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M. Böhm

N. I. Dewhurst-Richman

M. Seddon

C. Albrecht

D. Allen

See next page for additional authors

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Authors

M. Böhm, N. I. Dewhurst-Richman, M. Seddon, C. Albrecht, D. Allen, A. E. Bogan, K. Cummings, G. Darrigran, W. Darwall, and Kathryn E. Perez

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The conservation status of the world's freshwater molluscs

Böhm, M.[1,*], Dewhurst-Richman, N.I.[1,2], Seddon, M.[3], Albrecht, C.[4], Allen, D.[5], Bogan, A.E.[6], Cummings, K.[7], Darrigran, G.[8], Darwall, W.[5], Fehér, Z.[9], Graf ,D.[10], Köhler, F.[11], Lopes-Lima, M.[12], Pastorino, G.[13], Smith, K.[5], van Damme, D.[14], Vinarski, M.[15], von Proschwitz, T.[16], von Rintelen, T.[17], Aldridge, D.C.[18], Budha, P.B.[19], Do, V.T.[20,21], Haase, M.[22], Johnson, P.D.[23], Kebapçı, Ü.[24], Madhyastha, N.A.A.[25,26], Neubert, E.[27], Prié, V.[28], Radea, C.[29], Son, M.O.[30], + additional authors, Collen, B.[x]

1 – Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY

2 – Department of Geography, University College London, Gower Street, London, WC1E 6BT, United Kingdom

3 -

4 – Department of Animal Ecology and Systematics, Systematics and Biodiversity Group, Justus Liebig University Giessen, H.-Buff-Ring 26-32 (IFZ), D-35392 Giessen, Germany

5 – Freshwater Biodiversity Unit, IUCN Global Species Programme, The David Attenborough Building, Pembroke Street, Cambridge CB2 3QZ, United Kingdom.

6 – North Carolina Museum of Natural Sciences, 11 West Jones Street, Raleigh, NC 27601 USA

7 - Illinois Natural History Survey, Prairie Research Institute, University of Illinois, 607 E. Peabody Drive, Champaign, IL 61820, USA.

8 - Museo de La Plata, La Plata National University (UNLP), Paseo del Bosque sin numero, La Plata (1900). Argentina.

9 - Department of Zoology, Hungarian Natural History Museum, H-1088, 13 Baross street, Budapest, Hungary

10 - University of Wisconsin-Stevens Point, Stevens Point WI 54481, USA

11 – Australian Museum, Australian Museum Research Institute, 1 William Street, Sydney, NSW 2010, Australia

12 - CIBIO/InBIO - Research Center in Biodiversity and Genetic Resources, Universidade do Porto, Campus Agrário de Vairão, Rua Padre Armando Quintas, 4485-661 Vairão, Portugal

13 - Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Av. Angel Gallardo 470 3° piso lab. 80, C1405DJR Ciudad Autónoma de Buenos Aires, Argentina

14 – Department of Geology, Ghent University, Belgium

15 - Laboratory of Macroecology & Biogeography of Invertebrates, Saint-Petersburg State University, 7/9 Universitetskaya Emb. 199034 Russia

16 – Göteborg Natural History Museum, Sweden

17 – Museum für Naturkunde, Leibniz Institute for Evolution and Biodiversity Science, Invalidenstraße 43, 10115 Berlin, Germany

18 - University of Cambridge, Department of Zoology, The David Attenborough Building, Cambridge CB2 3QZ, United Kingdom

19 - Central Department of Zoology, Tribhuvan University, Kirtipur, Kathmandu, Nepal

20 - Institute of Ecology and Biological Resources, Vietnam Academy of Science and Technology, 18 Hoang Quoc Viet, Cau Giay, Hanoi, Vietnam

21 - Graduate University of Science and Technology, Vietnam Academy of Science and Technology, 18 Hoang Quoc Viet, Cau Giay, Hanoi, Vietnam

22 - Vogelwarte, Zoologisches Institut und Museum, Universität Greifswald, Soldmannstrasse 23, 17489 Greifswald, Germany.

23 - Alabama Aquatic Biodiversity Center, Alabama Department of Conservation and Natural Resources, 2200 Highway 175, Marion, AL 36756, USA.

24 - Mehmet Akif Ersoy, Science and Arts Faculty, Department of Biology, Burdur, Turkey.

25 - Suri Sehgal Center for Biodiversity and Conservation, Ashoka Trust for Research in Ecology and the Environment (ATREE), Royal Enclave, Srirampura, Jakkur PO Bangalore 560064, India.

26 - Yenepoya Research Center, Yenepoya University, University Road, Deralakatte, Mangalore 575018, India.

27 –

28 - Institut de Systématique, Évolution, Biodiversité ISYEB – Museum National d’Histoire Naturelle, CNRS, Sorbonne Université, EPHE, Université des Antilles, 57 rue Cuvier, CP26, F-75005 Paris, France.

29 - Department of Ecology and Systematics, Faculty of Biology, National and Kapodistrian University of Athens, Panepistimiopolis 15784, Greece.

30 - Institute of Marine Biology, NAS of Ukraine, 37 Pushkinska St. 65048, Odessa, Ukraine.

X - Centre for Biodiversity & Environment Research, University College London, Gower Street, London WC1E 6BT, United Kingdom.

* correspondence: monika.bohm@ioz.ac.uk; +44(0)207 449 6676

Abstract

With the biodiversity crisis continuing unchecked, we need to establish levels and drivers of extinction risk to effectively allocate conservation resources and develop targeted actions. Given that threat appears particularly high in freshwaters, we assessed the extinction risk of 1,500 randomly selected freshwater molluscs using the IUCN Red List Categories and Criteria, as part of the Sampled Red List Index project. We show that close to one third of species in our sample are estimated to be threatened with extinction, with highest levels of threat in the Palearctic, Australasia and Nearctic and among gastropods. Threat levels were higher in lotic than lentic systems. Twenty-seven species were classified as Extinct (eight bivalves and 19 gastropods), mostly from the Nearctic realm and lotic systems. Pollution and the modification of natural systems (e.g. through damming and water abstraction) were the most frequently reported threats to freshwater molluscs, with some regional variation. Given that we found little spatial congruence between species richness patterns of freshwater molluscs and other freshwater taxa, new additional conservation priority areas emerge from our study. We discuss the implications of our findings for freshwater mollusc conservation and important next steps to estimate trends in freshwater mollusc extinction risk over time.

Keywords:

IUCN Red List, extinction risk, threatened species, bivalves, gastropods, congruence

Introduction

With the biodiversity crisis continuing unchecked (Butchart et al. 2010; Tittensor et al. 2014), it is vital to determine levels and drivers of species' extinction risk to effectively allocate conservation resources and develop targeted conservation actions. In addition, monitoring changes in extinction risk over time allows us to track changing biodiversity status (Butchart et al. 2004) and evaluate our progress towards meeting global, regional and national biodiversity targets (e.g., Aichi Targets of the Convention on Biological Diversity [CBD] and the Sustainable Development Goals [SDGs]). Many studies have described threat patterns of various species groups using the data provided by the IUCN Red List of Threatened Species, which describes extinction risk, dominant threats and recommended conservation action (Mace et al. 2008). For example, Torres et al. (2018) used the IUCN Red List of Threatened Species to prepare the first comparative analysis of risk of freshwater Unionida bivalves from South America. Global analyses of these valuable data have shown that 25% of mammal species (Schipper et al. 2008), 42% of amphibians (Stuart et al. 2004), 19% of reptiles (Böhm et al. 2013), 32% of freshwater crabs (Cumberlidge et al. 2009), 14% of dragon- and damselflies (Clausnitzer et al. 2009) and 32% of crayfish (Richman et al. 2015) are threatened with extinction. These analyses have also revealed how predominant drivers of extinction risk differ between higher taxa and ecosystems. Consequently, Red Lists are important tools for prioritising resources towards species and ecosystems most in need and identifying necessary actions to combat threats.

Freshwater ecosystems are under extensive pressure from anthropogenic threats. Freshwaters constitutes < 1% of the total volume of the hydrosphere but maintain several tens of thousands of animal species not able to live in salinated water (e.g. Balian et al. 2008). Some are restricted in distribution to a single waterbody (such as Baikal Lake, Tennessee River Basin, or single waterfalls in the Western Ghats). It has been suggested that approximately 80% of the world’s human population faces threats to water security (Vörösmarty et al. 2010), and almost one in three freshwater species are estimated at risk of extinction worldwide (Collen et al. 2014), with habitat loss being the most commonly cited threat. A recent analysis of distribution and threat to freshwater megafauna (fish, mammals, amphibians, reptiles) showed that increasing human pressures occur in many biodiversity hotspots (He et al. 2018). Given the high connectivity of freshwater systems, threat processes and their detrimental effects are easily transported from one locality to another (Darwall et al. 2009; Dudgeon et al. 2006) and fragmentation can have profound effects on water flows, sedimentation, habitat loss and hence species loss (Revenga et al. 2005).

