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GHOTI

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Are domesticated freshwater fish an underappreciated culprit of ecosystem change?

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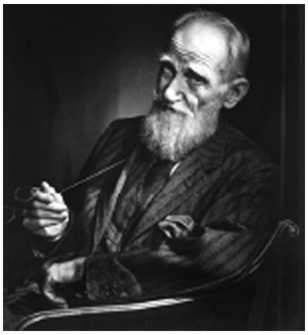
Abstract

In addition to accidental aquaculture escapees, an increasing number of freshwater fish expressing different domestication levels are voluntarily released into the wild primarily as stocking supplement for fisheries and for conservation programmes. Because domestication modifies individual traits and because subtle changes in intraspecific variability can impact ecological dynamics, we argue that these purposeful introductions of domesticated fish may impact the functioning of recipient ecosystems. We posit that purposely introduced domesticated fish could be considered as native invaders and be investigated and managed using frameworks developed for biological invasions. Studies identifying the relative importance of the different ecological mechanisms leading to these ecosystems impacts and quantifying how the intensity of introduction and the level of domestication modulate their ecosystem impacts are needed. This will lead to a better appreciation of how the benefits from releasing domesticated fish are offset by the ecological costs on freshwater ecosystem functioning caused by human-induced local modification of intraspecific diversity patterns.

KEYWORDS
domestication, ecosystem functioning, freshwater fish, intraspecific variability, phenotypes, stocking

1 | INTRODUCTsION

Humans have domesticated numerous species of plants and animals over thousands of years, primarily with the aim to bolster food production, transportation or recreational fishing and hunting opportunities (Diamond, 2002). Biologists have long recognized that the process of domestication, defined as the manipulation of species attributes in an effort to maximize some desired outcomes, profoundly changes the genotypes and phenotypes of domesticated



Ghoti papers

Ghoti aims to serve as a forum for stimulating and pertinent ideas. Ghoti publishes succinct commentary and opinion that addresses important areas in fish and fisheries science. Ghoti contributions will be innovative and have a perspective that may lead to fresh and productive insight of concepts, issues and research agendas. All Ghoti contributions will be selected by the editors and peer reviewed.

Etymology of Ghoti

George Bernard Shaw (1856-1950), polymath, playwright, Nobel prize winner, and the most prolific letter writer in history, was an advocate of English spelling reform. He was reportedly fond of pointing out its absurdities by proving that 'fish' could be spelt 'ghoti'. That is: 'gh' as in 'rough', 'o' as in 'women' and 'ti' as in palatial.

individuals (Milla, Osborne, Turcotte, & Violle, 2015). The number of domesticated species on the planet continues to show unprecedented growth, where the biomass of domesticated individuals now surpass that of wild counterparts for several taxa, including mammals and birds (Bar-On, Phillips, & Milo, 2018). Accidental introduction of domesticated species into the wild can result from individuals escaping from farms, aquaculture and horticulture facilities or pets being released by the public, leading to the "feralization" or establishment of self-sustained and free-living populations (Gering et al., 2019). A less appreciated introduction pathway of domesticated individuals in the wild is sanctioned (purposeful) introductions in support of conservation programmes, biomanipulation (e.g. pest control), ornamental practices and stocking supplement to improve commercial and recreational fishing and hunting.

Purposeful introductions are particularly common for freshwater fish as tens of billions individuals of varying domestication levels are introduced yearly into fresh waters worldwide (Carrera-García, Rochard, & Acolas, 2016; Halverson, 2008). For instance, 1.7 billion fish were stocked in the United States in the year 2004 (Halverson, 2008) and "some 40 billion individuals are stocked annually in European fresh waters" (Cooke & Cowx, 2006). When introduced into the wild, domesticated individuals can express combinations of (novel) traits that differ considerably from their wild counterparts, thus modifying patterns of local intraspecific diversity. Such alterations have important ecological implications because changes in phenotypic traits have been reported to modify consumers-resources dynamics, subsequently affecting important ecosystem functions (Des Roches et al., 2018; Raffard, Santoul, Cucherousset, & Blanchet, 2019). Introductions of domesticated fish can also impact ecological dynamics across multiple levels of biological organization, and we posit that they operate in a manner similar to invasive species (Cucherousset & Olden, 2011). To date, however, most investigations have focused on consequences of these introductions at lower levels of biological organization (i.e. genetic, individual and populations: disease transmission, introgression, heightened competition) (Bolstad et al., 2017; Fleming et al., 2000; Lorenzen, Beveridge, & Mangel, 2012), whereas potential effects manifested at higher level of biological organizations (i.e. community and ecosystems) remain largely unexplored (Buoro, Olden, & Cucherousset, 2016).

