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The cost of being valuable: predictors of extinction risk in marine invertebrates exploited as luxury seafood

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Extinction risk has been linked to biological and anthropogenic variables. Prediction of extinction risk in valuable fauna may not follow mainstream drivers when species are exploited for international markets. We use results from an International Union for Conservation of Nature Red List assessment of extinction risk in all 377 known species of sea cucumber within the order Aspidochirotida, many of which are exploited worldwide as luxury seafood for Asian markets. Extinction risk was primarily driven by high market value, compounded by accessibility and familiarity (well known) in the marketplace. Extinction risk in marine animals often relates closely to body size and small geographical range but our study shows a clear exception. Conservation must not lose sight of common species, especially those of high value. Greater human population density and poorer economies in the geographical ranges of endangered species illustrate that anthropogenic variables can also predict extinction risks in marine animals. Local-level regulatory measures must prevent opportunistic exploitation of high-value species. Trade agreements, for example CITES, may aid conservation but will depend on international technical support to low-income tropical countries. The high proportion of data deficient species also stresses a need for research on the ecology and population demographics of unglamorous invertebrates.

1. Introduction

Most countries have made slow progress in their global assignments to safeguard the Earth's biodiversity [1,2]. In an attempt to guide conservation efforts, research into attributes that predispose species to the risk of extinction has surged [3,4]. Extinction drivers are increasingly viewed as the combined effects of biological and anthropogenic variables. High-trophic level, large body size, low population density, slow life history (slow growth and late maturation) and small geographical range size are often the major biological drivers of extinction risk in marine species, in comparable importance to human-related factors such as habitat loss, over-exploitation, introduced species and chains of extinction [3,4].

In 1883, Thomas Huxley proclaimed the assumption that economic extinction (exploitation cessation) of marine species will precede ecological extinction because sparse populations are increasingly costly to exploit [4]. However, this notion has long been questioned [5]. Increased value can be attributed to rarity [6–8], thereby precipitating extinctions through the so-called anthropogenic Allee effect (AAE) [9]. Alternatively, valuable species can become rare from targeted exploitation arising from consumer preference, which can drive them to

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extinction through opportunistic exploitation [10]. Exacerbating both processes is the growing population and wealth of China—a dominant market for derivatives of rare and exceptional wildlife [11].

The oceans are inhabited by all but one of the currently described metazoan phyla and therefore host the largest part of the Earth's biodiversity [12]. Assessments of extinction risks in the ocean are particularly challenging [13]. The historical belief that exploitation cannot drive marine species to extinction has been refuted by the collapse of fisheries worldwide [14] and recent extinctions of marine species caused by exploitation [10,15]. Although marine extinctions are only slowly uncovered at the global scale [2], human-dominated marine ecosystems, for example coastal zones [16], are experiencing accelerated loss of populations and species [17]. Fishing through marine food webs is an alarming trend [18], leading to the rapid expansion and depletion of invertebrate fisheries [19]. Despite this trend, marine invertebrates are lagging in extinction-risk assessments and conservation research afforded to more charismatic vertebrate taxa such as mammals [20], turtles, birds and fishes [8,21]. This marked bias is at odds with the sheer domination of marine invertebrates (more than 30 phyla) in the oceans' faunal biodiversity [12].

International Union for Conservation of Nature (IUCN) Red List assessments are commonly used as a surrogate measure of extinction risk [13,20,21]. Alternative methods have produced similar results and the criteria under which declining species are assessed explicitly equate IUCN Red List categories to empirically estimated rates of decline in global population size [8]. A recent IUCN Red List assessment of all sea cucumbers (Echinodermata: Holothuroidea) in the order Aspidochirotida (electronic supplementary material, table S1) provided the opportunity to test the effects of drivers of extinction risk in a low-trophic-level group of invertebrates. At least 60 species of sea cucumbers are harvested worldwide, primarily by divers and waders in the tropics and by trawl in temperate and polar seas [22]. Sea cucumber is a prized seafood on Asian markets (electronic supplementary material, figure S1) and is one of five essential luxury foods in festive dinners alongside shark fin, bird nests (swiftlet saliva), fish maw (swim bladder) and abalone. In the non-perishable dried form, the temperate species *Apostichopus japonicus* can command up to US\$2950 kg^{-1} in Chinese markets, whereas high-value tropical species can fetch US\$140–1670 kg^{-1} [23]. Intensive aquaculture production of *A. japonicus*, especially in China, has not reduced market prices and cannot be considered to safeguard extinction in the wild. In recent decades, high market demand has intensified exploitation within existing sea cucumber fisheries and spurred new fisheries elsewhere [19,24].