Freshwater molluscs represent one of the most diverse groups of freshwater organisms. Close to 6,000 species of freshwater mollusc have been described; the majority being gastropods (almost 4,700 species; MollluscaBase 2020), while bivalves account for around 1,200 species (Bogan 2008, Graf 2013). Freshwater molluscs play key roles in freshwater systems by contributing to water quality, nutrient cycling and primary productivity, especially due to their roles as filter feeders and algal grazers, as well as to provide an ample food source for other species, including humans (Howard & Cuffey 2006, Brown & Lydeard 2010, Vaughn 2017).

Previous work has highlighted the plight of freshwater molluscs: for example, in 2000, 202 of nearly 300 unionid species from Canada and the United States were listed as either extinct, possibly extinct, or in the critical categories (critically imperilled, imperilled, vulnerable; Lydeard et al. 2004, Master et al. 2000); a recent assessment of freshwater gastropods showed that 67 of 703 US and Canadian species were considered extinct (Johnson et al. 2013), primarily due to the effects of damming and river channelisation. Within Europe, 44% of freshwater molluscs were assessed as threatened with extinction (Cuttelod et al. 2011) compared to 29% in continental Africa (Seddon et al. 2011) and 17% in the Indo-Burma region (Köhler et al. 2012). There are likely many more unnoticed extinctions of freshwater molluscs around the globe (Cowie et al. 2017, Régnier et al. 2009, Régnier et al. 2015). Such levels of threat mirror the general decline and threat in freshwater ecosystems (Collen et al. 2014).

The Sampled Red List Index (SRLI) provides a sampling strategy from which to derive – over time – broadly representative trends in extinction risk of species across highly species-rich species groups (Baillie et al. 2008). Freshwater molluscs are typically understudied and generally not represented in conservation planning, despite comparatively high levels of extinction (e.g. Régnier et al. 2015). Similar assessments have already been carried out for dragonflies (Clausnitzer et al. 2009) and reptiles (Böhm et al. 2013) and have acted as catalysts for increased conservation attention being afforded to these species groups (e.g., Tingley et al. 2016). Here, we report on the levels and drivers of threat in a random representative sample of 1,452 freshwater molluscs from across the globe, which was assessed as part of the SRLI project. This number constitutes roughly a quarter of described species in this group. We estimate extinction risk within our sample for molluscan orders/families; compare hotspots for freshwater molluscs with hotspots derived from other freshwater species groups to identify additional areas and regions of conservation priority; and set out important next steps to improve Red List assessments and extinction risk trend detection over time.

Materials and Methods

The Red List assessment process

Baillie et al. (2008) showed that a sample size of 900 non-Data Deficient species was sufficiently large to accurately report on trends in extinction risk, while buffering against falsely detecting improvements in extinction risk. Additionally, they recommended a sample size of 1,500 species for the sampled Red List approach to account for levels of data deficiency within the random sample of up to 40% (Baillie et al. 2008). We followed this approach and originally selected at random 1,500 species from a list of all described freshwater mollusc species (IUCN/SSC Mollusc Specialist Group). A full list of species in the sample (Table S1) is given in the Supplementary Materials. Our original sample consisted of 1,160 (77%) gastropod and 340 (23%) bivalve species, thus closely reflecting the contribution of both groups towards total freshwater mollusc diversity (Bogan et al. 2008; Strong et al. 2008). Subsequently, 48 selected species were found to inhabit brackish or marine systems and subsequently removed from analysis. Our reduced sample was still equal to or exceeding 900 non-Data Deficient species.

Overall, 371 of the 1,452 selected species were assessed as part of IUCN regional assessment projects, specifically Europe (Cuttelod et al. 2011), Pan-African (Darwall et al. 2009), Eastern Himalayas (Allen et al. 2010), the Western Ghats (Molur et al. 2011) and Indo-Burma (Köhler et al. 2012). For the remaining 1,081 species, new or updated assessments were produced through consultation with a global network of malacologists at an assessment workshop in January 2010. Species-specific data were collected on taxonomy, distribution, population trends, ecology and biology, threats, and conservation measures for all species in the assessment. Assessments followed the IUCN Red List Categories and Criteria (IUCN 2001) and all species were assessed against the quantitative thresholds of the five Red List criteria which indicate level of extinction risk (Mace et al. 2008): rate of population decline (Criterion A), population size (Criteria C and D/D1), geographic range size and decline (Criterion B), very small population size (Criterion D) or restricted range (Criterion D2) or quantitative analyses (Criterion E). Extinction risk ranges from the highest risk categories, Extinct (EX) and Extinct in the Wild (EW), via the threatened categories

Critically Endangered (CR), Endangered (EN) and Vulnerable (VU) to the lowest risk categories of Near Threatened (NT) and Least Concern (LC). Additionally, a species is listed as Data Deficient (DD) if insufficient data are available to make a conservation assessment. Through a centralised editorial and reviewing process, we ensured that the IUCN Red List Categories and Criteria were consistently applied between species and regions. A total of 248 species were re-assessed from previous assessments, with the remainder of 1,003 assessments representing first-time assessments of species. Since these assessments, 86 species have been reassessed and non-genuine changes in status (i.e. due to improved data availability; N = 28) have been incorporated into our results. All of the species assessments have been reviewed by the IUCN and are published online (www.iucnredlist.org, IUCN 2019), with the exception of one species of bivalve, *Arcidopsis footei* (Theobald, 1876), drafted as Endangered.

Summarising extinction risk

We summarised extinction risk within our sample across all freshwater molluscs and by taxonomic class (bivalves and gastropods), order and family, biogeographical realm (Afrotropical, Australasian, Indomalayan, Nearctic, Neotropical, Oceanian and Palearctic) and habitat system (lotic versus lentic systems). Following previous studies (Böhm et al. 2013, Clausnitzer et al. 2009, Richman et al. 2015), we estimated extinction risk in our sample as the proportion of threatened species (Critically Endangered, Endangered and Vulnerable species), assuming that Data Deficient species will fall into threatened categories in the same proportion as non-Data Deficient species:

$$\text{Prop}_{\text{threat}} = (\text{CR} + \text{EN} + \text{VU})/(\text{N} - \text{DD} - \text{EX}),$$

where N is the total number of species in the sample, CR, EN and VU are the numbers of species in each of the three threatened categories respectively, DD is the number of species in the Data Deficient category, and EX the number of species in the Extinct category. We provided upper and lower bounds of our estimate by assuming that (a) no Data Deficient species were threatened [lower margin: $Prop_{threat\_lower}$ = (CR + EN + VU)/(N – EX)], and (b) all Data Deficient species were threatened [upper margin; $Prop_{threat\_upper}$ = (CR + EN + VU + DD)/(N – EX)]. It should be noted that these are estimates and upper/lower bounds of extinction risk within our sample only and may not accurately reflect the proportion of freshwater molluscs threatened worldwide. This is because the sampled approach employed here was devised to accurately detect trend direction of the RLI over time, and was not devised to accurately reflect threat status for a species group as a whole at a particular point in time.

Assessment of drivers of extinction risk

During the assessment process, threat processes were recorded for each species and coded following Salafsky et al. (2008) (Table S1). We summarised the number of species affected (across the global sample and by biogeographic region) by each of the following high-level threat processes: residential and commercial development; agriculture and aquaculture; energy production and mining: transportation and service corridors; biological resource use; human intrusion and disturbance; natural system modification; invasive and other problematic species; pollution; geological events; and climate change and severe weather (Salafsky et al. 2008). Using permutation-based chi-square tests, we determined whether threat processes were randomly spread across Red List categories, by looking at a) threatened (CR, EN, VU) versus non-threatened (NT, LC) classification, and b) individual Red List categories (CR, EN, VU, NT, LC). We carried out permutation chi-square tests using a) all 518 threatened and non-threatened species which were affected by one or more threat processes (the remainder of species does not have any threats, or the threats are unknown, or species are DD), and b) all 142 species affected by a single threat process only. We permuted the tables 1,000 times, and supplemented the results of this analysis with Fisher exact tests where the data had low expected values of less than 5 (for single-threat species only).

Spatial patterns of freshwater molluscs and congruence with other species groups

We only included species which were considered extant or probably extant, resident, and native or reintroduced in our summary maps of freshwater mollusc species richness. We mapped species richness, threatened species richness and Data Deficient species richness of our sample by overlaying a grid with 1° grid cells onto the respective aggregated species' distribution and summing the number of species occurring in each grid cell. We normalised species richness relative to the richest cell in order to derive a synthetic pattern of species richness ranging from zero (no species present) to one (highest species richness), as described in Collen et al. (2014). We also mapped normalised species richness, threatened species richness and Data Deficient species richness of bivalves and gastropods in our sample, respectively (Figure S1 and S2, Supplementary Materials).

To assess spatial congruence between bivalves and gastropod spatial patterns, we generated spatial overlays of the three normalised measures of species richness – species richness, threatened-species richness, and Data Deficient-species richness – for the two groups. We estimated spatial congruence using Pearson's correlations, and accounted for spatial autocorrelation by implementing the method of Clifford et al. (1989), which estimates effective degrees of freedom based on spatial autocorrelation in the data and applies a correction to the significance of the observed correlation. We excluded cells where both species had no species present in order to overcome the double zero problem because these cells can inflate measures of covariation and association (Legendre & Legendre 1998). We mapped congruence of species richness hotspots between gastropods and bivalves in our analysis by selecting the top 10% of cells with the highest normalised richness values.

