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RESEARCH ARTICLE

Local knowledge enhances the sustainability of interconnected fisheries

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Abstract

1. Local knowledge (LK) refers to the ancestral understanding that Indigenous Peoples and local communities have developed over centuries through trial-and-error and hands-on management of natural resources. LK may provide valuable insights for biodiversity conservation and human well-being. However, its effectiveness remains under-explored at large scales, especially where multiple communities manage ecosystems. One example is fisheries, which form complex, interconnected networks where fish move across spatial boundaries between managed areas. Fisheries are critical for food security and income, yet face threats from overharvesting. Fisheries Co-Management (FCM)—a partnership between local communities and governments—leverages LK. However, the value of LK in designing protection strategies remains unclear.

2. Using a process-based dynamical model parameterized with empirical data, we evaluated FCM strategies for pirarucu (*Arapaima gigas*) fisheries, which form a metapopulation network of protected and unprotected lakes in the Brazilian Amazon. We combined our metapopulation model with LK, fish biology and network theory to assess how lake protection, fishing quotas and illegal fishing impact pirarucu population abundance at the riverscape scale.

3. By analysing 13 FCM-protected lakes and 18 unprotected lakes, we contrasted six hypothesis-driven management strategies against the current one, which is based on LK. In all strategies, protected lakes support higher pirarucu populations and buffer against increased fishing pressure, while unprotected lakes face population collapse due to the lack of fishing regulations. While a strategy that provides the best outcomes in terms of metapopulation persistence was based on pirarucu carrying capacity, the currently applied FCM strategy closely matched its efficacy.

4. *Synthesis and applications*. Our modelling approach allows managers to compare alternative conservation strategies under different socio-ecological scenarios, highlighting trade-offs and guiding investment of effort and resources. While immediately valuable for pirarucu management in the Middle Juruá, the framework scales across tiers of applicability, each requiring progressively greater model adaptation: from supporting FCM in other Amazonian regions (with minimal adjustment), to adaptation for other riverine fisheries and ultimately to broader socio-ecological systems. In this way, we provide both system-specific insights and a flexible tool for advancing sustainable management of natural resources across contexts.

1 | INTRODUCTION

Emerging conservation paradigms increasingly highlight the potential role of local communities in preserving ecosystem services through the protection and management of natural resources (Díaz et al., 2018; Levis et al., 2024; Naeem et al., 2016; Wood et al., 2018). Integrating local knowledge (hereafter, LK) into conservation enhances environmental governance, supports local development, promotes social justice and ensures biodiversity protection (Campos-Silva et al., 2021; Freitas et al., 2020). In the context of this study, LK is defined as the ancestral knowledge that Indigenous Peoples and local communities have gathered over centuries, and possibly over many trial-and-error methods and experimentations, regarding the use of natural resources and territorial management. Recent findings have revealed a long history of human coexistence with biodiversity across different biomes, demonstrating that sustainable interactions between people and nature have occurred under certain social and ecological conditions (Fletcher et al., 2021; Levis et al., 2024). This is particularly remarkable in Amazonia, where long-standing human–nature interactions have shaped complex socio-ecological systems where natural resource management is essential for maintaining biodiversity and ecosystem services (Levis et al., 2018). Nevertheless, limited evidence exists on whether combining LK with governmental regulations is effective when conservation strategies are upscaled to a regional level.

Fisheries have historically provided essential ecosystem services for various human cultures (Arantes et al., 2022; Freitas et al., 2020; Lopes et al., 2021). However, they are increasingly threatened by a range of stressors, including overexploitation of natural resources, market fluctuations and climate change (Andrew et al., 2007). Avoiding overexploitation and mitigating the challenges imposed on natural ecosystems by unsustainable practices need balancing multiple factors, including fish biology and ecology, management of fishing pressure and governmental regulations. Strategies to address these challenges typically fall into two broad categories. Top-down regulations enforce conservation through protected areas and exploitation quotas (Arantes et al., 2022; Campos-Silva et al., 2021), while participatory initiatives such as collaborative management integrate local communities into the decision-making process (Berkes, 2009; Freitas et al., 2020).

Understanding the impact of management decisions on ecosystem service provision is challenging due to the intricate interplay within and between ecological and human social systems (Felipe-Lucia et al., 2020; Preiser et al., 2018). Recent research on small-scale fishing emphasizes the importance of integrating ecological and social dimensions to promote sustainable practices (Cochrane et al., 2011; Reis-Filho et al., 2023). In that sense, Fisheries Co-Management (hereafter, FCM) strategies, in which local people and governmental entities cooperate, are particularly effective. Incorporating LK within FCM empowers local communities while enhancing compliance with top-down regulation and environmental justice (Jentoft et al., 2017; Lopes et al., 2021). Adopting a networked system perspective in which entities (ecological, social or both) interact is ideal to address dependencies and feedback loops typical of social-ecological systems (Biggs et al., 2021; Brodie et al., 2025; Keyes et al., 2021). However, we still lack comprehensive large-scale network studies that directly contrast LK with alternative management schemes using empirical data on ecological dynamics and spatial connectivity, making it difficult to quantify the impact of management decisions imposed at the regional level (but see Allen et al., 2022; Dee et al., 2017; Felipe-Lucia et al., 2020; Keyes et al., 2021; Windsor et al., 2022).

Here, we explore the FCM conservation programme of pirarucu (*Arapaima gigas* (Schinz, 1822)) from the Western Brazilian Amazon. Pirarucu is the world's largest freshwater fish, is protected against overfishing (CITES, 2024; Instituto Brasileiro do Meio Ambiente (IBAMA), 2004, 2005) and constitutes a major income for many local communities (Campos-Silva et al., 2018; Campos-Silva & Peres, 2016). Its floodplain ecosystem is characterized by seasonal flooding during which pirarucu moves along the main river

and among areas that remain isolated during the dry season, creating a metapopulation network of interconnected oxbow lakes with seasonal dynamics. LK from Indigenous and traditional fishing communities was pivotal to developing the current method used to count pirarucu individuals, based on their breathing behaviour (Castello, 2004). Such LK is the core of the current FCM strategy that protects several lakes from illegal fishing while allowing sustainable landings every year. This community-based strategy has been instrumental to the recovery of the historically overfished pirarucu (Campos-Silva, 2019; Castello et al., 2015) and is recognized as one of the most promising grassroots initiatives to tackle conservation, food security and poverty challenges across Amazonia (Campos-Silva et al., 2018; Lopes et al., 2021).

However, lake protection is costly and time-consuming for fishing communities, and it remains unclear what are the social, economic and ecological attributes that make this system successful. It is also unclear whether the current FCM strategy is optimal. The current strategy protects lakes on an *ad hoc* basis, guided by LK—that is, the historical designation of lakes to be protected based on fishers' perceptions of pirarucu abundance and accessibility for fishing and transport. To address this gap, we developed a process-based dynamical model (Cuddington et al., 2013) parameterized with empirical FCM data to evaluate the effects of alternative small-scale fishing protection strategies on the persistence of a pirarucu metapopulation formed by a network of interconnected lakes in the Juruá River Basin, Western Brazilian Amazon (Figure 1).

