

1 **The conservation status of the world's freshwater molluscs**

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126

127 **Abstract**

128 With the biodiversity crisis continuing unchecked, we need to establish levels and drivers of
129 extinction risk, and reassessments over time, to effectively allocate conservation resources
130 and track progress towards global conservation targets. Given that threat appears particularly
131 high in freshwaters, we assessed the extinction risk of 1,428 randomly selected freshwater
132 molluscs using the IUCN Red List Categories and Criteria, as part of the Sampled Red List
133 Index project. We show that close to one third of species in our sample are estimated to be
134 threatened with extinction, with highest levels of threat in the Nearctic, Palearctic and
135 Australasia and among gastropods. Threat levels were higher in lotic than lentic systems.
136 Pollution (chemical and physical) and the modification of natural systems (e.g. through
137 damming and water abstraction) were the most frequently reported threats to freshwater
138 molluscs, with some regional variation. Given that we found little spatial congruence between
139 species richness patterns of freshwater molluscs and other freshwater taxa, apart from
140 crayfish, new additional conservation priority areas emerged from our study. We discuss the
141 implications of our findings for freshwater mollusc conservation, the adequacy of a sampled
142 approach and important next steps to estimate trends in freshwater mollusc extinction risk
143 over time.

144

145 **Keywords:**

146 IUCN Red List, extinction risk, SRLI, bivalves, gastropods, congruence

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148

149 **Introduction**

150 With the biodiversity crisis continuing unchecked (Tittensor et al. 2014), it is vital to
151 determine levels and drivers of species' extinction risk to effectively allocate conservation
152 resources and develop targeted conservation actions. Many studies have described threat
153 patterns of various species groups using the IUCN Red List of Threatened Species, which
154 describes extinction risk, threats, and recommended conservation action: for example, 25% of
155 mammal species (Schipper et al. 2008), 42% of amphibians (Stuart et al. 2004), 32% of
156 freshwater crabs (Cumberlidge et al. 2009) and 32% of crayfish (Richman et al. 2015) are
157 threatened with extinction. In addition, the IUCN Red List Index (RLI; Butchart et al. 2004),
158 a biodiversity indicator, has been used to monitor changes in extinction risk over time and
159 evaluate our progress towards meeting global, regional and national biodiversity targets (e.g.,
160 Aichi Targets of the Convention on Biological Diversity [CBD] and the Sustainable
161 Development Goals [SDGs]).

162 The Sampled Red List Index (SRLI) is a derivative of the RLI and provides a
163 sampling strategy from which to derive – over time – broadly representative trends in
164 extinction risk of species across highly species-rich species groups (Baillie et al. 2008). For
165 the SRLI, a random sample of 1,500 species from a given taxon group is assessed using the
166 IUCN Red List Categories and Criteria (IUCN 2012); this sample size was found sufficiently
167 large to accurately report on trends in extinction risk while also buffering against up to 40%
168 of data deficiency in the sample (Baillie et al. 2008). Assessments for the SRLI have already
169 been carried out for dragonflies (Clausnitzer et al. 2009), reptiles (Böhm et al. 2013) and
170 plants (Brummitt et al. 2015) and have acted as catalysts for increased conservation attention
171 being afforded to these species groups (e.g., Tingley et al. 2016).

172 Freshwater ecosystems are under extensive pressure from anthropogenic threats
173 (Darwall et al. 2018). Freshwaters constitute < 1% of the total volume of the hydrosphere but
174 maintain several tens of thousands of animal species not able to live in salinated water (e.g.
175 Balian et al. 2008). It has been suggested that approximately 80% of the world's human
176 population faces threats to water security (Vörösmarty et al. 2010), and almost one in three
177 freshwater species have been estimated at risk of extinction worldwide (Collen et al. 2014),
178 with habitat loss being the most commonly cited threat. Increasing human pressures occur in
179 many freshwater biodiversity hotspots (He et al. 2018). Given the high connectivity of
180 freshwater systems, threat processes and their detrimental effects are easily transported from
181 one locality to another (Dudgeon et al. 2006; Darwall et al. 2009) and fragmentation can have
182 profound effects on water flows, sedimentation, habitat loss and hence species loss (Revenge
183 et al. 2005).

184 Compared to other, especially terrestrial taxa, freshwater molluscs are understudied
185 and often not represented in conservation planning, despite comparatively high levels of
186 extinction (e.g. Régnier et al. 2015). Freshwater molluscs represent one of the most diverse
187 groups of freshwater organisms. More than 6,000 valid species of freshwater molluscs are
188 accepted (MolluscaBase 2020); most are gastropods (almost 4,800 species; MolluscaBase
189 2020), while bivalves account for more than 1,200 species (Bogan 2008; Graf 2013).
190 Freshwater molluscs play key roles in freshwater systems by contributing to water quality,
191 nutrient cycling and primary productivity, especially due to their roles as filter feeders and
192 algal grazers (Howard & Cuffey 2006; Brown & Lydeard 2010; Vaughn 2018). Shells and
193 soft tissues of freshwater mussels have been used to monitor environmental conditions
194 (Schöne et al. 2004; Newton and Cope 2007), and suspension feeding by molluscs removes
195 particles from the water and increases water quality with resulting benefits to recreation and

196 aesthetics (Vaughn 2018). They also provide an ample food source for other species,
197 including humans (Vaughn 2018).

198 Freshwater molluscs are considered to be highly threatened as a group: for example,
199 in 2000, 202 of nearly 300 unionid species from the USA and Canada were listed as either
200 extinct, possibly extinct, or critical (critically imperilled, imperilled, vulnerable; Master et al.
201 2000; Lydeard et al. 2004). In addition, 67 of 703 US and Canadian gastropod species were
202 considered extinct (Johnson et al. 2013), primarily due to the effects of damming and river
203 channelisation. Within Europe, 44% of freshwater molluscs are threatened with extinction
204 (Cuttelod et al. 2011) compared to 29% in continental Africa (Seddon et al. 2011) and 17% in
205 the Indo-Burma region (Köhler et al. 2012). There are likely many more unnoticed
206 extinctions of freshwater molluscs around the globe (Régnier et al. 2009; Régnier et al. 2015;
207 Cowie et al. 2017). Such levels of threat mirror the general decline and threat in freshwater
208 ecosystems (Collen et al. 2014).

