Humans and seasonal climate variability threaten large-bodied coral reef fish with small ranges

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Coral reefs are among the most species-rich and threatened ecosystems on Earth, yet the extent to which human stressors determine species occurrences, compared with biogeography or environmental conditions, remains largely unknown. With ever-increasing human-mediated disturbances on these ecosystems, an important question is not only how many species can inhabit local communities, but also which biological traits determine species that can persist (or not) above particular disturbance thresholds. Here we show that human pressure and seasonal climate variability are disproportionately and negatively associated with the occurrence of large-bodied and geographically small-ranging fishes within local coral reef communities. These species are 67% less likely to occur where human impact and temperature seasonality exceed critical thresholds, such as in the marine biodiversity hotspot: the Coral Triangle. Our results identify the most sensitive species and critical thresholds of human and climatic stressors, providing opportunity for targeted conservation intervention to prevent local extinctions.
Understanding the processes that generate and maintain species occurrence patterns is challenging, partly due to confounding natural and human-mediated effects. The peak in marine biodiversity observed in the Coral Triangle has been explained by several non-mutually exclusive hypotheses that involve the roles of energy, habitat area, biogeography and geometric constraints on species range sizes. By contrast, the impact of cumulative human pressure (including fisheries, urban development and climate change) on global marine biodiversity patterns has long been overlooked. With the recent development of multifaceted metrics of cumulative anthropogenic pressures and geometric constraints on species range sizes, it is now possible to disentangle their impacts from ecological and evolutionary determinants of biodiversity patterns. Doing so now is critical to help identify and prioritize tractable options for conservation actions to mitigate accelerating human impacts on biological communities.

Most studies investigating biodiversity patterns implicitly consider species as comparable units. However, the ecological roles of species also matter, with many species—particularly those with restricted geographical ranges supporting unique and indispensable functions. Furthermore, different subsets of species respond differently to environmental and human stressors, most often in non-linear ways with critical thresholds. For example, fishing and climate change can differentially impact the abundance and biomass of fishes depending on their body sizes. Human pressure also has the potential to reduce species abundances, which in turn can cause ecological extinction (that is, when large population declines prevent species from performing their ecological roles), local extinction (that is, extinction) and, ultimately, global extinction. Yet compared with human-mediated decreases in abundances, the loss of species occurrences under human pressure remains largely unknown for coral reef fishes over broad spatial scales, and cannot be inferred from reduced local abundance because abundance and occupancy are unrelated for fishes on coral reefs. Thus, the extent to which human stressors shape species occurrence patterns within their geographical range, once natural and biogeographic factors have been accounted for, requires urgent assessment—as does the extent to which these relationships might be modulated by biological traits such as body size.

Our analyses of coral reef fishes combined data from 906 locations across the Indo-Pacific along with biological traits, including maximum adult total length, trophic group, home range size, mobility, diel activity, schooling behaviour and geographical range size estimated as the extent of occurrence. Coral reef fishes are ideal for examining correlates of broad-scale occurrence patterns because they (i) are species-rich (> 4,800 species within the Indo-Pacific), (ii) respond to environmental gradients at multiple scales, particularly in comparison to most other vertebrate taxa and (iii) include a wide range of body sizes (from a few cm to > 3 m total length), life histories, and reproductive strategies. We focused our analyses on 241 well-known and easily detected species of coral reef fishes that were consistently sampled on reefs across the Indo-Pacific and that encompass a wide spectrum of biological traits and geographical range sizes. We assessed how occurrence patterns in coral reef fishes respond to multiple indices of human pressure, which included past and present threats, the human impact index mostly reflecting intense artisanal fishing and dense human populations and the ocean health index. Using machine-learning techniques combined with detectability and null permutation models, we identified the main correlates of occurrence for each species and their associated thresholds among (i) indices of human pressure, (ii) energy proxies, including sea surface temperature and primary productivity, (iii) habitat area (both present and historical), and (iv) biogeography, including distances to land masses and the Coral Triangle. We considered energy proxies to be potentially important because temperature influences species occurrence through phenological and physiological constraints, while higher primary productivity supports larger populations that more effectively resist extinction. Reef area increases the probability of colonization from neighbouring reefs, while biogeographic isolation from the main coral reef habitats accounts for large-scale connectivity and long-term persistence through dispersal.

