

9-12-2020

The conservation status of the world's freshwater molluscs

M. Böhm

N. I. Dewhurst-Richman

M. Seddon

C. Albrecht

D. Allen

See next page for additional authors

Follow this and additional works at: https://scholarworks.utrgv.edu/bio_fac



Part of the [Animal Sciences Commons](#), [Biology Commons](#), and the [Fresh Water Studies Commons](#)

Recommended Citation

Böhm, M., Dewhurst-Richman, N.I., Seddon, M. et al. The conservation status of the world's freshwater molluscs. *Hydrobiologia* (2020). <https://doi.org/10.1007/s10750-020-04385-w>

This Article is brought to you for free and open access by the College of Sciences at ScholarWorks @ UTRGV. It has been accepted for inclusion in Biology Faculty Publications and Presentations by an authorized administrator of ScholarWorks @ UTRGV. For more information, please contact justin.white@utrgv.edu, william.flores01@utrgv.edu.

Authors

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

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

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

9 1 – Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY

10 2 – Department of Geography, University College London, Gower Street, London, WC1E
11 6BT, United Kingdom

12 3 -

13 4 – Department of Animal Ecology and Systematics, Systematics and Biodiversity Group,
14 Justus Liebig University Giessen, H.-Buff-Ring 26-32 (IFZ), D-35392 Giessen, Germany

15 5 – Freshwater Biodiversity Unit, IUCN Global Species Programme, The David
16 Attenborough Building, Pembroke Street, Cambridge CB2 3QZ, United Kingdom.

17 6 – North Carolina Museum of Natural Sciences, 11 West Jones Street, Raleigh, NC 27601
18 USA

19 7 - Illinois Natural History Survey, Prairie Research Institute, University of Illinois, 607 E.
20 Peabody Drive, Champaign, IL 61820, USA.

- 21 8 - Museo de La Plata, La Plata National University (UNLP), Paseo del Bosque sin numero,
22 La Plata (1900). Argentina.
- 23 9 - Department of Zoology, Hungarian Natural History Museum, H-1088, 13 Baross street,
24 Budapest, Hungary
- 25 10 - University of Wisconsin-Stevens Point, Stevens Point WI 54481, USA
- 26 11 – Australian Museum, Australian Museum Research Institute, 1 William Street, Sydney,
27 NSW 2010, Australia
- 28 12 - CIBIO/InBIO - Research Center in Biodiversity and Genetic Resources, Universidade do
29 Porto, Campus Agrário de Vairão, Rua Padre Armando Quintas, 4485-661 Vairão, Portugal
- 30 13 - Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Av. Angel Gallardo
31 470 3° piso lab. 80, C1405DJR Ciudad Autónoma de Buenos Aires, Argentina
- 32 14 – Department of Geology, Ghent University, Belgium
- 33 15 - Laboratory of Macroecology & Biogeography of Invertebrates, Saint-Petersburg State
34 University, 7/9 Universitetskaya Emb. 199034 Russia
- 35 16 – Göteborg Natural History Museum, Sweden
- 36 17 – Museum für Naturkunde, Leibniz Institute for Evolution and Biodiversity Science,
37 Invalidenstraße 43, 10115 Berlin, Germany
- 38 18 - University of Cambridge, Department of Zoology, The David Attenborough Building,
39 Cambridge CB2 3QZ, United Kingdom
- 40 19 - Central Department of Zoology, Tribhuvan University, Kirtipur, Kathmandu, Nepal

- 41 20 - Institute of Ecology and Biological Resources, Vietnam Academy of Science and
42 Technology, 18 Hoang Quoc Viet, Cau Giay, Hanoi, Vietnam
- 43 21 - Graduate University of Science and Technology, Vietnam Academy of Science and
44 Technology, 18 Hoang Quoc Viet, Cau Giay, Hanoi, Vietnam
- 45 22 - Vogelwarte, Zoologisches Institut und Museum, Universität Greifswald,
46 Soldmannstrasse 23, 17489 Greifswald, Germany.
- 47 23 - Alabama Aquatic Biodiversity Center, Alabama Department of Conservation and
48 Natural Resources, 2200 Highway 175, Marion, AL 36756, USA.
- 49 24 - Mehmet Akif Ersoy, Science and Arts Faculty, Department of Biology, Burdur, Turkey.
- 50 25 - Suri Sehgal Center for Biodiversity and Conservation, Ashoka Trust for Research in
51 Ecology and the Environment (ATREE), Royal Enclave, Srirampura, Jakkur PO Bangalore
52 560064, India.
- 53 26 - Yenepoya Research Center, Yenepoya University, University Road, Deralakatte,
54 Mangalore 575018, India.
- 55 27 –
- 56 28 - Institut de Systématique, Évolution, Biodiversité ISYEB – Museum National d’Histoire
57 Naturelle, CNRS, Sorbonne Université, EPHE, Université des Antilles, 57 rue Cuvier, CP26,
58 F-75005 Paris, France.
- 59 29 - Department of Ecology and Systematics, Faculty of Biology, National and Kapodistrian
60 University of Athens, Panepistimiopolis 15784, Greece.
- 61 30 - Institute of Marine Biology, NAS of Ukraine, 37 Pushkinska St. 65048, Odessa, Ukraine.

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

64

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

66

67

68

69 **Abstract**

70 With the biodiversity crisis continuing unchecked, we need to establish levels and drivers of
71 extinction risk to effectively allocate conservation resources and develop targeted actions.
72 Given that threat appears particularly high in freshwaters, we assessed the extinction risk of
73 1,500 randomly selected freshwater molluscs using the IUCN Red List Categories and
74 Criteria, as part of the Sampled Red List Index project. We show that close to one third of
75 species in our sample are estimated to be threatened with extinction, with highest levels of
76 threat in the Palearctic, Australasia and Nearctic and among gastropods. Threat levels were
77 higher in lotic than lentic systems. Twenty-seven species were classified as Extinct (eight
78 bivalves and 19 gastropods), mostly from the Nearctic realm and lotic systems. Pollution and
79 the modification of natural systems (e.g. through damming and water abstraction) were the
80 most frequently reported threats to freshwater molluscs, with some regional variation. Given
81 that we found little spatial congruence between species richness patterns of freshwater
82 molluscs and other freshwater taxa, new additional conservation priority areas emerge from
83 our study. We discuss the implications of our findings for freshwater mollusc conservation
84 and important next steps to estimate trends in freshwater mollusc extinction risk over time.

85

86 **Keywords:**

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

88

89

90 **Introduction**

91 With the biodiversity crisis continuing unchecked (Butchart et al. 2010; Tittensor et
92 al. 2014), it is vital to determine levels and drivers of species' extinction risk to effectively
93 allocate conservation resources and develop targeted conservation actions. In addition,
94 monitoring changes in extinction risk over time allows us to track changing biodiversity
95 status (Butchart et al. 2004) and evaluate our progress towards meeting global, regional and
96 national biodiversity targets (e.g., Aichi Targets of the Convention on Biological Diversity
97 [CBD] and the Sustainable Development Goals [SDGs]). Many studies have described threat
98 patterns of various species groups using the data provided by the IUCN Red List of
99 Threatened Species, which describes extinction risk, dominant threats and recommended
100 conservation action (Mace et al. 2008). For example, Torres et al. (2018) used the IUCN Red
101 List of Threatened Species to prepare the first comparative analysis of risk of freshwater
102 Unionida bivalves from South America. Global analyses of these valuable data have shown
103 that 25% of mammal species (Schipper et al. 2008), 42% of amphibians (Stuart et al. 2004),
104 19% of reptiles (Böhm et al. 2013), 32% of freshwater crabs (Cumberlidge et al. 2009), 14%
105 of dragon- and damselflies (Clausnitzer et al. 2009) and 32% of crayfish (Richman et al.
106 2015) are threatened with extinction. These analyses have also revealed how predominant
107 drivers of extinction risk differ between higher taxa and ecosystems. Consequently, Red Lists
108 are important tools for prioritising resources towards species and ecosystems most in need
109 and identifying necessary actions to combat threats.

110 Freshwater ecosystems are under extensive pressure from anthropogenic threats.
111 Freshwaters constitutes < 1% of the total volume of the hydrosphere but maintain several tens
112 of thousands of animal species not able to live in salinated water (e.g. Balian et al. 2008).
113 Some are restricted in distribution to a single waterbody (such as Baikal Lake, Tennessee
114 River Basin, or single waterfalls in the Western Ghats). It has been suggested that

115 approximately 80% of the world's human population faces threats to water security
116 (Vörösmarty et al. 2010), and almost one in three freshwater species are estimated at risk of
117 extinction worldwide (Collen et al. 2014), with habitat loss being the most commonly cited
118 threat. A recent analysis of distribution and threat to freshwater megafauna (fish, mammals,
119 amphibians, reptiles) showed that increasing human pressures occur in many biodiversity
120 hotspots (He et al. 2018). Given the high connectivity of freshwater systems, threat processes
121 and their detrimental effects are easily transported from one locality to another (Darwall et al.
122 2009; Dudgeon et al. 2006) and fragmentation can have profound effects on water flows,
123 sedimentation, habitat loss and hence species loss (Revenga et al. 2005).

