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Metacommunities, metaecosystems, and the environmental fate of chemical contaminants

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Running Headline
Dispersal and contaminant fate in metaecosystems

Abstract

1. Although pollution is a major driver of ecosystem change, models predicting the environmental fate of contaminants suffer from critical uncertainties related to oversimplifying the dynamics of the biological compartment.
2. It is increasingly recognized that contaminant processing is an outcome of ecosystem functioning, that ecosystem functioning is contingent on community structure, and that community structure is influenced by organismal dispersal. We propose a conceptual organization of the contribution of organismal dispersal to local contaminant fate. Direct dispersal effects occur when the dispersing organism directly couples contaminant stocks in spatially separate ecosystems by transporting contaminants in its biomass. Indirect dispersal effects occur when the dispersing organism indirectly influences contaminant fate via community assembly. This can occur either when the dispersing organism is a contaminant processor or when the dispersing organism alters, via species interactions, the abundance of contaminant biotransporters or processors already established in the ecosystem. The magnitude of direct and indirect dispersal effects are modulated by many factors, including other contaminants. These will influence population growth rates of the dispersing species in the donor ecosystem, or the probability that a dispersing individual reaches the recipient ecosystem.
3. We provide a review of pertinent literature demonstrating that these two mechanisms, and their chemical modulation, are well supported or likely to occur in many natural and human-modified landscapes. The literature also demonstrates that they can operate in concert with each other.
4. *Synthesis and applications*. This research provides recommendations for environmental management, monitoring, model development and funding policy. Managed ecosystems thought to be important contaminant and nutrient sinks, such as artificial ponds and constructed wetlands, should be monitored and controlled for in-and-out animal movement if contaminant export is found to be relevant. Uncontaminated fishing grounds linked to contaminated sites via movement of dispersing species should be monitored and resident species evaluated for health consumption advisories. Assessing the success of contaminated site remediation can be improved by better matching the spatial extent of site remediation and the home range of monitored species. Finally, interagency research fund programs should be developed that narrow the current gap between the fields of ecology and ecotoxicology.

Keywords

biotransport, biovector, dispersal, ecosystem function, ecotoxicology, keystone species, migration, pollution, metaecosystems, metacommunities

Introduction

Pollution is recognized as one of the five most important direct drivers of ecosystem change at the global scale, and a major contributor to the loss of biodiversity and degradation of human health (MEA, 2005). Nevertheless, the environmental fate of contaminants in complex food webs and landscapes is still inadequately understood. Fugacity-based models emphasize abiotic processes and physical transport, with simplified representations of organismal interactions to describe contaminant biomagnification across trophic levels (Diamond, Mackay, & Welbourn, 1992; Arnot, Mackay, Parkerton, Zaleski, & Warren, 2010). These models have been extremely useful for understanding basic transport and fate processes and guiding further studies, but tend to suffer from critical uncertainties due to a lack of site-specific data and of the realistic incorporation of the dynamical complexity within the biological compartment. This is true for studies aimed at assessing contaminant fate at scales ranging from local to global (Arnot et al., 2010).

At the same time ecosystem function, including processes that regulate contaminant fate, is modulated by community composition and structure, which in turn, is increasingly recognized as being influenced by organismal dispersal in space. This is the basis for the concepts of the metacommunity (a set of local communities that are linked by dispersal of multiple interacting species) and the metaecosystem (a set of local ecosystems that are linked by the flow of organisms, matter, or energy; Loreau, Mouquet, & Holt, 2003; Leibold et al., 2004; Leibold & Chase in press).

To our knowledge, a conceptual organization of the potential contributions of organismal dispersal to local contaminant fate has not been attempted, nor has the employment of a metacommunity and metaecosystem framework to understand the environmental fate of contaminants. There has been an effort in recent years to better incorporate ecological realism in ecotoxicology (Relyea & Hoverman, 2006; Rohr, Kerby, & Sih, 2006; Clements & Rohr, 2009); however, this effort has focused on *local* rather than *coupled* ecosystems and on *effects* of chemical contaminants rather than on their *fates* in the environment.

We propose two biologically-based mechanisms whereby organismal dispersal interacts with physical, chemical and biological processes to influence local contaminant fate. First, we recognize that individual organisms can influence local contaminant fate by sequestering, amplifying and temporarily storing contaminants in their biomass, and/or transforming a contaminant's physical and chemical structure via stabilization, activation and degradation (e.g. Moore, Kröger, & Jackson, 2011). We then differentiate *direct* and *indirect dispersal effects* depending on whether dispersing organisms directly couple contaminant stocks in spatially separate ecosystems or indirectly influence local contaminant processing via community assembly. Specifically, we term *direct dispersal effects* those that occur when dispersing organisms act primarily as biotransporters, carrying contaminants in their biomass and influencing contaminant concentrations both in donor (decreasing concentrations) and recipient (increasing concentrations) ecosystems. By contrast, *indirect dispersal effects* occur when dispersing organisms are primarily contaminant processors that colonize a previously unoccupied ecosystem, or when dispersing organisms alter, via species interactions, the abundance or biological activities of contaminant biotransporters or processors already established in the ecosystem (Fig. 1). The organisms we refer to could be species, functional groups, or even assemblages, and their role on contaminant fate can vary from subtle to keystone depending on contaminant body loads or per capita effects on contaminant processing, or on contaminant processors and transporters.

The magnitude of direct and indirect dispersal effects can be further modulated by any factor influencing numbers of dispersing organisms leaving donor ecosystems (via effects on population growth rates) and the probability that a dispersing individual reaches the recipient ecosystem (via effects on, e.g., individual mobility, habitat choice or matrix permeability). Given our general objective of narrowing the gap between ecology and ecotoxicology, we here review a role for contaminants acting as modulators of the environmental fate of other contaminants. We therefore need to differentiate chemical agents as either *target contaminants*, i.e., those that have their fate influenced in ecosystems, or *modulating contaminants,* i.e., those that modulate the fate of target contaminants via effects on the population growth rate, behaviour or performance of dispersing organisms.

