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Keywords: freshwater fisheries, biodiversity, functional richness, river continuum theory, community composition

JEL Classification: Q22, Q57

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Valuing biodiversity in freshwater fisheries: Evidence from Laos

Benjamin Chipperfield[1], Paulo Santos[2] & Carly Cook[3]

Abstract

Reducing the impact of large-scale biodiversity loss on ecosystem functioning and human wellbeing requires understanding which aspects of biodiversity are central to the ecosystem services on which humans rely. Despite this need, the impact of biodiversity on fishing yield in freshwater systems is not well understood. Using detailed data on fish catch and estimates of fish functional diversity in the Mekong River Basin, we build on the ecological notion of the river continuum concept (that links biological diversity with the natural variation in the physical environment along a river) to show that higher levels of diversity lead to economically significant increases in freshwater fish yield. We also show that local fisheries are vulnerable to the extinction of a small number of key species which, if lost, could compromise the productivity of local fisheries. Our analysis suggests that achieving win-win solutions that link biodiversity protection with improvements in economic outcomes in freshwater fisheries may require well targeted conservation efforts.

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1. Introduction

The current extinction of species is estimated to be 100-1,000 times greater than the baseline extinction rate, typically accepted to be 0.1-1 species per year for every one million species (Ceballos et al., 2015; Pimm et al., 2014; De Vos et al., 2014). The impacts of such large losses in biodiversity on human wellbeing are slowly being understood (see Dasgupta (2021) for a recent review) and drive much of the policy behind the expansion of protected areas (e.g., the recent targets established as part of the Kunming-Montreal Agreement of protecting 30% of land and water (Convention on Biological Diversity, 2022)).

Freshwater ecosystems are not an exception to this trend and have been losing biodiversity at alarming rates (Sala et al., 2000; Reid et al., 2019).[4] Twenty-five percent of freshwater fish species assessed by the IUCN are considered to be at risk of extinction, with 16 species being declared extinct in 2020 alone (IUCN 2023; Hughes, 2021). Concurrently, since 1970, populations of freshwater vertebrates have declined twice as quickly as those in marine and terrestrial biomes (WWF, 2016), with recent estimates suggesting a reduction of 83% of biomass (WWF, 2022). Furthermore, global migratory freshwater fish stocks have declined by 76% over the same period (Westveer et al., 2022).

Such losses are likely to have particularly negative consequences for local communities dependent on freshwater fish consumption (Heilpern et al., 2021). Catches from inland fisheries are heavily concentrated in low-income countries with high food insecurity (Funge-Smith & Bennett, 2019), where they provide a crucial source of protein and micronutrients in local diets (McIntyre et al., 2016; Allison & Mills, 2018). In our context, Lao People's Democratic

[4] Despite covering only 1% of the Earth's surface, freshwater ecosystems are home to 51% of known fish species and almost one quarter of all vertebrate species (Hughes, 2021).

Republic (hereafter, Lao PDR), freshwater fisheries play an essential role in local diets, with fish providing 42.5-78% of total animal protein intake (Baran et al., 2007).[5]

Reducing the effect of such losses on human wellbeing requires an understanding of which aspects of biodiversity matter most in these ecosystems. For example, Dasgupta and Levin (2023) note the importance of functional diversity in driving ecosystem's productivity from a human perspective. The importance of community composition on fish biomass and fisheries yield has been studied in aquatic ecosystems (Duffy et al., 2017); both marine (Lefcheck et al., 2021; Harrison et al., 2014) and freshwater (Brooks et al., 2016; McIntyre et al., 2016). However, existing analyses typically present estimates of the correlation between species richness and productivity, controlling for macroecological drivers, but omitting likely confounding factors such as fishing intensity, capture methods, and fisheries management rules and enforcement. The biodiversity productivity relationship has also been experimentally evaluated in marine (Gamfeldt et al., 2015) and freshwater (Vaughn, 2010) systems. While experiments can allow for causal interpretations, they may not generalize to natural ecosystems as the gains and losses of species in experiments may not mimic changes in species in nature (Dee et al., 2023). An approach that combines both the strength of experiments in facilitating causal inferences and observational data for facilitating generalizability about natural ecosystem processes is needed to overcome these limitations (Dee et al., 2023).

The present study seeks to fill this gap in the literature by using a quasi-experimental design to estimate the causal impact of biodiversity on the fishing yield of the Xe Banghieng River, one of the last undisturbed freshwater ecosystems in the Mekong Basin. Borrowing from the River Continuum Concept in ecology (Vannote et al., 1980), we exploit the variation in fish diversity along the river induced by its changing biophysical conditions as an exogenous source

[5] See Fluet-Chouinard et al. (2018) and Allison & Mills (2018) for further discussion of the importance of these fisheries in low-income nations. However, their services are underreported (Fluet-Chouinard et al., 2018) and rarely recognized in international development discussions and policy circles (e.g., the United Nations Sustainable Development Goals (Lynch et al., 2020)).

of variation in biodiversity and estimate its impact on fishing yield using an instrumental variable approach. We measure biodiversity as Functional Richness (Loreau et al., 2001), an approach that allows us to estimate the impact of fish community structure on fishing yield, as well as simulate the vulnerability of local fisheries to species extinctions.

Our analysis establishes that more biodiverse fish communities increase fisheries yields in freshwater ecosystems. Furthermore, simulations of the vulnerability of fishery productivity to reductions in biodiversity suggest significant economic consequences for the extinction of a few highly threatened key species, motivating the need for effective conservation to support fishing yield.

2. Data

To quantify the effect of fish biodiversity on fishing yield, we use primary data from 19 villages along the Xe Banghieng River, a tributary of the Mekong River Basin in Lao PDR; Figure 1). We use three sets of variables: fishing practices and outcomes, biodiversity and village characteristics.

Data on fishing technology and yield were obtained from fish catch monitoring diaries kept by a sample of 408 fishers and completed over a period of 30 consecutive days, primarily in September 2019. Diary entries recorded details of their fishing trips (n=2,558), including location and duration, weight of fish caught, and equipment used. We calculate fishing yield as the weight of fish caught per hour of fishing.

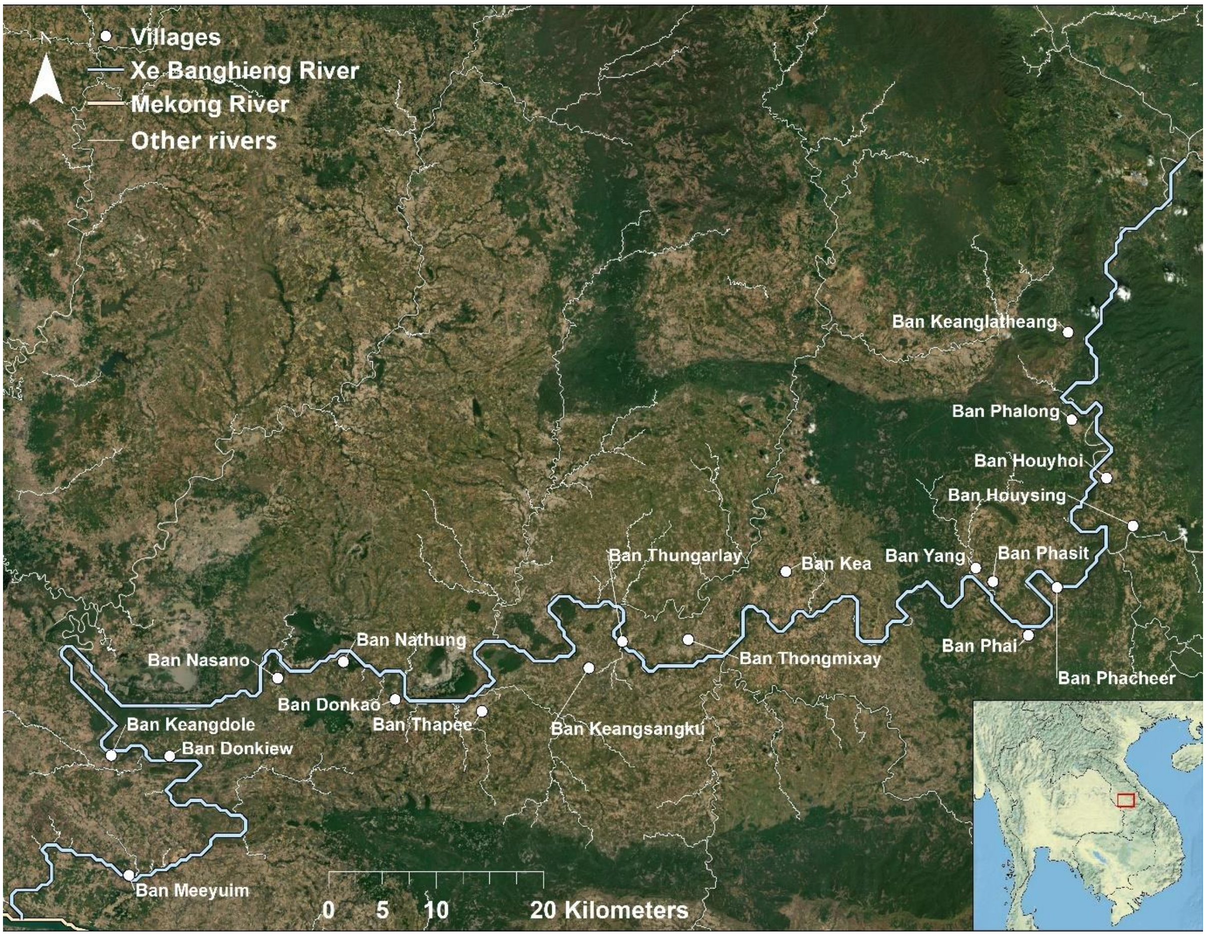

Fig. 1. Sample villages (n=19) and their locations along the Xe Banghieng River, Lao PDR. The inset shows the location within Southeast Asia as indicated by the red square.

Data on fish species were collected through a module included in a household survey fielded in June 2019 to a different random sample of households in each of the villages in our study (8-12 households per village, n=192). We interviewed household members who were primarily responsible for fishing in the household (or, in their absence, the household head) and asked them to identify whether a particular species was caught in the last 12 months. Figure 2 shows the format of a subset of questions used in this survey where each species was accompanied by a photograph of a typical specimen as well as its common Lao name to facilitate identification. Despite the relatively large number of species (131 species, presented in Appendix A.1), this module of the household survey was typically answered without difficulties.

ຊະນິດປາ/Species	ຊື່ພາສາລາວ Lao name	ຮູບປາ Fish picture	Tick if caught in past 12 months
Aaptosyax grypus	ປາສະນາກໃຫຍ່		
Pao suvattii	ປາເປົ້າ		
Wallago attu	ປາສະງົ້ວ		
Xenentodon canciloides	ປາສະໂຫງ		

Fig. 2. An example of questions used to identify species presence. While *Aaptosyax grypus* is a species with the morphological shape typically associated with fish, *Pao suvattii, Wallago attu,* and *Xenentodon canciloides* are unique in different ways and make larger contributions to functional diversity.

Additionally, we interviewed a key informant from each village, typically the head of the local Fisheries Management Committee who is responsible for the monitoring of local fisheries, or a member of the village leadership with deep knowledge of the village's fisheries management. These respondents provided information on the socioeconomic conditions, including access to roads, fishing rules and monitoring, prevalence of poverty and food insecurity, and the importance of fishing to local livelihoods.

Our data suggests that fishers did not move between villages to catch fish. The average distance between villages is 13.27 km, which is quite significant considering the quality of the roads, and that only half of the villages have road access throughout the year. Furthermore, the average reported travel time to the fishers' most common fishing location was 25 minutes (median = 15 minutes), a value consistent with people fishing in the river area adjacent to the village where they reside. Finally, 86.01% of respondents believe that people from their village respect village boundaries while fishing, and 77.20% believe the same of neighboring villages.

This survey has several advantages over more traditional ways of sampling fish communities that typically rely on capture or direct observation, including lower cost (and, with it, potentially larger coverage) and the fact that it avoids concerns about inter-seasonal variability in biodiversity. Fishing practices in these communities involve individuals retaining any fish caught, regardless of species or size. However, the species caught by fishing may not be representative of the full community composition if preferences for some fish species encourage fishers to target areas where those species are commonly found. Our data suggests that this concern is unlikely to be important in our context. Fishers identified 408 unique fishing locations, with the most frequent site accounting for only 4.14% of the trips, suggesting that no single site dominated fishing activity. In addition, there are very few restrictions to fishing activity: for example, no villages had limitations on the type of fish that could be caught (either in terms of species or size), and only one village imposes restrictions on the size of fishing gear (nets and traps).

The simplest measure of fish biodiversity is species richness (SR), which measures the number of species present in the ecosystem, and can be calculated in our data as the average number of species caught by fishers in each village, as recorded by the survey illustrated by Figure 2. Because all species contribute equally to this indicator, SR does not reflect the roles that different species may play in an ecosystem or their abundance.

