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The threespine stickleback (*Gasterosteus aculeatus*) as a modifier of ecological disturbances

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ABSTRACT

Background: The influence of human activity on ecological communities can be mediated as well as modulated by species with a central role in regulating community composition. The threespine stickleback is a common species in temperate aquatic ecosystems that could serve such a role.

Question: Does the threespine stickleback (*Gasterosteus aculeatus*) modulate the impact of human-induced eutrophication on ecological communities? If so, what are the pathways and mechanisms?

Methods: Review of studies investigating the influence of eutrophication on the dynamics and characteristics of stickleback populations, and how changes to the population mediate and modify the impact of eutrophication on other species.

Results: Eutrophication influences the abundance and characteristics of stickleback, which impacts other species through density- and trait-mediated effects on species interactions and the habitat. The effects can be complex and include feedback loops, and extend far beyond the stickleback population through the myriad of linkages among species. The changes can interact with other changes to the ecosystem, such as species invasions and climate change, and further alter the impact of ecological disturbances.

Conclusions: The threespine stickleback modulates the effects of eutrophication on communities and alters ecological and evolutionary processes. However, relatively little is known about the ultimate effects on ecosystems. Thus the complexity of ecological network architecture needs to be considered by combining experimental investigations of linkages among species with whole-ecosystem studies.

Keywords: eco-evolutionary dynamics, ecosystem engineer, ecosystem function, eutrophication, species interactions, trophic cascade

INTRODUCTION

Human activity is transforming ecosystems at an unprecedented rate. Whole communities are being affected through effects on both the species and their interactions, including consumer–resource and competitive interactions (Tylianakis *et al.*, 2008; Hoover and Tylianakis, 2012).

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These effects can in turn propagate throughout the ecological network, via species interactions, and influence the abundance and traits of species that are not directly affected [i.e. indirectly linked species (Wootton, 1994; Ohgushi *et al.*, 2012)]. For instance, the overfishing of Atlantic cod (*Gadus morhua*) has resulted in a trophic cascade that has altered the abundance of species at lower trophic levels (Frank *et al.*, 2005), while the introduction of the invasive mosquitofish (*Gambusia holbrooki*) has influenced the abundance and behaviour of native species, both directly through predation and competition for resources, and indirectly through linked species (Pyke, 2008). Feedback responses can further complicate the pattern and result in complex changes to the community, as when a species reacts to the responses of interacting species and further alters its traits.

The propagation of human disturbances through communities can be density- or trait-mediated (Abrams, 1995; Werner and Peacor, 2003; Schmitz and Trussell, 2016). Density-mediated effects occur when changes in the density of a species influence the species it is linked with, both directly and indirectly linked species. Trait-mediated effects occur when changes in the traits of a species, such as its morphology or behaviour, influence both directly and indirectly linked species. Some density-mediated effects are ultimately trait-mediated, as the traits of individuals influence the density of the population, while others are directly caused by humans, such as through harvesting (El-Sabaawi, 2017; Hendry, 2017). Density- and trait-mediated effects can also occur simultaneously, such as when an alteration in the density of a species and changes in its foraging behaviour combine to alter its predation pressure on prey species.

Relatively little attention has been paid to the role of species interactions in mediating the impacts of human disturbances on community structure and ecosystem processes (Gilman *et al.*, 2010; Ockendon *et al.*, 2014; Wong and Candolin, 2015; Nagelkerken and Munday, 2016; Urban *et al.*, 2016). Most studies have focused on the direct effects of human activities on species, without considering species interactions. Yet, when species interactions are considered, they are often found to alter the impact of human disturbances on communities (Alexander *et al.*, 2015; Palkovacs *et al.*, 2018). For instance, ocean acidification has cascading effects on communities; elevated CO_2 allows the expansion of common, competitively dominant species, through enhanced food resources and reduced predator abundance, which suppresses less common and behaviourally subordinate competitors (Nagelkerken *et al.*, 2017).

Species with a central role in regulating communities could mediate and modulate the impacts of human disturbances (Estes *et al.*, 2011; Bulleri *et al.*, 2018; Jurgens and Gaylord, 2018). Such species could be abundant species, species with links to many other species, or species that modify the environment, such as keystone species, niche constructors, ecosystem engineers, and foundation species (Jones *et al.*, 1994; Odling-Smee *et al.*, 2013; Matthews *et al.*, 2014). The threespine stickleback is a common mesopredator in temperate aquatic ecosystems of the northern hemisphere, and could play such a role. It is often highly abundant, feeds on a range of organisms, and can occupy different habitats (Wootton, 1984). An insidious, human-induced disturbance, the effects of which stickleback could modify, is eutrophication, an enrichment with nutrients that promotes primary production. Eutrophication alters habitat structure, reduces visibility, increases the amount of energy and material that flow through the food web (bottom-up effects), causes large daily fluctuations in oxygen levels in surface waters while reducing levels at the bottom (through increased amounts of decaying material), and induces toxic algal blooms (Smith and Schindler, 2009; Alexander *et al.*, 2017). These changes influence both ecological and evolutionary processes, and hence can impinge on the dynamics of populations and the structure of communities.

Here, I discuss the pathways through which the threespine stickleback can mediate and modulate the effects of anthropogenic eutrophication on communities and ecosystems. I present our current understanding of the processes and highlight some open questions to promote more research on the topic. I begin with a general presentation of how species mediate and modulate the effects of ecological disturbances on communities through density- and trait-mediated species interactions. I then proceed to discuss how the stickleback is affected by eutrophication, and how changes in the density and traits of the stickleback influence other species in the community. When no examples are available for the stickleback, I use information on other species to help anticipate how the changes might influence communities. I then discuss the consequences that the impact of the stickleback on the community can have for ecosystem processes, including ecosystem stability, biodiversity and services, and how any changes might impinge on eco-evolutionary dynamics and long-term changes in ecosystems. The threespine stickleback is considered a suitable model species for investigating the mechanisms and pathways through which anthropogenic disturbances influence communities and ecosystems. Yet, this review reveals a scarcity of studies on the ecological effects of the threespine stickleback in human-disturbed habitats. I thus end by highlighting some questions that require further investigation.

