



Joint Effects of Fragmentation and Mercury Contamination on Marsh Periwinkle (*Littoraria irrorata*) Movement

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Abstract: There are different ways contaminants can interact and enhance the effects of habitat fragmentation, such as modifying the movement of organisms. The present study tested the hypothesis that mercury exacerbates the effects of fragmentation by affecting the movement of the marsh periwinkle *Littoraria irrorata* and reducing the probability of snails crossing fragmented microlandscape experimental systems. How these changes could affect the search efficiency of organisms in the long term was assessed using hidden Markov models and random walks simulations. Bayesian nonlinear models were used to analyze the effects of fragmentation and contamination on the mean speed and mean directional change of organisms. Snail movement for control and two mercury-exposure treatments were recorded in microlandscapes with six different levels of habitat cover and three landscape replicates. The results indicated that exposed organisms had lower probabilities of crossing the landscape, reduced speed, and shifts in step length distributions. Both mercury exposure and habitat fragmentation affected the movement of the marsh periwinkle. Mercury exacerbated the effects of habitat fragmentation by affecting the cognition (e.g., route planning, orientation, and spatial learning) and movement of *L. irrorata*. Hence, the interaction of these stressors could further reduce the functional connectivity of landscapes and reduce the search efficiency of organisms. *Environ Toxicol Chem* 2022;00:1–12. © 2022 The Authors. *Environmental Toxicology and Chemistry* published by Wiley Periodicals LLC on behalf of SETAC.

Keywords: Mercury; Habitat fragmentation; Multiple stressors; Movement; Hidden Markov models

INTRODUCTION

The combination of habitat loss and fragmentation is currently one of the primary causes of global biodiversity loss (Vitousek et al., 1997; Wu et al., 2003). Habitat fragmentation is caused by the division of a habitat, leading to smaller and more isolated areas and reducing landscape connectivity and patch area and/or increasing patch edges (Fahrig, 2003). After decades of research, scientists have now amassed strong and consistent experimental evidence of the ecological effects on organisms and ecosystem processes caused by habitat fragmentation (see Alexander et al., 2012; Billings & Gaydess, 2008; Zartman, 2003). However, how fragmentation can

interact with other stressors, such as contaminants and climate change, is considered a key knowledge gap (Haddad et al., 2015). In fact, it has been predicted that interaction among fragmentation and other stressors could worsen the effects of fragmentation (Doerr et al., 2011; Haddad et al., 2015).

There are different ways that contaminants can interact with habitat fragmentation. For instance, increases in the number and size of edges in a landscape can lead to an increase in contaminant deposition and consequent reduction in habitat quality (Hasselrot & Grennfelt, 1987; Hester & Hobbs, 1992). Contaminants can also cause habitat loss, such as in oil spills (Beland et al., 2017) and nutrient-enriched salt marshes (Deegan et al., 2012), which could lead to habitat fragmentation. Deforestation and habitat fragmentation can also enhance soil erosion and leaching of mercury (Hg), becoming an important source of contamination to watersheds and aquatic life (Mainville et al., 2006; Roulet et al., 1999). Contaminants can also potentially act as chemical barriers in ecological systems, reducing the connectivity of the landscape even at lower concentrations (Araújo et al., 2016, 2018). For instance, *Poecilia reticulata* fishes avoided crossing waters contaminated with the

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herbicide atrazine, which can lead to isolation of populations and habitat fragmentation (Araújo et al., 2018).

Reduction of the structural connectivity of the landscapes (i.e., changes in the physical characteristics of the landscape) caused by habitat fragmentation may affect the ability of organisms to move and disperse across suitable and unsuitable patches (i.e., functional connectivity; Doerr et al., 2011; Offerman et al., 1995). In fact, increasing the structural connectivity among fragments, such as in the presence of corridors or stepping stone patches, may lessen the effects of fragmentation by increasing organisms' dispersion and functional connectivity (Doerr et al., 2011; Haddad, 1999; Pardini et al., 2005). However, contaminants can potentially affect organism movement and dispersion in the landscape. For instance, nonlethal concentrations of different classes of contaminants can affect speed, grazing (Bernot et al., 2005), habitat selection (Araújo et al., 2016; McCloskey & Newman, 1995), path tortuosity (i.e., how straight a path is; Kane et al., 2004), and predator avoidance (Zhou & Weis, 1999). Changes in these behaviors could further reduce animal movement and functional connectivity of the landscape and consequently worsen the effects of fragmentation.

Large-scale experiments would be impractical because of the ethical and legal constraints of releasing chemicals in ecosystems (Focks, 2014) and manipulating large landscape characteristics, so small-scale experimental model systems (Ims & Stenseth, 1989) are more suitable to test hypotheses about interactions among these two stressors. Smaller-scale experiments also allow easier landscape manipulation, larger sampling sizes, and higher statistical power (Wiens & Milne, 1989). Because the scale depends on the organism and process of interest, microlandscape experiments have been successfully used by ecologists to test hypotheses regarding the effects of fragmentation in the movement behavior of small organisms such as insects (see McIntyre & Wiens, 1999; Morales & Ellner, 2002; Wiens & Milne, 1989; Wiens et al., 1997; With et al., 1999). Microlandscape experiments are especially useful because they may accelerate the development of quantitative conceptual frameworks (Wiens & Milne, 1989) and may provide ways of testing assumptions of landscape ecology theories (Wiens et al., 1997). Experiments at this scale can also provide important insights about the searching behavior of organisms (see Kölzsch et al., 2015) which could be incorporated into simulations to test further hypotheses (Morales & Ellner, 2002).

The present study evaluates how habitat fragmentation and Hg exposure can interact and affect the movement of the marsh periwinkle *Littoraria irrorata*, using microlandscape experimental systems. The marsh periwinkle was selected as a model organism because of its (1) high abundance, (2) being an important organism in salt marsh food webs (Zengel et al., 2016), (3) slow dispersion and movements (Hamilton, 1977) that can be easily and precisely recorded, and (4) strong tendency to move toward vertical objects (Hamilton & Winter, 1982), which can be used as a stimulus to the movement of organisms and allows inferences about the cognitive behavior of organisms (Kabadayi et al., 2018).

During low tide, these organisms forage in the exposed marsh surface and avoid predation by climbing salt marsh grass stems (*Spartina alterniflora* and *Spartina cynosuroides*) as soon as a tide turns to flood the marsh (Bingham, 1972; Failon et al., 2020; Warren, 1985). Hence, being able to find and climb grass stems is crucial to the survival of marsh periwinkles. These snails graze not only detritus/algae (Bingham, 1972) but also live salt marsh cordgrass, primarily to consume invasive fungi on the cordgrass (Silliman & Newell, 2003). Mercury was selected as a contaminant of interest because it is a widespread persistent contaminant that can accumulate in the environment and in organisms' tissues (Krabbenhoft & Sunderland, 2013). Also, it is a well-recognized neurotoxin that can affect the cognitive behavior of organisms, animal movement, and search efficiency (Adams & Frederick, 2008; Bouton et al., 1999; Kobiela et al., 2015). Because the marsh periwinkle is an intertidal species, it can be exposed to Hg through different non-excluding environmental media, such as water, sediment surface, and grazing on *Spartina* blades. The hypotheses tested were that (1) Hg exposure worsens the effects of fragmentation by reducing the probability of snails crossing fragmented landscapes and reaching *S. alterniflora* blades and (2) by affecting the movement of organisms, Hg impacts their speed, path linearity, and step length distribution. The present study further explored how these changes in movement behavior might affect search efficiency of the marsh periwinkle in the long term using hidden Markov models (HMM) and random walks simulations.

METHODS

Test organisms

Organisms were collected in a relatively undisturbed saltmarsh with no known contamination point sources, located in Hayes, Virginia, USA (37°16'52.6"N, 76°23'23.8"W). Sampled organisms ($n=810$) had similar shell length (2.16 ± 0.1 cm; mean and standard deviation), width (1.52 ± 0.07 cm), and total weight (2.63 ± 0.33 g). Snails were acclimatized in aquariums with aerated water, sediments, and *S. alterniflora* blades for 2–3 weeks in the laboratory prior to the experiment. Water salinity was kept constant at 20 psu, the same salinity of the sampling site. Water changes occurred every 3–5 days. Organisms were kept in the laboratory for a maximum period of 2 months before being used in the experiment.

