




RESEARCH ARTICLE

Panama Canal expansion and shifts in fishing practices: A social-ecological network approach

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Handling Editor: Sebastian Villasante**Abstract**

1. Species introductions have spiked over the past two centuries due to globalization. These introductions impact ecosystems, but may also have long-term implications for human communities. In one of the world's hubs for global shipping, the Panama Canal, a recent canal expansion has coincided with an increase in marine fishes entering the freshwater portion of the canal, Lake Gatun. These introductions may impact the lake's fishers who depend on that ecosystem for their livelihoods.
2. Social-ecological network (SEN) modelling presents a powerful tool to understand the combined impacts of these marine fish introductions on ecosystems and people. Using information from interviews with key stakeholders and available ecological data, this study constructs two SENs to analyse how the fish community composition and trophic links, as well as potential consequences on fishers' livelihoods and income from fishing, have changed after the canal expansion and the subsequent rise in marine fish species incursions.
3. We found a less connected network after the expansion with a lower diversity of income sources for fishers, indicating decreased fisher, and thus network, resilience. Fishers in Lake Gatun widely reported sharp increases in populations of marine fishes coinciding with a decline in their catch of historically targeted species (e.g. the introduced freshwater Peacock Bass, *Cichla cf. monoculus*). Network indices revealed differences in diversity of species targeted between small-scale fishers and recreational fishing guides, and thus variable susceptibility to economic impacts from ecosystem changes as a result of marine fish incursions.

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4. Our results demonstrate the importance of income and target species diversification in small-scale fishers' adaptive capacity to network-wide impacts resulting from marine fish species moving into a freshwater lake ecosystem. This study framework highlights the value of local ecological knowledge in building a more holistic and nuanced understanding of the consequences of biological invasions.
5. This study provides a first suggestion on how to adopt a SEN perspective for the analysis of species' invasion impact on aquatic ecosystems with the potential for application in policy-making at the Panama Canal and in other case studies concerned with the pressing issue of species introductions.

KEYWORDS

biological invasions, invasive alien species (IAS), marine fishes, non-native species, Peacock Bass, recreational fishing guides, small-scale fisheries

1 | INTRODUCTION

Travel and trade have become unprecedentedly fast and easy in a globalized world, with enormous impacts on ecosystems and economies (Hulme, 2009). One such impact has been the introduction of non-native species, which can result in increased predation pressure, habitat degradation, competition for resources, hybridization, disease transmission, depletion of native species populations, and biotic homogenization (Blackburn et al., 2019; IPBES, 2023; Jones et al., 2021; Pyšek et al., 2020). This myriad of environmental impacts is compounded with other anthropogenic pressures, including pollution, climate change, habitat fragmentation, and natural resource depletion (Parris, 2016). Aside from the impact that non-native species have on recipient ecosystems, they can also have long-term implications for human societies and economies (Cuthbert et al., 2021; Diagne et al., 2021). Said implications can, in some instances, provide financial and recreational services for people, further complicating management strategies (Kourantidou et al., 2022). Non-native species can disproportionately affect the livelihoods of people who depend on those ecosystems for sustenance and income, and can also have tangible impacts on human quality of life (Jones, 2017). Marine non-native species introductions present a unique set of monitoring and management challenges, often lacking the physical boundaries to territorial expansion generally present in terrestrial environments. Globally, invasive fish species have caused economic losses of over US\$37 billion since the 1960s, compared with an estimated figure of US\$424 billion for invasive mammals and US\$7.52 billion for invasive bird species. (Haubrock et al., 2022).

International maritime trade is a prominent vector for aquatic species introductions (Briski et al., 2013; Seebens et al., 2013). Human-made canals connecting major bodies of water are known hotspots for biological invasions (Castellanos-Galindo et al., 2020; Galil et al., 2015). The Suez Canal and Panama Canal are thus important research grounds for understanding the mechanisms and impacts of marine species introductions. Following the completion of an expansion project in the Panama Canal in 2016, there has been

a nearly 30% increase in the number of marine species present in Lake Gatun (Castellanos-Galindo et al., 2020; Castellanos-Galindo et al., 2025), the freshwater lake created during the Panama Canal's construction in the early 20th century, which connects the Pacific and Atlantic sides of the waterway (Rogers & Barrelier, 2018). These introductions are hypothesized to have had tangible effects on the lake's ecosystem and fish community, and thus have the potential to impact fishers in the area who rely on the lake and on its native and introduced freshwater fish species for their livelihoods (Balzani et al., 2022; Castellanos-Galindo et al., 2020).

From a research perspective, it is a challenge to develop investigative frameworks that allow us to examine the system-wide impacts of such an introduction event on ecological and human levels simultaneously. Social-ecological network (SEN) approach is useful for understanding the complexity of human–nature interactions (cf. Bodin et al., 2019; Kluger et al., 2020; Sayles et al., 2019). Rooted in network science, with nodes and links representing actors and their interactions within a social-ecological (SE) system, SENs have been constructed to model a wide variety of regimes, including fisheries (e.g. Barnes et al., 2019; González-Mon et al., 2019; Kluger et al., 2019; Yletyinen et al., 2018). As yet, however, SENs have not often been applied to assess impacts of multispecies aquatic invasions, though they could be an invaluable tool in such a layered and multifaceted context. The capacity of the SEN approach to illuminate both direct and indirect impacts of non-native species introductions, as well as resulting system-wide transformations, make this a uniquely appealing framework for examining invasion events (Runghen et al., 2023). While current literature in invasion biology often employs economic or ecological indices such as cost of economic losses; alien species richness; or alien species cover to measure impacts of non-native introductions (Catford et al., 2011), a SEN approach offers a multidimensional, overarching perspective on the impacts of invasion on an entire SE system (Rickowski et al., 2026).

Herein, we use SEN theory for understanding the impacts of biological invasions in the Panama Canal system. We include both introduced freshwater species and marine fishes that have migrated into

the freshwater part of the canal. Using two SENS of Lake Gatun in the Panama Canal, representing the pre- and post-expansion systems, we examined the impacts of the introduction of these species on the lake's ecology and the fishers who rely upon it. For purposes of this study, we placed fishers into two main archetypes. Artisanal fishers we define as those who fish for commercial sale; for food for their families and communities, without financial compensation; or for both of these purposes. Recreational fishing guides are considered to be those that earn money by taking clients to fish on the lake, many fishing to catch and release. We hypothesized that changes in the lake's fish community, driven by marine fish incursions after the canal's expansion, have altered the SE connectivity of fishers. As a result, both fisher archetypes and the dynamics of their livelihoods and income may have shifted.

2 | METHODS

2.1 | Study site description

The Panama Canal, a maritime canal nearly 30m above sea level, was opened in 1914 (Panama Canal Authority, 2006). Its construction involved the excavation and flooding of the area around the Chagres River (Span. Río Chagres), the natural river which previously flowed from the interior of the isthmus of Panama to the Atlantic Ocean. The river was dammed between 1910 and 1914, forming Lake Gatun, which would become the canal passageway for cargo ships moving between the Atlantic and Pacific oceans. This freshwater

lake comprises the interior portion of the canal and currently covers an area of about 430 km² (Panama Canal Authority, 2006; cf. Figure 1). Its creation involved the forced displacement of human communities which had historically resided in the area surrounding the Chagres River, ultimately amounting to a number of people equivalent to around 14% of Panama's population of the time (Lasso, 2019). Beginning in 1904, the region which was to become the Panama Canal was designated the Canal Zone, and rights to control the land in the zone were passed via treaty to the United States (Lasso, 2019). Over the years following, native inhabitants of the newly Americanized zone were segregated from American Canal Zone residents (Lasso, 2019). Most of the communities in the region pre-canal had historically relied on agriculture as well as business from international commerce via the Panama Railroad's isthmian railroad line that ran through the region (Carse, 2016; Lasso, 2019). When these communities were mandated by U.S. authorities to leave their homes, they were then told to move to predetermined sites for new towns, often with less fertile land and located far away from the railroad or any commerce centres, and left to create new livelihoods for themselves (Lasso, 2019). Many of the displaced communities which had once been situated near the Chagres River had fished the river for both fish and turtles (Lasso, 2019). In present-day communities surrounding Lake Gatun, some residents fish the lake to support themselves; some fishers fish for their own food or to sell, while some run recreational fishing businesses as guides for paying clients. Some fishers support themselves by both small-scale fishing and operating recreational fishing guide businesses.

