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The conservation status of the world's freshwater molluscs

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Received: 17 May 2020/Revised: 7 August 2020/Accepted: 10 August 2020
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Abstract With the biodiversity crisis continuing unchecked, we need to establish levels and drivers of

extinction risk, and reassessments over time, to effectively allocate conservation resources and track progress towards global conservation targets. Given that threat appears particularly high in freshwaters, we assessed the extinction risk of 1428 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

Guest editors: Manuel P. M. Lopes-Lima, Nicoletta Riccardi, Maria Urbanska & Ronaldo G. Sousa / Biology and Conservation of Freshwater Molluscs

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10750-020-04385-w>) contains supplementary material, which is available to authorised users.

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Nearctic, Palearctic and Australasia and among gastropods. Threat levels were higher in lotic than lentic systems. Pollution (chemical and physical) 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, apart from crayfish, new additional conservation priority areas emerged from our study. We discuss the implications of our findings for freshwater mollusc conservation, the adequacy of a sampled approach and important next steps to estimate trends in freshwater mollusc extinction risk over time.

Keywords IUCN Red List · Extinction risk · SRLI · Bivalves · Gastropods · Congruence

Introduction

With the biodiversity crisis continuing unchecked (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. Many studies have described

threat patterns of various species groups using the IUCN Red List of Threatened Species, which describes extinction risk, threats, and recommended conservation action: for example, 25% of mammal species (Schipper et al., 2008), 42% of amphibians (Stuart et al., 2004), 32% of freshwater crabs (Cumberlidge et al., 2009) and 32% of crayfish (Richman et al., 2015) are threatened with extinction. In addition, the IUCN Red List Index (RLI; Butchart et al., 2004), a biodiversity indicator, has been used to monitor changes in extinction risk over time 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]).

The Sampled Red List Index (SRLI) is a derivative of the RLI and provides a sampling strategy from which to derive—over time—broadly representative trends in extinction risk of species across highly species-rich groups (Baillie et al., 2008). For the SRLI, a random sample of 1500 species from a given taxon group is assessed using the IUCN Red List Categories and Criteria (IUCN, 2012); this sample size was found sufficiently large to accurately report on trends in extinction risk while also buffering against up to 40% of data deficiency in the sample (Baillie et al., 2008). Assessments for the SRLI have already been carried

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out for dragonflies (Clausnitzer et al., 2009), reptiles (Böhm et al., 2013) and plants (Brummitt et al., 2015) and have acted as catalysts for increased conservation attention being afforded to these species groups (e.g. Tingley et al., 2016).

Freshwater ecosystems are under extensive pressure from anthropogenic threats (Darwall et al., 2018). Freshwaters constitute < 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). 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 have been estimated at risk of extinction worldwide (Collen et al., 2014), with habitat loss being the most commonly cited threat. Increasing human pressures occur in many freshwater 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 (Dudgeon et al., 2006; Darwall et al., 2009) and fragmentation can have profound effects on water flows, sedimentation, habitat loss and hence species loss (Revenge et al., 2005).

Compared to other, especially terrestrial taxa, freshwater molluscs are understudied and often not

represented in conservation planning, despite comparatively high levels of extinction (e.g. Régnier et al., 2015). Freshwater molluscs represent one of the most diverse groups of freshwater organisms. More than 6000 valid species of freshwater molluscs are accepted (MolluscaBase, 2020); most are gastropods (almost 4800 species; MolluscaBase, 2020), while bivalves account for more than 1200 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 (Howard & Cuffey, 2006; Brown & Lydeard, 2010; Vaughn, 2018). Shells and soft tissues of freshwater mussels have been used to monitor environmental conditions (Schöne et al., 2004; Newton and Cope, 2007), and suspension feeding by molluscs removes particles from the water and increases water quality with resulting benefits to recreation and aesthetics (Vaughn, 2018). They also provide an ample food source for other species, including humans (Vaughn, 2018).

Freshwater molluscs are considered to be highly threatened as a group: for example, in 2000, 202 of nearly 300 unionid species from the USA and Canada were listed as either extinct, possibly extinct, or critical (critically imperilled, imperilled, vulnerable;

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Master et al., 2000; Lydeard et al., 2004). In addition, 67 of 703 US and Canadian gastropod species were considered extinct (Johnson et al., 2013), primarily due to the effects of damming and river channelisation. Within Europe, 44% of freshwater molluscs are 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 (Régner et al., 2009, 2015; Cowie et al., 2017). Such levels of threat mirror the general decline and threat in freshwater ecosystems (Collen et al., 2014).

Here, we report on the levels and drivers of threat in a random representative sample of 1428 freshwater molluscs from across the globe, which was assessed as part of the SRLI project (Baillie et al., 2008). This number constitutes around a quarter of valid species in this group. We estimate extinction risk within our sample for molluscan orders/families; assess predominant threats impacting freshwater molluscs; 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 detect trends in extinction risk over time.

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Materials and methods

The Red List assessment process

Baillie et al. (2008) showed that a random sample of 900 non-Data Deficient species (non-DD) is sufficiently large to accurately report on trends in extinction risk. However, to account for potentially high levels of data deficiency within random samples of taxon groups, they recommended 1500 species for the sampled Red List approach, which allows for data deficiency of up to 40% (Baillie et al., 2008). We followed this approach and selected at random 1500 species from a list of all described freshwater mollusc species (provided by the 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 1160 (77%) gastropod and 340 (23%) bivalve species, thus closely reflecting the contribution of both groups towards total freshwater mollusc diversity (Bogan, 2008; Strong et al., 2008). Recent taxonomic work meant that 13 species were synonymised with species already included in the sample, and were replaced with new species randomly drawn from the species list (bivalves replacing bivalves, gastropods replacing gastropods). Of these 13 replacement species, seven had already been assessed on the IUCN Red List; these were

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included in this study, while the remaining six replacements are currently listed as Not Evaluated (NE). Finally, 65 species were found to inhabit brackish or marine systems, or to be otherwise not fully freshwater, and these were subsequently removed from analysis. Our final sample still met the threshold of 900 non-DD species.

Overall, 371 of the 1428 selected species were assessed as part of IUCN regional assessment projects, specifically Europe (Cuttelod et al., 2011), Pan-Africa (Darwall et al., 2009), Eastern Himalayas (Allen et al., 2010), Western Ghats (Molur et al., 2011) and Indo-Burma (Köhler et al., 2012). For the remaining 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. Assessments followed the IUCN Red List Categories and Criteria which evaluate species against five Red List criteria relating to extinction risk (IUCN, 2012): population reduction (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); probability of extinction (Criterion E). Extinction risk categories range

from 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 reassessed from previous assessments, while all others represented first-time assessments of species. Since these assessments, 86 species have been reassessed and 28 non-genuine changes in status (changes in species status due to increased knowledge and new information rather than an actual change in population or distribution due to an emerging threat; IUCN, 2012) have been incorporated into our results. All species assessments have been reviewed by the IUCN and were published online in 2012 and 2013 (IUCN, 2019), except for one species of bivalve, *Arcidopsis footei* (Theobald 1876), drafted as Endangered.

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Summarising extinction risk

We summarised extinction risk across the full sample 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 (Clausnitzer et al., 2009; Böhm et al., 2013; Richman et al., 2015), we estimated extinction risk in our sample as the proportion of threatened species (CR, EN, VU), assuming that Data Deficient species will fall into threatened categories in the same proportion as non-DD 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: $\text{Prop}_{\text{threat_lower}} = (\text{CR} + \text{EN} + \text{VU}) / (\text{N} - \text{EX})$], and (b) all Data Deficient species were threatened [upper margin: $\text{Prop}_{\text{threat_upper}} = (\text{CR} + \text{EN} + \text{VU} + \text{DD}) / (\text{N}$

– EX)]. Note 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 was devised to accurately detect trend direction of the RLI over time, and not to reflect threat status for a species group overall at a 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 S2). This included recording the timing of the threat (ongoing; past, unlikely to return; past, likely to return; future; unknown). Most threats (85%) were recorded as ongoing threats, and we focus on these ongoing threats in the following analyses. However, we present a breakdown of future threats in the Supplementary Materials (8% of recorded threats; Figure S12). We summarised the number of species affected (across the sample and by biogeographic region) by broadest hierarchical level of the IUCN Threat Classification Scheme (Salafsky et al., 2008): residential and commercial development; agriculture and aquaculture; energy production and mining; transportation and service corridors;

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biological resource use; human intrusion and disturbance; natural system modification (includes dams and abstraction of surface or ground water); invasive and other problematic species; pollution (includes domestic waste water, industrial and agricultural effluents, garbage and solid waste); geological events; and climate change and severe weather (Table S2). 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 ran this analysis on all 511 threatened and non-threatened species which were affected by one or more ongoing threat processes (the remainder of species does not have any threats, or the threats are unknown, or are past or future threats, or species are DD) and permuted the tables 1000 times.