For each species, we compiled data on a range of biological and anthropogenic explanatory variables: average body size, median depth of occurrence, geographical range size, market price, climate zone of occurrence, and human demographic and wealth indices in the geographical range. We performed univariate and multivariate analyses to examine the effect of these explanatory variables on extinction risk defined by the IUCN Red List categories ascribed to each species. The main objectives were to identify places in the world with high numbers of threatened sea cucumber species, determine which biological and anthropogenic variables relate to the extinction-risk categories assigned to species and test which of those variables can best predict extinction risks. Our findings of trends in extinction-risk drivers that differ from most other marine species are discussed in terms of the market forces affecting exploitation of sea cucumbers globally. These insights are valuable for understanding the drivers of extinction risk in animals exploited for luxury markets. Our study offers an important example that extinction risk may not relate closely to large body size, small geographical range and a species' rarity. Better understanding of the relative effect of these and other explanatory variables is pivotal for identifying species at risk of extinction and for choosing appropriate management measures to mitigate extinction risks [16,25]. We therefore conclude by advocating research for 'conservation hotspots' (places of critical need) and potential national and international management measures, which are relevant to biodiversity conservation of other high-value species under exploitation.

2. Material and methods

(a) Assessments of sea cucumbers, order Aspidochirotida

This study uses published results [26] of a global assessment that evaluated extinction risks in all 377 known sea cucumber species in the order Aspidochirotida, which contains most of the commercially exploited species (electronic supplementary material, table S1). Briefly, the IUCN Red List assessments were based on application of the IUCN Red List Categories and Criteria [27] and using a vast number of published reviews, studies and reports on the species. A species qualified for one of the three threatened categories (critically endangered (CR), endangered (EN) and vulnerable (VU)) by meeting the threshold for that category in one of five Criteria (see the electronic supplementary material, S1 Materials and Methods). Species that did not come close to meeting the thresholds were assessed as least concern (LC) and species with insufficient data to apply the Red List Criteria were assessed as data deficient (DD). The species assessments were reviewed and edited by a separate panel of international experts in taxonomy and IUCN Red List assessment methodology [28]. Most of the species that met the threshold for a threatened category were assessed under Criterion A [26], which measures extinction risk based on exceeding a threshold of population decline (30% for VU, 50% for EN and 80% for CR) over a time frame of the greater of 10 years or three generation lengths. The IUCN defines generation length as the average age of reproducing adults of the current cohort [28]. During the IUCN Red List assessment, generation length was approximated as 11–17 years according to IUCN methodology (see the electronic supplementary material, S1 Materials and Methods).

(b) Explanatory variables of each species

Species maps and analyses of geographical ranges were done in ArcGIS (v. 10.1) using the minimum convex polygon connecting all known points occurrence. For shallow species occurring primarily shallower than 200 m and those with limited records, the polygons were cut to a 100 km shoreline buffer and depth of 200 m. Intervals of 500–1000 m were used for deep-water species (more than 200 m). For species known from a single record at more than 200 m depth, a polygon was drawn at the appropriate 1000-m depth interval around the reported geographical area. The resulting polygons in square kilometres provided an estimate of geographical range size at 2011. Three latitude zones (tropical, temperate and polar) were determined based on Spalding *et al.* [29]. The latitude zone representing the majority of a species' range was designated where the range overlapped two or more zones.

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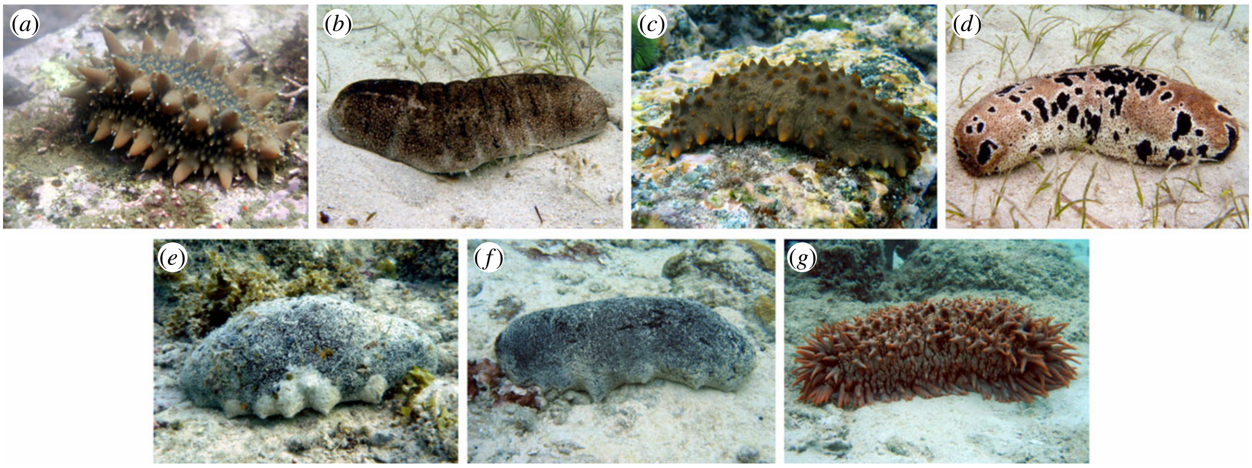