However, the functioning of freshwater fish ecosystems strongly depends on their composition (Loreau et al., 2001), whereby different species fill the range of ecological roles associated with the range of ecosystem functions (Villéger et al., 2017). Species-rich communities often possess a diverse range of functional traits enabling species to fill different roles in the ecosystem (Chesson 2000). As a result, they tend to use a greater fraction of available resources than species-poor communities (Levine and HilleRisLambers 2009). This occurs through a process known as resource partitioning (also commonly known as the complementarity effect), whereby more ecological niches are filled, supporting healthy ecosystem function and increasing biomass production (Griffin, 2011; Loreau et al., 2001; Leduc et al., 2015). Moreover, the likelihood of the presence of highly productive species (i.e., those with high biomass) increases in more biodiverse ecosystems; this is known as the sampling effect (Loreau et al., 2001).

Functional Richness (FR), our preferred measure of biodiversity, overcomes the limitations of SR, as it is a measure of the variety of functional roles carried out by all fish species present in the ecosystem, with higher functional richness associated with healthy and productive ecosystems (Loreau et al., 2001; Dasgupta & Levin, 2023). While the subsequent analysis uses FR to quantify the productive value of biodiversity, Appendix B presents this same analysis when we use SR as a measure of biodiversity.

FR is estimated using information on morphological traits, such as body size, mouth and jaw morphology, eye position, and fin structure (Brosse et al., 2021). These traits (and their combinations) can indicate attributes such as trophic level and feeding behavior which in turn explain several important fish functions such as nutrient cycling, and therefore the functional roles that species play in their ecosystem (Cirtwill & Eklöf, 2018; Brosse et al., 2021; Chea et al. 2021; Ghilardi et al., 2023).[6]

[6] For example, the vertical eye position trait can predict the position of the fish and/or its prey in the water column and is measured by dividing the eye position (distance between center of eye and bottom of body) of the species by its body depth. This can be seen in Figure 2, where carp species such as *Aaptosyax grypus* often have a lower vertical eye position (0.622) compared to catfish such as *Wallago attu* (0.755).

Following Cornwell et al. (2006) and Villéger et al. (2008), we calculate FR as the convex hull volume of the space formed by the 10 morphological traits of species caught by each fisher. Trait data were drawn from FISHMORPH, which holds traits for 8,342 freshwater fish species (48.69% of the world freshwater fish species) (Brosse et al, 2021). We average values at the village level to characterize the FR of the local fishery.[7, 8] The values of FR are standardized between 0 and 1 over the observed maximum across all species to ensure that the units of individual traits do not influence the magnitude of the FR values. Table 1 presents the descriptive statistics of our data.[9]

[7] Out of the 131 species in our sample, 18 are excluded from the calculation of FR due to 6 having no match and 12 lacking complete information on all 10 morphological traits in the FISHMORPH database (Brosse et al., 2021). Therefore, 113 species are included in the calculation.
[8] See Section A.2 in appendix for a description of the convex hull volume methodology. FR was calculated using the fundiversity package in R (Grenié & Gruson, 2023).
[9] In the analysis, we excluded 172 outliers (6.26% of the sample, identified using the -hadimvo- command in Stata).

Table 1: Descriptive statistics

	Mean	Std. Dev.	Median	Min	Max
Trip level (n=2,558, from 408 fishers)					
Fishing yield (kg per hour)	0.5	0.58	0.28	0	2.96
Overnight fishing (0 no; 1 yes)	0.33	0.47	0.00	0	1
Used fishing gear: nets (0 no; 1 yes)	0.76	0.43	1.00	0	1
Used fishing gear: traps (0 no; 1 yes)	0.05	0.21	0.00	0	1
Used fishing gear: lines (0 no; 1 yes)	0.18	0.38	0.00	0	1
Used fishing gear: other (0 no; 1 yes)	0.01	0.11	0.00	0	1
Village level (n=19)					
Average village species richness	120.11	7.29	123.20	104.7	128.3
Average village functional richness	0.37	0.12	0.43	0.19	0.51
Distance to river mouth (km)	156.26	72.03	157.86	18.97	257.81
No. poor households in village	12.84	12.08	9.00	0	40
No. food insecure households in village	14.74	19.22	7.00	0	60
No. fishing-dependent households in village	48.68	54.3	20.00	0	150
Car access during whole year (0 no; 1 yes)	0.53	0.51	1.00	0	1
Rules on gear and/or methods (0 no; 1 yes)	0.58	0.51	1.00	0	1
Paid compliance monitoring (0 no; 1 yes)	0.63	0.5	1.00	0	1

Note: 172 outliers in terms of fishing yield were excluded from the analysis. Trip level data are taken from the fish catch monitoring survey. Data on average village species and functional richness are from the biodiversity module in the household survey. Data on number of poor, food insecure and fishing dependent households; car access to village; fishing rules; and compliance monitoring are from the village survey. Distance to river mouth (km) estimated using coordinates from the village survey, spatial data of the Xe Banghieng River and the sfnetworks package in R (van der Meer et al., 2023).

Figure 3, Panel A, presents the relationship between distance to the river mouth and average fishing yield in each village.[10] Panel B presents the relationship between distance to mouth and FR. While the positive trend in Panel B resembles what is shown in Panel A, a large discontinuity is evident between villages 8 (Ban Keangsangku) and 9 (Ban Thungarlay), which coincides with the inflow of water from the Xe Thamouak River (Figure A.3 in Appendix).[11]

[10] As is noticeable, average fishing yield in Village 5 (in terms of order from the river mouth, see Ban Nathung in Figure 1) is 2-3 times greater than that in most other villages. While average fish weight per trip is slightly lower than in the other villages (3.79kg in village 5 vs 3.83kg in other villages), fishing time was significantly shorter (2.57 and 9.54 hours respectively),with no fisher averaging a fishing time greater than 5 hours. The source of these differences is unclear, but in Appendix C we present estimates of our main results when we exclude Village 5, showing that the inclusion of data from this village in the analysis does not substantially affect our results.

[11] Although our data does not allow us to fully explain this drop, we note that the headwaters of this river are near the location of the Sepon open-pit and underground Gold and Copper mine and its Western Tailings Storage Facility, where waste from the mining process is stored.

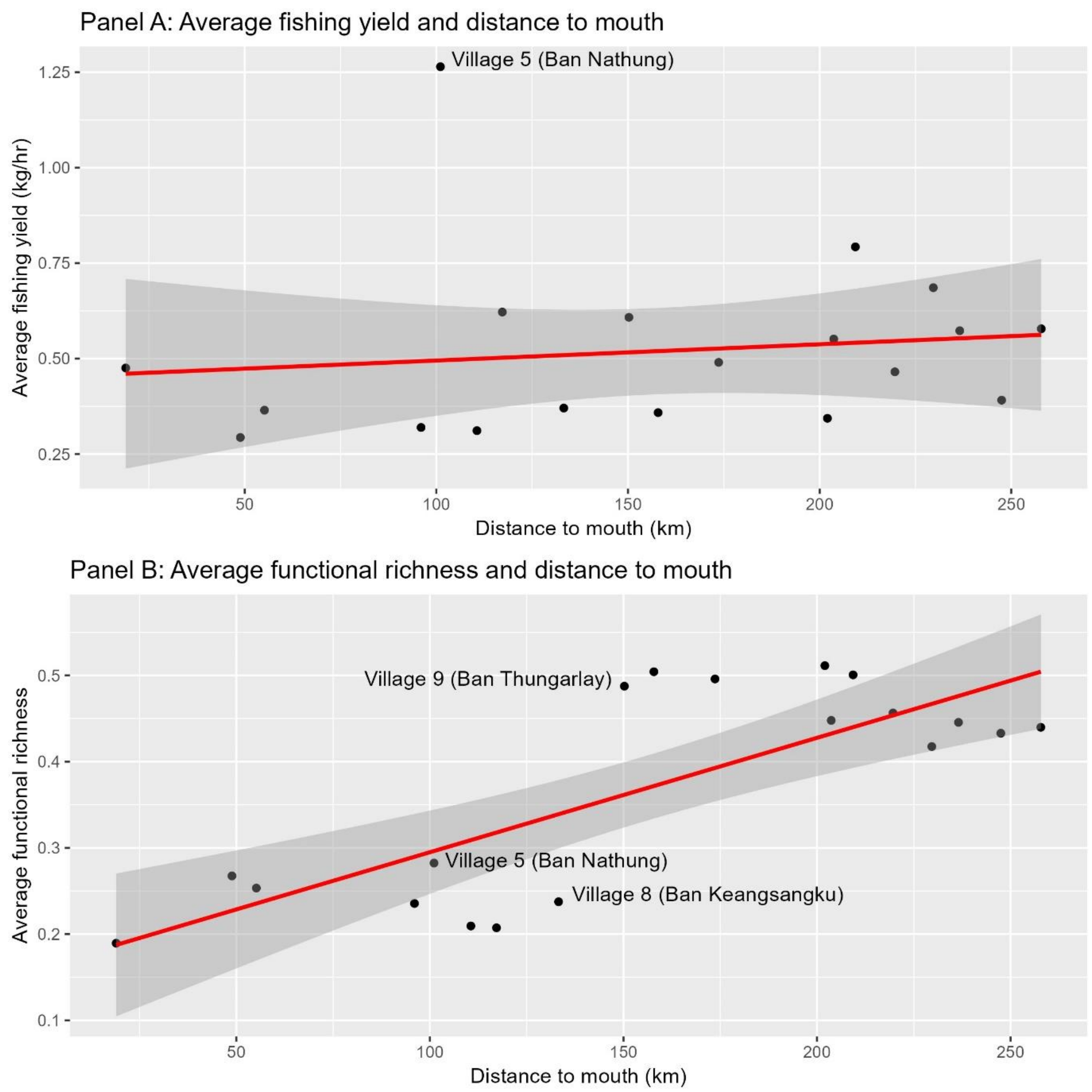

Fig. 3. Panel A: relationship between distance to mouth and average fishing yield. Panel B: relationship between distance to mouth and FR. The red line and shaded area represent the linear prediction and 95% confidence interval, respectively.

3. Identification strategy

As a first step in quantifying the impact of biodiversity on fishing yield, we estimate the following ordinary least squares (OLS) regression:

$$Y_{ijv} = \beta_1 B_v + \boldsymbol{\theta} \boldsymbol{X}_{ijv} + \boldsymbol{\gamma} \boldsymbol{Z}_v + \varepsilon_v \tag{1}$$

where Y_{ijv} refers to the yield (in kilograms per hour) of fishing trip i caught by fisher j at location v, a measure that is analogous to the catch per unit of effort (CPUE) commonly used in the analysis of fisheries productivity, B_v is the level of biodiversity measured by FR, $\boldsymbol{X}_{ijv}$ is a vector of trip-level controls (fishing equipment used and whether overnight fishing was conducted) and $\boldsymbol{Z}_v$ is a vector of village-level controls (fishing dependency, levels of poverty and food insecurity, all-year access to a road, rules on fishing equipment and paid monitoring of rules). The inclusion of these control variables reduces the variability in fishing yield, leading to more precise estimates of the impact of more diverse fish communities on our outcome (Angrist & Pischke, 2008). Conservatively, we cluster the error term (ε_v) at the village level (Abadie et al., 2023; Cameron et al., 2011).

We are particularly interested in β_1, which can be interpreted as the causal impact of biodiversity on fishing yield if we can assume that there are no unobserved confounders of this relationship once we account for fishing technology and other village characteristics. This is unlikely: for example, differences in water quality between villages due to factors such as adjacent land use (and associated runoff) might impact both biodiversity and overall fish biomass and, therefore, fishing yield.

To address this concern, we use the position of the village along the river, measured using the distance of the village from the river mouth and its squared term, and an indicator variable that measures whether the village is downstream of the Xe Thamouak, as two exogenous sources of variation in biodiversity, and estimate equation (1) using instrumental variable (IV) regression (Angrist & Pischke, 2008).[12]

The correlation between position along the river and biodiversity is central to the River Continuum Concept in ecology, first suggested by Vannote et al. (1980), who describe how the

[12] The distance from the village to the river mouth along its natural path was calculated using the R packages sf and sfnetworks (Pebesma, 2018; van der Meer et al., 2023). Village coordinates and spatial data of the Xe Banghieng River were obtained from Greater Mekong Subregion Environment Operations Center (2015).

position along a river predicts multiple attributes of the physical environment of a stream, including river depth, width, slope, discharge, substrate composition and size, which in turn influence light penetration, water temperature and chemistry (Doretto et al., 2020; McCabe, 2011; van der Sleen & Albert, 2021; Vannote et al. 1980). These attributes have implications for food availability and drive the composition of the fish community, including the presence of different species and functional groups (Miranda et al., 2019; Sanchez-Hernandez, 2023; van der Sleen & Albert, 2021). This complex interaction between position along the river, food availability, and biodiversity supports the relevance of our instrument (distance to the river mouth).[13] Despite this, position along the river may affect fishing yield other than through the variation it creates in terms of biodiversity. For example, in this setting, headwater villages may be different from those near the mouth of the river (and the Mekong plains, where most of the economic activity is concentrated) in ways that matter for fishing yield, such as levels of economic development or access to local markets. For that reason, in our analysis, we control for village characteristics, including the levels of poverty, food insecurity and fishing dependency, rules regulating the use of specific fishing equipment, and its monitoring and road access (as a proxy for integration in markets).

