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 that with LK, fish biology and network theory to assess how lake protection and fishing quotas, including illegal fishing, impact pirarucu population abundance at the riverscape scale.

3. Our analysis of 13 FCM-protected lakes and 18 unprotected lakes compares six hypothesis-driven management strategies with 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 preferential protection to lakes with high pirarucu carrying capacity provided the highest population persistence, the currently applied one closely matched its efficacy.

4. Our findings reveal that current FCM strategy, grounded in LK, is highly efficient but can still be optimised using ecological knowledge. Our modelling approach can be applied to strengthen strategies for scaling up areas of community-led protection in the Amazon, reinforcing the critical role of LK in contributing to key global conservation targets such as the Kunming-Montreal Global Biodiversity Framework under the Convention on Biological Diversity.

Keywords: conservation; ecosystem services; ecosystem management; fish ecology; metapopulation dynamics; socio-ecological systems; spatial networks

Introduction

Emerging conservation paradigms increasingly highlight the potential role of local communities in preserving ecosystem services through the protection and management of natural resources (Levis et al., 2024, Díaz et al., 2018, Wood et al., 2018, Naeem et al., 2016). Integrating local knowledge (hereafter, LK) into conservation enhances environmental governance, supports local development, promotes social justice, and ensures biodiversity protection (Freitas et al., 2020, Campos-Silva et al., 2021). 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 (Levis et al., 2024, Fletcher et al., 2021). 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 (Freitas et al., 2020, Lopes et al., 2021, Arantes et al., 2022). 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 needs 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 (Campos-Silva et al., 2021, Arantes et al., 2022), while participatory initiatives such as collaborative management integrate local communities into the decision-making process (Freitas et al., 2020, Berkes, 2009).

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, Andrew, and Parma, 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 (Lopes et al., 2021, Jentoft et al., 2017). 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 (Dee et al., 2017, Keyes et al., 2021). However, most network studies focused on ecosystem services vulnerability (Dee et al., 2017, Felipe-Lucia et al., 2020, Keyes et al., 2021) overlook the underlying ecological dynamics such as species movement and spatial connectivity, making it difficult to quantify the impact of management decisions imposed at the regional level.

Here, we explore the FCM conservation program 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, Instituto Brasileiro do Meio Ambiente (IBAMA), 2005), and constitutes a major income for many local communities (Campos-Silva and Peres, 2016, Campos-Silva et al., 2018). Its floodplain ecosystem is characterised 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 develop 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 (Lopes et al., 2021, Campos-Silva et al., 2018).

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. This strategy protects lakes on an ad hoc basis, guided by LK—that is, the historical designation of protected lakes based on fishers' perceptions of pirarucu abundance and logistical accessibility. 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 (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) can be protected or unprotected by FCM and managed according to governmental top-down regulatory policies that set fishing quotas. We show that current FCM strategies, grounded in LK, are highly efficient but can still be optimised by protecting lakes based on populations' 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.

