







Does non-native diversity mirror Earth's biodiversity?

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Abstract

Aim: Human activities have introduced numerous non-native species (NNS) worldwide. Understanding and predicting large-scale NNS establishment patterns remain fundamental scientific challenges. Here, we evaluate if NNS composition represents a proportional subset of the total species pool available to invade (i.e. total global biodiversity), or, conversely, certain taxa are disproportionately pre-disposed to establish in non-native areas.

Location: Global.

Time period: Present day.

Major taxa studied: Global diversity.

Methods: We compiled one of the most comprehensive global databases of NNS (36,822 established species) to determine if NNS diversity is a representative proportional subset of global biodiversity.

Results: Our study revealed that, while NNS diversity mirrors global biodiversity to a certain extent, due to significant deviance from the null model it is not always a representative proportional subset of global biodiversity. The strength of global biodiversity as a predictor depended on the taxonomic scale, with successive lower taxonomic levels less predictive than the one above it. Consequently, on average, 58%, 42% and 28% of variability in NNS numbers were explained by global biodiversity for phylum, class and family respectively. Moreover, global biodiversity was a similarly strong explanatory variable for NNS diversity among regions, but not habitats (i.e. terrestrial, freshwater and marine), where it better predicted NNS diversity for terrestrial than for freshwater and marine habitats. Freshwater and marine habitats were also greatly understudied relative to invasions in the terrestrial habitats. Over-represented NNS relative to global biodiversity tended to be those intentionally introduced and/or

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'hitchhikers' associated with deliberate introductions. Finally, randomness is likely an important factor in the establishment success of NNS.

Main conclusions: Besides global biodiversity, other important explanatory variables for large-scale patterns of NNS diversity likely include propagule and colonization pressures, environmental similarity between native and non-native regions, biased selection of intentionally introduced species and disparate research efforts of habitats and taxa.

KEYWORDS

alien species, class taxonomic level, family taxonomic level, invasive species, non-indigenous species, phylum taxonomic level

1 | INTRODUCTION

Invasions by non-native species (NNS; i.e. species established outside their native range), among other stressors, have drastically changed biogeography, biodiversity and community structure worldwide, with the cumulative documented global cost over the last four decades estimated to exceed US\$ 1 trillion and causing losses of vital ecosystem services (Blackburn et al., 2019; Britton et al., 2023; Capinha et al., 2015; Cuthbert et al., 2021; Diagne et al., 2021; Pyšek et al., 2008; Turbelin et al., 2017). As globalization and anthropogenic stressors intensify, rates of invasion are expected to persist or grow in the future, with the numbers of NNS projected to increase by 36% in coming decades, while the magnitude of adverse impacts associated with these invasions are also expected to increase rapidly (Blackburn et al., 2019; Cuthbert et al., 2021; Diagne et al., 2021; Essl et al., 2020; Pyšek et al., 2020; Seebens, Bacher, et al., 2021). Despite increased attention given to the growing impacts, predicting which species will become NNS and where they will invade remain fundamental challenges to science.

A mechanistic understanding of the drivers of NNS invasions has been achieved for a very small proportion of the world's biota (Bonnamour et al., 2021; Fournier et al., 2019), with species causing the greatest impacts tending to be the best studied (Crystal-Ornelas & Lockwood, 2020; Pyšek et al., 2008). Critical knowledge gaps often preclude robust analyses of whether certain taxa are predisposed to invade relative to other taxonomic groups at the global scale. Non-native species may more commonly represent taxa that possess biological traits (such as rapid population growth, dormancy, earlier flowering) that promote the ability to arrive, establish and spread (Briski et al., 2011; Cardeccia et al., 2018; Casties & Briski, 2019; Chrobok et al., 2011; Fournier et al., 2019; Ricciardi & Cohen, 2007; Richardson et al., 2011). Arthropods, molluscs and fishes have been most frequently reported as NNS in freshwater and marine habitats (Bailey et al., 2020; Karatayev et al., 2009; Ruiz et al., 2000; Schwindt et al., 2020). Furthermore, the number of NNS in certain plant and bird families is much higher than expected by chance (Blackburn & Cassey, 2007; Lockwood, 1999; Pyšek et al., 2017). Key alternative mechanisms to explain invasion success include introduction efforts, such as propagule pressure (i.e. the number of introduction events,

the number of individuals per event and individuals' viability) and colonization pressure (i.e. the number of species introduced to a specific geographic area; Blackburn et al., 2020; Duncan et al., 2019; Lockwood et al., 2009). Environmental similarity between native and non-native regions, potential for inter-regional spread and biased selection of species having traits that pre-adapt them to interface with human vectors and commerce have also been determined to be important (Jaric et al., 2020; Kinlock et al., 2022; Lenzner et al., 2022; Lovell et al., 2021; Redding et al., 2019; Ricciardi, 2006; Seebens, Blackburn, et al., 2021; van Kleunen et al., 2007).

Given expanding global trade and the burgeoning diversity of vectors of species introductions (e.g. intentional introductions for food, ornamentation, sport, aquaculture; Lockwood et al., 2013; Lenzner et al., 2022), species in general should have increasing opportunities for transportation to new locations over time. For example, shipping transports a highly representative range of aquatic biodiversity, from viruses and bacteria to algae, invertebrates and fishes (Briski et al., 2013; Lin et al., 2020). In addition, the increased frequency of vector movements and rapid development of trade and travel networks over the last 50 years (Hulme, 2009; Seebens et al., 2013) have increased the probability that species will be transported and that some of these transfers will be to sites that are environmentally suitable habitats (e.g. climatically and biotically). Analogous to Neutral Theory (Hubbell, 2001), one might therefore assume, as a null hypothesis, that all species are virtually identical with respect to their probability of being transported beyond their natural range. As this hypothesis also assumes an infinite time frame, based on random sampling theory where larger sample size increases the probability of inclusion of rare species (Preston, 1948), there is higher probability that current NNS will belong to species-rich groups (e.g. phyla) rather than to species-poor groups. Or, the higher the taxonomic diversity of a group (e.g. phylum), the greater the probability that at least one of the species will be included in a sample transported somewhere else. Accordingly, current diversity of NNS could be a subset of total global biodiversity for that group, with differences in global NNS patterns reflecting differences in total species diversity among taxonomic groups. In the case of birds, most variation in establishment success resides at the species level, with a weak phylogenetic signal implying that the successful NNS were effectively

drawn at random and in direct proportion to the number of species in each genus, family and order (Blackburn & Duncan, 2001; Redding et al., 2019). However, these findings could be obscured or distorted by intentional releases of species, unevenness in research or monitoring effort, or shifting trade and transport patterns, irrespective of the total species diversity of the taxonomic group (Cardeccia et al., 2018; Casties & Briski, 2019; Kinlock et al., 2022; Lockwood et al., 2013; Sardain et al., 2019; van Kleunen et al., 2007).

