Effects of invasive jumping worms (*Amynthas* spp.) on microhabitat and trophic interactions of native herpetofauna

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**Abstract** Invasive species can affect native communities through multiple mechanisms, including habitat modification and trophic interactions. In North America, invasive jumping worms (*Amynthas* spp.) may alter microhabitats used by native herpetofauna or serve as a novel prey resource for herpetofauna predators. We investigated effects of recently introduced *Amynthas* and previously established *Lumbricus* spp. earthworms on leaf litter microhabitat and trophic interactions of native herpetofauna using an outdoor mesocosm experiment, laboratory feeding trials, and field surveys of predator stomach contents in southern Wisconsin, USA. In mesocosms, *Amynthas* and *Lumbricus* reduced leaf litter biomass but did not have strong effects on soil conditions (pH, moisture, and temperature) or survival of American toad metamorphs (*Anaxyrus americanus*). In laboratory trials, American toads preyed on *Amynthas* but were less successful at capturing *Amynthas* than *Lumbricus* or crickets (*Acheta domesticus*). Attack success differences were likely due to unique defensive behaviors of *Amynthas*. *Amynthas* spent less time moving than *Lumbricus*, which was a behavior associated with delayed prey detection times by toads. In our diet surveys, we found novel evidence of *Amynthas* consumption by common garter snakes (*Thamnophis sirtalis*). We did not find *Amynthas* in stomach contents of American toads or red-bellied snakes (*Storeria occipitomaculata*), though additional surveys would help definitively determine whether these taxa are consuming *Amynthas*. Our findings highlight the importance of studying multiple mechanisms by which invasive species affect native communities and suggest that unique anti-predator behaviors may...
influence how *Amynthas* are incorporated into food webs as a novel prey resource.

**Keywords** Invasive earthworm · *Amynthas* · Herpetology · Trophic interactions · Ecosystem engineer

**Introduction**

Invasive species can affect recipient communities through a wide range of mechanisms, sometimes resulting in unforeseen consequences for native species. For instance, an invasive species may directly or indirectly influence trophic interactions, competition dynamics, disease transmission, or habitat structure (Crooks 2002; Carlsson et al. 2009; Vilcinskas 2015; Dueñas et al. 2018). Effects on native community members are generally not isolated to a single type of interaction (Bennett et al. 2011; Kaemingk et al. 2017), complicating efforts to understand and predict consequences of species invasions. Untangling multiple mechanisms through which an invasive species affects native species may require a combination of research techniques.

Some invasive species serve as ecosystem engineers by altering the physical habitat structure to which native species have adapted (Crooks 2002; Ransom 2011). Native species may be directly affected by the structural changes or indirectly affected by resulting shifts in habitat conditions or community composition. Overall effects of ecosystem engineers in invaded communities can be complex and multidirectional. For example, in a Mediterranean Sea community invaded by an algal ecosystem engineer (*Halimeda incrassata*), native fish may be attracted to, unafected by, or driven away from the altered ecosystem depending on the species (Vivó-Pons et al. 2020). Another invasive ecosystem engineer, the feral swine (*Sus scrofa*), dramatically reduced overall vegetation diversity in a Florida prairie, but promoted rapid growth of a single native forb (Boughton and Boughton 2014). Assessing net effects of invasive ecosystem engineers is further complicated when the invasive species also directly interacts with native taxa.

While the predatory roles of some invasive species have received longstanding research attention, the potential for invasive species to serve as novel prey has been recognized more recently. In some cases, nonnative prey can have positive population-level effects on native predators (Carlsson et al. 2009). This can be particularly important if an invasive species outcompetes native prey because it can mitigate the effect of reduced native prey availability (Dijkstra et al. 2013; Cava et al. 2018). For example, invasive round gobies (*Apollonia melanostomus*) in the Great Lakes have been incorporated into diets of native predators including fish, birds, and snakes (King et al. 2006; Hensler et al. 2008; Coleman et al. 2012) and have been linked to population recovery of native snakes (King et al. 2006). Alternatively, if predators are unable to effectively consume an invasive species, due for instance to dietary specialization (Suárez et al. 2000) or prey defensive traits, this may lead to population declines in native predators. In a well-studied example, the toxicity of invasive cane toads (*Rhinella marina*) to many native Australian predators (Phillips et al. 2003) has resulted in population declines of native snakes, lizards, and other species (Shine 2018).

Widespread on every continent but Antarctica (Hendrix et al. 2008), invasive earthworms can alter habitat structure and trophic interactions within invaded ecosystems. Earthworms act as ecosystem engineers by restructuring soil and leaf litter microhabitats, which subsequently alters community structure and ecosystem functions, including decomposition rates, nutrient cycling, and primary production (Craven et al. 2017; Freligh et al. 2019). In addition, invasive earthworms may be important prey for a variety of predators (Maerz et al. 2005; Gao et al. 2017; Virgin and King 2019), though research on their roles in trophic interactions is limited. Because earthworms reproduce with small cryptic cocoons, detection and widespread control are challenging, and nonnative earthworm range expansion may occur rapidly (Chang et al. 2021).