209 Here, we report on the levels and drivers of threat in a random representative sample
210 of 1,428 freshwater molluscs from across the globe, which was assessed as part of the SRLI
211 project (Baillie et al. 2008). This number constitutes around a quarter of valid species in this
212 group. We estimate extinction risk within our sample for molluscan orders/families; assess
213 predominant threats impacting freshwater molluscs; compare hotspots for freshwater
214 molluscs with hotspots derived from other freshwater species groups to identify additional
215 areas and regions of conservation priority; and set out important next steps to improve Red
216 List assessments and detect trends in extinction risk over time.

217 **Materials and Methods**

218 *The Red List assessment process*

219 Baillie et al. (2008) showed that a random sample of 900 non-Data Deficient species (non-
220 DD) is sufficiently large to accurately report on trends in extinction risk. However, to account
221 for potentially high levels of data deficiency within random samples of taxon groups, they
222 recommended 1,500 species for the sampled Red List approach, which allows for data
223 deficiency of up to 40% (Baillie et al. 2008). We followed this approach and selected at
224 random 1,500 species from a list of all described freshwater mollusc species (provided by the
225 IUCN/SSC Mollusc Specialist Group). A full list of species in the sample (Table S1) is given
226 in the Supplementary Materials. Our original sample consisted of 1,160 (77%) gastropod and
227 340 (23%) bivalve species, thus closely reflecting the contribution of both groups towards
228 total freshwater mollusc diversity (Bogan 2008; Strong et al. 2008). Recent taxonomic work
229 meant that 13 species were synonymised with species already included in the sample, and
230 were replaced with new species randomly drawn from the species list (bivalves replacing
231 bivalves, gastropods replacing gastropods). Of these 13 replacement species, seven had
232 already been assessed on the IUCN Red List; these were included in this study, while the
233 remaining six replacements are currently listed as Not Evaluated (NE). Finally, 65 species
234 were found to inhabit brackish or marine systems, or to be otherwise not fully freshwater, and
235 these were subsequently removed from analysis. Our final sample still met the threshold of
236 900 non-DD species.

237 Overall, 371 of the 1,428 selected species were assessed as part of IUCN regional
238 assessment projects, specifically Europe (Cuttelod et al. 2011), Pan-Africa (Darwall et al.
239 2009), Eastern Himalayas (Allen et al. 2010), Western Ghats (Molur et al. 2011) and Indo-
240 Burma (Köhler et al. 2012). For the remaining species, new or updated assessments were
241 produced through consultation with a global network of malacologists at an assessment

242 workshop in January 2010. Species-specific data were collected on taxonomy, distribution,
243 population trends, ecology and biology, threats, and conservation measures. Assessments
244 followed the IUCN Red List Categories and Criteria which evaluate species against five Red
245 List criteria relating to extinction risk (IUCN 2012): population reduction (Criterion A);
246 population size (Criteria C and D/D1); geographic range size and decline (Criterion B); very
247 small population size (Criterion D) or restricted range (Criterion D2); quantitative analyses of
248 extinction risk (Criterion E). Extinction risk categories range from Extinct (EX) and Extinct
249 in the Wild (EW), via the threatened categories Critically Endangered (CR), Endangered
250 (EN) and Vulnerable (VU) to the lowest risk categories of Near Threatened (NT) and Least
251 Concern (LC). Additionally, a species is listed as Data Deficient (DD) if insufficient data are
252 available to make a conservation assessment. Through a centralised editorial and reviewing
253 process, we ensured that the IUCN Red List Categories and Criteria were consistently applied
254 between species and regions. A total of 248 species were re-assessed from previous
255 assessments, while all others represented first-time assessments of species. Since these
256 assessments, 86 species have been reassessed and 28 non-genuine changes in status (changes
257 in species status due to increased knowledge and new information rather than an actual
258 change in population or distribution due to an emerging threat; IUCN 2012) have been
259 incorporated into our results. All species assessments have been reviewed by the IUCN and
260 were published online in 2012 and 2013 (IUCN 2019), except for one species of bivalve,
261 *Arcidopsis footei* (Theobald, 1876), drafted as Endangered.

262

263 *Summarising extinction risk*

264 We summarised extinction risk across the full sample and by taxonomic class (bivalves and
265 gastropods), order and family, biogeographical realm (Afrotropical, Australasian,
266 Indomalayan, Nearctic, Neotropical, Oceanian and Palearctic) and habitat system (lotic

267 versus lentic systems). Following previous studies (Clausnitzer et al. 2009; Böhm et al. 2013;
268 Richman et al. 2015), we estimated extinction risk in our sample as the proportion of
269 threatened species (CR, EN, VU), assuming that Data Deficient species will fall into
270 threatened categories in the same proportion as non-DD species:

$$271 \quad \text{prop}_{\text{threat}} = (\text{CR} + \text{EN} + \text{VU})/(\text{N} - \text{DD} - \text{EX}),$$

272 where N is the total number of species in the sample, CR, EN and VU are the numbers of
273 species in each of the three threatened categories respectively, DD is the number of species in
274 the Data Deficient category, and EX the number of species in the Extinct category. We
275 provided upper and lower bounds of our estimate by assuming that (a) no Data Deficient
276 species were threatened [lower margin: $\text{Prop}_{\text{threat_lower}} = (\text{CR} + \text{EN} + \text{VU})/(\text{N} - \text{EX})$], and (b)
277 all Data Deficient species were threatened [upper margin; $\text{Prop}_{\text{threat_upper}} = (\text{CR} + \text{EN} + \text{VU} +$
278 $\text{DD})/(\text{N} - \text{EX})$]. Note that these are estimates and upper/lower bounds of extinction risk
279 within our sample only and may not accurately reflect the proportion of freshwater molluscs
280 threatened worldwide. This is because the sampled approach was devised to accurately detect
281 trend direction of the RLI over time, and not to reflect threat status for a species group overall
282 at a point in time.

