

Research



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# Biodiversity underpins fisheries resilience to exploitation in the Amazon river basin

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Inland fisheries feed greater than 150 million people globally, yet their status is rarely assessed due to their socio-ecological complexity and pervasive lack of data. Here, we leverage an unprecedented landings time series from the Amazon, Earth’s largest river basin, together with theoretical food web models to examine (i) taxonomic and trait-based signatures of exploitation in inland fish landings and (ii) implications of changing biodiversity for fisheries resilience. In both landings time series and theory, we find that multi-species exploitation of diverse inland fisheries results in a hump-shaped landings evenness curve. Along this trajectory, abundant and large species are sequentially replaced with faster growing and smaller species. Further theoretical analysis indicates that harvests can be maintained for a period of time but that continued biodiversity depletion reduces the pool of compensating species and consequently diminishes fisheries resilience. Critically, higher fisheries biodiversity can delay fishery collapse. Although existing landings data provide an incomplete snapshot of long-term dynamics, our results suggest that multi-species exploitation is affecting freshwater biodiversity and eroding fisheries resilience in the Amazon. More broadly, we conclude that trends in landings evenness could characterize multi-species fisheries development and aid in assessing their sustainability.

## 1. Introduction

Inland capture fisheries play critical roles in food security and livelihoods across the world, particularly in the largest tropical river basins, such as the Amazon [1]. Thus, a boom in tropical hydropower development, together with climate change, has received considerable attention for their potential impact on fisheries [2,3]. Overexploitation, however, remains pervasive albeit rarely quantified, particularly because the lack of high-quality data offers few opportunities for traditional approaches (e.g. stock assessments [4]). Tropical riverine fisheries consist of many spatially diffuse operators using a variety of gears to exploit a wide diversity of species (i.e. multi-species) in regions difficult

to access and manage, which underlie the limited data flows [5]. Thus, aggregated landings data (i.e. retained catches) from regional ports are often among the few information sources available to examine patterns of community response to exploitation and, more generally, to diagnose their status.

The Amazon is one of the most productive and diverse freshwater ecosystems on the planet [1], and has among the highest rates of fish consumption in the world [6]. While vast portions of the region remain sparsely occupied, growing urban demand for fish has resulted in the overexploitation of key species [7,8]. Yet, deducing whether exploitation is affecting ecological communities more broadly, and linking these patterns to processes that maintain fishery resilience, is hampered by the paucity of fishery independent information and appropriate analytical tools. Developing and harnessing fisheries diagnostics based on landings data holds promise to understand whether communities are responding to exploitation and how these changes affect fisheries resilience.

Landings reflect a combination of fisher dynamics and the response of ecological communities to exploitation [9,10]. While often leveraged to examine patterns of exploitation, disentangling the relationship between landings and underlying community dynamics can be challenging [10,11]. Tropical inland fisheries such as the Amazon exploit complex food webs where large- and small-bodied species occupy a diversity of trophic positions (e.g. detritivory and predation). By exploiting multiple species, these fisheries may maintain consistent harvest biomass, although result in changes in taxonomic and functional composition [9,12]. Landings taxonomic trends, such as declines in species richness, may suggest a narrowing of the pool of exploitable species. Trait-based trends, such as declines in mean body size or trophic level, can correspond to the sequential replacement of long-lived species with low population growth rates (e.g. K-selected) with faster growing species (e.g. r-selected [9,13,14]). On the other hand, changes in economic-based indices, such as mean revenue or price of landings may provide evidence of trends in fishery behaviour [15]. But, because tropical inland fisheries target many taxa simultaneously with varying species-level selectivity, how economic indicators lead or lag compositional change is unclear [16].

Beyond characterizing patterns in the response of ecological communities, understanding how biodiversity changes affect processes that maintain harvests despite ongoing exploitation (i.e. fishery resilience) is critical for assessing fisheries status. Generally, resilience declines with biodiversity loss because communities with fewer species have lower potential for biomass compensation [17]. Exploitation, thus, by progressively depleting the pool of compensating species, could also decrease fisheries resilience [12]. Turnover in landings taxonomic or functional composition may be indicative of declining resilience, but few studies have linked these patterns to processes such as compensation. In fisheries that exploit simple food chains or specifically target predators, changes in resilience might correspond with declines in mean trophic levels since depleting predators can induce prey compensation [18,19]. Fisheries exploiting complex food webs, however, could cause compensatory responses in prey and competitors alike [19,20]. While previous work on tropical inland fisheries has linked exploitation to compositional turnover in landings [9,11,21], how these relate to fisheries resilience is unclear, but essential for diagnosing fishery status in regions such as the Amazon.

Further limiting diagnosis based on landings data is that patchy spatial and temporal coverage might only provide an incomplete snapshot of true community composition dynamics. Thus, complementary insights into the sustainability of data-depauperate multi-species fisheries can be obtained by analysing theoretical models that mimic landings dynamics [22,23]. These models can uncover mechanisms underlying observed patterns in landings and relate these to drivers of fishery resilience. For example, theory indicates that balanced-exploitation—when fishing is distributed across species in proportion to their natural productivity—can increase fishery resilience relative to selectively targeting large species [24,25]. Models incorporating food web interactions further suggest that harvests can be maintained through predator and competitor release, patterns which manifest through compositional turnover from K- to r-selected species [26]. More broadly, linking models to observed biodiversity trends in landings could provide a powerful approach to diagnose the status of multi-species fisheries in the Amazon and other similar geographies.

Here, by combining an extensive inland fisheries landings time series from the Amazon, Earth's largest river basin, with insights from a theoretical food web model, we evaluate how multi-species exploitation is affecting biodiversity, and in turn, how these changes in biodiversity affect fishery resilience. Specifically, our objectives are to (1) explore how landings biomass, taxonomic and trait-based diversity (i.e. mean trophic level, body size, price and revenue) are changing across time in the Amazon and (2) use theoretical food web modelling to infer changes in fishery resilience and advance diagnostic tools for multi-species fisheries. Given the predominance of fish as food across Earth's tropical river basins, but challenges associated with weak governance and monitoring, this study provides insights into the potential for landings data to inform the sustainability of data-limited fisheries.