4. Results

The OLS estimates of the relationship between biodiversity and fishing yield (controlling for trip-level and village-level determinates of fishing yield) show that biodiversity (as measured by FR) is a statistically significant predictor of fishing yield at the 1% level (Table

[13] However, it is important to notice that the RCC does not explicitly predict the direction of the relationship between distance to river mouth and biodiversity. For example, while Kang et al. (2018) present empirical evidence supporting higher SR and FR in the lower reaches of the Yangtze River in China when compared with its headwaters, Huang et al. (2022) present evidence that the middle catchment of the Pearl River in China is more biodiverse, both in terms of SR and FR, than either the headwaters or the river mouth.

2). However, as mentioned above, these estimates may also reflect unmeasured confounders at the village level.

Table 2: Relationship between biodiversity and fishing yield

Outcome:	Fishing yield (kg per hour)
Average functional richness	0.908*** (0.270)
Trip level controls	Yes
Village level controls	Yes
Observations	2,558
R-squared	0.108
Mean fishing yield	0.818

Note: OLS estimates. Robust standard errors clustered at the village level in parentheses. Observations at the fishing trip level, from 408 fishers. 172 outliers of fishing yield were excluded from the analysis. ***, **, * indicates statistical significance at the 1%, 5% and 10% level, respectively. See Table A.4 for full results.

Given our relatively small sample size, we use Limited Information Maximum Likelihood (LIML) to obtain the IV estimates of the relationship between biodiversity and fishing yield (Angrist & Pischke, 2008; Cameron & Trivedi, 2009; Flores-Lagunes, 2007).[14] Table 3 presents first-stage estimates of the relationship between our IVs (distance to river mouth, its squared term, and whether the village was downstream of Xe Thamouak) and biodiversity (column 1), and reduced form estimates of the relation between our IVs and fishing yield (column 2). Both models include trip and village level controls.

We find no evidence of under or weak identification, as measured by the Kleibergen–Paap tests, and the overidentification test supports our interpretation of the exclusion restriction. Downstream of Xe Thamouak and the square of distance to river mouth are significantly correlated with FR at the 1% and 10%, respectively.

[14] Main conclusions remain unchanged when using two-stage least squares or generalized method of moments estimation; see Tables A.5 and A.6.

Table 3: First-stage and reduced form estimates

Dependent variable:	Average functional richness (1)	Fishing yield (kg per hour) (2)
Exogenous Instruments		
Distance to river mouth (km)	0.0004	0.003
	(0.000)	(0.002)
Distance to river mouth (km) squared	-0.000003*	-00001*
	(0.000)	(0.000)
Downstream of Xe Thamouak	-0.275***	-0.181
	(0.022)	(0.133)
Trip level controls	Yes	Yes
Village level controls	Yes	Yes
P-value of overidentification test of all instruments	0.361	-
P-value of Kleibergen–Paap test for underidentification	0.0221	-
Kleibergen–Paap Wald F statistic for weak identification	157.9	-
Stock-Yogo weak identification test critical values: 10% maximal LIML size	6.46	-
P-value of GMM distance test statistic of endogeneity	0.408	-
Observations	2,558	2,558
R-squared	0.972	0.106
Outcome mean	0.364	0.818

Note: Robust standard errors clustered at the village level in parentheses. Observations at the fishing trip level, from 408 fishers. 172 outliers of fishing yield were excluded from the analysis. ***, **, * indicates statistical significance at the 1%, 5% and 10% level, respectively. See Table A.7 for full results.

IV estimates of the impact of biodiversity on fishing yield, are shown in Table 4.[15] As in Table 3, the specification controls for trip and village-level confounders of fishing yield. We find that FR increases fishing yield, significant at the 1% level. As FR is determined by the volume of the space formed by the morphological traits of species present in the community, the magnitude of these estimates cannot be directly interpreted.

When the productive value of biodiversity is estimated using SR (see Appendix B), we reach the same conclusion. SR significantly increases fishing yield (at the 1% level) such that

[15] Results are robust to using only distance to river mouth (and its squared term) or being downstream of Xe Thamouak as instruments (see Table A.8 and A.9 in appendix, respectively).

an additional species is estimated to increase fishing yield by 15 grams per hour, a two percent increase from the average fishing yield of 0.818. Given that households in our sample make, on average, 2.1 fishing trips per week, with an average duration of 9 hours, this value translates into an additional 284 grams per week per additional species.

Table 4: Impact of biodiversity on fishing yield

Outcome:	Fishing yield (kg per hour)
Average functional richness	0.800***
	(0.284)
Trip level controls	Yes
Village level controls	Yes
Observations	2,558
Mean fishing yield	0.818

Note: Limited Information Maximum Likelihood IV estimates. Standard errors clustered at the village level in parentheses. Observations at the fishing trip level, from 408 fishers. 172 outliers of fishing yield excluded from the analysis. Functional richness instrumented using distance to river mouth, distance to river mouth squared, and village downstream of Xe Thamouak as exogenous source of variation. ***, **, * indicates statistical significance at the 1%, 5% and 10% level, respectively. See Table 3 for IV test statistics. See Table A.10 for full results.

5. Quantifying the vulnerability of local fisheries to reductions in biodiversity

The IV estimate presented in Table 4 shows that greater functional richness increases the productivity of freshwater fisheries, consistent with the complementarity and sampling effects (Loreau et al., 2001). Given the threats to freshwater biodiversity (Deinet et al., 2020; Dudgeon et al. 2006), this is concerning news for communities that depend on this resource for either income or consumption. However, the impact of species extinction on fisheries productivity is likely to depend on which specific species are lost, rather than being uniform across all species. For example, large bodied 'mega-fish' function as top predators and keystone species, controlling the population of other fish species, indirectly regulating the availability of nutrients such as vegetation and thereby supporting overall ecosystem balance (He et al., 2019; Hui, 2012). However, these species are particularly vulnerable: between 1970 and 2012, their populations exhibited a 94% decline (He et al., 2020), a result that reflects their life-history traits (e.g., low reproduction rates (Barneche et al., 2018) and longer generation time (Froese & Binohlan, 2000)) and the associated vulnerability to disruption of their ecosystems (e.g., dams disrupting movement patterns (Baird & Hogan, 2023; Barbarossa et al., 2020) and overfishing (Ripple et al., 2019; Ripple et al., 2017)).

In this section we explore what we can learn about the vulnerability of local fisheries to losses in biodiversity from our estimate. We follow previous work that asked a similar question (McIntyre et al., 2007; Heilpern et al., 2021) and focus on the impact of each extinction on FR and of changes in FR on expected fishing yield in this river system.[16] However, unlike these studies, that start by simulating biodiversity loss through random extinction (McIntyre et al., 2007; Heilpern et al., 2021), we consider the worst-case scenario, in which extinctions occur in decreasing order of their contribution to FR. The simulation

[16] The answer to this question is trivial when we measure biodiversity using SR, given that each species contributes equally to this measure.

involves removing each species individually, calculating the change in FR that would result from their removal, and identifying the species that cause the largest reduction. We then repeat the process of individual deletion and FR calculation, with the species having the highest contribution to FR in these progressively less diverse sets of species becoming extinct until no species remain in the ecosystem. This approach provides evidence of vulnerability to the loss of key species (i.e., those that contribute most to FR) and establishes a benchmark against which we can evaluate the effect of particular extinctions on FR (and yield).

A more realistic alternative to both random and worst-case scenarios is to simulate the effect of progressive loss of biodiversity when each species is removed on the basis of its extinction risk. We explore two proxies for such risk. The first is the well-known IUCN Red List status of species, which uses established criteria such as declines in population size and geographic distribution to categorize species according to their extinction risk (IUCN, 2024). The second is the species' resilience through reproduction, a measure of population doubling time that predicts the capacity of species to respond to disturbance (Villéger, et al. 2017; Froese et al., 2017). Table A.11 provides a summary description of these indicators.[17]

5.1 Extinction simulation: worst case scenario

The impact of species extinctions (in decreasing order of their contribution to FR), on FR and average fishing yield is shown in Figure 5.[18] Removing the 5 largest contributors to FR sharply reduces the FR of this ecosystem by approximately 90% of its initial level (Figure 5A). Using the IV estimate of FR on fishing yield, the extinction of these species is estimated to reduce fishing yield from 818 to 101 grams per hour (Figure 5B).

[17] While these proxies are not specific to our research area in the Xe Banghieng River, the geographical distribution of the species included in the biodiversity module are primarily limited to the Mekong Basin (or wider Southeast Asian region), which should ensure they are robust for our study.

[18] Based on the 113 species in our sample, a total of 102 iterations were conducted as calculations of FR require strictly more species than traits.

Table 6 describes the characteristics of the top contributors to FR. While these species span a range of attributes, they are all carnivores (trophic level >3), are morphologically unusual, and include two of the largest fish species in the system (*Bagarius yarrelli,* the giant devil catfish and *Wallago Attu,* the helicopter catfish) which are classified as mega-fish. These characteristics are suggestive of habitat specialists that fill ecological roles no other species can, and whose presence or absence could have significant implications for the ecological balance in this ecosystem.

The results from this simulation motivate two conclusions. The first is that the extinction of species that make minimal contribution to FR has no impact on average fishing yield, a relatively straightforward implication of complementarity between species. The second is that, as shown in Table 6, the species that are the largest contributors to FR are not necessarily the most vulnerable to extinction according to the other criteria we considered. A more realistic analysis of the vulnerability of these fisheries to losses in biodiversity is presented next.

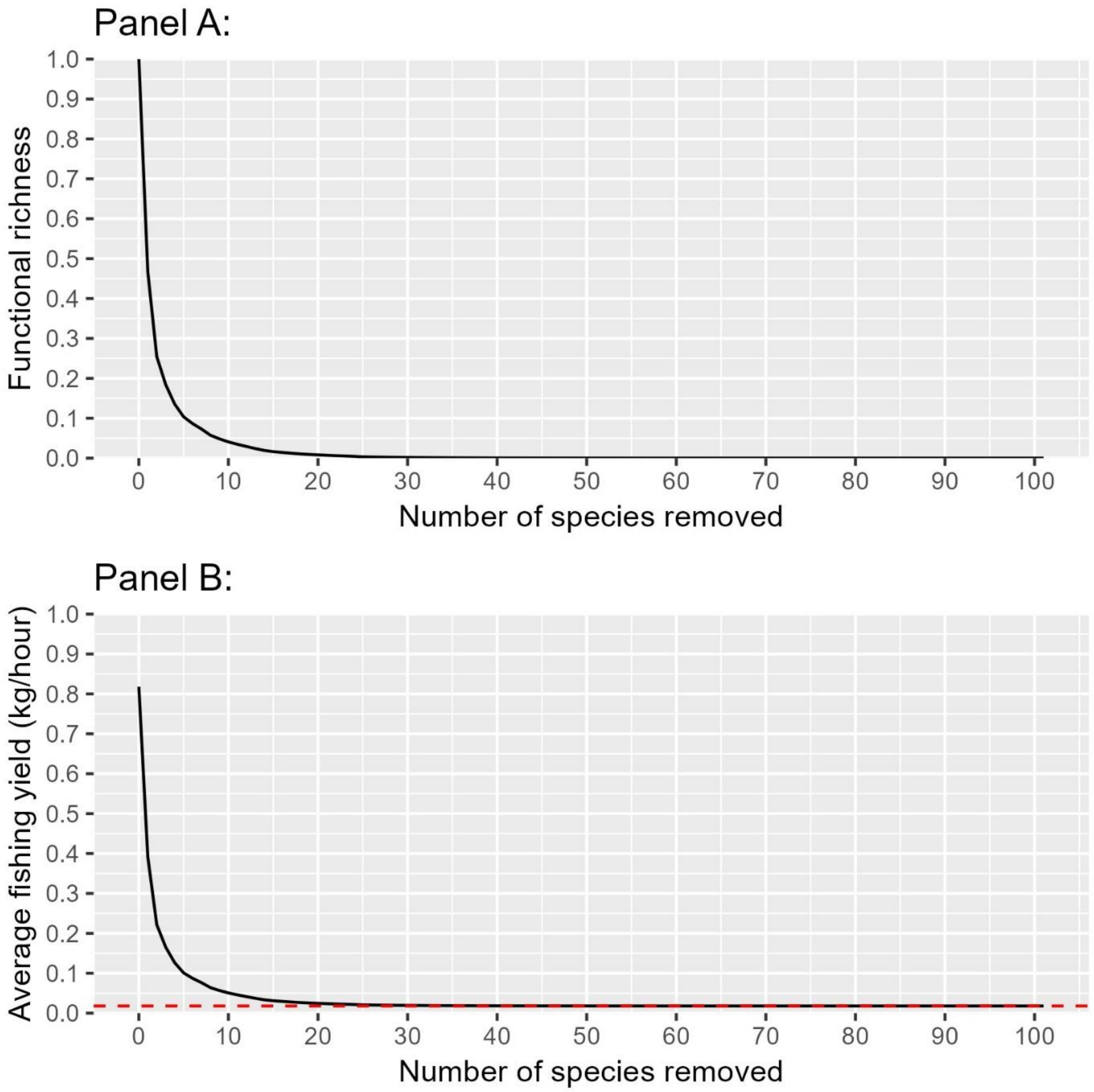

Fig. 5. Effect of species extinction (in decreasing order of contribution to functional richness) on functional richness (Panel A): functional richness declines sharply when the top contributors to FR are removed. As established in Section 4, this reduction negatively impacts on average fishing yield (Panel B).