283 *Assessment of drivers of extinction risk*

284 During the assessment process, threat processes were recorded for each species and coded
285 following Salafsky et al. (2008) (Table S2). This included recording the timing of the threat
286 (ongoing; past, unlikely to return; past, likely to return; future; unknown). Most threats (85%)
287 were recorded as ongoing threats, and we focus on these ongoing threats in the following
288 analyses. However, we present a breakdown of future threats in the Supplementary Materials
289 (8% of recorded threats; Figure S12). We summarised the number of species affected (across
290 the sample and by biogeographic region) by broadest hierarchical level of the IUCN Threat
291 Classification Scheme (Salafsky et al. 2008): residential and commercial development;

292 agriculture and aquaculture; energy production and mining; transportation and service
293 corridors; biological resource use; human intrusion and disturbance; natural system
294 modification (includes dams and abstraction of surface or ground water); invasive and other
295 problematic species; pollution (includes domestic waste water, industrial and agricultural
296 effluents, garbage and solid waste); geological events; and climate change and severe weather
297 (Table S2). Using permutation-based chi-square tests, we determined whether threat
298 processes were randomly spread across Red List categories, by looking at a) threatened (CR,
299 EN, VU) versus non-threatened (NT, LC) classification, and b) individual Red List categories
300 (CR, EN, VU, NT, LC). We ran this analysis on all 511 threatened and non-threatened
301 species which were affected by one or more ongoing threat processes (the remainder of
302 species does not have any threats, or the threats are unknown, or are past or future threats, or
303 species are DD) and permuted the tables 1,000 times.

304 *Spatial patterns of freshwater molluscs and congruence with other species groups*

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

310 Species distribution was also mapped – where possible - for all assessed species.

311 Given that some species have very poor data, we were unable to map several Data Deficient
312 species. For subsequent analysis, we selected only those parts of a species' distribution map
313 where the species was considered extant or probably extant, resident, and native or
314 reintroduced (RLTWG 2018). We mapped species richness, threatened species richness and
315 Data Deficient species richness of our sample by overlaying a grid with 1° grid cells onto the

316 respective aggregated species' distribution and summing the number of species occurring in
317 each grid cell. We normalised species richness relative to the richest cell to derive a synthetic
318 pattern of species richness ranging from zero (no species present) to one (highest species
319 richness), as described in Collen et al. (2014). We also produced species richness maps for
320 bivalves and gastropods in our sample, respectively (Figure S1 and S2, Supplementary
321 Materials).

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

333 To build on previous work on spatial patterns of freshwater species richness (Collen
334 et al. 2014), we also assessed spatial congruence between patterns of species richness,
335 threatened species richness and Data Deficient species richness of our sample of freshwater
336 molluscs and those derived for other freshwater species groups. First, we recalculated the
337 richness patterns for six freshwater taxon groups (amphibians, crabs, crayfish, fish, mammals
338 and reptiles) analysed by Collen et al. (2014) at our 1° spatial scale. We then produced
339 normalised species richness maps for each as described above to account for different sample
340 sizes in the various species groups (Collen et al. 2014). To assess spatial congruence between

341 species richness patterns of freshwater molluscs and other freshwater taxon groups, we again
342 generated spatial overlays of species richness patterns – species richness, threatened-species
343 richness, and Data Deficient-species richness – for each taxonomic group, and estimated
344 spatial congruence using Pearson’s correlations, as described above. We applied this using
345 only cells with non-0 normalised richness for molluscs. We mapped congruence of species
346 richness hotspots for all freshwater taxonomic groups in our analysis by selecting the top
347 10% of cells with the highest normalised richness value for each taxon group, and
348 summarising the number of taxon group hotspots overlapping in each grid cell. We
349 acknowledge that hotspot patterns within our sample of freshwater molluscs is highly
350 influenced by the random selection process; however, previous analyses have shown that
351 broad-scale richness patterns derived from such species samples are largely representative of
352 richness hotspot patterns obtained from comprehensive mapping of entire species groups.

353 **Results**

354 *Extinction risk in freshwater molluscs*

355 Nearly one-third of species in our final sample of 1,428 freshwater molluscs were estimated
356 to be threatened ($\text{prop}_{\text{threat}} = 0.31$; lower = 0.19, upper = 0.56; Table 1), with 520 Data
357 Deficient species (36.4%) and 908 species non-Data Deficient. Estimated threat was highest
358 in the Nearctic, Palearctic and Australasian realms (Nearctic: $\text{prop}_{\text{threat}} = 0.36$, lower = 0.30,
359 upper = 0.46; Palearctic: $\text{prop}_{\text{threat}} = 0.35$, lower = 0.19, upper = 0.64; Australasia: $\text{prop}_{\text{threat}} =$
360 0.34, lower = 0.26, upper = 0.50; Table 1). Data deficiency was highest in the Neotropics
361 (50.3% of species), Indomalaya (48.6% of species), Palearctic (45.1% of species) and
362 Oceania (43.5% of species). Estimated threat levels were higher in lotic than lentic systems
363 (lotic: $\text{prop}_{\text{threat}} = 0.31$, lower = 0.22, upper = 0.50; lentic: $\text{prop}_{\text{threat}} = 0.18$, lower = 0.13,
364 upper = 0.45).

