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OPINION

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The angled-web: Recreational angling as an underappreciated disruptor to the interconnectedness of terrestrial and freshwater food webs

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Abstract

1. The interconnectedness of adjacent freshwater and terrestrial ecosystems results in 'tangled-webs', where the cross-boundary exchange of materials results in energy flows that provide critical resources for ecosystem productivity. However, these energy flows can be disrupted by anthropogenic activities, resulting in modified ecosystem functioning.
2. A ubiquitous anthropogenic activity in fresh waters is recreational angling. Five major angling activities can disrupt the structure of the 'tangled-web' to produce an 'angled-web' (a tangled food web that is modified by angling activities). (1) Fish stocking increases the number and species available to exploit, but the increased fish abundances can have strong top-down effects and disrupt reciprocal prey subsidies. Following capture, fish are either (2) harvested or (3) released alive ('catch-and-release0'); both can both drive eco-evolutionary changes that can modify food-web structure. Where fish are exploited using baited hooks, (4) the release of 'ground-bait' is used as a fish attractant; its composition of novel protein and carbohydrate sources form novel trophic links in the food web and can accelerate eutrophication. Some angling styles also require (5) riparian and in-stream vegetation to be cleared to minimise gear fouling, potentially modifying fish spawning and nursery areas.
3. We suggest that each of these angling impacts (and their interactions) can contribute to transforming the 'tangled web' into an 'angled-web', with the strength and direction of the transformation dependent on angling pressure, prevailing fishery practices, regulations and management, and the extent of the interaction effects of the activities. These interactions and their impacts will vary globally given angling methods, practices and regulations differ across the world.
4. We argue that, in this era of substantial environmental change driven by climate change, habitat loss and nutrient enrichment of fresh waters, the extent to which angling impacts food webs should not be overlooked and underappreciated. We emphasise that when freshwater angling activities are poorly managed and/or unregulated, they can strongly modify the interconnectedness between terrestrial and freshwater food webs.

KEYWORDS
catch and release, fishing, groundbait, harvesting, stocking

1 | INTRODUCTION

Nearly 20 years ago, the tangled-web was described by Baxter et al. (2005) in *Freshwater Biology* (vol. 50) as close links between streams and their adjacent riparian zones formed by reciprocal flows of invertebrate prey. The emergence of adult insects from streams represent a substantial export of benthic production to riparian consumers (e.g. spiders, lizards and birds), especially in early summer, while fluxes of terrestrial invertebrates can produce up to half the annual energy budget for some fishes (Baxter et al., 2005). These mutual trophic interactions between contiguous habitats are important for maintaining communities in ecological landscapes (Nakano & Murakami, 2001), with the cross-boundary exchange of materials providing spatial resource subsidies for ecosystem productivity (Polis et al., 1997). The effects of aquatic subsidies for terrestrial ecosystems are still felt over 500 m from the water's edge (Richardson & Sato, 2015). This tangled-web provides the basis for testing how anthropogenic activities disrupt animal communities and ecosystems. For example, the concept has revealed how non-native fish impact the diet and growth of native fish via their usurping of terrestrial prey inputs (Baxter et al., 2007) and how stressors such as deforestation, climate change and dams can drive substantial declines in the foraging, growth and/or abundance of aquatic and terrestrial predators (Fausch et al., 2010).

Participation in recreational angling varies between countries, but with an average of approximately 11% of the populations having participated in angling within the last 2 years (Arlinghaus et al., 2015). Anglers typically benefit from their experiences through enhanced well-being and, where fish are harvested, consuming a valuable protein source (Britton, Pinder, et al., 2023). In many countries, anglers are the main local managers and users of freshwater ecosystems, and thus potentially play a key role in environmental stewardship (Shephard et al., 2023). Rod-and-line angling styles vary around the world, but with the primary methods involving either the use of a lure or a bait presented on the hook. These methods can be highly effective, with recreational anglers capturing approximately 10% of the annual global fish harvest (Lynch et al., 2024). Additionally, catch-and-release (C&R) practices have been increasing in popularity (Sass & Shaw, 2020). A high proportion of the global angling effort is expended on inland fisheries (Lynch et al., 2024). These fresh water fisheries are on generally closed systems ecosystems that can be strongly affected by environmental changes (Kao et al., 2020). Freshwater fisheries are often heavily regulated to promote responsible angling, where regulations such as limits on the size and number of fish that can be removed aim to prevent angling affecting stock sustainability (Sass & Shaw, 2020).

