



Contaminant fluxes across ecosystems mediated by aquatic insects

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Metals and organic contaminants in aquatic systems affect the coupling of aquatic and terrestrial ecosystems through two pathways: contaminant-induced effects on insect emergence and emergence-induced contaminant transfer. Consequently, the impact of aquatic contaminants on terrestrial ecosystems can be driven by modifications in the quantity and quality of adult aquatic insects serving as prey or contaminants entering terrestrial food webs as part of the diet of terrestrial predators. Here, we provide an overview of recent advances in the field, separating metals from organic contaminants due to their differential propensity to bioaccumulate and thus their potential contribution to either of the two pathways. Finally, this review highlights the knowledge gap in the relative impact of these pathways on terrestrial insectivores.

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Introduction

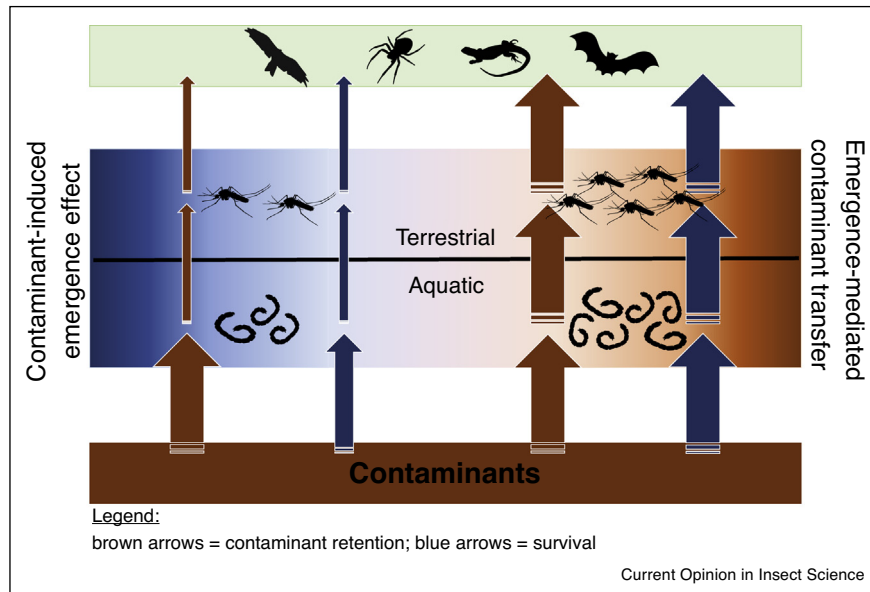
Ecosystems are connected by fluxes of nutrients, organic material, and organisms [1]. The emergence of aquatic insects is a highly relevant process linking aquatic with terrestrial food webs on the landscape scale. For example, along the Upper Mississippi River and western Lake Erie (USA) the emergence of mayflies was estimated at several thousand tons during a single event [2]. However, aquatic to terrestrial linkages can be impacted by anthropogenic activity in or near aquatic ecosystems that modify habitat quality and consequently emergence biomass and

its temporal availability to terrestrial insectivores. In recent years, mass emergence of mayflies has been reduced by approximately 50% due to eutrophication, algal blooms, and chemical contaminants (including pesticides) [2]. Indeed, recent evidence points towards anthropogenic land use as an important factor driving aquatic-terrestrial coupling at the landscape scale [3], which is supported by a negative correlation between emergent insect relative abundance in the benthic macroinvertebrate community and tolerance towards contaminants [4].

Increased concentrations of chemical contaminants are one of the effects of anthropogenic land use on aquatic ecosystems. These contaminants may be taken up by aquatic biota and can be transferred as part of the emerged insects to adjacent riparian terrestrial habitats and their food webs [reviewed in Ref. 5]. To understand the effects of aquatic contaminants on terrestrial insectivores, contaminants may – according to the heuristic model proposed by Kraus [6] – be categorized by their effects on emergence quantity, nutritious quality for terrestrial consumers, and emergence timing (contaminant-induced emergence effect, Figure 1). Thereby, the potential for aquatic contaminants to be retained during metamorphosis and ultimately transferred to the terrestrial ecosystems without affecting emergence biomass (emergence-induced contaminant transfer, Figure 1) should be considered [6]. For example, elevated concentrations of trace metals in aquatic ecosystems can reduce emergence of adult aquatic insects. In combination with a generally low retention during metamorphosis [7], metal fluxes to terrestrial systems via emerging aquatic insects is limited. On the contrary, some organic contaminants such as pesticides can be retained or even enriched during metamorphosis and may simultaneously affect emergence (e.g. insecticides) with yet rarely studied implications for pesticide fluxes [8]. Although the framework in Kraus [6] is helpful, more recent findings on effects of chemical contaminants on emergence and contaminant transfer have yet to be incorporated.

