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If you see one, have you seen them all?: Community-wide effects of insecticide cross-resistance in zooplankton populations near and far from agriculture[☆]



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ABSTRACT

The worldwide use of pesticides has led to increases in agricultural yields by reducing crop losses. However, increased pesticide use has resulted in pesticide-resistant pest species and recent studies have discovered pesticide-resistance in non-target species living close to farms. Such increased tolerance not only affects the species, but can alter the entire food web. Given that some species can evolve not only resistance to a single pesticide, but also cross-resistance to other pesticides that share the same mode of action, one would predict that cross-resistance to pesticides would also have effects on the entire community and affect community stability. To address this hypothesis, we conducted an outdoor mesocosm experiment comprised of 200 identical aquatic communities with phytoplankton, periphyton, and leopard frog (*Lithobates pipiens*) tadpoles. To these communities, we added one of four *Daphnia pulex* populations that we previously discovered were either resistant or sensitive to the insecticide of chlorpyrifos as a result of living close to or far from agriculture, respectively. We then exposed the communities to either no insecticide or three different concentrations of AChE-inhibiting insecticides (chlorpyrifos, malathion or carbaryl) or sodium channel-inhibiting insecticides (permethrin or cypermethrin). We discovered that communities containing sensitive *Daphnia pulex* experienced phytoplankton blooms and subsequent cascades through all trophic groups including amphibians at moderate to high concentrations of all five insecticides. However, communities containing resistant *D. pulex* were buffered from these effects at low to moderate concentrations of all AChE-inhibiting insecticides, but were not buffered against the pyrethroid insecticides. These data suggest that a simple change in the population-level resistance of zooplankton to a single insecticide can have widespread consequences for community stability and that the effects can be extrapolated to a wide variety of pesticides that share the same mode of action.

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1. Introduction

Synthetic pesticides are ubiquitous across the globe and have been largely responsible for increasing agricultural yields since their introduction in the late 1930s. It has been estimated that every \$1 spent on pesticide production and use has led to \$4 in

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crops being saved from their target pest species (Pimentel et al., 1992). Although overall pesticide use in the U.S. has been slowly declining over recent years, due to the phasing out of specific classes of pesticides (i.e. organophosphates), worldwide production of these chemicals has increased dramatically to the point where nearly 2.4 billion kg of pesticides are applied every year (Grube et al., 2011). These chemicals are designed to affect the physiology of target pest species by either deterring, incapacitating, or killing them. The pest species that are typically targeted by these chemicals can range broadly depending on the chemical formula of chosen pesticide. For instance, in agriculture, the most common pest species for which pesticides are used as a control measure would include an enormous array of insects such as beetles,

weevils, grasshoppers, crickets, aphids, and thrips (Oerke, 2006). However, widespread pesticide use can also cause direct, indirect, and sublethal effects on non-target organisms, as well as lead to the evolution of resistance. Evolved resistance in targeted pest species has received a lot of attention by researchers across the globe (Georghiou and Taylor, 1977; Hoy, 1998; Weill et al., 2003) and it is estimated that pesticide resistance causes more than \$1.5 billion in crop losses each year (Pimentel, 2005). What is far less understood, however, is whether evolved pesticide resistance also occurs in non-target species that are inadvertently exposed to these chemicals (Brausch and Smith, 2009a,b; Jansen et al., 2011).

Although there is less of an economic incentive to study evolved resistance in non-target species, such resistance may have important ecological and conservation implications (Hua et al., 2013). For instance, pesticides can decrease population-level genetic variation and this can be disadvantageous in terms of responding to future environmental change (Georghiou, 1990; Carriere et al., 1994). Pesticides can have a range of sublethal effects on non-target organisms (i.e. life history trade-offs) that can have direct effects on the survivorship and fecundity of the directly impacted species and can also have an array of indirect effects throughout the food web. On the other hand, populations of non-target species that have evolved resistance and play key roles in communities can buffer aquatic communities from the negative effects of a pesticide-induced trophic cascade (Bendis and Relyea, 2016).

Today there are more than 1055 active ingredients that are registered as insecticides in the United States (Goldman, 2007). Due to this large number of chemicals, insecticides are often classified by their mode of action, which is the method by which chemicals affect target pest species. An interesting aspect of considering pesticide modes of action is that target species can commonly evolve cross-resistance to multiple chemicals of the same class or mode of action and sometimes even cross-resistance among pesticides with different modes of action (Berengues et al., 2003; Brausch and Smith, 2009a; Mitchell et al., 2012; Hua et al., 2013). It is reasonable to predict that cross-resistance may also be common in non-target species, but we know very little about the prevalence of cross-resistance among non-target species. Furthermore, we know nothing about whether patterns of cross-resistance to pesticides that share a mode of action can have the same community-wide effects as pesticide that have different modes of action.

