PHILOSOPHICAL TRANSACTIONS B

rstb.royalsocietypublishing.org

Review

Cite this article: Alexander TJ, Vonlanthen P, Seehausen O. 2017 Does eutrophication-driven evolution change aquatic ecosystems? *Phil. Trans. R. Soc. B* **372**: 20160041. http://dx.doi.org/10.1098/rstb.2016.0041

Accepted: 26 September 2016

One contribution of 18 to a theme issue 'Human influences on evolution, and the ecological and societal consequences'.

Subject Areas:
ecology, evolution

Keywords:
eutrophication, eco-evolutionary dynamics, whitefish, lakes

Author for correspondence:
Timothy J. Alexander
e-mail: tjalexander001@gmail.com

Does eutrophication-driven evolution change aquatic ecosystems?

Timothy J. Alexander[1,2], Pascal Vonlanthen[1,2] and Ole Seehausen[1,2]

[1]Department of Fish Ecology and Evolution, Centre of Ecology, Evolution and Biogeochemistry, EAWAG Swiss Federal Institute of Aquatic Science and Technology, Seestrasse 79, 6047 Kastanienbaum, Switzerland
[2]Division of Aquatic Ecology and Evolution, Institute of Ecology and Evolution, University of Bern, Baltzerstrasse 6, 3012 Bern, Switzerland

TJA, 0000-0002-6971-6205

Eutrophication increases primary production and changes the relative abundance, taxonomic composition and spatial distribution of primary producers within an aquatic ecosystem. The changes in composition and location of resources alter the distribution and flow of energy and biomass throughout the food web. Changes in productivity also alter the physico-chemical environment, which has further effects on the biota. Such ecological changes influence the direction and strength of natural and sexual selection experienced by populations. Besides altering selection, they can also erode the habitat gradients and/or behavioural mechanisms that maintain ecological separation and reproductive isolation among species. Consequently, eutrophication of lakes commonly results in reduced ecological specialization as well as genetic and phenotypic homogenization among lakes and among niches within lakes. We argue that the associated loss in functional diversity and niche differentiation may lead to decreased carrying capacity and lower resource-use efficiency by consumers. We show that in central European whitefish species radiations, the functional diversity affected by eutrophication-induced speciation reversal correlates with community-wide trophic transfer efficiency (fisheries yield per unit phosphorus). We take this as an example of how evolutionary dynamics driven by anthropogenic environmental change can have lasting effects on biodiversity and ecosystem functioning.

This article is part of the themed issue 'Human influences on evolution, and the ecological and societal consequences'.

1. General introduction

Ecologically significant evolutionary change is increasingly recognized to occur over short timescales of tens of generations or fewer [1,2]. In parallel with this recognition comes the realization that human activities can rapidly change the course of evolution and even reverse the evolutionary processes generating biodiversity, resulting in homogenization of once-distinct populations and species. Cultural eutrophication, the human-derived increase in the supply of a limiting nutrient above natural levels, is one of the most pervasive forms of environmental change experienced by aquatic ecosystems, strongly influencing both biotic and the abiotic conditions. Eutrophication has affected most freshwater and coastal ecosystems of the world to some extent [3] and is generally caused by urban and industrial sewage, erosional run-off and leaching from agricultural areas and cleared land [4]. While the amount of nutrients entering aquatic ecosystems has probably been gradually increasing since humans first began clearing land for settlements and agriculture, the rate of nutrient supply increased dramatically in many aquatic ecosystems in the mid-1900s [5]. This increase was primarily driven by the rapid human population growth and connection of many households to main sewerage networks, which was discharged with minimal treatment into local waterways. The ecological impacts of eutrophication have been intensively studied [4]; however, the effects of these changes on the evolutionary dynamics of the systems

THE ROYAL SOCIETY
PUBLISHING

have received less attention. Lakes are particularly useful model systems in this context as the impact of evolutionary change on biodiversity and ecosystem services is likely to be most apparent in these semi-enclosed systems. In this paper, we briefly summarize ecological effects of eutrophication in aquatic ecosystems, review how these may lead to evolutionary change and finally discuss the potential consequences of evolutionary change for ecology and the services that humans derive from these ecosystems. The paper focuses mostly on lakes as this is where much research on recent and rapid evolutionary dynamics has been conducted, and fish because of their direct link to an important ecosystem service (i.e. fisheries).

2. Ecological changes with eutrophication

Understanding the ecological changes that occur during eutrophication is critical for recognizing changes to evolutionary dynamics, particularly with respect to changing selection pressures and the underlying fitness landscape. The direct effect of increasing nutrients in aquatic systems is to increase growth rates of primary producers. Increasing productivity generally corresponds with a shift among groups of primary producers and habitats from benthic periphyton, epiphytes and macrophytes to phytoplankton. Shifts also occur within groups, such as increasing dominance of the phytoplankton community by cyanobacteria in lakes with elevated nutrients [6]. In highly eutrophic lakes, primary production occurs mostly through phytoplankton in a relatively thin layer of water close to the lake surface. Increasing nutrient levels also alter the seasonality of phytoplankton dynamics, advancing the period of peak phytoplankton biomass [7] and delaying the onset of epilimnetic depletion of phosphorus [8]. While the link between nutrients and plant growth is well established, the flow of this energy/biomass to higher trophic levels is less predictable. The response of a particular trophic level to increased primary productivity also depends on how abiotic changes associated with increased nutrients affect the target trophic level, as well as trophic levels above (predators) and below (prey).

The increased primary production under eutrophication indirectly affects the physico-chemical conditions of aquatic ecosystems. High rates of primary production resulting from elevated nutrients can result in super-saturation of oxygen in the epilimnion during daylight hours of summer months. Respiration by the high density of organisms in surface waters of eutrophic systems (e.g. phytoplankton, zooplankton) also consumes large amounts of oxygen during night hours, resulting in large daily fluctuations. High concentrations of organic particles also affect the ambient light environment. Increased biogenic turbidity results in lower light penetration and a shallower photic zone. Organic particles absorb and scatter sunlight of certain wavelengths, resulting in changes in the spectrum of visible colours (e.g. [9]). When growth rates of primary producers and other trophic guilds exceed rates of consumption, large quantities of deceased organic material can also accumulate in the system. Decomposition of accumulated dead phytoplankton, aquatic macrophytes, zooplankton and other organic material occurs in the water column and on the lake floor. Decomposition of organic particles below the thermocline, and at the sediment–water interface, can result in oxygen depletion (hypoxia) in the hypolimnion of lakes. Eutrophication, therefore, changes the amount of biomass in a lake, its spatial distribution and allocation among trophic levels and taxa. Consequently, eutrophication alters the entire biological structure of a lake ecosystem, along with its physico-chemical conditions.

3. Changes in evolutionary dynamics

(a) Ecological fitness landscapes

Biotic and abiotic changes associated with eutrophication interact to influence the direction and strength of natural selection and thereby the shape of the ecological fitness landscape experienced by component populations. Cultural eutrophication in most aquatic ecosystems occurred as a result of rapidly increasing nutrients over just a few decades [10,11] (figure 2*a*). Algal-grazing zooplankters, such as cladocerans (e.g. *Daphnia* spp. [12,13]) and copepods (e.g. *Acartia* spp. [14]), have been shown to adapt to the changing diet under eutrophic conditions. Hairston *et al.* [15] resurrected dormant eggs of *Daphnia galeata* from Lake Constance in central Europe to show evolved resistance to the nutritionally poor and potentially toxic cyanobacteria that bloomed during the period of eutrophication. Frisch *et al.* [12] also used resurrection ecology to show that modern *Daphnia pulicaria* of South Center Lake, Minnesota, grew less efficiently under low-phosphorus conditions as they had adapted to take advantage of the high-phosphorus diet while the lake was eutrophic.