We also assessed spatial congruence between patterns of species richness, threatened species richness and Data Deficient species richness of our sample of freshwater molluscs and those derived from other freshwater species groups. First, we recalculated richness patterns for six different groups of freshwater species (amphibians, crabs, crayfish, fish, mammals and reptiles) obtained from a previous study on the spatial distribution of freshwater species and threat (Collen et al. 2014) at our 1° spatial scale. We then produced normalised species richness maps for each as described above to account for different sample sizes in the various species groups (Collen et al. 2014). To assess spatial congruence between species richness patterns of freshwater molluscs and other groups of freshwater species, we again generated spatial overlays of the three measures of species richness – species richness, threatened-species richness, and Data Deficient-species richness – for each taxonomic group, and estimated spatial congruence using Pearson's correlations, as described above. We applied this using only cells with non-0 normalised richness for molluscs, to minimise inflation of association (Legendre & Legendre 1998). We mapped congruence of species richness hotspots for all freshwater taxonomic groups in our analysis by selecting the top 10% of cells with the highest normalised richness values, and mapping the number of taxon groups overlapping in each grid cell.

Results

Extinction risk in freshwater molluscs

Nearly one-third of species in our sample of 1,450 freshwater molluscs were estimated to be threatened ($\text{prop}_{\text{threat}}$ = 0.31; lower = 0.19, upper = 0.57; Table 1), based on 532 Data Deficient species (36.7%) within the sample. Freshwater mollusc threat was highest in the

Nearctic, Palearctic and Australasian realms (Nearctic: $\text{prop}_{\text{threat}}$ = 0.36, lower = 0.30, upper = 0.46; Palearctic: $\text{prop}_{\text{threat}}$ = 0.35, lower = 0.19, upper = 0.65; Australasia: $\text{prop}_{\text{threat}}$ = 0.34, lower = 0.25, upper = 0.50; Table 1). Data deficiency was particularly high in tropical regions, especially the Neotropical and Indomalayan realms (50.3% and 49.0% of species, respectively), the Palearctic (45.5% of species) and Oceania (43.5% of species). Threat levels were estimated to be higher in lotic systems than lentic systems (lotic: $\text{prop}_{\text{threat}}$ = 0.31, lower = 0.22, upper = 0.50; lentic: $\text{prop}_{\text{threat}}$ = 0.18, lower = 0.12, upper = 0.45).

Estimated threat levels were higher in gastropods ($\text{prop}_{\text{threat}}$ = 0.33; lower = 0.19, upper = 0.61) than bivalves ($\text{prop}_{\text{threat}}$ = 0.26; lower = 0.20, upper = 0.43; Table 1). Threat and data deficiency levels varied greatly amongst families: for example, the bivalve family Unionidae was the most species-rich families within the sample (N= 191), with 33% of species estimated threatened (lower = 0.29, upper = 0.42) and a relatively low level of data deficiency (12% of species in the family), followed by the gastropod families Hydrobiidae (N= 157) with 67% species threatened (lower = 0.44, upper = 0.78) and a third of species listed as DD, and the Planorbidae (N= 155), with only 3% of species threatened (lower = 0.01, upper = 0.54), yet high levels of data deficiency (prop_{DD} = 0.52). The Margaritiferidae are another highly threatened family of bivalves in our sample (N= 7, $\text{prop}_{\text{threat}}$ = 0.67; lower = 0.57, upper = 0.71). For gastropods, other highly threatened families in our sample are the Moitessieriidae (N= 36, $\text{prop}_{\text{threat}}$ = 0.74; lower = 0.56, upper = 0.81), Semisulcospiridae (N= 12, $\text{prop}_{\text{threat}}$ = 0.63; lower = 0.42, upper = 0.75), Pachychilidae (N= 18, $\text{prop}_{\text{threat}}$ = 0.50; lower = 0.39, upper = 0.61), Emmericiidae (N= 5, $\text{prop}_{\text{threat}}$ = 0.50; lower = 0.20, upper = 0.80), and Tateidae (N= 91, $\text{prop}_{\text{threat}}$ = 0.49; lower = 0.42, upper = 0.56).

Overall, 27 species were assessed as extinct, of which eight were bivalves and 19 were gastropods. Nearly one-fifth of the gastropod family Pleuroceridae assessed in our sample were categorised as Extinct, by far the family with the highest percentage of Extinct species in our analysis. Number of extinct species was highest in the Nearctic realm (23 species listed as Extinct) and in lotic systems (15 species listed as Extinct). In addition, 23 species are currently listed in the CR category as possibly extinct (19 gastropods of which eight belong to the family Hydrobiidae, and four bivalves of which three are unionids).

Most threatened species were classified based on criterion B (geographic range size and decline: 60% of threatened species, with 57% listed under B criterion only), followed by criterion D2 (very restricted range: 28% of threatened species) and criterion A (population reduction: 13.5% of threatened species, with 11% listed solely under criterion A). Only one species was classed as threatened based on criteria C (small population size and reduction), and two species based on criterion D (very small population size).

Predominant threat processes affecting freshwater molluscs

Pollution and natural system modification were the most common threats affecting freshwater molluscs (Figure 2A), both when considering all species (27% and 24% of threats documented, respectively), threatened species only (27% and 26% of threats documented), and bivalves and gastropods separately (Figure 2B). Residential and commercial development, energy production and mining, invasive and other problematic species, agriculture and aquaculture, and biological resource use were also frequently reported threats (Figure 2A).

Regional splits showed that pollution was the most commonly cited threat in the Afrotropics, Palearctic and Indomalaya, with natural system modification being the predominant threat in Australasia (together with threats from agriculture and aquaculture) and the Neotropics. In the Nearctic, pollution and natural system modification affected the same number of species in the sample (Figure 2C).

The distribution of threats between gastropods and bivalves was significantly non-random when considering all species (chi-squared = 17.09, $p < 0.05$) and single-threat species only (chi-squared = 16.21, $p < 0.05$; Fisher test: $p = 0.013$). The distribution of threats between threatened and non-threatened Red List categories was borderline random when considering all species (chi-squared = 16.81, $p = 0.064$) and single-threat species only (chi-squared = 16.61, $p < 0.05$; Fisher test: $p = 0.001$). This remained true when only considering the two most frequently cited threats of natural system modification and pollution (chi-squared = 7.646, d.f. = 1, $p = 0.006$). The distribution of all threats between individual non-DD Red List categories (CR, EN, VU, NT, LC) was random when considering all species (chi-squared = 50.88, $p = 0.54$) and single-threat species only (chi-squared = 52.18, $p = 0.08$), although Fisher's test indicated a non-random distribution for single-threat species (Fisher test: $p = 0.018$).

However, natural system modification and human disturbance contributed more than expected to threatened status of species, while pollution and biological resource use contributed more than expected to non-threatened species threats (Figure 3). Natural system modification made a greater than expected contribution to the CR category and less than expected to LC in both analyses (Table 3). Pollution and biological resource use contributed less than expected to higher threat categories (CR) and more than expected to lower threat categories of NT and LC (Table 3). Human intrusion and disturbance contributed less than expected to low threat categories (LC) and more than expected to the lower end of the threatened category spectrum (VU), primarily due to application of IUCN Red List criterion D2 (restricted range and plausible future threat) (Table 3).

Spatial distribution of freshwater molluscs and congruence with other species groups

Normalised species richness in our sample was highest in the Eastern USA (especially Tennessee, Kentucky and surrounding states), Lake Baikal, parts of Central and Eastern Europe, and selected river systems in Southeast Asia (Figure 1A; see Supplementary Materials for spatial detail of the distribution pattern by region, for all species (Figure S3-S5), gastropods (Figure S6-S8) and bivalves (Figure S9-S11) in our sample, respectively). High species richness in Central and Eastern Europe, Lake Baikal and Southeast Asia was driven by high species richness of gastropods in these regions (Figure S1A). High species richness in the Eastern USA was primarily driven by bivalves (Figure S2A), although gastropods were also species rich in these areas (Figure S1A), and there was significant congruence in the spatial pattern of bivalve and gastropod species richness in our sample (Pearson's correlation = 0.692, F = 71.18, adjusted d.f. = 77.52, p < 0.001).

Data deficiency was highest also in Lake Baikal (again, due to relatively high richness of gastropods; Figure S1B), as well as the Caspian Sea region, Japan, and selected river systems in South and Southeast Asia (e.g. regions of the Brahmaputra and Irrawaddy rivers), while normalised threatened species richness in our sample was highest in the most species-rich states of the USA, and in Central Europe (Albania/North Macedonia, and Austria) (Figure 1B & C). Threatened species richness was highest for gastropods in parts of central Europe (Figure S1C) and for bivalves in the southeastern USA (Figure S2C), and overall the spatial distribution of threatened gastropods and bivalves was significantly negatively correlated (Pearson's correlation = -0.151, F = 6.62, adjusted d.f. = 283.03, p = 0.011). Data deficiency for bivalves in our sample was highest in eastern Asia (Russia and Japan; Figure S2B), and this pattern was incongruent with the DD species richness pattern of gastropods in our sample (Pearson's correlation = 0.07, F = 1.18, adjusted d.f. = 209.01, p = 0.279). Bivalve and gastropod congruence maps are shown in Figure S12 in the Supplementary Materials.