Organism exposure and chemical analysis. Mercury solutions were prepared daily by dissolving mercury chloride, HgCl_2 (purity $\geq 99.5\%$; Alfa Aesar), in fresh aerated artificial seawater kept at 20 psu. A 96-h survival experiment was conducted to select nonlethal concentrations of dissolved ionic Hg to be used in the experiment. Based on the results, two concentrations of Hg were selected for the microlandscape experiment, 100 and $250 \mu\text{g L}^{-1}$, both being below the concentration predicted to cause 5% lethality (LC5) of $370.4 \pm 74.1 \mu\text{g L}^{-1}$ (95% confidence interval). The marsh

periwinkle is extremely tolerant to inorganic Hg relative to other invertebrates (see Cabecinhas et al., 2015), and this information was not presented in the literature before. Prior to the experimental trials, snails were individually exposed in 60-ml plastic cups covered with perforated plastic lids to ensure the complete submersion of organisms and prevent them from escaping. Organisms were kept in an incubator for 96 h, with temperature set to 20 °C during the experiment with daily water changes. Mercury concentrations in the solutions were measured immediately after the solutions were prepared, and organisms were frozen after the experimental trials were over for Hg tissue analysis. Before water changes were performed, Hg concentrations in the water after 24 h of exposure were also measured. After 96 h of Hg exposure, organisms were immediately set on the experimental trials. Ten organisms from each Hg treatment and for each landscape replicate were cracked open with a hammer, sexed, and checked for the presence of trematode parasites ($n = 90$). Soft tissues were rinsed with deionized water and freeze-dried for 72 h or until constant weight was reached. Freeze-dried soft tissues were pulverized with a grinder. Both water and tissue analyses were measured using a Milestone DMA-80 Direct Mercury Analyzer (Shelton) following the same methods described in Holloman and Newman (2012) and Xu and Newman (2015). Standard curves and the accuracy and precision of the data were assessed using the tissue reference material DORM-3 (National Research Council of Canada) and an Hg standard water solution (BDH). Mercury concentrations (dry wt, milligrams per kilogram) for all snails analyzed were above the method detection limit ($0.0001 \text{ mg kg}^{-1}$) and limit of quantification ($0.0005 \text{ mg kg}^{-1}$). The results indicated good analytical precision and accuracy with an average recovery rate of $99 \pm 2\%$

($n = 40$) in the water and $100 \pm 7\%$ ($n = 12$) in the tissue samples.

Experimental setup

Random microlandscapes ($25.4 \times 38.1 \text{ cm}$) were created in $38.1 \times 38.1 \times 15.24 \text{ cm}$ Plexiglas trays. Six different levels of habitat loss were used (0%, 15%, 30%, 45%, 60%, and 75% of habitat loss). An example of the experimental setup is illustrated in Figure 1. The dimensions of the tray and microlandscapes were selected based on pilot experiments to maximize the movement of snails toward the other side of the landscape instead of moving toward the lateral edges of the tray. Microlandscapes were fragmented with $2.54 \times 2.54 \text{ cm}$ of copper tape, an electrically conductive material that repels the snail on contact with the moist foot integument (Cutter, 1988). Hence, in this experiment, habitat loss and fragmentation are caused by a type of chemical barrier where organisms are unable to cross unsuitable patches. Water was not added to the tray because the marsh periwinkle moves mainly in the low tide and the addition of water would likely lead to copper leaching from the tapes becoming a potential confounding factor. Because organisms are unable to cross fragmented patches but are still able to see the *Spartina* stems, inferences about the cognitive behavior of organisms can be made under the detour paradigm (e.g., route planning, orientation, and spatial learning; Kabadayi et al., 2018).

Copper tape was also placed on the tray sides to prohibit climbing and escaping. Microlandscape patterns were created using a function developed in the R environment (R Foundation for Statistical Computing, 2020) that samples random patterns given the area of the tray and the percentage of habitat loss.

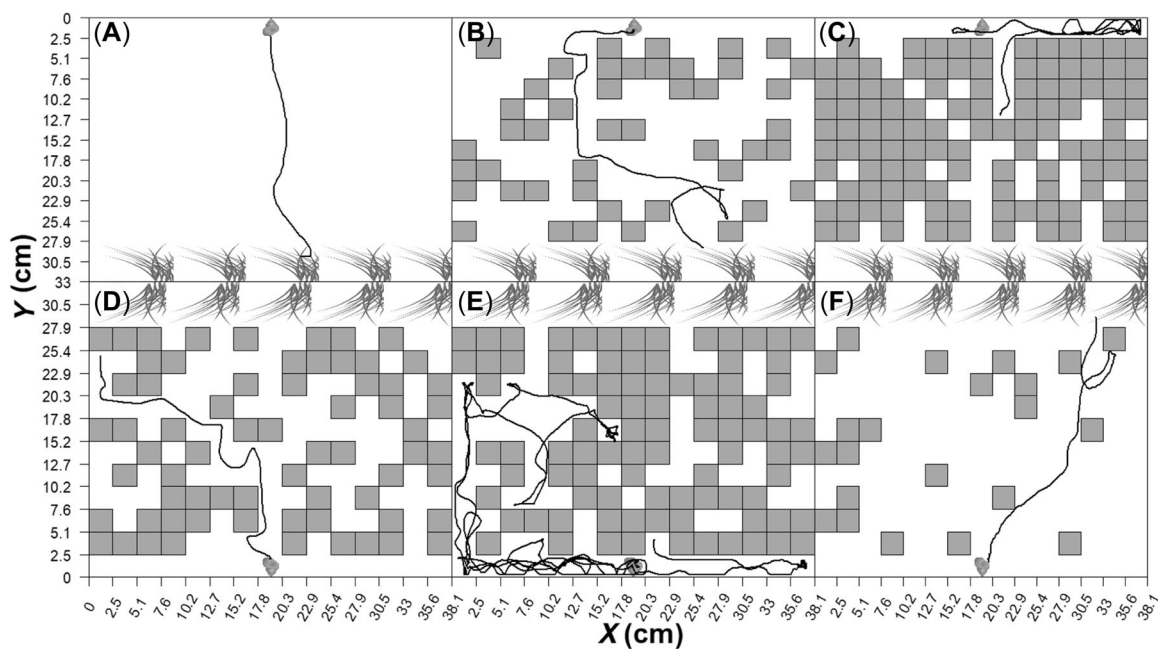


FIGURE 1: Experimental setup and examples of movement tracks (black solid line) in microlandscapes with (A) 0%, (B) 30%, (C) 75%, (D) 45%, (E) 60%, and (F) 15% of habitat loss. Gray squares represent the copper tape and the white background, the Plexiglas. The snails in the figure represent the initial position of their release, on the opposite side of the *Spartina* blades. Digital cameras were set approximately 1 m above the trays.

Only landscapes with a free path were selected (i.e., landscapes that percolate). Even though snails cannot directly cross the copper tape, they can still cross tapes diagonally (e.g., Figure 1E). Therefore, the movement of snails in the micro-landscape can be related to the eight nearest neighbors' rule in a percolation theory framework (see Pearson et al., 1996). Because a completely free path was very unlikely in landscapes with 25% of cover, landscapes with paths connected diagonally were considered in the experiment.

Fifteen organisms that were not used previously in any experiment were individually released in one side of the landscape. Clumps of *S. alterniflora* blades were set on the opposite side of the tray as a stimulus to the organisms to cross the landscape. For each level of cover, three random microlandscape patterns were created. Replication of different microlandscapes is necessary to enable inferences about the level of cover and not any particular landscape pattern. In this way, a total of 810 organisms were used in this experiment. The movement of control and Hg-exposed snails in the microlandscapes was recorded with a digital camera (Logitech C920 HD Pro). The experimental trials were finished after 4 h or when the periwinkle crossed the landscape. After experimental trials, snails were immediately frozen for analysis of Hg content in soft tissues. Therefore, each snail was used only once for each experimental trial. Videos were broken into every 5-s pictures, and the position of each organism was digitized to x/y coordinates using the software ImageJ/Fiji (Schneider et al., 2012) and the MtrackJ plugin (Tinevez et al., 2017). Because the marsh periwinkle produces a mucus trail that might be followed by other snails, trays were cleaned with ethanol 90% (v/v) and deionized water and dried after each trial, to ensure the independence of samples (Tankersley, 1989). All tracks and landscape configurations are provided in Supporting Information S1 (Figures S1–S3).