Jumping worms (*Amynthas* and *Metaphire* spp.) are widespread invasive species in the eastern United States and have recently invaded several midwestern and northeastern states (Chang et al. 2018). As only species of the *Amynthas* genus are considered in this study, jumping worms will hereafter be referred to as *Amynthas*. Originating in eastern Asia, including Japan and the Korean Peninsula (Blakemore 2003, 2014), these earthworms were likely spread to the United States through horticulture practices and use as fishing bait (Gates 1958; Görres and Melnichuk...
Arthropods, and common garter snakes (*Thamnophis sirtalis*), red-bellied snakes (*Storeria occipitomaculata*), and \( \textit{Anaxyrus americanus} \), habitat with and could potentially prey on Amynthas also home to native terrestrial herpetofauna that share 2002; Bohlen et al. 2004). Southern Wisconsin is spp.) (Hendrix and Bohlen Octolasion Lumbricus spp., spp., Aporrectodea earthworms (e.g., \( \textit{Aporrectodea, Lumbricus, and Octolasion spp.} \) (Chang et al. 2017)) (Chang et al. 2016a). Invasive jumping worms (*Amynthas spp.*) can reproduce parthenogenically, and produce cocoons throughout the summer months (Chang et al. 2016a). *Amynthas* have been known to outcompete previously established nonnative earthworms (e.g., \( \textit{Aporrectodea, Lumbricus, and Octolasion spp.} \) (Chang et al. 2016b; Laushman et al. 2018). *Amynthas* behaviors differ from other nonnative earthworms and their establishment may elicit changes in habitat structure and food webs (Chang et al. 2021), especially since *Amynthas* may outcompete and cause population declines of other earthworm species (Chang et al. 2016b; Laushman et al. 2018). Unlike many nonnative earthworms in North America, *Amynthas* live only on the surface and upper few centimeters of soil and create an aggregated casting layer on the soil surface that is distinct from other earthworm castings (Görres et al. 2019; Chang et al. 2021). *Amynthas* reduce leaf litter layers (Qiu and Turner 2017), though the extent to which this differs from other earthworms is largely unknown (Chang et al. 2021). Invasive *Amynthas* indirectly alter composition of leaf litter and soil invertebrate communities through mechanisms including resource competition (Snyder et al. 2011; Greiner et al. 2012; Gao et al. 2017). Additionally, invasive *Amynthas* potentially provide an abundant novel prey source, but anti-predator behavioral defenses such as their characteristic “jumping” behavior may make *Amynthas* challenging prey for native predators (Gorsuch and Owen 2014). Few studies have documented the role of invasive *Amynthas* in food webs (but see Gorsuch and Owen 2014 and Gao et al. 2017).

To examine how introduced *Amynthas* may affect native species through multiple mechanisms, we conducted a mesocosm experiment, laboratory feeding trials, and field diet surveys of native predators in Madison, Wisconsin, USA. In historically glaciated regions of the northern United States, including the Madison area, there are no native earthworm species but there are several established nonnative earthworms (e.g., \( \textit{Lumbricus spp.}, \textit{Aporrectodea spp.}, \textit{Octolasion spp.}, \textit{Eisenia. spp.} \) (Hendrix and Bohlen 2002; Bohlen et al. 2004). Southern Wisconsin is also home to native terrestrial herpetofauna that share habitat with and could potentially prey on *Amynthas*, including American toads (*Anaxyrus americanus*), red-bellied snakes (*Storeria occipitomaculata*), and common garter snakes (*Thamnophis sirtalis*) (Christoffel et al. 2008, 2009). American toads, particularly metamorphs, may be especially vulnerable to changes in cover and moisture content within leaf litter habitat and commonly co-occur with *Amynthas* in their invaded range (Heinen 1993; Rittenhouse et al. 2008). In the current study, we examined how *Amynthas* affect habitat and trophic interactions of terrestrial herpetofauna compared to established *Lumbricus* earthworms. We make comparisons with *Lumbricus* because they are a common local species who have experienced dramatic population declines associated with *Amynthas* invasion (Laushman et al. 2018). We expected differences in effects between the two species to reflect changes in local communities as *Amynthas* spread. We asked 1) how invasive *Amynthas* worms, *Lumbricus* worms, and native American toad metamorphs interact within leaf litter microhabitat, 2) how prey behavioral interactions with a generalist predator (American toads) compare between *Amynthas* and alternative prey, including *Lumbricus*, under laboratory conditions, and 3) whether native toads and snakes consume *Amynthas* in the field. We predicted that 1) *Amynthas* would directly reduce leaf litter mass via consumption, indirectly reduce moisture, and increase temperature of soil through litter depletion and soil aggregation, and indirectly reduce metamorphic toad survival because of these habitat changes; 2) toads would have reduced success at capturing *Amynthas* compared with alternative prey due to defensive behaviors of *Amynthas*, and 3) native toads and snakes would consume *Amynthas*, despite their status as a novel prey source in this region.