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

132 Previous work has highlighted the plight of freshwater molluscs: for example, in
133 2000, 202 of nearly 300 unionid species from Canada and the United States were listed as
134 either extinct, possibly extinct, or in the critical categories (critically imperilled, imperilled,
135 vulnerable; Lydeard et al. 2004, Master et al. 2000); a recent assessment of freshwater
136 gastropods showed that 67 of 703 US and Canadian species were considered extinct (Johnson
137 et al. 2013), primarily due to the effects of damming and river channelisation. Within Europe,
138 44% of freshwater molluscs were assessed as threatened with extinction (Cuttelod et al. 2011)
139 compared to 29% in continental Africa (Seddon et al. 2011) and 17% in the Indo-Burma

140 region (Köhler et al. 2012). There are likely many more unnoticed extinctions of freshwater
141 molluscs around the globe (Cowie et al. 2017, Régnier et al. 2009, Régnier et al. 2015). Such
142 levels of threat mirror the general decline and threat in freshwater ecosystems (Collen et al.
143 2014).

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

159 **Materials and Methods**

160 *The Red List assessment process*

161 Baillie et al. (2008) showed that a sample size of 900 non-Data Deficient species was
162 sufficiently large to accurately report on trends in extinction risk, while buffering against

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

174 Overall, 371 of the 1,452 selected species were assessed as part of IUCN regional
175 assessment projects, specifically Europe (Cuttelod et al. 2011), Pan-African (Darwall et al.
176 2009), Eastern Himalayas (Allen et al. 2010), the Western Ghats (Molur et al. 2011) and
177 Indo-Burma (Köhler et al. 2012). For the remaining 1,081 species, new or updated
178 assessments were produced through consultation with a global network of malacologists at an
179 assessment workshop in January 2010. Species-specific data were collected on taxonomy,
180 distribution, population trends, ecology and biology, threats, and conservation measures for
181 all species in the assessment. Assessments followed the IUCN Red List Categories and
182 Criteria (IUCN 2001) and all species were assessed against the quantitative thresholds of the
183 five Red List criteria which indicate level of extinction risk (Mace et al. 2008): rate of
184 population decline (Criterion A), population size (Criteria C and D/D1), geographic range
185 size and decline (Criterion B), very small population size (Criterion D) or restricted range
186 (Criterion D2) or quantitative analyses (Criterion E). Extinction risk ranges from the highest
187 risk categories, Extinct (EX) and Extinct in the Wild (EW), via the threatened categories

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

199

200 *Summarising extinction risk*

201 We summarised extinction risk within our sample across all freshwater molluscs and by
202 taxonomic class (bivalves and gastropods), order and family, biogeographical realm
203 (Afrotropical, Australasian, Indomalayan, Nearctic, Neotropical, Oceanian and Palearctic)
204 and habitat system (lotic versus lentic systems). Following previous studies (Böhm et al.
205 2013, Clausnitzer et al. 2009, Richman et al. 2015), we estimated extinction risk in our
206 sample as the proportion of threatened species (Critically Endangered, Endangered and
207 Vulnerable species), assuming that Data Deficient species will fall into threatened categories
208 in the same proportion as non-Data Deficient species:

$$209 \quad \text{Prop}_{\text{threat}} = (\text{CR} + \text{EN} + \text{VU}) / (\text{N} - \text{DD} - \text{EX}),$$

210 where N is the total number of species in the sample, CR, EN and VU are the numbers of
211 species in each of the three threatened categories respectively, DD is the number of species in
212 the Data Deficient category, and EX the number of species in the Extinct category. We

213 provided upper and lower bounds of our estimate by assuming that (a) no Data Deficient
214 species were threatened [lower margin: $\text{Prop}_{\text{threat_lower}} = (\text{CR} + \text{EN} + \text{VU})/(\text{N} - \text{EX})$], and (b)
215 all Data Deficient species were threatened [upper margin; $\text{Prop}_{\text{threat_upper}} = (\text{CR} + \text{EN} + \text{VU} +$
216 $\text{DD})/(\text{N} - \text{EX})$]. It should be noted that these are estimates and upper/lower bounds of
217 extinction risk within our sample only and may not accurately reflect the proportion of
218 freshwater molluscs threatened worldwide. This is because the sampled approach employed
219 here was devised to accurately detect trend direction of the RLI over time, and was not
220 devised to accurately reflect threat status for a species group as a whole at a particular point
221 in time.

222 *Assessment of drivers of extinction risk*

223 During the assessment process, threat processes were recorded for each species and coded
224 following Salafsky et al. (2008) (Table S1). We summarised the number of species affected
225 (across the global sample and by biogeographic region) by each of the following high-level
226 threat processes: residential and commercial development; agriculture and aquaculture;
227 energy production and mining; transportation and service corridors; biological resource use;
228 human intrusion and disturbance; natural system modification; invasive and other
229 problematic species; pollution; geological events; and climate change and severe weather
230 (Salafsky et al. 2008). Using permutation-based chi-square tests, we determined whether
231 threat processes were randomly spread across Red List categories, by looking at a) threatened
232 (CR, EN, VU) versus non-threatened (NT, LC) classification, and b) individual Red List
233 categories (CR, EN, VU, NT, LC). We carried out permutation chi-square tests using a) all
234 518 threatened and non-threatened species which were affected by one or more threat
235 processes (the remainder of species does not have any threats, or the threats are unknown, or
236 species are DD), and b) all 142 species affected by a single threat process only. We permuted

237 the tables 1,000 times, and supplemented the results of this analysis with Fisher exact tests
238 where the data had low expected values of less than 5 (for single-threat species only).

239

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

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

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

260 mapped congruence of species richness hotspots between gastropods and bivalves in our
261 analysis by selecting the top 10% of cells with the highest normalised richness values.

262 We also assessed spatial congruence between patterns of species richness, threatened
263 species richness and Data Deficient species richness of our sample of freshwater molluscs
264 and those derived from other freshwater species groups. First, we recalculated richness
265 patterns for six different groups of freshwater species (amphibians, crabs, crayfish, fish,
266 mammals and reptiles) obtained from a previous study on the spatial distribution of
267 freshwater species and threat (Collen et al. 2014) at our 1° spatial scale. We then produced
268 normalised species richness maps for each as described above to account for different sample
269 sizes in the various species groups (Collen et al. 2014). To assess spatial congruence between
270 species richness patterns of freshwater molluscs and other groups of freshwater species, we
271 again generated spatial overlays of the three measures of species richness – species richness,
272 threatened-species richness, and Data Deficient-species richness – for each taxonomic group,
273 and estimated spatial congruence using Pearson’s correlations, as described above. We
274 applied this using only cells with non-0 normalised richness for molluscs, to minimise
275 inflation of association (Legendre & Legendre 1998). We mapped congruence of species
276 richness hotspots for all freshwater taxonomic groups in our analysis by selecting the top
277 10% of cells with the highest normalised richness values, and mapping the number of taxon
278 groups overlapping in each grid cell.

279 **Results**

280 *Extinction risk in freshwater molluscs*

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

284 Nearctic, Palearctic and Australasian realms (Nearctic: $\text{prop}_{\text{threat}} = 0.36$, lower = 0.30, upper =
285 0.46; Palearctic: $\text{prop}_{\text{threat}} = 0.35$, lower = 0.19, upper = 0.65; Australasia: $\text{prop}_{\text{threat}} = 0.34$,
286 lower = 0.25, upper = 0.50; Table 1). Data deficiency was particularly high in tropical
287 regions, especially the Neotropical and Indomalayan realms (50.3% and 49.0% of species,
288 respectively), the Palearctic (45.5% of species) and Oceania (43.5% of species). Threat levels
289 were estimated to be higher in lotic systems than lentic systems (lotic: $\text{prop}_{\text{threat}} = 0.31$, lower
290 = 0.22, upper = 0.50; lentic: $\text{prop}_{\text{threat}} = 0.18$, lower = 0.12, upper = 0.45).

291 Estimated threat levels were higher in gastropods ($\text{prop}_{\text{threat}} = 0.33$; lower = 0.19,
292 upper = 0.61) than bivalves ($\text{prop}_{\text{threat}} = 0.26$; lower = 0.20, upper = 0.43; Table 1). Threat
293 and data deficiency levels varied greatly amongst families: for example, the bivalve family
294 Unionidae was the most species-rich families within the sample (N= 191), with 33% of
295 species estimated threatened (lower = 0.29, upper = 0.42) and a relatively low level of data
296 deficiency (12% of species in the family), followed by the gastropod families Hydrobiidae
297 (N= 157) with 67% species threatened (lower = 0.44, upper = 0.78) and a third of species
298 listed as DD, and the Planorbidae (N= 155), with only 3% of species threatened (lower =
299 0.01, upper = 0.54), yet high levels of data deficiency ($\text{prop}_{\text{DD}} = 0.52$). The Margaritiferidae
300 are another highly threatened family of bivalves in our sample (N= 7, $\text{prop}_{\text{threat}} = 0.67$; lower
301 = 0.57, upper = 0.71). For gastropods, other highly threatened families in our sample are the
302 Moitessieriidae (N= 36, $\text{prop}_{\text{threat}} = 0.74$; lower = 0.56, upper = 0.81), Semisulcospiridae (N=
303 12, $\text{prop}_{\text{threat}} = 0.63$; lower = 0.42, upper = 0.75), Pachychilidae (N= 18, $\text{prop}_{\text{threat}} = 0.50$;
304 lower = 0.39, upper = 0.61), Emmericiidae (N= 5, $\text{prop}_{\text{threat}} = 0.50$; lower = 0.20, upper =
305 0.80), and Tateidae (N= 91, $\text{prop}_{\text{threat}} = 0.49$; lower = 0.42, upper = 0.56).

