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When One Global Invasion Hides Another—Cryptic Interspecific Invasion in Freshwater Gastropods

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ABSTRACT

Aim: Cryptic invasions are an understudied phenomenon among species invasions, especially in freshwater invertebrates. We study the gastropod family Physidae, including the global invaders *Physella acuta* and several enigmatic *Stenophysa* species, their phylogenetic relationships and the presence of native species among African Physidae. We infer distribution pattern, colonisation history and invasion ecology across Africa. Finally, we reconstruct the colonisation pathways and their timing into, across (and out of) Africa and model future dispersal.

Location: Global, with a focus on Africa and Indian Ocean islands.

Methods: Based on extensive sampling, multi-gene phylogenetic, phylogeographic and ecological analyses, including species distribution modelling, we here examine Physidae globally.

Results: The Physidae probably originated in the Lower Cretaceous. A robust phylogeny showed four strongly supported genus-level clades corresponding to *Physella*, *Physa*, *Stenophysa* and *Aplexa*. *Physella acuta* thrives in continental African countries and Indian Ocean islands. The African continent was colonised at least six times independently.

For *Stenophysa*, the phylogeny suggests two independent transoceanic dispersal events into Africa and the Indian Ocean islands. *Physella acuta* occurs not only in artificial or highly disturbed habitats but also in large natural lakes. *Stenophysa marmorata*

Christian Albrecht and Björn Stelbrink contributed equally to this study.

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is ecologically flexible. The SDM for *S. marmorata* based on the selected climate variables predicted high probabilities of future occurrence in equatorial Africa and regions in the Indo-Malayan Archipelago, New Guinea and eastern Australia.
Main Conclusions: Physidae contains examples of both intraspecific cryptic and interspecific cryptic invasions, with an intraspecific invasion of *Physella acuta* and a prime example of an interspecific cryptic invasion of *Stenophysa* spp. This study highlights the importance of cryptic invasions in freshwaters and also calls for their management. *Stenophysa* is likely to become pan-tropical in the future. Physidae are an excellent model to study differential patterns and processes of intra- versus interspecific invasions at global and regional scales.

1 | Introduction

Invasive species are considered the second-most important threat to native biodiversity after habitat destruction (Dueñas et al. 2021; Gurevitch and Padilla 2004). Negative impacts on both communities and even whole ecosystems caused by invasive alien species (IAS) are well-documented for various freshwater systems (e.g., Ricciardi and MacIsaac 2011). As a result of these global processes, we witness an ever-increasing degree of biotic homogenisation in freshwater ecosystems on basically all continents (Petsch 2016), in both lotic and lentic systems (Dudgeon 2020).

Cryptic invasions represent a potentially widespread but underestimated and understudied phenomenon among IAS, two forms of which are distinguished, that is, intraspecific and interspecific cryptic invasions (Morais and Reichard 2018). According to Morais & Reichard (2018, 1439), 'interspecific refers to the invasion of non-native species that goes unnoticed due to misidentification as a native or another non-indigenous species, often closely related'. In contrast, 'intraspecific cryptic invasion refers to the invasion of another lineage of a species into the area where a distinct local lineage of the same species already exists' (Morais and Reichard 2018, 1439). These cases represent a continuum and are difficult to recognise and are often overlooked due to misidentification as a native or another IAS (Morais and Reichard 2018). Such misidentifications might hamper effective eradication or mitigation efforts. Interspecific cryptic invaders are numerous across all major taxa, including freshwater molluscs (e.g., de Lacerda et al. 2015; Van Bocxlaer et al. 2015), which, among others, represent the most notorious invasive species regularly damaging native faunas (Preston et al. 2022) and ecosystems (Kesner and Kumschick 2018). However, the mechanisms and consequences of cryptic invasions remain poorly documented (Morais and Reichard 2018).

Africa, although well-known for invasion cascades with resulting ecosystem collapses, best illustrated by the Nile perch introduction into Lake Victoria (Kaufman 1992), is not among the continents best known for freshwater invasions (Darwall et al. 2011, but see Weyl et al. 2020). Whereas this single fish introduction is textbook knowledge nowadays (Dudgeon 2020), much less is known about freshwater invertebrate invasions in Africa, even for globally recognised invaders such as the red swamp crayfish (*Procambarus clarkii*; see Madzivanzira, Weyl, and South 2022). The situation is similar for molluscs, which figure prominently as global invaders elsewhere (Madsen and Frandsen 1989; Pointier 1999; Preston et al. 2022). In fact, only a few studies, predominantly in South Africa (Appleton 2003; Appleton and Miranda 2015), highlighted the effects of such species on ecosystems (Miranda, Perissinotto, and Appleton 2011). Likewise, both interspecific and intraspecific invasion and the transmission of diseases such as schistosomiasis and fasciolosis have been identified for several African lacustrine environments (Carolus et al. 2019; Mahulu et al. 2019; Van Bocxlaer, Albrecht, and Stauffer Jr. 2014).

Pulmonate gastropods often become invasive (Preston et al. 2022), and the family Physidae is known explicitly for some globally invasive species (Albrecht et al. 2009). The plasticity of physid shell characters has led to several cryptic species (Wethington and Lydeard 2019) but also to oversplitting at the species (Taylor 2003) and even the genus level (Taylor 2003; Wethington and Lydeard 2019). The 'centre of diversity' of Physidae is North America (Taylor 2003), which is also underpinned by the fossil record (Wethington and Lydeard 2019). The most famous physid snail, *Physella acuta* (Physinae), discovered in 1805 in France has been mistakenly considered native to Europe for decades (Lydeard, Campbell, and Golz 2016). In fact, it is among the most invasive freshwater gastropods globally (Preston et al. 2022), best known for outcompeting native gastropods and carrying non-native parasites (Ebbs, Loker, and Brant 2018). Its ecological success, flexibility and competitive abilities (Dillon 2004; Dobson 2004) have repeatedly been shown in contrastingly different habitats. Although the species has the capacity to invade natural ecosystems, including ancient lakes, it remains restricted to ecologically disturbed littoral habitats (Albrecht et al. 2014, 2009; Brown 1994).

Whereas the spread of *P. acuta* has been well documented in Eurasia (Vinarski 2017), information about its spread in Africa is scanty (Brown 1994) except for South Africa (Appleton 2003; De Kock and Wolmarans 2007). Recent studies focussing on the phylogeography of *P. acuta* had a limited coverage of Africa (Ebbs, Loker, and Brant 2018; Lawton et al. 2018). Moreover, there are uncertainties about the status of presumably native physids outside of North America, that is, the Mascarene Islands, from where the potentially endemic *P. borbonica* has been described (Brown 1994; Griffiths and Florens 2006). Nevertheless, Lawton et al. (2018) and, more recently, Young et al. (2021) identified multiple lineages of *P. acuta* that invaded the African continent from North America. The species might thus well represent a case of intraspecific cryptic invasion.