Table 6: Characteristics of the top 10 contributors to functional richness

	Worst case scenario		Ecological attributes and vulnerabilities			Morphological traits			
Fish species	Order of removal	Reduction in functional richness	IUCN Red List Status	Resilience through reproduction	Trophic level	Maximum body length (cm)	Body elongation	Relative maxillary length	Relative eye size
Xenentodon canciloides	1	-0.533	LC	High	3.9	30	11.845	4.073	0.629
Doryichthys deokhatoides	2	-0.212	DD	High	3.2	18.5	24.779	0.431	0.611
Chaudhuria caudata	3	-0.070	DD	N/A	3.2	6	13.959	0.389	0.245
Bagarius yarrelli	4	-0.049	VU	Very Low	3.7	200	5.695	0.650	0.174
Pseudohomaloptera yunnanensis	5	-0.032	LC	N/A	3.2	6	7.298	0	0.348
Dermogenys aiamensis	6	-0.017	LC	N/A	3.1	6	8.432	1.184	0.507
Pao suvattii	7	-0.013	LC	High	3.3	12	3.282	0.183	0.243
Pao turgidus	8	-0.016	LC	High	3.4	18.5	3.074	0.091	0.361
Neodontobutis aurarmus	9	-0.009	LC	Medium	3.1	6	3.666	0.657	0.323
Wallago attu	10	-0.008	VU	High	3.7	240	5.671	1.108	0.262

Note: See Table A.12 for a description of the ecological attributes included in this table. Data on IUCN Red List status from IUCN (2024). The IUCN Red List status includes data deficient (DD), least concern (LC), near-threatened (NT), vulnerable (VU), endangered (EN), critically endangered (CR) and not evaluated (NE) categories. Data on trophic level and resilience through reproduction from FishBase (2024). N/A = not available. Data on morphological traits from Brosse et al. (2021). The *Pseudohomaloptera yunnanensis* has a relative maxillary length of 0 as its mouth/snout is on the base of its body.

5.2 Extinction simulation: The IUCN Red List and resilience through reproduction

Simulating the impact of species extinction on fisheries based on the IUCN Red List status reveals that the largest decrease in FR results from the loss of 11 species considered vulnerable (VU) to extinction (Figure 6A). Using the IV estimates of the effect of FR on fishing yield, the extinction of only the 2 CR species and 11 VU fish species is estimated to reduce yield by 0.362, effectively halving average fishing yield from 0.818 to 0.456 kilograms per hour (Figure 6B). Two mega-fish species categorized as vulnerable, *Bagarius yarrelli* and *Wallago attu*, drive this reduction, being the fourth and tenth largest contributors to FR, respectively. Importantly, the large decrease in FR that occurs through the loss of data deficient (DD) species highlights the need for additional information on the abundance and distribution of these species. Studies in other taxa suggest that data deficient species are more likely to be in higher threat categories once assessed (Bland, et al., 2015; Borgelt et al., 2022).

Assessing vulnerability according to reproductive capacity reveals that average fishing yield sharply reduces after the loss of only 7 species with very low resilience through reproduction, reducing FR to 0.597 (Figure 6C). This reduction is estimated to reduce fishing yield by 0.323 kilograms per hour, from an average of 0.818 to 0.495 kilograms per hour (Figure 6D). Again, the loss of *Bagarius yarrelli* was highly influential, with its life history traits conferring very low levels of resilience.

Importantly, the majority of the species in the system were considered least concern (LC) by the IUCN (81.68%) and had medium to high resilience to perturbation (72.52%). This suggests that these species likely have the capacity to recover quickly if external threats are attenuated. Despite this, the benefits of maintaining a diverse fish community for freshwater fisheries are clear, as at-risk species are key drivers of functional diversity and, as a result, fishing yield.

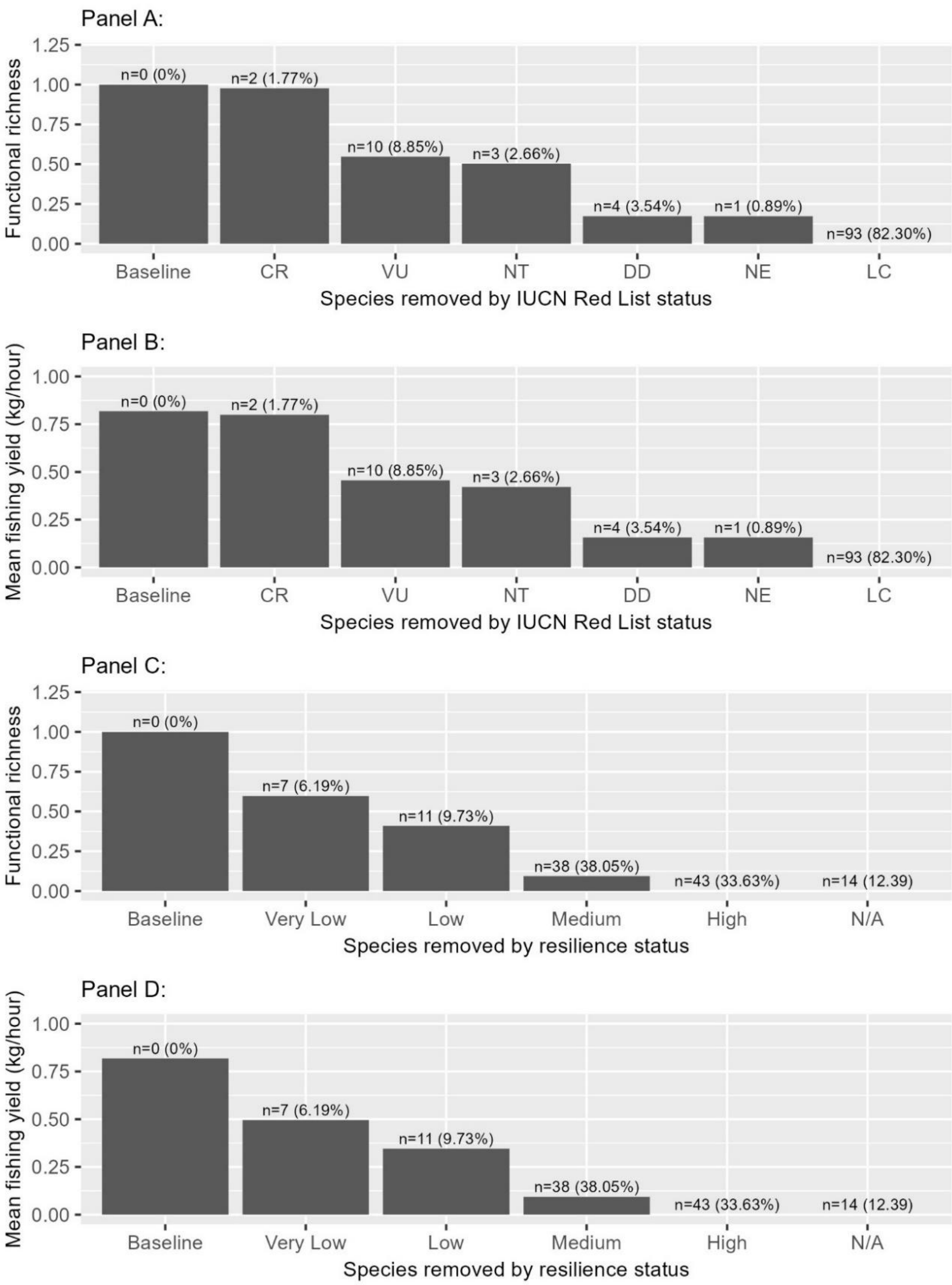

Fig. 6. Effect of species extinction on functional richness and mean fishing yield in order of IUCN Red List status (Panels A and B) and resilience through reproduction (Panels C and D). The IUCN Red List status categories include critically endangered (CR), vulnerable (VU), near threatened (NT), data deficient (DD), not evaluated (NE) and least concern (LC). Resilience status N/A represents no data available. No species are listed as endangered (EN) in our sample. Baseline represents no species removed (i.e., full sample). The total number of species is 113. A sharp decrease in fishing yield occurs after removing the species categorized as VU and subsequently DD as well as species with a very low resilience status.

6. Discussion

Freshwater ecosystems support the livelihoods of local communities in developing countries, with people in rural areas often depending on fish provision for protein and essential micronutrients (McIntyre et al., 2016; Allison & Mills, 2018). Despite their contributions to welfare, global freshwater fish populations are declining due to multiple external threats, with groups such as mega-fish disproportionately affected (Deinet et al., 2020). Habitats for freshwater fish are complex, vulnerable and often not supported by management actions (including fisheries management, habitat restoration, dam removal, the establishment of fish conservation zones, species-specific management, and legal protection), as international policy discussions have largely failed to acknowledge the essential services they provide (Lynch et al., 2020; Deinet et al., 2020).

This study evaluated the role that biodiverse fish communities play in facilitating fishing yields in freshwater ecosystems. We addressed a critical knowledge gap by using a quasi-experimental design to determine the causal impact of higher levels of freshwater fish biodiversity, measured as Functional Richness (FR), on fishing yield using detailed fish catch monitoring data collected from the Xe Banghieng River, Lao PDR. Functional richness captures an important dimension of biodiversity by measuring the variety of functional roles present in the community, and its effect is estimated using an instrumental variable approach that exploits the natural variation in biodiversity along the course of the river, through the distance to the river mouth and whether the location is downstream of Xe Thamouak.

We found that more biodiverse fish communities lead to increases in freshwater fish yield, offering potential win–win outcomes for biodiversity and food security in the effective conservation of these ecosystems. This finding is causal and robust to both measures of biodiversity (SR and FR). This is consistent with ecological theory (Loreau et al., 2001; Griffin, 2011) and highlights that the composition of fish communities matters for increasing fishing yield, with species that fill specific ecological niches in the ecosystem disproportionately contributing to this relationship. Furthermore, we found that the FR, and therefore, the productivity of this ecosystem, is vulnerable to the loss of a small number of key species from the community. The loss of the largest contributors to FR, species categorized by the IUCN as vulnerable, or species with very low resilience through reproduction would have significant economic consequences for local fisheries. Taken together, our results show that diverse communities promote better outcomes for freshwater fisheries.

Our results are consistent with the findings of Brooks et al. (2016) and McIntyre et al. (2016), who both found positive relationships between SR and freshwater fishing yield. However, while the SR serves as a well-known and easily quantifiable metric, the inability to consider the contribution of species to ecosystem function limits its value. By considering the impact of community composition (FR) on freshwater fish yield, our research makes a novel contribution to this literature.

Policies that can support diverse fish communities by imposing restrictions to prevent overfishing (e.g., no-take areas) can support the economic productivity of fisheries by providing species with a safe habitat for populations to recover (Koning et al., 2020). Moreover, policies that protect specific vulnerable species and key contributors to FR (e.g., breeding programs or bans on harvesting certain species or size classes) can also increase fishing yield. The extinction simulations provide important guidance for policies related to protecting key species. For example, *Bagarius yarrelli* contributes greatly to FR and is considered at risk across multiple measures of vulnerability (see Table 6). The loss of this species alone could have significant consequences for ecosystem health and fishery productivity; therefore, its protection should be prioritized.

The three mechanisms proposed in the literature underlying the relationship between biodiversity and productivity are the sampling, complementarity and resilience effect (Loreau et al., 2001). While we find evidence consistent with both the sampling effect and complementarity effect, we could not assess whether higher levels of biodiversity can act as a form of insurance against perturbations (the resilience effect). Communities with high diversity can be more resilient to shocks, as redundancy in the system (i.e., species that share a similar niche) fill the functional roles left by affected species, buffering the ecosystem against the loss of species (Loreau et al., 2001; Elmqvist et al., 2003). This process can maintain ecosystem function, resource utilization and therefore productivity in the face of species extinction. The analysis of the resilience effect requires panel data before and after changes in environmental conditions, which is absent in the data used in this study.

