Received: 18 March 2023 | Accepted: 29 July 2023

DOI: 10.1002/pan3.10535

PEOPLE AND NATURE | BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Identifying potential emerging invasive non-native species from the freshwater pet trade

James W. E. Dickey[1,2,3,4] | Chunlong Liu[1,2,3,5,6] | Elizabeta Briski[4] | Christian Wolter[1] | Simon Moesch[2,7,8] | Jonathan M. Jeschke[1,2,3]

[1]Leibniz Institute of Freshwater Ecology and Inland Fisheries (IGB), Berlin, Germany; [2]Institute of Biology, Freie Universität Berlin, Berlin, Germany; [3]Berlin-Brandenburg Institute of Advanced Biodiversity Research, Berlin, Germany; [4]GEOMAR Helmholtz Centre for Ocean Research Kiel, Kiel, Germany; [5]Fisheries College, Ocean University of China, Qingdao, China; [6]Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan, China; [7]Geography Department, Humboldt-Universität zu Berlin, Berlin, Germany and [8]Leibniz Institute for Zoo and Wildlife Research (IZW), Berlin, Germany

Correspondence
James W. E. Dickey
Email: jamesdickey03@gmail.com

Chunlong Liu
Email: liuchunlong113@gmail.com

Funding information
Alexander von Humboldt-Stiftung; Deutsche Bundesstiftung Umwelt, Grant/Award Number: 20020/652-33/0

Handling Editor: Helen Roy

Abstract

1. An increasingly globalised world has facilitated the movement of non-native species (NNS) via the poorly regulated international pet trade. While focus is increasingly being placed on preventative action to combat invasive NNS—often cheaper and less difficult than the management of established populations—successful prevention requires controlling potential pathways and obtaining baseline knowledge of species' availability.
2. Here we performed an in-depth analysis of the freshwater pet trade as one major vector of NNS, compiling its species inventory and deriving threats of NNS release and establishment in the wild. With Germany as our study region, we surveyed pet stores, websites and the country's largest online classified portal, eBay Kleinanzeigen, recording the taxa encountered. For each species, we determined the likelihood of release based on availability and price (cheaper and/or more readily available species have been shown to be of greater risk), and the likelihood of establishment based on ecological niche breadth and niche overlap with environmental conditions in Germany.
3. The survey revealed 669 species, of which 651 were non-native to Germany. Looking at release likelihood, more readily available species in pet stores and on websites proved to be cheaper. For websites, there was a significant effect of occurrence status (i.e. released, not released, native) on price, with released and native species being significantly cheaper. Species previously released in Germany and elsewhere demonstrated greater niche breadths and greater niche overlaps between their source regions and Germany; and for species released in Germany, there was a significantly positive relationship between the magnitude of niche overlap and the number of documented occurrences.

4. Finally, we combined our release and establishment likelihood findings under 'Release Risk' metrics to highlight the species most worthy of prioritisation. We propose these metrics as proactive methods for screening species in the trade, which can inform future policy direction and intervention.

KEYWORDS
aquatic invasive species, Invasive Alien Species (IAS), niche breadth, niche overlap, non-native species, pet trade, propagule pressure, Release Risk

1 | INTRODUCTION

Increasing globalisation has facilitated numerous pathways for non-native species (NNS) to be introduced (Hulme, 2009; Saul et al., 2017; Zieritz et al., 2016), with the number of NNS unlikely to saturate in the near future (Seebens et al., 2018). One crucial pathway that has benefited from international supply chains is the pet trade. While most animals within this poorly regulated trade remain in confinement throughout their lives (Raghavan et al., 2013), many individuals are intentionally released or escape from importers, sellers or consumers (Holmberg et al., 2015; Lockwood et al., 2019; Vall-Ilosera & Cassey, 2017). The pet trade, shown to specifically favour invasive NNS (those responsible for ecological and/or economic impacts), has facilitated their spread around the world (Gippet & Bertelsmeier, 2021; Mason et al., 2013). Indeed, it is deemed responsible for 53% of invasive vertebrate NNS (Gippet & Bertelsmeier, 2021; Saul et al., 2017) and one third of aquatic invasive NNS (Padilla & Williams, 2004).

The availability of species within the trade has been linked to more release events (Chucholl, 2013; Duggan et al., 2006) and propagule pressure is one key determinant of establishment success (Briski et al., 2012; Stringham & Lockwood, 2021). Due to the supply-and-demand characteristics of the pet trade, 'bandwagon species' emerge, namely those traded at higher volumes and lower prices. These are deemed more likely to be released (Lockwood et al., 2019). However, even if propagule pressure is high, abiotic barriers to growth and survival must be overcome (Blackburn et al., 2011), which have proven crucial to establishment success of numerous pet trade species (Standfuss et al., 2016; Veselý et al., 2015). Studies have shown that species' range size is a good predictor of invasiveness (Ricciardi & Rasmussen, 1998), which has led to the 'niche breadth—invasion success hypothesis', with generalist species with broad niches more likely to successfully invade than specialist species with narrow niches (Vázquez, 2006). Niche analysis also allows us to predict how a specific system could be at risk based on the niche overlap between source and recipient regions for NNS (Liu et al., 2019). This is because the niche of a species changes very slowly through space and time (i.e. niche conservatism: Liu et al., 2020; Petitpierre et al., 2012; but see Sexton et al., 2017).

Here, we used Germany as our focal country due to it being an important European Union (EU) member state and a major importing and re-exporting hub in the global aquarium trade (Dey, 2016). Germany shares land borders with nine countries including Switzerland, a non-EU hub for imports and trans-shipment throughout Europe (Biondo, 2018; Leal et al., 2016), and Czechia, a gateway for EU imports (Kalous et al., 2015; Novák et al., 2022). Despite a number of EU regulations relating to the pet trade, such as the Common Entry Veterinary Document (Regulation 338/1997), and prohibiting the import, transport, use and release of Invasive Alien Species of Union Concern (Regulation 1143/2014), a number of freshwater NNS have established feral populations in Germany, including fish (Wolter & Röhr, 2010), crayfish (Chucholl & Wendler, 2017), and turtles (Pieh & Laufer, 2006). Many species sold in Germany may be capable of establishing impactful populations, and that they have not yet done so may be entirely serendipitous (McDowall, 2004). Crucially, previously banned species may still be available in stores or on online marketplaces. Preventative measures are deemed the most effective NNS management options (Leung et al., 2002; Ricciardi & MacIsaac, 2022; Roy et al., 2014), but they require the identification of risky traded species with high likelihoods of introduction, establishment and spread (Liu et al., 2019). There is therefore a pressing need for a quantitative method that allows this.