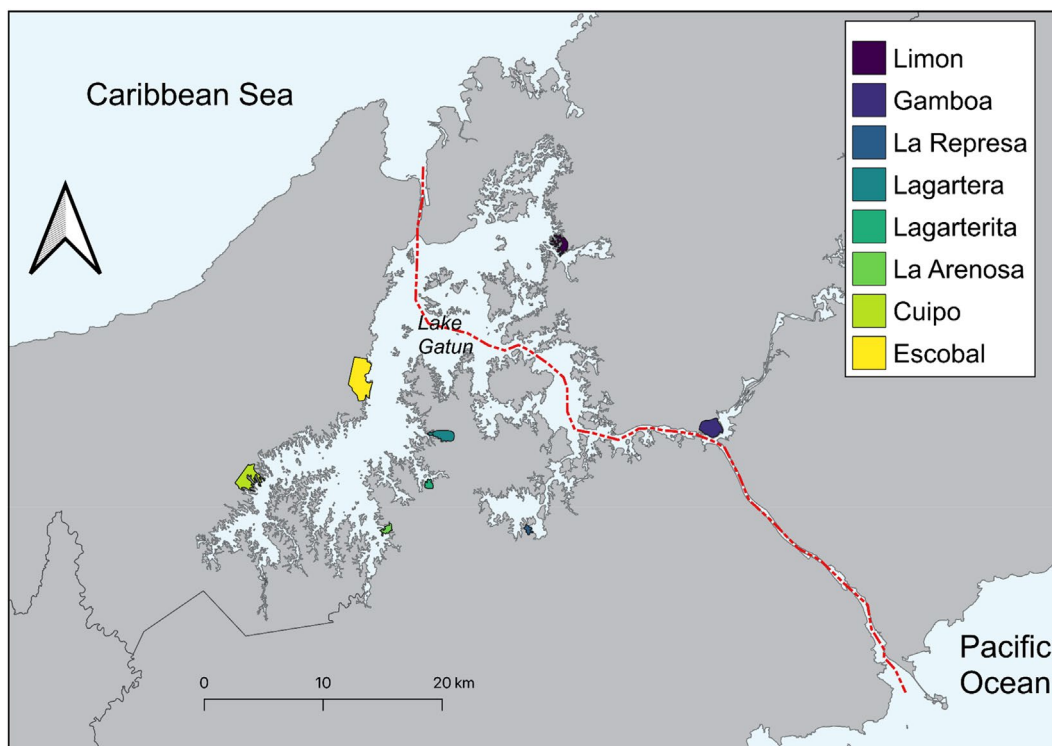


FIGURE 1 Map of the Panama Canal and Lake Gatun, showing locations of the eight communities in which fishers were interviewed. The red dotted line indicates the canal navigation path. Shape file of populated places around Lake Gatun taken from the STRI GIS Data Portal (<https://stridata-si.opendata.arcgis.com/>). Map created using QGIS software (QGIS.org, 2023).

Lake Gatun's fish community is composed of species from both the Pacific and Caribbean watersheds (Smith et al., 2004). The ecological system of this region has undergone several major shifts in the past, starting with the creation of the lake from the damming of the Chagres River during canal construction. The lake has remained as a freshwater system for over a century despite canal operation (Salgado et al., 2020). Nevertheless, for decades Lake Gatun has experienced the introduction of non-native freshwater fish species, mainly for aquaculture and recreational fishing purposes, and the incursion of marine fishes through the Panama Canal (Sharpe et al., 2023). The introduction of the freshwater South American Peacock Bass (*Cichla cf. monoculus*) in the early 1970s drastically altered the native littoral fish community of the lake, reducing it by over 95% (Sharpe et al., 2017; Zaret & Paine, 1973). Peacock Bass have become a staple species for consumption, income and recreation for the lake's fishers. By 1986, data from fishing communities around the lake estimated an annual catch of Peacock Bass of 212 tonnes per year, attributable mostly to community sustenance (45%), and in part also to recreational (29%) and small-scale fishing (25%) (Maturell & Tapia, 1991). Nile Tilapia (*Oreochromis niloticus*), a freshwater species native to Africa, is another major target of fishers in Lake Gatun. Nile Tilapia and other Tilapia species were first introduced to the lake in 1976 for sport fishing (Sharpe et al., 2023). Other introduced freshwater species include Jaguar guapote (*Parachromis managuensis*) and Oscar (*Astronotus ocellatus*) (Sharpe et al., 2017). Additionally, marine fish species have been reported in the lake over the years, including Atlantic Tarpon (*Megalops atlanticus*), present since at least 1935 (Hildebrand, 1937; Sharpe et al., 2023); Snooks (*Centropomus* spp.), first reported in 2017 (save for one reported sighting in 1944); and Jacks (*Caranx* spp.), also first reported in 2017. The newest wave of fish migrations into the Canal following expansion has altered the trophic structure of the lake yet again (Sharpe et al., 2023).

2.2 | SEN conceptualization

Broadly, networks consist of entities (nodes) and the connections between them (edges), and can be used to model many different types of systems depending on the research context (Strogatz, 2001). SENs represent relational structures of human or biological actors (nodes) and their interactions (links or edges). In SENs, three types of links may connect ecological (E) and social (S) actors (sensu Bodin & Tengö, 2012): between ecological nodes (ecological-ecological (EE) links), between social nodes (social-social (SS) links), or connecting social and ecological nodes (SE links).

For the present study, the networks' social dimension represents the supply chain from the lake's fishers to consumers, and the biological dimension depicts fisheries target species. The links between social nodes (SS links) then represent seller-buyer relationships. They thus indicate two types of "flows": monetary flow in one direction and biomass flow in the opposite direction (money for fish), with the only exception being social-social links between tourist nodes

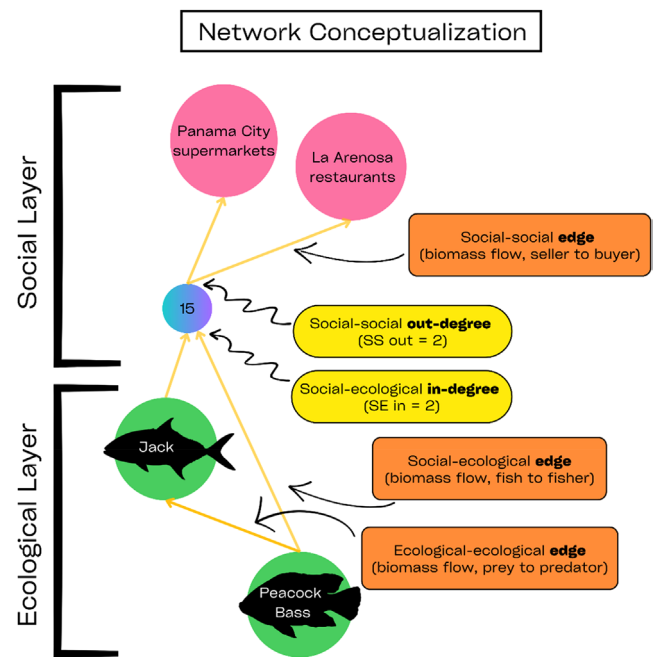


FIGURE 2 Conceptualization of the social-ecological network approach applied in the present work. Pink nodes represent supply chain actors (i.e. buyers of fish). Individual fishers are represented by blue (artisanal), purple (recreational guides), and blue-purple (both) nodes. The directed yellow connections between nodes represent biomass flow (i.e. from fish to fisher, from fisher to supermarket, or from prey fish to predator fish). In this example, Fisher 15 has an SE in-degree of two, as this fisher targets two fish species. Fisher 15 has an SS out-degree of two, because they sell fish to two buyers.

and fisher nodes, which only represent monetary flow in one direction, from tourists to fisher. The different types of "flows" (monetary and biomass) can be viewed as two distinct layers for analysis: one at the level of biomass transfer and the other at the level of monetary transfer. Biomass flow, in the context of this study, is defined qualitatively, rather than quantitatively, by the presence of a predation or harvest relationship from one node to another. For network analysis, the entire network level was used, complemented with a zoom-in on the SE connectivity of fishers via an ego-network approach (sensu Kluger et al., 2025). For this, the fisher – as the main agent at the human–nature interface – is placed in the centre of analysis (Figure 2), or the central node (the ego) of the ego-network, with their connections to actors (the alters) into the human and environmental realms characterizing particular archetypes of SE connectivity (Kluger et al., 2025).

2.3 | Network building and analysis

The goal of the analysis was to assess changes in the connectivity and robustness of the network, and in the fishing-dependent financial vulnerability of individual fishers. Edge density was calculated using the "igraph" package in R (Csárdi & Nepusz, 2006).

Node degrees were also calculated with “igraph”; these included out-degrees of biomass flow for both fish and fisher nodes, as well as in-degrees of monetary flow for fishers. Igraph was also used to estimate the diameter of each network. Analyses to compare both networks were performed using R statistical software (v4.3.0; R Core Team, 2023).