Spatial patterns of freshwater molluscs and congruence with other species groups

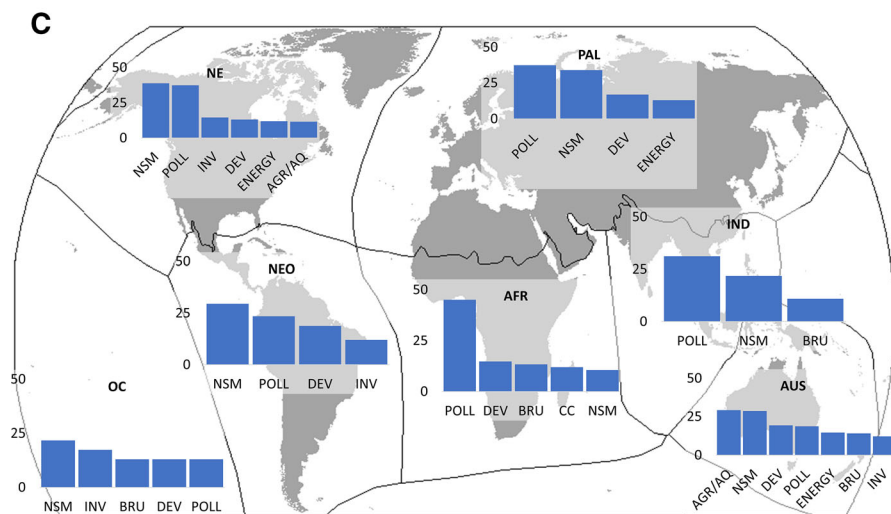
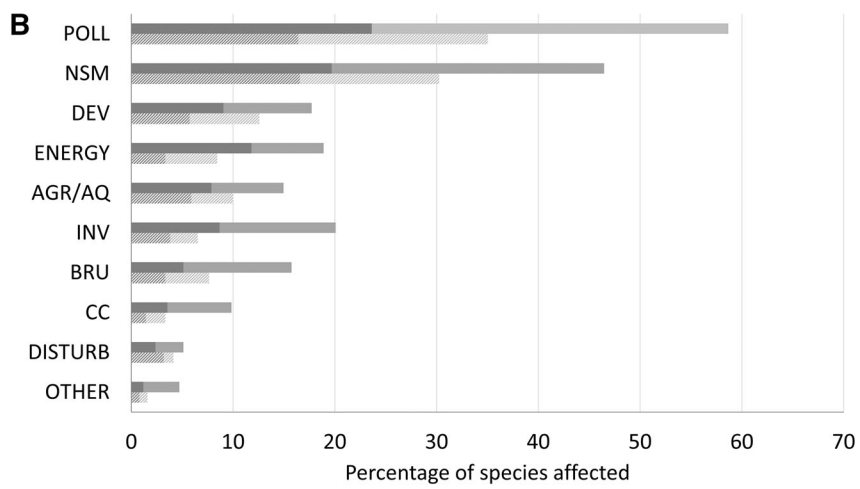
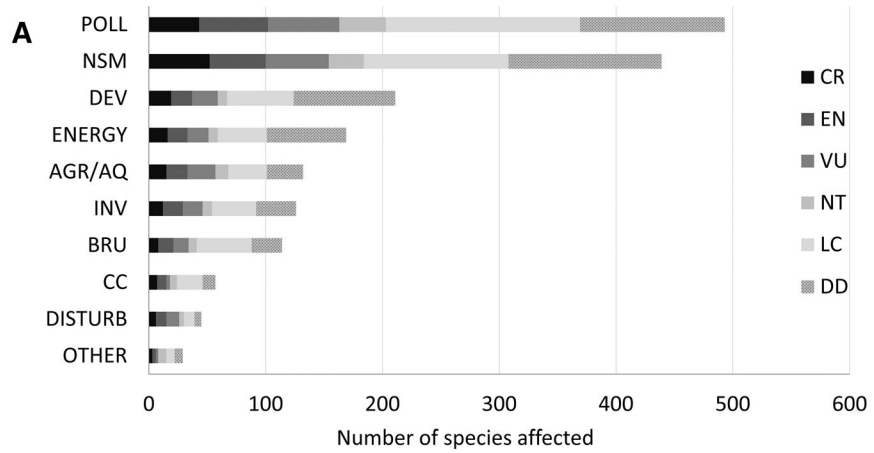
During IUCN Red List assessment, the countries in which a species is native, introduced, reintroduced, vagrant ('origin' codes), and extant, possibly extant, possibly extinct, extinct or has an uncertain presence ('presence' codes) are entered into the Red List database (for IUCN's 'seasonality' codes, we assumed species were resident within each recorded country). From this, we summarised the number of species native to a country in our sample.

Species distribution was also mapped—where possible—for all assessed species. Given that some species have very poor data, we were unable to map several Data Deficient species. For subsequent analysis, we selected only those parts of a species' distribution map where the species was considered extant or probably extant, resident, and native or reintroduced (RLTWG, 2018). 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 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 produced species richness maps for 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 taxa had no species present 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.

To build on previous work on spatial patterns of freshwater species richness (Collen et al., 2014), 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 for other freshwater species groups. First, we recalculated the richness patterns for six freshwater taxon groups (amphibians, crabs, crayfish, fish, mammals and reptiles) analysed by 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 freshwater taxon groups, we again generated spatial overlays of species richness patterns—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. 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 value for each taxon group, and summarising the number of taxon group hotspots overlapping in each grid cell. We acknowledge that hotspot patterns



◀ **Fig. 1** Number of species affected by different ongoing threat processes, showing **A** contribution of threat processes to Red List categories; **B** contribution of threats to non-threatened (light) and threatened species (dark) for bivalves ($n = 254$; solid bars) and gastropods ($n = 628$; hashed bars), as percentage of n (excluding DD and EX species); **C** predominant threats by biogeographical realm ($> 10\%$ of species affected), as % of species affected. Threats: *POLL* Domestic & urban waste, industrial effluent; *NSM* Natural system modification; *DEV* Residential and commercial development; *ENERGY* Energy production; *AGR/AQ* Agriculture and aquaculture; *INV* Invasive and other problematic species; *BRU* Biological resource use, mostly exploitation; *CC* Climate change; *DISTURB* Human intrusion and disturbance; *OTHER* Other threats, e.g. geological events, transportation & service corridors. Realms: *AFR* Afrotropical; *AUS* Australasian; *IND* Indomalayan; *NE* Nearctic; *NEO* Neotropical; *OC* Oceanian; *PAL* Palearctic

within our sample of freshwater molluscs is highly influenced by the random selection process; however, previous analyses have shown that broad-scale richness patterns derived from such species samples are largely representative of richness hotspot patterns obtained from comprehensive mapping of entire species groups (B. Collen, unpublished data).

Results

Extinction risk in freshwater molluscs

Nearly one-third of species in our final sample of 1428 freshwater molluscs were estimated to be threatened ($\text{prop}_{\text{threat}} = 0.31$; lower = 0.19, upper = 0.56; Table 1), with 520 Data Deficient species (36.4%) and 908 species non-Data Deficient. Estimated 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 = 0.64; Australasia: $\text{prop}_{\text{threat}} = 0.34$, lower = 0.26, upper = 0.50; Table 1). Data deficiency was highest in the Neotropics (50.3% of species), Indomalaya (48.6% of species), Palearctic (45.1% of species) and Oceania (43.5% of species). Estimated threat levels were higher in lotic than lentic systems (lotic: $\text{prop}_{\text{threat}} = 0.31$, lower = 0.22, upper = 0.50; lentic: $\text{prop}_{\text{threat}} = 0.18$, lower = 0.13, upper = 0.45).

Gastropods were more threatened ($\text{prop}_{\text{threat}} = 0.33$; lower = 0.19, upper = 0.61) than bivalves ($\text{prop}_{\text{threat}} = 0.26$; lower = 0.20, upper = 0.42; Table 1). Threat and data deficiency levels varied

Table 1 Extinction risk in a random sample of 1428 freshwater molluscs by class, biogeographic realm and habitat system (lentic versus lotic)

Taxon	DD	LC	NT	VU	EN	CR	EX	n	n non-DD	Prop. threatened	Lower prop	Upper prop
All	520	545	66	115	76	80	26	1428	908	0.307	0.193	0.564
Bivalves	74	173	16	19	27	19	7	335	261	0.256	0.198	0.424
Gastropods	446	372	50	96	49	61	19	1093	647	0.328	0.192	0.607
Realm												
Afrotropical	39	67	10	7	13	6	0	142	103	0.252	0.183	0.458
Australasian	41	79	5	24	7	13	2	171	130	0.344	0.260	0.503
Indomalayan	120	105	9	6	4	3	0	247	127	0.102	0.053	0.538
Nearctic	49	147	23	31	30	33	22	335	286	0.356	0.300	0.457
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
Palaeartic	206	143	19	40	24	23	2	457	251	0.349	0.191	0.644
Habitat system												
Lentic	180	294	16	30	22	18	0	560	380	0.184	0.125	0.446
Lotic	300	465	61	99	64	68	14	1071	771	0.305	0.219	0.502

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

greatly amongst families (Table 2): for example, the bivalve family Unionidae had the most species in our sample ($n = 190$), with 33% estimated threatened (bounds: 29–42%) and a relatively low level of data deficiency (12% of species in the family). Planorbidae ($n = 155$) had only 3% of species threatened (bounds: 1–54%), yet 52% of species listed as DD, and Hydrobiidae ($n = 145$) had 69% of species threatened (bounds: 48–79%) and around a third of species listed as DD. Margaritiferidae is 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 were the Moitessieriidae ($n = 33$, $\text{prop}_{\text{threat}} = 0.68$; lower = 0.52, upper = 0.76), 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 ($n = 91$, $\text{prop}_{\text{threat}} = 0.50$; lower = 0.43, upper = 0.57).

Overall, 26 species were assessed as Extinct, seven bivalves and 19 gastropods. Just over one-fifth of species in our sample belonging to the gastropod family Pleuroceridae were categorised as Extinct. The number of extinct species was highest in the Nearctic realm ($n = 22$) and in lotic systems ($n = 14$). Twenty species currently listed as CR are possibly extinct (17 gastropods, seven of which belong to Hydrobiidae, and three unionid bivalves).