There was limited evidence for cross-taxon congruence in patterns of species richness at the broad-scale, with normalised species richness of freshwater molluscs positively and significantly correlated with normalised species richness of crayfish (Pearson’s correlation = 0.513, F = 28.18, adjusted d.f. = 78.94, p < 0.001), freshwater reptiles (Pearson’s correlation = 0.342, F = 14.20, adjusted d.f. = 107.57, p <0.001) and freshwater mammals (Pearson’s correlation = 0.256, F = 6.70, adjusted d.f. = 95.98, p =0.011; Table 4). All other species richness patterns were not spatially congruent with that for freshwater molluscs (amphibians, freshwater crabs and overall freshwater species richness as estimated by Collen et al. (2014); Table 4).

There was significant positive congruence between threatened freshwater mollusc richness and all threatened crayfish species richness (Pearson’s correlation = 0.465, F = 9.51, adjusted d.f. = 34.50, p =0.004) and threatened freshwater species richness (Pearson’s correlation = 0.208, F = 4.78, adjusted d.f. = 105.83, p =0.031), and negative congruence with freshwater crabs (Pearson’s correlation = -0.046, F = 5.20, adjusted d.f. = 2146.15, p =0.023; Table 4). Congruence between patterns of Data Deficient species richness were significantly positive between freshwater molluscs and freshwater crayfish (Pearson’s correlation = 0.184, F = 26.23, adjusted d.f. = 746.2, p <0.001), freshwater fish (Pearson’s correlation = 0.203, F = 5.94, adjusted d.f. = 138.53, p =0.016) and all freshwater species (Pearson’s correlation = 0.177, F = 4.52, adjusted d.f. = 140.19, p =0.035; Table 4).

Discussion

Here, we presented the first global analysis of the extinction risk of freshwater molluscs by utilising an established method to assess a random sample of 1,452 species from the world’s freshwater mollusc species list (Baillie et al. 2008). This sample constitutes around a quarter of the global species diversity of freshwater molluscs and shows that 30% of species in our sample are threatened with extinction.

Patterns of threat

Extinction risk in freshwater taxa is known to exceed that of terrestrial or predominantly terrestrial taxonomic groups (Collen et al. 2014, McRae et al. 2017). For example, 25% of mammal species (Schipper et al. 2008) and 14% of birds are threatened (IUCN 2018), in comparison to levels of threat for freshwater molluscs which are comparable to those of freshwater crayfish and freshwater crabs (32%; Cumberlidge et al. 2009, Richman et al. 2015). Threat levels in our mollusc sample were lower than those for amphibians (42%; Stuart et al. 2004) and higher than those for Odonata (14%; Clausnitzer et al. 2009). Regional assessments of freshwater species, including molluscs, show a broadly similar pattern to our results, with high levels of threat in Europe (Cuttelod et al. 2011), although our current analysis fails to highlight the high levels of threat observed in continental Africa (Seddon et al. 2011).

Threat was particularly high in freshwater gastropods, for which more species had smaller ranges compared to the often large-ranged bivalves (median range size for gastropods in our sample was 28,723.75 km^2 compared to a median of 243,401.5 km^2 for bivalves; Figure S13). This has also been shown in previous regional analyses of freshwater threat, using the IUCN Red List Categories and Criteria, where gastropods, particularly "prosobranchs", consistently showed the highest levels of threat (Cuttelod et al. 2011, Seddon et al. 2011). Our analysis found threat levels for gastropods to be highest in Europe, which is also shown in the European Red List for these species (Cuttelod et al. 2011), and negatively correlated with threat levels in bivalves which had the highest threat levels in North America (Bogan 2006). Some of the highly threatened gastropod families, such as the Tateidae, are small species with restricted distributions; unsurprisingly, many species of Tateidae have also only recently been described in the past 30 years or so (Ponder 2019). In our sample, 60 of the 91 species of Tateidae were described in 1990 or later; despite this, data deficiency was relatively low at 14% of Tateid species in our sample. Species of the family Moitessieridae, also highly threatened in our sample, are small species, leading a mainly subterranean lifestyle, with patchy and restricted distributions and often known from few or only single localities; some species may be undersampled given the challenge to sample these subterranean species (Wilke 2019), though data deficiency in our sample was again low (25%) compared to other families.

Lower overall threat of freshwater bivalves is primarily due to the relatively low threat in the bivalve family Sphaeriidae, a family of almost cosmopolitan and widespread species with very few threats reported. However, these small bivalves may have attracted much less research attention by conservationists than the larger unionids, and have higher levels of data deficiency (36% versus 12% in the Unionidae; Table 2). Recent studies suggest that threat levels in freshwater bivalves may be higher than estimated here. For example, a recent study on the status and distribution of the world's freshwater bivalves suggested that 40% of bivalves are either Near Threatened, threatened or Extinct (Lopes-Lima et al. 2018). Including Extinct and Near Threatened species into our estimate, our results suggest that 35% of freshwater bivalve species are threatened or extinct (lower estimate: 26%; upper estimate: 50%). In addition, using alternative assessment processes, such as the one employed by the American Fisheries Society, showed that broadly equal levels of 74% and 72% of species are imperilled for gastropods and bivalves, respectively (Johnson et al. 2013). The fact that information on population trends may be missing for a large proportion of bivalve species, which are often long-lived (Vaughn & Taylor 2001) and therefore need long-term monitoring to detect trends, may lead to an underestimate of extinction risk, particularly when only range-based metrics are available to assess extinction risk (Torres et al. 2018).

Threat was higher in lotic versus lentic system, a finding corroborated in other studies on the conservation status of freshwater biodiversity (Clausnitzer et al. 2009, Collen et al. 2014). Establishment of dams and other barriers, one of the main threats to freshwater molluscs, presents a rising threat to freshwater biodiversity (He et al. 2018). Freshwater mussels require fish hosts for the completion of their life cycle and dispersal (Modesto et al. 2018). Movement of fish hosts is vital for connectivity of mussel populations and metapopulation dynamics (Zając et al. 2018). It was shown that there is reduced mussel species richness and abundance closer to river impoundments, suggesting an extinction risk gradient downstream of these structures (Vaughn & Taylor 2001). Dams may block migratory routes for fish (Maceda-Veiga 2013), which may be important hosts for molluscan larvae (Modesto et al. 2018). Local extinction rates of mussels have previously been predicted by their primary fish hosts: mussels that require large migratory fish to complete their life cycle had higher extinction rates due to river fragmentation (Vaughn 2012).

High levels of threat in freshwater species are expected in a system that is impacted by many different threats, especially given that freshwater systems are generally highly interconnected. To determine the importance of different threats to freshwater species, various studies have analysed large-scale datasets such as the IUCN Red List. For example, Collen et al. (2014) found three predominant drivers of freshwater threat: habitat loss and degradation (which includes urban development and dam building), pollution and overexploitation. Interestingly, using an alternative dataset on freshwater species trends, the Living Planet database (McRae et al. 2017), a recent unpublished analysis has shown that the most common threats affecting freshwater vertebrate populations are natural system modifications (24.1%), agriculture and aquaculture (16.4%) and pollution (15.2%) (Thorburn

2017). In our present analysis, pollution and natural system modification were again the most common threats affecting freshwater molluscs globally, and natural system modification was associated more than expected with CR listings. Not only do dams and barriers cause habitat fragmentation, they are also a major factor reducing climate change resilience of freshwater systems (Markovic et al. 2017). It is therefore of utmost importance that we address connectivity of freshwaters when identifying priority areas for conservation and identify the barriers that human perturbations pose to connectivity (Hermoso et al. 2018). In terms of pollution, we may still be underestimating the impact of this threat on freshwater molluscs, since sublethal effects of pollution, and how it may impact gene expression and ecological condition, are still under-researched (Ferreira-Rodríguez et al. 2019).

Species such as freshwater mussels were among the most sensitive freshwater species to several chemicals, even more so as juveniles (Wan et al. 2017). However, pollution was associated more than expected with lower threat categories of NT and LC globally, but was the most commonly-cited threat in the Afrotropics and Indomalayan. For example, pollution in form of agricultural runoff (especially from monoculture crops like rubber or palm oil plantations) and sedimentation are a major threat to freshwater molluscs in Indonesia (Gallardo et al. 2018, Zieritz et al. 2018). Therefore, regional analyses of threat are necessary to highlight regional differences in predominant threats, and to put in place regional action plans to combat threats in a meaningful and targeted way.