Dominator tree analysis, a method stemming from network analysis in ecology (REFs), was first applied to SEN analysis in Kluger et al. (2019), and was found useful to identify dominating pathways within a network describing flows; and as such useful for SENs depicting fisheries settings and fisheries products. Dominator tree analysis helps identify which nodes of the network are sequentially connected based on their dominance relations (Allesina & Bodini, 2004), with any node A dominating another node B if every path to B contains A. Identifying which actors dominate the SEN allows predicting the cascading effects and risks of secondary extinctions from the structure itself (Kluger et al., 2019).

Node degree ratios are a valuable tool for quantifying the resilience of network components (Ren et al., 2022). Our work follows the conceptualization of SE connectivity of fishers as introduced by Kluger et al. (2025) and as such considers the ratio of SE in-degrees (SE in-degrees) to social-social out-degrees (SS out-degrees) of

individual fishers a proxy for relative resilience of different nodes and between pre- and post-expansion. SE in-degrees depict qualitative biomass flows from fish to fisher and serve to quantify each fisher's number and diversity of target catch species. Social-social out-degrees represent qualitative biomass flows from seller to buyer. For fishers, they reflect the number and diversity of direct income sources to each fisher from fish sales. Therefore, the ratio of SE in-degrees to social-social out-degrees (SE-in: SS-out degree ratio) for each fisher can be interpreted as the ratio of their diversity of catch to their diversity of income sources. A high diversity of both indicates a higher adaptive capacity of individual fishers (Anderson et al., 2017; Subramaniam et al., 2023), which we hypothesize to increase overall network (system) resilience. A ratio below one is indicative of a higher diversity of income sources and a lower diversity of catch, while a ratio well above one indicates a relatively high diversity of catch and a low diversity of income sources.

The specific network parameters chosen for analysis were selected because they each represent different perspectives from which to examine the connectedness of a network, and of specific nodes within that network (Bodin & Tengö, 2012; Kluger et al., 2019; Table 1). We are, with our focus on value chain dynamics, interested in the flow of things throughout the network, and the analysis of

TABLE 1 List of network parameters, their technical definitions and how they can be interpreted in the context of this study.

Network parameter	Definition from the literature	Application in this work
Edge density	The number of links in existence in the network divided by the number of possible links in the network (Janssen et al., 2006). This parameter has a maximum value of 1	The relative connectivity of the pre- versus post-expansion networks (Bhattacharya et al., 2023)
In-degree	The number of links pointing into a node in a directed network (Wasserman & Faust, 1994)	The number of fishers targeting a particular species (fish nodes, as part of the SE-connectivity calculation) (Fornito et al., 2016; Masawi, Roy, & Ghosh, 2023)
Out-degree	The number of links coming out of a node in a directed network (Wasserman & Faust, 1994)	The number of income sources from fishing for an individual fisher (as part of the SE-connectivity) (Fornito et al., 2016; Masawi, Roy, & Ghosh, 2023)
Diameter	The longest geodesic (shortest possible path) between two nodes in the network (Csárdi & Nepusz, 2006)	The latency of exchange within the network and the longest path through the network (Bhattacharya et al., 2023)
Dominator tree	One vertex <i>v</i> which is dominated by another vertex <i>w</i> if every possible path from the starting vertex to <i>v</i> must travel through <i>w</i> (Knakkegaard Christensen, 2016)	Which nodes are exclusively dependent on a single node for income (in the case of monetary flow dominator trees) or fish (in the case of biomass flow dominator trees) (Kluger, Scotti, Vivar, & Wolff, 2019)

patterns on the entire network level. Edge density, diameter, and node degrees are parameters that give us insight into flow within the network and between specific nodes. Dominator tree analysis provides insights into which nodes are dominating flow pathways within the network, allowing us to evaluate changes in network structures following the introduction or disappearance of nodes, as is our focus. Since methodological and theoretical approaches in the rather new field of SEN research are still fragmented and would benefit from comparable measures (Sayles et al., 2019; Kluger et al., 2020), we decided to apply metrics that have been successfully used in published work.

2.4 | Data collection

Interviews and various literature sources were used to conceptualize and parametrize the SENs. Interviews were conducted with social actors between March and June of 2023. These included key experts ($n=6$) on the history of Lake Gatun and its ecosystem, as well as fishers ($n=38$) living in various communities around Lake Gatun. Key experts were considered to be individuals with in-depth knowledge and experience of the lake's SE system and its history. Conversations lasted between 5 and 45 min, depending on the disposition of the interviewee, in a location that best suited them. Of the six key expert interviews conducted, four were recorded and transcribed, while physical notes were taken during interviews with the remaining two. These interviews were conducted to inform the approach to the network building process, and the information gathered from key experts did not directly inform any nodes or links within the network. Rather, they were used to provide contextual information for framing the network conceptualization, and for interpreting network analysis results. They were conversational, with the aim of gaining as much background information on the history of the lake's system as possible, from an ecological, political, and sociological point of view.

Interviewees were identified and contacted using a snowball sampling method (Johnson, 2005), by which initial contacts provided further contacts. A total of 38 fisher interviews, with both small-scale fishers ($n=29$) and recreational fishing guides ($n=9$), were conducted and recorded using a handheld voice recorder after study goals were introduced and informed consent was obtained (cf. section Ethic and consent statement, and the interviewee guide provided in [Material S1](#)). A minimum of three individuals were interviewed per fishing town (Cuipo ($n=4$), Escobal ($n=5$), Limon ($n=8$), Lagartera ($n=5$), Lagarterita ($n=3$), La Arenosa ($n=6$), La Represa ($n=4$), and Gamboa ($n=3$)). These towns were chosen for both pre-existing contacts, as well as for their location around the lake, ranging from the Pacific to the Atlantic side of the canal ([Figure 1](#)). In communities in which no initial contact was present, we spent time around the fishing or gathering centres of the community, such as the public docks or town centres, and approached people to inquire about which members of the community they knew to be fishers.

Once initial contacts were established, further contacts were established by referral.

The snowball sampling method utilized in this study presents a potential source of sample bias in comparison with a completely randomized or stratified sample design. For example, individuals who had to leave the fishery entirely may have been missed, thus leading to an underestimation of livelihood losses. Though this may be a potential limitation of the study's sample design, a systematic survey design would have been logistically challenging and outside the scope of time and funding available for the project. Snowball sampling can be an effective method in ethnographic research of reaching groups or individuals who might otherwise be difficult to encounter (Naderifar et al., 2017). Furthermore, although sample bias introduced by snowball sampling methods hinders the capacity for generalization of study results to an entire population, it does allow for an in-depth and contextualized exploration of the central phenomenon being investigated (Creswell & Guetterman, 2019).

Interviews were semi-structured (Longhurst, 2003) using a pre-defined list of topics and questions (available in [Material S1](#)). They were conducted in Spanish in a conversational context. Interviewees were asked about which fish species they targeted when fishing; how their catch had changed between the two time periods of pre- and post-canal expansion; whether they fished artisanally, as recreational fishing guides, or both; and who they sold their fish or fishing services to. To avoid leading interviewees to draw causal relationships between the canal expansion and changes in their catch or in the ecosystem, questions about conditions pre-expansion were framed in a context of 10–15 years prior, without mentioning the expansion.

Fisher interviews were recorded using a handheld voice recorder. Interview recordings were transcribed, aided by the transcription function of Microsoft Word, and information was then coded and extracted. Information was coded based on a hybrid deductive and inductive approach for qualitative data (Vears & Gillam, 2022). Inductive coding was applied to identify and extract information describing links (SS, SE, EE) or nodes (ecological, social). Deductive coding was applied to sort other relevant information regarding overall ecosystem or sociological history and trends that were repeated by multiple fishers in separate interviews and was also identified in the analysis of interview texts. Coded interview data were then organized categorically in a spreadsheet to be utilized for quantitative network analysis.

Finally, ecological links were added: Trophic (EE) links in the ecological dimension of the network were gathered from a variety of literature sources ([Table S5](#)). Partially informed by the interviews, the pre-expansion period to be represented by the network was that of 2000–2010, due to the peak size and involvement of the fishing cooperatives in the towns of Cuipo and Escobal (see [Figure 1](#)) in the network of the lake during this time. The post-expansion period was defined as that of 2016 to the present, or following the completion of the canal expansion project.