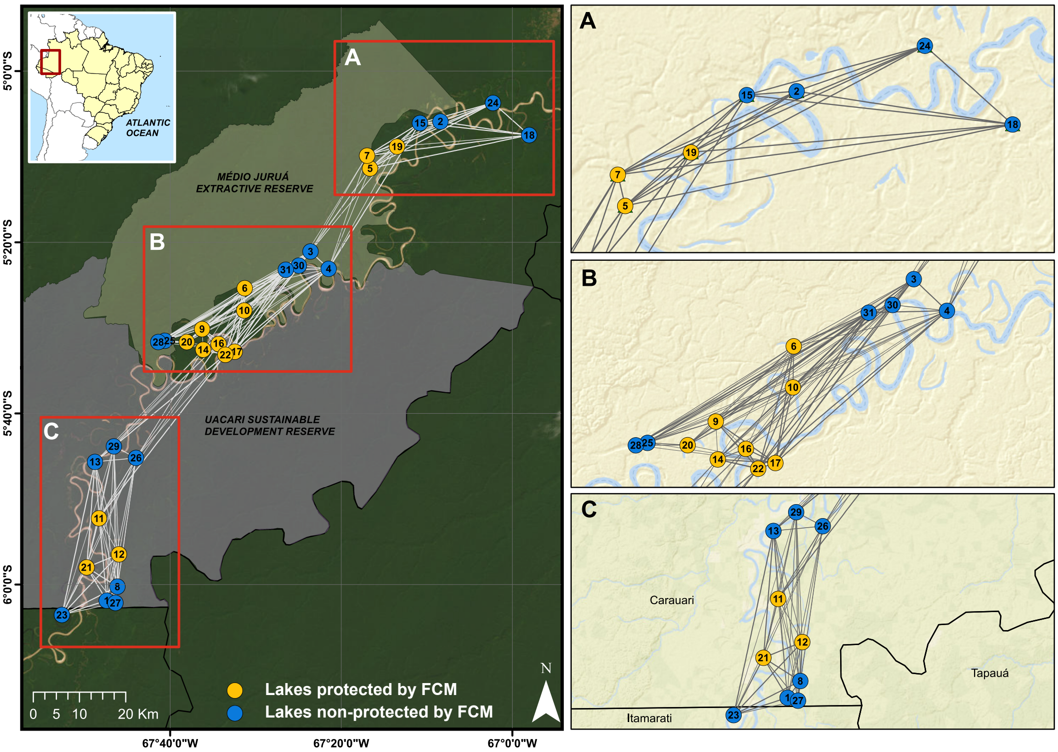

Figure 1. Study area and the metapopulation network of the pirarucu (*Arapaima gigas*) at the Middle Juruá River Basin, Western Brazilian Amazon. Each lake is a node in the network and is represented by a number; the list of lakes and their attributes can be found in Table S1. The position of each lake 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, B, and 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 the pirarucu movement. The links are drawn as straight lines for clarity, but were calculated based on the length of curved river courses (see Metapopulation network section in Methods). We used ArcGIS and Arcmap 10.825 to draw the map layout.

Methods

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 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 and 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 monopolised 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 around (Cavole, Arantes, and Castello, 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.

Data set

We gathered data on pirarucu population numbers across all studied lakes from a previous study (Campos-Silva and 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 which is validated in 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 2011-2022 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 were used as the baseline for modelling population dynamics (see below).

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. 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.

Protection scenario	**Hypotheses / predictions**	**Analyses**
1. Business-as-usual (BAU)	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 legal and illegal fishing quotas would lead to system collapse, which is faster in unprotected lakes (Cavole, Arantes, and Castello, 2015).	Keep the same 13 protected lakes as the current empirical protection strategy while increasing fishing effort for both protected and unprotected lakes.
2. Protect the most connected lakes (MC)	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.	Protect the 13 lakes with the highest strength (sum of dispersal link weights) (Barrat et al., 2004), given the empirical metapopulation network.
3. Protect the least connected lakes (LC)	H3: Because pirarucu tend to return to protected lakes (Gurdak et al., 2022, Campos-Silva, Hawes, and Peres, 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.	Protect the 13 lakes with the lowest strength (sum of dispersal link weights) (Barrat et al., 2004), given the empirical metapopulation network.
4. Protect larger lakes (Area)	H4: Larger lakes can sustain larger populations of pirarucu as their niche space is greater in terms of food resources and reproductive sites (Richard et al., 2018, Gilarranz et al., 2017). Therefore, larger lakes can serve as a 'source' of pirarucu in the metapopulation dynamics.	Protect the 13 lakes with the largest area (ha).
5. Protect lakes with higher carrying capacity (K)	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).	Protect the 13 lakes with the highest carrying capacity.
6. Protect lakes according to their geographic position (Geography)	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.	Protect the six northernmost and the seven southernmost lakes because these are more vulnerable to illegal fishing coming from outside Protected Areas.
7. Protect lakes randomly (Random)	H7: Protecting lakes with no biotic or abiotic criteria would lead to local population collapses and lowest metapopulation persistence.	Randomly select 13 lakes to protect.

Metapopulation network

We represented the riverscape formed by a set of Arapaima 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 point to the exit cost 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 entry and exit costs need to be Euclidean distances 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 cost of exit and entry are temporary river channels, which are not mapped from the hydrographic bases available. Moreover, these distances are very small compared to the river flow and therefore have only a minor effect on the overall distance.

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 $d = min(\mathcal{D})$, the minimum pairwise distance across all lakes ($\mathcal{D}$ 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, 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 and over two years Campos-Silva, Hawes, and Peres, 2019. Two years after the conclusion of this study, 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, 2019). Therefore, we applied a return rate only to 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:

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

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.

