



Freshwater crabs and the biodiversity crisis: Importance, threats, status, and conservation challenges

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ABSTRACT

Freshwater ecosystems in the tropics host a diverse endemic fauna including freshwater crabs, but the rapid loss and deterioration of habitat means that many species are now under imminent threat. Studies on freshwater fish and amphibians suggest a third to half of the species in some tropical freshwaters is either extinct or endangered, but the status of the freshwater crabs is not known. Freshwater crabs, with 1280 species, represent one-fifth of all the World's brachyurans. We therefore undertook a comprehensive IUCN Red List assessment of the freshwater crabs, which was the first time that such a study had been attempted on a global scale for any group of freshwater invertebrates. The conservation status of all known species from the Americas, Africa, Europe, Asia, and Australasia revealed unexpectedly high threat levels. Here we show that about one-sixth of all freshwater crab species have an elevated risk of extinction, only one-third are not at-risk, and although none are actually extinct, almost half are too poorly known to assess. Out of 122 countries that have populations of freshwater crabs, 43 have species in need of protection. The majority of threatened species are restricted-range semi-terrestrial endemics living in habitats subjected to deforestation, alteration of drainage patterns, and pollution. This is illustrated with a case study of one such species found in Singapore. This underlines the need to prioritize and develop conservation measures before species decline to levels from which they cannot recover. The proportion of freshwater crabs threatened with extinction is equal to that of reef-building corals, and exceeds that of all other groups that have been assessed except for amphibians. These results represent a baseline that can be used to design strategies to save the World's threatened freshwater crab species.

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1. Introduction

It is estimated that over a million species Worldwide rely on tropical freshwater ecosystems for their survival but the rapid deterioration of freshwater bodies, driven by human population growth and deforestation, is having a negative impact on inland aquatic biodiversity (Dudgeon, 1992, 2000; Dudgeon et al., 2006; Strayer, 2006). Moreover, all predictions are that global climate change is likely to further increase these negative impacts and accelerate the number of species that are under imminent threat (Carpenter et al., 1992). Studies on freshwater fish and amphibians

suggest a third to half of the species in some areas are either endangered or extinct (Sodhi et al., 2004, 2008; Xenopoulos et al., 2005; Kottelat and Freyhof, 2007; Jelks et al., 2008), but it is not known whether freshwater invertebrates have been similarly impacted. We therefore undertook the first global conservation status of all 1280 known species of freshwater crabs from the tropical regions of the Americas, Africa, Asia, and Australasia belonging to the families Pseudothelphusidae, Trichodactylidae, Potamonautidae, Potamidae, and Gecarcinucidae (Ng et al., 2008; Klaus et al., in press; Cumberlidge and Ng, in press; Appendix 1).

1.1. Importance of freshwater crabs

Most of the 6800 species of brachyurans are marine but a surprising one-fifth of all crabs on Earth are strictly freshwater (in four superfamilies, Gecarcinucoidea, Potamoidea, Pseudothelphusoidea, Trichodactyloidea, in which all members are independent of the sea for completion of the life cycle). This makes freshwater crabs the largest assemblage within the Brachyura, which in turn is the most species-rich of all decapod crustacean groups (Ng et al., 2008). Recent studies have overturned the notion that freshwater crabs are phylogenetically unimportant and biogeographically uninformative (Bossuyt et al., 2004; Daniels et al., 2006; Cumberlidge, 2008; Cumberlidge et al., 2008; Yeo et al., 2008a; Cumberlidge and Ng, in press; Klaus et al., in press). Freshwater crabs are also medically important as intermediate hosts of paragonimiasis in Asia, Africa, and the Neotropics (Nwokolo, 1974; Ng, 1988; Blair et al., 1998; Dai, 1999; Rodríguez and Magalhães, 2005). The fact that paragonimiasis is a food-borne zoonosis indicates that freshwater crabs are widely consumed by humans, which is underlined by the more than 20 million people infected Worldwide by one of the 15 species of lung flukes of the genus *Paragonimus* (World Health Organization, 1995; Maleewong, 2003; Blair et al., 2008). Freshwater crabs are also hosts to the developing larvae of biting blackflies (*Simulium* spp.) that are the vectors of the parasite *Onchocerca volvulus*, the cause of hundreds of thousands of human cases of onchocerciasis (river blindness) in Africa (Crosskey, 1990).

Freshwater crabs are one of the most ecologically important macro-invertebrate groups in tropical inland waters Worldwide (Dobson et al., 2007a,b; Magalhães, 1999, 2003; Rodríguez and Magalhães, 2005; Yeo et al., 2008a). These strictly freshwater decapods are found in almost all clean freshwater bodies in the tropics from moist lowland forests to rugged mountains. Crabs live in rivers, streams, waterfalls, wetlands, karsts, and caves, and many are semi-terrestrial (Yeo et al., 2008a). Almost all require pristine water conditions to survive and are excellent indicators of good water quality (Yeo et al., 2008a).