2.5 | Ethics and Consent Statement

This study was approved by the ethics committee at the Smithsonian Tropical Research Institute, and a permit was obtained for conducting research involving human subjects prior to initiating the study (Permit number HS23021). All identifying personal data were kept confidential and not included in results. Interviews were completely voluntary, and interviewees were informed of their right to opt out or refuse to be interviewed at any time. Interviewees were asked for their consent to be recorded prior to being interviewed and were verbally informed that their anonymity would be maintained and their identities would not be made public, as well as of other rights taken from a written statement of informed consent.

3 | RESULTS

The pre-expansion network consisted of 62 nodes and 234 links, and the post-expansion network of 64 nodes and 237 links. The number of sellers decreased from 36 pre-expansion to 30 post-expansion sellers. The number of ecological nodes increased from pre- to post-with the introduction of new marine fish species whose presence was not recorded prior to expansion. These were the Needlefish (*Strongylura marina*) and the Weakfish (*Cynoscion albus*), both species whose numbers were said by interviewees to have increased in the time following the Panama Canal expansion. Recent studies have found Needlefish to be markedly general predators in the lake, making them one of the more highly connected nodes in terms of predator-prey relationships in the ecological dimension of the post-expansion network (Strasiewsky, 2023).

About 92% ($n=35$) of fishers indicated that their catch was decreasing, compared with their catch 10–15 years prior. When asked to describe the changes in their catch, 95% ($n=36$) of fishers interviewed relayed that their catch of Peacock Bass had declined over the stated time period. Some interviewees stated that they used to be able to fill one bucket in 1 day, or even hours, with little fishing effort. In more recent times, more time and effort were required to achieve the same volume of catch. Many fishers stated that they now had to fish every day in the week, rather than 2–3 days of the week; others cited that they now needed to spearfish as opposed to fishing with a line, because it was the only way they could catch the same volume needed to sustain them. None of the fishers related this change directly, however, to the expansion of the canal. Instead, many associated the expansion with the appearance and proliferation of new marine fish species (Figure 3).

Network edge density decreased between pre- and post-expansion from 0.0608 to 0.0553, respectively. A comparison of monetary in-degrees for all fisher nodes in the networks, or all the direct income sources from fishing held by each fisher, revealed a shift between pre- and post-expansion in which a number of fishers saw a decrease in their monetary in-degree. In other words, these fishers lost one or more

income sources from the sale of fish caught in Lake Gatun. Fourteen (37%) of the 38 individuals interviewed reported a loss in the number of sources of income from fish sales, while six fishers (16%) lost all income sources from fish sales altogether.

The comparison between pre- and post-expansion out-degrees for all fish species, as a proxy for determining how fishing pressure on each species has changed, revealed little change between the two time periods. Two new species were added into the network post-expansion: Weakfish and Needlefish, while the species with the highest out-degrees, or the most heavily targeted, were consistently Peacock Bass, Snook, and Jack, consecutively.

Overall, fishers with a ratio of zero for either time period were those who either lost all their income sources from fish sales post-expansion, in the case of small-scale fishers, or never sold fish for income, in the case of most recreational fishing guides. Recreational fishing guides tended to have a higher diversity of catch in relation to a lower diversity of income sources compared with small-scale fishers. Both recreational fishing guides and small-scale fishers saw a ratio increase between pre- and post-expansion. This would suggest an increase in diversity of targets, a decrease in income sources, or both simultaneously. As many of them had a ratio of zero either pre-expansion, post-expansion, or both due to a lack of SS-out degrees from not selling fish, small-scale fishers overall had a lower average SE-in:SS-out ratio than recreational fishing guides.

In the case of small-scale fishers, the ratio increase from pre- to post-expansion likely reflects a decline in the number of income sources from fish sales, as few of them fished many new species post-expansion. This is also true for fishers who had a ratio of zero post-expansion, as these fishers lost all of their income sources. For recreational fishing guides, this ratio increase could be attributed to their targeting recently arrived marine species and maintaining income from tourism.

Peacock Bass was an immediate dominator of three fishers (14, 15, and 22) in the flow dominator trees for both time periods (Figure 4). It was the only fish species upon which some fishers relied exclusively for their catch in both time periods.

Post-expansion, the number of fisher nodes that were directly dominated by one income source increased; as resulting from the monetary flow dominator trees for both time periods. Examples of these are the higher number of fishers directly dominated by individual buyers, both from within and outside of their respective fishing communities (Figure 5), particularly in the communities of Lagarterita and Lagartera. Additionally, there was an overall decrease in the number of fisher nodes present in the post-expansion tree compared with that of pre-expansion, though this is not visible from the figures due to the exclusion of all nodes without an immediate dominator. The disappearance of some fisher nodes from the tree from pre- to post-expansion is indicative of a loss of all income sources from fish sales for those nodes. Overall, there was a higher number of dominance relationships in the post-expansion monetary flow tree, pointing to a decrease in the diversity of income sources from fishing for individual fishers.

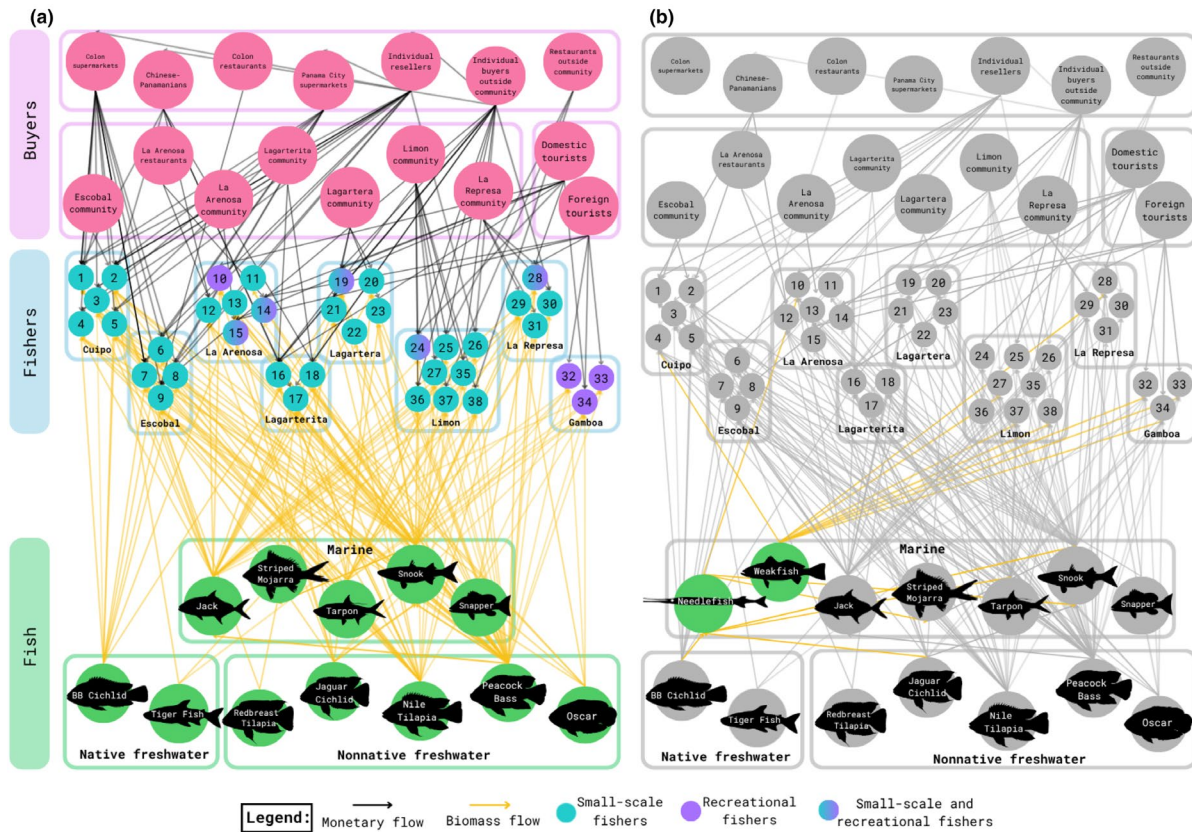


FIGURE 3 Full pre-expansion (a) and post-expansion (b) networks. Node sizes are not indicative of the relative size of each group. Pink nodes represent all buyers of fish and fish-related services. Fisher nodes are in blue (small-scale), purple (recreational guides), and blue-purple (both). Fisher nodes are grouped based on the fishing community (cf. the map in Figure 1). Green nodes represent fish species. Species in light green are those that were newly present in the post-expansion network only. The species represented in the network result from being listed by interviewed fishers as direct targets of their fishing. Black links represent monetary flows. Yellow links represent biomass flows. Links in colour in panel B represent edges associated with newly introduced marine species, also in colour.