Motivations to participate in freshwater angling are diverse and include psychological (e.g. emotional benefits of being in the outdoors), challenge-related (e.g. trying to catch a 'trophy' sized fish), social (e.g. interacting with other anglers), competitive (e.g. tournament fishing) and nutritional (capturing fish for food) (Britton, Pinder, et al., 2023). These varying angling motivations results in non-uniform angler behaviours that drive a range of diverse management strategies for increasing angler satisfaction (Britton, Pinder, et al., 2023). Nevertheless, most anglers participate in at least two of five general freshwater angling capture and management activities, irrespective of their global location: fish stocking, fish harvesting, C&R, ground-baiting and habitat manipulation (usually vegetation management) (Holder et al., 2020; Shephard et al., 2023). We thus propose that in fresh waters where angling is practised, these activities represent perturbations that can transform the tangled-web outlined by Baxter et al. (2005) into the 'angled-web', defined as a tangled food web that has been modified by various angling activities (Figure 1). The strength and direction of the impacts of the angling activities, and their interactions, determine the extent of divergence of the two food-web structures and energy flux. We explore this divergence between the tangled-web and angled-web by reviewing the relevant literature and outlining the angling and fishery management activities, and the processes by which these activities can modify community composition and the cross-ecosystem exchanges and energy flows. We place our focus on those activities that can strongly disrupt the tangled-web, but note anglers can also provide beneficial outcomes for freshwater ecosystems (Shephard et al., 2023).

2 | HOW FRESHWATER ANGLING MANAGEMENT AND CAPTURE ACTIVITIES MODIFY THE TANGLED-WEB

2.1 | Fish stocking

Fish stocking is a widespread and long-standing management measure in fresh water fisheries (Arlinghaus et al., 2015). It involves releasing fish into a managed water that were captured in a different ecosystem or, more commonly, produced semi-naturally or artificially in hatchery conditions (Cucherousset et al., 2021). Drivers of stocking include attempting to meet anglers' expectations at catching 'trophy/game fish' (Hickley & Chare, 2004) or by releasing larger numbers of smaller fishes to meet expectations of competition anglers (Britton et al., 2022). In put-and-take fisheries, the stocked fish (usually hatchery reared fish such as rainbow trout *Oncorhynchus mykiss*) are often caught and removed soon after their release. For example, 90% of stocked salmonids were captured within 45 days of stocking in a managed reservoir in England (North, 1983). In catch-and-release fisheries, all captured fish tend to be released alive, with

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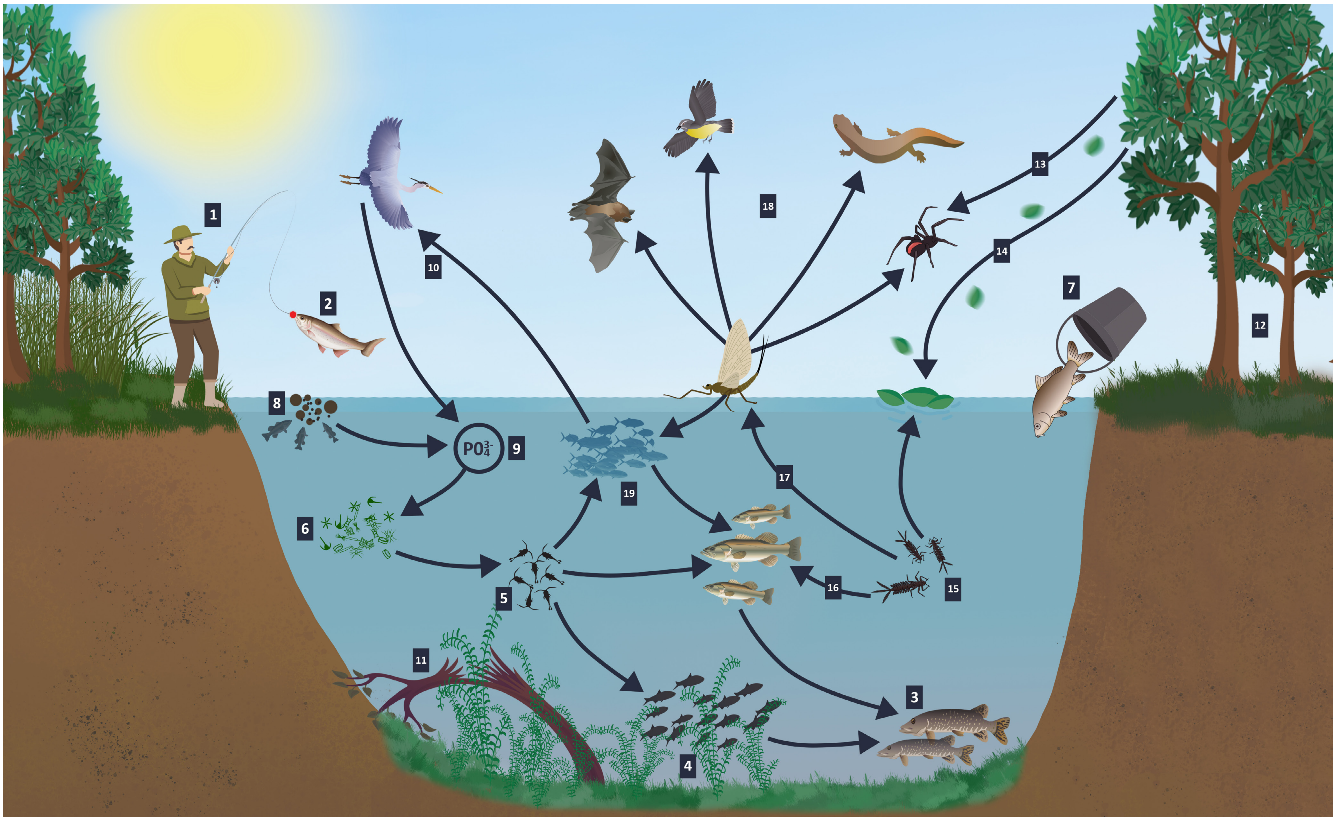