**Methods**

**Study site** – We conducted the mesocosm experiment and diet survey at the University of Wisconsin-Madison Arboretum (43.041293, −89.428252; hereafter referred to as the UW Arboretum), a 1,200-acre restored public natural area and research center surrounded by urban development. *Amynthas* were discovered in the UW Arboretum in 2013, and their range has expanded rapidly (Laushman et al. 2018). Laboratory feeding trials were conducted at the University of Wisconsin-Madison.

**Mesocosm experiment** – To examine effects of *Amynthas* on toad microhabitat, we performed a
2×2×2 factorial mesocosm experiment with the following treatments: 1) presence or absence of 4 American toad metamorphs, 2) presence or absence of 20 Amynthas worms, and 3) presence or absence of 20 Lumbricus worms. We randomly assigned treatments to 50-L plastic mesocosms (rim diameter = 45 cm, height = 38 cm). 46 total mesocosms were used, and each treatment was replicated in either 5 or 6 mesocosms (Table S1). We drilled holes in the bottom of the mesocosms for drainage and raised 70% shade cloth over them to simulate canopy cover. The mesocosms were covered on the bottoms with garden fabric and on the top with fiberglass mesh lids to prevent worms and toads from escaping. We filled each mesocosm to an approximate height of 30 cm with locally sourced screened topsoil from a nearby garden store, then topped the soil with an approximate wet mass of 460 g of hand mixed leaf litter collected randomly from an Amynthas-free area of an oak-dominated forest in the UW Arboretum. Litter was composed predominantly of black oak (Quercus velutina, ~ 66% by volume), white oak (Q. alba, ~ 14%), shagbark hickory (Carya ovata, ~ 14%), and black walnut (Juglans nigra, ~ 3%).

We collected Amynthas for the mesocosms by hand from beneath leaf litter, and we collected Lumbricus by applying a mustard solution to the soil (a method which draws worms to the surface by irritating the skin), after which they were rinsed with clean tap water. We only collected juveniles (worms lacking a clitellum) of all taxa, as Amynthas were predominantly in the juvenile life stage at the time. Worms were weighed (Table S1) and added to mesocosms within 12 h of collection. Based on known species compositions in the area (Laushman et al. 2018, Price-Christenson et al. 2020), Amynthas worms added to mesocosms were a combination of Amynthas tokioensis and A. agrestis, and Lumbricus worms in the experiment were Lumbricus terrestris and L. rubellus.

We collected American toad metamorphs around three ponds in Madison. Toads were weighed (Table S1) and added to mesocosms in similar size cohorts to minimize competition effects. Toads were presumed to feed on naturally occurring springtails, beetles, ants, and mites observed within leaf litter. We also added 10 to 20 flightless fruit flies evenly to each mesocosm every two days throughout the experiment to ensure adequate prey availability.

We began the experiment on July 26, 2019 and took soil measurements weekly. We measured soil pH and temperature (Hanna Instruments Direct Soil Measurement pH/Temperature Meter HI 99,121) and percent soil moisture (Extech Soil Moisture Meter MO750, range = 0–50%) by inserting probes at the soil surface to a depth of ~ 10 cm. On day 36 (Aug 31), we counted and weighed all toads and disassembled one toad + Amynthas + Lumbricus mesocosm to assess earthworm survival. Due to concerns about low numbers of observed Amynthas, both in the broken-down mesocosm and on the surfaces of other mesocosms, we added 10 newly collected Amynthas to all Amynthas-treated mesocosms (for a total of 30 Amynthas worms added). While Lumbricus had also declined in the broken-down mesocosm, we were more uncertain about their survival across tanks because Lumbricus were not easily visible compared to the surface-dwelling Amynthas, so we chose not to add more Lumbricus. On day 61 (Sep 25), we collected, counted, and weighed remaining toads and earthworms from all mesocosms. At this time, we also collected all leaf litter from each mesocosm and dried it in an oven for 24 h at 80° C to quantify litter dry mass.

Feeding experiments – To examine predator–prey behavioral interactions between toads and Amynthas, we conducted two no-choice feeding trial experiments in September 2019 (hereafter referred to as Exp. 1 and Exp. 2). For both experiments, we used the same 12 American toads (mean mass = 16.9 g; Table S2), collected from an Amynthas-free location (the UW-Madison Lakeshore Preserve). Toads were housed individually in 5.7-L plastic storage bins with moist peat moss substrate and access to distilled water, and they were fasted for at least 48 h prior to each experiment. We spot-cleaned habitats and replaced water daily.