Most threatened species (61%) were classified based on criterion B (geographic range size and decline), followed by criterion D2 (very restricted range: 28% of threatened species) and criterion A (population reduction: 15% of threatened species). Only one species each was threatened based on criteria C (small population size and reduction) and criterion D/D1 (very small population size).

Predominant threat processes affecting freshwater molluscs

Overall, ongoing threats were reported for 726 species (including DD) in our sample, with most species having one or two ongoing threats recorded (Figure S13). Pollution and natural system modification were the most frequently recorded ongoing threats affecting freshwater molluscs (Fig. 1A), both when considering all species (27% and 24% of documented

threats, respectively), threatened species only (26% and 25%), and bivalves (27% and 22%) and gastropods (27% and 25%; Fig. 1B). 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 (Fig. 1A).

Pollution was the most cited threat in the Afrotropics and Indomalaya, with natural system modification the predominant threat in Australasia (together with threats from agriculture/aquaculture) and the Neotropics. In the Palearctic and Nearctic, both pollution and natural system modification were the predominant threats (Fig. 1C).

The distribution of threats between threatened and non-threatened Red List categories was borderline random ($\chi^2 = 20.67$, $P = 0.054$). 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 (Fig. 2). The distribution of threats between individual non-DD Red List categories (CR, EN, VU, NT, LC) was random (Chi-squared = 48.274, $P = 0.342$). 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 threat) (Table 3).

Spatial distribution of freshwater molluscs and congruence with other taxonomic groups

More than 20% of species in our sample occurred in the USA (328 species, 38 of them recorded as extinct or possibly extinct), followed by Russia (201 species; 13 with uncertain presence in the country), Australia (114 species) and Thailand (101 species; Table 4). Within the USA, normalised species richness in our sample was highest in the Eastern USA (Tennessee, Kentucky and surrounding states); elsewhere, normalised species richness showed additional hotspots in

Table 2 Extinction risk in a random sample of 1428 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)

	No. species in sample	No. threatened	No. DD	% DD	Prop. Thr.	Lower prop	Upper prop	No. EX
Class Gastropoda	1093	206	446	40.8	0.328	0.192	0.607	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	772	190	299	38.7	0.416	0.251	0.647	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	524	157	207	39.5	0.505	0.303	0.703	6
Amnicolidae	26	3	17	65.4	0.333	0.115	0.769	0
Assimineidae	22	4	12	54.5	0.400	0.182	0.727	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	146	68	45	30.8	0.687	0.472	0.785	2
Lithoglyphidae	28	2	19	67.9	0.250	0.074	0.778	1
Moitessieriidae	33	17	8	24.2	0.680	0.515	0.758	0
Pomatiopsidae	52	5	29	55.8	0.217	0.096	0.654	0
Tateidae	91	38	13	14.3	0.500	0.427	0.573	2
Order Sorbeoconcha	149	28	45	30.2	0.298	0.201	0.525	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	33	3	17	51.5	0.188	0.091	0.606	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
Chiliniidae	12	1	7	58.3	0.200	0.083	0.667	0
Lymnaeidae	53	5	15	28.3	0.135	0.096	0.385	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	335	65	74	22.1	0.256	0.198	0.424	7
Subclass Heterodonta	105	6	42	40.0	0.095	0.057	0.457	0
Order Venerida	103	6	42	40.8	0.098	0.058	0.466	0
Cyrenidae	22	1	13	59.1	0.111	0.045	0.636	0
Sphaeriidae	81	5	29	35.8	0.096	0.062	0.420	0

Table 2 continued

	No. species in sample	No. threatened	No. DD	% DD	Prop. Thr.	Lower prop	Upper prop	No. EX
Subclass	227	59	31	13.7	0.312	0.268	0.409	7
Palaeoheterodonta								
Hyriidae	12	1	4	33.3	0.125	0.083	0.417	0
Unionidae	190	53	23	12.1	0.331	0.290	0.415	7

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

our sample in Lake Baikal, parts of Central and Eastern Europe, and selected river systems in South-east Asia (Fig. 3A; see Figures S3-S11 in the Supplementary Materials for spatial detail of the distribution pattern in our sample by region, and Table S1 for a full list of species in our sample by country). 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). There was significant congruence in the spatial pattern of bivalve and gastropod species richness in our sample (corr = 0.693, $F = 72.58$, adjusted d.f. = 78.74, $P < 0.001$).

Data deficiency was highest in Lake Baikal (due to high DD richness of gastropods; Figure S1B) and Japan, and selected river systems in South and Southeast Asia (e.g. regions of the Brahmaputra and Irrawaddy rivers; Fig 3B). Threatened species richness in our sample was highest in the most species-rich states of the USA (primarily driven by bivalves), and the Southeastern Alps and Balkans in Europe (primarily driven by gastropods; Fig. 3C and Figures S1C and S2C). Overall, the spatial distribution of threatened gastropods and bivalves in our sample was significantly negatively correlated (corr = -0.161, $F = 7.19$, adjusted d.f. = 270.60, $P = 0.008$). Data deficiency for bivalves in our sample was highest in eastern Asia (Russia and Japan) and South America (Figure S2B), and this pattern was incongruent with the DD species richness pattern of gastropods in our sample (corr = 0.07, $F = 1.10$, adjusted d.f. = 202.33, $P = 0.295$). Bivalve and gastropod congruence maps are shown in Figure S14 in the Supplementary Materials.

Normalised species richness, DD species richness and threatened species richness of freshwater molluscs was positively and significantly correlated with the respective species richness of crayfish (species richness: corr = 0.52, $F = 28.73$, adjusted d.f. = 79.03, $P < 0.001$; DD species richness: corr = 0.19, $F = 25.92$, adjusted d.f. = 716.24, $P < 0.001$; threatened species richness: corr = 0.46, $F = 9.09$, adjusted d.f. = 33.97, $P = 0.005$). In addition, normalised species richness of sampled freshwater molluscs was positively and significantly correlated with that of freshwater reptile (corr = 0.33, $F = 13.44$, adjusted d.f. = 108.35, $P < 0.001$) and freshwater mammals (corr = 0.26, $F = 6.90$, adjusted d.f. = 95.53, $P = 0.010$; Table 5). There was significant positive congruence between threatened freshwater mollusc richness and threatened freshwater species richness (corr = 0.20, $F = 4.41$, adjusted d.f. = 103.20, $P = 0.038$; as estimated by Collen et al. (2014)), and negative congruence with freshwater crabs (corr = -0.05, $F = 5.42$, adjusted d.f. = 2375.5, $P = 0.020$; Table 5). Congruence between Data Deficient species richness was significantly positive between freshwater molluscs and freshwater fish (corr = 0.21, $F = 6.12$, adjusted d.f. = 131.04, $P = 0.015$), and all freshwater species (corr = 0.18, $F = 4.54$, adjusted d.f. = 133.35, $P = 0.035$; Table 5). All other species richness patterns were not spatially congruent with that for freshwater molluscs (Table 5). Congruence of 10% of richest hotspots for freshwater species is shown in Fig. 4 as the number of taxon groups overlapping.

Discussion

Here, we present the first global analysis of the extinction risk of freshwater molluscs by utilising an established method to assess a random sample of

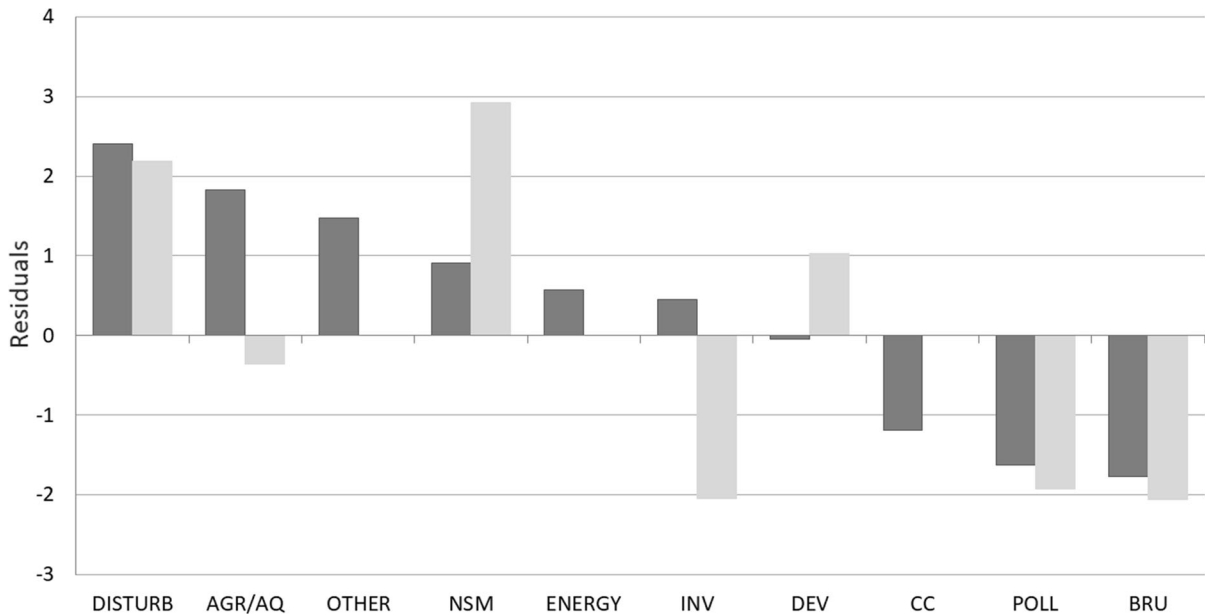


Fig. 2 Pearson's residuals from permutation-based Chi-square test of threat status (threatened versus non-threatened) by threat process, based on the full dataset of all non-DD species (dark grey) and non-DD species affected by a single threat process only (light grey). *AGR/AQ* agriculture and aquaculture; *BRU* biological resource use, mostly exploitation; *CC* climate

change; *DEV* residential and commercial development; *DISTURB* human intrusion and disturbance; *ENERGY* energy production; *INV* invasive and other problematic species; *NSM* natural system modification; *OTHER* other threats, e.g. geological events, transportation & service corridors; *POLL* domestic & urban waste, industrial effluent

freshwater mollusc species from around the world (Baillie et al., 2008). Our sample of 1428 species 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 taxonomic groups (Collen et al., 2014; McRae et al., 2017). Levels of threat for our sample of freshwater molluscs are comparable to those of freshwater crayfish and freshwater crabs (32%; Cumberlidge et al., 2009; Richman et al., 2015), 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 broadly distributed bivalves (median distribution size for gastropods in our sample was 26,863 km² compared to a median of 259,386 km² for bivalves; Figure S15). High gastropod threat levels have also been shown in regional analyses using the IUCN Red List Categories and Criteria, where gastropods, particularly “proso-branches”, 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, and negatively correlated with threat levels in bivalves which had the highest threat levels in North America. Some of the highly threatened gastropod families, such as the Tateidae, consist of small-sized 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%. Members of the Moitessieriidae, also highly threatened in our sample, are small snails, leading a mainly

