Assessing recovery of stream insects from pesticides using a two-patch metapopulation model

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HIGHLIGHTS

- modelled pesticide effects on survival, reproduction and emergence of univoltine insects
- populations in polluted and non-polluted patches linked through migration
- reductions in reproduction had strongest influence on recovery time
- extinction for some scenarios with annual exposure
- migration buffered against extinction and generally facilitated faster recovery
- migration led to indirect pesticide effects in the non-polluted patch

GRAPHICAL ABSTRACT
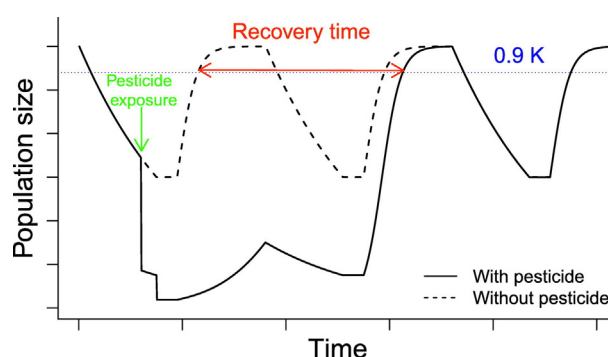
ABSTRACT

Pesticides can exert lethal and sublethal effects on streams organisms. Field studies have shown that non-polluted upstream patches promote population recovery from such effects. Nevertheless, the dynamics and potential carryover effects on the upstream patch are largely unknown. We used a metapopulation model with 2 patches to simulate lethal and sublethal effects on the downstream population of an insect with one generation per year, which was structured into early and late instars aquatic life stages, and an adult terrestrial life stage. We examined the implications for the recovery time of a range of scenarios covering different pesticide effect combinations, migration and exposure types. We found that recovery time responded most strongly to a reduction in reproduction in terms of the reduction of the intrinsic growth rate during the early instar aquatic life stage. For 60 of 96 scenarios with pesticide exposure in consecutive years, no recovery occurred within one year if the intrinsic growth rate was reduced by 50% or more. Without migration between patches (32 scenarios), the polluted downstream population went extinct in 5 of these scenarios. Migration lead overall to slightly faster recovery, albeit this was scenario dependent, but also to a carryover of the pesticide effect from the polluted downstream to the non-polluted upstream patch (up to 25% reduction in the minimal population size). A sensitivity analysis revealed that recovery time was most sensitive to the parameters length of the intrinsic growth phase during early instar aquatic life stage and to migration mortality of the late instar aquatic larvae, and least sensitive to the adult emigration rate and timing of pesticide application. Our study highlights the important role of sublethal effects for population responses to pesticides and that migration buffers against effects, but also carries effects over to non-polluted patches.

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1. Introduction

Pesticide exposure represents an important stressor in freshwater ecosystems (e.g. Malaj et al., 2014; Stehle and Schulz, 2015), particularly for macroinvertebrates that are of paramount importance for ecosystem functioning (Wallace and Webster, 1996). Several field studies found a reduction in pesticide-sensitive macroinvertebrate species with increasing pesticide exposure that also translated to a reduction in ecosystem functioning (Schäfer et al., 2012). However, upstream patches in the stream network without pesticide exposure have been shown to buffer effects (Orlinskiy et al., 2015; Schäfer et al., 2012). The presumed mechanism for the buffering of effects is immigration of individuals from non-polluted upstream patches, but related studies are scarce.

From a theoretical perspective, a habitat patch that requires immigration from a source patch to sustain the local population represents a sink (Pulliam, 1988). The migration between sources and sinks, i.e. source-sink dynamics, also affects the source patches (e.g. reduced productivity in the source patch). Such processes have also been shown for non-polluted habitat patches (sources) connected to polluted habitat patches (sinks) (Chaumot et al., 2003; Spromberg and Scholz, 2011; Willson and Hopkins, 2013). To our knowledge, to date the dynamics of merolimnic (species with both aquatic and terrestrial life stages) insects between pesticide-polluted patches and non-polluted upstream patches have not been studied. Thus, it is unknown under which conditions pesticide pollution turns the affected patch into a sink and how the dynamics affect the upstream patch in terms of carryover effects. Studying related research questions can also inform on recovery processes from pesticide stress, which has recently gained increasing attention in regulation through incorporation of an ecological recovery option in the guidance document for pesticide authorisation in the European Union (EFSA, 2013), while a systematic understanding of the processes driving recovery in risk assessment is still missing (Kattwinkel et al., 2015).