The two feeding trial experiments had slightly different designs. During each trial in Exp. 1, a toad was offered one live house cricket (Acheta domestica), one Amynthas worm, or one Lumbricus worm. Each toad in Exp. 1 underwent one trial per prey type (36 total trials). Crickets were purchased from a local pet store and used as a positive control because they were expected to be readily consumed by toads. Amynthas were collected from the UW Arboretum, and Lumbricus (specifically, L. terrestris) were purchased from a local bait store. The average mass of
the purchased _Lumbricus_ (mean = 2.7 g) was approximately 3 times the mass of the _Amynthas_ (0.9 g) in Exp. 1 (Table S2). Because we did not want prey size differences to confound possible differences in earthworm-toad interactions, we then conducted a follow-up experiment (Exp. 2) in which we used only comparably sized _Amynthas_ (mean = 0.6 g) and _Lumbricus_ (mean = 0.6 g) prey (Table S2). In Exp. 2, _Amynthas_ and _Lumbricus_ were hand-collected in the UW Arboretum. Toads were offered one _Amynthas_ worm or one _Lumbricus_ worm per trial, and we conducted two trials per toad per prey type (48 total trials). In both experiments, trials were performed two days apart, and the order of prey for each toad was rotated between individual toads (Table S2).

Feeding trials were conducted in a clear plastic arena with a rectangular base (29.7 × 19.3 × 20.3 cm.) and brown paper was attached to the walls to minimize external stimuli. During each trial, we placed a toad under a transparent cover in the arena for a five-minute acclimation period. A pre-weighed prey item was placed in front of the toad, and the cover was removed. The time of each attack or capture and total number of attacks were recorded. Attacks were defined as any attempt (successful or not) by the toad to capture prey with or without physical contact. A capture was an attack that resulted in the full consumption of a prey item. In Exp. 1, we removed the toad after prey consumption or after 15 min if the prey had not been consumed. Based on a lack of captures observed in the last 5 min of Exp. 1 trials, we reduced the time limit to 10 min for Exp. 2. Due to observed interspecific variation in worm movement in Exp. 1 (see “Discussion” Section), we recorded each trial in Exp. 2 using an iPhone SE 2016 to quantify the proportion of total trial time a worm spent moving (hereafter referred to as “prey movement proportion”) and the time at which the toad first visibly detected the earthworm (hereafter referred to as “prey detection time”). The latter response variable was a consistently observed behavior in which a toad would visibly turn its head toward the prey item, often followed by other characteristic hunting behavior (e.g., crouching, stalking, attacking).

_Diet Surveys_—To determine whether American toads or colubrid snakes were consuming _Amynthas_ worms in the field, we collected individual predators and nonlethally recovered their stomach contents. We opportunistically captured predators during visual encounter surveys and from beneath cover boards. Both survey methods were used in two disconnected areas of the UW Arboretum: an _Amynthas_-invaded site (“invaded”) and a site with no known _Amynthas_ presence (“uninvaded”). The invaded site consisted of deciduous forest, oak savannah, prairie, and mowed/garden spaces. The uninvaded site contained pine forest, deciduous forest, oak savannah, and prairie. We surveyed the uninvaded site with the goal of comparing diets between the two areas; however, the number of predators captured in each location was too low to robustly analyze diet differences. To survey cover boards, we haphazardly placed a total of 50 corrugated tin and 20 plywood boards evenly in the two areas of the Arboretum. We checked boards about twice a week from May to September 2020. Upon capture of each toad and snake, we recorded mass and snout-vent length (SVL) (Figs. S2 and S3). We collected snake stomach contents by gently palpating the stomach to induce regurgitation (Seigel et al. 1987). We collected toad stomach contents by using gastric lavage methods (Solé et al. 2005) with clean well water from an 8Fr (diameter = 2.3 mm) silicone veterinary feeding tube and 60 ml plastic syringe. Stomach contents were strained through a paper coffee filter. Retained prey items were preserved in 70% ethanol and later identified visually using a dissecting microscope.

_Analyses_—We analyzed treatment effects on leaf litter dry mass, soil parameters (pH, temperature, and log-transformed percent moisture), and toad survival within mesocosms. Our experimental design included toads as an independent variable to assess toad effects on earthworm survival, but we were unable to test this effect due to low earthworm survival in all treatments (see Table S1 and Discussion). Because toads did not affect leaf litter or soil responses and including toads as a predictor did not improve model performance, we grouped toad present and absent treatments for analyses of habitat variables. We tested effects on leaf litter dry mass using linear models (lm, ‘stats’ package) with fixed effects for presence/absence of _Amynthas_, presence/absence of _Lumbricus_, and their interaction. To test effects on soil responses, we used generalized additive mixed models (gamm, ‘mgcv’ package) with the same earthworm treatment predictors, a smoothing term for sample date, and a random intercept for mesocosm identity to account for repeated measurements (Wood 2017). We tested earthworm effects on
We analyzed feeding experiment data to test our hypothesis that toads would be less successful predators of *Amynthas* than alternative prey. Exp. 1 and 2 were analyzed independently. We analyzed effects of prey type on the total number of attacks per trial and on the binary success or failure of each attack (“attack success”) using generalized linear mixed effects models (glmer, ‘lme4’ package) with a fixed effect for prey type and a random intercept for toad identity (Bates et al. 2015). We specified a Poisson distribution for the attack number model and a binomial distribution for attack success. For Exp. 1, each model was followed by Tukey-adjusted pairwise comparisons (pairs, ‘emmeans’ package) to directly compare between the three prey types (Lenth et al. 2021). We used a linear model (lm, ‘stats’ package) to test for effects of prey type on prey movement proportion (time moving/total trial time; logit-transformed). Lastly, we assessed the relationship between earthworm movement and toad hunting behavior in Exp. 2 using a linear mixed effects model (lmer, ‘lme4’ package) with prey detection time (log-transformed) as the response, prey movement proportion (logit-transformed) as a predictor, and toad identity as a random intercept (Bates et al. 2015). All analyses were performed in R version 4.03 (R Core Team 2020).