Experimental trials were recorded three different times per day in six trays (each tray with a different level of cover) divided into two rows and three columns (Figure 1). The position of the trays was randomly chosen and changed daily to avoid any possible effect of the tray position on the snail movement. The walls of the trays were covered with white cardboard to avoid visual contact outside the tray and with other snails. Because it would be infeasible to record all experimental trials at the same time, each microlandscape replicate was recorded one at a time. After recording 15 organisms per treatment in one microlandscape pattern, the copper tape of all trays was removed. Trays were cleaned with ethanol 90% and deionized water, and a new pattern was set up. To avoid using snails that had remained in the laboratory more than 2 months, new organisms were sampled following the procedures described above each time a new pattern was set up. Pilot experiments showed that after long periods in the laboratory, snails were less tolerant to the effect of Hg.

Data analysis

A Bayesian generalized linear model with the Logit link function was used to evaluate the effects of fragmentation and

Hg exposure on the probability of snails crossing the landscape. A Cauchy distribution was set as prior for all parameters, with center and scale parameters set at 0 and 2.5, respectively, as recommended by Gelman et al. (2008). Models were fit using Markov chain Monte Carlo methods with a Hamiltonian sampler algorithm. Three independent chains were used in parallel with an initial 2000 iterations for adaptation. This was followed by another 2000 iterations, during which samples were monitored every three steps. Among the fixed effects included in the models were habitat loss, Hg exposure, length, weight, day of the experiment, landscape resistance, recording day, and landscape replicates. Model selection was performed based on the Watanabe (or widely applicable) Akaike information criterion (WAIC) weights. Evidence ratios (ERs) were used to test the hypothesis that parameters were different from zero or different between treatments, assuming a 95% credible interval.

For each pathway, the mean speed (centimeters per minute), net displacement, turning angles, and total time moving were calculated. Mean directional change was also calculated as a measurement of path nonlinearity (Kitamura & Imafuku, 2015). Because each snail started to move at different times, all metrics and tracks were analyzed after organisms left a radius of 2 cm from its starting position. Because movement tracks were sampled at a short temporal and spatial scale, and consequently were more sensitive to errors (Edelhoff et al., 2016), tracks were smoothed by applying a Savitzky-Golay filter with the *trajr* R package (McLean & Skowron Volponi, 2018). Bayesian nonlinear models (asymptotic regression) were used to analyze path metrics following the same procedures described above. The associated three-parameter asymptotic regression equation can be written as

$$y_{ji} = \Theta_i + (R_{0i} - \Theta_i)e^{-x_j e^{\beta_i}} \quad (1)$$

where y_{ji} is the response variable in the x_j level of cover in the i th treatment, R_{0i} is the parameter representing the response when the level of cover x_j is equal to zero, Θ_i is the asymptote on the right side, and β_i is the \log_e of the rate constant. In Bayesian nonlinear models, random and fixed effects are set on the nonlinear parameters. Because nonlinear models require stronger (i.e., narrower) priors for chain convergence (Bürkner, 2017) and no data were available on the effects of habitat fragmentation on the movement of snails, a normal distribution with mean of 0 and standard deviation of 2 was used. Other nonlinear models were considered, such as logistic and exponential regressions; but models did not converge. All Bayesian models were fit with the *brms* R package (Bürkner, 2017).

Stochastic state-switching HMMs were used to analyze how fragmentation and Hg exposure could affect the movement behavior and states of the marsh periwinkle. This type of model assumes that organisms can present different movement states such as slower (shorter step lengths with higher number of directional changes) or faster (longer step lengths with fewer directional changes). Hence, organisms can switch or remain in

a state through time with a certain probability. Because a single model with Hg exposure as a covariate would pool all step lengths into a single distribution, HMMs were fitted to the data for each independent Hg treatment using maximum likelihood methods. Habitat loss was \log_e -transformed before being analyzed as a covariate. A wrapped Cauchy distribution was fitted to the turning angles and an exponential, Weibull, or gamma distribution for the step length distribution. Model selection was performed based on the AIC weights. Differences in the parameter estimates were assessed based on the 95% confidence intervals. The HMMs were fitted using the moveHMM R package (Michelot et al., 2016). Pseudo-residuals and simulations of the speed and mean step length were used to assess model fit.

To evaluate how changes in the movement behavior of organisms could affect the search efficiency of organisms, simulations were used following similar procedures to Bartumeus et al. (2005). For each treatment, random paths of 50 organisms with 10×10^7 steps were drawn from the HMMs. Uniform randomly distributed targets (e.g., food, mates, or site) were set in a bidimensional continuous landscape with periodic boundaries. An encounter occurs if a target lies within a detection radius r . The search efficiency is calculated by dividing the number of encounters by the total distance traveled and scaled based on the mean free path parameter λ . The mean free path is calculated as

$$\lambda = \frac{L^2}{2rNt} \quad (2)$$

where L is the size of the system in one dimension, r is the detection radius, and Nt is the number of targets. Without loss of generality, λ was calculated by setting the size of the system at 128, the detection radius at 0.5, and the number of targets to 16. After an encounter, the target is removed, and a new target is randomly placed in the landscape to keep λ constant. Because the number of targets was held constant over the different levels of habitat cover, the simulations did not include the effects of habitat loss on resource availability and distribution. Hence, the effects of Hg exposure on the search efficiency of organisms can solely be related to changes in the movement behavior caused by fragmentation. Evidence of differences in the search efficiency among treatments and levels of cover were assessed based on the 95% high-density confidence interval.

RESULTS

Chemical analyses

Mean Hg concentrations in the water (\pm standard deviation) were $248 \pm 7 \mu\text{g L}^{-1}$ ($n = 78$), $100 \pm 3 \mu\text{g L}^{-1}$ ($n = 105$), and $0.0002 \pm 0.0002 \mu\text{g L}^{-1}$ ($n = 80$) in the $250 \mu\text{g L}^{-1}$, $100 \mu\text{g L}^{-1}$, and control treatments, respectively. Mean Hg concentrations in the water after 24 h of exposure were $40 \pm 29 \mu\text{g L}^{-1}$ ($n = 118$), $14 \pm 10 \mu\text{g L}^{-1}$ ($n = 188$), and $0.0003 \pm 0.0002 \mu\text{g L}^{-1}$ ($n = 65$) in the $250 \mu\text{g L}^{-1}$, $100 \mu\text{g L}^{-1}$, and control treatments, respectively. Mercury tissue concentration (dry wt) were $27 \pm 8 \text{ mg kg}^{-1}$ ($n = 30$), $19 \pm 5 \text{ mg kg}^{-1}$ ($n = 30$), and $0.8 \pm 0.2 \text{ mg kg}^{-1}$ ($n = 30$) in the highest Hg treatment to the lowest,

respectively. Mean Hg concentrations in the water and tissues per landscape replicate are presented in Supporting Information S2 (Table S1). No mortality was observed during the experiment. Trematode parasites were also not found in any opened organisms.

Probability of snails crossing the landscape. Based on the WAIC weights (WAICw), the best model selected was that including an interaction term of Hg and habitat loss plus the effect of landscape replicate (WAICw = 0.913). The results of model selection analyses are provided in Supporting Information S3 (Table S1) and parameter estimates in Supporting Information S4 (Table S1). Very strong evidence supports the hypothesis that both Hg treatment and habitat loss affected the probability of snails crossing the landscape (all ERs > 1000). There was also very strong evidence suggesting that those in the $250 \mu\text{g L}^{-1}$ Hg treatment had lower probability of crossing the landscape when compared to those in the $100 \mu\text{g L}^{-1}$ treatment (ER > 1000). Hence, control snails had a higher probability of crossing the landscape, which decreased with habitat loss and with Hg concentration (Figure 2). Very strong evidence supports the hypothesis that organisms from the Landscape Replicates 2 and 3 had a lower probability of crossing the landscape (ER = 799 and >1000, respectively). This indicates that snails had a higher probability of crossing the landscape in the first pattern replicate. However, there was very weak evidence to support differences between the second and third landscape replicates (ER = 1.5). The interaction of cover and the $250 \mu\text{g L}^{-1}$ Hg treatment was also significant (ER = 366), while there was no strong evidence in favor of an interaction of cover and the $100 \mu\text{g L}^{-1}$ Hg treatment (ER = 1.3).