Some zooplankton species also show behavioural adaptations to the effects of eutrophication. Estuarine copepod zooplankton (*Acartia tonsa*) exhibit geographical variation in adaptive behavioural responses to hypoxia caused by excess nutrients [14]. Field- and laboratory-reared individuals from a location with a steep vertical oxygen gradient avoided hypoxic bottom water under experimental conditions. On the other hand, individuals from a population with no history of hypoxia did not avoid lethal oxygen concentrations. The results suggest an evolved behavioural response to avoid hypoxia, allowing the adapted population to persist and perhaps thrive (as hypoxic conditions may provide a refuge from fish predation) despite the adverse environmental conditions caused by eutrophication. Physiological adaptation to tolerate hypoxic conditions has also been documented in invasive *Dreissena* mussels [16].

Ecosystem changes during eutrophication may also provide invasive species, usually arriving from more phosphorus rich habitats, with an ecological advantage over native species [17]. The resulting relatively larger population sizes of invasive species in the altered environment, consequently increase the likelihood of hybridization and invasion of the genome of closely related native species [18]. *Daphnia galeata* is an invasive species in Lake Constance that arrived only in the course of the eutrophication. As it invaded, it hybridized with the local *D. longispina* (formerly *D. hyalina)* to an extent that the current population, after restoration of the oligotrophic conditions, seems to be dominated by genetically admixed individuals [19].

Generally speaking, in ecosystems undergoing *strong* eutrophication, the rapid onset of change and higher temporal variability of biotic and abiotic conditions under newly eutrophic conditions may select for phenotypic plasticity [20] and provide a fitness advantage to generalist species (e.g. [21]). Empirical studies have shown that individuals and populations tolerant to toxins of cyanobacteria will also have a fitness advantage in lakes undergoing strong eutrophication. Organisms that live and breed in shallow water, and those with the capacity for physiological or behavioural adaption to hypoxia, are less likely to be negatively affected by abiotic changes. In ecosystems undergoing *weak* eutrophication, it is more difficult to generalize on the direction of natural selection for a specific population. Changes to the adaptive landscape certainly occur. However, rather than being driven by dramatic changes in the abiotic environment, selection pressures are altered more by changes in the distribution and flow of energy and biomass among species and trophic guilds throughout the food web.

(b) Sexual selection

The altered physical environment associated with eutrophication can affect visual signalling between mates and between competitors. When sexual selection is mediated by vision-based mate choice, as in many fish, eutrophication-induced loss of water clarity is predicted to weaken sexual selection. Male nuptial coloration of cichlid fish in Lake Victoria is less colourful (less bright and less diverse) in more strongly eutrophic sections of the lake [9]. Eutrophication also reduced the intensity of sexual selection in stickleback of the Baltic Sea via multiple pathways. In this species, expression of male nuptial coloration and courtship activity are influenced by the outcome of male–male contest competition. Dominant males courted more actively and exhibited a larger area of red coloration, which positively influenced female mate choice [22]. Under eutrophication-induced turbidity, social control of the signalling was relaxed and subordinate males were able to vigorously court females and express bright colours, despite the presence of males in better condition [23]. Eutrophication also resulted in a dense mat of filamentous algae around male stickleback nests. This further impaired visibility, resulting in smaller territories, fewer aggressive interactions and a higher density of nests, indicating that a higher proportion of males were able to reproduce [24]. Female choice was believed to be hampered by the higher turbidity and increased physical structure, which resulted in a more even distribution of eggs among male nests in nutrient-enriched waters [24]. These conditions constitute further evidence for relaxed sexual selection in the presence of eutrophication.

In addition to the Baltic stickleback, algae-induced turbidity hampers sexual selection in other marine fishes in eutrophic areas of the Baltic Sea. Mating success in the sand goby (*Pomatoschistus minutus*) was more evenly distributed and less skewed towards large males under turbid conditions compared with clear water [25]. The difference in mean length between mated and unmated males was also smaller in turbid water [25]. Also in the Baltic Sea, turbidity impeded mate choice in the broadnosed pipefish (*Syngnathus typhle*) [26]. Male pipefish spent less time assessing females and exhibited a weaker preference for large females under turbid conditions [26]. In these cases, algal turbidity weakened sexual selection, potentially leading to reduced phenotypic variation in affected populations and potentially affecting mean fitness. The possible consequences for ecosystem services in these cases have not been studied. Consequences for ecosystem functioning are more intuitive where eutrophication-induced breakdown of species-assortative mate choice led to gene flow between previously distinct species, as discussed in §3c.

(c) Reproductive isolation and gene flow

By changing the physical environment along with the form and strength of natural and sexual selection, eutrophication can affect environmentally mediated mechanisms of reproductive isolation among species. Closely related species are particularly prone to extinction via the breakdown of reproductive isolation after human-induced environmental changes [27]. This is because reproductive isolation is still dependent on prezygotic mechanisms (mate choice, habitat choice) and/or extrinsic (ecology-dependent) postzygotic mechanisms in the absence of strong intrinsic postzygotic hybrid dysfunction. Rare species are also at risk of being lost through introgression when environmental changes force them into increasing contact with abundant species [28].

In Lake Victoria, at least 200 of the 500 endemic species of cichlids have gone extinct over the past 30 years [29,30]. Eutrophication is believed to be a major contributor to this loss [9]. Increased turbidity reduced light penetration and narrowed the spectrum of transmitted light. Male coloration is an important component of intraspecific sexual selection (i.e. female mate choice) [31,32], as well as interspecific reproductive isolation among Lake Victoria cichlids [9,32,33], and the altered light environment impeded species-assortative mate choice [9,33]. Eutrophication-induced turbidity, therefore, reduced the intensity of sexual selection within species and removed the mechanism of reproductive isolation among species [9,34]. With the merging of many distinct species into fewer hybrid species, ecological diversity was also lost. The evolutionary response to the changes in the environment was thus the replacement of many species with diverse ecological adaptions by fewer species, many of which tend to be ecological generalists.

Eutrophication has also been suggested as a contributing factor to the collapse through hybridization of a species pair of benthic and limnetic stickleback in Enos Lake, Vancouver Island [35]. The morphological and genetic homogenization of the species corresponded with an increase in turbidity and reduction in abundance and distribution of aquatic vegetation. These physical changes were linked to the presence of an introduced crayfish and increased nutrient load from the catchment.

Eutrophication-associated consumption of oxygen in the profundal zone caused demographic extinctions and speciation reversal in the adaptive radiation of whitefish (*Coregonus* spp.) of central European subalpine lakes [36]. The breakdown of reproductive isolation and resulting gene flow led to losses of genetic, phenotypic and functional diversity in the species flock across the region. This case study is discussed in more detail in §3f.

The effects of eutrophication-elevated gene flow may be magnified when eutrophication occurs in combination with other anthropogenic-induced changes. For example, factors such as intense harvesting pressure [37] or competition with introduced species can lead to small population sizes. In combination with eutrophication-induced loss of reproductive isolation, this may increase the likelihood, speed and intensity at which species collapse may occur [34,38].

(d) Biodiversity dynamics

By changing natural and sexual selection, as well as reproductive isolation and gene flow, eutrophication influences key processes that generate and maintain biodiversity, reflected in differentiation and diversity among genes, phenotypes, populations and species.