MODULATION OF ECOLOGICAL DISTURBANCES

Individual species can modulate the impacts of ecological disturbances on communities through direct and indirect interactions with other species, and by modifying the abiotic environment (Fig. 1). Species may influence other species (1) directly, e.g. when an increased phytoplankton density promotes the growth of zooplankton; (2) indirectly via effects on other species, e.g. when the increased zooplankton density in turn promotes the growth of their consumers, the mesopredators; (3) by altering the impact of the disturbance on other species, e.g. when the phytoplankton growth ties up nutrients and limits the impact of eutrophication on other primary producers; and (4) by altering the habitat and the conditions for other species, e.g. when the growth of phytoplankton reduces light penetration and thereby limits the growth of other photosynthesizing organisms in deeper water.

The modulation of disturbances can be density- or trait-mediated, and influence the density or traits of other species. Below, I explain how density- and trait-mediated effects can influence species communities.

Density-mediated effects

The impact of altered population density on other species has been one focus of studies on trophic interactions (i.e. consumer–resource interactions) (Wootton, 1993; Golubski and Abrams, 2011; Terry *et al.*, 2017). Changes in the density of one species can influence other species both directly and indirectly through bottom-up and top-down effects. An example is commercial fishing of top predators that alters the abundance of species at lower trophic levels, sometimes even down to primary producers (Jackson *et al.*, 2001; Estes *et al.*, 2011). Similarly, nutrient enrichment that increases primary production promotes population growth at higher trophic levels, with effects that can propagate all the way to top predators (Hulot *et al.*, 2000). The traits of linked species can also be affected, particularly their behaviours. For instance, many shorebirds amend their prey selection when eutrophication alters the abundance of different prey species (Green *et al.*, 2015).

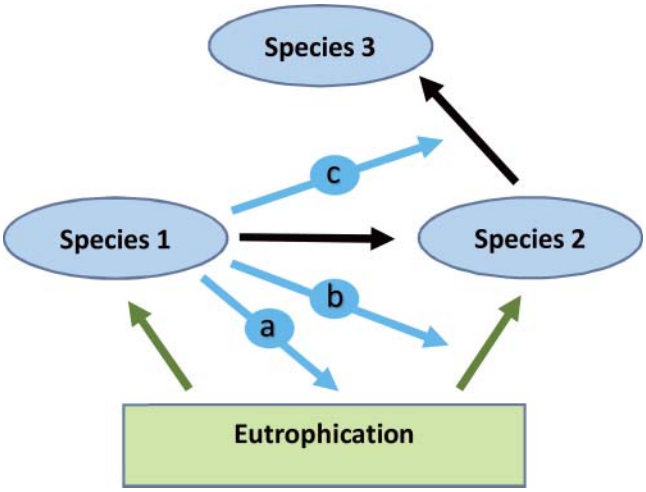

Fig. 1. The direct and indirect pathways through which changes in the density or traits of a species can influence other species. Eutrophication influences both species 1 and 2 through effects on their traits and population density and structure (green arrows). Changes in species 1 influence in turn species 2, both directly, for instance through predation (black arrow), and indirectly, by altering the effect of eutrophication on species 2 (blue arrows a and b). The latter scenario may arise if species 1 alters nutrient recycling and thereby modifies the level of eutrophication and its impact on species 2 (blue arrow a), or the distribution of species 2 and its exposure to eutrophication (blue arrow b). Changes in species 2 can in turn influence species 3 (black arrow), which is then an indirect effect of species 1. Species 1 can also modulate the effect of species 2 on species 3 by altering the environment, and thus encounters between species 2 and 3 (blue arrow c). Feedback responses can occur among species, with species 1 responding to changes in the other species, which may in turn alter the depicted impacts of species 1, but for clarity these are not shown.

Altered population density can also influence competitive interactions. For example, increases in the density of species after range contraction can increase the intensity of competition among those species for resources (Wootton, 1994). This might favour dominant species while wiping out weaker competitors. In the case of apparent competition (i.e. when prey species share a natural enemy), the effects of population density might also be felt by other prey species of the predator (Holt and Lawton, 1994). For instance, the current increase in Atlantic krill in the Barents Sea as a result of climate change is expected to promote the growth of the main zooplankton predator, the capelin *Mallotus villosus*, which in turn will reduce the biomass of another zooplankton group, the copepods (Stige *et al.*, 2018).

Changes in the density of species involved in host–parasite or mutualistic interactions can influence both the interacting partner and indirectly linked species (Holland and DeAngelis, 2010; Budria and Candolin, 2014). For example, the mass mortality of the Caribbean sea urchin *Diadema antillarum* in the 1980s shifted the reef system from coral-dominated to algae-dominated (Hughes, 1994).

Trait-mediated effects

Similar to density-mediated effects, human activities that alter trait expression (i.e. behavioural, morphological, physiological, developmental, or life-history traits) can affect interactions among species, including trophic (Schmitz *et al.*, 2004), competitive (Peacor and Werner, 1997), mutualistic (Kiers *et al.*, 2010), and parasitic interactions (Hatcher *et al.*, 2012). The responses of the interacting species can in turn influence any indirectly linked species (Ohgushi *et al.*, 2012). For instance, size-selective fishing that reduces the body size of fishes simultaneously increases predation on smaller prey species, which in turn influences their prey and competitors (Kuparinen *et al.*, 2016). Such trait-mediated effects have been proposed to have larger effects on community structure than density-mediated effects (Krivan and Schmitz, 2004). In support of this, a recent meta-analysis indicates that variation in traits within a species, such as in foraging or anti-predator behaviour, often has greater effects on community composition than the presence or absence of a species (Des Roches *et al.*, 2018). The initial trait change in response to environmental disturbances is usually a phenotypically plastic one (Pigliucci, 2001; van Buskirk, 2012). This is particularly likely in rapidly changing environments, as phenotypic changes occur within a generation, and hence are faster than genetic changes that occur across generations (Chevin *et al.*, 2010). However, plastic responses depend on earlier evolved reaction norms (i.e. on past selection), and thus need not be adaptive under novel conditions (Ghalambor *et al.*, 2007). Their expression depends on a range of conditions, such as the internal state of the individual and social conditions (Schmitz and Trussell, 2016), and can even result in changes that decrease the viability of the population. If there is genetic variation in the direction of selection, genetic changes may occur over time, which can lead to further changes to species interactions and hence to the species community (Barrett and Hendry, 2012).