Additionally, due to the structure of our fish monitoring data, we cannot fully explore the impact of varying abundance among different species on fishery productivity. A balanced system is achieved when the relative abundances of species are proportional to their roles within the ecosystem at any given time (Cleland, 2011). Disproportionate numbers could lead to instability and potentially disrupt ecosystem function. Future research could explore other measures of diversity, including response diversity and relative abundance, and their impacts on the productivity of freshwater systems, and subsequently, fishery yields.

Although we rely on the IUCN Red List status and resilience through reproductive capabilities as proxies for a species' vulnerability to extinction, further research is needed to precisely identify and understand the underlying factors that contribute to this vulnerability. Despite significant efforts dedicated to understanding this cause in marine ecosystems, freshwater systems require more attention, given their importance to food security for many communities and the myriad threats that impact them.

Furthermore, the generalizability of the findings in this study can be tested in future work. The causal impact of biodiversity on freshwater fishery productivity can be determined in other contexts and regions, such as Africa, where significant win–win opportunities with respect to environmental conservation and poverty alleviation may also exist.

While we recognize that more research in this space is necessary, our study fills a crucial gap in the literature by establishing the economic benefit in yield that biodiversity brings to freshwater fisheries, marking an important first step in building our understanding of how community composition affects productivity, and thereby fishing yields in freshwater ecosystems. Effective conservation actions, particularly those that target the most functionally important and vulnerable species, are critical for improving ecological health and livelihoods in communities dependent on the services provided by freshwater ecosystems.

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Appendix A

A.1 Species list from biodiversity module

1. *aaptosyax grypus*
2. *acanthopsoides delphax*
3. *acantopsis ioa*
4. *akysis hendricksoni*
5. *albulichthys albuloides*
6. *anabas testudineus*
7. *anematichthys repasson*
8. *bagarius yarrelli*
9. *bagrichthys obscurus*
10. *barbichthys laevis*
11. *barbodes aurotaeniatus*
12. *barbonymus altus*
13. *barbonymus gonionotus*
14. *belodontichthys truncatus*
15. *betta smaragdina*
16. *boraras micros*
17. *brachirus harmandi*
18. *brachygobius mekongensis*
19. *channa gachua*
20. *channa lucius*
21. *channa micropeltes*
22. *channa striata*
23. *chaudhuria caudata*
24. *chitala ornata*
25. *cirrhinus cirrhosus*
26. *cirrhinus molitorella*
27. *clarias batrachus*
28. *clupeichthys aesarnensis*
29. *crossocheilus reticulatus*
30. *ctenopharyngodon idella*
31. *cyclocheilichthys apogon*
32. *cyclocheilichthys armatus*
33. *cyclocheilichthys enoplos*
34. *cyclocheilichthys furcatus*
35. *cyprinus carpio*
36. *datnioides undecimradiatus*
37. *dermogenys siamensis*
38. *doryichthys deokhatoides*
39. *esomus malayensis*
40. *esomus metallicus*
41. *glyptothorax major*
42. *hampala dispar*
43. *helicophagus waandersii*
44. *hemibagrus nemurus*
45. *hemibagrus wyckioides*
46. *hemisilurus mekongensis*
47. *henicorhynchus ornatipinnis*
48. *henicorhynchus siamensis*
49. *hypophthalmichthys molitrix*
50. *hypsibarbus lagleri*
51. *hypsibarbus malcolmi*
52. *hypsibarbus vernayi*
53. *indostomus paradoxus*
54. *labeo barbatulus*
55. *labeo pierrei*
56. *labiobarbus leptocheilus*
57. *laides longibarbis*
58. *lepidocephalichthys hasselti*
59. *lobocheilos melanotaenia*
60. *lobocheilos rhabdoura*
61. *macrochirichthys macrochirus*
62. *macrognathus semiocellatus*
63. *macrognathus siamensis*
64. *mastacembelus armatus*
65. *mastacembelus favus*
66. *monopterus albus*
67. *mystacoleucus atridorsalis*
68. *mystacoleucus lepturus*
69. *mystacoleucus marginatus*
70. *mystus albolineatus*
71. *mystus atrifasciatus*
72. *mystus bocourti*
73. *mystus mysticetus*
74. *mystus pulcher*
75. *nandus oxyrhynchus*
76. *nemacheilus masyae*
77. *neodontobutis aurarmus*
78. *notopterus notopterus*
79. *ompok bimaculatus*
80. *opsarius koratensis*
81. *oreochromis niloticus*
82. *oryzias pectoralis*
83. *oryzias wolasi*
84. *osphronemus exodon*
85. *osteochilus lini*
86. *osteochilus melanopleurus*
87. *osteochilus microcephalus*
88. *osteochilus waandersii*
89. *oxyeleotris marmorata*
90. *oxygaster pointoni*
91. *pangasius bocourti*
92. *pangasius polyuranodon*
93. *pangio anguillaris*
94. *pao suvattii*
95. *pao turgidus*
96. *parachela maculicauda*
97. *parachela siamensis*
98. *paralaubuca barroni*
99. *paralaubuca typus*
100. *parambassis siamensis*
101. *phalacronotus apogon*
102. *poropuntius laoensis*
103. *poropuntius normani*
104. *pristolepis fasciata*
105. *probarbus jullieni*
106. *pseudohomaloptera yunnanensis*
107. *pseudolais pleurotaenia*
108. *puntioplites falcifer*
109. *puntioplites proctozystron*
110. *puntius brevis*
111. *raiamas guttatus*
112. *rasbora aurotaenia*
113. *rasbora borapetensis*
114. *rasbora dandia*
115. *rasbora paviana*
116. *rasbora rubrodorsalis*
117. *rasbora trilineata*
118. *rasbosoma spilocerca*
119. *scaphognathops stejnegeri*
120. *sundasalanx mekongensis*
121. *syncrossus helodes*
122. *systomus jacobusboehlkei*
123. *systomus orphoides*
124. *thynnichthys thynnoides*
125. *trichopodus trichopterus*
126. *wallago attu*
127. *xenentodon canciloides*
128. *yasuhikotakia eos*
129. *yasuhikotakia lecontei*
130. *yasuhikotakia modesta*
131. *yasuhikotakia morleti*

A.2 Convex hull methodology

The outcome measure of FR used in this study was determined using the convex hull methodology proposed by Cornwell et al., (2006) and applied to FR measurement by Villéger et al. (2008).

Figure A.2.1 shows graphical illustrations of convex hulls. In graph (a), the x-axis represents the specific leaf area (z score), and the y-axis represents wood density (z score). Each dot on the graph represents a different species, with the bold dots representing species present in the ecosystem. The convex hull is then defined as the area inside the outlined shape, known as the trait space. This shape is determined by species on the frontier of the trait space, with 'unique' species with respect to specific leaf area (z score) and wood density (z score) pushing out the frontier and increasing the area of the trait space. Graphs (b) and (c) extend graph (a) to the 3-dimensional space, including seed mass as an additional trait. As in graph (a), species present in the ecosystem are plotted according to these traits (shown in graph (b)), and the convex hull volume is determined by the multidimensional trait space occupied by these species. This methodology can be extended to n-dimensional spaces, with this study calculating the convex hull on a 10-dimensional morphological trait space.

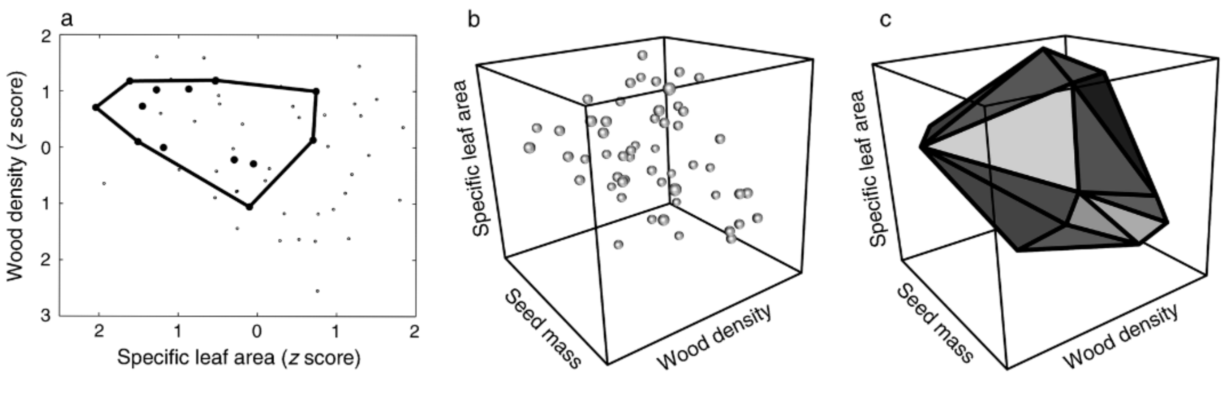

Fig. A.2.1 Graphical illustrations of convex hulls. Reproduced from Cornwell et al. (2006)

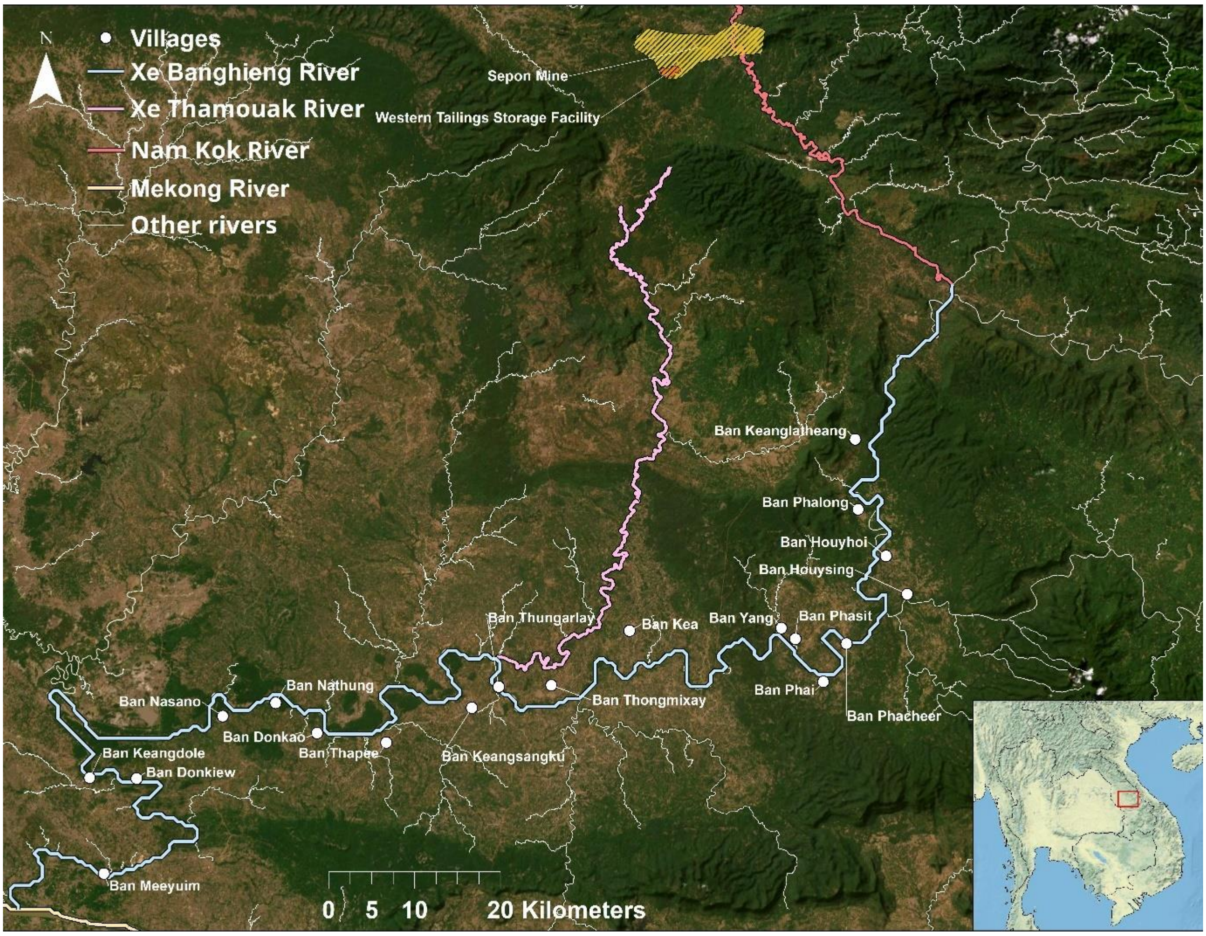

Fig. A.3. Sample villages in relation to the Sepon Gold and Copper mine and its Western Tailings Storage Facility. The inset shows the location within Southeast Asia indicated by the red square.

