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Pesticide alters habitat selection and aquatic community composition

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Abstract Anthropogenic chemical contamination is an important issue for conservation of aquatic ecosystems. While recent research highlights that community context can mediate the consequences of contaminant exposure, little is known about how contaminants themselves might determine this context by altering habitat selection and thus initial community composition. Here we show that the insecticide carbaryl and its commercial counterpart Sevin can affect aquatic community composition by differentially altering oviposition and colonization of experimental pools by amphibians and insects. On average, contaminated pools received 20-fold more adult beetle and heteropteran colonists and 12-fold more *Culex* mosquito and chironomid midge egg masses. On the other hand, ovipositing *Anopheles* mosquitoes and cricket frogs showed no preference and we have shown previously that gray treefrogs strongly avoid contaminated pools. Overall, initial richness doubled in contaminated pools compared with controls. By affecting colonizing taxa differently and increasing richness, the contaminant may alter the ecological context under which subsequent effects of exposure will unfold. Given that community context is important for evaluating toxicity effects, understanding the net effects of contaminants in natural systems requires an understanding of their effects on community assembly via shifts in habitat selection.

Keywords Carbaryl · Community assembly · Insecticide · Oviposition · Colonization

Introduction

Chemical contamination is an important threat to aquatic biodiversity (Wilcove and Master 2005), and has been associated with increased disease (Johnson et al. 2007; Kiesecker 2002; Rohr et al. 2008), reproductive abnormalities (Hayes et al. 2002) and population declines (Davidson 2004; Davidson et al. 2002) of non-target aquatic species. Although toxicological studies historically focused on single-chemical, single-species direct toxicity tests conducted in a laboratory setting, there is now a large and growing literature which examines the effects of contaminants on multispecies assemblages (Boone et al. 2004; Kreutzweiser et al. 2002; Relyea et al. 2005; Rohr and Crumrine 2005; Sibley et al. 1991). A number of these studies have enabled researchers to evaluate indirect effects of contaminants in aquatic communities and to test if community context alters toxicity (reviewed in: de Noyelles et al. 1994; Fleeger et al. 2003; Relyea and Hoverman 2006; Rohr et al. 2006). Collectively, these studies highlight that although environmentally realistic concentrations of contaminants can directly alter species' abundance, behavior and physiology, community context plays an important role in shaping these contaminant effects (Relyea et al. 2005; Rohr and Crumrine 2005). For example, laboratory and mesocosm experiments

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have revealed dramatic synergistic interactions between insecticide exposure and biotic stressors (i.e., predation and competition) in tadpoles (e.g., Boone and Semlitsch 2001; Boone et al. 2004; Relyea 2003; Relyea and Mills 2001; Semlitsch et al. 2000). Largely overlooked is the potential for contaminants themselves to play an important role in creating initial community context by influencing how taxa choose to colonize aquatic habitats.

The colonization and oviposition behavior of dispersing adults of many freshwater aquatic species (e.g., aquatic insects and amphibians) plays an important role in the assembly of individual aquatic communities (Resetarits et al. 2005). While most meta-population and meta-community theory assumes that colonization occurs randomly (Gotelli and Kelly 1993; Hanski and Gilpin 1997; Holyoak et al. 2005), empirical evidence suggests that this is often not the case. Many aquatic taxa, including species of anurans (Resetarits and Wilbur 1989), salamanders (Kats and Sih 1992), water boatmen (E. A. Garcia, unpublished data), midges (Petranka and Fakhoury 1991), phantom midges (Garcia 2006), mosquitoes (Chesson 1984), and beetles (Binckley and Resetarits 2005), have been shown to exhibit strong preferences during colonization and oviposition. These preferences may be in response to variation in biotic (e.g., Marsh and Borrell 2001; Resetarits and Wilbur 1989) or abiotic factors (e.g., Spieler and Linsenmair 1997; Viertel 1999), including anthropogenic chemicals (Vonesh and Buck 2007; Xue et al. 2006).