Knowledge of total NNS species diversity in relation to global species pools has remained limited, although it is central to understanding whether certain taxonomic groups are indeed disproportionately represented among NNS. Here, we compiled one of the most comprehensive global databases of NNS diversity to determine whether NNS are indeed representative proportional subsets of global biodiversity of particular taxonomic groups. In particular, we tested whether the proportion of NNS diversity among taxonomic groups is similar to the proportion of global species diversity of those same groups. First, to test whether all species have an equal probability of being established beyond their natural range, we compared global species diversity in phyla with and without NNS to determine if phyla with listed NNS contain more species than those without listed NNS—as random sampling theory would predict (Preston, 1948). Then, we tested the null hypothesis that there is no difference between the expected and observed NNS diversity, based on the proportional distribution of taxonomic groupings in global biodiversity. Finally, we determined the extent to which global biodiversity explains NNS diversity across taxonomic levels (i.e. phylum, class and family) at global and regional scales, and under geographic and environmental (i.e. terrestrial, freshwater and marine habitats) contexts.

2 | METHODS

2.1 | Data compilation

We assembled a comprehensive data set of NNS by combining the SInAS database of alien species occurrences (Seebens, 2021) with several other publicly available databases and NNS lists (Bailey et al., 2020; Campbell et al., 2016; Carlton & Eldredge, 2009; Casties et al., 2016; Eldredge & Carlton, 2015; Hewitt, 2002; Hewitt et al., 2004; Lambert, 2002; Meyer, 2000; National Exotic Marine and Estuarine Species Information System (NEMESIS): California non-Native Estuarine and Marine Organisms (Cal-NEMO) Database, 2017; National Exotic Marine and Estuarine Species Information System (NEMESIS): Chesapeake Bay Introduced Species Database, 2020; Paulay et al., 2002; Richardson et al., 2020; Schwindt et al., 2020; Sturtevant et al., 2019; U. S. Geological Survey, 2017; Wonham & Carlton, 2005) to examine NNS diversity globally (Table 1). The SInAS_AlienSpeciesDB_2.4.1 (Seebens, 2021) file was used as the base file for our data set. Species without assignment of invaded country/region were removed from the data set. Then, species assigned only as CASUAL and ABSENT in the

columns degreeOfEstablishment (N) and occurrenceStatus (L), respectively, were also removed due to their undetermined non-native establishment status in those particular regions (Groom et al., 2019). Next, species from other publicly available databases and NNS lists (Bailey et al., 2020; Campbell et al., 2016; Carlton & Eldredge, 2009; Casties et al., 2016; Eldredge & Carlton, 2015; Hewitt, 2002; Hewitt et al., 2004; Lambert, 2002; Meyer, 2000; National Exotic Marine and Estuarine Species Information System (NEMESIS): California non-Native Estuarine and Marine Organisms (Cal-NEMO) Database, 2017; National Exotic Marine and Estuarine Species Information System (NEMESIS): Chesapeake Bay Introduced Species Database, 2020; Paulay et al., 2002; Richardson et al., 2020; Schwindt et al., 2020; Sturtevant et al., 2019; U. S. Geological Survey, 2017; Wonham & Carlton, 2005) that had not been listed for particular region/s in the SInAS database were added to the file. The species that were both native and NNS within a continent were retained in the data set. For example, a species may be native to the Black Sea in Romania, but non-native in the Baltic Sea in Germany; in this case, the species is both native and non-native in Europe. Consequently, our data set consisted of 36,822 species established outside of their native regions, out of which 36,326 came from Seebens (2021) and 496 species from other databases and NNS lists. We emphasize here that our data set also contains subspecies, when those were accepted as such by the Global Biodiversity Information Facility (GBIF).

Binominal scientific names, phylum, class and family levels, were assigned to each species based on the SInAS_AlienSpeciesDB_2.4.1_FullTaxaList file (Seebens, 2021) that was originally determined following GBIF. When a species was not automatically assigned to binominal scientific name and/or taxonomic level, an additional manual search of GBIF, World Register of Marine Species (WoRMS) and a general internet search engine was conducted in June and July 2022 and September 2023. Furthermore, to examine NNS diversity among different habitats (i.e. terrestrial, freshwater and marine), we assigned one or more habitats for each species based on the Step2_StandardTerms_GRIIS file (Seebens, 2021); habitat data in the Step2_StandardTerms_GRIIS file originated from the Global Register of Introduced and Invasive Species (GRIIS). Again, if habitat(s) was(were) not automatically assigned to a species, an additional manual search of WoRMS and a general internet search engine was conducted from July to September 2022. We emphasize that due to the great number of species in our data set and changing information availability over time, there is a possibility that we did not list all potential habitats for all species. Brackish habitats were defined as marine based on the Venice System (1958). Regions were assigned based on the geographic continental definitions (i.e. North America, South America, Europe, Africa, Asia and Australia), with Pacific islands as a separate region due to their unclear/undefined continental affiliations (National Geographic Society, 2022). The raw data set of NNS assembled, containing information on non-native region, phylum, class, family, type of invaded habitat and underlying references can be found in Table S1 and at Pangaea: <https://doi.org/10.1594/PANGAEA.940752>. The regions not listed for a

TABLE 1 Results of regression analyses where global biodiversity of corresponding phyla, classes and families were predictor variables for diversity of non-native species in the same phyla, classes and families for different regions and habitats. Additionally, the number of families containing non-native species per region/habitat; the number of families per region/habitat that have only one non-native species; and mean, median and mode numbers of non-native species per family for each region/habitat are reported.