We compare the current FCM strategy with six other protection scenarios based on network topology, lake characteristics, geography and randomness (Table 1). Across scenarios, lakes (i.e. local patches in the metapopulation) are either protected or unprotected by FCM, and are managed according to governmental top-down regulatory policies that set fishing quotas. We show that the current LK-based FCM strategy, despite its high efficiency, could still be improved by prioritizing lake protection based on piraruru populations'
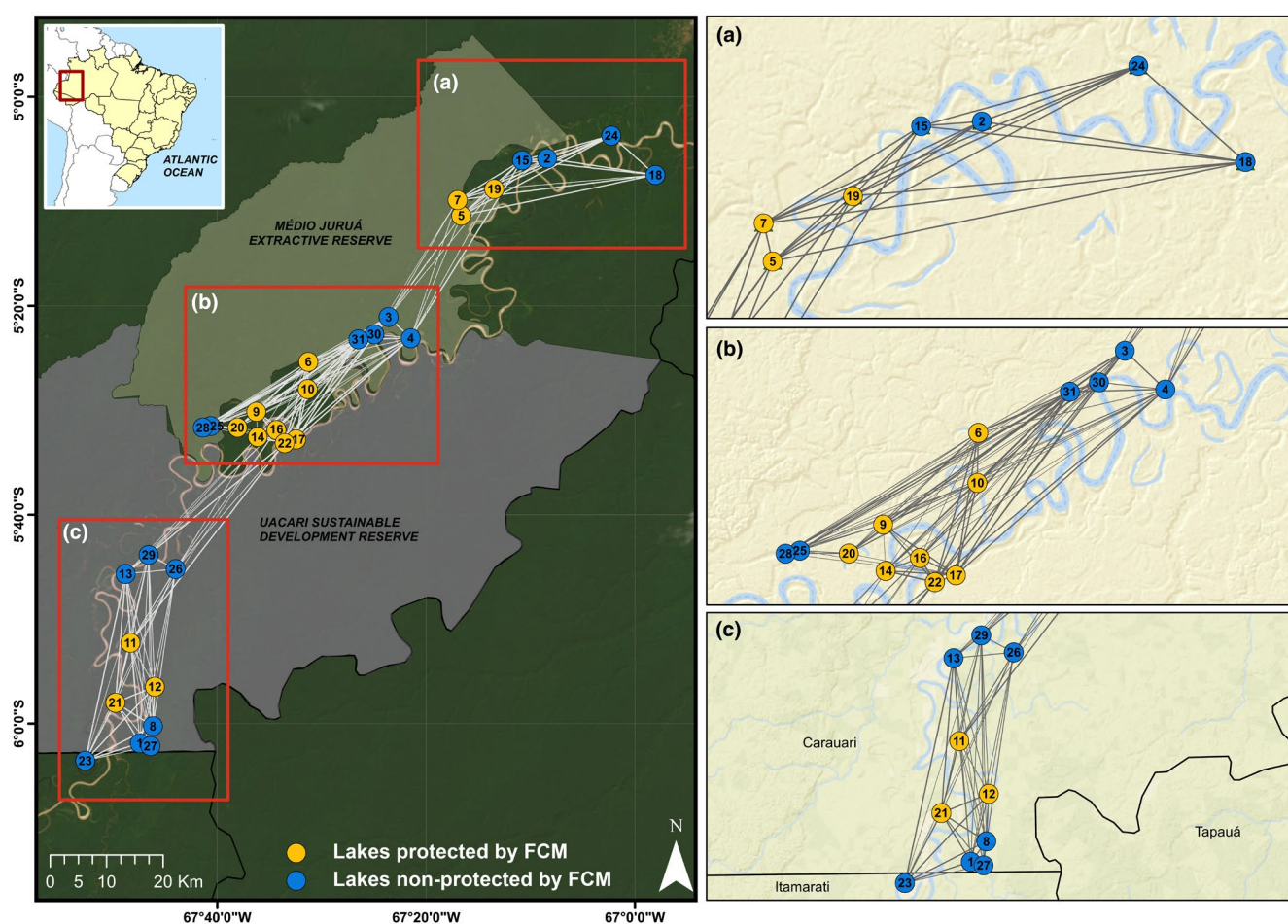
FIGURE 1 Study area and the metapopulation network of the pirarucu (*Arapaima gigas*) at the Middle Juruá River Basin, Western Brazilian Amazon. Each lake is a node in the network and is represented by a number; the list of lakes and their attributes can be found in Table S1. The position of each lake represents its latitude/longitude coordinates along the Juruá River. Links between nodes indicate whether two lakes are spatially connected by pirarucu movement during the flooding season. Network construction is described in the Methods. Panels (a–c) zoom in on the study area's north, central and south regions, respectively, showing detailed connections among protected (yellow nodes) and unprotected lakes (blue nodes) performed by pirarucu movement. The links are drawn as straight lines for clarity, but were calculated based on the length of the curved river courses (see Section 2.3 in Methods). We used ArcGIS and Arcmap 10.825 to draw the map layout.

TABLE 1 Description of the management scenarios used to assess the potential consequences of increasing fishing pressure on the abundance and persistence of pirarucu (*Arapaima gigas*) at the Middle Juruá River Basin, Western Brazilian Amazon.

Protection scenario	Management strategy	Rationale
1. Business-as-usual (BAU)	Keep the same 13 protected lakes as the current empirical protection strategy while increasing fishing effort for unprotected lakes to simulated increasing illegal fishing	H1: Current FCM strategy, built upon local knowledge to define which lakes to protect based on the counted number of pirarucu per lake, lake size and the distance to the main river, is optimal. However, increasing illegal fishing quotas would lead to system collapse, which is faster in unprotected lakes (Cavole et al., 2015)
2. Protect the most connected lakes (MC)	Protect the 13 lakes with the highest strength (sum of dispersal link weights) (Barrat et al., 2004), given the empirical metapopulation network	H2: The most connected lakes serve as a 'source' of pirarucu for the metapopulation dynamics at the riverscape scale (Dee et al., 2017; Keyes et al., 2021). Therefore, their protection would increase the abundance of pirarucu at the metapopulation level
3. Protect the least connected lakes (LC)	Protect the 13 lakes with the lowest strength (sum of dispersal link weights) (Barrat et al., 2004), given the empirical metapopulation network	H3: Because pirarucu tend to return to protected lakes (Gurdak et al., 2022; Campos-Silva et al., 2019), protecting the less connected lakes would facilitate its establishment in more isolated areas of the network, improving riverscape connectivity, facilitating migration and conserving higher risk populations
4. Protect larger lakes (area)	Protect the 13 lakes with the largest area (ha)	H4: Larger lakes can sustain larger populations of pirarucu as their niche space is greater in terms of food resources and reproductive sites (Gilarranz et al., 2017, Richard et al., 2018). Therefore, larger lakes can serve as a 'source' of pirarucu in the metapopulation dynamics
5. Protect lakes with higher carrying capacity (K)	Protect the 13 lakes with the highest carrying capacity	H5: Lakes with higher carrying capacity would function as a source of pirarucu fish, which then can disperse to safe sites and maintain overall positive growth rate (Castello, 2008)
6. Protect lakes according to their geographic position (geography)	Protect the six northernmost and the seven southernmost lakes because these are more vulnerable to illegal fishing coming from outside Protected Areas	H6: Protecting lakes farther from protected areas would help maintain population abundance and increase metapopulation connectivity by lowering illegal fishing (Campos-Silva, 2019) and buffering against external pressures
7. Protect lakes randomly (random)	Randomly select 13 lakes to protect	H7: Protecting lakes with no biotic or abiotic criteria would lead to local population collapses and lowest metapopulation persistence