FIGURE 1 The angling activities that modify naturally tangled-webs to angled-webs, where the extent of modification depends on the extent of angling activity. A typical tangled-web for comparison can be seen in Baxter et al. (2005). The recreational angling activities can involve: (1) capturing fish that are either harvested (2) or released (3), both of which drive angler induced selection, leading to decreased predation pressure, increased prey fish population abundances (4) and reduced zooplankton abundance (5) that leads to phytoplankton dominance (6). As both harvesting and catch-and-release can reduce the number of fish vulnerable to capture, fish stocking (especially of large-bodied non-native and/or domesticated fishes) is used to increase catch rates (7), inverting the trophic pyramid. Anglers might then exploit the stocked fishes with methods involving ground-bait (8), causing nutrient enrichment (9) and accelerating eutrophication and algal dominance (6). To protect the newly stocked fish, the presence of piscivorous fauna at the fishery is minimised (10). Angling activities manipulate the habitat through removal of submerged vegetation and wooden debris (11), reducing fish nursery and refuge areas. Anglers also alter riparian vegetation (12), leading to reductions in riparian invertebrate populations (13) and inputs of leaf litter into the freshwater ecosystem (14). Reduced volumes of freshwater leaf litter decrease macroinvertebrate population abundances (15), altering diets of fish (16), and with decreased rates of insect emergence (17), the weakened reciprocal prey subsidy alters the diets of terrestrial fauna (18) and pelagic fishes (19). In all cases, the arrows denote the direction of energy flow (but not the strength). Vectors in the figure were from the Integration and Application Network (ian.umces.edu/media-library).

positive relationships often apparent between stocked fish abundance and angler catch rates (North, 2002). Some individual fish can be captured on multiple occasions over short time periods (Britton et al., 2007), demonstrating a relatively high resilience to repeated capture events (Britton, Andreou, et al., 2023).

Stocking events also elevate fish densities and biomass in the receiving ecosystem. In France, over 90 million fishes were stocked into inland waters in 2013 (Cucherousset et al., 2021). In England, over six million non-native common carp *Cyprinus carpio* were consented by the fishery regulator to be released into inland waters for angling between 1998 and 2008 (Britton et al., 2010), despite recognition that this species is an ecological engineer that has strong bottom-up and top-down effects (Britton, 2022; Carvalho & Moss, 1995; Skeate et al., 2022). These stocked fishes can alter the tangled-web by modifying the patterns of size distribution in communities, trophic-structuring (inverting the trophic pyramid by releasing individuals of relatively high trophic position; Eby et al., 2006) and functional, genotype and phenotype diversity (Gimenez et al., 2023; Figure 1). The release of hatchery-reared and domesticated fishes can lead to the presence of individuals that can behave differently to the resident conspecifics (Cucherousset & Olden, 2020), and these stocked conspecifics can have stronger ecological impacts than alien fishes through their higher abundances (Buoro et al., 2016). Elevated fish abundances from stocking then decrease prey subsidies from aquatic to riparian ecosystems via strong top-down effects on aquatic life-stages of aerial insects (Pope et al., 2009). The stocked fish might also introduce novel parasites that can be transmitted to resident fishes, altering their foraging habitats and shifting the strength of existing trophic links and creating new ones (Britton, 2022).

