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REVIEW

Non-native freshwater snails: a global synthesis of invasion status, mechanisms of introduction, and interactions with natural enemies

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Abstract

1. Non-native freshwater snails can play important roles as consumers, hosts, and prey. Despite their potential ecological importance, global patterns in non-native snail taxonomy, geography, and ecology have not been documented. Our objectives were to use a semi-quantitative systematic review to describe non-native freshwater snail global diversity, distribution, mechanisms of introduction, and interactions with natural enemies, including parasites and predators.
2. Based on 506 relevant publications, we recorded 95 non-native freshwater snail species from 16 families. Six taxonomic families, and pulmonate snails as a group, were over-represented relative to the number of species expected by chance. Eight snail species represented 63% of the research records. A few snail taxa (15%) were widespread global invaders, reported from four or more continents, while most invasions were limited to a single continent. Australia and the Pacific Islands were the largest 'sink' for non-native snails, with the greatest difference in the number of non-native taxa relative to native taxa that had spread to other continents.
3. Aquarium hobby sales were implicated as the most common mechanism of introduction (41% of species), followed by "hitchhiking" on aquatic vegetation, human consumption, use for biocontrol, transportation in canals, commercial shipping, and outdoor recreation. A search of internet sales posts indicated that four of the six over-represented snail families were readily available for purchase online.
4. Non-native snails hosted parasites of wildlife, livestock, and human health importance, yet on average had 80% lower parasite richness in their non-native compared to native range. At least 65 taxa were documented as consumers of non-native snails, including native predators of conservation concern. These findings suggest that non-native snails often are released from parasitism, but may commonly experience biotic resistance from predators.
5. Our synthesis emphasizes the relatively high diversity of non-native snails, but the disproportionate role of a few taxonomic groups in driving ecological, economic, and public health challenges. Moving forward, it will be important to limit new snail introductions through policy, education, and monitoring, particularly as

the effective control of established snail invasions remains challenging in most ecosystems.

KEYWORDS

freshwater management, gastropod, host–parasite, introduced, predator–prey

1 | INTRODUCTION

Understanding and predicting the effects of non-native species can be challenging owing to a lack of basic information on the identity, distribution, and ecology of invading organisms. In some cases, new invasions are cryptic, with years passing before an invader has been identified in a new location and its ecological roles recognized (Morais & Reichard, 2018; Spear et al., 2021). Given the potential consequences of species invasions for biodiversity conservation, public health, and economics, increasing our knowledge of the taxonomic and geographical distribution of non-native species represents a key goal in ecology and resource management (Lockwood et al., 2013). Achieving this aim will help move towards strategies that emphasize prevention, monitoring, and early detection of invasions, rather than focusing efforts only on the control of well-established invaders (Reaser et al., 2020; Vander Zanden et al., 2010).

Freshwater snails are widespread non-native species that can exert significant ecological effects on recipient communities and ecosystems. For instance, they can alter primary production and nutrient cycling (Carlsson & Bronmark, 2006; Hall et al., 2003, 2006; Moslemi et al., 2012), outcompete other community members (Pointier et al., 2011), serve as prey for consumers (Cattau et al., 2016; Yamanishi et al., 2012), or transmit parasites of wildlife, livestock, and human health importance (Madsen & Frandsen, 1989; Pointier, 1999; Sauer et al., 2007). Owing to this diversity of interactions, non-native freshwater snails can cause undesirable impacts (e.g., economic losses from agricultural pests; Halwart, 1994; Naylor, 1996); or alternatively, they may provide valued ecological roles (e.g., positive effects on native species of conservation concern; Cattau et al., 2016). Despite their importance, several challenges have hindered a holistic understanding of the global status, ecology, and conservation implications of non-native freshwater snails. Among these issues are confusion over taxonomic identities, a limited knowledge of global geographical patterns, and gaps in understanding of ecology of non-native snails in their introduced ranges. To date, a number of papers have reviewed non-native freshwater snails in specific geographical areas (Araya, 2015; Cowie, 1998; Darrigran et al., 2020; Karatayev et al., 2009; Kesner & Kumschick, 2018; Naranjo-Garcia & Castillo-Rodriguez, 2017; Pointier, 2001; Roll et al., 2009) or have focused on specific snail taxa (Alonso & Castro-Díez, 2008, 2012; Hayes et al., 2015; Horgan et al., 2014; Pointier et al., 2005), but a global synthesis does not exist.

Our objectives for the current study were to use a semi-quantitative systematic review to describe the global diversity of non-native freshwater snails, their distribution, mechanisms of introduction, and interactions with natural enemies. Our specific questions included: (1) How many taxa of non-native freshwater snails have been reported, and are certain taxonomic groups over-represented? (2) At the global scale, do some regions serve as "sources" or "sinks" for non-native freshwater snails? (3) What mechanisms are most responsible for new anthropogenic introductions of non-native freshwater snails? and (4) How does the diversity of freshwater aquarium snails for sale online compare with the observed non-native taxa? We predicted that non-native freshwater snails would disproportionately come from a few taxonomic families, such that taxonomic richness was likely to be a relatively poor predictor of the number of non-native taxa within a family (Lockwood, 1999). This disproportionate taxonomic representation could be caused by shared traits that enhance invasion success and/or differences in the likelihood of human-aided transport between families. We also expected that regions with high freshwater snail diversity that also are sources of snails in the aquarium and aquatic plant trades would be most likely to act as geographical sources rather than as sinks. This prediction stems from the likelihood that the aquatic plant and animal trade is expected to be among the most important mechanisms of new introductions of aquatic organisms, including snails (Duggan, 2010). We also predicted that many of the non-native snail taxa recorded from our literature search would be available for purchase online, emphasizing the growing importance of online sales in the spread of non-native species (Olden et al., 2020).