In this review, we summarize recently (2019–2021) published evidence on the impact of chemicals – both metals and organic chemicals – on aquatic subsidy quantity and quality against the background of the heuristic model explained above [6]. We separate the published literature to (1) contaminant effects in aquatic subsidy and (2) emergence induced contaminant transfer into terrestrial

Figure 1



Graphical illustration of ‘contaminant-induced emergence effect’ and ‘emergence-induced contaminant transfer’. The black horizontal line indicates the boundary between the aquatic and terrestrial ecosystems and the developmental stages occurring therein, larvae and adults, respectively. Contaminant-induced emergence effects are characterized by a reduction in larval and adult abundance (thin blue arrows) and a low retention of contaminants during metamorphosis (thin brown arrows), resulting in a low flux of contaminants from the aquatic to the terrestrial food web. An emergence-induced contaminant transfer is defined by limited impact on emergence (thick blue arrow) and a high retention of contaminants in different developmental stages (thick brown arrow), resulting in an efficient contaminant transfer to the terrestrial food web.

ecosystems and food webs. We then compare newer results on contaminant retention to those previously incorporated in the model [7].

Contaminant-induced emergence effect

Contaminants affect emergence and thus the subsidy provided by aquatic to terrestrial ecosystems. Trace metals and organic contaminants at toxic concentrations were reported to mostly reduce emergence biomass, with nutrients having the opposite effect [9^{••}]. Some have suggested that emergence may be a more sensitive endpoint than larval abundance in detecting toxic effects of contaminants [10]. In recent years, evidence has pointed towards a more nuanced picture, calling for a developmental stage specific consideration of sensitivity [11].

In the case of trace metals, a field study on northern Swedish lakes impacted by mining reported that increasing zinc levels did not affect larval abundance; their emergence success was, however, reduced. The opposite pattern, namely a reduction in larval abundance but no effect on their emergence success, was observed in lakes dominated by lead contamination [12]. Similarly, chironomids exposed to a mixture of copper and zinc showed a substantial reduction in larval abundance but not emergence success; in fact, emergence success was even elevated [13]. Emergence success can be elevated as a

consequence of decreased larval density and thus less competition for resources [14]. This pattern was not confirmed by Ephemeroptera and Simuliidae tested simultaneously [13]. Moreover, field collected sediment contaminated with cadmium, lead, and zinc delayed chironomid emergence, increased levels of storage lipids, and reduced individual biomass of adults as well as the ratio between wing area and adult dry mass [15]. Similarly, metal (oxide) nanoparticles delayed emergence of a caddisfly species substantially and decreased subsidy quality by decreasing energy reserves [16]. These studies suggest that metals and metal-based nanoparticles impact the transfer of energy from aquatic to terrestrial ecosystems by reducing the number of emerged insects, shifting temporal emergence pattern, and modifying nutritious quality of emerged insects for terrestrial predators.

Similar to trace metals, organic contaminants can interfere with emergence. The antidepressant fluoxetine, at low concentrations (20 ng/L), induced an earlier emergence of Diptera [17]. This effect was not confirmed at 1000-fold higher concentrations, with the mechanisms causing this difference unknown [17]. Also, the anti-inflammatory drug naproxen and the preservative propylparaben reduced pupation and fecundity of the mosquito *Aedes aegypti* in the $\mu\text{g/L}$ range suggesting shifts in aquatic subsidy over time [18]. Studies addressing the impact

of pesticides on aquatic emergence have involved neonicotinoids nearly exclusively. Strong pesticide induced impairments in emergence of damselflies [19], chironomids [20] and insect communities [21] were seen in field-based mesocosms and natural wetlands. The study by Graf *et al.* [22**] is to our knowledge the only one that linked in-stream pesticide contamination to insectivore species richness and abundance in the adjacent riparian zone. Although insect emergence was not documented in this study [22**], these data point towards contaminant impacts on food webs across ecosystem boundaries: negative effects in insectivore riparian spiders (both species richness and number of spider individuals) could either be driven by a pesticide induced reduced emergence or the elevated flux of pesticides contained in the emerged adult insects [8*] [see also Ref. 23] serving as resource for riparian spiders. Despite increased attention on the effects of contaminants on emergence and the consequences for insectivores, data are still limited to support conclusions on the relevance of contaminant-induced emergence effects for riparian food webs.