We review the recent ecological and ecotoxicological literature and demonstrate that these two mechanisms, and their chemical modulation, are either well supported or likely to occur in many natural and human-modified landscapes. We further demonstrate that these two mechanisms may also operate in concert, generating complex outcomes involving organism-contaminant interactions in spatially structured ecosystems.

Direct Dispersal Effects

The most evident way that dispersal might affect the dynamics of contaminants is via direct transport. Any organism can be a reservoir for contaminants and therefore act as a dispersal vector for contaminants in the landscape. Contaminants are then released in the recipient ecosystem, in part or in full, modified or not, by individual consumption, reproduction and/or decomposition following leaching, excretion, defecation, shedding, and, especially, death. Indeed, the movement of organisms across habitats has been known to affect the movement of materials since at least the 1980s as ‘ecological subsidies’ (Polis et al., 2004). What is more recent is the appreciation that such subsidies can involve contaminants (referred to as ´the dark side of subsidies´; Walters, Fritz & Otter, 2008).

Biological transport of contaminants is relatively unique in that for many contaminants it may be the only form of ‘upgradient’ dispersal (upstream, upwind, uphill, water-to-land, deep-to-shallow water). Additionally, it may be the only form of dispersal of certain chemicals that are not amenable to atmospheric transport, like some pharmaceuticals and personal care products, or that are easily degraded outside of organisms, such as chlorinated fatty acids. Furthermore, biologically transported contaminants may be delivered in an easily bioavailable form to predators and scavengers, whereas those deposited by air or water currents are subject to various abiotic processes that may or may not favour bioaccumulation. Finally, unlike transport by air or water currents, which usually facilitate both the introduction and removal of contaminants, biological transport often lacks a viable loss route resulting in the amplification of contaminants in recipient ecosystems (Blais et al., 2007).

The degree to which biological transport contributes to the fate of a target contaminant depends on behavioural, morphological, physiological and life history traits of the biotransporting organism; on physico-chemical properties of the target contaminant; and, on the interaction between organism traits and contaminant properties (Table 1).

Organismal movement can either lead to the geographical focusing of contaminants in a particular recipient ecosystem that would otherwise be widely diluted across the landscape (´biovector transport´ according to Blais et al., 2007), or to dispersing contaminants that would otherwise be localized in concentrated donor ecosystems.

The amplification of contaminants in diluted donor ecosystems and focusing in recipient ecosystems

The geographical focusing of contaminants by biovector transport depends on three processes: (i) the collection and amplification of the contaminant from the donor ecosystem by the biovector, (ii) biovector transport to the recipient ecosystem , and (iii) deposition, release or transfer of the contaminant at the recipient ecosystem (Blais et al., 2007).

Anadromous fish provide one of the best examples of the massive transport of nutrients and contaminants across ecosystem boundaries. Pacific salmon (*Oncorhynchus* spp) acquire more than 95% of their biomass in the sea and return to natal streams and lakes in mass migrations to spawn. Because salmon are semelparous, the transfer of matter across marine and headwater systems is total. They are estimated to annually transport 305-606 million tons of biomass of marine origin to headwaters in the Pacific Northwest (Gresh, Lichatowich & Schoonmaker, 2000).

Pacific salmon, as top predators, are also efficient amplifiers of biomagnifying contaminants in marine food webs. In sockeye salmon, bioconcentration from water and biomagnification up the food chain can increase polychlorinated biphenyl (PCB) concentrations from 1 ng/L in seawater to 670,000 ng/kg lipid prior to migration. During the upstream migration, consumption of lipid reserves for energy and gonad maturation further increases PCB concentrations to 2,500,000 ng/kg lipid (a 7-order magnitude increase). Similarly, mercury (Hg) and dichlorodiphenyltrichloroethane (DDT) concentrations increase 6 and 9 orders of magnitude, respectively, in salmon lipid relative to seawater (Ewald, Larsson, Linge, Okla, & Szarzi, 1998; Sarica, Amyot, Hare, Doyon, & Stanfield, 2004).

Environmentally relevant focusing of contaminants then occurs because a large number of sizeable individuals, each carrying contaminant doses many orders of magnitude above environmental levels, migrate to specific headwater streams and lakes and die. Salmon may contaminate headwaters, sediment and resident biota including algae, zooplankton, benthic macroinvertebrates, young salmon, smolts, and various fish species as well as nearby terrestrial organisms such as calliphorid flies, bald eagles, and bears. Such transfer occurs either indirectly via the base of the food web after salmon biomass is decomposed and mineralized, or directly via predation and/or scavenging (Ewald et al., 1998; Sarica et al., 2004; Gregory-Eaves et al., 2007).

Comparable focusing of contaminants results from the activity of seabirds that congregate in breeding colonies, thereby depositing thousands to millions of kg of guano sometimes contaminated with DDT, DDE (dichlorodiphenyldichloroethylene), HCH (hexachlorocyclohexane), PCBs, polychlorinated naphthalenes, and brominated flame retardants of marine origin every year (Blais et al., 2007). Similarly, scarlet ibises transfer Hg used in gold mining in coastal South America, possibly through shedding feathers, to protected mangrove reserves in Trinidad. There, increased Hg contamination of sediments under roosters are correlated with increased mutation rates in mangrove trees (Klekowski, Temple, Siung-Chang, & Kumarsingh, 1999).

These impressive cases of massive transport and focusing of contaminants to otherwise pristine locations results from a combination of properties of the contaminant, such as environmental persistence and biomagnification, and traits of the dispersing species, such as gregarious, migratory behaviour with highly specific spatial targets (Table 1).