We also were particularly interested in how non-native snails interact with natural enemies (i.e., parasites and predators), with a focus on evaluating support for the "enemy release" and "biotic resistance" hypotheses, which have been advanced as a framework for predicting the establishment and spread of non-native species (Lockwood et al., 2013; Ricciardi et al., 2013). With this in mind, we additionally asked: (5) Do non-native snails have fewer parasites in their introduced than native range? and (6) Which predators utilize non-native freshwater snails as novel prey resources? We expected to find that non-native snails, in general, host fewer parasites in their introduced ranges, owing to a lack of obligate non-snail hosts for complex life cycle parasites in the introduced snail's range and/or the rare occurrence of parasites being transported to new areas with their hosts (Colautti et al., 2004; Torchin et al., 2003). This pattern has been observed for several individual snail taxa (Ebbs et al., 2018), but has not been synthesized across multiple non-native host species. Lastly, we predicted that many generalist aquatic predators would consume non-native snails, suggesting the potential for biotic control from native predators.

2 | METHODS

2.1 | Database search

We used a Web of Science database search to identify papers involving non-native freshwater snails. The search string was as follows: “TS=(("invasive" OR "non-native" OR "nonnative" OR "introduced" OR "exotic" OR "alien") AND ("freshwater" OR "lake" OR "pond" OR "stream" OR "river" OR "wetland") AND ("snail*" OR “gastropod*"))”. The search results included papers available in Web of Science up to August 2021. A total of 1,077 papers were returned, which initially were screened based on their titles and abstracts. We omitted all papers on marine snails, slugs, bivalves, terrestrial snails, and extinct taxa. We also excluded records of non-native snails in aquarium stores, unless those species also were reported in the field in the same paper. Table S1 includes the reference list of relevant papers that remained after the initial screening.

2.2 | Data extraction

From each relevant paper, we extracted information on the research focus, research venue, snail taxonomic identities, the regions where each snail was reported as native and non-native, the mechanism(s) of introduction, and data on parasitism and predation in the non-native range. Research focus was categorized into one or more of the following six groups for each paper: (1) range records of a non-native snail population; (2) ecological impacts on species, communities, or ecosystems in the non-native range; (3) non-native snail biology, including genetics, life-history, physiology, morphology, and behavior; (4) invasion drivers, defined as biotic and/or abiotic environmental factors influencing invasion success; (5) parasite–host ecology; and (6) studies testing or implementing non-native snail control or management. We categorized research venues into six groups: (1) field studies, (2) laboratory studies, (3) outdoor mesocosm experiments, (4) modelling, (5) literature reviews, or (6) mixed venues. Below we provide additional information defining the other response variables and how they were analyzed.

2.3 | Taxonomic patterns

Once we obtained a species list of non-native snails, we checked for synonymous taxonomic names within our list, using the original papers, an online nomenclatural database (www.molluscabase.org), and additional focused literature searches as needed. Synonymous taxonomic names returned in the literature search were combined to generate a species list of unique taxa for subsequent analyses. We also included notes on possible synonyms that were not found in the literature search (Table S2).

In order to examine whether any taxonomic groups were over-represented, we compared the observed number of non-native snails per family to the expected number if non-native taxa were distributed randomly across families. We also conducted this same analysis on all pulmonate snails combined, which were hypothesized to be over-represented. We followed the approach used by Lockwood (1999) to estimate the probability that the number of non-native snail species per family was equal or more extreme than the observed value due to random chance alone. The equation used to generate the probabilities (R) was:

$$R = \left(\frac{n\,!}{X\,!\,(n - X)\,!} \right) p^X q^{n-X}$$

where n is the total number of species in a family, X is the observed number of non-native species in the family, p is the overall proportion of all non-native species out of all families, and q is the overall proportion of species that were not documented as non-native from all families. We restricted the analyses to families that had at least one species of observed non-native snail. For the number of species per family, we followed the estimates from Lydeard and Cummings (2019). Galindo et al. (2016) was only used for the species count in the family Nassariidae, which included one freshwater non-native taxon in our dataset. See Table S3 for the observed and expected number of non-native species and the family richness values.

2.4 | Geographical patterns

Our analyses of geographical patterns focused on six continental regions: Australia and the Pacific Islands, Asia, Europe, Africa, Central and South America (including the Caribbean Islands), and North America. From each paper, we recorded which of these regions each snail was reported as being native and non-native. We combined this information across records for each snail species. We additionally cross-checked the resulting native and non-native localities with the Global Biodiversity Information Facility (www.gbif.org), an online database assembling occurrence observations of organisms. As a consequence of challenges in verifying the GBIF records, many of which are based on citizen science data, we analyzed the geographical patterns without the additional GBIF data, but we include those locality records in Table S2 as an additional resource.

In order to examine whether certain regions acted as “sources” or “sinks” for non-native freshwater snails, we calculated an index (K) representing asymmetry in the introductions or departures from each region, following Turbelin et al. (2017):

$$K = \frac{\left(\frac{NN_R}{NN_{Tot}} - \frac{N_R}{NN_{Tot}} \right)}{\left(\frac{NN_R}{NN_{Tot}} + \frac{N_R}{NN_{Tot}} \right)}$$

where NN_R is the number of non-native snail species in a region, N_R is the number of native snail species in a region that are also non-native somewhere, and NN_{Tot} is the total number of non-native taxa (values in Table S4). This index ranges from negative one (regions acting as sources of non-native snails, but with relatively few non-natives present) to positive one (regions acting as sinks of non-native snails, but with relatively few native snails that are also non-native somewhere). Values near zero indicate similar numbers of non-native and native snails in the region that are included in the dataset.