Freshwater crabs are omnivorous (with some tending more towards either herbivory or carnivory) and include species that feed on leaves, fallen leaves with attached algae, and beechnuts (Kasai and Naruse, 2003), and species that feed on aquatic insects, gastropods, dead frogs, or snakes (Dudgeon and Cheung, 1990; Kasai and Naruse, 2003; Maitland, 2003). Some species of freshwater crabs are detritivores that play an important role in nutrient cycling in tropical freshwater ecosystems (Dobson et al., 2002, 2007a,b). The large proportion of detritus measured in the diet of freshwater crabs in African river ecosystems suggests that these brachyurans may occupy the detritus-shredding guild that was thought to be almost completely absent from these tropical systems (Dobson et al., 2002). Freshwater crabs also comprise a large proportion (between 88% and 94%) of the overall biomass of all invertebrates in the streams and debris dams in the Eastern Usambara Mountains of Tanzania (Abdallah et al., 2004). The general abundance and high biomass of freshwater crabs in aquatic ecosystems, combined with their dominant detritus-shredding role, makes them potentially

very important to the dynamics of nutrient recycling in rivers both in Africa, and elsewhere in the World.

In addition, freshwater crabs are integral components of food webs in tropical aquatic ecosystems and provide food for a wide range of predators, as well as forming the basis of small-scale fisheries such as those in Lakes Malawi and Tanganyika in East Africa. African freshwater crabs are important prey items for otters, mongooses, civets, kites, egrets, herons, and kingfishers, as well as eels, bullfrogs, toads, monitor lizards, and crocodiles (Turnbull-Kemp, 1960; Rowe-Rowe, 1977; Hill and O'Keeffe, 1992; Purves et al., 1994; Butler and Marshall, 1996). In the Neotropics, pseudothelphusids are preyed upon by turtles (Teran et al., 1995) and tufted capuchin monkeys (Port-Carvalho et al., 2004), while in Asia, freshwater crabs are preyed upon by wild boars (Kasai and Naruse, 2003) and by stream snakes (*Opisthotropis kikuzatoi*) (Ota, 2004). The ecological importance of freshwater crabs in food webs in Africa is underlined by the impact of alien North American crayfish in the rivers of Western Kenya that out-competed and replaced the native crabs. The drop in freshwater crab populations in these systems led to a subsequent decline in clawless otter populations that fed on crabs, most likely due to increased competition with other predators attracted by the abundance of crayfish (Foster and Harper, 2007; Ogada, 2006).

The present study was prompted by a growing awareness of the true extent of freshwater crab diversity and of the possible threatened status of many narrowly distributed species given the current widespread destruction of tropical forests and aquatic ecosystems (Dudgeon, 1992, 2000; Sodhi et al., 2004; Bahir et al., 2005; Dudgeon et al., 2006; Strayer, 2006; Ng and Yeo, 2007; Cumberlidge and Daniels, 2008). Freshwater crab characteristics of low fecundity, direct development, and low vagility, combined with the fragmented nature of freshwater habitats have resulted in frequent isolation, rampant allopatric speciation and high levels of endemism (Cumberlidge, 1999; Ng and Yeo, 2007; Yeo et al., 2008a). Niche specialization has contributed to their diversity via sympatric speciation (Ng and Yeo, 2007), with one site having as many as five species occupying different habitats (Yeo et al., 1999a). A conservation assessment of the freshwater crabs is especially timely because studies on freshwater fish and amphibians in Southeast Asia suggest that a third to half of the species in some tropical freshwaters are either extinct or endangered (Sodhi et al., 2004, 2008), and studies in Malaysia indicate that many species of freshwater crabs may be facing the same fate (Ng and Yeo, 2007). The freshwater crab assessments for the 2008 International Union for Conservation of Nature (IUCN) Red List of threatened species covered the entire faunal assemblage from all five families, and increased the number assessed from 93 Asian and African species (Sri Lanka, East Africa, Southern Africa, West Africa) (Bahir et al., 2005; Ng and Yeo, 2007; Cumberlidge and Daniels, 2008) to 1280 species globally (IUCN, 2001).

2. Methods

2.1. Application of the IUCN Red List criteria

Conservation assessments were made using the IUCN (2001) Red List Categories and criteria (version 3.1) (IUCN, 2001) using the Species Information System Data Entry Module provided by the IUCN. Analysis of species-level data on taxonomy, distribution, population trends, ecology, life history, past and present threats, and conservation actions was conducted at Northern Michigan University as part of the Red List Index, Sampled approach project (Zoological Society of London; Baillie et al., 2008). Each species assessment was independently evaluated by the IUCN. Red List assessments were also conducted in regional workshops between

2005 and 2008 in South Africa (Stellenbosch), Ghana (Accra), USA (Washington, DC), and Singapore (National University) that brought together freshwater crab specialists and conservation professionals from 10 countries. The study involved the collation of an enormous amount of published and unpublished data on freshwater crabs. Those countries with the most threatened species, the highest species diversity, and the highest rates of endemism of freshwater crabs, were identified and the numbers of threatened species were correlated by family and region. The results were compared with similar studies of other groups of animals for which conservation assessments are available (Butchart et al., 2004; Stuart et al., 2004; Schipper et al., 2008; Carpenter et al., 2008; Clausnitzer et al., 2009).