Emergence-mediated contaminant transfer

The flux of contaminants through emerging aquatic insects to terrestrial ecosystems is a function of metamorphic retention and the biomass of insects emerging [6**]. Consequently, emergence-mediated contaminant transfer and thus the exposure risk for riparian insectivores partly depends on the impact of the same contaminants on aquatic life stages affecting their emergence success. Contaminants that bioaccumulate in larvae may be retained or lost during metamorphosis. Loss can occur during physiological processes: contaminants may be deposited in exuviae shed during final aquatic life stages or excreted with the metabolic waste generated during formation of adult tissues (i.e. meconium) [24]. Alternatively, the concentration of contaminants in adults can be elevated relative to the final larval life stage because energy reserves and weight are lost during metamorphosis in combination with a limited contaminant excretion [6**,7].

Recent examples of contaminant fluxes and metamorphic retention of contaminants, as well as evidence for their transfer from aquatic into terrestrial food webs, include studies of both metal and organic contaminants. For several trace metals, the concentration in adult aquatic insects was lower relative to their larval life stages (Figure 2), suggesting metamorphic losses, and thus decreasing their potential impact on concentrations of metals in riparian spiders [25], an observation confirmed for uranium by Bergmann and Graca [26]. Similarly, data on hemimetabolous and holometabolous insects (Odonata and Trichoptera, respectively), for which only five (copper, zinc, selenium, cadmium and silver) out of 22 metals had higher concentrations after emergence [27,28] [see for copper and *Aedes* 29], confirm the results

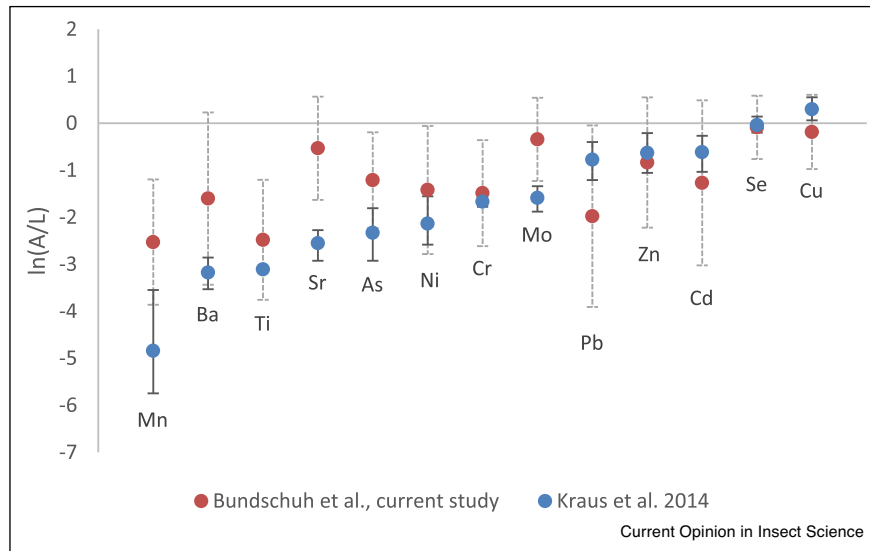
of previous field studies. A study by Naslund *et al.* [30] linked the selenium concentration of biofilms in mining impacted aquatic systems with selenium concentration in adult aquatic insects and finally riparian spiders, suggesting metamorphic retention of selenium [see also Ref. 23 and Figure 2] and a transfer from the aquatic into the terrestrial food web. A similar observation was made for methyl mercury, whose body burden in riparian spiders increased with increasing share of aquatic insects in their diet [31,32,33*]. Metal (oxide) nanoparticles data on the metamorphic retention are lacking but their transfer with insect emergence was recently confirmed [16].

Similarly, the flux of organic pesticides transported with emerged adult insects from prairie wetlands to terrestrial systems was elevated (50%) along an insecticide gradient despite a reduced (40%) emergence when contaminated with such insecticides [8*] [see also Ref. 23]. Although metamorphic retention of pesticides was not targeted in this study [8*], literature confirms that pesticides seem to be largely retained during metamorphosis, contributing to this observation (Figure 3). Moreover, recent evidence suggests that significant retention of pharmaceuticals, endocrine disrupting compounds [34*], and organophosphorus flame retardants over metamorphosis may be similar to that previously found in polychlorinated biphenyls, dioxins, and pesticides (Figure 3) [35]. Although perfluorinated and polyfluorinated substances [PFAS, 36,37*] are less efficiently retained, their concentrations in riparian spiders are directly related to the share of aquatic organisms in their diet [36], underpinning the relevance of aquatic emergence as exposure pathway.