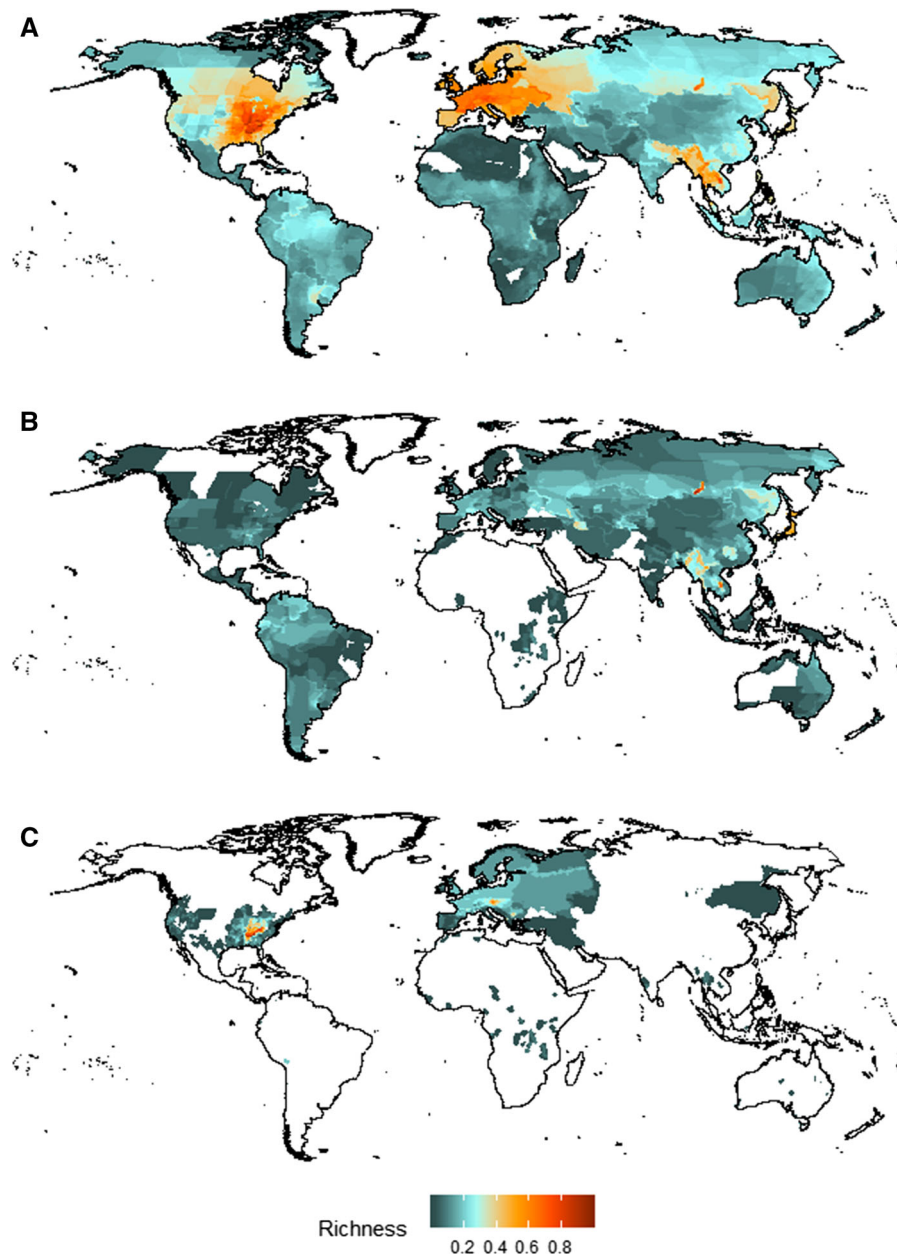


Fig. 3 **A** Species richness of the sampled assessment for freshwater molluscs ($n = 1384$ species of extant/probably extant, native or reintroduced species), showing normalised

species richness per grid cell; **B** Normalised species richness of Data Deficient (DD) species ($n = 503$); **C** Normalised threatened species richness (CR, EN, VU; $n = 271$)

subterranean lifestyle, with patchy and restricted distributions and often known from few or only single localities; some may be under-sampled given the challenge to collect and detect these subterranean species (Wilke, 2019), though data deficiency in our

sample was again relatively low (24%) compared to other families.

Lower overall threat of freshwater bivalves is primarily due to the relatively low estimated threat levels in the bivalve family Sphaeriidae, a family of

Table 3 Pearson's residuals of all threats per IUCN Red List category, from permutation-based Chi-square test

Threat	THR			NON-THR	
	CR	EN	VU	NT	LC
AGR/AQ	0.25	0.44	1.74	0.31	-2.03
BRU	-1.38	-0.40	-0.68	-0.66	2.20
CC	0.24	0.21	-1.99	0.70	0.78
ENERGY	0.55	0.16	0.10	-0.73	-0.14
DISTURB	0.25	1.17	1.80	0.05	-2.46
INV	-0.28	0.59	0.27	-0.43	-0.19
NSM	1.65	-0.38	0.05	-0.17	-0.81
POLL	-1.56	-0.18	-0.55	0.64	1.26
DEV	0.44	-0.56	0.09	-1.39	0.88
OTHER	0.13	-0.77	-1.48	3.76	-0.66

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). *AGR/AQ* agriculture and aquaculture; *BRU* biological resource use, mostly exploitation; *CC* climate change; *ENERGY* energy production; *DISTURB* human intrusion and disturbance; *INV* invasive and other problematic species; *NSM* natural system modification; *POLL* domestic & urban waste, industrial effluent; *DEV* residential and commercial development; *OTHER* other threats, e.g. geological events, transportation & service corridors

Table 4 Top ten countries with most native species in our random sample of 1428 freshwater molluscs, by IUCN presence code (full table available in the Supplementary Materials)

Country	Extant	Extinct/possibly extinct	Presence uncertain	No. species*
United States	288	38	2	328
Russian Federation	188	0	13	201
Australia	111	1	2	114
Thailand	94	0	7	101
France	83	1	4	88
India	76	0	4	80
Canada	68	2	7	77
China	65	0	5	70
Austria	65	2	1	68
Congo (DRC)	60	3	1	64

*Includes extant, extinct and uncertain presence codes

almost cosmopolitan and widespread species with very few threats reported. However, these small bivalves have attracted much less research attention by conservationists than the larger unionids, thus 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