| Region-habitat | # of species | Phylum | Class | Family | | | Mean # of spp. | Median # of spp. | Mode # of spp. |
|-----------------------------|--------------|--------|-------|--------|---------------|-------------------------------|----------------|------------------|----------------|
| | | r^2 | r^2 | r^2 | # of families | # of families with only 1 sp. | | | |
| Total | 36,822 | | | | 2733 | 970 | | | |
| North America | 13,326 | 0.691 | 0.546 | 0.263 | 1306 | 543 | 10.22 | 2 | 1 |
| South America | 4380 | 0.645 | 0.553 | 0.258 | 718 | 338 | 6.11 | 2 | 1 |
| Europe | 16,255 | 0.732 | 0.593 | 0.288 | 1799 | 722 | 9.10 | 2 | 1 |
| Africa | 6462 | 0.714 | 0.560 | 0.260 | 848 | 385 | 7.679 | 2 | 1 |
| Asia | 10,743 | 0.638 | 0.538 | 0.252 | 1326 | 545 | 8.15 | 2 | 1 |
| Australia | 6917 | 0.594 | 0.504 | 0.288 | 697 | 300 | 9.93 | 2 | 1 |
| Pacific Islands | 8249 | 0.664 | 0.491 | 0.357 | 1095 | 453 | 7.59 | 2 | 1 |
| North America—terrestrial | 11,405 | 0.623 | 0.474 | 0.260 | 813 | 297 | 14.06 | 2 | 1 |
| South America—terrestrial | 3864 | 0.671 | 0.515 | 0.235 | 493 | 212 | 7.85 | 2 | 1 |
| Europe—terrestrial | 13,938 | 0.681 | 0.517 | 0.283 | 1069 | 375 | 13.12 | 2 | 1 |
| Africa—terrestrial | 5756 | 0.662 | 0.552 | 0.234 | 542 | 213 | 10.70 | 2 | 1 |
| Asia—terrestrial | 8658 | 0.542 | 0.470 | 0.247 | 732 | 280 | 11.88 | 2 | 1 |
| Australia—terrestrial | 6396 | 0.501 | 0.369 | 0.275 | 479 | 175 | 13.36 | 2 | 1 |
| Pacific Islands—terrestrial | 7571 | 0.704 | 0.556 | 0.368 | 814 | 300 | 9.33 | 2 | 1 |
| North America—freshwater | 1721 | 0.650 | 0.490 | 0.134 | 302 | 136 | 5.79 | 2 | 1 |
| South America—freshwater | 414 | 0.536 | 0.361 | 0.180 | 129 | 63 | 3.20 | 2 | 1 |
| Europe—freshwater | 1326 | 0.626 | 0.453 | 0.133 | 305 | 148 | 4.39 | 2 | 1 |
| Africa—freshwater | 459 | 0.516 | 0.318 | 0.194 | 111 | 58 | 4.15 | 1 | 1 |
| Asia—freshwater | 1231 | 0.673 | 0.383 | 0.140 | 251 | 119 | 4.95 | 2 | 1 |
| Australia—freshwater | 357 | 0.392 | 0.271 | 0.182 | 71 | 36 | 5.01 | 1 | 1 |
| Pacific Islands—freshwater | 509 | 0.617 | 0.461 | 0.216 | 117 | 65 | 4.39 | 1 | 1 |
| North America—marine | 1093 | 0.548 | 0.300 | 0.086 | 455 | 261 | 2.49 | 1 | 1 |
| South America—marine | 362 | 0.443 | 0.283 | 0.127 | 201 | 131 | 1.81 | 1 | 1 |
| Europe—marine | 1904 | 0.452 | 0.241 | 0.110 | 688 | 355 | 2.80 | 1 | 1 |

(Continues)

TABLE 1 (Continued)

| Region-habitat | # of species | Phylum | | | Class | | Family | | |
|------------------------------|--------------|--------|-------|-------|---------------|-------------------------------|----------------|------------------|----------------|
| | | r^2 | r^2 | r^2 | r^2 | r^2 | r^2 | r^2 | r^2 |
| | | | | | # of families | # of families with only 1 sp. | Mean # of spp. | Median # of spp. | Mode # of spp. |
| Africa—marine | 581 | 0.420 | 0.149 | 0.114 | 293 | 178 | 2.00 | 1 | 1 |
| Asia—marine | 1613 | 0.513 | 0.330 | 0.160 | 561 | 270 | 2.90 | 2 | 1 |
| Australia—marine | 449 | 0.281 | 0.282 | 0.131 | 212 | 125 | 2.13 | 1 | 1 |
| Pacific Islands—marine | 585 | 0.378 | 0.157 | 0.103 | 268 | 153 | 2.32 | 1 | 1 |
| Average all habitats | 9476 | 0.575 | 0.418 | 0.280 | | | 8.397 | | |
| Average terrestrial habitats | 8227 | 0.626 | 0.493 | 0.271 | | | 11.471 | | |
| Average freshwater habitats | 860 | 0.572 | 0.391 | 0.168 | | | 4.554 | | |
| Average of marine habitats | 941 | 0.433 | 0.248 | 0.118 | | | 2.350 | | |

particular species in our database do not correspond to the native region of the species. Finally, global estimated biodiversity (i.e. numbers of species—taxa—per taxonomic group) of each particular phylum, class and family was obtained from the GBIF in October 2022 (Global Biodiversity Information Facility (GBIF), 2022). The raw data set of global estimated biodiversity can be found in Table S2 and at Pangaea: <https://doi.org/10.1594/PANGAEA.940752>.

2.2 | Statistical analyses

To determine if phyla with listed NNS contain more species than phyla without listed NNS, we conducted a *t*-test where species richness per phylum (i.e. number of species) was compared between phyla with and without NNS (using all phyla listed in Table S3). Additionally, a separate analysis was run including only phyla within Animalia and Plantae to control for differences and possible scientific biases among taxonomic groups, due to different physical sizes and taxonomic resolutions that more strongly impede research into other kingdoms (e.g. small vs. big species, charismatic vs. less well-studied taxa). Data were log-transformed (i.e. $\log_{10}(x+1)$) to meet the assumptions of a parametric test.

Then, to test the null hypothesis that there is no difference between the expected and observed NNS diversity, we compared the expected and observed number of species in each phylum, class and family. The expected number of species for each phylum, class and family was calculated by pooling all NNS and determining the percentage of global biodiversity represented by NNS. This percentage was then multiplied by global biodiversity (i.e. number of species) in each phylum, class and family to obtain expected proportion of NNS in particular taxonomic groups. The expected proportion of

NNS in taxonomic groups had a perfect correlative fit with global biodiversity ($r^2 = 1.00$) and represented the proportional subset of global biodiversity of particular taxonomic groups in the case of NNS diversity being a random subset of global biodiversity—the null model (Figure 1). Finally, observed and expected numbers of NNS in taxonomic groups were statistically compared using Pearson's chi-square tests. Three tests were run, for each of phylum, class and family level.