To assess which NNS in Germany's freshwater pet trade pose the greatest risk, a baseline knowledge of the available species is required. We determined those available via three ways: (1) physical pet stores and garden centres in the country's largest city, Berlin (including some Germany-wide chains); (2) German pet websites; and (3) eBay Kleinanzeigen, the country's largest online marketplace (such non-traditional marketplaces are becoming increasingly important: Lockwood et al., 2019; Olden et al., 2021). We addressed five key questions, with the first two questions focusing on likelihood of release, based on price and availability: (1) whether cheaper species are more likely to be released (i.e. have documented non-native occurrences); and (2) whether more readily available species in the pet trade are more likely to be released. Two other questions focused on likelihood of establishment, centred around climatic niche: (3) whether released species are more likely to have wider niche breadths; and (4) whether species with non-native occurrences in Germany are selected from regions with similar climates to the target region. Finally, we combined likelihood of release with likelihood of establishment under our novel Release Risk (RR) metric which accounted for availability, price and either niche breadth or climatic niche overlap with Germany using 2030 climatic projections. Using this metric, we addressed question (5): which species in the freshwater pet trade pose the highest risk of release and establishment and thus should be targeted by management intervention?

2 | METHODS

2.1 | Surveys

2.1.1 | In-person pet store survey

The survey of available species in pet stores and garden centres was conducted in Berlin between November 2020 and March 2021. Relevant stores were found using online business directory websites (gelbeseiten.de, goyellow.de, yelp.de) and the pet store directory of petnews.de (which allowed 'lebende Tiere'—'live animals'—to be specified). All listings were checked with Google/Google Maps to determine which stores were still open and sold live freshwater animals. In each store, listings (i.e. species identification cards featuring the common and/or binomial species name, and price: see Figure S1 for an example) were photographed and compiled. Due to the covert nature of the process and the high number of listings per store, it was difficult to confirm that all listings corresponded to species present in store. However, we treat all listings as featuring species that have at least been sold recently. In total, listings were compiled from 12 stores roughly evenly distributed across the city (Figure S2). When stores or websites offered different sizes, sexes or age groups of species, the cheapest price was used. Furthermore, when discounts were offered for buying higher numbers of certain species, the cheapest price was used (e.g. if a fish species was 3,00€ individually, or 6,00€ for 3×, the price was taken as 2,00€).

2.1.2 | Pet websites

Over the month of October 2020, online pet stores across Germany were surveyed. To reduce the search bubble effect from previous browsing history and cookies (Ćurković & Košec, 2018), three search engines (Google.de, duckduckgo.com and Bing.com) were accessed using 'private windows' on Mozilla Firefox. For duckduckgo.com and Bing.com, which offered results from a specific area, the location was set to Germany. The search terms "Zierfische kaufen" (i.e. "buy ornamental fish"), "Flusskrebs für Aquarium kaufen" ("buy crayfish for aquarium"), "Garnelen kaufen" ("buy shrimp"), "Wasserschildkröten kaufen" ("buy turtles"), "Aquarienschnecken kaufen" ("buy aquarium snails"), "Teich Tiere kaufen" ("buy pond animals") and "Muscheln für Aquarium kaufen" ("buy mussels for aquarium") were used. The first 50 websites from each search and each search engine were noted, and only websites with German domains (.de) featuring on all three search engines were used. Once websites were checked to confirm that they sold live freshwater species, all species listings were recorded, with common names, binomial species names, prices and availability (i.e. currently available or not currently available). All freshwater species across 31 pet store websites were recorded.

2.1.3 | eBay Kleinanzeigen

Berlin-based listings were taken from eBay Kleinanzeigen (ebay-kleinanzeigen.de) over 7 weeks within a 14-week period (week 1: 9–16 November 2020, week 2: 23–30 November, week 3: 7–14 December, week 4: 21–28 December, week 5: 4–11 January, week 6: 18–25 January, week 7: 1–8 February), featuring 3 weeks in the run-up to Christmas, a Christmas week, and three post-Christmas weeks to be assessed. To record listings, 'Fische' ('fishes') was selected from the 'Haustiere' ('pets') options and only 'Angebote' ('offers') listings (as opposed to 'Gesuche', 'wanted') were included. Note that the 'Fische' heading incorporated the sub-headings of 'Aquarium', 'Barsche' ('perch'), 'Diskusfische' ('discus fish'), 'Garnelen & Krebse' ('shrimp and crabs'), 'Koi', 'Schnecken' ('snails'), 'Wasserpflanzen' ('water plants'), 'Welse' ('catfish') and 'Weitere Fische' ('other fishes'), and fishes, crayfish, freshwater crabs, shrimp, amphibians, molluscs and terrapins were all found using this heading. Each day during the survey period, the website was checked at 12:05 PM, with all listings with a time stamp of 12:00 that day and going back to 12:01 the previous day recorded. All listings were saved as PDF files and the information was subsequently compiled in a spreadsheet, with the listing title, the common name, the binomial species name (where available), and reasons given for selling, where given, noted (see overview as per Table S1). The reasons given were grouped into 22 different categories, with definitions of each and examples given as per Table S2.

2.2 | Niche breadth and niche overlap analyses

Species names were validated using the Global Biodiversity Information Facility (GBIF) and carefully checked to avoid synonyms. Species native to Germany (henceforth 'native') were excluded from niche analysis. Occurrence data for each species were compiled from GBIF (using the 'rgbif' R package), which is currently the largest international database of geo-referenced species observations. GBIF compiles millions of occurrences from diverse sources including museum records, scientific databases and citizen science programmes, which have been extensively used to describe the up-to-date range of NNS across the globe (Lajeunesse & Fourcade, 2023). Each NNS (i.e. those with a native range not including Germany) needed to have at least five occurrences in their native ranges and in Germany or across the globe (i.e. both native and introduced ranges) to meet the requirement for niche analyses (see below). The environmental conditions for each species were determined according to eight variables describing projected (2030) climatic conditions at the worldwide scale from WorldClim at a 10 arc-min resolution (Hijmans et al., 2005): annual mean temperature (BIO1), temperature seasonality (BIO4), mean temperature of the warmest quarter (BIO10), mean temperature of the coldest quarter (BIO11), annual precipitation (BIO12), precipitation seasonality (BIO15), precipitation of the wettest quarter (BIO16) and precipitation of the driest quarter (BIO17). In summary: niche analysis involved 651 NNS with at least five occurrences in the native range, for which the dynamics of species niche were estimated between native countries and Germany in 2030; and 95 species with at least five occurrences in native countries and introduced non-native countries, for which the dynamics of species niche were estimated between their global ranges (i.e. native countries and introduced countries) and Germany in 2030.

Niche analyses was conducted using the COUE scheme (Centroid shift, Overlap, Unfilling, and Expansion) developed by Broennimann et al. (2012). The 'COUE' scheme is deemed the most appropriate approach to quantify and decompose niche changes (Figure S3). For a given species, all climatic variables associated with species occurrences in native and global ranges were used to produce a two-dimensional environmental space by principal components analysis. The native and introduced continents of each species were used as background regions to delineate the environmental conditions that a species can occupy via natural dispersal (Broennimann et al., 2012). All cells in the native and introduced continents, as well as species occurrences, were then projected into the environmental space calibrated by the environment across the global climatic conditions, so that all species are projected at the same environmental scale. A kernel density function was then used for smoothing the density of occurrences in the native and introduced environmental space respectively to account for the different sampling approaches applied in the native and introduced ranges (Broennimann et al., 2012; Petitpierre et al., 2012).