2.5 | Mechanisms of introduction

Whenever possible, we recorded the inferred mechanism of non-native snail introduction from each paper. In some cases, these mechanisms were based on expert opinions by the authors, and thus should be considered probable or inferred mechanisms. The mechanisms were grouped into the following seven categories: (1) transport and sale associated with the freshwater aquarium hobby; (2) "hitchhiking" with ornamental aquatic vegetation, often associated with outdoor water-gardens; (3) introductions associated with human consumption of snails, including aquaculture and field collection; (4) snails introduced as biological control agents; (5) introductions stemming from canals that connected previously isolated waterbodies; (6) transport associated with commercial shipping; and (7) movement associated with outdoor recreational activities. Because the aquarium hobby has been implicated as an important driver of non-native snail introductions, we also quantified how many taxa from our non-native snail list were reported from aquarium store surveys that were conducted in several different continents (Cowie & Robinson, 2003; Duggan, 2010; Mackie, 1999; Ng et al., 2016; Patoka et al., 2017; Yanai et al., 2017). Table S2 includes information on the mechanisms of introduction from both the original literature search and the aquarium store surveys.

In order to further explore patterns in freshwater snails sold in the aquarium hobby, we also utilized an online search of eBay sales posts (www.ebay.com) to evaluate which snail taxa commonly are sold on the internet. While multiple online sales forums exist in the aquarium hobby, we focused on eBay because of its growing use to sell live aquatic animals, its global presence, and its relatively easy-to-search records. We used the term "aquarium snail" to search the sales posts (search conducted on 1 March 2021). We then recorded the listed common names for each of these sales advertisements, as scientific names were rarely included and unreliable. Based on the common names, photographs in the advertisements, and additional online searches, we assigned family-level identifications to all snails returned in the eBay search. In some cases, we were able to also assign genus and species names for distinctive taxa, but these were considered tentative identifications (see Table S5 for details). We then compared this list to our species list of non-native freshwater snail taxa reported from the field.

2.6 | Non-native snails as hosts

A subset of papers from the Web of Science search examined whether non-native snails served as hosts to parasites. For each of these papers, we recorded the taxonomic identity and richness of parasites reported. We only included studies with data on parasites from field-collected snails in the non-native range (i.e., we excluded records based on laboratory exposures). We then combined these records across each snail taxon to estimate the total observed parasite richness in the non-native range, based on the available studies and sampling effort. For as many of these snail taxa as possible, we also obtained estimates of parasite richness within the native range, using the highest reported richness value that was found in the literature. We then used a linear regression with parasite richness in the native range as the predictor of parasite richness in the non-native range. A slope below one would provide evidence for release from parasites in the non-native range. References used to obtain parasite data, identities of parasites, and notes on the extent of sampling (e.g., sample sizes of hosts examined) are provided in Table S6.

2.7 | Non-native snails as prey

For papers reporting information on consumption of non-native snails, we recorded the species identities of all predators and whether they were native or non-native within the non-native range of the snail. We recorded the venue providing the evidence for consumption, including field data (diet studies or direct observations of predation events), laboratory data (e.g., feeding trials), outdoor mesocosms, or a mix of these approaches. Predator identities, references, and associated information are provided in Table S7.

3 | RESULTS

3.1 | Research trends

We found 506 articles that met our criteria, with the earliest paper published in 1985. The numbers of papers on non-native snails increased rapidly around 2000, reaching 52 per year in 2020 (Figure 1a). Most of the published studies focused on range records, snail biology, invasion drivers, or ecological impacts, with relatively fewer investigating parasite–host ecology and management (Figure 1b). In terms of research venues, most studies involved field-based data collection, followed by laboratory-based studies, review papers, outdoor mesocosm experiments, and modelling efforts (Figure 1c).

3.2 | Taxonomic patterns

The relevant articles collectively involved 129 snail taxonomic names. Of these, we determined 95 to be unique species after merging synonymous taxonomic names (Table S2). Some articles involved multiple non-native snail taxa, resulting in 845 unique article-by-snail species combinations (hereafter referred to as "records"). Research focus was disproportionately allocated to eight species, which accounted for 63% of all records (see Figure 2 for specific taxa). Most taxa were rarely found in the literature search, with 34 species in just one record each, and 69 species in three or fewer records each. The 95 non-native species represented