Interaction between density- and trait-mediated effects

Density-mediated and trait-mediated effects are often connected. The density of a population can influence the traits of individuals, particularly their behaviour, such as foraging and social behaviour, and their body size. This can in turn induce further changes to the density of the population. Thus, density- and trait-mediated effects can interact and amplify, weaken, or alter each other's effects on other species (Relyea and Yurewicz, 2002). For instance, the collapse of a population of the goby *Gymnogobius isaza* in Lake Biwa in Japan in response to multiple environmental disturbances coincided with an increase in the body size of the gobies. This resulted in the fish switching from feeding on zooplankton to feeding on zoobenthos, since the latter are more suitable prey for larger individuals and they became more abundant when the fish population collapsed (Briones *et al.*, 2012). Thus, changes in both density and prey selection behaviour of the fish population influenced the prey community. Density- and trait-mediated effects can also interact as they propagate through the web of species interactions, which can result in complex changes to the community (Doak *et al.*, 2008; Hatcher *et al.*, 2012). For instance, the population growth of herbivorous snails in eutrophic lakes in North America has enhanced the transmission of the trematode *Ribeiroia ondatrae* to higher trophic levels, through both increased abundance of snails and increased per-capita production of infectious parasites in larger snails with enhanced host vigour (Johnson *et al.*, 2007). The increased release of parasites has in turn increased infections in the predator of the snails, the amphibian *Rana clamitans*, and caused severe limb deformities, which in turn has increased their susceptibility to predation (Goodman and Johnson, 2011).

EFFECTS OF EUTROPHICATION ON THE THREESPINE STICKLEBACK

Human-induced eutrophication influences both the density and the traits of the threespine stickleback by impinging on its foraging, predation risk, parasite burden, and reproductive success. I will discuss these effects in more detail below.

Foraging

An enhanced growth of micro- and macroalgae alters the availability and quality of prey of the stickleback, as well as its ability to detect and catch those prey. The effect on prey depends on the degree of eutrophication, with moderate levels of eutrophication increasing prey availability (Kraufvelin, 2007; Korpinen *et al.*, 2010; Sieben *et al.*, 2011b) and higher levels reducing prey availability (Arroyo *et al.*, 2012; Olafsson *et al.*, 2013), as well as decrease foraging efficiency (Helenius *et al.*, 2013; Sohel *et al.*, 2017). This is because the vision-oriented feeding behaviour of the stickleback is sensitive to eutrophication-induced changes in light conditions and habitat structure (Wootton, 1984; Lazzaro, 1987; Utne-Palm, 2002).

Predation risk

Intensified algal growth can decrease exposure to predators and facilitate escape, as it reduces visibility and increases structural complexity (Candolin and Voigt, 1998; Ajemian *et al.*, 2015). However, algal growth can also hamper the ability of stickleback to detect predators (Sohel and Lindstrom, 2015), as well as change the composition of the predator community to one that the stickleback is not adapted to, thus making escape more difficult. The exact impact of eutrophication therefore depends on how the predator community is affected. Owing to a trade-off with predator avoidance (Lima and Dill, 1990), changes in predation risk can in turn influence fitness-enhancing behaviours, such as foraging (Rudman *et al.*, 2016), social behaviour (Hoare *et al.*, 2004), and reproductive behaviour (Magnhagen, 1991; Candolin, 1998). Eutrophication can influence predation risk also through effects on shoaling behaviour, as algal turbidity hampers the ability of stickleback to identify and choose larger shoals that provide better protection against predators (Fischer and Frommen, 2013).

Parasite infections

Parasite infections in stickleback generally increase in line with increasing eutrophication (Poulin and Fitzgerald, 1989; Heuschele and Candolin, 2010). This is because many parasites prefer vegetated habitats, such as the ectoparasite *Argulus canadensis* (Poulin and Fitzgerald, 1989), or because their intermediate or final hosts are more common in vegetation, such as snails that are the first host of eye flukes *Diplostomum* sp. (Bronmark, 1989). However, the relationship between eutrophication and infection can vary over time, particularly during the reproductive season when a higher mortality of infected fish reduces their proportion in the population (Budria and Candolin, 2015). Eutrophication influences resistance and tolerance to parasites, but the effect varies among populations (Anaya-Rojas *et al.*, 2016). Some populations become more resistant and tolerant when nutrient levels increase, probably because of improved prey availability and body condition, while others do not (Anaya-Rojas *et al.*, 2016). The evolutionary history of the population and past levels of eutrophication apparently have an impact (Budria and Candolin, 2014). Changes in risk and severity of infections can in turn influence behaviours, such as anti-predator behaviour (Demandt *et al.*, 2018), social behaviour (Rahn *et al.*, 2018), foraging (Barber and Huntingford, 1995), and reproductive behaviour (Bronseth and Folstad, 1997; Macnab *et al.*, 2011). This can be caused by the energetic costs of immunocompetence and infections, which see individuals limit the investment they put into those behaviours (Barber *et al.*, 2000), or because of direct manipulation by parasites of neurophysiological mechanisms (Adamo, 2013). Changes in infections can in turn influence population dynamics through effects on growth, reproduction, and survival (Barber *et al.*, 2008; Heins and Baker, 2008).

Reproduction

Moderate levels of eutrophication generally increase offspring production, whereas high levels reduce it (Candolin, 2009). This is because moderate levels increase food availability and fecundity, as well as reduce visibility and aggressive interactions, which allows more males to nest within an area (Candolin, 2004; Candolin and Vlieger, 2013; Candolin *et al.*, 2014). Eutrophication also reduces raids on nests by conspecifics and heterospecifics (Vlieger and Candolin, 2009), and improves oxygen levels during the day, which decreases the need for intense fanning at the nest entrance and accelerates embryo development (Candolin *et al.*, 2008). After hatching, more food and shelter improve juvenile growth rate and survival (Candolin and Selin, 2012; Rybkina *et al.*, 2017). However, at high levels of eutrophication, negative effects dominate: males are reluctant to nest (Candolin and Salesto, 2006), nests are of poorer quality (Wong *et al.*, 2012; Tuomainen and Candolin, 2013), mate encounter rate decreases (Heuschele *et al.*, 2012), mate choice becomes more random (Candolin *et al.*, 2007; Wong *et al.*, 2007), oxygen levels decrease (because of decomposing material), and cyanobacteria blooms produce toxins that have a negative effect on juvenile development and survival (Sotton *et al.*, 2015). The exact effect of eutrophication varies, however, among populations, depending on the levels of eutrophication experienced during its evolutionary history (Tuomainen *et al.*, 2011).