Using the most extensive data set on tropical reef fish occurrences (presences and absences) across the entire Indo-Pacific, we tested whether the vulnerability of fish occurrence to human pressure is modulated by fish body size and geographical range size, while controlling for energy, area and biogeography. We show that (i) the occurrence of relatively large-bodied tropical reef fishes (> 50 cm total length) is strongly and negatively associated with cumulative human pressure and, to a lesser extent, negatively associated with temperature seasonality; and that (ii) this effect is most pronounced for the large-bodied species with the relatively smallest geographical ranges (that is, within the first quartile of geographic range sizes; n = 13).

Results and Discussion

Quality control of the fish data. We found no evidence of any consistent data source or temporal effects in the fish occurrence data (permanova; 999 permutations, P > 0.05). Conversely, we found evidence for an effect of body size and behaviour on fish detectability (Supplementary Table 1; model1; weight of Akaike’s information criterion corrected for sample samples (wAICc) > 0.9). Detectability decreased with maximum body size (mean effect size ± s.e. = -0.006 ± 0.001), high mobility (−0.289 ± 0.053), a solitary behaviour (−0.562 ± 0.049) and high level in the water column (−1.035 ± 0.135). However, the models including geographic variation (model2) or important correlates (model3) received little support (wAICc < 0.1; Supplementary Table 1), and residuals of the first model were evenly distributed within the study area (Supplementary Fig. 1A). These results suggest that even though detectability differed among species, this effect was evenly distributed among samples and within the correlate space, and did not affect the relationships between different correlates and fish occurrence patterns. We also found no effect of fishing intensity on the probability of recording false absences, either for all species or targeted/large ones (Supplementary Fig. 1B). Locations with missing fish data were evenly distributed across the correlate space as indicated by a principal component analysis (Supplementary Fig. 2) based on correlates related to biogeography, energy, area and human pressure, suggesting that species–correlate relationships inferred by the models were not influenced by missing data.

Main correlates of fish occurrence patterns. Human pressure and energy had disproportionately large effects on the occurrence of large-bodied species (> 50 cm; Fig. 1a), with negative relationships between occurrence probability and both human impact and temperature seasonality (the most important human pressure and energy correlates; Fig. 2). By contrast, occurrences of smaller-bodied species were best explained by biogeographical correlates (Fig. 1a), with a positive relationship between reef area and occurrence probability (Fig. 2). Among large-bodied species,
which tend to have large geographic ranges (Supplementary Fig. 2), those with relatively smaller ranges (<90 × 10^6 km^2; with a mean range of 57 × 10^6 km^2, equivalent to half that of an average large-bodied fish) were particularly and negatively affected by human pressure and energy (Fig. 1a, foreground edge of the cube and Fig. 2, dotted lines). The total amount of variation explained in occurrence patterns declined from 71% for the smallest species to 39% for the largest, with 5 and 10%, respectively associated with human pressure (Supplementary Fig. 3) (that is, 8–23% in terms of relative contribution; Supplementary Fig. 4). Of the total variation explained in occurrence patterns among species (Supplementary Fig. 5), body size combined with range size explained 46% (Supplementary Table 2). These patterns were consistent with the typical trend of decreasing probability of occurrence (concomitant with decreasing abundance^29) as body size increases^30,31 (Supplementary Fig. 6). Other biological traits (for example, diet, home range size) did not explain additional variation in occurrence patterns (Supplementary Fig. 7; Supplementary Table 3).