Results

**Mesocosm experiment**—*Amynthas* and *Lumbricus* earthworms altered leaf litter but did not substantially affect soil conditions or toad survival. *Amynthas* presence reduced dry leaf litter mass by 16% compared to controls ($\beta = -16.43$, $SE = 4.20$, $t = -3.92$, $p < 0.001$) and *Lumbricus* reduced dry litter mass by 13% compared to controls ($\beta = -12.82$, $SE = 4.10$, $t = -3.13$, $p = 0.003$) (Fig. 1). Mesocosms with both earthworms present had 26% less dry litter mass than controls, but we did not see evidence of an interaction between earthworms ($\beta = 3.10$, $SE = 5.93$, $t = 0.52$, $p = 0.605$) (Fig. 1). Sampling date strongly affected all three soil responses (Fig. S1, Table S3). Toad survival across all treatments averaged 52% on day 36 and 34% at the end of the experiment on day 61 ($\beta = -1.77$, $SE = 0.89$, $t = -1.98$, $p = 0.063$). Mesocosms with both earthworms had the lowest mean final toad survival at 21% compared with 30% for *Amynthas* mesocosms, 46% for *Lumbricus* mesocosms, and 38% for control mesocosms (Fig. 2).

**Feeding experiments**—In both experiments, toads attacked *Amynthas* more times per trial on average than other prey types, but attacks were less likely to result in a capture. We observed at least one attack in most trials with crickets (92%), and in comparably fewer trials with *Amynthas* (Exp. 1: 58%, Exp 2: 42%) and with *Lumbricus* (Exp. 1: 33%, Exp. 2: 55%). In Exp. 1, the mean number of toad attacks per trial on *Amynthas* was over 2× the number on crickets (ratio = 2.21, $SE = 0.60$, $z = 2.94$, $p = 0.009$) and over 3× the number on *Lumbricus* (ratio = 3.82,
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SE = 1.26, z = 4.05, *p* < 0.001) (Fig. 3a). Similarly, the mean number of attacks per trial on *Amynthas* in Exp. 2 was 3 times the number on comparably sized *Lumbricus* (β = 1.11, SE = 0.25, z = 4.53, *p* < 0.001) (Fig. 3b). Mean attack success on *Amynthas* in Exp. 1 was over 13× lower than on crickets (odds ratio = 0.06, SE = 0.06, z = −3.06, *p* = 0.006) and 9× lower than on *Lumbricus* (odds ratio = 0.10, SE = 0.11, z = −2.15, *p* = 0.080) (Fig. 3c). In Exp. 2, mean attack success on *Amynthas* was again 9× lower than on comparably sized *Lumbricus* (β = 3.30, SE = 0.95, z = −3.48, *p* < 0.001) (Fig. 3d). During Exp. 2, prey movement proportion was lower for *Amynthas* than for *Lumbricus* (β = −2.18, SE = 0.54, t = −4.02, *p* < 0.001) (Fig. 4a). Lastly, prey detection time in Exp. 2 occurred earlier during trials in which worms spent a larger proportion of time in motion (β = −0.337 ± 0.129 SE, t = −2.615, *p* = 0.012) (Fig. 4b).

**Diet surveys** — *Amynthas* earthworms were detected in the stomach contents of common garter snakes, but not the other predators surveyed. We captured a total of 24 American toads, 35 red-bellied snakes, and 44 common garter snakes. We captured 11 of the toads at the *Amynthas*-invaded site and 14 at the uninvaded site. Only 1 toad was found under...
a cover board; all others were found incidentally. No *Amynthas* were identified in toad stomach contents, and only one earthworm (unidentifiable) was recovered from a toad in the *Amynthas*-uninvaded site. Other toad prey (reported as the % of total prey items) included 25% snails (2 toads), 19% ants (2 toads), 9% millipedes (4 toads), 7% dipterans (5 toads), 5% springtails (5 toads), and 7% unidentifiable prey (5 toads) (Table 1). “Unidentifiable prey” were prey items considered too degraded for any level of identification. Nearly all (96% of common garter and 91% of red-bellied) snakes were captured at the *Amynthas*-invaded site. Stomach contents were recovered from 37% of red-bellied snakes (13 individuals), and all identifiable prey consisted of nonnative slugs. Prey consisted of 65% *Deroceras reticulatum* (7 snakes), 12% *Arion subfuscus* (2 snakes), 18% unidentifiable slugs (3 snakes), and 6% unidentifiable prey (1 snake) (Table 1). Common garter snakes were the only species whose stomach contents contained *Amynthas*. We recovered stomach contents from 34% of common garter snakes (15 individuals). Prey items consisted of 26% *Amynthas* spp. (5 snakes), 26% *Lumbricus* spp. (3 snakes), 26% American toads (5 snakes), 11% unidentifiable earthworms, and 11% unidentifiable prey (2 snakes) (Table 1).