To determine to what extent global biodiversity explained diversity of NNS established in different regions and habitats around the world, we conducted regression analyses. Here, we considered global biodiversity of taxonomic groups (i.e. numbers of species) as the independent variable and diversity of NNS of the corresponding taxonomic groups (i.e. number of NNS) as the dependent variable. Independent regression analyses were conducted for different taxonomic levels (i.e. phylum, class and family), and for different regions (i.e. North America, South America, Europe, Africa, Asia, Australia and Pacific islands) and habitats within regions (i.e. all habitats, terrestrial, freshwater and marine habitats; indicated as e.g. North America—all habitats, North America—terrestrial, ...). In each regression analysis, only those taxonomic groups (phyla, classes and families) that contained NNS for that particular region/habitat were included; when there were no NNS reported for a particular group in a particular region/habitat, this group was not included in that regression analysis. Therefore, no analyses had dependent variables containing zeroes. In the case of classes and/or families, when there was one or more NNS belonging to class/family without that/these species being listed in the GBIF, that particular class/family was excluded from the regression analyses (i.e. 3 out of 161 classes and 12 out of 2733 families). All data were log-transformed (i.e. $\log_{10}(x+1)$) to meet the assumptions of parametric regression. To determine

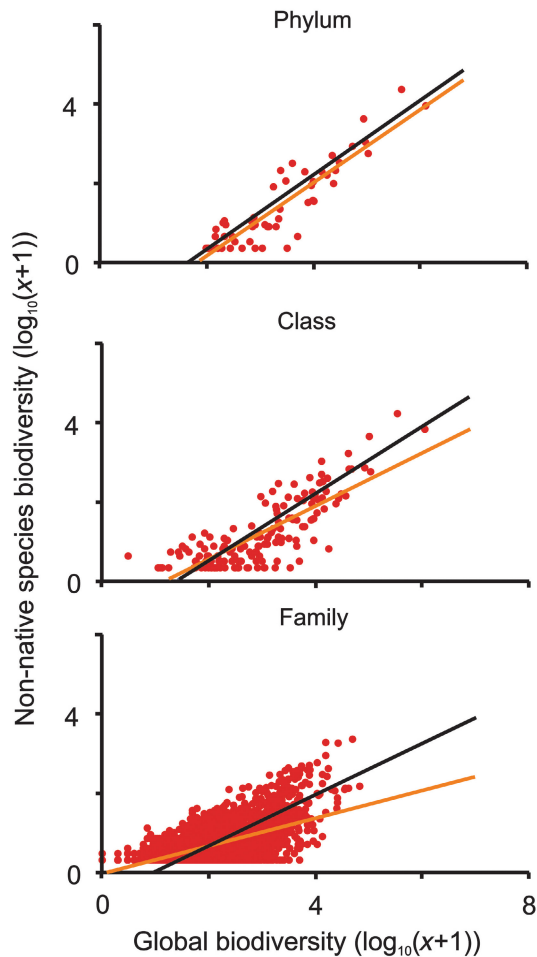


FIGURE 1 Scatterplots and fitted regression lines with global biodiversity of corresponding phyla, class and family as independent variables and diversity of non-native species of corresponding phyla, class and family as dependent variables, respectively. Black lines represent fitted regression lines when expected proportions of NNS in taxonomic groups were used for calculations. As these proportions have perfect correlational fit to global biodiversity ($r^2 = 1.00$), the dots were not shown as all of them lay exactly on the lines. Orange lines represent fitted regression lines when observed proportion of non-native species (NNS) in taxonomic groups were used. Red dots represent observed proportions of NNS in taxonomic groups. All data are log-transformed.

which phyla and classes were over- or under-represented, two distinct approaches were taken: (i) the expected number of NNS per taxon was plotted based on the distribution of global biodiversity, in addition to plots of the upper and lower quantiles of a binomial distribution between these variables (this distribution used a Bonferroni correction to an alpha of 0.01 based on the number of phyla and classes included, respectively, resulting in over- and under-represented groups being therefore outside of this distribution); and (ii) the regression residuals were calculated for regions and habitats in regions. To keep the analyses of the second approach conservative and ecologically relevant, we removed Bryozoa and Cnidaria phyla from terrestrial habitats, and Tracheophyta from marine habitats,

because of a low proportion of species from these taxonomic groups in those habitats. The number of regions with under- and over-represented taxa per phylum and class, respectively, was used to demonstrate repeatability of under- and over-representation of a taxonomic group across regions and habitats.

To determine if the explanatory strength of global biodiversity for NNS diversity differed among taxonomic levels (i.e. phylum, class and family), habitat types (i.e. terrestrial, freshwater and marine) and geographic regions (i.e. North America, South America, Europe, Africa, Asia, Australia and Pacific islands), the coefficients of determination (r^2) from the above regressions were compared among different taxonomic levels using beta regression (Cribari-Neto & Zeileis, 2010). Nested likelihood ratio tests were used to compare beta regression models with and without the taxonomic level, habitat type and geographic region terms (Zeileis & Hothorn, 2002). Post hoc pairwise comparisons were then made among the categories within these three predictor variables, using Tukey adjustments for multiplicity (Lenth, 2023).

Finally, we conducted additional regression analyses to discern the speed of accumulation of new families in a non-native region based on speed of establishment of NNS in that region (net accumulation of NNS), to explain differences in explanatory ability of NNS diversity by global biodiversity along the taxonomic scale (i.e. phylum, class and family). Here, we considered the number of species per region/habitat as the independent variable and the number of families per region/habitat as the dependent variable. Four different regression analyses were conducted in total: (i) all habitats, (ii) terrestrial, (iii) freshwater and (vi) marine habitats. Based on regression lines fitted and corresponding equations, we determined the rate of family accumulations among habitats. Statistical analyses were performed using SPSS (IBM SPSS Statistics 26.0 IBM Corp.) and R v4.0.2 (R Core Team, 2020).

3 | RESULTS

3.1 | Does non-native diversity mirror Earth's biodiversity?

Our data set identified a total of 36,822 NNS worldwide across all three habitats, with 31,160, 3561 and 4206 NNS being terrestrial, freshwater and marine species respectively. Non-native species belonged to six of seven kingdoms listed on GBIF, with only Archaea lacking reported NNS (Table S3). Of 244 phyla, 694 classes and 26,019 families considered (Global Biodiversity Information Facility (GBIF), 2022), we found that 58, 161 and 2733 contained reported NNS respectively (Table 1; Tables S3–S5). The majority of phyla without NNS belonged to the Bacteria and Protozoa kingdoms (Table S3).

A comparison of phyla with and without NNS revealed that the former were significantly more species-rich than the latter (t -test, $t = 15.05$, $df = 240$, $p < 0.001$ and $t = 4.88$, $df = 39$, $p < 0.001$, for all phyla in GBIF and only Animalia and Plantae respectively). In contrast, the comparative assessment of the expected and observed

NNS diversity revealed significant differences, leading to rejection of the null hypothesis at all taxonomic levels (Chi-square test, $p=0.006$, $p=0.003$ and $p<0.001$ for phylum, class and family taxonomic levels respectively; Figure 1).