Introgressive hybridization between conspecific populations and recently diverged species generally results in a homogenization of genetic and phenotypic diversity. This is reflected in a loss of alpha, beta and gamma diversity. Increased interspecific gene flow results in an increase in genetic variation within the hybrid population, as long as the genetic diversity of previously divergent populations is still present in the homogenized population. This may result in higher evolutionary potential in hybrid populations, which in turn could promote adaption to new environments, including to the conditions created by eutrophication. However, such potential will not be maintained indefinitely. Removal of the selective force(s) that led to the original divergence of the populations means that the ecologically relevant genetic variation will eventually be lost from the hybrid population through genetic drift. Previously adaptive alleles that no longer confer an advantage in the changed environment may be lost more rapidly through directional selection driven by the eutrophic conditions. The strength of selection under eutrophic conditions and the duration of the eutrophic period will determine how much genetic variation is lost in the hybridized populations. In some cases, genetic and phenotypic divergence lost through hybridization could in principle be re-established with reoligotrophication and the reinstatement of the original adaptive landscape (assuming that other factors remain the same; discussed in §4a). It is also possible that populations that have been exposed to several generations of selection in strongly eutrophied lakes, will have lower fitness in a re-oligotrophied lake and may require several generations to recover adaptations to the restored environment through evolution [12].

In one of the few documented examples of adaptation to eutrophic conditions in vertebrates, Tuckett *et al.* [39] identified variation in feeding and defence traits of white perch (*Morone americana*) that corresponded with differences in productivity among lakes. White perch in more eutrophic lakes tended to be larger, have more gibbous bodies, longer fins, more subterminal mouths and larger spacing among gill rakers. Given that white perch was introduced into some lakes in the 1970s, phenotypic plasticity is likely to be at least partially responsible for the observed changes. Such cases of adaptive divergence between lakes of different eutrophication status could contribute to intraspecific diversity. However, the negative impact of eutrophication on the volume and diversity of aquatic habitats, and the fast rate at which ecological changes occur, lead us to predict that eutrophication has predominantly negative effects on biodiversity. Short- to medium-term increases in species richness with nutrients are reported in some systems [40,41]. However, these are driven by invasion of widely distributed species into lakes where they were absent, rather than changes in evolutionary dynamics. Anthropogenically increased nutrient loads are driven by human use of the lake and catchment, which is associated with increased rates of immigration of non-native species. Increasing nutrients in oligotrophic systems may also shift them into a more common ecosystem state, thereby facilitating establishment of individuals from the larger pool of widely distributed species adapted to the more commonly occurring mesotrophic or eutrophic conditions.

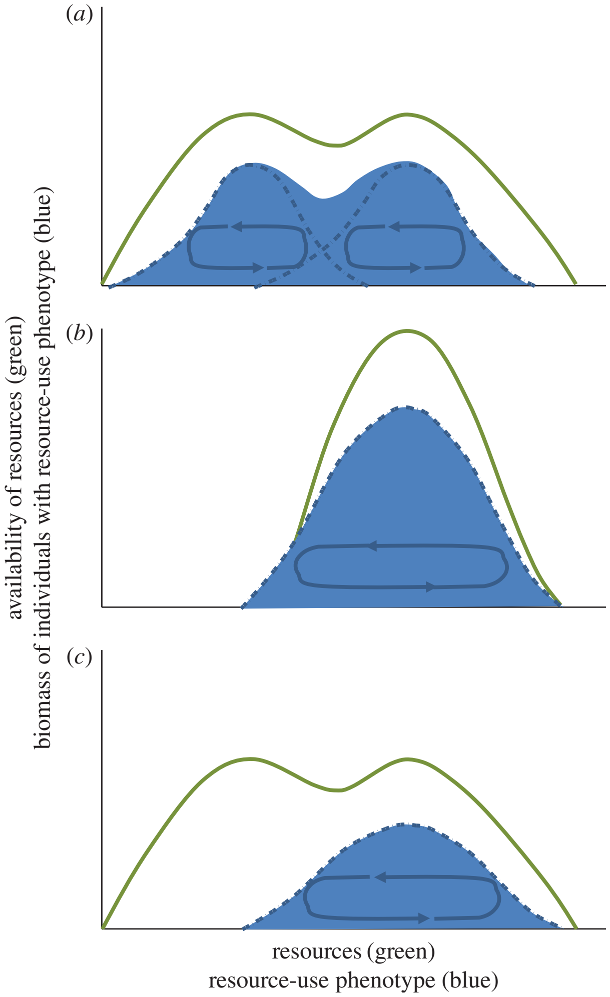

Figure 1. Ecological consequences of eutrophication-induced evolution are most apparent when the ecological function of a species assemblage in a restored ecosystem is compared with that in a pristine ecosystem. In the illustrated example, two species occupy two ecological optima along a gradient of resources in the pristine ecosystem at time t_1 (*a*). Example resource gradients include prey size and resources at different depths in a lake. Despite relatively low productivity in each niche, consumer biomass is high because of effective resource utilization. In the eutrophic ecosystem at time t_2 (*b*), one portion of the gradient of resources is increased (e.g. large zooplankton or shallow-water resources), while another portion is reduced or unavailable. This relaxes divergent selection between niches, causing the species pair to collapse. Consumer biomass is high, nevertheless, because of high productivity in one niche. Under the restored conditions at time t_3 (*c*), the original resource gradient may be restored but only one type of consumer remains. Its biomass is low because the reduced overall trait diversity precludes utilization of part of the resources (e.g. adaptation to feed on small zooplankton, or adaptations to deep water are lost). The result is reduced ecological functioning relative to the pristine state. Broken lines represent trait frequency distributions of consumer populations (species). Random mating and recombination within each population (arrows) enforces Gaussian distributions of resource-use phenotype.

(e) Ecological consequences and implications for society

The pervasiveness of the ecological effects of eutrophication means that the consequences of eutrophication-induced evolution can be most effectively determined in ecosystems where nutrient loads and their direct ecological effects have returned to near-natural levels. Comparisons between the ecological function of species assemblages between re-oligotrophied and pristine ecosystems provide the best opportunity to assess the consequences of eutrophication-induced evolution (figure 1). Even then, differentiating