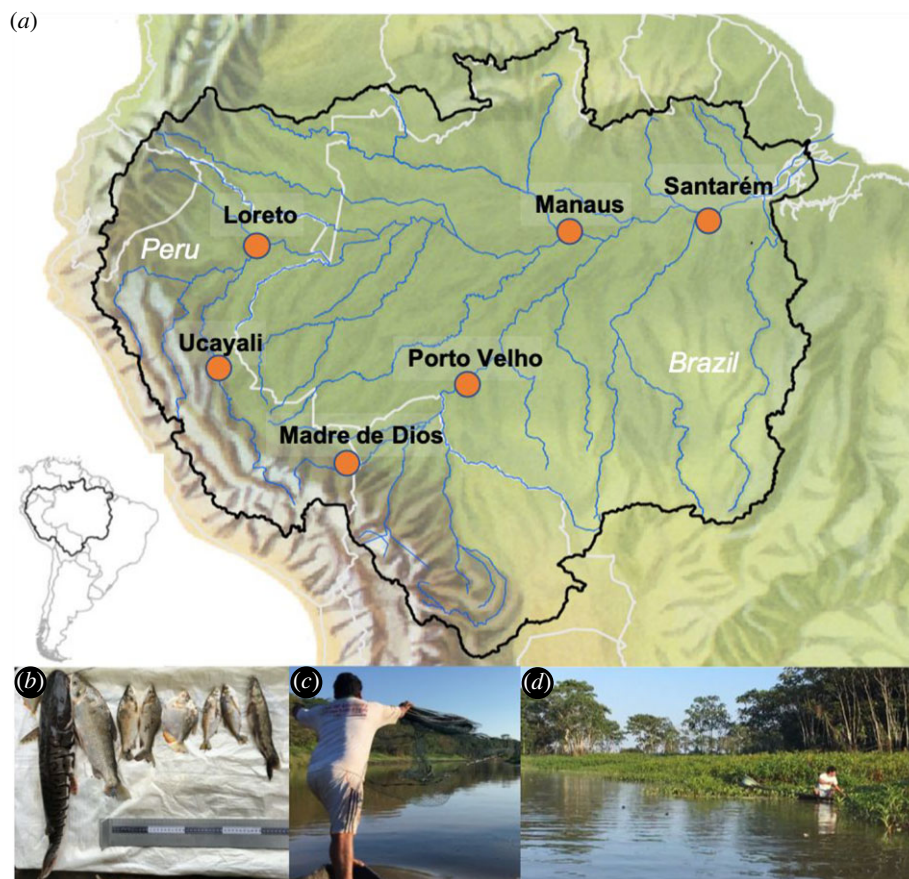
## 2. Methods

Our approach first examined biodiversity trends in landings and then complemented this analysis with insights from a theoretical food web model. For empirical landings analysis, we used six fisheries time series from the Amazon, including the Peruvian departments of Loreto, Ucayali and Madre de Dios, and the Brazilian cities of Porto Velho, Manaus and Santarém (figure 1a). For the theoretical food web model, we used a system of Generalized Lotka–Volterra equations where species negatively interact and incur fishing-induced mortality.

### (a) Data

In the Peruvian Amazon, we obtained data from the Ministry of Production, which records daily landings from the region's largest urban areas, including total volume and taxonomic information. In Brazil, academic institutions lead collection of daily landings information from key urban ports. For each region, we aggregated daily data by year (for time-series length, see electronic supplementary material, figure S1). For species that are commonly grouped into similar taxonomic units we used the lowest taxonomic unit possible (Extended Data in electronic supplementary material, table S1).

Trait information was obtained from several sources. Species body size and trophic position was downloaded from FishBase [27]. Species price information is collected at port and available from Loreto, Porto Velho and Manaus. To obtain a price and revenue index for each species, prices for landings within ports were



**Figure 1.** Map of the Amazon basin (a) detailing the location of the landings six time series from three Peruvian (Loreto, Ucayali and Madre de Dios) and three Brazilian regions (Puerto Velho, Manaus and Santarém). The black contour represents the extent of the Amazon basin. A variety of species are typically included in one landings (b), which aggregate across diffuse users employing a variety of techniques such as castnets (c), gillnets (d), seines and hooks (not shown). (Online version in colour.)

first adjusted for inflation using a baseline Consumer Price Index for 2010 (obtained from the World Bank) and standardized to US dollars using the average 2010 exchange rate for each country. Then, price index was calculated as the average yearly price for each species for each dataset. Since price data were unavailable for Santarém, we used the price from Manaus, the closest port within Brazil with information available. Additionally, since price data for Ucayali and Madre de Dios were also not available, we used information from Loreto. While species' prices could differ across markets, we expect the relative price differences between species should remain similar among regions within countries. The revenue index was calculated by multiplying each species average annual landed biomass within a region by its price index. For taxa that included multiple species, traits were averaged across the representative species.

### (b) Trait-based metrics

For each trait, we estimated landings biomass-weighted mean annual trait values for each region as

$$\text{Trait}_{\text{Landings}}(t) = \sum_{i=1}^{S(t)} p_{i,t} \text{Trait}_i, \quad (2.1)$$

where  $\text{Trait}_{\text{Landings}}(t)$  is the mean trait value of the landings for year  $t$ ,  $S$  is the number of species in the landings for year  $t$ ,  $p_{i,t}$  is the landings biomass of species  $i$  in year  $t$  divided by the total biomass landed in year  $t$  and  $\text{Trait}_i$  is the trait value for species  $i$ .

### (c) Taxonomic diversity trends

We estimated evenness for each year as  $\sum_{i=1}^{S(t)} p_{i,t} \ln(p_{i,t}) / \ln S_{\text{Max}}$ , where variables are as above. Additionally, we estimated temporal  $\beta$  diversity using the Jaccard dissimilarity index between the first year in each time series and each subsequent year, which ranges from 0 to 1, from similar to dissimilar. We further decomposed Jaccard dissimilarity into turnover and nestedness for the totality of each time series. Evenness and Jaccard dissimilarity were calculated using the *vegan* package in R [28], whereas decomposition was performed with the *betapart* package [29].

### (d) Species-level attributes and fisheries development

A time series of fishery development patterns was constructed using the landings data from each region. As an indicator of whether a taxon is a regular component of the harvest portfolio (i.e. an established fishery), a species was considered developed in the year where the annual market landings first reached 25% of its maximum observed level [15]. We tested different fishery development thresholds ranging from 10% to 50% of maximum observed annual landings and found no difference in development patterns.

### (e) Harvest model

To model multi-species fisheries, we simulated exploitation dynamics in communities using a system of Generalized Lotka–Volterra equations:

$$\frac{dN_i(t)}{dt} = N_i(t) \left( r_i + \sum_j^S A_{ij} N_j(t) \right) - E(t) N_i(t), \quad (2.2)$$



where  $N_i(t)$  is the abundance of population  $i$  at time  $t$ ,  $r_i$  is the intrinsic growth rate of species  $i$ ,  $S$  is the number of species,  $A_{ij}$  is the species self-regulation effects,  $A_{ji}$  is the per-capita effect of species  $j$  on the growth rate of species  $i$  and  $E$  is the exploitation rate [26]. Species self-regulating effects,  $A_{ii}$ , can be rewritten as  $r_i/K_i$ , where  $K_i$  is the carrying capacity of species  $i$  [30]. For notational convenience, the interaction coefficients  $A_{ij}$  were collected into the interaction matrix  $A$ , while the coefficients  $r_i$  and  $N_i$  were collected into the vectors  $r$  and  $N$ , respectively. Rather than randomly assembling communities, our simulated communities were built under the assumption that species lay along an  $r$ - to  $K$ -selected gradient, with initial biomass distribution skewed towards the latter species [31].  $r$ -selected species have high intrinsic growth rates and low initial biomass, whereas  $K$ -selected species have low intrinsic growth rates and high initial biomass. These are akin to short-lived and small-bodied species, and long-lived large-bodied species, respectively. Finally, we allowed  $E$  to vary with time so that a target community harvest,  $H$  was maintained:

$$E(t) = \frac{H}{\sum_i^S N(t)_i}. \quad (2.3)$$

Under these assumptions, we took two approaches to modeling species richness. First, to understand the impact of multi-species exploitation irrespective of biodiversity, we simulated 100 communities at three levels of species richness (low: 10; middle: 20; and high 40). Second, to explore the role of species richness, we simulated an additional 250 communities by drawing initial species richness from a vector of integers ranging from 1 to 40. For both approaches, total initial community biomass was held constant at 1000 for all simulations. Thus, the carrying capacities of each species,  $K_i$ , were drawn from a lognormal distribution (mean = 0, s.d. = 0.5) and their sum scaled to 1000 by dividing each species carrying capacity by the sum of all carrying capacities and subsequently multiplying those by 1000. Species intrinsic growth rates were also drawn from a lognormal distribution (mean = 0, s.d. = 0.5) plus 1, so that all species grew at each time step without interactions or harvest. Using a lognormal distribution to draw  $K$  and  $r$  parameters better represents natural communities, which tend to have biomass and traits such as body size lognormally distributed (electronic supplementary material, figure S2). Before assigning coefficients to species, the  $r$  and  $K$  vectors were sorted so that they were negatively correlated (mean correlation =  $-0.71 \pm 0.002$ ). Additionally, we assumed that most species were weakly interacting so that all elements were  $-0.01$ , with the exception of the diagonal, which contained the  $A_{ii}$  coefficients, and the subdiagonal elements which contained  $A_{ij}$  coefficients drawn from a uniform distribution (0,  $-0.50$ ) and sorted to positively correlate with  $r$ . We then determined species biomass at equilibrium in the absence of harvest by allowing community dynamics to run for 100 time steps using the `lsoda` function in the `desolve` R package [32]. Simulated communities that did not have positive biomass after 100 time steps were considered to not resolve and discarded prior to further analysis.

After establishing that communities resolved in the absence of harvest mortality, we fixed harvest amount across time at half of the total community biomass. This was done by first finding the species equilibrium biomass for each community without exploitation and then multiplying that biomass by 0.3, 0.5 and 0.6. These values were arbitrarily selected to represent low, medium and high harvests. Using these values for fixed harvest (i.e.  $H$  in equation (2.3)), community dynamics were again allowed to run for 100 time steps using the `lsoda` function in the `desolve` R package [32]. In the main text, we present results on  $H = 0.5$ , whereas other harvest targets are presented in the electronic supplementary material. Finally, for each time step, we back-calculated exploitation rate, community total biomass, total harvest, species harvests and evenness. We also calculated

cumulative species collapses as the count of species with biomass below 20% of their max biomass [12], and time to collapse as the last time point when yields fell to 25% of their maximum. The values used in all simulations are detailed in the electronic supplementary material, table S2.

### (f) Statistical analysis

Because each time series reflects regional dynamics, landings time series were analysed individually. Linear regressions were conducted on trait and taxonomic time trends, with year as the predictor and the trait-based or taxonomic index as the response variable. Similarly, to test for correlations between traits and fishery development patterns, we conducted linear regressions on individual time series with trophic level, body size, price index, revenue index and mean annual landed biomass, used as a proxy for productivity, as response variables and year as the predictor variable. Body size, price index, revenue index and mean annual landed biomass were log-transformed prior to inclusion in models. For Madre de Dios, we excluded years 2000 and 2001 from the analysis since taxonomic grouping was inconsistent with the rest of the years. All analyses and simulations were conducted in R [33].

## 3. Results and discussion

Our results support the notion that multi-species exploitation is affecting freshwater biodiversity and eroding long-term fisheries sustainability in the Amazon. We draw this inference from two key findings emerging from our observational and theoretical analysis. First, although changes in harvested biomass are variable across the Amazon, we observed turnover in species composition and declines in mean body size consistent with increasing exploitation of fish communities. Second, insights from theory suggest that these observational biodiversity patterns could be driven by the progressive reduction in the bank of potentially compensating species and therefore of fishery resilience. Together, both observational and theoretical results exhibited an inverted U-shaped evenness curve, which tracked a decline in fishery resilience. More broadly, this inverted U-shaped curve could be characteristic of multi-species fisheries exploitation and aid in evaluating their sustainability when other signatures of exploitation fail. Below, we expand on these key findings by first discussing trends in biomass, taxonomic diversity and trait-based indices observed from landings time series. Then, we interpret these results in light of the theoretical model. Finally, we conclude by drawing implications for management for the Amazon and other tropical inland fisheries.

### (a) Amazon landings trends

Across the six time series analysed, trends in landed biomass showed high interannual variation but no consistent trends: in Loreto and Ucayali trends slightly increased, whereas in Porto Velho, Madre de Dios, Manaus and Santarém trends were insignificant (electronic supplementary material, figure S1). Although these data correspond to the longest landings time series available in the Amazon, ranging from 12 to 34 years, they lack information on effort and on subsistence fisheries and thus should be considered as providing an incomplete snapshot of harvest dynamics (figure 1). Nevertheless, over the last 40 years, urban populations have grown exponentially, increasing both demand for fish and pressure on aquatic communities (electronic supplementary

material, figure S3). Indeed, this expansion has led to an 'urban shadow of defaunation' in some locations, with populations of key species showing clear signs of overexploitation, both in terms of reduced harvests and size spectra [7,8]. Other threats to fish biodiversity, including pollutants and dams, could also be contributing to declines in some taxa [34], although their impacts may be more locally constrained or concentrated on a few species compared to fishing exploitation, which we expand on below.

### (b) Taxonomic trends

We observed changes in taxonomic diversity that could reflect fish community responses under multi-species exploitation [12]. Over 120 fish taxa are represented in these landings data, ranging from approximately 40 to 70 species depending on the specific region (Extended Data in electronic supplementary material, table S1). Although migratory species dominated landings across regions, landings became less similar in species composition over time (electronic supplementary material, figure S4). Further partitioning Jaccard dissimilarity indicates that across years changes in taxonomic composition are driven by both nestedness and turnover, reflecting patterns of species additions as well as replacements, respectively [29]. However, some regions show stronger tendencies towards the nestedness (e.g. Madre de Dios and Porto Velho), whereas others show a combination of nestedness and turnover (e.g. Santarém).

Additionally, most regions exhibited significant trends in landings evenness, a metric that reflects the relative concentration of harvested species in landings, but patterns were region-specific (figure 2). In Loreto and Porto Velho evenness increased, in Ucayali evenness exhibited strong interannual variation but no long-term trend, and in Manaus, Santarém and Madre de Dios evenness declined. While the lack of consistent trends may be at first surprising, they suggest that where landings evenness is increasing, regions could be expanding harvest into new species as dominants decline. For example, *Prochilodus nigricans*, a medium-size migratory detritivore, decreased from 45% to 25% between 1984 and 2016 in Loreto, and from 21% to 8% between 1994 to 2009 in Porto Velho. Although the time series are shorter, where evenness is decreasing, *P. nigricans* also declined and harvests became dominated by a narrower variety of small species.