Introductions of non-native species to enhance angling can have cascading ecological consequences, including altering ecosystem functioning by bioturbation and reducing the diversity of prey fish communities by predation (Britton, 2022; Eby et al., 2006; Figure 1). For example, impacts of invasive common carp via middle-out processes involve multiple direct and indirect top-down and bottom-up processes that have profound influences on ecosystem functioning (Vilizzi et al., 2015). Indeed, the stocking of cyprinid fishes, especially common carp, has been strongly associated with the degradation of many lakes of conservation importance in England (Skeate et al., 2022). Introductions of piscivorous fishes, including largemouth bass *Micropterus salmoides* and peacock basses of the *Cichla* genus, are associated with substantial declines in the abundance and diversity of their prey in many areas of the world, including South America and Southeast Asia (Kim et al., 2022).

2.2 | Angling capture: harvesting and catch and release

Fish populations rarely comprise individuals expressing uniform behaviours, but instead individuals that consistently express specific behavioural traits that correlate into specific phenotypes (Alos et al., 2012). When these fish populations are exploited by angling, capture rates across different phenotypes tend to select for specific phenotypes (Lennox et al., 2017). The phenotypes most vulnerable to angling capture are usually those of high activity and stress resilience, although low activity phenotypes are more vulnerable in some species and contexts (Alos et al., 2012). Anglers often target trophy fish with specific trait combinations, such as large individuals that are also fast growing, bold and with relatively high metabolic rates (Koeck et al., 2019). Capture vulnerability of specific phenotypes is also a function of angling gear selectivity, with high activity phenotypes more likely to encounter and inspect novel objects (such as lures) compared with low activity phenotypes (Lennox et al., 2017).

Harvesting of specific phenotypes will alter phenotypic distribution and modify body-size structure, behaviour and life history traits of fish populations exploited by angling (Koeck et al., 2019). Such angling-induced selection drives strong directional selection for smaller body sizes and lower age at maturity, traits linked to lower fecundity, reduced recruitment and truncated age distribution, so impacting population structure and evolutionary dynamics (Diaz Pauli & Sih, 2017; Heino et al., 2015). Evolution driven by angler harvest has resulted in Northern pike *Esox lucius* populations with smaller body sizes and less bold behaviours (Monk et al., 2021), Atlantic salmon *Salmo salar* increasing in age and size at maturation (Hard et al., 2008) and largemouth bass having lower metabolic rates (Redpath et al., 2010). Changes in fish population size structure and intraspecific phenotypic variation in fish population affect both top-down and bottom-up processes, so can have marked effects on invertebrate community structure and ecosystem function (McQueen et al., 1989; Rudman et al., 2015). Consequently, it is suggested that angling induced changes in fish populations through harvesting will impact the flux of aquatic prey into the terrestrial ecosystem, with direction and magnitude of change dependent upon the extent of the changes in phenotype composition (Eby et al., 2006).

Catch-and-release angling is likely maintaining phenotypic diversity compared with harvesting. Thus, compared to harvested fisheries, angling-induced evolution might be less detrimental in C&R fisheries. However, post-release behaviours can be altered through responses in the fish to both capture and handling (e.g. from behavioural changes resulting from the physiological impacts of fight-time and air exposure; Pinder et al., 2019). Consequently, individual traits might be modified through, for example, individuals behaving more timidly, at least in the short term (Klefoth et al., 2008). Some behavioural changes can, however, be maintained over relatively long periods, with hook avoidance behaviours in common carp often lasting several months (Lovén Wallerius et al., 2020). Altered fish behaviour has the potential to impact foraging strategies, with bolder individuals being more susceptible to predation (Nannini et al., 2012). Thus, shifts in behaviour due to either previous capture experience or fisheries-induced evolution could result in angling-induced modification of the food web, most likely though behavioural changes in individuals altering their foraging behaviours and prey selectivity. However, the extent to which fish personality and associated behaviours affect diet composition (and so food-web structure and, ultimately, the tanged-web) is not clear (Mittelbach et al., 2014).