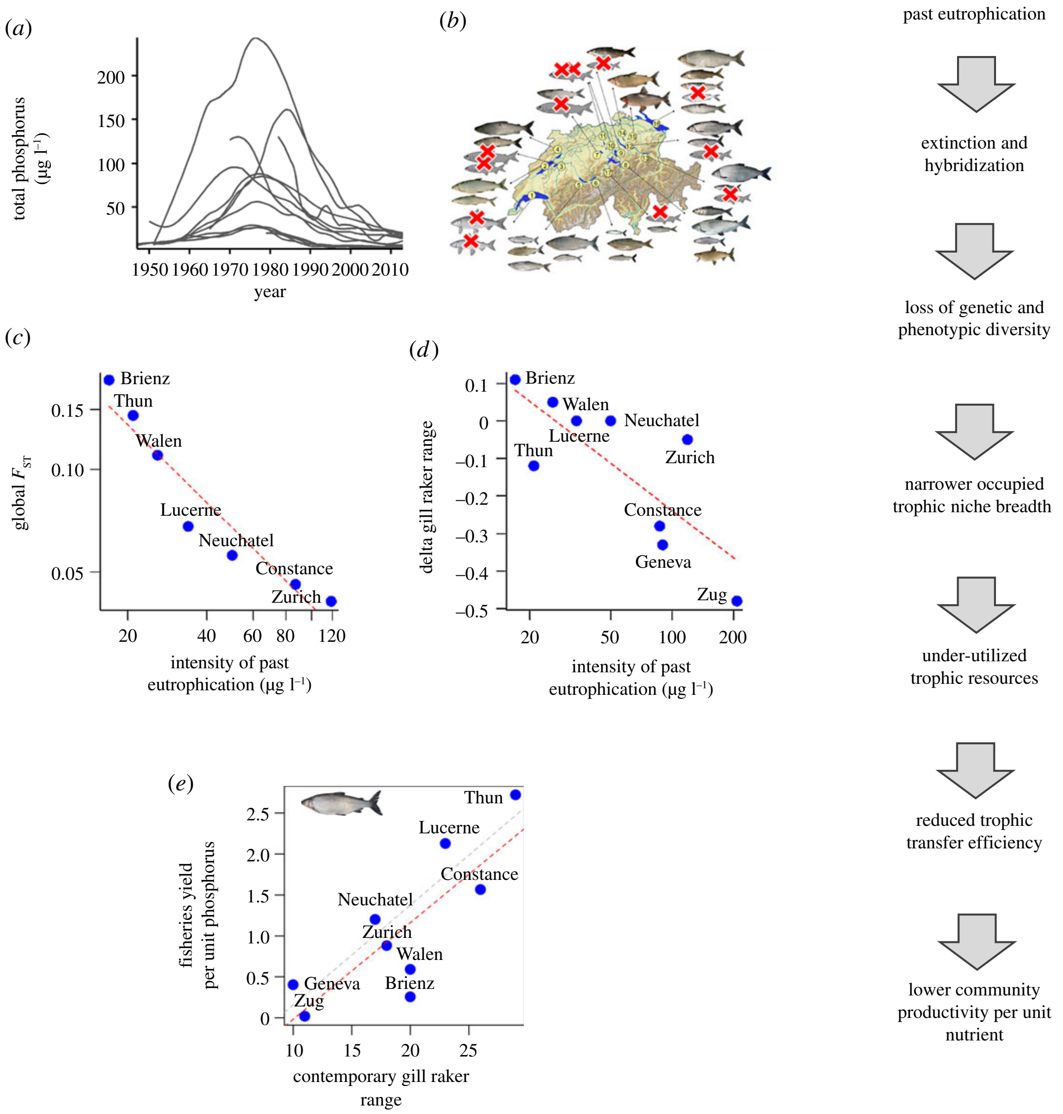

Figure 2. A possible eco-evolutionary feedback loop: changes in the ecosystem (eutrophication) changed the form of selection on whitefish in subalpine lakes. The evolutionary response (speciation reversal in whitefish) resulted in reduced trait diversity, which affected the ecology. (*a*) Temporal trajectories of total phosphorus in large Swiss lakes. Phosphorus data lightly smoothed with loess function (source: Swiss Federal Office of the Environment). (*b*) Extinctions of whitefish species in Swiss lakes between 1950 and early 2000. (*c*) Global genetic differentiation (F_{ST}) among whitefish species within each lake is negatively related to the intensity of past eutrophication (i.e. maximum phosphorus concentration; $\log(y) \sim \log(x)$, $p < 0.001$, $R^2 = 0.91$). (*d*) Change in gill raker range between historic and contemporary whitefish assemblages was also greater in lakes where eutrophication was more intense ($\log(x)$, $p < 0.05$, $R^2 = 0.61$). Ranges were calculated among individuals in each lake assemblage with correction for unequal sample sizes. Gill raker range is a form of functional diversity, reflecting the efficiency of the whitefish assemblage to feed on a diverse array of food items [54]. Panels (*b*–*d*) are adapted from [36]. (*e*) Whitefish fisheries yield per unit phosphorus after most lakes were restored was significantly related to the remaining functional diversity (contemporary gill raker range; $p < 0.01$, $R^2 = 0.67$). Whitefish yield is calculated as the annual catch (in kilograms) of whitefish by commercial and recreational fisheries (source: Swiss Federal Office of the Environment) divided by the surface area of the lake. Graph shows the mean of yield/phosphorus between 2005 and 2014. Lakes Brienz and Walen are influenced by sediment-rich glacial meltwater, resulting in high mineral turbidity, a narrower photic zone and lower potential productivity (excluding these lakes; grey dashed line; $p < 0.01$, $R^2 = 0.86$).

ecological effects of evolutionary changes from residual or hysteretic ecological effects of eutrophication requires careful consideration. For example, invasive species that established themselves during eutrophication may continue to retain a foothold for some time after nutrient recovery, affecting the functioning of the ecosystem. To make it more complicated, these invasive species may themselves have evolved in response to the changes in the environment they invaded [42].

Mesocosm experiments suggest that evolutionary diversification associated with divergent ecological adaptation, such as in adaptive radiations, may have considerable effects on ecosystems (e.g. [43,44]). The ecological effects of speciation *reversal* and associated loss of ecological specialists through relaxed selection and/or increased gene flow are, therefore, likely to be similarly pronounced. In the case of stickleback, species with only 10 000 years of divergence differentially affected prey community structure, total primary production and the light environment in experimental mesocosms [43]. Speciation reversal of stickleback in Enos Lake, British Columbia, also likely had significant ecosystem consequences [45]. The homogenized population exhibited a phenotype intermediate between benthic and limnetic species which previously inhabited the lake, and which still occur in more pristine lakes in the region. Field studies and mesocosm experiments suggested that the hybrid population influenced ecosystem functioning in a way that differed from both extant benthic and limnetic species pairs from other lakes, and generalist populations that had never diverged [45].

The loss of species and erosion of phenotypic and genetic diversity through speciation reversal, particularly in ecosystems where the locally radiated species occupy key niches, such as the cichlids of Lake Victoria, the Enos Lake stickleback and the whitefish of Swiss lakes, are likely to have ecological consequences for patterns of resource utilization and energy flow, leaving some resources or habitats unoccupied or less efficiently used. The primary niche dimensions affected by evolutionary changes caused by eutrophication are utilization of trophic resources and habitat (depth) occupation. In the case of central European whitefish, reduction in the range of a key functional trait, the number of gill rakers, potentially reflects a narrowing of the trophic resources efficiently accessed by whitefish in a lake (discussed in §3f).

(f) Case study of central European whitefish

The whitefish radiations (*Coregonus* spp.) of central European subalpine lakes are ecologically, commercially and recreationally important [46,47]. Since recolonization of the lakes after the last glacial maximum around 15 000 years ago, whitefish have undergone adaptive radiations within each large lake or set of connected lakes, resulting in up to six ecologically differentiated species within a lake [48]. At least 25 lakes supported native whitefish species, the majority of which were endemic [36]. Whitefish used to occupy all spatial niches of the lakes, from the shallow benthic to open pelagic and the profundal zone down to 300 m depth. No other group of fish occupied such a wide range of habitats in these lakes. Known ecologically relevant differences among species include body size, growth rate, diet and depth-habitat. Reproductive isolation among members of lake radiations is maintained by differences in spawning depth, spawning season, possibly mate choice ([49,50]; B. Lundsgaard-Hansen 2012, unpublished data) and natural selection against intermediate phenotypes [51,52].

The ecosystem changes resulting from eutrophication led to extinction and speciation reversal of whitefish species in many lakes in the second half of the nineteenth century [36]. Almost 40% of whitefish species went extinct across the region. These losses had significant effects on the functional diversity of the species flock with a mean reduction in the range of gill raker numbers (reflecting trophic niche breadth) within lakes by 14%. The difference in mean gill raker number between sympatric species was even reduced by 28%. Loss of genetic and functional differentiation in a lake was correlated to the extent of eutrophication [36].