Table A.4: Relationship between biodiversity and fishing yield

Outcome:	Fishing yield (kg per hour)
Biodiversity measure	
Average functional richness	0.908***
	(0.270)
Controls	
Overnight fishing (0 no; 1 yes)	-0.335***
	(0.067)
Used fishing gear: nets (0 no; 1 yes)	0.350***
	(0.083)
Used fishing gear: traps (0 no; 1 yes)	0.224**
	(0.100)
Used fishing gear: lines (0 no; 1 yes)	0.285***
	(0.085)
No. poor households in village	-0.006
	(0.004)
No. food insecure households in village	0.000
	(0.001)
No. fishing-dependent households in village	0.001
	(0.001)
Car access during whole year (0 no; 1 yes)	-0.135
	(0.114)
Rules on gear and/or methods (0 no; 1 yes)	0.041
	(0.142)
Paid compliance monitoring (0 no; 1 yes)	-0.006
	(0.084)
Constant	0.029
	(0.174)
Observations	2,558
R-squared	0.108
Mean fishing yield	0.818

Note: OLS estimates. Robust standard errors clustered at the village level in parentheses. Observations at the fishing trip level, from 408 fishers. 172 outliers of fishing yield were excluded from the analysis. ***, **, * indicates statistical significance at the 1%, 5% and 10% level, respectively.

Table A.5: Impact of biodiversity on fishing yield using two-stage least squares estimator

Outcome:	Fishing yield (kg per hour)
Biodiversity measure	
Average functional richness	0.800***
	(0.284)
Controls	
Overnight fishing (0 no; 1 yes)	-0.333***
	(0.063)
Used fishing gear: nets (0 no; 1 yes)	0.344***
	(0.079)
Used fishing gear: traps (0 no; 1 yes)	0.215**
	(0.095)
Used fishing gear: lines (0 no; 1 yes)	0.279***
	(0.080)
P-value of overidentification test of all instruments	0.361
P-value of Kleibergen-Paap test for underidentification	0.0221
Kleibergen-Paap test statistic for weak identification	157.9
Stock-Yogo weak identification test critical values: 10% maximal IV size	9.08
P-value of GMM distance test statistic of endogeneity	0.408
Observations	2,558
Mean fishing yield	0.818

Note: Two-stage least squares estimates. Robust standard errors clustered at the village level in parentheses. Observations at the fishing trip level, from 408 fishers. 172 outliers of fishing yield excluded from the analysis. Functional richness instrumented using distance to river mouth, distance to river mouth squared, and village downstream of Xe Thamouak as exogenous source of variation. Village controls and constant partialled out. ***, **, * indicates statistical significance at the 1%, 5% and 10% level, respectively.

Table A.6: Impact of biodiversity on fishing yield using generalized method of moments estimator

Outcome:	Fishing yield (kg per hour)
Biodiversity measure	
Average functional richness	0.916***
	(0.238)
Controls	
Overnight fishing (0 no; 1 yes)	-0.318***
	(0.054)
Used fishing gear: nets (0 no; 1 yes)	0.329***
	(0.078)
Used fishing gear: traps (0 no; 1 yes)	0.254***
	(0.090)
Used fishing gear: lines (0 no; 1 yes)	0.266***
	(0.079)
P-value of overidentification test of all instruments	0.361
P-value of Kleibergen-Paap test for underidentification	0.0221
Kleibergen-Paap test statistic for weak identification	157.9
Stock-Yogo weak identification test critical values: 10% maximal IV size	9.08
P-value of GMM distance test statistic of endogeneity	0.408
Observations	2,558
Mean fishing yield	0.818

Note: Generalized method of moments estimates. Robust standard errors clustered at the village level in parentheses. Observations at the fishing trip level, from 408 fishers. 172 outliers of fishing yield excluded from the analysis. Functional richness instrumented using distance to river mouth, distance to river mouth squared, and village downstream of Xe Thamouak as exogenous source of variation. Village controls and constant partialled out. ***, **, * indicates statistical significance at the 1%, 5% and 10% level, respectively.

Table A.7: First-stage and reduced form estimates

Dependent variable:	Average functional richness (1)	Fishing yield (kg per hour) (2)
Exogenous Instruments		
Distance to river mouth (km)	0.0004	0.003
	(0.000)	(0.002)
Distance to river mouth (km) squared	-0.000003*	-.00001*
	(0.000)	(0.000)
Downstream of Xe Thamouak	-0.275***	-0.181
	(0.022)	(0.133)
Controls		
Overnight fishing (0 no; 1 yes)	-0.001	-0.327***
	(0.003)	(0.066)
Used fishing gear: nets (0 no; 1 yes)	-0.006	0.338***
	(0.005)	(0.087)
Used fishing gear: traps (0 no; 1 yes)	-0.010*	0.211**
	(0.005)	(0.099)
Used fishing gear: lines (0 no; 1 yes)	-0.002	0.277***
	(0.004)	(0.087)
No. poor households in village	-0.000	-0.005
	(0.000)	(0.004)
No. food insecure households in village	-0.000	-0.000
	(0.000)	(0.001)
No. fishing-dependent households in village	-0.000	0.001
	(0.000)	(0.001)
Car access during whole year (0 no; 1 yes)	0.007	-0.132
	(0.015)	(0.127)
Rules on gear and/or methods (0 no; 1 yes)	0.004	-0.015
	(0.014)	(0.137)
Paid compliance monitoring (0 no; 1 yes)	-0.000	-0.001
	(0.015)	(0.074)
Constant	0.511***	0.305
	(0.033)	(0.224)
P-value of overidentification test of all instruments	0.361	-
p-value of Kleibergen–Paap test for underidentification	0.0221	-
Kleibergen–Paap Wald F statistic for weak identification	157.9	-
Stock-Yogo weak identification test critical values: 10% maximal LIML size	6.46	-
P-value of GMM distance test statistic of endogeneity	0.408	-
Observations	2,558	2,558
R-squared	0.972	0.106
Outcome mean	0.364	0.818

Note: Robust standard errors clustered at the village level in parentheses. Observations at the fishing trip level, from 408 fishers. 172 outliers of fishing yield were excluded from the analysis. ***, **, * indicates statistical significance at the 1%, 5% and 10% level, respectively.

Table A.8: Impact of biodiversity on fishing yield using only distance to mouth and its squared term as instruments

Outcome:	Fishing yield (kg per hour)
Biodiversity measure	
Average functional richness	0.864**
	(0.371)
Controls	
Overnight fishing (0 no; 1 yes)	-0.334***
	(0.063)
Used fishing gear: nets (0 no; 1 yes)	0.348***
	(0.080)
Used fishing gear: traps (0 no; 1 yes)	0.220**
	(0.093)
Used fishing gear: lines (0 no; 1 yes)	0.283***
	(0.080)
P-value of overidentification test of all instruments	0.185
P-value of Kleibergen-Paap test for underidentification	0.0110
Kleibergen-Paap test statistic for weak identification	27.07
Stock-Yogo weak identification test critical values: 10% maximal IV size	8.68
P-value of GMM distance test statistic of endogeneity	0.964
Observations	2,558
Mean fishing yield	0.818

Note: Limited Information Maximum Likelihood IV estimates. Robust standard errors clustered at the village level in parentheses. Observations at the fishing trip level, from 408 fishers. 172 outliers of fishing yield excluded from the analysis. Functional richness instrumented using distance to river mouth and distance to river mouth squared as exogenous source of variation. Village controls and constant partialled out. ***, **, * indicates statistical significance at the 1%, 5% and 10% level, respectively.

Table A.9: Impact of biodiversity on fishing yield using only downstream of Xe Thamouak as an instrument

Outcome:	Fishing yield (kg per hour)
Biodiversity measure	
Average functional richness	0.778**
	(0.306)
Controls	
Overnight fishing (0 no; 1 yes)	-0.333***
	(0.063)
Used fishing gear: nets (0 no; 1 yes)	0.343***
	(0.079)
Used fishing gear: traps (0 no; 1 yes)	0.213**
	(0.095)
Used fishing gear: lines (0 no; 1 yes)	0.278***
	(0.080)
P-value of Kleibergen-Paap test for underidentification	0.00214
Kleibergen-Paap test statistic for weak identification	235.4
Stock-Yogo weak identification test critical values: 10% maximal IV size	16.38
P-value of GMM distance test statistic of endogeneity	0.426
Observations	2,558
Mean fishing yield	0.818

Note: Limited Information Maximum Likelihood IV estimates. Robust standard errors clustered at the village level in parentheses. Observations at the fishing trip level, from 408 fishers. 172 outliers of fishing yield excluded from the analysis. Functional richness instrumented using village downstream of Xe Thamouak as exogenous source of variation. Village controls and constant partialled out. ***, **, * indicates statistical significance at the 1%, 5% and 10% level, respectively.

Table A.10: Impact of biodiversity on fishing yield

Outcome:	Fishing yield (kg per hour)
Biodiversity measure	
Average functional richness	0.800***
	(0.284)
Controls	
Overnight fishing (0 no; 1 yes)	-0.333***
	(0.063)
Used fishing gear: nets (0 no; 1 yes)	0.344***
	(0.079)
Used fishing gear: traps (0 no; 1 yes)	0.215**
	(0.095)
Used fishing gear: lines (0 no; 1 yes)	0.279***
	(0.080)
Observations	2,558
Mean fishing yield	0.818

Note: Limited Information Maximum Likelihood IV estimates. Robust standard errors clustered at the village level in parentheses. Observations at the fishing trip level, from 408 fishers. 172 outliers of fishing yield excluded from the analysis. Functional richness instrumented using distance to river mouth, distance to river mouth squared, and village downstream of Xe Thamouak as exogenous source of variation. Village controls and constant partialled out. ***, **, * indicates statistical significance at the 1%, 5% and 10% level, respectively. See Table A.7 for IV test statistics.

Table A.11: Description and measures of ecological attributes and vulnerabilities

Term	Description	Measure
IUCN Red List Status	Current extinction risk of species.	Expert assessment of extinction risk using standardized criteria, including population size and trend, geographic distribution and known threats. Categories include data deficient, least concern, near threatened, vulnerable, endangered, critically endangered, extinct in the wild, extinct and not evaluated (IUCN, 2024).
Resilience through reproduction	Level of resilience against external threats through reproduction.	Measured by population doubling time and categorized as very low, low, medium or high (Froese et al., 2017). Values from FishBase (2024)
Trophic level	Position species occupies in the food web.	Trophic level determined as 1 + trophic level of food items weighted by the contribution to diet (Pauly and Christensen, 1998). Values from FishBase (2024)

Appendix B: Measuring the productive value of biodiversity using SR

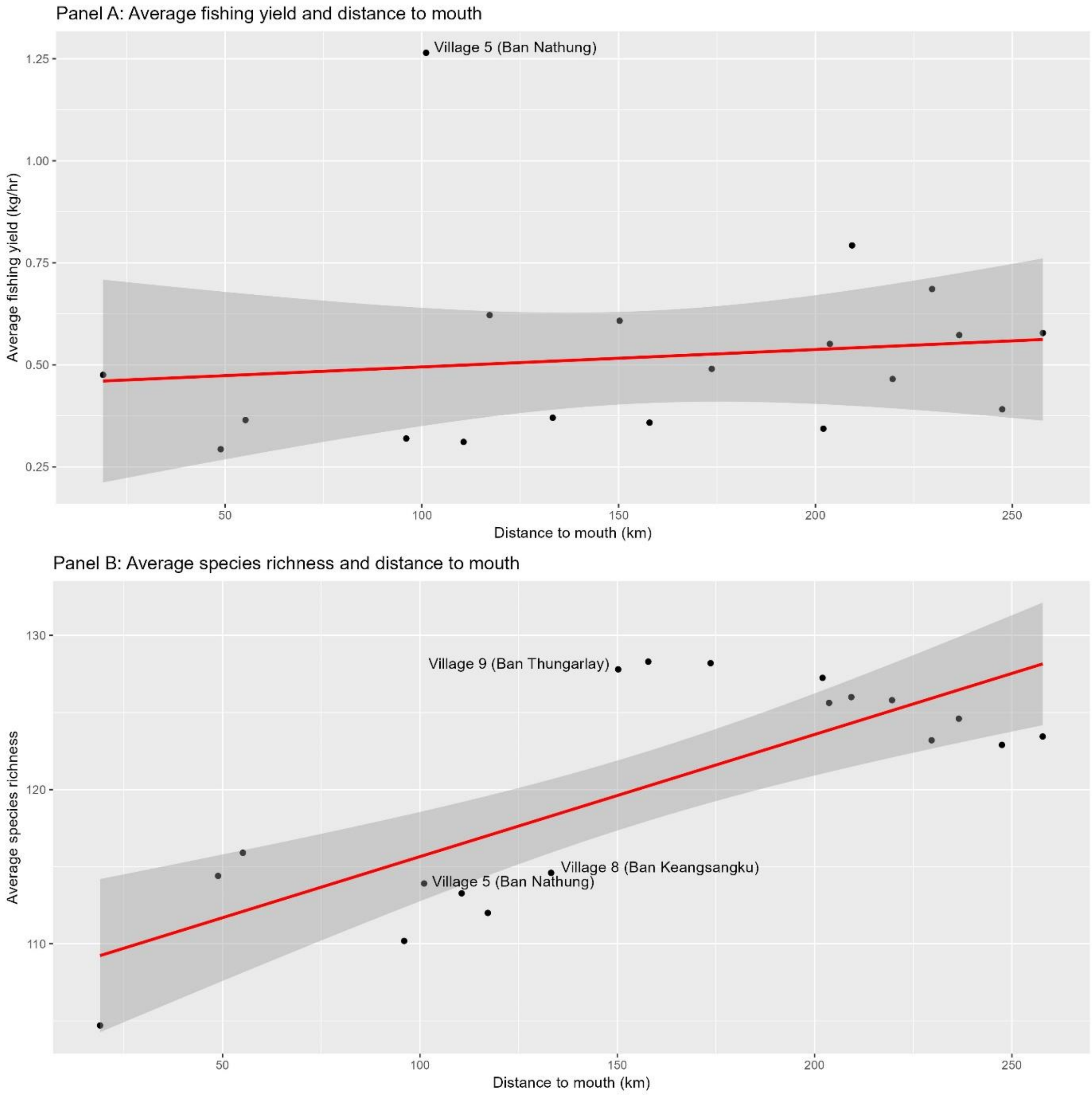

Fig. B.1. Relationship between distance to mouth and average fishing yield (Panel A), as well as the relationship between distance to mouth and SR (Panel B). The red line and shaded area represent the linear prediction and 95% confidence interval, respectively.