Population size

The effects of eutrophication on fitness-related behaviours and processes discussed above indicate that moderate levels of eutrophication generally promote the growth of stickleback populations, through increased prey availability, reduced predation risk, and improved reproductive success. In contrast, high levels of eutrophication reduce population growth through decreased foraging efficiency, increased risk of parasite infections, hampered mate choice, and poor water quality for offspring production. In support of this, the stickleback are more abundant in the less eutrophic outer archipelago of the Baltic Sea than in the heavily eutrophic middle archipelago (Gagnon *et al.*, 2017). It also varies among locally anthropogenically eutrophic habitats, with stickleback more abundant in moderately eutrophic habitats (Bergström *et al.*, 2016; Candolin *et al.*, 2016b).

Population structure

Eutrophication can influence not only the size of the population but also its structure: its age, size, and sex distribution. In particular, improved male survival in turbid water during the breeding season could alter the sex ratio, as the nuptially coloured, vigorously courting males are less exposed to predators when visibility is reduced (Johnson and Candolin, 2017). In addition, the survival and growth of different age classes could change if the composition of the predator or prey community changes in response to eutrophication (Smith and Schindler, 2009; Arroyo *et al.*, 2012).

Plastic adjustments

The threespine stickleback adjusts its behaviour to eutrophication and alterations in visibility, including its foraging (Helenius *et al.*, 2013; Sohel *et al.*, 2017), anti-predator behaviour (Ajemian *et al.*, 2015), reproductive behaviour (Candolin, 2009), and social behaviour (Fischer and Frommen, 2013). The plastic adjustments may be adaptive when the stickleback has encountered similar conditions in the past, as adaptive reaction norms could then have evolved (Sih *et al.*, 2011; Tuomainen *et al.*, 2011). However, when novel environmental conditions are encountered, the responses may just as likely be maladaptive, as adaptive reaction norms may not have evolved (Ghalambor *et al.*, 2007). In support of this, stickleback females are more likely to select a male that sires offspring of low viability when visibility is reduced by algal blooms (Candolin *et al.*, 2016b).

Evolutionary responses

Genetic adaptation to eutrophication may occur over time. The threespine stickleback is an evolutionarily flexible species that has repeatedly adapted to natural variation in environmental conditions (Schluter *et al.*, 2010; Kaeuffer *et al.*, 2012). For instance, two morphologically distinct ecotypes – limnetic and benthic – have repeatedly evolved in response to different habitat use (Schluter, 1993). However, the degree to which the stickleback can adapt to rapid anthropogenic eutrophication is unclear, as eutrophication can also promote the collapse of ecotypes. For instance, the hybridization between the limnetic and the benthic ecotypes in Enos Lake in Canada could have been caused by eutrophication and deteriorating visibility (Taylor *et al.*, 2006).

An inability to adapt to eutrophication occurs when the rate of environmental change exceeds the potential for evolutionary change (Chevin *et al.*, 2010). Thus, relaxed sexual selection in eutrophic habitat, as a result of less careful mate choice, could constrain adaptation (Candolin *et al.*, 2007; Engström-Öst and Candolin, 2007). However, relaxed sexual selection can also strengthen natural selection at the juvenile stage, as more offspring are produced in eutrophic environments (Candolin *et al.*, 2014, 2016b). This could result in a switch in the relative strength of selection among different selection episodes, which may not reduce the rate of adaptation (Winemiller, 1992).

IMPACT OF THE THREESPINE STICKLEBACK ON LINKED SPECIES

Changes in the density and traits of the threespine stickleback can in turn influence other species (Fig. 2). The effect can be direct, such as when a growing stickleback population decimates a prey population, or indirect, such as when stickleback decimate a prey population that is shared with other predators. The impact of the stickleback on species communities has recently received wider attention, but how the stickleback mediates, and

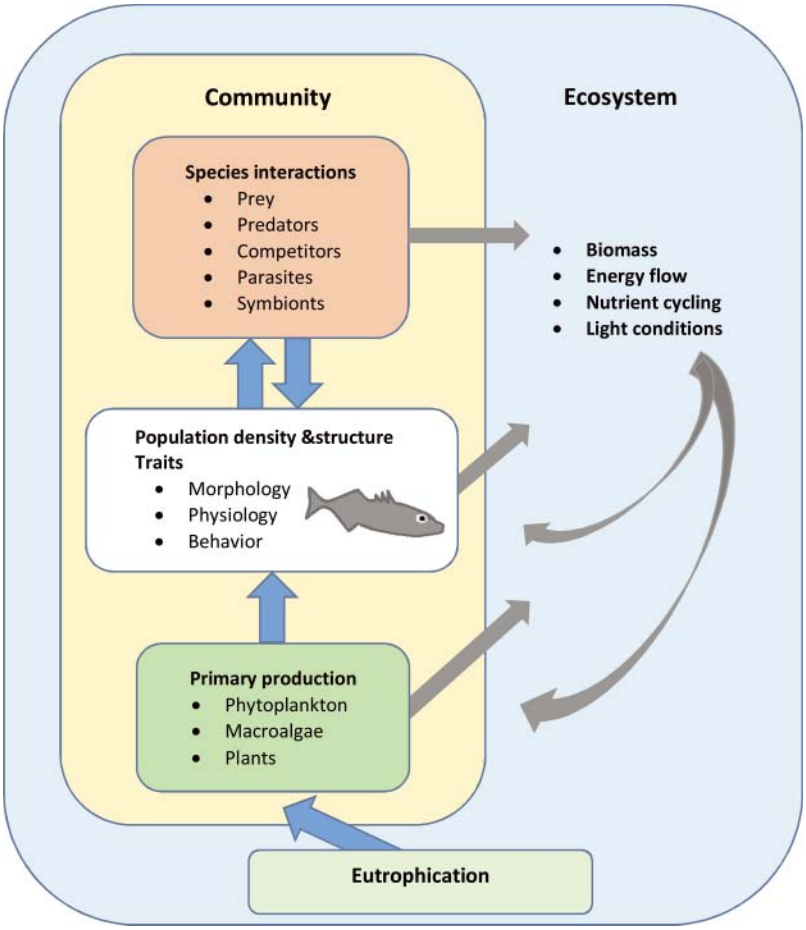

Fig. 2. Nutrient enrichment – eutrophication – influences primary production, which in turn can influence the population dynamics and traits of the threespine stickleback. Changes in the stickleback can in turn influence its interactions with other species, and hence the composition and structure of the species community. The responses of the stickleback to eutrophication can consequently influence ecosystem processes both directly, through changes in the population dynamics and traits of the stickleback, and indirectly, through the changes it induces in other species. Changes in ecological conditions can induce further changes to the stickleback population and its interactions with other species. Ecological changes can also induce evolutionary changes in the stickleback and the interacting species, but for clarity these are not shown.

possibly modulates, the effects of human-induced environmental changes is still poorly understood.