Figure 1. Endangered sea cucumbers. (*a*) *A. japonicus*, (*b*) *H. scabra*, (*c*) *I. fuscus*, (*d*) *H. lessoni*, (*e*) *H. nobilis*, (*f*) *H. whitmaei*, (*g*) *Thelenota ananas*. Photos: (*a*), Fukushima–Yoshioka Fisheries Cooperative Association (with permission); (*b*–*g*), S. W. Purcell.

Market prices of sea cucumbers were obtained in October 2011 from retail and wholesale shops in Hong Kong ($n = 7$) and Guangzhou ($n = 11$). Maximum market price seen in those shops was used for analyses to avoid bias from data on low-quality products of some species. Average live weights of sea cucumbers were based on averages of values from biological studies in various localities across the geographical range of each species [23].

Data on human population density and wealth in the geographical ranges of commercial species ($n = 61$) were obtained by compiling metrics for all countries in each range (electronic supplementary material, figure S1 and table S1). The raw data, relative to the geographical range of each species, included coastline (km), total population, coastal population, human development index (HDI) and gross domestic product (GDP) *per capita* converted at 2011 to international dollars (also called the 'Geary–Khamis dollar', has same purchasing power parity as US dollar at a given point in time). Individual country data were summed to obtain values in the whole range for total human population, coastal human population, cumulative HDI and cumulative GDP. We also calculated mean HDI and GDP, as well as HDI and GDP indices prorated to coastline and coastal human population. Finally, total and coastal human densities were calculated by dividing values of total and coastal human population by the species geographical range size in square kilometres.

(c) Statistical analyses

We firstly used univariate analyses to examine variations in the average values of explanatory variables (biological and anthropogenic) among Red List categories (response). This step also narrowed down the most appropriate wealth metric and human demographic metric (i.e. anthropogenic variables) that would be unique for subsequent multivariate tests. Homogeneity of variance in tests was confirmed using Levene's test. Using all available data in each case, one-way ANOVA tests examined differences among the four IUCN Red List assessment categories for the following explanatory variables: average live body weights ($n = 46$), median depth of occurrence ($n = 271$; $\log_{10}$ transformed), maximum market price ($n = 30$; $\log_{10}$ transformed), geographical range size ($n = 362$; $\log_{10}$ transformed) and a range of human density and wealth indices (see the electronic supplementary material, S1 Materials and Methods) in the range of commercial species ($n = 61$). The relationship between maximum market prices ($\log_{10}$ transformed) and average body weights of species ($n = 30$) was analysed using linear regression. The proportions of species in Red List categories between tropical and temperate–polar groups were tested using a Fisher exact test. Differences in averages of and among Red List categories were tested using one-way ANOVA tests.

Multinomial logistic regression analyses, using a forward stepwise process, were then performed on a reduced dataset of commercial species for which we had data on all of the selected six explanatory variables. The variables were: maximum market price, average adult body weight, median depth of occurrence, geographical range size, human density in geographical range and coastal GDP in geographical range. The univariate analyses had shown that the last two of these variables were the most significant demographic and wealth indices, respectively. Geographical range size was also a key factor in IUCN criteria B and D. The categorical response was the Red List category assigned to the species from the IUCN Red List assessment (LC, VU, EN, DD) [26]. The multinomial logistic regression analyses are robust to accommodate the unbalanced design concerning the number of species across the four response categories. These analyses were employed to model which explanatory variable(s) most strongly distinguished the Red List categories. VU and EN species were pooled into a single 'threatened' category. The explanatory variables were all transformed using natural log. The most appropriate relationship between the multinomial logistic regression estimated probabilities of being classed as EN or VU and the maximum market price of species was determined using Akaike's information criterion [30] on multiple functional forms.

3. Results

In brief, the IUCN Red List assessment determined that 4% of all of the 377 species in the Aspidochirotida were threatened, comprising seven EN (figure 1) and nine VU (see the electronic supplementary material, table S1, and [26]). Thirteen of these threatened species comprise 21% of the 61 commercially important species. Twenty-nine per cent of all 377 species were assessed as LC, while 66% were assessed as DD (electronic supplementary material, table S1). Fifty species are found in waters deeper than 200 m, at least 10 species are in need of taxonomic revision and approximately 15 species are thought to be heavily fished in at least a portion of their range, but data were insufficient to estimate population declines.