Regression analyses at the phylum, class and family taxonomic levels identified significant positive relationships between the number of NNS reported from a taxonomic group and the total species diversity of that taxonomic group (i.e. average $r^2=0.58$, 0.42 and 0.28 respectively; Table 1; Figure 2, Figures S1 and S2). However, the strength of global biodiversity as an explanatory variable of NNS diversity depended on taxonomic scale. On average, 58%, 42% and 28% of variability in NNS numbers was explained by global biodiversity for phylum, class and family levels, respectively (Table 1), with each subsequent taxonomic level being significantly less explanatory than the level above it (Likelihood ratio test, $p<0.001$; Tukey contrasts: $p<0.001$). There were a few regional differences in the explanatory strength of global biodiversity for NNS diversity (Likelihood ratio test, $p=0.004$). With the exception of Australia having lower r^2 compared to several other regions (Asia, Europe, North America, South America and Pacific islands; Tukey contrasts: $p<0.05$), explanatory strength did not significantly differ among regions (Tukey contrasts: $p>0.05$). Significant differences in explanatory strength were also found among habitat types (Likelihood ratio test, $p<0.001$), with terrestrial habitats having a significantly higher r^2 than freshwater and marine habitats (Tukey contrasts: $p<0.001$), and freshwater r^2 was significantly higher than that of marine systems (Tukey contrast: $p<0.001$). The slopes among habitat types follow the same pattern, with terrestrial being the steepest, followed by freshwater and then by marine ones, indicating few NNS relative to global biodiversity (Figure 2, Figures S1 and S2).

Finally, the relationship between the number of NNS and the number of families containing NNS was decelerating curvilinear, and revealed significant positive relationships for all three habitat types (Figure 3; i.e. $r^2=0.84$, 0.93 and 0.99 for terrestrial, freshwater and marine respectively). Based on the fitted regression lines, for each 20th terrestrial, 6th freshwater and 3rd marine NNS, a new family of NNS would be detected.

3.2 | Under- and over-represented taxa as NNS

Analysis of the binomial distribution and regression residuals revealed that, for many taxa, observed numbers of NNS were within the region expected based on global biodiversity. For some over- and under-represented taxa as NNS, a clear pattern was evident (Figures 4 and 5; Figure S3; Tables S4 and S5). In particular, the most over-represented phylum in almost all habitats and regions was Chordata (e.g. vertebrates), with Aves (birds), Reptilia and Mammalia classes being consistently over-represented in terrestrial habitats, Actinopterygii (bony fishes) in marine and freshwater and Ascidiacea (sea squirts) in marine ones (Figures 4 and 5; Figure S3; Tables S4 and S5). Terrestrial taxa within the phylum Tracheophyta (vascular plants), and Arachnida (spiders) and Insecta classes within the Arthropoda phylum were also

over-represented. Eight out of nine classes of Tracheophyta were consistently over-represented in terrestrial habitats (Figures 4 and 5; Figure S3; Tables S4 and S5). Mollusca were under-represented in terrestrial habitats but over-represented in freshwater and marine ones, with Bivalvia (e.g. clams, oysters and mussels) and Gastropoda (snails) being the most over-represented in marine habitats (Figures 4 and 5; Figure S3; Tables S4 and S5). Other over-represented phyla included Annelida (segmented worms), Rhodophyta (red algae) and Chlorophyta (green algae), whereas Bryozoa (moss animals) was under-represented in freshwater but over-represented in marine habitats. Cnidaria (e.g. hydroids) had mixed representation, being under-represented in freshwater systems but clearly over-represented in marine habitats, with particular over-representation by the Hydrozoa class (Figures 4 and 5; Figure S3; Tables S4 and S5). Bacteria, fungi and viruses were mixed and mostly under-represented in the majority of regions and habitats.

4 | DISCUSSION

4.1 | Does non-native diversity mirror Earth's biodiversity?

Our study demonstrated that, while more biodiverse taxa generally harbour more NNS, due to significant deviance from the null model, NNS diversity is not always a representative proportional subset of global biodiversity. Furthermore, the relationship depends on the taxonomic scale, with each subsequent lower taxonomic level being less representative than the level above it. On average, 58%, 42% and 28% of variability in NNS numbers were explained by global biodiversity for phylum, class and family levels respectively. Interestingly, independent of the number of estimated NNS in a region, such as 4380 NNS in South America, 16,255 NNS in Europe and 10,743 in Asia (Table 1), global biodiversity maintained similar explanatory ability across regions. Our results also suggest, for example, that there are more NNS among insects than birds, probably not only because the former could be better colonizers or that they have traits that make them more easily transported by human vectors, but to a certain extent because there are many more species of insects than birds on Earth. At the same time, a charismatic and well-studied taxonomic group such as phylum Echinodermata, including sea stars and sea urchins (and other groups), seems to have species characterized by poor colonizing ability. Likewise, Pyšek et al. (2017) and Liebhold et al. (2021) reported some plant and beetle families being over-represented and others under-represented respectively. Consequently, besides global biodiversity being a strong explanatory variable for NNS diversity, factors such as propagule and colonization pressures, environmental similarity between native and non-native areas, biased selection of intentionally introduced species and species traits that pre-adapt them to interfacing with human vectors may be additionally important (Blackburn et al., 2020; Duncan et al., 2019; Jaric et al., 2020; Kinlock et al., 2022; Lenzner et al., 2022; Lockwood et al., 2009;