Vast regions of continental Africa and all neighbouring islands remain unexamined. Moreover, no phylogenetic/phylogeographical study exists on a second physid group that

shows a disjunct distribution on the continent. *Physa mosambiquensis* was originally described from Mozambique, whereas *P. waterloti* was described from West Africa (Benin). The latter species has been treated as either a member of the genus *Aplexa* (e.g., Brown 1994; Dana and Appleton 2007) or *Stenophysa* (e.g., Starobogatov 1970), both traditionally representing the subfamily Aplexinae. Interestingly, a detailed morphological and anatomical examination found *P. waterloti* identical to *Stenophysa marmorata* from the Caribbean and South America (e.g., Appleton and Dana 2005), which has been widely accepted ever since. Taylor (2003) argued that a second monotypic genus exists alongside *Stenophysa* and that *P. waterloti* (and thus *Stenophysa marmorata*) from Africa is actually *Afrophysa brasiliensis*. The hypothesised mechanism of colonisation from South American sources links it to trans-oceanic dispersal related to the slave trade between the 16th and 19th century, particularly to regions in West Africa where it now occurs at least in Benin, Togo, Ghana, Nigeria and the Ivory Coast (Bony et al. 2008). Moreover, Appleton, Brackenbury, and Tonin (1989) proposed that *P. mosambiquensis* is also identical to *Stenophysa marmorata* (Appleton and Dana 2005).

Stenophysa marmorata in Africa has been proposed to prefer cleaner, particularly non-flowing water and more shaded conditions (Bony et al. 2008; Dana and Appleton 2007) compared to *P. acuta*. Apparently, no co-occurrences have been reported in Africa so far, and it remains unclear whether the co-occurrence in Argentina is indeed syntopic, that is, at the same place (Núñez 2010). Given the outlined situation and the frequent confusion of native and non-native physids in the literature record, African physids could be considered a cryptic interspecific invasion. However, uncertainties exist as to the taxonomic status of several of these species, the presence of native physids on the continent, the timing of introduction and the onset of subsequent spread, all of which call for a comparative examination of the invasion history in a broader framework.

Based on a comprehensive worldwide sampling and a suite of various analyses, we here study Physidae globally, focusing on Africa, in order to

1. infer interspecific relationships and to test for the presence of native species among African Physidae by using molecular phylogenetic methods,
2. determine the number of lineages of *P. acuta* and to infer their distribution pattern, colonisation history and invasion ecology across the continent using phylogeographical network analyses,
3. reconstruct colonisation pathways and their timing into, across and out of Africa of *Stenophysa* spp. and to model future spread using information of habitat preferences and community composition and by applying species distribution modelling.

We discuss intra- and interspecific cryptic invasions among the physid gastropods of Africa and beyond as well as current and potential future consequences for the native mollusc fauna and their ecosystems.

2 | Methods

2.1 | Sampling

The new sampling of physids compiled over 20 years focused on a pan-African coverage but also comprised several samples from the Palearctic, including the Arabian Peninsula. A particular focus was also put on the islands and archipelagos in the Indian Ocean and on key localities such as type localities of nominal taxa, that is, from places from which species were originally described and names are thus available (see Figure 1 and Table S1 for details). New material was obtained from 12 African countries, Oman, Indonesia, Brazil and Guadeloupe. All types of lacustrine and riverine ecosystems were surveyed, ranging from small temporal ponds to large ancient lakes, and natural and man-made systems. Categorical habitat characteristics were recorded (Table S2). Snails were hand-picked or collected with a scoop net or dredge and fixed in 80% ethanol. Specimen and DNA vouchers are stored in the Systematics and Biodiversity Collection of the Justus Liebig University (UGSB).

Material from Brazil was collected in the native range of *Stenophysa*. The type locality of *P. mosambiquensis* at Tete on the Zambezi in Mozambique was visited twice in 2006 and 2011 but did not yield material. However, a successful sampling was possible in the Zambezi catchment in close proximity to Malawi. Porto Novo in Benin is the type locality of *P. waterloti*, where we collected topotypic material in 2024. In addition, two Nigerian populations were sampled. African samples were supplemented with material of various global origins, biogeographical interests and previously published sequences of relevant samples. All available nominal taxa, particularly representatives of named genera, were retrieved in order to reconstruct a robust backbone phylogeny of Physidae.

2.2 | DNA Isolation, Amplification, Sequencing

DNA was isolated from muscle tissue using the mollusc-specific CTAB protocol (Winnepenninckx, Backeljau, and De Wachter 1993). We amplified and sequenced the two mitochondrial barcoding genes, cytochrome *c* oxidase subunit I (COI; primers: LCO1490/HCO2198 from Folmer et al. 1994) and 16S rRNA (16S; primers: 16Sar/16Sbr from Palumbi et al. 1991) as well as two nuclear markers, 18S rRNA (18S; primers: first forward primer listed in Winnepenninckx, Backeljau, and De Wachter 1994/Lym658, slightly modified, from Bargues and Mas-Coma 1997) and ITS2 (primers: LT1 from Bargues et al. 2001/ITS2-RIXO from Almeyda-Artigas, Bargues, and Mas-Coma 2000). Purification and bidirectional sequencing of PCR products were performed on an ABI 3730 XL sequencer at LGC Genomics (Germany).

2.3 | Phylogenetic Analyses

We compiled a multi-gene dataset including 105 specimens, covering a variety of *Physa* and *Physella*, several potential *Stenophysa* and two *Aplexa* species (Table S1). We used five Hygrophila representatives as outgroup: *Acroloxus lacustris*