Three species not currently targeted by fishers (*Bohadschia maculisparsa*, *Holothuria arenacava* and *Holothuria platei*) were listed as VU under Criterion D2. These species have very small reported distributions and are assumed to

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be intrinsically threatened owing to a current or projected plausible threat [28].

(a) Univariate tests

The average adult body weight (fresh and live) had little effect on a species risk of extinction (figure 2); the average body weights of EN (1138 ± 314 g; mean $\pm$ s.e.) and VU (1061 ± 440 g) species were similar to those of species assessed as LC (889 ± 217 g) and DD (1006 ± 314 g) ($F_{3,42} = 0.11$, $p = 0.953$). On the other hand, maximum market prices differed significantly among IUCN Red List categories for commercial species ($F_{3,26} = 8.24$, $p = 0.001$). The average maximum market price was significantly higher for EN species (US\$1030) than species assessed as VU (US\$158), LC (US\$124) and DD (US\$106) (p-values < 0.01). The linear relationship between market prices and average adult body weights of species was weak ($F_{1,28} = 1.76$, $p = 0.195$, $r^2 = 0.06$).

Globally, there is a much greater number of threatened sea cucumber species in the tropics than in temperate and polar regions (figure 3). The number of threatened species in countries in and surrounding the Coral Triangle were notably high. By contrast, just three threatened sea cucumber species (*A. japonicus*, *A. parvimensis* and *H. platei*) are found in temperate waters. However, the proportion of species in Red List categories out of the total number of species present did not differ significantly between tropical and temperate/polar climes (Fisher's exact test, $p = 0.425$; electronic supplementary material, figure S2). The proportion of DD species was high in all zones.

The average median depth of occurrence (middle of known depth range) of sea cucumbers differed significantly among the extinction-risk categories ($F_{3,233} = 3.88$; $p = 0.01$). The median depth at which species occur was highly variable in the DD and LC groups (figure 4*a*). Median depth of occurrence was at bathyal depths (200–4000 m) in 120 species examined (32%), and at abyssal depths (more than 4000 m) in 14 species (4%). By contrast, VU and EN aspidochirotid sea cucumbers were consistently found in shallow waters; means of median depths: 18 ± 9 m (mean $\pm$ s.d.) and 19 ± 6 m, respectively.

Average geographical range size differed significantly among the four extinction-risk categories ($F_{3,358} = 17.84$, $p < 0.001$; figure 4*b*). Specifically, DD species had smaller range sizes than species assessed as LC, VU and EN (post hoc LSD, p-values < 0.001–0.028). Many of the DD species are known only from one or few specimens, giving them presumably underestimated geographical ranges. The geographical range areas of VU (9.6 ± 3.1 million km^2) and EN species were more variable, and seemingly larger, than species of LC, but differences were statistically non-significant (figure 4*b*). The VU group included three species with very small known geographical ranges, meeting criterion D2 [27], in addition to species with very large geographical ranges that were assessed under Criterion A.

Human density within a species' range differed significantly among the IUCN Red List categories ($F_{3,56} = 3.36$, $p = 0.025$; figure 4*c*). Human populations were significantly denser for the EN species than species assessed as DD or LC (post hoc Holm-Sidak, $p < 0.05$). The average GDP *per capita* in coastal regions of countries in the species' ranges declined from LC to VU to EN species (figure 4*d*); differences were non-significant ($F_{3,57} = 1.99$, $p = 0.127$) but the same trend was consistent across all analyses of GDP metrics. On the other hand, no significant differences or clear trends

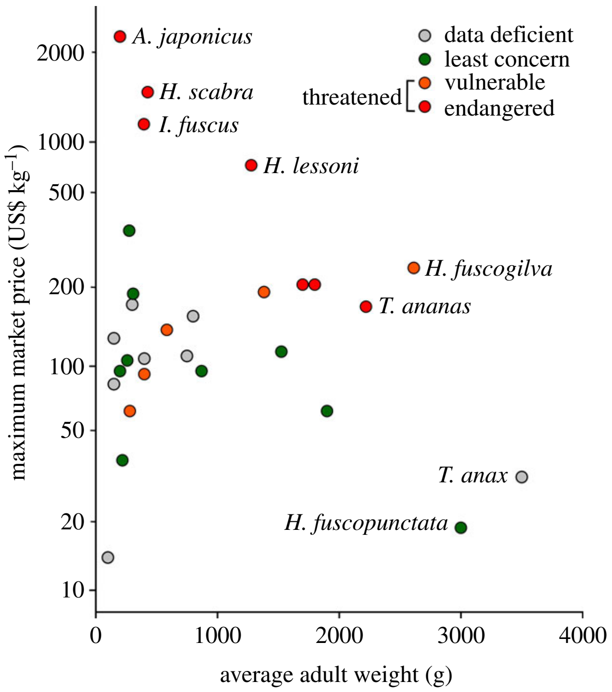

Figure 2. Value versus body size of commercially exploited sea cucumbers. Plot of maximum market prices of sea cucumber species in Chinese markets (Hong Kong and Guangzhou; axis is on a $\log_{10}$ scale) versus their average live adult weight. Only species for which market prices could be obtained are shown; $n = 29$.

among IUCN categories were found for the metrics of HDI (p-values: 0.424–0.997).