Anthropogenic chemicals have been shown to strongly deter oviposition in single-species studies of habitat selection. For example, several studies from the vector control literature show that commercial insect repellants can alter oviposition by mosquitoes. Xue et al. (2001; 2003; 2006) show that 18 of 21 commercial insect repellents tested in laboratory trials deterred oviposition by *Aedes albopictus*. Furthermore, two recent studies show that pesticides can alter oviposition site selection in some amphibians. Takahashi (2007) showed that gray treefrogs (*Hyla chrysoscelis/versicolor*) completely avoid pools treated with the glyphosphate-formulated herbicide Roundup. Similarly, Vonesh and Buck (2007) show in a series of experiments that the insecticide Sevin and its active ingredient, carbaryl, also reduce oviposition in gray treefrogs across several spatial and temporal scales. Thus, while there is evidence that anthropogenic chemicals can affect habitat selection of aquatic taxa, it is unclear from these few single-species studies how these chemicals might alter the colonization or composition of entire communities.

Given the growing evidence that community context can determine the impact of contamination, it is important to understand if and how aquatic community assembly is altered by changes in habitat selection in response to contaminants. Although there is some evidence that chemicals can affect oviposition by individual taxa, no studies have thus far examined the effects of contaminants on the assembly of communities as a whole. Vonesh and Buck (2007) presented a series of four experiments that examined the effects of a common pesticide, carbaryl, on a single amphibian species. In this study, we provide community-level analysis of one of these experiments to examine the effects of carbaryl and the commercially available form, Sevin, on habitat selection by the entire assemblage of insects and amphibians colonizing and ovipositing in aquatic mesocosms. Carbaryl is a widely applied insecticide and can contaminate aquatic habitats via a variety of pathways (e.g., Edwards 1973; Relyea and Mills 2001; USDA 1989). This research increases understanding of how behavioral shifts in response to pesticide treatments could alter the ecological context under which the post-colonization effects of exposure will be played out.

Materials and methods

To examine the effect of the insecticide Sevin on colonization of aquatic habitats we manipulated the presence of the pesticide in experimental pools arrayed in the field at Tyson Research Center and then monitored subsequent natural colonization and oviposition by frogs and insects in these pools (Vonesh and Buck 2007, Experiment 4). The experiment was designed to compare the impact of both the active ingredient, carbaryl (1-naphthyl N-methylcarbamate), and solvent with the commercially available version of the insecticide. This required four treatments: water control (water addition; WAT), solvent control (acetone; ACE), carbaryl + solvent (CAR), and Sevin (SEV). These four treatments were replicated 9 times in 36 wading pools filled with 140 l of well water using a randomized block design with three spatial blocks of 12 pools each. The experiment ran from 30 June to 17 July 2006. Colonists were removed every 3–6 days (mean = 4.3) and identified to the lowest taxonomic level possible (Vonesh and Buck 2008). Dipteran clutches were sorted into culicid genera and chironomid morphotypes (J. Epler, personal communication; Nolte 1993). Frog eggs were resolved to species using a taxonomic key (Parmelle et al. 2002). Adult insects were identified to family or genus (Merritt and Cummins 1996) and then assigned to morphospecies (Derraik et al. 2002; Rohr et al. 2007).

In both the carbaryl + solvent and Sevin treatments, initial carbaryl concentrations were established at 7 mg/l to reflect concentrations used in several recent ecological toxicity studies to facilitate comparison across studies (Boone et al. 2001; Boone and Semlitsch 2002; Boone and Semlitsch 2003; Boone et al. 2004; Relyea 2003). Although more research is needed on peak levels of carbaryl in the environment, it is worth noting that our initial concentrations are higher than previously reported for agricultural ponds (~5 mg/l; Norris et al. 1983). The half-life of carbaryl can be variable; however, it typically breaks down rapidly in mesocosm settings (e.g., half life ~4 days, Boone and Semlitsch 2001). By adding an initial pulse of carbaryl at the beginning of the experiment which breaks down over time (Boone and Semlitsch 2001), most of the behavioral responses we measured over the duration of our experiment were likely at lower concentrations. See Vonesh and Buck (2007, "Insecticide concentrations") for additional discussion of factors that determine the breakdown of carbaryl. Previous studies using these methods show that carbaryl treatment has no effect on pool pH, temperature or dissolved oxygen concentration (Vonesh and Buck 2007).