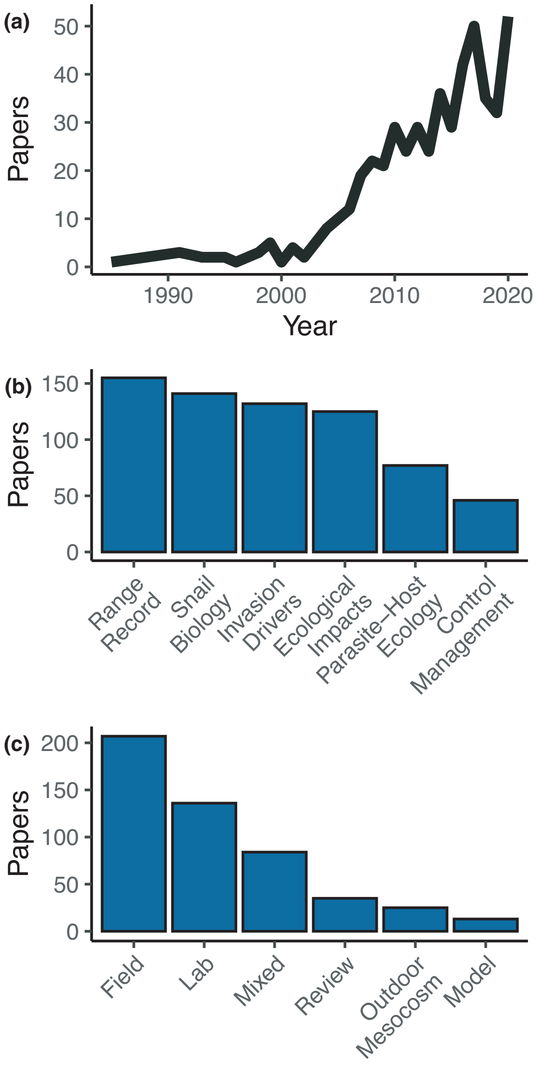

FIGURE 1 Trends in research articles involving non-native freshwater snails in terms of papers published per year over time (a), focal research areas (b), and research venues (c)

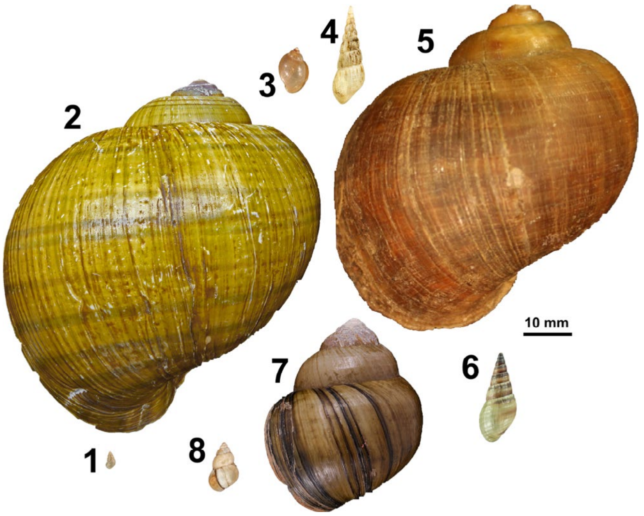

FIGURE 2 Eight non-native freshwater snail species that represented 63% of the research records from the Web of Science literature search. Snail species, clockwise from the lower left, include: (1) *Potamopyrgus antipodarum* (117 records), (2) *Pomacea canaliculata* (106 records), (3) *Physa* (=*Physella*) *acuta* (86 records), (4) *Melanoides tuberculata* (73 records), (5) *Pomacea maculata* (53 records), (6) *Tarebia granifera* (44 records), (7) *Bellamya* (=*Cipangopaludina*) *chinensis* (31 records), and (8) *Bithynia tentaculata* (25 records). All images have been scaled to the same 10 mm scale bar, reflecting the wide range of adult body sizes. The first six of these taxa are widespread global invaders, found on four or more continental regions. The first seven have been documented in the aquarium trade. Several taxa host parasites in their non-native range that infect native species of conservation concern (4,6,8) or have public health implications (5). Some are ecologically important as prey resources to threatened wildlife (5) or have become agricultural pests (1). Others have been documented to alter freshwater ecosystem processes at some locations in their non-native range (2). See Table S2 for additional information on each taxon. (Photos 1,4,6 by H. Zell; 2,3 from http://www.animalbase.uni-goettingen.de/; 5 from Museum of Comparative Zoology, Harvard University; 7 from A. E. Lincoln; 8 from University of Michigan Museum of Zoology)

16 snail families (Table S2). Of these, six families were represented with significantly more non-native taxa than expected by chance (Figure 3a; Table S3): Ampullariidae (17 species; $p < 0.001$), Lymnaeidae (nine species; $p = 0.005$), Physidae (seven species; $p < 0.001$), Planorbidae (20 species; $p < 0.0001$), Semisulcospiridae (seven species; $p = 0.009$), and Thiaridae (10 species; $p = 0.011$). As a group, more taxa of non-native pulmonate snails also were observed than expected by chance (36 of 95 snail taxa were pulmonates; $p < 0.0001$). Many families also were under-represented, and we found zero non-native taxa from 18 of the 34 recognized gastropod families in Lydeard and Cummings (2019). Five families had only one reported non-native species (Table S3).

3.3 | Geographical patterns

All continental regions had more non-native snails than native snails that were non-native somewhere ($K > 0$ for all regions; Table S4). Australia and the Pacific Islands appeared as the largest "sink" for non-native freshwater snails, with 20 non-native taxa and only five native taxa that also were non-native somewhere ($K = 0.60$). The regions with the highest number of non-native snails were Asia, followed by North America, and Central and South America (Figure 3b). A handful of taxa (15%) were widespread global invaders, reported from four or more continental regions (Figure 3b). The global invaders were pulmonates (six taxa from the families Planorbidae, Lymnaeidae, and Physidae), Ampullariidae (four taxa), Thiaridae three taxa), and one Tateidae (*Potamopyrgus antipodarum*). Of these globally invasive taxa, six were included in the top eight in terms of number of records in the database (see Figure 2 for specific taxa). Most non-native snail taxa (63%) were reported from only a single continental region (Figure 3b). Of this subset, exactly half were non-native within the same continental region that included their native range.