### (c) Trait-based trends

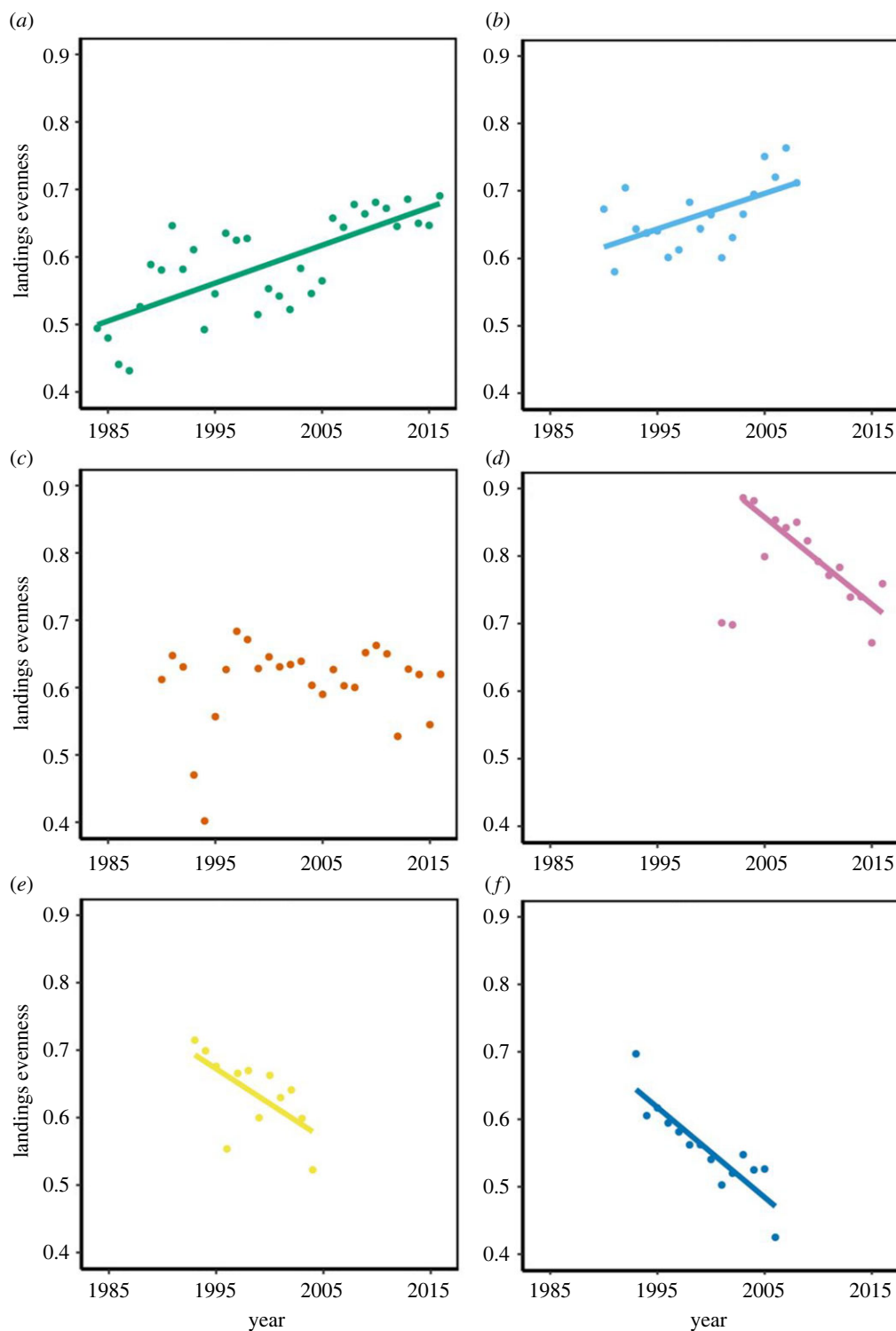
Trait-based trends varied across indices, but were consistent with turnover in species composition expected under increasing exploitation. In contrast with findings from other tropical inland fisheries [35], we found mixed evidence for a fishing down the food web pattern, with mean trophic level increasing or decreasing depending on the region (figure 3a). Additionally, trends in economic-based indices were also inconsistent, with mean price indices decreasing, but mean revenue indices both increasing and decreasing (figure 3b,d). While price information was not available for all regions (i.e. Ucayali, Madre de Dios and Santarém), our use of species prices for the closest ports within-country should broadly reflect relative price differences between species and are unlikely to alter these results.

In contrast with these mixed results, we observed persistent declines in landings mean body size commensurate with expectations of fishery-induced biodiversity change (figure 3c).

Specifically, across all regions, large-bodied species became less common in landings whereas smaller species increased. While there is evidence of declining large predatory species abundances (e.g. *Arapaima* sp., Pimelodid catfish), large-dominant detritivores have also experienced dramatic decreases [36,37]. These patterns suggest that Amazon fisheries exploit multiple species across all trophic levels, but life-history constraints are such that large-bodied species tend to have lower intrinsic population growth rates and are more sensitive to exploitation. In contrast with susceptible *K*-selected species, smaller *r*-selected species are becoming more common as exploitation increases. These trait-based trends concord with observations of overexploitation in complex tropical freshwater communities elsewhere [9,21,35] and suggest that Amazonian communities could be responding to increasing fishing pressure.

Considering that changes in mean trait values are only partially indicative of how fisheries exhibits trait-based targeting behaviour and can mask the signature of low-biomass species, we further analysed the sequential pattern in which species appear in landings records, or became developed [15]. This complementary trait-based index estimates the year when a species become a regular component of the harvest fish portfolio using the year in which species-specific harvests reached 25% of their maximum total harvest across all years. While the sequence of development varied across trophic levels, body sizes and price indices, species with high mean annual harvest biomass were consistently developed early on in four of the six time series (electronic supplementary material, figure S5). Development along a revenue gradient followed a similar trajectory as biomass-based development. While this analysis may fail to capture development patterns for shorter time series (e.g. Manaus and Santarém), the temporal window coincides with a significant expansion in population, consistent with increasing fishing pressure (electronic supplementary material, figure S3). Further altering fishery development thresholds (i.e. 10%, 50%) resulted in no qualitative differences.

Overall, patterns of early development of high biomass species suggest that multi-species fisheries in the Amazon, at an aggregate scale, exhibit relatively low selectivities and can alternate among species in response to shifting community composition. Similar patterns have been also been observed in other multi-species fisheries exploiting diverse food webs, such as coral reef systems [10,21]. Fishers in the Amazon employ a variety of gears, including gill nets, hooks, seines and cast nets with varying selectivities (figure 1b–d). Additionally, fishery subsectors in the Amazon exist, but these tend to target low-abundance and high-value species such as *Arapaima* spp. and migratory catfish [37,38]. However, effort among gear types and actors is distributed widely and often overlapping in space and time. Consequently, species composition in urban landings aggregate across diffuse users employing these different techniques [39]. Across time, fishers might adapt their selectivities and increase fishing effort to maintain harvests by first exploiting large-bodied and abundant species, and, as their populations decline, replacing them with smaller, *r*-selected species [9,40]. While gear typically meets a minimum mesh-size, selecting for species above a size threshold, in some locations gill net size is declining and people are fishing for longer time periods [41]. In the process, smaller characins, once relatively uncommon in landings (e.g. *Mylossoma* spp. and curimatids), are now increasing as other larger characins (e.g. *Prochilodus nigricans*) decline. Beyond this compensatory



**Figure 2.** Trends in landings evenness for the six time series analysed. Lines represent linear regressions with significant slopes ( $p \leq 0.05$ ). (a) Loreto, (b) Porto velho, (c) Ucayali, (d) Madre de Dios, (e) Santarém and (f) Manaus. (Online version in colour.)

behaviour from fishers, the sequential replacement of species could also be affected by ecological compensation, where competitive and predator release drive directional changes in landings species composition [18].