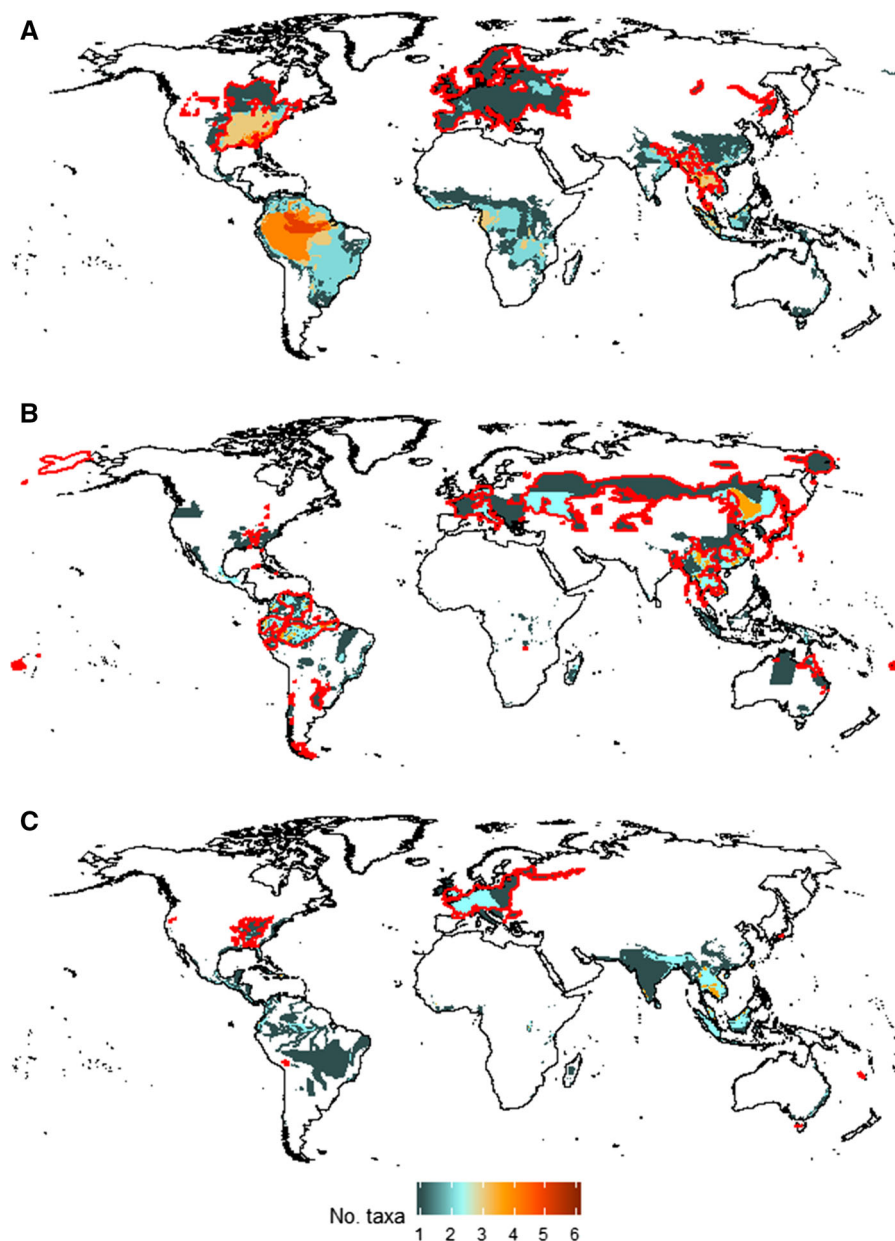


Fig. 4 Congruence of 10% of richest hotspots for freshwater species: **A** species richness hotspots; **B** Data Deficient richness hotspots; **C** threatened species richness hotspots. Congruence is shown by overlap of hotspots for seven different freshwater

taxonomic groups: amphibians, crabs, crayfish, fish, mammals, reptiles (based on Collen et al., 2014) and molluscs (this analysis). Red polygon outline delineates 10% freshwater mollusc hotspot area

species into our estimate, our results suggest that 34% of freshwater bivalve species are threatened or extinct (lower estimate: 26%; upper estimate: 48%). In addition, using alternative assessment processes, such as the one employed by the American Fisheries

Society, nearly 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 also be missing for many large bivalve species, which are often long-

Table 5 Spatial congruence between geographical ranges of freshwater molluscs and other freshwater taxa

Richness metric	Amphibians	Crabs	Crayfish	Fish	Mammals	Reptiles	All freshwater ¹
SR							
Corr	0.07	− 0.02	0.52***	0.15	0.26*	0.33***	0.15
<i>F</i>	0.34	0.04	28.73	1.47	6.90	13.44	1.41
d.f.	61.26	60.02	79.03	62.32	95.53	108.35	60.20
THR							
Corr	− 0.04	− 0.05*	0.46**	− 0.04	0.04	− 0.06	0.20*
<i>F</i>	1.70	5.42	9.09	1.27	1.28	1.44	4.41
d.f.	1083.6	2375.5	33.97	787.2	683.8	342.79	103.20
DD							
Corr	0.02	0.11	0.19***	0.21*	0.06	− 0.02	0.18*
<i>F</i>	0.23	3.20	25.92	6.12	0.28	0.78	4.54
d.f.	393.74	244.85	716.24	131.04	82.03	1712.3	133.35

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: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$)

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

lived (Vaughn & Taylor, 2001) and therefore requiring 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).

High levels of threat in freshwater species are expected in a system that is impacted by many different threats, especially given the high interconnectivity of freshwater systems. 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 habitat loss and degradation (which includes urban development and dam building), pollution and overexploitation to be the three most frequently reported threats. Interestingly, a recent analysis using an alternative dataset on vertebrate freshwater species trends, the Living Planet database (McRae et al., 2017), has shown natural system modifications (24.1%), agriculture and aquaculture (16.4%) and pollution (15.2%) as the most important threats (Thorburn, 2017). Assessing the predominant drivers of extinction risk and population decline is a complex task, given that species may be impacted by multiple, often synergistic threats, drivers of decline may vary from region to region (Fig. 1C) and that species experts may differ in their perception of the importance of different threat processes to species

decline or in their recording of drivers according to the IUCN Threat Classification Scheme (e.g. sedimentation is coded under pollution, but may be caused by logging of forest, which constitutes biological resource use). In a centrally led project, inconsistencies can be minimised through a rigorous review process and justification of identified threats.

In our present analysis, pollution and natural system modification were the most common threats affecting freshwater molluscs globally, ranking in the top two most prevalent threats in all biogeographical realms bar the Afrotropics, and natural system modification specifically was associated more than expected with CR listings. Establishment of dams and other barriers presents a major 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), and dams may block migratory routes for fish (Maceda-Veiga, 2013). Movement of fish hosts is vital for connectivity of mussel populations and metapopulation dynamics (Zajac et al., 2018). It has been shown that mussel species richness and abundance is reduced closer to river impoundments, suggesting an extinction risk gradient downstream of these structures (Vaughn & Taylor, 2001). Local extirpation 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 extirpation rates due to river fragmentation (Vaughn, 2012). 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). Some of these factors are likely behind the observed higher threat levels in lotic versus lentic system, a finding corroborated in other studies (Clausnitzer et al., 2009; Collen et al., 2014). 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).

Freshwater molluscs are among the most sensitive freshwater species to several chemicals, particularly as juveniles (Wang et al., 2017). While pollution was associated more than expected with lower threat categories of NT and LC globally, it was the most commonly cited threat in the Afrotropics and Indomalaya. For example, pollution in form of agricultural run-off (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., 2018a). Therefore, regional threat analyses are vital to highlight regional differences in predominant threats, and to put in place regional action plans to combat threats in a meaningful and targeted way. We may still be underestimating the impact of pollution 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).

Global change and trade globalisation have spurred an increase in bioinvasions and their subsequent impacts on ecosystems (Darrigran & Damborenea, 2011; 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), is a vital step to identify hotspots for conservation action.

Climate change is likely to have an impact on freshwater molluscs, yet this was not reflected in our analysis. Climate change is often not highlighted in

IUCN Red List assessments as an ongoing threat, given the Red List's focus on immediate impacts on species over relatively short timeframes, depending on the generation length of the species in question (Trull et al., 2017; IUCN Standards and Petitions Committee, 2019). However, our knowledge gap on climate change impacts on freshwater molluscs has started to be filled with climate change vulnerability analyses, e.g. following Young et al. (2011) and Foden & Young (2016), and other research activities. With a reassessment of the SRLI for freshwater molluscs about to commence, we envisage that we will see the threat from climate change increase in our assessments, given some of the recent work on climate change impacts on freshwater species identifying range contractions and shifts (e.g. Markovic et al., 2014; Gallardo et al., 2018). Already, climate change is the joint most frequently recorded future threat to our freshwater molluscs, together with natural system modification and pollution (Figure S12).

Incongruence between spatial patterns of freshwater mollusc species richness in comparison to other taxonomic groups, with the exception of crayfish which have hotspots in North America and Europe (Richman et al., 2015), 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) and its evolutionary history. Therefore, conservation priority areas are likely to vary, depending on the focal species group. High aquatic species richness in parts of North America and Southeast Asia reflect known hotspots of freshwater molluscs (e.g. Lydeard & Mayden, 1995; Zieritz et al., 2018a). High species richness in our sample in parts of Europe is likely a reflection of a larger number of taxonomists working there, 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, reflects understudied species groups where threats have not yet been adequately reported. Central America is also a vastly understudied region demonstrated by the fact that no native bivalves and only a dozen gastropod species found in the area are included here. In addition, recently completed assessment work in West Africa is showing that the situation for freshwater molluscs is rapidly deteriorating, primarily due to conversion of wetlands for food production (D. van Damme, pers.

comm.). These new findings will be integrated into our upcoming reassessment of the SRLI species set.

East Asia also harboured hotspots of freshwater molluscs in our sample, specifically for gastropod species richness and Data Deficient bivalves, which did not emerge during previous study of spatial patterns of freshwater richness and threat (Collen et al., 2014). Recent molecular studies have unearthed the presence of morphologically cryptic species which have increased species richness in the area (Zieritz et al., 2018a). Despite a recent increase in research attention on diversity, biogeography, evolution and—most recently—conservation of freshwater molluscs in the region (e.g. Saito et al., 2018; Zieritz et al., 2018a, Huang et al., 2019; Bolotov et al., 2020b; Lopes-Lima et al., 2020), primary sources on species distributions and biogeography in many countries are still outdated (Zieritz et al., 2018a). Future reassessments of our species sample are likely to see decreasing levels of data deficiency in this and other regions, while it is likely that the taxonomy of our sample will undergo additional changes as molecular studies and field surveys are carried out. New species hotspots are gradually emerging with increased molecular study, e.g. Honshu, Kyushu and Hokkaido in Japan and the Korean peninsula in East Asia (Lopes-Lima et al., 2020), and it is vital that protective measures are put in place to not repeat the fate of the better-studied freshwater mollusc fauna of Europe and North America.