For each species, the niche breadth in the native range and across the globe was used for representing the range of environmental space in which species can survive, and niche overlap represents the similarity in occupied environmental space between the source regions and Germany. Niche breadth was quantified via a minimum convex polygon estimator using the 'adehabitatHR' R package, and Schoener's *D* was quantified to assess an overall match between two niches using the 'ecospat' R package. The detailed process for collecting occurrence, range and climate data, and the niche analysis methods are further outlined as per 'Supporting Information: Methods', with cited material therein referenced under Data Sources at end of manuscript.

2.3 | Data analysis

2.3.1 | Survey findings

A three-sample test for equality of proportions was used to compare the proportions of species with non-native occurrences in Germany across the three surveys. A three-sample test for equality of proportions was also used to test for differences in the proportion of unique species (i.e. those not found in other surveys) available across the three surveys.

2.3.2 | Likelihood of release

The relationship between species availability and average lowest price from the pet store and website surveys was assessed using linear models, with availability and price both log-transformed. The effect of occurrence status (i.e. species with non-native occurrences globally, species without non-native occurrences, German native species) on average lowest price of species from pet store and website surveys was assessed using a Kruskal–Wallis rank sum test, and a post-hoc Dunn's Test with Benjamini Hochberg continuity correction. We investigated the relationship between the number of German occurrences, or elsewhere occurrences, and price, by fitting Quasi-Poisson generalised linear models (GLMs). To test whether there was a relationship between the number of occurrences in Germany (for species with German occurrences) or elsewhere (for species with elsewhere occurrences) and their availability using GLMs (family stated in Results).

2.3.3 | Likelihood of establishment

Using (1) native and (2) global ranges, the climatic niche breadths of species with occurrences in (a) Germany and (b) elsewhere were compared to those species without occurrence data using a Wilcoxon rank sum test with continuity correction. Furthermore, we used linear models with Box-Cox transformation to assess the relationship between the number of (a) German and (b) elsewhere non-native occurrences, and the species' (1) native and (2) global niche breadths. Next, using the (1) native ranges and then the (2) global ranges, we assessed whether species with invasion histories in Germany have greater climatic niche overlaps (Wilcoxon rank sum test with continuity correction), and whether the number of occurrences in Germany were explained by the degree of overlap (linear model with Box-Cox transformation).

2.4 | RR metrics

To determine the risk of any given species in the pet trade, it is important to account for both the likelihood of release, and the likelihood of establishment. Cheaper and more available species were expected to have greater risks of release (Chucholl, 2013; Lockwood et al., 2019), species with wider niche breadths to be more likely to establish in more regions (Carscadden et al., 2020), and species with higher degrees of niche overlap to be more likely to establish in Germany, our focal region (Bates et al., 2020). We therefore propose two RR assessment metrics: the first based on a relative availability score, a relative price score and a niche breadth score (Equation 1: RR_b; NB = niche breadth), and the second based on a niche overlap score (Equation 2: RR_o; NO = niche overlap). We applied these to species found in the pet shop survey and the pet website survey as follows:

$$RR_b = \frac{\text{Availability focal species}}{\text{Availability most prevalent species}} \times \frac{\text{Price cheapest species}}{\text{Price focal species}} \times \frac{\text{NB focal species}}{\text{NB species with greatest NB}}, \quad (1)$$

$$RR_o = \frac{\text{Availability focal species}}{\text{Availability most prevalent species}} \times \frac{\text{Price cheapest species}}{\text{Price focal species}} \times \frac{\text{NO focal species}}{\text{NO species with greatest NO}}. \quad (2)$$

All statistical analyses were performed using R v4.1.2 'R Core Team' (2021).

3 | RESULTS

3.1 | Survey findings

A total of 669 species with at least five documented occurrences in their native ranges were found across all three surveys, with 18 native species and 651 NNS (Figure S4; Supporting Information: Results). Of those, 24 NNS had at least one introduced, non-native occurrence in the wild across the globe, and 22 of these had at least one non-native occurrences in Germany (Figure S4; Supporting Information: Results). From the in-person survey of 12 pet stores, 365 species were identified, with 15 of the 356 NNS having at least one documented occurrence in Germany (Figure S4; Supporting Information: Results). From the survey of 31 websites, 531 species were identified, with 17 of the 516 NNS having documented occurrences in Germany (Figure S4; Supporting Information: Results). From the eBay Kleinanzeigen survey, 3229 listings were saved with 207 species identified. There were 204 NNS, with eight having documented occurrences in Germany (Figure S4; Supporting Information: Results). No significant effect of survey type (pet stores, websites, eBay Kleinanzeigen) on the proportion of species with documented non-native occurrences in Germany was found ($p = 0.759$; Figure S4).

Of the three surveys, the website survey featured not only the most identified species, but also had the greatest proportion of unique species (i.e. not found in the other two surveys, 44.4%: Figure 1). The pet store survey featured the second highest number of unique species (28.5%), with the eBay Kleinanzeigen survey third (11.6%). There was a significant effect of survey type on the proportion of unique species available ($\chi^2 = 77.706$, df = 2, $p < 0.001$; Figure 1). Of the unique species encountered, the pet store survey featured the most unique species with documented non-native occurrences ($n = 6$, 5.7%), and the website survey featured the most native species ($n = 9$, 3.8%). None of the unique species recorded from the eBay Kleinanzeigen survey had non-native occurrences, and none were native species (Figure 1). There were 129 species that featured in all three surveys.

In terms of the taxonomic breakdown of species encountered across all three surveys, fishes were the most prevalent, accounting for 89.5% of all species, with molluscs at 4.3%, crustaceans at 3.9% (shrimps: 2.1%; crayfish and freshwater crabs: 1.8%), amphibians 1.2% and reptiles 1.0% (Figure 2; Figures S5 and S6). Two species that feature on the ISSG's 100 of the World's Worst Invasive Alien Species list (Lowe et al., 2000), and three species from the EU's Invasive Alien Species of Union Concern (Regulation (EU) 1143/2014) list, were encountered in the three surveys. From the former list, *Cyprinus carpio* (fish) featured in all three, and *Clarias batrachus* (fish) featured in the website and the eBay Kleinanzeigen survey. A listing