Note: We compare the current FCM strategy (business-as-usual) to five hypothesis-driven alternative management scenarios and to a random protection scenario. Note that in each scenario, we fixed the number of protected lakes to 13, matching the current FCM configuration to allow a fair comparison of alternative protection strategies under the same overall level of protection effort. See Table S2 for the list of protected lakes in each scenario.

carrying capacity. Our results demonstrate that management strategies of a networked fisheries system guided by LK can outperform other approaches, highlighting the importance of incorporating LK into conservation for a sustainable future.

2 | METHODS

2.1 | Study system

We studied 31 oxbow lakes along the Juruá River Basin, Western Brazilian Amazon, harbouring a set of 13 local fisheries that rely on the sustainable harvest of pirarucu for subsistence and income (Figure 1, Table S1). Lakes and fishing communities are part of both: (i) territorial management, which includes two protected areas (PA; Uacari Sustainable Development Reserve and Médio Juruá Extractivism Reserve); (ii) a FCM strategy, which includes agreements

among local communities, regional associations and the federal government aiming to guarantee the pirarucu fishing sustainability. Lakes within PAs are protected by law; therefore one could assume illegal fishing to be absent. However, it is clear from LK that PAs are not enough to guarantee pirarucu conservation in the region. In turn, the current FCM strategy at Juruá River works equally well for lakes within and outside PAs (Campos-Silva et al., 2021; Campos-Silva & Peres, 2016). Within this FCM strategy, local communities are legally empowered to protect their fishing grounds (most oxbow lakes) against large-scale commercial and illegal fishing. During the dry season, oxbow lakes are discrete units in the riverscape that can be monopolized by one or a few fishing communities.

Fishing quotas for each community are granted according to the pirarucu population size in each managed lake, which has been monitored for at least three consecutive years before entering the FCM strategy. Fishing quotas are granted by the federal governmental agency (Instituto Brasileiro do Meio Ambiente (IBAMA)) in

accordance with fishing communities and local associations, and can vary over time. The legal fishing quota applies only to lakes within the FCM strategy and can reach up to 30% of the pirarucu population of a given lake. Lakes outside FCM and/or conservation units may experience illegal fishing all year round (Cavole et al., 2015). For modelling assumptions of this study, protected lakes (13 lakes) correspond to 'no-take' areas designed to ensure pirarucu reproduction, in which fishing is not allowed apart from sustainable 'off-take' for a short period once a year and based on a strict fishing quota; protected lakes are co-managed by local communities that follow IBAMA regulations. In turn, unprotected lakes (18 lakes) are not managed by FCM nor IBAMA and are prone to exploitation by commercial fisheries that are generally uncontrolled, and to all sorts of illegal fishing.

2.2 | Data set

We gathered data on pirarucu abundances across all studied lakes from a previous study (Campos-Silva & Peres, 2016) and FCM information from our local partner institution (Juruá Institute, institutojurua.org.br). The pirarucu population dataset contains the number of adults in each lake in 2013, counted by local experts from local communities. LK was pivotal for developing the counting method, which is based on their breathing behaviour and validated by Castello (2004). Additionally, we retrieved temporal pirarucu population data from annual reports submitted by the local associations (Associação de Produtores Rurais de Carauari (ASPROC) and Associação de Moradores Extrativistas da Comunidade São Raimundo (AMECSARA) to IBAMA. We compiled a temporal series from 2011 to 2022 containing the number of pirarucu juveniles and adults in each of the 31 study lakes, also counted by local expert fishers as part of the FCM. However, the year that FCM started in each lake was different and 21 of them did not have continuous information. Therefore, only a subset of lakes was used as the baseline for modelling population dynamics (see below).

2.3 | Metapopulation network

We represented the riverscape formed by a set of pirarucu populations and their spatial connectivity as a weighted directed network in which nodes represent local patches of habitats (i.e. oxbow lakes) and links between them represent dispersal corridors that the species can use to move across the riverscape. Links between lakes were defined quantitatively as a combination of three components of the riverscape: the distance between lakes, the pirarucu's dispersal ability and its return rate after high-tide migration, as follows:

(i) *Distance*: the pairwise river flow geographic distance (km) between lakes i (source) and j (target), d_{ij}, during the flooding season when the high tides of the Juruá River allow fish movement from lake to lake. Distance was estimated using the 'Base Hidrográfica Ottocodificada (BHO) Multiescalas 2017 5k', an hydrographic database available from the National Water Agency of Brazil (Agência Nacional de Águas, 2020). The hydrographic basin follows the Pfafstetter Coding System that includes topological information within the code, extracted from the Shuttle Radar Topography Mission (SRTM), mapped from 11 to 22 February 2000 with a 30-m spatial resolution. Distances were calculated using Quantum GIS 3.3233 software and the analytical extension called QNEAT3. We calculated the river-flow geographic distance among lakes as the combination of three measurements resulting from: (i) the Euclidean distance from the source lake i to the nearest river channel; (ii) the river channel distance from the entry to the exit point towards lake j following the river course; and (iii) the Euclidean distance from the exit point to the destination lake j.

The length of the main river channel includes its curves, and is therefore not Euclidean. Only the distance to the entry and exit points (i.e. the distance from the border of the river to the nearest border of the target lake) needs to be Euclidean as there are no river channels that could be mapped for those. This is a limitation of the satellite images and the dynamics of the study system: the distance of exit and entry are temporary river channels, which are not mapped by the hydrographic bases available. Moreover, these distances are very small compared to the main river flow and therefore have only a minor effect on the overall distance between lakes.