Data Deficiency

High levels of data deficiency preclude our ability to adequately represent species groups in conservation action plans and prioritisation schemes. Data deficiency in freshwater molluscs (36%) was greater than in 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 leave the species status of many freshwater molluscan taxa in dispute; 3) lack of

monitoring of abundance and status of freshwater molluscan populations, especially in hotspots of freshwater biodiversity in developing countries. Many nominal species of freshwater molluscs have not been studied (or even recorded) since their taxonomic description. 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 changed species richness estimates (e.g. Osikowski et al., 2018; Bolotov et al., 2020a; Lopes-Lima et al., 2020), and conservation status of individual species. For example, there has been an increase in the numbers of new species with often restricted ranges, e.g. in Southeast Asian Unionids (Bolotov et al., 2020b). 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 may be used to assess the most likely threat status of Data Deficient species within our sample, and have been carried out for other species groups (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, 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). Given the nature of a random sample, it will also omit some smaller families, here for example the Mycetopodidae. Throughout the project, species had to be replaced due to synonymy; future taxonomic revisions are likely to lead to more replacements, and we have to ensure that we use up-to-date species lists to draw replacements from. In addition, we will also replace those species excluded from the current assessment because they were not fully freshwater, to regain a sample size of 1500 species. Twenty-seven of the 74 excluded species were assessed as DD, 39 as LC and one as CR; several of these species were from the Caspian Sea region, for which latest data suggest deteriorations in status for many species (Wesselingh et al., 2019). It is therefore also important that brackish or other semi-freshwater species do not fall through the cracks of conservation.

Spatially, our random sample highlights hotspots of freshwater mollusc richness in the Southeastern USA and across parts of Europe; however, given the random species selection and relatively small sample size compared to the total richness of freshwater molluscs, it is unlikely to accurately highlight regional detail. For example, threatened hotspots previously highlighted in other, regional assessments, such as for example the Anatolian hotspot identified during a Mediterranean assessment (Smith et al., 2008) are not captured in our sampled assessment, while the Alps and Balkan hotspots for threatened species in Europe (Cuttelod et al., 2011) only just show up on our maps. In addition, the low congruence of spatial patterns of hotspots with those for other freshwater species groups (e.g. fish) may be a reflection of the sampled approach, especially as the fish pattern itself is also derived from a sampled approach (Collen et al., 2014). As the number of comprehensively assessed species groups is increasing on the IUCN Red List, we need to test how richness patterns obtained from sampled assessments compare to global richness patterns of comprehensive groups, at which spatial scale they may be adequately depicting spatial conservation status, or how large samples would have to be to provide an adequate reflection.

Apart from spatial bias, 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. These shortcomings are to be expected 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. Thus, we cannot make any conclusions from our sample on overall level of threat within this species group, although work is ongoing to test the accuracy of sampled status estimates. This is important since we do not have the resources to run comprehensive assessments for all species groups, especially highly species-rich ones; for example, a recent study shows that 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). This will be tested with the upcoming reassessment of freshwater molluscs in the coming years.

The future of freshwater molluscs

Freshwater molluscs provide invaluable functions 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, which depend on them, given the manifold threats impacting these fragile systems. While this sampled global assessment gives an overview of issues impacting freshwater molluscs across the globe and at the broad regional level, it is vital that comprehensive action plans are drawn up to preserve freshwater systems and its biodiversity at regional, national or sub-national scales, given that drivers of threat may vary from region to region. However, natural system modification, especially through dams, and pollution are frequently recorded and are likely to have a substantial impact on freshwater molluscs worldwide. While pollution was not particularly associated with high extinction risk, it is vital to combat water pollution to ensure healthy mollusc populations which may be more robust to withstand other threats. Establishment of riparian buffers to minimise run-off within impacted areas, improvements to wastewater treatment and regulation of pesticides and fertilisers are all actions which have previously been suggested (e.g. Zieritz et al., 2018b; Tickner et al., 2020), especially in areas such as Southeast Asia. Where water is heavily managed for energy generation, flood risk reduction or is abstracted for agriculture, environmental flows need to be considered in environmental impact assessments, infrastructure design and watershed management to minimise impacts on

biodiversity; identification and monitoring of introduction pathways is needed to prevent further detrimental species invasions, as is protection of critical habitat to prevent extinctions (Darrigran et al., 2020; Tickner et al., 2020). In addition, research should focus 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). More research on the systematics, ecology, and status of freshwater molluscs, particularly in the Neotropics and Southeast Asia, are sorely needed to better assess their conservation status.

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. Establishment of protected areas aimed at freshwater species conservation, targeted in situ conservation programmes and clear freshwater policies are needed to safeguard freshwater systems into the future. 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 show 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. The planned reassessment of the sample of freshwater molluscs, to commence this year, will provide a first glimpse into extinction risk trends of freshwater species globally. To underpin this and future reassessments to track status of freshwater molluscs, there is a vital need for wide-spread monitoring of freshwater species.

Acknowledgements This paper is dedicated to our co-author, friend and mentor Ben Collen, champion of the sampled approach to Red Listing and friend of understudied species. The authors would like to acknowledge the Esmée Fairbairn Foundation (NIDR and MB) and the Rufford Foundation (MB) for their generous support. MV is supported by the Russian Fund for Basic Research (project No. 19-04-00270). We are grateful to the Biodiversity Synthesis Center for funding a major assessment workshop in London in 2010. For data compilation and workshop group facilitation, we thank Anne-Marie Soulsby, Ellie Dyer, Felix Whitton, Gita Kasthala and Shane McGuinness; for additional work on draft assessments,

we thank Clare Duncan, Amy Collins, Kirsten McMillan, Suzanne Offord, Julia Thorley, Rebecca Herdson, Harriet Milligan, Greta Carrete-Vega and Jordi Corbella.

References

- Agnarsson, I. & M. Kuntner, 2007. Taxonomy in a changing world: seeking solutions for a science in crisis. *Systematic Biology* 56: 531–559.
- Allen, D. J., S. Molur & B. A. Daniel, 2010. The Status and Distribution of Freshwater Biodiversity in the Eastern Himalaya. IUCN and Zoo Outreach Organisation.
- Baillie, J. E., B. Collen, R. Amin, H. R. Akcakaya, S. H. Butchart, N. Brummitt, T. R. Meagher, M. Ram, C. Hilton-Taylor & G. M. Mace, 2008. Toward monitoring global biodiversity. *Conservation Letters* 1: 18–26.
- Balian, E. V., H. Segers, C. Lévêque & K. Martens, 2008. The Freshwater Animal Diversity Assessment: an overview of results. *Hydrobiologia* 595: 627–637.
- Bland, L. M., C. D. L. Orme, J. Bielby, B. Collen, E. Nicholson & M. A. McCarthy, 2015. Cost-effective assessment of extinction risk with limited information. *Journal of Applied Ecology* 52: 861–870.
- Bogan, A., 2008. Global diversity of freshwater mussels (Mollusca, Bivalvia) in freshwater. *Hydrobiologia* 595: 139–147.
- Böhm, M., B. Collen, J. E. Baillie, P. Bowles, J. Chanson, N. Cox, G. Hammerson, M. Hoffmann, S. R. Livingstone, M. Ram, A. G. Rhodin, et al., 2013. The conservation status of the world's reptiles. *Biological Conservation* 157: 372–385.
- Bolotov, I. N., A. V. Kondakov, E. S. Konopleva, I. V. Vikhrev, O. V. Aksenova, A. S. Aksenov, Y. V. Bepalaya, A. V. Borovskoy, P. P. Danilov, G. A. Dvoryankin, M. Y. Gofarov, et al., 2020a. Integrative taxonomy, biogeography and conservation of freshwater mussels (Unionidae) in Russia. *Scientific Reports* 10: 3072.
- Bolotov, I. N., E. S. Konopleva, I. V. Vikhrev, M. Y. Gofarov, M. Lopes-Lima, A. E. Bogan, Z. Lunn, N. Chan, T. Win, O. V. Aksenova, A. A. Tomilova, K. Tangmuangpak, S. Tumpeesuwan & A. V. Kondakov, 2020b. New freshwater mussel taxa discoveries clarify biogeographic division of Southeast Asia. *Scientific Reports* 10: 6616.
- Brown, K.M. & C. E. Lydeard, 2010. Mollusca: Gastropoda. In Thorpe, J. H. & A. P. Covich (eds), *Ecology and classification of freshwater invertebrates of North America*. Academic Press, Burlington, MA 01803, USA: 277–307.
- Brummitt, N. A., S. P. Bachman, J. Griffiths-Lee, M. Lutz, J. F. Moat, A. Farjon, J. S. Donaldson, C. Hilton-Taylor, T. R. Meagher, S. Albuquerque, E. Aletrari, et al., 2015. Green Plants in the Red: a Baseline Global Assessment for the IUCN Sampled Red List Index for Plants. *PLoS ONE* 10: e0135152.
- Butchart, S. H., A. J. Stattersfield, L. A. Bennun, S. M. Shutes, H. R. Akcakaya, J. E. Baillie, S. N. Stuart, C. Hilton-Taylor & G. M. Mace, 2004. Measuring global trends in the status of biodiversity: Red List Indices for birds. *PLoS Biology* 2: e383.