(b) Multivariate tests

The final model provided by the multinomial logistic regression analysis determined that the significant variables that best explained the Red List categories among species were maximum market price ($\chi^2 = 13.6$; $p = 0.001$) and geographical range ($\chi^2 = 7.3$; $p = 0.026$). Large geographical ranges and high market prices tended to distinguish threatened species. This result does not contradict the significant univariate results for other explanatory variables. Rather, it infers that maximum market price and geographical range were the variables that together could best explain the Red List categories assigned to the commercial species. The pairwise comparisons of the final model showed that maximum market price significantly distinguished the threatened species (EN and VU) from species assessed as LC or DD (electronic supplementary material, table S2). The modelled probabilities from the multinomial logistic regression revealed that the likelihood of a species being classified as EN or VU increases steeply with market value ($p < 0.001$, $r^2 = 0.80$; electronic supplementary material, figure S3).

4. Discussion

Market price stands out as the key driver of extinction risk in commercially exploited aspidochirotid sea cucumbers, seconded by large geographical range, accessibility (shallow depth of occurrence), as well as dense human populations and coastal poverty in the geographical ranges. Our study provides a clear example from marine invertebrates in which widely distributed species can become threatened through familiarity (being well known) in the marketplace that makes them valuable. Our findings also highlight that extrinsic factors can be significant determinants of extinction

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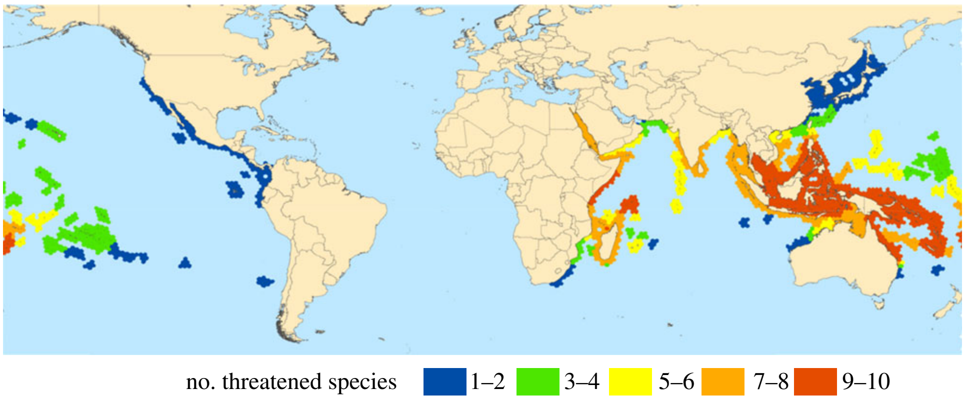

Figure 3. Global prevalence of threatened sea cucumbers. Number of sea cucumber species within the order Aspidochirotida that were classed as EN or VU among locations worldwide.