306 Overall, 27 species were assessed as extinct, of which eight were bivalves and 19
307 were gastropods. Nearly one-fifth of the gastropod family Pleuroceridae assessed in our
308 sample were categorised as Extinct, by far the family with the highest percentage of Extinct

309 species in our analysis. Number of extinct species was highest in the Nearctic realm (23
310 species listed as Extinct) and in lotic systems (15 species listed as Extinct). In addition, 23
311 species are currently listed in the CR category as possibly extinct (19 gastropods of which
312 eight belong to the family Hydrobiidae, and four bivalves of which three are unionids).

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

319 *Predominant threat processes affecting freshwater molluscs*

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

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

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

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

354

355 *Spatial distribution of freshwater molluscs and congruence with other species groups*

356 Normalised species richness in our sample was highest in the Eastern USA (especially
357 Tennessee, Kentucky and surrounding states), Lake Baikal, parts of Central and Eastern
358 Europe, and selected river systems in Southeast Asia (Figure 1A; see Supplementary
359 Materials for spatial detail of the distribution pattern by region, for all species (Figure S3-S5),
360 gastropods (Figure S6-S8) and bivalves (Figure S9-S11) in our sample, respectively). High
361 species richness in Central and Eastern Europe, Lake Baikal and Southeast Asia was driven
362 by high species richness of gastropods in these regions (Figure S1A). High species richness
363 in the Eastern USA was primarily driven by bivalves (Figure S2A), although gastropods were
364 also species rich in these areas (Figure S1A), and there was significant congruence in the
365 spatial pattern of bivalve and gastropod species richness in our sample (Pearson's correlation
366 = 0.692, $F = 71.18$, adjusted d.f. = 77.52, $p < 0.001$).

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

381 There was limited evidence for cross-taxon congruence in patterns of species richness
382 at the broad-scale, with normalised species richness of freshwater molluscs positively and
383 significantly correlated with normalised species richness of crayfish (Pearson's correlation =
384 0.513, $F = 28.18$, adjusted d.f. = 78.94, $p < 0.001$), freshwater reptiles (Pearson's correlation
385 = 0.342, $F = 14.20$, adjusted d.f. = 107.57, $p < 0.001$) and freshwater mammals (Pearson's
386 correlation = 0.256, $F = 6.70$, adjusted d.f. = 95.98, $p = 0.011$; Table 4). All other species
387 richness patterns were not spatially congruent with that for freshwater molluscs (amphibians,
388 freshwater crabs and overall freshwater species richness as estimated by Collen et al. (2014);
389 Table 4).

390 There was significant positive congruence between threatened freshwater mollusc
391 richness and all threatened crayfish species richness (Pearson's correlation = 0.465, $F = 9.51$,
392 adjusted d.f. = 34.50, $p = 0.004$) and threatened freshwater species richness (Pearson's
393 correlation = 0.208, $F = 4.78$, adjusted d.f. = 105.83, $p = 0.031$), and negative congruence
394 with freshwater crabs (Pearson's correlation = -0.046, $F = 5.20$, adjusted d.f. = 2146.15, p
395 $= 0.023$; Table 4). Congruence between patterns of Data Deficient species richness were
396 significantly positive between freshwater molluscs and freshwater crayfish (Pearson's
397 correlation = 0.184, $F = 26.23$, adjusted d.f. = 746.2, $p < 0.001$), freshwater fish (Pearson's
398 correlation = 0.203, $F = 5.94$, adjusted d.f. = 138.53, $p = 0.016$) and all freshwater species
399 (Pearson's correlation = 0.177, $F = 4.52$, adjusted d.f. = 140.19, $p = 0.035$; Table 4).

400

401 **Discussion**

402 Here, we presented the first global analysis of the extinction risk of freshwater molluscs by
403 utilising an established method to assess a random sample of 1,452 species from the world's
404 freshwater mollusc species list (Baillie et al. 2008). This sample constitutes around a quarter

405 of the global species diversity of freshwater molluscs and shows that 30% of species in our
406 sample are threatened with extinction.

407 *Patterns of threat*

408 Extinction risk in freshwater taxa is known to exceed that of terrestrial or predominantly
409 terrestrial taxonomic groups (Collen et al. 2014, McRae et al. 2017). For example, 25% of
410 mammal species (Schipper et al. 2008) and 14% of birds are threatened (IUCN 2018), in
411 comparison to levels of threat for freshwater molluscs which are comparable to those of
412 freshwater crayfish and freshwater crabs (32%; Cumberlidge et al. 2009, Richman et al.
413 2015). Threat levels in our mollusc sample were lower than those for amphibians (42%;
414 Stuart et al. 2004) and higher than those for Odonata (14%; Clausnitzer et al. 2009). Regional
415 assessments of freshwater species, including molluscs, show a broadly similar pattern to our
416 results, with high levels of threat in Europe (Cuttelod et al. 2011), although our current
417 analysis fails to highlight the high levels of threat observed in continental Africa (Seddon et
418 al. 2011).

419 Threat was particularly high in freshwater gastropods, for which more species had
420 smaller ranges compared to the often large-ranged bivalves (median range size for gastropods
421 in our sample was 28,723.75 km² compared to a median of 243,401.5 km² for bivalves;
422 Figure S13). This has also been shown in previous regional analyses of freshwater threat,
423 using the IUCN Red List Categories and Criteria, where gastropods, particularly
424 “prosobranchs”, consistently showed the highest levels of threat (Cuttelod et al. 2011, Seddon
425 et al. 2011). Our analysis found threat levels for gastropods to be highest in Europe, which is
426 also shown in the European Red List for these species (Cuttelod et al. 2011), and negatively
427 correlated with threat levels in bivalves which had the highest threat levels in North America
428 (Bogan 2006). Some of the highly threatened gastropod families, such as the Tateidae, are

429 small species with restricted distributions; unsurprisingly, many species of Tateidae have also
430 only recently been described in the past 30 years or so (Ponder 2019). In our sample, 60 of
431 the 91 species of Tateidae were described in 1990 or later; despite this, data deficiency was
432 relatively low at 14% of Tateid species in our sample. Species of the family Moitessieridae,
433 also highly threatened in our sample, are small species, leading a mainly subterranean
434 lifestyle, with patchy and restricted distributions and often known from few or only single
435 localities; some species may be undersampled given the challenge to sample these
436 subterranean species (Wilke 2019), though data deficiency in our sample was again low
437 (25%) compared to other families.

438 Lower overall threat of freshwater bivalves is primarily due to the relatively low
439 threat in the bivalve family Sphaeriidae, a family of almost cosmopolitan and widespread
440 species with very few threats reported. However, these small bivalves may have attracted
441 much less research attention by conservationists than the larger unionids, and have higher
442 levels of data deficiency (36% versus 12% in the Unionidae; Table 2). Recent studies suggest
443 that threat levels in freshwater bivalves may be higher than estimated here. For example, a
444 recent study on the status and distribution of the world's freshwater bivalves suggested that
445 40% of bivalves are either Near Threatened, threatened or Extinct (Lopes-Lima et al. 2018).
446 Including Extinct and Near Threatened species into our estimate, our results suggest that 35%
447 of freshwater bivalve species are threatened or extinct (lower estimate: 26%; upper estimate:
448 50%). In addition, using alternative assessment processes, such as the one employed by the
449 American Fisheries Society, showed that broadly equal levels of 74% and 72% of species are
450 imperilled for gastropods and bivalves, respectively (Johnson et al. 2013). The fact that
451 information on population trends may be missing for a large proportion of bivalve species,
452 which are often long-lived (Vaughn & Taylor 2001) and therefore need long-term monitoring

453 to detect trends, may lead to an underestimate of extinction risk, particularly when only
454 range-based metrics are available to assess extinction risk (Torres et al. 2018).

455 Threat was higher in lotic versus lentic system, a finding corroborated in other studies
456 on the conservation status of freshwater biodiversity (Clausnitzer et al. 2009, Collen et al.
457 2014). Establishment of dams and other barriers, one of the main threats to freshwater
458 molluscs, presents a rising threat to freshwater biodiversity (He et al. 2018). Freshwater
459 mussels require fish hosts for the completion of their life cycle and dispersal (Modesto et al.
460 2018). Movement of fish hosts is vital for connectivity of mussel populations and
461 metapopulation dynamics (Zajac et al. 2018). It was shown that there is reduced mussel
462 species richness and abundance closer to river impoundments, suggesting an extinction risk
463 gradient downstream of these structures (Vaughn & Taylor 2001). Dams may block
464 migratory routes for fish (Maceda-Veiga 2013), which may be important hosts for molluscan
465 larvae (Modesto et al. 2018). Local extinction rates of mussels have previously been
466 predicted by their primary fish hosts: mussels that require large migratory fish to complete
467 their life cycle had higher extinction rates due to river fragmentation (Vaughn 2012).

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

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

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

Global change and trade globalization have spurred an increase in bioinvasions and their subsequent impacts on ecosystems (Darrigran and Damborenea 2011). Introduction of non-native species (potential invasive species) is a main cause of biodiversity loss (Gallardo et al. 2018). Darrigran et al (2020) identified four hotspot areas for non-native species of molluscs (both aquatic and terrestrial) in South America, which require special attention for biodiversity conservation, not only because they are potential entry points for non-native

503 species, but also because they coincide with hotspots of high endemism (Darrigran et al.
504 2020). Identifying entry points of non-native molluscs, such as through large cities, ports, or
505 airports (Darrigran et al. 2020), are a vital step to identify hotspots for conservation action.

