI & al. 2014, PISA & al. 2015). In addition to exposure via baits, unintentional neonicotinoid exposure routes include contact with spray droplets, contaminated soils, foliage, and water (BONMATIN & al. 2015). Furthermore, it is known that neonicotinoids cascade along food webs, resulting in foodborne exposure via plant material such as nectar, pollen, guttation fluid and seeds, honeydew secreted by aphids and some scale insects, and prey that was directly or indirectly exposed (KRUPKE & al. 2012, BONMATIN & al. 2015, JUNG & al. 2018, CALVO-AGUDO & al. 2019, MÜLLER & al. 2019, FRANK & TOOKER 2020). Given that many ant species are characterised by perennial sedentary colonies and queens with exceptionally long lifespans, the long persistence of neonicotinoids in the environment may render ants especially vulnerable due to potential long-term exposure (Keller & Genoud 1997, Goulson 2013, Schläppi & al. 2020). Indeed, colonies may face chronic exposure in the nesting area as well as intermittent acute exposure during foraging. Yet, the relative importance of different exposure routes or of acute versus chronic exposure remains to be investigated.

Previous studies on sublethal effects of neonicotinoid exposure in ants revealed changes in food consumption, activity and aggression, digging and foraging behaviours, as well as impaired locomotion, adverse impacts on brood care and colony growth, and reduced grooming behaviour resulting in elevated mortality upon co-exposure with entomopathogenic fungi (Santos & al. 2007, Barbieri & al. 2013, Galvanho & al. 2013, Wang & al. 2015a, b, Pan & al. 2017, Penn & Dale 2017, Li & al. 2019, Cramer 2020). In general, the concentrations used in these studies are higher than expected under field-realistic exposure scenarios. Nonetheless, adverse effects of some neonicotinoids can be detected even at environmentally relevant neonicotinoid doses. Using field-realistic concentrations and a combination of multiple exposure routes expected under natural conditions, Sappington (2018) showed impacts on nest building and foraging success. Furthermore, a long-term laboratory study at field-realistic concentrations revealed decreased colony growth in chronically exposed *Lasius niger* colonies (Schläppi & al. 2020). Even the smallest sublethal effects may accumulate for as long as a colony persists, potentially with dramatic impacts on fitness. Unfortunately, none of the mentioned studies directly assessed fitness, that is, lifetime reproductive success, which would be required to estimate the real risk neonicotinoids impose on ants at a population level (Straub & al. 2020). Whilst the effects of neonicotinoid exposure on ovaries or the quality of sperm have been investigated in honey bees (Straub & al. 2016), no study has yet addressed the effects of neonicotinoids on fertility in ants. The reproductive division of labour that characterises eusocial insects (Wilson 1971) could potentially confer them superorganismic resilience against neonicotinoid exposure as the loss of usually non-reproductive workers, which are analogous to somatic cells, may have little effect so long as the germline remains protected (Straub & al. 2015). Moreover, recent evidence suggests that ant queens might have superior detoxification capabilities compared with workers, which could contribute to the extreme difference in longevity observed between these castes (Schläppi & al. 2020). However, differences in susceptibility between castes or sexes, or between monogynous or polygynous species, remain to be clarified. Similarly, it is still unknown whether compartmented nest architectures or polydomous organisation may influence the impact of neonicotinoids on ant colonies by limiting or enhancing exposure.

Ants are crucial players in food webs, both as generalist predators and prey. Indirect effects of neonicotinoids could therefore impose an even more significant threat to ecosystems than previously assumed (Frank & Tooker 2020). For example, insecticides have been shown to disrupt interspecific prey-predator interactions by altering the responsiveness of ants towards exposed prey or by changing their behaviour after they consume exposed prey (Jung & al. 2018, Müller & al. 2019). If neonicotinoid treatments affect non-target predators such as ants, natural pest control can be inhibited, thereby allowing pests to resurge (Kilpatrick & al. 2005, Peck & Olmstead 2010). Furthermore, competitive interactions among ants may change upon neonicotinoid exposure: aggressive behaviours of ants and consequently the outcome of interspecific confrontations have indeed been shown to change depending on whether or not the interacting species have been exposed to neonicotinoids (Barbieri & al. 2013, Thiel & Köhler 2016, Wang & al. 2020). Competition is a crucial factor in structuring ant communities (Cerdá & al. 2013), and therefore changes in interspecific interactions or differential susceptibility to neonicotinoids potentially interfere with dominance hierarchies. For example, neonicotinoid applications can decrease the abundance of a dominant species, which in turn allows for increased ant diversity (Penn & Dale 2017). Furthermore, neonicotinoid exposure may influence the outcome of interactions between native and invasive species. One could assume that invasive ants may cope better with contamination compared with native ants as they might face fewer other stressors. However, it has been shown that neonicotinoid-exposed invasive Argentine ants, *Linepithema humile*, produced significantly less brood, while no such effect was observed for native Southern ants, *Chelaner antarcticus* (see Barbieri & al. 2013, referred to as "*Monomorium antarcticum*"). The potential influence of neonicotinoids on biological invasions thus remains unclear. Although non-target native species are also affected by control measures against invasive ants, they may recover to pre-invasion levels once invasion pressure is released (Sakamoto & al. 2019). Ultimately, neonicotinoid exposure is likely to change the structure and dynamics of ant communities via complex feedback mechanisms.

Under real-world conditions, ants are simultaneously exposed to multiple stressors, including a variety of agrochemicals and co-infections with several pathogens (Feldhaar & Otti 2020). Interactive effects with other stressors, for example, pathogens, malnutrition, or climate change, are inevitable and need to be investigated (Kaunisto & al. 2016, Tosi & al. 2017). Direct and indirect effects of neonicotinoids, as well as stressor interactions, are notoriously difficult to disentangle, and consequently, impacts of widespread environmental contamination with neonicotinoids on ant communities remain poorly understood. Although judicious use of neonicotinoids is a useful tool to combat pest and invasive ants, negative consequences should not be neglected given the global scale of the problem and the number of potentially endangered species. Sublethal effects can be detected even at field-realistic concentrations, potentially jeopardising ecological services provided by ants. Unintentional effects of widespread environmental contaminations with neonicotinoids on non-target ants are alarming and possibly have far-reaching consequences. The highlighted knowledge gaps necessitate further investigation on all effect levels, from cells and tissues, via individuals and different castes to the colony and the population level. Comprehensive long-term field-studies looking at ant communities are required to grasp the actual ecotoxicological risks imposed by neonicotinoids. Further, data needs to be gathered to grasp the state of natural ant communities and how they change, with particular attention to rare and endangered species. Periodical mapping is required to detect potential changes in time for adequate conservation measures. Accordingly, there is an urgent need to improve future ecological risk assessments of neonicotinoids by incorporating (i) ants as key representatives of soil-dwelling arthropods, (ii) effects of acute and long-term exposure, (iii) stressor interactions, and ultimately (iv) effects on fitness, the essential factor governing wild populations, to prevent further damages to ecosystem functioning (Straub & al. 2020). Agricultural practices need to become more sustainable to prevent further damages to natural ecosystems and ultimately to human food security and well-being. Abandonment of the use of neonicotinoids and other substances that are clearly harmful to the environment, for example by promoting biological control agents (Oi & al. 2015), would be a step in the right direction.

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