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Competition magnifies the impact of a pesticide in a warming world by reducing heat tolerance and increasing autotomy[☆]

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ABSTRACT

There is increasing concern that standard laboratory toxicity tests may be misleading when assessing the impact of toxicants, because they lack ecological realism. Both warming and biotic interactions have been identified to magnify the effects of toxicants. Moreover, while biotic interactions may change the impact of toxicants, toxicants may also change the impact of biotic interactions. However, studies looking at the impact of biotic interactions on the toxicity of pesticides and vice versa under warming are very scarce. Therefore, we tested how warming (+4 °C), intraspecific competition (density treatment) and exposure to the pesticide chlorpyrifos, both in isolation and in combination, affected mortality, cannibalism, growth and heat tolerance of low- and high-latitude populations of the damselfly *Ischnura elegans*. Moreover, we addressed whether toxicant exposure, potentially in interaction with competition and warming, increased the frequency of autotomy, a widespread antipredator mechanism. Competition increased the toxicity of chlorpyrifos and made it become lethal. Cannibalism was not affected by chlorpyrifos but increased at high density and under warming. Chlorpyrifos reduced heat tolerance but only when competition was high. This is the first demonstration that a biotic interaction can be a major determinant of 'toxicant-induced climate change sensitivity'. Competition enhanced the impact of chlorpyrifos under warming for high-latitude larvae, leading to an increase in autotomy which reduces fitness in the long term. This points to a novel pathway how transient pesticide pulses may cause delayed effects on populations in a warming world. Our results highlight that the interplay between biotic interactions and toxicants have a strong relevance for ecological risk assessment in a warming polluted world.

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1. Introduction

There is increasing concern that evaluating the impact of pollution under ideal laboratory conditions may be misleading (Liess et al., 2016; Rohr et al., 2016). For example, a striking recent finding was that declines in aquatic biodiversity in Europe have been observed at pesticide concentrations that are regarded as safe by current risk assessment based on laboratory toxicity tests (Beketov et al., 2013). This discrepancy between observations from ecotoxicological testing and natural field situations can be attributed to the presence of environmental stressors that magnify the impact of pesticides in natural systems (Holmstrup et al., 2010; Liess et al., 2016). A recent meta-analysis demonstrated that the

presence of both biotic and abiotic stressors can increase the sensitivity to pesticides with a factor of up to 100 (Liess et al., 2016). Warming is such an important abiotic stressor that may interact with pollution and is getting increased attention because of climate change. Exposure to toxicants can impair an organism's ability to cope with warming, and vice versa, warming can change the impact of toxicants (Sokolova and Lannig, 2008; Noyes and Lema, 2015). Examining the impact of toxicants under more realistic ecological conditions is therefore key to develop a better understanding of the impact of toxicants in natural systems in a warming world.

While most multi-stressor studies with toxicants considered abiotic stressors, also stress imposed by biotic interactions may strongly magnify the impact of toxicants (reviewed in Relyea and Hoverman, 2006; Holmstrup et al., 2010; Jackson et al., 2016; Liess et al., 2016). In this context, most attention went to the effect of predation risk (e.g. Relyea and Mills, 2001; Campero et al., 2007), while studies integrating competition are less frequent. Competition, however, is also a major structuring force in aquatic

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communities that may strongly change the impact of toxicants (e.g. Boone and Semlitsch, 2001; Jones et al., 2011; Knillmann et al., 2012). For example, the negative effects of the pesticide esfenvalerate in the water flea *Daphnia magna* increased with a factor up to 100 with increasing intraspecific competition (Knillmann et al., 2012). Biotic interactions are also sensitive to warming. Indeed, organisms typically show increased metabolic and growth rates at higher temperatures, this increases their energetic requirements and often results in an increased foraging effort (Angiletta, 2009). This will increase the encounter rates among species and intensify predator-prey and competitive interactions (Gilman et al., 2010). Therefore, biotic interactions have been identified as crucial to be able to predict the fate of populations under global warming (Gilman et al., 2010; Urban et al., 2016; Stoks et al., 2017). This indicates that it is important to include biotic interactions when assessing the impact of toxicants in a warming world. Although studies like this are rare, there have been a few of such studies. For example, Janssens and Stoks (2017) looked at the effects of predation risk imposed by visual and chemical predator cues, warming and exposure to the pesticide chlorpyrifos on physiological traits. In the study of Knillmann et al. (2013) the influence of warming, interspecific competition, and exposure to the insecticide esfenvalerate on the zooplankton community composition and population recovery was assessed.

Toxicants can also change the impact of biotic interactions just like biotic interactions can change the impact of toxicants. One of the ways by which a toxicant can do this is by changing antipredator mechanisms such as behavioural changes in response to predator cues and changes in escape performance (Teplitsky et al., 2005; Brooks et al., 2009; Van Gossum et al., 2009; Janssens and Stoks, 2012). One widespread antipredator mechanism that has been ignored so far in ecotoxicology is autotomy, where an animal sacrifices a body part to escape predation (Fleming et al., 2007). While autotomy has immediate survival benefits, it is costly in the long term as it will increase the vulnerability to future encounters with predators and energy is needed to regrow the autotomized body part (Fleming et al., 2007). Autotomy increases with the number of encounters with predators, and animals may become more active when exposed to toxicants (e.g. Janssens and Stoks, 2012) and warming (e.g. Janssens et al., 2014) since they need to forage more in order to meet the higher energy demand for detoxification and damage repair under pesticide exposure (Congdon et al., 2001), and to sustain their higher metabolism under warming (Angiletta, 2009). It may therefore be expected that both stressors increase the frequency of autotomy (for warming: Start et al., 2017). As such, autotomy may be an overlooked mechanism how transient exposure to toxicants generates delayed costs.