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

520

521 *Data Deficiency*

522 High levels of data deficiency preclude our ability to adequately represent species groups in
523 conservation action plans and conservation prioritisation schemes. Data deficiency in
524 freshwater molluscs (37%) was greater than amongst crayfish (20%; Richman et al. 2015),
525 roughly comparable to that in the Odonata (35%; Clausnitzer et al. 2009), but much lower
526 than in freshwater crabs (49%; Cumberlidge et al. 2009). The most obvious causes for the

527 high prevalence of DD species in our sample are: 1) a deficiency of experts in the field of
528 invertebrate systematics (Agnarsson & Kuntner 2007, Kotov & Gololobova 2016; 2)
529 discrepancies among molluscan systematists with regard to species rank and the methods of
530 species delimitation (e.g. Vinarski 2018), which lead to species status of many freshwater
531 molluscan taxa remaining disputable; 3) lack of monitoring of abundance and status of
532 freshwater molluscan populations, especially in developing countries in hotspots of
533 freshwater biodiversity. Many nominal species of freshwater snails and bivalves have not
534 been studied (or even recorded) since their taxonomic description, thus pushing these taxa
535 into the limbo of Data Deficient species. Outdated, morphology-based taxonomies persist in
536 many groups of freshwater molluscs (Graf 2007, Torres et al. 2018), though usage of modern
537 molecular techniques show that some are incomplete. In the few genera and families where
538 revisions have been made, drastic reassessment of the commonly accepted taxonomies
539 changes changed species richness estimates (e.g. Bolotov et al. 2015, Osikowski et al. 2018),
540 and likely conservation status of individual species. Since data deficiency was high amongst
541 most of the taxonomic sub-groups in our study, increased efforts are needed across orders and
542 families of freshwater molluscs to improve our knowledge on this ecologically important
543 group. In addition, predictive techniques are needed to assess the most likely threat status of
544 Data Deficient species within our sample. Such assessments have already been carried out for
545 several other taxonomic groups to improve threat estimates (Bland & Böhm 2016, Bland et
546 al. 2015). Reducing the number of DD species in our study and for freshwater molluscs in
547 general will allow not only for more accurate biodiversity indicators, but initiate better
548 conservation actions for individual species and/or regions.

549 *Adequacy of sample, sample size and sRLI process*

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

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

568 *The future of freshwater molluscs*

569 Freshwater molluscs provide invaluable function to freshwater ecosystems and ecosystem
570 services to humans, but are under high levels of threat. It is vital that conservation actions are
571 increased to safeguard freshwater ecosystems and the species, including molluscs, that
572 depend on them, given the manifold threats impacting these fragile systems, particularly
573 riverine ecosystems. While this targeted global assessment gives an overview of issues

574 impacting freshwater molluscs across the globe and at the regional level, it is vital that
575 comprehensive action plans are drawn up to preserve freshwater systems and its biodiversity.
576 In addition, research needs to be focused on priorities for conservation of these species and
577 better understanding of the impact of threats, such as pollution and climate change (Ferreira-
578 Rodríguez et al. 2019).

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

590 **Acknowledgements**

591 The authors would like to acknowledge the Esmée Fairbairn Foundation (NIDR and MB) and
592 the Rufford Foundation (MB) for their generous support. MV is supported by the Russian
593 Fund for Basic Research (project No. 19-04-00270). We are grateful to the Biodiversity
594 Synthesis Center for funding a major assessment workshop in London in 2010. For data
595 compilation and workshop group facilitation, we thank Anne-Marie Soulsby, Ellie Dyer,
596 Felix Whitton, Gita Kasthala and Shane McGuinness; for additional work on draft
597 assessments, we thank Clare Duncan, Amy Collins, Kirsten McMillan, Suzanne Offord,

598 **References**

- 599 Agnarsson I, Kuntner M. 2007. Taxonomy in a changing world: seeking solutions for a
600 science in crisis. *Systematic Biology* 56: 531–559.
- 601 Allen DJ, Molur S, Daniel BA. 2010. The Status and Distribution of Freshwater Biodiversity
602 in the Eastern Himalaya. IUCN and Zoo Outreach Organisation.
- 603
- 604 Baillie JE, Collen B, Amin R, Akcakaya HR, Butchart SH, Brummitt N, Meagher TR, Ram
605 M, Hilton-Taylor C, Mace GM. 2008. Toward monitoring global biodiversity. *Conservation*
606 *Letters* 1: 18-26.
- 607
- 608 Balian EV, Segers H, Lévêque C, Martens K. 2008. The Freshwater Animal Diversity
609 Assessment: an overview of results. *Hydrobiologia* 595: 627-637.
- 610
- 611 Bland LM, Orme CDL, Bielby J, Collen B, Nicholson E, McCarthy MA. 2015. Cost-effective
612 assessment of extinction risk with limited information. *Journal of Applied Ecology* 52: 861-
613 870.
- 614
- 615 Bland LM, Böhm M. 2016. Overcoming data deficiency in reptiles. *Biological Conservation*
616 204: 16-22.
- 617
- 618 Bogan A. 2006. Conservation and extinction of the freshwater molluscan fauna of North
619 America. Pages 373-383 in Sturm CF, Pearce TA, Valdés A, eds. *The Mollusks: A Guide to*
620 *Their Study, Collection, and Preservation*. American Malacological Society.
- 621
- 622 Bogan A. 2008. Global diversity of freshwater mussels (Mollusca, Bivalvia) in freshwater.
623 *Hydrobiologia* 595: 139–147.
- 624
- 625 Böhm M, Collen B, Baillie JE, Bowles P, Chanson J, Cox N, Hammerson G, Hoffmann M,
626 Livingstone SR, Ram M, Rhodin AG et al. 2013. The conservation status of the world's
627 reptiles. *Biological Conservation* 157: 372-385.
- 628

629 Böhm M, Williams R, Bramhall H, McMillan K, Davidson A, Garcia A, Bland LM, Bielby J,
630 Collen B. 2016. Correlates of extinction risk in squamate reptiles: the relative importance of
631 biology, geography and threat. *Global Ecology and Biogeography* 25: 391-405.
632

633 Bolotov IN, Bespalaya YV, Vikhrev IV , Aksenova OV, Aspholm PE, , Gofarov MY,
634 Klishko OK, Kolosova YS, Kondakov AV, Lyubas AA, Paltser IS, Konopleva ES,
635 Tumpeesuwan S, Bolotov NI, Voroshilova IS. 2015. Taxonomy and distribution of
636 freshwater pearl mussels (Unionoida: Margaritiferidae) of the Russian Far East. *PLoS ONE*
637 10: e0122408. doi:10.1371/journal.pone.0122408.
638

639 Brown KM, Lydeard CE. 2010. Mollusca: Gastropoda. Pages 277–307 in Thorpe JH, Covich
640 AP, eds. Ecology and classification of freshwater invertebrates of North America. Elsevier.
641

642 Butchart SH, Stattersfield AJ, Bennun LA, Shutes SM, Akçakaya HR, Baillie JE, Stuart SN,
643 Hilton-Taylor C, Mace GM. 2004. Measuring global trends in the status of biodiversity: Red
644 List Indices for birds. *PLoS Biology* 2: e383.
645

646 Butchart SHM, Walpole M, Collen B, van Strien A, Scharleman JP, Almond RE, Baillie JE,
647 Bomhard B, Brown C, Bruno J, Carpenter KE et al. 2010. Global biodiversity: indicators of
648 recent declines. *Science* 328: 1164-1168. doi: 10.1126/science.1187512.
649

650 Clausnitzer V, Kalkman VJ, Ram M, Collen B, Baillie JE, Bedjanič M, Darwall WR, Dijkstra
651 KD, Dow R, Hawking J, Karube H et al. 2009. Odonata enter the biodiversity crisis debate:
652 the first global assessment of an insect group. *Biological Conservation* 142: 1864-1869.
653

654 Clifford P, Richardson S, Hemon D. 1989. Assessing the significance of the correlation
655 between two spatial processes. *Biometrics* 45: 123–134.
656

657 Collen B, Whitton F, Dyer EE, Baillie JEM, Cumberlidge N, Darwall WRT, Pollock C,
658 Richman NI, Soulsby A-M, Böhm M. 2014. Global patterns of freshwater species diversity,
659 threat and endemism. *Global Ecology and Biogeography* 23: 40-51. doi: 10.1111/geb.12096.
660

661 Cowie RH, Régnier C, Fontaine R, Bouchet P. 2017. Measuring the Sixth Extinction: What
662 do mollusks tell us? *The Nautilus* 131: 3-41.

663

664 Cumberlidge N, Ng PK, Yeo DC, Magalhães C, Campos MR, Alvarez F, Naruse T, Daniels
665 SR, Esser LJ, Attipoe FY, Clotilde-Ba F et al. 2009. Freshwater crabs and the biodiversity
666 crisis: Importance, threats, status, and conservation challenges. *Biological Conservation* 142:
667 1665-1673. doi: 10.1016/j.biocon.2009.02.038.

668

669 Cuttelod A, Seddon M, Neubert E. 2011. European Red List of Non-marine Molluscs.
670 Publications Office of the European Union.

671

672 Darrigran G, Damborenea C. 2011. Ecosystem engineering impacts of *Limnoperna fortunei*
673 in South America. *Zoological Science* 28: 1-7.

674

675 Darrigran G, Agudo-Padron I, Baez P, Belz C, Cardoso F, Carranza A, Collado G, Correoso
676 M, Cuezco MG, Fabres A, Gutiérrez Gregoric DE, et al. 2020. Non-native mollusks
677 throughout South America: emergent patterns in an understudied continent. *Biological*
678 *Invasions* 22: 1-19.

679

680 Darwall W, Smith K, Allen D, Seddon M, McGregor Reid G, Clausnitzer V, Kalkman V.
681 2009. Freshwater biodiversity: a hidden resource under threat. Pages 43 -53 in Vie JC,
682 Hilton-Taylor C, Stuart SN, eds. *Wildlife in a changing world: an analysis of the 2008 IUCN*
683 *Red List of Threatened Species*. IUCN.