The eight Red List Categories used were Extinct (EX), Extinct in the Wild (EW), Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), Least Concern (LC), and Data Deficient (DD). Freshwater crab species included here were mostly assessed under Criterion B (geographic range), Criterion C (small population size and decline), and Criterion D (very small or restricted population). In those cases where sufficient long-term species-specific monitoring data were insufficient to calculate actual population trends, Criterion A (declining population levels) was used based on literature records, museum holdings, and the number of sites at which a species was present. The majority of the 34 species assigned to CR were in Criterion B1 based on Extent of Occurrence (EOO, the area contained within the shortest continuous imaginary boundary encompassing known sites of occurrence), or Criterion B2 based on Area of Occupancy (AOO, the available habitat within the EOO which is actually occupied by the taxon). Other factors used included (a) whether a species was known from only a small number of locations, and (b) whether there was a continuing decline in some or all of quantitative values (i–v). Similarly, most of the 52 species assigned to EN, and the 123 species assigned to VU, were listed under Criterion B or Criterion D, with only a few species assessed under Criterion C. Criterion E was not applied here to any species of freshwater crab because of the lack of quantitative population data (IUCN, 2001). No criteria were applied to the 628 species of freshwater crabs that were listed as DD due to insufficient information on abundance, distribution, and threats that prevented the assessment of extinction risk (IUCN, 2001). The freshwater crab species in this study have been included in the IUCN Red List of threatened species online database. A table of the resulting Red List Categories and supporting data for each species is provided online (Appendix, Table A1).

3. Results

3.1. Global patterns of diversity

The five families of freshwater crabs currently recognized (Klaus et al., in press; Cumberlidge and Ng, in press) showed differences in diversity, species richness, threatened status, endemism, and data deficiency (Tables 1 and 2, Fig. 1a and b). Global diversity

patterns of the freshwater crabs at the family level were strikingly uneven. Species richness was concentrated in Southeast Asia where the two most diverse families occur – Potamidae (505 species, 95 genera) and Gecarcinucidae (344 species, 59 genera) (Fig. 1a). The Afrotropical freshwater crab fauna was the least diverse (133 species, 18 genera, 2 families), while the Neotropical fauna was intermediate (298 species, 50 genera, 2 families). Seven of the top 10 most species-rich countries were in Asia, including China – with the highest number of species globally (224 species), Thailand (101 species), and Malaysia (92 species) (Table 2). These countries were among those that have been surveyed recently (Ng, 1988; Ng and Naiyanetr, 1993; Dai, 1999; Yeo et al., 1999b; Ng and Yeo, 2007; Yeo and Ng, 2007), but others such as Indonesia (83 species), India (78 species), and the Philippines (42 species) are almost certainly undercounted due to lower survey efforts. The number of species in the Philippines was thought likely to double once a large amount of unsorted material has been published. Colombia (101 species), Mexico (63 species), Brazil (45 species), and Venezuela (42 species) were all relatively well surveyed for freshwater crabs (Rodríguez, 1982, 1992; Magalhães and Türkay, 1996a–c; Campos, 2005), and it was surprising that Brazil was ranked only third of the New World countries and only 9th most diverse globally (Table 2). Species numbers in poorly sampled countries such as Ecuador (27 species), Peru (25 species), and Panama (14 species), and indeed most countries in Central America, are almost certainly underestimates. The relatively species poor Afrotropical region included only two of the World's top 20 most diverse countries – the Democratic Republic of Congo (36 species) and Tanzania (25 species). Only the latter has received significant survey efforts in recent decades (Reed and Cumberlidge, 2006) and large increases in species totals can be predicted for the Democratic Republic of Congo (and other countries in the Congo Basin) where there has been almost no freshwater crab survey work for over 50 years.

3.2. Threatened species between families and countries

Some 628 out of the 1280 species of freshwater crabs had insufficient data to complete a Red List assessment (DD, Tables 1 and A1) and were excluded from subsequent calculations. Of the remaining 651 species, 209 were listed in the three threatened categories, and 227 were in the threatened (VU, EN, CR) and NT categories combined (Table 1). Well over half (59%) of the threatened species belonged to just two families – the Asian Gecarcinucidae (43% of species Threatened) and the New World Pseudothelphusidae (34.2% of species Threatened). The proportion of threatened African Potamonautidae (27.5%) and Asian Potamidae (26.5%) is less than the global average (32.1%), while only 10.3% of the New World species of Trichodactylidae appear to be at-risk. The Red List assessment indicated that semi-terrestrial species tended to be the most threatened in all families, particularly stenotopic endemics. Although restricted to different continents, the Potamidae and Pseudothelphusidae each include primarily semi-terrestrial air-

Table 1

Current Red List categories for freshwater crab species by family. Conservation status is derived using the IUCN (2001) Red list criteria; VU = vulnerable, EN = endangered, CR = critically endangered, NT = near threatened. Percentages in combined threatened categories (Thr.) include all non-data-deficient species listed as VU, EN, or CR. Spp. = species, No. = number.