The inflection points and 95% fitted credible interval of the control treatment were 31% (27–36), 23% (19–28), and 24% (20–29) of habitat loss for the first, second, and third landscape replicates, respectively. In the $100 \mu\text{g L}^{-1}$ Hg treatment, the inflection points were approximately 10% lower in comparison to the control with 19% (14–23), 10% (5–15), and 11% (6–16), respectively. It was not possible to estimate the inflection point of the $250 \mu\text{g L}^{-1}$ Hg treatment

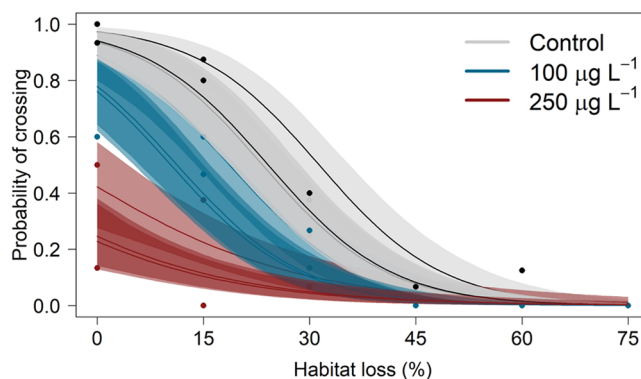


FIGURE 2: Probability of control and mercury-exposed snails crossing the landscape and 95% predicted credible interval (shaded lines) for each landscape replicate. Solid lines represent the predicted lines from the model for each landscape replicate.

because most snails did not cross the landscape even in the case of no habitat loss.

Movement tracks

Snails present high variability within treatments relative to their time to start moving, total distance traveled, and total time moving (Figure 3). On average, control organisms started moving first, with a mean and 95% credible interval of 5 min (0.3–12.5). Exposed organisms started to move on average after 9 min (0.3–31) and 25 min (0.3–122) for the 100 and 250 $\mu\text{g L}^{-1}$ Hg treatments, respectively. Control organisms also had a higher total displacement and were active for longer periods of time, with an average of 75 cm (5–192) in 24 min (3–58). In the Hg treatments, snails moved on average shorter distances, 55 cm (3–166) and 30 cm (1–75), in an average period of 19 (3–50) and 17 min (2–39) in the 100 and 250 $\mu\text{g L}^{-1}$ Hg treatments, respectively.

Based on model selection, asymptotic regression provided a better fit to the data than linear models for both mean speed and mean directional change. For both mean speed and mean directional change, the best model selected (WAICw = 1 each) included Hg, landscape replicate, and whether the organisms crossed the landscape or not. Models that included the interaction term of habitat loss and Hg did not converge. The results of model selection analyses are provided in Supporting Information S3 (Tables S2 and S3) and parameter estimates in Supporting Information S4 (Tables S2 and S3). Regarding the

mean speed of organisms, there was strong evidence that the asymptote parameter θ of the highest Hg exposure concentration is lower in comparison to the control (ER = 69) and moderate evidence that it is different from the 100 $\mu\text{g L}^{-1}$ Hg treatment (ER = 12.3). However, there was no evidence to support the hypothesis that there were differences between the asymptote parameter of the control and the 100 $\mu\text{g L}^{-1}$ Hg treatment (ER = 0.7). There was also strong evidence to support the hypothesis that R_0 (i.e., mean speed without fragmentation) is higher in the control treatment in comparison to the lowest (ER = 554) and highest (ER = 999) Hg exposure concentrations. There was only weak support for the hypothesis that there were differences between the two Hg concentrations (ER = 2.8). Regarding the decay rate constant (β), 100 $\mu\text{g L}^{-1}$ Hg was the only treatment that had a lower decay rate in comparison to the other treatments (ER = 67). Moderate and weak evidence suggests that there was a difference among landscape replicates for all three parameters (ER ranging from 3.4 to 9.9) except for the rate constant parameter in the third landscape replicate, which indicated strong evidence (ER = 49). Organisms that crossed the landscape also had a higher mean speed without fragmentation (ER > 1000) and higher asymptote parameter (ER = 134), but there was no evidence to support the hypothesis that the rate constant was lower (ER = 0.5).

Regarding the mean directional change, there was weak and moderate evidence of effects of Hg in the asymptote of both treatments (ER = 2.2 and 5.1 for the lowest and highest exposure concentrations, respectively). For the constant rate, there was moderate evidence of effects of Hg (ER = 5.2 and

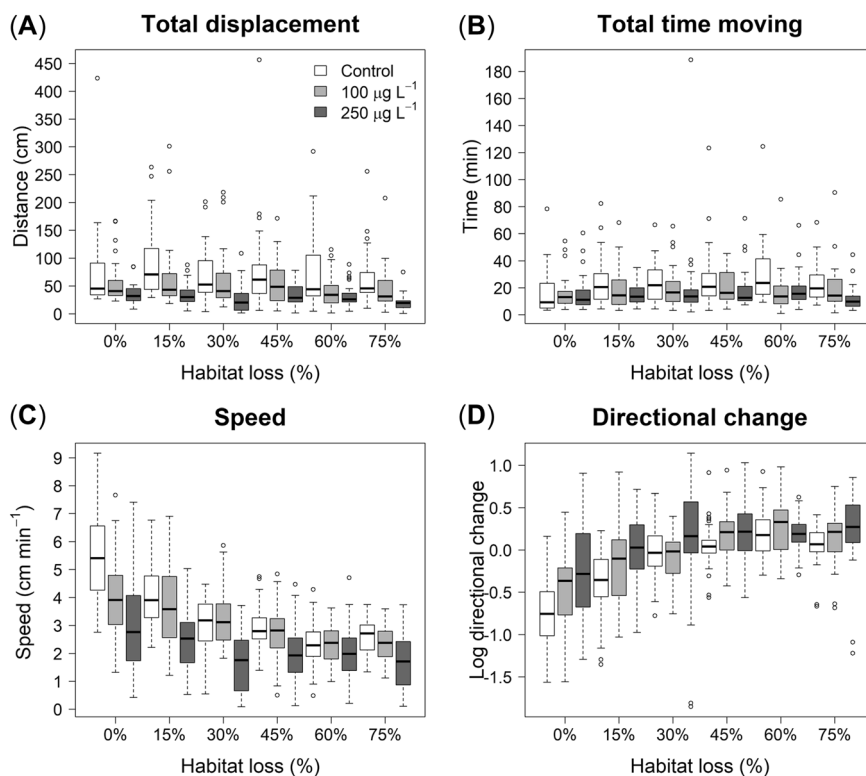


FIGURE 3: Boxplot of the (A) total displacement, (B) total time moving, (C) mean speed, and (D) mean \log_e directional change of control and exposed organisms. Data one and a half times the interquartile range are indicated as white circles.

12.8). However, there was strong evidence that the mean directional change of organisms without fragmentation (i.e., R_0) was higher in organisms exposed to $250 \mu\text{g L}^{-1}$ Hg (ER = 56) and moderate evidence (ER = 12.8) for the lowest Hg concentration. Organisms that crossed the landscape also had a lower directional change without fragmentation (ER > 1000) with a higher decay rate (ER = 29) but with no effects on the asymptote (ER = 1.8). Moderate evidence suggests a difference in the asymptote of the second and third landscape replicates (ER = 7.4 and 5.1, respectively), but there is only weak evidence for differences in the constant rate among replicates (ER = 3 and 1.5). Thus, there was only strong evidence of differences in the mean directional change of control and exposed organisms in the highest concentrations without habitat fragmentation.

HMMs and random walk simulations

For all treatments, a gamma distribution provided a best fit to step length distribution (AICw = 1 for all treatments). The results of model selection are provided in Supporting Information S3 (Table S4) and parameter estimates in Supporting Information S4 (Table S4). Organisms in the first state (i.e., resting or detouring) presented smaller steps and less correlated turning angles in comparison to the second state (i.e., directional movement; Figure 4). Hence, organisms in the first state could be characterized as sedentary, searching, or detouring movements, whereas organisms in the second state could be classified as active directional movement. As expected, the probability of snails remaining in the active state was higher at low levels of fragmentation in all treatments. Exposed organisms had lower shape and scale parameters in comparison to control in both states, with lower parameter estimates in the $250 \mu\text{g L}^{-1}$ Hg treatment (Supporting Information S4, Table S4). Without fragmentation, control organisms also had a higher probability of staying in the active state, suggesting more directional movements than exposed organisms. The probability of snails remaining in the active state decreased with habitat loss in all treatments and with a faster rate in exposed organisms. Simulations generally provided good agreement with the data based on the mean step length and mean speed (Supporting Information S5, Figure S1). However, the mean speed of organisms in lower habitat loss (i.e., 0% and 15%) was generally underestimated in all treatments.