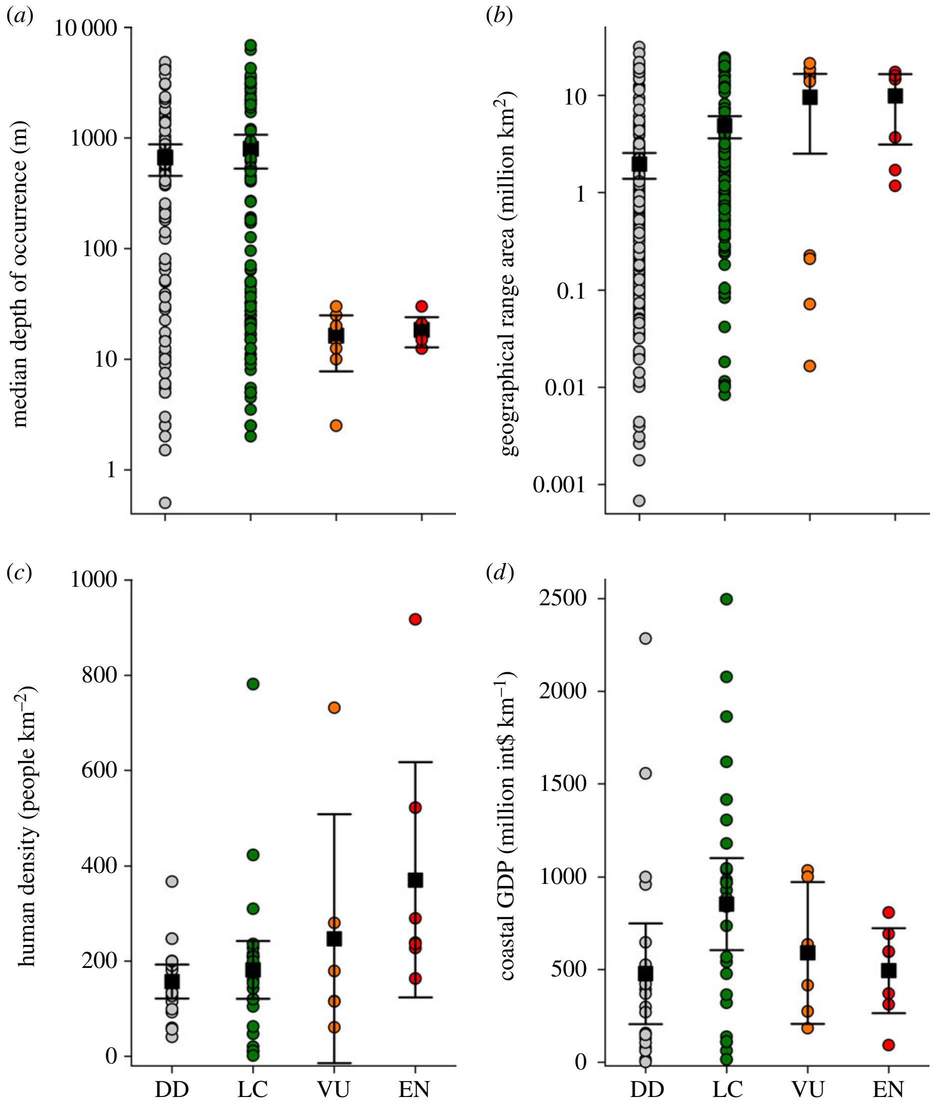

Figure 4. Error bar and scatter plots of comparisons among IUCN Red List categories for (*a*) depth at which sea cucumbers can be found in the oceans ($n = 226$), (*b*) their geographical range area ($n = 362$), (*c*) human population density in geographical range of each species ($n = 60$) and (*d*) GDP per kilometre of coastline in geographical range of each species ($n = 61$). Axes for (*a*,*b*) are on a $\log_{10}$ scale; data for the four extinction-risk categories are untransformed. Squares are means and error bars are 95% CIs. Categories: DD, data deficient; LC, least concern; VU, vulnerable; EN, endangered. (Online version in colour.)

risk, even for species once considered to be locally common and with wide geographical distributions.

(a) Paying the price of being valuable

The AAE happens when a species' market value increases disproportionately as it becomes rare, motivating exploitation at very low abundance and leading to extinction [9]. The rarer they become, the greater the demand to exploit every last one; i.e. rarity causes their high value. However, in contrast to the AAE, high-value drives rarity in sea cucumbers, not vice versa. None of the naturally rare species are particularly high value. The seven species classified as EN, have been previously common and widely distributed. Their populations have

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declined considerably through intense exploitation throughout most of their native ranges, but none are yet rare at a global scale.

Over-exploitation has reduced wild populations of the most expensive species (*A. japonicus*) by more than 60% across its geographical range, despite vast mariculture of these sea cucumbers in China. Billions of juveniles are now produced in hatcheries and grown-out in ponds or sea farms but, from all accounts, wild populations have not been repopulated [26]. *Holothuria scabra*, also EN, attracts the highest market price of any tropical species [23,31], is widely distributed and has always been favoured by southern Chinese, even when once abundant [32]. Sea cucumbers are valued by Asian consumers for their familiarity in dishes, health and medicinal benefits, and good eating qualities but not for their rareness. By comparison, sea cucumbers in naturally low abundance (e.g. *Thelenota rubralineata*, *Actinopyga flammea*, *Stichopus pseudohorrens*), do not attract higher prices [23].

This appraisal demonstrates that high value can be a key driver of extinction risk in low-trophic-level animals as has been shown for high-trophic-level tunas, billfishes [8] and groupers [33]. Globally, high-revenue fisheries develop before low-revenue fisheries [34], and high-value sea cucumber species are often targeted first before fishers move to lower value species [35,36]. The corollary is that low-value species with small populations or small geographical ranges, for example the three VU species not currently targeted by fishers, could be easily fished to extinction. In view of the importance of predicting vulnerability, estimating extinction risk and prioritizing species for conservation attention [13], we submit that highly desirable sea cucumbers are under greatest threat of extinction, as has been the case for many marine and terrestrial species [10]. In the past decade, export-driven exploitation has caused the collapse of numerous sea cucumber fisheries and populations of high-value species were always reported as the first to be affected [24].