These patterns differed from those expected under a null model of randomized occurrences within each species’ geographical range. Null boosted regression trees converged for 121 species only (~50% of all species considered) and explained between 1.0 and 23.1% deviance in fish occurrence patterns (mean = 5.3 ± standard deviation = 5.3 ± 4.7%). We found no evidence for a relationship between the total deviance explained and body size (Supplementary Fig. 8; Supplementary Table 4), or between the relative contributions of the different correlates and body or range sizes (Supplementary Fig. 9; Supplementary Table 4).

Our findings indicate an increasing negative influence of human pressure and temperature seasonality on fish occurrence as body size increases and species range size decreases. Small species tend to disperse less than large ones^32, and their occurrences are primarily a function of biogeography, suggesting that isolation from source populations (decreasing dispersal rates) plays an important role in shaping their regional-scale occurrences^28. For larger species with slower growth rates, fishing or habitat degradation can more effectively reduce fish stocks, affecting local and regional patterns of population size and biomass^15. Our results show that human pressure and temperature seasonality can potentially affect not only local population size, but also regional occurrence patterns of large-bodied and small-ranging fishes in particular.

**Human impact and fish occurrence patterns.** Large fishes tend to occur less frequently on human-impacted reefs (Fig. 3b), highlighting a gradient of increasing occurrence with distance from the Coral Triangle. This pattern contrasts with the well-known gradient in marine biodiversity^2 that peaks in the Coral Triangle. Large species occurrence was negatively related to the human impact index^8 (the most important human pressure variable we examined). This pattern was stronger for large-bodied, relatively small-ranging fishes (Fig. 2) for which the contribution of human impact was greatest (Fig. 1a). Owing to the non-linear and negative relationship between human impact and the occurrence of large-bodied fishes, high occurrence probabilities of large-bodied and small-ranging species were only observed where human impact was low to moderate (Fig. 2 and Supplementary Fig. 10) with critical thresholds (Table 1). This means that under such thresholds, even a small reduction in human impact was associated with a much higher probability of encountering those large fish species. More specifically, reefs subject to a human impact index > 9.9 (equivalent to conditions encountered in the Solomon Archipelago and currently representing 30% of all Indo-Pacific coral reefs) have a probability <0.3 of hosting large fishes. This low probability of occurrence represents a 60% reduction (67% for large-bodied, small-ranging fishes) from the greatest occurrence probabilities (0.7) that characterize less impacted reefs in New Caledonia or on
the Great Barrier Reef (Fig. 3). This spatial gradient of large fish occurrence probabilities due to decreasing human impact from the Coral Triangle towards the south-west Pacific contrasts with the gradient of fish species richness and corroborates recent results showing that large species, and large-bodied and small-ranging fishes in particular, might contribute only marginally to high local species richness within the Coral Triangle, but much more to the richness of less-diverse assemblages at its periphery. Conversely, human pressure was in general positively, but weakly, associated with the occurrence of small-bodied species (Fig. 2), with small fishes tending to be more frequent on impacted reefs (that is, subject to a human impact >36.4; Table 1). This result corroborates previous studies documenting an increase in the relative abundances of small fishes on highly disturbed or fished reefs.

Climate seasonal variability and fish occurrence patterns. The probability of occurrence of large (and small-ranging) fishes was also greater where sea surface temperatures were less seasonally variable (Fig. 2). This generally resulted in higher probabilities of occurrence at low latitudes (Fig. 3d); although large species, which tend to have larger ranges than smaller ones, are still likely to occur in more variable environments than smaller species (as a consequence of their generally larger ranges). Temperature can affect marine organisms through

Figure 2 | Predicted probability of occurrence and associated thresholds for species of increasing body size in response to biogeography, energy, area-related correlates and human impact. Only the relationships with the strongest correlates in each category are shown, with Dist2Land: distance to nearest land mass, in km; ReefArea50: reef area, in km²; SSTdev: seasonal deviation (that is, seasonality) in sea surface temperature, in °C. For each plot, the continuous line represents the mean effect across species and the envelope indicates the 95% confidence interval. Red dots indicate critical thresholds in the mean effect across species (Davies test, P < 0.05). Dotted lines show the response of small-ranging species (first quartile of geographic range sizes), truncated to represent only the range of values where they occur (up to the 98th percentile). Contribution daggers reflect the change in correlate contribution as body size increases.