Global change and trade globalization have spurred an increase in bioinvasions and their subsequent impacts on ecosystems (Darrigran and Damborenea 2011). Introduction of non-native species (potential invasive species) is a main cause of biodiversity loss (Gallardo et al. 2018). Darrigran et al (2020) identified four hotspot areas for non-native species of molluscs (both aquatic and terrestrial) in South America, which require special attention for biodiversity conservation, not only because they are potential entry points for non-native species, but also because they coincide with hotspots of high endemism (Darrigran et al. 2020). Identifying entry points of non-native molluscs, such as through large cities, ports, or airports (Darrigran et al. 2020), are a vital step to identify hotspots for conservation action.

Incongruence between spatial patterns of freshwater mollusc species richness in comparison to other taxonomic groups suggests that macroecological patterns of species richness and range may be governed by different determinants, depending on the species group in question (Collen et al. 2014). Therefore, conservation priority areas are likely to vary, depending on the species group under focus; similar discrepancies between richness patterns have recently been shown in terrestrial vertebrates, where the addition of reptiles has highlighted new conservation priorities for lizards worldwide (Roll et al. 2017). High species richness in parts of the United States and Southeast Asia reflect known hotspots of freshwater molluscs (e.g. Lydeard & Mayden 1995, Zieritz et al. 2018). However, the general pattern of high species richness in our sample in parts of Europe could be simply a reflection of a larger number of taxonomists working here, with well-defined species boundaries as a result. In contrast, the comparatively lower species richness and levels of threat in our sample in South America, despite the presence of similar threats, may reflect understudied species groups where threats have not yet been adequately reported.

Data Deficiency

High levels of data deficiency preclude our ability to adequately represent species groups in conservation action plans and conservation prioritisation schemes. Data deficiency in freshwater molluscs (37%) was greater than amongst crayfish (20%; Richman et al. 2015), roughly comparable to that in the Odonata (35%; Clausnitzer et al. 2009), but much lower than in freshwater crabs (49%; Cumberlidge et al. 2009). The most obvious causes for the high prevalence of DD species in our sample are: 1) a deficiency of experts in the field of invertebrate systematics (Agnarsson & Kuntner 2007, Kotov & Gololobova 2016; 2) discrepancies among molluscan systematists with regard to species rank and the methods of species delimitation (e.g. Vinarski 2018), which lead to species status of many freshwater molluscan taxa remaining disputable; 3) lack of monitoring of abundance and status of freshwater molluscan populations, especially in developing countries in hotspots of freshwater biodiversity. Many nominal species of freshwater snails and bivalves have not been studied (or even recorded) since their taxonomic description, thus pushing these taxa into the limbo of Data Deficient species. Outdated, morphology-based taxonomies persist in many groups of freshwater molluscs (Graf 2007, Torres et al. 2018), though usage of modern molecular techniques show that some are incomplete. In the few genera and families where revisions have been made, drastic reassessment of the commonly accepted taxonomies changes changed species richness estimates (e.g. Bolotov et al. 2015, Osikowski et al. 2018), and likely conservation status of individual species. Since data deficiency was high amongst most of the taxonomic sub-groups in our study, increased efforts are needed across orders and families of freshwater molluscs to improve our knowledge on this ecologically important group. In addition, predictive techniques are needed to assess the most likely threat status of Data Deficient species within our sample. Such assessments have already been carried out for several other taxonomic groups to improve threat estimates (Bland & Böhm 2016, Bland et al. 2015). Reducing the number of DD species in our study and for freshwater molluscs in general will allow not only for more accurate biodiversity indicators, but initiate better conservation actions for individual species and/or regions.

Adequacy of sample, sample size and sRLI process

Taxonomically, comparison to published literature suggests that our study sample broadly represents freshwater mollusc diversity at the global scale. For example, based on globally available estimates of freshwater bivalve species richness (Lopes-Lima et al. 2018), our sample broadly represents bivalve families adequately (Table SX), although it over-represents Sphaeriidae (18% of the world's freshwater bivalve species, represented by ~24% of species in our sample). Other studies have found a similar broad-scale representativeness of the random sampling technique for other species groups, such as fish, where the sample adequately represented both marine and freshwater fish diversity and traits (R. Miranda, unpublished data).

Estimating threat status of freshwater molluscs, and sub-groups thereof, based on a sample of only around 25% known freshwater molluscs may introduce bias into our estimate, especially since the sample size of 900 non-DD species recommended by Baillie et al. (2008) was only devised to accurately detect extinction risk trends in a species group over time. In fact, we cannot make any conclusions from our sample on overall level of threat within this species group. However, recent studies show that in future we may be able to utilise a smaller sample of around 400 non-DD species to accurately depict extinction risk trends over time (Henriques et al. 2020), a suggestion which will be tested with the upcoming re-assessment of freshwater molluscs in the coming years.

The future of freshwater molluscs

Freshwater molluscs provide invaluable function to freshwater ecosystems and ecosystem services to humans, but are under high levels of threat. It is vital that conservation actions are increased to safeguard freshwater ecosystems and the species, including molluscs, that depend on them, given the manifold threats impacting these fragile systems, particularly riverine ecosystems. While this targeted global assessment gives an overview of issues impacting freshwater molluscs across the globe and at the regional level, it is vital that comprehensive action plans are drawn up to preserve freshwater systems and its biodiversity. In addition, research needs to be focused on priorities for conservation of these species and better understanding of the impact of threats, such as pollution and climate change (Ferreira-Rodríguez et al. 2019).

With globally agreed policy targets aiming to combat species extinctions and declines, while also protecting the services that underpin human livelihoods and well-being, this study demonstrates that we must step up our commitment to the conservation of freshwater systems if we want to achieve these targets. While species assessments and action plans are highlighting species conservation priorities and relevant action, we require an ecosystem approach to safeguard healthy freshwater systems for all. Climate change in particular will strain both freshwater species and human water use (Strayer & Dudgeon 2010), so ecosystem approaches are required to mitigate impacts of climate change. In addition, our data shows that freshwater extinctions are already underway; it has previously been stated that the time to act is now (Strayer & Dudgeon 2010). Incomplete knowledge should not be a barrier to carrying out conservation actions for those species known or thought to be most at risk.

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Table 1. Extinction risk in a random sample of 1,452 freshwater molluscs by class, biogeographic realm and habitat system (lentic versus lotic). The number of species falling into each IUCN Category are listed: DD – Data Deficient; LC – Least Concern; NT – Near Threatened; VU – Vulnerable; EN – Endangered; CR – Critically Endangered; EX - Extinct. No species were listed as Extinct in the Wild (EW). Proportion threatened: assumes DD species are threatened in the same proportion as non-DD species; Lower proportion: no DD species threatened; Upper proportion: all DD species threatened.

Taxon	**DD**	**LC**	**NT**	**VU**	**EN**	**CR**	**EX**	***N***	***N non-DD***	**Prop. threatened**	**Lower prop**	**Upper prop**
All	532	552	65	115	77	82	27	1,450	918	0.308	0.193	0.566
Bivalves	75	175	16	19	27	20	8	340	265	0.257	0.199	0.425
Gastropods	457	377	49	96	50	62	19	1,110	653	0.328	0.191	0.610
Realm												
Afrotropical	38	67	10	7	13	6	0	141	103	0.252	0.184	0.454
Australasian	41	80	5	23	7	13	2	171	130	0.336	0.254	0.497
Indomalayan	120	104	8	6	4	3	0	245	125	0.104	0.053	0.543
Nearctic	52	148	23	31	30	33	23	340	288	0.355	0.297	0.461
Neotropical	75	66	0	6	0	2	0	149	74	0.108	0.054	0.557
Oceanian	10	12	0	1	0	0	0	23	13	0.077	0.043	0.478
Palaearctic	217	148	19	41	25	25	2	477	260	0.353	0.192	0.648
Habitat system												
Lentic	189	299	16	30	22	19	0	575	386	0.184	0.123	0.452
Lotic	302	476	61	100	67	69	15	1,090	788	0.305	0.220	0.500

Table 2. Extinction risk in a random sample of 1,450 freshwater molluscs by subclass, superorder or order, and family (only families with more than ten species and at least one threatened species are listed here). A full taxonomic summary is available in the Supplementary Materials, Table S1. Proportion of threatened species has been calculated as described in the methods section.