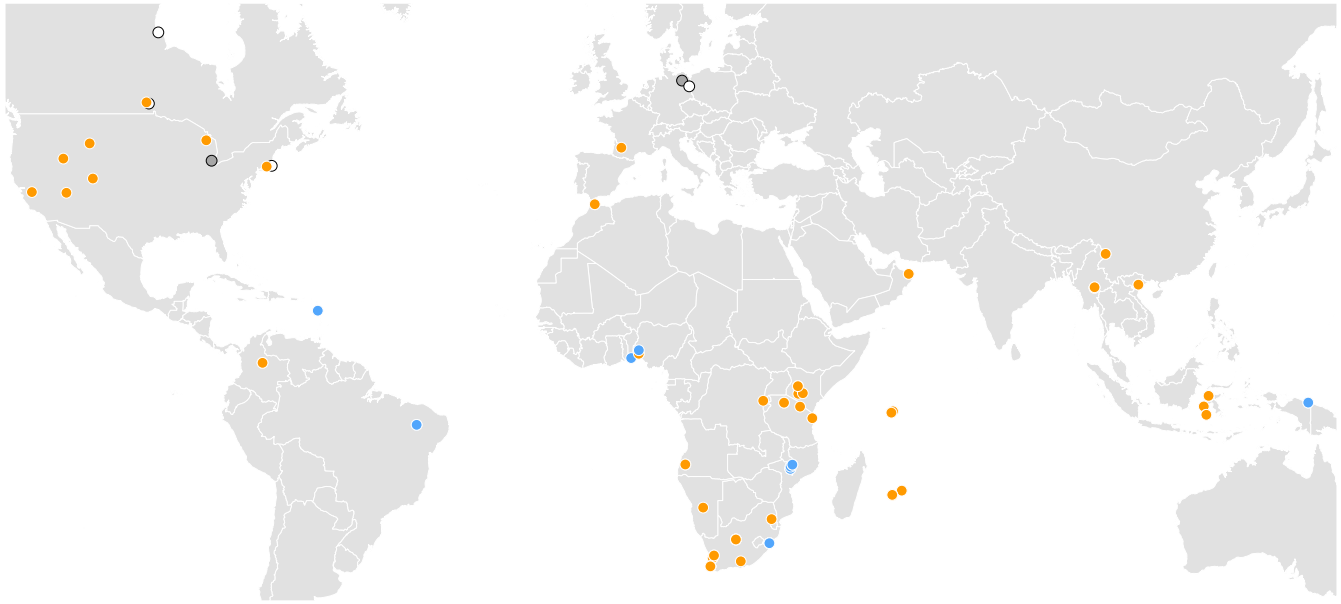

FIGURE 1 | Localities of samples (this study and other sources) used for molecular phylogenetic analyses (grey circles = *Aplexa*, white circles = *Physa*, orange circles = *Physella* and blue circles = *Stenophysa*). Note that the populations of *Physella* and *Stenophysa* from Nigeria occur syntopically (Ona River).

(Acroloxidae), *Ancylus fluviatilis* (Planorbidae), *Latia neritodes* (Latiidae), *Lymnaea stagnalis* (Lymnaeidae) and *Planorbarius corneus* (Planorbidae).

For the final phylogenetic analyses, the dataset was reduced to 51 samples, reflecting the number of haplotypes identified for the concatenated (all four genes combined) dataset (see Figures S1 and S2 for a 75-taxon dataset). The MAFFT Web Service (Katoh and Toh 2008; Katoh and Standley 2013) and Gblocks Server v. 0.91b (Castresana 2000) were used to align the 16S, 18S and ITS2 datasets. PartitionFinder 2 (Guindon et al. 2010; Lanfear et al. 2012, 2016) was used for selecting the best-fit partition scheme and substitution models (AICc, linked branch lengths, MrBayes models, greedy algorithm, codon partitioning for COI: 16S = GTR + I + Γ, 18S = GTR + I, COI^{1st} = GTR + Γ, COI^{2nd} = GTR + Γ, COI^{3rd} = GTR + I and ITS2 = GTR + I + Γ).

Phylogenetic trees were reconstructed with RAxML-HPC BlackBox v. 8.2.12 (Stamatakis 2014; GTR + Γ model for all partitions, stop rule for bootstrapping) and MrBayes v. 3.2.6 (Ronquist et al. 2012) on the CIPRES Science Gateway (Miller, Pfeiffer, and Schwartz 2010). The MrBayes analyses were run for 5,000,000 MCMC generations, sampling every 250 trees and applying a 50% burn-in. Convergence between the two runs was reached, all ESS values were > 200, as assessed in Tracer v. 1.7 (Rambaut et al. 2018).

2.4 | Estimation of Divergence Times

Divergence times were estimated for the reduced dataset (51 taxa) using BEAST v. 1.8.4 (Drummond et al. 2012). Although the fossil record of freshwater pulmonates is rather depauperate and temporarily scattered compared to marine molluscs, a considerable body of literature exists thereupon. Fossil record data were evaluated from various literature sources (e.g., Bandel 1991; Gray 1988; Huckriede 1967; Taylor 1988; Tracey, Todd, and Erwin 1993; Yen and Reeside Jr. 1946; Zilch 1960) and evaluated for their reliability to constrain certain splits in the phylogenetic tree. The first Physidae are described from the Upper Triassic of India (Nath, 1999), however, more reliable records are from the uppermost Jurassic and Lower Cretaceous from Europe (Bandel 1991). We here employed the fossil *Haitia taylori* from the Cerro del Pueblo Formation (Upper Campanian, 72.74–73.63 Myr; Vega et al. 2019) to date the node of *Physa* + *Physella* to account for taxonomic uncertainties. Both a strict-clock analysis and a birth–death analysis were run with a gamma prior for the fossil-calibrated node applying a hard minimum age of 72.74 Myr and a soft maximum age of 100 Myr (95% quantile of the prior) to further account for the incompleteness of the fossil record. Because of convergence problems, a less complex partition scheme (no codon-position data blocks) and less complex substitution models (HKY) were applied. The analyses were run for 50,000,000 generations, sampling every 2500th tree. Convergence was assessed using Tracer v. 1.7 (Rambaut et al. 2018). The different analyses were compared a posteriori using the marginal likelihood estimation (MLE) derived from the path sampling (PS) and stepping-stone (SS) sampling as implemented in BEAST (Baele et al. 2012). Maximum clade credibility (MCC) trees were obtained using TreeAnnotator v. 1.8.4 (BEAST package) by applying a burn-in of 50%.

2.5 | Phylogeographical Analyses

Haplotype networks were generated for the mitochondrial COI dataset of *Physella acuta* specimens using the TCS algorithm (Clement, Posada, and Crandall 2000) as implemented in PopART (Leigh and Bryant 2015). The dataset comprised our newly acquired sampling and the data of Lawton et al. (2018),

resulting in a total of 193 specimens. All *Stenophysa* specimens totalling 26 COI sequences were used in a separate haplotype network analysis.

2.6 | Species Distribution Modelling

To investigate suitable habitats and the potential distribution of the species, we applied a species distribution modelling approach. Geo-referenced occurrence data for *S. marmorata* were retrieved from the Global Biodiversity Infrastructure Facility (GBIF) (data request DOI: 10.15468/dl.3xng5z). The records were cleaned by removing obviously wrong (i.e., outside coordinate system) and imprecise coordinates (i.e., at least two digits after the comma), and by applying tests of the R package 'coordinateCleaner'. This package was designed to clean GBIF records by, for example, performing outlier tests and removing entries associated with museums or country centroids. This cleaning resulted in the removal of 58 records of 188 altogether from GBIF. Thus, 120 GBIF records remained for subsequent analyses. This dataset was supplemented with records from the literature (29 localities in Appleton and Dana 2005) and our own new records (26), resulting in a total of 175 records used for modelling the species distribution.

For the species distribution model, we used a generalised additive model (GAM) with a binomial error distribution. Six climatic variables to simulate the species distribution were considered, which are annual mean temperature, temperature seasonality, temperature annual range, annual precipitation, precipitation of driest month and precipitation seasonality. Spatial layers of these variables were obtained from WorldClim (https://www.worldclim.org; Fick and Hijmans 2017) at a 2.5 min resolution. For a robust parameterisation of the SDM, pseudo-absences were generated by sampling randomly from the environmental layers (Barbet-Massin et al. 2012). This was repeated 10 times to avoid biased representations of the samples (Araújo et al. 2019). A cross-validation of model results was conducted by fitting the GAM to 30% of the full dataset and validating the results using the remaining 70%. The goodness-of-fit was estimated using the True Skill Statistic (TSS) measure. The cross-validation was repeated 10 times for each of the 10 pseudo-absence datasets, resulting in 100 model fits. Only model runs with a TSS > 0.6 were kept, which resulted in the selection of the ca. 50% best models, and their mean used as the main model output. A change in the cut-off value did only marginally influence the predictions. The fitted models were used to predict the potential species distribution for the entire region. Finally, the habitat suitability values from all models were averaged per grid cell to obtain the final map of predicted habitat suitability. The analyses were performed using the R packages mgcv v. 1.9 (Wood 2011, 2017) and PresenceAbsence v. 1.1.11 (Freeman and Moisen 2008) for the R statistical environment v. 4.3.2 (R Core Team 2023). The code and occurrence data to run the model are publicly available (https://zenodo.org/doi/10.5281/zenodo.13305293). The environmental layers can be directly used as provided by WorldClim. To ensure the transparency of our approach, we provide the ODMAP protocol for reporting species distribution models (Zurell et al. 2020) in the online repository.