Family	DD	LC	NT	VU	EN	CR	Total species	NT + Thr. (%)	Thr. (%)
Trichodactylidae	8	35	0	3	1	0	47	10.3	10.3
Pseudothelphusidae	140	72	1	33	3	2	251	35.1	34.2
Potamonautidae	31	72	2	16	10	2	133	29.4	27.5
Potamidae	305	139	8	38	12	3	505	30.5	26.5
Gecarcinucidae	144	107	7	33	26	27	344	46.5	43.0
Total	628	425	18	123	52	34	1280		

Table 2

Current Red List categories for freshwater crab species for all 43 countries that have threatened species of freshwater crabs. Conservation status is derived using the IUCN (2001) Red List criteria. Percentages in threatened categories (Thr.) include all non-data-deficient species listed as VU, EN, or CR. The numbers endemic species and rate of endemism (%) are also shown. VU = vulnerable, EN = endangered, CR = critically endangered, NT = near threatened (IUCN, 2001).

No.	Country	DD	LC	NT	VU	EN	CR	Total Spp.	No. Thr.	Thr. (%)	Endemic (%)
1	Sri Lanka	0	8	2	5	10	25	50	40	80.0	98
2	Malaysia	10	51	1	20	9	1	92	30	36.6	95
3	Thailand	42	40	0	11	8	0	101	19	32.2	86
4	Colombia	41	45	1	13	0	1	101	14	23.3	75
5	Indonesia	46	23	1	10	3	0	83	13	35.1	88
6	Taiwan	11	13	1	7	2	2	36	11	44.0	97
7	Ecuador	8	12	0	7	0	0	27	7	36.8	44
8	Tanzania	0	16	2	6	1	0	25	7	28.0	16
9	Venezuela	11	24	0	7	0	0	42	7	22.6	45
10	Liberia	0	3	0	1	3	2	9	6	66.7	33
11	Mexico	44	13	0	2	3	1	63	6	31.6	86
12	Brazil	7	34	0	3	1	0	45	4	10.5	29
13	China	174	46	0	3	1	0	224	4	8.0	96
14	Guinea	1	2	0	1	3	0	7	4	66.7	29
15	Kenya	2	8	2	3	1	0	16	4	28.6	31
16	Philippines	29	9	0	3	1	0	42	4	30.8	98
17	Viet Nam	28	8	0	3	1	0	40	4	33.3	88
18	Cameroon	2	8	0	1	2	0	13	3	27.3	23
19	India	50	22	3	3	0	0	78	3	10.7	82
20	Laos	10	4	0	2	1	0	17	3	42.9	82
21	Peru	4	18	0	3	0	0	25	3	14.3	32
22	Singapore	0	1	0	1	0	2	4	3	75.0	75
23	Australia	0	4	1	2	0	0	7	2	28.6	100
24	Democratic Republic of Congo	7	22	0	0	2	0	31	2	8.3	32
25	Costa Rica	6	5	0	2	0	0	13	2	28.6	69
26	Dominican Republic	0	0	0	2	0	0	2	2	100.0	100
27	El Salvador	2	4	0	2	0	0	8	2	33.3	38
28	Guatemala	6	5	0	2	0	0	13	2	28.6	46
29	Honduras	0	4	0	2	0	0	6	2	33.3	17
30	Hong Kong	1	1	0	1	1	0	4	2	66.7	100
31	Japan	2	16	1	1	1	0	21	2	10.5	100
32	Madagascar	5	7	0	2	0	0	14	2	22.2	100
33	Malawi	0	2	0	2	0	0	4	2	50.0	50
34	Myanmar	32	5	0	2	0	0	39	2	28.6	69
35	Nigeria	1	7	0	2	0	0	10	2	22.2	40
36	Uganda	2	7	0	0	2	0	11	2	22.2	18
37	Ethiopia	0	3	0	1	0	0	4	1	25.0	50
38	Ghana	0	5	0	1	0	0	6	1	16.7	17
39	Haiti	0	0	0	1	0	0	1	1	100.0	100
40	Panama	10	3	0	1	0	0	14	1	25.0	79
41	South Africa	0	12	0	1	0	0	13	1	7.7	54
42	Suriname	1	9	0	1	0	0	11	1	10.0	9
43	Turkey	0	4	4	1	0	0	9	1	11.1	22

breathing, burrow-living species that divide their time between water and land, a lifestyle that is apparently the most susceptible to anthropogenic habitat disturbances. Most of these species also have a very restricted distribution. More positively results showed roughly two-thirds of all species belonging to all five families in 79 countries Worldwide to be either LC or NT (Tables 1, 2, and A1).