	No. species in sample	**No. threatened**	**No. DD**	**% DD**	**Prop. Thr.**	**Lower prop**	**Upper prop**	**No. EX**
Class Gastropoda	1,110	208	457	41.2	0.328	0.191	0.610	19
Subclass Neritimorpha	32	3	7	21.9	0.120	0.094	0.313	0
Neritidae	30	3	7	23.3	0.130	0.100	0.333	0
Subclass Caenogastropoda	789	192	310	39.3	0.415	0.248	0.649	16
Order Architaenioglossa	99	5	47	47.5	0.096	0.051	0.525	0
Ampullariidae	50	4	26	52.0	0.167	0.080	0.600	0
Viviparidae	49	1	21	42.9	0.036	0.020	0.449	0
Order Littorinimorpha	539	159	216	40.1	0.492	0.295	0.696	6
Amnicolidae	26	3	17	65.4	0.333	0.115	0.769	0
Assimineidae	23	4	12	52.2	0.364	0.174	0.696	0
Bithyniidae	38	6	17	44.7	0.286	0.158	0.605	0
Bythinellidae	21	5	7	33.3	0.385	0.250	0.600	1
Cochliopidae	44	8	25	56.8	0.421	0.182	0.750	0
Hydrobiidae	157	68	53	33.8	0.667	0.439	0.781	2
Lithoglyphidae	28	2	19	67.8	0.250	0.074	0.778	1
Moitessieriidae	36	20	9	25.0	0.741	0.556	0.806	0
Pomatiopsidae	51	5	29	56.9	0.227	0.098	0.667	0
Tateidae	91	37	13	14.3	0.487	0.416	0.562	2
Order Sorbeoconcha	151	28	47	31.1	0.298	0.199	0.532	10
Melanopsidae	11	1	3	27.3	0.125	0.091	0.364	0
Pachychilidae	18	7	4	22.2	0.500	0.389	0.611	0

Paludomidae	26	3	11	42.3	0.200	0.115	0.538	0
Pleuroceridae	47	9	5	10.6	0.281	0.243	0.378	10
Semisulcospiridae	12	5	4	33.3	0.625	0.417	0.750	0
Thiaridae	35	3	19	54.3	0.188	0.086	0.629	0
Subclass Heterobranchia	289	13	140	48.4	0.089	0.045	0.535	3
Valvatidae	15	2	5	33.3	0.200	0.133	0.467	0
Superorder Hygrophila	270	11	133	49.3	0.082	0.041	0.539	3
Chilinidae	12	1	7	58.3	0.200	0.083	0.667	0
Lymnaeidae	54	5	16	29.6	0.135	0.094	0.396	1
Physidae	18	2	12	66.7	0.333	0.111	0.778	0
Planorbidae	155	2	80	51.6	0.027	0.013	0.536	2
Class Bivalvia	340	66	75	22.1	0.257	0.199	0.425	8
Subclass Heterodonta	109	7	43	39.4	0.106	0.064	0.459	0
Order Venerida	104	6	43	41.3	0.098	0.058	0.471	0
Cyrenidae	23	1	14	60.9	0.111	0.043	0.652	0
Sphaeriidae	81	5	29	35.8	0.096	0.062	0.420	0
Subclass Palaeoheterodonta	228	59	31	13.6	0.312	0.268	0.409	8
Hyriidae	12	1	4	33.3	0.125	0.083	0.417	0
Unionidae	191	53	23	12.0	0.331	0.290	0.415	8

Table 3. Pearson's residuals of all threats per IUCN Red List category, from permutation-based chi-square test. Grey cells show the largest negative deviance from the model, per threat; red cells show the largest positive deviance from the model, per threat. THR – Threatened IUCN Red List categories (CR – Critically Endangered, EN - Endangered, VU - Vulnerable); NON-THR – Non-threatened IUCN Red List categories (NT – Near Threatened; LC – Least Concern). AGRI/AQUA – Agriculture and aquaculture; BRU – Biological resource use, mostly exploitation; CC – Climate change; ENERGY – Energy production; DISTURBANCE – Human intrusion and disturbance; PROBLEM SP - Invasive and other problematic species; NSM – Natural system modification; POLLUTION - Domestic & urban waste, industrial effluent; DEV – Residential and commercial development; OTHER – Other threats, e.g. geological events, transportation & service corridors;

	THR			**NON-THR**	
Threat	**CR**	**EN**	**VU**	**NT**	**LC**
AGRI/AQUA	0.34	0.36	1.63	0.22	-1.9
BRU	-1.41	-0.39	-0.39	-0.9	2.13
CC	0.34	0.16	-1.89	0.42	0.85
ENERGY	0.59	0.02	0.2	-0.88	-0.05
DISTURBANCE	0.24	0.98	2.25	-0.4	-2.39
PROBLEM SP.	-0.14	0.2	0.12	-0.39	0.1
NSM	1.73	-0.11	-0.01	0.18	-1.25
POLLUTION	-1.76	0.24	-0.75	0.92	1.11
DEV	0.33	-0.51	0.02	-1.28	0.9
OTHER	0.07	-1.3	-0.92	3.07	-0.23

Table 4. Spatial congruence between geographical ranges of freshwater molluscs and other freshwater taxa. Richness metrics investigated are: SR – normalised species richness; THR – normalised threatened species richness; DD – normalised Data Deficient species richness. Richness patterns for taxa other than freshwater molluscs are based on Collen et al. 2014. Stars denote significance levels: * p<0.05; ** p<0.01; *** p<0.001).

Richness metric		**Amphibians**	**Crabs**	**Crayfish**	**Fish**	**Mammals**	**Reptiles**	**All freshwater**[1]
SR	Corr	0.07	-0.03	0.52***	0.14	0.26*	0.33***	0.15
	F	0.31	0.05	28.38	1.31	6.66	13.27	1.32
	d.f.	60.94	59.59	78.34	61.83	94.67	107.32	59.82
THR	Corr	-0.04	-0.05*	0.46**	-0.04	0.04	-0.06	0.20*
	F	1.65	5.45	9.12	1.25	1.02	1.41	4.46
	d.f.	1121.82	2445.2	33.67	809.5	647.7	345.47	103.33
DD	Corr	0.03	0.11	0.18***	0.20*	0.05	-0.02	0.18*
	F	0.25	3.32	26.23	5.93	0.22	0.83	4.52
	d.f.	404.62	257.12	745.26	138.14	82.70	1801.7	139.81

[1] as defined in Collen et al. 2014, excluding freshwater molluscs

Figure legends

Figure 1. A) Species richness of the sampled assessment for freshwater molluscs (N = 1,406 species of extant/probably extant, native or reintroduced species), showing normalised species richness per grid cell; B) Normalised species richness of Data Deficient (DD) species (N = 517); C) Normalised threatened species richness (CR, EN, VU; N = 274).

Figure 2. Number of species affected by different threat processes, showing A) contribution of threat to Red List categories, B) contribution of threats to non-threatened (light) and threatened species (dark) for bivalves (solid bars) and gastropods (hashed bars), respectively, C) predominant threats by biogeographical realm.

Figure 3. Pearson's residuals for threatened species by threat process, from permutation-based chi-square test, based on the full dataset (dark grey) and species affected by a single threat process only (light grey). AGRI/AQUA – Agriculture and aquaculture; NSM – Natural system modification; DISTURBANCE – Human intrusion and disturbance; ENERGY – Energy production; PROBLEM SP - Invasive and other problematic species; DEV – Residential and commercial development; OTHER – Other threats, e.g. geological events, transportation & service corridors; CC – Climate change; BRU – Biological resource use, mostly exploitation; POLLUTION - Domestic & urban waste, industrial effluent.

Figure 4. Congruence of 10% of richest hotspots for freshwater species: A) species richness hotspots; B) Data Deficient richness hotspots; C) threatened species richness hotspots**.** Congruence is shown by overlap of hotspots for seven different freshwater taxonomic groups: amphibians, crabs, crayfish, fish, mammals, reptiles (based on Collen et al. 2013) and molluscs (this analysis). Red polygon outline delineates 10% freshwater mollusc hotspot area.

Figure 1.