3 | Results

3.1 | Phylogenetic Relationships and Species Identities

According to the MLE, the relaxed-clock analysis was favoured compared to the strict-clock analysis [$PS_{relaxed} = -12{,}643.53$, $SS_{relaxed} = -12{,}645.31$ vs. $PS_{strict} = -12{,}741.76$, $SS_{strict} = -12{,}742.63$, and thus the Bayes factors (BF) is $\log(BF)_{PS} = 1.99$ vs. $\log(BF)_{SS} = 1.99$].

A robust phylogeny with four highly supported genus-level clades corresponding to *Physella*, *Physa*, *Stenophysa* and *Aplexa* (RAxML bootstrap, BS = 100, MrBayes posterior probability, PP = 1.0, BEAST posterior probability, BPP = 1.0) was inferred (Figure 2). *Physella* and *Physa* form a clade, which, however, is not (well) supported (BS = 58, PP = 0.83, BPP = 0.48) and represents the sister to *Stenophysa* (BS = 100, PP = 1.0, BPP = 1.0), which together form the subfamily Physinae. North American and European *Aplexa*, representing the subfamily Aplexinae, form a well-supported but rather distinct clade that is sister to all other Physinae.

According to the molecular-clock analysis, the Physidae probably originated in the Lower Cretaceous c. 115.1 Ma (mean age, 95% highest posterior density, HPD = 88.8–149.9 Ma; Figure 2). The onset of diversification of Physinae is dated to the Upper Cretaceous around c. 82.2 Ma (72.7–97.7 Ma), whereas the Aplexinae likely started to diversify at the Palaeocene-Eocene transition c. 56.5 Ma (11.5–100.9 Ma; Figure 2). The initial divergence time of *Physella* is estimated to c. 64.1 Ma (50.2–79.1 Ma) in the Palaeocene, whereas *Physa* started to diversify in the Eocene c. 48.8 Ma (28.6–69.7 Ma). *Physella acuta* comprises a couple of other nominal taxa (e.g., *P. anatina* and *P. winnipegensis*; see Table S1) and consists of several clades in a comparatively shallow topology (Figure 2). It started to diversify in the Miocene–Pliocene transition c. 6.2 Ma (3.5–9.0 Ma). *Physella spelunca* is the sister species to *P. acuta* in this molecular phylogeny, but the splitting has been estimated to c. 19.6 Ma (10.4–29.2 Ma) already.

Our molecular analyses confirm that *P. waterloti* and *P. mosambiquensis* are synonyms of *S. marmorata* (see Introduction), which thus represents a non-indigenous species in Africa and on Indian Ocean islands. There is no indication of an endemic *P. borbonica* from the Mascarene Islands; all studied specimens were *P. acuta*. Genetic variation exists in the *Stenophysa* clade, but the topology is mostly unresolved. One clade of very closely related populations consists of samples from geographically very distant places ranging from Africa (Malawi and South Africa), Mauritius, to Indonesia (Sulawesi and New Guinea), to which specimens from Nigeria probably represent the sister (BS = 79, PP = 92, BPP = 99). *Stenophysa* specimens from Brazil do not cluster together, and *S. marmorata* from Guadeloupe is sister to specimens from Seychelles, though this relationship is not supported (BS = 58, PP = 0.59, BPP = 0.62). Diversification within *Stenophysa* started in the Miocene c. 10.5 Ma (5.4–16.3 Ma), whereas the clade from Nigeria and the remaining populations from southern Africa and the Indian Ocean diverged c. 1.9 Ma (0.7–3.5 Ma) in the Early Pleistocene.