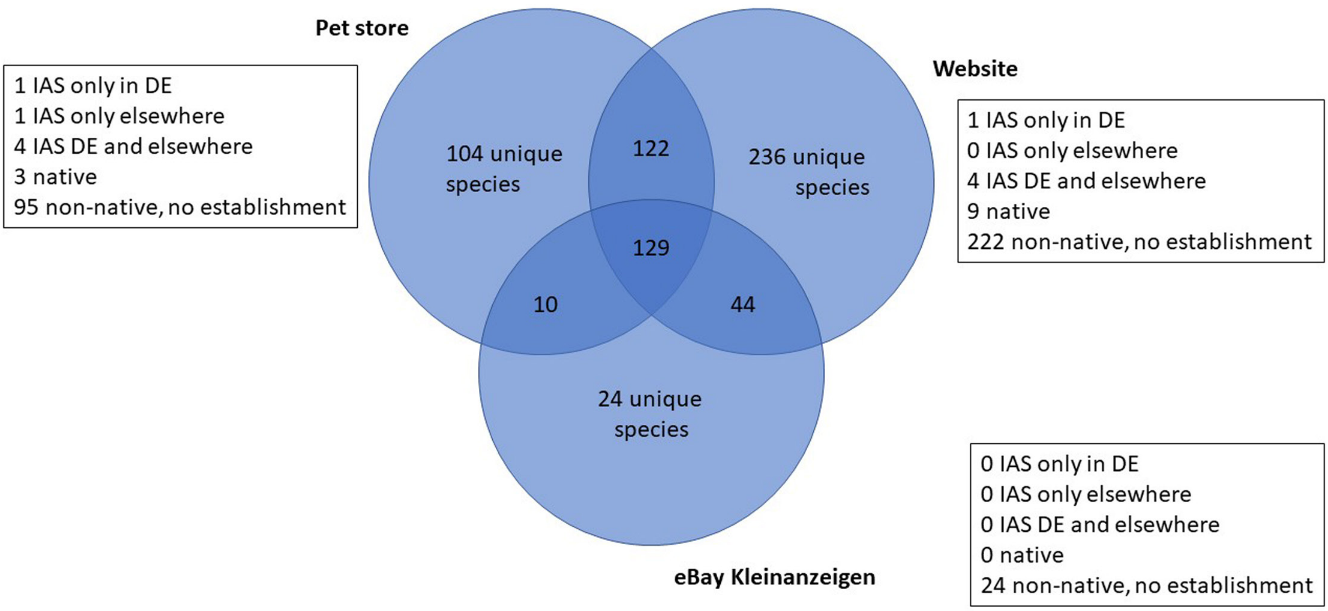

FIGURE 1 Breakdown of species found in each survey, with a focus on species unique to each survey.

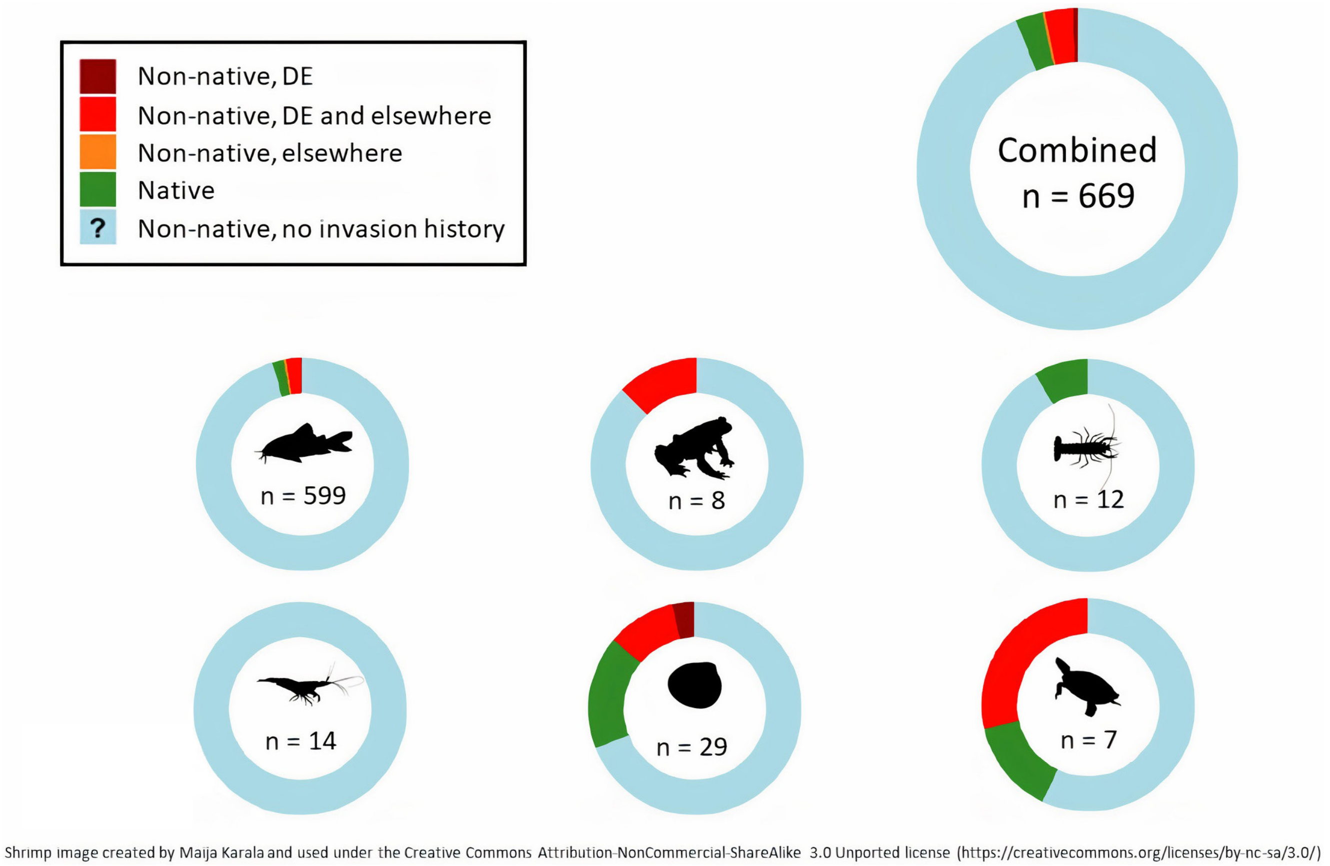

FIGURE 2 A breakdown of all species encountered into six taxonomic groups (fishes, amphibians, crustaceans—crayfish and crabs, crustaceans—shrimp, molluscs and reptiles) and their native/non-native status. Status information was acquired from Global Biodiversity Information Facility, with non-native occurrence data, where applicable, relating to Germany or elsewhere in the world. Native species are those either currently or historically present (i.e. extirpated but previously present) in Germany. Only taxa listed/identified to species level included.

only identifiable as *Clarias* sp. (fish) also featured in the eBay Kleinanzeigen survey. From the recently updated EU list of Union Concern (Regulation (EU) 2022/1203), we found *Xenopus laevis* (amphibian; website and eBay Kleinanzeigen), *Lepomis gibbosus* (fish; website) and *Ameiurus melas* (fish; in person). A number of congenerics of Invasive Alien Species of Union Concern were also found, namely *Xenopus tropicalis* (amphibian), *Channa gachua* and *C. stewartii* (both fish; *C. argus* is on the list). While outside the focus of this study, a number of native protected species were also encountered, namely *Rhodeus amarus* (fish), which features on Annex II (Animal and plant species of community interest whose conservation requires the designation of special areas of conservation), and *Emys orbicularis* (reptile), which features on Annex II and IV (Animal and plant species of community interest in need of strict protection) of Council Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora.