Altered density

Changes in the density of threespine stickleback can influence other species through (1) species interactions, including indirect interactions through other species, and (2) habitat modification. Effects on trophic species interactions have received most attention, with several studies finding that an increased density of stickleback reduces the abundance of various prey species, particularly herbivorous zooplankton and epibenthos (Jakobsen *et al.*, 2003; Eriksson *et al.*, 2009; Sieben *et al.*, 2011a, 2011b; Candolin *et al.*, 2018). This can in turn induce trophic cascades that increase the biomass of primary producers, which can further aggravate the effects of eutrophication on ecosystems (Candolin *et al.*, 2016a). Moreover, increased density can cause individual stickleback to switch to alternative prey, which may change the composition of the prey community (Svanbäck and Bolnick, 2007; Araujo *et al.*, 2008).

Alterations in stickleback density also have an effect on higher trophic levels. For example, the recent increase in the abundance of the great cormorant (*Phalacrocorax carbo sinensis*) in the Baltic Sea appears to be related, at least in part, to the growth of the stickleback population there. The stickleback is the main prey of the bird and the growth of the bird population coincides with the growth of the stickleback population (Boström *et al.*, 2012). Similarly, the decline of piscivorous fishes in the Baltic Sea, such as European perch (*Perca fluviatilis*) and pike (*Esox lucius*), could be related to the growth of the stickleback population, as the stickleback predates on their eggs and juveniles (Byström *et al.*, 2015). Such predation could result in a reinforcing feedback loop, with the growth of the stickleback population increasing predation on early-life stages of the predators, which reduces their abundance and, in so doing, further promotes the growth of the stickleback population. Invasion of stickleback into areas that have become more suitable for them because of eutrophication could similarly affect higher trophic levels. For instance, the invasion of the threespine stickleback into Upper Lake Constance has increased predation pressure on juvenile whitefish (*Coregonus* sp.), which has likely contributed to their decline (Roch *et al.*, 2018; Rosch *et al.*, 2018).

A growing stickleback population affects not only trophic interactions but also competitive interactions. The stickleback is an aggressive fish dominant over many other species (Huntingford, 1982; Wootton, 1984). Thus, its population growth intensifies competition with other mesopredators for space and food (Bergström *et al.*, 2015; Byström *et al.*, 2015). For example, the decline of whitefish in Lake Constance could in part be caused by competition for food between juvenile whitefish and stickleback (Roch *et al.*, 2018; Rosch *et al.*, 2018). Competition can also influence the behaviour and population dynamics of invading species. For instance, the invasive shrimp *Palaemon elegans* consumes more filamentous algae when competing with stickleback for animal prey (Candolin *et al.*, 2018). This reduces algal biomass, which counteracts the trophic cascade induced by a growing stickleback population (Fig. 3). Interestingly, the shift in diet by the shrimp could also moderate the population growth of the invasive shrimp, as the filamentous algae are less nutritious than animal prey (Lesutiene *et al.*, 2014).

Changes in stickleback density also affect other species through apparent competition, by influencing the abundance of shared predators. For instance, the great cormorant is a shared predator between the threespine and the ninespine stickleback (*Pungitius pungitius*) in the Baltic Sea. Thus, its increase in abundance in the area at the same time as that in the threespine stickleback population has increased predation pressure on the ninespine stickleback (Boström *et al.*, 2012). This could have contributed to the present decline of the ninespine stickleback in the area (Baden *et al.*, 2012).

Parasite transmission can further mediate effects of altered stickleback density on other species. In particular, the increased prevalence of parasitized stickleback in eutrophic environments could influence infections in other species, particularly the predators of stickleback, and hence their population dynamics. However, while such effects have been noted in other species [e.g. freshwater snails that transfer more trematodes to amphibians in

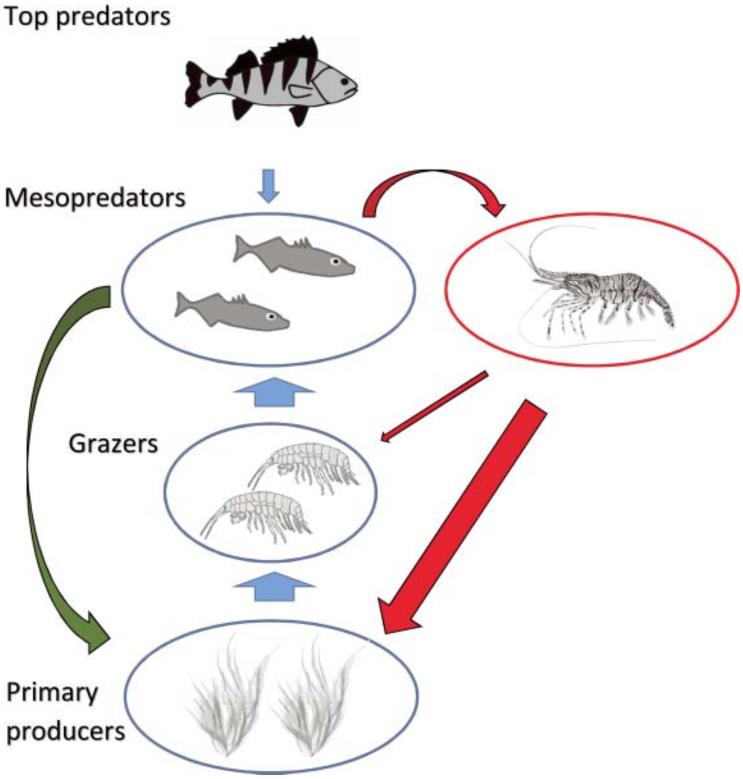

Fig. 3. The growth of the threespine stickleback population in the Baltic Sea has been promoted by eutrophication that has enhanced the growth of primary production, and hence the growth of grazers, and by overfishing of top predators (the blue arrows, which indicate direct effects). This has intensified competition among mesopredators (stickleback and shrimp) for animal food. In response to the competition, omnivorous shrimp have increased their consumption of filamentous algae. This has reduced the biomass of primary producers, i.e. counteracted the effects of eutrophication on the biomass (Candolin *et al.*, 2018). Thus, while the stickleback promotes the growth of algal biomass through a trophic cascade, it also mitigates its growth by inducing changes in the foraging behaviour of the shrimp (the red arrows indicate direct effects and the green arrow an indirect effect). The size of the arrows indicate changes in the impact of the components of the community.

eutrophic habitats (Johnson *et al.*, 2007)], little is known about the ecological effects of an increased abundance of infected stickleback (Budria and Candolin, 2014).