We scaled d_{ij} to reflect the intuition that fish are more likely to disperse between nearby lakes. Scaling followed the formula:

$$d'_{ij} = \frac{1}{\frac{\log(d_{ij})}{\log(d)}}, \tag{1}$$

where $d = \min(D)$, the minimum pairwise distance across all lakes (D is the set of pairwise distances). This transformation yields values of d'_{ij} ranging from 1 for the closest lake pair to approximately 0.11 for the most distant pair. We used the inverse of the log ratio so that closer lakes receive higher weights. We normalized the outgoing links from each lake i by dividing each link weight by the sum of all outgoing weights from that lake (i.e. row normalization), using the formula:

$$v_{ij} = \frac{d'_{ij}}{\sum_j d'_{ij}}. \tag{2}$$

This provided the relative probability of fish to move to any lake j from a source lake i. This method is analogous to calculating the flow of information in social and ecological networks (Rosvall, Axelsson and Bergstrom, Rosvall et al., 2009, Farage et al., 2021).

(ii) *Dispersal capacity*: In a previous study, the movement of 13 individuals was monitored via GPS radio tracking during the dry and wet seasons (Campos-Silva et al., 2019). Two years after release, one of the tagged individuals was recaptured nearly

90 km from its original capture site. Therefore, we set 90 km as the maximum potential riverscape connectivity facilitated by pirarucu adults. Rather than assuming that fish evaluate distances and selectively disperse, we assume that attempted dispersal beyond this threshold is physiologically or environmentally constrained and therefore unlikely to succeed. Accordingly, we first computed dispersal probabilities between lakes based on scaled distances, and then set to zero any links where the pairwise distance exceeded 90 km, thereby removing unsuccessful dispersal attempts from the network.

(iii) *Return rate*: The average return rate of adult pirarucu individuals to their lake of origin, where they stay during the dry season. Previous studies reported pirarucu site fidelity to FCM protected lakes, meaning that a high proportion of individuals from lakes under FCM strategies return to their lake of departure, ranging from 71% to 83% (Gurdak et al., 2022, Campos-Silva, Hawes, and Peres, Campos-Silva et al., 2019). Therefore, we applied a return rate only to source lakes under the FCM strategies, using an average return rate (λ) of 0.77. Lake connectivity was then multiplied by $1 - \lambda$, reflecting the proportion of individuals that will not return to the departure lake, thus effectively contributing to network connectivity.

We integrated these three components into a single metric for pairwise connectivity between lakes, which is the weight of a link in the metapopulation network, ω_{ij}, as follows:

$$\omega_{ij} = \begin{cases} 0, & \text{if the distance between a pair of lakes is above 90 km} \\ v_{ij}, & \text{if lake } i \text{ is not under FCM} \\ v_{ij}(1-\lambda), & \text{if lake } i \text{ is under FCM} \end{cases} \quad (3)$$

The inclusion of the return rate introduces asymmetry in the link weights between pair of lakes: if one lake is under FCM protection and the other is not, then $w_{ij} \neq w_{ji}$. This asymmetry results in a directed network structure.

2.4 | Metapopulation model

To investigate the potential effects of changing fishing policies on pirarucu across the riverscape shown in Figure 1, we considered the set of lakes connected via the metapopulation network described above as a metapopulation composed of local pirarucu populations / habitat patches. We modelled each lake's local population growth using a density-dependent growth equation and dispersal following the established connectivity between lakes (see Metapopulation network). We used the Ricker population equation (Ricker, 1954), with an added stochastic term to account for the effects of year-to-year environmental variability on population growth, to model local population dynamics:

$$N_{t+1} = N_t e^{r(1 - N_t/K) + \varepsilon} \quad (4)$$

where N_t is the abundance of the population at time t, r is the intrinsic growth rate of the population and K is its carrying capacity. ε is a normally distributed stochastic variable representing stochastic environmental variability in population growth $\varepsilon \approx N(0, \sigma)$.

To leverage the data collected from our study system, we derived empirical values for the model parameters from the temporal abundance data of local pirarucu populations in specific lakes (see the Dataset subsection above). From this dataset, we selected a time series of adult pirarucu population abundance within specific lakes, focusing on those with at least seven consecutive data points (years) available between 2011 and 2022 (see Table S3). This criterion yielded 10 lakes for which population abundances were considered to have sufficient resolution to calculate parameters r and K for the model above (Equation 4). The lakes selected were: Branco (5), Dona Maria (6), Janiceto (9), Manaria (10), Mandioca (11), Marari (12), Onça (14), Sacado do Juburi (19), Samaúma (20) and Santo Antônio (22) (Figure 1).

To calculate r and K, we conducted a robust linear regression analysis over the per-capita growth rate, calculated as $\ln(N_{t+1}/N_t)$, against N_t, with r being the y-intercept and K the x-intercept, respectively. We performed the analysis for each of the 10 populations independently. Robust fitting of the linear models was performed using the function *rlm* from the MASS package in R (Venables & Ripley, 2002). Linearity and homoscedasticity assumptions were visually assessed using scatter plots of the relationship among variables and residuals versus fitted values respectively. Normality of the residuals was assessed through Shapiro–Wilk tests (using the *shapiro. test* function in R) independently for each regression. Residuals were normally distributed for all the regressions performed ($p > 0.1$ for all tests). The average value or r calculated across these 10 populations was $r = 1.05$. We used this value as the growth rate of fish in the model (Campos-Silva, Hawes, and Peres, Campos-Silva et al., 2019). We additionally calculated σ as the variance of this set of r values ($\sigma = 0.096$). This sigma was used to draw the stochastic term for each iteration of the model in Equation 4 (ε) as specified above. We validated the K values calculated from the available time series by plotting them against LK-derived values for those lakes (Figure S1). We found good agreement between the values calculated from the data versus the ones derived from LK (Pearson correlation coefficient $r = 0.86$, p-value < 0.01). This indicated that LK-based K values are generally valid. Therefore, we complemented the K values for the 21 lakes for which we did not have good-enough time series with local fisher expert knowledge. At the end, each of the 31 lakes had its own carrying capacity value, K_i (Table S3).

We connected local populations growing according to Equation 4 through dispersal, as defined by the metapopulation network. To do so, we incorporated influx and outflux terms into the model:

$$N_{t,i} = N_{t-1,i} e^{r\left(1 - \frac{N_{t-1,i}}{K_i}\right) + \varepsilon} + \sum_{\substack{j=1 \\ i \neq j}}^{L} \omega_{ji} N_{t-1,j} - \sum_{\substack{j=1 \\ j \neq i}}^{L} \omega_{ij} N_{t-1,i} \quad (5)$$

where $N_{t,i}$ is the abundance of pirarucu population in lake i at time t, L is the total number of lakes and rates ω_{ij} and ω_{ji} are the dispersal rates from lake i to j and from lake j to i, respectively. Goodness of fit of the metapopulation model was quantified using Kolmogorov–Smirnov (KS) tests to compare the population abundance values for the 10 lakes from which data were used to infer parameter values against the abundance at the corresponding patches in the metapopulation from outcomes of model simulations. To perform this analysis we parameterized the model with the values of initial abundance, r and K extracted and calculated for the target lakes. We then ran the model for a number of time steps equal to the number of data points present in the time series ($n = 10$). We performed independent KS tests to compare the empirical time series with the time series extracted from the simulation outputs corresponding to each of the 10 target lakes. All tests supported the null hypothesis (i.e. no difference between empirical and simulated data, $p > 0.05$) suggesting a good fit of model outcome to the data. KS tests were performed using the *ks.test* function in R.