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:

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

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 (Eq. 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 and Ripley, 2002). Linearity and homoscedasticity assumptions were visually assessed using scatter plots of the relationship among variables and residuals vs 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 ten populations was $r = 1.05$. We used this value as the growth rate of fish in the model (Campos-Silva, Hawes, and Peres, 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 Eq. 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 vs. 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 Eq. 4 through dispersal, as defined by the metapopulation network. To do so, we incorporated an influx and outflux terms into the model:

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

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 Eq. 5 to:

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

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 their 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 (Gurdak et al., 2022, Campos-Silva, Hawes, and Peres, 2019), 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.

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:

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 (*Arapaima gigas*) at Middle Juruá River Basin, Western Brazilian Amazon. 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: $log10(pop.means + 1) \sim scenario + protected + fishing\_effort + scenario : protected + protected : exploitation\_effort + scenario : fishing\_effort + (1|lake)$.

	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

$$\begin{aligned} \log_{10}(\text{mean population abundance} + 1) &\sim \text{scenario} + \text{prot\_status} + \text{fishing effort} \\ &\quad + \text{scenario} : \text{protected} + \text{prot\_status} : \text{fishing effort} + (1|\text{lake}) \end{aligned} \tag{7}$$

Results

The metapopulation network had 338 links among the 31 lakes (13 protected, 18 unprotected). Network density (proportion of realised 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 ± 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 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 carrying capacity (i.e., protecting lakes that can harbour the larger number of fish, H5) consistently showed the highest population of pirarucu, followed by business-as-usual (H1) (Figure 3).

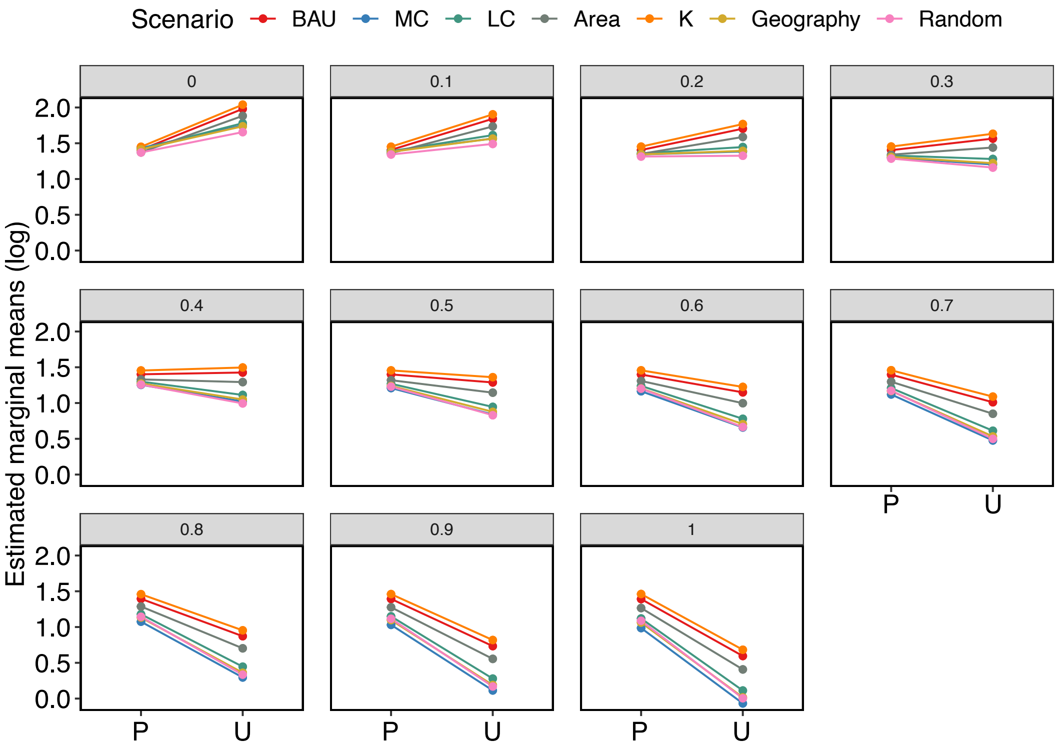

Figure 2. The effect of protection and fishing quota on pirarucu abundance. Each data point is the Estimated Marginal Means of log fish abundance, calculated from the statistical model and adjusted according to the other variables in the model, for protected (P) and unprotected (U) lakes. Each line represents the change in the Estimated Marginal Means for a specific scenario. Scenarios (depicted by color) correspond to those described in Table 1. Each panel is a fishing quota; quotas above 0.3 are considered illegal fishing.