<u>The diffuse dispersal of contaminants from concentrated point source-donor ecosystems</u>

In reverse, biotransporters can accelerate the removal of contaminants from donor ecosystems. In fact, this may be a more common phenomenon both because it does not require gregariousness, coordinated migration, or selectivity of the migration target by the biotransporter and also because complex life cycles with obligatory niche shifts across ecosystem boundaries are common in the animal kingdom. Indeed, insect metamorphosis and emergence can provide important resource subsidies from aquatic to terrestrial ecosystems, often exceeding the spatial scale of subsidies generated by hydrological processes (Muehlbauer, Collins, Doyle, & Tockner, 2014). Metamorphosing stream insects have been shown to export PCBs and Hg from contaminated streams to the riparian zone and its insectivore community (Runck, 2007; Cristol et al., 2008; Walters et al., 2008; Raikow, Walters, Fritz, & Mills, 2011). Midges, in particular, appear to be keystone in the removal and export of contaminants from polluted freshwater ecosystems through a combination of complex life cycle (and therefore obligatory emergence of adults), high potential secondary productivity, high demographic responsiveness to eutrophication, tolerance to hypoxia, and tolerance to environmental contamination (Runck, 2007; Raikow et al., 2011).

Albeit diffuse, organism-mediated contaminant dispersal can be both sizeable and widespread. Emerging aquatic insects were estimated to export 6.1 g/yr of PCBs from a 25-km stream section historically contaminated by a capacitor plant (Walters et al., 2008) and midges exported 41 g/yr of PCBs from the lake receiving water from a stream (Raikow et al., 2011). These amounts are comparable to the PCB mass delivered by 50,000 and 310,000 returning chinook salmon, respectively (Compton et al., 2006; Walters et al., 2008). Organism-mediated contaminant dispersal may also be widespread as comparable scenarios of industrial pollution are found in drainage networks around the world. For example, 166, 123 and 129 thousand stream km and 3.2, 0.4 and 1.2 million hectares of lakes, reservoirs and ponds are classified as ´impaired´ in the USA due to contamination with mercury, other metals and PCBs (US EPA, 2015).

Indirect Dispersal Effects

Dispersing organisms that act primarily as contaminant processors can influence contaminant fate upon colonization of the recipient ecosystem (Fig. 1). Zebra mussels (*Dreissena polymorpha*) invaded the Great Lakes in 1986 and, because of remarkably high population densities (up to 700,000 individuals per square meter) and individual filtration rates (~1L per individual per day), were estimated to filter the entire volumes of Lake Saint Clair, Lake Erie and Lake Ontario in as little as 3, 5 and 333 days, respectively (Bruner, Fischer, & Landrum, 1994; Vanderploeg et al., 2002). By means of water, phytoplankton and suspended particle filtration, zebra mussels were found to rerout dissolved and particle bound contaminants including PCBs, DDT and PAHs (polycyclic aromatic hydrocarbons) from pelagic to benthic food webs through the production of feces or pseudofeces (Bruner et al., 1994; Gossiaux, Landrum, & Fisher, 1998).

Alternatively, dispersing organisms can influence contaminant fate in recipient ecosystems if upon colonization they change the abundance of biotransporters or processors. As with zebra mussels, various macrophyte species can be keystone contaminant processors in freshwater ecosystems. Indeed, the importance of macrophytes is so well established that they are used for remediation of waste sites and for wastewater treatment in constructed wetlands. Macrophytes can influence contaminant fate through uptake and subsequent elimination, accumulation and/or volatilization. Macrophytes can also influence contaminant fate by increasing structural complexity and thereby reduce water flow, trapping particles and associated nutrients and contaminants. Furthermore, macrophytes influence key abiotic properties such as dissolved oxygen and organic carbon, and serve as substrate for bacteria, fungi and periphyton communities, which themselves influence contaminant fate (Moore et al., 2011).

It follows that the dispersal of herbivores could have major indirect effects in local contaminant dynamics via macrophyte consumption. Wetlands occupy only 3.8% of the Earth´s land surface, yet are responsible for 20 to 39% of the global emissions of methane (CH_4), a powerful greenhouse gas (IPCC, 2007). Because decomposing macrophyte litter and root exudates provide organic carbon for the production of methane by methanogenic bacteria, high macrophyte production is associated with high methane production. Interestingly, the fate of produced methane is strongly influenced by macrophyte functional type composition and the intensity of herbivory (Laanbroek, 2010; Dingemans, Bakker & Bodelier, 2011). Emergent macrophytes function as a gas conduit facilitating the escape of methane from sediments to the atmosphere via the aerenchyma. This effect can be greatly exacerbated by waterfowl herbivory, as the per-unit area diffusive methane flux to the atmosphere is up to 5 times greater in reed plots grazed by waterfowl than in ungrazed exclosures or in plots with no plants (Dingemans et al., 2011). This occurs because clipping the aerial parts reduces resistance to gas flux. Rhizome and tuber grubbing also regulate methane emissions. Waterfowl grubbing activity reduces wetland CH_4 emissions to the atmosphere both directly through bioturbation – which, by increasing sediment oxygenation reduces the activity of the anaerobic methanogenic bacteria and increases CH_4 oxidation into CO_2 by aerobic NH_3-oxidizing bacteria – and indirectly by reducing macrophyte density and therefore methane production (Bodelier, Stomp, Santamaria, Klaassen, & Laanbroek, 2006).

Herbivore movement patterns can generate widely different spatial signals in contaminant processing. The predictable movements of gregarious migratory waterfowl, yearly returning to the same summer breeding grounds, staging areas and wintering grounds translate into massive and sustained damage to macrophytes. Snow geese (*Chen caerulescens caerulescens*), for example, congregate in tens to hundreds of thousands of individuals, denuding marsh vegetation, creating large openings and exposing underlying glacial gravels (Kerbes, Kotanen, & Jefferies, 1990). This contrasts with the diffuse movements of dispersal-limited herbivores. The rusty crayfish *Orconectes rusticus,* for example, introduced in many lakes surrounding its native range in the Ohio River Drainage by anglers spread steadily over years to decades resulting in macrophyte depletion over broad areas of the landscape rather than the focused impacts of migrating waterfowl (Wilson et al., 2004).