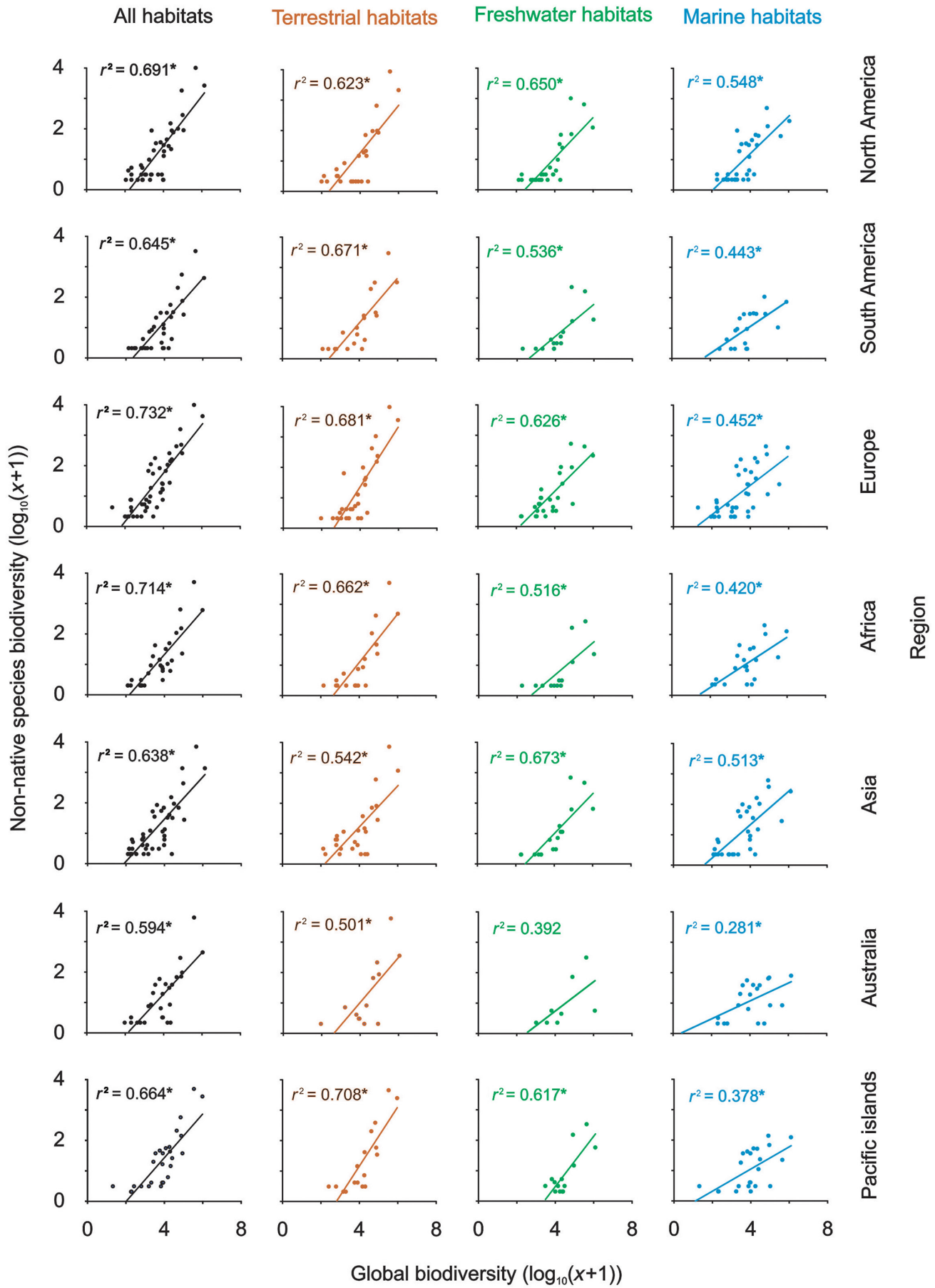


FIGURE 2 Scatterplots and fitted regression lines with global biodiversity of corresponding phyla as independent variables and diversity of non-native species of corresponding phyla as dependent variables for different regions and habitats. All data are log-transformed. Coefficients of determinations (r^2) are shown as well. Asterisks denote significant r^2 .

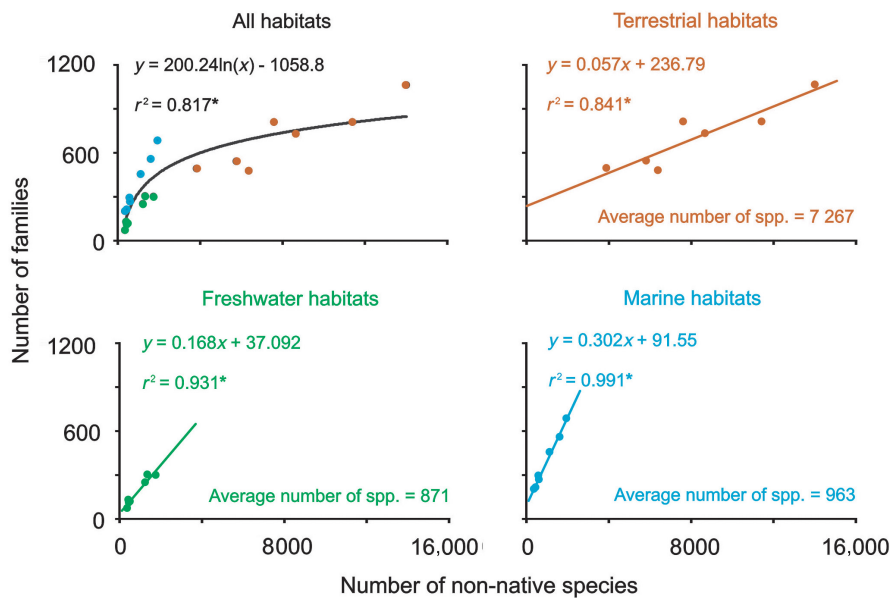


FIGURE 3 Scatterplots and fitted regression lines with number of non-native species as independent variables and number of families as dependent variables for all habitats per region, and terrestrial, freshwater and marine, separately. Regression equations, coefficients of determinations and average number of species per region are shown in addition. Asterisks denote significant r^2 . Brown, red and blue colours denote terrestrial, freshwater and marine habitats respectively.

Lovell et al., 2021; Redding et al., 2019; Ricciardi, 2006; Seebens, Blackburn, et al., 2021; van Kleunen et al., 2007).

4.2 | Under- and over-represented taxa as NNS

While relationships between global biodiversity and non-native diversity are significant, an average of 43% and 58% of variation in the NNS/global diversity relationships remained unexplained at the phylum and class levels, respectively, due to both under- and over-represented taxa. Under-represented taxa could result for at least four reasons: (i) biased research interest and effort, analysis and/or taxonomic expertise towards certain groups (Bortolus, 2008; Carlton, 2009; Ruiz et al., 2000); (ii) poor taxon association with current and/or historic transport vectors and pathways (Jaric et al., 2020; Ricciardi, 2006); (iii) the conservative nature of our analysis, which used total global biodiversity of phyla and classes when considering particular habitats or regions, while in some cases, species in these groups might be predominantly represented in specific habitats (e.g. terrestrial vs. marine, temperate vs. tropical climates and coastal vs. shelf taxa); or (iv) certain taxonomic groups could be relatively poor colonizers. Conversely, over-represented taxa may result from disproportionate interest in and/or monitoring effort of invasion ecologists; environmental managers and/or scientists in general; and strong taxon association with current and/or historical transport vectors and pathways.