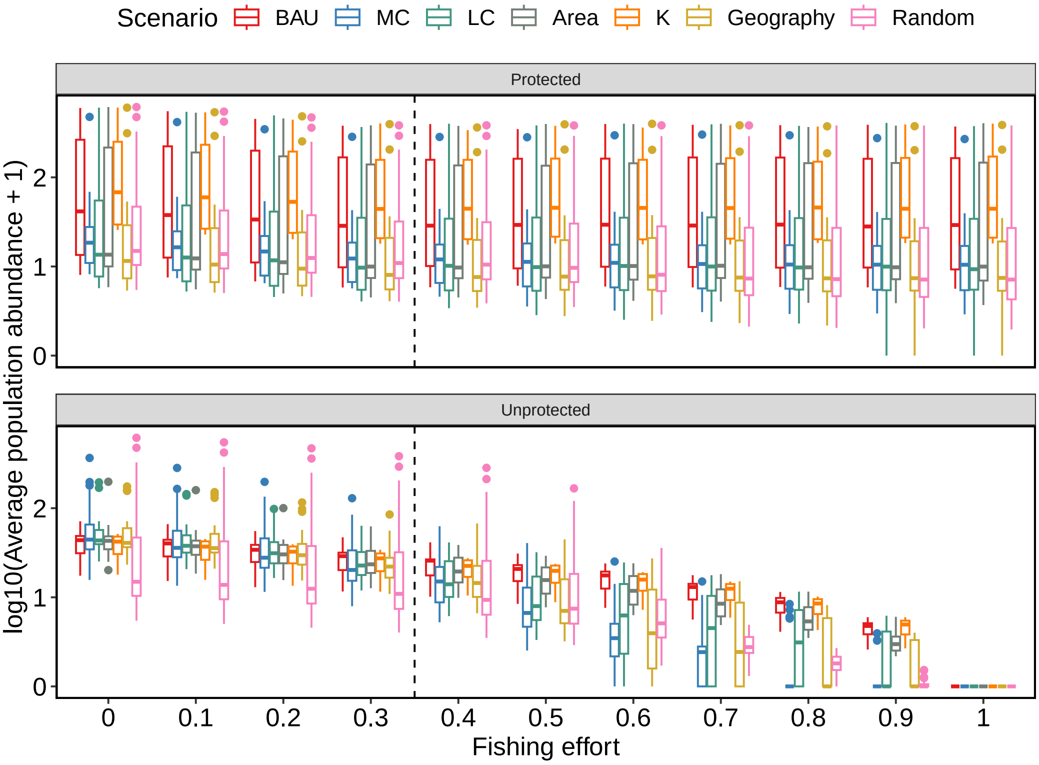

Figure 3. Effects of fishing effort across scenarios for protected and unprotected lakes. The plots show the average population abundance (log scale) across scenarios and increasing fishing pressure for protected and unprotected lakes. Vertical dashed lines mark the maximum fishing quota allowed by governmental 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 quartile 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 color) correspond to those described in Table 1.

Furthermore, protecting lakes with the highest carrying capacity (H5) 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 (H1), protecting lakes under the carrying capacity scenario (H5) 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 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 (H2), least connected (H3) and the geography (H6) 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).

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; Figure S4, S5). Therefore, we first considered binary persistence (i.e., the proportion of lakes with pirarucu abundances larger than zero). While business-as-usual (H1), area (H4) and carrying capacity (H5) scenarios performed similarly, scenarios based on the most and least connected (H2, H3) and geography (H6) (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.