Modulating contaminants could influence the magnitude of direct and indirect dispersal effects

Modulating contaminants could influence the magnitude of direct and indirect dispersal effects by affecting the probability that a dispersing individual reaches the recipient ecosystem – for example by altering movement behaviour, locomotion, and homing ability. In fact, effects of contaminants on movement behaviour and locomotion are so widespread that they are the most widely used behavioural biomarkers of effect (Little & Finger, 1990; Dew, Wood & Pyle, 2012). Contaminants may influence the rate, location and circadian pattern of activity, the propensity for exploring the environment, and physiological attributes that are key to animal movement, such as oxygen uptake, oxygen-carrying capacity of the blood, metabolism and energy budget (e.g., Marentette et al., 2012). Moreover, contaminants may have strong effects on spatial orientation, homing, and movement endurance, all necessary components in long distance migration. Classical experimental studies have shown that olfaction is the primary sensory mechanism by which salmon discriminate and reach natal headwaters during upstream migration (Scholtz, Horrall, Cooper, & Hasler, 1976). However, water-born contaminants including metals, pesticides, surfactants and hydrocarbons may disrupt olfactory-based responses in fish by acting as signals, modifying odor perception, and/or acting on neural or physiological responses (Baldwin, Sandahl, Labenia, & Scholz, 2003; Tierney et al., 2010; Dew et al., 2012). For example, reduced homing rates were recorded for chinook salmon exposed for

24h to the acetyl-cholinesterase inhibiting insecticide diazinon, at concentrations observed in many salmon rivers (Scholz et al., 2000). Thus, a modulating contaminant can alter the fates of target contaminants that are transported from marine to headwater ecosystems. Other than that, long distance migrations are energetically costly and require the accumulation of large lipid stores via hyperphagia. Organochlorine pesticides such as dieldrin and other cyclodienes inhibit GABA, a neuroreceptor linked to appetite stimulation, causing anorexia and weight loss in a variety of bird species, including migrating waterfowl (Elliott & Bishop, 2012) with consequent effects on dispersal success. Because movement behaviour can be extremely sensitive to environmental contamination, manifesting at concentrations well below water quality standards (Dew et al., 2012), it is likely that contaminant-induced changes in movement behaviour are widespread in human dominated waterways where a plethora of contaminants exist. Another way by which modulating contaminants can influence the probability a dispersing individual effectively reaches a recipient ecosystem is habitat selection. Gray treefrogs, for example, avoid ovipositing in water contaminated with pesticides (Vonesh & Buck, 2007).

Alternatively, modulating contaminants could influence the magnitude of direct or indirect dispersal effects by increasing or decreasing the population growth rates of a dispersing species. This would occur anytime that a dispersing species is simultaneously exposed to at least two contaminants (that is, a target contaminant and a modulating contaminant), and is more sensitive to some contaminants (i.e. the modulating contaminant) than to others (i.e. the target contaminant). Both conditions are commonly satisfied: on one hand, exposure to contaminant mixtures is a widespread scenario in human dominated environments; while on another, species sensitivity to chemicals varies widely.

Eutrophication, a common environmental scenario, may cause indirect contaminant effects, with nutrients assuming a role of modulating contaminants. Runck (2007) found remarkably high production of *Cricotopus* midges (479 kg AFDM/yr in a 2.1 km stream section) in streams subject to wastewater contaminated with Hg and other metals. This occurred because the warm, illuminated and nutrient-rich water led to an abundance of nutritious periphyton, but also because *Cricotopus* appeared to be more tolerant to metal contamination than the pollution-intolerant mayflies (Ephemeroptera), stoneflies (Plecoptera) and caddisflies (Trichoptera). Without interspecific competition, *Cricotopus* dominated the assemblage with 96% of all macroinvertebrates (Runck, 2007). Through the ingestion of Hg-contaminated periphyton as larvae and subsequent emergence of metamorphosing adult, it was estimated that *Cricotopus* exported 4.1 g Hg(II)/yr to the riparian zone (Fig. 2).

Networks of Effects

Above we highlight the distinct ways direct and indirect dispersal effects can work independently of each other, and how their magnitude could be influenced by modulating contaminants. However, these mechanisms may work in concert and under the influence of other ecological processes, and therefore it may be useful to think of them as elements in a larger network of causal effects influencing local contaminant fate.

This is illustrated by recent studies linking freshwater community structure and the contamination of terrestrial food webs by methyl-mercury (MeHg) (Tweedy, Drenner, Chumchal, & Kennedy, 2013; Buckland-Nicks, Hillier, Avery, & O´Driscoll, 2014; Chumchal & Drenner, 2015). Highly toxic and biomagnifying MeHg is not normally produced in terrestrial systems; instead, it results from the methylation of inorganic mercury of atmospheric origin by iron- and sulfur-reducing bacteria in freshwater sediments. Contamination of terrestrial food webs is thus largely dependent on a water-to-land export of MeHg by biotransporters, but this export is strongly regulated by freshwater community structure. In semi-permanent ponds, dragonfly and damselfly (Odonata) naiads are top predators accumulating very high MeHg tissue concentrations; upon metamorphosis dragonflies effectively export MeHg to terrestrial food webs. By contrast, in permanent ponds, strong size-selective predation by fish suppresses MeHg export by large insects. Comparatively small amounts of MeHg mercury export occurs via the emergence of small and usually lower-trophic level taxa such as chironomids and mosquitos, and instead MeHg tends to recirculate in the system via fish biomass decomposition. Overall, there is up to 5 times greater insect-mediated MeHg export in fishless than in fish ponds (Tweedy et al., 2013). Finally, in fishless temporary ponds, insect-mediated MeHg export is even smaller because only small and usually lower-trophic level taxa such as chironomids and mosquitoes emerge (Fig. 3).

Interestingly, because food web structure changes over space and time, so does the potential for MeHg export. On one hand, winterkills, eutrophication-mediated harmful algal blooms and oxygen depletions eliminate fish; on another, erosion and siltation transform permanent ponds into semi-permanent and temporary ponds (Chumchal & Drenner, 2015). The keystone biological agents, however, differ widely in colonization ability: fish are strongly dispersal-limited whereas dragonflies are highly mobile. Therefore, an increase in the production and export of MeHg to terrestrial systems is expected both by the globally high rates of pond construction (Downing et al., 2006) and the net tendency for fish elimination in such small artificial ponds.