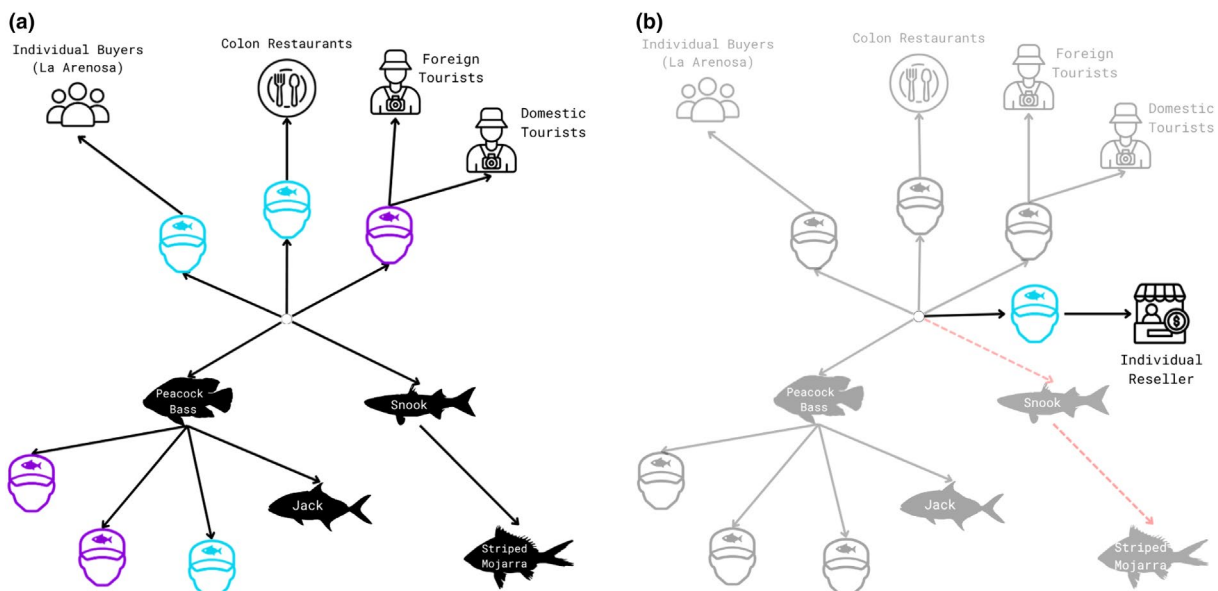


FIGURE 4 Pre-expansion (a) and post-expansion (b) dominator trees of biomass flows. Recreational fishing guides are in purple, while artisanal fishers are in blue. Edges and nodes in colour in panel B are new in the post-expansion tree, while edges in red were lost between pre- and post-expansion. The figure displays only branches of the trees that held dominator relationships. Nodes which are only dominated by the root node are not displayed.

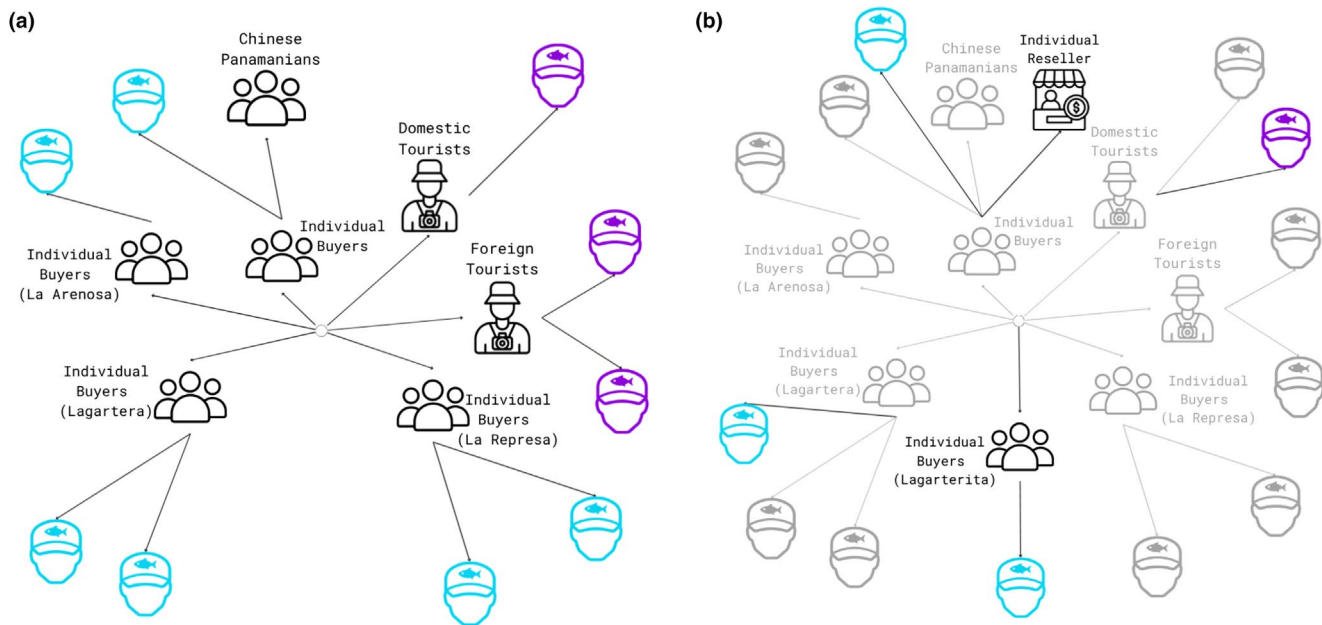


FIGURE 5 Pre-expansion (a) and post-expansion (b) dominator trees of monetary flows. Recreational fishing guides are in purple, while artisanal fishers are in blue. Edges and nodes in colour in panel b are new in the post-expansion tree. The figure displays only branches of the tree that depict dominator relationships. Nodes that are only dominated by the root node are not displayed.

4 | DISCUSSION

We hypothesized that accelerated marine fish incursions into Lake Gatun following canal expansion would alter the way in which fishers operated and the fishes they caught, affecting the connectivity of the SEN and fishers' livelihoods from fishing. Overall, our results indicate that the post-expansion SEN of Lake Gatun is less connected than the pre-expansion network. This is evidenced by the decrease in edge density and an increase in dominance structures: a greater number of fishers who are now reliant upon only one or zero income sources from fishing. A higher diversity of target species and income sources among recreational fishing guides afforded them greater adaptive capacity, in network terms, than their purely small-scale counterparts. The causes of these overall network changes between the pre- and post-expansion networks appear to be both multifaceted and highly contextual.

4.1 | Ecological shifts and reduced catch per unit effort

Among interviewees, there was a widely reported decrease in catch per unit effort (CPUE). This shift appears to have coincided with a decrease in the overall connectivity of the network. Not only were fishers unable to catch as many fish, but some were no longer able to sell fish because they were able to catch only enough to feed their families and communities. It is important to note, though, that reports by fishers can be influenced by recall bias, which can sometimes influence fishers to overestimate catch in the short term

(Gundeland et al., 2023) while underestimating or recalling declining trends in the long term (Aylesworth & Kuo, 2018).

The reported decrease in CPUE can be hypothetically attributed to several factors, in addition to the trophic changes taking place as a result of increased number of marine predators inside the canal (Castellanos-Galindo et al., 2025). One such factor is overexploitation due to the potential influx of fishers into the lake during the COVID-19 pandemic due to the resulting spike in unemployment (CEPAL, 2022) and the following increase in Panamanian employment in the agricultural sector (Statista, 2023). Another is that fishing activity in communities around the lake is relatively unregulated by any of the governmental bodies managing the canal and the surrounding environment.

4.2 | Adaptive capacity of Lake Gatun fishers

The adaptive capacity of fishers in the lake appears to have been adversely impacted between pre- and post-expansion, based on the decrease in network edge density, increase in monetary dominance relationships, and changes in SE-in:SS-out degree ratios for fishers. All of these network changes point to the decreased diversity of income for the lake's small-scale fishers in particular, likely caused by changes in fish abundances as well as loss of self-organization (fishing cooperatives) among the fishers themselves. Recreational fishing guides appeared to be better suited to withstand network disruptions, as evidenced by their generally higher SE-in to SS-out degree ratios when compared with those of small-scale fishers.