365 Gastropods were more threatened ($\text{prop}_{\text{threat}} = 0.33$; lower = 0.19, upper = 0.61) than
366 bivalves ($\text{prop}_{\text{threat}} = 0.26$; lower = 0.20, upper = 0.42; Table 1). Threat and data deficiency
367 levels varied greatly amongst families: for example, the bivalve family Unionidae had the
368 most species in our sample ($n = 190$), with 33% estimated threatened (bounds: 29–42%) and a
369 relatively low level of data deficiency (12% of species in the family). Planorbidae ($n = 155$)
370 had only 3% of species threatened (bounds: 1–54%), yet 52% of species listed as DD, and
371 Hydrobiidae ($n = 145$) had 69% of species threatened (bounds: 48–79%) and around a third of
372 species listed as DD. Margaritiferidae is another highly threatened family of bivalves in our
373 sample ($n = 7$, $\text{prop}_{\text{threat}} = 0.67$; lower = 0.57, upper = 0.71). For gastropods, other highly
374 threatened families in our sample were the Moitessieriidae ($n = 33$, $\text{prop}_{\text{threat}} = 0.68$; lower =
375 0.52, upper = 0.76), Semisulcospiridae ($n = 12$, $\text{prop}_{\text{threat}} = 0.63$; lower = 0.42, upper = 0.75),
376 Pachychilidae ($n = 18$, $\text{prop}_{\text{threat}} = 0.50$; lower = 0.39, upper = 0.61), Emmericiidae ($n = 5$,
377 $\text{prop}_{\text{threat}} = 0.50$; lower = 0.20, upper = 0.80), and Tateidae ($n = 91$, $\text{prop}_{\text{threat}} = 0.50$; lower =
378 0.43, upper = 0.57).

379 Overall, 26 species were assessed as extinct, seven bivalves and 19 gastropods. Just
380 over one-fifth of species in our sample belonging to the gastropod family Pleuroceridae were
381 categorised as Extinct. The number of extinct species was highest in the Nearctic realm ($n =$
382 22) and in lotic systems ($n = 14$). Twenty species currently listed as CR are possibly extinct
383 (17 gastropods, seven of which belong to Hydrobiidae, and three unionid bivalves).

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

389 *Predominant threat processes affecting freshwater molluscs*

390 Overall, ongoing threats were reported for 726 species (including DD) in our sample, with
391 most species having one or two ongoing threats recorded (Figure S13). Pollution and natural
392 system modification were the most frequently recorded ongoing threats affecting freshwater
393 molluscs (Figure 2A), both when considering all species (27% and 24% of documented
394 threats, respectively), threatened species only (26% and 25%), and bivalves (27% and 22%)
395 and gastropods (27% and 25%; Figure 2B). Residential and commercial development, energy
396 production and mining, invasive and other problematic species, agriculture and aquaculture,
397 and biological resource use were also frequently reported threats (Figure 2A).

398 Pollution was the most cited threat in the Afrotropics and Indomalaya, with natural
399 system modification the predominant threat in Australasia (together with threats from
400 agriculture/ aquaculture) and the Neotropics. In the Palearctic and Nearctic, both pollution
401 and natural system modification were the predominant threats (Figure 2C).

402 The distribution of threats between threatened and non-threatened Red List categories
403 was borderline random (chi-squared = 20.67, $p = 0.054$). Natural system modification and
404 human disturbance contributed more than expected to threatened status of species, while
405 pollution and biological resource use contributed more than expected to non-threatened
406 species threats (Figure 3). The distribution of threats between individual non-DD Red List
407 categories (CR, EN, VU, NT, LC) was random (chi-squared = 48.274, $p = 0.342$). Natural
408 system modification made a greater than expected contribution to the CR category and less
409 than expected to LC in both analyses (Table 3). Pollution and biological resource use
410 contributed less than expected to higher threat categories (CR) and more than expected to
411 lower threat categories of NT and LC (Table 3). Human intrusion and disturbance contributed
412 less than expected to low threat categories (LC) and more than expected to the lower end of

413 the threatened category spectrum (VU), primarily due to application of IUCN Red List
414 criterion D2 (restricted range and plausible threat) (Table 3).

415

416 *Spatial distribution of freshwater molluscs and congruence with other taxonomic*
417 *groups*

418 More than 20% of species in our sample occurred in the USA (328 species, 38 of them
419 recorded as extinct or possibly extinct), followed by Russia (201 species; 13 with uncertain
420 presence in the country), Australia (114 species) and Thailand (101 species; Table 4). Within
421 the USA, normalised species richness in our sample was highest in the Eastern USA
422 (Tennessee, Kentucky and surrounding states); elsewhere, normalised species richness
423 showed additional hotspots in our sample in Lake Baikal, parts of Central and Eastern
424 Europe, and selected river systems in Southeast Asia (Figure 1A; see Figures S3-S11 in the
425 Supplementary Materials for spatial detail of the distribution pattern in our sample by region,
426 and Table S1 for a full list of species in our sample by country). High species richness in
427 Central and Eastern Europe, Lake Baikal and Southeast Asia was driven by high species
428 richness of gastropods in these regions (Figure S1A). High species richness in the Eastern
429 USA was primarily driven by bivalves (Figure S2A), although gastropods were also species-
430 rich in these areas (Figure S1A). There was significant congruence in the spatial pattern of
431 bivalve and gastropod species richness in our sample ($\text{corr} = 0.693$, $F = 72.58$, adjusted d.f. =
432 78.74 , $p < 0.001$).