Five of the top six countries with the highest numbers of threatened species are in tropical Asia, which is the global center of freshwater crab biodiversity (Table 2). Important concentrations of at-risk species are found in the highland forests of Sri Lanka and Taiwan, and in the rain forests of Indochina, Thailand, the Malay Peninsula, Borneo, and New Guinea. In Latin America, the countries with the highest numbers of threatened species are Colombia, Ecuador, and Venezuela, while in Africa, Tanzania, and Liberia stand out. When the relative size of the regional fauna is taken into account, the speciose Asian countries again have the highest percentage of threatened species (34.8%), followed by the Afrotropical and Neotropical countries (27.5% and 28%, respectively). In the Dominican Republic and Haiti (admittedly species-poor), the entire fauna is threatened, while about one-third of all species (31.6–36.8%) are threatened in Mexico, El Salvador, Honduras, and Ecuador. In several African countries (Liberia, Guinea, and Malawi) alarmingly high proportions of the freshwater crabs (50–66.7%) are threatened (Table 2).

No species of freshwater crabs could be confirmed either Extinct or Extinct in the Wild, but extinctions are notoriously difficult to confirm (Harrison and Stiassny, 1999), and this is thought likely to be an underestimate given that many tropical freshwater ecosystems are under severe real-time threat from forest destruction and illegal produce extraction (Sodhi et al., 2004; Bahir et al., 2005; Ng and Yeo, 2007). Of great concern are the many DD species that have not been found in recent years. For example, the terrestrial crab *Thaipotamon siamense* and waterfall crab *Demanietta manii* from Thailand may well be extinct because there have been no records of them for over a century and their original habitats are now part of urban landscapes (Ng and Naiyanetr, 1993; Sodhi et al., 2008). Anecdotaly, it is often the case that researchers return to a site only to find that a species has disappeared since their last visit. However, a species cannot be formally classified as extinct until exhaustive surveys probing its disappearance have been carried out.

3.3. Comparisons of threat levels between families and other assessed groups

In comparison with other globally assessed groups, the proportion of freshwater crab species threatened with extinction (32%, range 16–65%) was equal to that of reef-building corals (Carpenter et al., 2008), less than that of amphibians (Stuart et al., 2004), but