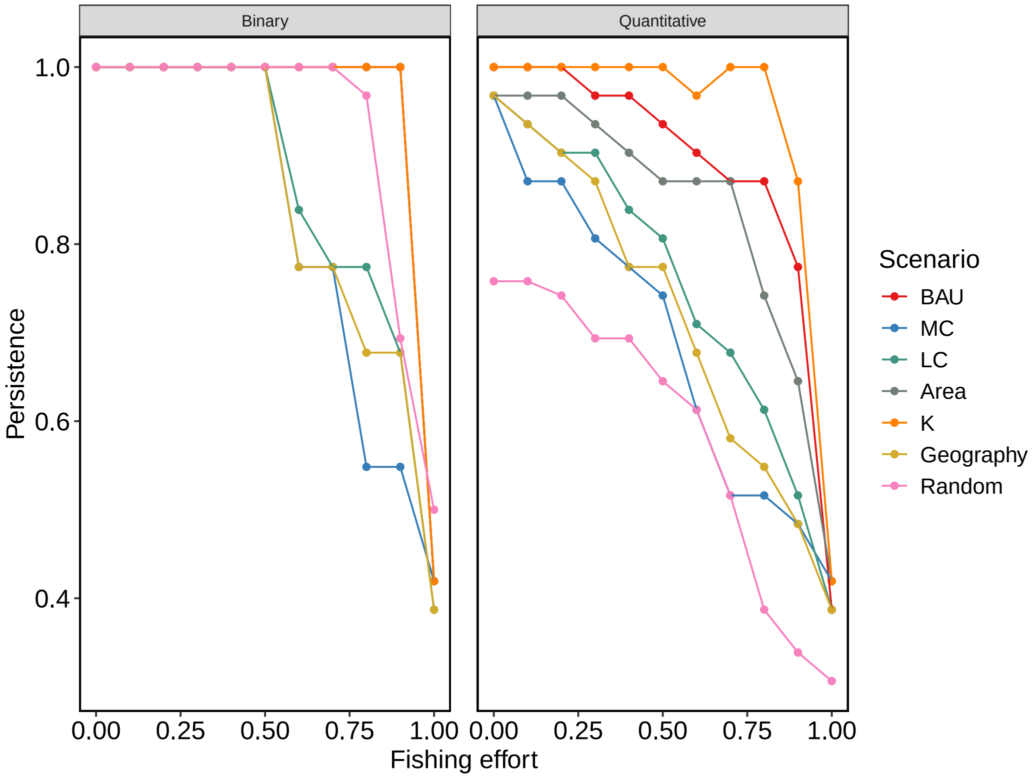

Figure 4. Effect of fishing effort on pirarucu metapopulation persistence. The plots show the proportion of lakes persisting at the metapopulation level across increasing fishing pressure for the seven simulated scenarios (Table 1). Binary persistence (left panel) considers a lake to persist in the metapopulation 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.

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 (H5) 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 (H7) 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, which always ensures the replenishment of individuals after harvesting, even at low population levels.

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, alternatives 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.

The interconnected lakes in the metapopulation network are crucial for sustaining the pirarucu socio-ecological system in the Juruá region. Pirarucu can travel up to 90 km, facilitating dispersal and buffering against local disturbances. Their high site fidelity ($\approx 77\%$ return to protected lakes; Gurdak et al., 2022) stabilises local populations, while positive growth rates help offset moderate fishing pressure in unprotected lakes, because protected ones serve as sources of juvenile fish. However, without effective FCM these mechanisms fail, as shown by the sharp population declines when harvesting exceeds 60%, aligning with findings from other regions (Castello, Stewart, and Arantes, 2011).

Historically, Juruá fishers have selected lakes for protection through trial-and-error, like many other small-scale fisheries (Cochrane, Andrew, and Parma, 2011). This strategy started as a random scenario, and we show that protection without any criteria is the least effective strategy. As the system evolved, nowadays experienced fishers choose lakes to be managed 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 (Dee et al., 2017, Campos-Silva et al., 2021). However, the geography 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).

Applications

Effective management must 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 serves as an interdisciplinary tool that integrates LK with scientific evidence. By testing socio-ecological scenarios in silico, it helps identify optimal configurations and supports decision-makers in exploring community-based strategies for the sustainable use of natural resources (Andrew et al., 2007, Cochrane, Andrew, and Parma, 2011). In many developing countries, small-scale fisheries operate without formal protection frameworks (Andrew et al., 2007). Our approach can support the design of such frameworks. Within the Amazon basin, our framework can be extended to other pirarucu fishing regions interested in implementing FCM and potentially form a corridor of FCM that would facilitate pirarucu movement at the larger riverscape scale. Furthermore, our results support the strategy of scaling up areas of community-led protection, reinforcing the critical role of Indigenous Peoples and local communities in contributing to key global conservation targets, including the Kunming-Montreal Global Biodiversity Framework under the Convention on Biological Diversity, as well as the earlier Aichi Biodiversity Targets. Moreover, evidence from other river systems in the Amazon shows that single-species FCM strategies can positively affect broader fish assemblages and improve ecological integrity (Medeiros-Leal et al., 2021). Expanding similar FCM strategies across the Amazon could further enhance sustainable fishing services as well as biodiversity conservation and local well-being.

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.