2 | DOMESTICATION-INDUCED CHANGES IN FRESHWATER FISH

Compared to land animals such as mammals (e.g. dogs, pigs, sheep, cows and horses), the history of freshwater fish domestication is relatively recent, with the exception of two species (Common carp (*Cyprinus carpio*, Cyprinidae) in Europe and Asia and Nile tilapia (*Oreochromis niloticus*, Cichlidae) in Africa) which have a history of domestication of 8,000 and 2,500 years (Nakajima, Hudson, Uchiyama, Makibayashi, & Zhang, 2019; Teletchea & Fontaine, 2014). The rearing of fish in captivity and their domestication have primarily occurred for food production (i.e. aquaculture), for supporting recreational fisheries and for the ornamental (aquarium) trade (Teletchea, 2016; Teletchea & Fontaine, 2014). Freshwater fishes span a wide range of domestication levels with respect to the proportion of the life cycle completed in captivity, inputs of wild individuals and existence of selective breeding. Examples include Dorado (*Salminus maxillosus*, Characidae) and White bream (*Blicca bjoerkna*, Cyprinidae) (Domestication level 1: initial trials of acclimatization to captivity), Redbelly tilapia (*Tilapia zillii*, Cichlidae) and Largemouth bass (*Micropterus salmoides*, Centrarchidae) (Domestication level 2: part of the life cycle is completed in captivity), Nile perch (*Lates niloticus*, Latidae) and Roach (*Rutilus rutilus*, Cyprinidae) (Domestication level 3: entire life cycle is closed in captivity, but with wild inputs), Northern pike (*Esox Lucius*, Esocidae) and North African catfish (*Clarias gariepinus*, Clariidae) (Domestication level 4: entire life cycle is closed in captivity without wild inputs) and Atlantic salmon (*Salmo salar*, Salmonidae), Rainbow trout (*Oncorhynchus mykiss*, Salmonidae) and Common carp (Domestication level 5: entire life cycle is closed in captivity without wild inputs and selective breeding is used) (Teletchea & Fontaine, 2014). For a given species, the level of domestication can also be highly variable between systems and over time. Levels of domestication soared starting in the 1950s with the intensification of food production in aquaculture and the creation of selective breeding programmes.

The domestication process can cause fish species to develop sets of "domesticated traits" such as high prolificacy, resistance to disease and rapid growth rate (Teletchea & Fontaine, 2014). An emblematic example of intensive and fast domestication is Atlantic salmon (Glover et al., 2017). Domestication has induced profound modification of the developmental and evolutionary forces acting on farmed Atlantic salmon, leading to individuals with better performance with respect to food production and to significant changes in phenotypic and life history traits compared to wild specifics: smaller eggs, reduced predator response, lower genetic diversity, decreased stress response and modified morphology (Gross, 1998). Trait consequences are also evident for lower levels of domestication. For example, comparative analyses have revealed vital commercial trait differences between domesticated and wild-type Eurasian perch (*Perca fluviatilis*, Percidae), including reproduction, immunology, skin colour and diet (Ben Khadher, Fontaine, Milla, Agnèse, & Teletchea, 2016). Recent investigations reveal that changes can rapidly occur when individuals are reared in hatchery conditions. For instance, differences in the expression of hundreds of genes were observed in the offspring of first-generation hatchery steelhead trout (*Oncorhynchus mykiss*, Salmonidae) compared to the offspring from wild parents. These differences were associated with adaption to hatchery conditions such as very high raising densities (Christie, Marine, Fox, French, & Blouin, 2016). In Coho salmon (*Oncorhynchus kisutch*, Salmonidae), hypermethylation and epigenetic reprogramming were caused by captive rearing in the absence of genetic differences between individuals (Le Luyer et al., 2017). Overall, this research revealed that even limited captivity can have large consequences on individual traits that are subsequently released in the wild.