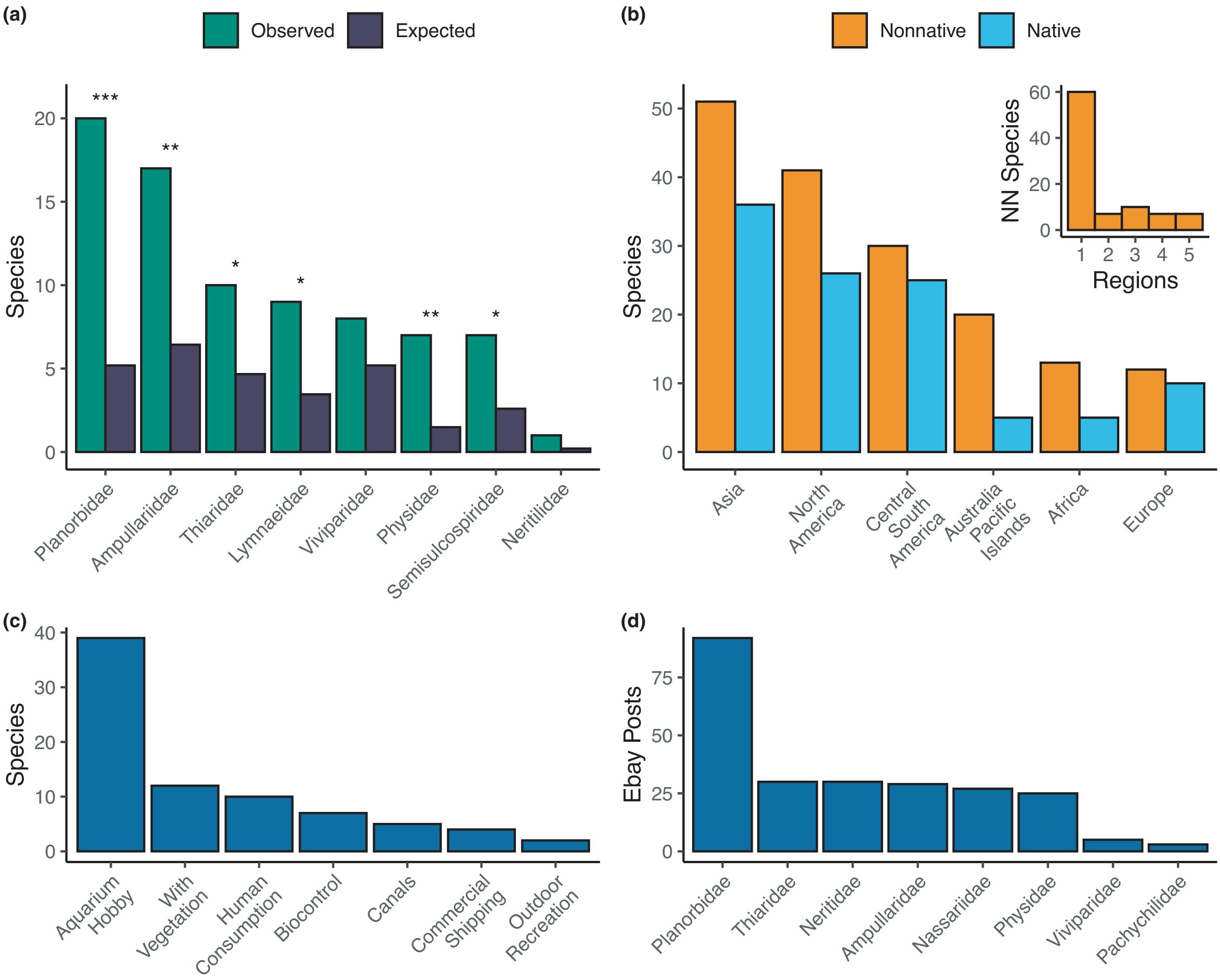

FIGURE 3 Observed numbers of taxa in seven snail families that were over-represented relative to the number expected by chance (a). Expected values are based on the relative richness within each family and the asterisks indicate statistical significance values (*, $p < 0.05$; **, $p < 0.001$; ***, $p < 0.0001$). In the top right panel (b), the bars indicate species counts of non-native snails found in each continental region (orange) and the number of non-native taxa originating from each continental region (blue). The inset panel shows the distribution of non-native species based on the number of regions in which they were reported as non-native. The right-skewed distribution shows a tail of widespread global invaders, while most taxa are non-native within a single continental region. The bottom panels show mechanisms of introduction reported for non-native snails (c) and counts of sales posts for freshwater taxa being sold on eBay (d). Five of the seven non-native families that were over-represented were found in eBay sales posts

3.4 | Mechanisms of introduction

The most commonly implicated mechanism of introduction was via the aquarium hobby (41% of non-native snail taxa; Figure 3c). Seven of the top eight most studied taxa (Figure 2) were involved in the aquarium trade. The next most common mechanism (13% of taxa) was "hitchhiking" with ornamental aquatic plants that are transported and sold commercially, followed by transport associated with human consumption (i.e., field collection for sale and/or aquaculture) and intentional introduction for biocontrol (Figure 3c), the latter of which typically targeted undesirable aquatic plants and/or other snail taxa that host parasites of public health concern. Transport via canals, commercial shipping, and outdoor recreation represented the other observed mechanisms of introductions.

The eBay search indicated that four of the six snail families that were taxonomically over-represented as non-native species were currently being sold online (Figure 3d; Table S5). The eBay search returned 352 sales posts, of which 241 were freshwater snails. The most commonly sold taxa on eBay belonged to the family Planorbidae, representing 38% of all records. Next most common in terms of the proportion of sales posts was the family Thiaridae (12%), which appeared to be primarily *Melanoides tuberculata*. Other taxa that were observed in the non-native snail literature records and also sold on eBay included Ampullariidae (12%), Physidae (10%), Viviparidae (2%), and Nassariidae (1%). All Nassariidae appeared consistent with the *Anentome helena* species complex on eBay. Only one family (Pachychilidae) was observed in eBay sales posts but was not observed in the literature records of non-native snails.