The generalizability of 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.

Conclusion Our study underscores the importance of data-driven management strategies to sustain local fisheries. While the current FCM strategy successfully stabilizes pirarucu populations, resilience could be further enhanced by prioritizing lake protection based on carrying capacity, particularly in regions facing high illegal fishing pressure. Expanding such effective FCM approaches across Amazonia holds significant promise for biodiversity conservation and local community well-being. Adopting a network perspective, as demonstrated here, is crucial for addressing the complex dependencies and feedback loops inherent in social-ecological systems. Our study highlights the value of explicitly incorporating ecological dynamics, such as species movement and temporal information, into network analyses to better assess the impacts of regional management decisions. Future modelling efforts should continue to thoughtfully integrate local knowledge and empirical data, carefully considering socio-ecological complexities and data constraints. Ultimately, strategies that balance ecological sustainability and community needs are essential to the long-term success of co-management initiatives and related conservation practices.

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Data and code availability statement

The data and code used for the analysis are available at the GitHub repository: `https://github.com/carineemer/pirarucu_metapop`.

Authors' contributions

Carine Emer – Writing – original draft, Conceptualization, Data curation, Formal Analysis, Funding acquisition, Investigation, Methodology, Project administration, Visualization.
João Vitor Campos-Silva – Writing – review and editing, Investigation, Conceptualization.

Sergio Timoteo – Writing – review and editing, Conceptualization, Formal Analysis, Investigation, Methodology.
Miguel Lurgi – Writing – review and editing, Conceptualization, Formal Analysis, Investigation, Methodology.
Shai Pilosof – Writing – review and editing, Conceptualization, Formal Analysis, Investigation, Methodology, Validation.

Conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

Agência Nacional de Águas (2020). *Base Hidrográfica Ottocodificada 1:250.000 (BHO250)*. Agência Nacional de Águas (ANA).

Andrew, Neil L et al. (Sept. 1, 2007). "Diagnosis and management of small-scale fisheries in developing countries". In: *Fish Fish (Oxf.)* 8 (3), pp. 227–240. DOI: 10.1111/j.1467-2679.2007.00252.x.

Arantes, Caroline C et al. (Mar. 2022). "Institutional effects on ecological outcomes of community-based management of fisheries in the Amazon". In: *Ambio* 51 (3), pp. 678–690. DOI: 10.1007/s13280-021-01575-1.

Barrat, A et al. (Mar. 16, 2004). "The architecture of complex weighted networks". In: *Proc. Natl. Acad. Sci. U. S. A.* 101 (11), pp. 3747–3752. DOI: 10.1073/pnas.0400087101.

Berkes, Fikret (Apr. 1, 2009). "Evolution of co-management: role of knowledge generation, bridging organizations and social learning". In: *J. Environ. Manage.* 90 (5), pp. 1692–1702. DOI: 10.1016/j.jenvman.2008.12.001.

Brown, Christopher J et al. (Oct. 1, 2015). "Fisheries and biodiversity benefits of using static versus dynamic models for designing marine reserve networks". In: *Ecosphere* 6 (10), pp. 1–14. DOI: 10.1890/ES14-00429.1.

Campos-Silva, João V et al. (Nov. 13, 2018). "Unintended multispecies co-benefits of an Amazonian community-based conservation programme". In: *Nat. Sustain.* 1 (11), pp. 650–656. DOI: 10.1038/s41893-018-0170-5.

Campos-Silva, João Vitor (Oct. 1, 2019). "Giant fish bucks population decline". In: *Nature* 574 (7776), p. 36. DOI: 10.1038/d41586-019-02926-5.

Campos-Silva, João Vitor, Joseph E Hawes, and Carlos A Peres (July 1, 2019). "Population recovery, seasonal site fidelity, and daily activity of pirarucu (Arapaima spp.) in an Amazonian floodplain mosaic". In: *Freshw. Biol.* 64 (7), pp. 1255–1264. DOI: 10.1111/fwb.13301.

Campos-Silva, João Vitor and Carlos A Peres (Oct. 12, 2016). "Community-based management induces rapid recovery of a high-value tropical freshwater fishery". In: *Sci. Rep.* 6, p. 34745. DOI: 10.1038/srep34745.

Campos-Silva, J et al. (Sept. 27, 2021). "Sustainable-use protected areas catalyze enhanced livelihoods in rural Amazonia". In: *Proc. Natl. Acad. Sci. U. S. A.* 118. DOI: 10.1073/pnas.2105480118.