684

685 Dudgeon D, Arthington AH, Gessner MO, Kawabata ZI, Knowler DJ, Lévêque C, Naiman
686 RJ, Prieur-Richard AH, Soto D, Stiassny ML, Sullivan CA. 2006. Freshwater biodiversity:
687 importance, threats, status and conservation challenges. *Biological Review* 81: 163–182.

688

689 Ferreira-Rodríguez N, Akiyama YB, Aksenova OV, Araujo R, Barnhart MC, Bessalaya YV,
690 Bogan AE, Bolotov IN, Budha PB, Clavijo C, Clearwater SJ, Darrigran G et al. 2019.
691 Research priorities for freshwater mussel conservation assessment. *Biological Conservation*
692 231: 77-87.

693

694 Gallardo B, Bogan AE, Harun S, Jainih L, Lopes-Lima M, Pizarro M, Rahim KA, Sousa R,
695 Virdis SGP, Zieritz A. 2018. Current and future effects of global change on a hotspot's

696 freshwater diversity. *Science of the Total Environment* 635: 750-760.
697 <https://doi.org/10.1016/j.scitotenv.2018.04.056>
698

699 Graf DL. 2007. Palearctic freshwater mussel (Mollusca: Bivalvia: Unionoida) diversity and
700 the Comparative Method as a species concept. *Proceedings of the Academy of Natural*
701 *Sciences of Philadelphia* 156: 71-88.

702 Graf DL. 2013. Patterns of freshwater bivalve global diversity and the state of phylogenetic
703 studies on the Unionoida, Sphaeriidae, and Cyrenidae. *American Malacological Bulletin* 31:
704 135-153.
705

706 He F, Bremerich V, Zarfl C, Geldmann J, Langhans SD, David JNW, Darwall W, Tockner K,
707 Jähnig SC. 2018. Freshwater megafauna diversity: patterns, status and threats. *Diversity and*
708 *Distributions* 24: 1395-1404. DOI: 10.1111/ddi.12780.
709

710 Henriques S, Böhm M, Collen B, Luedtke J, Hoffmann M, Hilton-Taylor C, Cardoso P,
711 Butchart SHM, Freeman R. 2020. Accelerating the monitoring of global biodiversity:
712 revisiting the sampled approach to generating Red List Indices. *Conservation Letters*:
713 e12703.
714

715 Hermoso V, Filipe AF, Segurado P, Beja P. 2018. Freshwater conservation in a fragmented
716 world: Dealing with barriers in a systematic planning framework. *Aquatic Conservation:*
717 *Marine and Freshwater Ecosystems* 28: 17-25.
718

719 Howard JK, Cuffey KM. 2006. The functional role of native freshwater mussels in the fluvial
720 benthic environment. *Freshwater Biology* 51: 460-474. doi: 10.1111/j.1365-
721 2427.2005.01507.x.
722

723 IUCN. 2001. IUCN Red List Categories and Criteria: Version 3.1. IUCN.
724

725 IUCN. 2018. IUCN Red List Summary statistics. (20 November 2018;
726 <https://www.iucnredlist.org/about/summary-statistics>).
727

728 IUCN. 2019. The IUCN Red List of Threatened Species, version 2019.3 (23 December 2019;
729 <http://www.iucnredlist.org>).

730

731 Johnson PD, Bogan AE, Brown KM, Burkhead NM, Cordeiro JR, Garner JT, Hartfield PD,
732 Lepitzki DA, Mackie GL, Pip E, Tarpley TA et al. 2013. Conservation Status of Freshwater
733 Gastropods of Canada and the United States. *Fisheries* 38: 247-282.

734

735 Köhler F, Seddon M, Bogan AE, Van Tu D, Sri-Aroon P, Allen D. 2012. The status and
736 distribution of freshwater molluscs of the Indo-Burma region. Pages 66-88 in Allen DJ,
737 Smith KG, Darwall WRT, eds. The Status and Distribution of Freshwater Biodiversity in
738 Indo-Burma. IUCN.

739

740 Kotov AA, Gololobova MA. 2016. Traditional taxonomy: Quo vadis? *Integrative Zoology*
741 11: 490–495.

742 Legendre L, Legendre P. 1998. Numerical ecology, 2nd edn. Elsevier Science.

743 Lopes-Lima M, Burlakova LE, Karatayev AY, Mehler K, Seddon M, Sousa R. 2018.
744 Conservation of freshwater bivalves at the global scale: diversity, threats and research needs.
745 *Hydrobiologia* 810: 1-14.

746

747 Lydeard C, Mayden RL. 1995. A diverse and endangered aquatic ecosystem of the southeast
748 United States. *Conservation Biology* 9: 800–805.

749

750 Lydeard C, Cowie RH, Ponder WF, Bogan AE, Bouchet P, Clark SA, Cummings KS, Frest
751 TJ, Gargominy O, Herbert DG, Hershler R et al. 2004. The global decline of nonmarine
752 mollusks. *Bioscience* 54: 321-330.

753

754 Mace GM, Collar NJ, Gaston KJ, Hilton-Taylor C, Akcakaya HR, Leader-Williams N,
755 Milner-Gulland EJ. 2008. Quantification of Extinction Risk: IUCN's System for Classifying
756 Threatened Species. *Conservation Biology* 22: 1424-1442. doi: 10.1111/j.1523-
757 1739.2008.01044.x.

758

759 Maceda-Veiga A. 2013. Towards the conservation of freshwater fish: Iberian rivers as an
760 example of threats and management practices. *Review in Fish Biology and Fisheries* 23: 1-
761 22.

762

763 Markovic D, Carrizo SF, Karcher O, Walz A, David JNW. 2017. Vulnerability of European
764 freshwater catchments to climate change. *Global Change Biology* 23: 3567-3580. doi:
765 10.1111/gcb.13657.

766

767 Master LL, Stein BA, Kutner LS, Hammerson GA. 2000. Vanishing assets: conservation
768 status of U.S. species. Pages 93-118 in Stein BA, Kutner LS, Adams JS, eds. *Precious
769 Heritage: The Status of Biodiversity in the United States*. Oxford University Press.

770

771 McRae L, Deinet S, Freeman R. 2017. The Diversity-Weighted Living Planet Index:
772 Controlling for Taxonomic Bias in a Global Biodiversity Indicator. *PLoS One* 12: e0169156.
773 <https://doi.org/10.1371/journal.pone.0169156>.

774

775 Modesto V, Ilarri M, Souza AT, Lopes-Lima M, Douda K, Clavero M, Sousa R. 2018. Fish
776 and mussels: Importance of fish for freshwater mussel conservation. *Fish and Fisheries* 19:
777 244–259.

778

779 MolluscaBase eds. 2020. MolluscaBase. Accessed at <http://www.molluscabase.org> on 2020-
780 02-27

781

782 Molur S, Smith KG, Daniel BA, Darwall WRT. 2011. The Status and Distribution of
783 Freshwater Biodiversity in the Western Ghats, India. IUCN and Zoo Outreach Organisation.

784

785 Osikowski A., Hofman S., Rysiewska A., Sket B., Prevorčnik S., Falniowski A. 2018. A case
786 of biodiversity overestimation in the Balkan *Belgrandiella* A. J. Wagner, 1927
787 (*Caenogastropoda: Hydrobiidae*): molecular divergence not paralleled by high morphological
788 variation. *Journal of Natural History* 52: 323-344.

789 Ponder, W. 2019. Tateidae Thiele, 1925. Pages 134-138 in Lydeard C, Cummings KS, eds.
790 *Freshwater mollusks of the world: a distribution atlas*. Johns Hopkins University Press.

791 Régnier C, Fontaine B, Bouchet P. 2009. Not knowing, not recording, not listing: Numerous
792 unnoticed mollusk extinctions. *Conservation Biology* 23: 1214-1221. doi: 10.1111/j.1523-
793 1739.2009.01245.x.

794 Régnier C, Achaz G, Lambert A, Cowie RH, Bouchet P, Fontaine B. 2015. Mass extinction
795 in poorly known taxa. *Proceedings of the National Academy of Sciences USA* 112: 7761-
796 7766.

797 Revenga C, Campbell I, Abell R, de Villiers P, Bryer M. 2005. Prospects for monitoring
798 freshwater ecosystems towards the 2010 targets. *Philosophical Transactions of the Royal
799 Society of London B* 360: 397-413.

800

801 Richman NI, Böhm M, Adams SB, Alvarez F, Bergey EA, Bunn JJ, Burnham Q, Cordeiro J,
802 Coughran J, Crandall KA, Dawkins KL et al. 2015. Multiple drivers of decline in the global
803 status of freshwater crayfish (Decapoda: Astacidea). *Philosophical Transactions of the Royal
804 Society B-Biological Sciences* 370: 20140060. doi: 10.1098/rstb.2014.0060.

805

806 Roll U, Feldman A, Novosolov M, Allison A, Bauer AM, Bernard R, Böhm M, Castro-
807 Herrera F, Chirio L, Collen B, Colli GR, et al. 2017. The global distribution of tetrapods
808 reveals a need for targeted reptile conservation. *Nature Ecology and Evolution* 1: 1677-1682.

809

810 Salafsky N, Salzer D, Stattersfield AJ, Hilton-Taylor CR, Neugarten R, Butchart SH, Collen
811 BE, Cox N, Master LL, O'Connor SH, Wilkie D. 2008. A standard lexicon for biodiversity
812 conservation: Unified classifications of threats and actions. *Conservation Biology* 22: 897-
813 911. doi: 10.1111/j.1523-1739.2008.00937.x.