We used a generalized linear mixed model (GLMM) framework (GLIMMIX procedure in SAS 9.1; SAS 2006; Wolfinger and O'Connell 1996) to test the fixed effect of pesticide treatment on colonization and oviposition in artificial pool habitats. Due to low numbers, data were summed over time instead of being treated as repeated measures. GLMMs fit statistical models to data using maximum and pseudo-likelihood where the response is not necessarily normally distributed and contains random effects (here, Block; Pinheiro and Bates 2000; Venables and Ripley 2002). Since our response data were counts, we assumed Poisson error distribution unless data were over-dispersed, in which case models were fit assuming a negative binomial error distribution (Ver Hoef and Boveng 2007; White and Bennetts 2005).

Results

All of the pools received colonists either in the form of eggs, egg masses or adults starting on the first sample date. A total of 87 adult insects, 26,682 frog eggs and 738 clutches of dipteran eggs colonized or were oviposited in the pools. Peak oviposition for amphibians, *Acris crepitans* (cricket frogs) and *Hyla chrysoscelis* (gray treefrogs), occurred between 7 and 13 July. Insect oviposition peaked between 30 June and 3 July and included *Culex* sp. and *Anopheles* sp. mosquitoes, and two morphospecies of chironomid. Peak adult insect colonization occurred 30 June–7 July and consisted of ten taxa, including seven morphospecies of Dytiscidae, one Hydrophilidae, one Gerridae and one Corixidae. The three most common predaceous diving beetles were *Copelatus* sp., *Laccophilus* sp., and *Acilius* sp.; other adult insects were not identified below the family level. These taxa commonly colonize both natural and artificial pools in the area (Shulman and Chase 2007; J. M. Chase, unpublished data).

Colonization by adult insects differed significantly among treatments ($F_{3,32} = 10.34$, $P < 0.001$; Fig. 1). Pools treated with Sevin received 22 times more adults on average than both the water and acetone treatments [Tukey honest significant difference (HSD) $P = 0.002$ for both; Fig. 1]. Pools treated with carbaryl received about 19 times more adults on average than both water and acetone treatments (Tukey HSD $P = 0.001$ for both; Fig. 1). Sevin and carbaryl (Tukey HSD $P = 0.96$) and water and acetone treatments (Tukey HSD $P = 1.00$) received similar numbers of adults. Although all ten adult insects tended to prefer to colonize contaminated pools, most taxa were not well enough represented to provide a powerful statistical test of their individual colonization patterns (Table 1). Statistical tests for individual taxa only revealed significant preference for contaminated pools in one dytiscid morphospecies ($F_{3,32} = 4.77$, $P = 0.007$; Table 1). Pooling the contaminated and uncontaminated results did not alter these results. However, if we assume that colonization by each species represents an independent event, it is highly unlikely that all ten taxa would prefer the carbaryl pools by chance (sign test, $P < 0.001$).

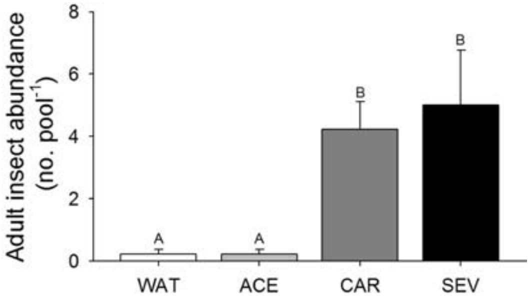

Fig. 1 Adult insect abundance (mean number per pool + 1 SE) of water (*WAT*)-, solvent control (acetone; *ACE*)-, carbaryl (*CAR*)- and Sevin (*SEV*)-treated pools at Tyson Research Center, St. Louis, Missouri, USA in 2006. Colonization varied significantly among treatments ($F_{3,32} = 10.34$, $P < 0.001$). CAR- and SEV-treated pools received higher abundance than both WAT and ACE controls (Tukey $P = 0.002$ for both); significant differences indicated by *different letters* above bars

Oviposition responses to pesticide treatments were varied. Similar to adult insects, *Culex* mosquitoes showed a preference for contaminated pools ($F_{3,32} = 7.46$, $P < 0.001$): there were about 26 times more *Culex* clutches in carbaryl pools than in controls (Tukey HSD $P_{ACE} = 0.008$, $P_{WAT} = 0.004$). Midges also showed a preference for contaminants [chironomid morphospecies 1 (chironomid 1) $F_{3,30} = 14.94$, $P < 0.001$; chironmid morphospecies 2 (chironmid 2) $F_{3,30} = 6.77$, $P = 0.001$; Fig. 2]. In this case, both carbaryl and Sevin pools received about an 8 times greater number of chironomid 1 egg masses on average than either control treatment (Tukey HSD $P < 0.001$ for all four comparison; Fig. 2). Chironomid 2 oviposition was 64 times higher in carbaryl pools compared to acetone controls (Tukey HSD $P = 0.03$), and trended towards more clutches in carbaryl than in water or Sevin ($P_{WAT} = 0.07$,