In the 1980s, three groups of fishing cooperatives were established among fishers in communities around the lake, with the help

of the Panamanian Aquaculture Authority (Maturell, 1984). These cooperatives were formed by groups of fishers to produce enough fishing yield to make agreements with supermarkets in the nearest major cities, Colón and Panama City, to sell them fish. In network terms, the presence of fishing cooperatives afforded fishers a generally higher monetary in-degree than when the cooperatives were no longer present in the post-expansion time period. The deterioration of these fishing cooperatives, which were important for small-scale fishing businesses and network connectivity, was the result of a number of coinciding factors. According to an ARAP official, the cooperatives disappeared in part due to their limited capacity to transport their catch to nearby major cities, for lack of cars and well-paved roads, as well as due to an inability to consistently meet supermarket volume demands for widely marketable species such as Peacock Bass and Nile Tilapia. By the late 2000s, following the disappearance of most of the lake's fishing cooperatives, fishers no longer had the capacity to maintain their prior sales relationships with the supermarkets, leading to the loss of a number of buyer-seller links in the social dimension of the network from pre- to post-canal expansion. The decrease in edge density and loss of income sources for small-scale fishers can therefore be attributed in part to the loss of these organizations. The self-organization of the fishing community served to strengthen the adaptive capacity of fishers in the pre-expansion network in that it allowed them to establish a communication channel with supermarket buyers, diversify their sale portfolios by enabling those relationships with supermarket buyers, and generally advocate for themselves and their livelihoods from fishing, all factors which contribute to the adaptive capacity of small-scale fisheries supply chains (Basurto et al., 2013).

Reliance on few or a single species can be another factor that increases the sensitivity of nodes within a network to disturbance (Bassett & Pasqualetti, 2020; Kluger et al., 2019). In this case, the high degree of reliance of the network as a whole on Peacock Bass could be a source of vulnerability. However, the second- and third-most targeted species among fishers, Snook and Jack, are both marine species. This would indicate that fishers, particularly recreational fishing guides, have already begun to adapt their fishing practices to newly introduced species and may continue to do so.

4.3 | Implications for the future of Lake Gatun's fish and fishers

The results of this study are a snapshot of the many complex and coinciding changes taking place within this system following the canal expansion. These findings allow us to make some predictions for how this system might change in the future: We might expect to see the presence of marine species continue to grow, while CPUE of more traditionally targeted species such as *Cichla* cf. *monoculus* and *O. niloticus* could continue to decline. Fishers' livelihoods will likely be increasingly impacted by these ongoing ecological changes. Recreational fishing guides may become a more popular vocation for some fishers around the lake, and they may find that it can provide

a more consistent income. However, this may also be limited by a lack of infrastructure to support tourism in some regions around Lake Gatun. Both recreational guides and small-scale fishers may increasingly target more recently available marine species. For recreational fishing guides, this is already the case, as many of these marine fish are also popular game fish for recreational fishing. All of these implications could be relevant to environmental planning and policy-making around Lake Gatun and the Panama Canal, as well as for social policies in the fishing towns surrounding the lake.

4.4 | SENs as a tool for capturing the wider implications of biological invasions

To the best of our knowledge, this is one of only a few attempts to examine the impacts of species invasions through a SEN lens. Its novelty calls for some reflection upon successes and opportunities for improvement for future applications of this method in other SE systems. This framework for examining impacts of biological invasions yields a much more complex chain of impacts than when such events are examined from an ecological perspective alone. This makes it difficult to conclusively determine direct causality between species invasion events and consequent network-wide changes. However, this study serves to show that the value of such a framework lies, in fact, in this same capacity to reveal overarching impacts on an ecosystem in the context of the other inevitably numerous and interconnected social and ecological shifts taking place concurrently within the system. This trade-off is also recognized by Downing et al. (2014), in which a SEN approach was used to attempt to disentangle the drivers of change in fisheries in East Africa's Lake Victoria. A birds-eye view of overarching impacts on ecosystems and people is desirable and sought-after in policy-making; SENs could play an important role in aiding and informing policymakers.

Bodin and Tengö (2012) discussed the potential for SENs to be used to gain information about overall trends within a SE system, to make informed hypotheses to be investigated more closely and specifically. In the case of this study, this was a major advantage of this framework for analysis, due to how many factors were really at play, both social (e.g. COVID-19 pandemic) and ecological (e.g. previous freshwater fish introductions), that would determine the effects of marine species incursions on this system. The network attribute of node degrees allows for the identification of weak points for further investigation within the network. In the case of the networks created for this study, the nodes of particular interest were fisher nodes with low monetary in-degrees or low biological in-degrees and fish nodes with high out-degrees, because these metrics revealed which fisher nodes were highly specialized in their income source or catch and which fish nodes were most heavily fished. Highly specialized fisher nodes have been documented in the SE literature to be those most likely to be affected negatively by network disturbances (Kluger et al., 2019), and therefore are of great interest to researchers investigating potential impact mitigation, in the case of species invasions as well as other anthropogenic ecological disturbances. In other words, the SEN approach can provide an overview of the network and its "weak" points, or points of

particular interest for disturbance mitigation, and make informed hypotheses for further investigation from this overview.

Finally, the integration of data collected from local ecological knowledge into SENs allows for the inclusion of human perspectives on the impacts of non-native species introductions. The local ecological knowledge possessed by fishers and other individuals is indispensable for ecosystem management, and by extension for the management of impacts of relevant species invasions. Not only is local ecological knowledge important for ecosystem-based management approaches, it also includes fishers and other stakeholders in the development of management strategies (Haggen et al., 2007), which is ultimately crucial.

AUTHOR CONTRIBUTIONS

Gustavo A. Castellanos-Galindo and Lotta C. Kluger conceived the ideas and designed the methodology, with input from Michelle Hübel, Jonathan M. Jeschke, and Elizabeta Briski. Michelle Hübel, Victor Bravo, and Gustavo A. Castellanos-Galindo collected the data. Interviews were conducted by Victor Bravo and Michelle Hübel. Michelle Hübel, Gustavo A. Castellanos-Galindo, and Lotta C. Kluger analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication. The nature of the framework of this study is to include input and knowledge from local stakeholders in the analysis. As such, our study and the authors ensured that intellectual input from stakeholders in the region was not only included but central to our analysis.

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CONFLICT OF INTEREST STATEMENT


All authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and supplementary materials are available on figshare at <https://doi.org/10.6084/m9.figshare.31830214>.

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REFERENCES

- Allesina, S., & Bodini, A. (2004). Who dominates whom in the ecosystem? Energy flow bottlenecks and cascading extinctions. *Journal of Theoretical Biology*, 230(3), 351–358. <https://doi.org/10.1016/j.jtbi.2004.05.009>
- Anderson, S. C., Ward, E. J., Shelton, A. O., Adkison, M. D., Beaudreau, A. H., Brenner, R. E., Haynie, A. C., Shriver, J. C., Watson, J. T., & Williams, B. C. (2017). Benefits and risks of diversification for individual fishers. *Proceedings of the National Academy of Sciences of the United States of America*, 114(40), 10797–10802. <https://doi.org/10.1073/pnas.1702506114>
- Aylesworth, L., & Kuo, T.-C. (2018). Reporting time period matters: Quantifying catch rates and exploring recall bias from fisher interviews in Thailand. *Canadian Journal of Fisheries and Aquatic Sciences*, 75(12), 2114–2122. <https://doi.org/10.1139/cjfas-2017-0169>
- Balzani, P., Cuthbert, R. N., Briski, E., Galil, B., Castellanos-Galindo, G., Kouba, A., Kourantidou, M., Leung, B., Soto, I., & Haubrock, P. J. (2022). Knowledge needs in economic costs of invasive species facilitated by canalization. *Neobiota*, 78, 207–223. <https://doi.org/10.3897/neobiota.78.95050>
- Barnes, M. L., Bodin, Ö., McClanahan, T. R., Kittinger, J. N., Hoey, A. S., Gaoue, O. G., & Graham, N. A. J. (2019). Social-ecological alignment and ecological conditions in coral reefs. *Nature Communications*, 10(1), 2039. <https://doi.org/10.1038/s41467-019-09994-1>
- Bassett, D., & Pasqualetti, F. (2020). Network-based approaches for understanding intrinsic control capacities of the human brain. In *The Cognitive Neurosciences* (pp. 729–738). MIT Press. <https://doi.org/10.7551/mitpress/11442.003.0079>
- Basurto, X., Gelcich, S., & Ostrom, E. (2013). The social-ecological system framework as a knowledge classificatory system for benthic small-scale fisheries. *Global Environmental Change*, 23(6), 1366–1380. <https://doi.org/10.1016/j.gloenvcha.2013.08.001>
- Bhattacharya, S., Sinha, S., Dey, P., Saha, A., Chowdhury, C., & Roy, S. (2023). *Online social-network sensing models* (pp. 113–140). Elsevier eBooks. <https://doi.org/10.1016/b978-0-32-390535-0.00010-0>
- Blackburn, T. M., Bellard, C., & Ricciardi, A. (2019). Alien versus native species as drivers of recent extinctions. *Frontiers in Ecology and the Environment*, 17(4), 203–207.
- Bodin, Ö., Alexander, S. M., Baggio, J., Barnes, M. L., Berardo, R., Cumming, G. S., Dee, L. E., Fischer, A. P., Fischer, M., Mancilla Garcia, M., & Guerrero, A. M. (2019). Improving network approaches to the study of complex social-ecological interdependencies. *Nature Sustainability*, 2, 551–559. <https://doi.org/10.1038/s41893-019-0308-0>
- Bodin, Ö., & Tengö, M. (2012). Disentangling intangible social-ecological systems. *Global Environmental Change*, 22, 430–439. <https://doi.org/10.1016/j.gloenvcha.2012.01.005>
- Briski, E., Bailey, S. A., Casas-Monroy, O., DiBacco, C., Kaczmarek, I., Lawrence, J. E., Leichsenring, J., Levings, C., MacGillivray, M. L., McKindsey, C. W., Nasmith, L. E., Parenteau, M., Piercey, G. E., Rivkin, R. B., Rochon, A., Roy, S., Simard, N., Sun, B., Way, C., ... MacIsaac, H. J. (2013). Taxon- and vector-specific variation in species richness and abundance during the transport stage of biological invasions. *Limnology and Oceanography*, 58(4), 1361–1372. <https://doi.org/10.4319/lo.2013.58.4.1361>
- Carse, A. (2016). “Like a work of nature”: Revisiting the Panama Canal's environmental history at Gatun Lake. *Environmental History*, 21(2), 231–239. <http://www.jstor.org/stable/24691582>