433 Data deficiency was highest in Lake Baikal (due to high DD richness of gastropods;
434 Figure S1B) and Japan, and selected river systems in South and Southeast Asia (e.g. regions
435 of the Brahmaputra and Irrawaddy rivers). Threatened species richness in our sample was
436 highest in the most species-rich states of the USA (primarily driven by bivalves), and the

437 Southeastern Alps and Balkans in Europe (primarily driven by gastropods; Figures 1B & C
438 and Figures S1C and S2C). Overall, the spatial distribution of threatened gastropods and
439 bivalves in our sample was significantly negatively correlated ($\text{corr} = -0.161$, $F = 7.19$,
440 adjusted d.f. = 270.60, $p = 0.008$). Data deficiency for bivalves in our sample was highest in
441 eastern Asia (Russia and Japan) and South America (Figure S2B), and this pattern was
442 incongruent with the DD species richness pattern of gastropods in our sample ($\text{corr} = 0.07$, F
443 = 1.10, adjusted d.f. = 202.33, $p = 0.295$). Bivalve and gastropod congruence maps are shown
444 in Figure S14 in the Supplementary Materials.

445 Normalised species richness, DD species richness and threatened species richness of
446 freshwater molluscs was positively and significantly correlated with the respective species
447 richness of crayfish (species richness: $\text{corr} = 0.52$, $F = 28.73$, adjusted d.f. = 79.03, $p < 0.001$;
448 DD species richness: $\text{corr} = 0.19$, $F = 25.92$, adjusted d.f. = 716.24, $p < 0.001$; threatened
449 species richness: $\text{corr} = 0.46$, $F = 9.09$, adjusted d.f. = 33.97, $p = 0.005$). In addition,
450 normalised species richness of sampled freshwater molluscs was positively and significantly
451 correlated with that of freshwater reptiles ($\text{corr} = 0.33$, $F = 13.44$, adjusted d.f. = 108.35, $p <$
452 0.001) and freshwater mammals ($\text{corr} = 0.26$, $F = 6.90$, adjusted d.f. = 95.53, $p = 0.010$;
453 Table 4). There was significant positive congruence between threatened freshwater mollusc
454 richness and threatened freshwater species richness ($\text{corr} = 0.20$, $F = 4.41$, adjusted d.f. =
455 103.20, $p = 0.038$; as estimated by Collen et al. (2014)), and negative congruence with
456 freshwater crabs ($\text{corr} = -0.05$, $F = 5.42$, adjusted d.f. = 2375.5, $p = 0.020$; Table 4).
457 Congruence between Data Deficient species richness was significantly positive between
458 freshwater molluscs and freshwater fish ($\text{corr} = 0.21$, $F = 6.12$, adjusted d.f. = 131.04, $p =$
459 0.015), and all freshwater species ($\text{corr} = 0.18$, $F = 4.54$, adjusted d.f. = 133.35, $p = 0.035$;
460 Table 4). All other species richness patterns were not spatially congruent with that for
461 freshwater molluscs (Table 4).

462

463 **Discussion**

464 Here, we present the first global analysis of the extinction risk of freshwater molluscs by
465 utilising an established method to assess a random sample of freshwater mollusc species from
466 around the world (Baillie et al. 2008). Our sample of 1,428 species constitutes around a
467 quarter of the global species diversity of freshwater molluscs and shows that 30% of species
468 in our sample are threatened with extinction.

469 *Patterns of threat*

470 Extinction risk in freshwater taxa is known to exceed that of terrestrial taxonomic groups
471 (Collen et al. 2014; McRae et al. 2017). Levels of threat for our sample of freshwater
472 molluscs are comparable to those of freshwater crayfish and freshwater crabs (32%;
473 Cumberlidge et al. 2009; Richman et al. 2015), lower than those for amphibians (42%; Stuart
474 et al. 2004) and higher than those for Odonata (14%; Clausnitzer et al. 2009). Regional
475 assessments of freshwater species, including molluscs, show a broadly similar pattern to our
476 results, with high levels of threat in Europe (Cuttelod et al. 2011), although our current
477 analysis fails to highlight the high levels of threat observed in continental Africa (Seddon et
478 al. 2011).

479 Threat was particularly high in freshwater gastropods, for which more species had
480 smaller ranges compared to the often broadly distributed bivalves (median distribution size
481 for gastropods in our sample was 26,863 km² compared to a median of 259,386 km² for
482 bivalves; Figure S15). High gastropod threat levels have also been shown in regional analyses
483 using the IUCN Red List Categories and Criteria, where gastropods, particularly
484 “prosobranchs”, consistently showed the highest levels of threat (Cuttelod et al. 2011; Seddon
485 et al. 2011). Our analysis found threat levels for gastropods to be highest in Europe, and

486 negatively correlated with threat levels in bivalves which had the highest threat levels in
487 North America. Some of the highly threatened gastropod families, such as the Tateidae,
488 consist of small-sized species with restricted distributions; unsurprisingly, many species of
489 Tateidae have also only recently been described in the past 30 years or so (Ponder 2019). In
490 our sample, 60 of the 91 species of Tateidae were described in 1990 or later; despite this, data
491 deficiency was relatively low at 14%. Members of the Moitessieriidae, also highly threatened
492 in our sample, are small snails, leading a mainly subterranean lifestyle, with patchy and
493 restricted distributions and often known from few or only single localities; some may be
494 under-sampled given the challenge to collect and detect these subterranean species (Wilke
495 2019), though data deficiency in our sample was again relatively low (24%) compared to
496 other families.

497 Lower overall threat of freshwater bivalves is primarily due to the relatively low
498 estimated threat levels in the bivalve family Sphaeriidae, a family of almost cosmopolitan and
499 widespread species with very few threats reported. However, these small bivalves have
500 attracted much less research attention by conservationists than the larger unionids, thus have
501 higher levels of data deficiency (36% versus 12% in the Unionidae; Table 2). Recent studies
502 suggest that threat levels in freshwater bivalves may be higher than estimated here. For
503 example, a recent study on the status and distribution of the world's freshwater bivalves
504 suggested that 40% of bivalves are either Near Threatened, threatened or Extinct (Lopes-
505 Lima et al. 2018). Including Extinct and Near Threatened species into our estimate, our
506 results suggest that 34% of freshwater bivalve species are threatened or extinct (lower
507 estimate: 26%; upper estimate: 48%). In addition, using alternative assessment processes,
508 such as the one employed by the American Fisheries Society, nearly equal levels of 74% and
509 72% of species are imperilled for gastropods and bivalves, respectively (Johnson et al. 2013).
510 The fact that information on population trends may also be missing for many large bivalve

511 species, which are often long-lived (Vaughn & Taylor 2001) and therefore requiring long-
512 term monitoring to detect trends, may lead to an underestimate of extinction risk, particularly
513 when only range-based metrics are available to assess extinction risk (Torres et al. 2018).