3.2 | Likelihood of release

From the pet store and website survey data, there were significant effects of availability on price for both, with more readily available species proving to be cheaper (LM: pet store: adjusted $R^2=0.140$, $F_{1,363}=60.2$, $p<0.001$; website: adjusted $R^2=0.1212$, $F_{1,529}=74.09$, $p<0.001$). A significant effect of occurrence status on price was found in the website survey ($\chi^2=34.319$, df=2, $p<0.01$), and species with non-native occurrence data were found to be significantly cheaper than those without ($z=2.991$, $p<0.005$; Figure 3). Native species were also significantly cheaper than species without non-native occurrence data ($z=5.130$, $p<0.001$; Figure 3). There was no significant relationship between the number of German non-native occurrences (GLM, Quasi-Poisson: pet store: $p=0.568$; website: $p=0.657$), or elsewhere occurrences (GLM, Quasi-Poisson: pet store: $p=0.531$; website: $p=0.507$), and price. The number of German occurrences (GLM: pet store: Quasi-Poisson, $p=0.567$; website: Quasi-Poisson, $p=0.824$; eBay Kleinanzeigen: negative binomial, $p=0.792$), and elsewhere occurrences (GLM: pet store: Quasi-Poisson, $p=0.522$; website: negative binomial, $p=0.999$; eBay Kleinanzeigen: negative binomial, $p=0.792$) were not related to availability.

Of the 3229 eBay Kleinanzeigen listings from the study period, 465 listings featured reasons for selling, with 483 reasons given (some listings featured more than one reason; Tables S1 and S2). Of the 22 main categories of reasons offered, the top 5 were high reproduction/hobby breeding (18.2%), tank conversion/redesign/change of stock/does not fit stocking (17.0%), size/space (9.7%),

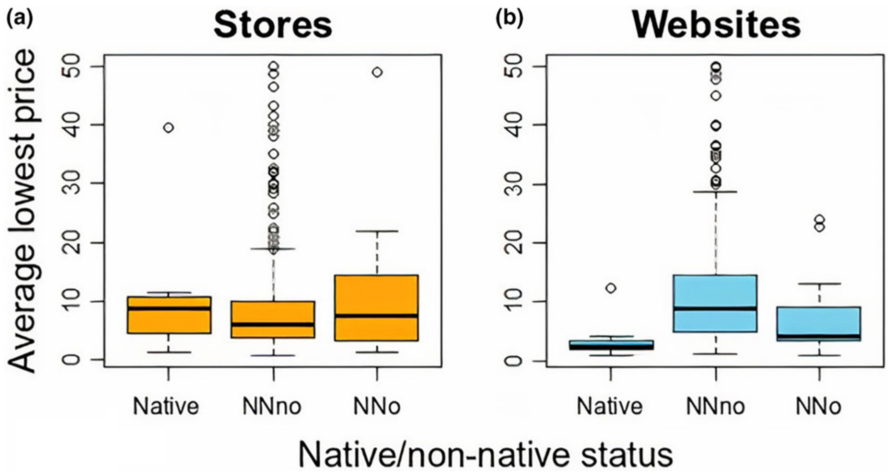

FIGURE 3 The average of the lowest price (€) for species found (a) in pet stores and (b) online. Native relates to species currently or historically native to Germany, NNno to non-native species (NNS; i.e. those with a native range not including Germany) without documented occurrences in Germany or elsewhere, and NNo to NNS with documented occurrences in Germany or elsewhere. Only species with average lowest prices less than or equal to €50 shown in figure for ease of interpretation, but all species (some with prices above €50) used for Kruskal-Wallis test. A significant effect of occurrence status on price was found in the website survey ($\chi^2=34.319$, df = 2, $p<0.01$), with species with non-native occurrence data (NNo) and native species, found to be significantly cheaper than those without, NNno ($z=2.991$, $p<0.005$; $z=5.130$, $p<0.001$).

aquarium dissolution/giving up hobby (9.3%) and incompatibility with tankmates/other pets (7.0%). Four hundred and one of the 465 listings with reasons featured fish, with 381 featuring just fish being sold, and 20 featuring mixed taxonomic groups.

3.3 | Likelihood of establishment

Species with occurrences in the wild, both in Germany and elsewhere, were found to have significantly greater native niche breadths than those without ($p<0.001$ for both). There were no significant relationships found between the number of German or elsewhere occurrences and the size of native or global niche breadths (LM: German, native: $p=0.524$; German, global: $p=0.512$; elsewhere, native: $p=0.296$; elsewhere, global: $p=0.289$). Species with German occurrences were found to have significantly greater native niche overlaps ($W=1303$, $p<0.001$) and global niche overlaps ($W=181$, $p<0.001$) than those without. For species with documented German occurrences, there was a significant relationship between the native niche overlap and the number of German occurrences (LM: adjusted $R^2=0.198$, $F_{1,20}=6.183$, $p<0.05$). A similar pattern was shown when assessing global niche overlap (LM: adjusted $R^2=0.496$, $F_{1,18}=19.7$, $p<0.001$). For top 20 rankings of species by climatic niche breadth and niche overlap see Tables S3–S6.

3.4 | RR metrics

Our RR metrics were applied to 561 NNS from the pet store and website surveys (Figure 4) that had at least five documented occurrences in their native ranges (allowing species niche to be estimated between native countries and Germany in 2030), and 95 NNS with at least five documented native and introduced ranges (allowing species niche to be estimated between their global ranges and Germany in 2030). From the native and global RR_b and RR_o ranking tables (Table 1; Table S7), many high-scoring species already have documented non-native occurrences in Germany. Applying RR based on native niche breadth (RR_b; Table 1a), five of the top 20 highest risk species already have documented non-native occurrences in Germany and elsewhere (fishes: *Carassius auratus*, *Xiphophorus hellerii*, *Poecilia reticulata*; molluscs: *Melanoides tuberculata*, *Tarebia granifera*). RR based on native niche overlap with Germany (RR_o; Table 1b) highlighted 10 species with non-native occurrences in Germany and elsewhere (fishes: *C. auratus*, *Pimephales promelas*, *Cyprinus carpio*, *Rhodeus sericeus*, *Lepomis gibbosus*, *Ctenopharyngodon idella*, *P. reticulata*, *Ameiurus melas*, *Misgurnus anguillicaudatus*; mollusc: *M. tuberculata*), with *Acipenser ruthenus* (fish), having documented occurrences elsewhere, ranked in 20th place. RR based on global niche breadth (Table S7a) identified six species with non-native occurrences in Germany and elsewhere in the top 20 (fishes: *P. reticulata*, *C. auratus*, *X. hellerii*, *C. idella*; molluscs: *M. tuberculata*, *T. granifera*), while RR based on global niche overlap (Table S7b) had the greatest proportion of species with non-native occurrences in Germany and elsewhere with 12 (fishes: *C. auratus*, *C. idella*, *R. sericeus*, *P. pomelas*, *C. carpio*, *Lepomis gibbosus*, *Hypophthalmichthys molitrix*, *M. anguillicaudatus*, *A. melas*; mollusc: *Sinanodonta woodiana*; reptile: *Mauremys reevesii*; amphibian: *Xenopus laevis*).