Consequently, while the majority of phyla and classes displayed no clear pattern of over- or under-representation of NNS (Figures 4 and 5; Figure S3), taxa that were over-represented as NNS

consistently belonged to groups that were, or still are, intentionally introduced into new habitats for cultural and socio-economic purposes, either directly or indirectly. For example, in both the past and present, fish, birds, mammals, plants, shellfish and macroalgae have been translocated globally for agriculture, aquaculture, sport and decoration purposes, and have been closely associated with different human dimensions (Bortolus & Schwindt, 2022; Kim et al., 2017; Lockwood et al., 2013). Insects, parasitic spiders, sea squirts and segmented worms are often connected with those activities, and are unintentionally transported indirectly as ‘fellow travellers’/‘hitchhikers’ or associated with intentionally transported species or on contaminated farming/fishing gear or in soil (Lockwood et al., 2013; Zhan et al., 2015). A number of studies conducted on horticultural plants also showed that the human-biased selection of species translocated for gardening purposes demonstrate more colonizing traits than their conspecifics (Chrobock et al., 2011; Kinlock et al., 2022; Maurel et al., 2016; Omer et al., 2021; van Kleunen et al., 2007). Our results suggest that phyla and classes that contain more NNS than expected are those that contain species of human interest, or those associated with them, and consequently are linked to intentional introductions globally, whereas those predominantly containing unintentionally introduced taxa do not show any clear pattern or predictability.

4.3 | Decreasing predictive ability of NNS diversity across taxonomic groups

Decreasing predictive ability of NNS diversity towards finer taxonomic levels likely stems from the currently estimated number of

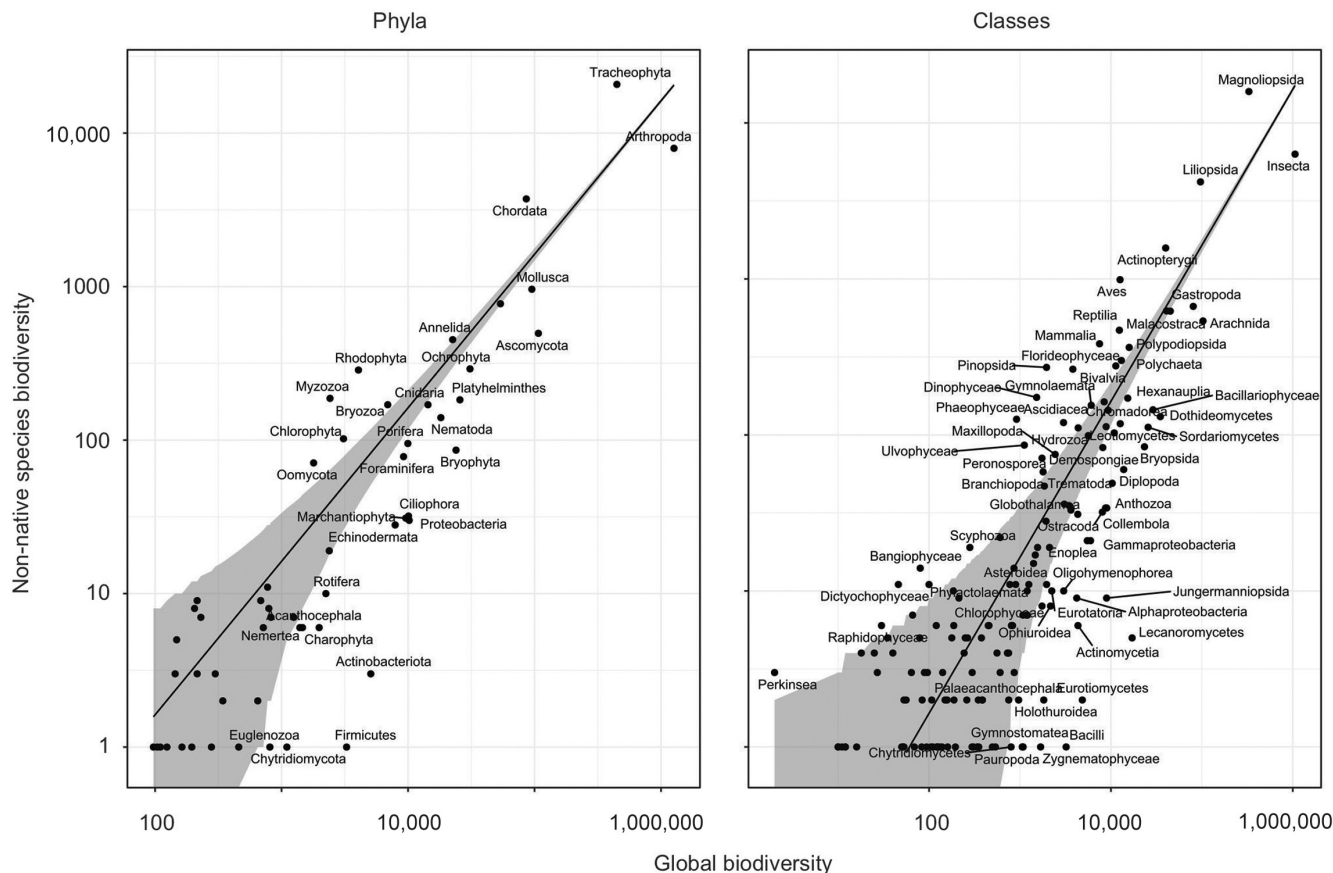


FIGURE 4 Scatterplots showing the total number of non-native species per phylum/class pooled among all regions/habitats versus numbers of species per phylum/class for the global biodiversity. The black lines show the expected numbers of non-native species per phylum/class if they were in the same proportions as global biodiversity. Grey shading shows the range outside of which a phylum/class would be deemed to be over- or under-represented at the $\alpha=0.01$ level, assuming a binomial distribution and using a Bonferroni correction to account for the number of phyla/classes compared. The labelled phyla/classes are those over- or under-represented. Note the axes are on a \log_{10} scale.