To incorporate the effects of harvesting into our metapopulation model, we added an extra term for harvesting rate, extending Equation 5 to:

$$N_{t,i} = N_{t-1,i} e^{r\left(1 - \frac{N_{t-1,i}}{K_i}\right) + \varepsilon} + \sum_{\substack{j=1 \\ i \neq j}}^{L} \omega_{ji} N_{t-1,j} - \sum_{\substack{j=1 \\ j \neq i}}^{L} \omega_{ij} N_{t-1,i} - h N_{t-1,i}, \quad (6)$$

where h is the harvesting rate, or fishing effort (i.e. the fraction of pirarucu fishes extracted from the population). For each of the scenarios (Table 1) we varied h across a range of values from 0 to 1 at 0.1 intervals, for unprotected lakes only. This yielded a total of 11 values of harvesting rate. For protected lakes we used 0.3 for values of $h > 0.3$ to ensure protection.

We ran numerical simulations for each management scenario by starting the metapopulation at random initial abundances across local lakes, chosen from a uniform distribution across the values of K (i.e. $N_{1,i} \sim U(\min(K_i), \max(K_i)) \forall i$, where i refers to the lakes in the system). We used a different metapopulation network for each scenario because we varied the protected and unprotected lakes (Table 1). For instance, when choosing to protect larger lakes (H4), we changed the metapopulation network by defining the 13 lakes with the greater area as protected and the 18 remaining ones as unprotected. This was repeated for all scenarios based on the criterion used. For scenario 7 (protected lakes selected randomly), we ran 1000 replicates in which the identity of the 13 protected lakes was drawn randomly and independently for each replicate. This procedure, however, inherently results in lakes being assigned either protected or unprotected status across different replicates (since they are assigned protection status randomly). To circumvent this, the resulting population abundances and harvested biomass were averaged across replicates of the same lake and protection status.

Then, we applied the protocol described in the 'Metapopulation model' section. This was necessary because return rates only apply to protected lakes (Campos-Silva et al., 2019; Gurdak et al., 2022),

which indeed change from scenario to scenario (Table S2). We ran simulations for 50 time steps, where each time step represents a year, where the first 10 time steps / years were run without harvesting. This initial time period was found to be enough for transient dynamics to occur and the system to reach its stochastic equilibrium (i.e. random fluctuations around the lakes' carrying capacities). At time step 11, harvesting was introduced and maintained for the rest of the simulation (i.e. the further 39 time steps). This time period was enough for the system to reach its new stochastic equilibrium with harvesting. To quantify the simulation outcomes, we calculated lake occupancy (i.e. whether a lake's abundance was greater than 0) and the mean population abundance across the last 10 time steps for each lake.

2.5 | Statistical analyses

To identify the main determinants of mean population abundance over the last 10 time steps of the model simulations across lakes, we performed a linear regression considering the following fixed effects: (i) scenario, (ii) protection status (prot_status), (iii) fishing effort and the pairwise interactions between each of these variables. To account for the non-independence of observations from the same lake, we added lake as a random effect variable to the model. The fitted full model was as follows:

$$\log_{10}(\text{mean population abundance} + 1) \sim \text{scenario} + \text{prot\_status} + \text{fishing effort} + \text{scenario: protected} + \text{prot\_status: fishing effort} + (1 | \text{lake})$$

$$(7)$$

3 | RESULTS

The metapopulation network had 338 links among the 31 lakes (13 protected and 18 unprotected). Network density (proportion of realized links) was 0.36 and the average node degree (number of connections per lake) was 21.8 ± 6.01. Lake out-strength centrality (i.e. the sum of a lake's outgoing links), which is a measure of a lake's importance in providing fish for riverscape connectivity through pirarucu dispersal (used in scenarios 2 and 3), varied from 0.17 to 0.43 (mean $\pm$ SD: 0.32 ± 0.07) (Table S1; see Figure S2 for node and out-strength distribution).

Pirarucu abundance was significantly affected by lake protection status, scenario, fishing effort and their statistical interactions (Table 2, Table S4). Lake protection had a positive effect on pirarucu population abundance across all scenarios above the 0.3 fishing quota. Below that threshold, however, unprotected lakes occasionally supported equal or even higher pirarucu abundance than protected ones. To assess the effects of protection status in the different management scenarios across fishing efforts while controlling for lake identity, we used Estimated Marginal Means (EMMs also known as least-squares means). EMMs provide adjusted model predictions for each factor level while accounting for other variables in the model (Lenth, 2016). We applied Tukey's post hoc

TABLE 2 Results from the linear mixed model showing the effects of lake protection, management scenario and fishing effort as well as the interactions among them on the population of pirarucu at Middle Juruá River Basin, Western Brazilian Amazon.

	Sum Sq	Mean Sq	df	F value	Pr(>F)
Fishing effort	203.362	203.362	1.000	2805.678	0
Protected	31.745	31.745	1.000	437.973	3.39E-90
Scenario	4.434	0.739	6.000	10.195	3.52E-11
Fishing effort: protected	125.151	125.151	1.000	1726.649	1.20E-291
Fishing effort: scenario	6.502	1.084	6.000	14.951	6.82E-17
Protected: scenario	8.514	1.419	6.000	19.576	1.79E-22