3 | FROM MODIFIED TRAITS TO ECOSYSTEM IMPACTS

Freshwater fish have been used as model group for exploring the importance of phenotypic variability on ecosystem functioning and subsequent eco-evolutionary feedbacks (Des Roches et al., 2018; Raffard et al., 2019). Local adaptation to predation in Trinidadian guppy (*Poecillia reticulata*, Poeciliidae), associated with changes in phenotypic and life history traits, resulted in modified algae production and nutrient cycling (Bassar et al., 2010). In alewife (*Alosa pseudoharengu*s, Clupeidae), phenotypic differences in foraging traits caused by anadromous migration strongly modify the community of zooplankton (Palkovacs & Post, 2009). Such ecosystem changes are important because they can affect the evolutionary trajectory of populations. In threespine stickleback (*Gasterosteus aculeatus*, Gasterosteidae), modifications of environmental conditions induced by individuals from different populations were demonstrated to affect the survival and growth rates of the following generation (Matthews, Aebischer, Sullam, Lundsgaard-Hansen, & Seehausen, 2016). Therefore, we posit that the introduction of new phenotypes and their subsequent impacts on ecosystems share important similarities with the introduction of invasive species.

The effects of fish invasions on the highest levels of biological organization are numerous (Cucherousset & Olden, 2011), including changes in food web structure caused by competitive exclusion (Vander Zanden, Casselman, & Rasmussen, 1999), modification of energy fluxes between freshwater and terrestrial ecosystems (Baxter, Fausch, Murakami, & Chapman, 2004) and changes in nutrient cycling (Figueredo & Giani, 2005), to name just a few. The introduction of domesticated fish, displaying different genetic and phenotypic traits that their wild conspecifics, has been reported to impact individuals and populations of wild conspecifics (*intraspecific level*). Research on the introduction of domesticated (farmed) salmonids provides insightful examples. Although domestication can reduce the fitness of hatchery-reared individuals when released in the wild (Araki, Cooper, & Blouin, 2007), investigations on Atlantic salmon have revealed that hatchery-reared individuals can, through competitive interactions, decrease the productivity of wild populations (Fleming et al., 2000) and, through introgression, modify the life history (size and age at maturity) of wild conspecifics (Bolstad et al., 2017). Although empirical evidence remains limited (Buoro et al., 2016), the introduction of domesticated fish may also affect higher levels of biological organization from changes in biotic interactions with competitors and predators to alteration of prey communities and ecosystem functions (*interspecific level*). In addition, these ecosystem effects can subsequently feedback to individuals and modify their evolutionary trajectories in the wild (Hendry, 2018).

Studies assessing the ecosystem impacts of domesticated fish are notably scant in the literature (Buoro et al., 2016), but we posit that several predictions could be tested empirically. For instance, we predict that hatchery-raised fish with higher metabolism released into the wild could modify the structure of prey density by consuming more of the same prey. As well, such introductions could lead to the competitive exclusion of wild conspecifics that would modify their trophic niche towards a functionally different prey (e.g. shredders) and modify the associated ecosystem function (e.g. organic matter recycling). Finally, behavioural differences between wild and domesticated individuals (e.g. activity, boldness) may be associated with different microhabitat use and prey selectivity (e.g. prey quality), leading to differences in ecosystem functions such as primary productivity driven by modified nutrient excretions. The mechanisms observed in biological invasions to drive such ecosystem impacts (e.g. competition, predation, nutrient recycling) could serve as a basis developing a hypothesis-driven approach aimed to quantify the ecosystem impacts of purposely introduced domesticated fish. They will occur through: (a) "ecological" effects that are independent of domesticated fish phenotypes and caused by an overall increased density of fish, (b) "direct evolutionary" effects that are driven by domesticated fish phenotypes and (c) "indirect evolutionary" effects of that are driven by the number of released domesticated fish which is modulated by their phenotypic traits (Figure 1). In addition, various interactions and feedbacks between these effects can modulate the overall ecosystem outcomes induced by these ecological and evolutionary effects (Hendry, 2018).