2.3 | Ground-baiting

Many freshwater angling methods using baited hooks are associated with ground-baiting, which is used as a fish attractant to increase capture probability. Ground-baits usually comprise allochthonous plant- and animal-derived materials (including marine-derived nutrients), so represent novel trophic subsidies in fresh waters (Britton et al., 2022). Elemental composition can vary among commercially available ground-baits, with high variations in nitrogen and phosphorous content (Imbert et al., 2022). These trophic subsidies can be released into fresh waters in high volumes, particularly in Europe, with German anglers using an average of 7.3 kg of bait per year, while some specialist anglers use up to 200 kg (Arlinghaus & Niesar, 2005; Niesar et al., 2004). Anglers targeting European barbel *Barbus barbus* in rivers in England regularly use over 1 kg of pelletised fishmeal per angling visit (De Santis et al., 2019), with competition anglers targeting smaller cyprinids stocked into pond fisheries using a wide variety of manufactured baits of varying sizes that enable the capture of fishes across a broad size spectrum (Britton et al., 2022).

The effects of using ground-baits on the aquatic food web are fourfold. First, the diet of both lotic and lentic cyprinid fish populations can comprise of high proportions of these baits (Britton et al., 2022; De Santis et al., 2019; Mehner et al., 2019). This means their use in fresh waters creates new trophic links with this novel resource, including new energy pathways that tropically transfer these nutrients from cyprinid prey fish to large piscivores (Nolan et al., 2019), including piscivorous mammals and birds (Britton et al., 2005). These baits also alter the strengths of existing trophic links, with individual dietary specialisations increasing population trophic niche sizes (Britton et al., 2022). Second, the availability of these baits over extended time periods resulted in increased catches of common carp, as shown by individual fish altering their foraging areas and time budgets in relation to the availability of these baits across lakes in Hungary, France, Slovakia and the Czech Republic (Žák, 2021). In consuming these baits, individual fish potentially reduce their foraging for invertebrate prey (Nolan et al., 2019), decreasing grazing pressure and increasing insect emergence into terrestrial environments. Third, these baits can accelerate eutrophication processes, especially where there are synergistic interactions with stocking (e.g. releases of large volumes of bait by anglers when targeting stocked fishes that drive bioturbation) (Britton, 2022; Fazekas et al., 2023) (Figure 1). However, it is acknowledged that other inputs of phosphorous from anthropogenic activities might have stronger effects on eutrophication (McDowell et al., 2020; Section 3). As eutrophication generally decreases invertebrate diversity (Wang et al., 2021), this will impact the diversity of emerging insects from the aquatic to terrestrial ecosystems. Finally, groundbaits can contain substantial amounts of microplastics (de Carvalho et al., 2021), which are then ingested by the fish, which could lead to physiological and behavioural shifts that affect food-web structure and energy flow (Parker et al., 2021) and so have cascading effects on insect emergence into the terrestrial environment.

2.4 | Habitat modification

To assist angling access in freshwater fisheries, riparian and freshwater habitats are often managed (e.g. vegetation clearance). This is usually related to angling activity from the shore that involves the localised clearing of plant growth in the riparian zone (Müller et al., 2003) and the partial or full removal of macrophytes and woody debris in the littoral zone that represent a hazard to angling activities (O'Toole et al., 2009; Schiemer et al., 1995). Macrophyte growth is also purposely being reduced in some recreational fisheries through dyeing of the water, where reduced light penetration caused by dyeing mediates plant growth to help control biomass and coverage (Crane et al., 2022). Reducing macrophyte growth can reduce the subsequent abundances of emerging insects from the aquatic to terrestrial system, as higher macrophyte biomass generally correlates positively with macroinvertebrate abundances (Cremona et al., 2008; Shupryt & Stelzer, 2009). The substantial clearing of riparian and aquatic vegetation to facilitate angler and angling access weakens the transfer of terrestrial subsidies (such as tree leaves and terrestrial invertebrates) into freshwater ecosystems (Baxter et al., 2005; O'Toole et al., 2009; Figure 1). Submerged materials, such as woody debris, are often removed to prevent the loss of angling gear, despite these materials providing fish refugia and nursery areas that are more successful in enhancing natural recruitment than stocking in lakes (Radinger et al., 2023). Moreover, increasing woody debris in rivers can have positive effects for freshwater biodiversity, including increases in fish population abundances (e.g. Thompson et al., 2018) and macroinvertebrate diversity (e.g. Deane et al., 2021). Accordingly, reducing aquatic and riparian vegetation for increasing angling access is likely decreasing the reciprocal exchange of material between the fresh water and terrestrial ecosystems (Knight et al., 2005).