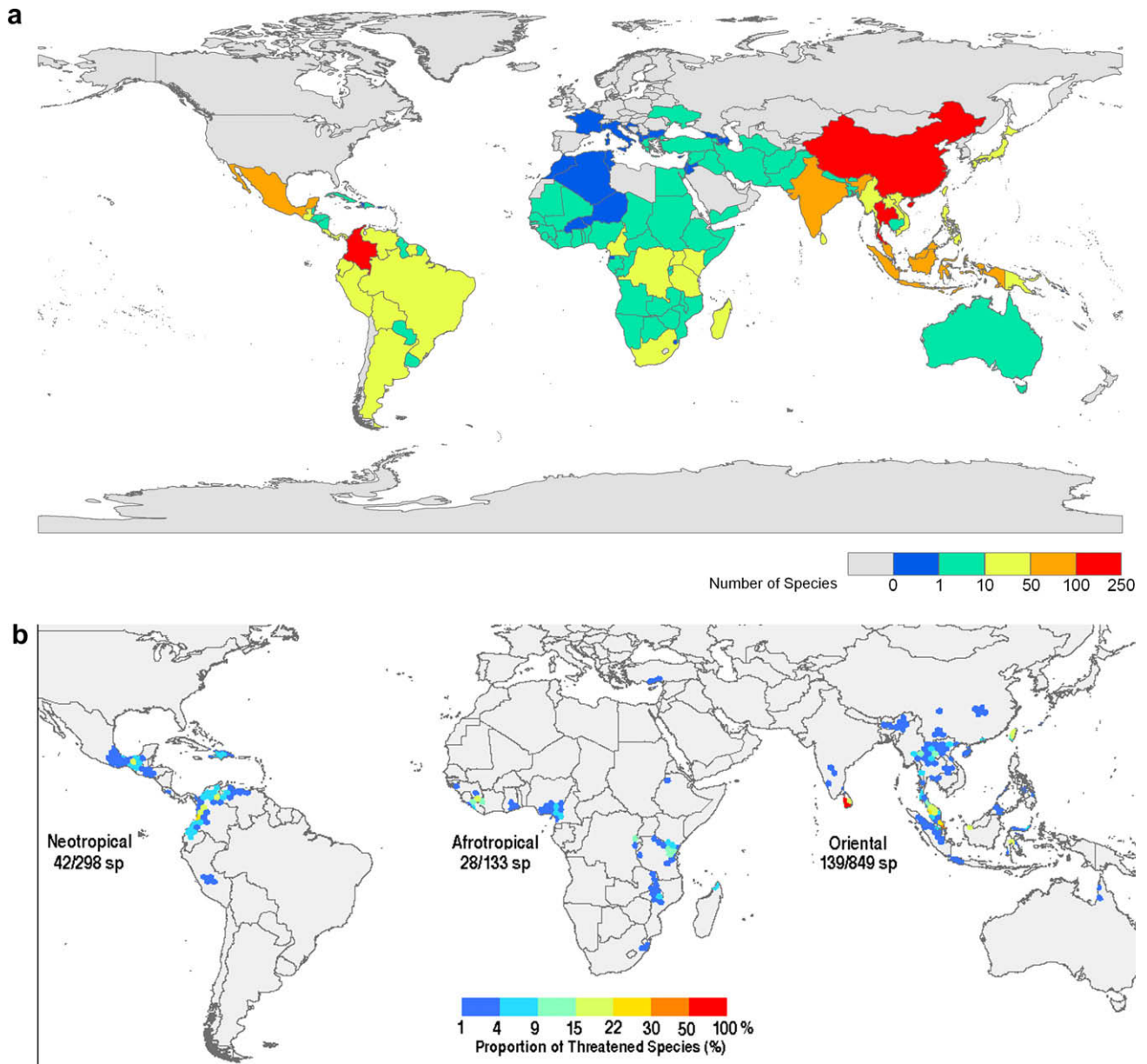


Fig. 1. (a) Global diversity of freshwater crabs in the 122 countries where they occur. The countries where freshwater crabs are absent are shown in grey and (b) global distribution of 191 of the 209 threatened species of freshwater crabs that could be mapped and included in the figure. Threatened here includes species assessed as VU, EN, and CR (conservation status derived using the IUCN (2001) Red List criteria). The colored areas show the proportion of threatened species (%) found in each country (dark blue, lowest range 1–4%; red, highest range 50–100%). The number of threatened species/total number of species is also provided for three regions. 'Neotropical' shows these numbers for the Pseudothelphusidae and the Trichodactylidae combined, 'Afrotropical' shows these numbers for the Potamonautidae found in this region, and 'Oriental' shows these numbers for the Potamidae and Gecarcinucidae found in Europe, Asia, and Australasia. See Table 2 and text for details.

greater than that of five other groups that have been assessed regionally or globally (Table 3). Of concern is that among the 209 threatened species of freshwater crabs, 34 (16.3%) were assessed as CR, and may well be on the brink of extinction. This is a similar proportion to that reported for birds, odonates, and mammals, greater than that for corals, but fewer than that for freshwater fish, reptiles, and amphibians (Table 3).

Sri Lanka, Tanzania, South Africa, Liberia, Australia, Honduras, Singapore, Ethiopia, and Malawi are all countries with no DD species where the entire freshwater crab fauna has been assessed (in non-DD categories). However, it is of concern that some 50 other countries include high numbers of DD species that together make

up nearly half of the global faunal assemblage (628/1280 species, 49.1%). The high level of data deficiency reflects the general lack of scientific attention paid to the freshwater crabs in the past and contrasts with better-studied groups such as birds (1/9791 = 0.01%), mammals (867/5893 = 14.71%), corals (141/845 = 16.69%), reptiles (284/1500 = 18.93%), and amphibians (1533/6260 = 24.49%) (Butchart et al., 2004; Stuart et al., 2004; Schipper et al., 2008; Carpenter et al., 2008).

Threat was not found to be evenly distributed across families of freshwater crabs. The Trichodactylidae and the Potamonautidae had the lowest percentage threat of any families, while the Potamidae and Pseudothelphusidae were found to have the highest threat

Table 3

Comparison of the results of the conservation assessments of eight groups of animals showing the number of species in each red list category. Data for groups other than freshwater crabs downloaded (www.iucnredlist.org) 11th September 2008. The percentage of threatened species is shown using three different assumptions. Assumption 1, that all DD species are non-threatened (Threatened/Assessed) \times 100; Assumption 2, that DD species are threatened in the same proportion as non-DD species (Threatened)/(Assessed – DD) \times 100; and Assumption 3, that all DD species are threatened ((Threatened + DD)/Assessed) \times 100. The midpoint (Assumption 2) is the least biased estimate of the threat status, and the range between the three assumptions incorporates the uncertainty. All animal groups were assessed comprehensively at the global level, except for the freshwater fish and Odonata, where a representative sample of the World's species was used (SRLI, the Red List Index, sampled approach) (Butchart et al., 2004, 2005, 2007).