Changes in the structure of stickleback populations, such as age or body size, could also influence species interactions. This has not been investigated in the threespine stickleback, but work on Trinidadian guppies (*Poecilia reticulata*) shows that size structure influences trophic interactions, and thus the composition of the prey community and algal biomass (Bassar *et al.*, 2015). Altered population structure could similarly influence competitive interactions, particularly as the diet and habitat use of the stickleback change with body size and age (Wootton, 1984).

In general, the impact of altered threespine stickleback density on other species is complex and includes both positive and negative effects. The effects can transcend far beyond the stickleback population, through the myriad of linkages among species, as well as interact with other changes to the ecosystem, such as overfishing, climate change, and the invasion of new species. Ultimately, the outcome will depend on the responses shown by the directly and indirectly interacting species, which stresses the importance of understanding the interactions that occur in species communities when attempting to elucidate the impact of changes in the population dynamics of stickleback.

Altered traits

Similar to changes in density, alterations to the traits of the threespine stickleback, such as its behaviour or morphology, can influence species interactions. Although relatively little is known about such effects in rapidly changing environments, studies on populations adapted to naturally varying habitats show that trait differences can influence community structure and composition (Harmon *et al.*, 2009; Ingram *et al.*, 2012; Des Roches *et al.*, 2013; Matthews *et al.*, 2016; Best *et al.*, 2017). For instance, Harmon *et al.* (2009) showed that ecologically differentiated threespine stickleback populations – benthic and limnetic ecotypes – have contrasting effects on the ecosystem; they differ in their diet and thereby in how they influence the species community, both directly through consumption and indirectly by influencing primary production and light conditions. Similarly, studies of other fish species have found that differences in traits among populations have an effect on community composition (Bassar *et al.*, 2010; Palkovacs *et al.*, 2012; Lundsgaard-Hansen *et al.*, 2014). For example, Post *et al.* (2008) showed that differences in foraging traits between landlocked and anadromous alewives (*Alosa pseudoharengus*) influenced the zooplankton community, which in turn affected phytoplankton abundance.

Changes in traits in response to eutrophication could have similar impacts on communities. Behavioural changes are usually the first response to rapid environmental change, such as altered foraging or habitat choice (Tuomainen and Candolin, 2011). For instance, the reduced foraging efficiency of stickleback in turbid water could have an effect on the prey community. In support of this, individuals foraging in algal-turbid water reduced their consumption of fast-moving copepods while increasing their consumption of slower-moving cladocerans, as they are easier to catch (Helenius *et al.*, 2013). Such plastic changes in diet could have cascading effects on the species community. This is supported by a recent study by Rudman and Schluter (2016), who found that rapid changes in morphology and prey selection, because of gene flow, altered the composition of the prey community.

Alterations in foraging behaviour can also influence competitive interactions. Species that are better than the stickleback at finding food in dense micro- or macroalgae growth could proliferate at the expense of stickleback. In particular, invasive species preadapted to eutrophic conditions could have a competitive advantage, especially if the stickleback – and other species in the community – have not experienced eutrophic conditions in their recent evolutionary past, and hence have not evolved adaptive strategies for dealing with such conditions.

Reduced aggressive interactions in eutrophic habitats, because of poor visibility, could similarly influence population dynamics and the traits of other species. This is especially likely during the reproduction period of the stickleback, when males establish territories and aggressively defend these against both conspecifics and heterospecifics (Candolin *et al.*, 2014). A reduction in aggression might then favour species that occupy the same habitat but which are subordinate to the stickleback. For instance, shrimps are at a disadvantage in the competition for space with stickleback in clear water, while dense algal growth and reduced visibility facilitates their co-existence (Candolin *et al.*, 2018). Such co-existence could have further effects on the species community, as shrimps consume both animal prey and algae, while stickleback consume only animal prey.

Eutrophication can also affect the ability of stickleback to avoid predation, as they use turbid water and dense macroalgal growth as refuges against predators (Candolin, 1998; Engström-Öst *et al.*, 2009). This could impinge on the population dynamics of their predators, and thus indirectly other prey of the predators. On the other hand, the current decline of top predators because of overfishing and habitat destruction (Estes *et al.*, 2011) could allow stickleback to venture out of refuges. This could in turn influence the prey community of the stickleback, as demonstrated in a study adding a predator, the cutthroat trout (*Oncorhynchus clarkii*), to ponds containing stickleback (Rudman *et al.*, 2016). The predator caused the stickleback to alter its diet, which induced a trophic cascade that changed the community composition of both the affected aquatic ecosystem and the connected terrestrial ecosystem, by changing the abundance of emerging insects.

Alterations in traits can also influence parasite transmission, as the stickleback is the intermediate and final host of several parasites. Changes in body condition can affect resistance to parasites, while behavioural alterations influence exposure (Barber, 2013), both of which can be influenced by eutrophication. Changes in parasite load can in turn influence the transmission of parasites to other species and thereby alter their population dynamics. It can also induce changes in the behaviour of the stickleback, such as its anti-predator behaviour or prey selection, which in turn can have an effect on these species (Barber, 2013; Anaya-Rojas *et al.*, 2016). For instance, stickleback infected with the common fish parasite *Gyrodactylus* spp. alter their prey selection, which has an impact on the zooplankton community (Brunner *et al.*, 2017).

Changes in mate choice and nest site selection can result in the merging of ecotypes, as observed between limnetic and benthic ecotypes in lakes with reduced visibility (Taylor *et al.*, 2006). This can in turn alter the species community, as the different ecotypes inhabit different habitats and vary in their prey choice (Matthews *et al.*, 2010; Rudman and Schluter, 2016). For instance, the merging of limnetic and benthic stickleback in Enos Lake in British Columbia has had cascading effects on both aquatic prey and on insects emerging into the terrestrial ecosystem (Rudman and Schluter, 2016). The predator fauna and competitors for food and space could similarly be affected by the merging of ecotypes.