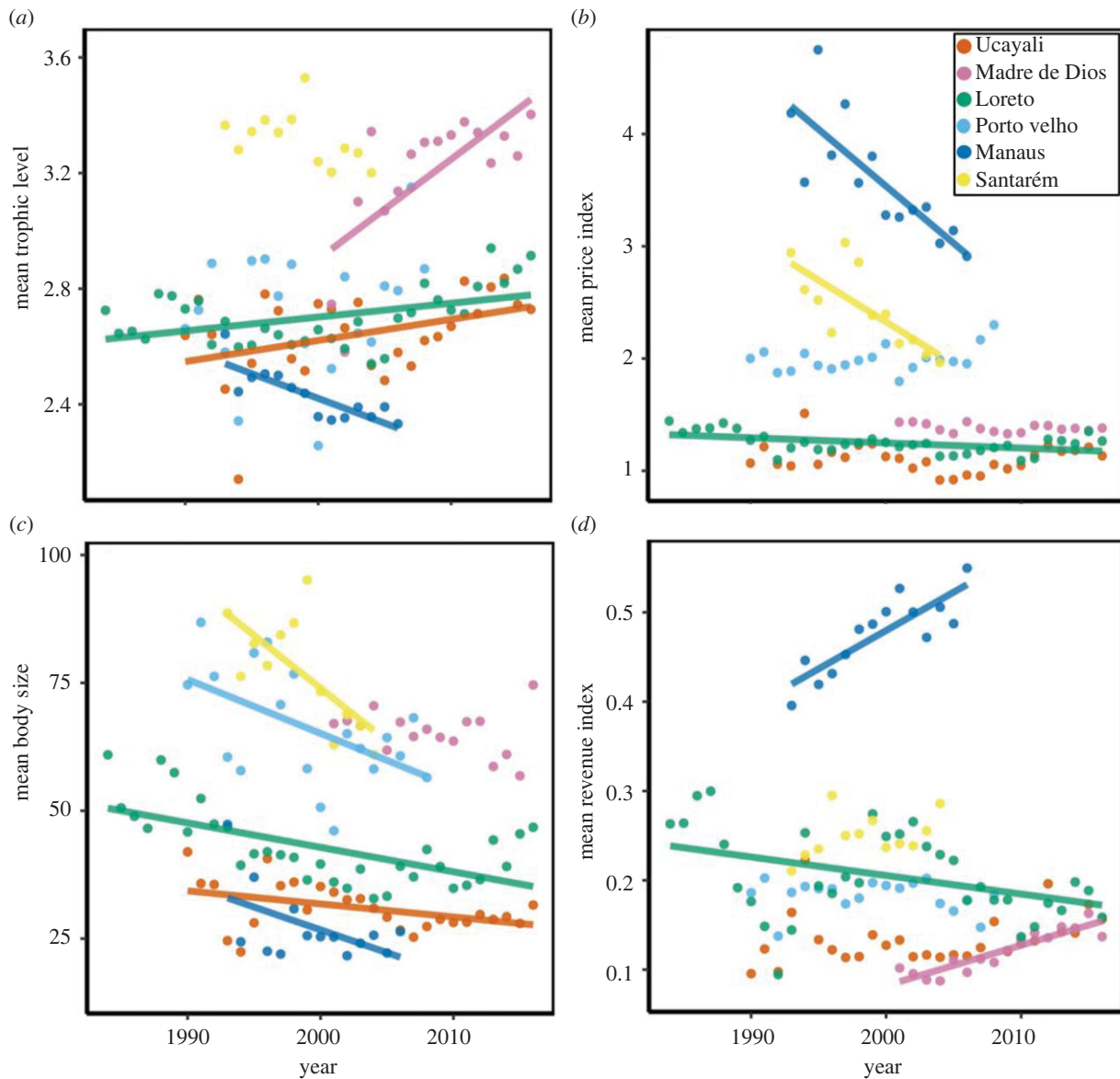
#### (d) General biodiversity-based theory of multi-species exploitation

A key limitation of the time series analysed is the lack of both long-term fishery independent ecological data and of effort data, which provides information to characterize how fishery behaviour induces changes in ecological communities [7].

Thus, to provide insights into the potential mechanisms underlying the observed biodiversity patterns and how these changes may affect fisheries resilience, we analysed a generalized Lotka–Volterra harvest model. Combining approaches further allowed us identify community level metrics that could explain fishery development patterns in the Amazon and other multi-species fisheries.

We found that maintaining harvests requires an increase in exploitation rates over time, but compensation and high species richness can reduce the probability of community collapse (figure 4). Increasing exploitation rates causes a sequential turnover in species composition similar to patterns



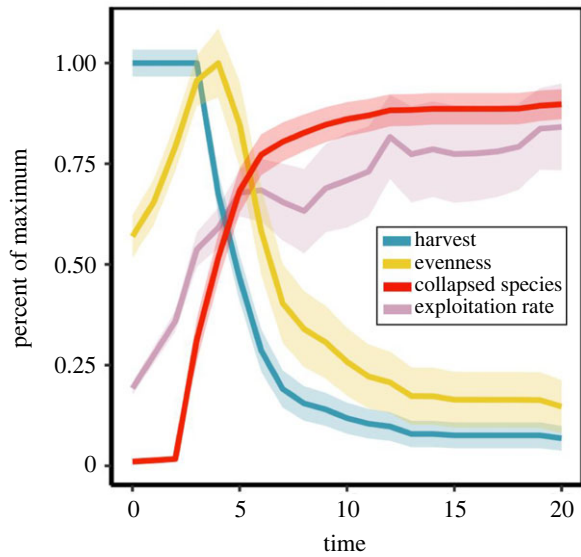


**Figure 3.** Temporal trends in landings (a) mean trophic level, (b) mean price index, (c) mean body size and (d) mean revenue index across six regions in the Amazon. Colours represent the different regions. Lines are only included for significant trends ( $p \leq 0.05$ ). (Online version in colour.)