Easy access by fishers to the sea cucumbers close to shore is the most probable underlying source of the significant relationship we found between densities of human populations in the species geographical range and their risk of extinction. The accompanying trend of lower GDP of coastal populations in the geographical ranges of threatened species reinforces the notion that harvesting of sea cucumbers is most attractive to low-income communities. Similarly, dense human populations and poor regional economies have been important predictors of extinction risk in birds [37] and mammals [38,39]. Our study illustrates that anthropogenic variables can also play a key role in driving extinction risks in the sea, even for animals at low-trophic levels.

The incentives to exploit high-value species are intuitive but the process of exploiting them to extinction is more complex. Continued exploitation of depleted populations is possible through ‘opportunistic exploitation’, arising from a pernicious synergy between sympatric exploitation and high value [10]. A silent accomplice to this threat is the (demographic) Allee effect; when wild populations decline in abundance to a threshold at which low reproductive success results in negative *per capita* population growth, sending them into an extinction vortex [15,40].

(b) Effects of geographical range size

Greater geographical range often affords species with resilience to extinction [20,41], although there are a few exceptions, for example groupers [33]. Within marine invertebrates specifically, large geographical range size was the most important determinant of resilience to extinction in recent geological history [41,42]. Our findings exemplify an important exception, underpinned by modern market drivers and human exploitation. Sea cucumber species in both VU and EN categories tended to be distributed across larger areas compared with least threatened species. Future genetic studies may split some of these species, reducing their known geographical ranges. The effect of large geographical range size on extinction risk can be explained by the effect of marketplace familiarity on extinction risk—widely traded species with desirable qualities become well known, which increases prices and spurs over-exploitation. This phenomenon is known from other previously common, widely distributed and heavily exploited species, such as big-leaf mahogany *Swietenia macrophylla*, passenger pigeon *Ectopistes migratorius* and Atlantic cod *Gadus morhua* [43], and certain groupers [33]. Typical threatening processes that are associated with significant declines in once common species relate to exploitation rate, habitat loss, natural demographic variability, population growth rates and hazardous behaviours like aggregating for reproduction [43]. Our study shows that high market value, accessibility (ease of exploitation), proximity to areas of high human density and poverty can be important extrinsic traits that can help identify species at greatest risk. Moreover, these traits appear to override the resilience to extinction normally afforded by broad geographical range.

(c) Does size matter?

Although body size is a good predictor of extinction vulnerability in marine fishes [15,44] and marine mammals [20], it was not a significant predictor for sea cucumbers. Across commercial species for which market prices were obtained, we found little correspondence between the average size of a species and its value. Both large and small species have roles in Chinese cuisine; e.g. small specimens of the spiky species, categorized as *ci-shen*, are served in small dishes in Beijing-style cuisine (electronic supplementary material, figure S1*e*), whereas the larger, smooth species, categorized as *guang-shen*, are served on large plates in Cantonese-style cuisine. The message is that large body size is not a universally reliable indicator of extinction risk.

(d) Is deeper safer?

Depth of fishing grounds can be a proxy for the costs of fishing, and species in shallow waters have been shown to be preferentially impacted by global overfishing [34]. Our univariate analyses revealed that threatened species systematically inhabit relatively shallow waters. This trend points to a strong effect of resource accessibility on extinction risk. In certain places where compressed-air diving is practiced, stocks in deeper waters no longer have refuge from exploitation [35].

Greater fishing pressure in shallow waters is corroborated by our findings that EN species tended to be from tropical coasts with dense human populations with poor economies. In low-income tropical countries, sea cucumbers are harvested in small-scale fisheries by hand in shallow waters accessible to waders and breath-hold divers [24]. We further point out that shallow-water species in the tropics are imperilled by broad-scale threats to coral reef ecosystems from ocean

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acidification and warming seas [45], which can additively amplify the extinction risks from over-exploitation [46].

(e) Knowledge gaps and uncertainties

(i) Estimating generation length

Under IUCN Red List assessment methodology, Criterion A requires estimation of generation length of each species. When unknown empirically, generation length is approximated from biological parameters of related species (see the electronic supplementary material, S1 Materials and Methods). However, little knowledge exists on longevity or ages of the vast majority of Aspidochirotida species [24]. The IUCN Red List assessment of the Aspidochirotida conservatively estimated three generation lengths to be 30–50 years. This time frame could be under- or over-estimated for certain species and requires future research.