3.5 | Non-native snails as hosts

We found records of parasites in wild non-native snails for 19 snail taxa (Table S6). Of these, we obtained estimates of parasite richness in the non-native and native range for nine taxa, all of which had fewer parasites in the introduced range (Figure 4). Nearly all of the records involved trematodes, with one notable case involving nematodes (*Angiostrongylus cantonensis* in *Pomacea* spp.; Table S6). Non-native range parasite richness was not significantly correlated with native range parasite richness ($T = 1.7$, $df = 8$, $r^2 = 0.29$, $p = 0.13$). The slope of the relationship between native and non-native range parasite richness was below one, suggesting release from parasites in the non-native range ($\beta = 0.12$, ± 0.07 *SE*).

3.6 | Non-native snails as prey

We found 95 records that involved 65 taxa of predators consuming nine different species of non-native snails (Table S7). Of these, 35 records involved documented cases of consumption of non-native snails in the field. The other records involved laboratory trials or mesocosm experiments. The consumers of non-native freshwater snails included 27 fish, 26 invertebrates, six birds, four reptiles, and two mammals (Table S7). Nineteen of the consumer taxa (and 30% of the total records) were non-native predators.

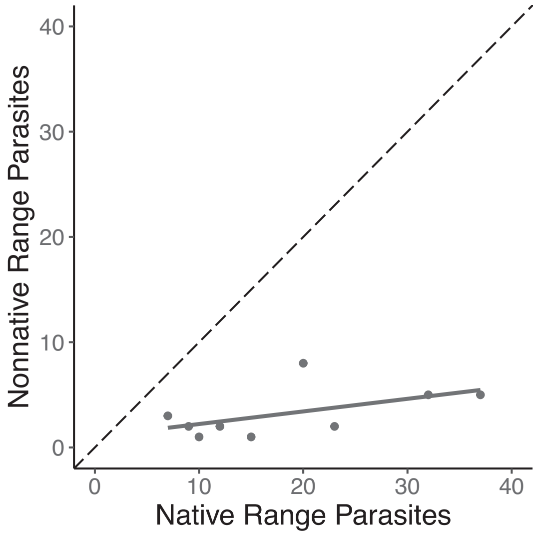

FIGURE 4 Relationship between observed parasites in the non-native and native range of freshwater snail taxa. The dashed line shows the relationship if the number of parasites was similar between native and non-native ranges. The solid line corresponds to a Poisson linear regression. See Table S6 for the specific taxa included in the figure and information on sampling effort

4 | DISCUSSION

In the last two decades, the number of studies involving non-native freshwater snails per year has increased more than six-fold. Here, we used a systematic review to synthesize this growing literature, allowing analysis of snail invasion trends at the global scale. The literature search results highlight several patterns of interest, including the disproportionate occurrence of specific taxonomic groups, the importance of limited snail range expansions versus global invasions, the role of different introduction mechanisms, and the potential of snail parasites and predators to influence invasion outcomes. In the following sections we discuss the implications of these results for the invasion ecology and management of non-native freshwater snails.

4.1 | Taxonomic patterns and snail traits

Research effort has been disproportionately focused on eight species of non-native freshwater snails, which together represented nearly two-thirds of the literature records (see Figure 2). Most of these taxa are highly successful invaders with large geographical ranges; six of the eight are globally invasive, occurring on four or more continental regions. Most can be considered trophic and habitat generalists with fairly wide environmental tolerances in lentic and lotic habitats (Alonso & Castro-Díez, 2008; Hayes et al., 2015; Miranda et al., 2010). They all have a relatively fast "pace of life", with rapid growth and high reproductive potential, which are traits associated with invasiveness in freshwater molluscs (Keller et al., 2007) and other taxa (Allen et al., 2017). Interestingly, while non-native pulmonate snails were highly over-represented relative to the number expected by chance, the majority of the most-researched non-native snails (seven of eight) were prosobranchs.

Several prosobranch taxa cause well-documented undesirable impacts, including parasite transmission to native species (Sauer et al., 2007) and damage to agricultural crops (Horgan, Felix, et al., 2014). Efforts to inform their management therefore have contributed towards their research attention.

The eight most highly studied invasive snail taxa share characteristics, yet they also show significant diversity in some life-history traits. This observation suggests there is no single "recipe" for what makes a successful invasive freshwater snail. For instance, adult shell height varies over 30-fold across the eight most well-studied invasive snail taxa (Figure 2), ranging from c. 5 mm for *Potamopyrgus antipodarum* to c. 150 mm for *Pomacea canaliculata* and *P. maculata*. This large range suggests that body size may be a poor predictor of invasion success in freshwater snails, which contrasts with a prior analysis on marine bivalves (Roy et al., 2002), but is relatively consistent with a large analysis of invasive vertebrates (Jeschke

& Strayer, 2006). Furthermore, while all of the most invasive snail taxa have high fecundity, there is nonetheless a wide range of reproductive strategies represented in the top eight taxa: three are parthenogenetic (*Potamopyrgus antipodarum*, *M. tuberculata*, and *Tarebia granifera*), four are dioecious (*Pomacea canaliculata*, *Pomacea maculata*, *Bithynia tentaculata*, and *Bellamya chinensis*), and one is a simultaneous hermaphrodite (*Physa acuta*; Berry & Kadri, 1974; Richter, 2001; Dillon et al., 2002; Alonso & Castro-Díez, 2008; Stephen et al., 2013; Hayes et al., 2015; Veeravechsukij et al., 2018). Of these taxa, half are viviparous (egg-laying) and half are oviparous (live-bearing). Thus, invasion success may not be closely linked to any specific snail reproductive strategy. This reproductive diversity also is prominent across the over-represented snail families. Moving forward, a quantitative analysis of how snail traits affect invasion success is warranted. This analysis could compare traits of the highly invasive non-native snails identified here to a representative sample of snail taxa that are not invasive. While our study provides the most complete list of non-native snails to-date, it also probably underestimates the true number of non-native snails. We did not compile studies that were in languages other than English, and we did not directly search museum records, which could contain additional unpublished information. Furthermore, the taxonomic status of some snails in our list was uncertain (see Table S2), and cryptic species of non-native snails are probably undocumented in many cases.