814

815 Schipper J, Chanson JS, Chiozza F, Cox NA, Hoffmann M, Katariya V, Lamoreux J,
816 Rodrigues AS, Stuart SN, Temple HJ, Baillie J et al. 2008. The status of the world's land and
817 marine mammals: diversity, threat, and knowledge. *Science* 322: 225-230.

818

819 Seddon M, Appleton C, Van Damme D, Graf D. 2011. Freshwater molluscs of Africa:
820 diversity, distribution, and conservation. Pages 92-125 in Darwall W, Smith K, Allen D,
821 Holland R, Harrison I, Brooks E, eds. *The diversity of life in African freshwaters:
822 underwater, under threat. An analysis of the status and distribution of freshwater species
823 throughout mainland Africa.* IUCN.

824
825 Strayer DL, Dudgeon D. 2010. Freshwater biodiversity conservation: recent progress and
826 future challenges. *Freshwater Science* 29: 344-358.
827
828 Strong EE, Gargominy O, Ponder WF, Bouchet P. 2008. Global diversity of gastropods
829 (Gastropoda; Mollusca) in freshwater. *Hydrobiologia* 595: 149-166. doi: 10.1007/s10750-
830 007-9012-6.
831
832 Stuart SN, Chanson JS, Cox NA, Young BE, Rodrigues AS, Fischman DL, Waller RW.
833 2004. Status and trends of amphibian declines and extinctions worldwide. *Science* 306: 1783-
834 1786.
835
836 Thorburn D-MJ. 2017. Anthropogenic threats predict likelihood and severity of decline in
837 global freshwater populations. MRes Thesis, University College London.
838
839 Tingley R, Meiri S, Chapple DG. 2016. Addressing knowledge gaps in reptile conservation.
840 *Biological Conservation* 204: 1-5.
841
842 Tittensor DP, Walpole M, Hill SL, Boyce DG, Britten GL, Burgess ND, Butchart SH,
843 Leadley PW, Regan EC, Alkemade R, Baumung R et al. 2014. A mid-term analysis of
844 progress toward international biodiversity targets. *Science* 346: 241-244. doi:
845 10.1126/science.1257484.
846
847 Torres S, Cao L, Gutiérrez Gregoric DE, de Lucía M, Brea F, Darrigran G. 2018. Distribution
848 of the Unionida (Bivalvia, Paleoheterodonta) from Argentina and its conservation in the
849 Southern Neotropical Region. *PLoS ONE* 13(9): e0203616.
850
851 Vaughn CC, Taylor CM. 2001. Impoundments and the decline of freshwater mussels: a case
852 study of an extinction gradient. *Conservation Biology* 13: 912-920.
853
854 Vaughn CC. 2012. Life history traits and abundance can predict local colonisation and
855 extinction rates of freshwater mussels. *Freshwater Biology* 57: 982-992.
856

857 Vaughn CC. 2017. Ecosystem services provided by freshwater mussels. *Hydrobiologia* 810:
858 15-27. DOI 10.1007/s10750-017-3139-x.
859

860 Vinarski MV. 2018. The species question in freshwater malacology: From Linnaeus to the
861 present day. *Folia Malacologica* 26: 39-52.

862 Vörösmarty CJ, McIntyre PB, Gessner MO, Dudgeon D, Prusevich A, Green P, Glidden S,
863 Bunn SE, Sullivan CA, Liermann CR, Davies PM. 2010. Global threats to human water
864 security and river biodiversity. *Nature* 467: 555-561. doi: 10.1038/nature09440.
865

866 Wilke, T. 2019. Moitesseriidae Bourguignat, 1863. Pages 122-125 in Lydeard C, Cummings
867 KS, eds. Freshwater mollusks of the world: a distribution atlas. Johns Hopkins University
868 Press.

869

870 Zajac K, Florek J, Zajac T, Adamski P, Bielański W, Ćmiel A, Klich M, Lipińska
871 AM. 2018. On the reintroduction of the endangered thick-shelled river mussel *Unio*
872 *crassus*: the importance of the river's longitudinal profile. *Science of the Total Environment*
873 624: 273–282.
874

875 Zieritz A, Bogan AE, Rahim KA, Sousa R, Jainih L, Harun S, Razak NF, Gallardo B,
876 McGowan S, Hassan R, Lopes-Lima M. 2018. Changes and drivers of freshwater mussel
877 diversity and distribution in northern Borneo. *Biological Conservation* 219: 126-137.
878 <https://doi.org/10.1016/j.biocon.2018.01.012>
879

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

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

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

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

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

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

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

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

Richness metric		Amphibians	Crabs	Crayfish	Fish	Mammals	Reptiles	All freshwater¹
SR	Corr	0.07	-0.03	0.52***	0.14	0.26*	0.33***	0.15
	F	0.31	0.05	28.38	1.31	6.66	13.27	1.32
	d.f.	60.94	59.59	78.34	61.83	94.67	107.32	59.82
THR	Corr	-0.04	-0.05*	0.46**	-0.04	0.04	-0.06	0.20*
	F	1.65	5.45	9.12	1.25	1.02	1.41	4.46
	d.f.	1121.82	2445.2	33.67	809.5	647.7	345.47	103.33
DD	Corr	0.03	0.11	0.18***	0.20*	0.05	-0.02	0.18*
	F	0.25	3.32	26.23	5.93	0.22	0.83	4.52
	d.f.	404.62	257.12	745.26	138.14	82.70	1801.7	139.81

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

Figure legends

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

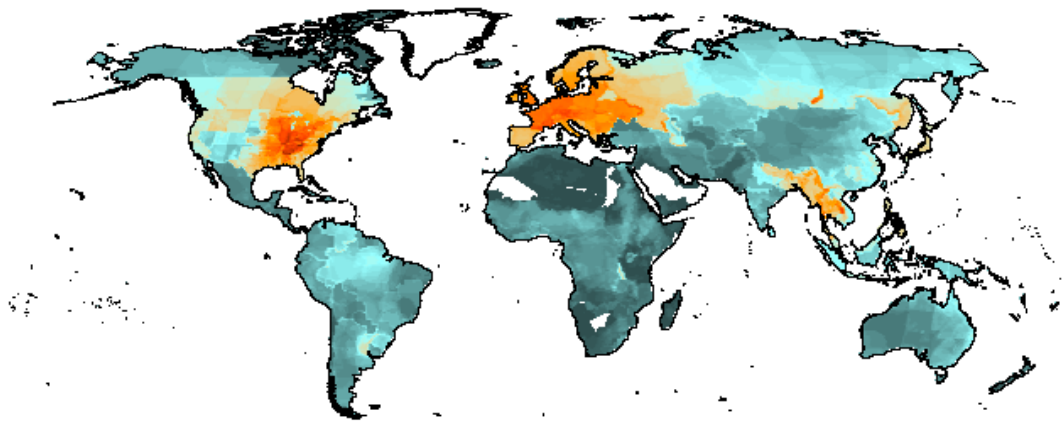
Figure 2. Number of species affected by different threat processes, showing A) contribution of threat to Red List categories, B) contribution of threats to non-threatened (light) and threatened species (dark) for bivalves (solid bars) and gastropods (hashed bars), respectively, C) predominant threats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

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

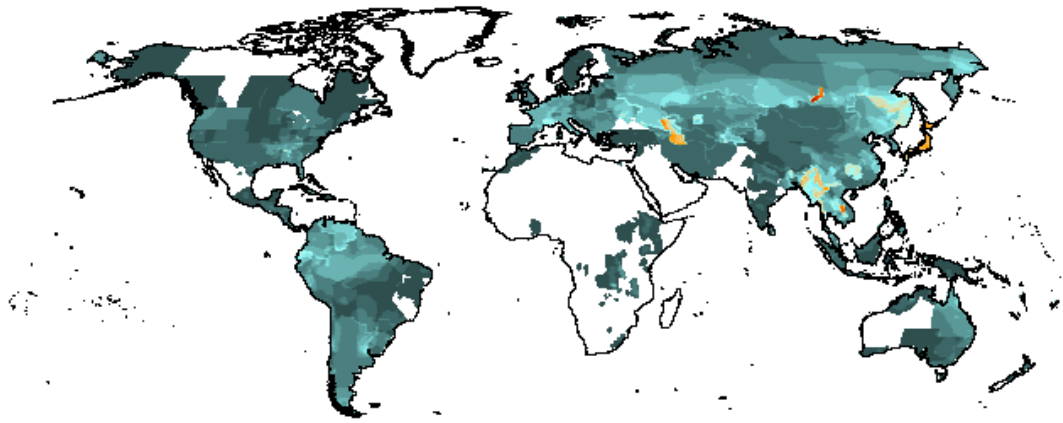
Figure 4. Congruence of 10% of richest hotspots for freshwater species: A) species richness hotspots; B) Data Deficient richness hotspots; C) threatened species richness hotspots. Congruence is shown by overlap of hotspots for seven different freshwater taxonomic groups: amphibians, crabs, crayfish,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

Figure 1.