4 | DISCUSSION

In an increasingly globalised world, the need to effectively anticipate invasive NNS is great. Having facilitated introductions of NNS globally, the pet trade is finally being recognised as a priority introduction

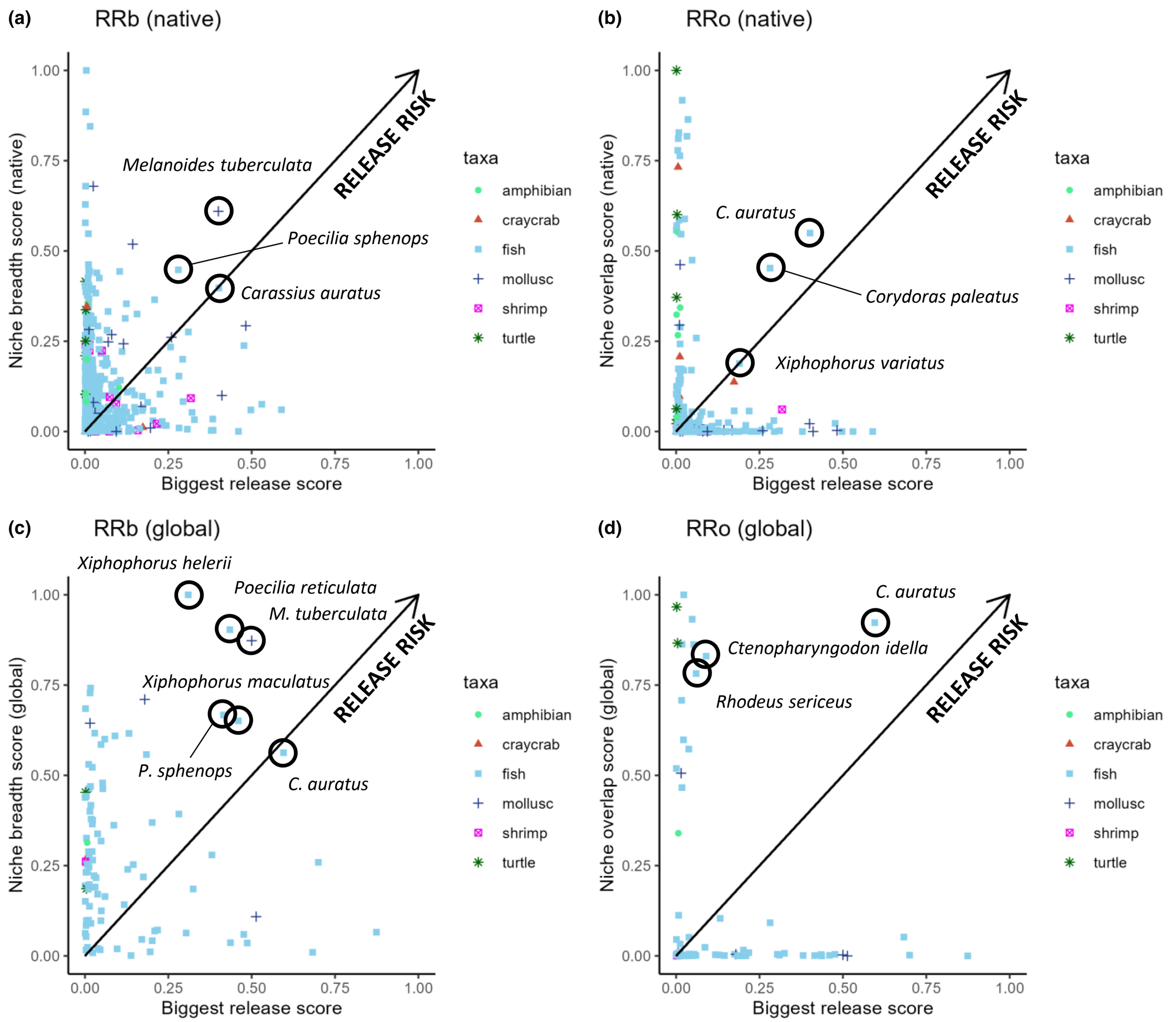

FIGURE 4 Release Risk (RR) plots combining "biggest release score" (i.e. the highest store or website score based on availability and lowest price) and (a) the breadth of niche in native range, (b) the overlap of niche between Germany and native range, (c) niche breadth in global range, and (d) niche overlap in global range. RR increases from bottom left to top right.

pathway by a number of EU member states (EU Commission, 2021). There is a need to account for likelihood of release and establishment when assessing pet trade NNS, and here we did this first separately and then in tandem using our RR metrics.

4.1 | Likelihood of release

Both pet store and website surveys demonstrated clear links between price and availability, backing the idea of cheap, readily available 'bandwagon species' (Lockwood et al., 2019). Websites were shown to have the highest proportion of unique species (i.e. those not found in the other surveys) and website species with documented non-native occurrences were found to be cheaper than those without.

Despite the high number of listings, eBay Kleinanzeigen had the fewest species that could be identified, highlighting the difficulty in regulating informal online marketplaces (Mazza et al., 2015; Olden et al., 2021). The prevalence of generic names (sometimes as vague as 'Tiere', i.e. 'animals') is concerning, suggesting that sellers are perhaps unaware of the species they are offering. However, such marketplaces can also connect highly informed buyers and sellers, facilitating global NNS dispersal pathways (Lenda et al., 2014; Olden et al., 2021). From the selling reasons listed on eBay Kleinanzeigen, high reproduction (most common), pet size relative to the tank (third) and aggression towards other pets (fifth) were all major reasons for selling, similar to previous findings (Duggan et al., 2006; Fujisaki et al., 2009; García-Díaz et al., 2015). The second most common reason, however, suggested a prioritisation of tank aesthetics over the inhabitants, with owners

TABLE 1 Species encountered in the pet store and website surveys with highest Release Risk (RR) scores based on *native* (a) niche breadth, availability and price (RR_b), and (b) niche overlap, availability and price (RR_o). Where species had both store and website RR scores, the highest is presented. Species were ordered by decreasing score. 'DE' refers to documented non-native occurrences in Germany from Global Biodiversity Information Facility (GBIF), 'elsewhere' refers to documented non-native occurrences outside Germany from GBIF, 'N/a' refers to no known documented non-native occurrences from GBIF, 'N/a*' indicates authors are aware of reported non-native occurrences in scientific literature.