Such a complex scenario involving both direct (emerging insect MeHg export) and indirect (food web structure regulating MeHg export) dispersal effects most likely also involves chemical modulation. The Texas Great Plains where the abovementioned studies were conducted is subject to widespread contamination from agriculture and cattle ranching (TCEQ, 2008, 2011). Chemical modulation of organismal dispersal are plausible outcomes as detected insecticides carbaryl and imidacloprid (TCEQ, 2008) increase fluctuating asymmetry in dragonfly wings (Hardersen & Wratten, 1998) and affect insect navigation, olfactory learning and memory, visual learning, motor function and postural control (Williamson, Willis & Wright, 2014). Likewise, chemical modulation of dispersing organism population growth rates are plausible outcomes as well as larval odonate production is increased by nutrient enrichment (90% of Texas reservoirs are either eutrophic or hypertrophic; TCEQ, 2008) but reduced by detected insecticides carbaryl (Hardersen & Wratten, 1998), imidacloprid, and fipronil (Jinguji, Thuyet, Uéda, & Watanabe, 2013).

Conclusions

The environmental fate of chemical contaminants depends on a complex suite of physical, chemical and biological processes. Yet, except for contaminant amplification, most previous work has ignored or greatly simplified the biological component. Here we propose an organizing scheme for how organismal movement can influence both the spatial dynamics and local transformation of contaminants. New insights appear as we bring together these two previously unrelated areas of ecology in what should be fundamentally seen as a question of 'applied metaecosystems ecology´ (Loreau et al., 2003; Massol & Petit 2013; Harvey, Gounand, Ward, & Altermatt, 2017). First, that animal transport may be the most important non-human agent of upgradient movement of contaminants in the landscape, as well as of products that easily degrade outside of living tissues. Second, that animals can be important agents in focusing as well as dispersing contaminants in a landscape, and that species traits may give us hints as to how strong these effects can be, and what species to look at. Third, that contrary to most previous work in metaecosystems ecology focused on nutrients and/or energy, contaminant transport may not be proportional to the movement of biomass of the usual organismal categories (trophic levels or functional groups). In other words, because organisms can vary so dramatically in their contaminant loads given processes such as bioamplification, asymmetries in exchanges between ecosystems can depend on species that may be uncommon or have distinct movement ecologies. There again, species traits and contaminant properties may help us identify when such asymmetries are more likely to be important. Finally, all these effects may interact with each other in a complex network of causal relations that can affect the fates of contaminants both at the local and landscape scale. Overall, then, the establishment of such connections contributes to narrowing the gap that exists between ecology and ecotoxicology.

This conceptual approach can have several applications for environmental management, monitoring, and research policy:

Implications for environmental management. If we recognize that contaminants can be exported from freshwater to terrestrial ecosystems via animal movement, and that such an export can be exacerbated by nutrient pollution, then we may be ignoring environmental impacts associated with the globally widespread trend of artificial wetland construction (Downing et al., 2006; Mitsch & Gosselink, 2015). Constructed wetlands include farm ponds, wetlands for compensatory mitigation, and treatment wetlands for nutrient pollution, domestic wastewater, mine drainage, stormwater runoff, landfill leachate, and confined livestock operations; not to mention the confined disposal facilities for contaminated dredged material in ports, maintenance projects or mines. Many of these are meant to act as nutrient and/or contaminant sinks but could conceivably become relevant exporters of contaminants via organismal attraction, production, activities and further movement - thereby becoming ´attractive nuisances´ in the landscape. Interestingly, whereas several governmental programs promote, encourage or fund wetland creation (Mitsch & Gosselink, 2015), we know of no program or research agenda monitoring their potential role as contaminant exporters. If such exports are found to be sizeable and/or if the contaminant under consideration is highly hazardous, then risk management might include controlling organismal movement in the landscape, if at all possible, or preventing colonization of important sources by keystone animal species. For example, automated bird hazing devices have been used to avoid birds landing in contaminated areas such as oil spills (Gorenzel & Salmon, 2008) or heavily polluted Superfund Sites (such as the Rocky Mountain Arsenal; State of Colorado, 2007). Although these were intended to protect the birds, they may be just as important in mitigating their effects as dispersers of contaminants across ecosystems or processors of contaminants in the ecosystem.

Recommendations for better models and monitoring. Contaminant fate models rarely build on detailed local data on contaminant loads or community structure; many extrapolate scenarios of exposure and bioaccumulation from water or sediment contaminant loads alone (MacKay & Arnot, 2011; Suhring et al., 2016). Not surprisingly then, even less frequent is the consideration of animal movement as source of upgradient dispersal of contaminants or as a source of error in interpreting correspondence between organism and environment contaminant loads. In the first case, ignoring animal-mediated contaminant transport may have already proved to be problematic. Salmonines introduced for recreational fisheries in the heavily polluted Great Lakes were later found to transfer a variety of persistent organic pollutants (POPs) to tributaries via upstream spawning migrations. Not only was the upstream transport of POPs unanticipated, but it resulted in the contamination of resident brook trout, a species avidly sought by fishermen that is not regularly assessed for contaminant levels to establish health consumption advisories (Janetski et al., 2002). In the second case, many monitoring programs present a mismatch between the scale of fate analysis and the home range of monitored organisms. For example, at ´Superfund´ sites the effectiveness of remediation is assessed by comparing contaminant levels in sediments and fish before and after remediation, with the expectation that fish tissue contaminant levels will improve after sediment remediation. However, since fish move and are exposed to many other areas and pollution sources there is rarely a relationship between site contamination and fish tissue levels (NRC, 2007).

Recommendations for better research policies. Finally, scientists and the general public alike would be surprised to know how little funding exists for studies on the environmental impacts of contaminants. They amount to only 2.6% of all funds given by the US National Science Foundation, who asserts this is responsibility of other federal agencies. However, the US Department of Agriculture funds research on the beneficial but not adverse effects of agrochemicals, whereas the Environmental Protection Agency extramural funding, which declined steadily since the 1980s, is mostly geared towards human health and climate change (Burton, Giulio, Costello, & Rohr, 2017). Taking the USA as an example, thus, it is of paramount importance that new funding programs (possibly co-funded across agencies) bridging the knowledge gaps between ecology and ecotoxicology are created. This would enable important advances in real-world issues such as the ones we are addressing here; but that now would not be funded.