Regarding the search efficiency simulation, control organisms generally had a higher search efficiency in comparison to both Hg exposure treatments (Figure 5). The highest Hg treatment had the lowest search efficiency. Differences between control and the $100 \mu\text{g L}^{-1}$ Hg treatment were only observed in the lowest levels of cover, until 30% of habitat loss. The effects of habitat fragmentation were less apparent or not significant in both Hg exposure concentrations because all 95% confidence intervals overlapped the search efficiency estimates in all levels of habitat loss. The effects of fragmentation, in comparison to no habitat loss, were more pronounced in the control treatment after 45% of habitat loss. However,

confidence intervals of all levels of habitat loss (from 15% to 75%) overlapped in the control treatment, suggesting no differences among these levels.

DISCUSSION

Movement of individuals is a fundamental element of almost any ecological and evolutionary process, especially when dealing with habitat fragmentation where a direct causal link with movement and environmental changes can be established (Nathan et al., 2008). Indeed, most of the advances in our understanding of habitat connectivity came from animal movement behavior studies (Doerr et al., 2011). The results from the present study showed that Hg exposure can worsen the effects of fragmentation by affecting a snail's cognition (e.g., route planning, orientation, and spatial learning) and movement and, consequently, the probability of snails crossing the landscape. The effects of fragmentation were pronounced at higher levels of habitat loss where most snails were unable to cross the landscape independent of Hg exposure. However, the effects of contamination were evident even without habitat loss, where most snails were unable to cross the landscape in the highest Hg treatment. Shifts in the inflection points of the probability of crossing the landscape were observed in exposed organisms (Figure 2). These results indicate that fragmentation can lead to reduction in the functional connectivity of landscapes.

There was also an effect of landscape replicate in the probability of snails crossing the landscape, which suggests an effect of the landscape configuration. However, it could also be a result of organisms' state at the time they were sampled. For instance, the resistance of the landscape had no or negligible improvement in any model fitted (Supporting Information S3, Tables S1–S3). Also, landscape replicate was among the variables included in the models for both mean speed and mean directional change, which could indicate different behavior among organisms. Previous studies also showed temporal variation in the sensitivity of organisms sampled in the field to contaminants even with a few months sampling difference (Kater et al., 2000; McGee et al., 1998). The marsh periwinkle also presented a monthly difference in respiration rate and caloric content related to seasonal effects, with higher respiration rates during the summer (Shirley et al., 1978). The marsh periwinkle also has monthly differences in activity time, with lower activity in the warmer months (Iacarella & Helmuth, 2012). Because control organisms also had a lower probability of crossing the landscape in the second and third landscape replicates, it is likely that the overall condition of organisms, such as metabolic states, could be an important factor. Therefore, the effect of landscape replicate could also be caused by the organism's condition at the time it was sampled. Nevertheless, the reduction in the ability of snails crossing the landscape was consistent in all landscape replicates and treatments.

The effects of fragmentation depend on how organisms perceive the landscape, their ability to disperse, and the quality

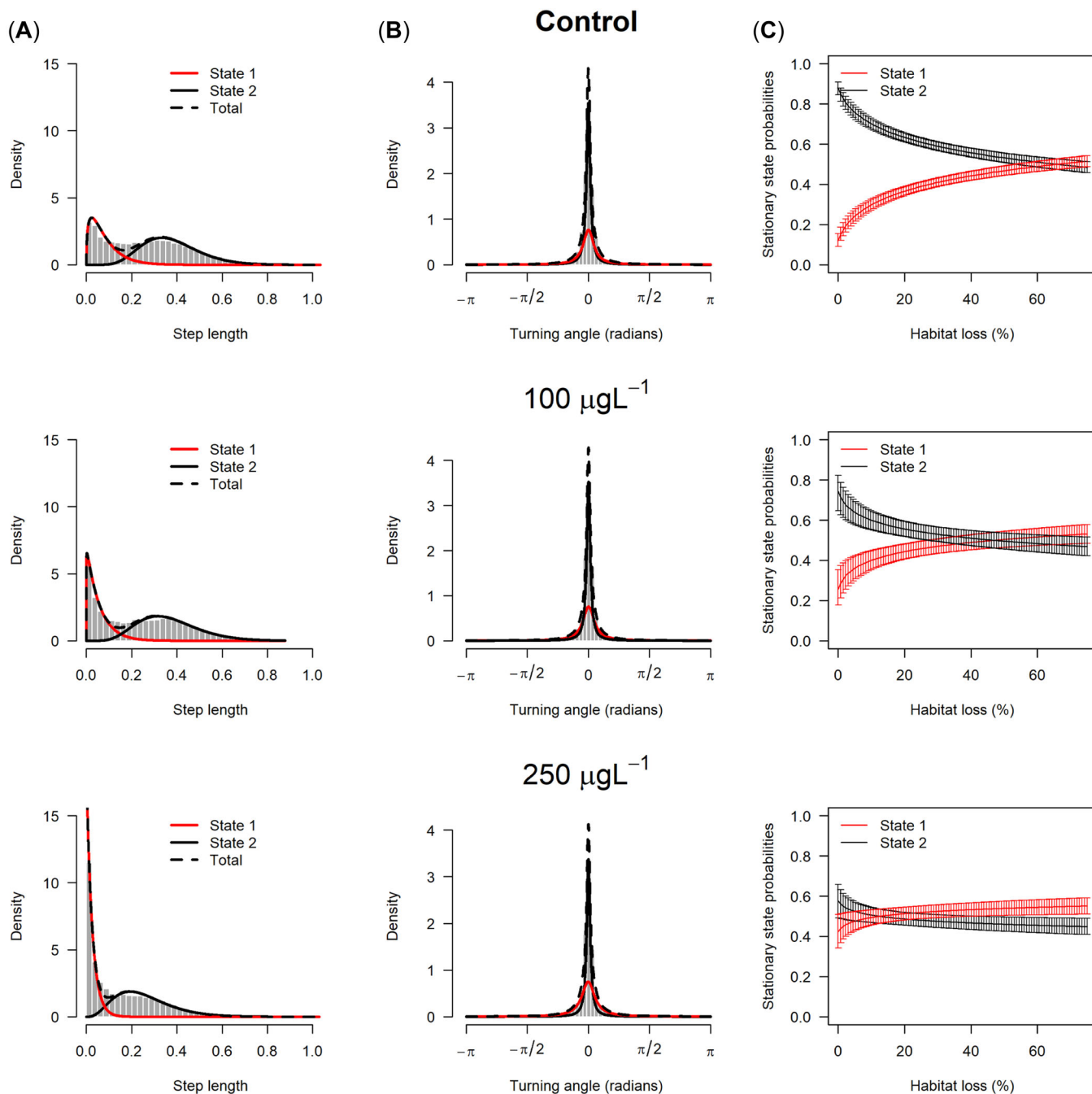


FIGURE 4: Results from the hidden Markov model for the control, 100 µg L⁻¹ Hg, and 250 µg L⁻¹ Hg treatments: (A) histogram and fitted gamma distribution to the step length; (B) histogram and fitted wrapped Cauchy distribution to the turning angles; and (C) stationary state probability of both states in function of habitat loss (percentage) and 95% confidence intervals.

of the surrounding nonhabitat matrix (Metzger & Décamps, 1997; With et al., 1999). Because fragmentation was generated using chemical barriers in the present study, the effects of fragmentation on movement behavior could be overestimated when compared with fragmented areas where organisms can cross unsuitable patches. In the case of chemical and physical barriers such as dams (Anderson et al., 2018; Wu et al., 2003), the effects of fragmentation on animal movement might be exacerbated because fragmentation can completely arrest dispersion among patches or force organisms to detour around

unsuitable areas. For instance, Garner et al. (2017) found that approximately 20% of marsh periwinkle reached *S. alterniflora* blades in trays completely covered with oil within 4 h. Fragmentation can reduce the interpatch movement of butterflies, though interpatch movement was still observed in patches 384 m apart (Haddad, 1999). However, changes in movement behavior could reduce the maximum amount of distance an organism can travel and reach other patches. The results from the HMM showed that Hg exposure can cause shifts in the step length distribution and consequently may reduce the searching