Speciation reversal resulting from the loss of reproductive isolation between species was implicated in several extinctions and in the reduction of genetic and phenotypic distinctiveness in many of the remaining species. The primary mechanism was driven by oxygen deficiencies that were most severe in the deeper parts of the lake. This led to a narrowing of the depth-range over which species could partition the habitat for feeding and reproduction. Species that originally spawned in the deep zones were either forced to spawn in shallower water (in cases where deep water was hypoxic) or only the shallowest of their eggs would hatch (in cases where water in the deeper parts of the lake contained oxygen but the lake sediment was hypoxic). Both situations led to increased interbreeding between deep and shallow species. Altered resource availability (e.g. decreased macroinvertebrates and increased zooplankton biomass) may have additionally influenced the relative survival of hybrids [52]. The spawning time of some sympatric whitefish species also shifted towards greater overlap in some lakes during the period of high nutrients [53]. The overall outcome was genetic and phenotypic homogenization of whitefish species flocks in each lake, with the extent of diversity loss correlating with the severity of eutrophication.

Here we extend the work of Vonlanthen *et al.* [36] to determine whether the evolutionary changes that occurred during the eutrophication period resulted in lasting effects on ecosystem functioning. Such effects would be reflected in the capacity of the whitefish assemblage to access and use available resources, which may consequently affect the productivity of the fishery. We test this hypothesis with data on changes in functional disparity, biomass and productivity of whitefish assemblages in lakes that were affected by eutrophication to variable extents (figure 2*a*). We focus on lakes with maximum depth of more than 100 m because these harboured the most endemic whitefish species and largest phenotypic diversity [36] and, therefore, are most likely to suffer losses as a result of eutrophication.

Vonlanthen *et al.* [36] found that loss of differentiation and species (figure 2*b*,*c*) through speciation reversal resulted in a reduction of the range of gill raker numbers among individuals in each lake assemblage (gill raker ranges corrected for unequal sample sizes; Table 1 in [36] and figure 2*d* in this paper). Gill rakers in whitefish are a highly heritable trait and variation in gill raker number is associated with differences in feeding efficiency on prey type [55] and size [54], among [54,55] and within [54] species. This, therefore, leads to the prediction that the homogenized whitefish assemblages remaining in lakes after eutrophication are feeding on a narrower range of prey items than before eutrophication. The loss of phenotypic disparity in a trait closely related to feeding efficiency also implies that a portion of the food resource is no longer being used as effectively as before, and less energy/biomass is integrated into the whitefish population. Consistent with these predictions, we see that a wider range of gill raker numbers in an assemblage, i.e. potential trophic niche breadth, tightly correlates with a higher fishery yield (combined commercial and recreational catches of whitefish) in a lake relative to its level of primary production as measured by phosphorus content (figure 2*e*; linear regression: $p < 0.01$, $R^2 = 0.67$).

Bringing this together, assemblages of whitefish lost functional diversity through speciation reversal and extinction (figure 2*b*,*c*), and the extent of cultural eutrophication in the past (figure 2*a*) predicts the extent of functional diversity lost (figure 2*d*). The functional trait identified by Vonlanthen *et al.* [36] to be affected by eutrophication-driven speciation reversal, gill raker number, tightly correlates with present-day whitefish productivity per unit phosphorus (figure 2*e*). That is, eutrophication-driven evolution influenced an aspect of functional diversity that is closely associated with how efficiently the whitefish assemblage make use of trophic resources. Greater niche overlap among individuals and a larger portion of the resource base that remains underused appears to result in decreased trophic transfer efficiency.

4. Discussion

We conclude that there is abundant evidence to suggest that eutrophication-driven evolution changes aquatic ecosystems in profound ways. Eutrophication tends to reduce the volume and diversity of aquatic habitats, as well as the diversity and distribution of resources, both of which can affect the form and strength of ecological and sexual selection, and can weaken reproductive isolation between species. The combined effect of these impacts often results in loss of diversity and rapid homogenization of biotic assemblages. The impacts of lost functional diversity become most pronounced when nutrient levels in aquatic ecosystems have been restored to their pre-eutrophication state [12]. As long as parts of the system have increased productivity stimulated by higher nutrient availability, some effects on ecosystem functioning, particularly functions linked to production, may be masked or compensated (figure 1).

(a) Recovery potential

In Lake Constance, speciation reversal driven by eutrophication in the second half of past century resulted in the complete loss of a deep water species and losses of genetic and phenotypic distinctiveness of the others [36]. Recent evidence suggests that one of the remaining whitefish species that received gene flow from the now extinct deep water species, may have begun extending its spawning range towards greater water depth [56]. Restoration of the lake to near-natural nutrient conditions has brought it closer to the original ecological conditions under which the endemic whitefish species once arose. The stickleback of Paxton Lake, Texada Island, Canada, are also believed to have experienced historical introgression during a period of human-induced environmental change, yet recovered their genetic distinctiveness with the return of the lake to near-natural conditions [57]. The extent and duration of hybrization (linked to the extent of eutrophication and duration of the eutrophic phase [36]) likely determine the probability that ecologically and genetically distinct species will re-emerge from hybrid populations after habitat restoration. In theoretical explorations of this problem, Gilman & Behm [58] found that the re-emergence of species was most likely when disturbances were of short duration, but even temporary bouts of hybridization commonly led to substantial homogenization of species pairs.

(b) Characteristics of vulnerable ecosystems

Characteristics that make evolutionary dynamics in lake ecosystems particularly vulnerable to the effects of eutrophication are their relatively young age, large ecosystem size and limited connectivity. Most vertebrate species can hybridize in the first 2–5 Myr after speciation due to little, if any, intrinsic postzygotic hybrid breakdown [59]. Nearly all large lakes of the world fall within that age range (notable exceptions being Baikal and Tanganyika). Therefore, evolutionary dynamics and species diversity in lakes that are large and deep enough to contain *in situ* evolved endemic species pairs or radiations will be vulnerable to the effects of eutrophication. Lake morphometry can influence the ecological sensitivity of a lake to eutrophication [60] and the vulnerability of evolutionary dynamics to eutrophication. Larger lakes generally contain more species [61] which may absorb or compensate for shifts in energy/biomass, thereby reducing changes in the adaptive landscape for individual species. On the other hand, large lakes also tend to support more endemic species owing to a higher opportunity for intralacustrine speciation through their greater environmental heterogeneity and niche dimensionality, as well as their capacity to support larger population sizes [61]. Erosion of this endemic diversity though the effects of eutrophication has major consequences for biodiversity conservation as this diversity cannot be replaced by recolonization. Finally, the evolutionary dynamics of aquatic ecosystems that have limited connectivity, with corresponding low potential for gene flow and arrival of new species, are more likely to be vulnerable to the effects of eutrophication. These systems may be more likely to have experienced a greater extent of local adaptation and a relatively stable biotic network over recent evolutionary history.

(c) Vulnerability of ecosystem services

The likelihood and severity of societal consequences arising from eutrophication-induced changes to evolutionary dynamics are determined by the ecological importance of affected species, characteristics of the service providing units (*sensu* [62]), and the importance of the ecosystem service to society. The importance of a species to an ecosystem can be determined by the impact of a change in the abundance of this species on the structure and dynamics of an ecosystem. Although difficult to quantify exactly, characteristics such as high relative abundance, keystone species, ecosystem engineers and/or high centrality within the biological network are likely to reflect ecological importance and the corresponding impact that evolutionary and ecological changes to these taxa will have on ecosystem functioning.