**Discussion**

Using mesocosm experiments, laboratory feeding trials, and field diet surveys, we were able to increase understanding of the mechanisms through which a recent *Amynthas* invasion affects native herpetofauna in the upper Midwest, USA. *Amynthas* reduced litter mass, but did not cause strong changes to soil conditions or toad survival. Our laboratory feeding trials and diet surveys indicated that *Amynthas* are a viable prey source for native herpetofauna, particularly common garter snakes, though their defensive behaviors may make them difficult to capture for some species. Overall, we found that *Amynthas* alter microhabitat by reducing leaf cover and affect prey availability for native herpetofauna. The ability of herpetofauna to tolerate or benefit from these changes may depend on microclimatic requirements, hunting behaviors, and dietary flexibility. More broadly, our results suggest that combining experimental and field studies can be a useful approach to isolate distinct mechanisms mediated by invasive species and quantify their importance in communities.

*Amynthas* reduced leaf litter biomass in our mesocosms, which supports prior research (Greiner et al. 2012; Ziemba et al. 2015; Qiu and Turner 2017). *Lumbricus* also reduced litter mass, but the extent to which the functional roles of *Amynthas* and *Lumbricus* in leaf litter breakdown differ is unclear from our experiment, and we found no evidence of interactive effects. Our results show weak evidence that *Amynthas* may raise soil temperatures, but this effect was inconclusive, and we saw no other effects of *Amynthas* or *Lumbricus* on soil responses. Prior studies of *Amynthas* effects on soil conditions show mixed results, but studies have found *Amynthas* to be associated with increased pH (Laushman et al. 2018; Bethke and Midgley 2020), altered thermal properties (Görres et al. 2019), and increased moisture loss (Görres et al. 2019). Litter decomposition processes and soil aggregation through casting are proposed indirect mechanisms for these soil effects (Chang
et al. 2021). In our study, remaining unconsumed leaf litter and ambient environmental conditions (e.g., light levels, relative humidity, and rainfall) may have buffered soil from meaningful temperature and moisture changes. Both *Amynthas* and *Lumbricus* survival was very low at the end of the experiment (Table S1). While we cannot be certain of the cause, heavy flooding that prevented proper mesocosm drainage during the week before the experiment ended likely caused at least a portion of the mortality. Nevertheless, the substantial differences in leaf litter masses between controls and earthworm treatments provide strong evidence that enough earthworms of both species survived long enough to cause leaf litter reduction, which was the main mechanism we predicted to have cascading effects on soil conditions and toad survival. That said, the magnitude of earthworm effects on leaf litter, soil properties, and amphibians in our experiment was likely affected by changes in earthworm densities over time. Future experiments in which *Amynthas* densities are carefully manipulated across the range of naturally observed densities would be useful to further clarify their direct and indirect effects.

The combination of *Amynthas* and *Lumbricus* had an increasingly negative association with toad survival over time, but this effect was relatively weak. Toad survival was low (<50% on average) across all treatments but tended to be slightly lower in tanks with *Amynthas* (Fig. 2). Earthworms reduced leaf

date

### Table 1

Prey identified in stomach contents of herpetofauna predators from field diet surveys at the UW Arboretum (Madison, WI, USA). Prey count is the total number of individuals of a certain prey type across all predator individuals of a certain species. Predator count is the total number of predators that consumed one or more of each prey type.