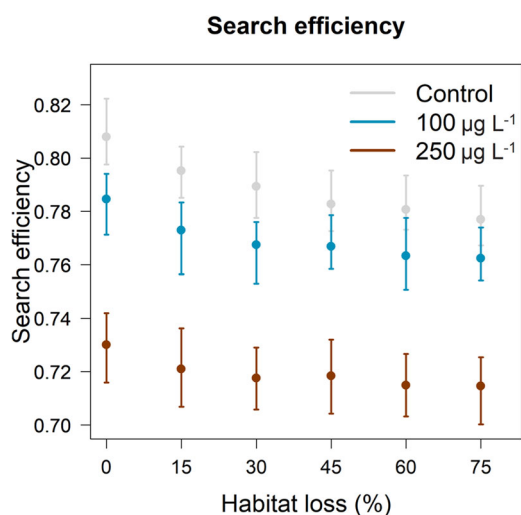


FIGURE 5: Search efficiency simulations of control and exposed organisms for each level of habitat loss. Error bars represents the 95% high-density confidence interval.

behavior and distances organisms can travel. Changes in the step length distribution and search strategies can potentially lead to a substantial increase in mortality of individuals in fragmented landscapes (Niebuhr et al., 2015).

Moreover, increases in habitat loss and fragmentation seem to have a nonlinear impact on animal movement state probabilities, search efficiency, mean speed, and mean directional change. These findings are in agreement with the notion that fragmentation may have nonlinear effects on movement potential and strategies (Doerr et al., 2011). The effects of fragmentation on path metrics were also similar to those shown in previous works conducted with beetles that were able to move through unsuitable patches. A decrease in mean speed and step length and an increase in path tortuosity (another metric for path linearity) were also reported for beetles and crickets in microlandscapes (McIntyre & Wiens, 1999; Wiens et al., 1997; With et al., 1999). In fact, these results also showed that the movement response of beetles to habitat fragmentation may present strong nonlinear responses (Wiens et al., 1997). Yet, short-term movement of insects and snails is expected to show less complexity and variability than long-term movement of larger organisms such as many vertebrates (Doerr & Doerr, 2005). Hence, the effects of fragmentation in higher spatial scales on the mean speed and step length distribution are extremely important to understand more complex scenarios.

Based on random walk simulations, Hg exposures can have a greater impact on the long-term movement and search efficiency of organisms in comparison to habitat fragmentation. Adams and Frederick (2008) also reported a reduction in search efficiency of birds, measured as consumption of fish during a given time, chronically fed low doses of methylmercury. However, because of limitations associated with extrapolating complex long-term movement behaviors from short-term experiments (Morales & Ellner, 2002), the effects of fragmentation

could be underestimated. In fact, the speed of organisms was generally overestimated in lower levels of habitat loss in all treatments (Supporting Information S5, Figure S1), which could possibly be linked to individual variation. Also, the possible effects of fragmentation on resource distribution and the emergence of barriers in the landscape were not considered in this simulation. In fact, random walk simulations showed that the distribution of resources may have a key role on the survival probability of organisms in fragmented landscapes (Niebuhr et al., 2015). Only the effects of fragmentation and Hg exposure on the movement of organisms were included, and further investigation is necessary to test such hypotheses. Also, the exposed concentration is an important factor because the decrease in the search efficiency was higher in the 250 µg L⁻¹ Hg than the 100 µg L⁻¹ Hg treatment.

Because the marsh periwinkle is very tolerant of inorganic Hg, it is unlikely that the concentrations of Hg used in the present study would be encountered in nature, unless a large accidental discharge occurred. Nevertheless, the concentrations used in the present study are below the LC50 predicted for the effects of inorganic Hg on the marsh periwinkle. Non-lethal effects of many other classes of contaminants may cause similar behavioral effects on a broad range of organisms. In fact, long-term exposures may also cause changes in animal behavior in much lower concentrations and affect the amount of time organisms stay in a movement state (see Kobiela et al., 2015). For instance, Henry et al. (2012) showed that the pesticide thiamethoxam, a selective agonist of nicotinic acetylcholine receptors, affects the movement of bees and increases homing failure. Pentachlorophenol, carbaryl, copper, sulfate, dichlorodiphenyltrichloroethane, cadmium, zinc, and cyanide can also affect swimming behavior in different species of fish (Little & Finger, 1990). Studies that used HMM also showed that diazinon and formaldehyde can affect animal movement speed and states of *Daphnia magna* and *Danio rerio* (Li et al., 2013; Liu et al., 2011; Nguyen et al., 2011). Chevalier et al. (2015) evaluated the effects of different contaminants on the behavior of *Daphnia magna* and concluded that chemicals with dissimilar modes of action can show similar behavioral effects and that no distinct behavioral profiles could be drawn from the chemical mode of action. These studies illustrate that broad classes of contaminants with different modes of action affect movement of organisms. Hence, the effects of fragmentation could also be exacerbated by contaminants other than Hg and affect other classes of organisms. This is especially worrisome because contaminants are detected even in the most remote places of the planet (Maltby, 2013). Also, nearly 20% of the world's remaining forest is within 100 m of an edge, and 70% are within 1 km of an edge (Haddad et al., 2015). Hence, most of the world's remaining forests are close to agricultural, industrial, or urban areas, where there are many point and non-point contaminant sources. The world's largest rivers have also been extensively fragmented by dams and face many contaminant sources and other stressors (Best, 2018). It is also likely that other factors such as increases in diseases, parasites, introduced species, and temperature could co-occur and interact with both fragmentation and contamination.

CONCLUSION

The effects of contamination and habitat fragmentation on animal movement behavior are well recognized in the literature; however, how these effects interact is crucial knowledge in a rapidly changing world. Microlandscape experiments allowed us to test initial hypotheses about the joint effect of such widespread stressors. The results of the present study indicated that both chemical contaminant exposure and habitat fragmentation affected the movement of the marsh periwinkle. These results suggest that Hg worsened the effects of habitat fragmentation by affecting the cognition and movement of *L. irrorata*. Based on our current understanding of habitat fragmentation and contamination, the interaction of these stressors could further reduce the functional connectivity of landscapes and reduce the search efficiency of organisms. This could lead to changes in metapopulation dynamics, such as the colonization of new patches. The present study also shows that nonlethal concentrations of contaminants may affect ecological processes that are not commonly considered in risk assessments. These results underscore the importance of incorporating landscape ecology and spatial distribution of contaminants in ecological risk assessments. They also suggest that management of fragmented areas should consider sources and potential effects of contaminants on animal movement behavior and functional connectivity. With advances in radio-telemetry, satellite tracking technology, and modeling techniques, more evidence should be gathered and further hypotheses tested by long-term and large-scale experiments.

Supporting Information—The Supporting Information is available on the Wiley Online Library at <https://doi.org/10.1002/etc.5351>.

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This article has earned both an Open Data and Open Materials badge for making publicly available the digitally shareable data necessary to reproduce the reported results. The data and the materials are available at <https://github.com/krullm/marsh-periwinkle-ETC-2022/blob/main/README.md>. Learn more about the Open Practices badges from the Center for Open Science: <https://osf.io/tvyxz/wiki>.