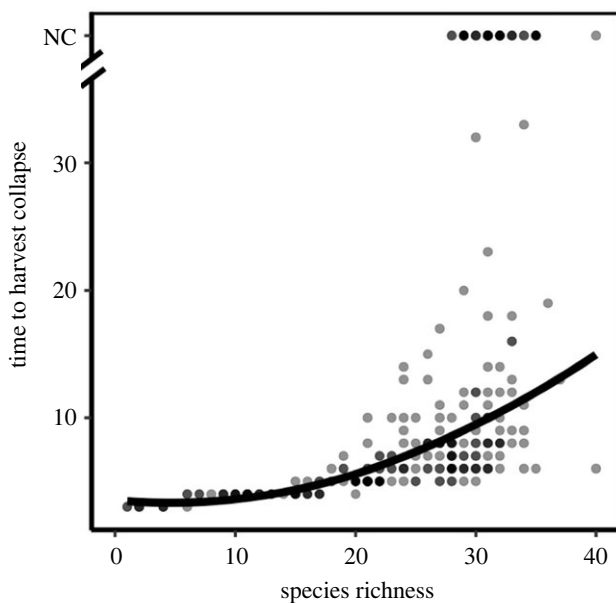
observed in landings, with a low number of dominant but slow-growing species (e.g. K-selected species) being replaced by a variety of faster growing species (r-selected species; electronic supplementary material, figure S6). Further, compensation, driven by release from negative interactions, together with increasing exploitation rates, expands harvests into new species. Simulated communities with higher species richness were more resilient to exploitation, with their harvests collapsing later than communities with low species richness (figure 5). These changes in biodiversity are consistent with other modelling studies that describe how multi-species exploitation fish down size-spectra gradients, decrease resiliency and could lead to dominance of few r-selected species [11,12,23,24,26]. Theoretical studies have also uncovered the important role of negative interactions in driving compensation [17], and our model suggests that similar mechanisms may underlie the resiliency of multi-species fisheries.

At the community level, patterns in species turnover and declining compensatory potential manifest along a hump-shaped harvest evenness curve, corresponding to a three-staged model of multi-species fisheries development

(figure 4). In early stages, light to moderate exploitation rates cause harvest evenness to increase as dominant, K-selected species decrease in abundance and are complemented with a diversity of other species. Only a small percentage of species are collapsed in these early stages. In middle stages, when exploitation is moderate, harvest evenness plateaus, reflecting their spread across taxa. The number of collapsed species increases rapidly, as exploitation depletes the pool of potentially compensating species. Finally, in later stages, harvest evenness declines as faster growing species dominate the harvest portfolio. This stage could be characterized as a 'productive monoculture' (*sensu* [26]), with few species available for compensation. This trajectory implies that as exploitation rates increase, harvest biomass is maintained at the expense of declining resilience. Communities with lower species richness harbour decreased compensating potential and thus progressed more rapidly towards collapse (electronic supplementary material, figure S7). At lower harvest targets, species turnover and exploitation rates increased less rapidly, harvests had a lower probability of collapse, and the decreasing portion of the evenness curve did not emerge (electronic supplementary material, figure S8A). By contrast, at higher



**Figure 4.** Three-staged model of multi-species fisheries development, resulting from a theoretical food web model with initial species richness equal to 20. In early stages, when exploitation rate is low, harvest evenness first increases as dominant and slow-growing species are replaced by faster growing species, and biomass is maintained. In middle stages, when exploitation rate is medium, evenness peaks as the number of collapsed species increases. Finally, in late stages, when exploitation rate is high, evenness decreases, as fewer fast-growing species remain to be exploited and harvests collapse. The lines in the main figure represent mean values for each time point for 250 simulations whereas the ribbons represent the 95% confidence intervals. (Online version in colour.)



**Figure 5.** Communities with higher species richness show greater resilience under multi-species exploitation. Time to harvest collapse is estimated as the time point at which total yields fall below 25% of the maximum for that community. The break on the y-axis depicts communities that do not collapse (NC). These are not included in the loess smoother (span = 2). Darker shades represent higher point densities. (Online version in colour.)

harvest targets, communities moved through the cycle of replacement, depletion and collapse more rapidly (electronic supplementary material, figure S8B). While previous work has linked multi-species exploitation patterns of turnover along K- to r-selected species gradients [9,11,24,42], our

modelling exercise further reveals how changes in evenness are linked to fishery resilience and community collapse.

These theoretical results provide insights into the diversity patterns observed in Amazonian landings time series. Evenness trends for Loreto and Porto Velho, which have lower, albeit growing, human populations and lie in the speciose lowlands, suggest that these regions are in earlier stages of development but transitioning (figure 2*a–c*; [36,37]). As mentioned above, we observed long-term declines in dominant species in both regions. For Porto Velho, the time period covered does not include the completion of dams in the area (in 2009), which has led to significant changes in landings [36]. In Ucayali, the lack of consistent evenness patterns could indicate that the region is in middle stages of development. Ucayali has relatively lower species diversity and experienced rapid population growth after a road to Lima, Peru's capital, was built in the mid-twentieth century. For Manaus and Santarém, decreasing evenness could potentially reflect later stages of fisheries development (figure 2*e,f*). Manaus and Santarém have high species richness but also a long history of human disturbance through deforestation and fishing. Strong evidence of overharvesting exists from these regions [7,8]. Finally, in Madre de Dios, declines in evenness follow theoretical expectations associated with high fishing pressure, but are challenging to disentangle. The region harbours lower species richness, and exogenous threats associated with deforestation, goldmining and dam development, are affecting aquatic ecosystems and potentially exacerbating fishing-related pressure [36]. However, poor data management in Madre de Dios warrants caution in interpreting these results. Nevertheless, taken together, our observational and theoretical results suggest that landings patterns reflect differences in development stages among these regions. Ascertaining whether biological communities are experiencing similar trends with complementary fishery independent information (e.g. fish surveys and local ecological knowledge) will be critical for assessing the overall status of Amazonian fisheries [7,41].

Broader interpretation of our modelling and empirical results rests on several key assumptions. First, given inconsistent trends in biomass landed, in our model, we fixed harvest targets across time steps. Yet, in the Amazon, harvested biomass likely changes overtime: increasing targets could lead to more rapid community collapse, whereas decreases could lead to slower or no collapse (electronic supplementary material, figure S8). Second, in our model, harvest targets and exploitation rates were set at the community level, rather than being species-specific. However, some degree of selectivity in the Amazon likely exists, such as for K-selected species (e.g. large migratory catfish) [38]. In line with theory from balanced-fisheries [24,42], integrating selectivity towards K-selected species could lead to more rapid species turnover and progression through the inverted U-shaped evenness curve. Third, our model only included negative interactions, under the assumption that Amazonian fish communities are partially structured by competition and predation [43]. Indeed, the release from negative interactions, driven by increasing exploitation rates, underlays compensation and the inverted U-shaped evenness curve. Although compensation is ubiquitous in ecological communities, its strength can vary depending on myriad factors including environmental context and temporal fluctuations in species abundances associated with migration [17]. While our results suggest that compensation partially drives observed landings



trends, improving the diagnosis of Amazonian and other data-depauperate fisheries requires pluralistic approaches that more fully capture their socio-ecological complexity.