| Species                      | Prey type                        | Prey count | Predator count |
|------------------------------|----------------------------------|------------|----------------|
| *Anaxyrus americanus* (n=24) | Araneae                          | 4          | 3              |
|                              | Blattodea                        | 9          | 2              |
|                              | Chilopoda                        | 5          | 4              |
|                              | Coleoptera                       | 5          | 5              |
|                              | Collembola                       | 5          | 5              |
|                              | Diplopoda                        | 9          | 4              |
|                              | Diptera (adult)                  | 1          | 1              |
|                              | Diptera (larva)                  | 6          | 4              |
|                              | Gastropoda (snail)               | 24         | 2              |
|                              | Gastropoda (slug—*Deroceras reticulatum*) | 1 | 1             |
|                              | Hymenoptera (Formicidae)         | 18         | 4              |
|                              | Hymenoptera (unknown)            | 1          | 1              |
|                              | Isopoda                          | 1          | 1              |
|                              | Nematoda                         | 1          | 1              |
|                              | Oligochaeta                      | 1          | 1              |
|                              | Trombidiformes                   | 1          | 1              |
|                              | unidentified                     | 7          | 5              |
|                              | no prey recovered                | –          | 6              |
| *Storeria occipitomaculata* (n=35) | *Arion subfuscus*              | 2          | 2              |
|                              | *Deroceras reticulatum*          | 11         | 7              |
|                              | unidentified slug                | 3          | 3              |
|                              | unidentified                     | 1          | 1              |
|                              | no prey recovered                | –          | 22             |
| *Thamnophis sirtalis* (n=44)  | *Amynthas* spp.                  | 5          | 5              |
|                              | *Anaxyrus americanus*            | 5          | 5              |
|                              | *Lumbricus* spp.                 | 5          | 3              |
|                              | unidentified earthworm           | 2          | 2              |
|                              | unidentified                     | 2          | 2              |
|                              | no prey recovered                | –          | 29             |
litter, which in turn might have reduced cover, humidity, and prey habitat (Rittenhouse et al. 2008; Kazemi et al. 2009) which may have affected toad mortality. Earthworm invasions have been linked to effects on other terrestrial amphibians, namely eastern red-backed salamanders (Plethodon cinereus) (Maerz et al. 2009; Ransom 2011, 2012; Ziemba et al. 2015). For example, nonnative Lumbricus earthworms are associated with declines in salamander abundance in the northeastern United States (Maerz et al. 2009), and consumption of leaf litter by Amynthas can have sublethal effects on salamanders through increasing movement and thus energy expenditures (Ziemba et al. 2015). American toads are somewhat less susceptible to desiccation than other amphibians (Rittenhouse et al. 2008), so negative effects of earthworms may have been stronger on other amphibian species. Research comparing lethal and sublethal effects of Amynthas among multiple litter-dependent herpetofauna taxa would help assess habitat modification effects across a broader native community.

In the feeding experiments, American toads hunted and attacked Amynthas, Lumbricus and crickets, but toads were often unsuccessful when attacking Amynthas compared with alternative prey. We observed a higher number of attacks on Amynthas per trial because of the frequent failed attacks. The repeated attacks on Amynthas suggest that low attack success was likely a result of worm defensive behaviors rather than unpalatability (e.g., toxins or distasteful compounds). Gorsuch and Owen (2014) found that, compared with other nonnative earthworms (Aporrectodea longa and L. rubellus), Amynthas are more successful at evading capture by nonnative wandering broadhead planarians (Bipalium adventitium), native seal salamanders (Desmognathus monticola), and native ribbon leeches (Nepholopsis obscura). We observed three distinct defensive behaviors by Amynthas: jumping, freezing, and autotomy (tail separation). The jumping defense is a behavior characterized by rapid undulations by an Amynthas worm to propel itself away from a physical disturbance and potentially startle a predator (Gorsuch and Owen 2014). Freezing was characterized by an immediate cease in movement for seconds to minutes at a time following a physical disturbance. This behavior has not been previously reported in the literature to our knowledge. As sight-based hunters, the toads commonly stopped displaying hunting behaviors when worm movement ceased, making this an effective strategy. Autotomy was the complete detachment of the tail region; this response occurred only once during our trials and has also been reported in prior research (Gorsuch and Owen 2014). In our study the toad consumed the separated tail and afterward captured and consumed the full worm, further evidencing the palatability of Amynthas to toads.

Overall movement patterns of Amynthas differed substantially from those of Lumbricus. Amynthas movement was sporadic and varied, due in part to the freezing behavior, while Lumbricus typically moved throughout most of the trial regardless of attacks. Additionally, Amynthas movement sometimes only involved the head or mouthpart while the rest of the body was stationary, which may have influenced toad hunting behavior. Worm movement patterns were associated with toad hunting behavior; prey detection time and thus hunting activity occurred earlier during trials with more active worms. Divergent life histories of Amynthas and Lumbricus may help explain movement differences. Amynthas dwell on or near the soil surface (epigeic to epi-endogeic) and are not known to create vertical burrows (Richardson et al. 2009; Qiu and Turner 2017), while Lumbricus are shallow-dwelling to deep-burrowing (epi-endogeic to anecic), depending on species (Shipitalo et al. 1988; Hale et al. 2006). For Lumbricus, especially anecic species like L. terrestris, constant movement may itself be a defense mechanism if its purpose is to seek a burrow to escape. Amynthas may have evolved more diverse behavioral defenses because living on the soil surface results in more frequent exposure to a wide range of terrestrial predators in their native range. Amynthas are highly abundant on the soil surface in recently invaded areas (Laushman et al. 2018), so although they are likely harder to capture than Lumbricus, they also may be more readily available to certain predators. While laboratory trials can help us predict the outcome of novel trophic interactions between invasive and native species, field studies are needed to reveal more clearly how invasive species integrate into natural food webs.