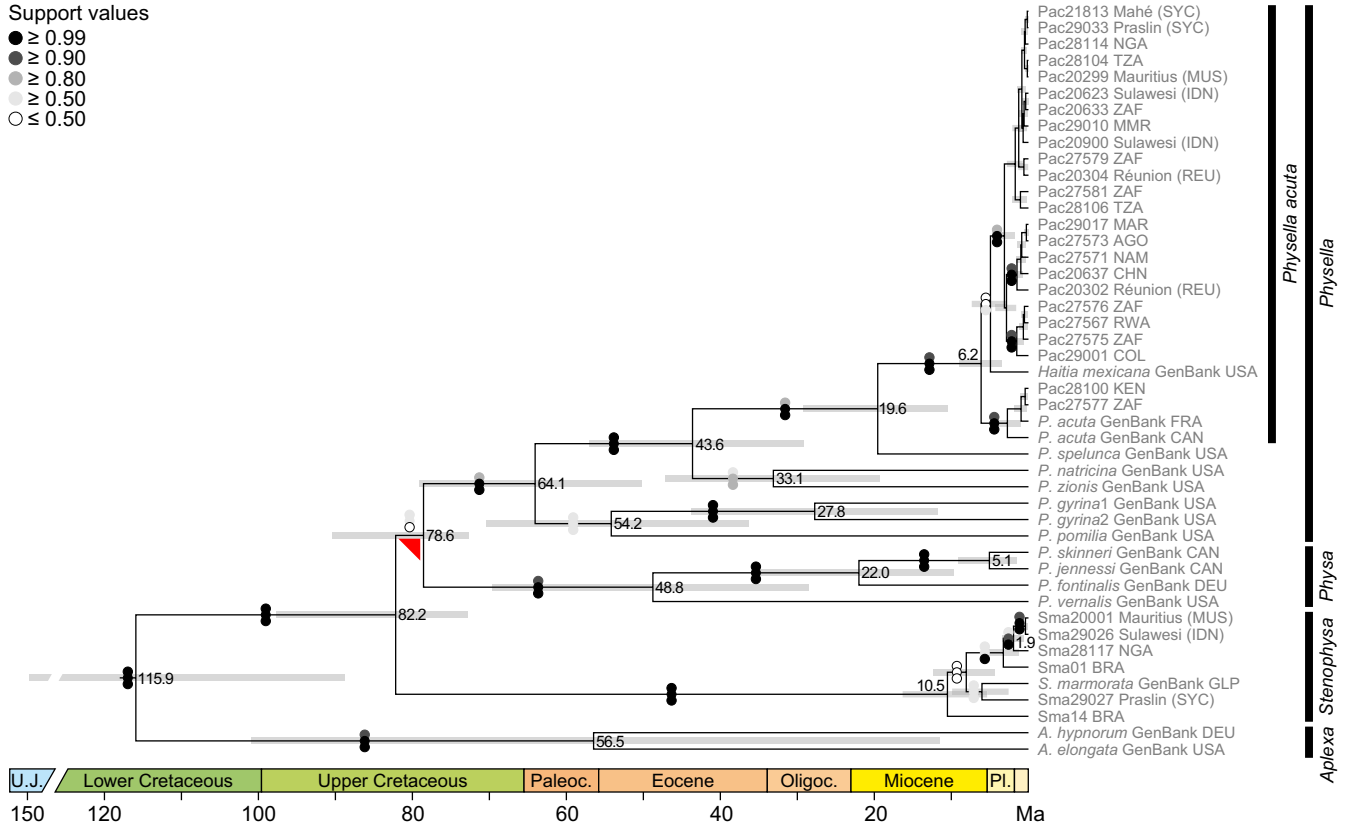

FIGURE 2 | Fossil-calibrated phylogeny performed in BEAST (outgroup taxa removed) including node ages, 95% HPD intervals (grey bars) and support values (from top to bottom: RAxML bootstrap values, MrBayes posterior probabilities and BEAST posterior probabilities). For simplicity, not all mean ages and support values are shown. The node that has been used for calibration is marked with a red triangle.

3.2 | Colonisation/Invasion Patterns

Physella acuta, as a global invader, is present in Africa from regions as distant to each other as Morocco, South Africa, Nigeria and Kenya. The species occurs in both continental African countries (plus Oman) and the islands of Mauritius, La Réunion, Seychelles (Mahé and Praslin) and Sulawesi. The *P. acuta* clade comprises multiple and genetically distinct African and Indian Ocean Island lineages, suggesting multiple independent colonisation events. However, the overall unresolved phylogenetic relationships make it difficult to assess their number and origins. According to the haplotype network analysis, 14 and 3 haplotypes were identified as belonging to African and island populations respectively. The haplotype network suggests that Africa was colonised at least six times independently, considering HT01/HT07, HT04, HT26, HT33, HT45 and HT20-HT23/HT15/HT16/HT17/HT19 as separate haplogroups that did not evolve on the continent (Figure 3), also following the conclusions of Lawton et al. (2018) and their analysis.

For *Stenophysa*, the phylogeny suggests two independent transoceanic dispersal events leading to the colonisation of Africa and the Indian Ocean islands. One is from the Caribbean (Guadeloupe) to the Seychelles (Figure 2), whereas the other is from Brazil to West Africa and subsequently to southeast Africa and the Indian Ocean islands. The haplotype network analysis revealed seven haplotypes with a single haplotype dominating present in South Africa, Malawi (representing nominal *P. mosambiquensis*), Mauritius and the distant Indonesian islands of Sulawesi and New Guinea (Figure 3). The West African specimens (representing nominal *A. waterloti* from Benin and Nigeria) are equally linked to the main haplotype as to the two specimens studied from Brazil, suggesting a colonisation of West Africa from Brazil. Interestingly, the Brazilian samples (representing *Afrophysa braziliense*) revealed two genetically distinct haplotypes, though they originate from the same population. The haplotypes of the genus' native range (Brazil and Guadeloupe) are not closely related (Figure 3) as already evident from the molecular phylogeny.

3.3 | Habitat Preferences

Physella acuta in continental Africa was found as the only gastropod species in more than half of all occurrences (54%), was associated with a single other gastropod family in 36% and with two other gastropod families in 10% of the cases (Table S2). Riverine habitats dominated (73%) over a dam lake, a coastal lake and an irrigation canal (9% each). Similarly, on islands, the species preferred riverine settings (75%) over rice fields and irrigation canals (12.5% each). The species never occurred solely and was associated with one to four (mean = 2.3) families per locality on islands. *Physella acuta* nowadays occurs not only in man-made or highly disturbed habitats but has been found in large natural lakes such as Lake Victoria, where it was established locally in 2018 or slightly before and was re-confirmed after spreading in 2023 (FC, pers. obs.).