3 | RELATIVE STRENGTH OF MODIFICATIONS TO THE TANGLED-WEB VERSUS OTHER ENVIRONMENTAL CHANGES

A fundamental question when considering the extent of food-web modification resulting from angling activities is how angling relates to other agents of environmental change, including climate change, nutrient enrichment and biological invasions. Climate change effects in freshwaters include shifts in the distribution of climatically vulnerable species as they seek climate refugia (Barbarossa et al., 2021). However, these distribution shifts are generally occurring over relatively extended timescales (e.g. decadal) (Buisson et al., 2013; Comte & Grenouillet, 2013). Conversely, stocking can have an immediate effect on the fish assemblage, especially where the stocked species increase predation pressure on native fishes (Eby et al., 2006; Kim et al., 2022) and/or is an ecosystem engineer (Skeate et al., 2022). Consequently, stocking is more likely than climate change to result in rapid changes in the physical environment (e.g. increasing turbidity through benthic foraging) and biotic communities (e.g. reduced macrophyte and macroinvertebrate biomass and diversity biomass) (Vilizzi et al., 2015). These changes in the fresh water ecosystem could then strongly disrupt the tangled-web, including by reducing the abundance of insects emerging from aquatic to terrestrial ecosystems.

Nutrient enrichment from anthropogenic activities is considered the primary stressor impacting lake ecosystems (Birk et al., 2020). Accordingly, nutrient enrichment resulting from the use of groundbait by anglers might increase the rate of eutrophication but is unlikely to be the major driver (Amaral et al., 2013). The impacts of eutrophication on the tangled-web (including the consequences arising from increased primary production, and decreased macrophyte abundance and reduced macroinvertebrate diversity; Amaral et al., 2013) are thus relatively minor from angling compared with other anthropogenic sources. The modification of river systems globally by engineering activities has been extensive globally, with only 37% of global rivers remaining free-flowing (Grill et al., 2019). There are also over one million barriers present on European rivers (Belletti et al., 2020). The extent of this habitat loss likely overrides the effect of angling activities in such rivers. However, the impounded sections of river provide new angling opportunities (Britton & Orsi, 2012). The impoundments are often stocked with piscivorous fishes for sport angling, such as the introduction of invasive peacock basses *Cichla* spp. into Brazilian hydropower reservoirs that have resulted in substantial decreases in prey fish diversity and abundance (e.g. Franco et al., 2022). The ecological engineering and usually invasive common carp is also often released into reservoirs for angling, whose foraging behaviours further modify the fresh water ecosystem (Vilizzi et al., 2015). Thus, while these angling activities are occurring in an already heavily modified ecosystem (and so are not the principal driver of ecosystem change), their impacts on the ecosystem increase the perturbations to the tangled-web by weakening the reciprocal exchange of materials between the freshwater and terrestrial ecosystems.

4 | CONCLUSIONS

We suggest that the angling activities outlined can drive strong food-web transformations in fresh waters used as recreational fisheries. While there will be high context dependency on the strength and directions of the angling-induced modifications, we suggest that where these are of management concern then increased regulation through more sustainable management actions can return heavily impacted ecosystems closer to their original state (if that is the desired goal). We also argue that in this current era of environmental changes driven by climate change, nutrient enrichment and habitat fragmentation, these angling-driven transformations of the tangled-web are often overlooked and underappreciated. Moreover, we have suggested that these angling-driven transformations can be strong and direct (e.g. stocking, harvesting), as well as more subtle and indirect, where the angling activity often acts as an additional stressor on an already highly stressed environment (e.g. C&R, groundbaiting). In all cases, the tangled-web is disrupted, usually through reduced energy flux between the adjacent ecosystems.

Our arguments are based on empirical evidence generated from Europe, and North and South America, but where long-term studies testing the impacts of angling activities (including interactions) across different levels of biological organisation remain limited. Knowledge gaps remain, including the long-term effects on the tangled web of high stocking densities in recreational fisheries and the management of vegetation through methods including water dyeing. We argue that a key next step is identifying the context-dependency of these effects by understanding the interaction effects of angling activities and environmental conditions. These findings will then ultimately contribute to the sustainable management of adjacent terrestrial and freshwater ecosystems, and their provision of connections between people and nature.

AUTHOR CONTRIBUTIONS

Conceptualisation: JRB, JC; literature summaries: all authors; Writing the original draft of the manuscript: all authors; Reviewing, commenting and editing drafts: all authors; Preparation of figures: all authors.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

ETHICS STATEMENT

Ethics approvals were not required for this study.

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