Red List category	FW crabs	Odonata	Corals	FW fish	Amphibians	Reptiles	Birds	Mammals
NE								14
EX								83
EW					1		4	2
CR	34	24	5	30	489	28	190	246
EN	52	42	25	28	787	109	363	537
VU	123	70	201	91	715	135	669	558
NT	18	65	176	26	381	69	835	352
LC	425	773	297	421	2316	875	7729	3234
DD	628	526	141	108	1533	284	1	867
Assumption 1 (%)	16	9	27	21	32	18	13	23
Assumption 2 (%)	32	14	33	25	42	22	13	27
Assumption 3 (%)	65	44	44	37	56	37	13	38

(Table 1). This result may be distorted by the fact that each of the latter two families includes a very high number of DD species, especially in China and Colombia where the biodiversity is richest. The high numbers of DD species for some families has almost certainly led to underestimations of the proportion of threatened species. For example, only a small part of the fauna in important species-rich countries such as China (22.3% of the Potamidae) and India (35.9% of the Gecarcinucidae) could be assigned conservation status (Dai, 1999; Bahir and Yeo, 2007; Yeo and Ng, 2007). While the eventual status of DD species is difficult to estimate, they are likely to add to the number of threatened species, and will have the greatest impact in Asia (52.9% DD) and the Neotropics (49.5% DD). When we reach the point in the future that all of the DD species have been included in the assessment, our least biased estimate (Assumption 2) is that 32% of all species of freshwater crabs globally will be listed in a threatened category (Table 3). Table 3 also gives the range for this value based on best-case (16% threatened) and worst-case (65% threatened) assumptions (Assumptions 1 and 3, respectively), and compares these estimates with data from seven other assessed groups of animals. These estimates for the freshwater crabs are similar to those for reef-building corals and greater than those for most other groups assessed (except for amphibians) (Table 3).

3.4. Threats and endemism

The freshwater crabs as a group showed very high numbers of endemic species at the country level (Table 2). In general, countries with the most endemic species (such as China, Malaysia, Thailand, Indonesia, India, Colombia, Mexico, Sri Lanka, and the Philippines) tend to be those with the largest total species diversity (Table 2). The percentage of a country's fauna that was found to be endemic showed a very different pattern, and islands such as Sri Lanka, Borneo, and New Guinea (with up to 98% endemism) stood out, as did other islands (Cuba, Hispaniola, Taiwan, Socotra, São Tomé, Príncipe, and Madagascar) and island groups (Japan, Hong Kong, and the Seychelles) with lower species numbers where the entire fauna was endemic. Endemism in continental countries tended to be lower than that for islands, but could also reach high levels (Table 2). A surprising number of endemic species were high-risk stenotopic species found in streams in rugged forested mountains, small isolated offshore islands, or specialist habitats such as caves. Studies on endemic amphibians in Southeast Asia suggest that specialist stenotopic species are extremely vulnerable to threats (Sodhi et al., 2008), and freshwater crabs fitting this description could be among the first to be lost.

4. Discussion

4.1. Threats to freshwater crabs

Threats to freshwater crabs living in the inland waters of tropical regions include widespread anthropogenic environmental impacts. For example, in Malaysia, and in most parts of Southeast Asia, the widespread loss of natural forest as a result of land development and agriculture has impacted almost every habitat where freshwater crabs are found (Ng and Yeo, 2007). Terrestrial or semi-terrestrial species (*Phricotelphusa hockpingi* (CR) and *Johora punicea* (CR)), aquatic species (*Johora tiomanensis* (NT) and *Heterothelphusa fatum* (VU)), cave-dwelling species (*Stygothelphusa bidensis* (VU)), highland species (*Johora gapensis* (VU)), and species on small islands (*Johora singaporensis* (CR) and *Parathelphusa reticulata* (CR)) all are vulnerable to disturbance and pollution (Ng and Yeo, 2007). Lowland forests have been particularly affected by land development and agriculture, so it is perhaps surprising that some widespread Malaysian freshwater crab species (such as *Parathelphusa maculata* and *Sayamia sexpunctata*, both LC) that are adapted to life in rivers or marshy lowlands in tropical forests still thrive in undisturbed rivers and streams as well as in relatively less polluted altered wetland habitats such as plantation waterways and rice fields (Ng and Yeo, 2007).

Given the widespread ecological disturbance in Sri Lanka (Pethiyagoda, 1994), it is perhaps not unexpected that over 80% of all freshwater crab species found on that island are either CR, EN, or VU (Bahir et al., 2005), and that many of these threatened species with restricted distributions pose serious problems for conservation. Over half of Sri Lanka's freshwater crab species are restricted to montane and sub-montane habitats where the threats include pollution from pesticides, deforestation, and increasing silt loads in streams and rivers from soil erosion (Pethiyagoda, 1994). As in Malaysia, a few species of Sri Lankan freshwater crabs assessed as LC thrive in altered habitats such as rice fields (e.g., *Oziothelphusa* spp.) and tea plantations (e.g., *Ceylonthelphusa rugosa* and *C. soror*) and have a wide distribution. However, even these apparently tolerant species could suffer catastrophic declines were they to be subjected to sudden changes in land management and development, pesticide-use regimes, or hydrology (Pethiyagoda, 1994; Bahir et al., 2005; Dudgeon et al., 2006).