4 | ECOSYSTEM IMPACT DRIVERS AND CONTEXT DEPENDENCY

Based on growing knowledge of the implications of aquatic species invasions (Anton et al., 2019; Gallardo, Clavero, Sánchez, & Vilà, 2016; Thomaz, Kovalenko, Havel, & Kats, 2015), we expect that the ecosystem impacts of purposely introduced fish will be largely determined by a combination of two factors. First, the direction and magnitude of effects are likely dependent upon the degree of introduction, including "propagule pressure" defined as the frequency and number of fish introductions, and the spatial and temporal extent over which the introductions have occurred. Second, although fish stocking is a global and ubiquitous phenomenon, the level of domestication of purposely introduced fish is highly variable both between and within species. Indeed, some species have reached higher domestication levels compared to others but also, within species, different domestication levels could be used for stocking. Because domestication level is an important determinants of trait variability (Teletchea & Fontaine, 2014), it can strongly modulate their ecosystem impacts (Figure 1). Understanding how stocking purposes (e.g. conservation, biocontrol, recreational and commercial fisheries) are associated with different levels of domestication of released fish is therefore needed to better anticipate their potential ecosystem impacts.

We predict that introduction intensity and domestication level shapes the intensity of ecosystem impacts of domesticated fish (Figure 2). This is expressed as a linear relationship for purely illustrative purposes, but these impacts will undoubtedly manifest in complex and nuanced ways that additional scientific study is needed