4.2 | Geographical patterns

The analysis of geographical patterns indicates that while a small subset of snails are globally widespread invaders, the majority have expanded only within their original continent of origin. For instance, the pleurocerid and semisulcospirid snails in the dataset all were translocated relatively short distances, including seven *Semisulcospira* spp. that have been introduced from Lake Biwa in Japan into other nearby waterbodies in association with aquaculture activities (Sawada et al., 2020). Four pleurocerid species in North America also expanded their historical range as a consequence of human activities, but are not currently widespread (Hayes et al., 2007; Mills et al., 1993, 1996). In general, most aquatic non-native species have relatively small range sizes, which limits the spatial scale of their impacts (Vander Zanden et al., 2017). The right-skewed distribution of the number of occupied continents per non-native snail species (inset Figure 3b) appears to be representative of non-native species range sizes in general, with many small and a few very large non-native range sizes (Vander Zanden et al., 2017).

4.3 | Mechanisms of introduction

Global trade in pets and ornamental organisms has increased greatly in recent decades and has been directly linked to species invasions by numerous taxa (Lockwood et al., 2019; Padilla & Williams, 2004). Previous studies have surveyed the diversity of freshwater snail taxa offered in the aquarium trade and noted the high likelihood of the aquarium hobby as a primary vector for new aquatic snail invasions (Cowie & Robinson, 2003; Duggan, 2010; Mackie, 1999; Ng et al., 2016; Patoka et al., 2017; Yanai et al., 2017). The ease at which live aquatic animals can now be purchased online has exacerbated this trend (Olden et al., 2020). Yet it has been challenging to quantify how many non-native freshwater snails at the global scale are likely to have been introduced through the aquarium trade. Our results indicate that at least 38 taxa (42% of the total) have potentially been introduced via this mechanism. Interestingly, recent research suggests that the pet trade actually favours animals that have the highest potential to become invasive, and taxa with large range sizes that are habitat generalists tend to be most commonly sold commercially, presumably because they make hardy captives (Gippet & Bertelsmeier, 2021). Our findings support this idea, as nearly all of the most widely distributed invasive snail taxa (based on number of continents occupied) were habitat generalists found in the aquarium trade. This included seven of eight of the most highly studied and globally invasive taxa shown in Figure 2.

The eBay sales posts showed concordance with the most over-represented non-native snail families, with five of the seven over-represented families observed for sale online. Among the most common eBay aquarium taxa were Planorbidae, which include hosts of parasites causing human disease (Madsen & Frandsen, 1989), and Thiaridae (namely *M. tuberculata*), which has been associated with spread of fish parasites in its non-native range (Tolley-Jordan & Chadwick, 2019). One of the families sold on eBay for freshwater aquaria consists largely of brackish or marine species (Nassariidae), which probably explains the relatively low number of freshwater invasions in this group. However, one notable exception (the *Anentome helena* species group) was commonly sold on eBay and has recently become invasive in freshwater, which may have significant ecological consequences due to its specialized diet of other snails (Strong et al., 2017). In some cases (e.g., Ampullariidae and Viviparidae), multiple species were being sold under the same common names, adding confusion to exactly which species are being traded, and highlighting the need for more thorough monitoring and regulation of which taxa are commercially sold and shipped globally.

4.4 | Interactions with natural enemies

Our literature search found evidence that non-native freshwater snails tend to have fewer parasites in their non-native ranges. The enemy release hypothesis posits that a lack of natural enemies (e.g., parasites and predators) in an organism's non-native range can contribute towards invasion success (Ricciardi et al., 2013). Prior evidence for individual snail species supports this hypothesis (Ebbs et al., 2018; Larson & Krist, 2020). By combining data across nine snail taxa, our results show that snails in their non-native ranges have, on average, at least 80% lower parasite richness than in their native ranges. The sampling extent varied across non-native snails in both number of sites and hosts examined (notes in Table S6). Two taxa had relatively small samples sizes of hosts dissected in the introduced range (*Radix auricularia* and *Valvata piscinalis*). However, it is unlikely that the lower parasite richness in the introduced ranges is solely the result of sampling differences, and removing these two taxa did not change the results of the analysis. In several cases, many thousands of snails were screened for infections in the non-native ranges (e.g., *Potamopyrgus antipodarum* and *Physa acuta*), and parasite richness was still significantly lower in the introduced ranges. This finding aligns with results for plants and their pathogens (Mitchell & Power, 2003), and a range of other invertebrates and vertebrates (Torchin et al., 2003). One of the likely mechanisms explaining this pattern is a lack of all obligate host taxa needed to complete the multi-host life cycles of trematode parasites in the new range; virtually all of the snail-parasite records were for trematodes. Lower parasite richness in the non-native range may contribute towards invasion success because trematode parasites castrate their snail hosts, sometimes causing population-level effects (Negovetich & Esch, 2008).