Table B.2: Relationship between biodiversity and fishing yield

Outcome:	Fishing yield (kg per hour)
Biodiversity measure	
Average species richness	0.015***
	(0.004)
Controls	
Overnight fishing (0 no; 1 yes)	-0.334***
	(0.067)
Used fishing gear: nets (0 no; 1 yes)	0.344***
	(0.085)
Used fishing gear: traps (0 no; 1 yes)	0.223**
	(0.095)
Used fishing gear: lines (0 no; 1 yes)	0.276***
	(0.087)
No. poor households in village	-0.007*
	(0.004)
No. food insecure households in village	0.000
	(0.001)
No. fishing-dependent households in village	0.001
	(0.001)
Car access during whole year (0 no; 1 yes)	-0.154
	(0.114)
Rules on gear and/or methods (0 no; 1 yes)	0.047
	(0.139)
Paid compliance monitoring (0 no; 1 yes)	-0.033
	(0.083)
Constant	-1.442**
	(0.583)
Observations	2,558
R-squared	0.108
Mean fishing yield	0.818

Note: OLS estimates. Robust standard errors clustered at the village level in parentheses. Observations at the fishing trip level, from 408 fishers. 172 outliers of fishing yield were excluded from the analysis. ***, **, * indicates statistical significance at the 1%, 5% and 10% level, respectively.

Table B.3: First-stage and reduced form estimates

Dependent variable:	Average species richness (1)	Fishing yield (kg per hour) (2)
Exogenous Instruments		
Distance to river mouth (km)	0.104***	0.003
	(0.031)	(0.002)
Distance to river mouth (km) squared	-0.0004***	-.00001*
	(0.000)	(0.000)
Downstream of Xe Thamouak	-12.939***	-0.181
	(1.145)	(0.133)
Controls		
Overnight fishing (0 no; 1 yes)	0.117	-0.327***
	(0.159)	(0.066)
Used fishing gear: nets (0 no; 1 yes)	-0.068	0.338***
	(0.250)	(0.087)
Used fishing gear: traps (0 no; 1 yes)	-0.681*	0.211**
	(0.364)	(0.099)
Used fishing gear: lines (0 no; 1 yes)	0.360	0.277***
	(0.272)	(0.087)
No. poor households in village	0.046*	-0.005
	(0.024)	(0.004)
No. food insecure households in village	-0.018	-0.000
	(0.012)	(0.001)
No. fishing-dependent households in village	-0.020**	0.001
	(0.009)	(0.001)
Car access during whole year (0 no; 1 yes)	2.020*	-0.132
	(0.969)	(0.127)
Rules on gear and/or methods (0 no; 1 yes)	-1.938	-0.015
	(1.220)	(0.137)
Paid compliance monitoring (0 no; 1 yes)	1.661	-0.001
	(0.968)	(0.074)
Constant	119.312***	0.305
	(2.880)	(0.224)
P-value of overidentification test of all instruments	0.748	-
p-value of Kleibergen–Paap test for underidentification	0.0218	-
Kleibergen–Paap Wald F statistic for weak identification	93.89	-
Stock-Yogo weak identification test critical values: 10% maximal LIML size	9.08	-
P-value of GMM distance test statistic of endogeneity	0.780	-
Observations	2,558	2,558
R-squared	0.960	0.106
Outcome mean	119.8	0.818

Note: Robust standard errors clustered at the village level in parentheses. Observations at the fishing trip level, from 408 fishers. 172 outliers of fishing yield were excluded from the analysis. ***, **, * indicates statistical significance at the 1%, 5% and 10% level, respectively.

Table B.4: Impact of biodiversity on fishing yield

Outcome:	Fishing yield (kg per hour)
Biodiversity measure	
Average species richness	0.015***
	(0.005)
Controls	
Overnight fishing (0 no; 1 yes)	-0.333***
	(0.065)
Used fishing gear: nets (0 no; 1 yes)	0.343***
	(0.082)
Used fishing gear: traps (0 no; 1 yes)	0.221**
	(0.093)
Used fishing gear: lines (0 no; 1 yes)	0.275***
	(0.083)
Observations	2,558
Mean fishing yield	0.818

Note: Limited Information Maximum Likelihood IV estimates. Robust standard errors clustered at the village level in parentheses. Observations at the fishing trip level, from 408 fishers. 172 outliers of fishing yield were excluded from the analysis. Species richness instrumented using distance to river mouth, distance to river mouth squared, and village downstream of Xe Thamouak as exogenous source of variation. Village controls and constant partialled out. ***, **, * indicates statistical significance at the 1%, 5% and 10% level, respectively. See Table A.3 for IV test statistics.

Table B.5: Impact of biodiversity on fishing yield using two-stage least squares estimator

Outcome:	Fishing yield (kg per hour)
Biodiversity measure	
Average species richness	0.015***
	(0.005)
Controls	
Overnight fishing (0 no; 1 yes)	-0.333***
	(0.065)
Used fishing gear: nets (0 no; 1 yes)	0.343***
	(0.082)
Used fishing gear: traps (0 no; 1 yes)	0.221**
	(0.093)
Used fishing gear: lines (0 no; 1 yes)	0.275***
	(0.083)
P-value of overidentification test of all instruments	0.748
P-value of Kleibergen-Paap test for underidentification	0.0218
Kleibergen-Paap test statistic for weak identification	93.89
Stock-Yogo weak identification test critical values: 10% maximal IV size	9.08
P-value of GMM distance test statistic of endogeneity	0.780
Observations	2,558
Mean fishing yield	0.818

Note: Two-stage least squares estimates. Robust standard errors clustered at the village level in parentheses. Observations at the fishing trip level, from 408 fishers. 172 outliers of fishing yield were excluded from the analysis. Species richness instrumented using distance to river mouth, distance to river mouth squared, and village downstream of Xe Thamouak as exogenous source of variation. Village controls and constant partialled out. ***, **, * indicates statistical significance at the 1%, 5% and 10% level, respectively.

Table B.6: Impact of biodiversity on fishing yield using generalized method of moments estimator

Outcome:	Fishing yield (kg per hour)
Biodiversity measure	
Average species richness	0.017***
	(0.004)
Controls	
Overnight fishing (0 no; 1 yes)	-0.313***
	(0.056)
Used fishing gear: nets (0 no; 1 yes)	0.328***
	(0.080)
Used fishing gear: traps (0 no; 1 yes)	0.233***
	(0.088)
Used fishing gear: lines (0 no; 1 yes)	0.261***
	(0.080)
P-value of overidentification test of all instruments	0.748
P-value of Kleibergen-Paap test for underidentification	0.0218
Kleibergen-Paap test statistic for weak identification	93.89
Stock-Yogo weak identification test critical values: 10% maximal IV size	9.08
P-value of GMM distance test statistic of endogeneity	0.780
Observations	2,558
Mean fishing yield	0.818

Note: Generalized method of moments estimates. Robust standard errors clustered at the village level in parentheses. Observations at the fishing trip level, from 408 fishers. 172 outliers of fishing yield were excluded from the analysis. Species richness instrumented using distance to river mouth, distance to river mouth squared, and village downstream of Xe Thamouak as exogenous source of variation. Village controls and constant partialled out. ***, **, * indicates statistical significance at the 1%, 5% and 10% level, respectively.

Table B.7: Impact of biodiversity on fishing yield using only distance to mouth and its squared term as instruments

Outcome:	Fishing yield (kg per hour)
Biodiversity measure	
Average species richness	0.015***
	(0.005)
Controls	
Overnight fishing (0 no; 1 yes)	-0.333***
	(0.064)
Used fishing gear: nets (0 no; 1 yes)	0.343***
	(0.083)
Used fishing gear: traps (0 no; 1 yes)	0.222**
	(0.090)
Used fishing gear: lines (0 no; 1 yes)	0.275***
	(0.083)
P-value of overidentification test of all instruments	0.453
P-value of Kleibergen-Paap test for underidentification	0.0108
Kleibergen-Paap test statistic for weak identification	28.93
Stock-Yogo weak identification test critical values: 10% maximal IV size	8.68
P-value of GMM distance test statistic of endogeneity	0.943
Observations	2,558
Mean fishing yield	0.818

Note: Limited Information Maximum Likelihood IV estimates. Robust standard errors clustered at the village level in parentheses. Observations at the fishing trip level, from 408 fishers. 172 outliers of fishing yield were excluded from the analysis. Species richness instrumented using distance to river mouth and distance to river mouth squared as exogenous source of variation. Village controls and constant partialled out. ***, **, * indicates statistical significance at the 1%, 5% and 10% level, respectively.

Table B.8: Impact of biodiversity on fishing yield using only downstream of Xe Thamouak as an instrument

Outcome:	Fishing yield (kg per hour)
Biodiversity measure	
Average species richness	0.014**
	(0.005)
Controls	
Overnight fishing (0 no; 1 yes)	-0.332***
	(0.064)
Used fishing gear: nets (0 no; 1 yes)	0.340***
	(0.081)
Used fishing gear: traps (0 no; 1 yes)	0.216**
	(0.094)
Used fishing gear: lines (0 no; 1 yes)	0.272***
	(0.082)
P-value of Kleibergen-Paap test for underidentification	0.00214
Kleibergen-Paap test statistic for weak identification	138.4
Stock-Yogo weak identification test critical values: 10% maximal IV size	16.38
P-value of GMM distance test statistic of endogeneity	0.538
Observations	2,558
Mean fishing yield	0.818

Note: Limited Information Maximum Likelihood IV estimates. Robust standard errors clustered at the village level in parentheses. Observations at the fishing trip level, from 408 fishers. 172 outliers of fishing yield were excluded from the analysis. Species richness instrumented using village downstream of Xe Thamouak as exogenous source of variation. Village controls and constant partialled out. ***, **, * indicates statistical significance at the 1%, 5% and 10% level, respectively.