- Castellanos-Galindo, G. A., Robertson, D. R., Sharpe, D. M. T., & Torchin, M. E. (2020). A new wave of marine fish invasions through the Panama and Suez canals. *Nature Ecology & Evolution*, 4, 1444–1446. <https://doi.org/10.1038/s41559-020-01301-2>
- Castellanos-Galindo, G. A., Sharpe, D. M. T., Robertson, D. R., Bravo, V., Jeschke, J. M., & Torchin, M. E. (2025). New fish migrations into the Panama Canal increase likelihood of interoceanic invasions in the Americas. *Current Biology*, 35, 1–9. <https://doi.org/10.1016/j.cub.2025.01.049>
- Catford, J. A., Vesik, P. A., Richardson, D. M., & Pyšek, P. (2011). Quantifying levels of biological invasion: Towards the objective classification of invaded and invadable ecosystems. *Global Change Biology*, 18(1), 44–62. <https://doi.org/10.1111/j.1365-2486.2011.02549.x>
- CEPAL. (2022). *Economic survey of Latin America and the Caribbean*. CEPAL.
- Creswell, J. W., & Guetterman, T. C. (2019). *Educational research: Planning, conducting, and evaluating quantitative and qualitative research* (6th ed.). Pearson.
- Csárdi, G., & Nepusz, T. (2006). The Igraph software package for complex network research. *InterJournal, Complex Systems*, 1695, 1–9.
- Cuthbert, R., Pattison, Z., Taylor, N., Verbrugge, L., Diagne, C., Ahmed, D., Leroy, B., Angulo, E., Briski, E., Capinha, C., Catford, J., Dalu, T., Essl, F., Gozlan, R., Haubrock, P., Kourantidou, M., Kramer, A., Renault, D., Wasserman, R., & Courchamp, F. (2021). Global economic costs of aquatic invasive alien species. *Science of the Total Environment*, 775, 145238. <https://doi.org/10.1016/j.scitotenv.2021.145238>
- Diagne, C., Leroy, B., Vaissière, A.-C., Gozlan, R. E., Roiz, D., Jarić, I., Salles, J.-M., Bradshaw, C. J. A., & Courchamp, F. (2021). High and rising economic costs of biological invasions worldwide. *Nature*, 592, 1–6. <https://doi.org/10.1038/s41586-021-03405-6>
- Downing, A. S., van, N., Baliwra, J. S., Beuving, J., Bwathondi, P. O. J., Chapman, L. J., Ilse, C., Iain, G., Kees, G., Hecky, R. E., Janse, J. H., Annette Kaufman, L., Kishemachumu, M. A., Kolding, J., Ligtoet, W., Mbabazi, D., Medard, M., Mkuumbo, O. C., & Mlaponi, E. (2014). Coupled human and natural system dynamics as key to the sustainability of Lake Victoria's ecosystem services. *Ecology and Society*, 19(4), art31. <https://doi.org/10.2307/26269672>
- Fornito, A., Zalesky, A., & Bullmore, E. T. (2016). *Fundamentals of brain network analysis*. Elsevier.
- Galil, B. S., Boero, F., Campbell, M. L., Carlton, J. T., Cook, E., Fraschetti, S., ... Ruiz, G. M. (2015). 'Double trouble': The expansion of the Suez Canal and marine bioinvasions in the Mediterranean Sea. *Biological Invasions*, 17(4), 973–976. <https://doi.org/10.1007/s10530-014-0778-y>
- González-Mon, B., Bodin, Ö., Crona, B., Nenadovic, M., & Basurto, X. (2019). Small-scale fish buyers' trade networks reveal diverse actor types and differential adaptive capacities. *Ecological Economics*, 164, 106338. <https://doi.org/10.1016/j.ecolecon.2019.05.018>
- Gundeland, C., Venturelli, P. A., Hartill, B., Hyder, K., Olesen, H. J., & Skov, C. (2023). Spatiotemporal and multispecies comparisons between a citizen science platform and recall surveys in recreational fisheries. *Marine Policy*, 155, 105780. <https://doi.org/10.1016/j.marpol.2023.105780>
- Haggan, N., Neis, B., & Baird, I. G. (2007). *Fishers' knowledge in fisheries science and management*. Coastal Management Sourcebooks.
- Haubrock, P. J., Bernery, C., Cuthbert, R. N., Liu, C., Kourantidou, M., Leroy, B., Turbelin, A. J., Kramer, A. M., Verbrugge, L. N. H., Diagne, C., Courchamp, F., & Gozlan, R. E. (2022). Knowledge gaps in economic costs of invasive alien fish worldwide. *Science of the Total Environment*, 803, 149875. <https://doi.org/10.1016/j.scitotenv.2021.149875>
- Hildebrand, S. F. (1937). The Tarpon in the Panama Canal. *Scientific Monthly*, 44, 245–246.
- Hulme, P. E. (2009). Trade, transport and trouble: Managing invasive species pathways in an era of globalization. *Journal of Applied Ecology*, 46(1), 10–18. <https://doi.org/10.1111/j.1365-2664.2008.01600.x>
- IPBES. (2023). Thematic assessment report on invasive alien species and their control of the intergovernmental science-policy platform on biodiversity and ecosystem services. In H. E. Roy, A. Pauchard, P. Stoett, & T. Renard Truong (Eds.), *IPBES secretariat*. <https://doi.org/10.5281/zenodo.7430682>
- Janssen, M. A., Bodin, Ö., Anderies, J. M., Elmqvist, T., Ernstson, H., McAllister, R. R. J., Olsson, P., & Ryan, P. (2006). Toward a network perspective of the study of resilience in social-ecological systems. *Ecology and Society*, 11(1), art15. <https://doi.org/10.5751/es-01462-110115>
- Johnson, T. P. (2005). Snowball sampling: Introduction. In *Wiley StatsRef: Statistics reference online*. Wiley. <https://doi.org/10.1002/9781118445112.stat05720>
- Jones, B. A. (2017). Invasive species impacts on human well-being using the life satisfaction index. *Ecological Economics*, 134, 250–257. <https://doi.org/10.1016/j.ecolecon.2017.01.002>
- Jones, P. E., Tummers, J. S., Galib, S. M., Woodford, D. J., Hume, J. B., Silva, L. G. M., Braga, R. R., Garcia de Leaniz, C., Vitule, J. R. S., Herder, J. E., & Lucas, M. C. (2021). The use of barriers to limit the spread of aquatic invasive animal species: A global review. *Frontiers in Ecology and Evolution*, 9, 611631. <https://doi.org/10.3389/fevo.2021.611631>
- Kluger, L. C., Gorriss, P., Kochalski, S., Mueller, M. S., & Romagnoni, G. (2020). Studying human–nature relationships through a network lens: A systematic review. *People and Nature*, 2, 1100–1116. <https://doi.org/10.1002/pan3.10136>
- Kluger, L. C., Mercer, S., Partelow, S., Roque-Sánchez, M. A., Higaki Moyano, K. O., & Salazar, M. (2025). *Connecting sea to market: Using network analysis to understand social-ecological dynamics in seafood value chains in Pisco, Southern Peru*. *People and Nature*. <https://doi.org/10.1002/pan3.70063>
- Kluger, L. C., Scotti, M., Vivar, I., & Wolff, M. (2019). Specialization of fishers leads to greater impact of external disturbance: Evidence from a social-ecological network modelling exercise for Sechura Bay, northern Peru. *Ocean and Coastal Management*, 179, 104861. <https://doi.org/10.1016/j.ocecoaman.2019.104861>
- Knakkegaard Christensen, H. (2016). Algorithms for finding dominators in directed graphs.
- Kourantidou, M., Haubrock, P. J., Cuthbert, R. N., Bodey, T. W., Lenzner, B., Gozlan, R. E., Nuñez, M. A., Salles, J.-M., Diagne, C., & Courchamp, F. (2022). Invasive alien species as simultaneous benefits and burdens: Trends, stakeholder perceptions and management. *Biological Invasions*, 24(7), 1905–1926. <https://doi.org/10.1007/s10530-021-02727-w>
- Lasso, M. (2019). *Erased: The untold story of the Panama Canal*. Harvard University Press.
- Longhurst, R. (2003). Semi-structured interviews and focus groups. In *Key methods in geography* (pp. 143–156). Sage.
- Masawi, A. F., Roy, S., & Ghosh, P. (2023). Examining indicators of complex network vulnerability across diverse attack scenarios. *Scientific Reports*, 13(1), 18208. <https://doi.org/10.1038/s41598-023-45218-9>
- Maturell, G. (1984). Recopilación sobre las características generales y potencial pesquero de los embalses Gatún, Alajuela y Bayano en la República de Panamá. Taller Internacional Sobre Ecología Y Manejo de Peces En Lagos Y Embalses. Taller internacional sobre ecología y manejo de peces en lagos y embalses, Santiago, Chile <https://www.fao.org/fishery/docs/CDrom/aquaculture/a0844t/docrep/008/AD772S/AD772S07.htm>
- Maturell, G., & Tapia, F. (1991). La pesquería de *Cichla ocellaris* en el lago Gatún, Panamá. Memorias del Segundo Taller ecología y Manejo de Peces en Lagos y Embalses. Copescal Doc. Tec. 9, 91–99.
- Naderifar, M., Goli, H., & Ghaljaie, F. (2017). Snowball sampling: A purposeful method of sampling in qualitative research, 14(3) Strides in development of medical education. <https://doi.org/10.5812/sdme.67670>