514 High levels of threat in freshwater species are expected in a system that is impacted
515 by many different threats, especially given the high interconnectivity of freshwater systems.
516 To determine the importance of different threats to freshwater species, various studies have
517 analysed large-scale datasets such as the IUCN Red List. For example, Collen et al. (2014)
518 found habitat loss and degradation (which includes urban development and dam building),
519 pollution and overexploitation to be the three most frequently reported threats. Interestingly, a
520 recent analysis using an alternative dataset on vertebrate freshwater species trends, the Living
521 Planet database (McRae et al. 2017), has shown natural system modifications (24.1%),
522 agriculture and aquaculture (16.4%) and pollution (15.2%) as the most important threats
523 (Thorburn 2017). Assessing the predominant drivers of extinction risk and population decline
524 is a complex task, given that species may be impacted by multiple, often synergistic threats,
525 drivers of decline may vary from region to region (Figure 2C) and that species experts may
526 differ in their perception of the importance of different threat processes to species decline or
527 in their recording of drivers according to the IUCN Threat Classification Scheme (e.g.
528 sedimentation is coded under pollution, but may be caused by logging of forest, which
529 constitutes biological resource use). In a centrally-led project, inconsistencies can be
530 minimised through a rigorous review process and justification of identified threats.

531 In our present analysis, pollution and natural system modification were the most
532 common threats affecting freshwater molluscs globally, ranking in the top two most prevalent
533 threats in all biogeographical realms bar the Afrotropics, and natural system modification
534 specifically was associated more than expected with CR listings. Establishment of dams and
535 other barriers presents a major threat to freshwater biodiversity (He et al. 2018). Freshwater

536 mussels require fish hosts for the completion of their life cycle and dispersal (Modesto et al.
537 2018), and dams may block migratory routes for fish (Maceda-Veiga 2013). Movement of
538 fish hosts is vital for connectivity of mussel populations and metapopulation dynamics (Zajac
539 et al. 2018). It has been shown that mussel species richness and abundance is reduced closer
540 to river impoundments, suggesting an extinction risk gradient downstream of these structures
541 (Vaughn & Taylor 2001). Local extirpation rates of mussels have previously been predicted
542 by their primary fish hosts: mussels that require large migratory fish to complete their life
543 cycle had higher extirpation rates due to river fragmentation (Vaughn 2012). Not only do
544 dams and barriers cause habitat fragmentation, they are also a major factor reducing climate
545 change resilience of freshwater systems (Markovic et al. 2017). Some of these factors are
546 likely behind the observed higher threat levels in lotic versus lentic system, a finding
547 corroborated in other studies (Clausnitzer et al. 2009, Collen et al. 2014). It is therefore of
548 utmost importance that we address connectivity of freshwaters when identifying priority
549 areas for conservation and identify the barriers that human perturbations pose to connectivity
550 (Hermoso et al. 2018).

551 Freshwater molluscs are among the most sensitive freshwater species to several
552 chemicals, particularly as juveniles (Wang et al. 2017). While pollution was associated more
553 than expected with lower threat categories of NT and LC globally, it was the most
554 commonly-cited threat in the Afrotropics and Indomalaya. For example, pollution in form of
555 agricultural runoff (especially from monoculture crops like rubber or palm oil plantations)
556 and sedimentation are a major threat to freshwater molluscs in Indonesia (Gallardo et al.
557 2018, Zieritz et al. 2018a). Therefore, regional threat analyses are vital to highlight regional
558 differences in predominant threats, and to put in place regional action plans to combat threats
559 in a meaningful and targeted way. We may still be underestimating the impact of pollution on
560 freshwater molluscs, since sublethal effects of pollution, and how it may impact gene

561 expression and ecological condition, are still under-researched (Ferreira-Rodríguez et al.
562 2019).

563 Global change and trade globalization have spurred an increase in bioinvasions and
564 their subsequent impacts on ecosystems (Darrigran & Damborenea 2011; Gallardo et al.
565 2018). Darrigran et al. (2020) identified four hotspot areas for non-native species of molluscs
566 (both aquatic and terrestrial) in South America, which require special attention for
567 biodiversity conservation, not only because they are potential entry points for non-native
568 species, but also because they coincide with hotspots of high endemism (Darrigran et al.
569 2020). Identifying entry points of non-native molluscs, such as through large cities, ports, or
570 airports (Darrigran et al. 2020), is a vital step to identify hotspots for conservation action.

571 Climate change is likely to have an impact on freshwater molluscs, yet this was not
572 reflected in our analysis. Climate change is often not highlighted in IUCN Red List
573 assessments as an ongoing threat, given the Red List's focus on immediate impacts on
574 species over relatively short timeframes, depending on the generation length of the species in
575 question (Trull et al. 2017; IUCN Standards and Petitions Committee 2019). However, our
576 knowledge gap on climate change impacts on freshwater molluscs has started to be filled with
577 climate change vulnerability analyses, e.g. following Young et al. (2011) and Foden &
578 Young (2013), and other research activities. With a reassessment of the SRLI for freshwater
579 molluscs about to commence, we envisage that we will see the threat from climate change
580 increase in our assessments, given some of the recent work on climate change impacts on
581 freshwater species identifying range contractions and shifts (e.g. Markovic et al. 2014;
582 Gallardo et al. 2018). Already, climate change is the joint most frequently recorded future
583 threat to our freshwater molluscs, together with natural system modification and pollution
584 (Figure S12).