Castello, L (Mar. 1, 2008). "Lateral migration of *Arapaima gigas* in floodplains of the Amazon". In: *Ecol. Freshw. Fish* 17 (1), pp. 38–46. DOI: 10.1111/j.1600-0633.2007.00255.x.

Castello, L, D J Stewart, and C C Arantes (Sept. 11, 2011). "Modeling population dynamics and conservation of arapaima in the Amazon". In: *Rev. Fish Biol. Fish.* 21 (3), pp. 623–640. DOI: 10.1007/s11160-010-9197-z.

Castello, L et al. (Oct. 1, 2015). "Understanding fishing-induced extinctions in the Amazon". In: *Aquatic Conservation-marine and Freshwater Ecosystems* 25, pp. 587–598. DOI: 10.1002/AQC.2491.

Castello, Leandro (May 1, 2004). "A method to count pirarucu *Arapaima gigas*: Fishers, assessment, and management". In: *N. Am. J. Fish. Manag.* 24 (2), pp. 379–389. DOI: 10.1577/m02-024.1.

Cavole, L, C Arantes, and L Castello (Aug. 1, 2015). "How illegal are tropical small-scale fisheries? An estimate for arapaima in the Amazon". In: *Fisheries Research* 168, pp. 1–5. DOI: 10.1016/J.FISHRES.2015.03.012.

CITES (2024). *Arapaima gigas. CITES Appendix II.* Retrieved from CITES Species Database: https://cites.org/eng/

Cochrane, Kevern L, Neil L Andrew, and Ana M Parma (Sept. 1, 2011). “Primary fisheries management: a minimum requirement for provision of sustainable human benefits in small-scale fisheries: Primary management of small-scale fisheries”. In: *Fish Fish (Oxf.)* 12 (3), pp. 275–288. DOI: 10.1111/j.1467-2979.2010.00392.x.

Cuddington, K et al. (Feb. 1, 2013). “Process-based models are required to manage ecological systems in a changing world”. In: *Ecosphere* 4 (2), pp. 1–12. DOI: 10.1890/es12-00178.1.

Dee, Laura E et al. (Feb. 2017). “Operationalizing network theory for ecosystem service assessments”. In: *Trends Ecol. Evol.* 32 (2), pp. 118–130. DOI: 10.1016/j.tree.2016.10.011.

Díaz, Sandra et al. (Jan. 19, 2018). “Assessing nature’s contributions to people”. In: *Science* 359 (6373), pp. 270–272. DOI: 10.1126/science.aap8826.

Farage, Carmel et al. (May 2021). “Identifying flow modules in ecological networks using Infomap”. In: *Methods Ecol. Evol.* 12 (5), pp. 778–786. DOI: 10.1111/2041-210x.13569.

Felipe-Lucia, María R et al. (Nov. 10, 2020). “Land-use intensity alters networks between biodiversity, ecosystem functions, and services”. In: *Proc. Natl. Acad. Sci. U. S. A.* 117 (45), pp. 28140–28149. DOI: 10.1073/pnas.2016210117.

Fletcher, Michael-Shawn et al. (Oct. 5, 2021). “Indigenous knowledge and the shackles of wilderness”. In: *Proc. Natl. Acad. Sci. U. S. A.* 118 (40), e2022218118. DOI: 10.1073/pnas.2022218118.

Freitas, Carolina Tavares et al. (Mar. 2020). “Co-management of culturally important species: A tool to promote biodiversity conservation and human well-being”. In: *People Nat. (Hoboken)* 2 (1), pp. 61–81. DOI: 10.1002/pan3.10064.

Gilarranz, Luis J et al. (July 14, 2017). “Effects of network modularity on the spread of perturbation impact in experimental metapopulations”. In: *Science* 357 (6347), pp. 199–201. DOI: 10.1126/science.aal4122.

Gravel, Dominique et al. (July 1, 2010). “Source and sink dynamics in meta-ecosystems”. In: *Ecology* 91 (7), pp. 2172–2184. DOI: 10.1890/09-0843.1.

Gurdak, Daniel J et al. (Dec. 2022). “Local fisheries conservation and management works: implications of migrations and site fidelity of Arapaima in the Lower Amazon”. In: *Environ. Biol. Fishes* 105 (12), pp. 2119–2132. DOI: 10.1007/s10641-021-01171-y.