Note: The full model was selected as the best model according to Akaike Information Criteria (LogLik = −420, Delta = 0, AICc = 888.4, weight = 1); therefore, only the results of this model are shown. The full model: $\log 10(\text{pop. means} + 1) \sim \text{scenario} + \text{protected} + \text{fishing\_effort} + \text{scenario: protected} + \text{protected: exploitation\_effort} + \text{scenario: fishing\_effort} + (1|\text{lake})$.
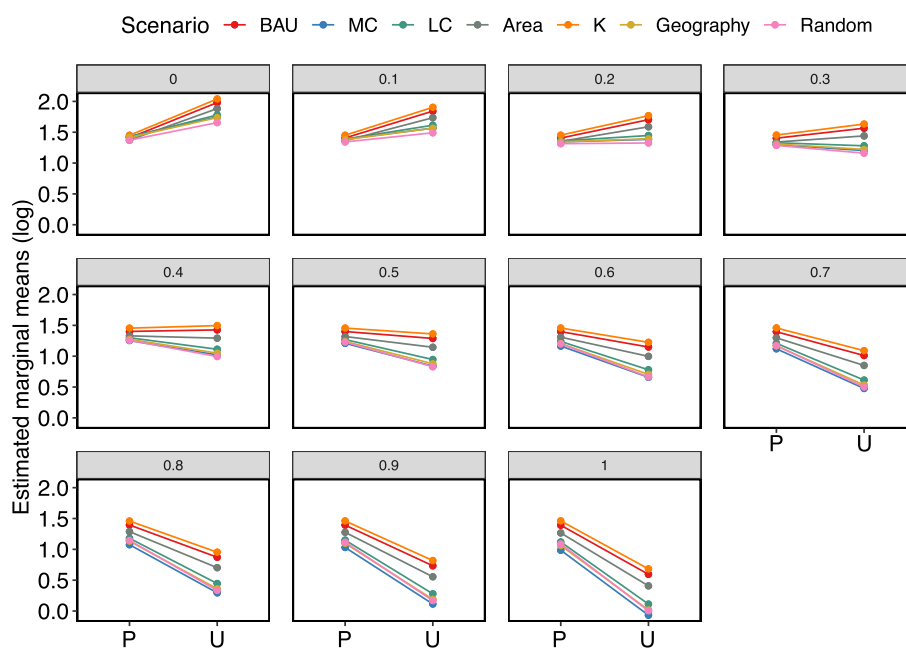
FIGURE 2 The effect of protection and fishing quota on pirarucu abundance. Each data point is the Estimated Marginal Means of log fish abundance, calculated from the statistical model and adjusted according to the other variables in the model, for protected (P) and unprotected (U) lakes. Each line represents the change in the Estimated Marginal Means for a specific scenario. Scenarios (depicted by colour) correspond to those described in Table 1. Each panel is a fishing quota; quotas above 0.3 are considered illegal fishing.

test for pairwise comparisons between scenarios and protection statuses, correcting for multiple testing (Tukey, 1949). These analyses revealed that the relative benefit of protection becomes consistently positive only as fishing pressure increases (Figure 2; Table S5), supporting the idea that local protection serves as a buffer under unsustainable exploitation levels.

Overall, increasing fishing effort significantly reduced the average population of pirarucu across all scenarios for unprotected lakes (Figure 3; Table S6). The expected adverse effect of fishing on FCM-protected lakes was avoided by the 0.3 maximum quota established in these lakes. Maintaining this quota allowed the pirarucu population to remain stable in protected lakes across all scenarios, even under high fishing pressure in unprotected lakes. However, for unprotected lakes, the scenario based on the K carrying capacity

(i.e. protecting lakes that can harbour the larger number of fish) consistently showed the highest population of pirarucu, followed by business-as-usual (BAU) (Figure 3).

Furthermore, protecting lakes with the highest carrying capacity (K) showed the lowest overall difference in pirarucu abundance between protected and unprotected lakes (Est = −0.10, SE = 0.03, $t = -3.00$; Figure 2; Table S5), generating a better balance between protected and unprotected lakes at the riverscape scale. Similar to business-as-usual (BAU), protecting lakes under the carrying capacity scenario (K) proved efficient for unprotected lakes under higher fishing efforts. This was due to the magnitude of the decline in pirarucu population being less abrupt than in other scenarios (Figure 3; Table S4). Interestingly, the carrying capacity and the business-as-usual scenarios showed the highest differences between protected
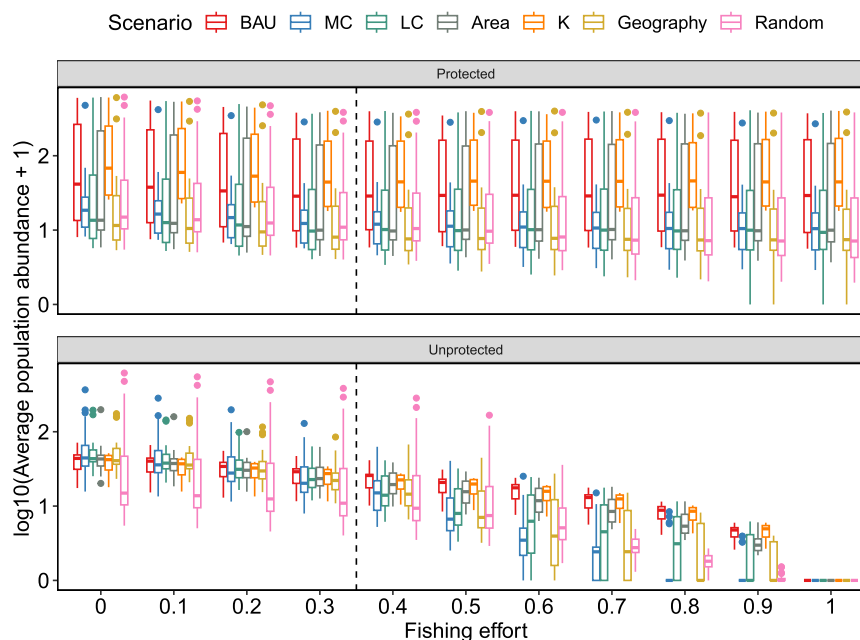
FIGURE 3 Effects of fishing effort across scenarios for protected and unprotected lakes. The plots show the average population abundance (log scale) across scenarios and increasing fishing pressure for protected and unprotected lakes. Vertical dashed lines mark the maximum fishing quota allowed by governmental authorities for lakes within the FCM. Fishing efforts to the right of the line are considered illegal. Thus, in protected lakes, the fishing effort to the right of the line is always 0.3, meaning that protected lakes are not fished for more than 30% of their pirarucu population in any scenario. Each data point represents a lake; therefore, each boxplot shows the median of population abundance (log10) across the 31 studied lakes, the minimum and maximum values, the first and third quartiles of data distribution and the outliers. Simulations were run for 50 time steps for each scenario. The abundance value of each point is the average abundance over the last 10 time steps. Scenarios (depicted by colour) correspond to those described in Table 1.

and unprotected lakes at low fishing pressure (≤ 0.3), in which unprotected lakes harboured more pirarucu than protected ones (Figure S3, Table S5). Conversely, the difference between protected and unprotected lakes was relatively lower at higher fishing effort (> 0.3) in both cases (Figure S3).

Pirarucu population in unprotected lakes was similar among scenarios at low fishing effort (< 0.3), and differences among scenarios were only noticeable at high efforts (Figure 3). The system started to collapse at intermediate levels of fishing effort (≥ 0.6) for the most connected (MC), least connected (LC) and the geography scenarios (Figure 3, Table S6). Randomly protecting lakes was generally less efficient than implementing a purposely designed management strategy, highlighting the importance of decision-making in FCM (Figure 3).

3.1 | Persistence at the metapopulation level

The choice of management scenario also had implications for the regional persistence of the pirarucu metapopulation (Figure 4). Our temporal data showed that at the beginning of FCM, lakes that had very few individuals (e.g. Onça and Santo Antônio), or even none (Janiceto) still recovered with the onset of FCM initiatives (Table S3; Figures S4 and S5). Therefore, we first considered binary persistence (i.e. the proportion of lakes with pirarucu abundances larger than zero). While business-as-usual (BAU), area

and carrying capacity (K) scenarios performed similarly, scenarios based on the most and least connected (MC, LC) and geography (Figure 4, left panel) resulted in a faster collapse of the metapopulation, starting at a fishing quota of 0.5. For the more robust scenarios, pirarucu populations only went extinct at the riverscape level above a 0.9 fishing effort.