- Clausnitzer, V., V. J. Kalkman, M. Ram, B. Collen, J. E. Baillie, M. Bedjanić, W. R. Darwall, K. D. Dijkstra, R. Dow, J. Hawking, H. Karube, et al., 2009. Odonata enter the biodiversity crisis debate: the first global assessment of an insect group. *Biological Conservation* 142: 1864–1869.
- Clifford, P., S. Richardson & D. Hemon, 1989. Assessing the significance of the correlation between two spatial processes. *Biometrics* 45: 123–134.
- Collen, B., F. Whitton, E. E. Dyer, J. E. M. Baillie, N. Cumberlidge, W. R. T. Darwall, C. Pollock, N. I. Richman, A.-M. Soulsby & M. Böhm, 2014. Global patterns of freshwater species diversity, threat and endemism. *Global Ecology and Biogeography* 23: 40–51.
- Cowie, R. H., C. Régnier, R. Fontaine & P. Bouchet, 2017. Measuring the Sixth Extinction: what do mollusks tell us? *The Nautilus* 131: 3–41.
- Cumberlidge, N., P. K. Ng, D. C. Yeo, C. Magalhães, M. R. Campos, F. Alvarez, T. Naruse, S. R. Daniels, L. J. Esser, F. Y. Attipoe, F. Clotilde-Ba, et al., 2009. Freshwater crabs and the biodiversity crisis: importance, threats, status, and conservation challenges. *Biological Conservation* 142: 1665–1673.
- Cuttelod, A., M. Seddon & E. Neubert, 2011. European Red List of Non-marine Molluscs. Publications Office of the European Union.
- Darrigran, G. & C. Damborenea, 2011. Ecosystem engineering impacts of *Limnoperna fortunei* in South America. *Zoological Science* 28: 1–7.
- Darrigran, G., I. Agudo-Padron, P. Baez, C. Belz, F. Cardoso, A. Carranza, G. Collado, M. Correoso, M. G. Cuzzo, A. Fabres, D. E. Gutiérrez Gregoric, et al., 2020. Non-native mollusks throughout South America: emergent patterns in an understudied continent. *Biological Invasions* 22: 1–19.
- Darwall, W., K. Smith, D. Allen, M. Seddon, G. McGregor Reid, V. Clausnitzer & V. Kalkman, 2009. Freshwater biodiversity: a hidden resource under threat. In Vie, J. C., C. Hilton-Taylor & S. N. Stuart (eds), *Wildlife in a changing world: an analysis of the 2008 IUCN Red List of Threatened Species*. IUCN, Gland: 43–53.
- Darwall, W., V. Bremerich, A. DeWever, A. I. Dell, J. Freyhof, M. O. Gessner, H.-P. Grossart, I. Harrison, K. Irvine, S. C. Jähnig, J. M. Jeschke, et al., 2019. The Alliance for Freshwater Life: a global call to unite efforts for freshwater biodiversity science and conservation. *Aquatic Conservation: Marine and Freshwater Ecosystems* 28: 1015–1022.
- Dudgeon, D., A. H. Arthington, M. O. Gessner, Z. I. Kawabata, D. J. Knowler, C. Lévêque, R. J. Naiman, A. H. Prieur-Richard, D. Soto, M. L. Stiassny & C. A. Sullivan, 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Review* 81: 163–182.
- Ferreira-Rodríguez, N., Y. B. Akiyama, O. V. Aksenova, R. Araujo, M. C. Barnhart, Y. V. Bespalaya, A. E. Bogan, I. N. Bolotov, P. B. Budha, C. Clavijo, S. J. Clearwater, G. Darrigran, et al., 2019. Research priorities for freshwater mussel conservation assessment. *Biological Conservation* 231: 77–87.
- Foden, W.B. & B. E. Young (eds), 2016. IUCN SSC Guidelines for Assessing Species' Vulnerability to Climate Change. Version 1.0. Occasional Paper of the IUCN Species Survival Commission No. 59. IUCN Species Survival Commission, Cambridge, UK and Gland, Switzerland.
- Gallardo, B., A. E. Bogan, S. Harun, L. Jainih, M. Lopes-Lima, M. Pizarro, K. A. Rahim, R. Sousa, S. G. P. Virdis & A. Zieritz, 2018. Current and future effects of global change on a hotspot's freshwater diversity. *Science of the Total Environment* 635: 750–760.
- Graf, D. L., 2007. Palearctic freshwater mussel (Mollusca: Bivalvia: Unionoida) diversity and the Comparative Method as a species concept. *Proceedings of the Academy of Natural Sciences of Philadelphia* 156: 71–88.
- Graf, D. L., 2013. Patterns of freshwater bivalve global diversity and the state of phylogenetic studies on the Unionoida, Sphaeriidae, and Cyrenidae. *American Malacological Bulletin* 31: 135–153.
- He, F., V. Bremerich, C. Zarfl, J. Geldmann, S. D. Langhans, J. N. W. David, W. Darwall, K. Tockner & S. C. Jähnig, 2018. Freshwater megafauna diversity: patterns, status and threats. *Diversity and Distributions* 24: 1395–1404.
- Henriques, S., M. Böhm, B. Collen, J. Luedtke, M. Hoffmann, C. Hilton-Taylor, P. Cardoso, S. H. M. Butchart & R. Freeman, 2020. Accelerating the monitoring of global biodiversity: revisiting the sampled approach to generating Red List Indices. *Conservation Letters*: e12703.
- Hermoso, V., A. F. Filipe, P. Segurado & P. Beja, 2018. Freshwater conservation in a fragmented world: dealing with barriers in a systematic planning framework. *Aquatic Conservation: Marine and Freshwater Ecosystems* 28: 17–25.
- Howard, J. K. & K. M. Cuffey, 2006. The functional role of native freshwater mussels in the fluvial benthic environment. *Freshwater Biology* 51: 460–474.
- Huang, X.-C., J.-H. Su, J.-X. Ouyang, S. Ouyang, C.-H. Zhou & X.-P. Wu, 2019. Towards a global phylogeny of freshwater mussels (Bivalvia: Unionida): Species delimitation of Chinese taxa, mitochondrial phylogenomics, and diversification patterns. *Molecular Phylogenetics and Evolution* 130: 45–59.
- IUCN, 2012. IUCN Red List Categories and Criteria: Version 3.1, 2nd ed. IUCN, Gland.
- IUCN, 2019. The IUCN Red List of Threatened Species, version 2019.3 (23 December 2019); <http://www.iucnredlist.org>.
- IUCN Standards and Petitions Committee, 2019. Guidelines for Using the IUCN Red List Categories and Criteria. Version 14. Prepared by the Standards and Petitions Committee. Downloadable from <http://www.iucnredlist.org/documents/RedListGuidelines.pdf>.
- Johnson, P. D., A. E. Bogan, K. M. Brown, N. M. Burkhead, J. R. Cordeiro, J. T. Garner, P. D. Hartfield, D. A. Lepitzki, G. L. Mackie, E. Pip, T. A. Tarpley, et al., 2013. Conservation status of freshwater gastropods of Canada and the United States. *Fisheries* 38: 247–282.
- Köhler, F., M. Seddon, A. E. Bogan, D. Van Tu, P. Sri-Aroon & D. Allen, 2012. The status and distribution of freshwater molluscs of the Indo-Burma region. In Allen, D. J., K. G. Smith & W. R. T. Darwall (eds), *The Status and Distribution of Freshwater Biodiversity in Indo-Burma*. IUCN, Gland: 66–88.
- Kotov, A. A. & M. A. Gololobova, 2016. Traditional taxonomy: Quo vadis? *Integrative Zoology* 11: 490–495.
- Legendre, L. & P. Legendre, 1998. *Numerical ecology*, 2nd ed. Elsevier Science, Oxford.