Appendix C: Measuring the productive value of biodiversity excluding Village 5

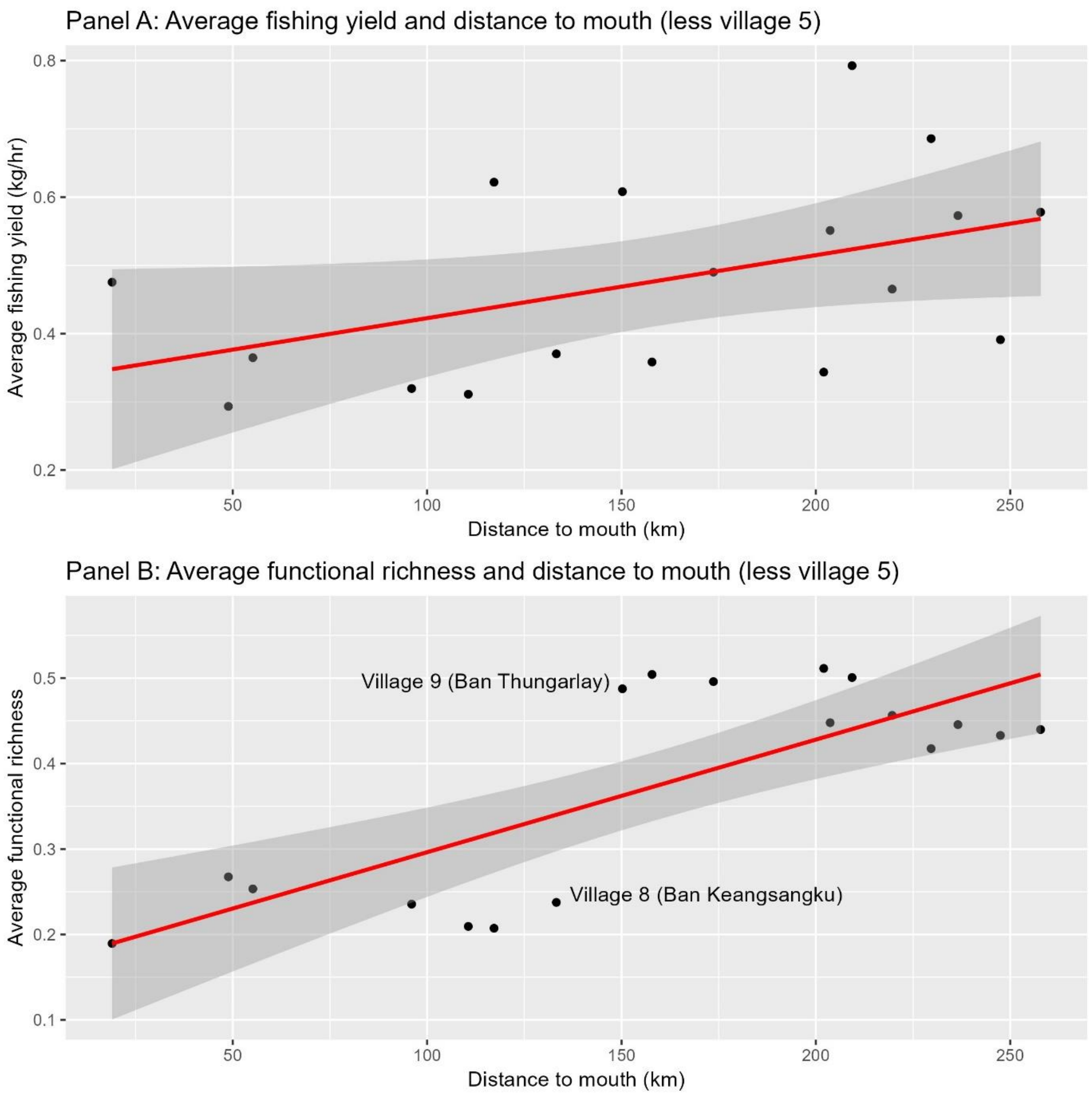

Fig. C.1. Relationship between distance to mouth and average fishing yield (Panel A), as well as the relationship between distance to mouth and FR (Panel B) when excluding village 5. The red line and shaded area represent the linear prediction and 95% confidence interval, respectively.

Table C.2: Relationship between biodiversity and fishing yield

Outcome:	Fishing yield (kg per hour)
Biodiversity measure	
Average functional richness	0.869***
	(0.161)
Controls	
Overnight fishing (0 no; 1 yes)	-0.287***
	(0.052)
Used fishing gear: nets (0 no; 1 yes)	0.315***
	(0.087)
Used fishing gear: traps (0 no; 1 yes)	0.200*
	(0.099)
Used fishing gear: lines (0 no; 1 yes)	0.231**
	(0.087)
No. poor households in village	-0.003
	(0.002)
No. food insecure households in village	0.000
	(0.001)
No. fishing-dependent households in village	0.001
	(0.001)
Car access during whole year (0 no; 1 yes)	-0.028
	(0.045)
Rules on gear and/or methods (0 no; 1 yes)	-0.103*
	(0.052)
Paid compliance monitoring (0 no; 1 yes)	0.057
	(0.049)
Constant	-0.032
	(0.126)
Observations	2,445
R-squared	0.108
Mean fishing yield	0.818

Note: OLS estimates. Robust standard errors clustered at the village level in parentheses. Observations at the fishing trip level, from 401 fishers. 172 outliers of fishing yield and a further 113 outliers from Ban Nathung were excluded from the analysis. ***, **, * indicates statistical significance at the 1%, 5% and 10% level, respectively.

Table C.3: First-stage and reduced form estimates

Dependent variable:	Average functional richness (1)	Fishing yield (kg per hour) (2)
Exogenous Instruments		
Distance to river mouth (km)	.0004	0.003*
	(0.000)	(0.001)
Distance to river mouth (km) squared	−0.000002*	−0.000008
	(0.000)	(0.000)
Downstream of Xe Thamouak	-0.275***	-0.184*
	(0.022)	(0.092)
Controls		
Overnight fishing (0 no; 1 yes)	0.000	-0.281***
	(0.002)	(0.054)
Used fishing gear: nets (0 no; 1 yes)	-0.008	0.313***
	(0.005)	(0.090)
Used fishing gear: traps (0 no; 1 yes)	-0.011*	0.198*
	(0.005)	(0.100)
Used fishing gear: lines (0 no; 1 yes)	-0.004	0.231**
	(0.004)	(0.090)
No. poor households in village	0.000	-0.003
	(0.000)	(0.002)
No. food insecure households in village	-0.000	-0.000
	(0.000)	(0.001)
No. fishing-dependent households in village	-0.000	0.001
	(0.000)	(0.001)
Car access during whole year (0 no; 1 yes)	0.013	-0.009
	(0.015)	(0.051)
Rules on gear and/or methods (0 no; 1 yes)	-0.002	-0.146***
	(0.013)	(0.044)
Paid compliance monitoring (0 no; 1 yes)	0.003	0.063
	(0.015)	(0.041)
Constant	0.507***	0.216
	(0.035)	(0.159)
P-value of overidentification test of all instruments	0.245	-
p-value of Kleibergen–Paap test for underidentification	0.0206	-
Kleibergen–Paap Wald F statistic for weak identification	153	-
Stock-Yogo weak identification test critical values: 10% maximal LIML size	9.08	-
P-value of GMM distance test statistic of endogeneity	0.261	-
Observations	2,445	2,445
R-squared	0.977	0.113
Outcome mean	0.364	0.818

Note: Robust standard errors clustered at the village level in parentheses. Observations at the fishing trip level, from 401 fishers. 172 outliers of fishing yield and a further 113 outliers from Ban Nathung were excluded from the analysis. ***, **, * indicates statistical significance at the 1%, 5% and 10% level, respectively.

Table C.4: Impact of biodiversity on fishing yield

Outcome:	Fishing yield (kg per hour)
Biodiversity measure	
Average functional richness	0.942***
	(0.161)
Controls	
Overnight fishing (0 no; 1 yes)	-0.288***
	(0.051)
Used fishing gear: nets (0 no; 1 yes)	0.319***
	(0.084)
Used fishing gear: traps (0 no; 1 yes)	0.206**
	(0.096)
Used fishing gear: lines (0 no; 1 yes)	0.235***
	(0.084)
Observations	2,445
Mean fishing yield	0.818

Note: Limited Information Maximum Likelihood IV estimates. Robust standard errors clustered at the village level in parentheses. Observations at the fishing trip level, from 401 fishers. 172 outliers of fishing yield and a further 113 outliers from Ban Nathung were excluded from the analysis. Functional richness instrumented using distance to river mouth, distance to river mouth squared, and village downstream of Xe Thamouak as exogenous source of variation. Village controls and constant partialled out. ***, **, * indicates statistical significance at the 1%, 5% and 10% level, respectively. See Table B.3 for IV test statistics.

Table C.5: Impact of biodiversity on fishing yield using two-stage least squares estimator

Outcome:	Fishing yield (kg per hour)
Biodiversity measure	
Average functional richness	0.942***
	(0.161)
Controls	
Overnight fishing (0 no; 1 yes)	-0.288***
	(0.051)
Used fishing gear: nets (0 no; 1 yes)	0.319***
	(0.084)
Used fishing gear: traps (0 no; 1 yes)	0.206**
	(0.096)
Used fishing gear: lines (0 no; 1 yes)	0.235***
	(0.084)
P-value of overidentification test of all instruments	0.245
P-value of Kleibergen-Paap test for underidentification	0.0206
Kleibergen-Paap test statistic for weak identification	153
Stock-Yogo weak identification test critical values: 10% maximal IV size	9.08
P-value of GMM distance test statistic of endogeneity	0.261
Observations	2,445
Mean fishing yield	0.818

Note: Two-stage least squares estimates. Robust standard errors clustered at the village level in parentheses. Observations at the fishing trip level, from 401 fishers. 172 outliers of fishing yield and a further 113 outliers from Ban Nathung were excluded from the analysis. Biodiversity measures are instrumented using distance to river mouth, distance to river mouth squared, and village downstream of Xe Thamouak as exogenous source of variation. Village controls and constant partialled out. ***, **, * indicates statistical significance at the 1%, 5% and 10% level, respectively.

Table C.6: Impact of biodiversity on fishing yield using generalized method of moments estimator

Outcome:	Fishing yield (kg per hour)
Biodiversity measure	
Average functional richness	0.869***
	(0.148)
Controls	
Overnight fishing (0 no; 1 yes)	-0.304***
	(0.047)
Used fishing gear: nets (0 no; 1 yes)	0.285***
	(0.081)
Used fishing gear: traps (0 no; 1 yes)	0.216**
	(0.095)
Used fishing gear: lines (0 no; 1 yes)	0.210**
	(0.082)
P-value of overidentification test of all instruments	0.245
P-value of Kleibergen-Paap test for underidentification	0.0206
Kleibergen-Paap test statistic for weak identification	153
Stock-Yogo weak identification test critical values: 10% maximal IV size	9.08
P-value of GMM distance test statistic of endogeneity	0.261
Observations	2,445
Mean fishing yield	0.818

Note: Generalized method of moments estimates. Robust standard errors clustered at the village level in parentheses. Observations at the fishing trip level, from 401 fishers. 172 outliers of fishing yield and a further 113 outliers from Ban Nathung were excluded from the analysis. Biodiversity measures are instrumented using distance to river mouth, distance to river mouth squared, and village downstream of Xe Thamouak as exogenous source of variation. Village controls and constant partialled out. ***, **, * indicates statistical significance at the 1%, 5% and 10% level, respectively.

Table C.7: Impact of biodiversity on fishing yield using only distance to mouth and its squared term as instruments

Outcome:	Fishing yield (kg per hour)
Biodiversity measure	
Average functional richness	1.065***
	(0.236)
Controls	
Overnight fishing (0 no; 1 yes)	-0.290***
	(0.050)
Used fishing gear: nets (0 no; 1 yes)	0.326***
	(0.084)
Used fishing gear: traps (0 no; 1 yes)	0.216**
	(0.096)
Used fishing gear: lines (0 no; 1 yes)	0.241***
	(0.084)
P-value of overidentification test of all instruments	0.223
P-value of Kleibergen-Paap test for underidentification	0.0102
Kleibergen-Paap test statistic for weak identification	27.02
Stock-Yogo weak identification test critical values: 10% maximal IV size	8.68
P-value of GMM distance test statistic of endogeneity	0.197
Observations	2,445
Mean fishing yield	0.081

Note: Limited Information Maximum Likelihood IV estimates. Robust standard errors clustered at the village level in parentheses. Observations at the fishing trip level, from 401 fishers. 172 outliers of fishing yield and a further 113 outliers from Ban Nathung were excluded from the analysis. Functional richness instrumented using distance to river mouth and distance to river mouth squared as exogenous source of variation. Village controls and constant partialled out. ***, **, * indicates statistical significance at the 1%, 5% and 10% level, respectively.

Table C.8: Impact of biodiversity on fishing yield using only downstream of Xe Thamouak as an instrument

Outcome:	Fishing yield (kg per hour)
Biodiversity measure	
Average functional richness	0.938***
	(0.172)
Controls	
Overnight fishing (0 no; 1 yes)	-0.288***
	(0.051)
Used fishing gear: nets (0 no; 1 yes)	0.319***
	(0.084)
Used fishing gear: traps (0 no; 1 yes)	0.206**
	(0.096)
Used fishing gear: lines (0 no; 1 yes)	0.235***
	(0.084)
P-value of Kleibergen-Paap test for underidentification	0.00199
Kleibergen-Paap test statistic for weak identification	228.6
Stock-Yogo weak identification test critical values: 10% maximal IV size	16.38
P-value of GMM distance test statistic of endogeneity	0.179
Observations	2,445
Mean fishing yield	0.082

Note: Limited Information Maximum Likelihood IV estimates. Robust standard errors clustered at the village level in parentheses. Observations at the fishing trip level, from 401 fishers. 172 outliers of fishing yield and a further 113 outliers from Ban Nathung were excluded from the analysis. Functional richness instrumented using village downstream of Xe Thamouak as exogenous source of variation. Village controls and constant partialled out. ***, **, * indicates statistical significance at the 1%, 5% and 10% level, respectively.