A



B



C

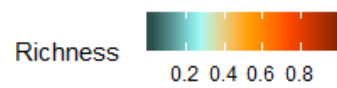
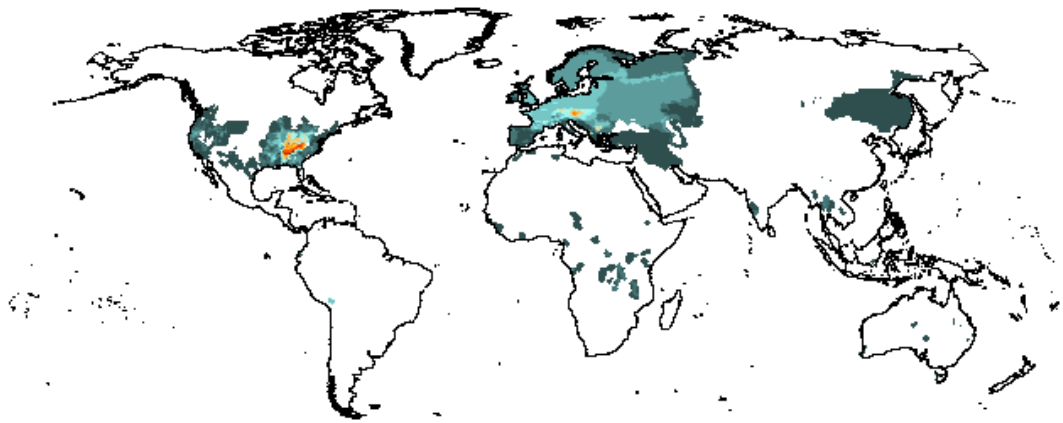
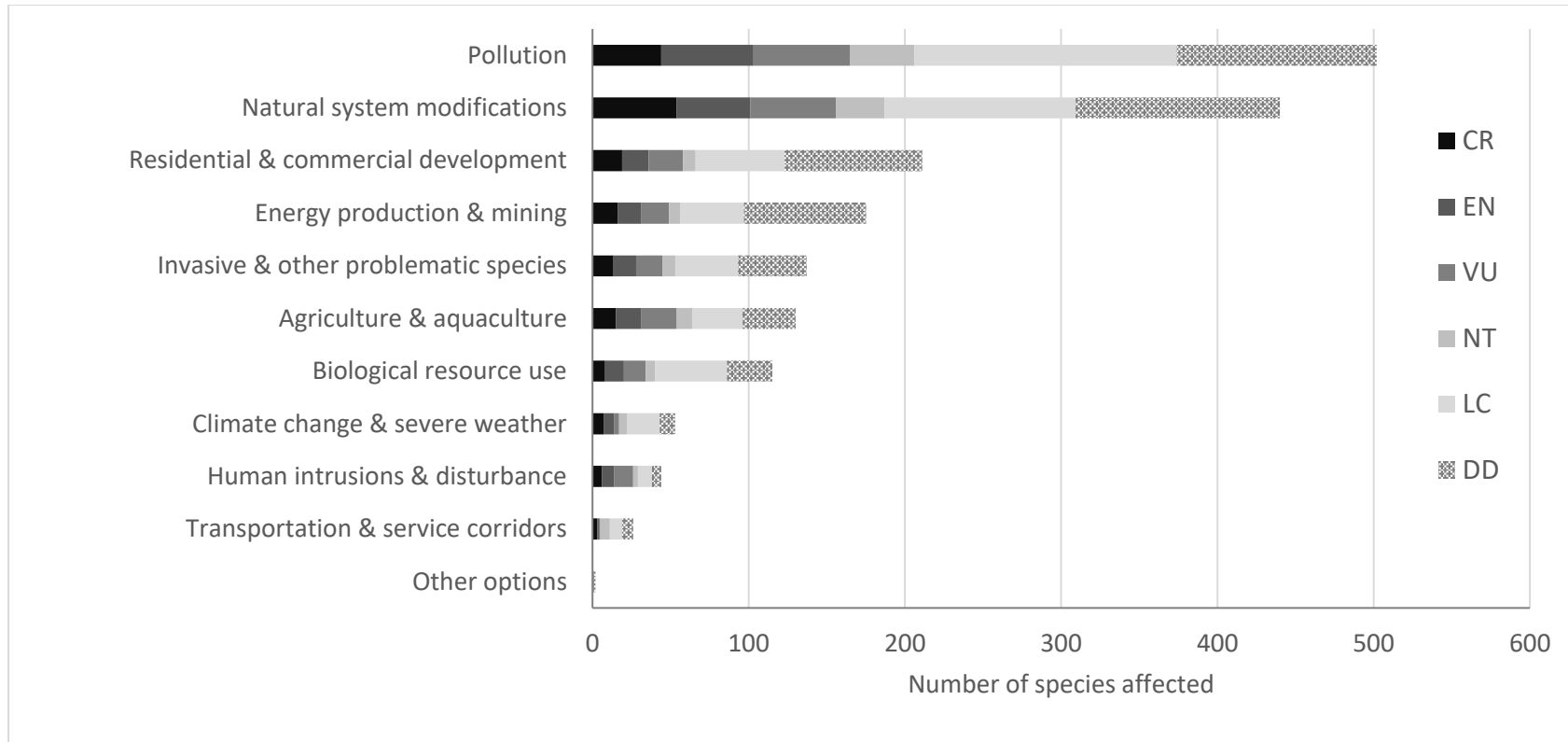
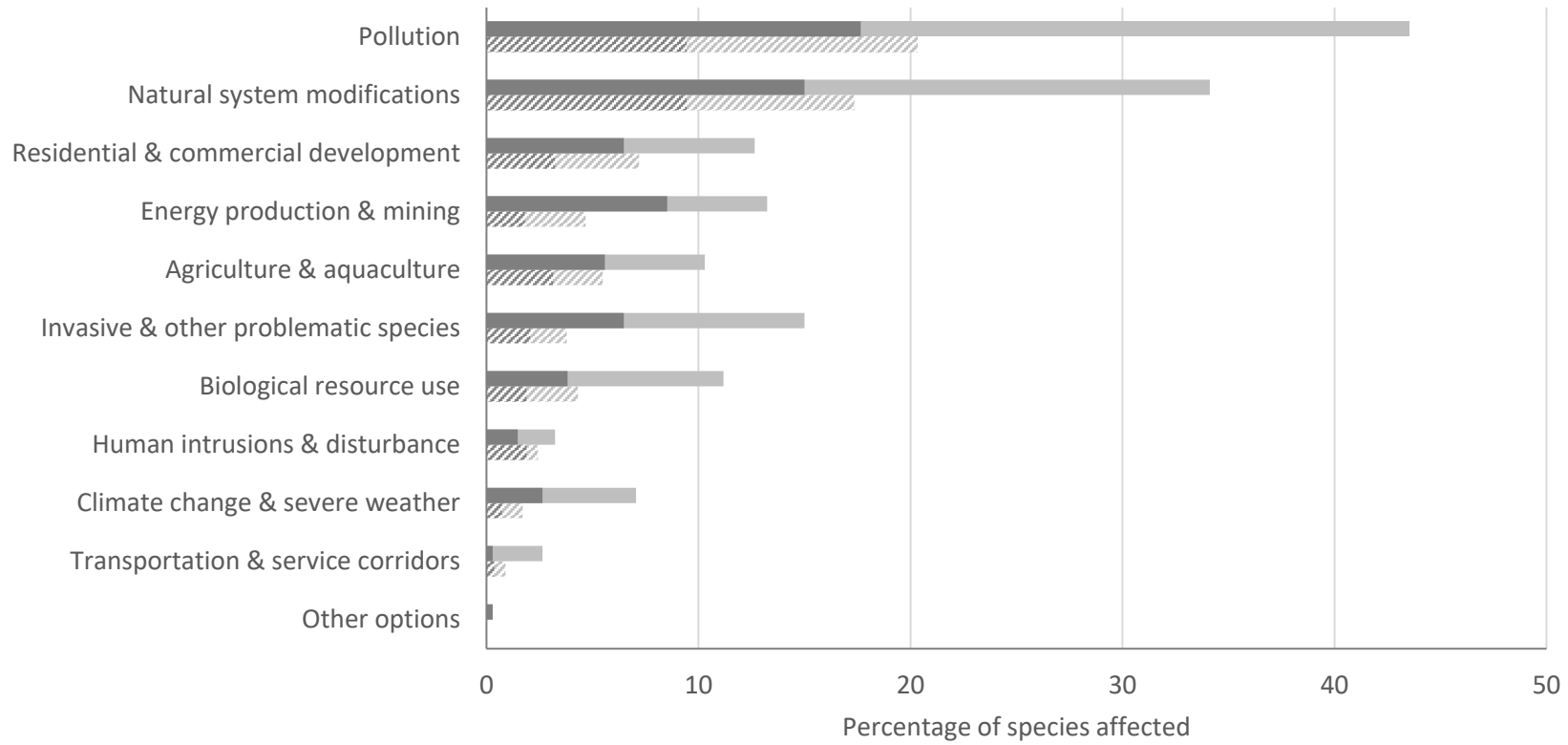


Figure 2.

A.