We also quantified metapopulation-level persistence as the proportion of lakes in the riverscape where pirarucu abundance reached at least 50% of the lake's carrying capacity (K) (Figure 4, right panel). This way of assessing metapopulation persistence considers that viable populations should be large enough to be resilient to stochastic extinctions and maintain a stock that is large enough in the long term to ensure sustainability. The carrying capacity management strategy (K) emerged as the best scenario, suggesting that it better allows the metapopulation to support harvesting. The current FCM was the second-best scenario as lakes dropped below the 50% threshold when reaching a 0.5 fishing effort. A random choice of lake protection performed the worst, as even in the absence of fishing pressure, only about 80% of the lakes can maintain fish populations at this level. This indicates that protecting lakes without any criteria is an ineffective strategy at the riverscape scale. The metapopulation does not entirely collapse in any scenario as there are always some lakes remaining in the system (around 40% of the lakes persist at the highest fishing effort in all scenarios; Figure 4). This is likely due to the positive growth rate of local populations adopted in our models,
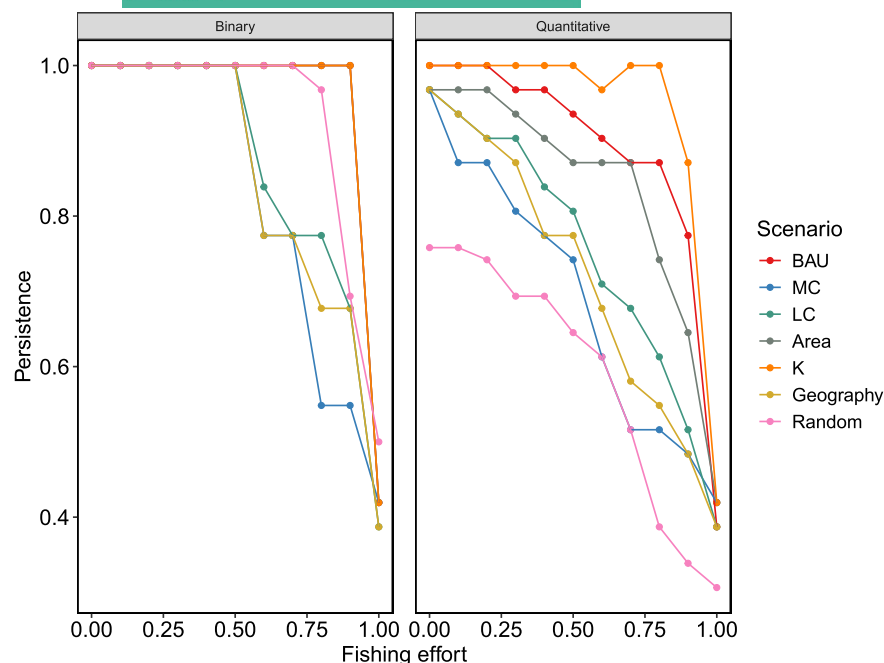
FIGURE 4 Effect of fishing effort on pirarucu metapopulation persistence. The plots show the proportion of lakes persisting at the metapopulation level across increasing fishing pressure for the seven simulated scenarios (Table 1). Binary persistence (left panel) considers a lake to persist in the metapopulation if the pirarucu abundance is >0. Quantitative persistence (right panel) considers that a given lake persists in the system only if pirarucu abundance is at least half of the carrying capacity of that lake. Scenarios (depicted by colour) correspond to those described in Table 1.

which always ensures the replenishment of individuals after harvesting, even at low population levels.

4 | DISCUSSION

Our study demonstrates the critical role of LK in shaping effective conservation strategies within complex socio-ecological systems. By evaluating FCM strategies for the pirarucu metapopulation in Amazonia, we show that strategies rooted in local insights can perform as well as, or better than, alternative scenarios even at large geographical scales. While the strategy based on protecting lakes with higher carrying capacity provided the highest population persistence, the approach based on LK closely matched its efficacy. This underscores the value of integrating LK in management strategies of interconnected systems at large geographical scales, for sustaining ecosystems and building resilience to exploitation pressures.

Adopting a network perspective is crucial for capturing the dependencies and feedbacks of social-ecological systems. Our study shows the value of incorporating ecological dynamics—such as species movement and temporal variation—into network analyses to better assess regional management. In the Juruá, the interconnected lakes sustain the pirarucu system: individuals disperse up to 90 km, buffering local disturbances, while high site fidelity (≈ 77% return to protected lakes; Gurdak et al., 2022) stabilizes local populations. Positive growth rates in protected lakes further offset moderate harvest in unprotected ones, as they act as sources of juvenile fish. However, without effective FCM these mechanisms collapse, with sharp population declines when harvest exceeds 60%, consistent with previously reported patterns (Castello et al., 2011).

Historically, Juruá fishers have selected lakes for protection through trial-and-error, like many other small-scale fisheries (Cochrane et al., 2011). This strategy started as a random scenario,

and we show that protection without any criteria is the least effective strategy. As the system has evolved, contemporary fishers selected lakes for management based on a combination of area, capacity, and proximity to the main river. Our findings suggest that the current FCM strategy is effective in maintaining the pirarucu population. However, it could be improved by prioritizing the protection of lakes based on their carrying capacity, as meta-ecosystem theory predicts that spatial flows from productive source habitats support population persistence in less productive sinks (Gravel et al., 2010).

In particular, protecting high-capacity lakes likely increases the overall reproductive output and surplus biomass, which can disperse to nearby, unprotected areas. This mechanism is analogous to the spillover effect observed in marine reserve networks (Brown et al., 2015). Spillover enhances regional persistence by facilitating the movement of individuals from well-protected, high-density areas into adjacent habitats, thereby reinforcing the resilience of the broader metapopulation. In our system, this effect may be especially critical under high fishing pressure, where unprotected lakes are more vulnerable to depletion and rely on inflows from better-managed areas to avoid collapse. These findings reinforce the idea that spatially strategic protection, informed by ecological attributes like carrying capacity, can enhance both local and regional conservation outcomes.

Enhancing ecosystem services is a primary goal of designating protected areas (Campos-Silva et al., 2021; Dee et al., 2017). However, the geographic scenario, which focused on lakes at the borders of two regional PAs, proved ineffective for pirarucu conservation, especially when illegal fishing exceeded 30%. These protected lakes had some of the lowest pirarucu populations, indicating that top-down management and simple land demarcation are insufficient without controlling illegal fishing, at least in this region. This aligns with recent findings showing that co-management arrangements, where communities participate in decision-making, significantly

increase the effectiveness of PAs in reducing overfishing and enhancing ecological outcomes (Lopes Carvalho et al., 2025).