- Lopes-Lima, M., L. E. Burlakova, A. Y. Karatayev, K. Mehler, M. Seddon & R. Sousa, 2018. Conservation of freshwater bivalves at the global scale: diversity, threats and research needs. *Hydrobiologia* 810: 1–14.
- Lopes-Lima, M., A. Hattori, T. Kondo, J. Hin Lee, S. Ki Kim, A. Shirai, H. Hayashi, T. Usui, K. Sakuma, T. Toriya, Y. Sunamura, et al., 2020. Freshwater mussels (Bivalvia: Unionidae) from the rising sun (Far East Asia): phylogeny, systematics, and distribution. *Molecular Phylogenetics and Evolution* 146: 106755.
- Lydeard, C. & R. L. Mayden, 1995. A diverse and endangered aquatic ecosystem of the southeast United States. *Conservation Biology* 9: 800–805.
- Lydeard, C., R. H. Cowie, W. F. Ponder, A. E. Bogan, P. Bouchet, S. A. Clark, K. S. Cummings, T. J. Frest, O. Gargominy, D. G. Herbert, R. Hershler, et al., 2004. The global decline of nonmarine mollusks. *Bioscience* 54: 321–330.
- Maceda-Veiga, A., 2013. Towards the conservation of freshwater fish: Iberian rivers as an example of threats and management practices. Review in *Fish Biology and Fisheries* 23: 1–22.
- Markovic, D., S. Carrizo, J. Freyhof, N. Cid, S. Lengyel, M. Scholz, H. Kasperdius & W. Darwall, 2014. Europe's freshwater biodiversity under climate change: distribution shifts and conservation needs. *Diversity and Distributions* 20: 1097–1107.
- Markovic, D., S. F. Carrizo, O. Karcher, A. Walz & J. N. W. David, 2017. Vulnerability of European freshwater catchments to climate change. *Global Change Biology* 23: 3567–3580.
- Master, L. L., B. A. Stein, L. S. Kutner & G. A. Hammerson, 2000. Vanishing assets: conservation status of U.S. species. In Stein, B. A., L. S. Kutner & J. S. Adams (eds), *Precious Heritage: The Status of Biodiversity in the United States*. Oxford University Press, Oxford: 93–118.
- McRae, L., S. Deinet & R. Freeman, 2017. The diversity-weighted Living Planet Index: controlling for taxonomic bias in a global biodiversity indicator. *PLoS One* 12: e0169156.
- Modesto, V., M. Ilarri, A. T. Souza, M. Lopes-Lima, K. Douda, M. Clavero & R. Sousa, 2018. Fish and mussels: importance of fish for freshwater mussel conservation. *Fish and Fisheries* 19: 244–259.
- MolluscaBase (eds), 2020. MolluscaBase. Accessed <http://www.molluscabase.org> 2020-02-27.
- Molur, S., K. G. Smith, B. A. Daniel & W. R. T. Darwall, 2011. *The Status and Distribution of Freshwater Biodiversity in the Western Ghats*. IUCN and Zoo Outreach Organisation, India.
- Newton, T. J. & W. G. Cope, 2007. Biomarker responses of unionid mussels to environmental contaminants. In Ferris, J. L. & J. H. Van Hassel (eds), *Freshwater Bivalve Ecotoxicology*. CRC Press, Boca Raton, Florida, USA: 257–284.
- Osikowski, A., S. Hofman, A. Rysiewska, B. Sket, S. Prevorčnik & A. Falniowski, 2018. A case of biodiversity overestimation in the Balkan *Belgrandiella* A. J. Wagner, 1927 (Caenogastropoda: Hydrobiidae): molecular divergence not paralleled by high morphological variation. *Journal of Natural History* 52: 323–344.
- Ponder, W., 2019. Tateidae Thiele, 1925. In Lydeard, C. & K. S. Cummings (eds), *Freshwater mollusks of the world: a distribution atlas*. Johns Hopkins University Press, Baltimore: 134–138.
- Red List Technical Working Group (RLTWG), 2018. Mapping Standards and Data Quality for the IUCN Red List Categories and Criteria v. 1.16. Available at: https://nc.iucnredlist.org/redlist/resources/files/1539098236-Mapping_Standards_Version_1.16_2018.pdf.
- Régnier, C., B. Fontaine & P. Bouchet, 2009. Not knowing, not recording, not listing: numerous unnoticed mollusk extinctions. *Conservation Biology* 23: 1214–1221.
- Régnier, C., G. Achaz, A. Lambert, R. H. Cowie, P. Bouchet & B. Fontaine, 2015. Mass extinction in poorly known taxa. *Proceedings of the National Academy of Sciences USA* 112: 7761–7766.
- Revenga, C., I. Campbell, R. Abell, P. de Villers & M. Bryer, 2005. Prospects for monitoring freshwater ecosystems towards the 2010 targets. *Philosophical Transactions of the Royal Society of London B* 360: 397–413.
- Richman, N. I., M. Böhm, S. B. Adams, F. Alvarez, E. A. Bergey, J. J. Bunn, Q. Burnham, J. Cordeiro, J. Coughran, K. A. Crandall, K. L. Dawkins, et al., 2015. Multiple drivers of decline in the global status of freshwater crayfish (Decapoda: Astacidea). *Philosophical Transactions of the Royal Society B-Biological Sciences* 370: 20140060.
- Saito, T., L. Prozorova, T. Sitnikova, P. Surenkhorloo, T. Hirano, Y. Morii & S. Chiba, 2018. Molecular phylogeny of glacial relict species: a case of freshwater Valvatidae molluscs (Mollusca: Gastropoda) in North and East Asia. *Hydrobiologia* 818: 105–118.
- Salafsky, N., D. Salzer, A. J. Stattersfield, C. R. Hilton-Taylor, R. Neugarten, S. H. Butchart, B. E. Collen, N. Cox, L. L. Master, S. H. O'Connor & D. Wilkie, 2008. A standard lexicon for biodiversity conservation: unified classifications of threats and actions. *Conservation Biology* 22: 897–911.
- Schipper, J., J. S. Chanson, F. Chiozza, N. A. Cox, M. Hoffmann, V. Katariya, J. Lamoreux, A. S. Rodrigues, S. N. Stuart, H. J. Temple, J. Baillie, et al., 2008. The status of the world's land and marine mammals: diversity, threat, and knowledge. *Science* 322: 225–230.
- Schöne, B. R., E. Dunca, H. Mutvei & U. Norlund, 2004. A 217-year record of summer air temperature reconstructed from freshwater pearl mussels (*M. margaritifera*, Sweden). *Quaternary Science Reviews* 23: 1803–1816.
- Seddon, M., C. Appleton, D. Van Damme & D. Graf, 2011. Freshwater molluscs of Africa: diversity, distribution, and conservation. In Darwall, W., K. Smith, D. Allen, R. Holland, I. Harrison & E. Brooks (eds), *The diversity of life in African freshwaters: underwater, under threat. An analysis of the status and distribution of freshwater species throughout mainland Africa*. IUCN, Gland: 92–125.
- Smith, K. G., V. Barrios, W. R. T. Darwall & C. Numa (eds), 2014. *The Status and Distribution of Freshwater Biodiversity in the Eastern Mediterranean*. IUCN, Cambridge.
- Strayer, D. L. & D. Dudgeon, 2010. Freshwater biodiversity conservation: recent progress and future challenges. *Freshwater Science* 29: 344–358.

- Strong, E. E., O. Gargominy, W. F. Ponder & P. Bouchet, 2008. Global diversity of gastropods (Gastropoda; Mollusca) in freshwater. *Hydrobiologia* 595: 149–166.
- Stuart, S. N., J. S. Chanson, N. A. Cox, B. E. Young, A. S. Rodrigues, D. L. Fischman & R. W. Waller, 2004. Status and trends of amphibian declines and extinctions worldwide. *Science* 306: 1783–1786.
- Thorburn, D.-M. J., 2017. Anthropogenic threats predict likelihood and severity of decline in global freshwater populations. MRes Thesis, University College London.
- Tickner, D., J. J. Opperman, R. Abell, M. Acreman, A. H. Arthington, S. E. Bunn, S. J. Cooke, J. Dalton, W. Darwall, G. Edwards, et al., 2020. Bending the curve of global freshwater biodiversity loss: an emergency recovery plan. *BioScience* 70: 330–342.
- Tingley, R., S. Meiri & D. G. Chapple, 2016. Addressing knowledge gaps in reptile conservation. *Biological Conservation* 204: 1–5.
- Tittensor, D. P., M. Walpole, S. L. Hill, D. G. Boyce, G. L. Britten, N. D. Burgess, S. H. Butchart, P. W. Leadley, E. C. Regan, R. Alkemade, R. Baumung, et al., 2014. A mid-term analysis of progress toward international biodiversity targets. *Science* 346: 241–244.
- Torres, S., L. Cao, D. E. Gutiérrez Gregoric, M. de Lucía, F. Brea & G. Darrigran, 2018. Distribution of the Unionida (Bivalvia, Paleoheterodonta) from Argentina and its conservation in the Southern Neotropical Region. *PLoS ONE* 13: e0203616.
- Trull, N., M. Böhm & J. Carr, 2017. Patterns and biases of climate change threats in the IUCN Red List. *Conservation Biology* 32: 135–147.
- Vaughn, C. C., 2012. Life history traits and abundance can predict local colonisation and extinction rates of freshwater mussels. *Freshwater Biology* 57: 982–992.
- Vaughn, C. C., 2018. Ecosystem services provided by freshwater mussels. *Hydrobiologia* 810: 15–27.
- Vaughn, C. C. & C. M. Taylor, 2001. Impoundments and the decline of freshwater mussels: a case study of an extinction gradient. *Conservation Biology* 13: 912–920.
- Vinarski, M. V., 2018. The species question in freshwater malacology: from Linnaeus to the present day. *Folia Malacologica* 26: 39–52.
- Vörösmarty, C. J., P. B. McIntyre, M. O. Gessner, D. Dudgeon, A. Prusevich, P. Green, S. Glidden, S. E. Bunn, C. A. Sullivan, C. R. Liermann & P. M. Davies, 2010. Global threats to human water security and river biodiversity. *Nature* 467: 555–561.
- Wang, N., C. D. Ivey, C. G. Ingersoll, W. G. Brumbaugh, D. Alvarez, E. J. Hammer, C. R. Bauer, T. Augspurger, S. Raimondo & M. C. Barnhart, 2017. Acute sensitivity of a broad range of freshwater mussels to chemicals with different modes of toxic action. *Environmental Toxicology and Chemistry* 36: 786–796.
- Wesselingh, F. P., T. A. Neubauer, V. V. Anistratenko, M. V. Vinarski, T. Yanina, J. J. ter Poorten, P. Kijashko, C. Albrecht, O. Y. Anistratenko, A. D’Hont, P. Frolov, et al., 2019. Mollusc species from the Pontocaspian region – an expert opinion list. *ZooKeys* 827: 31–124.
- Wilke, T., 2019. Moitessieriidae Bourguignat, 1863. In Lydeard, C. & K. S. Cummings (eds), *Freshwater mollusks of the world: a distribution atlas*. Johns Hopkins University Press, Baltimore: 122–125.
- Young, B. E., E. Byers, K. Gravuer, K. Hall, G. Hammerson & A. Redder, 2011. Guidelines for using the NatureServe Climate Change Vulnerability Index. NatureServe, Arlington, VA.
- Zajac, K., J. Florek, T. Zajac, P. Adamski, W. Bielański, A. Ćmiel, M. Klich & A. M. Lipińska, 2018. On the reintroduction of the endangered thick-shelled river mussel *Unio crassus*: the importance of the river’s longitudinal profile. *Science of the Total Environment* 624: 273–282.
- Zieritz, A., A. E. Bogan, E. Froufe, O. Klishko, T. Kondo, U. Kovitvadhi, S. Kovitvadhi, J. H. Lee, M. Lopes-Lima, J. M. Pfeiffer, R. Sousa, T. V. Do, I. Vikhrev & D. T. Zanatta, 2018a. Diversity, biogeography and conservation of freshwater mussels (Bivalvia: Unionida) in East and Southeast Asia. *Hydrobiologia* 810: 29–44.
- Zieritz, A., A. E. Bogan, K. A. Rahim, R. Sousa, L. Jainih, S. Harun, N. F. Razak, B. Gallardo, S. McGowan, R. Hassan & M. Lopes-Lima, 2018b. Changes and drivers of freshwater mussel diversity and distribution in northern Borneo. *Biological Conservation* 219: 126–137.

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