The immediate importance of affected species to ecosystem functioning and ecosystem services depends on their functional redundancy [62]. Where multiple species are functionally similar, the provision of a particular ecosystem service may not be severely affected by changes in the evolution and ecology of either one of them (although the long-term stability of the service will likely require redundancy). Where assemblages of ecologically dominant species have arisen by *in situ* adaptive radiation, as in the case study of central European whitefish, functional redundancy is expected to be low because sympatric species originated through divergent adaptation to different ecological niches. The immediate ecosystem effects of diversity losses in such cases are likely to be particularly pronounced.

The simplest way to quantify changes in ecosystem services and their consequences for society, although certainly not comprehensive, is to measure it in terms of economic value. This is relatively straightforward in the case of productivity-based ecosystem services such as production of fish biomass. However, the influence of eutrophication-induced changes to evolutionary dynamics on this value is difficult to quantify, particularly given the many and severe ecological changes that have simultaneously occurred in these lakes over the past decades. In addition to effects on income, non-material benefits and cultural services, such as the availability of diverse local produce and preservation of fishing culture, should also be included in such an assessment, but are also difficult to quantify.

(d) Management options

Theory and a limited amount of empirical data suggest that rapid restoration of near-natural ecosystem conditions is critical to maximize the recovery potential of adaptive differentiation after disturbance-mediated speciation reversal [35,56,58]. In the case of eutrophication, this involves restoration of ecosystems to near-natural nutrient levels. After restoration of natural nutrient conditions, careful management of harvesting might increase the likelihood that collapsed species can re-establish by adaptation to the restored habitats based on remaining genetic variation [56].

In lake fish populations, if stocking practices are necessary to support natural reproduction, efforts could be made to ensure that stocking can facilitate restoration by maintaining differentiation among populations [56]. Incautious stocking practices that do not distinguish among still differentiated or again diverging populations may impede the progress of re-differentiation and re-adaptation [63]. In the end, however, recovery of lost traits and species is not guaranteed. Strong selection during the period of eutrophication may have removed the genetic and phenotypic variation required to use a broader range of prey resources and adapt to the deep habitats restored through re-oligotrophication. In such cases, evolution would be limited by the rate at which new beneficial mutations arise, which in most cases will be a very slow process.

Management strategies aiming to facilitate recovery from the effects of eutrophication on evolutionary dynamics must additionally consider other anthropogenic drivers of evolutionary change, such as harvesting-induced evolution [37,64], the effect of stocking with hatchery bred fish [65], pollution [66] and climate change [67].

Efforts to restore natural ecological and evolutionary dynamics may sometimes appear to conflict with goals of some resource users and the delivery of some ecosystem services. For instance, moderately elevated nutrients can increase fisheries catches [68] through increased productivity in the shallow parts of a lake, which can result in faster growth rates [69] and concentration of fish into surface waters [70]. A return to oligotrophic conditions can result in slower growth of some species, reducing the amount of biomass available to a fishery each year. Restoration of environmental conditions, particularly in deep water, allows fish populations to spread out throughout the water column and use resources across the entire lake, which can cause fishing to be less efficient. Re-adaptation could partially restore lost resource-use efficiency and production-based ecosystem services; however, the rate at which this would proceed remains uncertain.

5. Knowledge gaps and future directions

One of the most pressing needs is to explore and carefully document the consequences of eutrophication-induced evolution on ecosystem function and ecosystem services. This requires a combination of experimentation at multiple scales of spatial and biological integration, from performance of individual organisms in the laboratory [12,54,55], to their effects on mesocosms [43,44], to quantifying predicted effects in large natural lakes, as well as theoretical modelling. Next to this, methods need to be developed to assess the demographic and evolutionary recovery potential of affected populations and assemblages. The key to this is to determine the extent and genetic identity of diversity lost through eutrophication, and thereby estimate the possibility and potential rates of recovery, re-divergence and the restoration of associated ecosystem function. This firstly requires a better understanding of the network of traits that underlie particular ecosystem functions and the genomic underpinning of trait variation and species differentiation. It further requires knowledge of how variation in the traits underlying ecosystem functions influences the services that these functions provide to society. Finally, it requires a deeper understanding of the evolutionary dynamics of ecosystems in their natural state. None of these are easy tasks; however, advancements in evolutionary ecology and ecological genomics, including high throughput DNA sequencing methods and bioinformatics, provide hope of deepened insights in the future. Understanding these conditions will allow us to better understand the processes behind the origins of biodiversity and its interaction with ecology, and to manage ecosystems with due consideration to evolutionary processes.

Authors' contributions. All authors contributed to the conceptual development of the manuscript. T.J.A. and O.S. wrote the manuscript with input from P.V.

Competing interests. The authors declare no competing interests.

Funding. We received no funding for this study.

Acknowledgements. The authors are grateful to A. Hendry, K. Gotanda, E. Svensson and G. Rolshausen for the invitation to contribute to this special issue. We thank Carmela Dönz and two anonymous reviewers for constructive comments on an earlier version of the manuscript.

References

1. Carroll SP, Hendry AP, Reznick DN, Fox CW. 2007 Evolution on ecological time-scales. *Funct. Ecol.* **21**, 387–393. (doi:10.1111/j.1365-2435.2007.01289.x)
2. Hendry AP, Gotanda KM, Svensson EI. 2017 Human influences on evolution, and the ecological and societal consequences. *Phil. Trans. R. Soc. B* **372**, 20160028. (doi:10.1098/rstb.2016.0028)
3. Smith VH, Tilman GD, Nekola JC. 1999 Eutrophication: impacts of excess nutrient inputs on freshwater, marine, and terrestrial ecosystems. *Environ. Pollut.* **100**, 179–196. (doi:10.1016/S0269-7491(99)00091-3)
4. Smith VH, Schindler DW. 2009 Eutrophication science: where do we go from here? *Trends Ecol. Evol.* **24**, 201–207. (doi:10.1016/j.tree.2008.11.009)
5. Smith VH. 2003 Eutrophication of freshwater and coastal marine ecosystems a global problem. *Environ. Sci. Pollut. Res.* **10**, 126–139. (doi:10.1065/espr2002.12.142)
6. Watson SB, McCauley E, Downing JA. 1997 Patterns in phytoplankton taxonomic composition across temperate lakes of differing nutrient status. *Limnol. Oceanogr.* **42**, 487–495. (doi:10.4319/lo.1997.42.3.0487)
7. Wetzel RG. 2001 *Limnology: lake and river ecosystems*. New York, NY: Academic Press.
8. Gaedke U, Schweizer A. 1993 The first decade of oligotrophication in Lake Constance. I. The response of phytoplankton biomass and cell-size. *Oecologia* **93**, 268–275. (doi:10.1007/Bf00317681)
9. Seehausen O, van Alphen JJ, Witte F. 1997 Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science* **277**, 1808–1811. (doi:10.1126/science.277.5333.1808)
10. Hecky R. 1993 The eutrophication of Lake Victoria. *Proc. Int. Assoc. Theoret. Appl. Limnol.* **25**, 39.
11. Beeton AM. 1965 Eutrophication of the St. Lawrence Great Lakes. *Limnol. Oceanogr.* **10**, 240–254. (doi:10.4319/lo.1965.10.2.0240)
12. Frisch D, Morton PK, Chowdhury PR, Culver BW, Colbourne JK, Weider LJ, Jeyasingh PD. 2014 A millennial-scale chronicle of evolutionary responses to cultural eutrophication in *Daphnia*. *Ecol. Lett.* **17**, 360–368. (doi:10.1111/ele.12237)
13. Jiang X, Liang H, Chen Y, Xu X, Huang D. 2015 Microgeographic adaptation to toxic cyanobacteria in two aquatic grazers. *Limnol. Oceanogr.* **60**, 947–956. (doi:10.1002/lno.10067)
14. Decker MB, Breitburg DL, Marcus NH. 2003 Geographical differences in behavioral responses to hypoxia: local adaptation to an anthropogenic

stressor? *Ecol. Appl.* **13**, 1104–1109. (doi:10.1890/1051-0761(2003)13[1104:GDIBRT]2.0.CO;2)