The next step in improving our understanding of how biotic interactions involving dispersal influence the fate of contaminants is make these ideas quantitative and explore their consequences more fully using modelling. Some of the important considerations in developing these models include an evaluation of the consequences of (i) contaminant properties such as fugacity constants, and bioaccumulation (BAF) and biomagnification factors (BMF) (ii) individual-level and population-level parameters governing the effectiveness of the dispersing organisms as biotransporters (detailed in Table 1), processors or intermediate interacting species (iii) relaxing the assumption that organisms act either as biotransporters or processors (i.e. exploring an overlap in the roles performed by the organism), or that contaminants act either as target or modulating contaminants (i.e., exploring an overlap in the roles of contaminants, such as the contaminant both affecting and being affected by the ability of the organism to transport or process contaminants); and, finally, (iv) interactions between the abovementioned attributes and landscape characteristics, such as connectivity and matrix permeability, affecting the dynamics of contaminants in spatially structured landscapes.

Authors´ Contributions

L.S. and M.A.L. conceived the original scientific idea. All authors contributed to literature review and to manuscript writing, and gave final approval for publication.

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Data accessibility

Data have not been archived because this article does not use data.

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Figure 1. *The two mechanisms by which organismal dispersal influences the fate of a target contaminant (three-point star) in local ecosystems. Direct dispersal effects occur when individuals of a biotransporter organism (triangle) transport, in their biomass, target contaminants from a donor ecosystem to a recipient ecosystem. Predation, scavenging and/or decomposition of the dispersing individuals eventually transfer target contaminants to other organisms (diamond) in the recipient ecosystem. Indirect dispersal effects occur when dispersing species influence local contaminant fate via community assembly. This can happen either because the dispersing species is a contaminant processor (square) or because, upon arrival, the dispersing species alters the abundance of a contaminant biotransporter (not shown) or of a contaminant processor (square) via species interactions.*

Figure 2. *In scenarios of exposure to contaminant mixtures, one contaminant (a ´modulating contaminant´) can have an effect on the environmental fate of another (the ´target contaminant´) through effects on the population growth rate of the dispersing species. Nutrients could commonly act as modulating contaminants both in urban (sewage) and rural (fertilizer) environments. In streams subject to release of process wastewater contaminated with mercury, nutrient supplementation strongly influences the per-unit area export of mercury by emerging midges (after Runck, 2007). Black arrows represent the flow of biomass, red arrows represent the flow of mercury; curved arrows represent the biological export of biomass and MeHg to terrestrial ecosystems via insect emergence.*

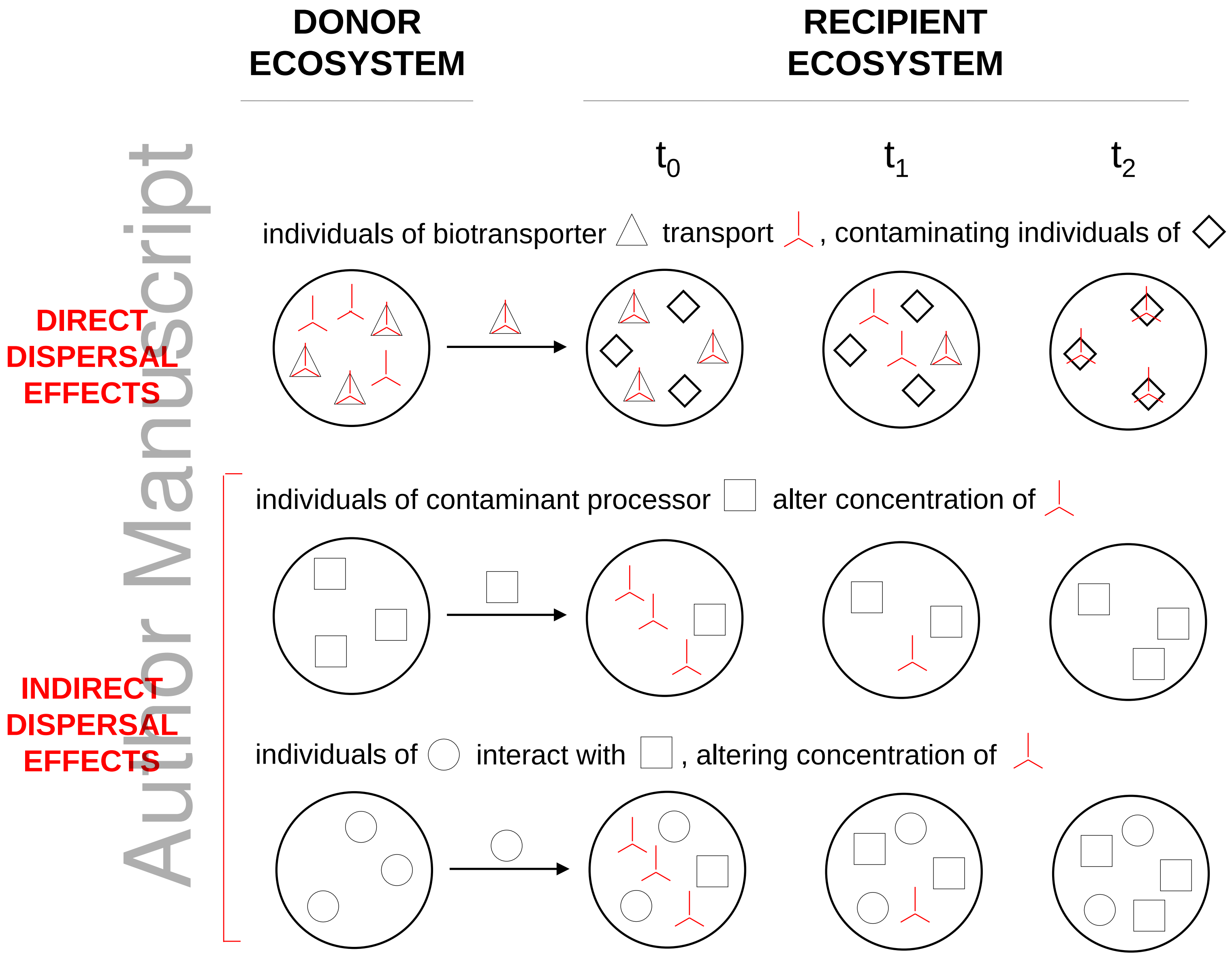
Figure 3. *The influence of food web structure on the fate of methylmercury in ponds distributed across a gradient of hydroperiod. Black arrows represent the flow of biomass, red arrows represent the flow of mercury; curved arrows represent the biological export of biomass and MeHg to terrestrial ecosystems via insect emergence. Based on Henderson et al. (2012), Jones et al. (2013), Tweedy et al. (2013), and Chumchal and Drenner (2015).*