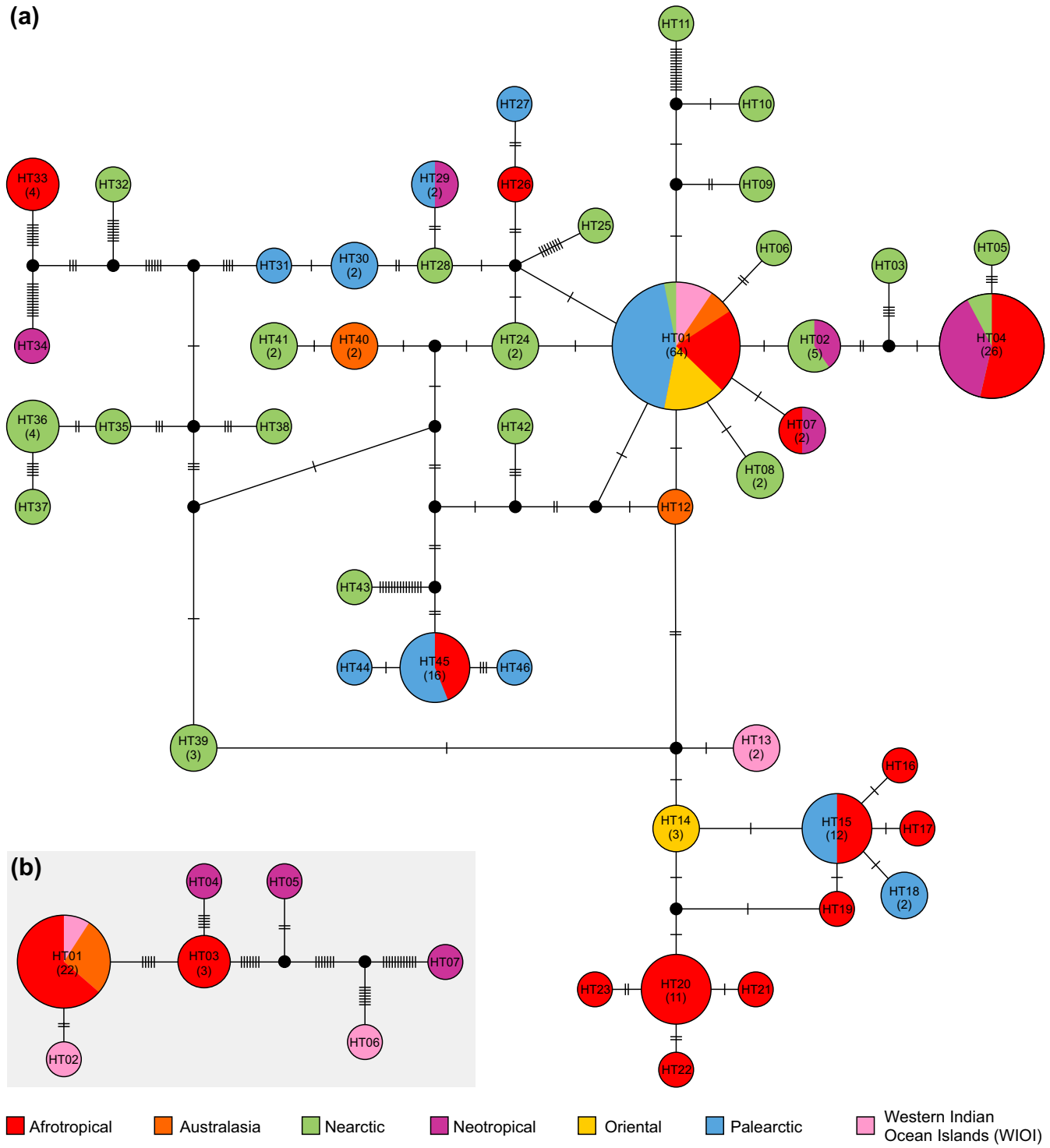

FIGURE 3 | Haplotype networks of *P. acuta* (a) and *S. marmorata* (b) created in PopART using the TCS algorithm (see Table S1 for haplotype codes). Number of specimens shared by the respective haplotype are shown in brackets. Black hatch marks and circles represent mutational steps and unsampled haplotypes respectively.

It also established populations with high abundances in isolated crater lakes (Lake Duluti, Tanzania) or desert settings (Namibia, Oman). The actual habitats in the systems though were mostly affected by anthropogenic disturbance such as eutrophication.

Generally, *S. marmorata* from its native range were collected from a river (Brazil) and an intermittent reservoir (Guadeloupe). In continental Africa, edges of riverine habitats (56%) predominated, followed by waterholes in a nature reserve (22%) and a rice field (11%) as well as a large coastal lake (11%; Table S2). The species was found on islands in natural habitats, perennial streams, temporary pools and artificial systems such as in a botanical garden. Except for this botanical garden, where *S. marmorata* was the single gastropod species, it occurred in

communities of one to six non-physid family-level mollusc taxa (mean = 2.6). Remarkably, only the Ona River in urban Ibadan (Nigeria) supported two syntopic populations of *S. marmorata* and *P. acuta*.

3.4 | Suitable Habitats

In general, the SDM for *S. marmorata* predicted occurrences well (means of best, that is, TSS > 0.6, model runs: AUC = 0.94, $R^2 = 0.57$, TSS = 0.64; Figure 4). The predicted hotspots in South America and West Africa are represented by actual records. In contrast, regions of high occurrence probabilities in equatorial Africa and regions in the Indo-Malayan Archipelago, New Guinea and Eastern Australia lack such records. These regions are characterised by suitable conditions for the establishment of invasive species. Occurrences in eastern and southern Africa are less well predicted.

4 | Discussion

4.1 | Phylogenetic Patterns and Species Identities

The current molecular phylogeny is the most comprehensive multi-gene phylogeny of Physidae currently available, including the type species of the four widely accepted genera and all available genus-level taxa. Although the present phylogeny (Figure 2) further stabilises the systematics of Physidae, some nominal taxa of Taylor (2003) remain to be phylogenetically studied. Nevertheless, we could test some of the phylogenetic hypotheses that were previously postulated. According to our data (1) *Aplexa* is not the sister-group of *Stenophysa*, and both thus do not form the proposed subfamily Aplexinae; rather, this circum-Caribbean/South American taxon forms a highly supported clade with *Physa* and *Physella*. The Aplexinae thus consists only of *Aplexa* species, including *A. elongata*, also known as *Sibirenauta elongata*; (2) *Afrophysa brasiliensis*, that is, *P. waterloti* from Africa, as well as *P. mosambiquensis* are likely synonyms of *Stenophysa marmorata* and thus of Caribbean-South American origin and not belonging to the Aplexinae; (3) *Stenophysa* was found to be a member of Physinae and not Aplexinae as previously assumed. However, the substantial genetic difference between *Physa* + *Physella* clearly supports a distinct genus *Stenophysa*, instead of the inclusion in *Physa* as proposed by Wethington and Lydeard (2007); (4) Another long-standing debate of *Physa* versus *Physella* becomes further enlightened given our phylogenetic placements of *P. acuta* and *P. fontinalis*. Although both groups are highly supported, the sister-group relationship between them is not. This is important as findings based on single-gene phylogenies have been contradictory (Wethington and Lydeard 2007; Young et al. 2021) and did not recover monophyletic genera *Physella* and *Physa*. Finally, *Haitia* as Taylor (2003) proposed, has to be synonymised with *Physella*.

The time-calibrated tree (Figure 2) is in good concordance with the scarce fossil record of the family. However, given that only a single and comparatively old fossil calibration point was available for dating the phylogeny, younger splits might be overestimated (i.e., older) due to the lack of further internal calibration points. Thus, the onset of diversification within *Stenophysa* and *P. acuta* may be considered with caution. However, our data clearly show that the diversification in *Stenophysa* started considerably earlier than in *P. acuta*.

4.2 | Invasion Histories

Physella acuta has long been established as an alien invasive species in parts of Africa, as early as 1954 in South Africa (De Kock and Wolmarans 2007) and latest in the 1980s in central Kenya (Brown 1994). Its spread has been described to be rapid (De Kock and Wolmarans 2007), often following the decline or complete disappearance of native snail faunas (Brown 1994). Brown's (1994) account listed *P. acuta* to be present in eight countries in sub-Saharan Africa and suspected it to be a 'composite taxon' of American origin. We showed that *P. acuta* is present in many African countries and that multiple invasions occurred as already proposed by Lawton et al. (2018), although their dataset was based on a limited sampling from three countries (i.e., Angola, Burundi and South Africa).

We confirmed most of the haplotypes recognised earlier but found a considerable number of new ones (Figure 3). The most common one, however, is new for Africa and occurs throughout

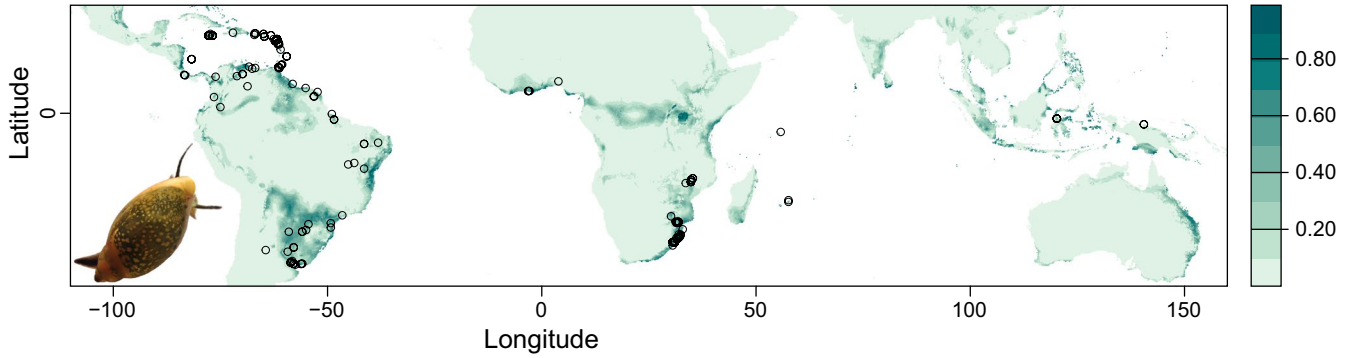

FIGURE 4 | Predictive species distribution modelling for *Stenophysa marmorata*. Black circles represent records from the present study and other resources (see text for details). Predicted occurrences and hotspots are represented by a colour gradient from light mint-green to dark mint-green (see scale on the right side of the map). The living gastropod depicted represents a *Stenophysa marmorata* specimen from a rice paddy close to Lake Malawi.