(ii) Data deficiency

Marine invertebrates comprise more than 95% of all marine animal species but most are poorly known [47]. The high proportion (66%) of DD sea cucumber species contrasts with a predominance of data sufficiency in IUCN assessments of charismatic marine vertebrates; e.g. 28% of marine mammals, 31% of elasmobranchs (sharks and rays) and 17% of marine turtles are DD [20,21]. In addition to needing basic biological data on described species, more taxonomic studies are required on undescribed aspidochirotid species, excluded from this IUCN assessment, some despite being harvested in several countries. Marine invertebrates, for example sea cucumbers, attract less funding for basic biological research than corals, fishes and other charismatic marine fauna [21]. The limited understanding of life-history traits of sea cucumbers [24], and many other marine invertebrate groups [47], will continue to hinder conservation efforts and assessments of extinction risk.

A number of sea cucumber species are relatively rare and, although not the prime targets of fishers, are exploited. Rare species require a large number of samples to assess population abundance and declines with any accuracy and that is especially labour intensive on coral reefs [13]. Although their rarity does not make them especially valuable, their populations may already be reproductively precarious and vulnerable to incidental exploitation. Thus, special attention needs to be given to rare species in resource assessments.

(f) Implications for biodiversity conservation

(i) National and local measures

Sea cucumbers contribute value to coral reef ecosystems through nutrient recycling and sediment bioturbation (reviewed in [24,48]) and might help to buffer reef biota from ocean acidification [49]. A modern explosion of studies on the medicinal benefits of sea cucumber products [50] reveals vast opportunities for pharmaceutical uses. Additionally, some of the EN species, such as *H. scabra*, *Holothuria lessoni* and *Isostichopus fuscus*, are showing promise as alternative aquaculture commodities [31]. Therefore, sea cucumbers are nationally valuable for export revenue, ecosystem services, and commercial and mariculture opportunities.

Our findings emphasize that high-value species, particularly those in shallow waters easily accessible to fishers, are likely to be at greatest risk of extinction of wild populations, even if they were once common and broadly distributed. High-value species need most stringent regulatory measures for their exploitation [10], because they can still be collected opportunistically after fishers shift to targeting lower value species [24], and conservation must not lose sight of threats to common species [43]. Species-specific bans have been placed on threatened sea cucumbers in a few instances [51] but these regulations do not prevent serial depletion of other species further down the value chain. An alternative is to set a shortlist of allowable species, which excludes threatened species and those important for ecosystem functions [10,24]. This regulatory measure should be accompanied by others, such as capacity and effort limitations (e.g. short fishing seasons), to keep exploitation of fishable populations at sustainable rates.

(ii) International and regional measures

Administrative burdens of compliance and inability to effectively enforce national bans are problematic for CITES listing of sea cucumbers [52]. Our finding that low-income countries have many threatened species to manage illustrates a dilemma that exacerbates those constraints—threats to biodiversity loss are greatest where capacity is weakest to manage them.

CITES can help in conservation broadly because importing countries should be part of the solution. To date, only *I. fuscus* is listed in CITES, within Appendix III, by Ecuador [52]. We contend that this species and the six other EN species should qualify for listing within CITES Appendix II. The CITES criterion relating to detrimental exploitation of species is consistent with the IUCN Red List criteria and assessments reported here. All seven EN species are well known in the marketplace and distinguishable in the dried form [23], dismissing the 'lookalike' clause [25,52] as an impediment to CITES listing.

The task for exporting countries of making non-detriment findings (for CITES Appendix II listing) is notoriously tricky, especially when multiple species are harvested [53,54], as is the case with most tropical sea cucumber fisheries. Importing countries need only determine non-detriment findings for trade of species in Appendix I [54]. Recent regional reviews and studies have taken large steps in filling previous knowledge gaps about certain sea cucumber populations and fisheries [22,35,55] but population data are still limited in many countries. We therefore echo the call for increasing research and capacity building in 'conservation hotspot' countries where biodiversity threats are most acute [56]. Technical support to assess exploitation and wild populations is needed in countries in the western Indian Ocean and Coral Triangle, because they have dense human populations, coastal poverty and a high number of threatened sea cucumber species.

Whereas the USA, the European Union and Japan are the main final destinations of most biodiversity-implicated commodities [57], harvested sea cucumbers are mostly destined for China [58]. Lenzen *et al.* [57] surmised that the responsibility for biodiversity loss should be allocated between producers and consumers. This concept has been largely overlooked in recent prescriptions to remedy sea cucumber fisheries. Management actions by source countries need parallel conservation efforts not only by consuming countries but also via multi-lateral agreements and the civil society itself [21], although multi-stakeholder involvement is no guarantee for sustainable exploitation [59]. We conclude

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that biodiversity conservation of exploited species, for example sea cucumbers, will depend on both local-level regulatory measures and international instruments that regulate trade to conserve populations and species at risk.

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