585 Incongruence between spatial patterns of freshwater mollusc species richness in
586 comparison to other taxonomic groups, with the exception of crayfish which have hotspots in
587 North America and Europe (Richman et al. 2015), suggests that macroecological patterns of
588 species richness and range may be governed by different determinants, depending on the
589 species group in question (Collen et al. 2014) and its evolutionary history. Therefore,
590 conservation priority areas are likely to vary, depending on the focal species group. High
591 aquatic species richness in parts of North America and Southeast Asia reflect known hotspots
592 of freshwater molluscs (e.g. Lydeard & Mayden 1995; Zieritz et al. 2018a). High species
593 richness in our sample in parts of Europe is likely a reflection of a larger number of
594 taxonomists working there, with well-defined species boundaries as a result. In contrast, the
595 comparatively lower species richness and levels of threat in our sample in South America,
596 despite the presence of similar threats, reflects understudied species groups where threats
597 have not yet been adequately reported. Central America is also a vastly understudied region
598 demonstrated by the fact that no native bivalves and only a dozen gastropod species found in
599 the area are included here. In addition, recently completed assessment work in West Africa is
600 showing that the situation for freshwater molluscs is rapidly deteriorating, primarily due to
601 conversion of wetlands for food production (D. van Damme, pers. comm.). These new
602 findings will be integrated into our upcoming reassessment of the SRLI species set.

603 East Asia also harboured hotspots of freshwater molluscs in our sample, specifically
604 for gastropod species richness and Data Deficient bivalves, which did not emerge during
605 previous study of spatial patterns of freshwater richness and threat (Collen et al. 2014). Recent
606 molecular studies have unearthed the presence of morphologically cryptic species which have
607 increased species richness in the area (Zieritz et al. 2018a). Despite a recent increase in research
608 attention on diversity, biogeography, evolution and – most recently – conservation of
609 freshwater molluscs in the region (e.g. Saito et al. 2018, Zieritz et al. 2018a, Huang et al. 2019,

610 Bolotov et al. 2020, Lopes-Lima et al. 2020), primary sources on species distributions and
611 biogeography in many countries are still outdated (Zieritz et al. 2018a). Future reassessments
612 of our species sample are likely to see decreasing levels of data deficiency in this and other
613 regions, while it is likely that the taxonomy of our sample will undergo additional changes as
614 additional molecular studies and field surveys are carried out. New species hotspots are
615 gradually emerging with increased molecular study, e.g. Honshu, Kyushu and Hokkaido in
616 Japan and the Korean peninsula in East Asia (Lopes-Lima et al. 2020), and it is vital that
617 protective measures are put in place to not repeat the fate of the better-studied freshwater
618 mollusc fauna of Europe and North America.

619

620 *Data Deficiency*

621 High levels of data deficiency preclude our ability to adequately represent species groups in
622 conservation action plans and prioritisation schemes. Data deficiency in freshwater molluscs
623 (36%) was greater than in crayfish (20%; Richman et al. 2015), roughly comparable to that in
624 the Odonata (35%; Clausnitzer et al. 2009), but much lower than in freshwater crabs (49%;
625 Cumberlidge et al. 2009). The most obvious causes for the high prevalence of DD species in
626 our sample are: 1) a deficiency of experts in the field of invertebrate systematics (Agnarsson
627 & Kuntner 2007; Kotov & Gololobova 2016; 2) discrepancies among molluscan systematists
628 with regard to species rank and the methods of species delimitation (e.g. Vinarski 2018),
629 which leave the species status of many freshwater molluscan taxa in dispute; 3) lack of
630 monitoring of abundance and status of freshwater molluscan populations, especially in
631 hotspots of freshwater biodiversity in developing countries. Many nominal species of
632 freshwater molluscs have not been studied (or even recorded) since their taxonomic
633 description. Outdated, morphology-based taxonomies persist in many groups of freshwater
634 molluscs (Graf 2007; Torres et al. 2018), though usage of modern molecular techniques show

635 that some are incomplete. In the few genera and families where revisions have been made,
636 drastic reassessment of the commonly accepted taxonomies changed species richness
637 estimates (e.g. Osikowski et al. 2018; Bolotov et al. 2020; Lopes-Lima et al. 2020), and
638 conservation status of individual species. For example, there has been an increase in the
639 numbers of new species with often restricted ranges, e.g. in Southeast Asian Unionids
640 (Bolotov et al. 2020). Since data deficiency was high amongst most of the taxonomic sub-
641 groups in our study, increased efforts are needed across orders and families of freshwater
642 molluscs to improve our knowledge on this ecologically important group. In addition,
643 predictive techniques may be used to assess the most likely threat status of Data Deficient
644 species within our sample, and have been carried out for other species groups (Bland et al.
645 2015). Reducing the number of DD species in our study and for freshwater molluscs in
646 general will allow not only for more accurate biodiversity indicators, but initiate better
647 conservation actions for individual species and/or regions.

648 *Adequacy of sample, sample size and SRLI process*

649 Taxonomically, comparison to published literature suggests that our study sample broadly
650 represents freshwater mollusc diversity at the global scale. For example, based on globally
651 available estimates of freshwater bivalve species richness (Lopes-Lima et al. 2018), our
652 sample broadly represents bivalve families adequately, although it over-represents
653 Sphaeriidae (18% of the world's freshwater bivalve species, represented by ~24% of species
654 in our sample). Other studies have found a similar broad-scale representativeness of the
655 random sampling technique for other species groups, such as fish, where the sample
656 adequately represented both marine and freshwater fish diversity and traits (R. Miranda,
657 unpublished data). Given the nature of a random sample, it will also omit some smaller
658 families, here for example the Mycetopodidae. Throughout the project, species had to be

659 replaced due to synonymy; future taxonomic revisions are likely to lead to more
660 replacements, and we have to ensure that we use up-to-date species lists to draw replacements
661 from. In addition, we will also replace those species excluded from the current assessment
662 because they were not fully freshwater, to regain a sample size of 1,500 species. Twenty-
663 seven of the 74 excluded species were assessed as DD, 39 as LC and one as CR; several of
664 these species were from the Caspian Sea region, for which latest data suggest deteriorations
665 in status for many species (Wesselingh et al. 2019). It is therefore also important that
666 brackish or other semi-freshwater species do not fall through the cracks of conservation.