Despite having lower parasite richness overall, our literature search results indicate that non-native snails nonetheless serve as hosts for a range of parasites that cause significant diseases in wildlife, livestock, and humans. This trend is exemplified by *Bithynia tentaculata*, a European native introduced to the upper Midwest United States where it hosts four non-native trematode taxa that cause severe pathology and mortality in tens of thousands of waterbirds each year (Bachtel et al., 2019; Sauer et al., 2007). In this case, the North American waterfowl have not co-evolved with the introduced trematodes, which would not be present without the introduced *Bithynia* snails that are obligate hosts. In another example, non-native pulmonate snails (e.g., *Galba* and *Lymnaea* spp.) have been responsible for the spread of *Fasciola* spp. trematodes in South America, which cause disease in livestock leading to significant economic losses (Caron et al., 2017; Pereira et al., 2020). The most significant human health issues surrounding non-native snails involve the introduction of *Biomphalaria* spp. into new areas, where they serve as hosts for human schistosomes (Madsen & Frandsen, 1989; Pointier, 1999; Pointier et al., 2005). The widespread non-native ampullariid snails (e.g., *Pomacea maculata*) also host the nematode *Angiostrongylus cantonensis*, which presents a human disease risk (Teem et al., 2013; Yang et al., 2013). Collectively, the spread of disease may be the most consequential ecological mechanism underlying impacts of non-native freshwater snails, particularly when non-native parasites are transmitted to naïve host populations.

While non-native snails are commonly released from parasitism, we found a wide diversity of invertebrate and vertebrate predators consuming non-native snails, most of which were generalist consumers (Yusa et al., 2006). In most cases, the consequences of introduced prey for native predators are not well documented (Carlsson et al., 2009). In one informative case, endangered raptors (snail kites; *Rostrhamus sociabilis*) that are highly specialist consumers of snails, have expanded their geographical range in Florida, show increased population growth rates, and now face reduced local extinction risk due to invasion by South American apple snails (*Pomacea maculata*; Cattau et al., 2016). The non-native apple snails are significantly larger than the native apple snails in Florida, and snail kites have increased the size of their bills, tarsus, and total body mass at invaded sites in response to the highly abundant novel prey source (Cattau et al., 2018). In other cases, consumption of non-native snails may lead to mixed effects on predators; for instance, freshwater fish consume New Zealand mud snails in North America and Europe, but they are a poor-quality resource, and probably do not cause positive population-level effects on their predators (Rakauskas et al., 2016, 2018; Vinson & Baker, 2008). Non-native snails also may help support populations of non-native predators (Twardochleb & Olden, 2016), potentially facilitating invasions by consumers at higher trophic levels. Conversely, the degree to which predators can limit the successful establishment or spread of non-native snails has been quantified only rarely, based on our literature search. In one exception, field surveys and experimental data from streams in Japan suggest native predators may be limiting the spread of non-native *Pomacea canaliculata*, providing evidence for biotic resistance (Yamanishi et al., 2012). Testing the degree to which native communities can prevent or limit non-native snail establishment through biotic resistance represents an important future research direction.

4.5 | Management and future directions

We initially planned to explore patterns in management activities reported in the literature related to non-native snails, yet we found relatively few papers that were actively employing non-native snail management in natural settings. Most examples focused on non-native apple snails in relation to their roles as crop pests in agricultural settings (Horgan, Stuart, et al., 2014). The relative paucity of studies implementing management for other taxa in natural environments may reflect limitations in management strategies for freshwater snails once they are established. In cases where non-native snails have strong negative effects on species of conservation concern or on economic interests, the feasibility of snail elimination may be relatively low. Possible strategies include biocontrol, chemical treatments, drying of waterbodies, or manual removal of snails (Carmosini et al., 2018; Halwart, 1994; Horgan, Felix, et al., 2014; Joshi, 2007; Olivier et al., 2016; Unstad et al., 2013). Of these, biocontrol has been utilized in a handful of cases. Predatory fish (Halwart et al., 2014), freshwater prawns (Savaya et al., 2020), and competition from other snails (Pointier et al., 2011) can reduce populations of non-native snails. The efficacy of these approaches in natural habitats is likely context-specific and effects on non-target species should be evaluated (Ip et al., 2014), especially considering how some previous gastropod biocontrol efforts have caused disastrous unintended consequences (Murray et al., 1988). Habitat modifications to enhance population abundance and/or individual predation rates of native predators provides another approach, which may be useful in specific cases while minimizing unintended consequences (Horgan, Felix, et al., 2014; Pias et al., 2012). Other approaches (e.g., chemical treatments and waterbody drying) are likely to cause loss of non-target organisms, making their use in natural settings challenging. Increasing public knowledge and outreach efforts to limit new introductions represents a complementary approach to control strategies.

Moving forward, it will be important to clearly establish the impacts of non-native snails relative to management goals. Neutral or desirable effects of non-native snail populations (Cattau et al., 2016) may reduce the need to prioritize limited resources towards freshwater snail management, but frequently the ecological roles of newly introduced snails are unknown within the invaded ecosystem. Filling this knowledge gap will require efforts to monitor and detect new invasions, coupled with experimental and observational approaches to disentangle the community- and ecosystem-level effects of the introduced snail populations. Preventing new introductions, rather than managing established invasive populations, is likely to be among the most viable strategies in the future. At the policy level, our results also emphasize the relative importance of the aquarium hobby as a vector of snail introductions, and further regulating this global trade may be among the most impactful actions to limit new introductions.

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DATA AVAILABILITY STATEMENT

Data from this article is included in the Supporting Information and will be publicly available upon publication.

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