Table 1. *Species traits and contaminant properties favoring a strong contribution of biological transport of contaminants in metaecosystems. In this Table the relationship between trait and property states and biological transport of contaminants is considered in isolation (that is, ´all else being equal, state 1 should favor a significant role of biological transport of contaminants´), but in many cases covary. For example, predators tend to have larger body sizes, greater longevity and greater dispersal abilities than their prey (positive correlations among several of the abovementioned traits). If compounds biomagnify, predators could have contaminant loads many orders of magnitude greater than background environmental levels, or than that of other organisms. Because of high dispersal ability, they could be effective vectors for the dispersal of contaminants at broad spatial scales. Moreover, because of high mobility they could have high selectivity/specificity of sites where these contaminants are released.*

	NEGATE biological transport of contaminants	**FAVOR biological transport of contaminants**	**Justification**
Organismal traits			
Mobility	sessile, stationary or philopatric	vagile, migratory	Mobility and propensity to dispersal are required for biological transport of contaminants.
Propensity to dispersal	low	high	
Selectivity of dispersal target	low	high	High selectivity of dispersal target increases potential contaminant loading in recipient ecosystems (focusing).
Sociality	solitary	gregarious	Gregarious behavior and dominance in community increase potential contaminant loading in recipient ecosystems.
Dominance in community	low	high	

Breeding strategy	iteroparous	semelparous	When habitats used for breeding are different than habitats used for contaminant amplification and growth, export of contaminants is total in semelparous organisms due to obligatory mortality following reproductive event.
Life cycle	simple life cycle	complex life cycle	Metamorphosis is usually associated with habitat shifts, therefore satisfying the conditions ´mobility´ and ´propensity to dispersal´.
Trophic level	low	high	For biomagnifying contaminants, contaminant concentration increases with trophic level.
Age	young	old	Age and lifespan usually correlate with total and per-unit-biomass contaminant body loads by length of exposure to contaminant.
Lifespan	short	long	
Body mass	small	large	For a given tissue concentration of contaminant, larger body loads will be found in larger individuals; body mass also correlated with mobility, age and lifespan.
Growth rates	fast growth	slow growth, starvation, tissue catabolism	Faster growth leads to greater biomass and therefore more contaminants per individual in absolute terms; however, faster growth tends to promote contaminant dilution and therefore less contaminant per individual in relative terms.
Population growth rate	low	high	High population growth rate and secondary productivity lead to more biomass to transport the contaminant; however, as above, tendency for contaminant dilution.
Productivity	low	high	
Contaminant properties			

Environmental persistence	low	high	Relevance of biological transport increases with the contaminant being persistent or, if not persistent, continuously pumped in the environment as a subsidy.
Supply of contaminants	pulsed	continuous	
Bioaccumulation potential	low	high	Contaminant amplification (through bioconcentration, bioaccumulation, biomagnification) in organisms is required for effective biological transport.
Biomagnification potential	low	high	
Bioconcentration factor	low	high	
Mobility	high	low	Highly mobile or volatile contaminants are more likely to be subject to physical than biological transport.
Volatility	high	Low	
Lipophilicity	low or high	intermediate	Log half life (i.e. persistence), log assimilation efficiency and log biomagnification factors peak at intermediate log Kow (i.e. lipophilicity) (Fisk et al. 1998).
Interaction between organism and contaminant			
Body contaminant loads	low	high	
Biotransporter species sensitivity to pollutant	high	low	Sensitive species are unlikely to be effective biotransporters because are negatively affected by the contaminant. It follows that the more dissimilar the biotransporter is relative to the local community in terms of the sensitivity to contaminant, the highest the likelihood that biological transport will be relevant.
Similarity in species responses to pollutants	similar	dissimilar: biotransporters tolerant, other species intolerant	