Table 1 Abundance (mean ± SD) per pool of adult colonists summed over the 23-day experiment ($n = 9$ tanks per treatment)

Taxa[a]	Treatment			
	Water	Acetone	Carbaryl	Sevin
Gerridae NS	0	0	0.1 ± 0.3	0
Corixidae NS	0.1 ± 0.3	0	0.3 ± 0.5	0
Hydrophilidae NS	0	0	0.2 ± 0.7	0
Dytiscidae				
Laccophilus sp.**	0.1 ± 0.3	0.1 ± 0.3	0.7 ± 1.2	1.8 ± 1.5
Acilius sp. NS	0	0.1 ± 0.3	0.2 ± 0.4	0.6 ± 0.9
Copelatus sp. NS	0	0	1.9 ± 2.1	1.9 ± 3.5
Species 4 NS	0	0	0.2 ± 0.4	0.3 ± 0.7
Species 5 NS	0	0	0.3 ± 0.7	0.2 ± 0.7
Species 6 NS	0	0	0.2 ± 0.7	0.1 ± 0.3
Species 7 NS	0	0	0	0.1 ± 0.3

Raw data are presented

** $P < 0.01$

[a] Each taxon represents one morphospecies within each family

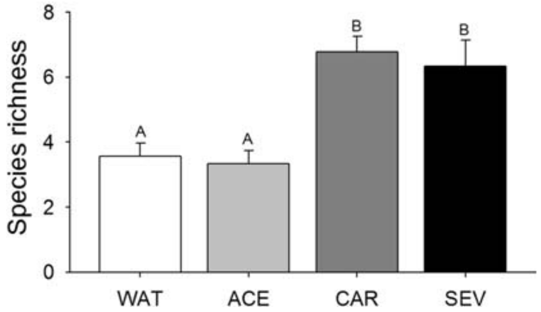

Fig. 3 Species richness (mean number of taxa per pool + 1 SE) colonizing or ovipositing in WAT-, solvent control (ACE)-, CAR- and SEV-treated pools. Taxa resolution is to species for frogs, genera for mosquitoes (*Culex* = 3 spp., *Anopheles* = 2 spp.), and morphospecies for Chironomidae (two), Dytiscidae (seven), Gerridae (one), Hydrophilidae (one), and Corixidae (one). Richness varied significantly among treatments ($F_{3,30} = 13.55$, $P < 0.001$). SEV- or CAR-treated pools received higher taxa richness than both WAT and ACE controls (Tukey, $P < 0.002$ for all). *Different letter* above bars indicate statistically different means. For abbreviations, see Fig. 1

$P_{SEV} = 0.052$). Some ovipositing taxa did not respond to the insecticide. Cricket frogs (*Acris crepitans*) and *Anopheles* mosquitoes did not lay eggs or clutches differentially by treatment (*Acris* $F_{3,30} = 1.00$, $P = 0.41$; *Anopheles* $F_{3,30} = 0.29$, $P = 0.83$; Fig. 2). Oviposition responses were similar within the contaminated and control treatments: Sevin and carbaryl (Tukey HSD, *Acris* $P = 1.00$, *Culex* $P = 0.32$, chironomid 1 $P = 1.00$, chironomid 2 $P = 0.052$) and water and acetone (*Acris* $P = 0.87$, Culex $P = 0.81$, chironomid 1 $P = 0.97$, chironomid 2 $P = 0.98$) received similar numbers of eggs. Including block as a random effect improved model fit for all taxa except *Culex* sp.

Finally, richness, as measured by number of colonizing and ovipositing morphotypes, differed significantly among treatments ($F_{3,30} = 13.55$, $P < 0.001$; Fig. 3). Pools treated with Sevin or carbaryl received about twice the number of taxa than both water and acetone controls (Tukey, $P < 0.002$ for all four comparison; Fig. 3).