4.2. Conservation actions

Endemic species perhaps present the greatest challenge for conservation because undisturbed habitats outside of protected areas

are especially vulnerable to sudden disruption (e.g., by island effects from fragmentation, pollution from pesticides, changes in local climate, and invasive species) and rapid declines are unlikely to be observed taking place given the lack of monitoring for most species (Ng and Yeo, 2007; Sodhi et al., 2008). While anthropogenic disturbance associated with development in most countries with threatened species of freshwater crabs is almost inevitable, it is clear that a balance between development and habitat protection will have to be made if some species are to survive. For example, switching to low impact forestry (where forest cover is not completely removed and where water drainages are not diverted or polluted) may reduce the extinction risk of endemic species of freshwater crabs. In Asia, many disturbed habitats that are now lowland plantations, estates, and rice fields have been recolonized by some of the more adaptable species of gecarcinucids, but montane potamidids with specialized habitat requirements may not be able to adapt to change as readily (Ng and Yeo, 2007). The freshwater crabs that live in the major rivers of the Amazon basin and have the lowest proportion of threatened species (Fig. 1b) appear to have been spared the direct effects of pollution and habitat loss by deforestation that is impacting semi-terrestrial stream and wetland-living highland species around the World (Bahir et al., 2005; Ng and Yeo, 2007). However, even widely distributed species with an apparent tolerance of land-use changes could suffer catastrophic declines as a result of changes in land developments, hydrology or pesticide-use regimes. Acid rain and climate change events also pose grave challenges.

4.3. Case study: crabs on the brink of extinction in Singapore?

The conservation of freshwater crabs relies heavily on preserving patches of natural forest large enough to maintain good water quality because many species of these decapods are extremely sensitive to polluted or silted water and cannot survive exposure. Given this, it is of concern that water quality of drainages is deteriorating even in key natural habitats (Ng, 1988, 1989, 1990a,b, 2008; Brook et al., 2003; Tan et al., 2007; Yeo et al., 2008b). A case in point is *Johora singaporensis*, an endemic potamid from Singapore that was known only from two drainages in the center of the island, one of which was Bukit Timah Nature Reserve (BTNR). A small patch of primary forest (about 39 ha) in the reserve has until now been sufficient to maintain a thriving population of these crabs (Ng, 2008; Yeo et al., 2008b), despite the deterioration of the rest of the BTNR (about 124 ha) into secondary forest and abandoned farmland. Although there is strict control of the BTNR, anthropogenic acidification of the streams has resulted in the extirpation of all of the crabs in the reserve, leaving the remaining population in an unprotected area of less than 10 ha that is currently subject to development (Ng, 2008; Yeo et al., 2008b). Similarly, the Singapore endemic gecarcinucid *Parathelphusa reticulata* is restricted to a small (5 ha) remnant patch of primary freshwater swamp forest, and although protected, could easily be destroyed through careless drainage planning or pollution (Yeo et al., 2008b). Decade-long monitoring of these populations has revealed that crabs can persist even in small habitat fragments if these are managed well. However, sudden events such as the drying up of stream habitats due to anthropogenic activities upstream could well lead to the extirpation of freshwater crab populations, and even extinction (Yeo et al., 2008b).

4.4. Conservation challenges

Our analysis indicates that the extinction risk for many species of freshwater crabs is significant. The assessment is likely to underestimate the true gravity of the situation, making the conservation of this fauna a matter of the highest priority. Further attention

should be paid to the roughly half of the group that were assessed as Data Deficient. The lack of conservation plans for most threatened taxa means that dozens of species of freshwater crabs now face imminent extinction. The IUCN Red List has the potential to be combined with other information to design strategies to save the World's threatened freshwater crabs through the development of national recovery plans that manage and monitor at-risk species before they decline to levels from which they cannot recover. Equally importantly, the Red List also has the credibility to persuade governments to initiate measures to conserve critically endangered taxa (Ng and Yeo, 2007; Sodhi et al., 2008). Whether or not the first species of freshwater crabs will actually become extinct this century depends on the severity of environmental disturbances they face. In view of the pressing human needs for water together with climate change and environmental degradation in the developing World (where most freshwater crab species are found), the challenges on a global scale are very severe. While no species of freshwater crab has been confirmed extinct, the available data suggest that many tropical species are at the brink, and if the pressures continue unabated, we are likely to see a precipitous escalation of extinction events in these crabs in the decades ahead.

The freshwater crab Red List assessment represents an easily accessible baseline resource that can alert, inform, and raise awareness about the threats faced by more than 200 species of these tropical brachyurans. As such, these data have the potential to be used by conservation managers to design strategies to save the World's threatened freshwater crab species.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.biocon.2009.02.038.

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