Vulnerability of large-bodied fishes with small ranges. Large-bodied, small-ranging fishes represent only 7% of all the species we examined here (Supplementary Data 1), yet because of their unique functional roles and ecosystem services they provide, their greater sensitivity to human pressure could have cascading effects on entire reef ecosystems. Some of these species are commercially exploited and sustain local artisanal fisheries in many developing nations, but their conservation status remains largely unassessed. This oversight is partly due to the recent focus of conservation strategies to protect particular functional groups like herbivores, which are deemed to play an essential role in the prevention of phase shifts from coral- to algae-dominated states. However, we found no evidence that herbivore occurrences were particularly affected by human pressure at the scale of the entire Indo-Pacific, possibly because the broad spatio-temporal scales at which these data were aggregated masked the importance of recent environmental changes at individual reefs, to which trophic affiliation often regulates species responses. Instead, the combination of large body size (usually associated with slow growth rates) and restricted geographical range (suggesting limited physiological tolerance) puts these species at higher risk of local extinction, irrespective of their other traits.

Large-bodied, small-ranging fishes are likely to be particularly susceptible to local extinction over the coming decades because (i) their restricted geographical ranges imply that any additional stressors would have a disproportionate effect on their occurrence patterns compared with more widely distributed species, and (ii) such stressors are expected to increase over the coming decades. The vulnerability of coral reef fishes to global change might thus depend strongly on the interplay between the body sizes and geographic range sizes of these species. Our results strongly indicate that these potential drivers of extinction urgently need to be incorporated into conservation strategies aimed at minimizing local biodiversity loss and thus maximizing ecosystem resilience to future disturbances.
Methods
Fish occurrence data and biological traits. We obtained fish occurrence (presence/absence) data from 9,828 samples, of which 93% were transects and the remaining point counts, from 906 locations of similar spatial extent within the Indo-Pacific (Supplementary Fig. 12; Supplementary Table 5). These data were collected by underwater visual census based on either fixed-length belt transects\textsuperscript{52} or stationary point counts\textsuperscript{53} in shallow reef habitats (depth 0–30 m), where all fishes sighted in the survey area were recorded on an underwater slate by divers. A detailed description of the methods used for fish sampling is provided in Supplementary Table 5 and references therein.

We selected 241 species from 10 families (Supplementary Data 1) for analysis based on the following criteria: (i) they satisfied minimum detection criteria (that is, we excluded cryptic and rare species, and those \(< 3 \text{ cm total maximum length}\)), and (ii) they covered the broadest range of life-history traits\textsuperscript{21} and geographical ranges\textsuperscript{52} possible with minimal uncertainty around those estimates. We used an independent data set of expert-verified checklists\textsuperscript{24} to delineate each species’ geographical range (convex hull, defined as the smallest convex polygon containing all species records) as the basis for calculations of geographic range sizes (i.e., extent of occurrence\textsuperscript{23}; in \(10^6 \text{ km}^2\)). For each species, we calculated range size (defined as the total area of the convex hull minus total land area) in ArcGis 10.0 using a global equal-area Behrmann projection. For each species, we also collated the following life-history traits\textsuperscript{21,22}: trophic group, body size (i.e., maximum adult total length, in cm), home range, mobility, diel activity pattern and schooling behaviour. Some species were occasionally not sampled because two data sets (WCS and PROCFish; Supplementary Table 5) used a restricted species list. This resulted in 8% of all records missing; therefore, we did not use these records during model calibration and verified that missing data did not affect our analyses (see ‘Missing fish data’ section).