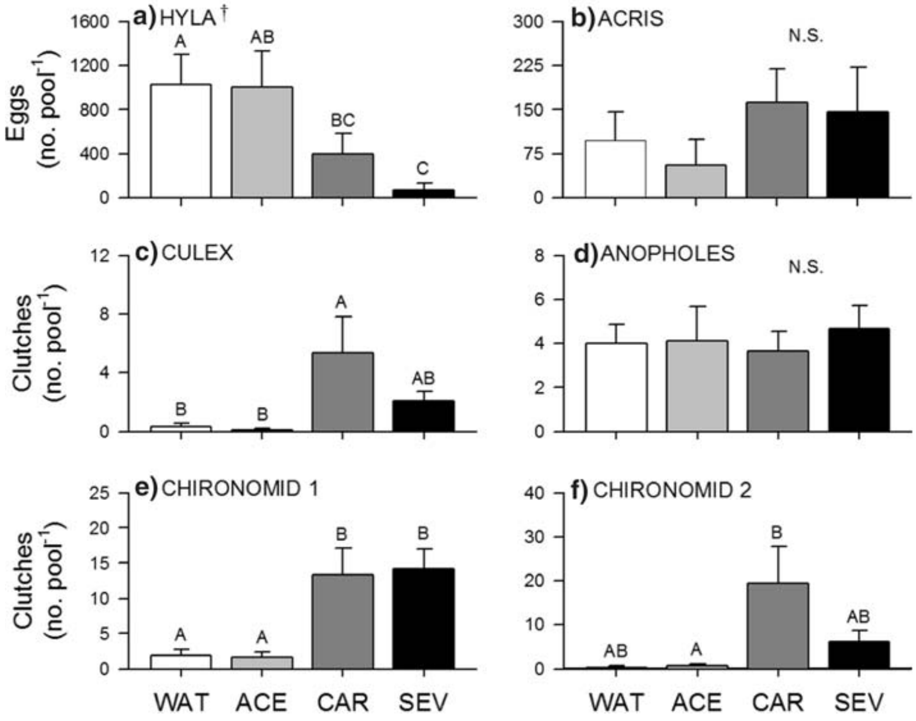

Fig. 2 Eggs or clutches (mean number per pool + 1 SE) oviposited in WAT-, solvent control (ACE)-, CAR- and SEV-treated pools for **a** *Hyla chrysoscelis* (*HYLA*) († data replotted from Vonesh and Buck 2007); **b** *Acris crepitans* (*ACRIS*); **c** *Culex pipiens*, *Culex restuans*, *Culex salinarius* (*CULEX*); **d** *Anopheles punctipennis*, *Anopheles quadrimcaulatus* (*ANOPHELES*), **e** chironomid morphospecies 1 (*CHIRONOMID 1*) and **f** chironomid morphospecies 2 (*CHIRONOMID 2*). Species of chironomids are unknown. *Different letters* above bars indicate statistically different means (Tukey, $P < 0.05$), *NS* indicates no significant treatment differences. For other abbreviations, see Fig. 1

Discussion

Despite a growing understanding of the effects of contaminants on aquatic communities, almost nothing is known about how contaminants alter the colonization component of community assembly. The importance of filling this gap in our understanding of contaminant effects on aquatic communities has been highlighted in recent literature (Relyea and Hoverman 2006; Rohr et al. 2006; Vonesh and Buck 2007). In the current study, we found that a common pesticide, carbaryl, can change the composition and increase diversity of the initial community in open experimental mesocosms by altering habitat selection simultaneously in multiple taxa. Colonization and oviposition of many insect taxa increased in contaminated pools, while other insects and cricket frogs showed no preference. This general pattern contrasted with the findings from Vonesh and Buck (2007) that gray tree frogs avoided contaminated pools (e.g., there were about 15 times fewer *Hyla* eggs on average in Sevin treatments than either water or acetone treatments). Below we interpret these patterns and discuss the potential importance of these results for understanding toxic effects of contaminants on aquatic communities in nature.