Ranking	Score type	Species	Taxonomic group	Score	Status
(a) Native RR_b					
1	RR_b website	*Melanoides tuberculata*	Mollusc	0.244	DE, elsewhere
2	RR_b store	*Carassius auratus*	Fish	0.160	DE, elsewhere
3	RR_b store	*Poecilia sphenops*	Fish	0.125	N/a
4	RR_b website	*Danio rerio*	Fish	0.113	N/a
5	RR_b store	*Xiphophorus maculatus*	Fish	0.085	N/a
6	RR_b store	*Xiphophorus hellerii*	Fish	0.076	DE, elsewhere
7	RR_b website	*Tarebia granifera*	Mollusc	0.074	DE, elsewhere
8	RR_b website	*Neritina pulligera*	Mollusc	0.068	N/a
9	RR_b store	*Corydoras aeneus*	Fish	0.060	N/a
10	RR_b store	*Poecilia reticulata*	Fish	0.059	DE, elsewhere
11	RR_b website	*Pethia conchonius*	Fish	0.051	N/a
12	RR_b website	*Poecilia latipinna*	Fish	0.046	N/a
13	RR_b store	*Trichopodus trichopterus*	Fish	0.043	N/a
14	RR_b store	*Corydoras paleatus*	Fish	0.043	N/a
15	RR_b website	*Anentome helena*	Mollusc	0.041	N/a*[a]
16	RR_b store	*Paracheirodon axelrodi*	Fish	0.040	N/a
17	RR_b store	*Megalechis thoracata*	Fish	0.038	N/a
18	RR_b store	*Hyphessobrycon eques*	Fish	0.037	N/a
19	RR_b store	*Paracheirodon innesi*	Fish	0.036	N/a
20	RR_b store	*Hyphessobrycon sweglesi*	Fish	0.033	N/a
Ranking	**Score type**	**Species**	**Taxonomic group**	**Score**	**Invasion status**
(b) Native RR_o					
1	RR_o store	*Carassius auratus*	Fish	0.221	DE, elsewhere
2	RR_o store	*Corydoras paleatus*	Fish	0.127	N/a
3	RR_o store	*Xiphophorus variatus*	Fish	0.036	N/a
4	RR_o store	*Pimephales promelas*	Fish	0.031	DE, elsewhere
5	RR_o store	*Cyprinus carpio*	Fish	0.027	DE, elsewhere
6	RR_o website	*Cambarellus patzcuarensis*	Crayfish	0.024	N/a
7	RR_o website	*Rhodeus sericeus*	Fish	0.023	DE, elsewhere
8	RR_o website	*Caridina multidentata*	Shrimp	0.019	N/a
9	RR_o website	*Lepomis gibbosus*	Fish	0.017	DE, elsewhere
10	RR_o store	*Ctenopharyngodon idella*	Fish	0.016	DE, elsewhere
11	RR_o store	*Oryzias latipes*	Fish	0.015	N/a
12	RR_o store	*Hyphessobrycon eques*	Fish	0.012	N/a
13	RR_o website	*Danio rerio*	Fish	0.011	N/a
14	RR_o website	*Barbodes semifasciolatus*	Fish	0.010	N/a
15	RR_o store	*Poecilia reticulata*	Fish	0.009	DE, elsewhere
16	RR_o website	*Melanoides tuberculata*	Mollusc	0.009	DE, elsewhere
17	RR_o store	*Ameiurus melas*	Fish	0.009	DE, elsewhere
18	RR_o store	*Misgurnus anguillicaudatus*	Fish	0.008	DE, elsewhere
19	RR_o store	*Enteromius fasciolatus*	Fish	0.008	N/a
20	RR_o store	*Acipenser ruthenus*	Fish	0.007	Elsewhere

[a]Ng, Foon, et al. (2016).

redesigning their tank or changing stock. Indeed, selling reasons lay along a spectrum, with some focused on the ornamental, aesthetic value of the pets, and some being focused on the welfare of the pets (the space available to the pet, the happiness or stress of the pet in the presence or absence of others). How such viewpoints determine the likelihood of pet releases warrant further study. Some reasons also hint at an inherent incompatibility of aquarium ownership with 21st century city life, with moving house and a lack of time two commonly offered excuses (note that more ambiguous reasons like aquarium dissolution and downsizing were prevalent and may be linked). This, in combination with a large number of the reasons hinting at insufficient research being done prior to purchase, may indicate that unwanted pets will remain a problem without owner suitability checks (Perdomo et al., 2021).

While uncertainty surrounded the eBay Kleinanzeigen listings, taxonomic ambiguity featured heavily during the pet store and website surveys too. A large number of species were only listed to genus level (and therefore could not be risk assessed in this study), and out-of-date species names were common. One 'species', the bivalve *Corbicula javanicus*, does not have a taxonomically accepted name, and a Polish report found the invasive NNS *C. fluminea* sold under this pseudonym (Łabęcka et al., 2018). Furthermore, where species were listed using taxonomically accurate names, we cannot confirm that they were correctly applied.

4.2 | Likelihood of establishment

After pooling the species from all three surveys, NNS with documented German and elsewhere occurrences had wider niche breadths (when accounting for both native niche and global niche), even if the degree of niche width did not significantly affect the number of recorded occurrences. This is in line with the 'niche breadth–invasion success' hypothesis (Abellán et al., 2017; Vázquez, 2006). We also found that species with German non-native occurrences had greater niche overlaps with Germany, using both native and global ranges, however, again the number of occurrences was not significantly affected by the degree of overlap. This is consistent with Broennimann et al. (2021) who found climate matching to the realised native climatic niche to be a key determinant of mammal introduction success, and with Duncan et al. (2001) who found that introduced birds with larger geographical ranges in Australia had a greater area of climatically suitable habitat and larger overseas ranges.

4.3 | RR metrics

To limit potential releases and escapes, assessment measures that address propagule pressure and establishment factors are needed. Here, our three-pronged RR metrics incorporated relative availabilities and prices alongside niche breadth (RR_b) and niche overlap (RR_o) with Germany. One species clearly highlighted as high-risk by our native and global RR_o and RR_b metrics was *C. auratus*, which is consistent with its extensive invasion history in Germany, elsewhere in Europe and around the world. With impacts stemming from high feeding rates (Dickey et al., 2022), generalist diets (Monello & Wight, 2001; Richardson et al., 1995), disruptive foraging behaviour and genetic introgression with other *Carassius* species (Britton, 2022), there is evident need to curtail its risk through price or availability. Other highlighted species with extensive invasion histories that scored highly on at least one RR_b and at least one RR_o list include the fishes *Ctenopharyngodon idella* and *Poecilia reticulata*, and the snail *Melanoides tuberculata*. Despite no evidence of reproduction in Germany so far (C. Wolter, pers. comm.), established populations of *C. idella* are present on every continent except Antarctica and have been linked with ecological and economic impacts including the consumption of vegetation vital for spawning fish and nesting waterfowl, increased turbidity in waterbodies, shoreline erosion (Dibble & Kovalenko, 2009) and the damage of recreational fishing gear (Robinson et al., 2021). Non-native populations of *P. reticulata* are similarly widespread due to releases for mosquito control as well as the aquarium trade (Jordan, 2008). Impacts include harassment and forced copulation with native species (Valero et al., 2008) and invertebrate species declines (Englund, 1999). Introductions of the parthenogenic *M. tuberculata* have extirpated native snail species through competition and egg predation, and acted as an intermediate host and transmission vector for trematode parasites posing threats to human health (Ladd & Rogowski, 2012; Rader et al., 2003). Focus should also be placed on species lacking invasion histories to date, like fishes *Hyphessobrycon eques* and *Xiphophorus variatus*, which featured on all four RR top 20 lists, and fishes *Corydoras paleatus*, *Danio rerio*, *Pethia conchonius* and *Poecilia latipinna*, which featured on at least one RR_b and RR_o top 20 list.