In our herpetofauna diet surveys, we found Amynthas in the stomach contents of garter snakes but not of American toads or red-bellied snakes. American toad stomach contents were primarily composed of arthropods and gastropods, though one toad consumed a non-Amynthas earthworm (Fig. S3). This
aligns with prior, though limited, findings that toads predominantly consume arthropod prey (Smith and Bragg 1949; Bellocq et al. 2000; Bolek and Coggins 2000), but may opportunistically prey on earthworms (Bush 1959). Earthworms have also been recorded in diets of other amphibians (Careddu et al. 2020), including the related genus Bufo (Evans and Lampo 1996; Vallvé and Sánchez-Iglesias 2018; Kolenda et al. 2019) and may be especially important prey after rain events (Maerz et al. 2005). Our sample size of American toads was relatively small, particularly at the Amynthas-invaded site, and a larger dataset would be useful to definitively conclude whether or not American toads are consuming Amynthas in the field. Additionally, soft-bodied prey like earthworms are digested more quickly than arthropod prey and therefore may be missed more often in visual stomach contents surveys (Pompanon et al. 2012). Surveying at night when toads are more likely to be feeding can help reduce this bias (Dodd 2010). Based on our laboratory trials, American toads may opportunistically consume Amynthas if they can capture them, but due to the inefficient hunting behavior we observed, hunting Amynthas may result in a higher energy expense and lower prey yield compared to alternative prey. This is important because Amynthas-induced extirpations of earthworms including Lumbricus (Chang et al. 2016b; Laushman et al. 2018) and shifts in broader invertebrate communities (Snyder et al. 2011; Gao et al. 2017) may change the prey assemblages available to American toads and other species. More field-based research, including quantification of energy flows into herpetofauna predators, would be needed to test this idea. Additionally, while we captured similar numbers of toads in invaded and uninvaded areas, research over a longer time period and larger sample size could more clearly assess whether Amynthas have population-level effects on toads.

Our study provides the first evidence that we are aware of for common garter snake consumption of Amynthas. Common garter snakes are highly opportunistic predators and are known to consume non-native prey including Lumbricus and Apporectodea earthworms (Virgin and King 2019). We expect that as Amynthas compete with and reduce populations of other earthworm taxa (Chang et al. 2016b; Laushman et al. 2018), Amynthas will become an increasingly important component of common garter snake diets. This trend may have significance for other snakes of local conservation concern, such as the Butler’s garter snake (Thamnophis butleri), which is an earthworm specialist and is considered a species of conservation concern in areas including Wisconsin (Wisconsin Department of Natural Resources 2017). Possibly, garter snakes and other predators that hunt using chemoreception may be able to better overcome some of the defensive behaviors of Amynthas, such as jumping and freezing, compared with predators that depend largely on sight-based hunting strategies (e.g., toads). Two other taxa, native centipedes (families Cryptopidae and Scolopocryptopidae) and native rusty crayfish (Orometes rusticus), have displayed relative success at capturing invasive Amynthas (Gorusch and Owen 2014; Gao et al. 2017) and are also known to use chemoreception (Müller et al. 2011; Kraus-Epley et al. 2015). Laboratory feeding trials testing chemoreception of snakes or other species (see Burger 1991) with Amynthas prey could test this idea. Additionally, it is unclear how the nutritional and energetic value of Amynthas as prey compare with other prey species, which could be another informative research direction.

Interestingly, red-bellied snakes in our study consumed only nonnative slugs, which corroborates previous research (Virgin and King 2019). Common garter and red-bellied snakes are both widespread and relatively common in urban areas (Kjoss and Litvaitis 2001). The dietary flexibility that allows predators to opportunistically switch to nonnative prey may also help them succeed in urban areas because anthropogenic disturbances strongly affect prey availability (Seress et al. 2018; Siqueira and Marques 2018). Accordingly, we suggest future research focus on species-specific traits that make native predators successful at utilizing nonnative prey. Further, we captured far more common garter and red-bellied snakes where Amynthas were present, which could be associated with differing prey availabilities due to nonnative species, though we have little evidence for this relationship. Research investigating direct and indirect effects of nonnative prey (e.g., Amynthas and slugs) on snake populations while controlling for environmental and habitat variables could assess this possible mechanism.

Due to the potential for multiple, multidirectional effects of invasive species on native communities, an integrative approach to invasive species research is essential. While teasing apart the individual
mechanisms that affect native species can be complex, from a conservation standpoint it is important to understand the net effects of invasive species interactions within native communities. Our research helps to advance understanding of the effects of *Amynthas* on native herpetofauna microhabitat and trophic interactions. More generally, our findings emphasize the potential importance of nonnative species as novel food resources to native consumers (Carlsson et al. 2009). This often-overlooked ecological role should be evaluated alongside the more commonly studied effects of invasive species as consumers, competitors, and disease vectors to obtain a more holistic understanding of invasion biology.

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**Authors’ contributions** EC, DP, BH, and DD conceived the ideas and designed the studies. EC, ES, and DP helped with mesocosm setup and statistical analyses. EC collected data and wrote the manuscript draft. All authors contributed to revisions.

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**Availability of data and material** The datasets and code generated during the current study are available from the corresponding author on reasonable request.

**Declarations**

**Conflict of interest** The authors declare no conflicts of interest.

**Ethics approval** All use of research animals was approved by UW-Madison College of Agriculture and Life Sciences IACUC (Protocols A006183-A02 and A006186-A03). Permits were obtained from the Wisconsin Department of Natural Resources for sampling and collection (#SRLN-19-32 and #SRLN-20-12).

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