Figure 3 | Maps of human and climate seasonal variability, and predicted probabilities of large fish occurrence. (a) Human impact and (b) predicted probability of occurrence of large fishes (body size \(\geq 50 \text{ cm}\)) within Indo-Pacific reefs in response to human impact; (c) Seasonal deviation (that is, seasonality) in sea surface temperature (SST\textsubscript{dev}) and (d) predicted probability of occurrence of large fishes in response to SST\textsubscript{dev}. (a,c) Insets show the distribution of (a) human impact and (c) SST\textsubscript{dev} across the study area. (b,d) Insets show the partial effect of (b) human impact and (d) SST\textsubscript{dev} averaged across large fishes and the 95% confidence interval. The triangle indicates the location of the Coral Triangle. On each plot, the mid-point of the colour scale corresponds to the critical threshold in the mean effect across species (Davies test, \(P < 0.05\)).
Environmental and anthropogenic variables. We selected environmental correlates related to major hypotheses attempting to explain variation in fish diversity in previous studies and based on general ecological theory. Considering the spatially aggregated nature of our data, we focused on large-scale environmental correlates that were mostly relevant to our analysis of occurrence patterns across locations (typically 10–100 km apart), instead of finer-scale environmental correlates (for example, benthic cover) that were inconsistently available across all sites. We considered the following large-scale environmental correlates: (i) biogeography, because it is related to dispersal rates through local connectivity; (ii) habitat area, because it is related to the probability of colonization from neighbouring reefs or patches within and to other Tects; and (iii) energy, because its availability can constrain species occurrence based on their physiological tolerances and because greater energy availability can sustain larger populations. We also considered a range of proxies for (iv) human pressure (past and present threat), human impact54 and ocean health index53) to account for potential pressures on coral reefs resulting from fisheries exploitation, pollution, urban development, aquaculture and past thermal stress (Supplementary Table 6), which can affect coral reef ecosystems at a global scale2,54. Many coastal centres of high species richness overlap with regions of medium to high human impact52. Human population density correlates with fishing and coastal development; and land-use stressors disproportionately impact fish biomass at more diverse reefs54. Specifically, the present local threat to coral reefs55 (from “low” to “very high”) combines threats from overfishing and destructive fishing, coastal development, watershed- and marine-based pollution and damage. The present integrated threat that accounts for past climatic stress56 (from “low” to “very high”) additionally incorporates severe stress potentially responsible for mass coral bleaching events between 1997 and 2008.

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For coral reefs, the human impact model is mostly driven by three main factors: artisanal fishing (FAO-based artisanal catch rates), climate change (frequency and intensity of sea temperature anomalies between 1985 and 2005) and direct human impact4. Coral reefs and economies, (vii) sense of place, (viii) coastal protection. We used principal component analysis (Supplementary Fig. 13) and analysed the resulting correlation matrix to ensure that correlations among the ocean health sub-components we considered here were reasonably low. We did this because, like most statistical modelling techniques, boosted regression trees are sensitive to high multicollinearity among predictors27, so a correlation coefficient r should ideally be kept under 0.7. For all correlations among the ocean health index sub-components we considered, r < 0.7 (range = (−0.46; 0.69); mean = 0.23; median = 0.27).

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Data management and quality control of fish data. Data classification and data source effects. The extent and quality of the data used in the study has only been possible because of collaborative data sets that have been collected and processed independently (Supplementary Table 5). Merging these data required a set of sample qualifiers (for example, country, island and location), reclassification of each data set according to these qualifiers, and testing for potential data source effects, and potential temporal effects that could result from differences in the timing of data collection.