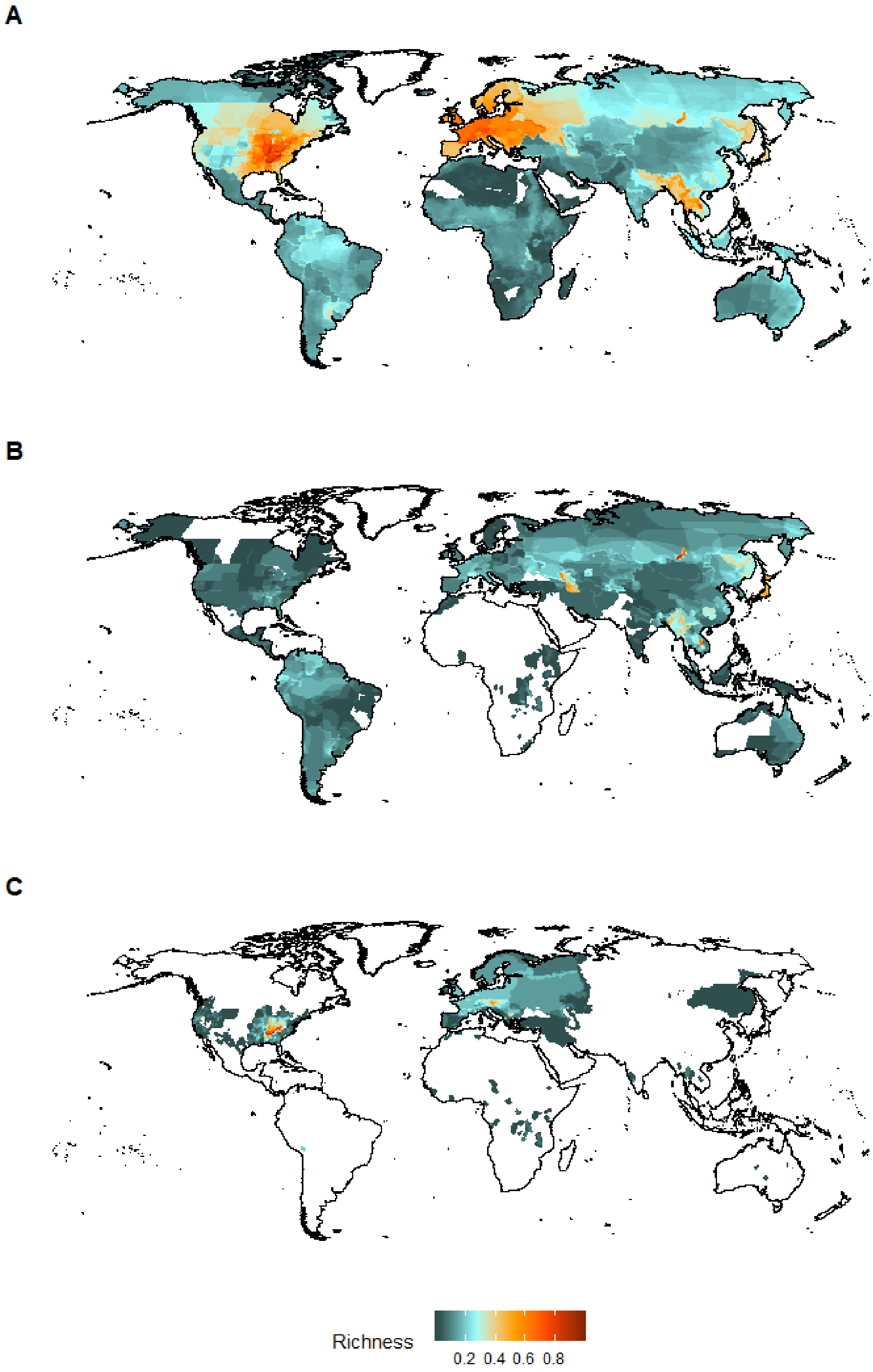
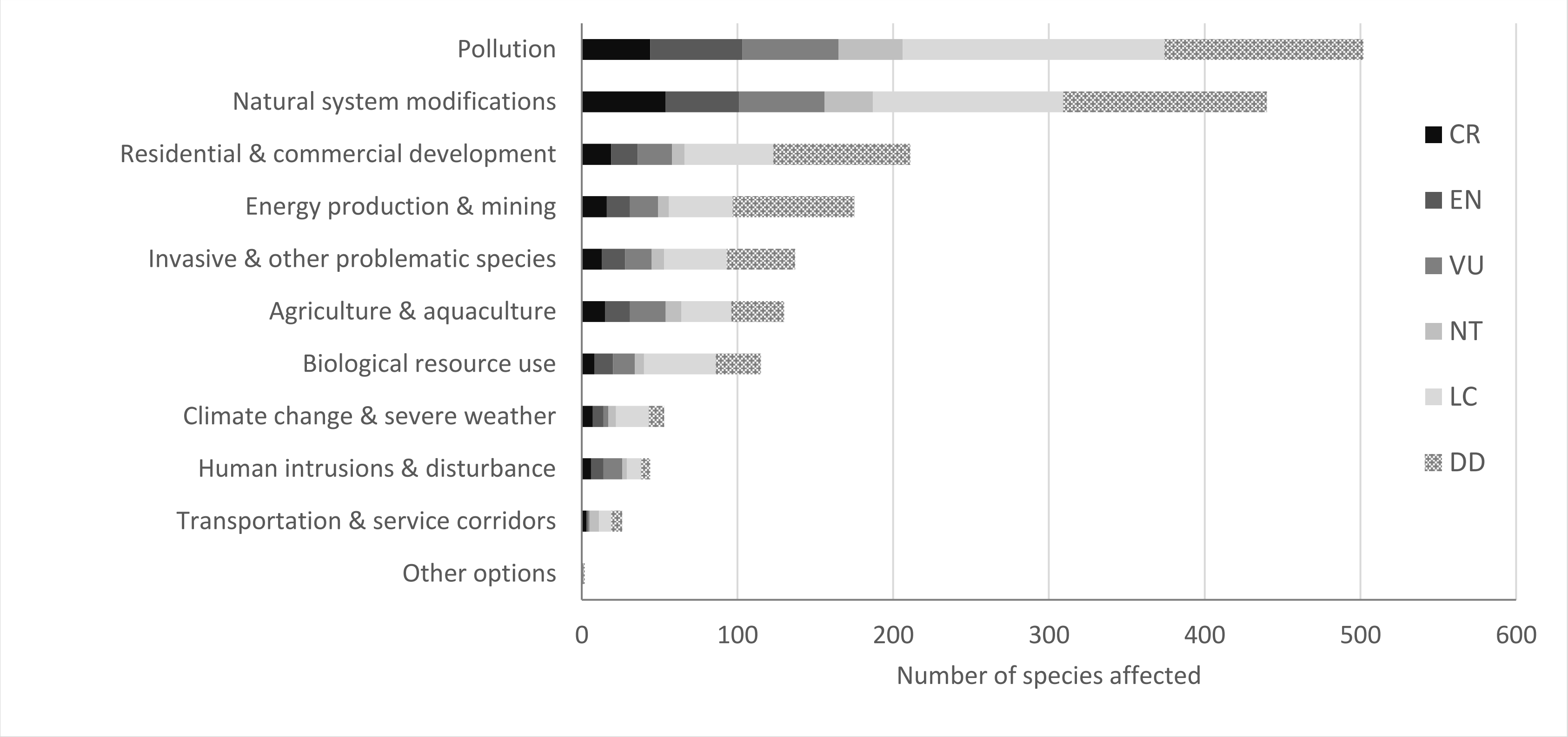


Figure 2.

A.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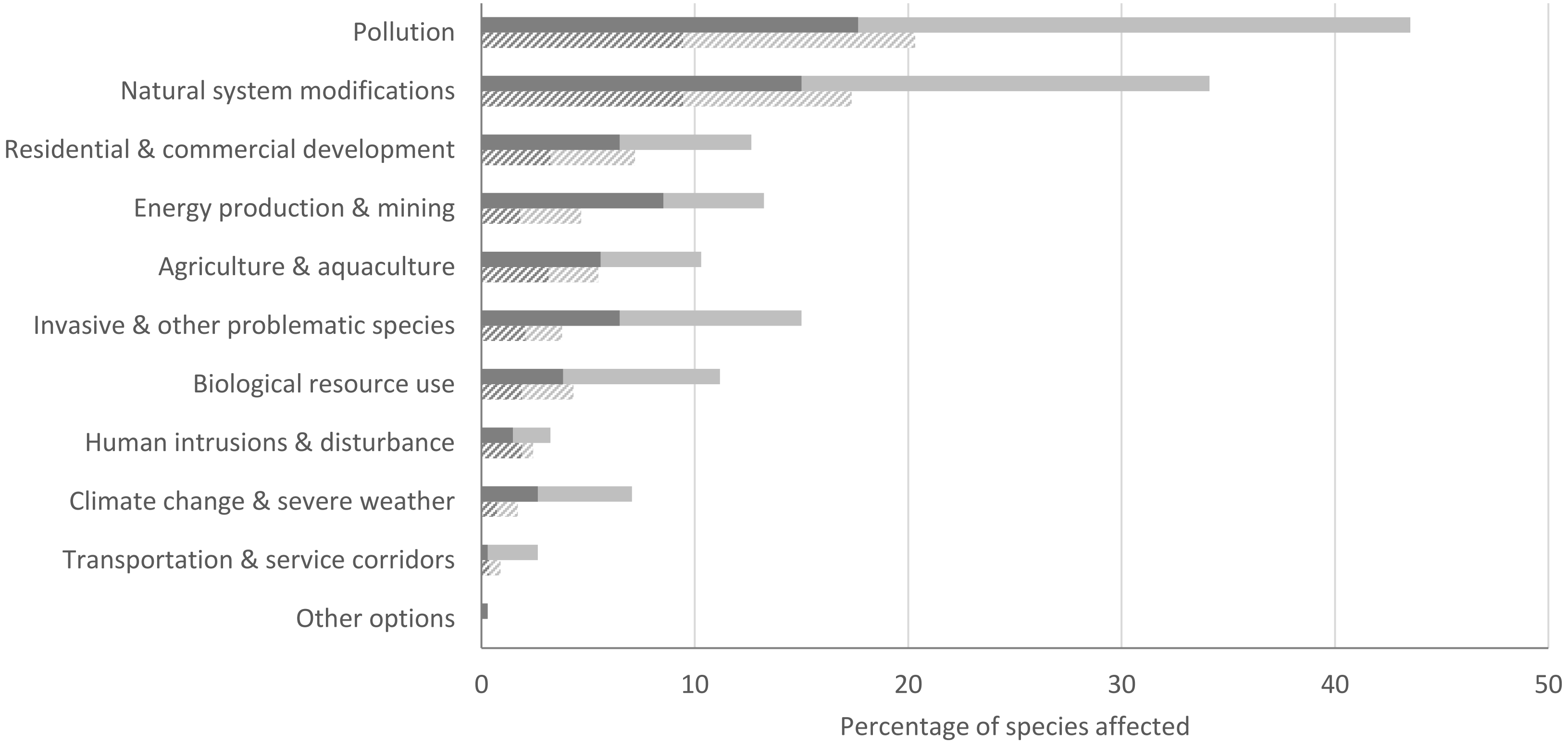
Natural system modifications
Residential & commercial development
Energy production & mining
Invasive & other problematic species
Agriculture & aquaculture
Biological resource use
Climate change & severe weather
Human intrusions & disturbance
Transportation & service corridors
Other options
0
100
200
300
400
500
600
Number of species affected
CR
EN
VU
NT
LC
DD