Through habitat selection, carbaryl has the potential to indirectly affect communities by altering the ecological context within which contaminant effects are played out. Changes in community composition (e.g., presence of predators or competitors) can cause contaminant concentrations that are sublethal in isolation to become lethal, either by altering the traits of prey species or decreasing their physiological tolerance to make them more sensitive to stressors (Relyea 2003; Relyea and Mills 2001; Schulz and Dabrowski 2001). Here we show that contaminant-treated pools received more abundant and diverse colonists than controls, suggesting that both intra- and interspecific interactions will be more frequent in contaminated habitats, possibly exacerbating the effects of subsequent exposure post-colonization. Alternatively, changes in community composition resulting from habitat selection could indirectly offset negative effects of contaminants by reducing a particular species' predators or competitors (Relyea et al. 2005). For example, in our study, we show that pesticide-induced shifts in colonization result in the partial removal of certain functional groups within one food web (i.e., herbivorous tadpoles). This removal could reduce competition and potentially toxic effects on other members of that trophic group. Thus, contaminant-induced shifts in colonization and oviposition could impact aquatic communities via the emergent effects of community composition on toxicity, potentially magnifying or in some cases decreasing toxic effects by altering the strength of species interactions after colonization. Recent studies showing context dependence of toxicity, even in fairly simple communities (e.g., Rohr and Crumrine 2005), suggest that feedbacks between effects on habitat selection and subsequent exposure are likely.

Besides altering initial community composition, pesticide-induced changes in habitat selection per se could have longer term consequences for aquatic populations and communities by deterring colonization of contaminated habitats. For example, by causing breeding habitats to appear unsuitable, even non-toxic contaminants could cause potentially important reductions in reproductive rates of animals with complex life cycles (see Vonesh and Buck 2007 for further discussion). However, in most cases, evaluating the consequences of pesticide-induced shifts in habitat selection will require interpreting how they combine with post-colonization effects of exposure. For example, in this experiment, *Culex* mosquitoes showed a strong preference for contaminated pools. In a similar oviposition study conducted in 2006 using smaller containers, we observed a fourfold increase in *Culex* egg rafts in pools treated with Sevin (mean ± SE rafts pool^{-1}: WAT 0.7 ± 0.28; SEV 3.033 ± 0.54) but found 6 times fewer larvae in these pools compared to controls (mean ± SE larvae sample^{-1}: WAT 12.73 ± 3.04; SEV 2.07 ± 1.89; J. R. Vonesh and J. C. Buck, unpublished data). This lack of correlation between oviposition rates and aquatic larval abundance in the carbaryl treatments suggest that the insecticide may have reduced larval survival. Similarly, adult beetles and heteropterans were 20 times more likely to colonize our contaminated pools. Relyea (2005) found that some diving beetles (*Dysticus* sp. and *Acilius semisulcatus*) were extremely sensitive to even low levels of Sevin, i.e., no survivorship at initial concentrations of 0.51 mg carbaryl/l. These two examples with mosquitoes and diving beetles highlight the possibility that contamination of natural pools by Sevin could act as an ecological trap for some taxa (sensu Battin 2004; Robertson and Hutto 2006), attracting insects to habitats that are ultimately lethal to them (Horvath and Zeil 1996; Kriska et al. 1998). This trap scenario has the potential to cause greater local and metapopulation declines than those predicted by habitat degradation alone (e.g., Delibes et al. 2001a, 2001b; Kristan 2003).

Whether contaminants alter patterns of colonization or not has important implications for understanding their effects in natural systems and should inform how we design studies to evaluate contaminant effects on communities. If contaminants alter habitat selection, studies conducted in open systems (e.g., uncovered mesocosms, experimental pond systems, natural habitats) that do not measure colonization may confound direct effects of toxicity with effects on habitat selection. Similarly, experimental studies of contaminant effects often start with closed systems (e.g., covered mesocosms) containing experimentally assembled communities thought to reflect an initially undisturbed state. The impacts of contaminant exposure are then evaluated in terms of interactions within this original assemblage. However, if contaminants alter the abundance of functionally important taxa, and such shifts in community composition change the subsequent effect of pesticide exposure, experimental communities mimicking an uncontaminated condition may not be the most relevant backdrop for evaluating subsequent contaminant effects. More research is needed to evaluate how commonly contaminants themselves act to shape initial community assembly. Elucidating the role of habitat selection in response to chemical contaminants may have important implications for understanding context-dependent effects of stressors in general.

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