Outlook for insectivores and future research

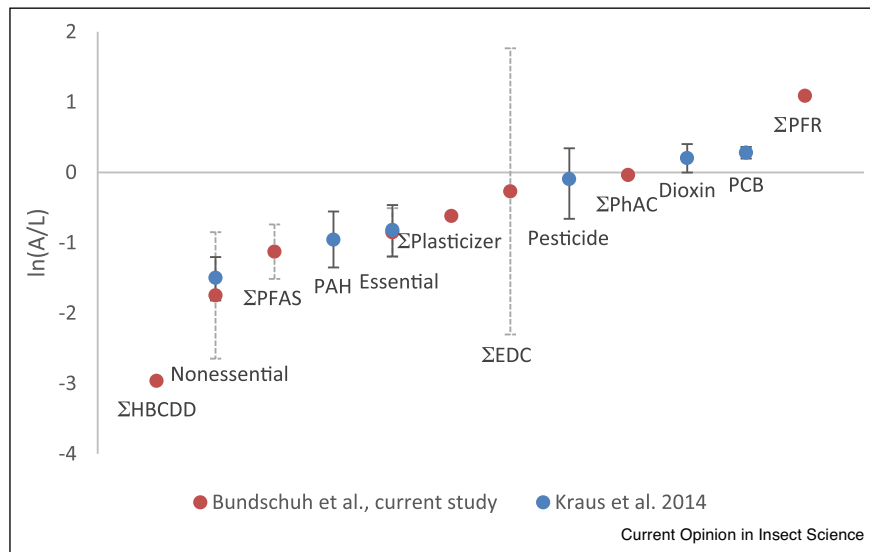
Despite recent advancements in understanding the impact of contaminants across ecosystem boundaries, the relative contribution of the two main effect pathways, that is contaminant-induced emergence effect and emergence-mediated contaminant transfer, on terrestrial insectivores remains largely unknown. Mechanistic studies are needed that separate these two effect pathways by modifying contaminant load or the quantitative, qualitative, or temporal characteristics of emergence. Studies are also needed that evaluate the implications of contaminant transfer for behavior, life history strategies, abundance and diversity of riparian insectivores to better understand and predict the impact of contaminants and their mixtures in these meta-ecosystems. We see a particular risk for unexpected ecological outcomes when contaminants with little impact on aquatic life stages of insects are efficiently retained during metamorphosis and have a toxic mode of action targeting hormone-driven processes in riparian insectivores. The publication by Previsic *et al.* [34*], for instance, points towards higher levels of endocrine disrupting compounds in adults relative to larval trichopterans. It is, moreover, evident from the present overview that the number of classes of (organic)

Figure 2



Overview of metamorphic retention of trace metals expressed as natural logarithm of the ratio between the concentration in adult (A) and larvae (L). Red (with standard deviation) and blue (with 95% confidence interval) data points represent the central tendencies of recent publications (2019–2021) covered in Bundschuh *et al.*, current study and in Kraus *et al.* [7], respectively. Both analyses are in agreement for most elements, pointing towards highest metamorphic retention of copper, selenium, cadmium, zinc, lead, and (particularly for the most recent published studies) strontium as well as molybdenum. Nonetheless, metamorphic retention is low for most elements.

Figure 3



Overview of metamorphic retention of organic contaminants from a range of classes (ΣHBCDD = sum of hexabromocyclododecane (3 types), ΣPFAS = sum of 24 perfluoroalkyl and polyfluoroalkyl substances, PAH = polyaromatic hydrocarbons, ΣPlasticizer = sum of 10 ten plasticizers, mainly phthalates, ΣEDC = sum of two endocrine disrupting chemicals, ΣPhAC = sum of four pharmaceuticals, PCB = polychlorinated biphenyl, ΣPFR = sum organophosphorus flame retardants) as well as non-essential (Nonessential) and essential (Essential) trace metals expressed as natural logarithm of the ratio between the concentration in adult (A) and larvae (L). Values of trace metals have been added for comparison and are based on Figure 2. Red (with standard deviation) and blue (with 95% confidence interval) data points represent the central tendencies of recent publications (2019–2021) covered in Bundschuh *et al.*, current study and in Kraus *et al.* [7], respectively. Both analyses are in agreement for essential and nonessential metals. It is evident that recent research expanded on the classes of organic contaminants relative to the earlier work (with partly high variability in the mean retention across taxa, for example, EDCs), with most classes being lost during metamorphosis.

contaminants and the number of observations per class (Figure 3) assessed is relatively limited, suggesting a need for further laboratory and field studies to measure concentrations of a wider range of contaminants with diverse physico-chemical properties in insects at the larval and adult life stages.

Conflict of interest statement

Nothing declared.

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