We defined country based on geopolitical units (for example, French Polynesia), which included multiple islands typically 100–1,000 km apart, and with different sampled locations on each island (for example, ocean-facing barrier reef) typically 10-100 km apart. Countries comprised archipelagos or sets of island-effect could easily be classified according to this scheme; however, for larger countries with extended reef systems (for example, Australia), a set of reefs (for example, Cairns) was classified as the island and a particular reef within that set (for example, Green Island Reef) as the location. This allowed us to keep a consistent definition of the spatial extent and resolution corresponding to each qualifier across data sets. Within each location, a sample typically corresponded to a site or a station where several replicates (transects or stationary point counts) were collected, across which we pooled the fish data for analysis. For the analysis, location was used as the sampling unit (corresponding to an average total sampled area of 2,760 m², range 1,200–4,000 m²), which allowed us to minimize issues of spatial autocorrelation and random sampling error.

We tested for potential data source effects using countries and species that were sampled in multiple data sets. These countries included, for example, French Polynesia, New Caledonia, Tonga, Samoa. We compared the probability of presence of each species in each country, according to each data set, and tested for potential data source effects using five separate GLMMs. Models included a random effect coding for genus (for example, for the same species, different from those expected by chance, we ran null models where we randomized the presences and absences of each species within its range. We then repeated the (i) BRT and (ii) GLMM analyses as described above. We applied a single randomization of the 241 species-specific BRT (to keep the time required to code all models reasonable) as opposed to the null model (zero) as well as their interactions.

Null models. To test the null hypothesis that the patterns we observed were not different from those expected by chance, we ran null models where we randomized the presences and absences of each species within its range. We then repeated the (i) BRT and (ii) GLMM analyses as described above. We applied a single randomization of the 241 species-specific BRT (to keep the time required to code all models reasonable) as opposed to the null model (zero) as well as their interactions.

Relationship between range and body size. We predicted geographical range size as a function of body size (that is, maximum adult total length) using separate GLMM with a Gaussian error distribution and a log link function, and other parameters as described above.

Partial effects of occurrence correlates and mapping of global patterns. We identified the strongest correlates of occurrence and plotted their partial effects.
(individual correlate effect, once the effect of other correlates had been accounted for) for each species. We then plotted the mean partial effects, averaged across species of three body size classes (≤15, 16–50, >50 cm), along with their 95% confidence intervals. For each body size class, we also plotted the mean partial effects for small-ranging species, defined as species within the first quartile of geographic range size, to test for critical thresholds in these partial effects using the Davies test and, where present (p < 0.05), identified their values based on a segmented linear regression. We mapped a raster surface of the mean partial effect of human impact and temperature seasonality on the occurrence of large tropical reef fishes (>50 cm body size) across the Indo-Pacific using bilinear interpolation in ArcGIS 10.3.

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1. Nogues-Bravo, D., Araujo, M. B., Romdal, T. & Rahbek, C. Scale effects for each species. We then plotted the mean partial effects, averaged across species of three body size classes (≤15, 16–50, >50 cm), along with their 95% confidence intervals. For each body size class, we also plotted the mean partial effects for small-ranging species, defined as species within the first quartile of geographic range size, to test for critical thresholds in these partial effects using the Davies test and, where present (p < 0.05), identified their values based on a segmented linear regression. We mapped a raster surface of the mean partial effect of human impact and temperature seasonality on the occurrence of large tropical reef fishes (>50 cm body size) across the Indo-Pacific using bilinear interpolation in ArcGIS 10.3.
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Author contributions
C.M., M.K., C.J.A.B., L.V., D.A.F., D.M. and M.J.C. conceived the ideas; M.K., L.V., R.E.B., P.C., G.J.E., A.M.F., T.R.M., R.D.S.S., I.W. and many others collected the data; C.M. led the writing of the paper, M.K., C.J.A.B., D.A.F., V.P., R.D.S.S., G.J.E., D.M. and M.J.C. helped draft the paper, with input from all authors; C.M., M.K. and A.M.M.S. analysed the data; C.M. and A.M.M.S. prepared the maps.

Additional information
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