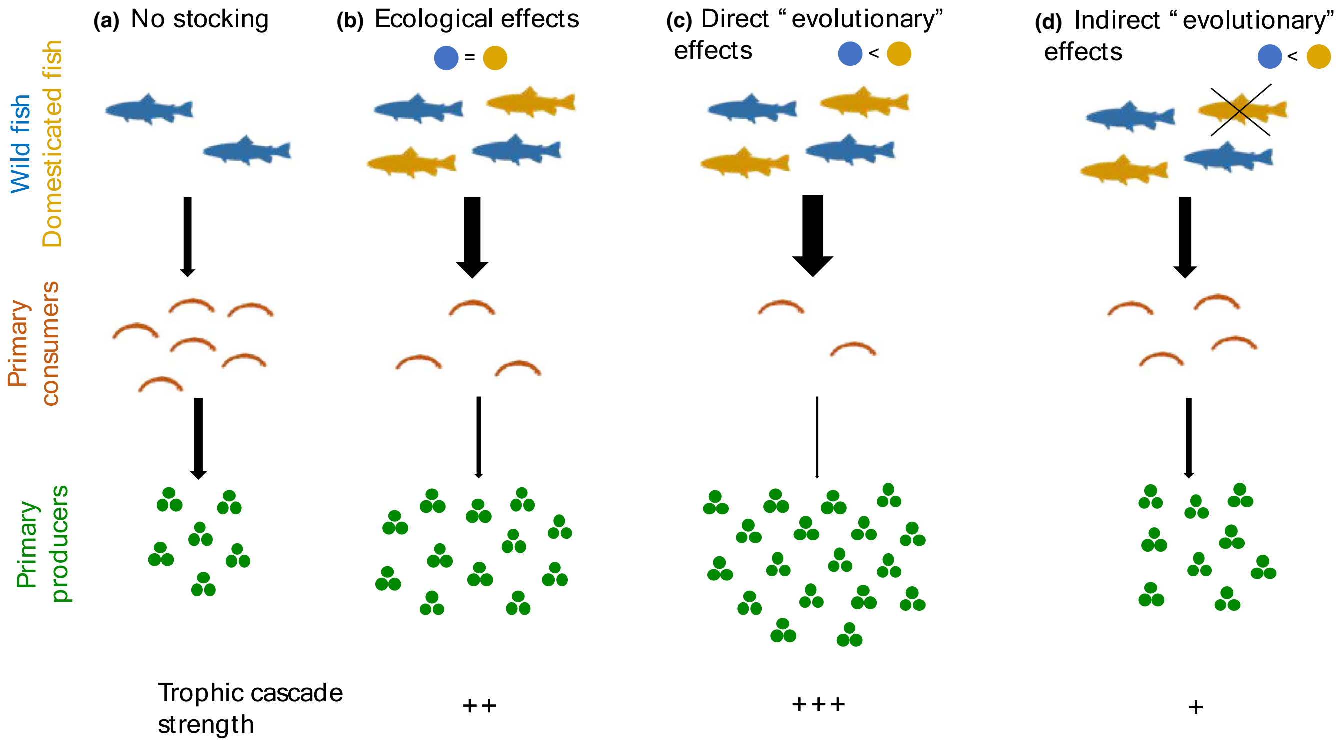


FIGURE 1 Potential ecological and evolutionary effects of domesticated fish in the wild on a simplified food chain. (a) Without stocking, wild fish (secondary consumers) control the biomass of invertebrates (primary consumers) that regulate primary production (biomass of algae). (b) "Ecological" effects of domesticated fish are independent of their phenotypes (e.g. same per-capita consumption rate) and caused by an overall increased density of fish (wild and domesticated) that increases the overall consumption pressure on primary consumers, leading to a trophic cascade. (c) "Direct evolutionary" effects of released domesticated fish are driven by their phenotypes (e.g. higher per-capita consumption rate) and increase the intensity of the stronger trophic cascade compared to the one induced purely by "ecological" effects. (d) "Indirect evolutionary" effects of released domesticated fish are driven by the number of released individuals which is modulated by their phenotypic traits that affect, for instance, their survival in the wild (e.g. maladaptation) [Colour figure can be viewed at wileyonlinelibrary.com]

to help reveal. For example, increased domestication may induce strong phenotypic changes leading to greater ecosystem impacts, yet it has been demonstrated that, in Salmonids, domesticated individuals may have reduced fitness in the wild compared to their conspecifics (Araki et al., 2007; Fleming et al., 2000). In addition, it is intuitive to expect that, in a given ecosystem, species with a long history of continuous introduction to support fisheries will likely induce stronger ecosystem impacts when compared to species with a limited level of domestication and stocked more recently at much smaller extents. However, the ecological impacts of an invasive species could decrease with time since introduction (Závorka, Buoro, & Cucherousset, 2018) and this might offset some of the ecosystem effects of a long history of continuous introduction. Consequently, the long-term ecosystem effects of purposely introduced domesticated organisms remain a pressing knowledge gap requiring greater attention in the future.

It is particularly important to understand how the fitness of domesticated fish modulates the temporal dynamic of these ecosystem impacts. Although their reproductive fitness could be low (Araki et al., 2007), released individuals, without spawning, can change ecosystem functioning, notably through consumptive effects that induce trophic cascades because they display very different phenotypic traits from wild individuals (Figure 1). These effects could occur rapidly, and the subsequent implications for ecosystem resilience are unknown. Through introgression with wild conspecifics, they can also impact ecosystem functioning over a longer period of time. This is because phenotypic changes induced by introgression can be important (Bolstad et al., 2017) and, although this remains to be tested, could subsequently impact ecosystem functioning.