15. Hairston NG, Lampert W, Cáceres CE, Holtmeier CL, Weider LJ, Gaedke U, Fischer JM, Fox JA, Post DM. 1999 Lake ecosystems: rapid evolution revealed by dormant eggs. *Nature* **401**, 446. (doi:10.1038/46731)
16. Ventura LD, Sarpe D, Kopp K, Jokela J. 2016 Variability in phenotypic tolerance to low oxygen in invasive populations of quagga and zebra mussels. *Aquat. Invasions* **11**, 267–276. (doi:10.3391/ai.2016.11.3.05)
17. Byers JE. 2002 Impact of non-indigenous species on natives enhanced by anthropogenic alteration of selection regimes. *Oikos* **97**, 449–458. (doi:10.1034/j.1600-0706.2002.970316.x)
18. Mallet J. 2005 Hybridization as an invasion of the genome. *Trends Ecol. Evol.* **20**, 229–237. (doi:10.1016/j.tree.2005.02.010)
19. Brede N, Sandrock C, Straile D, Spaak P, Jankowski T, Streit B, Schwenk K. 2009 The impact of human-made ecological changes on the genetic architecture of *Daphnia* species. *Proc. Natl Acad. Sci. USA* **106**, 4758–4763. (doi:10.1073/pnas.0807187106)
20. Hendry AP, Farrugia TJ, Kinnison MT. 2008 Human influences on rates of phenotypic change in wild animal populations. *Mol. Ecol.* **17**, 20–29. (doi:10.1111/j.1365-294X.2007.03428.x)
21. Johnson PT, Carpenter SR. 2008 Influence of eutrophication on disease in aquatic ecosystems: patterns, processes, and predictions. In *Infectious disease ecology: effects of ecosystems on disease and of disease on ecosystems* (eds R Ostfeld, F Keesing, V Eviner), pp. 71–79. Princeton, NJ: Princeton Unviersity Press.
22. Candolin U. 1999 Male–male competition facilitates female choice in sticklebacks. *Proc. R. Soc. Lond. B* **266**, 785–789. (doi:10.1098/rspb.1999.0706)
23. Wong BM, Candolin U, Lindström K. 2007 Environmental deterioration compromises socially enforced signals of male quality in three-spined sticklebacks. *Am. Nat.* **170**, 184–189. (doi:10.1086/519398)
24. Candolin U. 2004 Effects of algae cover on egg acquisition in male three-spined stickleback. *Behaviour* **141**, 1389–1399. (doi:10.1163/1568539042948268)
25. Järvenpää M, Lindström K. 2004 Water turbidity by algal blooms causes mating system breakdown in a shallow-water fish, the sand goby *Pomatoschistus minutus*. *Proc. R. Soc. Lond. B* **271**, 2361–2365. (doi:10.1098/rspb.2004.2870)
26. Sundin J, Berglund A, Rosenqvist G. 2010 Turbidity hampers mate choice in a pipefish. *Ethology* **116**, 713–721. (doi:10.1111/j.1439-0310.2010.01787.x)
27. Seehausen O. 2006 Conservation: losing biodiversity by reverse speciation. *Curr. Biol.* **16**, R334–R337. (doi:10.1016/j.cub.2006.03.080)
28. Rhymer JM, Simberloff D. 1996 Extinction by hybridization and introgression. *Annu. Rev. Ecol. Syst.* **27**, 83–109. (doi:10.1146/annurev.ecolsys.27.1.83)
29. Witte F, Goldschmidt T, Wanink J, van Oijen M, Goudswaard K, Witte-Maas E, Bouton N. 1992 The destruction of an endemic species flock: quantitative data on the decline of the haplochromine cichlids of Lake Victoria. *Environ. Biol. Fishes* **34**, 1–28. (doi:10.1007/bf00004782)
30. Seehausen O, Witte F, Katunzi EF, Smits J, Bouton N. 1997 Patterns of the remnant cichlid fauna in southern Lake Victoria. *Conserv. Biol.* **11**, 890–904. (doi:10.1046/j.1523-1739.1997.95346.x)
31. Maan ME, van der Spoel M, Jimenez PQ, van Alphen JJM, Seehausen O. 2006 Fitness correlates of male coloration in a Lake Victoria cichlid fish. *Behav. Ecol.* **17**, 691–699. (doi:10.1093/beheco/ark020)
32. Selz OM, Thommen R, Pierotti MER, Anaya-Rojas JM, Seehausen O. 2016 Differences in male coloration are predicted by divergent sexual selection between populations of a cichlid fish. *Proc. R. Soc. B* **283**, 20160172. (doi:10.1098/rspb.2016.0172)
33. Selz OM, Pierotti MER, Maan ME, Schmid C, Seehausen O. 2014 Female preference for male color is necessary and sufficient for assortative mating in 2 cichlid sister species. *Behav. Ecol.* **25**, 612–626. (doi:10.1093/beheco/aru024)
34. Seehausen O, Takimoto G, Roy D, Jokela J. 2008 Speciation reversal and biodiversity dynamics with hybridization in changing environments. *Mol. Ecol.* **17**, 30–44. (doi:10.1111/j.1365-294X.2007.03529.x)
35. Taylor EB, Boughman JW, Groenenboom M, Sniatynski M, Schluter D, Gow JL. 2006 Speciation in reverse: morphological and genetic evidence of the collapse of a three-spined stickleback (*Gasterosteus aculeatus*) species pair. *Mol. Ecol.* **15**, 343–355. (doi:10.1111/j.1365-294X.2005.02794.x)
36. Vonlanthen P *et al.* 2012 Eutrophication causes speciation reversal in whitefish adaptive radiations. *Nature* **482**, 357–362. (doi:10.1038/nature10824)
37. Kuparinen A, Festa-Bianchet M. 2017 Harvest-induced evolution: insights from aquatic and terrestrial systems. *Phil. Trans. R. Soc. B* **372**, 20160036. (doi:10.1098/rstb.2016.0036)
38. Colautti RI, Alexander JM, Dlugosch KM, Keller SR, Sultan SE. 2017 Invasions and extinctions through the looking glass of evolutionary ecology. *Phil. Trans. R. Soc. B* **372**, 20160031. (doi:10.1098/rstb.2016.0031)
39. Tuckett QM, Simon KS, Saros JE, Halliwell DB, Kinnison MT. 2013 Fish trophic divergence along a lake productivity gradient revealed by historic patterns of invasion and eutrophication. *Freshw. Biol.* **58**, 2517–2531. (doi:10.1111/fwb.12229)
40. Jeppesen E, Peder Jensen J, Søndergaard M, Lauridsen T, Landkildehus F. 2000 Trophic structure, species richness and biodiversity in Danish lakes: changes along a phosphorus gradient. *Freshw. Biol.* **45**, 201–218. (doi:10.1046/j.1365-2427.2000.00675.x)
41. Brucet S *et al.* 2013 Fish diversity in European lakes: geographical factors dominate over anthropogenic pressures. *Freshw. Biol.* **58**, 1779–1793. (doi:10.1111/fwb.12167)
42. Lucek K, Lemoine M, Seehausen O. 2014 Contemporary ecotypic divergence during a recent range expansion was facilitated by adaptive introgression. *J. Evol. Biol.* **27**, 2233–2248. (doi:10.1111/jeb.12475)
43. Harmon LJ, Matthews B, Des Roches S, Chase JM, Shurin JB, Schluter D. 2009 Evolutionary diversification in stickleback affects ecosystem functioning. *Nature* **458**, 1167–1170. (doi:10.1038/nature07974)
44. Lundsgaard-Hansen B, Matthews B, Seehausen O. 2014 Ecological speciation and phenotypic plasticity affect ecosystems. *Ecology* **95**, 2723–2735. (doi:10.1890/13-2338.1)
45. Rudman SM, Schluter D. 2016 Ecological impacts of reverse speciation in threespine stickleback. *Curr. Biol.* **26**, 490–495. (doi:10.1016/j.cub.2016.01.004)
46. Vonlanthen P, Périat GC, Alexander TJ, Seehausen O. 2015 Artenvielfalt und Zusammensetzung der Fischpopulation im Thunersee. Projet Lac, Eawag. Kastanienbaum, Switzerland. See http://www.eawag.ch/fileadmin/Domain1/Abteilungen/fishec/projekte/lac/Projet_Lacs_Thunersee_final.pdf.
47. FOEN. 2016 Fischerei Statistik. Bern, Switzerland: Federal Office for the Environment. See http://www.fischereistatistik.ch.
48. Steinmann P. 1950 Monographie der schweizerischen Koregonen: Beitrag zum Problem der Entstehung neuer Arten. *Schweiz. Z. Hydrol.* **12**, 109–112. (doi:10.1007/bf02486030)
49. Vonlanthen P, Roy D, Hudson A, Largiader C, Bittner D, Seehausen O. 2009 Divergence along a steep ecological gradient in lake whitefish (*Coregonus* sp.). *J. Evol. Biol.* **22**, 498–514. (doi:10.1111/j.1420-9101.2008.01670.x)
50. Eckmann R. 2015 Absence of intrinsic post-zygotic incompatibilities in artificial crosses between sympatric coregonid species from upper Lake Constance. *J. Fish Biol.* **86**, 1601–1611. (doi:10.1111/jfb.12673)
51. Woods PJ, Müller R, Seehausen O. 2009 Intergenomic epistasis causes asynchronous hatch times in whitefish hybrids, but only when parental ecotypes differ. *J. Evol. Biol.* **22**, 2305–2319. (doi:10.1111/j.1420-9101.2009.01846.x)
52. Hudson AG, Vonlanthen P, Bezault E, Seehausen O. 2013 Genomic signatures of relaxed disruptive selection associated with speciation reversal in whitefish. *BMC Evol. Biol.* **13**, 1–18. (doi:10.1186/1471-2148-13-108)
53. Numann W. 1972 Bodensee: effects of exploitation and eutrophication on salmonid community. *J. Fish. Res. Board Can.* **29**, 833. (doi:10.1139/f72-127)
54. Roesch C, Lundsgaard-Hansen B, Vonlanthen P, Taverna A, Seehausen O. 2013 Experimental evidence for trait utility of gill raker number in adaptive radiation of a north temperate fish. *J. Evol. Biol.* **26**, 1578–1587. (doi:10.1111/jeb.12166)
55. Lundsgaard-Hansen B, Matthews B, Vonlanthen P, Taverna A, Seehausen O. 2013 Adaptive plasticity and genetic divergence in feeding efficiency during parallel adaptive radiation of whitefish (*Coregonus* spp.). *J. Evol. Biol.* **26**, 483–498. (doi:10.1111/jeb.12063)