NNS (i.e. 36,822 ~ 1% of total global biodiversity) and the decreasing detection probability of NNS within more granular taxonomic levels (i.e. 244 phyla, 694 classes and 26,019 families; Global Biodiversity Information Facility (GBIF), 2022). Accordingly, the decreasing explanatory ability could be easily explained by random sampling theory, where the currently estimated number of NNS is a relatively large number when the small number of phyla has been taken into account, but conversely is relatively small when the large number of families is considered (Preston, 1948). This is evidenced by the average of 632 NNS per phylum and 8 NNS per family in our study, with a relatively large number of families having only one NNS reported (Table 1; Figure S2). In concordance, the relationship between the number of NNS and the number of families containing NNS shows that the number of families has a decelerating curvilinear relationship with the

number of NNS (Figure 3). This trend suggests that, at first, the number of families will increase rapidly as the number of NNS increases, such as in the case of our freshwater and marine NNS data (i.e. a new family for each 6th and 3rd NNS respectively). However, as the number of NNS increases, the number of families saturates as newly detected species are likely to be within already reported families. This is reflected differently among habitats, with an order of magnitude more in terrestrial than freshwater or marine NNS (i.e. a new family for each 20th terrestrial NNS) meaning that the taxonomic plateau has nearly been approached on land (Figure 3). In line with the greater number of NNS in terrestrial habitats compared to freshwater and marine ones, the explanatory ability of NNS biodiversity by global biodiversity of families in terrestrial habitats is much higher than that in freshwater and marine habitats (i.e. Table 1; 27%, 17% and 12%

FIGURE 5 Number of regions with under- and over-represented taxa per phylum based on the regression residuals of fitted regression lines with global biodiversity of corresponding phyla as independent variables and biodiversity of non-native species of corresponding phyla as dependent variables for different regions and habitats. All species, terrestrial, freshwater and marine species are shown in black, brown, green and blue colours respectively. Note that under- and over-represented taxa are highlighted in lighter and darker colours respectively.

Number of regions/habitats with negative and positive residuals



respectively). Consequently, as the number of NNS increases, we expect that the strength of global biodiversity as an explanatory variable of NNS diversity among taxonomic levels will become more similar—that is, class and family explanatory strength will approach that of phylum. Importantly, this trend is indicative of massively unrealized invasion potential, particularly for freshwater and marine habitats, or that greater detection efforts towards these habitats could relatively rapidly unravel previously unreported NNS diversity.

4.4 | Under-estimated number of NNS globally

Our study also demonstrates that freshwater and marine habitats are severely understudied in comparison to terrestrial habitats. As with Archaea which completely lacked NNS, the limited representation in aquatic habitats is unsurprising given that there is a paucity in understanding of the ecology, biogeography or even evolutionary origin of most of these species, potentially leading to a significantly under-estimated number of NNS globally. Owing to severe taxonomic and biogeographic challenges, including the perception of natural cosmopolitanism and scientists neglecting the native/non-native status of taxa, organisms smaller than 1 mm are reported as NNS far less often than larger organisms (Carlton, 2009). This pattern has been referred to as the 'small rule' of invasion ecology (Carlton, 2009), where a large number of smaller bodied taxa, such as microalgae, protists, rotifers, nematodes, flatworms, hydroids, copepods and ostracods, remain largely or completely unexplored relative to their invasion status. For example, out of 500 distinct phytoplankton taxa in San Francisco Bay, with 396 of these identified to species level, none have been recognized as NNS (Cloern & Dufford, 2005), which is implausible considering historical and current shipping traffic in the region (Kaluza et al., 2010; Seebens et al., 2013). Even in the case of larger bodied organisms, depending on the history of taxonomical and ecological studies in an area and the availability of taxonomic expertise, many groups of species remain classified as cryptogenic (e.g. because of unclear taxonomy and/or evolutionary history of taxa; Carlton, 2009; Carlton & Fowler, 2018; Hewitt et al., 2004). Finally, besides under-reporting of NNS biodiversity, there are also many taxonomic groups in respect to total global biodiversity that are widely regarded as severely under-described. For example, the phylum Nematoda contains 18,174 species (Table S3); however, the estimated number of nematode species possibly varies from 500,000 to 1,000,000, and even up to 100,000,000 (Morand et al., 2015). Despite this, it is probable that the underestimation of total global species richness does not qualitatively affect the outcomes of our analyses, as we trust that taxonomic groups that are largely under-described in global species richness will be even less recorded as NNS. We accordingly acknowledge that existing constraints on data quality across taxonomic groups may contribute to the variation across taxonomic groups we include here.

5 | CONCLUSIONS

While global biodiversity intuitively contributes to NNS numbers within corresponding taxonomic groups, current NNS diversity is not a representative proportional subset of global biodiversity, owing to other factors that mediate invasion success. Propagule and colonization pressures, environmental similarity between native and non-native areas, intentional introduction of species and traits that pre-adapt species to interfacing with human vectors and increasing their establishment success may be just some of the important factors (Blackburn et al., 2020; Duncan et al., 2019; Jaric et al., 2020; Kinlock et al., 2022; Lenzner et al., 2022; Lockwood et al., 2009; Lovell et al., 2021; Redding et al., 2019; Ricciardi, 2006; Seebens, Blackburn, et al., 2021; van Kleunen et al., 2007). Moreover, randomness might also be of high importance, but our current data set was not able to demonstrate this. Taking into account that: (i) current estimated number of NNS is a very small subset of global biodiversity (i.e. ~1% of total global biodiversity); (ii) out of all phyla globally, those with listed NNS contained more species than phyla without listed NNS—as random sampling theory would predict (Preston, 1948); (iii) a relatively large number of families have only one NNS reported; and (iv) the explanatory ability of NNS biodiversity by global biodiversity increases as the number of NNS increases (e.g. stronger explanatory ability of global biodiversity for terrestrial than for freshwater and marine habitats, where currently there are an order of magnitude higher numbers of terrestrial than freshwater and marine NNS), we propose that randomness is likely to play an important role in establishment success of NNS, and that this could be further elucidated in the future as invasion rates persist.

AUTHOR CONTRIBUTIONS

Elizabeta Briski conceived the study; Elizabeta Briski, Syrmalenia G. Kotronaki, Alejandro Bortolus, Marnie L. Campbell, Paul Fofonoff, Bella S. Galil, Chad L. Hewitt, Anthony Ricciardi, Gregory Ruiz, Evangelina Schwindt and James T. Carlton collected and curated the data. Elizabeta Briski and Ross N. Cuthbert analysed and visualized the data and led the writing of the manuscript. All authors revised and contributed critical intellectual content to the manuscript and approved submission.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Raw data supporting the findings of this study are in [Tables S1](#) and [S2](#), as well as deposited at Pangaea and publicly available at: <https://doi.org/10.1594/PANGAEA.940752>. There was no custom code or mathematical algorithm used in the study.

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BIOSKETCH

Elizabetha Briski is interested in a broad variety of questions pertaining to invasion biology and global change ecology. Her current work focuses on examining if species from particular regions (e.g., Ponto-Caspian area) have inherent advantages over other species in colonizing new areas. This work also leads to an interest in the natural dispersal of aquatic organisms and genetic mechanisms underlying adaptive responses of these organisms to novel environments and stressors. All authors are interested in invasion ecology, particularly in vectors and pathways by which non-indigenous species are introduced.

SUPPORTING INFORMATION

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

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