Despite these caveats, taken together, observed biodiversity patterns in landings concord with increasing fishing pressure and declining resilience, and carry important implications for management across the region. While changing market forces could also shape these biodiversity patterns, consumer demand rarely evolves towards smaller species, even though these may be the most nutritious and Amazonian consumers show complex fish preferences [44]. Rather, declines and sequential replacement of large-bodied species is a well-documented effect of overexploitation [14,41]. Less well documented is how trends in species turnover track compensation and changes in fishery resilience. Because fishers can alternate among a larger pool of species, our results suggest that single-species approaches, with a few key exceptions (e.g. *Arapaima* spp.), will be challenging to implement. Beyond body size, the most heavily exploited species are also migratory, and while we analysed these time series as independent, long-distant migrants might form part of the same effective population across multiple regions. Thus, our study further underscores the need to manage fisheries at a relevant spatial scale, which in the Amazon is a basin-wide approach for many key species [3]. Finally, despite the clear need for integrated river basin management in the Amazon, our findings on different fishery development stages among regions also call for complementary local approaches. Doing so is particularly critical considering the potentially heterogeneous changes in hydrology and human behaviour associated with climate change and dam development across the region [34].

## 4. Conclusion

The ecological sustainability of fisheries relies on maintaining overall harvest biomass while also minimizing changes in community and ecosystem structure [12]. Our empirical and theoretical analyses indicate that, for multi-species fisheries, this may be challenging because even at low exploitation rates, maintaining harvests results in biodiversity changes. Further increasing exploitation to maintain harvests can ultimately lead to a depletion the pool of compensating species and eventual collapse. While similar patterns have been observed in other fisheries and theoretical exercises [9,11,24,26], we extend these findings and uncover how fisheries resilience depends on two factors: (i) the initial number of exploitable species and (ii) the potential for compensation driven by competition and predation release. Detecting these

factors is imperative for ascertaining fishery status and ensuring their long-term sustainability.

Tropical inland fisheries, such as the Amazon, are characterized by many diffuse fishers and limited data flows; thus, landings information collected at regional ports are often the only data available to assess fishery status. While these only account for a portion of catches in the Amazon, using landings data we found a consistent decline in large-bodied species occupying a range of trophic levels. Complementing empirical data with theory, we link observed patterns to a hump-shaped landings evenness curve, indicating the sequential replacement of dominant slow-growing species with smaller and faster growing species in the harvest portfolio, and reduction of the bank of compensating species. In the absence of other data, declining evenness, in combination with declines in mean body size, may signal that fisheries are losing resilience and progressing towards possible collapse. Importantly, communities with low species richness could move through this cycle of depletion, replacement and collapse more rapidly. Ultimately, without implementing large-scale innovations to improve monitoring (e.g. citizen science), analysing evenness trends may provide a practical approach to leverage landings data and assess patterns of exploitation, declining resilience and, ultimately, the sustainability of data-limited multi-species fisheries.

**Data accessibility.** All code and data supporting the findings of this study are available as electronic supplementary material [45].

**Authors' contributions.** S.A.H.: conceptualization, data curation, formal analysis, methodology, project administration, visualization, writing—original draft and writing—review and editing; S.A.S.: conceptualization, methodology, visualization, writing—original draft and writing—review and editing; R.B.B.: data curation and writing—review and editing; C.R.C.D.: data curation and writing—review and editing; A.G.V.: data curation and writing—review and editing; M.G.: data curation and writing—review and editing; V.I.: data curation and writing—review and editing; V.S.B.: data curation and writing—review and editing; F.D.: data curation and writing—review and editing; S.N.: conceptualization and writing—review and editing; A.S.F.: conceptualization and writing—review and editing.

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## References

- McIntyre PB, Liermann CAR, Revenga C. 2016 Linking freshwater fishery management to global food security and biodiversity conservation. *Proc. Natl Acad. Sci. USA* **113**, 12 880–12 885. (doi:10.1073/pnas.1521540113)
- Flecker AS *et al.* 2022 Reducing adverse impacts of Amazon hydropower expansion. *Science* **375**, 753–760. (doi:10.1126/science.abj4017)
- Goulding M *et al.* 2019 Ecosystem-based management of Amazon fisheries and wetlands. *Fish Fish.* **20**, 138–158. (doi:10.1111/faf.12328)
- Costello C, Ovando D, Hilborn R, Gaines SD, Deschenes O, Lester SE. 2012 Status and solutions for the world's unassessed fisheries. *Science* **338**, 517–520. (doi:10.1126/science.1223389)
- Smith H, Basurto X. 2019 Defining small-scale fisheries and examining the role of science in shaping perceptions of who and what counts: a systematic review. *Front. Mar. Sci.* **6**, 236. (doi:10.3389/fmars.2019.00236)
- Heilpern SA, Fiorella K, Cañas C, Flecker AS, Moya L, Naeem S, Sethi SA, Uriarte M, DeFries R. 2021 Substitution of inland fisheries with aquaculture and chicken undermines human nutrition in the Peruvian Amazon. *Nat. Food* **2**, 192–197. (doi:10.1038/s43016-021-00242-8)
- Keppeler FW, de Souza AC, Hallwass G, Begossi A, de Almeida MC, Isaac VJ, Silvano RAM. 2018