56. Hirsch PE, Eckmann R, Oppelt C, Behrmann-Godel J. 2013 Phenotypic and genetic divergence within a single whitefish form - detecting the potential for future divergence. *Evol. Appl.* **6**, 1119–1132. (doi:10.1111/eva.12087)
57. Gow JL, Peichel CL, Taylor EB. 2006 Contrasting hybridization rates between sympatric three-spined sticklebacks highlight the fragility of reproductive barriers between evolutionarily young species. *Mol. Ecol.* **15**, 739–752. (doi:10.1111/j.1365-294X.2006.02825.x)
58. Gilman RT, Behm JE. 2011 Hybridisation, species collapse, and species reemergence after disturbance to premating mechanisms of reproductive isolation. *Evolution* **65**, 2592–2605. (doi:10.1111/j.1558-5646.2011.01320.x)
59. Coyne JA, Orr HA. 2004 *Speciation*. Sunderland, MA: Sinauer Associates.
60. Nixdorf B, Deneke R. 1997 Why 'very shallow' lakes are more successful opposing reduced nutrient loads. *Hydrobiologia* **342**, 269–284. (doi:10.1023/a:1017012012099)
61. Wagner CE, Harmon LJ, Seehausen O. 2014 Cichlid species-area relationships are shaped by adaptive radiations that scale with area. *Ecol. Lett.* **17**, 583–592. (doi:10.1111/ele.12260)
62. Luck GW *et al.* 2009 Quantifying the contribution of organisms to the provision of ecosystem services. *Bioscience* **59**, 223–235. (doi:10.1525/bio.2009.59.3.7)
63. Eckmann R. 2012 Massive stocking with hatchery larvae may constrain natural recruitment of whitefish stocks and induce unwanted evolutionary changes. *Adv. Limnol.* **63**, 325–336.
64. Kuparinen A, Hutchings JA. 2017 Genetic architecture of age at maturity can generate divergent and disruptive harvest-induced evolution. *Phil. Trans. R. Soc. B* **372**, 20160035. (doi:10.1098/rstb.2016.0035)
65. Anneville O, Lasne E, Guillard J, Eckmann R, Stockwell JD, Gillet C, Yule DL. 2015 Impact of fishing and stocking practices on coregonid diversity. *Food Nutr. Sci.* **6**, 1045. (doi:10.4236/fns.2015.611108)
66. Hamilton PB, Rolshausen G, Webster TMU, Tyler CR. 2017 Adaptive capabilities and fitness consequences associated with pollution exposure in fish. *Phil. Trans. R. Soc. B* **372**, 20160042. (doi:10.1098/rstb.2016.0042)
67. Lancaster LT, Morrison G, Fitt RN. 2017 Life history trade-offs, the intensity of competition, and coexistence in novel and evolving communities under climate change. *Phil. Trans. R. Soc. B* **372**, 20160046. (doi:10.1098/rstb.2016.0046)
68. Gerdeaux D, Anneville O, Hefti D. 2006 Fishery changes during re-oligotrophication in 11 peri-alpine Swiss and French lakes over the past 30 years. *Acta Oecol. Int. J. Ecol.* **30**, 161–167. (doi:10.1016/j.actao.2006.02.007)
69. Eckmann R, Gerdeaux D, Müller R, Rösch R. 2007 Re-oligotrophication and whitefish fisheries management—a workshop summary. *Adv. Limnol.* **60**, 353–360.
70. Thomas G, Rosch R, Eckmann R. 2010 Seasonal and long-term changes in fishing depth of Lake Constance whitefish. *Fish. Manage. Ecol.* **17**, 386–393. (doi:10.1111/j.1365-2400.2010.00734.x)