the continent (South Africa, Tanzania, Kenya, Nigeria and Oman) and all studied islands (except New Guinea). It is a global haplotype also found in Europe, continental Asia and central parts of the United States. Such a pattern indicates a 'flash invasion' (Lounnas et al. 2017) but hampers an inference on the trajectory (Ebbs, Loker, and Brant 2018). Because the sampling is not yet continent-wide we assume that more than six independent invasions of continental Africa have occurred. The published record suggests an early invasion hub in South Africa, followed slightly later by eastern parts of the continent and potentially last in western Africa as suggested by the earliest published record from Nigeria (Kristensen and Ogunnowo 1992). However, there is always a considerable time lag between establishing a non-native species and recognition, especially in inconspicuous species such as the physids that even resemble native bulinids by their general shell shape (see e.g., Brown 1994). It might also be due to the indistinctness of shell shapes that led early malacologists to describe native endemic *P. borbonica* from the Mascarene Islands. Given the natural range of Physidae (see Wethington and Lydeard 2019) and our findings of *P. acuta* on these islands, we conclude that this species has established vital populations almost as early as in Europe, that is, in the early 19th century (Vinarski 2017). Occurrences on basically all studied Indian Ocean islands (see Figure 3) support the tremendous dispersal capacity of this most invasive global freshwater pulmonate species. The means of dispersal are not simple to trace, and several modes have been discussed for medium distances (Banha, Marques, and Anastácio 2014; Van Leeuwen et al. 2013). Aquarium trade and the introduction of water plants have repeatedly been suggested for long-distance translocation (Albrecht et al. 2009; Madsen and Frandsen 1989; Pointier, David, and Jarne 2005), and the role of water birds as vectors has been emphasised several times (e.g., Reynolds, Miranda, and Cumming 2015).

As stated above, we here interpret the African samples as belonging to a single, though genetically highly variable and thus phylogenetically old species, that is, *Stenophysa marmorata* (Figures 2 and 3). Both the colonisation of Africa via the slave trade and the more recent fast spread of the species in South Africa, which started in 1986 or even earlier, have been discussed in detail (e.g., Appleton, Brackenbury, and Tonin 1989; Appleton and Dana 2005). It remains unclear whether our findings along the Zambezi River system and in the Lake Malawi Basin represent a recent expansion from the localities in Mozambique. Given the close proximity of our recent records to the Lake Malawi proper and the species' habitat preferences, there is a great potential for invading this ecosystem with its unique biodiversity. Invasions of physids to ancient lakes have been demonstrated elsewhere (Albrecht et al. 2009, 2014) and are evident already in Africa as for Lake Victoria (see above). In West Africa, *S. marmorata* has been present since at least the early 20th century and probably much earlier (Appleton and Dana 2005) and has grown to large population sizes, whose introduction has been linked mainly to human activities (Bony et al. 2008).

Physidae have never been considered a native faunal component of the freshwater fauna of Africa nor the Indian Ocean islands (but see *P. borbonica* above). However, an alternative scenario must be discussed in view of our findings, specifically the estimated divergence times in the phylogeny (Figure 2) as well as the considerably high haplotype diversity (Figure 3). Accordingly, a much earlier non-human-mediated dispersal from South America at Plio-Pleistocene times would potentially be possible as proposed for *Biomphalaria* (Jørgensen, Kristensen, and Stothard 2007). However, unlike in *Biomphalaria* there is no fossil record of *Stenophysa* in Africa. As discussed earlier, we only used a single, comparatively old fossil calibration point, and thus node ages towards the tips of the phylogeny might be overestimated. Moreover, the distribution remains localised to two hubs on opposite sides of the continent with only very recent spreading tendencies according to malacological surveys (e.g., Appleton 2003). It further remains unclear why the Benin-Nigerian haplotype is so distinct from the main haplotype occurring in the rest of Africa and the Indian Ocean islands (Figure 3b), which shows the typical pattern of invasive species when a single haplotype becomes dominant over large geographical areas in a short time (Lounnas et al. 2017). Interestingly, the single specimen from Praslin Island (Seychelles) is genetically very distinct from populations from Guadeloupe and not closely related to any other population in the haplotype network. This suggests another independent colonisation and, more importantly, hints further to the following interpretation. Both the lineages from Benin and Nigeria and the Seychelles likely represent a random sample from the ancestral *Stenophysa* population in the Caribbean and South America. This scenario is supported by our identification of two highly distinct haplotypes of *S. marmorata* in a single locality in Brazil (Figure 3b). More extensive geographical sampling of continental South American Physidae is expected to reveal greater biodiversity (Taylor 2003). It is thus very likely that many more lineages exist among *S. marmorata* and that this taxon should be considered a species complex.

Likewise, the invasive species scenario for *S. marmorata* is more conclusive and parsimonious compared to a prehuman introduction to Africa. Based on our phylogenetic patterns and haplotype diversity, we hypothesise a very recent expansion across the Indian Ocean. Although determining the exact origin of that invasion is challenging with the data at hand, the role of the Dutch East India Company trade routes is as plausible as more recent connections and human migrations facilitating transportation in both directions, that is, from Africa to Indian Ocean islands or vice versa. The fit of occurrences and the predictions is comparatively good in the native range of the species (Figure 4). In addition, the SDM also corroborates the potential for a global tropical invasion of *S. marmorata*. The vast regions in Africa, Asia and Australia where the species lacks records currently might be under-sampled. In contrast, it might simply reflect the ongoing phase of the invasion with large potential regions not being invaded yet. Records from climatically less optimal regions such as in South Africa are likely due to the highly stochastic nature of the human-mediated introductions and subsequent establishment.

4.3 | Intra- Versus Interspecific Invasions

Physidae in Africa and across the Indian Ocean represent both intraspecific and interspecific cryptic invasions. Several lineages of *P. acuta* independently invaded Africa from several sources (Figure 3). Though recognised for decades, the extent of the spread has been clearly underestimated. Nowadays, there

are concerns not only about disturbed habitats close to urban regions. The species occurs in natural systems far from urban centres. Such a pattern is typical of an intraspecific cryptic invasion (Morais and Reichard 2018). It is likely that many more records will be obtained when dedicated surveys are conducted on other regional freshwater mollusc faunas throughout Africa. Part of the underestimation of the spread of this species lies in the fact that *P. acuta* is often confused with native *Bulinus* spp. by superficial examination or unaware collectors (CA, pers. obs.).