B



C

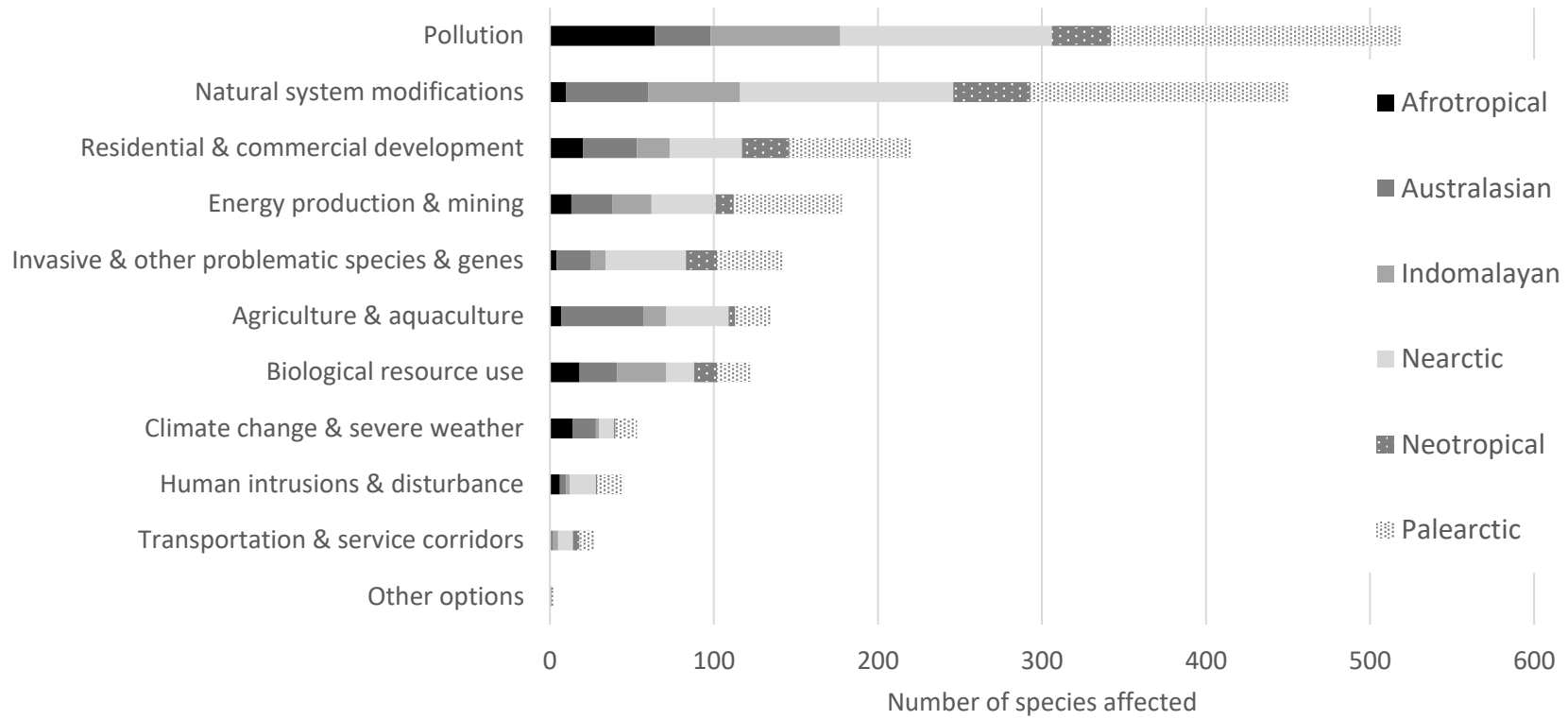


Figure 3.

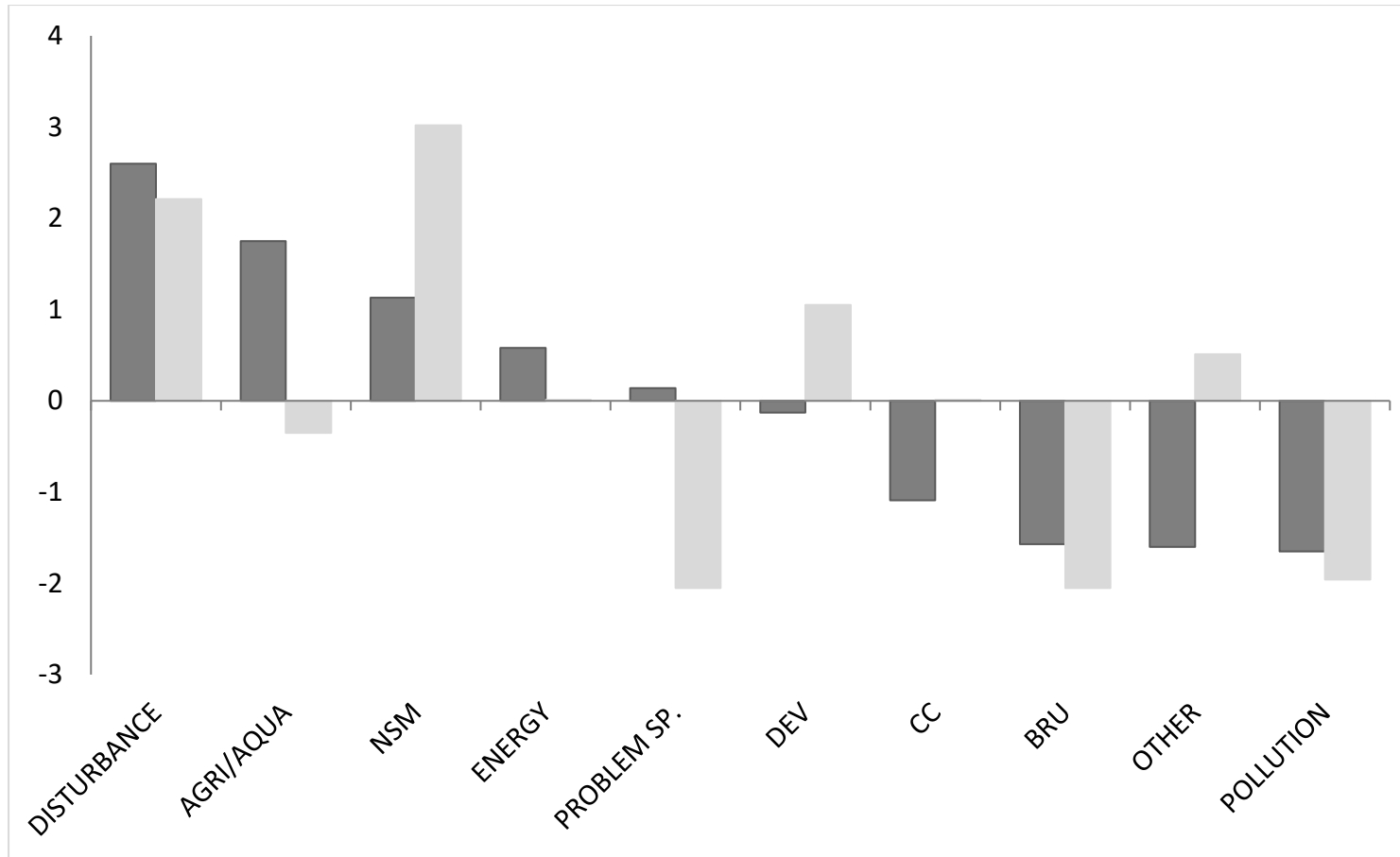
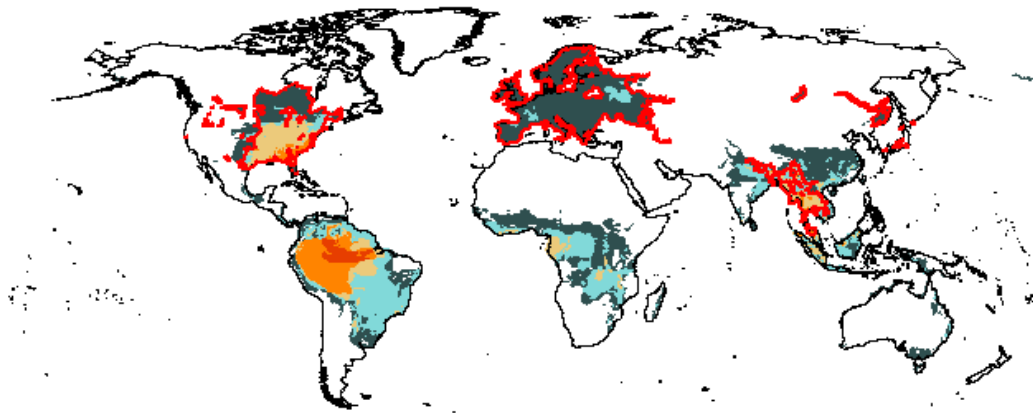
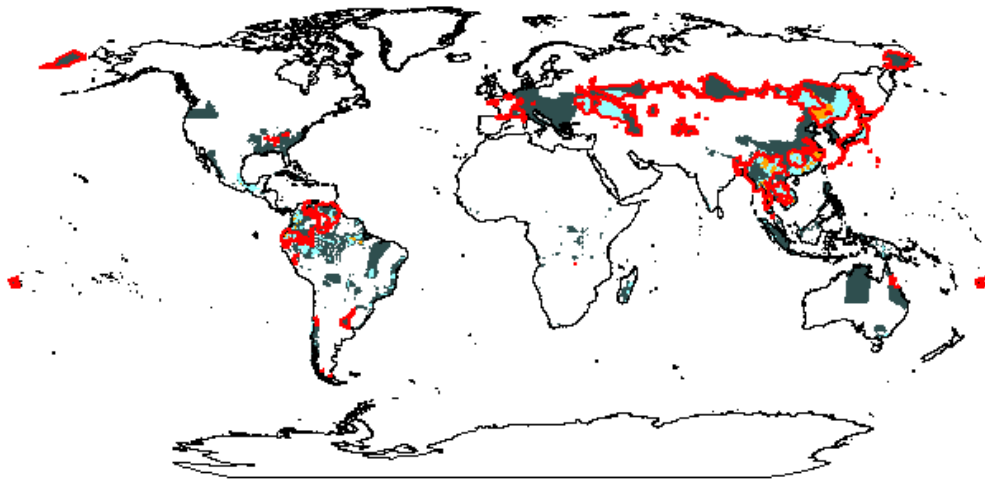


Figure 4.

A



B



C