REFERENCES

- Adams, E. M., & Frederick, P. C. (2008). Effects of methylmercury and spatial complexity on foraging behavior and foraging efficiency in juvenile white ibises (*Eudocimus albus*). *Environmental Toxicology and Chemistry*, 27, 1708–1712.
- Alexander, H. M., Foster, B. L., Ballantyne, F., Collins, C. D., Antonovics, J., & Holt, R. D. (2012). Metapopulations and metacommunities: Combining spatial and temporal perspectives in plant ecology. *Journal of Ecology*, 100, 88–103.
- Anderson, E. P., Jenkins, C. N., Heilpern, S., Maldonado-Ocampo, J. A., Carvajal-Vallejos, F. M., Encalada, A. C., Rivadeneira, J. F., Hidalgo, M., Cañas, C. M., Ortega, H., Salcedo, N., Maldonado, M., & Tedesco, P. A. (2018). Fragmentation of Andes-to-Amazon connectivity by hydropower dams. *Science Advances*, 4, 1–7.
- Araújo, C. V., Martinez-Haro, M., Pais-Costa, A. J., Marques, J. C., & Ribeiro, R. (2016). Patchy sediment contamination scenario and the habitat selection by an estuarine mudsnail. *Ecotoxicology*, 25, 412–418.
- Araújo, C. V., Silva, D. C., Gomes, L. E., Acayaba, R. D., Montagner, C. C., Moreira-Santos, M., Ribeiro, R., & Pompêo, M. L. (2018). Habitat fragmentation caused by contaminants: Atrazine as a chemical barrier isolating fish populations. *Chemosphere*, 193, 24–31.
- Bartumeus, F., da Luz, M. G. E., Viswanathan, G. M., & Catalan, J. (2005). Animal search strategies: A quantitative random-walk analysis. *Ecology*, 86, 3078–3087.
- Beland, M., Biggs, T. W., Roberts, D. A., Peterson, S. H., Kokaly, R. F., & Piazza, S. (2017). Oiling accelerates loss of salt marshes, southeastern Louisiana. *PLoS One*, 12, Article e0181197.
- Bernot, R. J., Kennedy, E. E., & Lamberti, G. A. (2005). Effects of ionic liquids on the survival, movement, and feeding behavior of the freshwater snail, *Physa acuta*. *Environmental Toxicology and Chemistry*, 24, 1759–1765.
- Best, J. (2018). Anthropogenic stresses on the world's big rivers. *Nature Geoscience*, 7, 7–21.
- Billings, S. A., & Gaydess, E. A. (2008). Soil nitrogen and carbon dynamics in a fragmented landscape experiencing forest succession. *Landscape Ecology*, 23, 581–593.
- Bingham, F. O. (1972). The influence of environmental stimuli on the direction of movement of the supralittoral gastropod *Littorina irrorata*. *Bulletin of Marine Science*, 22, 309–335.
- Bouton, S. N., Frederick, P. C., Spalding, M. G., & McGill, H. (1999). Effects of chronic, low concentrations of dietary methylmercury on the behavior of juvenile great egrets. *Environmental Toxicology and Chemistry*, 18, 1934–1939.
- Bürkner, P. C. (2017). brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software*, 80, 1–28.
- Cabecinhas, A. S., Novais, S. C., Santos, S. C., Rodrigues, A. C., Pestana, J. L., Soares, A. M., & Lemos, M. F. (2015). Sensitivity of the sea snail *Gibbula umbilicalis* to mercury exposure—Linking endpoints from different biological organization levels. *Chemosphere*, 119, 490–497.
- Chevalier, J., Harscoët, E., Keller, M., Pandard, P., Cachot, J., & Grote, M. (2015). Exploration of Daphnia behavioral effect profiles induced by a broad range of toxicants with different modes of action. *Environmental Toxicology and Chemistry*, 34, 1760–1769. <https://doi.org/10.1002/etc.2979>
- Cutter, J. W. (1988). Snail barrier (US Patent No. 4756116 A). US Patent and Trademark Office.
- Deegan, L. A., Johnson, D. S., Warren, R. S., Peterson, B. J., Fleeger, J. W., Fagherazzi, S., & Wollheim, W. (2012). Coastal nutrient enrichment as a driver of salt marsh loss. *Nature*, 490, 388–392.
- Doerr, E. D., & Doerr, V. A. (2005). Dispersal range analysis: Quantifying individual variation in dispersal behaviour. *Oecologia*, 142, 1–10.
- Doerr, V. A., Barrett, T., & Doerr, E. D. (2011). Connectivity, dispersal behaviour and conservation under climate change: A response to Hodgson et al. *Journal of Applied Ecology*, 48, 143–147.
- Edelhoff, H., Signer, J., & Balkenhol, N. (2016). Path segmentation for beginners: An overview of current methods for detecting changes in animal movement patterns. *Movement Ecology*, 4, 1–21.
- Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 34, 487–515.