- Ecological influences of human population size and distance to urban centres on fish communities in tropical lakes. *Aquat. Conserv.* **28**, 1030–1043. (doi:10.1002/aqc.2910)
8. Tregidgo DJ, Barlow J, Pompeu PS, de Almeida Rocha M, Parry L. 2017 Rainforest metropolis casts 1,000-km defaunation shadow. *Proc. Natl Acad. Sci. USA* **114**, 8655–8659. (doi:10.1073/pnas.1614499114)
  9. Welcomme RL. 1999 A review of a model for qualitative evaluation of exploitation levels in multi-species fisheries. *Fish. Manag. Ecol.* **6**, 1–19. (doi:10.1046/j.1365-2400.1999.00137.x)
  10. Lorenzen K, Almeida O, Arthur R, Garaway C, Nguyen Khoa S. 2006 Aggregated yield and fishing effort in multispecies fisheries: an empirical analysis. *Can. J. Fish. Aquat. Sci.* **63**, 1334–1343. (doi:10.1139/f06-038)
  11. Halls AS, Welcomme RL, Burn RW. 2006 The relationship between multi-species catch and effort: among fishery comparisons. *Fish. Res.* **77**, 78–83. (doi:10.1016/j.fishres.2005.08.005)
  12. Worm B *et al.* 2009 Rebuilding global fisheries. *Science* **325**, 578–585. (doi:10.1126/science.1173146)
  13. Jennings S, Pinnegar JK, Polunin NVC, Boon TW. 2001 Weak cross-species relationships between body size and trophic level belie powerful size-based trophic structuring in fish communities. *J. Anim. Ecol.* **70**, 934–944. (doi:10.1046/j.0021-8790.2001.00552.x)
  14. Graham N, Dulvy N, Jennings S, Polunin N. 2005 Size-spectra as indicators of the effects of fishing on coral reef fish assemblages. *Coral Reefs* **24**, 118–124. (doi:10.1007/s00338-004-0466-y)
  15. Sethi SA, Branch TA, Watson R. 2010 Global fishery development patterns are driven by profit but not trophic level. *Proc. Natl Acad. Sci. USA* **107**, 12163–12167. (doi:10.1073/pnas.1003236107)
  16. Reddy SMW, Wentz A, Aburto-Oropeza O, Maxey M, Nagavarapu S, Leslie HM. 2013 Evidence of market-driven size-selective fishing and the mediating effects of biological and institutional factors. *Ecol. Appl.* **23**, 726–741. (doi:10.1890/12-1196.1)
  17. Gonzalez A, Loreau M. 2009 The causes and consequences of compensatory dynamics in ecological communities. *Ann. Rev. Ecol. Evol. Syst.* **40**, 393–414. (doi:10.1146/annurev.ecolsys.39.110707.173349)
  18. Szuwalski CS, Burgess MG, Costello C, Gaines SD. 2017 High fishery catches through trophic cascades in China. *Proc. Natl Acad. Sci. USA* **114**, 717–721. (doi:10.1073/pnas.1612722114)
  19. Dulvy NK, Freckleton RP, Polunin NVC. 2004 Coral reef cascades and the indirect effects of predator removal by exploitation. *Ecol. Lett.* **7**, 410–416. (doi:10.1111/j.1461-0248.2004.00593.x)
  20. Heilpern SA, DeFries R, Fiorella K, Flecker A, Sethi SA, Uriarte M, Naeem S. 2021 Declining diversity of wild-caught species puts dietary nutrient supplies at risk. *Sci. Adv.* **7**, eabf9967. (doi:10.1126/sciadv.abf9967)
  21. McClanahan TR, Mangi SC. 2004 Gear-based management of a tropical artisanal fishery based on species selectivity and capture size. *Fish. Manag. Ecol.* **11**, 51–60. (doi:10.1111/j.1365-2400.2004.00358.x)
  22. Christensen V, Walters CJ. 2004 Ecosim with ecosim: methods, capabilities and limitations. *Ecol. Model.* **172**, 109–139. (doi:10.1016/j.ecolmodel.2003.09.003)
  23. Christensen V. 1998 Fishery-induced changes in a marine ecosystem: insight from models of the Gulf of Thailand. *J. Fish Biol.* **53**, 128–142. (doi:10.1111/j.1095-8649.1998.tb01023.x)
  24. Law R, Plank MJ, Kolding J. 2012 On balanced exploitation of marine ecosystems: results from dynamic size spectra. *ICES J. Mar. Sci.* **69**, 602–614. (doi:10.1093/icesjms/fss031)
  25. Law R, Plank MJ, Kolding J. 2016 Balanced exploitation and coexistence of interacting, size-structured, fish species. *Fish Fish.* **17**, 281–302. (doi:10.1111/faf.12098)
  26. McCann KS, Gellner G, McMeans BC, Deenik T, Holtgrieve G, Rooney N, Hannah L, Cooperman M, Nam S. 2015 Food webs and the sustainability of indiscriminate fisheries. *Can. J. Fish. Aquat. Sci.* **73**, 656–665. (doi:10.1139/cjfas-2015-0044)
  27. Froese R, Pauly D. 2019 FishBase. See [www.fishbase.org](http://www.fishbase.org), version (02/2019) (accessed on 20 June 2019).
  28. Oksanen J *et al.* 2019 *Vegan: Community Ecology Package*. See <https://CRAN.R-project.org/package=vegan>.
  29. Baselga A, Orme CDL. 2012 betapart: an R package for the study of beta diversity. *Methods Ecol. Evol.* **3**, 808–812. (doi:10.1111/j.2041-210X.2012.00224.x)
  30. Vandermeer JH. 1975 Interspecific competition: a new approach to the classical theory. *Science* **188**, 253–255. (doi:10.1126/science.188.4185.253)
  31. Winemiller KO, Rose KA. 1992 Patterns of life-history diversification in North American fishes: implications for population regulation. *Can. J. Fish. Aquat. Sci.* **49**, 2196–2218. (doi:10.1139/f92-242)
  32. Soetaert K, Petzoldt T, Setzer RW, authors odepack. 2019 *deSolve: Solvers for Initial Value Problems of Differential Equations (ODE, 'DAE', 'DDE')*. See <https://CRAN.R-project.org/package=deSolve>.
  33. R Core Team. 2020 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. See <https://www.R-project.org/>.
  34. Castello L, Macedo MN. 2016 Large-scale degradation of Amazonian freshwater ecosystems. *Glob. Change Biol.* **22**, 990–1007. (doi:10.1111/gcb.13173)
  35. Ngor PB, McCann KS, Grenouillet G, So N, McMeans BC, Fraser E, Lek S. 2018 Evidence of indiscriminate fishing effects in one of the world's largest inland fisheries. *Sci. Rep.* **8**, 8947. (doi:10.1038/s41598-018-27340-1)
  36. Doria CRC *et al.* 2018 Review of fisheries resource use and status in the Madeira River Basin (Brazil, Bolivia, and Peru) before hydroelectric dam completion. *Rev. Fish. Sci. Aquacult.* **26**, 494–514. (doi:10.1080/23308249.2018.1463511)
  37. Garcia A, Tello S, Vargas G, Duponchelle F. 2009 Patterns of commercial fish landings in the Loreto region (Peruvian Amazon) between 1984 and 2006. *Fish Physiol. Biochem.* **35**, 53–67. (doi:10.1007/s10695-008-9212-7)
  38. Tregidgo D, Parry L, Barlow J, Pompeu P. 2021 Urban market amplifies strong species selectivity in Amazonian artisanal fisheries. *Neotrop. Ichthyol.* **19**, e210097. (doi:10.1590/1982-0224-2021-0097)
  39. Hallwass G, Silvano RAM. 2016 Patterns of selectiveness in the Amazonian freshwater fisheries: implications for management. *J. Environ. Planning Manage.* **59**, 1537–1559. (doi:10.1080/09640568.2015.1081587)
  40. Bieg C, McCann KS, McMeans BC, Rooney N, Holtgrieve GW, Lek S, Bun NP, Kc KB, Fraser E. 2018 Linking humans to food webs: a framework for the classification of global fisheries. *Front. Ecol. Environ.* **16**, 412–420. (doi:10.1002/fee.1933)
  41. Hallwass G, Schiavetti A, Silvano RAM. 2020 Fishers' knowledge indicates temporal changes in composition and abundance of fishing resources in Amazon protected areas. *Anim. Conserv.* **23**, 36–47. (doi:10.1111/acv.12504)
  42. Jacobsen N, Gislason H, Andersen K. 2014 The consequences of balanced harvesting of fish communities. *Proc. R. Soc. B* **281**, 20132701. (doi:10.1098/rspb.2013.2701)
  43. Correa SB, Winemiller KO. 2014 Niche partitioning among frugivorous fishes in response to fluctuating resources in the Amazonian floodplain forest. *Ecology* **95**, 210–224. (doi:10.1890/13-0393.1)
  44. Begossi A, Hanazaki N, Ramos RM. 2004 Food chain and the reasons for fish food taboos among Amazonian and Atlantic Forest Fishers (Brazil). *Ecol. Appl.* **14**, 1334–1343. (doi:10.1890/03-5072)
  45. Heilpern SA *et al.* 2022 Biodiversity underpins fisheries resilience to exploitation in the Amazon river basin. Figshare. (<https://doi.org/10.6084/m9.figshare.c.6033812>)