While the study biological invasion provides an insightful framework for understanding the ecosystem impacts of purposely introduced fish, it also represents an opportunity to improve their management. Stemming from the trait changes caused by domestication and the potential impacts induced by their introduction into the wild, purposely introduced domesticated fish could be considered as native invaders, defined as the introduction of novel genotypes or phenotypes within their native range in ecosystems where wild individuals are present but also in specific locations where wild individuals are not present (Carey, Sanderson, Barnas, & Olden, 2012; Simberloff & Rejmánek, 2011). Consequently, the development of prevention and risk assessments that seek to minimize their potential ecological impacts is needed. This includes balancing the potential benefits obtained from releasing domesticated fish

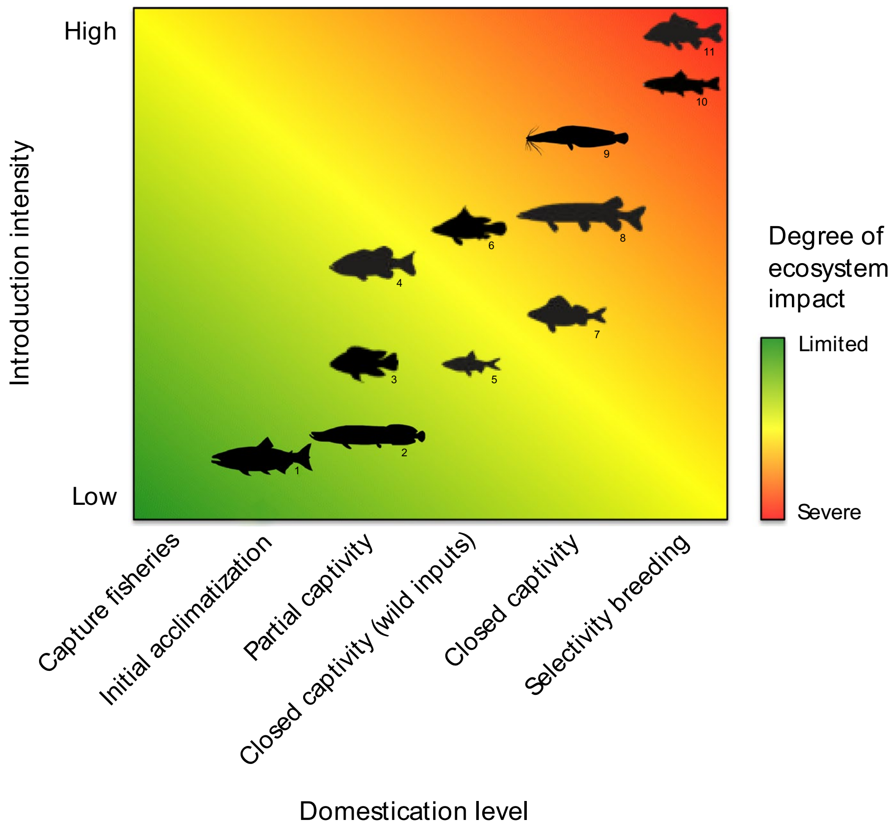


FIGURE 2 The temporal dynamics of the ecosystem impacts of purposely introduced domesticated organisms. Examples of domesticated freshwater fish species are positioned according to current evidence, representing potential case studies for future investigation, and include: (1) Dorado (*Salminus maxillosus*, Characidae), (2) Arapaima (*Arapaima gigas*, Arapaimidae), (3) Redbelly tilapia (*Tilapia zillii*, Cichlidae), (4) Largemouth bass (*Micropterus salmoides*, Centrarchidae), (5) Roach (*Rutilus rutilus*, Cyprinidae), (6) Nile perch (*Lates niloticus*, Latidae), (7) Eurasian perch (*Perca fluviatilis*, Percidae), (8) Northern pike (*Esox lucius*, Esocidae), (9) North African catfish (*Clarias gariepinus*, Clariidae), (10) Rainbow trout (*Oncorhynchus mykiss*, Salmonidae) and (11) Common carp (*Cyprinus carpio*, Cyprinidae). Domestication levels following definition by Teletchea and Fontaine (2014) [Colour figure can be viewed at wileyonlinelibrary.com]

for conservation or fisheries management with the risks of modifying the intraspecific diversity patterns and freshwater ecosystem functioning.

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DATA AVAILABILITY STATEMENT

No data were analysed in this article.

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