B


Pollution
Natural system modifications
Residential & commercial development
Energy production & mining
Agriculture & aquaculture
Invasive & other problematic species
Biological resource use
Human intrusions & disturbance
Climate change & severe weather
Transportation & service corridors
Other options
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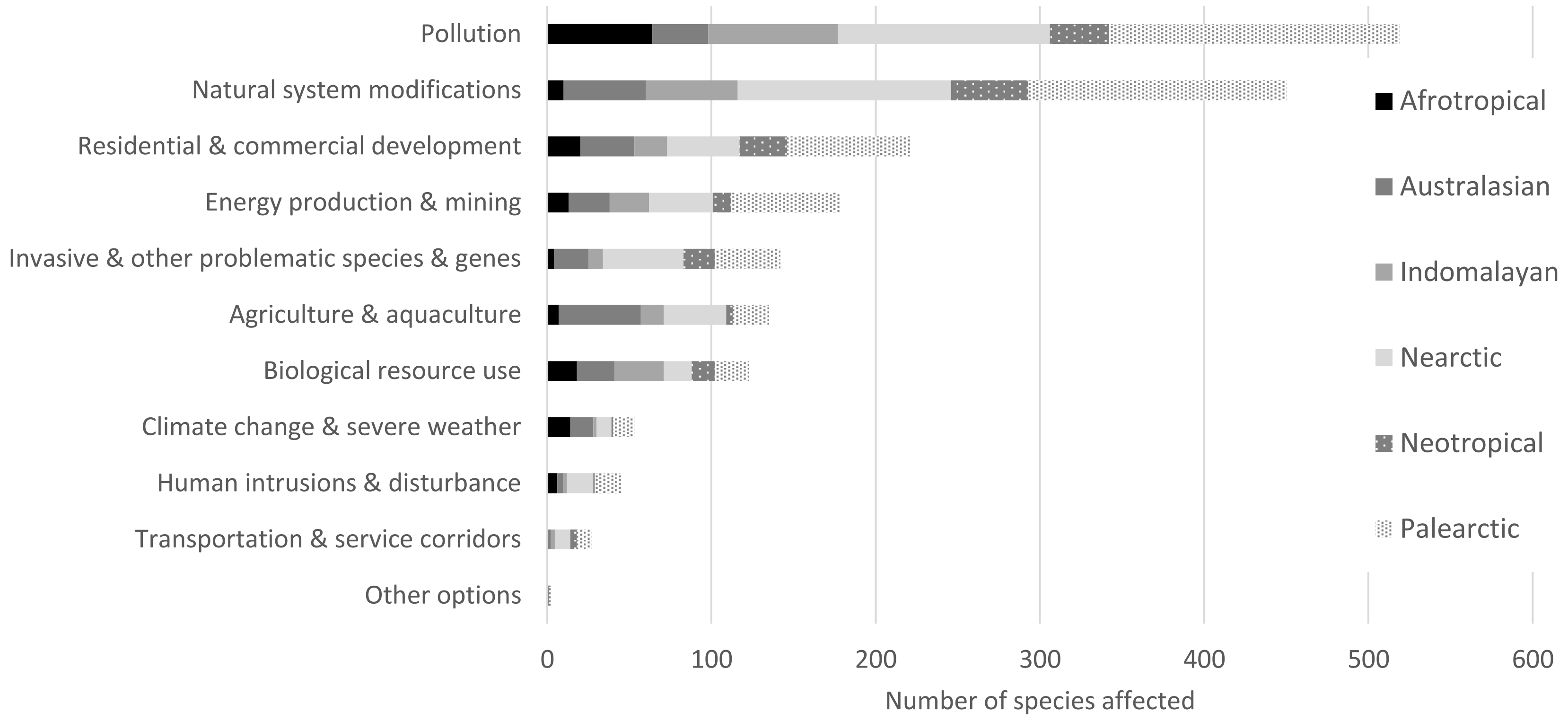
40
50
Percentage of species affected

C


Pollution
Natural system modifications
Residential & commercial development
Energy production & mining
Invasive & other problematic species & genes
Agriculture & aquaculture
Biological resource use
Climate change & severe weather
Human intrusions & disturbance
Transportation & service corridors
Other options
0
100
200
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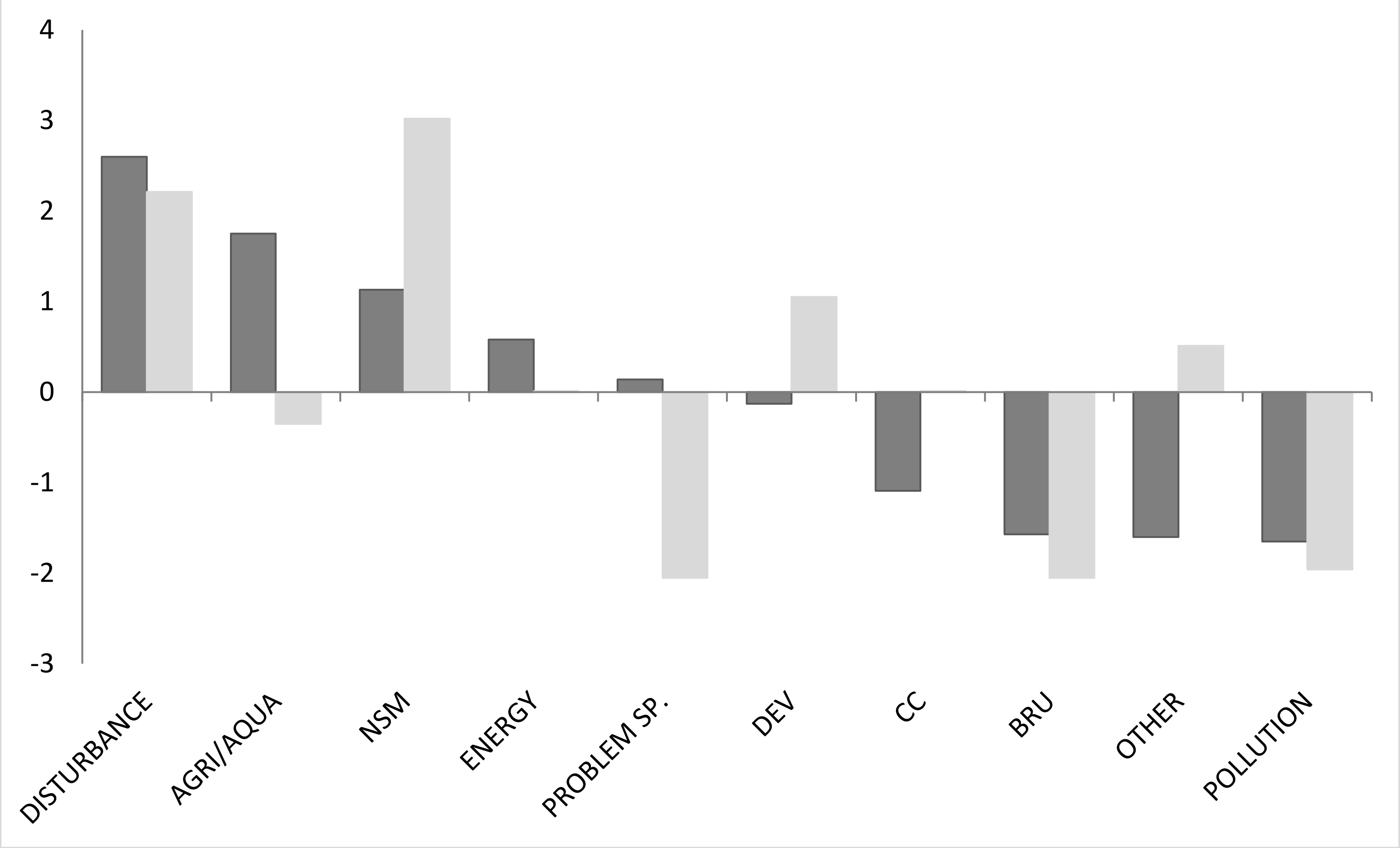
400
500
600
Number of species affected
Afrotropical
Australasian
Indomalayan
Nearctic
Neotropical
Palearctic

Figure 3.


4
3
2
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-3
DISTURBANCE
AGRI/AQUA
NSM
ENERGY
PROBLEM SP.
DEV
CC
BRU
OTHER
POLLUTION

Figure 4.