Ecological models can be employed for multiple purposes including the generation and testing of ecological hypotheses (e.g. De Laender et al., 2015), identification of research gaps and explanation of observed patterns (e.g. Becker and Liess, 2015). Several models have been used to study the dynamics of (meta-)populations between different habitat patches under toxicant influence. A few studies on predator-prey dynamics between insecticide-sprayed and non-sprayed fields found that prey populations, representing a pest, can reach higher densities with spraying, conditional on factors such as the dispersal rates of the predator and prey (Sherratt and Jepson, 1993; Trumper and Holt, 1998). A study on single species metapopulation dynamics highlighted the carryover of impacts on a contaminated patch to other non-contaminated patches (Spromberg et al., 1998). Similarly, a metapopulation model with multiple patches of toad populations showed that depending on the distance between patches the contamination of one patch influences the extinction risk of non-contaminated patches (Willson and Hopkins, 2013).

The aim of this study was to examine the influence of lethal and sublethal pesticide effects on the metapopulation dynamics of a merolimnic insect between a pesticide-polluted downstream and an unpolluted upstream patch, including carryover effects from the polluted to the non-polluted patch. Pesticide effects and the influence of metapopulation dynamics were quantified based on the time to recovery following an approach of Barnthouse (2004). The extinction risk in a patch was evaluated based on the minimal population size. We selected a univoltine (i.e. one generation per year) merolimnic insect with three life stages as model organism, however, we provide the full computer code to allow for adaptation to species with different generation times or life cycles.

2. Methods

2.1. Model species selection and general autecology

As model species, we selected a merolimnic stream invertebrate (i.e. the stonefly *Nemoura* sp.) that is generally sensitive to pesticides in comparison to other stream invertebrates (Rico and Van den Brink, 2015; von der Ohe and Liess, 2004). The species was considered univoltine, i.e. has one generation per year (Elliott, 1984). The life cycle of univoltine insects consists of several stages: several consecutive aquatic larval stages followed by a metamorphosis to a terrestrial adult stage that emerges from the water body. The terrestrial adults mate and oviposit. The larvae hatch from the eggs and represent the new generation of aquatic larvae.

The overall dynamic of the life cycle of the modelled species was matched to observations from a study on a permanent small stream in southern Ontario (Turner and Williams, 2000), which has a temperate climate. This study found highest densities of *Nemoura trispinosa* larvae in winter (from November to January), presumably due to the emergence covering almost 4 months and consequently larvae hatching until winter. Subsequently, the density of aquatic larvae declined steadily towards summer due to natural mortality (owing to e.g. predation) and emergence. Several studies reported that the emergence of *Nemoura* sp. peaked around early summer (June) (Dobrin and Giberson, 2003; Turner and Williams, 2000; Williams and Williams, 1993), though emergence was variable as mentioned above and asynchronous emergence has also been reported (Speirs et al., 2000).

The dispersal in merolimnic insects represents an autecological research area with several unresolved questions (Didham et al., 2012; Humphries and Ruxton, 2002). Given that the aquatic larvae of meroliminic insects are subject to downstream drift with stream flow, upstream directed flight of emerging adults has been suggested as mechanism that counteracts the upstream depletion of invertebrates several decades ago (Müller, 1982, 1954). Nevertheless, other studies showed that processes such as in-stream upstream migration or random flight coupled with density dependent processes may be sufficient to counter depletion (Humphries and Ruxton, 2002; Speirs and Gurney, 2001). For *Nemoura sp*., different terrestrial dispersal strategies have been reported. Studies found directed upstream flight (Müller, 1982), undirected flight (Madsen et al., 1973; Turner and Williams, 2000) and even downstream directed flight (Williams and Williams, 1993). Thus, we analyzed the potential influences of the dispersal strategy on the model results by testing two different dispersal strategies (1. asymmetric: downstream drift and directed upstream flight, 2. symmetric: undirected aquatic and terrestrial migration).

2.2. Conceptual model

We used a two-patch metapopulation model to investigate the combined roles of pesticide effects and migration on the populations of the model species. The two patches represent spatially separated habitats of the model species, which may originate from spatially variable resources (Lancaster and Downes, 2014). They are within in-stream migration distances, located upstream and downstream and pesticides only affect the local population in the downstream patch directly.

We considered three consecutive life stages: (1) late instars aquatic larvae, (2) terrestrial adults and (3) early instars aquatic larvae, representing a new generation. The model initialises with the late instars stage because this stage is subject to pesticide effects. We split the life cycle into the aquatic and terrestrial stage to allow for simulation of asymmetric migration in the aquatic and terrestrial stage. Moreover, we distinguished between early and late instars of aquatic larvae to account for differences in migration (see below). Furthermore, this classification offers a simplified approach to reproduce the pattern found in the Ontario stream with an increasing number of larvae until winter (early instars aquatic larvae stage in our model) and a subsequent decrease (late instars aquatic larvae stage in our model) (Turner and Williams, 2000). As outlined above the increasing number of larvae until winter presumably results from an extended period of emergence and hatching. Instead of implementing this pattern through the three underlying processes (temporally variable emergence, hatching and background mortality of hatched larvae), we modelled the pattern as