The aim of this study was to test the effect of intraspecific competition on the sensitivity of an aquatic insect to toxicants under global warming. We therefore documented in a common garden warming experiment how warming, competition and pesticide exposure in isolation and in combination affected mortality, growth and heat tolerance. Moreover, we addressed whether toxicant exposure, potentially in interaction with competition and warming, increased the frequency of autotomy. We studied this in the damselfly *Ischnura elegans*. Damselflies are important intermediate predators in aquatic systems (Stoks and Córdoba-Aguilar, 2012), and are vulnerable to both global warming (Hassall and Thompson, 2008) and toxicant exposure (Liess and Von der Ohe, 2005), since the obligate aquatic stage cannot escape exposure to these stressors. Competition is an important biotic interaction in larval damselfly populations (e.g. Anholt, 1990; McPeck and Peckarsky, 1998), and damselfly larvae rely on autotomy of their caudal lamellae to escape predation (Stoks, 1998a). We exposed *I. elegans* larvae from replicated high- and low-latitude populations

of this species in Europe in a common garden warming experiment. Common garden experiments are a standard method to demonstrate local adaptation (Kawecki and Ebert, 2004). In this type of experiments organisms from both latitudes are reared under common conditions with the manipulation of one environmental variable for which local adaptation is tested. In our case we reared animals from both latitudes under common conditions either at the mean summer water temperature of the high latitude (20 °C) or the low latitude (24 °C). This approach allows testing how the latitude-associated thermal adaptation in the species (De Block et al., 2013; Shama et al., 2011; Op de Beeck et al., 2017a), and the latitudinal differences in life history (the low-latitude larvae grow and develop faster, Shama et al., 2011; Stoks et al., 2012) may generate changes in the sensitivity to toxicants. For this study, we used chlorpyrifos as the toxicant of interest. Chlorpyrifos is an organophosphate and one of the most frequently used insecticides worldwide (Eaton et al., 2008) and a priority pollutant in the European Water Framework Directive (2000/60/EC). We choose to apply the pesticide under an environmental realistic multiple pulse scenario without renewal of the medium, thereby mimicking as series of releases/emissions of a pesticide in a pond. For the study species, the sensitivity to CPF increases under warming as evidenced when the CPF concentration is kept constant (Dinh Van et al., 2014), yet, the net impact of CPF under warming may decrease under a multiple pulse scenario because of higher pesticide degradation and less pesticide accumulation (Op de Beeck et al., 2017a).

2. Material & methods

2.1. Collecting and housing

Mated females (12–15 per population) of the damselfly *I. elegans* were collected from replicated populations in the low-latitude and high-latitude regions of the species' distribution in Europe (Gosden et al., 2011). Per latitude three populations were chosen randomly and sampled end June – early July 2014. For the low-latitude region (southern France) we sampled at Saint-Martin-de-Crau (43°38'16.61"N, 4°50'49.05"E), Camaret-sur-Aigues (44°9'15.0"N, 4°51'20.36"E), and Valcros (43°10'9.06"N, 6°16'11.36"E). For the high-latitude region we sampled the Danish population Ahl Hage (56°10'59.66"N, 10°39'1.69"E) and the Swedish populations Nöbelövs mosse (55°44'6.00"N, 13°9'10.00"E) and Eriksö (58°56'4.90"N, 17°39'21.50"E). All sampling sites were shallow lakes with a rich aquatic vegetation. Details on the study sites can be found in Op de Beeck et al. (2017b).

To obtain eggs, mated females were placed individually in plastic cups with wet filter paper as substrate for oviposition. The deposited eggs were transferred to the lab in Belgium, where they were incubated. Larvae were reared individually in 200 ml plastic cups filled with 100 ml dechlorinated water at one of two water temperatures (20 °C or 24 °C) and a photoperiod of L:D 14:10 h until they reached the final instar. For more details on the housing of damselfly larvae see Op de Beeck et al. (2017b). One day after their moult into the final instar, larvae were introduced in the pesticide exposure experiment at their respective rearing temperature. In this way all larvae had been acclimated to their experimental temperature (starting from the egg stage) for more than 14 weeks before we tested effects of the pesticide and competition. This also ensured that all larvae were standardized for the same "physiological age" when the exposure started. The chosen temperatures match the average summer water temperature of the water bodies inhabited by the study species at low (24 °C) and high (20 °C) latitude in Europe (De Block et al., 2013). Moreover, the 4 °C temperature difference matches the predicted warming at high latitudes by the year 2100 under IPCC (IPCC, 2013) scenario RCP 8.5.

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