- Failon, C. M., Wittingham, S. S., & Johnson, D. S. (2020). Ecological associations of *Littoraria irrorata* with *Spartina cynosuroides* and *Spartina alterniflora*. *Wetlands*, 40, 1317–1325.
- Focks, A. (2014). Why we need landscape ecotoxicology and how it could be advanced—An academic perspective. *Environmental Toxicology and Chemistry*, 33, 1193–1194.
- Garner, T. R., Hart, M. A., Sweet, L. E., Bagheri, H. T., Morris, J., Stoeckel, J. A., & Roberts, A. P. (2017). Effects of deepwater horizon oil on the movement and survival of marsh periwinkle snails (*Littoraria irrorata*). *Environmental Science & Technology*, 51, 8757–8762.
- Gelman, A., Jakulin, A., Pittau, M. G., & Su, Y. S. (2008). A weakly informative default prior distribution for logistic and other regression models. *Annals of Applied Statistics*, 2, 1360–1383.
- Haddad, N. M. (1999). Corridor and distance effects on interpatch movements: A landscape experiment with butterflies. *Ecological Applications*, 9, 612–622.
- Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., Lovejoy, T. E., Sexton, J. O., Austin, M. P., Collins, C. D., Cook, W. M., Damschen, E. I., Ewers, R. M., Foster, B. L., Jenkins, C. N., King, A. J., Laurance, W. F., Levey, D. J., Margules, C. R., ... Townshend, J. R. (2015). Habitat fragmentation and its lasting impact on earth's ecosystems. *Science Advances*, 1, 1–9.
- Hamilton, P. V. (1977). Daily movements and visual location of plant stems by *Littorina irrorata* (Mollusca: Gastropoda). *Marine and Freshwater Behaviour and Physiology*, 4, 293–304.
- Hamilton, P. V., & Winter, M. A. (1982). Behavioural responses to visual stimuli by the *Littorina irrorata*. *Animal Behavior*, 30, 752–760.
- Hasselrot, B., & Grennfelt, P. (1987). Deposition of air pollutants in a wind-exposed forest edge. *Water, Air, and Soil Pollution*, 34, 135–143.
- Henry, M., Beguin, M., Requier, F., Rollin, O., Odoux, J. F., Aupinel, P., Tchamitchian, A., & Decourtye, A. (2012). A common pesticide decreases foraging success and survival in honey bees. *Science*, 336, 348–350.
- Hester, A. J., & Hobbs, R. J. (1992). Influence of fire and soil nutrients on native and non-native annuals at remnant vegetation edges in the Western Australian wheatbelt. *Journal of Vegetation Science*, 3, 101–108.
- Holloman, E. L., & Newman, M. C. (2012). Expanding perceptions of subsistence fish consumption: Evidence of high commercial fish consumption and dietary mercury exposure in an urban coastal community. *Science of the Total Environment*, 416, 111–120.
- Iacarella, J. C., & Helmuth, B. (2012). Body temperature and desiccation constrain the activity of *Littoraria irrorata* within the *Spartina alterniflora* canopy. *Journal of Thermal Biology*, 37, 15–22.
- Ims, R. A., & Stenseth, N. C. (1989). Divided the fruitflies fall. *Nature*, 342, 21–22.
- Kabadayi, C., Bobrowicz, K., & Osvath, M. (2018). The detour paradigm in animal cognition. *Animal Cognition*, 21, 21–35.
- Kane, A. S., Salierno, J. D., Gipson, G. T., Molteno, T. C. A., & Hunter, C. (2004). A video-based movement analysis system to quantify behavioral stress responses of fish. *Water Research*, 38, 3993–4001.
- Kater, B. J., Hannewijk, A., Postma, J. F., & Dubbeldam, M. (2000). Seasonal changes in acute toxicity of cadmium to amphipod *Corophium volutator*. *Environmental Toxicology and Chemistry*, 19, 3032–3035.
- Kitamura, T., & Imafuku, M. (2015). Behavioural mimicry in flight path of Batesian intraspecific polymorphic butterfly *Papilio polytes*. *Proceedings of the Royal Society B: Biological Sciences*, 282, Article 20150483. <https://doi.org/10.1098/rspb.2015.0483>
- Kobiela, M. E., Cristol, D. A., & Swaddle, J. P. (2015). Risk-taking behaviours in zebra finches affected by mercury exposure. *Animal Behavior*, 103, 153–160.
- Kölzsch, A., Alzate, A., Bartumeus, F., de Jager, M., Weerman, E. J., Hengeveld, G. M., Naguib, M., Nolet, B. A., & van de Koppel, J. (2015). Experimental evidence for inherent Lévy search behaviour in foraging animals. *Proceedings of Royal Society B: Biological Sciences*, 282, Article 20150424. <https://doi.org/10.1098/rspb.2015.0424>
- Krabbenhoft, D. P., & Sunderland, E. M. (2013). Global change and mercury. *Science*, 341, 1457–1458.
- Li, Y., Lee, J. M., Chon, T. S., Liu, Y., Kim, H., Bae, M. J., & Park, Y. S. (2013). Analysis of movement behavior of zebrafish (*Danio rerio*) under chemical stress using hidden Markov model. *Modern Physics Letters B*, 27, 1–13.
- Little, E. E., & Finger, S. E. (1990). Swimming behavior as an indicator of sublethal toxicity in fish. *Environmental Toxicology and Chemistry*, 9, 13–19. <https://doi.org/10.1002/etc.5620090103>
- Liu, Y., Lee, S. H., & Chon, T. S. (2011). Analysis of behavioral changes of zebrafish (*Danio rerio*) in response to formaldehyde using self-organizing map and a hidden Markov model. *Ecological Modelling*, 222, 2191–2201.
- Mainville, N., Webb, J., Lucotte, M., Davidson, R., Betancourt, O., Cueva, E., & Mergler, D. (2006). Decrease of soil fertility and release of mercury following deforestation in the Andean Amazon, Napo River Valley, Ecuador. *Science of the Total Environment*, 368, 88–98.
- Maltby, L. (2013). Ecosystem services and the protection, restoration, and management of ecosystems exposed to chemical stressors. *Environmental Toxicology and Chemistry*, 32, 974–983.
- McCloskey, J. T., & Newman, M. C. (1995). Sediment preference in the Asiatic clam (*Corbicula fluminea*) and viviparid snail (*Campeloma decusum*) as a response to low-level metal and metalloid contamination. *Archives of Environmental Contamination and Toxicology*, 28, 195–202.
- McGee, B. L., Wright, D. A., & Fisher, D. J. (1998). Biotic factors modifying acute toxicity of aqueous cadmium to estuarine amphipod *Leptocheirus plumulosus*. *Archives of Environmental Contamination and Toxicology*, 34, 34–40.
- McIntyre, N. E., & Wiens, J. A. (1999). How does habitat patch size affect animal movement? An experiment with darkling beetles. *Ecology*, 80, 2261–2270.
- McLean, D. J., & Skowron Volponi, M. A. (2018). trajr: An R package for characterisation of animal trajectories. *Ethology*, 124, 440–448.
- Metzger, J. P., & Décamps, H. (1997). The structural connectivity threshold: A hypothesis in conservation biology at the landscape scale. *Acta Oecologica*, 18, 1–12.
- Michelot, T., Langrock, R., & Patterson, T. A. (2016). moveHMM: An R package for the statistical modelling of animal movement data using hidden Markov models. *Methods in Ecology and Evolution*, 7, 1308–1315.
- Morales, J. M., & Ellner, S. P. (2002). Scaling up animal movements in heterogeneous landscapes: The importance of behavior. *Ecology*, 83, 2240–2247.
- Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., & Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences of the United States of America*, 105, 19052–19059.
- Nguyen, T. V., Liu, Y., Jung, I. H., Chon, T. S., & Lee, S. H. (2011). Unraveling Markov processes in movement patterns of indicator species in response to chemical stressors. *Modern Physics Letters B*, 25, 1143–1149.
- Niebuhr, B., Wosniack, M. E., Santos, M. C., Raposo, E. P., Viswanathan, G. M., da Luz, M. G. E., & Pie, M. R. (2015). Survival in patchy landscapes: The interplay between dispersal, habitat loss and fragmentation. *Scientific Reports*, 5, 1–10.
- Offerman, H. L., Dale, H. V., Pearson, S. M., Bierregaard, R. O., Jr., & O'Neill, R. V. (1995). Effects of forest fragmentation on neotropical fauna: Current research and data availability. *Environmental Reviews*, 3, 191–211.
- Pardini, R., Souza, S. M., Braga-Neto, R., & Metzger, J. P. (2005). The role of forest structure, fragment size and corridors in maintaining small mammal abundance and diversity in an Atlantic forest landscape. *Biological Conservation*, 124, 253–266.
- Pearson, S. M., Turner, M. G., Gardner, R. H., & O'Neill, R. V. (1996). An organism-based perspective of habitat fragmentation. In R. C. Szaro & D. W. Johnston (Eds.), *Biodiversity in managed landscapes: Theory and practice* (pp. 77–95). Oxford University Press.
- R Foundation for Statistical Computing. (2020). *R: A language and environment for statistical computing*.
- Roulet, M., Lucotte, M., Farella, N., Serique, G., Coelho, H., Passos, C. S., de Jesus da Silva, E., Scavone de Andrade, P., Mergler, D., Guimarães, J. R. D., & Amorim, M. (1999). Effects of recent human colonization on the presence of mercury in Amazonian ecosystems. *Water, Air, and Soil Pollution*, 112, 297–313.
- Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, 9, 671–675. <https://doi.org/10.1038/nmeth.2089>
- Shirley, T. C., Denoux, G. J., & Stickle, W. B. (1978). Seasonal respiration in the marsh periwinkle, *Littorina irrorata*. *The Biological Bulletin*, 154, 322–334.
- Silliman, B. R., & Newell, S. Y. (2003). Fungal farming in a snail. *Proceedings of the National Academy of Sciences of the United States of America*, 100, 15643–15648.
- Tankersley, R. A. (1989). The effect of trail-following on the locomotion of the marsh periwinkle *Littorina irrorata* (mesogastropoda: Littorinidae).

- Marine Behaviour and Physiology, 15, 89–100. <https://doi.org/10.1080/10236248909378721>
- Tinevez, J.-Y., Perry, N., Schindelin, J., Hoopes, G. M., Reynolds, G. D., Laplantine, E., Bednarek, S. Y., Shorte, S. L., & Eliceiri, K. W. (2017). TrackMate: An open and extensible platform for single-particle tracking. *Methods*, 115, 80–90. <http://fiji.sc/TrackMate>
- Vitousek, P. M., Mooney, H. A., Lubchenco, J., & Melillo, J. M. (1997). Human domination of earth's ecosystems. *Science*, 277, 494–499.
- Warren, J. H. (1985). Climbing as an avoidance behaviour in the salt marsh periwinkle, *Littorina irrorata* (Say). *Journal of Experimental Marine Biology and Ecology*, 89, 11–28.
- Wiens, J. A., & Milne, B. T. (1989). Scaling of "landscapes" in landscape ecology, or, landscape ecology from a beetle's perspective. *Landscape Ecology*, 3, 87–96.
- Wiens, J. A., Schooley, R. L., & Weeks, R. D., Jr. (1997). Patchy landscapes and animal movements: Do beetles percolate? *Oikos*, 78, 257–264.
- With, K. A., Cadaret, S. J., & Davis, C. (1999). Movement responses to patch structure in experimental fractal landscapes. *Ecology*, 80, 1340–1353.
- Wu, J., Huang, J., Han, X., Xie, Z., & Gao, X. (2003). Three-Gorges dam—Experiment in habitat fragmentation? *Science*, 300, 1239–1240.
- Xu, X., & Newman, M. C. (2015). Mercury exposure as a function of fish consumption in two Asian communities in coastal Virginia, USA. *Archives of Environmental Contamination and Toxicology*, 68, 462–475.
- Zartman, C. E. (2003). Habitat fragmentation impacts on epiphyllous bryophyte communities in central Amazonia. *Ecology*, 84, 948–954.
- Zengel, S., Montague, C. L., Pennings, S. C., Powers, S. P., Steinhoff, M., Fricano, G., Schlemme, C., Zhang, M., Oehrig, J., Nixon, Z., Rouhani, S., & Michel, J. (2016). Impacts of the deepwater horizon oil spill on salt marsh periwinkles (*Littoraria irrorata*). *Environmental Science & Technology*, 50, 643–652.
- Zhou, T., & Weis, J. S. (1999). Predator avoidance in mummichog larvae from a polluted habitat. *Journal of Fish Biology*, 54, 44–57.