Instituto Brasileiro do Meio Ambiente (IBAMA) (2004). *Instrução Normativa 34, de 18 de junho de 2004*. https://www.ibama.gov.br/component/legislacao/?view=legislacao&legislacao=111150.

– (2005). *Instrução Normativa 1, de 01 de junho de 2005*. https://www.ibama.gov.br/component/legislacao/?view=

Jentoft, S et al. (June 26, 2017). *The small-scale fisheries guidelines: Global implementation*. Ed. by Svein Jentoft et al. 1st ed. Vol. 14. MARE Publication Series. Report. Basel, Switzerland: Springer International Publishing. 858 pp.

Keyes, Aislyn A et al. (Mar. 11, 2021). “An ecological network approach to predict ecosystem service vulnerability to species losses”. In: *Nat. Commun.* 12 (1), p. 1586. DOI: 10.1038/s41467-021-21824-x.

Lenth, Russell V (Jan. 2016). “Least-Squares Means: The R Package lsmeans”. In: *J. Stat. Softw.* 69, pp. 1–33.

Levis, Carolina et al. (Jan. 17, 2018). “How people domesticated amazonian forests”. In: *Front. Ecol. Evol.* 5. DOI: 10.3389/fevo.2017.00171.

Levis, Carolina et al. (May 19, 2024). “Contributions of human cultures to biodiversity and ecosystem conservation”. In: *Nat. Ecol. Evol.* 8 (5), pp. 866–879. DOI: 10.1038/s41559-024-02356-1.

Lopes, Priscila F M et al. (May 19, 2021). “Just Aquatic Governance: The Amazon basin as fertile ground for aligning participatory conservation with social justice”. In: *Aquat. Conserv.* 31 (5), pp. 1190–1205. DOI: 10.1002/aqc.3586.

Lopes Carvalho, Giulia Cristina et al. (Apr. 1, 2025). “Fisheries co-management strengthen the effectiveness of protected areas in Amazonian floodplain lakes”. In: *Fish. Manag. Ecol.* 32 (2), e12768. DOI: 10.1111/fme.12768.

Medeiros-Leal, Wendell M et al. (Mar. 2, 2021). “Single-species co-management improves fish assemblage structure and composition in a tropical river”. In: *Front. Ecol. Evol.* 9, p. 604170. DOI: 10.3389/fevo.2021.604170.

Naeem, S et al. (Dec. 14, 2016). “Biodiversity and human well-being: an essential link for sustainable development”. In: *Proceedings of the Royal Society B: Biological Sciences* 283, p. 20162091. DOI: 10.1098/rspb.2016.2091.

Preiser, Rika et al. (Dec. 19, 2018). “Social-ecological systems as complex adaptive systems: organizing principles for advancing research methods and approaches”. In: *Ecol. Soc.* 23 (4). DOI: 10.5751/es-10558-230446.

Reis-Filho, J A et al. (Apr. 15, 2023). “-I fish, therefore I monitor: Participatory monitoring to assess inland small-scale fisheries”. In: *Environ. Manage.* 72, pp. 1–18. DOI: 10.1007/s00267-023-01819-8.

Richard, Jordan C et al. (Dec. 1, 2018). “Size-structured habitat selection by arapaima in floodplain lakes of the Lower Amazon: Size-structured habitat selection by arapaima in floodplain lakes of the Lower Amazon”. In: *Aquat. Conserv.* 28 (6), pp. 1403–1413. DOI: 10.1002/aqc.2969.

Ricker, W E (May 1, 1954). “Stock and recruitment”. In: *J. Fish. Res. Board Can.* 11 (5), pp. 559–623. DOI: 10.1139/f54-039.

Rosvall, M, D Axelsson, and C T Bergstrom (Nov. 2009). “The map equation”. In: *Eur. Phys. J. Spec. Top.* 178 (1), pp. 13–23. DOI: 10.1140/epjst/e2010-01179-1.

Tukey, J W (June 1949). “Comparing individual means in the analysis of variance”. In: *Biometrics* 5 (2), pp. 99–114. DOI: 10.2307/3001913.

Venables, W N and B D Ripley (2002). *Modern Applied Statistics with S.* ISBN 0-387-95457-0. New York.

Wood, S et al. (Feb. 1, 2018). “Distilling the role of ecosystem services in the Sustainable Development Goals”. In: *Ecosystem services* 29, pp. 70–82. DOI: 10.1016/J.ECOSER.2017.10.010.