On the other hand, *Stenophysa marmorata* is a prime example of an interspecific cryptic invasion because it has been mistaken as either *Physa waterloti* or *P. mosambiquensis*, or even referred to under the generic names *Aplexa* or *Afrophysa*. This taxonomic confusion reflects the uncertainty surrounding the status of these two taxa, which we consider synonyms of the invasive alien species *S. marmorata*. Moreover, its invasion has been cryptic in two ways, taxonomically and spatially. It is more widespread in southwestern Africa than anticipated, but also cryptically invaded geographically very distant islands across the Indian Ocean as far as the Indo-Australian Archipelago (Figures 2 and 3). This has reached an extent that ranks it among the top 10 most invasive freshwater gastropods globally (see Preston et al. 2022). Interestingly, besides being interspecifically cryptic invasive (relative to *P. acuta*), *S. marmorata* definitely shows characteristics typical for intraspecific cryptic invasions. Here, the potentially independent colonisations of West and East Africa, the Seychelles and other islands in the Indian Ocean by specific distinct lineages from different sources in the native range went unnoticed.

The example of the Physidae outlines the complexity of the phenomenon of cryptic invasions and evaluates the mechanisms involved. Cases such as this can also help to understand the success and impact of such kinds of invasions. Human-mediated introduction is likely to play the dominant role in *S. marmorata*. Whereas no direct data exist on differential invasive behaviour of certain genetic lineages of the two physid species, clear differences have been shown between the two species in Argentina. *Physella acuta* had higher fecundity and better life-history parameters in the native range of *S. marmorata* (Núñez 2010, 2011). This might also explain why only a single case of co-occurrence was found in our study (see Figure 1). Nonetheless, this is a remarkable finding as previous studies suggested distinct ecological preferences for the two species (Appleton and Dana 2005), with slow-flowing waters for *S. marmorata* and running waters for *P. acuta*. A stable co-existence of the two species was predicted for populations in Guadeloupe (Dubart et al. 2019) due to reduced competition. Even though the number of habitats studied is rather low, and the categories of habitats are coarse, our findings do not support habitat preferences for either species (Table S2). Both *P. acuta* and *S. marmorata* colonise natural and remote systems, not limited to disturbed habitats with already depauperated mollusc communities. Remarkably, *P. acuta* occurred in many cases only as a sole species or with one other species in the community, at least in continental African settings. This is of concern given the competitive abilities shown, at least for *P. acuta*, leading to the decline and even local extinction of ecologically similar planorbid snails in Africa (Brackenbury and Appleton 1991) and Australia (Zukowski and Walker 2009). 'Enemy release', that is, the escape from native-range parasites, has been shown for *P. acuta* and likely is one component for its global invasion success (Ebbs, Loker, and Brant 2018). The extent to which this applies to *S. marmorata*, however, is currently unclear.

Impacts of cryptic invaders are even more difficult to detect and assess than in regular invasions. Invasions of the scale of the physids will undoubtedly affect the ecosystems they colonise, and although such impacts have not been well-studied, they could be more rapid and more severe in small insular systems. Such colonisation-extinction-recolonisation dynamics can be very complex as recent long-term studies on Guadeloupe have shown (Dubart et al. 2022). In fact, freshwater mollusc faunas in the Indian Ocean experience severe transformation, with many endemics being (cryptically) replaced by non-indigenous species, not only physids (CA, pers. obs.). Such impacts will become more evident in future as revealed by our modelling that identified suitable habitat conditions beyond the currently known range at least for *S. marmorata*.

4.4 | Conservation and Management Aspects

The management of freshwater gastropod species is a major challenge, particularly under natural conditions and especially in Africa (Rollinson et al. 2009). Despite their global invasiveness and documented impacts on native species and ecosystems, there is no formal risk assessment for Physidae. A key point in potential mitigation strategies is the recognition of a second major player, that is, *S. marmorata*. It is also important to realise that both species are not limited to disturbed sites and are not directly linked only to human activities (plant introductions, etc.). We do not have sufficient information on the actual impacts of either species, although it is clear that they will compete with native gastropods for food and other resources and will have direct impacts given the population sizes they can build up so quickly (Appleton 2003).

As usual, disruption of the transmission chain would be an intervention to stop further introductions to the continent and intracontinental translocations (Havel et al. 2015). The movement of fish, including ornamental species, and aquatic plants should be strictly regulated and controlled. It is foreseeable that aquaculture and the blue economy, in general, will dramatically increase the introduction of freshwater gastropods and other invertebrate groups into African waters in the near future.

Another important aspect is the creation of many new habitats such as large hydroelectric dam projects, which are already underway or planned for the near future and may increase the rates of establishment for these and other invasive species.

Coordinated control efforts in relation to medically important intermediate host snails (Sokolow et al. 2018) could have side effects on physids, potentially reducing their populations. Reducing the invasibility of ecosystems by enhancing their natural state, minimising pollution, and supporting native fauna could also contribute to controlling the spread of physids. However, given the biological characteristics of physid snails and their worldwide success as invaders, eradication and even halt of the ongoing invasion seems very unrealistic.

Managers are therefore left with awareness raising, impact assessment and monitoring as well as habitat improvement for native fauna.

4.5 | Future Scenarios and Conclusions

Physella acuta is likely to continue its global spread, including in Africa and the Indian Ocean islands. A parallel hidden but potentially also global invasion is rising, with *S. marmorata* having already invaded two continents outside its native range. A notable difference to *P. acuta* is its less pronounced climatic tolerance, as *S. marmorata* is predicted to spread primarily through tropical and subtropical regions. This spread is assumed to be accelerated by ever-increasing traffic and intercontinental trade. Adequate sampling should be carried out in regions where occurrence is predicted. The current distribution is certainly also underestimated, given the cryptic character of the invasion. It is thus generally advisable to follow up more closely on the invasion dynamics and potential interaction with *P. acuta* and other potentially invasive physids. The *Stenophysa* invasion would also provide an interesting study model for testing the 'enemy-release hypothesis' along the lines of research of Ebbs, Loker, and Brant (2018) in *P. acuta*. Because both species now rank among the most globally invasive freshwater gastropods, detailed comparative studies should be considered to further study patterns and processes on cryptic invasions. A major challenge in cryptic invasions is the initial recognition of them, and future investigations of physid introductions may build on the framework outlined here.

Author Contributions

Christian Albrecht designed research and coordinated sampling. Christian Albrecht, Fred D. Chibwana, Edson Lourenço da Silva, Manuella F. Leal, Frank Riedel, Roger Lingofo Bolaya, Alexander Odaibo, Michael O. Popoola and Ristiyanti M. Marwoto sampled in the field. Catharina Clewing, Tamaris G. Pinheiro, and Björn Stelbrink did molecular laboratory work. Björn Stelbrink, Catharina Clewing, and Hanno Seebens performed analyses. Christian Albrecht and Björn Stelbrink wrote the paper, with contributions of all co-authors.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in the Supporting Information (Figures S1 and S2 and Tables S1 and S2). Genetic data are deposited in NCBI GenBank under the GenBank accession numbers PP931039–PP931126 (COI), PP937600–PP937655 (16S), PP937656–PP937685 (ITS2), and PP930947–PP930974 (18S).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.