- Panama Canal Authority (ACP). (2006). Proposal for the expansion of the Panama Canal—Third set of locks project.
- Parris, K. M. (2016). *Ecology of urban environments*. Chichester Wiley Blackwell.
- Pyšek, P., Hulme, P. E., Simberloff, D., Bacher, S., Blackburn, T. M., Carlton, J. T., Dawson, W., Essl, F., Foxcroft, L. C., Genovesi, P., Jeschke, J. M., Kühn, I., Liebhold, A. M., Mandrak, N. E., Meyerson, L. A., Pauchard, A., Pergl, J., Roy, H. E., Seebens, H., & Kleunen, M. (2020). Scientists' warning on invasive alien species. *Biological Reviews*, 95(6), 1511–1534. <https://doi.org/10.1111/brv.12627>
- QGIS.org. (2023). QGIS geographic information system. QGIS Association. <http://www.qgis.org>
- R Core Team. (2023). R: A language and environment for statistical computing (version 4.2.1) [Computer software]. R Foundation for Statistical Computing. <https://www.R-project.org>
- Ren, Y., Sarkar, A., Veltri, P., Ay, A., Dobra, A., & Kahveci, T. (2022). Pattern discovery in multilayer networks. *IEEE/ACM Transactions on Computational Biology and Bioinformatics*, 19(2), 741–752. <https://doi.org/10.1109/TCBB.2021.3105001>
- Rickowski, F. S., Ruland, F., Bodin, Ö., Evans, T., Fowler, M. S., Kluger, L. C., Latombe, G., Lenzner, B., Macêdo, R. L., Adriaens, T., Arlinghaus, R., Castellanos-Galindo, G. A., Dick, J. T. A., Dickey, J. W. E., Essl, F., Gallardo, B., Hilt, S., Itescu, Y., Jarić, I., ... Jeschke, J. M. (2026). A systems perspective: How social-ecological networks can improve our understanding and management of biological invasions. *BioScience*, 76(2), 127–146. <https://doi.org/10.1093/biosci/biaf174>
- Rogers, J. D., & Barrelier, M. H. (2018). Gatun dam—Megastructure of the Panama Canal. *Environmental & Engineering Geoscience*, 24(1), 1–22. <https://doi.org/10.2113/EEG-1935>
- Runghen, R., Llopis-Belenguer, C., McNeill, M. R., Riva, G. V., & Stouffer, D. B. (2023). Using network analysis to study and manage human-mediated dispersal of exotic species. *Biological Invasions*, 25(11), 3369–3389. <https://doi.org/10.1007/s10530-023-03122-3>
- Salgado, J., Vélez, M. I., González-Arango, C., Rose, N. L., Yang, H., Huguet, C., Camacho, J. S., & O'Dea, A. (2020). A century of limnological evolution and interactive threats in the Panama Canal: Long-term assessments from a shallow basin. *Science of the Total Environment*, 729, 138444. <https://doi.org/10.1016/j.scitotenv.2020.138444>
- Sayles, J., Mancilla Garcia, M., Hamilton, M., Alexander, S. M., Baggio, J. A., Fischer, A. P., Ingold, K., Meredith, G. R., & Pittman, J. (2019). Social-ecological network analysis for sustainability sciences: A systematic review and innovative research agenda for the future. *Environmental Research Letters*, 14, 93003. <https://doi.org/10.1088/1748-9326/ab2619>
- Seebens, H., Gastner, M. T., Blasius, B., & Courchamp, F. (2013). The risk of marine bioinvasion caused by global shipping. *Ecology Letters*, 16(6), 782–790. <https://doi.org/10.1111/ele.12111>
- Sharpe, D. M. T., De León, L. F., González, R., & Torchin, M. E. (2017). Tropical fish community does not recover 45 years after predator introduction. *Ecology*, 98(2), 412–424. <https://doi.org/10.1002/ecy.1648>
- Sharpe, D. M. T., Valverde, M. P., De Leon, L. F., Hendry, A. P., & Torchin, M. E. (2023). Biological invasions alter the structure of a tropical freshwater food web. *Ecology*, 104, e4173. <https://doi.org/10.1002/ecy.4173>
- Smith, S. T., Bell, G., & Bermingham, E. (2004). Cross-cordillera exchange mediated by the Panama Canal increased the species richness of local freshwater fish assemblages. *The Royal Society*, 271(1551), 1889–1896. <https://doi.org/10.1098/rspb.2004.2796>
- Statista. (2023). Panama—Employment by economic sector 2009–2019. Statista. <https://www.statista.com/statistics/454827/employment-by-economic-sector-in-panama/>
- Strasiewsky, D. (2023). Metabarcoding to evaluate the potential success of marine fish predators within the Panama Canal from a trophic perspective.
- Strogatz, S. H. (2001). Exploring complex networks. *Nature*, 410(6825), 268–276.
- Subramaniam, R. C., Ruwet, M., Boschetti, F., Fielke, S., Fleming, A., Dominguez-Martinez, R. M., Pláganyi, É. E., Schrobback, P., & Melbourne-Thomas, J. (2023). The socio-ecological resilience and sustainability implications of seafood supply chain disruption. *Reviews in Fish Biology and Fisheries*, 33(4), 1129–1154. <https://doi.org/10.1007/s11160-023-09788-1>
- Vears, D. F., & Gillam, L. (2022). Inductive content analysis: A guide for beginning qualitative researchers. *Focus on Health Professional Education: A Multi-Professional Journal*, 23(1), 111–127. <https://doi.org/10.3316/informit.455663644555599>
- Wasserman, S., & Faust, K. (1994). *Social network analysis: Methods and applications*. Cambridge University Press. <https://doi.org/10.1017/CBO9780511815478>
- Yletyinen, J., Hentati-Sundberg, J., Blenckner, T., & Bodin, Ö. (2018). Fishing strategy diversification and fishers' ecological dependency. *Ecology and Society*, 23(3), 28. <https://doi.org/10.5751/ES-10211-230328>
- Zaret, T. M., & Paine, R. T. (1973). Species introduction in a Tropical Lake: A newly introduced piscivore can produce population changes in a wide range of trophic levels. *Science*, 182(4111), 449–455. <https://doi.org/10.1126/science.182.4111.449>

SUPPORTING INFORMATION

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

Data S1: Fish species names (English, Spanish, scientific).

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