Some species with high niche breadths and/or niche overlaps with Germany did not have high RR scores, due to low availability or high price. While currently low priority for management focus, RR could increase with future availability or price fluctuations.

4.4 | Future directions

Invasion ecology has relied heavily on invasion histories for determining NNS risks, but this approach is limited against a dynamic industry adding new species from around the world. With our RR metrics, we propose a forward-focused risk assessment method, capable of accounting for fluctuations in the trade and climate projections. Furthermore, with these metrics based on niche analyses rather than number of occurrences, they remain robust to potential issues such as time lags in species detectability. Such methods provide a starting point for prioritisation and can be followed up with methods of predicting ecological impact (note that two species with similar availabilities and climatic tolerances can have very different behaviours and impacts: Dickey et al., 2022). For example, species with high RR scores could be assessed using methods to determine resource uptake rates across relevant abiotic contexts relative to native trophic analogues, which have in the past proven to be effective at highlighting damaging invasive NNS (e.g. Comparative Functional Response: Dick et al., 2014; Dickey et al., 2021). Alternatively, morphology has been used to determine trophic overlap between natives and NNS (Luger et al., 2020; Nagelkerke et al., 2018). Such combinations would address many of the 14 minimum standards for risk assessments proposed by Roy et al. (2018), and quantify risk to proactively inform legislation. This could help policymakers determine threshold 'risk' levels, with species scoring above this having imports or sales curtailed (Dickey et al., 2022).

The 'release likelihood' findings of this study are somewhat limited due to their snap-shot nature, with no accounting for seasonal changes (see Shivambu et al., 2020) or how, for example, the Covid-19 pandemic affected availability. One potential solution to this for the website and eBay Kleinanzeigen surveys could be to use a web crawler (Olden et al., 2021), however, repeated surveying of pet stores, where staff were unable, or unwilling, to provide a stock listing and were not receptive to the documenting of stock by hand (pers. obs.) would prove difficult.

Going forward, there is a need to address the prevalence of potentially ecologically damaging species being sold in the pet trade, as well as the causes of pet abandonment. The reactive, rather than proactive, nature of pet trade legislation (and animal importation more broadly: Simberloff, 2006) has been highlighted as a problem, and issues surround enforcement, often leading to 'dead letters' (Patoka et al., 2018). While pet abandonment is a criminal offence in many countries, the covert nature of releases makes prosecution difficult (Maceda-Veiga et al., 2019; Perdomo et al., 2021). Perdomo et al. (2021) suggest a lack of external controls and verifications facilitate impulsive pet acquisitions, and call for owner suitability accreditation. Furthermore, they propose that compulsory health and survival insurance could benefit owners and pet welfare, while providing financial support for approved shelters. Concerns have been raised about banning species, which may increase their value through illegal channels (Maceda-Veiga et al., 2019), however, with the species most at risk of release tending to be the cheap and readily available (Lockwood et al., 2019), limiting availability and raising the prices of these species would lead to reduced RR. Our metrics could also provide a starting point for the creation of low-risk species lists to be sold in place of riskier species (Patoka et al., 2018; Simberloff, 2006). Of course, such lists would warrant 'serious expert scrutiny' (Simberloff, 2006), requiring traits beyond ecological niche, such as potential for disease spread (Tilmans et al., 2014) or zoochorous dispersal of other invasive NNS (Dickey et al., 2023) to be accounted for.

In the context of a highly dynamic, global industry with compulsive, ill-equipped pet owners, border security officials facing a near impossible task of inspecting large volumes of shipments (Ng, Tan, et al., 2016) and sellers being capable of evading regulations (Biondo, 2018; Olden et al., 2021), pet species releases will likely continue. Screening tools such as the RR metrics proposed here can highlight species most likely to be released and to establish, and in turn facilitate preventative action.

AUTHOR CONTRIBUTIONS

James W. E. Dickey and Jonathan M. Jeschke conceived the study, pet species present in the German pet trade were recorded by James W. E. Dickey with assistance from Simon Moesch, species niche modelling was performed by Chunlong Liu. All authors provided valuable input to the development of the final manuscript and have given approval for publication.

ACKNOWLEDGEMENTS

JWED was supported by the Alexander von Humboldt Foundation. SM was supported by the Deutsche Bundesstiftung Umwelt (20020/652-33/0). Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

'Supporting Information: Methods', 'Results' and 'Tables and Figures' available on data archive platform Figshare.com (https://doi.org/10.6084/m9.figshare.23613036) under CC BY 4.0 licence.

ORCID

James W. E. Dickey https://orcid.org/0000-0001-7288-5555
Chunlong Liu https://orcid.org/0000-0002-3376-4555
Elizabeta Briski https://orcid.org/0000-0003-1896-3860
Christian Wolter https://orcid.org/0000-0002-2819-2900
Simon Moesch https://orcid.org/0000-0002-3186-9644
Jonathan M. Jeschke https://orcid.org/0000-0003-3328-4217

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. An example listing from a pet store giving the common name, binomial species name and price.

Figure S2. Map of twelve visited pet stores and garden centres in Berlin.

Figure S3. Schematic representation of the indices of niche changes (unfilling, stability, and expansion) in two-dimensional environmental space calibrated by the principal components analysis.

Figure S4. Breakdown of the species encountered combined and in each of the three surveys: pet store survey, website survey and eBay Kleinanzeigen survey.

Figure S5. Histograms of Release Risk scores based on native niche breadth (a, c) and overlap (b, d) for species found in the pet store (a, b) and pet website (c, d) surveys.

Figure S6. Histograms of Release Risk scores based on global niche breadth (a, c) and overlap (b, d) for species found in the pet store (a, b) and pet website (c, d) surveys.

Table S1. eBay Kleinanzeigen summary table.

Table S2. The twenty-two reasons given, with definitions, translated examples and prevalence, for selling species from eBay Kleinanzeigen listings.

Table S3. Ranking of species by native climatic niche overlap (Schoener's *D*) with Germany.

Table S4. Ranking of species by global climatic niche overlap (Schoener's *D*) with Germany.

Table S5. Ranking of species by native niche breadth (minimum convex polygon estimator).

Table S6. Ranking of species by global niche breadth (minimum convex polygon estimator).

Table S7. Species encountered in the pet store and website surveys with highest Release Risk scores based on global (a) niche breadth, availability and price (RR_b), and (b) niche overlap, availability and price (RR_o).

Appendix S1. Supplementary species niche breadth and niche overlap analyses.

Appendix S2. Pet store, website and eBay Kleinanzeigen survey findings and Release Risk results.

How to cite this article: Dickey, J. W. E., Liu, C., Briski, E., Wolter, C., Moesch, S., & Jeschke, J. M. (2023). Identifying potential emerging invasive non-native species from the freshwater pet trade. *People and Nature*, *5*, 1948–1961. https://doi.org/10.1002/pan3.10535