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

682 Apart from spatial bias, estimating threat status of freshwater molluscs, and sub-
683 groups thereof, based on a sample of only around 25% known freshwater molluscs may

684 introduce bias into our estimate. These shortcomings are to be expected especially since the
685 sample size of 900 non-DD species recommended by Baillie et al. (2008) was only devised to
686 accurately detect extinction risk trends in a species group over time. Thus, we cannot make
687 any conclusions from our sample on overall level of threat within this or any sampled species
688 group, although work is ongoing to test the accuracy of sampled status estimates. This is
689 important since we do not have the resources to run comprehensive assessments for all
690 species groups, especially highly species-rich ones; for example, a recent study shows that we
691 may be able to utilise a smaller sample of around 400 non-DD species to accurately depict
692 extinction risk trends over time (Henriques et al. 2020). This will be tested with the upcoming
693 re-assessment of freshwater molluscs in the coming years.

694 *The future of freshwater molluscs*

695 Freshwater molluscs provide invaluable functions to freshwater ecosystems, and ecosystem
696 services to humans, but are under high levels of threat. It is vital that conservation actions are
697 increased to safeguard freshwater ecosystems and the species, including molluscs, that
698 depend on them, given the manifold threats impacting these fragile systems. While this
699 sampled global assessment gives an overview of issues impacting freshwater molluscs across
700 the globe and at the broad regional level, it is vital that comprehensive action plans are drawn
701 up to preserve freshwater systems and its biodiversity at regional, national or sub-national
702 scales, given that drivers of threat may vary from region to region. However, natural system
703 modification, especially through dams, and pollution are frequently recorded and are likely to
704 have a substantial impact on freshwater molluscs worldwide. While pollution was not
705 particularly associated with high extinction risk, it is vital to combat water pollution to ensure
706 healthy mollusc populations which may be more robust to withstand other threats.
707 Establishment of riparian buffers to minimise run-off within impacted areas, improvements to

708 wastewater treatment and regulation of pesticides and fertilizers are all actions which have
709 previously been suggested (e.g. Zieritz et al. 2018b, Tickner et al. 2020), especially in areas
710 such as Southeast Asia. Where water is heavily managed for energy generation, flood risk
711 reduction or is abstracted for agriculture, environmental flows need to be considered in
712 environmental impact assessments, infrastructure design and watershed management to
713 minimise impacts on biodiversity; identification and monitoring of introduction pathways is
714 needed to prevent further detrimental species invasions, as is protection of critical habitat to
715 prevent extinctions (Darrigran et al. 2020, Tickner et al. 2020). In addition, research should
716 focus on priorities for conservation of these species and better understanding of the impact of
717 threats, such as pollution and climate change (Ferreira-Rodríguez et al. 2019). More research
718 on the systematics, ecology, and status of freshwater molluscs, particularly in the Neotropics
719 and Southeast Asia, are sorely needed to better assess their conservation status.

720 With globally agreed policy targets aiming to combat species extinctions and declines,
721 while also protecting the services that underpin human livelihoods and well-being, this study
722 demonstrates that we must step up our commitment to the conservation of freshwater systems
723 if we want to achieve these targets. Establishment of protected areas aimed at freshwater
724 species conservation, targeted in-situ conservation programmes and clear freshwater policies
725 are needed to safeguard freshwater systems into the future. Climate change in particular will
726 strain both freshwater species and human water use (Strayer & Dudgeon 2010), so ecosystem
727 approaches are required to mitigate impacts of climate change. In addition, our data shows
728 that freshwater extinctions are already underway; it has previously been stated that the time to
729 act is now (Strayer & Dudgeon 2010). Incomplete knowledge should not be a barrier to
730 carrying out conservation actions for those species known or thought to be most at risk. The
731 planned reassessment of the sample of freshwater molluscs, to commence this year, will
732 provide a first glimpse into extinction risk trends of freshwater species globally. To underpin

733 this and future reassessments to track status of freshwater molluscs, there is a vital need for
734 widespread monitoring of freshwater species.

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Table 1. Extinction risk in a random sample of 1,428 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	<i>n</i>	<i>n non-DD</i>	Prop. threatened	Lower prop	Upper prop
All	520	545	66	115	76	80	26	1,428	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	1,093	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
Palearctic	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	1,071	771	0.305	0.219	0.502

Table 2. Extinction risk in a random sample of 1,428 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	1,093	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
Chilinidae	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
Subclass Palaeoheterodonta	227	59	31	13.7	0.312	0.268	0.409	7
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

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). 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;

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

Table 4. Top ten countries with most native species in our random sample of 1,428 freshwater molluscs, by IUCN presence code (full table available in the Supplementary Materials). * includes extant, extinct and uncertain presence codes

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

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 freshwater¹
SR	Corr	0.07	-0.02	0.52***	0.15	0.26*	0.33***	0.15
	F	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*
	F	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*
	F	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

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 = 1,384 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).

Figure 2. 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 (AGR/AQ – Agriculture and aquaculture; BRU – Biological resource use, mostly exploitation; CC – Climate change; DEV – Residential and commercial development; ENERGY – Energy production; INV - Invasive and other problematic species; NSM – Natural system modification; POLL - Domestic & urban waste, industrial effluent).

Figure 3. 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 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.

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.