4.1 | Limitations

Our framework represents one of the first efforts to integrate LK, fish biology and metapopulation modelling to inform conservation on a regional scale in a tropical system. However, it has several limitations. Although based on the best available data, the model is constrained by limited empirical information: parameterization relied on 11 years of monitoring from only 10 lakes, which may not fully capture long-term trends or regional variability. As FCM initiatives continue and more data become available, future analyses will be essential to assess the persistence of current patterns and the long-term impacts of sustained fishing pressure, even under co-management. Moreover, regenerating the network based on the specific spatial configuration of each system is critical. Lake connectivity varies across regions, and the positive growth rates observed in the Middle Juruá may not hold in more degraded habitats. Such differences could undermine key processes—such as site fidelity and long-distance dispersal—that are integral to the network structure and population persistence.

Our model across the Amazon basin is limited by regional socio-ecological variation. In areas with elevated levels of illegal fishing—driven by geographic isolation, weak enforcement, deforestation or other pressures—increased fishing effort may exert stronger impacts on pirarucu metapopulation dynamics. Under such conditions, even FCM strategies may be insufficient to maintain source populations across the riverscape. In addition, the model does not account for certain ecological and evolutionary processes that may affect long-term sustainability. For instance, repeated reliance on the same lakes under FCM could reduce genetic diversity by limiting gene flow from other areas. This loss of genetic variation may compromise population resilience and adaptive capacity in the face of future environmental, climate and/or anthropogenic changes.

4.2 | Applications

Effective management should address local and regional socio-ecological factors. Given the complexity and scale of social-ecological systems, empirically testing management scenarios is impractical. Our modelling framework provides a practical means to contrast alternative socio-ecological management scenarios *in silico*, allowing decision-makers to rank strategies based on empirical evidence. As demonstrated in this study, the framework can seamlessly integrate LK to explore community-based strategies for the sustainable use of natural resources (Andrew et al., 2007; Cochrane et al., 2011), although it can also be applied without LK. To illustrate its broader applicability, we identify four tiers of use, ranging from direct transfer without modification (Tier 1) to application in different socio-ecological contexts requiring substantial adaptation (Tier 4).

- *Tier 1: Regional co-management of pirarucu.* Our framework can be directly applied to guide management strategies of pirarucu under FCM at the Middle Juruá River Basin.
- *Tier 2: Scaling up within the Amazon.* The framework can be extended to other pirarucu fishing regions across the Amazon that are considering FCM. Scaling up could potentially create a FCM corridor, facilitating pirarucu movement at a larger riverscape scale. In this case, model parameters remain the same, but the spatial network configuration must be tailored to each region.
- *Tier 3: Other riverine fishery systems.* Applying the framework to other fisheries requires adjusting both metapopulation network parameters (e.g. dispersal capacity, return rates, spatial configuration) and species-specific dynamics (e.g. growth rates, temporal fluctuations). Evidence from other Amazonian river systems shows that single-species FCM can benefit broader fish assemblages and improve ecological integrity (Medeiros-Leal et al., 2021). Adapting the framework to other riverine species could therefore enhance biodiversity conservation, local livelihoods and sustainable fishing services.
- *Tier 4: Beyond fisheries.* The framework may also be adapted to non-fishery landscapes. This includes terrestrial landscapes in which a target, valued species and its territory needs to be protected according to certain conditions involving community and political decisions. For example, in Palenque National Park, Mexico, howler monkeys (*Alouatta pigra*) inhabit fragmented forest patches within an agricultural matrix (Klass, 2024). By parameterizing the framework to reflect howler monkey biology and patch-level metapopulation dynamics, managers could evaluate alternative conservation scenarios and guide resource allocation for long-term species persistence.

In conclusion, our study highlights the importance of data-driven management for sustaining local fisheries. While the current FCM scheme stabilizes pirarucu populations, resilience could be improved by prioritizing lakes with higher carrying capacity, especially where illegal fishing pressure is high. Scaling up community-led protection emphasizes the critical role of Indigenous Peoples and local communities in meeting global biodiversity targets, such as the Kunming-Montreal Framework. Future modelling should continue to integrate local knowledge with empirical data, while accounting for socio-ecological complexities and data limitations. Ultimately, balancing ecological sustainability with community needs is essential for the long-term success of co-management and related conservation strategies.

AUTHOR CONTRIBUTIONS

Carine Emer: Writing—original draft, writing—review and editing, conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, visualization. Miguel Lurgi: Writing—original draft, writing—review and editing, conceptualization, formal analysis, investigation, methodology. Sérgio Timóteo: Writing—original draft, writing—review and editing, conceptualization, formal analysis, investigation, methodology. João

Vitor Campos-Silva: Writing—review and editing, investigation, conceptualization. Shai Pilosof: Writing—original draft, writing—review and editing, conceptualization, investigation, methodology, project administration, validation.

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FUNDING INFORMATION

CONFLICT OF INTEREST STATEMENT

DATA AVAILABILITY STATEMENT

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Relationship between carrying capacity (K) values inferred from empirical data (see Methods in the main text for details) versus those extracted from local knowledge from local communities in the Juruá system.

Figure S2. Distribution of centrality metrics of the Arapaima spatial metapopulation network based on the 31 studied lakes from Middle Juruá River Basin, Western Brazilian Amazon.

Figure S3. Differences between protected and unprotected lakes in the gradient of increasing fishing effort across the seven scenarios of Fishery CoManagement (FCM).

Figure S4. Population dynamics of pirarucu modelled from empirical data.

Figure S5. Simulated population dynamics of pirarucu.

Table S1. The studied lakes at the Middle Juruá River Basin, Western Brazilian Amazon, and their respective characteristics.

Table S2. List of lakes protected in each scenario, as follows: H1—Business-as-usual; H2—Protecting most connected lakes; H3—Protecting least connected lakes; H4—Protecting larger lakes; H5—Protecting lakes with higher carrying capacity; H6—Protecting lakes according to geographic position.

Table S3. Temporal data from 2009 to 2022 of arapaima population used in the metapopulation model followed by the corresponding carrying capacity (K) (see main text: Methods—Metapopulation Model for details on how K was estimated).

Table S4. Results from the Linear Mixed Model showing the effects of lake protection, management scenarios and different levels of fishing effort as well as the interactions among them on the population of pirarucu (*Arapaima gigas*) at Middle Juruá River Basin, western Amazon.

Table S5. Post-hoc Tukey test of the Estimated Average Means (EMMeans) of arapaima population in protected and unprotected lakes in each Fishery CoManagement (FCM) scenario, following the linear mixed effect model. Only comparisons between unprotected and protected lakes within each scenario are shown.

Table S6. Post-hoc Tukey test for the Estimated Marginal Means (EMMeans) of Arapaima population, showing pairwise differences between fishing effort in each scenario.