Similarly, altered morphology, whether caused by the merging of ecotypes or by selection, can influence behaviour and thereby trophic interactions. Changes to the predator fauna induces selection on morphology (Ingram *et al.*, 2012), which in turn influences behaviour, such as habitat choice and prey selection (Schluter, 1993; Berner *et al.*, 2008; Matthews *et al.*, 2010; Snowberg *et al.*, 2015). Similarly, changes in competition for prey could induce morphological changes that influence prey selection. For instance, when limnetic and benthic stickleback have to compete for the same prey, selection on their morphology changes (Schluter, 1994). Moreover, changes in the prey community could induce morphological alterations that improve foraging efficiency, as noted in fishes such as alewives (Palkovacs and Post, 2008).

CONSEQUENCES

This review of the literature has shown that the threespine stickleback can mediate and modify the impact of nutrient enrichment on community structure, through species interactions and by altering habitat. Such changes could in turn influence ecological processes such as energy flow and nutrient cycling (Fig. 2). This is supported by several studies showing that changes in the traits of the stickleback influence ecological processes, including primary production, decomposition, nutrient cycling and translocation, and light penetration (Harmon *et al.*, 2009; Sieben *et al.*, 2011b; Des Roches *et al.*, 2013; Rudman *et al.*, 2015; Best *et al.*, 2017; Limberger *et al.*, 2019). For instance, Rudman *et al.* (2015) showed that differences in the diet of the stickleback influence bottom-up effects caused by nutrient subsidies from terrestrial litter, i.e. they influence primary and secondary production and light extinction. Other studies have found that changes in the density of stickleback (Jakobsen *et al.*, 2003; Sieben *et al.*, 2011a; Candolin *et al.*, 2016a), and in the presence of competing species (Candolin *et al.*, 2018), influence the ecological impact of the stickleback.

This ecosystem engineering effect of the stickleback suggests that it could have a major impact on ecosystem stability, biodiversity, and services in human-disturbed habitats. In addition, it could influence evolutionary processes through reciprocal interactions between ecological and evolutionary changes, i.e. through eco-evolutionary dynamics (Hendry, 2017). This could result in longer-term consequences of ecological changes. These are, however, difficult to predict, as the pathways are complex and intertwined, as has become evident in this review. Below, I discuss some effects that the stickleback could have on ecological and evolutionary processes in anthropogenically eutrophic habitats.

Ecosystem stability, biodiversity, and services

The ecological flexibility of the threespine stickleback – particularly in relation to diet and habitat choice – combined with its often high abundance and multiple interactions with other species, suggests that it could influence the stability of human-disturbed ecosystems. Changes in traits can stabilize or destabilize the dynamics of populations, depending on how they influence the abiotic environment and species interactions (Ives and Carpenter, 2007). Changes in population dynamics can in turn influence the stability of the community and, ultimately, the probability of regime shifts from one ecosystem state to another in human-disturbed habitats (Oliver *et al.*, 2015; Dakos *et al.*, 2019). Thus, changes in stickleback population dynamics and traits could either buffer ecosystems against further change or, alternatively, amplify ongoing changes, depending on how the stickleback influences the population dynamics of other species. For instance, if the stickleback increases its consumption of prey whose populations are growing, it could moderate their growth and buffer against further changes to the ecosystem. However, if it increases its consumption of the most easily detected or caught species, and these are not the most abundant species, it could amplify disturbances brought on by humans. For example, the increased consumption of larger, slower-moving zooplankton in algal-turbid water (Helenius *et al.*, 2013) could influence the zooplankton fauna, which in turn could influence the phytoplankton community and other predators of the zooplankton, thus amplifying the effects of human-induced eutrophication on the ecosystem.

Current research indicates that the stickleback mainly aggravates the impact of eutrophication on ecosystems, at least at moderate levels of eutrophication. The stickleback population grows when primary production increases, through higher fecundity and a lower mortality rate, as detailed above. A larger population reduces in turn the abundance of grazers, which increases the biomass of primary production not transferred to higher trophic levels, as the biomass of primary production grows faster than that of grazers (Sieben *et al.*, 2011a, 2011b; Candolin *et al.*, 2016a). This causes further changes to the ecosystem by altering light conditions, decomposition, nutrient recycling, and energy flow (Smith, 2003). The ultimate outcome depends, however, on how the effects of the stickleback interact with other changes to the ecosystem (Ratajczak *et al.*, 2018). For instance, in many human-disturbed habitats, the decline of top predators is further promoting the growth of stickleback populations, and in interaction with eutrophication is aggravating the impact of the stickleback on ecological conditions (Bergström *et al.*, 2015; Estes *et al.*, 2011). At very high levels of eutrophication, stickleback populations decline. However, this can also influence the ecosystem, as the stickleback plays a central role in many food webs through its high abundance and myriad species interactions.

The stickleback is an important link between coastal and offshore areas, given its seasonal migration. Thus, changes in the density and behaviour of the stickleback can influence the redistribution of resources between habitats, as has been noted for other fishes, such as salmon (Gende *et al.*, 2002). Similarly, the stickleback influences the flow of material and energy between aquatic and terrestrial ecosystems, by feeding on terrestrial insects with aquatic larvae stages (Rudman *et al.*, 2016), and by being the prey of piscivorous birds (Boström *et al.*, 2012). These processes may be altered by changes to the abundance and traits of the stickleback.

Changes in stickleback density and traits can also influence ecosystem services, such as fish production and recreational use (Barbier *et al.*, 2011). In particular, the increased biomass of primary production caused by the stickleback (by feeding on grazers) increases hypoxia, with known negative effects on secondary production and organic matter cycling (Levin *et al.*, 2009). It also alters habitat structure and thus the provision of shelter for juveniles and adults of commercially or recreationally important species (Mineur *et al.*, 2015).

Eco-evolutionary dynamics

Changes in ecological processes can in turn influence evolutionary processes, which, through feedback loops, can influence ecological processes, resulting in eco-evolutionary dynamics (Pelletier *et al.*, 2009; Post and Palkovacs, 2009; Hendry, 2017). In support of this, several studies have found that stickleback populations exposed to different ecological conditions during their recent evolutionary history have evolved into different ecotypes that vary in their ecological impact, as discussed earlier (e.g. Harmon *et al.*, 2009; Des Roches *et al.*, 2013). Recent experiments have further shown that the ecological effects of different ectomorphs and evolutionary lineages can influence selection on the next generation (Matthews *et al.*, 2016; Best *et al.*, 2017; Brunner *et al.*, 2017). Similar interactions between ecological and evolutionary processes have been recorded for other species such as Trinidadian guppies, which evolve earlier maturity and altered dietary preferences when exposed to predators, which in turn influence ecological conditions (Bassar *et al.*, 2010).