DONOR ECOSYSTEM

RECIPIENT ECOSYSTEM

t_0 t_1 t_2

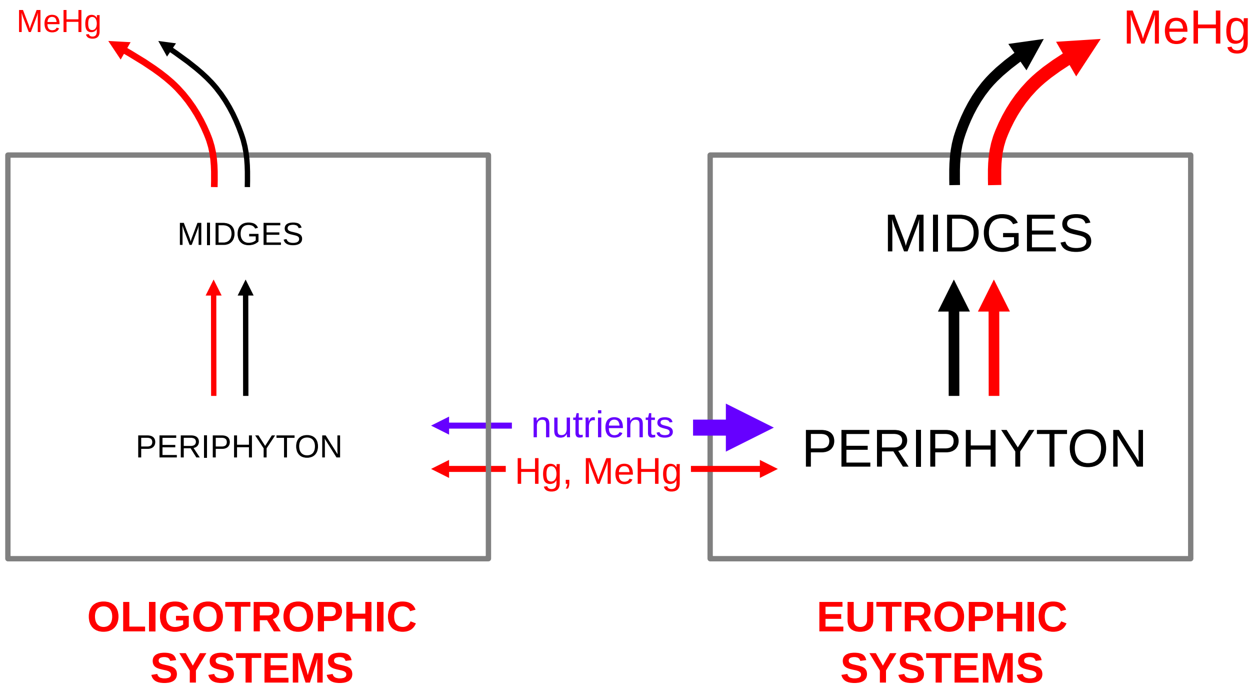
DIRECT DISPERSAL EFFECTS

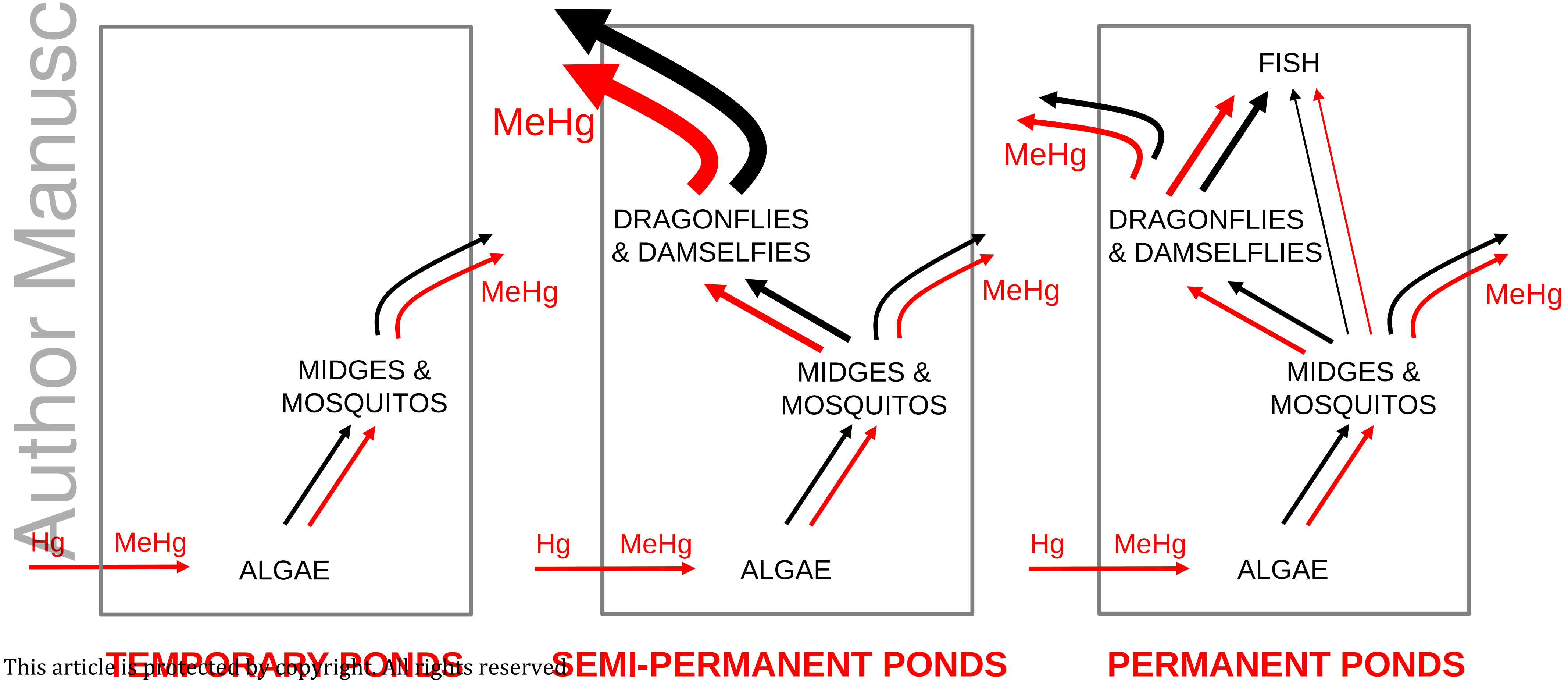
individuals of biotransporter △ transport ⅄, contaminating individuals of ◇

INDIRECT DISPERSAL EFFECTS

individuals of contaminant processor □ alter concentration of ⅄

individuals of ○ interact with □, altering concentration of ⅄


MeHg
MIDGES
PERIPHYTON
OLIGOTROPHIC SYSTEMS
nutrients
Hg, MeHg
MeHg
MIDGES
PERIPHYTON
EUTROPHIC SYSTEMS


Hg
MeHg
ALGAE
MIDGES & MOSQUITOS
MeHg
TEMPORARY PONDS
Hg
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MIDGES & MOSQUITOS
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DRAGONFLIES & DAMSELFLIES
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SEMI-PERMANENT PONDS
Hg
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MIDGES & MOSQUITOS
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DRAGONFLIES & DAMSELFLIES
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FISH
PERMANENT PONDS