Pond communities are ideal for studying the community-wide effects of cross-resistance to insecticides because they are found across a wide range of distances from agricultural areas and are therefore subjected to a variety of pesticide types and application frequencies (De Meester et al., 2005). Habitats with higher proportions of surrounding agriculture and closer distances to agricultural areas have proven to be useful proxies of historic pesticide exposures that lead to populations evolving higher pesticide resistance (Coors et al., 2009; Cothran et al., 2013; Bendis and Relyea, 2014). For example, recent studies have shown that wood frog populations (*Lithobates sylvaticus*) living closer to agricultural areas have higher resistance to the insecticide carbaryl (Cothran et al., 2013). A subsequent study found that these populations that were not only resistant to this one acetylcholine esterase (AChE)-inhibiting insecticide, but they also exhibited cross resistance to two additional AChE-inhibiting insecticides, thereby indicating that cross-resistance may be common among non-target species (Hua et al., 2013). AChE-inhibiting insecticides, like these, inhibit the acetylcholinesterase enzyme from breaking down the neurotransmitter acetylcholine at neuromuscular junctions. This causes overstimulation of the muscles which then leads to paralysis and, eventually, death (Fukuto, 1990). Recent studies have also shown that zooplankton populations in the genus *Daphnia* can vary

in their resistance to commonly applied insecticides such as carbaryl (*Daphnia magna*, Coors et al., 2009) and chlorpyrifos (*Daphnia pulex*, Bendis and Relyea, 2014) and that these patterns of resistance are also related to agricultural land use surrounding the ponds. Such evolved resistance is important because zooplankton are one of the most sensitive taxonomic groups to insecticides, and they play a key role in the function of pond communities as consumers, as prey, and as cyclers of nutrients (Hanazato, 1998; 2001). When zooplankton are exposed to an insecticide, they can experience large declines in abundance and their food resource (i.e. phytoplankton) typically experiences a dramatic increase in abundance. The increase in phytoplankton can, in turn, cause a further trophic cascade that has numerous deleterious effects throughout the community (Barry and Logan, 1998; Boone and James, 2003; Fleeger et al., 2003; Boone et al., 2004; Mills and Semlitsch, 2004, Relyea and Diecks, 2008). However, we recently discovered that communities containing resistant populations of *D. pulex* (hereafter referred to as '*Daphnia*' for simplicity) can buffer the entire aquatic communities from the impacts of insecticides (Bendis and Relyea, 2016). Although this is an important finding, we need to know if zooplankton can evolve cross-resistance to other pesticides with the same or different modes of action, and whether this allows the zooplankton to buffer communities from pesticide exposures.

We addressed this question using populations of *Daphnia* that vary in their resistance to the insecticide chlorpyrifos (Bendis and Relyea, 2014). We created identical aquatic communities that varied only in the population of *Daphnia* that the community received (two "resistant" populations collected from ponds near agriculture, two "sensitive" populations collected from ponds far from agriculture). We hypothesized that communities containing populations of chlorpyrifos-resistant *Daphnia* would be buffered from the effects of low concentrations of not only chlorpyrifos, but also carbaryl and malathion, which have the same mode of action as chlorpyrifos (i.e. they inhibit AChE). In contrast, communities exposed to low concentrations of permethrin and cypermethrin, two pyrethroid insecticides which have a different mode of action (i.e. Na⁺ channel-inhibitors which disrupt the normal transmission of nerve impulses by blocking Na⁺ channels in nerve cells – Vijverberg et al., 1982), should not exhibit any differences in resistance to these insecticides, regardless of the *Daphnia* population included and should therefore not be buffered from its effects.

2. Methods

We conducted a mesocosm experiment at the University of Pittsburgh's Donald S. Wood Field Laboratory at the Pymatuning Laboratory of Ecology. Using mesocosms allowed us to replicate aquatic communities, while simultaneously subjecting these communities to a range of pesticide applications (Relyea and Diecks, 2008). The experimental design was a full factorial using four *Daphnia* populations: two resistant populations from ponds with surrounding agriculture (>30% agricultural land within a 300-m radius) and two sensitive populations from ponds with little or no surrounding agriculture (<5% agricultural land within a 300-m radius). These four populations were each exposed to 16 insecticide treatments ([0.25, 0.50 and 1.0 µg/L chlorpyrifos], [12.5, 25 and 50 µg/L carbaryl], [0.5, 1.0, and 2.0 µg/L malathion], [0.5, 1.0, and 2.0 µg/L permethrin], [0.5, 1.0 and 2.0 µg/L cypermethrin], and a negative control).

The insecticide concentrations were determined from our review of published data on recorded LC50s for *Daphnia* for each insecticide, a comparison of LC50 values from other LC50 pilots performed within our lab, and from a series of LC50 experiments that we performed prior to the setup of the mesocosm experiment

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