Whether the stickleback can adapt fast enough to rapid human-induced environmental changes, such as eutrophication, to result in eco-evolutionary dynamics is unknown. The first responses to rapid environmental changes are usually plastic responses (Tuomainen and Candolin, 2011). Yet, these can influence ecological conditions and thus induce selection on the next generation (Miner *et al.*, 2005; Hendry, 2016). However, whether populations can in turn respond to these changes with genetic alterations, as well as the rate of such alterations, depends on the existence of genetic variation in the direction of selection and the size of the population. The stickleback is an evolutionarily flexible species that has adapted to a range of conditions (Schluter *et al.*, 2010; Kaeuffer *et al.*, 2012). Thus, many populations could harbour the genetic variation needed to adapt to eutrophication, but the rate at which this could occur is not known.

The responses of the stickleback to eutrophication (whether plastic or genetic) could in turn influence the evolution of linked species. For instance, increased predation by the stickleback on slow-moving cladocerans in turbid water could induce selection for smaller body size of cladocerans, or for morphological structures that protect against predators. Such evolutionary changes could cause further changes to the ecosystem; reduced body size of cladocerans could alter their food selection, while the evolution of anti-predator structures could influence the population dynamics of other predators of the cladocerans.

Eco-evolutionary dynamics can also help to maintain ecosystem services in rapidly changing environments [i.e. evosystem services (Faith *et al.*, 2010; Rudman *et al.*, 2017)]. The stickleback could contribute to this, considering the central role that it plays in many ecosystems. In particular, it could promote evolutionary changes in other species with shorter generation time, such as plankton, which could influence the diversity and productivity of ecosystems. However, little is still known about such effects.

CONCLUSIONS, OPEN QUESTIONS, AND FUTURE DIRECTIONS

It is clear that anthropogenic eutrophication affects threespine stickleback populations, their density, and individual traits. Research shows that the stickleback is a highly plastic species, particularly behaviourally, that can adjust rapidly to changes in the environment. The evolution of this plasticity and how it depends on previously encountered conditions – the evolutionary history of the species – is less well known. More research is needed on the evolution of plasticity and the factors that influence it. This would improve our ability to predict under which conditions the stickleback is able to adjust to eutrophication, and how different populations may respond. More research is also needed on the potential of the stickleback to adapt genetically to human-induced rapid environmental changes, and on the interaction between plasticity and genetic changes in promoting this adaptation.

Research on the impact of stickleback responses on species interactions has mostly concentrated on trophic interactions. Research shows that changes in density and foraging behaviour influence the abundance of other species, especially at lower trophic levels. The recorded effects are strong, which indicates that the stickleback is a major player in mediating the impact of eutrophication on the composition and structure of communities in many ecosystems. Research has concentrated on effects on the abundance of the interacting species, while effects on their traits, such as foraging behaviour or activity, have received less attention. Little is known either about effects on other forms of species interactions, such as competitive and host–parasite interactions. More attention should be paid to the multitude of pathways through which the stickleback can influence communities in eutrophic habitats. This would give us a more complete picture of how, when, and why the stickleback mediates the impact of human disturbances on communities.

Changes in the composition and structure of species communities can in turn influence ecological processes, such as primary production, decomposition, nutrient recycling and translocation, and light extinction. Information on such effects is beginning to accumulate, such as that trophic interactions in particular influence ecological processes. The impact of the stickleback through other forms of species interactions, such as competitive and host–parasite interactions, is not well understood. Thus, more information is needed on the various pathways through which the stickleback can influence ecological processes, both direct and indirect pathways, as well as the underpinning mechanisms. Related to this, more attention should be paid to the impact of the stickleback on ecosystem services. This is a growing field of research and the stickleback could influence both the recreational and commercial value of habitats through its effects on algal biomass, water quality, and habitat structure.

Changes in ecological conditions in turn influence evolutionary processes, which feed back to influence ecological conditions. Another field of research which the stickleback has much to offer is eco-evolutionary dynamics. Information is needed not only on how the stickleback adapts to eutrophication, but also how it influences the evolution of other species, and how this can feed back to further alter the ecosystem.

To investigate the pathways through which the stickleback mediates the impact of eutrophication on ecosystems, and the underlying mechanisms, experimental studies on species interactions need to be integrated with whole-ecosystem studies. This would allow us to evaluate the relative contribution of single interactions to ecosystem processes. For instance, mesocosm experiments that manipulate the presence of stickleback and other species, or particular traits of the species, under high and low nutrient levels, can reveal their impact on community structure and ecosystem processes (e.g. Harmon *et al.*, 2009). The results can then be compared to processes in nature to evaluate the relative impacts of the species and their traits (Candolin *et al.*, 2016a). Similarly, exclosure experiments, or the introduction of species, can reveal the impact of individual species on ecological processes (e.g. Sieben *et al.*, 2011b). Comparisons of populations in space and time can in turn reveal the progress of changes and how they depend on specific conditions and evolutionary processes (Simon *et al.*, 2017).

Empirical data can combined with theoretical models and simulations to reveal the pathways and underpinning mechanisms, as well as to predict possible responses to rapid environmental changes. For instance, weighted interaction network models can be used to predict changes in interaction frequencies in disturbed habitats. This can be achieved by combining field data on abundance and behaviour with mathematical models (Staniczenko *et al.*, 2017).

Interactions with other changes occurring in ecosystems also need to be considered, as many ecosystems are exposed to multiple disturbances. For instance, many fish populations are affected not only by eutrophication, but also by climate change and overfishing of top predators. In addition, long-term data on the processes in nature are required to reveal evolutionary changes that play out over longer time-scales.

In summary, attention needs to be paid to the impact of altered ecological interactions on ecosystem processes. This would improve our ability to understand, predict, and mitigate the effects of human activities on ecosystems. The stickleback can serve as an excellent model species, given its abundance in many aquatic ecosystems, the central role that it plays in many food webs, the ease with which it can be used in experimental work, and the amount of information that has already been gathered on its ecology and differences in characteristics among populations.

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